INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

SMR.853 - 39

ANTONIO BORSELLINO COLLEGE ON NEUROPHYSICS

(15 May - 9 June 1995)

"The Segregation of Function in the Nervous System: Why Do Sensory Systems Have So Many Subdivisions?"

Jon H. Kaas
Department of Psychology
Vanderbilt University
Nashville, TN 37240
U.S.A.

The Segregation of Function in the Nervous System:

Why Do Sensory Systems Have So Many Subdivisions?

JON H. KAAS

DEPARTMENTS OF PSYCHOLOGY AND ANATOMY
VANDERBILT UNIVERSITY
NASHVILLE, TENNESSEE

I. INTRODUCTION

Until recently, sensory systems in mammals were thought to have few parts (for review, see Merzenich and Kaas, 1980; Diamond, 1979). For a typical system, sensory input from the periphery was portrayed as entering a single

CONTRIBUTIONS TO
SENSORY PHYSIOLOGY, VOL. 7

ISBN 0-12-151807-8

thalamic nucleus for "relay" to "primary" sensory cortex with elementary sensory functions, then processed in an adjacent band of "secondary sensory" or "psychic" cortex with more complex sensory perceptual functions, and finally sent on to large rather homogeneous multimodal "association" areas for all higher order abilities. With the advent of more powerful electrophysiological and anatomical methods of revealing sensory representations and patterns of connections in the brain, it has become abundantly clear that advanced mammals such as cats and monkeys have many sensory representations within separate areas in cortex and nuclei in the thalamus, and that the earlier view of sensory systems is too simple. The evidence that we need more complex models to reflect accurately forebrain organization is impressive, and a number of schemes have been offered (e.g., Merzenich and Brugge, 1973; Merzenich *et al.*, 1977; Strick and Preston, 1978; Allman, 1977; Kaas, 1978; Zeki, 1978; Diamond, 1979; Van Essen, 1979; Tusa and Palmer, 1980; Graybiel and Berson, 1981; Kaas *et al.*, 1981). The number of cortical subdivisions suggested by these proposals raises the question, "Why so many?" A related question is, "How did such complex systems evolve?" And because there is not complete agreement on the number of proposed subdivisions, an initial question might be, "How are subdivisions defined?" These are the questions of concern in this article.

II. HOW ARE SUBDIVISIONS DEFINED?

Powerful evidence against the theory of cerebral equipotentiality was first presented by Fritsch and Hitzig in the 1870s when they used electrical stimulation to demonstrate the localization of motor functions. Other critical evidence was presented by Broca, J. Hughlings Jackson, and others, and by the time of Brodmann (1909), there had been wide acceptance of the "principle of localization of function," and the goal of subdividing the cortex into functionally distinct "areas." Other investigators divided the thalamus into nuclei. Areas and nuclei, as equivalent structures, are one level of subdivision in the brain. It is also useful and important to recognize both larger and smaller levels of subdivision, somewhat in the manner of taxonomic levels (Fig. 1). Areas and nuclei can be grouped into a larger unit variously referred to as a complex, domain, province, or constellation. Individual areas and nuclei can also be divided into layers and sublayers, as well as modules and columns. Since these terms have been used in different ways, and there may be some confusion, the purpose of this section is to define levels of subdivisions, and state assumptions behind those levels.

A related issue is whether functions are sharply segregated in the brain. Brodmann (1909) distinguished two types of areas in his maps. One type consisted of structural zones with sharply delimited morphological boundaries, and presumably sharply delimited functions. This type is typified by striate cortex, or area

2.

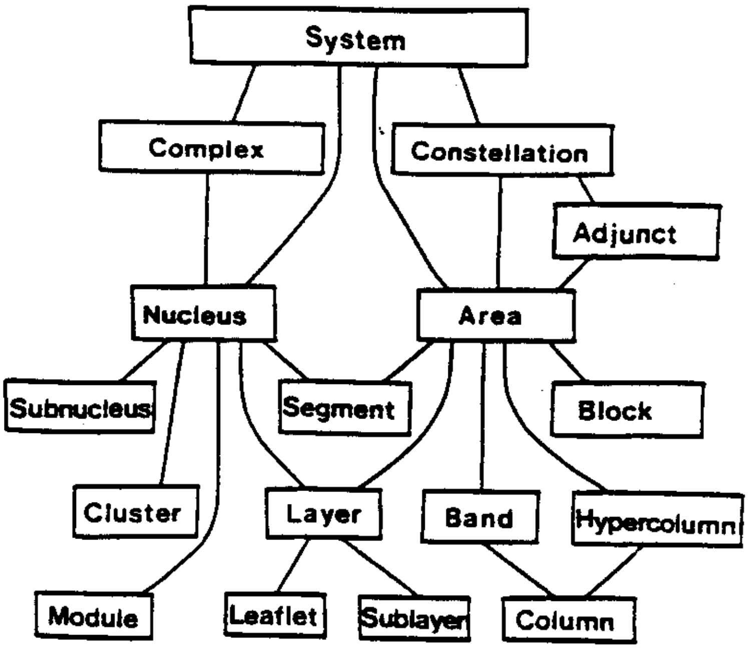

FIG. 1. A hierarchical arrangement of concepts of subdivisions of sensory systems (see text).

