Experimental Brain Research (2018) 236:3113–3119
https://doi.org/10.1007/s00221-018-5360-x

RESEARCH ARTICLE

The effects of instrumental action on perceptual hand maps

Matthew R. Longo[1]

Received: 2 April 2018 / Accepted: 10 August 2018 / Published online: 21 August 2018

Abstract
Perceiving the external spatial location of body parts using position sense requires that immediate proprioceptive afferent signals be integrated with information about body size and shape. Longo and Haggard (Proc Natl Acad Sci 107:11727–11732, 2010) developed a method to measure perceptual hand maps reflecting this metric information about body size and shape. In this paradigm, participants indicate the perceived location of landmarks on their occluded hand by pointing with a long baton held in their other hand. By comparing the relative location of judgments of different hand landmarks, perceptual hand maps can be constructed and compared to actual hand structure. The maps show large and highly stereotyped distortions. Here, I investigated the potential effect of biases related to active motor control of the hand doing the pointing in these distortions. Participants localized the fingertip and knuckle of each finger on their occluded left hand either by actively pointing with a baton held in their right hand (pointing condition) or by giving verbal commands to an experimenter on how to move the baton (verbal condition). Similar distortions were clearly apparent in both conditions, suggesting that they are not an artifact of motor control biases related to the pointing hand.

Keywords Proprioception · Position sense · Somatosensation · Body representation · Body model

Introduction

Several types of sensory signal provide information about the location of the limbs in space (Burgess et al. 1982; Proske and Gandevia 2009, 2012), including receptors in joints (Ferrell et al. 1987; Macefield et al. 1990), in the skin (Edin and Johansson 1995; Collins et al. 2005), and in muscle spindles (Goodwin et al. 1972; Matthews 1972). Critically, each of these signals provides information about joint angles, that is the degree of flexion or extension at each joint. This provides information about body posture, but to determine the absolute location of a body part in space, information about joint angles needs to be integrated with information about the length of body segments between joints (Longo et al. 2010). Such metric information about the body is not obviously signaled by any afferent signal or combination of signals, and therefore, likely arises from a central representation of body size and shape, what my colleagues and I have referred to as a 'body model' (Longo et al. 2010; Longo and Haggard 2010).

We developed a simple procedure to try and isolate and measure this mental representation (Longo and Haggard 2010). Participants localized the knuckle and tip of each finger on their occluded hand by pointing with the opposite hand on an occluding board. By comparing the relative locations of judgments of each landmark, we constructed perceptual maps of hand structure, which we could then compare to the actual structure of participants' hands. These maps showed large and highly stereotyped distortions, including: (1) overall underestimation of finger length, (2) a gradient of increasing underestimation of finger length from the thumb to little finger, and (3) overall overestimation of hand width.

This overall pattern has been replicated numerous times in several labs (Cocchini et al. 2018; Coelho et al. 2017; Coelho and Gonzalez 2018; Ferrè et al. 2012; Ganea and Longo 2017; Longo 2014, 2015a, 2017b; Longo and Haggard 2012a, b; Longo et al. 2012, 2015a, b; Longo and Morcom 2016; Lopez et al. 2012; Mattioni and Longo 2014; Medina and Duckett 2017; Saulton et al. 2015, 2016, 2017; Stone et al. 2018; Tamè et al. 2017). Nevertheless, the interpretation of such effects remains uncertain. While my colleagues and I have interpreted these distortions as

✉ Matthew R. Longo
m.longo@bbk.ac.uk

1 Department of Psychological Sciences, Birkbeck, University of London, Malet Street, London WC1E 7HX, UK

reflecting a central body model (e.g., Azañón et al. 2016; Longo 2015c, 2017a; Longo and Haggard 2010; Longo et al. 2015a), some researchers have proposed that they may result from more general perceptual and motor processes (Medina and Duckett 2017; Saulton et al. 2015, 2016, 2017).

This study investigates one potential source of domain-general bias in these maps, namely whether they might relate to motor control of the contralateral hand doing the pointing. In our original paper using this paradigm (Longo and Haggard 2010), we attempted to control for this possibility by comparing conditions in which the hand being judged was oriented in different postures, either with the fingers pointing away from the participant or pointing to the side. The logic of this manipulation was that any biases related to motor control should be defined in a torso-centred frame of reference and thus reverse when the hand was rotated by 90°. Several other experiments have also used similar controls (e.g., Longo et al. 2015a; Saulton et al. 2015). In each case, qualitatively similar distortions have been found in both postures, though sometimes with differences in their quantitative magnitudes. These results suggest that the existence of the distortions is not an artifact of motor control biases, but does suggest some possible influence thereof.

