The study of phantom limbs has received tremendous impetus from recent studies linking changes in cortical topography with perceptual experience. Systematic psychophysical testing and functional imaging studies on patients with phantom limbs provide 2 unique opportunities. First, they allow us to demonstrate neural plasticity in the adult human brain. Second, by tracking perceptual changes (such as referred sensations) and changes in cortical topography in individual patients, we can begin to explore how the activity of sensory maps gives rise to conscious experience. Finally, phantom limbs also allow us to explore intersensory effects and the manner in which the brain constructs and updates a “body image” throughout life.

The phenomenon of phantom limbs has been known since antiquity and has always been shrouded in mystery. After Lord Nelson lost his right arm during an attack on Santa Cruz de Tenerife, he experienced compelling phantom limb pain, including the strange sensation of fingers digging into his phantom palm. The emergence of these ghostly sensations led the Sea Lord to proclaim that he now had “direct proof” for the existence of the soul. For if an arm can survive physical annihilation, why not the whole person?

The first clear clinical description of phantom limbs was by Silas Weir Mitchell in 1872 (see review by Melzack). Although there have been hundreds of case studies since that time, systematic experimental work began only 7 years ago, inspired in part by the demonstration of striking changes in somatotopic maps following deafferentation. Pons et al demonstrated that 11 years after dorsal rhizotomy in adult monkeys, the region corresponding to the hand in the cortical somatotopic map, area 3b, can be activated by stimuli delivered to the monkey’s ipsilateral face—direct evidence that a massive reorganization of topography had occurred in area 3b. That a similar reorganization occurs in the adult human cortex over distances of 2 to 3 cm was first shown by our group using magnetoencephalography (Figure 1). After amputation of an arm, sensory input from the face begins to activate the hand area of the Penfield homunculus in cortical area S1.

Given this massive reorganization, what would the person feel if his face were touched? Since the stimulus now activates the hand area of the cortex, would the person feel that he was being touched on his hand as well?

REFERRED SENSATIONS IN PHANTOM LIMBS

We tested 18 patients with either arm amputation or brachial avulsion, and found that 8 patients systematically referred sensation from the face to the phantom limb. In many of them, there was a topographically organized map of the hand on the lower face region (Figure 2) and the referred sensations were modality specific. For example, hot, cold, vibration, rubbing, metal, or massage are felt as hot, cold, vibration, rubbing, metal, and massage at precisely localized points on the phantom limb. Points on other parts of the body were usually ineffective in eliciting referred sensations in the phantom limb, but there was often a second topographically organized map proximal to the am-
Our results suggest, instead, that referred sen-
to stump neuromas or to activation of a “diffuse neural
and the referred sensations were often attributed either
to track the time course of perceptual changes in hu-
man subjects. We have recently seen at least one pa-
tient in whom this prediction was confirmed. He had a left
cerebrovascular accident and clearly referred sensations
from normal skin to the deafferented zones on his right
arm. Referral usually occurred from the adjacent normal
skin but also occasionally from the ipsilateral leg (Eric
Altschuler, MD, and V.S.R., unpublished observations,
1998). The reason for this is obscure but may be related
to the fact that in S2 cortex, the foot representation is right
next to the arm and deafferentation of cortex correspond-
ing to the arm in S1 may lead to a reorganization in S2 so
that leg stimulation begins to activate arm cortex. These
conjectures are important because they would imply that
reorganization can occur even in the adult human cortex
analogous to what is seen after S1 lesions in monkeys or
after limb amputation in humans.

SYNESTHESIA

Some patients claim that they can experience vivid vol-
tary movements in their phantom limb, presumably
because reafference signals from motor commands sent
to the phantom limb are monitored in the cerebellum and
parietal lobes. However, over time, the phantom limb be-
comes “frozen” or “paralyzed,” perhaps because of a con-
tinuous absence of visual and proprioceptive confirma-
tion that the commands have been obeyed. Some patients
experience excruciatingly painful involuntary clenching
spasms in the phantom limb; they experience their
nails digging into their phantom palm and are unable to
open the hand voluntarily to relieve the pain.

