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Visuoproprioceptive Conflict in Hand Position Biases Tactile Localization on the Hand Surface

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The location of touch can be represented in a somatotopic reference frame and, combined with proprioceptive information, in an external reference frame. There is evidence that body position influences where individuals feel touch on the skin surface, indicating that proprioceptive information affects tactile localization in a somatotopic reference frame. In conditions with visual and proprioceptive mismatch of body position, where do individuals feel touch on the body? We used the mirror box illusion to address this question. Participants placed 1 hand on each side of a mirror aligned with the body midline, such that the hand reflection in the mirror looked like the hand hidden behind the mirror. The illusion creates a spatial mismatch between the actual hidden hand position and where the participant perceives their hand to be (the mirror image location). Across three experiments, localization judgments on the hidden hand were consistently and systematically biased toward the actual hand position relative to the viewed hand position. These findings provide evidence that proprioceptive estimates of limb position influence tactile localization and are discussed in relation to two models of tactile localization.

Public Significance Statement

Where do people feel a touch when the viewed hand is displaced from its actual position? In the classic rubber hand illusion, people feel touch on the seen rubber hand when it is brushed in synchrony with their unseen actual hand. But does the actual hand still influence tactile perception? Using the mirror box illusion, we found that when there was spatial mismatch between visual and proprioceptive information of hand position, the perceived location of tactile stimuli on the skin surface was systematically biased toward the proprioceptively-defined hand position compared to baseline. These results provide evidence that the actual hand position exerts influence on tactile localization, adding to past findings that information from external space affects tactile localization in somatotopic space.

Keywords: tactile localization, somatotopic, external, visuoproprioceptive, mirror box

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Upon receiving a tactile stimulus, the brain represents its location in multiple spatial reference frames. Tactile location can be encoded in a *somatotopic* reference frame with coordinates fixed on the skin surface (Penfield & Boldrey, 1937). In this reference frame, a touch on the right index finger would be represented as the same location regardless of where the right hand itself is positioned. Beyond the skin surface, tactile location can also be represented in an external reference frame (Azañón et al., 2010; Heed & Azañón, 2014; Heed et al., 2015). Here, "external" refers to nonsomatotopic frames of reference with midlines that project from the body (e.g., trunk, gaze, hand) into external space. Tactile location in external space changes following movement of the touched body part.

While studies have provided evidence for somatotopic and external location representations of touch (e.g., Azañón & Soto-Faraco, 2008; Medina et al., 2019; Medina et al., 2014; Moscovitch & Behrmann, 1994; Overvliet et al., 2011), an interesting question is how information from these representations is integrated. Previous models have suggested that tactile localization is a serial process in which the brain first estimates tactile location on the skin surface, then maps tactile location to external space by

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referencing body position (Longo et al., 2010; Medina & Coslett, 2010). This seems intuitive, as our percept of touch on the skin surface does not seem to vary based on changes in limb position. An alternative framework has been proposed in which the brain integrates tactile location representations within multiple reference frames in making localization judgments (Badde & Heed, 2016; Badde et al., 2016; Heed et al., 2015). Studies have shown that gaze and head orientation influence tactile localization on the skin surface (Ho & Spence, 2007; Medina et al., 2018). For example, when asked to localize touch on the back of the unseen hand, participants made more distal errors (i.e. mislocalization toward the fingers) when the head and gaze were directed away from versus toward the touched hand (Medina et al., 2018). Other studies found that localizing touch to a specific body part was influenced by the relative position between the potentially stimulated body parts (Badde et al., 2019; Haggard et al., 2006; Overvliet et al., 2011; Riemer et al., 2010). These findings indicate that localizing touch on the skin surface is influenced by information from external space.

Past studies examining the influence of body position on tactile localization have had participants rely on proprioception alone (i.e. no vision of the stimulated limb, see Haggard et al., 2006; Harrar & Harris, 2009; Overvliet et al., 2011; Riemer et al., 2010), or have full vision of the stimulated body part (Ho & Spence, 2007; Medina et al., 2018). Although we typically see and feel our body in the same location, body illusions can separate information from vision and proprioception. When visual and proprioceptive input regarding limb position is dissociated, where do participants feel touch? In the rubber hand illusion, participants not only reported embodying the rubber hand, but also felt touch where they saw the rubber hand being touched, providing evidence that the location of perceived touch can shift to the embodied hand (Azañón & Soto-Faraco, 2007; Botvinick & Cohen, 1998; Gallace & Spence, 2005). Our preliminary work with the mirror box illusion found a similar phenomenon—people reported feeling touch on the viewed hand in the mirror location when the illusion was successful. Furthermore, this touch seemed fairly specific—after stimulation of the index finger, participants reported sensation on the index finger of the mirror reflection. This suggests a process in which touch is mapped to a location on the skin surface and then localized in external space to the embodied limb.

Even though touch is felt on the embodied hand, is there any influence of true limb position on tactile localization? To examine this question, we presented individuals with tactile stimulation on the back of the hand during the mirror box illusion. In the mirror box illusion, an individual places one hand on each side of a mirror that is aligned with the sagittal plane of the body, such that the hand reflection in the mirror (the "mirror hand") looks like the hand hidden behind the mirror (Ramachandran & Rogers-Ramachandran, 1996). When the two hands are placed at different distances from the mirror, the hidden hand is displaced from where it appears, creating a mismatch between the proprioceptive estimate (i.e. from the actual hand) and the visual estimate (i.e. from the mirror hand) of the hidden hand position. In this circumstance, the hidden hand is localized nearer to the viewed hand, as opposed to where it is actually positioned (Holmes et al., 2006; Holmes & Spence, 2005; Medina et al., 2015). The illusion is stronger when the individual moves both hands synchronously (e.g., in-phase tapping of the index fingers), such that the movements seen on the mirror hand are congruent with the movements performed by the hidden hand (Holmes & Spence, 2005; Medina et al., 2015).

After the mirror box illusion was established, we presented single touches to the participant's hidden hand and asked where on the hand surface the touch was perceived. If the actual position of the hidden hand does not influence tactile localization on the skin surface such that tactile sensations are veridically mapped onto the viewed hand, then one would predict unbiased localization judgments. However, if the actual position of the hidden hand influences tactile localization on the skin surface, then one would predict biases in localization judgments. Specifically, it is possible that tactile sensation is mapped to the viewed hand, but proprioceptive information informs the brain that touch occurred further away, biasing tactile localization in external space toward the actual hand position. This external bias influences tactile localization on the skin surface, biasing tactile localization toward the actual hand position. We will refer to this as the anchoring hypothesis, as touch is anchored to the embodied, viewed limb and is then pulled in the direction of the proprioceptively-defined limb. Alternatively, it is possible that touch is originally mapped to external space based on the actual proprioceptively-defined hand position, then biased toward the viewed hand resulting in the opposite localization bias. We conducted three experiments to test these possibilities. In Experiment 1, we altered the relative position between the actual and viewed hand and found that tactile localization on the skin surface was consistently biased toward the actual hand. Results from Experiments 2 and 3 confirmed these findings and ruled out potential alternative accounts. We then discussed potential mechanisms in the General Discussion section.