There are other ways, however, in which the act of pointing might affect responses. A substantial literature has demonstrated important differences between mechanisms underlying overt motor behavior and conscious perceptual experience (cf. Milner and Goodale 1995). For example, Aglioti and colleagues (1995) reported that the classic Titchener circles illusion was not apparent when instead of making a perceptual judgment about the size of the central circle, participants were asked to reach and grasp it. Similarly, other work has reported double dissociations in neurological patients between the ability to overtly describe or recognize objects and to act effectively with them (e.g., Carey et al. 2006; Goodale et al. 1991). Importantly, similar dissociations between perceptual judgments and motor responses have also been described in proprioceptive localization of the hand (Jones et al. 2010, 2012). While the interpretation of these results remains controversial (e.g., Pavani et al. 1999; Pisella et al. 2006), such dissociations raise the possibility that active pointing judgments by a participant in the paradigm of Longo and Haggard (2010) may not correspond directly to the location where they subjectively experience part of their body as being located. Thus, obtaining proprioceptive localization responses by pointing with the contralateral hand is not an entirely neutral method, and could potentially contribute to the pattern of distortions observed in perceptual hand maps. Indeed, given suggestions that motor responses may be more directly in line with veridical reality than perceptual judgments (e.g., Anema et al. 2009; Paillard et al. 1983; Rossetti et al. 1995), it is possible that the use of motoric pointing responses in previous studies may have led to underestimation of the magnitude of distortions.

In one study, we tested an individual (C.L.) who was born without a left arm, to investigate perceptual maps of her 'phantom' left hand (Longo et al. 2012). While she was able to point with her intact right hand to locations at which she experienced parts of her non-existent left hand as being, there was no way for her to point manually at landmarks on her right hand. We, therefore, obtained maps of her right hand by asking her to give verbal commands to an experimenter who moved the baton on the occluding board under her instruction. Importantly, these maps looked very similar to those obtained through active pointing in other participants, and maps of her 'phantom' hand obtained by active pointing and verbal instructions were very similar. These results suggest that active manual pointing does not drive the organization of perceptual hand maps. However, as we only tested one individual in that study, I therefore, compared perceptual hand maps in a sample of two-armed individuals obtained in conditions in which the participant responded by actively pointed (*pointing* condition) or by giving verbal instructions to an experimenter (*verbal* condition).

Methods

Participants

Twelve members of the Birkbeck community (four female, mean age: 31.2 years, SD: 9.5 years) participated after giving informed consent. All but one were right-handed as assessed by the Edinburgh Inventory (Oldfield 1971; M 73.8, range −90.9 to 100). Procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London. The study was conducted in accordance with the principles of the Declaration of Helsinki.

A weighted average of effect sizes from 15 previous experiments in my lab (283 total participants) using this paradigm produced an average Cohen's d of 1.78 for underestimation of finger length and 1.89 for overestimation of hand width. A power analysis using G*Power 3.1 on the smaller of these two effect sizes with alpha of 0.05 and power of 0.95 suggested that six participants were needed. Thus, the present sample size is well-powered to detect distortions in the verbal condition.

Procedure

The paradigm was similar to our previous experiments using this paradigm (e.g., Longo and Haggard 2010, 2012a). Participants sat at a table with their left hand resting flat on a board with the palm down. Their hand was approximately aligned with their body midline. Their hand was covered by an occluding board (40 × 40 cm) resting on four pillars (6 cm in height). Participants were asked to judge the perceived location of ten landmarks on their occluded left hand by indicating the location on the occluding board directly above each landmark. Judgments were record by a webcam (Logitech Webcam Pro 9000) suspended 27 cm above the table, under control of a custom MATLAB (Mathworks, Natick, MA) script. The photographs were saved as JPEG images at 1600 by 1200 pixels resolution and stored for offline coding.

At the beginning of each block, a photograph was taken without the occluding board to obtain information about actual hand size and position. A 10 cm ruler on the table allowed conversion between distances in pixels and cm. Before the start of the experiment, a small black mark was made with a felt pen on each knuckle to facilitate coding of location from photographs. The landmarks judged were the tip of each finger (the most distal bit of the skin) and the centre of the knuckle at the base of each finger (i.e., the metacarpophalangeal joint). Participants were given a verbal instruction at the beginning of each trial about which landmark to judge.

