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Vestibular contributions to bodily awareness

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ABSTRACT

The vestibular system has widespread interactions with multisensory cortical networks, including the somatosensory areas. Several clinical observations suggested that vestibular signals are essential to compute more abstract cognitive representations of the body. However, the existing literature is generally based on isolated reports. We aimed to provide both a theoretical framework, and an experimental method to investigate potential vestibular contributions to somatic cognition. Accordingly, we have investigated effects of galvanic vestibular stimulation (GVS) on the localisation of a stimulus on the skin of the hand (a process that we define as somatoperception) and on the implicit representation of the hand size and shape (involving a different process which we define as somatorepresentation).

Vestibular input influenced the localisation of tactile stimuli on the hand: touches on the dorsum of the hand were perceived as shifted toward the wrist. The specific polarity of vestibular stimulation influences the localisation errors. Right anodal and left cathodal, which influences both cerebral hemispheres, induced a stronger localisation bias compared to left anodal and right cathodal GVS, which influences primarily the right hemisphere. Although our data confirmed previous findings that the body model of the shape of the hand is massively distorted, vestibular inputs do not contribute to these distortions.

Our results suggest that vestibular input influences the registration of somatosensory input onto a map of the body (somatoperception), but does not influence stored knowledge about the spatial organisation of the body as a physical object (somatorepresentation).

1. Introduction

Information from the vestibular peripheral organs in the inner ear is integrated with several other classes of signals about the body, generated by eyes, muscles and joints. The resulting signals provide a coherent sense of body posture and orientation in surrounding space (Berthoz, 1996). Multiple lines of evidence indicated the importance of a functional link between vestibular and somatosensory systems. On the one hand, neuroimaging studies revealed an anatomical overlap of vestibular and somatosensory projections (Bottini et al., 1995; Fasold et al., 2000; review in Lopez, Blanke, & Mast, 2012). On the other hand, clinical reports described temporary modulation of somatosensation in brain damaged patients induced by artificial vestibular stimulation (Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990; Kerkhoff et al., 2011). Similarly, psychophysical studies showed that vestibular inputs directly influence primary somatosensory processing: vestibular stimulation facilitates detection of faint somatosensory stimuli in healthy volunteers (Ferrè, Bottini, & Haggard, 2011) and enhances specific somatosensory evoked potential components originating in the right opercular region (Ferrè, Bottini, & Haggard, 2012). These results were interpreted as a vestibular-induced modulation in the level of primary processing of somatic stimuli, consistent with multisensory regulation of the gain in somatosensory cortical processing pathways.

However, the vestibular contribution to other, more cognitive, aspects of body perception is not yet clear. Several clinical observations suggested that vestibular signals are essential to compute more abstract cognitive representations of the body. For instance, caloric vestibular stimulation (CVS) can have dramatic effects on neurological disorders that involve altered bodily awareness, including disownership of body parts (somatoparaphrenia, Bisiach, Rusconi, & Vallar, 1991), somatoagnosia (Rode et al., 2012) and anosognosia (Cappa, Sterzi, Vallar, & Bisiach, 1987). Additionally, CVS modifies or reduces phantom limbs sensations in both paraplegic (Le Chapelain, Beis, Paysant, & André, 2001) and amputees patients (André, Martinet, Paysant, Beis, & Le Chapelain, 2001).

Here we have focussed on a cardinal aspect of somatosensory representation, namely the localisation of somatosensory stimuli,

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Abbreviations: GVS, galvanic vestibular stimulation; CVS, caloric vestibular stimulation; PIVC, parieto-insular vestibular cortex; TPJ, tempo parietal junction; SI, primary somatosensory cortex

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and their relation to the sense of one's own body. Sensory information from the body surface projects to the well-known sensory homunculus of the primary somatosensory cortex. The neurons in this area form an ordered, though characteristically distorted, map of the contralateral body surface. This map is often thought to underlie the perception of where on the skin a sensory stimulus is located. To give just one well-known example, appropriately-timed presentation of two nearby stimuli on the skin can produce the percept of a third stimulus located at the midpoint of the two. This illusion was accompanied by a somatosensory cortical response in a cortical region midway between the projections of the two actual stimuli (Friedman, Chen, & Roe, 2008). Interestingly, the same somatosensory cortical maps may underlie the sense of one's own body, as well as the sensation of a bodily stimulus. Thus, anaesthesia or amputation of the digits affects both the organisation of primary somatosensory cortex (Gandevia & Phegan, 1999) and also produces a feeling of enlargement or distortion of the relevant body parts.

However, both tactile localisation, and the sense of one's own body require a range of other cognitive processes in addition to primary somatosensation. In a recent review, Longo, Azañón, and Haggard (2010) distinguished between two such processes. These were (i) somatoperception: 'the processes of constructing percepts and experiences of somatic objects and events, and of one's own body' and (ii) somatorepresentation: knowledge about 'the body's character as a physical object in the external world' (Longo et al., 2010). Somatoperception involves an on-line percept of the state of the body, based on the integration of multisensory inputs, while somatorepresentation involves both explicit and implicit knowledge related to body, which may be less directly related to immediate input.

