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Conceptual distortions of hand structure are robust to changes in stimulus information



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ABSTRACT

Previous studies showed stereotyped distortions in hand representations. People judge their knuckles as farther forward in the hand than they actually are. The cause of this bias remains unclear. We tested whether both visual and tactile information contribute to the bias. In Experiment 1, participants judged the location of their knuckles by pointing to the location on their palm with: (1) a metal baton (using vision and touch), (2) a metal baton while blindfolded (using touch), or (3) a laser pointer (using vision). Distal mislocalisations were found in all conditions. In Experiment 2, we investigated whether judgments are influenced by visual landmarks such as creases. Participants localized their knuckles on either a photograph of their palm or a silhouette. Distal mislocalisations were apparent in both conditions. These results show that distal biases are resistant to changes in stimulus information, suggesting that such mislocalisations reflect a conceptual misrepresentation of hand structure.

1. Introduction

Hands are ubiquitous in our daily lives. It is through the hands that we experience the world around us most directly. They are especially important for goal-directed action and in learning to manipulate objects (Klatzky, Pellegrino, McCloskey, & Doherty, 1989; Reed, Grubb, & Steele, 2006). From infancy, humans use their hands for two primary functions: to acquire information and to manipulate their environments (Jones & Lederman, 2006). Hands are also a valuable source of social knowledge, providing information about other people's intentions (Woodward, 2009) as well as aiding language comprehension (Goldin-Meadow & Wagner, 2005; McNeill, 1992). We use hands to communicate before we learn language. By 11 months, infants can recognize and use pointing gestures (Carpenter, Nagell, & Tomasello, 1998), and show shifts of attention in the direction of dynamic points even earlier (Bertenthal, Boyer, & Harding, 2014; Rohlfing, Longo, & Bertenthal, 2012). A recent study which analyzed data from head cameras worn by infants found that while faces are a dominant visual input during the first year of life, hands emerge as dominant in the second year (Fausey, Jayaraman, & Smith, 2016).

With all the experience we gather through the lifespan, it seems intuitively that we really should know hands like the proverbial “back of our hand”. Recent research, however, has revealed that their representations can be strikingly distorted. For example, in a study by Longo and Haggard (2010) participants were asked to judge the perceived location of landmarks (i.e. knuckles and fingertips) of their occluded left hand. By comparing the relative position of judgments of each landmark, implicit perceptual maps of hand structure were constructed and compared to actual hand structure. These maps were highly distorted in a stereotyped way across people, with the hand represented as wider than it actually is and the fingers as shorter than they actually are. Similarly, the distance between two unseen touches aligned with the medio-lateral hand axis is perceived as substantially larger than the same

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distance aligned with the proximo-distal axis (Green, 1982; Longo & Haggard, 2011). Other studies, involving explicit judgments of body part size have also revealed similar distortions (D'Amour & Harris, 2017; Linkenauger et al., 2015; Longo & Haggard, 2012).

In two recent studies, we have found that people have highly distorted conceptual knowledge of the configuration of landmarks within their hand, believing their knuckles (i.e., the metacarpophalangeal joints) to be substantially farther forward in the hand than they actually are (Longo, 2015; Margolis & Longo, 2015). Longo (2015) asked participants to lay their hand palm-up on a table (in a position in which knuckles are not visible) and to use a long baton to indicate the location on the palm directly opposite the knuckle of each finger using the other hand. Participants consistently judged their knuckles as farther forward in the hand than they actually are, showing a clear distal bias for all fingers aside from the thumb. In the study of Margolis and Longo (2015), similar distal biases were apparent when participants were asked to judge the location of their knuckles by clicking the mouse cursor on an empty silhouette, created from an image of the dorsal side of their hand, presented on a screen in front of them.

In Experiment 3 of Longo (2015), similar biases were also found when participants were asked to judge the location of the knuckles of the experimenter's hand, suggesting that the distortion reflects conceptual knowledge about the configuration of hands in general, rather than self-specific representation of one's own hand. These results show that healthy participants can demonstrate behavior similar to this observed in disorders characterized by distorted body representations such as autotopagnosia, a condition resulting from damage to the left parietal cortex, in which patients are impaired in judgments about the configuration and location of body parts (Buxbaum & Coslett, 2001; Sirigu, Grafman, Bressler, & Sunderland, 1991). Autotopagnosic patients are generally impaired when asked to point to parts of their own body, and are also impaired when asked to point to parts of other people's bodies or mannequins (Gerstmann, 1942; Ogden, 1985; Sirigu et al., 1991). Autotopagnosia is generally thought to reflect damage to a representation called the *body structural description*, which mediates knowledge of the spatial layout of bodies (Corradi-Dell'Acqua et al., 2008; Longo, Azañón, & Haggard, 2010; Schwoebel & Coslett, 2005). The distal biases we recently described (Longo, 2015; Margolis & Longo, 2015), thus, suggest that even in healthy people the body structural description does not provide a fully veridical representation of body configuration, but is systematically distorted in stereotyped ways across people.

