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Domain-General Biases in Spatial Localization: Evidence Against a Distorted Body Model Hypothesis

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A number of studies have proposed the existence of a distorted body model of the hand. Supporting this hypothesis, judgments of the location of hand landmarks without vision are characterized by consistent distortions—wider knuckle and shorter finger lengths. We examined an alternative hypothesis in which these biases are caused by domain-general mechanisms, in which participants overestimate the distance between consecutive localization judgments that are spatially close. To do so, we examined performance on a landmark localization task with the hand (Experiments 1–3) using a lag-1 analysis. We replicated the widened knuckle judgments in previous studies. Using the lag-1 analysis, we found evidence for a constant overestimation bias along the mediolateral hand axis, such that consecutive stimuli were perceived as farther apart when they were closer (e.g., index-middle knuckle) versus farther (index-pinky) in space. Controlling for this bias, we found no evidence for a distorted body model along the mediolateral hand axis. To examine whether similar widening biases could be found with noncorporeal stimuli, we asked participants to localize remembered dots on a hand-like array (Experiments 4–5). Mean localization judgments were wider than actual along the primary array axis, similar to previous work with hands. As with proprioceptively defined stimuli, we found that this widening was primarily due to a constant overestimation bias. These results provide substantial evidence against a distorted body model hypothesis and support a domain-general model in which responses are biased away from the uncertainty distribution of the previous trial, leading to a constant overestimation bias.

Public Significance Statement

In past research (e.g., Longo & Haggard, 2010; PNAS), individuals judged where landmarks (e.g., knuckles, fingertips) of their hand were without seeing or touching their hands. Several studies have shown that people consistently misjudge the distance between their knuckles—reporting them as wider than they actually are. Previous researchers have concluded that our brains have highly distorted representations of our hands. However, our research provides evidence that the observed patterns in previous research are not caused by a distorted body representation, but are instead a by-product of uncertainty. More specifically, when individuals judge consecutive stimuli that are close in space, but hard to localize, they overestimate the distance between the 2 stimuli. This was found both in a trial-by-trial analysis of hand landmark judgments, and by observing these same widening patterns for a simple dot-array, showing that it is not specific to the body.

Keywords: landmark localization, body model, overestimation bias

Inputs from a number of different modalities contribute to body perception in space. For example, joint receptors and muscle spindle fibers provide information regarding joint angles (Proske & Gandevia, 2012). However, knowledge of joint position is not sufficient to localize body parts in space, as one also needs to represent the size and shape of body parts. Interestingly, proprioceptive and tactile information alone does not provide the necessary information to specify the size and shape of the body (Craske, Kenny, & Keith, 1984; Gurfinkel & Levick, 1991). Based on this, researchers have proposed the existence of a representation that stores information about the metric properties of body parts, called either a body form representation (Medina & Coslett, 2010) or a *body model* (Longo, Azañon, & Haggard, 2010).

Longo and Haggard (2010) developed a task designed to understand the properties of this body model representation. They instructed a participant to place one hand underneath an occluding board, and asked them to localize the position of easily identifiable hand landmarks (e.g., fingertips and the metacarpophalangeal joints of the hand—what we will call "knuckles" in this article). The partici-

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pants did not have vision of their hand during the entire task, nor were they instructed to move their hand during the task. Longo and Haggard (2010) specifically examined, not overall localization bias in external space, but the bias in localization judgments of different landmarks relative to each other. For example, the distance from the mean localization judgments of the index and pinky knuckle could be compared to the actual distance between these two knuckles. Longo and Haggard claimed that differences between actual and perceived hand landmark distances would be indicative of a body model distortion.

Using this landmark localization task, Longo and Haggard (2010) found that judgments of the knuckles were significantly wider, and that judgments of the fingers were significantly shorter, than the actual dimensions of the hand. Furthermore, they also found that these biases were evident when the hand was turned 90°, and occurred on both the left and right hand. The authors concluded that this implicit body model for the hand is "massively distorted." This landmark localization task has been used in a number of other studies, including a replication of the main finding while showing no shape biases in a separate visual template matching task (Longo & Haggard, 2012b), demonstrating that these biases are not changed with galvanic vestibular stimulation (Ferrè, Vagnoni, & Haggard, 2013) but may be changed with caloric vestibular stimulation (Lopez, Schreyer, Preuss, & Mast, 2012), that these biases are greater on the dorsal versus palmar surface of the hand (Longo & Haggard, 2012a) and with vision versus when blindfolded (Longo, 2014), that these biases exist in upper-limb amputees (Longo, Long, & Haggard, 2012), that changes in hand position alter these biases (Longo, 2015b), that perceptual and conceptual distortions may contribute to these biases (Longo, Mattioni, & Ganea, 2015), and that there is a relationship between tactile and landmark localization task biases (Longo, Mancini, & Haggard, 2015; Margolis & Longo, 2015; Mattioni & Longo, 2014). Furthermore, the results of this task have been cited in a number of review papers providing evidence for a distorted body model (e.g., Longo, 2015a, 2017; Proske & Gandevia, 2012).

However, there are a number of potential issues with concluding the existence of such a distorted body model from this landmark localization task. First, there is no direct experimental evidence supporting the distorted body model hypothesis outside of evidence from the landmark localization task. It is important to carefully consider whether the landmark localization task truly assesses the body model, and not some other aspect of spatial processing. Second, the ecological validity of this finding is unclear. For example, on the palmar surface of the hand, the perceived distance between knuckle judgments is approximately 50% greater than veridical. However, when grasping an object with vision (which likely provides more veridical information about hand shape) versus without vision (which would likely rely more on this distorted body model), participants do not experience similarly massive distortions in haptic performance—for example, holding a sphere without vision is not perceived as holding an oblong, egg shape. To our knowledge, findings like this have not been reported, and it is unclear how this distorted body model is involved in the integration of action information with the body schema. Third, a recent study using a landmark localization task has found similar biases for nonhand body parts. Saulton, Dodds, Bülthoff, and de la Rosa (2015) were instructed to localize landmarks on either their own hand or noncorporeal objects. The authors found that symmetrical objects (such as Post-it notes and CD cases) were perceived as significantly wider than normal. Furthermore, they found that landmark localization on a rake demonstrated the same biases as demonstrated for the hand—namely an overestimation of rake width and an underestimation of rake length. These biases in rake localization judgments persisted in multiple orientations, suggesting that these biases were encoded in an object-centered reference frame. Overall, these results suggest that mechanisms other than a distorted body model may explain results in landmark localization tasks with the hands.

Longo and Haggard (2010) claimed that the biases observed in the landmark localization task for hands are due to a massively distorted body model. In this paper, we first present evidence from three experiments that were initially designed, not to question the distorted body model account, but to examine the relationship between distortions in landmark and tactile localization judgments. In our landmark localization experiments, we also observed widening in knuckle localization judgments as in previous papers. However, although the relative position of landmark localization judgments were quite consistent and somatotopically organized, we also noticed that overall accuracy was quite variable across participants, with some consistently making judgments that were quite distant from the actual position of their hand. Given how distant some of these landmark localization judgments were from the actual hand, we considered whether they may not actually be referencing the participant's actual body model. Instead, we developed an alternative hypothesis in which the previously observed landmark localization biases were caused, not by a distorted body model, but by biases in spatial localization for remembered targets. More specifically, we propose that given noise in proprioceptive estimation, participants make an initial guess regarding the location of their hand. For subsequent localization judgments, participants reference the position of the previous localization judgment and make a distance estimation based on a fairly veridical representation of their own hand. We propose that the observed biases in past landmark localization studies are, in large part, due to biases in which the distance between consecutive, relatively close localization judgments are consistently overestimated. To examine this further, we analyzed landmark localization performance using a novel lag-1 analysis, in which we observed how localization judgments on trial n influenced the perceived location on trial $n + 1$. We found evidence that consecutive localization judgments that were closer in space were overestimated, but no evidence for a distorted body model. Then, we examined whether this close overestimation is domain-general, occurring not only for localization of hand landmarks, but for spatial localization of noncorporeal remembered targets. In Experiments 4 and 5, we conducted a landmark localization task with, not hands, but dot arrays. Consistent with our hypothesis, we found that the distance between localization judgments for two close stimuli were overestimated—providing further evidence for a domain-general account.

Experiments 1–3

Method

Participants. All participants were recruited from the University of Delaware's Introduction to Psychology research pool, and received credit for participation. We made an a priori decision to stop testing for each experiment after testing 14 individuals that met criteria. However, a number of participants were excluded from analysis for excessive hand movement (see Procedure for criteria; 10 excluded in Experiment 1, six in Experiment 2, and 14 in Experiment 3). Therefore, 24 participants were tested in Experiment 1, 20 in Experiment 2, and 28 in Experiment 3. All subjects were right-handed by self-report (Experiment 1, $n = 14$ [4 females], mean age: 19.0 years, $SD = .55$; Experiment 2, $n = 14$ [eight females], mean age 19.3 years, $SD = 1.02$; Experiment 3, $n = 14$ [eight females], mean age 18.56 years, $SD = 0.77$). No participants reported any neurological condition that would affect their hands, such as neuropathy or brain damage. All experimental protocols were approved by the University of Delaware's Institutional Review Board.

