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Projecting the self outside the body: Body representations underlying proprioceptive imagery

Nataşa Ganea, Matthew R. Longo *

Department of Psychological Sciences, Birkbeck, University of London, United Kingdom

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ABSTRACT

Recent research has shown that proprioception relies on distorted representations of body size and shape. By asking participants to localise multiple landmarks on their occluded hand, perceptual maps of hand size and shape can be constructed and compared to actual hand structure. These maps are different from the actual size and shape of the occluded hand, revealing underestimation of finger length and overestimation of hand width. Here we tested whether the same distorted body model underlies proprioceptive imagery (i.e. imagining the hand at a specific location, and in a different posture than it actually is). In Experiment 1, participants placed their left hand under an occluding board (*real* condition) or imagined their left hand under the board (*imagined* condition). Highly similar distortions were found in both conditions. Furthermore, results across the two conditions were strongly correlated. In Experiment 2, participants completed the *real* condition and two *imagined* conditions. In the *imagined-fist* condition, participants held their left hand in a fist, in their lap, while in the *imagined-flat* condition, participants held their left hand flat, with palm down, in their lap. In both *imagined* conditions, participants were asked to imagine their left hand lying flat, with palm down, under the occluding board. A similar pattern of distortions was found in all three conditions. These results suggest that both proprioception and proprioceptive imagery reply on a common stored model of the body's metric properties.

1. Introduction

The ability to form mental images of stimuli in their absence is a fundamental component of human cognition. It facilitates action planning and decision-making, and provides a revealing window into the contents of mental representations (Kosslyn, Thompson, & Ganis, 2006). Imagery has been investigated most thoroughly in the case of vision, for example in the seminal studies of Kosslyn and colleagues (Kosslyn, Ganis, & Thompson, 2001; Kosslyn et al., 2006). Numerous studies have also described imagery in other modalities, including audition (e.g., Zatorre, Halpern, Perry, Meter, & Evans, 1996), touch (e.g., Schmidt, Ostwald, & Blankenburg, 2014), gustation (e.g., Kobayashi et al., 2004), olfaction (e.g., Bensafi et al., 2003), vestibular sensations (e.g., zu Eulenburg, Müller-Forell, & Dieterich, 2013), and action (e.g., Decety et al., 1994; Parsons, 1987). A general finding across modalities is that imagery relies on mental and neural representations subserving perception and action, functioning in effect as a "weak form of perception" (Pearson, Naselaris, Homles, & Kosslyn, 2015, p. 590).

Here, we investigated mental imagery for proprioception, that is the ability to imagine one's limbs in a different posture or location than they are actually in. Many studies of motor and kinaesthetic imagery have, of course involved a proprioceptive component. For example, in studies of imagined walking (e.g., Decety, Jeannerod, & Preblanc, 1989) the limbs are certainly imagined to change posture. Similarly, in Parsons' (1987, 1994) classic hand rotation task, participants judge whether a picture is of a right or a left hand. Research has suggested that participants perform this task by mentally rotating their hand from its current posture to match the seen hand (Parsons, 1987). Indeed, when the posture of the participant's own hand does not match that of the picture, responses are slowed (Funk, Shiffrar, & Brugger, 2005; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Shenton, Schwoebel, & Coslett, 2004). The focus of these studies, however, has been on the ability to imagine *movement* of the body, not on proprioception. To our knowledge, no research has specifically focused on the ability to imagine the limbs at a specific location different from their actual location.

* Corresponding author at: Department of Psychological Sciences, Birkbeck, University of London, Malet Street, London WC1E 7HX, United Kingdom.

E-mail address: m.longo@bbk.ac.uk (M.R. Longo).

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There are reasons to think that investigating imagery for precise location may be particularly informative. For example, in a classic study, Kosslyn, Ball, and Reiser (1978) showed that the time taken to mentally scan between landmarks on a previously seen map was directly proportional to the distance between landmarks. This showed that mental imagery preserves precise metric information about imagined objects. Indeed, recent fMRI studies have shown that visual perception and imagery rely on shared representations of location in higher-order visual cortices (Cichy, Heinzle, & Haynes, 2012; Stokes, Saraiva, Rohenkohl, & Nobre, 2011).

Given that Kosslyn et al. (1978) showed that visual imagery preserves precise metric spatial relations, we investigated whether the same is true for proprioceptive imagery. We employed a paradigm we recently developed to construct perceptual maps of hand size and shape underlying proprioception (Longo & Haggard, 2010). Participants use a long baton to indicate the perceived location of landmarks (i.e., fingertips and knuckles) of their occluded hand. By comparing the relative locations of judgments of different landmarks, perceptual maps of hand size and shape can be constructed and compared to actual hand form. These maps show massive distortions, which are highly stereotyped across people, for example, overall underestimation of finger length and overestimation of hand width. Longo and Haggard (2010) interpreted this result as suggesting that immediate proprioceptive signals are combined with a distorted mental representation of body size and shape, which they called the *body model*. This task is unusually suited to studies of mental imagery in that it does not require any stimulation to be delivered to the judged body part, or even for that part to exist at all. Indeed, Longo, Long, and Haggard (2012) used this paradigm to map the phantom hand of a person born without a left arm.

