The role of visual similarity and memory in body model distortions

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Abstract

Several studies have shown that the perception of one's own hand size is distorted in proprioceptive localization tasks. It has been suggested that those distortions mirror somatosensory anisotropies. Recent research suggests that non-corporeal items also show some spatial distortions. In order to investigate the psychological processes underlying the localization task, we investigated the influences of visual similarity and memory on distortions observed on corporeal and non-corporeal items. In experiment 1, participants indicated the location of landmarks on: their own hand, a rubber hand (rated as most similar to the real hand), and a rake (rated as least similar to the real hand). Results show no significant differences between rake and rubber hand distortions but both items were significantly less distorted than the hand. Experiment 2 and 3 explored the role of memory in spatial distance judgments of the hand, the rake and the rubber hand. Spatial representations of items measured in experiment 2 and 3 were also distorted but showed the tendency to be smaller than in localization tasks. While memory and visual similarity seem to contribute to explain qualitative similarities in distortions between the hand and non-corporeal items, those factors cannot explain the larger magnitude observed in hand distortions.

Keywords: body representation, body model, memory, hand, distortions

1. Introduction

There is probably no more familiar object to us than our own body. This might give rise to the impression that we know our body better than anything else. This impression partly comes from the fact that we receive constant and immediate sensory information about our body. A single glance at one's hand and we know its location in space as well as its relative proportions with other limbs (e.g., the hand is smaller than the arm). Consequently, it seems natural to assume that we have an accurate perception of the size and shape of our body and its parts. However, multiple studies indicate the presence of systematic distortions in the perception of bodily proportions (Linkenauger et al., 2015; Longo & Haggard, 2010, 2011, 2012; Saulton, Dodds, Bülthoff, & Rosa, 2015). Those distortions were demonstrated in visual estimations tasks (Linkenauger et al., 2015; Longo & Haggard, 2012) as well as in tactile and localization tasks (Longo & Haggard, 2010, 2011). In this study, we are particularly interested in better understanding the origin of the distortions measured in localization tasks (Longo & Haggard, 2010).

Localizing one's body in space is important for perception and action (Frith, Blakemore, & Wolpert, 2000). For instance, one needs to know the location of one's hand in order to grasp objects (Frith et al., 2000). Research suggests that localization judgments related to our body parts are based on the combination of proprioceptive signals (e.g. joint angles) and stored representation of body size and shape (Beers, Sittig, & van der Gon, 1998; Longo & Haggard, 2010; Soechting, 1982). This stored representation of the body metric properties, referred to as the body model, was measured in a localization task for the hand (Longo & Haggard, 2010). Participants were asked to point towards the felt location of their occluded finger tips and knuckles. By analyzing the spatial configuration of the felt locations of the finger tips and knuckles, implicit maps of hand shape were created. Those maps showed large distortions of hand shape. This pattern of distortion was characterized by an overestimation of hand width and an underestimation of finger length.

Interestingly, distortions of hand shape measured in localization tasks matched those found in tactile size perception of the hand (Linkenauger et al., 2015; Longo & Haggard, 2011; Weber, 1834/1996). Hand distortions measured in localization tasks were consistent with anisotropies characterizing the hand's tactile acuity and receptive field geometry (Longo &

Haggard, 2010, 2011). Hand distortions were therefore interpreted as retaining “vestigial traces of the primary somatosensory homunculus of Penfield” (p.11729, Longo & Haggard, 2010).

However, there is no direct evidence that hand distortions in the localization task are due to somatosensation. Particularly, the localization task does not involve tactile perception, as the hand is not touched during the experimentation (see method in, Longo & Haggard, 2010; Saulton et al., 2015). As such, there may be no direct link between anisotropic tactile sensitivity of the hand and hand shape distortions measured in localization tasks.

Indeed, localization tasks distortions were not limited to the hand and appeared to generalize onto certain types of objects, particularly in the case of a rake (Saulton et al., 2015) Distortions measured on the rake item were more similar to the one found on the participant’s hand than on other objects depicting square and rectangular shapes. Although the amount of distortion was significantly smaller on the rake than on the hand, it was also characterized by an overestimation of the width axis compared to a large underestimation of the length. The purpose of the present paper is to better understand why distortions would be more similar across a rake and a hand than across a hand and other geometrical objects. We will explore both body and non-body related factors that might account for these results.

We explored whether an item’s visual similarity to a real hand was behind the greater performance similarity between the hand and the rake. Due to structural similitudes between the hand and the rake (e.g. five fingers/ five tines), it could be that participants partly matched the representation of their hand onto the stored spatial representation of the rake. Hand shapes are more familiar to participants than tools. Hence, matching strategies could be used in localization task as an attempt to improve one’s performance in the localization task. If this is the case, an object with greater visual similarity to a real hand (e.g. a rubber hand) might depict distortions that are closer to the hand than the rake. This idea would be in line with research on embodiment showing that objects can be experienced as part of one’s body (i.e. as embodied) when they share important structural and visual information about the body part (Bertamini & O’Sullivan, 2014; Holmes, Snijders, & Spence, 2006; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005). Studies on the rubber hand illusion suggest that the degree to which fake body parts (rubber hand and non-biological mechanical hand) can be embodied depends on the similarity between the actual body part and the tested stimulus. For instance, embodiment of a rubber hand is facilitated and obtained to a larger degree compared to a non-biological hand made of wires (Bertamini & O'Sullivan, 2014). Although embodiment mechanisms are unlikely to occur in the localization task (no visuo-tactile stimulation applied onto the participant's hand and the tested stimulus), one cannot exclude the possibility that greater visual similarity between an item and a real hand contribute to an increase in localization task distortions. This aspect was investigated in experiment 1 by comparing participants' estimates of landmarks located on a rubber hand, a rake and the participants' hand in a localization task.

