# Double Representation of the Body Surface within Cytoarchitectonic Areas 3b and 1 in "SI" in the Owl Monkey *(Aotus trivirgatus)*

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*ABSTRACT* Microelectrode multiunit mapping studies of parietal cortex in owl monkeys indicate that the classical "primary" somatosensory region (or "SI") including the separate architectonic fields 3a, 3b, 1, and 2 contains as many as four separate representations of the body rather than one. An analysis of receptive field locations for extensive arrays of closely placed recording sites in parietal cortex which were later related to cortical architecture led to the following conclusions: (1) There are two large systematic representations of the body surface within "SI." Each is activated by low threshold cutaneous stimuli; one representation is coextensive with Area 3b and the other with Area 1. (2) While each of these representations contains regions of cortex with topological or "somatotopic" transformations of skin surface, the representations have many discontinuities where adjoining skin surfaces are not adjoining in the representations. Thus, the representations can be considered as composites of somatotopically organized regions, but cannot be accurately depicted by simple continuous homunculi. Lines of discontinuity often cut across dermatomes and seldom follow dermatomal boundaries, i.e., neither cutaneous representation constitutes a systematic representation of dermatomal skin fields. (3) While the two cutaneous fields are basically similar in organization and are approximate mirror images of each other, they differ in important details, i.e., lines of discontinuity in the representations and the sites of representations of different specific skin surfaces differ significantly in the two representations. (4) The two cutaneous representations also differ in size and in the relative proportions of cortex devoted to representation of various body parts. Because the proportions in each representation differ, they cannot both be simple reflections of overall peripheral innervation density. (5) All or part of Area 2 contains a systematic representation of deep body structures.

These conclusions are consistent with a view of the anterior parietal region as containing functionally distinct fields at least partially related to different subsets of receptor populations and coding or representing different aspects of somatic sensation. We suggest that the "SI" region of primates be redefined as a *parietal somatosensory strip,* the Area 1 representation as the *posterior cutaneous field,* and, for reasons of probable homology with "SI" of other mammals, the Area 3b representation as *SI proper.*

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Over the last four decades, electrophysiological mapping experiments conducted in a number of mammalian species have established the view that the parietal cortex of all mammals contains at least two systematic representations of the body surface, i.e., the first (first discovered) and second somatosensory areas, SI and SII. Many of the early pioneering experiments were on macaque monkeys (Marshall et al., '37; Woolsey et al., '42). These studies demonstrated an orderly progression or representation of body parts in a wide band of post-central parietal cortex that later became known as "SI" (Woolsey and Fairman, '46). From the beginning, it was recognized that this "SI" of macaque monkeys encompassed three of the architectonic fields of Brodmann ('09), Areas 3, 1 and 2. The more caudal parietal Areas 5 and 7, and the precentral motor field, Area 4, were excluded from the representation on the basis of a sharp decline in the amplitude of potentials evoked by somatosensory stimuli whenever the recording electrode was moved onto the surface of these Areas.

Initial reports on the postcentral parietal cortex in macaques emphasized the mediolateral organization. The mediolateral sequence of representation was found to parallel that defined concurrently by electrical stimulation in the anterior parietal cortex in man (Penfield and Boldrey, '37). That is, stimulating the tail evoked surface potentials from recording sites in the extreme medial aspect of the representational region; more laterally, the postaxial leg, then the foot, the preaxial leg, the body, the arm, the hand, and finally the head were successively represented (Woolsey et al., '42). In these studies, the rostrocaudal changes in the body surfaces represented in "SI" were less dramatic; receptive fields tended to remain in the same general body region. Determination of the rostrocaudal order of the representation was aggravated by the fact that the most rostral half of the responsive region including nearly all of Area 3 was buried in the central sulcus, and was accessible for exploration by surface electrodes only after extensive cortical ablations. Possibly for these reasons, the rostrocaudal organization of the responsive zones was not stressed. In later reviews of the organization of somatosensory cortex in mammals, Woolsey ('54, '58, '64) summarized both the mediolateral and rostrocaudal organization of postcentral parietal cortex of macaque monkeys with the now familiar distorted "homunculus" (or "simiunculus") of the contralateral half of the body surface, which was superimposed on a lateral view of the brain to show the major features of "SI" organization. The homunculus portrayed the body on the brain with the distal digits of the hands and feet pointing rostrally along the rostral border of Area 3 (actually, of 3a), the head laterally, and the back of the animal caudally (along the caudal border of Area 2).

A difficulty with the concept of the organization of postcentral parietal cortex as a homunculus overlying three or four major architectonic fields became evident with the publication of the microelectrode studies of the properties of single neurons in parietal cortex, by Powell and Mountcastle ('59a,b) and Mountcastle and Powell ('59). These investigators demonstrated that neurons in each of three architectonic fields (actually, 3b, 1, 2) of "SI" tended to have different modes of response to sensory stimuli. Thus, cells of Area 2 responded almost exclusively to the stimulation of deep rather than cutaneous receptors; neurons in Area 1 responded to both types of stimulation; and cells in Area 3b were predominantly activated by light tactile stimulation of cutaneous receptors. This discovery meant that if the proposed concept of the rostrocaudal organization of postcentral parietal cortex were valid, then different body parts would be subserved by populations of neurons with decidedly different functional properties. However, it was still possible to conclude that distal and proximal body parts have different roles in sensory experience, and to argue that the homunculus made functional sense in that the input from cutaneous receptors would be predominant rostrally in Area 3b, where the highly sensitive finger tips were located in the representation, while neurons activated by the stimulation of joints and deep body tissues would be predominant in Area 2, where the less sensitive proximal parts of the limbs and the back were represented.

The concept of an unequal distribution of receptor inputs to a single cortical representation, "SI," became less attractive as further microelectrode studies of neurons in parietal cortex extended the basic discoveries of Powell and Mountcastle. It gradually became apparent that neurons in Area 2 are principally responsive to the rotation of joints and the stimulation of periosteum for fascia (or other "deep" structures); Area 1 neurons are activated by cutaneous input from quickly adapting receptors; Area 3b derives its input from cutaneous quickly and slowly adapting receptor classes; while Area 3a processes information from muscle afferents and other deep receptors (Mountcastle and Powell, '59; Powell and Mountcastle, '59b; Werner and Whitsel, '68; Phillips et al., '71; Paul et al., '72a; Yumiya et al., '74; Lucier et al., '75; Tanji, '75; Heath et al., '76; Krishnamurti et al., '76). Furthermore, the boundaries between neurons with different response properties were often recognized as being sharp rather than gradual, and were felt to coincide with cytoarchitectonic boundaries. Such stepwise changes in functional zones are obviously less compatible with the concept of a single body representation overlying these fields than was the earlier postulation of gradients of functional change.

A second concept of the organization of the postcentral parietal cortex in primates avoided the apparent inconsistency of the single neuron data with the idea of a single homunculus extending over Areas 3, 1 and 2. Powell and Mountcastle ('59b) first suggested that the afferent fibers relayed from a single dorsal root relate to a narrow rostrocaudal band across all the "SI" architectonic fields. While such a statement is not clearly in conflict with the single homunculus viewpoint, it is not far from the more specific concept that each body part is represented in a band across the three or four architectonic fields, so that each body part is in all fields and can be subserved by all neuronal types. This "rostrocaudal band" concept received support from observations that neurons at the same mediolateral level in the separate architectonic fields were found to have similar receptive field locations (Powell and Mountcastle, '59b; Werner and Whitsel, '71; Pubols and Pubols, '71). However, even strong supporters (Pubols and Pubols, '72) of the "rostrocaudal band" concept recognized evidence for somatotopic organization within "rostrocaudal bands" that was clearly inconsistent with a simple rostrocaudal "isorepresentation" of all body surfaces in the postcentral region (which is, in fact, a topological impossibility).

A third viewpoint on the organization of the "SI" region of primates emerged from an extensive series of microelectrode mapping studies on squirrel and macaque monkeys, first initiated by Werner and Whitsel ('68, '71; Dreyer et al., '74, '75; Whitsel et al., '71). While these authors concentrated on definition of the mediolateral organization of the postcentral parietal cortex (which they described as a dermatomal sequence), they also indicated the general features of their concept of the rostrocaudal organization. As in the original reports of Woolsey et al. ('42), these investigators regarded "SI" as encompassing several architectonic fields, i.e., Areas 3a, 3b, 1 and 2. Larger body units such as the face, arm, hand, trunk, and leg were portrayed as rostrocaudal bands extending across all of these architectonic divisions (fig. 12 of Whitsel et al., '71). In this regard, their viewpoint was similar to the "rostrocaudal band" concept stemming from the experiments of Powell and Mountcastle ('59b). However, in their view, a general somatotopy is preserved within these rostrocaudal bands. The representation of some body surfaces are depicted as extending over several architectonic divisions; others are confined to one or two divisions; still others are duplicated in the representation, so as to occur both rostrally in Areas 3a and 3b and caudally in Areas 1 and 2 (see, for example, fig. 9 in Whitsel et al., '71). For example, the volar surface of the hand is shown as extending over Areas 3a, 3b, 1 and 2 with the distal tips of the digits at the rostral margin of 3a and the proximal part of the hand near the caudal margin of Area 2. By contrast, the representation of the dorsal hand is shown exclusively or mainly in Area 3b. Finally, the abdomen is shown both rostrally in Areas 3a and 3b and caudally in Areas 1 and 2. These two representations of the abdomen are separated by the back, located near the border of Areas 3b and 1. It is clear that even this complicated scheme only partially solves the problem of the incongruency of receptor segregation within distinct architectonic fields and the orderly map of the body surface across these fields.

A quite different possibility for the organization of the postcentral parietal cortex was suggested by the experiments of Paul et al. ('72a,b, '75). In microelectrode mapping experiments of the hand region of Areas 3b and 1 of macaque monkeys, they discovered two separate and topographical representations of the volar hand "in its entirety." Each of the two representations was found to correspond to a separate architectonic subdivision with distinct neural properties. Thus, the rostral representation of the hand was confined to Area 3b and was dominated by input from quickly and slowly adapting cutaneous mechanoreceptors, while the caudal representation was limited to Area 1 and was activated by input from quickly adapting cutaneous mechanoreceptors. Area 2 was not systematically explored, but limited recordings there suggested a third representation of the hand responsive to higher threshold stimulation of "deep" receptors. The results of Paul et al. ('72a) raise the possibility that architectonic subdivisions of the postcentral parietal cortex actually constitute separate representations of the body, each processing input from a distinct subset of receptors. The present mapping experiments were designated to gather evidence for or against this last possibility.

The owl monkey *(Aotus trivirgatus)* was used in these experiments because the central sulcus consists of only a very shallow, short dimple on the cortical surface (e.g., see fig. 15), and because there are no sulci in parietal cortex caudal to the parietal somatosensory cortical region. Thus, the entire surfaces of cytoarchitectonic Areas 4, 3a, 3b, 1, 2, 5 and 7, except those buried in the medial wall or Sylvian fissure, are exposed on the lateral cortical surface. The results demonstrate that there are separate and apparently complete representations of the contralateral body within the separate architectonic fields of the "SI" region.

A preliminary report of some of these results has been published elsewhere (Kaas et al., '76).

## METHODS

Experiments were conducted with nine adult owl monkeys *(Aotus trivirgatus)*. Animals were initially anesthetized with ketamine hydrochloride (50 mg/kg, IM). They were maintained with supplementary injections of ketamine at a surgical level of anesthesia. Body temperature was monitored, and kept at 37° throughout these long (20-50 hours) recording experiments. Parietal cortex was exposed *via* a wide craniotomy. An acrylic dam was constructed around this skull opening to maintain a pool of silicone over the exposed brain surface. A high resolution photograph of the brain surface was then taken. The surface vasculature (observed with a dissecting microscope) was used to site electrode penetrations on this photograph.

Glass-coated platinum-iridium microelectrodes with impedances of 2-3 M$\Omega$ were introduced in penetrations perpendicular to the surface of the anterior parietal cortex. The amplified electrode output was fed to an oscilloscope, and to a loudspeaker. Mapping was usually initiated just posterior to a shallow dimple (a poorly developed central sulcus) commonly falling at or near the boundaries of somatosensory cortex and motor cortex. The vertical axis of penetrations was set so that penetrations about midway between the midline and the crest of the Sylvian sulcus were precisely normal to the cortical surface. All penetrations in any given experiment over the relatively flat parietal cortex were parallel with this axis.

In most experiments, an effort was made to map a given sector of the somatosensory cortex in great detail. Up to nearly 500 (usually several hundred) penetrations were made in each hemisphere studied. Electrode penetrations were usually spaced at 200- to 300-$\mu$m intervals. The most extensive mapping experiments were within cytoarchitectonic Areas 3b and 1, as later verified in serial sagittal brain sections. More limited recordings were obtained rostrally in motor cortex, and caudally in Areas 2 and 5.

Within Areas 3b and 1, neurons in the middle cortical layers were strongly driven by light tactile stimulation. Receptive fields were defined using fine black glass probes while the relevant body part was carefully stabilized to prevent movement. All receptive fields derived in these maps were minimum fields, defined as the skin region from which a distinct response could be evoked by very light tactile stimulation. There was a consistent attempt to determine whether input arose from cutaneous receptors, or from joint or other deep receptors. Outlines of receptive fields were drawn on enlarged photographs of body surfaces of the owl monkey.

