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

Femke Maij[3], W. Pieter Medendorp[3], Tobias Heed[1,2]

[1]Faculty of Psychology and Movement Science, Bielefeld University, Bielefeld, Germany

[2]Center of Excellence Cognitive Interaction Technology (CITEC), Bielefeld University, Bielefeld, Germany

[3]Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands

Running head: Post-hoc construction of tactile external location

Correspondence: Tobias Heed, tobias.heed@uni-bielefeld.de

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 different 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, Schütz, & Henriques, 2011; Thompson, Byrne, & Henriques, 2014), but also on salient world-centered landmarks (Schütz, Henriques, & Fiehler, 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, Djidjeli, & Durand, 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, Engel, & Röder, 2015). Indeed, there is evidence that external tactile locations can be coded in a gaze-centered reference frame (Harrar & Harris, 2010; Mueller & Fiehler, 2014b, 2014a), but also relative to anchors such as the head, torso, and hand (Alsmith, Ferrè, & Longo, 2017; Heed, Backhaus, Röder, & Badde, 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, Wolpert, & Haggard, 2002), as well as top-down information such as task-constraints (Badde, Heed, & Röder, 2015; Schubert, Badde, Röder, & Heed, 2017), action context (Mueller & Fiehler, 2014a), and cognitive load (Badde, Heed, & Röder, 2014) can affect the relative

contributions of different reference frames, presumably in a weighted manner (Angelaki, Gu, & DeAngelis, 2009; Atsma, Maij, Koppen, Irwin, & Medendorp, 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 in dependence of 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, Rösler, & Spence, 2004). The most common experimental manipulation underlying this claim is limb crossing. For a right-hand tactile stimulus, part of the right body side lies on the left side of space when the right arm is crossed over. 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, Camacho, & Soto-Faraco, 2010; Azañón & Soto-Faraco, 2008). 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, Spry, & Spence, 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 in an 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. 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 slightly reduces errors in TOJ (Gallace & Spence, 2005; Roberts, Wing, Durkin, & Humphreys, 2003; Shore, Gray, Spry, Spence, & others, 2005), and the TOJ crossing effect is smaller when the hands' positions additionally differ in height or depth (Azañón, Mihaljevic, & Longo, 2016). These graded modulations of the TOJ have led to the claim that the TOJ paradigm is an implicit index of tactile remapping

(Azañón, Stenner, Cardini, & Haggard, 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, Grave, Brenner, & Smeets, 2011; Maij, Wing, & Medendorp, 2013, 2017; Watanabe, Nakatani, Ando, & Tachi, 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, together 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

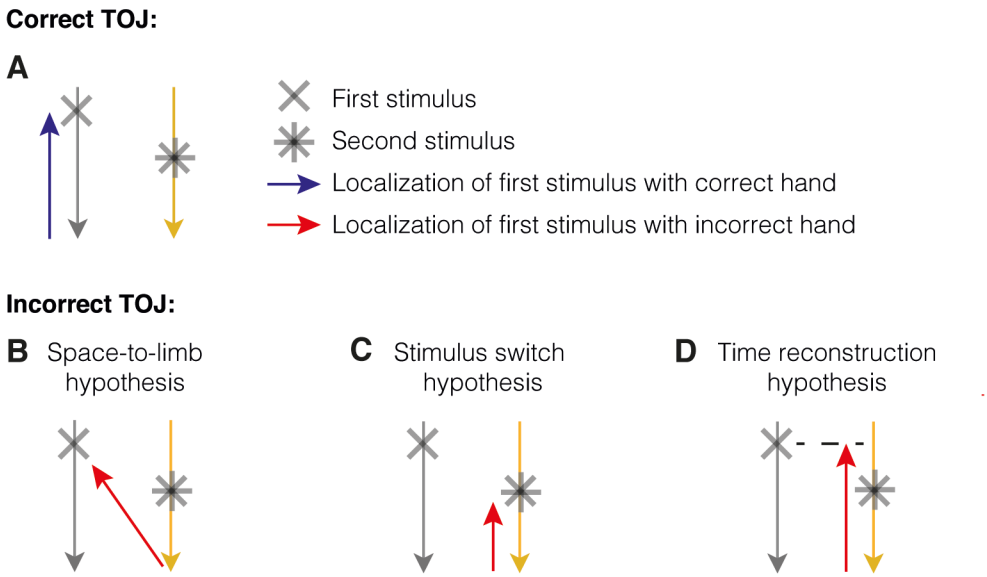

Figure 1. *Hand assignment and tactile localization in a TOJ task with bimanual movements. Grey trace, right arm trajectory; yellow trace: left arm trajectory; red trace: reach-to-point movement to external location of the tactile stimulus. A. Correct TOJ trial: the stimulus is assigned to the correct 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 thelocation 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, in a single experiment, 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, in a single experiment, 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 Figure 1. Because tactile stimuli were presented near the time of a 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 wrong hand, they reported stimulus location at where that hand been 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

