THE JOURNAL OF COMPARATIVE NEUROLOGY 317:1–30 (1992)

Five Topographically Organized Fields in the Somatosensory Cortex of the Flying Fox: Microelectrode Maps, Myeloarchitecture, and Cortical Modules

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ABSTRACT

Five somatosensory fields were defined in the grey-headed flying fox by using microelectrode mapping procedures. These fields are: the primary somatosensory area, SI or area 3b; a field caudal to area 3b, area 1/2; the second somatosensory area, SII; the parietal ventral area, PV; and the ventral somatosensory area, VS. A large number of closely spaced electrode penetrations recording multiunit activity revealed that each of these fields had a complete somatotopic representation. Microelectrode maps of somatosensory fields were related to architecture in cortex that had been flattened, cut parallel to the cortical surface, and stained for myelin. Receptive field size and some neural properties of individual fields were directly compared. Area 3b was the largest field identified and its topography was similar to that described in many other mammals. Neurons in 3b were highly responsive to cutaneous stimulation of peripheral body parts and had relatively small receptive fields. The myeloarchitecture revealed patches of dense myelination surrounded by thin zones of lightly myelinated cortex. Microelectrode recordings showed that myelin-dense and sparse zones in 3b were related to neurons that responded consistently or habituated to repetitive stimulation respectively. In cortex caudal to 3b, and protruding into 3b, a complete representation of the body surface adjacent to much of the caudal boundary of 3b was defined. Neurons in this area habituated rapidly to repetitive stimulation. We termed this caudal field area 1/2 because it had properties of both area 1 and area 2 of primates.

In cortex caudolateral to 3b and lateral to area 1/2 (cortex traditionally defined as SII) we describe three separate representations of the body surface coextensive with distinct myeloarchitectonic appearances. The second somatosensory area, SII, shared a congruent border with 3b at the representation of the nose. In SII, the overall orientation of the body representation was erect. The lips were represented rostrolaterally, the digits were represented laterally, and the toes were caudolateral to the digits. The trunk was represented caudally and the head was represented medially. A second complete representation, PV, had an inverted body representation with respect to SII and bordered SII at the representation of the distal limbs. The proximal body parts were represented rostrolaterally in PV. Finally, caudal to both SII and PV, an additional representation, VS, shared a congruent border with the distal hindlimb representation of both SII and PV. VS had a crude topography, and receptive fields of neurons in VS were relatively large. Many neurons in VS responded to both somatosensory and auditory stimulation.

Key words: SI, SII, parietal ventral area, ventral somatosensory area, area 1, area 2, electrophysiology, architecture

By using microelectrode mapping procedures and myeloarchitecture, we have delineated five topographically organized cutaneous fields in the cerebral cortex of the grey-headed flying fox, *Pteropus poliocephalus* and the little red flying fox, *Pteropus scapulatus*. Since no clear distinction in

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Accepted September 20, 1991.

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somatosensory cortical organization was noted between these species, they were considered together throughout this investigation. We chose these bats for several reasons. First, in an earlier investigation in the flying fox (Calford et al., '85) that described the organization of the primary somatosensory area, SI or 3b, limited recordings outside of 3b suggested a highly developed somatosensory cortex. The present investigation extends this earlier study by describing the detailed somatotopy for a number of fields, in addition to 3b, in parietal cortex. Second, because the flying fox has a smooth neocortex with a very shallow lateral sulcus, all of these somatosensory areas are readily accessible on the surface of cortex (Fig. 1). Another reason we chose the flying fox is that relatively little is known about the organization of its somatosensory neocortex. Comparative studies are inherently interesting, and if we are to appreciate how the brain changes or varies across species filling different ecological niches, and what features of organization are preserved in neocortical evolution, it is important that we study many species to assess similarities or homologies accurately. For example, there is accumulating evidence that mammals in general may have more somatosensory areas in common than just the first (SI) and second (SII) somatosensory fields. Recently, another somatosensory area, the parietal ventral area, PV, has been identified in squirrels (Krubitzer et al., '86), New World primates (Krubitzer and Kaas, '90b) and rats (Fabri et al., '90). However, only by examining a variety of species can we confidently assign PV as a homologous cortical area in mammals. The final reason we chose the flying fox for these experiments is the recent suggestion that megachiropteran bats may have a closer relationship to primates than other archontans (Pettigrew et al., '89). The Grandorder Archonta was first described by Gregory ('10) to include primates, megachiropteran and microchiropteran bats, Dermoptera (gliding lemurs), Scandentia (tree shrews), and Macroscelididae (elephant shrews). Macroscelididae have since been removed from the archontan group (McKenna, '75), and some investigators (Pettigrew and Cooper, '86) consider only primates, Dermoptera, and megachiropterans to be archontans. The complex origins of the cortical organization of primates are presently poorly understood. Study of the cortical organization of a putative close sister group, such as megachiropteran bats, could help illuminate the gap in understanding between primate and nonprimate neocortical organization.

We posed several questions in this study. First, how are the somatosensory representations in the anterior parietal cortex of the megachiropteran bat organized? In most New and Old World primates there is clear evidence for at least four topographically organized fields in the anterior parietal cortex (Merzenich et al., '78; Kaas et al., '79; Nelson et al., '80; see Kaas and Pons, '88 for review). These fields include the primary somatosensory area 3b (SI proper), area 3a, area 1, and area 2. It has been proposed that this expansion of cortical fields in anterior parietal cortex in primates is a recent phenomenon found only in simian primates (Krubitzer and Kaas, '90b). All other mammals examined have a primary somatosensory area, SI (see Kaas, '83, for review). However, other somatosensory areas adjacent to this primary field have only been described in some species and it is unclear whether these fields are homologous with the anterior parietal fields described in primates. Since there appears to be this dichotomy in organizational schemes between primates and other mammals, we thought it would be beneficial to examine the cortical organization in an archontan, other than a primate, to see which features are shared by archontans, in general, and other mammals.

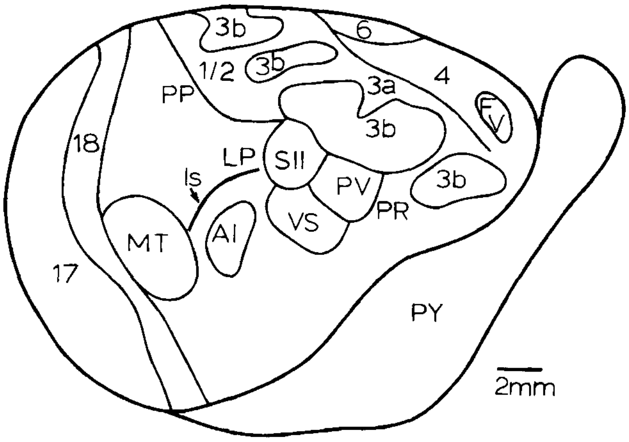


Fig. 1. Lateral view of *Pteropus poliocephalus* brain. Solid lines mark the location of somatosensory, auditory and visual areas of the neocortex. Arrow marks the shallow lateral sulcus. Primary visual area, 17; second visual area, 18; middle temporal visual area, MT; primary auditory area, AI; posterior parietal cortex, PP; primary somatosensory area, SI or 3b; caudal somatosensory field area 1/2; rostral somatosensory area, 3a; second somatosensory area, SII; parietal ventral area, PV; ventral somatosensory area, VS; parietal rhinal area, PR; lateral parietal area, LP; motor cortex, area 4; supplementary motor area, area 6; frontal ventral area, FV; pyriform cortex, PY; lateral sulcus, ls.

A second question we addressed in this study is what is the organization of cortex caudolateral to 3b in the flying fox? This area corresponds to the lateral sulcus region in primates, and the anterior ectosylvian sulcus region in cats. In previous work on the grey squirrel, several fields lateral to SI were defined. These include the classically defined SII region, the parietal ventral area, PV, and the parietal rhinal area, PR (Krubitzer et al., '86). SII has been described in a number of mammals including rodents (Lende and Woolsey, '56; Woolsey, '67; Welker and Sinha, '72; Nelson et al., '79; Pimentel-Souza et al., '80; Carvell and Simons, '86; Krubitzer et al., '86), carnivores (Haight, '72; Burton et al., '82; Herron, '78; Clemo and Stein, '82), tree shrews (Sur et al., '81), prosimian primates (Burton and Carlson, '86), and simian primates (Whitsel et al., '69; Friedman et al., '80; Robinson and Burton, '80b; Pons et al., '88; Cusick et al., '89; Krubitzer and Kaas, '90b). However, there is little consensus on the organization of other somatosensory fields in addition to SII in cortex lateral to SI. Recently, PV has been defined in marmosets (Krubitzer and Kaas, '90b) and rats (Fabri et al., '90). In cats, a topographically organized field adjacent to SII, termed SIV (Clemo and Stein, '82, '83; Burton and Kopf, '84) has been described, and in Old World primates the granular insular cortex, Ig, is in the relative location of PV. Although there are some features of SIV and Ig that are similar to PV described in squirrels and marmosets, it is uncertain whether these fields are homologous with PV. By examining cortex lateral to SI in the flying fox we can determine whether there are areas in addition to SII involved in somatosensory processing and, if so, whether they are similar to fields described in other mammals such as carnivores, rodents, and archontans.

MATERIALS AND METHODS

The electrophysiological recording experiments in this study were of two types. In one set of experiments, multiunit recordings were made to determine the physiological extent of identified fields so that injections of anatomical tracers could be restricted to a particular field of interest. In this group of experiments, the density of recording sites was low, and only a crude somatotopy of fields was determined. In the other group of experiments, maps in which electrode penetrations were 200–300 μm apart were made of areas 1/2, SII, PV, and VS to determine the detailed somatotopy of these areas. The internal organization has been described for the primary somatosensory area, SI (3b), in the flying fox (Calford et al., '85). However, this is the first detailed description of fields caudal and lateral to 3b in the flying fox.

Multiunit mapping methods were used to investigate the somatotopic organization of areas 3b, 1/2, SII, PV, and VS in five grey-headed flying foxes, (*Pteropus poliocephalus*) and five little red flying foxes, (*Pteropus scapulatus*). In some of these animals, the cortical connections of fields were determined by using anatomical tracers and these results have been briefly described (Calford and Krubitzer, '90). At the beginning of each experiment, the animal was anesthetized with ketamine hydrochloride (30 mg/kg) and xylazine (4 mg/kg). Maintenance doses of approximately one-half of the initial dose of ketamine were administered as needed throughout the experiment to maintain surgical levels of anesthesia. Standard sterile surgical procedures were maintained in experiments in which the animals were allowed to recover. Once the animal was anesthetized, the scalp was cut, the skull over the somatosensory cortex was removed, and the dura retracted. An acrylic well was built around the opening in the skull and filled with viscous silicone fluid to prevent desiccation and decrease pulsation. A clamp was attached to the skull and the animal was removed from the stereotaxic frame so that the entire body surface contralateral to the opening in the skull was easily accessible. The head was tilted in a plane perpendicular to the recording electrode. A photograph (enlarged 20 times) was made of the cortex so that electrode penetrations could be related to cortical vasculature.

Electrode recordings were made with low impedance (~1 MΩ at 1000 Hz) glass-insulated tungsten microelectrodes with exposed tips (30–40 μm) designed to record from single units and multiunit clusters. The electrode was manually moved in X/Y coordinates and a stepping microdrive advanced the electrode through the cortical layers. When a stimulus was applied to the relevant receptive field, the depth at which maximal neuronal activity was sampled was 700–1000 μm below the pial surface. Neurons in superficial and deeper layers also responded to somatosensory stimulation, where receptive fields were centered around the same location as those defined in middle layers. Because of the good responses, receptive fields were easier to define in middle layers. The vast majority of receptive fields in this study were determined with electrodes placed at a depth of 900 μm. Receptive fields for neurons in any given penetration were determined by stimulating the body surface with fine wires, brushes, or small puffs of air, and receptive fields were defined as the region on the skin surface that, when stimulated, produced a clear neural response. By using our recording procedures, neural responses in somatosensory cortex could be readily defined by large bursts of activity exhibited on an oscilloscope and amplified through a loudspeaker. Neural responses were easily distinguished from recordings from axons in the white matter below cortex, where activity increased above resting rate when the skin was stimulated, but no large spikes on the recorded waveform could be distinguished. In all cases, recordings were from identified postsynaptic unit clusters (~2–5 units), or from single units. Stimulation elicited a characteristic burst or series of bursts from these units. When cutaneous stimulation was ineffective, sensitivity to joint manipulation, pressure, or tapping was tested. These fields were drawn onto outline diagrams of the animals. The type of stimulation that best drove neurons in cortex was dependent on the cortical area being mapped. For instance, neurons in 3b were non-habituating to somatosensory stimulation, while neurons in area 1/2 habituated to somatosensory stimulation. A stimulus that was presented at a steady rate of stimulation would cause neurons in area 1/2 to fire upon the first few stimulus presentations and then cease firing even though the stimulus was still being presented. Neurons in area 3b would fire to every presentation of a repeated stimulus and would cease firing only with the cessation of the stimulus. Habituating and non-habituating responses of neurons should not be confused with the rapidly and slowly adapting response classification of cutaneous sensitivity (Dykes and Gabor, '81). A rapidly adapting neuron would fire only at the onset of a continuous, non-interrupted stimulus, while a slowly adapting neuron would respond throughout the presentation of a continuous, non-interrupted stimulus. Both habituating and non-habituating neurons observed in the present investigation would be classified as rapidly adapting.

By identifying the receptive fields for a number of closely spaced recording sites in a given cortical field, the somatotopic organization of that field could be readily determined. In some experiments, recordings were made from neurons in adjacent auditory and visual fields. In these animals, clicks were used to stimulate neurons in auditory cortex and moving bars of light were used to stimulate neurons in visual cortex. At the conclusion of all experiments, microlesions (10 microamps for 6 seconds) were placed at physiologically identified boundaries. In some animals, after a somatosensory field was defined, an injection of an anatomical tracer was placed into a body part representation.

When the experiments were complete, animals were administered a lethal dose of sodium pentobarbitone and, when areflexive, were transcardially perfused with 0.9% saline followed by 3% paraformaldehyde in phosphate buffer and then 3% paraformaldehyde and 10% sucrose in phosphate buffer. The brain was removed from the cranium, and cortex was peeled from the brainstem and thalamus. With the aid of several cuts, the cortex was flattened between glass slides and soaked overnight in 30% sucrose phosphate buffer. The flattened cortex was cut into 40 μm sections on a freezing microtome and alternate sections were stained for myelin (Gallayas, '79). By matching lesions in brain sections stained for myelin with electrophysiological data from the enlarged photograph, the architectonic boundaries of fields could be identified and related to physiological results.

RESULTS

The somatotopic organization of a cortical field was the strongest physiological evidence for subdividing somatosensory cortex into various fields. If a region of cortex that was responsive to somatosensory stimulation had a complete representation of the body surface coextensive with a distinct architectonic appearance, it was considered a separate field. Using this criterion, we describe five somatosensory fields in flying fox neocortex responsive to light cutaneous stimulation. Some of these areas have sufficient parallels in position, myeloarchitecture, and somatotopy (connections of fields have been briefly described elsewhere, Calford and Krubitzer, '90) to fields described in other species, to allow assigning of names to these fields in the flying fox. Our results will be presented according to the areas defined which include: the primary somatosensory area, SI, or 3b; a caudal somatosensory area, 1/2, which has properties of both areas 1 and 2 in primates; three subdivisions in lateral parietal cortex, SII, the parietal ventral area, PV, and the ventral somatosensory area, VS. In addition, we describe responses of neurons in adjacent fields and directly compare neural response properties across fields. A total of 1396 recording sites were examined in and around these cortical fields in ten animals. In this section we also describe qualitative observations on the response properties of neurons and their receptive field size.

The primary somatosensory area, SI (area 3b)

The somatotopic organization of the primary somatosensory area in the grey-headed flying fox has been described previously (Calford et al., '85) and will be described only briefly here. In this study, 459 recording sites in 3b were made to determine the topographic organization of this field and its boundaries with adjacent fields. Area 3b contained a complete representation of the contralateral body surface (Figs. 3 and 4) with the distal foot represented most medially on the medial wall of cortex. The representation of the hindlimb, arm, and trunk were observed progressively lateral. The distal forelimb representation was lateral to that of the trunk and arm.

Within the representation of the distal forelimb, the digits and associated finger membranes were represented caudally and the forearm was represented rostrally. This is the reverse of the representation of the forelimb in primates, carnivores, and rodents where the digits are represented rostrally and the palm is represented caudally. Distal D1 was represented caudal to the middle and proximal portions of D1. Digits 2 and 3 were represented medial to D1. Distal D2 and D3 and associated finger membranes were represented caudomedially while the middle and proximal portions of D2 and D3 were represented more rostrolaterally. Digits 4 and 5 and the finger membrane between them were represented most medially in the representation of the digits. The distal representation of D4 and D5 was medial and caudal to the middle and proximal representation of these digits. The representation of the arm membrane was split. Portions of the arm membrane adjacent to the hindlimb and foot in the periphery were adjacent to hindlimb and foot representations in cortex, while portions of the arm membrane adjacent to the proximal forelimb in the periphery were adjacent to the forelimb representation in cortex. Finally, regions of the arm membrane adjacent to digit 5 in the periphery were represented adjacent to the D5 representation in cortex. The prowing was represented lateral to the representation of the forelimb and D1.

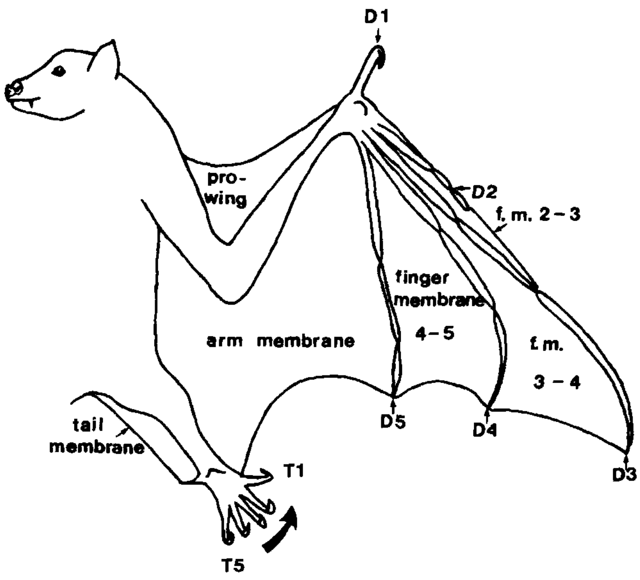


Fig. 2. A ventral view of the grey-headed flying fox with body parts identified. The wing span of the grey-headed flying fox is approximately 150 cm, while the wing span of a little red flying fox is approximately 130 cm. Digits, D; toes, T.

Lateral to the representation of the forelimb was the representation of the head and face. Although no receptive field in this study was restricted to a single vibrissa, the different sets of vibrissae (snout, chin, below nares, below eyes) were represented separately and occupied a large amount of cortical space. Within the face representation, the nose was represented caudolateral to the vibrissae and was adjacent to the nose representation in SII. There was a reversal of receptive fields as recording sites progressed from the nose representation in 3b to the nose representation in SII (Fig. 16). The lips were represented rostral and lateral to the nose and the representation of the chin formed the rostrolateral boundary of 3b. Finally, the representation of the oral structures occupied the most lateral position in 3b.

