Organization of Somatosensory Cortex in Monotremes: In Search of the Prototypical Plan

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ABSTRACT

The present investigation was designed to determine the number and internal organization of somatosensory fields in monotremes. Microelectrode mapping methods were used in conjunction with cytochrome oxidase and myelin staining to reveal subdivisions and topography of somatosensory cortex in the platypus and the short-billed echidna. The neocortices of both monotremes were found to contain four representations of the body surface. A large area that contained neurons predominantly responsive to cutaneous stimulation of the contralateral body surface was identified as the primary somatosensory area (SI). Although the overall organization of SI was similar in both mammals, the platypus had a relatively larger representation of the bill. Furthermore, some of the neurons in the bill representation of SI were also responsive to low amplitude electrical stimulation. These neurons were spatially segregated from neurons responsive to pure mechanosensory stimulation. Another somatosensory field (R) was identified immediately rostral to SI. The topographic organization of R was similar to that found in SI; however, neurons in R responded most often to light pressure and taps to peripheral body parts. Neurons in cortex rostral to R were responsive to manipulation of joints and hard taps to the body. We termed this field the manipulation field (M). The mediolateral sequence of representation in M was similar to that of both SI and R, but was topographically less precise. Another somatosensory field, caudal to SI, was adjacent to SI laterally at the representation of the face, but medially was separated from SI by auditory cortex. Its position relative to SI and auditory cortex, and its topographic organization led us to hypothesize that this caudal field may be homologous to the parietal ventral area (PV) as described in other mammals. The evidence for the existence of four separate representations in somatosensory cortex in the two species of monotremes indicates that cortical organization is more complex in these mammals than was previously thought. Because the two monotreme families have been separate for at least 55 million years (Richardson, B.J. [1987] Aust. Mammal. 11:71-73), the present results suggest either that the original differentiation of fields occurred very early in mammalian evolution or that the potential for differentiation of somatosensory cortex into multiple fields is highly constrained in evolution, so that both species arrived at the same solution independently. © 1995 Wiley-Liss, Inc.

Indexing terms: evolution, development, SI, echidna, platypus

Monotremes are egg-laying mammals belonging to two surviving families (Ornithorhynchidae and Tachyglossidae) that have intrigued scientists since the improbable platypus was first described (Shaw, 1799). One reason for this continuing interest is that taxonomic studies have shown that, of all extant mammals, monotremes are the most distantly related to humans and other placental mammals, having diverged from therian mammals in the early Cretaceous, over 130 million years ago (MYA; Clemens, 1989; Flannery, 1989; Westerman and Edwards, 1992). As such, they help define the range of characteristics that we consider mammalian, one of which is the elaboration of those parts of the forebrain known as the neocortex. However, it is also the differences in the nervous system (Bullock, 1993), in particular the neocortex, that characterize differences between groups of mammals. We undertook this study of monotremes as part of a more extensive, comparative effort to deduce what features of neocortex characterize all major lines of mammalian evolution, and

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Abbreviations

Cortical fields		CN DIG	chin digits
1	cutaneous somatosensory field	DOR	dorsal
1/2	area 1/2 of somatosensory cortex	FA	face
1/2 0	deen sometosensory field	FL	forelimb
20	deep somatosensory area	FL EL	forelimb elevation
<i>ы</i> Л	auditory field	FP	forepaw
A + S	mixed auditory and somatosensory responses	FP (VIB)	forepaw vibration
A + W	mixed auditory and visual responses	FW	finger webs
	mixed additory and visual responses	G	genitals
	primary additory area	GLAB	glabrous
AUD	auditory contex	HE	head
	dorsolateral visual area	HL	hindlimb
DM	dorsomediai visual area	HLEL	hindlimb elevation
FEF	frontal eye movement field	HLEYT	hindlimb extension
FST	fundal superior temporal area	UD	hindnew
FV	frontal ventral eye movement field	III VN	knoo
Н	hippocampus	LAT	latoral
M	manipulation area	LAI	lowor
MI	primary motor held	MID	middle
MST	medial superior temporal visual area	MID	nadule
MT	middle temporal visual area	NA	naris
PM	premotor cortex	NE	nan beus
PP	posterior parietal cortex	NE	neck
PV	parietal ventral somatosensory area	NK	no response
R	rostral somatosensory area	PIN	pinna
SI	primary somatosensory area (3b)	PROX	proximal
SII	second somatosensory area	SH	shoulder
SMA	supplementary motor area	SHI	shield
TA	temporal anterior field	SP	spur
UZ	unresponsive zone	Т	toes
V	visual field (possibly VI)	TA	tail
V + S	mixed visual and somatosensory responses	TAST	tail stub
VI	primary visual area	TON	tongue
VII	second visual area	TR	trunk
VIS	visual cortex	UP	upper
VP	ventral posterior visual area	VEN	ventral
vs	ventral somatosensory field	W	wrist
		WE	webs
Body parts			
		Other abbreviations	
A + B	auditory and bill mixed responses		
В	bill	М	medial
BO	body	NR	no response
CK	cheek	R	rostral

thus are likely to have been retained from the first emergence of mammals from reptiles in the middle to late Triassic, over 200 MYA (Clemens, 1970, 1989; Crompton and Jenkins, 1973). By determining cortical organization in monotremes and comparing results with those obtained from various metatherian and eutherian mammals, it should be possible to reconstruct the cortical organization of the common ancestor from traits that have been retained, and to determine how this organization has been modified in the different lines. A second reason for continuing scientific curiosity about monotremes is the unique bill-like structure of the platypus and the related bill of the echidna. These specializations are reflected in the fossils of the latest modern-like monotreme (Miocene, ~ 22 MYA; e.g., Archer et al., 1992a,b) and are likely to represent long-standing modifications that may have been essential to their survival. In both animals, the long rostrum is covered with a rubbery, sensitive skin that is important in tactile exploration and prey capture. However, it appears that only the platypus has well-developed electroreception as an additional sensory elaboration of the bill (Scheich et al., 1986; Gregory et al., 1987, 1988; Iggo et al., 1992).

Variable numbers of somatosensory fields have been reported in mammals (see Johnson, 1990, for review), and there is evidence that at least three of these fields, the primary somatosensory area (SI), the second somatosensory area (SII), and the parietal ventral area (PV, see Abbreviations) are basic to eutherians (e.g., Krubitzer et al., 1986; Krubitzer and Kaas, 1990b; see Krubitzer and Calford, 1992, for review) and, perhaps, metatherian mammals (Beck and Kaas, 1993; Elston et al., 1993). Previous electrophysiological recording studies provide evidence for a large somatosensory region in both monotremes (Lende, 1964; Bohringer and Rowe, 1977) with much of the region devoted to the bill. The general organization and location of this region suggests that much or all of it is SI (see Abbreviations). There is also evidence for a separate motor area in the echidna (Abbie, 1938; Lende, 1964; Ulinski, 1984) and the platypus (Bohringer and Rowe, 1977) as well

A note on terminology: Three different terms are used to describe the specialized, anterior feeding apparatus of monotremes: viz. bill, beak, and snout. We have chosen the term bill to refer to this apparatus in both the platypus and the echidna for the following reasons: 1) Consistency; because both structures are clearly homologous, sharing the same tactile specializations as well as a similar bony support, it seems rational to adopt the same name for the structure whether we are referring to the platypus or the echidna; 2) semantics; to us, the word beak has the connotations of a horny, keratinous appendage like the beak of a fowl. In contrast, the more encompassing term bill includes, to our way of thinking, a more elaborate feeding apparatus such as the rhyncokinetic mechanism of scolopacid birds (Pettigrew and Frost, 1985). The word snout seems inappropriate because of the bony skeleton found in both the platypus and the echidna. Short of coining a totally new term, we believe that bill is an unambiguous and appropriate term for the feeding appendage of both monotremes, and this is the usage that has been adopted in this paper.

as separate auditory and visual regions in the echidna (Lende, 1964). Most importantly, architectonic studies in the echidna suggest further complexity of the neocortex and the existence of several subdivisions of sensory and motor cortex (e.g., Ulinski, 1984).

We embarked on the present investigation with several goals. First, we hoped to describe the somatotopic organization of SI in detail. This would allow us to make comparisons with SI in other mammals and to determine common and specialized features in monotremes. In particular, we wanted to see if the previously described large bill representation (Bohringer and Rowe, 1977) of the platypus had subdivisions that might relate to electroreceptors, as has been suggested in a previous study (Scheich et al., 1986). Thus, another goal in the present investigation was to determine how the organization of neocortex in monotremes reflects their facial specializations, and whether the differences in these specializations are reflected in their cortical organization. Third, we wanted to see if any additional somatosensory fields could be identified. Previously, only SI had been identified electrophysiologically in monotremes, but a more detailed study could reveal additional representations, as suggested by architectonic studies. Fourth, we wanted to see how somatosensory fields relate to auditory and visual fields. In most other mammals, a primary visual area (VI) and an auditory field, presumably the primary auditory area (AI), can be identified by architectonic and other criteria. Separate auditory and visual regions have been proposed in echidnas (Lende, 1964), whereas almost completely overlapping auditory and visual regions were identified in the platypus by Bohringer and Rowe (1977).

Our approach differed from previous studies in that we combined electrophysiological and several architectonic procedures in the same animals, and cortex was flattened and cut parallel to the cortical surface. This preparation facilitates comparisons of the two sets of data and allows direct visualization of the extents and relative positions of architectonic fields. This allows us to relate present results to those obtained in a number of recent studies in eutherian mammals conducted using similar procedures, e.g., flying foxes (Krubitzer and Calford, 1992; Krubitzer et al., 1993a), marmosets (Krubitzer and Kaas, 1990b), owl monkeys (Cusick et al., 1989), macaque monkeys (Krubitzer et al., 1993b), squirrels (Krubitzer et al., 1986), and metatherians (Beck and Kaas, 1993; Elston et al., 1993), and to elaborate the theory of the evolution of cortical fields derived from our recent work in flying foxes (Krubitzer and Calford, 1992; Krubitzer et al., 1993a).

MATERIALS AND METHODS

Microelectrode mapping procedures similar to those used previously in this laboratory (e.g., Krubitzer and Calford, 1992) were used to study somatosensory cortex of six platypuses (Ornithorhyncus anatinus) and seven echidnas (Tachyglossus aculeatus). At the beginning of each experiment, the animal was anesthetized with ketamine hydrochloride (40 mg/kg) and xylazine (4 mg/kg). Dexamethasone (0.2 mg/kg) was administered to prevent edema, and glucose supplements were also given. Half the initial dose of ketamine was given as required to maintain anesthetic levels throughout the experiment.

After the animal was anesthetized, the scalp was cut, and a large opening was made in the skull to expose all of sensory cortex. The dura was retracted and an acrylic well, built around the opening in the skull, was filled with silicone fluid. A photograph of the exposed cortex was taken and enlarged so that recording sites could be marked relative to vasculature. Multiunit and single-unit activity was recorded through a tungsten-in-glass electrode. The electrode was manually moved in X/Y coordinates and advanced through the cortex with a stepping microdrive. Electrical activity was amplified, filtered, displayed on an oscilloscope, and transduced through a loud speaker. Responses of neurons at 928 recording sites in platypuses and 2,338 recording sites in echidnas were obtained and analyzed. Receptive fields for neurons at these sites were defined by lightly brushing or lightly tapping the skin, lightly squeezing the skin, manipulating joints, or vigorously tapping the skin. Stimuli consisted of brushes, fine glass probes, and pointed and blunt sticks. The recording sites at which neurons responded to light brushing of glabrous skin or deflection of hairs are termed "cutaneous." Recording sites at which neurons responded to light tapping of skin, gentle squeezing, or light pressure are termed "deep." Although neurons that responded best to manipulation of body parts are also likely to be receiving inputs from deep peripheral receptors, we have classified them as "manipulation" sites. Neurons at such sites often responded to hard taps as well. The stimulus needed to elicit a response was one useful criterion for distinguishing cortical fields (Table 1). A receptive field was defined as the maximal area of the body surface that, when stimulated with a given stimulus, produced a neural response. When we compared receptive field size, the same investigator mapped the receptive fields, and the same stimulus was applied to the receptive fields with maximal strength to reduce variation. Furthermore, we compared receptive fields for a similar body part in a single animal.

