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The present review outlines studies of electrophsyiological organization, cortical architecture and thalmocortical and corticocortical connections in monotremes. Results of these studies indicate that the neocortex of monotremes has many features in common with other mammals. In particular, monotremes have at least two, and in some instances three, sensory fields for each modality, as well as regions of bimodal cortex. The internal organization of cortical fields and thalamocortical projection patterns are also similar to those described for other mammals. However, unlike most mammals investigated, the monotreme neocortex has cortical connections between primary sensory fields, such as SI and VI.

The results of this analysis lead us to pose the question of what monotremes can tell us about brain evolution. Monotremes alone can tell us very little about the evolutionary process, or the construction of complex neural networks, as an individual species represents only a single example of what the process is capable of generating. Perhaps a better question is: what can comparative studies tell us about brain evolution? Monotreme brains, when compared with the brains of other animals, can provide some answers to questions about the evolution of the neocortex, the historical precedence of some features over others, and how basic circuits were modified in different lineages. This, in turn, allows us to appreciate how normal circuits function, and to pose very specific questions regarding the development of the neocortex.

Keywords: somatosensory cortex; visual cortex; auditory cortex; evolution; neural networks

1. INTRODUCTION

Extant monotremes include the duck-billed platypus (*Ornithorhynchus anatinus*) and two species of echidna (*Tachyglossus aculeatus* and *Zaglossus bruijnii*). To most, monotremes are interesting creatures because of their unusual appearance. The platypuses' rubbery bill and webbed extremities, and the echidna's elongated bill and spiny trunk, give these animals an other-worldly appearance, an appearance quite out of the realm of what we often consider mammalian. Likewise, the nature of their reproduction is unlike that of other mammals. These animals lay eggs, like reptiles, rather than having viviparous births. In addition to these morphological curiosities, monotremes are also interesting for issues regarding evolution, particularly that of the brain.

The ancestors of present-day monotremes emerged over 130 million years ago (Ma BP) (Clemens 1989; Flannery 1989; Westerman & Edwards 1992; see Penny & Hasegawe (1997) for alternative relationships and times), well before the major radiation of eutherian mammals, which occurred about 50–65 Ma BP (Hedges *et al*. 1996; Morell 1996). Because of their early emergence, and the number of features that are retained from their therapsid reptile forebears (Clemens 1970, 1989; Crompton & Jenkins 1973), extant monotremes may represent the ancestor of all mammals, possibly more than any other mammal. Even if monotremes radiated early from the marsupial line, as some current theories suggest (Penny & Hasegawe 1997; Kirsch & Mayer, this issue), the idea that their ancestors emerged early in mammalian evolution, and their retention of primitive features, remains unchanged.

It is important to appreciate, however, that no species represents the ancestral form (Northcutt & Kaas 1995). In addition, no morphological or neural structure in any animal represents the 'normal' state of that characteristic, with any other derivation in that characteristic being a variant from the normal state. Thus, while I initially described monotremes as being curious and unique looking, this description should hold for any mammal, including *Homo sapiens*. Despite the idea that all mammals are specialized or derived, there are many features of extant species that can be traced back to the common ancestor. Such features are possessed by all or most living relatives, and are considered to be homologous. For the brain, a cortical field is the product of a retained developmental program that all species share, as well as changes in that program that were independently acquired in different lineages over time. Thus, a homologous cortical field shared by a number of mammals may not have the same function.

It is particularly difficult to identify ancestral features of the brain as neural tissue does not fossilize, and groups of homologous neurons can often be recruited in different lineages to form different regions within a structure, or completely different structures over time. For example, it has been proposed that the deep structure termed the dorsal ventricular ridge (DVR) in reptiles is homologous to the cerebral neocortex in mammals (for reviews, see Northcutt & Kaas (1995) and Karten (1997)).

In this review of monotreme neocortex organization, I have tried to keep the limitations of the comparative approach in mind. However, the strength of my conclusions regarding the evolution of the neocortex is based not only on observations of extant monotremes, but on comparisons between monotremes and other extant mammals that represent a number of major lineages of mammalian evolution. In the first part of this review I describe electrophysiological, anatomical and architectonic data that form the basis of our current understanding of cortical organization in monotremes. The second part of this review compares the organization of monotreme neocortex with that of other mammals. Finally, I raise several questions regarding the evolution of the neocortex that comparative studies, particularly those in monotremes, will help address.

2. THE ORGANIZATION OF NEOCORTEX IN MONOTREMES

(a) *External morphology*

The appearance of the platypus brain is quite different from that of the echidna brain (figure 1). The platypus brain is smooth, whereas the echidna brain is highly fissured with approximately one-half of the cortical surface buried in very deep sulci. The relative size of the platypus and the echidna brain differs, with the platypus having a brain that measures 2.5 cm rostrocaudally and 2 cm mediolaterally, and the echidna having a brain that measures 4 cm rostrocaudally and 3.5 cm mediolaterally. The sensory cortex in both animals covers a large caudal region, and in the echidna resides caudal to one of the two large sulci of the brain, the beta sulcus (figure 1). Neurons in cortex rostral to this sulcus are unresponsive to sensory stimulation. In the echidna there appears to be an extraordinary expansion of this frontal region, since much of the cortex is buried in the fissures. However, when cortex is flattened and the sulci opened, the proportion of this cortex relative to sensory cortex is actually much less than it appears to be in the intact brain, although it is still appreciable (Krubitzer *et al*. 1995, fig. 2; see also figure 13).

(b) *Somatosensory cortex*

(i) *Electrophysiological recording studies*

The earliest electrophysiological recording experiments in a monotreme were performed by Lende (1964) using evoked potentials in the echidna to ascertain the cortical representation of different body parts. Lende described one representation of the sensory epithelium within and around the alpha sulcus (figures 1 and 2). A topographic map of the body surface was obtained and was proposed to be homologous to the primary somatosensory area (SI) described in other mammals, with the foot represented most medially, followed by the representation of the hand and face more laterally (figure 2). This pioneer study provided detailed descriptions of the internal organization of SI, later confirmed for the platypus in microelectrode mapping studies by Bohringer & Rowe (1977). As in the echidna, these investigators found evidence for only a single representation of the body surface, SI, in which neurons responded to cutaneous stimulation (figure 2).

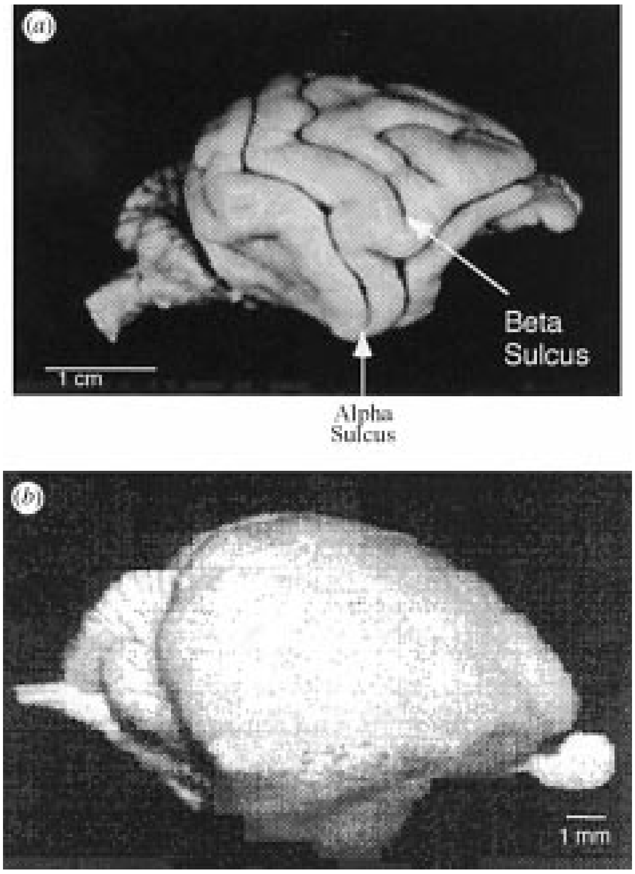

Figure 1. Dorsolateral views of the neocortex of (*a*) the echidna and (*b*) the platypus. In the echidna, a number of fissures are visible and include sulci alpha (α) and beta (β). All of sensory cortex is located caudal to these two major sulci. The platypus neocortex is smooth, and much smaller than that of the echidna. In this and the following figures, rostral is to the right and dorsal is to the top.

More recent studies using microelectrode recording techniques investigated the organization of somatosensory cortex in both the platypus and echidna, and confirmed the location and internal organization of SI reported in previous studies (figure 3; Krubitzer *et al.* 1995). Two additional representations of the body surface were found in both the echidna and the platypus: a rostral deep field, R, and a caudal field termed the parietal ventral area/second somatosensory area, PV/SII. Unlike SI, R contains neurons that respond to stimulation of deep receptors, rather than cutaneous receptors, and receptive fields of these neurons are somewhat larger than for neurons in SI. The mediolateral organization of R is similar to that of SI. A field immediately caudal to SI was also identified in both the echidna and platypus and was termed PV/SII because it had features of both fields in other mammals. Although more data need to be gathered, PV/SII is more similar in organization to PV than to SII. Therefore, for the sake of clarity, I will refer to this field as PV throughout the rest of this review. PV also contains a complete representation of the sensory epithelium in which neurons respond to stimulation of cutaneous receptors, but these neurons have larger receptive fields than those in either SI or R. It should be noted that the rostrocaudal extent of SI in

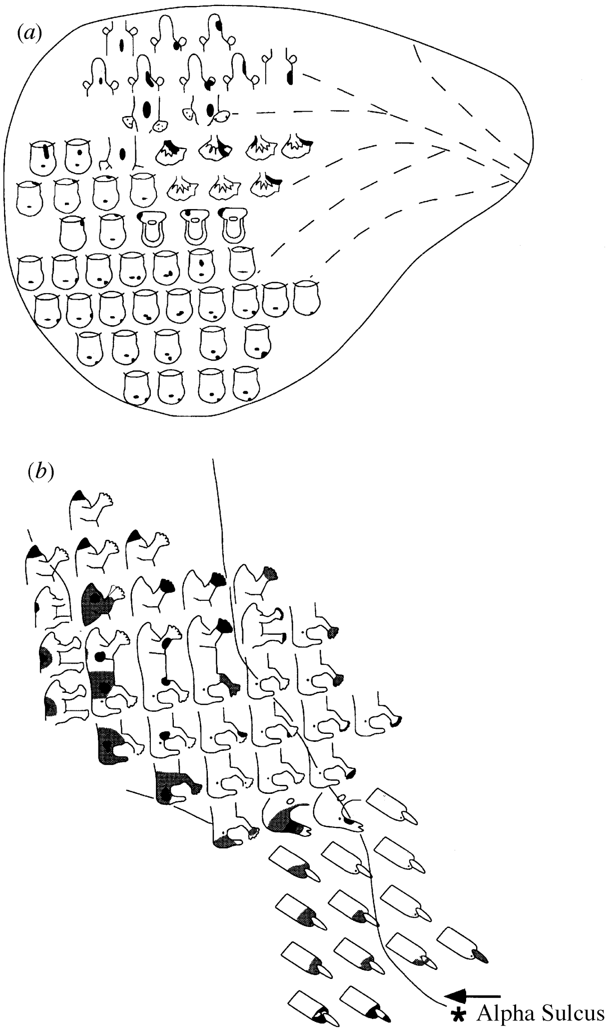

Figure 2. Maps of the primary somatosensory area, SI, in (*a*) the platypus and (*b*) the echidna, redrawn from Bohringer & Rowe (1977) and Lende (1964), respectively. The organization of SI is similar in both species with the face represented most laterally and the tail most medially. Shaded and darkly filled regions on the figures indicate the receptive field for neurons at that site in the cortex.

the echidna and platypus in the two early studies was much larger than in the most recent study, and it is likely that SI, R and PV are contained in the region that early studies term SI.

All electrophysiological recording studies demonstrate a remarkable cortical magnification of the bill. In the platypus, for instance, the bill representation for all sensory fields defined occupies more than one-half of the entire neocortex.