Procedure. Participants were seated at a table and instructed to place their left hand palm down. To facilitate coding, a washable marker was used to mark the metacarpophalangeal joints (which we will refer to as knuckles) of each finger for the landmark localization task. For the tactile localization task, a washable marker was used to draw a 3 cm × 3 cm grid of nine tactile targets with each target 1.5 cm away from adjacent targets on the dorsum of the participant's hand. Participants never saw these marks (either the knuckle or tactile targets) and did not see their hand again until the end of the entire session. Hand position varied by experiment. In Experiments 1 and 3, the participant's left hand was aligned with their trunk midline, with their fingers spread comfortably and pointed away from their trunk, with their wrist approximately 30 cm from their trunk midline (see Figure 1). In Experiment 2, participants aligned the mediolateral axis of their hand with the long axis of their trunk midline, such that the hand was rotated 90° from the Experiment 1/3 position, with their fingers pointed to their right. Because of biomechanical constraints, the participant's wrist was approximately 20 cm from body midline in Experiment 2. Tactile grid position also varied by experiment. In Experiments 1 and 2, the center of the grid was located approximately 4.5 cm distal from the participants' wrist with the mediolateral grid axis parallel to a line from the index to pinky knuckle. The original goal of this study was to examine the relationship between distortions in landmark and tactile localization. To examine whether previously observed widening of tactile localization judgments (Longo, Mancini, et al., 2015) was relative to a hand-centered or array-centered reference frame, the tactile grid was rotated approximately 20° medially from the axis created by the index and pinky knuckles and parallel to the participant's wrist in Experiment 3.

Two blocks were conducted for both the landmark localization and tactile localization tasks for a total of 4 blocks counterbalanced in an ABBA design. The task of the first block was also counterbalanced across participants. Participants were allowed to take breaks in between blocks to move their hands, but could not see their hand until testing was complete.

Before and after each experimental block, a picture was taken of the participant's hand using a Logitech C920 camera suspended over the center of the table. The participant's hand was then covered by a 50 cm × 50 cm occluding board resting on 10 cm high pillars, providing sufficient space for tactile stimulation. Participants' hands remained covered for the duration of the block. When the block concluded, the board was removed and another picture of their hand was taken. Pictures were taken before and after each block to ensure that the participant's hand had not moved under the board during the course of the block. We made the following a priori decision for inclusion: If any of the knuckle points moved more than .25 cm in the before-block versus after-block picture, then the participant was excluded from analysis. We note that a large percentage of participants (42%) were excluded. In our study, we selected a particular strict exclusion criterion to ensure that our results were not contaminated by any shift in hand position.

In the landmark localization task, on each trial the experimenter said a particular landmark on the hand (e.g., "index knuckle"), corresponding to one of the five knuckles on the left hand. Prior to the start of the session (before the hands were marked), the experimenter pointed to and verbally labeled each knuckle of interest on the participant's hand to eliminate confusion about which knuckles participants were to localize. Participants then used a 15.25 cm long pointer to indicate the location of the landmark on top of the occluding board. Each landmark block

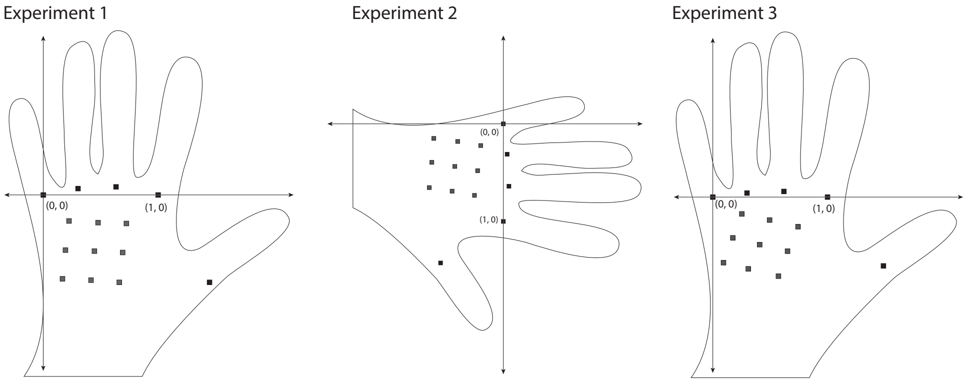

Figure 1. Hand position (relative to the trunk), landmark, and tactile stimulus location for each of the three experiments. Landmark locations are shown in black, with Bookstein coordinates for the index (1,0) and pinky knuckle (0,0) along with the axes for this coordinate system (black lines with arrows) also shown. Tactile stimulation locations are shown in dark gray.

consisted of 30 trials ($n = 6$ per landmark) presented in a randomized order.

In the tactile localization task, the experimenter used a Semmes-Weinstein monofilament (10 g force) to present suprathreshold tactile stimulation to one of the nine grid locations. All participants reported it as clearly suprathreshold but not painful. After stimulation, the participant made a localization judgment in the same manner as in the landmark localization task. Each tactile block consistent of 54 trials ($n = 6$ per target) was presented in a random order. For both the landmark and tactile tasks, after each localization judgment, a picture was taken to record each response. After the picture was taken, participants were instructed to return their pointing hand to the starting position, located at the near right corner of the occluding board. Approximately 3 s elapsed between each trial in both tasks.

Data coding. Pictures were coded using an in-house program written in PsychoPy (Peirce, 2007) to record the Cartesian coordinates for the location of targets and localization judgments. For landmark localization, these raw coordinates were converted to Bookstein coordinates (Bookstein, 1997) with the pinky knuckle designated as point (0, 0) and the index knuckle designated as point (1, 0). Note that this coordinate system remained "hand-centered", even for experiments where the hand was rotated relative to the trunk (Experiment 2). For tactile localization, the same coordinate scale was used as in landmark localization (e.g., the length from index to pinky knuckle was 1 Bookstein Unit). However, the coordinate system was shifted such that the x-axis was aligned with the mediolateral axis of the tactile grid for each participant. Shift is described relative to the radial-ulnar (toward the pinky-thumb) and distal-proximal (toward the fingertips-base of hand) hand axes.

Results

Mean localization judgments. Figure 2 shows the mean landmark localization judgments for each individual participant with lines connecting each landmark (within subject) from pinky to thumb knuckle. From this figure, it is clear that there was considerable variability in constant error (i.e., the signed distance from target to localization judgment) across participants. To examine overall shift in landmark localization in the radial-ulnar and distal proximal dimensions, we found the constant error for each trial, and then found the average shift over all trials in an experiment. We then used one-sample t tests to examine whether the overall constant error along each axis was significantly greater compared to a null hypothesis of no shift. Positive values indicate a radial/distal shift; negative values indicate an ulnar/proximal shift. Along the radial-ulnar dimension, there was a significant ulnar shift in Experiment 1—$M = -0.76$ Bookstein units [BU], $SE = 0.084$, $t(13) = -9.06$, $p < .001$, 95% confidence interval [CI]: $-.57$ to $-.93$, Cohen's $d = -2.42$—and Experiment 3—$M = -0.55$ BU, $SE = 0.15$, $t(13) = -3.68$, $p = .003$, 95% CI: $-.22$ to $-.87$, Cohen's $d = -.98$. There was a nonsignificant radial shift in Experiment 2: $M = 0.15$ BU, $SE = 0.19$, $t(13) = 0.783$, $p = .448$, 95% CI: $-.25$ to $.55$, Cohen's $d = .21$. We next examined whether constant error differed across experiments. A one-way analysis of variance (ANOVA) with experiment entered as a factor revealed that there was a difference between experiments in radial-ulnar shift, $F(2, 39) = 10.468$, $p < .001$. Tukey's HSD post hoc analysis showed that Experiment 2 significantly differed from Experiment 1 ($p < .001$) and Experiment 3 ($p = .005$). Experiments 1 and 3 did not significantly differ from one another ($p = .581$). Along the distal-proximal dimension, there was a significant proximal shift in all three experiments—Experiment 1: $M = -0.52$ BU, $SE = 0.12$, $t(13) = -4.32$, $p = .001$, 95% CI: $-.26$ to $-.79$, Cohen's $d = -1.16$; Experiment 2: $M = -0.73$ BU, $SE = 0.18$, $t(13) = -4.13$, $p = .001$, 95% CI: $-.35$ to -1.11, Cohen's $d = -1.10$; and Experiment 3, $M = -0.79$ BU, $SE = 0.16$, $t(13) = -4.86$, $p < .001$, 95% CI: $-.44$ to -1.13, Cohen's $d = -1.29$. A one-way ANOVA with experiment entered as a factor indicated that there were no significant differences between the experiments, $F(2, 39) = 0.804$, $p = .455$.