In this study, we tested whether proprioceptive imagery preserves precise metric relationships among landmarks, analogous to that seen in visual imagery by Kosslyn et al. (1978), and if so, whether it utilises the same distorted body model as actual proprioception. In Experiment 1, we used the pointing task developed by Longo and Haggard (2010) to construct perceptual hand maps both when the hand was on table, underneath the occluding board (*real* condition), and when the participant merely imagined the hand as being there (*imagined* condition). Based on previous imagery research, which has found that imagery preserves metric relations, we predicted the same stereotyped pattern of distortions (i.e., an underestimation of finger length and overestimation of knuckle spacing) in both conditions. In Experiment 2, we controlled for the posture and the position of the participant's actual hand in the *imagined* condition, asking participants to hold their left hand in their lap flat, with fingers straight, and palm down (*imagined-flat* condition), or in the shape of a fist (*imagined-fist* condition). For comparison, we also included a *real* proprioceptive condition.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Thirteen individuals (5 females) aged between 18 and 51 years old (M: 28.57) participated. All were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), *M*: 70.96; range: 47.37 – 100. Data from one additional participant could not be analysed due to random responses.

2.1.2. Design & procedure

Fig. 1 shows the experimental setup. Participants sat at a table and made judgments about the perceived location of different parts of their left hand in two conditions. The *real* condition was similar to our previous studies using this paradigm (Longo & Haggard, 2010, 2012a, 2012b; Longo et al., 2012). Participants sat with their left hand resting on the table approximately aligned with their body midline. The hand was then covered by a 40 x 40 cm board which rested on four pillars (6 cm high). Participants used a baton (35 cm length; 2 mm diameter) held in their right hand to indicate the perceived location of landmarks on the dorsum of their occluded hand. The *imagined* condition was similar except that the participant's left hand rested in their lap, with palm up, while they imagined it lying flat on the table, with palm down, in a position and posture similar to the *real* condition. Like in the *real* condition, participants were asked to indicate where they felt each landmarks was located. In both conditions, participants wore a black cloth which covered their body from neck downwards.

Responses were captured by a camera (Logitech Webcam Pro 9000) suspended 27 cm above the table. The photographs (1600×1200 pixels) were taken under the control of a custom Matlab (Mathworks, Natick, MA) script. Participants localised ten landmarks: the centre of the knuckle at the base of each finger and the tip of each finger (i.e., the most distal bit of the finger). On each trial, participants were verbally instructed which landmark to judge. They placed the tip of the baton on the board directly above the perceived location of that landmark. Participants were asked to take their time, be precise, avoid ballistic pointing and avoid using strategies such as tracing the outline of the hand. When the participant made their response, a photograph was taken and stored for offline coding. To avoid response biases, after each trial participants moved the tip of the baton to a dot at the edge of the board.

Both before and after each block of the *real* condition, a photograph was taken without the occluding board to obtain measures of actual hand size, shape, and posture, and to ensure that the hand had not moved during the block. Clearly, no such pictures could be taken in the *imagined* condition. A 10 cm ruler on the table appeared in the photographs without the occluder, allowing conversion between pixels and cm. At the beginning of the experiment, a small black mark was made on the knuckle of each finger to facilitate coding from photographs. There were four blocks of 50 trials, two of each condition. Each block consisted of five mini-blocks of 10 trials (one trial for each landmark), presented in random order. The blocks were presented in ABBA order, with the initial condition counterbalanced across participants.

2.1.3. Analysis

The analysis methods were similar to those we have used previously with this paradigm. The x-y pixel coordinates of each landmark were coded using a custom Matlab script and were averaged across trials within a block. This resulted in one map of the hand for each block. Distances between pairs of knuckles and between the tip and the knuckle of each finger were calculated and converted into cm. We then calculated the percent overestimation between pairs of landmarks as: 100 x (judged length – actual length) / actual length.

