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

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CONTENTS

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

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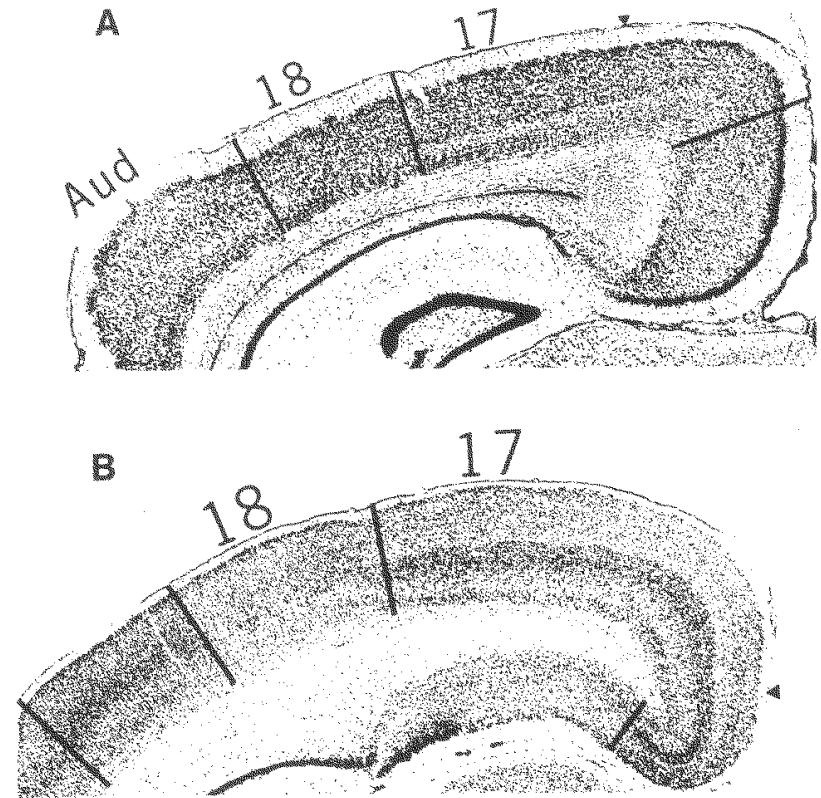
Figure 1. Cortical areas 17 and 18 in (*A*) a hedgehog and (*B*) a tree shrew. While these fields are clearly homologous in these two mammals, they differ considerably in appearance. Lines mark borders, while a small triangle indicates the junction of binocular and monocular portions of area 17. A standard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

