THE JOURNAL OF COMPARATIVE NEUROLOGY 403:5–32 (1999)

Organization of Somatosensory Cortex in Three Species of Marsupials, *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: Neural Correlates of Morphological Specializations

KELLY J. HUFFMAN,[1] JOHN NELSON,[2] JANINE CLAREY,[3] AND LEAH KRUBITZER[1,3]*
[1]Department of Psychology and Center for Neuroscience, University of California, Davis, Davis, California 95616
[2]Department of Biological Sciences, Monash University, Clayton, VIC 3168 Australia
[3]Vision, Touch, and Hearing Research Centre, University of Queensland, QLD, 4072 Australia

ABSTRACT

The organization of somatosensory neocortex was investigated in three species of marsupials, the northern quoll (*Dasyurus hallucatus*), the striped possum (*Dactylopsila trivirgata*), and the short-tailed opossum (*Monodelphis domestica*). In these species, multiunit microelectrode mapping techniques were used to determine the detailed organization of the primary somatosensory area (SI). In the striped possum and quoll, the topography of somatosensory regions rostral (R), and caudal (C) to SI were described as well. Lateral to SI, two fields were identified in the striped possum, the second somatosensory area (SII) and the parietal ventral area (PV); in the quoll, there appeared to be only one additional lateral field which we term SII/PV. Visual and auditory cortices adjacent to somatosensory cortex were also explored, but the details of organization of these regions were not ascertained. In these animals, electrophysiological recording results were related to cortical myeloarchitecture and/or cytochrome oxidase staining. In one additional species, the fat-tailed dunnart (*Sminthopsis crassicaudata*), an architectonic analysis alone was carried out, and compared with the cortical architecture and electrophysiological recording results in the other three species. We discuss our results on the internal organization of SI in relation to the morphological specializations that each animal possesses. In addition, we discuss the differences in the organization of SI, and how evolutionary processes and developmental and adult neocortical plasticity may contribute to the observed variations in SI. J. Comp. Neurol. 403:5–32, 1999.

Indexing terms: SII; PV; the primary somatosensory area; evolution

When one thinks of marsupials, inevitably a few stereotypic animals such as the Australian kangaroo or the North American opossum come to mind. Marsupials represent a branch of mammals that emerged very early in evolution, approximately 135 million years ago (Clemens et al., 1989; Flannery, 1989), which includes at least 240 species comprising 76 genera (Grzimek, 1990). These mammals are extremely diverse, and different species are adapted for semiaquatic, terrestrial, subterranean, and arboreal habitats. Mammals within this order can be found on three continents in locations ranging from the canopy of tropical rain forests to semiarid planes and deserts.

Grant sponsor: NIH; Grant number: 1 RO1 NS35103–01A1; Grant sponsor: Whitehall Foundation; Grant number: M20–97; Grant sponsor: Australian Research Council (ARC); Grant sponsor: ARC Special Research Centre.

*Correspondence to: Leah Krubitzer, Center for Neuroscience, 1544 Newton Court, Davis, CA 95616. E-mail: lakrubitzer@ucdavis.edu

Received 15 April 1998; Revised 29 July 1998; Accepted 4 August 1998

One reason for examining a range of marsupials, or a range of mammals from any lineage, is that the morphological characteristics of these animals as well as their lifestyles are highly diverse. For instance, the striped possum inhabits the canopy of tropical rain forests. This animal has a remarkable specialization of the forepaw; the fourth digit of the forepaw is elongated and is used for extracting insects from the bark of trees (Fig. 1f; Van Dyck, 1983). The terrestrial quoll also possesses a specialization of the forepaw and hindpaw in the form of raised striations on the pads of the forepaw, hindpaw, and digit tips (Fig. 1e), which are thought to assist in climbing over rocky surfaces (Begg, 1983). In addition, the quoll has well-developed wrist, chin, and snout vibrissae. The nocturnal, terrestrial fat-tailed dunnart is a voracious hunter that possesses large eyes and ears. It has raised pads on the hindpaw and forepaw (Morton, 1983). All of these Australian marsupials use their forepaw to manipulate insect prey. Finally, the South American short-tailed opossum lives close to the ground and feeds on plants, insects, and small vertebrates. It too is an active hunter with large eyes and pinnae (Fig. 1d), raised pads on the forepaw and hindpaw, an elongated snout, well-developed snout vibrissae, and dexterous forepaws. One might expect unique neural specializations, specifically differences in neocortical organization, to reflect these morphological and behavioral specializations. Conversely, one would also expect that there would be common patterns of neocortical organization, due to common ancestry (homologous or generalized features), that all marsupials possess.

Although limited, studies on marsupials confirm that there are characteristics of neocortical organization that all marsupials share, such as a primary (SI) and a second (SII) somatosensory area (see Johnson, 1990; Rowe, 1990; Krubitzer, 1995 for review), as well as some features that are restricted to a particular species, such as a barrel field in SI (Weller, 1972, 1993). In addition, in three species of marsupials an auditory area, possibly the primary auditory area, AI, has also been described (see Aitkin, 1995 for review), and striate cortex or VI has been characterized architectonically, anatomically (see Rowe, 1990 for review), and physiologically (e.g., Sousa et al., 1978; Vidyasagar et al., 1992). However, the details of the internal organization of these fields have only been described in a few species of marsupials (e.g., Sousa et al., 1978; Beck et al., 1996). There is no study in which a direct comparison of the internal organization of a field has been made between several species. Furthermore, no direct correlation has been demonstrated between the organization of somatosensory cortex and the morphological specializations that the animal possesses, other than the vibrissae and the accompanying barrels in SI.

In the present investigation, the organization of somatosensory cortex was determined in three species of marsupials, the northern quoll (*Dasyurus hallucatus*), the striped possum (*Dactylopsila trivirgata*), and the short-tailed opossum (*Monodelphis domestica),* and the architecture of somatosensory cortex was determined in these species and one additional species, the fat-tailed dunnart (*Sminthopsis crassicaudata*; Fig. 1a–d). We have chosen these particular animals because of their unique morphological and behavioral specializations, and because of their availability. In the northern quoll, striped possum and short-tailed opossum, the cortex was explored by using electrophysiological recording techniques, and these results were related to cortical myeloarchitecture or cytochrome oxidase (CO) staining. In the fat-tailed dunnart, only the cortical architecture was examined, and cortical subdivisions were ascertained and compared with the three other species examined in this study. Our goal was to determine characteristics of somatosensory cortical organization that were common to all of these species, and likely to be common to all marsupials, as well as to elucidate the details of somatosensory cortical organization that were unique to each species, that might reflect morphological and behavioral differences.

MATERIALS AND METHODS

Four northern quolls (*Dasyurus hallucatus*) with an average weight of 750 g, one striped possum (*Dactylopsila trivirgata*) with a weight of 435 g, and three short-tailed opossums (*Monodelphis domestica*) with an average weight of 150 g, were used to determine the internal organization of SI and surrounding cortex by using electrophysiological recording techniques. Animals of both genders were used in this study. Prior to electrophysiological recording, each animal was anesthetized with either an i.p. injection of sodium pentobarbital (30 mg/kg for the northern quolls and 25 mg/kg for the striped possum), or a combination of ketamine (40 mg/kg), xylazine (5 mg/kg), and sodium pentobarbital (20 mg/kg) administered intramuscularly and intraperitoneally, respectively, for the short-tailed opossum. To maintain surgical levels of anesthesia, supplements of sodium pentobarbital (10 mg/kg), or ketamine (15 mg/kg) were given throughout the experiment. Body temperature was maintained by placing the animal on a heating pad and monitoring its temperature with a rectal thermometer; heart rate and respiration rate were continually monitored.

Once the animal was anesthetized, an incision was made along the midline of the scalp, the skin and temporal muscle were retracted, and a craniotomy was performed over somatosensory cortex. In the short-tailed opossum, a larger craniotomy was made over the entire hemisphere. The dura was retracted, an acrylic well was built around the opening, and the well was filled with silicone oil to help maintain cortical temperature and to protect the exposed cortex from desiccation. To stabilize the head, a metal bar was cemented to the head at one end, and attached to a magnetic base at the other. The magnetic base was then attached to the floor of the stereotaxic frame upon which the micromanipulator was placed. During surgery, images of the exposed cortex were made either by taking a photograph, or by using a CCD video camera system (Optronics Engineering, Zeiss, Thornwood, NY) attached to a computer. The image was saved, and then printed. Locations of electrode penetrations were marked on the photograph or image, using blood vessel patterns as landmarks.

Electrophysiological recording

A tungsten-in-glass electrode (1 MΩ at 1 kHz) was used to record extracellularly from multiple units. The electrode was attached to a micromanipulator, oriented perpendicular to the pial surface, and lowered with a stepping hydraulic microdrive (model 650 micropositioner, David Kopf Instruments, Tujunga, CA) to a depth of 300–700 μm. Recordings were routinely made in the middle cortical layers as judged by the depth from the cortical surface, and

Fig. 1. Photographs of the quoll, 750 g (**a**), striped possum, 435 g (**b**), fat-tailed dunnart, 20 g (**c**), and the short-tailed opossum, 150 g (**d**). The quoll has a number of distinct body vibrissae in addition to those on the snout. The forepaw specialization of the quoll takes the form of corrugated pads on the distal digits and distal pads (**e**). The striped possum has a very unique forepaw with an elongated fourth digit (**f**).

the amplitude and the consistency of the driven activity. Multiple electrode penetrations were made (50–240 in any given animal), and spaced approximately 100–500 μm apart in SI, and further apart in areas surrounding SI. Recordings were also made along the medial wall, i.e., the electrode was advanced parallel to the cortical layers.

Once the electrode was advanced into the cortex, the body surface was stimulated. Stimulation consisted of the displacement of hairs, light brushing of skin, light taps to the skin, pressure, and joint manipulation. For stimulation of deep receptors, the body part on which they were located was isolated by firmly pressing adjacent skin regions to prevent them from being stimulated. By changing the place that was firmly held and the place that was stimulated, we could define the receptive field with a high degree of accuracy. Although the size of the receptive field for neurons that responded to stimulation of deep receptors may actually be somewhat smaller than what we have defined, we believe that this difference is minimal, and would not effect our results, nor the interpretation of our results. The neural response to deep receptors was vigorous, and our isolation procedures allowed us to determine if a receptive field encompassed an entire digit, for instance, or only the distal phalanx of the digit.

In all animals, visual and auditory cortex surrounding somatosensory cortex was explored to a limited extent. For neurons in visual cortex, stimulation consisted of full field flashes of light, moving bars of light, and spots or flickering spots of light. Auditory stimuli were crude and consisted of complex sounds made by the experimenter, e.g., tapping pencils together, snapping fingers and whistling.

The neural responses were amplified, observed on an oscilloscope, and played through a speaker. The receptive field (RF) was defined as the area of the body surface that when stimulated, produced a neuronal response. Receptive fields were obtained for neurons at all recording sites in somatosensory cortex, and were drawn on pictures of the body. Receptive fields were not determined for neurons in auditory or visual cortex. The neuronal response properties and stimulus preferences for neurons were noted. Electrolytic lesions (10 μA for 10 sec) were made, or probes were inserted at strategic locations in order to relate electrophysiological recording results to histologically processed tissue.

Tissue processing

After the mapping was completed, the animal was given a lethal dose of sodium pentobarbital and transcardially perfused with 0.9% saline, then 3% paraformaldehyde in 0.1 M phosphate buffer, pH 7.4, and finally a solution of 3% paraformaldehyde, 10% sucrose in phosphate buffer. The brain was removed from the skull, the cortex was peeled from the brainstem and thalamus, the medial wall was retracted, and the cortex was flattened between two glass slides.

With a freezing microtome, the cortex was cut parallel to the pial surface into 40-μm- thick sections in the northern quoll, 35-μm sections in the striped possum and short-tailed opossum, and 20- to 35-μm sections in the fat-tailed dunnart. For the striped possum, northern quoll, and fat-tailed dunnart, the sections were alternatively stained for myelin (Gallyas, 1979), and assayed for cytochrome oxidase (Carroll and Wong-Riley, 1984). For the short-tailed opossum, sections were stained for myelin only, because related studies in our laboratory in the short-tailed opossum indicated that CO stains were not as useful in identifying cortical field boundaries such as SI, VI and presumptive primary auditory area (A).

Data analysis

For the quoll, striped possum, and short-tailed opossum, the electrophysiological recording results were related to architectonic boundaries by matching the lesions, probes, and blood vessel patterns in the processed tissue to their locations on the photograph or video image of the cortex. The entire series of sections was used to determine the cortical field boundaries. The final boundary was the average border traced through all cortical layers. For the quoll and the short-tailed opossum, the boundaries of SI were most easily distinguishable in the sections stained for myelin. For the striped possum, the boundaries of SI were most easily distinguishable in the sections assayed for CO, and for the fat-tailed dunnart, SI could be clearly identified in both the sections reacted for CO and those stained for myelin.

In the quoll and striped possum, in cases in which complete maps of SI were obtained, area measurements of SI and individual as well as groups of body part representations within SI were made by using NIH IMAGE 1.61 software (National Institutes of Health). Body part representations of interest were measured and the percentage of SI that they occupied was calculated. Several different body part representations are overlapping in SI, and often multiple body part representations together formed the representation of interest (e.g., Fig. 2, snout and lip vibrissae; dorsal digits 4–3). Thus, it was necessary to calculate measurements of small groups of body part representations, some of which were subsets of others. Because all body part representations were not discretely measured, and because some areal measurements are a subset of other measurements (e.g., tip of tongue is a subset of tongue in the striped possum), the representations in Table 2 do not add up to 100% of SI. Both the northern quolls and striped possum were caught under the appropriate collecting and housing permits issued by the Queensland government. The dunnart and short-tailed opossum were bought from breeding colonies specifically created for use in research. All protocols for these experiments were approved by either the University of Queensland Animal Experimentation Ethics Committee (UAEEC), or by the Animal Use and Care Administrative Advisory Committee (AUCAAC) of the University of California, Davis.

RESULTS

Electrophysiological recording results in the quoll, striped possum, and short-tailed opossum revealed a large portion of the neocortex in which neurons were responsive to somatosensory stimulation. Within this region, several distinct cortical areas or fields were present. Because any given cortical field does not always meet all criteria used to define it, to accurately subdivide the neocortex, it is critical to use a number of different criteria (Kaas, 1982). In the present study a cortical field was defined using one or more of the following criteria: 1) the presence of a complete representation of the sensory epithelium; 2) a change in stimulus preference for neurons in the different fields; 3) receptive field reversals across boundaries of fields; 4) a rerepresentation of the same receptive field in different

cortical locations; and 5) a distinct architectonic appearance. There were 2 fields that did not possess a complete representation of the body surface, but did meet a number of other criteria; we call them regions rather than fields. We were able to identify at least four somatosensory fields or regions in the quoll (n = 4) and five somatosensory fields or regions in the striped possum (n = 1). Due to the lower recording density in the short-tailed opossum (n = 3) compared to the quoll and striped possum, only a single field, SI, could be defined with confidence. In the following results we describe the organization of the separate somatosensory fields in the quoll, striped possum, and short-tailed opossum, and briefly review the morphological and behavioral characteristics of these species.

Organization of the primary somatosensory area

In the quoll, there was a large region of cortex in which neurons were responsive to stimulation of cutaneous receptors. SI contained a complete representation of the sensory epithelium, with the tail represented most medially, progressing in a mediolateral sequence of representation to the hindpaw and toes, onto the trunk, forelimb, and forepaw, and then onto the face and snout most laterally (Figs. 2, 3). Neurons in SI had small receptive fields, and were securely driven by cutaneous stimulation to the contralateral body surface. In all cases, the rostrocaudal extent of SI was not uniform in size and measured 1–3 mm, and the mediolateral extent measured 8–9 mm. When recording sites progressed beyond the rostral and caudal boundaries of SI, the stimulus preference for neurons changed from cutaneous to deep, the progression of receptive fields often reversed, and the architectonic appearance of cortex changed (see below).

Within the forepaw representation, D5 was represented most medially followed by digits 4–1 in a lateral progression (Figs. 2–4). The distal digits were represented rostrally, whereas more proximal digits and the palmar surface were represented caudally (Figs. 2–4). The representation of the forepaw in SI occupied 21–22% of the entire representation in the two quolls in which complete maps of SI were obtained (Table 2). The representations of the snout, chin, cheek, and lip vibrissae assumed 35–40% of SI, the wrist vibrissae 3–4%, the elbow vibrissae 4%, and the tail, hindlimb, forelimb (excluding the forepaw), and trunk 13–17%. When all vibrissae were included in the measurements (wrist + all others), it was found that they occupy the largest portion of the representation (42–44%). In addition to the enlarged forepaw representation in the quoll, the receptive field configuration for neurons here was unique. Often, receptive fields were restricted to an individual striated pad on the digit tip (e.g., Fig. 11, RFb), or to a group of specialized pads (Fig. 11, RFd).

In the striped possum, as in the quoll, there was a large portion of cortex in which neurons were responsive to cutaneous stimulation (Fig. 5). SI contained almost a complete representation of the body surface, and neurons in SI of the striped possum had small receptive fields, and responded to cutaneous stimulation of the contralateral body surface. As with the quoll, when recording sites extended beyond the boundaries of SI, the stimulus preference for neurons in these sites changed from cutaneous to deep, the progression of receptive fields reversed at some of the boundaries (see below), and a rerepresentation of receptive fields was found.

