External location of touch is constructed post-hoc based on limb choice

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Abstract (150 words)

When humans indicate on which hand a tactile stimulus occurred, they often err when their hands are crossed. This finding seemingly supports the view that the automatically determined touch location in external space affects limb assignment: the crossed right hand is localized in left space, and this conflict presumably provokes hand assignment errors. Here, participants judged on which hand the first of two stimuli, presented during a bimanual movement, had occurred, and then indicated its external location by a reach-to-point movement. When participants incorrectly chose the hand stimulated second, they pointed to where that hand had been at the correct, first time point, though no stimulus had occurred at that location. This behavior suggests that stimulus localization depended on hand assignment, not vice versa. It is, thus, incompatible with the notion of automatic computation of external stimulus location upon occurrence. Instead, humans construct external touch location post-hoc and on demand.

Introduction

Spatial perception and actions rely on multiple spatial codes, often associated with different reference frames. For instance, the accuracy of pointing or reaching with an arm or finger to a visual target depends not only on the position of target relative to gaze (Fiehler et al., 2011; Thompson et al., 2014), but also on salient world-centered landmarks (Schütz et al., 2013). Similarly, judgment of visual location during whole-body movement is influenced by a target's position relative to gaze, as well as by the location of the target relative to the body (Tramper & Medendorp, 2015).

In touch, too, space is coded in several reference frames. Touch activates specialized sensory receptors embedded in the skin, and the arrangement of the peripheral sensors is reflected in the homuncular organization of primary somatosensory cortex (Penfield & Boldrey, 1937; Roux et al., 2018), referred to as a skin-based or somatotopic layout. However, because our body can take various postures, the stimulus location in space – often referred to as its external location – must be derived by combining skin location and body posture, a process termed tactile remapping (Heed, Buchholz, et al., 2015). Indeed, there is evidence that external tactile locations can be coded in a gaze-centered reference frame (Harrar & Harris, 2010; Mueller & Fiehler, 2014a, 2014b), but also relative to anchors such as the head, torso, and hand (Alsmith et al., 2017; Heed et al., 2016).

It is less clear, however, according to which principles these different spatial codes are employed. Both bottom-up features such as the availability of sensory information (Bernier & Grafton, 2010) and the spatial reliability of a sensory channel (Ernst & Banks, 2002; van Beers et al., 2002), as well as top-down information such as task-constraints (Badde et al., 2015; Schubert et al., 2017), action context (Mueller & Fiehler, 2014b), and cognitive load (Badde et al., 2014) can affect the relative contributions of different reference frames, presumably in a weighted manner (Angelaki et al., 2009; Atsma et al., 2016; Badde & Heed, 2016;

Ernst & Di Luca, 2011; Kayser & Shams, 2015; Lohmann & Butz, 2017; Tramper & Medendorp, 2015). Yet, whereas there is widespread consensus that each spatial code can have more or less influence depending on the specific situation, it is currently not known whether all putative codes are always constructed, or whether they are only computed based on demand.

For touch, it has been suggested that the construction of spatial location is an automatic process, implying that any tactile input is remapped into an external code, irrespective of its relevance (Heed & Azañón, 2014; Röder et al., 2004). The most common experimental manipulation underlying this claim is limb crossing. Crossing, say, a right arm over to the left side of space leads to different skin-based (here: right body side) and external (here: left side of space) spatial codes of a tactile stimulus delivered to the right hand. A task-irrelevant tactile stimulus delivered to a crossed right hand accelerates visual discrimination in the right visual field if it precedes the visual target stimulus by 60 ms, but on the left side if it leads by 180 ms or more (Azañón et al., 2010; Azañón & Soto-Faraco, 2008). Thus, responses to visual targets were faster after anatomically congruent tactile cues (e.g., tactile stimulus on [crossed] right hand, visual target in right hemifield) at short cue-stimulus intervals, but after externally congruent tactile cues (e.g., tactile stimulus on the left hand crossed over to the right side, visual target in right field) at long cue-stimulus intervals. Such effects are usually interpreted as evidence that tactile remapping – the precise computation of the external tactile stimulus location – is automatic and forms the basis for the performance enhancement at this external location.

The same conclusion has also been drawn from results obtained with the tactile temporal order judgment (TOJ) task; in this task, participants report which of two successive tactile stimuli, each presented to a different body part – typically the two hands – occurred first (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). When the time interval between the two stimuli is short, participants sometimes choose the wrong stimulus. Notably, stimulus

confusion is much more prominent when the arms are in a crossed than uncrossed posture. This is surprising because the TOJ task asks about the identity of the touched limb, and, in theory, it would be irrelevant to this question where the hand was in space. That limb crossing, nevertheless, affects TOJ implies that posture cannot be strategically ignored, but is automatically incorporated into the hand assignment.

Several explanations have been put forward to account for crossing effects in tactile localization. First, it has been suggested that touch location, once it is remapped, is retained only in an external spatial code, and the original skin location is discarded in the process. To report which body part has been touched, the brain must then reversely determine which limb was located at the computed external location at the time of the touch (Kitazawa, 2002; Kitazawa et al., 2008; Yamamoto & Kitazawa, 2001). We refer to this suggestion as the *space-to-limb reconstruction hypothesis*. When applied to errors in the TOJ task, this hypothesis implies that participants correctly remap the two tactile stimuli into external space, but then reconstruct erroneously which hand was at the first spatial location.

A second explanation assumes that TOJ errors reflect the conflict between different codes used for stimulus location. When the limbs are crossed, skin-based and external spatial codes point to different sides of space, and this conflict must be resolved, a process that takes time and is error-prone (Röder, Kusmierek, Spence, & Schicke, 2007; Simon, Hinrichs, & Craft, 1970). In this view, the TOJ crossing effect is a marker for the presence of conflict and, thus, for the fact that remapping into an external spatial code has taken place. Notably, the interpretation that the TOJ crossing effect derives from a remapped stimulus location is indirect because participants only report a binary decision about which hand was stimulated, not the spatial location of the perceived stimulus. Increasing the distance between the uncrossed hands can slightly reduce errors in TOJ (Gallace & Spence, 2005; Roberts et al., 2003; Shore et al., 2005), and the TOJ crossing effect is smaller when the hands' positions additionally differ in height or depth

(Azañón et al., 2016). These graded modulations of the TOJ have led to the claim that the TOJ paradigm is an implicit index of tactile remapping (Azañón et al., 2015; Badde & Heed, 2016; Heed & Azañón, 2014). We refer to this suggestion as the *stimulus switch hypothesis*. It implies that participants have correctly remapped the two stimuli into space, but have incorrectly resolved the conflict between the different spatial codes of the first stimulus, consequently assigning the incorrect stimulus to the first time point; as a consequence, participants incorrectly report the hand that received the second stimulus.

Importantly, both hypotheses outlined above assume that touch is automatically and accurately remapped to its external location. However, recent experiments have cast doubt on whether this is actually the case. For instance, if a tactile stimulus is presented during an arm movement, and participants indicate the stimulus's location by pointing to its external location after the movement, they make systematic localization errors (Dassonville, 1995; Maij et al., 2011, 2013, 2017; Watanabe et al., 2009). Importantly, because these errors differ for fast and slow movements, it has been suggested that participants do not compute the precise spatial location of a stimulus when it occurs, but instead infer spatial location post-hoc by estimating hand location at the perceived time of the tactile stimulus (Maij et al., 2017). We refer to this suggestion as the *time reconstruction hypothesis*. Accordingly, errors in the TOJ task would occur because participants first choose the incorrect hand, and then derive stimulus location based on that hand's location at the time of the first stimulus. Note, that here participants merge the correct, first stimulus's time with the incorrect, second stimulus's hand. Importantly, the claim of the *time reconstruction hypothesis* that tactile location is not determined by integrating posture and skin location at the time of stimulus

occurrence – in the case of TOJ errors, this is the time point of the second stimulus