Alternatively, the similarity in localization task distortions between the hand and rake might be explained by non-body specific factors. Previous work suggests the presence of viewer-centered biases and immediate vision on hand distortions in localization tasks (Longo, 2014; Saulton et al., 2015). In line with these ideas, people might also partially rely on a general form of memory (e.g. spatial memory) that is not directly related to proprioception. Overall, memory distortions have been observed in multiple studies, from tasks involving the recollection of stories or experienced events (Bartlett, 1932; Nourkova, Bernstein, & Loftus, 2004) to psychophysical experiments measuring object size perception, localization and distance estimations on maps and figures (Cooper, Sterling, Bacon, & Bridgeman, 2012; Huttenlocher, Hedges, Corrigan, & Crawford, 2004; Tversky, 1981, 1992; Tversky & Schiano, 1989). For instance, distances stored in memory between entities of the same categories (cities on map) are perceived relatively smaller compared to distances between entities of different categories (Tversky, 1992). Semantically, fingers often constitute a separate body part category (Enfield, Majid, & Van Staden, 2006). Hence, memory biases related to finger categorization could explain why underestimation of finger length compared to hand width were found in localization tasks (Longo, Mancini, & Haggard, 2015; Mattioni & Longo, 2014). To assess whether memory of distances between landmarks can create the distortions measured on items in the localization task, we ran a second experiment. In experiment 2, we asked participants to indicate on a line, the memorized distance between landmarks marking the finger/branches length and width of the hand, the rake and the rubber hand. We compared the ratio of length over width distortions obtained in this distance memory task (experiment 2) with the same length to width ratio calculated in localization task (experiment 1) for the same items.

In order to investigate whether the distortions measured on the participant's hand in the distance memory task can be behaviorally dissociated from distortions coming from the somatosensory feeling associated with one's own hand, we ran a third experiment. In experiment 3 participants indicated on a line, both the memorized and the felt distance between landmarks on their hand. Different results between the felt and memorized distance conditions of experiment 3 would favor the hypothesis that memory information about hand parts can be dissociated from information related to the somatosensory feelings associated to the hand.

2. Experiment 1

In experiment 1, we investigated the extent to which the similarities between the item and the participant's hand modulate the distortion measured in the localization task. In order to measure the contribution of visual similarity on the items' distortions, it is important to choose stimuli that gradually increase in visual similarity with a hand: a rake which only had a similar structure to a real hand; a rubber hand which had the structure and the visual configuration/form of a real hand and the participant's own hand. We used typical localization task methods (Longo, 2014; Longo & Haggard, 2010, 2012; Saulton et al., 2015) to estimate the relative distance between 10 predefined landmarks on the hand, the rubber hand and the rake. We then compared the aspect ratio of the hand with the ones from hand-like items (rake and rubber hand). If the magnitude of the distortions increases with the items visual similarity to a real hand, the difference in distortions between the participant's hand and the rubber hand should be smaller than the one obtained with the rake. In other words, the estimated shape of the rubber hand should be more distorted than the rake.

Before starting the main experiment, we ran a pilot study to assess whether individuals (N=16; Age M=28.8) judged the rubber hand to be perceptually more similar to the real hand compared to the rake. Participants were seated at a table and items were presented separately in front of them in a random order, for 30 sec each. After each item presentation (the rake, the rubber hand and their own hand) participants had to rate how similar the item was to a real hand on a continuous interval scale from 0 to 10. Participants had to answer the question: How similar is this item to a real hand in terms of visual appearance? 0 corresponded to "the item is not at all similar to a real hand" and 10 corresponded to "the item is exactly like a real hand". Both the rubber hand [M=8; SD=.77; $t(15)=-10.32$; $p<.001$; $r=.93$] and the rake [M=3.81; SD=1.98;

$t(15)=-12.48$; $p<.001$; $r=.95$] were rated as differing from a real hand [M=10; SD=0] in terms of visual similarity. More importantly, participants considered the rubber hand to look significantly more like a real hand than the rake [$t(15)=7.78$; $p<.001$; $r=.89$]. Thus, the visual similarity to the hand significantly increased from the rake to the rubber hand.

2.1. Method

2.1.1. Participants.

Sixteen right handed individuals (5 males) between 20 and 34 years of age (M=24.5) participated in the localization task. Participants gave written informed consent prior to the study. The research was approved by the ethics committee of the University of Tübingen.

2.1.2. Materials.

The items consisted of the participant's right hand, a rake and a right rubber hand. The items can be seen in Figure 1. The length and width dimensions of each item are reported in the analysis section.

2.1.3. Procedure.

Participants sat at a table with their body midline aligned with a mark on the table which indicated the placing position (a cross) for the items. An item was placed centrally with its lower edge at the center of the cross. Participants viewed the item for 15 seconds while the position of the item was photographed using an overhead mounted camera (Canon, EOS 40D; Zoom lens, EF- 28-135mm). The photographs were used to derive the exact size of the items (Fig. 1). Afterwards a computer monitor (Dell U2412M monitor with a 16:10 widescreen aspect ratio) was slid in parallel to the table top, over the item thereby occluding it (Fig. 2). Instead of doing the localization task with a stick (see method; Longo & Haggard, 2010), participants used a mouse cursor to point on the monitor (see method; Saulton et al., 2015).

To minimize variation in task difficulty, ten landmarks were used in the localization task for each of the three items on similar locations: the finger tips and center of the knuckles at the bottom of each finger for hands and the rubber hand and the top and bottom of the five branches for the rake (Fig. 2).

Each participant was familiarized with the landmark names and their corresponding locations on an item resting on a flat surface (for about two minutes). None of the items were touched nor held in front of participants by the experimenter. An experimental block measured participants' ability to localize predefined landmarks on a particular item (hand, rubber hand or rake). For the rake and the rubber hand, participants were told to imagine the screen to be transparent so that they could 'see' the landmarks below it. For the hand, participants had to perform the task while relying exclusively on the felt location of their finger tips and knuckles. They were instructed not to use visual imagery of their hand.

