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RESEARCH ARTICLE

Whole-hand perceptual maps of joint location

Kasia A. Myga[1] · **Klaudia B. Ambroziak**[1] · **Luigi Tamè**[1,2] · **Alessandro Farnè**[3,4,5,6] · **Matthew R. Longo**[1]

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Abstract

Hands play a fundamental role in everyday behaviour. Nevertheless, healthy adults show striking misrepresentations of their hands which have been documented by a wide range of studies addressing various aspects of body representation. For example, when asked to indicate the location within the hand of the knuckles, people place them substantially farther forward than they actually are. Previous research, however, has focused exclusively on the knuckles at the base of each finger, not considering the other knuckles in the fingers. This study, therefore, aimed to investigate conceptual knowledge of the structure of the whole hand, by investigating judgements of the location of all 14 knuckle joints in the hand. Participants localised each of the 14 knuckles of their own hand (Experiment 1) or of the experimenter's hand (Experiment 2) on a hand silhouette. We measured whether there are systematic localisation biases. The results showed highly similar pattern of mislocalisation for the knuckles of one's own hand and those of another person's hand, suggesting that people share an abstract conceptual knowledge about the hand structure. In line with previous reports, we showed that the metacarpophalangeal joints at the base of the fingers are judged as substantially father forward in the hand than they actually are. Moreover, for the first time we showed a gradient of this bias, with progressive reduction of distal bias from more proximal to more distal joints. In sum, people think their finger segments are roughly the same, and that their fingers are shorter than they are.

Keywords Body representation · Conceptual knowledge · Hand · Metacarpophalangeal joints

Humans are busy with their hands and fingers even in utero (De Vries et al. 1985; Sparling et al. 1999). Our hands attract our attention from infancy. Babies as old as 3 months spent time staring at (Huang et al. 2019) and exploring (Piaget 1952) their hands in motion. Hands emerge as a dominant sensory input in the second year of human life (Fausey et al. 2016). Hands serve us for goal-directed action, grasping, object manipulation, and allow us fine dexterous movements (Gibson 1962; Klatzky and Lederman 1992). Thus, hands are the source through which we explore and learn about the environment. Moreover, hand gestures support communication (Goldin-Meadow and Wagner 2005). Children produce hand gestures prior to acquiring language skills and verbally referring to people, objects or places (Iverson and Goldin-Meadow 2005). In adults, hand gestures convey how they think (Goldin-Meadow 2003; McNeill 1992).

One might expect that such great familiarity with our hands would ensure accurate representation of the hand. After all, we use the expression 'to know something like the back of our hand' to express depth of expertise in a given matter. Recent studies, however, have shown that this assumption is far from being true. Healthy adults show striking misrepresentations of their hands which have been documented by a wide range of studies addressing various aspects of body representations, including: position sense (e.g., Longo and Haggard 2010; Longo 2014; Ganea and

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✉ Kasia A. Myga
kasia.a.myga@gmail.com

[1] Department of Psychological Sciences, University of London, Malet Street, Bloomsbury, London WC1E 7HX, UK

[2] School of Psychology, University of Kent, Keyenes College, Canterbury CT2 7NO, UK

[3] Integrative Multisensory Perception Action & Cognition Team—ImpAct, Lyon Neuroscience Research Center, INSERM U1028, CNRS U5292, Lyon, France

[4] Claude Bernard University Lyon 1, 43 Boulevard du 11 Novembre 1918, 69100 Villeurbanne, France

[5] Hospices Civils de Lyon, Neuro-immersion, Villeurbanne, Lyon, France

[6] Centre for Mind/Brain Sciences, University of Trento, Corso Angelo, Corso Bettini, 31, 38068 Rovereto, TN, Italy

Longo 2017; Coelho et al. 2017; Peviani and Bottini 2018), tactile distance perception (e.g., Longo and Haggard 2011; Longo and Golubova 2017; Fiori and Longo 2018), tactile localisation (e.g., Mancini et al. 2011; Steenberger et al. 2012; Medina et al. 2018), and the conscious body image (e.g., Longo and Haggard 2012a, b; Linkenauger et al. 2015, 2017; Sadibolova et al. 2019). Such perceptual misrepresentations may be even stronger during development, evolving into adulthood (Cardinali et al. 2019; Giurgola et al. 2020). Thus, the intimate familiarity we have with our hands, does not imply that our perception of the hand veridically reflects its true physical structure.

Recent research has also suggested that not only is our immediate perception of the hand and stimuli on the hand distorted, but that more abstract conceptual knowledge about hand structure may also be systematically biased. Longo (2015a, b) asked participants to use a long baton to indicate the location on their palm directly opposite the knuckle at the base of each finger (i.e., the metacarpophalangeal joints). Participants consistently judged their knuckles as being substantially farther forward in the hand than they actually were. Two other studies (Margolis and Longo 2015; Longo et al. 2015a, b, c) found similar results when using a task in which participants localised their knuckles by clicking a mouse cursor on a silhouette of their hand. Such a result was consistent across different type of responses used by participants suggesting that the bias is not a motor control artefact. Ambroziak et al. (2018) investigated whether any specific sensory signal drives this bias by asking participants to indicate the location of their knuckles using a long baton touching directly their skin with eyes open (Visuo-Tactile Condition), (2) while blindfolded (Tactile Condition), or (3) using a laser pointer instead of a metal baton with their eyes open (Visual Condition). In all three cases, a similar stereotyped pattern of distal biases was found, suggesting that these distal biases are not related to any specific sensory signal. Furthermore, Longo (2015a, b) found very similar biases when participants made judgments about the location of the knuckles of their own hand or of the experimenter's hand. Collectively, these results indicate systematic distortions of conceptual knowledge of hand structure.

