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# Primary somatosensory cortex hand representation dynamically modulated by motor output

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The brain's primary motor and primary somatosensory cortices are generally viewed as functionally distinct entities. Here we show by means of magnetoencephalography with a phantom-limb patient, that movement of the phantom hand leads to a change in the response of the primary somatosensory cortex to tactile stimulation. This change correlates with the described conscious perception and suggests a greater degree of functional unification between the primary motor and somatosensory cortices than is currently realized. We suggest that this may reflect the evolution of this part of the human brain, which is thought to have occurred from an undifferentiated sensorimotor cortex.

**Keywords:** phantom; reference field; sensorimotor cortex; somatosensory cortex; motor cortex

## Report

In the human brain the primary motor (M1) and somatosensory cortices (S1) are distinct anatomical structures, located in the pre- and post-central gyri respectively, and current clinical and scientific practice is to treat them as functionally distinct (Penfield & Jasper, 1954; Ramachandran & Hirstein, 1998; Ramachandran, Rogers-Ramachandran, & Stewart, 1992). However, it has been observed that direct stimulation of M1 (during awake brain surgery) evokes a sensory response in about a fifth of occasions, and vice versa (Penfield & Jasper, 1954). Here we show in a phantom-limb patient that the response of S1 to a tactile stimulus varies according to M1 activity, suggesting that functional interactions between the two structures occur.

After a hand is amputated its representation persists in the contralateral S1, and can become cross-activated by neighboring areas of S1, one of which represents the face (McGeoch & Ramachandran, 2012; Ramachandran & Hirstein, 1998; Ramachandran et al., 1992). This phenomenon is postulated to play an important role in generating the frequently reported tactile illusion that an amputated hand is still present – i.e. a phantom. Reflecting this some amputees experience a touch to their face both locally and as a referred sensation on the phantom hand, making it possible to draw on their face a map of the phantom hand with clearly delineated digits (termed "reference fields") (Ramachandran, Brang, & McGeoch, 2010; Ramachandran & Hirstein, 1998; Ramachandran et al., 1992). Some amputees also report being able to volitionally move their phantom hand, and this capability has been linked to activation of the hand area of M1 (by direct stimulation and functional imaging studies) (Mercier,

Reilly, Vargas, Aballea, & Sirigu, 2006). We have to date identified three individuals with upper limb amputations who both had facial reference fields and could move their phantom hand. In all, such movements caused an immediate and reproducible shift in the location on the face of the reference fields (Ramachandran et al., 2010).

After ethical approval one of these amputees, DS, consented to a magnetoencephalography (MEG) study. Now aged 44, DS had suffered a left brachial-plexus injury at the age of 18 and 1 year later undergone a left above-elbow amputation. He reported that the rest position of his phantom hand was with fingers extended but that with effort he could oppose his phantom thumb towards the little finger. Somatosensory evoked fields were recorded in the MEG scanner in response to tactile stimulation (tapping) to the same point on DS's left cheek (marked with ink) during two conditions: first, while his phantom was in the rest position; and second with his phantom thumb opposed. He stated that in the rest condition he experienced the touch on both face and phantom thumb (Figure 1(a)), but on opposing his phantom thumb, tapping at the same location was experienced only on his face (Figure 1(b)). The difference in MEG activations was calculated by subtracting the thumb-opposed condition from the rest condition (see online Materials and Methods).

Inspection of the resulting data set showed two adjacent but distinct loci of contralateral (right) S1 activity that started at around 40 ms and peaked at 60 ms. The raw waveforms extracted from these two regions of S1 (Figure 2) showed a polarity inversion in their activity between the two conditions. This suggests the involvement of separate neuronal populations with different orientations relative to the MEG sensors. These two activation

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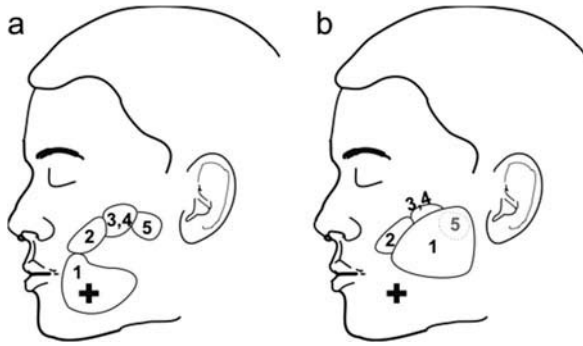Paul D. McGeoch and David Brang contributed equally.

Figure 1.  (a) Reference field map with phantom hand in rest position. Digits numbered from thumb (1) to little finger (5). Cross shows stimulation site. (b) Map after opposition of thumb. (Modified with permission from Wolters Kluwer Health; Ramachandran et al., 2010.)

locations appear to correspond superiorly to the hand, and inferiorly to the face areas of S1 (Penfield & Jasper, 1954; Ramachandran & Hirstein, 1998; Ramachandran et al., 1992). A significant difference in right superior parietal lobule (SPL) activity was also seen (Figure 2), which is explained by this area of association cortex (which is involved in body image) being a major projection site for S1 activity (McGeoch et al., 2011).