An experimental trial started by presenting the name of an item's landmark (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 indicated as accurately as possible the perceived location of the queried landmark by positioning the mouse cursor over the corresponding position on the computer screen and left-clicking with the mouse. The 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. After testing each landmark in random order five times, the computer monitor was removed for 15 seconds making the item visible to the participant and the item's location was photographed to ensure that it had not moved. Then each landmark was again tested five times. The ten measures for each landmark constituted one experimental block. Each experimental block probed all landmarks of an item (three items) in one specific orientation (upright or 90° anticlockwise rotation). There were a total of 6 blocks. The testing order of experimental blocks was randomized across participants. At the beginning of the localization task participants received one experimental block as training with a different object (pen). The training data were not included in the analysis.

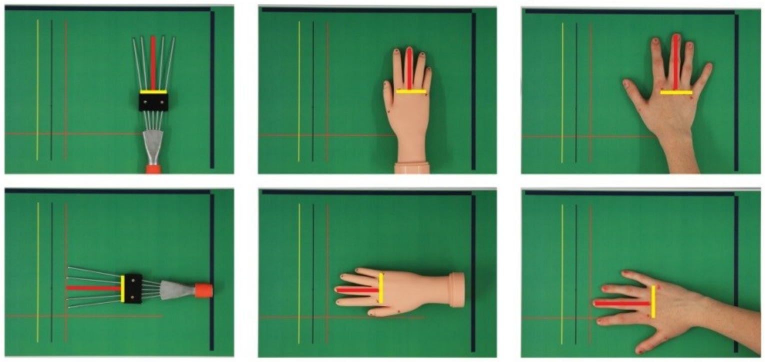

Fig.1. Images of the items used in the localization task. From left to right: rake, rubber hand, participant's hand positioned in upright (top row) and rotated (bottom row) orientation. The yellow and red lines on the items were not present during experimentation and have been drawn to illustrate the item-centric width (yellow) and length (red) dimensions used to calculate the Normalized Shape Index of the items.

Fig.2. Experimental setup for the localization task. The right hand is lying in upright position on the table while being covered by the screen and thereby hidden from the participant's view. The localization of the right hand's landmarks was done by directing the mouse cursor (with the left hand) to the corresponding location on the screen. Participants were asked to place the mouse pointer on the screen directly above where it felt like the tip or knuckle of their finger was positioned.

2.1.4. Analysis.

We measured the relative distance between judged positions of landmarks along the length and width of each item, irrespective of the landmarks' true locations. In Fig. 1, the width of an item is marked with a yellow line, and the length is marked with a red line. For both the rubber hand and the participant's hand, length was defined as the distance between the knuckle and the tip of the middle finger (Mean length (cm): rubber hand= 7.13 cm, SD=.04; hand= 9.25; SD=.49). Hand width corresponded to the distance between the knuckles of the little to the index finger (Mean width (cm): rubber hand= 4.81, SD= .02; hand= 5.64, SD=.32). For the rake, the length was defined as the distance between the bottom and top of the middle branch (Mean length = 9.84; SD=.04) while the width was the distance between the bottom of the first and fifth branches (Mean width= 3.97; SD=.015). We quantified the item's shape using its width to length ratio, referred to as Shape Index (SI=100*width/length). This measure is assumed to reflect the overall aspect ratio of the item (see method, Longo & Haggard, 2012). We calculated the Shape Index for the participants' hands (SI=61.13; SD=4.41), the rake (SI = 40.34; SD=.22) and the right rubber hand (SI =67.47; SD=.54). In order to allow comparisons between items, we normalized each item's Shape Index (SI) by dividing the estimated SI by the actual item's SI (Normalized Shape Index= NSI). A value of 1 indicates veridical Shape index estimates.

2.1.5 Statistics.

For statistical analysis, we used the Mauchly's sphericity test to assess sphericity violations. In cases of sphericity violations, we reported the results with Greenhouse-Geisser sphericity corrections.

2.2. Results

2.2.1. Do we observe items' distortions in the localization task?

As shown previously with the human hand (Longo & Haggard, 2010), all items showed distortions characterized by significant underestimation of length relative to width in both orientations (see Table 1). The rubber hand was the only item to show no differences in length compared to width estimations in the rotated orientation (NSI close to 1). To assess differences in distortions between items we conducted a within-subjects analysis of variance (ANOVA) on the Normalized Shape Index (NSI) with items (hand, rake, rubber hand) and orientation (upright vs. rotated) as within-subject factors. There was a significant effect of item [$F(1.35, 20.22)=9.76$, $p=.0028$, $\eta^2=.13$] and orientation [$F(1, 15)=7.24$, $p=.017$, $\eta^2=.059$] on the NSI. The interaction effect between orientation and item was non-significant [$F(2, 30)=0.88$, $\eta^2= .0068$]. The effect of orientation on the NSI presumably reflects the presence of viewer center biases. Indeed, the items distortions were larger in the upright compared to the rotated orientation (for visual comparison see Fig.3).

Items	Rake		Right Hand		Rubber Hand	
Orientation	Upright	Rotated	Upright	Rotated	Upright	Rotated
Mean Estimated Length	M length -18.86% SD=21.14	M length -16.28% SD=22.69	M length -38.22% SD=14.66	M length -39.07% SD=12.22	M length -20.09% SD=21.67	M length -12.77% SD=25.05
Mean Estimated Width	M width 27.02% SD=29.32	M width 22.05% SD=30.94	M width 25.80% SD=36.27	M width 7.39% SD=23.34	M width 3.67 % SD=24.11	M width -3.75% SD=20.98
Comparisons between width & length estimates	*t(15)=4.21 p=.002 r=0.74*	*t(15)=3.30 p=.010 r=0.65*	*t(15)=6.92 p<.001 r=0.87*	*t(15)=8.45 p<.001 r=0.90*	*t(15)=2.59 p= .020 r=0.56*	*t(15)=1.17 p= .250 r=0.29*

Table.1. Localization task results for all items across different orientation. Mean estimated length overestimation (first row) and width (second row) of each item are reported in percent overestimation e.g. for an item's length: [100*(judged length-actual length)/actual length]. Third row: comparisons between width and length estimates of each item in upright and rotated orientations. P-values are Holm-corrected. Positive t values indicate that width estimates were larger than length.