The overall mediolateral organization was like that described for the quoll, and was 2–3 mm in its rostrocaudal extent and approximately 12 mm in its mediolateral extent. Although the quoll was almost twice as large as the striped possum, the size of the neocortex of the striped possum was about twice that of the quoll, and SI was proportionately larger as well (Table 2). One difference in the internal organization of SI in the striped possum was the amount of cortical space allotted to processing input from different body parts (Table 2). In the striped possum, the entire forepaw accounted for 29% of the total area of SI, with the representation of the specialized fourth digit occupying 33% of the forepaw representation and 10% of the entire representation in SI. The representation of the tip of the tongue was large and occupied 16% of the entire representation of SI, and 67% of the entire tongue representation. The vibrissae on the snout, chin, cheek, and lip occupied 24% of SI, the snout occupied 6% of SI, and the toes occupied 3% of SI (Table 2). Within the enlarged representation of digit 4, the receptive fields for neurons were smaller than RFs for other parts of the forepaw. For instance, a receptive field was often restricted to a small portion of distal digit 4, whereas receptive fields for neurons in other digit representations were larger, and encompassed more of the digit, or multiple digits (Fig. 9).

The organization of SI in the short-tailed opossum was determined from more limited data (Figs. 6, 7). However, some similarities were observed between the organization of SI in the short-tailed opossum and the other two species. First, neurons here tended to respond best to stimulation of cutaneous receptors on the contralateral body surface. However, unlike other animals in this study, under our recording conditions, there were regions within SI that contained neurons unresponsive (X), or very weakly responsive (ss) to cutaneous stimulation. Furthermore, in one case (Fig. 6), there were locations in SI that contained neurons responsive to auditory and somatosensory stimulation, whereas in the other case (Fig. 7), there were regions that contained neurons responsive to deep and cutaneous stimulation of a given body part. Second, the oral structures (tongue and lips), and snout were represented most laterally in the field. The vibrissae, face, and orbital region were represented medially, and the forepaw was represented further medially. In one case (Fig. 6), the tail and caudal trunk were represented in a far medial location, similar to the quoll and striped possum.

The relative size and location of SI was similar to that of the other species. The rostrocaudal extent of SI measured approximately 3 mm, whereas the mediolateral extent measured about 5 mm. Because the mapping density was low and some of the boundaries were estimated from myeloarchitecture, detailed measurements were not possible. However, from the data that were collected, it appears as if a large proportion of the entire extent of SI was devoted to representations of the face and head. There was a small densely myelinated island rostral to SI; however, the density of recording was too low to determine if this island was a portion of SI or a separate field.

Organization of somatosensory cortex rostral to and caudal to SI

In all quolls and the single striped possum, there was a region just rostral to SI (termed the rostral region, R) in which neurons were responsive to stimulation of deep receptors in the skin and muscle. The field was termed R

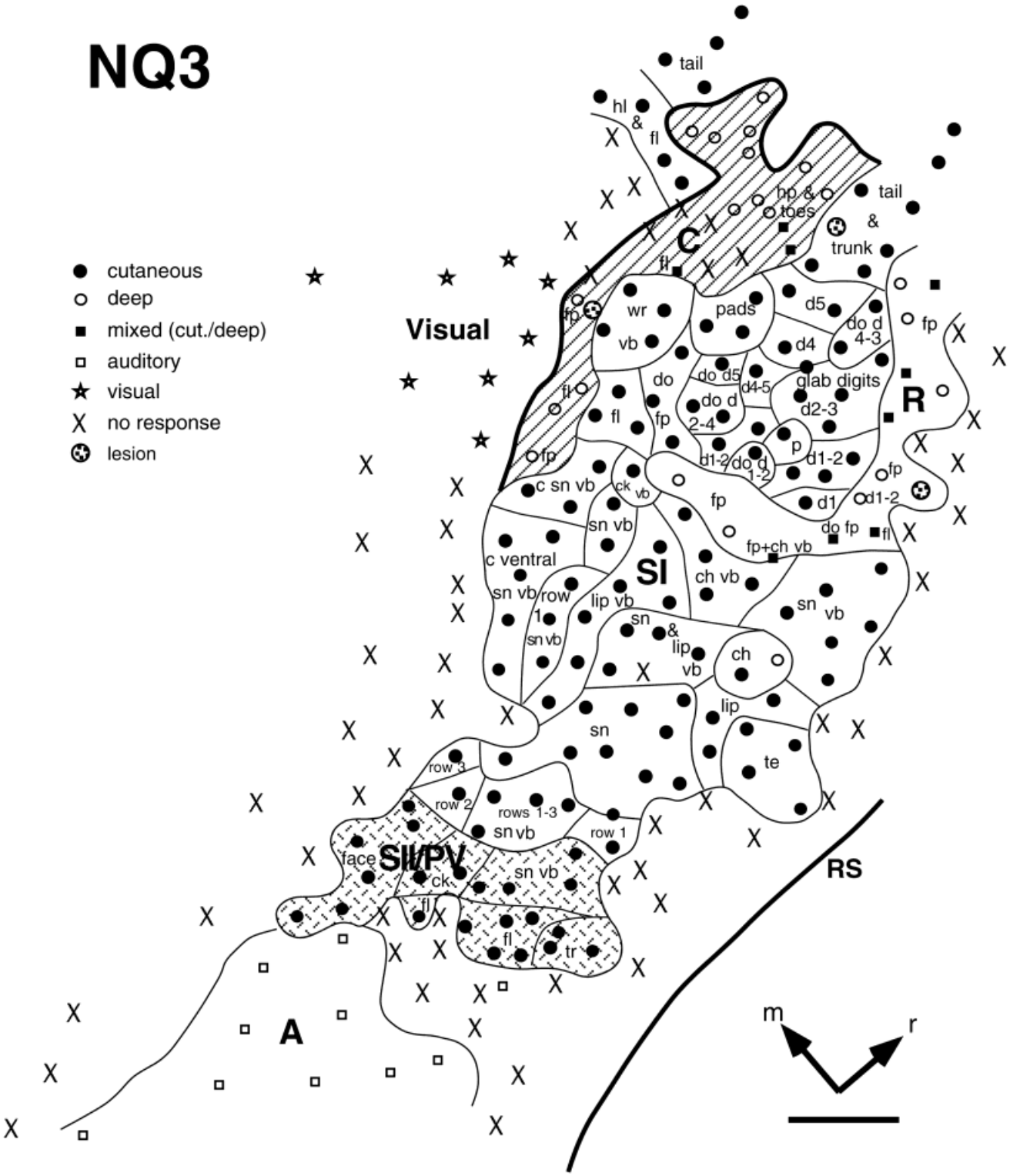


Fig. 2. A reconstructed map of the somatosensory cortex of northern quoll (NQ)3. In this case, recording sites in primary somatosensory area (SI; filled circles) were made at distances of 200–400 µm apart, and the details of the internal organization could be clearly discerned. In the quoll, four somatosensory areas were observed, the primary SI, the caudal somatosensory region (C, striped), the rostral somatosensory region (R, shaded), and the second somatosensory area/ parietal ventral area (SII/PV, stipple). As in other mammals, the primary somatosensory area had a mediolateral organization with the tail and hindlimb represented most medially, followed by representation of the forelimb, trunk, forepaw, face, and snout vibrissae in a lateral progression. A large proportion of the field is devoted to representing the forepaw, and the snout, face, and wrist vibrissae. Thin lines indicate physiological boundaries. Thick lines represent combined physiological and architectonic boundaries. For abbreviations in this and subsequent figures, see Table 1. Scale bar = 1 mm.

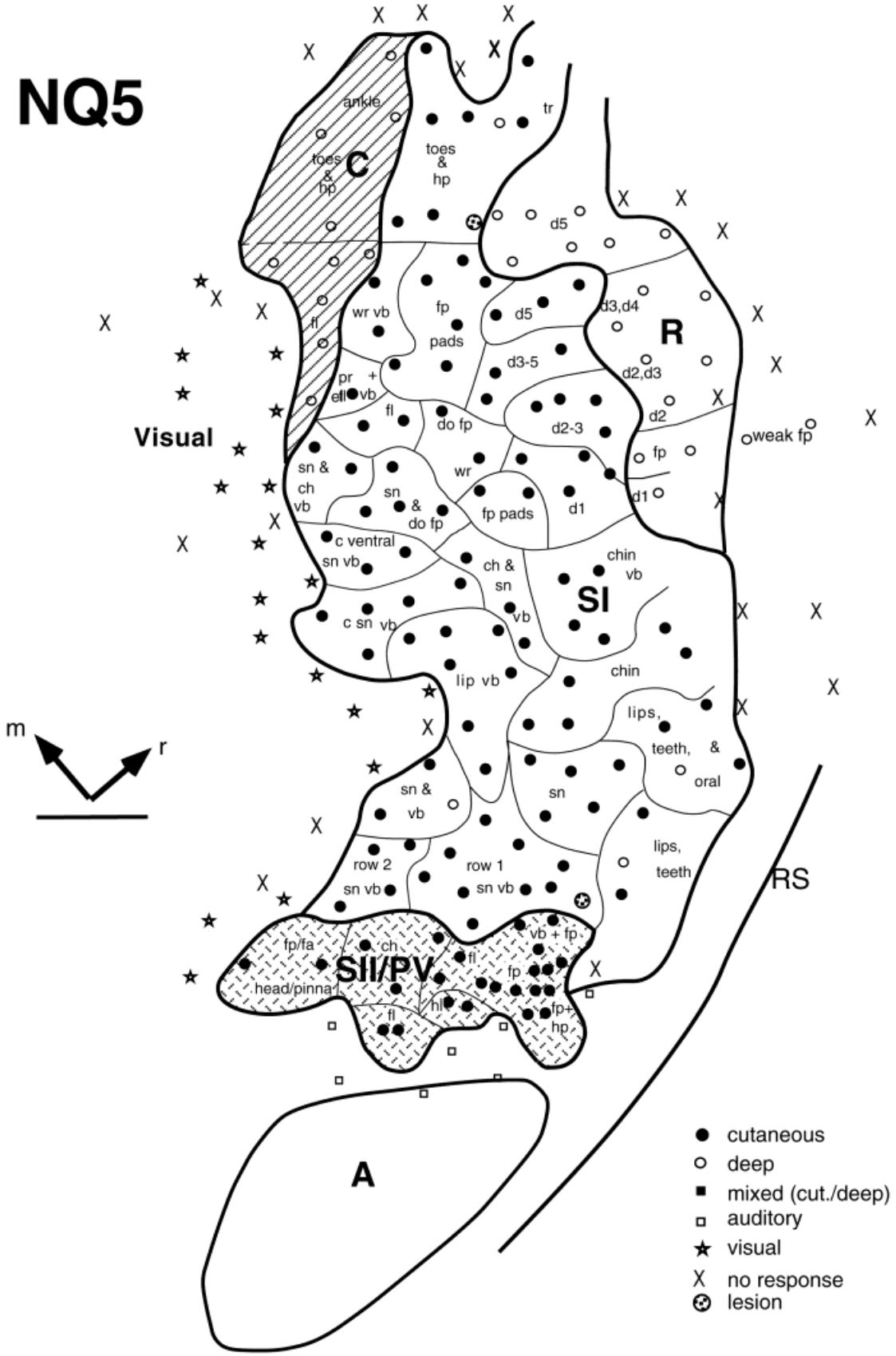


Fig. 3. A reconstruction of the somatosensory cortex of northern quoll (NQ)5. The internal organization, and location of cortical fields is very similar to the previous case. Conventions as in previous figure. Scale bar = 1 mm.

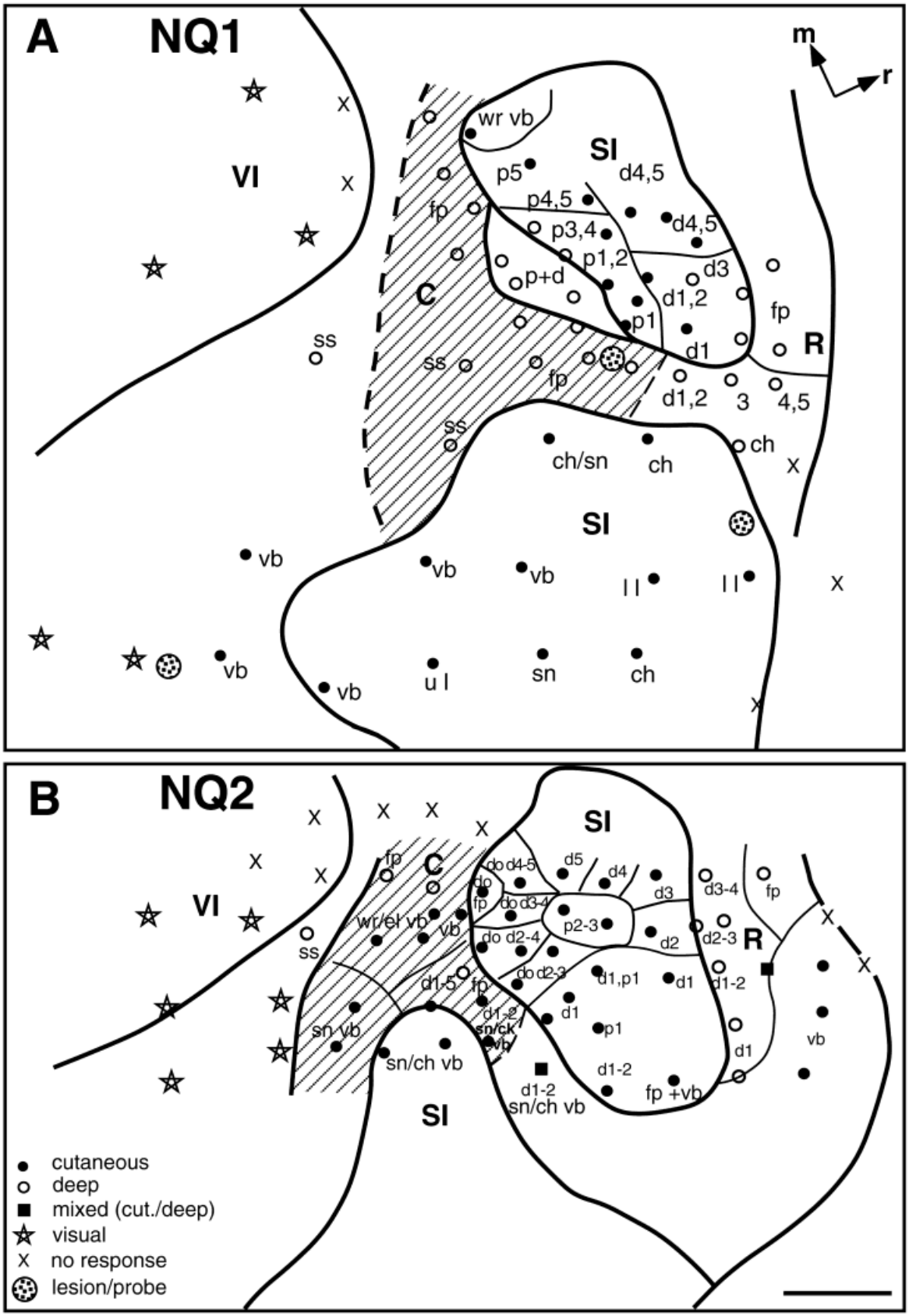


Fig. 4. A reconstruction of partial maps from northern quoll (NQ)1 (**A**), and NQ2 (**B**). In these cases, the details of the forepaw representation in primary somatosensory area (SI) are apparent. NQ1 clearly demonstrates the rostral location of the digits relative to the proximal portion of the forepaw. In NQ2, the electrophysiological recordings in rostral somatosensory region (R) demonstrate that the vibrissae representation contains neurons that respond to cutaneous stimulation, unlike other cases in which R contains only neurons responsive to deep stimulation. Dashed lines indicate approximated boundaries. Conventions as in previous figures. Scale bar = 1 mm.

TABLE 1. List of Abbreviations

Cortical areas and regions	
A	Presumptive primary auditory area
AI	Primary auditory area
C	Caudal somatosensory region
CT	Caudal temporal area
M	Presumptive motor cortex
OB	Olfactory bulb
Ps	Peristriate cortex
PV	Parietal ventral area
PYR	Pyriform cortex
R	Rostral somatosensory region
RS	Rhinal sulcus
SC	Caudal somatosensory area
SI	Primary somatosensory area
SII	Second somatosensory area
SR	Rostral somatosensory area
VI	Primary visual area
VII	Second visual area
Vis	Visual
Body parts	
ch	Chin
ck	Cheek
d, dig	Digit
el	Elbow
fa	Face
fl	Forelimb
fp	Forepaw
glab	Glabrous
hl	Hindlimb
hp	Hindpaw
ll	Lower lip
p	Pads
sn	Snout
ss	Somatosensory, unable to identify RF (receptive field)
te	Teeth
ton	Tongue
tr	Trunk
ul	Upper lip
vb, vib	Vibrissae
wr	Wrist
Direction terms	
c	Caudal
do	Dorsal
m	Medial
pr	Proximal
r	Rostral
Animals	
NQ	Northern quoll, or native cat
SP	Striped possum
StO	Short-tailed opossum
Other	
CO	Cytochrome oxidase

TABLE 2. Area Measurements and Percentages of Body Part Representations Within Primary Somatosensory Area (SI) of the Northern Quoll (NQ), and Striped Possum (SP)[1]

	NQ3		NQ5		SP1	
Body representation	Area (mm^2)	% of SI	Area (mm^2)	% of SI	Area (mm^2)	% of SI
Entire contralateral body	16.1	100	19.5	100	36.7	100
Dorsal + glab forepaw	3.5	22	4.1	21	10.5	29
Forepaw pads (glab palm)	0.5	3	1.4	7	4.6	13
Dorsal + glab digit 4	0.8	5	0.6	3	3.5	10
Dorsal + glab d1, d2, d3, d5	2.9	18	2.5	13	2.4	7
Wrist vibrissae	0.6	4	0.5	3	*	*
Elbow vibrissae	*	*	0.7	4	*	*
Face vb (sn, ch, ck, lip vb)	6.4	40	6.9	35	8.7	24
Snout	1.5	9	1.3	7	2.3	6
Oral + lips	1.1	7	2.4	12	4.6	13
Tongue	*	*	*	*	8.6	23
Tip of tongue	*	*	*	*	5.8	16
Tail, hl, toes, tr, fl (no forepaw)	2.1	13	3.3	17	1.1	3

[1]For abbreviations, see Table 1.

because of the similarities in position, architecture, and stimulus preference to the rostral field in monotremes and some insectivores (Krubitzer et al., 1995a, 1997b; Pobirsky et al., 1998). Neurons in R responded to light to moderate taps to the body, and to manipulation of the limbs, but, with a few exceptions, did not respond to cutaneous stimulation. A number of criteria were used to distinguish this region from SI, including a change in stimulus preference, a rerepresentation of body parts, a unique myeloarchitectonic appearance, and reversals in receptive field progression across the boundaries of SI and R. However, a complete representation of the sensory surface was not observed in R. Many of the locations in R contained neurons responsive to stimulation of the forepaw or digits, and the mediolateral organization of the forepaw representation in R was similar to that described for SI (Figs. 3–5). At many locations within R, neuronal responses reflected the RFs of neurons in immediately neighboring sites in SI (Fig. 11), and RF sequences reversed across the SI-R border (Figs. 10, 12). Also, the representations of the digits and forepaw in R appear to form a mirror image of the same body parts in SI (Fig. 4b; in this animal there were also clear cutaneous responses to stimulation of the vibrissae in R). Similarly, in the striped possum, the representation of the digits and forepaw pads was a mirror reversal of the representation of the same body parts in SI (Fig. 12).