In initial experiments, the receptive field boundaries were determined for different neurons or clusters of neurons at a number of depths across the active depths of cortex within single penetrations. They were found to be remarkably constant throughout vertical penetrations into the cortex, as described by others in other species (e.g., Mountcastle, '57; Powell and Mountcastle, '59b; Werner and Whitsel, '68; Whitsel et al., '71; Paul et al., '72a; Dreyer et al., '75). In later experiments (in which the most extensive maps were derived), one or two very careful receptive field determinations were made in each penetration. Although receptive fields of isolated neu-

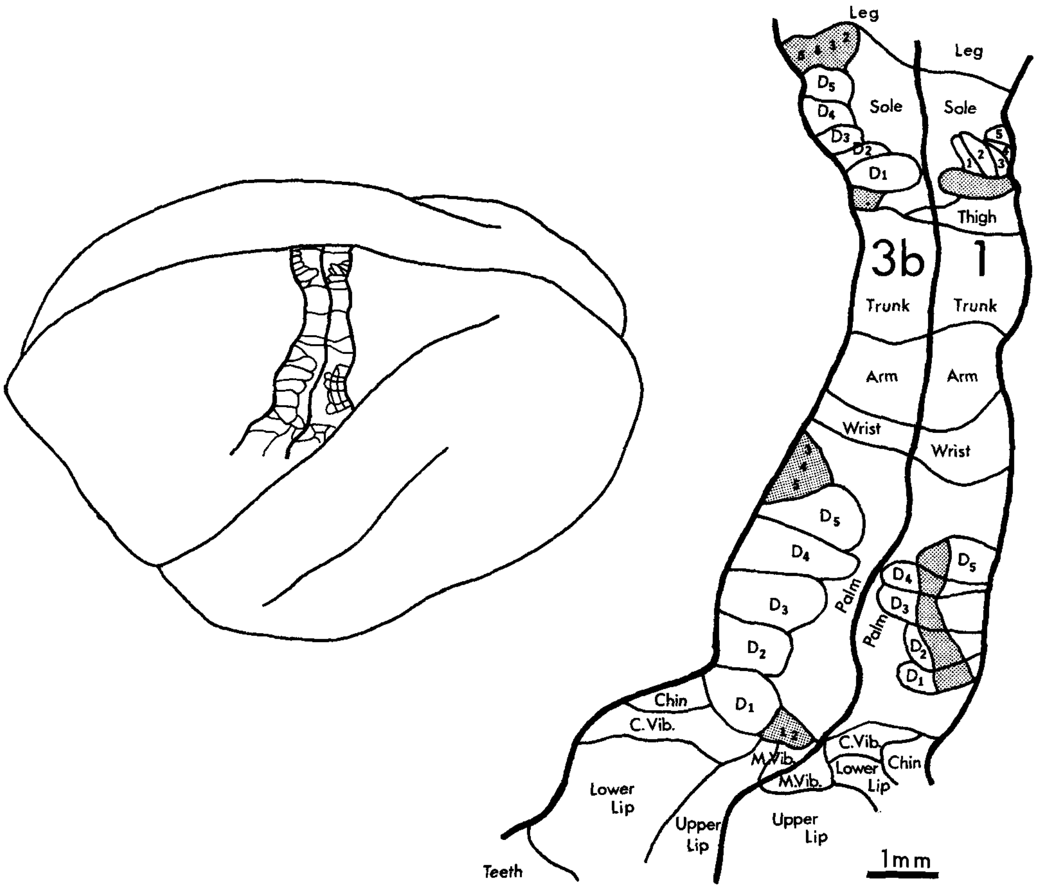

Fig. 1 The organization of the two representations of the contralateral body surface within two cytoarchitectonic fields (3b, 1) in the anterior parietal cortex of the owl monkey, *Aotus trivirgatus*. Sectors within each map representing the surfaces of the leg, sole, individual toes, preaxial thigh, trunk, arm, wrist, palm, individual fingers, chin, chin vibrissae, mandibular vibrissae, lower lip and upper lip are demarcated. Cortex representing the dorsal hairy surfaces of the fingers and toes are shaded. This reconstruction is based on receptive fields from 486 electrode penetrations in the "SI" region in a single owl monkey. Similar patterns of organization were found in other monkeys.

rons were sometimes mapped, any given receptive field in the illustrated maps must be assumed to have been derived for small clusters of neurons (Paul et al., '72a; Allman and Kaas, '74; Merzenich et al., '75). *Without exception,* all neurons studied at any given cortical locus had identical or nearly identical receptive fields.

Following recording experiments, small injections of horseradish peroxidase and/or tritiated proline were introduced at physiological defined locations. At this time, small electrolytic lesions were introduced at physiologically significant landmarks (usually at the borders of representations), and a series of surface locations were marked with carbon black to facilitate transfer of mapping data to photographs of the brain surface in that monkey. The animal was maintained with ketamine anesthesia for 20 to 30 hours after the termination of the recording experiment in order to allow the transport of the anatomical tracers. (Cerebral edema was, surprisingly, not a serious problem in these very long procedures in the owl monkey.) The animal was then perfused intracardially with saline followed by 8% formol-saline. The brain was kept overnight in fixative (at 4°C), passed through several increasing concentrations of sucrose in formalin ending in 30% sucrose, and the cor-

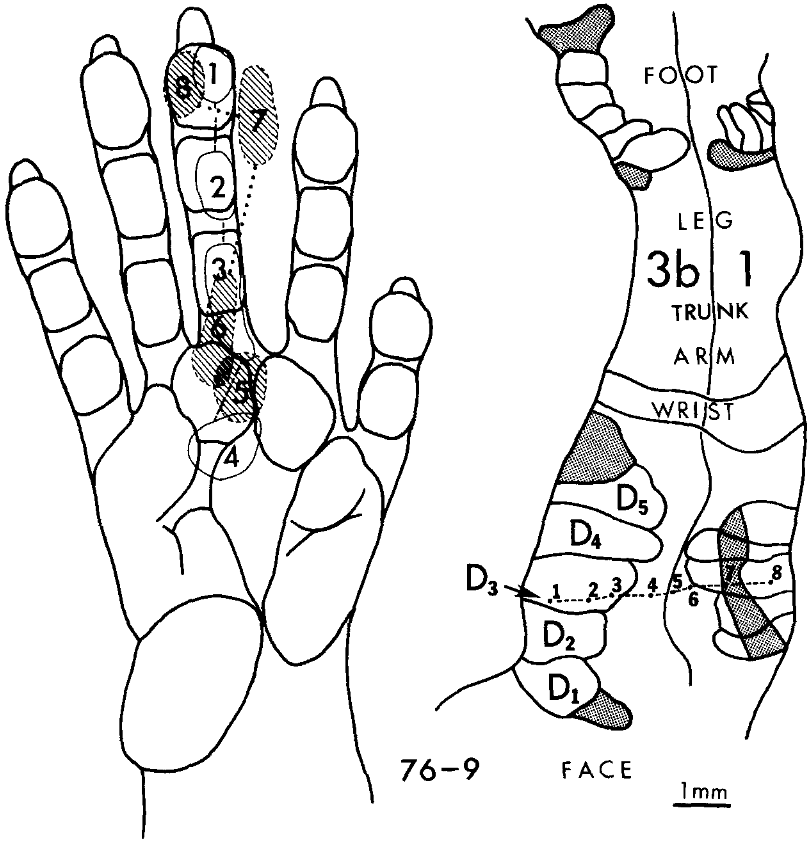

Fig. 2 Receptive fields defined within a row of electrode penetrations crossing the regions of Areas 3b and 1 representing the third digit and distal palm. The locations of electrode penetrations are shown on the right on a reconstruction of the mapped portion of Areas 3b and 1. The border between Areas 3b and 1 was defined architectonically. Receptive fields defined within penetrations in Area 3b are outlined with a solid line; those defined within Area 1 are crosshatched. Receptive fields drawn off the digits are on the dorsal hairy surfaces of the fingers at that location. The shaded areas in the reconstruction of the experiment are the regions of representation of the hairy surfaces of the digits.

tex cut frozen in the sagittal plane at 25 or 50 μm section thickness. Usually, every fifth brain section was processed for autoradiography and counterstained with cresyl violet. Another set of every fifth section was stained for myelin with hematoxylin. All remaining sections were stained with cresyl violet for cells. Experiments were later reconstructed, so that results of brain cytoarchitecture could be systemically related to mapping and tracer studies. Results of HRP and tritiated amino acid tracer studies are described elsewhere (Lin et al., '78).

## RESULTS

There are two highly ordered representations of the contralateral body surface within the "primary somatosensory cortex" ("SI") in the owl monkey. The basic pattern of representation of the body surface within these two large cortical subdivisions is shown schematically in figure 1. The relationship of the two areas is complex when considered in detail, and they are not identical. The two representations have been found to occupy cytoarchitectonic Areas 3b and 1 (as will be described later). In order to appreciate how body surface regions are represented in somatosensory cortex, it is useful to consider in detail the pattern of representation of specific skin surfaces within these two fields.

### *Representation of the hand in cytoarchitectonic Areas 3b and 1*

The hand is represented completely within

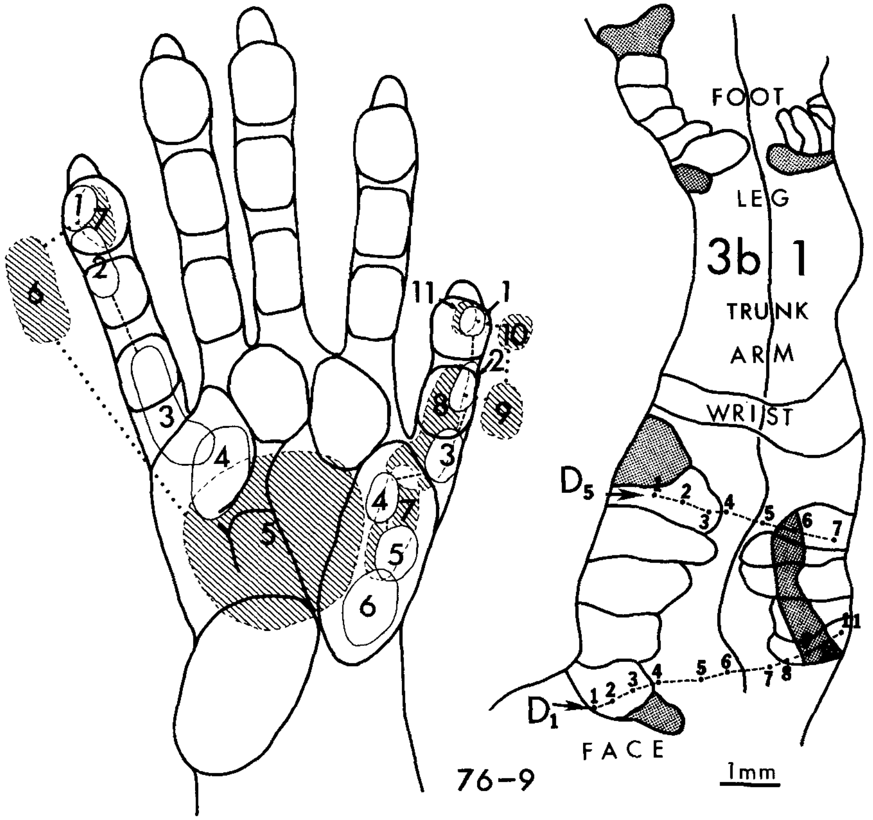

Fig. 3 Receptive fields defined for neurons within two rows of penetrations crossing Area 3b and Area 1 in the region representing the thumb and thenar eminence (row $D_1$ in the reconstruction to the right), and in the region representing the fifth digit and fourth interdigital and insular palmar pads (row $D_5$).

Area 3b and completely within Area 1. The two representations are roughly "mirror images." The tips of the fingers in Area 3b are represented along its anterior border and in Area 1 along its posterior border (fig. 4; figs. 2, 3). The rest of the glabrous skin of the fingers is represented twice in between with a reversal along the palm at the 3-1 border (figs. 2-5).

There is a highly ordered representation of the palmar pads in both representations (figs. 4, 5). The basic pattern of representation, derived from a relatively complete map of the hand obtained in a single experiment, is shown diagrammatically in figure 5. Within each representation, the thenar and hypothenar eminences are displaced from each other and represented in regions lateral and medial (respectively) to the representation of the interdigital pads and fingers. This split representation of the basal palm is more exaggerated in Area 1 than in Area 3. In rows of penetrations extending across the middle of the hand (i.e., the row illustrated in fig. 2), the line of reversal (in fig. 2, between electrode penetrations 4 and 5) runs across the base of the interdigital and insular pads. Thus, the representation of the glabrous surface of the hand is discontinuous. Topological discontinuities were found between the adjoining surfaces of the thenar and hypothenar eminences, the radial and ulnar insular pads, part of the border of both thenar and hypothenar eminences with adjacent interdigital pads, and in Area 1, between the most proximal and the more distal aspects of the thenar eminence.

The representation of the glabrous surfaces of the hand in Area 3b is a precisely ordered array. This order is evident in very fine grained mapping, such as that conducted in experiment 76-10, from which receptive fields derived in a continuous row of penetrations across the Area 3b hand representation are shown in figure 4. Penetrations over most of

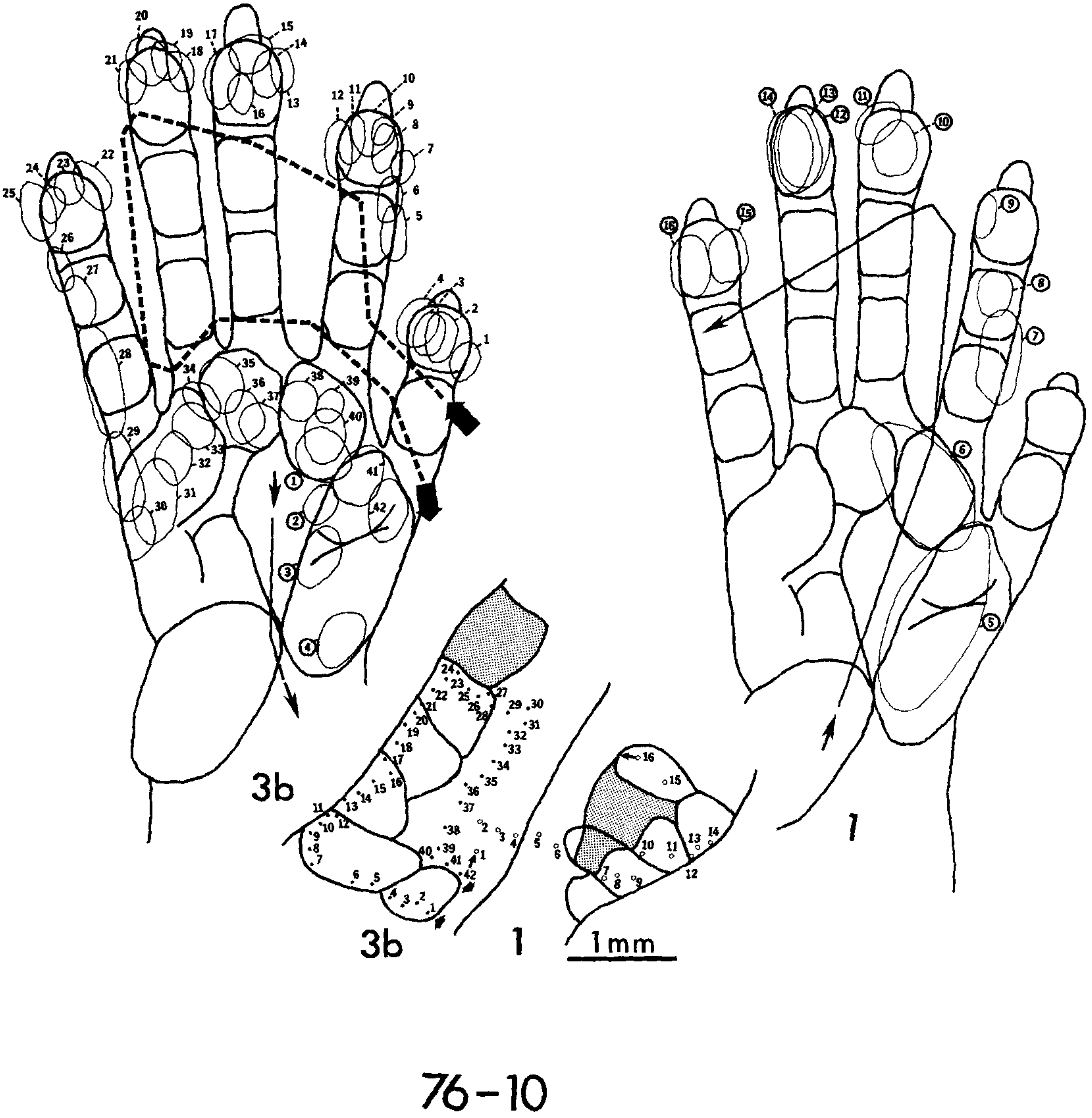

Fig. 4 Receptive fields defined for neurons within penetrations along two long rows within the hand representations in Areas 3b and 1. Receptive fields for penetrations in Area 3b are on the left; receptive fields for penetrations in Area 1 are on the right. The locations of penetrations in the two rows (dots and open circles) are shown in the reconstruction of the map derived in this study (bottom).

this row were about 200-250 μm apart. In this and similar rows, the centers of successively defined fields shifted in a highly predictable way, usually with significant overlap of minimum receptive fields (like the partially shifted overlap for receptive fields defined in adjacent cortical columns, by Mountcastle, '57, and Powell and Mountcastle, '59b). The representation of the ventral, glabrous surface of the hand in Area 3b was strictly segregated from the representation of the dorsal surfaces of the fingers and hand.

