

Tactile Perception: Beyond the Somatotopy of the Somatosensory Cortex

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New research demonstrates systematic errors of tactile localisation, involving confusions of body parts and body sides. Such errors do not follow the organisation of topographic maps in somatosensory cortex, suggesting that tactile localisation involves coding of abstract features of limbs.

The skin can convey many sensations, which are translated into our ability to perceive, for instance, the smooth texture of a marble statue or the pinprick of a mosquito bite. Common to all these sensations is the phenomenological experience that they occur somewhere on the body. Indeed, unlike other bodily sensations such as hunger or fatigue, it is difficult to conceive of a tactile sensation which can be felt but not localized, whether in its current true spatial location or in an erroneous one [1]. Even in the extreme case of patients who are unable to locate tactile sensations correctly, touches are not perceived floating in the air but as happening somewhere within the confines of their body [2,3].

Touches on the body are initially represented in the cortex in an orderly topographic manner, so that adjacent parts of the skin are represented by adjacent bits of the brain [4]. This has been famously illustrated in textbook depictions of Penfield's sensory homunculus in the primary somatosensory cortex, S1 (Figure 1). Given this cortical topography, one might assume that the problem of localising a touch on the skin reduces to localising a corresponding peak of activation in these somatotopic maps. Indeed, several studies have shown that the brain can represent tactile location via population coding within somatotopic maps [5], and some reports of mislocalizations in amputees suggest a dependency on homuncular organization, as when touches on the ipsilateral face, which is adjacent to the hand in the homunculus, evoke tactile sensations on the phantom hand and fingers [6]. A new study by

Badde *et al.* [7], reported in this issue of *Current Biology*, challenges this 'homuncular' view and delivers important new insight into how our nervous system relies on abstract features or categorical information to locate touch.

Existing neurocognitive models of somatosensory processing have suggested that localizing a touch within a somatotopic map is not by itself sufficient to localize the stimulus on the body surface, but that this requires higher-order body representations (for example [8]). In the early 20th century, before the discovery of the topographical architecture of the somatosensory cortex [4], Head and Holmes [3] had already proposed a mental representation of the body surface to account for the deficits of patients who could detect touch but were unable to localize where on the body the touch was. This representation has come to be called the superficial schema.

We do not have to go so far from our daily routines to envision the need for such representation. Now spare a thought for the kid who is learning to play the guitar. With training, the cortical representation of the fingertips of her left hand, which she uses for fingering the strings on the fretboard, will enlarge compared with that of other kids of her age [9]. But how, after such cortical changes, is she still able to localize touch without producing massive mislocalizations? This is where a body representation such as the superficial schema comes into play in some neurocognitive models, as a link between cortical maps and body locations that is updated to reflect plastic changes to those maps, and that accounts for their

inherent distortions and magnifications [8]. Nevertheless, such models have difficulty accounting for puzzling mislocalizations observed in some amputees, where tactile stimuli on a foot are occasionally attributed to the absent hand [6], because the hand and foot representations are far apart in the somatosensory homunculus (Figure 1).

More than a century after Head and Holmes' [3] first insights into tactile localization, Badde *et al.* [7] have provided remarkable evidence for mislocalizations in healthy individuals that are, as in the example with the amputees, not determined either by the sensory homunculus or the superficial schema. They have found that, when touched on a limb, healthy adults occasionally — but systematically — misattribute the touch to a limb that was not touched at all. Many of these 'phantom errors' were attributed to the homologous contralateral limb, for example the right hand for a touch on the left hand. This pattern could potentially be explained by reliance on the somatosensory homunculus, given growing evidence of the existence of bilateral receptive fields [10] and inter-hemispheric interactions [11] as early as in S1 (reviewed in [12]). However, a smaller set of phantom errors were systematically attributed to opposite limb types, for example a foot for a hand and *vice-versa*, which excludes overlapping representations in S1 as a source of these phantom errors, because the hand and foot representations are far apart in S1.