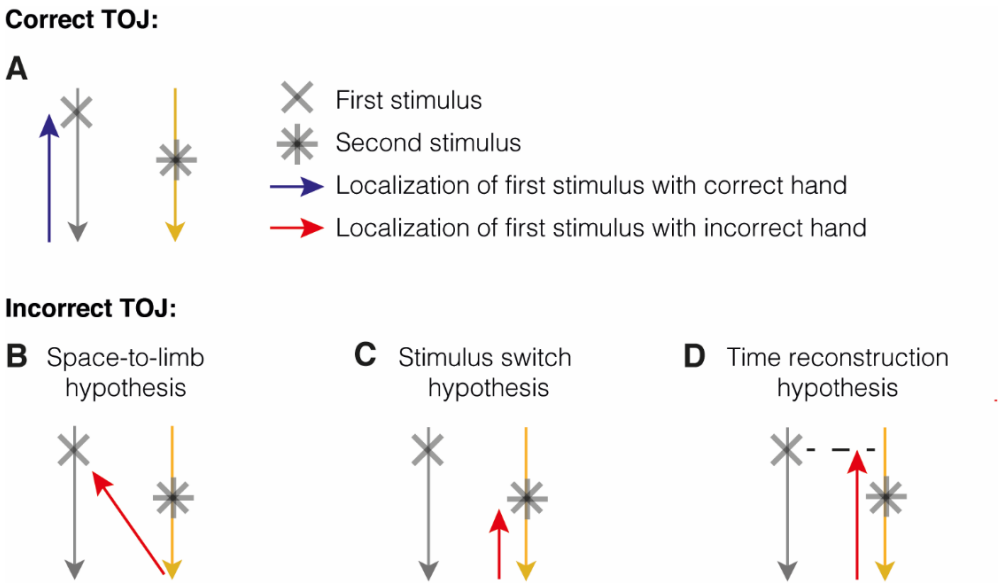


Figure 1. *Hand assignment and tactile localization in a TOJ task with bimanual movements. Grey trace, left arm trajectory; yellow trace: right arm trajectory; red trace: reach-to-point movement to external location of the tactile stimulus. A. Correct TOJ trial: the stimulus is assigned to the correct hand, which points to the correct location. B-D Three hypotheses for tactile location in incorrect TOJ trials. B. Space-to-limb reconstruction hypothesis: participants point with the incorrect hand at the external location of the first stimulus. C. Stimulus switch hypothesis: participants point with the incorrect hand at the external location of the second stimulus. D. Time reconstruction hypothesis: participants point with the incorrect hand at the location at which that hand was at the time of the first stimulus.*

– is at odds with the idea that tactile judgments are based on precise spatial remapping.

Here, we assessed hand assignment and spatial localization of tactile stimuli presented during movement. Our objective was to test whether TOJ responses mark the use of the stimulus's precise, external-spatial location constructed in response to the stimulus, or whether instead participants estimate the precise stimulus location post-hoc by integrating the hand movement trajectory with stimulus time. In other words, we aimed to directly contrast the three

discussed hypotheses for tactile localization: the space-to-limb reconstruction hypothesis, the stimulus switch hypothesis, and the time reconstruction hypothesis.

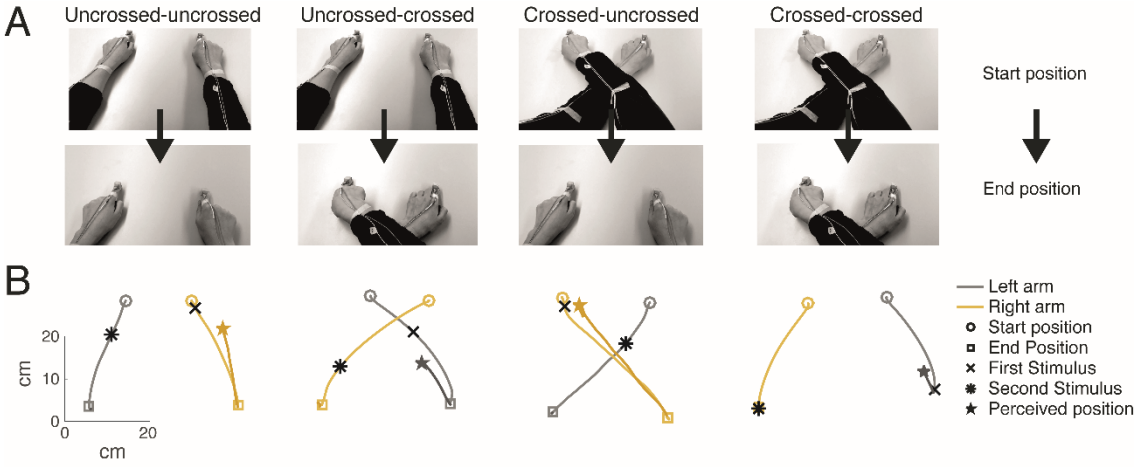
We presented human participants with two tactile stimuli during a bimanual movement and assessed which hand participants perceived to have been stimulated first (TOJ hand assignment), as well as exactly where in space participants had perceived it (tactile stimulus localization). The experimental logic, and its relation to the three tested tactile localization hypotheses, are illustrated in Fig. 1. Because tactile stimuli were presented shortly before, after, and during the time of movement, their precise spatial location depended on their timing relative to the movement. This allowed us to determine the precise tactile spatial location participants had perceived when they had made a hand assignment error in the TOJ task. Contrary to common opinion, TOJ errors were not associated with the location of the second, incorrect stimulus. Instead, when participants chose the incorrect hand, they reported its location at the time point at which the other, correct stimulus had occurred. Thus, participants constructed stimulus location by combining the position of the incorrectly chosen hand with the stimulus timing that belonged to the other, non-chosen hand's stimulus, resulting in reported locations at which no stimulus had ever occurred. This finding invalidates current explanations of crossing effects as being based on the precise, remapped external spatial location of the tactile stimulus.

Results

Experiment 1

Participants assumed a start posture with their hands resting on a table and their arms stretched out in an uncrossed or crossed posture (see Fig. 2 for an illustration of experimental conditions and trial timing). A tone then instructed a movement of the two hands about 30 cm towards their body, bringing the arms

173 into either an uncrossed or crossed arm end posture (see Fig. 2A). Shortly



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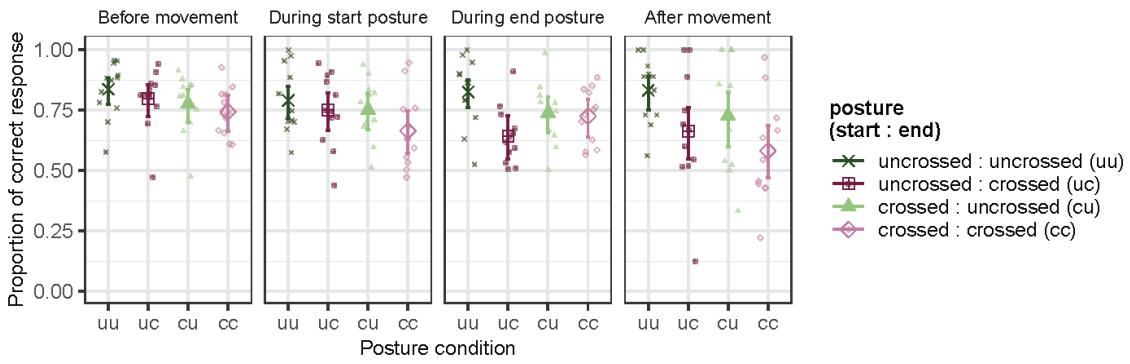
175 ***Figure 2.*** *Experimental conditions. A. The arms moved from an uncrossed (u) or crossed (c) start*
176 *posture to either an uncrossed or crossed arm end posture. B. Example TOJ trial of a representative*
177 *subject, showing the bimanual movement (grey: left arm, yellow, right arm) and the reach-to-point*
178 *movement of the assigned hand for the tactile localization response.*

179 before, during, or shortly after the movement, participants received two tactile
180 stimuli, one on each hand, with a stimulus onset asynchrony (SOA) of 110 ms. At
181 this SOA, participants often misreport which of the two stimuli occurred first, both
182 when the arms are still (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto &
183 Kitazawa, 2001) and during movement (Heed, Möller, et al., 2015; Hermosillo et
184 al., 2011). After the bimanual movement, participants reported on which of the two
185 hands the first stimulus had occurred by reaching with this hand to the perceived
186 external location of the stimulus (see Fig. 2B). The response, thus, contained two
187 components: the hand to which the first stimulus was assigned, and explicit spatial
188 localization of this stimulus.

