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Overlapping representation of fingers in the somatosensory cortex (area 2) of the conscious monkey

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Finger representation on the first somatosensory cortex was mapped in conscious monkeys by single-unit recording. While representation was somatotopic in area 3, this was not the case in area 2, where the representation of different fingers overlapped. Our results indicate that area 2 is not a pure replica of the receptor sheet of the body surface.

Since it was first proposed[1,13,16] the concept of somatotopic representation of the body in the first somatosensory cortex (SI) has found wide acceptance and it has been expanded by a number of studies which suggested that this representation is multiple within SI[2,6,7,10,12]. Kaas et al.[10] postulated that each of the four cytoarchitectonic subdivisions of SI: areas 3a, 3b, 1 and 2, has an independent and somatotopic representation of the contralateral side of the body. Their hypothesis is based on the observation that the receptive fields of neurons in area 1 or 2 of the finger region were as fine and topical as those of the neurons in area 3b. However, their experiments were performed in anesthetized animals, so that the loss of sophisticated receptive field properties could not be ruled out. In fact, the most recent single-unit studies in SI of unanesthetized monkeys[3–5,8] and cats[6,7] have demonstrated that SI has neurons with far more complex receptive field properties than previously thought. This was particularly true in area 2, where units with converging inputs from multiple loci as well as from receptors of different submodalities were found. We now report that the representation of fingers in area 2 is not strictly somatotopic.

A series of experiments were carried out with both rhesus and Japanese macaques. The monkeys were reasonably cooperative during the experiments, allowing us to explore their hands to determine the receptive fields. Extracellular recordings from well-isolated single units were made with glass-coated platinum–iridium microelectrodes. Receptive fields and submodality preferences of the units were examined with hand-held probes, paint-brushes and other tools.

Fig. 1 shows typical and contrasting examples of receptive fields of neurons in area 3b (A) and area 2 (D). Neurons in area 3b were predominantly skin type, either rapidly or slowly adapting. Their receptive fields were fine and topical as illustrated in Fig. 1A. Neurons in area 3a were predominantly deep type, responding to the