Neurons in 3b were highly responsive to cutaneous stimulation of the skin and to small displacement of hairs. Responses could also be elicited by lightly brushing either glabrous or hairy skin. Most neurons in 3b gave consistent responses to repetitive stimulation (Figs. 5, 11B, 12B) and had relatively small receptive fields. However, there were several recording sites within 3b where neurons rapidly habituated to a stimulus. These recording sites were generally clustered together (Figs. 5, 11, 12). Receptive fields on digit 1, and on portions of the rostral face were quite small compared to receptive fields on the same body parts in other cortical fields such as SII, PV, and VS (Figs. 19 and 20). Receptive fields on the limbs were larger than those on the face and digits, and those on the trunk were the largest in area 3b. Also, most receptive fields were restricted to a particular body part so that receptive fields on the digits were confined to the digits and associated finger membranes and did not encompass portions of the wrist or arm; receptive fields on the trunk were restricted to the trunk and did not encompass portions of the adjacent limb. Further details on the responsiveness, receptive field size,

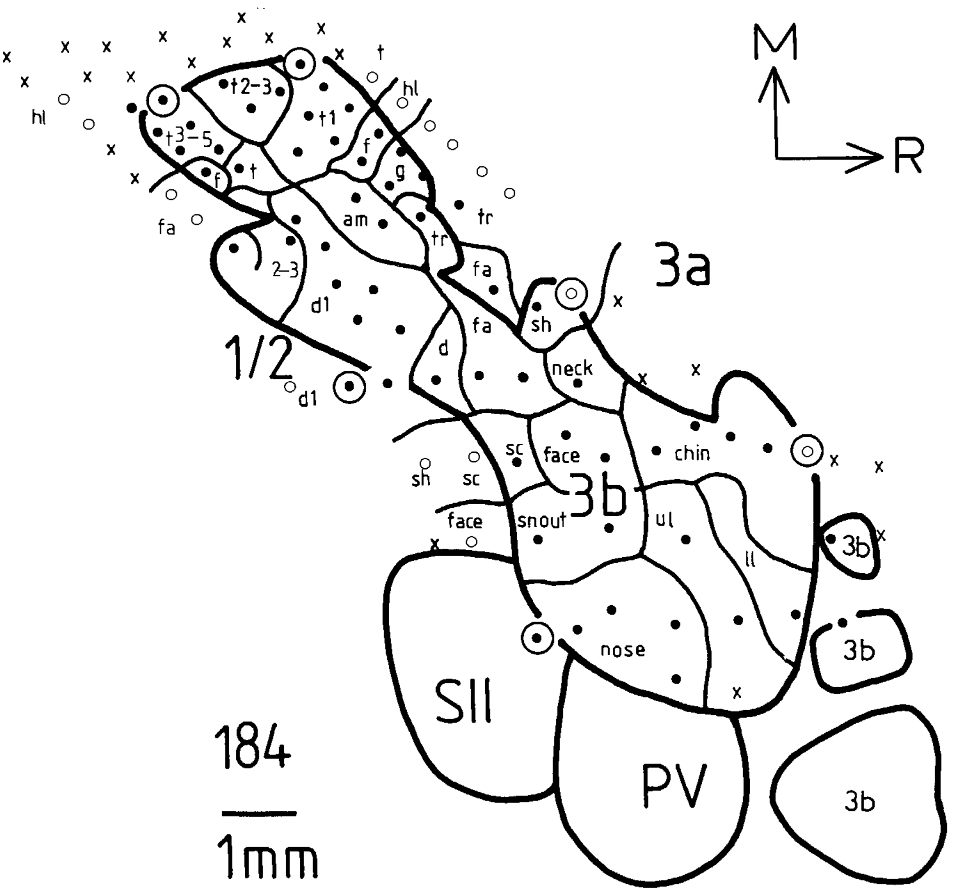


Fig. 3. A microelectrode map of area 3b in the flying fox (*Pteropus poliocephalus*). As recording sites move from medial (top) to lateral (bottom) in cortex, receptive fields on the body progress from toes, to forelimb, to digits and face. Filled circles mark electrode penetrations where neurons respond to cutaneous stimulation, small open circles mark electrode penetrations where neurons respond to deep stimulation or manipulation of peripheral body parts. X's mark regions of no response. Large open circles mark microlesions placed at physiological boundaries. Solid lines mark myeloarchitectonic boundaries. Toes, t; foot, f; genitals, g; arm membrane, am; forearm, fa; hindlimb, hl; trunk, tr; digits, d; shoulder, sh; scalp, sc; upper lip, ul; lower lip, ll.

progression, and plasticity of receptive fields have been provided elsewhere (Calford et al., '85; Calford and Tweedale, '88, '91). As in other mammals studied, the digits and lips occupied a large amount of cortex, while the trunk and proximal limbs occupied less cortical space (Figs. 3 and 4). Unlike primates, the vibrissae representation was extensive in the flying fox (e.g., Fig. 4), but there was no specialized area equivalent to the barrel field vibrissae representation in rodents (Woolsey and Van der Loos, '70).

The primary somatosensory area, defined physiologically, was coextensive with the architectonically defined area 3b. Area 3b is distinguished by dense staining for myelin (Vogt and Vogt, '19) and by a distinct granular appearance of layer IV in Nissl preparations in primates (Sanides, '68, '70; Jones et al., '78). In cortex that has been flattened and cut parallel to the cortical surface, area 3b, or SI proper, is a myelin-dense area in rodents (Krubitzer et al., '86) and primates (Krubitzer and Kaas, '90b). In the flying fox, this field was densely myelinated throughout all cortical layers, but stained most densely in the deepest cortical layers. Area 3b was quite narrow medially and widened laterally (Fig. 6). At the caudal boundary of area 3b, where the forelimb representation bordered the representation of the face, there was often an indentation that corresponded to a discontinuity in the physiological representation in this field (Figs. 4, 6, 7). Just lateral to this indentation, area 3b curved rostrally so that the most lateral boundary of area 3b was also the most rostral portion of the field. The most rostrolateral regions usually show a distinct island of myelin-dense staining. This region was not investigated in most of the animals of the present study. However, comparison with the maps of Calford et al. ('85), reveal that this island corresponds to the tongue representation. Thus, the overall shape of area 3b was a stretched out L (Fig. 9). In more superficial layers of cortex, the myelin staining in area 3b was not homogeneous. Rather myelin-dark patches were surrounded by myelin-light zones (Figs. 6–9). This discontinuous pattern was even more distinct in middle cortical layers. In deep cortical layers, the myelin-dense regions began to merge and form a continuous myelin-dense region. Electrophysiological recordings indicated that these myelin-dense patches in the hand and face representation were coextensive with the non-habituating cutaneous receptors associated with area 3b (Figs. 6 and 7). The myelin-light

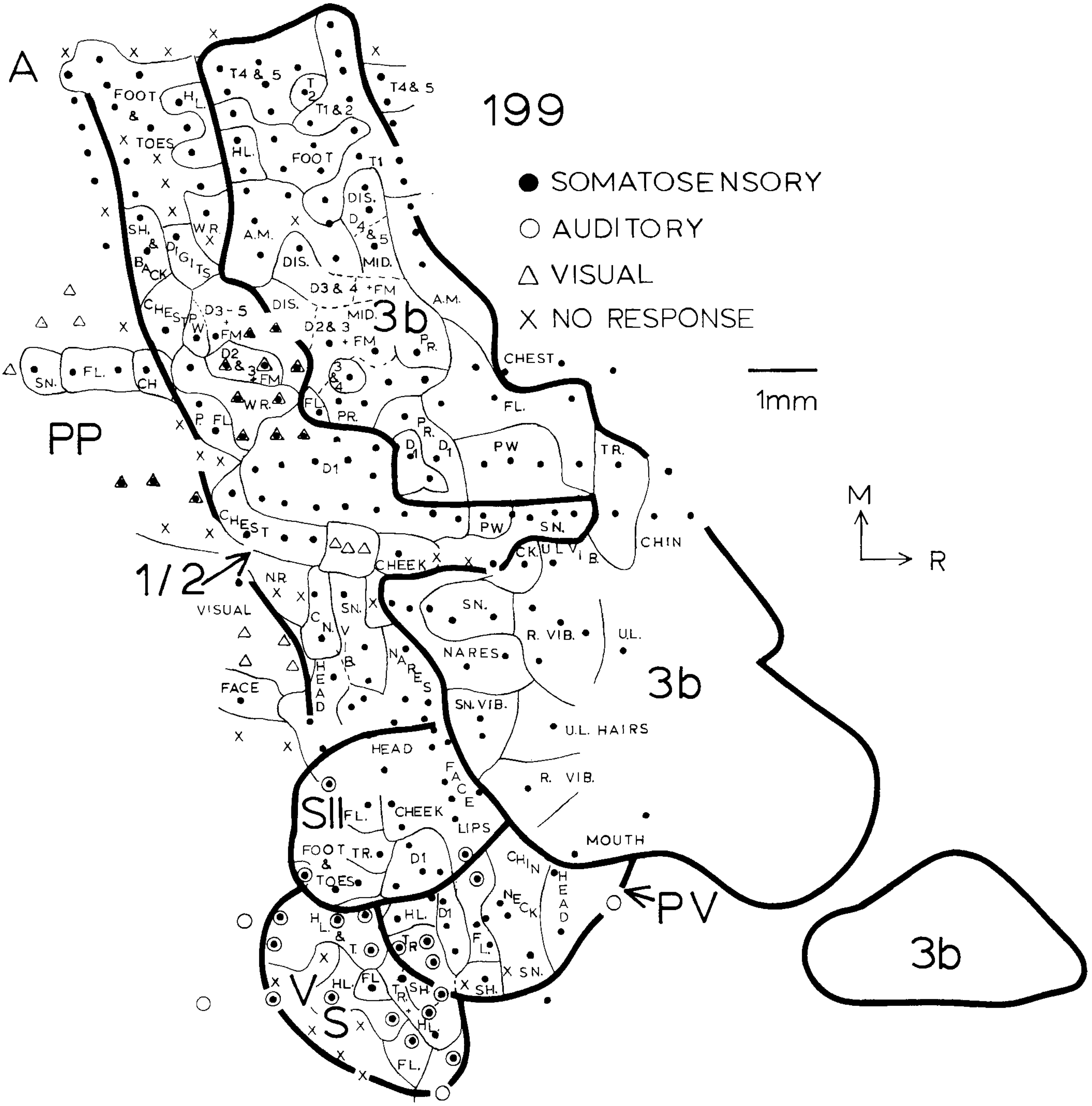


Fig. 4. Microelectrode maps of 3b, area 1/2, SII, PV, and VS obtained in a single animal (*Pteropus poliocephalus*). Area 1/2 is a mirror reversal representation of 3b. Both 3b and area 1/2 have a large representation of the digits, particularly D1. The representation of the face in 3b is much more extensive than the face representation in area 1/2. SII, PV and VS each contains a complete representation of the body surface. Most neurons in VS in this case respond to both somatosensory and auditory stimulation. Prowing, PW; snout, SN; finger membrane, FM; chin, CN; wrist, WR; vibrissae, VIB; cheek, CK; chest, CH; forelimb, FL; distal, DIS; middle, MID; proximal, PR; rostral, R. Other conventions as in previous figures.

zones between the hand and face representations contained neurons that rapidly habituated to repetitive stimulation.

Somatosensory cortex caudal to 3b, area 1/2

Immediately caudal to area 3b was another complete representation of the body surface. A total of 178 recording sites was obtained from this field. The topography of this field is much like that described for area 3b, with the foot represented most medially on the medial wall of cortex, and the trunk, forelimb, and face represented progressively more lateral (Fig. 4). However, overall the topography appears to be less precise than in area 3b. The position of the field and the mirror reversal along the dorsal midline of the representation with 3b (Figs. 10 and 21) suggest a

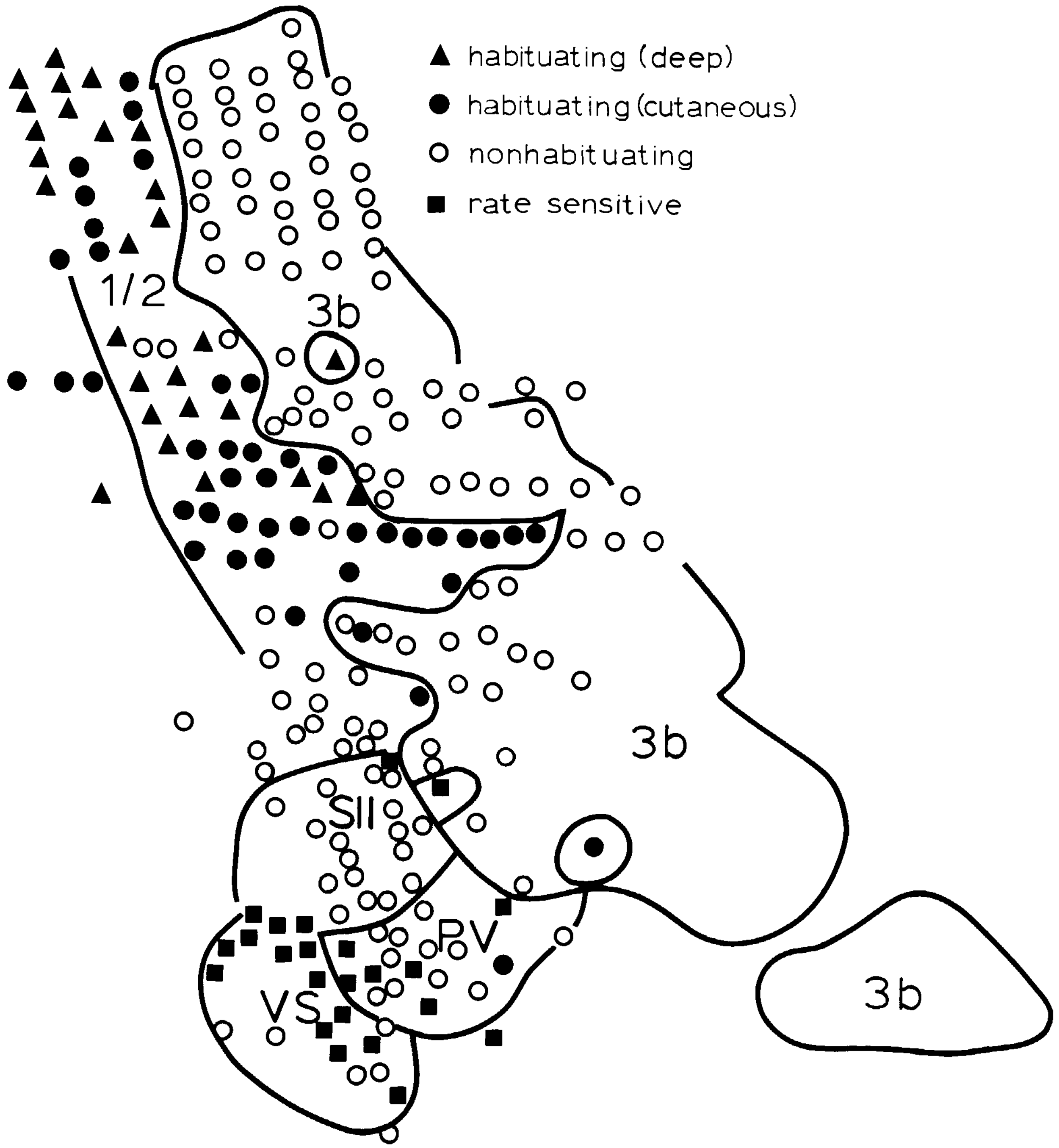


Fig. 5. Microelectrode map of 3b, area 1/2, SII, PV, and VS of the same animal illustrated in Figure 3. Different types of stimulation were required to elicit a neural response in the different fields mapped (cutaneous or deep), or different types of neural responses were elicited under similar stimulation conditions (e.g., habituating vs. nonhabituating). These differences help to distinguish boundaries between cortical fields. There is a clear division between areas 3b and 1/2 since most neurons in area 1/2 rapidly habituate to cutaneous stimulation. Neuronsin SII and PV are nonhabituating while neurons in VS are rate sensitive. Solid lines mark myeloarchitectonic boundaries.

parallel with area 1 described in primates (Merzenich et al., '78; Kaas et al., '79; Nelson et al., '80; Felleman et al., '83a). As in area 1, neurons in this field responded well to cutaneous stimulation of peripheral body parts. Receptive field sizes for most neurons in area 1/2 were generally small, especially on the hand, but larger than those in area 3b (Figs. 10, 19, 20). Some aspects of the neural response suggest a parallel with area 2 of primates. As in area 2 (Powell and Mountcastle, '59; Merzenich et al., '78; Pons et al., '85), some neurons in area 1/2 responded well to hard taps to the body or to manipulation of a limb (Fig. 5). Receptive fields for these neurons were generally quite large. Because of the similarities with both areas 1 and 2, we term this field area 1/2. A distinctive feature of area 1/2

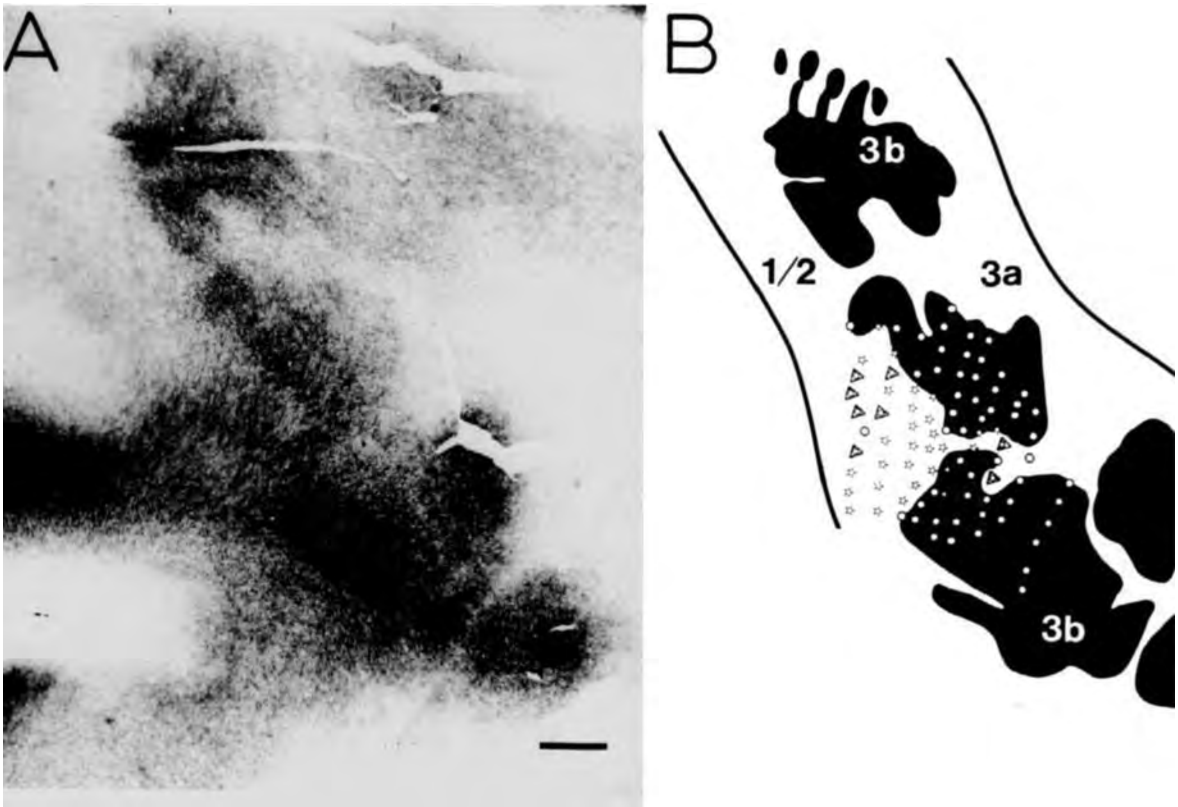


Fig. 6. Lightfield photomicrograph (**A**), and a schematic reconstruction with recording sites added (**B**) in flying fox 205 (*Pteropus poliocephalus*). In A, cortex has been flattened and cut parallel to the cortical surface and stained for myelin. Myelin-dense regions are coextensive with non-habituating neural responses (circles), while myelin-light invaginations into myelin-dark regions are coextensive with habituating neurons (stars). The myelin-dark regions are area 3b, and the myelin-light regions are portions of area 1/2. The lateral sulcus is myelin-light. The very dark regions immediately above and below the lateral sulcus are portions of MT and AI respectively. Triangles indicate responsiveness to deep stimulation. Scale bar = 1 mm.

that was generally not noted in any of the other somatosensory fields, was that neurons in this field rapidly habituated to repetitive stimulation (Figs. 5, 11B, 12B). Thus, when stimulation was administered by lightly tapping the body or brushing hairs in a repetitive fashion, neurons in area 1/2 would fire vigorously and then stop after the third or fourth stroke. If an interval of approximately 5 seconds was allowed to elapse before tapping resumed, the neuron or neurons would again fire and cease firing at the third or fourth stimulus presentation. This is in contrast to area 3b where neurons continued to fire with each presentation (tap or brush) of the stimulus. Even when neurons in area 1/2 had small and very sensitive receptive fields, repeated presentation of a stimulus at 0.5–1.0 second intervals led to habituation within a few seconds. A repetitive stimulus presented in one segment of a receptive field led to habituation to stimuli throughout the receptive field. The boundary of area 1/2 with area 3b was quite distinct because of the change in this aspect of the response. The area 3b and area 1/2 boundary was also readily determined by somatotopic changes, since receptive field sequences across the boundary of these fields reversed (Fig. 10). For example, neurons in rostral locations in 3b had receptive fields on the chest, and with a progression of recording sites caudally in 3b, receptive fields moved to the forelimb and digits. As recording sites crossed the area 3b area 1 border, receptive fields reversed back onto the digits and forelimb and finally the chest (Fig. 10, receptive fields A–G).