Another example of systematic distortions becomes apparent when healthy people are asked to draw a face. A study by Carbon and Wirth (2014) showed that in all drawings the eyes are positioned much higher in the head than they really are. The authors explained this bias by suggesting that people do not take into account the convexity of the forehead. Similarly, Longo (2015) suggested that distal bias in knuckles localization reflects "intuitive anatomy", a naïve belief about the hand structure.

Could these distortions instead reflect a more basic perceptual bias resulting from specific sensory cues present while participants perform the task? One potential interpretation of this effect is that participants, in giving their judgments, were visually influenced by the crease at the base of the fingers on the palmar hand surface, which is substantially farther forward in the hand than the knuckle. However, while responses in Longo (2015) were clearly distal to the actual location of the knuckle, they were also clearly proximal to the crease, suggesting that participants had not simply confused the crease for the knuckle. Furthermore, in Experiment 2 of the study of Longo (2015) similar distal biases were found when participants were blindfolded, suggesting that the bias is not a purely visual bias in the direction of the crease.

Hands are common in our visual experience of the world, but are ubiquitous in touch, in which the hands form a 'fovea' for tactile perception (Mancini et al., 2013). In the study by Longo (2015) participants showed distal biases in knuckles localization on the palm even when blindfolded, providing some indication that immediate vision may not be required to elicit this effect. However, it is not possible to assess how similar in magnitude the biases are considering that the comparison of visual-tactile and tactile-only judgments was between experiments. Therefore, it remains unclear what kind of sensory information affects these distal biases, and how and to what extent visual and tactile cues might affect them. The present study aimed to systematically investigate whether information from different modalities contributes to these biases and whether they are affected by visual cues such as the crease. Experiment 1 used the paradigm of Longo (2015) to investigate the contribution of vision and touch to knuckle mislocalization. Participants judged the location of their knuckles (the metacarpophalangeal joints) by pointing on their palm in three conditions: (1) using a baton on the skin providing both visual and tactile cues (*VisuoTactile* condition), (2) using a laser pointer resulting in only visual cues (*Visual* condition), or (3) using that baton while blindfolded resulting in just tactile cues (*Tactile* condition). Experiment 2 used the paradigm of Margolis and Longo (2015) to directly assess the potential role of the creases at the base of the fingers as a visual cue in producing the bias. Participants localized their knuckles by clicking the mouse cursor on either a photograph of their palm or on a blank white silhouette of the palm, in which visual cues such as the crease were removed.

2. Experiment 1

Experiment 1 tested whether both visual and tactile information contribute to the distorted representation of hand structure we recently described (Longo, 2015). Participants were asked to localize their knuckles by indicating the location on their palm directly opposite to each knuckle. In the *VisuoTactile* condition, participants used a long baton to make their judgments and could see where they were pointing, providing both visual and tactile information about their response. In the *Tactile* condition, participants used the same baton, but were blindfolded, and thus forced to rely on tactile information to make their judgments. In the *Visual* condition, participants used a laser pointer to indicate their response, resulting in similar visual cues to the *VisuoTactile* condition, though tactile information was not present on the palm. If the distal biases in knuckle localization are driven by visual signals, then they should emerge in the *VisuoTactile* and *Visual* conditions, but not in the *Tactile* condition. If the biases are driven by tactile signals, then they should appear in the *VisuoTactile* and *Tactile* conditions, but not in the *Visual* condition. By contrast, if the biases reflect genuine misconceptions about hand structure, they should appear in all three conditions, irrespective of which sensory cues are available.

2.1. Methods

2.1.1. Participants

Twenty participants (mean age \pm SD = 29.9 \pm 13.6, range: 19–75, 13 females) took part in this experiment. Nineteen were right-handed and one person was left-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean: 82; range: –61 to 100). All participants gave informed consent and were paid for their participation. The procedures were approved by the local ethics committee.

2.1.2. Procedure

The experimental procedure was similar to that of Longo (2015). Participants sat with their left hand resting palm up on a table. Based on the results from Longo (2015) who found no significant difference in knuckle mislocalization between left and right hands, we decided to test only the left hand to reduce the length of the experiment. A webcam (Logitech Webcam Pro 9000 HD) was suspended from a tripod directly above the table. On each trial, a photograph (1600 \times 1200 pixels) of the participant's response was taken using a custom MATLAB (Mathworks, Natick, MA) script. A 10 cm ruler on the table allowed conversion between distances defined in pixels and in cm.

The experimenter explained to the participant that their task was to indicate the location on the palm directly opposite to the knuckle “as if you were to drill directly through the hand”. Then the experimenter pointed at the knuckles all the way at the base of the fingers of her own hand (on the dorsal side) to make sure participants understood which landmark they were asked to localize (i.e., the metacarpophalangeal joint). Across trials, participants were asked to localize the knuckles of each of the five fingers of their left hand.

