

Multiple Somatosensory Areas in the Anterior Parietal Cortex of the California Ground Squirrel (*Spermophilus beecheyii*)

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ABSTRACT

Multiunit electrophysiological recording techniques were used to explore the somatosensory cortex of the California ground squirrel (*Spermophilus beecheyii*). Cortex rostral and caudal to the primary somatosensory area (SI) contained neurons that responded to stimulation of deep receptors and to muscle and joint manipulation. The region of cortex rostral to SI was termed the rostral field (R) because of possible homologies with a similar field described in other mammals. Cortex caudal to SI had neurons that responded to stimulation of deep receptors and has been termed the parietal medial area (PM), as in previous investigations in squirrels. Like SI, both R and PM contained a complete or almost complete representation of the body surface, although the receptive field size for clusters of neurons in these regions was somewhat larger than those for clusters of neurons in SI. Electrophysiological recording results were correlated with histologically processed tissue that had been sectioned tangentially. Although SI was clearly identified as a myelin-dense region, both R and PM stained much less densely for myelin. Our results indicate that as in a number of other mammals including monotremes, marsupials, carnivores, and primates, the anterior parietal cortex of the California ground squirrel contains multiple representations of the sensory epithelium. This work, as well as a growing body of studies of somatosensory cortex organization in a variety of mammals, indicates that anterior parietal fields other than SI existed early in mammalian evolution, and were present in the common ancestor of all mammals. *J. Comp. Neurol.* 416:521–539, 2000. © 2000 Wiley-Liss, Inc.

Indexing terms: parietal medial area; SI; area 3a; area 2; area 1; evolution

The concept that some cortical fields are older or more primitive than others originated from early architectonic studies that demonstrated the ubiquity of certain fields (e.g., areas 17, 3, and 41; the primary sensory fields) across mammalian species (Brodmann, 1909; Vogt and Vogt, 1919; von Bonin and Bailey, 1961; see Krubitzer, 1995 for review). Other areas were only identified in mammals with large brains, and thus were believed to be more recently evolved. Comparative studies in which the functional organization of the brain was explored appeared to support these early architectonic studies (Abbie, 1938; Adrian, 1941; Lende and Sadler, 1967; Lende, 1969). Indeed, the presence of only primary areas in some species led to the assumption that primary fields must be evolutionarily older, and that other fields differentiated later in the evolution of the mammalian cerebral cortex. These newly evolved fields were proposed to play a more sophisticated role in sensory processing than primary fields.

Historically, the evidence for primacy of processing may appear compelling, but the identification and importance of primary areas was due in part to precedence of discovery (Woolsey and Fairman, 1946), and to less refined recording techniques. Primary areas are relatively large, are typically located on the dorsal surface of the cortex in gyrencephalic brains, and contain neurons that are readily driven using simple stimuli, even in the anesthetized animal. Therefore, it is not surprising that they were the first fields to be described.

Probably the best piece of evidence to support the contention that primary fields are evolutionarily the oldest

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fields comes from early studies in species whose ancestral lineage became distinct early in evolution, such as monotremes (Lende, 1964; Bohringer and Rowe, 1977), marsupials (Lende, 1963, 1969), edentates (Meulders et al., 1966; Royce et al., 1975; Saraiva and Magalhães-Castro, 1975), and insectivores (Lende and Sadler, 1967). In these studies, only a single auditory, anterior parietal somatosensory, and visual area were described. These fields were originally described as partially overlapping so that physiological boundaries were blurred or indistinct. These findings provided strong support for the view that primary fields are the oldest fields, and secondary and tertiary fields evolved later. Also postulated from the above observations was the idea that the neocortex of the common ancestor was both physiologically and architectonically indistinct. Thus, it was proposed that early mammals had a generalized neocortex, rather than a highly differentiated structure (Diamond and Hall, 1969; Ebner, 1969; Kaas et al., 1970).

However, results from recent studies on mammals with long and distinct evolutionary histories run counter to previous observations by demonstrating multiple sensory representations with distinct architectonic boundaries (see Krubitzer et al., 1997 for review). For instance, multiple topographically organized somatosensory areas have been described in monotremes (Krubitzer et al., 1995b; Krubitzer, 1998), marsupials (Beck et al., 1996; Huffman et al., 1999), and insectivores (Krubitzer et al., 1997; Catania et al., 1998; Pobirsky et al., 1998). In these studies, cortical boundaries were found to be distinct, and no overlap of sensory representations was observed.

Likewise, there is a growing body of evidence for multiple fields in anterior parietal cortex in eutherian mammals such as cats (Garraghty et al., 1987), raccoons (Johnson et al., 1982; Feldman and Johnson, 1988), ferrets (LeClerc et al., 1993), megachiropteran bats (Krubitzer and Calford, 1992), and primates (Kaas, 1983; Kaas and Pons, 1988; see Johnson, 1990 for review). However, less is known about the organization of anterior parietal cortex in eutherian mammals such as rodents, which have a small neocortex, and a relatively simply organized brain.

Rodents are one of the most commonly used mammals in neurobiological research, and often serve as a model for understanding general principles of sensory processing, development, and plasticity. However, relatively little is known about the organization of somatosensory cortex in rodents other than mice and rats. Even in these species, the majority of information concerning somatosensory cortical organization is focused on the vibrissae barrel fields. There are some suggestions that anterior parietal cortex contains more than just a primary somatosensory area. These ideas stem mainly from studies of connections (Krubitzer et al., 1986; Li et al., 1990; Fabri and Burton, 1991). However, electrophysiological recording studies are limited to SI, and these studies have only explored cortex rostral to SI (Sur et al., 1978; Chapin and Lin, 1984; Welker et al., 1984).

In the present investigation, we examined the organization of anterior parietal cortex in the California ground squirrel (*Spermophilus beecheyii*), using electrophysiological recording techniques combined with myeloarchitectonic analysis, to determine the number and internal organization of cortical fields that reside there. We chose the squirrel because it has a large cortex relative to that of commonly used mice and rats. Also, the somatosensory system of these animals is well developed in that much of the cortex is devoted to processing somatic inputs, and several areas lateral to SI have been well described. Finally, much is already known about the organization and connections of visual (Kaas et al., 1972, 1989; Sereno et al., 1991) and auditory cortex (Merzenich et al., 1976; Luethke et al., 1988) in these animals. Although there are several studies on the functional organization of SI in squirrels (Sur et al., 1978; Gould and Kaas, 1981; Krubitzer et al., 1986), and of two areas lateral to SI (SII and PV; Krubitzer et al., 1986), there is little known about the functional organization of other portions of anterior parietal cortex.

This study is part of a growing body of evidence that indicates that multiple somatosensory fields exist in anterior parietal cortex of all mammals. The present results are considered in the larger context of the evolution of sensory fields, and have led us to reevaluate current theories of anterior parietal cortex evolution.

MATERIALS AND METHODS

Multiunit recording methods were used to investigate subdivisions of the somatosensory cortex in five adult California ground squirrels (*Spermophilus beecheyii*). Partial or entire maps of the primary somatosensory area (SI), the parietal medial area (PM), and the rostral area (R) were obtained from these animals. Electrophysiological recording results were related to cortical myeloarchitecture.

Abbreviations

Cortical hemi-spheres

LH	left hemisphere
RH	right hemisphere

Cortical areas

1	caudal somatosensory area (cutaneous)
2	caudal somatosensory area (deep)
3a	rostral somatosensory area (deep)
3b	primary somatosensory area
PM	parietal medial area
PV	parietal ventral area
R	rostral area
SI	primary somatosensory area
SII	second somatosensory area
TA	temporal anterior area
TI	temporal intermedial area
TP	temporal posterior area
VI	primary visual area
VII	second visual area

Representations

dlt	dorsal lower trunk
eb	eyebrow
el	elbow
fa	forearm
fav	forearm vibrissae
fp	forepaw
hd	head
hl	hindlimb
hp	hindpaw
kn	knuckles
j	lower jaw
n	naris
sn	snout
sh	shoulder
tr	trunk
ul	upper lip
vib	vibrissae
wr	wrist

Each squirrel was initially anesthetized with ketamine hydrochloride (25 mg/kg, IM) and xylazine hydrochloride (5 mg/kg, IM). In some squirrels, atropine (0.1 ml, IM) was given, and 0.1 ml of 1% lidocaine hydrochloride was administered subcutaneously where the earbars entered the auditory meatus. Maintenance doses of half of the initial dose of ketamine were given as needed to maintain a surgical level of anesthesia. Subcutaneous injections of 0.9% sodium chloride with 2.5% dextrose were administered every 3–4 hours to maintain hydration.

Once a surgical level of anesthesia was reached, the skin along the midline was cut, a craniotomy was performed, and the dura was retracted to expose all or most of the somatosensory cortex. The head was tilted in a plane that allowed the electrode to penetrate the cortex perpendicularly to the surface of the cortical area of interest. An acrylic well was built around the opening and filled with dimethylpolysiloxane to prevent desiccation and to maintain cortical temperature. The exposed cortex was digitally imaged using a CCD camera (Optronics), and the image was printed. The image was used as a reference map to relate the electrode penetrations to cortical vasculature. All experimental protocols were approved by the Animal Use and Care Advisory Committee of the University of California, Davis, and conformed to National Institutes of Health guidelines.

Extensive mapping of the somatosensory cortex was undertaken using tungsten microelectrodes (0.025-cm diameter, 5 M Ω) designed to record small clusters of neurons. The electrode was advanced with a micromanipulator to a depth of 500 μ m from the pial surface. To determine the receptive fields for a cluster of neurons in a given penetration, the body surface was stimulated with brushes and fine wooden probes. Cutaneous stimulation consisted of small indentations of the glabrous surface of the skin, displacement of hairs and vibrissae on the hairy surface of the skin, and lightly brushing the skin. When cutaneous stimulation was ineffective, responsivity to joint manipulation, pressure, or taps was tested. The somatotopic organization of a region of the cortex was determined from receptive fields for neurons at a number of closely spaced recording sites.

At the end of the experiment, each squirrel was euthanized with a lethal dose of pentobarbital sodium (1.5 ml, IP) and transcardially perfused with 0.9% saline, followed by 3% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4), and finally 3% paraformaldehyde with 10% sucrose in 0.1 M phosphate buffer. The fixed brain was removed from the skull and the cortex was then removed from the rest of the brain and manually flattened between two glass slides. The flattened cortices were soaked overnight in 30% sucrose in 0.1 M phosphate buffer, and then cut on a freezing microtome into 35–50- μ m sections in a plane parallel to the cortical surface. Alternate sections were stained either for myelin using the Gallyas (1979) silver procedure, or reacted for cytochrome oxidase (CO) (Wong-Riley, 1979).

For each case, camera lucida drawings of individual sections were made using a stereomicroscope. Each drawing contained the outline of the section, blood vessels, tissue artifacts, and architectonic borders determined from myelin-stained and CO-reacted sections. All drawn sections were then aligned using blood vessels and tissue

artifacts and compiled into one map. Finally, using probes and blood vessel patterns obtained from the image of the exposed cortex, the electrode penetrations were plotted and aligned with drawn sections containing architectonic boundaries to produce one comprehensive reconstruction of electrophysiological maps with architectonic borders of cortical fields.