2.2.2. Is there an effect of visual similarity on the distortions?

To understand the effect of items on the distortions, we ran paired t-tests on each item's normalized shape index averaged across orientation. We used the error term of the above interaction from the overall analysis of variance as the error estimate in the a priori t-tests comparisons between items. The participant's hand (M=1.85; SD=0.67) was significantly more distorted than the rubber hand [Rubber hand $t(15)=5.98$, $p<.001$, $r=.84$] and the rake [$t(15)=2.056$, $p=.012$, $r=.47$] . These findings are in line with the idea that localization tasks can measure body model specific distortions. According to our initial hypothesis, if hand shape similarity plays a role on spatial distortions measured in localization tasks, then the distortions measured on the rubber hand should be larger than the one measured on the rake. However, we observed a trend in the opposite direction. Descriptively, the rake (M=1.50; SD=.72) was more distorted than the rubber hand (M=1.27; SD=.53). Yet, despite a trend in the data, this difference did not reach significance [$t(15)=1.94$, $p=.09$, $r=.44$]. This result contrasts with the hypothesis that larger visual similarity between corporal and non-corporal items leads to an increase in localization task distortion.

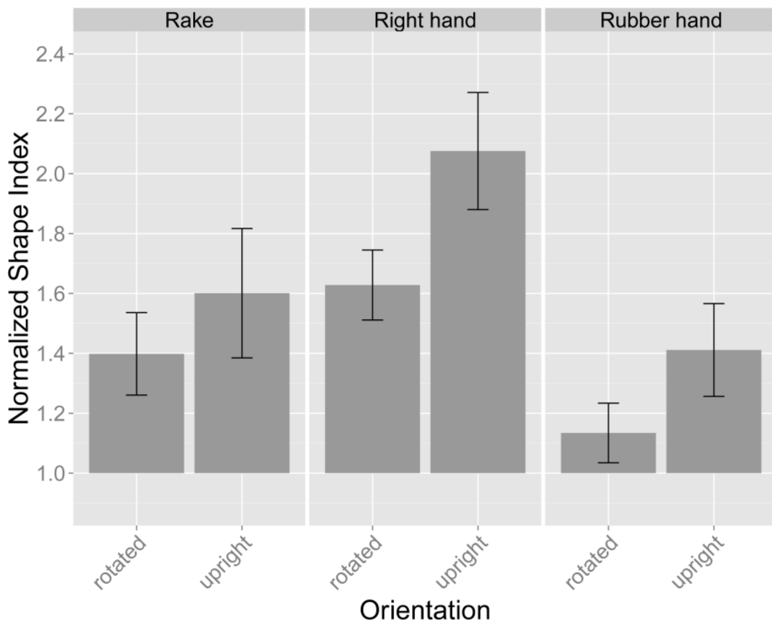

Fig.3. Results of the localization task. The Normalized shape index (NSI) of the participants' hand, the rubber hand and the rake estimated in the localization task in upright and rotated orientation in experiment 1. Bars indicate +/- 1 SE from the mean.

2.3. Discussion

Experiment 1 investigated the relation between an item's visual similarity with a real hand and the spatial distortions in a localization task by varying the extent of the items' resemblance to a real hand (rubber hand and rake). We hypothesized that differences in distortions between corporeal and non-corporeal items could be positively related to the visual similarity between the item and the real hand. Results of our pilot study showed that subjects judged the rubber hand as significantly more similar to a real hand compared to the rake. Hence, we expected the rubber hand's distortions to be larger than distortions measured on the rake. This is not what we observed. Descriptively, the rubber hand was less distorted than the rake but this difference was non-significant. It seems that greater visual similarity between corporeal and non-corporeal items tested in our study were not associated with an increase in localization task distortions.

Because the body related hypothesis tested in the first experiment is inconclusive, we examined the influence of non-body specific factor on localization distortions between the rake and the hand, such as memory effects (Huttenlocher et al., 2004; Tversky, 1992). In particular, memory biases related to distances between landmarks of the same category (e.g. rake's tines or finger length) could explain the relative underestimation of the item's length compared to width found in our localization tasks (Longo et al., 2015; Mattioni & Longo, 2014; Saulton et al., 2015). To investigate the contribution of memory to the distortions of items, we used a different task to compare spatial biases in the recall of previously visually learned distances on the participant's hand, the rubber hand and the rake.

3. Experiment 2

In experiment 2, we want to know whether directly *memorizing the relative distance* between landmarks located on the participant's hand, a rubber hand and a rake can retain distortions typically associated with localization judgment tasks. In the localization task, participants had to point on a screen towards *the felt location* of predefined landmarks on their hand (absolute landmark location). To decrease the participants' reliance on proprioception during body estimates, we used a memory task in which participants had to indicate on a line, the remembered *relative distance* between those landmarks. Those distances corresponded to the length and width axis used for each item to calculate the NSI in experiment 1(see Fig.1). We then compared NSI for all items between the two tasks. If the effects seen in the localization task merely reflect memory distortions, the difference in distortions measured across items in experiment 2 should be similar to the one measured in the localization task.

3.1. Method

3.1.2. Participants.

A different group of participants, sixteen right handed individuals (3 males) between 23 and 37 years of age (Mean=28.8) took part in experiment 2. Participants gave written informed consent prior to the study.

3.1.3. Materials.

Stimuli were the same as for experiment 1. Participants had to remember the length or width of an item along the dimensions marked with yellow and red in Fig.1. The dimensions of the item's width and length are reported in the analysis section of experiment 1. The middle finger of the right hand (knuckle to tip of the finger) and the middle branch of the rake (bottom to top of the branch) were chosen as representative distances along the length dimension. For the width, we chose the distance between the bottom of the first and fifth branches of the rake and the distance between the knuckles of the little and index fingers of the hands. All landmarks were indicated by a red cross on the item, like in the localization task.

