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"The Organization of Neocortex in Mammals: Implications for Theories of Brain Function"

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THE ORGANIZATION OF NEOCORTEX IN MAMMALS: Implications for Theories of Brain Function

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INTRODUCTION

Over the last several years, microelectrode mapping procedures and highly sensitive methods of revealing anatomical connections, used in conjunction with classical cell and fiber stains and new histochemical protocols for studying cortical architecture, have led to new insights on cortical organization and major revisions of longstanding viewpoints. These revised concepts

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are outlined here because they can limit and direct theories of brain function. This review is concerned with how cortex is divided into areas or fields, how areas are subdivided into processing modules, how areas are interconnected, how cortical organization develops and is maintained, and how species differ and are similar. We start with the premise that newer procedures have led to an improved understanding of cortical organization.

TRADITIONAL ARCHITECTONIC THEORIES OF CORTICAL ORGANIZATION

Until recently, the main way of subdividing cortex was by architectonic differences. Before and since the extensive reports of Brodmann (1909), many investigators have described regional differences in cortical architecture, and have used such descriptions to subdivide cortex and develop theories of cortical organization (for review, see Kemper & Galaburda 1984). Such investigators have not agreed on how cortex is subdivided, on homologies and differences across species, or even on whether cortical fields are sharply defined or gradually change from one to the other. Largely because of such disagreements, the architectonic method has been subjected to major criticism (e.g. Lashley & Clark 1946). Yet, the comprehensive proposals that have been produced by architectonic studies have continued to influence how we think about cortical organization.

The problem of identifying cortical fields has been a major one in traditional architectonic studies for several reasons. First, for any complex mammal with a large brain, there is the general supposition, not agreed upon by all, that there must be a large number of subdivisions. Yet, the cell and fiber stains reveal only a few obvious subdivisions and most proposed borders and areas have been based on such subtle differences that there is little agreement among investigators. In fact, many researchers have concluded that large expanses of cortex are basically uniform in structure, even though they have been subdivided in various ways in architectonic studies. Another difficulty in architectonic studies is that observed differences usually had uncertain significance. The "clear border" of one investigator could be attributed to random variation, variation within a field, or distortions produced by sulci by another investigator. A third difficulty is that species differ profoundly, not only in amount of cortex, but in the relative differentiation of cortex.

An appreciation of the magnitude of the difficulty of recognizing the same field across species by architectonic criteria alone can be realized by comparing the cytoarchitecture of the primary and secondary visual areas (V-I or area 17 and V-II or area 18) in a hedgehog, which has a small brain and poorly differentiated cortex, and a tree shrew, which has a somewhat larger brain and obviously greater cortical differentiation (Figure 1). The point of using area 17 as an example is that it is perhaps the most distinctive and easily recognized of neocortical fields, and yet species differences are so great that it is not immediately apparent that the fields designated as area 17 are homologous (the same field). In fact, area 17 was completely misidentified in some early comparative studies (e.g. Mott 1907), and even Brodmann (1909) mistook the less-developed monocular portion of striate cortex as another field (area 18) in some mammals. Several recent investigators have been so impressed with the species differences in cortical structure that they have disagreed with Brodmann's (1909) contention that area 17 is present in hedgehogs, and have concluded instead that hedgehogs have no primary visual or other primary fields (von Bonin & Bailey 1961; Sanides 1972). We now know from other

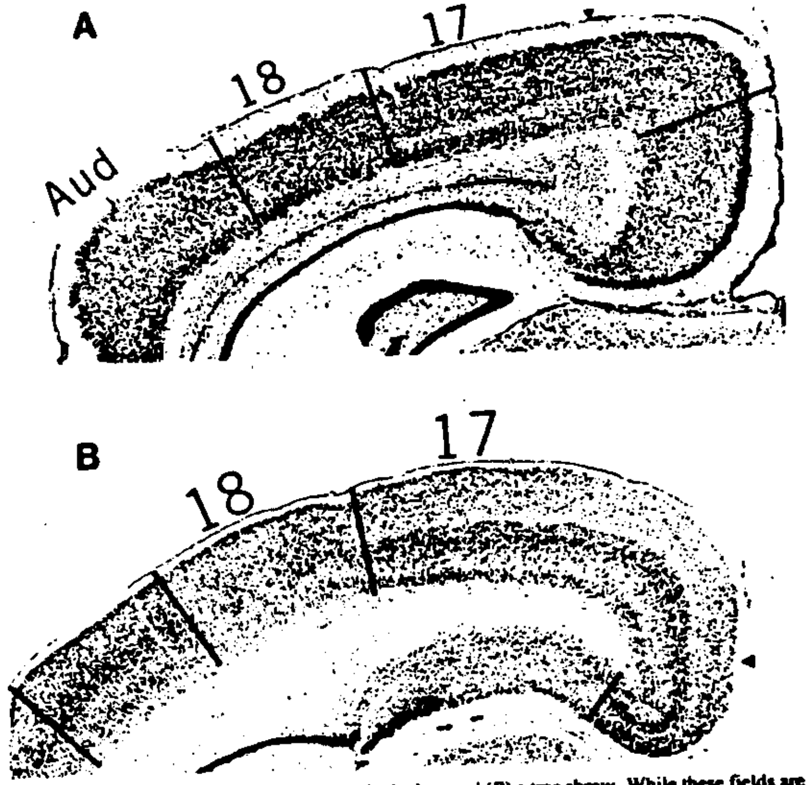

Figure 1. Cortical areas 17 and 18 in (*A*) a hedgehog and (*B*) a tree shrew. While these fields are clearly homologous in these two mammals, they differ considerably in appearance. Lines mark borders, while a small triangle indicates the junction of binocular and monocular portions of area 17. A standard Nissl preparation for cell bodies. Frontal brain sections with medial to the right.

types of evidence (see Kaas et al 1970) that Brodmann correctly identified area 17 in hedgehogs, but the nature of the difficulty is clear: species differences in cortical structure are so great that homologies can be difficult to recognize even for the most distinctive of fields.

In brief, the traditional proposals of cortical organization, based on architecture, have been unreliable because regional differences in cortical structure are often unimpressive, species differences in cortical differentiation are considerable, and, above all else, there has been little attempt to evaluate the significance of the variation that exists.

DEFINING FIELDS BY MULTIPLE CRITERIA

Brodmann (1909) viewed cortical areas as "organs" of the brain, and this is the way areas are usually considered. Each area, as an "organ" of the brain with a unique function or set of functions, should differ from other areas in a number of ways related to its functional role. The list of potentially useful differences is not necessarily limited, but only a few can be easily revealed by current techniques (for a review of methods of revealing subdivisions, see Kaas 1982).

The early architectonists had stains for cells and fibers. They correctly assumed that functionally distinct fields should have morphological differences, but clearly many fields are not obvious in traditional preparations. Fortunately, traditional stains are now being supplemented with techniques for revealing distributions of cellular enzymes, evoked and resting metabolic levels, and neurotransmitters (Figures 2 and 3; also see Livingstone & Hubel 1984; Tootell et al 1985). In addition, new recipes have greatly improved the usefulness of fiber stains (e.g. Maunsell & Van Essen 1983; Krubitzer et al 1986).

Functionally distinct subdivisions of cortex often contain a systematic representation or map of a sensory surface or a motor map of body movements. Such a map is fairly compelling evidence for a cortical area. Early studies with surface recordings and stimulations resulted in much progress, but these procedures were not accurate enough to reveal important details about where the pattern contained in one map ended and where a new pattern began. Microelectrode mapping methods allow representations to be revealed in great detail, and with considerable accuracy, and large portions of cortex have been found to be devoted to sensory and motor maps (Figure 6). A difficulty is that "higher" sensory and motor areas may be relatively unresponsive under many typical recording and stimulation conditions, and that maps with complex organization may be difficult to discern.

The uniqueness of cortical areas should also be reflected in connections.

Figure 2. Area 18 and adjoining cortex in a squirrel monkey. The cortex has been separated from the brain, unfolded, flattened, cut parallel to the surface, and reacted for cytochrome oxidase (an enzyme related to levels of neural activity). The plane of section passes from layer IV to layer III in area 17 more caudally (upper figure) and laterally along 17/18 border (right in figure). Note that the 17/18 border (open arrows) is "line-sharp," even in layer III. In addition, a sharp border is apparent over much of the rostral extent of area 18. Area 18 is characterized by alternating light and dark bands, and thus clearly has subunits. Four of the dark bands are marked by thick arrows, which also indicate the rostral border of area 18. Thin arrows mark three of the dense cytochrome oxidase puffs that are distributed in layer III of area 17. The photomicrograph was kindly supplied by L. A. Krubitzer.

nections. Each cortical area should have a systematic pattern of connections with a number of other areas. Once the validity of an area has been established, its connections can reveal the locations and internal topography of other areas.

Other methods of indicating areas are potentially useful, but have not been widely applied. Thus, areas can be distinguished by overall differences in the responses of neurons to sensory stimuli, but such recordings have been used more often to help establish the validity of an area rather than to help discover areas. Likewise, ablation-behavior studies can help demonstrate the functional role of a proposed area, and thus help establish its validity, but ablation studies have not often uncovered the presence of previously unknown fields.

Each experimental approach has its value, but each is also subject to its own problems of interpretation. It follows that errors in identifying cortical

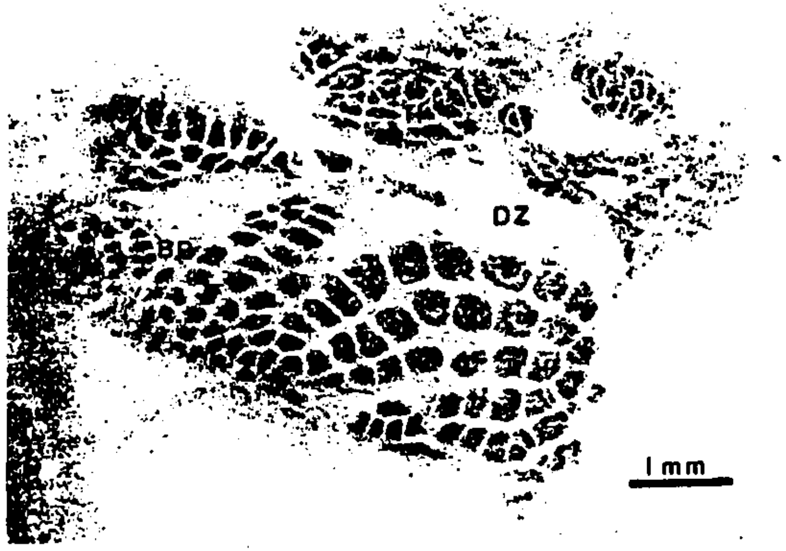

Figure 3. The architecture of primary somatosensory cortex in the rat. The brain section was cut parallel to the surface of an artificially flattened brain and stained for the enzyme, succinic dehydrogenase. Dense clusters of staining reveal the pattern of dense thalamic inputs. The pattern indicated that S-I is sharply defined and has a precise somatotopic organization. Labels indicate where in S-I various body parts are represented: H = "hand"; F = foot; T = trunk; a-1 = rows of mystacial vibrissae from dorsal to ventral on the face; BP = bucal pad; LL = lower lip; DZ = dysgranular zone. The photomicrograph was kindly supplied by H. P. Killackey and D. R. Dawson. See Kaas 1983 for references on S-I organization in rats.

areas are best avoided by using multiple criteria. It has long been held that potential neurotransmitters are presumptive until a list of defining criteria are met. The evidence for proposed cortical areas varies from weak to very strong, and it must be admitted that most proposed fields in complex brains are now only presumptive. However, much progress has been made, specific proposals have been made for further testing, and the methods are available for rapid progress.

