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Connections of Somatosensory Cortex in Megachiropteran Bats: The Evolution of Cortical Fields in Mammals

LEAH A. KRUBITZER, MIKE B. CALFORD, AND LEISA M. SCHMID
Vision, Touch and Hearing Research Centre, Department of Physiology and Pharmacology, The University of Queensland, Queensland, 4072, Australia

ABSTRACT

The cortical connections of the primary somatosensory area (SI or 3b), a caudal somatosensory field (area 1/2), the second somatosensory area (SII), the parietal ventral area (PV), the ventral somatosensory area (VS), and the lateral parietal area (LP) were investigated in grey headed flying foxes by injecting anatomical tracers into electrophysiologically identified locations in these fields. The receptive fields for clusters of neurons were mapped with sufficient density for injection sites to be related to the boundaries of fields, and to representations of specific body parts within the fields. In all cases, cortex was flattened and sectioned parallel to the cortical surface. Sections were stained for myelin and architectonic features of cortex were related to physiological mapping and connection patterns. We found patterns of topographic and nontopographic connections between 3b and adjacent anterior parietal fields 3a and 1/2, and fields caudolateral to 3b (SII and PV). Area 1/2 had both topographic and nontopographic connections with 3b, PP, and SII. Connections of SII and PV with areas 3b, 3a, and 1/2 were roughly topographic, although there was clear evidence for nontopographic connections between these fields. SII was most densely connected with area 1/2, while PV was most densely connected with 3b. SII had additional connections with fields in lateral parietal cortex and with subdivisions of motor cortex. Other connections of PV were with subdivisions of motor cortex and pyriform cortex. Laminar differences in connection patterns of SII and PV with surrounding cortex were also observed. Injections in the ventral somatosensory area revealed connections with SII, PV, area 1/2, auditory cortex, entorhinal cortex, and pyriform cortex. Finally, the lateral parietal field had very dense connections with posterior parietal cortex, caudal temporal cortex, and with subdivisions of motor cortex. Our results indicate that the 3b region is not homogeneous, but is composed of myelin dense and light regions, associated with 3b proper and invaginations of area 1/2, respectively. Connections of myelin dense 3b were different from invaginating portions of myelin light area 1/2. Our findings that 3b is densely interconnected with PV and moderately to lightly interconnected with SII supports the notion that SII and PV have been confused across mammals and across studies. Our connectional evidence provides further support for our hypothesis that area 1/2 is partially incorporated in 3b and has led to theories of the evolution of cortical fields in mammals.

Key words: area 3b, second somatosensory area, parietal ventral area, area 1, neocortical evolution

In a recent investigation (Krubitzer and Calford, '92) using microelectrode mapping techniques and myeloarchitectonic staining patterns, we described the detailed organization of five somatosensory cortical fields in the flying fox including areas 3b, 1/2, SII, PV, and VS (Fig. 1). In that study we found that 3b was not a homogeneous field. Rather, the somatotopically organized 3b, in which neurons show consistent responses to low threshold cutaneous stimulation, is interspersed with regions in which neurons habituate to repetitive stimulation. The nonhabituating neurons were related to myelin dense zones that are striking in tangentially sectioned tissue (Figs. 2B,C, 3A,D). These myelin dense zones are considered homologous to 3b, or SI, in other mammals. Myelin light regions, coextensive with rapidly habituating neurons, share properties of the field caudal to 3b, termed area 1/2 in the flying fox. We hypothesized that these myelin light islands containing habituating neurons are actually portions of area 1/2, rather than "modules" within 3b. In the present investigation we hoped to confirm this hypothesis by comparing the

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connections of 3b proper with connections of area 1/2 and area 1/2 invaginations into 3b. Also, we wanted to determine the connections of somatosensory fields SII, PV and VS with 3b and the area 1/2 invaginations into 3b, as well as with other cortical fields.

Several other important issues were raised in our earlier study about the organization of anterior parietal somatosensory cortex. First, an area just caudal to 3b had a cortical organization similar to that described for area 1 of primates, but had some neurons with properties of area 1 and other neurons with properties of area 2 (Fig. 1). Hence, we termed the field area 1/2. We hope to support the hypothesis that area 1/2 is really a combination of both area 1 and area 2 in primates by examining connections of cutaneous and deep neural clusters in area 1/2 in the same animal. Another issue is whether 3a exists in the flying fox. Limited electrophysiological mapping in cortex rostral to 3b has revealed an area in which neurons have deep receptive fields, suggesting that the flying fox does have an area 3a. In primates, 3a receives topographically organized input from 3b and SII (e.g., Krubitzer and Kaas, '90c). We reasoned that by injecting different body part representations in electrophysiologically identified fields such as 3b, area 1/2, SII, and PV, we could infer topographic organization of fields such as 3a by connection patterns.

In the present study we also wanted to describe the connections of cortical fields caudolateral to 3b. This region of cortex is occupied by the second somatosensory area, SII, as described in other mammals (see Johnson, '90, for review). In the flying fox we found 3 fields (SII, PV, and VS) in this area of cortex. We wanted to see how connections of these fields relate to myelin light and dark area 1/2 and 3b, respectively, as well as to other regions of cortex. The connections of these fields have never been described for any chiropteran and it is important to determine how they compare with connections of homologous fields described in other mammals. But a question even more pertinent to our understanding of somatosensory cortical organization in mammals was: What is the real SII? With the first description of PV in squirrels (Krubitzer et al., '86) it was proposed that PV and SII may have been confused in other mammals since both are in a similar location relative to SI, both are organized in a similar topographic fashion, and both receive dense connections from the primary somatosensory area, SI, or 3b (e.g., Jones and Powell, '69; Akers and Killackey, '78; Vogt and Pandya, '78; Krubitzer et al., '86; Krubitzer and Kaas, '90c; but see Johnson, '90, for review). Since we now appreciate that 3b is not a homogeneous field but is composed of two separate fields in the flying fox and probably in a number of other mammals (see Krubitzer and Calford, '92), the third criterion for distinguishing PV and SII needs to be re-examined.

The final reason we undertook this study was to gain some insights into the evolution of complex sensory systems in mammals. Many evolutionary biologists consider that flying foxes are archontans, and as such, are closely related to primates (e.g., Gregory, '10; McKenna, '75; Pettigrew and Cooper, '86). By examining a less complexly organized brain of a sister group, we hope to understand how a complexly organized neocortex, such as that found in

Abbreviations

Cortical fields

A-I	primary auditory area
cc	corpus callosum
FV	frontal ventral eye movement field
H	hippocampus
L	limbic cortex
LP	lateral parietal area
ls	lateral sulcus
MT	middle temporal visual area
PM	parietal medial area
PP	posterior parietal cortex
PR	parietal rhinal area
PV	parietal ventral area
PY	pyriform cortex
SMA	supplementary motor area
SII	second somatosensory area
SIIl	somatosensory area caudolateral to 3b in cats
SIV	somatosensory area lateral to SII in cats
R	rostral auditory field
Ri	retroinsular area
T	temporal cortex
UZ	unresponsive zone
VS	ventral somatosensory area
1	somatosensory area caudal to 3b in primates
2	somatosensory area caudal to area 1 in primates
1/2	somatosensory area caudal to 3b (SI) in flying fox
3a	somatosensory area rostral to 3b (SI)
3b	primary somatosensory area (SI)
4	primary motor area
5	subdivision of posterior parietal cortex
7b	subdivision of posterior parietal cortex
17	primary visual area (VI)
18	second visual area (VII)

Body parts

AM/am	arm membrane
CH/ch	chest
CK	cheek
CN/cn	chin
CNV	chin vibrissae
D/d	digits
F/f	foot
FA	forearm
FL/fl	forelimb
FM/fm	finger membrane
G	genitals
H	head
HL/hl	hindlimb
L	lips
LL	lower lip
LTR	lower trunk
M	mouth
N/n	naris
NE/ne	neck
P	pinna
PW/pw	prowing
SH	shoulder
SN	snout
SNV	snout vibrissae
T/t	toes
TM/tm	tail membrane
TR	trunk
UL	upper lip
ULV	upper lip vibrissae
UTR	upper trunk
V	vibrissae
W	wrist

Anatomical tracers

DY	diamidino yellow
FB	fast blue
FG	fluorogold
WGA-HRP	wheatgerm agglutinin conjugated to horseradish peroxidase

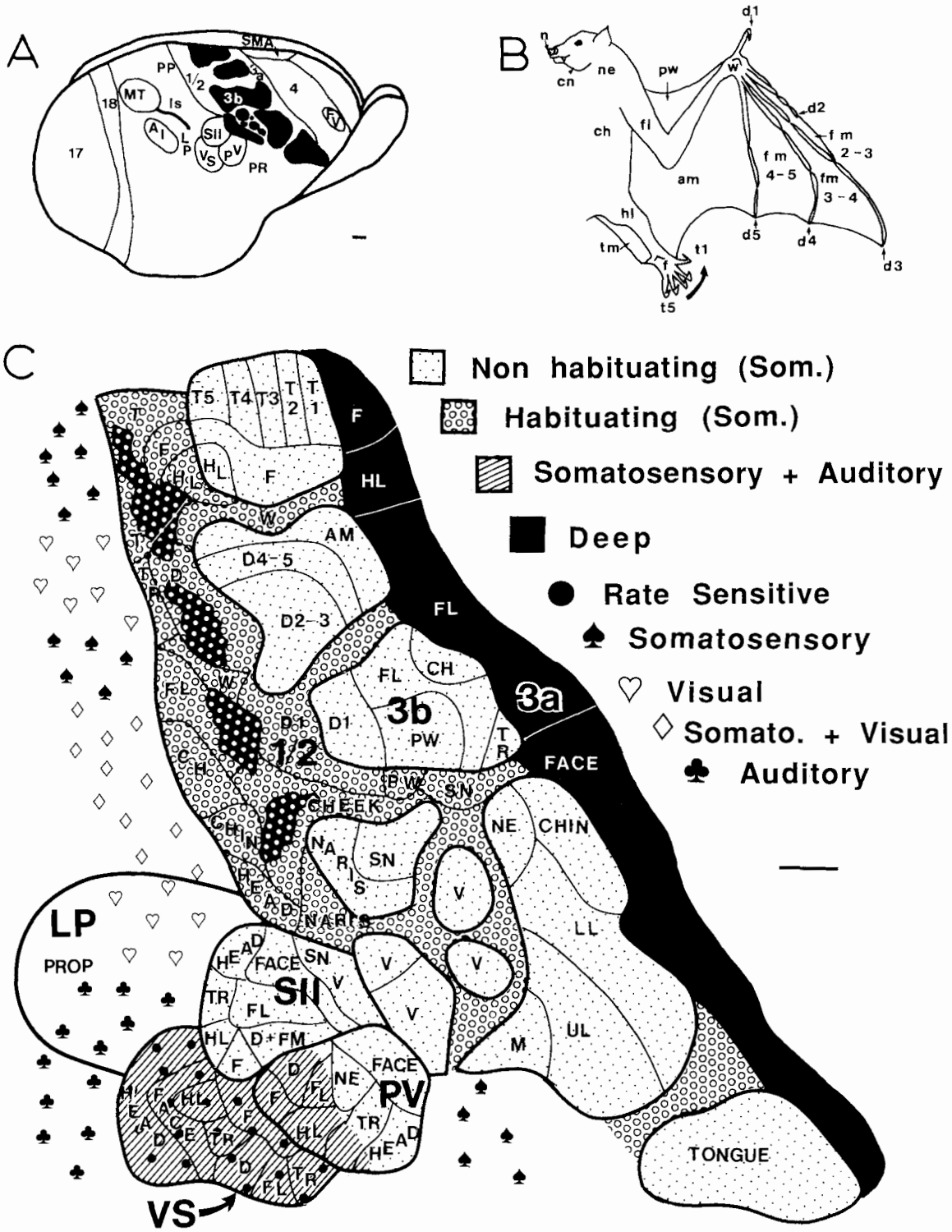


Fig. 1. **A:** A dorsolateral view of the flying fox neocortex with somatosensory, visual, and auditory fields outlined. **B:** A ventral view of the flying fox with body parts identified. **C:** A summary map of the topographic organization of five somatosensory fields described in the flying fox neocortex. This map has been modified from Krubitzer and Calford ('92). Both the primary somatosensory area, SI or 3b, and area 1/2 have a similar medial to lateral organization with the foot represented most medially, followed by the leg, trunk, forelimb, digits, and face represented progressively laterally. Portions of area 1/2 jut into area 3b. Most neurons in area 1/2 rapidly habituate to a stimulus, while most neurons in 3b do not habituate to the stimulus. Just rostral to 3b, in 3a, neurons respond to pressure on body parts or joint manipulation. The mediolateral organization of 3a appears to be similar to that of 3b and area 1/2. Three topographically organized fields are located lateral to 3b. SII is adjacent to the vibrissae representation in 3b and the naris and head representations in area 1/2. Within SII, the face and head are represented rostrally and the forelimb and hindlimb progressively caudal. The trunk is represented caudomedially. PV has a similar organization to that of SII except the trunk is represented laterally. Also, some neurons in PV respond to both somatosensory and auditory stimulation. Finally, just caudal to SII and PV is the ventral somatosensory field, VS. The topographic organization of VS is less precise than either that of SII or PV. Generally, the feet are represented rostromedially, the forelimb and trunk are represented in the middle of the field, and the face is represented caudolaterally. Neurons in VS are sensitive to the rate of presentation of a stimulus and most neurons in the field respond to both auditory and somatosensory stimulation. Solid lines mark architectonic boundaries. Scale bars equal 1 mm. In this and the following figures rostral is to the right and medial is to the top. Prop, proprioceptive; Som./Somato., somatosensory. See list of abbreviations for other conventions.

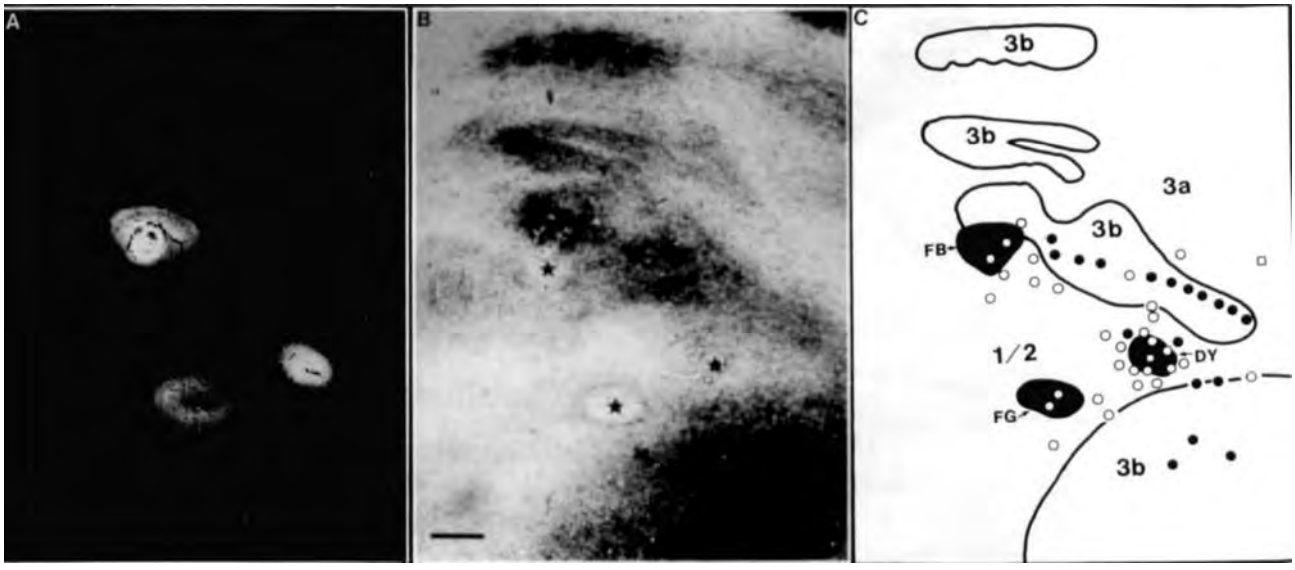


Fig. 2. An example of how injections of anatomical tracers (**A**) are related to myeloarchitecture (**B**) and electrophysiological mapping (**C**). In case 212, the region to be injected was mapped with microelectrodes in enough detail to ensure accurate placement of the injections (C). Several tracers were then injected into the electrophysiologically defined locations. In this case, fast blue was injected into the representations of D1, diamidino yellow was injected into the deep head and neck representation, and fluorogold was injected into the representation of the chin and snout vibrissae (A). Sectioned tissue was processed for fluorescence microscopy or stained for myelin (B). Myeloarchitecture was then related to electrophysiological mapping in C and the injection sites in A by aligning blood vessels, tissue artifact, and injection sites (stars) throughout the series of sections. Further analysis of this case is illustrated in figures 8 and 9. Electrode tracks in C are marked by filled circles (nonhabituating neurons) and open circles (habituating neurons). Solid lines in C mark architectonic boundaries. Scale bar equals 1 mm. Other conventions as in previous figure.

primates, and ultimately humans, evolves. In mammalian brains that are simply organized, only SI and SII have been described (see Johnson, '90, for review). Mammals such as primates, carnivores, and megachiropterans have a number of somatosensory fields. Primates have at least 10 somatosensory fields (Kaas, '87) and it is likely that humans have an even greater number of fields. How does the somatosensory neocortex evolve from a simple 2–3 area processing network to a processing network with as many as 10–12 interconnected fields? We reasoned that examining a brain that may reflect an intermediate form between primates and other mammals might provide some insight into how cortical areas increase in number and complexity.

Our approach to answering these questions raised in electrophysiological mapping studies in the flying fox is quite different from most studies of connections of somatosensory cortex. First, we not only define our injection sites electrophysiologically (e.g., Figs. 2C, 4, 6), but in many cases, we define the expected targets of fields by making high density, electrophysiological maps in the field (Figs. 8, 15, 17). We have confidence from our analysis of physiological experiments that most of the boundaries between the 5 cutaneous cortical representations can be readily defined with the aid of indicators such as changes in response properties, receptive field size, and reversals in somatotopic sequences. To achieve this, over 1,000 recording sites were made in 8 animals.

Another difference in the present investigation is the use of multiple anatomical tracers to infer topography of unknown fields as well as to compare directly differences and similarities in the connections of separate fields (Figs. 2A, 4–8, 15, 16). Only two other published reports have used multiple tracers in the same animal to define the somatotopic connections with adjacent fields, and to compare directly thalamic connections, and some cortical connections of different fields (Krubitzer and Kaas, '90c, '92). In this investigation, we use up to three tracers in a single animal. In these same animals, dense electrophysiological maps were made for the injected fields as well as target fields (e.g., Figs. 8, 15). Finally, cortical myeloarchitecture was related to injection sites and target areas defined electrophysiologically and connectionally (e.g., Figs. 2, 3). In this study, we flatten the neocortex and cut it parallel to the cortical surface. This type of tissue preparation has been described for a number of studies on visual cortex (Livingstone and Hubel, '84; Hubel and Livingstone, '87; Cusick and Kaas, '88; Krubitzer and Kaas, '90a,b) and several studies of somatosensory (e.g., Krubitzer et al., '86; Krubitzer and Kaas, '90b; Krubitzer and Calford, '92), and auditory cortex (e.g., Luethke et al., '88), and allows reconstruction of electrophysiological recordings in the lissencephalic neocortex of the flying fox to be done without the inaccuracies introduced by tracing electrode tracks through several sections of coronally or sagittally sectioned tissue. Also, myeloarchitectonic differences, especially between separate neural groups within the 3b region, are strikingly clear in tangentially sectioned tissue (Figs. 2B, 3A,D). Finally, areal patterns of connections in relation to electrophysiological mapping and myeloarchitectonic patterns can be directly observed, often in a single section.

