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The Self *in* Its Brain: neural representations of the body

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1   Abstract

The psychological construct of the body schema (or body image), was invoked to explain some curious clinical 'disturbances' following central nervous system lesions. Only when Penfield began electrical exploration of the cerebral cortex in the late 1920's, did neurophysiological evidence pertaining to the representation of the body in the brain become available. This paper puts forward two lines of evidence in support of a model for neural body representations. Firstly, the clinical phenomena and neural correlates of phantom limbs are reviewed. Melzack's *neuromatrix hypothesis*, and the *reorganisation hypothesis* of Ramachandran and co-workers are then discussed in some detail. Secondly, the effects of empirical sensory manipulations in primates and man demonstrate significant plasticity in both neural and perceptual domains. Evidence of somato-cortical reorganisation following selective deafferentation is reviewed, and two hypotheses for reorganisation mechanisms (*unmasking of latent connectivity* and *axonal sprouting*) are discussed. Finally, muscle vibration-induced perceptions of anatomically impossible body configurations are examined.

Six aspects of the representation of the body are highlighted. The representations are multi-modal, distributed, constrained, dynamic, use-dependent, and co-incident. A speculative model of sensory integration, depending on direct connections between corresponding positions in abstract topographic or computational maps is used to account for some of the findings of the reviewed research. The function of the representation of the body in the brain is seen as that of piloting the organism through the environment, attending only to salient details in order to produce a 'best fit' working body schema.

2 Introduction

2.1 A short history

> The abundance of speculation and theoretical constructs in the doctrine of the loss of awareness of the body… is inversely proportional to factual observations (Poeck and Orgass, 1971, p 254, citing Pick, 1922)

Poeck and Orgass (1971) suggested that the concept of the body schema (the psychological construct proposed to subserve the perception of the body[1]) arose from the need to explain some curious clinical phenomena. Some patients suffer from body image disturbances following central nervous system (CNS) lesions, as classically reported by neurologists such as Gerstmann (1942), L'Hermitte, and Wernicke. Empirical support for this 'body consciousness' was lacking, however, and conceptual confusions often led to misunderstandings and disagreements both within and between medical and psychological communities (Bromage and Melzack, 1974).

The most influential early account was put forward by Head and Holmes (1911). They saw the body schema as "formed and constantly changed by individual experience" (Bromage and Melzack, 1974, p 267), multi-modal, and based primarily on somatosensory input. Pick (1908, 1915, 1922) approached the problem from a clinical perspective, and suggested that visual input was the primary influence in the construction of the body schema.

The terms used by researchers to describe clinical syndromes, where a 'body image disturbance' may be a primary or only secondary manifestation of the disorder, have often been used interchangeably or arbitrarily (Cumming, 1988). As a consequence, the concept of the body schema has become virtually useless (Poeck and Orgass, 1971). That there exists a functional organisation subserving the perception of the body is not doubted, but it is only through neurophysiology that this mechanism will be elucidated (Poeck and Orgass, 1971).

It was not until Penfield's work on the functional organisation of the human cerebral cortex that any such neurophysiological evidence existed. It is to Penfield's work that we now turn.

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[1] The terms 'body schema,' 'body image,' and 'representation of the body' are equivalent and used interchangeably for the purpose of the present report, though see Gallagher *et al*., 1998 for distinctions.

2.2   Penfield's legacy

In late 1920's Montreal, Wilder Penfield began electrical exploration of the cerebral cortices of patients during neurosurgery for epilepsy (Penfield and Boldrey, 1937, see Figure 1A and B, below).
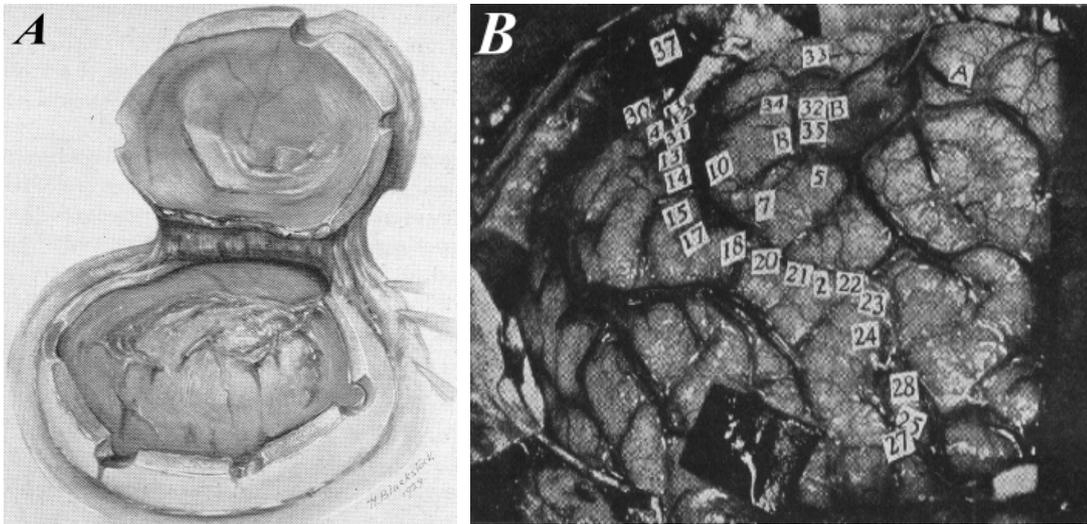
Figure 1. Penfield's procedure for electrical exploration of the exposed brain surface during neurosurgery for epilepsy. **A**. The anaesthetised scalp and cranium were cut to produce a 'flap,' which was folded back to expose the brain. The dura mater was cut and folded back, the brain was kept moist and warm during exploration and surgery. **B**. Paper tickets were placed on stimulation points that elicited a response during exploration of the postcentral gyrus of the right hemisphere, from the infero-lateral (27 – facial regions) to the supero-medial (30 – upper arm and trunk regions). Figure 1A was adapted from Penfield and Erickson (1941); Figure 1B was adapted from Penfield and Rasmussen (1957).

During electrical stimulation, the current was increased until a response was elicited from the patient. Responses varied according to the area of the brain stimulated, for example visual phenomena were elicited on stimulation of the occipital lobe, while stimulation of the post-central gyrus of the anterior parietal lobe led to patients reporting sensations pertaining to the body.

By systematically exploring the post-central gyrus, Penfield obtained a somatosensory 'map' of the body. Significantly, this map exhibited topographic organisation, such that adjacent parts of the body were 'represented' adjacently on the surface of the cortex. Figure 2 below illustrates this organisation.
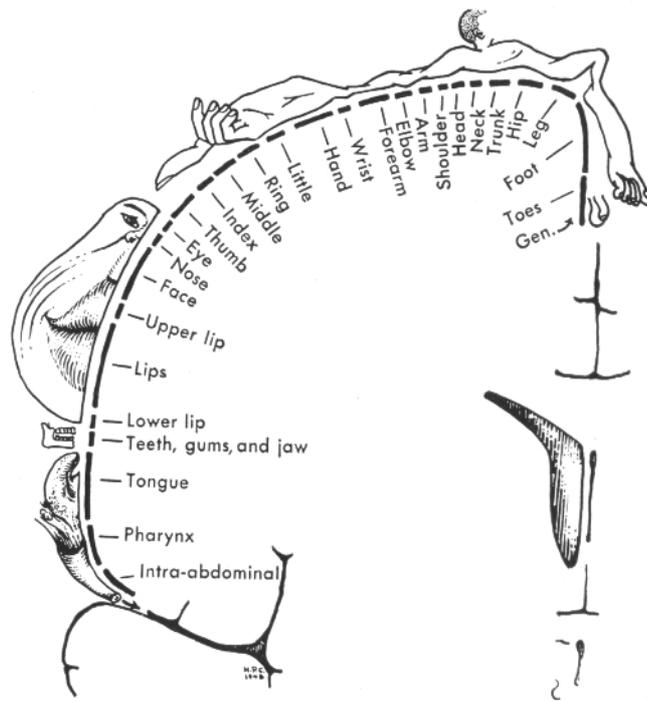
Figure 2. Somatotopic organisation of post-central gyrus. Note that there are discontinuities in the topography, for example the face is represented laterally to the hand, and the genitalia infero-medial to the feet. Note also that there is considerable 'cortical magnification' (high cortical to body surface area ratio) of the face, hands and feet, and in particular the lips and thumbs. The 'homunculus' drawn reclining on the surface of the brain is a useful metaphor for this somatotopy. Adapted from Penfield and Rasmussen (1957).