On each trial, the experimenter gave the participant a verbal instruction about which of their knuckles to localize, by naming one of the five fingers. In each condition, participants judged the location of their knuckles by pointing to the location on their palm directly opposite each knuckle. In the VisuoTactile condition, the participant indicated their response using a metal baton for precision (35-cm length and 2-mm diameter) (see Fig. 1A). In the Tactile condition, the participant used the same metal baton while blindfolded. In the Visual condition, the participant used a laser pointer (see Fig. 1B). The diameter of the laser on the solid surface was approximately 2 mm, on the skin the light dispersed to 5–6 mm.

Participants were instructed to be careful and deliberate in their responses, which were unsped. They were free to move the baton or the pointer as much as they liked and to adjust their response until they were satisfied. When the participant indicated verbally that they were happy with their response, the experimenter pressed a button on the keyboard to capture the photograph. To avoid hysteresis effects, participants moved the baton to the right side of the table after each response.

There were six experimental blocks (two blocks of each condition) presented in ABCBBA order, with the order of the first three conditions randomized for each participant. Each block consisted of 25 trials, each including five trials of each finger in random order. To allow calculation of the actual location of each knuckle, at the end of the experiment a photograph was taken of the back of the participant's left hand. To avoid ambiguity in coding, a small black mark was made by the experimenter on each knuckle in the center of the bump formed by each knuckle when the participant made a fist.

2.1.3. Analysis

As in the study of Longo (2015), for each photograph the x–y pixel coordinates were coded for the tip of the finger being judged and for the participant's response (the judged location of the knuckle). From these coordinates, we calculated the distance from the participant's judgment to the location of the fingertip in pixels and then converted this number to centimeters. The actual distance from each knuckle to the fingertip was calculated from the photograph of the back of the hand taken at the end of the experiment. Next, the distal bias was calculated as the difference between the distances from the tip to the responses and the actual distance

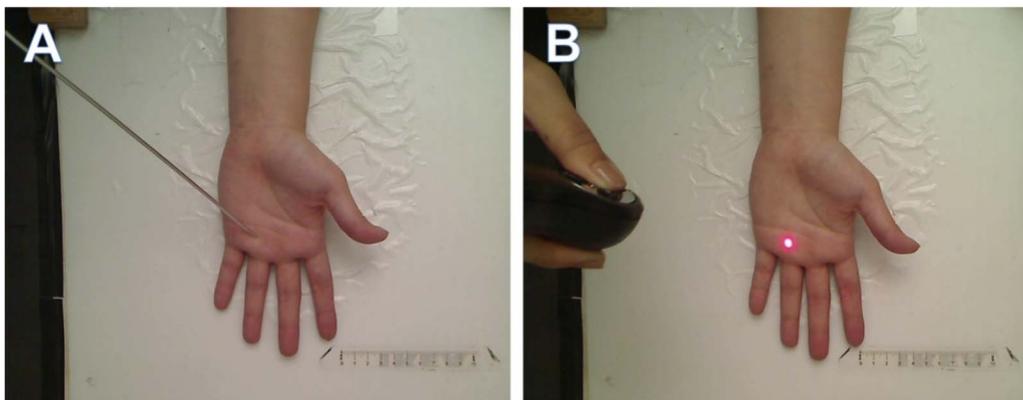


Fig. 1. Conditions in Experiment 1. *Panel A*: In the VisuoTactile and Tactile conditions, participants used a long metal baton to indicate the location on their palm directly opposite each of their knuckles. In the VisuoTactile condition participants could also see their response, whereas in the Tactile condition they were blindfolded. Responses were captured by an overhead camera. *Panel B*: In the Visual condition, participants used a laser pointer to indicate their responses.

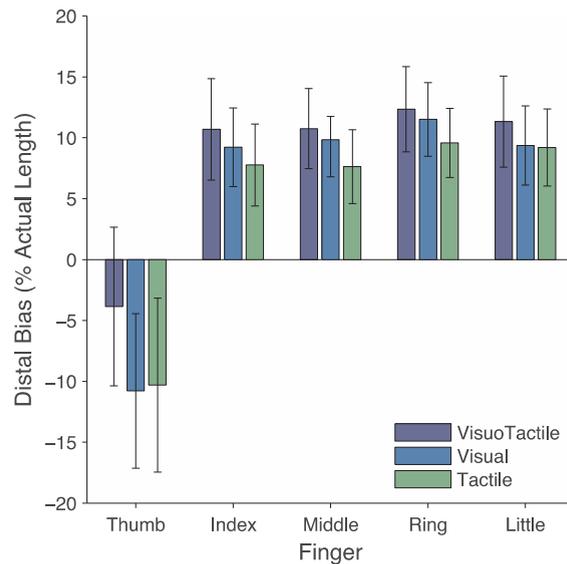


Fig. 2. Results from Experiment 1. Clear distal biases were apparent for all fingers except the thumb. Error bars represent 95% confidence intervals. Positive values indicate a distal bias (too close to the fingertips), negative values indicate proximal bias (too close to the wrist).

between the fingertip and the knuckle location. Finally, this difference (distal bias) was expressed as a percentage of the actual finger’s length. Thus, values greater than 0 indicate that participants judged the knuckle as too far forward in the hand (too close to the fingertip), while values less than 0 indicate that they judged the knuckle as too far back (too close to the wrist).