189 **Hand assignment**

190 We measured TOJ performance as the percentage of correct reports of
191 which hand had been stimulated first in the TOJ task, as indicated by the hand that

192 participants used for their localization response (see Fig. 3). Stimuli could occur
193 during all times (see Methods for details), so we binned the binary



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195 ***Figure 3.*** *Proportion of correct hand assignment across movement conditions (uu, uc, cu, uu, with*
196 *c=crossed, u=uncrossed posture) in the four phases of the bimanual movement (before movement,*
197 *during start posture, during end posture, after movement). For uc and cu conditions, stimuli were*
198 *classified according to whether the first stimulus occurred while the hands were still in the start*
199 *posture, or already in the end posture. For uu and cc conditions, trials were assigned as "during*
200 *start posture" if stimuli had been presented during the first temporal half of the movement, and as*
201 *"during end posture" otherwise. Error bars denote 2 s.e. from the mean; asymmetry is due to*
202 *nonlinear conversion from the GLMM's logit scale to percentage correct. Large symbols are group*
203 *means, small symbols are individual participants' performance.*

204 (correct/incorrect) TOJ response data into four movement phases – stimulation
205 before movement onset, during first and second half of movement, and after
206 movement offset – to assess the modulation of TOJ performance by stimulus time
207 relative to the bimanual movement.

208 In accordance with previous findings, TOJ performance declined in the
209 crossed compared to the uncrossed posture (Heed & Azañón, 2014), and
210 depended on the posture at the time of stimulation (Heed, Möller, et al., 2015;
211 Hermosillo et al., 2011). For instance, for the uncrossed-uncrossed movement
212 condition (see Fig. 3, uu), the probability of correct response was high compared
213 to the crossed-crossed movement condition (see Fig. 3, cc) throughout all

movement phases. For the conditions with a postural change (see Fig. 3, uc & cu) the probability of correct responses was modulated by the posture at the time of stimulation. A generalized mixed model (GLMM) with factors Start Posture, End Posture, and Movement Phase revealed significance for all main effects and

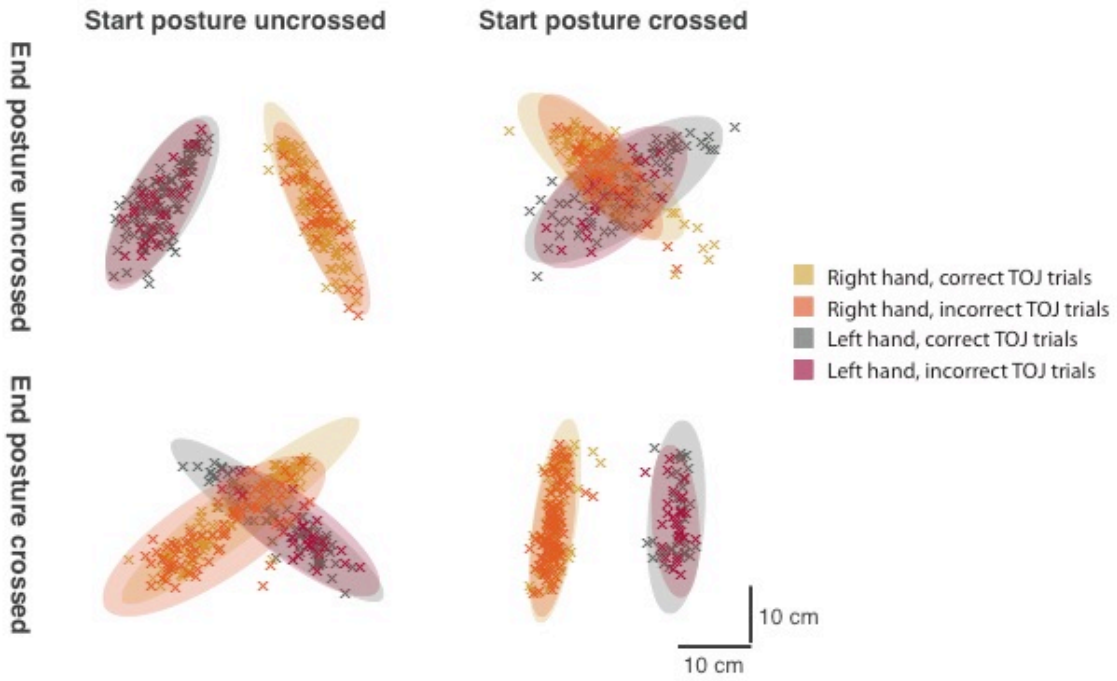

Figure 4. *Reach end points, as measures of localization responses, in the horizontal plane for the different movement conditions. Data are from a single participant with substantial end point variability. Ellipses cover 95% of the variability. Ellipses cover virtually identical spaces when participants give correct and incorrect responses. The space-to-limb reconstruction hypothesis would predict that, during error trials, participants point with the incorrectly chosen hand to the location of the correct stimulus; thus, if this hypothesis were correct, orange ellipses should overlay with grey ellipses, and red ellipses should overlay with yellow ellipses.*

interactions (see Supplementary Table 1). With movement phase, the effect of Start Posture (see Fig. 3, dark vs. light colors) declined, whereas the effect of End Posture (see Fig. 3, green vs. magenta colors) increased. For instance, for

movements from an uncrossed to a crossed posture, TOJ performance was better during the first two movement phases, that is, when the hands were still uncrossed, than during the last two movement phases, that is, when the hands were crossed.

In sum, TOJ performance in our first experiment reflected known modulations of hand posture and movement timing. Participants made, on average, more than 15% TOJ errors even with uncrossed hands. This high error rate is due to the use of the short SOA of 110 ms (Heed, Möller, et al., 2015; Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001), and is an intended outcome of the experimental paradigm, allowing, as a next step, comparison of spatial localization responses for erroneous TOJ trials across all postures.

Explicit stimulus localization in space

Localization responses in TOJ error trials allow differentiating between the three hypotheses about how participants determine stimulus localization in tactile decision paradigms (see Fig. 1). The *space-to limb reconstruction hypothesis* posits that the spatial location of the first tactile stimulus is represented correctly, and that a limb assignment entails computing which limb was at that spatial location when the stimulus occurred. Thus, in our task, responses with the incorrect hand would result from assigning the incorrect hand to the correct spatial location of the first tactile stimulus (see Fig. 1B). Accordingly, the chosen, incorrect hand should be directed to the location at which the stimulus of the other, correct hand had occurred, and the reported stimulus location in TOJ error trials should scatter around the movement trajectory of the correct hand. Contrary to this prediction, participants pointed to locations scattered around the movement trajectory of the chosen, incorrect hand (see also Fig. 2B), indicating that the chosen stimulus had been perceived on the incorrect hand (see Fig. 4 for the localization responses of the participant with the largest variability in localization errors). Thus, localization behavior did not support the implication of the *space-to-*

limb reconstruction hypothesis that the correct external spatial location is simply assigned to a wrong limb.

Having established that participants appear to have perceived the stimulus at the reporting hand, two possibilities remain as to which stimulus location was associated with erroneous responses (see Fig. 1). The *stimulus switch hypothesis* posits that the two stimuli were localized correctly, and one is chosen for the response. In TOJ error trials, participants would confuse the two stimuli and report the second stimulus by pointing at its location with the respective, incorrect hand. In this case, spatial localization errors in the reach-to-point task should scatter around the position of the hand at the time point of the *second*, erroneously chosen stimulus (referred to as time 2 from hereon). In contrast, the *time reconstruction hypothesis* assumes that participants always use the correct, first time point (time 1 from hereon), and determine the chosen response limb's location at this time point. This hypothesis predicts that, in TOJ error trials, participants point to the location of the erroneously chosen, incorrect hand at the correct time, that is, time 1. Note, that no tactile stimulus occurred at this external spatial location, because it combines the time of the first, correct stimulus with the movement trajectory of the second, incorrect stimulus's hand.