In our studies, we placed a midvertical sagittal mir-
ror on the table in front of the patient. If the patient's
paralyzed phantom limb was, say, on the left side of the
mirror, he placed his right hand in an exact mirror-
symmetric location on the right side of the mirror
(Figure 3). If he looked into the shiny right side of the

Figure 1. Changes in cortical topography in S1 revealed by
topography stump. Since the hand area in the Penfield map
is flanked on one side by the upper arm and the other
side by the face, this is precisely the arrangement of points
that one would expect if the afferents from the upper arm
skin and face skin were to invade the hand territory from
either side.

The fact that stimulating certain trigger points near
the stump, or sometimes remote from the stump, can elicit
referred sensation in the phantom limb has been noted
before in the older clinical literature, but the oc-
currence of a topographically organized map on the face
and modality-specific referral from face to phantom limb
has not been described. Consequently, no attempt was
made to relate these findings to somatotopic brain maps,
and the referred sensations were often attributed either
to stump neuromas or to activation of a “diffuse neural
matrix.” Our results suggest, instead, that referred sen-
sations emerge as a direct consequence of the changes
in topography following deafferentation—an idea that we
refer to as “the remapping hypothesis.”

Based on the remapping hypothesis, we also pre-
dicted that after trigeminal nerve section, one should
observe a map of the face on the hand, and this has been
confirmed in a study by Clarke et al. Also, after ampu-
tation of the index finger in one patient, a map of the in-
dex finger was found neatly draped across the ipsilat-
eral cheek. Finally, our suggestion that these effects are
based partly on unmasking of preexisting connections
rather than sprouting receives support from our recent
observation that modality-specific referral from the face
to the phantom limb can occur even a few hours after
amputation.

Taken collectively, these findings provide strong sup-
port for the remapping hypothesis. They may allow us
to track the time course of perceptual changes in hu-
mans and relate these in a systematic way to anatomy.
The occurrence of topography and modality specificity
rules out any possibility of the referral being due to non-
specific arousal.

Finally, we predicted that if the remapping were at
least partly cortical (rather than thalamic), then after de-
afferentation caused by central white matter lesions, one
should observe sensations by referral from normal skin ar-
as to the deafferented zones. For instance, if a stroke pro-
duces partial sensory loss, touching the spared “islands”
of normal skin should evoke sensations referred to the de-
afferented regions. We have recently seen at least one pa-
tient in whom this prediction was confirmed. He had a left
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Figure 2. Points on the face of a patient that elicit precisely localized,
modality-specific referral in the phantom limb 4 weeks after amputation of
the left arm below the elbow. Sensations were felt simultaneously on the face
and phantom limb.
mirror, the reflection of his own right hand is optically superimposed on the felt location of his phantom limb so that he has the distinct visual illusion that the phantom limb had been resurrected. If he now made mirror-symmetric movements while looking in the mirror, he received visual feedback that the phantom limb was obeying his command.

Remarkably, 6 of 10 patients using this procedure claimed that they could now actually feel—not merely see—movements emerging in the phantom limb. This was often a source of considerable surprise and delight to the patient.18

Indeed, 4 patients were able to use the visual feedback provided to them by the mirror to “unclench” a painfully clenched phantom hand and this seemed to relieve the clenching spasm, as well as associated cramping pain (the burning and lancinating pains in the phantom limb remained unaffected by the mirror procedure, suggesting that the relief of the clenching was probably not confabulatory in origin). The elimination of the spasm is a robust effect that was confirmed in several patients. Patients reported the elimination of the associated pain but this requires confirmation with double-blind control subjects, given the notorious susceptibility of pain to placebo and suggestion. In one patient, repeated use with the mirror for 2 weeks resulted in a permanent and complete disappearance of the phantom arm and elbow (and a “telescoping” of fingers into the stump) for the first time in 10 years. The associated pain in the elbow and wrist also vanished. This may be the first known instance of a successful amputation of a phantom limb!

Visual Feedback for Other Neurological Syndromes?

Other syndromes such as focal dystonia, dyspraxia, and hemiparesis (following strokes) usually result from destruction of neural tissue but is it conceivable that there is a “learned paralysis” component to some of these disorders14? If so, can this component caused by a temporary neural inhibition or “block” be overcome by using a mirror? We are currently exploring these possibilities.

