Conceptual biases explain distortion differences between hand and objects in localization tasks

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Abstract

Recent studies have shown the presence of distortions in proprioceptive hand localization tasks. Those results were interpreted as reflecting specific perceptual distortions bound to a body model. It was especially suggested that hand distortions could be related to distortions of somatotopic cortical maps. In this study, we show that hand distortions measured in localization tasks might be partly driven by a general false belief about hand landmark locations (conceptual biases). We especially demonstrate that hand and object distortions are present in similar magnitude when correcting for the conceptual bias of the knuckles (Experiment 1) or when asking participants to directly locate spatially well-represented landmarks (i.e. without conceptual biases) on their hand (Experiment 2). Altogether our results suggest that localization task distortions are non-specific to the body and that similar perceptual distortions could underlie localization performance measured on objects and hands.

Keywords: body representation, position sense, somatosensation, conceptual distortions

Public statement

The present study suggests that distortion differences between one's hand and objects measured in body model localization tasks are more likely to be explained by inaccurate knowledge about hand landmarks than somatosensory distortions. Correcting for this inaccurate knowledge or using a better known configuration of hand landmarks led to a similar magnitude of distortions between hand and objects. Our results confirm the idea that localization task distortions involving non-direct somatosensory stimulations are non-specific to the body and that similar perceptual distortions might underlie localization performance for hands and objects.

Introduction

Body representations are important for perception and action. Traditionally, a dissociation is made between the conscious body image, primarily involved in perceptual judgments and the postural schema used during motor actions (de Vignemont, 2010; Gallagher, 1986). The postural schema is generally considered as an unconscious dynamically updated representation relying on proprioceptive signals from the joints, muscles and skin (Head & Holms, 1911). This representation has long been considered as necessary for the maintenance of posture and perceptual localization of our limbs in external space. Accurately perceiving the location of body parts through proprioception requires that sensory signals about the angles of each joint (i.e., body posture) are combined with information about the size and shape of the body segments between joints (Beers, Sittig, & Gon, 1998; Soechting, 1982). In line with this idea, Longo and Haggard (2010) argued that the human postural schema also referred to as position sense, must rely on a stored body model of the body's metric properties (i.e., size and shape).

Longo and colleagues (Longo, 2014a; Longo & Haggard, 2010, 2012; Longo, Mattioni, & Ganea, 2015) used a proprioceptive localization task in order to investigate the properties of this body model in the case of the human hand. Participants laid their hand on a table under an occluding board and had to indicate with a pointer the location of their finger tips and knuckles at the base of each finger (metacarpophalangeal joint). Perceptual maps of hand structure were constructed based on the relative judged location of each tip and knuckle of the participants' fingers. Results showed highly distorted hand maps. Those distortions were characterized by an underestimation of finger length (especially an increase in finger length underestimation from the thumb to little finger) and an overestimation of the spacing between the knuckles.

Despite multiple studies reporting hand shape distortions in localization tasks, the nature of hand distortions remains unclear. Longo and colleagues suggested that hand distortions measured in localization tasks could be influenced by perceptual distortion characteristic of early somatosensory maps (e.g. Penfield homunculus; see: Longo & Haggard, 2010). For instance, the authors propose that the gradient in finger size measured in localization tasks could mirror the cortical magnification of the fingers and their relative spatial tactile acuity (Duncan & Boynton, 2007). Hence the findings of localization tasks are assumed to hinge upon the proprioceptive feedback of the hand landmarks. On this interpretation, hand representations measured in proprioceptive localization tasks would rely on a perceptual model that is specific to the body. However, a number of studies also indicate the presence of cognitive/perceptual factors other than somatosensation (e.g., memory biases) playing a role in localization task distortions, thereby raising the possibility that localization tasks might measure biases that are non-specific to the hand (Longo, 2014b, 2015; Saulton, Dodds, Bülthoff, & Rosa, 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016).

The somatosensory interpretation of distortions in the localization task makes an interesting prediction. Distortions in localization tasks should only occur when pointing to landmarks on the human body as somatosensory feedback is only available for the human body. In other words, no such distortions are expected when pointing to landmarks on non-bodily items, e.g. objects. We recently started investigating the specificity of hand distortions measured in localization tasks by comparing hand distortions with a range of objects going from a simple geometrical form, e.g., a CD-case, to items sharing the structural shape of a hand (e.g., rake; rubber hand; for more details see: Saulton et al., 2015, 2016). In line with hand distortions, biases measured on objects were also characterized by significant length underestimation compared to width across different orientations. Hence the presence of length and width distortions was not special to the hand. However, the magnitude of hand distortions was specific to the hand, with larger distortions along the length (but not width) dimension for the hand than for other objects (e.g. rake). These results suggest that the larger magnitude of distortions present on the hand might be indicative of somatosensory processing.

Yet, recent work suggests that the greater distortions found for finger length estimates could be due to a conceptual misunderstanding of the hand structural configuration, e.g., an incorrect belief of the hand's anatomical landmarks (Longo, 2015; Longo et al., 2015; Margolis & Longo, 2014). In Longo et al., (2014, 2015) participants were asked to indicate the believed location of their knuckles (metacarpophalangeal joint) on a silhouette image of their hand. Localizing hand landmarks in this silhouette task is, therefore, assumed to assess the spatial knowledge or conceptual representation associated to the spatial layout of the hand (Longo, 2015; Longo et al., 2015; Margolis & Longo, 2014). Results showed that the knuckle location was judged higher up on the hand, towards the crease of the finger. This finding was replicated in a pointing task in which participants had to place the tip of a baton on the knuckle on the palm side of their own hand and another person's hand (Longo, 2015). In both conditions, participants judged the knuckles above its actual location suggesting that the bias in knuckle location arises from an *inaccurate spatial knowledge* of the hand structure, which we will refer to as *conceptual bias* (similar to Longo, 2015). One reason for this conceptual bias might be that anatomical location of the knuckle does not coincide with the visually perceived end of the finger (point where the finger protrudes from the palm).