The source of these distortions remains uncertain. Several clinical studies have found that knowledge of human bodies can be selectively impaired or spared following stroke (Coslett et al. 2002; Kemmerer and Tranel 2008; Laiacona et al. 2006). Other studies have documented a condition called autotopagnosia, in which patients are impaired in pointing to parts of their body and in judging the spatial relation and configuration between body parts (Buxbaum and Coslett 2001; Gerstmann 1942; Schwoebel and Coslett 2005; Sirigu et al. 1991), not only for oneself, but also for other people's bodies and mannequins (Gerstmann 1942; Ogden 1985; Sirigu et al. 1991; Buxbaum and Coslett 2001). Autotopagnosia is thought to be related to damage to a body representation known as the *body structural description*, which has been localised by neuroimaging studies to the left posterior parietal cortex (Corradi-Dell'Acqua et al. 2008; Felician et al. 2004; Rusconi et al. 2014), in line with the location of lesions that cause autotopagnosia. The mislocalisation of the knuckles described above may reflect systematic distortions of the body structural description, though very few studies have attempted to investigate the actual content of this representation in healthy individuals.

Notably, autotopagnosia generally affects the entire body, rather than specific parts (Kinsbourne, 1998), with the one intriguing exception of finger agnosia (Kinsbourne and Warrington 1962). This raises the possibility that the hand may be a distinct semantic domain from the rest of the body, in line with recent work showing that the hand appears to be a distinct category within the visual system (Bracci et al. 2010, 2012). To date, distortions of conceptual knowledge of hand structure have only been shown for the knuckles at the very base of each finger (i.e., the metacarpophalangeal joint). It, therefore, remains unclear whether such biases are an idiosyncratic aspect of that specific landmark, or reflective of a more general pattern of misrepresentation of hand structure.

Joints are thought to be critical for the emergence of spatial structure in bodily experience (Bermúdez 1998). They play a key role in segmenting the body for lexical naming (Andersen 1978; Brown 1976; McClure 1975), provide categorical boundaries for tactile distance estimates (de Vignemont et al. 2009; Le Cornu Knight et al. 2014; Le Cornu Knight et al. 2017; Le Cornu Knight et al. 2020), and serve as reference points for tactile localisation (Cholewiak and Collins 2003; Weber 1834/1996; Weigel et al. 2017). While the metacarpophalangeal joints at the base of the fingers are the only ones that form lexical boundaries (at least in English), there are two additional joints in each of the four fingers (i.e., the proximal and distal interphalangeal joints) and one interphalangeal joint in the thumb (Lewis 1989; Owen 1849/2007). To our knowledge, no study has investigated people's intuitions about the locations of these other joints.

This study, therefore, aimed to investigate conceptual knowledge of hand structure in a more detailed manner than previous research by investigating judgments of the location of all 14 knuckle joints in the hand. It is possible that the distortions reported in previous studies for the metacarpophalangeal joints to be localised too far forward in the hand are an idiosyncrasy of these joints, perhaps related to the fact that they extend quite low into the hand beyond the skin connecting adjacent fingers. On the other hand, the fact that the metacarpophalangeal joints are lexically-coded (i.e., by separating the 'fingers' from the 'hand'), whereas the interphalangeal joints are not, may also be relevant, although this would most naturally be a reason for the representation of the metacarpophalangeal joints to be more, rather than less, accurate. Alternatively, it is also possible that distal biases are a general feature of the conceptual representation of hand structure, in which case they should be found for all the joints. We thus asked participants to localise each of the 14 knuckles of their own hand (Experiment 1) or of the experimenter's hand (Experiment 2) on a hand silhouette and measured whether there are systematic localisation biases.

Experiment 1

In Experiment 1 we investigated whole-hand perceptual maps of joint localization.

Participants were asked to localise knuckles of their hand on the white silhouette representing their palm, with anatomical characteristics such as creases removed.

Method

Participants

Twenty individuals participated in the first experiment. One participant showed unsystematic confusions of knuckles and fingers and was removed from further analysis. Of the remaining nineteen participants (M = 26.4 years, SD = 7.6, range 18–48, 12 females), 16 were right-handed (above 50), one was ambidextrous (between − 50 and 50) and two were left-handed (below − 50) as assessed by the Edinburgh Handedness Inventory (EHI: Oldfield 1971; mean: 63.9; range − 75 to 100). All participants gave written informed consent and were paid for their participation. The procedures were approved by the Department of Psychological Sciences ethics committee at Birkbeck, University of London.

Procedures

The experimental procedures were similar to those of Margolis and Longo (2015) and Ambroziak et al. (2018). At the start of the experiment, a photograph of the participant's left palm against a black background was taken using a 16-megapixel mobile phone camera (4608 × 3456 pixels), Samsung Galaxy A5(2017). A ruler was placed next to the participant's hand and captured in the photograph to allow conversion from pixels to centimetres (cm) later in the analysis. This photograph was then edited using the GNU Image Manipulation Program (GIMP, version 2.8.8). It was first cropped so that the image included the ruler and the hand, extending 1–2 cm below the wrist. The photograph was then resized and cropped to 800 × 800 pixels. This edited photograph was then used to create the stimulus: a white hand silhouette with creases and landmarks removed, against the black background, using the Threshold Tool in GIMP (see Fig. 1). While the researcher edited the photographs, the participant completed the EHI.

The participant sat in front of a 24-inch monitor at a distance of approximately 45 cm. An occluding board was placed above the participant's hands so that no visual cues of hand anatomy were available. The experimenter explained that the task required the participant to judge the location