(ii) *Cortical architecture*

An early analysis of the cytoarchitecture of the monotreme neocortex by Abbie (1940) demonstrated a granular region of cortex, termed PPy3 in both the echidna and the platypus. In the platypus, this region appears to correspond at least partly to the SI representation (compare figure 2 with figure 4). In the echidna, the rostral boundary of PPy3 is on the floor of the alpha sulcus and also occupies the caudal bank of the alpha sulcus and the adjacent caudal gyrus. This corresponds in location to the electrophysiologically identified SI, although in the echidna this granular region is more extensive than the SI defined in microelectrode recording studies (compare figure 2 with figure 4).

A modern architectonic analysis of the neocortex was done by Ulinski (1984) in the echidna. Like Abbie, he identified a granular region in the caudal bank of sulcus alpha, which continues on the caudal gyrus. He proposed that this region is coextensive with the physiologically identified SI region of Lende (1964). This description is consistent with the location of SI described in recent electrophsyiological studies (Krubitzer *et al.* 1995). Ulinski also described a rostral field on the rostral bank of the alpha sulcus in which layer IV contains a dense packing of granule cells, although slightly less so than his caudal field, and a more developed fifth layer that contains medium size pyramidal cells. He concludes that the functionally identified SI is composed of two separate architectonic fields. Ulinski's results are consistent with modern microelectrode mapping studies that demonstrate two separate, complete representations, SI and R, in cortex that corresponds to his caudal and rostral architectonic subdivisions, respectively.

In the early electrophysiological studies in both the echidna and platypus, architectonic descriptions of somatosensory cortex were not provided, and in the Bohringer & Rowe (1977) study, cytoarchitecture was used only to verify the location of the electrode tracks for reconstruction. In the most recent electrophysiological study (Krubitzer *et al.* 1995), recording results were related to cortical myeloarchitecture and to cytochrome oxidase (CO) stains, and it was found that SI was coextensive with a darkly myelinated, CO-dense field. Both R and PV were moderately to lightly myelinated.

(iii) *Connections*

Studies of connections of somatosensory cortex are limited. In an early investigation by Welker & Lende (1980), lesions were made in different regions of the echidna neocortex, and degenerating cells in the thalamus were identified. Lesions in the region of the trunk representation in SI resulted in degeneration in a location dorsal and caudal to the ventral posterior nucleus (VP), whereas lesions that incorporated almost the entire SI representation resulted in degenerated neurons throughout most of the VP. Lesions in cortex that incorporated the rostral field, but also included portions of motor cortex, resulted in degeneration of the ventrolateral nucleus (VL); but examination of the figures suggests that there may have been portions of the ventral posterior nucleus that contained degenerating neurons as well (see figure 5). In addition, some investigators (e.g. Ulinski 1984; Regidor & Divac 1987) indicate the VP runs throughout almost the entire rostrocaudal length of the thalamus (Ulinski 1984, fig. 4), suggesting that portions of VP were indeed labelled in the Welker & Lende (1890) study. More recent studies of thalamocortical connections of somatosensory fields using horseradish peroxidase (HRP) demonstrate that the rostral field receives input from the ventroposterior nucleus as does the caudal field (Ulinski 1984). No other thalamic nucleus appears to project to these two architectonically distinct fields.

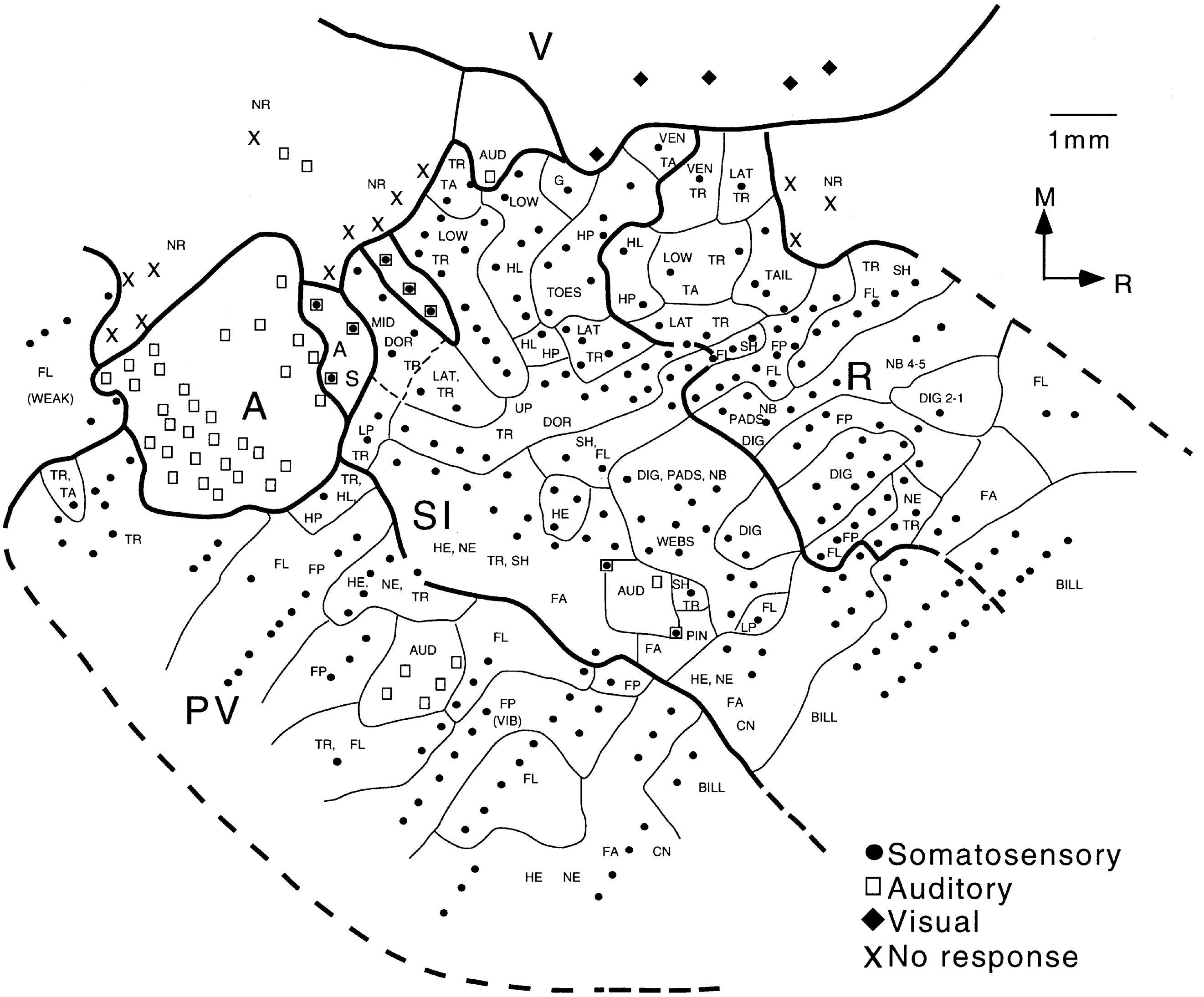

Figure 3. Microelectrode map of SI, PV and R in the echidna, redrawn from Krubitzer *et al.* (1995). The overall organization of SI is similar to that described in early studies. In this study, two additional fields have been identified, R and PV. The location of auditory and visual cortex relative to somatosensory cortex can also be appreciated.

Studies of cortical connections of the somatosensory cortex in monotremes have been briefly documented in our laboratory (Krubitzer *et al.* 1991), where we made small injections of wheatgerm agglutinin (WGA)–HRP into the approximate location of the forelimb representation of SI. This location corresponds to Ulinski's caudal field. Transported tracer was observed in cortex immediately rostral and caudal to the injection site (in fields R and PV) at the same mediolateral level as the injection site in SI (figure 6). Small amounts of labelled cell bodies and axon terminals were also observed in cortex rostral to R, in motor cortex (M, see below). Finally a small amount of tracer was observed in visual cortex.

In summary, both the platypus and the echidna have three separate somatosensory fields. A primary somatosensory area, SI, a rostral deep field, R, and a caudal field, PV. The primary somatosensory area has corticocortical connections with R, PV, M and visual cortex (possibly VI), and receives projections from the ventral posterior nucleus (VP) of the thalamus. The rostral field receives thalamic input from VP, and possibly from VL as well. The cortical and thalamic connections of PV are unknown.

(c) *Electrosensory cortex*

Until recently, it was a mystery how the platypus could accurately detect and capture prey under water while closing its eyes, ears and nose. Indeed, Burrell (1927) speculated that these peculiar animals must have a 'sixth sense'. Today we appreciate that the platypus does have an additional sense, electroreception, which allows it to detect changes in electrical currents generated by prey. The discovery of this remarkable sense was first made by Scheich *et al.* (1986), who observed both behavioural and neural correlates consistent with the presence of electroreceptivity. In this study, neurons responsive to electrical stimulation of the bill were found in the bill representation of SI. In a related 2-deoxyglucose study, Langner & Scheich (1986) demonstrate a series of rostrocaudal rows in this region when weak electrical stimulation was applied to the bill.

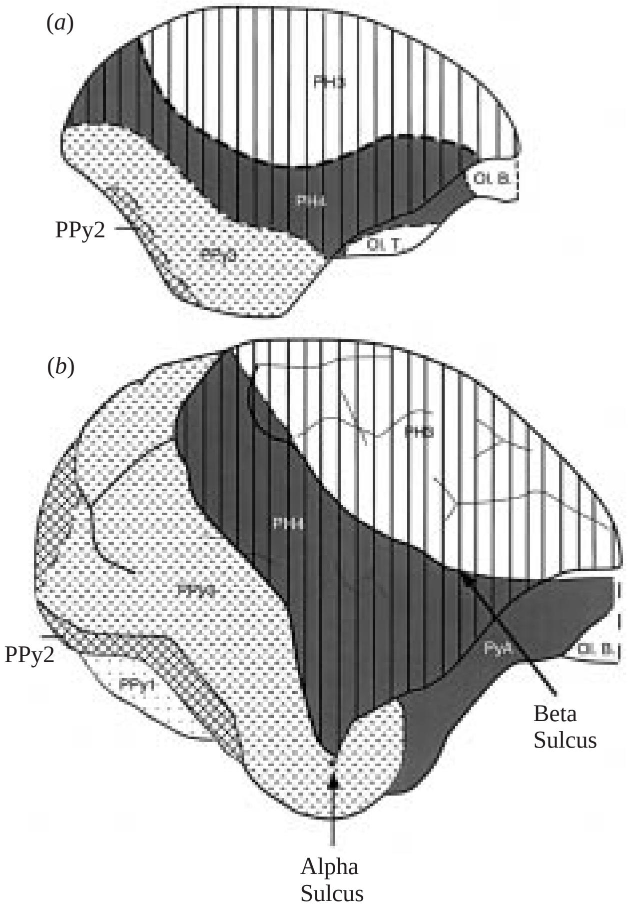

Figure 4. Cytoarchitectonic subdivisions of the neocortex of (*a*) the platypus and (*b*) the echidna, redrawn from Abbie (1940). To some extent, some fields such as PPy3 correspond to physiologically identified fields, such as SI (compare with figure 2 by matching up the asterisk for sulcus alpha).

Recently, the cortex in which neurons are responsive to electrosensory stimulation has been identified and related to cortical myeloarchitecture and CO staining (Krubitzer *et al.* 1995). The details of the platypus electrosensory system will be described elsewhere in this issue. Here, I only wish to describe the relationship between inputs from electrosensory and mechanosensory receptors on the bill, to their ultimate representation in the cerebral cortex. Our electrophysiological mapping experiments demonstrated that the electrosensory system is interdigitated with the mechanosensory system in the primary somatosensory area of the cerebral cortex, and this functional segregation can be distinguished histochemically with CO and myelin stains (figure 7). The electrosensory cortex, like the mechanosensory cortex, is topographically organized with more proximal portions of the bill represented caudomedially and more distal portions of the bill represented rostrolaterally. However, unlike the mechanosensory representation, there appears to be local discontinuities and topographic re-representation within this map.