For some neurons in the platypus, electrical stimulation was used to elicit a response. In these experiments, the bill was immersed in water to just below the nares. Electrical stimuli were produced by battery-operated pulse generators and delivered through a pair of stainless steel electrodes (1 mm in diameter and 20 mm in length) by placing the electrodes in the water bath near the submerged bill. The amplitude of the stimuli ranged from 20 μ V/cm to 900 $\mu V/cm$. An electrical receptive field was defined as the area of the skin surface that, when stimulated electrically, produced a neural response. The location of electrosensory receptive fields was determined by moving the electrode pair around the submerged bill while adjusting the amplitude of the stimulus to find both approximate threshold and the best location for stimulation. The position of the electrosensory receptive field did not vary with stimulus amplitude. A precise determination of threshold was made by placing the electrodes on either side of the receptive field and adjusting the field voltage until a neural response could no longer be elicited. Stimulus voltage was calibrated for each individual experiment by placing the immersed stimulating electrodes 10 cm apart and measuring the $\mu V/cm$ directly with two stainless steel electrodes connected to an oscilloscope.

Because we hoped to determine the entire extent of somatosensory cortex in these animals, cortex adjacent to somatosensory cortex was often mapped so that the boundaries (but not the internal organization) of auditory and visual fields could be determined. Full-field flashes of light and moving bars of light produced a vigorous response from neurons in visual cortex. Neurons in auditory cortex responded well to free-field clicks. In one echidna, free-field pure tones were used to determine the tonotopic organiza264

tion of auditory cortex. However, results of that experiment will be provided in a subsequent paper.

In the sensory mapping experiments in the echidna, many electrode tracks were advanced through the sulci of neocortex and ran parallel to cortical layers. Recordings were obtained every 400–600 μ m. In the platypus, most of the electrode penetrations were on the surface of cortex except for recording sites in the caudal field, which we term PV (see Results). Because PV was located at the posteromedial pole of the cortex, electrodes were often advanced down the posterior medial wall and recordings were made every 400–600 μ m. Recording sites on the surface of cortex were placed 400–1,000 μ m apart. In all experiments, electrolytic lesions (10 μ A for 6 seconds) were placed at a number of locations for later identification in processed tissue, to aid in the reconstruction.

At the end of a recording session, the animal was administered a lethal dose of sodium pentobarbitone and transcardially perfused with 0.9% saline; this was followed by 3% paraformaldehyde in phosphate buffer and then 3% paraformaldehyde and 10% sugar in phosphate buffer. When perfusion was complete, the brain was removed from the cranium, the cortices were dissected from the brainstem and thalamus, the sulci were gently pried apart, and the cortex was manually flattened and placed between glass slides. After the cortex was immersed in 30% sugar phosphate buffer for approximately 15 hours, it was cut on a freezing microtome into 40-µm sections. In two echidna hemispheres and one platypus hemisphere, cortex was sectioned parasagittally at 50 µm. Alternate sections were reacted for cytochrome oxidase (CO; Carroll and Wong-Riley, 1984) and stained for myelin (Gallyas, 1979) or Nissl substance.

Data analysis

In order to match electrophysiological findings to architectonic boundaries, lesions or probe markers were located on stained tissue, scales were adjusted, and electrophysiological data from the enlarged photograph were added to results from tissue processed for CO or stained for myelin (e.g., Figs. 11, 25). In this way, a comprehensive reconstruction of our data could be obtained. We have chosen to present our data in several ways. Because a good criterion for defining a somatosensory cortical field is a complete representation of the body surface, we first reconstructed recording sites and identified the receptive fields associated with neurons in those sites to make maps of the body surface. This allowed us to determine the number of times a single body part was represented in cortex and to assess the number of cortical areas present (e.g., Figs. 4, 8, 14). Second, we considered the type of stimulation required to elicit a neural response at a given location in cortex (e.g., Figs. 5, 15). Third, we illustrated a number of receptivefield progressions within and across areas. We did this to detail the topographic organization within an area and to show reversals and changes in receptive field size across areas. Finally, we matched cortical architecture to our electrophysiological mapping results to determine whether our physiological boundaries were coextensive with architectonic boundaries. Thus, our criteria for subdividing cortex were: 1) demonstration of a complete representation of the body surface, 2) discrete architectonic appearance, 3) changes in stimulus type required to elicit a response, and 4) changes in receptive field size. When all of these criteria are used in combination, it is possible to delineate neocortical fields with accuracy.

RESULTS

Here we describe the detailed topographic organization of four somatosensory fields in echidnas and platypuses. In the first section of our results, we outline the surface morphology of the platypus and echidna cortices. We then describe the relative location and extent of somatosensory, auditory, and visual cortex in both species. In the next section of our results, we describe four separate representations of the body surface in both species. Based on topographic organization, neural response properties, and architectonic appearance, we have termed these fields the primary somatosensory area, the rostral field (R), as described in previous studies of monotreme cortex (Lende, 1964; Bohringer and Rowe, 1977; Ulinski, 1984), and the parietal ventral area (PV), as described in previous studies in other mammals. The description of the topographic organization of an additional field, rostral to R, which we term M, is brief, because only limited recordings were made in this field. The internal organization of fields will be detailed, and the receptive field progression within and across these fields will be described. In this section, we also describe the correlation of functionally distinct groups of neurons in the bill representation of SI, associated with electrosensory and mechanosensory processing, with architectonic features of the bill representation in SI. In the third section of our results, we describe the neural response properties of the different somatosensory fields and the preferred stimulus of neurons in each field. We then compare receptive-field sizes between fields. In the next section of these results, we describe the architectonic appearance of each of these fields in cortex that has been flattened, cut parallel to the cortical surface, and stained for myelin or cytochrome oxidase. In two cases, cortex was sectioned parasagittally, which allows us to describe the cytoarchitecture of somatosensory cortex in both species. Finally, we describe the location, extent. and architecture of visual and auditory cortex.

The location and extent of somatosensory fields

The surface morphology of the neocortex of the platypus and the echidna is strikingly different. Whereas the platypus has a smooth, small neocortex, the echidna has a convoluted, relatively large brain (Fig. 1A,B) with an expanded area of neocortex rostral to the alpha (α) sulcus. In the intact echidna brain, the amount of neocortex devoted to sensory representations appears small compared to the large "frontal" cortex (Abbie, 1938; Lende, 1964; Divac et al., 1987). However, when the α and zeta (ζ) sulci (approximately 5–8 mm in depth) are opened completely, the extent of sensory cortex can be appreciated with respect to the entire cortex (Fig. 2) and is as large, or almost as large, as that of "frontal" cortex. Although cortex rostral to the manipulation field (M) in echidnas has been termed frontal cortex, it is unclear if it is homologous to frontal cortex described in other animals, such as primates.

In both the platypus and the echidna, somatosensory cortex accounted for almost three-quarters of sensory cortex. Neurons responsive to cutaneous stimulation were located in the caudal half of the platypus cortex and the caudolateral one-fourth of the echidna cortex. Neurons responsive to other types of somatic stimulation were found in cortex just rostral to cortex in which neurons were responsive to cutaneous stimulation. In the platypus, this rostral somatic cortex extended almost to the rostral pole of the neocortex. In the echidna, it was located on the rostral



Fig. 1. Dorsolateral views of a platypus (\mathbf{A}) and an echidna (\mathbf{B}) brain illustrating the locations of cortex responsive to sensory stimulation. Cortex in which neurons were responsive to cutaneous stimulation occupied the caudal pole in both species. In the platypus, approximately one-third of the entire neocortex contained neurons responsive to cutaneous stimulation. Cortex in which neurons were responsive to stimulation of deep peripheral receptors was rostral to cortex where

neurons were responsive to cutaneous stimulation. Visual cortex was located medial to somatosensory cortex in both species. Auditory cortex was lateral to visual cortex, and was bordered by somatosensory cortex rostrally, laterally, and caudally. In the echidna, auditory cortex was deep in the ζ sulcus and sometimes spread onto the adjacent rostral gyrus. Major sulci are indicated (α , β , and ζ). Rostral is to the left, and medial is to the top. Scale bars = 1 mm.



Fig. 2. A dorsolateral view of the echidna brain (bottom right), and an unfolded echidna cortex (top) with the different sensory fields outlined. In the small bottom figure, the major sulci (alpha, α ; beta, β ; and zeta, ζ) have been partially opened, and the fields that lie within them are outlined in thick lines. Somatosensory cortex assumes most of

and caudal banks of sulcus $\boldsymbol{\alpha}$ and onto the adjacent rostral gyrus.

In both species, cortex in which neurons were responsive to somatic stimulation appeared to be divisible into four separate fields, which we have termed the primary somatosensory area (SI), the rostral deep field (R), the manipulation field (M), and the parietal ventral field (PV). Electrophysiological and architectonic evidence has been previously provided for SI in the platypus (Bohringer and Rowe, 1977) and for SI and R in the echidna (Lende, 1964; Ulinski, 1984), and the most caudal somatic field in both echidnas and platypuses has a number of parallels with a field termed the parietal ventral area (PV) described in other mammals (see below). For this reason, we have termed the field PV in both species. As in R, neurons in M responded to stimulation of deep receptors; however, the type of stimulus required to elicit a neural response, the internal organization, and the architectonic appearance of M distinguished it from the rostral field. In both species, all four somatosensory fields were similar in size, and each contained a complete representation of the body surface. The manipulation field was the rostralmost field and, in echidnas, was located on the rostral bank of sulcus α and the adjacent gyrus (Fig. 1B). The rostral field was located immediately

sensory cortex. As in the platypus, auditory cortex is embedded in somatosensory cortex. Visual cortex is medial to somatosensory cortex and is relatively larger than visual cortex in the platypus. See Abbreviations list for this and subsequent figures. Scale bars = 2 mm.

caudal to M and, in echidnas was located deep in the caudal bank of sulcus α (Fig. 1B), although it sometimes spread onto the adjacent caudal gyrus. Immediately caudal to R was SI. In the echidna, SI was found on the rostral bank of sulcus ζ and spread onto the adjacent rostral gyrus. Finally, PV was located immediately caudal to SI on the caudal bank of sulcus ζ and onto the adjacent caudal gyrus.

Although detailed maps were obtained only for somatosensory fields, the relative location and extent (Figs. 1, 2) of visual cortex and auditory cortex were easily obtained with simple auditory and visual stimuli. In both monotreme species, neurons responsive to visual stimulation were located just medial to cortex in which neurons were responsive to somatic stimulation. In the echidna, visually responsive cortex occupied a comparatively larger region of the neocortex than in the platypus. The position of auditory cortex with respect to visual and somatosensory cortex was similar in both species of monotremes. Auditory cortex was surrounded rostrally, laterally, and caudally by cortex responsive to cutaneous stimulation. In the echidna, auditory cortex was located on the rostral bank of sulcus ζ and often spread onto the adjacent rostral gyrus. Medially, auditory cortex was bounded by cortex in which neurons responded to visual, or visual plus auditory stimuli, or by

cortex in which neurons were unresponsive to any type of stimulation used in our experiments. There were small regions of cortex between auditory and somatosensory cortex in which neurons responded to both somatosensory and auditory stimulation.

The topographic organization of somatosensory cortex

The overall organization of sensory cortex appeared quite similar in the platypus and the echidna. Likewise, the architectonic appearance of fields in the platypus and the echidna were similar. For these reasons, we propose that the four somatosensory representations identified in the platypus and echidna are homologous, and, thus our results are grouped according to the cortical area described rather than by species. However, the figures are grouped according to species, so that comparisons across cases of the same species can be made with ease. Figures 3–11 are devoted to the platypus, and Figures 12–24 are devoted to the echidna.