Reality of Phantom Limbs

We also studied intermanual “interference” in patients with phantom limbs. A person with intact limbs finds it very difficult to tap his head with one hand while making circular movements on his belly simultaneously with the other hand. We now find that if a patient with a “moveable” phantom limb (ie, one he can control volitionally) tries to produce dissimilar movements with his phantom limb and his real arm, he experiences a similar interference. But no interference occurs in a patient with a “paralyzed” phantom limb who simply imagines that he is moving his phantom limb.19 Thus, the interference must be of cortical origin and is not a result of feedback from the arm.

What Use is Plasticity?

Is the remapping that occurs in the adult somatosensory cortex beneficial to the organism? Or is it an “epi-phenomenon”—a manifestation, in the adult, of a process that is ordinarily expressed only in early brain development?

Since a larger amount of cortex is now devoted to the region proximal to the stump, would there be an improvement in tactile acuity in these regions? An early study by Teuber et al20 hinted at this possibility but further experiments are needed to confirm this. It would be especially interesting to see if such an improvement also occurs on the face skin ipsilateral to amputation. It seems likely that such improvement would occur more readily for tactile hyperacuity rather than 2-point discrimination. Also, perhaps such improvement would be seen only after the referred sensations have faded so that sensory stimulation on the face is felt only on the face.

PHANTOM LIMBS IN NONAMPUTATED INDIVIDUALS

Phantom limbs are not unique to amputees. Indeed, even in individuals with intact limbs, the body image is highly malleable; one can lengthen one’s nose, or even project one’s sensations onto external objects, such as Halloween masks, tables, and chairs merely by using appropriate patterns of tactile stimulation. For instance, if you watch the experimenter stroking a shoe or a table surface while he simultaneously, in perfect synchrony, strikes and taps your knee hidden from you under the table, you will experience the touch sensations as emerging from the shoe or table. If the experimenter then hits the shoe or table with a hammer, you will register a strong galvanic skin response, as though the object was now part...
of your body. But if the shoe (or table) and your hand are stimulated out of synchrony, no illusion occurs and no galvanic skin response is seen (so the response is not just due to startle).

CONCLUSIONS

The experiments on referred sensations in phantom limbs are important for 2 reasons: First, they suggest that, contrary to the static picture of brain maps provided by neuroanatomists, topography is extremely labile. Even in the adult brain, massive reorganization can occur over extremely short periods, and referred sensations can therefore be used as a “marker” for plasticity in the adult human brain. Second, the findings allow us to relate perceptual qualia (subjective sensations) to the activity of brain maps and to test some of the most widely accepted assumptions of sensory psychology and neurophysiology, such as Müller’s law of specific nerve energies, “pattern coding” vs “place coding” (ie, the notion that perception depends exclusively on which particular neuron fires rather than the overall pattern of activity), and, more generally, to understand how neural activity leads to conscious experience. For instance, after arm amputation, patients usually have dual sensations, ie, sensations are experienced in both the face and the hand, presumably because 2 separate points are activated on the cortical map. But after section of the fifth nerve, the patient felt the sensation only on the face when the hand was touched.15 Perhaps there is an initial “overshoot” during remapping so that the anomalous input from the hand to the face territory actually comes to dominate perception and masks or suppress the “real” sensation from the hand.

The experiments with mirrors have 3 implications. First, they may be clinically useful in alleviating abnormal postures and spasms in phantom limbs. Indeed, it is not inconceivable that even other neurological syndromes such as focal dystonias, dyspraxias, and hemipareses may be caused, at least in part, by a temporary “inhibition” of sorts and may therefore benefit from visual feedback provided by the mirror. Second, it suggests that the modular, hierarchical, “bucket brigade” model of the brain popularized by computer engineers needs to be replaced by a more dynamic view of the brain in which there is a tremendous amount of back-and-forth interaction between different levels in the hierarchy and across different modules. The fact that the mere visual appearance of the moving phantom limb feeds all the way back from the visual to the somatosensory areas of the brain to relieve a spasm in a nonexistent hand shows how extensive these interactions can be. Third, the resurrection of a long-lost phantom in some patients, and its “amputation” in others, suggest that the body image, despite all its appearance of durability and permanence, is in fact a purely transitory internal construct, a mere shell that our brain creates temporarily for passing on our genes to the next generation.

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