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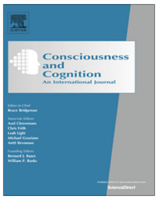

Posture modulates implicit hand maps

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ABSTRACT

Several forms of somatosensation require that afferent signals be informed by stored representations of body size and shape. Recent results have revealed that position sense relies on a highly distorted body representation. Changes of internal hand posture produce plastic alterations of processing in somatosensory cortex. This study therefore investigated how such postural changes affect implicit body representations underlying position sense. Participants localised the knuckles and tips of each finger in external space in two postures: the fingers splayed (*Apart* posture) or pressed together (*Together* posture). Comparison of the relative locations of the judgments of each landmark were used to construct implicit maps of represented hand structure. Spreading the fingers apart produced increases in the implicit representation of hand size, with no apparent effect on hand shape. Thus, changes of internal hand posture produce rapid modulation of how the hand itself is represented, paralleling the known effects on somatosensory cortical processing.

1. Introduction

Several aspects of perception requires that immediate sensory signals be combined with information about the size and shape of the body, including binocular vision (Banks, 1988), and auditory localisation (Clifton et al., 1988). This need is especially acute in somatosensation, given that the primary receptor surface (the skin) is physically co-extensive with the body. Recent studies have investigated the nature of these body representations underlying somatosensory abilities such as position sense (e.g., Ferrè, Vagnoni, & Haggard, 2013; Hach & Schütz-Bosbach, 2010; Longo & Haggard, 2010, 2012a, 2012b; Lopez, Schreyer, Preuss, & Mast, 2012; Saulton, Dodds, Bülthoff, & de la Rosa, 2015) and tactile size perception (e.g., Anema, Wolswijk, Ruis, & Dijkerman, 2008; Canzoneri et al., 2013; Le Cornu Knight, Longo, & Bremner, 2014; de Vignemont, Ehrsson, & Haggard, 2005; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller, Longo, & Saygin, 2014; Tajadura-Jiménez et al., 2012; Taylor-Clarke, Jacobsen, & Haggard, 2004). A general finding across these studies is that the body representations mediating somatosensory processing are highly distorted, in ways that appear related to distortions of somatotopic maps in somatosensory cortex. Other recent studies have demonstrated that the internal postural configuration of the hand alters somatotopic maps (e.g., Hamada & Suzuki, 2003, 2005; Stavrinou et al., 2007). Thus, the present study investigated whether hand posture also modulates implicit body representations mediating position sense.

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1.1. Implicit body representations

In their classic work, which has set the agenda for the field ever since, Head and Holmes (1911) argued that somatosensory processing required that incoming sensory signals from the peripheral nerves had to be interpreted in terms of stored representations, or 'schemas'. There were two main schemas which Head and Holmes postulated. The first, commonly referred to as the 'postural schema' or 'body schema', is a dynamically-updated representation of the configuration of the limbs, required for perceiving where the limbs were in external space. The second, commonly referred to as the 'superficial schema', serves localisation of stimuli on the skin surface. Recently, my colleagues and I (Longo, Azañón, & Haggard, 2010) argued that, in addition to the postural and superficial schemas, a third class of body representation was required for several types of somatosensory information processing, specifically a 'body model' providing information about the metric properties (i.e., the size and shape) of the body.

For example, consider position sense, the ability to perceive the external spatial location of body parts. Proprioceptive afferent signals from joints, muscle tendons, and the skin provide information about the degree of flexion or extension of each joint (Burgess, Wei, Clark, & Simon, 1982; Proske & Gandevia, 2012), that is about body *posture*. To determine the absolute spatial position of a limb, however, information about joint angles (which is specified by proprioceptive afferent signals) needs to be combined with information about the length of each body segment between joints (which is not), as a matter of simple trigonometry. Thus, position sense requires that immediate proprioceptive signals be combined with a stored body model (Longo et al., 2010). We recently developed a novel method to isolate and measure this body model (Longo & Haggard, 2010). Participants laid their hands on a table underneath an occluding board and used a long baton to judge the location of the knuckle and tip of each finger. By comparing the relative judged location of each landmark, we constructed perceptual maps of hand structure, which could then be compared with actual hand structure. These maps were massively distorted, in very consistent ways across people. Specifically, there were three clear distortions apparent across people: (1) overall overestimation of hand width, (2) overall underestimation of finger length, and (3) increasing underestimation of finger length across the hand from the thumb to little finger. This overall pattern has been replicated in a number of subsequent studies (e.g., Ferrè et al., 2013; Longo, 2014; Longo & Haggard, 2012a, 2012b; Longo, Long, & Haggard, 2012; Mattioni & Longo, 2014). In contrast, when participants selected from an array of hand pictures the one most like their own, responses were generally accurate (Longo & Haggard, 2010), suggesting that position sense relies on a class of *implicit body representation*, distinct from the conscious body image.