Penfield noticed variable overlap in the representations of body parts, and variability within and between individuals over time and space respectively (e.g. Penfield and Welch, 1948; Penfield, 1947; Penfield and Boldrey, 1937). The important features to note are that the medial-lateral sequence of representations and the extent of cortical magnification are largely invariant. The 'homunculus' created by this electrical mapping is a useful metaphor for the organisation of somatosensory input to this area (Brodmann's cytoarchitectonic areas 3, 1, and 2), however;

> …although a given response follows point stimulation it is not to be concluded that functions are localised in these points. (Penfield, 1946 p 343)

What Penfield's homunculus does *not* imply, is that there is a 'little man,' localised *in* the somatotopic map, who reads the topographic map, processes information, and sends output to other areas (Churchland, 1986). To fall victim to this 'homunculus fallacy' is to invoke the Cartesian infinite regress, and merely to reduplicate the problem – if the brain represents the body in a homunculus, how does the homunculus represent the body? (Weinberg, 1997; Hacker, 1987). So what is meant by "the representation of the body?"

2.3 The nature of representations

The *re*-presentation of afferent information at 'higher' levels of the somatosensory pathway must serve a purpose, be it computation, analysis, or integration, else nothing is gained and the infinite regress is invoked. Melzack, (1992) writes;

> …signals are analysed, information about them is shared [among parallel systems] and converted into an integrated output, which is sent to other parts of the brain. (p 93)

The present review takes sensory-motor integration and computation as the function of somatosensory representations of the body. It is not clear whether the topographic organisation of these representations is fundamental to their functional properties (Kaas, 1997; Stryker *et al*., 1988; Calford *et al*., 1985), or is simply a matter of efficiency and 'housekeeping' (Weinberg, 1997; Mountcastle, 1988).

How does the representation and integration of sensory-motor information result in the conscious perception of the body? Melzack (1992) continues;

> Somewhere in the brain the output is transformed into a conscious perception, although no-one knows exactly where the transformation that leads to awareness takes place. (p 93)

To assert that there is a place (and therefore a time) where neural information reaches conscious awareness, is to make the mistake that Dennett and Kinsbourne (1992) discuss at length – it is once again to invoke a 'Cartesian Theatre' of consciousness. It is beyond the scope of the present review to ask this question, and it is the author's opinion that the answer is, at least at present, beyond the conceptual bounds of psychology and neuroscience.

2.4 The task

Berlucchi and Aglioti's (1997) paper "*The body in the brain: neural bases of corporeal awareness*" reviews many aspects of the representation of the body in the brain, and readers are referred to this paper for broader discussion. The present work reviews findings from research on phantom phenomena (3.1), and empirical investigation of neural representations of the body (3.2) in more detail, and attempts a synthesis of this research in terms of a geometrical co-ordinate model of body representation.

That the experience of a part of the body continues despite the absence of that part has great implications for theories of the brain's body representation. If a body part is not necessary for its continued perception, then a theory based on peripheral input alone is insufficient. Equally, if phantom perceptions change over time, or occur only under certain conditions, then theories of their origin and maintenance must reflect this (3.1).

The majority of empirical research on the manipulation of somatosensory input in humans, non-human primates, and other animals, involves the capacity for plasticity within the somatic neocortex (and to a lesser extent the thalamus and spinal cord), and the conditions under which this plasticity is induced and maintained. This research is examined below (3.2.1). Another intriguing line of research focuses on the manipulation of proprioceptive input in conscious human subjects, who subsequently report bizarre and 'impossible' perceptual phenomena (3.2.2).

Various important and relevant lines of evidence are beyond the scope of this review, and are only listed here; clinical syndromes including the 'Alice in Wonderland' syndrome (micro- and macro- somatoparagnosia – e.g. Kew *et al*., 1998; Leker *et al*., 1996; Todd, 1955), awareness or denial disorders (alocognosia, anosognosia, asomatognosia, somatoparaphrenia, "non-belonging", anosodiaphora – see Berlucchi and Aglioti, 1997; Vuilleumier, 1997; Halligan *et al*., 1993; Poeck and Orgass, 1971). Similarly, works on motor aspects of body representation, the perception of extra-personal space (see e.g. Bisiach *et al*., 1993, Bisiach, 1985), and psychogenic, psychoanalytic and other 'psychological' accounts of the body image (see Berlucchi and Aglioti, 1997; Weiss, 1955) are not considered.

3   Evidence

3.1   Evidence from phantom phenomena

Comprehensive reviews of phantom phenomena are available elsewhere (especially Ramachandran and Hirstein, 1998; see also Davis, 1993; Katz and Melzack, 1990; Simmel, 1956). The following review covers only aspects relevant to the present discussion.

3.1.1 Phantom phenomena

> And yet I have learned from some persons whose arms or legs have been cut off, that they sometimes seemed to feel pain in the part which had been amputated. (Descartes, 1642/1997, p 180)

Reports, like Descartes' above, of the continued perception of body parts following their amputation or deafferentation, can be found in a wide range of literature dating back hundreds of years to Paré, in 1551 (Davis, 1993; Shukla *et al*., 1982; Weiss, 1955). Both Admiral Lord Nelson, in the late 18th century, and Captain Ahab in Melville's 'Moby Dick' (1851), complained of phantoms (Park *et al*., 1999, Ramachandran and Hirstein, 1998). It was following the manifold surgical amputations of the American Civil War, however, that Silas Weir Mitchell published the first scientific account, and coined the term 'phantom limbs' (anonymously in *Atlantic Monthly*, 1866; then in *Lippincott's Magazine*, 1871).

Phantoms are experienced by 80 – 100 % of amputees (Park *et al*., 1999; Flor *et al*., 1998; Jensen *et al*., 1983), and following traumatic nerve palsy, brachial plexus avulsion, paralysis, dorsal root removal, and temporary anaesthetic block (Halligan *et al*., 1993; Shukla *et al*.,1982; Bromage and Melzack, 1974). Phantoms may require specific sensory triggers (e.g. Kaas, 1998; Katz and Melzack, 1990; James, 1890), or be permanently present. Between 33% and 75% of phantoms appear immediately after deafferentation, and most appear within a few weeks (Ramachandran and Hirstein, 1998; Jensen *et al*, 1983). Phantoms are more common in dominant than non-dominant arms (Shukla *et al*., 1982), in traumatic amputation than gradual denervation (Park *et al*., 1999; Shukla *et al*., 1982), and in adults than in children (but see 3.1.3 below).

Phantom perceptions may pertain to a normal limb or body part, to only selected submodalities of somatosensation, such as pain, tingling, vibration, or burning, to changes in length or volume, even to movements or paralysis in the missing body part (Franz and Ramachandran, 1998; Jensen *et al*., 1983; Weiss, 1955). Phantom arms may swing during locomotion; phantom penises may become erect, and bladders distended (Melzack, 1992, 1990; Katz and Melzack, 1990). Jacome (1978) reported an extraordinary case where a phantom itch was relieved by scratching the phantom foot! Supernumerary phantom limbs (Vuilleumier *et al*., 1997; Halligan and Marshall, 1995; Halligan *et al*., 1993; Lacroix *et al*., 1992; Ohry *et al*., 1989), or an entire phantom body (Melzack, 1990) often occur following thoracic or cervical spinal transections (Simmel, 1956) or brain damage (Berlucchi and Aglioti, 1997).