The primary somatosensory area. SI contained a complete representation of the body surface coextensive with a unique architectonic appearance. The detailed topographic organization and neural characteristics of SI were similar to those described previously for both monotreme species (Lende, 1964; Bohringer and Rowe, 1977) as well as for other mammals (see Kaas, 1983; Johnson, 1990; Rowe, 1990, for review). Neurons in SI responded best to cutaneous stimulation of the contralateral body surface, and receptive fields were quite small, especially on the bill. Generally, the tail and tail stub in echidnas were represented in the mediocaudalmost portion of SI. Immediately rostral and/or rostrolateral to the tail representation was the representation of the lower trunk, hindlimb, hindpaw, and toes in a caudorostral sequence in both platypuses and echidnas (Figs. 4, 14, 18, 21A). In one echidna, the lower trunk was represented caudal to the tail (Fig. 12A). As recording sites moved from caudal to rostral in the lower body representation, receptive fields moved from lower trunk and tail to hindlimb, and then to toes, and then reversed back onto the hindlimb, lower trunk, and tail when crossing the SI/R boundary, and moving rostrally in R (e.g., Figs. 6, 20).

The representation of the trunk in both the echidna and the platypus was just lateral to the representations of the hindlimb and tail. Generally, the lower trunk was represented most medially, followed by the representation of the middle trunk, and, finally, the upper trunk most laterally (Figs. 3, 4, 12A, 14, 18, 21A). The dorsal trunk was represented caudally, and the ventral trunk was represented rostrally. As recording sites moved from medial to lateral in the representation of the trunk, receptive fields moved from the lower to upper trunk (e.g., Fig. 13), and as recording sites moved from caudal to rostral in the trunk representation of SI, receptive fields moved from dorsal to ventral (e.g., Figs. 13, 17, recording sites D-F). As recording sites moved rostrally from SI into R the receptive-field progression reversed back towards the dorsal trunk (e.g., Fig. 17, recording sites D-I).

In both the echidna and the platypus the representation of the forelimb was rostrolateral to the representation of the trunk. Within the forelimb representation, the digits of the forepaw were represented most rostrally, followed caudally by the representation of the forepaw, and, finally, the forelimb and shoulder representations most caudally (Figs. 3, 4, 12A, 14, 22A, 23). Thus, as recording sites progressed from caudal to rostral in the representation of the forelimb in SI, receptive fields moved from proximal to distal forelimb (e.g., Fig. 6, recording sites 1–4; Fig. 16, recording sites A–D). As recording sites crossed the SI/R boundary, a reversal of the sequence of receptive fields was observed, and receptive fields progressed from the distal forepaw caudally in R to proximal forepaw rostrally in R (e.g., Fig. 6, recording sites 1–7; Fig. 16, recording sites A–G).

The representations of the face, head, and neck were located laterally and often caudal to the representation of the forelimb, although this was most apparent in the echidna. Generally, the upper dorsal trunk, head, and neck representations were located caudal to the representation of the forelimb, and the face and chin representations extended farther laterally (Figs. 3, 4, 14, 18). Within the representation of the head and face, the dorsal head was represented most caudally in SI and the ventral neck most rostrally (e.g., Figs. 17, D-F). In some echidnas, a representation of the pinna was observed caudally in SI (Figs. 14, 23) and, in one case, was located just rostral to cortex in which neurons were responsive to auditory stimulation (Fig. 23). The face and chin representations were lateral to the head and neck representations, and, finally, the bill and oral structures were represented most laterally (Figs. 3, 4, 14, 18, 23). In both the echidna and the platypus the representation of the bill assumed disproportionately more space than any other body part representation. This was especially apparent for the platypus (Figs. 3, 4, 11; see below), which is not surprising, because approximately 100,000 receptors have been counted for half of the platypus bill (Manger et al., 1993). Functional specialization in the form of electrosensory input has been identified in the bill representation in SI (Scheich et al., 1986) and in fields ${\rm R}$ and PV (Manger et al., 1993), but a complete description of the bill representation is beyond the scope of the present report and is only dealt with briefly here.

The bill representation of SI of the platypus. In most cases, we observed a striking architectonic pattern in the bill representation of SI in the platypus (e.g., Fig. 11). In cortex that was flattened and cut parallel to the cortical surface, myelin-dense bands coextensive with CO-dense bands were observed in the bill representation. In some cases, this pattern was observed in SI immediately medial to the representation of the bill in other body part representations. In several experiments, we attempted to determine if these architectonic distinctions were related to physiological specializations. Previous reports have indicated that the platypus can detect electrical potentials, and that neurons in cortex respond to low amplitude electrical stimulation of the bill (e.g., Langner and Scheich, 1986; Scheich et al., 1986; Iggo et al., 1992). Furthermore, the platypus has specialized receptors on the bill that require electrical stimulation to be activated (Gregory et al., 1987, 1988). Thus, the most obvious choice of stimulus type to apply, in addition to mechanosensory stimulation, was electrical stimulation. In two animals, we identified regions where neurons responded only to cutaneous stimulation of the bill and separate, interdigitating regions where neurons responded to both cutaneous and electrical stimulation, although simultaneous stimulation was not required to elicit a response (Fig. 10). The receptive fields for neurons in the latter regions were somewhat larger than those of neurons in regions where only cutaneous stimulation elicited a response. Furthermore, there was a clear correspondence of these functionally distinct zones with the cortical architec-



Fig. 3. A reconstructed map of sensory cortex in platypus 4 (P4). Filled circles, spades, and squares mark electrode penetrations (see key in this figure). Solid lines mark architectonic and electrophysiological boundaries. Dashed lines mark approximated boundaries. Note that three representations of the body, SI, R, and PV (M was not mapped) in

this case were coextensive with architectonic boundaries. Within SI, myelin dense and light regions separate major body parts. Auditory cortex is embedded within somatosensory cortex, and a visual field is medial to somatosensory cortex.

ture described above. Regions where neurons responded only to cutaneous stimulation (in SI proper) were coextensive with myelin dark/CO-dense regions, and portions of cortex where neurons responded to both cutaneous and electrical stimulation were coextensive with the myelin/COlight regions of cortex (Figs. 10, 11). Across these CO-poor regions, the thresholds to electrical stimuli varied widely, with some neurons responding to stimuli as low as 20 μ V/cm and others responding to stimuli as great as 2,400 μ V/cm. In addition, closely spaced recording sites repetitively represented the same portion of the electroreceptive periphery. These areas were between 500 and 800 μ m wide. Although electroreceptors have been identified in the echidna bill (e.g., Gregory et al., 1989; Andres et al., 1991; Manger and Hughes, 1992), the number is substantially smaller than the number of electroreceptors found in the platypus bill (approximately 100 in the echidna bill compared to 40,000 in the platypus bill). The responsiveness of cortical neurons to electrical stimulation was not systematically investigated in the echidna.

The parietal ventral area. There was good evidence for another complete representation of the contralateral body surface caudal to SI and auditory cortex. We termed this field PV rather than SII, because the relative location of the

field, its internal organization, and its cortical architecture were consistent with PV, as described in a number of other mammals, rather than SII (see Discussion for alternative interpretations).

The data indicate that PV is not a caudal extension of SI. For example, in one echidna, E11 (Fig. 17, receptive fields 1-9), a clear topographic progression from the PV hindlimb representation into the PV forelimb and head and neck representations, and into similar representations in SI was observed. As recording sites moved from caudomedial PV toward SI, receptive fields for neurons in PV began on the tail and trunk and progressed to the upper trunk and forelimb. When the SI boundary was encountered, receptive fields for neurons became smaller (e.g., Fig. 17, compare receptive fields 4 and 5), and then the receptive-field progression reversed and moved laterally on the trunk, onto the forelimb, middle trunk, and finally lower trunk and tail. A reversal in receptive-field progression and change in the size of receptive fields was also observed for neurons at the PV/SI boundary of the bill representation (e.g., Fig. 7, receptive fields A-G).

The most dense maps of PV were obtained from two platypuses (Figs. 4, 8) and one echidna (Fig. 14). Partial maps in a number of other cases also helped determine the topography of PV. As in SI, neurons in PV responded most often to cutaneous stimulation. However, receptive fields for neurons in PV were generally large and often encompassed as much as one-third of the body in both species (e.g., Fig. 7, receptive field B; Fig. 9, receptive field 5; Fig. 17, receptive field 4). Thus, the topography of PV was less precise than that of SI. The mediolateral organization of PV in both platypuses and echidnas was similar to that described for SI in these species. As recording sites progressed from medial to lateral in PV, receptive fields progressed from tail to hindlimb, trunk, forelimb, and face (Fig. 7, receptive fields 1-7; Fig. 9, receptive fields 1-7; Fig. 14). The hindlimb, lower trunk, and tail representations occupied a very small portion of the medial part of PV, with the tail generally located most medially in the field (e.g., Figs. 4, 8, 14), followed by the hindlimb and trunk representations more laterally. In some cases, separate representations of the toes were observed at the far rostral boundary of the field (e.g., Fig. 21A). However, most often, the hindlimb, hindpaw, and trunk or the trunk and tail (e.g., Fig. 7, receptive fields 1,2; Fig. 9, receptive field 1; Fig. 14, receptive field 1), were contained in the same receptive field.

Lateral to the representation of the hindlimb were the representations of the forelimb, forepaw, shoulder, and upper trunk. These representations occupied slightly more space than the hindlimb/lower trunk representations. As with the hindlimb representation, the distal forelimb (forepaw) was generally represented more rostrally in PV, and the more proximal forelimb was represented more caudally in both species (Figs. 3, 4, 8, 14, 21A). This was not always the case; sometimes, additional portions of PV would have neurons with receptive fields on the forepaw (e.g., Fig. 4), or have separate forelimb representations (e.g., Fig. 14). However, there was still a trend for pure forepaw to be represented in the rostral portion of PV (e.g., Figs. 3, 8, 21, 23). These variations were due, in part, to the large sizes of receptive fields.

Lateral to the representation of the forelimb were the representations of the head, neck, face, and chin. These representations occupied only a small portion of PV. Immediately lateral and caudal to these representations was the representation of the bill. As in SI, the bill representation in PV appeared to occupy a disproportionately large region (e.g., Fig. 4), especially in the platypus, although the rostrolateral extent of the bill representation in PV was not determined. The bill representation in PV was adjacent to the bill representation in SI, and receptive fields for neurons at recording sites crossing the PV/SI boundary reversed and became smaller for neurons in SI (Fig. 7, receptive fields A–G).

The rostral somatosensory area. Unlike neurons in SI and PV, neurons in R responded most often to stimulation of deep receptors, so that light taps or light pressure to the body surface were required to elicit a response. Receptive fields for neurons in R were somewhat larger than for neurons in SI (see below). As in SI, the mediolateral organization of R in both platypuses and echidnas progressed from tail to hindlimb, trunk, forelimb, and face. However, the rostrocaudal organization of R was reversed from that of SI, so that the ventral midline was represented caudally in the field adjacent to the ventral midline representation in SI, and the dorsal midline was represented rostrally. Thus, R formed a mirror image of SI, as demonstrated by receptive-field reversals across the SI/R boundary (Figs. 6, 16, 20). As recording sites progressed from caudal to rostral in SI, receptive fields for neurons at those recording sites progressed from the dorsal midline, to the ventral midline (e.g., Fig. 17, receptive fields D-I) or from proximal to distal limbs (e.g., Figs. 6, 16). As recording sites crossed the SI/R boundary and progressed from caudal to rostral in R, a reversal of receptive fields was observed, and receptive fields for neurons in R progressed from the ventral midline to the dorsal midline (e.g., Fig. 17, receptive fields G-I), or from distal to proximal limbs (e.g., Fig. 6, receptive fields D-F and 5-7; Fig. 20, receptive fields 6-9). Although neurons in R responded best to stimulation of deep receptors, receptive fields were generally small (e.g., Fig. 23), and the topography of R was quite precise.