The representation of the glabrous surfaces of the hand in Area 1 was, at first glance, a mirror image of that in Area 3b, but when considered in detail several obvious differences were apparent. The orderliness of the Area 1 representation was not as strict as that of

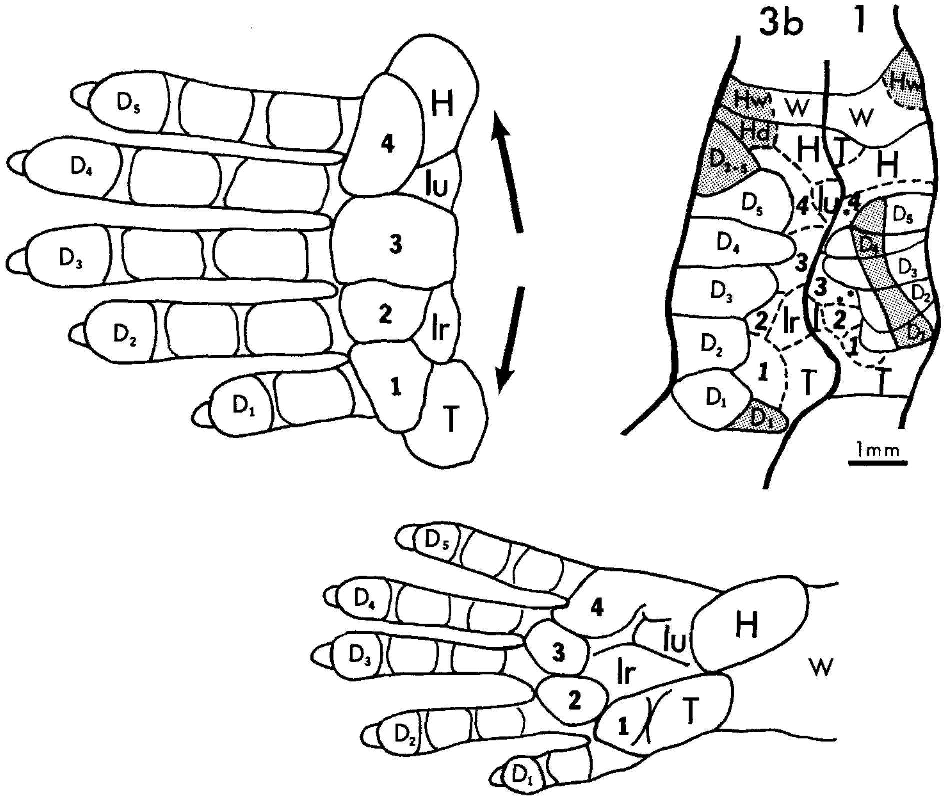

Fig. 5 The representations of the glabrous hand in Areas 3b and 1. The hand surface (below) is split between the pads of the palm and distorted (upper left) to fit the confines of area 3b in the cortical representation (upper right). The Area 1 representation is roughly a mirror image of the Area 3b representation. The detailed reconstruction of the hand representations shown on the upper right is based on a single extensive experiment. Receptive fields in Area 1 frequently extended over more than one pad, so that the indicated boundaries in the representation are not absolute. Asterisks in Area 1 indicate penetrations with neurons with very large receptive fields suggestive of Pacinian corpuscle input. The representations of the dorsum of the hand are shaded. Receptive fields in Hd (hand dorsum) were restricted to the hand dorsum; receptive fields for Hw (hand and wrist dorsum) included both parts of the wrist and hand dorsum. The digits ($D_1$-$D_5$) and interdigital pads (1-4) are numbered in the standard manner. Ir and Iu, radial and ulnar insular pads, T and H, thenar and hypothenar pads.

Area 3b. Receptive fields were commonly significantly larger within Area 1 than within Area 3b (see fields illustrated in figs. 2-4). Fields over the palmar pads, for example, frequently extended over an entire pad, or over broad sectors of adjacent pads. Nonetheless, the sequence of representation of the pads was very similar to that of Area 3b, with two exceptions. First, there was a small representation of the basal aspect of the thenar eminence in the extreme medial aspect of the Area 1 hand representation, adjacent to the representation of the wrist, and far from the representation of the rest of the thenar eminence on the extreme lateral side of the hand representation (fig. 5). Second, receptive fields along the base of the palm for neurons in Area 1 commonly included both the glabrous skin and some of the hairy skin of the wrist. Receptive fields for neurons in the Area 3b glabrous representational region never crossed the glabrous-hairy skin boundary.

The most striking difference in the hand representation of the two Areas, however, was in the pattern of representation of the dorsal hairy surface (fig. 5). Within Area 3b, the representation of the dorsal surfaces of the fingers was split. The representation of the hairy surfaces of the first and sometimes the second digit were on the far lateral aspect of

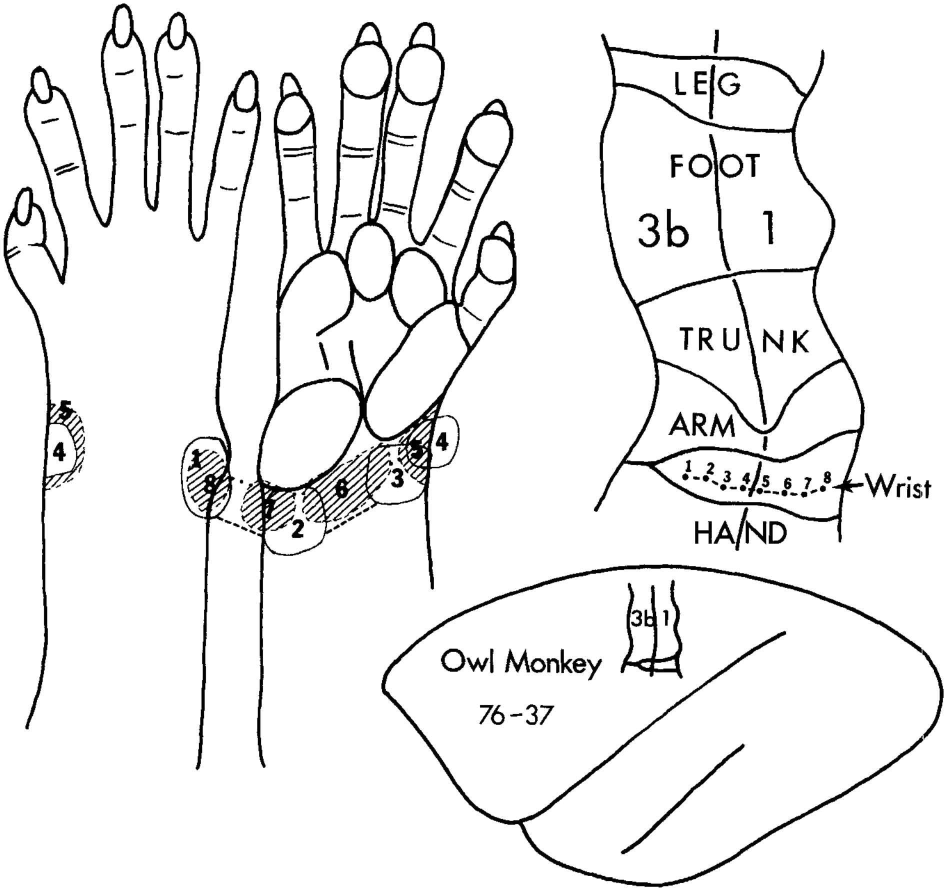

Fig. 6 Receptive fields defined within a row of penetrations crossing Area 3b and 1 in the region representing the volar wrist. Details as in figure 2.

the hand representation adjacent to the glabrous thumb. The hairy surfaces of the fifth, fourth, third and sometimes the second digits were on the extreme medial aspect of the hand representation adjacent to the glabrous surfaces of the fifth digit. The hairy surfaces were represented as a continuation of glabrous surfaces. Thus, the representation of the outer glabrous margin of the thumb in the lateral region moved onto the dorsal surface and marched across the hairy surfaces of digits 1 and sometimes 2. In the medial region, the representation progressed from the outer glabrous margin of digit 5 and then, in order across the hairy surfaces of digits 5, 4, 3 and sometimes 2. The representation of the back of the hand in Area 3b was continuous with the medial representation of the hairy finger surfaces (digits 5,4,3,2-var.). The representation of the hairy surfaces of the hand within Area 1 was very different. There, the dorsal surfaces of the fingers were represented within a band of cortex between the representation of the distal and middle phalangeal pads (fig. 5), or (in one case see fig. 4) between the representation of the proximal phalangeal pads and the palm. Thus, the dorsal hairy surfaces of the fingers in Area 1 were represented in an island of cortex completely encircled by the representation of the glabrous surfaces of the hand, and thereby creating a discontinuity in their representation by separating fingertips (or fingers) from the rest of the fingers (or palm). The hairy skin of the hand dorsum in Area 1 was represented in a region medial to the representation of the hand and volar wrist, far separated from the representation of the dorsal surfaces of the fingers. The piecemeal rep-

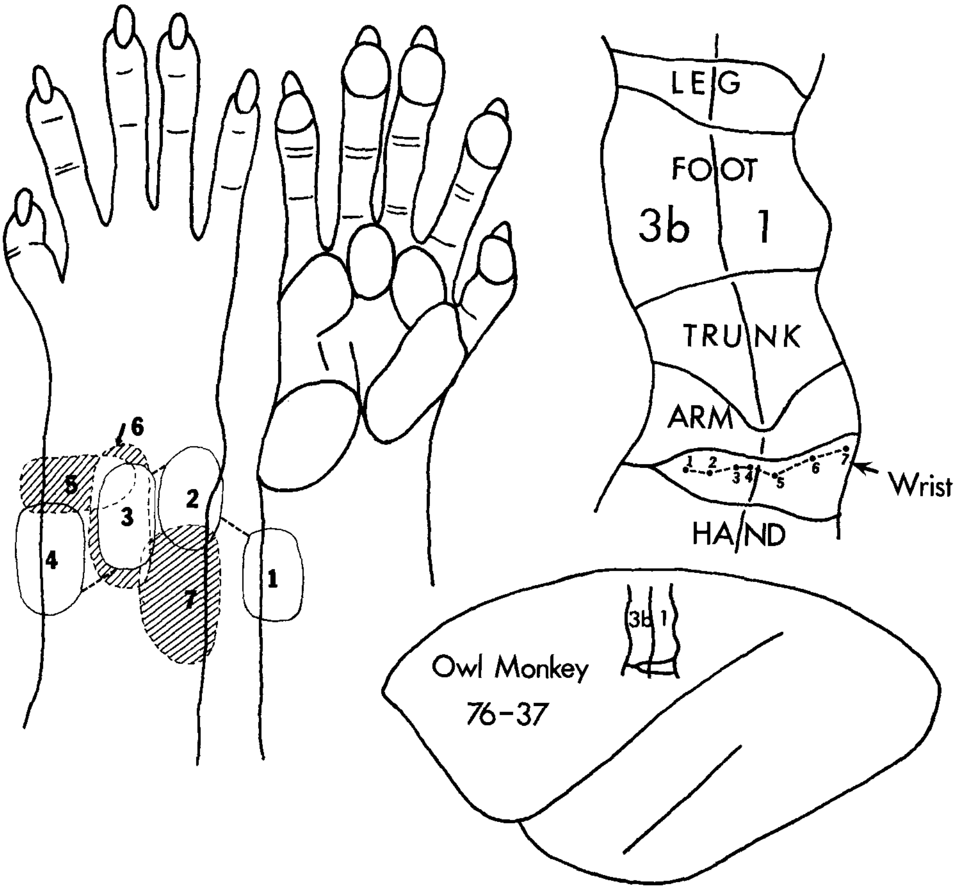

Fig. 7 Receptive fields defined within a row of penetrations crossing Areas 3b and 1 in the region of representation of the dorsal surface of the wrist. Details as in figure 2.

resentation of the hairy surfaces of the hand in Areas 3b and 1 is again illustrated in detail in the schematic drawing in figure 5.

### *Representation of the wrist and arm in Areas 3b and 1*

There are also two separate representations of the wrist and arm in Areas 3b and 1. The pattern of organization is complicated by the fact that the volar wrist surface was represented separately, and by the fact that the order of representation of the arm in Area 1 was often marked by discontinuities which differed in detail from monkey to monkey.

The volar wrist was represented within a narrow strip of cortex immediately adjacent to the representation of the hypothenar eminence, in both Areas 3b and 1. Volar wrist fields were in continuous sequence with fields on the eminence. As noted earlier, in Area 1 fields commonly overlapped the hairy wrist and glabrous hypothenar (or thenar) eminence surfaces, while in Area 3b, fields did not cross the hairy-glabrous skin boundary. The ulnar side of the volar wrist was represented toward the anterior margin of Area 3b, and near the posterior margin of Area 1 (fig. 6). Proceeding toward the 3-1 border in either field, successively defined receptive fields shifted over the wrist toward its radial margin, which was represented along the 3-1 border.

