fMRI evidence for an inverted face representation in human somatosensory cortex

Philip Servos,CA Stephen A. Engel,1 Joseph Gati2 and Ravi Menon2

Department of Psychology, Wilfrid Laurier University, Waterloo, ON N2L 3C5 Canada; 1Department of Psychology, University of California, Los Angeles, CA 90095 USA; 2Robarts Research Institute, London, ON N6A 5K8 Canada

Key words: Cortex; Face; fMRI; Somatosensory

CA Corresponding Author

Introduction

The face component of the well-known somatosen-
sory homunculus originally described by Penfield [1] has long been thought to be oriented right-side
top (forehead in a superior position, chin in an inferior position) along the central sulcus of the human brain. This is in contradistinction to the analogous sensory map of the face in the monkey, which is upside down [2]. This arrangement positions the face upside down compared to the rest of the homunculus, which is inverted relative to the sulcal anatomy.

Because Penfield’s studies involved epileptic pa-
tients, and the stimulating electrodes were typically placed on lateral portions of cortex (not deep within the sulci), we still do not have detailed information about the somatotopic organization of human somato-
sensory cortex. Moreover, the actual surface of the face was never accurately characterized due to more pressing pre-operative concerns such as mapping of the fingers and speech-related structures.

Ramachandran and his colleagues [3,4] reported a neural reorganization of human somatosensory cortex following the loss of a limb. They described a series of patients who report having referred sensation in a phantom arm following mechanical stimulation of their ipsilateral chin, but never following stimulation of their ipsilateral forehead. This reorga-
nization is consistent with the encroachment of the face representation onto what would be the arm representation. However, if the Penfield map is correct, one would expect such referred sensations to follow stimulation of the forehead and not the chin, given the forehead’s putative location adjacent to the arm representation on the somatosensory homunculus. Hence, these neurological reports strongly suggest that the human facial representation is inverted compared to the Penfield map. We stimulated the forehead and chin of neurologically intact humans to demonstrate with functional magnetic resonance imaging (fMRI) [5,6] that the face representation in the post-central gyrus of humans is inverted relative to the Penfield map.

Materials and Methods

Air puffs were delivered to the forehead and chin of six healthy right-handed adult volunteers (age range 22–34 years) using a pneumatic stimulation tech-
nique [7]. A plastic frame mounted on the head bay of the scanner held a series of eight air jets that were lowered to within 3 mm of the subject’s face. Four jets were positioned to stimulate the right side of the forehead; four jets were used to stimulate the right side of the chin and portions of the lower jaw. Each 27 s bout of stimulation was alternated with a 27 s rest period. Two experiments were used, each lasting 216 s and consisting of four 54 s stimulus cycles. In one experiment the forehead was stimulated; in the other experiment the chin was stimulated. A PowerPC controlled a series of manifold-mounted
high-speed air valves through custom-built relay junctions. During a stimulation bout (27 s), an individual jet was activated for 60 ms, followed by a 40 ms interval between the end of the stimulation from that jet and the start of stimulation from another jet (randomly sampled from the set of four jets for a given experiment). Within the bout of stimulation these stimulation episodes had random durations ranging from 1000 to 2000 ms and were interspersed with randomly determined 500–1400 ms periods of no stimulation.

Activation images were acquired on a 4 T whole body imaging system (Varian, Palo Alto, CA; Siemens, Erlangen, Germany) with a 14 cm quadrature surface coil which was placed proximally over the left cortex of each individual. A bite bar was used for head stabilization. T1-weighted sagittal scout images were acquired to select nine contiguous 5 mm slices in a coronal orientation across the brain. Each functional volume was acquired using a navigator echo corrected, interleaved multi-shot (four shots) echo planar imaging (EPI) pulse sequence with a 128 × 128 matrix size and a total volume acquisition time of 3 s (TE = 18 ms, flip angle = 50°, FOV = 19.2 cm). Each imaging run consisted of 72 continuous acquisitions of the selected brain volume. During each imaging session, high-resolution (256 × 256) 3D T1-weighted anatomical volumes were acquired in the same FOV and orientation as the functional images (TE = 6 ms, TR = 11 ms, TI = 500 ms, flip angle = 11°). The resulting acquisition produced 64 contiguous structural images each with a slice thickness of 1.0 mm.

Results

The 72 fMR images acquired in each experiment comprised a time series of images. At each pixel this timeseries was cross-correlated with a reference sinusoid at the stimulus alternation frequency (1/54 Hz) [8]. The maximum correlation, and associated phase were recorded for each pixel and were used to generate the map shown below and to identify peak activations. After identifying the course of the central sulcus (and hence the post-central gyrus) on the series of 64 contiguous high-resolution anatomical images, these 256 × 256 anatomical images were subsampled to the matrix size of the functional images (128 × 128).

The correlation maps generated from the chin and forehead stimulation were plotted on the anatomical images. A correlation cutoff of 0.38 (p < 0.0005) was used with a 0–9 s phase window (to minimize any large vessel effects) [9], and a Gaussian spatial filter (σ = 1.5 mm) was applied to the correlation maps. The most active regions were identified on the post-central gyrus in each of the scanning planes. In each subject the most active regions on the post-central gyrus for both experiments occurred within the same scanning plane. The position of the peak (voxel containing the highest correlation) of the active region on the post-central gyrus was measured relative to the fundus of the central sulcus for both experiments. Thus, for a given scanning plane, an

<table>
<thead>
<tr>
<th>Subject</th>
<th>Forehead</th>
<th>Chin</th>
</tr>
</thead>
<tbody>
<tr>
<td>AM</td>
<td>45</td>
<td>16</td>
</tr>
<tr>
<td>TJ</td>
<td>31</td>
<td>15</td>
</tr>
<tr>
<td>MB</td>
<td>72</td>
<td>59</td>
</tr>
<tr>
<td>KN</td>
<td>73</td>
<td>42</td>
</tr>
<tr>
<td>JD</td>
<td>14</td>
<td>14</td>
</tr>
</tbody>
</table>

*Table 1. Cortical distance of the center of activation from the fundus of the central sulcus. Note how the activity caused by stimulation of the forehead is found in inferior regions of the post-central gyrus relative to the activity caused by stimulation of the chin (t(4) = 3.14, p < 0.05)*

![FIG. 1. Determining the orientation of the somato-sensory representation of the face. (A) Correlation map resulting from forehead stimulation in subject KN. (B) Correlation map of the identical plane in the same subject during chin stimulation. Blue arrows indicate the post-central gyrus; yellow arrows indicate the fundus of the central sulcus.](1394 Vol 10 No 7 14 May 1999)
active region whose center falls along a shorter cortical distance from the fundus of the central sulcus relative to another center corresponds to a relatively more superior position on the post-central gyrus. Table 1 summarizes these distances for five of the six subjects (one subject showed poor post-central gyrus activation in both experiments). Figure 1 shows a representative activation pattern in which forehead stimulation causes the greatest activation in a relatively inferior region of the post-central gyrus relative to chin stimulation in the same subject.

Conclusion

Our data support the hypothesis that the representation of the face in human somatosensory cortex is upside down and suggest that the Penfield map of human somatosensory cortex should be revised such that the orientation of the face is inverted as in the monkey.

References


ACKNOWLEDGEMENTS: This research was supported by an NSERC operating grant and a Research Fellowship funded by Wilfrid Laurier University to P.S.

Received 10 February 1999;
accepted 3 March 1999