The hindpaw and toes were represented mediocaudally in R, with the hindlimb, lower trunk and tail progressively rostral (e.g., Figs. 4, 12A, 14, 18). As recording sites moved from caudal to rostral in the hindlimb representation of R, receptive fields moved from distal hindlimb to proximal hindlimb (Fig. 6, receptive fields D–F; Fig. 20, receptive fields 6–9). Lateral and caudal to the representation of the hindlimb was the representation of the trunk. The lower trunk was represented most medially, followed by the middle trunk and upper trunk representations laterally (e.g., Figs. 3, 12A, 18). The dorsal trunk was represented rostrally, whereas the ventral trunk was represented caudally (e.g., Fig. 17, receptive fields F–I).

In both platypuses and echidnas, the representation of the forelimb was caudal and lateral to the representation of the trunk. Within the representation of the forelimb, the digits were represented most caudally followed by the forepaw, forelimb, and shoulder representations rostrally (Figs. 4, 12A, 14). However, there was some variation in this pattern (e.g., Fig. 3). Thus, as recording sites moved from caudal to rostral in R, receptive fields moved from the distal to the proximal forelimb (e.g., Fig. 6, receptive fields 5–7; Fig. 16, receptive fields E–G). Rostral and lateral to the representation of the forelimb in R were the representations of the head, neck, upper trunk, and face. The face and chin were represented more laterally, whereas the head, neck, and upper trunk were represented more medially (Figs. 4, 14, 18). As in SI and PV, the representation of the









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Fig. 6. A reconstruction of receptive-field progressions for neurons in SI and R in P8. Receptive fields are marked with solid lines on body drawings and relate to recording sites marked with the same letter or number on the cortical reconstruction in the upper left. Only a partial map for case P8 is shown here. As recording sites move from caudal to rostral in SI (A–C







Fig. 8. A reconstruction of a map of PV and surrounding fields for platypus 5 (P5). The organization of PV in monotremes is similar to that described for other mammals, except that the rostrocaudal and mediolateral coordinates are interchanged. The A + S region, adjacent

oral structures and the bill were located most laterally in R, with a large magnification of the bill, especially in the platypus.

The manipulation field. In one platypus (Figs. 4, 5) and two echidnas (Figs. 12A, 12B, 22A, 22B), electrophysiological recordings were obtained from neurons in cortex immediately rostral to R. The boundary between R and this field, which we term M, was defined using architectonic as well as electrophysiological criteria. First, neurons in M responded to manipulation of joints and hard taps to peripheral body to the rostral border of PV, is not a part of PV, because the receptive fields for neurons in the A + S region are discontinuous with the representation in PV. Dashed lines mark approximated boundaries.

parts rather than to light taps and pressure, as in R. Also, the proportion of recording sites where neurons responded to manipulation of the limbs vs. light taps or pressure to different body parts differed for R and M (Table 1). Second, the internal organization of M was different from and less precise than that of R. Finally, the architectonic appearance of M was quite different from that of R (see below).

Although there was a general medial-to-lateral organization in M with the hindlimb represented most medially followed by the trunk, forelimb, and face in a lateral



Fig. 9. A simplified reconstruction of the map in P5 (left) illustrating recording-site progressions and corresponding receptive fields (right). With a progression from medial to lateral in PV, receptive fields for neurons progress from tail, hindlimb, trunk, forelimb, and face, respectively. Receptive fields are often quite large for neurons in PV and incorporate several body parts (e.g., receptive field 5). In addition, receptive fields are sometimes split in PV and incorporate several, noncontinuous body parts (e.g., receptive field 3).



Fig. 10. A: Photomicrograph of cortex that has been flattened and stained for cytochrome oxidase (CO) through the bill representation of SI of the platypus. **B,C:** Reconstructions of electrophysiological recording data from the same case where CO boundaries, determined from an entire series of sections, are superimposed on the recording data. In B, the recording sites where neurons responded to mechanosensory stimulation only (m) are in CO-dense regions (shaded areas), whereas recording sites in which neurons responded to combined mechanosensory and electrosensory stimulation although simultaneous stimula-

tion was not required to elicit a response (c) are in the CO-light regions of cortex (unshaded areas). Recordings in the rostral sensory field are marked as r. A,C are at the same magnification, and arrows in each mark probes made in the tissue. C details the thresholds of neurons for electrical stimulation at some sites, and the regions designated with an i or an ii contain neurons with corresponding receptive fields illustrated in **D**. In D, electrosensory (e) receptive fields are marked in black, and somatosensory (s) receptive fields are shown in outlines.



Fig. 11. **A,B:** Lightfield photomicrographs of cortex that has been cut tangentially and stained for CO in two different platypuses. Within the bill representation of SI, CO-dark regions are surrounded by COlight regions. The CO-dense regions contain neurons that responded to

mechanosensory stimulation (Fig. 10), whereas the CO-light region contained neurons that responded to both electrosensory and mechanosensory stimulation. Scale bar = 2 mm.

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Figure 12

progression, the overall topographic organization was not precise. Unlike in SI and R, several representations of a similar manipulation were observed in the same animal. For instance, in the echidna (E10; Fig. 12A), hindlimb extension representations were found in three separate locations within the field. Although receptive fields tended to be large, smaller receptive fields limited to the digits were also noted (e.g., Fig. 22A). Although field M appears to be a separate field and previous investigations in echidnas suggest that this is the case (Ulinski, 1984), details of the internal organization of the field need to be obtained in future studies.

Neural response properties, stimulus types, and receptive-field sizes of somatosensory fields

Neural response properties. In the present investigation, neural response, preferred stimulus, and receptive field size were useful in distinguishing between the different fields. Most neurons in both species of monotremes responded transiently to the onset of a repeated stimulus. Such responses described for peripheral receptors (e.g., Harrington and Merzenich, 1970; Johansson and Vallbo, 1979; see Kaas and Pons, 1988, for review) and neurons in central representations (e.g., Paul et al., 1972; Hyvärinen and Poranen, 1978; Dykes and Gabor, 1981; Dykes et al., 1981; Sur et al., 1984) in eutherian mammals are termed rapidly adapting (RA). At some recording sites, neurons in R and M responded to the onset of the stimulus and throughout the application of the stimulus. We termed these slowly adapting (SA) responses, similar to those described in previous investigations in other mammals (see above citations). Because the number of recording sites at which neurons slowly adapted to the stimulus was low, we do not illustrate them here. Some neurons in somatosensory cortex responded to the onset of the stimulus but ceased responding after the first few stimulus presentations. We termed these habituating responses, and have described such responses in detail elsewhere (Krubitzer and Calford, 1992). The number of recording sites at which neurons habituated to the stimulus was inconsistent both across and within animals.

Stimulus type. Although a complete representation of the sensory epithelium is one of the best criteria for subdividing cortical fields, the type of stimulus needed to elicit a response from neurons was also very useful in subdividing fields when used in combination with other criteria (Figs. 5, 12B, 15, 19, 21B). Cutaneous stimulation consisted of lightly brushing the glabrous surface of the skin or deflecting hairs or spines. Deep stimulation was of several types. Light taps and pressure often elicited a neural response. We termed these "deep" responses, and distinguish them from the manipulation responses (although deep receptors of joints and muscles are likely to be stimulated during both), because the strength and type of stimulus needed to elicit a response from neurons at deep vs. manipulation recording sites was significantly different.

Neurons in SI were responsive to cutaneous stimulation of the contralateral body in 84% of the recording sites, whereas 11.5% of the recording sites had neurons responsive to deep stimulation and 4.5% had neurons responsive to both deep and cutaneous stimulation (Table 1). Likewise, a large proportion (75%) of recording sites in PV had neurons responsive to cutaneous stimulation; the remaining 25% of recording sites contained neurons responsive to light taps or pressure. We encountered no recording sites in PV in which neurons were responsive to both cutaneous and deep stimulation.

An interesting observation in the present investigation was that in two echidnas, E11 (Figs. 14, 15) and E9 (not shown), a specialized forepaw region was found in the forelimb representation of PV. Neurons in this region responded to vibratory stimulation applied to the surface on which the forepaw rested, with a very precise locking of the response to the stimulus. When the forepaw was lifted during this type of stimulation, the neurons ceased firing. Thus, neurons responsive to vibratory stimulation could be distinguished from neurons responding to bone-conducted auditory stimulation. This region was within the overall forelimb representation and, in both cases, was very close, or adjacent, to a patch of cortex in which neurons were responsive to auditory stimulation. It is possible that this region is receiving input from Pacinian-like receptors. Neurons responsive to this type of stimulation were not observed in any of the other cortical fields. Although this was only observed in two of the seven echidnas, the other echidnas did not have recording sites in this region. This specialized region was not observed in the platypus.

Unlike in SI and PV, a large proportion of the recording sites in R contained neurons responsive to stimulation of deep receptors (Table 1). Sixty-four percent of the recording sites contained neurons that responded to light taps or pressure, whereas neurons in 24% of the recording sites responded to cutaneous stimulation. The remaining recording sites had neurons that responded to either manipulation of body parts (7%) or both manipulation and light taps or pressure (5%). Thus, the boundary between SI and R not only coincided with reversals in receptive fields, but often with a change from cutaneous to deep stimulation (e.g., compare Figs. 5 and 6). Finally, neurons in 51% of the recording sites in M responded to manipulation of the limbs and joints, whereas neurons in 43% of the recording sites in M responded to other types of deep stimulation (Table 1). Unlike neurons in R, neurons in M required a substantially greater stimulus intensity to deep peripheral receptors to evoke a response. Neurons in only 6% of recording sites in M responded to cutaneous stimulation. The stimulus type needed to elicit a response from neurons in the different fields, when used in combination with architecture, receptive-field progressions, and complete representations of the body surface, was a useful criterion in helping to subdivide cortex.

Receptive fields areas. To make receptive field area comparisons across fields, we chose receptive fields from a single case and then chose the smallest receptive field for a

Fig. 12. A: A reconstructed map of echidna 10 (E10). In this case, most of the body representations have been defined for fields SI, R, and M. Although the mediolateral sequence of organization is similar across all three fields, the topography is most precise in SI and least precise in M. Body parts in M often are represented in several separate locations. Visual cortex is immediately medial to somatosensory cortex, and auditory cortex is just caudal to SI. B: A reconstruction of the preferred stimulus required to elicit a response for neurons in SI, R, M, A, and V in E10. Neurons in SI showed a preference for cutaneous stimulation, although, in several sites, they responded to both cutaneous stimulation and light taps and pressure and, in some sites, responded to light taps and pressure and manipulation, whereas, in M, neurons responded to manipulation.



Fig. 13. A simplified reconstruction of E10 (top) illustrating recording-site sequences from medial to lateral in both the caudal and rostral portions of SI, and corresponding receptive fields (**bottom**) for neurons in those recording sites. As recording sites progress from medial to

lateral in SI, receptive fields progress from lower to upper body, respectively. Caudal locations in SI represent the dorsal surface of the body (bottom right), whereas more rostral portions of SI represent ventral portions of the body (bottom left).

particular body part in each area. For neurons with cutaneous receptive fields (e.g., SI and PV), a similar stimulus was applied with the same strength by the same investigator within an individual animal. In this way, variation due to investigator differences, individual animal differences, and body part on which the field occurred could be kept to a minimum. Although light taps were required to elicit a response from neurons in R, neurons responded well and consistently to this lightly applied stimulus, and it was possible to determine the receptive-field boundaries with accuracy. Although not quantitatively studied, we observed that receptive fields appeared to be smallest for neurons in SI and progressively larger for neurons in R and PV (e.g., Fig. 24). Receptive fields on the forepaw or hindpaw for

neurons in SI were often restricted to the ventral or dorsal surface of one or two digits (Fig. 6, receptive field 4; Fig. 16, receptive fields D,4; Fig. 24). In R, receptive fields for neurons in a similar representation incorporated the dorsal and ventral surfaces of one to three digits (e.g., Fig. 16, receptive fields E,F,5; Fig. 24), whereas, in PV, the entire forepaw or hindpaw was contained in the receptive field (Fig. 9, receptive field 2; Fig. 24). Receptive fields in M often contained the joints of the digits, wrist, and elbow. The progressive trend for larger receptive fields in M than in other fields was also noted for other body parts as well. For instance, receptive fields on the trunk for neurons in SI were often restricted to a small patch of skin, whereas the receptive fields on the trunk for neurons in R and PV incorporated more skin and included almost the entire trunk for neurons in PV (e.g., Fig. 7, receptive field 3; Fig. 17, receptive fields 4,5; Fig. 24). A difference in receptive-field size for neurons in PV and SI was noted for receptive fields on the bill of the platypus (Fig. 7, receptive fields A-G). This difference, in addition to the reversals in receptive fields, was useful in distinguishing between the bill representation in SI and the bill representation in PV. Receptive fields for neurons in PV more often than not included a number of different body parts, and it was not unusual for a receptive field to include the entire forepaw, shoulder, and upper trunk (e.g., Fig. 7, receptive field 1; Fig. 9, receptive field 5; Fig. 17, receptive field 4). Thus, it was difficult to make precise maps of the topography of PV (e.g., Fig. 9, receptive field 3).