RESULTS

In the present experiment, multiunit recording techniques were used to define the boundaries and the features of organization of three somatosensory areas—SI, PM, and R. The electrophysiological results were related to architectonically defined subdivisions of anterior parietal cortex in the same animals.

Three distinct fields—PM, SI, and R—were observed by use of multiple criteria. First, the areas had distinct architecture. Second, all three areas contained complete or almost complete representations of the sensory epithelium (i.e., the body surface). Third, neurons in each area had different stimulus preferences in that neurons in SI responded preferentially to stimulation of cutaneous receptors, whereas neurons in PM and R responded to stimulation of deep receptors. Finally, there were differences in the size of the receptive fields for the neurons in each area. For example, SI contained neurons that had small receptive fields, whereas PM and R contained neurons that had relatively larger receptive fields.

Myeloarchitecture of cortex

Myeloarchitectonic distinctions were identified on a number of brain sections cut parallel to the cortical surface. Although some cortical boundaries were obvious on a single section (Fig. 1), the boundaries on the illustrations were determined by examining a series of sections through the entire cortex encompassing all cortical layers (Fig. 2). The first visual area, VI or area 17, is a densely myelinated area located at the caudomedial pole of the cortex (Fig. 1A,C). It is adjoined along its rostrrolateral border by the second visual area, VII or area 18 (Kaas et al., 1972; 1989). VII is moderately myelinated, which makes it easy to distinguish from the darkly myelinated VI. The temporal posterior region (TP) is an area located lateral to VII. TP is a densely myelinated area surrounded by lightly myelinated cortex (Fig. 1A,C). Therefore, its borders are very distinct and easy to identify. The temporal anterior region (TA), which includes the primary auditory field AI (Merzenich et al., 1976), is another densely myelinated area (Fig. 1A,C). It is located rostral to the lightly myelinated temporal intermedial area (TI) and lateral to the somatosensory cortex. The nomenclature for these temporal regions is taken from Kaas et al. (1972).

Somatosensory cortex explored in this investigation is located medial to TA and rostral to VII. Much of this region has been described in the Eastern grey squirrel (Sur et al., 1978; Nelson et al., 1979; Krubitzer et al., 1986). The primary somatosensory area is the largest, most densely myelinated somatosensory area, as well as the most cytoarchitectonically distinct area (Fig. 1A,B). SI is bordered caudolaterally by the second somatosensory area

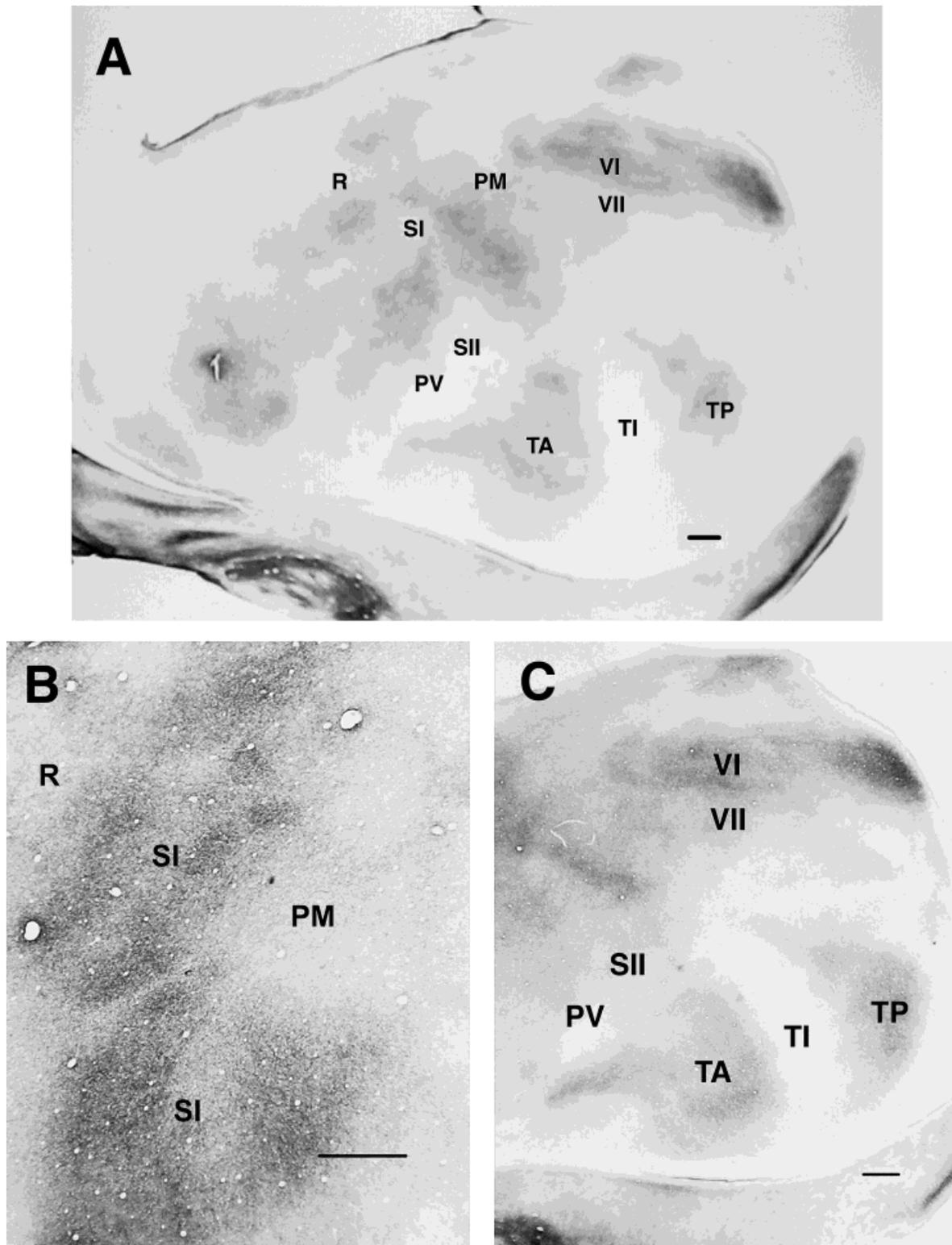


Fig. 1. Lightfield digital images of cortex in the California ground squirrel that have been flattened, cut parallel to the cortical surface, and stained for myelin (Gallyas, 1979). Although boundaries of cortical fields are drawn from a series of sections through the neocortex, often a number of the boundaries are visible on a single section (A). In (A), the relative relationships of different cortical fields to each other can be readily appreciated. **B:** High-power photograph of the parietal

cortex. In this photograph, SI is a densely myelinated area that covers the majority of the anterior parietal cortex. PM is a lightly myelinated area caudal to SI. R is lightly to moderately myelinated and is rostral to SI. In (C), regions of occipital and temporal cortex are depicted. The primary visual area, VI, stains darkly to moderately for myelin, as do temporal areas TP and TA. Rostral is to the left and medial is to the top. For abbreviations, see list. Scale bars = 1 mm.

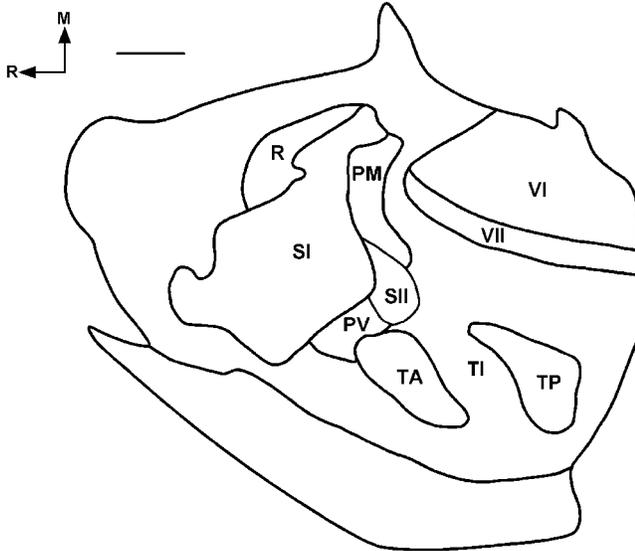


Fig. 2. A reconstruction of a series of sections through the entire dorsoventral extent of the neocortex. Solid lines mark architectonic boundaries. Scale bar = 2 mm.

(SII), and the parietal ventral area (PV). These areas are moderately myelinated, making the SI/SII and SI/PV borders distinct.

The parietal medial area is located along the caudomedial border of SI. PM is a lightly myelinated region, which distinguishes it from the densely myelinated SI rostrally (Fig. 1B), and from the darkly myelinated VI and moderately myelinated VII caudomedially. Along its caudal border, there is a narrow region of lightly myelinated cortex that makes this border difficult to distinguish. The lateral border of PM adjoins the moderately myelinated SII. The rostral area, R, bounds SI rostromedially. R is a lightly to moderately myelinated region, which makes the SI/R border very distinct (Fig. 1B). R is bordered rostrally by the presumptive primary motor cortex, which is moderately myelinated (Krubitzer and Kaas, unpublished observations).

CO-reacted sections were also used to determine architectonic boundaries, but they were not as effective as the myelin-stained sections for distinguishing the different cortical fields. However, the CO-reacted sections were especially useful for delineating SI because densely staining barrels were observed in the middle cortical layers in the lateral portion of SI (Fig. 3). The vibrissa barrels, originally described cytoarchitectonically, form dense patches in layer IV in several species of rodents including rats, mice, hamsters, and squirrels (Woolsey, 1967; Welker, 1971; Woolsey et al., 1975). In the California ground squirrel, the barrels are small, densely reacted, polygonal areas closely clustered in the lateral region of SI in the middle cortical layers (Fig. 3).

Representation of the body surface in SI, PM, and R

There was a general pattern of parallel topographic organization that could be distinguished in SI, PM, and R (Fig. 4). The receptive fields of the neurons in all three areas were located on the contralateral body surface, and the representations of the body were inverted, with the

tail, trunk, and hindlimb represented most medial and the face and vibrissae represented most lateral (Fig. 4).

The primary somatosensory area, SI. The organization of SI was consistent with that described in a previous study for the eastern grey squirrel (Sur et al., 1978). The hindpaw, hindlimb, and trunk were represented in the most medial portion of the area (Figs. 5–9). This was followed laterally by the representation of the forearm, forepaw, and digits (Figs. 6–10). Lateral to this was a large vibrissae representation, including the barrel field cortex (Figs. 6, 7, and 9). Finally, the naris, upper lip, lower lip, and intraoral structures were represented most laterally (Figs. 5–10). In all cases, SI was coextensive with the large darkly myelinated field described above (Fig. 1).

The parietal medial area, PM. The organization of PM was not as topographically precise as SI. However, the topographic organization in several of the cases shows the same general mediolateral organization that was observed in SI. In case 96–5 RM (Fig. 8), the tail representation was located most medially. The tail representation was adjoined laterally by the hindlimb and trunk representations. Lateral to these representations was the representation of the forearm and then the forepaw. Finally, the face was represented most lateral.