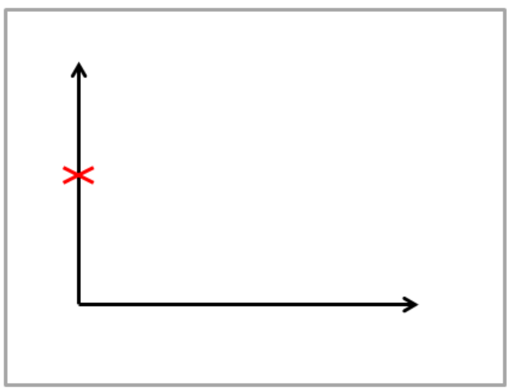

Fig.4. The distance memory task. Representation of the answer sheet for the distance memory task used in experiment 2 and 3. Participants gave their answer by means of marking the estimated distance with a cross on the respective axis (here the red cross) on an A4 sheet of paper.

3.1.4. Procedure.

Each item was presented in upright position on a table in front of the participant. Depending on the trial, participants had to remember the relative distance between either two landmarks along the length or two landmarks along the width of the item. Participants had about 40 seconds to memorize the distance between those two landmarks. After the learning period, the item was hidden from view by positioning it under a cardboard box. After a retention period of about 10 sec, participants were shown the answer sheet (Fig.4) which showed a coordinate system. The coordinate system's width to length aspect ratio (24.5 by 15.5 cm; ratio=1.58) was designed to match in proportions the aspect ratio of the computer screen used in experiment 1

(52 by 33 cm; ratio =1.58). Participants were asked to estimate on each axis, the remembered length or width of an item in relation to the point of origin of the graph**.** The distance along the length dimension (e.g. finger length) had to be indicated by a cross on the y axis and the distance along the width dimension (e.g. hand width) had to be marked on the x axis. Participants performed the task with their left hand. The left hand used to mark the landmarks location on the axis was covered by long sleeves. We controlled for any landmark matching strategies by presenting the items to the participants at a different location from the paper on which they performed the task. A new answer sheet was given at each trial (2 trials per item: one for the width and one for the length). Each trial assessed a different dimension and/or different item. The trials order was randomized across items and participants.

3.2. Results

3.2.1. Do we observe distortions in the distance memory task?

In experiment 2 (distance memory task), all normalized SIs were significantly larger than 1 (all $p<.001$, all effect sizes $r\geq.74$; p values were Holm-corrected, see Table 2) suggesting that all items showed underestimation of length relative to width (mean length estimate < mean width; see Table 2). Hence, we observe distortions in the distance memory task. Yet, the results are very similar for all items as indicated by the non-significant effect of item on the distance memory task [$F(2, 30)=.19$, $p=.82$, $\eta^2=.0052$]. This result contrasts with the differences in distortions found between items in the localization task of experiment 1 (see Fig.5).

3.2.2. Localization vs memory task distortions.

To assess differences in distortions between experiment 1 (localization task) and experiment 2 (distance memory task), we conducted a mixed analysis of variance (ANOVA) on the normalized shape index in the upright orientation with items (hand, rake, rubber hand) as a within-subject factor and experiment as between subject factor (see Fig.5).There was a significant effect of item [$F(1.36, 40.70)=5.56$, $p=.01$, $\eta^2=.061$] and experiment on the NSI [$F(1, 30)=9.99$, $p=.036$, $\eta^2=.17$]. The interaction effect between experiment and item was significant [$F(1.36, 40.70)=6.14$, $p=.010$, $\eta^2=.07$]. These results suggest that the distortions present on the items vary between experiments. Specifically, items were more distorted in the localization compared to the distance estimation task (see Fig.5). We used post-hoc Welch two sample t-tests with Holm correction to analyze the interaction between experiment and item. We compared the effect of the experiment on the NSI for each item separately. The participants' hand had significantly larger distortions in the localization task compared to the distance memory task [$t(16.52)=4.42$; $p=.0012$; $r=.74$]. The difference in distortions between the two experiments for the rake and the rubber hand were not statistically significant [rake: $t(15.76)=1.76$; $p=.19$; $r=.41$; rubber hand: $t(16.94)=1.32$; $p=.20$; $r=.31$]).

We further noticed smaller between-subject variability in the distance memory task compared to the localization task. This indicates that participants in the memory task had not only a tendency to be better at estimating the hand dimensions but they were also more consistent with their judgments as a group compared to the localization task. We cannot exclude the possibility that the larger variability in the localization task might have obscured some of the differences between the localization and the distance memory task.

Item	**Rake**	**Right hand**	**Rubber hand**
Comparison of NSI to Baseline	M= 1.21; SD=.14 *t(15) = 6.22* *p<.001* *r=.85*	M= 1.19; SD=.18 *t(15) = 4.25* *p<.001* *r=.74*	M= 1.2; SD=.16 *t(15) = 5.03* *p<.001* *r=.79*
Comparisons between width & length estimates	M length= -12.62% SD=8.9 M width= 6.25% SD=16.9 *t(15) = 5.95* *p<.001* *r=.84*	M length= -11.50% SD=9.74 M width=4.68% SD=16.6 *t(15) = 4.31* *p<.001* *r=.74*	M length= -10.47% SD=13.25 M width=6.37% SD=14.52 *t(15) = 5.30* *p<.001* *r=.80*

Table.2. Distance memory task results. First row: Mean NSI values and comparison of NSI to baseline for the rake, the right hand and the rubber hand. All items were significantly distorted from baseline. Second row: for each item, mean width and length percent overestimation e.g. for an item's length [100*(judged length-actual length)/actual length] and comparison between width and length estimates. P-values are Holm-corrected. Positive t values indicate that width estimates were larger than length.