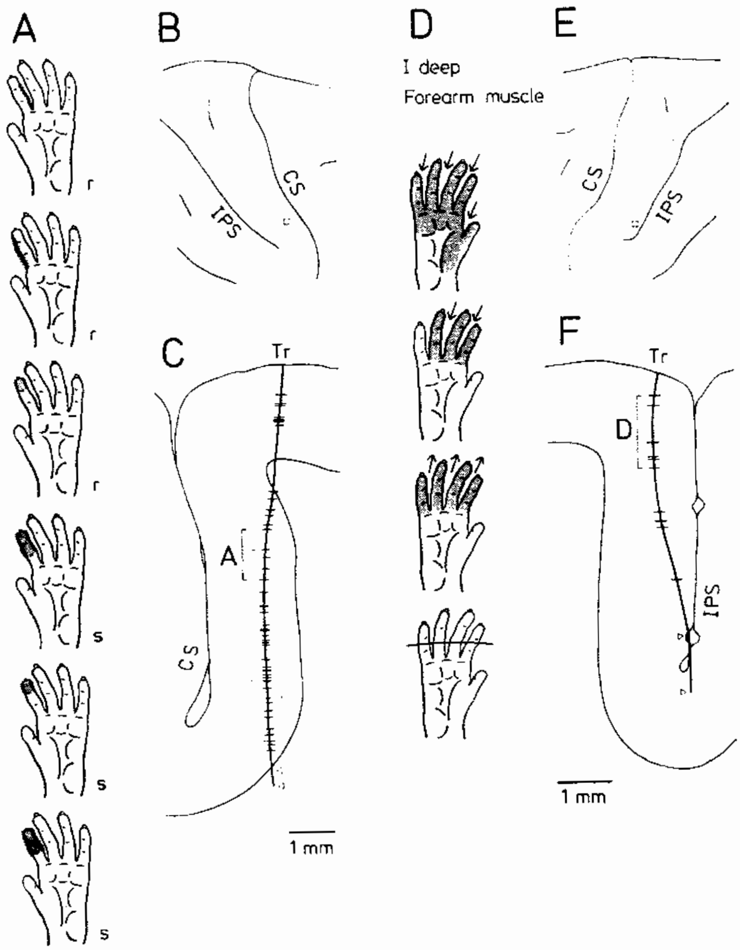

Fig. 1. Comparison of receptive fields in area 3b and 2. A: receptive fields of 6 units recorded in area 3b. The recording sites were in the posterior bank along the central sulcus as illustrated in C. B: the square indicates the site of penetration over the dorsal surface of the cortex. CS, central sulcus; IPS, intraparietal sulcus. C: recording sites of units shown in A and other units (bars) along the profile of the electrode track reconstructed on histological slides. The sites were estimated from depth measurements made during the experiment. The small triangles at the end of the track indicate the site of electrolytic lesions. D: receptive fields of 6 units recorded in area 2. The initial two were deep units, the next three, skin units responding to skin stimuli moving in the directions indicated by the arrows. The bottom unit responded only to the contact of an edge across the fingers. The recording sites were in the anterior bank along the intraparietal sulcus as illustrated in F. E: site of penetration, identified by the square. F: recording sites of the units shown in D.

manipulation of a single finger joint. Thus, the receptive field of neurons in both area 3a and 3b was localized to a single finger.

In contrast, units with small receptive fields were rare in area 2. The receptive fields involved two to five fingers, or both fingers and palmar skin (Fig. 1D). Many skin units responded to tapping, to a stimulus moving in a certain direction, or to contact with objects of particular shapes, but not to punctate stimulation. Many other units in area 2 responded to various combinations of multiple joint manipulation and sometimes, these units responded to both skin and joint stimulation. This indicates

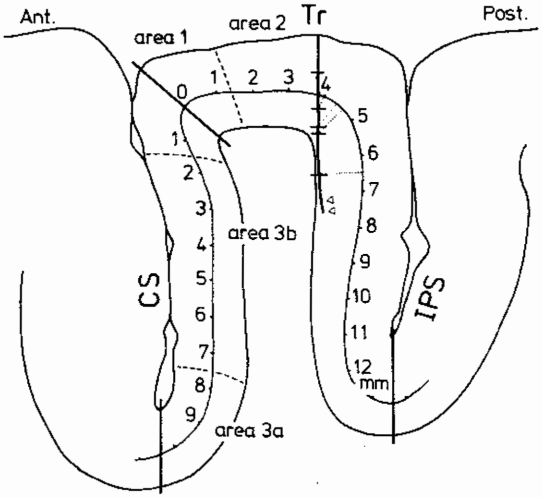

Fig. 2. Reconstruction from a histological slide, showing how the cortex was unfolded. The electrode track (Tr) was reconstructed and the recording sites (horizontal bars) were estimated from distance measurements made during the recordings. The anterior turn of the gyrus, at the corner of the central sulcus, was taken arbitrarily as the zero point of the coordinate, and the distance from this point along layer IV was measured either anteriorly or posteriorly and scaled in mm. The depth of the recording site of each unit was then represented in mm as the distance along this line. Broken lines indicate the border between two cytoarchitectonic areas. CS, central sulcus; IPS, intraparietal sulcus.