The key manipulation was that participants responded in two different ways. The pointing condition was similar to previous studies using this paradigm (e.g., Longo and Haggard 2010, 2012a, b). Participants used a long baton (35 cm in length; 2 mm in diameter) held in their right hand to indicate the perceived location of each landmark by positioning the tip of the baton on the occluding board. They were asked to be precise in their responses, to avoid ballistic pointing, and to avoid strategies such as tracing the outline of the hand. After each trial, they were asked to move the tip of the baton to a blue dot at the edge of the occluding board to make responses as independent as possible. In the verbal condition, in contrast, the experimenter (author MRL) held the baton and moved it over the occluding board based on verbal instructions from the participant. On each trial, the experimenter moved the tip of the baton to a dot at the middle of the far edge of the occluding board and moved it at a slow and approximately constant speed (~ 1 cm/s) towards the centre of the board. Participants could give whatever verbal instructions they liked to the experimenter until the tip of the baton was at the desired location. Examples of typical sorts of instructions were “now to the left”, “just a bit farther down”, and “too far, back slightly”.

There were four blocks of 30 trials each, two blocks of the pointing condition and two of the verbal condition. The blocks were presented in ABBA order, with the initial condition counterbalanced across participants. Each block consisted of three mini-blocks of 10 trials each (one trial for each landmark), in random order (Fig. 1).

Analysis

Analysis methods were similar to those my colleagues and I have used in previous studies with this paradigm. The *x*/*y* pixel coordinates of each response were coded using a custom MATLAB script and averaged across trials within a block. This produced one perceptual maps of the hand in each block. Distances between pairs of landmarks were calculated and converted into cm. The pairs of landmarks analysed reflected the length of each finger (i.e., the distance

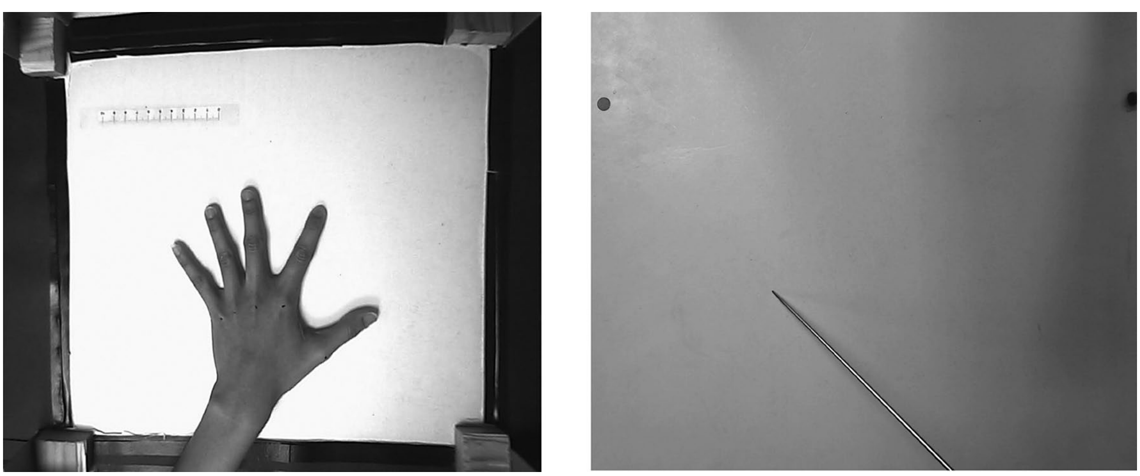

Fig. 1 The experimental setup. Participants placed their left hand palm down on the table (left panel) and it was then covered by an occluding board (right panel). Their task was to judge the location of the fingertip and knuckle of each finger by positioning the tip of a long baton on the occluding board, directly above the perceived location of each landmark (right panel). In the pointing condition, participants held the baton with their right hand and positioned it manually. In the verbal condition, the experimenter held the baton and participants gave verbal instructions about where the baton should be moved. After the participant was satisfied with the location of the baton, a photograph of each response was captured by a camera suspended above the board

between the knuckle and fingertip) and the overall width of the hand (i.e., the distance between the knuckles of the index and little fingers). I then calculated percent overestimation for each distance as: 100 × (judged length − actual length)/actual length.