Therefore, we can propose a hierarchy of somatosensory cognition (Fig. 1), extending from primary somatosensation, to somatoperception and finally somatorepresentation. This hierarchy does not correspond directly to the somatosensory afferent pathway. In particular, somatosensation is a necessary condition for somatoperception, because perceiving the current state of the body will always involve integrating a range of somatosensory afferent signals. In contrast, somatorepresentation can persist in the absence of any particular somatosensory input: one knows what one's body is like even in the absence of any tactile afferents (Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013). We suggest that each level of the hierarchy can be tapped by different somatosensory tasks: tactile detection measures the first, somatosensory level, tactile localisation the somatoperceptual level, and judgements about body part size, or shape the somatorepresentational level (Fig. 1). Previous work already showed strong vestibular modulation of somatosensory detection (Ferrè et al., 2011). Here we investigate whether vestibular input can also influence the somatoperceptual and somatorepresentational levels.

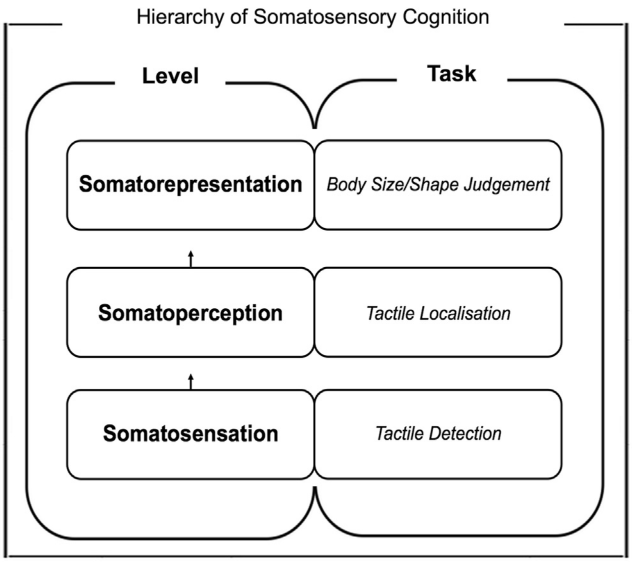

Fig. 1. The hierarchy of somatosensory cognition. The hierarchy of somatosensory cognition extends from primary *somatosensation*, to *somatoperception* and finally *somatorepresentation*. Somatosensation represents the first stage of somatosensory processing, resulting from activation of tactile receptors in the skin. *Somatoperception* involves an on-line percept of the state of the body, based on the integration of multiple somatosensory inputs. Finally, somatorepresentation involves both explicit and implicit knowledge related to body, which may be less directly related to immediate input. Each level of the hierarchy can be tapped by different somatosensory tasks: tactile detection measures the somatosensory level, tactile localisation measures the somatoperceptual level, and judgements about body shape, size and configuration measure the somatorepresentational level.

Experiment 1 investigated the vestibular influence in recognising the location of a stimulus on the skin surface (topognosis). Clinical reports described brain-damaged patients unable to indicate where they have been touched, though their ability to detect that they had been touched was unimpaired (Head & Holmes, 1911). On the basis of these observations, it has been proposed that the ability to localise stimuli on the skin is subserved by a cognitive representation of the body surface, namely the superficial schema. Localising the activation produced by a stimulus within a somatotopic map is, in fact, not by itself sufficient to identify its position on the body surface. Rather, a two-stage process is required (Longo et al., 2010). First, the stimulus-evoked activity is localised within the somatotopic map. Second, the somatotopic location must be mapped onto a corresponding bodily location. This second step requires a body model, relating the receptor surface of the skin to locations on the body, and thus involves at least an implicit somatoperception according to the definition of Longo et al. (2010). Consistent with this two-step model for somatoperception, localising a tactile stimulus involves both the somatotopic maps in the primary somatosensory cortex (SI) (Seyal, Siddiqui, & Hundal, 1997), and also additional somatosensory processes in parietal areas posterior to SI (Porro et al., 2007; Van Boven, Ingeholm, Beauchamp, Bikle, & Ungerleider, 2005). Interestingly, recent studies in patients (Rapp, Hendel, & Medina, 2002) and in healthy volunteers (Mancini, Longo, Iannetti, & Haggard, 2011) highlighted systematic biases in localizing tactile stimuli on the hand. In healthy volunteers, these biases involved a distal and radial shift of the estimated spatial locations for stimuli delivered on the dorsum of the hand and on the proximal segments of the fingers, but not on the middle segments of the fingers. Patients with left parietal lesions, in contrast, showed a proximal shift, mainly on the fingers (Rapp et al., 2002).

Second, we assessed whether vestibular inputs interact with a model of body size and shape (Experiment 2). No peripheral receptors are directly informative about the size and shape of body parts. Thus, the knowledge about these features are linked to an internal stored model of the body's metric properties (Longo & Haggard, 2010). It has recently demonstrated that this 'body model' is strongly distorted (Longo & Haggard, 2010). At least for the hand, these distortions included a radial–ulnar gradient of magnification of the digits and shrinkage toward the proximo-distal axis. These internal models appear to be independent of any specific somatosensory input for two reasons. First, people can judge the configuration and location of the body, including its metric properties, in the absence of specific somatosensory stimulation (Longo & Haggard, 2010). Second, these metric properties are accessible even for congenital phantoms (Longo, Long, & Haggard, 2012). For this reason, the internal body model involves a level of somatorepresentation, independent of any particular somatosensory event or stimulus.