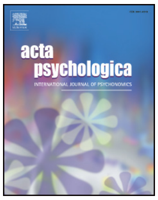
Acta Psychologica 153 (2014) 60–65

Contents lists available at ScienceDirect

Acta Psychologica

journal homepage: www.elsevier.com/locate/actpsy



The effects of verbal cueing on implicit hand maps

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ARTICLE INFO

Article history:
Received 7 June 2014
Received in revised form 18 September 2014
Accepted 22 September 2014
Available online xxxx

PsycINFO classification:
2320
2340

Keywords:
Body representation
Touch
Proprioception
Position sense

ABSTRACT

The use of position sense to perceive the external spatial location of the body requires that immediate proprioceptive afferent signals be combined with stored representations of body size and shape. Longo and Haggard (2010) developed a method to isolate and measure this representation in which participants judge the location of several landmarks on their occluded hand. The relative location of judgements is used to construct a perceptual map of hand shape. Studies using this paradigm have revealed large, and highly stereotyped, distortions of the hand, which is represented as wider than it actually is and with shortened fingers. Previous studies using this paradigm have cued participants to respond by giving verbal labels of the knuckles and fingertips. A recent study has shown differential effects of verbal and tactile cueing of localisation judgements about bodily landmarks (Cardinali et al., 2011). The present study therefore investigated implicit hand maps measuring through localisation judgements made in response to verbal labels and tactile stimuli applied to the same landmarks. The characteristic set of distortions of hand size and shape were clearly apparent in both conditions, indicating that the distortions reported previously are not an artefact of the use of verbal cues. However, there were also differences in the magnitude of distortions between conditions, suggesting that the use of verbal cues may alter the representation of the body underlying position sense.

1. Introduction

Several forms of afferent signal provide information about the posture of the limbs, including receptors in joints, muscle spindles, and skin (Proske & Gandevia, 2012). Each of these signals provides information about the extent to which joints are flexed or extended, that is about body posture. In order to perceive the absolute location in external space, information about joint angles must be combined with information about the length of bodily segments between joints, information which is not specified by immediate afferent signals from the periphery. Thus, accurate position sense requires that immediate proprioceptive afferent signals be informed by a stored *body model* (Longo, Azañón, & Haggard, 2010).

Recently, we have developed a procedure to isolate and measure this body model in which participants are asked to indicate the perceived location of different landmarks on their occluded hand. By comparing the relative locations of judgements of different landmarks, implicit perceptual maps of hand shape can be constructed (Longo, 2014; Longo & Haggard, 2010, 2012a,b; Longo, Long, & Haggard, 2012). These studies have revealed that the body model of the hand is massively distorted, with several consistent patterns of distortion across people, including: (1) overall overestimation of hand width, (2) overall underestimation of finger length, and (3) a radio-ulnar gradient, with underestimation of finger length increasing from the thumb to little finger. In contrast, when asked to compare the perceive shape of their hand to a visual template, participants perform accurately (Longo & Haggard, 2010,b), suggesting that they have explicit awareness of the true shape of their hand. Longo and Haggard (2010) argued on the basis of this dissociation that the distorted body model is distinct from the conscious body image.

In the present paper we focus on one aspect of the procedure we used in previous studies with this paradigm, namely the fact that participants have been asked to localise bodily landmarks indicated by verbal labels. A large literature in neuropsychology has suggested that lexico-semantic knowledge about the body is a distinct domain, which can be doubly-dissociated from other aspects of semantic cognition (e.g., Coslett, Saffran, & Schwoebel, 2002; Goodglass, Klein, Carey, & Jones, 1966; Kemmerer & Tranel, 2008; Laiacona, Allamano, Lorenzi, & Capitani, 2006). The studies of Dennis (1976) and Suzuki, Yamadori, and Fujii (1997) both reported patients who were unable to point to parts of their own body when verbally labelled, but could point to body parts described functionally (e.g., 'with which organ do you see?') or by association to other objects (e.g., 'which parts do you put your socks on?'). Thus, the use of verbal labels to indicate landmarks may have important implications for the representations of the body involved in generating responses.