We decided to focus our analysis on the distal-proximal dimension for two reasons. Firstly, we wanted to keep the analysis as similar as possible to the method used in previous studies investigating distal bias (Longo, 2015; Margolis & Longo, 2015). Secondly, our analysis revealed very little variability in the dimension perpendicular to the finger midline (calculated as the line going through the middle of the tip and the middle of the crease). For each finger we calculated the angle between the midline (defined as a line going through the middle of the tip and the middle of the crease) and the line going from the tip to the response. This angle was on average 1.52° with very small variability (SD: 0.008°), indicating that responses did not deviate much from the midline (M: 0.20 cm, SD: 0.02).

2.2. Results and discussion

Fig. 2 shows distal bias for each finger as a percentage of actual finger length. Consistent with the results of Longo (2015), clear distal biases were apparent for all fingers except the thumb. Participants judged their knuckles to be closer to the fingertips than they really are. Critically, these biases were clearly apparent in all three experimental conditions. Table 1 summarizes the results, presenting distal biases in centimeters and as a percentage of actual finger length.

Collapsing across the five fingers, clear distal biases were found in the VisuoTactile condition (M: 8.25%, $t(19) = 4.24$,

Table 1

The results of Experiment 1: distal biases presented in centimeters and as a percentage of finger’s length.

Condition	Finger	Mean distal bias in cm	SE	Mean distal bias as% of finger’s length	SE
VisuoTactile	Thumb	-0.21	0.20	-3.86	3.32
	Index	0.95	0.19	10.68	2.13
	Middle	1.06	0.17	10.75	1.68
	Ring	1.14	0.17	12.33	1.78
	Little	0.82	0.14	11.33	1.91
Visual	Thumb	-0.64	0.19	-10.78	3.23
	Index	0.81	0.15	9.22	1.65
	Middle	0.97	0.14	9.85	1.38
	Ring	1.06	0.14	11.50	1.55
	Little	0.67	0.12	9.36	1.66
Tactile	Thumb	-0.61	0.22	-10.31	3.64
	Index	0.68	0.15	7.76	1.72
	Middle	0.75	0.15	7.63	1.54
	Ring	0.88	0.13	9.57	1.45
	Little	0.67	0.12	9.19	1.62

$p < .0005$, $d = 1.81$, the Visual condition ($M: 5.83\%$), $t(19) = 3.67$, $p < .002$, $d = 0.95$, and the Tactile condition ($M: 4.77\%$), $t(19) = 2.78$, $p < .02$, $d = 0.62$. This bias was even stronger removing the thumb from the analysis, with clear distal biases in the VisuoTactile condition ($M: 11.27\%$), $t(19) = 7.80$, $p < .00001$, $d = 2.47$, the Visual condition ($M: 9.98\%$), $t(19) = 6.96$, $p < .00001$, $d = 2.20$, and the Tactile condition ($M: 8.54\%$), $t(19) = 4.31$, $p < .0005$, $d = 1.36$. These results clearly replicate the bias in knuckle localization described by Longo (2015), and show that neither visual nor tactile cues are necessary to elicit this effect.

To directly compare the magnitude of biases in the different conditions, we conducted a 3×5 repeated measures analysis of variance (ANOVA) including Condition (VisuoTactile, Tactile, Visual) and Finger (Thumb, Index, Middle, Ring, Little) as within-subjects factors. There was a significant main effect of condition, $F(2, 38) = 6.35$, $p < .005$, $\eta_p^2 = 0.25$, and a significant main effect of finger, $F(4, 76) = 40.93$, $p < .0001$, $\eta_p^2 = 0.68$. There was also a significant interaction between condition and finger, $F(8, 152) = 5.34$, $p < .005$, $\eta_p^2 = 0.22$. A similar ANOVA excluding the thumb revealed a significant main effect of condition, $F(2, 38) = 5.13$, $p = 0.011$, $\eta_p^2 = 0.21$, but no effect of finger, $F(3, 57) = 2.52$, $p = .091$, $\eta_p^2 = 0.12$, nor an interaction, $F(6, 114) = 4.27$, $p = .147$, $\eta_p^2 = 0.09$.

To investigate the effect of condition we collapsed across the four fingers, excluding the thumb. There was a significant difference between the Tactile and VisuoTactile conditions, $t(19) = 3.10$, $p < .01$, $d_z = 0.73$, and a marginal trend for a difference between the VisuoTactile and Visual conditions, $t(19) = 1.87$, $p = .078$, $d_z = 0.47$, but no difference between the Tactile and Visual conditions, $t(19) = 1.49$, $p = .15$, $d_z = 0.33$. Thus, the bias appears to be strongest in the VisuoTactile condition.