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

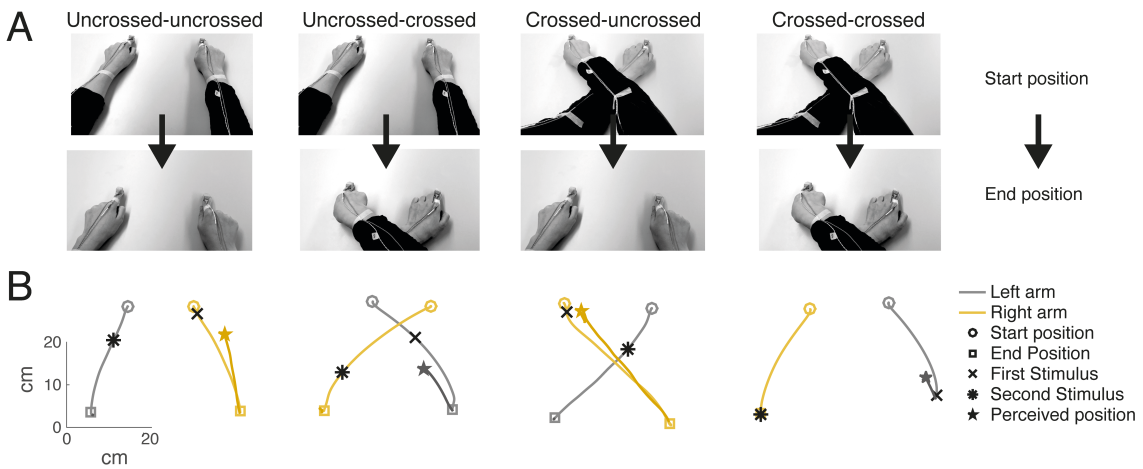

Figure 2. *Experimental conditions. A. The arms moved from an uncrossed (u) or crossed (c) start posture to either an uncrossed or crossed arm end posture. B. Example TOJ trial of a representative subject, showing the bimanual movement (grey: left arm, yellow, right arm) and the reach-to-point movement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

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

Hand assignment

We measured TOJ performance as the percentage of correct reports of which hand had been stimulated first in the TOJ task, as indicated by the hand that participants used for their localization response (see Figure 3). Stimuli could occur during all times (see Methods for details), so we binned the binary (correct/incorrect) TOJ response data into four movement phases – stimulation before movement onset, during first and second half of movement, and after

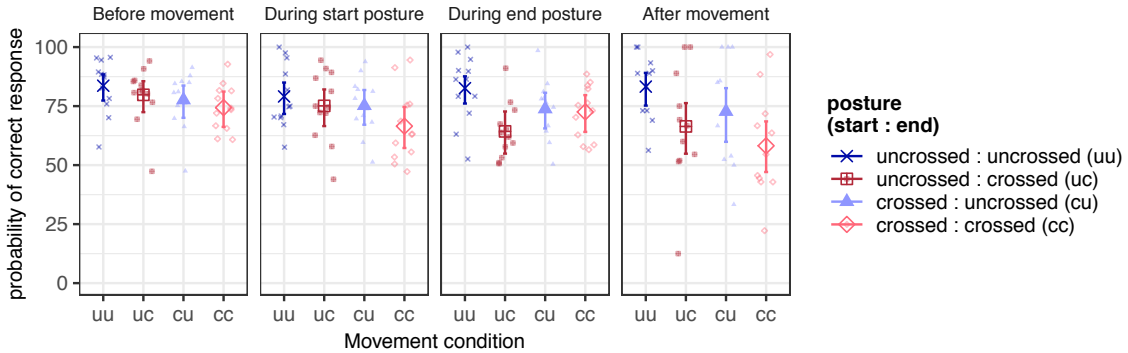

Figure 3. *Probability of correct hand assignment across movement conditions (uu, uc, cu, uu, with c=crossed, u=uncrossed posture) in the four phases of the bimanual movement (before movement, during start posture, during end posture, after movement). For uc and cu conditions, stimuli were classified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

movement offset – to assess the modulation of TOJ performance by stimulus time relative to the bimanual movement.

