The body in the brain: neural bases of corporeal awareness

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Recent studies have begun to unravel the brain mechanisms that underlie the mental representation of the body. Imitation of movements by neonates suggests an implicit knowledge of the body structure that antedates the adult body schema. This can include inanimate objects that bear systematic relations to the body, as shown by the elimination from self awareness of a body part and its associated paraphernalia after selective brain lesions. Dynamic aspects of the body schema are revealed by spontaneous sensations from a lost body part as well as by orderly phantom sensations elicited by stimulation of body areas away from the amputation line and even by visual stimulation. The mechanisms of the body schema exhibit stability, since some brain regions seem permanently committed to representing the corresponding body parts in conscious awareness, and plasticity, since brain regions deprived of their natural inputs from a body part become reactive to inputs from other body parts.

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THE CAPABILITY OF OUR BRAIN to represent the body and to entertain a model of human anatomy has probably a quite precocious if not downright innate origin. Hours or even minutes after delivery, neonates can imitate orofacial and head movements performed by adults in front of them[1]. To the extent that they identify a movement of a specific bodily part of the adult model, and then produce a similar movement in the corresponding part of their own anatomy, babies must in some sense be cognisant of the general body structure. A neural basis for this deceptively simple visuomotor performance is probably constituted by neurones that become active either during the observation of a specific movement made by another individual, or during the performance of the same movement[2]. It is conceivable that primates are born equipped with this mechanism for the imitation of elementary actions, and that during maturation the mechanism undergoes a gradual refinement as a consequence of systematic interactions between tactile, proprioceptive and vestibular inputs, as well as between such inputs and the visual perception of the structure and movements of one's own and other people's bodies. The final result, a mental construct that comprises the sense impressions, perceptions and ideas about the dynamic organization of one's own body and its relations to that of other bodies, is variously termed body schema, body image and corporeal awareness[3]. Somatosensory inputs to the brain, especially from proprioceptors, are no doubt essential for bodily awareness, as attested by enduring changes caused in it by short-lasting muscle vibration and other somatic manipulations[4]; however, the importance of vision is attested by the anatomical distortions evident in the misshapen attempts of congenitally blind subjects at drawing or sculpting their own and other people's bodies[3]. The finding that normally sighted adults are facilitated in the visual discrimination of postural changes in another person's arms during movements of their own arms but not legs, and vice versa[5], argues for the existence of at least partly common, mutually reinforcing mechanisms for the representation of corresponding parts of one's own and other people's bodies.

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Brain lesions affect the representation of the body

Brain lesions can induce profound changes in the way the body is perceived and represented. In some cases such changes can be ascribed to a disorder of a specific cognitive domain, such as language or spatial attention. Disturbances of body awareness that are caused by lesions of the left posterior parietal lobe, such as autotopagnosia, finger agnosia and left–right disorientation, seem to depend on an altered conceptual, mainly linguistic representation of body parts[6]. Similarly, neglect of the left hemisoma that follows right posterior parietal lesions usually occurs within the context of a general neglect of the left hemispace, and appears to depend on an impairment of spatial attention or space representation rather than on selective disruption of the body schema. Some disturbances, however, might reflect a specific alteration of the body schema or parts of it, as, for example, in those stroke patients who are anosognosic for their motor and sensory defects so as to deny that they are impaired at all[7,8]. When it occurs in the absence of extrapersonal neglect, personal neglect in the form of hemisomatoagnosia suggests a specific alteration in the body schema[9]. Feelings of non-belonging, denial of ownership of a body part and misoplegia (hatred of hemiparetic limbs) can occur following right brain damage[10,11]. The neglected or disowned body parts are expunged from the mental body representation, and the material existence of these parts is justified with confabulatory explanations[12,13]. Although anosognosia for hemiplegia and somatoparaphrenia have occasionally been observed after large left-hemisphere lesions[14], they occur mostly following right-hemisphere

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lesions, hence their incidence is much greater on the left side of the body than on the right.