Other recent studies have revealed similar effects for tactile size perception. Specifically, the perceived distance between two touches on the hand dorsum is perceived as bigger when the two points are oriented medio-laterally (running *across* the hand) than when they're oriented proximo-distally (running *along* the hand) (e.g., Canzoneri et al., 2013; Le Cornu Knight et al., 2014; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller et al., 2014). This pattern suggests that tactile size perception may, like position sense, rely on a distorted body model, with the hand represented as squatter and fatter than it actually is.

1.2. Postural effects on somatosensory processing

Numerous studies have demonstrated that body posture modulates somatosensory processing in various ways. For example, Medina and Rapp (2008) described a patient with a condition known as *synchiria*, in which tactile stimulation of the left hand frequently elicited bilateral sensations on both the left and right hands. Remarkably, the strength of synchiria was modulated by the positions of the hands in space, declining as the hands were moved from the contralesional right hemispace to the ipsilesional left hemispace.

Another clear instance in which posture is critical for somatosensory processing is in perceiving the external spatial location of touch (*tactile spatial remapping*), in which information about the location of touch on the body surface is integrated with proprioceptive information about the location of the body in external space. Intriguingly, there is some evidence that tactile remapping may operate differently at different spatial scales. For example, when the hands are crossed the initial processing of tactile stimuli appears to be based on canonical rather than actual posture, but is rapidly remapped based on actual posture within 200–300 ms (e.g., Azañón & Soto-Faraco, 2008; Heed & Röder, 2010; Overvliet, Azañón, & Soto-Faraco, 2011; Schicke & Röder, 2006; Yamamoto & Kitazawa, 2001). In contrast, when individual fingers are crossed, tactile information does not appear to be updated to reflect this, even as long as 700 ms after stimulation (de Haan, Anema, & Dijkerman, 2012). This can be seen in the well-known *Aristotle illusion* in which a single object placed between crossed fingertips is perceived as two distinct objects (Benedetti, 1985). Indeed, Haggard and colleagues (Haggard, Kitadono, Press, & Taylor-Clarke, 2006) found that webbing the fingers of the two hands impaired judgments of which *hand* had been touched, but not of which *finger* had been touched, suggesting that hand identity is coded in external coordinates, while finger identity is coded in somatotopic coordinates (but for a different interpretation see, Riemer, Trojan, Kleinböhl, & Hölzl, 2010).

Other studies have demonstrated that the internal postural configuration of the hand modulates processing in primary somatosensory cortex (SI). Hamada and Suzuki (2003, 2005), for example, used MEG to compare SI activations elicited by electrical stimulation of the index finger and thumb while the hand was in an 'open' posture (with fingers spread apart) and in a 'closed' posture (with the fingers close together, without touching, as if to pick up a small object). In their first study, they found that hand configuration altered interactions between the representations of the two fingers, measured by comparing activations elicited by simultaneous stimulation of both fingers to the sum of activations from stimulation of each finger separately (Hamada & Suzuki, 2003). More remarkably, in their second study they showed that the distance between the equivalent current dipoles elicited by stimulation of each finger actually decreased when the hand was in the closed posture (Hamada & Suzuki, 2005). These findings suggests that changes in the internal configuration of the hand rapidly stretch and shrink the somatosensory homunculus, changing the overall configuration of SI maps and the way that representations of different skin surfaces interact.