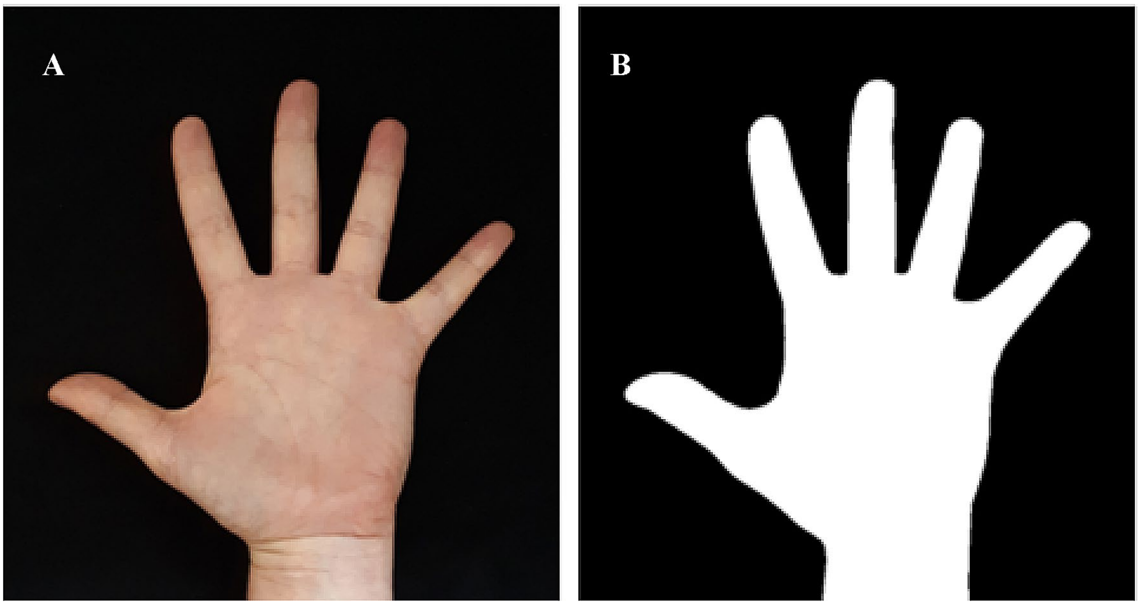

Fig. 1 Stimulus creation. At the start of each experiment, a photograph of the participant's left palm against a black background was taken and resized to 800 by 800 pixels (Panel **a**). This image was then edited to create a silhouette (Panel **b**) without internal detail about hand features

of each of the knuckles of their left palm on the silhouette as if they could see through the knuckles to the dorsum of the hand. To make sure that participants understood which landmarks they were being asked to judge, the experimenter demonstrated on her own hand by making a fist.

Across trials, participants were asked to localise all 14 knuckles: two for the thumb and three for each of the four non-thumb fingers. Before the start of the experiment, the researcher explained to the participant that the distal interphalangeal joint in each finger would be labelled '1st', the middle joint '2nd'', and the metacarpophalangeal joint as '3rd'. For the thumb, the interphalangeal joint was labelled '1st' and the metacarpophalangeal joint as '2nd'. A written instruction indicating which knuckle to localise (e.g., 'Ring Finger 1st') appeared on the screen under the image on each trial. Participants used a crosshair controlled by the mouse to judge the location of each knuckle. To avoid hysteresis effects and make the responses as independent from each other as much as possible, on each trial the mouse cursor appeared in a different, random location on the screen. The size of the silhouette was approximately life size.

During each trial, a silhouette of the participant's hand appeared on the computer screen, 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 instruction indicating which knuckle to localise appeared under the silhouette. Each landmark was judged twice in each block, six times in total. There were three blocks each consisting of 28 trials formed by 2 repetitions of each landmark presented in random order.

At the end of each experiment, a photograph of the dorsum of the participant's left hand was taken to allow calculation of the actual location of each knuckle. To avoid ambiguity in coding knuckle location from photographs, each knuckle was marked with a black pen.

Analysis

Initial analysis of the data showed that one participant systematically confused the little finger with the index finger so this data was re-labelled and included in the analysis. Another dataset was removed from the analysis due to randomness of the answers.

The logic of the analysis was similar to that used by Longo (2015a, b) and Ambroziak et al. (2018). For each response, we calculated the distance in pixels from the participant's response to the tip of the finger being judged. The ruler that appeared in the original image of the hand allowed this distance to be converted into cm on the hand. The actual distances from each knuckle to the fingertip as well as actual distances between each knuckle (i.e., segment lengths) were calculated from the photograph of the dorsum of the hand taken at the end of the experiment.

Next, distal bias was calculated as the difference between these two distances and actual knuckle location, as a percentage of the actual distance of the knuckle from the fingertip. Values greater than 0 indicate that participants judged the knuckle location as too close to the fingertip (i.e., distal bias), whereas values less than zero indicate that the judged location of the knuckles was too close to the wrist (i.e., proximal bias).

Unlike previous studies which only measured a single knuckle location, the present study allows estimation of the length of each segment of the finger by comparing the judged locations of pairs of knuckles. The length of the proximal phalanx was calculated as the distance between the metacarpophalangeal and proximal interphalangeal joints. The length of the middle phalanx was calculated as the distance between the proximal and distal interphalangeal joints. The length of the distal phalanx was calculated as the distance between the distal interphalangeal joint and the fingertip. Each of these distances was calculated both for the participant's actual hand and for the judgments of the location of each knuckle (Note that no explicit judgment of the location of the fingertip was collected, since this was visually specified in the silhouette). For each segment we calculated percent overestimation as 100 × (Judged Length—Actual Length)/Actual Length. Positive values indicated that participants judged the distances as larger than they really are, and negative values indicated underestimation of the distances between the two landmarks.

A two-way (knuckle × finger) repeated measures analysis of variance (ANOVA) was run to determine whether there were statistically significant differences in the distal bias in localising three different knuckles on four fingers of the hand (thumb excluded), followed by simple main effects analysis. A two-way (segment × finger) repeated measures ANOVA was run to determine whether there were significant differences in the percent segment overestimation of the segment lengths on four non-thumb fingers. Where Mauchley's test indicated a violation of the sphericity assumption, the Greenhouse–Geisser correction was applied.

Mean distal bias and mean percent segment overestimation were compared to zero using one-sample *t* tests.