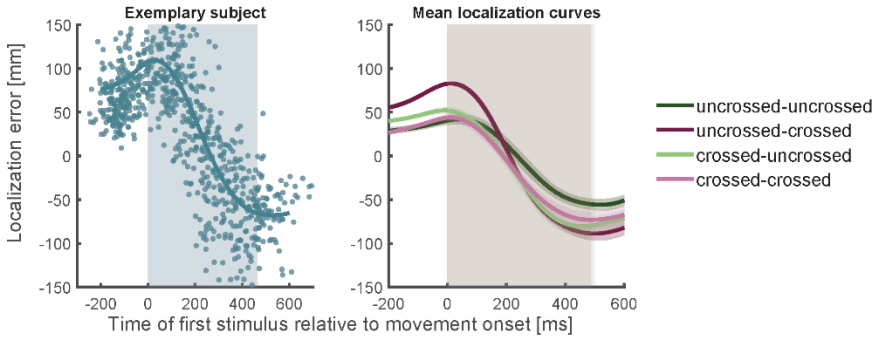

Figure 5. *Localization errors systematically vary in dependence of the progression of the movement. A. Mean localization error (teal line) of all correct localization trials of a single participant. Each dot represents the error of a single trial, that is the difference between actual hand position at the time of tactile stimulation and indicated hand position at the end of the trial. Blue shading represents the average movement time, with 0 = movement start. Note, that localization bias is positive at the beginning of the movement, but negative towards the end of the movement. These biases reflect mislocalization in the direction of movement at the beginning, and in the opposite direction at the end of the movement. B. The error pattern in A was evident across all subjects for all posture combinations. Traces reflect the mean, shaded areas around the traces reflect s.e.m. The shaded regions in the background indicate movement times, which differed slightly between conditions.*

Assessment of whether participants pointed to the hand's position at the first or second time point during TOJ error trials is based on comparison of the localization error curve in correct and erroneous TOJ trials. When participants retrospectively point to the spatial location of a tactile stimulus presented while the target limb was moving, their location judgment errors are systematically biased in the direction of the movement during the initial part of a movement, and in the opposite direction during the final part of the movement (Dassonville, 1995; Maij et al., 2013, 2017; Watanabe et al., 2009), resulting in systematic localization error curves. Such movement time-related biases were evident also in the present data (see Fig. 5). In the case of correct TOJ trials, we assume that participants aimed, as instructed, at the location of the correct hand at time 1. Therefore, we derive the localization error curve as the spatial difference of reaching endpoint and hand location at time 1 (see Fig. 6, dark blue lines). However, we can also derive a

second localization error curve by computing localization error relative to time 2

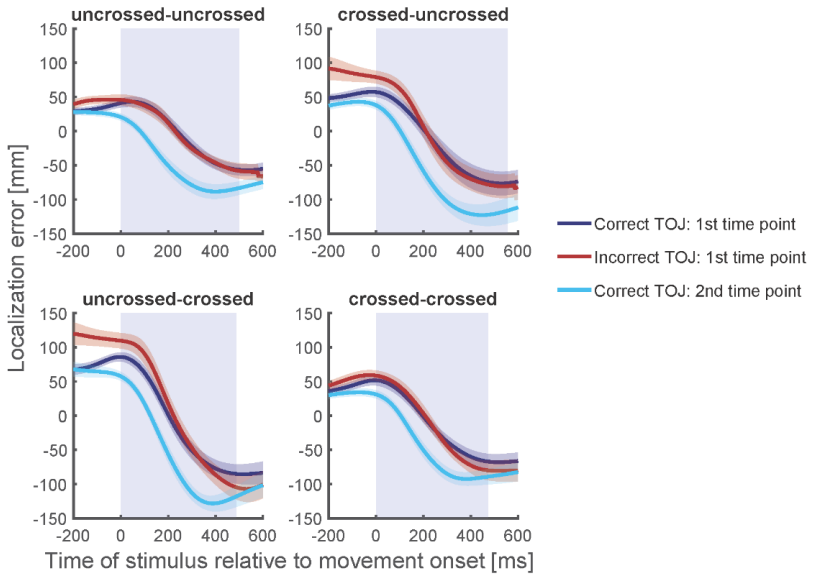

Figure 6*. Localization curves, averaged across participants, for each of the four posture conditions. Curves of incorrect TOJ trials (red) show a similar pattern as the localization curves of the correct TOJ trials at time 1 (dark blue), but not as the localization curves of the correct TOJ trials at time 2 (light blue). Traces reflect the mean, shaded areas around the traces reflect s.e.m. The shaded regions in the background represent the average movement time.*

(see Fig. 6, light blue lines). This hypothetical error curve is shifted to the left of the first curve, because time 2 is later in time relative to movement start (and, accordingly, closer in time to movement end), so that the movement time-related localization errors should be shifted backwards in time by the 110 ms time difference of the two stimuli. In other words, this second error curve reflects the pattern we would expect if participants had aimed for hand location at time 2.

The two localization error curves computed on the basis of correct TOJ trials serve as templates against which we compare the localization error curve of TOJ error trials (see Fig. 6 and Methods). Localization errors of incorrect TOJ trials overlapped with localization errors of correct TOJ trials at time 1, for each of the

four start and end posture combinations. To quantify this further, we computed by how much reaching endpoints of TOJ error trials had to be shifted to best match either template curve derived from correct TOJ trials. If, in incorrect TOJ trials, participants aimed for the incorrect hand's position at time 1, then the temporal shift should be zero relative to the localization error curve in correct TOJ trials relative to time 1; furthermore, it should be about -110 ms (negative denoting a shift towards left, see above) compared to the localization error curve of correct TOJ trials relative to time 2. If, however, participants aimed for the incorrect hand's position at time 2, the shift pattern should be exactly reverse, that is, zero compared to the second template curve, and near +110 ms compared to the first template curve.

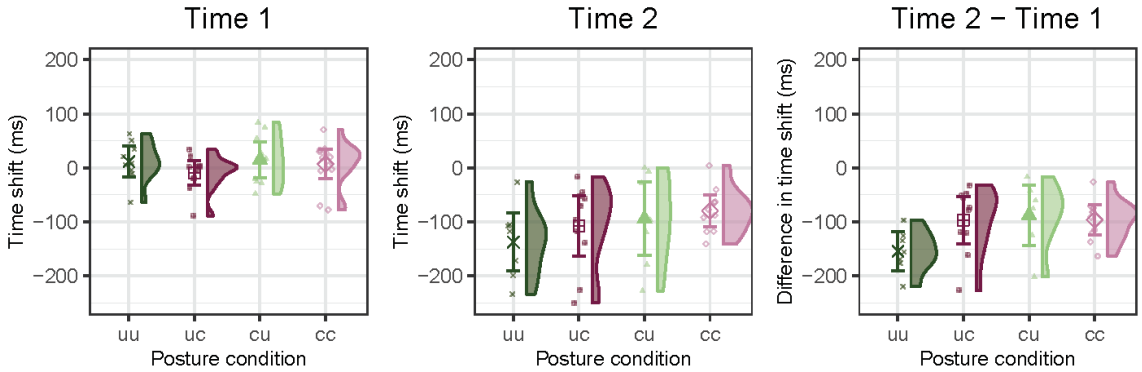

Figure 7. *Time shift of stimulus localization error in TOJ error trials relative to time 1 (left panel) and time 2 (middle panel) for the four posture conditions. The temporal shift of the localization error curve was significantly different from zero when calculated relative to time 2, but not relative to time 1; this result is consistent with the time reconstruction hypothesis, but not with the stimulus switch hypothesis. This pattern was similar across all participants as demonstrated by the differences in time shift between time 2 and time 1 (right panel). Data are visualized with raincloud plots (Allen et al., 2019) displaying probability density estimates, condition averages (large symbols), and individual participants (small symbols). Error bars denote 95% confidence intervals.*

