

Magazine
R170**Primer**

Tactile perception, cortical representation and the bodily self

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The sensory information we receive from our own bodies is unique, both from epistemological and neurological points of view. Philosophers have noted the immediate, private quality of bodily sensation. I can understand your visual percepts by looking in the same direction as you, but understanding your tactile sensation would require being in your skin! Descartes took an additional step, arguing that because bodily sensation is immediate, it is also reliable: *“nor was it without some reason that I believed that that body which, by a special right, I call mine, belonged to me more properly and closely than any other; for, in truth, I could never be separated from it as from other bodies”* (6th Meditation).

The reliability of bodily sensation implies accurate transmission of peripheral information to the higher brain centres of conscious perception. We shall argue here that Descartes was wrong, at least as regards the sense of touch. Higher cortical regions which underlie tactile perception also provide several top-down influences which modulate perception: so the brain constructs our sense of the body, rather than passively receiving it.

Bodily sensation is also unique in its neurophysiological basis. The body has many different classes of sensory receptor, each transducing a specific type of stimulus. We shall focus on information from the mechanoreceptors in the skin. Tactile perception may have a special role in body representation, because the skin forms the interface between the body and the outside world. Other sensory

systems, notably pain and body position sense, also contribute to body representation. Nociception lacks the spatial specificity of touch, and proprioceptive contributions to body representation are difficult to dissociate from the tactile and motor events normally correlated with them. So the brain's processing of touch is perhaps the clearest way to study the construction of our sense of our own body.

We shall give three examples of this construction process. First, we shall describe visual enhancement of the sense of touch. Second, we shall consider how changes in body posture modulate tactile inputs. And third, we shall discuss the problem of attribution: that is, of how a perceptual input may be assigned either to the self or to the body of another person.

The structure and function of the peripheral and subcortical somatosensory system is well known. Tactile information is conveyed to the primary somatosensory cortex (SI) of the contralateral hemisphere. Here, tactile perception and body representation begin to converge. SI contains a somatotopic map of the contralateral side of the body (Figure 1A). Early studies emphasised its role as a veridical, organised projection, faithfully transmitting peripheral inputs. For example, intracranial stimulation of sites in the SI map produces sensation on the corresponding body part. More recent studies suggest that SI processes may be modulated by context, in particular the general perceptual experience of the body provided by other senses such as vision.

Visual-tactile interactions

The spatial organisation of touch was studied by Weber in 1834, using two-point discrimination thresholds (2PDTs). Subjects report whether they are touched by one or two tactile stimulators. The spatial separation of the two stimulators is varied to find the threshold distance at which they can no longer be resolved and are perceived as a single tap. The 2PDT is a perceptual measure of

tactile acuity and varies systematically across the body surface, being lowest where tactile receptor density is high (Figure 1B). The SI map of the body surface may play a key role in such tasks: tactile discrimination of different body parts correlates well with the size of their representation in SI. And disruption of SI by transcranial magnetic stimulation (TMS) increases tactile thresholds, while tactile discrimination training enlarges the corresponding representation in SI.

To investigate whether tactile acuity depends on a raw, sensor-driven afferent process, or is modulated by general bodily representation context, we compared 2PDT in conditions where subjects could see their arm, a magnified view of their arm, a neutral object appearing at the location of their arm, or nothing at all (darkness). Gaze and spatial attention were always directed towards the stimulated portion of the arm. Critically, looking at the arm provided only a general visual body representation, but did not provide any task-relevant information about the tactile stimulation itself. Tactile acuity improved when viewing the arm relative to both darkness and viewing a neutral object. Increasing visual detail with a magnifying lens improved tactile acuity further (Figure 2).

A subsequent experiment used event-related cortical potentials to measure cortical activity evoked by double taps in the view-arm and view-object conditions. There was no difference between these conditions 50 ms after the tactile stimulus — the time of the first wave of afferent input to the cortex from the skin. A later component of the brain's response, 80 ms post-stimulus, was significantly enhanced when vision of the arm was available, but only when subjects had to make an explicit judgement about the tactile inputs (that is, when touch was task-relevant). This component has been identified with a second wave of cortical processing within SI, possibly involving a local network of interneurons. These results suggest that any bodily

representation context provided by vision occurs within the primary cortex itself, rather than by gating cortical inputs. Visual effects on light touch do not block or unblock afferent signals, but change the efficiency with which they are processed, perhaps by a cortical tuning process involving lateral inhibition.