The lack of a complete representation in this narrow region is difficult to interpret. It is possible that more detailed sampling of this region may have revealed a complete representation of the body surface. However, in the quolls illustrated in Figures 2 and 3 and the striped possum (Fig. 5), almost the entire rostral boundary of R was defined by both a change in responsiveness (i.e., sites of no response rostral to R) and distinct myeloarchitecture. There appears to be very little cortex in which the rest of the body surface could have been represented.

In two of the quolls and the single striped possum, R interdigitated with SI and separated the representations of the hand and face in the primary field (Figs. 4, 5). In the other two quolls, the interdigitation was either incomplete (Fig. 2) or not present (Fig. 3). R was bounded rostrally by cortex in which neurons were mostly unresponsive to any type of stimulation we tried (Figs. 2, 3, 5). At a few sites in one quoll (Fig. 3), and in the striped possum (Fig. 5), neurons were responsive to high threshold stimulation of deep receptors.

There were too few recording sites rostral to SI in the opossum to comment on whether or not there is a similar region in this species. In one animal there were a few locations containing neurons responsive to stimulation of deep receptors on the forepaw and wrist (Fig. 7), and in another case (not illustrated), there were four sites that contained neurons responsive to stimulation of deep receptors on the snout and chin. However, most of this region was not architectonically distinct.

In the striped possum, there was a region of cortex caudal (C) to SI, and in the quoll caudomedial to SI, that contained neurons that generally responded to stimulation of deep receptors. The number of recording sites obtained in C in any given animal was too low for the details of the organization of this region to be reliably obtained. However, the data that we did obtain indicate that most of this region was devoted to the representation of the forepaw. There were some exceptions: in the two quolls in which more detailed results were obtained, a representation of the hindpaw was observed (Figs. 2, 3). In another quoll (Fig. 4b), neurons responsive to cutaneous

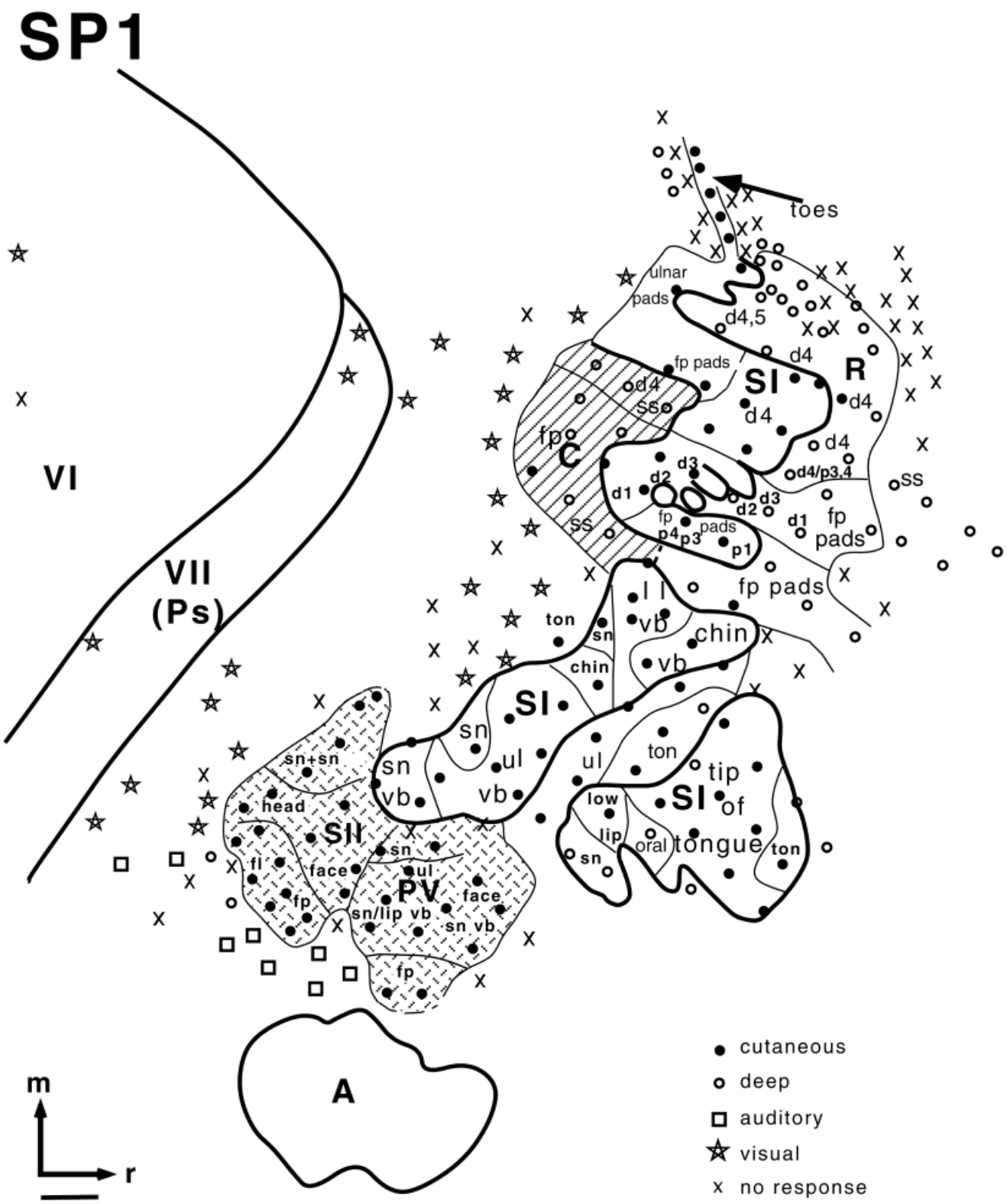


Fig. 5. A reconstruction of electrophysiological recordings from the striped possum. Although the gross mediolateral organization of primary somatosensory area (SI) is similar to that of the quoll, the representations of the fourth digit and the tip of the tongue are greatly magnified. Unlike the quoll, a clear distinction between second somatosensory area (SII) and parietal ventral area (PV) can be identified. Conventions as in previous figures. Scale bar = 1 mm.

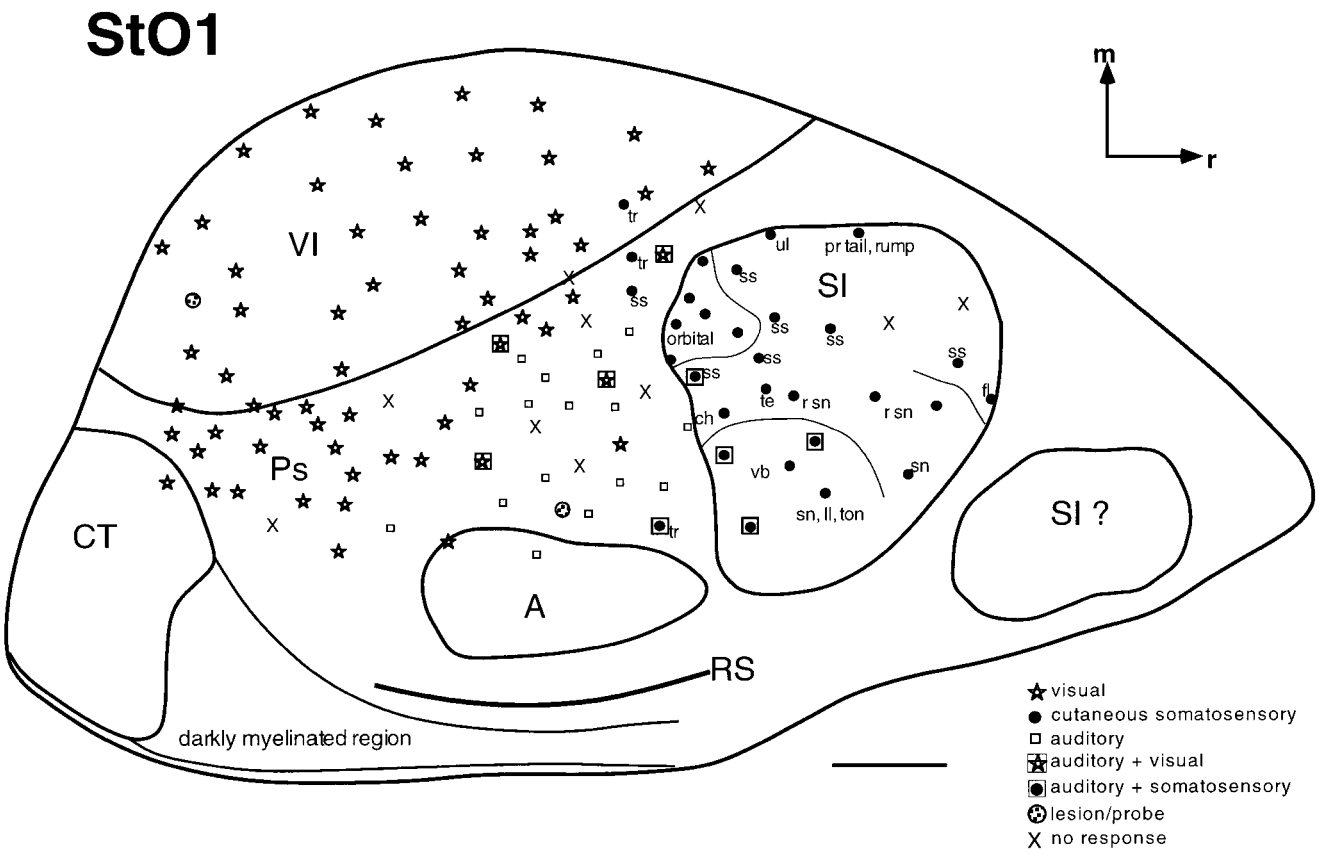


Fig. 6. A reconstruction of electrophysiological recordings across a large extent of the neocortex in short-tailed opossum 1. Although primary somatosensory area (SI) has not been explored in the same detail as the quoll and striped possum, it is clear that the representations of the orbital region and the vibrissae occupy over half of the entire SI. Our electrophysiological recording results indicate that much of the neocortex in the short-tailed opossum is devoted to processing visual inputs. A relatively large portion of the neocortex also appears to be involved in processing auditory inputs. There was a darkly myelinated island just rostral to SI, termed SI?. It is unclear if this island is a part of SI proper, or a separate field. Conventions as in previous figures. Scale bar = 1 mm.

stimulation of the elbow, wrist, and snout vibrissae were observed. As in R, there was no evidence for a complete representation of the body surface within C. In contrast to R, we did not observe any clear examples of a RF sequence that reversed across the SI-C border in any of the animals. Again, this outcome would not appear to be a result solely of low recording density because most of the outer boundary of C was defined physiologically and architectonically in the detailed maps (Figs. 2, 3, 5).

This caudal region differed in architectonic appearance from SI (see below), and in the quoll and striped possum was bounded caudally by either neurons unresponsive to any type of stimulation that we used, or by neurons responsive to visual stimulation. In the short-tailed opossum, neurons immediately caudal to SI were responsive to auditory or visual stimulation. Thus, there does not appear to be an equivalent region in this species.

The regions designated R and C were not considered to be part of SI in quolls and the striped possum for several reasons. First, they were dominated by neurons that respond to stimulation of deep receptors. Second, RFs for neurons in both R and C tended to be somewhat larger than for neurons in SI (Figs. 8, 9). Third, there were some examples of rerepresentation of body parts at distantly located regions of cortex (Figs. 10, 12) which, in a few instances, formed a sequence of RFs that mirrored a parallel sequence in SI (Fig. 11). Finally, the architectonic appearance of both R and C was different from that of SI (Fig. 13). However, because neither region appears to contain a complete representation of the body surface, their status as classically defined somatosensory fields remains unclear.

Organization of the second somatosensory area and the parietal ventral area

In the striped possum, there was evidence for two separate representations of the body surface (Fig. 5). One of these fields in the striped possum was termed the second somatosensory area (SII), due to its similarity to SII described in other mammals (Krubitzer et al., 1986, 1995a; see Johnson, 1990 for review). The second field was termed the parietal ventral area (PV) for similar reasons (Krubitzer et al., 1986; Krubitzer and Kaas, 1990; Krubitzer, 1996). Both SII and PV contained neurons that responded to cutaneous stimulation of the body surface; however, receptive fields for neurons in these regions were larger than for neurons in SI (Fig. 9). SII was located caudal to SI, and shared a common border with SI at the representations of the snout vibrissae and snout (Fig. 5). The snout

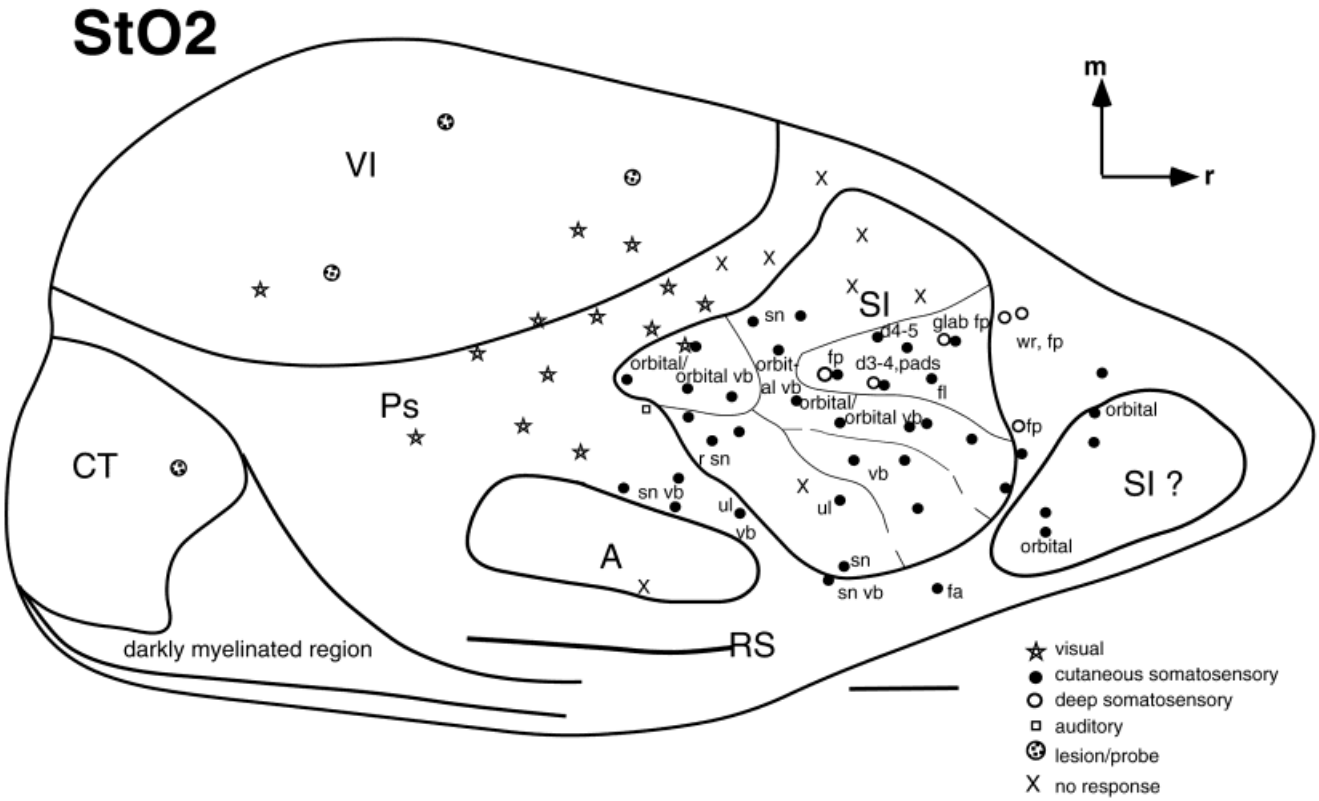


Fig. 7. A reconstruction in which more limited electrophysiological recording data were gathered in short-tailed opossum (StO)2. The organization of primary somatosensory area (SI) appears to be similar in some respects to that in the previous case, although the data are too sparse to make accurate comparisons. Again, a large portion of SI is devoted the orbital region, snout, and snout vibrissae. Cortex just rostral and lateral to SI contains neurons responsive to somatic inputs. Conventions as in previous figures. Scale bar = 1 mm.

vibrissae in SII were represented caudal to the representation of the snout vibrissae of SI, and the face and head representations of SII were lateral to the snout vibrissae representation of SII. The forelimb and forepaw were represented lateral to this, with the forelimb representation caudomedial to that of the forepaw (Fig. 5). As described for other mammals, SII was a noninverted, or upright representation with respect to the animal's head.