MATERIALS AND METHODS

In the present investigation 16 injections into electrophysiologically defined somatosensory fields were made in 8 grey-headed flying foxes (*Pteropus poliocephalus*). In all of these animals, multiple or single injections of different anatomical tracers were made and cortical connections of

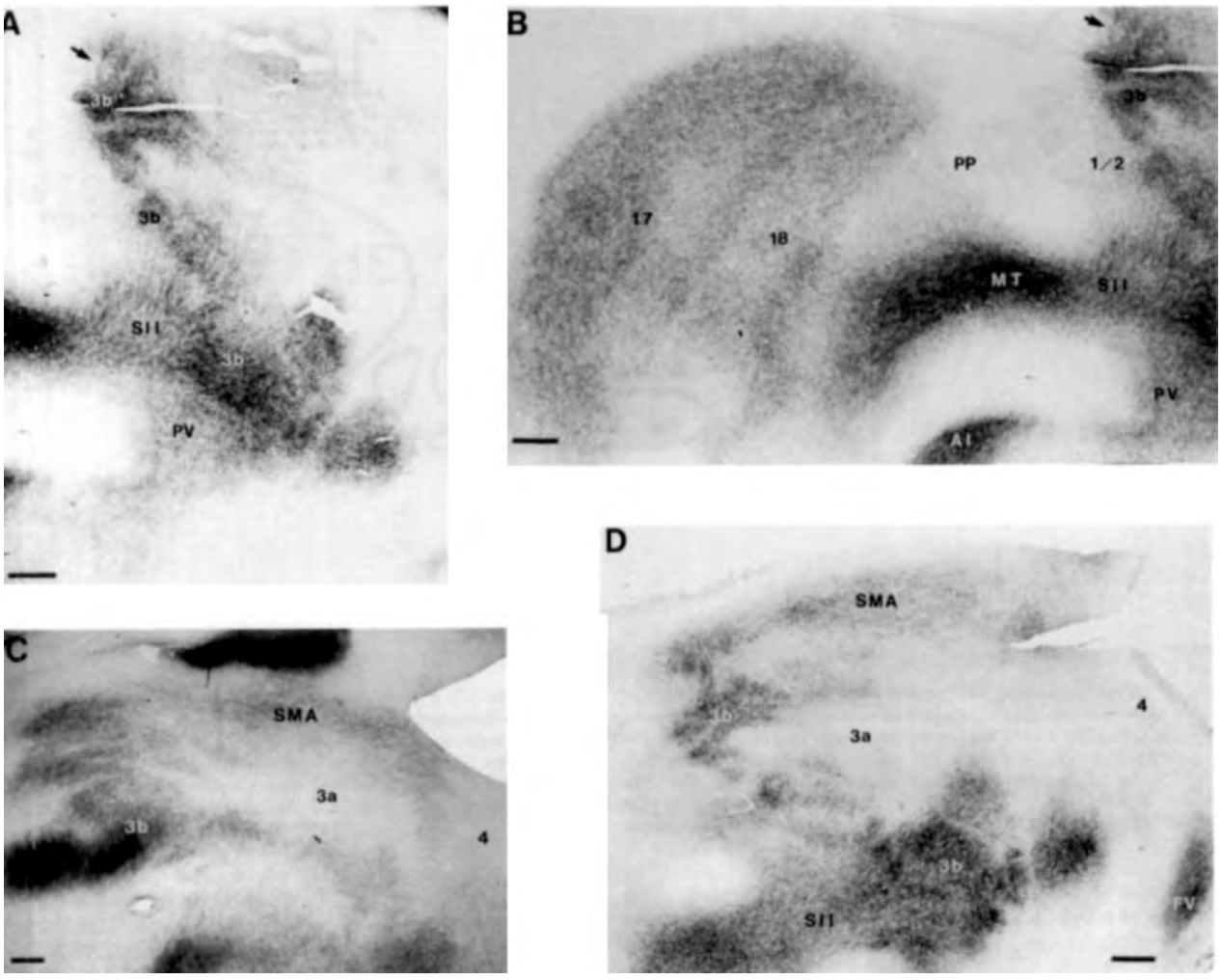


Fig. 3. Lightfield photomicrographs of the myeloarchitecture of somatosensory and surrounding cortex. **A** and **D** demonstrate the patchy, darkly myelinated area 3b in two different flying foxes. The lightly myelinated regions invaginating into 3b are coextensive with the rapidly habituating neurons of area 1/2. The interdigitated myelin dark 3b and myelin light area 1/2 regions in the foot representation in A are striking (arrow). In A, SII and PV stain moderately for myelin. In **C** and **D,** area 3a stains very lightly for myelin relative to 3b caudally and SMA rostromedially. Although area 4 is also lightly stained for myelin it is more myelinated than 3a. In D, FV is easily distinguished as a darkly myelinated oval of cortex lateral to M. **B:** A lightfield photomicrograph that demonstrates the staining of other visual and auditory fields in the neocortex of the flying fox. Photomicrographs A and B are from the same case and photomicrographs C and D are from different cases. Scale bars equal 1 mm. Conventions in list of abbreviations.

five topographically organized fields were determined. Experiments were of three types. In the first type of experiment, an area of interest was mapped and boundaries of the field located. Multiple tracers were then injected into different body part representations within a single field so that the topography of connections of unknown fields could be deduced. In the second type of experiment, the boundaries of several fields were mapped electrophysiologically and different tracers were placed in a similar body part representation in separate fields. In this way differences and similarities in the connection patterns of fields could be directly assessed. In the third type of experiment, a single injection or multiple injections were placed into an electrophysiologically identified location in a particular field, and adjacent fields were then mapped in detail. This type of experiment provided very specific details on the connections of fields with electrophysiologically identified representations of adjacent fields.

At the start of each experiment, the animal was deeply anaesthetized with a combination of ketamine hydrochloride (40 mg/kg) and xylazine (4 mg/kg). At this time, the animal was administered amoxycillin (7.5 mg/kg) to prevent post-operative infection. Standard sterile surgical procedures were followed throughout the experiment. After the animal was anaesthetized, the scalp was cut and retracted, the skull over somatosensory cortex was removed, and the dura was cut. Silicone fluid was placed on the cortex to prevent desiccation and reduce pulsation. An enlarged photograph was made of the exposed cortex and electrode penetrations were marked relative to the vascular pattern. Tungsten-in-glass electrodes with tips designed to record from single units and neural clusters were used to define the cortical area of interest and microlesions (10 μA for 6 seconds) were placed at electrophysiological boundaries and marked on the photograph for later identification in processed tissue. Twenty-two to 69 recording sites were

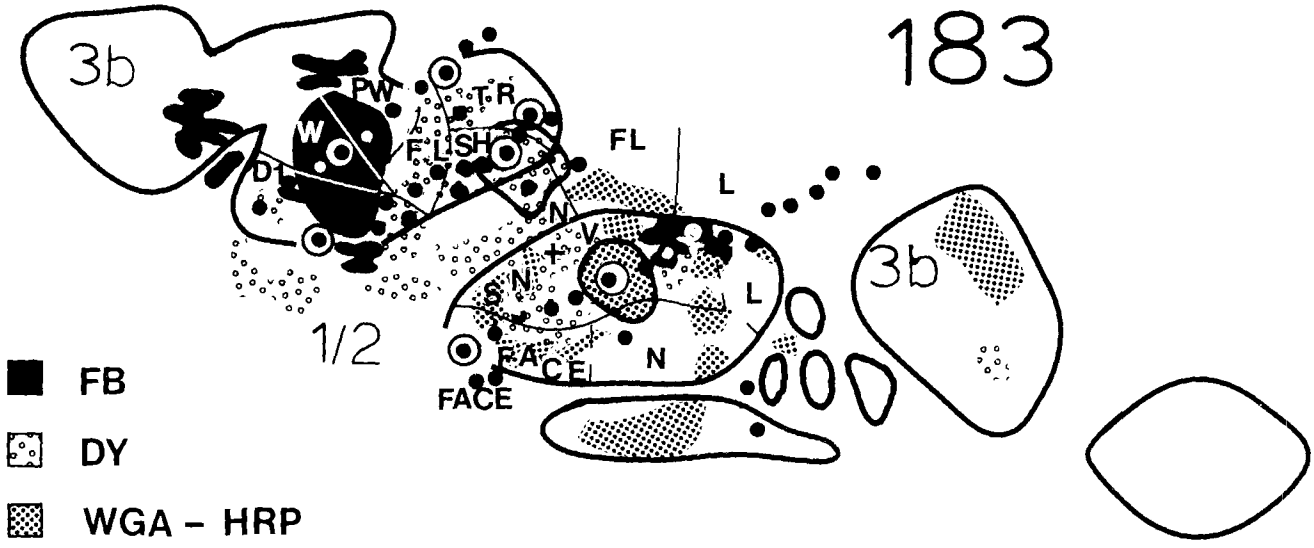


Fig. 4. A reconstruction of injection sites and intrinsic patterns of label in area 3b in case 183 in relation to electrophysiological mapping. Forty-six recording sites were used to define the location for the placement of injections in area 3b. The most medial injection is fast blue centred in the representation of the wrist. Lateral to the fast blue (FB) injection is an injection of diamidino yellow (DY) centred in the shoulder representation of 3b, but spreading into the neck representation of area 1/2. Finally the black circle is an injection of WGA-HRP centred in the snout vibrissae representation of area 3b. Architectonic boundaries are marked in solid thick lines. Open circles surrounding filled circles mark lesions at electrophysiological boundaries. Small filled circles mark 49 recording sites used to identify area 3b before injections were made. Scale bar equals 1 mm.

used initially to define the fields to be injected. The numbers of recording sites used to define the injected fields are provided for individual cases in the figure legends of each case. Details of electrophysiological recording procedures are provided elsewhere (Krubitzer and Calford, '92).

When the region of interest was mapped in sufficient detail, anatomical tracers were injected into the area. The anatomical tracers included the fluorescent dyes fast blue (FB), diamidino yellow (DY), fluorogold (FG), and wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP). Microcrystals (~10–20 μm in diameter) of fast blue and diamidino yellow were inserted directly into the cortex. The small hole in cortex was then plugged with a minute piece of absorbable gelatin sponge to prevent the tracer from escaping from the injection hole and artifactually labelling cells. Approximately 0.2–0.3 μl of 3% fluorogold or 0.03–0.05 μl of 0.1% WGA-HRP were injected with a 1 μl syringe coupled to a micropipette. Injections varied in size from small (~500 μm in diameter; e.g., Figs. 8 and 15, DY injections) to large (~2 mm diameter; e.g., Figs. 12, 19). Although the placement of microcrystals was used for some fluorescent tracers, we refer to these as injections throughout the text. After injections were complete, a soft contact lens was placed over the cortex, and covered with a thin sheet of absorbable gelatin sponge. The opening in the skull was then covered with an acrylic cap. The temporal muscle and attached fascia were sutured and then the scalp was sutured closed. The animal was allowed to recover for the appropriate survival time for each tracer (approximately 3–5 days for fast blue, diamidino yellow, and fluorogold and 2–3 days for WGA-HRP). In some cases, cortical areas away from the injection site were studied electrophysiologically in greater detail on the day of perfusion. The animal was then administered a lethal dose of pentobarbitone and transcardially perfused with 0.9% saline followed by 3% paraformaldehyde in phosphate buffer and then 3% paraformaldehyde in 10% sucrose phosphate buffer. When perfusion was complete, the brain was removed from the cranium. The corpus callosum was cut and each cortical hemisphere was carefully removed from the brainstem and thalamus. With the aid of several small cuts, the cortex was manually flattened between weighted glass slides and both the cortex and thalamus were soaked overnight in 30% sugar phosphate buffer. The flattened cortex was cut on a freezing microtome into 40 μm sections and alternate sections were processed for HRP with tetramethylbenzidine (Mesulam, '78; as modified by Gibson et al., '84), stained for myelin (Gallyas, '79) or mounted for fluorescence microscopy (Zeiss Axioplan MC100).

In all cases, sections processed for HRP or mounted for fluorescence microscopy were plotted with a camera lucida. In sections processed for HRP, both labelled cell bodies and axon terminals were apparent. In animals that received injections of fluorescent tracers, only labelled cell bodies were apparent. Thus, retrograde, or anterograde and retrograde label were plotted for all sections in the series of a single case. Blood vessels, lesions, and local tissue artifacts were drawn on the same sections so that individual sections could be aligned and a comprehensive reconstruction made. Lesions placed at physiological boundaries of cortical fields

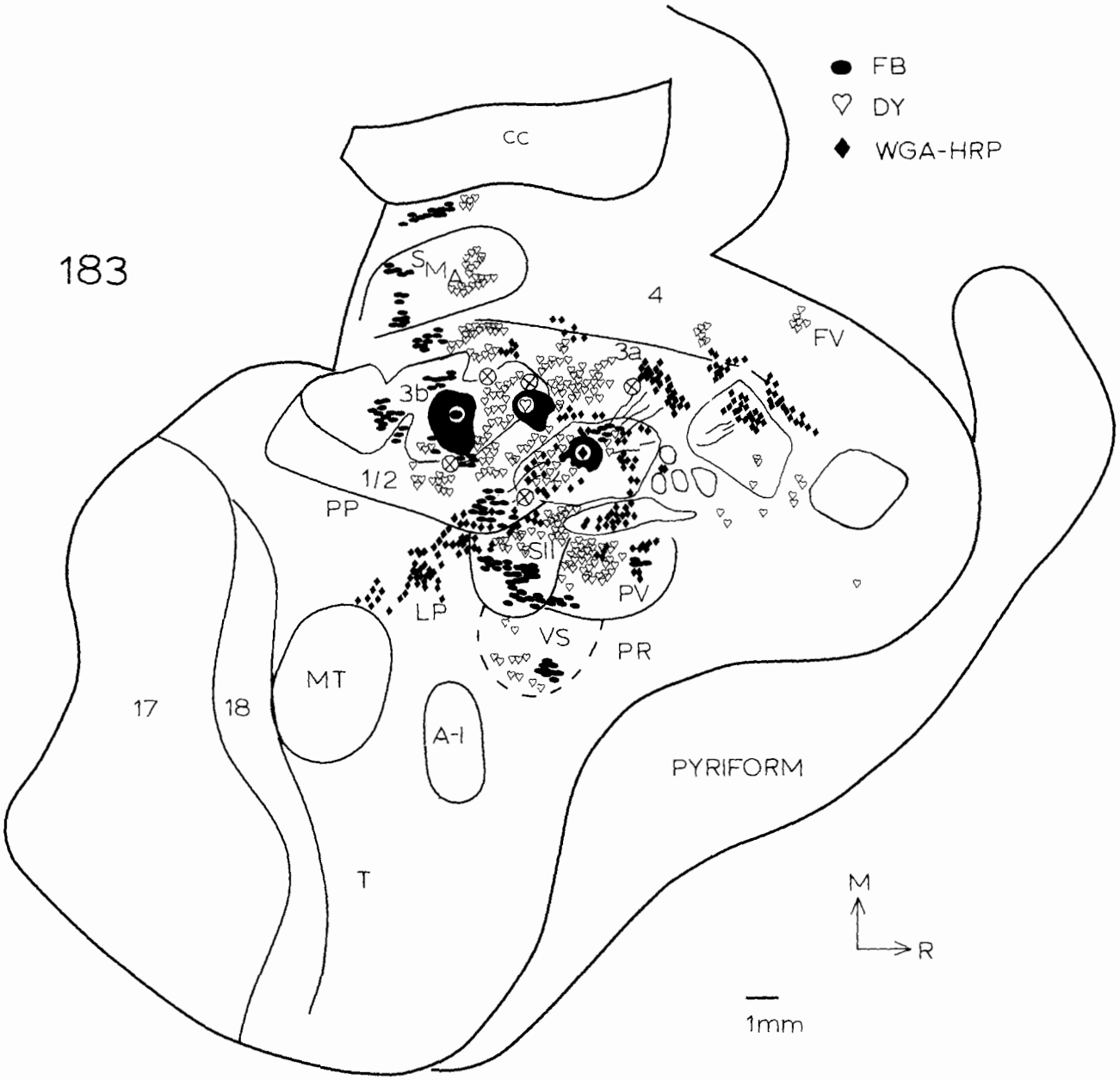


Fig. 5. A reconstruction of three injections in flying fox 183. Body part representations injected in 3b are illustrated in Figure 4. There are both topographic and nontopographic connections with areas 1/2, 3a, SII, and PV. Intrinsic connections of 3b are to close, related representations, and to distant, unrelated body part representations. M, medial; R, rostral. Conventions as in list of abbreviations.

were identified in sections stained for myelin. Both blood vessels and lesions were aligned in myelin stained sections and reconstructions of transported tracer so that architectonic boundaries could be added to the reconstruction. Electrophysiological mapping data, plotted from the enlarged photograph, were fitted to the reconstruction by using injection sites, blood vessels, and electrolytic lesions to scale and align, and were related to transported tracer as well as myeloarchitecture. Figure 2 illustrates the initial process of data analysis in all cases beginning with electrophysiological mapping, anatomical reconstruction of the injection site, and finally placement of architectonic boundaries. Further data analysis for this case is illustrated in Figures 8 and 9.

Although exact laminar patterns of label could not be defined with our flattened cortex preparation, general laminar levels could be ascertained by estimating the depth of the entire series of 40 μm sections through the cortex. Sections reconstructed from 0 to ~600 μm from the pial surface are likely to contain mostly supragranular layers. Sections reconstructed from ~600 to ~800 μm are likely to contain mostly layer IV and are considered to be granular

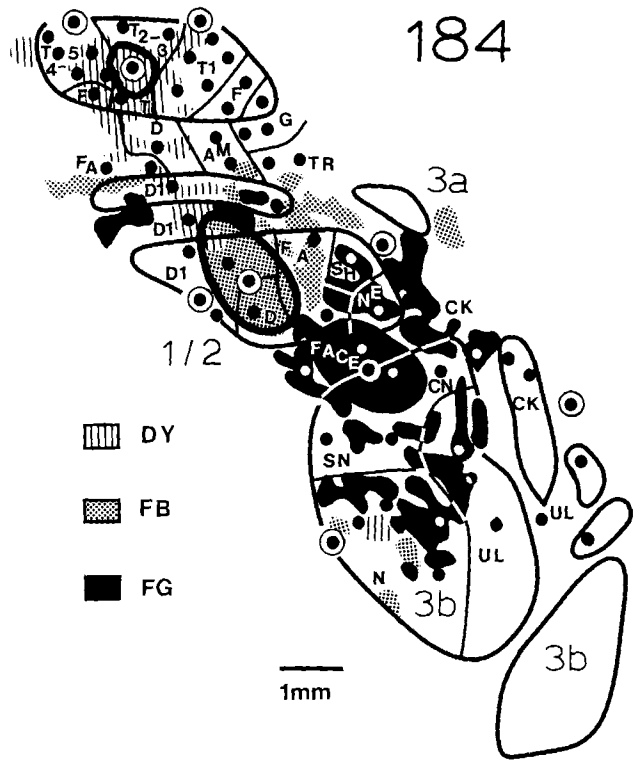


Fig. 6. A reconstruction of three injections and intrinsic patterns of connections in 3b in relation to electrophysiological mapping in case 184. Sixty-four recording sites were used to define the location for the placement of injections in area 3b. Diamidino yellow (DY) was injected in the toe 2–3 representation, fast blue (FB) was injected in the digit representation, and fluorogold (FG) was injected in the face representation. Intrinsic connections are to close, related body part representations as well as to distant body part representations. Other conventions in list of abbreviations.

layers; sections taken from cortex from ~800 to 1,400 μm are considered to contain mostly layers V and VI and are termed infragranular layers.

Connectional data has been illustrated in two ways. First, the overall patterns of density are illustrated with dots or symbols to denote labelled cell bodies. In cases where WGA-HRP was injected, dots of different sizes denote retrograde and anterograde label. Although reconstructions of labelled cell bodies and terminals are made directly from the magnified cortical tissue, there is not a one-to-one correspondence between a single labelled cell or axon terminal and a single symbol in an illustration. Rather, the pattern of density throughout the cortical layers is illustrated. Illustrating a one-to-one correspondence would not accurately depict the data since the changes in magnification from actual tissue to microscope reconstruction to illustration to final photographic reduction would make all label appear equally dense and would not reflect true density patterns. In our illustrations, very dense label is depicted by clustering symbols tightly, while sparse label is depicted by a few symbols, often spread far apart. Densities of label are depicted in this same manner within a case and across cases.