So real is the phantom perception that the patient may attempt to reach out with, rest, or walk on the ghostly appendage (Gallagher *et al*., 1998; Melzack, 1992, 1990; Simmel, 1956). With time, phantom limbs are often felt to dissipate and foreshorten (a phenomenon known as 'telescoping'), with the most vivid and salient portions (e.g. hand, fingers, or feet - Simmel, 1956, Weiss, 1955) seeming to float in mid air or become attached to the stump (Katz and Melzack, 1990; Melzack, 1990). The phantom may disappear spontaneously, or following CNS damage (Halligan *et al*., 1993; Yarnitsky *et al*., 1988; Weiss, 1955; Head and Holmes, 1911). Injury to, or surgery on the stump may induce or re-induce a phantom (Park *et al*., 1999; Simmel, 1956), or reverse telescoping (Melzack, 1990) years after the initial deafferentation.
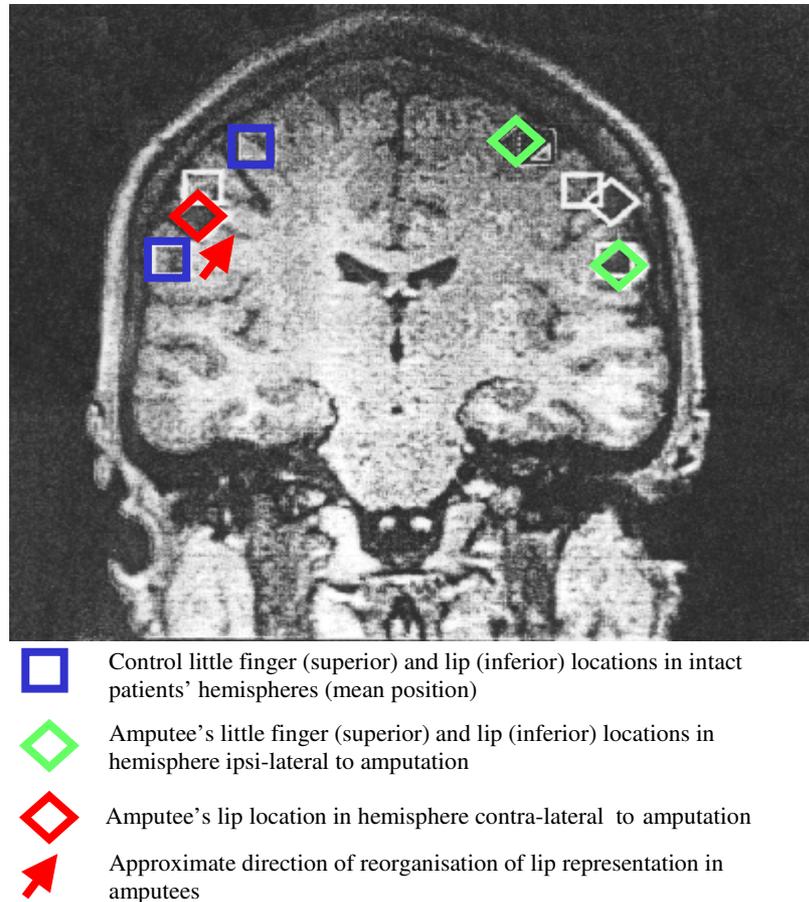
Many patients enjoy their phantoms – they 'flesh-out' the prostheses that they wear (Park *et al*., 1999; Melzack, 1990), and some patients experience orgasm despite total spinal transection (Davis, 1993; Melzack, 1990). Conversely, 50% - 98% of patients complain of phantom pain (primarily burning and cramping - Birbaumer *et al*., 1997; Weiss, 1955). Treatment for phantom pain, paralleling contemporary technology and understanding of the brain, has ranged from pounding the amputation stump with a mallet, to stereotactic thalotomies (Davis, 1993). With 50 available treatments, however, only seven percent of patients experience long term relief (Katz and Melzack, 1990). Chemotherapy, neurosurgery and anaesthesia are often ineffective (Melzack, 1999, 1992; Birbaumer *et al*., 1997; Weiss, 1955), while holistic therapies, including pre-amputation anaesthesia and counselling may prevent phantom pain (Davis, 1993).

A complete neuroscience must account for these phenomena, and many researchers have offered accounts for these bizarre experiences (Birbaumer *et al*., 1997). So what neural processes can be seen to accompany such illusory perceptions?

3.1.2   Neural correlates of phantoms

The invasiveness of neurosurgery has meant that systematic cortical stimulation and mapping studies, like those carried out by Penfield and co-workers, have not been repeated on phantom patients (Yang *et al*., 1993; Narici *et al*., 1991). With the advent of modern brain-imaging techniques, however, the opportunity to sample structure-activity-function relationships in the alert brain has been regained. Magnetoencephalography

(MEG), magnetic source imaging (MSI), and neuroelectric source imaging (NeSI) have been employed to map the somatosensory homunculus in patients and control subjects, and offer distinct advantages over other techniques (Gallen *et al.*, 1994; Rossini *et al.*, 1994; Yang *et al*., 1993; Narici *et al*., 1991). See Figure 3, below.

▢ (blue square)	Control little finger (superior) and lip (inferior) locations in intact patients' hemispheres (mean position)
◇ (green diamond)	Amputee's little finger (superior) and lip (inferior) locations in hemisphere ipsi-lateral to amputation
◇ (red diamond)	Amputee's lip location in hemisphere contra-lateral to amputation
➤ (red arrow)	Approximate direction of reorganisation of lip representation in amputees

Figure 3. Magnetoencephalographic recording of somato-cortical responses to one thousand brief pneumatic stimulations of the first and fifth digit and lip in upper extremity amputees (diamonds), and intact controls (squares). The electrical activity in the brain is detected, averaged, and background activity subtracted, yielding a point representation of the stimulated body site on the somatosensory cortex. White squares - control thumb representation; white diamonds - amputees' thumb representations ipsi-lateral to amputation. The red arrow shows the approximate direction and extent of reorganisation occurring in amputees as compared both to non-amputee controls and amputees' hemisphere ipsi-lateral to amputation. Adapted from Elbert *et al*., (1997).

Such imaging studies in phantom hand and arm patients have shown that substantial cortical reorganisation occurs following deafferentation (Kaas, 1998; Davis *et al*., 1998; Knecht *et al*., 1996, 1995, and see Table 1, below).

Table 1 Extent of Cortical Reorganisation Following Alteration of Somatic Input in Humans

Study	Altered Input Type	Technique	Cortical Representation	Reorganisation* (mm)
Yang *et al.*, 1994	amputation	MEG	face, upper arm	30 - 35
Flor *et al.*, 1995	"	MEG	face	21
Knecht *et al.*, 1996	"	MSI	lip	39
Elbert *et al.*, 1997	"	MEG	lip	14
Montoya *et al.*, 1998	"	NeSI	lip	24
Flor *et al.*, 1998	"	NeSI	mouth	22
Birbaumer *et al.*, 1997	amputation,	NeSI	lip	20
	(anaesthesia)‡	NeSI	lip	(18)
Mogilner *et al.*, 1993	separation of syndactyl† fingers	MEG	fingers	3 - 9
Flor *et al.*, 1997	chronic pain	MSI	back	25

* Reorganisation is given as a mean or range over several subjects. † Patients with webbed fingers' (syndactyly) underwent surgical separation of the conjoined fingers. Brain imaging was carried out before and 3 weeks after surgery. ‡ Brachial plexus anaesthesia resulted in acute reorganisation of chronically reorganised post-amputation cortical representations. All other studies involve comparisons with the unaffected (ipsilateral) hemisphere. MEG – magnetoencephalography; MSI – magnetic source imaging; NeSI – neuroelectric source imaging

The deafferented arm representation of the somatosensory cortex (bordered by the head and face representations infero-laterally and by the shoulder and upper trunk supero-medially, see Figure 2) of deafferented patients is 'invaded' by the face and trunk representations; electrical activity in cortex previously responsive to hand and arm stimulation is now elicited by stimulation of body parts with adjacent representations (Knecht *et al.*, 1998, 1996, 1995; Kaas, 1998; Elbert *et al.*, 1997). Tactile stimulation of the face or trunk may elicit modality-specific, topographically organised sensations in the phantom arm (Borsook *et al.*, 1998; Ramachandran, 1994; Ramachandran *et al.*, 1992), and conversely, stimuli applied to the arm may elicit sensations in a phantom face (Clarke *et al.*, 1996) see