The distal forelimb in area 1/2 was represented in a fairly tight topographic fashion, with the digit tips and associated finger membranes represented rostrally, adjacent to the digit tip representation in 3b, and more proximal digit representations were found progressively caudal in area 1/2 (Fig. 4). As with the forelimb representation in area 3b, this is reversed from that described for primates where the distal digits are represented caudally in area 1. D1 was represented in most detail and was lateral in the representation of the distal forelimb, while digits 2–5 and associated finger membranes were represented progressively more medial in less detail so that often, two to three digits were represented in a single recording site. Within the hand representation, the wrist was represented caudal to the digits, and the proximal forelimb was represented caudal to the wrist. The prowing was represented rostrolateral to the digits, between the digit and face representation of area 3b. As in area 3b, the distal forelimb representation in area 1/2 comprised a large portion of the entire body representation.

The face representation in area 1/2, just lateral to the representation of the hand, was less extensive than the face representation in area 3b. The cheek was represented lateral to the representation of D1, and the snout was represented lateral to the cheek and formed a border with

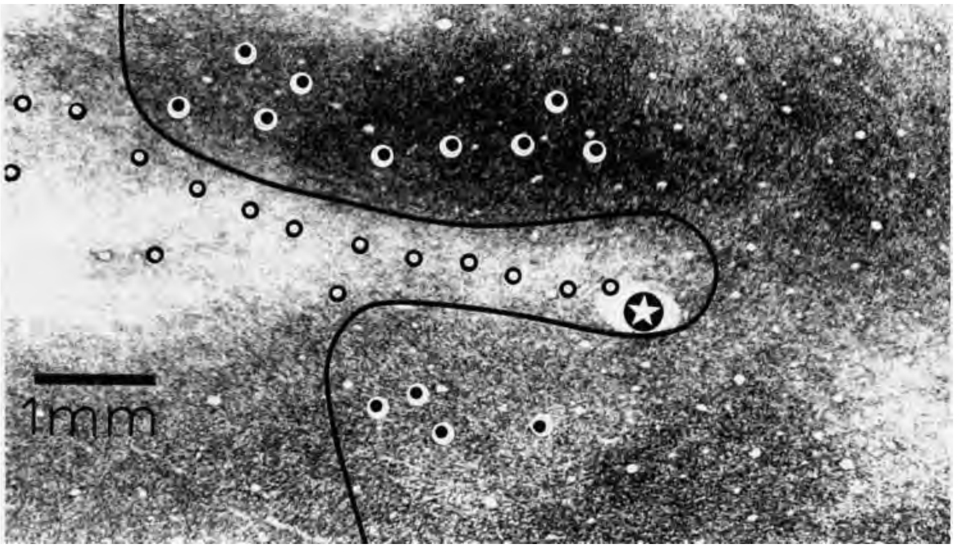


Fig. 7. Lightfield photomicrograph of myelin-light and dense patches in 3b, and their relationship to non-habituating (black centered circles) and habituating (white centered circles) neurons in 3b and area 1/2 respectively. Myelin-dark regions are coextensive with non-habituating neurons while myelin-light regions correspond to the habituating neurons. The hole (star) marks a probe placed in cortex during physiological mapping for later identification in cortex stained for myelin.

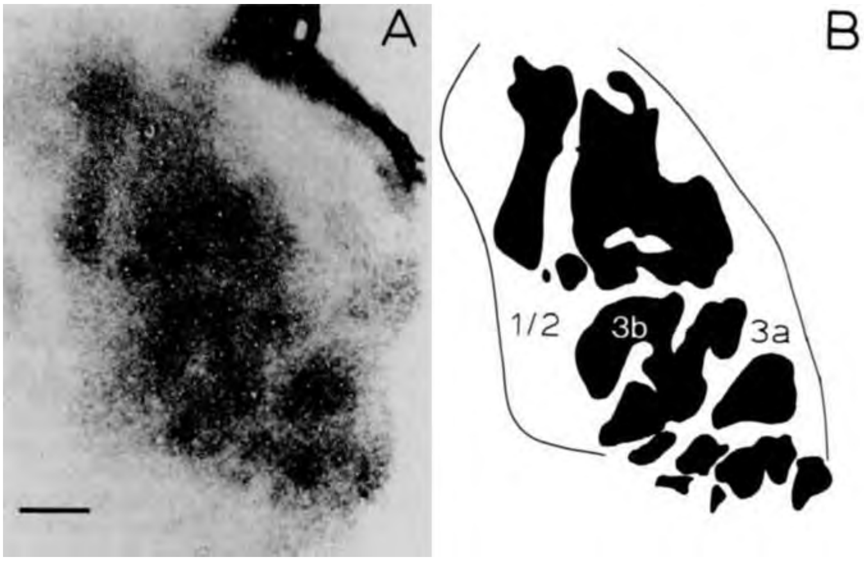


Fig. 8. Lightfield photomicrograph (**A**), and a schematic reconstruction (**B**) of cortex in flying fox 184 (*Pteropus poliocephalus*) that has been cut parallel to the cortical surface and stained for myelin. In 3b, myelin-dense zones are surrounded by myelin-light patches throughout the field. Area 1/2 stains lightly for myelin, and SII and PV are moderately myelinated. Note that the density of electrode tracks in this experiment (Fig. 3) was not sufficient to delineate the modular nature of area 3b as was possible in other experiments e.g., Figs. 5–7. Scale bar = 1 mm.

the snout representation in 3b (Fig. 10, receptive fields a–f) and partially invaginated rostrally into area 3b (Figs. 4, 5, 11, 12). Caudal to the representation of the cheek and snout was the representation of the snout vibrissae, and the chin. The head and neck representation in area 1/2 was represented caudolaterally in the field. The nares were represented at the rostrolateral edge of area 1/2 adjacent to the nares of area 3b.

Medial to the representation of the forelimb in area 1/2 was the representation of the hindlimb and foot. The representation of the hindlimb was adjacent to the representation of the hindlimb in area 3b. The foot and toes in area 1/2 were represented caudomedial to the representation of the hindlimb. Unlike the representation of the foot and toes in area 3b, the foot and toes in area 1/2 were generally represented together so that receptive fields encompassed both toes and feet (Fig. 10, receptive field 6). The chest and back in area 1/2 were represented most caudally. The back and shoulders were represented caudolateral to the representation of the foot and toes, and the chest was repre-

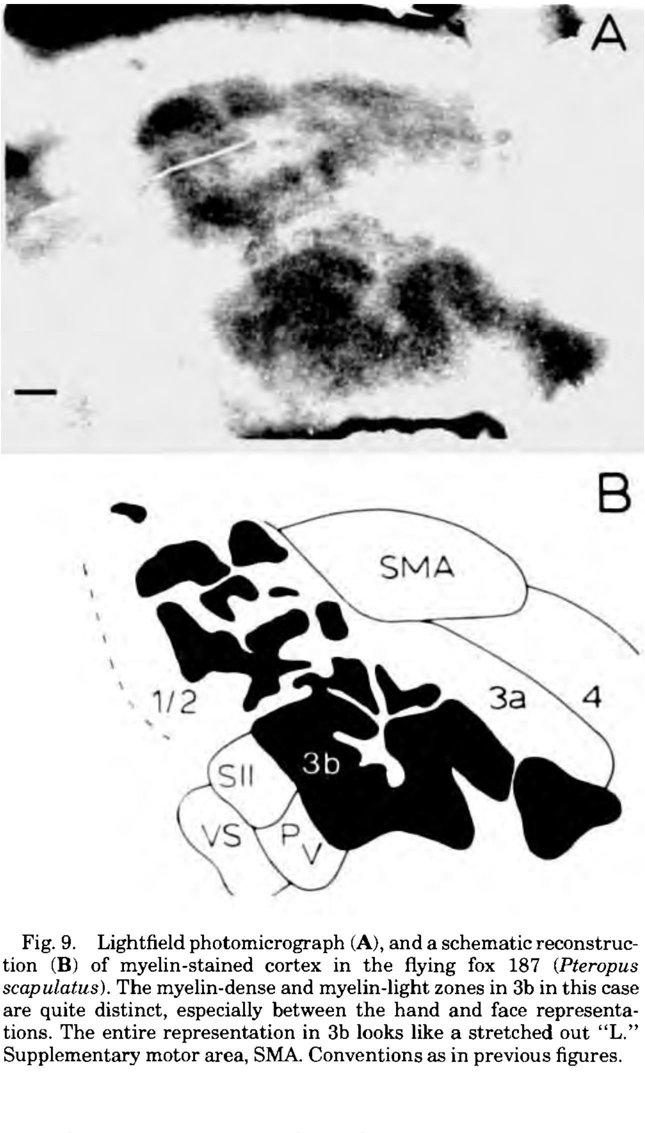


Fig. 9. Lightfield photomicrograph (**A**), and a schematic reconstruction (**B**) of myelin-stained cortex in the flying fox 187 (*Pteropus scapulatus*). The myelin-dense and myelin-light zones in 3b in this case are quite distinct, especially between the hand and face representations. The entire representation in 3b looks like a stretched out "L." Supplementary motor area, SMA. Conventions as in previous figures.

sented immediately lateral to the representation of the shoulders and back, and caudal to the proximal hand. The representation of the lower ventral and dorsal trunk was not defined in area 1/2, possibly because it was a small portion of the representation. Also, recording density in the expected location of this representation was low, due to the curvature of the cortex at the midline.

In area 1/2, some groups of neurons responded to cutaneous stimulation, while other groups of neurons responded to deep stimulation of peripheral body parts. When area 1/2 is examined as a single field and all receptive fields are taken together, regardless of responsiveness to deep or cutaneous stimulation, there appear to be multiple representations of the same body parts. For instance, an extra digit representation of all digits was found just medial to the D3–5 representation in case 199 (Fig. 4). Also, there were two representations of the chest in this same case, one medial to the digit representation and one caudal to the digit representation. However, where double representations were found, one representation had neurons responsive to cutaneous stimulation while the other had neurons responsive to deep stimulation. Thus, if the cutaneous and deep receptive fields are considered separately in area 1/2, there is only a single body representation of cutaneous receptors and a single body representation of deep receptors. In a few cases (Figs. 4 and 13A), responses to somatosensory and visual stimulation were observed. However, the somatosensory responses were always stronger compared to responses to visual stimulation which were weak and inconsistent.

Area 1/2 was distinguished architectonically as a moderately myelinated field much like area 1 described in primates (Krubitzer and Kaas, '90b) (Figs. 6, 8, 9). This moderately myelinated strip of cortex immediately caudal to SI conformed closely to the representation of rapidly habituating receptors described above. The field shared a common boundary with 3b from the far medial extent of 3b to the lateral portion of 3b just dorsal to the SII/3b boundary. Caudal and medial to area 1/2, cortex stained very lightly for myelin.

Incursions of area 1/2 into area 3b

There was physiological and architectonic evidence that area 1/2 invaginates into area 3b between the representation of the face and forelimb and may actually interdigitate with area 3b throughout its entire representation. In animals in which a high density of recording sites was made (e.g., Figs. 4, 6, 11), the head and forelimb representations in area 3b were separated by neurons with the rapidly habituating properties of area 1/2. Thus, neurons in this region had receptive fields roughly in register with those in adjacent portions of area 3b, but rapidly habituated to the stimulus.

There was a close correspondence between these physiological results and the myeloarchitecture of this region where area 1/2 juts into area 3b. Sections stained for myelin revealed a clear break in the myelin-dense 3b between the forelimb and the face representation (Figs. 6–9). The cortex between the forelimb and the face representations in area 3b stained moderately for myelin and was continuous with area 1/2 architecture. There were possibly smaller incursions or interdigitations of area 1/2 into area 3b (e.g., Figs. 6, 8, 9) because there were small islands of neurons interspersed throughout 3b that rapidly habituated to cutaneous stimulation (Figs. 5, 11B, 12B). Also, 3b did not stain homogeneously for myelin. Rather, myelin-dense patches were separated by narrow zones of myelin-light zones throughout the entire representation. It is possible that these myelin-light regions correspond to the rapidly habituating zones identified physiologically, as is the case for the forelimb and head representation.

Second somatosensory area, SII

Neurons from 135 electrode penetrations were recorded from SII in five animals, with up to 43 recording sites in a single animal. Because SII occupies a relatively small portion of the neocortex (4 mm^2), the density of recording sites in some of these animals was quite high, allowing the topography of the field to be determined. The topography of SII in the flying fox is much like that described for other eutherian mammals. Although SII occupied considerably less space than the primary somatosensory area, a complete representation of the contralateral body surface was still observed. The overall representation in SII had an upright orientation with the trunk represented centromedially and the distal limbs pointing laterally. The face representation was adjacent to the face representation in 3b and the nose representation formed a congruent boundary with the nose

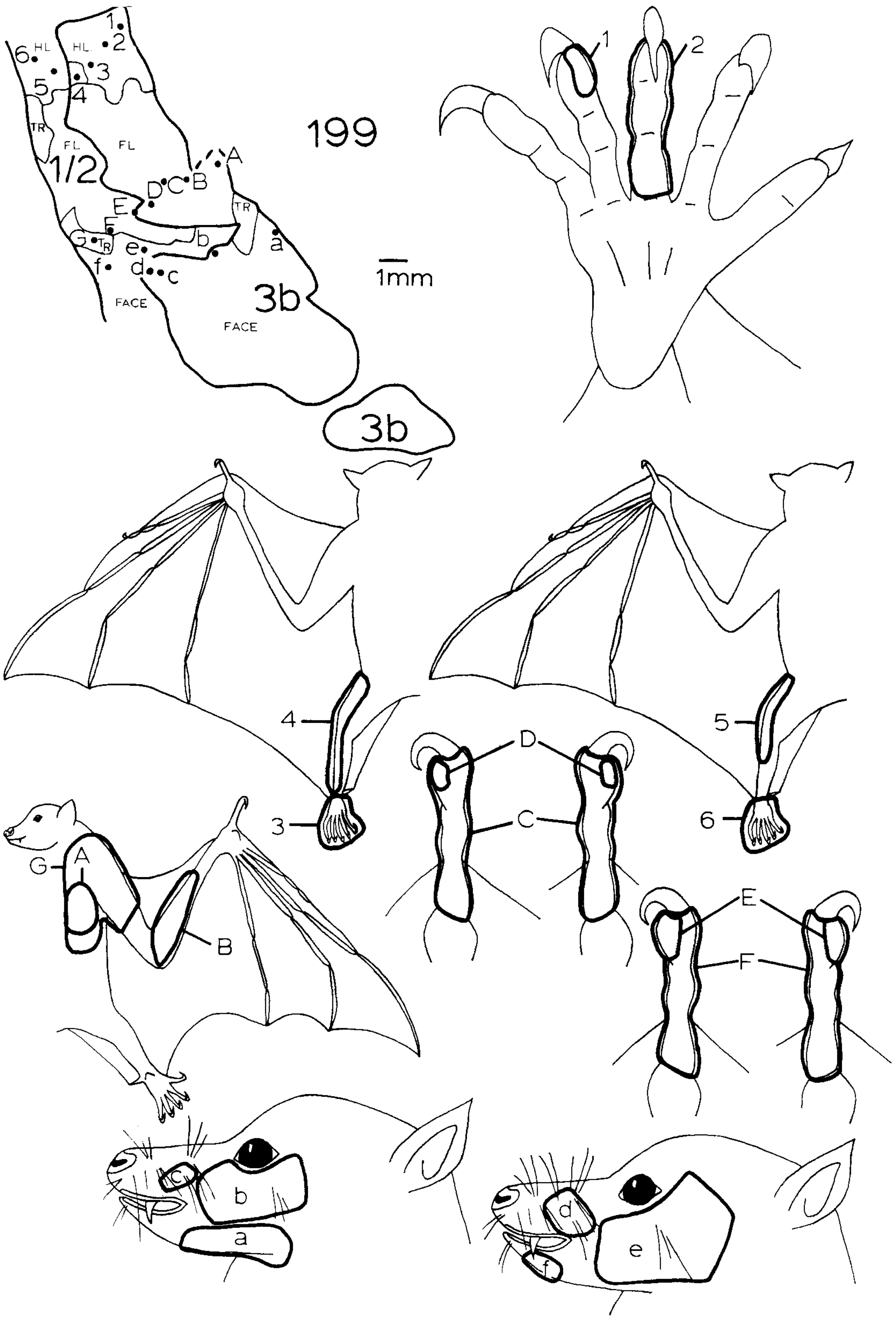


Fig. 10. A simplified map (upper left) illustrating recording site progression from 3b to area 1/2 in flying fox 199. Numbered and lettered receptive fields drawn on body parts correspond to electrode penetrations (filled circles). Receptive fields reverse at the area 3b/area 1/2 border at the representation of the hindlimb (1–6), forelimb (A–G) and face (a–f).

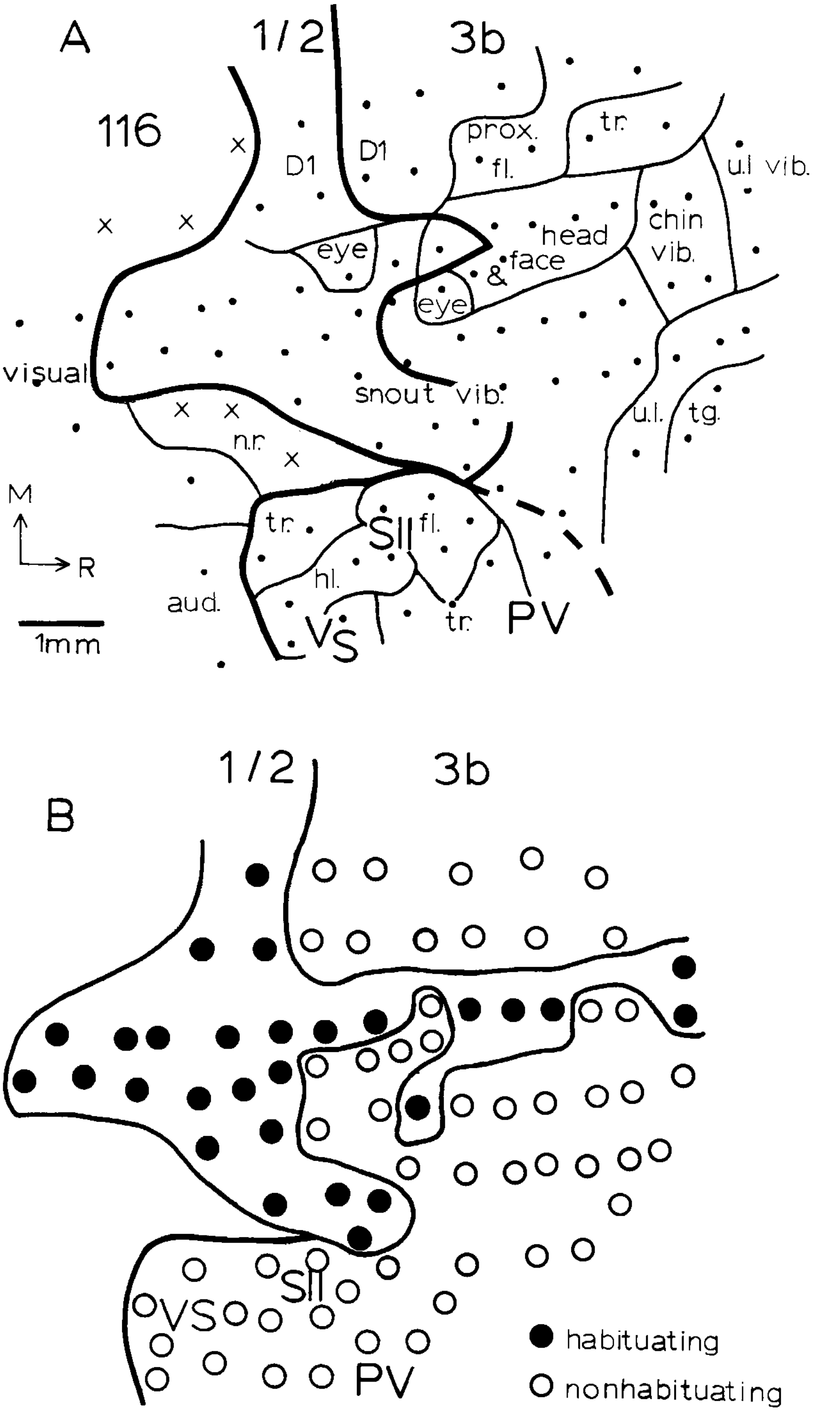


Fig. 11. A reconstruction of recording sites in lateral 3b and 1/2 and in SII, PV, and VS in *Pteropus scapulatus* (**A**). Non-habituating neurons in area 1/2 protrude into 3b (**B**) and separate representations of the face in 3b from the forelimb. Neurons in SII, PV, and some in VS are non-habituating to cutaneous stimulation. A small zone of no response, nr, separates most of the ventral border of area 1/2 from SII. Neurons caudal to the face representation in area 1/2 are responsive to visual stimulation, while neurons caudal to SII and VS are responsive to auditory stimulation. Tongue, tg. Other conventions as in previous figures.

representation in 3b (Figs. 13A,B; 16, upper left). Within the representation of the face and head, the face was represented most rostrally, and the head rostromedially. The lips were far rostral and the chin caudal in the face representation (Figs. 13 and 16). Compared to receptive fields on the face in 3b, receptive fields on the face in SII were relatively large (Fig. 16).