Just rostral to SII in the striped possum, there was evidence for another field, PV. This field represented some of the body parts that were in SII, and contained almost a complete representation of the body surface. In PV, neurons with receptive fields on the snout and face were medial, adjacent to neurons in SI with receptive fields on the vibrissae. The snout vibrissae were represented lateral to this. Finally, the forepaw was represented most laterally in the field. Figure 12 illustrates a sequence of RFs from adjacent cortical sites across the SI-PV border, and demonstrates a rerepresentation of parts of the snout and vibrissae in the two fields, and a rough mirror image reversal of these body parts about the border. We did not find a representation of the trunk or hindlimb in either SII or PV. It is likely that the representations of these body parts are very small, especially because the amount of cortex that they assume in SI is small (e.g., hindlimb), or not defined (e.g., trunk). Because the size of SII and PV is small, a greater recording density may be necessary to observe these very small representations within the fields.

In the two quolls in which more complete data were obtained, there was evidence for a representation lateral to SI (Figs. 2, 3). We termed this area SII/PV because it was unclear to which of these fields it corresponds. Because the recording density was relatively low, the details of the internal organization of this field were difficult to determine. However, like SII and PV in the striped possum, the face and snout representation shared a common border with similar representations in SI. The limbs were represented lateral to this. In one case (Fig. 3), there was a representation of the forepaw in both caudal and rostral locations of this SII/PV region, suggesting that SII/PV may be two separate fields in the quoll, as in the striped possum.

In the short-tailed opossum, the presence of a lateral field was not demonstrated, possibly because this region was only coarsely sampled in two animals (Figs. 6, 7).

Organization of cortex surrounding somatosensory areas

In all animals in which electrophysiological recordings were made, cortex surrounding somatosensory cortex was explored. In the quoll and striped possum, neurons in cortex caudal to SI and C were either unresponsive to any type of sensory stimulation, or were responsive to visual stimulation (Figs. 2–5). With a further progression caudally in the striped possum and short-tailed opossum

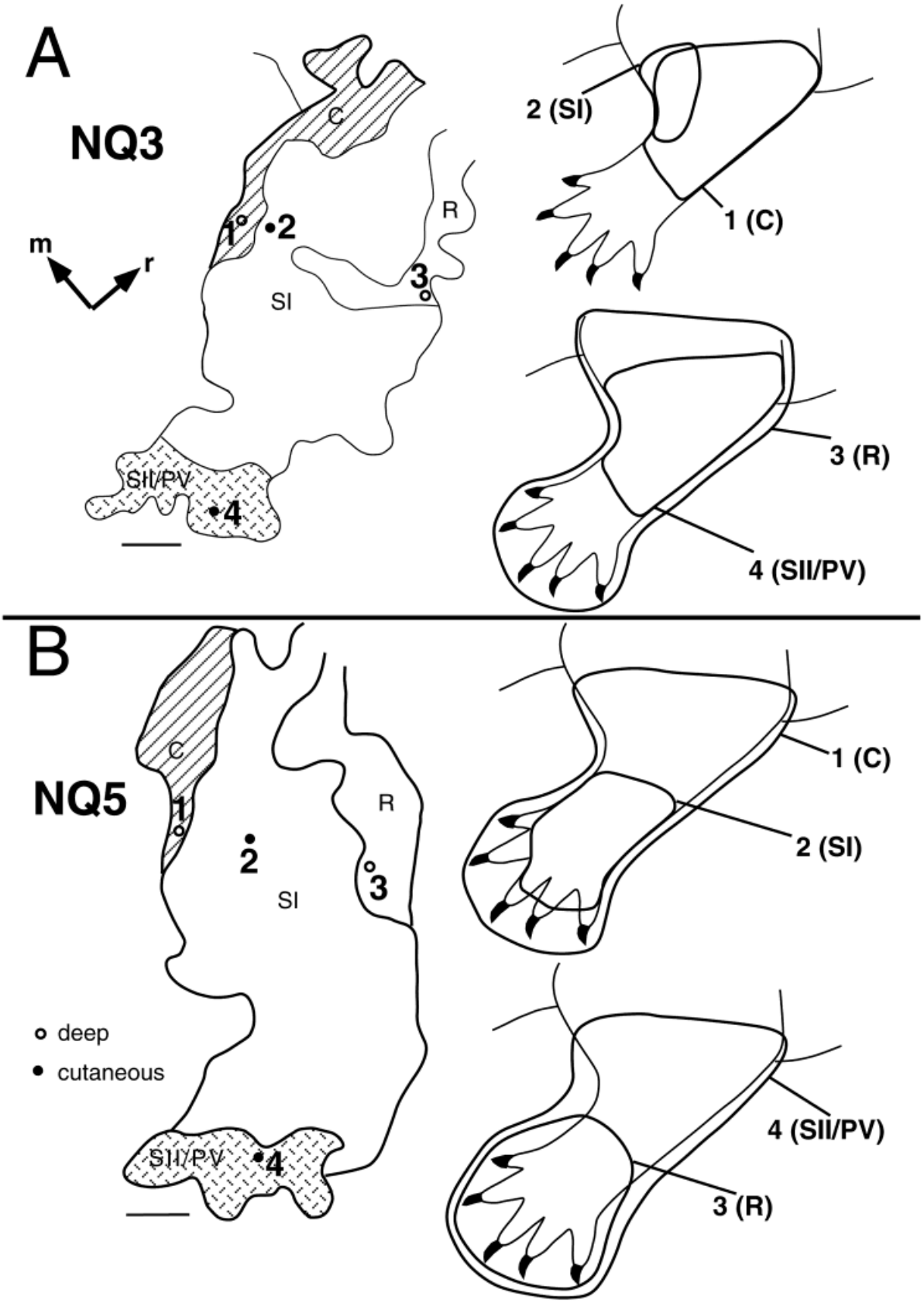


Fig. 8. Receptive fields for neurons in rostral somatosensory region (R), primary somatosensory area (SI), caudal somatosensory region (C), and second somatosensory area/ parietal ventral area (SII/PV) in quoll 3 (**A**) and 5 (**B**). These illustrations demonstrate that neurons in distant locations in cortex (sites 1, 2, 3, and 4) have receptive fields that are on the same body part, indicating the presence of four separate fields or regions. Receptive field sizes for neurons in each of these representations differed, with SI neurons having the smallest receptive field (RF 2), neurons in regions R and C having larger receptive fields (RFs 1 and 3), and those in SII/PV having the largest receptive fields (RF 4). Conventions as in previous figures. Scale bar = 1 mm.

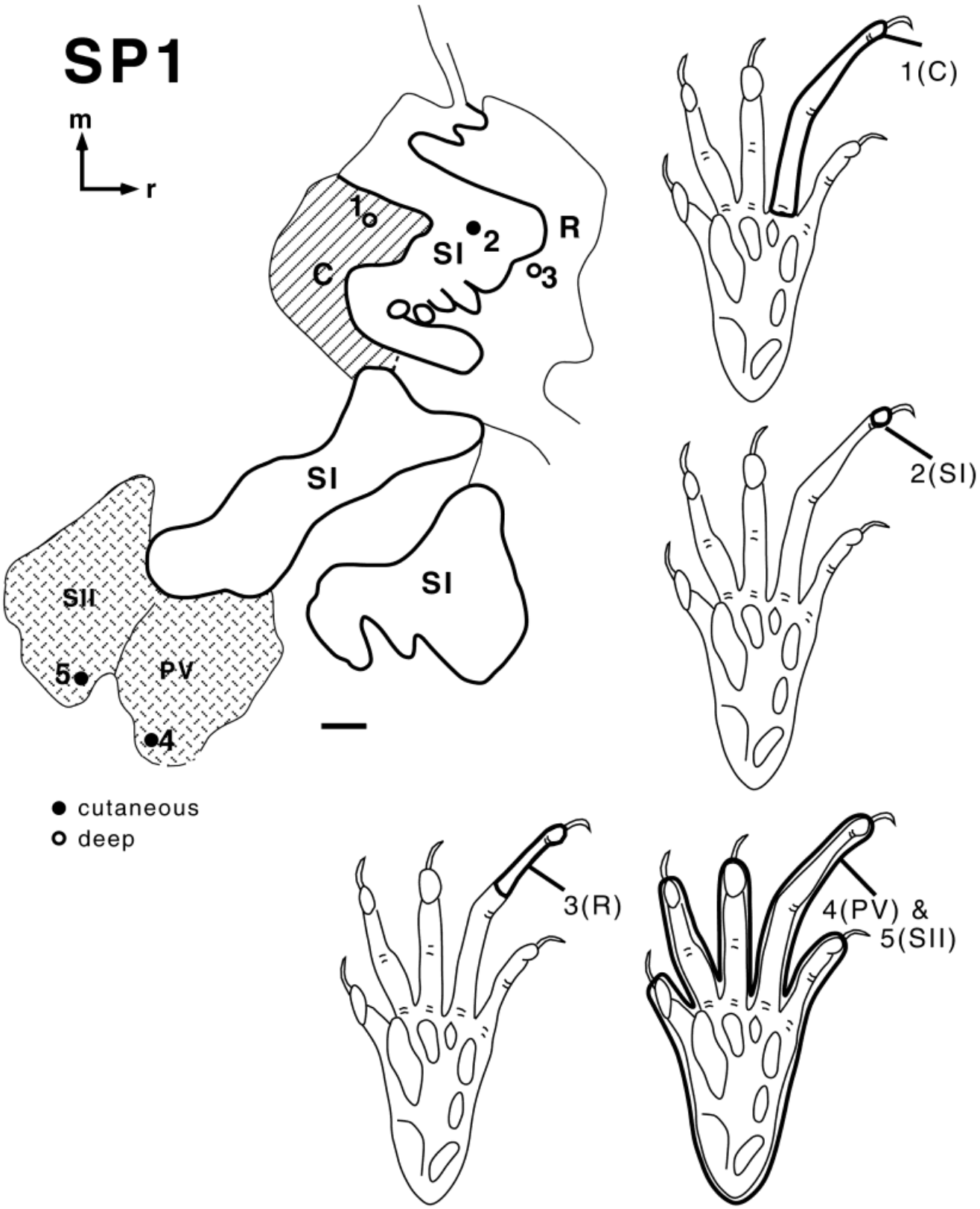


Fig. 9. Receptive fields for neurons in primary somatosensory area (SI), caudal somatosensory region (C), rostral somatosensory region (R), second somatosensory area (SII) and parietal ventral area (PV) in the striped possum. This illustration demonstrates that neurons at distant locations in cortex rerepresent the same body part, such as the forepaw. This figure also demonstrates that the size of receptive fields is different for neurons in the different fields or regions. Neurons in SI have the smallest receptive fields; e.g., RF 2 is restricted to a small portion of the distal digit; neurons in C and R have larger receptive fields that encompass more of a digit or an entire digit (RFs 1 and 3), and neurons in SII and PV have large receptive fields that include the entire glabrous forepaw (RFs 4 and 5). Conventions as in previous figures. Scale bar = 1 mm.

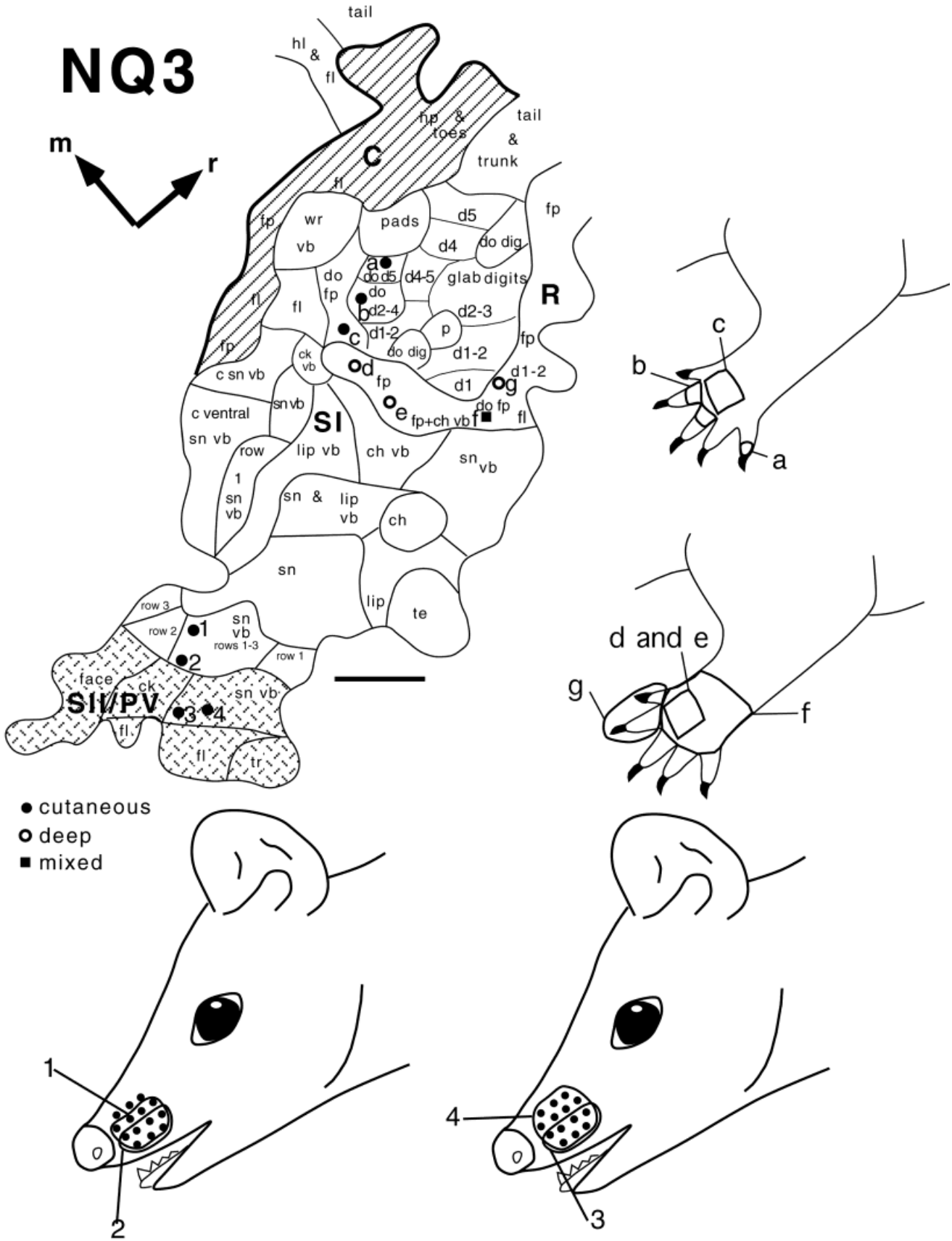


Fig. 10. Recording sites in primary somatosensory area (SI) and rostral somatosensory region (R) and their corresponding receptive fields on different body parts (RFs a–g). As recording sites move from SI (a–c) into R (d–g), receptive fields move from the distal digits onto the dorsal hand (a–c), and as recording sites cross the SI/R border, receptive fields for neurons at those sites move from the dorsal hand (d–f) back onto the distal digits. Receptive fields for neurons in R are larger than for those in SI, and the stimulus preference for neurons changes from cutaneous in SI, to deep in R. Recording sites across the SI/(second somatosensory area/ parietal ventral area, SII/PV) border are illustrated in sites 1–4. As sites move from SI into SII/PV, receptive fields reverse at the boundary, and neurons come to rerepresent similar body parts in SII/PV as those represented in SI. Conventions as in previous figures. Scale bar = 1 mm.