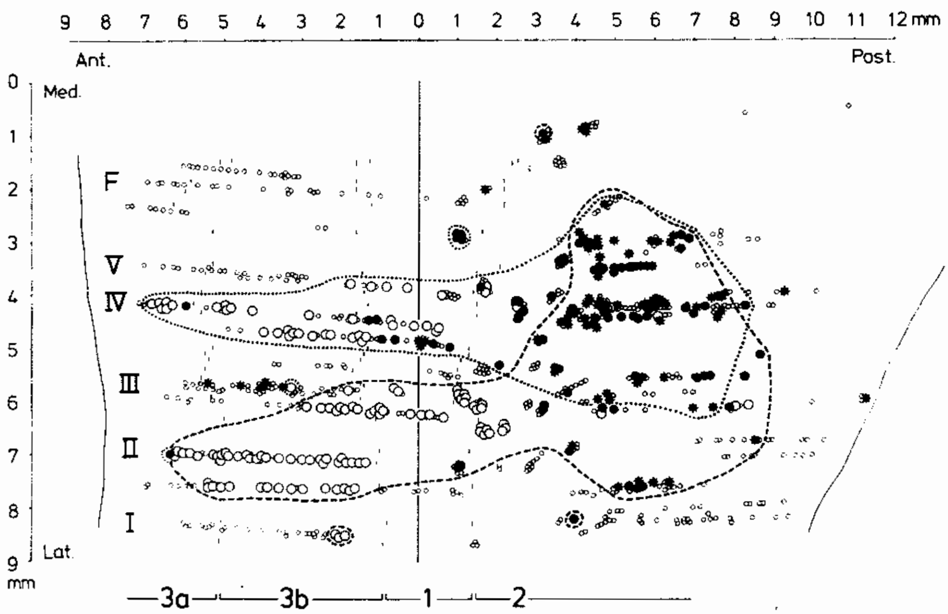

Fig. 3. Scatter map illustrating somatotopic and converging representation of fingers in SI. The abscissa represents the antero-posterior direction and the ordinate, the medio-lateral direction over the cortical surface. Large open circles, units with receptive fields on either the second or fourth finger; solid circles, units whose receptive fields involve two or three fingers including either the second or fourth finger; stars, units whose receptive fields involve three or more fingers including both the second and fourth fingers; small open circles, all other units recorded in the two hemispheres. The lines encircle the area in which the majority of units receiving inputs from the second (broken line, II) or the fourth (dotted line, IV) finger distribute. The vertical bars indicate the border between cytoarchitectonic subareas (areas 3a, 3b, 1 and 2, see designation at the bottom of the figure), which were determined in each histological slide. The long lines at the right and left end of the figure indicate the extreme bottom of the intraparietal and central sulcus, respectively. The letter F and the Roman numerals I–V indicate the location of representation of the forearm and the 5 fingers.

that the receptive fields tend to be larger in both skin and joint manipulation units of area 2. Moreover, these two submodalities often converged in area 2 neurons. Many other units had no receptive field at all, but were activated in relation to the animal's active hand or arm movements[3–5,8,11].

The results of receptive field mapping were plotted on a two-dimensional map of the cortex. Fig. 2 shows a reconstruction from a histological slide and explains how the cortex in the sulci was unfolded. Fig. 3 is a scatter map in which the data collected from 776 units in the two hemispheres of one monkey were combined. The circumscribed portions are the areas of representation of the second (II) and fourth (IV) finger over areas 3a, 3b, 1 and 2. Each finger had an almost completely separate projection field in area 3, indicating that this region is somatotopically arranged. There was an exceptional spot where both of these, as well as other fingers, converged (see solid stars and circles). However, this finding did not alter the overall picture of segregated representation of individual fingers in area 3. In area 2, there was considerable scattering and overlapping of the units which receive inputs from either the second or fourth finger, indicating that in this area the representation of the two fingers overlaps. Therefore we conclude that, differently from area 3, the representation of each finger in area 2 is not somatotopically segregated from others and that the somatosensory representation of area 2 is not a pure replica of the receptor sheet of the body surface. The altered mode of representation of fingers in area 2 reflects the presence of more specialized functional processes of integration. Our results support the hypothesis that area 2 is a site for the integration of neuronal messages essential for various tactile performances of perceptual processes[3–5,8,14,15].

We think that it is misleading to use the concept of multiple representation in terms of cytoarchitectonic subareas in SI if the concept is based on the assumption that these subareas receive independent afferent projections from different submodality sources, and if the concept disregards the important integratory processes through the corticocortical connections of neurons across the boundaries of these subareas.[9]

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