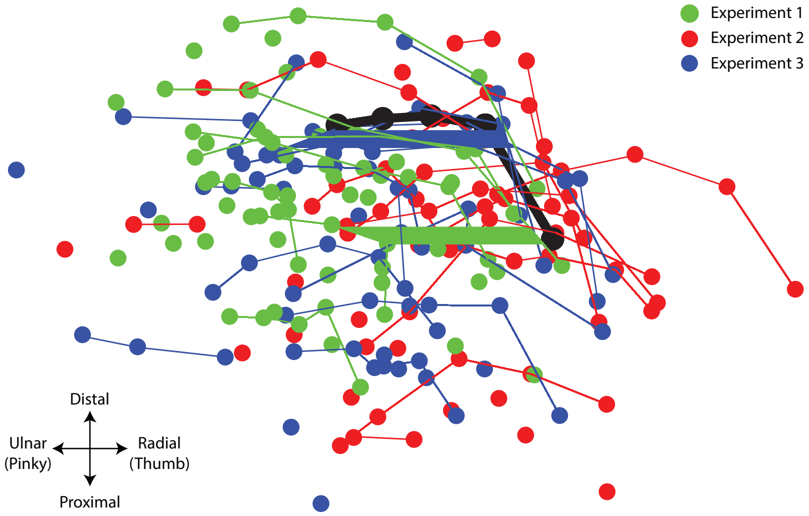

Figure 2. Mean localization judgment for each individual participant in Experiments 1 (red/grey), 2 (blue/dark grey), and 3 (green/light grey). The location of the participants' own knuckles is shown in black. For each individual, a line connecting mean localization judgments for each knuckle, going from the pinky (left) to the thumb (right) knuckle. See the online article for the color version of this figure.

However, Figure 2 also shows that the relative location of each landmark was well-preserved within subjects—as illustrated by the lines connecting the mean landmark localization judgment for each finger. As done in Longo and Haggard (2010), we plotted the data across individuals using a generalized Procrustes superimposition in MATLAB. Given that hand size and the absolute location of landmark judgments vary across participants (e.g., Figure 2), the generalized Procrustes superimposition adjusts each individual's localization judgments onto a single hand shape, highlighting the relative locations of landmark judgments within each individual's hand. As seen in Figure 3, landmark judgments for the second and fifth knuckles were wider than the actual landmark locations. To examine if participants widened localization judgments of the knuckles as in previous experiments, we calculated the distance from the mean perceived location of the index knuckle to the mean perceived location of the pinky knuckle for each subject, and then compared this to the actual distance between the participant's index and pinky knuckle to derive an estimate of landmark widening or contraction. Using one-sample t tests (comparing these groups to the null hypothesis of no widening), we found significant widening of landmark judgments in all three experiments—Experiment 1: $M = 26.74\%$, $SE = 9.59$, $t(13) = 2.79$, $p = .015$, 95% CI: 6.0% to 47.5%, Cohen's $d = .74$; Experiment 2: $M = 18.67\%$, $SE = 6.88$, $t(13) = 2.71$, $p = .018$, 95% CI: 3.8% to 33.5%, Cohen's $d = .72$; and Experiment 3: $M = 37.40\%$, $SE = 11.69$, $t(13) = 3.20$, $p = .007$, 95% CI: 12.2% to 62.6%, Cohen's $d = .86$. A one-way ANOVA with experiment entered as a factor revealed that widening did not significantly differ across experiments, $F(2, 39) = 0.962$, $p = .392$.

Mechanisms of landmark localization—assessing the overestimation hypothesis. Taken at face value, this analysis provides evidence that individuals perceive their knuckles to be significantly more separated than on their actual hand, consistent with a distorted body model hypothesis. However, simply taking the average localization judgment for each knuckle may fail to capture other biases that may lead to the widening observed in our and other data sets using this task. For example, Figure 4 shows the first five trials of the landmark localization task for a selected participant. In our notation, the location of the actual stimulus will be marked as ACT_N, and the position of the localization judgment will be PER_N, with N being the trial number. On the first trial (localizing the pinky knuckle), the localization judgment for this response (PER_1) is quite distant from the actual location of the pinky knuckle (ACT_1). However, even though the initial judgment is relatively inaccurate, the vector ($\text{PER}_{1\text{–}2}$) from the localization judgment at Trial 1 (pinky) to Trial 2 (thumb) looks to be a general approximation of the vector from the actual pinky to the actual thumb ($\text{ACT}_{1\text{–}2}$). Importantly, this vector does not seem to be referencing the location of the actual pinky knuckle as a starting point, but may instead be using the initial localization judgment of the pinky knuckle as the vector starting point. One possibility is that, when doing a relatively difficult localization task, people rely strongly on their last localization judgment (as opposed to the actual landmark position) and then use a mental approximation of the distances between points on the hand to make the next localization judgment. Using a trial-by-trial lag-1 analysis, we can examine potential biases in representing the hand in more depth.

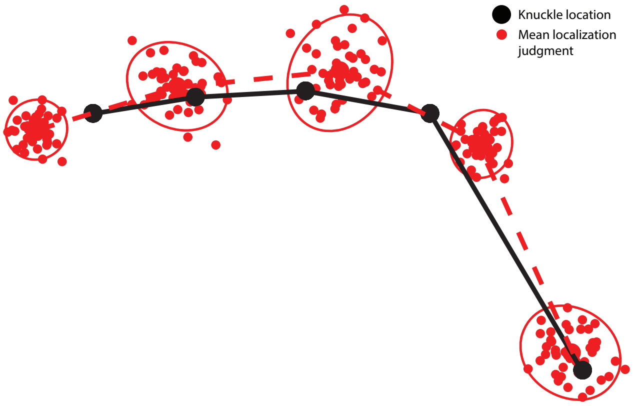

Figure 3. Generalized Procrustes superimposition (GPS) for landmark localization judgments for each participant across all three experiments (red/grey), along with the mean GPS for each knuckle (black). Ovals are 95% confidence intervals. See the online article for the color version of this figure.

To do so, we developed two variables. First, we found the position vector from the actual stimulus location on trial n-1 to the actual stimulus location on trial n—what we will call the actual lag-1 vector (e.g., $\text{ACT}_{1\text{–}2}$ in Figure 4). Next, we measured the distance from the participant's localization judgment on trial n-1 to their localization judgment on trial n—the perceived lag-1 vector (e.g., $\text{PER}_{1\text{–}2}$ in Figure 4). Using these variables, we first examined whether individuals used the perceived or actual stimulus location as the origin on trial n-1 to make a localization judgment on trial n. First, we found the "perceived origin error," which was the difference in Euclidean vector distance and angle between the actual lag-1 vector and perceived lag-1 vector. Next, we found the "actual origin error," which was the difference in euclidean vector distance and angle between the actual lag-1 vector and a vector with its origin at the position of the actual stimulus at trial n-1, and its terminus at the perceived stimulus location at trial n (see gray dotted line, Figure 4). If participants are using the perceived location of the landmark on trial n-1 as the origin for their localization judgment on trial n more than the position of the actual landmark, then we would expect less perceived origin error versus actual origin error. For each subject, we found the mean predicted absolute vector error and euclidean distance error using the actual versus perceived origin. These values were entered into separate mixed-design ANOVAs with experiment as a between-subjects factor.

For absolute vector error, we found that participants demonstrated substantially more error when using the actual stimulus location as the trial n-1 origin (mean actual origin error: 129.2°, SE: 2.35°, 95% CI: 124.4° to 133.9°) compared to the perceived stimulus location (mean perceived origin error: 18.4°, SE: 1.12°, 95% CI: 16.1° to 20.7°), $F(1, 39) = 1619.3$, $p < .001$, $\eta_p^2 = .976$. There was no main effect of experiment, $F(2, 39) = .197$, $p = .822$, $\eta_p^2 = .010$, nor an experiment by error type interaction $F(2, 39) = .349$, $p = .707$, $\eta_p^2 = .018$. We also found significantly more euclidean distance error when using the actual stimulus location as the origin (mean error: .738 BU, SE: .054, 95% CI: .629 to .846) compared to the perceived stimulus location (mean error: .309 BU, SE: .014, 95% CI: .280 to .337), $F(1, 39) = 58.2$, $p < .001$, $\eta_p^2 = .599$. There was no main effect of experiment, $F(2, 39) = .309$,