The organization of electrosensory cortex in the platypus was characterized further by Manger *et al.* (1996) using single-unit studies to explore the spatial and temporal parameters of the neural response. They propose that the electrosensory cortex is composed of modules in which neurons within the module have the same receptive field on the bill, but respond to different intensities of the stimulus (in addition, see Krubitzer *et al.* (1995) and figure 7). Because these neurons have a limited dynamic range of response, together with a different threshold to electrical stimulation, they suggest that the differential activation of modules for different locations on the bill is the neural substrate for determining stimulus origin (electrical fields decay as they pass through water: see Pettigrew *et al.* (this issue) and Fjällbrant *et al.* (this issue)). In addition, the latency of a neuron's response for mechanosensory and electrosensory stimuli differs, and there is a facilitation of the latency of response when both stimuli are presented simultaneously. Because a single natural stimulus is likely to stimulate both electrosensory and mechanosensory receptors, Manger *et al.* (1996) propose that this differential firing rate could be used to determine stimulus distance. Thus, the arrangement of electrosensory cortex, and the differences in the latency of response of neurons to mechanosensory and electrosensory stimulation, allows the platypus to determine both the direction of an

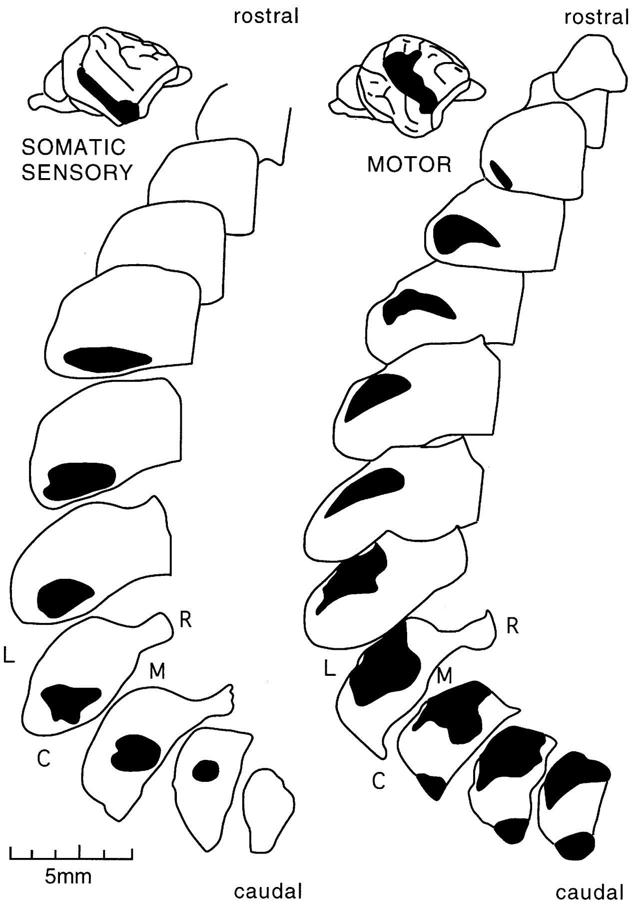

Figure 5. Patterns of degeneration through the thalamus (below; dark filled regions) resulting from lesions in somatosensory (top left) and motor (top right) cortex. After lesioning somatosensory cortex, degenerated neurons were found in the ventral posterior nucleus of the thalamus, which runs through a large portion of the thalamus. Lesions in motor cortex result in degenerating neurons in VL (upper dark patches through the series), as well as in a posterior ventral portion of the thalamus (lower dark patch). This figure is redrawn from Welker & Lende (1980).

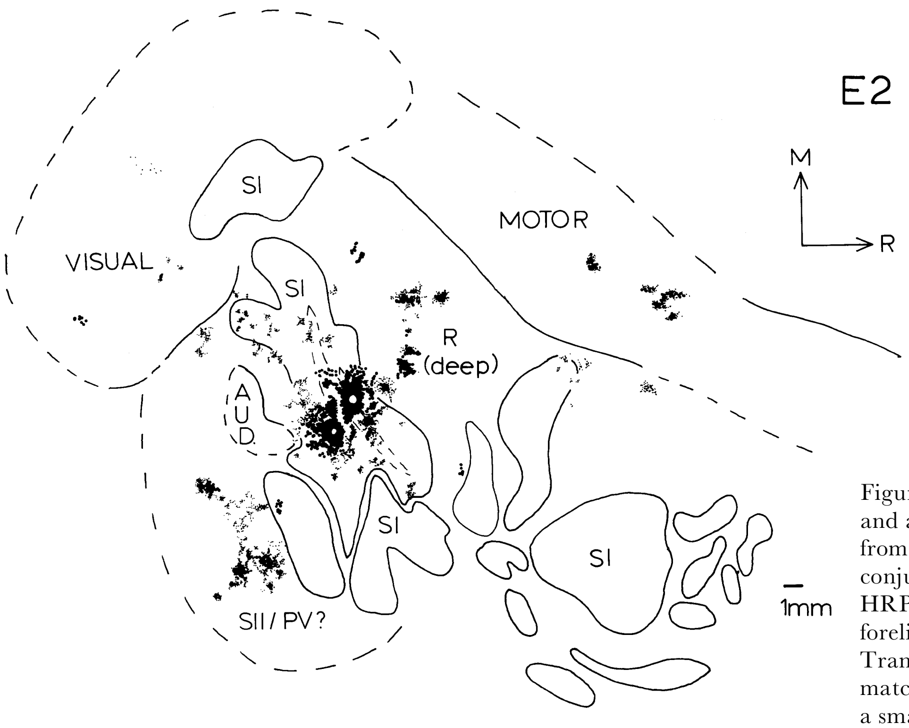

Figure 6. Labelled cell bodies (large dots) and axon terminals (small dots) resulting from an injection of wheatgerm agglutinin conjugated to horseradish peroxidase (WGA–HRP) in the approximate location of the forelimb representation in SI of the echidna. Transported tracer is in a topographically matched location in R, PV/SII and MI, and a small amount of label is in VI.

electrical signal and possibly its distance, respectively (Pettigrew *et al.*, this issue).

(d) *Motor cortex*

(i) *Electrophysiological recording studies*

The earliest study in which the cerebral cortex in a monotreme was electrically stimulated was done a century ago by Martin (1898). Although the precision of this study was limited, he provided evidence that movements of the forelimb, head and eyelids could be elicited when large currents were applied to the cerebral cortex (figure 8). Four decades later, Abbie (1938) used bipolar faradic electrodes to stimulate portions of the cerebral cortex in both the echidna and platypus. He found that almost the entire dorsolateral surface of the platypus neocortex, when stimulated, evoked movements of body parts. A rough topography was reported with the trunk represented most caudally, followed by the tail and leg representation laterally. The forelimb and head representations were rostral to this (figure 8). This physiologically defined representation spanned three architectonic regions.

In the echidna, on the other hand, the region defined as motor cortex was more limited and resided between the alpha and beta sulci. The topography of this field was similar to that described for other mammals with the tail and hindlimb represented most medially, followed by the representation of the trunk, forelimb and head most laterally (figure 8). This report was later confirmed by Goldby (1939), in which electrical stimulation of the cortex between sulci alpha and beta produced a map similar to Abbie's, although some of the details of the map differed slightly. Abbie found that this motor field coincided with a distinct architectonic field, PH4 (Abbie 1940).

More recent investigations in both the echidna (Lende 1964) and platypus (Bohringer & Rowe 1977) confirm the location of excitable cortex (figure 8), and provide more detailed maps of motor cortex. Both of these studies examined the location and internal organization of somatosensory cortex in the same animals, and for the platypus, almost a complete overlap of somatosensory and motor cortex was described. In the echidna, motor cortex was shown to be separate from somatosensory cortex.

(ii) *Cortical architecture*

Only a few studies of cortical architecture have been done for motor cortex in monotremes. Abbie's study (1940) demonstrated a 'granular' region of cortex termed PH4 that resides in the location of motor cortex in both the echidna and platypus (figure 4). Examination of his figures indicates that PH4 also contains medium size pyramidal cells in layer V, although this distinction is not extreme. In a more recent investigation in echidnas by Ulinski (1984), it was found that the cortex just rostral to his rostral area, in the location of MI defined electrophysiologically by Lende, had a poorly developed layer IV, and a thick layer V, which contained a number of large pyramidal neurons. In our recent study (Krubitzer *et al.* 1995), the region in which motor cortex is located is lightly myelinated in both the platypus and echidna.

(iii) *Connections*

Studies of connections of motor cortex in monotremes are few. In a degeneration study by Goldby (1939), the cortex between the alpha and beta sulci was lesioned and degenerating axons were found in the pars lateralis of the ventral nucleus of the thalamus (VL), and in the cerebral peduncle of the midbrain. The degenerated fibres decussated in the upper part of the pons, and then travelled in the lateral column of the spinal cord (the corticospinal tract). More recently, Welker & Lende (1980) made lesions in motor cortex, as defined previously by Lende (1964), and found thalamic degeneration in VL. However,

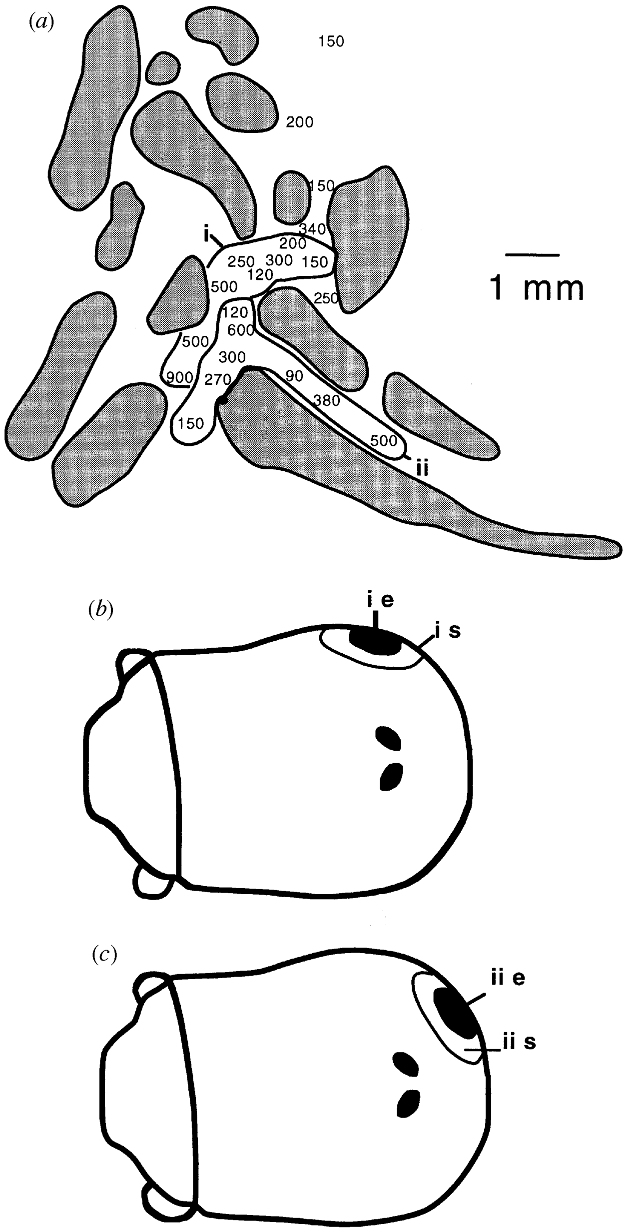

Figure 7. (*a*) A patch of electrosensory cortex in the platypus. The shaded areas represent regions of high CO density. These regions contain neurons responsive to mechanosensory stimulation. In the enclosed white areas, the individual numbers represent electrode penetrations at which neurons responded to electrosensory and mechanosensory stimulation. The numbers themselves are the threshold in $\mu V\,cm^{-1}$ for neurons at those sites. The receptive field location for neurons at all of the sites within the enclosed white area was the same. For instance, the electrosensory field for neurons in the 'i' enclosed region is drawn in (*b*) and is indicated as 'ie'. The somatosensory receptive field is indicated in (*b*) as 'is'. (*c*) The same relationship exists for neurons in the 'ii' enclosed area. Note that the electrosensory receptive field and somatosensory receptive field are completely overlapping, although the electrosensory receptive field is smaller. This figure is redrawn from Krubitzer *et al.* (1995).

examination of the series of sections through the thalamus in which degenerating neurons were defined shows that a large region of the thalamus was affected, larger than the size of VL, and that degeneration occurred at two separate loci, suggesting more than just the involvement of VL (figure 5).