Cardinali et al. (2011) recently reported an intriguing difference between localisation of body part based on verbal versus tactile cues. They asked participants to indicate the location of their occluded right elbow, wrist, and middle fingertip, either by pointing with their left hand or by indicating the corresponding number on a ruler laid over their arm.

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http://dx.doi.org/10.1016/j.actpsy.2014.09.009
0001-6918/

When the location to be judged was cued by touching that part of the right arm, the authors replicated their previous finding (Cardinali et al., 2009) that the distance between the judged locations of the elbow and wrist increased following a period of tool use with the right arm. The authors interpreted this result as evidence that tool use induces functional updating of the body schema, leading to an elongation of the representation of the forearm. Critically, however, when participants were asked to indicate the location of the same body parts indicated by verbal labels, no such updating from tool use was found. Thus, while the manner in which the participant *responded* had no apparent effect, the manner in which body-part locations were *indicated* critically determined whether or not tool-use induced plasticity was obtained. Cardinali et al. (2011) interpret this dissociation as evidence that changing the sensory modality of the input (tactile or verbal) affects the degree of access of the body schema.

The dissociation localisation of bodily landmarks cued through touch versus vision reported by Cardinali et al. (2011) has important implications for understanding the nature of the distorted hand maps described above. Longo and Haggard (2010) argued that the distorted representation they described was distinct from the conscious body image since in a more overt measure of body image in which participants were asked to select from an array of hand images the one most like their own, they were on average unbiased. Nevertheless, it is true that all studies investigating these representations have used verbal cues to indicate which landmarks participants should localise (Ferrè, Vagnoni, & Haggard, 2013; Longo, 2014; Longo & Haggard, 2010, 2012a,b; Longo et al., 2012; Lopez, Schreyer, Preuss, & Mast, 2012). The results of Cardinali et al. (2011) indicate that this aspect of the procedure may have important consequences for which mental representations of the body are being measured.

It is thus a critical question whether the distorted representation underlying position sense reported in recent studies may result from activation of the conscious body image or lexico-semantic representations of the body resulting from the use of verbal cues. The present study addressed this issue by comparing distortions of implicit hand maps when participants were verbally cued to point to the knuckles and tips of their occluded left hand and when they were asked to point to the location of touches applied to those same landmarks. If the distortions reported by Longo and Haggard (2010) reflect access to the conscious body image, they should arise only when locations are verbally cued, and disappear when participants are asked to localise touch. In contrast, if the distortions reflect implicit body representations underlying position sense, they should appear regardless of the manner in which locations are cued.

2. Methods

2.1. Participants

Twenty healthy individuals (eleven female) between 18 and 73 years of age participated. All but two were right-handed as assessed by the Edinburgh Handedness Inventory (*M*: 63.56; range: −100 to 100).

2.2. Procedure

Procedures were similar to our previous studies using this paradigm (Longo, 2014; Longo & Haggard, 2010, 2012a,b; Longo et al., 2012). Participants placed their left palm-down on a table, aligned with their body midline (see Fig. 1). An occluding board (40 × 40 cm) was placed over the hand, resting on four pillars (6 cm high). A camera (Logitech Webcam Pro 9000 HD) suspended on a tripod above the occluding board (27 cm high) captured photographs (1600 × 1200 pixels) controlled by a custom Matlab (Mathworks, Natick, MA) script.