Another example of this topographic organization can be seen in case 96–31 LM (Fig. 9). In this case, the trunk was located medially, followed by the lower dorsal trunk and hindlimb representations. The shoulder representation was lateral to the representation of the trunk, and in this case, rostral to the representation of the hindlimb. The shoulder representation was adjoined rostrally by the forepaw and forearm representations. The digit representation, naris, and snout were represented most lateral in PM.

There were some differences between cases in the internal organization of PM, but the general topography remained constant. The receptive fields for the caudal portion of the animal—the hindpaw, toes, tail, hindlimb, and lower trunk—were located in the most medial section of PM (Figs. 5, 6, 8, and 9). The upper body representations, including the shoulder, forelimb, forepaw, and digits were located lateral to this in the middle section of the area (Figs. 5–9). Finally, the head and face representations, including the vibrissae, naris, lips, and snout, were located in the most lateral portion of the area (Figs. 5–8). Coextensive with the electrophysiologically defined PM was a lightly myelinated field described above (Fig. 1). The match between the architecture and electrophysiological recording results was good, but not as consistent as for SI (Fig. 5). For instance, there were several cases in which neurons did not respond to our stimuli, and these were included in the architectonically defined PM region. These no-response zones tended to be on the caudal and medial boundary of PM.

The rostral area, R. The rostral area contained a nearly complete representation of the contralateral body surface. Although the entire extent of architectonically defined R was not surveyed, the partial maps obtained from most of the cases do provide information on the organization of the area. Like PM, R was not as topographically precise as SI, but did show the same general mediolateral organization (Fig. 4). An example of this can be seen in case 96–2 (Fig. 6). The trunk representation was located most medial in R. The trunk representation was adjoined laterally by the hindpaw representation. Lateral to the

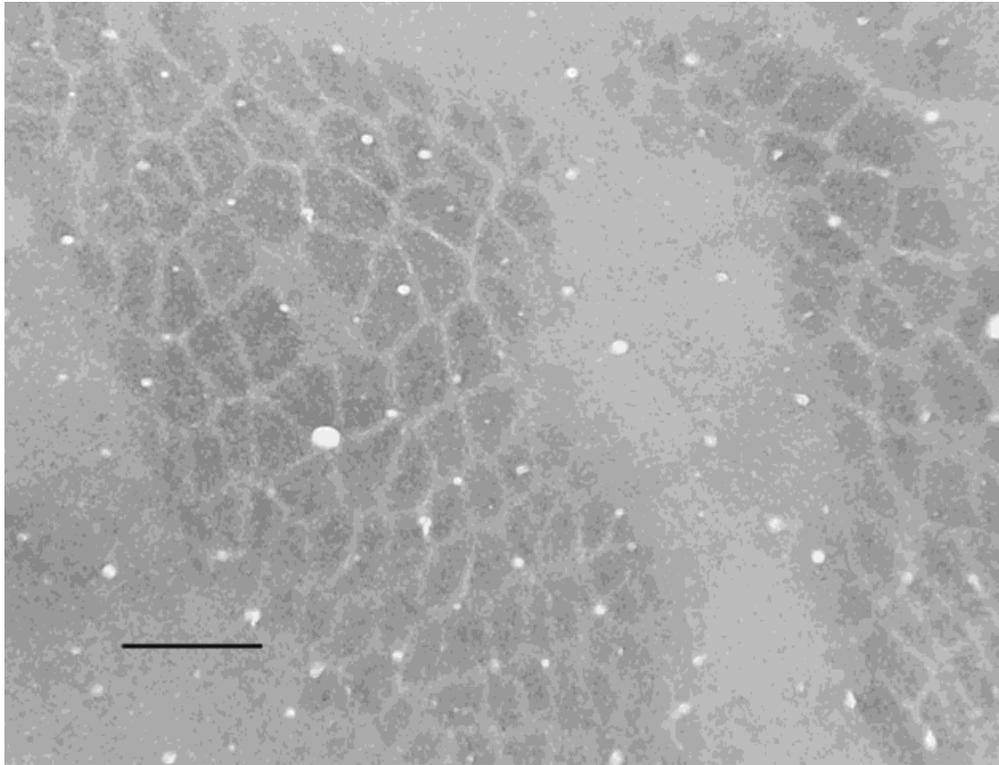


Fig. 3. A lightfield digital image of a section of cortex that has been flattened, cut tangentially, and reacted for cytochrome oxidase (Wong-Riley, 1979). The portion of the barrel field depicted in this image is

located in the lateral portion of the primary somatosensory area and contains neurons that respond to stimulation of the vibrissae. Conventions as in previous figures. Scale bar = 500 μ m.

hindpaw representation was the forepaw, forearm, and then the digit representations.

Another example can be seen in case 96-31 (Fig. 10), which had the same general mediolateral organization. The tail was located most medial followed by the hindlimb representation in a more lateral location. The wrist, elbow, forepaw, and digit representations continued in a lateral progression in R.

Recordings in the lateral portion of R were restricted by blood vessel patterns or the restricted size of the opening in the skull. Therefore, receptive fields on the face were only recorded for R in one penetration in one case, 96-1 (Fig. 5). It was located, as expected, in the most lateral portion of R. The electrophysiologically described R was coextensive with a lightly myelinated strip of cortex described above (Fig. 1). The match between cortical architecture and electrophysiological recording results was good, although as with PM, there were some regions of cortex that were unresponsive to our stimulation that were included within the architectonically defined R (Fig. 6).

Differences in stimulus preference and receptive field size

The types of stimuli that produced a neural response were different for the different areas. Neurons in SI responded to light cutaneous stimulation, which included small indentations of the glabrous skin, light brushing of the skin, and the displacement of hairs or vibrissae. These responses were typically vigorous and nonhabituating. The receptive fields for the neurons in SI were small and the borders were easily defined. For example, in case 96-2

(Fig. 11), the neurons at recording sites 3-7 responded to cutaneous stimulation and had receptive fields restricted to small portions of the glabrous forepaw.

The neurons in PM responded to stimulation of deep receptors. The types of stimuli that proved most effective in eliciting a response included moderate-to-hard taps and squeezes to the body surface and joint and limb displacements. In some instances, these responses would habituate. Also, the receptive fields were typically larger than those observed for neurons in SI. For instance, in case 96-2 (Fig. 11), the neurons in SI at recording sites I and III had small receptive fields on the elbow vibrissae, wrist, and knuckles, respectively, whereas the neurons in PM at recording sites IV and VI had large receptive fields that rerepresented those for neurons in SI.

The neurons in R, like those in PM, responded to stimulation of deep receptors. However, the intensity of the stimulus needed to elicit a response was greater and included taps, squeezes, joint manipulations, and limb displacement. Thus, the receptive fields of these neurons were also larger than those found in SI. An example can be seen in case 96-2 (Fig. 11), where receptive fields for the neurons in different parts of the forepaw representation are shown. The receptive fields for the neurons at recording sites 1 and 2 in R are much larger than those found for neurons in similar regions of SI, like 4 and 5.

Receptive field progressions

A reversal of receptive field progressions can be seen across the PM/SI border for neurons in all of the body part representations. Case 96-5 shows a reversal of the recep-

96-2 LH

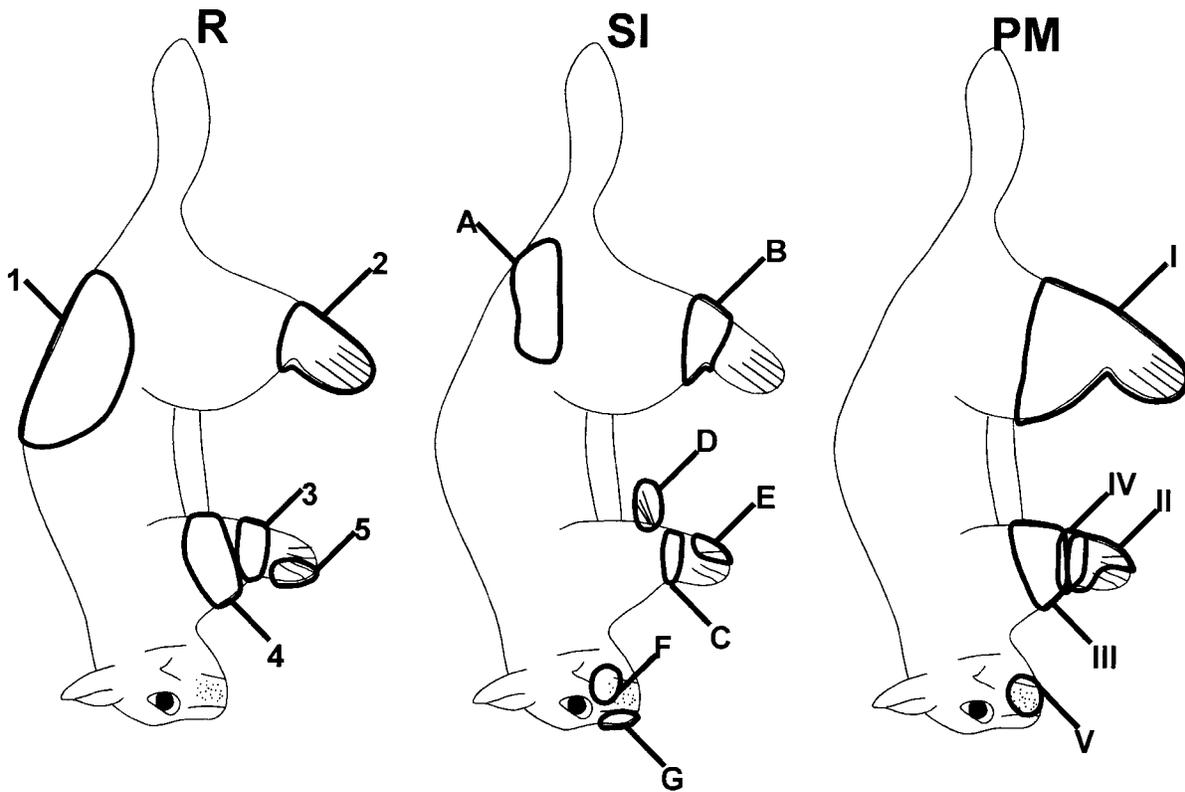
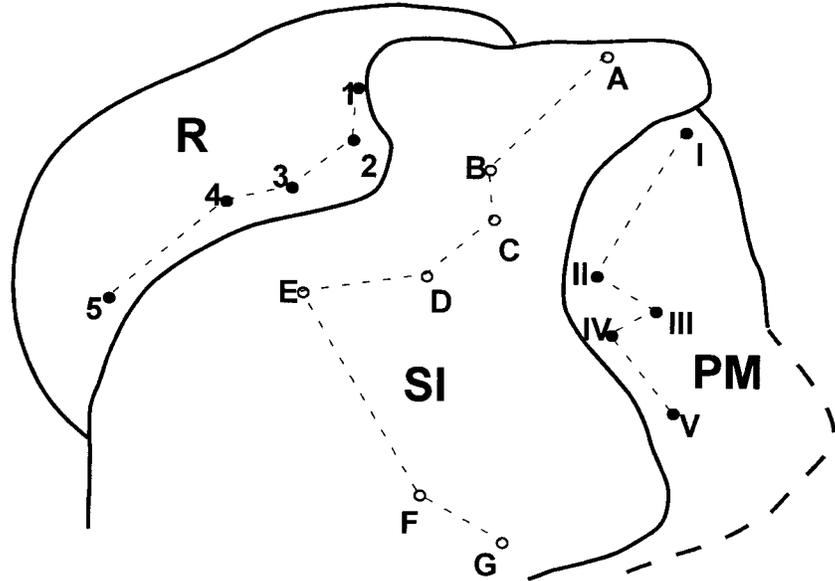
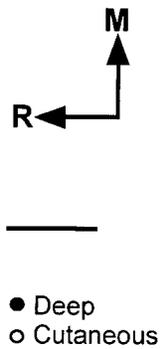