All studies are consistent with the hypothesis that a primary motor cortex, or MI, is present in echidnas. This region appears to be separate from the somatosensory areas defined in modern microelectrode mapping studies (Krubitzer *et al.* 1995) and architectonic studies (Ulinski 1984). In the platypus, it is possible that motor cortex is also separate from SI, since the area of cortex in which movements could be evoked with electrical stimulation did not extend as far caudal as the region in which tactile stimulation elicited a neural response (Bohringer & Rowe 1977; compare figures 2 and 8). In addition, the region of cortex considered as SI in this earlier study was later broken into three separate fields. MI is interconnected with the primary somatosensory area (Krubitzer *et al.* 1991), and receives projections from the ventrolateral nucleus of the thalamus (Welker & Lende 1980) and possibly other nuclei as well.

(e) *Auditory cortex*

(i) *Electrophysiological studies*

Although the location of auditory cortex has been described in evoked potential studies in both the echidna (Lende 1964) and the platypus (Bohringer & Rowe 1977) (figure 9), and has been more precisely placed in more recent microelectrode mapping studies (Krubitzer *et al.* 1995), the details of the functional organization of auditory cortex have only been described in a brief report for the echidna (Krubitzer *et al.* 1991). In this study, in both the platypus and the echidna, auditory cortex was found to be almost completely embedded in somatosensory cortex (figure 3). The position of this field is similar to that described in earlier studies by Lende (1964) and Bohringer & Rowe (1977). Unlike more recent studies, the cortex caudal to auditory cortex in these studies was undefined, and in the Bohringer & Rowe study, they proposed that auditory cortex overlaps with visual cortex (figure 9).

In the Krubitzer *et al.* (1995) study, microelectrode recording techniques were used to determine the response of neurons to free-field, pure-tone stimuli ranging from 500 Hz to 20 kHz. The best frequencies were defined at the lowest amplitude at which a neural response could be elicited, and a tuning curve was obtained for neurons at each recording site. Some neurons responded to the onset and offset of the stimulus, but this was not consistently limited to a single field.

There was evidence for two tonotopic representations in auditory cortex: a rostromedial field and a caudolateral field. The rostromedial field contained a tonotopic representation from 1 to 16 kHz, with lower frequencies represented caudally and higher frequencies represented rostrally. The caudolateral field contained a cochleotopic representation from 3 to 13 kHz, with low frequencies represented rostrally and high frequencies caudally. Because of its internal organization and myeloarchitectonic appearance (see below), I hypothesize that this caudal field is homologous to the primary auditory field described in other mammals, although further electrophysiological, connectional and architectonic studies need to be done to test this hypothesis. Both of these fields were bordered by neurons that responded to visual and auditory stimulation caudally, and rostrally by SI, or neurons that

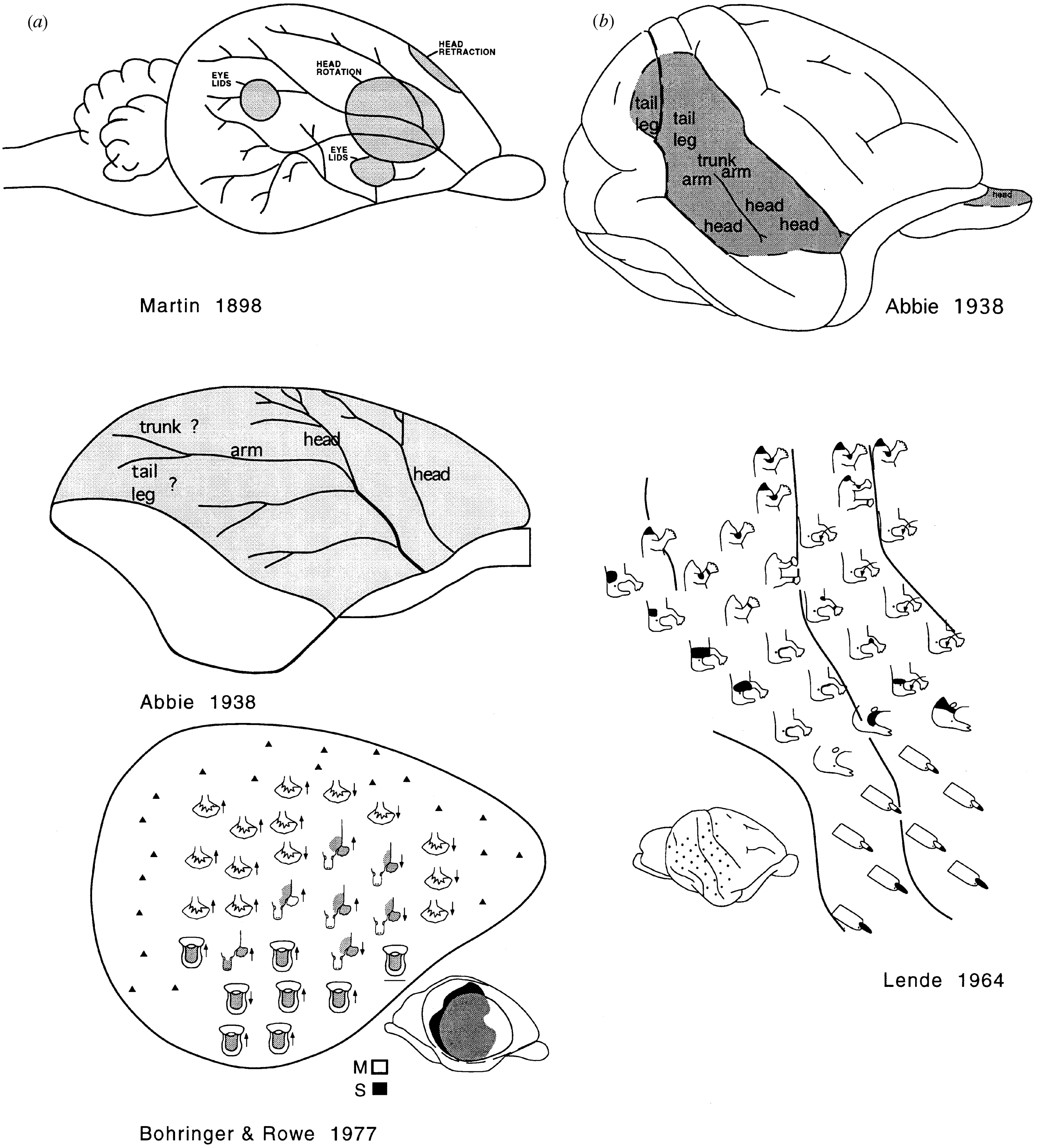

Figure 8. Maps of motor cortex in (*a*) the platypus and (*b*) the echidna, obtained by stimulating this region. Although crude, the early maps of motor cortex in the echidna showed a similar pattern of organization as the more detailed maps of Lende (1964). All of the maps are redrawn form the studies cited in the figure.

responded to both auditory and somatosensory stimulation.

(ii) *Cortical architecture and connections*

Early architectonic studies of Abbie (1940) failed to make a distinction in this region of cortex, and based on relative location, auditory cortex would be assimilated in his much larger region termed PPy2 (figure 4). In the study by Krubitzer *et al.* (1991), both fields were contained predominantly within a darkly myelinated region of cortex.

In other mammals, MG is the major auditory projection nucleus of the thalamus. Studies of connections by Welker & Lende (1980) did not distinguish a medial geniculate nucleus (MG) in the thalamus, although a cortical ablation in a portion of auditory cortex resulted in degeneration in the posterior lateral portion of the thalamus, in the expected location of the medial geniculate complex. Interestingly, an earlier architectonic study in the echidna by Campbell & Hayhow (1971), and a more recent study by Ulinski (1984) did not distinguish a medial geniculate complex. However, in the platypus, the

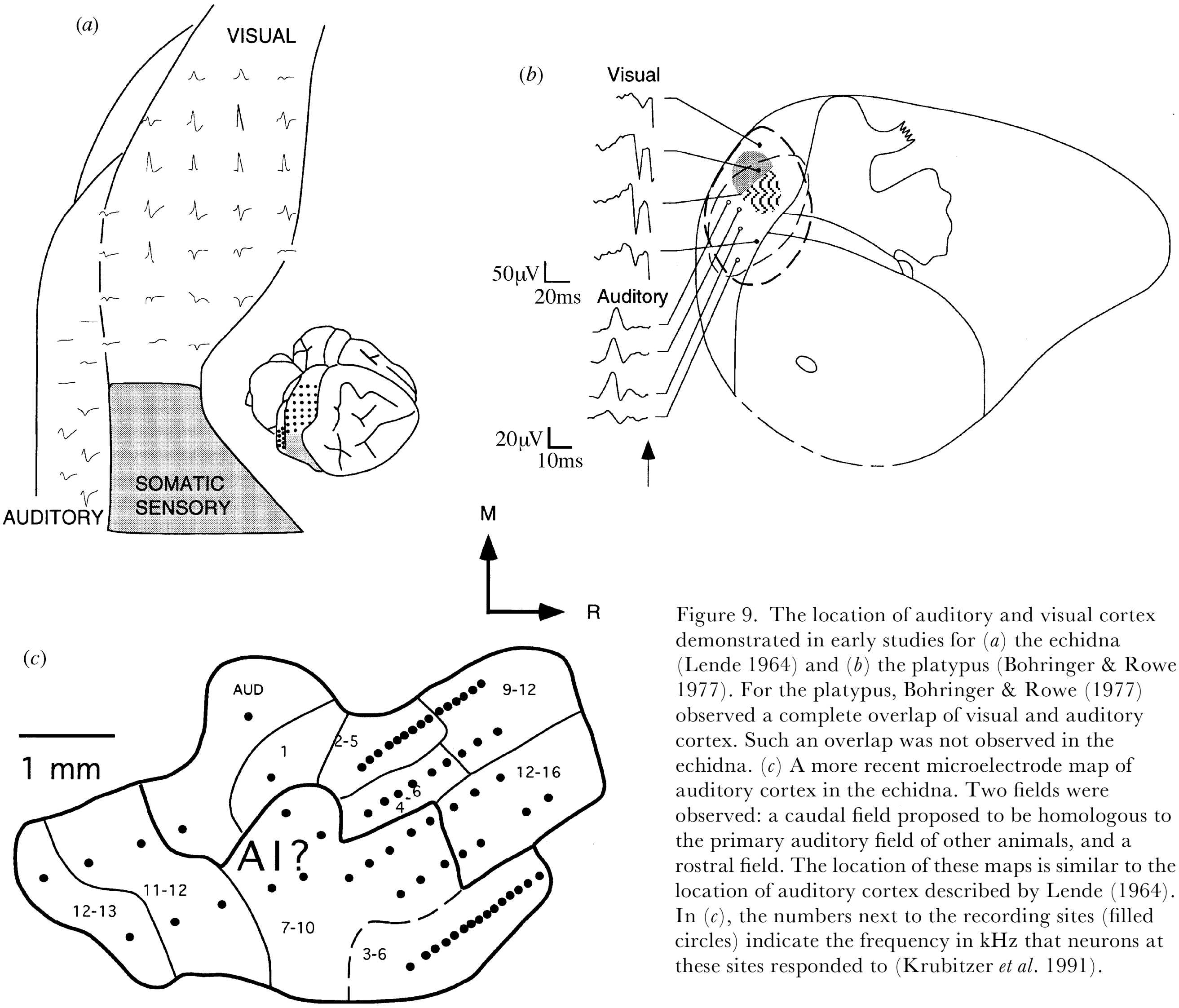

Figure 9. The location of auditory and visual cortex demonstrated in early studies for (*a*) the echidna (Lende 1964) and (*b*) the platypus (Bohringer & Rowe 1977). For the platypus, Bohringer & Rowe (1977) observed a complete overlap of visual and auditory cortex. Such an overlap was not observed in the echidna. (*c*) A more recent microelectrode map of auditory cortex in the echidna. Two fields were observed: a caudal field proposed to be homologous to the primary auditory field of other animals, and a rostral field. The location of these maps is similar to the location of auditory cortex described by Lende (1964). In (*c*), the numbers next to the recording sites (filled circles) indicate the frequency in kHz that neurons at these sites responded to (Krubitzer *et al.* 1991).

medial geniculate body has been identified by Hines (1929) and Campbell & Hayhow (1972).