More recently, Stavrinou et al. (2007) taped the four fingers of participants' hands together to induce an experimental form of 'syndactyly', as has been studied following surgical interventions in monkeys (Allard, Clark, Jenkins, & Merzenich, 1991). Like Hamada and Suzuki, Stavrinou and colleagues measured changes in Euclidean distance between MEG dipoles of two digits (D2 and D5) following electrical stimulation. Unlike the earlier studies, however, these effects were measured at several time points up to five hours following the onset of the intervention. In the immediate period following taping the fingers (tested at 30 min), the distance between dipoles was reduced compared to baseline, suggesting that the representations of the fingers had become less distinct, consistent with the postural effects reported by Hamada and Suzuki (2005). Over the next two hours, however, this effect reversed, with the distance between the dipoles increasing over baseline, before reducing towards baseline towards the end of the intervention period.

1.3. The present study

Previous studies of distorted body representations underlying position sense (Longo & Haggard, 2010) and tactile size perception (Longo & Haggard, 2011), have shown that the distortions are not dependent on the global orientation of the body part (the hand) with respect to the rest of the body. When the hand is rotated 90° with respect to the rest of the body, the biases remain unchanged. This demonstrates that the distortions are defined in a hand-centred reference frame, rather than with respect to, for example, the torso or retina. However, given findings that the *internal* posture of the hand modulates somatosensory processing (Hamada & Suzuki, 2003, 2005; Stavrinou et al., 2007), I suspected that it might also affect implicit body representations. This experiment used the 'psychomorphometric' method (Longo & Haggard, 2010) to measure body representations mediating position sense with the hand in two different internal configurations. I compared conditions in which the fingers were spread apart (*Apart posture*) or pressed together (*Together posture*).

2. Methods

2.1. Participants

Eighteen individuals (nine female) between 17 and 41 years of age participated after giving informed consent. All participants but one were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971), *M*: 75.94, range: −27.27 to 100. Procedures were approved by the local ethics committee.

2.2. Procedure

Procedures for this task were similar to those of Longo and Haggard (2010). Participants sat with their left hand palm-down on a table. A board (40 × 40 cm) could be placed on four pillars (6 cm high) to occlude the hand. A webcam (Logitech Webcam Pro 9000) was suspended 27 cm above the occluding board and captured photographs (1600 × 1200 pixels) under control of a custom Matlab (Mathworks, Natick, MA) script.

The participant's task on each trial was to use a long baton (35 cm length; 2 mm diameter) to indicate the perceived location of a specific landmark on their occluded left hand. As in my previous studies, ten landmarks were used: the knuckles (i.e., centre of the knuckle at the base of each finger) and tips (i.e., most distal point) of each finger. On each trial, participants were verbally instructed which landmark to localise. They were instructed to be precise and avoid ballistic pointing or strategies such as tracing the outline of the hand. To ensure independent responses, participants moved the baton to a dot at the edge of the board between trials. When participants indicated their response, a photograph was taken and stored for offline coding. Both before and after each block, 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. 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.

The key experimental manipulation was the posture of the judged left hand. In the *Together* posture participants were asked to place their hand with the fingers pressed together, while in the *Apart* posture participants were asked to spread their fingers apart as much as they could hold comfortably for the duration of each block (see Fig. 1). There were two experimental blocks of each posture in ABBA order. The first condition was counterbalanced across participants.

3. Results

The posture of the participant's actual hand in each condition and of implicit hand maps was quantified by calculating the angle between a line passing between the knuckle and tip of each finger and a line passing between the knuckles of the index