What are the potential consequences of this conceptual bias for the localization task? Because participants believe their knuckles to be closer to the crease (and thereby the finger tips) than they actually are, this conceptual bias leads to participants believing that the distance between knuckles and finger tips is smaller than it actually is. If participants were to rely on this belief also in localization tasks, the conceptual bias alone should lead to an underestimation of the finger length in the localization task. As for objects, landmarks are usually associated to a clear physical location (e.g. see tips and bottoms of the rake' branches in Figure 2). Hence, participants should have a much smaller conceptual bias with objects than with hands. In other words, the influence of the conceptual bias in object localization tasks should be smaller than in hand localization tasks. Consequently, one might observe a hand specific additional distortion in the localization tasks due to this conceptual bias. Is it possible that this larger conceptual bias with the hand than with objects explains the larger hand distortions in the location task?

In this study, our goal was to investigate whether conceptual biases could account for the larger distortions in the hand compared to objects in the localization task (as per Saulton et al. 2015, 2016). To do so, we measured the conceptual biases for hand and rake landmarks in a silhouette task similar to the one used by Longo and colleagues (Longo et al., 2015; Margolis & Longo, 2014). We then used a localization task to measure somatosensory distortions of the hand and compared it with rake distortions measured within the same localization task (similar to Saulton et al., 2015, 2016). We could therefore assess whether the magnitude of localization distortions was specific to the hand. In Experiment 1 we wanted to mathematically correct hand localization distortions for the conceptual biases and compare the magnitude of the corrected hand and rake distortions. If the larger magnitude of hand distortions previously measured in localization task is specific to a perceptual body model, as previously suggested (Longo et al., 2015), we should be able to measure significant differences in hand and rake distortions after correcting for the conceptual biases. In contrast, a similar magnitude of distortions (after correction of the conceptual bias) between hand and rake would suggest that the conceptual biases can account for differences between hand and rake in localization tasks.

Experiment 1

Method

Participants. 16 right handed individuals (9 males) between 19 and 35 years of age (M=26.6) participated in the experiment. One subject was excluded from the study due to hand movements during the task. Participants gave written informed consent prior to the study. The research was reviewed by the local Ethics Committee of the University of Tübingen and done in line with their recommendations.

Procedure. The participant's left hand and a rake item were used as stimuli in the experiment. The rake and the hand share a similar structure (5 branches/5 fingers). Participants were first introduced to the name and locations of 10 landmarks on their hand and the rake. On the rake, the 10 landmarks corresponded to the top and bottom of each of the 5 branches. On the hand, the 10 landmarks corresponded to the tip and knuckle (metacarpophalangeal joint) of each finger. To avoid any ambiguities in showing landmarks on the hand, we drew a small red cross in the middle of each nail to indicate the position of the tips and another one in the middle of the knuckle at the base of each finger. We did the same for the rake. We later refer to those actual landmarks as the *anatomical locations* of the rake and hand's landmarks. The experiment was split into two parts: a localization task and a silhouette task (see setups in Fig.1). The silhouette task might make participants aware that we were interested in the hand structure. Consequently, if the silhouette task precedes the localization task, participants might use their knowledge about the hand structure to localize individual landmarks instead of relying on the proprioceptive feeling associated to each individual landmark (as instructed). To avoid this type of confound, we therefore always conducted the localization task before the silhouette task. The experiment lasted 1 hour.

Localization task. The localization task procedure was similar to the one used in Saulton et al (2015). Subjects had to localize on a screen the perceived location of the tips and knuckles of the 5 fingers of their hidden left hand (condition 1) and the bottom and top of the 5 branches of a hidden rake (condition 2). The condition order (hand vs. rake) was counterbalanced. For both conditions, participants sat with the item lying on a table aligned with their body midline. The subject's left hand and the rake were positioned at the same location on the table. The stimulus was visible during 15 seconds while being photographed. We used this photograph to make sure that subjects did not move their hand across trials but also to extract the exact dimensions of each stimulus. After 15 seconds, a computer monitor (Dell U2412M monitor with a 16:10 widescreen aspect ratio) was slid in parallel to the table top (16 cm above the table) to occlude the hand/rake from the participant's view. An experimental trial started by presenting the name of one of the item's landmarks (e.g., tip of middle finger) in white font at the top center of the black computer screen. After a 2 s delay, the mouse cursor was presented at a random y-axis location on the right edge of the screen. Participants were instructed to indicate the perceived location of the queried landmark by positioning the mouse cursor over the corresponding position on the computer screen and clicking with the mouse. For the hand, subjects had to rely on the felt location (proprioceptive sensations) associated to each individual landmark to guide their location judgments. No tactile or somatosensory stimulations were delivered onto the subjects' hand. For the rake, subjects had to rely on the memorized location of each individual landmark. The right hand directing the mouse pointer was hidden from view. The answer interval was not time restricted and provided no feedback. Then the next trial started. A condition ended after testing each landmark in random order 10 times within two blocks. There were 5 repetitions per landmark within each block. Before and after each block, we photographed the stimulus (15 seconds visibility of the stimulus) using an overhead mounted camera (Canon, EOS 40D; Zoom lens, EF-28–135 mm). The hand and rake pictures taken during the localization task were later used by a custom written Matlab script to extract a black silhouette of the rake and each individual's hand.

Silhouette task. Participants sat in front of a computer monitor (Dell U2412M monitor with a 16:10 widescreen aspect ratio) with their hands hidden under a cardboard box. The hand was aligned perpendicular to the monitor screen. A black silhouette of the participant's hand or the rake was displayed in the center of the screen at the same size as the real item. An experimental trial started by presenting the name of an item's landmark (e.g. knuckle of middle finger). Participants had to indicate the location where they believed the pre-indicated landmarks to be, by directly clicking on corresponding location on the silhouette. Participants had the opportunity to adjust their judgments as much as they wanted before going to the next trial. The task ended after testing each landmark in random order 6 times.