In a more recent study of connections in the echidna, Dann & Buhl (1995) placed small crystals of DiI into the region of cortex defined by Lende (1964) as auditory. They found patchy connections in surrounding auditory cortex. Because of the presence of labelled fibres in the white matter, they suggest that these patches of label are cortico-cortical connections to adjacent auditory fields.

Taken together these studies indicate that both the platypus and echidna have a distinct auditory region of the cerebral cortex, separate from somatosensory and visual representations. It is likely that at least two separate fields are contained within a darkly myelinated region, A and Ar (Krubitzer *et al.* 1991), one of which may be the homologue of the primary auditory area, AI, described in other species (see below). Studies of corticocortical connections by Dann & Buhl (1995) support the hypothesis that more than one field is present. Although the specific thalamocortical connections are not known, this region of cortex in the echidna receives projections from the posterior lateral portion of the dorsal thalamus, in the expected location of the medial geniculate nucleus.

(f) *Visual cortex*

(i) *Electrophysiological recording studies*

Like auditory cortex, relatively little is known about the organization, architecture and connections of visual cortex in monotremes. Early evoked potential studies identified the location of visual cortex in the platypus, and report that it is completely overlapping with auditory cortex (Bohringer & Rowe 1977; figure 9), whereas Lende's (1964) study in echidnas designated a separate auditory and visual region of the cortex (figure 9). A recent micro-electrode mapping study defined the location of neurons responsive to visual stimulation relative to other cortical fields, and in relation to cortical myeloarchitecture and CO stains (Krubitzer *et al.* 1995). In the echidna, the location of the visual cortex was similar to that identified by Lende; in the platypus, it was medial to SI and auditory cortex.

Only recently have we defined the internal organization of visual cortex in the platypus, and the relationship of different fields to cortical myeloarchitecture (L. Krubitzer, unpublished observations). In this study, microelectrode mapping procedures, similar to those used in an earlier study (Krubitzer *et al.* 1995), were used to identify the

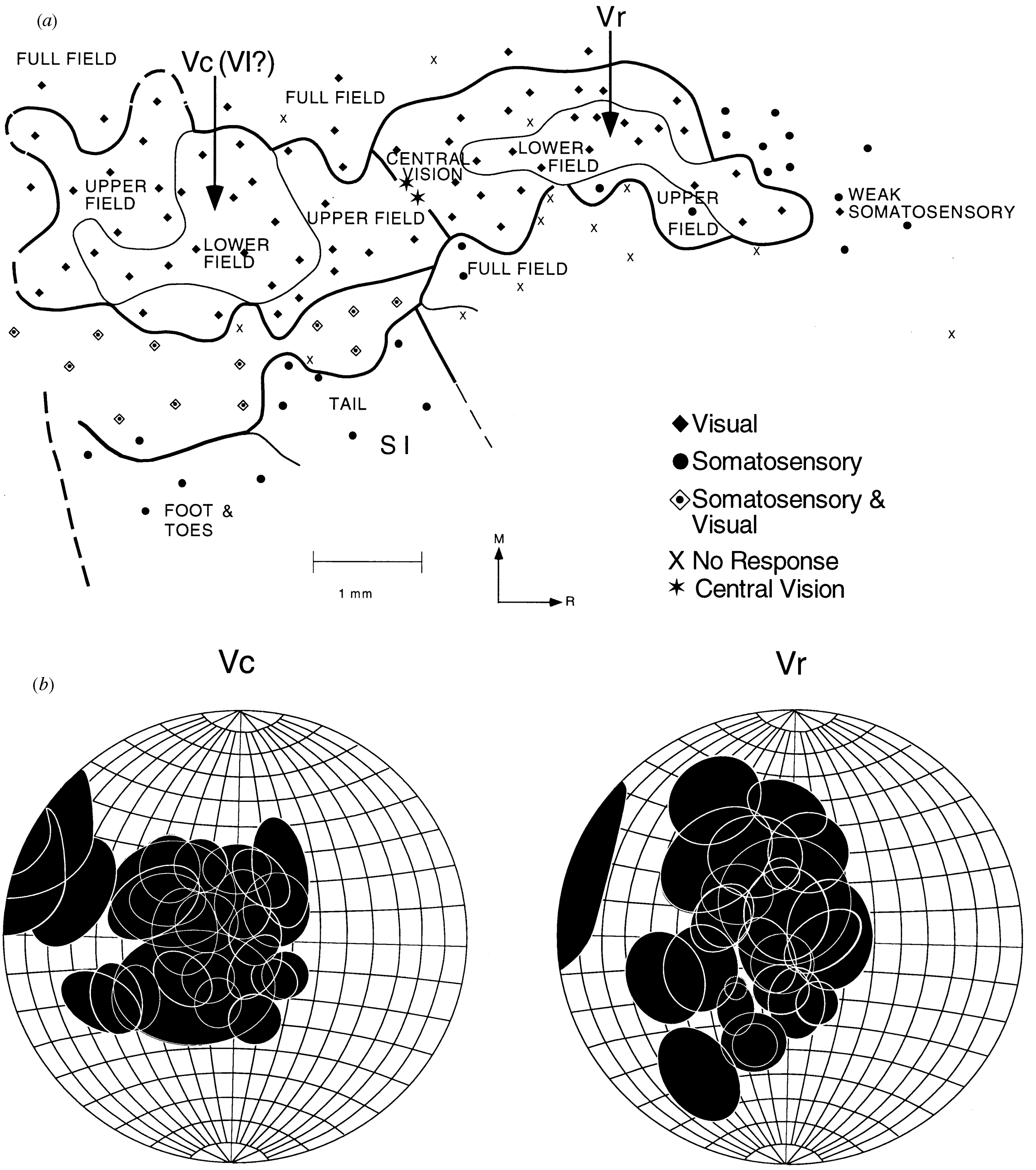

Figure 10. (*a*) A map of visual cortex organization in the platypus and (*b*) the amount of visual space represented in each field of the two cortical areas identified. It is clear from (*b*) that at least two complete representations of the visual field exist, a caudal field, Vc, and a rostral field, Vr. Although a clear lower and upper field representation can be identified in each cortical area, the topography is not precise. The caudal field, Vc, is proposed to be homologous to the primary visual area defined in other mammals. The region of cortex bordering Vc and Vr contains neurons that respond to full-field flashes. Cortex just lateral contains neurons that respond to visual and somatosensory stimulation, and cortex rostral contains neurons that respond to weak somatosensory stimulation. These data were collected with P. Manger and M. Rosa.

receptive field location for neurons responsive to visual stimulation. The results indicate that at least two representations of the visual field can be identified in the platypus, one of which is located medial to SI (Vc), and one of which is just rostral and medial to SI (Vr) (figure 10). Each field contains a relatively complete representation of the visual field, although the topographic organization of these fields is imprecise. The caudal field contains neurons that respond more vigorously to visual stimulation, and the receptive fields range in size from 15° to 50° with a trend for the central visual representation to have neurons with smaller receptive fields (figures 10 and 11). Although some receptive fields for neurons in the rostral field are small (15°), more neurons have large receptive fields than do neurons with receptive fields at the same eccentricity in Vc. Further, neurons in Vr respond less vigorously to visual stimulation than neurons in Vc. There is a clear separation of upper and lower field representations in each area, and the representation of central vision can be clearly defined. The representation of central vision formed the boundary of the two fields. Because a number of fractures in the map, or jumps in receptive field progression, were observed in both fields, it was difficult to obtain a clear topographic organization for Vr or Vc (figure 11). It is possible that these jumps in receptive field progression are due to movement of the eyes. However, the eyes were sutured to a metal ring to prevent movement, and a number of recording sites were re-checked throughout the experiments to ensure that receptive fields for neurons at those sites remained constant.

(ii) *Cortical architecture*

In the above study, both fields were coextensive with a darkly myelinated, CO-dense region. However, Vr was slightly less myelinated than Vc. In Abbie's (1940) architectonic analysis, he did not distinguish a separate visual cortex. In the echidna it would be included in the portion of his PPy3, and in the platypus in his PPy3 or PH4.

(iii) *Connections*

There is only one study in which the thalamocortical connections of visual cortex are described (Welker & Lende 1980), and two studies in which the corticocortical connections of the visual cortex are described (Krubitzer *et al*. 1991; Dann & Buhl 1995). All of these connections studies were done in the echidna. In the Welker & Lende study, a region of the thalamus designated as OP (occipital pole region) contained degenerated fibres after visual cortex lesions. No degeneration was observed in the major retinal target of other mammals, the dorsal lateral geniculate nucleus (LGN). Almost all studies in which the architecture of the echidna thalamus was investigated place the LGN in the same location (Campbell & Hayhow 1971; Welker & Lende 1980; Ulinski 1984). The study by Regidor & Divac (1987) place the LGN in a different location, just lateral to the ventral posterior nucleus. Given the rather large size of the visual cortex in echidnas, and the degeneration demonstrated in OP, it is possible that OP is really the LGN, or that OP is homologous to the pulvinar in other mammals, and that connections have changed in different lineages. Campbell & Hayhow (1971, 1972) demonstrate that two subdivisions of the LGN (LGNa and LGNb), the pretectum and the superior colliculus receive retinal input in both the echidna and the platypus. However, examination of the data indicate that the amount of label in the superior colliculus, at least in the echidna, far exceeds that in either division of the LGN (e.g. Campbell & Hayhow 1972, fig. 5). This suggests that the retino-geniculo-striate pathway may be a more recently evolved system in mammals. A related hypothesis is that the visually responsive cortex in the platypus and echidna is not homologous to VI, and that VI evolved later and connections with the LGN are a new feature observed in marsupial and eutherian mammals. Further study is needed to resolve this issue.

In one of the studies of cortical connections (Krubitzer *et al*. 1991), WGA–HRP was injected into visual cortex in the echidna, and patches of label were noted within the myelin dense region (the injected area), possibly in separate subdivisions. Patches of label were also observed outside of this region, in lightly myelinated cortex, and a small amount of transported tracer was observed in SI (figure 12). Finally, in a recent study by Dann & Buhl (1995), the connections of the region that Lende (1964) defined as visual were determined by placing small crystals of DiI into this area. Transported tracer was found in small patches up to 6 mm from the injection site. Because labelled fibres were identified in the white matter, the authors conclude that some of these patches were indicative of corticocortical connections. In addition, the columnar nature of the connections and the morphology of labelled neurons was much like that of other mammals.

In summary, both the platypus and the echidna have more than one visual field. In the platypus, this has been demonstrated electrophysiologically where two, nearly complete representations of the visual field have been identified. I believe one of these fields, Vc, is homologous to the primary visual area defined in other mammals based on receptive field size, location, vigour of response and cortical architecture. Connectional studies also support the existence of more than one visual field. Neurons in cortex surrounding these two fields respond to full-field flashes, so it is possible that there is another visual area as well.

(g) ***Association cortex***

I have included all regions outside of the known sensory cortex as association areas. For the platypus and echidna these include multimodal regions interspersed between auditory, visual and somatosensory cortex, as well as cortex rostral to motor cortex, termed the prefrontal cortex in a previous investigation (see below).