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

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, and today we have a number of sensitive procedures for determining con-
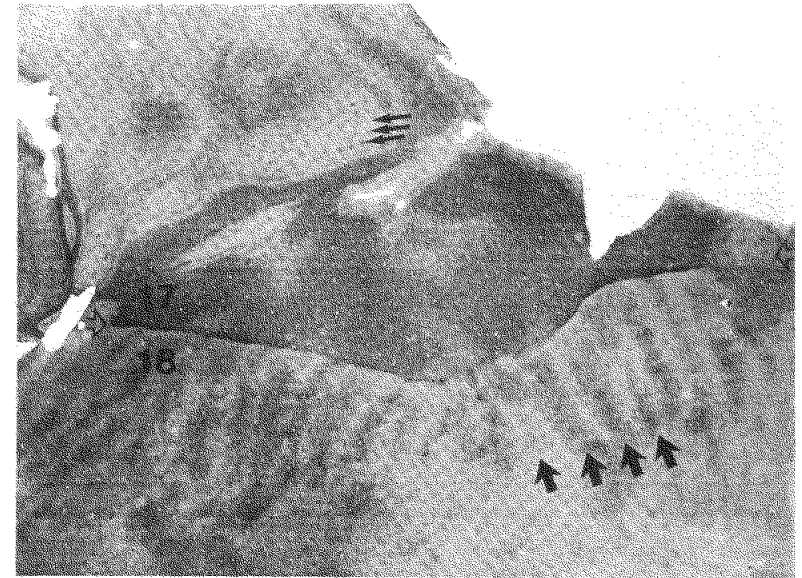
Figure 2.   Area 18 and adjoining cortex in a squirrel monkey. The cortex has been separated from the brain, unfolded, flattened, cut parallel to the surface, and reacted for cytochrome oxidase (an enzyme related to levels of neural activity). The plane of section passes from layer IV to layer III in 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
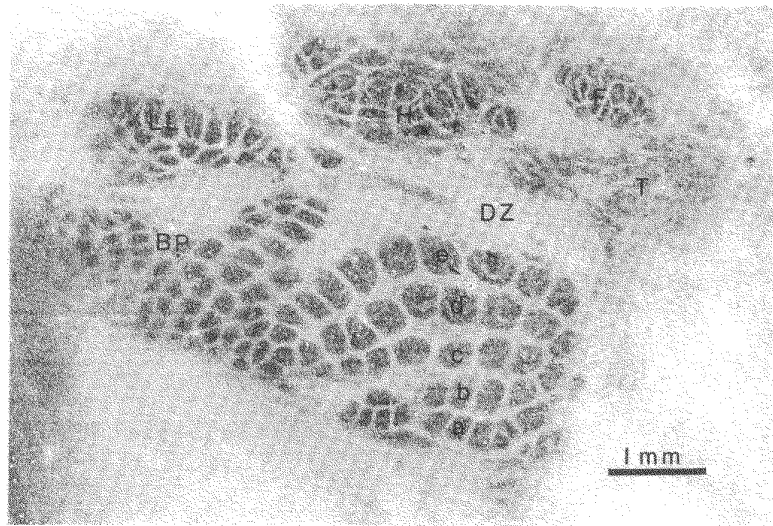
Figure 3.   The architecture of primary somatosensory cortex in the rat. The brain section was cut parallel to the surface of an artificially flattened brain and stained for the enzyme, succinic dehydrogenase. Dense clusters of staining reveal the pattern of dense thalamic inputs. The pattern indicated 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
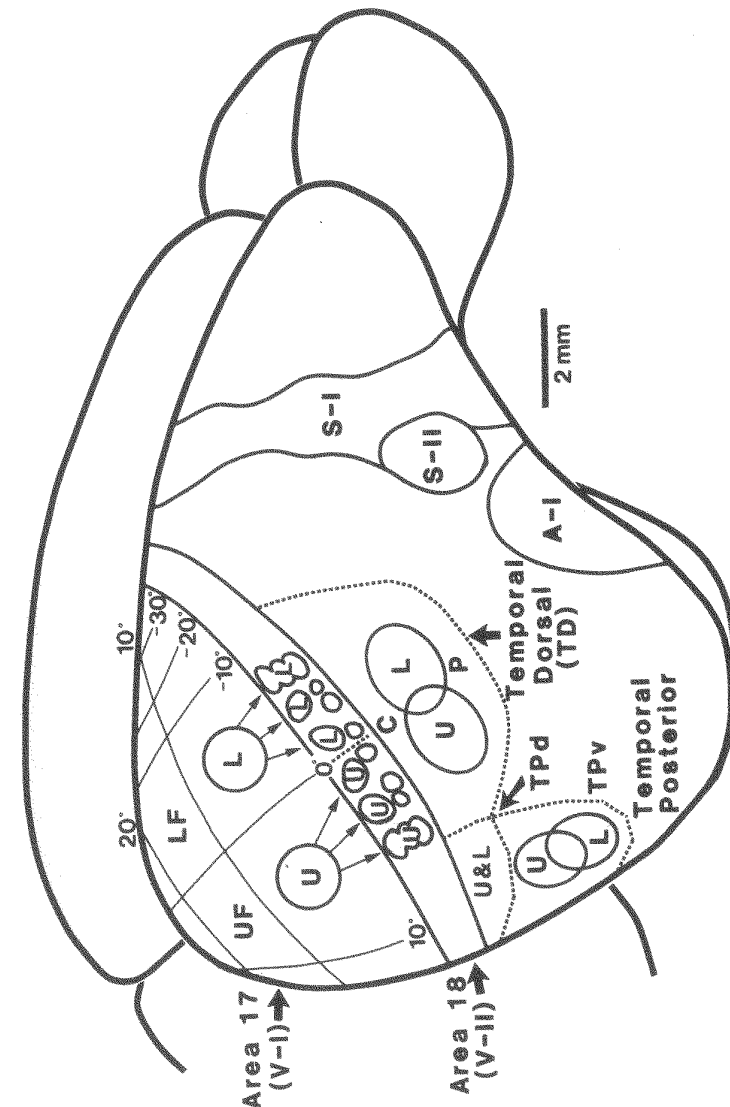