The second way we have illustrated the data is spatially. In these illustrations, our goal was to show the spatial location of label relative to electrophysiological mapping. We used different stipples for this, since individual symbols would be confused with electrophysiological recording points. The perimeter of the labelled regions was used to mark spatial location. Within the stippled region, the actual density of labelled cells and axon terminals may vary. When only one or two labelled cells were noted, no stipple was used.

RESULTS

In these results we describe the cortical organization of five fields (areas 3b, 1/2, SII, PV, and VS) in the somatosensory cortex of the flying fox that systematically represent the cutaneous body surface. Also, in one animal, we injected an anatomical tracer into a region of cortex defined predominantly by connections from known somatosensory and visual fields. We term this field the lateral parietal field, LP, and describe its connections as well. In the first part of these results the myeloarchitecture of somatosensory neocortex in the flying fox is described. Detailed descriptions of the topographic organization and neural response properties of fields are provided elsewhere (Krubitzer and Calford, '92). Next, the topographic patterns of connections of area 3b and area 1/2 with adjacent fields in anterior parietal cortex and fields in lateral somatosensory cortex are described. Then we describe the patterns of connections of SII, PV, and VS, three topographically organized fields lateral to 3b. Patterns of connections with each other, and with subsets of rapidly habituating neurons in area 1/2 incursions into 3b and with nonhabituating neurons in 3b are described as well as connections with other fields. In some animals, somatosensory fields adjacent to the injected areas were mapped in detail. Where this was done, correlation between connection patterns and electrophysiological maps are described. Finally, we describe the connections of the lateral parietal area, LP.

Myeloarchitecture of somatosensory cortex

The organization of 3b, area 1/2, SII, PV, and VS in the flying fox was described in a previous study (Krubitzer and Calford, '92; Fig. 1) where over 1,300 recording sites were made in 10 animals. We found evidence for at least five topographically organized fields in somatosensory cortex of the flying fox, coextensive with a unique myeloarchitectonic appearance. Area 3b is coextensive with myelin dense zones (Fig. 3A,D), best viewed in tangentially sectioned cortex. An important finding in the previous investigation was that these myelin dense zones, containing nonhabituating neurons, are surrounded by lightly myelinated zones whose neurons rapidly habituate to the stimulus. These myelin light, habituating regions appear to be extensions of the caudally adjacent area 1/2 into 3b (Figs. 1, 3).

The physiological organization of fields caudolateral to 3b (SII, PV, and VS) has also been described. These three fields were distinguished by myeloarchitectonic criteria as well. Both SII and PV stain moderately to densely for myelin while VS stains somewhat lighter (Fig. 3A).

Electrophysiological recordings were made in regions of cortex where we have not yet defined the physiological organization: rostral to 3b; caudal to 1/2, SII, and VS; and lateral to PV. Caudal to area 1/2, posterior parietal cortex (PP) was a myelin light region interspersed between the moderately myelinated second visual area (VII) caudally, and area 1/2 rostrally (Fig. 3B). The lateral parietal area, LP, was also myelin light and wedged between moderately myelinated SII rostrally, darkly myelinated middle tempo-

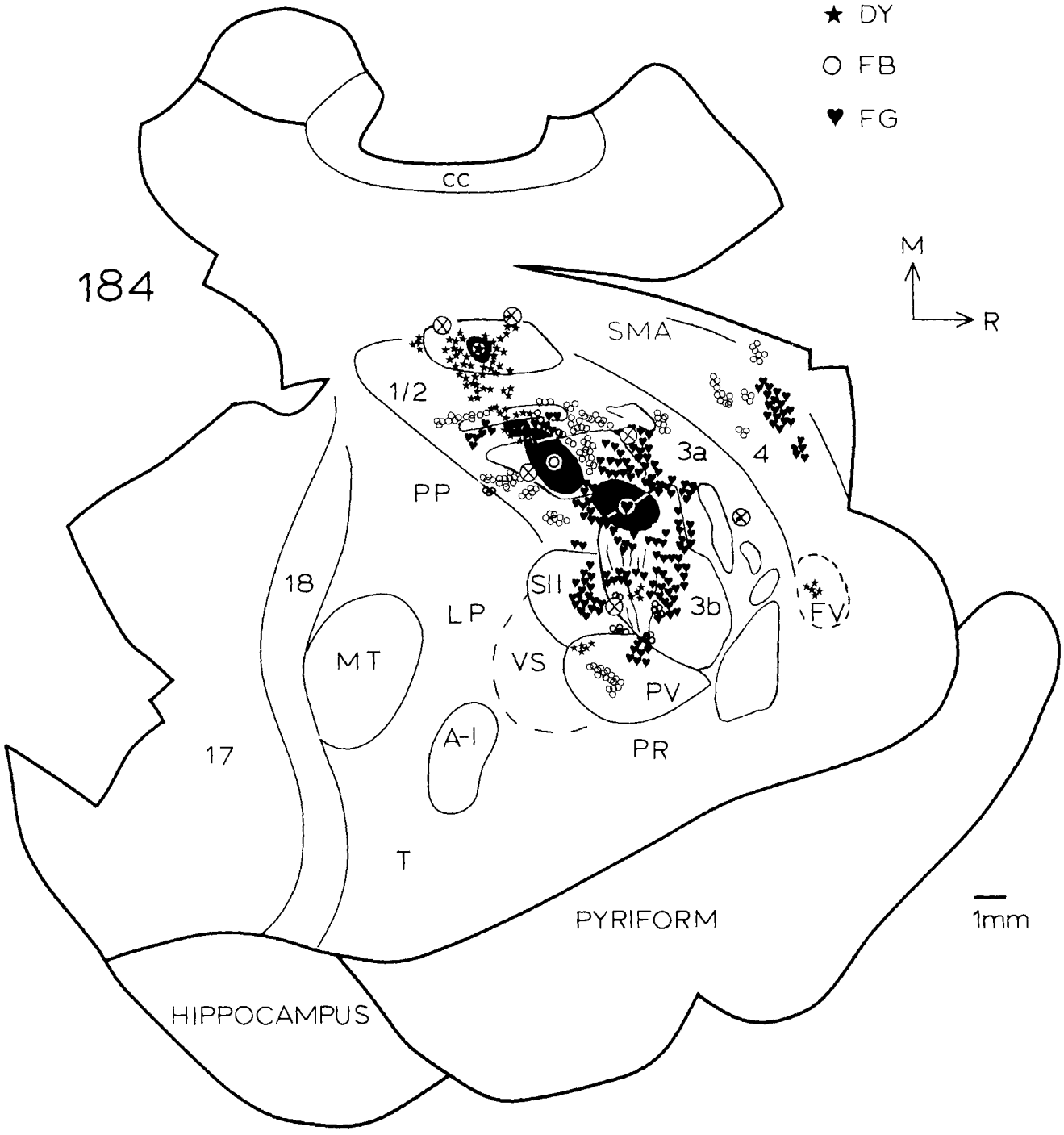


Fig. 7. An illustrated reconstruction of three injections in area 3b and resulting transported tracer in flying fox 184. Body part representations injected in 3b are illustrated in Figure 6. The connections are generally consistent for all three tracers although the diamidino yellow injection had substantially less transport than the fast blue and fluorogold injections. Label in both areas 1/2 and 3a was topographically organized in that the most medial injections in 3b labelled medial portions of areas 3a and 1/2, and progressively lateral injections in 3b labelled more lateral regions in areas 3a and 1/2. Injections of FG into the face representation labelled both SII and PV in portions adjacent to the 3b boundary, in representations of the face. Injections of FB into the digit representation labelled SII in a lateral location and PV in a far medial location, in representations of the digits, and injection of DY in the representation of the toes in 3b labelled a caudomedial location in PV in the approximate location of the toe representation. Other connections of 3b were with area 4. Solid lines mark architectonic boundaries, dashed lines mark approximated boundaries. Circled X's mark lesions at physiological boundaries. M, medial; R, rostral. Other conventions in list of abbreviations.

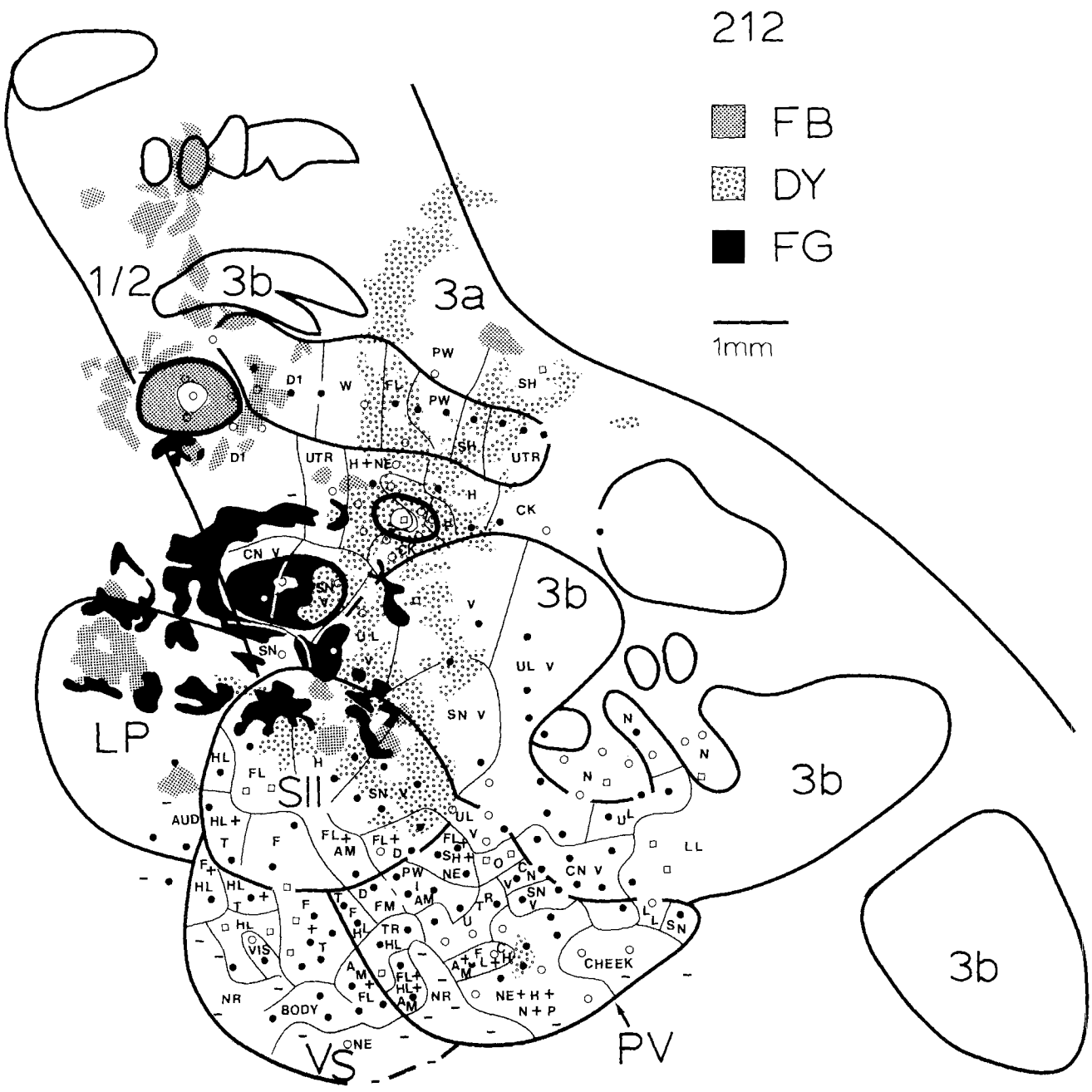


Fig. 8. Electrophysiological mapping in relation to injection sites and transported tracer from three injections in area 1/2 in case 212. Fifty recording sites were used to define the location for the placement of injections in area 1/2. Fast blue was centred in the representation of D1, diamidino yellow was centred in the deep head and neck representation, and fluorogold was centred in the chin vibrissae representation. As for injections in 3b, intrinsic connections of area 1/2 were to both closely related and distantly related body part representations. Connections with 3b were to topographically matched and mismatched locations as well. Label in SII was quite dense and restricted to the rostral portion of the field where the face and the forelimb are represented. Label in LP was also very dense. Only sparse label was noted in the head and neck representation in PV after an injection in the deep head and neck representation in area 1/2. Finally, label in area 3a was most dense after an injection in the head/neck representation in area 1/2. Filled circles mark electrode tracks in which neurons did not habituate to a cutaneous stimulus. Open circles mark electrode tracks in which neurons habituated to a cutaneous stimulus, and open squares mark electrode tracks in which neurons habituated to a deep stimulus. Dashes mark electrode tracks in which neurons did not respond to sensory stimulation. Aud, auditory; NR, no response. Other conventions in list of abbreviations.

ral visual area (MT) caudodorsally, and the darkly myelinated auditory area (AI) ventrally (Fig. 2B). Just ventral to PV, a lightly myelinated region of cortex, PR, was observed. The rostral and caudal boundaries of PR were difficult to distinguish since much of this cortex was lightly myelinated.

Immediately rostral to 3b was a narrow, lightly myelinated strip of cortex that appeared to abut most of the

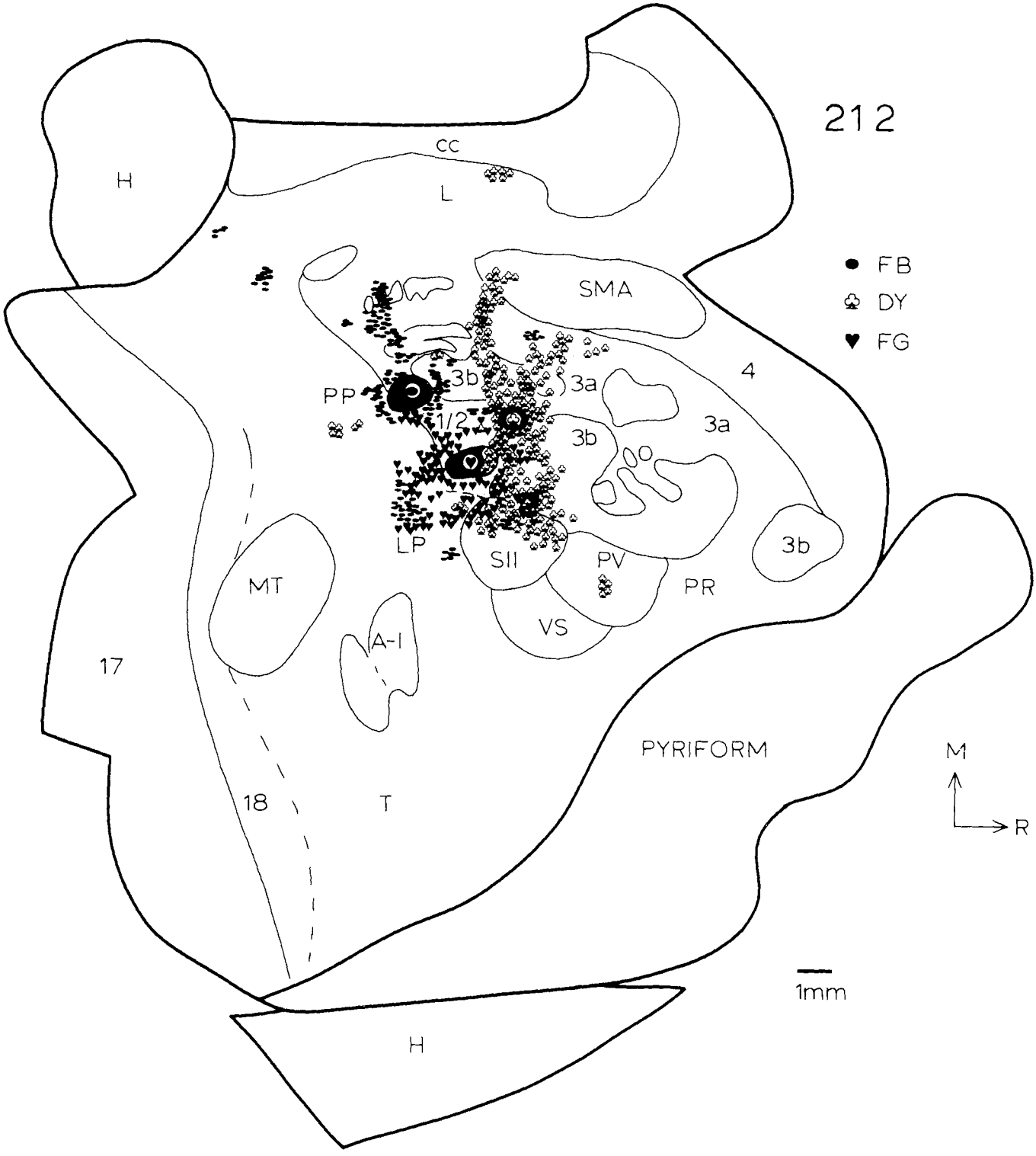


Fig. 9. A reconstruction of injections in case 212 that illustrates the entire pattern of connections of area 1/2. The representations injected in area 1/2 are described in the previous figure. Note that the injection in the region of cortex in which neurons responded to deep stimulation (DY, open clubs) resulted in somewhat different patterns of connections from those injections centred in cortex in which neurons responded to cutaneous stimulation. For example, area 3a is heavily labelled from the injection in the deep representation, while little or no label is observed in 3a after injections in cutaneous representations. Also, SMA, PV, and rostral limbic cortex contain transported tracer from injections in deep area 1/2 but not from injections of cutaneous area 1/2. M, medial; R, rostral. Other conventions in list of abbreviations.

TABLE 1. A Summary of the Injections in Different Cortical Areas and the Resulting Connections Observed[1]

Injections			Connected to																
			3b	1/2	3a	PP	4	SMA	FV	SII	PV	VS	LP	PR	PY	T	Vis	Aud	Other
Case	Area	Tracer																	
183	3b	FB	++	++	++	–	–	++	–	++	+	+	–	–	–	–	–	–	+
183	3b, 1/2	DY	+++	+++	+++	–	++	++	–	++	+++	+	–	–	–	–	–	–	+
183	3b	WGA	+++	+++	++	–	+	–	–	+	+	–	++	–	–	–	–	–	–
184	3b, 1/2	DY	+++	++	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–
184	3b	FB	+++	++	+++	–	+++	+	–	+	++	–	–	–	–	–	–	–	–
184	3b, 1/2	FG	+++	+	+++	–	+++	–	–	+++	+	–	–	–	–	–	–	–	–
212	1/2(c)	FB	+++	+++	+	++	–	–	–	+++	–	–	+++	–	–	–	–	–	+
212	1/2(d)	DY	+++	+++	+++	+	–	–	–	+++	+	–	+	–	–	–	–	–	+
212	1/2(c)	FG	++	+++	–	++	–	–	–	+++	–	–	+++	–	–	–	–	–	–
188	SII	WGA	+	+++	–	–	–	++	+	++	+++	+++	+++	–	–	–	–		–
189	SII, PV	WGA	+	++	+	–	–	+	+	++	++	++	++	–	–	–	–		–
199	SII	DY	+	+++	–	+	–	+	+	+	++	+	+++	–	–	–	–	–	+
199	PV	FG	+++	+	+++	–	–	+	–	+++	++	++	–	+++	+++	+	–	–	+
186	PV	WGA	+++	+	+	++	+	+	–	+++	+	+++	+	+	–	–	–	+	–
199	VS	FB	–	++	–	–	–	–	–	++	+	+	–	–	+	+++	–	–	–
202	LP	WGA	+	++	++	+++	+	++	+++	+++	–	–	+	–	–	+++	+++	++	+

+++	Dense Labelling
++	Moderate Labelling
+	Sparse Labelling
–	No Labelling
	Superficial anterograde

[1]Connections of areas 3b and 1/2 are most dense with other anterior parietal fields. Connections of the second somatosensory area (SII), the parietal ventral area (PV), and the ventral somatosensory area (VS) are most dense with other lateral parietal fields. Connections of the lateral parietal area (LP) are very dense with posterior parietal (PP), temporal (T), and motor cortex (area 4). Vis, visual cortex; Aud, auditory cortex. (c) = cutaneous; (d) = deep. Other conventions in list of abbreviations.

mediolateral length of 3b (Fig. 3A,C,D). This field was termed 3a. Just rostral to 3a, in area 4, cortex was moderately myelinated. In a lateral location in area 4, a darkly myelinated oval of cortex was observed (Fig. 3D). Based on relative location and connections (see below) we term this field the frontal ventral eye movement field, FV. Finally, cortex immediately dorsal to area 4 and rostral to 3a, in the approximate location of the supplementary motor area (SMA) described in other mammals, stained moderately to darkly for myelin (Fig. 3C,D). In related microstimulation studies (Kennedy, '91), cortex in this location, when microstimulated, evoked body part movement.