In both species of monotremes, a small belt of cortex surrounding the ventral half of AI and Ar contained neurons responsive to both auditory and somatosensory stimulation (Krubitzer *et al*. 1995, fig. 4 and 8; in addition, see figure 3). Cortex just medial to A and PV and lateral to visual cortex was found to have neurons responsive to both auditory and visual stimulation (Krubitzer *et al*. 1995, fig. 5 and 18). Finally, in some animals, neurons just medial to SI and lateral to visual cortex had neurons that responded to both visual and somatosensory stimulation.

Cortex immediately rostral to motor cortex in both species is electrically silent using standard microelectrode mapping procedures. This cortex is remarkably large in the echidna and is proposed to be similar to prefrontal cortex in other mammals (Divac *et al*. 1987*a*,*b*). In a series of studies in the echidna, investigating the connections of prefrontal cortex with the thalamus and other subcortical structures, a large mediodorsal nucleus of the thalamus was identified (Regidor & Divac 1987), and was found to be strongly interconnected with the 'silent' cortex rostral to MI (Divac *et al*. 1987*a*,*b*). These investigators also report

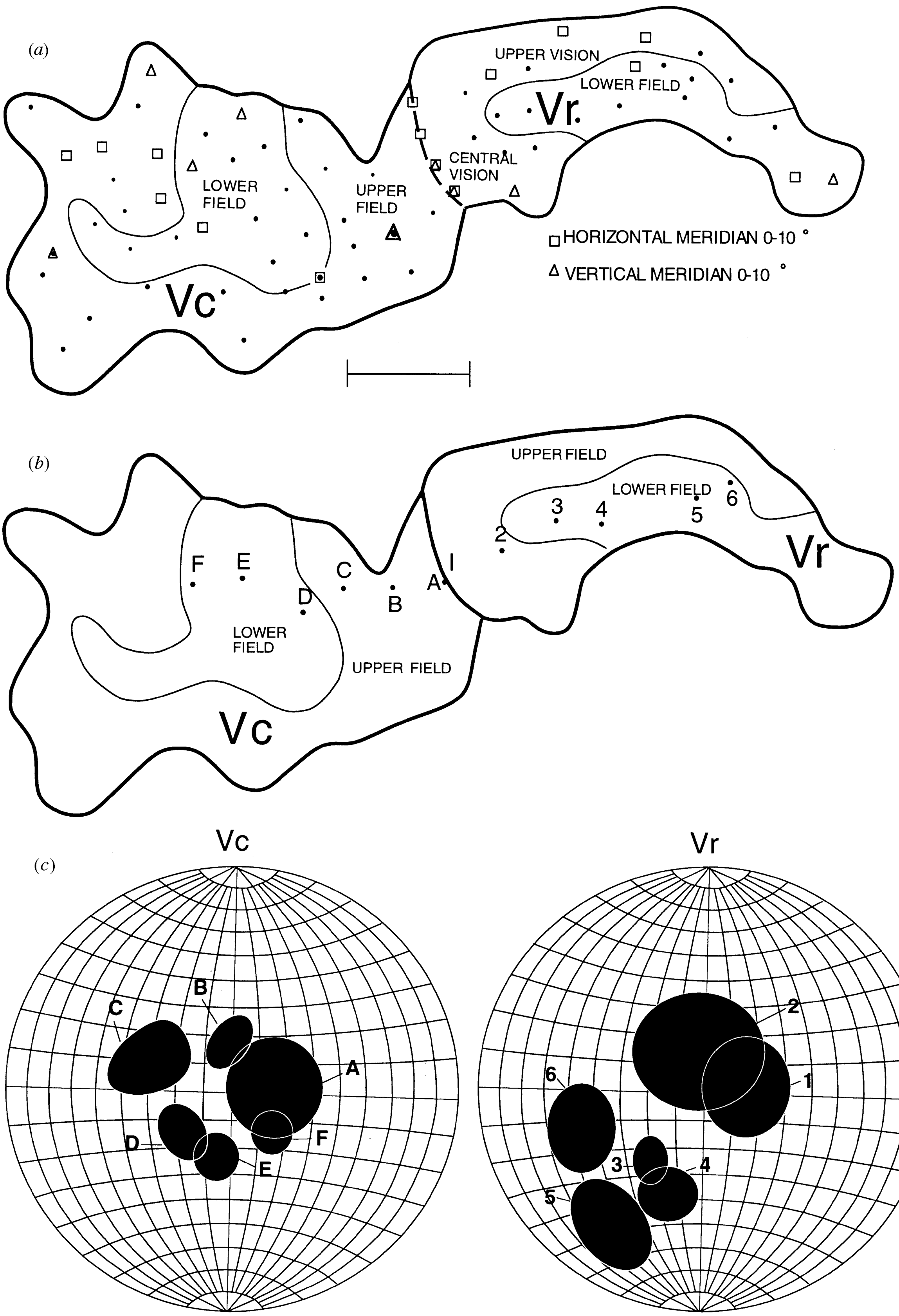

Figure 11. (*a*) A simplified map of Vc and Vr, shown in figure 10, demonstrating the location of neurons that had receptive fields whose centres were within 1° to 10° of the horizontal (open squares) and vertical (open triangles) meridians. (*b*) Receptive field progressions through each field (letters and dots), and (*c*) corresponding receptive fields for neurons at those sites. Although there is not a re-representation within a particular field, the receptive field progressions are not smooth. These data were collected with P. Manger and M. Rosa.

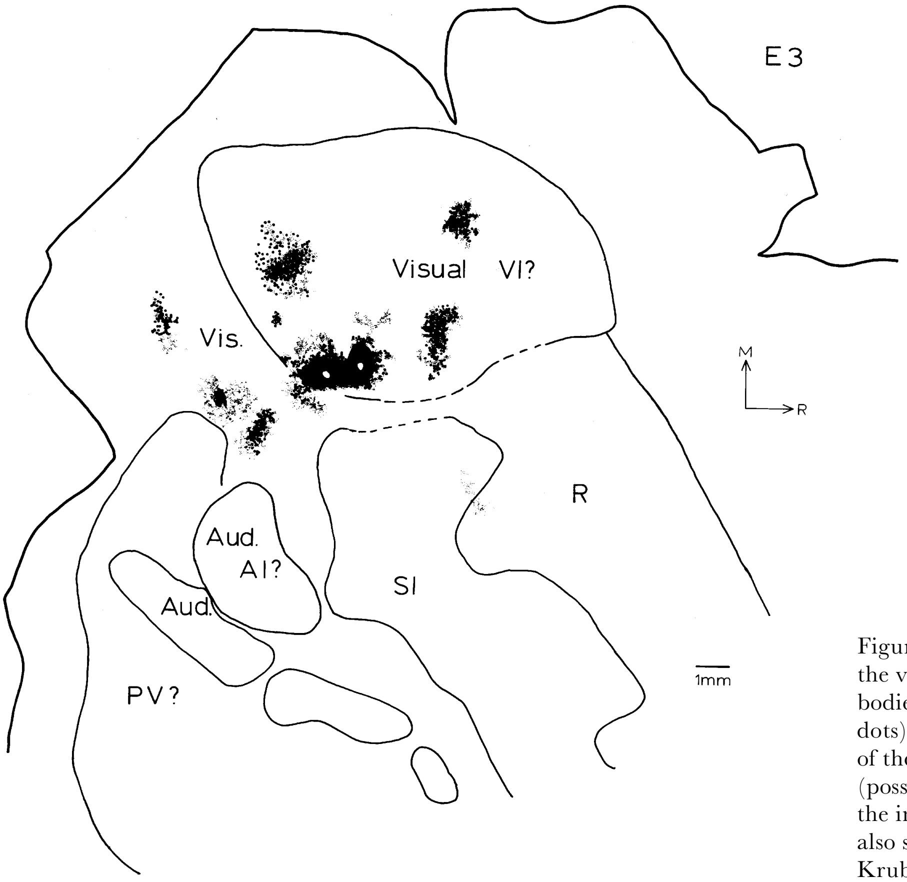

Figure 12. An injection of WGA–HRP into the visual cortex of the echidna. Labelled cell bodies (large dots) and axon terminals (small dots) were found in several separate patches of the darkly myelinated visual cortex (possibly VI), and in visual cortex caudal to the injected area. A small patch of label was also seen in SI. This figure is redrawn from Krubitzer *et al.* (1991).

afferent connections from the entorhinal cortex, basal forebrain, amygdala, pyriform cortex, substantia nigra and ventral tegmental area. Efferent connections were observed with prefrontal cortex in the opposite hemisphere, and the medial dorsal nucleus of the thalamus, the ventral tegmental area, the hypothalamus and the pons. Bilateral connections were observed with the neostriatum and the palaeocortex. Based on these connection studies, Divac and colleagues conclude that this region of cortex is similar to the prefrontal cortex described in eutherian mammals. Indeed, their terminology of 'prefrontal' strongly implies homology. An earlier study of thalamocortical connections of this region by Welker & Lende (1980) also demonstrates a substantial amount of degeneration in the medial dorsal nucleus after lesions to several regions of this prefrontal cortex.

3. COMPARISONS WITH OTHER MAMMALS

(a) *Somatosensory cortex*

When the echidna and platypus somatosensory neocortical organization (figure 13) is compared with the organization and connections of somatosensory cortex in other mammals (figure 14), there are a number of features of organization that are similar. First, like other mammals, monotremes contain a complete representation of cutaneous receptors, coextensive with a myelin dark, layer IV dense region that receives input from the ventral posterior nucleus of the thalamus. This is the primary somatosensory area. To date, all mammals investigated have this field, and it is believed to be homologous across mammals (for reviews, see Kaas (1983) and Johnson (1990)). Further, the cortical connections of SI in monotremes are similar to those described for other mammals and support electrophysiological studies demonstrating more than a single somatosensory field. The presence of a small caudal field, termed PV, and a rostral field, R, also corresponds well to subdivisions in other mammals (figures 13 and 14). For instance, a field rostral to the primary somatosensory area whose neurons respond to stimulation of deep receptors has been identified in a number of mammals and is termed area 3a in primates (see Kaas & Pons (1988) for a review), cats (Dykes *et al.* 1980; McKenna *et al.* 1981) and flying foxes (Krubitzer & Calford 1992), the kinaesthetic cortex in raccoons (Johnson *et al.* 1982; Feldman & Johnson 1988), and the rostral field in marsupials (Elston *et al.* 1993; Beck *et al.* 1996) and insectivores (Krubitzer *et al.* 1997). Finally, the caudal field, PV, has a counterpart in most or all other mammals investigated. In monotremes, this field was termed the parietal ventral area (in this review), although it could be homologous to SII in other mammals. Thus far SII and PV have been identified in most other mammals investigated (see Krubitzer (1996) for a review).