The main statistical comparisons involve percent overestimation. In order to visualise the data, however, we also placed the maps from each condition into Procrustes alignment with actual hand shape. Procrustes alignment translates, rotates, and dilates maps of homologous landmarks in order to place them into optimal alignment (Bookstein, 1991; Rohlf & Slice, 1990). Because the fingers can rotate independently, they were rotated to a common posture before being put into Procrustes alignment. For each finger this posture was defined by the angle formed by the intersection of two lines – one running through the tip and the knuckle of that finger and another running through the knuckles of the index and little fingers. We calculated the average angle across participants for each finger of the actual hand, and then rotated

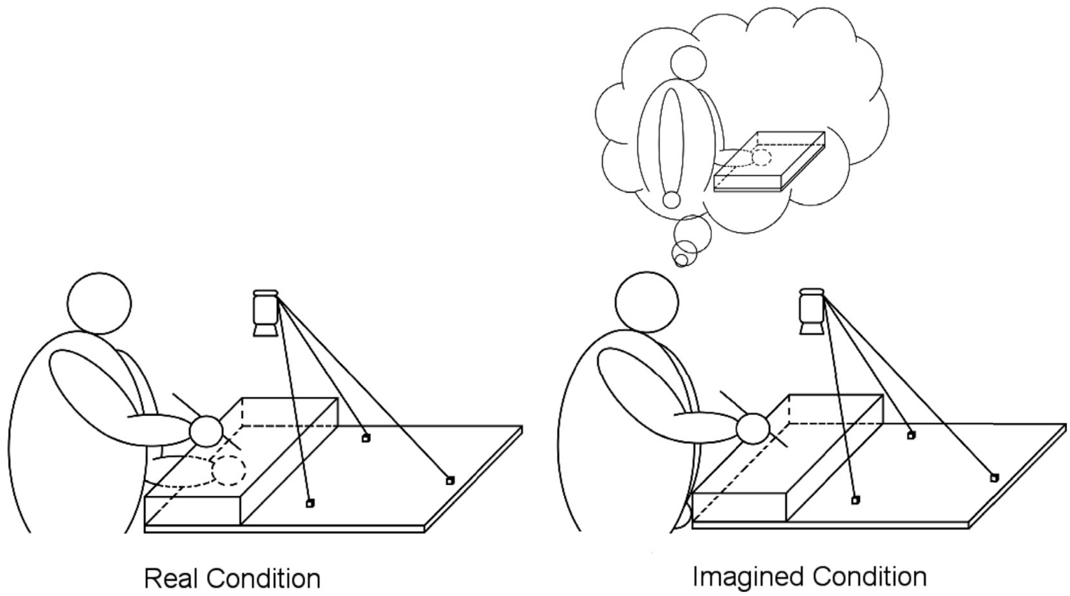

Fig. 1. Experimental setup. *Left panel:* The *real* condition. Participants placed their hand underneath an occluding board and used a long baton to indicate the perceived location of the tip and knuckle of each finger. *Right panel:* The *imagined* condition. Participants rested their hand in their lap with palm facing up while imaging their hand to be underneath the occluding board, in a posture and location similar to the *real* condition. They made judgments of the perceived location of landmarks on the mental image.

the tip of each finger in every map (actual and judged), taking the knuckle as a pivot point. This resulted in hand maps having the same posture, allowing comparisons of shape.

The hand shapes were then compared using Generalised Procrustes Superimposition (GPS) with CoordGen software, part of the Integrated Morphometrics Program (IMP; H. David Sheets, Canisius College, http://www.canisius.edu/~sheets/morphsoft.html). Because there were two experimental blocks of each condition, maps from each condition were first put into GPS and averaged, resulting in a single map for each participant for the actual hand and for judgments in each of the two experimental conditions. Then a second group-level GPS was run, putting the judged maps from each condition into GPS alignment with actual hand shape.

2.2. Results and discussion

Fig. 2 shows grand average maps of actual and represented hand shape in the two conditions, placed into Procrustes alignment. Clear and well-organised spatial maps were apparent in both conditions, demonstrating that proprioceptive imagery supports organised spatial judgments which preserve spatial relations among landmarks. Consistent with our previous results, we found clear distortions, including: (1) overestimation of hand width, (2) underestimation of finger length, and (3) a radial-ulnar gradient of magnification of finger length underestimation. Crucially, these distortions were present in both the *real* condition and the *imagined* condition.

The left panel of Fig. 3 shows percentage overestimation of finger length. Averaging across fingers, overall underestimation of finger length was apparent in both the real (M: 21.89%), $t(12) = 3.55$, $p < 0.005$, $d = 0.98$, and imagined (M: 24.74%), $t(12) = 2.90$, $p < 0.02$, $d = 0.81$, conditions. There was no significant difference in the magnitude of finger underestimation across the two conditions, $t(12) = 0.66$, $p = 0.52$, $d_z = 0.18$, which were strongly correlated, $r(11) = 0.875$, $p < 0.0001$. An analysis of variance (ANOVA) revealed a significant main effect of finger, $F(1.94, 23.29) = 5.24$, $p < 0.02$, $\eta_p^2 = 0.30$. However, there was no main effect of condition, $F(1, 12) = 0.43$, *n.s.*, nor an interaction between finger and condition, $F(4, 48) = 0.70$, *n.s.*