Fig. 4. Recording sites (top), and corresponding receptive fields for neurons at those sites (bottom) in three separate body representations in anterior parietal cortex. All three areas (R, SI and PM) exhibit the same mediolateral organization. Neurons in the three areas had different stimulus preferences and different-size receptive fields. Neurons in SI typically had small receptive fields and responded best to cutaneous stimulation, whereas neurons in R and PM had larger

receptive fields and responded best to taps and limb manipulations. The thick lines mark architectonic boundaries and thick dashed lines mark approximate boundaries. Thin dashed lines mark recording site progressions. For abbreviations, see list. In this and the following figures, the scale bar = 1 mm. Other conventions as in previous figures.

tive field (r.f.) progression in the trunk, hindlimb, and hind paw representations (Fig. 12, r.f. A-H). The receptive fields for the neurons in SI progress from the trunk, onto the proximal hindlimb, and then onto the distal hindlimb as

recording sites move from rostral to caudal (Fig. 12, r.f. A-E). As the SI/PM border was crossed, the r.f. progression for neurons reversed. With a progression of sites from rostral to caudal in PM, r.f. for neurons at those sites

96-1 LH

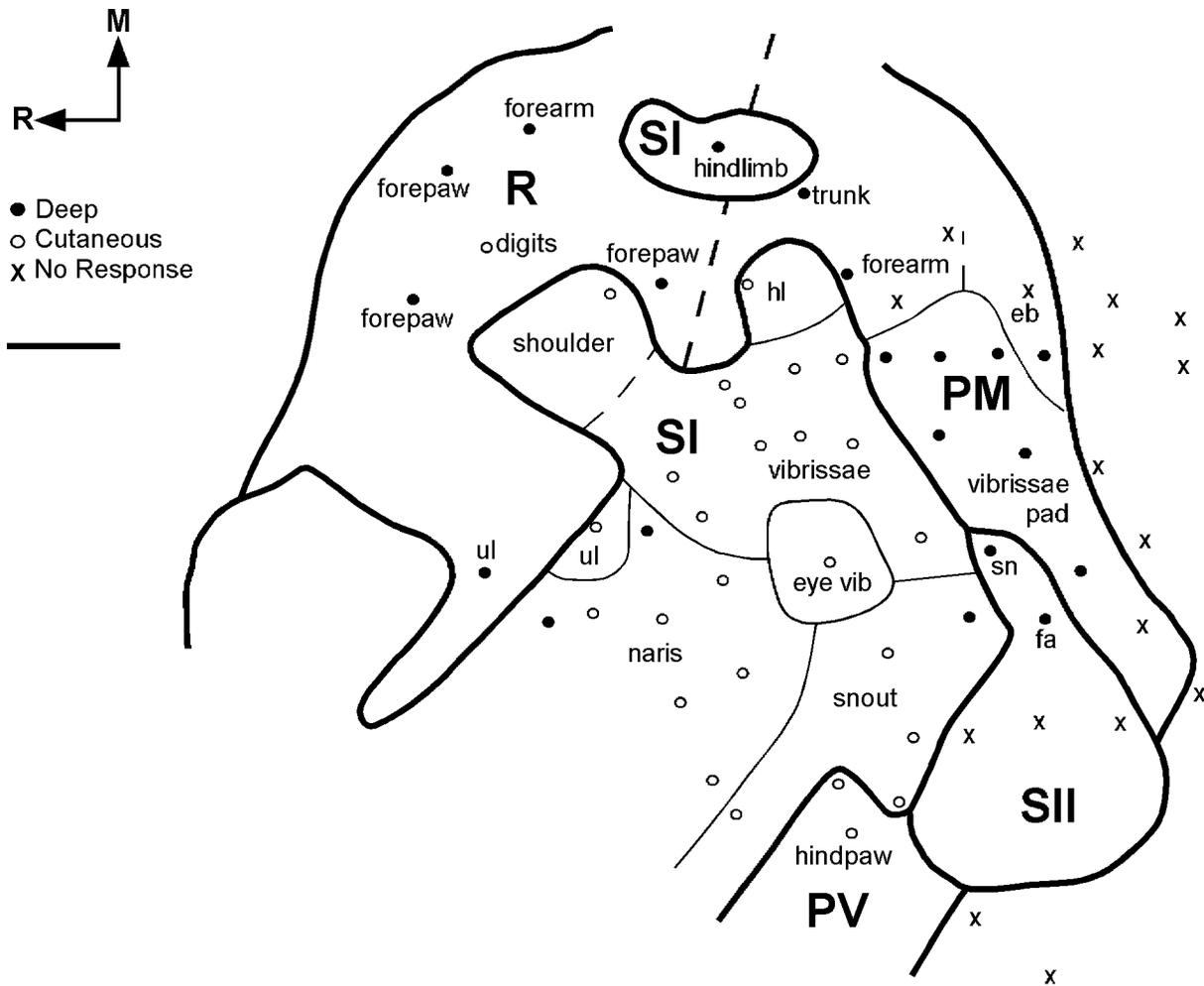


Fig. 5. A reconstruction of electrophysiological recording results from squirrel 96-1. Multiple recording sites were made in the somatosensory cortex, which enabled us to determine the gross topography of several areas. The mediolateral organization of SI is consistent with other studies such that the hindlimb is represented medially, followed by representations of the forelimb and face laterally. An area caudal to SI, termed PM, had the same general mediolateral organization as SI.

Another area was identified immediately rostral to SI and was termed R because of its similarity to the rostral deep field described in other mammals. Thick lines mark architectonic boundaries, dashed lines mark approximate boundaries, thin lines within a field separate different body part representations. For abbreviations, see list. Other conventions as in previous figures.

progressed from distal to proximal hindlimb and trunk (Fig. 12, r.f. F-H).

A similar reversal can be observed in the forearm, forepaw, and digit representations in case 96-2 (Fig. 11, r.f. I-VI). Receptive fields progress from the forearm, to the wrist, and to the forepaw as they move from rostral to caudal in SI. As the SI/PM border was crossed, the receptive field progression reversed and moved from the forepaw, to the wrist, and on to the forearm.

Finally, a receptive field reversal can also be seen in the face representation. For case 96-31, as recording sites moved from rostromedial to caudolateral in SI, corresponding receptive fields moved from the side of the face to the naris (Fig. 13, r.f. 1-4). As the SI/PM border was crossed,

receptive field progression reversed back onto the side of the face (Fig. 13, r.f. 5 and 6). Similar reversals were observed in other cases as well (Fig. 11, r.f. A-F).

No reversals in r.f. progressions across the SI/R border were identified. This may be because of the low recording density in R in most cases. However, it was still possible to observe a rerepresentation of the body parts between areas R and SI.

DISCUSSION

The results of the present study demonstrate that three cortical areas are located in the anterior parietal cortex of the California ground squirrel. These fields include the

96-2 LH

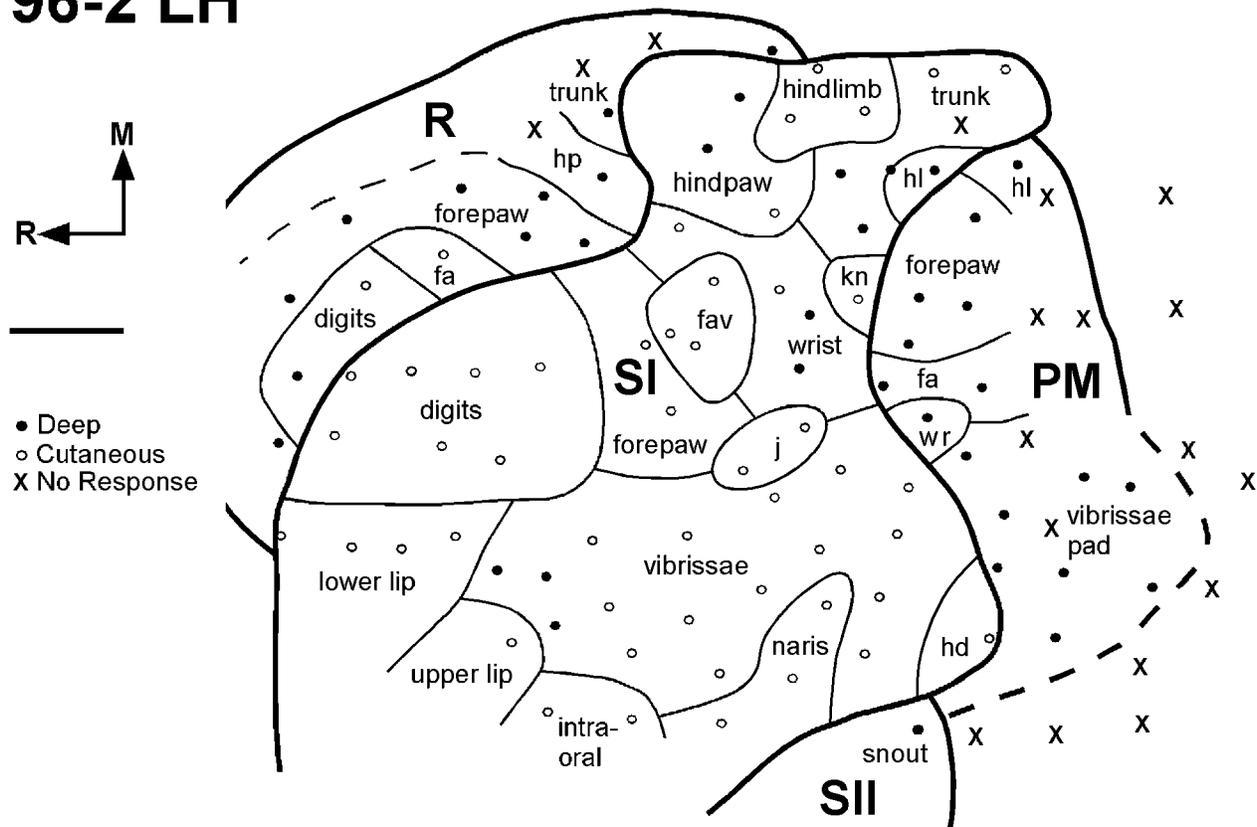


Fig. 6. A reconstruction of a detailed map of PM, R, and SI in squirrel 96-2. In a medial location in SI, the trunk, hindlimb, and hindpaw are represented. These representations are followed more laterally by the representations of the forearm, forepaw, and digits. Finally, the vibrissae and other facial structures are located most medial in SI. The physiological recordings indicate similar organiza-

tions of R and PM. From medial to lateral in R, there is a representation of the trunk, hindpaw, forepaw/forearm, and digits. For PM, the mediolateral organization is from the hindlimb, to the forepaw, forearm, and vibrissae representation most lateral. Conventions as in previous figures. For abbreviations, see list.

primary somatosensory area (SI), a rostral area (R), and the parietal medial area (PM). All fields are distinguished by a complete or almost complete representation of the body surface and neurons with different stimulus preferences and r.f. sizes. In addition, all fields are distinct in myeloarchitectonic appearance. In the following discussion, we outline similarities in somatosensory cortical organization described in other rodents and in other mammals, and propose possible homologies across species. The presence of multiple representations in a variety of nonprimate mammals suggests that the ancestral somatosensory cortex was likely to be more complexly organized than was previously thought.