Cortical connections of 3b

A total of six injections of neuroanatomical tracers were placed into different body part representations in 3b of two flying foxes (Table 1; Figs. 4–7). Because of the invaginations of area 1/2 between myelin dense portions of 3b, it was difficult to produce an injection that was strictly limited to area 3b. Nevertheless, three of the six injections appeared to be completely confined to 3b, while 3 of the injections (Table 1) appeared to spread into area 1/2. In case 183, the injection of the fluorescent dye fast blue was centred in the wrist representation, but spread into the adjacent prowing and D1 representation. A diamidino yellow injection was centred in the shoulder and chest representation but spread into the naris and face representation in area 1/2. WGA-HRP was injected into the snout and vibrissae representations in 3b. In case 184, the FB injection was almost completely restricted to the representation of the digits in 3b, but spread slightly into the digit representation of area 1/2 (Fig. 6). The DY injection was placed in the representation of toes 2 and 3 in 3b and the FG injection was placed in the snout representation of 3b, but spread into the representation of the face in area 1/2 (Fig. 6).

Intrinsic connections of 3b. All injections into 3b retrogradely labelled adjacent regions of 3b immediately surrounding the injection site (Table 1). Only the injection of WGA-HRP in the vibrissae representation in case 183 (Figs. 4, 5) resulted in anterograde label as well. In this case, both anterograde and retrograde label were in similar locations in the cortex. Injections that appeared to be restricted to myelin dense regions (e.g., FB and WGA-HRP injections in case 183, Fig. 4; FB injection in case 184, Fig. 6) labelled adjacent, myelin dense regions of cortex within the same myelin dense clump as that injected. This locally transported tracer was related to body part representations adjacent to that injected. For example, the injection into the digit representation in case 184 labelled the adjacent forearm representation (Fig. 6).

In addition to intrinsic label observed near the injection site, retrograde label, and for the WGA-HRP injection, anterograde label, was noted in myelin dense zones separated from the injection zone by a myelin light area 1/2 invagination. For example, the WGA-HRP injection in case 183 (Figs. 4, 5) into the vibrissae representation, not only had bidirectionally transported tracer in adjacent myelin dense regions of 3b (in snout, lips, nose and face representations), but also had transported tracer in a large myelin dense island rostrolaterally and a small thin island caudolaterally (Figs. 4, 5). These myelin dense zones relate to the lips and naris/snout representations respectively. Likewise, the injection of FB in case 183 (Figs. 4, 5) into the wrist/digit representations, labelled a nearby myelin dense region of cortex in the representation of the shoulder and the expected location of the forelimb representation, as well as myelin dense zones further medially, in the approximate location of the representation of the hindlimb, and laterally, in the snout and vibrissae representations. In case 184 (Figs. 6, 7), an injection of FB into the digit representation resulted in small clumps of transported tracer in the myelin dense zone immediately adjacent to the injection site, and distant from the injection site. Local transport was to representations of the forearm. Label in a medial myelin dense zone was in the D1 representation and sparse label in a lateral myelin dense clump was in the representation of the naris. An injection of FG into the representation of the snout (Figs. 6, 7) labelled clumps of cells laterally in the representation of the naris and lips. In the myelin dense zone medial to the injection site, in the representation of the shoulder and neck, a large clump of labelled cells resulted from the injection in the snout representation. Finally, in a more medial myelin dense zone, where D1 was represented, a sparse patch of label was also noted. Thus, it appears that the intrinsic connections of 3b are with adjacent body part representations as well as distant body part representations.

Connections with areas 1/2 and 3a. Connections of 3b with other cortical fields were consistent across injections (Table 1). There was one exception. In case 184 (Figs. 6, 7), the far medial injection of DY, centred in the representation of the toes, had only limited amounts of transported tracer in other cortical fields. This may be because this injection was made on the medial wall and ran parallel to cortical layers rather than perpendicular to them. Reconstruction of this injection revealed that the injection did not encompass all cortical layers, but involved mostly middle cortical layers. Sparseness of transported tracer in cortex is likely to be the result of limiting the injection to only a few cortical layers.

Injections into a far medial location in 3b (DY injection in case 184, Figs. 6, 7) labelled cells in myelin light area 1/2, caudal to the injection site in the representation of the foot (see Fig. 1), and lateral to the injection site in an area 1/2 invagination representing the forearm and digits (Figs. 6, 7). Injections centred in representations of the digits and shoulder (FB, DY injections in case 183, Fig. 4; and FB injection in case 184, Fig. 6) retrogradely labelled cortex immediately caudal to the injection site, in area 1/2 in the expected location of the representation of the digits, and in area 1/2 invaginations around the injection site in representations of the forelimb and face (Figs. 4–7). These injections also labelled cells in cortex immediately rostral to 3b, in area 3a, at similar mediolateral levels. Injections centred in the face representation of 3b (WGA-HRP injection in case 183, Figs. 4, 5; FG injection in case 184, Figs. 6, 7) also labelled cells, or cells and axon terminals for the WGA-HRP injection, in adjacent caudal portions of area 1/2 and area 1/2 invaginations into 3b. This caudal portion of area 1/2 represents the head and neck and more medial invaginations represent the face and portions of the forelimb (Fig. 1). Retrograde label was also noted immediately rostral to the injection sites in area 3a. Both retrograde and anterograde label were observed in area 3a and area 1/2 after the injection of WGA-HRP in the snout representation in case 183.

In addition to the topographically appropriate connections between 3b and area 1/2 and 3b and 3a, connections also appeared nontopographic. Retrograde label was observed in both area 1/2 and 3a at different mediolateral

levels from the injection site (e.g., FB injection in case 183, Fig. 5; FB and FG injections in case 184, Fig. 7). Thus, injections in forelimb or digit representations not only labelled cells in the approximate location of the forelimb and digit representation in area 1/2, but also labelled cells in portions of the face representation (e.g., FB injection in Fig. 5) or trunk and face representations (e.g., FB injection in digits in Fig. 7).

Connections with frontal cortex. Connections between area 3b and 4 were observed for four of the six injections in 3b (Table 1). Connections with area 4 were roughly topographic in that injections in the forelimb representation labelled more medial portions of area 4 than injections in the face representation (Figs. 5, 7). Cortex in area 4, when microstimulated, produces movements of various body parts, in rough topographic sequences similar to the mediolateral sequence of body part representation in 3b (Vogt and Vogt, '07; Kennedy, '91) indicating that this region of cortex has motor functions.

Connections with SII and PV. An interesting result in the present investigation was that PV, rather than SII, was more densely interconnected with area 3b. This finding is even more pronounced when one examines transported tracer in 3b and area 1/2 after injections were placed in SII and PV, probably because it is difficult to make an injection completely limited to 3b without involving small portions of area 1/2 (see below). Connections between 3b and PV were dense and roughly topographic. An injection into the toe representation in 3b (DY injection in case 184, Figs. 6, 7) labelled cells in a caudomedial portion of PV, where the foot is represented (Fig. 1). Injections in the digit representation in 3b (FB injection in case 183, Figs. 4, 5; FB injection in case 184; Figs. 6, 7) labelled cells in middle and medial portions of PV, rostral to the foot/hindlimb representations, in the approximate location of the forelimb representation (Fig. 1). Finally, injections in the face representation in 3b (WGA-HRP injection in case 183, Figs. 4 and 5; FG injection in case 184, Figs. 6 and 7) resulted in labelled cell bodies and axon terminals in rostral portions of PV, where the face is represented.

Although sparse to moderate, connections of 3b with SII were consistent across injections and roughly topographic. Injections that resulted in moderate to dense label in SII usually involved area 1/2 (Table 1). Injections in the forelimb or digit representations labelled more middle portions of SII (where the forelimb and digits are represented, Fig. 1), while injections into the face representation in 3b labelled rostral portions of SII (Figs. 5, 7), where the face is represented (Fig. 1). Injections into the digit representation in 3b (FB injection in case 184, Figs. 6, 7) retrogradely labelled cells in lateral portions of SII, and injections in the forearm representation in 3b (FB injection in case 183, Figs. 4, 5) labelled cells in medial portions of SII, where the forelimb is represented (Fig. 1). Finally, injections into the shoulder/chest representation in 3b labelled rostral and rostromedial portions of SII. Labelled cell bodies and axon terminals also spread beyond the location of approximate matched body parts into other adjacent body part representations. When the injection in 3b involved area 1/2 to a greater extent (e.g., compare FB and FG injections in case 184, Figs. 6, 7), transported tracer was predominantly in SII and less dense in PV.

Other connections of 3b. In one case (183), additional connections were noted for some of the injections (Table 1). Both the injection of FB into the forelimb representation and the injection of DY into the shoulder representation (Figs. 4, 5) retrogradely labelled VS and cortex just lateral (dorsal in the intact brain) to the corpus callosum. In one case, a sparse patch of transported tracer was found in the frontal ventral area, FV (DY injection in case 184, Fig. 7). Finally, the WGA-HRP injection into the face representation in case 183 (Figs. 4, 5) anterogradely and retrogradely labelled LP.

Cortical connections of area 1/2

Three injections of retrogradely transporting fluorescent tracers were made into different body part representations in area 1/2. Two of these injections were centred in an electrophysiologically identified location where neurons responded to cutaneous stimulation (FB and FG, Fig. 8), and one injection was centred in an electrophysiologically identified location where neurons responded to deep stimulation (DY, Fig. 8). In our physiological study of this area we identified neurons in area 1/2 that rapidly habituated to cutaneous stimulation to peripheral body parts, and other neurons in area 1/2 that rapidly habituated to deep stimulation of peripheral body parts. Although the pattern of retrogradely transported tracer from all injection sites was very similar, there were several differences between connections of deep and cutaneously responsive cortex in area 1/2. A consistent finding was that the major sources of projections to area 1/2 were from 3b, SII and LP (Table 1).

Connections with 3b and 3a. All fluorescent injections in area 1/2 retrogradely labelled area 3b in locations topographically matched to the injection site, as well as representations of other body parts (Figs. 8, 9). Injections in the D1 representation in area 1/2 retrogradely labelled the D1 representation in 3b. Transported tracer was also noted in darkly myelinated medial clumps where the forelimb and hindlimb are represented (Fig. 1). Injections centred in the head and neck representation in area 1/2 labelled 3b in representations of the upper lip vibrissae and snout vibrissae. More medially represented body parts in 3b, including the wrist, forelimb, prowing, shoulder, and upper trunk were retrogradely labelled as well (Figs. 8, 9). Finally, injections in the snout vibrissae representation in area 1/2 retrogradely labelled the snout vibrissae and upper lip vibrissae representations in 3b.

Two of the injections in area 1/2 labelled cells in cortex immediately rostral to 3b, in area 3a. The injection centred in the deep head and neck representation in area 1/2 (DY), retrogradely labelled cells in area 3a in a portion of the shoulder representation. Additional labelled cells were noted medially, in 3a, presumably in other portions of the forelimb representation. This injection had the densest connections with 3a. The injection centred in the D1 representation in area 1/2 (FB) resulted in a small patch of labelled cells in the shoulder representation of 3a.

Connections with SII and LP. Injections in both deep and cutaneous representations in area 1/2 resulted in dense retrogradely labelled cells in SII (Table 1). Connections were topographically matched and mismatched to that of the representation injected. For example, the injection centred in the snout vibrissae representation in area 1/2 retrogradely labelled cells in SII in the snout vibrissae, head, and forelimb representations. The injection centred in the head/neck representation in area 1/2 retrogradely labelled cells in snout vibrissae, head, and forelimb representations in SII. Finally, the injection in the D1 representation in area 1/2 retrogradely labelled the head, and portions

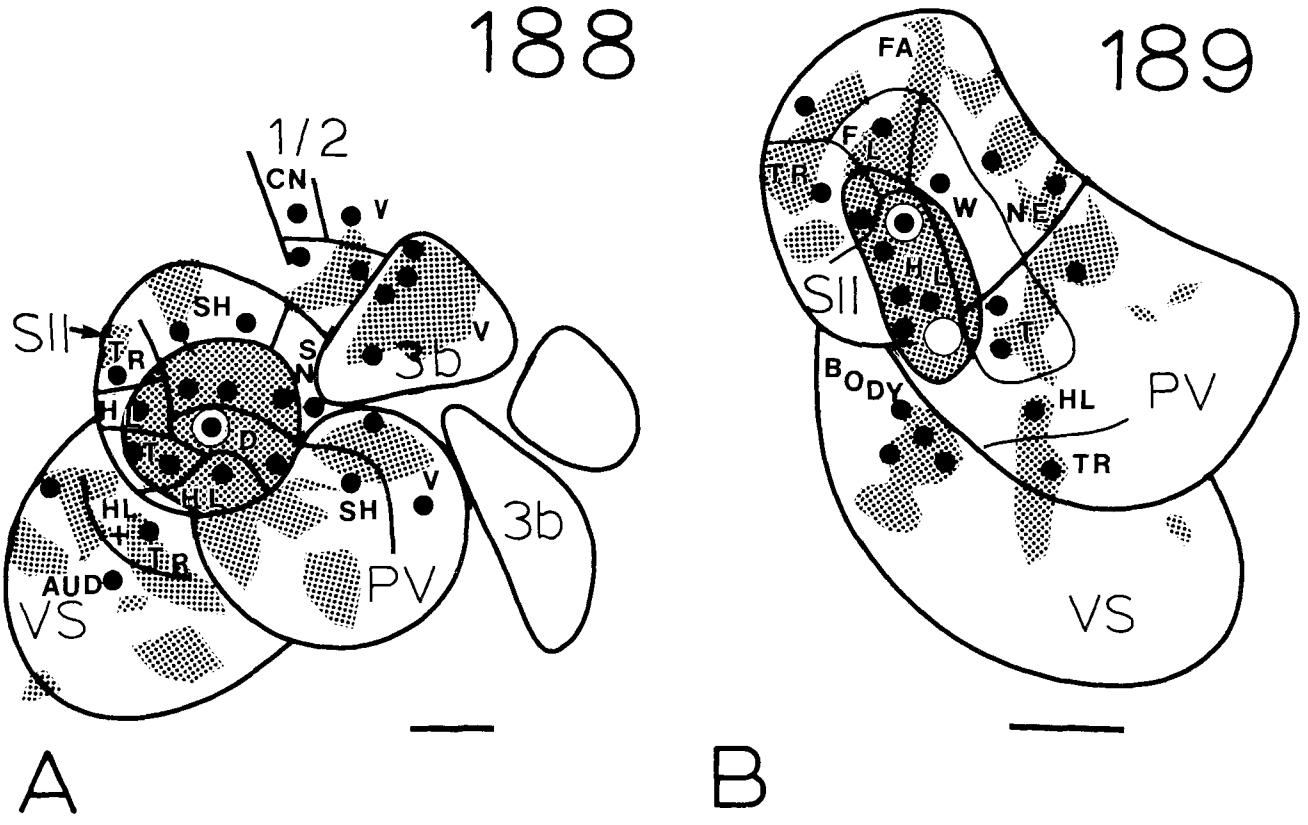


Fig. 10. **A:** An injection centred in the digit representation in SII in case 188 and the relation of the injection site to microelectrode mapping and myeloarchitecture. The spatial distribution of locally transported tracer in relation to electrophysiological mapping is also illustrated. In this case, 27 recording sites helped identify the boundaries of SII before the injection was made. **B:** An injection centred in the hindlimb representation in SII in case 189. The injection spread slightly into the representation of the hindlimb in PV. In this case, 22 recording sites helped identify the boundaries of SII before the injection was made. As in A, patterns of locally transported tracer in relation to electrophysiological mapping and myeloarchitecture are illustrated in stipple. Aud, auditory. Scale bar equals 1 mm. Other conventions in list of abbreviations.

of the snout vibrissae representation in SII (Figs. 8, 9). After area 1/2 injections, retrogradely labelled neurons were also noted in the lateral parietal area, LP (Fig. 9). The DY injection in the deep head/neck representation had the lightest label in LP.

Other connections of area 1/2. There were several areas of cortex inconsistently labelled from injections in area 1/2 (Table 1). The injection centred in the representation of D1 in area 1/2 resulted in two sparse patches of label medial to posterior parietal cortex. The injection centred in the cluster of neurons that responded to deep stimulation of the head and neck (DY, Figs. 8, 9) resulted in labelled neurons in a middle portion of PV, in posterior parietal cortex, in SMA and in cortex adjacent to the corpus callosum. Thus, deep islands in area 1/2 have somewhat different connections from cutaneous islands in area 1/2, although the majority of connections were similar.

Cortical connections of SII

Electrophysiologically identified body part representations in SII were injected in three animals (Table 1). In two cases where WGA-HRP was injected into SII, laminar differences in patterns of connections were observed. In cortex ~0–200 μm from the pial surface (in superficial supragranular cortex), a large area of dense anterograde label was noted around the injection site. Differences in superficial anterograde and deeper anterograde and retrograde label are depicted by showing two reconstructions for some cases. One reconstruction illustrates the distribution of superficial anterograde label in relation to cortical boundaries, and the other illustrates patterns of anterograde and retrograde label from the same case for deeper cortical layers.

In one case (188), an injection of WGA-HRP was centred in the digit representation in SII, but spread into adjacent representations of the shoulder, hindlimb, and toes (Fig. 10A). This injection was limited to the electrophysiological and architectonic borders of SII. In another case (189), an injection of WGA-HRP was centred in the dorsal hindlimb representation of SII (Fig. 10B), and spread into the representation of the trunk and forelimb. This injection appears to have involved a small medial portion of PV. In the third case (199), the fluorescent dye diamidino yellow was centred in the cheek representation in SII, but spread into adjacent head and forelimb representations (Fig. 15). Injections of WGA-HRP resulted in labelled cells and axon terminals in moderately dense clumps throughout the SII representation, regardless of the body part injected in SII.

Patterns of superficial anterograde label. In case 188, patterns of superficial anterograde label differed markedly from the deeper areal patterns of connections (compare Fig.

Fig. 11. Darkfield photomicrograph of WGA-HRP injections in SII in case 188 and resulting superficial anterograde label in cortex immediately surrounding the injection site. In this case, the injection was centred in the representation of the digits and patches of transported tracer were observed locally, in representations of the shoulder and trunk in SII and in related representations in PV and VS. Scale bar equals 1 mm.

12A with 12B). Superficial anterograde label was denser in PV, VS and area 1/2 than in the deeper layers (Figs. 11, 12A). In addition, densely labelled axon terminals were also noted in AI, LP, and cortex caudal to AI and rostral to AI. These regions were not labelled in deeper layers of cortex. Patterns of superficial anterograde label in case 189 (Fig. 14A) were also more broadly distributed around the injection site than the anterograde and retrograde label in deeper layers (Figs. 13, 14B). Densely labelled superficial axon terminals were noted in PV, VS, area 1/2, and 3b. Superficial anterograde label was also noted in LP, AI, cortex caudal to AI and in PP. In both cases 188 and 189, supragranular anterograde label formed bands that stretched across the rostrocaudal extent of AI (Figs. 12A, 14A).