Limb amputees usually report a single phantom limb that can change in size and form over time. By contrast, brain-damaged patients without amputations might report the presence of multiple supernumerary body parts, in most cases hands or feet[15–17]. Reports of supernumerary limbs can coexist with denial of hemiplegia and feeling of non-belonging of the contralesional limb[18], suggesting that negative and positive symptoms can share common mechanisms. Unlike the phantom sensations of amputees, the sensations from supernumerary limbs are illogically believed by patients to reflect the real existence of these limbs, even when awareness of the rest of the body is normal[19].

Brain areas for perceiving and representing the body

According to Melzack[20], corporeal awareness relies upon a large neural network where somatosensory cortex, posterior parietal lobe and insular cortex play crucial and different roles, as indicated by the effects of selective lesions in this network. Lesions of the primary somatosensory cortex induce deficits in the tactile and proprioceptive spheres, but there is no evidence that they can cause alterations of higher-order body awareness, such as anosognosia for hemianesthesia, feelings of non-belonging, somatoparaphrenia and hemisomatoagnosia. By contrast, all these symptoms are frequently observed after lesions that involve the right posterior parietal lobe. Further, phantom-limb perceptions of amputees can be suppressed by right posterior parietal lesions[21,22] but not by excisions of primary somatosensory cortex[23]. Posterior parietal lesions can cause both negative (for example, disownership of body parts) and positive symptoms (for example, supernumerary limbs). A positron emission tomographic (PET) study has shown that a posterior parietal system, comprising superior parietal cortex, intraparietal sulcus, and adjacent rostral-most part of inferior parietal lobule, is activated during mental transpositions of the body in space[24]. The insular cortex is also involved in the body awareness, particularly in relation to the emotional aspects of it, since insular lesions can cause somatic hallucinations[25], and electrical stimulation near the insula induces illusions of changes in body position and feelings of being outside one's body[26].

Psychiatric disorders and body image

Body-centred delusions, such as underestimation of the size of bodily parts, are often observed in major psychiatric illnesses like schizophrenia, where such symptoms are more frequently related to the left side, and depression, where they are more frequently related to the right side. Also, hypochondriacs tend to refer their complaints (for example, an aching arm) more frequently to the right side of the body than to the left. These side differences might be pathological expressions of the asymmetrical functioning of the cerebral hemispheres[27]. In the depersonalization syndrome there is a persistent feeling of living outside one's own body, while patients with dysmorphophobia are morbidly preoccupied with real or imaginary physical flaws, concerning, for example, the shape of the nose, the size of the penis or breast, to the point of seeking unnecessary surgical corrections or suffering from self-inflicted injuries. The neural activities that underlie these complex psychiatric conditions will no doubt be explored in the near future with functional brain imaging.

The extended body schema

The body schema can be extended to include non-corporeal objects that bear a systematic relation to the body itself, such as clothes, ornaments and tools. Published examples range from the feather in the hat of Edwardian women to the surgeon's knife and so on[3,28]. These inclusions of inanimate objects into the body schema are generally regarded as temporary and contingent on the actual association between body and object: when the cyclist dismounts from his bike this ceases to be part of his body schema. The temporary character of the extended body schema is also manifest in the operation of one of its probable neuronal mechanisms. Neurones in the monkey's caudal postcentral gyrus respond to somatosensory and visual stimuli arising from the hands. If the monkey retrieves food with one hand the visual receptive fields of these neurones are limited to that hand, but if the retrieval is done with a rake, visual receptive fields expand to include both hand and tool, and the modification is strictly limited to the time of tool usage[29]. Recently we made a clinical observation that, in addition to upholding the concept of an extended body schema, hints at the existence of more complex and longer-lasting relations between such a schema and the objects incorporated into it[30]. After a large right-hemisphere stroke, a 73-year-old woman, while showing no sign of being demented, exhibited a total unawareness of her severe left-arm paralysis and in fact repeatedly affirmed that the paralysed hand belonged to someone else. The peculiarity about this patient was that while she was able to see and describe the rings she had worn for years and was currently wearing on her left, now disowned hand, she resolutely denied their ownership. By contrast, she immediately recognized these rings as her own (and produced much veridical autobiographical information about them) when they were shifted to her right hand, or displayed in front of her. Similarly, she promptly acknowledged ownership of other personal belongings that, in her previous experience, had not been ordinarily associated with the left hand (for example, a keyholder or a comb), even when she saw such objects in contact with that hand. Denial of ownership of the left-hand rings was thus conditional not only on their being seen on the disowned hand, but also on the existence of a previous systematic association between them and that hand. It was as if a conjoint visual representation of the left hand and its rings had been retained in her memory but expunged from her self awareness, implying that before the stroke the rings thus represented had become part of an extended, primarily visual body schema. William James remarked that bodily parts and personal belongings alike can be experienced in self awareness sometimes as 'mine' and sometimes as 'me'[31]. As the above results suggest, somatoparaphrenia suppresses both the me and the mine experiences of the disowned body part and related paraphernalia, but the latter, if removed from the disowned hand, prove apt to activate a mine visual representation that is independent