In accordance with previous findings, TOJ performance declined in the crossed compared to the uncrossed posture (Heed & Azañón, 2014), and depended on the posture at the time of stimulation (Heed, Möller, et al., 2015; Hermosillo et al., 2011). For instance, for the uncrossed-uncrossed movement condition (see Fig. 3, uu), the probability of correct response was high compared 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 interactions (see Table 1 at the end of this manuscript). With movement phase, the effect of Start Posture (see Fig. 3, dark vs. light colors) declined, whereas the effect

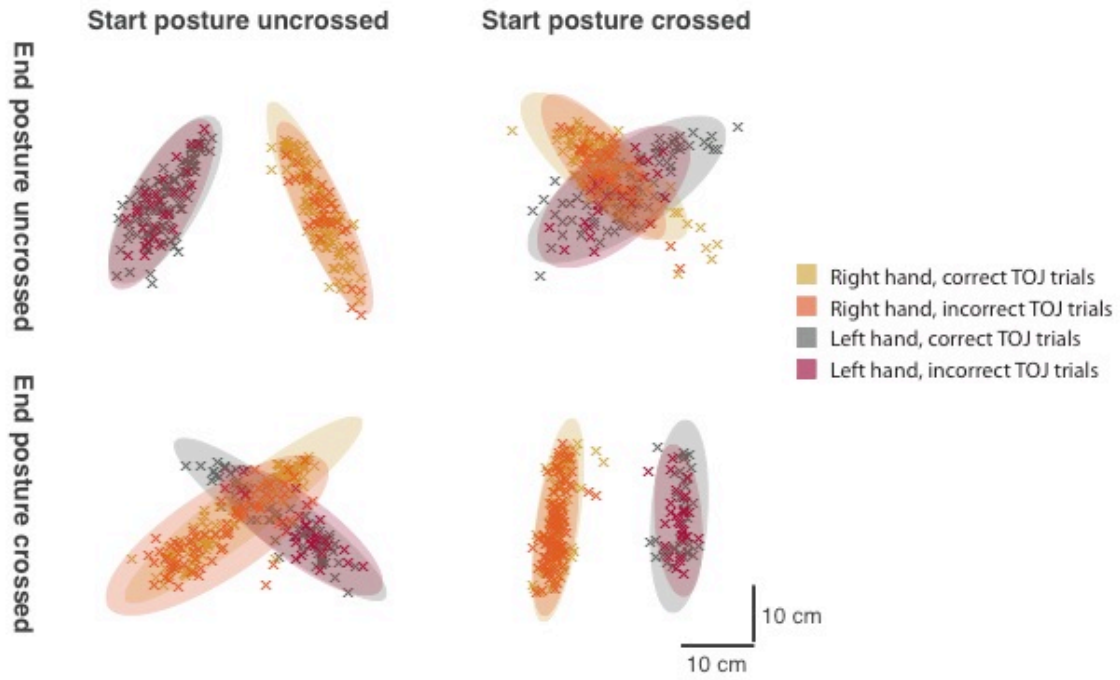

Figure 4. *Reach end points, as measures of localization responses, in the horizontal plane for the different movement conditions. Data are from a single participant with substantial end point variability. Ellipses cover 95% of the variability. Ellipses cover virtually identical spaces when participants 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.*

of End Posture (see Fig. 3, blue vs. red colors) increased, over time. Note that, due to our randomized stimulus timing strategy, this fourth movement phase contained fewer trials than the other phases (see Materials and methods).