The dorsal wrist was represented within a narrow strip of cortex just medial to the representation of the volar wrist in an ulnar to radial to ulnar sequence identical to that of the volar wrist. Thus, as shown by example in figure 7, the ulnar side of the wrist dorsum

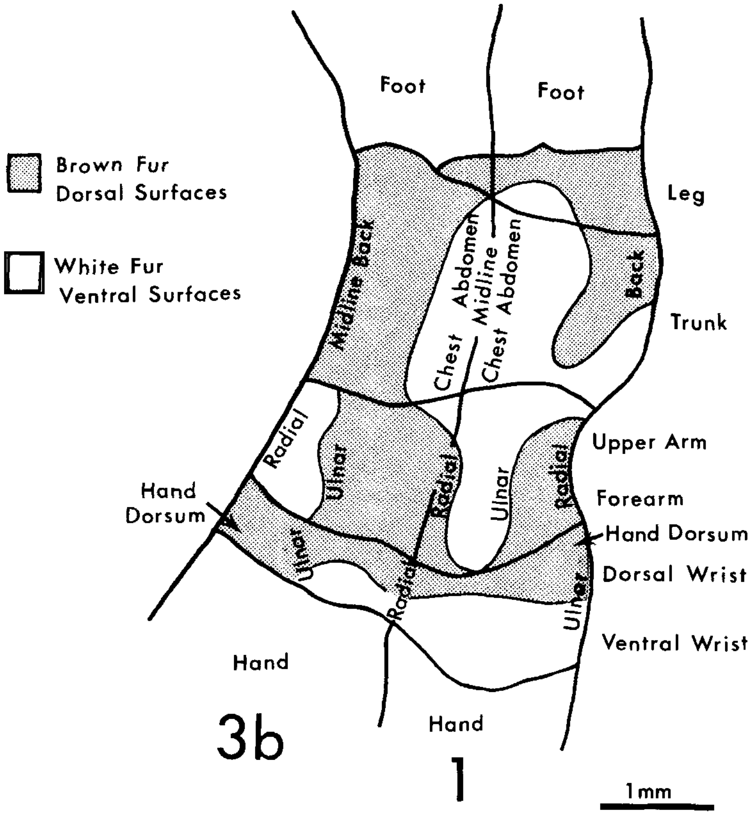

Fig. 8 The patterns of representation of the arm and trunk in Areas 3b and 1 in a single monkey (76-9). Representation of the brown fur of the arm dorsum, side and back of the trunk and lateral thigh (shaded region) and of the white fur of the ventral arm, axilla, chest, abdomen and medial thigh (not shaded) are shown. The patterns of representation of the arm and trunk differ in detail among individual monkeys (see text).

was represented near the anterior border of Area 3b and near the posterior border of Area 1. Proceeding toward the 3-1 border in either field, successively defined receptive fields shifted systematically toward the radial margin of the wrist dorsum, which was, again, represented along the 3-1 border. Note that given identical sequences in representation of the dorsal and ventral surfaces of the wrist, much of the representations of the two surfaces are discontinuous. Thus, recording sites 6 in figure 6 and 6 in figure 7 are close to each other on the brain but correspond to distant receptive fields located on the middle of the ventral and dorsal surfaces of the wrist, respectively.

The forearm and upper arm were also represented twice within Areas 3b and 1. Receptive fields defined near the anterior border of Area 3b or near the posterior edge of Area 1 were usually found to lie along or near the radial margin of the arm. Proceeding toward the 3-1 border within Area 3b, successively defined receptive fields shifted across the ventral surface of the arm toward the ulnar margin, and moved around the arm over the dorsal surface to return to a location near the radial margin, which was again represented along the 3-1 border. Thus, one can imagine the skin of the arm as being slit down the radial margin and laid out on the cortex of Area 3b with the ventral surface represented more anteriorly and the dorsal surface toward the 3-1 boundary.

The representation of the arm within Area 1 was difficult to reconstruct in detail. For some anterior-posterior recording sequences, successively defined receptive fields for Area 1 marched around the arm a second time in the

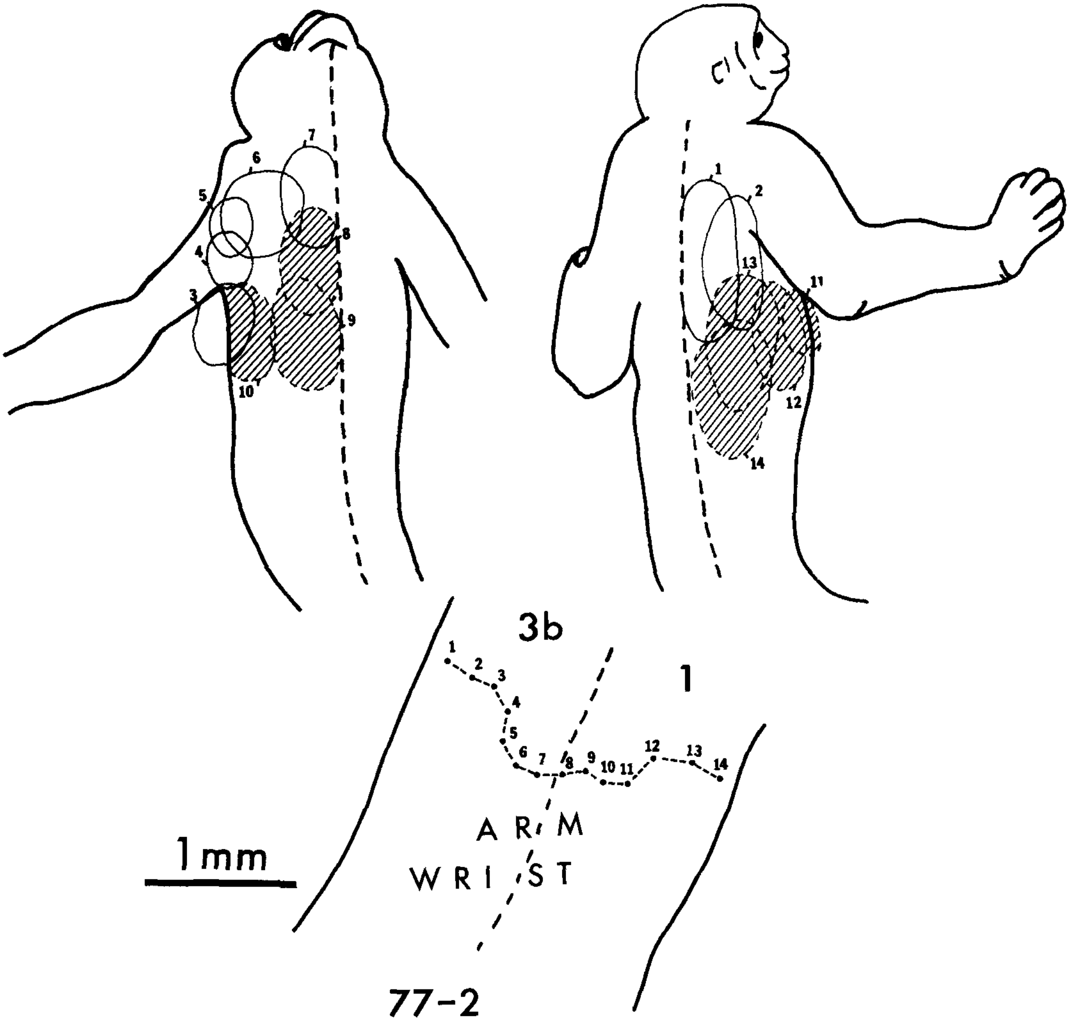

Fig. 9 Receptive fields defined within a long row of penetrations crossing Areas 3b and 1 in the region representing the chest and anterior back. Note the reversal in representational sequence across the 3b-1 border. Details as in figure 2.

same direction as was seen in Area 3b (as in the experiment illustrated in fig. 8). In other sequences, reversals or discontinuities in represented skin location were recorded within the Area 1 arm representation. Thus, although it is clear that there is a single and complete representation of arm surfaces in Area 1, as in the more clearly ordered Area 3b, a simple pattern of representation could not be defined that fit all derived mapping data in the several monkeys in which the arm representation was relatively completely mapped. These data indicated that, in fact, there must be significant variation in the way arm surfaces are represented within Area 1 in different individual monkeys.

### *Representation of the trunk*

The double representation of the trunk was difficult to illustrate completely in most monkeys because we found the representation of the back in Area 1 to be small (as in the case illustrated in fig. 8). Only a small number of receptive fields on the back have been defined in all experiments. On the other hand, the representation of the skin of the chest and abdo-

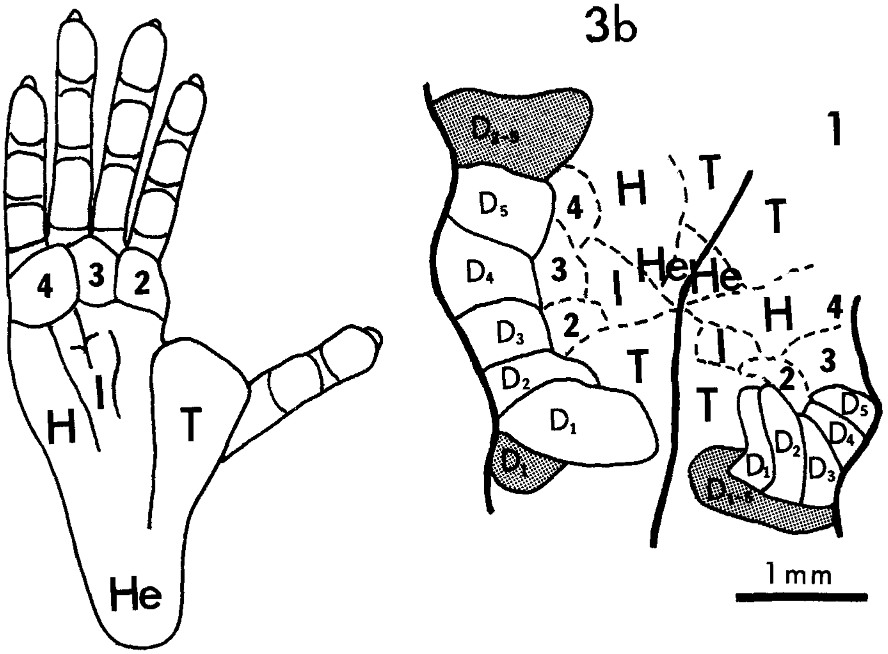

Fig. 10 Reconstruction of a detailed map of the representations of the foot, from an experiment in one of several monkeys in which the foot region was completely mapped. The heel and the interdigital, insular, hypothenar and thenar pads are identified on the diagram at the left. Boundaries between the pads of the sole (dashed lines) are not absolute in Area 1 since receptive fields frequently extended over more than one pad.

men actually appeared to be larger within Area 1 than within Area 3b. However, all mapping data were consistent with a crude mirror-image representation of the trunk, with the top of the back represented along the anterior margin of Area 3b and near the posterior margin of Area 1, and with the skin along the contralateral side of the midline of the chest and abdomen (the line of reversal) represented along the 3-1 boundary (fig. 9). The shoulder and back of head were located in the lateral aspect of the trunk representation, continuous with the arm, and far removed from the topologically adjacent face. In rows of penetrations passing in the lateral to medial direction within the trunk representation of either field, there was a systematic shift of receptive fields down the trunk, from the neck and shoulders and upper chest to the lower back and abdomen.

### *Representation of the foot in Areas 3b and 1*

Figure 10 is a schematic drawing of the representation of the contralateral foot within Areas 3b and 1. The figure was based upon one of several reconstructions of complete maps of the foot derived in individual monkeys. Again there was a double representation of foot surfaces in the two fields. The representation of the glabrous surfaces of the foot within Area 3b was highly ordered, and was similar in many respects to the Area 3b representation of the hand. The great toe (D1) was in the lateral aspect of the representation. The other digits were represented in order, progressing toward the midline, in a lateral-to-medial sequence. The distal phalanges of the toes were represented along the anterior border of Area 3b (figs. 11, 12). Proceeding toward the 3-1 border, successively defined receptive fields shifted down the digits onto the pads of the sole toward the base of the foot, which was represented along the 3-1 border. The representations of the foot pads in Area 3b were not separated from each other as were those of the palmar pads (fig. 10). The one notable exception was that some of the receptive fields on the thenar eminence were recorded in the medial aspects of foot representations in Areas

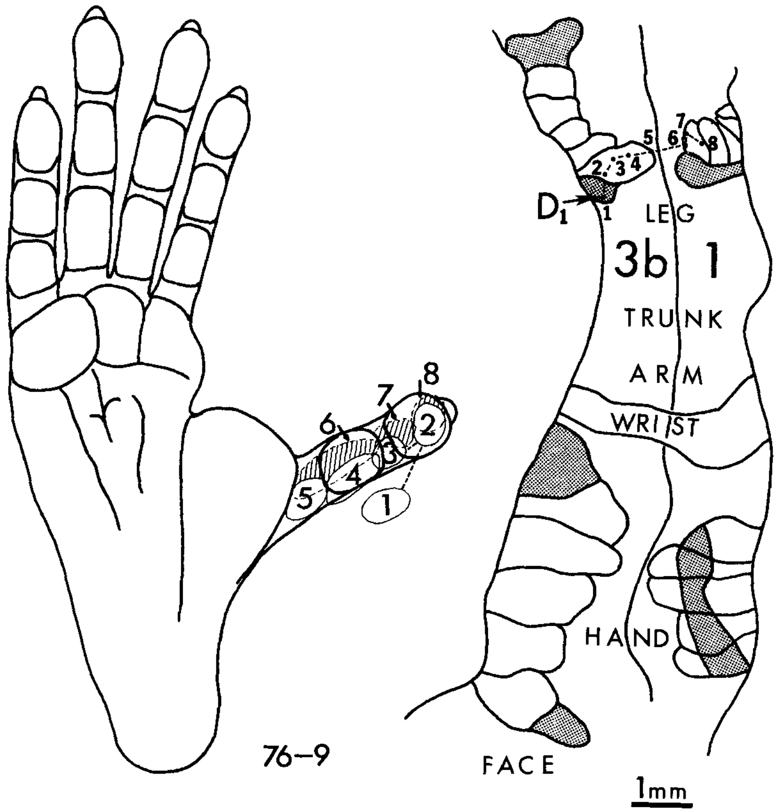

Fig. 11 Receptive fields defined within a row of penetrations crossing Areas 3b and 1 in the region representing the great toe. Details as in figure 2.

3b and 1. Therefore, these recording sites related to the thenar eminence were separated from those related to the representation of the rest of the thenar eminence.

Within Area 1, digits were represented in a largely anterior to posterior sequence, with the great toe near the middle of Area 1 and only the third (variable), fourth and fifth digits in contact with the posterior border of Area 1 (figs. 10-12). Thus, the representation of the foot within Area 1 was *not* a mirror image of that in Area 3b, although they were topographically very similar. The representation of the sole in Area 1 was like that in Area 3b. As in the hand representations, receptive fields for the pads of the sole were much larger in Area 1 than in Area 3b, and commonly extended over entire pads, or over adjacent pads.

The dorsal surfaces of the toes (as with the fingers) were ordered in a very different way within the two representations. In the Area 3b foot, the representation of the dorsal, hairy surfaces of the toes was split (in a manner similar to the split of the representation of the hairy fingers in Area 3b), with the dorsum of the great toe represented in a region lateral to that of the glabrous surface of the great toe, and with the hairy surface of digits 5, 4, 3 and 2 represented in order in the region medial to the representation of the glabrous surfaces of the fifth digit. As with the hand, the representational sequence moved around the outer surfaces of the first and fifth digits onto the adjacent hairy skin, and then marched over the hairy surfaces of the toe or toes. The representation of the foot dorsum was continuous with that of the fifth, fourth, third and second digits on the medial side of the Area 3 foot representation.

