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Review

Touch and the body

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ABSTRACT

The dual nature of touch has long been understood. The sense of touch seems to carry information at the same time about the external object touching our skin, and also about our body itself. However, how these two interact has remained obscure. We present an analytic model of how tactile information interacts with mental body representations in the brain. Four such interactions are described: the link between the body surface and the maps in primary somatosensory cortex, the contribution of somatosensory cortical information to mental body representations, the feedback pathway from such higher representations back to primary tactile processing in somatosensory cortex, and the modulation of tactile object perception by mental body representations.

Contents

1. Introduction and model

Touch is often considered by neuroscientists under the general heading of somatosensation. This already reveals a strong link between tactile sensation and perception on the one hand, and the body on the other. Indeed, the receptor organ for touch, the skin, also forms the surface of the physical body. Although the interdependence between the sense of touch and the body is well recognised, this interaction can take place at a range of different levels within the nervous system, with quite different consequences and mechanisms. Moreover, the brain contains several mental representations of the physical body. These include descriptions of the parts of the body, their arrangement into a structural whole, and the positions of these parts in space at a given moment. In this review, we first present an analytical model of the relation between touch and the body, and then use this to

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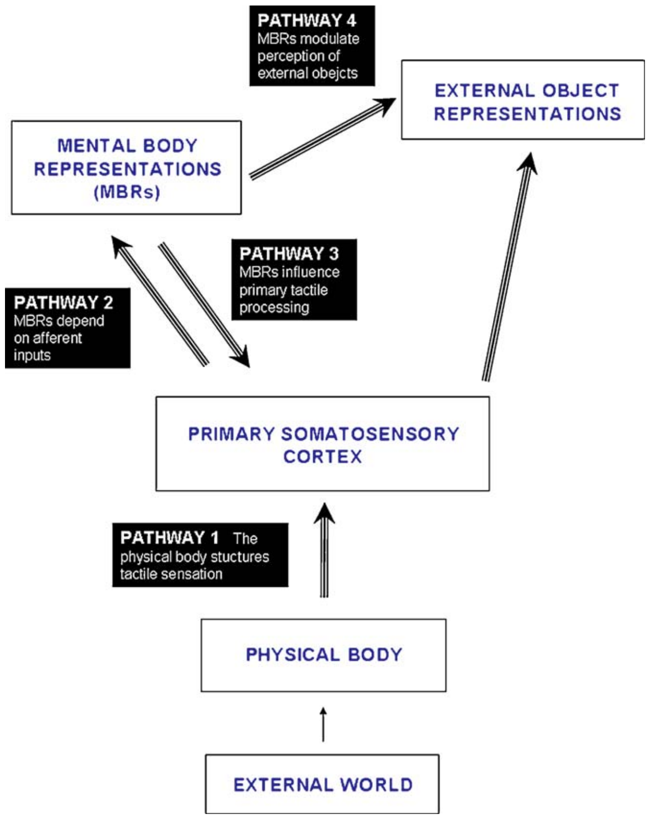

Fig. 1. An analytical model of the relation between touch and the body. Four different ways (double arrows with black boxes) by which tactile afferent information can either be influenced by, or have influence upon, higher mental representations of the body. See text for explanation.

distinguish four different ways in which tactile afferent information can either be influenced by, or have influence upon, mental representations of the body.

The model is shown in Fig. 1. External stimuli ("objects") impinge upon the physical body, through contact with the skin. Tactile afferents convey information about mechanical contact via the dorsal column-medial lemniscus pathway, and the thalamus, to the primary somatosensory cortex (SI) of the contralateral hemisphere. The afferent projections to SI preserves the spatial organization of receptors in the skin, so that SI contains an essentially *spatial* representation of the physical body surface. That is, the physical body structures tactile sensation, because the receptor surface covers the physical body (Pathway 1 in Fig. 1).