Somatosensory cortical organization in rodents

The topographic organization, architectonic appearance, and neuroanatomical connections of SI, SII, and PV have been well documented in previous studies in the grey squirrel (Sur et al., 1978; Nelson et al., 1979; Gould and Kaas, 1981; Krubitzer et al., 1986; Krubitzer and Kaas, 1987). Detailed descriptions of the organization of SI demonstrate a topographic organization similar to that observed in the present study. SI in previous studies was coextensive with a region of cortex that was densely

myelinated (Krubitzer et al., 1986), and that contained a well-developed layer IV (Sur et al., 1978). As in the present investigation, neurons in SI in those studies responded best to cutaneous stimulation. This area also contained a physiologically defined "barrel field," similar to that found in other rodents (Sur et al., 1978).

Relatively little is known about the functional organization of anterior parietal fields other than SI in rodents. The present findings of two fields in addition to SI, one rostral and one caudal (R and PM, respectively), are important for two reasons. First, they extend our current understanding of anterior parietal cortex organization in rodents. Second, they demonstrate that rodent neocortex is complexly organized and is more similar in organization to the neocortex of other eutherian mammals, such as carnivores and primates, than was previously believed.

In the present investigation, neurons in areas R and PM responded best to stimulation of deep receptors. Although Sur et al. (1978) did not describe a separate representation rostral to SI, they found a double representation of the forepaw. They noted that some of the neurons in this forepaw representation would respond to "substantially harder taps" to the dorsal skin. It is possible that the rostral representation of the hand in the previous study corresponds to the hand representation identified in R in

96-3 LM

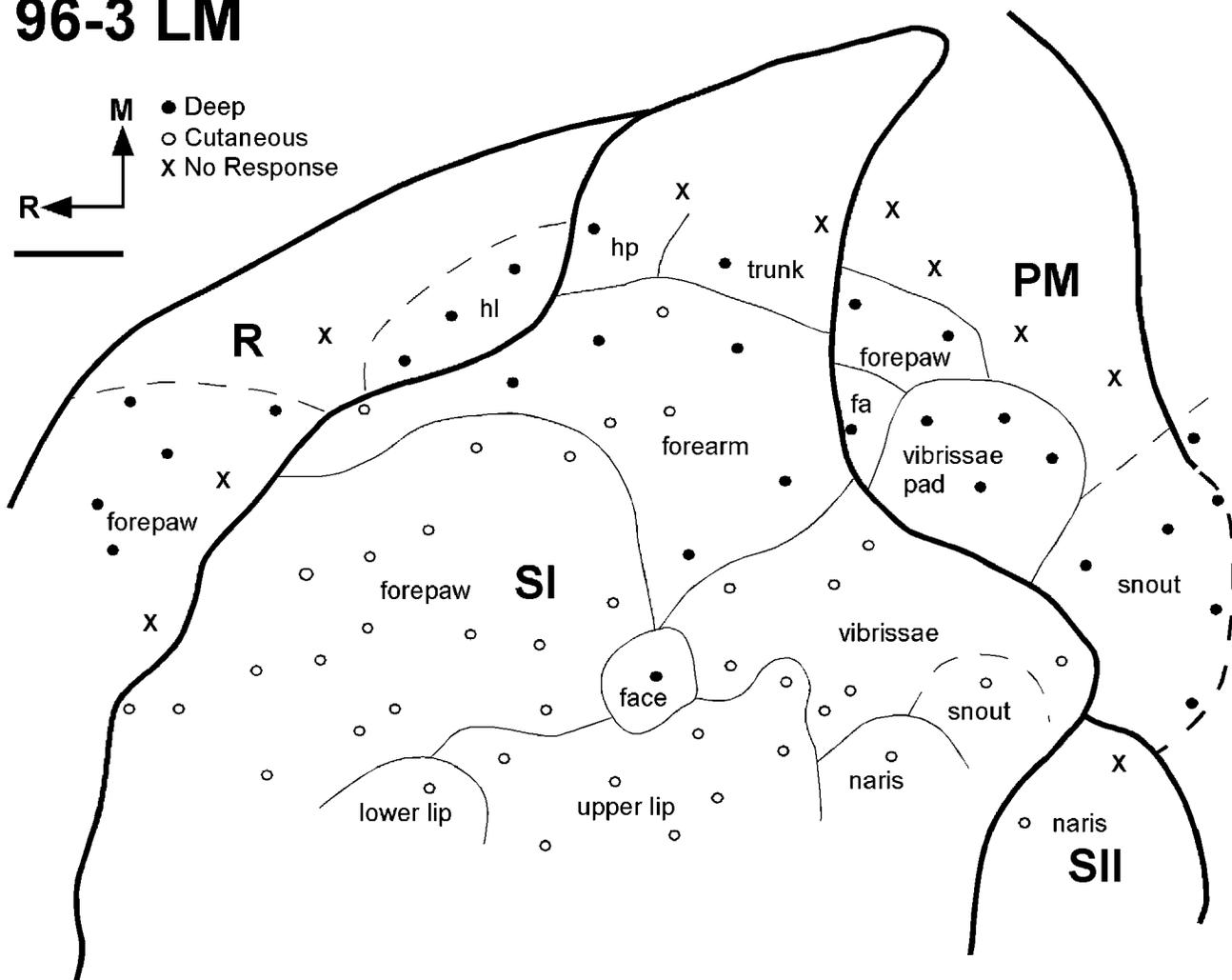


Fig. 7. Partial maps of SI, R, and PM in case 96-3. The mediolateral organization of these fields is similar to that described in the previous cases. Conventions as in previous figures. For abbreviations, see list.

the present investigation. However, in the present study, neurons in R were not driven by cutaneous stimulation and fell outside of the darkly myelinated SI.

The topography of the parietal medial area was explored in the grey squirrel using anatomical tracing techniques by Krubitzer et al. (1986). Injections in the electrophysiologically identified lateral portion of SI, where the face was represented, projected to the lateral portion of PM. Injections in the more medial portion of SI, where the forelimb was identified using electrophysiological recording techniques, projected to a more medial portion of PM. Our descriptions of the mediolateral organization of PM are consistent with these previous results.

Cortical regions rostral and caudal to SI in which neurons respond to stimulation of deep receptors have also been described for other rodents. For example, Chapin and Lin (1984) described a small strip of dysgranular cortex, called the transitional zone (TZ) in rats, just rostral to the representations of the forepaw and hindpaw in SI, like R in the present study. This zone contained neurons that consistently responded to passive joint manipulations.

Welker and colleagues (1984) described a complete representation of deep receptors in the dysgranular zone (DZ) of rats, which was rostral to and embedded within granular SI. The rostral dysgranular zone corresponds to TZ described by Chapin and Lin (1984). The mediolateral topography of this dysgranular zone including TZ is like that of R described in the present study. A rostral representation of the body surface that parallels that of SI has also been described in the agranular cortex in the guinea pig (Rapisarda et al., 1990). However, this area resides rostral and medial to the area described in rats and squirrels and corresponds to motor cortex.

Fabri and Burton (1991), using neuroanatomical tracing techniques, described an area of cortex similar to PM in rats. This region displayed a rough topography similar to that found in PM of the ground squirrel. In this same study, an area of cortex rostral to SI also had topographically organized inputs from SI that paralleled the pattern of representation in SI. This region was termed TZ, as in the previous studies of rats. Finally, corticospinal projections in the rat arise in cortex caudal to SI in a topographic

96-5 RM (reversed)

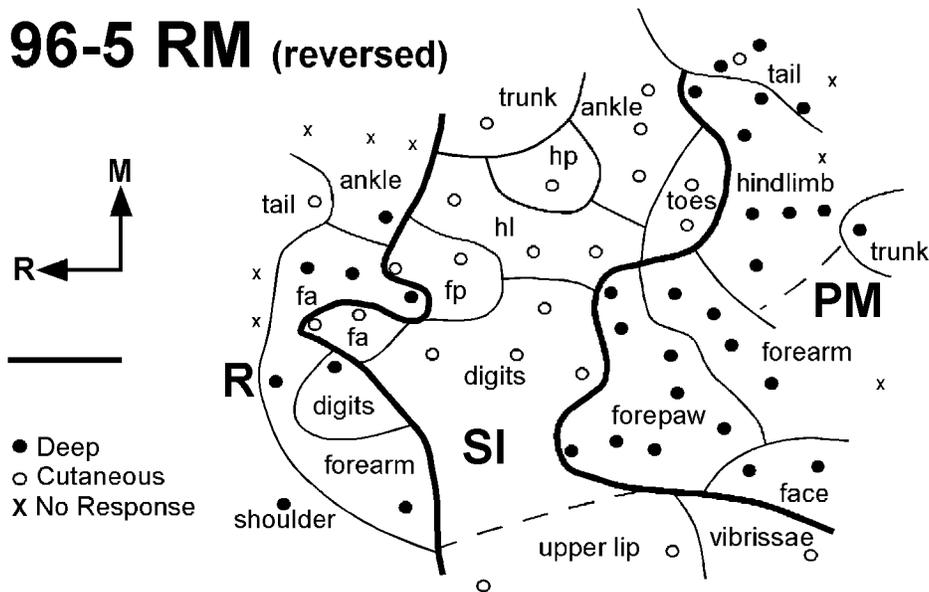


Fig. 8. A detailed map of PM, and more limited recording in SI and R in case 96-5. The mediolateral organization in PM is clear with the tail representation located most medially, followed by the hindlimb, trunk, forearm, forepaw, and face representations in a lateral progres-

sion. Thick lines mark physiological boundaries, and thin lines within a field separate different body part representations. Conventions as in previous figures. For abbreviations, see list.