Results and discussion

Distal biases

The left panel of Fig. 2 shows mean distal biases for all 14 knuckles. The positive values indicate that the knuckles are perceived more distally compared to their actual location, (i.e., closer to the fingertip). Consistent with previous studies (Longo 2015a, b; Margolis and Longo 2015; Ambroziak

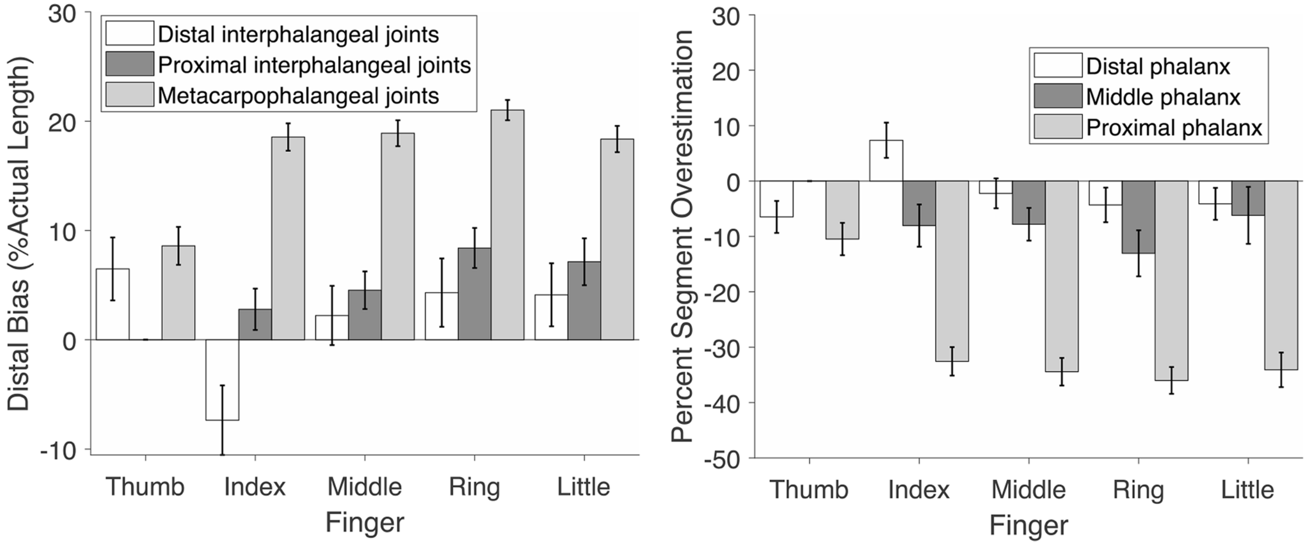

Fig. 2 Results from Experiment 1. *Left panel*: Distal bias for each joint in each finger. There were clear distal biases for the third knuckle, replicating previous results (Longo 2015a, b; Margolis and Longo 2015; Ambroziak et al. 2018). These biases are substantially reduced (proximal interphalangeal joint) or eliminated (distal interphalangeal joint). Thumb's only one interphalangeal join is represented as distal interphalangeal joint. Error bars represent standard error. *Right panel:* Percent Segment Overestimation. Negative values indicate underestimation of the segment length. In the case of thumb only distal and proximal segments are shown. Error bars represent standard error

et al. 2018), clear distal biases for the metacarpophalangeal joints were apparent for all non-thumb fingers. More modest distal biases were also observed also for the thumb, in some contrast to previous studies which have either found slight proximal biases or close to no overall bias. Importantly, we show for the first time a full implicit map of the perceived configuration of all the knuckles of the hand. These distal biases are substantially reduced for the proximal interphalangeal joint and essentially eliminated for the distal interphalangeal joint (with the exception of the index finger).

Collapsing across four non-thumb fingers, clear distal biases were apparent for the metacarpophalangeal joint at the base of the finger (*M*: 19.204% of finger length), $t(18)=20.481$, $p<0.0001$, $d_z=4.699$, in line with previous studies. Furthermore, mean distal bias for the proximal interphalangeal joint was also significantly different from zero (*M*: 5.715% of finger length), $t(18)=3.565$, $p=0.002$, $d_z=0.818$. In contrast, no significant bias was apparent for the distal interphalangeal joint *(M*: 0.823% of finger length*)*, $t(18)=0.314$, $p=0.757$, $d_z=0.072$.

An ANOVA was run to analyse the data with repeated-measures factors knuckle (metacarpophalangeal, proximal interphalangeal, distal interphalangeal) and finger (index, middle, ring, little). There were significant main effects of knuckle, $F(2, 36)=38.417$, $p<0.001$, $\eta_p^2=0.681$, and of finger, $F(3, 54)=8.512$, $p<0.001$, $\eta_p^2=0.321$. These main effects were modulated by a significant interaction between knuckle and finger, $F(3.890, 70.011)=7.692$, $p<0.001$, $\varepsilon=0.60$, $\eta_p^2=0.299$.

To explore this interaction, we conducted simple main effects analyses investigating the effect of finger on each of the three knuckles separately. For the metacarpophalangeal joint, there was no significant effect of finger on distal bias, $F(2.154, 38.769)=2.550$, $p=0.087$, $\eta_p^2=0.124$. This is consistent with the results of other studies using this paradigm, which have generally found similar distal biases for all the (non-thumb) fingers. In contrast, there were significant effects of finger on distal bias for both the proximal interphalangeal joint, $F(3, 54)=4.528$, $p=0.007$, $\eta_p^2=0.201$, and the distal interphalangeal joint, $F(3, 54)=11.326$, $p<0.001$, $\eta_p^2=0.386$. For both the interphalangeal joint, distal bias in general decreased from the ulnar (little finger) to radial (index finger) side of the hand.

Finger length

A number of recent studies have found that people underestimate the length of their fingers, both in tasks, where length is inferred from the proprioceptive localisation of knuckles and fingertips (e.g., Longo and Haggard 2010; Mattioni and Longo 2014) and in explicit judgments of finger length using a visual comparison task (e.g., Longo and Haggard 2012a, b; Tamè et al. 2017a, b). The distal mislocalisation of knuckle location within the hand could be an explanation for such underestimation of length, as noted by Longo et al. (2015b). That study measured distal bias of knuckle localisation and underestimation of finger length using both proprioceptive localisation and explicit length estimates. Distal mislocalisation of knuckles correlated across participants with underestimation in the proprioceptive task, but not explicit judgments.