The newer methods have led to a number of conclusions, but one seems particularly relevant for discussion of cortical organization. Theories of cortical organization based solely on the study of architecture have not been supported by the results of newer methods, with the significant and important exceptions of the proper identification of a few fields in some species by some investigators. But even judgments that proved to be correct for some investigators for some species have been confounded by different opinions of other investigators and even by the same investigator in other species. For example, it appears that the proposed somatosensory fields 3a, 3b, 1, and 2 of

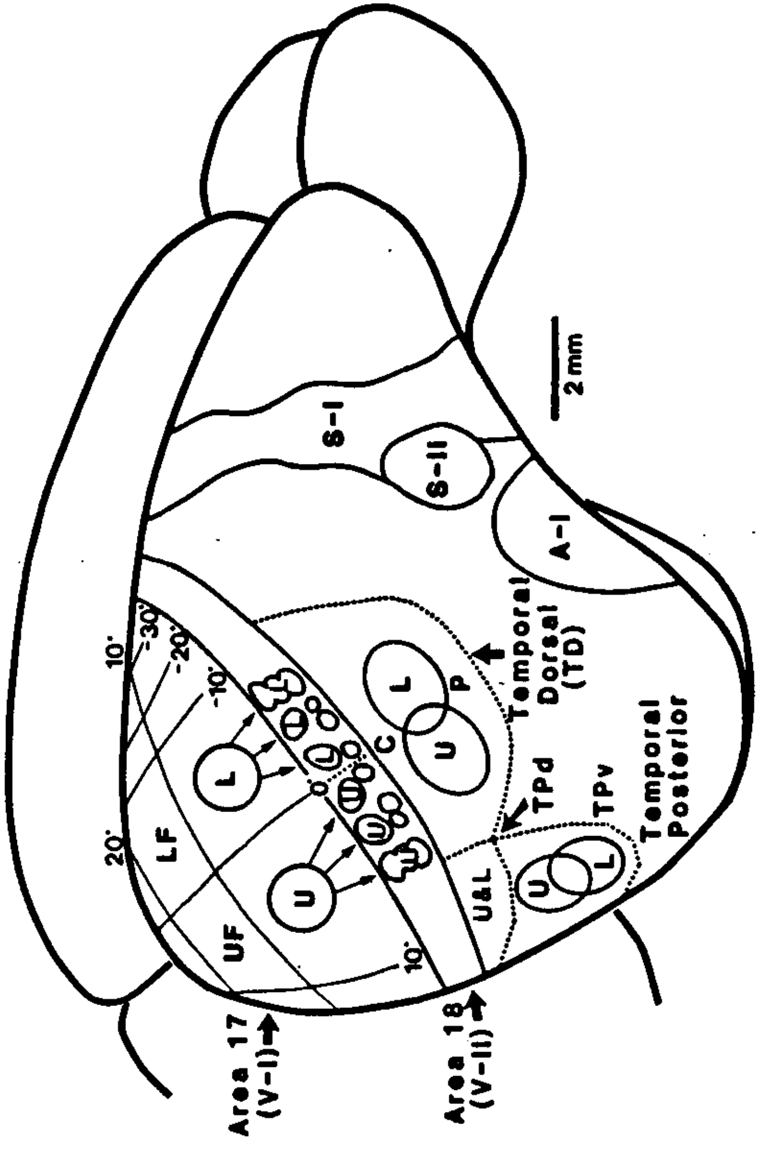

Figure 4. Projections from primary visual cortex, V-I or area 17, to secondary visual cortex, V-II or area 18, and regions of temporal cortex in a tree shrew as revealed by injections of an anatomical tracer (circles with arrows). Each location in area 17 produces several distinct bands of terminations in area 18, providing evidence for separate processing "modules." Similar uneven distributions of projections from area 17 to area 18 are found in other mammals. A dorsolateral view of the brain with visual field coordinates indicated in area 17. Ovals indicate projection zones from the upper field (U) and lower field (L) injections. Primary auditory (A-I) and primary (S-I) and secondary (S-II) somatosensory fields are indicated. From Sesma et al (1984).

Brodmann (1909) and Vogt & Vogt (1919) actually do correspond to functionally distinct areas in macaque monkeys (see Kaas 1983), but these areas have been illustrated as fairly different in extent and exact location in macaque monkeys by other investigators, and they have been combined and misidentified in other monkeys and other primates by Brodmann and other investigators. In non-primates, these architectonic terms have been applied in a number of different ways that do not correspond to the way they are used in macaque monkeys.

CURRENT CONCEPTS OF CORTICAL ORGANIZATION

Evidence has rapidly accumulated to support a number of conclusions about cortical organization. Each of these conclusions has implications for theories of cortical functions.

Cortical Areas Are Sharply Defined

Whether cortical localization is precise or not has been a classical issue of debate. Eliot Smith (1907) concluded that at least 50 fields in the human brain had "exact boundaries," von Economo & Koskinas (1925) extended this list to 107 fields, while von Bonin and coworkers (e.g. von Bonin & Bailey 1961) have emphasized the view that there are fewer fields and that the fields gradually change from one to another. Brodmann (1909) believed in both absolute and relative localization; that is in fields with sharp boundaries and in fields that gradually change to the next. The issue is not completely resolved, but recent evidence that many borders are sharp supports the conclusion that boundaries in general are sharp so that one field changes to the next within 100 μm or so. The evidence comes from microelectrode recordings, reconsiderations of cortical architectonics, and from studies of connections. An example is the second visual area, V-II, or "area 18," which in tissue sections with standard stains for cell bodies is clearly different and sharply separated from primary visual cortex, V-I or area 17, but is often indistinctly separated from other adjoining fields at its rostral boundary. Thus, Brodmann (1909) failed to correctly identify the rostral border of area 18 in Old World monkeys, and included cortex within "area 18" that we now know is occupied by other fields. As can be seen in Figure 2, current histochemical stains indicate that both the caudal and rostral borders of area 18 are sharply defined. Similar conclusions would stem from studies of patterns of retinotopic organization, neural properties, or connections. As an example of an elegant demonstration of the existence of sharp boundaries using microelectrode recordings, Rasmusson et al (1979) recorded from sequences of neurons in microelectrode penetrations passing parallel to the cortical surface and perpendicular to the border between primary somatosensory cortex and the adjoining rostral field "3a," in cats (see Figure 6 for the location of these fields). In each electrode penetration, the response properties of neurons changed sharply and completely from those activated by noncutaneous receptors (muscle spindles) in area 3a to cutaneous receptors in S-I.

Historically, it has been common to acknowledge sharp borders between fields in advanced species, while suggesting a lack of such borders in primitive species. There is no compelling evidence to support this viewpoint. Borders seem to be just as sharp in the cortex of the hedgehog (Kaas et al 1970) as in advanced primates and carnivores. Certainly anyone who has seen a properly prepared "surface view" tangential section through somatosensory cortex of a rat (Figure 3) will agree that S-I is sharply defined in these rodents.

The evidence for sharp boundaries has accumulated rapidly, while there is no clear evidence for gradual borders between areas. Thus, the conclusion seems warranted that functional boundaries are usually and perhaps always sharp.

Cortical Areas Are Functionally Heterogeneous

Mountcastle (1978) is known for stressing that cortical areas are subdivided into mosaics of functionally distinct "columns" or processing modules. While areas may not contain groups of cells with all of the features of columns as outlined by Mountcastle (1978), a number of cortical areas have now been shown to be heterogeneous in structure and function, and it seems reasonable to postulate from this sample of fields that areas in general are heterogeneous. The best example of a field with clear subdivisions is primary visual cortex of macaque monkeys where occular dominance bands, orientation bands, and cytochrome oxidase dense "puffs" (Figure 2) of neurons that are non-selective for orientation have been demonstrated as subunits (see Livingstone & Hubel 1984). Evidence is also accumulating for subunits within area 18 or V-II. The uneven pattern of projections from V-I to V-II that is found in most mammals is shown in Figure 4. A given location in V-I projects to several locations in V-II, and two nearby locations in V-I project to locations in V-II that are partially separate and partially interdigitated. These observations argue that given locations in V-I send the same information to several spatially separate modules in V-II. The internal organization of V-II is better understood in monkeys, where "thick bands," "thin bands," and "interbands" crossing the width of the field in cytochrome oxidase (Figure 2; also see Livingstone & Hubel 1984; Tootell et al 1985) and fiber stain preparations have been related to neurons and connections mediating different functions (see Hubel & Livingstone 1985). As a third example, primary somatosensory cortex of monkeys (area 3b, see Kaas 1983) is divided into alternating and irregularly shaped strips of neurons that respond in a rapidly adapting (RA) or slowly

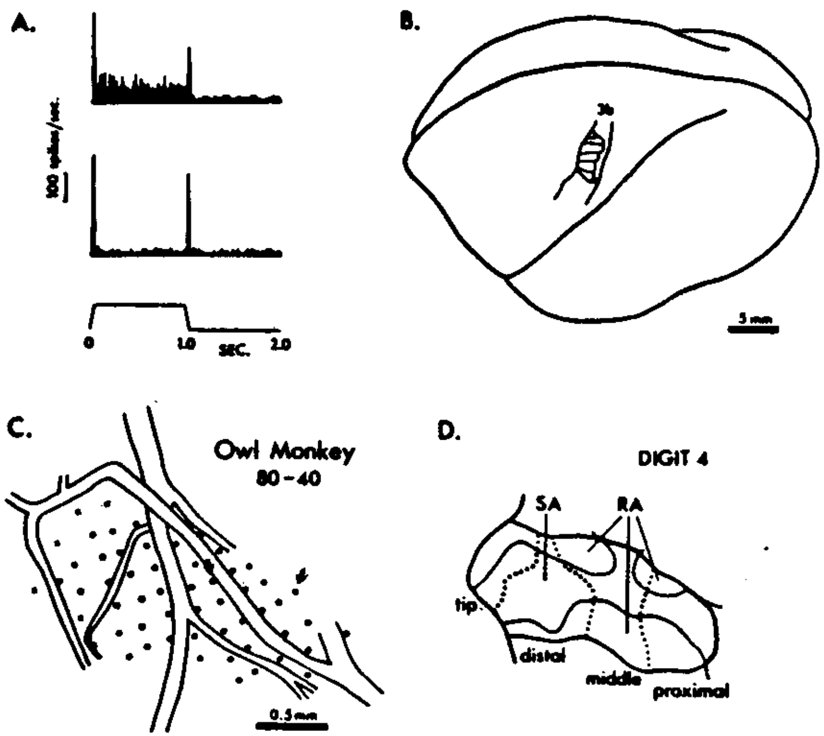

Figure 5. The spatial distribution of neurons that adapt slowly (SA) or rapidly (RA) to maintained skin indentation in primary somatosensory cortex (area 3b) of an owl monkey. The bandlike regions, which are shown only for the representation of a finger, were determined by multiple recordings with microelectrodes. The distinctly separate regions were only apparent in middle layers of cortex. *A.* Peristimulus time histograms of a slowly adapting *(top)* and rapidly adapting *(bottom)* neuron. Trace shows waveform of the skin indentation probe. *B.* The region of the hand representation in area 3b on a dorsolateral view of the brain. *C.* An enlarged view of cortex representing filled circles mark penetrations outside the field. *D.* An enlarged view of the representation of digit 4 with the RA and SA regions. The results support the notion of modular organization in somatosensory cortex. From Sur et al 1981a; also see Sur et al 1984.

adapting (SA) manner to maintained pressure on the skin (Figure 5; Sur et al 1981a, 1984).

Species Vary in Number of Areas

Brodmann (1909) and most other investigators have long contended that mammals with large complex brains, especially humans, have more cortical areas than mammals with small primitive brains, but without compelling evidence it was still possible to argue, as Lashley did, that mammals have few fields, on the order of 10 or so, and that there was no reason to suppose that the number differed in rats and humans (e.g. Lashley & Clark 1946). Figure 6 illustrates current theories of how cortex is divided into areas in hedgehogs, squirrels, cats, and New World monkeys. Some of the fields are well supported, others are tentative, and revisions and additions will undoubtedly occur. Yet, the evidence for enough of the fields is so solid that there is no escaping the conclusion that species differ in numbers of areas. Furthermore, as Brodmann (1909) and Eliot Smith (1907) proposed, advanced mammals have more fields.

All Mammals Have Some Fields in Common

One major conclusion stemming from modern evidence on cortical organization is that a few basic areas of cortex are present in most or all mammals. Hedgehogs, with cortex that is probably not much different from that of the first Eutherian mammals, have primary and secondary visual fields (areas 17 or V-I and 18 or V-II), primary and secondary somatosensory fields (S-I and S-II), a motor field (M-I), a primary auditory (A-I) and perhaps one or two other auditory fields, probably taste cortex, prefrontal cortex related to the mediodorsal nucleus of the thalamus, several subdivisions of limbic cortex related to the anterior and lateral dorsal nuclei of the thalamus, a small region of temporal cortex that is probably visual with input from area 17, and a perirhinal strip of transitional cortex that probably relates other neocortical fields with the amygdala and the hippocampus (see Kaas 1982). These same fields have been identified in a wide range of placental mammals (Figure 6), and they can be considered basic to Eutherian mammals, evolving early in the divergence of mammals and retained in most or all subsequent lines of divergence.

Studies on opossums and other marsupials indicate that these same fields, with the exception of motor cortex, are part of the basic plan of the Metatherian radiation as well. Opossums apparently do not have a primary motor field (M-I), but instead the motor functions of primary somatosensory cortex (S-I) are emphasized (Lende 1963). S-I receives both somatosensory information from the ventroposterior thalamus and cerebellar information, normally projected to motor cortex, from the ventroanterior thalamus (Killackey & Ebner 1973). Much less is known about cortical organization in monotremes, but available evidence (Lende 1964) suggests that they have at least primary visual, auditory, and somatosensory areas, and, as in marsupials, no primary motor field. Hence, a few fields appear to be common to all mammals and undoubtedly were present in reptilian ancestors.