Analysis. We used two indices to assess the spatial distortions observed with hand and rake. The Normalized Shape Index (NSI), which measures distortions of aspect ratio of an item and the percent overestimation, which measures distortions separately along the length and width dimensions.

NSI. We quantified each item's shape using its width to length ratio, referred to as its Shape Index (SI = 100*width/length). The Shape index is assumed to reflect the overall aspect ratio of an item (Longo & Haggard, 2012; Napier & Tuttle, 1993). We then normalized the shape index for each item by dividing the estimated SI by the actual SI of that item; thereby creating a baseline of NSI=1. An NSI value that is superior to the baseline of 1 indicates the presence of larger estimation of width relative to length (mean width estimate > mean length). The width and length dimensions used to calculate the SI can be seen in Fig. 2 marked by yellow and blue lines.

Percent Overestimation. To be consistent with previous work (Longo et al., 2010; Saulton et al., 2015), we also calculated and compared the percent overestimation between the rake and hand's length and width (e.g., 100*(judged hand width- actual hand width)/ actual hand width). Judged hand width corresponds to the average relative distance measured in cm between the estimated location of the little, ring, middle and index knuckles. Judged finger length corresponds to the averaged relative distance measured in cm between the estimated location of the finger's tip and knuckles indicated by each subject. The length dimension of the rake corresponds to the average length of its branches (from bottom to top of the branches) and the width to the average distance between the bottoms of its branches (for additional methodological details see methods in Saulton et al 2015, 2016).

We checked whether assumptions of the statistical tests were met. All data met the assumption of normality and sphericity.

Results

Do conceptual biases exist for hand and rake?

In the silhouette task, subjects were relatively accurate in judging the location of the rake landmarks (see Fig.4). Indeed, the percent length and width overestimation of the rake dimensions did not significantly differ from 0 [Percent length: M=-.6%, t(14)=-2.08, p=.06, r=.48; Percent width: M=- .1%, t(14)=-.88, p=.39, r=.22]. In contrast, subjects were extremely biased in judging the location of their hand knuckles (but not the tips) on the silhouette of their hand (for a visual appreciation see Fig.3). Indeed, the percent length and width overestimation of the hand dimensions significantly differed from 0 [Percent length underestimation M=-14.7%, t(14)=-13.3, p<.0001, r=.96; Percent width overestimation M= 11.86%, t(14)=5.35, p<.001, r=.82]. This confirms the fact that subjects consider their knuckles to be positioned higher up on the hand but also further apart (for more statistical details see S1 of the supplementary material). Hence, results of the silhouette task show the presence of significant conceptual biases for the hand and little to no conceptual biases for the rake. In order to compare hand and rake distortions more directly, we conducted a priori paired t-tests on the percent length and width separately. Hand distortions were significantly larger for the hand than the rake for the length [t(14)=-11.5, p<.0001, r=.95] but also the width [t(14)=5.5, p<.001, r=.82; see Fig.4]. These results clearly show that the amounts of conceptual biases present in the silhouette task for the hand are significantly larger for the hand than for the rake.

Can these conceptual biases account for localization distortion differences between hand and rake?

In order to assess whether conceptual biases of hand landmarks can account for the distortion differences between hand and rake in the localization task, we calculated localization distortions with and without correcting for the conceptual bias. For the uncorrected localization judgments (correction absent condition) we calculated distortions with the actual distances between landmarks based on the anatomical/physical locations from the photographs (e.g. NSI= [100*hand width/ hand length from localization task]/ [100*hand width/hand length from photograph]). To apply the correction for conceptual biases (correction present condition), localization task distortions were calculated with the actual distance between landmarks based on the estimated landmark locations indicated by participants on the silhouette (e.g. NSI= [100*hand width/ hand length from localization task]/ [100*hand width/hand length from silhouette task]). This was done for the hand and the rake. If the conceptual bias of the hand is responsible for larger hand than rake localization distortions, correcting for this bias should reduce this difference significantly.

To compare hand and rake distortions, we conducted a within-subject ANOVA on the NSI with items (hand and rake) and correction (absent vs. present) as within-subjects factors. There was a significant main effect of the correction factor [$F(1,14)=95.30$, $p<.001$, $\eta^2=.04$] as well as a significant interaction between the items and the correction factors [$F(1,14)=78.19$, $p<.001$, $\eta^2=.037$]. This significant interaction means that the difference in distortion between hand and rake depended on the correction (see Fig.5). Without correcting for the conceptual bias, the hand is significantly more distorted than the rake [a priori paired T-test: t(14)=2.4, p=.03, r=.54]. Importantly, *after correction* for the conceptual bias, the NSI associated to the hand and the rake distortions was not significantly different [a priori paired T-test: t(14)=.09, p=.9, r=.024].

Because one cannot infer from the null effect that the distortions between rake and hand are similar in the corrected condition of the localization task, we determined the likelihood that the localization distortions of the items (rake vs. hand) come from the same distribution rather than different distributions using Bayes factor on the NSI values ("BayesFactor" package in R). We obtained a Bayes factor of 3.8 which means the data was about 4 times more likely to come from the null hypothesis than from the alternative hypothesis. In this specific case, this indicates that the rake and the hand distortions are more likely to come from the same distribution rather than from different distributions when correcting for the conceptual bias.

To ensure that observed NSI differences indicate conceptual biases along the length dimension, we compared corrected and uncorrected hand and rake length estimates in terms of percent overestimation. In the uncorrected condition, length underestimation of the fingers (M=-34.9%, SD=2.03) was significantly larger compared to the rake branches (M=-18.4%, SD=2.13) [t(14)=-3.15; p=.007, r=64]. In the corrected condition, there were no significant differences between hand (M=-23.2%, SD=2.6) and rake (M=-18%, SD=2.1) in terms of percent length underestimation [t(14)=-.92, p=.37, r=.24]. Note that there were no differences between hand and rake width overestimations in the corrected [t(14)=-.35; p=.72, r=.09] and the uncorrected [t(14)=-1.5, p=.16, r=.37] condition.