96-31 LH

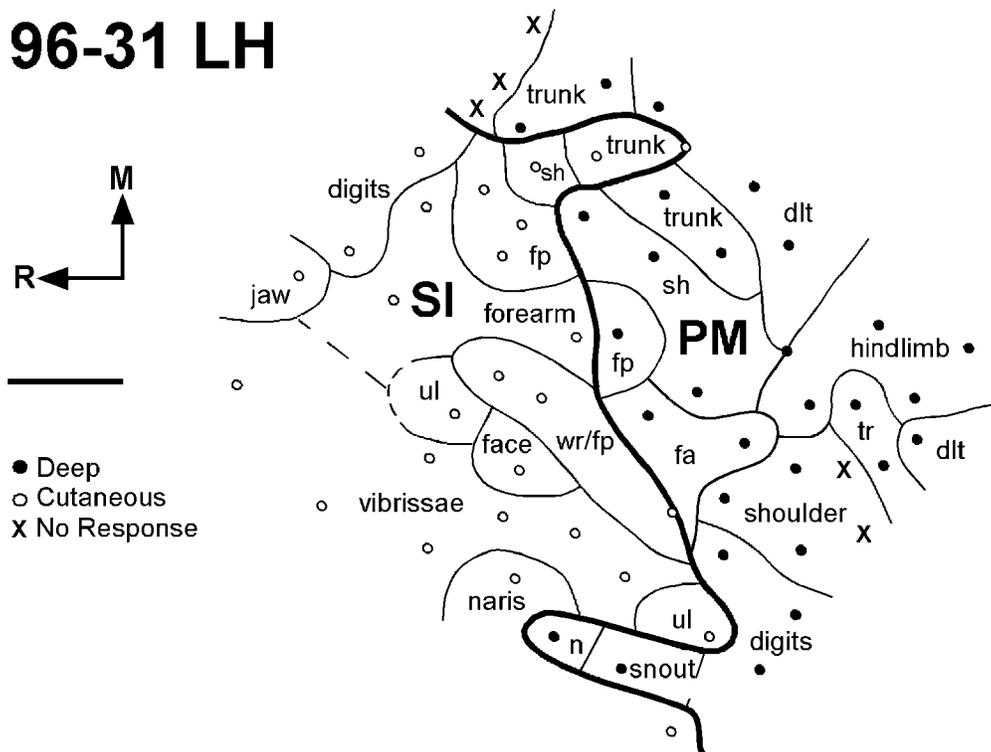


Fig. 9. The organization of SI and PM in case 96-31. This case shows a more complete map of PM. The parallel mediolateral topographic order in SI and PM is clear. Thick lines mark physiological boundaries, and thin lines within a field separate different body part representations. For abbreviations, see list. Conventions as in previous figures.

fashion consistent with our descriptions of PM (Li et al., 1990). Thus, the electrophysiological recording and neuro-anatomical tracing studies in other rodents support the

finding of the present investigation in squirrels that three separate areas exist in anterior parietal cortex of rodents: SI, PM, and R (TZ + DZ).

96-31 RH (reversed)

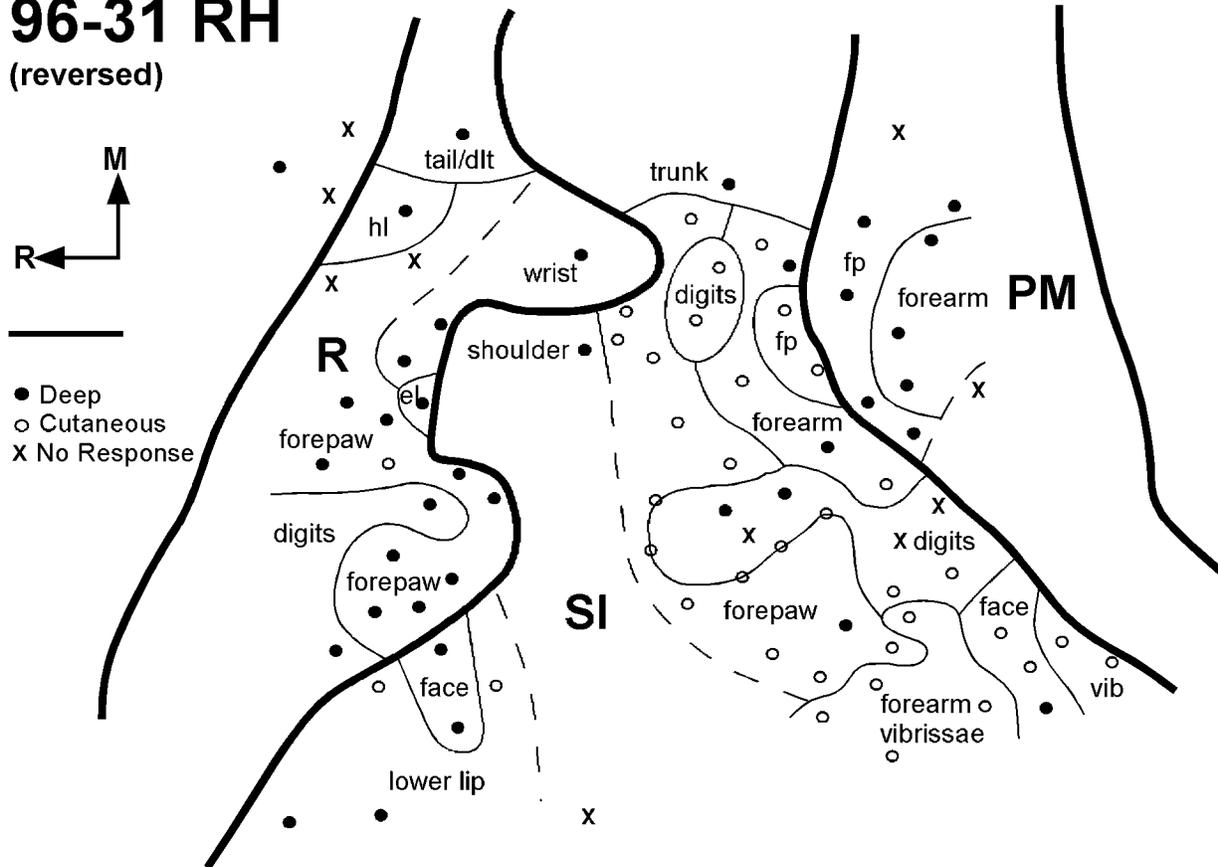


Fig. 10. Recording sites in SI, R, and PM in the right hemisphere of case 96-31. The mediolateral organization is similar to that in the previous cases. In this case, we have a more extensive map of R. A large blood vessel located over the rostral portion of SI prevented

mapping of most of SI by the SI/R border. Thick lines mark architectonic boundaries. For abbreviations, see list. Conventions as in previous figures.

Comparisons with other eutherian mammals

Similar topographic organizations, architectonic appearances, and cortical and subcortical connections of SI have been described in all mammals investigated (see Kaas, 1983 and Johnson, 1990 for review). Cortical fields in addition to SI have been described in the anterior parietal cortex of a number of other eutherian mammals. For instance, a field rostral to SI (3b) in primates in which neurons respond to stimulation of deep receptors on the contralateral body surface has been termed 3a (Sur et al., 1982; Nelson et al., 1980; see Kaas and Pons, 1988 for review). Only recently has the complete somatotopic organization of this field been described in primates (Huffman et al., 1996, 1999). Compared to SI, this area contains a less developed layer IV and a more densely packed layer V (Vogt and Vogt, 1919). In cortex that has been flattened and stained for myelin, area 3a is moderately myelinated, as is R in the present investigation (Huffman et al., 1996, 1999). Neurons in this region respond best to more complex stimulation and have large receptive fields that extend over more than one joint or group of muscles. Thus, area 3a in primates shows similarities in architecture, somatotopic organization, relative position, and stimulus preference to R in the ground squirrel.

In carnivores, a somatotopically organized field in a similar location has been described for the raccoon and

termed kinesthetic cortex (KC; Johnson et al., 1982; Feldman and Johnson, 1988; Doetsch et al., 1988). In ferrets, four representations of the face have been described using electrophysiological recording techniques. However, all four representations were interpreted to be a single field, SI (LeClerc et al., 1993), despite the fact that they reside in four separate architectonic zones (Rice et al., 1993). In another study in ferrets (McLaughlin et al., 1998), two distinct forepaw representations were identified. One was in SI (3b), and the other was a rostral field (area 3a) that received inputs from both deep and cutaneous receptors. In rabbits, cortex rostral to SI was found to contain neurons that only responded to taps or squeezes (Gould, 1986). However, this area was not systematically investigated. In the flying fox, a field rostral to 3b has been identified and termed area 3a (Krubitzer et al., 1998). The internal organization, stimulus preference, and myeloarchitecture of 3a in the flying fox is much like that described for area 3a in primates and R in the present study. Finally, in insectivores (Krubitzer et al., 1997; Pobirsky et al., 1998), a field just rostral to SI was found to contain neurons that responded to stimulation of deep receptors, but this field was not described in detail.

Like the rostral field, a representation of deep receptors has been described in a region caudal to SI and termed area 2 in primates (Pons et al., 1985; see Kaas and Pons,