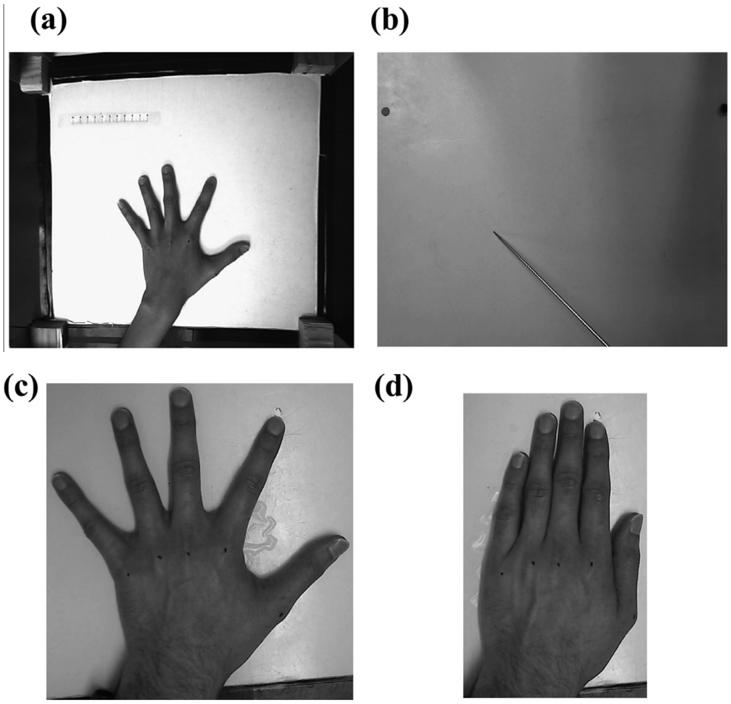

Fig. 1. The experimental paradigm and examples of hand postures. Panel (a) shows an example of the photographs taken at the start and end of each block, showing the actual location of the hand. Panel (b) shows an example of a pointing response. Panels (c) and (d) show examples of the *Apart* (c) and *Together* (d) postures.

and little fingers. These angles are shown in Fig. 2. An analysis of variance (ANOVA) was used to analyse these data with repeated-measures factors *Modality* (Actual, Judged), *Posture* (Apart, Together), and *Finger* (thumb, index, middle, ring, little). Unsurprisingly, there was a clear interaction of posture and finger, $F(4, 68) = 172.23$, $p < .0001$, indicating that the hands were in fact in different postures in the two conditions, and were judged as such. More interestingly, there was a significant interaction of modality and finger, $F(4, 68) = 14.08$, $p < .0001$, indicating the posture of implicit hand maps was systematically biased from actual hand posture, and a three-way interaction, $F(4, 8) = 8.56$, $p < .0001$, indicating that these biases for the judgment of posture differed between the apart and together conditions. As is clear from Fig. 2, in the together posture participants judged their fingers as being more widely splayed than they actually were. In the apart posture, in contrast, there was a bias to judge fingers as rotated slightly towards the radial (i.e., thumb) side of the hand, but no bias in terms of overall splay.

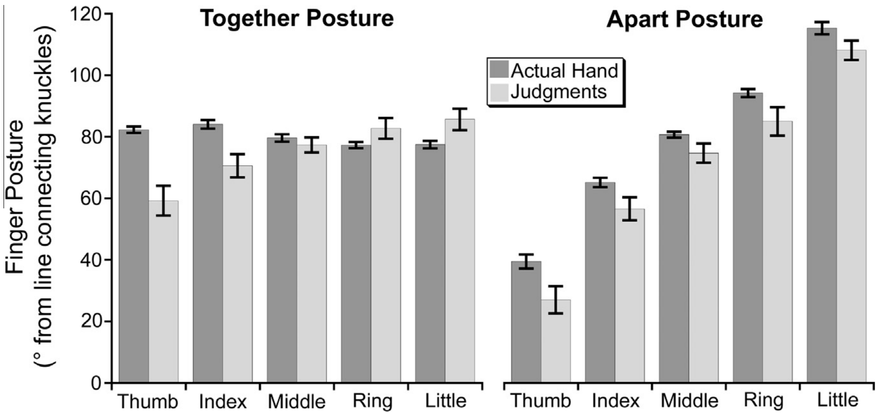

Fig. 2. The posture of each finger, quantified as the angle between a line connecting the knuckle and tip of each finger and a line connecting the knuckles of the index and little finger. Error bars are ±SEM.