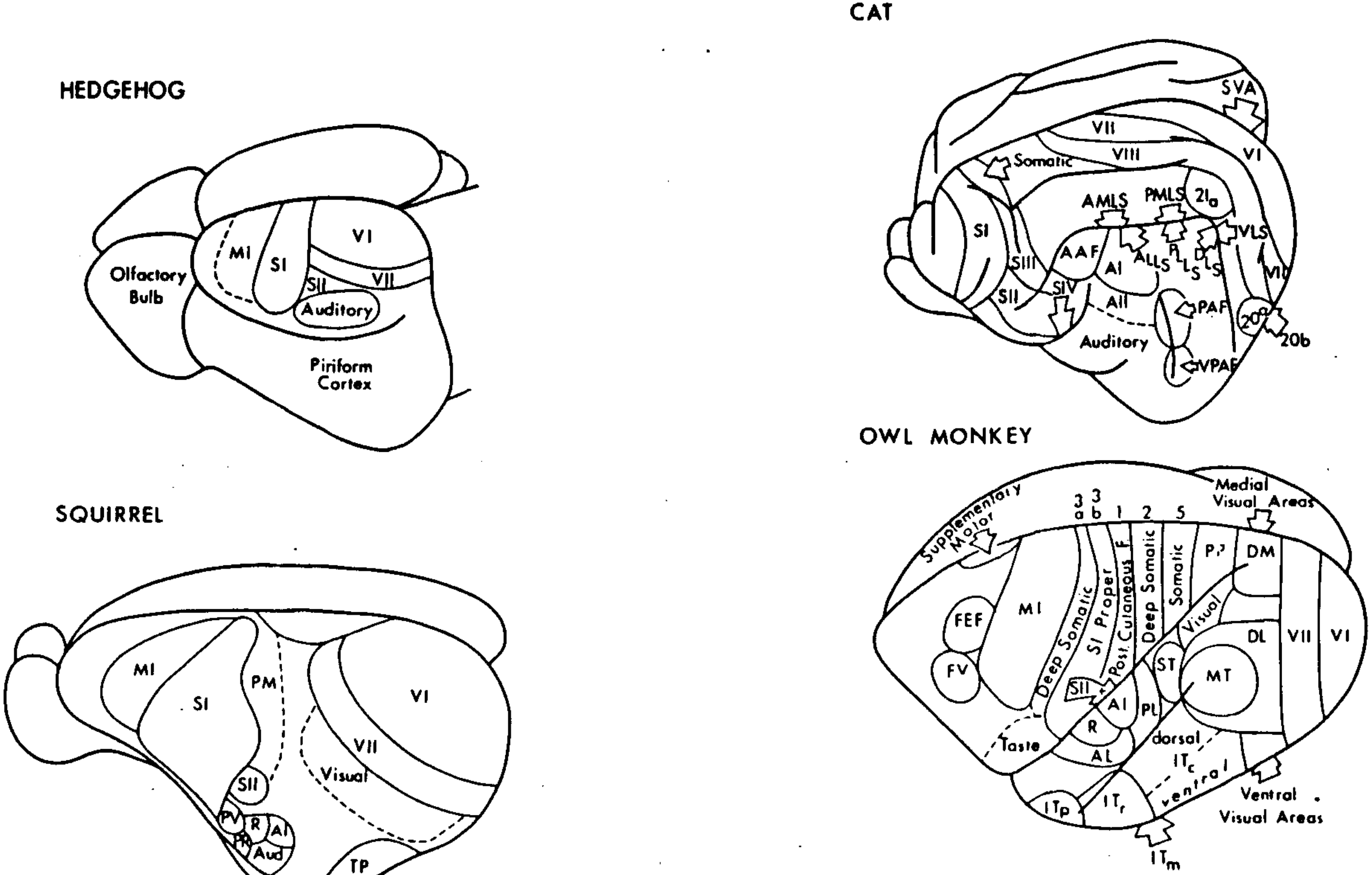

Figure 6. Subdivisions of cortex in a primitive mammal (hedgehog), a mammal with a somewhat advanced brain (squirrel), and two mammals with moderately advanced brains (cat and owl monkey). The primary motor (M-I), primary and secondary somatic (S-I and S-II), and primary and secondary visual areas (V-I and V-II) are present in all. Other fields have been named by location (e.g. anterior auditory field, AAF; middle temporal area, MT) or related to a traditional architectonic field of Brodmann (1909) by various authors (for details and additional references, see Kaas 1982; Krubitzer et al 1986).

Major Advances in Brain Evolution Have Been Marked by Increases in Numbers of Unimodal Sensory Areas

Of the mammals with relatively advanced brains, only monkeys and cats have been studied to an extent where reasonable comparisons can be made. The primate and carnivore lines diverged at a time when brain development was probably not much different from that now found in the hedgehogs, and both of these lines have the basic areas found in hedgehogs. However, both lines have additional somatosensory, visual, and auditory areas. Both cats and monkeys have more than 10 visual areas, and perhaps as many as 15–20. Cats have at least five and monkeys at least eight somatosensory areas, and both lines have on the order of five or more auditory fields. All of the above fields are dominated by one modality and most exclusively code inputs of only one modality. Generalizing from cats and monkeys, it appears that evolutionary advance in brain organization is marked by increases in the numbers of unimodal sensory fields, not by increases in multimodal association cortex, as traditionally thought. Of course, it should be stressed that the lines leading to cats and monkeys, and almost certainly those leading to other advanced brains, independently increased the number of sensory areas, and therefore most sensory fields in these different lines are not homologous.

Areas Are Multiply Interconnected; Connections Are Species-Variable

Some of the demonstrated connections of visual cortex of owl monkeys are shown in Figure 7. Typically, each field is interconnected with 3–6 other fields in the same hemisphere. In addition, each field connects callosally with its counterpart and 1–3 other fields in the opposite hemisphere. Finally, subcortical connections with subdivisions of the pulvinar complex, the lateral geniculate nucleus, the claustrum, the basal ganglia, the superior colliculus, and pontine nuclei add to the complexity of the wiring diagram (see Weller & Kaas 1981; Kaas & Huerta 1987). Thus, neurons in any field are subject to a multitude of influences from other fields. Somatosensory, auditory, and motor areas have connection patterns that are similarly complex, and such complexity is seen across species. It follows that even simple stimuli delivered to a receptor surface would, in advanced mammals, activate an array of interacting locations in the multitude of cortical areas and subcortical nuclei related to that modality. Thus, processing is distributed across a large expanse of the forebrain.

Of course, not all pathways shown in Figure 7 are equivalent. They differ in magnitude and type. The so-called "feedforward" connections terminate most densely on the middle (receiving) layers of cortex, IV and inner III, which contain the stellate neurons that initiate the processing in an area. Connections that terminate in the upper and lower layers largely relate to the

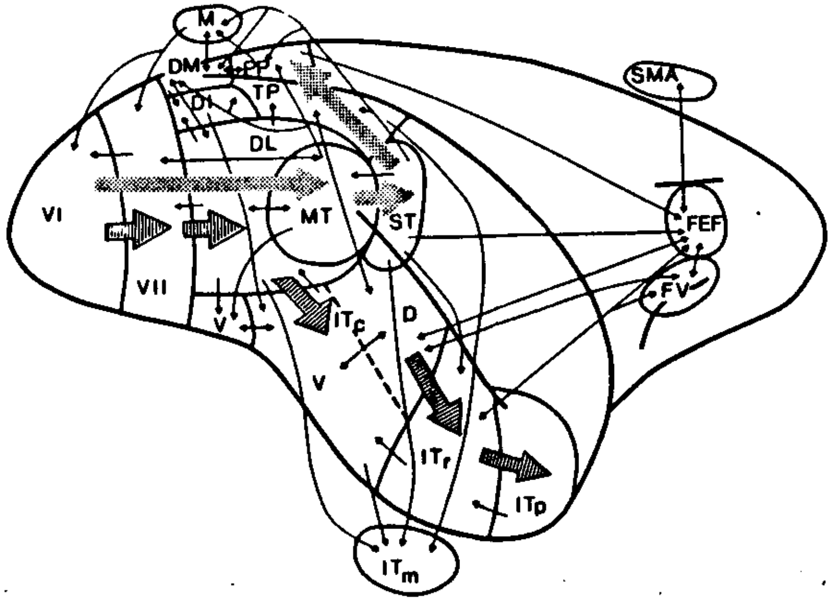

Figure 7. Some of the interconnections of visual cortex in owl monkeys. Major visual processing sequences are indicated by the thick arrows. Thin arrows indicate other connections. V-I and V-II, primary and secondary fields; FEF and SMA are the frontal eye field, and the eye movement portion of the supplementary motor area. FV is a frontal visual area of uncertain significance. Other visual areas are named by location (e.g. dorsolateral, DL; dorsomedial, DM; dorsointermediate, DI) or by location in a lobe (e.g. IT_C, caudal area of the inferior temporal lobe). See Weller & Kaas (1986) for details. Note that each area is interconnected with several other visual areas. Major processing sequences are directed toward the temporal lobe for object vision (thick hatched arrows) and posterior parietal cortex (thick stippled arrows) for visual attention (see Ungerleider & Mishkin 1982; Kaas 1986).

dendrites of pyramidal cells that project to other structures. These "feedback" connections appear to modulate the outflow of information after much of the local processing has occurred (see Maunsell & Van Essen 1983; Weller & Kaas 1981 for review). Pathways also differ in effectiveness. For example, the neurons in the central nucleus of the inferior pulvinar with visual inputs from striate cortex and the superior colliculus, depend on the striate cortex and not the superior colliculus for activation (Bender 1983).

By considering only the major feedforward projections that presumably provide most of the activation, it is possible to construct the dominant processing streams or hierarchies. Thus, in the visual cortex of owl monkeys, there is a stream from striate cortex to the inferior temporal lobe that appears to mediate form vision, and a stream to the posterior parietal cortex that is important in visual attention (Weller & Kaas 1986; Kaas 1986; see Ungerleider & Mishkin 1982 for "two cortical visual systems"). While the processing hierarchies, such as those in Figure 7, are tempting frameworks for theories of cortical processing, the true complexity of the system should be remembered. Processing has both parallel and hierarchical components, but "later" stations receive inputs from both "intermediate" and "early" stations, confounding simple hierarchical schemes.

It is also important to recognize that species can differ considerably in connections. Both areas 17 and 18 receive major inputs from the lateral geniculate nucleus in cats, for example, while these projections are almost exclusively to area 17 in monkeys. There is also some evidence that a type of "corticalization of function" occurs so that higher stations tend to acquire more direct sensory inputs as an advance in evolution. In anterior parietal cortex of monkeys, information is relayed from the ventroposterior nucleus to area 3b (S-I), from area 3b to area 1, and from area 1 to area 2 (see Kaas 1983). Thus, areas 3b, 1, and 2 can be considered a processing hierarchy. In both New and Old World monkeys, some projections from the ventroposterior nucleus also terminate directly in area 1 of monkeys, but no such projections have been found in prosimians. In Old World monkeys, there is an additional projection from the ventroposterior nucleus to the part of area 2 that represents the hand (Pons & Kaas 1985). Such observations suggest that behavioral advances sometimes are achieved by rerouting relatively unprocessed information to higher stations, rather than completely depending on cortical processing sequences. In some systems this may be more important than others. For example, most of the auditory areas in the cortex of cats receive direct thalamic auditory information in addition to cortically relayed information (see Merzenich & Kaas 1980).

Detailed Organization Is Dynamically Maintained

The excitatory receptive fields of cortical neurons reflect only a portion of their total inputs. Maps of receptor surfaces in cortex can have organization that supercedes that of the anatomical distribution of inputs. Retinotopic organization clearly exists within the overlapping distributions of the terminal arbors of single geniculostriate axons (Blasdel & Lund 1983), and somatotopic organization is found within the distance covered by the arbors of ventroposterior axons that terminate in area 3b (Pons et al 1982). Thus, the axons drive neurons only within a portion of their arbors. In this sense, connections are superabundant, and superabundant connections occur at all levels in sensory systems. Obviously, neurons somehow select inputs from a menu of possibilities. The selection may be based on intrinsic mechanisms that tend to preserve a fairly constant level of synaptic activation, and a favoring of synapses that are active during the firing of the postsynaptic cell, and thereby temporally correlated with the activity of other synapses (see Constantine-Paton 1982 for review).

When the sources of activation for cortical neurons are altered, they rapidly acquire new sources of activation. One way of altering input has been to section a nerve to the skin of part of the hand or some other region (see Kaas et al 1983; Wall & Kaas 1985 for review). Neurons in somatosensory cortex formerly with receptive fields exclusively within the denervated skin rapidly recover new receptive fields in adjoining innervated skin. At first, the new receptive fields are abnormally large, but over weeks they reduce in size to that appropriate for the region of cortex, rather than for the normal representation of the skin field. These results suggest that cortex is constantly in a state of flux, and stability results from a balance of competing factors.

Self-Organization Occurs During Development

As the adult nervous system is characterized by neurons that select a portion of potential inputs from a menu of inputs from widespread axon terminal arbors, an analogous but more extensive selection process takes place during development. Neurons and neural connections in the developing nervous system are superabundant, and the prevailing view is that neurons are in competition with each other for synaptic space and survival (e.g. Killackey & Chalupa 1986; Rakic et al 1986). It is clear from many experiments that the selection process is related to neural activity, and it appears likely that the co-activation of inputs results in a selective increase in synaptic efficacy and survival (for reviews, see Constantine-Paton 1982, Easter et al 1985; Schmidt & Tieman 1985). Such a process would account for at least four features of cortical fields that systematically represent sensory surfaces.

