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Implicit body representations and tactile spatial remapping

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ABSTRACT

To perceive the location of a tactile stimulus in external space (*external tactile localisation*), information about the location of the stimulus on the skin surface (tactile localisation on the skin) must be combined with proprioceptive information about the spatial location of body parts (position sense) — a process often referred to as 'tactile spatial remapping'. Recent research has revealed that both of these component processes rely on highly distorted implicit body representations. For example, on the dorsal hand surface position sense relies on a squat, wide hand representation. In contrast, tactile localisation on the same skin surface shows large biases towards the knuckles. These distortions can be seen as behavioural 'signatures' of these respective perceptual processes. Here, we investigated the role of implicit body representation in tactile spatial remapping by investigating whether the distortions of each of the two component processes (tactile localisation and position sense) also appear when participants localise the external spatial location of touch. Our study reveals strong distortions characteristic of position sense (i.e., overestimation of distances across vs along the hand) in tactile spatial remapping. In contrast, distortions characteristic of tactile localisation on the skin (i.e., biases towards the knuckles) were *not* apparent in tactile spatial remapping. These results demonstrate that a common implicit hand representation underlies position sense and external tactile localisation. Furthermore, the present findings imply that tactile spatial remapping does not require mapping the same signals in a frame of reference centred on a specific body part.

1. Introduction

The appropriate frame of reference for localising bodily sensations varies according to circumstances. When we have an itch on our hand, for example, we care primarily about where the itch is located on the surface of the body. In contrast, when we grope in a dark room looking for a light switch, we may be aware of which part of our hand has contacted the switch, but our primary aim is to localise the switch as an object in external space. A large recent literature has begun to investigate this ability to localise tactile stimuli in external space (e.g., Azañón, Camacho, & Soto-Faraco, 2010; Azañón & Soto-Faraco, 2008; Azañón et al., 2010; Bolognini & Maravita, 2007; Buchholz, Jensen, & Medendorp, 2011; Heed, Backhaus, & Röder, 2012; Heed & Röder, 2010; Overvliet, Azañón, & Soto-Faraco, 2011; Schicke & Röder, 2006). *External spatial localisation* requires that tactile information about the location of a stimulus in contact with the skin surface be integrated with proprioceptive or other information about body posture — a process known as *tactile spatial remapping*. While considerable research has studied the reference frames used for external spatial localisation, little research has investigated the specific representations of the body involved in these computations.

Information about body size and shape is critical for somatosensation. We have recently demonstrated that large distortions of the body representations underlie somatosensory abilities (for review, see Longo, 2015). In particular, tactile localisation of stimuli on the skin surface appears to use a highly distorted representation (Mancini, Longo, Iannetti, & Haggard, 2011), as does localisation of the body in external space (Longo & Haggard, 2010, 2012a). Thus, both of the component processes of external spatial localisation rely on highly distorted body representations. In the present study, we investigate the role of these body representations in remapping by investigating the extent to which these respective distortions appear when participants localise touch in external space.

In the case of position sense, proprioceptive afferent signals specify the extent to which each joint is flexed or extended (Proske & Gandevia, 2012). In order to perceive the absolute spatial location of a part of our body, however, this angular information is not sufficient, and needs to be combined with metric information about the length of segments between joints. Critically, however, information about body size and shape is not directly specified by any of the known somatosensory afferent signals, suggesting that it must be provided by a stored representation of body size and shape. We termed this

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representation of the body's metric properties the "body model", and recently developed a "psychomorphometric" procedure to isolate and measure it (Longo & Haggard, 2010). Participants used a long baton to indicate the perceived location in external space of several landmarks of their occluded hand. By comparing the internal configuration of judgments of each landmark with respect to each other landmark, we constructed perceptual maps of represented hand shape and compared them to actual hand shape. These perceptual maps were highly distorted in a stereotyped fashion, with the hand represented as wider than it actually is and the fingers represented as shorter. In contrast, when participants were explicitly asked to judge the perceived shape of their hand, responses were generally veridical, suggesting that the body model is a form of implicit body representation, distinct from the body image that underlies the conscious experience of our own body.

Localisation of a tactile stimulus on one body part also requires referencing to a body representation — a point that is often ignored in the literature. The stimulus location is first mapped in somatotopic maps in primary somatosensory cortex (Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Mancini, Haggard, Iannetti, Longo, & Sereno, 2012; Penfield & Boldrey, 1937). However, to localise the stimulus to a body part requires an additional linking function, which relates skin regions to the underlying body parts where they are located. This linking function resembles the classical *superficial schema* (Head & Holmes, 1911; Longo, Azañón, & Haggard, 2010; Mancini et al., 2011). To investigate this linking function, we (Mancini et al., 2011) asked participants to localise a tactile stimulus by clicking the mouse cursor at the corresponding point on a silhouette of their own hand on a computer monitor. We found large and highly stereotyped distortions of the superficial schema. On the hairy skin of the hand dorsum, participants perceived touch as being located substantially more distally than it actually was. Intriguingly, this distal bias was highly similar regardless of which class of peripheral afferent fibre was stimulated (i.e., Aβ mediating touch, Aδ mediating first pain, C-fibres mediating second pain), suggesting that it reflects distortions of a supramodal representation of the body surface. In contrast, no such distal bias was found on the glabrous skin of the palm. This suggests that the superficial schema represents the body as a collection of distinct skin surfaces, rather than a coherent, volumetric object.