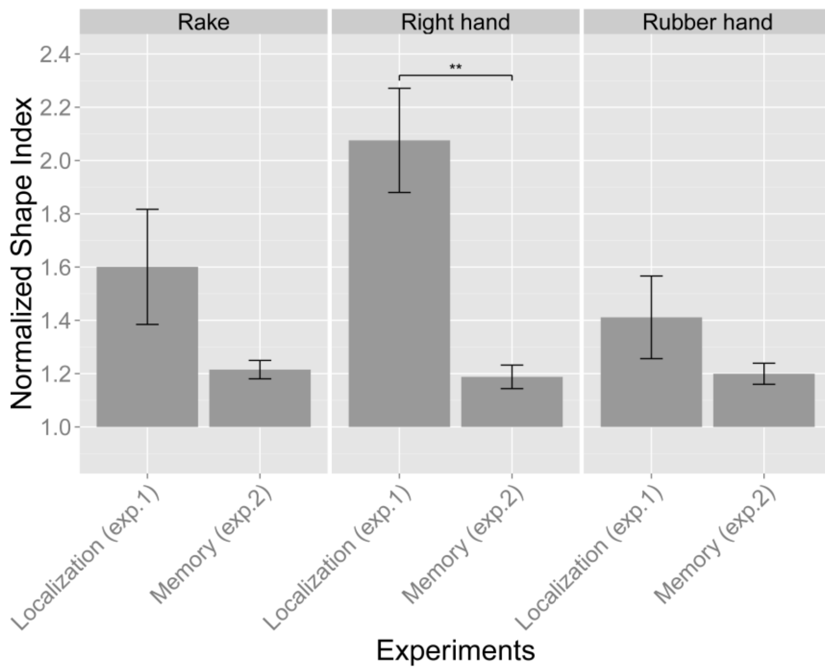

Fig.5. Comparisons of Normalized Shape Index between experiment 1 (localization task) and experiment 2 (distance memory task). The participant's right hand is significantly more distorted in experiment 1 (localization task) compared to experiment 2 (distance memory task). Data of experiment 1 correspond to the results obtained in upright orientation in the localization task for all trials (for a visual comparison between experiments at trial number N=1, see supplementary material S1).

3.3. Discussion

Experiment 2 investigated whether memory distortions could contribute to explain the biases observed in the localization task. To investigate this point, we used a distance memory task in which participants had to remember the relative distance between two landmarks along the length and width of an item. If memory was entirely contributing to distortions in the localization tasks, we would have expected to find similar relative differences across items in the distance memory task. Results of the distance memory task indicated that all items were rather equally distorted. This finding contrasts with the large relative differences in distortions found in the localization task between the participant's hand and non-corporeal items. Hence, memory cannot fully explain distortions measured in localization tasks.

A direct comparison of the two experiments showed that distortions on the hand were observed in smaller magnitude compared to the localization task results. Evidence suggests that tasks involving relative distance judgments about hand parts can lead to attenuated hand distortions compared to localization tasks results (Longo & Haggard, 2012).This is the case of a line length task in which subjects are asked to judge whether a line is shorter or longer than the *felt* length of their finger and hand width. Although we did not ask participants to *feel* but to use *stored visual information* about distances on their hand, we cannot exclude that participants relied on somatosensory information instead of memory in experiment 2. Relying on somatosensation could have influenced the distortions measured on the hand in our distance memory task (experiment 2), although other factors could also play a role. To investigate this point, we ran a third experiment.

4. Experiment 3

We performed a third experiment in which we asked two groups of participants to assess the distance between landmarks on their hand either by relying on their *memory* (stored visual information about hand parts) or by *feeling* (somatosensory information about hand parts) the distance (Longo & Haggard, 2012). The procedure was the same as in experiment 2 except for the looking time which was matched to the one used in the localization task (15 sec). If participants predominantly relied on somatosensation in the distance memory task, results of experiment 3 should indicate similar distortions regardless of whether we instruct participants to memorize group 1) or to feel (group 2) the distances on the hand. On the other hand, a significant difference between these two groups (feeling vs. memory) would speak in favor of the distance memory condition involving different mechanism than the feeling (somatosensory) condition.

4.1 Method

4.1.1 Participants

Two groups of participants took part in experiment 3 in order to avoid interferences between the different conditions (feeling vs. memorizing distances on the hand). Group 1 (memory condition) consisted of 16 participants (8 males) aged between 22 and 36 years old (Mean=28.87). Group 2 (feeling condition) consisted of 16 other participants (12 males) all aged between 20 and 33 years old (Mean=26.94). All individuals were right handed.

4.1.2 Procedure

Experiment 3 was only performed on the participant's right hand. The method and procedure used in experiment 3 was the same as in experiment 2 except for the following. The looking time associated to learning the hand was 15 seconds instead of 40 seconds. Group 1 was asked to retrieve landmark distances via stored visual information about the hand (memory condition) while group 2 was instructed to retrieve the same distance information from the felt locations (feeling condition; group 2). In group 2, we especially insisted that participants should focus on the somatosensory feeling of their hand and avoid the use of mental visualization strategies.

4.2 Results

4.2.1 Feeling the hand led to larger distortions than memorizing the hand.

To assess differences in distortions in the distance memory task between the two conditions (memory or feeling), we conducted an independent Welch t-test on the NSI values. NSI values were significantly more distorted in the feeling compared to the memory condition [$t(18.031)=2.49$; $p=.02$; $r=.51$]. Hence, changing instructions from memorizing to feeling hand parts significantly increased the amount of distortion present on the hand in the distance task.

4.2.2 Different hand distortions across experiments.

Interestingly, the direction of the effect measured in experiment 3 (increase in distortion from memory to feeling) is in line with the larger hand distortions measured in localization tasks (see Fig.6). To further analyze differences in hand distortions across the localization (exp.1) and distance tasks (exp.3), we used independent Welch t-tests on NSI values measured in experiment 1 with the feeling and memory conditions of experiment 3. The hand was significantly more distorted in the localization task compared to the feeling condition [Group2: $t(20.117)=2.61$; $p=.016$; $r=.50$] and memory condition [Group1: $t(15.54)=3.89$; $p=.0013$; $r=.70$] of experiment 3. The significant difference found between the feeling condition and the localization task suggests that factors other than somatosensation (e.g. relative distances vs. absolute position judgments) are susceptible to induce differences in the results. This point will be discussed in the general discussion.