In contrast to the Area 3b representation, the dorsal surfaces of the foot within Area 1 were represented entirely on the *lateral* side of the foot representation, adjacent to the representation of the distal phalanges of digits 1, 2

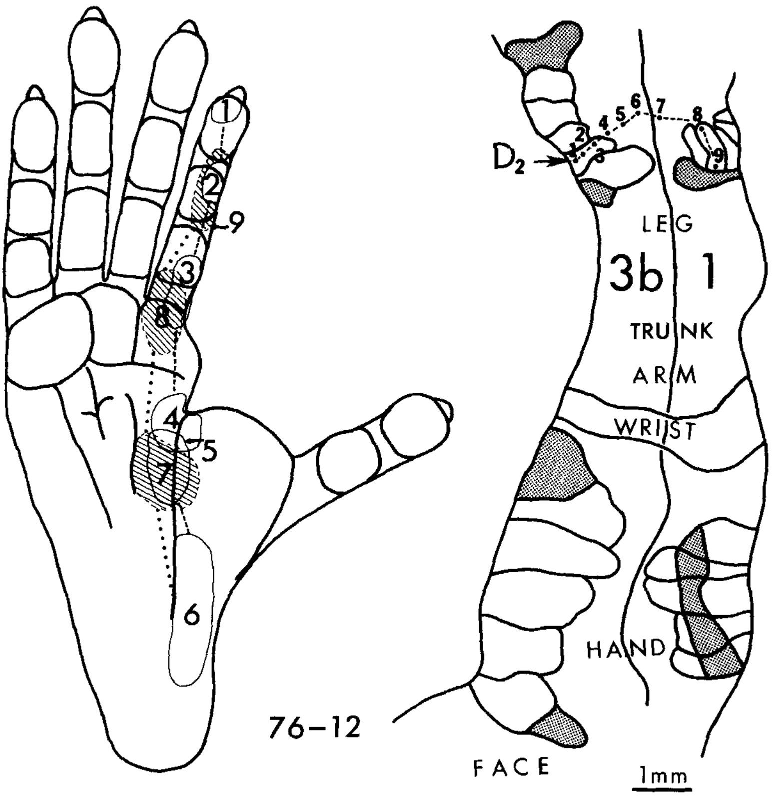

Fig. 12 Receptive fields defined within a row of penetrations crossing areas 3b and 1 in the region representing the second pedal digit, second interdigital pad, insular pad and heel. The representational sequence reverses between penetrations 6-7, near the proximal end of the glabrous foot. Details as in figure 2.

and 3 (figs. 10-12). Successively defined receptive fields in a lateral-to-medial sequence in this region marched from the proximal foot to the distal foot. Hairy surfaces on the distal phalanges of the toes were represented in the cortex adjacent to the representation of glabrous phalanges.

### *Representation of the leg*

The region representing the leg on the lateral surface of the cortex was explored, but since much or most of the leg representation was on the medial wall in the owl monkey, derived representational data were fragmentary. Available data were consistent with a re-representation of leg surfaces in Areas 3b and 1. The preaxial surface of the thigh was mapped in entirety within both representations. A few postaxial fields were also defined in Area 1 and 3b in this region.

As in some other species of primates (DISCUSSION), part of the leg was found both medial and lateral to the foot representation in somatosensory cortex of owl monkeys. While most of the leg was represented medial to the foot, significant portions were represented in cortex immediately lateral to the foot in both Areas 3b and 1. Both lateral leg representations were small (table 1), but the leg representation lateral to the foot was consistently larger in Area 1 than in Area 3b (in some experiments, no leg representation could be found lateral to the foot in Area 3b). The lateral representation of the leg in Area 1 was almost totally restricted to the preaxial surface of the thigh, which appeared to be represented there in its entirety. Receptive fields for sequences of recording sites in this region formed continuous sequences with those on the abdomen and lower back, indicating that the representations of the thigh and adjoining abdomen and back, are continuous. In contrast, rows of recording sites never revealed continuous sequences of receptive fields from the thigh to the lower leg. For example, in lateromedial rows of recording sites in the lateral leg representation in Area 1, a discontinuity was consistently found such that skin from the knee was adjacent to the cortical representation of the dorsal foot.

Surprisingly, the complete preaxial thigh in Area 3b was found on the *medial* side of the foot representation, where it has been mapped in detail. Thus, there are double representations of parts of the preaxial thigh in each of Areas 3b and 1, with the two representations lying on different sides of the representation of the foot.

### *Representation of the face in Areas 3b and 1*

The region of the face representation of the lateral surface of the cortex has been mapped in detail, but the representational area buried within the Sylvian fissure has not been systematically explored. The buried portion includes significant parts of the Area 3b and especially the Area 1 face representations. Nonetheless, the general pattern of representation of the face was evident. There is clearly a double representation of the face within the two cytoarchitectonic fields. The midline of the lower face (lower lip, chin vibrissae, chin) was represented at or near the anterior border of Area 3b, and at or near the posterior border of Area 1 (fig. 13). The region of the representation of the contralateral upper lip and mandibular vibrissae at or near the midline was along the 3-1 border. The two representations in Areas 3b and 1 were topographically similar, with areas on the face represented in roughly mirror-image sequence proceeding away from the 3-1 border. An example of this re-representation of the face is illustrated by the receptive fields for a long row of penetrations illustrated in figure 13. Beginning with a receptive field near the midline on the chin in the Area 3b representation (penetration 1, fig. 13), successive receptive fields were located first near the midline on the chin and lower lip, then progressing toward the corner of the mouth on the lower lip, and then toward the midline on the upper lip. A reversal in the sequence of the representation was recorded at the 3-1 border (between penetrations 8 and 9 in fig. 13). Receptive fields for the remaining recording sites crossing Area 1 retraced a sequence similar to that of Area 3b.

It should be noted that the representation of the chin was immediately adjacent to that of the glabrous skin of the first digit in Area 3b, and to the thenar eminence in Area 1 (figs. 5, 13). The representation of the chin vibrissae was adjacent to that of the glabrous thumb in Area 3b, and of the thenar eminence in Area 1. Finally, the representation of the mandibular vibrissae was adjacent to the representation of the dorsum of the finger in Area 3b, and to the thenar eminence in Area 1. No transition from the radial hand to the face *via* intervening skin could be recorded. This step was discontinuous, within the finest possible grain of recording. As noted earlier, contiguous interconnecting skin surfaces (arm, shoulder, side of head) were found to be represented within the cortex in a region medial to the representation of the hand and wrist, and far from that of the face.

A very large representation of the contralateral teeth was mapped within Area 3b. Our maps never extended into the probable location of the Area 1 representation of the teeth, or the tongue. The teeth were represented lateral and rostral to the lower lip in Area 3b. In penetration rows directed rostralward in Area 3b, successive receptive fields shifted from near the midline on the lower lip onto the lower incisors and then to the more lateral lower teeth. Still further rostralward, receptive fields crossed to the lateral upper teeth, and then moved medialward toward the upper incisors.

### *The proportion areas of cortex devoted to different skin surfaces within Area 3b and Area 1*

It is of interest to note that the proportional representation of different body surfaces within the Area 3b representation is similar, but definitely *not* identical to that within the Area 1 representation. These two large body surface representations are *not* scale versions of each other.

To illustrate how the areas of representation of different body surfaces vary in the two fields, areas from maps have been measured planimetrically. Measurements derived from one extensively studied owl monkey (consistent with similar, more fragmentary data derived in other monkeys) are recorded in table 1. Excluding the incompletely mapped face, leg, tail and genital representations, the Area 3b representation was about 35-40% larger than that in Area 1. The representation of the hand was about one and a half times larger in

TABLE 1

*Area of representation of different body surfaces within areas 3b and 1 in Owl Monkey 76-9*

| Represented body surface | Area 3b representation (mm²) | | Area 1 representation (mm²) | | Area 3b/area 1 |
|---|---|---|---|---|---|
| Hand | 11.5 | | 7.6 | | 1.51 |
| Glabrous digits | | 5.8 | | 2.3 | 2.52 |
| Palm | | 4.6 | | 4.2 | 1.10 |
| Dorsum | | 1.1 | | 1.1 | 1.00 |
| Wrist | 0.8 | | 1.5 | | 0.53 |
| Arm | 1.9 | | 1.8 | | 1.06 |
| Trunk | 2.7 | | 2.3 | | 1.17 |
| Leg (lateral to foot) | 0.1 | | 0.7 | | 0.14 |
| Foot | 4.9 | | 2.7 | | 1.81 |
| Glabrous digits | | 1.9 | | 0.6 | 3.17 |
| Sole | | 2.2 | | 1.6 | 1.38 |
| Dorsum | | 0.8 | | 0.5 | 1.60 |
| Total [1] | 21.8 | | 15.9 | | 1.37 |

[1] Excluding leg lateral to foot, and incompletely mapped face, leg medial to foot, tail and genital representations.

Area 3b than in Area 1. The representation of the foot was nearly twice as large. In contrast, the representation of the trunk and arm were nearly equal in the two Areas, and the representation of the wrist was actually larger in Area 1 than in Area 3b.

It is evident from table 1 that the biggest disparity between Areas 1 and 3b was in the proportional areas of the representations of subdivisions of the hand and foot. The area representing the glabrous surfaces of the hand digits in Area 3b, for example, was over twice as large as that in Area 1; while the areas representing the palm and the dorsal hand were nearly equal in Area 3b and Area 1. As an even more striking example, the area of representation of the glabrous surfaces of the foot digits in the Area 3b representation was over three times as large as in Area 1. In contrast, the representations of the sole and dorsal foot in Areas 3b and 1 were more nearly equal. Thus, it would appear that much of the difference in the overall sizes of the two representations can be attributed to a proportionately larger representation of the glabrous surfaces of the fingers and toes in Area 3b.

### *Fields bordering Areas 3b and 1*

Penetrations were introduced into Areas 3a, 4 and 2 in all mapping experiments. The cortical region posterior to Area 1 (including Area 2) was extensively mapped in two experiments.

In penetrations anterior to Area 3b, neurons were not driven by light tactile stimulation. Numerous lesions were introduced along this anterior border of the anterior cutaneous somatosensory representation. Medially, this boundary fell along a distinct Area 3b-3a border; laterally, Area 3a was very narrow or absent, and Area 3b appeared to directly border Area 4. In some penetrations into Area 3a, neurons were driven by deep (never cutaneous) stimuli, while in other penetrations neurons were driven poorly if at all even by stimulation of deep body tissues. If neurons in Area 3a were responsive to deep stimuli, the Area 4 border could be detected by a marked reduction in responsiveness.

In some instance, intracortical stimulation was employed to confirm the position of the caudal border of Area 4. Those experiments were conducted in Area 4 adjacent to the Area 3b representation of the face and hand. Within this region, Area 3a is very narrow or absent. The rostral boundary of Area 3b defined through use of light tactile stimulation corresponded closely (within a few 100 μm) to the caudal border of Area 4 defined by low threshold movements produced by intracortical "microstimulation."

Two classes of responses were encountered in a broad region caudal to Area 1. In a very

Fig. 13 Some features of representations of the face within Areas 3b and 1. As in other primates, there is a disproportionately large representation of the anterior face, especially of the lips and the vibrasse of the chin and upper jaw. These skin surfaces (indicated in the drawing at the upper right) are represented in Areas 3b and 1 as shown in the drawing at the lower left. Receptive fields defined within a long row of penetrations crossing the Area 3b and Area 1 face representations are drawn at the lower right (Area 1 fields, right Area 3b fields, left). Penetrations in this irregular row were chosen to show approximately corresponding lines of receptive fields for both cytoarchitectonic areas.

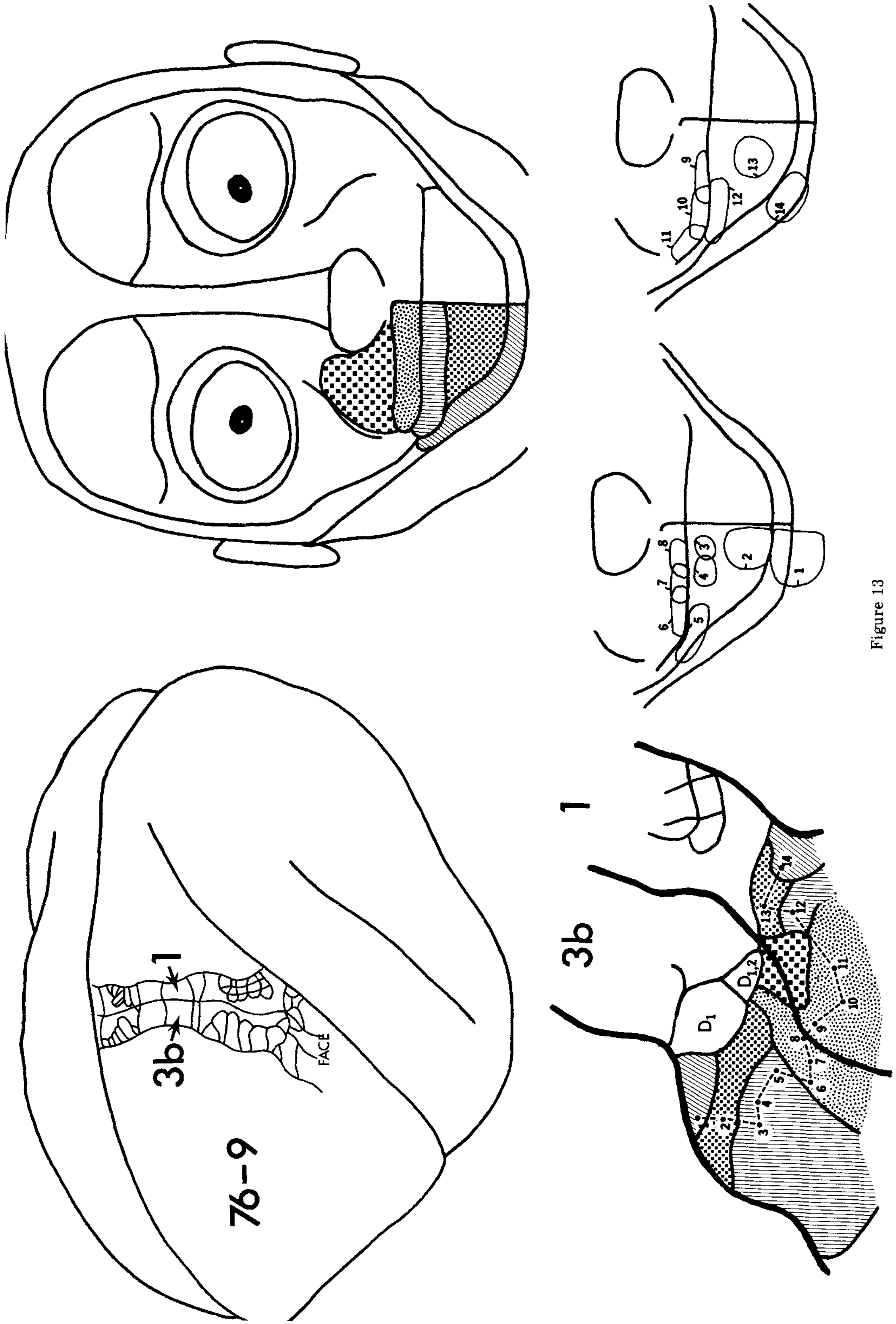

Figure 13

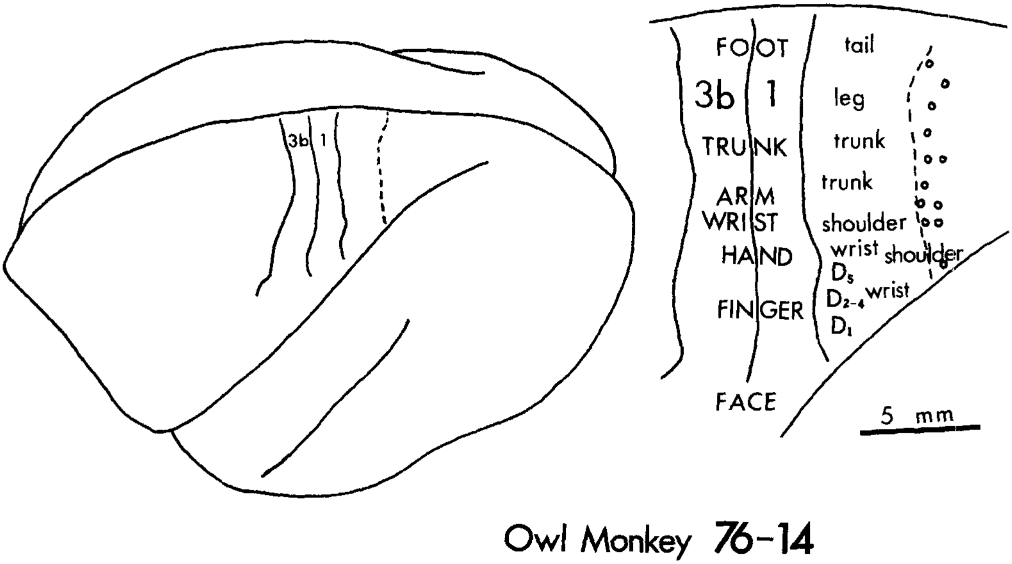

Fig. 14 The basic pattern of the representation of deep body structures within the cortical region caudal to Area 1. This schematic drawing summarized results obtained in an extensive mapping experiment conducted in Areas 3b and 1 and the cortex caudal to Area 1. In the caudal representation (including and possibly coextensive with Area 2), neurons responded specifically to stimulation of joint or other "deep" receptors in the indicated body regions (see text). Circles mark penetrations within which neurons were not obviously driven by tactile or deep somatic stimulation.

