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15. We are grateful to M. Barkley and the late I. I. Geschwind for *Gillichthys* UII and to K. Lederis for *Catostomus* UI and UII. We also thank T. Machen and R. Gunther for advice during the experiments. Supported by National Research Council of Canada and Killam (Canada) postdoctoral fellowships to W.S.M. and by NSF grant PCM-16345 to H.A.B.

18 December 1978

Multiple Representations of the Body Within the Primary Somatosensory Cortex of Primates

Abstract. *Microelectrode mapping experiments indicate that the classical primary somatosensory cortex of monkeys consists of as many as four separate body representations rather than just one. Two complete body surface representations occupy cortical fields 3b and 1. In addition, area 2 contains an orderly representation of predominantly "deep" body tissues. Area 3a may constitute a fourth representation.*

Many of our current concepts of the organization of the somatosensory cortex in primates stem from the early studies of C. N. Woolsey and his colleagues, first published more than 40 years ago (*1*).

Using surface-evoked potential methods, these pioneering investigators concluded that there was a large single representation of the contralateral body surface within the anterior parietal cortex of macaque monkeys. The "representation" [later termed SI (*2*)] included four distinct cytoarchitectonic fields, areas 3a, 3b, 1, and 2 of Brodmann (*3*). The basic organization of the representation was later summarized by Woolsey for several primate species by a "homunculus," a distorted drawing of the body surface reflecting the proportions of different skin surfaces in SI as well as the overall somatotopic organization of SI (*4*). This body figure was drawn with the digits of the hand and foot represented rostrally in the parietal cortex, the back caudally, the tail medially, and the face laterally (Fig. 1A).

Observations recorded in later single unit studies (*5*) were not consistent with the concept of SI as a simple, continuous somatotopic representation of the contralateral body surface. Cutaneous receptors signaling light touch were reported to provide the major input to area 3b; mixed cutaneous and deep receptor input activated mosaically distributed neuron groups in area 1; and deep receptor input was predominant in area 2. Thus, if there was a single body surface representation in SI (as portrayed by a homunculus overlying the architectonic fields), different regions of the body surface would relate to quite different classes of neurons in SI.

Powell and Mountcastle (*5*) suggested a second concept of SI that appeared to be more compatible with the uneven cortical distribution of receptor inputs than the homunculus concept. They noted that the same body region could activate neurons in different electrode penetrations across the rostrocaudal dimension of SI. Thus, a reasonable alternative to the homunculus concept was that any given body region be represented within a rostrocaudal band extending across areas 3a, 3b, 1, and 2. All body surface locations would thereby be subserved by peripheral receptors of all classes, and areas 3a, 3b, 1, and 2 would be considered parts of a single representation. Variants or aspects of the rostrocaudal bands concept have been forwarded in more recent investigations of SI organization in spider, squirrel, and macaque monkeys (*6*) (Fig. 1B).

A third view of SI organization was suggested by the microelectrode mapping studies of Paul, Merzenich, and Goodman (*7*) who described two "complete" representations of the glabrous hand within SI of macaque monkeys; one representation was within area 3b, the other was related to area 1. Area 3a was not included in either representation, and there was partial evidence for a third representation in area 2. Although the organizations of areas 3b, 1, and 2 were not further investigated, these stud-