Discussion

We found that conceptual biases measured in the silhouette task were significantly larger for the hand than the rake. While judgments performed on the rake were relatively accurate (no conceptual bias), judgments performed on the hand were significantly distorted (conceptual bias). Those hand distortions appear to be driven by an incorrect knowledge of the knuckle position (but not the tips). Specifically, subjects think their knuckles are located higher up on their fingers, which might lead to a greater finger length underestimation in localization tasks. To understand whether these differences in conceptual biases can account for the larger hand than rake distortions in the localization task, we mathematically corrected for these conceptual biases. Interestingly, we found that removing these conceptual biases significantly changed the differences in distortions measured between hand and rake in the localization task. Without correction for these conceptual biases, we found that distortions were significantly larger for the hand than the rake, as shown in previous work (Saulton et al., 2015, 2016). However, after correction of these conceptual biases, the differences in distortions between hand and rake decreased and no significant difference was detected between them (Fig.5). Hence, results of Experiment 1 indicate that it is possible for conceptual biases of the hand to account for localization differences between hand and rake.

In Experiment 1, we mathematically corrected for hand conceptual biases to compare hand and rake distortions in the localization task. In Experiment 2, we were interested in providing more direct evidences for the suggestion that conceptual biases of hand landmarks are the basis for the larger localization task distortions with the hand compared to objects. To do so, we directly manipulated the amount of conceptual bias on the hand and examined its effect on localization distortions. Instead of using the subjects' conceptual knowledge about their tips and knuckles positions (silhouette task data) to correct localization task data, we chose to evaluate subjects' localization task results on hand landmarks for which subjects already have a relatively good conceptual knowledge. This way, we can compare objects to hand localization task distortions directly, without requiring to mathematical corrections to remove conceptual bias influences. If our hypothesis is correct, we should observe a similar magnitude of distortion differences between objects and hand when using well conceptualized hand landmarks.

Experiment 2

Experiment 2 sought to provide more direct causal evidence for the suggestion that conceptual biases of hand landmarks are the basis for the larger localization task distortions with the hand compared to objects. We manipulated the magnitude of conceptual biases by having participants point to hand landmarks that were either associated with large (i.e. hand knuckles, as in Experiment 1) or small conceptual biases (bottom of fingers). Colloquially speaking, the bottom of the fingers corresponds to the point where a finger protrudes from the palm (see representation on Fig.6). We anticipated that the location of these more visually salient landmarks would be better known than the location of the knuckles. In order to check this assumption, we ran a pilot study in which subjects indicated the believed location of either their finger bottoms or their knuckles on a hand silhouette.

Pilot study

The goal of the pilot study was to check whether the bottom of the finger was associated with a smaller conceptual bias than the knuckle of the finger using a silhouette task (as per Experiment 1). Interference effects are known to occur in perceptual judgments associated with spatially close landmarks that are probed in a successive manner (Huttenlocher, Hedges, Corrigan, & Crawford, 2004; Huttenlocher & Lourenco, 2007). To avoid this type of bias, subjects were split into two groups of 16 participants. The first group (5 males, M = 27.7) had to indicate the believed location of the bottom of their finger on a hand silhouette (bottom group). The second group (7 males, M=27.2) had to indicate the believed position of the knuckles of their finger on the hand silhouette (knuckle group). We compared the locations of the judged hand landmarks averaged across fingers on the silhouette to the actual anatomical location of the same landmarks. This was done using paired t-tests in each group along the y (corresponding to the length dimension) and x (corresponding to the width dimension) axis of the hand. We then compared data of the two groups using independent Welch t-tests. In both groups, the knuckles were relatively well located along the x axis [Group 1: t(15)=-0.47, p=.64, r=.12 ; group 2: t(15)= -.15, p=.88, r=.038] and no significant difference between groups was detected [Welch T-test: t(16.22)= -.88, p=.38, r=.21]. This was not the case for the y axis. In the bottom group, participants had the tendency to position the bottom of their finger 0.15 cm (on average) above the actual bottom of the fingers [t(15)=2.7, p<.02, r=.57]. In the knuckle group, participants judged their knuckles to be 1.09 cm higher (on average) than their actual location position [t(15)=11.63, p<.0001, r=.94]. The position error of the knuckle group was significantly larger (by a factor of 7) than the bottom group [Welch T-test: t(22.56)= -9.49, p<.0001, r=.89]. Hence, this pilot study confirmed that finger bottoms were associated with a statistically significantly smaller conceptual bias than the knuckles of the finger.

Main Experiment

Experiment 2 compared hand distortions associated with large (knuckles) and small (bottoms) conceptual biases to object distortions within the same localization task. If conceptual biases are the main driving force behind the larger localization distortions found on the hand, we should observe a decrease in hand distortions when participants point to hand landmarks associated with a small (bottom of finger) compared to a large (knuckles) conceptual bias. Specifically, we expect significant localization distortion differences between hand and objects only when participants point to hand landmarks associated with large conceptual biases (e.g. knuckles). In contrast, when participants point to hand landmarks with little conceptual biases (bottom of fingers), we would expect a similar magnitude of distortions between objects and hand.

Furthermore, we wanted to avoid that our results simply reflect an artifact of using objects with a hand like structure (e.g. rake or rubber hand; see previous work: Longo et al., 2015; Saulton et al., 2016). We therefore chose objects of simple geometrical shape, namely an inverted T shape and L shape. Those shapes allowed us to keep certain geometrical characteristics of the hand (vertical finger crossing the palm see Fig.6) while avoiding any clear resemblances with a hand. Extending our study to other control objects also increases the generalizability of our results.