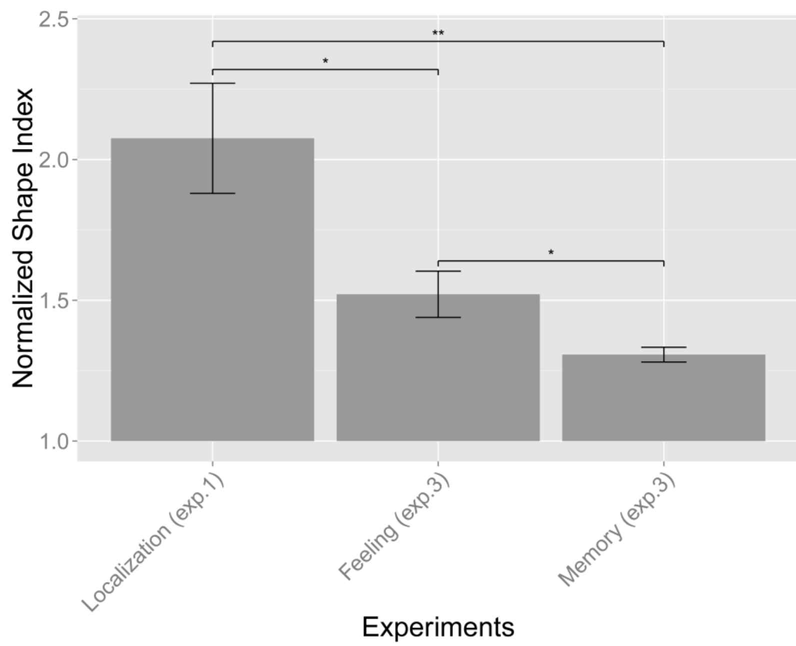

Fig.6. Comparisons of Normalized Shape Index between experiments 1 and 3 for the participant's hand. Experiment 1 corresponds to the "localization (exp.1)" results obtained for the hand in upright posture for 16 participants. Results of experiment 3 are presented for group 2 "feeling (exp.3)" and group 1 "memory (exp.3)" with the hand in upright posture with 16 participants in each group. Localization task results for the hand are more distorted than in the feeling condition of experiment 3. In experiment 3, the feeling condition results (group2) are more distorted than in the memory condition (group1).

5. General Discussion

The goal of the study was to better understand the psychological processes underlying localization task results for corporeal and non -corporeal items. Specifically, we assessed the plausibility of visual similarity (experiment 1) and memory (experiments 2 and 3) as the driving force behind the distortions in the localization task.

5.1 The role of visual similarity on hand distortions in experiment 1.

In experiment 1, we measured localization task distortions with objects that varied with respect to their visual similarity to a real hand, namely a rake and a rubber hand. The magnitude of the distortions in the localization task did not increase with the structural/visual similarity of the item to a real hand: although the rubber hand was rated as the most similar item to a real hand it was also the least distorted item. Therefore, it seems that increasing the visual similarity between corporeal and non-corporeal items cannot explain the difference in the magnitude of distortions across items in the localization task. It might be that the rubber hand used in our experiment is too different from a real hand (despite being rated as more similar to the hand than the rake) to detect an effect of visual similarity on our results. Using a more realistic hand shape could increase the chance of finding similar distortions to the participant's own hand. Apart from visual similarities there are several other factors that might influence the localization distortions, e.g. different action affordances associated with different items. The examination of these factors is interesting for future work.

5.2 The role of memory in experiment 2.

In experiment 2, we investigated whether larger hand distortions in the localization task could be due to a memory effect. To decrease the participants' reliance on proprioception during body estimates, we used a memory task in which participants had to remember the relative distance between two landmarks along the length and width of each item. Interestingly, distortions measured in experiment 2 were found in similar magnitude across all items. This result contrasts with the findings of the localization task which indicated larger hand shape distortions compared to non-corporeal items. If participants had used similar cognitive processes to perform the localization task and the distance memory experiments, we should also have measured an effect of items on the distortions. This is not what we observed. Hence, different mechanisms might be at play in the localization task and the distance memory task.

5.3 Memorizing vs. feeling one's hand in experiment 3

It has been suggested that subjects can rely on somatosensation when comparing the length of a line to a distance on their hand (Longo & Haggard, 2012). This type of task is very similar to our distance memory task. Hence, biases measured on the hand representation in experiment 2 could have been influenced by the somatosensory feeling of one's own hand. In order to investigate whether participants' own hand memory judgments are directly influenced by the feeling of their own hand, we ran a third experiment. In experiment 3, we asked different groups of subjects to perform the distance memory task either by memorizing (stored visual information condition: group 1) or feeling parts of their hand (somatosensory information condition: group 2). If the results of experiment 2 were dominated by somatosensory processing of hand shape, we would have predicted similar performance between groups in which participants feel or memorize parts of their hand (experiment 3). Results of experiment 3 indicated larger distortions in the “feeling group” compared to the “memory group” for the hand. Hence, our results do not seem to support this suggestion.

5.4 Differences between localization and distance memory tasks.

Distances vs. location judgments. In the distance memory task, the spatial representations of items were all characterized by significant length underestimation compared to width. These types of biases were also found in the localization task but in larger magnitude. This was especially the case for the participants’ hands. Evidence from visual perception indicates that distance judgments rely on different sources of information than location judgments (Abrams & Landgraf, 1990; Loomis, Silva, Philbeck, & Fukusima, 1996). Although this fact might contribute to explaining the presence of larger distortions in experiment 1, it cannot explain why all items are perceived rather equally in the distance memory task but differently in the localization task.