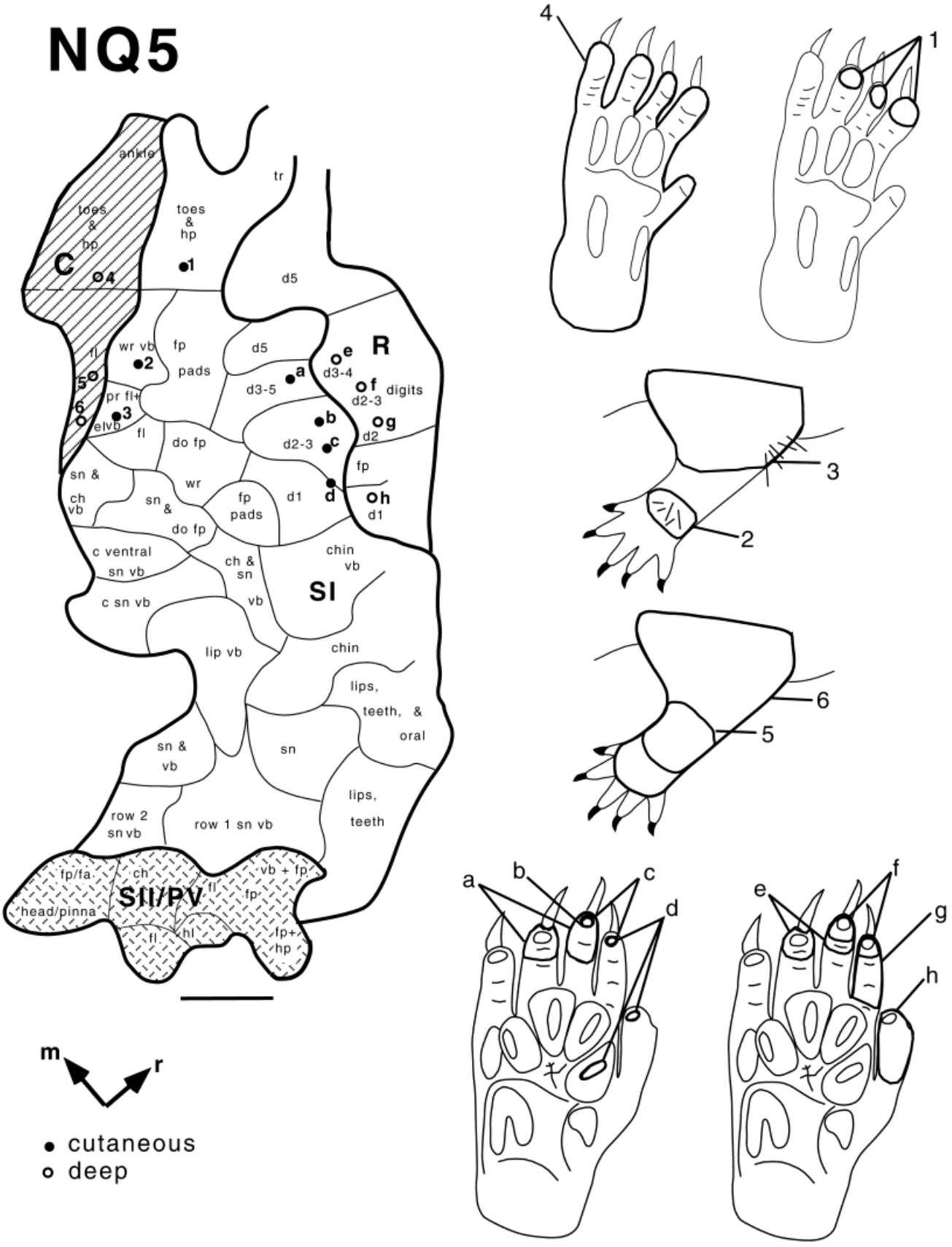


Fig. 11. Receptive fields for neurons at the boundary of primary somatosensory area (SI), and caudal somatosensory region (C; 1–6), and SI and rostral somatosensory region (R; a–h). This illustration demonstrates a rerepresentation of body parts in C and R in cortex in which neurons respond to deep stimulation, and reflects the mirror image of fields, at least at the border. Thus, for neurons in SI, we see a mediolateral progression from hindpaw to forelimb to forepaw, and a rerepresentation of these same body parts in C. Note that receptive fields for neurons in C are larger than neurons in SI. A similar rerepresentation is seen for neurons in SI and R (receptive fields [RFs] a–h). Neurons in SI have smaller receptive fields than do neurons in R. Also, the receptive field configuration for neurons in SI is unique in that they generally contain either one or several of the specialized, striated pads on the forepaw. Receptive fields for neurons in R contain these pads, but also include adjacent skin. Conventions as in previous figures. Scale bar = 1 mm.

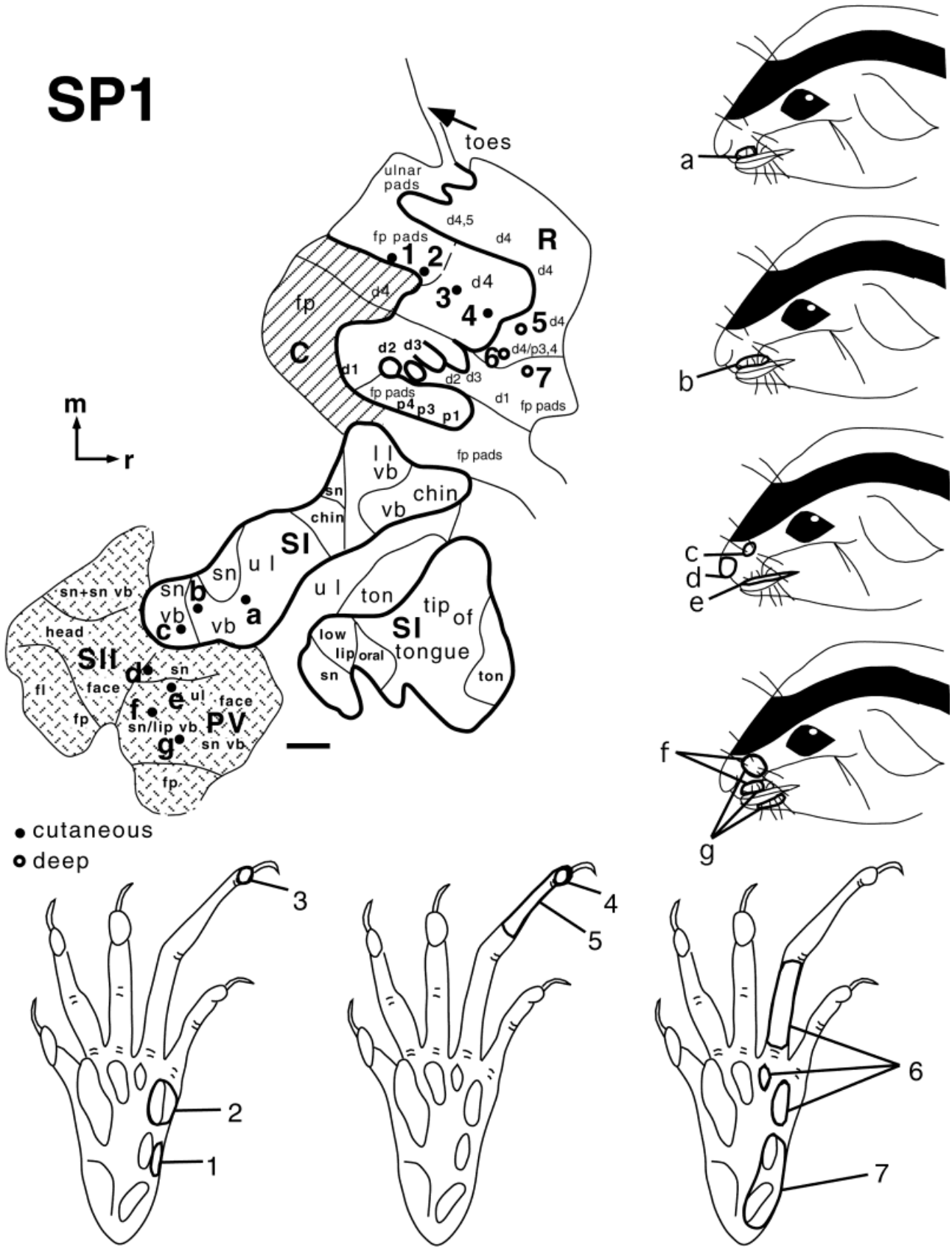


Fig. 12. Receptive field progression for neurons in primary somatosensory area (SI) and rostral somatosensory region (R; 1–7), and SI and parietal ventral area (PV; a–g). As recording sites move from the caudal portion of SI into the rostral portion, corresponding receptive fields for neurons at those sites move from the proximal forepaw to the distal digit (RFs 1–4). As recording sites cross the SI/R boundary, a reversal in the progression of recording sites is seen so that receptive fields for neurons at those sites move from the distal digit back to the proximal forepaw (RFs 5–7). There is also an increase in receptive field size for neurons in R compared to neurons in SI, and neurons in R respond to stimulation of deep receptors. A progression of recording sites from SI into PV (a–g) demonstrates a rerepresentation of body parts as well as a reversal in the progression of receptive fields for neurons a those sites. Neurons in both SI and PV respond to cutaneous stimulation. Conventions as in previous figures. Scale bar = 1 mm.

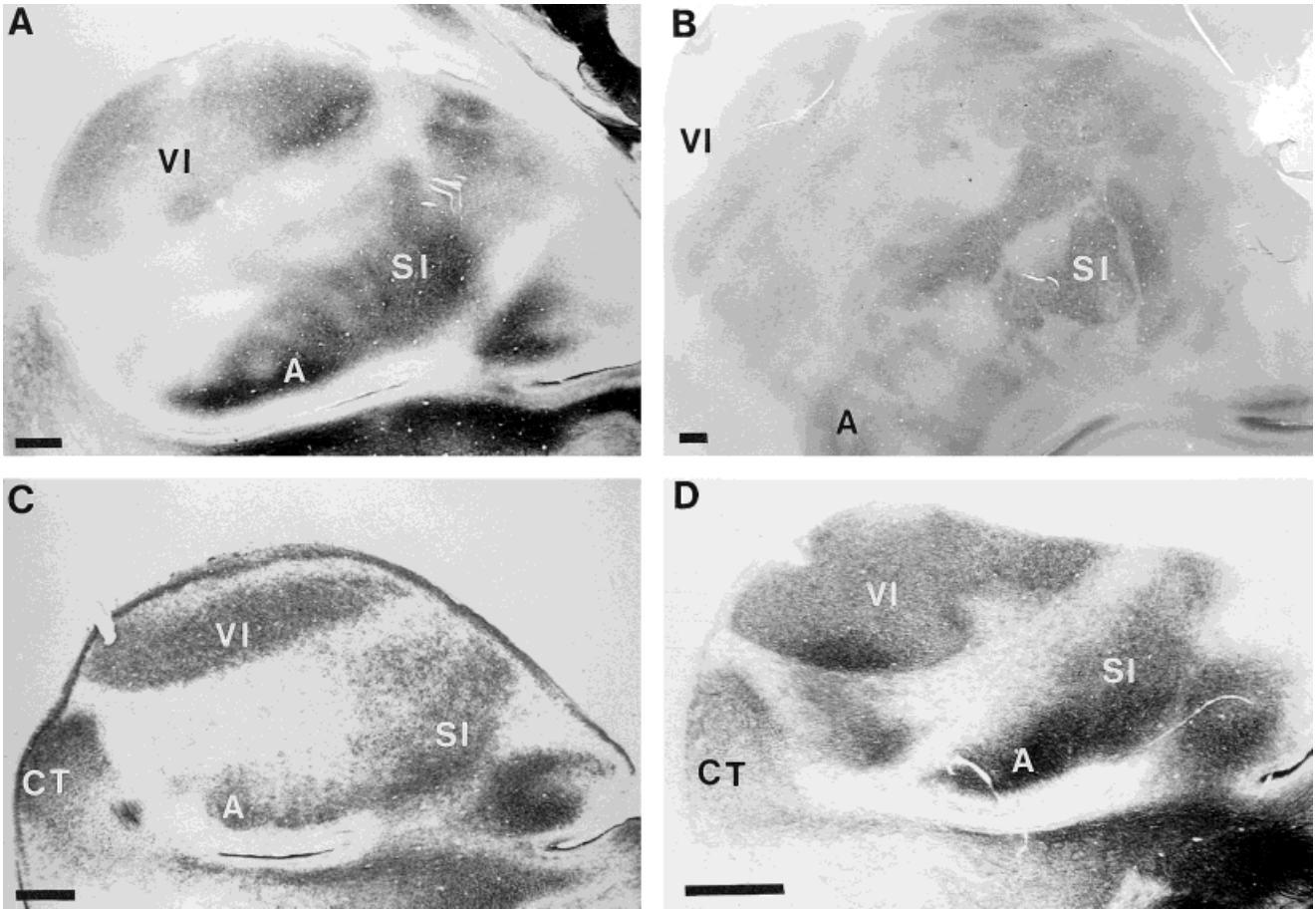


Fig. 13. Lightfield photomicrographs of cortex that has been flattened, and cut parallel to the cortical surface in the quoll (**A**), striped possum (**B**), short-tailed opossum (**C**), and fat-tailed dunnart (**D**). In the quoll, short-tailed opossum and fat-tailed dunnart, the myelin-stained cortex reveals several heavily myelinated areas including primary somatosensory area (SI), primary visual area (VI), and presumptive primary auditory area (A). Cortex just caudal and rostral to SI stains moderately for myelin and corresponds to caudal and rostral somatosensory regions (C and R), respectively. The SI/ second somatosensory area/ parietal ventral area (SII/PV) is not easily identified because SII/PV is darkly myelinated like SI. In the striped possum, cortex assayed for cytochrome oxidase (CO) reveals a very darkly staining SI, in which the major body part representations within it appear as darkly staining islands. Rostral is to right and medial is to the top. Scale bars = 1 mm.

(Figs. 5–7), neurons consistently responded to visual stimulation. When matched with architecture in the occipital lobe, it was found that these neurons were in the primary (striate) and second (peristriate) area, VI and VII, respectively (see below).

In one short-tailed opossum, in which more detailed maps were obtained, cortex caudal to SI contained neurons that responded to auditory stimulation (Fig. 6). In two of the quolls and in the striped possum, neurons in cortex lateral to SII and PV responded to auditory stimulation (Figs. 2, 3, 5). In one animal (Fig. 2), neurons that responded to pure auditory stimulation were related to cortical architecture (see below), and were found to be in a region in which a tonotopic map has been described previously by Aitkin et al. (1986).

Neurons in cortex rostral to R were most often unresponsive to any type of sensory stimulation that we presented (Figs. 2–5). In the case of the striped possum, and in one quoll (Figs. 3, 5), some neurons in this region responded weakly to stimulation of deep receptors. Finally, in cortex medial to somatosensory areas SI, C, and R, in cingulate cortex, neurons were unresponsive to sensory stimulation.

Multiple representations of the sensory epithelium, and receptive field progressions within and across fields

In this investigation, we identified four somatosensory fields in the quoll, five in the striped possum, and one in the short-tailed opossum. In the quoll, duplicate RFs were found in distantly located electrode penetrations in SI, SII/PV, C, and R, indicating a rerepresentation of similar body parts in often widely spaced regions of the somatosensory cortex (Fig. 8A,B). The receptive fields on the forearm and forepaw for neurons in SI were smaller than those for neurons in any of the other fields (compare RF 2 with RFs 1, 3, and 4 in Fig. 8A, and RF 2 with RFs 1, 3, and 4 in Fig. 8B). A similar rerepresentation of body parts was seen in the different fields in the striped possum (Fig. 9). For the representation of the forepaw, distal D4 or receptive fields encompassing distal D4 were observed at five separate locations, in SI, R, C, SII, and PV (Fig. 9, RFs 1–5). As in the quoll, the receptive fields for neurons in SI were much smaller than for neurons in the other fields (compare RF 2 with RFs 1, 3, 4, and 5 in Fig. 9).

The progressions of receptive fields demonstrate reversals across the boundaries of some fields (Figs. 10, 12), and in some instances demonstrate mirror images of fields at the boundaries (Fig. 11). For instance, in the quoll (Fig. 10) and striped possum (Fig. 12), as electrode penetrations cross the SI/R boundary, a reversal in the progression of receptive fields on the forepaw is observed (Fig. 10, RF a–g; Fig. 12, RF 1–7), a change in stimulus preference is seen, and a difference in the architectonic appearance of fields can be identified (see below). In the quoll and striped possum, an enlargement of receptive fields for neurons in R is also observed. Similar reversals in receptive field progression can also be identified between SI and SII and SI and PV (Figs. 10, RFs 1–4; 12, RFs a–g).

Finally, when parallel rows of recording sites and their corresponding receptive fields are examined for C, SI, and R, three separate representations can be identified (Fig. 11). For instance, in two parallel mediolateral sequences of recording sites in SI and C, a clear progression of recording sites from the toe representation to the forelimb representation is seen in both fields as well as an almost exact duplication of receptive fields for neurons at those sites (Fig. 11, compare RF 1 and 4, 2 and 5, 3 and 6). Two parallel rows of mediolateral recording sites in SI and R demonstrate similar points (Fig. 11, RF a–h).

Relationship of electrophysiological recording results to architectonic boundaries

SI. In the quoll, striped possum and short-tailed opossum, SI was very darkly myelinated compared to surrounding cortex (Fig. 13A,C). SI was also correlated with a cytochrome oxidase-dense region which was particularly striking in the striped possum (Fig. 13B). Close examination of the CO stain in the striped possum reveals a barrel-like arrangement of CO dense regions, much like that described in the brush-tailed possum by Weller (1993). In the quoll, SI was not a contiguous field, but was broken into two mediolateral islands, and in the striped possum, several islands (Fig. 13). This was in good agreement with electrophysiological results which also demonstrated the discontinuous nature of SI.

R and C. In quolls and striped possums, cortex immediately rostral and caudal to SI was moderately myelinated, and was largely coextensive with the regions that contained neurons responsive to deep stimulation (R and C, respectively). In CO stains, this cortex stained much less densely than did SI. Cortex just rostral to R stained lightly for myelin, and in most instances, the rostral boundary of R could be identified. Cortex immediately caudal to the caudal region stained lightly for myelin, which sometimes allowed the caudal boundary of C to be identified.

SII and PV. In the quoll and striped possum, cortex immediately lateral to SI stained moderately to darkly for myelin, and in the striped possum, moderately for CO. This region was coextensive with SII and PV or SII/PV identified electrophysiologically. It was often difficult to identify the boundaries of SII and PV architectonically. Thus, we relied predominantly on electrophysiological identification of these boundaries.

Other cortical areas. In most cases, there were several very prominent regions of cortex that had clear architectonic boundaries. One of these was the presumptive primary auditory area (A). In the quoll, striped possum, and short-tailed opossum, A was located caudolateral to SII and PV. The auditory area stained very darkly for myelin, and in one quoll, neurons here responded vigorously to auditory stimulation.

Another very clear architectonic subdivision of cortex was in the occipital pole. We termed this caudal region, the primary visual area (VI), because its location and architectonic appearance conform to VI described in other mammals. More importantly, related studies in our laboratory in the short-tailed opossum (Krubitzer et al., 1997a), and previous studies in other marsupials (Sousa et al., 1978; Crewther et al., 1984; Vidyasagar et al., 1992) indicate that the physiological organization and connections of this field are similar to those described for VI in other mammals. VI in this study stained very darkly for myelin and cytochrome oxidase, particularly in the middle cortical layers. Its rostral and lateral boundary was readily identified because cortex beyond it stained much less densely for myelin. In most of these animals, most neurons in VI generally responded vigorously to visual stimulation.