As recording sites in SII progressed from rostral to caudal, receptive fields on the body progressed from head to forelimb to hindlimb (Figs. 13–17). Within the representa-

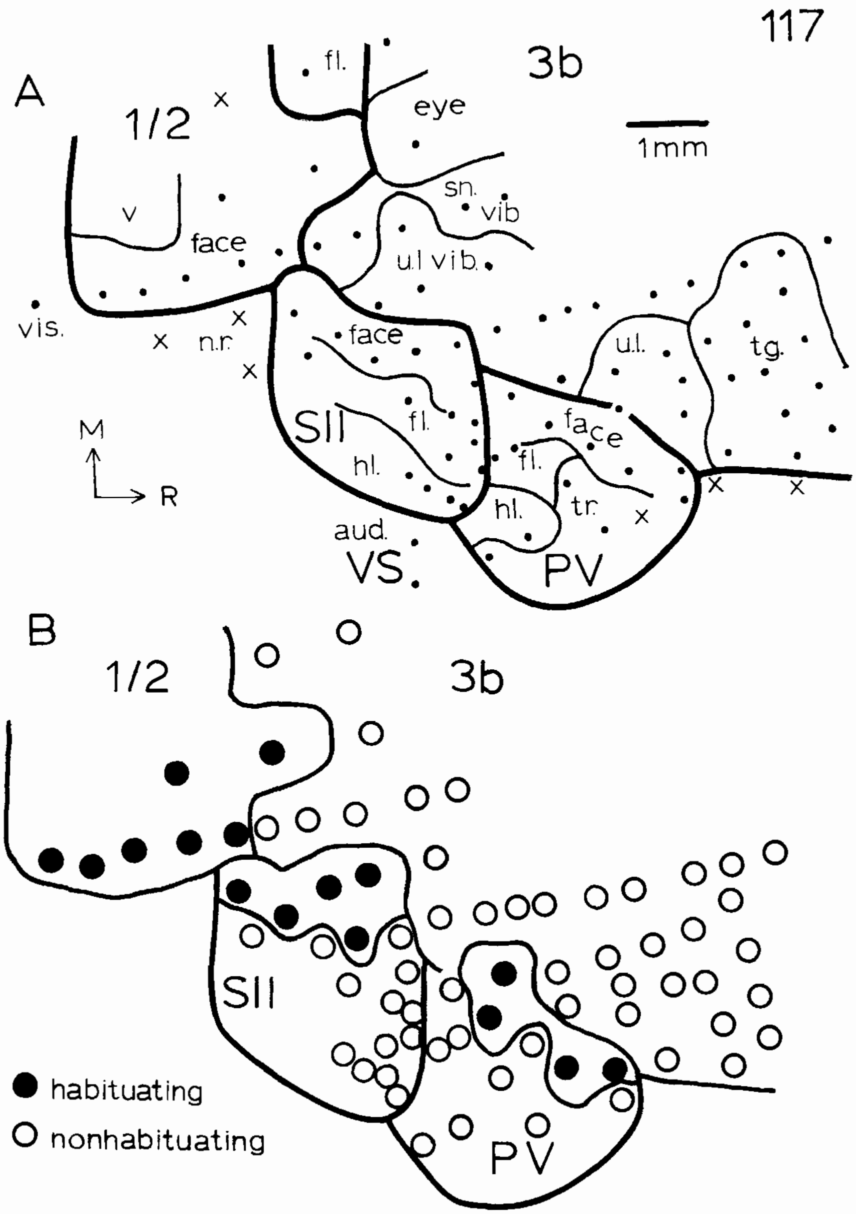


Fig. 12. A reconstruction of recording sites in lateral 3b and 1/2 and in SII and PV in *Pteropus scapulatus*. There is a slight incursion of habituating neurons from area 1/2 into 3b. There are also two small islands of habituating neurons at the 3b/SII and 3b/PV boundaries. Neurons in the location of VS in this case respond only to auditory stimulation. As in the previous figure, there is a small zone of unresponsive cortex between area 1/2 and SII.

tion of the forelimb, the proximal forelimb and associated wing membranes were represented most medially and the distal forelimb and finger membranes were represented more laterally. The position of the digits with respect to the rest of the forelimb was similar to that described for other mammals with no apparent aberrations like those reported for 3b and area 1/2. Often, small receptive fields restricted to D1 phalanges were noted (Fig. 20). However, most often, receptive fields on D1 also included portions of the wrist, finger membranes, and portions of other digits (Fig. 14, receptive fields B and C). Medial to the distal forelimb representation were the representations of the arm, arm membrane, prowing, and shoulder. Receptive fields were generally large and often included portions of the trunk.

The representation of the hindlimb was much like that of the forelimb, with the toes and foot represented most laterally and the proximal portion of the hindlimb and tail membrane represented more medially. Receptive fields restricted to individual toes were never identified. For the most part, both the dorsal and ventral caudal trunk were included in receptive fields of the proximal hindlimb. Thus, the trunk was generally not represented separately in SII. Rather, receptive fields on the lower trunk included portions of the hip and sometimes the upper leg, and receptive

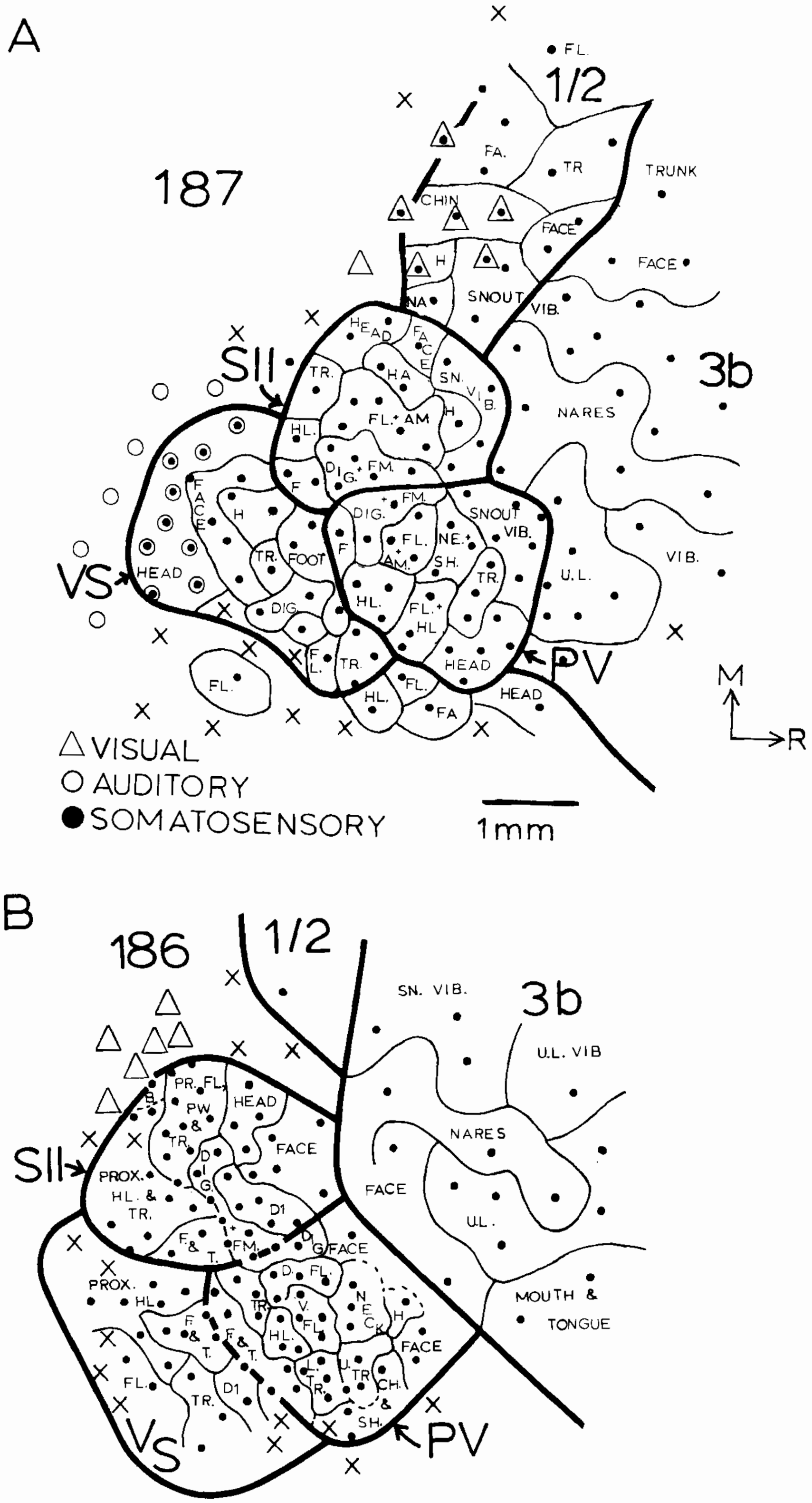


Fig. 13. Summary maps of SII, PV, and VS in case 187 (*Pteropus scapulatus*) (**A**) and 186 (*Pteropus poliocephalus*) (**B**). The density of recording sites in both cases is quite high in all three cortical fields. Neurons in VS in case 187 responded to both somatosensory and auditory stimulation. SII and PV are nearly mirror representations of each other. In both cases, VS reverses off the foot representation in SII and PV. Neurons caudal to area 1/2 and a few within area 1/2 respond to visual stimulation, while neurons caudal to SII and VS respond to auditory stimulation in case 187. In case 186, there is an unresponsive zone between area 1/2 and SII as in previous Figures (8 and 9). Neurons caudomedial to SII are responsive to visual stimulation. Neck, NE; foot, F; nares, NA; body, B; head, H; digits, D. Conventions as in previous figures.

fields on the upper trunk also encompassed portions of the shoulder and sometimes the upper forelimb as well (Fig. 17, receptive field 2). This was never observed in area 3b and only rarely in area 1/2.

The lateral boundary of SII coincided with PV at the representation of the distal limbs. Thus, as recording sites progressed from medial SII to lateral SII into PV, receptive fields on the body progressed from proximal to distal in SII, and from distal to proximal in PV (Figs. 14 and 17). The responses of neurons in SII to cutaneous stimulation, although good, were less vigorous than those observed in area 3b. As in area 3b, responses were elicited by lightly tapping or brushing the skin or displacing hairs. Neurons in SII gave consistent responses to repetitive stimulation (Figs. 5 and 11B), and receptive fields were often very large (Figs. 19 and 20). The representations of the head, forelimb and hindlimb occupied a similar amount of cortical space.

Several fields caudolateral to 3b were distinct in sections stained for myelin. Generally, a single section did not reveal all cortical boundaries. Thus, architectonic boundaries were determined from a series of sections throughout cortical layers. The second somatosensory area was apparent as a moderate to darkly myelinated field adjacent to the lateral portion of 3b, just where 3b begins to curve rostrally (Figs. 9 and 18). In superficial sections, SII stained moderately to lightly for myelin, while in middle and deeper layers, SII was more darkly myelinated. The shape and size of this darkly myelinated field corresponded to the physiological representation described in the previous section. Because SII stained darkly for myelin at deeper levels, the boundary between SII and 3b was most apparent in more superficial layers where SII was lightly myelinated and 3b was still darkly myelinated (Fig. 18). Cortex immediately dorsal and caudal to SII was lightly to moderately myelinated.

Parietal ventral area, PV

One hundred and fifteen closely spaced electrode penetrations were made in the parietal ventral area, PV, just lateral to SII and caudolateral to 3b in five animals. In individual animals, up to 39 electrode penetrations were made so that high density maps of this field could be constructed. PV occupied approximately the same cortical area as SII (4 mm^2) and contained a complete representation of the body surface. The body map in PV was inverted with respect to SII, with the trunk located laterally and the distal limbs represented medially. Thus, it formed a mirror reversal of the body map in SII (Figs. 13, 14, 17, 21). The face representation in PV was adjacent to the face representation in 3b and formed a border at the representation of the upper lip. As recording sites progressed across the 3b/PV border, receptive fields progressed from the snout and upper lip in 3b back onto snout and head in PV (Fig. 16). Within the face and head representation in PV, the face was represented rostromedially and the head was represented caudolaterally to the face. In some cases (Fig. 16) the oral structures in PV were represented most laterally in the representation of the face. In two cases, the chin was represented in a lateral position in PV (Figs. 13B and 16). Caudal to the face and head representation was the representation of the neck.

The representation of the forelimb in PV was caudal to the face and head representation. Within the forelimb, the distal forelimb and finger membranes were represented most medially and were adjacent to the distal forelimb representation in SII. The forelimb, arm membrane, prowing, and shoulder were represented lateral to the representation of the distal forelimb and the upper trunk was represented lateral to the representation of the forelimb. Thus, with a progression of recording sites from SII to PV in the forelimb representation, receptive fields on the body progressed from upper trunk/forelimb and distal forelimb in SII, to distal forelimb, forelimb and upper trunk in PV (Figs. 14 and 17). Unlike SII, the trunk was distinct and represented separately from the representation of the limbs (e.g., Fig. 16, receptive fields H–K). Also, within the representation of the forelimb, separate islands of the dorsal and ventral forelimb were found in some, but not all, cases (Fig. 13B).

The hindlimb was represented in the most caudal portion of PV, with the foot represented caudomedially and the proximal hindlimb and tail membrane represented more laterally. Immediately lateral to the representation of the hindlimb was the representation of the lower trunk. As in the representation of the forelimb and upper trunk, islands of ventral and dorsal trunk representations could be observed in some cases. In one animal, 187 (Fig. 13A), there was a small zone of cortex between the forelimb and hindlimb representations, where neurons had receptive fields on both the forelimb and the hindlimb. Within the trunk representation, the upper trunk was rostral to the lower trunk. In one case, the head was represented below the representation of the trunk (Fig. 13A).

Neurons in PV were consistently responsive to cutaneous stimulation of the body surface. Receptive field sizes were generally larger than those in SII (Figs. 19 and 20), and receptive fields on the trunk were generally smaller in PV than in SII, since they never included portions of the limbs. As in SII, major body parts assumed a similar amount of cortical space with the face/head, forelimb, hindlimb, and trunk representations each occupying approximately one-fourth of the total area in PV.

PV could also be distinguished myeloarchitectonically as a lightly to moderately stained area adjacent to the darkly stained 3b (Fig. 18). PV was similar to SII in size and shape and, because of the similarity in architecture, it was sometimes difficult to define the SII/PV boundary. However, because PV was less well-myelinated than SII in most layers, this boundary could usually be distinguished (Figs. 9

Fig. 14. A simplified map for case 186 (Fig. 13B) showing progressions of receptive fields from SII into PV. Receptive fields in SII are located on the trunk in caudomedial portions of the field and progress to distal limbs as recording sites move rostrolaterally (r.f.'s A–E and 1–3). As recording sites move into PV, receptive fields are located on distal limb representations and then move onto proximal body parts as recording sites move rostrolaterally (F–I and 4–8). Thus, there is a reversal of receptive fields at the SII/PV boundary. Conventions as in previous figures.

Fig. 15. A simplified map for case 186 showing progressions of receptive fields from SII into VS, and from PV into VS. As recording sites progress medial to lateral in SII, receptive fields progress from forelimb/trunk to hindlimb/foot (r.f.'s 1–5). As recording sites move from SII to VS, receptive fields move from hindlimb/foot to forelimb (r.f.'s 6 and 7). When recording sites in PV move from rostromedial to caudolateral, receptive fields move from forelimb to hindlimb and foot (r.f.'s A–C). As recording sites move into VS, receptive fields move from foot to hindlimb to forelimb (r.f.'s D–G). In both SII and PV there is a reversal of receptive fields at the representation of the foot as recording sites move into VS. Scale bar as in Fig. 14.

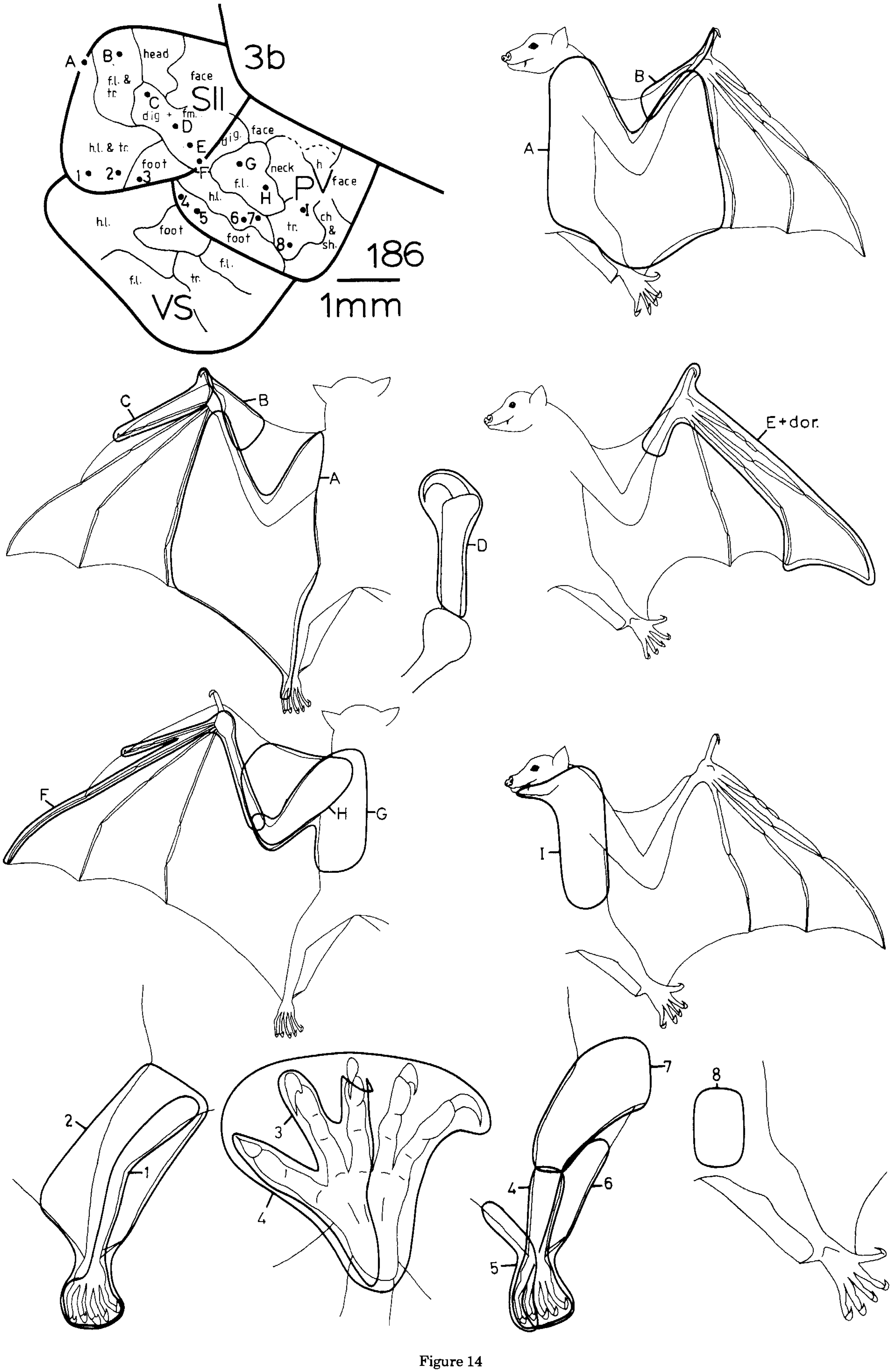

3b
SII
head
face
f.l. & tr.
dig + fm.
h.l. & tr.
foot
A
B
C
D
E
F
1
2
3
dig.
face
neck
h
PV
face
G
f.l.
H
h.l.
I
tr.
ch & sh.
4
5
6
7
8
foot
h.l.
foot
f.l.
f.l.
tr.
VS
186
1mm
E+dor.