Figure 4, below.
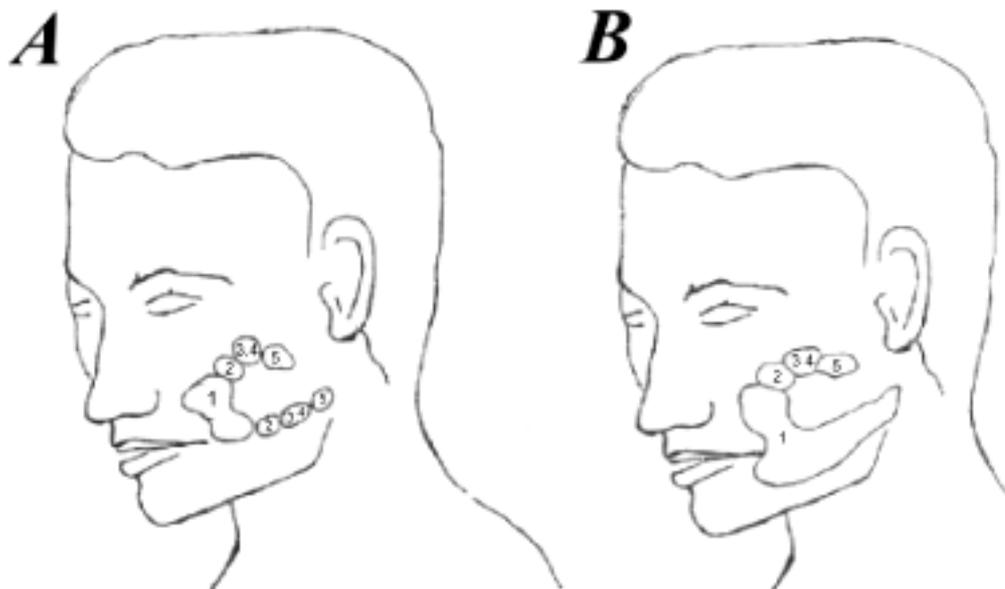
Figure 4. Ramachandran's (1994) patient DS. Stimulation of the face produced modality-specific sensations felt in the phantom hand. Furthermore, stimulation points on the face exhibited topography, such that there was a systematic relationship between points on the face and on the phantom limb. **A**. Referral map at the initial study point. **B**. Referral map after 6 months, indicating plasticity in the topography of referred sensations. Numbers in A and B denote finger representations; 1 – thumb, 2 – index, 3,4 – middle and ring, 5 – little. Adapted from Ramachandran and Hirstein (1998).

Phantom breasts may be elicited by stimulation of the ear; phantom feet and legs by genital or anal stimulation (Park *et al*., 1999, Ramachandran and Hirstein, 1998; Aglioti *et al*., 1994). This is termed 'referred sensation,' 'mislocalisation,' or 'ectopic representation,' and also occurs in partial nerve injury (Schultz and Melzack, 1999) and chronic pain states (Katz and Melzack, 1987). Several 'referral maps' may be found in the same individual, and maps may disappear, expand, or shift over time or with muscular extension of the stump (Berlucchi and Aglioti, 1997; Knecht *et al*., 1996, see Figure 4). Repeated experimental stimulation of a facial loci may induce *de novo* sensations referred to the phantom limb (Ramachandran, 1994).

Ectopic representations have been interpreted in terms of adjacency of body-part representations on the Penfield homunculus (see Figure 2, e.g. Aglioti *et al*., 1994; Ramachandran, 1994). Not all ectopic representations fit the predictions made from these proximity relations, however (Park *et al*., 1999; and see Borsook *et al*., 1998), and strict referral topography and modality-specificity is not always observed (Knecht *et al*., 1998, 1996, 1995). We should note in this regard Penfield's caveats about inter-individual variability (see 2.1, above).

Phantom pain is closely and positively correlated with the extent of post-amputation cortical reorganisation (Flor *et al*., 1998, 1995; Birbaumer *et al*., 1997; Knecht *et al*., 1996, 1995), and there are indications that painful and non-painful phantom phenomena may arise from separate neural mechanisms (see Davis, 1993 for a review). Ojemann and Silbergeld's (1995) patient had not experienced phantom phenomena for two decades prior to presentation, yet phantoms were readily elicited on cortical stimulation of the silent representation. This patient showed pre-central motor, but not post-central somatosensory cortical reorganisation following amputation.

3.1.3   Neural causes of phantoms

> The voluminous literature covering almost a century of discussion concerning the origin of phantom experiences can be summarised in a single sentence: Is the seat of the phantom to be located in the periphery, specifically the neuroma; in the brain, or in the soul? (Simmel, 1956, p 646)

Initially, neurobiological accounts of phantom phenomena fell into two broad theoretical types: peripheral nerve activation (e.g. Mitchell, Foerster, Pitres, Livingston, Falconer – see Weiss, 1955) and central body schema explanations (e.g. Riddoch, 1941; Head and Holmes, 1911). It was later found that peripheral anaesthesia, complete spinal section, and surgery at many levels of the somatosensory system failed to abolish phantoms (Melzack, 1992, 1990; Bromage and Melzack, 1974), ruling out the possibility that phantom experiences *required* anomalous peripheral input. Consequently, recent theories have focused on the CNS (Shukla *et al*., 1982). Two such theories are summarised below.

The neuromatrix hypothesis

Melzack and co-workers (1999, 1992, 1990) suggested that a genetically determined neural network, or 'neuromatrix,' incorporating the somatosensory cortex, limbic system, and posterior parietal lobes "generates the experience of the body" (Saadah and Melzack, 1994, p 484) by means of parallel, distributed, cyclical processing of afferent and efferent information. Under this hypothesis, phantoms arise when the neuromatrix spontaneously *generates* the experience of the body in the absence of input from a missing or deafferented limb.

Melzack's theory is consistent with Hebbian, neural Darwinist, (e.g. Edelman, 1992; Pearson *et al*., 1987), parallel distributed processing, and neural-migratory developmental

theories (Davis, 1993; Melzack, 1992, 1990), giving it solid theoretical support. There are several lines of experimental evidence offered in support of the neuromatrix.

Phantom elbow or knee joints are typically perceived as lying in the middle 40% to 70% of joint range (Ramachandran and Hirstein, 1998; Melzack, 1990; Melzack, 1971, see also James, 1890, p 39), where joint sensory receptors and activating muscles are maximally responsive. This stereotyped posture is interpreted by Melzack as an expression of an adaptive evolutionary 'factory setting' of the optimal body position – like that of a "wrestler or knife fighter" (Melzack, 1972 p 273). This posture confers maximum motor responsivity on the animal, with obvious 'fight or flight' survival value.

The genetic basis of the neuromatrix and, by extension, the perception of the body, is supported by the reports of phantoms in amelia or phocomelia (congenital absence of, or defect in, a limb respectively – see Gallagher *et al.* (1998) for neurodevelopmental hypotheses of their origin; Berlucchi and Aglioti, 1997; Melzack *et al.*, 1997; Saadah and Melzack, 1994; Lacroix *et al.*, 1992; Poeck, 1964; Weinstein *et al.*, 1964; Weinstein and Sersen, 1961), and in young children (Ramachandran and Hirstein, 1998; Flor *et al.*, 1998; Simmel, 1962, 1961, 1956) who, according to various authors (Riese and Bruck, 1950; Pick, 1915; Head and Holmes, 1911), would not have had sufficient experience of the body part in order for post-amputation phantoms to emerge. Several authors have failed to find phantoms in amelics (Montoya *et al.*, 1998; Flor *et al.*, 1998), or doubt that the reported experiences are *bona fide* phantoms (Skoyles, 1990; Simmel, 1964, 1961). Such phantoms may be more transitory than in adult traumatic amputees (Scatena, 1990), and the issue of amelic phantoms is still controversial (Montoya *et al.*, 1998).

Melzack does not claim that the body image is entirely genetically determined (Saadah and Melzack, 1994), and has also researched 'somatosensory memories' in which the position or state of the pre-amputation body part is retained, 'imprinted' in the phantom (Melzack *et al.*, 1997; see Katz and Melzack, 1990 for a review and detailed account; Simmel, 1956). Thus, corns may still be felt on phantom feet, and rings on phantom fingers. One patient felt blood trickling down his phantom arm (Katz and Melzack, 1990). Before the amputation, one patient had arthritic 'flare-ups' in cold, damp weather conditions; the phantom responded similarly pot-amputation (Ramachandran and Rogers-Ramachandran, 1996).