narrow strip immediately adjacent to Area 1, neurons were commonly driven by light tactile (cutaneous) stimulation over very large receptive fields. These receptive fields commonly extended over the entire body surface region represented in adjacent Area 1. Thus, adjacent to the representation of the abdomen in Area 1, for example, neurons in this narrow zone might have receptive fields that extended over part of the chest, the entire abdomen, and the medial surface of the leg. In a few exceptional cases, such receptive fields appeared to extend across the midline. Input to these neurons appeared to be cutaneous, and not from the Pacinian receptors. These responses were never recorded more than a few 100 $\mu$m from the border of Area 1, and frequently neurons in penetrations just posterior to Area 1 could not be driven by cutaneous stimulation. Nonetheless, these data suggest that there might be a very narrow, third cutaneous or mixed modality representation of the body surface in "SI" of the owl monkey.

In a much broader and clearly delimited field behind Area 1 (probably coextensive with Area 2), neurons could be driven by manipulation of joints or other "deep" stimulation, and were *never* excited by cutaneous stimulation. Rows of recording sites revealed that there is an orderly representation of deep body structures within this region, with the sequence of representation paralleling that of skin surfaces represented in the nearby cutaneous sensory strip (fig. 14). Input at many loci within this field appeared to be derived from joint receptors. However, it was not possible to unequivocally define the receptor source of this "deep" input (especially when the effective stimulation required movement of the shoulder girdle, neck, back or hips).

### *The relation of electrophysiological results to cortical architecture*

The cytoarchitecture of the somatosensory and motor areas of the cerebral cortex of New World monkeys had been described for marmosets by Brodmann ('09) and Peden and von Bonin ('47), for squirrel monkeys by Rosabal ('67), Sanides ('67) and Jones ('75), and for cebus monkeys by von Bonin ('38). Since characteristics of the somatic fields appear to be very similar in these monkeys and in owl monkeys, the major architectonic features are only briefly reviewed below. These features are apparent in figure 15, which shows photomicrographs of Areas 4, 3a, 3b, 1 and 2 in owl monkeys. Since they have general acceptance, Brodmann's ('09) numbers are used, although Sanides ('68), Peden and von Bonin ('47) and von Bonin ('38) used other nomenclature. The two architectonic fields of most interest for the present study are Areas 3b and 1.

The major features of Area 3b are easy to appreciate in the owl monkey because this subdivision is located in relatively flat cortex (see, for example, fig. 15A). Unlike most primates there is no central fissure to distort the architectonic features. However, owl monkeys generally do have a short, shallow dimple in the expected location of the middle part of the central fissure, and this dimple is shown in figures 15B and C. The dimple is rarely deeper than that shown in figure 15, and it does not significantly alter the laminar pattern of the underlying cortex. When the dimple occurs, it is over Area 3b with usually more of 3b rostral than caudal to the dimple. Therefore the dimple is a good landmark in recording experiments.

Area 3b is a koniocortical or hypergranular field identified by the densely packed granular cells in the outer cell layers. The cell packing in layer IV is most dense, but cells are also tightly packed in layers II and III so that layers II-IV sometimes appear to fuse (fig. 15A). Layer VI is slightly more dense than in adjoining cortex so that the relatively light layer V stands out in contrast to the layers above and below. Area 1 is marked by a less dense but obvious inner granular cell layer, and a less dense layer V. The transition from Area 1 to more caudal parietal cortex, Area 2, is denoted by an increase in layer III and layer V pyramidal cells and more densely packed cells in layer IV. Area 3a has both the larger pyramidal cells in layer V characteristic of motor cortex and a clear inner granular layer characteristic of sensory fields, and therefore has been called a transitional or intermediate field. However, Area 3a has distinct boundaries with Areas 4 and 3b, and does not appear as a gradual transition from motor to sensory fields. Rather, we agree with Sanides ('68) that Area 3a is a separate field with a "character" that does not "allow one to consider it a subdivision of Area 3." The motor field or Area 4 is rostral to the central dimple, and is characterized by large pyramidal cells in layer V, overall low density of neurons, and the lack of a clear granular cell layer. Area 4 is several millimeters wide, and gradually merges laterally with cortex having smaller pyramidal cells. Stimulation experiments suggest that this cortex is also part of the motor representation.

In alternate brain sections stained for myelinated fibers, Area 3b is more densely myelinated than is Area 1, and we found this feature useful in distinguishing between the two fields. The myeloarchitecture of postcentral cortex has been described in detail in the squirrel monkey by Sanides ('68) and Jones ('75) and the overall features are similar in owl monkeys.

In all recording experiments, electrolytic lesions were made along the boundaries of the two body surface representations in order to relate the recording results to cortical architecture. Two examples of brain sections with such marking lesions are shown in figures 15B and C. Cytoarchitectonic field boundaries were completely reconstructed from this histological material. The field boundaries drawn in all illustrations represent such objectively defined lines, drawn solely from histological reconstructions. Coincidence of the distinct cytoarchitectonic and functional boundaries of these fields is remarkable. *In all instances:* (1) Lesions placed at the electrophysiologically defined border between the rostral and the caudal cutaneous representation of body surfaces were later found to be along the border between cytoarchitectonically defined Areas 3b and 1 (fig. 15B); (2) lesions placed along the caudal border of the caudal cutaneous field were between Areas 1 and 2 (fig. 15B); (3) lesions located along the rostral border of the rostral cutaneous field were between Areas 3a and 3b (fig. 15C).

### *Individual variations in the organization of Areas 3b and 1*

As has been noted earlier, these mapping studies have revealed that there is unequivocal variation in the detailed pattern of representation in different individual monkeys. Examples include: (1) The arm representation in Area 1 was different in detail in every mapped monkey. In Area 3b, the region of the rostral margin of the arm representation was different in individual owl monkeys. (2) In most owl monkeys, the hairy skin of the dorsal fingers in Area 1 was represented continuously between the representation of the glabrous fingertips and that of the middle and proximal phalanges. In one extensively mapped exceptional case, they were represented in a region between a representation of the entire glabrous surface of the digits and the distal palm. (3) In one monkey, the representation of the back in Area 1 was clearly defined throughout the mediolateral extent of the representation, and the back representation occupied a relatively large proportion of the total Area 1 trunk representation. In all other monkeys, the Area 1 back representation was very small, and receptive fields on the back were defined only a few penetrations in the most posterior aspect of the field. The pattern of representation appeared to differ in fine detail in each owl monkey. Certainly, individual variation in the organization of sensory areas is much greater than has been generally appreciated.

## DISCUSSION

The microelectrode mapping results of the present study lead to the conclusions that each of two separate architectonic fields in owl monkeys is occupied by a map of the skin surface, that the two maps differ in organization, and that a third architectonic zone is devoted to non-cutaneous "deep" receptors. The results obviously require modifications and revisions of some of the current concepts of "SI" organization in primates, and new terminology will be needed to reflect these changed concepts. In addition, the results and conclusions raise the important questions: (1) What are the homologues of these separate representations in other mammals, and (2) how did these multiple representations evolve? These issues are considered further below.

### 1. *Current tenets of somatosensory organization*

The parietal somatosensory region has been mapped in a number of primate species, including the slow loris, marmoset, squirrel monkey, cebus monkey, spider monkey, macaque monkey, gibbon, chimpanzee, and man. From these studies, a concept of the organization of the primate parietal somatosensory cortex has arisen that includes at least six principal tenets. *First,* there is a single representation of the contralateral body surface ("SI") within the parietal sensory strip. *Second,* this representation overlies more than one clearly delimitable cytoarchitectonic field. *Third,* the two-dimensional organization of "SI" is (a) a somatotopic homunculus; (b) a sequence of rostrocaudal bands each devoted to a single body part; or (c) some combination of these two views. *Fourth,* the representation of the body surface follows a dermatomal sequence. *Fifth,* the proportional representation of different body surface regions is a reflection of peripheral innervation density. *Sixth,* "SI" is the primary functional division of somatosensory cortex. While investigators have derived evidence contrary to almost all of these commonly held tenets, these concepts of somatosensory cortex still dominate. Therefore, it is useful to start by reviewing evidence for and against each of these ideas, and to suggest modifications and revisions that are consistent with present and previous results.

#### (a) There is a single representation of the body surface in the parietal somatosensory strip in primates

Investigators who have studied the representation of the body surface within the parietal somatosensory strip using microelectrode and surface evoked potential mapping techniques have described a single representation of the body occupying the "SI" region in the New World marmoset (Woolsey, '52, '54), squirrel monkey (Benjamin and Welker, '57; Werner and Whitsel, '68), cebus monkey (Hirsh and Coxe, '58) and spider monkey (Chang et al., '47; Pubols and Pubols, '71, '72); in the Old World rhesus monkey (Marshall et al., '37; Woolsey et al., '42; Mountcastle and Powell, '59; Werner and Whitsel, '68; Whitsel et al., '71; Dreyer et al., '74, '75); in the gibbon (Woolsey et al., '60; Welt, '63); the chimpanzee (Woolsey et al., '43; Woolsey et al., '60; Welt, '63); and in humans (Penfield and Boldrey, '37; Penfield and Rasmussen, '50). However, there have been notable exceptions to the idea of a single "SI" representation. Most importantly, Paul et al. ('72a) presented evidence for two complete and separate cuta-

Fig. 15 Some features of the cytoarchitecture of the parietal somatosensory strip illustrated in Nissl-stained parasagittal sections. Boundaries of cytoarchitectonic Areas 4, 3a, 3b, 1 and 2 are indicated by arrows. Lesions in B were introduced at locations determined physiologically to mark the approximate boundaries of the posterior body surface representation. In all such instances, these marks fell at or very near the Area 1 boundaries. The lesion in C was one of the many introduced at the site of the first penetration rostral to the anterior body surface representation. All such lesions fell along the 3b-3a (or far laterally, along the 3b-4) boundary. Boundaries of Areas 3b and 1 were defined solely on cytoarchitectonic bases from material like that shown in A-C in all illustrated cases. Note the very shallow, incomplete (absent at the level shown in A) central sulcus. It is rarely deeper than as seen in B and C. Marker bar, 1 mm.

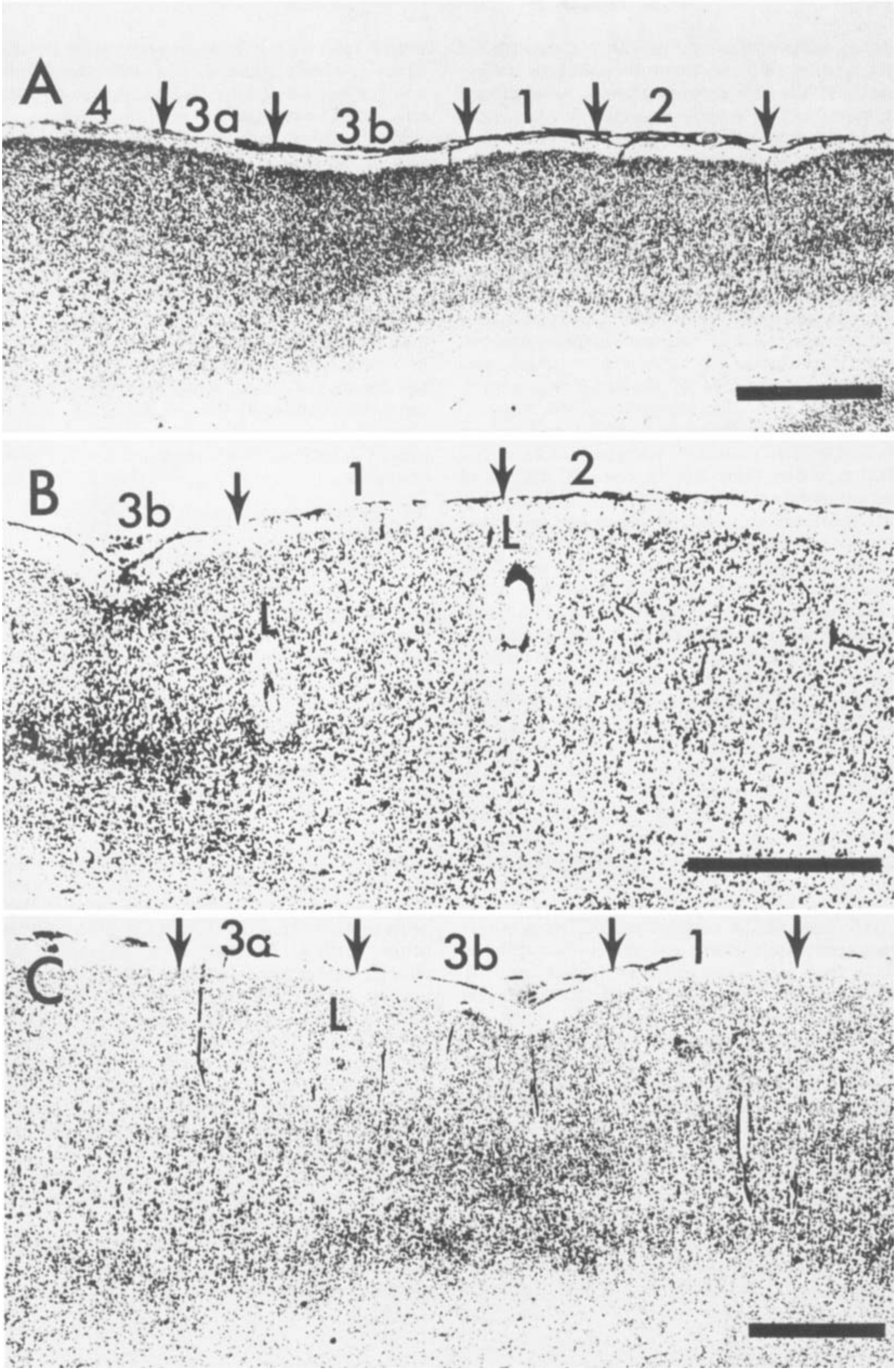

Figure 15

neous representations of the glabrous hand surface in "SI" of macaque monkeys (other parts of "SI" were not explored). A second exception is the recent report of a cutaneous body representation completely within only one of the architectonic fields of the "SI" region of the prosimian, slow loris (Krishnamurti et al., '76). While further representations were not identified in these experiments, the finding of a complete representation restricted to only part of "SI" clearly challenges the concept of "SI" as a single representation. Furthermore, cortex adjoining the cutaneous representation was responsive to somatosensory stimulation. A third report which was strongly suggestive of multiple representations was that of Zimmerman ('68). This investigator noted separate rostral and caudal foci of evoked responses to light tactile stimulation of the digit tips in the "SI" region of somatosensory cortex of the squirrel monkey. Zimmerman argued that these foci indicated two "entirely separate and differently organized sensory areas" for three reasons. First, the rostral and caudal foci were discontinuous; second, the two zones differed in response characteristics such as the latency, following frequency and threshold; third, experiments involving spreading depression showed that responses in the two foci were independent. Unfortunately, the experiments of Zimmerman had limited impact, perhaps because he regarded the rostral somatosensory zone as within "somatomotor" cortex rather than as a functional division of "SI" cortex. To us, it appears that both the rostral and caudal foci were within the region commonly considered the "SI" field in squirrel monkeys.