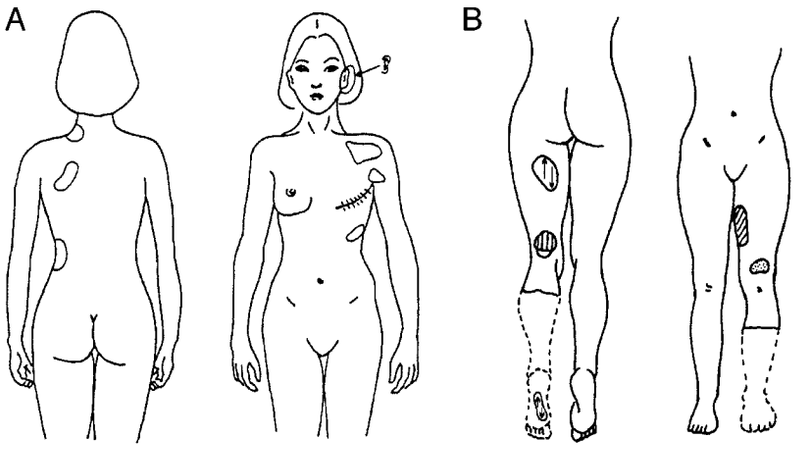

Fig. 1. ***Schematic drawing of the skin areas that elicit phantom sensations in lower limb and breast amputees.*** **(A)** *Somatic stimuli delivered to the circled areas elicited sensations on the phantom nipple in addition to local sensations.* Reproduced from Ref. 41. **(B)** *Stimuli delivered to the vertically lined region were mislocated to the sole of the phantom foot. Stimuli to the unfilled area elicited sensations on the calf. Sliding stimuli to the stump region marked with the arrows were referred as directional stimuli to the area marked by the arrows on the phantom foot. The dotted and the hatched areas elicited sensations to the dorsum of the foot and the hallux, respectively. It is noteworthy that this patient reported sensations on the foot during sexual intercourse and defaecation. Thus, in this patient, a topographic remapping might have occurred.* Modified from Ref. 40.

of that hand, thus arousing an appropriate experience of ownership.