96-2 LH

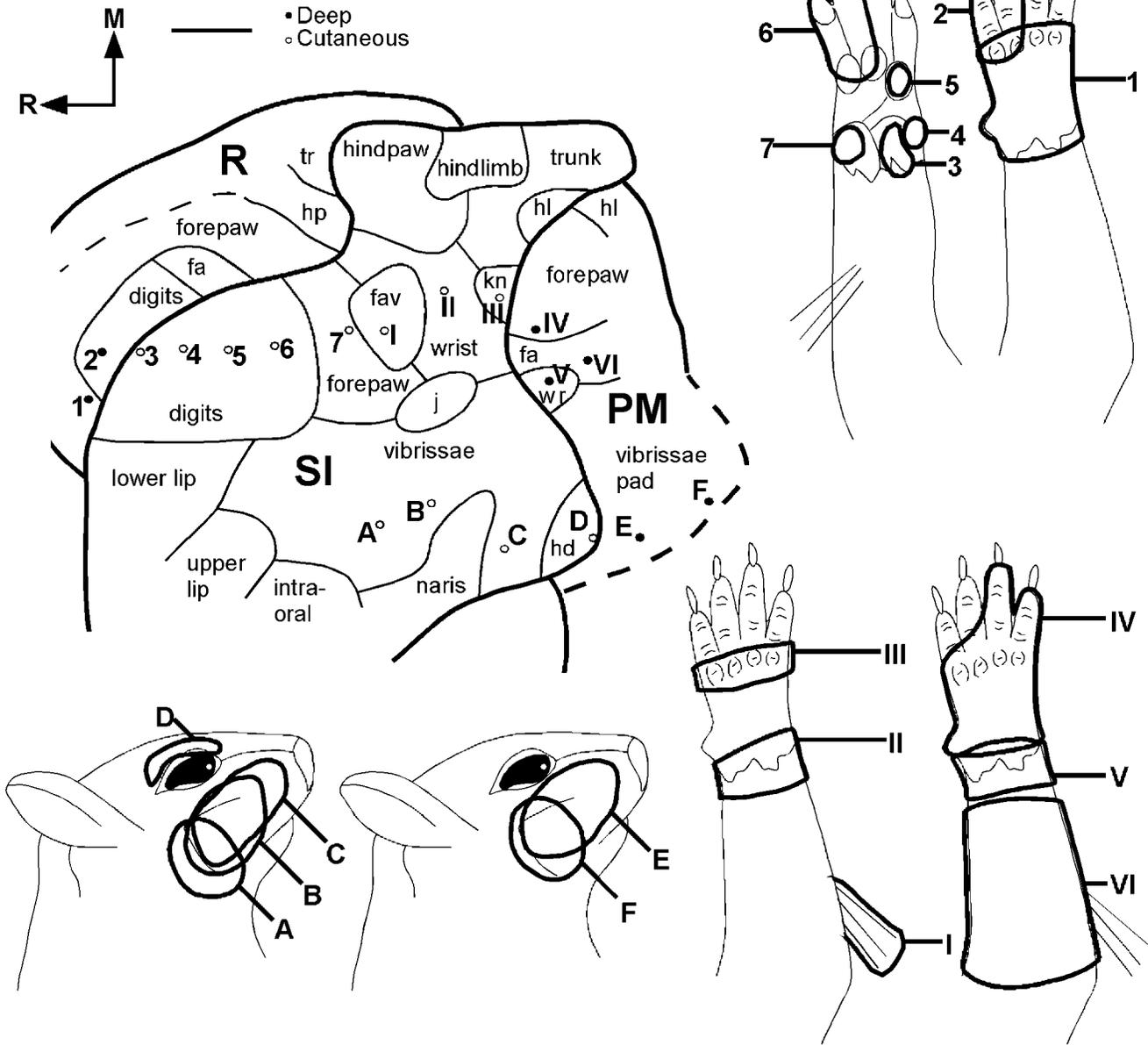


Fig. 11. Recording sites in R, SI, and PM (top left), and corresponding receptive fields for neurons at those sites (right and bottom) in case 96-2. As recording sites move from SI into PM, receptive fields for neurons at those sites reverse, and often increase in size (e.g., compare receptive fields I and III for neurons in SI with receptive fields VI and IV for neurons in PM). Although no clear reversal is observed across

the SI/R boundary, a rerepresentation of receptive fields is seen. In addition, an increase in the size of receptive fields is observed for neurons in R compared to neurons in SI (e.g., compare receptive fields 1 and 2 with receptive fields 3-7). For abbreviations, see list. Conventions as in previous figures.

1988 for review). However, in primates, area 2 is not immediately caudal to 3b. Rather, a cutaneous representation, area 1, resides immediately adjacent to 3b in the location of PM of the present study. In flying foxes, a caudal field was also described and termed area 1/2. Area 1/2 resembles both areas 1 and 2 in primates in its relative location, stimulus preferences for neurons therein, and organization (Krubitzer and Calford, 1992). Area 1/2 in the flying fox was proposed to represent a primitive form of

both areas 1 and 2 in primates. In cats, a field immediately caudal to 3b has been termed SIII (Garraghty et al., 1987). However, neurons there, as in area 1 in primates, respond to cutaneous stimulation. In rabbits, a high-threshold field caudal to SI was identified but not systematically studied (Gould, 1986). Insectivores such as tenrecs (Krubitzer et al., 1997) and hedgehogs (Pobirsky et al., 1998) have a caudal field in which neurons respond to stimulation of deep receptors. This area was termed the caudal field (C).

96-5 RH (reversed)

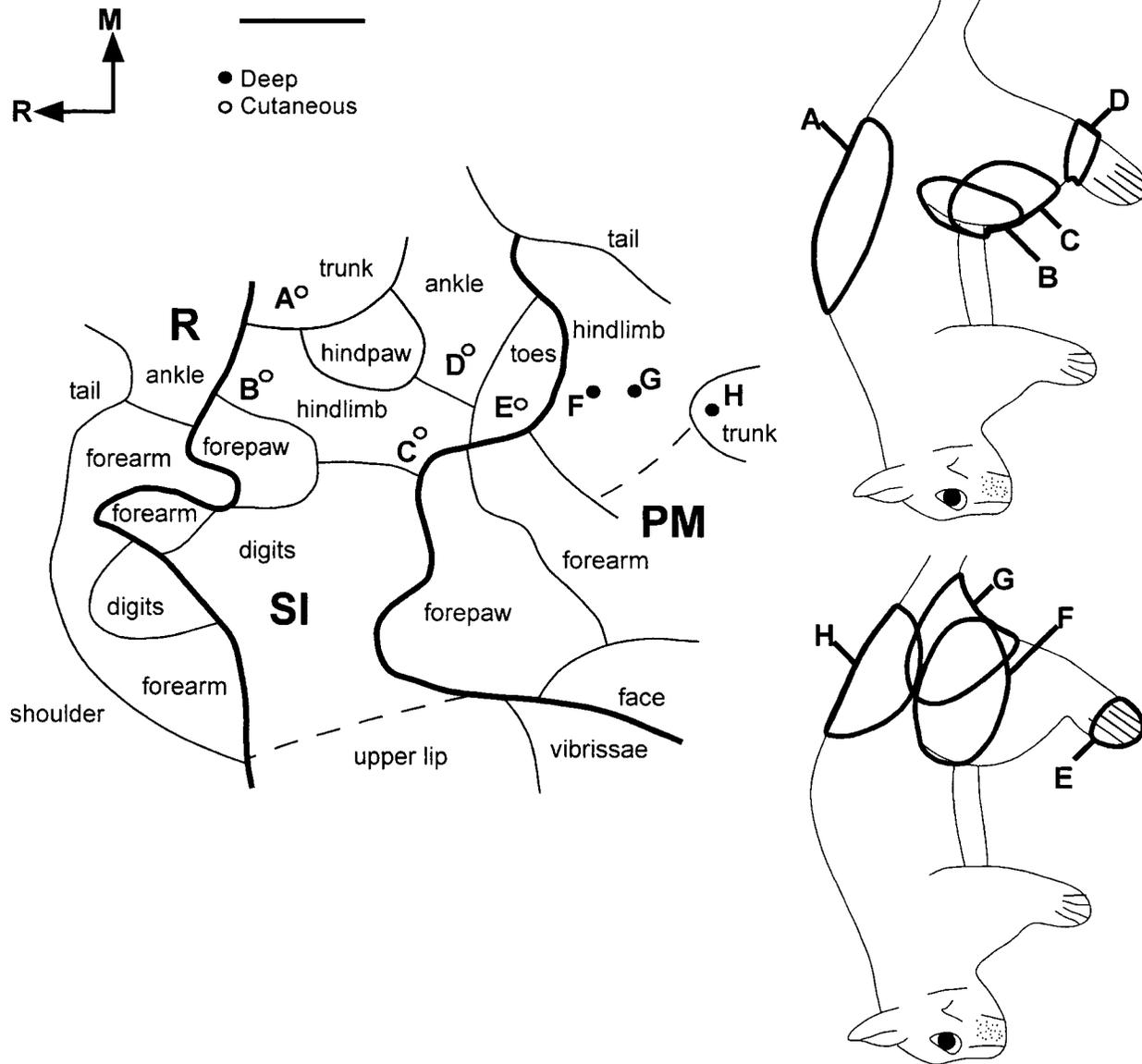


Fig. 12. Recording sites in SI and PM (left), and corresponding receptive fields for neurons at those sites (right) in case 96-5. As the SI/PM border is crossed, a clear reversal in receptive field progression is observed. Also, neurons change their stimulus preference from cutaneous (in SI), to deep (in PM). For abbreviations, see list. Conventions as in previous figures.

Taken together, the results from studies in a variety of different eutherian mammals indicate that at least three representations of the body surface exist in anterior parietal cortex (Fig. 14). Two of these fields include the primary somatosensory area (SI or 3b) and a rostral field (R, 3a, TZ + DZ, KC). The similarities in location, topographic organization, architectonic appearance, and r.f. size and progression suggest that all of these areas are homologous and were likely to be present in the ancestor of

eutherian mammals. The status of the third field is less certain. In monkeys, two fields (areas 1 and 2) are located caudal to 3b. Area 1 contains a representation of cutaneous receptors, whereas area 2 contains a representation of deep receptors. One hypothesis, based on location, is that PM in squirrels and the caudal field in other eutherian mammals represent high-threshold cutaneous receptors, and therefore are homologous to area 1 in primates and SIII in cats. A second hypothesis is that PM or C is

96-31 LH

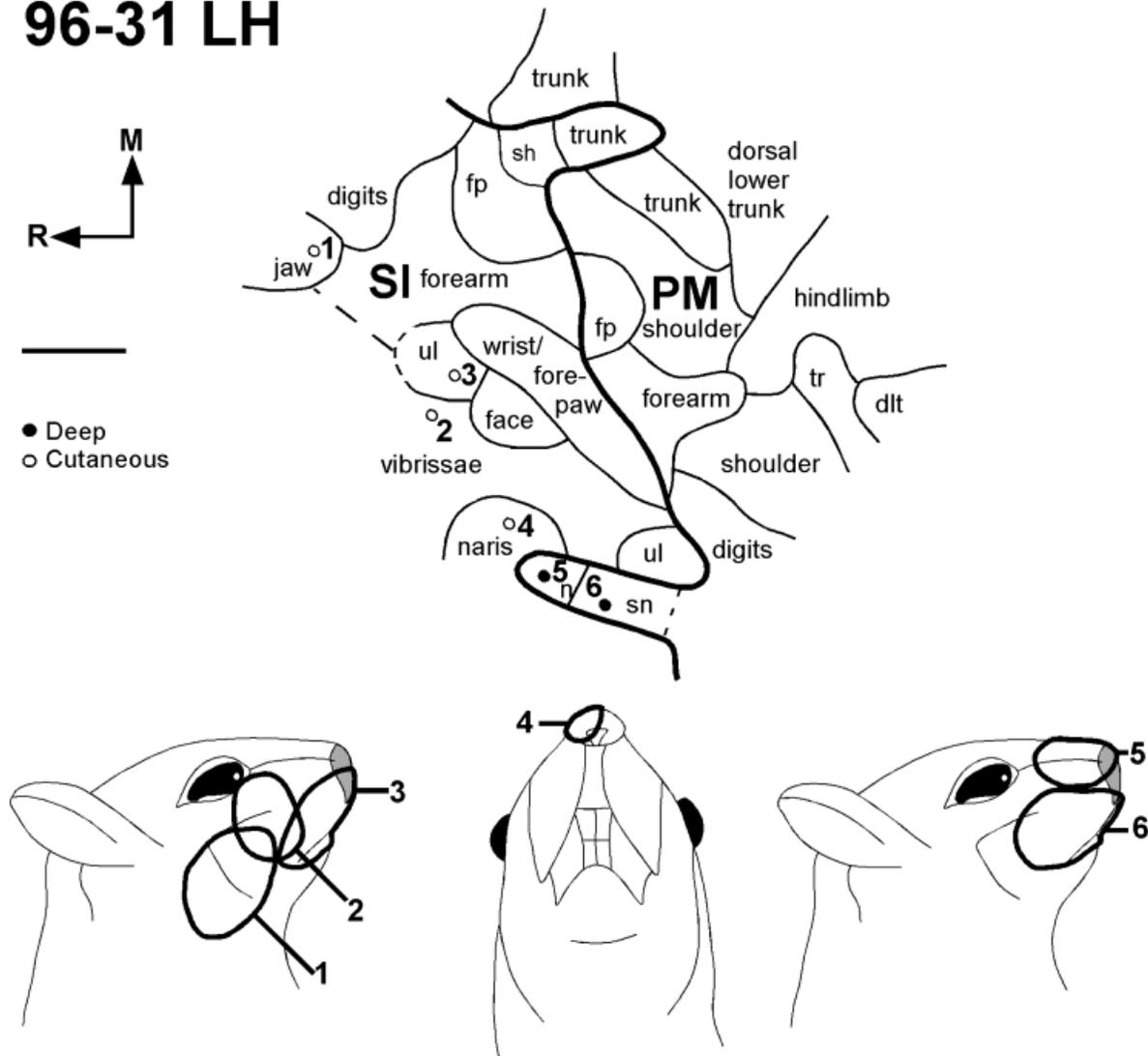


Fig. 13. Recording sites in SI and PM (top), and corresponding receptive fields for neurons at those sites (bottom) in case 96-31. As recording sites cross the SI/PM boundary, receptive fields for neurons at these sites reverse in their progression. For abbreviations, see list. Conventions as in previous figures.