Method

Participants. 18 right handed individuals (10 males) between 23 and 38 years of age (M=28.6), all different to participants in the pilot study and Experiment 1 took part in Experiment 2. Participants gave written informed consent prior to the study. The research was reviewed by the local Ethics Committee of the University of Tübingen and done in line with their recommendations.

Material. The localization task consisted of four conditions each probing a different item (Hand Bottom, T shape, L shape and Hand Knuckle; see Fig.5). In the case of the L and T shapes, subjects made judgments from memory about the locations of landmarks localized at each top of the vertical and horizontal sticks associated to each geometrical shape (3 for the L shape and 4 for the T shape : see red landmarks on Fig.5). The sticks which formed the L and T shapes had a length of 8 cm (corresponding to an average finger length). For the hand, subjects had to rely on proprioceptive judgments of the location of the hand's landmarks: either the bottoms and tips of the finger (hand bottom condition) or the knuckles and tips of the finger (hand knuckle condition).

Procedure. The localization procedure was the same as in Experiment 1. The hand and geometrical shapes were positioned at the same location under the screen. Each stimulus was visible during 15 seconds while being photographed. The screen was then pulled above the stimulus and the trials associated to the condition started. To maximize the time in between the two hand conditions and minimize potential carry over effects, participants always started and finished the experiment by one of the hand conditions (Hand Bottom or Hand Knuckle). Participants performed the other two conditions in between (L and T shape).The conditions' order was counterbalanced between participants. There were 10 randomized repetitions per landmark in each condition. Before the experiment started, we introduced each landmark to the participants by drawing a red cross at the corresponding location (see Fig.5). To ensure that no conceptual biases were present for the L and T shape objects, we also checked that subjects had a good understanding/knowledge of each landmark position by asking them to point with their finger at the exact location of the pre-defined landmarks on the sticks (see red landmarks on Fig.5). All subjects were all relatively accurate and precise in their answers.

Analysis. The hand and geometrical stimuli have different shapes. In order to compare the shape representation of the geometrical stimuli with the shape of a hand, we quantified each item's shape using its NSI. As per Experiment 1, we also used the percent length and width overestimation to calculate the distortions associated to each separate dimension. The width and length dimensions used to calculate the NSI can be seen in Fig.5 marked by yellow and blue rectangles. All errors were normally distributed (Shapiro-Wilk test non-significant). We report Greenhouse-Geisser correction when the assumption of sphericity was violated.

Results

Can the conceptual bias explain distortion differences between hand and objects?

In line with previous work (Saulton et al., 2015, 2016) NSI distortions for all item conditions were significantly greater than 1 (all p<.001 with Holm correction, see Fig.6 left). To investigate differences in distortions between the item conditions, we used a within-subject ANOVA with NSI as the dependent variable and item conditions (Hand

Knuckle, Hand Bottom, L-shape, T-shape) as factors. Results showed a significant main effect of item conditions [F(2.0, 34.15)=19.22 p<.0001, η^2=.45]. This result suggests that the amount of distortion varies across the different item conditions. In line with our hypothesis, the hand knuckle condition (condition associated with large conceptual biases) was characterized by larger distortions than all other conditions (paired t-tests with Holm correction: L-shape t(17)= 5.83, p<.0001, r=.65; T-shape t(17)= 3.61, p<.003, r=.73; Hand bottom t(17)=5.11 p<.0002, r=.77). There were no significant differences in distortions between the hand bottom condition and the L and T shapes (paired t-tests with Holm correction: L-shape t(17)= 2.31, p=.07, r=.48 and T-shape t(17)= -1.02, p=.32, r=.24). Hence, the hand condition associated with relatively small conceptual biases (hand bottom) appears to be significantly less distorted than the hand condition associated with large conceptual biases (hand knuckle) in the localization task.

To better understand the differences in NSI between the item conditions, we also conducted a within-subject ANOVA on length and width percent overestimation separately (See Fig.7. right). In line with the NSI results, we found a significant main effect of item conditions on percent overestimation for width [F(3,51)=17.23, p<.0001, η^2=.27] and length [F(3,51)=5.43, p<.003, η^2=.11] confirming the presence of differential distortions between item conditions. As before, paired t-tests (with Holm correction) showed that the Hand knuckle condition (condition associated with large conceptual biases) differed from all other conditions (width comparisons: for all p<.004; Length comparisons: for all p<.02). There were no significant differences in length and width distortions between the T shape, L shape and hand bottom conditions (all p>.05, except the L shape that significantly differed from the T shape and hand bottom condition for width estimates: all p<.02). To provide more evidence for the similarity of length and width distortions between objects and hands in the hand bottom condition, we correlated hand and object distortions.

Correlation on percent length dimensions. There was a significant correlation across participants between the magnitude of length underestimation on the hand bottom and each of the L and T shape configurations [T shape: r= .49, p<.038; L shape: r=.57, p<.014]. There were no correlations between the Hand Knuckle conditions and the T/L shape conditions [T shape: r= .28, p=.25; L shape: r= .34, p=.17].There was a significant correlation between the hand bottom and hand knuckle conditions [r= .54, p<.02].

Correlation on percent width dimensions. We measured significant width correlations between all geometrical items and the Hand Bottom condition [T shape: r = .51, p<.030; L shape: r= .50, p <.031]. There were no correlations between the Hand Knuckle conditions and the T/L shapes conditions [T shape: r= .38, p=.11; L shape: r= .46, p=.053]. There was a significant correlation between the hand bottom and hand knuckle conditions [r= .70, p<.002].