Looking time. Alternatively, the difference in accuracy between the two tasks might be due to differences in looking time between the distance memory task (40 seconds) and the localization task (15 seconds). In line with this hypothesis, additional analysis performed on experiment 3 suggests that shorter looking time (15seconds) increased hand distortions compared to the distance memory task [$t(24.38)=-2.32$; $p=.03$; $r=.42$]. However, this result did not change our main conclusion. Even after matching looking time between the localization task and the distance memory task (experiment 3) hand distortions were significantly less pronounced compared to the one measured in the localization task (see Fig 6). Hence, difference in looking time cannot explain why hand distortions are larger in the localization compared to the distance memory task.

Different body representations. According to previous work, different types of body representations might be accessed depending on task demands (Longo & Haggard, 2012). It has been suggested that localization task distortions were more likely to reflect biases from somatosensory processing than tasks referring to visual relative distance judgments (Longo & Haggard, 2012). This idea could explain why hand distortions were larger in the localization task than in other conditions of experiment 3. Compared to the localization task, the distance memory task might rely to a larger degree on visual information. Even in the “hand feeling group” participants have to match the felt represented distance between two landmarks on their hand onto a visual line. This judgment implies a transfer of distance information from the somatosensory modality to the visual modality. Ultimately, this estimation cannot be totally immune to visual influences (Vignemont, 2014). It is very difficult to dissociate visual from somatosensory or proprioceptive influences in tasks aiming to assess body representations as there are no tasks which directly and only assess somatosensation. The same could be said about visual estimates of the body. Hence, interpretations regarding different sensory processing underlying hand shape perception in different tasks need to be discussed with caution.

Variability difference between experiments. Overall results suggest that participants instructed to feel landmarks on their hand estimate their own hand shape with more variance compared to conditions in which they are told to use stored visual information about their hand. Individual differences in susceptibility to proactive interference (Anderson & Neely, 1996; Peterson & Peterson, 1959) could play a role in the increased variability measured on the hand in experiment 1. However, additional results related to this aspect, suggest this is unlikely to be the case in our study (for more details on proactive interference, see section S2 of the supplementary material). Alternatively, the smaller variability measured in the memory condition could indicate that assessing memory representation is generally more reliable than assessing somatosensory representation associated to the feeling of one's own body. Further investigations are needed to fully understand the variability differences between the two experiments.

5.5 Alternative hypotheses regarding larger hand distortions in localization tasks.

Somatosensory influences. Overall, the fact that localization tasks results were more distorted for the participants' hand than the rake and the rubber hand suggests that the participant's hand is treated differently from the other hand-like items chosen in our study. One difference, among others between corporeal and non-corporeal items is the presence of proprioceptive/somatosensory information about one's own body. Such information is not available in the case of the rake and the rubber hand. In fact, 81.25% of participants freely reported that "feeling their hand was helping them localizing the landmarks". Hence, one cannot exclude the possibility for hand distortions to be more distorted due to somatosensory influences. Yet, importantly, our results do not provide direct evidence for this. This hypothesis would need to be directly tested to be confirmed. This means other mechanisms than somatosensation could contribute or explain the differential distortions observed between the participants' hand and other items.

Viewer-dependent representations. The observation of orientation viewpoint dependent biases in hands (see supplementary material S3 for comparisons with the left hand) and non-corporeal item representations (see results of experiment 1) suggests that factors other than somatosensation contribute to the localization task distortions. Items were characterized by a decrease in distortions in the rotated compared to the upright orientation. A decrease in item's distortion can be indicative of biases in torso or eye centered reference frames as demonstrated in the literature on visual illusions (see results of the bisecting line illusion or vertical horizontal illusion affected by a change in head orientation; Finger & Spelt, 1947; Hamburger & Hansen, 2010; Künnapas, 1955; Künnapas, 1958). If biases were only reflecting an internal representation of the hand, we would have expected to observe a similar pattern of distortion across orientation. Hence, the presence of orientation sensitive distortions shows that other factors than somatosensation are likely to contribute to the distortions.

Holistic perception. Research on visual holistic perception indicates that the perception of faces and bodies is sensitive to stimulus inversion (turning the stimulus upside-down). This inversion effect has been taken as evidence that the perception of faces and bodies rely on a holistic percept, e.g. the perception of the configuration of facial features. This effect contrasts with that of objects, which seem to be perceived in a feature-based manner (objects are less sensitive to stimulus inversion). One major difference between feature-based and holistic perception is that the properties of isolated features can be more readily accessed in feature-based perception than in holistic processing. For instance, Tanaka and Farah (1993) have shown that the identification of isolated facial features is more difficult when facial features are presented in isolation compared to when they are presented as part of the face (Tanaka & Farah, 1993). As for the localization task, one could argue that the localization of object landmarks is more accurate than that of real hands because isolated features can be more readily accessed for objects than for real hands. Assuming that the rake and rubber hand are treated as any other objects, holistic perception of the hand could potentially explain our experimental findings, in particular why the landmarks of the rake and the rubber hand are more accurately localized than landmarks on the hand. However, this explanation cannot fully account why participants show a systematic bias rather than a random error in the localization task. Hence, further investigations are needed to understand the real impact of holistic perception on our data.

Conceptual hand knowledge. Recent work has shown that conceptual knowledge of one's own hand is distorted (Longo, 2015). In particular the study demonstrates that healthy participants misjudge their knuckles towards the crease of their fingers (Longo, 2015). It is unclear whether participants also adopt such strategies in the localization task. If it is the case, this hypothesis could explain why hand distortions appear larger in the case of the hand than other items as the knuckle- tip distance was considered as a baseline for finger length. This is a promising hypothesis to pursue.

6. Conclusion

In the study, we investigated some psychological processes underlying localization task distortions measured on corporeal and non-corporeal items. We have shown that visual similarity and memory factors are unlikely to fully explain localization task distortions. Hence, other factors related to body perception like viewer dependent representation (Künnapas, 1958), holistic perception (Tanaka & Farah, 1993), distorted conceptual knowledge of the hand (Longo, 2015) and somatosensory processing (Longo & Haggard, 2010, 2012) might also contribute to hand shape distortions measured in the localization task. Those hypotheses provide interesting perspectives for future work.

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