Experiment 1: Effects of Visuoproprioceptive Conflict on Tactile Localization

Method

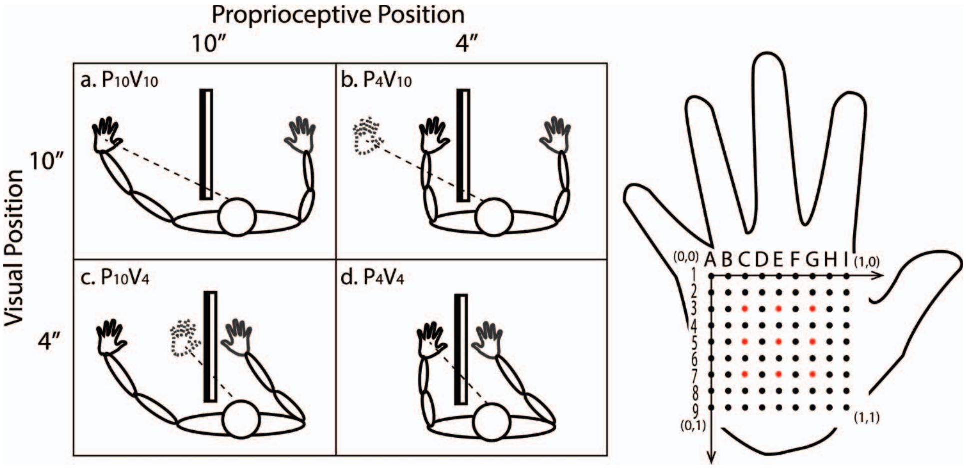
Design

A 2 × 2 design was used (see Figure 1): Participants placed their right hand in front of the mirror, with the middle finger either 4" (10.2 cm) or 10" (25.4 cm) away from the mirror. The left hand was hidden behind the mirror, either 4" or 10" away. Each condition is named as P_xV_y, with P representing the proprioceptive position and V the visual position of the hand, and x and y denoting the distance of proprioceptive and visual position from the mirror respectively. Previous studies have shown that a mismatch of 6" between the proprioceptive and visual hand position in the mirror box reliably induced shifts in felt hand position toward the visual position (Liu & Medina, 2018; Medina et al., 2015). In each condition, participants were touched on the dorsum of the hidden left hand and reported where on the skin surface they felt the stimulus (see Procedures below).

Participants

In a pilot experiment with two conditions (Figure 1c and 1d), we found significantly more lateral localization biases (i.e. toward the little finger) when the proprioceptive estimate was lateral to the visual estimate ($P_{10}V_4$) versus when both estimates were at 4" from the mirror (P_4V_4). With 10 participants, the effect size (Cohen's d) was 1.37 and the power was 0.97. Considering that the

Figure 1
Manipulations in Experiment 1



Note. Left: Participants placed their right hand in front of the mirror, either 4” or 10” away from the mirror. The left hand was hidden behind the mirror, at either 4” or 10” from the mirror. The reflection of the right hand in the mirror (dashed hand outlines) looks like the hidden left hand. Dashed straight black lines indicate gaze direction. Right: A 9 × 9 dot grid was drawn on the back of the hidden left hand. A coordinate system with A-I on the columns and 1–9 on the rows was labeled for the participants to make response. The dot grid was transformed to Bookstein coordinates with the most distolateral dot as (0,0) and the most distomedial (1,0) for analyses. Of the 81 dots, only the nine dots in red (gray) were stimulated, with the rest of dots providing a wider response range covering the entire dorsum surface. See the online article for the color version of this figure.

effect size could be inflated by a small sample size due to sampling biases, a smaller effect size was assumed in designing new experiments. With a moderate to high effect size of 0.8, 19 participants were needed to obtain a power of 0.9.

With the goal of 19 participants, 22 participants were recruited from the University of Delaware (mean age: 24.6 years, $SD = 5.1$ years, 8 males), assuming attrition. One participant did not complete the experiment and was excluded from the analyses. In addition, given that tactile localization performance decreases with tactile detection ability (Harris et al., 2004), participants were excluded if the number of trials where tactile stimuli were not felt exceeded the criterion (3 SDs of group mean; see Procedure below). One participant was excluded for this reason. In total, data from 20 participants were analyzed. All participants signed informed-consent forms and received monetary reimbursement of $10/hr. All studies were approved by the University of Delaware Institutional Review Board.

Apparatus

The mirror box used in the experiments consists of an acrylic mirror aligned with the body midsagittal plane (16” (40.6 cm) deep × 12” (30.5 cm) tall), mounted on a flat wooden base (36” (91.4 cm) wide × 16” (40.6 cm) deep). Two black curtains hung from each side of the mirror to prevent participants from seeing their forearms in the mirror box.

Tactile stimuli were delivered using Semmes-Weinstein monofilaments (North Coast Medical Inc., CA, U.S.). To induce tactile localization biases that could be modulated by experimental conditions, we used monofilaments with a bending weight of 0.6*g*. For most participants, this monofilament was light but suprathreshold. For participants who could not reliably detect the 0.6*g* filament, a filament of 1.0*g* was used (see Procedure below).

Procedure

At the beginning of the experiment, the experimenter drew a 9 × 9 dot grid (0.75 cm between adjacent dots; Figure 1, right) on the dorsum of the left hand. The midline of the dot grid was aligned with a virtual line connecting the wrist center and the knuckle of the middle finger. Then a picture of the left hand was taken and printed out with the hand in real size. On the picture, the dot-grid was labeled as A-I from the ulnar (little finger) to radial (thumb) side, and the rows as 1–9 from the knuckles to the wrist (Figure 1, right). Participants used this picture to make verbal localization judgments by stating the grid coordinates (e.g., “B7”). Unknown to the participant, only nine of the 81 dots were stimulated (marked red [gray] in Figure 1, right), with the rest of the dots providing a wider response range covering the entire space. After the hand picture was taken, the nine target dots were redrawn with a different color for the experimenter to locate.

To ensure that the participant could reliably detect tactile stimuli of this intensity, the experimenter tapped random locations on the dorsum of the left hand using the 0.6*g* filament before the experiment. If the participant reported not feeling the stimuli in more than three consecutive trials, a filament of one scale higher (1.0*g*) was used for that participant. Two out of the 20 participants included in the analyses were tested with the 1.0*g* filament in this experiment.

At the beginning of each block, the experimenter placed the participant’s hands such that the middle fingertips were at the instructed distances from the mirror. The left hand was placed with the participant's eyes closed, hence its exact location was unknown to the participant. To facilitate visuoproprioceptive integration, participants first tapped the index finger of both hands synchronously for 20 s at a metronome set at 120 beats per minute, while focusing on the hand in the mirror. The tactile stimulation trials started immediately after the tapping was completed. In each trial, the experimenter stimulated the instructed location on the participant's left hand. Then, the participant referred to the hand picture to verbally report the dot coordinate on which they felt the touch. The experimenter then typed the response to a computer for off-line coding. Trials in which the participant reported not feeling the stimulus were noted without being repeated.

Participants' hands remained at the same positions throughout each block. Each of the four conditions were tested in two blocks. Each block contained 27 trials, with three trials per stimulus location. Block and trial orders were randomized for each individual. The entire experiment lasted close to one hour.