1. A fundamental feature of cortical maps, their topographic organization, may largely be the outcome of selection for receptor surface neighborhood correlations. Simple, two-dimensional arrangements of receptor sheets, such as the cochlea or hemiretina, can be represented in simple topographic maps, having distortions but no splits. However, even representation of the hemiretina can be "split" along the representation of the horizontal meridian in such fields as V-II and DL (Figure 6), apparently due to constraints imposed by form and a long matched border at the representation of the zero vertical meridian. The more complex receptor surface of the contralateral body surface cannot be represented in a cortical sheet without "folds" and "splits." Folds occur when skin regions that are not normally next to each other are represented by adjacent blocks of neurons in cortex. For example, the thumb is commonly represented next to the lower lip in S-I (Kaas 1983). Splits occur when two or more parts of a continuous skin surface are represented in separate cortical locations within a field. As dramatic examples, the upper back is separated from the lower back by the representation of the wing in S-I

of bats (Calford et al 1985), and the upper trunk is separated from the lower trunk by the representation of the hindlimb in tree shrews (Sur et al 1981b). Despite the folds and splits, there is remarkable topography in cortical maps, as if every effort is made to preserve neighborhood relationships. Thus, it is usually possible to trace maze-like lines of continuity throughout cortical maps. For example, there is complete somatotopic continuity along the caudal border of S-I in tree shrews, and other parts of S-I have somatotopic continuity with that border (Sur et al 1981b). It is as if S-I in tree shrews developed from caudal to rostral in cortex with a somatotopic continuity rule that initially could be met due to a large degree of freedom, but soon led to discontinuities based on the constraints of having "used up" some skin surfaces.

The locations of folds and, to a greater extent, splits, are species-variable. Other species variations appear to occur for skin surfaces that are relatively isolated somatotopically in S-I and other fields. For instance, the enlarged representations of the hand and foot in areas 3b of monkeys tend to somatotopically isolate the representation of the trunk from the limbs. Perhaps as a result, the back is represented rostrally in area 3b of some monkeys and caudally in others (Sur et al 1982). The species variability, and the lesser individual variability in the relative locations of parts of receptor surfaces in sensory maps, suggest that details are not genetically specified, but related to other factors, such as the relative sequencing of correlated activity during development.

2. Features related to somatotopic "folds" in cortical maps suggest that a second developmental feature is shaped by activity. Folds result in adjacent groups of neurons with inputs from quite different skin regions, the lower lip and thumb, for example. Apparently, arbors of entering axons select one block of tissue or the other, and avoid a narrow "no-man's land" in between. Thus, the hand-face border in area 3b of monkeys remains stable while the hand representation does not when nerves to the hand are cut (Merzenich et al 1983). Borders between folds are often apparent as narrow, poorly differentiated regions. In the thalamus, such folds are marked by cell-poor zones or laminae that partially separate cell groups in nuclei. Thus, the face, hand, and foot representations are separated in the ventroposterior nucleus (see Kaas et al 1984 for review), and there is a cell-poor zone in the lateral geniculate nucleus separating neurons with inputs from either side of the optic disc of the retina (Kaas et al 1973). In cortex, the "folds" in the map and the resulting narrow zones of poor differentiation (e.g. the dysgranular zones in Figure 3) apparently result in a physically "weaker" zone that favors the development of an actual fold or fissure. Thus, representations of the hand and face, for example, are often separated in cortex by a shallow fissure (e.g. Welker & Campos 1963).

3. In addition, carefully timed selection for correlated activity in development could account for many local features of organization such as the sequencing of orientation-selective neurons in cortical modules in area 17 and MT (see Kaas 1986), the variability in the presence of ocular dominance columns in striate cortex of monkeys and other mammals (see Florence et al 1986), the segregation by sublamina or patches of "on center" and "off center" receptive field classes of inputs in area 17 of some mammals (Norton et al 1983; McConnell & LeVay 1984) and classes of geniculate inputs in area 17 of monkeys (see Kaas 1986), and even the specific response properties of cells throughout cortex. The grouping of neurons with similar response properties within areas is a logical outcome of a selection process based on correlated activity.

4. Typically, cortical maps of receptor surfaces are precisely matched at common borders. Visual fields are commonly matched along representations of the zero vertical or portions of the zero horizontal meridians (see Allman & Kaas 1976; Kaas 1980; Van Essen 1985). The match is so precise that receptive fields overlap for neurons slightly displaced from the border in either direction. Similar matches occur between somatosensory fields and between auditory fields. For example, primary and secondary somatosensory fields are aligned along a common representation of the top of the head (e.g. Krubitzer et al 1986), the adjoining maps of the body surface in steplike areas 3b and 1 of monkeys are somatotopically aligned along their complete borders (see Kaas 1983), and auditory fields in cats and monkeys are matched at borders for representing high or low tones (see Merzenich & Kaas 1980). Such matched borders, because of the exactness of the alignment, have been called "congruent" (Allman & Kaas 1975). Such border alignments have no obvious function. They do allow short interconnections between areas at the border region, but other parts of the fields thereby have longer interconnections. Thus, it seems unlikely that border alignments would develop for functional reasons. However, the alignments would be an obvious outcome of selection for correlated activity.

CONCLUSIONS

Current viewpoints on how cortex is organized can usefully restrict and direct theories of brain function. Some of the conclusions that follow from these viewpoints are listed below.

1. Architectonic methods, when used alone, have not reliably determined functionally valid subdivisions of cortex. Subdivisions identified by architecture alone should be treated as hypothetical, subject to evaluation with other techniques. Studies of patterns of connections, topographic organization, neuron response properties, and the behavioral consequences of lesions have been valuable sources of additional information. Cortical subdivisions can be

most reliably identified by multiple criteria. A common practice in studies of cortex has been to refer to regions studied by architectonic terms, even when the architectonic fields have not been shown to be functionally significant, and even when the investigators fail to demonstrate that they have identified the fields by architecture in the experimental animals. This practice, by implying a state of understanding and accuracy that does not exist (see Lashley & Clark 1946, for further discussion), discourages and hinders further efforts to understand cortical organization. It is better to refer to cortical regions by reference to surface landmarks (e.g. posterior parietal cortex) if that is the actual practice.

2. Cortical areas, as functionally distinct divisions of the brain, frequently and perhaps always, are precisely localized. Therefore, restricted lesions can produce very specific and irreversible changes in behavior. However, because many of the details of internal organization within cortical areas are dynamically maintained, brain lesions are followed by a progression of alterations that may effectively compensate for aspects of the damage (see below).

3. Functional heterogeneity within fields permits parallel processing of information, and one field can function as several. However, more complex processing and the resulting behavioral advances have not been achieved by simply increasing the sizes and internal complexity of cortical areas. Thus it seems likely that no more than a few independent channels or types of processing modules coexist within a field. In addition, evidence for processing modules does not necessarily imply that an area mediates more than one function, since an uneven distribution of neurons with certain properties could relate to a single function. For example, neural mechanisms for discrimination of the orientation of line segments may require the grouping for local interactions of orientation-selective cells with similar preferences.

4. Behavioral advances are commonly dependent on increases in number of fields. This mechanism has been used in a number of lines of evolution. As a result, most areas in advanced mammals of different lines have been independently acquired and are not homologous, but they may function in similar ways and be highly analogous. However, because most fields are not homologous, generalizations across major taxonomic groups should be made with great caution.

5. In primitive to at least moderately advanced mammals, most of cortex is occupied by orderly sensory representations. Thus, sensory processing is the dominant cortical function, and most processing is concerned with a single modality.

6. In advanced mammals, perception is based on the coactivation of a number (5–20 for a single modality) of cortical fields. Even simple attributes of stimuli (such as color, motion, form) are unlikely to be based on processing within a single field. However, each activated area undoubtedly makes a field-specific contribution to the resulting perception

7. Cortical maps function while having a number of different organizations across and even within species. It does not appear that the normal function of a field is seriously limited by the specifics of the internal representation of the receptor surface.

8. The microorganization of cortex is constantly in a state of flux, and stability results from a balance of competing factors. Receptors activate cortical space to an extent that is influenced by competition between inputs and relative use, so that increasing use probably increases cortical space and decreasing use probably decreases cortical space. Such a mechanism could account for the improvements in perceptual and motor skills that occur with practice, and the remarkable recoveries that often follow central nervous system injuries. It also follows that it will be very difficult to study the contribution of specific cortical areas in sensory-perceptual systems by deactivating (ablating) the areas, because reactions to lesions immediately start to alter the synaptic strengths of other connections. A partial solution to this problem may be to determine changes immediately after lesions, but changes can be very rapid.

9. The apparent importance of self-organizing processes in development, based on activity patterns, suggests that some specific features of cortical organization, such as the topographic details of sensory and motor representations, the border alignments of fields, and types of modular grouping of neurons, could be side-products of timing sequences in the building of brains. Thus, specific features of cortical organization may be necessary outcomes of the building process rather than features designed for maximizing function.

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Chapter Fourteen

THE ORGANIZATION AND EVOLUTION OF NEOCORTEX

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INTRODUCTION

This chapter provides a brief overview of some of the major similarities and differences in the organization of neocortex in different lines of mammalian evolution, and discusses how these differences could have evolved. Several longstanding and obvious observations provide a basic framework for further discussion. First, brains are extremely variable, especially the major subdivision, neocortex. Neocortex varies tremendously in size, shape, fissure pattern, and regional proportions (e.g., Fig. 1, also see Ariëns Kappers et al., 1936; Papez, 1929). Second, neocortex is quite variable in histological structure, both from region to region in the same brain and in the same field across species (e.g., Campbell, 1905; Brodmann, 1909; Elliot Smith, 1910). Third, the fossil record and comparative studies indicate that the first mammals had small brains with proportionately little neocortex, and that mammals with large brains and proportionately more neocortex have evolved a number of times in different lines of descent (e.g., Jerison, 1973; Ulinski, 1983; Hofman, 1982). Finally, the evolution of different brains obviously has something to do with the remarkable diversity in the behavioral abilities of mammals. Mammals with small brains and little neocortex are rather limited behaviorally, while mammals with large brains and much neocortex have variable and complex behavior (see Welker, 1976 for review). Hence, the old Greek poem fragment, "The fox has many tricks, the hedgehog only one . . ."

Because brains with more neocortex have evolved a number of times from brains with little neocortex, it is tempting and productive to concentrate on overall proportions and relate these to behavior (e.g., Jerison, 1973). However, the long-noticed variability in fissure patterns and the relative proportions of the major lobes of the brain, as well as the appreciable variability in histological structure of cortex (see Kaas, 1987), indicates

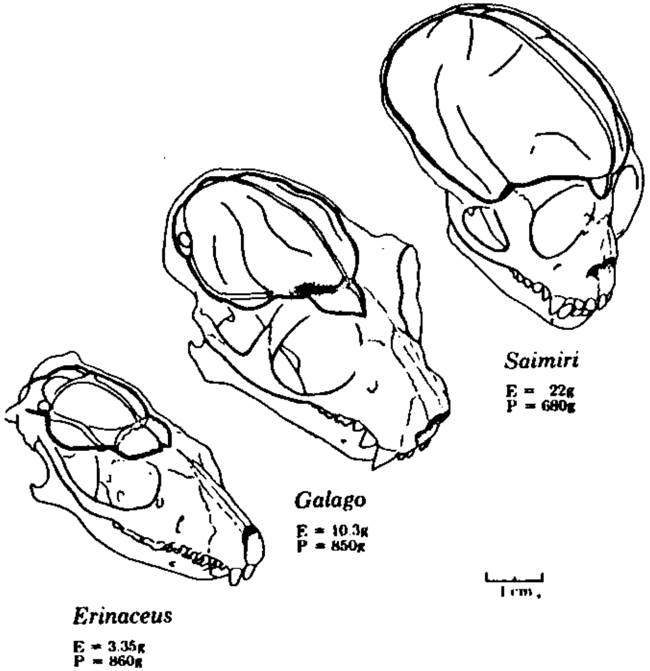

FIGURE 1. An example of how brains vary in size, fissure patterns, and proportions. Outlines of the brains are superimposed on the skulls of a hedgehog (*Erinaceus*), a galago crassicaudatus (*Galago*), and a squirrel monkey (*Saimiri*), representing basal insectivores, prosimian primates, and New World monkeys. All are drawn to the same scale. E = brain weight; P = body weight. Reproduced from Figure 1 of Radinsky (1975).

that there is more to the story. Cortex did not just get bigger, but it clearly changed as well. However, it is less obvious how cortex changed and whether changes were similar or different in various lines of descent. Since investigators have had different opinions on how the forebrain evolved, it is instructive to review concepts of cortical evolution. The early theories were greatly limited by the sparseness of comparative information on cortical organization which was largely obtained from histological studies of normal brains. However, within the last 20 years, major technical advances have permitted investigators to accumulate an impressive amount of detail on the organization of neocortex in at least a few well-studied species. In the following pages, we briefly discuss these methods, review current concepts of cortical organization and hypotheses of cortical organization and construct from comparative studies hypotheses of the progressions of change that occurred in different lines of descent. The mechanisms of change are much less certain, but some possibilities are reviewed.