Participants used a long baton (35 cm length; 2 mm diameter) to indicate with their right hand the perceived location of several landmarks on their occluded left hand. Ten landmarks were used: the knuckles at the base of each finger and the tip of each finger. The critical difference between conditions was the manner in which participants were cued to each landmark. In the *Verbal* condition, participants were verbally instructed which landmark to localise, as in previous studies with this paradigm. In the *Tactile* condition, in contrast, the experimenter delivered unseen tactile stimuli to the same landmark using a von Frey hair (255 milliNewtons) applied for approximately one second. They were instructed to be precise in their judgements and avoid ballistic pointing or strategies such as tracing the outline of the hand. To ensure that they judged each landmark individually, participants moved the baton to a yellow dot at the edge of the board before the start of each trial. When the participants indicated their response, a photograph was taken and saved for offline coding.

There were four blocks of 30 trials: two blocks for the verbal condition and two blocks for the tactile condition. The two conditions were counterbalanced across the four blocks in ABBA fashion, with the first condition counterbalanced across participants. Each block included three mini-blocks of one trial of each landmark in random order. At the beginning and the end of each block a photograph of the participant's hand was taken to measure the true hand proportions and to check that the hand hadn't moved during the course of the block. To facilitate coding, a black mark was made on the centre of each knuckle with a non-permanent felt pen. A 10 cm ruler appeared in the photographs of the participant's hand and allowed conversion between pixel units and centimetres.

2.3. Analysis

The analysis was similar to our previous studies (Longo & Haggard, 2010, 2012a,b). The x–y pixel coordinates of each landmark on the images of actual hands and of all responses were coded using a custom Matlab script using Cogent Graphics (John Romaya, Wellcome Department of Imaging Neuroscience, University College London). Mean coordinates were then calculated for each landmark in each experimental block. The set of mean coordinates in each block comprises two maps, one reflecting actual hand shape, the other reflecting represented hand shape. Distances between mean pixel coordinates of the tip and knuckle of each finger and between pairs of knuckles were calculated and converted into cm.

We also used Generalised Procrustes Analysis (GPA) to compare the overall shape of hand maps. GPA aligns configurations of homologous landmarks, removing differences in location, rotation, and overall size to isolate differences in shape (Bookstein, 1991; Rohlf & Slice, 1990). Because the fingers are articulated structures, differences in posture could be confused with differences in shape (Adams, 1999). Although this will not affect analysis of distances between pairs of adjacent landmarks, it will affect analyses of overall hand shape, like GPA. We therefore rotated each finger to a common posture, defined for each finger as the angle formed by the intersection of the line running through the knuckles of the index and little fingers and the line running through the knuckle and tip of a particular finger. We used the same angles used in our original study (Longo & Haggard, 2010), namely 44.4°, 64.4°, 77.4°, 86.8°, and 106.1° for digits 1–5, respectively. For hand maps in each block, the tip of each finger was rotated so that the finger was at the appropriate angle, while preserving the distance between the knuckle and tip of each finger. This results in hand maps which have a common posture, allowing comparison of overall shape with GPA.

GPA was conducted using CoordGen software (Integrated Morphometrics Program, H. David Sheets, Canisius College, http://www3.canisius.edu/~sheets/morphsoft.html). Because there were two experimental blocks of each condition, maps of represented hand shape from the two blocks of each condition for a particular participant were first placed in GPA alignment with each other and the average hand shape calculated. Then a second, group-level, GPA was conducted to align maps of each condition across participants. The maps of actual