For the thumb, there was a significant difference between the Visual and VisuoTactile conditions, $t(19) = 4.43$, $p < .0005$, $d_z = 0.99$, and between the VisuoTactile and Tactile conditions, $t(19) = 2.76$, $p < .02$, $d_z = 0.62$, but not between the Tactile and Visual conditions, $t(19) = 0.22$, $p = .824$, $d_z = 0.05$. Looking at each condition individually, there were significant proximal biases for the thumb in both the Visual condition ($M: -10.78\%$), $t(19) = -3.33$, $p < .005$, $d = 0.75$, and the Tactile condition ($M: -10.31$), $t(19) = -2.83$, $p = .01$, $d = 0.63$, but no significant bias in the VisuoTactile condition ($M: -3.86$), $t(19) = -1.16$, $p = .26$, $d = 0.26$. This general pattern is quite similar to that found by Longo (2015), in which a proximal bias was found for the thumb when only tactile cues were available, but no bias was found when both vision and touch were available, although in that study it was a between experiments comparison.

Across the four non-thumb fingers the magnitude of distal biases was strongly correlated between conditions, with large correlations between the Visual and VisuoTactile conditions, $r(18) = 0.93$, $p < .00001$, the Tactile and VisuoTactile conditions, $r(18) = 0.87$, $p < .00001$, and the Tactile and Visual conditions, $r(18) = 0.79$, $p < .00005$.

These results clearly replicate the distal bias in judging the location of the knuckles reported by Longo (2015). Critically, our results show that neither visual nor tactile cues are necessary to produce this effect. Clear distal biases were found for all non-thumb fingers in the absence of visual cues (i.e., in the Tactile condition) and in the absence of tactile cues (i.e., in the Visual condition). Furthermore, the magnitude of biases in individual participants was strongly correlated between the conditions. These results demonstrate that the mislocalization of the knuckles is not an artifact of any specific sensory signal available during responses. This is consistent with the proposal that these biases result from distortions of modality-independent conceptual knowledge of hand structure (Longo, 2015).

Nevertheless, our results do suggest that the type of information available for making judgments does affect the size of the mislocalization bias. For the non-thumb fingers, the bias was strongest in the VisuoTactile condition in which participants used both vision and touch to make their judgments. Thus, the bias became larger the more information was available. This effect seems counterintuitive, as normally people are expected to be more accurate the more information they have. However, the results of the present study showed that in knuckles localization the opposite seems to be the case. Taken together, our findings strongly suggest that distal biases arise from a common modality-independent cause.

3. Experiment 2

The results of Experiment 1 showed that neither vision nor touch is necessary to elicit distal mislocalization of the knuckles. In Experiment 2, we investigated more directly the potential role of visual cues, such as the crease at the base of each finger, in producing these biases. In order to manipulate visual information, we used the paradigm of Margolis and Longo (2015) in which participants respond by clicking the mouse cursor on an image of their hand. In the study by Margolis and Longo (2015) participants localized their knuckles on an empty silhouette created from an image of the dorsal side of the hand. Here we used the same paradigm but with a silhouette created from an image of participant's palm. Participants were asked to indicate the location directly opposite their knuckles on either a full-colour photograph of their palm (*Photo* condition) or on a silhouette of the palm where visual cues such as crease were removed (*Silhouette* condition). To the extent that distal biases in knuckle localization are driven by the presence of visual landmarks, biases should be larger in the Photo condition than the Silhouette condition.

3.1. Methods

3.1.1. Participants

Twenty participants (mean age \pm SD = 25 ± 8.07 , range: 18–49, 17 females) took part in this experiment. Initial analysis of the data showed that one of the participants confused the ring and index fingers on approximately half of the trials and his data was therefore excluded from further analysis. Of the remaining nineteen participants (mean age \pm SD = 25.26 ± 8.2 , range: 18–49, 17 females), seventeen were right-handed (above 50) and two were mixed-handed (between -50 and 50) as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean: 75; range: -40 to 100). Participants gave informed consent and received payment for