The change in underestimation across fingers was quantified using least-squares regression. Percent overestimation was regressed on digit number (i.e., D1 = thumb, D5 = little finger, separately for each participant and condition). There was a clear radial-ulnar gradient of underestimation in the *real* condition (mean $\beta = -3.92$%/finger), $t(12) = -3.54$, $p < 0.005$, $d = 0.98$. This

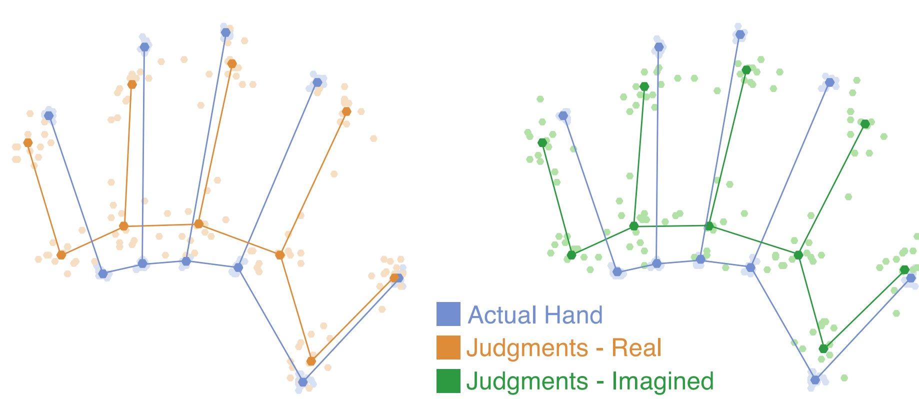

Fig. 2. Generalised Procrustes alignment of landmark positions of the actual hand (blue) and perceptual hand maps in the *real* condition (orange), and in the *imagined* condition (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

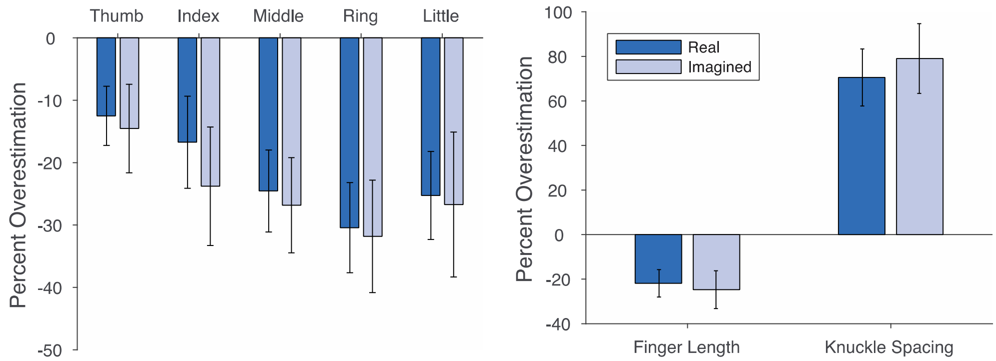

Fig. 3. *Left panel:* Underestimation of finger length as a function of the five fingers in the *real* and the *imagined* conditions. *Right panel:* Underestimation of finger length (i.e., the data from the left panel collapsed across fingers) and overestimation of hand width (i.e., the distance between the knuckles of the index and little fingers). Error bars indicate one S.E.M.

effect was only marginally significant in the *imagined* condition (mean β = -3.24%/finger), $t(12) = -2.00$, $p = 0.069$, $d = 0.55$, but there was no significant difference between the two conditions, $t(12) = 0.81$, $p = 0.435$, $d_z = 0.22$.

The right panel of Fig. 3 shows percentage overestimation of the spacing between pairs of knuckles. Taking the distance between the knuckles of the index and little fingers as an overall measure of hand width, clear overestimation of hand width was apparent in both the *real* (*M*: 70.57%), $t(12) = 5.51$, $p < 0.0001$, $d = 1.53$, and the *imagined* (*M*: 79.02%), $t(12) = 5.04$, $p < 0.0005$, $d = 1.40$, conditions. No significant difference in the magnitude of overestimation in the two conditions, $t(12) = 1.72$, $p = 0.11$, $d_z = 0.48$, was found, overestimation across the two conditions being strongly correlated, $r(11) = 0.961$, $p < 0.0001$.