Figure 14

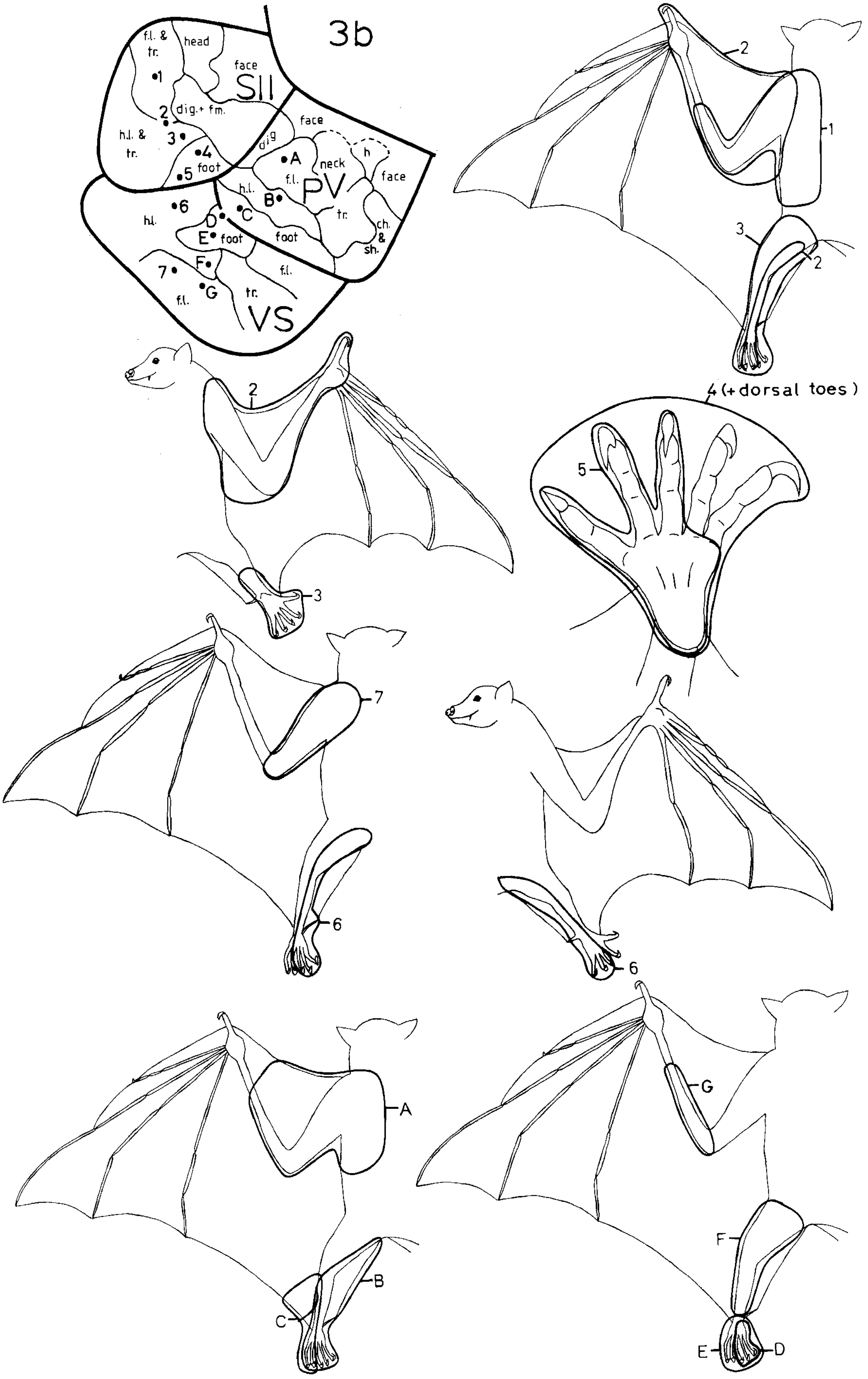

3b
f.l. &
tr.
head
face
SII
•1
2
dig.+ fm.
h.l. &
tr.
3
4
5
foot
face
dig
h
A
neck
face
f.l.
PV
h.l.
B
tr.
6
h.l.
D
C
E
foot
foot
ch.
&
sh.
F
f.l.
7
G
tr.
f.l.
VS
2
1
3
2
2
3
4 (+ dorsal toes)
5
7
6
6
A
G
B
C
F
E
D

Figure 15

and 18). The boundary between the darkly myelinated 3b and the moderately myelinated PV could also be identified at most laminar levels. Cortex immediately lateral to PV was lightly myelinated in superficial sections and moderately myelinated at deeper cortical levels. Cortex caudal to PV was moderately myelinated and coextensive with a third representation of the body surface, the ventral somatosensory field, VS.

Ventral somatosensory area, VS

A third topographically organized field caudolateral to SII and PV was explored in the present investigation by placing as many as 29 electrode penetrations in this field in a single animal, and a total of 80 penetrations in four animals. Although the total area of VS was similar to that of SII and PV, the shape of the field was more elongated in the dorsolateral plane. VS was adjacent to both SII and PV at the representation of the foot. The topography of this field was less precise than that observed in SII and PV, but there appeared to be a complete representation of the body surface in some preparations (e.g., Fig. 13A). The threshold of neurons in VS was relatively high so it was often difficult to drive neurons in this field and in some cases, no responses were elicited from VS (e.g., Fig. 16).

Maps of VS demonstrated a rough topography in this field and although the detailed internal organization of VS varied from animal to animal, the overall topography was consistent (Figs. 4 and 13). The foot in VS was represented rostromedially adjacent to the foot representation in SII and PV. The digits, finger membranes, and forelimb were represented adjacent to the ventral border of the foot representation, and the trunk was represented ventral to the forelimb representation in one case (Fig. 13A), and caudoventral to the digit representation in another case (Fig. 13B). An additional representation of the trunk was noted just caudal to the foot in the former case, and an additional representation of the forelimb was adjacent to the trunk representation in the latter case (Fig. 13). The proximal hindlimb was represented caudomedially, adjacent to the representation of the foot, and the face was represented most caudally in VS. Despite the internal variation in VS across animals, there was a monotonic topographic progression of receptive fields through the field (Fig. 15). A clear reversal in the receptive field progression was noted as recording sites moved from either SII or PV into VS (Fig. 15).

Responses of neurons in VS to cutaneous stimulation were markedly weaker than those of neurons in SII and PV, and receptive fields in VS were generally larger than those in SII (Figs. 19 and 20). We refer to neurons in VS as rate-dependent because a low rate of stimulus repetition (around 1–5 Hz) was a crucial feature in driving them (Fig. 5). Another feature of neurons in VS was that they were often driven by both somatosensory and auditory stimulation (Figs. 4 and 13A).

In cortex stained for myelin, VS was a lightly to moderately myelinated oblong area that was most distinct in middle cortical layers. In superficial sections, VS was very lightly myelinated (Fig. 9), while at middle and deeper cortical layers, VS was more moderately myelinated (Fig. 18). The SII/VS boundary was generally distinct since SII stained more densely for myelin than VS. However, the PV/VS boundary was sometimes difficult to define since both fields were lightly to moderately myelinated. Usually, the boundary of these two fields was most apparent in superficial sections where VS was less well myelinated than PV. Cortex surrounding VS was generally lightly myelinated. The densely stained field caudal to VS is assumed to be the primary auditory area, since it has a similar appearance in a number of other species including rodents (Merzenich et al., '76; Luethke et al., '88), tamarins (Luethke et al., '89), and owl monkeys (Morel et al., '89).

Other areas with somatosensory responses

In some animals, the cortex surrounding the somatosensory fields described above was mapped. In cortex immediately caudal to area 1/2, neurons often responded to both visual and somatosensory stimulation (Fig. 4), although in some cases, only a visual stimulus could elicit a response. Strong taps or limb displacement were needed to elicit a response from neurons caudolateral to area 1/2 and receptive fields here were difficult to define and were often quite large. In some cases, no responses were obtained from neurons caudal to area 1/2. Immediately lateral to area 1/2 and caudomedial to SII was a small zone of unresponsive cortex where no mode of stimulation could elicit a neural response. This pocket of unresponsive cortex was observed in every animal in which this region was mapped (Figs. 4, 11A, 12A, 13). Caudal to this zone of unresponsive cortex, neurons responded to visual stimulation (Figs. 11A, 12A, 13B).

The type of stimulation needed to elicit a response from neurons caudal to SII varied across animals. In some animals (Fig. 13B), neurons responded to visual stimulation, while in other animals (Figs. 4 and 11A), neurons responded to auditory stimulation. In cortex immediately caudal to VS, neurons responded well to auditory stimulation (Figs. 4, 11A, 12A, 13A). Responses of these neurons were non-habituating and thresholds were very low. Cortex lateral to VS was generally unresponsive to any type of stimulation (Fig. 13A), but in some animals, an island of neurons responded to deep taps to the forelimb (Fig. 13A). Cortex immediately lateral to PV had neurons that were often unresponsive, but in one case, somatosensory stimulation could evoke responses here (Fig. 13A). Unlike PV, hard taps to the body surface were needed to stimulate neurons in this region. Because of the difference in architecture and response properties of neurons, and because the receptive fields of neurons here were unrelated to the topography of adjacent fields, these recording sites were not included within the PV or VS fields. Connectional evidence (Calford and Krubitzer, '90) suggests that some of these fringe areas surrounding known somatosensory fields may be involved in somatosensory processing. Because neural groups were often bimodal, these areas are probably higher in the processing stream of somatosensory information and may constitute what is traditionally considered as "association" cortex. Finally, in cortex immediately rostral to 3b, neurons could be driven by movement of joints or hard taps to body parts (Fig. 3). We termed this field area 3a because the relative position, myeloarchitecture, and neural response properties of this field resembled somatosensory area 3a described in primates.

Comparison of properties of cutaneous somatosensory areas

Although primary descriptions of cortical areas are based on somatotopy of fields, there were important qualitative observations which helped distinguish the five somatosensory areas. For instance, neurons in area 1/2 were distinct from neurons in area 3b because they rapidly habituated to the stimulus, while most neurons in 3b were nonhabituating to the stimulus (Figs. 4, 11B, 12B). Neurons in VS were rate-sensitive, responding only to a specific rate of stimulus presentation, while neurons in neighbouring fields such as SII and PV were generally not rate-sensitive, although in one case, several recording sites in PV had neurons that were rate-sensitive (Fig. 4). Finally, in VS and PV, neurons responded to both somatosensory and auditory stimulation (Figs. 4 and 13). This bimodal response was only noted for a few penetrations at the borders of SII in one case (Fig. 4). Another important feature that could be directly compared across all cortical fields was the size of a receptive field. Because the receptive fields within a single field varied with the part of the body stimulated, one had to compare receptive fields on the same body part across cortical fields. To do this, we chose the smallest receptive field for a given body part across all cortical fields. For fields on the snout (Fig. 19), it was possible to compare receptive fields obtained from the same animal. The size of receptive fields was smallest in 3b and progressively increased in areas 1/2, SII, PV, and VS for the representation of the face (Fig. 19). This was also true for receptive fields on the thumb (Fig. 20), although both PV and VS had very similar receptive field sizes. This progressive increase in receptive field size from 3b to VS was noted for receptive fields on all body parts.

DISCUSSION

In the present investigation, we have demonstrated that the somatosensory cortex in the flying fox is composed of a number of topographically organized fields (Fig. 21). In anterior parietal cortex, there are at least three somatosensory fields, including the primary somatosensory area (3b or SI proper), a field just caudal to 3b, area 1/2, in which neurons have response properties of areas 1 and 2 of primates, and a field rostral to 3b, 3a, in which neurons respond to manipulations of body parts. In cortex caudolateral to 3b in the region traditionally defined as SII, there are at least three topographically organized fields. All regions identified electrophysiologically have been related to myeloarchitecture in cortex that has been flattened and cut parallel to the cortical surface.

The cortical topography, response properties, and myeloarchitecture of anterior parietal cortex

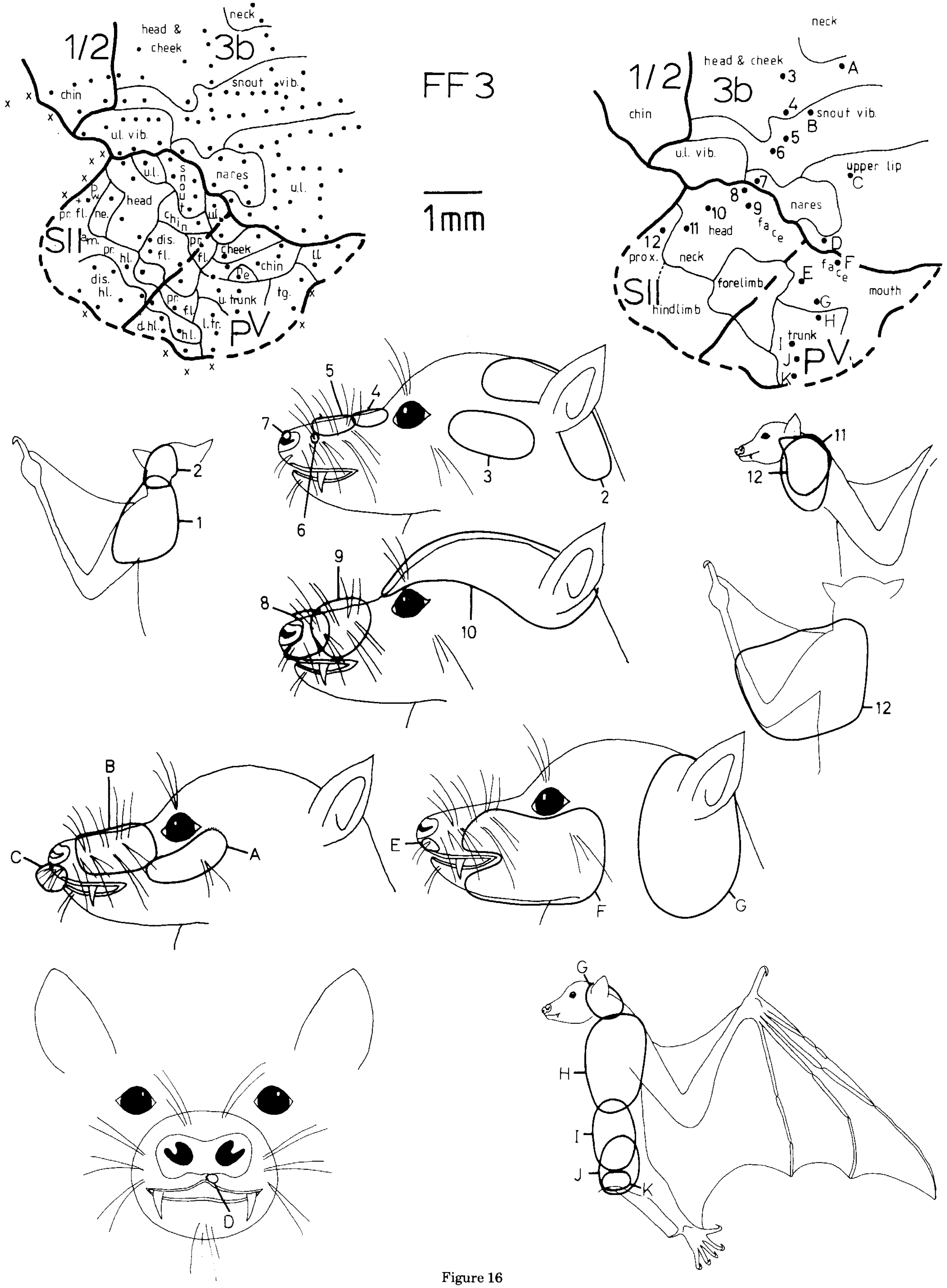
Area 3b. The present findings on the topographic organization and response properties of neurons in the primary somatosensory area, 3b or SI, are in agreement with previous results on 3b in the flying fox (Calford et al., '85), as well as reports on the organization of SI in other eutherian mammals (rodents: Lende and Woolsey, '56; Woolsey, '67; Carlson and Welker, '76; Sur et al., '78; Pimentel-Souza, '80; Chapin and Lin, '84; carnivores: Welker and Seidenstein, '59; Dykes et al., '80; Felleman, '83b; tree shrews: Sur et al., '81; primates: Merzenich et al., '78; Nelson et al., '80; Sur et al., '80; '82; Felleman et al., '83a; Carlson et al., '86; Krubitzer and Kaas, '90b; and microchiropteran bats: Wise et al., '86; but see Kaas, '83 for review), although the representation of the forelimb is reversed rostrocaudally from that described for other mammals. As in other mammals, 3b in the flying fox contains a complete representation of the body surface with the hindlimb represented most medially, on the medial wall of cortex, and the forelimb and face represented in a mediolateral progression. In the representation of the face, the oral structure representation curves rostrally so that 3b appears to be a stretched out "L". A similar shape of 3b has been described in the marmoset (Krubitzer and Kaas, '90b). Neurons in 3b respond to cutaneous stimulation and are best stimulated by lightly tapping the skin surface, displacing hairs, or brushing the skin surface. Because of the similarities in organization, response properties, and connections (Calford and Krubitzer, '90), it is believed that SI is a homologous field in all mammals.

Although most neurons in 3b have a consistent response to cutaneous stimulation, there were some islands of neurons in 3b in the flying fox that rapidly habituated to cutaneous stimulation. These regions were related to myelin-light zones in cortex that was flattened and cut parallel to the cortical surface. The idea that neurons in SI are heterogeneous is not new. There have been a number of reports of modality-specific neural groups in 3b of primates (Mountcastle and Powell, '59; Paul et al., '72; Hyvärinen and Poranen, '78; Darian-Smith et al., '82; Sur et al., '84), and SI of cats (Mountcastle, '57; Rasmusson et al., '79; Dykes and Gabor, '81) and rats (Chapin and Lin, '84; Dawson and Killackey, '87). These reports imply that modularity of SI may be a general feature of mammalian somatosensory neocortex. It is important to distinguish between habituating and non-habituating neural responses defined in the flying fox, and rapidly and slowly adapting neural responses described in other mammals (e.g., Paul et al., '72; Sur et al., '84). No slowly adapting responses were observed in the flying fox in the present investigation. Both habituating and non-habituating neurons in areas 1/2 and 3b respectively would be classified as rapidly adapting. Thus, segregation of functional neural groups in 3b in the flying fox does not relate to the rapidly adapting and slowly adapting segregates described in 3b in primates (Paul et al., '72; Sur et al., '84) and SI of cats (Dykes and Gabor, '81).

The discovery of vibrissae barrel fields in mice (Woolsey, '67; Woolsey and Van der Loos, '70; Welker and Woolsey, '74; Woolsey et al., '75) and rats (Welker, '71) was the first hint that representations in the neocortex of mammals may segregate into clear anatomical compartments based on afferent inputs from the periphery. Since this early discovery, it has been noted that all of the representation in SI in the rat is separated into distinct granular (GZ) and dysgranular (DZ) patches, each related to a specific body part representation (Chapin and Lin, '84). Granular SI is coex-

Fig. 16. Dense microelectrode map (upper left) for SII and PV in flying fox 3 (*Pteropus poliocephalus*) and receptive field progressions from 3b into area SII, and from 3b into PV (upper right). Receptive fields reverse on the face at the border of 3b with both SII and PV. Thus, as recording sites progress from 3b into SII, receptive fields move from trunk, head, cheek, snout, and nose (r.f.'s 1–7) in 3b, to snout, head and trunk in SII (r.f.'s 8–12). In PV a similar reversal of receptive fields is noted (r.f.'s A–K). Note that receptive fields in 3b are smaller than in SII and PV.