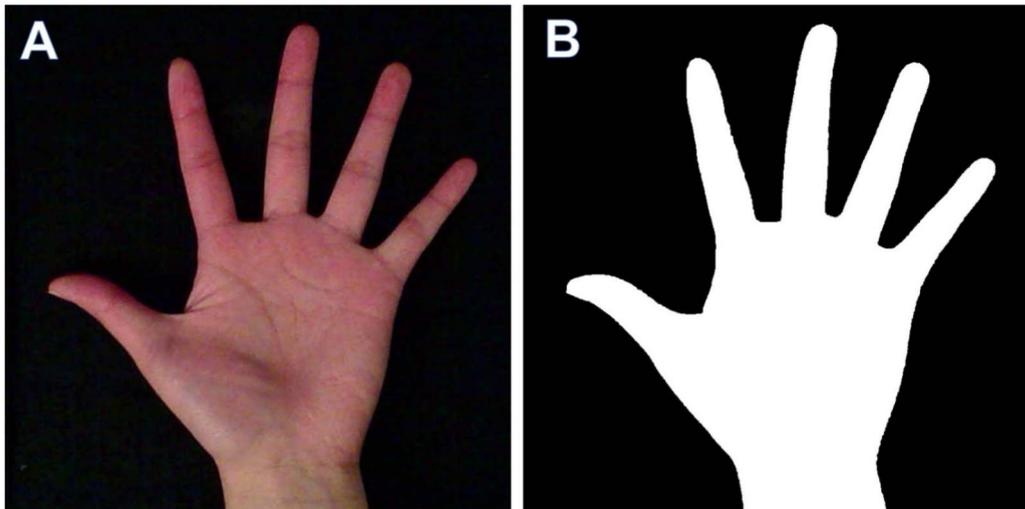


Fig. 3. Conditions in Experiment 2. *Panel A:* Sample stimulus in the Photo condition. A photograph was taken of the participant's hand at the beginning of the session and incorporated into the experimental script. *Panel B:* Sample stimulus in the Silhouette condition. The silhouette was made directly from the photograph of each participant's hand using the GNU Image Manipulation Program. The two hands thus had exactly the same size, posture, and overall contour. In both conditions participants localized their knuckles by clicking the mouse cursor (a cross) on the corresponding location of the hand image.

their participation. The procedures were approved by the local ethics committee.

3.1.2. Procedure

At the start of the experiment, a photograph of the palm of the participant's left hand against a black background was taken by a webcam (Logitech Webcam Pro 9000 HD) suspended from a tripod directly above the table. A ruler was placed next to participant's hand and included in the photograph to allow conversion from pixels to centimeters later in the analysis. This photograph was then cropped and edited in the GNU Image Manipulation Program (GIMP, version 2.8.8) to create two images (800 pixels \times 800 pixels) that were identical in size, shape and location of the hand (see Fig. 3). The ruler was not included in the final images. The second image was additionally edited using the Threshold tool in GIMP to obtain a white silhouette of participant hand on a black background with cues such as creases removed from the image (see Fig. 3B). While the experimenter was editing the pictures the participant filled in the handedness questionnaire.

Next, the experimenter explained that the task involved identifying the location directly opposite to the knuckles on either a photograph or a silhouette of the participant's palm. As in Experiment 1, the experimenter explained that we were interested in the knuckle all the way at the base of the finger (i.e., the metacarpophalangeal joint), and pointed at the knuckles all the way at the base of the fingers of her own hand (on the dorsal side) to make sure the participant understood which landmark they were being asked to localize.

During the task, on each block either the cropped photograph of the palm of the participant's hand (Photo condition) or the silhouette (Silhouette condition) was shown under control of a custom MATLAB script using Cogent Graphics (developed by John Romaya, Laboratory of Neuroscience, Wellcome Department of Imaging Neuroscience, University College London) and the participant was asked to localize their knuckles. The size of the image presented on the screen roughly matched the actual size of the participant's hand. On each trial, a written instruction was shown at the bottom of the screen, indicating one of the fingers so that the participant knew which knuckle to localize. The participant indicated their response by clicking the mouse cursor (a thin cross) at the corresponding location on the hand image. After each response, the mouse cursor appeared again at a random location on the monitor to reduce hysteresis and make responses as independent from each other as possible.

There were four blocks (two blocks of the photograph and two blocks of the silhouette) presented in ABBA order, with the first condition counterbalanced across participants. Each block consisted of 25 trials, each including five trials of each finger in random order. At the end of the experiment, a photograph was taken of the back of the participant's left hand to allow calculation of actual knuckle location. As in Experiment 1, to avoid ambiguity in coding of knuckle location, a small black mark was made by the experimenter on each knuckle.

3.1.3. Analysis

On each trial, the x–y pixel coordinates of the response (i.e., the judged location of the knuckle) were recorded. During the analysis, the experimenter coded the pixel coordinates of the tip of each finger on the monitor as they were shown to each participant. Then, from these coordinates, the distance from the tip to the response was calculated for each trial and converted to centimeters using the ruler from the original photograph. As in Experiment 1, the actual distance from each knuckle to the fingertip was calculated from the photograph of the back of hand taken at the end of the experiment and converted to centimeters. Next, the distal bias was calculated as the difference between these two distances as a percentage of actual distance, as in Experiment 1.

Table 2
The results of Experiment 2: distal biases presented in centimeters and as a percentage of finger's length.