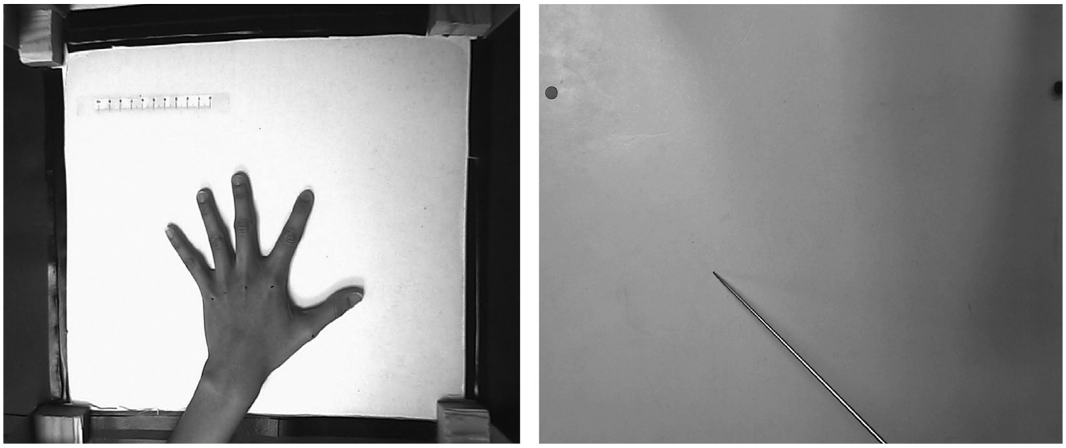

Fig. 1. The experimental setup. Participants placed their hand palm down on a table (left panel) which was then occluded with a board (right panel). They judged the perceived external spatial location of landmarks which were either verbally specified (verbal condition) or touched (tactile condition) by positioning the tip of a long baton on the board, and responses were recorded with a camera.

hand space were analysed in the same way, except that the maps from all four blocks were analysed together, since actual hand shape will not differ across conditions.

3. Results

Fig. 2 shows grand average maps of actual and represented hand shape, placed into alignment with GPA. Previous studies (Longo, 2014; Longo & Haggard, 2010, 2012a,b) have shown three main characteristic distortions of the implicit representation of the hand: (1) overall underestimation of finger length; (2) a radial–ulnar gradient of this underestimation, increasing from thumb to little finger; and (3) overall overestimation of hand width. Here, we investigated each of these three distortions in both the verbal and tactile conditions.

First, we investigated underestimation of finger length. Fig. 3 shows overestimation of finger length as a percentage of actual finger length for each finger in both conditions. Collapsing across the five fingers, there was significant underestimation of finger length in both the verbal condition (*M*: -40.66% overestimation), $t(19) = -15.79$, $p < .0001$, $d = 3.53$, and the tactile condition (*M*: -38.66% overestimation), $t(19) = -12.77$, $p < .0001$, $d = 2.86$. The magnitude of underestimation did not differ significantly between the two conditions, $t(19) = 0.52$, *n.s.*, $d_z = 0.12$. There was significant underestimation of all five fingers in both conditions (all *p*'s < .0001). Thus, the overall magnitude of finger length underestimation was highly similar in the two conditions.

We next investigated how this underestimation changed from the thumb to the little finger. This gradient was quantified using least-squares regression to assess the change in underestimation per digit. As we have reported previously (Longo & Haggard, 2010, 2012a,b), in the verbal condition there was a clear gradient with underestimation increasing from thumb to little finger (mean $\beta = -5.2\%$ per finger), $t(19) = -5.27$, $p < .0001$, $d = 1.18$. In striking contrast, there was no such gradient in the tactile condition (mean $\beta = -1.0\%$ per finger), $t(19) = -1.01$, *n.s.*, $d = 0.23$. There was a clearly significant difference in mean regression coefficients between the two conditions, $t(19) = -3.33$, $p < .01$, $d_z = 0.75$. An ANOVA comparing percent overestimation of finger length for the verbal and tactile conditions revealed a significant effect of finger, $F(2.69, 51.10) = 6.23$, $p < .005$, $\eta_p^2 = 0.25$, with bias increasing monotonically across the hand from the thumb to the little finger in the verbal condition but not in the tactile condition. There was no significant effect of input type (verbal vs tactile), $F(1,19) = 0.27$, $p = .61$, $\eta_p^2 = 0.01$. Critically, however, there was a significant interaction between the condition and finger, $F(4, 76) = 5.50$, $p < .001$, $\eta_p^2 = 0.23$, consistent with the difference between condition in regression coefficients.