17, where a sharp boundary is unanimously recognized. Areas of this type have "absolute localization." Brodmann also concluded that there are regions of cortex without fixed boundaries and where neighboring fields "more or less mix and overlap." In such fields, functions are not sharply localized and these areas were said to have "relative localization." It is not certain whether areas of relative localization exist, but areas with sharp localization such as striate cortex certainly do, and the overwhelming evidence supports the conclusion that sensory systems consist of areas and nuclei with absolute boundaries (for review, see Merzenich and Kaas, 1980).

Layers in cortex and nuclei, of course, are recognized by sharp boundaries, although gradients within layers may exist. Columns or modules have usually been discussed as having absolute localization, but the possibility of relative localization must also be considered (see below).

A. Areas and Nuclei

In Brodmann's view, the areas (and nuclei) are the histologically differentiated "organs" of the brain. Given this concept, each area or nucleus has a distinct function or set of functions. Furthermore, each structure mediates these functions as a whole, and therefore subunits in an area or nucleus have processing features in common. Because of subunits, an area or nucleus need not be spatially uniform in function. Areas and nuclei, but not necessarily the subunits within them, are unique and are not identically replicated elsewhere in the brain.

3.

While the concept of an area or nucleus as a basic subdivision of the brain is clearly related to function, it has not been possible to specify precisely the function or functions of most subdivisions of the brain. This difficulty does not, however, invalidate the usefulness of the concept. The concept of homology has been very valuable in biology, for example, but homologous structures, defined as coming from a common ancestor, are never actually demonstrated by tracing the structures back through an unbroken genealogical series to a common ancestral form. Instead, criteria for assessing the probability of homology have been specified. In a like manner, it is useful to distinguish between the definition of an area or nucleus, and the criteria for its recognition.

Because an area or nucleus is functionally defined, all evidence, both direct and indirect, that a region of the brain is functionally distinct, argues for its validity as an area or nucleus. It follows that no list of criteria for identifying an area is complete, and that it would be difficult to assign a precise weight or significance to any type of evidence (see Tyner, 1975; Rowe and Stone, 1977). Hence, debates over the validity of postulated subdivisions are possible and expected, and the arguments for each subdivision should be carefully evaluated. As an aid to this evaluation process, some features of areas and nuclei will now be discussed.

1. SEPARATE AREAS AND NUCLEI SHOULD HAVE MORPHOLOGICAL DIFFERENCES

The basic assumption is that structural differences reflect functional differences. The structural differences can be of any sort, but obviously certain structural differences are more likely to reflect function than others. Brodmann and other classical anatomists stressed differences in individual cell types, but also considered patterns of cell grouping and fiber architecture. Investigators have also used differences in blood vessel distribution [striate cortex, for example, is highly vascular (see Cowey, 1964)] and the presence of pigment granules (see Braak, 1978). Additional methods for revealing "morphological differences" based on histochemical and metabolic factors have also become available. Thus, it is now possible to distinguish brain structures by revealing different distributions of certain cellular enzymes (Wong-Riley *et al.*, 1978; Killackey and Belford, 1979; Graybiel and Berson, 1981) and levels of glucose metabolism (see Durham *et al.*, 1981). In addition, traditional fiber stains have been improved and extended (Lin and Kaas, 1977; Van Essen *et al.*, 1981). As a result of these newer methods, it is becoming easier to characterize brain regions. These new technical developments will diminish one traditional problem for architectonic studies: that the proposed morphological distinctions are so subtle that there is little agreement between investigators. Thus, we can look forward to more interobserver reliability.

A problem that will remain is how to evaluate the significance of the perceived

4.

differences. A histological change might signify the border of an area, a border of subdivisions in an area, or the border of a group of areas. It is the inability of the architectonic method to denote levels of organization that is its major weakness.

2. EACH SENSORY AREA OR NUCLEUS USUALLY CONTAINS A SINGLE SYSTEMATIC REPRESENTATION OF A SENSORY SURFACE

A single complete map implies that at least one function is distributed throughout the map. Since an area can be expected to mediate a function or functions for all parts of the related sensory surface, each area should have a complete map, and except locally (see modules, below), areas should not replicate parts of sensory surfaces. It is possible, however, that some areas either replicate some part of a sensory surface, or omit some part. The primary somatic field (S-I) of squirrels, for example, appears to include two adjoined forepaw representations in a single area (Sur *et al.*, 1978). Each of the six lateral suprasylvian visual areas in the cat is thought to exclude most of the upper and lower extremes of the retina (Palmer *et al.*, 1978). But, in general, the suspicion must be maintained that "partial" duplications are actually part of another complete area, and that "incomplete" representations have been incompletely mapped.