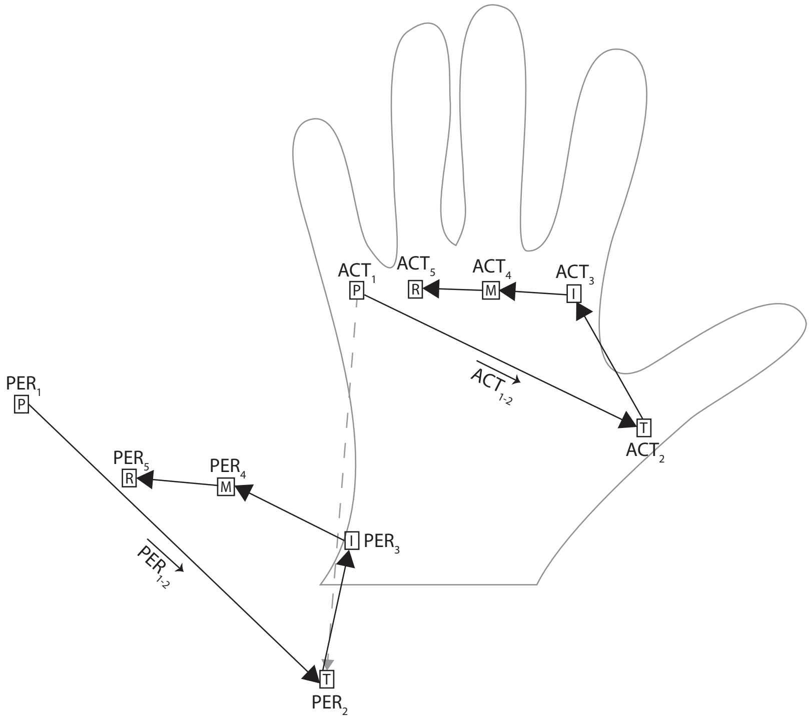

Figure 4. Diagram showing the first five trials of a selected subject. ACT$_1$ denotes the actual stimulus position, with the trial number as the subscript. PER$_1$ shows the localization judgment for the first trial. In each rectangle is the abbreviation for each knuckle. Arrows show vectors going from landmark judged (ACT) or localization judgment (PER) for consecutive trials. The dotted gray line shows the vector from the actual landmark location on Trial 1, and the perceived stimulus location on Trial 2.

p = .736, $\eta_p^2 = .016$, and no experiment by origin interaction, $F(2, 39) = .673$, $p = .516$, $\eta_p^2 = .033$.

Examining perceptual biases using a lag-1 analysis. The previous analyses provide evidence that participants are using the location of the previous (n-1) localization judgment, combined with some knowledge of the actual distance and direction from trial (n-1) to trial n, to make a localization judgment on trial n. However, this knowledge of the distance and direction between two points on the hand may be distorted in a systematic manner. For example, previous studies (e.g., Longo & Haggard, 2010) have claimed that individuals utilize a body model when making landmark judgments, and that this body model is systematically distorted such that the knuckles are represented as wider than actual. In these studies, the authors found the mean localization judgments for each landmark, and then compared the distance between the mean localization judgments to the distance between the actual landmarks. With regards to the knuckles, studies have found a systematic widening of the perceived location of the landmarks, ranging anywhere from 20% (Saulton et al., 2015) to 78% (Longo & Haggard, 2010). As in previous studies, we found the distance between the mean localization judgments of the index and pinky knuckles to range from 19% in Experiment 2% to 37% in Experiment 3.

If individuals rely on a distorted body model, then these same widening biases should also be observed using a lag-1 analysis. For example, suppose that trial (n-1) was a localization judgment of the pinky knuckle, followed by a localization judgment of the index knuckle on trial n. In BU, the change in actual landmark position from trial n-1 (coordinates 0,0) to trial n (coordinates: 1,0) would be one unit along the mediolateral, hand-centered (x) axis, and zero units along the distal-proximal (y) axis. If participants were referencing a body model with distorted, widened knuckles, one would predict that the displacement between the perceived location judgments on trial n-1 and trial n (perceived lag-1 displacement) along the mediolateral axis would be increased relative to the actual displacement (actual lag-1 displacement). Importantly, this increased displacement should be in addition to any potential confounding effects. To examine this relationship, we used linear mixed models to find if the actual displacement between consecutive stimuli predicts the perceived displacement between consecutive stimuli. Given that previous studies have reported widening of the knuckles (mediolateral axis) and shortening of the fingers (distal-proximal axis), we examined this relationship separately along the mediolateral and distal-proximal hand axes using linear mixed models with subject as a random effect. For our initial model, we examined whether actual lag-1 displacement predicted perceived lag-1 displacement. Next, we added the following factors (fixed effects) to the model in a stepwise manner: displacement direction, experiment and block. Displacement direction coded whether the change in actual stimulus position from trial n-1 to trial n was medial (+1) or lateral (−1) when examining mediolateral shift, distal (+1) or proximal (−1) when examining distal-proximal shift, or (0) if there was no change in stimulus position along the selected axis. Then, to account for within-subject differences, we included the following random effects: an intercept for subject, and a by-subject random slope for the effect of actual lag-1 displacement. For every model, adding the random slope resulted in a significantly better model fit than a model without the random slope. After adding a factor to the model, we used ANOVAs to compare the simpler model to the model with the additional factor. Factors were only included if they significantly improved model fit ($\alpha = .05$). All analyses were done using R 3.3.1 (using the lmer command in the lmerTest package).

First, we examined the relationship between perceived lag-1 displacement and actual lag-1 displacement along the mediolateral hand axis on the landmark localization task. The final model that best predicted perceived lag-1 displacement (see Figure 5) included actual lag-1 displacement ($\beta = 1.012$, $SE = .052$, 95% CI: .910 to 1.11, $t = 19.4$, $p < .001$) and the actual displacement direction ($\beta = .084$, $SE = .016$, 95% CI: .052 to .115, $t = 5.13$, $p < .001$), with no significant change in intercept ($\alpha = -.0005$, SE: .007, 95% CI: $-.014$ to .014, $t = .075$, $p = .94$).

We will discuss two critical findings in this analysis. First, we found that displacement direction was a significant predictor. Note that both actual lag-1 and perceived lag-1 displacement variables are signed, and encode the direction of actual displacement. The actual displacement direction variable is fixed at +1 for any medial shifts, −1 for any lateral shifts, and zero if there are no shifts. For the regression equation, this serves to create a separate *y*-intercept for trials depending on the direction of actual lag-1 shift (see red line, Figure 5). This *y*-intercept is a measure of constant overestimation on any trials where there is displacement along that particular dimension from trial n-1 to trial n. Our analysis provides evidence that our participants, on average, always overestimate mediolateral shift .084 BU in the direction of the actual displacement, independent of the actual distance between the two localization judgments. Furthermore, this bias would be manifest as a greater overestimation of the distance between two consecutive localization judgments when the two consecutive stimuli are closer versus farther along the mediolateral dimension. To provide an example, the actual vector from the pinky to the ring finger is approximately +.30 BU along the mediolateral axis. In the regression equation, the perceived vector (+.384 BU) would be the actual vector (+.30 BU) in addition to this constant shift (+.084 BU). This would result in a predicted 28% overestimation of distances between these two fingers, whereas judgments between the index and pinky finger (+1 BU) would be overestimated only by 8.4%.

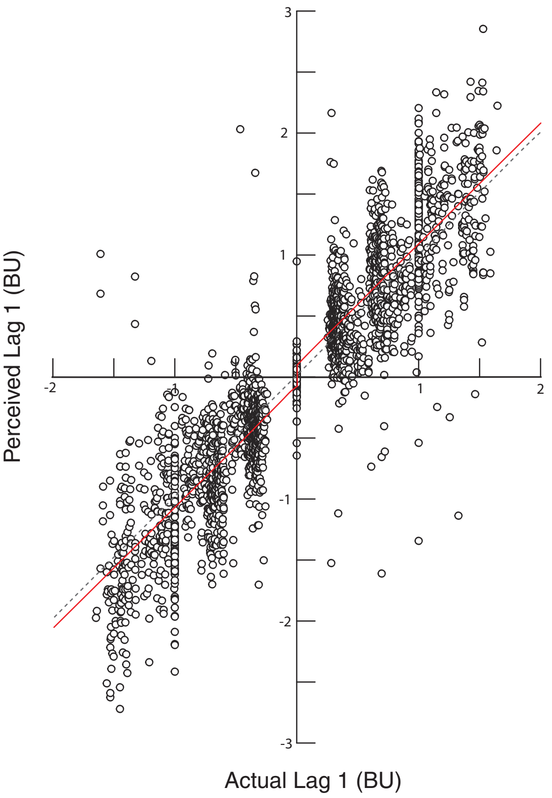

Figure 5. The relationship between the actual lag-1 (*y*-axis) and perceived lag-1 (*x*-axis) vector for each trial (shown as a circle) along the mediolateral hand axis. The regression line is shown in red/grey. The dotted line shows the line if there was a one-to-one relationship between the actual and perceived lag-1 vectors. See the online article for the color version of this figure.