3. Experiment 2

In Experiment 1, we found that irrespective of the actual location of the hand, participants underestimated the length of their fingers, and overestimated the width of their hands. Although these results speak to the fact that participants can imagine their hands in a different location and posture than they actually are, it could be argued that asking participants to hold their hands open, with palm up, in their lap, during the *imagined* condition, might have facilitated responses. That is, could participants in the *imagined* condition have actually been pointing towards the location of landmarks on their actual hand on their lap? We consider this interpretation unlikely, given that the participant's lap was not directly underneath the occluding board, because the hand was resting palm up in a relaxed posture, in contrast to the imagined hand which was palm down with fingers straight. Nevertheless, to address this point, we ran a second study in which we manipulated the posture of the hand during the imagined condition. More specifically, in the *imagined-flat* condition we asked participants to hold their hand flat on their lap, with palm facing down and fingers straight. In the *imagined-fist* condition, in contrast, we asked participants to hold their left hand in a fist in their lap. Irrespective of the actual hand posture, participants had to imagine their left hand lying flat, with palm down, under the occluding board. For comparison with Experiment 1, we also ran a *real* proprioceptive condition, in which we asked participants to place their hand flat, with palm down, under the occluding board.

3.1. Methods

3.1.1. Participants

Fifteen participants (10 females) aged between 20 and 42 years old (M: 27.66) took part in the study. With the exception of one participant who was left-handed, all the other participants were right-handed as assessed by the by the Edinburgh Handedness Inventory (Oldfield, 1971), *M*: 77.04; range: -47.37 to 100. Two additional participants were tested, but excluded from the analysis due to inattentiveness and random pointing (N = 1), or because they moved their hand during 3 blocks (N = 1).

3.1.2. Design & procedure

Procedures were similar to Experiment 1. The *real* condition was exactly as in Experiment 1. In the *imagined-flat* condition, participants were asked to hold their left hand flat on their lap, with the palm resting flat and with fingers straight. In the *imagined-fist* condition, they were asked to hold their left hand on their lap in the shape of a fist. As in the *imagined* condition of Experiment 1, in both imagined conditions participants were asked to imagine the hand lying flat, with palm down, and straight fingers, under the board. The coding and the analysis of data was similar to Experiment 1.

3.2. Results and discussion

Fig. 4 shows grand average maps of actual and represented hand shape in the three conditions, placed into Procrustes alignment. Clear and well-organised spatial maps were apparent in all three conditions, similar to Experiment 1. Overestimation of hand width, underestimation of finger length, and a radial-ulnar gradient were clearly present in all conditions. This pattern replicates the results from Experiment 1 and shows that the presence of these distortions in the imagery condition does not rely on the actual hand being in any single posture.

The left panel of Fig. 5 shows percent overestimation of finger length. Collapsing across the five fingers, there was clear underestimation of finger length in the *real* condition (*M*: 30.27%), $t(14) = -8.36$, $p < 0.0001$, $d = 2.16$, in the *imagined-flat* condition (*M*: −35.66%), $t(14) = -8.53$, $p < 0.0001$, $d = 2.20$, and in the *imagined-fist* condition (*M*: −34.46%), $t(14) = -8.38$, $p < 0.0001$, $d = 2.16$. The amount of underestimation was strongly inter-correlated across conditions, with clear correlations between the *real* and *imagined-flat* conditions, $r(13) = 0.765$, $p < 0.001$, the *real* and *imagined-fist* conditions, $r(13) = 0.819$, $p < 0.0005$, and the two imagined conditions, $r(13) = 0.897$, $p < 0.0001$. An ANOVA revealed a significant main effect of finger, $F(4, 56) = 27.48$, $p < 0.0001$, $\eta_p^2 = 0.66$. There was a marginal trend towards a main effect of condition, $F(2,28) = 2.90$, $p = 0.072$, $\eta_p^2 = 0.17$, and a significant interaction between finger and condition, $F(8,112) = 3.12$, $p < 0.005$, $\eta_p^2 = 0.18$. As can be seen in the left panel of Fig. 5, this interaction was driven by less underestimation of thumb length in the *real* condition than in either of the two imagery conditions. Generally,

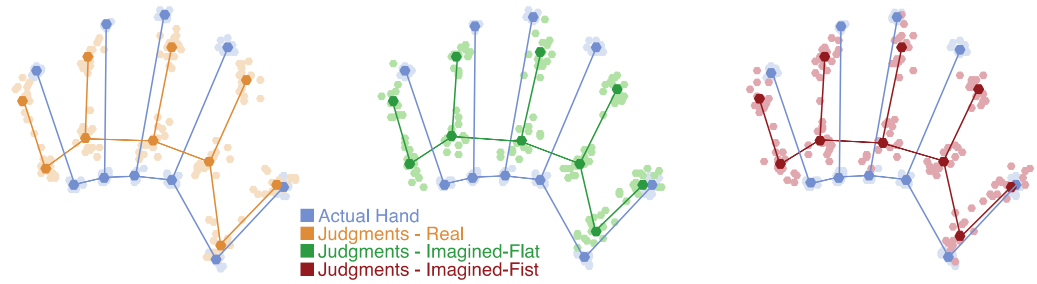

Fig. 4. Generalised Procrustes alignment of landmark positions of the actual hand (blue) and perceptual maps in the *real* condition (orange), the *imagined-flat* condition (green), and the *imagined-fist* condition (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

