

## Opinion

## Stability of Sensory Topographies in Adult Cortex

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**Textbooks teach us that the removal of sensory input to sensory cortex, for example, following arm amputation, results in massive reorganisation in the adult brain. In this opinion article, we critically examine evidence for functional reorganisation of sensory cortical representations, focusing on the sequelae of arm amputation on somatosensory topographies. Based on literature from human and non-human primates, we conclude that the cortical representation of the limb remains remarkably stable despite the loss of its main peripheral input. Furthermore, the purportedly massive reorganisation results primarily from the formation or potentiation of new pathways in subcortical structures and does not produce novel functional sensory representations. We discuss the implications of the stability of sensory representations on the development of upper-limb neuroprostheses.**

**Plasticity in Sensory Cortical Topographies**

One of the key concepts in contemporary neuroscience is that experience shapes the central nervous system throughout life. The ability of the brain to adaptively change how it processes inputs based on new experience is termed ‘plasticity’ and underlies our ability to mature, learn new skills, and recover from injury. Our current understanding of neuroplasticity has been moulded by the work of Hubel and Wiesel [1–3] in the 1960s, who studied the visual cortex of cats following temporary occlusion of visual input from one eye. They found that input loss to one eye in early development drives profound physiological and behavioural changes: neurons in the visual cortex normally devoted to the occluded eye respond to input from the non-occluded eye. Accordingly, when forced to rely on the previously occluded eye, the kittens showed profound visual impairments. This line of research demonstrated the brain’s extraordinary capacity for change: Loss of primary input to a brain area does not lead to the abolishment of processing but rather to a reassignment of processing, resulting in increased functional representation of an alternative input. This process, termed cortical reorganisation, is perhaps the most extreme form of brain plasticity. According to these early studies, however, reorganisation is much more restricted in the adult brain: adult cats subjected to visual occlusion did not exhibit the same deficits and cortical changes as did kittens [3] (see [4] and [5] for related evidence in monkeys and humans; see [6] for current debate on the adult’s visual cortex capacity for reorganisation).

Perhaps the most striking example of the adult brain’s capacity to reorganise comes from electrophysiological studies of primary somatosensory cortex (SI) after the loss of peripheral input (e.g., as a result of limb amputation). A well-known characteristic of SI in intact individuals is the well-defined topographic map of the body – so-called somatotopic organisation – with neighbouring neurons responding to adjacent and overlapping regions of the body [7] (Figure 1A). Removal of input from a body part (due to amputation [8] or nerve transection [9]) results in changes in the somatotopic organisation, such that the representation of cortically adjacent body parts seems to take over the ‘freed up’ brain territory (see [10] for a review of

## Trends

The reorganisation of primary somatosensory cortex (SI) following arm amputation is considered a prime example of neural plasticity in the adult brain and of its consequences on altered perception.

Recent evidence from human and non-human primates shows that the reorganisation in SI does not result in novel functional sensory representations and that somatotopic organisation persists despite drastic loss of sensory input.

Perceptual reports from human subjects suggest that the loss of sensory input does not result in a replacement of the original representation: activation of the missing hand area evokes sensations referred to the missing (phantom) hand and not to the ‘invading’ body regions (e.g., the face).

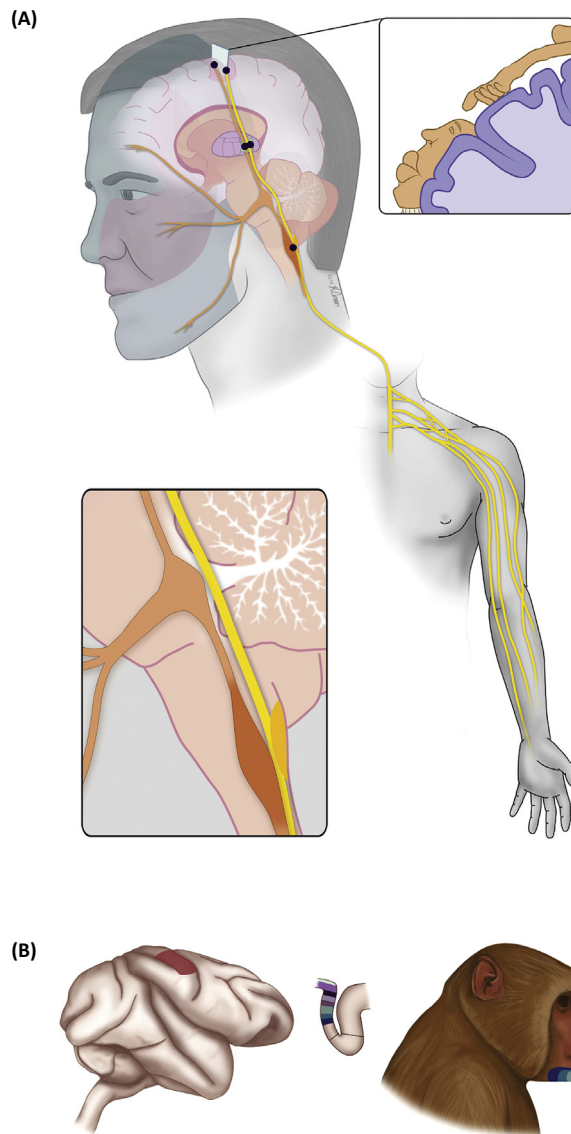
The evidence for preserved somatotopy following long-term deafferentation has important implications for providing artificial touch through electrical interfaces with the nervous system.

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## Trends in Cognitive Sciences

**Figure 1. Somatosensory Pathways and the Basic Phenomenon of Remapping.** (A) Diagram of the somatosensory pathways from the limb (yellow) and face (orange) to primary somatosensory cortex. The somatosensory nerves from the limb synapse onto the cuneate nucleus, located in the brainstem, which then sends projections to the ventroposterior lateral nucleus of the thalamus, which in turn projects to primary somatosensory cortex. The somatosensory nerves from the face project to the trigeminal nucleus, also in the brainstem, which then projects to the ventroposterior medial nucleus of the thalamus, then to cortex. The primary somatosensory cortex comprises a complete map of the body, where adjacent body parts are represented in adjacent patches of cortex (with some necessary discontinuities, see cartoon in top right inset). In S1 of monkeys, the hand representation borders the lower part of the face. (B) Following arm deafferentation, the cortical territory of the (deafferented) limb becomes responsive to stimulation of the lower face. Adapted, with permission from AAAS, from [11].

similar results from the barrel cortex of rodents). When input is lost from the entire hand and arm, for example, the cortical territory of the missing hand begins to respond to the lower part of the face, resulting in what appears to be massive reorganisation, sometimes spanning half of the sensory homunculus [11,12] (see [13] for review) (Figure 1B).

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