Discussion

Experiment 2 investigated whether manipulating the degree of conceptual distortion with the hand could influence distortions in the localization task. We varied the amount of conceptual bias by having participants point to two types of landmarks. One type of landmark was associated with a large conceptual bias (hand knuckle) and the other with a small conceptual bias (bottom of fingers). We compared the results of these two conditions to localization task estimates of objects. We found that the smaller conceptual biases (hand bottom condition) were associated with significantly smaller distortions in the localization task, which rendered differences between the hand and objects non-significant. Moreover, we found that distortions of hand landmarks for which participants have accurate spatial knowledge, are significantly related to distortions of object landmarks. This demonstrates similarities between hand and object distortions in the localization task.

Can the number of probed landmarks used in Experiment 2 affect localization performance? In this study, we compared an item with three/four landmarks (L and T shapes) to the hand that has 10 landmarks. It might be that the number of landmarks affects localization performance. For example, we have previously shown that a square box and a post-it each having four landmarks were significantly less distorted than the rake (with 10 landmarks: see Supplementary material in Saulton et al., 2015). The results are less clear for the current study (see Fig.5 for the rake and Fig.7 (left) for T and L shapes). Yet, we would like to highlight that choosing fewer landmarks does not play in favor of our hypothesis. We were interested in showing that distortion differences between hand and objects can be minimized by considering the conceptual bias. In other words, we wanted to show that distortions between hand and objects could be present in similar magnitude when we remove conceptual bias influences. Assume that objects with fewer landmarks indeed lead to smaller distortions. In this case, our choice to use an object with fewer landmarks is increasing the difference that we try to explain by the conceptual bias. In our study, despite the possibility that larger distortion differences exist (objects have fewer landmarks), we find that the conceptual bias can account for this larger difference. We therefore deem it unlikely that choosing an object with fewer landmarks helped us in finding the reported results.

Overall the results of Experiment 2 show that conceptual biases significantly increase distortions in the localization task and that minimizing these distortions leads to similar performance in object and hand localization tasks. Hence, we suggest that conceptual biases are likely to be an important factor for larger distortions observed with hands than with objects in localization tasks.

General discussion

In this study, we demonstrate that participant's visual knowledge about the spatial location of the hand's knuckles is inaccurate (referred to as conceptual bias, see Experiment 1, silhouette task). We therefore examined whether these conceptual biases could account for the distortion difference between objects and hand in localization tasks. In Experiment 1 we found that mathematically correcting for these conceptual biases results in similar distortions in object and hand localization tasks.

Experiment 2 was geared towards finding more direct evidence for the influence of conceptual biases on localization performance differences between hands and objects. To this end, we manipulated the amount of conceptual bias by having participants point to different types of hand landmarks i.e. the knuckles or bottom of the finger, each associated to different degrees of conceptual biases. We found that using hand landmarks that are associated with small conceptual biases (i.e. participants have good knowledge about the spatial location of the landmarks) removes differences between objects and hands in localization tasks. Overall these results speak strongly in favor of conceptual bias being a likely candidate for causing larger hand distortions compared to objects in localization tasks.

Why are localization distortions different between L and T shapes in Experiment 2? Studies investigating vertical-horizontal and bisecting line illusions have reported length underestimation relative to width estimates in the case of objects and figures depicting vertical segments crossing horizontal ones (Chapanis & Mankin, 1967; Finger & Spelt, 1947; Hamburger & Hansen, 2010). In some sense, the L and T-shape stimuli chosen in our last study can be considered as representative of such illusions. In line with this idea, it is known that the configuration of the figure (whether the stimulus looks like a T or a L shape) is susceptible to generate different amount of perceptual distortions in metric estimates associated to each figure (especially due to an additional bisection bias present in the T shape figure). This could potentially account for the differential distortions found along the width between the L and T shapes in Experiment 2.

Similar to the T shape, the hand bottom might also present an additional bisection bias (finger crossing the palm) compared to the L shape. This could contribute to the differential amount of perceptual distortions found along the width dimension between the L shape and hand bottom conditions. Nevertheless, the exact causes underlying the width differences between the L shape and hand bottom/ T shapes remain unclear. Further work would be needed to investigate this question.

Interestingly, the presence of conceptual biases in hand knuckles in this study is not an isolated finding. Previous work already reported conceptual biases in knuckle judgments (Longo, 2015; Longo et al., 2015; Margolis & Longo, 2014). Here we go beyond these previous reports by providing evidence that correcting for these conceptual biases (mathematically, as in Experiment1) or through direct manipulation (Experiment 2) results in the observation of similar localization distortions between hand and objects (see significant correlation in Experiment 2).

Our results are interesting for the interpretation of hand distortions found in localization tasks. It has been suggested that localization task distortions could retain vestigial traces of the primary somatosensory homunculus of Penfield including an overestimation of the mediolateral (width) over the proximo-distal axis (length) (Longo & Haggard, 2010). Our results cast doubt on this strict interpretation. If those characteristics were specifically bound to a somatosensory representation of the hand, we should only observe them in the case of the hand. We have previously shown that the *magnitude* of these distortions – not the simple presence of distortions, which was also found on objects – was specific to the hand (Saulton et al., 2015, 2016). Here we provide further evidence that even the magnitude of the distortions can be explained by non-somatosensory factors, namely conceptual biases. Overall, our results favor the idea that the localization task taps into perceptual cognitive processes that might not be related to somatosensation but rather reflect general cognitive/perceptual biases that can be measured both with hands and objects.

It is important to note that our results do *not* question the existence of a body model that is based on somatosensation. Rather our findings suggest that the localization task distortions are not specific to the body and consequently the type of localization task used in Body model investigations (Longo et al., 2010) cannot be reliably linked to somatosensation. Hence our results point to a methodological challenge in the interpretation of results associated to this type of localization task (Saulton et al., 2015; Longo et al., 2010) in the sense that one cannot assume that localization tasks which do not provide direct somatosensory stimulations measure body model specific effects. This ability of a method to measure the intended process is also referred to as internal validity. We therefore suggest for a revision of the internal validity of the localization task to measure body specific effects. Please note that other types of localization tasks involving more direct somatosensory stimulation (either by touch, painful or thermal stimuli) might be valid to measure body specific effects.