Fig. 17. A simplified map of FF3 (upper left) showing receptive field progressions from SII into PV. As recording sites progress from medial to lateral in SII, receptive field progress from trunk to distal limbs (r.f.'s 1–4, A and B). As recording sites move into PV and progress laterally, receptive fields move from distal limbs to proximal limbs and trunk (r.f.'s 5–8, C and D). Scale bar as in Fig. 16.


neck
head &
cheek
1/2
3b
chin
snout vib.
u.l. vib.
u.l.
snout
nares
u.l.
p.w.
pr. fl.
ne.
head
chin
u.l.
SII
am.
pr.
hl.
dis.
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fl.
cheek
chin
ne
l.l.
dis.
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d. hl.
hl.
l. tr.
PV
FF3
1mm
neck
head & cheek
1/2
3b
A
3
4
snout vib.
B
5
6
chin
u.l. vib.
upper lip
C
7
8
9
10
11
head
face
nares
D
12
prox.
neck
SII
hindlimb
forelimb
E
face
F
mouth
G
H
trunk
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PV
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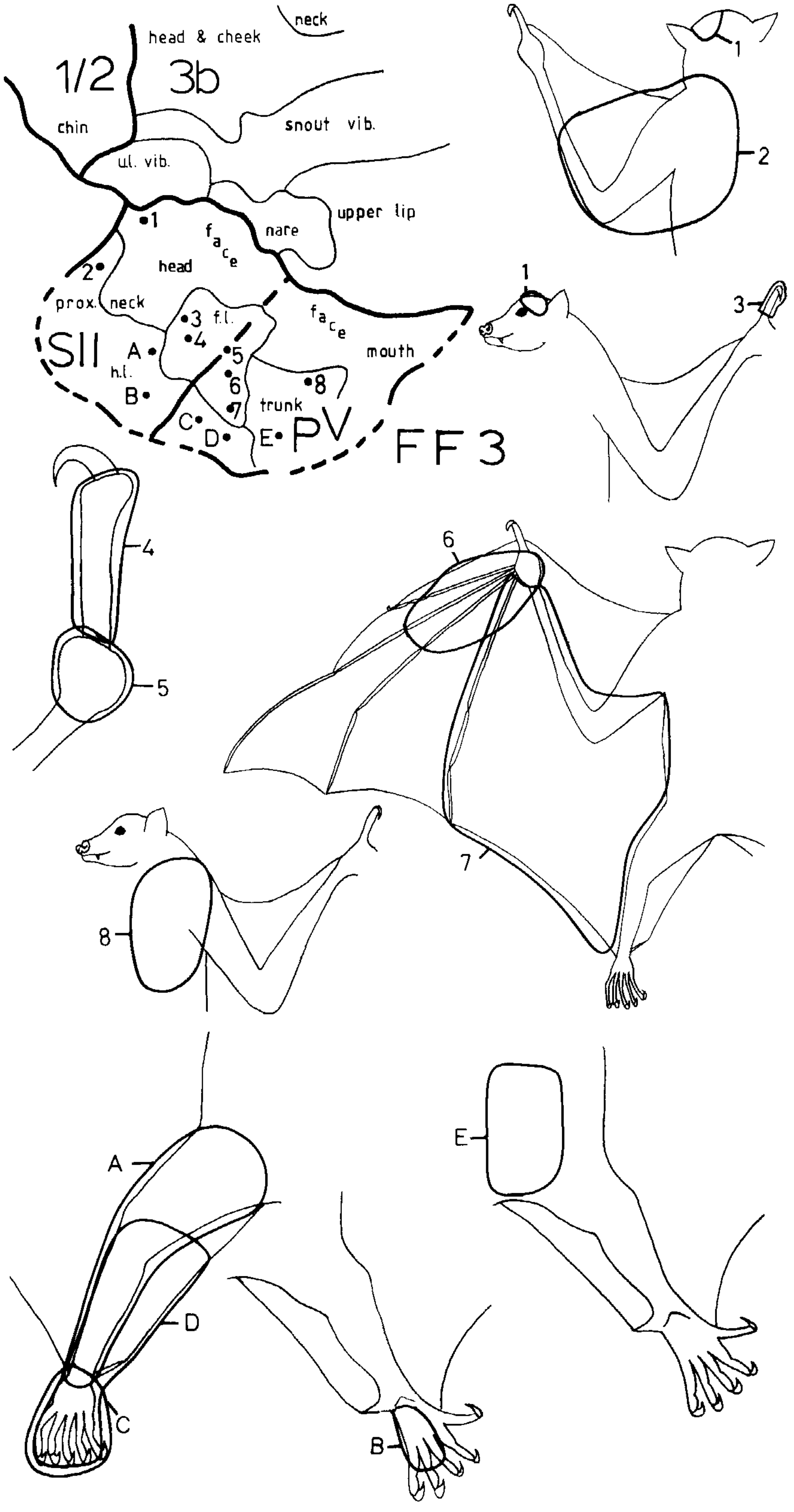
Figure 16


neck
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4
face
mouth
SII
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h.l.
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Figure 17

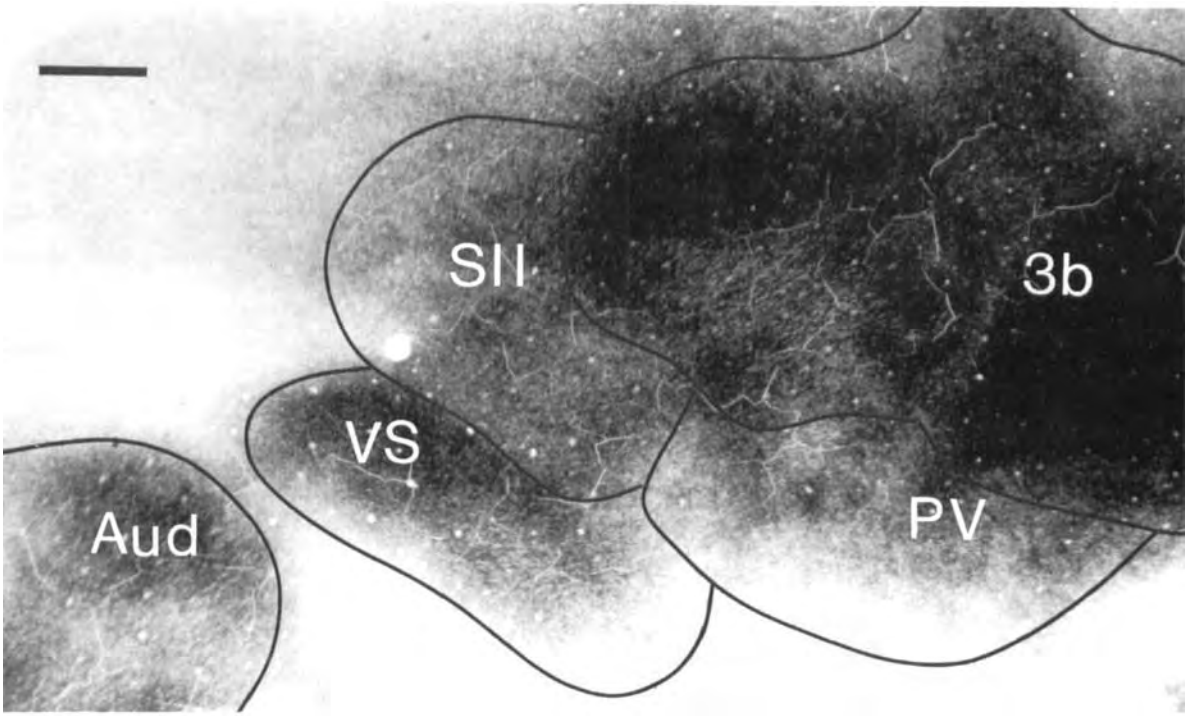

Fig. 18. Lightfield photomicrograph of cortex stained for myelin. The myelin dense SI cortex (3b) is bordered caudolaterally by three moderately myelinated fields, SII, PV, and VS. Cortex surrounding SII, PV, and VS stains very lightly for myelin. Auditory cortex (Aud) stains moderately for myelin at this laminar level. Scale bar = 1 mm. Rostral is right and medial is top.

tensive with the representation of cutaneous receptors, while dysgranular SI has a higher proportion of neurons responsive to joint stimulation. In a more recent investigation, a complete representation of cutaneous receptors was found to be directly related to dense staining using succinic dehydroxinase (Dawson and Killackey, '87). Although receptive fields on a particular body part spread across structural boundaries in cortex in this study, it is likely that minimal receptive fields would be restricted to a structural segregate in cortex.

In this investigation, we provide descriptions of functional submodalities in 3b coextensive with a unique architectonic appearance. While myelin-light and dark regions were noted in a previous investigation in marmosets (Krubitzer and Kaas, '90b), a direct relationship between the cortical physiology and myeloarchitecture was not made. Our descriptions of a modular 3b in the flying fox are most similar to descriptions of SI in rats where clear correlations between functional neural groups and architecture have been made.

This correspondence of functional units with architectonic distinctions in SI is reminiscent of the modular organization described for the first (V-I) and second (V-II) visual area in primates. In visual cortex, the relation between functional neural specializations to cytochrome oxidase staining patterns in V-I and V-II in primates is well documented (Livingstone and Hubel, '84; Hubel and Livingstone, '87) and has recently been described in cats (Murphy et al., '90). In the primary auditory area, aural dominance modules have been identified in a range of mammals (Imig and Adrian, '77; Imig and Brugge, '78; Middlebrooks et al., '80). The modulation of the primary somatosensory area described in this report indicates that sensory neocortex in general may have a predisposition to subdivide into functional units within a cortical field.

All of the features that constitute a "module" in cortex are unknown. However, it is possible that different combinations of afferent input help create modules in cortex. In the visual system of primates, some evidence suggests that cortical fields are the result of different combinations of modular inputs (Krubitzer and Kaas, '90a). Thus, the same forces that contribute to the uniqueness of a cortical field, may also contribute, on a smaller scale, to creating a module within a field.

Mosaic hypothesis. Recently, Favorov and colleagues have described a mosaic organization within SI of cats (Favorov et al., '87; Favorov and Diamond, '90) and area 1 of macaque monkeys (Favorov and Whitsel, '88a,b). The mosaic is formed of segregates, approximately 300–600 μm in diameter, within which the threshold of receptive fields of neurons is constant. The center of all receptive fields within a segregate is the same, although maximum receptive fields may be highly variable. A somatotopic organization exists across but not within segregates. No anatomical correlate of the segregates has been described. The methods we have employed in the study of the flying fox do not allow for the evaluation of such segregates. However, the discrete myelin-dark patches which correspond to neurons that are non-habituating to cutaneous stimuli in the present study, need to be evaluated as a possible anatomical substrate for the mosaic segregates described by Favorov and colleagues.

The patches in the flying fox are larger (~ 4 mm^2) than the functional segregates described in cats or monkeys, and there is somatotopy within patches. In the studies on cats and monkeys in which closely spaced electrode tracks were placed across the borders of segregates (e.g., Figures 4 and 5

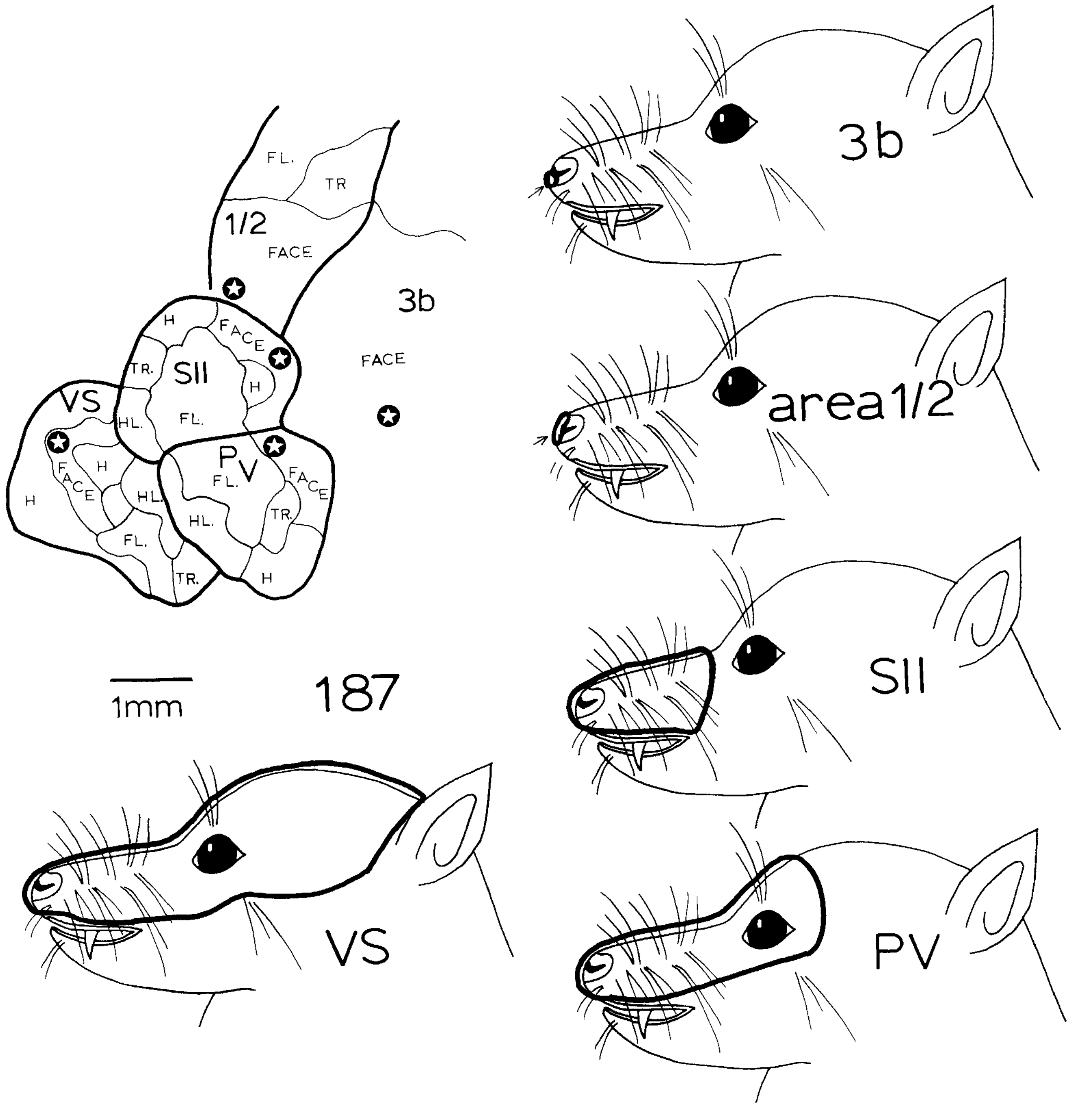

Fig. 19. Receptive fields for starred penetrations in areas 1/2, 3b, SII, PV, and VS in simplified map (upper left) of flying fox 187. To allow a rough comparison of receptive field extent in the five cutaneous sensitive fields, the smallest receptive field that included any part of the nares in each area is illustrated. In area 3b, the smallest receptive field is restricted to a small region of the nares. The field in area 1/2 is about twice the size, covering approximately half of the nares. The illustrated receptive fields in the others areas are much larger with an increase from SII to PV to VS. The increase in receptive field size from 3b to VS was a general feature that was apparent for representations of all body areas.

of Favorov and Diamond, '90) there was no evidence for weaker or different response properties of neurons as that seen between patches in the flying fox. Thus, it appears that if the organization of myelin-dark patches and common minimum receptive field segregates coexist in a species, then the proposed mosaic organization of segregates would occur within the patches.

Implications for studies of plasticity. The identification of patches in 3b also has implications for the interpretation of the capacity for plasticity of the representation in 3b. Functional limits have been demonstrated in the extent of long-term reorganization of the topographic representation in 3b following partial denervation of the periphery (Merzenich et al., '83a,b, '84; Wall and Cusick, '84). Thus, if

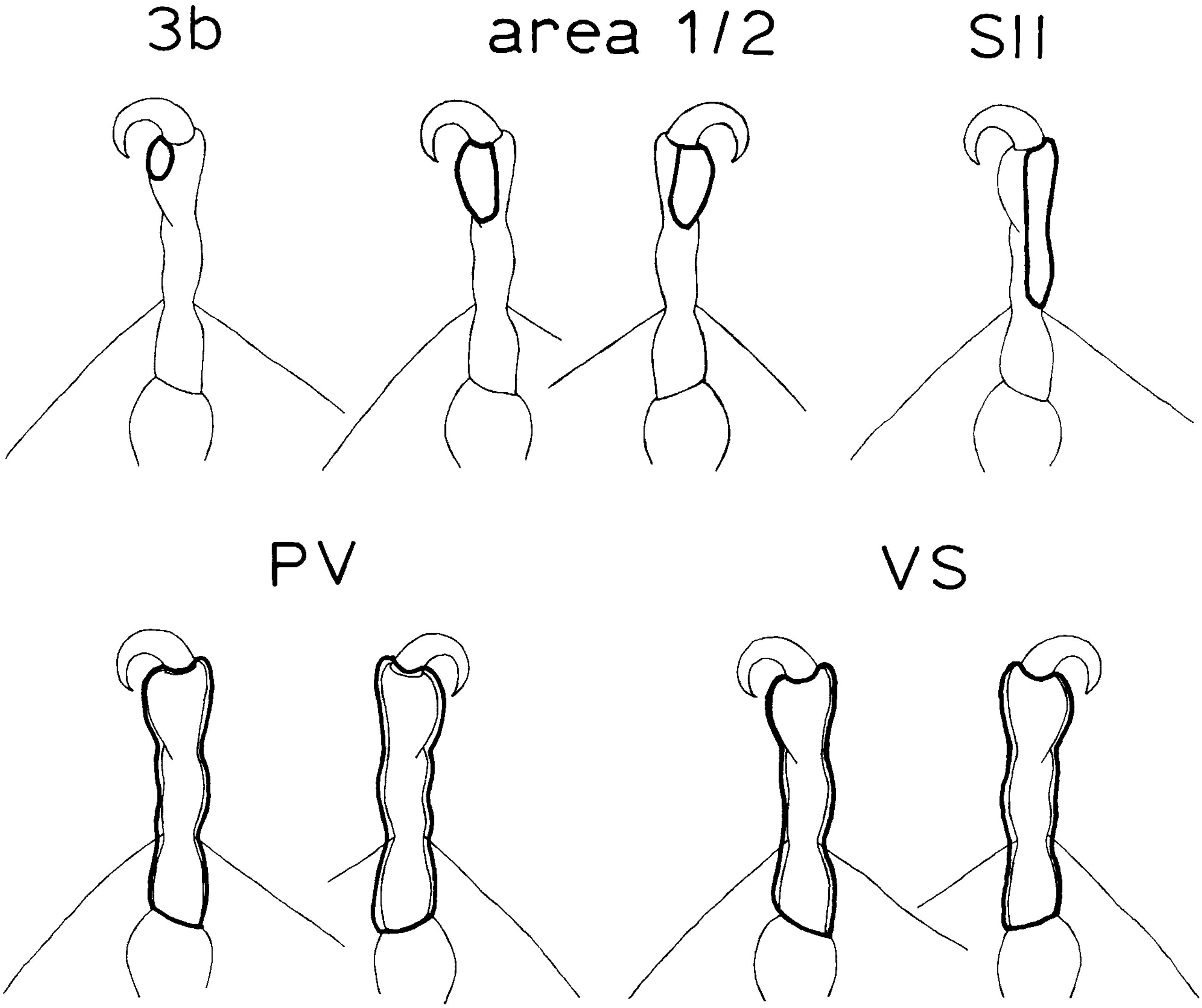

Fig. 20. Receptive fields on D1 for neurons in all cortical fields mapped. As in the previous figure, receptive fields are smallest in 3b and include only the distal tip of D1. In area 1/2, receptive fields are slightly larger and in SII larger still. In PV and VS, receptive fields on the distal D1 also include middle and proximal portions of D1.

two fingers are amputated in an owl monkey, a nonresponsive area remains in the center of the affected representation, whereas if one finger is amputated, the expansion of the representation of adjacent fingers and the palm completely encompasses that of the amputated finger (Merzenich et al., '84). Topographic limits are also apparent in the extent of expanded receptive fields of neurons in 3b that are seen within a few minutes of a small peripheral denervation (Calford and Tweedale, '88, '90, '91). In both cases, the limits have been related to the presence of inputs to a cortical locus that are not normally expressed (Snow et al., '88), afforded by the extensive arborization of thalamocortical afferents (Landry and Deschênes, '81; Garraghty and Sur, '90). The limit on plasticity appears to be about 1 mm across the cortical representation, and functional changes in cortex never cross cortical representational boundaries (e.g., between the hand and face) that are not also topographic on the body surface (e.g., digits to palm). Two mechanisms for the way in which the weaker inputs to a cortical locus may come to be expressed after loss of its major input have been proposed: changes in excitatory efficacy (Merzenich et al., '84; Pearson et al., '87) and disinhibition (Calford and Tweedale, '88, '91). Both, however, rely on utilization of existing connectivity and the rough topography of the thalamocortical projection. It is interesting that although the basis for plasticity can be explained in terms of overlap of thalamocortical inputs and the heightened expression of the input provided by the distal arborization of afferents that primarily connect to neighbouring cortical regions, the role of structural "edges" in cortex has never been discussed. The myelin-dark patches demonstrated in the present investigation may provide structural "edges" over which plasticity does not occur. The relationship of thalamocortical afferents to the myelin-light and dense patches is unknown but is an important question for future studies.