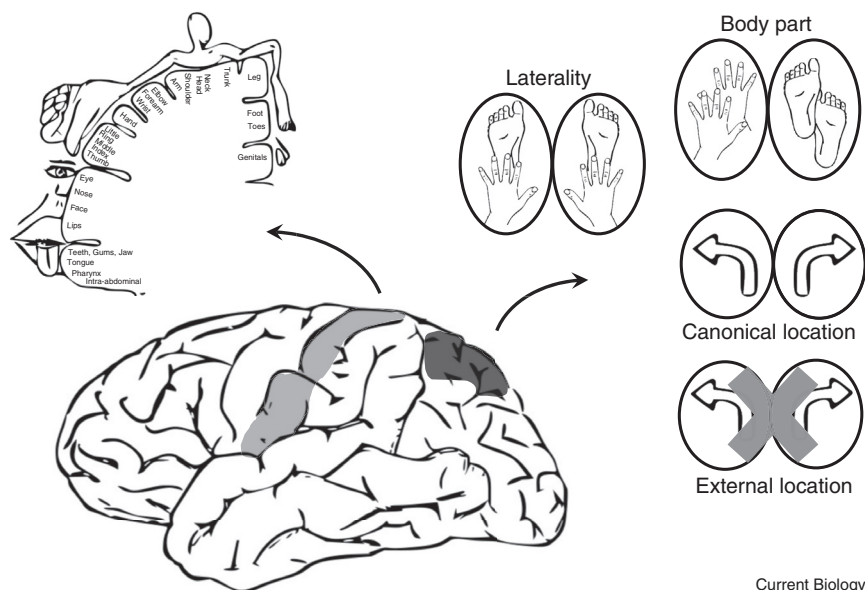
One possibility could be that these mislocalizations might arise from overlapping representations in secondary somatosensory cortex, S2, where the

foot and hand representations are adjacent, at least in monkeys [13]. But an explanation based on adjacent representations in S2 could only partially account for the pattern of mislocalizations observed in Badde *et al.*'s study [7]: while it could explain why phantom errors are more frequent across feet and hands sharing the same body side, it cannot account for the fact that mislocalizations are more often than chance referred to the limb placed at the stimulated limb's canonical side of space (which for the right hand would be the right side of space, for example).

The mislocalizations reported by Badde *et al.* [7] are therefore consistent with their resulting from representations in which touch is coded in terms of a number of abstract features, rather than as a spatial map. This way of representing touch may be related to some other results in the literature. For example, interleaving the fingers of a hand can lead to confusions about which hand is touched, but not which finger, despite the fact that finger type and laterality could both rely on the same activity in S1 [14]. Similarly, the pattern of mislocalizations at the hairy and glabrous skin are virtually identical, despite being clearly different at the level of S1, which suggest the use of a representation abstracting away from the details of each individual skin surface [15].

The pattern of mislocalizations reported by Badde *et al.* [7] provides new and exciting insight into the type of information that is needed to encode location, and appears to implicate the use of representations based on body-related categorical information. This idea fits with recent studies showing that motor representations of the body in the posterior parietal cortex show substantial degrees of mixed selectivity, with common responses to movements made with different body parts, or by the left and right hands (for example [16]). The new results suggest that similar mixed coding may also be employed in touch (Figure 1).

A representation based on high-dimensional mixed-selectivity would produce very different patterns of confusions and errors than one based on topographic maps. The phantom errors reported by Badde *et al.* [7] emphasise three relevant features, in decreasing order of importance: body part's identity (a hand or a foot); body laterality (right or left);



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Figure 1. Continuous versus categorical representations in tactile localization.