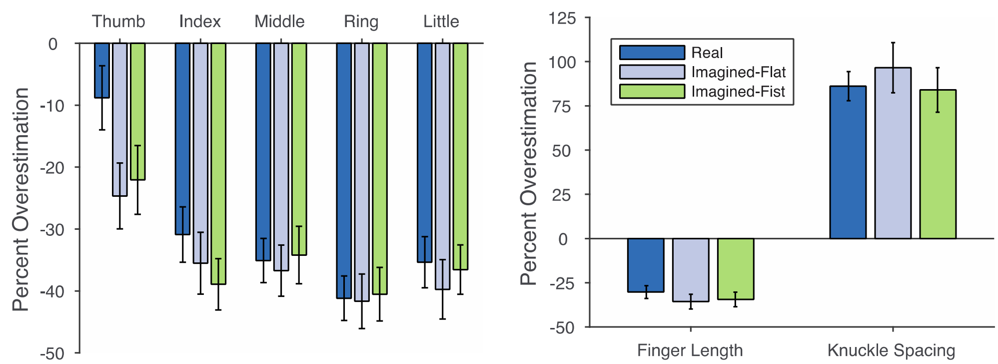

Fig. 5. *Left panel*: Underestimation of finger length across the five fingers in each of the three conditions. *Right panel*: Underestimation of finger length (i.e., the data from the left panel collapsed across fingers) and overestimation of hand width (i.e., the distance between the knuckles of the index and little fingers). Error bars indicate one S.E.M.

however, the same radial-ulnar gradient with underestimation increasing from the thumb to little finger was apparent in all three conditions.

As in Experiment 1, this change across the hand was quantified using least-squares regression. Clear gradients were found in the *real* condition (mean $\beta = -6.34\%$/finger), $t(14) = -5.85$, $p < 0.0001$, $d = 1.51$, in the *imagined-flat* condition (mean $\beta = -3.63\%$/finger) $= t(14) = -3.17$, $p < 0.01$, $d = 0.82$, and in the *imagined-fist* condition (mean $\beta = -3.06\%$/finger), $t(14) = -4.09$, $p < 0.002$, $d = 1.06$.

The right panel of Fig. 5 shows overestimation of the spacing between the knuckles of the index and little fingers. Clear overestimation of hand width was apparent in the *real* condition (M: 86.12%), $t(14) = 10.46$, $p < 0.0001$, $d = 2.70$, in the *imagined-flat* condition (M: 96.53%), $t(14) = 6.81$, $p < 0.0001$, $d = 1.76$, and the *imagined-fist* condition (M: 83.97%), $t(14) = 6.68$, $p < 0.0001$, $d = 1.73$. The amount of overestimation was strongly intercorrelated between conditions, with clear correlations between the *real* and *imagined-flat* conditions, $r(13) = 0.751$, $p < 0.002$, the *real* and *imagined-fist* conditions, $r(13) = 0.804$, $p < 0.0005$, and the two imagined conditions, $r(13) = 0.936$, $p < 0.0001$. An ANOVA comparing the amount of overestimation in the three conditions did not reveal a significant effect, $F(1.39, 19.45) = 1.52$, $p = 0.240$, $\eta_p^2 = 0.098$.

4. General discussion

Similar perceptual maps of hand structure were obtained when participants judged the location of landmarks on their occluded hand using proprioception and when they merely imagined their hand underneath the occluder. Moreover, in both cases these maps were highly distorted, consistent with previous results (e.g., Longo & Haggard, 2010). Specifically, the maps featured: (1) overestimation of hand width, (2) underestimation of finger length, and (3) increased underestimation of finger length from the thumb to the little finger. The results of Experiment 2 showed that similar maps of imagined hand posture can be obtained, even when the actual posture of the hand is very different. In both experiments, the magnitude of distortions in real and imagined conditions was strongly correlated across participants. That these distortions were present in the imagined condition as well as the real condition suggests that both proprioception and proprioceptive imagery utilise a common stored body model. To our knowledge this is the first attempt to systematically test the properties of proprioceptive imagery. By looking at the distances between points rather than the localization of individual landmarks, which can be influenced by various factors such as distance from the body's medial axis, or visual depth, we show that proprioceptive imagery mimics actual proprioception, and that a stored representation of the body's metric properties informs both processes.