Given that the current study measured localisation of all three knuckles, we can estimate the implicitly judged length of each of the three segments of the finger by comparing the distances between judged locations of adjacent knuckles. We, therefore, calculated the length of each segment and then compared it to the actual length of that segment on the participant's actual hand, expressing these values as percent overestimation of actual size. The length of the proximal segment was calculated as the distance between the metacarpophalangeal and proximal interphalangeal joints. The length of the middle segment was calculated as the distance between the proximal and distal interphalangeal joints. The length of the distal segment was calculated as the distance between the distal interphalangeal joint and the fingertip. In the case of the thumb, there were only proximal and distal segments.

The overestimation of segment lengths is shown in the right panel of Fig. 2. Positive values indicate overestimation of length and negative values indicate underestimation. It is apparent that apart from the first segment of the index finger, all the segment lengths were underestimated, with the largest underestimation of the third segment. We conducted a two-way repeated measures ANOVA on the four non-thumb fingers with repeated measures factors segment (proximal, middle, distal) and finger (index, middle, ring, little). There was a significant main effect of segment, $F(2, 36) = 38.326$, $p < 0.001$, $\eta_p^2 = 0.680$. Irrespective of finger, there was a significant difference between the percent segment overestimation between the third segment (M = − 34.266%) and the first segment (M = − 0.823%), $t(18) = 8.969$, $p < 0.001$, $d_z = 2.058$, and the third segment and the second segment (M = − 8.766%), $t(18) = 6.406$, $p < 0.001$, $d_z = 1.470$. Percentages overestimations between the first and the second segment did not differ significantly, $t(18) = 1.872$, $p = 0.078$, $d_z = 0.491$ (Bonferroni corrected).

There was also a significant main effect of finger, $F(2.237, 40.261) = 4.195$, $p = 0.019$, $\varepsilon = 0.746$, $\eta_p^2 = 0.189$. There was a statistically significant increase in percent segment overestimation between the index (M = − 11.084%) and the ring finger (M = − 17.788%), $t(18) = 3.041$, $p = 0.007$, $d_z = 0.698$) and a statistically significant increase in the percent segment overestimation between the middle (M = − 14.816%) and the ring finger, $t(18) = 3.219$, $p = 0.007$, $d_z = 0.738$. There were no statistically significant differences between the other fingers (all ps > 0.008, Bonferroni corrected). There was no statistically significant two-way interaction between segment and finger, $F(2.906, 52.314) = 1.391$, $p = 0.256$, $\varepsilon = 0.484$, $\eta_p^2 = 0.072$, meaning that finger parts were underestimated regardless of the finger.

Percentage overestimation and mean value for each segment was calculated on collapsed four non-thumb fingers. There was substantial underestimation of the proximal segment (M: − 34.266%), $t(18) = - 15.582$, $p < 0.001$, $d_z = - 3.575$. There was also more modest underestimation of the middle segment (*M*: − 8.776), $t(18) = - 3.333$, $p = 0.004$, $d_z = 0.765$. In contrast, there was no overall bias for the distal segment (*M*: − 0.823%), $t(18) = - 0.314$, $p = 0.757$, $d_z = 0.072$. These results suggest that underestimation of finger length changes in a proximal–distal gradient across the finger, with the largest underestimation of the most proximal segment and no underestimation of the most distal segment.

These results provide a clear replication of the mislocalisation of the metacarpophalangeal joints that we have reported previously (Ambroziak et al. 2018; Longo 2015a; Margolis and Longo 2015). They further demonstrate that this bias is not an idiosyncrasy of that specific joint, as analagous biases (though of smaller magnitude) were found for the proximal interphalangeal joints as well. There was a clear gradient for this mislocalisation to get smaller from the more proximal to the more distal joints in the fingers.

Experiment 2

Longo (2015b) argued that the mislocalisations of the metacarpophalangeal knuckles reflect conceptual knowledge of hand structure given that they appeared both when participants made judgments about the knuckles of their own hand, or those of another person's hand. In Experiment 2, we aimed at generalising this conclusion to the mislocalisations we found in Experiment 1 for the interphalangeal joints by comparing the whole-hand perceptual maps of joint location between oneself and others. To test this we asked participants to judge the location of the knuckles of their own hand on a white silhouette representing their palm (like in Experiment 1; 'Self' condition). Additionally, participants were also asked to give their judgements for knuckles localisation on a silhouette another person's hand ('Other' condition). The hand silhouette for the 'Other' condition was created of the actual hand photograph of the female researcher (KM) who did the testing, and was the same for all participants.

Methods

Participants

Twenty individuals participated (M = 29.6 years, SD = 9.0, range 19–50, 12 females). Eighteen were right-handed (above 50), two were ambidextrous (between − 50 and 50) as assessed by the EHI (Oldfield 1971; mean: 80.8; range 5.9–100).

Procedure

Procedures were identical to Experiment 1 except that across blocks judged the location of all 14 landmarks both on a silhouette of their own hand ('Self' condition) and on the silhouette of the researcher's hand ('Other' condition). The stimulus for the 'Other' condition was prepared ahead of time, and was identical for all participants. There were four blocks of trials counterbalanced between participants in an ABBA order, with the first condition counterbalanced across participants. There were eight judgements of each landmark in a block (56 trials in each block).

Participants were explicitly told at the start of the experiment that in some blocks they would have to judge the location of the knuckles of their own hand, and sometimes the knuckles of the experimenter's hand. The experimenter was a woman (KM) and showed her hand to the participant which giving them instructions so they could see the shape and configuration of her hand. At the beginning of each block, the participant was told either that they would be judging "your hand" or "Kasia's hand".

Analysis

The analysis was identical to Experiment 1, except that the statistics were calculated for judgements on both participant's palm ('Self' condition) and researcher's palm ('Other' condition). ANOVAs included identity (Self, Other) as an additional within-subject factor.