The real body and the body in the brain

The body schema is not a simple percept of the body, but involves mnemonic and imaginative components as well, as clearly demonstrated by the compelling amputees' experience of the continued existence of the amputated body part. Recently, the time-honoured knowledge about the 'consciousness of lost limbs'[32] has been complemented by fresh evidence of phantom phenomena localized to other removed or denervated body parts, like the breast, the jaw, the penis and so on[21,33,34]. Visual, auditory and olfactory phantom sensations have been reported after deafferentation of the corresponding sense organs[21], but the most obvious phantom phenomena are undoubtedly somaesthetic in nature, all submodalities, from pain to feeling of movement, from touch to thermoception, being represented in the phantom experience. Activation of sensory nerves in the amputation scar can contribute to such an experience, but it is now clear that phantom phenomena have a primarily central origin. As already mentioned, according to Melzack[20] the body schema is subserved by a distributed neural network or neuromatrix, largely prewired by genetics but open to continuous shaping influences of experience, which includes the somatosensory system, reticular afferents to the limbic system, and cortical regions that are important to self-recognition and recognition of external objects and entities. Phantom phenomena would be caused primarily by the persisting activity of neuromatrix components that have been deprived of their normal inputs because of the loss of a body part, and by the brain's interpretation of this activity as originating from the lost part. It would seem obvious that if the lost body segment is, for example, a foot, the central activity decoupled from the periphery should be exclusively somatosensory, justifying Dennett's quip[35] that if amputees can feel a lost foot, they cannot hear, smell or see it. Hear and smell it they might not, but the Ramachandrans have shown recently that an amputated limb can be seen as well as felt[36]. The reflection of the normal arm in a vertical mirror generated in six arm amputees a compelling visual perception of the missing arm. This visual perception interacted with the somatic phantom sensations so effectively as to succeed, for example, in relieving painful spasms in the phantom. Further, subjects reported vivid tactile sensations on the phantom when they viewed the experimenter touching the mirror image of their normal arm, as if the virtual but 'realistic' visual inputs that arise from the non-existing limb could activate neurones that normally receive tactile, proprioceptive and visual inputs from that limb[37,38].

Evoked phantom sensations

While previously attention has been focused on spontaneous phantom sensations[39], modern studies have examined in greater detail the phantom sensations evoked in amputees by appropriate sensory stimulation. Tactile stimulation of the stump of an amputated limb can elicit sensations in the phantom limb, and more recently it has been found that similarly vivid phantom sensations can arise in lower limb or breast amputees as a result of tactile stimulation of regions distant from the amputation line[40,41] (Fig. 1).

In hand amputees, sensations in the phantom hand can be elicited by tactile stimuli that are delivered to the lower face on the amputation side. Like concurrent veridical facial sensations, elicited phantom sensations convey precise information about form, numbers, motion and temperature of the facial stimuli, and there is usually a point-to-point correspondence between the actual location of the eliciting stimulus and its felt position on the phantom, so that it is possible to construct an orderly map of a phantom hand or finger on the face[42]. Since in the somatosensory cortex the representation of each hemiface lies side by side with that of the ipsilateral hand, phantom hand sensations from facial stimulation are probably caused by an appropriation of the original cortical representation of the lost hand by sensory inputs inherent to the adjacent face representation. Strong support for this hypothesis is provided by the demonstration that deafferented portions of the primary somatosensory cortex of experimental animals become responsive to sensory inputs that are normally routed to adjacent cortical regions[43]. Similarly, electrical stimulation of motor cortex regions that originally represented denervated muscles tends to activate muscles that are normally represented in contiguous portions of the cortex[44]. These results from animal experiments have been extended to human amputees in studies that used magnetoencephalographic recordings, electrical or magnetic cortical stimulations, and brain-imaging techniques, all of which have revealed expansions of sensory and motor central representations of intact body segments at the expense of deafferented adjacent representations[45–48]. The anatomo–functional constitution of sensory and motor body maps in the brain proves to be highly dynamic and subject to the influence of experience even in the adult organism, and even in cortical areas that were previously thought to possess a strongly fixed and stereotyped organization[50,51].