(b) *Motor cortex*

The complete topographic organization of MI has only been fully explored in a few mammals, including some primates (Killackey *et al.* 1983; Gould *et al.* 1986; Stepniewska *et al.* 1993) and rats (e.g. Hall & Lindholm 1974; Donoghue & Wise 1982). The organization of MI is less precise than SI, and fractures in the map are often

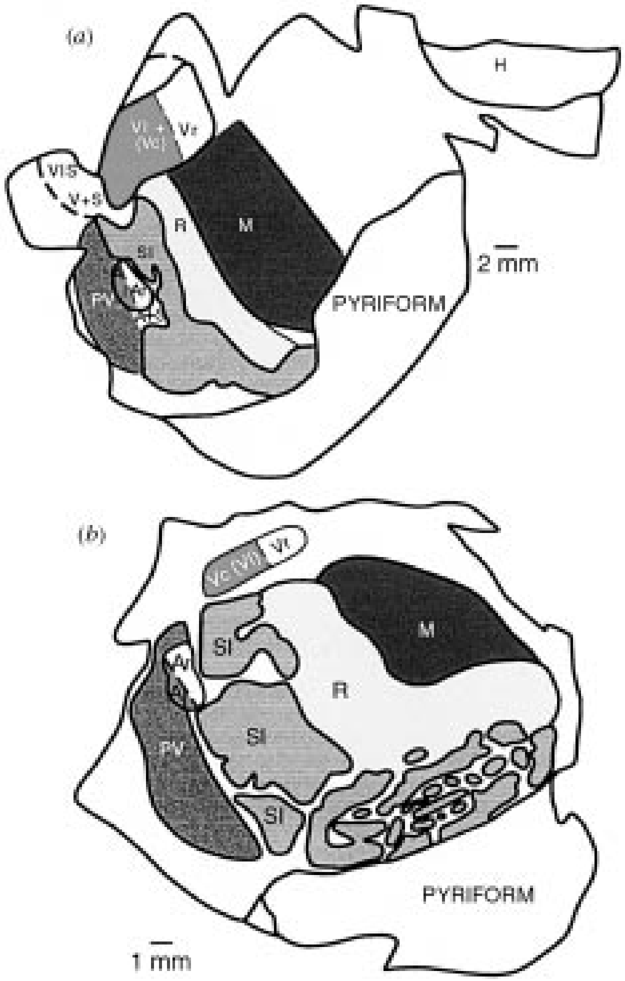

Figure 13. The proposed organization of the neocortex of (*a*) the platypus and (*b*) the echidna. Both species have an SI, R, PV, AI, Ar, Vc (VI), Vr, M, multimodal cortex, and an unresponsive frontal region. In the platypus, the representation of the bill also contains islands of neurons that respond to electrosensory stimulation. The colour coding is used to indicate homologous areas in each species. From Krubitzer *et al*. (1995).

observed. However, the gross mediolateral organization mirrors that of SI with the feet represented most medially, followed by representations of the trunk, forelimb and face most laterally. The partial overlap of somatosensory cortex and motor cortex reported for marsupials and monotremes in early studies (see Rowe (1990) for a review) is often used to promote the notion that a sensory/motor amalgam exists in primitive mammals (Lende 1963). It should be noted that all mammals investigated with microstimulation techniques and microeclectrode recording techniques, including primates (Stepniewska *et al*. 1993, fig. 7 and 14), demonstrate an overlap of somatosensory and motor cortex. Further, the corticospinal tract has been demonstrated to incorporate portions of both motor and somatosensory cortex in a variety of mammals (Nudo & Masterton 1990*a*,*b*). Connections of MI with the ventrolateral nucleus of the thalamus have been demonstrated in a number of mammals (see Jones (1985) for a review), including monotremes. It appears that all mammals have a primary motor cortex that shares a number of common organizational and connectional features. However, the extent of overlap with somatosensory cortex may be variable across species.

(c) *Visual cortex*

To date, all mammals investigated have a primary visual cortex, VI or area 17, that receives dense input from the lateral geniculate nucleus of the thalamus, and a VII that receives input from the LGN in some animals (e.g. Sherman 1985), as well as the pulvinar (for reviews, see Kaas & Huerta (1988) and Kaas & Krubitzer (1991)). The region designated as visual in echidnas receives input from a large nucleus termed OP of the thalamus, rather than the LGN. However, in the platypus, two separate visual fields exist, and studies of connections in the echidna also suggest that more than a single field is present. It is possible that one of these fields is VI, and the study in which lesions were made did not include this field. An alternative explanation is that this region is not VI, but either homologous with VII or some other extrastriate region identified in other mammals, or a completely different field that evolved independently in the monotreme line. Although I have tentatively termed the caudal field in the platypus VI, owing to the vigour of neural response, receptive field size and the densely myelinated appearance of cortex in which it is contained, the data are equivocal, and a different interpretation is certainly plausible. The presence of an LGN in the thalamus of both platypus and echidnas indicates homology, at least at the thalamic level. What is needed is a more precise study of thalamocortical connections, as well as more detailed maps of visual cortex in both the platypus and echidna. Regardless of homology, an interesting difference between monotremes and other mammals is the presence of direct connections between the primary somatosensory area and visual cortex in monotremes.

(d) *Auditory cortex*

All mammals investigated have a primary auditory area (figure 14) that receives input from the medial geniculate nucleus of the thalamus (see Clarey *et al*. (1992) for a review). In addition, a number of animals have also been shown to possess a second field just rostral to AI, the rostral auditory field (Luethke *et al*. 1988, fig. 19; Morel & Kaas 1992; Morel *et al*. 1993). Cortex designated as auditory in monotremes also contains tonotopic representations of the cochlea. As in other mammals, this region of cortex is coextensive with dark myelination. I have termed the caudal field in echidnas AI, owing to similarity in organization, myeloarchitecture and indirect support from thalamocortical connection studies. However, like the visual cortex, more data are needed to make firm conclusions regarding homology between auditory cortex in monotremes, and auditory cortex in other mammals.

(e) *Association cortex*

As described above, both the platypus and echidna have cortex in which neurons respond to more than one type of sensory stimulation (e.g. somatosensory and auditory), and a 'silent' frontal cortex. Although multimodal regions have been described in other mammals (e.g. Barnes & Pandya 1992), the number of species in which these observations were made is too limited to make any firm conclusions regarding homology. However, it is interesting that the

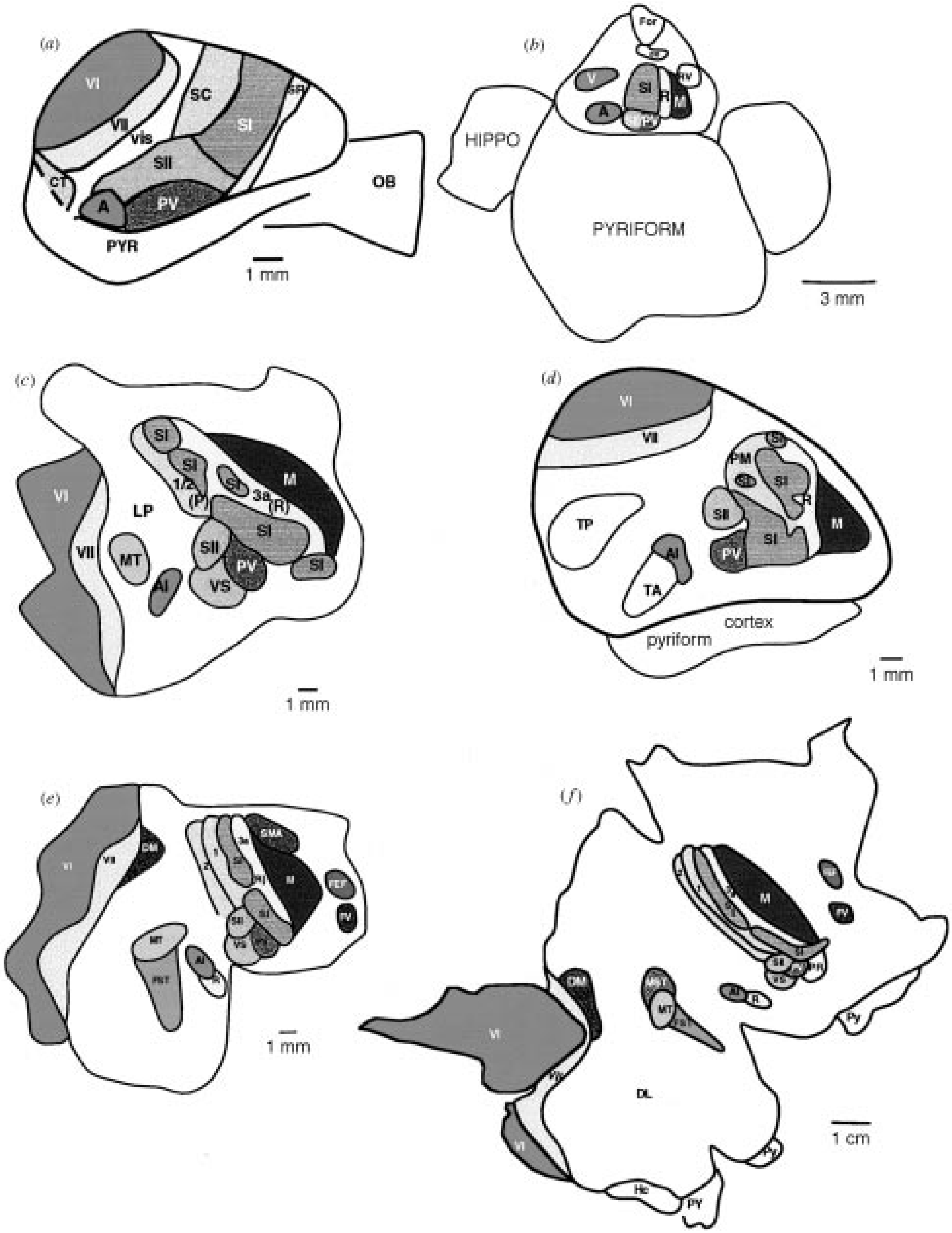

Figure 14. The organization of neocortex in mammals from different lineages. (*a*) Virginia opossum; (*b*) tenrec; (*c*) flying fox; (*d*) squirrel; (*e*) marmoset; (*f*) macaque monkey. Despite the differences in the size of the neocortex in different species, common or homologous fields (indicated by the same colour) can be identified. These fields are similar to those described for the platypus and echidna, and are proposed to be retained from the common ancestor of all mammals. Although not drawn, the areas of the cortex that are not coloured contain other cortical fields, often restricted to a given lineages. Thus, in any species, the neocortex is composed of a number of primitive or retained areas, and more recently added areas. The opossum is redrawn from Beck *et al.* (1996); the tenrec is redrawn from Krubitzer *et al.* (1997); the boundaries for the rest of the species are from a variety studies, and have been described in detail in Krubitzer (1995).

location of these multimodal fields is between the sensory cortices which they apparently integrate. This is also observed in other mammals, suggesting that the arrangement of cortical fields in any given animal is constrained, possibly by selection for optimal connection lengths (Ringo 1991; Cherniak 1994; Ringo *et al*. 1994; see Manger *et al*. (1997) for full discussion).

The cortex just rostral to motor cortex in the echidna is proposed to be similar to prefrontal cortex in eutherian mammals. Indeed, the terminology is suggestive of homology. In humans, prefrontal cortex is involved in future planning, construction of alternative interpretations of an event, detection of novelty and monitoring behaviour (Knight & Grabowecky 1995). The supposition that echidnas have a prefrontal cortex is based predominantly on patterns of connections. Specifically, this region of cortex in the echidna receives projections from the medial dorsal nucleus of the thalamus. However, the assertion of homology of PF in the echidna lacks parsimony when phylogenetic relationships are considered.

The ancestors of modern echidnas are proposed to have branched off of the platypus line approximately 65 Ma BP (Griffiths *et al*. 1991; Westerman & Edwards 1992). In the platypus, most marsupials investigated, and even a number of eutherian mammals such as insectivores, this prefrontal region appears to be very small or absent. If one were to argue for homology between PF in echidnas and PF in eutherian mammals, the evolutionary scenario would be as follows: the ancestor of both the platypus and echidna had prefrontal cortex that was lost in the platypus, and was subsequently lost in most or all marsupials, and even in insectivores and some other eutherian mammals, and retained in only a few lineages. A more likely scenario is that the common ancestor did not have a prefrontal cortex, or had only a very small prefrontal cortex, and that the expansion of prefrontal cortex in some eutherians and the echidna was independent (homoplaseous), not homologous. Although there may be some overlap of connection patterns, it is likely that the prefrontal cortex as classically defined by connections with MD is not homologous across species (Preuss 1995).

So, what then is the function of this region in echidnas? A visual examination of the external morphology of the echidna brain reveals a striking expansion of the olfactory system, including the pyriform cortex and olfactory bulb. Indeed, the surface area of the olfactory bulb is so large that this structure is fissured. It is possible that this large expansion of the frontal lobe is part of an olfactory specialization, and may be homologous to orbital cortex or anterior cingulate cortex as has been previously suggested for other animals (Preuss 1995).