Results and discussion

Distal biases

The top row of Fig. 3 shows mean distal bias as a percentage of finger length for all 14 knuckles in both the 'Self' and 'Other' conditions. Nearly identical patterns were apparent for judgments of the participant's own hand and of another person's hand. As in Experiment 1 and previous studies, clear distal biases were present for the third knuckle. Collapsing across four non-thumb fingers, there was clear distal bias for the metacarpophalangeal joint in both the 'Self' condition (M: 18.955%), $t(19) = 13.089$, $p < 0.0001$, $d_z = 2.927$, and in the 'Other' condition (21.274%), $t(19) = 16.730$, $p < 0.0001$, $d_z = 3.741$. The magnitude of bias in the two conditions was strongly correlated across participants, $r(18) = 0.886$, These results replicate the finding of Longo (2015a, b, Experiment 3) that similar distal biases occur for judgments of one's own and another person's hand. Unlike in that previous study, however, there was a significant difference in the magnitude of distal biases between conditions, $t(19) = 3.455$, $p < 0.003$, $d_z = 0.770$, with larger distal biases for the other person's hand. One possible explanation for this difference between experiments is that the other person's hand in Longo (2015a, b) was a relatively large man's hand, whereas in the present study it was a relatively small woman's hand.

On the proximal interphalangeal joint the magnitude of distal bias was clearly smaller than on the metacarpophalangeal joint in both conditions. There was no significant distal bias for participant's own hand (M: 3.183%), $t(19) = 1.704$, $p = 0.105$, $d_z = 0.381$. There was, however, significant distal bias for the other person's hand (M: 7.818%), $t(19) = 3.745$, $p = 0.001$, $d_z = 0.837$, which was significantly larger than on the participant's own hand, $t(19) = 3.698$, $p = 0.002$, $d_z = 0.827$. Despite these differences, the magnitude of bias was strongly correlated in the two conditions, $r(18) = 0.805$, $p < 0.0001$.

On the distal interphalangeal joint, there were significant proximal biases (i.e., judgments were biases away from the fingertip), both in the 'Sel' condition (M: $-$ 13.901%), $t(19) = -4.227$, $p < 0.001$, $d_z = 0.945$, and in the 'Other' condition (M: $-$ 9.614%), $t(19) = -3.567$, $p = 0.002$, $d_z = 0.798$. There was a marginally significant difference between the magnitude of bias in the two conditions, $t(19) = 2.100$, $p = 0.049$, $d_z = 0.470$, which were strongly correlated, $r(18) = 0.785$, $p < 0.0001$.

We conducted a three-way repeated measures ANOVA on distal bias, including knuckle (metacarpophalangeal, proximal interphalangeal, distal interphalangeal), finger (index, middle, ring, little), and condition (Self, Other) as within-subject factors. There were a significant two-way interaction between finger and condition, $F(3, 57) = 11.036$, $p < 0.001$, $\eta_p^2 = 0.367$, and between knuckle and finger, $F(3.116, 59.213) = 32.789$, $p < 0.001$, $\eta_p^2 = 0.633$. These effects were modulated by a significant three-way interaction, $F(3.071, 58.353) = 4.039$, $p = 0.011$, $\eta_p^2 = 0.175$.

To follow up this significant three-way interaction, we ran separate two-way ANOVAs on data from the 'Self' condition and from the 'Other' condition. In the 'Self' condition there was a significant interaction, $F(3.550, 67.458) = 19.670$, $p < 0.001$, $\varepsilon = 0.592$, $\eta_p^2 = 0.509$, as well as significant main effects of knuckle, $F(2, 38) = 71.875$, $p < 0.001$, $\eta_p^2 = 0.791$, and of finger, $F(3, 57) = 15.634$, $p < 0.001$, $\eta_p^2 = 0.451$. Similar effects were observed in the 'Other' condition, with a significant interaction, $F(2.872, 54.565) = 20.610$, $p < 0.001$, $\varepsilon = 0.479$, $\eta_p^2 = 0.520$, as well as main effects of knuckle, $F(2, 38) = 79.419$, $p < 0.001$, $\eta_p^2 = 0.807$, and of finger, $F(3, 57) = 148.344$, $p < 0.001$, $\eta_p^2 = 0.886$. Thus, despite the significant three-way interaction, qualitatively similar patterns were apparent in both the 'Self' and 'Other' conditions.