Second, as expected, the actual lag-1 displacement predicted the perceived lag-1 displacement—that is, there was a strong relationship between the actual distance between the two consecutively localized points on the hand and the two consecutive localization judgments. However, the slope of the line showing the relationship between actual and perceived lag-1 displacement is of critical importance. If there are distortions in the representation of landmark location separate from the constant overestimation bias as characterized by the main effect of displacement direction, the actual lag-1 slope should be significantly different from 1. However, the β for actual lag-1 displacement is not significantly different from 1 ($t = .230$, $p = .818$). Therefore, the only significant source of bias along the mediolateral axis was the constant overestimation effect, with no evidence for any additional widening between localization judgments. Outside of this constant overestimation bias, there is no evidence for any distortion in the perceived location of hand landmarks.

We did the same analysis examining predictors of perceived lag-1 displacement along the distal-proximal axis of the hand. As before, the model that best predicted perceived lag-1 displacement (see Figure 6) included actual lag-1 displacement ($\beta = .597$, $SE = .005$, 95% CI: .497 to .695, $t = 11.8$, $p < .001$) and the actual displacement direction ($\beta = .119$, $SE = .009$, $t = 13.6$, 95% CI: .102 to .136, $p < .001$) as significant predictors, along with an intercept that was significantly different from zero ($\alpha = -.020$, SE: .006, 95% CI: $-.008$ to $-.031$, $t = -3.46$, $p = .0005$). Contrasting the model for mediolateral shift, this model does show a large contraction of perceived distances along the distal-proximal dimension, even when accounting for constant displacement over each trial. We note that this contraction along the distal-proximal axis is similar to the reported distortions in body representation—shorter fingers—in Longo and Haggard (2010). However, we observe this distal-proximal bias on landmark trials that do not involve any judgments of finger position—suggesting that the previously reported shorter finger representations may be due to a general foreshortening along the distal-proximal hand axis. Next, given that our dependent variable is the perceived shift along the

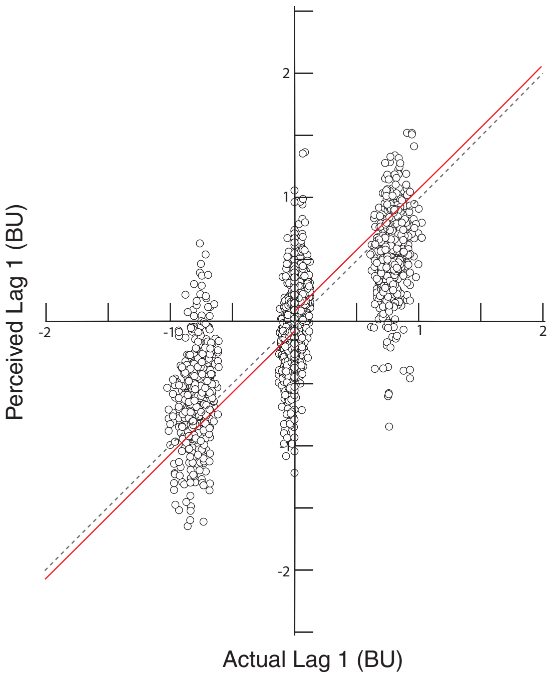

Figure 6. The relationship between the actual lag-1 (*y*-axis) and perceived lag-1 (*x*-axis) vector for each trial (shown as a circle) along the distal-proximal hand axis. These clusters reflect that, along the distal-proximal axis, most changes in actual stimulus position are either from one nonthumb knuckle to the other (middle cluster) or from thumb to index-pinky knuckle (outside clusters). See the online article for the color version of this figure.

distal-proximal axis between two trials, a significant intercept reflects a consistent bias in localization judgments between two trials. The significant negative intercept in our regression analysis reflects a small, but consistent, proximal bias for each localization judgment. This intercept likely indexes proprioceptive drift (Wann & Ibrahim, 1992), a phenomenon in which proprioceptive judgments drift toward the body without vision of the body. As a secondary analysis, we found the slope of distal-proximal error over trial for each participant. This slope was significantly negative (e.g., proximal shift over the course of a block) for all three experiments (Experiment 1., −.013, Experiment 2, −.011, Experiment 3, −.015, all *ps* < .001 using one-sample *t* tests with the null hypothesis being zero), providing additional evidence for proprioceptive drift. In Experiments 1 and 3, the significant shift is both toward the trunk (the typical direction of proprioceptive drift) and the wrist. Interestingly, in Experiment 2 the observed shift is also toward the wrist but to the left of the body. Although not the purpose of this analysis, our results may suggest that proprioceptive drift for the hand goes toward the arm, and not the trunk.

To further explore these effects, we separately examined the ratio of the perceived distance between two consecutive landmark judgments to the actual distance between two consecutive landmark judgments. First, we only examined trials in which the two consecutive judgments (on trial *n* and trial n-1) did not involve the thumb knuckle, and only when the two consecutive trials were on different knuckles (e.g., index-thumb and index-index were not included, whereas index-middle was included). Furthermore, as participants occasionally made errors that may be due to forgetting the instructed trial, we excluded any trials in which the vector of two consecutive localization judgments was in the opposite direction of the vector from the first to second stimulus location (2.4% of trials—though we note that all significant findings remain significant with these trials included). We then ran a mixed-design ANOVA with experiment as a between-subjects factor and "knuckle distance" (the distance between localization judgments, in knuckles) as a within-subjects factor. If localization judgment distance is influenced by the distance between two consecutive stimuli, we would predict a significant effect of knuckle distance—with greater overestimation for consecutive judgments that are closer in hand space. We found a significant main effect of knuckle distance between consecutive trials, $F(1.702, 66.38) = 45.0$, $p < .001$, $\eta_p^2 = .570$, Greenhouse-Geisser corrected, as judgments were significantly more overestimated at the one-knuckle distance (+62.8% overestimation) versus two- (+40.2%) and three-knuckle (+31.5%) distances (all pairwise comparisons between conditions were significant, all *ps* < = .003). There was no main effect of experiment, $F(2, 39) = 2.17$, $p = .127$, nor an experiment by knuckle distance interaction, $F(3.4, 66.4) = 1.84$, $p = .141$). A similar analysis that included trials to/from the thumb had similar results. We found a significant main effect of knuckle distance, $F(2.002, 78.06) = 78.3$, $p < .001$, Greenhouse-Geisser corrected, with no main effect of experiment, $F(2, 39) = 1.53$, $p = .230$ nor a knuckle distance by experiment interaction, $F(4.0, 78.1) = 1.92$, $p = .115$). Participants demonstrated the most overestimation with the shortest knuckle distances, with all pairwise comparisons being significant (1 knuckle apart, 43.0%; 2 knuckles, 22.2%, 3 knuckles, 16.8%, 4 knuckles, 1.9%; all *ps* <.05).

To summarize, we found an overestimation of hand width when simply analyzing the mean localization judgment location. However, we found that as consecutive localization judgments were for targets that were closer in space (e.g., index knuckle on Trial 1, middle finger knuckle on Trial 2), participants consistently overestimated the distance between the two landmarks compared to consecutive comparisons that were farther in space (e.g., index knuckle on Trial 1, pinky knuckle on Trial 2). Controlling for such an overestimation effect, we found no evidence for a wider representation of hand width.

Tactile localization. Given that we also have tactile localization data for each individual tested in these three experiments, we can examine if the biases seen for localizing proprioceptively defined targets also exist for localizing touch. To examine overall shift in tactile localization in the radial-ulnar and distal-proximal dimensions, we found the constant error for each trial, and then found the average shift over all trials in an experiment. As for landmark localization, positive values indicate a radial/distal shift; negative values indicate an ulnar/proximal shift. Along the radial-ulnar dimension, there was a significant ulnar shift in Experiment 1—$M = -0.63$ BU, $SE = 0.06$, $t(13) = -9.88$, $p < .001$, 95% CI: −.49 to −.77, Cohen's $d = -2.64$—and Experiment 3—$M = -0.30$, $SE = 0.11$, $t(13) = -2.68$, $p = .021$, 95% CI: −.05 to −.54, Cohen's $d = -.70$. There was a nonsignificant radial shift in Experiment 2: $M = 0.28$, $SE = 0.21$, $t(13) = 1.33$, $p = .205$, 95% CI: −.17 to .73, Cohen's $d = .36$. A one-way ANOVA with experiment entered as a factor revealed that there was a difference between the experiments in radial-ulnar plane, $F(2, 39) = 10.46$, $p < .001$. Tukey's HSD post hoc analysis showed that Experiment 2 significantly differed from Experiment 1 ($p < .001$), and Experiment 3 ($p = .018$). Experiment 1 and Experiment 3 did not significant differ from one another ($p = .234$). Along the distal-proximal dimension, there was a significant proximal shift in all three experiments—Experiment 1: $M = -0.46$, $SE = 0.15$, $t(13) = -3.09$, $p = .009$, 95% CI: $-.13$ to $-.78$, Cohen's $d = -.82$; Experiment 2: $M = -0.38$, $SE = 0.12$, $t(13) = -3.13$, $p = .008$, 95% CI: $-.12$ to $-.64$, Cohen's $d = -.84$; and Experiment 3: $M = -0.68$, $SE = 0.13$, $t(13) = -5.26$, $p < .001$, 95% CI: $-.40$ to $-.97$, Cohen's $d = -1.40$. A one-way ANOVA with experiment entered as a factor indicated that there were no significant differences between the experiments, $F(2, 39) = 1.37$, $p = .265$.