To visualize maps, I also placed the maps from each condition into Generalized Procrustes alignment across participants to construct grand-average perceptual maps. Procrustes alignment translates, rotates, and scales maps of homologous landmarks to place them into optimal alignment (Bookstein 1991; Rohlf and Slice 1990). Because the fingers can rotate independently, differences in hand posture could be conflated with differences in hand shape (Adams 1999). I thus 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 index and little fingers and the line running through the knuckle and tip of each finger. I used the same angles as in our original study (Longo and Haggard 2010), namely 44.4°, 64.4°, 77.4°, 86.8°, and 106.1° for the thumb through little finger, respectively. For each map (both maps of actual hand structure and perceptual maps), the tip of each finger was translated so that the finger was oriented at the appropriate angle, while preserving the distance between the tip and knuckle of each finger. Because there were two experimental blocks of each condition, the two maps from each condition for each participant were first put into Procrustes alignment to produce a single average perceptual map for each participant for each condition. Similarly, the four maps of the actual hand for each participant were placed into Generalized Procrustes alignment to construct a grand-average map for each participant. Then, a second group-level Generalized Procrustes alignment was run, putting the judged maps from each condition into alignment across participants and conditions.

Results

Figure 2 shows perceptual maps placed into Procrustes alignment with actual hand shape in the pointing condition (left panel) and the verbal condition (right panel). Clear and well-organized maps were apparent in both cases. Most importantly, similar patterns of distortions were apparent in both conditions, including: (1) overall underestimation of finger length, (2) a radial-ulnar gradient in the magnitude of finger length underestimation, and (3) overestimation of hand width.

The left panel of Fig. 3 shows underestimation of finger length across the five fingers in each condition. Clear underestimation was apparent in both conditions for all fingers, except the thumb. Collapsing across the five fingers, there was overall underestimation of finger length in both the pointing condition (*M* 18.0%), $t(11) = -3.15$, $p < 0.01$, $d = 0.910$, and the verbal condition (*M* 25.6%), $t(11) = -4.23$, $p < 0.002$, $d = 1.22$. The differences between conditions were investigated by a repeated-measures analysis of variance (ANOVA) with factors condition (pointing vs. verbal) and finger (thumb, index, middle, ring, little). There was a clear main effect of finger, $F(1.48, 16.32) = 19.24$, $p < 0.0005$, $\eta_p^2 = 0.636$, and a non-significant trend towards a main effect of condition, $F(1, 11) = 3.92$, $p = 0.073$, $\eta_p^2 = 0.263$. There was no hint of an interaction, $F(2.10, 23.08) = 0.91$, n.s., $\eta_p^2 = 0.076$. Across fingers, there was a strong correlation between the magnitude of underestimation