THEORIES OF CORTICAL EVOLUTION

There are two major themes in the various theories of brain evolution. Most investigators concluded that, as brains advanced and acquired proportionately more neocortex, more subdivisions of functional significance were acquired. Typically, the presumed mechanism of increasing the number of subdivisions was a gradual differentiation over many generations of new from previously existing subdivisions. This is basically the view of the classical architechtonists such as Brodmann (1909), Campbell (1905), and von Economo (1929). Brodmann (1909), for example, illustrated few subdivisions within the neocortex of hedgehogs and other small-brained mammals, and many more subdivisions for advanced mammals such as several carnivores and higher primates. The more complex brains had subdivisions not shown for the simpler brains. For example, hedgehogs were seen as having field "1" of somatic cortex, but not fields "2" and "3" of advanced brains. In addition, some of the single fields in the simpler brains were "combined" from several in more complex brains. For example, fields "1, 2, and 3" of monkeys, apes, and humans were combined in a single "1–3" field in lemurs (also see LeGros Clark, 1931 for a similar viewpoint). The implication is that fields "1–3" differentiated into three separate fields in some lines of descent. Von Economo (1929) called the proposed evolutionary process of adding areas, the "progressive differentiation of architectonically specific structures" or "progressive cerebration." In von Economo's view, this process resulted in an increase in intelligence and depended, most probably, upon natural selection. The alternative theme for the evolution of the brain is that the number of subdivisions has not changed over the course of mammalian evolution, and that the changes seen represent only an expansion of cortex or particular divisions of cortex. The main proponent of this second view was Lashley, who argued that there was no real evidence that the number of functionally distinct subdivisions varied, and that humans and rats probably had the same number, around ten (e.g., "the total number of functionally diverse areas demonstrated in primates, even including man, does not exceed the number found in lower mammals," Lashley and Clark, 1946). A common version of the "expansion" theory suggests that all mammals have rather stable sensory and motor areas, together with "association cortex" which expands greatly from generalized to advanced brains. Within the frameworks of the themes of expansion and the acquisition of new subdivisions, a number of more specific theories have been proposed. Four of these proposals are outlined here.

Bishop

Of the relatively modern theories of brain evolution, an early, but influential, plan was proposed by George Bishop (1959). Figure 2 summarizes the main points of the theory. Following the arguments of Herrick (1956) and others, Bishop recognized that the dorsal area of pallium in amphibians and the dorsal (general) cortex of reptiles was the precursor of neocortex in mammals. Dorsal cortex in turtles was known from surface recordings to be sensory, and little organization was apparent. Thus, it was reasonable to postulate that the reptiles leading to mammals had rather diffusely organized, multimodal sensory cortex. The existence of the "primary" and "secondary" sensory and motor fields was also known at the time (named in order of discovery), with the secondary fields having larger receptive (or movement) fields, and a less specialized histological appearance. In particular, the primary fields were more densely myelinated. Myelination is associated with axon size in sensory pathways, and Bishop argued that thicker axons evolved later in phylogeny than thinner axons. Because the secondary fields were less myelinated, and apparently less precisely organized and less specialized, Bishop argued that the secondary fields evolved before the primary fields by differentiating out of general cortex. Thus, a hypothetical premammalian stage of cortical organization was characterized by secondary motor and sensory fields surrounded by general cortex. Later, the primary fields, together with association cortex, evolved, while remnants of general cortex and the secondary fields were preserved.

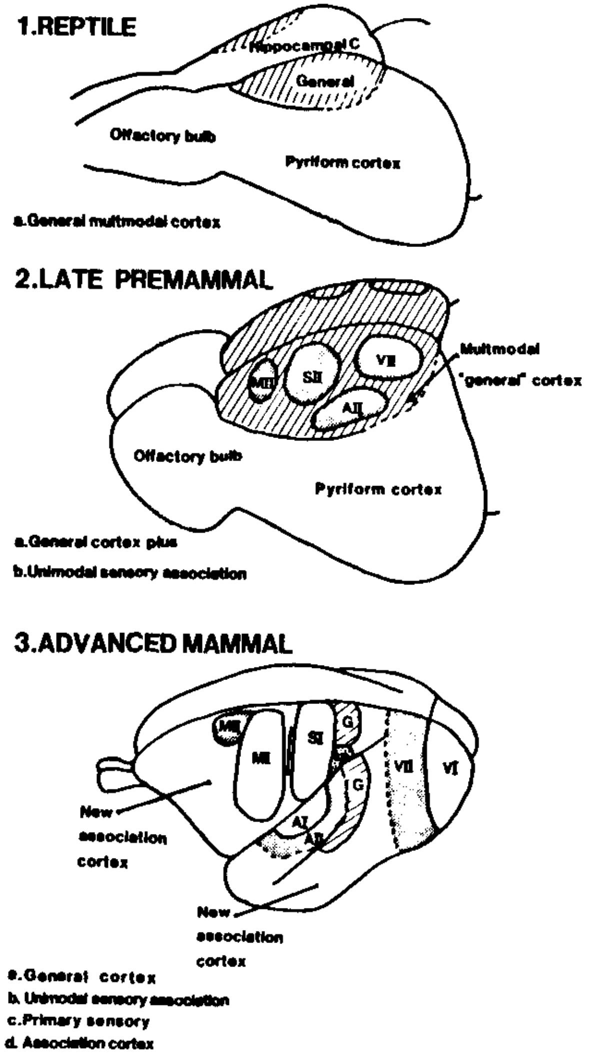

FIGURE 2. Three stages of cortical evolution according to Bishop (1959). General, multimodal, dorsal cortex of reptiles gives rise to the secondary sensory and motor areas at a later premammalian stage. At later stages, primary sensory and motor areas, and then areas of new "association" cortex are added.

Von Bonin

A somewhat similar but less specific theory was outlined at about the same time by von Bonin and Bailey (1961). These investigators studied the histological structure of cortex of a number of mammals, and in general were critical of earlier portrayals which presented a great number of subdivisions in advanced mammals. They considered the neocortex of hedgehogs as representing an early stage of cortical organization, and concluded there was little evidence for subdivisions and that the primary fields were missing. They concluded that the region described by Brodmann (1909) as primary visual cortex has "none of the characteristics" of that cortex in primates. From their studies of cortical histology in tree shrews and a number of primates, they concluded that the differentiation of specific fields occurred gradually in a line that ran from tree shrews to man (see Le Gros Clark, 1959 on this "primate series"). Primary visual cortex first evolved out of generalized cortex at an early primate or preprimate stage, followed in time by motor cortex. Primary somatosensory cortex evolved by the occurrence of the first monkeys, with primary auditory and premotor fields evolving histologically by the advent of Old World monkeys. However, for the most part, cortex by the time of the first monkeys was seen as consisting of a few sensory and motor fields, together with more generalized association cortex, and little change in cortex, other than in proportions and size, was believed to have occurred after that. The brain of the small and somewhat primitive New World marmoset monkey was seen as "essentially . . . in the mold in which it remains up to man." New World cebus monkeys were "amazingly like" macaque monkeys which showed "only minor elaborations over marmosets," with the brain of chimpanzees "merely a larger edition" of that of the macaque monkey. The human brain was seen as a larger chimpanzee brain with the possibility of the addition of a specialized speech (Broca's) area.

Lende

At about the same time, Lende (1969) based a theory of cortical evolution largely on the results of his comparative electrophysiological studies (e.g., Lende 1964, 1963). Lende's cortical surface recordings and stimulation studies suggested that almost all of the cortex in the small-brained hedgehog was sensory or motor and that auditory, visual, somatosensory, and motor fields overlapped widely. We know now from later studies using microelectrodes with finer resolution (Kaas et al., 1970) that apparent overlap was the result of volume conduction in the small brain. Nevertheless, it was reasonable at the time for Lende to hypothesize an ancestral stage to hedgehogs with almost complete overlap of sensory and motor fields, with gradual and varying degrees of separation in different lines of descent (Fig. 3). In addition, nonsensory association cortex came to occupy large expanses of cortex in different locations in some lines of evolution.

Sanides

Finally, a theory developed by Sanides (1970, 1972) from comparative architectonic studies of cortex requires special mention because the theory continues to receive support (e.g., Morgane et al., 1985; Mesulam and Mufson, 1982; Goldberg, 1985). In brief, this theory (Fig. 4) holds that the neocortex that evolved in reptiles differentiated out of medial hippocampal (archicortex) cortex and lateral pyriform (paleocortex) cortex. Thus, the first neocortex, the primitive general cortex of reptiles, had a dual origin with

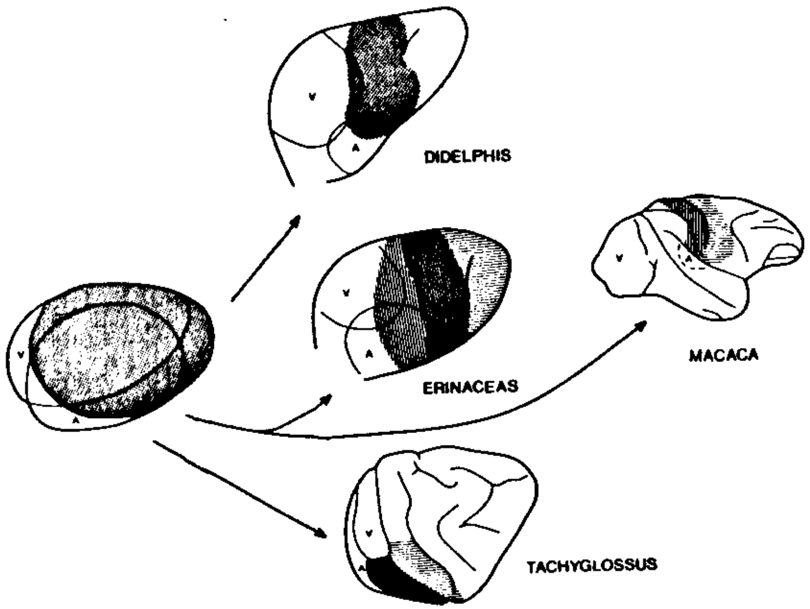

FIGURE 3. The course of cortical evolution according to Lende (1964). A hypothetical premammalian stage had extensively overlapping sensory and motor fields. According to the theory, these fields became incompletely separate in lines of descent leading to hedgehogs and opossums, and completely separate in lines leading to the echidna and macaque monkey. Regions of nonsensory association cortex expanded differently in the separate lines. Reproduced from Figure 10 of Lende (1964).

the medial half originating from hippocampal cortex and the lateral half originating from pyriform cortex. At a later premammalian stage, this first "growth ring" of neocortex gave rise to a center region of proisocortex. The medial or limbic proisocortex was derived from medial periarchicortex, while the lateral insular proisocortex was derived from lateral peripaleocortex. This second "growth ring" subsequently gave rise to the secondary motor and sensory fields. More specifically, at an early mammal stage of evolution, limbic proisocortex produced the supplementary motor area, and the "true" medially located, second visual area (prostriata), while insular proisocortex produced the secondary motor (premotor) field, the secondary somatic area (somatic prokoniocortex), and the secondary auditory area (auditory prokoniocortex). According to the theory, most but not all mammals (e.g., hedgehogs) reached a further stage of cortical evolution, when the third growth ring gave rise in its center to primary motor and sensory fields (the fourth growth ring). Primary motor and primary somatic fields had a dual origin, with lateral portions derived from parainsular isocortex and medial portions derived from paralimbic isocortex. Primary visual cortex (visual koniocortex) derived only from paralimbic cortex (prostriata) and primary auditory cortex (auditory koniocortex) originated from secondary (A-II) auditory cortex of parinsular isocortex. At even later stages, sensory belt regions and association regions evolved.

All of the above theories have currently supportable and unsupportable elements. I argue later that the idea that the primary sensory fields evolved after the advent of mammals is clearly wrong.

MODERN APPROACHES TOWARD UNDERSTANDING CORTICAL ORGANIZATION

Until recently, evaluation of theories of cortical evolution were limited by the insensitivity of the methods used to determine brain organization. Architectonic studies tended to dominate, and histological examinations of brains depended on a limited number of fiber and Nissl stains that failed to reveal obvious differences between many cortical fields. Thus, large regions of cortex were seen as essentially homogeneous in structure, and the arguments for the fewer, poorly defined fields of von Bonin and Bailey (1961) and others were at least as supportable from arthitectonic evidence alone, as the more elaborate schemes of Brodmann (1909), the Vogts (1919), and others. In the last few years, however, fiber stains have been improved and methods for visualizing other components of neurons have been shown to be extremely useful. In particular, reactions for the cellular enzyme, succinic dehydrogenase, have revealed with great clarity the location and even the somatotopic distribution of body parts in the primary somatosensory cortex of rodents (see Fig. 1 of Killackey, 1983, for example). Stains for the cellular enzyme, cytochrome oxidase, clearly distinguish primary and other sensory fields, as well as substructures within these fields (see Tootell et al., 1985 for example). Most recently, mono-

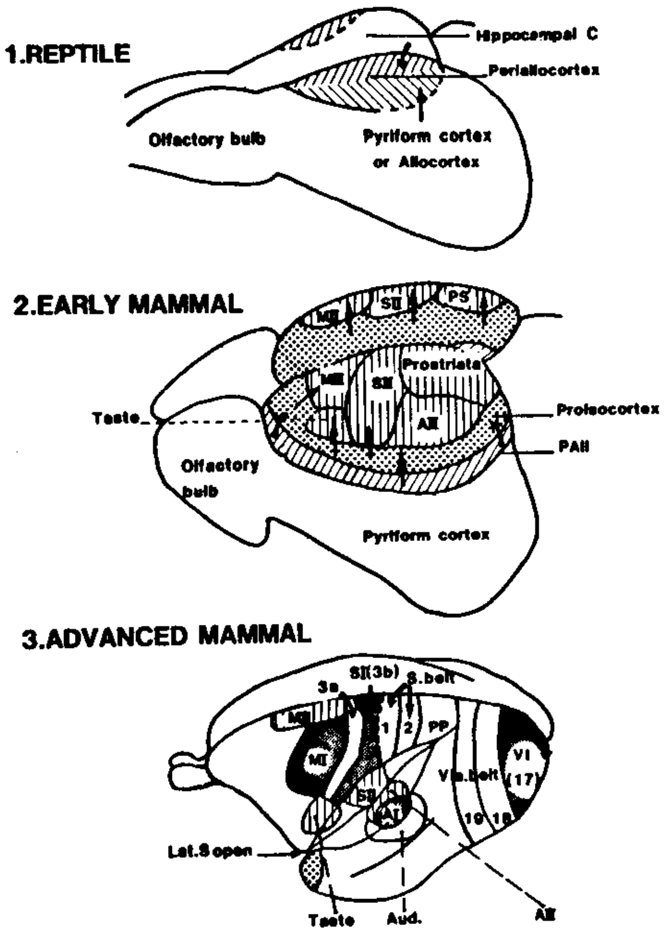

FIGURE 4. Stages of cortical evolution according to Sanides. Neocortex has a dual origin in reptiles with the lateral part derived from paleocortex and the medial part derived from archicortex. This original neocortex gives rise to proisocortex, and then in early mammals to secondary sensory and motor fields. Primary motor and sensory fields originate later in some but not all lines of descent. Subsequent additions include the sensory belts and ultimately new association fields. Based on Sanides (1970, 1972); also see Pandya and Sanides (1973), and Morgane et al. (1985).

clonal antibodies have been produced that recognize specific cell surface antigens that are concentrated on only certain classes of neurons, and such antibodies have been used to delimit distinct cortical areas and subdivisions within areas (see De Yoe et al., 1986). These powerful new techniques are reviving and revising the "architectonic" approach, and are revealing subdivisions of cortex in previously homogeneous regions in astonishing detail. Clearly the idea of many subdivisions of Brodmann (1909), rather than the idea of few of von Bonin and Bailey (1961), more accurately reflects the actual organization in advanced mammals.