To see if participants widened the tactile grid as they widened their knuckles in the landmark localization task, we calculated the actual and perceived distances between Targets 1 and 3, Targets 4 and 6, and Targets 7 and 9. The perceived distance was divided by the actual distance so that values greater than 1 indicated widening of the row. These three values were averaged together to calculate one overall percentage for tactile grid widening. Significant widening did occur in all three experiments—Experiment 1: $M = 76.76\%$, $SE = 15.39$, 95% CI, 43.50% to 110.01%, $t(13) = 4.99$, $p < .001$; Experiment 2: $M = 63.87\%$, 95% CI, 40.53% to 87.21%, $SE = 10.80$, $t(13) = 5.91$, $p < .001$; and Experiment 3: $M = 76.72\%$, 95% CI, 46.37% to 107.09%, $SE = 14.05$, $t(13) = 5.46$, $p < .001$ (see Figure 7). A one-way ANOVA with experiment entered as a factor revealed no significant differences between experiments, $F(2, 39) = 0.302$, $p = .741$. However, tactile localization judgments were not different from veridical along the distal-proximal grid axis—Experiment 1: $M = 3.06\%$, $SE = 8.69$, 95% CI: -15.72 to 21.84%, $t(13) = .352$, $p = .731$; Experiment 2: $M = 6.42\%$, $SE = 8.99$, 95% CI: -13.00 to 25.86%, $t(13) = .715$, $p = .487$; and Experiment 3: $M = 5.42\%$, $SE = 9.96$, 95% CI: -16.10 to 26.94%, $t(13) = .544$, $p = .596$.

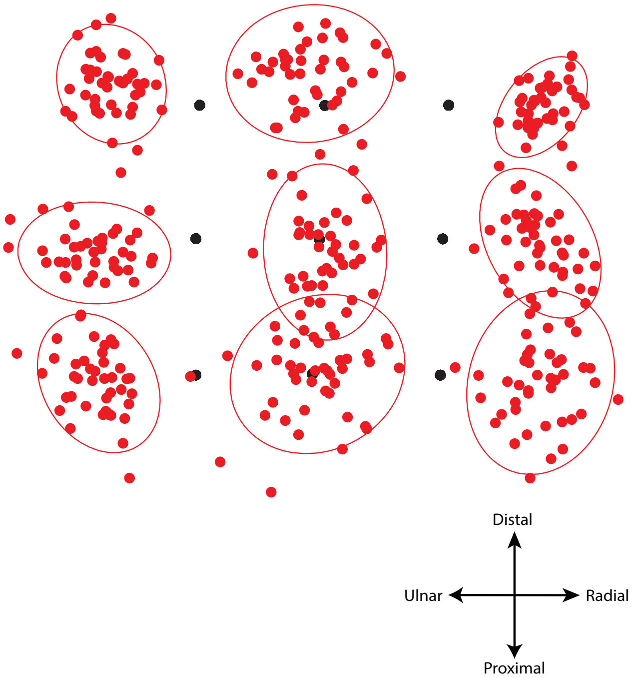

Figure 7. Mean localization judgments across all three experiments (red/grey) for each tactile stimulation location (black). Each dot is the mean for one participant at one target. The oval shows the 95% confidence interval. Data are displayed with the target grid rotated and shown such that the most distal row (relative to the participant's hand) is on top. See the online article for the color version of this figure.

As with the landmark localization data, we also did a lag-1 analysis to examine what factors predicted perceived displacement. For this analysis, the following fixed effects were entered in a stepwise manner: actual lag-1 displacement, actual displacement direction, hand orientation (parallel or perpendicular with the trunk axis), tactile array orientation (straight or rotated relative to hand), trial, and block. As before, we included subject as a random intercept, and a by-subject random slope for the effect of actual lag-1 displacement. For the mediolateral dimension, the only significant factor that predicted perceived lag-1 displacement was actual lag-1 displacement ($\beta = 1.593$, $SE = .081$, $t = 19.7$, $p < .001$, 95% CI: 1.43 to 1.75), with a nonsignificant intercept ($\alpha = .0003$, SE: .005, $t = 0.06$, $p = .949$, 95% CI: $-.014$ to .006). This model predicts a 59.3% widening of tactile localization judgments. Interestingly, adding neither displacement direction ($p = .398$), hand position ($p = .828$) nor array orientation ($p = .915$) significantly improved the model. For distal-proximal displacement, the only significant factor that predicted perceived lag-1 displacement was actual lag-1 displacement ($\beta = .996$, $SE = .051$, $t = 19.6$, $p < .001$, 95% CI: .896 to 1.096), with a nonsignificant intercept ($\alpha = -.004$, SE: .005, $t = -.79$, $p = .43$, 95% CI: $-.014$ to .006). The slope of the regression line was not significantly different from 1, $t = .077$, $p = .939$, providing additional evidence for no bias along the distal-proximal axis. Furthermore, as seen in the mediolateral dimension, adding hand position ($p = .561$) or array orientation ($p = .809$) did not significantly improve the model. In summary, we find a clear widening of tactile localization judgments on the hand using multiple analyses that is not explained by a constant overestimation bias. This will be discussed in more detail in the General Discussion.

Experiments 4 and 5

Our analysis of the landmark localization data found the following. (a) Participants likely use an estimate of the location of their previous localization judgment as an origin for the subsequent localization judgment. (b) When examining the vector between consecutive localization judgments and the consecutive stimuli to be localized, participants consistently overestimated the vector along the mediolateral dimension. (c) Controlling for this overestimation bias, participants' knowledge of distances between hand landmarks are veridical along the mediolateral axis, suggesting that individuals utilize a nondistorted representation of the distance between the knuckles when making localization judgments. With regards to the second point, one possibility is that this constant overestimation bias is specific to localizing body-related stimuli. If so, this would provide evidence that the overestimation is specific to the hand.

An alternative hypothesis is that this overestimation bias is not specific to the hand, but is caused by a domain-general spatial bias. In the landmark localization task with the hands, proprioceptive noise may result in moderate uncertainty regarding absolute stimulus position but high certainty regarding the relative position of consecutive stimuli (e.g., on my left hand with my palm down, the pinky knuckle is to the left of my index knuckle). One possibility is that, when individuals make a localization judgment for trial n, they have a memory of that localization judgment along with an uncertainty estimate for the location of that judgment. On trials where consecutive stimuli are in different positions, there may be a mechanism to avoid making a response in the same location when consecutive trials are in different locations, such that the localization judgment on trial $n + 1$ does not fall within the uncertainty estimate for trial n. Given that the participant knows the spatial relationship between the two stimuli, the participant may shift the second localization judgment outside of the trial *n* uncertainty estimate. This would result in an overestimation bias that is exaggerated when two consecutive trials are closer in space.

In the next experiments, we endeavored to (a) examine whether the observed biases in the landmark localization task with the hand could be domain-general and (b) examine the effects of trial-to-trial proximity on overestimation bias. To do so, we replicated the landmark localization task from Experiments 1–3. However, instead of having participants localize their knuckles, we instructed participants to localize a remembered visual array of five dots located under an occluding board—a task that should have moderate uncertainty regarding absolute stimulus position, but high certainty regarding the relative location of two stimuli. If there is a domain-general mechanism that causes this bias, we should observe the same overestimation biases for localizing nonbody stimuli that were observed with body stimuli. Furthermore, we manipulated the size of the array, predicting that there would be a larger overestimation bias for closer versus more spaced-out dot arrays.

Method

Participants. Twenty-six participants were tested each in Experiment 4 (19 females, *M* age = 18.7, *SD* = .74) and Experiment 5 (19 females, *M* age =, 19.0, *SD* = .82). All participants were recruited from the Introduction to Psychology pool at the University of Delaware.

Procedure. The procedure for both experiments was the same as in the landmark localization task, with the following differences. Instead of localizing one's own knuckles, participants were asked to instead localize a dot from a remembered dot array presented in the same location as the hand in Experiments 1–3. Participants were tested in six blocks (block order randomized across participants), in which the spatial dimensions of the dot array varied. The "default" dot array was designed to have similar dimensions as the metacarpophalangeal joints (knuckles) on the human hand. The array consisted of four dots in a straight line, with a fifth dot offset from the other four dots. In Experiment 4, the straight line was arrayed horizontally relative to the viewer (see Figure 8a); whereas in Experiment 5, it ran vertically relative to the viewer (see Figure 8b). The six arrays varied based on the size of the array relative to the default array (1/2x, 1x, and 2x) and the position of the offset dot relative to the viewer (whether the offset dot was the nearest or farthest from the participant in Experiment 4; and whether it was left or right of the participant in Experiment 5). In Experiment 4, half of the participants were tested with the offset dot to their left, with the other half to their right. Because of an experimental oversight, all of the participants in Experiment 5 were tested with the offset dot near to their body. To ensure that participants did not consciously reference their own hand when doing the task, we asked each participant to report what they thought the experiment was about after it was completed. No participants made mention of the hand or body.