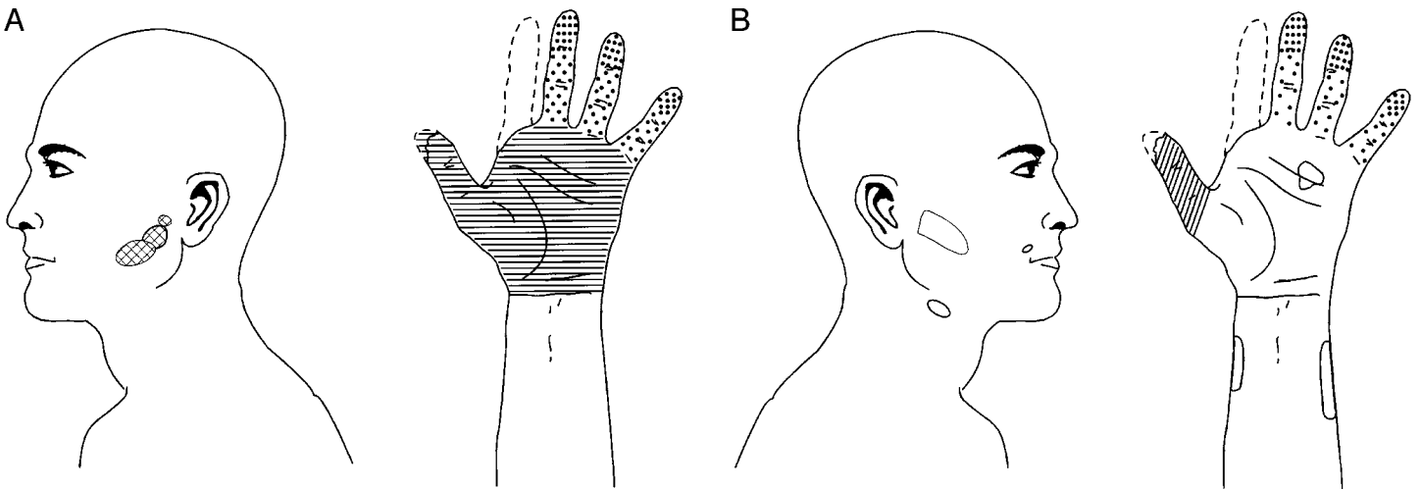

Fig. 2. ***Topographic changes over time of the areas that elicit phantom sensations in a left-index amputee patient.*** **(A)** *Five months after the amputation, stimuli on the remnant fingers (dotted areas) and the face ipsilateral to the amputation (hatched areas) elicited topographic phantom sensations. Lined areas on the hand were not stimulated for they were covered by a bandage.* **(B)** *About three years after the amputation the finger maps were virtually unchanged. By contrast, non-topographic facial maps (circled areas) were found only contralaterally to the amputation. Circled areas on the forearm and hand elicited only diffuse and vague phantom sensations.* Modified from Ref. 52.

The somatosensory reorganization that follows amputation appears to rely on diverse mechanisms. Prompt appearance of reactivity of deafferented cortical regions to previously ineffective inputs from intact body regions can be accounted for by an increased synaptic efficacy of already existing but normally silent connections, whereas an actual restructuring or destructuring of neural networks can account for later effects. Indirect clues about the operations of these mechanisms are afforded by the temporal changes in the pattern of elicited phantom phenomena, such as those we have observed in a left-index amputee who experienced consistent, mostly unpleasant, spontaneous phantom sensations[52]. About six months after the amputation, tactile stimulations of either the left hemiface or the third, fourth and fifth fingers of the left, mutilated hand revealed the existence of orderly topographic maps of the missing index on both face and remaining fingers. About three years later, spontaneous and elicited phantom sensations were still present, and the orderly topographic maps of the amputated index on the ipsilateral fingers were unchanged, but the index map on the ipsilateral hemiface had totally disappeared. Some phantom sensations could now be aroused by touching the right hemiface, but there was no precise correspondence in kind, intensity and location between the facial stimuli and the sensations elicited by them on the phantom finger (see Fig. 2).