In sum, our recent research has demonstrated large, stereotyped distortions of body representations underlying both component processes that contribute to external spatial localisation of touch: namely, tactile localisation (Mancini et al., 2011) and proprioceptive localisation (Longo & Haggard, 2010). In this study, we investigated the implicit body representations underlying tactile spatial remapping. In particular, we studied how the different patterns of perceptual bias we described previously affect the perceived external spatial location of touch. In Experiment 1, we adapted our psychomorphometric paradigm for estimating body representations underlying position sense (Longo & Haggard, 2010) in order to investigate tactile spatial remapping. Rather than judging the location of verbally-specified landmarks, participants judged the perceived location in external space of touches applied to the back of their hand. In Experiment 2, we designed a series of tasks to isolate the effects of biases due to tactile localisation and of proprioceptive localisation. If tactile spatial remapping reflects a simple sequential process of first localising touch on the skin, which is then localised on external space, the distortions characteristic of tactile localisation and position sense should add *linearly*. By investigating whether these distortions appear in external spatial localisation of touch, we can therefore investigate the role of implicit body representations in tactile spatial remapping.

2. Experiment 1

The first experiment aimed at unmasking implicit body representations underlying external spatial localisation of touch. To this purpose, we adapted the procedures we have previously developed to measure body representations underlying position sense (Longo & Haggard, 2010).

2.1. Method

2.1.1. Participants

Twelve individuals (eight females) between 19 and 34 years of age participated. All but one were right handed as assessed by the Edinburgh Inventory (*M*: 74.88, range: −100–+100). All procedures were approved by the local ethics committee.

2.1.2. Procedure

The procedure was similar to our previous studies using this paradigm (Longo, 2014; Longo & Haggard, 2010, 2012a,b; Longo, Long, & Haggard, 2012; Mattioni & Longo, 2014). Participants sat with their left hand resting on a table with the palm facing down. The hand rested flat on the table, with fingers completely straight. An occluding board (40 × 40 cm), resting on four pillars (6 cm high) was placed above the hand. A camera (Creative Live Webcam Voice) was suspended directly above the board, pointing straight down, and collected photographs of the participant's hand or responses (JPEG images, 1280 × 960 pixels).

In separate blocks, participants made two types of localisation judgement. In the *Verbal* task, participants judged the location of either the knuckle or the tip of each finger by pointing with a long baton on a board placed above their hand (Fig. 1), as in our previous studies. The critical new aspect of this experiment was to extend the logic of this paradigm to investigate continuous skin surfaces without relying on the presence of landmarks with verbal labels. Accordingly, in the *Tactile* task, participants were touched using a wooden stick at one of the nine locations marked on their left hand dorsum in a 3-by-3 square grid (5 × 5 cm; see Fig. 1b). Participants were required to point with a baton on an occluding board placed above their hand to the point which corresponded to the location of their tactile sensation. Note that because different sets of points were judged in the two tasks, they cannot be compared directly. The purpose of including both tasks was to replicate the distortions we have previously observed using the Verbal task and then to investigate whether comparable distortions can be found for a continuous skin surface using the Tactile task in the same participants.

There were two experimental blocks of each task, in an ABBA order, with the initial condition counterbalanced across participants. Within each block, there were three sequential mini-blocks, each with one trial of each landmark in random order. Before and after each block a photo was taken without the occluding board to obtain a measure of true hand position and to ensure that the hand had not moved during the block. A 10 cm ruler on the table appeared in these images, allowing conversion between pixels and cm.

The use of a baton for pointing was similar to our other studies using this paradigm and was motivated by three considerations. First, because a baton has a much narrower tip than a fingertip, it allows substantially greater precision in responses. Second, it reduces concerns that proximal constant errors might result from the participant having difficulty reaching to the location they actually perceived. Third, it prevents the participant from seeing their pointing hand continuously during the task, which could bias responses.

2.1.3. Analysis

Fisheye distortion in the photographs was corrected using the Panotools plug-in (http://www.panotools.org/) for Adobe Photoshop CS2. The x–y pixel coordinates of each landmark on the images of the actual hand and the corresponding judged locations were coded using ImageJ (Abramoff, Magelhaes, & Ram, 2004).

We conducted two main analyses. First, to investigate whether external spatial localisation relies on the distorted body representations that underlie position sense (Longo & Haggard, 2010), we analysed