Connections with PV, VS, and LP. In all cases dense label was found in the adjacent fields PV and VS (Table 1). Bidirectionally transported tracer from the WGA-HRP injection which was centred in the digit representation in SII (Figs. 11, 12) labelled PV in a region immediately adjacent to the SII boundary. This region of PV is known to represent the digits (Fig. 1). Additional label in PV was found in the approximate location of the face and hindlimb representations. Label in VS in this case was scattered in clumps throughout the field and probably related to portions of the hindlimb, forelimb and face representations.

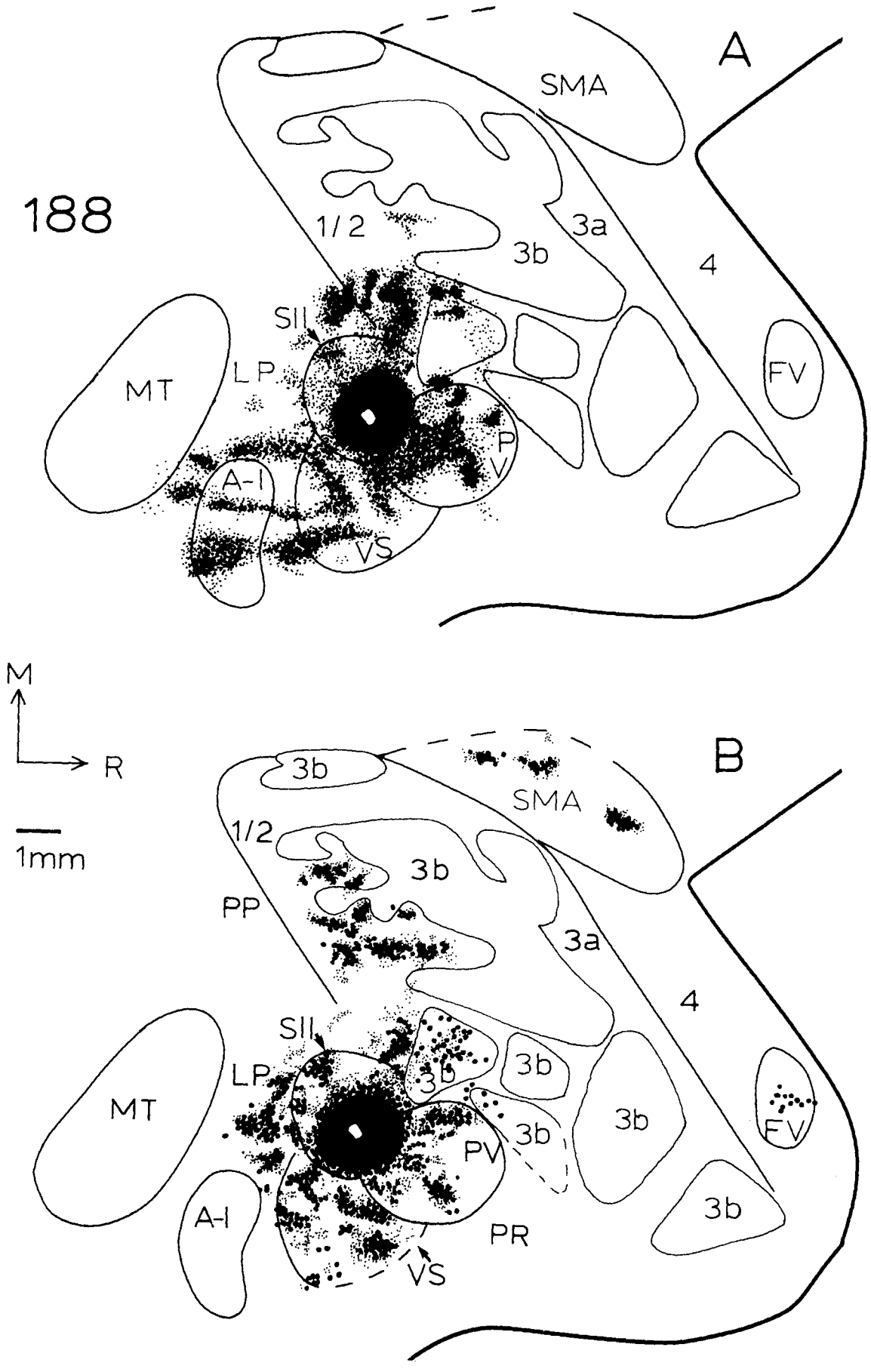
An injection in the dorsal hindlimb representation in SII (Fig. 10B), anterogradely and retrogradely labelled PV in a caudal location where the hindlimb and foot are represented (Fig. 14). Sparse patches of bidirectionally transported tracer were also observed rostromedially in the representation of the digits. Label in VS was in a dense clump adjacent to the PV and SII boundary, in the general location of the foot representation (Fig. 1), although sparse mapping in this general region in VS demonstrated that label was in the representation of the body (Fig. 10B). A smaller patch of transported tracer was also noted lateral to this large dense clump.

Finally, a small injection of DY centred in the cheek representation in SII (Figs. 15, 16) labelled cells in PV in several locations medially and in a larger clump caudoventrally. Electrophysiological mapping in this same case showed that the densest clump of label was in the representation of the snout and smaller clumps of label were in the digit, chin, and hindlimb representations (Fig. 15). Labelled cells in VS were sparse and in a middle dorsal location, in the representation of the hindlimb and toes (Fig. 15). Connections between SII and PV and VS were largely matched for topographic location, but transported tracer was also present in other unrelated body part representations.

Dense patches of transported tracer were consistently noted in a region of cortex immediately caudal to SII, in LP (Figs. 12, 14, 16). Neurons in the dorsal part of this region responded best to visual stimulation, while neurons in the ventral part of LP responded best to auditory stimulation.

Connections with 3b and area 1/2. Connections between SII and the 3b region, which includes 3b proper and invaginations of area 1/2, were both topographically matched and mismatched to the injected representation. An injection centred in the digit representation in SII (Figs. 10A, 12), resulted in anterograde and retrograde label in medial and middle portions of area 1/2, in the expected location of the forelimb representation (Fig. 1). Sparse patches of bidirectionally transported tracer were also noted laterally, in the representation of the face (Figs. 11A, 12B). Anterograde and retrograde label was much lighter in myelin dense 3b and was found in the lateral portion of 3b. An injection in the hindlimb representation (Fig. 10B) produced anterograde and retrograde label in dorsal, middle, and lateral representations of 3b and area 1/2 (Fig. 14B), in the representations of the hindlimb, forelimb, and

Fig. 12. A reconstruction of a WGA-HRP injection centred in the digit representation in SII, and patterns of superficial anterograde (**A**) and deeper patterns of anterograde and retrograde label (**B**). Patterns of superficial anterograde label are very dense and more broadly distributed than deeper labelled cells and axon terminals. In both A and B dense patches of transported tracer are in PV and VS. In B, the lateral parietal cortex also contains dense clumps of transported tracer. Label in the myelin light invaginations of area 1/2 into 3b is quite dense and label in myelin dense 3b is moderate to light. Other patches of transported tracer were in SMA, and the frontal ventral area, FV. Small dots denote anterogradely transported tracer and large dots denote retrogradely transported tracer. M, medial; R, rostral. Other conventions in list of abbreviations.


A
188
SMA
1/2
3a
3b
4
SII
LP
MT
FV
PV
A-I
VS
M
R
1mm
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SMA
1/2
3b
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SII
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Figure 12

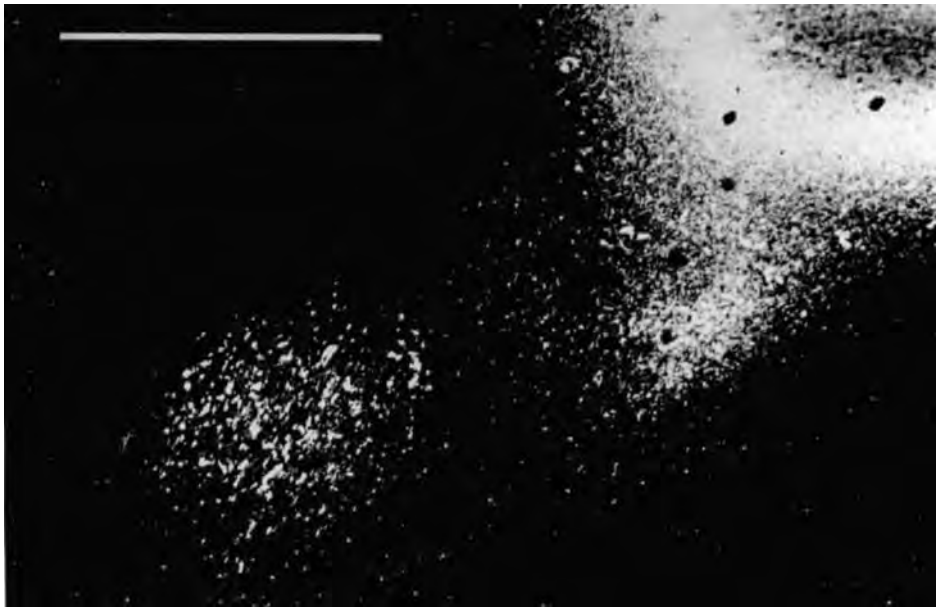

Fig. 13. A darkfield photomicrograph of a portion of a WGA-HRP injection in SII and resulting transported tracer in VS. Labelled cell bodies in VS are moderately to densely packed. Scale bar equals 1 mm.

face, respectively. Again, transported tracer was dense in area 1/2 and area 1/2 invaginations, and sparse in area 3b. An injection in the cheek representation in SII retrogradely labelled neurons in middle and lateral portions of area 1/2, in representations of the cheek, forelimb, D1, and vibrissae, and lightly labelled the snout and D1 representations in area 3b (Figs. 15, 16).

Connections of SII with 3b and area 1/2 were topographically matched with the representation injected in SII, but adjacent body part representations in 3b and area 1/2 were also labelled. The best example of this is from case 199 (Fig. 15) where extensive microelectrode mapping was carried out in area 3b and 1/2 on the day of perfusion so that connections from SII, PV, and VS could be accurately related to specific body part representations of 3b and area 1/2. Injections in the cheek representation in SII resulted in dense, retrogradely labelled cells in the cheek and upper lip vibrissae representations in area 1/2, and in sparsely labelled cells in the snout and naris representations in area 3b. Additional patches of retrograde label were noted in the forelimb and D1 representations in area 1/2 and the D1 representation in area 3b. In all cases transported tracer in the 3b region resulting from injections in SII was found predominantly in the myelin light regions coextensive with rapidly habituating neurons of area 1/2 (Figs. 11–16). Only sparse label was found in the myelin dense zones considered to be 3b proper.

Other connections of SII. Retrograde, or both retrograde and anterograde, label was consistently found in a myelin dark oval rostrolateral to area 4 (Figs. 12B, 14B, 16). The relative position and size of this myelin dark oval is similar to the frontal eye field or the frontal ventral eye movement field described in primates (Huerta et al., '87; Kaas and Krubitzer, '88; Krubitzer and Kaas, '90b). Also, label was found medial to area 4, in SMA. The amount of transported tracer observed in SMA was moderate to sparse (Figs. 12B, 14B, 16). Finally, in one of the three cases (189), transported tracer was noted in area 3a, just rostral to 3b (Fig. 14B). This consisted of moderately dense bidirectionally transported tracer found in medial portions of 3a, at the same mediolateral level as label in 3b and area 1/2. Since label in area 3a was not found in any other cases that received an SII injection, it is possible that it is the result of the slight spread of the injections into PV (Fig. 10B), which does have connections with 3a (see below).

Connections of PV

The parietal ventral area, PV, was injected in two animals (Table 1). In one animal, 199 (Fig. 15), an injection of fluorogold was centred in the representation of the neck, and spread into adjacent representations of the snout, forelimb, shoulder and digits. In the second case, 186 (Fig. 17), an injection of WGA-HRP was centred in the representation of the forelimb, and spread into adjacent representations of neck, trunk, digits and hindlimb. In case 199, where the injection was centred in the representation of the neck, intrinsic connections were observed in cortex far lateral in

Fig. 14. A reconstruction of an injection of WGA-HRP centred in the hindlimb representation of SII in case 189 that illustrates superficial anterograde label (**A**) and the entire pattern of connections of SII (**B**). Superficial anterogradely labelled axon terminals (A) are more broadly distributed 2–4 mm from the injection site than deeper patterns of anterograde and retrograde label. In B, dense patches of transported tracer are in PV, VS, and LP. Area 1/2 also contains dense patches of transported tracer while darkly myelinated 3b contains moderate to light patches of transported tracer. Additional label is present in SMA and FV, and a small patch of label is in area 3a. M, medial; R, rostral. Other conventions in list of abbreviations.

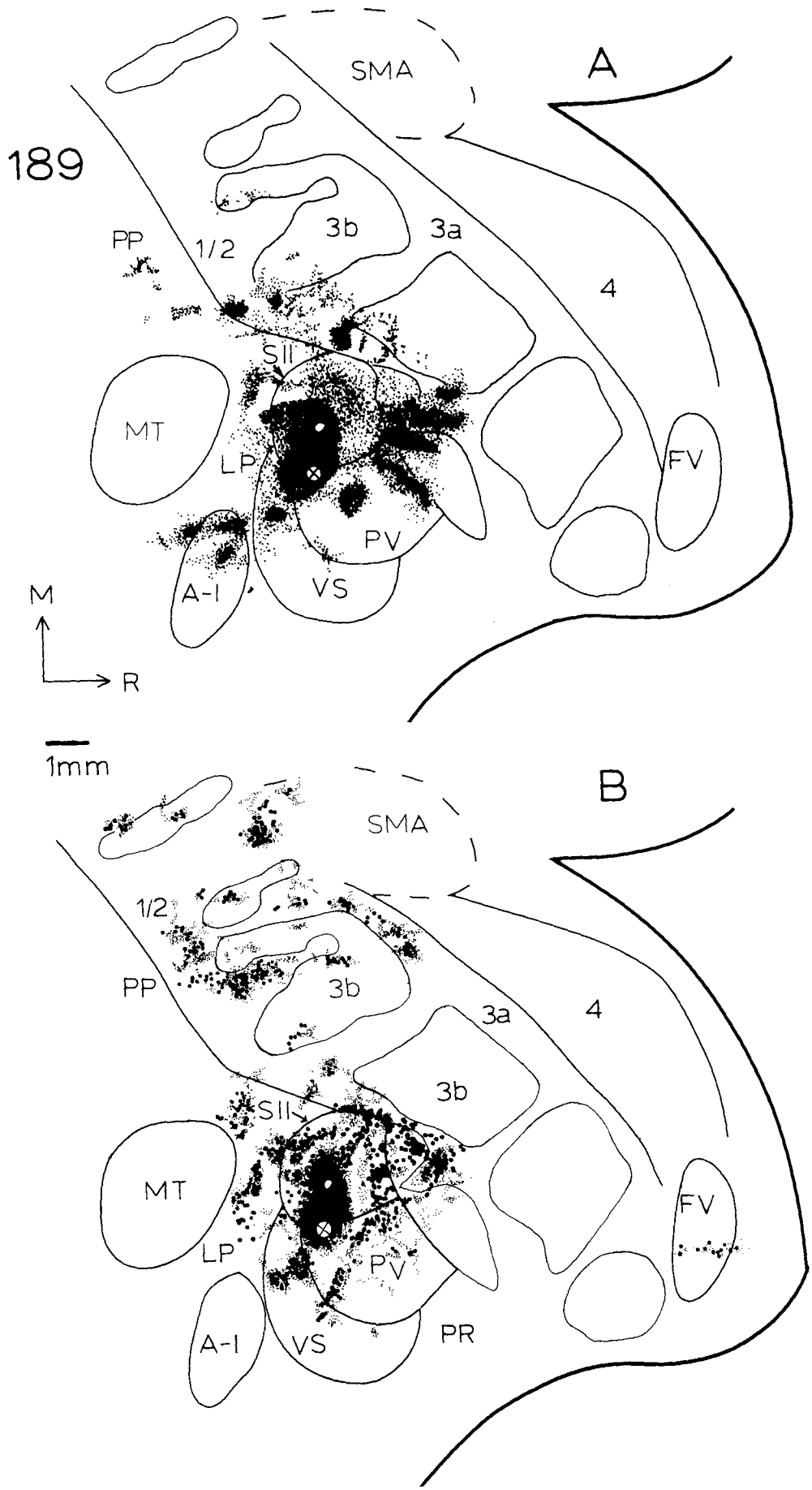
A
189
SMA
PP
1/2
3b
3a
4
SII
MT
LP
FV
PV
A-I
VS
M
R
1mm
B
SMA
1/2
PP
3b
3a
4
3b
SII
MT
FV
LP
PV
A-I
VS
PR

Figure 14

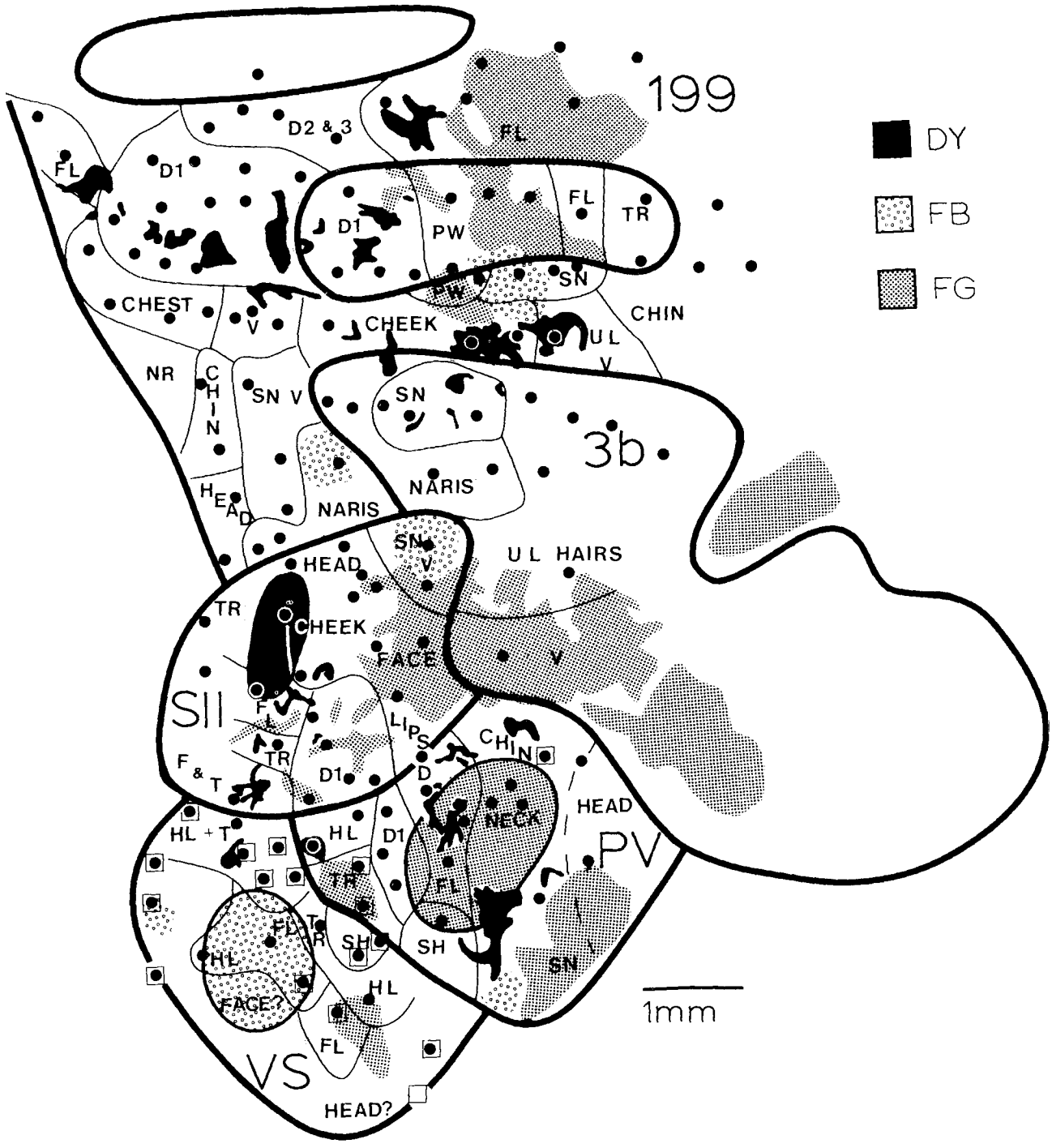

Fig. 15. A graphic reconstruction of transported tracer and injection sites from case 199 in relation to microelectrode mapping in areas 3b and 1/2 in the same case. Sixty-nine recording sites helped identify the boundaries between SII, PV, and VS prior to the injections of anatomical tracers. In this case, diamidino yellow was injected in the cheek representation of SII, fast blue was injected in the face and forelimb representations in VS, and fluorogold was injected in the neck and forelimb representations in PV. Connections of SII, PV, and VS with 3b and area 1/2 are topographically matched for the representation injected. However, connections are also with distant unrelated body part representations. Note that SII is more densely connected with area 1/2, while PV has stronger connections with 3b. Filled circles mark electrode tracks in areas 3b and 1/2. VS has only sparse connections with area 1/2. NR, no response. Other conventions in list of abbreviations.