Melzack's position, then, is that the neuromatrix can account for many phantom phenomena, but that the system is to a certain extent plastic, especially for pain-related 'memories.'

The reorganisation hypothesis

Ramachandran and co-workers (1998, 1996, 1994) offered an alternative hypothesis. They maintained that the perception of the body is more plastic than allowed by Melzack's genetic pre-wiring. Within anatomical limits (e.g. of thalamocortical neural arborisation) the body representations are dynamic, modality-specific and experientially modifiable. Ramachandran asserts that phantom limbs arise following the 'invasion' of deafferented cortex by adjacent body representations. This is supported by the presence of ectopic representations as described above (3.1.2), and the large body of evidence on cortical reorganisation in primates (see 3.2.1 below).

The re-mapping hypothesis is different from, but not inconsistent with, Melzack's neuromatrix (Ramachandran 1994). The important difference between the theories is that Melzack believes phantoms are an *expression* of the inbuilt neuromatrix, whereas Ramachandran suggests they result from cortical *reorganisation*. Melzack's view implies a certain genetic determinism to the perception of the body, which is not unreasonable given the relative stability of the gross physical form throughout our phylogeny (*Homo sapiens* has always had two arms, two legs, and a short tail, for example). Ramachandran, on the other hand, believes that the experience of the body is a temporary, dynamic and therefore relatively manipulable, *construction*, maintained in real time. This view would tend to stress the ontogeny of *Homo sapiens*' body image – the ability to adapt to growth, injury, tool use, and bodily adornments dynamically, without literally tripping over your own feet. More will be said about these aspects below (4).

A recent review (Ramachandran and Hirstein, 1998) adopts a more interactionist approach to the experience of the body. These authors suggested that phantom phenomena (and the body image) arise through the interaction of five or more neural sources: stump neuromas; cortical remapping; corollary motor discharge monitoring; a primordial genetic body image; and vivid somaesthetic memories of previous postural, anatomical or physiological states. Discrepancies and mismatches between these various components lead in some cases to supernumerary phantoms, and in others to perceptions of impossible bodily configurations (see 3.2.2 below).

3.2 Evidence from empirical investigation

3.2.1 Somatotopic reorganisation

The literature on experimentally induced cortical reorganisation in animals[2] is vast. The reader is referred to several reviews dealing more thoroughly with this research (Killackey *et al*., 1995; Kaas, 1991; Merzenich *et al*., 1988; Wall, 1988; Merzenich and Kaas, 1982). A summary is provided below.

Before 1991, the limit for cortical reorganisation[3] was thought to be set by the extent of thalamocortical arborisation, at 1-2 mm medio-laterally (Lund *et al*., 1994; Pons *et al*., 1991; e.g. Kaas, 1991; Rakic and Singer, 1988; Merzenich *et al*., 1984; Merzenich and Kaas, 1982). Pons and co-workers (1991) reported on the 'Silver Spring Monkeys,' who had undergone upper limb deafferentation 12 years previously and displayed "massive reorganisation" over 10 to 14 mm of somatosensory cortex (see Figure 5, below).
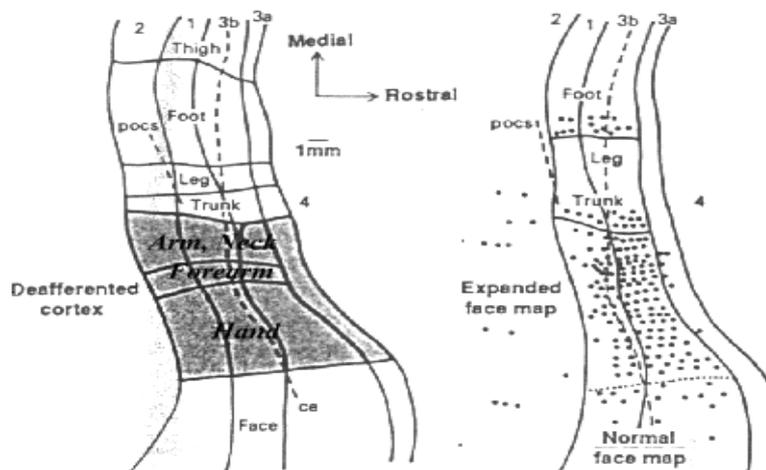
Figure 5. Cortical reorganisation over 10 to 14 mm in cynomulgous monkey post-central gyrus. Over a period of 12 years, the deafferented region of cortex (shaded region of the left map, containing representations of the hand, forearm, arm, and neck) became responsive to stimulation of the face and trunk. Insulated microelectrodes were passed through the post-central gyrus cortex at 0.75mm spatial separation. Body sites were stimulated tactually, and electrical activity was recorded in the tip of the microelectrode. Lines in both maps represent borders between representations (transverse lines), and between cytoarchitectonic fields (vertical lines). Numbers denote cytoarchitectonic fields according to Brodmann's classification. Dots in the right hand map indicate recording sites respondive to stimulation of the appropriate body part, as indicated by the expanded representations of face and trunk. Adapted from Pons *et al*., (1991).

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[2] Two animal models are dominant in this research – the representation of the digits and glabrous skin of the primate hand, and the barrel-field representation of the rodent vibrissae.

[3] As defined above (3.1.2); where a cortical locus previously responsive to stimulation of the (now deafferented) body part, becomes responsive to stimuli from a body part with an adjacent cortical representation.

Other researchers have since found functional reorganisation of 5 mm in macaques (Florence and Kaas, 1995; Lund *et al*., 1994), and of up to 4 cm in humans (see Table 1, above), though Schady and co-workers (1994) question the extent and functional significance of experimentally-induced changes in central neuronal responsivity.

Two hypotheses have been put forward to explain cortical functional reorganisation. *The 'unmasking' hypothesis* (e.g. Borsook *et al*., 1998; Pascal-Leone and Torres, 1993; Ramachandran *et al*., 1992; Smits *et al*., 1991; Merzenich *et al*., 1988, 1984; Merzenich and Kaas, 1982; Wall, 1977) suggests that recruitment of adjacent neurons occurs following deafferention. This implies that there are latent connectivity patterns (normally held below threshold by lateral inhibition[4]), which are sufficient for functional reorganisation over large cortical distances. Unmasking of existing pathways by release from inhibition is supported by evidence from acute experimental reorganisation, for example Calford and Tweedale (1988), who demonstrated functional reorganisation immediately following surgical amputation of a digit, and Rossini and co-workers (1994), who showed anaesthesia-induced shifts in human finger representations. Such reorganisation (see also Borsook *et al*., 1998; Kaas *et al*., 1990) is so rapid that it "undoubtedly reflect[s] changes in the effectiveness of pre-existing pathways." (Merzenich and Kaas, 1982, p 436).

The 'sprouting' hypothesis can account for reorganisation occurring beyond the extent of thalamocortical arborisation, and for longer-term changes (e.g. Florence and Kaas, 1995). Through new axonal and synaptic growth, deafferented neurons become responsive to stimuli outside their original receptive fields. This process takes longer than unmasking, and is unlikely to be effective for at least 4 weeks following deafferention (Ramachandran, 1992).

It is likely that cortical reorganisation involves both unmasking and sprouting (Elbert *et al*., 1997; Flor *et al*., 1995; Florence and Kaas, 1995; Aglioti *et al*., 1994; Calford and Tweedale, 1988; Merzenich and Kaas, 1982), but may also reflect subcortical reorganisation at spinal, brainstem, or thalamic levels (Kaas, 1998; Florence and Kaas, 1995; Pons, 1992; Kaas, 1991; Pons *et al*., 1991; Wall, 1988; Pearson *et al*., 1987; Merzenich *et al*., 1984; Merzenich and Kaas, 1982; Devor and Wall, 1978). Sub-cortical

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[4] which serves to sharpen receptive fields (Calford and Tweedale, 1988).

stimulation and recording investigations in humans are difficult, but a recent report using functional stereotactic mapping suggests that some thalamic reorganisation occurs in amputees with phantom pain[5] (Davis *et al.*, 1998).