Condition	Finger	Mean distal bias in cm	SE	Mean distal bias as% of finger's length	SE
Silhouette	Thumb	-0.01	0.14	-0.31	2.37
	Index	1.15	0.14	12.90	1.52
	Middle	1.56	0.17	15.54	1.58
	Ring	1.45	0.17	15.70	1.72
	Little	1.31	0.14	17.88	1.86
Photo	Thumb	0.02	0.14	0.37	2.42
	Index	1.23	0.12	13.86	1.24
	Middle	1.66	0.15	16.60	1.31
	Ring	1.51	0.16	16.32	1.61
	Little	1.32	0.13	18.03	1.67

Again, for each finger we calculated the angle between the midline and the line going from the tip to the response ($M: 1.52^\circ$, $SD: 0.007^\circ$), to show that responses did not deviate much from the midline ($M: 0.19$ cm; $SD: 0.02$).

3.2. Results

In both conditions, clear distal mislocalizations of the knuckles were found for all fingers except the thumb (Table 2). Fig. 4 shows this distal bias as a percentage of actual finger length. This effect was significant for all four non-thumb fingers (all p values < .0001). Across all fingers, the distal bias was significant for both the Silhouette condition ($M: 12.34\%$), $t(18) = 8.83$, $p < .00001$, $d = 2.03$, and the Photo condition ($M: 13.04\%$), $t(18) = 10.64$, $p < .00001$, $d = 2.44$. As in Experiment 1, the effect was stronger after removing the thumb from the analysis, with clear distal biases in both the Silhouette condition ($M: 15.51\%$), $t(18) = 10.11$, $p < .00001$, $d = 2.32$, and the Photo condition ($M: 16.20\%$), $t(18) = 12.28$, $p < .00001$, $d = 2.82$.

We conducted an ANOVA including Condition (Silhouette, Photo) and Finger (Thumb, Index, Middle, Ring, Little) as within-subjects factors. There was a significant main effect of finger, $F(4, 72) = 31.00$, $p < .001$, $\eta_p^2 = 0.63$, reflecting the gross difference between the thumb and the other fingers. There was, however, no significant interaction between condition and finger, $F(4, 72) = 0.50$, $p = .736$, $\eta_p^2 = 0.03$. There was also no significant main effect of condition, $F(1, 18) = 3.10$, $p = .095$, $\eta_p^2 = 0.15$.

A subsequent ANOVA in which we removed the thumb from the analysis, showed, unlike Experiment 1, a significant main effect of finger, $F(3, 54) = 6.25$, $p = .001$, $\eta_p^2 = 0.26$, with the magnitude of distal bias increasing from the index finger to the little finger. Again, there was no main effect of condition, $F(1, 18) = 2.89$, $p = .107$, $\eta_p^2 = 0.14$, nor a significant interaction, $F(3, 54) = 1.89$, $p = .142$, $\eta_p^2 = 0.10$. There was a strong correlation between the amount of distal bias on the non-thumb fingers between the two conditions, $r(17) = 0.97$, $p < .00001$. These results suggest that participants did not use creases as landmarks in their judgments of knuckle location.

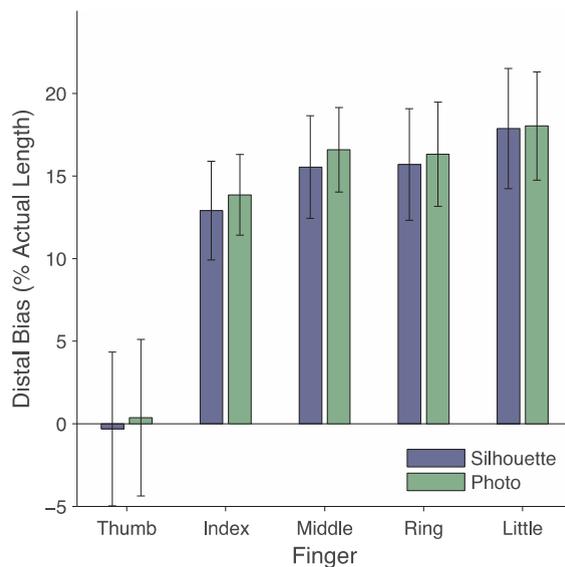


Fig. 4. Results from Experiment 2. Clear distal biases were apparent for judgments of the location of knuckles of all the fingers except the thumb. These biases were clearly apparent in both the Photo and Silhouette conditions. No significant differences between the two conditions were found. Error bars represent 95% confidence intervals. Positive values indicate distal bias (too close to the fingertip), negative values indicate proximal bias (too close to the wrist).

4. General discussion

In both experiments, clear mislocalizations of the knuckles were found, of generally similar magnitude across conditions. The results of Experiment 1 showed that people misjudge the location of the knuckles whether they are asked to make the judgment using both vision and touch, or vision and touch separately. These results indicate that neither vision nor touch is necessary to elicit these biases. Furthermore, the results of Experiment 2 showed that responses do not appear to be influenced by visual cues such as the creases at the base of the fingers on the palm. In both experiments, biases in all conditions were strongly correlated. These results replicate our recent findings of systematic mislocalization of the knuckles (Longo, 2015; Margolis & Longo, 2015) and extend them by providing clear evidence showing the robustness of the effect to differences in sensory cues available for response and the nature of the task.