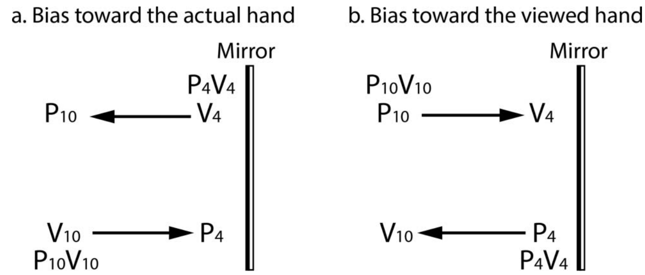
Data Analyses and Predictions

We converted the raw dot coordinates to Bookstein units (BU, Bookstein, 1997). The most distolateral and distomedial dots were designated as (0,0) and (1,0) respectively (Figure 1, right). As a result, the *x*-axis of the Bookstein coordinate was aligned with the mediolateral axis of the hand and *y*-axis with the proximodistal axis (Longo et al., 2015). Tactile localization error was calculated as the distance in Bookstein units between the responded dot and the actual dot in the mediolateral and proximodistal dimension respectively. Negative values denote lateral and distal biases. Prior studies showed that integration of visual and proprioceptive information is direction-specific (Snijders, Holmes, & Spence, 2007), we therefore only present hypotheses regarding the mediolateral localization bias and present the proximodistal bias in online supplemental materials.

To investigate the effects of visual and proprioceptive hand position on tactile localization, localization bias in each dimension was first analyzed using an omnibus repeated-measures ANOVA with proprioceptive position (10" and 4") and visual position (10" and 4") as independent variables. Different hypotheses on how visuoproprioceptive conflict influences tactile localization predict different main effects. First, if tactile sensation is mapped to the viewed hand but still influenced by the actual hand position (anchoring hypothesis), we would predict tactile localization bias toward the actual hand position (Figure 2a). For example, in both P_4V_4 and $P_{10}V_4$ (Figure 2a, top), tactile sensation is mapped to the viewed hand at 4." However, in the $P_{10}V_4$ condition, the actual hand position would cause additional lateral localization bias away from the mirror. We therefore predict a main effect of proprioceptive position, such that at each visual position, tactile localization bias occurs in the same direction as the incongruent actual hand position.

Alternatively, it is possible that tactile localization is biased toward the viewed hand, as with the perceived hand position (Figure 2b). For example, in both $P_{10}V_{10}$ and $P_{10}V_4$ (Figure 2b, top), the veridical tactile location is at 10." However, in the $P_{10}V_4$ condition, the viewed hand would cause additional medial localization bias toward the mirror. If this were the case, we would predict a main effect of visual position such that at each actual

Figure 2
Prediction of Each Hypothesis in Experiment 1



Note. Arrows denote the expected directions of tactile localization bias. a. With tactile sensation mapped to the viewed hand, tactile localization would be biased toward the proprioceptive estimate in incongruent versus congruent condition. b. With touch represented on the actual hand, tactile localization would be biased toward the viewed hand.

hand position, tactile localization bias occurs in the same direction as the incongruent viewed hand position.

Previous studies provide evidence that when the body is perceived as enlarged, the distance between two tactile stimuli is judged as farther apart (de Vignemont, Ehrsson, & Haggard, 2005; Taylor-Clarke et al., 2004). These findings indicate that tactile perception is influenced by perceived body size and shape. In the analyses described above, if tactile localization bias differed across conditions, one possibility is that manipulating proprioceptive and visual positions altered perceived tactile location per se. Alternatively, it is possible that visuoproprioceptive conflicts modulated perceived hand size and shape, which in turn influenced tactile localization. We therefore performed additional analyses to test these possibilities.

To quantify the size of the response space, we calculated the root mean squared distance between the average response on each dot to the center of the response space (Medina et al., 2018). An ANOVA was then performed with proprioceptive position and visual position as independent variables. To compare the shape of the response space across conditions, a generalized Procrustes analysis (GPA) was performed using the *geomorph* package in R (Adams & Otárola-Castillo, 2013; Longo et al., 2015; Medina et al., 2018). This analysis focuses on shape variance while aligning the size, position, and orientation across maps. The shape variance was then analyzed using an ANOVA with proprioceptive position and visual position as independent variables, using the procD.lm function in the geomorph package. All data from this study can be found on the Open Science Framework, see https://osf.io/z38hc/

Results

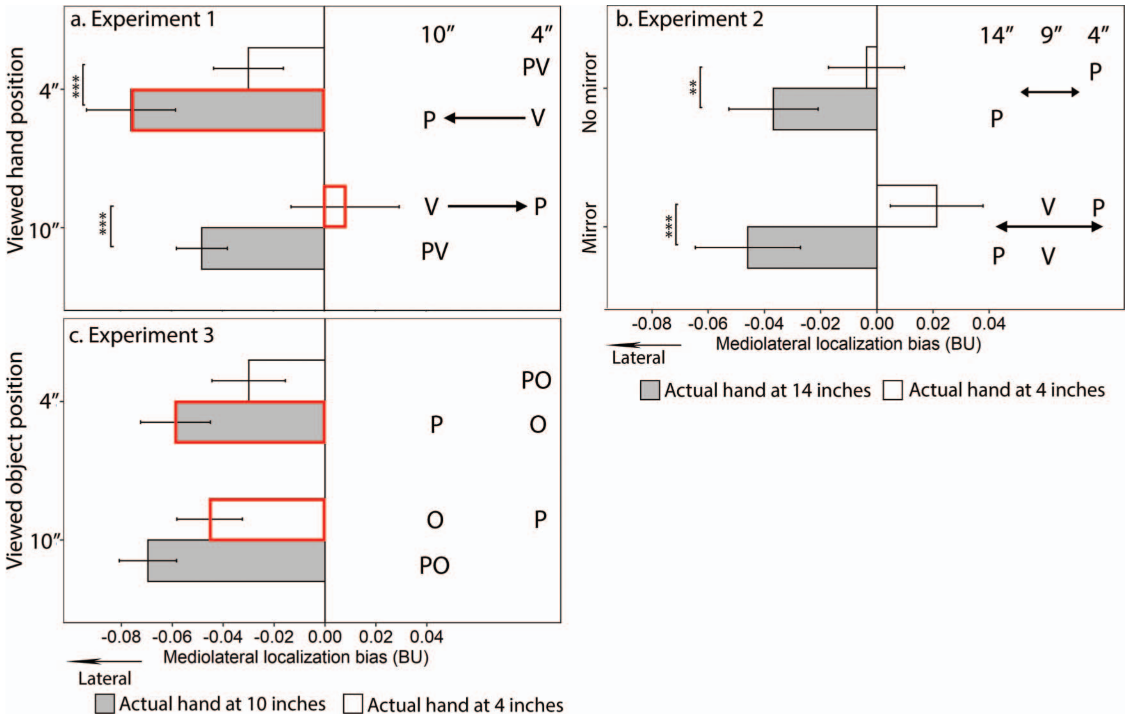
Overall participants reported not feeling touch on 3.8% (SD = 3.2%) of trials. Trials in which participants did not detect the stimulus were excluded from the analyses of localization bias.