Research on kinaesthetic imagery has focused largely on the role of biomechanical constraints in shaping imagery. For example, it has been consistently shown that people are slower to mentally rotate their hands or feet into awkward postures than into postures that are biomechanically easier to achieve (Funk et al., 2005; Parsons, 1987, 1994; Shenton et al., 2004). For example, judging the laterality of a picture of the palm of a hand orientated 90° away from the medial axis (with the thumb pointing away from the body) is more difficult than for the same picture orientated towards the medial axis (Parsons, 1994). In contrast, little if any research has investigated whether imagery preserves precise metric information about the spatial configuration of the body. Our results demonstrate that metric relations about body parts, like biomechanical constraints on bodily movement, are preserved in mental imagery. In this sense, our results in proprioception mirror those of Kosslyn's classic studies (1973; Kosslyn et al., 1978) on scanning of visual images.

A central finding in research on visual imagery is that mental images preserve functional characteristics as actual vision (e.g., Kosslyn et al., 1978) and rely on common neural bases (e.g., Kosslyn, Thompson, Kim, & Alpert, 1995; Stokes et al., 2011). Analogous findings have been reported for several other modalities, including audition (e.g., Zatorre et al., 1996), touch (Schmidt et al., 2014), olfaction (e.g., Bensafi et al., 2003), and motoric behaviour (e.g., Decety et al., 1989; Parsons 1994). Our findings extend this result to proprioceptive imagery, showing that judgments about both actual and imagined limb positions rely on a common representation of body size and shape. Pearson et al. (2015), in a recent review, describe mental imagery as a "weak form" of actual perception. Our results are consistent with this characterisation in the case of proprioceptive imagery, showing that it operates very much like actual proprioception, both in terms of allowing precise metric judgments about the locations of specific parts of the body and in showing massive distortions of body size and shape.

What is the function of proprioceptive imagery? Like kinesthetic imagery, proprioceptive imagery may have a role in action planning. As important as planning movements, is planning the desired final configuration of the limbs. Indeed, much research on action planning suggests that many motor representations code primarily for the desired end state of actions, regardless of the specific movement pattern used to achieve that end state (Jeannerod, 1997; Rizzolatti et al., 1988). Proprioceptive imagery, by specifying the end state of a potential action, may thus be particularly useful for planning the eventual goal of an action, whereas kinesthetic imagery may be more useful for planning the specific means used to achieve this goal. Further, proprioceptive imagery may be useful for determining whether an action being considered is possible to perform. For example, the ability to grasp an object depends not only on the size of one's hand, but also on the spacing between one's fingers in a specific hand posture. Thus, to determine if an object is graspable, proprioceptive imagery could be used to imagine one's hand in a grasping posture around the object.

The origins of the distorted representation of the hand seen in this and previous studies remain uncertain. Longo and Haggard (2010) argued that since proprioceptive afferent signals only provide information about joint angles, the absolute localisation of the body in space requires that these signals are combined with a stored body model specifying the size and shape of the segments between joints. Together with a recent case-study of an individual born without a left arm (Longo et al., 2012), the present results provide strong evidence for this interpretation, showing that the distorted hand representation cannot be an artifact of afferent proprioceptive signals, since such signals are absent in the imagined condition. Thus, the distortions must arise from a central representation of body size and shape. Some evidence suggests that this body model is not specific to proprioception, as some aspects of these distortions appear in touch (Longo & Haggard, 2011), visual judgments of body-part size (Longo & Haggard, 2012b), and visual memory for non-body objects (Saulton, Dodds, Bülthoff, & de la Rosa, 2015). For example, Saulton et al. (2015) found that when participants were asked to localize landmarks on previously-seen objects, somewhat similar distortions were apparent, suggesting that some aspects of these distortions may reflect perceptual biases extending beyond proprioception. However, there is also evidence of important differences between the distortions found for one's own body compared to other objects. When participants judged the location of the fingertips and knuckles of a previously seen rubber hand, they showed clear underestimation of finger length, but no overestimation of hand width (Longo, Mattioni, & Ganea, 2015; for similar results, see Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). This suggests that while underestimation of finger length may reflect a quite general conceptual misrepresentation of hand structure (cf. Longo, 2015), the overestimation of hand width is more specific to the representation of one's own body. Our finding of nearly identical overestimation of hand width in the *real* and the *imagined* conditions is in striking contrast to the lack of such overestimation when making judgments from visual memory about the same landmarks on a rubber hand. This suggests that visual memory of the hand cannot fully account for our results.

