Consciousness and Cognition 36 (2015) 96–102

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog

Posture modulates implicit hand maps

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ARTICLE INFO

Article history:
Received 20 February 2015
Revised 12 June 2015
Accepted 15 June 2015

Keywords:
Position sense
Body representation
Posture
Plasticity

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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http://dx.doi.org/10.1016/j.concog.2015.06.009

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