Mediolateral Localization Bias

We first tested if tactile localization judgments were biased toward the actual hand at each visual position (Figure 2a). Consistent with this prediction, there was a main effect of Proprioceptive Position (Figure 3a), $F(1, 19) = 20.94$, $p < .001$, $\eta_p^2 = .52$,

Figure 3

Mediolateral Localization Bias in a. Experiment 1, b. Experiment 2, and c. Experiment 3



Note. Negative values denote lateral biases. Manipulations are illustrated on the right side of each bar, with the numbers on the top denoting distances from the mirror. V: visual position. P: proprioceptive position. O: object position. Arrows denote the predicted direction of localization bias from the anchoring hypothesis. Bars in red (dark gray) rectangles are conditions in the critical analysis across Experiment 1 and Experiment 3. Bias bars indicate 95% within-subjects confidence intervals (Cousineau, 2005). * $p < .05$. ** $p < .01$. *** $p < .001$. See the online article for the color version of this figure.

with more lateral biases when the hand was at a more lateral (10”: $M = -0.06$ BU, $SD = 0.07$ BU) versus medial position (4”: $M = -0.01$ BU, $SD = 0.08$ BU), indicating that localization judgments were biased toward the incongruent proprioceptive position, consistent with the anchoring hypothesis.

In testing the alternative hypothesis that tactile localization is biased toward the viewed hand, we also found a main effect of visual position, $F(1, 19) = 8.81$, $p = .008$, $\eta_p^2 = .32$. However, the direction of the effect was opposite the prediction of the alternative hypothesis. Specifically, there was a more lateral bias when the viewed hand was at a more medial position (4”: $M = -0.05$ BU, $SD = 0.07$ BU) versus lateral (10”: $M = -0.02$ BU, $SD = 0.08$ BU), showing bias away from the viewed hand at each proprioceptive hand position. There was no interaction between proprioceptive position and visual position, $F(1, 19) = 0.57$, $p = .459$, $\eta_p^2 = .03$. Taken together, the results are consistent with the anchoring hypothesis such that touch is anchored to the embodied, viewed limb and is then biased in the direction of the proprioceptively defined limb.

Finally, we did a paired t test between the two congruent conditions, $P_{10}V_{10}$ and P_4V_4, to examine the effect of absolute hand position when no visuoproprioceptive conflict was introduced. Although biases were more lateral in $P_{10}V_{10}$ ($M = -0.05$ BU, $SD = 0.08$ BU) versus P_4V_4 ($M = -0.03$ BU, $SD = 0.07$ BU), the difference was not significant, $t(19) = 1.60$, $p = .125$, 95% CI [−0.005, 0.04], Cohen’s $d = 0.41$.

Internal Configuration of the Response Space

We then examined if the size and shape of response space varied across conditions. First, there were no main effects or interaction on the size, calculated as the root mean square distance between response on each dot to the centroid (main effect of proprioceptive position: $F(1, 19) = 0.02$, $p = .878$, $\eta_p^2 = .001$; main effect of visual position: $F(1, 19) = 0.50$, $p = .487$, $\eta_p^2 = .03$; interaction: $F(1, 19) = 0.81$, $p = .381$, $\eta_p^2 = .04$). See online supplemental materials for tactile localization bias for each target location in each condition. Similarly, no main effects or interaction were found on the shape of the response (main effect of proprioceptive position: $F(1, 76) = 0.43$, $p = .93$; main effect of visual position: $F(1, 76) = 0.77$, $p = .68$; interaction: $F(1, 76) = 0.54$, $p = .87$). These findings indicate that manipulating proprioceptive and visual hand position more likely changed tactile localization per se, rather than altering the perceived size and shape of the hidden hand.

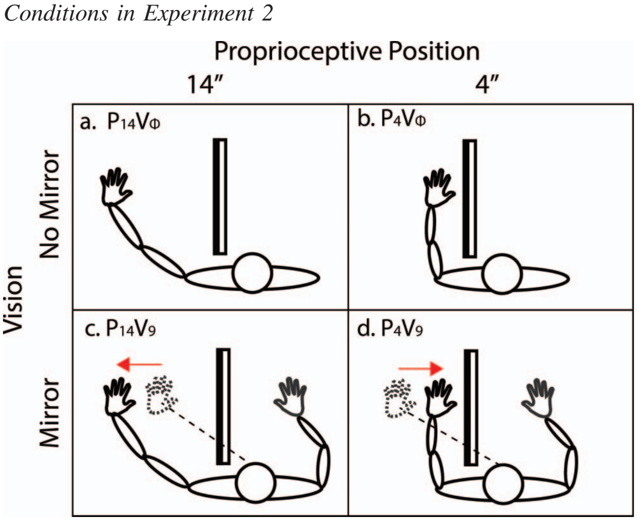
Discussion

The aim of this experiment was to investigate the influence of visuoproprioceptive conflict on tactile localization. The findings are consistent with the hypothesis that with tactile sensation mapped to the visual estimate, information from the proprioceptively-defined hand position would bias tactile localization on the skin surface away toward the proprioceptive estimate. These findings will be further confirmed in later experiments and are discussed in the General Discussion. Moreover, the size and shape of the response space were not influenced by hand position, indicating that the tactile localization biases were not likely attributed to changes in perceived hand size or shape. Finally, there was no significant difference between the two congruent conditions, that is, P_4V_4 and $P_{10}V_{10}$, indicating that absolute hand position did not strongly affect tactile localization when there were no visuoproprioceptive conflicts.

Experiment 2: Controlling for the Effects of Hand Position on Tactile Localization

In Experiment 1, tactile localization was biased toward the proprioceptive hand position, away from the visual position. However, Experiment 1 also found an overall main effect of proprioceptive hand position, suggesting that simply placing the hand at different positions, regardless of visual hand position, biased tactile localization. Moreover, in Experiment 1 there was an effect of proprioceptive position at each visual position. It is possible that simply changing hand position, regardless of visuoproprioceptive conflict, could have caused the observed effects. We therefore introduced a no-mirror condition in Experiment 2 to investigate the effect of hand position alone on tactile localization in the absence of visual information and to dissociate the effect of proprioceptive position alone from visuoproprioceptive conflict. A 2 (vision) by 2 (proprioceptive position) design was used (see Figure 4). The hidden left hand was placed either 14" or 4" from the mirror. In the no mirror condition (Figure 4a and 4b), the right hand was not placed in the mirror box, and participants closed their eyes during tactile stimulation. In the mirror condition, participants viewed a mirror hand at 9" from the mirror. As a result, the proprioceptive hand position was either 5" lateral (Figure 4c) or 5" medial (Figure 4d) to the same visual hand position. This was designed for performing the comparison described below.

Figure 4
Conditions in Experiment 2



Note. Red (gray) arrows in the mirror conditions denote predicted tactile localization bias directions. The null symbol in $V_Ø$ denotes no visual information. See the online article for the color version of this figure.

The effect of proprioceptive hand position alone on tactile localization were examined by comparing $P_{14}V_Ø$ (Figure 4a) and $P_4V_Ø$ (Figure 4b) when no visual information was available. If hand position alone biases tactile localization in a consistent direction, there would be more lateral localization bias when the hand was placed laterally ($P_{14}V_Ø$) versus medially ($P_4V_Ø$). Importantly, the unique effect of visuoproprioceptive conflict, beyond the effects of hand position, were examined by comparing the effects of proprioceptive hand position between the two vision conditions (i.e. $P_{14}V_Ø$-$P_4V_Ø$ vs. $P_{14}V_9$-P_4V_9). In the no mirror condition, any differences in mediolateral localization bias between $P_{14}V_Ø$ and $P_4V_Ø$ would be solely driven by different proprioceptive hand positions. In the mirror condition, in addition to the absolute hand position, the two proprioceptive positions were on the opposite sides relative to the viewed hand. If visuoproprioceptive conflict biases tactile localization, tactile localization would be "pulled" toward each proprioceptive position (Figure 4c and 4d, red arrows). This would add to the effects of hand position alone, magnifying the difference between the two proprioceptive hand positions. As a result, the difference between $P_{14}V_9$ and P_4V_9 would be larger than that between $P_{14}V_Ø$ and $P_4V_Ø$. This finding would provide additional evidence for the anchoring hypothesis by demonstrating the pure effects of visuoproprioceptive conflict on tactile localization, controlling for the effects of hand position alone.