Fig. 7 displays the temporal shift between the localization error curve of incorrect TOJ trials and the error curves at time 1 and time 2, as derived from correct TOJ trials. A linear mixed model with factors Posture Condition and Reference Time Point (localization errors for correct TOJ trials computed relative to time 1 or time 2) and time shift of the error curve between correct and erroneous TOJ trials as dependent variable revealed a significant effect of Reference Time Point ($\chi^2(9,10) = 15.55$, $p < 0.001$), but no effect of Posture Condition ($\chi^2(7,10) = 1.57$, $p = 0.67$) or interaction ($\chi^2(7,10) = 4.53$, $p = 0.21$) between the two factors. The time shift between localization errors for correct TOJ trials at time 1 and TOJ error trials, averaged across all four posture conditions, was 6 (s.e., 3) ms; if this value is not significantly different from 0, then an LMM of only this condition should not improve by inclusion of an intercept, as the latter would model the deviation of the average shift away from 0. Indeed, comparison of a model with and without intercept did not provide statistical evidence to reject a zero time shift ($\chi^2(1) = 0.84$, $p = 0.36$). In line with this result, a Bayesian analysis of a model with a random participant factor and a population-level intercept estimated the population intercept at 6 ms, and the 95% confidence range [-8.28; 19.27 ms] included 0. Model comparison via leave-one-out cross-validation found a model without population intercept to be more credible (difference of expected log predictive density, ELPD, for second as compared to first model: -0.6, s.e. 0.9). In contrast, the average time shift between localization errors for correct TOJ trials at time 2 and TOJ error trials was -105 (s.e., 7) ms, and a model without intercept fit this condition siginificantly worse than a model that included the intercept ($\chi^2(1) = 19.38$, $p < 0.001$). The significant difference to time 2 suggests that participants did not aim at the position of the second stimulus in TOJ error trials. While neither the non-significant difference to time 1 in the LMM analysis, nor the Bayesian parameter estimate including 0 statistically imply equality of the error curves in correct and incorrect TOJ trials, these statistical results are consistent with the two conditions being equal, and they suggest that, if a difference exists, it is small. Furthermore, the time shift of -105 ms for time 2 closely matches the stimulus SOA

of 110 ms, further suggesting that, in error trials, participants did not aim for hand location at the second, but rather at the first time point. Corroborating this conclusion, the Bayesian 95% interval [-138; -76 ms] of the intercept estimate includes -110 ms, and comparison of Bayesian models for time 2 with and without intercept strongly favored the model including the intercept (difference in ELPD from first to second model, -1.4, s.e. 1.9).

Experiment 2

The results of Experiment 1 suggest that when asked to localize the external location of the first of to two tactile stimuli applied in succession to different hands, participants chose which hand received the stimulus and then inferred the location of the chosen limb at the time point of the first stimulus. Consequently, when participants chose the incorrect limb, stimulus location was determined as the location at which the incorrect hand was at the correct (first) time point. While these results support the *time reconstruction hypothesis*, it should be realized that Experiment 1 tested only a single SOA of 110 ms between the two tactile stimuli. If our conclusions drawn from Experiment 1 are correct, then localization of stimuli assigned to the incorrect hand should always depend on the first stimulus's time, independent of SOA.

Experiment 2 tested this conjecture. Again, participants judged which hand had received the first of two tactile stimuli during a bimanual movement and then located the stimulus perceived to have occurred first. We presented tactile stimuli with four different SOAs: 60, 85, 110, and 135 ms. As the estimated localization error curves in Experiment 1 were similar for all combinations of the hands' start and end posture, Experiment 2 involved only reaches from an uncrossed to an uncrossed posture and from a crossed to a crossed posture. This strategy minimized marker obstruction and homogenized movement time across conditions. Experiment 2 was conducted in a different lab than Experiment 1, using different equipment, re-written experimental code, different experimenters, and new

analysis scripts (see Material and methods for details). To further scrutinize the reliability of our results, we increased our sample size and acquired a higher number of trials.

Hand assigment

In accordance with Experiment 1 and previous findings (Heed, Möller, et al., 2015; Hermosillo et al., 2011), TOJ performance in Experiment 2 was modulated by hand posture and SOA. At all SOA, participants made large amounts of errors, ensuring that a sufficient number of trials were available to analyze incorrect hand choice trials. Detailed results are reported in the Supplementary Information.

Explicit stimulus localization in space

Complementing the findings from Experiment 1 and further corroborating the *time reconstruction hypothesis*, localization errors of the incorrect TOJ trials largely overlapped with the localization errors of correct TOJ trials at time 1 for each of the four SOAs (see Fig. 8) and for each subject and posture condition (see Supplementary Fig. 2-7).

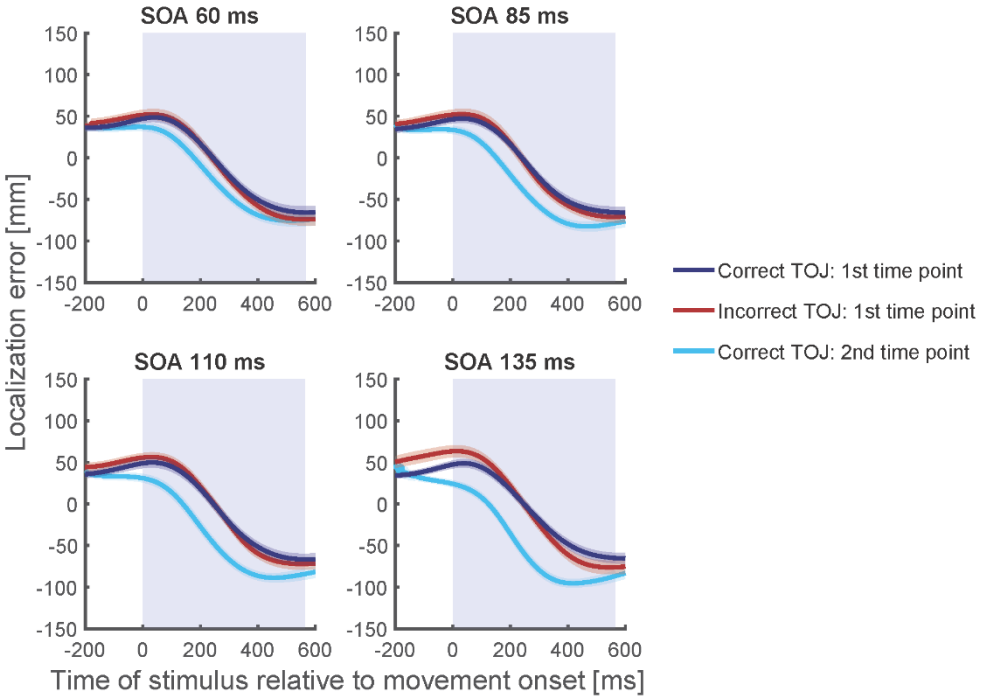

Figure 8. *Localization curves, averaged across participants and posture, for each of the four SOAs. Curves of incorrect TOJ trials (red) show a similar pattern as the localization curves of the correct TOJ trials at time 1 (dark blue), but not as the localization curves of the correct TOJ trials at time 2 (light blue). This pattern was highly similar across all subjects (see Supplementary Information) and also when calculated separately for each posture condition (see Supplementary Information). Traces reflect the mean, shaded areas around the traces reflect s.e.m. The shaded regions in the background represent the average movement time.*

Fig. 9 shows the temporal shift between the localization error curves of incorrect TOJ trials and the error curves of correct TOJ trials relative to time 1 and time 2 four all four SOAs.

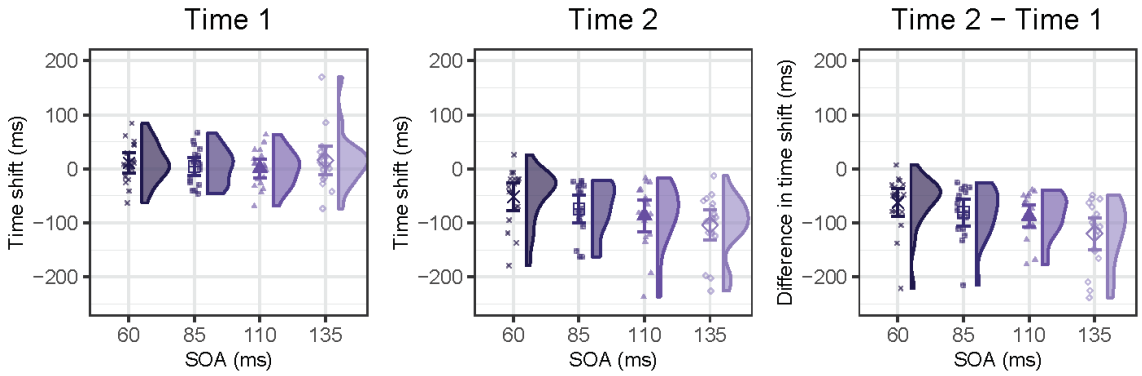

Figure 9. *Time shift of stimulus localization error in TOJ error trials relative to time 1 (left panel) and time 2 (middle panel) for the four SOAs. For all SOAs, the temporal shift relative to time 1 was not significantly different from 0. In contrast, the time shift was significantly different from zero for all SOAs when calculated relative to time 2, and it was numerically similar to the respective SOA. These results are consistent with the time reconstruction hypothesis, but not with the stimulus switch hypothesis. This pattern was similar across all participants as demonstrated by the differences in time shift between time 2 and time 1 (right panel). Data are visualized with raincloud plots (Allen et al., 2019) displaying probability density estimates, condition averages (large symbols), and individual participants (small symbols). Error bars denote 95% confidence intervals.*