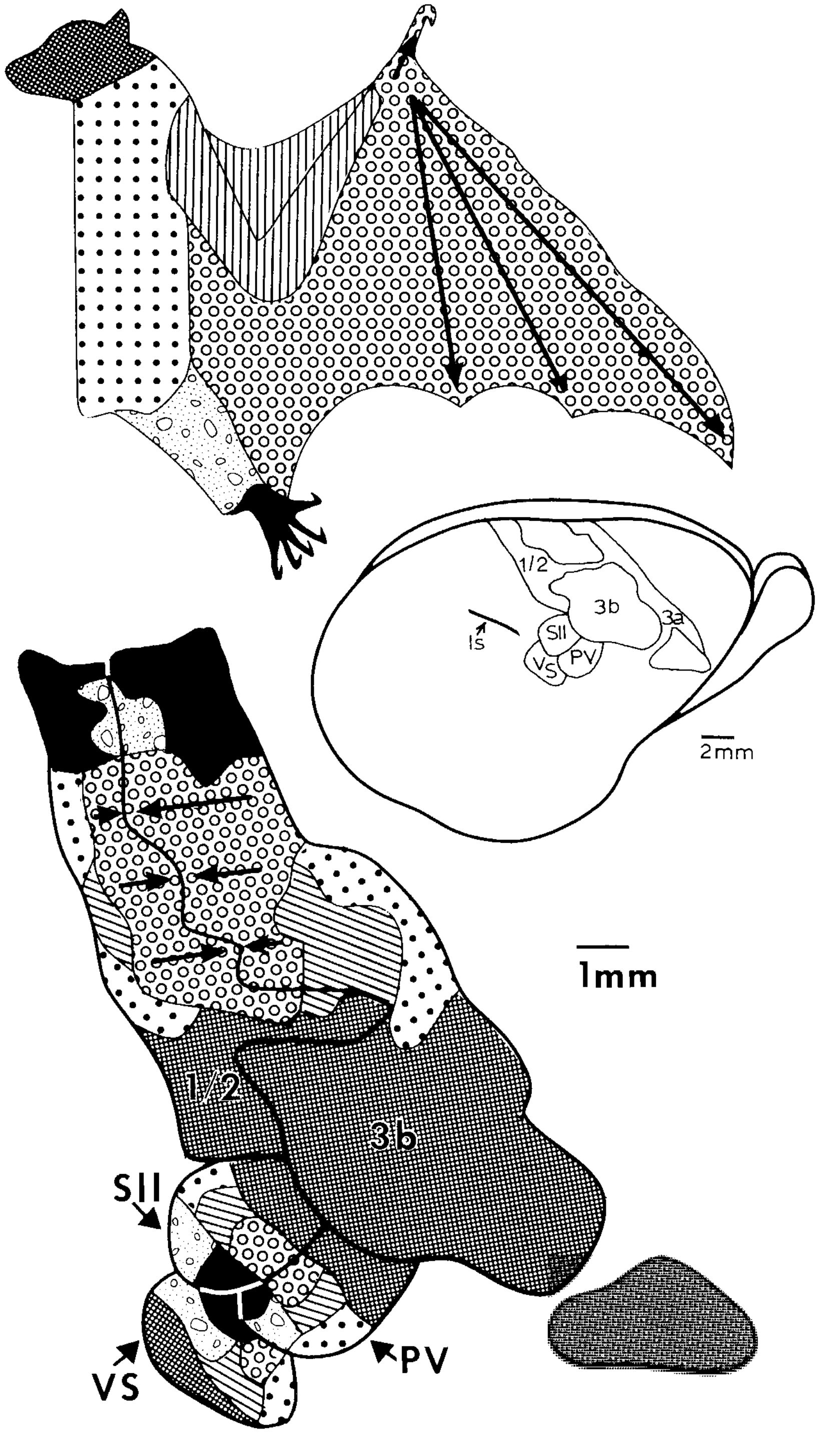

Fig. 21. A summary of the topographic organization of somatosensory fields described in this study and their position in the neocortex (inset at right). Flying fox body parts are stipple coded (top), and correspond to a specific location in cortical fields (bottom). Notice the mirror reversal organization between area 3b and area 1/2, and between SII and PV. Arrows in 3b and 1/2 point to distal wing and digit representations.

Area 1/2. In this investigation in the flying fox, we define a topographically organized field just caudal to 3b that contains some neurons with properties of area 1, and some neurons with properties of area 2 as described in primates. In most simian primates, area 1 responds to cutaneous stimulation of peripheral body parts, forms a mirror reversal of area 3b (Fig. 21) with a very fine somatotopy (Merzenich et al., '78; Kaas et al., '79; Nelson et al., '80; Sur et al., '82; Felleman et al., '83a) and has a distinct architecture (Merzenich et al., '78; Sur et al., '82), and myeloarchitecture (Krubitzer and Kaas, '90b). In the flying fox, the area caudal to 3b, area 1/2, shares these properties with area 1 of primates. However, neurons in area 1/2 rapidly habituate to cutaneous stimulation. Area 2 in primates forms a separate topographically organized representation just caudal to area 1 (Pons et al., '85). Unlike area 1 and 3b, neurons in area 2 respond to deep stimulation of peripheral body parts (Powell and Mountcastle, '59; Merzenich et al., '78; Pons et al., '85). In area 1/2 of the flying fox, there are groups of neurons that duplicate body part representations. However, these "redundant" representations contain neurons that respond best to deep stimulation of peripheral body parts, much like area 2 in primates. Responsiveness of cortex caudal to SI in other mammals traditionally grouped with archontans such as microchiropteran ghost bats (Wise et al., '86), and tree shrews (Sur et al., '81) has not been noted. In prosimian galagos (Sur et al., '80), limited responsiveness was noted in cortex caudal to SI and very hard taps were needed to drive neurons here. However, receptive fields for neurons caudal to SI in the galago were in topographic register with 3b.

It is possible that area 1/2 in the flying fox may have homologies with cortical fields described in other mammals. However, evidence for this is limited. In rodents, a field immediately caudal to SI, the parietal medial area, PM, receives a topographically organized input from SI and SII (Krubitzer et al., '86). However, neurons in PM are unresponsive to cutaneous stimulation in the anesthetized animal and a precise topography cannot be ascertained from connections alone. In cats, a field caudal to SI, SIII (Darian-Smith et al., '66; Garraghty et al., '87), is similar to area 1/2 in the flying fox in several ways. SIII in the cat is in the same relative location as area 1/2 in the flying fox and neurons respond well to cutaneous stimulation of peripheral body parts (Darian-Smith et al., '66; Garraghty et al., '87). However, the topography of SIII is quite different from that described for the flying fox (compare Figure 3 of this study with Figure 2 of Garraghty et al., '87), and only some parts of SIII are responsive to cutaneous stimulation. Also, there are no neurons in SIII that respond to deep stimulation of peripheral body parts.

An homology between SIII in the cat and area 1 in primates has been considered and rejected by most investigators for several reasons. First, area 1 in primates is highly responsive to cutaneous stimulation throughout the representation, while only the face and forepaw representations have neurons responsive to cutaneous stimulation in SIII in the cat (Garraghty et al., '87). Second, some (McKenna et al., '81) but not all (Felleman et al., '83b) investigators define SI in cats to include architectonic areas 3a, 3b, and 1. Finally, some investigators (Iwamura and Tanaka, '78) feel that portions of cortex defined as SIII are really portions of area 3b. Given the complexity of the issue and the conflicting data on the organization of cat anterior parietal cortex, it is difficult to evaluate whether SIII is homologous to area 1 of primates or area 1/2 of the flying fox.

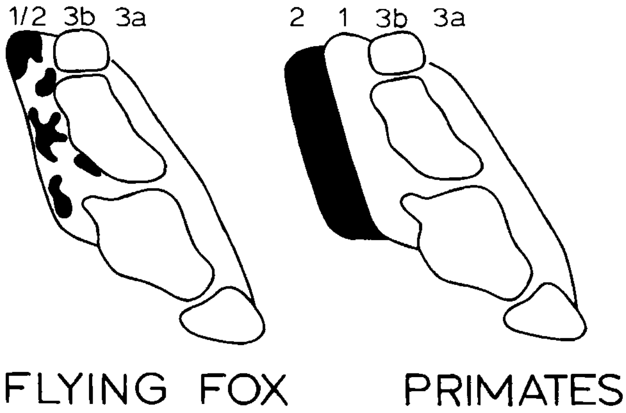

Fig. 22. A stylized figure illustrating our interpretation of the differentiation of areas 1 and 2 identified in extant mammals, from a single field, area 1/2 that has neural groups related to both area 1 and 2. Area 1/2 in the flying fox possibly represents a more primitive single field from which areas 1 and 2 evolved.

Traditionally, proposed homologies across species are in one-to-one correspondence so that a single field in one animal is homologous to a single field in another animal. However, theories on how sensory maps evolve in the neocortex have taken into account that different neural groups within the same cortical area in primitive brains may differentiate over time to form separate cortical fields (Kaas, '87, '89). It has been postulated that additional sensory representations may evolve by the process of local segregation within a field, gradual separation, and finally, fusion of segregated neural populations to form separate fields (Kaas, '89, see Fig. 1). We suggest this is the case with the cortex caudal to 3b. In the flying fox, this single field, in topographic register with 3b, contains neural groups of either cutaneous or deep representations. We hypothesize that area 1/2 in the flying fox reflects an earlier state of organization compared to that found in extant primates. At some point in primate evolution, there was sufficient selective pressure for neurons that respond to deep stimulation in area 1/2 to completely aggregate and form a separate representation (Fig. 22). In other evolutionary branches, such as that including the flying fox, there was little or no pressure for complete segregation and the field retained features of its original form (Fig. 22). However, the split between the primate and megachiropteran lines occurred 65 million years ago (Eisenberg, '81) so it is likely that the original field from which area 1/2 evolved underwent some changes in both lines.

An alternative hypothesis is that cortex does not evolve by gradual segregation of existing parts. For instance, modules observed in the visual system of primates in areas V-I and V-II have undergone little or no change in simian evolution. However, because some modularly organized fields have remained relatively unchanged over time, it does not mean that eventual segregation could not or would not occur. It only suggests that there may have been no selective pressure for such aggregation and eventual segregation to take place.

Area 3a. Physiological evidence for an area 3a in the present investigation is limited and our best evidence for a somatotopically organized field just rostral to 3b comes from studies of connections (see Calford and Krubitzer, '90). However, physiological evidence for the existence of an area rostral to 3b, responsive to deep stimulation and joint manipulation, has been obtained in flying foxes by Kennedy ('91). In our study, the region of cortex just rostral to 3b has a distinct appearance in cortex that has been stained for myelin. Like 3a described in a similar preparation in the marmoset, this region in the flying fox stains lightly for myelin and forms a very thin strip. Because of the neural response properties (Zarzeki et al., '78; Merzenich et al., '78), relative position, architectonic appearance, and topographic input from 3b (Calford and Krubitzer, '90), we feel this field is homologous with 3a described in other mammals. As with the boundary of area 1/2 with area 3b, there is some indication that area 3a interdigitates with area 3b in myelin light regions.

Somatosensory cortex caudolateral to 3b

The second somatosensory area, SII. The organization of SII in the flying fox is much like that described in other mammals with the representation of the face adjacent to the face representation in 3b and the forelimb, and hindlimb represented progressively caudal in the field. A similar organization has been described for rodents (Nelson et al., '79; Pimentel-Souza et al., '80; Carvell and Simons, '86; Krubitzer et al., '86), carnivores (Haight, '72; Burton et al., '82; Herron, '78; Clemo and Stein, '82), tree shrews (Sur et al., '81), and primates (Whitsel et al., '69; Friedman et al., '80; Robinson and Burton, '80b; Burton and Carlson, '86; Pons et al., '88; Cusick et al., '89; Krubitzer and Kaas, '90b). In microchiropteran bats (Wise et al., '86), a complete representation of the body surface homologous to SII in other mammals has not been described, but portions of what appear to be SII have been identified electrophysiologically. Receptive fields of neurons in SII in the flying fox were similar in size to those described for other mammals, and neural responses were also similar. Generally, neurons responded consistently to cutaneous stimulation, but neurons at some sites in SII showed habituation properties similar to those seen for neurons in area 1/2 (Fig. 12). No embedded zones within SII were observed, such as the "rostral complex" region identified by Robinson and Burton in the macaque monkey. Also, no portion of SII was responsive to deep stimulation of peripheral body parts as was seen in owl monkeys (Cusick et al., '89).

In the present investigation, SII was immediately adjacent to 3b and there was no incursion of area 1/2 between 3b and SII. Because SII is on the cortical surface, the spatial relationship of SII to 3b could be easily established and receptive field progressions from 3b to SII were similar to those described in other mammals (see Krubitzer and Kaas, '90b).

The parietal ventral area, PV. To date, only limited information exists on the topographic organization of fields lateral to 3b in mammals; most investigators have only described an SII and may have included PV within SII (Robinson and Burton, '80b) or termed the region now known as PV as SII (Welker and Sinha, '72). Recently, a third topographically organized field rostrolateral to SII, PV, has been described in rodents (Krubitzer et al., '86; Fabri et al., '90) and New World monkeys (Krubitzer and Kaas, '90b). In this investigation, we provide evidence for a topographically organized field rostrolateral to SII in the flying fox (Fig. 21). Because of its relative location, topographic organization, neural properties, architectonic appearance, and connections (Calford and Krubitzer, '90), we term this field PV. The possibility that PV exists in other mammals has been discussed in detail in previous investigations (see Krubitzer et al., '86 for full discussion).

In cats, SIV (Clemo and Stein, '82, '83; Burton and Kopf, '84) has a similar relative position and size to PV, and the overall organization of the body surface is like PV. Receptive field progression from SII to SIV in the cat reverses off the forelimb. However, the detailed topography of this field (Clemo and Stein, '83) and its cortical connections (Burton and Kopf, '84; Clarey and Irvine, '90b) vary to such an extent that it is considered unlikely that this field is homologous to PV described in the present investigation or in other mammals. In primates such as Old World macaque monkeys, granular insular cortex, Ig, is in a similar location to PV and has been implicated in somatosensory processing since it receives strong input from both SI and SII (Friedman et al., '86), and neurons here respond to somatosensory stimulation (Robinson and Burton, '80a; Burton and Robinson, '81 for review) as they do in PV in other mammals (Krubitzer et al., '86; Krubitzer and Kaas, '90b; Fabri et al., '90). However, Ig is considered a general region of cortex, and receptive fields are large and difficult to define. Ig is quite large, and probably encompasses several fields, although it has not been split into functional subdivisions. SII described in macaque monkeys by Robinson and Burton ('80b) is relatively large and contains duplicate representations of certain body parts (see Fig. 9 of Robinson and Burton, '80b). It is possible that the "single" field described in macaque monkeys actually contains 2 mirror reversal fields, SII and PV.

Because PV appears to be homologous in such distantly related species as rodents, bats, and monkeys, it is probable that it is a field found in a wide range of Toketherian mammals, including humans.

Ventral somatosensory field, VS. A ventral somatosensory field, VS, was first described in owl monkeys by Cusick et al. ('89). VS is located immediately lateral to SII on the ventral bank of the lateral sulcus. VS, as defined in owl monkeys, contains a complete representation of the body surface with the foot adjacent to the foot in SII, and the hand representation adjacent to the hand representation in SII. The face and head are represented most laterally in this field. The topography of VS as described in owl monkeys is very similar to that described for VS in the present investigation in the flying fox. Neurons in VS in owl monkeys were mostly responsive to cutaneous stimulation, although some neurons responded well to deep stimulation and Pacinian stimulation. Responses to auditory stimulation were not systematically investigated in the owl monkey. While both SII and PV receive dense direct input from SI in squirrels (Krubitzer et al., '86), marmosets (Krubitzer and Kaas, '90b) and flying fox (Calford and Krubitzer, '90), VS in both owl monkeys and flying foxes is not a cortical projection target of 3b. Although there are some differences in response properties of neurons in VS described in owl monkeys and flying fox, the relative location and overall topographic organization implies that VS is a homologous field in both species. The general position of VS in owl monkeys and flying foxes is close to that described for SIV in cats and there may be more parallels between these fields, particularly since there is an overlap of auditory and somatosensory responses in SIV in the cat, although individual neurons are rarely bimodal (Clarey and Irvine, '90a). Thus, VS in owl monkeys and flying foxes may be homologous to SIV in the cat.

The large receptive field sizes in VS, and its responsiveness to both auditory and somatosensory stimulation, indicate that this field is involved in higher levels of somatosensory processing, possibly in sensory integration of somatosensory and auditory stimuli.

Cortex surrounding somatosensory cortex. In general, cortex caudomedial and caudolateral to somatosensory area 1/2 is visual or visual and somatosensory, while cortex caudal to the lateral somatosensory fields is auditory or auditory and somatosensory. Cortex caudal to area 1/2 is analogous and probably homologous to certain portions of posterior parietal cortex as classically defined (see Kaas and Pons, '88 for review). This region receives input from both somatosensory (Calford and Krubitzer, '90) and visual cortex (Krubitzer and Calford, '90). Cortex caudal to SII, VS, and PV receives input from somatosensory cortex (Calford and Krubitzer, '90). The auditory connections of this region are unknown. The bimodal response properties of these medial and lateral cortical regions and the inputs from different sensory modalities, make it likely that these regions are involved in sensory integration. These bimodal regions are what is generally defined as "association" cortex. Remarkably, it is sensory cortex, with clear response properties and whole body somatotopy, that occupies the most cortical space and these "association" areas that occupy only a small amount of cortical space. They are parsimoniously located between the sensory modalities they integrate.

Conclusions

Our results lead to several important conclusions about somatosensory cortex. First, theories on the organization of SI in mammals need to consider the present evidence that SI may not be a homogeneous field. Rather, it is composed of separate populations of neurons with distinct physiological properties and architectonic appearances. Specifically, our study has important implications for theories of plasticity of somatosensory neocortex. A second conclusion in this investigation is that mammals may have more somatosensory fields in common than just SI and SII. Because the flying fox is the fourth mammal in which PV has been described, covering three orders of mammals, it is probable that it is a cortical field found in all Toketherian mammals. A third conclusion is that the somatosensory cortex of the flying fox is complexly organized and contains a number of functional subdivisions. It is surprising that the organization of somatosensory cortex in the flying fox is more like that of simian primates than prosimian primates. However, only limited information exists on the organization of somatosensory cortex in prosimians. Finally, the recent suggestion that megachiropteran bats are more closely related to primates than other archontans is supported by the present investigation. Thus, by investigating the neocortex of the flying fox, we have uncovered some basic principles about the evolution of somatosensory neocortex in primates, and more specifically, the differentiation of areas 1 and 2 from a single field.

ACKNOWLEDGMENTS

This research was supported by the Vision, Touch and Hearing Research Centre and NHMRC. We thank Soumya Ghosh, Lorraine Jolly, Jack Pettigrew, and Rowan Tweedale for helpful comments on this manuscript. Data in Figure 12 came from an earlier study and we thank Mal Graydon, Mike Huerta, Jon Kaas, and Jack Pettigrew who participated in that experiment.

LITERATURE CITED

Burton, H., and M. Carlson (1986) Second somatic sensory cortical area (SII) in a prosimian primate, *Galago crassicaudatus*. J. Comp. Neurol. *247:*200–220.

Burton, H., and E.M. Kopf (1984) Ipsilateral cortical connections from the second and fourth somatic sensory areas in the cat. J. Comp. Neurol. *225:*527–553.