Aside from histological approaches, the main way of defining subdivisions of cortex has been to determine movement maps with electrical stimulation or sensory maps by recording evoked neural activity. The early studies depended on surface electrodes that had the potential of stimulating or recording from neurons some distance from the electrode tip, and therefore detail was lost. Nevertheless, these procedures, especially in the hands of Woolsey and colleagues (for reviews see Woolsey, 1958, 1960, 1971), provided the more accurate information on cortical organization and revealed many of the errors and inconsistencies of the earlier purely architectonic approaches. Yet, surface recording and stimulation procedures (1) tended to overestimate receptive and movement field sizes, (2) were of limited usefulness in small brains or for examining the organization of small fields, (3) often failed to indicate borders accurately, (4) incorrectly suggested overlap of adjacent fields, and (5) sometimes failed to distinguish separate adjacent fields. Depth recordings with microelectrodes were used in the early 1940s by Adrian, (e.g., 1941), but the method was not widely employed until revived and improved by Welker (e.g., Welker and Campos, 1963). The microelectrode approach, by stimulating or recording from neurons only very close to the electrode tip, allowed sensory and motor maps to be determined with great precision, and these maps have provided the most extensive and valuable information to date about cortical organization.

The other principal method used to reveal cortical organization has been to examine patterns of connections. The basic premise is that determining the connections of known or better understood areas (or nuclei) can reveal other cortical or thalamic subdivisions and aspects of their internal organization. Until the advent of the Nauta method for staining degenerating axons in the 1950s (referred to as "the Nauta revolution" by Ebbesson, 1984), studies were limited to examining parts of the brain, typically the thalamus, for degenerated neurons after lesions damaged their axon projections to some other structure, typically the cortex, and to tracing degenerating myelin in axon paths after lesions. Today we have a number of sensitive procedures for accurately determining connections, most using the normal transport mechanisms of neurons (e.g., horseradish peroxidase, wheat germ agglutinin, fluorescent dyes). These anatomical procedures, now in wide use, are providing a steady flow of information on cortical organization.

Of course, each method has its problems as well as its advantages (see Kaas, 1982), and therefore specific proposals of cortical organization should be subjected to careful test by employing a number of procedures. Often it is most powerful to combine microelectrode mapping, the use of anatomical tracers of connections, and histological procedures in the same experiment. Given the rapid progress of the last ten years, together with the power of the new techniques, it seems reasonable to conclude that we are at the beginning of a "Golden Age" in terms of understanding cortical organization.

THE CONTRIBUTIONS OF MODERN APPROACHES

The progress that is possible with modern approaches can be illustrated with an example. We have been interested in how neocortex is subdivided into areas of functional significance in rodents. Although rodents constitute a highly successful and adaptive order of mammals, members of the order do not differ extensively in brain size relative to body size or in brain proportions. Thus, it seems likely that different rodent species are highly similar in basic subdivisions of the brain, with most variability in proportions and intrinsic organization within fields. Given this assumption, at least rough comparisons can be made across species.

Our studies in rodents have been concentrated on the common grey squirrel (see Fig. 8), because these rodents are easily available and have the advantages of a somewhat larger brain (the brain is also larger relative to body size than that of most rodents; see Eisenberg, 1981) and greater architectonic differentiation than the rodents more typically used as experimental animals. In visual cortex, a primary field, V-I, was identified by histological structure, connections with the lateral geniculate nucleus, a systematic "first-order" representation of the contralateral visual hemifield, and projections to other visual structures. A second field, V-II or area 18, was identified by histological structure, connections with V-I, and a systematic "second-order" representation of the visual hemifield. A band of cortex lateral to V-II was shown to be visual by projections from V-I and V-II (see Hall et al., 1971; Kaas et al., 1972a; Cusick et al., 1980; Johanson et al., 1986). Projections from V-II also demonstrate that more lateral cortex in the temporal lobe is visual, and we expect that much of the temporal cortex caudal to the auditory fields will be found to be visual, and will be found to consist of several fields (an architectonic subdivision of unknown significance, TP, is obvious). Thus, two visual areas have been established with certainty, one additional visual area is presumptive and deserves further investigation, and other visual areas are likely to be discovered in the near future.

Similar statements can be made for regions of cortex devoted to other functions. Three somatosensory areas have been identified with certainty by multiple criteria (S-I, S-II, and parietal ventral or PV), and two other somatosensory fields have been suggested by less complete evidence (see Krubitzer et al., 1986). Likewise, two auditory fields have been delimited by tonotopic maps, architectonics, neuronal response properties, and cortical and subcortical connection patterns, while the existence of at least one other field is supported by less complete data (see Merzenich et al., 1976; Luethke et al., 1985). Finally, primary motor cortex, M-I, has been identified by a motor map, architectonics, and connections, and a second motor field has been suggested (M. Huerta and L. Krubitzer, personal communication).

The developing picture of cortical organization that emerges from modern studies in squirrels can be compared and contrasted to earlier portrayals of cortical organization in rodents. Brodmann (1909), restricted by having only histological information about cortical organization, clearly only had limited success in correctly delimiting functional subdivisions of cortex in squirrels. Brodmann located part, but not all, of primary motor cortex (his area 4). In addition, part of the primary visual field (area 17) was correctly identified, but the medial, less differentiated portion, was mistakenly thought to be a secondary field (area 18). In somatosensory and auditory cortex no fields were correctly identified, although part of the primary somatic field (which Brodmann termed area 3 in higher primates, see Kaas, 1983) was seen as a secondary somatic area (area 1). Kreig (1946), also largely depending on architectonic criteria, made some improvements, including the placement of area 18 lateral to area 17 and the identification of some of S-I as area 3 in rats. Later, Woolsey, using surface recording and stimulating electrodes, demonstrated the existence and nearly correct location of M-I, S-I, S-II, and A-I in rats (see Woolsey, 1958). However, the recording methods did not distinguish separate visual fields, the correct organization of S-II or somatosensory fields in addition to S-I and S-II; in addition, the second auditory field (A-II) was assumed, rather than demonstrated. We conclude from these comparisons that a more exact

understanding of cortical organization has been obtained, although much further progress can be expected. Furthermore, it seems obvious that early conclusions, based almost solely on cortical architecture, were not reliable.

CURRENT CONCEPTS OF CORTICAL ORGANIZATION AND THE COURSE OF CORTICAL EVOLUTION

The Phylogenetic Tree

Mammals emerged from reptiles about 250 million years ago, and have subsequently diverged into a number of independent lines. There are many uncertainties about the branch points and time course of this radiation, but broad outlines can be sketched, and valuable data, especially comparative molecular data, are rapidly accumulating and allowing revisions and improvements in phylogenetic classifications. Figure 5 is based on recent estimates (e.g., Eisenberg, 1981) and is accurate enough to guide a general discussion of cortical evolution. The first mammals branched into prototherian (modern monotremes) and therian mammals, and therian mammals later branched into metatherian (marsupials) and eutherian (placental) mammals. Following the great wave of extinctions some 65 million years ago, the present orders of eutherian mammals radiated extensively. Some eutherian orders have been very successful without much advance in brain organization (e.g., rodents), and some have great diversity in brain structure (e.g., primates), but have failed to demonstrate robust reproductive success in many of its species (e.g., certain apes).

A correct and independently established phylogenetic tree is critical for deducing the course of brain evolution from comparative studies on extant mammals (see Northcutt, 1984, 1985 for review). Because the fossil record can tell us little about cortical organization, we are largely limited to comparisons across the top of the phylogenetic tree. In general, brain stuctures (areas or nuclei) observed in many lines of descent can be assumed to be primitive, and those that are restricted to a few lines can be considered new or derived. It is possible that quite similar subdivisions of the brain have evolved independently. To help discern homologous from homoplastic subdivisions, it is important to compare both closely related (sister groups) and distantly related (outgroups) mammals. Such comparisons, for example, have led Florence et al. (1986) to conclude that the "ocular dominance columns" in primary visual cortex of cats and some primates evolved independently in several lines, and were not present in the common ancestor.

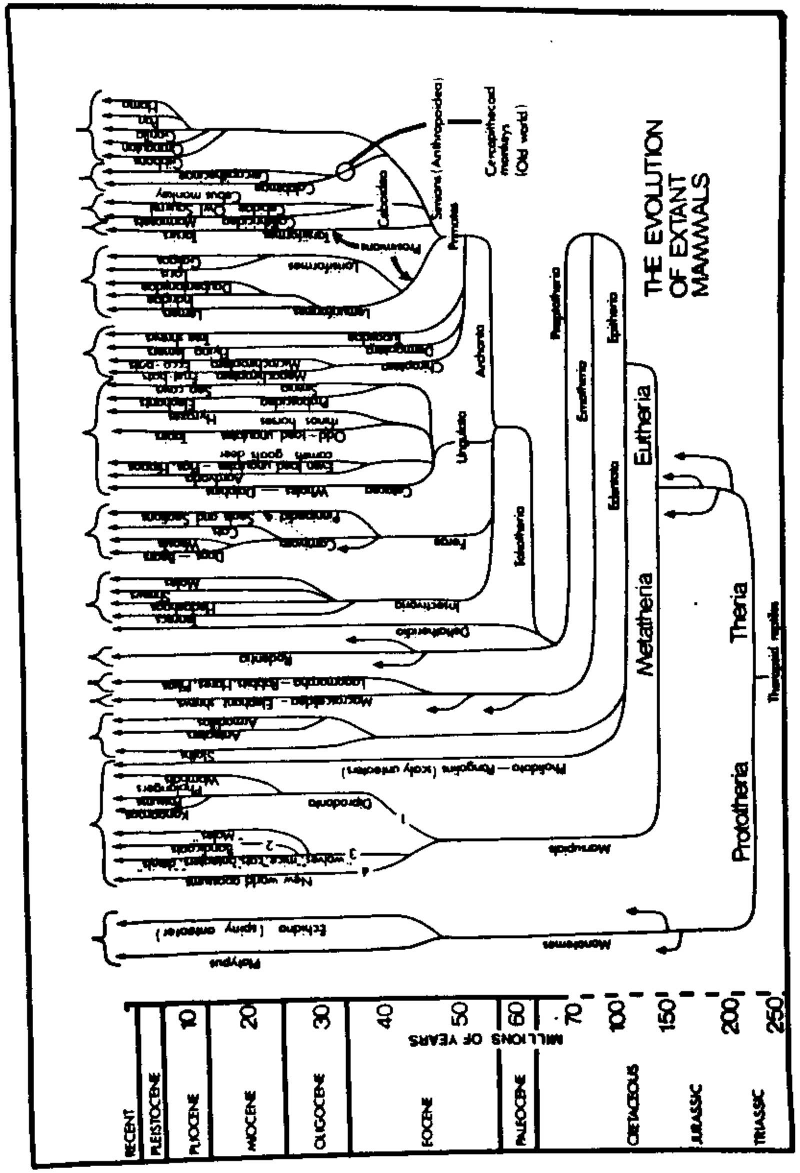

FIGURE 5.