A linear mixed model with factors SOA and Reference Time Point (localization errors for correct TOJ trials computed relative to time 1 vs. time 2) and time shift of the error curve between correct and erroneous TOJ trials as dependent variable revealed a significant main effect of Reference Time Point ($\chi^2(9,10) = 21.33$, $p < 0.001$) and a significant Reference Time Point × SOA interaction ($\chi^2(7,10) = 9.90$, $p = 0.02$). The time shift between localization errors for correct TOJ trials at time 1 and TOJ error trials, averaged across all four SOA conditions, was 8 ms. As in Experiment 1, a LMM with a common intercept for all SOAs did not fit the data better than a model without an intercept ($\chi^2(1) = 1.24$, $p = 0.27$). Similarly, allowing for individual intercepts per SOA did not improve the goodness of fit, ($\chi^2(3) = 2.74$, $p = 0.43$). Thus, none of the tested models provided statistical evidence to reject a zero time shift with respect to time 1. These results were again supported by parameter estimates of Bayesian models equivalent to

the afore-mentioned LMMs, which estimated both an intercept across all SOAs and individual intercepts per SOA to lie in intervals that included 0 (see Supplementary Information). Model comparison via leave-one-out cross-validation found a model without population intercept to be more credible than a model with a common intercept (difference of expected log predictive density, ELPD: -0.2, s.e. 0.6) and a model with individual intercepts per SOA (ELPD: -2.2, s.e. 2.2).

In contrast, the average time shifts between localization errors for correct TOJ trials at time 2 and TOJ error trials were -52 (s.e., 12) ms, -75 (s.e., 12) ms, -87 (s.e., 14) ms, and -104 (s.e., 13) ms for the SOA 60 ms, 85 ms, 110 ms, and 135 ms, respectively. A model with a common intercept for all SOAs explained the data significantly better than a model without an intercept ($\chi^2(1) = 29.27$, $p < 0.001$). A model allowing for different intercepts for each SOA further improved the goodness of fit ($\chi^2(3) = 14.3$, $p = 0.003$), indicating that localization curve's time shift relative to time 2 depended on the respective SOA (see Supplementary Table 3 for Bayesian model estimates). Model comparison via leave-one-out cross-validation found a model with individual SOA intercepts to be more credible than a model with a common intercept (difference of expected log predictive density, ELPD: -5.4, s.e. 3.8) and a model without intercept (ELPD: -7.2, s.e. 4.7).

Somewhat unexpectedly, the time shift value for the 110 ms SOA in Experiment 2 (-87 ms) diverged more from the SOA compared to Experiment 1 (-105 ms, averaged across all four posture conditions). However, in Experiment 2, average time shift values generally underestimated the true SOA. Nontheless, the Bayesian 95% intervals of the intercept estimates included the true SOA for all but the largest SOA (i.e., 135 ms, see Supplementary Table 3). Furthermore, at time 1, the estimated intercepts were all slightly (albeit non-significantly) positive (Fig. 9 left panel, Supplementary Table 3), and when one considers the difference in time shift (i.e., Time 2 – Time 1), the estimated values match the true SOA more closely (-63 ms, -81 ms, -88 ms, and -120 ms for SOAs 60 ms, 85 ms, 110 ms , and 135 ms, respectively; Fig. 9 right panel).

Discussion

The aim of our study was to test whether participants represent the remapped spatial location of tactile stimuli when they make spatial decisions about tactile stimuli. Participants indicated both the target limb and the perceived location in space of the first of two tactile stimuli in a tactile TOJ task. Presentation of stimuli during movement implied that stimulus location depended on stimulation time, allowing us to determine the relationship of stimulus timing and perceived stimulus location in space. If participants had first computed the spatial location, and then derived which limb had occupied this location at time of stimulation (*space-to-limb reconstruction hypothesis*, see Kitazawa, 2002), incorrect hand assignment should have been associated with external localization along the trajectory of the correct hand; we did not find any evidence for such behavior. If participants had represented stimulus location and stimulated limb together, and simply confused the two due to conflict between different spatial codes (*stimulus switch hypothesis*), incorrect hand choice should have been associated with spatial localization at the location of the incorrect limb at the second stimulus's time. Localization error curves were incompatible with this view, as their systematic bias differed significantly from a hypothetical localization curve, derived from correct trials, relating to stimulus time 2. Instead, when participants chose the incorrect hand, their localization errors implied that they had aimed at that hand's location at the time of the first, correct stimulus, evident in a close match of localization curves of correct and erroneous TOJ trials when computed relative to stimulus time 1. In other words, participants derived the reported stimulus location by combining the time of the first, correct stimulus with the trajectory of the second, incorrectly chosen hand, effectively indicating a location at which no stimulus had occurred – consistent with the *time reconstruction hypothesis*. This behavior was evident for all combinations of uncrossed and crossed start and end postures, as well as for all tested SOAs between the two tactile stimuli. TOJ errors, thus, did not simply reflect temporal confusion of two stimuli; instead, localization in TOJ error trials

marks the computation of tactile stimulus location based on correct stimulus timing and movement information of a (correctly or incorrectly) implied body part. Accordingly, limb crossing affected hand assignment, but not stimulus localization.

The pattern of hand assignment errors was in line with previous studies: Participants made more TOJ hand assignment errors in conditions that involved hand crossing than in conditions in which the hands were uncrossed (see Fig. 3; Heed, Möller, et al., 2015; Hermosillo et al., 2011; Shore et al., 2002; Yamamoto & Kitazawa, 2001). These reliable findings support the interpretation that categorical decisions in touch, such as choosing which limb was stimulated, are affected by weighted integration of different spatial aspects of the tactile stimulus and configuration of the body (Badde et al., 2019; Badde & Heed, 2016; Heed & Azañón, 2014). In contrast, localization error patterns were similar across uncrossed and crossed start and end hand posture conditions, suggesting that arm posture during stimulation did not affect reach-to-point localization (see Fig. 4, 5). In particular, localization errors exhibited comparable spatial biases over time in uncrossed and crossed conditions. Furthermore, localization error scattered around the chosen hand was not biased towards the other hand (see Fig. 4), an effect one might have expected if, like hand assignment, spatial localization was subject to weighted influence of the tactile stimulus's anatomical origin as coded by a body-based reference frame.

The dissociation between TOJ hand choice and localization responses indicates that the two phenomena do not reflect the same process. It is widely assumed that the weighted integration of spatial factors reflected by tactile limb crossing effects trades off the anatomical and the external location of a tactile stimulus (Badde & Heed, 2016; Cadieux & Shore, 2013; Kitazawa, 2002; Shore et al., 2002; Yamamoto & Kitazawa, 2001). This assumption requires that an external location is constructed as a prerequisite for assigning a stimulus to a hand. Our present finding that participants incorrectly localize tactile stimuli associated with

incorrect limb choice, in contrast, implies that not stimulus location determines hand choice, but vice versa, hand choice determines perceived stimulus location.

In turn, this conclusion is incompatible with the common view that crossing effects, obtained in experiments that require categorical decisions such as TOJ, are an implicit indicator of precise tactile localization and, thus, tactile remapping. This is a seemingly surprising conclusion given that limb crossing quite obviously creates conflict between the anatomical body side and the side of space, and it is a strong claim that seems to invalidate the experimental logic of numerous papers that have applied this logic. Our conclusion is, however, in fact compatible with that of another recent study in which participants performed TOJ of tactile stimuli presented to the hands and feet (Badde et al., 2019). In that study, stimuli were presented to two of the four limbs (hands and feet), but it was unknown to the participant which two limbs would be stimulated in a given trial. Accordingly, four rather than just two response options were always available. In a percentage of trials, participants systematically assigned the first touch to a limb that had not received a tactile stimulus at all during the respective trial. For instance, after stimulation of the left hand and the right foot, a participant may have indicated that the first stimulus had occurred on the right hand. These errors depended on whether the arms and/or legs were crossed. Importantly, neither the side of space of the limb that had received the correct stimulus, nor the spatial distance between stimulus and response limb, were indicative of the erroneously chosen, unstimulated limb – again incompatible with the prevailing view that crossing effects reflect conflict during the integration of anatomical and spatial stimulus location. Instead, participants responded with unstimulated limbs that occupied the space anywhere around the body side of the correct, first tactile stimulus, independent of whether that limb was crossed or not. Thus, what mattered for limb assignment was not the precise, spatial location of the stimulus, but much broader, global spatial stimulus features such as an entire side of the body and its surrounding space. Critically, these global features explained behavior without

562 having to recur to the use of external-spatial coding of touch location, consistent
563 with the present finding that the latter is only computed when necessary.