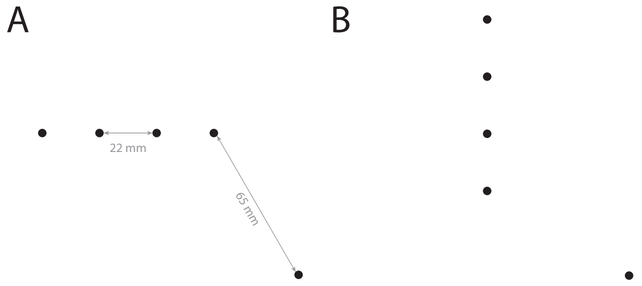

Figure 8. Examples of the horizontally (A) and vertically (B) oriented dot-arrays used in Experiments 4 and 5. The distance between dots for the 1× condition are shown in gray (arrows are for display purposes only and were not on the dot array).

To begin each block, participants were shown one of the six dot arrays (attached to a testing board using Velcro) for 30 s and were told that the dots were numbered 1–5, from left-right (Experiment 4) or from top to bottom (Experiment 5). During this 30-s period, they were told to study and memorize the location of the dots in the array. After 30 s, a 6-cm tall occluding board (40 × 40 cm) was placed over the array. We previously used a larger, taller occluding board to ensure sufficient room for the experimenter to touch the participant using Semmes-Weinstein filaments. The experimenter would call out a number referring to the dot number, and the participant would localize the dot as in Experiments 1–3. Each block consisted of 30 trials (six trials for each of the five dots).

Pictures were coded offline as in Experiments 1–3. Given that the dot arrays were constant across participants, we coded stimulus and response locations in Cartesian coordinates (in mm), with the *x*-axis aligned with the long axis of the participant's trunk (left: negative).

Results

As in Experiments 1–3, we first examined whether overall bias along the x- and y-axes were significantly different from the null hypothesis of no bias using one sample *t* tests. We found no significant bias along the left-right axis for Experiment 4—*M* bias, +0.26 cm, 95% CI: −.36 cm to +.89 cm; Cohen's *d* = .170, *t*(25) = .87, *p* = .394—or Experiment 5—*M* bias, −0.14 cm, 95% CI −0.58 to +0.30 cm; Cohen's *d* = −.129, *t*(25) = −.66, *p* = .516. There was a slight shift in the near-far dimension that was not significant for Experiment 4—*M* = +0.81 cm, 95% CI: −0.12 cm to +1.76 cm; Cohen's *d* = .350, *t*(25) = 1.78, *p* = .087—but was significant for Experiment 5—*M* = +0.91 cm, 95% CI: +0.17 cm to +1.65 cm; Cohen's *d* = .496, *t*(25) = 2.53, *p* = .018.

Next, we examined whether participants' average responses widened along the primary axis of the dot array (see Figure 9). First, we found the mean localization judgments for the two most separated dots along the array line (i.e., excluding the offset dot). We then quantified overestimation as the distance between these

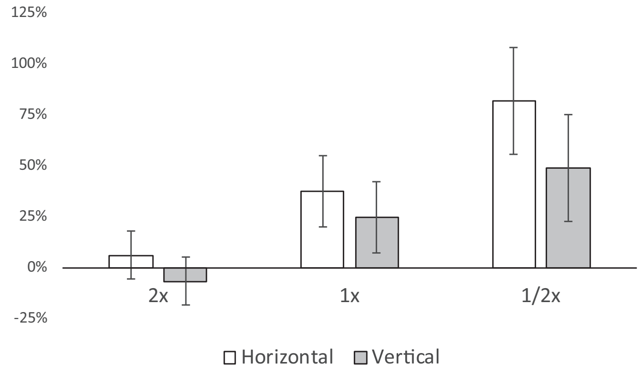

Figure 9. Widening of localization judgments along the horizontal (Experiment 4) and vertical (Experiment 5) array axes. Bars show the 95% confidence interval.

two mean localization judgments divided by the actual distance of these two points. Given that there was no difference in overestimation based on the position of the offset dot, we collapsed these trials for this analysis. Data was analyzed in a mixed-design ANOVA, with array distance (2x, 1x, 1/2x) as a within-subjects factor, and experiment array orientation (horizontal vs. vertical relative to the subject) as a between-subjects factor. First, we found a significant effect of array distance, $F(2, 100) = 72.5$, $p < .001$, $\eta_p^2 = .592$. There was virtually no widening of localization judgments in the 2x array condition (−0.4% overestimation, 95% CI: −9.0% to +8.1%), moderate widening in the 1x array condition (+31.3% overestimation, 95% CI: 18.7% to 43.8%) and substantial widening in the 1/2x array condition (+65.4% overestimation, 95% CI: 46.4% to 84.4%). All pairwise comparisons between these conditions were significant (*p*s < .001). Although there was more overestimation with the horizontal (+41.8%, 95% CI: 24.0% to 59.5%) than the vertical array orientation (+22.4%, 95% CI: +4.6% to +40.1%), there was no main effect of array orientation, $F(1, 50) = 2.41$, $p = .127$, $\eta_p^2 = .046$, nor was there a significant interaction, $F(2, 100) = 2.19$, $p = .117$, $\eta_p^2 = .042$. These results demonstrate the same pattern as observed in our experiments with hands—a significant widening in mean localization judgments along the major axis of the dot array. Furthermore, we also found that the observed widening varied as a function of dot spacing in the array—with substantial widening with the smallest array and no widening with the largest array.

Next, we examined these results using the same lag-1 analysis as in Experiments 1–3. We used linear mixed models to examine the relationship between the perceived displacement between two stimuli and the actual displacement between two stimuli, with separate analyses for displacement along the left-right and near-far axes (relative to the viewer). For our initial model, we examined whether actual lag-1 displacement predicted perceived lag-1 displacement, and then added the following factors in a stepwise manner: displacement direction, experiment and block. Model selection, random effects, and random slopes were done as in Experiments 1–3.

First, we present the results for the left-right axis. The final model that best predicted perceived lag-1 displacement included actual lag-1 displacement ($\beta = .936$, $SE = .041$, 95% CI: .855 to 1.017, $t = 22.7$, $p < .001$) and actual displacement direction ($\beta =$ 6. 96, $SE = .324$, 95% CI: 6.32 to 7.60, $t = 21.5$, $p < .001$), with no significant change in intercept ($\alpha = -.0027$, *SE*: .217, 95% CI: −.423 to .428, $t = -.01$, $p = .99$). The actual lag-1 displacement is not significantly less than 1 ($t = 1.55$, $p = .122$). Importantly, there was a significant effect of displacement direction, providing additional evidence for this constant overestimation bias even with noncorporeal stimuli. Neither adding experiment ($p = .972$) nor block ($p = .722$) resulted in a significantly improved model.

Next, we ran a similar model examining bias along the distal-proximal axis; with the only difference being the addition of trial as a factor, to examine if something analogous to proprioceptive drift was occurring with noncorporeal stimuli. The final model that best predicted perceived lag-1 displacement included actual lag-1 displacement ($\beta = .861$, $SE = .036$, 95% CI: .789 to .933, $t = 23.4$, $p < .001$) and the actual displacement direction ($\beta = 5.65$, $SE = .271$, 95% CI: 5.11 to 6.18, $t = 20.8$, $p < .001$), with no significant change in intercept ($\alpha = -.083$, *SE*: .182, 95% CI: −.440 to .275, $t = -.45$, $p = .65$). The actual lag-1 displacement is significantly less than 1 ($t = 3.78$, $p < .001$), suggesting a 14% underestimation of distal-proximal distance when taking constant overestimation into account. Neither adding experiment ($p = .741$), block ($p = .636$), nor trial ($p = .058$) resulted in a significantly improved model.