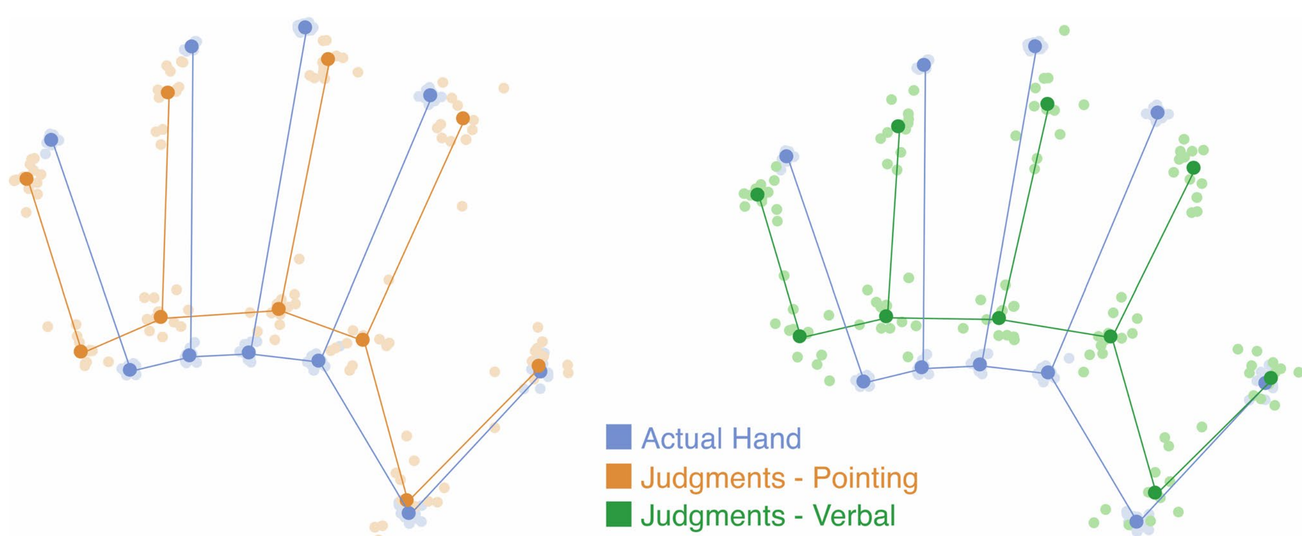

Fig. 2 Generalized Procrustes alignment of hand maps of the actual hand (blue) and perceptual maps in the pointing condition (orange) and the verbal condition (green). The pale dots indicate maps from individual participants. The dark colored dots and lines indicate grand-average maps

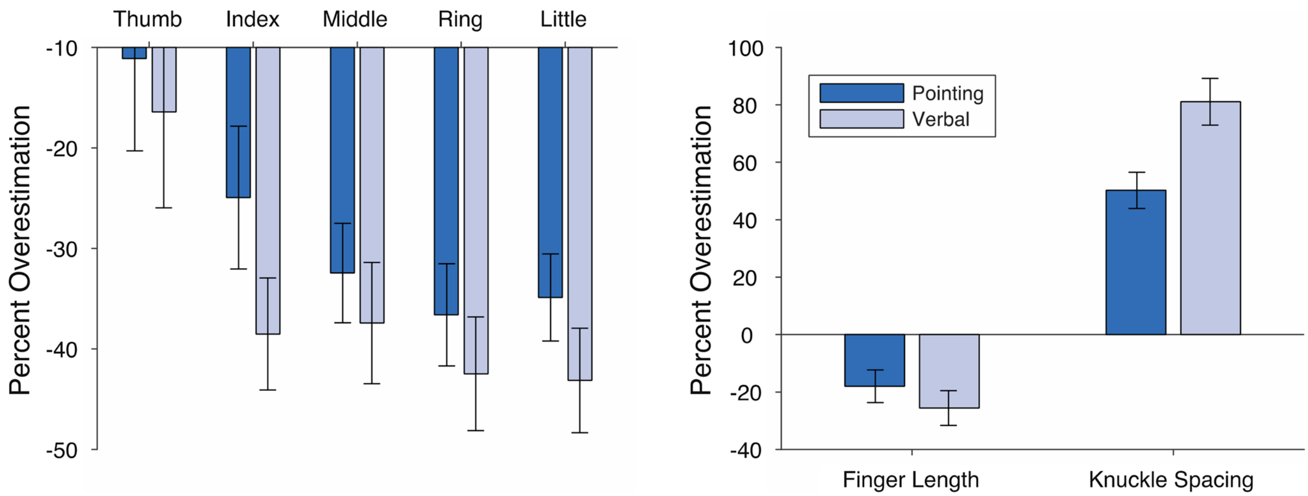

Fig. 3 Left panel: underestimation of finger length across the five fingers in the pointing and verbal conditions. Clear underestimation was apparent in both conditions, which increased from the thumb to the little finger. Right panel: underestimation of finger length (i.e., the data from the left panel averaged across the five fingers) and overestimation of hand width (i.e., the distance between the knuckles of the index and little fingers). Error bars are one standard error

in the two conditions, $r(10) = 0.788$, $p < 0.005$. Thus, clear underestimation of finger length was found irrespective of whether participants actively pointing in making their response. Indeed, if anything, there was a trend for this bias to be larger when the participants did not actively point.

I quantified the change across the five fingers using least-squares regression, regressing percent overestimation on finger number (i.e., thumb = 1 to little finger = 5). There were clear gradients in both the pointing condition (*M* 5.9% per finger), $t(11) = 4.36$, $p < 0.002$, $d = 1.26$, and the verbal condition (*M* 5.7% per finger), $t(11) = 5.69$, $p < 0.0002$, $d = 1.64$, which did not differ from each other, $t(11) = 0.16$, n.s., $d_z = 0.05$ (Fig. 3, left panel).