PV, in the representation of the snout and head. A smaller patch of transported tracer was observed caudomedially, in the representation of the trunk.

Like injections of WGA-HRP in SII, injections of WGA-HRP in PV resulted in two patterns of transported tracer in surrounding fields. Dense superficial anterograde label was

broadly distributed in surrounding regions of cortex including SII, VS, and PR (Fig. 18A). Labelled axon terminals were also noted in LP, 3b, PP and area 1/2. Overall patterns of supragranular anterograde label for both SII and PV injections were most dense in cortex 2–4 mm from the injection sites, were more broadly distributed locally than granular and infragranular label, and often were in areas that were not labelled in deeper layers of cortex.

Connections with SII, VS, and PR. In middle and deeper layers of cortex (granular and infragranular layers respectively), transported tracer was observed in roughly matched topographic locations in SII. In case 199, where the injection was centred in the representation of the neck (Figs. 15, 16), retrogradely labelled cells in SII were most dense in the representation of the face, and smaller patches of transported tracer were observed in the digit, forelimb and trunk representations of SII (Fig. 15). A small patch of labelled cells was also noted in VS in the forelimb, hindlimb, and head representations. An injection centred in the forelimb representation in PV in case 186 (Figs. 17, 18B) resulted in a large patch of anterograde and retrograde label in the forelimb and digit representations in SII (Fig. 17). Lighter patches of bidirectionally transported tracer were observed in the finger membrane, foot and toe, and hindlimb representations as well (Fig. 17). Also, in case 186, bidirectionally transported tracer in VS was scattered throughout the field, and found predominantly in hindlimb, forelimb, and trunk representations.

In cases 186 and 199, clumps of transported tracer were noted within the parietal rhinal area, just lateral to PV (Figs. 16, 18B), and in case 186, anterograde and retrograde label was moderately dense (Fig. 18B). In the other case (199), retrograde label was very dense (Fig. 16). In both cases, additional label was noted in cortex lateral to VS (Figs. 16, 18). Patches of retrograde label were found in pyriform and hippocampal cortex only in case 199 (Fig. 16). It is possible that the larger injection is responsible for these additional connections noted with pyriform and hippocampal cortex. Connections between PV and pyriform and hippocampal cortex may be very sparse and uneven in distribution and a large injection may be required to reveal them. Another possibility is that representations of the face in PV relate strongly to pyriform and hippocampal cortex, while representations of the forelimb do not.

Connections with 3b, area 1/2, and 3a. Dense connections were observed between PV and 3b. Connections with 3b were both topographically matched and mismatched to representations injected in PV. Injections centred in the neck representation in PV retrogradely labelled cells in lateral portions of 3b adjacent to SII and PV (Figs. 15, 16) in the representation of the vibrissae and upper lip hairs. Labelled neurons were also noted in a more medial portion of 3b where the prowing, digits, and forelimb are represented. Injections in the forelimb representation of PV (Figs. 17, 18) resulted in labelled cell bodies and axon terminals in medial portions of 3b, in the approximate location of the forelimb representation (see Fig. 1). A small patch of labelled cells and terminals was also noted in a lateral portion of 3b where the face is represented.

Light patches of retrogradely transported tracer were found in the myelin light, rapidly habituating invaginations of area 1/2 into area 3b in one case where the neck/forelimb representation was injected (Figs. 15, 16). This label was in the representations of the prowing, forelimb, and cheek of area 1/2. In the second case, where the forelimb representation in PV was injected, anterograde and retrograde label was in a far medial location in area 1/2, just caudal to the label in area 3b, in the expected location of the forelimb representation (Fig. 1). Thus, in both cases, connections between area 1/2 and PV were sparse to moderate and topographically matched.

Injections in PV resulted in label in cortex rostral to 3b, in area 3a. Connections between PV and 3a were to topographically matched and mismatched locations. Injections in the neck representation in PV (Figs. 15, 16), labelled middle and lateral portions of 3a immediately rostral to label in 3b. Injections in the forelimb representation in PV (Figs. 17, 18), labelled more medial portions of 3a in cortex immediately rostral to label in 3b. In both cases PV was sparsely connected with SMA (Figs. 16, 18).

Other connections of PV. Other connections of PV were inconsistent between the two cases. In the case where the neck representation was injected, large patches of transported tracer were in pyriform cortex and hippocampal cortex. The injection centred in the forelimb representation in PV (Fig. 18), had additional label in auditory cortex, in cortex immediately caudal to SII and in posterior parietal cortex. Responses to auditory as well as somatosensory stimulation were found in neurons in caudal portions of PV where the limbs are represented. Neurons in rostral portions of PV generally did not respond to auditory stimulation. Label in auditory cortex in case 186 (Fig. 18), but not in case 199 (Fig. 16) may be the result of injecting portions of PV that also respond to auditory stimulation.

Connections of VS

The connections of the ventral somatosensory area, VS, were investigated in one case, 199 (Figs. 15, 16), where an injection of fast blue was placed in the representation of the forelimb and part of the face. There was some spread into other portions of the face and hindlimb representations (Fig. 15). Labelled cell bodies were noted in both SII and PV. Connections with SII were in a far rostral location, where the snout is represented, and connections with PV were in a caudolateral location, where the snout is represented (Fig. 15). Patches of retrogradely transported tracer were in a far lateral location in area 1/2, where the naris is represented, and in the portion of 1/2 that invaginates into area 3b, in the representations of the snout (Fig. 15). No label was noted in myelin dense 3b.

Large clumps of labelled cells were present in rostral temporal cortex. One patch of labelled cells was adjacent to the caudal boundary of VS (Fig. 16). This region of cortex contains neurons responsive to auditory stimulation (see Fig. 1). Another clump of labelled neurons was rostrolateral in temporal cortex, just medial to the rhinal sulcus in entorhinal cortex. Finally, several small patches of transported tracer were found in a lateral portion of pyriform cortex.

Connections of LP

In one animal, an injection was placed just caudal to SII (Fig. 19), in the lateral parietal area, LP. Patterns of connections of LP differed greatly from those in other somatosensory fields in that densely transported tracer was widely distributed throughout the cortex. In this case, the injection was placed in a portion of LP where neurons responded to proprioceptive stimulation of the head and neck. In some cases, neurons in LP responded to both somatosensory and visual stimulation or somatosensory


H
cc
199
DY
FB
FG
SMA
1/2
M
R
3a
4
PP
3b
FV
SI
17
LP
PV
18
PR
A-I
MT
VS
PYRIFORM
T
1mm
H

Figure 16

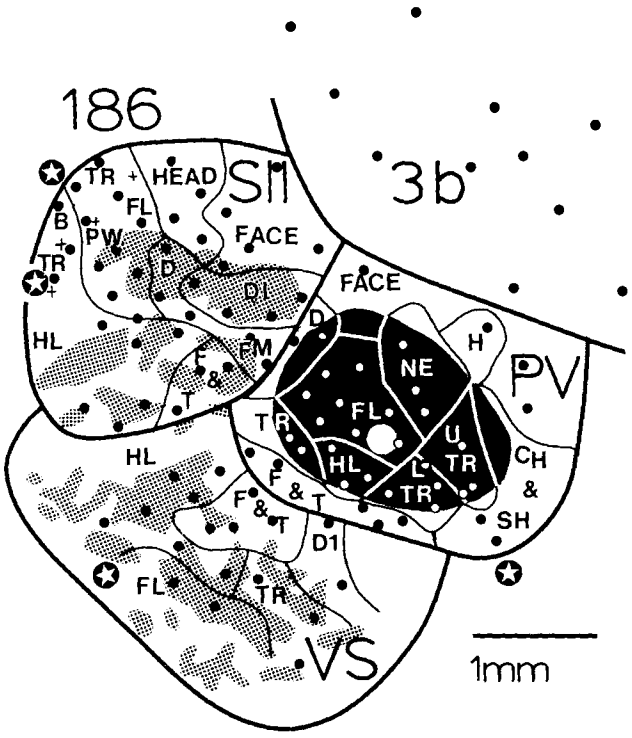

Fig. 17. A graphic reconstruction of an injection in the forelimb representation in PV and transported tracer in adjacent fields from case 186 in relation to microelectrode mapping. Forty-eight recording sites helped identify the boundaries of PV prior to the injection of WGA-HRP. The injection in PV labelled adjacent digit, finger membrane, and forelimb representations in SII. Label was also in the hindlimb and trunk representations of SII. Label in VS was in forelimb, hindlimb, and trunk representations. Little or no label was in the foot and toe or D1 representations of VS. Starred circles mark lesions at electrophysiological boundaries. Conventions in list of abbreviations.

and auditory stimulation (see Fig. 1). The injection of WGA-HRP in LP resulted in dense anterograde and retrograde label throughout posterior parietal cortex (PP), and in caudal portions of temporal cortex. Label in PP was in dense clumps spanning its rostrocaudal extent. Connections with temporal cortex, although dense, were less dense than those observed with posterior parietal cortex. Label was restricted to caudal portions of temporal cortex, lateral to auditory cortex and rostral to area 18 of visual cortex. Dense connections were noted with the middle temporal visual area, MT, caudal to LP. SII, immediately rostral to LP, was densely labelled, and connections with auditory cortex, AI, were noted as well.

LP also had connections with other somatosensory fields. Area 1/2 had moderate amounts of label in its middle portion, while area 3b had only sparse connections at middle and lateral levels. Sparse label was also observed with middle and lateral portions of 3a. Moderately dense patches of label were in area 4 and SMA. The frontal ventral area was densely labelled so that transported tracer filled almost the entire field. Finally, a sparse patch of transported tracer was located just medial to 3b and another moderate patch of label was just medial to area 17, in cingulate cortex.

Fig. 16. An illustrated reconstruction of three different tracers injected in areas SII, PV, and VS in flying fox 199. The placement of tracers into different body part representations is illustrated in the previous figure. In this figure, the total pattern of connections of SII, PV, and VS are illustrated. Also, this case best illustrates the differences and similarities in connection patterns of SII, PV, and VS. M, medial; R, rostral. Other conventions in list of abbreviations.

DISCUSSION

The present investigation was not undertaken to provide yet another description of somatosensory cortical connections in a different mammal. Rather, we hoped to address more global issues about somatosensory processing networks in mammals, about the evolution of cortical fields, and about the importance of defining homologies across species. In the present investigation, the connections of areas 3b, 1/2, SII, PV, VS, and LP were investigated in grey-headed flying foxes by injecting anatomical tracers into electrophysiologically identified body part representations within these fields. Both physiological and architectonic boundaries were determined in cortex that was flattened and cut parallel to the cortical surface so that injections could be evaluated and the regions of cortex with transported tracer could be identified. Using this preparation, areal patterns of connections of fields can be visualized, often in a single section. We found that 3b had connections with adjacent areas 3a and 1/2, and with PV. Area 1/2 had connections with 3b, SII, and LP. Furthermore, our results indicate different patterns of connections for deep and cutaneous portions of area 1/2. SII was interconnected with PV, VS, LP, and area 1/2, and PV was interconnected with SII, VS, and 3b. Surprisingly, 3b was densely interconnected with PV, while area 1/2 was densely interconnected with SII. VS had connections with cortex in the temporal lobe, and LP was interconnected with posterior parietal cortex, rostral temporal cortex, and portions of motor cortex. Finally, laminar differences in patterns of connections were observed. Major connections of somatosensory cortex in the flying fox are summarized in Figure 20.

While this investigation produced many interesting results, we will focus on only some of these in the discussion. In the first part of the discussion we will describe the major interconnections of cortical fields and how they compare with connections of homologous fields in other mammals. In this section we hope to establish some homologies between areas in the flying fox and areas in other mammals. Next we discuss the importance of correctly establishing homologies across mammals. As a specific example, we argue that PV and SII may have been confused across studies and across mammals. We then discuss the possible significance of topographic and nontopographic connections in the neocortex. Finally we discuss the implications of our results for theories of the evolution of cortical fields.

Interconnections of anterior parietal cortex

Connections of areas 3b and 1/2 with area 3a. Injections of anatomical tracers into different electrophysiologically identified body part representations in 3b revealed connections with adjacent fields rostral and caudal to 3b. Limited microelectrode recordings rostral to 3b in closely related primates and more distantly related carnivores, reveal a field in which neurons respond to hard taps to the body surface and joint manipulation. This field, termed 3a, has been observed in squirrel monkeys (Kaas et al., '79),

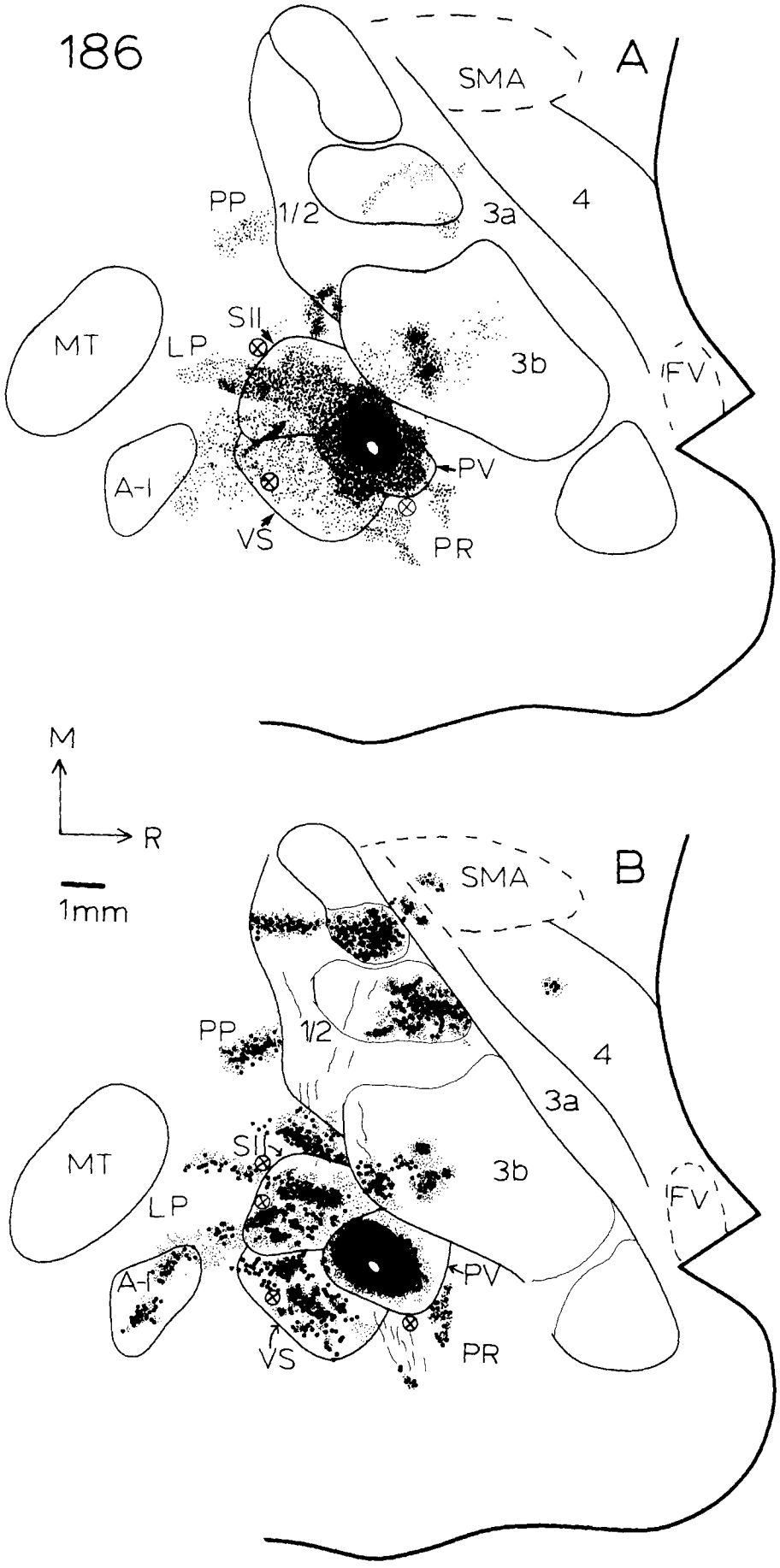
186
A
SMA
PP
1/2
3a
4
MT
LP
SII
3b
FV
A-I
PV
VS
PR
M
R
1mm
B
SMA
PP
1/2
4
3a
MT
SII
3b
LP
FV
A-I
PV
VS
PR

Figure 18

owl monkeys (Merzenich et al., '78; Kaas et al., '79), marmosets (Carlson et al., '86), macaque monkeys (Kaas et al., '79; Nelson et al., '80), prosimian lorises (Krishnamurti et al., '76; Carlson and Fitzpatrick, '82), prosimian galagos (Sur et al., '80a; Kaas, '82), tree shrews (Sur et al., '80b), and cats (Zarzeki et al., '78; Dykes et al., '80; Dykes and Gabor, '81; McKenna et al., '81; Felleman et al., '83). Surprisingly, there are no detailed maps of 3a in any archontan, and only partial maps have been made in cats (Dykes et al., '80; McKenna et al., '81). As in 3a of other mammals, neurons in the location of 3a in the flying fox are responsive to light pressure and hard taps to the body surface (Calford et al., '85; Krubitzer and Calford, '92; Finnigan et al., '92).

In the present investigation, injections into medial portions of 3b, where the hindlimb and trunk are represented, labelled medial portions of 3a, while injections placed progressively lateral in 3b, in representations of the forelimb and face, labelled more lateral portions of 3a. Connections between 3b and 3a have been described in primates (Jones and Powell, '69; Jones and Wise, '77; Vogt and Pandya, '78; Krubitzer and Kaas, '90c) and cats (Jones and Powell, '68). Connections between SI (3b) and cortex immediately rostral to 3b have also been reported in rodents (Akers and Killackey, '78; Krubitzer et al., '86; Paperna and Malach, '91), but this cortex has been defined as motor cortex (see Donoghue and Wise, '82; Donoghue and Parham, '83; Sanderson et al., '84).

Connections between area 1/2 and 3a in the flying fox were observed. However, while the injection centred in neurons responding to deep stimulation of peripheral body parts had very dense connections with 3a, injections into cutaneous portions of area 1/2 had few or no connections with 3a. We proposed in a previous investigation that area 1/2 was homologous to both area 1 and area 2 in primates, with the deep islands being a primitive, embedded form of area 2, much like area 1/2 is partially embedded in 3b. Strong connections between deep area 1/2 and 3a and sparse or no connections between cutaneous area 1/2 and area 3a support this idea. In primates, area 2 has dense connections with 3a while area 1 has sparse and inconsistent connections with 3a (Vogt and Pandya, '78; Pons and Kaas, '86).