564 Notably, other manipulations that have been used to argue for the relevance
565 of precise spatial representations in tactile decisions can be framed in such a
566 feature-based account as well. For instance, the TOJ crossing effect was reduced
567 when the two hands' positions differed in height or in depth (Azañón et al., 2016).
568 However, this manipulation may have simply introduced an additional, non-metric
569 feature that helped representing the two choice options as different, thus improving
570 TOJ choice based on a categorical feature rather than on metric distance.
571 Similarly, whereas effects of distance between the two hands during a TOJ have
572 been interpreted as implying a metric representation of stimulus location (Roberts
573 et al., 2003; Shore et al., 2005), others have reported such effects only for very
574 small (3cm), but not other (10 cm and larger), distances between the hands (Kim
575 & Cruse, 2001), again suggesting that they may reflect categorically coded spatial
576 features, not metric stimulus location.

577 The reason for the apparent contradiction between previous research and
578 these new findings stems from the fact that typical experimental designs, in which
579 tactile stimuli are presented to the two stationary hands, do not allow disentangling
580 the prevailing view of crossing effects indicating conflict between tactile anatomical
581 and (precise) spatial stimulus location from the view that the conflict apparent in
582 limb crossing must indicate other spatial aspects, such as those identified in our
583 previous study (Badde et al., 2019). Thus, limb crossing paradigms that require
584 limb choices about the origin of touch likely reflect the integration of categorical,
585 tactile-spatial stimulus features. We propose that automatic effects, such as
586 crossmodal, tactile-visual cueing (Azañón & Soto-Faraco, 2008), too, are based
587 on such feature-based processing. In contrast, precise stimulus location is,
588 contrary to what has regularly been implied, not among the pieces of information
589 that are integrated for automatic, tactile-spatial coding. Instead, precise location of
590 the tactile stimulus in space is inferred post-hoc only when required.

Furthermore, our proposal contrasts with the suggestion that TOJ errors are due to temporal confusion of the two stimuli, hypothesized to occur due to slowing of a neural clock mechanism because crossed postures induce higher cognitive load as compared to uncrossed postures (Kitazawa et al., 2008). This hypothesis is based on the assumption that tactile locations are represented correctly but ordered incorrectly in time. It is incompatible with our finding that participants localized touch in incorrect TOJ trials at the location of the incorrect hand at the correct, first stimulus time point. Moreover, an account based on time confusion is specific to the TOJ paradigm, in which participants compare two stimuli. In contrast, a feature-based account generalizes to other experimental paradigms, including ones that present only a single tactile stimulus (Azañón et al., 2010; Azañón & Soto-Faraco, 2008; Badde et al., 2015, 2019).

Our study exploited known variations in localization bias when touch is presented during movement. We have previously proposed a computational model for tactile localization errors that faithfully replicates these biases assuming that participants are uncertain about the time at which the stimulus occurred relative to the movement, and combine a probability distribution of the possible stimulus time with the perceived arm movement trajectory (Maij et al., 2013, 2017, see also Maij et al., 2011 for a visual analogue). The present results are compatible with the temporal uncertainty model. Independent of which hand the stimulus was assigned to, the temporal estimate of the tactile stimulus was identical, resulting in identical localization error profiles, based on the trajectory of the chosen hand, in correct and erroneous TOJ trials.

To summarize, we observed the typical dependence of tactile TOJ responses on limb posture, with higher error rates when the hands are crossed rather than uncrossed. Explicit localization responses of the stimulus chosen as having occurred first were incompatible with theoretical accounts that posit confusion of yoked stimulus representations that encompass the independently determined external-spatial location of tactile stimuli, or projection of a body part

onto the determined spatial location of a stimulus. Instead, participants chose one hand presumably based on categorical, spatial stimulus characteristics such as the stimulated body side (Badde et al., 2019), and then combined the time point associated with the first stimulus with the chosen arm's trajectory. After hand assignment errors, participants, thus, effectively referenced a post-hoc constructed spatial location at which no stimulus had ever occurred.

Materials & methods

Data for the presented analyses as well as code to run analyses and create figures are provided at the Open Science Framework website, https://osf.io/ybxn5/.

Participants

Experiment 1 was performed at the Faculty of Psychology and Human Movement Science of the University of Hamburg. Twelve right-handed participants (aged 19-31 years, 7 female) gave informed consent to take part in the experiment. The study was part of a research program approved by the ethics committee of the German Psychological Society (DGPs). Experiment 2 was preregistered at the Open Science Framework website (https://osf.io/qyzgb). A sample size of 20 participants was defined a priori. We collected data from 20 individuals from Bielefeld University. We excluded data of 1 participant from analyses as s/he did not follow the instructions and most of the time localized the tactile stimulus at the start or end position, but not along the movement trajectory. Furthermore, we excluded data of another participant as s/he only completed 384 trials in total. As any form of data acquisition was stopped in our lab beginning of March 2020 due to the spread of the corona virus, we did not collect data from replacement participants. Our sample thus constisted of 18 participants (aged 18-25 years, 15 female). The experiment was approved by the ethics committee at Bielefeld University (Ethical Application Ref: 2017-114).

Participants provided written informed consent and were compensated with €7/hr or received course credit. All participants had normal or corrected-to-normal vision and did not have any known perceptual, motor, or neurological disorders. Participants took part only if, in a screening experiment, they exhibited a TOJ crossing effect at the SOA used in the main experiment. We used this screening procedure because individual response patterns in tactile experiments involving hand crossing are quite variable (Badde et al., 2015; Cadieux et al., 2010; Yamamoto & Kitazawa, 2001); however, crossing effects are highly reliable across the entire population, so that our screening procedure does not preclude generalization.

General setup

Participants were blindfolded. They sat on a chair at a table. A tactile stimulator (Oticon BC 461-0/12, Oticon Ltd., London, UK) was attached to the phalanx media of each index finger. Stimulation consisted of 200 Hz vibration for 10 ms. To mask any noise of the vibrators, participants wore earplugs and heard white noise through speakers (Experiment 1) or wore sound-attenuating headphones (Superlux HD669, Superlux Enterprise Development, Shanghai, China; Experiment 2).

Experiment 1

Apparatus, task and procedure

The position of each index finger in space was recorded with an Optotrak active, infrared marker motion tracking system (Northern Digital Inc., Waterloo, Ontario, Canada) at a sampling rate of 1000 Hz. One marker was positioned on the nail of each index finger, directly next to the tactile stimulator. A data acquisition unit (Odau; Northern Digital Inc., Waterloo, Ontario, Canada; sampling rate 1000 Hz) synchronized marker position and timing of the tactile stimuli. The experiment was controlled with Matlab (Mathworks, Natick, MA, USA), using the Psychophysics

673 Toolbox (Brainard, 1997) and the Optotrak Toolbox (http://webapp6.rrz.uni-
674 hamburg.de/allpsy/vf/OptotrakToolbox).

675 Participants moved both hands from a position of about 40 cm away from their
676 body towards their body to a position about 10 cm away from their body. Hand
677 start and end posture were uncrossed and crossed, varied in blocks of 50 trials in
678 pseudo-randomized order (see Fig. 2A). In each trial, a tone instructed the
679 movement start. At a random time (presented between 50-800 ms after the tone,
680 drawn from a square distribution) before, during, or after the movement, two tactile
681 stimuli were applied, one to each hand, at an SOA of 110 ms; the left-right order
682 of stimuli was pseudo-random. Upon movement completion, participants moved
683 the index finger that they had perceived to have been stimulated first to the location
684 of the first stimulus on the table. The hand remained in this location until a tone,
685 presented 2.5 s after the initial movement cue instructed them to lift the index
686 finger; this finger lift was used to identify the response hand during trajectory
687 analysis. Subsequently, participants repositioned the hands to their start locations.
688 We acquired 300 trials of each posture combination. To compensate for
689 obstruction of motion tracking markers, we acquired more trials for 2 participants
690 in the uncrossed to crossed posture and vice versa movement condition. The
691 experiment took approximately 4 hours, split in two-hour sessions held on different
692 days. Practice trials were included on each day before the experiment started until
693 the participant had understood, and felt confident with, the task. In total we
694 acquired 14.776 trials.