Finally, Fig. 4 shows overestimation of the distance between pairs of knuckles. Taking the distance between the knuckles of the index and

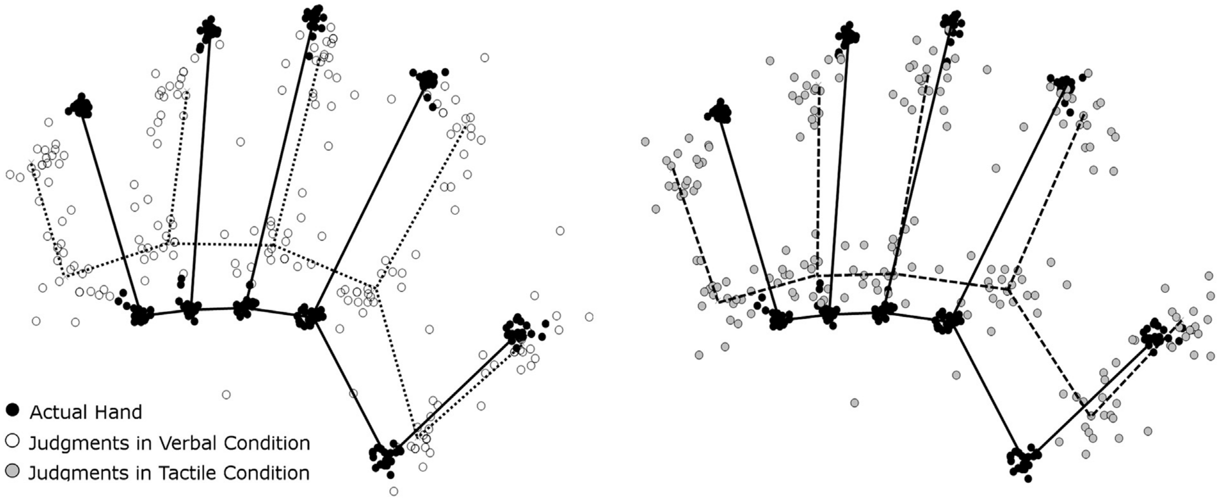

Fig. 2. Generalised Procrustes analysis (GPA) alignment of maps of actual (black dots, solid lines) and represented hand shape in the verbal (left panel, open circles, dotted lines) and tactile (right panel, grey circles, dashed lines) conditions.

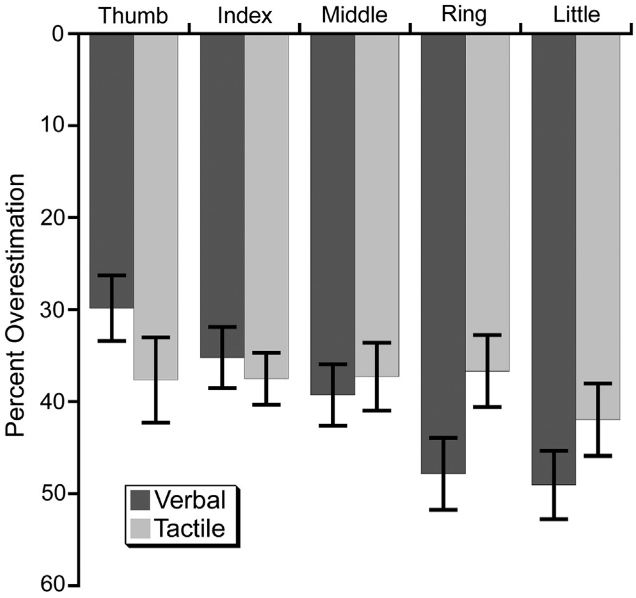

Fig. 3. Percent overestimation [i.e., 100 × (judged length − actual length) / actual length] of finger lengths for judgements cued by verbal and by tactile stimuli. Error bars are one S.E.M. Clear underestimation was apparent in all conditions, but the pattern across fingers was completely different in the two conditions. In the verbal condition, a clear gradient was observed, with underestimation increasing progressively from thumb to little finger; in the tactile condition, in contrast, no such change was observed, with generally constant underestimation across fingers.