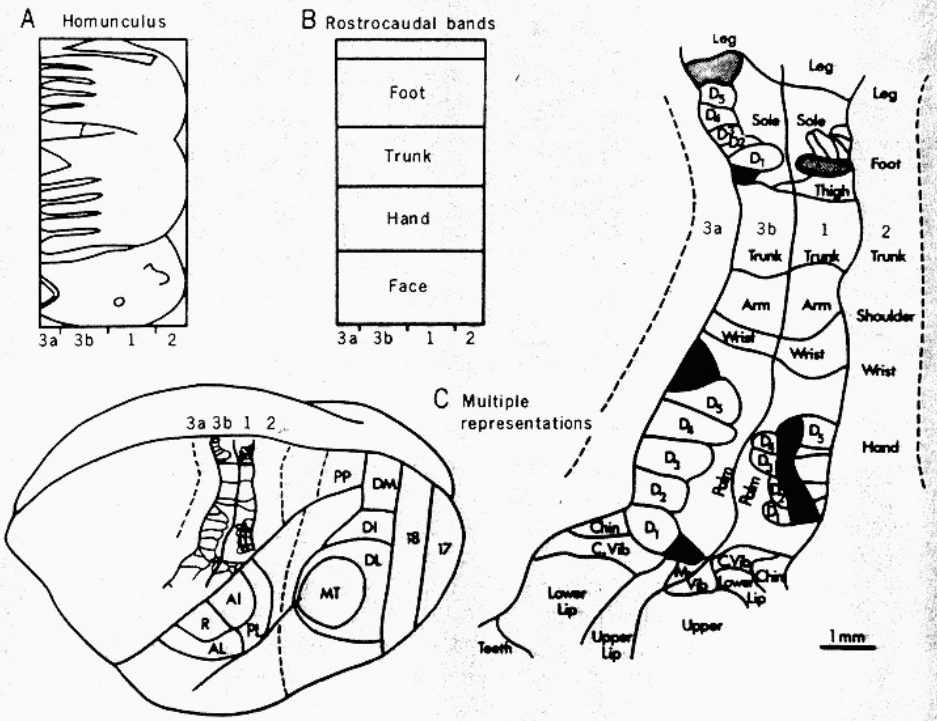

Fig. 1. Three conceptions of the organization of postcentral parietal somatosensory cortex (SI). (A) A distorted body figure (homunculus) over the four architectonic fields. In this view a single topographic body representation constitutes SI. (B) The SI as rostrocaudal bands. Major body parts are represented in all architectonic fields. (C) Multiple representations of the body within the cortex formerly designated as SI. Each architectonic field contains a representation. The organizations of the two cutaneous representations, SI proper (3b) and the posterior cutaneous field (1), and some of the organizations of the area 2 representation are shown for the owl monkey (*Aotus*). Sectors within each map limit the representations of body parts. The digits of the foot (upper) and hand (lower) are numbered, and the dorsal hairy surfaces are shaded. Chin and mandibular vibrissae are indicated. The positions of the fields on the brain are shown on the lower left. Visual and auditory areas are also shown (*14*).

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ies raised the possibility that each of the traditional architectonic fields of SI in primates constitutes a separate and complete body representation, each with a different functional role and relationship to peripheral receptor categories. This third hypothesis is characterized in Fig. 1C as the multiple representations hypothesis.

We now summarize the results of an extensive series of microelectrode mapping studies (*8*) undertaken to determine which of these concepts of SI organization is correct. Our conclusions are based on approximately 3500 recording sites in 19 New World monkeys (*Aotus trivirgatus, Cebus capucinus*, and *Saimiri sciureus*), and 4400 recording sites in 13 Old World monkeys (*Macaca fascicularis*) (*9*). Results on owl monkeys (*Aotus*) have been published (*8*); these findings can be compared with those from other primates, and more inclusive statements are now possible. Our experiments unequivocally support the multiple representations hypothesis.

The most detailed results have been obtained from areas 3b and 1. Because neurons in these areas respond to low-threshold cutaneous stimulation within small restricted receptive fields, patterns of somatotopic organization are relatively easy to reveal. In all monkeys, these two fields form two separate and complete maps of the body surface that are roughly, but not precisely, mirror images of each other. Thus, rostrocaudal rows of recording sites across the two areas yield progressions of receptive fields across the body surface for sites in area 3b that reverse at the border between 3b and 1 and retrace the same body surface for sites in area 1 in a manner analogous to the reversal and retracing of the retinal position one finds with rows of recording sites across the first and second areas of visual cortex. Rows of recording sites at different mediolateral locations showed that all major body parts are represented twice. Examples of receptive field progressions with reversals and retracing on the digits of the hand are shown for a macaque monkey in Fig. 2A, and details of the two representations are summarized for owl monkeys in Fig. 1C. The digits point in opposite directions in the two representations (*10*). This was observed in all four species of monkeys; there were some clear species differences, however. As a minor difference, the hand representations in areas 3b and 1 adjoined along the pads of the palm in owl and squirrel monkeys, but largely along the base of the digits in macaques (Figs. 1C and 2A). As examples of more striking differences, both the trunk and parts of the face representations in both areas 3b and 1 were reversed in orientation in squirrel monkeys compared with owl and macaque monkeys. The two representations also differed from each other in several clear and consistent ways in all monkeys. The area 1 representation was smaller, the neurons had larger receptive fields, and some neurons received Pacinian receptor input. The arrangement of body parts in area 1 also differed from that in area 3b, especially in the locations of glabrous and hairy skin surfaces of the hand (Fig. 1C).