The flexibility of the local neuronal network in SI ensures the brain's map of the body is not fixed; each cortical neuron may have the connections required to represent touch over a wide region of the body. Merzenich and colleagues found that amputation of a single digit from a monkey led to rapid changes in the SI map: within minutes those neurons that represented the amputated digit respond to touch on adjacent parts of the hand. These wider connections must have been latent, but inhibited by a dominant input from the amputated digit. These results suggest a metaphor of different parts of the body surface competing with each other to 'own' cortical representation. By biasing this competition, the brain's representation of the body can be rapidly and functionally changed.

Earlier studies of cross-modal links between vision and touch focussed either on a common system for spatial attention, or on optimal fusion of information about the same dimension provided by different senses. Neither model explains this visual enhancement of touch adequately, as spatial attention was controlled for and visual information about the tactile stimulus was not present. Instead, we suggest vision of a body part exerts a top-down influence on primary tactile sensation.

Analogous context effects of non-informative vision on proprioception and motor control have also been reported. The neural mechanism underlying this influence could involve multimodal representations in the parietal cortex biasing local networks within SI. These results suggest that our tactile perceptions are not raw and immediate, but are constructed

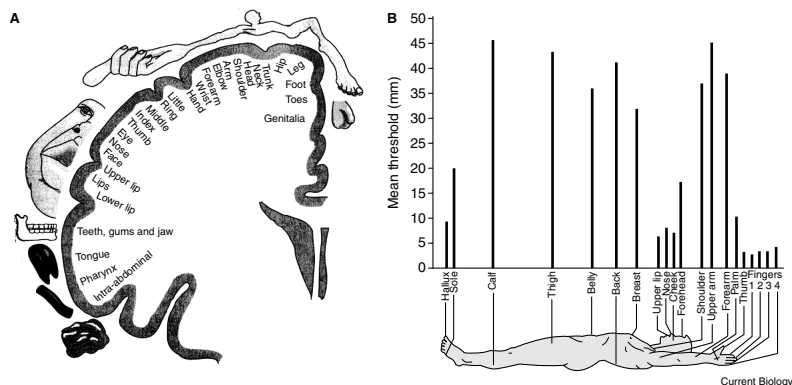


Figure 1.

(A) The sensory homunculus in each hemisphere contains a distorted representation of the contralateral side of the body. Note enlarged representation of the fingers and face. (B) Tactile spatial resolution varies dramatically between different body parts. Spatial resolution correlates well with the size of the corresponding representation in somatosensory cortex. Here, spatial resolution is measured as the two point discrimination threshold: the smallest distance between two simultaneous point contacts which are felt as two touches rather than one. (Adapted from: (A) Penfield, W. and Rasmussen, T. (1950). The cerebral cortex of man. A clinical study of localization of function. (Macmillan, New York); and (B) Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex and laterality. In *The Skin Senses*, D.R. Kenshalo, ed. (Thomas, Springfield, Illinois), pp. 195–218.)

with reference to a general abstract body representation. This hypothesised body representation recalls the traditional concept of *body schema*. This classical concept, introduced in 1911 by Head and Holmes, implies an unconscious and passively updated representation of the position of the body in space, often identified with the parietal lobes. The body schema has typically been used in neuropsychology in a descriptive, rather than an explanatory way. Earlier studies in normal subjects, however, confirm that both visual and proprioceptive inputs contribute to the body schema.

This interaction between vision and touch may be unsurprising, given the unique way we perceive our body. We see our body as a spatially-extended object like any other; and we *feel* our body 'from the inside'. The sense of touch, unusually, embodies both the exteroceptive and interoceptive functions within a single sensory system. As such, interaction between vision and touch would seem essential to produce a single coherent sense of our own bodily self, as opposed to a series of fractionated and independent sensory maps.