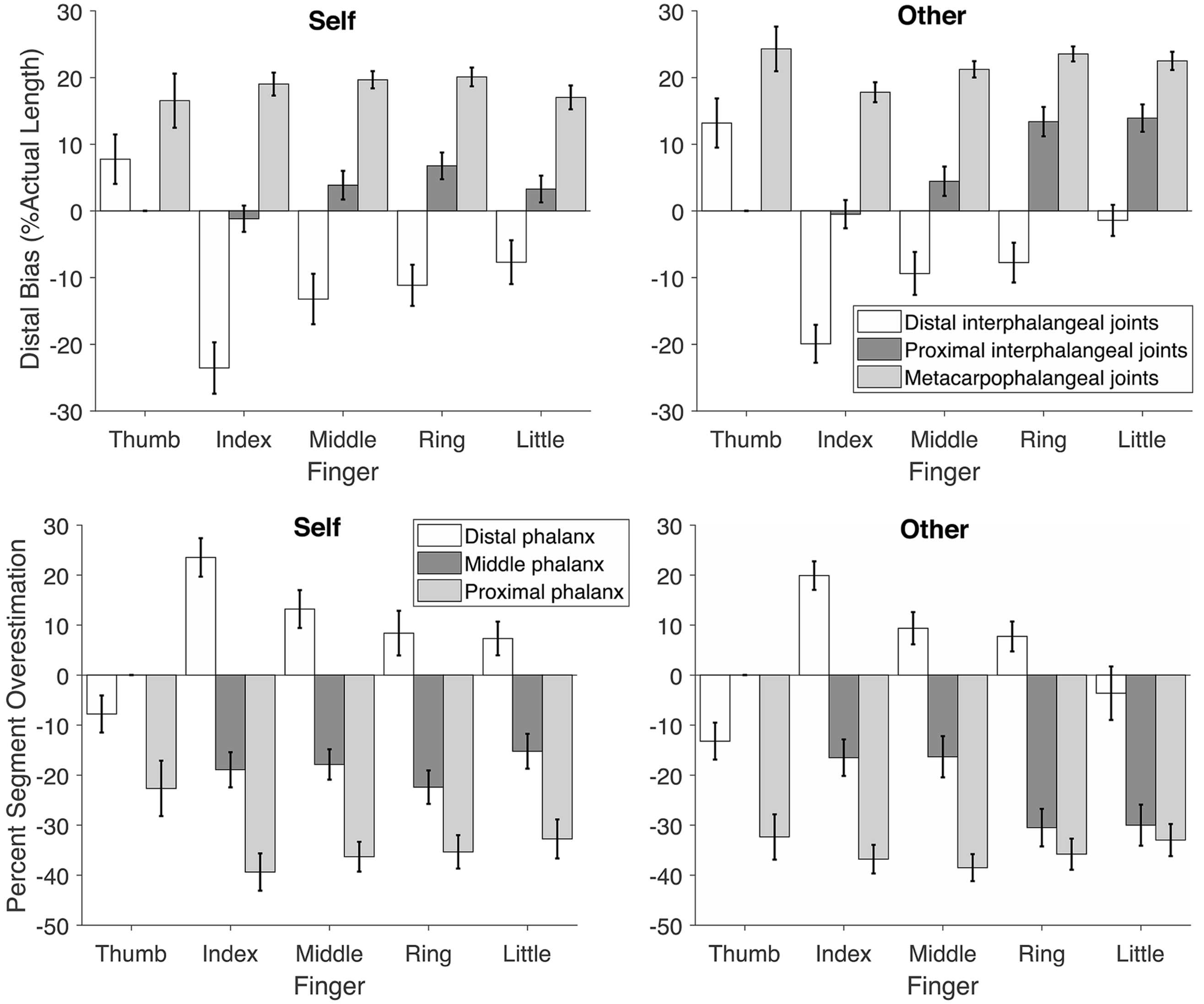

Fig. 3 Results from Experiment 2. *Top row*: distal biases in localising knuckles on one's own hand ('Self' condition, top left) and another person's hand ('Other' condition, top right). The single interphalangeal joint in the thumb is labeled as distal. Error bars represent standard error. *Bottom row*: Percent Segment Overestimation on one's own hand ('Self' condition, bottom left) and another person's hand ('Other' condition, bottom right). Negative values indicate underestimation of the segment length. In the case of thumb only distal and proximal segments are shown

Finger length

The bottom row of Fig. 3 shows overestimation of the length of each segment of the fingers. Broadly similar patterns were apparent in the two conditions. Collapsed across the four non-thumb fingers, there was clear underestimation of the length of the proximal finger segment both in the 'Self' condition (*M*: − 35.931%), $t(19) = -10.804$, $p < 0.0001$, $d_z = -2.416$, and the 'Other' condition (*M*: − 36.010%), $t(19) = -12.519$, $p < 0.0001$, $d_z = 2.799$. For the middle segment there was also clear underestimation in both the 'Self' condition (*M*: − 18.592%), $t(19) = -6.086$, $p < 0.0001$, $d_z = 1.361$, and the 'Other' condition (*M*: − 23.324%), $t(19) = -6.297$, $p < 0.0001$, $d_z = 1.408$. For the distal finger segment, there was, conversely, significant overestimation both in the 'Self' condition (*M*: 13.122%), $t(19) = 3.806$, $p < 0.002$, $d_z = 0\ 0.851$, and in the 'Other' condition (*M*: 8.361%), $t(19) = 2.941$, $p = 0.008$, $d_z = 0.658$. There were strong correlations between percent segment overestimation in the two conditions for the proximal segment, $r(18) = 0.898$, $p < 0.0001$, the middle segment, $r(18) = 0.871$, $p < 0.0001$, and the distal segment, $r(18) = 0.689$, $p < 0.001$.

We conducted a three-way repeated measures ANOVA with within-subject factors segment (proximal, middle, distal), finger (index, middle, ring, little) and condition (self, other). There was a significant three-way interaction,

$F(3.593, 6.2630) = 3.354$, $p = 0.018$, $\varepsilon = 0.599$, $\eta_p^2 = 0.150$, as well as two-way interactions between segment and finger, $F(3,149, 59.8250) = 15.846$, $p < 0.001$, $\varepsilon = 0.525$, $\eta_p^2 = 0.455$, and between finger and condition, $F(1.842, 35.000) = 12.844$, $p < 0.001$, $\varepsilon = 0.614$, $\eta_p^2 = 0.403$.

To explore this three-way interaction, we conducted separate two-way ANOVAs on data from the 'Self' and 'Other' conditions. In the 'Self' condition there was a significant interaction, $F(6, 114) = 9.275$, $p < 0.001$, $\eta_p^2 = 0.328$, as well as main effects of segment, $F(2, 38) = 46.039$, $p < 0.001$, $\eta_p^2 = 0.708$, and of finger, $F(2.345, 44.551) = 5.932$, $p = 0.003$, $\varepsilon = 0.782$, $\eta_p^2 = 0.238$. Analogously, in the 'Other' condition there also an interaction, $F(6, 114) = 10.906$, $p < 0.001$, $\eta_p^2 = 0.365$, as well as main effects of segment, $F(2, 38) = 41.258$, $p < 0.001$, $\eta_p^2 = 0.685$, and of finger, $F(1.204, 22.870) = 28.073$, $p < 0.001$, $\varepsilon = 0.401$, $\eta_p^2 = 0.596$. Thus, despite the significant three-way interaction, there were broadly similar patterns in the two conditions.

Taken together, despite some variations in distortions between the two experiments and between the two conditions of Experiment 2, these results here presented contribute to previous findings, showing clear, distinctive distal biases in localising metacarpophalangeal joints both, for one's own hand and another person's hand (e.g., Longo 2015a, b; Margolis and Longo 2015; Longo et al. 2015b; Ambroziak et al. 2018). Furthermore, the biases on one's own hand and on the other person's hand were strongly correlated. Globally, most distal finger segments tend to be perceived accurately or overestimated, whereas the proximal and middle finger segment lengths are underestimated, collectively lengths of all non-thumb fingers are clearly underestimated, making them perceived as shorter.