Method

Participants

Twenty-one participants (mean age: 18.6 years, $SD = 1.0$ years, one male) were tested in the experiment. All participants were recruited from the General Psychology course at the University of Delaware and reimbursed with research participation credits. One participant who did not complete the experiment was excluded. Twenty participants were included in the final analyses.

Design

As discussed above, a 2 (proprioceptive position: 14" and 4") × 2 (vision: mirror and no mirror) design was used (see Figure 4). Constrained by the width of the mirror box, the spatial mismatch between the visual and proprioceptive position was reduced to 5" (as opposed to the 6" in Experiment 1).

Procedure

The procedure for the mirror condition was the same as in Experiment 1. For the no mirror condition, only the left hand was placed in the mirror box. At the beginning of the no mirror blocks, participants tapped the left index finger for 20 s with the eyes closed. Then, in each trial, participants closed their eyes as the experimenter applied touch, then opened their eyes and verbally reported the coordinates of the perceived stimulus location.

As with Experiment 1, each condition was tested in two blocks. Within each block, each of the nine stimulus locations was tested in three trials. The block and trial orders were randomized for each individual.

Data Analyses and Predictions

As with Experiment 1, a repeated-measures ANOVA was performed on the mediolateral and proximodistal bias separately, with proprioceptive position (14" and 4") and vision (mirror and no mirror) as independent variables. Paired *t* tests were then performed to test specific hypotheses. First, to examine if hand position alone biases tactile location, mediolateral bias was compared between $P_{14}V_{Ø}$ and $P_4V_{Ø}$ (Figure 4a vs. Figure 4b) where no visual information was presented. If tactile localization is biased toward the direction of hand position, there would be more lateral localization bias in $P_{14}V_{Ø}$ versus $P_4V_{Ø}$. Importantly, to examine the pure effects of visuoproprioceptive conflict while controlling for the effects of hand position alone, differences between the two proprioceptive positions were compared across vision conditions ($P_{14}V_9$-P_4V_9 vs. $P_{14}V_{Ø}$-$P_4V_{Ø}$). In the mirror condition, visuoproprioceptive conflicts would bias tactile localization toward the opposite directions (i.e. toward each proprioceptive hand position), magnifying the effects of hand position alone. As a result, there would be a larger difference between $P_{14}V_9$ and P_4V_9 versus between $P_{14}V_{Ø}$ and $P_4V_{Ø}$, leading to a proprioceptive Position × Vision interaction. Since these analyses are hypothesis-driven, we did not perform multiple-comparison correction on the *t* tests. Finally, the size and shape of the internal configuration of the response space were analyzed using the same methods as in Experiment 1.

Results

Overall, participants reported not feeling the stimulus on 2.0% of trials (SD = 3.9%).

Mediolateral Localization Bias

First, a repeated-measures ANOVA was performed on mediolateral bias (Figure 3b). As with Experiment 1, there was a main effect of proprioceptive position, $F(1, 19) = 24.20$, $p < .001$, $\eta_p^2 = .56$. Placing the left hand at a lateral position (14": $M = -0.04$ BU, $SD = 0.06$ BU) induced more lateral localization biases than when the left hand was at 4" ($M = 0.01$ BU, $SD = 0.06$ BU). There was no main effect of vision, $F(1, 19) = 0.62$, $p = .442$, $\eta_p^2 = .03$, (mirror: $M = -0.01$ BU, $SD = 0.06$ BU; no mirror: $M = -0.02$ BU, $SD = 0.06$ BU). Importantly, there was a significant proprioceptive Position × Vision interaction, $F(1, 19) = 4.56$, $p = .046$, $\eta_p^2 = .19$, indicating that the effect of proprioceptive information differed based on the availability of visual information.

As described earlier, if visuoproprioceptive conflict biases tactile localization, we predicted a larger effect of proprioceptive hand position in the mirror versus no mirror condition. First, for both the mirror and no mirror conditions, there were significantly more lateral biases when the left hand was at 14" versus 4" ($ps < .007$; Figure 3b). These findings indicate that proprioceptive hand alone biased tactile localization toward the hand position, with more lateral bias in $P_{14}V_{Ø}$ versus $P_4V_{Ø}$, when visual information was not presented. Importantly, the effect was larger in the mirror (*Mean difference* = −0.07 BU) versus the no mirror (*Mean difference* = −0.03 BU) condition, *Mean difference* = 0.03 BU, *SE*(difference) = 0.02 BU, $t(19) = 2.14$, $p = .046$, 95% CI [−0.07, −0.001] BU, Cohen's $d = 0.48$ (Figure 3b), driving the proprioceptive Position × Vision interaction presented above. This finding indicates that in addition to different tactile localization biases caused by hand position alone (i.e. in no mirror condition), visuoproprioceptive conflicts biased tactile localization further toward each proprioceptive position, leading to a larger difference in the mirror condition between the two proprioceptive hand positions.

Finally, as with Experiment 1, no effects of proprioceptive and visual hand positions were found on the shape or size of the internal configuration of the response space. Detailed results are presented in the online supplemental materials.

Discussion

This experiment was designed to further test the effect of visuoproprioceptive conflict on tactile localization, dissociating it from the effect of proprioceptive position alone. First, without any viewed hand, simply placing the hidden hand at a lateral position ($P_{14}V_{Ø}$) led to more lateral tactile localization bias than when the hand was at a medial position ($P_4V_{Ø}$). This finding indicates that proprioceptive hand position alone biases tactile localization in the direction of hand position. Importantly, the difference in mediolateral bias between proprioceptive positions was larger in the mirror versus no mirror condition, indicating that beyond the effects of hand position alone, visuoproprioceptive conflicts introduced additional tactile localization bias toward each proprioceptive position. This finding provides additional and confirmatory evidence that tactile localization is biased toward the proprioceptive hand position relative to the visual position under visuoproprioceptive conflict.

In Experiment 1, no statistical differences were found between the two congruent conditions, P_4V_4 and $P_{10}V_{10}$, although there was a trend toward more lateral localization bias when the hand was placed laterally (i.e. in $P_{10}V_{10}$ vs. P_4V_4). In contrast, Experiment 2 demonstrated that proprioceptive position alone, without visual information, biased tactile localization toward the direction of hand position. One possibility is that hand position does bias tactile localization but is more salient with larger distances between the hands (10" in Experiment 2, 6" in Experiment 1).

Taken together, results from both Experiment 1 and Experiment 2 are consistent with the hypothesis that when visual and proprioceptive hand positions are spatially incongruent, tactile localization on the skin surface is biased toward the proprioceptive position. In Experiment 3, we address one additional alternative account to these findings.