The body in space

Tactile stimuli occur within an anatomical space defined by the body surface. A largely somatotopic organisation is found in SI, and with somewhat less precision in secondary cortical areas. But the body itself has a very complex shape and is in constant motion. So the relation between location on the body surface and external spatial location is both complex and dynamic. Several results suggest that tactile information is referred to external spatial locations. Even dimensions of touch which appear to be well coded in SI are influenced by body configuration. Yamamoto and Kitazawa investigated temporal order judgement between two vibrating tactile stimuli mounted on sticks held in the left and right hands. When subjects crossed their arms, the normal psychophysical curve was sometimes disrupted. For example, subjects might have accurately judged the temporal order when a buzz occurs on the stick held in the right hand shortly after one on the left hand, with the hands in their normal positions, but judged the order much less accurately when the hands or the sticks were crossed. At some high level of neural coding, therefore, subjects

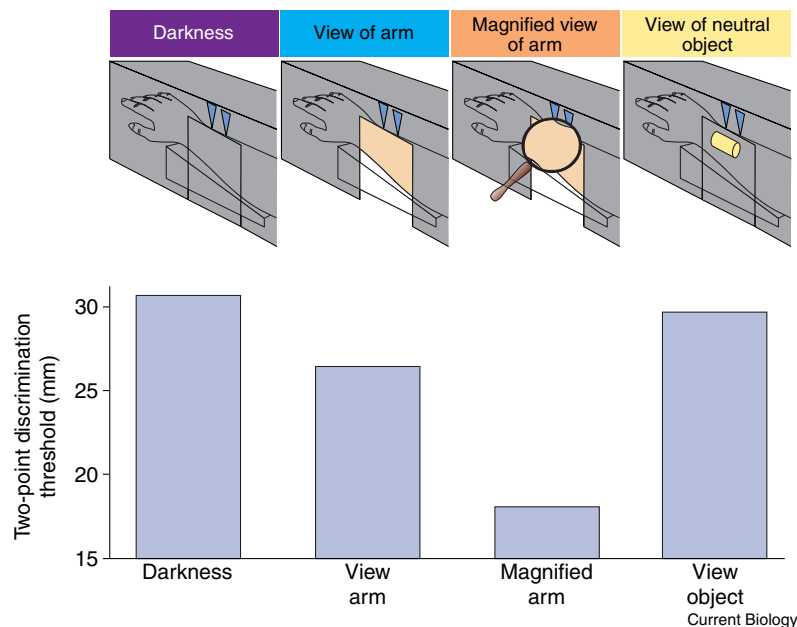


Figure 2. Non-informative vision enhances tactile spatial resolution. Two-point discrimination thresholds (2PDT) measured on the forearm under different visual conditions. Viewing the arm gives better tactile resolution than either performance in darkness or viewing a neutral object projected via mirrors to appear in the same location as the arm. Magnifying the view of the arm further improves tactile resolution. The moment of tactile stimulation is never seen, preventing trivial vision of the stimulators. (Adapted from Kennett *et al.*, (2001).)

must represent the stimuli, not by location on the body surface, but by their external spatial location. More compellingly, when both the hands and the sticks were crossed so the buzzers occupied their standard uncrossed location, former levels of accuracy were reattained. Clearly, the vibratory percept represented in SI must be modulated by neural representations of external space. Previous studies using crossed hands had shown the importance of external spatial location in selective attention to signals, but it is surprising that the primary elements of tactile perception, so firmly anchored in the body space organisation of skin receptors, show the same influences. One possible criticism of crossed hands experiments may be that they capitalise on a particularly drastic and unusual spatial manipulation.

We have also studied the effects of crossing the fingers on tactile perception. Subjects judged whether a metal bar applied to the pad of the right index or middle fingers at random did or did not contain a small gap. The tests were

performed in a normal finger posture, and in a crossed posture in counterbalanced order. Subjects were touched on a single finger on each trial, and posture was irrelevant to the task. Tactile thresholds were worse in the crossed posture than in normal posture. Even basic tactile acuity is also modulated by external spatial location. Poor tactile acuity with fingers crossed may reflect a mismatch between the stimulus location in body space and its unusual location in external space. Postural modulations of tactile perception are not restricted to the special posture and large spatial displacements of crossed hands, nor to tasks involving discrimination between the crossed body parts. These spatial effects on primary dimensions of tactile processing again suggest strong modulation of tactile perception by higher aspects of body representation.

Several studies suggest that primary sensory input from the body also strongly influences more abstract processing of body representations. For example,

when subjects are asked to discriminate between another person's imagined hands, their reaction time is influenced by the posture of their own unseen hands. General spatial body representations are strongly influenced by afferent proprioceptive signals from the subject's own body. The abstract body schema may have evolved from somatosensory association cortex to generalise to the bodies of others.