In sum, TOJ performance in the present 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 & Azañón, 2014; Heed, Möller, et al., 2015; 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 Figure 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 Figure 1A). 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 Figure 2B), indicating that the chosen stimulus had been perceived on the incorrect hand (see Figure 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* assumes 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

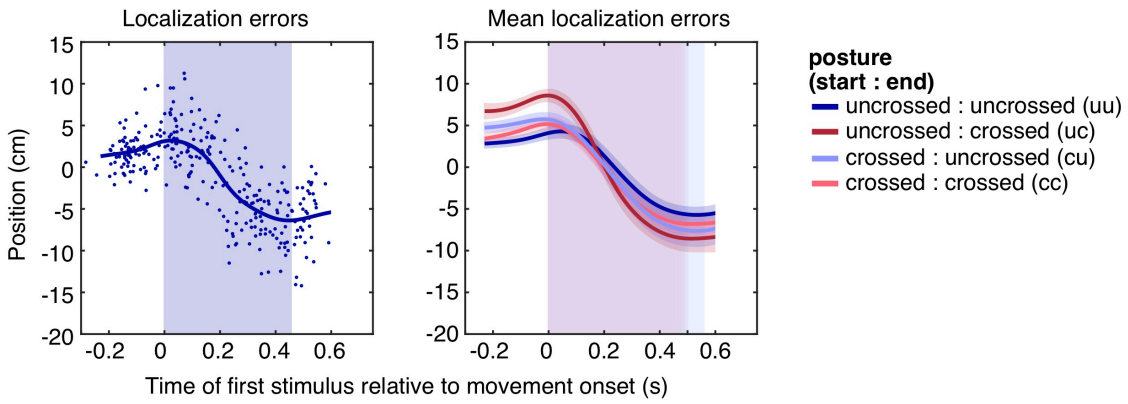

Figure 5. *Localization errors systematically vary in dependence of the progression of the movement. A. Mean localization error (blue line) of all correct localization trials of a single participant. Each dot represents the error of a single trial, that is the difference between true hand position at 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 toward the movement start point at the beginning, and toward the movement endpoint 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.*

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.

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

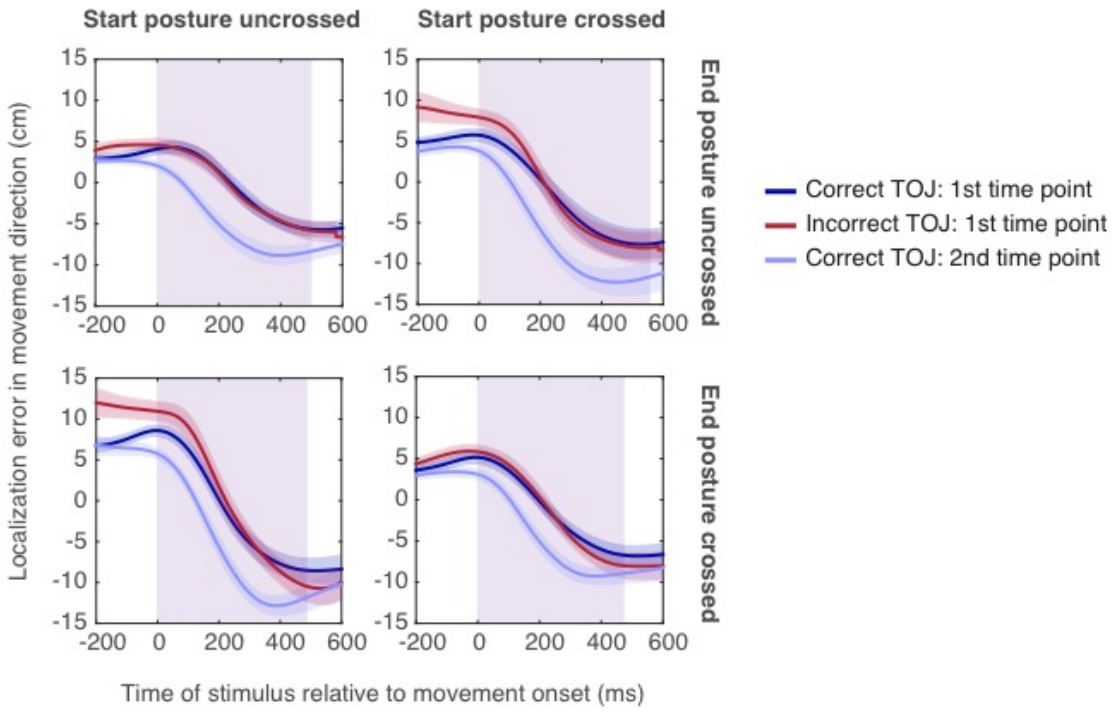

***Figure 6**. Localization curves of incorrect TOJ trials (in red), averaged across subjects, for each of the four movement conditions. Curves show a similar pattern as the localization curves of the correct TOJ performance (light blue), but shifted by the stimulus onset asynchrony (dark blue).*

retrospectively point to the spatial location of a tactile stimulus presented while the target limb was moving, their location judgment errors are systematically biased towards the movement start point during the initial part of a movement, and towards the movement end point 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 Figure 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 (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