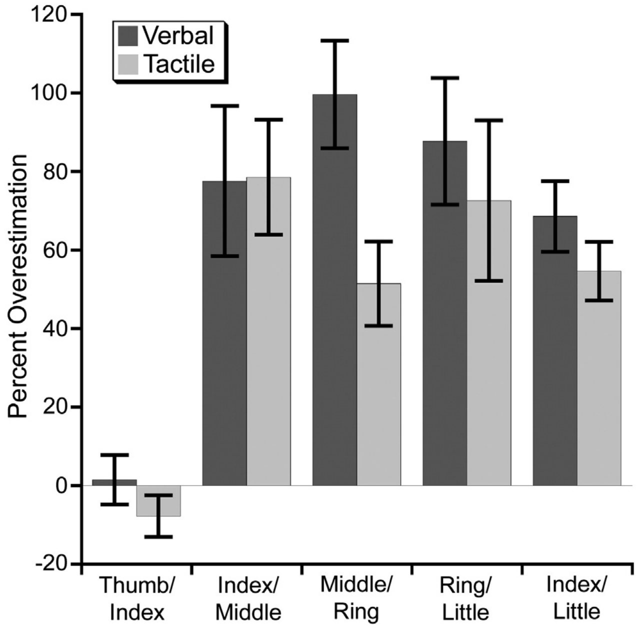

Fig. 4. Percent overestimation of the distance between pairs of knuckles. Clear overestimation of hand width was observed. The distance between the knuckles of the index and little fingers was taken as an overall measure of hand width. While clear underestimation was observed in both conditions, it was clearly reduced in the tactile condition.

little fingers as an overall measure of hand width, there was significant overestimation of hand width in both the verbal condition (*M*: 69.0%), $t(19) = 7.63$, $p < .0001$, $d = 1.71$, and the tactile condition (*M*: 54.9%), $t(19) = 7.39$, $p < .0001$, $d = 1.65$. The magnitude of overestimation was significantly reduced in the tactile compared to the verbal condition, $t(19) = 2.17$, $p < .05$, $d_z = 0.49$.

The scatterplots in Fig. 5 show the relation between the magnitude of underestimation of finger length (left panel) and overestimation of hand width (right panel) between the two conditions. Previous studies with this paradigm have found clear correlations between the magnitude of these effects across different conditions (Table 1), including the right and left hands (Longo & Haggard, 2010, Exp. 2), the left hand in two different postures (Longo & Haggard, 2010, Exp. 3), the dorsal and palmar surfaces of the left hand (Longo & Haggard, 2012a), and the left hand with vision and while blindfolded (Longo, 2014). In the present study, there was a significant correlation between overestimation of hand width in the two conditions, $r(18) = 0.706$, $p < .0005$, consistent with previous results. In striking contrast, however, there was no correlation between the magnitude of finger length underestimation in the two conditions, $r(18) = 0.046$, *n.s.*.

Hand shape was quantified using Napier's *shape index* (Napier, 1980), a ratio of hand width to length, reflecting the overall aspect ratio of the hand. Hand width was quantified as the distance between the knuckles of the index and little fingers, hand length as the length of the middle finger. SI = 100 × (width / length). The shape index