Experiment 3. Controlling for the Effects of Gaze-Proprioceptive Spatial Mismatch on Tactile Localization

While manipulating visual and proprioceptive hand positions in Experiment 1 and 2, the relative position between the proprioceptive hand position and gaze direction also varied in conjunction. Previous literature reported effects of gaze-proprioceptive spatial mismatch on tactile localization on the skin surface (Medina et al., 2018). It is thus possible that the tactile localization bias found in the previous experiments was driven by hand position encoded relative to gaze direction, as opposed to visuoproprioceptive conflicts. To test this alternative account, participants viewed an object in the mirror instead of a mirror hand. The position of the object and hidden left hand was manipulated across conditions (see Figure 5). The left hand was positioned at either 10" or 4" from the mirror, and the mirror reflection of the object appeared at either 10" or 4" from the mirror. The object was a vertically oriented cylinder placed where the middle fingertip was located in Experiment 1. The object hence served as a "fixation point". Conditions in this experiment are denoted as P_xO_y, with O standing for "object".

Method

Participants

Twenty-one participants were recruited (mean age: 23.6 years, *SD* = 4.4 years, 9 males) from the General Psychology course, assuming attrition. One participant who did not complete the experiment was excluded. Overall, 20 participants were included in the analyses.

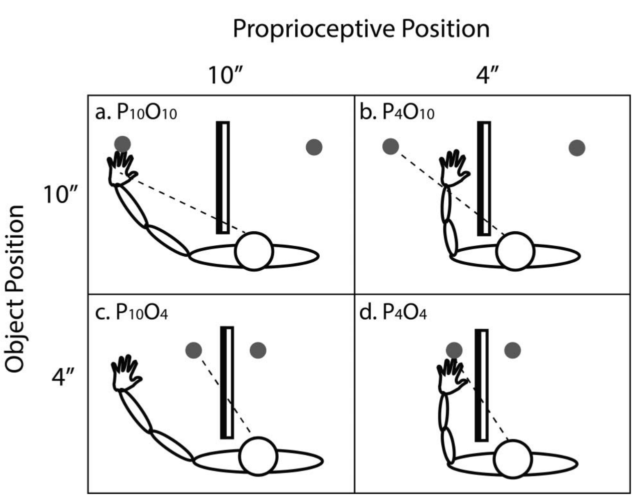
Design

As presented before (see Figure 5), a 2 (proprioceptive position) by 2 (object position) design was used.

Procedure

The procedure was the same as in Experiment 1, except for the following differences. At the beginning of each block, the experimenter placed the cylinder in front of the mirror and the participant's left hand behind the mirror, at the instructed locations. Then

Figure 5
Conditions in Experiment 3



Note. The left hand was positioned at either 10" or 4" behind the mirror. An object (the gray circle) was positioned at either 4" or 10" in front of the mirror, with its position in the mirror either congruent or incongruent with the hidden hand.

the participant tapped the left index finger for 20 s while looking at the mirror reflection of the cylinder. After tapping, the experimenter started tactile stimulation trials, while the participants kept gazing at the cylinder in the mirror.

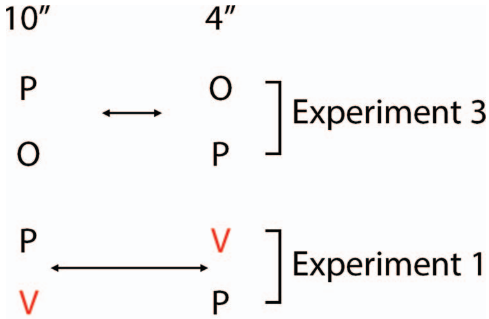
Data Analyses and Predictions

We first ran an ANOVA on mediolateral and proximodistal bias separately, with proprioceptive position (4" and 10") and object position (4" and 10") as independent variables. Then, the main purpose of this experiment was to examine whether visuoproprioceptive conflict biases tactile localization while controlling for gaze direction. For this reason, the critical comparison was the visuoproprioceptive/gaze-proprioceptive incongruent conditions across Experiment 1 and Experiment 3 (Figure 3a and 3c, bars with red squares). An ANOVA was performed with proprioceptive position (4" and 10") as a within-subjects factor and visual content (hand or object) as a between-subjects factor. If visuoproprioceptive conflict introduced additional tactile localization bias beyond the effects of gaze-proprioceptive mismatch, an interaction would be expected. Specifically, in Experiment 3, any difference between P_4O_{10} and $P_{10}O_4$ (Figure 6, top two conditions) was caused by gaze-proprioceptive mismatch in opposite directions. Similarly, in Experiment 1, P_4V_{10} and $P_{10}V_4$ entailed the same difference in gaze-proprioceptive mismatch (Figure 6, bottom two conditions). If localization bias observed in Experiments 1 and 2 was solely induced by gaze-proprioceptive mismatch, the difference between P_4V_{10} and $P_{10}V_4$ (Experiment 1) would be the same as difference between P_4O_{10} and $P_{10}O_4$ (Experiment 3). However, if localization bias was driven by visual-proprioceptive mismatch in hand position, there would be additional localization bias toward the proprioceptively defined location in P_4V_{10} and $P_{10}V_4$ conditions in Experiment 1, resulting in a larger difference between P_4V_{10} and $P_{10}V_4$ versus between P_4O_{10} and $P_{10}O_4$ (Figure 6, longer arrow on the bottom vs. top). We tested these predictions by comparing the difference between P_4O_{10} and $P_{10}O_4$ in Experiment 3 and then comparing this distance with the difference between P_4V_{10} and $P_{10}V_4$ in Experiment 1.

In the conditions in Figure 6, viewing a hand introduced two differences from viewing an object. First, participants viewed a hand stimulus versus a nonhand stimulus. Second, viewing a hand led to a visually defined spatial representation of hand position, creating visuoproprioceptive conflict in the hand position estimate. Whereas the expected direction-specific tactile location bias described in the previous paragraph is unlikely caused by viewing a hand stimulus per se, we performed an additional analysis to confirm this. An additional ANOVA was performed across Experiment 1 and 3, focusing on conditions with *no* mismatch between proprioceptive position and visual hand position (P_4V_4 and $P_{10}V_{10}$ in Experiment 1) or object position (P_4O_4 and $P_{10}O_{10}$ in Experiment 3). Studies have shown that noninformative vision of the hand improves tactile acuity (Kennett et al., 2001; Longo et al., 2008) but not tactile localization (Medina et al., 2018). We therefore predict that mediolateral localization bias would not differ whether participants were viewing a hand or object. Such findings would provide a control result that simply presenting a visual hand stimulus is not sufficient for biasing tactile localization compared with viewing an object.

Figure 6

Illustration of the Critical Analysis Across Experiment 1 and Experiment 3, Focusing on the Incongruent Conditions



Note. The numbers on the top denote distances from the mirror. P, O, and V stand for proprioceptive hand position, object position, and visual hand position, respectively. Red (gray) labels highlight conditions from Experiment 1. Arrows denote a larger difference in mediolateral bias between conditions in Experiment 1 than between conditions in Experiment 3 if visuoproprioceptive conflicts bias tactile localization. See the online article for the color version of this figure.

Results

Overall participants reported not feeling touch on 2.7% (*SD* = 3.0%) of trials.