Finally, as in the previous experiments using the hand, we examined the ratio of the perceived distance between two consecutive landmark judgments to the actual distance between two consecutive landmark judgments. As in our analyses for Experiments 1–3, we excluded any trials in which either of the two judgments included the offset dot, and any trials in which the vector of two consecutive localization judgments was in the opposite direction (along the primary array axis) of the two dots that were localized (1.2% of trials). We then ran a mixed-design ANOVA with primary array axis as a between-subjects factor, and with "dot distance" (the distance between consecutive localization judgments, in dots) and array size as within-subjects factors. First, we found a significant effect of dot distance, $F(1.634, 65.89) = 23.6$, Greenhouse-Geisser corrected, $p < .001$, $\eta_p^2 = .325$, as there was significantly more overestimation when trials were separated by one (46.8%) versus two (40.1%) or three (35.8%) dots (all pairwise comparisons between conditions, *p*s < = .001). There was also an expected significant main effect of array size, $F(1.345, 65.89) = 86.8$, Greenhouse-Geisser corrected, $p < .001$, $\eta_p^2 = .639$, with the most overestimation for the smallest arrays (small array, +78.2%; medium array, +39.3%, large array, +5.2%). There was a main effect of array axis, $F(1, 49) = 4.71$, $p = .035$, $\eta_p^2 = .088$), with more overestimation along the horizontal (+53.5%) versus vertical main axis (+28.5%). Finally, there was a significant array size by dot distance interaction, $F(3.46, 169.6) = 2.99$, Greenhouse-Geisser corrected, $p = .026$, $\eta_p^2 = .057$, as the increase in overestimation from 3-dots-apart to 1-dot-apart decreased as array size increased (large array, +7.5%, medium array, +10.1%, small array, +15.5%).

Overall, these results provide evidence for overestimation biases with nonbody stimuli, similar to what has been observed with the hand. Furthermore, these overestimation biases are modulated based on the relative location of the two stimuli, with significantly greater overestimation of two consecutive localization judgments when the two localized stimuli are closer in space.

Discussion

We examined whether previously reported biases in localizing landmarks on the hand are due to a distorted body model, or can be explained by an alternative process. We proposed that previously reported biases on the landmark localization task could be caused by a domain-general process in which participants overestimate the distance between consecutive localization judgments of close stimuli. Supporting this hypothesis, we found that participants overestimated the distance between landmark localization judgments of stimuli on the hand, with this overestimation decreasing as the distance between consecutive targets increases (Experiments 1–3). When accounting for this constant overestimation, we did not find evidence for a widening bias along the mediolateral axis of the hand—providing additional evidence against the distorted body model account. However, we did find evidence for contraction of consecutive landmark localization judgments along the distal-proximal hand axis. Given that we did not have any fingertip landmark judgments, yet there was still distal-proximal contraction, this suggests that the observed contraction in previous studies may not be due to a distorted body model. In Experiments 4 and 5, we examined whether overestimation of localization judgments of close stimuli would be observed on a task that does not involve the body at all—reporting the location of dots on a remembered array. First, when examining the mean localization judgments in this task, we found widening of dot localization judgments along the array's axis of elongation—similar to what has been reported with hand landmark judgments. Second, this widening varied depending on the relative distance between the dots, as closer dot arrays led to increased widening. Third, a lag-1 analysis revealed that this bias was caused by a constant overestimation, and that controlling for this constant estimation demonstrated minimal additional bias. Overall, these results provide substantial evidence against the distorted body model account. Instead, the previously observed findings are more likely explained by domain-general bias in spatial localization that cause the observed patterns of performance. Furthermore, we predict that a reanalysis of previous body model studies, taking into account the distance between consecutive localization judgments, would not find evidence for a distorted body model.

What mechanism would result in this pattern of performance? In our experiments, there is strong evidence that participants use the position of their initial localization judgment as a reference point to make their next localization judgment. The memory of the initial localization judgment is inexact, and the estimates of this localization judgment can be characterized with an uncertainty distribution. Huttenlocher, Hedges, and Duncan (1991) proposed the category adjustment model in which memories are encoded at two levels of representation. In the fine-grained level, a particular location is retrieved from a distribution around the mean of the most likely stimulus value. The categorical level includes a distribution of all potential stimulus locations, with boundaries at the extreme values of this distribution. When remembering the location of a stimulus, participants sample from the fine-grained stimulus distribution. However, any samples selected from outside of the categorical boundaries are discarded. This model has been used to explain biases in spatial memory for stimuli near categorical boundaries (see also Huttenlocher, Hedges, Lourenco, Crawford, & Corrigan, 2007).

One possibility is that individuals represent the location of the initial localization judgment as a categorical distribution—a range of potential locations where the initial localization judgment could have been. On any trial in which the first and second localization judgment are not in the same location, there may be a constraint such that the second localization judgment does not occur within the initial localization judgment category. In other words, individuals may be biased to avoid making a second localization judgment in the same location as the first localization judgment when they have clear knowledge that the two localization judgments differ. If so, this would create a bias such that the second localization judgment is not located within the category for the initial localization judgment. According to the category adjustment model, when attempting to localize the second stimulus, participants select from a distribution of potential response locations. Importantly, we suggest that any samples for this second stimulus distribution that fall within the initial localization judgment category are discarded. If so, this would be manifest as a constant overestimation bias. For two consecutive stimuli that are relatively distant (i.e., the second stimulus is outside of the distribution for the initial localization judgment), little to no overestimation bias should be observed. However, consecutive localization judgments that are relatively close in space would be biased, such that the distance between the two judgments would be overestimated. Such a model is consistent with our results, which found a strong relationship between the relative distance of two targets and the amount of overestimation bias. However, we note that this is only one potential explanation, and that other models may also be able to account for our findings.

We argue that our findings are inconsistent with a distorted body model hypothesis. One potential argument against this is that our landmark localization task (Experiments 1–3) only used the knuckles, and not the fingertips as in previous studies. We have yet to directly examine whether results would have been different if participants were instructed to localize both the fingertips and knuckles. However, if there is a distorted body model, these distortions should be evident for the knuckles regardless of whether fingertip landmark judgments are collected or not. A second potential argument is that there may still be a distorted body model, in addition to the overestimation effects demonstrated for nonbody stimuli in our and other experiments (e.g., Saulton et al., 2015). For example, Saulton, Longo, Wong, Bülthoff, and de la Rosa (2016) recently examined biases in landmark localization using a rake, rubber hand, and actual hand. Distortions in perceived size were observed for all three objects, with significantly larger distortions found for the participant's actual hand compared to the rubber hand and rake. Although one could interpret these results as evidence for distortions specific to one's actual hand, an alternative explanation is that the increased uncertainty in proprioceptive estimates led to this result. Given that proprioceptive estimates are relatively noisy compared to vision, drift over time without visual information (Wann & Ibrahim, 1992), and that hands typically move (compared to stationary objects), one possibility is that proprioceptive estimates of a specific hand landmark have more uncertainty than judgments of the remembered position of a stationary rubber hand or rake. If so, given our suggested mechanism, we would predict that noisier modalities would lead to a larger uncertainty estimate for the initial localization judgment, which would lead to increased overestimation for consecutive localization judgments. However, additional research would be necessary to examine whether uncertainty differs in hand versus object landmark judgments.

Contrasting the findings for landmark localization, we did find significant widening for tactile localization judgments in addition to the constant overestimation bias. These results are consistent with other studies that have examined tactile localization judgments made without vision of the hand. For example, Longo et al. (2015) stimulated the dorsal surface of participants' hands that were placed underneath an occluding board, on which participants responded without vision of the hand. Participants demonstrated a significant widening of localization judgments (approximately 70%) along the mediolateral axis of the hand, with no significant distortions along the distal-proximal axis. This bias is not observed in experiments where participants respond on a hand outline (see Mancini, Longo, Iannetti, & Haggard, 2011; Margolis & Longo, 2015). Furthermore, Longo and Haggard (2011) presented two tactile stimuli to the dorsal surface of the left hand, one along the proximodistal hand axis and one along the mediolateral hand axis, and asked participants to judge which distance was longer. Participants demonstrated a consistent bias—distances on the mediolateral axis were judged to be longer than those along the proximodistal axis. These effects were not observed on the glabrous, palmar surface and were consistent regardless of whether the proximodistal axis of the hand was aligned with the short or long axis of the trunk midline. We note that these tactile widening effects are found only on tasks in which individuals are not referencing hand boundaries in making a localization judgment. Various studies have shown that tactile localization judgments reference body part boundaries (see Medina & Coslett, 2016 for a review). One possibility is that these tactile widening biases are only evident when making judgments without referencing body part boundaries, and that localization judgments onto the hand are mapped within these boundaries. It is unclear what mechanism causes such tactile widening distortions. Potential mechanisms include tactile receptive fields that are elongated along the distal-proximal hand axis (Longo & Haggard, 2011; Stevens & Patterson, 1995), uneven distribution of skin surface receptors, or central factors (see Gibson & Craig, 2005 for a discussion). Regardless, our results provide evidence that these tactile distortions are separate from body model distortions.

In summary, our results provide strong evidence against the distorted body model hypothesis. Instead, we found evidence that the remembered location of stimuli, both hand landmarks and dot arrays, are influenced by the location of the previous localization judgment. This results in a bias, such that the location of the second stimulus is an overestimation of the vector from the first to the second localization judgment. This overestimation bias increases when consecutive trials are closer in space. These results may be consistent with a model in which individuals reference and store the location of the initial localization judgment. Participants may be biased to not respond within the potential distribution of the initial localization judgment, resulting in overestimation biases that are modulated by the distance between consecutive localization judgments.

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