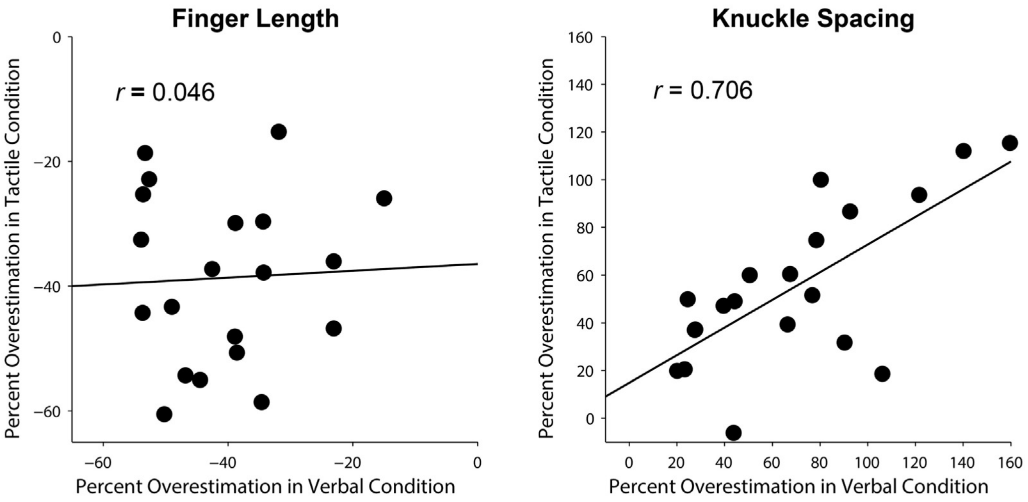

Fig. 5. Scatterplots showing correlations between underestimation of finger length (left panel) and overestimation of hand width (distance between knuckles of index and little fingers; right panel).

Table 1
Correlations between distortions in different conditions of previous published studies using this paradigm and the present study.

Experiment	Comparison	*N*	Finger length	Hand width
Longo and Haggard (2010), Exp. 2	Left hand in 'normal' vs. 'rotated' posture	12	0.685	0.719
Longo and Haggard (2010), Exp. 3	Left hand vs. right hand	12	0.666	0.927
Longo and Haggard (2012a)	Left dorsal vs. palmar hand surface	12	0.751	0.834
Longo (2014)	Left hand with vision vs. blindfolded	12	0.381	0.508
This study	Tactile vs. verbal cueing	20	0.046	0.706

allowed comparison of overall hand shape across conditions as well as the actual hand. Shape indices were significantly higher than actual in both the verbal (177.8 vs. 58.2), $t(19) = 6.16$, $p < .0001$, $d = 1.38$, and the tactile (150.9 vs. 58.2), $t(19) = 10.58$, $p < .0001$, $d = 2.37$, conditions. There was no significant difference in shape indices between the two experimental conditions, $t(19) = 1.13$, *n.s.*, $d_z = 0.25$. These results suggest that the overall aspect ratio of represented hand shape is similar in the two conditions.

4. Discussion

Similar distortions of hand size and shape were found whether participants were asked to localise landmarks indicated by verbal labels or by touch. These results demonstrate that the distorted hand maps previously reported (Ferrè et al., 2013; Longo, 2014; Longo & Haggard, 2010, 2012a,b; Longo et al., 2012; Lopez et al., 2012) are not an artefact of the use of verbal instructions. Longo and Haggard (2010, 2012a,b) have previously shown three characteristic distortions of the implicit representation of the hand: (1) overall overestimation of hand width, (2) overall underestimation of finger length; and (3) a radial–ulnar gradient of this underestimation, increasing from thumb to little finger. Here we clearly replicated these results in the verbal condition. In the tactile condition the first two distortions were clearly apparent: participants overestimated the width of their hand and underestimated the length of their fingers. In contrast, however, the third type of distortion was not apparent in the tactile condition: the magnitude of underestimation of finger length was approximately constant across the five fingers. Thus, while the overall pattern of distortion is largely similar across conditions, there is evidence that the use of verbal cues does affect performance on this task.