In conclusion, we argue that an implicit representation of the hand underlies both actual proprioception and proprioceptive imagery. The fact that highly similar perceptual maps of hand structure are obtained whether localization judgments are based on actual proprioceptive signals of limb location or on imagery provides further evidence that the body model underlying position sense is stored centrally, and is not an artifact of proprioceptive afferent signals. Our results show that, as in the case of vision (Kosslyn et al., 1978), proprioceptive imagery maintains detailed metric information about the body. More generally, our results add to a growing literature showing that across domains mental imagery relies on mechanisms shared with actual perception and action.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2017.01.021.

References

Bensafi, M., Porter, J., Pouilot, S., Mainland, J., Johnson, B., Zelano, C., et al. (2003). Olfactory activity during imagery mimics that during perception. *Nature Neuroscience, 6*, 1142–1144.
Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge: Cambridge University Press.
Cichy, R. M., Heinzle, J., & Haynes, J.-D. (2012). Imagery and perception share cortical representations of content and location. *Cerebral Cortex, 22*, 372–380.
Decety, J., Jeannerod, M., & Preblanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research, 34*, 35–42.
Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., et al. (1994). Mapping motor representations with positron emission tomography. *Nature, 371*, 600–602.
Funk, M., Shiffrar, M., & Brugger, P. (2005). Hand movement observation by individuals born without hands: Phantom limb experience constrains visual limb perception. *Experimental Brain Research, 164*, 341–346.
Ionta, S., Fourkas, A. D., Fiorio, M., & Aglioti, S. M. (2007). The influence of hands posture on mental rotation of hands and feet. *Experimental Brain Research, 183*, 1–7.
Jeannerod, M. (1997). *The cognitive neuroscience of action*. Oxford: Blackwell.
Kobayashi, M., Takeda, M., Hattori, N., Fukunaga, M., Sasabe, T., Inoue, N., et al. (2004). Functional imaging of gustatory perception and imagery: "Top-down" processing of gustatory signals. *NeuroImage, 23*, 1271–1282.
Kosslyn, S. M. (1973). Scanning visual images: Some structural implications. *Perception and Psychophysics, 14*, 90–94.
Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance, 4*, 47–60.
Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience, 2*, 635–642.
Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery*. Oxford: Oxford University Press.
Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature, 378*, 496–498.
Longo, M. R. (2015). Intuitive anatomy: Distortions of conceptual knowledge of hand structure. *Cognition, 142*, 230–235.
Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 11727–11732.
Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance, 37*, 720–726.
Longo, M. R., & Haggard, P. (2012a). A 2.5-D representation of the human hand. *Journal of Experimental Psychology: Human Perception and Performance, 38*, 9–13.

Longo, M. R., & Haggard, P. (2012b). Implicit body representations and the conscious body image. *Acta Psychologica, 141*, 164–168.

Longo, M. R., Long, C., & Haggard, P. (2012). Mapping the invisible hand: A body model of a phantom limb. *Psychological Science, 23*, 740–742.

Longo, M. R., Mattioni, S., & Ganea, N. (2015). Perceptual and conceptual distortions of implicit hand maps. *Frontiers in Human Neuroscience, 9*, 656.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

Parsons, L. M. (1987). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology, 19*, 178–241.

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 709–730.

Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental imagery: Functional mechanisms and clinical applications. *Trends in Cognitive Sciences, 19*, 590–602.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research, 71*, 491–507.

Rohlf, F. J., & Slice, D. E. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology, 39*, 40–59.

Saulton, A., Dodds, T. J., Bülthoff, H. H., & de la Rosa, S. (2015). Objects exhibit body model like shape distortions. *Experimental Brain Research, 233*, 1471–1479.

Saulton, A., Longo, M. R., Wong, H. Y., Bülthoff, H. H., & de la Rosa, S. (2016). The role of visual similarity and memory in body model distortions. *Acta Psychologica, 164*, 103–111.

Schmidt, T. T., Ostwald, D., & Blankenburg, F. (2014). Imaging tactile imagery: Changes in brain connectivity support perceptual grouping of mental images in primary sensory cortices. *NeuroImage, 98*, 216–224.

Shenton, J. T., Schwoebel, J., & Coslett, H. B. (2004). Mental motor imagery and the body schema: Evidence for proprioceptive dominance. *Neuroscience Letters, 370*, 19–24.

Stokes, M., Saraiva, A., Rohenkohl, G., & Nobre, A. C. (2011). Imagery for shapes activates position-invariant representations in human visual cortex. *NeuroImage, 56*, 1540–1545.

Zatorre, R. J., Halpern, A. R., Perry, D. W., Meter, E., & Evans, A. C. (1996). Hearing in the mind's ear: A PET investigation of musical imagery. *Journal of Cognitive Neuroscience, 8*, 29–46.

zu Eulenburg, P., Müller-Forell, W., & Dieterich, M. (2013). On the recall of vestibular sensations. *Brain Structure and Function, 218*, 255–267.