In addition to connectional evidence for 3a, our investigation provided architectonic support for this field. In marmosets in which cortex has been flattened, cut parallel to the cortical surface, and stained for myelin, 3a has been described as moderately to lightly myelinated (Krubitzer and Kaas, '90c), especially compared to 3b. A similar appearance of 3a is observed in the flying fox. Taken together, electrophysiological, architectonic and topographically organized connections from electrophysiologically identified fields support the contention that the field rostral to 3b in the flying fox may be homologous with 3a as described in other mammals. However, extensive microelectrode mapping of 3a in the flying fox, as well as in primates and other mammals, is needed to define the overall organization of this field accurately.

Connections between 3b and area 1/2. Connections of 3b in the flying fox were observed with area 1/2, immediately caudal to 3b and invaginating into 3b. Connections between 3b and area 1 have been previously identified in primates (Jones and Powell, '69; Jones and Wise, '77; Vogt and Pandya, '78; Pons and Kaas, '86; Krubitzer and Kaas, '90c). Connections between area 2 and 3b have also been identified in macaque monkeys (Vogt and Pandya, '78; Pons and Kaas, '86). In carnivores such as cats, connections between SI and the caudally located SIII have also been reported (Jones and Powell, '68; Garraghty et al., '87), and in rodents such as squirrels, strong connections have been reported between SI and cortex immediately caudal to SI, the parietal medial area, PM (Krubitzer et al., '86). Similar patterns of connections have been reported in rats (Akers and Killackey, '78), although cortex caudal to SI is not always referred to as PM. In a recent investigation in rats, interconnections were noted between granular, SI cortex, and interdigitating dysgranular (DGZ) and perigranular (PGZ) cortex (Chapin et al., '87). Although rodents have been evolving independently from other Toketherian mammals for over 50 million years (Eisenberg, '81), these interdigitating dysgranular and perigranular zones in rodents may reflect the primitive precursor of area 1/2 described in flying fox (see Krubitzer and Calford, '92, for further discussion). We appreciate that evolutionary development is not a continuum (Hodos and Campbell, '69), and that the window in time provided by extant species is limited since tens of millions of years of independent evolution have occurred in major lines of descent. However, some features are retained in evolution, and extant mammals may reflect some features of their primitive ancestors. Interconnections between SI and cortex caudal to SI or interdigitating into SI suggest that area 1/2 in the flying fox may be homologous to SIII in cats, PM, or PGZ/DGZ in rodents, as well as area 1 and area 2 in primates. However, comparisons of topographic organization and response properties of neurons in fields caudal to SI in mammals cast some doubt as to whether these fields are homologous across species (see Krubitzer and Calford, '92, for further discussion). On the other hand, carnivores, archontans, and rodents have been independently evolving for at least 50 million years, certainly enough time for topographic organization and response properties to be altered. To assign homologies confidently to cortex caudal to SI in mammals, representative mammals from different branches of evolution need to be examined as well.

Connections between area 1/2 and posterior parietal cortex. Connections were observed between area 1/2 and cortex immediately caudal to area 1/2, which we term posterior parietal cortex. In rhesus and macaque monkeys (Vogt and Pandya, '78; Pons and Kaas, '86) connections between area 2 and cortex immediately caudal to area 2 have been reported. Traditionally, two architectonic subdivisions have been described for primates, area 5 or PE, immediately caudal to area 2, and area 7 or PG, caudolateral to area 5 on the inferior parietal lobule (Brodmann, '09; Von Economo, '29). More recently, these fields have been further subdivided (see Hyvärinen, '82; Andersen, '87). Area 5 receives input from anterior parietal cortex (Jones and Powell, '69; Vogt and Pandya, '78; Pons and Kaas, '86), and area 7 receives input from anterior parietal

Fig. 18. A reconstruction of a WGA-HRP injection centred in the forelimb representation in PV in case 186. This figure illustrates superficially labelled axon terminals (**A**) and the areal patterns of deeper anterograde and retrograde label (**B**) resulting from a PV injection. Dense connections are with SII and VS. The myelin dense portions of 3b contain dark patches of transported tracer while area 1/2 and 3a contain only sparse patches of transported tracer. Other label is in posterior parietal cortex, PR, LP, and AI. M, medial; R, rostral. Other conventions as in previous figures.

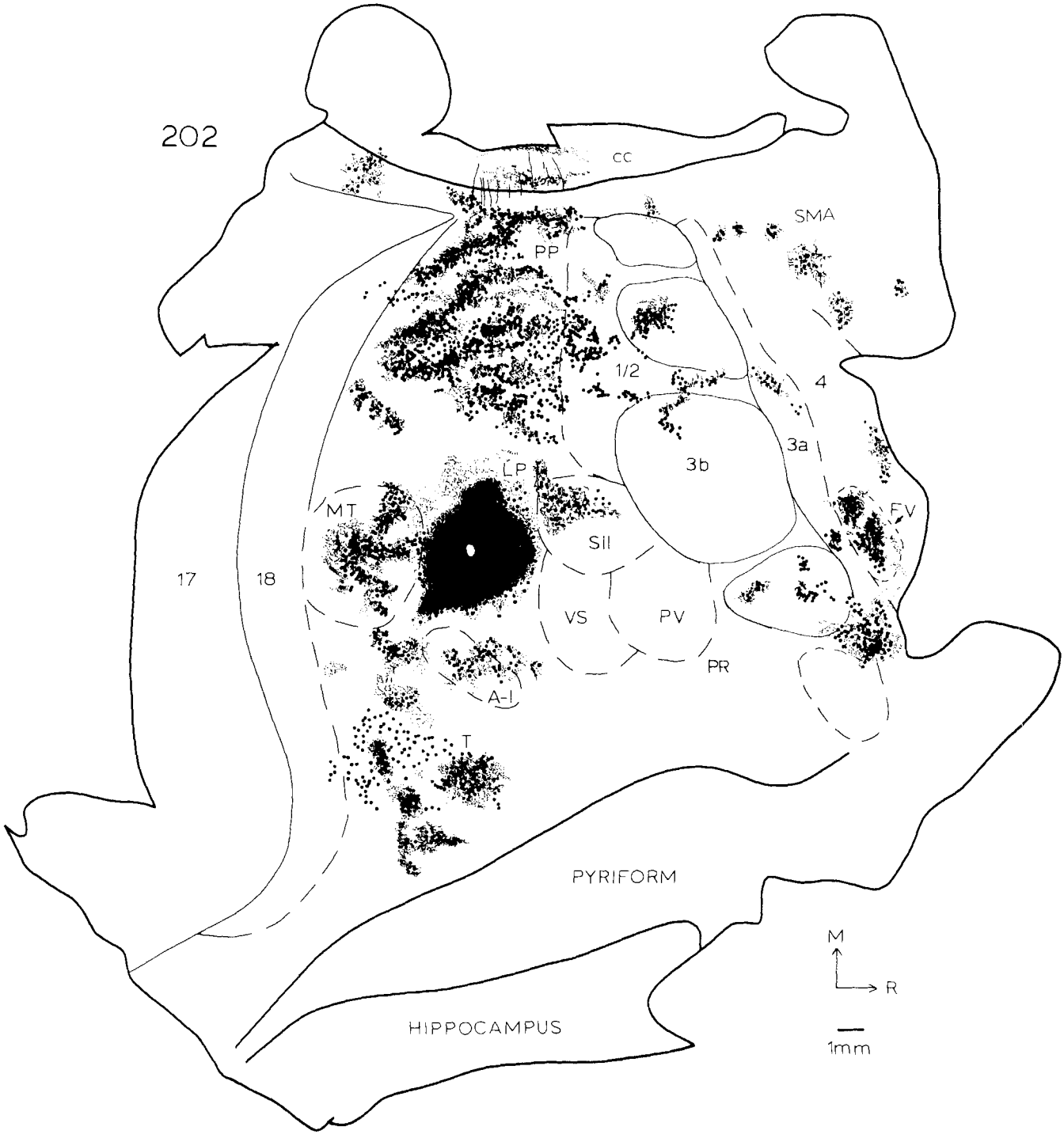

Fig. 19. A reconstruction of a WGA-HRP injection in the lateral parietal area, LP, of case 202. Resulting transported tracer was most dense throughout posterior parietal cortex. Posterior temporal cortex contained numerous retrogradely labelled cell bodies and anterogradely labelled axon terminals as well. Adjacent fields MT and SII were densely labelled. Sparse patches of label were in area 1/2, 3b, 3a, area 4, and SMA. Finally, FV was densely labelled. M, medial; R, rostral. Other conventions in list of abbreviations.

cortex and dense input from visual cortex (Cavada and Goldman-Rakic, '89a; Andersen et al., '90). The status of PP in the flying fox with respect to the larger subdivisions of posterior parietal cortex in primates (area 5 and area 7) is unclear.

Interconnections of anterior parietal areas with lateral somatosensory areas

Connections of 3b and area 1/2 with SII and PV. Injections into different electrophysiologically identified

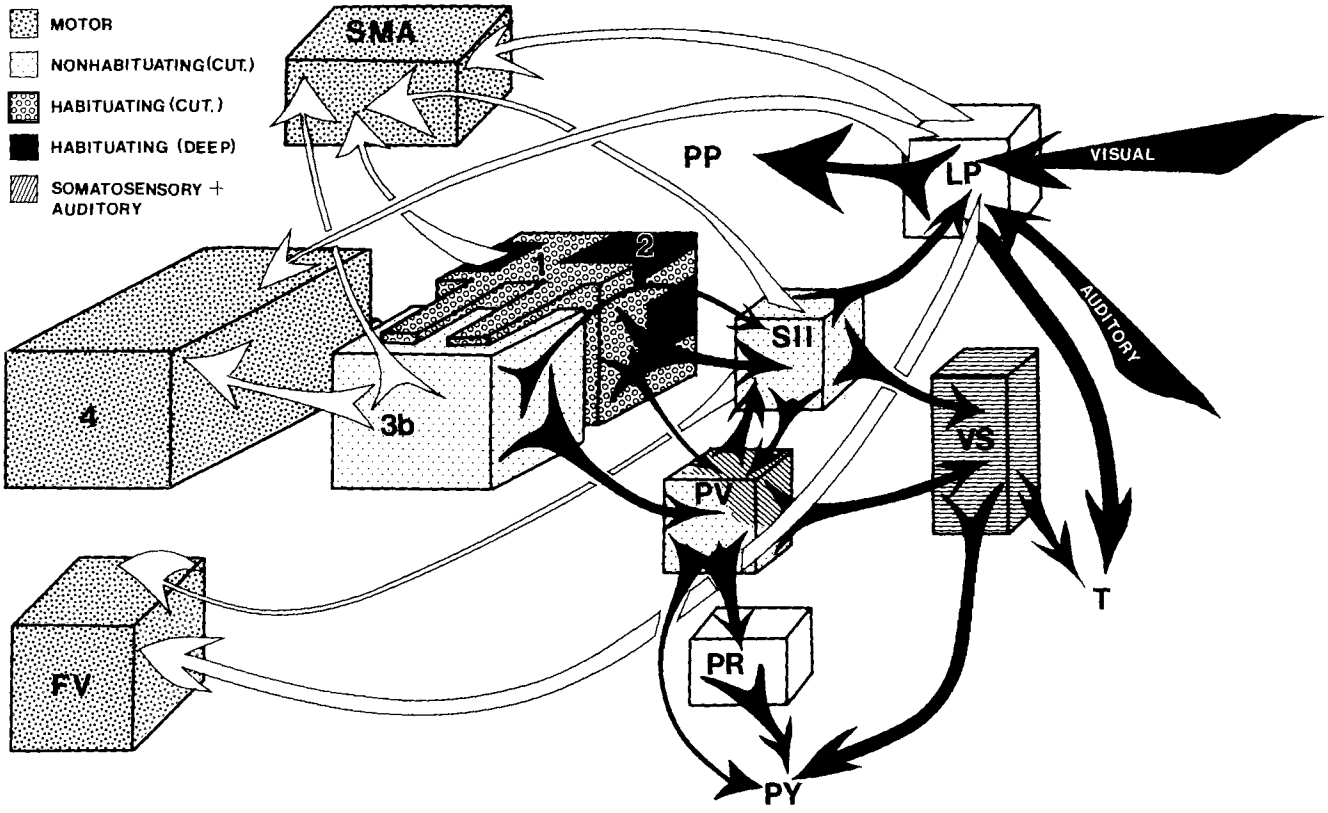

Fig. 20. A summary of the major connections of five somatosensory fields in the flying fox. Filled arrows denote connections with sensory fields and open arrows denote connections with motor fields. Note that although processing sequences are hierarchical, they are also distributed so that somatosensory information can be sent to posterior parietal, temporal, and motor areas of the neocortex via several different pathways. Cut, cutaneous. Other conventions in list of abbreviations.

body part representations in 3b labelled both SII and PV in small patches in portions of these fields where representations matched those injected in 3b. Injections into both the deep and cutaneous portions of area 1/2 resulted in dense patches of transported tracer in SII, and only the islands of deep representation in area 1/2 had connections with PV. Injections in SII resulted in dense connections with area 1/2 and only sparse connections with area 3b, while injections in PV resulted in dense connections with 3b and sparse connections with area 1/2.

Connections between SII, or the SII region, and the primary somatosensory cortex, SI (3b), have been reported for a number of mammals, including rodents (White and De Amicis, '77; Akers and Killackey, '78; Krubitzer et al., '86; Carvell and Simons, '87; Paperna and Malach, '91), carnivores (Jones and Powell, '68; Manzoni et al., '79; Graziosi et al., '82; Burton and Kopf, '84; Alloway and Burton, '85; Barbaresi et al., '87; Herron and Johnson, '87; Standage and Doetsch, '88), and primates (Jones and Powell, '69; Vogt and Pandya, '78; Friedman et al., '80, '86; Cusick et al., '89; Krubitzer and Kaas, '90c). However, at the time at which most of these studies were conducted, three important aspects of the organization of somatosensory cortex were not appreciated. First, the traditional "SI" is actually composed of four separate fields, 3a, 3b, 1, and 2. Second, the 3b region may not be a homogeneous region, but may actually be composed of either separate modules or interdigitating areas with differential connections. Third, the SII region contains more than one field. We now appreciate that only 3b should be termed SI across mammals (Kaas, '83), that SI in some mammals such as rats (e.g., Chapin and Lin, '84; Chapin et al., '87; Dawson and Killackey, '87), primates (Mountcastle and Powell, '59; Paul et al., '72; Hyvärinen and Poranen, '78; Sur et al., '84), megachiropteran bats (Krubitzer and Calford, '92), and cats (Mountcastle, '57; Rasmusson et al., '79; Dykes and Gabor, '81) is composed of functionally distinct neural groups (although the functional distinctions may be the result of parallel or convergent homoplasy rather than homology, Northcutt, '85), and that the region caudolateral to SI contains at least two and possibly three distinct fields (e.g., Clemo and Stein, '83; Krubitzer et al., '86; Cusick et al., '89; Krubitzer and Kaas, '90c; Krubitzer and Calford, '92).

When one examines earlier studies describing connections of 3b (SI) with SII, several features become apparent. In the first investigation describing connections between SI and PV and SI and SII, connections are clearly stronger between SI and PV in some cases (e.g., see Figs. 10 and 11, Krubitzer et al., '86). Second, in studies of SII connections in marmosets, connections with area 1 are denser than with area 3b, and the label in 3b is in the approximate location of the myelin light band separating the hand and face representations (see Figs. 17 and 18, Krubitzer and Kaas, '90c). Finally, in studies where connections from SI (3b) are used to define the topography of SII (e.g., Friedman et al., '80; Alloway and Burton, '85), "SII" has been described as an inverted representation, much like PV, suggesting that

connections from SI were actually with PV. Thus, our results demonstrating dense connections between PV and area 3b may be a general feature of most mammals.

Connections between 3b (SI) and PV have been reported for grey squirrels (Krubitzer et al., '86), rats (Fabri et al., '90); and New World marmoset monkeys (Krubitzer and Kaas, '90c). However, because PV has only been identified recently, earlier studies on connections of 3b may not have reported connections with PV. Connections between 3b and the general location of PV in primates (Ig cortex) have also been described (e.g., Jones and Powell, '69; Vogt and Pandya, '78; Mesulam and Mufson, '82).

Because the connection patterns between SI and a field lateral to SI in the general location of SII and PV have been well established in such a wide range of mammals, it is likely that this relationship is phylogenetically old and may be common to all mammals. Indeed, a recent investigation in monotremes demonstrates such a connection (Krubitzer et al., '91). However, because SII may have been misidentified in some species, it is uncertain whether this original field is homologous to SII or PV.

What is the "real" SII in mammals?

The existence of parallel, dense interconnections between 3b and PV and between area 1/2 and SII is a surprising result since it is generally supposed that one of the criteria for defining SII is a strong projection from SI (3b) (e.g., Akers and Killackey, '78; Friedman et al., '80; Alloway and Burton, '85; Barbaresi et al., '87). However, as suggested above, PV and SII may have been confused across studies and across species and evidence from several lines of research support this hypothesis. In some investigations, SII is described as an inverted representation of the body surface in mammals such as marsupials (opossum, Lende, '63), insectivores (Lende and Sadler, '67), rodents (porcupine, Lende and Woolsey, '56; mouse, Woolsey, '67; rat, Welker and Sinha, '72) carnivores (cat, Berman, '61; Burton et al., '82), and primates (macaque monkey, Friedman et al., '80; Pons et al., '88), while in other investigations, SII is described as an upright representation of the body surface in marsupials (opossum, Pubols, '77), rodents (squirrel, Nelson et al., '79; Krubitzer et al., '86; agouti, Pimentel-Souza et al., '80; mouse, Carvell and Simons, '86), rabbits (Gould, '86), carnivores (cat, Haight, '72; raccoon, Herron, '78) and archontans (tree shrew, Sur et al., '81; megachiropteran bat, Krubitzer and Calford, '92; galago, Burton and Carlson, '86; owl monkey, Cusick et al., '89; marmoset, Krubitzer and Kaas, '90c). Finally, in some investigations, SII has been described as somewhere in between inverted and non-inverted in cats (Clemo and Stein, '83) and monkeys (macaque, Whitsel et al., '69; Robinson and Burton, '80) (Fig. 21). Interestingly, in some of the same species (opossums, cats, and mice) SII has been alternately described as inverted and non-inverted by different investigators. We now know that PV rather than SII is an inverted representation. In some investigations, SII is reported as having some neurons that respond to auditory stimulation in mammals such as marsupials (Lende, '63; Magalhães-Castro and Saraiva, '71; Pubols, '77), rodents (porcupine, Lende and Woolsey, '56; mouse, Woolsey, '67; Carvell and Simons, '86; agouti, Pimentel-Souza et al., '80) and cats (Berman, '61), while in other investigations, SII neurons are only driven by cutaneous stimulation in mammals such as rodents (rat, Welker and Sinha, '72; squirrel, Nelson et al., '79; Krubitzer et al., '86), carnivores (cat, Haight, '72; Burton et al., '82; raccoon, Herron, '78) and archontans (tree shrew, Sur et al., '81; megachiropteran bat, Krubitzer and Calford, '92; galago, Burton and Carlson, '86; marmoset, Krubitzer and Kaas, '90c; owl monkey, Cusick et al., '89; macaque monkey, Whitsel et al., '69; Friedman et al., '80; Robinson and Burton, '80; Pons et al., '88). It has recently been appreciated that PV often has an auditory overlap zone while SII is purely cutaneous. Finally, in some mammals, lesions in SI deactivate SII (macaque, Pons et al., '87; marmoset, Garraghty et al., '90), and in other mammals lesions to SI have no effect on neural responses in SII (prosimians and tree shrew, Garraghty et al., '91; cat, Manzoni et al., '79; Burton and Robinson, '87; Burton et al., '88). While differences in thalamic input from VP to SII may account for differences observed, other sources of variation may account for differing results. First, "SI" is not being consistently defined across studies. Sometimes areas 3a, 3b, 1, and 2 were lesioned (Pons et al., '87), other times 3b, 3a, and "adjacent cortex" were lesioned (Garraghty et al., '90), and still other times 3b and adjoining areas 3a, 4, and 1 were lesioned (Garraghty et al., '91). Finally, in cats, only 3b was lesioned (e.g., Burton et al., '88). Another source of variation may arise from some investigators mapping SII after SI ablation and some investigators mapping PV after SI ablation. In our own mapping experiments, it often takes 20–40 electrode recordings to distinguish SII from PV. We now appreciate that in the flying fox and possibly all mammals, both SII and PV have differential connections, with 3b densely interconnected to PV, and area 1/2 densely interconnected to SII. Taken together, it seems highly likely that SII and PV have been confused across studies.