Burton, H., and C.J. Robinson (1981) Organization of the SII parietal cortex-Multiple somatic sensory representations within and near the second somatic sensory area of cynomolgus monkeys. In M. Carlson and C. Welt (eds): *Cortical Sensory Organization*. Clifton: The Humana Press, pp. 67–119.

Burton, H., G. Mitchell, and D. Brent (1982) Second somatic sensory area in the cerebral cortex of cats: somatotopic organization and cytoarchitecture. J. Comp. Neurol. *210:*109–135.

Calford, M.B., and L.A. Krubitzer (1990) The organization and connections of somatosensory cortex in the megachiropteran bat (*Pteropus poliocephalus*). Soc. Neurosci. *16:*228 (Abstract).

Calford, M.B., and R. Tweedale (1988) Immediate and chronic changes in responses of somatosensory cortex in adult flying-fox after digit amputation. Nature *332:*446–448.

Calford, M.B., and R. Tweedale (1990) Interhemispheric transfer of plasticity in the cerebral cortex. Science *249:*805–807.

Calford, M.B., and R. Tweedale (1991) Acute changes in cutaneous receptive fields in primary somatosensory cortex following digit denervation in adult flying fox. J. Neurophysiol. *65:*178–187.

Calford, M.B., M.L. Graydon, M.F. Huerta, J.H. Kaas, and J.D. Pettigrew (1985) A variant of the mammalian somatotopic map in a bat. Nature *313:*477–479.

Campos, G.B., and W.I. Welker (1976) Comparisons between brains of a large and a small hystricomorph rodent: Capybara, *Hydrochoerus* and guinea pig, *Cavia;* neocortical projection regions and measurements of brain subdivisions. Brain Behav. Evol. *13:*243–266.

Carlson, M., and W.I. Welker (1976) Some morphological, physiological and behavioral specializations in North American beavers (*Castor canadensis*). Brain Behav. Evol. *13:*302–326.

Carlson, M., M.F. Huerta, C.G. Cusick, and J.H. Kaas (1986) Studies on the evolution of multiple somatosensory representations in primates: the organization of anterior parietal cortex in the New World Callitrichid, *Saguinus*. J. Comp. Neurol. *246:*409–426.

Carvell, G.E., and D.J. Simons (1986) Somatotopic organization of the second somatosensory area (SII) in the cerebral cortex of the mouse. Somatosens. Res. *3:*213–237.

Chapin, J.K., and C.-S. Lin (1984) Mapping the body representation in the SI cortex of anesthetized and awake rats. J. Comp. Neurol. *229:*199–213.

Clarey, J.C., and D.R.F. Irvine (1990a) The anterior ectosylvian sulcal auditory field in the cat: I. An electrophysiological study of its relationship to surrounding auditory cortical fields. J. Comp. Neurol. *301:*289–303.

Clarey, J.C., and D.R.F. Irvine (1990b) The anterior ectosylvian sulcal auditory field in the cat: II. A horseradish peroxidase study of its thalamic and cortical connections. J. Comp. Neurol. *301:*304–324.

Clemo, H.R., and B.E. Stein (1982) Somatosensory cortex: A 'new' somatotopic representation. Brain Res. *235:*162–168.

Clemo, H.R., and B.E. Stein (1983) Organization of a fourth somatosensory area of cortex in cat. J. Neurophysiol. *50:*910–925.

Cusick, C.G., J.T. Wall, D.J. Felleman, and J.H. Kaas (1989) Somatotopic organization of the lateral sulcus of owl monkeys: Area 3b, S-II, and a ventral somatosensory area. J. Comp. Neurol. *282:*169–190.

Darian-Smith, I., J. Isbister, H. Mok, and T. Yokota (1966) Somatic sensory cortical projection areas excited by tactile stimulation of the cat: A triple representation. J. Physiol. *182:*671–689.

Darian-Smith, I., M. Sugitani, J. Heywood, K. Karita, and A. Goodwin (1982) Touching textured surfaces: Cells in somatosensory cortex respond both to finger movement and to surface features. Science *218:*906–909.

Dawson, D.R., and H.P. Killackey (1987) The organization and mutability of the forepaw and hindpaw representations in the somatosensory cortex of the neonatal rat. J. Comp. Neurol. *256:*246–256.

Dykes, R.W., and A. Gabor (1981) Magnification functions and receptive field sequences for submodality-specific bands in SI cortex of cats. J. Comp. Neurol. *202:*597–620.

Dykes, R.W., D.D. Rasmusson, and P.B. Hoeltzell (1980) Organization of primary somatosensory cortex in the cat. J. Neurophysiol. *43:*1527–1546.

Eisenberg, J.F. (1981) The Mammalian Radiations. Chicago: University of Chicago Press.

Fabri, M., K. Alloway, and H. Burton (1990) Multiple ipsilateral connections of SI in rats. Soc. Neurosci. *16:*228 (Abstract).

Favorov, O.V., and M.E. Diamond (1990) Demonstration of discrete place-defined columns-segregates-in the cat SI. J. Comp. Neurol. *298:*97–112.

Favorov, O., and B.L. Whitsel (1988a) Spatial organization of the peripheral input to area 1 cell columns. I. The detection of 'segregates'. Brain Res. Rev. *13:*25–42.

Favorov, O., and B.L. Whitsel (1988b) Spatial organization of the peripheral input to area 1 cell columns. II. The forelimb representation achieved by a mosaic of segregates. Brain Res. Rev. *13:*43–56.

Favorov, O.V., M.E. Diamond, and B.L. Whitsel (1987) Evidence for a mosaic representation of the body surface in area 3b of the somatic cortex of cat. Proc. Natl. Acad. Sci. U.S.A. *84:*6606–6610.

Felleman, D.J., R.J. Nelson, M. Sur, and J.H. Kaas (1983a) Representations of the body surface in areas 3b and 1 of postcentral parietal cortex of cebus monkeys. Brain Res. *268:*15–26.

Felleman, D.J., J.T. Wall, C.G. Cusick, and J.H. Kaas (1983b) The representation of the body surface in S-I of cats. J. Neurosci. *3:*1648–1669.

Friedman, D.P., E.G. Jones, and H. Burton (1980) Representation pattern in the second somatic sensory area of the monkey cerebral cortex. J. Comp. Neurol. *192:*21–41.

Friedman, D.P., E.A. Murray, J.B. O'Neill, and M. Mishkin (1986) Cortical connections of the somatosensory fields of the lateral sulcus of macaques: Evidence for a corticolimbic pathway for touch. J. Comp. Neurol. *252:*323–347.

Gallayas, F. (1979) Silver staining of myelin by means of physical development. Neurology *1:*203–209.

Garraghty, P.E., and M. Sur (1990) Morphology of single intracellularly stained axons terminating in area 3b of macaque monkeys. J. Comp. Neurol. *294:*583–593.

Garraghty, P.E., T.P. Pons, M.F. Huerta, and J.H. Kaas (1987) Somatotopic organization of the third somatosensory area (SIII) in cats. Somatosens. Res. *4:*333–357.

Gregory, W.K. (1910) The orders of mammals. Bull. Am. Mus. Nat. Hist. *27:*1–524.

Haight, J.R. (1972) The general organization of somatotopic projections to SII cerebral neocortex in the cat. Brain Res. *44:*483–502.

Herron, P. (1978) Somatotopic organization of mechanosensory projections to SII cerebral neocortex in the raccoon (*Procyon lotor*). J. Comp. Neurol. *181:*717–728.

Hubel, D.H., and M.S. Livingstone (1987) Segregation of form, color, and stereopsis in primate area 18. J. Neurosci. *7:*3378–3415.

Hyvärinen, J., and A. Poranen (1978) Receptive field integration and submodality convergence in the hand area of the post-central gyrus of the alert monkey. J. Physiol. *283:*539–556.

Imig, T.J., and H.O. Adrián (1977) Binaural columns in the primary field (A1) of cat auditory cortex. Brain Res. *138:*241–257.

Imig, T.J., and J.F. Brugge (1978) Sources and terminations of callosal axons related to binaural and frequency maps in primary auditory cortex of the cat. J. Comp. Neurol. *182:*637–660.

Iwamura, Y., and M. Tanaka (1978) Functional organization of receptive fields in the cat somatosensory cortex. II: Second representation of the forepaw in the ansate region. Brain Res. *151:*61–72.

Jones, E.G., J.D. Coulter, and S.H.C. Hendry (1978) Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. J. Comp. Neurol. *181:*291–348.

Kaas, J. (1987) The organization and evolution of neocortex. In S.P. Wise (ed) Higher Brain Functions. New York: John Wiley and Sons, pp. 347–378.

Kaas, J.H. (1983) What, if anything, is SI? Organization of first somatosensory area of cortex. Physiol. Rev. *63:*206–231.

Kaas, J.H. (1989) The evolution of complex sensory systems in mammals. J. Exp. Biol. *146:*165–176.

Kaas, J.H., and T.P. Pons (1988) The somatosensory system of primates. In H.P. Steklis (ed): Comparative Primate Biology, Vol 4. New York: Alan R. Liss, pp. 421–468.

Kaas, J.H., R.J. Nelson, M. Sur, C.-S. Lin, and M.M. Merzenich (1979) Multiple representations of the body within the primary somatosensory cortex of primates. Science *204:*521–523.

Kennedy, W. (1991) Origins of the corticospinal tract of the flying fox: correlation with cytoarchitecture and electrophysiology. Masters Thesis, University of Queensland.

Krubitzer, L.A., and M.B. Calford (1990) Cortical connections of the primary visual area, V-I, of the grey headed flying fox (*Pteropus poliocephalus*): Evidence for multiple extrastriate cortical fields. Soc. Neurosci. *16:*621 (Abstract).

Krubitzer, L.A., and J.H. Kaas (1990a) Convergence of processing channels in extrastriate cortex of monkeys. Vis. Neurosci. *5:*609–613.

Krubitzer, L.A., and J.H. Kaas (1990b) The organization and connections of somatosensory cortex in marmosets. J. Neurosci. *10:*952–974.

Krubitzer, L.A., M.A. Sesma, and J.H. Kaas (1986) Microelectrode maps, myeloarchitecture, and cortical connections of three somatotopically organized representations of the body surface in the parietal cortex of squirrels. J. Comp. Neurol. *250:*403–430.

Landry, P., and M. Deschênes (1981) Intracortical arborizations and receptive fields of identified ventrobasal thalamocortical afferents to the primary somatic sensory cortex in the cat. J. Comp. Neurol. *199:*345–371.

Lende, R.A., and C.N. Woolsey (1956) Sensory and motor localization in cerebral cortex of porcupine (*Erethizon dorsatum*). J. Neurophysiol. *19:*544–563.

Livingstone, M.S., and D.H. Hubel (1984) Anatomy and physiology of a color system in the primate visual cortex. J. Neurosci. *4:*309–356.

Luethke, L.E., L.A. Krubitzer, and J.H. Kaas (1988) Cortical connections of electrophysiologically and architectonically defined subdivisions of auditory cortex in squirrels. J. Comp. Neurol. *268:*181–203.

Leuthke, L.E., L.A. Krubitzer, and J.H. Kaas (1989) Connections of primary auditory cortex in the New World monkey, *Saguinus*. J. Comp. Neurol. *285:*487–513.

McKenna, M.C. (1975) Toward a phylogenetic classification of the mammalia. In W.P. Luckett and F.S. Szalay (eds): Phylogeny of the Primates. A Multidisciplinary Approach. New York and London: Plenum Press, pp. 21–46.

McKenna, T.M., B.L. Whitsel, D.A. Dreyer, and C.B. Metz (1981) Organization of cat anterior parietal cortex: Relations among cytoarchitecture, single neuron functional properties, and interhemispheric connectivity. J. Neurophysiol. *45:*667–697.

Merzenich, M.M., J.H. Kaas, and G.L. Roth (1976) Auditory cortex in the grey squirrel: Tonotopic organization and architectonic fields. J. Comp. Neurol. *166:*387–402.

Merzenich, M.M., J.H. Kaas, M. Sur, and C.-S. Lin (1978) Double representation of the body surface within cytoarchitectonic areas 3b and 1 in "SI" in the owl monkey (*Aotus trivirgatus*). J. Comp. Neurol. *181:*41–74.

Merzenich, M.M., J.H. Kaas, J. Wall, R.J. Nelson, M. Sur, and D. Felleman (1983a) Topographic reorganization of somatosensory cortical areas 3b and 1 in adult monkeys following restricted deafferentation. Neuroscience *8:*33–55.

Merzenich, M.M., J.H. Kaas, J.T. Wall, M. Sur, R.J. Nelson, and D.J. Felleman (1983b) Progression of change following median nerve section in the cortical representation of the hand in areas 3b and 1 in adult owl and squirrel monkeys. Neuroscience *10:*639–665.

Merzenich, M.M., R.J. Nelson, M.P. Stryker, M.S. Cynader, A. Schoppmann, and J.M. Zook (1984) Somatosensory cortical map changes following digit amputation in adult monkeys. J. Comp. Neurol. *224:*591–605.

Middlebrooks, J.C., R.W. Dykes, and M.M. Merzenich (1980) Binaural response-specific bands in primary auditory cortex (AI) of the cat: Topographical organization orthogonal to isofrequency contours. Brain Res. *181:*31–48.

Morel, A.E., L.A. Krubitzer, and J.H. Kaas (1989) Connections of auditory cortex in owl monkeys. Soc. Neurosci. *15:*111 (Abstract).

Mountcastle, V.B. (1957) Modality and topographic properties of single neurons of cat's somatic sensory cortex. J. Neurophysiol. *20:*408–434.

Mountcastle, V.B., and T.P.S. Powell (1959) Neural mechanisms subserving cutaneous sensibility, with special reference to the role of afferent inhibition in sensory perception and discrimination. Bull. Johns Hopkins Hosp. *105:*201–232.

Murphy, K.M., R.C. Van Sluyters, and D.G. Jones (1990) Cytochrome-oxidase activity in cat visual cortex: Is it periodic? Soc. Neurosci. *16:*292 (Abstract).

Nelson, R.J., M. Sur, and J.H. Kaas (1979) The organization of the second somatosensory area (SmII) of the grey squirrel. J. Comp. Neurol. *184:*473–490.

Nelson, R.J., M. Sur, D.J. Felleman, and J.H. Kaas (1980) Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. J. Comp. Neurol. *192:*611–643.

Paul, R.L., M.M. Merzenich, and H. Goodman (1972) Representation of slowly and rapidly adapting cutaneous mechanoreceptors of the hand in Brodmann's areas 3 and 1 of *Macaca mulatta*. Brain Res. *36:*229–249.

Pearson, J.C., L.H. Finkel, and G.M. Edelman (1987) Plasticity in the organization of adult cerebral cortical maps–a computer simulation based on neuronal group selection. J. Neurosci. *7:*4209–4223.

Pettigrew, J.D., and H.M. Cooper (1986) Aerial primates: Advanced visual pathways in megabats and gliding lemurs. Soc. Neurosci. *12:*1035 (Abstract).

Pettigrew, J.D., B.G.M. Jamieson, S.K. Robson, L.S. Hall, K.I. McAnally, and H.M. Cooper (1989) Phylogenetic relations between microbats, megabats and primates (Mammalia: Chiroptera and Primates). Phil. Trans. R. Soc. Lond. B. *325:*489–559.

Pimentel-Souza, F., R.M. Cosenza, G.B. Campos, and J.I. Johnson (1980) Somatic sensory cortical regions of the agouti, *Dasyprocta aguti.* Brain Behav. Evol. *17:*218–240.

Pons, T.P., P.E. Garraghty, and M. Mishkin (1988) Lesion-induced plasticity in the second somatosensory cortex of adult macaques. Proc. Natl. Acad. Sci. U.S.A. *85:*5279–5281.

Pons, T.P., P.E. Garraghty, C.G. Cusick, and J.H. Kaas (1985) The somatotopic organization of area 2 in macaque monkeys. J. Comp. Neurol. *241:*445–466.

Powell, T.P.S., and V.B. Mountcastle (1959) Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey: A correlation of findings obtained in a single unit analysis with cytoarchitecture. Bull. Johns Hopkins Hospital *105:*133–162.

Rasmusson, D.D., R.W. Dykes, and P.B. Hoeltzell (1979) Segregation of modality and submodality information in SI cortex of the cat. Brain Res. *166:*409–412.

Robinson, C.J., and H. Burton (1980a) Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of *M. fascicularis.* J. Comp. Neurol. *192:*69–92.

Robinson, C.J., and H. Burton (1980b) Somatotopographic organization in the second somatosensory area of *M. fascicularis.* J. Comp. Neurol. *192:*43–67.

Sanides, F. (1968) The architecture of the cortical taste nerve areas in squirrel monkey (*Saimiri sciureus*) and their relationships to insular sensorimotor and prefrontal regions. Brain Res. *8:*97–124.

Sanides, F. (1970) Functional architecture of motor and sensory corticies in primates in light of a new concept of neocortical evolution. In C.R. Noback and W. Montagna (eds): The Primate Brain. New York: Appleton-Century-Crofts, pp. 137–208.

Snow, P.J., R.J. Nudo, W. Rivers, W.M. Jenkins, and M.M. Merzenich (1988) Somatotopically inappropriate projections from thalamocortical neurons to the SI cortex of the cat demonstrated by the use of intracortical microstimulation. Somatosens. Res. *5:*349–372.

Sur, M., R.J. Nelson, and J.H. Kaas (1978) The representation of the body surface in somatosensory area I of the grey squirrel. J. Comp. Neurol. *179:*425–450.

Sur, M., R.J. Nelson, and J.H. Kaas (1980) Representation of the body surface in somatic koniocortex in the prosimian *Galago.* J. Comp. Neurol. *189:*381–402.

Sur, M., R.J. Nelson, and J.H. Kaas (1982) Representations of the body surface in cortical areas 3b and 1 of squirrel monkeys: Comparisons with other primates. J. Comp. Neurol. *211:*177–192.

Sur, M., J.T. Wall, and J.H. Kaas (1984) Modular distribution of neurons with slowly adapting and rapidly adapting responses in area 3b of somatosensory cortex in monkeys. J. Neurophysiol. *51:*724–744.

Sur, M., R.E. Weller, and J.H. Kaas (1981) The organization of somatosensory area II in tree shrews. J. Comp. Neurol. *201:*121–133.

Vogt, C., and O. Vogt (1919) Allgemeinere ergebnisse unserer Hirnforschung. J. Psychol. Neurol. *25:*279–462.

Wall, J.T., and C.G. Cusick (1984) Cutaneous responsiveness in primary somatosensory (S-I) hindpaw cortex before and after partial hindpaw deafferentiation in adult rats. J. Neurosci. *4:*1499–1515.

Welker, C. (1971) Microelectrode delineation of fine grain somatotopic organization of SmI cerebral neocortex in albino rat. Brain Res. *26:*259–275.

Welker, C., and M.M. Sinha (1972) Somatotopic organization of SmII cerebral neocortex in albino rat. Brain Res. *37:*132–136.

Welker, C., and T.A. Woolsey (1974) Structure of layer IV in the somatosensory neocortex of the rat: Description and comparison with the mouse. J. Comp. Neurol. *158:*437–454.

Welker, W.I., and S. Seidenstein (1959) Somatic sensory representation in the cerebral cortex of the racoon (*Procyon lotor*). J. Comp. Neurol. *111:*469–501.

Whitsel, B.L., L.M. Pertrucelli, and G. Werner (1969) Symmetry and connectivity in the map of the body surface in somatosensory area II of primates. J. Neurophysiol. *32:*170–183.

Wise, L.Z., J.D. Pettigrew, and M.B. Calford (1986) Somatosensory cortical representation in the Australian ghost bat, *Macroderma gigas.* J. Comp. Neurol. *248:*257–262.

Woolsey, T.A. (1967) Somatosensory, auditory and visual cortical areas of the mouse. Johns Hopkins Med. J. *121:*91–112.

Woolsey, T.A., and H. Van der Loos (1970) The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex: The description of a cortical field composed of discrete cytoarchitectonic units. Brain Res. *17:*205–242.

Woolsey, T.A., C. Welker, and R.H. Schwartz (1975) Comparative anatomical studies of the SmI face cortex with special reference to the occurrence of "barrels" in layer IV. J. Comp. Neurol. *164:*79–94.

Zarzecki, P., Y. Shinoda, and H. Asanuma (1978) Projection from area 3a to the motor cortex by neurons activated from group I muscle afferents. Exp. Brain Res. *33:*269–282.