Architecture of somatosensory cortex

Coextensive with the electrophysiologically identified body representations described above was a distinct cortical architecture in both the platypus and the echidna. In cortex that was flattened and cut tangential to the cortical surface, M stained very lightly for both myelin and CO (Figs. 11, 25). In cortex cut parasagittally, M contained very large pyramidal neurons in layer V and a reduced granule cell layer. Thus, its appearance was similar to descriptions of this region previously reported for echidnas [see Figs. 2 (Ulinski, 1984), 6 (Abbie, 1938)]. In tangentially sectioned cortex, R stained lightly for myelin in both echidnas and platypuses (Fig. 25), but somewhat darker than cortex immediately rostral, in M (see below). In cortex cut parasagittally and stained for Nissl substance, layer V in R contained fewer, less densely packed pyramidal cells and a moderately packed granule cell layer. Again, this is similar to previous descriptions of R in echidnas (Abbie, 1938; Ulinski, 1984). SI was not homogeneous in appearance in cortex cut parallel to the cortical surface and stained for myelin and CO. In cortex stained for myelin, myelin-dense regions were surrounded by myelin-light regions (Fig. 25). This was particularly apparent in the representation of the bill in the platypus. Myelin-dense stripes, running rostrocaudally in cortex, were interdigitated with myelin-light stripes. This pattern was also apparent in cortex processed for CO (Fig. 11). However, unlike the myelin-dense stripes, the CO-dense stripes were often composed of separate puffs strung together to form a stripe. Both myelin-dense and CO-dense regions in the SI representation were related to mechanosensory neurons (Figs. 11, 25). The myelin-dense and CO-dense regions of SI overlapped to a large extent, but were not identical. Whereas this interdigitating pattern was most consistent for the bill representation, there were also architectonic discontinuities observed for some portions of the body representation in SI. In cortex sectioned parasagittally and stained for Nissl substance, SI had a darkly staining and densely packed granule cell layer in both echidnas and platypuses. In the bill representation of SI in the platypus, CO-dense and CO-light regions were observed in the superficial layers of cortex; these were most obvious in layer IV in cortex sectioned parasagittally. Finally, PV was moderately myelinated and stained lightly for CO. In cortex stained for Nissl substance, a densely packed layer IV was observed in PV, but this was not as distinct as in SI.

Location, extent, and architecture of auditory and visual cortex

Neurons in cortex adjacent to somatosensory cortex often responded well to free field flashes of light and clicks. Thus, we could reliably map the boundaries of visual cortex and auditory cortex. Neurons responsive to auditory stimulation were often observed in cortex in several separate locations in each species. One large region, field A (Figs. 1, 2; approximately 2×3 mm in platypus, 3×3 mm in echidna), just caudal to SI and rostral to PV was observed in all cases, and a smaller region (approximately 1 mm²) embedded within SI or R (see Figs. 3, 14 for examples in platypuses and echidnas, respectively) was also observed in several cases. Both of these regions of cortex were almost completely embedded within somatosensory cortex. This type of organization has never been reported for any mammal. In two echidnas, a third region of cortex in which neurons were responsive to auditory stimulation was observed (Figs. 14, 15; other case not shown). This region was very close to a specialized forepaw representation in PV (see above for details) and occupied only about a 1 mm² region of cortical space. In most platypuses and echidnas, neurons in regions surrounding the large auditory field (A) were responsive to both auditory and somatosensory stimulation (e.g., Figs. 4, 8, 14), and we termed this region A + S. Whereas these bimodal regions were found in patches in the echidna, they formed a belt-like region surrounding auditory cortex in the platypus. Because the somatosensory receptive fields for neurons in these bimodal regions were not part of a sequence of receptive fields continuous with those of adjacent somatosensory fields, we believe these neurons are part of a separate field rather then belonging to either SI or PV. Thus, our interpretation is not that SI and PV overlap auditory cortex, but that there is a separate bimodal area adjacent to somatosensory and auditory cortex. The somatotopic arrangement supports this interpretation, because the body parts represented in the bimodal area duplicate those represented in adjacent areas PV and SI.

The region of cortex where neurons responded only to auditory stimulation, field A, was heavily myelinated and stained darkly for both myelin and CO throughout all cortical layers in both echidnas and platypuses (Figs. 11, 25). In the belt of cortex surrounding A, where neurons

TABLE 1. Preferred Stimulus as a Percentage of Recording Sites

Cortical	Cutan-	Light taps and	Manipu-	Mixed cutaneous/ light taps and	Mixed light taps and pressure/ manipu-	Total number of recording
	eous 84	11.5	lation	4 5		484
R	24	64	7	—	5	442
РV M	75 6	25 43	51	_	_	248 115



responsive to auditory and somatosensory stimulation (A + S) were observed. An additional two regions in which neurons were responsive to pure auditory stimulation (AUD) were observed in PV and SI. As in other cases, visual cortex was immediately medial to somatosensory cortex.

Fig. 14. A reconstructed map of PV, SI, R, A, and surrounding cortex for echidna 11 (E11). In this case, the extensive mapping allowed most of the body to be detailed. The three complete representations found in these fields are coextensive with the architectonic boundaries of the fields. In this case, an auditory field (A) and two small pockets of cortex in which neurons were





and PV). In R, most recording sites contained neurons that responded to light taps and pressure, but a number of sites contained neurons that responded to both cutaneous and deep stimulation or cutaneous stimulation alone. In this case, recording sites in PV contained neurons that responded to cutaneous stimulation, but, at a few sites, neurons responded to deep stimulation. A patch of cortex in PV, where neurons responded to vibrations, was observed.

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responded to both auditory and somatosensory stimulation, cortex was only very lightly myelinated throughout all cortical layers (Fig. 11A).

The location of visual cortex was similar in both species, although cortex containing neurons responsive to visual stimulation occupied a much larger area in the echidna brain than in the platypus brain (Figs. 3, 19). As for auditory cortex, the location of visual cortex was unusual compared to other mammals. In all cases, neurons responsive to visual stimulation were in cortex just medial to SI. Neurons responsive to visual stimulation were in cortex that was architectonically divisible into at least two separate regions in both species. One region (V) just medial to SI, formed a small, heavily myelinated, CO-dense oval (approximately $3.5 \text{ mm} \times 2 \text{ mm}$, Figs. 1, 3, 11) in the platypus, and a large, heavily myelinated, CO-dense rectangle (approximately 10 mm \times 7 mm; Figs. 2, 25) in the echidna. This region had the appearance of area 17 (VI), as described in other mammals, although further electrophysiological mapping studies are necessary to address this issue. Neurons in cortex rostral and caudal to this region were also responsive to visual, visual and somatosensory, or visual and auditory stimulation in both species (e.g., Figs. 4, 5, 18). However, neurons in these areas were not driven as effectively as those in V using the simple visual stimuli of our experiments. It is unknown whether these surrounding regions contained one or more fields.

DISCUSSION

The major contribution of the present report is to demonstrate that the two species of monotremes investigated have at least four topographically organized subdivisions of somatosensory cortex. In addition, we have demonstrated a remarkable specialization in the bill representation of the platypus, related to electrosensory inputs. The results provide a broader view of the organization of sensory cortex in monotremes and allow comparisons with marsupials and placental mammals to be made in greater detail.

As the title of this paper suggests, we undertook this study in the hope that we could describe some prototypical or ancestral plan of cortical organization. Interestingly, the presence of complex, multiple representations observed in these species is generally not associated with primitive brains. We appreciate that, irrespective of our findings, we would have difficulty deducing the ancestral organization by examining only monotremes (Johnson, 1988). However, the similarity in cortical organization in both species of monotremes, despite at least 55 million years of independent evolution (Richardson, 1987) and the acquisition of morphological as well as cortical specializations, suggests that some features of organization have been retained from their common ancestor. Furthermore, the similarities in cortical organization that monotremes share with eutherian and metatherian mammals can be attributed to common descent from early mammals and, therefore may reflect, at least in part, the plan of organization that existed over 130 million years ago, when prototherian and therian mammals diverged. It should be noted that inferences about the ancestral state can be made from studying a broad range of extant mammals that need not necessarily be primitive in their cortical organization.

Subdividing cortex and evaluating homologies

Before addressing questions about origins and homologies of cortical fields, it is necessary to clarify what we consider to be the features of a cortical field. Very broadly defined, a cortical field is considered a valid subdivision if it possesses a distinctive cortical architecture, has a complete, systematic representation of the sensory surface, contains neurons that respond in a particular fashion to a defined stimulus, and has a unique pattern of connections (see Kaas, 1982, for review). The relative position of a field and behavioral consequences resulting from lesions to the field also can be used to assess whether it is a valid subdivision (Kaas, 1982). However, the absence of any of these features does not mean that a region of cortex is not a separate subdivision. The use of as many of these features as possible will provide the most accurate description of how a particular cortex should be subdivided, and allow comparisons with other mammals to be made with greater precision.

When evaluating homologies, we consider as many of the distinctive characteristics of a field as have been investigated in the mammal in question, and compare them with similar features in other mammals. It is unlikely that there will be a strict one-to-one correspondence between individual features across mammals. Indeed, if one only considered a single feature (e.g., topography), enormous differences would be found. For example, the rostrocaudal organization of SI in megachiropteran bats is reversed from that in other eutherians (Calford et al., 1985), and in some species, the organization of SI is distorted by the disproportionate representation of some body parts. For instance, the vibrissae representation in rats (e.g., Chapin and Lin, 1984), the hand representation in raccoons (Welker and Seidenstein, 1959; Johnson et al., 1982; Feldman and Johnson, 1988), the digits of the hand and foot in lorises (Krishnamurti et al., 1976), the lips of the llama (Welker et al., 1976), and the bill in the platypus make up most of the SI representation in these animals. Thus, if one examined only the topography of SI in these mammals, one might conclude that these were different, nonhomologous fields. Yet, if we consider additional features such as relative position with respect to major sulci and other known fields, architectonic appearance, neural response properties, preferred stimulus, and cortical and thalamic connections, we would conclude that in all of these mammals, the fields in question are homologous and have undergone specialized changes in different lineages. Although these points may seem obvious, it is critical to establish our criteria for subdividing cortex, and the use of the terminology of the subdivisions we have described, because the question of homology is the basis for most of the following discussion.

Comparisons of cortical organization with other mammals: Deducing the primitive form

The primary somatosensory area. In the present investigation, we identified SI on the basis of its architectonic appearance and topographic organization, as well as preliminary results on cortical connections of this field with other cortical fields and the thalamus (Krubitzer et al., 1991). The primary somatosensory area (SI or area 3b) has been described in all mammals investigated including primates, bats, tree shrews, carnivores, ungulates, rodents, lagomorphs, edentates, insectivores, marsupials, and monotremes (e.g., Fig. 17; see Kaas, 1983; Johnson, 1990; Rowe, 1990, for reviews) as having a complete, systematic representation of the body surface, and as containing neurons responsive to cutaneous stimulation. Furthermore, SI (area 3b) in all mammals is characterized by a myelin-dense appearance when cortex has been sectioned tangentially, and by the presence of a dense granule cell layer (koniocor-





Fig. 16. A simplified reconstruction of maps in SI and R in E11 illustrating recording-site progressions from SI to R (upper left). Corresponding receptive fields for neurons in those recording sites are drawn at the right and bottom of this figure. As recording sites move from caudal to rostral in the forelimb representation of SI (recording sites A–D), receptive fields for neurons in those recording sites move from the dorsal midline of the upper trunk to the shoulder,



Figure 17

tex) when sectioned sagittally or coronally. Because SI has been described in so many species, many of which are very distantly related, it is reasonable to assume that it is a phylogenetically old field retained from the common ancestor of all mammals.