Less can be said about the organizations of areas 3a and 2. Area 3a usually required deep pressure, hard taps, or body movement to activate recording sites, an observation consistent with the prevailing view that this subdivision of

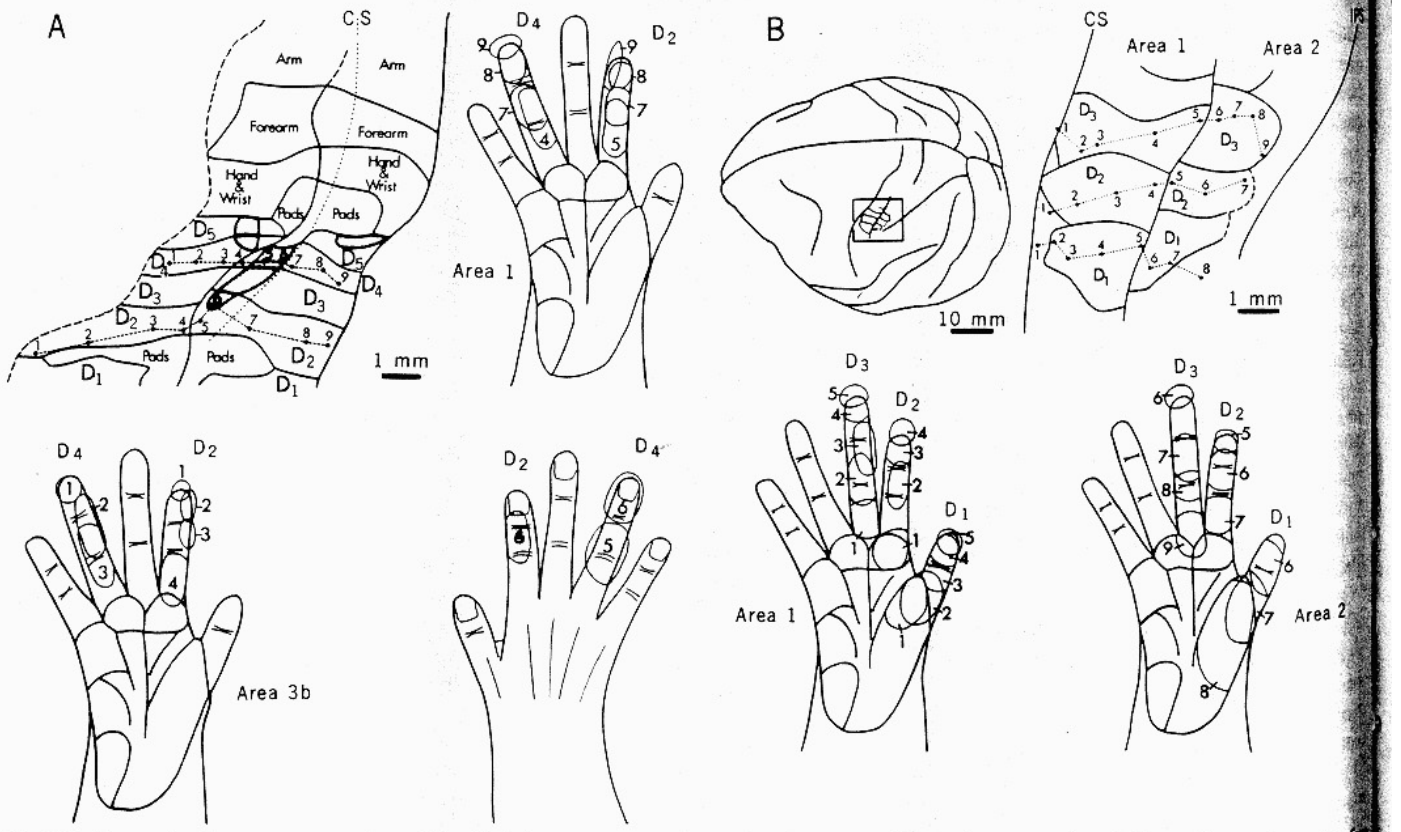

Fig. 2. Evidence for three representations of the digits in macaque monkeys. For purposes of illustration, receptive fields are shown for only a few recording sites from much more extensive mapping experiments. (A) Receptive fields for rows of recording sites across the representations of digits 2 and 4 in areas 3b and 1 in monkey 77-52. Cortex to the left of the dotted line is buried in the central sulcus (*CS*). Shaded areas indicate the representation of dorsal hairy surfaces of digits. Each architectonic field separately represents the digits, the representations are joined along the bases of the fingers (rather than the palm as in the owl monkey), and the finger tips point in opposite directions. (B) Receptive fields for rows of recording sites across the representations of the first three digits in areas 1 and 2 of monkey 77-39. The digits are represented separately in each architectonic field and the two representations are joined at the finger tips so that the representations are approximately mirror images of each other.

cortex is the principle target of receptors in muscles (*11*). When area 3a recording sites were activated, they related to body locations that roughly corresponded to those activating adjoining recording sites in area 3b. Thus, our observations are consistent with the concept of a representation in area 3a that is parallel to that in area 3b, but further details are unclear.