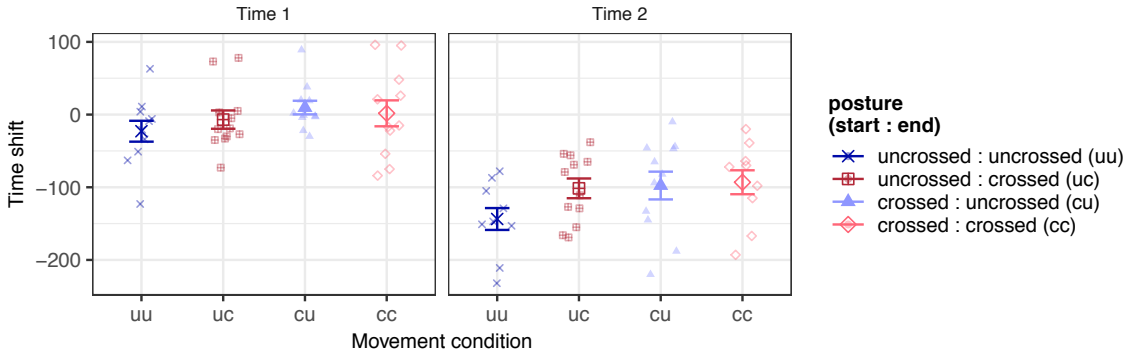

Figure 7. *Time shift of individual participants (small symbols) and average time shift (large symbols) in the four movement conditions when stimulus localization error in TOJ error trials is calculated relative to time 1 (left panel) and time 2 (right panel). Localization error was siginificantly different 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.*

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 around -110 ms (negative denoting a shift towards left, see above) – compared 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 second template curve, and near +110 ms compared to first template curve.

Figure 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 ($\chi^2(1) = 22.67$, $p < 0.001$), but no effect of Posture Condition ($\chi^2(3) = 6.82$, $p = 0.078$) or interaction ($\chi^2(3) = 2.40$, $p = 0.49$) 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 -5 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 ($\chi^2(1) = 0.36$, $p = 0.55$). In contrast, the average time shift between localization errors for correct TOJ trials at time 2 and TOJ error trials was -109 ms, and a model without intercept fit this condition siginificantly worse than a model that included the intercept ($\chi^2(1) = 26.68$, $p < 0.001$). The significant difference to time 2 suggests that participants did not aim at the position of the second stimulus in TOJ error trials. While the non-significant difference to to time 1 does not statistically imply equality of the error curves in correct and incorrect TOJ trials, it suggests that, if a difference exists, it is small.

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. Had participants 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. Had participants 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. 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 & 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 Figures 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 Figure 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; Badde et al., 2015; Cadieux & Shore, 2013; Heed & Azañón, 2014; 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, Röder, & Heed, 2018). In that study, the limbs that would receive the two stimuli for the TOJ were unknown prior to a given trial, so that 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 having to recur to the use of external-spatial coding of touch location, consistent with the present finding that the latter is only computed when necessary.

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

The reason for the apparent contradiction between previous research and these new findings stems from the fact that typical experimental TOJ designs, in which stimuli are presented to the two stationary hands, do not allow disentangling the prevailing view of crossing effects indicating conflict between tactile anatomical and (precise) spatial stimulus location from the view that the conflict apparent in limb crossing must indicate other spatial aspects, such as those identified in our previous study (Badde et al., 2018). Thus, limb crossing paradigms that require limb choices about the origin of touch likely reflect the integration of categorical, tactile-spatial stimulus features. We propose that automatic effects, such as crossmodal, tactile-visual cueing (Azañón & Soto-Faraco, 2008), too, are based on such feature-based processing. In contrast, precise stimulus location is, contrary to what has regularly been implied, not among the pieces of information that are integrated for automatic, tactile-spatial coding. Instead, precise location of 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, 2018).