Discussion

These results provide further evidence that people misunderstand the locations of the knuckles in their hands. Our results directly replicate recent findings that the metacarpophalangeal joints at the base of the fingers are judged as substantially farther forward in the hand than they actually are (e.g., Longo 2015a, b; Margolis and Longo 2015; Ambroziak et al. 2018). Previous studies, however, only tested that single knuckle on each finger. By obtaining data on all 14 knuckle joints in the hand, we obtained a more complete picture of understanding of joint location. Our results show a gradient of bias, with progressive reduction of distal bias from more proximal to more distal joints. By showing that mislocalisations are not idiosyncratic to the metacarpophalangeal joint, these results provide further evidence that these biases reflect distortions of conceptual knowledge of hand structure. Furthermore, consistent with a previous study that tested the metacarpophalangeal joint (Longo 2015a), we show highly similar patterns of mislocalisation for the knuckles of one's own hand and for those of another person's hand, suggesting that the biases reflect abstract conceptual knowledge about hand structure.

At first glance, some inconsistencies in knuckle judgements for oneself (between Experiment 1 and 2) and between judgements for one's own and another person's hand (Experiment 2) emerged, despite identical experimental setup and similar instructions given by the same researcher. First, while in Experiment 1 participants' judgements about the most distal knuckles (the distal interphalangeal joints) were unbiased, and the proximal interphalangeal knuckles were mislocalised more distally, in Experiment 2 both sets of responses were more proximal, with significant proximal biases for the distal interphalangeal joints and no overall bias for the proximal interphalangeal joints. Next, in the second experiment participants' judgements for the proximal interphalangeal joints were accurate on their own hand, but localised more distally on another person's hand. Overall, however, analyses on the joint results from Experiment 1 and 2 for 'Self' judgements yielded proximal mislocalisations for the distal interphalangeal joints, and distal biases for middle and proximal distal interphalangeal joints. Moreover, these results echoed distortions observed for another person's hand which overall, yields universal character of distortions of hand configuration. The inconsistencies in judgements given for interphalangeal joints, and reduced biases may result from the fact that people are visually drawn to upper parts of their fingers for instance while caring for their nails or while performing fine finger movements. These activities coupled with prolonged visual attention directed to the most distal finger parts, may contribute to a better knowledge of hand anatomy and consequently, to attenuating the biases in localising those joints of the hand.

It might have been assumed that if joints, described as the 'hinges' of the body (Bermúdez 1988), are critical for the emergence of spatial structure in bodily experience, facilitate categorical boundaries for tactile distance estimates (de Vignemont et al. 2009), and serve as a reference point for tactile localisations (Cholewiak and Collins 2003; Weber 1834/1996; Weigel et al. 2017), their location would be judged accurately. Previous literature, at least for the metacarpophalangeal knuckles has shown this line of thought to be incorrect. The explanation for observed previously large distal biases for the metacarpophalangeal joints might be due to the fact that these joints are embedded within the hand by which they are less visually salient, and less movable than the rest of the finger joints; therefore, people misallocate their position as if they were localised further up in the finger (i.e., more distally). As the interphalangeal joints are undoubtedly visibly more pronounced, and fingers can afford a larger range of movements, the distal biases for these joints are decreased or attenuated, which partly goes along with the aforementioned hypothesis stating the importance of joints in spatially segmenting bodily form. In this respect, recent studies from our group have shown that postural changes modulate representation of hand structure in tactile localization tasks of the first phalange of the participants' fingers, revealing dynamic interactions between structural and sensorimotor body representations (Tamè et al. 2017a, b; Dolgilevica et al. 2020). Therefore, the lower or absence of distal bias for the more distal joints may derive by a combination of factors such as their greater motor mobility and an attentional component.

The origins of the distortions observed here are not fully understood. More attention has been given so far to distorted body representations in clinical populations. For instance, patients with autotopagnosia show difficulties in localising body parts in relation to whole body for oneself and others (Ogden 1985). Autotopagnosia is thought to be caused by a lesion in the left parietal lobe (Ogden 1985; Corradi-Dell'Acqua et al. 2008, Felician et al. 2004), and is related to damage of a body representation known as the body structural description. As body structural description is largely understudied, it is difficult to state whether knuckle mislocalisations reflect distortions of this representation. Nevertheless, the present results provide further evidence that conceptual knowledge of body structure appears to be systematically distorted in the non-clinical adult human population.

For the first time, we show the conceptual knowledge of the location of all landmarks on the hand. Hand representation is highly distorted, with biggest distal biases of the metacarpophalangeal joints, and attenuated biases for interphalangeal joins. Generally, people think finger segments have roughly the same length, and they are perceived significantly shorter than they actually are. The most basal segments of the fingers were underestimated the most, whereas the second and most distal finger-part size-estimations, were distorted to a lesser extent, and the patterns of distortions showed more variability. It appears that people believe that the parts forming fingers are approximately of the same length. Our suggestion that people conceptual understand finger segments as having equal length has an interesting correspondence with the proposal of Cicmil et al. (2016) that people may judge the toes as being equal in width, which was based on the systematic pattern of confusions they observed between toes in a tactile localisation task. Together, these results suggest that mental representations of body parts may be built up from combinations of a set of interchangeable part-based representations, perhaps analogous to the idea of 'geons' in visual object representation (Biederman 1987).

Critically, similar distortions were found when participants made judgements for their own hand as well as for another person's hand, which contributes to the evidence that these distortions are not self-specific, but reflect a more general, universal belief of a hand structure shared by all humans. These results mirror distortions observed in judgements underlying tactile localisation and position sense, and resemble distortions of somatotopic maps in somatosensory cortex. Further research is needed to shed more light into the character and origins of these distortions.

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Availability of data and material The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability The study was run 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 code is available upon from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The procedures were approved by the Department of Psychological Sciences ethics committee at Birkbeck, University of London.

Consent to participate All participants gave written informed consent and were paid for their participation.

Consent for publication Participants signed informed consent to publish their data.

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