Taking the distance between the knuckles of the index and little fingers as an overall measure of hand width, there was clear overestimation in both the pointing condition (*M* 50.2% overestimation), $t(11) = 7.96$, $p < 0.0001$, $d = 2.30$, and in the verbal condition (*M* 81.1% overestimation), $t(11) = 9.93$, $p < 0.0001$, $d = 2.87$. The magnitude of this bias was significantly larger in the verbal than in the pointing condition, $t(11) = 4.43$, $p < 0.001$, $d_z = 1.28$. There was a moderate correlation between the magnitude of overestimation in the two conditions, $r(10) = 0.563$, $p = 0.057$.

As an overall measure of hand aspect ratio, I adapted Napier's (1980) shape index, defined as: SI = 100 × (width/length). Thus, large values of the shape index indicate a squat, fat hand, whereas small values indicate a long, slender hand. As a measure of hand width, I used the distance between the knuckles of the index and little fingers; as a measure of hand length, I used the length of the middle finger. The shape index was calculated for both the actual shape of participants' hands as well as for perceptual maps in the two conditions. On average, participants' actual hands had a shape index of 57.26. Shape indices were significantly larger than for actual hands, both in the pointing condition (*M* 114.44), $t(11) = 7.70$, $p < 0.0001$, $d = 2.22$, and the verbal condition (*M* 153.96), $t(11) = 6.29$, $p < 0.0001$, $d = 1.82$. Shape indices were significantly larger in the verbal than in the pointing condition, $t(11) = 2.85$, $p < 0.02$, $d_z = 0.82$.

Discussion

Similarly distorted perceptual hand maps were found whether participants indicated the perceived location of hand landmarks by pointing with a long baton or by giving verbal instructions to an experimenter. The stereotyped set of distortions described in previous studies (e.g., Longo and Haggard 2010) was clearly apparent in both conditions, including underestimation of finger length, a gradient with finger length being underestimated progressively more from the thumb to little fingers, and overestimation of hand width. There was, if anything, a trend for these effects to be larger in the verbal condition than in the pointing condition, though this was only statistically significant for overestimation of hand width. These results indicate that the distortions of perceptual hand maps are not a result of biases related to motor control of the hand doing the pointing, as comparable biases occur even when no such pointing is involved.

In a previous study (Longo et al. 2012), we reported a case study of an individual (C.L.) born without a left arm, for whom we used a method similar to the verbal condition in the present study. C.L. showed very similar distortions in perceptual maps of her non-existent left hand whether pointing to landmarks with her intact right hand or giving verbal instructions to an experimenter. Similarly, maps of her intact right hand (collected only using the verbal condition) showed similar distortions to those described in other studies. The present results generalize the results of that case study to a sample of people with two arms. Together, the present results and those from C.L. indicate that the highly stereotyped distortions found for perceptual hand maps do not result from motor control of the contralateral hand used for making localization judgments.

One limitation of the present study was that the experimenter who moved the baton in the verbal condition (i.e., the author) was not naïve to the experimental hypotheses. Because of the active role of the experimenter in this condition, this potentially raises concerns about experimenter bias over and above those potentially influencing any study in experimental psychology. The correlation between the magnitude of distortions in the two conditions is noteworthy in this context, since it suggests that the distortions in the verbal condition are not a result of biases related to the experimenter holding the baton, which only occurred in one of the two conditions.

Several recent studies have suggested that these distortions may result from general processes operating beyond the context of proprioception, including biases to judge elongated objects as more isotropic than they actually are (e.g., Saulton et al. 2015, 2016), confusion about the locations of landmarks within the hand (e.g., Ambroziak et al. 2018; Longo 2015b; Longo et al. 2015b; Saulton et al. 2017), and carryover effects from trial-to-trial (Medina and Duckett 2017). The present results do not exclude any of these potential influences, but they do indicate that any such effects cannot occur at the level of motor output.

Clear distortions were apparent in both conditions, which were qualitatively similar to each other and to previous studies using this paradigm. Quantitatively, however, there was a trend for the distortions to be larger in the verbal than in the pointing condition. This effect was not predicted, and should therefore, be interpreted cautiously. One possibility is that these differences could relate to the duration of the experimental blocks, given the known tendency of limb proprioception to drift over time (Wann and Ibrahim 1992). An analysis of the image timestamps indeed showed that the average trail length was substantial longer in the verbal condition than in the pointing condition (13.8 vs. 5.9 s). Even if there was drift in the perceived location of the hand, it is not clear that this should affect perceptual maps using this technique. Indeed, in our first experiment using this paradigm (Experiment 1 in Longo and Haggard 2010), we used quite long blocks (100 trials), but found no apparent change in the magnitude of distortions across the duration of individual blocks.