Figure 4.   Projections from primary visual cortex, V-I or area 17, to secondary visual cortex, V-II or area 18, and regions of temporal cortex in a tree shrew as revealed by injections of an anatomical tracer (circles with arrows). Each location in area 17 produces several distinct bands of terminations 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
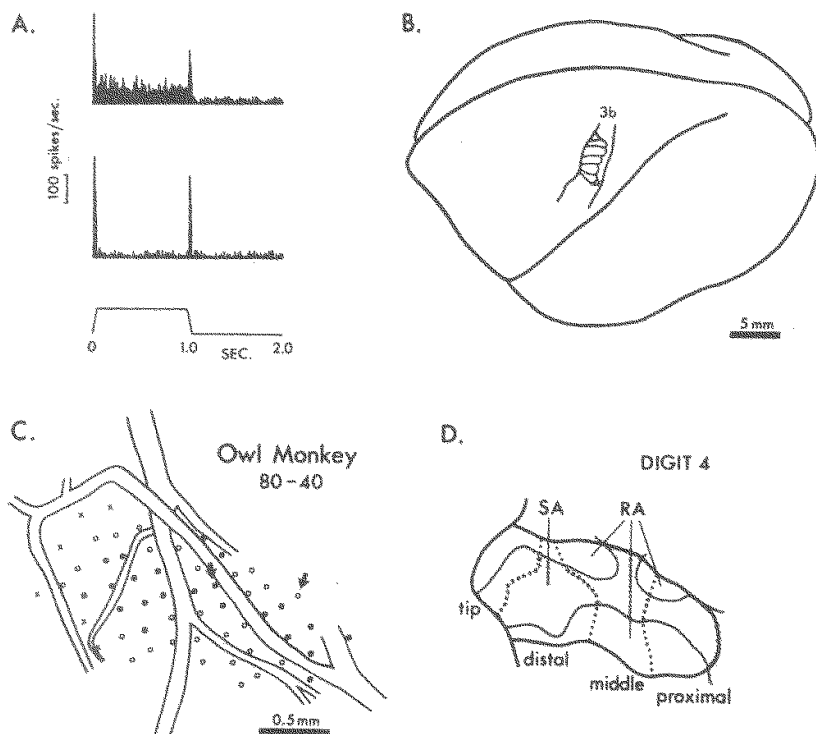
Figure 5. The spatial distribution of neurons that adapt slowly (SA) or rapidly (RA) to maintained skin indentation in primary somatosensory cortex (area 3b) of an owl monkey. The bandlike regions, which are shown only for the representation of a finger, were determined by multiple recordings with microelectrodes. 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.