Our study exploited known variations in localization biases 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 analague). 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., 2018), 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/.

The study 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. All participants were free of any known sensory, perceptual, or motor disorders. The study was part of a research program approved by the ethics committee of the German Psychological Society (DGPs). Participants were compensated with €7/hr or received course credit. Participants took part only if, in a screening experiment, they exhibited a TOJ crossing effect at the SOA used in the main experiment (see Supplementary Information).

Experimental 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 each index finger, close to the fingernail. 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.

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 Toolbox [17] and the Optotrak Toolbox (http://webapp6.rrz.uni-hamburg.de/allpsy/vf/OptotrakToolbox).

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

Data analysis. Start and end of the movement were determined based on a velocity threshold of 5 cm/s. We interpolated missing motion tracking data, for instance due to obstruction when the hands passed each other or due to rotation of the hands, using splines, with the restriction that movement onset and offset 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%;

500 mean±sem); (3) movement duration is less than 200 ms (0.2±0.05%; mean±sem).
501 In total, 17.5±2.9% (mean±sem) of trials were removed.

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

505 *Localization error.* We calculated the localization error, that is, the difference
506 between the true location of the index finger at the time of stimulation and the
507 reported location, that is, index finger pointing location just before finger lifting.
508 Errors are reported relative to the direction of the movement as a straight line
509 between start and end position of the hand, with positive values indicating errors
510 in movement direction towards the end position of the hand. The localization error
511 varies systematically with the stimulus time relative to movement onset
512 (Dassonville, 1995; Maij et al., 2011, 2013, 2017; Watanabe et al., 2009); for each
513 participant and posture condition, the localization errors were converted to an
514 estimated localization curve by averaging errors using a moving Gaussian window
515 of 75 ms.

516 *Comparison of localization errors in correct and incorrect TOJ trials.* To determine
517 whether participants localized the stimulus relative to the first or the second
518 stimulus, we calculated the temporal shift that minimized the squared difference
519 between the localization error curve constructed for the correct TOJ trials with the
520 moving window relative to the first and second stimulus time points, and the
521 reaching endpoints of the incorrect TOJ trials. In other words, we shifted the
522 endpoints of incorrect TOJ trials in time until the correct TOJ trial localization error
523 curve provided the best achievable fit for localization in incorrect TOJ trials. We
524 restricted this search to a time window of [-200 to 600 ms] around the respective
525 correct TOJ localization error curve. We refer to the time value that minimized the
526 squared difference as time shift. As the time shift was assessed for both stimulus
527 times, we obtained two shift values per participant. In some instances, we were

unable to construct a time shift due to a low number of incorrect TOJ trials for that specific condition (11 cases out of 4 postures x 2 stimulus times x12 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 3.4.3 (R Core Team, 2014) through the package lme4, version 1.1-7 (Bates, Mächler, Bolker, & Walker, 2015), and afex version 0.21-2 (Singmann, 2015). 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. GLMM for TOJ analysis used only random intercepts, because models did not reliably converge across all trial phases when random slopes were included. LMM for time shift analysis used main effects, because a there was not enough data to include the interaction. 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 with against a model without an intercept, effectively testing whether a non-zero intercept significantly improved the time shift fit.

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Tables

Table 1. Generalized Linear Mixed Models of temporal order judgment accuracy.

	df	χ^2	**p**
all trial phases (full model)			
start posture	16, 17	21.92	<0.001
end posture	16, 17	82.94	<0.001
movement phase	14, 17	69.36	<0.001
start posture : end posture	16, 17	10.48	0.001
start posture : movement phase	14, 17	8.26	.04
end posture : movement phase	14, 17	15.41	0.001
start posture : end posture : movement phase	14, 17	12.34	0.006
phase 1: before movement onset			
start posture	1	23.09	<0.001
end posture	1	8.48	0.004
start posture : end posture:	1	< 0.01	0.96
phase 2: first half of movement			
start posture	1	8.85	0.003
end posture	1	23.20	<0.001
start posture : end posture:	1	2.55	0.11
phase 3: second half of movement			
start posture	1	1.54	0.21
end posture	1	68.24	<0.001
start posture : end posture:	1	24.96	<0.001
phase 4: after movement offset			
start posture	1	4.15	0.04
end posture	1	22.67	<0.001
start posture : end posture:	1	2.33	0.13