We found that area 2 of the owl monkey was almost exclusively activated by stimulating deep body tissues. Because it was difficult to stimulate selectively restricted regions of deep receptors, it was possible to obtain only a crude idea of the organization of area 2 in this monkey. Yet it was clear that the overall organization of area 2 was in parallel with areas 3b and 1 and that body parts were represented for a third time in area 2. In macaque monkeys, area 2 responded to cutaneous as well as deep stimuli. We do not know if this difference between monkeys reflects a difference in the susceptibility of cutaneous input to suppression by anesthetics, but the difference did allow a more detailed analysis of the organization of area 2 in macaques. Progressions of receptive fields for rows of recording sites across areas 1 and 2 indicate a mirror reversal of somatotopic organization at the border (Fig. 2B). Thus, areas 3b and 1 and areas 1 and 2 are approximately mirror reversals of each other. The data from the many rows of recording sites that were typically obtained in each experiment made it also apparent that none of the three representations was a simple distortion of the body without splits or disruptions. Disruptions may be necessary for the distorted map to fit in an architectonic strip. However, it is important to note that the discontinuities are not predicted strictly by the dermatomal sequence, and that they differ in location in the separate representations.

We conclude that the classical primary somatosensory cortex consists of four functionally distinct strips. At least areas 3b, 1, and 2 contain separate body representations. We believe this interpretation is required by the mapping data. Furthermore, the multiple representations hypothesis is clearly more consistent with the microelectrode studies that indicate that each architectonic area has its own pattern of sensory activation (*5*, *7*, *8*, *11*), recent anatomical studies that demonstrate distinctive patterns of connections for each of the architectonic fields (*8*, *12*), and ablation-behavioral investigations showing specific impairment associated with lesions restricted to specific fields (*13*). There is little doubt that the four fields 3a, 3b, 1, and 2—and not SI—are the subdivisions of functional significance of the parietal somatosensory cortex of monkeys, and perhaps of all higher primates.

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9. Our studies also include 1800 recording sites in ten prosimian primates (*Galago senegalensis* and *Galago crassicaudatus*). Only one low-threshold cutaneous representation was found, although cortex rostral and caudal to this representation was responsive to more intense stimuli. These observations are consistent with those of two other recent microelectrode mapping studies in prosimians [A. Krishnamurti, F. Sanides, W. I. Welker, *Brain Behav. Evol.* **13**, 367 (1976); M. Carlson and C. Welt, *Soc. Neurosci. Abstr.* **3**, 478 (1977)]. The organization of the low-threshold representation identifies it as the 3b field. We are still uncertain whether areas 1 and 2 exist in prosimians.
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25 October 1978; revised 26 December 1978

Intraretinal Distribution of Cone Pigments in Certain Teleost Fishes

Abstract. *Microspectrophotometric investigations of visual pigments in the teleost family Cichlidae determined that morphological "twin cones" need not be "pigment twins" as well. In each species there were two pigments that could be found in these cells; a "longwave" and a "shortwave" type whose precise spectral location varies for each species, making the terms red and green inadequate to describe them. Studies of the receptor mosaic with the nitro-blue tetrazolium chloride reduction technique permitted the sampling of larger receptor populations and confirmed that twin cones in several cichlid species could be either longwave-longwave, longwave-shortwave, or shortwave-shortwave pairs, and that the relative proportions of these twin cone types vary in different parts of the retinas. Nonuniform distribution of pigment types was also evident in the eyes of several other species from a variety of piscine taxa.*

The retinas of many fish species exhibit single, double, and twin cones. Double cones, such as those described in the goldfish (*Carassius auratus*), are characterized by members of dissimilar appearance in both fixed and fresh preparations. One member of the pair has an ellipsoid body and an outer segment which are broader and longer than those of the other member. This cell usually contains

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