HEDGEHOG

CAT
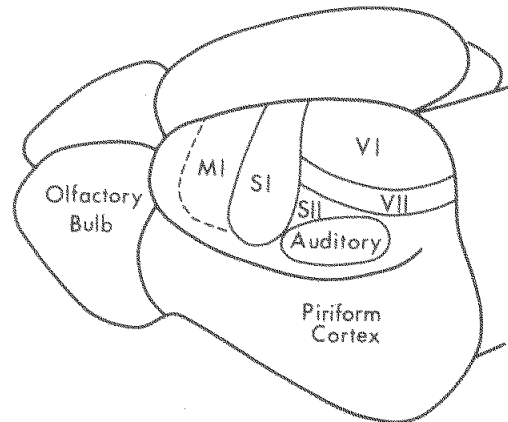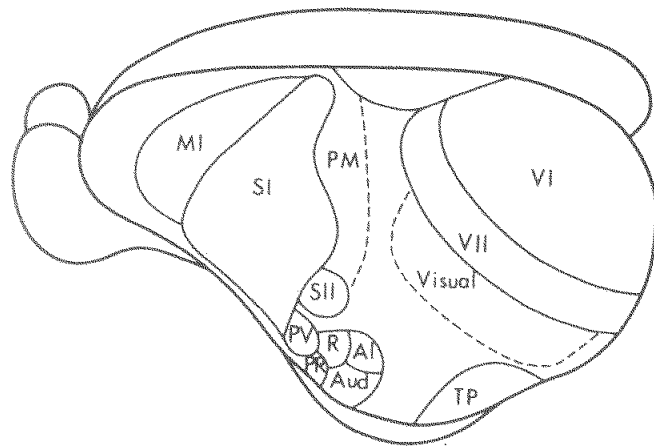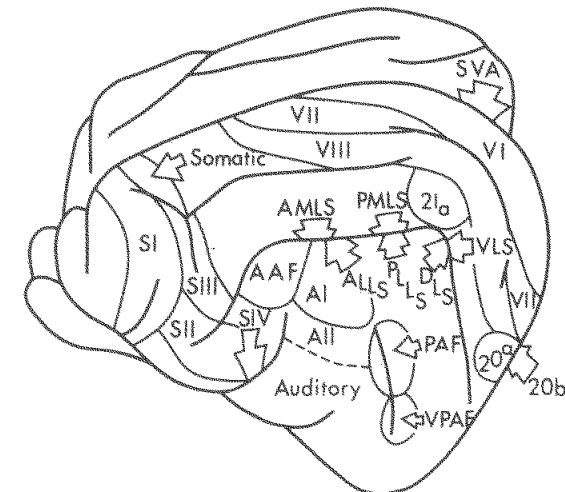
SQUIRREL
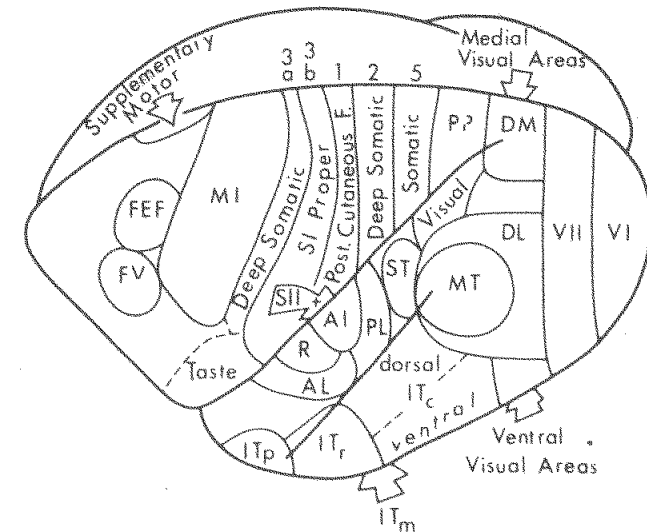
OWL MONKEY

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
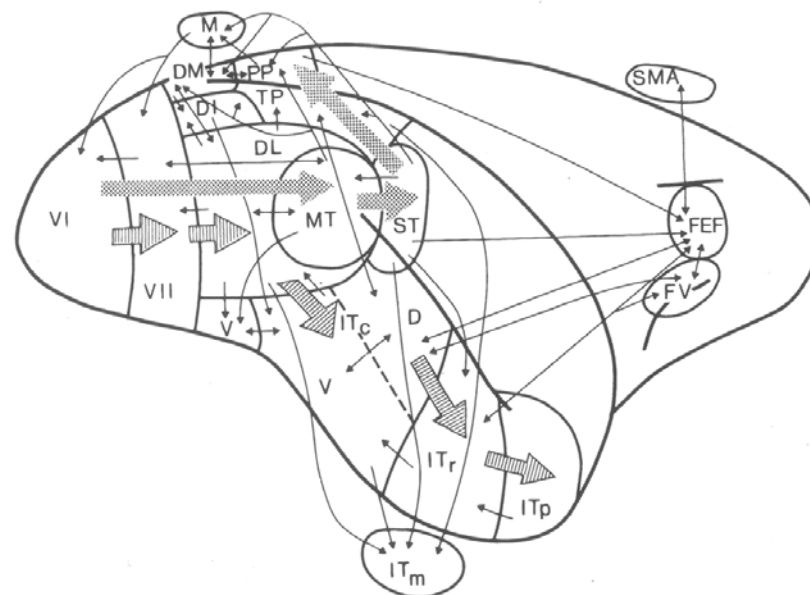
Figure 7. Some of the interconnections of visual cortex in owl monkeys. Major visual processing sequences are indicated by the thick arrows. Thin arrows indicate other connections. V-I and V-II, primary and secondary fields; FEF and SMA are the frontal eye field, and the eye movement portion of the supplementary 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. ITc, 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 develop-

ment 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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