Immediately rostral and lateral to VI was a region of cortex that stained lightly to moderately for myelin. We term this region, the second visual area (VII), or the peristriate area (PS), because it has been similarly named in other marsupials and other mammals (Rowe, 1990; see Kaas and Krubitzer, 1991; Rosa, 1997, for review). A small, darkly myelinated region was identified in cortex lateral to the caudal portion of VI. We term this field the caudal temporal area (CT) because a similar field has been identified in a recent studies in the Virginia opossum (Beck et al., 1996) and the short-tailed opossum (Krubitzer et al., 1997a).

Cortical architecture of the fat-tailed dunnart. Although no electrophysiological recordings were made in the fat-tailed dunnart, cortex was flattened, sectioned, and stained for both cytochrome oxidase and myelin (see myelin stain, Fig. 13D). There were three areas of cortex that had a striking architectonic appearance, the presumptive SI, A, and VI. As in the other species, SI was a darkly myelinated, CO-dense field (myelin, Fig. 13D). In addition to similarities in its architectonic appearance, SI in the fat-tailed dunnart was similar in shape, and relative location to SI in the quoll and short-tailed opossum. Thus, we propose that this region is homologous to SI described in the other marsupials in this study, and other mammals. A darkly myelinated, CO-dense oval of cortex just caudal to the lateral border of SI was also easily discernible (myelin, Fig. 13D). We term this field A because its shape, relative location, and architectonic appearance are similar to those described for other animals in this study, and other mammals in general. A very darkly myelinated, CO-dense wedge of cortex that formed the caudal pole of the cortex was identified (myelin, Fig. 13D). This region had a similar location, shape, and appearance to VI described in this study and other mammals. For these reasons, we designate it as VI. Just lateral to VI, a darkly myelinated oval of cortex was observed. The location of this region and its architectonic appearance are similar to those of the CT described in previous studies in the Virginia opossum (Beck et al., 1996), and the short-tailed opossum (Krubitzer et al., 1997a).

DISCUSSION

In the present study, using electrophysiological recording techniques and architectonic analysis, we describe the organization of four somatosensory areas in the quoll, five areas in the striped possum, and one area in the short-

tailed opossum. Our results demonstrate that these three marsupials have a primary somatosensory area, SI. In the two species in which complete maps of somatosensory cortex were made, the striped possum and quoll, a rostral and caudal somatosensory region (R and C, respectively), and either one or two lateral somatosensory fields, SII, and the PV were identified. Most of these areas had a distinct myeloarchitectonic or CO appearance, and neurons within these fields had different stimulus preferences. Reversals of receptive field progressions for neurons were observed across some of the cortical field boundaries, and a rerepresentation of body parts was also found in these different fields or regions. However, only in SI was a complete representation of the sensory surface observed. We only found partial representations in regions C, R, SII, and PV. In an additional species, the fat-tailed dunnart, we describe the architecture of the neocortex, and relate these findings to those in which both electrophysiological analysis and architecture were combined in the other species.

The following discussion describes the morphological specializations of these mammals, and compares the similarities in cortical organization described in this study with other studies of marsupials and eutherians. This is done in an effort to determine the basic pattern of organization of somatosensory cortex that all marsupials, and perhaps all mammals possess. We then outline the differences in organization of SI described in the present study and compare our findings with descriptions of SI in other mammals. We attempt to correlate differences in the internal organization of SI across species to distinct morphological and behavioral characteristics. In this section we also discuss briefly the overall organization of the neocortex in a variety of mammals. Finally, we relate these observed differences across species to the changes that occur in an individual animal within the course of its life.

Morphological specializations

All mammals have morphological features that are unique, or are considered variants of a standard pattern or form. For example, although all mammals have homologous forepaw skeletal patterns, the shape and function of the "forepaw" ranges from a cat's clawed forepaw, to a cetacean flipper, to the human hand. Yet all are considered to be homologous. In the present investigation, each species investigated was obviously unique in appearance; however, some physical features were more exaggerated than others.

For instance, the quoll has a specialized forepaw in which the digit and palmar pads contain striated ridges (Fig. 1e). The quoll also has a number of vibrissae in addition to those on the snout, namely, around the eye, and on the chin, cheek, wrist, and elbow. These vibrissae play an important role in prey capture, particularly in orienting the attack (Pellis et al., 1992). The striped possum has snout vibrissae, but does not possess the exaggerated body vibrissae nor the glabrous forepaw specializations observed in the quoll. Rather, the striped possum has an elongated fourth digit that is approximately 40% longer than the other digits (Fig. 1f), which is used to extract insects from holes in tree bark. The gums of the striped possum have evenly spaced protrusions or flaps that cover the lateral and frontal base of the incisors (John Nelson, personal observation). The striped possum also has a very long, pointed tongue which is used for extracting insects. The fat-tailed dunnart and the short-tailed opossum have large eyes and pinnae, a well- developed snout, and a number of specialized vibrissae on the snout and face (Fig. 1c and d).

Organization of somatosensory cortex in marsupials and other mammals: Common patterns of organization

Since the advent of electrophysiological recording techniques, SI and SII have been consistently described in all mammals studied (for reviews, see Johnson, 1990; Rowe, 1990; Krubitzer, 1996), including a number of marsupials such as the brush-tailed possum (*Trichosurus vulpecula*: Adey and Kerr, 1954; Bodemer and Towe, 1963; Weller and Haight, 1973; Elston et al., 1993; Weller, 1993), the wallaby (*Thylogale eugenii*: Lende, 1963b), and the opossum (*Didelphis virginiana*: Lende, 1963a, b; Pubols et al., 1976; Pubols, 1977; Beck et al., 1996; Fig. 14), and *Didelphis azarae azarae* (Magalhâes-Castro and Saraiva, 1971). The organization of SI described in all previous studies is similar in mediolateral organization to SI described in the present investigation in the quoll and striped possum. The tail and foot are represented most medially, followed by the representation of the hindlimb, trunk, forelimb, forepaw, and face in a mediolateral sequence. The more limited data on the organization and myeloarchitecture of SI in the short-tailed opossum, to some extent, are similar to previous descriptions of SI in other marsupials.

SII described in previous studies was similar to SII described in the present investigation for the striped possum. It is a small representation lateral to SI that forms a congruent boundary with SI at the representation of the vibrissae (e.g., Pubols, 1977; Elston et al., 1993; Beck et al., 1996). SII is considered to be an upright representation with respect to the head, with the trunk represented medially, the forepaw and hindpaw represented laterally or rostrolaterally, and the hindlimb represented caudal or caudolateral to the forelimb. In all studies in which cortical architecture was examined, SI corresponded to a darkly myelinated, CO-dense region with a cell-dense layer IV (granular). In a previous investigation in the opossum (Beck et al., 1996), SII was found to be darkly myelinated and CO-dense. In the present investigation, SII in the striped possum corresponds to a region of cortex that stained moderately dark for CO. Some aspects of SII/PV in the quoll look like SII described in other mammals in that in one case (Fig. 3), the head and pinna are represented caudally in the field, although the rest of the representation does not appear to correspond to SII.

Additional regions caudal and rostral to SI have been described in the brush-tailed possum (C and R, respectively; Elston et al., 1993), and in the Virginia opossum (caudal somoatosensory area [SC] and rostral somatosensory area [SR], respectively; Beck et al., 1996). Neurons in these regions were outside of SI, and were either unresponsive to somatic stimulation, or responded to stimulation of deep receptors, as do C and R in the present investigation in the quoll and the striped possum. Although the mediolateral organization of R and C in previous studies grossly mirrored that of SI (Elston et al., 1993), these fields were smaller than SI, in most instances did not contain a complete representation of the sensory epithelium, and were less densely myelinated than SI. These findings are similar to findings in the quoll and striped possum of the present study, although R and C in this study did not

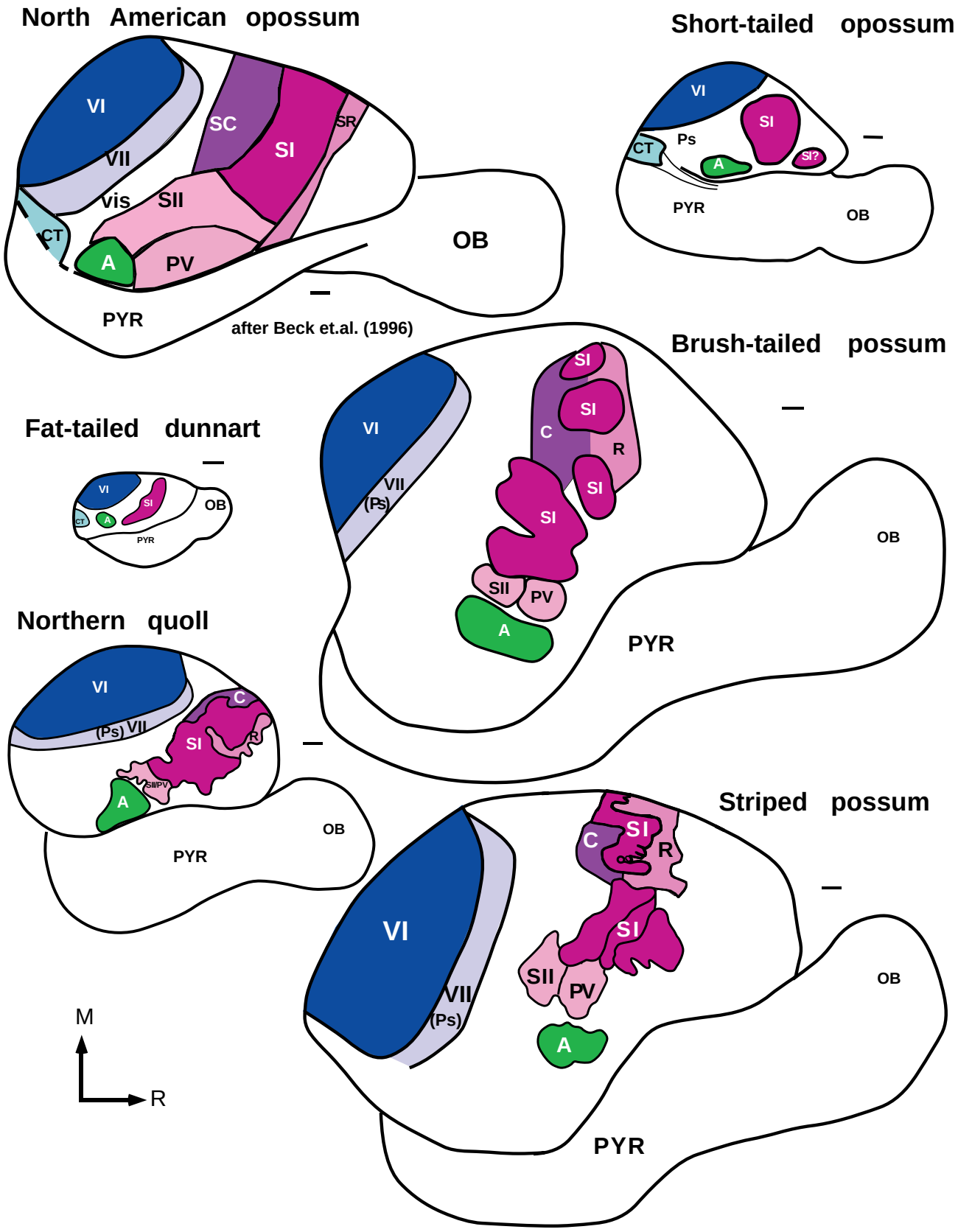


Fig. 14. A summary of cortical organization in a variety of marsupials. Proposed homologies are indicated in the same color. Although all of these animals have the primary fields primary visual area (VI; blue), primary somatosensory area (SI; red), and presumptive primary auditory area (A) or AI (green), the relative size and shape of these fields varies in the different species. In a number of species, lateral fields (second somatosensory area/ parietal ventral area [SII/PV] or SII and PV) have been described. In three of these species, a rostral and caudal region has also been described. The summary of the Virginia opossum is from Beck et al. (1996), and the summary of the brush-tailed possum is from Elston et al. (1993). Conventions as in previous figures and Table 1. Scale bar = 1 mm.

border the entire mediolateral length of SI. Additionally, Beck et al. (1996) provide evidence for a fifth field, PV, in the Virginia opossum. These findings are similar to our results in the striped possum, although PV in the Virginia opossum occupied a relatively larger area of cortex (Fig. 14). PV is located lateral to SI, but is an inverted representation of the body surface (See Krubitzer et al., 1986).

In the short-tailed opossum, neurons responsive to somatosensory stimulation were found at a few locations rostral to SI in one animal. However, the small size of the neocortex and the low density of mapping, particularly lateral to SI, prevents us from drawing any conclusions about the presence of somatosensory areas other than the primary field.

All studies on marsupial neocortex are consistent with the notion that all, or most, marsupials have two representations of the body surface, SI and SII. In most recent studies of marsupials, rostral and caudal regions immediately adjacent to SI have been identified (e.g., Elston et al., 1993; Beck et al., 1996). Because they do not contain a complete representation of the body surface (present study; Elston et al., 1993) or are largely unresponsive to somatosensory stimulation (Beck et al., 1996) their status as traditionally defined somatosensory fields remains uncertain. In three species, the striped possum, the brush-tailed possum, and the Virginia opossum, an additional area, PV, is present (Fig. 14). The difficulty in distinguishing PV from SII is especially exaggerated in animals with a small neocortex, because the size of the field is quite small and the mapping density is relatively sparse. Despite this, in marsupials with a larger neocortex, such as the striped possum and Virginia opossum, PV can be separated from the SII region.

In most marsupials investigated, SI, at least one lateral field (SII), and a rostral (R) and caudal (C) region have been identified, suggesting that these fields were retained from a common ancestor (Fig. 14). This supposition is supported by observations in monotremes (prototherian) and basal placental (eutherian) mammals such as tenrecs (Krubitzer et al., 1997b) and hedgehogs (Porbirsky et al., 1998). In all of these animals SI, SII/PV, and a rostral field, R, have been identified. SI, SII, PV, as well as a rostral field, area 3a, and one or two caudal fields, area 1 and 2 or area 1/2, have also been identified in a wide variety of eutherians representing major lineages (see Feldman and Johnson, 1988; Johnson, 1990; Krubitzer, 1996, 1998).

Organization of cortex surrounding somatosensory cortex

Visual cortex. In most cases in which electrophysiological recordings were made, neurons in cortex surrounding somatosensory cortex were surveyed and results were related to cortical architecture. In all cases, cortex immediately caudal to C contained neurons that were either unresponsive to any type of stimulation, or were responsive to visual stimulation. When architecture was related to electrophysiological recording results, it was found that visually responsive neurons at the far caudal pole of cortex were in the primary visual area, VI (striate), and those located rostral and lateral to this were in the presumptive second visual area, VII (peristriate), defined in other marsupials (Packer, 1941; Benevento and Ebner, 1971a,b; Sousa et al., 1978; Haight et al., 1980; Crewther et al., 1984; Volchan et al., 1988; Martinich et al., 1990; Vidyasagar et al., 1992; Rosa et al., personal communication). Preliminary studies in our laboratory on the topographic organization and connections of visual cortex in the short-tailed opossum support these earlier findings (Krubitzer et al., 1997a). The CO staining and myeloarchitecture are also consistent with descriptions of VI in other marsupials in which VI was described as a CO-dense (Martinich et al., 1990) and myelin-dense region with a well-developed layer IV (Benevento and Ebner, 1971a; Haight et al., 1980). Although the presence of a VII in the striped possum and short-tailed opossum is not conclusive, the presence of neurons that respond vigorously to visual stimulation, the geographic location, and the myeloarchitectonic appearance of the presumptive VII region in the present study, suggests that it is homologous to VII in other mammals (see Kaas and Krubitzer, 1991; Rosa, 1997 for review).

Auditory cortex. In the present investigation, most animals in which electrophysiological recordings were made had regions of cortex lateral, caudolateral, or caudal to somatosensory cortex in which neurons responded to crude auditory stimulation. This is the region where Lende (1963a,b) recorded evoked potentials to auditory stimulation in the Virginia opossum, and where frequency maps were obtained in the quoll (Aitkin et al., 1986), and brush-tailed possum (Gates and Aitkin, 1982). In addition, this region receives projections from the medial geniculate complex of the thalamus in the brush-tailed possum (Aitkin and Gates, 1983), the quoll (Kudo et al., 1989), and the Virginia opossum (Kudo et al., 1986). The cortical architecture of portions of this region in previous studies and in the present study corresponds to AI described in other mammals using a similar preparation (e.g., Luethke et al., 1988, 1989). Taken together, all studies indicate that marsupials have a primary auditory area with neuroanatomical and physiological characteristics similar to those described for other mammals (see Aitkin, 1995).

Motor cortex. In the quoll and striped possum, the vast majority of sites in cortex immediately rostral to R contained neurons that were unresponsive to any type of sensory stimulation. This cortex stained lightly for myelin and was in the geographic location of the primary motor area described in eutherians (Stepnieska et al., 1993). Although some early studies described a somatosensory-motor amalgam in marsupials such as the Virginia opossum (Lende, 1963a–c), azarae (Magalhâes-Castro and Saraiva, 1971), and brush-tailed possum (Rees and Hore, 1970), the currents used to evoke movement were relatively high (0.2–0.7 mA; Magalhâes-Castro and Saraiva, 1971; 0.1–1.2 mA, see Fig. 3 of Lende, 1963a), compared to recent microstimulation studies of the primary motor area, MI, in which current levels are on the order of 1–10 μA, or 100–10× smaller than in these earlier reports (e.g., Gould et al., 1986). A recent microstimulation study by Beck et al (1996) in the opossum found that movements could be elicited from neurons in SI and R, but they were generally of too high a threshold to be considered normal for motor cortex. Thus, the amount of overlap of motor cortex with somatosensory cortex in marsupials remains uncertain.