695 ***Analysis***

696 *Data preprocessing.* Start and end of the movement were determined based on a
697 velocity threshold of 5 cm/s. We interpolated missing motion tracking data, for
698 instance due to obstruction when the hands passed each other or due to rotation
699 of the hands, using splines, with the restriction that movement onset and offset
700 could be determined. Trials were discarded when (1) marker data were missing at

movement onset and/or movement offset (11.9±2.6%; mean±sem); (2) no stimulus localization response, indicated by finger lifting, could be detected (5.4±1.3%; mean±sem); (3) movement duration is less than 200 ms (0.2±0.05%; mean±sem). In total, 17.5±2.9% (mean±sem) of trials were removed.

Analysis of Temporal Order Judgements (TOJ). We considered the TOJ to be correct when the hand used for the localization response had indeed been stimulated first.

Localization error. We calculated the localization error, that is, the difference between the true location of the index finger at the time of stimulation and the reported location, that is, index finger pointing location just before finger lifting. Errors are reported relative to the direction of the movement as a straight line between start and end position of the hand, with positive values indicating errors in movement direction towards the end position of the hand. The localization error varies systematically with the stimulus time relative to movement onset (Dassonville, 1995; Maij et al., 2011, 2013, 2017; Watanabe et al., 2009). The localization errors were converted to an estimated localization curve by averaging errors using a moving Gaussian window of 75 ms across a time window of -200 to 600 ms (step size 1ms) with respect to movement onset. For each participant and posture condition, we calculated localization curves for correct TOJ trials relative to onset of the first stimulus, for correct TOJ trials relative to onset of the second stimulus, and for incorrect TOJ trials relative to onset of the first stimulus.

Comparison of localization errors in correct and incorrect TOJ trials. To determine whether participants localized the stimulus relative to hand position at the first or the second stimulus timepoint, we calculated – separately for each participant and posture condition – the temporal shift that would produce the smallest deviations around a single, common localization curve of the compared conditions 1) between the incorrect TOJ localization curve and the correct TOJ localization curve relative to the first stimulus time point and 2) between the incorrect TOJ localization curve

and the correct TOJ localization curve relative to the second stimulus time point. Specifically, we shifted the data points of the incorrect TOJ localization curves in time from 300 – 300 ms in steps of 1 ms and calculated the squared localization error differences with an localization curve calculated from data points of the two compared conditions using a common moving Gaussian average for each time shift. We refer to the time value that minimized the summed squared error differences with this overall construction curve as time shift (Maij et al., 2009, 2017).

We assessed the time shift for both stimulus times and, accordingly, obtained two shift values per participant and posture condition. In some instances, we were unable to construct a time shift due to a low number of incorrect TOJ trials for that specific condition (18 cases out of 4 postures x 2 stimulus times x 12 participants = 96); these data points were treated as missing data in the linear mixed model analysis.

Statistical analysis. We assessed statistical significance of the reported results using (Generalized) Linear Mixed Models ([G]LMM) (Bolker et al., 2009, 2009) as implemented in R version 3.6.1 (R Core Team, 2014) using packages lme4, version 1.1-21 (Bates et al., 2015), and afex version 0.26-0 (Singmann, 2015). We estimated intercept parameters of Bayesian mixed factorial models equivalent to LMM using packages brms, version 2.12.0 (Bürkner, 2017, 2018), and loo, version 2.2.0 (Vehtari et al., 2017).

GLMM are adequate for analysis of binary variables such as correct vs. incorrect responses in our TOJ task (Jaeger, 2008). Furthermore, (G)LMM and are robust against missing data and account for differences in trial numbers across conditions, as present in our data. All reported statistics were computed using type 3 sums of squares, as implemented in afex. For the random structure of LMM and GLMM for TOJ analysis, we included only random intercepts, because models did not reliably converge when random slopes were included. Models that tested time

shifts against zero used only the data corresponding to one particular reference time point of correct trials (localization error relative to time 1 or time 2); given that posture did not significantly modulate time shift, the respective models excluded this factor. Accordingly, we compared a model without intercept [shift ~ 0 + (1 | participant] against a model with intercept [shift ~ 1 + (1 | participant], effectively testing whether a non-zero intercept significantly improved the time shift fit.

The brms R package uses STAN as backend. We ran LMM to estimate the 95% interval of the intercepts in the different time shift models. We compared Bayesian models using the loo_compare() function of the loo R package. This function uses leave-one-out cross-validation to compare models by assessing the models' predictive density when each data point is omitted from fitting (Vehtari et al., 2017).

Experiment 2

Apparatus, task and procedure

Kinematic data of the fingers was recorded using an optical motion capture system (Visualeyez II VZ4000v, Phoenix Technologies Inc, Vancouver, BC, Canada) at 250Hz sampling frequency with markers placed on the nail of the two index fingers. The experiment was controlled with Matlab (The MathWorks Version R2015a; Natick, MA, USA) using the Psychophysics Toolbox (Brainard, 1997). Stimulus presentation was controlled via custom-made hardware and triggered through a digital acquisition card (PCI-6509, National Instruments, Austin, USA).

The procedure was largely similar to Experiment 1, except that 1) participants made only reaches from an uncrossed to an uncrossed posture or from a crossed to a crossed posture and 2) tactile stimuli were separated by SOAs of 60, 85, 110, or 135 ms. Posture was varied in blocks of 64 trials in a pseudo-randomized order. Within each block, SOA and which hand was stimulated first were pseudo-randomized. Participants performed 28 blocks (14 of each posture combination) for a total of 1792 trials. To compensate for marker obstruction and failure to

785 reliably detect finger lifting, 2 participants performed 10 additional blocks (5 of each
786 posture combination). As we stopped any form of data acquisition in our lab for an
787 indefinite time period beginning of March 2020, 2 participants performed only 19
788 and 23 blocks, respectively. The experiment took about 5-6 hours to complete,
789 split in two-hour sessions held on different days. Practice trials were included prior
790 to each experimental session.

791 ***Analysis***

792 *Data preprocessing.* We used custom-written Matlab scripts for processing of
793 kinematic data. We first interpolated missing data points and resampled the data
794 to 1000 Hz using splines, and low-pass filtered the data using a second-order
795 butterworth filter with a cut-off frequency of 6 Hz. We determined movement onset/
796 offset of each hand as the time of the sample in which the resultant velocity of the
797 respective finger marker exceeded/ dropped below 5 cm/s. We excluded trials
798 when missing marker data could not be adequadetely interpolated (8 %), when no
799 stimulus localization response, indicated by finger lifting, could be detected (4.2
800 %), and when participants did not perform smooth, continuous, and synchronous
801 movements (6.8 %). In total we removed 18.2 % of the trials.

802 *Analysis of Temporal Order Judgements (TOJ) and localization error.* TOJ and
803 localization errors were determined as in Experiment 1. Because localization error
804 curves were similar regardless of start and end posture in Experiment 1, we
805 collapsed across postures in Experiment 2 to calculate the localization error
806 curves; we calculated individual curves for each participant and SOA (60, 85, 110,
807 and 135 ms). Localization error curves calculated separately for Experiment 2's
808 two posture conditions yielded qualitatively similar results (see Supplementary
809 Information).

810 *Comparison of localization errors in correct and incorrect TOJ trials.* Time shift
811 values were calculated as in Experiment 1 (separately for each participant and
812 SOA) using a shifting window of -300 to 300 ms (step size 1ms).

Statistical analysis. We assessed TOJ performance using a generalized mixed model (GLMM) with factors Posture (uncrossed-uncrossed, crossed-crossed), and SOA (60, 85, 110, 135 ms). The analysis approach for the dependence of time shifts on SOAs followed a similar logic as Experiment 1. We first assessed the significance of main effects and interaction of the experimental design with afex. We then assessed whether time shifts were 0 relative to time 1 and time 2. To this end, we compared models with a random participant factor but no fixed factors and intercept [shift ~ 0 + (1 | participant], with a common intercept for all SOAs [shift ~1 + (1 | participant], and with individual intercepts per SOA [shift ~ SOA + 0 + (1 | participant] separately for shift values relative to time 1 and time 2, respectively.

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