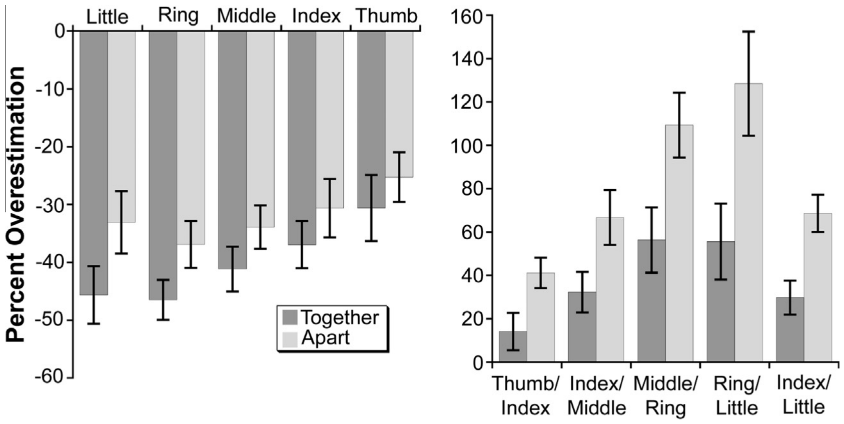

Fig. 3. Percent overestimation of finger length (left panel) and knuckle spacing (right panel) for the Together and Apart postures. Error bars are ±SEM.

Previous studies using this paradigm (e.g., Longo & Haggard, 2010, 2012a, 2012b) have revealed three characteristic distortions of hand shape: (1) overall underestimation of finger length, (2) increase of finger underestimation from the thumb to the little finger, and (3) overestimation of hand width. Each of these effects was replicated in the present data in both postures (see Fig. 3). First, collapsing across the five fingers, there was significant underestimation of finger length in both the apart (31.9% underestimation), $t(17) = 8.13$, $p < .0001$, and together (40.2% underestimation), $t(17) = 10.12$, $p < .0001$, postures (Fig. 3, left panel). Second, the gradient of underestimation across fingers was quantified by regressing percent underestimation on digit number (i.e., thumb = 1, little finger = 5). Underestimation of finger length increased from the radial to ulnar side of the hand, both in the apart (2.2% underestimation/finger), $t(17) = 3.38$, $p < .005$, and together (4.0% underestimation/finger), $t(17) = 3.91$, $p < .005$, postures. Finally, there was significant overestimation of hand width in both the apart (86.4% overestimation), $t(17) = 9.46$, $p < .0001$, and together (39.6% overestimation), $t(17) = 4.77$, $p < .0005$, postures (Fig. 3, right panel). These results replicate the characteristic set of distortions my colleagues and I have reported previously and demonstrate that qualitatively similar patterns of distortions are found in both postures.

While the same basic pattern of distortions was found in both conditions, posture nevertheless had clear effects on the magnitude of these distortions (Fig. 2). First, to investigate effects on finger length, an analysis of variance (ANOVA) was conducted including finger (Thumb–Little) and posture (together, apart) as factors. Consistent with the above results, there was a significant main effect of finger, $F(4,68) = 8.09$, $p < .0001$, revealing that underestimation increased from the thumb to the little finger. Critically, there was also a clear effect of posture, $F(1,17) = 45.61$, $p < .0001$, with significantly less underestimation in the apart than the together posture. There was no significant interaction of finger and posture, $F(4,68) = 0.84$, $p > .50$. Effects for hand width went in the same direction (Fig. 2, right panel). Overestimation of distances between knuckles was significantly greater in the apart than the together posture. Taking the distance between the knuckles of the index and little fingers as an overall measure of hand width, overestimation was significantly larger in the apart than the together posture (68.6% vs. 29.8%), $t(17) = 4.03$, $p < .001$.