3.2.2 Proprioceptive manipulation

> Proprioception is the inner sense by which the body is aware of itself. (Oliver Sacks, 1995, p X)

Cole's (1995) patient Ian Waterman vividly demonstrates the importance of proprioception in the maintenance of posture, balance and movement. This unfortunate but courageous man lost all proprioception subserved by large diameter, rapid-conduction afferents[6]; only pain and temperature sensation was preserved. The (temporary) functional consequence of this loss was a near-complete paralysis, yet "he consider[ed] his body image quite normal" (Cole, 1995, p 136). Similarly, in children with high and complete spina-bifida, tactile and proprioceptive input is not necessary for the derivation of an 'image' of the insensate body (Robinson *et al.*, 1986). How, then, does proprioception contribute to the neural representation of the body?

Several reports of experimental proprioceptive manipulations, and their effects on the perception of the body are available (e.g. Lackner and Levine, 1979; Goodwin *et al.*, 1972a, b) and make scintillating reading. The results of several studies (Lackner 1988; Lackner and Taublieb, 1984; Craske, 1977, see also Ramachandran and Hirstein, 1999, 1998) have a striking implication: that *we can perceive anatomically impossible body positions* given the appropriate input.

When a vibrating stimulus is applied to a muscle or tendon, mechanoreceptors (primarily muscle spindles, but also Golgi tendon organs and secondary spindle endings, Goodwin *et al.*, 1972a, b) are stimulated, and action potential frequency in the Ia-afferents serving the muscle increases. Normally, this signal is 'interpreted' by the CNS as an increase in muscle stretch resulting from limb motion, and involuntary compensatory movements via α-motoneurone reflex pathways (the tonic vibration reflex (TVR); Lackner, 1984; Lackner and Levine, 1979; Craske, 1977; Goodwin *et al.*, 1972b) are initiated. If a

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[5] Recall that phantom pain is strongly positively correlated with extent of cortical reorganisation (3.1.2).
[6] This form of sensory loss also occurs in tabes dorsalis (tabetic neurosyphilis), resulting in inability to maintain balance when denied vision (Lackner and Levine, 1979).

blindfolded subject's TVR-induced limb motion is restrained, illusory, apparent motion (extension or flexion) will be felt. Prolonged vibration may cause the subject to feel a wrist hyperextend up to 50º beyond normal anatomical limits, or the hand may be perceived to be "going through [the] shoulder" (Craske, 1977, p 73).

Lackner (1988) vibrated either the biceps, triceps, or one of various leg muscles of blindfolded subjects in 10 postural configurations. After 10 or 20 seconds, bizarre perceptual phenomena were reported. When subjects grasped their nose and received biceps vibration to the same arm, for example, the nose would be felt to 'grow' up to 30cm in length (the so-called 'Pinocchio effect' – Brady, 1999, personal communication, see also Ramachandran and Hirstein, 1999, 1998). Similarly, when the triceps muscle of an arm with its hand held on the head was vibrated, the hand was felt to submerge into the cavity of the head! The skin was felt to remain intact, the skull concaved, yet no pain was perceived[7].

The perceptions vary considerably between individuals – verbal interpretations include a 'heaviness', 'flickering up and down', a 'multiple image' of the arm, or that it was in two places at once, while others report a break or bend in the arm (Craske, 1977). Cody (1999, personal communication) notes that the Pinocchio effect is difficult to produce in the laboratory – subjects often experience a leaning or tilting of the head, rather than an extended nose. Lackner's (1988) subjects showed diverse responses – one reported no bizarre perceptions over all ten manipulations, others experienced various quantitative or qualitative variations on the conceivable 'interpretations' of the mismatched inputs, and some reported dissociations between perceived movement and position.

What is remarkable about these findings, is that they seem to suggest that the brain has the latent capacity to represent perceptually, anatomical situations that could not have arisen either in phylogenetic or ontogenetic experience. The hand could never have been perceived actually to be *inside* the volume of the head, or the nose to be 30cm long. How, then, can such a perception be instantiated in the CNS? Craske (1977) suggests a mechanism that relies on at least two sensory input modalities, and an extrapolative system that requires experiential calibration, based on joint motion. A speculative explanation will also be offered below (4.1).

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[7] Craske reports that although no pain is felt, "subjects displayed the overt signs which often accompany pain, such as writhing, sweating and gasping." (1977, p 73).

If additional inputs (vestibular, skin, joint, or visual) do not correlate with the apparent motion-inducing inputs, the latter may be overridden and the system[8] will relax into a coherent and meaningful interpretation. When aberrant input is sufficient for impossible perceptions, the system will relax into a meaningful, synergistic, but impossible interpretation; the perceived position of the hand, nose, and head, and the hand-nose contact, for example, may be combined into the coherent but impossible perception of an extended nose (Lackner, 1988).

Lackner and Taublieb (1984) manipulated the visual input in vibration-induced apparent limb motion experiments. They showed a dissociation between felt and seen positions of the hand or finger in a well-lit room, often to the point of producing proprioceptive perceptions of anatomically impossible configurations. In a dark room with a phosphorescent-painted finger or hand, however, the visually-fixated extremity was *actually seen* to move with the apparent motion of the limb, despite eye-movement recordings showing no appreciable movement compared to unseen extremity conditions (see also Lackner and Levine, 1979 for whole-body apparent motion – the so-called 'proprio-gyral illusion').

Lackner and Taublieb (1984) suggested a reciprocal relationship between the importance of vision and muscle afferents under varying conditions of visibility, and questioned the well-accepted primacy of vision under certain conditions. They conclude:

> It seems unlikely… on the basis of the findings reported here that the position of the body can be coded solely in the activity patterns of [thalamic and cortical] somatotopic maps; instead, reference and correlation with other afferent domains also seems to be involved… [the perception of anatomically impossible limb positions] points to the multi-modal nature of position sense representation. (1984, p 104 – 105)

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[8] By system is meant whatever neurofunctional system(s) subserves the representation and perception of the body.

4   Synthesis

From consideration of the evidence cited above, several general conclusions can be drawn about the representation of the body. These conclusions are set out below, and further evidence is adduced in their support.

I.   The representations are multimodal and distributed

The body is represented in multiple modalities and sub-modalities, widely distributed in the brain. All submodalities of somatosensation are represented in phantoms. Some phantoms are *actually seen* (Berlucchi and Aglioti, 1997; Halligan and Marshall, 1995), although there are no reports of phantoms being heard[9] or smelt! Ramachandran and co-workers (1996, 1995; Ramachandran, 1994) showed that seeing the reflection of an intact arm in a mirror positioned along the midline of the body gave phantom arms an immediate and striking reality. Touching the intact hand produced an identical sensation in the phantom, while pain and paralysis could be relieved and telescoping induced. Moreover, looking at the flexing fingers of the experimenters' upturned gloved right hand (in place of the downturned phantom left hand) could induce feelings of (anatomically impossible) hyperextension of the phantom fingers (Ramachandran and Rogers-Ramachandran, 1996)!

Research has focused on the multiple somatosensory maps of the post-central gyrus (areas, 3b, 3a, 1, 2; Kaas, 1991; Mountcastle, 1988; Kaas *et al.*, 1979), but there are somatosensory maps in other parts of the CNS. Spinal (Devor and Wall, 1978), midbrain (Soper and Melzack, 1982), thalamic (Penfield and Jasper, 1954), and insular cortical (Bonda *et al.*, 1995; Schneider *et al.*, 1993) maps have been shown, and somatosensory information is widely distributed throughout the brain (Wall, 1988).

Parietal areas are strongly implicated in body-representations (Bonda *et al.*, 1996, 1995), and inter-hemispheric transfer of somatosensory information occurs (Franz and Ramachandran, 1998; Knecht *et al.*, 1996, 1995; Ramachandran and Rogers-Ramachandran, 1996, 1995; Iwamura *et al.*, 1994; Calford and Tweedale, 1990).

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[9] I wrote to Professor Ramachandran to ask whether a phantom arm patient who 'clapped' his intact with his phantom hand would hear a phantom clapping. At the time of writing no reply had been received.