Attribution

Finally, an important interaction between tactile perception and body representation occurs at the highest psychological level of processing: the conscious sense of self. Baumeister recently wrote "All over the world, self begins with body". The development of the sense of self is based on sensory signals which discriminate internal from external events. These signals may either be efferent ('I am whatever my motor commands can cause to move) or afferent ('I am the receiver of peripheral information). Separating the contributions of these two signals has proved difficult experimentally, and obscures the interesting issue of how they are combined: we experience a single coherent self, rather than separate efferent and afferent selves. Tactile information plays a unique role in this process, because it can describe both external objects and the body itself. Tactile perception plays a major role in defining the boundary between the self and the external world.

This process has been investigated in attribution experiments. A typical experimental method uses combined tactile and visual information to 'persuade' subjects that an external object is in fact part of their own body. Subjects might view a fake hand being stroked while they experience a similar stroking movement applied to their own unseen hand. The correlated visual and tactile input causes subjects to attribute the fake hand to themselves. These illusions can be extremely powerful. For example, a blow to the fake body part after attribution

will elicit a physiological response in the observer. In this case, a purely visual input from an external object elicits a response appropriate to a tactile input to one's own body. This finding seems opposed to the traditional philosophical view of tactile sensations as private.

Associations between visual and tactile inputs can clearly be very strong and contribute to our sense of bodily self. Interestingly, attribution has some important properties in common with both visual enhancement and postural modulation of touch, suggesting a common neural mechanism. Attribution may depend on the rubber hand having an appropriate postural configuration. Pavani and colleagues found that a light on a rubber hand maximally interfered with a simultaneous tactile input when the rubber hands were seen to have the same postural configuration as the subject's own hands.

The dual nature of the body as both an external and internal object was mentioned above. Neural integration of vision and touch may be essential for developing and maintaining this sense of bodily self. Some neural mechanism must therefore bind internal and external representations. Single neurons in monkey parietal cortex responded when the monkey viewed a stuffed arm being stroked, while experiencing synchronous stroking on its own arm. When the timing of the viewed and felt stroking was made asynchronous, these neurons were less active. This suggests a special role of parietal cortex in integrating visual and tactile inputs to create a coherent representation of the bodily self.

Involvement of parietal cortex in body representation has been confirmed by neuropsychological studies of patients with focal lesions. A crucial distinction can be made here between right and left hemisphere lesions. Patients with right hemisphere lesions may disown a plegic left limb or attribute it to another person. We speculate that the affected limb is *dis*attributed from the bodily self, because the normal correlation between visual and tactile input is

lacking as a result of the sensory loss. Impaired spatial attentional mechanisms in the right parietal cortex may also fail to resolve the lack of visual-tactile correlation. In contrast, left parietal lesions may produce a specific difficulty in localising body parts. When asked to point to the elbow, for example, patients will typically point to another body part, such as the shoulder or forearm. The parietal lobe of the left hemisphere may contain an abstract body representation used for purposes of localisation. The left hemisphere maintains an abstract representation of the spatial organisation of body parts, while the right hemisphere may correlate multisensory stimuli to maintain a sense of bodily self.

The condition of heterotopagnosia, after left parietal damage, seems to involve a higher processing stage, in which body parts are assigned to persons. When asked to point to their own elbow, these patients repeatedly point to the examiner's elbow. The localisation within the body map is correct, but the body representation is transposed to another person. This puzzling condition could arise if a left parietal abstract body representation fails to integrate attribution information from visual-tactile correlation processes. In normal function, a generalised body representation is activated for processes involving the spatial organisation of body parts in one's own body, and also when viewing the bodies of others. The ownership of the body concerned — the answer to the question: is that part of 'me'? — would be computed by a process of correlating visual and proprioceptive inputs. The left parietal cortex would use this information to assign the body part to a particular person. This process of binding spatial body part information to attribution information may be impaired in heterotopagnosia.

Conclusion

The human sense of touch relies on a specialised neural system for transmission of afferent input. Afferent inputs to primary

somatosensory cortex result in tactile perceptions, characterised by their phenomenological vividness. Epistemologists have found these perceptions intriguing because they appear to be private: another person cannot know what I am feeling, because only 'I' am connected to my tactile receptors. However, epistemologists have confused the correct close connection of touch with the bodily self, with the incorrect idea of tactile perception as a raw sense datum. Neuroscience can clarify how tactile perception contributes to a conscious sense of the bodily self, by describing the neural mechanisms underlying the mutual and interactive relation between primary tactile perception and higher cortical representations of the body. Even highly abstract cognitive representations, such as 'self', may be understood in terms of their sensorimotor bases.

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