Mediolateral Localization Bias

Within Experiment 3, there was a main effect of proprioceptive position, $F(1, 19) = 7.55$, $p = .013$, $\eta_p^2 = 0.05$. Consistent with Experiments 1 and 2, placing the hand laterally (at 10," $M = -0.06$ BU, $SD = 0.07$ BU) induced more lateral localization bias than when the hand was at a medial position (at 4," $M = -0.04$ BU, $SD = 0.05$ BU; Figure 3c). There was also a main effect of object position, $F(1, 19) = 7.74$, $p = .012$, $\eta_p^2 = 0.01$, with more lateral bias when the participants gazed at a lateral position (10," $M = -0.06$ BU, $SD = 0.05$ BU) versus medial (4," $M = -0.04$ BU, $SD = 0.06$ BU). Note that here the effect of gaze direction occurs in the opposite direction as the effect of viewed hand position in Experiment 1 and 2, where more medial visual hand position led to more lateral localization bias. The Proprioceptive Position × Object Position interaction was not significant, $F(1, 19) = 0.15$, $p = .707$, $\eta_p^2 = 0.001$.

We then analyzed the incongruent conditions across Experiment 1 and Experiment 3 (Figure 3a and 3c). There was a main effect of proprioceptive position, $F(1, 38) = 18.86$, $p < .001$, $\eta_p^2 = .33$. As previously found, there was a more lateral bias when the proprioceptive position was at a more lateral (10": $M = -0.06$ BU, $SD = 0.07$ BU) versus medial (4": $M = -0.02$ BU, $SD = 0.08$ BU). The main effect of visual content was not significant, $F(1, 38) = 0.78$, $p = .384$, $\eta_p^2 = .02$ (View hand: $M = -0.03$ BU, $SD = 0.07$ BU; View object: $M = -0.05$ BU, $SD = 0.06$ BU). Importantly, there was a significant proprioceptive Position × Visual Content interaction, $F(1, 38) = 9.41$, $p = .004$, $\eta_p^2 = .20$, consistent with the anchoring hypothesis. We then performed pairwise comparisons below to investigate the interaction effect.

In Experiment 3, the difference between $P_{10}O_4$ and P_4O_{10} did not reach significance, *Mean difference* = −0.01 BU, *SE*(difference) = 0.01 BU, $t(19) = 1.23$, $p = .233$, 95% CI [−0.04, 0.01] BU, Cohen's $d = 0.28$. In contrast, in Experiment 1, $P_{10}V_4$ induced more lateral bias than P_4V_{10}, *Mean difference* = −0.08 BU, *SE*(difference) = 0.02 BU, $t(19) = 4.31$, $p < .001$, 95% CI [−0.12, −0.04] BU, Cohen's $d = 0.96$. Importantly, the difference between $P_{10}V_4$ and P_4V_{10} is larger than difference between $P_{10}O_4$ and P_4O_{10}, *Mean difference* = −0.07 BU, *SE*(difference) = 0.02 BU, $t(38) = 3.09$, $p = .004$, 95% CI [−0.11, −0.02] BU, Cohen's $d = 0.98$. These findings indicate that visuoproprioceptive conflict biased tactile localization beyond the effect of gaze-proprioceptive mismatch. With gaze-proprioceptive mismatch controlled, tactile localization was biased toward proprioceptive estimate when participants were viewing a hand, providing further evidence for the anchoring hypothesis. Moreover, the size and shape of the response space did not differ across conditions (see online supplemental materials), indicating that the effects were on tactile localization per se.

To test if simply viewing a hand versus nonhand stimulus influences tactile localization, an additional ANOVA was performed across Experiment 1 and Experiment 3, focusing on the congruent conditions. The main effect of visual content was not significant, $F(1, 38) = 0.32$, $p = .575$, $\eta_p^2 = .008$ (View hand: $M = -0.04$ BU, $SD = 0.07$ BU; View object: $M = -0.05$ BU, $SD = 0.06$ BU), nor was the proprioceptive Position × Visual Content interaction, $F(1, 38) = 2.40$, $p = .130$, $\eta_p^2 = .06$. These findings indicate that the additional localization bias in the view hand versus view object condition described in the previous paragraph was driven by visuoproprioceptive spatial conflict, not viewing a hand stimulus per se. Finally, consistent with previous results, there was a main effect of proprioceptive position, $F(1, 38) = 14.65$, $p < .001$, $\eta_p^2 = .28$, with more lateral bias when the hand was at a lateral position (10," $M = -0.06$ BU, $SD = 0.07$ BU) versus a medial position (4," $M = -0.03$ BU, $SD = 0.07$ BU).

Discussion

This experiment further examined the effect of visuoproprioceptive conflict on tactile localization while controlling for the potential effects of gaze-proprioceptive mismatch. First, with gaze direction and proprioceptive hand position controlled, viewing a mirror hand induced additional tactile localization bias toward the proprioceptive hand position. Moreover, the additional effect of viewing a hand cannot be explained by viewing a hand stimulus per se. Second, the overall effect of gaze direction on tactile localization was in the opposite direction of the overall effect of visual hand position in Experiment 1. These findings indicate that tactile localization bias under visuoproprioceptive conflict cannot be fully attributed to gaze-proprioceptive mismatch.

General Discussion

Using the mirror box illusion, we examined the effect of visuoproprioceptive conflict on tactile localization on the hand. Across multiple experiments, we found that when visual and proprioceptive information regarding hand position was dissociated, tactile localization on the skin surface was biased toward the proprioceptive hand position. This bias was observed when controlling for hand position alone (Experiment 2), or gaze-proprioceptive mismatch (Experiment 3). Taken together, these findings provide evidence that proprioceptive information influences tactile localization on the skin surface. Past studies have examined tactile localization on single body parts (e.g., on either hand) by manipulating the relative position between different body parts (e.g., crossing the two hands; Badde et al., 2019; Haggard et al., 2006; Overvliet et al., 2011; Riemer et al., 2010). We provide clear evidence that perceived tactile location on the skin surface is also influenced by body position (see also Canzoneri et al., 2014).

Currently, there are two major accounts for how we localize tactile stimuli. In the remapping account, tactile information is first represented in a somatotopic frame of reference. Then, information from these somatotopic representations is combined with information regarding body position to represent stimulus position in an external frame of reference (Longo et al., 2010; Medina & Coslett, 2010). In a second integration account, information from multiple spatial representations exist in parallel and are integrated in a weighted manner (Badde & Heed, 2016; Badde et al., 2016; Heed et al., 2015). Our results can be considered in light of both models and will be discussed in the next paragraphs.

In the mirror box illusion, spatial mismatch is created between a visual and proprioceptive estimate regarding hidden hand position. To form a coherent percept, information from multiple sensory modalities is integrated by weighting unimodal information in proportion to its relative precision (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Van Beers et al., 1999). In the original rubber hand illusion study (Botvinick & Cohen, 1998), visual information was more strongly weighted such that participants reported that tactile sensation originated from the seen rubber hand. In our study, when participants make synchronous hand movements, the movements seen on the mirror hand match the movements made on the actual hand, providing congruent visual–motor information and facilitating integration between visual and proprioceptive estimates. This process also biased where participants felt touch. Our preliminary work showed that individuals felt touch on the mirror hand and externally localized touch to the visually defined location of the hand. These results demonstrate that tactile percepts can be mapped to nonveridical locations (see also Badde et al., 2019). We and others have proposed that information from primary somatosensory cortex is mapped onto a representation of body size and shape used to localize touch on the body surface (body form representation, Medina & Coslett, 2010; superficial schema, Head & Holmes, 1911; Longo et al., 2010). In this framework, participants are localizing touch onto the viewed, embodied hand. In serial models of tactile localization, this linking process from somatosensory maps to a representation of body size and shape has been conceptualized as somatotopic and not needing information about hand position in external space.