Neurophysiological and psychophysical evidence shows that other brain areas house additional mental body representations (MBRs), over and above the somatosensory maps in SI. We will show that MBRs depend on afferent inputs, relayed through primary representations (Pathway 2 in Fig. 1). However, MBRs are typically multimodal rather than unimodal, and persist even in the absence of current stimulation: they are representations of the body, not just perceptions of particular somatic stimuli. This abstraction from primary sensation allows MBRs to contribute to *cognitive* functions including memory, mental imagery, etc. Here, we make the further strong claim that these MBRs reciprocally influence primary tactile processing in SI (Pathway 3 in Fig. 1). A second strong claim from this review will be that MBRs contribute not only to perception of one's own body, but also to perception of other objects in the external world. Specifically, tactile and visual perception of external objects may be *body-referenced* (Pathway 4 in Fig. 1).

The structure of our review is based on these four critical pathways linking the physical body, the sense of touch and the mental representation of one's own body. Therefore, we review, in turn, key psychophysical and neurophysiological evidence that (1) the physical body structures tactile sensation, (2) that tactile sensations contribute to a mental body representation (MBR), (3) that MBRs reciprocally influence primary tactile processing, and (4) that MBRs mediate the formation of a object representations from primary tactile sensations.

2. Pathway 1—the physical body structures tactile sensation

The sense of touch is the phenomenal counterpart of afferent input from mechanoceptors on the body surface. Peripheral signals from the skin are transmitted through the dorsal columns of the spinal cord to the medulla, and project via the postero-lateral thalamus, to contralateral primary (SI; area 3b and 1 in the monkey) and secondary (SII) somatosensory cortices. These are located, respectively in the postcentral gyrus and parietal operculum. Somatosensory cortical areas, and SI in particular, generally receives a wide range of somatosensory inputs from different peripheral receptors, such as mechanoreceptors, thermoreceptors, and nociceptors. They therefore process several different kinds of somatic information, and leading to a range of sensations including pressure, vibration, thermal sensation, pain, and itch. Here we concentrate on the cortical mechanisms of light touch only. For details on other somatosensory modalities and a wider view on somatosensation see Craig (2003).

SI neurons encode physical properties of tactile stimuli within a spatial map. Tactile sensations are localized on a given part of the body due to the organization of primary somatosensory cortex. SI of each hemisphere contains a complete topographically organized representation of the contralateral side of the body. This "somatosensory homunculus" is inverted relative to the physical body, with the legs represented medially and the face and hands more laterally (Penfield and Boldrey, 1937; see Fig. 1). The relationship between location on the body and in SI homunculus has been clearly demonstrated by classic neurophysiological experiments. Tactile stimuli administered on a given body part elicit a neural response in a specific portion of SI the homunuculus, matching the same body part. Conversely, the electrical stimulation of the same region of SI induces a tactile perception localized on the corresponding part of the body (see also Kaas et al., 1979 and Tommerdahl et al., 1993 for data on animals and Yang et al., 1993; Shoham and Grinvald, 2001; Sato et al., 2005 for data on humans).

Neurophysiological studies on the structure of postcentral gyrus showed that SI is organized in cortical columns, up to 500 μm wide, that receives projections from a restricted population of mechanoceptors (Kaas et al., 1979; Mountcastle, 1997). Thus each column has a well-defined receptive field. Adjacent neurons on SI surface tend to have adjacent receptive fields on the body (Blankenburg et al., 2003; Penfield and Rasmussen, 1950).

Within this somatotopic map, there is a three-way relation between receptive field size, extent of representation in SI, and tactile acuity. The size of individual receptive fields on the skin varies among body parts and therefore among regions of SI also. At the same time the size of SI representations varies among body parts. For instance, skin regions such as lips and fingers have large SI representations, while the back and torso have small representations. Skin regions differ in the degree of tactile information they supply: tactile spatial acuity on the finger is for instance about twenty times greater than on the back. Tactile spatial acuity is an inverse function of the receptive field size of SI neurons (Brown et al., 2004): skin regions with high tactile acuity are densely innervated by mechanoreceptors supplying the skin, are represented by individual cortical neurons with small receptive fields, and have relatively large representations in SI. Other skin regions