Another possibility is that even if aspects of motor control of the pointing hand are not responsible for the overall pattern of distortions, such factors may nevertheless influence responses. The more veridical maps obtained with pointing responses could be related to dissociations between perception and action such as reported for both neurological patients (e.g., Goodale et al. 1991) and healthy individuals (e.g., Aglioti et al. 1995). Indeed, Kammers and colleagues (2009) showed that proprioceptive biases induced by the rubber hand illusion were apparent for perceptual judgments, but disappeared when participants responded by active pointing. Cardinali and colleagues (2011), in contrast, found that proprioceptive updated induced by tool-use was apparent for both motoric and perceptual tasks, but only when locations were cued by touch and not verbally. It is possible that even more veridical maps might be found if participants were asked to point quickly and ballistically, rather than in a deliberate and controlled way.

Acknowledgements This research was supported by European Research Council Grant ERC-2013-StG-336050 under the FP7.

Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

References

Adams DC (1999) Methods for shape analysis of landmark data from articulated structures. Evol Ecol Res 1:959–970

Aglioti S, DeSouza JF, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Ambroziak KB, Tamè L, Longo MR (2018) Conceptual distortions of hand structure are robust to changes in stimulus information. Conscious Cogn 61:107–116

Anema HA, van Zandvoort MJE, de Haan EHF, Kappelle LJ, de Kort PL, Jansen BPW et al (2009) A double dissociation between somatosensory processing for perception and action. Neuropsychologia 47:1615–1620

Azañón E, Tamè L, Maravita A, Linkenauger SA, Tajadura-Jiménez A, Longo MR (2016) Multimodal contributions to body representation. Multisens Res 29:635–661

Bookstein FL (1991) Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge

Burgess PR, Wei JY, Clark FJ, Simon J (1982) Signaling of kinaesthetic information by peripheral sensory receptors. Ann Rev Neurosci 5:171–187

Cardinali L, Brozzoli C, Urquizar C, Salemme R, Roy AC, Farnè A (2011) When action is not enough: tool-use reveals tactile-dependent access to body schema. Neuropsychologia 49:3750–3757

Carey DP, Dijkerman HC, Murphy KJ, Goodale MA, Milner AD (2006) Pointing to places and spaces in a patient with visual form agnosia. Neuropsychologia 44:1584–1594

Cocchini G, Galligan T, Mora L, Kuhn G (2018) The magic hand: plasticity of mental hand representation. Quart J Exp Psychol. https://doi.org/10.1177/1747021817741606

Coelho LA, Gonzalez CLR (2018) The visual and haptic contributions to hand perception. Psychol Res. https://doi.org/10.1007/s00426-017-0870-x

Coelho LA, Zaninelli G, Gonzalez CLR (2017) A kinematic examination of hand perception. Psychol Res 81:1224–1231

Collins DF, Refshauge KM, Todd G, Gandevia SC (2005) Cutaneous receptors contribute to kinesthesia at the index finger, elbow and knee. J Neurophysiol 94:1699–1706

Edin BB, Johansson N (1995) Skin strain patters provide kinaesthetic information to the human central nervous system. J Physiol 487:243–251

Ferrè ER, Vagnoni E, Haggard P (2012) Vestibular contributions to bodily awareness. Neuropsychologia 51:1445–1452

Ferrell WR, Gandevia SC, McCloskey DI (1987) The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. J Physiol 386:63–71

Ganea N, Longo MR (2017) Projecting the self outside the body: body representations underlying proprioceptive imagery. Cognition 162:41–47

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349:154–156

Goodwin GM, McCloskey DI, Matthews PBC (1972) The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. Brain 95:705–748

Jones SA, Cressman EK, Henriques DY (2010) Proprioceptive localization of the left and right hands. Exp Brain Res 204:373–383

Jones SA, Fiehler K, Henriques DY (2012) A task-dependent effect of memory and hand-target on proprioceptive localization. Neuropsychologia 50:1462–1470

Kammers MPM, de Vignemont F, Verhagen L, Dijkerman HC (2009) The rubber hand illusion in action. Neuropsychologia 47:204–211

Longo MR (2014) The effects of immediate vision on implicit hand maps. Exp Brain Res 232:1241–1247