4. Discussion

The internal posture of the hand produces rapidly modulation of implicit hand maps. When the fingers were splayed, the hand appeared to be represented as larger than when the fingers were pressed together. This effect is in striking contrast to previous findings showing that postural *rotations* of the hand with respect to the rest of the body have no influence on either position sense (Longo & Haggard, 2010), tactile size perception (Longo & Haggard, 2011), or tactile localisation (Mancini, Longo, Iannetti, & Haggard, 2011). It is thus the *configuration* of the hand that drives these effects, not its *location* or *orientation* in external space. These findings add to the growing literature showing that the position of the body in space has important influences on the processing of somatosensory information (e.g., Azañón, Longo, Soto-Faraco, & Haggard, 2010; Azañón & Soto-Faraco, 2008; de Haan et al., 2012; Haggard et al., 2006; Hamada & Suzuki, 2003, 2005; Heed & Röder, 2010; Kim & Cruse, 2001; Medina & Rapp, 2008; Overvliet, Anema, Brenner, Dijkerman, & Smeets, 2011; Overvliet, Azañón, et al., 2011; Riemer et al., 2010; Sanabria, Soto-Faraco, & Spence, 2005; Schicke & Röder, 2006; Stavrinou et al., 2007; Tamè, Farnè, & Pavani, 2011; Yamamoto & Kitazawa, 2001; Zampini, Harris, & Spence, 2005).

Do the present results reflect an alteration of the represented size of the hand as a function of posture, or could they reflect differences in the act of estimating spatial location? Many studies have shown systematical spatial biases in estimating locations from visual memory (e.g., Huttenlocher, Hedges, Corrigan, & Crawford, 2004; Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Newcombe, & Sandberg, 1994; Spencer & Hund, 2002). For example, Huttenlocher et al. (1991) showed that estimates of the location in which a stimulus had appeared within a circular frame were biases towards the centres of the four wedges created by segmenting the circle along the vertical and horizontal axes. Similarly, young children searching for a toy they had previously seen hidden in a long thin sandbox were biased in their search towards the centre of the box, while more complex biases were found in older children and adults (Huttenlocher et al., 1994). Huttenlocher and colleagues interpret these effects as reflecting a Bayesian integration of an imperfect memory trace with information from spatial categories. To my knowledge, analogous biases have not been described in position sense, though it seems highly plausible that they might exist. In a recent paper (Mattioni & Longo, 2014), we discussed a form of such bias, namely the possibility that the underestimation of finger length and overestimation of knuckle spacing might reflect a form of categorical perception. On this interpretation, landmarks labeled as belong to the same part (e.g., the knuckle and tip of a single finger) would be perceptually attracted, resulting in underestimation, whereas landmarks labeled as belonging to different parts (e.g., the knuckles of adjacent fingers) would be perceptually repulsed.

It is possible that the changes in posture in this experiment might lead to differences in the spatial categorisation of the hand, and thus changes in the estimation of perceived location, analogous to the effects described in visual memory by Huttenlocher and colleagues. For example, a rectangular bounding box surrounding the hand would be larger and more square-like with the fingers in the apart than in the together posture. This could potentially create different constant error biases, producing effects like those reported. On this interpretation, posture would not alter the representation of hand size per se, but would influence performance at the level of location estimation. The present data do not exclude such an interpretation. However, there are some considerations that weigh against it. First, the present analysis focuses on distances between judgments of pairs of knuckles and between the knuckle and tip of each individual finger. Critically, however, these specific distances are not altered by changes in hand splay. For example, splay dramatically changes the distance between judgments of the knuckles of the middle and ring fingers. But the distance between these landmarks is constant across conditions. This bias would predict baseline distortions exactly opposite to those actually found: the spacing between adjacent knuckles should be underestimated relative to finger length since the knuckles are very close together compared to the tip and knuckle of each finger.

Previous studies using MEG have revealed that internal hand posture modulates the organisation of primary somatosensory cortex (Hamada & Suzuki, 2003, 2005; Stavrinou et al., 2007). Specifically, spreading the hand apart appears to increase the distinctiveness of the different fingers, as reflecting by increases in the distance between representations of different fingers (Hamada & Suzuki, 2005; Stavrinou et al., 2007). Thus, when the fingers are pressed together, the hand may be represented more as a single functional unit, whereas with the fingers splayed it may be represented more as a collection of distinct parts. This difference may reflect a transition between different functional modes of hand representation corresponding to power grips, in which the fingers work together collectively, vs. precision grips, in which the fingers operate more individually (cf. Napier, 1956).

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