While there are few examples of direct challenges to the concept of "SI" as a single representation, there are many examples of data that are inconsistent with that concept. Starting with the initial pioneering studies on macaque monkeys, Woolsey et al. ('42) described a second representation of the thumb on the caudal bank of the central fissure that was "at some distance" from the representation of the thumb on the dorsal surface of postcentral parietal cortex. Likewise, microelectrode single unit and mapping studies (Powell and Mountcastle, '59b; Whitsel et al., '71; Dreyer et al., '75) have consistently noted the activation of nonadjacent cortical locations within "SI" from the stimulation of a single body location. Dreyer et al. got so far as to conclude that, for each body part of "SI," "a single region in the periphery is represented several times in widely separate locations." This viewpoint is not far from a formal rejection of the single "SI" concept.

While there have been a few conclusions and many observations in conflict with the concept of "SI" as a single representation in primates, this concept has persisted. We believe that the present extensive mapping of the "SI" region of the owl monkey presents unequivocal evidence that there are two cutaneous representations in owl monkeys. Furthermore, more limited mapping results indicate a third representation that is devoted to non-cutaneous receptors. Thus, we feel that the concept of a single representation in "SI" must be abandoned for owl monkeys, and in view of these and previous results, must be placed in serious doubt or abandoned for other primates.

### (b) The body representation in the parietal somatosensory strip occupies more than one architectonic field

It has been recognized from the first surface evoked potential somatosensory mapping studies (Marshall et al., '37; Woolsey et al., '42) that "SI," as described in macaque monkeys, would include more than one cytoarchitectonic field. These authors concluded that the "SI" representation occupied Brodmann's Areas 3, 1 and 2, but not the adjoining Areas 4 and 5. The viewpoint that "SI" includes Areas 3, 1 and 2 has prevailed for macaques and other primates (Whitsel et al., '71; Whitsel et al., '72; Dreyer et al., '74, '75).

However, it has been puzzling why a single representation should have distinct architectonic subdivisions. Such distinct and different architectonic "subunits" are not found within other cortical sensory representations (although subregions of some structural specialization occur; the monocular and binocular portion of striate cortex can be distinguished, for example). The usual way to account for the architectonic differences within "SI" has been to relate them to varying extents of submodality segregation within the field (Powell and Mountcastle, '59b; Werner and Whitsel, '68; Whitsel et al., '71; Dreyer et al., '75). Such segregation, of course, implies either separate maps or rostrocaudal bands of "isorepresentation" (see below).

Not all investigators have included more than one architectonic field within "SI." In macaque monkeys Paul et al. ('72a,b) argued for a representation of the hand within Area 3b, a second representation of the hand within Area 1, a possible third "deep" representation in Area 2, and other non-cutaneous activation within Area 3a. Krishnamurti et al. ('76) reported a complete body surface representation that was coextensive with somatic koniocortex or Area 3b of the slow loris (Sanides and Krishnamurti, '67). These conclusions agree with the present results, which indicate that there is a large body surface representation that is coextensive with Area 3b and a second somewhat smaller body surface representation that is congruent with Area 1. Area 3a is outside this cutaneous sensory strip. And there is an orderly representation of deep body structures (probably coextensive with Area 2) within the cortical region caudal to Area 1.

### (c) The representation of the body surface is a homunculus, or forms rostrocaudal bands of isorepresentation

There have been two different basic viewpoints as to how a single body representation, "SI," lies across the several architectonic fields in primates. Many investigators have summarized the pattern of the representation of the body surface on the parietal cortex by describing or drawing a "homunculus" (or "simiunculus"), a body figure distorted to illustrate the proportional representation of different skin surfaces. The homunculus has been shown or described as having the same overall orientation on the brain of prosimians (Krishnamurti et al., '76, where it was confined to Area 3b), marmosets (Woolsey, '52), squirrel monkeys (Benjamin and Welker, '57), macaques (Woolsey, '58, '64), chimpanzees (Woolsey, '64), and humans (Penfield and Boldrey, '37; Penfield and Rasmussen, '50). The distal limbs and digits are rostral, and back and dorsal midline are caudal, the head is lateral, and the tail medial in these figurative illustrations of representational patterns.

Other investigators have concluded that each different body region is represented (at least for the most part) across "SI" within a rostrocaudal cortical strip extending from margin to margin. The concept of rostrocaudal bands was first introduced in the landmark studies of Powell and Mountcastle ('59b) in describing the functional organization of "SI" in macaque monkeys. The concept has also been advanced in a study of spider monkey somatosensory cortex by Pubols and Pubols ('71, '72), and to some extent for squirrel and macaque monkeys by Werner and Whitsel ('68, '71) and macaque monkeys by Whitsel et al. ('71) and Dreyer et al. ('74, '75).

Both points of view reasonably account for certain sets of observations. For example, progressions of recording sites in "SI" commonly result in simple somatotopic sequences of receptive fields. And recording sites at different positions at the same rostrocaudal level are often activated by the same body part. But most investigators recognized that a strict adherence to either point of view would not account for all the observations. In particular, it has been necessary to admit to some degree of somatotopic organization within "rostrocaudal bands," and major discontinuities and re-representations in "the single somatotopic map" have been noted. We have presented evidence for a third point of view (also see Paul et al., '72a). There are clearly not rostrocaudal strips across the architectonic fields in owl monkeys. Rather, separate architectonic fields have separate representations. Furthermore, the concept of a homunculus does not accurately reflect the organization of either of the two cutaneous representations that we have demonstrated. Rather, the representations are better described as composites of subunits or sectors, each of which is internally somatotopic. Within each sector, progressions of recording sites produce simple progressions of receptive fields. However, adjoining neurons on two sides of a "sector" border might relate to quite distant or discontinuous body parts. Thus, the representations are not simple or topological transformations of the complete contralateral body surface, and therefore are not homunculi. We prefer to consider the representations as *composites of somatotopic regions.*

### (d) The representation follows a dermatomal sequence

All three concepts of somatosensory cortex organization could, in principle, be reasonably (but not completely) consistent with a further postulate or organization: that the medial-to-lateral sequence of representation follows the dermatomal order. There has been some disagreement as to the actual order of the medial-to-lateral sequence of body surface representation in primates, but a number of investigators suggested (as did earlier neurologists such as Head, '20, and Benisty, '28) that this sequence follows the dermatomal order (Bard, '38; Woolsey et al., '42; Woolsey et al., '43;

Powell and Mountcastle, '59b; Werner and Whitsel, '68, '71). Holding a more extreme form of the concept of dermatomal organization of "SI," Powell and Mountcastle ('59b) and Werner and Whitsel ('68, '71) argued that the representation of the body in "SI" is actually a simple representation of the dermatomes, which are laid out over the rostrocaudal dimension of "SI," and represented in order in its lateral-to-medial dimension.

On the other hand, many investigators have described exceptions to the dermatomal sequence of representation. Woolsey and colleagues ('42) first noted the discontinuity between the representation of the hand and two parts of the head, i.e., the dorsal head is represented in the cortical region medial to the hand, while adjoining head surfaces are represented lateral to the hand. This "splitting of the occiput" has been recorded in nearly all the primate species that have been studied. Other exceptions to dermatomal sequences were reported later in the chimpanzee and gibbon (genitalia adjacent to trunk representation, foot lateral to a complete leg representation) (Woolsey et al., '60); in humans (entire leg lateral to foot) (Penfield and Rasmussen, '50); in cebus monkeys (genitalia represented on both sides of the foot) (Hirsch and Coxe, '58); and in spider monkeys (head lateral to hand) (Pubols and Pubols, '71, '72).

The detailed maps of the two cutaneous fields in the owl monkeys allow us to evaluate the usefulness of considering these representations as "metameric maps", i.e., maps of the dorsal root cutaneous fields. For both representations there are numerous examples, both of regions where the dermatomal sequence is not followed, and where discontinuities between the representations of adjoining skin surfaces are not along "dermatomal boundaries." Among obvious examples are the following: (1) As many others have noted, the representation of the face is immediately adjacent to that of the thumb and thenar eminence in both fields. In the dermatomal sequence, of course, fields on the arm, shoulder and head dorsum should be represented between the hand and face. The skin field represented in the dermatomes innervating the arm and shoulder are actually represented in both cortical fields 3b and 1 in cortex distant from the representation of the hand. This separation of the hand from adjoining skin surfaces has also been described in other species (Woolsey et al., '42; Benjamin and Welker, '57; Woolsey et al., '60; Penfield and Boldrey, '37; Paul et al., '72a; Pubols and Pubols, '72). (2) The representation of the dorsal surfaces of the fingers is separated from that of the rest of their dermatomal fields on the hand and arm. Moreover, the dorsal fingers are represented differently in Areas 3b and 1. Especially in Area 1, lines of discontinuity in the representations of fingers fail to follow even a short part of any dermatomal boundary. A similar segregation of the Area 3b representation of the volar and dorsal hand was also recorded in the slow loris, by Krishnamurti et al. ('76). (3) The representation of the hand and volar wrist is discontinuous with that of the rest of the arm. Given this discontinuity, the dermatomes would be cut off at the wrist, and in the hand-wrist sector there would be fragments of several dermatomes. (4) If dermatomal fields occur in the region of representations of the arm, they are aligned successively in the mediolateral and not the rostrocaudal cortical dimension in both fields. (5) The representation of part of the preaxial leg is found lateral to the foot within Area 1 (the lateral representation in Area 3b is very small or absent). The split of the preaxial and postaxial leg is along dermatomal lines, and this finding in other primates has been one of the major arguments for a systematic representation of dermatomes in cortex (Woolsey et al., '42), i.e., according to the dermatomal sequence, and the preaxial leg should be represented lateral to the foot.[6] However, at least most of the preaxial leg in Area 3 is clearly represented in the cortex *medial* to the foot representation, and out of the dermatomal sequence. (6) The hairy skin of the toes is not represented with the remainder of the dermatomes covering these surfaces, in either Areas 3b or 1. Again, the pattern of representation of the dorsal digits is different for the two fields, and again, in both instances, lines of discontinuity that cut across these skin fields cut through dermatomes. (7) In somewhat different ways in Areas 1 and 3b the representation of the foot is largely discontinuous with that of the leg. However, dermatomes in this region cross the dorsal foot to extend up onto the leg.

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[6] The preaxial leg has been described as being represented on the lateral side of the foot representation in squirrel monkeys (Benjamin and Welker, '57; Werner and Whitsel, '68), spider monkeys (Pubols and Pubols, '72) and rhesus monkeys (Woolsey et al., '42; Werner and Whitsel, '68). Investigations of somatosensory cortex organization in apes and man (Penfield and Boldrey, '37; Penfield and Rasmussen, '50; Woolsey et al., '60) report that the entire leg is represented lateral to the foot.

Can *any* discontinuities really be described as falling along dermatomal boundaries? It is possible that the lines of discontinuity along the arm and leg representations follow dermatomal boundaries. Our mapping data is not precise enough to define these lines with sufficient accuracy to resolve this question. The lines splitting the hairy skin of the toes (and possibly the fingers) in Area 3b (but not Area 1), and lines of discontinuity which split the palm and which separate off a sector of the thenar eminence could conceivably follow a dermatomal boundary over a short distance. The dermatomal boundaries defining the preaxial thigh may be followed over a part of their length in the Area 1 representation of the thigh. In all of these instances, on the other hand, *the sector of the skin field represented discontinuously would probably never include all of any one dermatome.* We conclude that while both the dermatomal sequence and the body maps reflect in a general way the spatial outlay of the skin surface, the organizations of the body maps are not a consequence of the dermatomal sequence.

### (e) The proportion of representation of different body surface regions is a simple reflection of cutaneous peripheral innervation density

As the observation that the parts of body surfaces with the greatest peripheral innervation density occupy proportionately more of "SI" became appreciated, the idea has arisen that there might be a simple relation between numbers of peripheral receptors per unit area and the cortical area representing the peripheral unit. Beginning with the insightful discussion of the somatosensory cortex in the report of Woolsey et al. ('42), most mapping studies have alluded to this basic concept. However, quantitive evidence for the hypothesis that the somatosensory cortical representations are simply a reflection of peripheral innervation density is limited to that presented in the report of Lee and Woolsey ('75). These investigators found a proportional relationship between the numbers of fibers innervating individual vibrissae on the face and the number of neurons in distinct groupings (termed barrels) of cells in layer IV of SI cortex devoted to individual vibrissae. Although the numbers of peripheral fibers and the numbers of layer IV neurons for each whisker varied, there was a constant proportion of 17 central neurons for each peripheral fiber. From these findings, Lee and Woolsey ('75) proposed that the distortion of the body representation is directly related to the quantity of peripheral innervation and is the result of a "peripheral scaling factor."