Similar side shifts and degradation over time of facial maps of a phantom have been observed in an arm amputee by Halligan and co-workers[53]. We believe that the different fate of the orderly maps of the phantom index on the remnant fingers, which persisted for years, and that on the face, which did not, depends on different associations between veridical and phantom sensations that occur during ordinary behaviour. As is typical of amputees, our subject was particularly aware of sensations from the phantom index when he manipulated objects with the mutilated hand. Phantom and veridical sensations from the fingers were so congruent and correlated that he sensed his motor commands to be directed to the missing finger as much as to the other fingers. By contrast, although he knew that facial stimuli could elicit sensations in the phantom index, he was rarely if at all aware of such sensations in everyday life, in agreement with the behavioural and cognitive irrelevance of the association between veridical facial sensations and phantom index sensations. The meaning of stimuli for the behaving organism's attention and intentions seems to be crucial for the overall dynamics of the organisation of sensory cortical maps, so that foreign inputs that become expressed in a deafferented portion of the somatosensory cortex should be maintained only if they can command attention and be useful for motor control. In turn, time-related changes in the location of skin areas that elicit phantom sensations in amputees suggest that the expression of foreign inputs in a deafferented somatosensory cortical area might reflect a hierarchical organization of different inputs to that area. Normally, the dominant input from the index finger to its representation in the somatosensory cortex would hold in check less powerful inputs from ipsilateral fingers and hemiface, as well as the even less powerful callosal inputs from the opposite hemiface. Removal of the dominant input by amputation would unmask the latent inputs from the ipsilateral fingers and hemiface, which in turn would keep the callosal inputs mostly silent. The functional associations between veridical and phantom digital sensations would favour the stabilization of the inputs from the remnant fingers, but the synaptic efficacy of the input from ipsilateral hemiface would be lost because of its functional insignificance for behaviour. The consequent expression of the unmasked callosal input from the opposite hemiface, attested by the appearance of weak phantom sensations that are elicited from that hemiface, would also be doomed to disappear because of its behavioural irrelevance. Much anatomical, physiological and neurochemical evidence supports the notion that cortical reorganization that follows partial deafferentation occurs in a staged fashion, involving, first, the immediate expression of latent inputs, second the formation of new synapses, and third the stabilization or

elimination of synapses in accordance with their functional usefulness[54,55].

The meaning of stability and plasticity in sensory cortical maps

While attesting the plasticity of central somatosensory representations, psychophysical studies of human amputees provide a unique documentation of a permanent commitment of specific brain regions to conscious representation of specific body parts. Spontaneous and elicited phantom sensations arise from central neural activities that were linked originally to the conscious representation of the lost body part. A persistent functional link between regions of primary somatosensory cortex and bodily regions is proven by direct electrical stimulation during neurosurgical operations under local anaesthesia. In a patient who had lost his right arm almost a quarter of a century before the operation and had not experienced phantom phenomena for many years, stimuli applied to the standard hand and arm representations in the left somatosensory cortex brought back into his conscious experience long-lost sensations from the missing hand and arm[56]. Phantom sensations reported by phocomelic children who were born without one or more limbs[57,58], as well as the visuomotor imitation abilities of newborn babies, similarly suggest that the brain might be genetically predisposed to represent a prototypical human body, regardless of the correspondence or lack thereof between ideal model and actual body. Nevertheless, there is plasticity in the somatosensory cortex insofar as inputs from intact body parts become able to activate deafferented cortical regions. Further, skill learning with a body part leads to an increased representation of that body part in the cortex[59,60], and the total loss of a sense modality increases the cortical representation and the functional performance of other sensory modalities[61]. Does the appropriation in the amputees' cortex of additional space by the invading inputs give a functional advantage to the body regions that are represented by such inputs? Old studies have provided some evidence that the skin near an amputation line or on the stump of a congenitally lacking limb has an advantage over the corresponding contralateral side in terms of tactile reaction time, tactile threshold, and tactile two-point discrimination[62–64]. These effects could be partly accounted for by sensory nerve regeneration in the stump, but they could also be due to central readjustments that impart to the stump some of the functional characteristics of the amputated limb. These investigations must now be repeated with more controlled methods, and above all they should be carried out on regions far from the amputation line. It would be important, for example, to monitor changes in tactile sensitivity in a facial region whose stimulation elicits veridical sensations and sensations localized to a phantom hand or finger. To the best of our knowledge, this work remains to be done.

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