The Brain of the Reptilian Ancestor

Little is known about the brains of the reptiles that gave rise to mammals, other than that the fossil endocasts indicate that the sizes and shapes of these brains approached those of the most primitive of mammals (Ulinsky, 1983). In terms of proportion of neocortex relative to pyriform and hippocampal cortex, these reptiles were probably only slightly different from the condition seen in extant turtles where a cap of general cortex resides on the dorsal surface of the brain (Fig. 6). Turtles are thought to have changed little from the basic reptilian stock from which all reptiles, and therefore mammals, descended (Romer, 1972), and hence the forebrain of turtles has often been studied and compared to that of mammals. The proportion of neocortex found in the most primitive of extant mammals (some insectivores, especially tenrics and hedgehogs, and some opossums) is not much more than the proportion of general cortex in turtles (Fig. 7). An obvious change, when the cortical structures of turtle and hedgehogs are compared, is from the simple arrangement of a thin layer of neurons between cell-sparse fiber layers in general cortex of turtles to the thick stacking of neurons and slight differentiation into cell layers in neocortex of hedgehogs. Most or all of general cortex in turtles is sensory, and there is some evidence for separate somatosensory and visual fields (see Hall and Ebner, 1970; Ulinski, 1983). We can presume from this that the ancestors of mammals had a rather simple precursor to neocortex that was sensory in function, but contained few subdivisions.

Primitive Mammalian Brains

The fossil record of endocasts indicates that the first mammals had little neocortex and that the amount has increased, often dramatically, in many lines of descent (Jerison, 1973). In using studies of present-day mammals to deduce the condition of cortex in the first mammals, it is logical to most strongly consider those mammals in which the general shape and proportions of the brain have not changed much from the time of the first mammals. This condition is met by most insectivores (see Stephan and Andy,

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FIGURE 5. The major phylogenetic radiations of mammals. The earliest branch was between therian and prototherian mammals. Monotremes exist today as a remnant of the early radiation of prototherian mammals. By late cretaceous marsupial (metatherian) and eutherian radiations were distinct. The eutherian radiation dominated, with some branches becoming highly successful. Both scientific and common names are used in the chart. In many instances, precise times of divergences, and sometimes points of origins are presently uncertain. Based on Eisenberg (1981) and other sources.

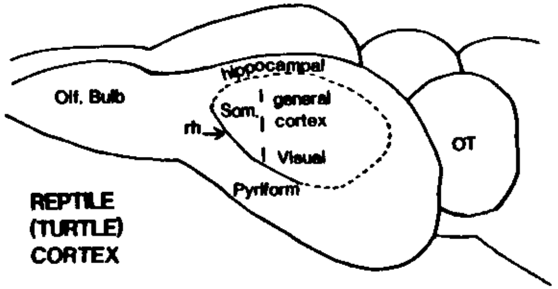

FIGURE 6. Subdivision of cortex in a reptile (turtle). The homologue of neocortex in mammals, the dorsal or general cortex of reptiles appears to be sensory throughout. A somatosensory (som.) sector may be rostral to the visual sector. Rh, rhinal fissure (dimple); OT, optic tectum. Based on Hall and Ebner (1970); also see Northcutt (1981) and Ulinski (1983).

1982), especially the hedgehogs and Madagascar tenrecs, and several small opossums, although even the common and rather stupid Virginia opossum shows some expansion of the temporal lobe compared to the ancestral condition. Of these mammals, cortical organization has been studied experimentally only in opossums and hedgehogs (see Ebner, 1969 for review). Histologically, the brains of tenrecs closely resemble those of hedgehogs (unpublished observations; Stephan and Andy, 1982). The experimental and architectonic studies give us a rough idea of what cortical organization must have been like in the first mammals.

Basic features of cortical organization in hedgehogs are summarized in Figure 7. The cortex is almost completely filled with a few motor and sensory representations. The primary visual area, V-I, primary somatosensory area, S-I, and primary motor area, M-I, have been identified with a high degree of certainty. A second somatosensory area, almost certainly S-II, and a second visual area, almost certainly V-II, clearly exist. Auditory cortex in all probability contains A-I, but other auditory fields may be present. There may be one or more additional visual fields in the small corner of unclaimed temporal cortex. Limbic, prefrontal, and entorhinal fields also exist, but there can be few other areas. For example, primary visual cortex borders directly on primary somatosensory cortex. Thus, there is no room for undiscovered, intervening areas. If cortex of opossums is considered for comparison, we find clear evidence for S-I, S-II, V-I, V-II, and auditory cortex (see Pubols, 1977; Pubols et al., 1976: Kaas, 1980; Kudo et al., 1986) but no separate motor cortex exists (Lende, 1963). Instead, the thalamic projections designated for motor cortex in other mammals go to S-I (Killackey and Ebner, 1972; Donoghue and Ebner, 1981). However, a

partially separate motor area may exist in some marsupials (see Haight and Neylon, 1979).

If we now assume that cortical areas found in a wide range of mammals are present because they were retained from a common ancestor (see Northcutt, 1985), and that cortical fields, once evolved, are seldom lost, we can support certain assumptions about the first mammals with results from more advanced mammals. We conclude that the organization of cortex in

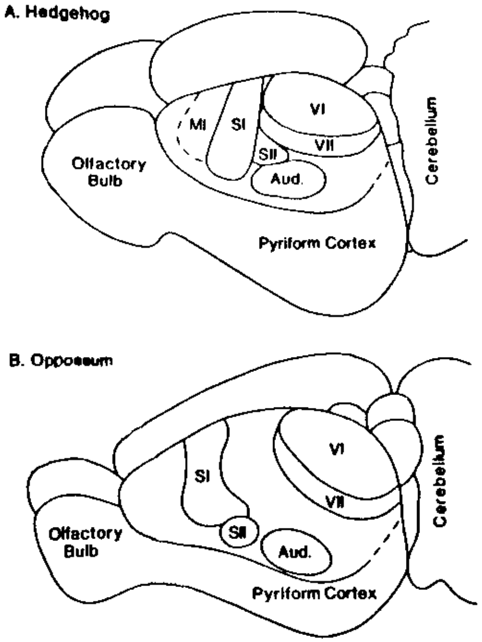

FIGURE 7. Subdivisions of neocortex in mammals reflecting primitive stages of organization. (*a*) A dorsolateral view of the brain of a hedgehog (*Erinaceus europaeus*) with primary and secondary visual (V-I and V-II), somatic (S-I and S-II) areas, and primary motor cortex (M-I). The auditory region (aud), undoubtedly contains primary auditory cortex, but it may include other auditory areas as well. Other subdivisions include a small prefrontal region, several subdivisions of limbic cortex on the medial wall of the cerebral hemisphere, entorhinal cortex, a cortex region on lateral S-I, and caudotemporal cortex of uncertain significance. Based on Kaas et al. (1970) and Lende (1969). (*b*) Sensory areas in the Virginia opossum (*Didelphis virginiana*). No separate motor cortex is apparent (Lende, 1963). Somatosensory areas are from Pubols (1977) and Pubols et al. (1976). Visual areas are from Kaas (1980). The auditory region appears to include primary auditory cortex (see Kudo et al., 1986). In comparison to hedgehogs there is more prefrontal cortex (see Benjamin and Golden, 1985) and more cortex of uncertain significance exists between the primary and secondary sensory fields. Projections from V-I indicate that some of the cortex lateral to V-II is visual (see Kaas, 1980 for review).

early mammals was not much different from that expressed in present-day hedgehogs. There were few areas, and these were mostly sensory in function. Primary visual, somatic, and auditory fields, which apparently exist in all mammals, were almost certainly present. The primary sensory fields were, of course, less differentiated architectonically than in most extant mammals, but the conclusion, based on histological structure by some investigators (e.g., Sanides, 1972; von Bonin and Bailey, 1961), that the primary fields evolved after the advent of mammals is clearly wrong. If the secondary fields evolved before the primary fields (Figs. 2 and 4), this must have occurred in the reptilian ancestors of mammals. However, it seems at least equally probable that the primary sensory fields are the oldest of neocortical fields. Primary motor cortex, however, apparently evolved as a separate field after the metatherian–eutherian divergence, and may have evolved independently in monotremes. The secondary somatosensory and visual fields were probably present in the first mammals.

Moderately Advanced Brains

Modern methods of investigations have revealed some of the subdivisions of neocortex in several mammals with moderately advanced brains (Fig. 8). Rabbits, megachiropteran bats, squirrels, and tree shrews all have S-I, S-II, V-I, V-II, A-I, and M-I fields, strengthening our conviction that these fields were present in the first eutherian mammals. In addition, there is evidence for other sensory fields in some of these mammals. Squirrels, for example, appear to have at least five somatosensory fields and tree shrews appear to have at least five visual fields. All these mammals have expanded temporal cortex of uncertain but probably visual function, and some enlargement of frontal cortex.

Highly Advanced Brains

The brains of domestic cats, New World monkeys such as owl monkeys, and Old World macaque monkeys have greatly expanded amounts of neocortex (although not nearly as much as in apes and humans), and the brains of these mammals have been extensively studied (Fig. 9). Most of the neocortex in these advanced brains is sensory or motor in broad overall function. Each "sensory" (sensory–perceptual–cognitive; see Merzenich and Kaas, 1980) field is dominated by a single modality. Cortex is divided into a large number of functionally distinct areas, only some of which can be homologized (see Campbell and Hodos, 1970) with fields in primitive mammals (Fig. 8). Cats and monkeys have many fields not found in each other, while New World and Old World monkeys have many, but appar-

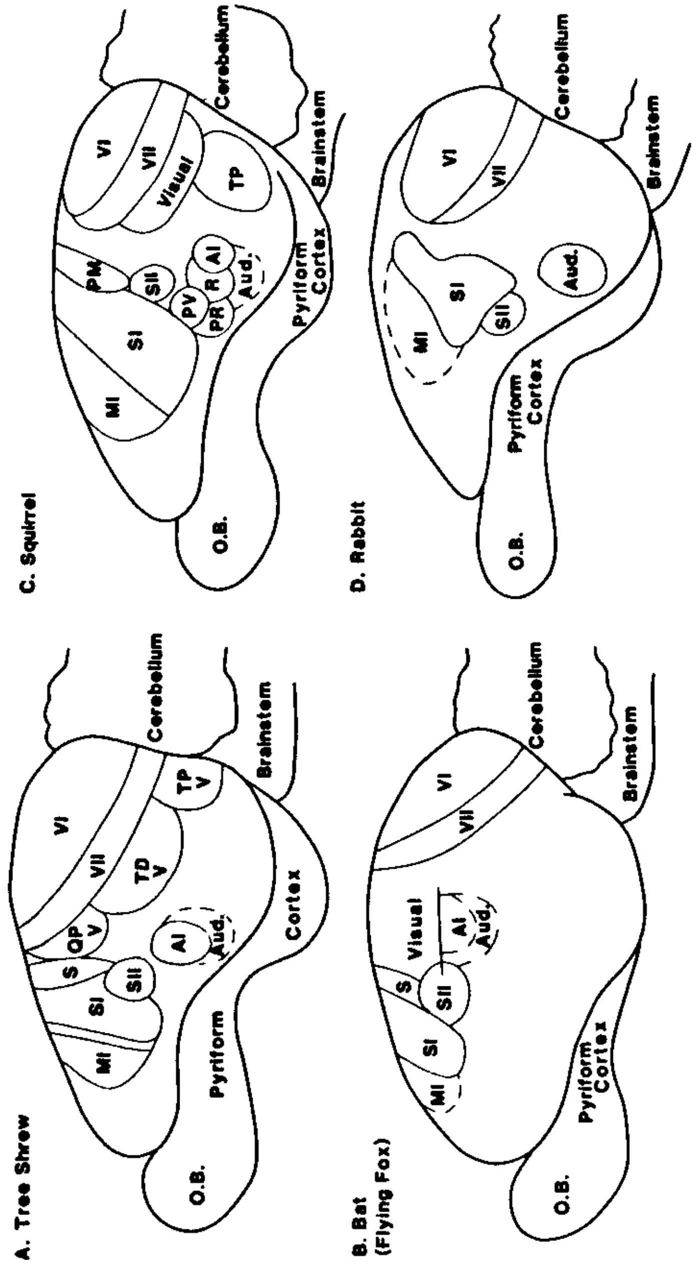

FIGURE 8. Subdivisions of cortex in mammals with moderately advanced brains. (*a*) A lateral view of the brain of a tree shrew (*Tupaia*). Visual areas include primary and secondary fields (Kaas et al., 1972b) and temporal posterior (TP), temporal dorsal (TD), and occipital-parietal (OP) fields defined by projections from V-I and V-II (Sesma et al., 1984). Primary auditory cortex and adjoining auditory cortex were defined by Oliver et al. (1976). Somatosensory areas are from Sur et al. (1981a, b), and motor cortex is based on Lende (1970) and unpublished studies. (*b*) Sensory and motor areas of the Megachiropterian bat, *Pteropus poliodephalus*. Based on Calford et al. (1985) and unpublished observations. Motor cortex was estimated from architectonic characteristics. (*c*) Subdivisions in the grey squirrel, *Sciurus carolinensis*. Somatic subdivisions including parietal medial (PM), parietal ventral (PV), and parietal rhinal (PR) areas are from Krubitzer et al. (1986). Motor cortex is from ongoing studies of L. Krubitzer and M. Huerta. Visual areas are based on Johanson et al. (1986), Cusick et al. (1980), and Hall et al. (1971). Temporal posterior (TP) cortex is architectonically defined (Kaas et al., 1972a). (*d*) Sensory and motor fields in the rabbit (*Oryctolagus cuniculus*). Somatosensory areas are from Gould (1986). See Kaas (1980) for visual areas, and Woolsey (1958) for auditory and motor areas.