The parietal ventral area and second somatosensory area. PV has also been described in several different mammals including squirrels, marmosets, flying foxes, rats, and, recently, macaque monkeys (Krubitzer et al., 1993b; and see Krubitzer et al., 1993a, for review) as a small representation of the body surface lateral to SI. PV is an "inverted" representation with respect to the brain, in that the organization of the body within the cortex is upside-down with respect to its real position in space. Thus, the distal limbs are directed medially, whereas the trunk is represented laterally in the brain. Even in the absence of its position relative to the brain, the internal organization of PV is consistent when rotated around a single axis (see Fig. 28).

SII, on the other hand, has been described in a number of different mammals (e.g., primates, carnivores, rodents, marsupials, ungulates; see Johnson, 1990; Krubitzer et al., 1993a, for review), as a small, "noninverted" representation of the body surface lateral to SI. Thus, the overall representation of SII is reversed from that of PV.

Like neurons in SI, neurons in PV respond to cutaneous stimulation; however, receptive fields for neurons in PV are larger. In some mammals, portions of PV contain neurons responsive to auditory stimulation (e.g., Krubitzer et al., 1986). All of these features, except an auditory overlap zone, are observed in the caudal somatosensory field in monotremes. Neurons in SII also respond to cutaneous stimulation, and receptive fields for neurons in SII are generally larger than for SI. Therefore, the neural properties and receptive-field sizes in both SII and PV are similar.

Although there are many similarities between PV and SII, we have called the caudal field in monotremes PV for two main reasons. First, when one considers the rotations in cortex that have occurred in other mammals (see below and Fig. 28), the internal organization of this caudal field relative to other fields is inverted like that of PV. SII is a noninverted representation. Second, in a related study on the connections of somatosensory fields in monotremes (Krubitzer et al., 1991), this caudal field has been shown to have dense connections with SI (area 3b), as does PV in other mammals. Although connections between SI and SII have been reported, they do not appear to be as dense as those between SI and PV (SII may have been misidentified in other investigations; see Krubitzer et al., 1993a, for review). Although we believe that the evidence supports our hypothesis that the field caudal to SI in monotremes is PV rather than SII, it is difficult to say with certainty that this is the case, because the internal organization of fields can vary (e.g., organization of SI representation in megachiropteran bats).

The rostral field. A field immediately rostral to SI (area 3b) in which neurons are often responsive to the stimulation of deep peripheral receptors has been identified in a number of species including carnivores (Zarzecki et al., 1978; Dykes et al., 1980; Dykes and Gabor, 1981; McKenna et al., 1981; Felleman et al., 1983; Feldman and Johnson, 1988; Gugino et al., 1990; Rasmusson et al., 1991; Avendaño and Verdu, 1992; Leclerc et al., 1993), primates (e.g., Krishnamurti et al., 1976; Merzenich et al., 1978; Kaas et al., 1979; Nelson et al., 1980; Sur et al., 1980a; Carlson et al., 1986), flying foxes (Krubitzer and Calford, 1992; Finnigan et al., 1992; Krubitzer et al., 1993b), and tree shrews (Sur et al., 1980b). This field is termed area 3a, although its status in carnivores (R2 or KC, kinesthetic cortical field) remains controversial (e.g., see Felleman et al., 1983; Feldman and Johnson, 1988; Leclerc et al., 1993). Many studies have concentrated on the group Ia afferent (muscle spindles) responses in this region (Zarzecki et al., 1978; Feldman and Johnson, 1988; Gugino et al., 1990), but inputs from joint receptors and cutaneous receptors have also been found (e.g., Feldman and Johnson, 1988; Finnigan et al., 1992; Leclerc et al., 1993). Despite the general consensus that cortex rostral to SI in these species is architectonically unique and receives inputs from more than just cutaneous afferents, a complete topographic description of the field has only been given for raccoons (Feldman and Johnson, 1988) and flying foxes (Finnigan et al., 1992) with partial maps existing for cats (Dykes et al., 1980; McKenna et al., 1981).

The existence of a somatosensory field homologous to area 3a in other species is still unclear. For instance, cortex rostral to SI in rodents has been described differently by different investigators. In rats, a thin portion of cortex just rostral to SI has been distinguished by some investigators (e.g., Akers and Killackey, 1978; Donoghue et al., 1979; Donoghue and Wise, 1982; Sanderson et al., 1984; Welker et al., 1984). This cortex appears to be contiguous with the dysgranular SI cortex (DG), where low-threshold movements can be elicited. In addition, in somatosensory mapping studies, DG embedded in SI and just rostral to SI contains neurons that respond to stimulation of deep peripheral receptors (Chapin and Lin, 1984; Sievert and Neafsey, 1986). In guinea pigs, agranular cortex (Agr), just rostral to SI, contains neurons responsive to deep stimulation, and microstimulation in this area evokes body part movements (Rapisarda et al., 1990). In squirrel cortex, the unresponsive zone (UZ) has the architectonic appearance of DG in rats (Sur et al., 1978; Krubitzer et al., 1986), and the connections of UZ (Gould, 1981) and DG appear similar in both species.

In the present investigation, area R has been described as containing a complete representation of the body surface in which neurons respond to stimulation of deep peripheral

Fig. 17. A simplified reconstruction of PV, SI, and R (upper left) for E11 illustrating recording-site progressions from PV into \hat{SI} (1-9), and from PV into SI and R. Corresponding receptive fields for neurons in those recording sites are shown at the right and bottom of this figure. As recording sites move from medial to lateral in PV, receptive fields progress from the lower half to the upper half of the body (1-4). When the PV/SI border is crossed, receptive fields reverse, become smaller in size (compare receptive fields 4 and 5), and move back towards the lower half of the body as recording sites move medially. Thus, a receptive field in SI (9), similar to that at the beginning of the progression in PV (1) is observed. Neurons in PV and SI associated with these receptive fields are separated by auditory cortex and are over 7 mm apart. Laterally in PV, recording-site progressions from caudal to rostral correspond to receptive-field progressions from the ventral neck and face to lateral neck to dorsal head and face (A-C). As the PV/SI boundary is crossed, receptive fields become smaller, reverse, and move from dorsal head, to lateral neck, to ventral neck and face, as recording sites move from caudal to rostral in SI (D-F). Note that very similar receptive fields are observed at recording site A (caudal in PV) and recording site F (rostral in SI). As the SI/R boundary is crossed, another reversal of receptivefield progression is observed (G-I), and receptive fields move from ventral to lateral neck, to face and upper dorsal trunk as recording sites move caudal to rostral in R. Thus, in this sequence, two clear reversals of receptive field progressions are observed, one at the PV/SI boundary and one at the SI/R boundary.



Fig. 18. A reconstruction of maps for SI, R, PV, and surrounding cortex for echidna 3 (E3). As in the previous maps, tail, hindlimb, and trunk are represented medially, followed by the forelimb, face, and bill laterally in all three fields. Visual cortex is immediately medial to somatosensory cortex, and auditory cortex is almost completely embedded in somatosensory cortex.

receptors. A previous investigation in echidnas (Ulinski, 1984) also provides convincing architectonic evidence for a separate subdivision of sensory-motor cortex in the same location as R in the present study. Ulinski (1984) also demonstrated that thalamic connections of this rostral field

were different from those of the caudal field (SI) and proposed that the rostral field may be homologous to area 3a as described in other mammals. A similar field has been found in possums (Elston et al., 1993), and the marsupial quoll (unpublished observations, L. Krubitzer), and it may

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Figure 19 (See overleaf.)

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Fig. 20. A simplified reconstruction of SI and R (upper left) from E3 illustrating recording-site progressions for the hindlimb representations in these fields. Corresponding receptive fields for neurons in those recording sites are illustrated at the right and bottom of this figure. As recording sites move from caudal to rostral in SI (1-5), receptive fields

progress through tail, lower trunk, proximal hindlimb, foot, and toes. As recording sites cross the SI/R boundary and move from caudal to rostral in R, a reversal of receptive fields is observed, and receptive fields progress back to the proximal hindlimb and tail (6-9).

Fig. 19. A reconstruction of the stimulus type required to elicit a response for neurons in SI, R, PV, and surrounding cortex in E3. Most neurons in SI and PV responded to cutaneous stimulation, whereas most neurons in R responded to deep stimulation. Neurons that responded to auditory stimulation were for the most part restricted to

the boundaries of A, although a small patch of cortex in SI contained neurons responsive to auditory stimulation. Neurons that responded to visual stimulation were found both in a densely myelinated region of cortex (V) and outside of this myelinated region.

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Fig. 21. Reconstructed maps illustrating the body part representation (A) and the preferred stimulus (B) for SI, PV, R, and surrounding cortex for echidna 6 (E6). The topographic organization and relative locations of somatosensory, auditory, and visual cortex are similar to those illustrated in previous cases. A large number of recording sites in

SI contained neurons that responded to cutaneous stimulation, whereas, in R, most recording sites contained neurons that responded to light taps and pressure. PV contained neurons that responded to either cutaneous or deep stimulation.

be homologous to R as described in monotremes. Indeed, it is possible that DG in rats, UZ in squirrels, R in monotremes, and area 3a in primates, flying foxes, tree shrews, and carnivores (R2 and KC of some studies) are all homologous cortical fields, but that the width and shape of the field is different in different lines (Fig. 26). In all cases, the region is moderately to lightly myelinated compared to area 3b (SI) and contains a moderately to lightly packed granule cell layer. In addition, area 3a contains a complete representation of the body surface (Dykes et al., 1980; Finnigan et al., 1992) as does KC in raccoons, and both are organized much like area R in the present investigation. Area 3a in



Fig. 22. Reconstructions of body part representations (A), and preferred stimulus (B) for neurons in recording sites in R and M in E4. The map in M is less precise than that in R, and some representations (e.g., FL, W, FP) are represented in several discontinuous patches. Most recording sites in R contained neurons that responded to light taps and pressure, although, at a few locations, neurons responded to manipula-

tion or cutaneous stimulation. In M, approximately half of the neurons responded to manipulation, and half responded to light taps and pressure. A few recording sites contained neurons that responded to cutaneous stimulation. Solid lines mark architectonic boundaries, and dashed lines mark approximated boundaries.



Fig. 23. A reconstruction of a map of SI and surrounding cortex for echidna 2 (E2). Although the hindlimb representation has not been mapped in this case, the rest of the body, including the representation of the bill, has been defined. Auditory cortex is completely embedded in somatosensory cortex and is adjacent to representations of the head and pinna. Visual cortex is medial to somatosensory cortex.

primates, KC in raccoons, and UZ/DG in squirrels and rats, respectively, also have connections with SI, as does R in monotremes (e.g., Jones and Powell, 1969, 1968; Akers and Killackey, 1978; Krubitzer et al., 1986, 1991; Chapin et al., 1987; Doetsch et al., 1988; Krubitzer and Kaas, 1990b). However, detailed maps of areas 3a, UZ, and DG need to be constructed in a number of species, and cortical and subcortical connections of these fields (and R) need to be determined before homologies can be assigned with assurance.