We would like to point out that there is good reason to believe that participants use different strategies when conducting hand and object localization tasks. We frequently observed that participants report qualitative differences in solving object and hand localizations tasks (e.g. I rely on the feeling of my hand location in the hand but not in the object condition). Hence, it seems that participants rely on feeling their body in the hand task but not in the object task. These reports are encouraging for the discussion about which method to use in order to measure these effects reliably.

Conclusion

In the present study, we investigated the impact of conceptual biases (knuckle misrepresentation) on comparative localization judgments of hands and objects. While the magnitude of localization task distortions appeared to be specific to the hand when using misrepresented landmarks (knuckles), this specificity vanished when asking participants to perform localization judgments for landmarks whose conceptual bias was much smaller. We therefore suggest that the conceptual bias associated with the knuckles might be behind the larger distortions observed with the hand compared to other objects in localization tasks. These results suggest that localization task distortions are not specific to the hand and call for caution when interpreting this type of localization task distortion in terms of body specific effects. We therefore suggest revisiting the internal validity of localization task results involving non-direct somatosensory stimulations.

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Fig.1 Localization task and silhouette task setups . The localization task setup on the left and the silhouette task setup on the right. In both experiments, the participants’ hands were hidden from view.

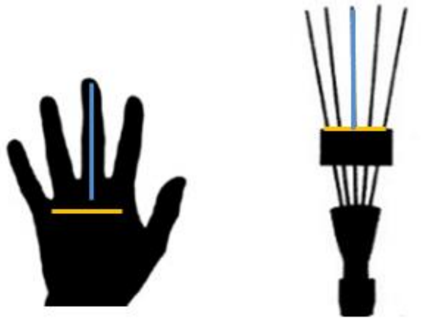

Fig.2 Black silhouette of hand and rake. The blue and yellow lines on the items were not present during experimentation and have been drawn to illustrate the length and width dimensions used to calculate the Shape Index (SI). On the hand, the yellow line corresponds to the distance between the little and index knuckles and the blue line to the distance between the tip and knuckle of the middle finger (as per Longo et al. 2010). On the rake, the yellow line corresponds to the distance between the first and fifth bottom branches and the blue line to the distance between the top and bottom of the middle branch (as per Saulton et al., 2015).

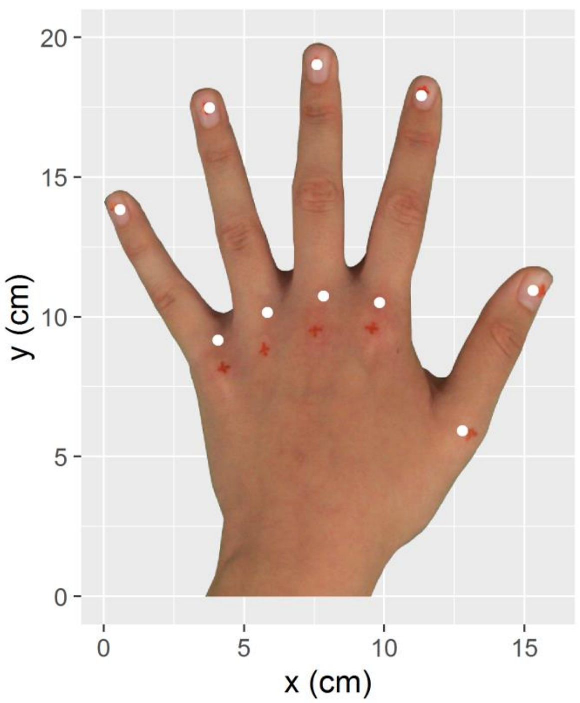

Fig.3 Averaged positions of the finger tips and knuckles as judged by participants in the silhouette task. The red crosses appearing on the hand picture correspond to the middle of the knuckles and tips as drawn by the experimenter on each participant's hand (anatomical locations). The white circles correspond to the estimated average (across participants) positions of the finger tips and knuckles as judged by participants in the silhouette task (conceptual locations). While participants were quite accurate in judging the position associated to the finger tips, they considered the knuckles as being higher up on the hand and further apart (to see the mean and standard error associated with each knuckle, see table 1 in supplementary material). This bias in knuckle location results in a significant underestimation of finger length and significant overestimation of hand width (see result section).

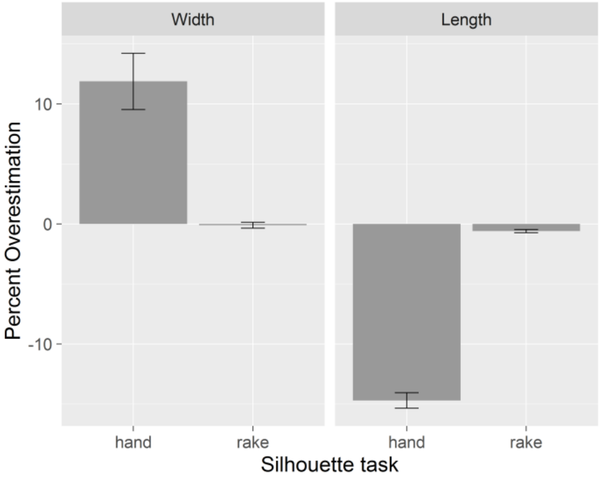

Fig.4 Percent Overestimation of length and width dimensions for the hand and the rake in the silhouette task. The hand presents significant length underestimation of the fingers and significant width overestimation as a result of the knuckle mislocation on the hand silhouette (Fig.3)**.** In contrast no significant length or width distortions are observed for the rake meaning that rake landmarks were accurately positioned on the silhouette. Errors bars represent ±1 standard error of the mean.