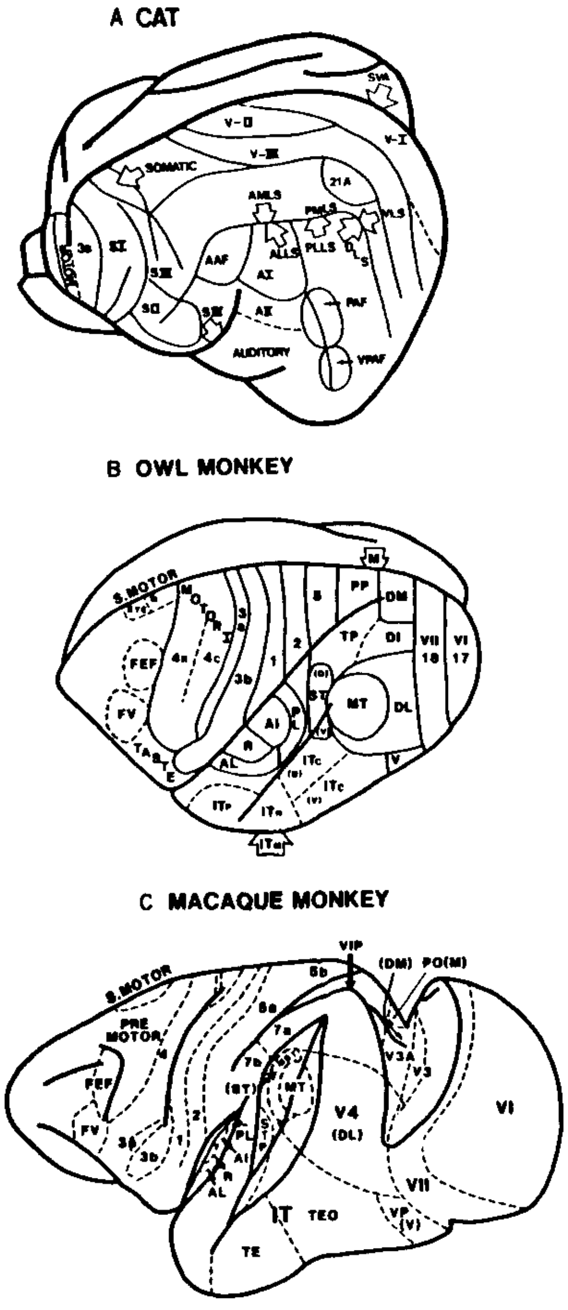

FIGURE 9.

ently not all, fields in common. (Some fields presently given different names may prove to be homologous.) Cats have at least 12 visual areas, 6 auditory areas, 5 somatosensory areas, and 2 motor areas. Monkeys have 15 or more visual areas, 10 or so somatosensory areas, and 3 or more motor areas. Brains of other mammals with expanded amounts of neocortex may also contain many subdivisions, but this has not been investigated as thoroughly in cats and monkeys.

Other Advanced Brains

Although it is obvious that there is much more to be learned about cortical organization in the few intensively studied species mentioned above, little is known about the specifics of cortical evolution in some of the most interesting lines of descent. The monotremes, for example, represent a separate line of mammalian evolution. This line, consisting now of only a few remnant species in two specialized families, has not been very successful in populating the planet. However, these monotremes have moderately advanced brains, as least in brain size relative to body size: platypuses are at the mammalian average, echidnas are somewhat less than average (Eisenberg, 1981). Studies of cortical organization could provide information critical for understanding the limits and possibilities of independent advance, as well as the likely organization, by comparisons with other mammals, of cortex at the reptilian–mammalian transition. The two families, platypuses and echidnas (spiny anteaters), have been studied experimentally to only a limited extent. Most of what is known is from the electrophysiological studies of Lende on echidnas (1963; also see Griffiths, 1968 for review and Ulinski, 1983 for more recent studies). A very valuable

FIGURE 9. Subdivisions of cortex in several extensively studied mammals with highly advanced brains. (*a*) Domestic cats. Twelve visual areas have been defined (V-I, V-II, V-III, SVA, AMLS, ALLS, PMLS, PLLS, DLS, VLS, 21a, 20a, and 20b; see Tusa and Palmer, 1980; Graybiel and Berson, 1981). Somatosensory areas (S-I, S-II, S-III, and S-IV) were reviewed by Garraghty et al. (1987). See Merzenich and Kaas (1980) for auditory areas (A-I, A-II, AAF, PAF, and VPAF) and Woolsey (1958) for motor cortex. (*b*) Owl monkeys (*Aotus*). See Weller and Kaas (1986) for visual areas (Medial, V-I, V-II, DL, Ventral, MT, DM, PP, ST, IT_C, IT_R, IT_M, IT_P and FV). Gould et al. (1896) for motor area (MI, supplementary motor, FEF), Imig et al. (1977) for auditory (A-I, R, PL, and AL), and somatic (S-I, S-II, and adjoining fields not shown, 1, 2, and 5) areas. (*c*) Macaque monkeys (*Macaca*). To show some of the cortex in fissures, the brain has been schematically expanded to open lunate, temporal, and lateral fissures. Visual areas (V-I, V-II, V3, V3a, V4, MT, MST, VIP, PO, and STP) are from Ungerleider and Desimone (1987) and Van Essen (1985), somatosensory areas (3a, S-I, 1, 2, 5, S-II, Ig, Id) are from Pons and Kaas (1985) and Robinson and Burton (1980). See Wise (1985) for motor (MI), premotor (PM), supplementary motor (SMA) fields. See Huerta et al. (1987) for frontal eye fields and Merzenich and Brugge (1973) for auditory fields (A-I, R, PL, AL).

electrophysiological study of cortical organization has been more recently published on platypuses (Bohringer and Rowe, 1977). The interesting finding is that the motor and sensory fields in both groups (Fig. 10; Bohringer and Rowe, 1977) are all located in the caudal half of the brain. The unknown significance of the rostral half of the brain raises the possibility that the major advance in the brains of monotremes, unlike that of the well-studied eutherian mammals, has been in the expansion and possible subdivision of nonsensory frontal cortex.

The brains of dolphins and other cetacea are also extremely intriguing. Cetacea have obviously expanded brains (twice the size expected from body size; Eisenberg, 1981), yet they have rather indistinct architectonic divisions of cortex (see Morgane et al., 1985). They also have remarkable behavioral abilities (see Bullock and Gurevich, 1979). Unfortunately, the brains are difficult to study, and most of what is known is from the physiological experiments of Lende and Welker (1972) and several Russian investigators (reviewed by Bullock and Gurevich, 1974; Morgane et al., 1985). However, what is clear from these studies is that the known motor and sensory fields are located dorsomedially in the brain, and that there is a huge lateral expanse of cortex of unknown significance (Fig. 10). Again, the possibility exists that this expansion is not of sensory cortex.

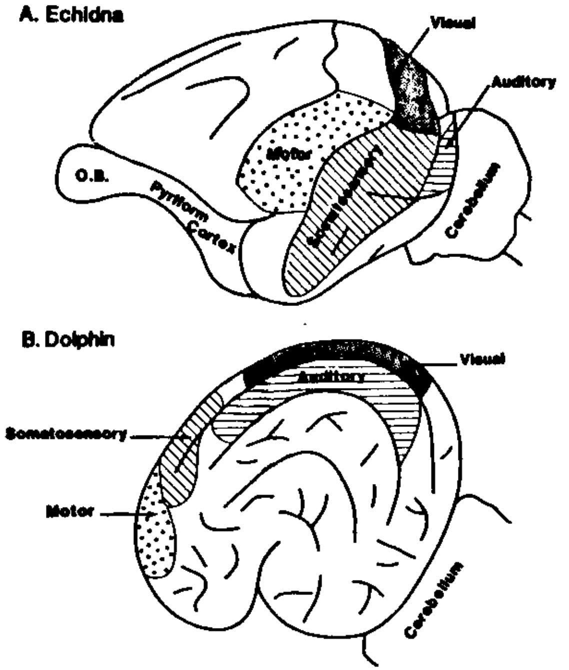

FIGURE 10. Sensory and motor fields in two unusual mammals. (*a*) The echidna or spiny anteater (*Tachyglossus aculeatus*). Most or all of the indicated somatosensory cortex appears to be S-I. Visual and auditory areas may contain subdivisions. There also appears to be a separate motor area. Note the large expanse of undefined frontal cortex. Based on Lende (1964, 1969). (*b*) The dolphin (*Tursiops*). Note the large amount of undefined cortex lateral to auditory cortex. Fields may contain subdivisions. Based on findings reviewed by Morgane et al. (1985) and studies of Lende and Welker (1972).

MECHANISMS OF CORTICAL EVOLUTION

Experimental studies on the organization of cortex in the brains of various extant mammals tell us much about what happened in the course of evolution, but little about how it happened. We presently have little idea of how cortex changed from a few fields to many in several lines of descent, but several possibilities have been considered (see Welker, 1976 for an extensive review).

1. New areas are created by subdividing old areas through a gradual process (over many generations) of differentiation. Generally, this process has been seen as the result of a gradual change of connections in a field (see Ebbesson, 1984; Northcutt, 1984 for reviews). New inputs invade and alter the functions of part of a field (the invasion hypothesis) or connections are lost, altering the functions of part of a field (the segregation or parcellation hypothesis). A specific form of the invasion hypothesis is that cortex is invaded by afferents originally destined for subcortical structures, thereby creating new cortical fields (e.g., Kudo et al., 1986). There is comparative evidence that connections do change for given fields (see Kaas, 1987), and sometimes this process may subdivide existing fields into two or several. However, it is difficult to see how systematic (topographic) cortical representations of sensory surfaces, which apparently dominated cortex through at least the early stages of evolution, could easily subdivide without losing functions for parts of the representation (see Kaas, 1982 for further discussion).

2. New cortical areas are created by cell migration and growth. The concept that new cortical areas might be created by cell migration from other regions of the brain has been stated or implied by a number of investigators. One possibility for the early stages of evolution of neocortex is that neurons constituting subcortical thalamic receiving zones in the

dorsal ventricular ridge migrate to cortex to form new subdivisions of cortex (Nauta and Karten, 1970; Sidman and Rakic, 1973). Cell groups in different locations, according to a specific form of this theory (Karten, 1969), can be homologous and are considered "equivalent cells" (see Northcutt, 1984 for review). Another possibility is that new cortical areas are formed by gradual (over generations) changes in the ontogeny of cortex so that cortical neurons generated in the ventricular and subventricular zones migrate to different locations and are generated in greater numbers to create new fields. Such a process presumably is implied, but not specifically stated, by Sanides (1972) with his concept of cortical growth rings giving rise to new subdivisions of cortex, since the generation of neurons does not take place in cortex itself (e.g., Sidman and Rakic, 1973).

3. Cortical areas could originate via the process of sudden replication of existing fields (from one generation to another due to a genetic mutation), and the gradual (over many generations subject to natural selection) modification of one or both fields so that they acquire different and new connections and functions (see Allman and Kaas, 1974; Kaas, 1982, 1987). Such a mechanism has been common in evolution. For example, lobsters evolved, in part, by a serial replication of appendages and the gradual differentiation and specialization of the replicated parts (Gregory, 1935). More specifically, replication could occur if two mirror image cortical maps with mirror image patterns of thalamic inputs were induced to form rather than one. Such a possibility is suggested by the experiments of Chung and Cooke (1975, 1978) in which two mirror image maps of the retina were induced to form in the optic tectum of frog embryos, and by the common occurrence of mirror image cortical representations (Kaas, 1987).

It is difficult to experimentally support or refute the above possibilities. But more information on what has happened in the evolution of cortex may provide further insights on the mechanisms of cortical change.

CONCLUSIONS

1. The first mammals had proportionately little neocortex, and this cortex was occupied largely by a few sensory representations. Most cortex was sensory or sensorimotor. Primary visual, V-I, auditory, A-I, and somatosensory, S-I, areas had certainly evolved by the time of the first mammals, and it is highly probable that the secondary fields, S-II and V-II, were present as well. A separate primary motor area (M-I) occurred early in mammalian evolution, apparently after the radiation of eutherian and metatherian mammals. If so, there is evidence that a partially or completely separate motor field evolved independently in all three major branches of the mammalian radiation (monotremes, marsupials, and eutherian mammals).

2. There is no clear evidence that secondary sensory fields evolved before (or after) the primary fields. Both types of fields occurred early in the history of mammals. Theories of cortical evolution holding that primary sensory fields evolved after the advent of mammals are not supported by the results of experimental studies in primitive extant mammals.

3. In a number of lines of descent, an increase in cortical size was accompanied by an increase in the number of sensory representations. This increase occurred independently in different lines, and thus the added cortical fields are not homologous. In advanced mammals such as cats and monkeys, the numbers of sensory fields for each modality is in the range of 5–10 or more, with the visual system having the most cortical subdivisions. There is no evidence for large expanses of multimodal association cortex.

4. In cats and monkeys, the new sensory fields have evolved in cortex located between the older primary fields, thus displacing the primary fields from their primitive adjacent positions. However, in some advanced brains, specifically those in echidnas and dolphins, the sensory areas appear to be close together (although the number of subdivisions of sensory cortex is not yet apparent), while large amounts of cortex have evolved rostral (echidnas) or lateral (dolphins) to sensory cortex. The significance of these expansions is completely unknown, but they raise the possibility that, unlike cats and monkeys, the major expansion of cortex in monotremes and cetacea has been of nonsensory fields.

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