The question of defining the "real" SII has broad implications for subdividing neocortex in any mammal and assigning homologies across species. If we are to understand how the neocortex evolves in mammals, and how complex processing networks evolve from simpler forms, we must accurately assign homologies across species to make meaningful comparisons. The present investigation does not answer the question of which is the "real" SII or which field is phylogenetically older. The important issue is not which field, PV or SII, we call SII, but that we consistently assign the term SII to the same field across mammals.

Interconnections of lateral somatosensory fields

In all cases, there were dense, topographic interconnections between SII and the parietal ventral area, PV. Connections between SII and PV have been reported for the grey squirrel (Krubitzer et al., '86) and New World marmoset monkeys (Krubitzer and Kaas, '90c). In Old World macaque monkeys, cortex in the general region of PV, in granular insular cortex (Ig) is connected with SII (Mufson and Mesulam, '82; Mesulam and Mufson, '82; Friedman et al., '86). Connections between SII and cortex called SIV, which is in the general location of PV, have been described in cats as well (Burton and Kopf, '84). However, it is uncertain whether SIV and PV are homologous since the patterns of connections of these fields vary.

Dense connections were also noted between SII and the ventral somatosensory area, VS. Because VS has only been identified in one other mammal (owl monkey, Cusick et al., '89), it is difficult to make precise comparisons between the flying fox and other mammals. However, it has been proposed that VS may be homologous to SIV in cats

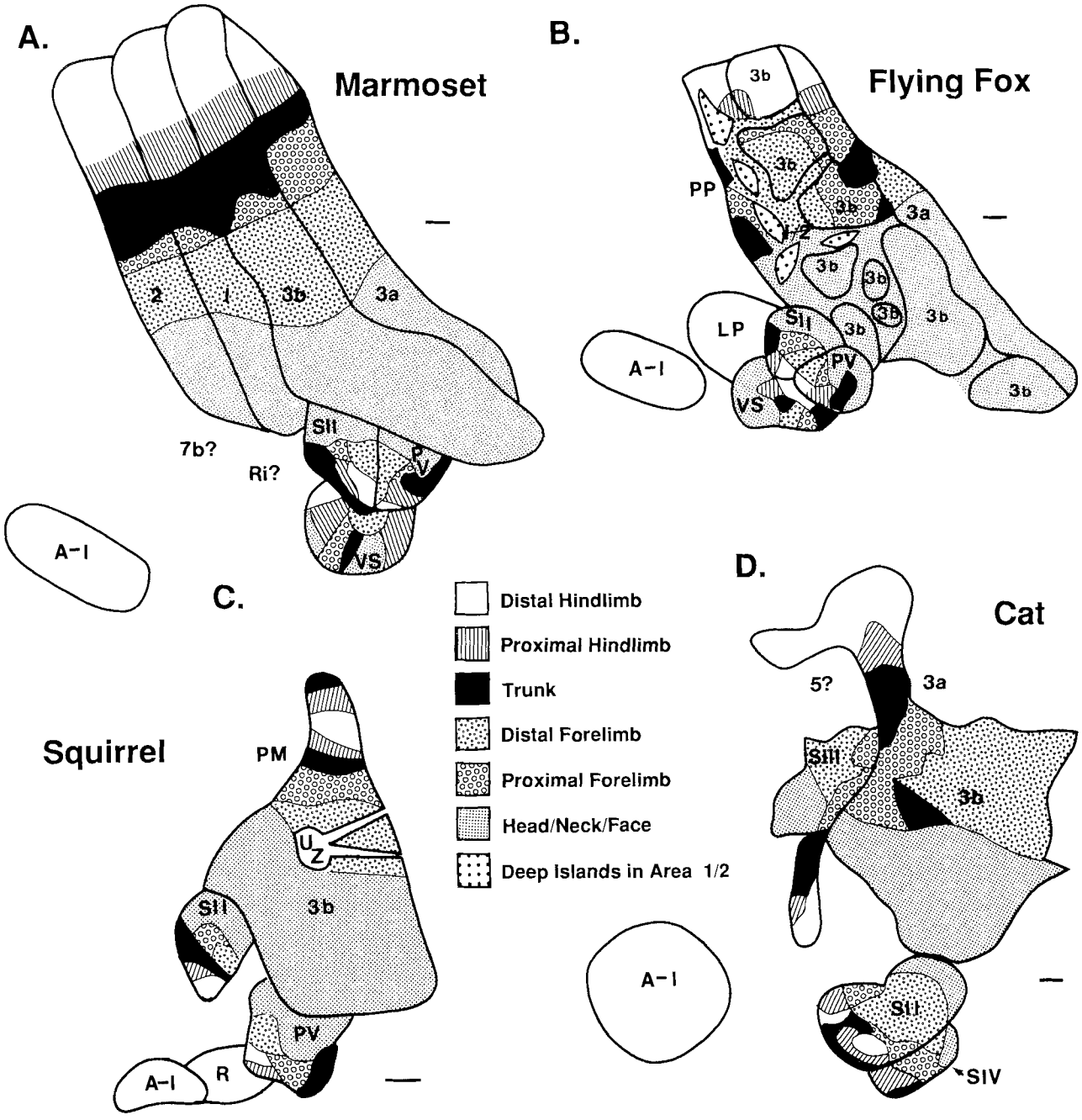

Fig. 21. A summary of the relative location and topographic organization of somatosensory fields in mammals from several major lines of evolution (**A–D**). At least two fields exist in cortex lateral to 3b in these mammals. Only in some mammals (A and B) is there a clear expansion of anterior parietal cortex. In all figures, rostral is right and medial is to the top. Scale bars equal 1 mm. Other conventions in list of abbreviations.

(Krubitzer and Calford, '92). VS is in the approximate location of SIV in cats (Fig. 21), the topography of VS and SIV are similar, both VS and SIV are responsive to auditory stimulation, and both VS and SIV receive dense input from SII, and have little or no input from SI.

Connections were consistently identified between PV and VS in the flying fox. Connections between PV and cortex in the general location of VS have been described in marmosets (Krubitzer and Kaas, '90c). In squirrels, cortex in the general location of VS is termed the rostral auditory field, R (Merzenich et al., '76) (Fig. 21). Although R has dense interconnections with PV in squirrels (Krubitzer et al., '86; Luethke et al., '88), neurons in R do not respond to somatosensory stimulation. It is possible that R and VS are homologous and that VS has gained responsiveness to somatosensory stimulation in the archonton line. An alter-

nate explanation is that R in squirrels, SIV in cats, and VS in flying foxes and owl monkeys are not homologous and that VS is a field that has only recently evolved in the archontan line. One way to resolve this issue is to examine a number of species from different lines of evolution.

The significance of interconnections between SII and PV and VS is unknown, but several lines of evidence suggest that VS is a "higher order" somatosensory area. First, receptive fields are larger in VS than in SII and PV (Krubitzer and Calford, '92). Second, VS receives no consistent projections from the primary somatosensory area or area 1/2. Third, neurons in VS respond to both somatosensory and auditory stimulation. Finally, VS has projections to entorhinal and pyriform cortex, and these regions are closely linked to hippocampal cortex. Thus, VS may be an area involved in somatosensory and auditory integration and may be part of the pathway involved in somatosensory recognition and the formation of memories.

LP connections. Dense connections were observed between area 1/2 and LP in the flying fox. Connections between area 1 and area 2 with area 7b, which is in the general location of LP, have been reported in primates (Jones and Powell, '69; Vogt and Pandya, '78; Pons and Kaas, '86). Connections between SII and lateral parietal cortex, LP, were consistent in all cases. Limited electrophysiological recordings in LP in the present investigation indicate that neurons respond to somatosensory, auditory, and visual stimulation. In some cases, proprioceptive stimulation of the head and neck evoked responses in LP. In a related study on the visual cortex, connections between MT and LP have been observed (Krubitzer and Calford, '90), and connections between auditory cortex and LP have also been identified in the present investigation. Hence, LP appears to be an association region of cortex where different sensory modalities converge. Connections of SII and area 1/2 with this field support this notion.

Injections in LP revealed very dense connections with both posterior parietal cortex and temporal cortex as well as with subdivisions of the frontal lobe. Connections are similar to those described for 7b in Old World monkeys (Cavada and Goldman-Rakic, '89a,b), where injections in 7b resulted in strong connections with more dorsal portions of PP, with temporal cortex, and with frontal cortex in the location of the frontal eye field and the frontal ventral area. However, the connections of LP in the flying fox and 7b in monkeys described by Cavada and Goldman-Rakic ('89a), differ markedly from connections of 7b recently described by Andersen and colleagues ('90). The relative location and cortical connections suggest that LP in the flying fox is homologous to 7b described in monkeys.

Topographic and nontopographic connections of somatosensory cortex

Our results provide evidence for both topographic and nontopographic connections of somatosensory cortex. One can imagine that topographic connections may serve to link different types of receptor input from the same body part (e.g., deep and cutaneous input from D1). However, the role of nontopographic connections is less clear. For instance, why would cutaneous digit representations have dense connections with cutaneous and deep representations of the face as in case 184? Or why would cutaneous digit representations have connections with head, trunk, and toe representations? There is evidence that the organization of the representation in SI is dependent on the animal's normal body position in space since variant postures (e.g., in the flying fox) result in variant representations in SI cortex (Calford et al., '85). Apparently, sensory maps contribute to the proprioceptive sense. Nontopographic connections of cortical representations would be required to integrate the somesthetic sense of the entire body. If an animal desired to touch a particular body part with another body part, it would need to have an integrated sense of the limbs to know where to target the movement, and it would need to know that the task was accomplished. Nontopographic connections in cortex may contribute to an integrated sense of the limbs.

Can laminar differences in patterns of connections help build processing hierarchies?

Patterns of connections in this study add to accumulating evidence that superficial anterograde connections are not equal to deeper patterns of anterograde and retrograde connections. All connections do not appear to be reciprocal (e.g., Krubitzer and Kaas, '89, '90b). For the past decade, investigators have worked on the premise that laminar patterns of connections can help build processing hierarchies in the neocortex (see Van Essen and Maunsell, '83, for review). Rockland and Pandya ('79) observed that laminar patterns of connections vary for different cortical fields and that some patterns (feedforward) reflect termination patterns of the thalamus onto cortex and therefore must serve to drive the field. Patterns of termination to superficial layers of the "driving" field from other fields reflects feedback information to the "driving" field. Areas that feedforward to cortical areas and receive feedback from these areas are lower on the processing hierarchy of sensory information. From this notion, complex processing hierarchies have been proposed for visual cortex (e.g., Van Essen et al., '92). One important tenet of this theory is that connections between cortical fields are reciprocal (Van Essen and Maunsell, '83). The present investigation does not support this contention. Although hierarchies may exist in cortical processing networks, laminar patterns of connections may not always define them. Superficial connections may serve to strongly modulate surrounding cortex, regardless of whether it receives input from the field. However, describing these connections as feedback would be a misnomer.

Connections of SII and PV with area 3b and area 1/2 invaginations, and implications for theories on evolution of cortical fields

In a previous investigation in the flying fox, functionally and architectonically distinct neural groups in 3b were identified (Krubitzer and Calford, '92). It was found that neurons in myelin dark and myelin light regions in 3b were related to nonhabituating and habituating neural responses, respectively. We do not interpret these results as evidence for a "modular" 3b, but instead propose that the geometric limits of the region containing 3b incorporate two functionally, architectonically, and connectionally distinct sets of neurons, those distinguished as SI proper (3b) and invaginations of a separate field, area 1/2, into 3b. This is different from a "modular" organization in SI in that topography within these invaginations is continuous with area 1/2. Indeed, without these invaginated parts, the topography of area 1/2 would be incomplete. The present investigation provides further evidence for the segregation

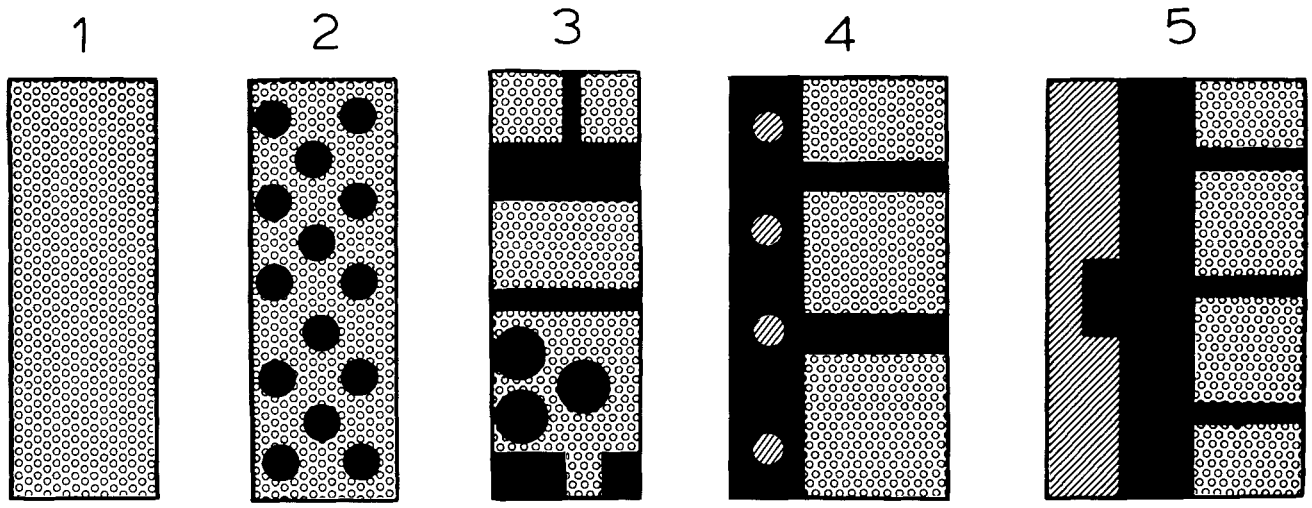

Fig. 22. An illustration depicting our hypothesis of the evolution of a cortical field. Fields may begin as homogeneous (**1**), and with an invasion of new afferent input (**2**), become modular. These modules may then begin to aggregate (**3** and **4**), and eventually completely segregate into new cortical fields (**5**). That all of these stages can and often are observed in the neocortex of extant mammals provides support for this hypothesis.

of the 3b region by showing differential connections of areas 1/2 and 3b.

A good example of functional segregation in SI has been demonstrated in rodents. Neurons in SI that respond to cutaneous and deep stimulation have been related to granular and dysgranular regions of cortex respectively (Chapin and Lin, '84; Chapin et al., '87). Although the heterogeneity of SI has been appreciated in rats for some time, no attempt has been made to distinguish between the connections of granular and dysgranular SI with SII. In the grey squirrel, myelin light and dense zones were noted (Krubitzer et al., '86), but differences in connections of myelin light and dark regions of SI with other fields were not reported. In marmosets, myelin light and dense regions have been identified, but the relationship of the myelin light and dense regions to different neural groups has not been established. However, differences in callosal connections of these myelin dense and light regions have been described (Krubitzer and Kaas, '90c). Furthermore, myelin light and dense regions have been observed in 3b in owl monkeys and Old World macaque and talapoin monkeys (personal observations), but have not been related to physiological response properties of neurons. In addition to observed architectonic distinctions, segregation of neural response properties have been noted in primates (Mountcastle and Powell, '59; Paul et al., '72; Hyvärinen and Poranen, '78; Sur et al., '84) and carnivores (Mountcastle, '57; Rasmusson et al., '79; Dykes and Gabor, '81). Thus, heterogeneity in SI, such as that described in the flying fox, may exist to a greater or lesser extent in a wide range of mammals.

Examples of modular segregation are found in other sensory systems in a variety of mammals. For instance, functional segregation, coextensive with architectonic distinctions and connectional distinctions has been described for VI and VII in primate neocortex (e.g., Livingstone and Hubel, '84; De Yoe and Van Essen, '85; Shipp and Zeki, '85; Hubel and Livingstone, '87; Krubitzer and Kaas, '89, 90a,b). In addition, aural dominance bands associated with differential connections have been described in cats (Imig and Adrián, '77; Imig and Brugge, '78; Middlebrooks et al., '80). In many examples of modularity, heterogeneities observed within a field have always been attributed to a single field. We propose that the heterogeneity in 3b in the flying fox is actually an intermediate state between modular segregation within a field, analogous to granular and dysgranular zones in rodents, and the almost complete segregation of anterior parietal fields observed in primates (Fig. 22). We believe that modular segregation within a field may eventually lead to complete segregation of fields. Thus, the evolution of cortical fields is not a spontaneous phenomenon, but is a continuum of modular segregation, partial separation, as seen in the flying fox, and perhaps eventual complete segregation as seen in primates (Fig. 22). It is important to note that any stage can be, and often is, observed in extant mammals, and that moving from a modular stage to a completely segregated stage does not imply that a particular cortical area is "more evolved" than a cortical area at an earlier stage. It means there was no selective pressure for modules within a field to completely segregate. Indeed, there may be selective pressure to preserve modules to maintain discreteness of representations such as barrel fields in SI of mice and rats or blobs in VI of primates. One of the most important implications of this theory is that new cortical fields gradually evolve from existing cortical fields and therefore are not added hierarchically. "Newer" or more recently evolved fields are likely to be interspersed among phylogenetically older fields.

Like our theory of neocortical evolution, the parcellation theory (Ebbesson, '80, '84) proposes that cortical fields evolve by the gradual segregation of existing fields. However, Ebbesson proposes that cortical fields evolve by the selected loss of existing diffuse, undifferentiated connections. We believe that an invasion of new correlated afferent inputs is responsible for initial modulation of a field and eventual segregation. It is possible that a combination of thalamic, ipsilateral, and contralateral cortical connections defines a cortical field. If this were so, only a slight change in any of these inputs would be necessary to reweight all

inputs, resulting in a large change in the final outcome, a new or different cortical field. There is evidence in developing mammals that cortex can be assigned a functional role by incoming thalamic input (Roe et al., '90; Schlaggar and O'Leary, '91).

CONCLUSIONS

Our results lead to several conclusions about the organization and connections of somatosensory cortex in the flying fox. Since many similarities exist between somatosensory cortex in the flying fox and other mammals (Krubitzer and Calford, '92), these conclusions may be generally applicable to all mammals. First, our results support the notion that area 3b is not a homogeneous field, but is composed of a myelin dark region (homologous to SI proper), and myelin light invaginations of area 1/2 into 3b, by demonstrating differential connections of these areas. Second, deep islands in area 1/2 have somewhat different connections from cutaneous islands, some of which are similar to area 2 described in primates. Thus, area 1/2 may be a reflection of a primitive form of both area 1 and area 2. Third, PV, rather than SII has stronger connections with 3b. If one defines SII as the recipient zone of inputs from 3b (SI), as is often the case (e.g., Akers and Killackey, '78; Friedman et al., '80; Graziosi et al., '82; Alloway and Burton, '85; Barbaresi et al., '87), then PV rather than SII may be the "real" or homologous SII region across mammals. It is likely that PV and SII have been confused across studies and animals. Fourth, patterns of connections are both topographic and nontopographic. Both types of connections may contribute to the general proprioceptive sense of the animal. Fifth, there are laminar differences in connection patterns of SII and PV. Although processing hierarchies in cortex are likely to exist, laminar patterns of connections may not define them in all instances. Rather, there appears to be a strong modulation of adjacent cortex (within 2–4 mm) regardless of whether adjacent areas provide input to the area of cortex injected. Finally, these results support the hypothesis that an individual cortical field may evolve by a gradual aggregation and eventual segregation of functionally distinct neural groups within a field, and that "modules" within a cortical field may be a stage in the evolution of a new cortical field.

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