The manipulation field. In early investigations in echidnas (Abbie, 1938; Goldby, 1939), low-voltage stimulation in a region of cortex in the location of M in the present study evoked body part movements. This region, between sulci α and β , contained a complete motor representation of the body with a similar mediolateral sequence of organization to that of M. More recent investigations in the platypus (Bohringer and Rowe, 1977) and the echidna (Lende, 1964) describe an overlap of sensory and motor cortex. In the

echidna, a single motor representation was found to overlap all regions of cortex responsive to somatosensory stimulation (in our investigation, this would include fields SI, R, and PV). However, surface stimulation was used, and the cortex within the deep fissures was not explored. In the platypus, Bohringer and Rowe (1977) found that the motor representation only partially overlapped with somatosensory cortex and extended further rostrally than the somatosensory (cutaneous) representations. Furthermore, in some cases, two motor representations of the distal forelimb were observed. This previous study is in good agreement with the present investigation, where M extends far rostrally in cortex. R is located caudal to M and is in the approximate location of the caudal distal limb representation of the Bohringer and Rowe study. This suggests that neurons in the R region, when stimulated, evoked body movements. Furthermore, in architectonic studies (Abbie, 1938; Ulinski, 1984), cortex in the location of M has the appearance of the primary motor area (MI) as described in other mam-



Fig. 24. Comparison of receptive field sizes for the trunk (left) and forepaw (right) in the different somatosensory fields in echidna 11 (E11). To make these comparisons, we chose a case that had recordings in all of the fields. We then chose the smallest receptive field for a particular body part in each of the three fields. Receptive fields are smallest for SI, somewhat larger for R, and largest for PV. Receptive fields are illustrated with solid lines.

mals; however, the myeloarchitecture of M in the present investigation is not similar to that of MI. In mammals where MI has been explored extensively (e.g., Gould et al., 1986; Stepniewska et al., 1993), multiple representations of body part movements have been observed. This cluster arrangement of multiple representations is very similar to the organization of M described in monotremes in the present investigation. Thus, there is some evidence for a topographically organized sensory-motor field distinct from SI and R that receives inputs from muscle and joint receptors. Based on topographic organization, connections with subcortical structures (Ulinski, 1984), and architecture (Abbie, 1938; Ulinski, 1984; present investigation), we suggest that M in monotremes is homologous to primary motor cortex in other species. An alternate interpretation is that M in monotremes and MI in other mammals may be products of convergent evolution. However, detailed microstimulation maps are needed in monotremes and other species to resolve this issue.

The platypus bill representation. An interesting observation in the present investigation was that the bill representation in SI of the platypus was divided into physiologically distinct subregions of neurons that were coextensive with architectonic subdivisions. A similar pattern was observed by Langner and Scheich (1986) using 2-deoxyglucose staining to identify the electrosensory representation of the bill in platypus cortex. In the present study, neurons responsive to mechanosensory stimulation were observed in myelin and CO-dense portions of the bill representations in SI, whereas neurons responsive to electrosensory plus mechanosensory stimulation were seen in CO- and myelin-light zones. Because both mechanoreceptors and electroreceptors share a common location on the bill, and because their respective receptive fields are nearly superimposed for



Fig. 25. Lightfield photomicrographs of platypus cortex that has been flattened, sectioned tangentially, and stained for myelin. In both A and B, SI can be distinguished as a myelin dark region. Fields A and V, adjacent to SI, also stain darkly for myelin. R and PV are more moderately myelinated. Rostral is right, and medial is to the top. Scale bars = 1 mm.



Fig. 26. A: Lightfield photomicrograph of platypus cortex that has been flattened, sectioned tangentially, and processed for myelin. SI, A, and V stain darkly for myelin, PV and R stain moderately for myelin, and M stains very lightly for myelin. The body representation is not visible in the myelin stain in this section, but is darkly myelinated in deeper sections **B**: A lightfield photomicrograph of an echidna cortex that has been flattened, sectioned tangentially, and stained for myelin. The primary somatosensory area, SI, stains darkly and unevenly for myelin, so that myelin-dense regions are surrounded by myelin-light regions. In A, myelin-light and myelin-dark bands in the representation of the bill are apparent. Both A and V also stain darkly for myelin. R and PV stain moderately, whereas M stains very lightly. Thin solid lines mark architectonic boundaries. Arrows in A mark electrode tracks through PV. Scale bars = 2 nm.



Fig. 27. A summary of the organization of sensory cortex in a number of different species including the platypus. We have not illustrated the echidna here, because the organization of sensory cortex in the echidna is very similar to that of the platypus. Thus, the platypus illustration in this instance represents both species of monotremes investigated. The fields we consider to be homologous are depicted in the different cortices in the same stipple type. Note that in the platypus, all sensory cortex adjoins. Unlike other mammals, auditory cortex is embedded in somatosensory cortex, and visual cortex is just medial to somatosensory and auditory cortex. In other mammals, the positions of some fields have changed (e.g., A and PV), but the position of fields relative to each other has been maintained. It is possible that the overall change in the position of cortical fields is due to a rotation of auditory cortex away from the caudal border of SI. PV has also rotated with auditory cortex so that in mammals other than the platypus, it now lies lateral (hedgehog) and rostral (other mammals) to auditory cortex. In a number of mammals, additional cortical fields are interspersed between the defined homologous fields, and cortex between A and PV is expanded, as is cortex between visual, somatosensory, and auditory cortex. Much of this expanded cortex contains new (additional) sensory fields. Subdivisions for the hedgehog cortex are from Kaas et al., 1972; Kaas, 1980, 1987; Batzri-Izraeli et al., 1990; and personal observations. Subdivisions of squirrel cortex come from Hall et al., 1971; Sur et al., 1978; Merzenich et al., 1976; Nelson et al., 1979; Krubitzer et al., 1986; Luethke et al., 1988; and Kaas et al., 1989. Subdivisions for the flying fox are from Calford et al., 1985; Kennedy, 1991; Krubitzer and Calford, 1992; Krubitzer et al., 1993a; and Rosa et al., 1993, 1994. Subdivisions for marmoset cortex are from Carlson et al., 1986; and Krubitzer and Kaas, 1990a,b, 1993. Subdivisions for macaque monkey come from Merzenich and Brugge, 1973; Nelson et al., 1980; Pons et al., 1985; Huerta et al., 1987; Kaas and Krubitzer, 1991; Krubitzer and Kaas, 1993; and Krubitzer et al., 1993b. Scale bars = 1 mm (except in macaque = 1 cm).



Fig. 28. Schematic diagrams illustrating the hypothesized changes in cortex that have occurred in different lines. A: The form in extant monotreme cortex. B: How this form may have changed, and which regions of cortical space increased or interspersed between existing fields. C: The organization observed in a number of extant eutherian mammals (see Fig. 26) showing additional expansions and rotations in the cortex.

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neurons at a given cortical site, it is not immediately obvious why there should be the clear functional parcellation that we have observed in the cortex. There are, nevertheless, many differences between mechanoreception and electroreception that might help explain the need for strict segregation at early stages of processing before the difficult task of locating an electrical stimulus is achieved. These include the fact that a suprathreshold stimulus excites all electroreceptors simultaneously (within nanoseconds, according to the speed of electromagnetic waves in water) in contrast to the punctate and sequential stimulation that is possible for mechanoreceptors. Determining the location of a tactile stimulus is a different and easier operation than the task of deriving the location of a dipole from the simultaneous activity of all electroreceptors. Hence, the separate tasks may be performed by separate cortical modules. Certainly, the activity of neurons receiving electrosensory and mechanosensory inputs would be related at any given location on the bill but poorly correlated temporally across the extent of the bill.

Although little is known about the organization of electrosensory inputs at other levels of the platypus nervous system, our results provide a clue in how central processing allows the platypus to detect the origin of an electrical dipole. We observed that similar electrosensory inputs from the bill are rerepresented in different, although adjacent, portions of SI electrosensory cortex, with variation in the threshold at different points within the region. This representation of different preferred-field strengths might be a necessary prerequisite for the calculation of the decay of an electrical field in water. By comparing the neural responses to electrical-field strength at each of these points, the platypus would be able to gain a map of the strength of electrical fields and determine how electrical fields decay across the bill.

The type of modular organization that we observed for the bill representation in SI of the platypus has been observed in a number of different mammals in all sensory systems. For instance, functionally distinct neural groups have been related to CO-light and CO-dense portions of the primary (VI) and second visual area (VII) in primates (e.g., Livingstone and Hubel, 1984; Hubel and Livingstone, 1987), vibrissae barrels have been identified in rat SI (Woolsey, 1967; Woolsey and Van der Loos, 1970), binaural summation and suppression bands related to differential interhemispheric connections have been identified in cat auditory cortex (Imig and Adrian, 1977; Imig and Brugge, 1978; Middlebrooks et al., 1980), and recently, CO modules have been described in human perirhinal and entorhinal cortex (Hevner and Wong-Riley, 1992). In addition, such specializations have also been identified in animals that are considered to have "generalized" brains. For instance, vibrissae barrels have been identified in SI in some marsupials (Weller, 1972, 1994), and recently a CO staining pattern related to nose specializations has been identified in SI of the insectivore, the star-nosed mole (Catania et al., 1993).

These findings, together with observations of modules in eutherian mammals, have important implications for neocortical evolution and development. First, there may be general rules that govern how the nervous system deals with related but separate information and how the addition of new sensory inputs or the modification of existing inputs manifests on the cortical sheet (e.g., Fig. 29). Second, there are certain areas in the cortex (primary areas) where these changes are most often observed. Finally, all mammals appear to have the capacity for this type of cortical segrega-

tion. Thus, although modules may be selected for, perhaps because they increase efficiency of cortical processing, their presence in such a wide range of mammals may be a reflection of ontogenetic processes that have been retained throughout mammalian, and possibly all vertebrate evolution (e.g., Constantine-Paton and Law, 1978; Meyer, 1982; Boss and Schmidt, 1984; Reh and Constantine-Paton, 1985).

Visual and auditory cortex. Probably the most important result of our electrophysiological and architectonic identification of visual and auditory cortex in both the echidna and the platypus was determining the position of these fields relative to somatosensory cortex. Auditory cortex was almost completely embedded in somatosensory cortex, and visual cortex was immediately medial to somatosensory cortex. These relative positions have been described only in monotremes.

Although visual cortex has not been systematically studied in either species of monotreme using electrophysiological recording procedures, in the present investigation, limited electrophysiological mapping and architectonic evidence suggests that monotremes possess a primary visual area (V), and possibly an additional visual area. Neurons responsive to visual stimulation were located in darkly myelinated cortex, similar in appearance to area 17 (VI) described in other mammals (see Kaas, 1980; Kaas et al., 1989; Kaas and Krubitzer, 1991; Sereno et al., 1991; Krubitzer and Kaas, 1993). In addition, limited electrophysiological mapping in echidnas and platypus (personal observation) suggests that the field is topographically organized. Lightly myelinated cortex surrounding area V was also responsive to visual stimulation, and preliminary investigations (Krubitzer et al., 1991) demonstrate dense interconnections between V and surrounding cortex. Thus, monotreme cortex may contain more than one visual area.

The primary auditory area, AI, has been described as a tonotopically organized representation coextensive within a darkly myelinated oval of cortex in primates (e.g., Imig et al., 1977; Brugge, 1982; Luethke et al., 1989), carnivores (e.g., Reale and Imig, 1980), rodents (e.g., Merzenich et al., 1976; Hellweg et al., 1977; Redies et al., 1989), marsupials (Aitkin et al., 1986), and insectivores (Batzri-Izraeli et al., 1990; but see Clarey et al., 1992, for comprehensive review). Although the frequency representation in area AI is subject to variation, the architectonic appearance and many of the connections of the field are similar across mammals. In most mammals investigated, additional, tonotopically organized auditory fields have been described (see Clarey et al., 1992, for review). However, homologous areas have not been clearly identified.

Auditory cortex has been identified in previous investigations in both the platypus (Bohringer and Rowe, 1977) and the echidna (Lende, 1964), but tonotopically organized maps of auditory fields have not been obtained. Preliminary studies of auditory cortex in echidnas indicate that at least one tonotopically organized field exists (Krubitzer et al., 1991) that is coextensive with a darkly myelinated region of cortex just caudal to SI (see Figs. 25, 26). To date, no tonotopic maps have been obtained in the platypus, but there is a darkly myelinated area of cortex similar in location and appearance to that observed in the echidna where auditory stimulation evokes a response. Cortex surrounding this darkly myelinated region in both the platypus and echidna is also responsive to auditory stimulation, and often somatosensory stimulation, suggesting that an additional auditory field exists in monotremes.