II.   The representations are constrained

Genetic and anatomical factors constrain representational plasticity. Coarse topography is apparent in thalamocortical projections in the absence of peripheral stimulation during cortical map development (Killackey *et al*., 1995; Kaas, 1988). Functional reorganisation and referred sensation in amputees is limited to areas of adjacent cortical representation, and often by the limits set by thalamocortical arborisation. Following extensive deafferentation or regeneration after nerve damage, reorganisation is incomplete, and areas of 'silent' cortex remain (Jain and Catania, 1997; Kaas, 1991; Kaas *et al*., 1990; Merzenich *et al*., 1988, 1984).

III.   The representations are dynamic

Cortical somatotopography is developed and maintained dynamically, operating on principles consistent with neuronal group selection (Knecht *et al*., 1998; Elbert *et al*., 1997; Wang *et al*., 1995; Braune and Schady, 1993; Pascal-Leone and Torres, 1993; Merzenich *et al*., 1988, 1984; von der Malsberg and Singer, 1988; Pearson *et al*., 1987). The body is maintained in a continuous interactive relation with the external world (Bonda *et al*., 1995) and with itself. Mechanisms of plasticity (sprouting and unmasking) operate over various time scales (Calford and Tweedale, 1990, 1988; Wall, 1988), and "any given skin surface can be represented by many alternative functional maps at different times in life" (Merzenich *et al*., 1984, p 592).

IV.   The representations are use-dependent

Representations reflect use and importance of body parts. Cortical representation size decreases following deafferentation, and is increased in the Braille reading finger (Pascal-Leone and Torres, 1993), in the contralateral hand following amputation (Elbert *et al*., 1997), in the fingering hand of string players (Elbert *et al*., 1995), and following differential heavy stimulation of the receptor sheet (Merzenich *et al*., 1988).

V.   The representations are co-incident

Representations are based on co-incident and co-variant input. Synchronous stimulation or surgical fusion of adjacent digits results in neurons developing receptive fields across areas defined by co-incident stimulation, rather than anatomical distinction (Wang *et al*., 1995; Clark *et al*., 1988; Merzenich *et al*., 1988). Similarly, separation of syndactyl fingers leads to a division of the syndactyl representation, and the emergence of two separate finger representations (Mogilner *et al*., 1993).

The importance of correlated, co-incident input for the body image is vividly demonstrated by some recent experiments (Ramachandran and Hirstein, 1999, 1998). In the first experiment, two subjects are seated one behind the other. The experimenter takes the rear subject's finger, and uses it to pseudo-randomly tap the nose of the front subject, while tapping the rear subject's nose with his own finger in perfect synchrony. With eyes closed, the rear subject soon feels that, despite his arm being extended over 50 cm from his face, he is tapping his own nose, which feels elongated, dislocated, or duplicated[10].

Similarly, another experiment uses a screen to shield the subject's hand, which is placed on a table. The experimenter then taps the concealed hand in perfect synchrony with a dummy hand which protrudes from the screen in view of the subject. The illusion of an extended arm can be produced by this synchronous tapping (see also Ramachandran and Hirstein, 1999 for an illusion of decapitation and telekinesis!).

These experiments suggest that the brain functions as a correlation detector (see also Cynader *et al*., 1988), and may do so more efficiently within an organised topography (Stryker *et al*., 1988). If two inputs are sufficiently correlated in time and space, then it is parsimonious that they are associated and represented as a single entity. Conversely, uncorrelated inputs may be differentiated, and contrasts enhanced.

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[10] Initial experiments by the present author have confirmed the phenomenon – at first, two distinct percepts are experienced, but soon, the unmistakable feeling of touching your own nose is produced.

4.1 A geometrical analysis?

Can the representation of the body be modelled? What kind of system could allow multi-modal, distributed, constrained, dynamic, use-dependent, and co-incident representations? Importantly, what kind of system could allow the representation and perception of impossible anatomical configurations?

The Churchlands (PM Churchland, 1986; PS Churchland, 1986) propose a general model for sensory-motor integration in multi-modal, massively parallel laminar cerebral cortex, which may also be implemented in the superior colliculus (see also Knudsen *et al*., 1987). If the brain *represents* by means of positions in abstract two-dimensional co-ordinate frames, instantiated in the nervous system by a physical, neural grid or network, and *computes* via fast, direct connections between positions in these frames, then some complex computational problems become relatively simple. Figure 6 presents a model of the sensory-motor integration problem based on Churchland (1986).
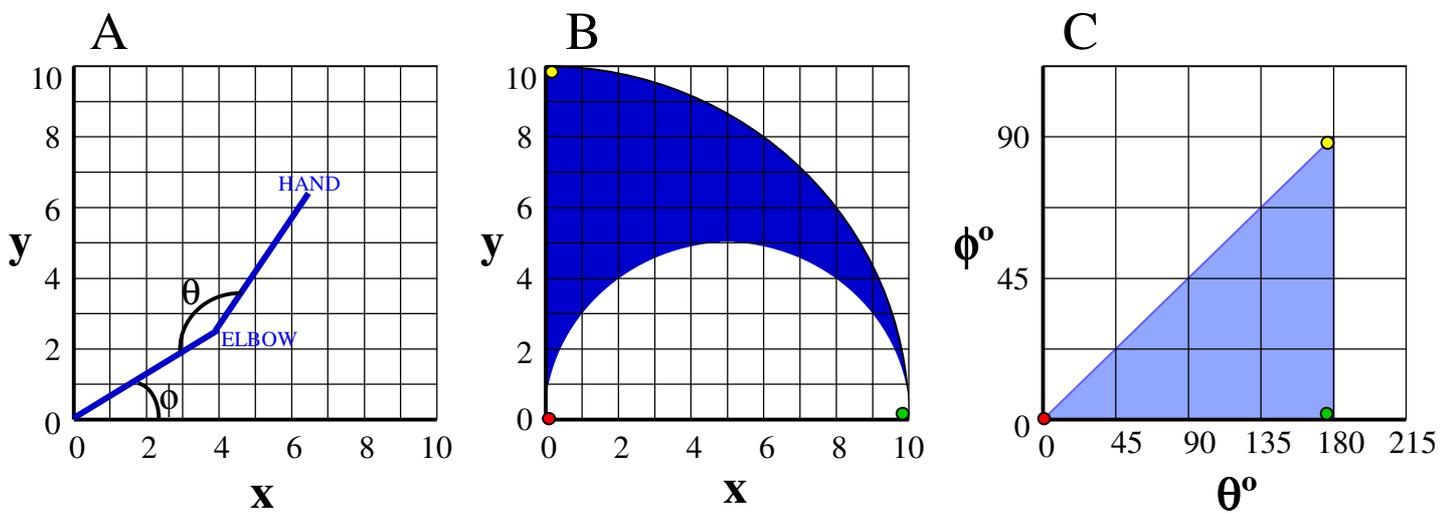
Figure 6. Hypothetical two-joint arm movement in visual and proprioceptive space. **A**. The arm, as seen in visual (x, y) space by a distant, fixed, cyclopean eye, consists of two segments (upper and lower arms), attached at one end (the shoulder). The upper arm forms the angle ϕ with the visual x-axis, and the lower arm forms the angle θ with the upper arm. A fixed hand is attached at the end of the lower arm. The arm is free to move in the two dimensions of visual space, under the constraints ($0^\circ \leq \phi \leq 90^\circ$; $0^\circ \leq \theta \leq 180^\circ$). **B**. The shaded area is the area of visual space within which a target can be reached by the moving hand. **C**. The shaded area represents the area in B in terms of 'proprioceptive' (ϕ, θ) co-ordinate space. Coloured dots denote corresponding points in visual and proprioceptive space.