Variation in the amount of SI devoted to particular body parts. Despite the similarities in the number and organization of somatosensory fields in the neocortex observed across species, there are clear differences in the internal organization of SI. In the present investigation, we attempted to relate these internal differences in SI to differences in morphological structure. When we examine the behavior of some of these animals, such as the striped

possum and the quoll, it appears as if the magnification of different body parts in SI may be related to high level discrimination abilities of each species. For example, in some instances the face and body vibrissae in the quoll are used for guiding the hand to prey items and orienting prey items (Nelson, personal observation; Pellis et al., 1992), and the forepaws are often used to manipulate insect prey (Begg, 1983). In the striped possum, initial observations suggest that the glabrous forepaw, particularly D4, may be used for discriminating different frequencies of vibration that various insects and larvae generate (Nelson, personal observation).

We calculated the percentage of the total area of SI that each body part representation or combined representations occupied, and compared these percentages in the quoll and striped possum. We found that the largest portion of SI is devoted to the representation of specialized body parts. Although there were no measures of receptor density for a given body part, these specialized body parts could be identified by an increase in the size of a structure (indicating an absolute increase in the number of receptors), or by the presence of a particular body part in some species that is not found in others. For example, the quoll and dunnart both have raised striations on the pads of their forepaws and hindpaws, and both use their forepaw extensively to manipulate insect prey (Begg, 1983; Morton, 1983). In quolls, the representation of the glabrous forepaw, which includes these pads, occupied 3–7% of SI. Although this percentage does not seem large compared to the striped possum for instance, the neuronal RFs in SI were often restricted to these pads (Fig. 11). Thus, the total skin surface area represented in this region of cortex was quite small, and not necessarily inclusive of the entire glabrous forepaw. Similarly, the prominent body vibrissae are a feature observed in the quoll, but not the other species in this study, and we found that the representations of the mystatial, chin, cheek, lip, elbow, and wrist vibrissae occupy 42–44% of SI in this species (Table 2, Fig. 16), compared to 24% in the striped possum.

This relationship between overrepresentation of a given body part in SI and that body part's specialized use is probably best exemplified by the fourth digit of the striped possum. This digit is approximately 40% larger than the other digits, and behavioral observations indicate that it plays an important role in prey capture, possibly by contributing to highly refined sensory discriminations for locating prey. When the prey have been located, the striped possum pulls the bark from the tree with specially modified jaws that enable maximum leverage (Cartmill, 1974), and then extracts insects from the holes in the tree with its elongated fourth digit, and elongated tongue. In the neocortex, the representation of D4 in SI assumes approximately 33% of the entire forepaw representation and 10% of the entire representation of SI. This is especially striking when compared to the D4 representation in the quoll which assumes 14–22% of the forepaw representation and only 3–5% of the entire field (Fig. 15).

Abundant examples of this relationship are evident in studies of prototherian and eutherian mammals (e.g., Johnson et al., 1982; Chapin and Lin, 1984; see Johnson, 1990 for review). For instance, in the platypus, Krubitzer et al. (1995b) demonstrated that at least 85% of SI, and most of the entire somatosensory neocortex (which includes somatosensory areas in addition to SI) is devoted to representing the bill. This electrosensory organ has long been considered a unique morphological specialization in both structure and function, and clearly has an exaggerated neural representation.

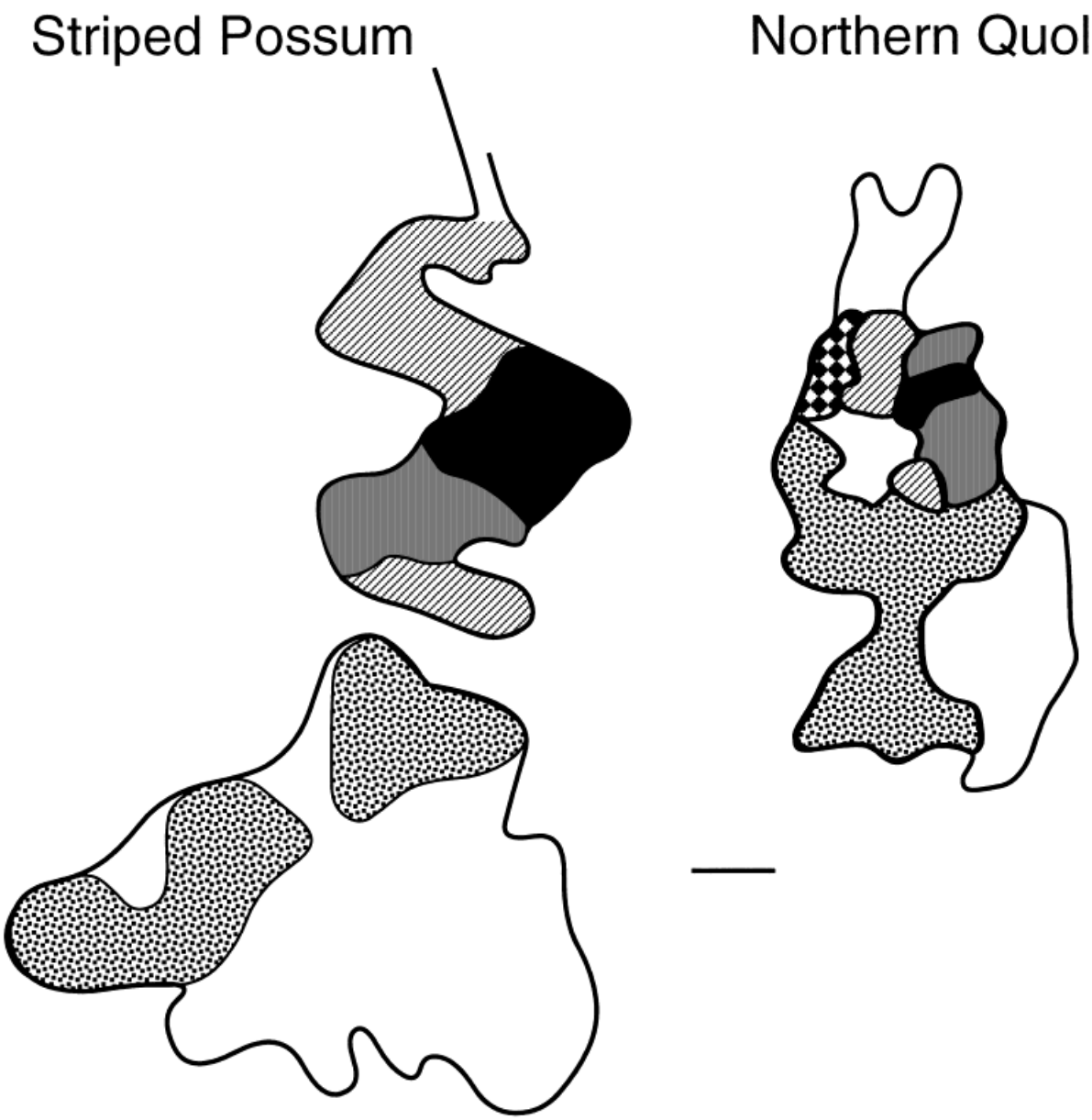
Studies in eutherian mammals have likewise shown neural correlates of specializations. Barrels (Woolsey and Van der Loos, 1970) in the SI cortex of rodents (Fig. 16), which correspond to the vibrissae, occupy 28 % of SI in rats (Chapin and Lin, 1984), compared to the gray squirrel, in which the vibrissae representation occupies only 9% of SI (Fig. 16; Sur et al., 1978). In the raccoon (*Procyon lotor*), the forepaw representation occupies 50% of SI (Fig. 16; Welker and Seidenstein, 1959, Johnson et al, 1982; Feldman and Johnson, 1988). Although the raccoon feeds on a variety of plants and animal species, the forepaw is used for prey capture in shallow water. By splaying their forepaws below the surface of the water, they identify and capture small fish and arthropods with their forepaws. Although the closely related cat uses its forepaws for prey capture as well, the structure of its forepaw with its retracted digits, is quite different, and apparently not used for discriminating prey. This difference is reflected in the organization of SI (Felleman et al., 1983), and the size of the forepaw representation in the cat, which occupies a much smaller portion of SI (24%) than in the raccoon (Fig. 16).

In primates, a large proportion of SI (area 3b) is devoted to processing inputs from the digits and the face (e.g., Kaas et al., 1979; Nelson et al., 1980; Sur et al., 1980; see Johnson 1990; and see Kaas and Pons, 1988 for review). This enlarged representation of the hand and face has been identified in adjacent anterior parietal fields such as areas 1 and 2 (e.g., Kaas et al., 1979; Pons et al., 1985; see Kaas and Pons, 1988; Johnson, 1990 for review). The classic study of Penfield and Rasmusson (1950) demonstrated that cortex on the postcentral gyrus in humans has enlarged representations of the hand and oral structures.

These observations in a variety of mammals indicate that differences in the organization of SI in different lineages are related to morphological structure and the use of that structure. The presence of such differences, even in some closely related species, indicates that such changes may occur relatively rapidly in evolution. How are these different types of organizations accomplished in evolution? Are these differences the result of genetic changes in the developmental programs that generate cortical fields, or are they wrought by simple genetic changes that regulate the size, innervation density, or receptor type of a peripheral structure? The present results, as well as previous investigations on the internal organization of SI in a variety of mammals, indicate that the characteristics under genetic control that might be selected for include an elongated digit, increased receptor density, or the emergence of a new receptor type, each of which confers some advantage to that animal. Thus, one factor that can account for the differences in SI organization that we observe in extant mammals is differences in morphological structure that are genetically mediated.

Variation in the neocortex within the life of an individual: Developmental and adult plasticity

A second factor that can account for the differences we observe in the neocortical organization in mammals is the ability of the neocortex to change its pattern of organization throughout an individual's life (Merzenich et al.,



	% SI, in SP	% SI, in NQ
D4	10%	3-5%
other digits	7%	13-18%
glabrous pads	13%	3-7 %
face vibrissae	24%	35-40%
body vibrissae	0%	4-7%

Fig. 15. A summary of primary somatosensory area (SI) in the striped possum and quoll showing enlarged representations of different body parts each indicated with different stipples. In the striped possum, the representation of D4 is very large and assumes 10% of SI, compared to the relatively smaller D4 representation in the quoll which occupies only 3% of SI. Conversely, the representation of the vibrissae on the face and body assume most of the representation of SI in the quoll, whereas a relatively smaller region of cortex in the striped possum represents the face vibrissae. Some vibrissae in the quoll, such as those on the wrist and elbow (body vibrissae), are not represented at all in SI of the striped possum. Conventions as in previous figures. Scale bar = 1 mm.

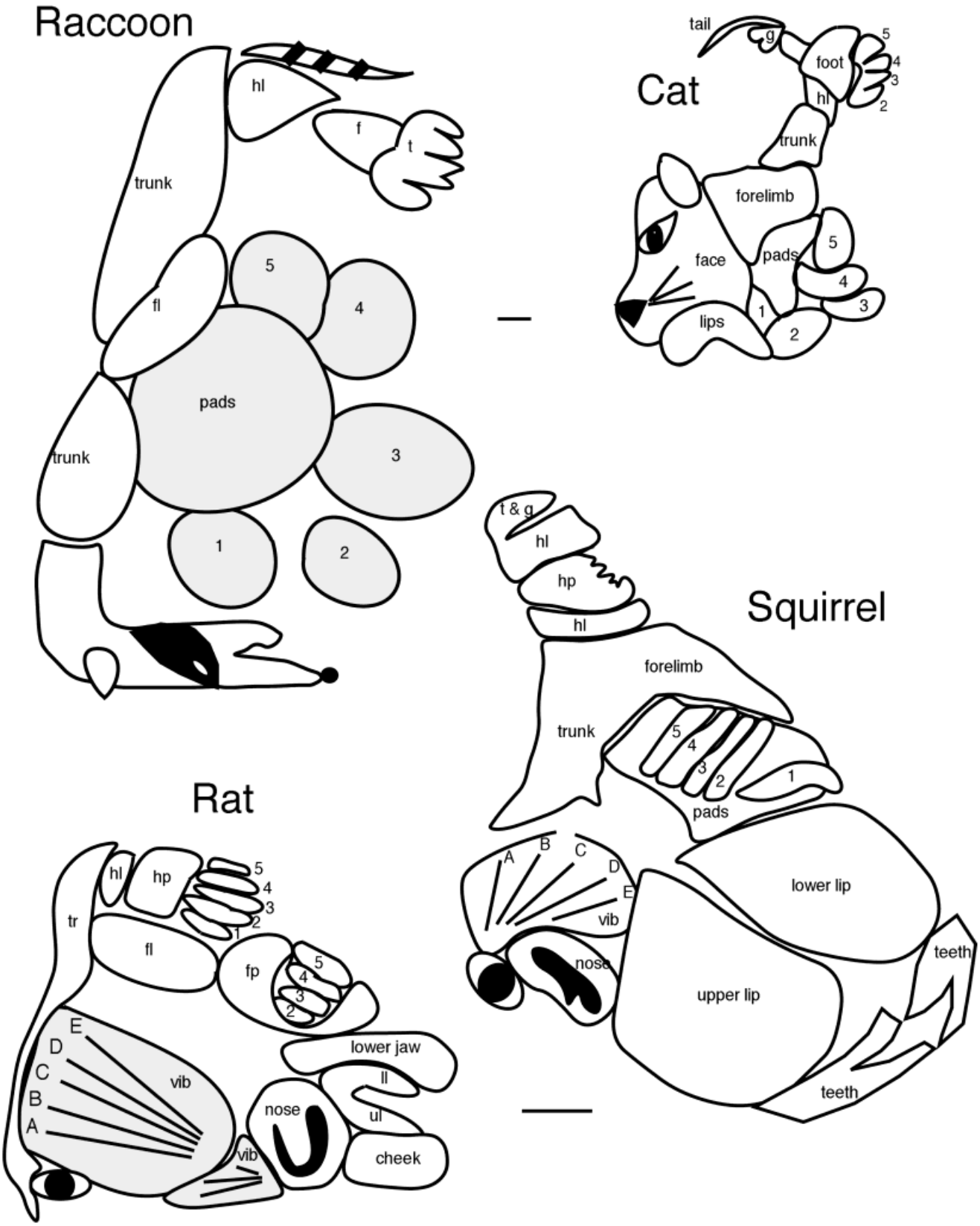


Fig. 16. Illustrations of body representations in primary somatosensory area (SI) in the raccoon (Johnson et al., 1982), cat (Felleman et al., 1983), rat (Chapin and Lin, 1984), and squirrel (Sur et al., 1978). These animals demonstrate that representations of different body parts occupy different proportions of SI. The forepaw representation in the raccoon occupies most of the representation in SI (50%), compared to the forepaw representation in the cat which occupies much less of SI (24%). Some rodents, such as rats, have much of SI devoted to representing the vibrissae (28%), whereas substantially less of SI in squirrels (9%) is devoted to representing the vibrissae. Conventions as in previous figures. Scale bars = 1 mm.

1987). Studies of adult mammals suggest that there is an inherent tendency for the neocortex to be plastic. For example, studies in which sensory input from a given body part has been increased by overstimulating that body part, have shown an expansion in the representation of those over stimulated digits in SI (e. g. Recanzone et al., 1992a,b; Jenkins et al., 1990), and in motor cortex (Nudo et al., 1996). A decrease in inputs to the cortex due to amputation, nerve crush, or nerve cut has resulted in a decrease in the amount of cortical space devoted to the affected body part, and an expansion of the representation of the adjacent body surface (Merzenich et al., 1983; Donoghue and Sanes, 1988; Donoghue et al., 1990; see Kaas, 1991; see Recanzone, 1998 for review). This plasticity has been demonstrated in all sensory systems in a variety of animals representing a number of different mammalian lineages (e.g., Kaas et al., 1990; Recanzone et al., 1993; Armstrong-James et al., 1994; Elbert et al., 1995; Bjordahl et al., 1998), suggesting that the mechanisms that allow for such changes are evolutionarily old, and would likely be present in all extant species. It has been proposed that this plasticity in cortical maps in adults is largely accomplished by changing the synaptic weights at different cortical locations, allowing for a change in the efficacy of existing connections with changing environmental demands (see Kaas, 1991; Merzenich et al., 1991; Recanzone, 1998 for review).

Thus, in addition to selection operating on the peripheral structure, or the receptors therein, as discussed above, selection is also likely to operate at the level of the synapse to allow Hebbian-like (Hebb, 1949) changes throughout the life of an individual. The molecular substrate that generates synaptic changes with differential use is likely to be highly conserved and genetically mediated.

A final factor that can account for the organization of neocortex in adult mammals is developmental in origin. Studies of developmental plasticity have demonstrated that the environment in which the animal develops plays an important role in the resultant neocortical organization. Early studies of Wiesel and Hubel (1965), and subsequent studies (e.g., Blakemore and Cooper, 1970; Pettigrew and Freeman, 1973; Tretter et al., 1975) demonstrated that differences in visual experience during the critical period can result in changes in the physiological properties of neurons, and in the organization of the neocortex. More dramatic changes in connection patterns, in the form of reduction of ocular dominance width determined through transneuronal transport from eye injections, after enucleation of one eye, suggests that the very wiring of the developing nervous system is, to a large extent, under environmental control (Hubel et al., 1977). For the somatosensory system, changes in the topography of cortical maps have been observed when the periphery is altered during different stages of development (e.g., Killackey and Belford, 1979; Belford and Killackey, 1980; Dawson and Killackey, 1987).