Longo MR (2015a) Posture modulates implicit hand maps. Conscious Cogn 36:96–102

Longo MR (2015b) Intuitive anatomy: distortions of conceptual knowledge of hand structure. Cognition 142:230–235

Longo MR (2015c) Implicit and explicit body representations. Euro Psychol 20:6–15

Longo MR (2017a) Distorted body representations in healthy cognition. Quart J Exp Psychol 70:378–388

Longo MR (2017b) Expansion of perceptual body maps near—but not across—the wrist. Front Hum Neurosci 11:111

Longo MR, Haggard P (2010) An implicit body representation underlying human position sense. Proc Natl Acad Sci 107:11727–11732

Longo MR, Haggard P (2012a) A 2.5-D representation of the human hand. J Exp Psychol Hum Percept Perform 38:9–13

Longo MR, Haggard P (2012b) Implicit body representations and the conscious body image. Acta Psychol 141:164–168

Longo MR, Morcom R (2016) No correlation between distorted body representations underlying tactile distance perception and position sense. Front Hum Neurosci 10:593

Longo MR, Azañón E, Haggard P (2010) More than skin deep: body representation beyond primary somatosensory cortex. Neuropsychologia 48:655–668

Longo MR, Long C, Haggard P (2012) Mapping the invisible hand: a body model of a phantom limb. Psychol Sci 23:740–742

Longo MR, Mancini F, Haggard P (2015a) Implicit body representations and tactile spatial remapping. Acta Psychol 160:77–87

Longo MR, Mattioni S, Ganea N (2015b) Perceptual and conceptual distortions of implicit hand maps. Front Hum Neurosci 9:656

Lopez C, Schreyer H-M, Preuss N, Mast FW (2012) Vestibular stimulation modifies the body schema. Neuropsychologia 50:1830–1837

Macefield G, Gandevia SC, Burke D (1990) Perceptual responses to microstimulation of single afferents innervating joints, muscles and skin of the human hand. J Physiol 429:113–129

Matthews PBC (1972) The mammalian muscle receptors and their central actions. Edward Arnold, London

Mattioni S, Longo MR (2014) The effects of verbal cueing on implicit hand maps. Acta Psychol 153:60–65

Medina J, Duckett C (2017) Domain-general biases in spatial localization: evidence against a distorted body model hypothesis. J Exp Psychol Hum Percept Perform 43:1430–1443

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford

Napier J (1980) Hands. Princeton University Press, Princeton

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Paillard J, Michel F, Stelmach G (1983) Localization without content: a tactile analogue of 'blindsight'. Ann Neurol 40:548–551

Pavani F, Boscagli I, Benvenuti F, Rabuffetti M, Farnè A (1999) Are perception and action affected differently by the Titchner circles illusion? Exp Brain Res 127:95–101

Pisella L, Binkofski F, Lasek K, Toni I, Rossetti Y (2006) No double-dissociation between optic ataxia and visual agnosia: multiple sub-streams for multiple visuo-manual integrations. Neuropsychologia 44:2734–2748

Proske U, Gandevia SC (2009) The kinaesthetic senses. J Physiol 587:4139–4146

Proske U, Gandevia SC (2012) The proprioceptive senses: their roles in signaling body shape, body position and movement, and muscle force. Physiol Rev 92:1651–1697

Rohlf FJ, Slice DE (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst Zool 39:40–59

Rossetti Y, Rode G, Boisson D (1995) Implicit processing of somaesthetic information: a dissociation between where and how? NeuroReport 6:506–510

Saulton A, Dodds TJ, Bülthoff HH, de la Rosa S (2015) Objects exhibit body model like shape distortions. Exp Brain Res 233:1471–1479

Saulton A, Longo MR, Wong HY, Bülthoff HH, de la Rosa S (2016) The role of visual similarity and memory in body model distortions. Acta Psychol 164:103–111

Saulton A, Bülthoff HH, de la Rosa S (2017) Conceptual biases explain distortion differences between hand and objects in localization tasks. J Exp Psychol Hum Percept Perform 43:1444–1453

Stone KD, Keizer A, Dijkerman HC (2018) The influence of vision, touch, and proprioception on body representation of the lower limbs. Acta Psychol 185:22–32

Tamè L, Bumpus N, Linkenauger SA, Longo MR (2017) Distorted body representations are robust to differences in experimental instructions. Atten Percept Perform 79:1204–1216

Wann JP, Ibrahim SF (1992) Does limb proprioception drift? Exp Brain Res 91:162–166