Attractive as this concept is, it cannot be applied without modification to the parietal somatosensory strip. Since the proportional representations of different skin areas are different in these two fields, the same peripheral scale factor obviously cannot be applied to both. It is also apparent that several features of at least the Area 1 somatosensory representation do not follow overall peripheral innervation patterns. The relatively small representations of the glabrous surfaces of the fingers and toes as compared with the relatively large representations of the palm and sole in Area 1 are examples (table 1). Thus, there is not a simple relationship between peripheral innervation density and cortical expansion. An alternative view is that functional specialization within cortex is a factor in the distortion of the representations, and consequently, the number of cortical neurons related to the peripheral input varies within representations, and from representation to representation. It is also possible that a modified form of the peripheral-central relationship exists, but that it applies for distributions of different specific afferents or submodalities for each cortical representation. Thus, each representation would reflect the differential distribution of a separate set of peripheral receptor or primary fiber types. Nonetheless, any application of the "peripheral scaling" principal to parietal somatosensory cortical fields must await further direct evidence of the kind derived by Lee and Woolsey ('75).

### (f) "SI" is the basic functional subdivision of somatosensory cortex

Most anatomical, ablation-behavioral, and electrophysiological studies of "SI" have been predicated on the concept that "SI" is a single large functional unit. As a result, and despite the clear architectonic subdivisions, limited attention has been paid to where recording sites, lesions, or injections have been located within this strip. Perhaps the most compelling argument against considering "SI" of primates as a single functional unit is the evidence that this region of cortex contains separate, complete and detailed representations of receptor surfaces that are coextensive with the separate and distinct architectonic fields. However, three other types of evidence support the hypothesis of functionally separate areas within "SI."

The first type of additional evidence is that the overall response characteristics of neurons differ in each of the "SI" architectonic subdivisions. This difference was noted in the early study of Powell and Mountcastle ('59b), although they regarded "SI" as a functional unit and argued that there was a graded distribution of neurons with different response characteristics across the architectonic fields. Subsequently, a number of investigators have presented evidence that different receptor populations ultimately project to Areas 3a, 3b and 2 (Paul et al., '72a,b; Krishnamurti et al., '76; Tanji, '75; Heath et al., '76). From their studies, it is reasonable to conclude that muscle afferents feed into Area 3a, input from perhaps different types of cutaneous receptors into Areas 3b and 1, and joint and other "deep" receptors into Area 2.

There may be some differences in the overall neuronal response properties of the architectonic fields in different primates. While neurons in Areas 3b and 1 of macaque monkeys apparently differ in adaptation rate to a steady cutaneous stimuli (Paul et al., '72a) we have been unable to demonstrate this segregation of slowly and quickly adapting inputs in the owl monkey. While neuronal responses were not studied in detail for adaptation properties, both fields appeared to have neurons that were basically quickly adapting. (This does not mean, of course, that differences in adaptation rate do not exist or that both populations derive their input solely from quickly adapting receptor classes.) On the other hand, the response properties of neurons in Areas 3b and 1 in owl monkeys were different in receptive field size and numbers of discharges in response to transient stimuli. Furthermore, as in macaque monkeys (Paul et al., '72a), Pacinian-like responses (Mountcastle et al., '69) were limited to Area 1 recording sites and were not found in Area 3b. Also in concurrence with the observations of Paul et al. ('72a), no joint receptor input was recorded in Areas 3b and 1 in anesthetized owl monkeys; joint receptor input was found in Area 2.

A second additional reason for considering "SI" of primates as several functionally distinct fields is that each of the separate representations has a different pattern of anatomical connections. Most significantly, Vogt ('76) found that Areas 3b and 1 are reciprocally interconnected, a finding that might be expected between separate cutaneous representations but would be surprising between parts of a single representation. Similarly, electrophysiological evidence indicates that Area 3a is topographically interconnected with motor cortex (Zarzechi et al., '76). It is also of interest that the commissural connections revealed by lesions restricted to Areas 1 and 2 result in three contralateral bands of degeneration corresponding to Area 3a, the boundary of Areas 3b and 1, and the boundary of Areas 2 and 5 (Shanks et al., '75). Such multiple connections between somatosensory cortex of one hemisphere and somatosensory cortex of the other hemisphere would be puzzling if the region contains only a single representation. The idea of a single representation across the somatosensory architectonic fields also is difficult to relate to other anatomical observations. Thus, the different "SI" architectonic fields project to different loci in the dorsal column nuclei (Weisberg and Rustioni, '76) and spinal cord (Jones, '76; Coulter and Jones, '76). In addition, the results of several types of experiments (Clark and Powell, '53; Jones and Powell, '70; Jones, '75; Lin et al., '78) have suggested that the ventroposterior nucleus projects heavily to Area 3b, and less heavily to Areas 1 and 2. All of these patterns of connections are more readily explained by the present concept of separate representations occupying separate architectonic fields than by the traditional concept of a single body representation and functional field.

A third type of evidence suggesting the subdivision of "SI" of primates into more than one unit of functional significance comes from a recent report of Randolph and Semmes ('74) on the behavioral consequences of ablating parts of Areas 3b, 1, or 2 in macaque monkeys. These investigators trained monkeys on tactile discrimination tasks and found that lesions of the hand region of Area 2 were followed by impairments on tasks involving the discrimination of angles; similar lesions of Area 1 affected discriminations of texture; while lesions of Area 3b led to severe impairments on both types of tasks.

In summary, the electrophysiological mapping data of the present report, studies of the distributions of neurons with different response characteristics, the cortical architecture, the connections of the parietal lobe, and

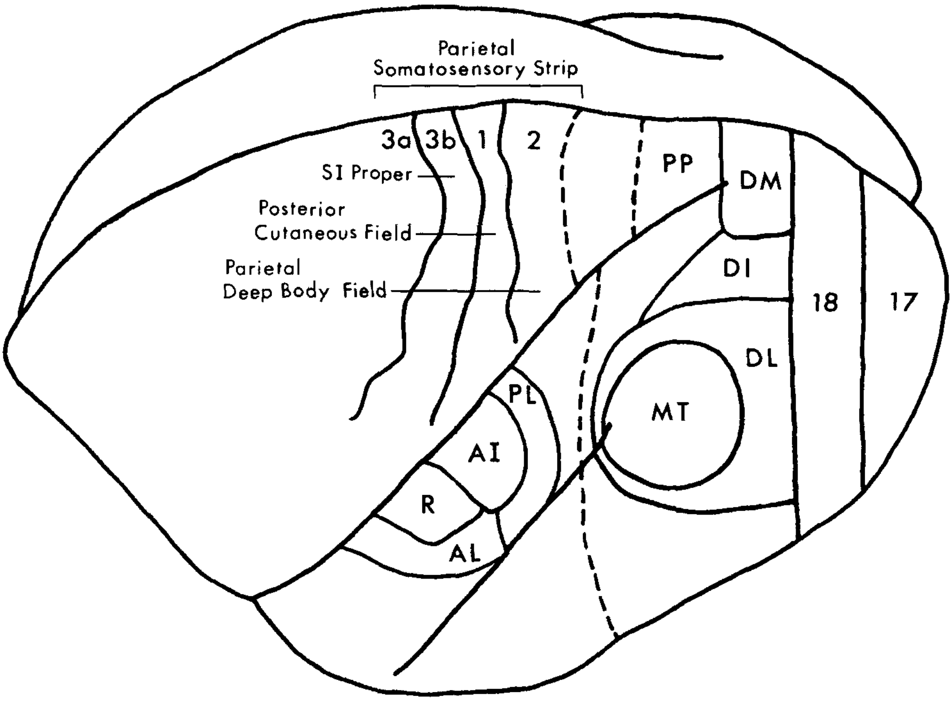

Fig. 16 Visual, auditory and somatosensory areas in the owl monkey. The schematic maps of the auditory representations are redrawn from the studies of Imig et al. ('77); the summary of visual mapping studies is redrawn from Allman and Kaas ('76). The posterior broken line marks the approximate boundaries of visually responsive cortex. The anterior broken line marks the posterior border of cortex activated by somatic stimuli in the present experiments. Refer to figure 1 for a detailed reconstruction of Area 3b and Area 1 body surface representations.

the behavioral effects of ablations of architectonic subdivisions of postcentral cortex all argue against the concept of "SI" as the basic functional subdivision of somatosensory cortex.

### 2. *A redefinition of the primate "SI" and suggested terminology*

Our conclusion that there are two separate representations of the body surface within Areas 3b and 1 of the classically defined "primary somatosensory cortex" or "SI" introduces the problem of redefining the cortical subdivisions of somatosensory cortex in primates. We believe that there are enough similarities between the representation in Area 3b of monkeys and the "SI" representation of most other mammals to argue that Area 3b is the homologue of the non-primate "SI." Therefore, we suggest the term "SI proper" for the 3b subdivision of primate somatosensory cortex, to distinguish it from the traditional primate "SI," which these studies suggest is comprised of as many as four body representations in monkeys, apes and man.

Three types of evidence suggest the homology of "SI proper" of primates with "SI" of other mammals. First, the overall organization of "SI," as generally described for non-primates (see Sur et al., '78, for review), is basically similar to that of "SI proper." For example the representations of the digits of the forepaw and foot are oriented rostrally in both "SI" and "SI proper." The most significant reported difference is that the dorsal trunk is usually portrayed as caudal to the abdomen in "SI" (e.g., see Woolsey, '64), while the reverse order occurs in "SI proper." However, the proportionately small representation of the trunk has been poorly documented in most species, and in "SI" of at least one mammal, the grey squirrel (Nelson and Sur, '77; Sur et al., '78), the representation of the trunk is like that of the owl monkey, with the dorsum rostral and the abdomen caudal in the field.

The cytoarchitecture of "SI proper" and non-primate "SI" is also very similar. Both fields are characterized by a well-developed layer IV with small, tightly packed granule cells. Finally, both "SI" of non-primates (Jones and Powell, '69; Hand and Morrison, '72) and "SI proper" (Jones, '75; Jones and Powell, '70; Clark and Powell, '53) receive a major input from the ventroposterior nucleus, and this input terminates largely in layer IV. For these reasons, we feel that it is probable that Area 3b of primates is homologous with "SI" as described for most non-primates, and that the term "SI proper" both suggests the likely homology, and distinguishes the Area 3b representation from the rest of the postcentral somatosensory strip of monkeys.

With the exception of "SIII" in the cat (Darian-Smith et al., '66), a systematic somatic representation has not been described for cortex caudal to "SI" in nonprimates. Thus, there is little data to suggest that the representation in Area 1 of monkeys is or is not homologous with any field in other mammals. For the present, we prefer the term, "posterior cutaneous field" (PCF) for the Area 1 representation, since it is both non-committal in regard to homologies, and descriptive with regard to location and function.

Finally, we suggest that the "deep" and cutaneous somatosensory fields, 3a, 3b, 1, and 2, of parietal cortex which currently are collectively termed "SI," be renamed the "parietal somatosensory strip" (PSS).

### 3. *Evolution of the parietal somatosensory strip in primates*

The generality of finding a body representation with the same relative location, the same overall orientation and arrangement of the body parts, a characteristic cytoarchitecture, and similar connections from the ventroposterior nucleus in "SI" of a wide range of mammalian species[7] and in "SI proper" of monkeys indicates that this subdivision of neocortex must have arisen early in mammalian or premammalian evolution, and is a basic feature of mammalian neocortex probably common to all mammals. On the other hand, the same argument cannot be made for the posterior cutaneous field. There is a general lack of evidence for a second cutaneous representation (except, perhaps, for cats; see above) that is posterior to "SI" in non-primates. Furthermore, the posterior cutaneous field appears to vary significantly in response characteristics and in organization within the primate order. In the prosimian, slow loris, the somatosensory field on the caudal border of "SI proper" requires rather strong stimuli for activation (Krishnamurti et al., '76), and probably for this reason the organization of the representation remains uncertain. In both New World monkeys (present study) and Old World monkeys (Paul et al., '72a), the PCF responds to low threshold cutaneous stimuli, but the neural responses appear to be more rapidly adapting in Old World monkeys. Finally, the organization of at least part of the PCF appears to be quite different in Old and New World monkeys. The evidence indicates that the hand representation in PCF is oriented with the fingertips caudally in New World monkeys (present study) and rostrally in Old World monkeys (Paul et al., '72a). These variations in PCF characteristics suggest that the field was not well developed in early primates, and perhaps existed as a high-threshold, crudely organized fringe such as it appears to be in present day prosimians.

We know too little about the interspecies comparative features of the Area 3a and Area 2 fields to make reasonable suggestions about their evolution. There is evidence for muscle afferent input to a narrow band of cortex between "SI" and motor cortex in a range of mammals, and the 3a field may be a widespread feature of mammalian brains. The Area 2 "deep" body field is, of course, only known for Old and New World monkeys, and even in these primates, the organization has not been determined in very much detail.

The significance of differences in the organization of the cutaneous fields in the various primates is not known. In reviewing earlier studies, there are difficulties in determining whether the described representational organization applies to Area 3b, to Area 1, or to both fields. Nonetheless, there is no question that quite marked differences in the representational sequence in either or both fields occur. For example, as reviewed earlier, the entire leg is represented lateral to the foot in

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[7] Among the more complete maps of non-primate mammals are those derived in the opossum (Lende, '63; Pubols et al., '76), the marsupial wallaby (Lende, '63), the pig and sheep (Woolsey and Fairman, '46; Johnson et al., '74), rabbit (Woolsey, '64), rat (Woolsey, '64; C. Welker, '71), grey squirrel (Sur et al., '78), dog (Pinto Hamuy et al., '56) guinea pig and capybara (Campos and Welker, '76), llama (Welker et al., '76), hyrax (Welker and Carlson, '76), beaver (Carlson and Welker, '76), and raccoon (Welker et al., '64).

apes and humans; the leg is represented almost completely on the medial side of the foot in owl monkeys; and the leg is split with the postaxial leg medial and the preaxial leg lateral to the foot in Old World monkeys. Perhaps, other differences among parietal somatosensory strip representations in different primates will be described as the organization of the PSS fields in more primates are mapped in detail. However, it is hardly surprising that species differences exist when the representations differ in organization to some extent from owl monkey to owl monkey. Thus, field organization in primates appears to be less constant and more subject to intraspecies and interspecies variation than formerly thought.

### 5. *A note on multiple representation of sensory epithelia in the neocortex*

With the completion of the present studies, most of the neocortex caudal to the central sulcus has been mapped in the owl monkey. Nearly all of the parietal, occipital, and temporal cortex has been found to be occupied by retinotopically, cochleotopically, or somatotopically organized fields (fig. 16) (Allman and Kaas, '76; Imig et al., '77). For each of the six visual, the three somatic, and the four auditory areas that have been mapped in the owl monkey, there is evidence that the representations occupy delimitable cytoarchitectonic fields. Given the present redefinition of the organization of somatosensory cortex, no representations of the sensory epithelia in the neocortex overlie more than one generally recognized cytoarchitectonic field. There can be little question that the functional subdivisions of neocortex can be distinguished by structural characteristics. And it is of great theoretical significance to concepts of the genesis of perception in the forebrain that *all or nearly all of these fields* in the parietal, occipital and much of the temporal cortex *embody systematic spatial representations of individual sensory epithelia.*

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