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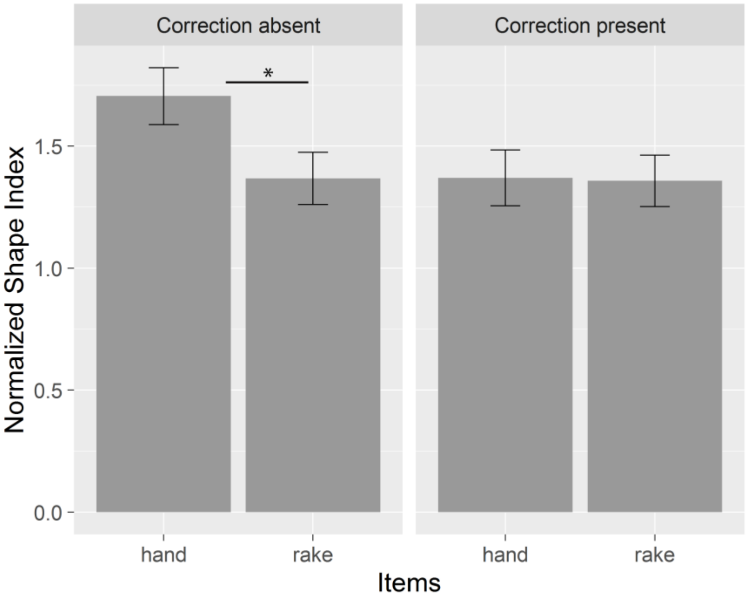

Fig.5. Normalized Shape Index of the rake and the hand measured in the localization task without Correction (Correction absent) and with correction (Correction present) in Experiment 1. In the "Correction absent" condition, we calculated the NSI (estimated SI/actual SI) with the actual SI corresponding to the anatomical/physical locations determined from the photographs. In the **"**Correction present condition" we calculated the NSI with the actual SI corresponding to the estimated landmark locations indicated by participants on the silhouette. The baseline of 1 corresponds to the actual size of the item. While significant differences in distortions are observed between hand and rake without correction, there are no significant differences between hand and rake distortions with correction. Errors bars represent ±1 standard error of the mean.

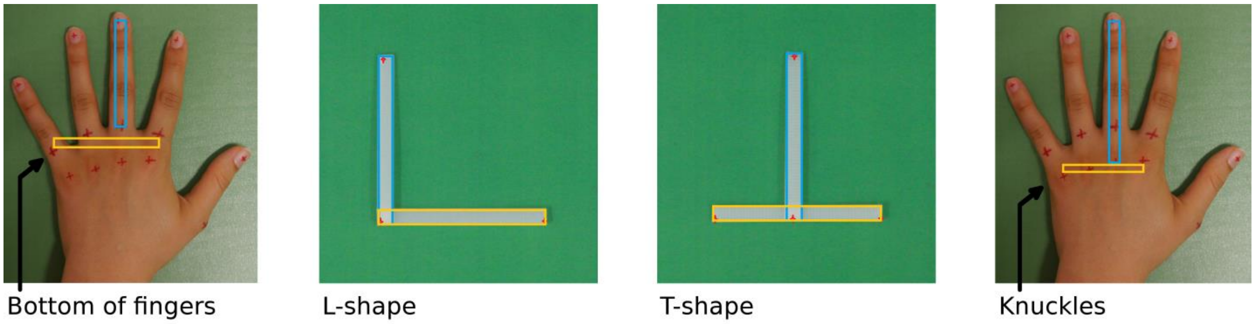

Fig. 6 Images of the item conditions used in Experiment 2. From left to right: Bottom of fingers (Hand Bottom condition), L-shape, inverted T-shape, knuckles (Hand Knuckle condition). The red crosses were drawn by the experimenter on the item to indicate the different landmarks location. The width dimension of the items is marked by a yellow rectangle and the length dimension by a blue rectangle; those colors were not present during experimentation. Those dimensions were used to calculate the Shape Index (width/length *100) associated to each condition.

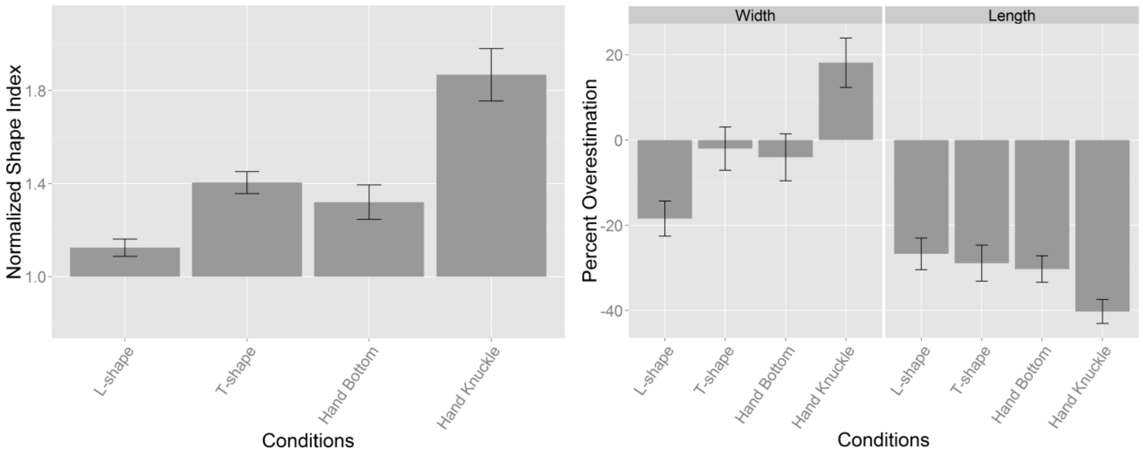

Fig.7 Experiment 2: Normalized Shape Index values (left) and percent overestimation of length and width (right) dimensions measured for the item conditions: L shape, T shape, Hand Bottom (bottoms and tips of fingers) and Hand Knuckle (knuckles and tips of fingers). Errors bars represent ±1 standard error of the mean.