In addition to the homologous cortical fields listed above, there are several general characteristics of cortical organization that all mammals possess. First, sensory fields are topographically organized. This common feature found throughout the nervous system in all mammals and even throughout vertebrates is likely to be a reflection of neural development, and is fundamental for sensory processing (Kaas 1997). Another common feature of cortical organization is that different portions of the sensory epithelium within a sensory system have varying degrees of representation within a cortical field. For instance, particular body parts of different mammals have a larger representation in the cerebral cortex than other body parts. Finally, cortical fields are architectonically distinct in both the tangential plane of section, and in frontal and parasagittal planes.

There are also certain characteristics of the monotreme neocortex that are not usually observed in other species. For instance, at least for visual cortex, the topography is somewhat rough, with breaks or fractures in the representations. Further, the corticocortical and thalamocortical connections of monotremes are somewhat limited. This is likely a reflection of having only a few cortical fields and thalamic nuclei. This may be a general feature in any species that has only a few cortical fields for each sensory system, and not particular to monotremes. This issue can be resolved by examining other species (e.g. insectivores) that also have a small number of cortical fields, and determining if their connection patterns are restricted as well. Finally, a feature not found in species with very large brains and multiple sensory is the presence of connections between primary sensory fields.

One might hypothesize that a cortex that contains few processing nodes for each sensory system (a maximum of three has been proposed for the somatosensory system of monotremes) is more likely to integrate sensory information at early levels of processing, since early levels in a configuration of three are not that far removed from later levels. The notion that multimodal integration takes place early in processing hierarchies is supported by the relatively small amount of multimodal cortex observed in these animals. Thus, in animals with large brains and a number of processing stations, sensory information is integrated much later in processing than in animals with smaller brains and fewer cortical fields. However, one would think a system with multiple fields may suffer from a lag in response time, and that processing would need to be more distributed rather than hierarchical (see Bullier & Nowak (1995) for a review). This seems to be the case.

For instance, in primates, the primary visual area has connections with VII, which in turn has connections with DM or V3, which connects to MT and the posterior parietal cortex (Krubitzer & Kaas 1993). VII also has direct connections with MT, as does VI (Krubitzer & Kaas 1990). MT in turn has connections with posterior parietal cortex, and areas of the frontal lobe involved in moving the eyes (Krubitzer & Kaas 1990). These are only a few of the connections described for VII, DM and MT. The point is that there are a number of alternate routes of information flow, some with more nodes or cortical fields in the circuit, and other more direct routes (e.g. VI-MT-FEF). Presumably even large brains can functionally reduce their circuitry, and thus have similar temporal characteristics of processing as smaller brains. The question is what causes the brain to activate particular combinations of connections in a vast array of interconnections at any one time? Perhaps studies of the neural mechanisms of attention will help resolve this issue.

4. WHAT IS THE PRIMITIVE OR ANCESTRAL PLAN OF CORTICAL ORGANIZATION IN MAMMALS?

Recent studies of monotreme cortical organization and connections, along with comparisons made in other mammals, suggest that the ancestor of all mammals was likely to posses the following: a primary somatosensory area; a rostral field; a smaller caudolateral field, PV or SII; a motor area; at least two auditory areas (an AI and a rostral field); a primary visual area and another extrastriate field; bimodal cortex located between sensory fields; and a small region of frontal cortex rostral to motor cortex. This small array of about ten cortical areas was likely to have had limited thalamic connections, and integration of sensory input between primary sensory areas via corticocortical connections may have been present (figures 6 and 12). Although the number of cortical fields and thalamic nuclei was small, the behaviour of this presumptive mammal need not have been simple, as the behaviour of the platypus in terms of prey identification and capture can be quite sophisticated (see Manger & Pettigrew 1995).

It is not clear why mammals with large brains were selected for, since small-brained mammals have obviously been highly successful. It is possible that larger brains confer an advantage when large social groups are formed, for interspecific communication, and when food sources are varied and separated in space and time.

5. HOW HAS THE CORTEX BEEN MODIFIED OVER TIME, AND WHAT ARE THE DEVELOPMENTAL MECHANISMS THAT MIGHT ACCOUNT FOR SUCH CHANGES?

The above proposition of ancestral neocortex is supported by a wealth of comparative studies of cortical organization in a variety of mammals, including the platypus and echidna. By examining the products of the evolutionary process, we can determine changes or modifications to the basic or ancestral plan of organization and infer possible mechanisms that generate those changes. In short, we find ourselves asking the same questions posed by developmental neurobiologists who study the process itself (Deacon 1989; Karten 1997).

The types of modifications to the conserved network have been outlined in detail in a previous review of neocortical organization in mammals (Krubitzer 1995). These modifications include:

1. A change in the internal organization, size and shape of a cortical field.
2. A change in the relative location of cortical fields.
3. A change in the amount of cortex devoted to a particular sensory or cognitive system.
4. A change in the number of cortical fields.
5. The addition of modules, or smaller processing units, to an existing field.
6. A change in the connections of a cortical field.

The presence of a retained cortical network, and the limited types of changes to this network, suggest that there are constraints imposed on the developing nervous system that significantly affect the evolution of the brain.

A number of theories of cortical development have been proposed to account for the differentiation of cortical fields, but few have proposed how developmental regimes are modified in evolution to produce the different types of cortex observed in extant mammals. Any theory of the evolution of the development of the neocortex must explain several important observations. First, the general expansion of the neocortex in different lineages must be explained in light of known developmental mechanisms. Second, the addition of new fields to the existing network, and the changes in patterns of connections in different lineages, must also be explained. Finally, the differences in the allotment of cortical territory to different sensory systems in different mammals must be accounted for.

A few recent theories on cortical development can account for some of the differences observed in mammals. For instance, Rakic (1995) proposes that the expansion of the neocortex in different lineages could be accounted for in development simply by prolonging the stage of horizontal proliferation of precursor cells in the ventricular zone. Although there is still some debate over how cortical fields differentiate in development (e.g. Rakic 1988; O'Leary 1989; Molnar & Blakemore 1991, 1995; Schlagger & O'Leary 1991; Levitt 1995), such changes in the timing of events, and the evolution of new receptor types, are likely candidates to explain the accompanying changes in organization that are coupled to the expansion of the cerebral cortex.

6. HOW DO SUCH CHANGES CONFER INCREASED PROCESSING CAPACITY?

This is the hard question. Although I have outlined changes in different mammalian lineages over time, I have not discussed how such changes result in changes in behaviour, or how these changes increase the animal's capacity to process information.

We know that brains have increased in size and in the number of fields present. We also know that connections between homologous fields, or nodes in a processing network, are often retained. With the addition of new fields, new connections appear and old connections are likely to be re-weighted (figure 15). For instance, in the somatosensory system, comparative studies indicate that a simple processing network was likely to be present in early mammals (figure 15). Since then, a number of major radiations have occurred, and at some point in different lineages, new fields were added, and the retained network was modified. There is evidence for the addition of a few new thalamic nuclei (such as PO) in some lineages (figure 15), and for the addition of one or two fields (such as area 1); these additions could confer a large increase in processing capacity simply by increasing the number of nodes that potentially could be interconnected (Herrick 1926). Observations in animals such as primates suggest that this network has been further elaborated with the addition of more cortical fields and thalamic nuclei (figure 15). Although simplified, this theory of evolutionary change can explain the presence of homologous circuits, as well as the remarkable changes in sensory processing abilities and behaviours that occur with modifications to existing circuits. Whereas one might argue that the human neocortex is extremely different from that of the platypus neocortex, I would argue that the difference in the modifications made to the brain is quantitative, and that the construction principles for both brains are relatively simple.

What studies in monotremes and other mammals with simply organized brains demonstrate is that simple networks were likely to be the forerunners of more

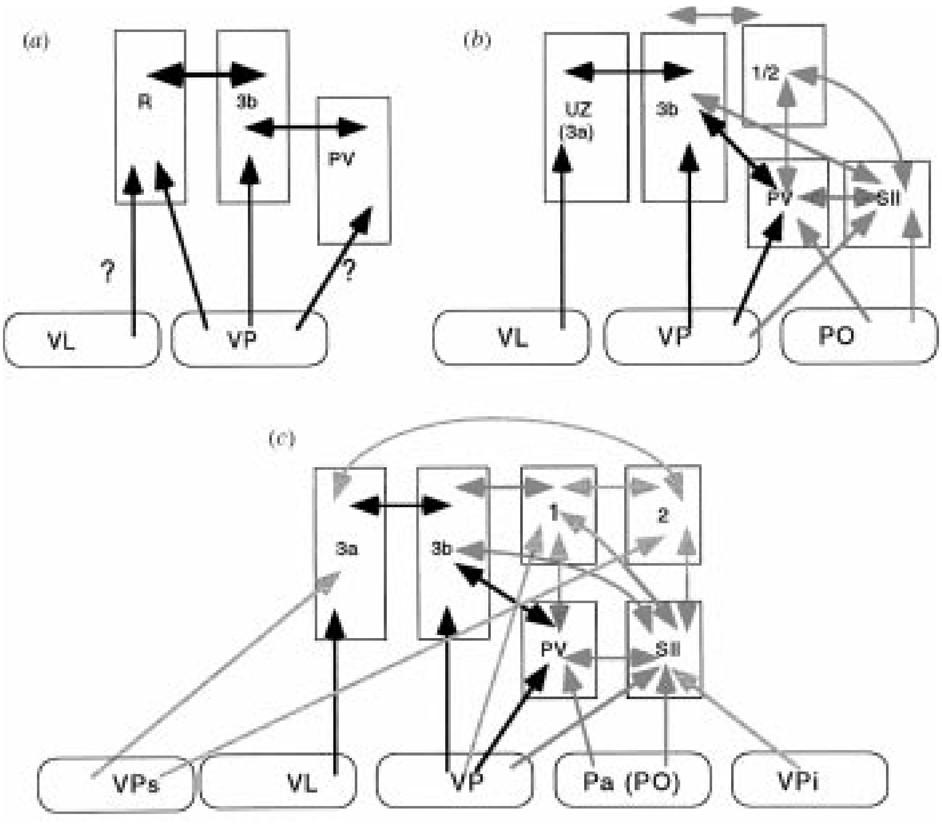

Figure 15. A diagram of how new circuits evolve in different lineages. (*a*) Representation of a circuit that early mammals with few cortical fields may have possessed. In some lineages, such as eutherians (*b*), new cortical fields were added. Although the network that early mammals had is retained, the addition of new fields would obviously re-weight this more primitive circuit. Thus, a homologous cortical field, like SI or area 3b, would not have an identical function, simply because its inputs and outputs have changed. (*c*) An elaboration of the somatosensory system in which certain fields were added in the lineages leading to primate. Although much more complicated, only a few cortical fields and a few thalamic nuclei have been added. Yet, these changes can confer a large increase in processing ability. Arrows of the same colour indicate retained neural circuits.

complex networks, and that the latter did not arise spontaneously in evolution, but are the result of both old, retained features, and newer, more specialized features. These changes are likely to be due to the modification of a few developmental events. If heritable, these changes are ultimately under genetic control.

Regardless of what the mechanisms of evolutionary change are, or even the abruptness with which these changes occur, the fact that there are clear differences in the size and organization of the neocortex in different mammals has important implications for current theories of cortical processing in general. The field of neuroscience is overrun with diagrams, my own included, demonstrating the hierarchical relationship of some cortical fields to others, the direction of information flow and the modulation or feedback of incoming sensory information to lower processing levels. Although such diagrams are useful, I believe that they can also be misleading, as they imply that understanding the neural circuitry in one particular group of animals (e.g. Old World monkeys) allows one to directly extrapolate the condition of another type of animal (e.g. humans). Given what we know about brain evolution, particularly that cortical fields are not added sequentially, and that their emergence is related to significant changes in connections which re-weights the existing circuits, direct extrapolation across species is simply not possible, unless one assumes that the nervous system is static over time. This is obviously not the case. An appreciation of how complex circuits evolve, and the types of structural and functional changes that are imposed on existing circuits, allows us to appreciate, to some extent, how these circuits work.

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