We hypothesize that even in the absence of any changes to developmental programs that construct a viable nervous system, a number of differently organized brains can develop, and what might originally have been considered as true evolutionary change exclusively, is actually a reflection of genetic, evolutionary processes, as well as epigenetic processes. Morphological changes within an evolving and developing organism cannot account for changes in the size of the cortical sheet. However, if size is held constant, changes in morphology (via genetic changes) and differences in the environment in which the organism develops and is maintained, from use of a particular body part to differences in social interactions, can account for many of the differences we observe in the brains of different mammals.

ACKNOWLEDGMENTS

We thank Elizabeth Disbrow, Dianna Kahn, Natalie Pobirsky, Gregg Recanzone, and Rowan Tweedale for helpful comments on this manuscript. We also thank Monika Sum for technical assistance with tissue processing. This work was supported in part by an NIH grant (1 RO1 NS35103–01A1), a Whitehall Foundation grant (M20–97), and an Australian Research Council (ARC) Fellowship to Leah Krubitzer; and by an ARC Special Research Centre grant to the VTHRC.

LITERATURE CITED

Adey WR, Kerr DIB. 1954. The cerebral representation of deep somatic sensibility in the marsupial phalanger and the rabbit; an evoked potential and histological study. J Comp Neurol 100:597–626.

Aitkin LM. 1995. The auditory neurobiology of marsupials: A review. Hearing Res 82:257–266.

Aitkin LM, Gates GR. 1983. Connections of the auditory cortex of the brush-tailed possum, *Trichosurus vulpecula*. Brain Behav Evol 22:75–88.

Aitkin LM, Irvine DRF, Nelson JE, Merzenich MM, Clarey JC. 1986. Frequency representation in the auditory midbrain and forebrain of a marsupial, the northern native cat (Dasyurus hallucatus). Brain Behav Evol 29:17–28.

Armstrong-James M, Diamond ME, Ebner FF. 1994. An innocuous bias in whisker use in adult rats modifies receptive fields of barrel cortex neurons. J Neurosci 14:6978–6991.

Beck PD, Pospichal MW, Kaas JH. 1996. Topography, architecture, and connections of somatosensory cortex in opossums: Evidence for five somatosensory areas. J Comp Neurol 366:109–133.

Begg RJ. 1983. In R. Strahan (ed): The Complete Book of Australian Mammals. Angus and Robertson: Sydney, p. 23.

Belford GR, Killackey HP. 1980. The sensitive period in the development of the trigeminal system of the neonatal rat. J Comp Neurol 193:335–350.

Benevento LA, Ebner FF. 1971a. The areas and layers of corticocortical terminations in the visual cortex of the Virginia opossum. J Comp Neurol 141:157–190.

Benevento LA, Ebner FF. 1971b. The contribution of the dorsal lateral geniculate nucleus to the total pattern of thalamic terminations in striate cortex of the Virginia opossum. J Comp Neurol 143:243–260.

Bjordahl TS, Dimyan MA, Weinberger NM. 1998. Inductions of long term receptive field plasticity in the auditory cortex of the waking guinea pig by stimulaton of the nucleus basialis. Behav Neurosci (in press).

Blakemore C, Cooper G. 1970. Development of the brain depends on the visual environment. Nature 228:477–478.

Bodemer CW, Towe AL. 1963. Cortical localization patterns in the somatic sensory cortex of the opossum. Exp Neurol 8:380–394.

Carroll EW, Wong-Riley MTT. 1984. Quantitative light and electron microscopic analysis of cytochrome oxidase-rich zones in the striate cortex of the squirrel monkey. J Comp Neurol 222:1–17.

Cartmill M. 1974. Daubentonia, Dactylopsila, *woodpeckers and klinorhynchy*. In RD Martin, GA Doyle, and AC Walker (eds): Prosimian Biology. Pittsburg: University of Pittsburg Press. pp. 655–670.

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

Clemens WA, Richardson BJ, Baverstock PR. 1989. Biogeography and phylogeny of the metatheria. In DW Walton and BJ Richardson (eds): Fauna of Australia. Canberra: Australian Government Publishing Service, pp. 527–548.

Crewther DP, Crewther SG, Sanderson KJ. 1984. Primary visual cortex in the brushtailed possum: Receptive field properties and corticocortical connections. Brain Behav Evol 24:184–197.

Dawson DR, Killackey HP. 1987. The organization and mutability of the forepaw and hindpaw representations in the somatosensory cortex of the neonatal rat. J Comp Neurol 256:246–256.

Donoghue JP, Sanes JN. 1988. Organization of adult motor cortex representation patterns following neonatal forelimb nerve injury in rats. J Neurosci 8:3221–3232.

Donoghue JP, Suner S, Sanes JN. 1990. Dynamic organization of primary motor cortex output to target muscles in adult rats II. Rapid reorganization following motor nerve lesions. Exp Brain Res 79:492–503.

Elbert T, Pantev C, Wienbruch C, Rockstroh B, Taub E. 1995. Increased cortical representation of the fingers of the left hand in string players. Science 270:305–307.

Elston G, Krubitzer L, Manger P, Calford M, Day T. 1993. The organization and connections of somatosensory cortex in the Australian marsupial, brush tailed possum (*Trichosurus vulpecula*). Soc Neurosci Abst 19:764.

Feldman SH, Johnson JI. 1988. Kinesthetic cortical area anterior to primary somatic sensory cortex in the raccoon *(Procyon lotor)*. J Comp Neurol 277:80–95.

Felleman DJ, Wall JT, Cusick CG, Kaas JH. 1983. The representation of the body surface in S-I of cats. J Neurosci 3:1648–1669.

Flannery TF. 1989. Origins of the Australo-Pacific mammal fauna. Austral Zool Rev 1:15–24.

Gallyas F. 1979. Silver staining of myelin by means of physical development. Neurology 1:203–209.

Gates GR, Aitkin LM. 1982. Auditory cortex in the marsupial possum *Trichosurus vulpecula*. Hear Res 7:1–11.

Gould HJI, Cusick CG, Pons TP, Kaas JH. 1986. The relationship of corpus callosum connections to electrical stimulation maps of motor, supplementary motor, and the frontal eye fields in owl monkeys. J Comp Neurol 247:297–325.

Grzimek B. 1990. Grzimek's Encylcopedia of Mammals. New York: McGraw-Hill Publishing Company. p. 210.

Haight JR, Sanderson KJ, Neylon L, Patten GS. 1980. Relationships of the visual cortex in the marsupial brush-tailed possum, *Trichosurus vulpecula*, a horseradish peroxidase and autoradiographic study. J Anat 131:387–413.

Hebb DO. 1949. The Organization of Behavior: A Neuropsychological Theory. New York: Wiley.

Hubel DH, Wiesel TN, LeVay S. 1977. Plasticity of ocular dominance columns in monkey striate cortex. Phil Trans Roy Soc Lond B 278:377–409.

Jenkins WM, Merzenich MM, Ochs MT, Allard T, Gu'c-Robles E. 1990. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. J Neurophysiol 63:82–104.

Johnson JI. 1990. Comparative development of somatic sensory cortex. In EG Jones and A Peters (eds): Cerebral Cortex. New York: Plenum, pp 335–449.

Johnson JI, Ostapoff E-M, Warach S. 1982. The anterior border zones of primary somatic sensory (SI) neocortex and their relation to cerebral convolutions, shown by micromapping of peripheral projections to the region of the fourth forepaw digit representation in raccoons. Neuroscience 7:915–936.

Kaas JH. 1982. The segregation of function in the nervous system: Why do the sensory systems have so many subdivisions? Contrib Sens Physiol 7:201–240.

Kaas JH. 1991. Plasticity of sensory and motor maps in adult mammals. Annu Rev Neurosci 14:137–167.

Kaas JH, Krubitzer LA. 1991. The organization of extrastriate visual cortex. In B Drehr and SR Robinson (eds): Neuroanatomy of Visual Pathways and Their Development: Vision and Visual Dysfunction. London: Macmillan Press, pp. 302–323.

Kaas JH, Pons TP. 1988. The somatosensory system of primates. Comp Primate Biol 4:421–468.

Kaas JH, Nelson RJ, Sur M, Lin C-S, Merzenich MM. 1979. Multiple representations of the body within the primary somatosensory cortex of primates. Science 204:521–523.

Kaas JH, Krubitzer LA, Chino YM, Langston AL, Polley EH, Blair N. 1990. Reorganization of retinotopic cortical maps in adult mammals after lesions of the retina. Science 248:229–231.

Killackey HP, Belford GR. 1979. The formation of afferent patterns in the somatosensory cortex of the neonatal rat. J Comp Neurol 183:285–304.

Krubitzer L. 1995. The organization of neocortex in mammals: Are species differences really so different? TINS 18:408–417.

Krubitzer L. 1998. What can monotremes tell us about brain evolution? Phil Trans Roy Soc Lond B 353:1127–1146.

Krubitzer L, Clarey J, Tweedale R, Elston G, Calford M. 1995a. A redefinition of somatosensory areas in the lateral sulcus of macaque monkeys. J Neurosci 15:3821–3839.

Krubitzer L, Manger P, Pettigrew J, Calford M. 1995b. Organization of somatosensory cortex in monotremes: In search of the prototypical plan. J Comp Neurol 351:261–306.

Krubitzer L, Huffman KJ, Sum ME. 1997a. Cortical connections of primary visual cortex in a metatherian mammal (*Monodelphis domestica*). Soc Neurosci Abstr 23:1031.

Krubitzer L, Künzle H, Kaas J. 1997b. Organization of sensory cortex in a madagascan insectivore, the tenrec (*Echinops telfairi*). J Comp Neurol 379:399–414.

Krubitzer LA. 1996. The organization of lateral somatosensory cortex in primates and other mammals. In O Franzen, R Johansson, and L Terenius (eds): Somesthesis and the Neurobiology of the Somatosensory Cortex. Basel: Birkhauser Verlag. pp. 173–185.

Krubitzer LA, Kaas JH. 1990. The organization and connections of somatosensory cortex in marmosets. J Neurosci 10:952–974.

Krubitzer LA, Sesma MA, Kaas JH. 1986. Microelectrode maps, myeloarchitecture, and cortical connections of three somatotopically organized representations of the body surface in the parietal cortex of squirrels. J Comp Neurol 250:403–430.

Kudo M, Glendenning KK, Frost SB, Masterton RB. 1986. Origin of mammalian thalamocortical projections. I. Telencephalic projections of the medial geniculate body in the opossum (*Didelphis virginiana*). J Comp Neurol 245:176–197.

Kudo M, Aitkin LM, Nelson JE. 1989. Auditory forebrain organization of an Australian marsupial, the northern native cat (*Dasyurus hallucatus*). J Comp Neurol 279:28–42.

Lende RA. 1963a. Sensory representation in the cerebral cortex of the opossum *(Didelphis virginiana)*. J Comp Neurol 121:395–403.

Lende RA. 1963b. Cerebral cortex: A sensorimotor amalgam in the marsupialia. Science 141:730–732.

Lende RA. 1963c. Motor representation in the cerebral cortex of the opossum (*Didelphis virginiana*). J Comp Neurol 121:405–415.

Luethke LE, Krubitzer LA, Kaas JH. 1988. Cortical connections of electrophysiologically and architectonically defined subdivisions of auditory cortex in squirrels. J Comp Neurol 268:181–203.

Luethke LE, Krubitzer LA, Kaas JH. 1989. Connections of primary auditory cortex in the New World monkey, *Saguinus*. J Comp Neurol 285:487–513.

Magalhâes-Castro B, Saraiva PES. 1971. Sensory and motor representation in the cerebral cortex of the marsupial *Didelphis azarae azarae*. Brain Res 34:291–299.

Martinich S, Rosa MGP, Rocha-Miranda CE. 1990. Patterns of cytochrome oxidase activity in the visual cortex of a South American opossum (*Didelphis marsupialis aurita*). Braz J Med Biol Res 23:883–887.

Merzenich MM, Kaas JH, Wall J, Nelson RJ, Sur M, Felleman D. 1983. Topographic reorganization of somatosensory cortical areas 3b and 1 in adult monkeys following restricted deafferentation. Neuroscience 8: 33–55.

Merzenich MM, Nelson RJ, Kaas JH, Stryker MP, Jenkins WM, Zook JM, Cynader MS, Schoppmann A. 1987. Variability in hand surface representations in areas 3b and 1 in adult owl and squirrel monkeys. J Comp Neurol 258:281–296.

Merzenich MM, Grajski KA, Jenkins WM, Recanzone GH, Peterson B. 1991. Functional cortical plasticity. Cortical network origins of represetation changes. Cold Spring Harbor Symp Quant Biol 55:873–887.

Morton SR. 1983. In R Strahan (ed): The Complete Book of Australian Mammals. Sydney: Angus and Robertson, p. 61.

Nelson RJ, Sur M, Felleman DJ, Kaas JH. 1980. Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. J Comp Neurol 192:611–643.

Nudo RJ, Milliken GW, Jenkins WM, Merzenich MM. 1996. Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16:785–807.

Packer AD. 1941. An experimental investigation of the visual system in the phalanger, *Trichosurus vulpecula*. J Anat 75:309–329.

Pellis SM, Vanderlely R, Nelson JE. 1992. The roles of vision and vibrissae in the predatory behaviour of Northern Quolls *Dasyurus Hallucatus* (Marsupialia: Dasyuridae). Austral Mammalogy 15:55–60.

Penfied W, Rasmussen T. 1950. The Cerebral Cortex of Man. New York: Macmillin.

Pettigrew J, Freeman R. 1973. Visual experience without lines: Effect on developing cortical neurons. Science 182:599–601.

Pons TP, Garraghty PE, Cusick CG, Kaas JH. 1985. The somatotopic organization of area 2 in macaque monkeys. J Comp Neurol 241:445–466.

Pobirsky N, Molnar Z, Blakemore C, Krubitzer L. 1998. The organization of somatosensory cortex in the west European hedgehog (*Erinaceus europaeus*). Soc Neurosci Abst 24:1125.

Pubols BH. 1977. The second somatic sensory area (SmII) of opossum neocortex. J Comp Neurol 174:71–78.

Pubols BH, Pubols LM, DePette DJ, Sheely JC. 1976. Opossum somatic sensory cortex: A microelectrode mapping study. J Comp Neurol 165:229–246.

Recanzone GH. 1998. Cerebral cortical plasticity, perception, and skill acquisition. In M Gazzaniga (ed.): The Cognitive Neurosciences. Cambridge, London: MIT Press, (in press).

Recanzone GH, Merzenich MM, Jenkins WM, Grajski KA, Dinse HR. 1992a. Topographic reorganization of the hand representation in cortical area 3b of owl monkeys trained in a frequency - discrimination task. J Neurophysiol 67:1031–1056.

Recanzone GH, Merzenich MM, Schreiner CE. 1992b. Changes in the distributed temporal response properties of SI cortical neurons reflect improvements in performance on a temporally based tactile discrimination task. J Neurophysiol 67:1071–1091.

Recanzone GH, Schreiner CE, Merzenich MM. 1993. Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. J Neurosci 31:87–103.

Rees S, Hore J. 1970. The motor cortex of the brush-tailed possum (*Trichosurus vulpecula*): Motor representation, motor function and the pyramidal tract. Brain Res 20:439–452.

Rosa MGP. 1997. Visuotopic organization of primate extrastriate cortex. In K Rockland, JH Kaas, and A Peters (eds.): Cerebral Cortex, Extrastriate Cortex in Primates, Volume 12. New York, London: Plenum Press, pp. 127–203.

Rosa MGP, Krubitzer LA, Molnar Z, Nelson JE. 1998. Organisation of visual cortex in the northern quoll, *Dasyurus hallucatus*. Evidence for a homologue of the second visual area in marsupials. in press J Euro Neurosci

Rowe M. 1990. Organization of the cerebral cortex in monotremes and marsupials. In EG Jones and A Peters (eds): Cerebral Cortex. Plenum, New York, pp. 263–334.

Sousa APB, Gattass R, Oswaldo-Cruz E. 1978. The projection of the opossum's visual field on the cerebral cortex. J Comp Neurol 177:569–588.

Stepniewska I, Preuss TM, Kaas JH. 1993. Architectonics, somatotopic organization, and ipsilateral cortical connections of the primary motor area (MI) of owl monkeys. J Comp Neurol 330:238–271.

Sur M, Nelson RJ, Kaas JH. 1978. The representation of the body surface in somatosensory area I of the grey squirrel. J Comp Neurol 179:425–450.

Sur M, Nelson RJ, Kaas JH. 1980. Representation of the body surface in somatic koniocortex in the prosimian *Galago*. J Comp Neurol 189:381–402.

Tretter F, Cynader M, Singer W. 1975. Modification of direction selectivity of neurons in the developing visual cortex of kittens. Brain Res 84:143–149.

Van Dyck SM. 1983. In R Strahan (ed.): The Complete Book of Australian Mammals. Sydney: Angus and Robertson, pp. 144–145.

Vidyasagar TR, Wye-Dvorak J, Henry GH, Mark RF. 1992. Cytoarchitecture and visual field representation in area 17 of the tammar wallaby (*Macropus eugenii*). J Comp Neurol 325:291–300.

Volchan E, Bernardes RF, Rocha-Miranda CE, Gleiser L, Gawryszewski LG. 1988. The ipsilateral field representation in the striate cortex of the opossum. Exp Brain Res 73:297–304.

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

Weller WL. 1972. Barrels in somatic sensory neocortex of the marsupial *Trichosurus vulpecula* (brush-tailed possum). Brain Res 43:11–24.

Weller WL. 1993. SmI cortical barrels in an Australian marsupial, *Trichosurus vulpecula* (brush-tailed possum): Structural organization, patterned distribution, and somatotopic relationships. J Comp Neurol 337:471–492.

Weller WL, Haight JR. 1973. Barrels and somatotopy in SI neocortex of the brush-tailed possum. J Anat 116:473–474.

Wiesel TN, Hubel DH. 1965. Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens. J Neurophysiol 28:1029–1040.

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