The ability to locate where on the continuous body surface touch has occurred putatively depends on the topographic maps observed in the primary somatosensory cortex (marked in soft grey). This is illustrated in what is known as the sensory homunculus, as an orderly topography of body parts in the cortex (left panel). Alternatively, the ability to locate touch on the skin might be based on abstract features or categorical information related to the touched body part. This second view is supported by Badde *et al.*'s [7] pattern of mislocalisations across hands and feet, which are clearly not determined by proximity in the homunculus. These mislocalizations follow a systematic pattern consistent with the use of three main categorical features: first, body part's identity, by which a touch on the right hand might be misperceived to the left hand (the homologous limb); second, body laterality, by which a touch on the right hand might be misperceived to the right foot; and third, canonical side of the touched body, by which a touch on the crossed right hand might be misperceived to the foot placed at the right side, even though the touched right hand was located at the left side of external space. Intriguingly, the external location of the touched limb did not predict the pattern of mislocalizations across hands and feet. The four types of categorical feature are schematically represented on the right panel. We refer to posterior parietal brain regions (marked in dark grey) as the source for such putative representations, following evidence that these regions might represent categorical information, such as body parts and body sides in a partially mixed fashion [16].

and canonical spatial location. The illusory percepts resemble those obtained in vision, the so-called illusory conjunctions, in which people report single objects having a combination of features which were not actually presented [17]. Indeed, Badde *et al.*'s [7] results can be thought of as a form of illusory conjunction on touch based on the features of limbs.

Studies of illusory conjunctions in vision show that such conjunctions are modulated by stimulus similarity [17]. The results of Badde *et al.* [7] suggest that a similar process might take place in touch, and demonstrate at least three relevant categorical features along which similarity is defined. For instance, phantom errors typically matched the correct limb with respect to limb type and body side. Interestingly, a third feature is the body part's *canonical* location. Several accounts have highlighted, based on

indirect evidence, the role of the body part's canonical location in tactile localization at initial stages of sensory processing. For instance, by assuming that immediately following stimulation touch is referred to a stored representation of the default posture [8] (reviewed in [12]). Badde *et al.*'s [7] results provide direct evidence for the existence of such canonical representations.

Perhaps one of the most surprising findings of Badde *et al.* [7] is that the *external* location of the touched limb did not predict the pattern of mislocalizations across hand and foot. This contradicts the widespread idea that touch takes the posture of the touched limb into account even in situations where there is no overt reaction to touch [18]. On the contrary, Badde *et al.* [7] propose that when explicit continuous localization is not needed, for instance to report or move

the touched limb, tactile processing can abstract away from topographic representations (somatotopic or external), and use bodily related categories relevant to the task itself. This raises a potentially interesting analogy to studies in vision which have argued for two distinct systems for spatial representation, one based on precise spatial coordinates, the other based on categorical spatial relations [19].

A question that remains to be answered, however, is under which circumstances touch relies on categorical versus coordinate spatial relations. For example, the so-called ‘crossed-hands deficit’, in which the ability to tell which of the hands was touched first is impaired when the hands are crossed, has been widely-used as an experimental model of tactile localisation in external space [20]. The results of Badde *et al.* [7], however, raise the possibility that the deficit may not result from the precise coding of touch in continuous external space, but from an incorrect assignment of touch to a particular limb.

The results of Badde *et al.* [7] raise fundamental questions about our experience of touch. The immediacy of tactile experience has sometimes led touch to be thought of as privileged among senses and even infallible, as in Bishop Berkeley’s famous claim that “touch tutors vision”. By documenting novel ways in which touch goes wrong, this paper shows that we may need to think twice when we feel an insect land on our arm, or we may swat the wrong limb entirely. Good news if you’re a mosquito.

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Animal Cognition: The Benefits of Remembering

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How cognitive abilities evolve through natural selection is poorly understood. Two new studies show that a good spatial memory helps birds that hide their food to survive and produce more offspring.

Every morning, houses across the world are filled with the despairing refrain: “where have I left my keys?” We use our keys every day, yet we still manage to forget where we left them. Contrast this with a Clark’s nutcracker, which every winter hides over 30,000 seeds in locations across the forest and still

manages to find most of them again several months later [1]. For such food-caching birds, it would seem obvious that being able to learn and remember locations must be advantageous, but until now direct evidence has been lacking. In fact, food-cachers have long been at the heart of acrimonious debates on the

