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

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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.

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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