Association cortex. Previous studies in monotremes reported that sensory fields were partially overlapping (Lende, 1964; Bohringer and Rowe, 1977). Although our observations are consistent with those of previous investigations in that we identified regions of cortex in which neurons responded to two types of stimuli (i.e., somatosensory and auditory, somatosensory and visual, visual and auditory; Figs. 4, 8, 14, 18), we did not interpret this as an overlap of fields, because the body part representations in these bimodal regions did not belong to the representations in adjacent fields. Furthermore, these regions were architectonically distinct from adjacent sensory fields. Thus, these fields appeared to be similar (although not necessarily homologous) to association cortex as described in other mammals (see Barnes and Pandya, 1992). It has been proposed that only "higher" mammals have

It has been proposed that only "higher" mammals have association (bimodal) regions of cortex (e.g., Sanides, 1969, 1975; see Van Hoesen, 1993). The presence of bimodal cortex in monotremes suggests that even mammals with simply organized brains may have regions of cortex where sensory information from different modalities converge. It is counterintuitive that any sensory system functions independently of other sensory systems.

What was the ancestral plan of cortical organization?

It is implicit in a number of theories of cortical evolution that extant monotremes and other basal mammals are "more primitive" or "lower" and will, therefore, have less differentiated brains with fewer cortical subdivisions than "more advanced" or "higher" mammals (Brodmann, 1909; von Economo, 1929; von Bonin and Bailey, 1961; Diamond and Hall, 1969; Ebner, 1969; Ebbesson, 1984; see Deacon, 1990, for review and refutation), and that the ancestral cortical organization, prior to the radiation of eutherian mammals, was simple. Although existing evidence in somatosensory cortex in mammals whose ancestors branched off early in evolution appears to support this idea by suggesting that only a few, architectonically undifferentiated fields exist in these species (e.g., Lende, 1964; Meulders et al., 1966; Saraiva and Magalhães-Castro, 1975; Bohringer and Rowe, 1977; Regidor and Divac, 1992), the present investigation does not. The presence of multiple sensory areas, association cortex, and anatomical and functional specializations within a cortical field indicate that monotreme brains are not "generalized and undifferentiated."

Although the relative position of fields in monotremes is quite different from that described for other mammals, a number of features of the neocortex are similar. Based on results from the present investigation as well as comparisons with other studies, we hypothesize that the basic mammalian plan of cortical organization includes fields SI, PV, A (AI), V (VI), R (3a/KC/UZ), motor cortex (M/MI), and, possibly, association cortex. The presence of SII in both metatherian and eutherian mammals suggests that it too is part of therian neocortical organization. It is possible that this second representation, caudolateral to SI and in the general region occupied by PV, evolved after PV.

How has the retained plan been modified in different lines?

The organization of neocortex in monotremes is, in some ways, very different from that described in other mammals (Figs. 1, 2, 27). First, auditory cortex is almost completely embedded within somatosensory cortex and lies between SI and PV, and there are other regions embedded within somatosensory cortex in which neurons respond to auditory stimulation. Second, visual cortex is immediately medial to SI. Finally, it appears since all or most of sensory cortex is accounted for, there are no unknown spaces between the sensory fields we have mapped. It is possible that in most metatherians and eutherians, auditory cortex rotated away from the caudal portion of SI leaving the relationship between PV and SI and the relationship between PV and auditory cortex intact (Fig. 28). Cortex between auditory cortex and SI may have expanded, and in some lines, PV eventually separated from A and other fields interspersed between pure somatosensory and pure auditory cortex. Similarly, visual cortex may have shifted caudally, away from SI, as cortex between SI and visual cortex (posterior parietal cortex) expanded (Figs. 27, 28).

An important question that arises from our results is: how are the dramatic changes and rotations in cortical organization accomplished in different lineages? One possibility is that the actual piece of cortex moves from one location to another via the dynamics of growth patterns of various fields. In this scenario, one cortical field or piece of cortex is homologous to another cortical field or piece. Thus, there is some inherent SI- or A-like component that makes that piece of cortex, and only that piece, SI or A. We consider this possibility unlikely, because the physical constraints of moving a segment of cortex with its attendant subcortical and cortical networks would be significant. A second possibility is that these changes occurred through a gradual shifting and reweighting of the connections (thalamic, cortical, and callosal) that we believe define a field. If this is the case, then what we are observing are homologous patterns of activation and interconnection upon the cortex that have been modified in different lines. These two possibilities relate to the current debate over how cortical areas differentiate during development (Rakic, 1988; O'Leary, 1989; Blakemore and Molnár, 1990; Schlagger and O'Leary, 1991; Kennedy and Dehay, 1993).

Theories of evolution of cortical fields in mammals

Recent work in the flying fox has led us (Krubitzer and Calford, 1992; Krubitzer et al., 1993a) and others (Kaas, 1989) to propose that new cortical fields evolve from existing cortical fields by a process of initial segregation of correlated inputs, followed by an aggregation (module formation) of these inputs and, finally complete separation of a new cortical field (Fig. 30). Inherent in this theory is that cortex is performing similar computations across its extent, and that it is the unique combination of inputs that defines a cortical field. This theory is supported by the present results as well as observations in a number of other mammals.

Dense electrophysiological maps of cortical fields in monotremes indicate that cortical fields are not functionally homogeneous, in that somatosensory fields were never purely cutaneous or deep (e.g., Figs. 5, 15). An extreme example is observed for the bill representation of the platypus, where there is a clear segregation of mechanosensory and bimodal electrosensory/mechanosensory inputs coincident with architectonic distinctions. Similarly, electrophysiological mapping in a number of other species indicates that cortical fields are composed of small clusters of neurons responsive to different types of stimulation, such as rapidly adapting (RA) and slowly adapting (SA) bands in SI of primates (e.g., Sur et al., 1984) and cats (Dykes and Gabor, 1981), orientation-selective and color-opponent modules in VI of monkeys (e.g., Livingstone and Hubel, 1984), and binaural suppression and summation bands in AI of cats (e.g., Middlebrooks et al., 1980). Furthermore, cortical connections are generally patchy (e.g., Kaas and Morel, 1993; Krubitzer and Kaas, 1993; Krubitzer et al., 1993a) regardless of the cortical field injected. Even when functional and/or architectonic distinctions within a field are difficult to define, cortex is not homogeneously interconnected, which suggests that aggregations or modules exist throughout cortex.

Regardless of the sensory system or the mammal, cortex appears to segregate functionally separate but related (correlated) information within a cortical field in a similar fashion (Fig. 29). For instance, the CO-dense bands in the SI-bill representation of the platypus, related to the segregation of electrosensory and mechanosensory information (Figs. 11, 12) are remarkably similar to ocular dominance columns in primates (Fig. 29), and the bands observed in VII of monkeys. More compelling examples include the presumably independent evolution of blobs in VI of monkeys (Livingstone and Hubel, 1984) and cats (Murphy et al., 1990), ocular dominance columns in VI of monkeys (Hubel and Weisel, 1968; 1978) and cats (Löwel and Singer, 1987). vibrissae barrels in SI of rodents (Woolsey, 1967) and marsupials (Weller, 1972), and slowly adapting and rapidly adapting bands in SI of monkeys (Sur et al., 1984) and cats (Dykes and Gabor, 1981). Observed homoplasy in extant species may reflect some inherent (homologous) cortical infrastructure (as suggested in previous studies; Rockel et al., 1980), compatible with homologous developmental programs. Although the different species may have undergone tens of millions of years of independent evolution, the outcomes (modules, fields) may look strikingly similar because they are highly constrained by the rules that govern development. For example, Purves and colleagues (1992) have recently proposed that module formation does not reflect principles of cortical function, but that it is a by-product of synaptic development.

Support for the theory that we propose here also comes from recent developmental studies demonstrating that cortical fields may not be preassigned. Experiments in which visual input is rerouted to auditory cortex in developing mammals demonstrate that auditory cortex becomes responsive to visual stimulation (Pallas et al., 1990; Roe et al., 1990). Investigations where cortex is transplanted from one location to another in the developing brain show that the transplanted cortex takes on properties of the cortex it replaced (Stanfield and O'Leary, 1985; O'Leary, 1989; Schlagger and O'Leary, 1991). In developing brains, new thalamic afferents do not show a preference for a particular region of neocortex but only prefer neocortex in general, as opposed to the hippocampus or striatum (Blakemore and Molnár, 1990; Molnár and Blakemore, 1991). Some investigators have proposed that spatial molecular gradients in cortex guide axons to their appropriate target (e.g., Boltz et al., 1993).

Taken together, the present results, along with observations in developing mammals and extant adult mammals, indicate that new cortical fields may evolve from existing cortical fields by an initial invasion of new correlated input or an intrinsic differentiation of discorrelated subchannels. Although thalamocortical afferents may be the main driving force of this phenomenon, ipsilateral, intrinsic, and callosal connections may also play a role in shaping a field. A gradual aggregation of similar inputs may occur to form modules, followed by a complete separation of modules to form a new field (Fig. 30). A novel afferent input is not



Fig. 29. Lightfield photomicrographs of cortex that has been flattened, sectioned tangentially, and processed for CO. A: Photograph of the bill representation of the platypus. The CO-light regions are coextensive with neurons that respond to electrosensory and mechanosensory stimulation, whereas the CO-dense regions contain neurons responsive to mechanosensory stimulation alone. B: Photograph taken from area VI of the Old World Talapoin monkey. CO-dense and

CO-light regions mark the inputs from the separate eyes (ocular dominance columns). C: Photograph of area VII in an owl monkey, depicting dark and light bands related to functionally and connectionally distinct cell groups. Despite tens of millions of years of independent evolution of some of these species, and the occurrence of these modules in different fields and sensory systems, there is a remarkable similarity in the patterns observed in cortex. Scale bars = 1 mm.



Aggregation of similar groups (modules)

Fig. 30. This figure graphically depicts how we believe cortical fields are modified, expanded, and eventually how new fields are added to the existing neocortical plan. A: Three separate, adjacent cortical fields. The different symbols (open hearts, filled diamonds, and open clubs) represent afferent patterns of activation to the particular field, which we believe defines a field. A is a hypothetical state, because cortical fields are usually not homogeneous in neural response properties, connections, and often architecture. B: The invasion of existing fields by new inputs may create modules within a field, and the realignment of existing afferents may contribute to variations observed in similar fields across species. C: An aggregation of similar groups of afferents, a further realignment, and an invasion of new inputs may occur together, or any one process may occur alone. Any or all of these processes may contribute to the modification of the existing plan so that modules and partially embedded fields may be observed. **D:** A complete aggregation of similar afferent groups (first observed in B) may occur and a new, separate field develops. It should be noted that all of these states are observed in extant mammalian brains. Furthermore, the process does not necessarily move from A–D but can move in both directions. Finally, this figure demonstrates the difficulty of subdividing cortex and determining homologies, especially in nonprimary areas, because cortex is often in flux and may be at different stages in different lines.

necessarily required for the evolution of a cortical field; a new combination of existing inputs may also result in the evolution of a new cortical field, or an existing input may evolve into two slightly different types that, in turn, ultimately segregate on the cortical sheet. For example, polymorphism of a particular receptor type could lead to selection of separate populations, which then results in modules in cortex and, eventually, a separate field. However, it should be noted that modules do not necessarily coalesce to form a cortical field. If there is no selection to separate, then the modules may stabilize, and no further aggregation occurs (Fig. 30). It should also be noted that this process can occur in either direction.

There appear to be cortical fields common to all mammals that constitute parts of the basic plan of mammalian cortical organization. This plan may have been inherited from the ancestor of the three groups of mammals, or the potential to derive this plan through convergent or parallel evolution may have been present in the common ancestor. The presence of discreet multiple representations and modular specializations in most or all mammals examined suggests that at least the potential for cortical field differentiation was present in our earliest ancestors. Perhaps mammals have been so successful not only because they have retained a plan which can be readily enlarged, condensed, and elaborated, but also because they have retained several basic rules of modification that allow that plan to be so easily changed.

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