The study by Margolis and Longo (2015) showed distal biases in knuckles localization when participants were localizing their knuckles on an empty silhouette created from an image of the back of the hand. Here, we show that similar biases occur when participants are presented with a silhouette of the palm, suggesting that these biases are not specific to one side of the hand but rather reflect a more general misconception about the location of the knuckles.

Furthermore, our findings suggest that distal biases arise from a common, modality-independent cause. These results show that the distal bias is resistant to changes in the stimulus information and does not rely on any specific stimulus cue or even single sensory modality, suggesting that such mislocalisations reflect a conceptual misrepresentation of hand structure.

Most previous studies of the body structural description have been in the context of patients with autotopagnosia (e.g., Buxbaum & Coslett, 2001; Ogden, 1985; Sirigu et al., 1991) or finger agnosia (e.g., Anema, Overvliet, Smeets, Brenner, & Dijkerman, 2011; Kinsbourne & Warrington, 1962). Several recent studies, however, have investigated the body structural description in healthy people (e.g., Corradi-Dell'Acqua et al., 2008, 2009; Rusconi, Gonzaga, Adriani, Braun, & Haggard, 2009; Rusconi et al., 2014; Tamè, Dransfield, Quettier, & Longo, 2017). In each of these studies, however, the focus has been on identifying its neural bases (e.g., Di Vita, Boccia, Palermo, & Guariglia, 2016), rather than revealing its representational content. Our results suggest there may be interesting deviations from actual body structure in the normal body structural description. Importantly, however, we are not suggesting that our participants showed evidence of a mild form of autotopagnosia. It is not the case that our participants were unable to perform the task or gave judgments which were random or disorganized. On the contrary, localization judgments were precise and highly structured. Yet these judgments were also systematically distorted, in a highly consistent and stereotyped way across people. Understanding the nature, extent, and functional role of these distortions is an important goal for future research.

The distortions we show for the body structural description contribute to a growing literature showing that far from being a sure sign of pathology, distorted body representations are a normal part of healthy cognitive life (for a recent review see Longo, 2017). As mentioned in the introduction, recent results have revealed large and stereotyped distortions underlying perceptual abilities including position sense (e.g., Ferrè, Vagnoni, & Haggard, 2013; Longo & Haggard, 2010, 2012; Lopez, Schreyer, Preuss, & Mast, 2012), tactile distance perception (e.g., Anema, Wolswijk, Ruis, & Dijkerman, 2008; Longo & Haggard, 2011; Taylor-Clarke, Jacobsen, & Haggard, 2004), localization of somatosensory stimuli (e.g., Mancini, Longo, Iannetti, & Haggard, 2011; Medina, Tamè, & Longo, *in press*; Trojan et al., 2006), and even more abstract processes such as the conscious body image (e.g., Fuentes, Longo, & Haggard, 2013; Linkenauger et al., 2015; Longo & Haggard, 2012).

The present results showing distal mislocalization of the knuckles fit within this general pattern, but also have interesting potential connections to other distortions. For example, the fact that people think their knuckles are farther forward in their hand than they actually are provides a potential explanation for the underestimation of finger length seen in body representations underlying position sense (Longo & Haggard, 2010) and explicit judgments of finger length (Longo & Haggard, 2012). In a recent study, we found that the magnitude of knuckle mislocalization correlated across participants with underestimation of finger length in a proprioceptive localization task, but not with explicit judgments of finger length where participants compared the perceived size of parts of their finger with a line visually presented on a monitor (Longo, Mattioni, & Ganea, 2015). This suggests important functional connections between different types of body representation. The number and nature of distinct body representations has been a highly controversial issue, with little consensus (for discussion of this issue, see Kammers, Mulder, De Vignemont, & Dijkerman, 2009; Longo et al., 2010; Medina & Coslett, 2010; Schwoebel & Coslett, 2005). Distortions of representations provide a potential means for differentiating between body representations based on the nature and magnitude of their distortions, and for investigating functional relations between different representations.

Our hands are an ever-present part of our perceptual experience starting from early childhood (Fausey et al., 2016), and an important source of information about the world. It may thus seem odd, or even incredible, that our knowledge of their structure is so systematically distorted. This is especially true since joints, such as the knuckles, are frequently taken to be especially critical for providing spatial structure to the body (Bermúdez, 1998), reference points for touch (Boring, 1942; Cholewiak & Collins, 2003; Weber, 1834/1996), and boundaries for categorical perception on the body (de Vignemont, Majid, Jola, & Haggard, 2009; Le Cornu Knight, Longo, & Bremner, 2014). Hand shapes inform perceivers about the properties of objects (Gibson, 1962; Klatzky et al., 1989) and prioritize spatial attention (Reed et al., 2006). It may be that hands direct attention to objects rather than to themselves. As the Chinese proverb goes, “When the finger is pointing at the sky, only the fool looks at the finger.”

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