Each of the quantities (x, y, ϕ, θ) are scalar, and refer to one dimension of visual or proprioceptive co-ordinate space. Visual dimensions are the familiar left-right (x) and up-

down (y) dimensions, while proprioceptive dimensions relate to ϕ and θ joint angles (coded by the CNS, for example, as a ratio of agonist to antagonist muscle contraction or muscle spindle activation[11]). Correspondence between proprioceptive and target visual positions may be implemented directly, see Figure 7, below.
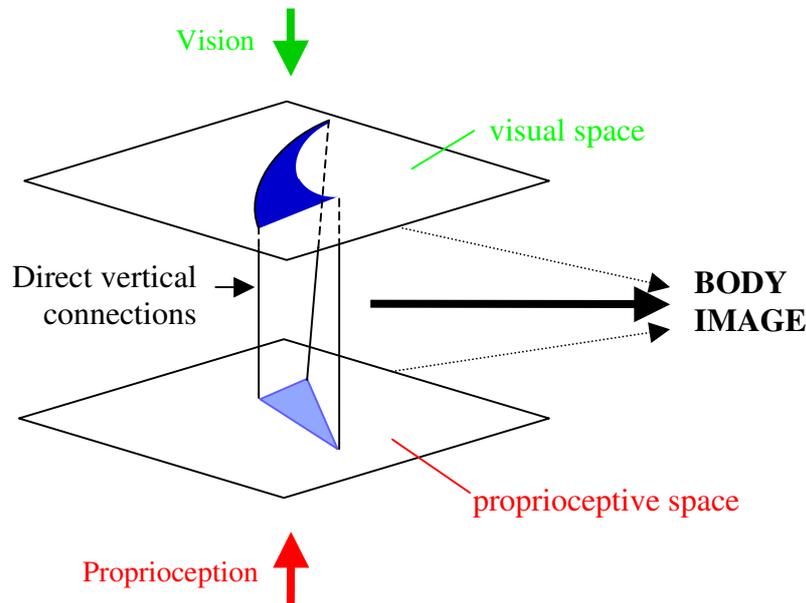
Figure 7. Correspondence between visual and proprioceptive spaces is directly instantiated by vertical connections. The upper space represents locations in two-dimensional visual space, while the lower, proprioceptive space, represents limb position in two-dimensional joint-angle space. Visual input enters the space from above, and proprioceptive input from below. Possible hand-spaces are shown in the shaded geometrical shapes (see Figure 6B, C) Direct vertical connections between the visual and proprioceptive spaces effect co-ordinate transformations between spaces. The combined activation of visual and proprioceptive representations, or of either representation alone, may be sufficient for the perception of the body. Original model, based on PM Churchland (1986) and PS Churchland (1986).

In terms of the whole brain, multiple modalities and sub-modalities of body representation, and vast parallel interconnection of corresponding positions in sensory spaces would be involved. This scheme would be consistent with Melzack's distributed neuromatrix, and may help to pin down the finer points of corporeal representation. How might the evidence given above be explained?

Phantom phenomena

If such an integrative system encompasses multiple modalities of representation, then it is conceivable that activity in one modality may be sufficient to produce the perception of the (phantom) body, or of somatosensory memories (Katz and Melzack, 1990) despite little sensory activity in other modalities. Visual input concerning prosthetic limbs may activate the corresponding portions of proprioceptive and tactile space, and the prosthesis

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[11] Bizzi (1988) suggests the CNS may code for posture most simply in the scalar ratio of agonist to antagonist forces.

may feel 'fleshed out'. Similarly, hyperexcitability of spinal, thalamic, or cortical cells, or increased peripheral 'noise' following traumatic deafferentation (Flor *et al*, 1998) may activate representations in many submodalities and be imprinted as phantoms (Kew *et al*., 1994).

Organisation and reorganisation

Connections between positions in sensory, motor, and computational spaces (state spaces) may be established by correlated and co-variant input, according to simple Hebbian synaptic rules. Incorporation of wide-branching lateral connections, with extensive lateral inhibition (as is common in cerebral cortex), will allow only those neurons that respond maximally to both representational dimensions to represent positions in state spaces. Following deafferentation or selective strengthening of synapses, the dynamic inhibitory balance will alter, and allow neurons to acquire new functional receptive fields.

Impossible perceptions

With limb position coded by combinations of scalar quantities, manipulation of these quantities might produce perceptions of anatomically impossible limb positions. In the absence of visual input, it may be possible to activate portions of the abstract proprioceptive space that would otherwise be 'impossible' – the brain "[derives] position information by extrapolating from the previously calibrated position domain." (Craske, 1977, p 73).

Into hyperspace?

These hypothetical situations may be modelled relatively easily by a two-dimensional model, but real situations are immeasurably more complex. Many natural co-ordinate systems are multi dimensional – for example gaze direction may best be modelled in 6 dimensions, corresponding to each of the extra-ocular muscles controlling eye position. Discussion of multidimensional systems is beyond the scope of the current review, but the representation and transformation of positions in and between state spaces may be taken as a general feature of brain function. Cerebellar cortex may carry out higher-dimensional 'matrix multiplications' in more complex sensory-motor integrations (PM and PS Churchland, 1986). This possibility may best be modelled by Tensor Network Theory (Pellionisz and Llinás, 1979).

4.2   What the little man does

> The central nervous system had from its beginning the main function of *steering* or *piloting* the moving organism. A knowledge of its location (the location of the body image) relative to the biologically most relevant aspects of the environment is a crucial prerequisite of this piloting function (Popper and Eccles, *The Self and Its Brain*, 1977, p 129)

Figure 8. Combined sensory and motor homunculus, adapted from Penfield and Boldrey, 1937

In piloting the organism through the environment, the little man (see Figure 8, above) must co-ordinate many facets of the interior and exterior world. He must learn which combinations of anatomical positions and visual locations correspond to each other, and account for changes in these correspondences over time – perhaps by detecting correlation and covariance (see Kuperstein's, 1988 model of hand-eye co-ordination). He must learn how to reach unseen portions of the world, to grope in the dark, or scratch his head – perhaps by a dynamic proprioceptive system. He may find some movements and portions of the sensed world more useful and important than others – perhaps he should delegate more cortical resources for these functions (see Knudsen *et al*., 1987), and perhaps some are innately pre-wired (e.g. the hand-mouth co-ordination of infants and neonates; Gallagher *et al*., 1998).

The direct association of sensory and motor spaces by means of multimodal topographic or abstract computational maps may simplify the pilot's job, though at a price. Inter-modal discrepancies may arise when one modality is inhibited, becomes unreliable, or signals discordant information. The pilot's job, then, is like that of a general, co-ordinating information about the battlefield from many scouts, trying "to arrive at the

most probable and globally consistent interpretation of the evidence derived from multiple sources" (Ramachandran, 1994, p 325).

The little man-pilot-general might represent the body most effectively as a 'best fit,' based on all the information available to him. Congruent, consistent information is enhanced and integrated. Incongruent, inconsistent information may ether be ignored or transformed and incorporated into the current working body schema. Such multi-modal, dynamic integration is no easy task, even with a brain the size of ours. My final example from a woman with anosognosia graphically demonstrates this complexity!

> When she was being tested for apraxia, the left hand grasped the right hand performing a task. She tried to let the right hand go to no avail. Then she started talking towards the left hand, "Grandma, would you please let me go. You are warm, but my hand is sweating and uneasy" (Nagumo and Yamadori, 1995, p 549)

4.3   What further questions should we ask him?

Several lines of research are especially interesting, such as Ramachandran and Hirstein's recent experiments. Further investigation of such dynamic inter-modal phenomena in normal individuals may tell us much about the general function of the brain as a sensory-motor co-ordinator, and more specifically about the representation of the body.

Iriki and co-workers (1996) discovered neurons in the caudal post-central gyrus of macaque monkeys whose hand-centred visual receptive fields elongated to encompass a tool as it was being used! It would be fascinating to know how such cells respond in Ramachandran's recent experiments and in phantoms that telescope or 'flesh out' with prostheses.

Finally, studying the interaction of the body schema with 'higher' attentional mechanisms may prove fruitful. Directing attention to a specific body part may facilitate localisation of stimuli applied to that part (O'Boyle, ongoing research), and body part-specific expectation of analgesia has been shown selectively to activate opioids within the somatotopic representation of that body part (Benedetti *et al*., 1999). Phantoms become more salient when attended to (Melzack *et al*., 1997), and central attentional gradients may explain two-point discrimination differences between equally innervated regions of skin (Braune and Schady, 1993).

5   Acknowledgements

6   References

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