homologous to area 2 in primates and that area 1 was differentiated later in primate evolution and interspersed between 3b and 2. A final hypothesis is that PM or C represent some primitive form of both areas 1 and 2, like area 1/2 in the flying fox (Krubitzer and Calford, 1992).

Comparisons with marsupials and monotremes

Until recently, it was believed that mammals whose ancestors represent early radiations in evolution, such as marsupials and monotremes, contained only a primary somatosensory area in anterior parietal cortex. Recent electrophysiological recordings in species from both mammalian orders indicate that this is not the case. In two of the three species of monotremes investigated, an architectonically distinct rostral field (Ulinski, 1984) in which neurons respond to stimulation of deep receptors was

identified and termed R (Krubitzer et al., 1995b). In a variety of marsupials, SI has been well described, and a rostral field, like that described in this study, has been identified and termed R (Huffman et al., 1999) or SR (Beck et al., 1996). A caudal field (SC or C) has also been described in marsupials (Beck et al., 1996; Huffman et al., 1999, respectively). Like PM, neurons in C respond to stimulation of deep receptors.

Fields R in monotremes, and R (SR) and C (SC) in marsupials contain complete or almost complete representations of the body surface, have similar architectonic appearances, and have similar topographic organizations to R and PM described in the present investigation. Thus, it is likely that all mammals possess at least two anterior parietal areas, SI (or 3b) and R (3a, TZ + DZ, KC), and that these fields are homologous (Fig. 14). The caudal field (C, SC, PM) may have arisen somewhat later in evolution or

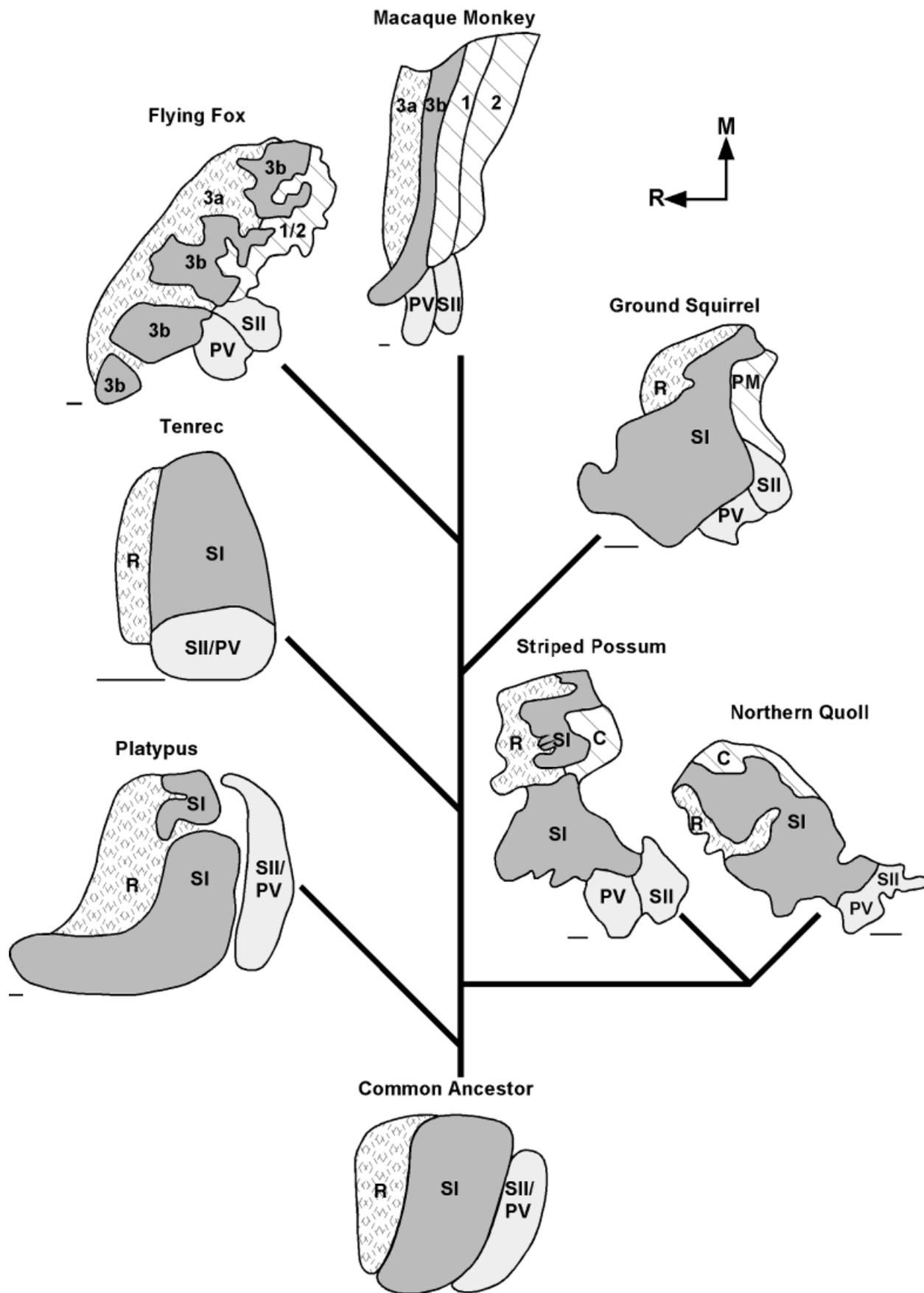


Figure 14

may have been lost, because it was not found in monotremes but has been identified in marsupials, insectivores, and rodents. Comparative studies of the connections of PM, C, SIII, and areas 1 and 2 may help resolve the issue of whether these fields are homologous across mammals.

Are primary fields the oldest fields?

There is a general consensus regarding the order of progression of sensory cortical field addition in evolution. Primary fields are commonly considered to be the oldest or most primitive cortical fields, secondary fields are somewhat newer, and "higher order" cortical fields, located in posterior parietal cortex, temporal cortex, and frontal cortex, are the newest fields. These ideas stem, in part, from early work on monotremes, whose ancestors emerged early in mammalian evolution. Studies by Lende (1964) and Bohringer and Rowe (1977), in the echidna and platypus, respectively, described only a single somatosensory, visual, and auditory field in the neocortex of these species.

Another factor that contributes to these misconceptions is the timing of discovery for primary versus secondary fields. Secondary fields were identified in a variety of mammals some time after the identification of primary fields. Adrian (1940) was the first to describe a double representation of the paws in the cat in cortex lateral to SI. In subsequent studies, a second somatosensory area (SII) was defined in the dog (Woolsey, 1943), monkey (Woolsey 1943, 1944), rabbit (Woolsey and Wang, 1945), sheep, and pig (Woolsey and Fairman, 1946). Around the same time, second sensory areas were found and described in the auditory cortex of cats (Talbot, 1942; Woolsey and Walzl, 1942) and dogs (Tunturi, 1944) and the visual cortex of rabbits (Talbot et al., 1946). These areas in all sensory systems were termed somatic areas I and II, auditory areas I and II, and visual areas I and II. As explained by Woolsey and Fairman (1946), "This terminology was chosen because it carries no anatomic or functional implications and because it can be applied to each of the three systems. . . . Area II in each case was second with respect to area I in time of discovery." In fact, they and others (Sanides, 1969, 1970) even postulated that the second sensory areas might be phylogenetically older, based on location and lack of cytoarchitectonic distinctiveness. Sanides (1969) argues that heavy myelination and a distinct granular cortex, features of primary areas, are evolutionarily newer features of the cortex. He also proposes that as the neocortex expanded away from paleocortex and hippocampal cortex, cortical fields were added concentrically. Thus, primary fields, which reside furthest from paleo- and hippocampal cortex, are more recent additions in mammalian evolution.

Fig. 14. The organization of anterior parietal cortex and lateral somatosensory areas in different mammals. Homologous areas across species are depicted in the same type of stipple. Comparisons across species, including monotremes and marsupials, indicate that multiple somatosensory areas are a common feature of all mammals, and were likely to be present in a common ancestor. Tenrec (Krubitzer et al., 1997); platypus (Krubitzer et al., 1995b); striped possum and northern quoll (Huffman et al., 1999); ground squirrel (present investigation and Sur et al., 1978; Nelson et al., 1979; Krubitzer et al., 1986); flying fox (Krubitzer and Calford, 1992); and Macaque monkey (Nelson et al., 1980; Krubitzer et al., 1995a). For abbreviations, see list. Conventions as in previous figures.

In the past 2 decades, a number of studies have explored cortex beyond primary and secondary areas and have found that multiple representations of the sensory epithelium exist in the cortex of a number of different mammals, including monotremes, marsupials, and basal eutherian mammals (see above). Despite these recent findings, early observations in extant monotremes, and to a large extent the timing of discovery, still hold sway and have led to the notion that the primary sensory fields are evolutionarily the oldest.

This issue of cortical field evolution is important for two reasons. The first is that it clearly impacts our current thinking of cortical processing, particularly our notions regarding cortical hierarchical processing (Felleman and Van Essen, 1991) and feedforward and feedback connections (Rockland and Pandya, 1979). Second, these old ideas are likely the impetus for a number of modern lesioning studies in which the contribution of primary fields to processing in "higher order" fields is examined (Pons et al., 1987; Garraghty et al., 1990; Girard et al., 1991a,b). Because results from the present investigation, as well as studies on a variety of different mammals, indicate that primary fields are not necessarily the oldest fields, current theories of cortical processing should be reevaluated.

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