If this process were strictly serial, with no influence of hand position on tactile localization in somatotopic space, then the prediction would be that localization judgments on the skin surface would not differ when the actual position of the hidden hand changes. However, we consistently observed a shift in localization judgments toward the proprioceptively defined hand. How is tactile localization biased toward the actual proprioceptive hand position within such a framework? We hypothesize that proprioceptive information from the actual hand is also referenced when localizing touch to external space. As a result, in addition to the visually defined location, tactile stimuli on the hidden hand are also localized in external space at the proprioceptively defined location. Even though tactile sensation is mapped to the viewed hand, the proprioceptively defined tactile information still exerts influence, biasing the tactile location estimate in external space toward the actual hand position. This bias in external space then influences tactile localization on the skin surface. One potential mechanism could be feedback from later external to earlier somatotopic representations. If these somatotopic representations are utilized for judging where on the hand tactile stimuli are located, this feedback would result in biases toward the proprioceptively defined hand. Note that this somatotopic representation is not necessarily in S1 but is simply one that represents the location of tactile stimuli in a somatotopic frame of reference and is utilized to localize touch on the skin surface. Previous serial models have been agnostic as to whether there is feedback from external representations to representations utilized in localizing touch on the skin surface. Our results suggest the possibility for feedback mechanisms within this framework.

Integrating Information Across Reference Frames

Our findings are also consistent with a Bayesian framework where the brain integrates information from multiple reference frames in making tactile location judgments (Badde & Heed, 2016; Badde et al., 2016; Goldreich & Tong, 2013; Heed et al., 2015; Shore et al., 2002). In this framework, multiple representations exist in parallel—a somatotopic representation of stimulus location on the skin surface, and a second representation of that position in external space. These accounts propose that the relative weighting of these inputs vary as a function of the task (e.g., Gallace et al., 2008; Medina et al., 2019). As noted before, multisensory integration leads to an estimate of hand position that is close to, or at the same location as, the mirror-reflected hand. In previous studies using the mirror box with a 6” displacement between viewed and actual hand position, perceived hand position was displaced approximately 70% (Medina et al., 2015) to 85% toward the mirror (Medina, unpublished data). Given this, one could assume that the biased localization judgments reported from the dot grid is simply due to equally integrating visual and proprioceptive estimates of the tactile stimulus position. However, the observed shift in tactile localization judgments in our experiment is much smaller than previously observed shifts in perceived limb position in the mirror box. Our task involves localizing touch on the hand surface and responding on a hand drawing, a somatotopic task. Given task-specific weighting of information from both representations (Badde & Heed, 2016), the nature of our task could lead to much stronger contributions from somatotopic versus external representations, resulting in a small but consistent bias toward perceived hand position in external space. While the task-specific weighting could account for our results, we note that in the current Bayesian accounts, the specific weighting mechanism is underspecified. Future studies are required to investigate how information from different reference frames are weighted during tactile perception.

Can our results also be explained by spatial attention? Past studies showed that when individuals attended to a location different from where they were touched, the perceived tactile location shifted in the direction of attention (Harrar & Harris, 2009; Kilgard

& Merzenich, 1995). In Experiments 1 and 2, localization judgments were biased in the direction of the actual hand position in external space relative to the viewed hand position in the mirror. A brief attentional shift toward the stimulus location in external space, perhaps caused by the tactile stimulus itself, is consistent with our results. However, we believe that the results in Experiment 3 make this account less likely. In this experiment, participants are told to fixate on an object in the mirror and are then stimulated on the hand behind the mirror. Of critical importance are the conditions in which there is a mismatch between the position of the viewed object in the mirror and the actual hand. If our effect was primarily attentional, these conditions would also involve an attentional shift from the viewed object to the actual hand location in external space, thus resulting in a similar tactile localization shift as observed in Experiment 1. We directly compared conditions in Experiment 1 and 3 that differed only in whether there was a viewed object or viewed hand. A primarily attentional hypothesis would predict similar localization bias in these conditions. Instead, we found significantly more tactile localization shift in Experiment 1 (viewed hand) versus Experiment 3 (viewed object). Although it is possible that attention plays some role in our findings, we do not believe that they explain our primary results. Moreover, past studies demonstrated localization bias toward the initially attended location (Harrar & Harris, 2009; Kilgard & Merzenich, 1995). On the same logic, given that participants were initially attending the viewed hand and touched on their actual hand, we would observe localization bias toward the viewed hand. However, localization judgments were consistently biased toward the proprioceptive position, inconsistent with attentional effect reported previously.

In addition to finding an effect of visuoproprioceptive conflict on tactile localization, we found that proprioceptive hand position alone biases tactile localization with a more lateral localization bias when the hidden hand was placed more laterally. Past studies have shown that hand position relative to the trunk midline influences tactile processing. For example, tactile temporal order judgment performance was better when the hands were far versus near from the trunk midline (Shore et al., 2005), even if this distance is just apparent (Gallace & Spence, 2005). With regards to tactile localization itself, although previous studies have demonstrated that changes in gaze (Harrar & Harris, 2009; Medina et al., 2018), head (Ho & Spence, 2007), and finger position influence tactile localization (Overvliet et al., 2011), this is the first finding to our knowledge demonstrating an effect of hand position on the perceived location of single touches. We had no a priori hypotheses regarding this bias and were not testing this specifically. Furthermore, given that our results were found using the mirror box setup, we do not know whether they will generalize to a standard tactile localization task without a mirror. To speculate, past studies that show changes in tactile temporal order judgment as a function of body position provide evidence for the influence of external representations on tactile performance. Interestingly, auditory stimuli also demonstrate a peripheral bias that increases for more peripheral stimuli, whereas visual stimuli are centrally biased (Garcia et al., 2017; Odegaard et al., 2015; Parise et al., 2012). One possibility is that both tactile and auditory external representations demonstrate an opposing bias to visual representations that result in a more accurate response for multisensory integration (Odegaard et al., 2015). However, we note that this account is quite speculative and needs to be tested in future studies.

Finally, overall we found distal bias in tactile localization across experiments, consistent with past findings (Mancini et al., 2011; Margolis & Longo, 2015; Medina et al., 2018). However, we found overall lateral bias whereas past studies reported medial bias on the hand (Longo et al., 2015; Mancini et al., 2011; Margolis & Longo, 2015). One possibility is that the hand was positioned overall more laterally than in previous experiments, leading to more lateral localization bias. In addition, whereas participants responded by mouse-clicking on a hand silhouette in the majority of previous studies (Longo et al., 2015; Mancini et al., 2011; Margolis & Longo, 2015), our participants made verbal response using a dot grid shown on their own hand picture. There is evidence that features of the response space influence tactile localization judgments (Margolis & Longo, 2015). It is therefore possible that different response modalities have led to differences in localization bias.

In summary, by dissociating visual and proprioceptive estimates of hand position using the mirror box illusion, we demonstrated for the first time that tactile localization on the hand is biased toward the proprioceptive hand position. These findings indicate that although touch is felt on the seen hand, the actual hand still influences tactile localization. These results add to past models on tactile localization and inform how visual, proprioceptive, and tactile information is integrated in making judgments of tactile location on the skin surface.

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