First, there was significant overestimation of hand width in both the verbal condition and the tactile condition, but the magnitude of this overestimation was significantly reduced in the tactile compared to the verbal condition. We also found a significant underestimation of all five fingers either when the stimulus was delivered in the verbal and tactile fashion. However, this underestimation in the verbal condition clearly increased from the thumb to little finger, as we have reported previously (Longo, 2014; Longo & Haggard, 2010, 2012a,b). In striking contrast, there was no such gradient of underestimation in the tactile condition, with approximately constant underestimation across the five fingers. Equally striking was the lack of correlation between the magnitude of underestimation of finger length in the verbal and tactile conditions. This null correlation stands in stark contrast to the significant correlations observed in several previous studies, as well as in this study between overestimation of hand width in the two conditions. This result suggests that the use of verbal cues may have more fundamental effects on the representation of finger length than of hand width. In our previous studies we have generally discussed the distortions we have observed as if they reflected a single underlying source. The present results suggest that there may be interesting differences between the different distortions we have reported, both in terms of their underlying causes and their implications for understanding the nature of body representations.

The present results are consistent with the recent results of Cardinali et al. (2011) who found tool-use induced plasticity on represented arm length using a similar task only when landmarks were cued through touch. No such plasticity was apparent when landmarks were cued verbally. Such specificity was found regardless of whether the participant's response was a motoric point or a verbal judgement of location from a ruler. Like the results of Cardinali et al. (2011), the present results show differences in represented body part size depending on whether localisation judgements are cued verbally or by touch. Whereas Cardinali et al. only found differences in terms of whether plastic changes were apparent, the present results show that verbal labels can also affect the baseline representation of the body.

What drives differences between the verbal and tactile conditions? There are several aspects of the present task that may be relevant to explaining the observed differences between the tactile and the verbal conditions. First, one possible interpretation of the overestimation of distance between knuckles and underestimation of finger length is in terms of categorical perception. The knuckles of different fingers are verbally labelled as being part of different fingers, whilst the tip and knuckle of a given finger are verbally labelled as being part of the same finger. The distance between the knuckle and tip of a single finger might therefore be more susceptible to categorical perception effects than the knuckles of adjacent fingers. If categorical perception produces perceptual contraction within categories and perceptual expansion across categories, a pattern like that observed might be predicted. The reduction in overestimation of hand width in the tactile condition could be considered consistent with this interpretation. However, the categorical interpretation also predicts that the underestimation of finger length should also be reduced in the tactile condition, which was not the case. Another possibility is that although touch was applied to the same landmarks which were cued verbally, the perceived location of touch may nevertheless have differed from the landmarks. For example, Mancini et al. (Mancini, Longo, Iannetti, & Haggard, 2011) showed large distal biases in localising touch on dorsal surface of the hand. Thus, it is possible that participants were pointing to different locations in the two conditions. Given that it was exactly on landmarks that we stimulated, we consider this unlikely. Further, as distal biases cannot affect localisation of the fingertips (since there's no more distal bit of the skin for localisation to be biased), distal localisation biases for touch would predict increased underestimation of finger length in the tactile compared to the verbal condition, which were not found. Finally, tactile and verbal cues may provide differential access to different types of body representations, as suggested by Cardinali et al. (2011). This interpretation is consistent with evidence that lexico-semantic information about the body may be a distinct domain of semantic cognition (e.g., Coslett et al., 2002; Kemmerer & Tranel, 2008) and for specific neuropsychological deficits in pointing to body parts on the basis of verbal body-part labels (e.g., Dennis, 1976; Suzuki et al., 1997).

Finally, the present results have interesting methodological implications for future studies. The use of verbal labels severely limits the ability to map the body surface, since the majority of locations on the body do not have names. The finding that similar implicit representations emerge from tactile and verbal cues, however, offers the possibility of mapping regions of the skin surface, which do not have convenient verbal labels. By having participants localise where they were touched, continuous regions of the skin can be mapped with the paradigm. This has the potential to greatly expand the utility of this method, allowing the entire body (not just the hand) to be investigated.

Acknowledgements

This research was supported by a European Research Council award (ERC-2013-StG-336050) under the FP7 to MRL.

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