The red/yellow areas of MEG activity in Figure 2 indicate where activity was positive, and thus stronger in the rest condition, when the stimulus was experienced in both the face and phantom thumb. Here we see activation of an area of S1, in keeping with the known positions of the representations of the hand (superiorly) and face (inferiorly) (Penfield & Jasper, 1954). Conversely, the blue MEG activity is negative and thus stronger in the thumb-

opposed condition, when the stimulus was felt in the face alone. And here we see a smaller, more inferior pattern of activity, in keeping with the S1 face area alone.

## Discussion

Based on comparative anatomical studies the division between M1 and S1 in placental mammals is believed to have evolved from an undifferentiated sensorimotor cortex (Karlen & Krubitzer, 2007; Lende, 1969). The data presented here suggest human M1 is capable of dynamically altering the response of S1 to a stimulus, and with it the correlated conscious experience. Thus, rather than a rigid demarcation existing between these brain areas the sensory and motor cortices appear to remain functionally connected, possibly reflecting their evolutionary past.

It is thought that cross-activation between the face and hand areas of S1 underlies the phenomenon of a touch to the face being referred to a phantom hand; as experienced here by DS in the rest position (Ramachandran & Hirstein, 1998; Ramachandran et al., 1992). However, it seems that by sending a motor signal to oppose his phantom thumb toward the little finger, the subject alters the configurational layout of the hand area of S1 so that the thumb representation no longer lies adjacent to the same part of the face map, but instead dynamically shifts to lie next to the other fingers, and to actually engulf the representation of the little finger. Such a change in the configuration of how the fingers are mapped in S1 mirrors the changes in spatial relationship that would occur in a physical hand carrying out the same movement.

As noted above, a significant difference in right SPL activity was observed, with the activity stronger in the rest
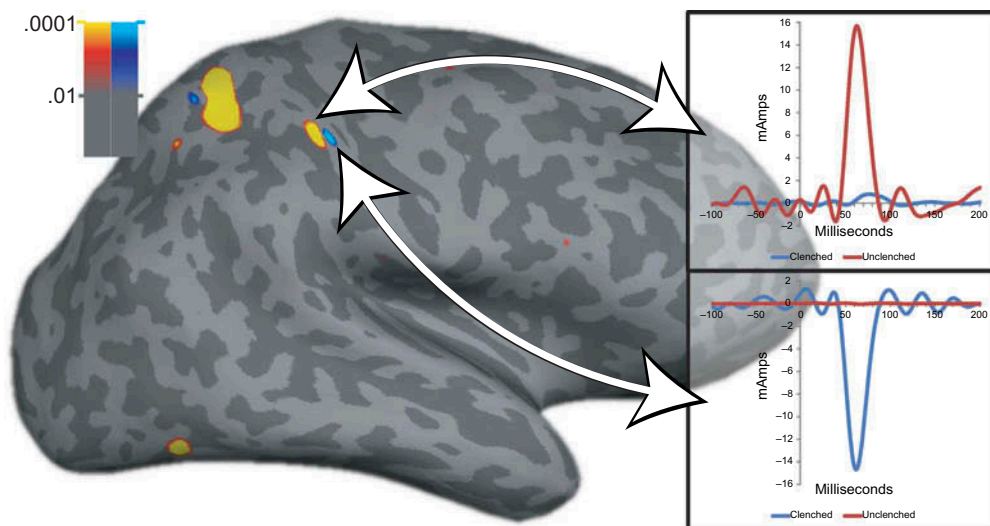


Figure 2.  Inflated FreeSurfer reconstruction of the lateral right hemisphere superimposed with difference in MEG activations between two conditions. Red/yellow areas indicate where activity was positive – i.e. was stronger in rest condition when touch was felt in both face and phantom thumb. Blue areas indicate where the activity was negative – i.e. was stronger in the thumb-opposed condition when touch felt solely on the face. Panels to right display the raw MEG waveforms for the two S1 sites where activity differs between the conditions. [To view this figure in color, please see the online version of this journal.]

condition, when touch was felt both in DS's face and his phantom thumb. As well as being a major projection target for S1 activity (McGeoch et al., 2011) this area of cortex is thought to be involved in receiving an "efference copy" of motor output, which is an important component of forward models of motor control (Blakemore, 2003). In these models the efference copy is used to predict the sensory consequences of actions, to compare them to the desired and actual outcomes. Moreover, these models propose that the brain can filter and modulate the responsiveness of the sensory cortex to distinguish, for instance, between self-touch and touch from another (as evinced by the fact that one cannot tickle oneself). Our data raise the possibility that changes in the somatotopic layout of S1 may play a role in mediating this modulation.

Finally, as mentioned above, a hypothesis used to explain the genesis of phantom sensations is that of cross-activation between neighboring cortical areas. However, it has been questioned whether this fully explains the phenomena, and there is evidence that other factors, such as cross-callosal activity, may also play a role (Bogdanov, Smith, & Frey, 2012; Ramachandran & Hirstein, 1998). Nonetheless, the findings of this study do fit well with the cross-activation hypothesis.

In conclusion, M1 appears to input to S1 in a way that dynamically modulates its topographic layout and hence response to tactile stimulation. It seems likely the function of this lies in correctly mapping the spatial relationship of the various body parts (in this case fingers) to one another. As well as affording insights into the genesis of body image, such fluidity in the ability of S1 to alter itself, would necessitate a re-evaluation of how exactly we think the cortex works.

## Supplementary Material

Supplementary (content) is available via the 'Supplementary' tab on the article's online page (http://dx.doi.org/10.1080/13506285.2013.873060).

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