3. EACH AREA OR NUCLEUS SHOULD HAVE A UNIQUE SET OF CONNECTIONS WITH OTHER AREAS AND NUCLEI

If a subdivision is functionally unique, then this uniqueness should be reflected in its anatomical connections. In addition, to the extent that functions are distributed throughout, all parts of the areas and nuclei should have equivalent connections. Thus, pronouncements that part of an area, but not the rest, projects to a certain target should be treated with suspicion that (1) the complete pattern of projections from the source has not revealed; (2) the projection is part of a pattern from a second area accidentally involved in the injection or lesion; or (3) the target area has been incorrectly identified.

There *are* clear exceptions to the expectation that all parts of an area or nucleus have the same pattern of connections, but it is not always obvious what exceptions to expect. Modules and layers within areas and nuclei differ in connections, and this is both expected and not particularly confusing. For example, the parvocellular and magnocellular layers of the lateral geniculate nucleus in primates project to different sublayers in striate cortex. Projections from one structure to another also may be nonuniform in compliance with functional differences in the structures. Thus, projections from the retina to the superior colliculus of monkeys are less dense from the central than from the periperal retina. There is also evidence that some visual areas with large representations of central vision "demagnify" central vision in projections to the pons by having fewer projecting neurons in cortex devoted to central vision (Glickstein *et al.*, 1972). Striate

5.

cortex, of course, has a binocular portion with input relayed from both eyes, and a monocular portion with input relayed from only the contralateral eye. Such variations in connections within areas are not disconcerting because hypotheses concerning the functional meanings of these variations can be generated. However, the evidence that only a limited portion of striate cortex, part of the representation of the lower visual quadrant, projects to a "V3" (Van Essen, 1979) is disturbing, since it is hard to imagine functions that relate to the lower but not to the upper visual quadrant. Since the validity of striate cortex as a single area can hardly be questioned, the possibilities that the projection to V3 either does not exist, or that V3 is not a complete area should be carefully considered. If, however, a visual area such as V3 with input from only part of another visual area is clearly demonstrated, it will be necessary to use patterns of connections for subdividing the brain with greater caution.

4. THE RESPONSE PROPERTIES OF NEURONS IN SEPARATE AREAS OR NUCLEI SHOULD DIFFER

If each area has distinct functions, and these functions are mediated by the neurons in the area, then each area should have a population of neurons with characteristic response properties. It may be that two or more areas differ only in the proportion of neurons of different physiological types. It is more likely, however, that different types of neurons also will be found in different areas. The "simple cell" type (Hubel and Wiesel, 1965) of visually responsive neuron is found in striate cortex of monkeys but not in the lateral geniculate nucleus, which provides input to striate cortex, or in the middle temporal visual area (MT), a target of striate cortex.

Demonstrating clear differences in response properties for neurons in two proposed subdivisions of the brain is strong support for the proposed separation. However, it is also necessary to consider the particular characteristic, and evaluate the possibility that regional variations within an area or nucleus are being reflected. Neurons in the parvocellular and magnocellular layers of the lateral geniculate nucleus of primates are markedly different in response properties (see Sherman *et al.*, 1976; Dreher *et al.*, 1976; Norton and Casagrande, 1982). Neurons in the part of striate cortex representing central vision have smaller receptive fields and may be proportionately more related to color and other factors (Gouras and Kruger, 1979). On the other hand, evidence that neurons are alike in two locations does not necessarily mean that they are in the same area, since electrophysiological experiments typically consider only a few stimulus parameters and important differences could be missed.

5. LESIONS IN DIFFERENT AREAS AND NUCLEI SHOULD PRODUCE DIFFERENT BEHAVIORAL IMPAIRMENTS

Ideally, a lesion in area A should produce behavioral change X and not Y and a lesion in area B should produce change Y and not X (a double dissociation).

6.

For example, lesions of the hand representation in area 1 of somatosensory cortex of macaque monkeys reportedly impair judgments of texture, but not of object shape, whereas lesions of area 2 produce the reverse (Randolph and Semmes, 1970). Behavioral tests after lesions can serve as a test for hypothesized subdivisions of the brain. However, negative results are not very meaningful, since it is often difficult to anticipate what abilities will be impaired and devise appropriate behavioral tests.

6. MULTIPLE CRITERIA MOST RELIABLY DEFINE AN AREA OR NUCLEUS

It is obvious that there can be problems and difficulties of interpretation with any single method of delimiting an area or nucleus, and errors are best avoided by the use of as many criteria as possible. The power of combining methods was clearly shown, for example, when Rose and Woolsey (1948) used both patterns of connections with the nuclei of the anterior thalamus and cytoarchitecture to determine subdivisions of limbic cortex, and when they used connections, cytoarchitecture, and electrophysiological maps to subdivide auditory cortex (Rose and Woolsey, 1949). Postulated subdivisions of the brain should be recognized for what they are: arguments for subdivision based on certain types of evidence. The evidence should be considered carefully, and other types of evidence for or against the proposed subdivisions should be sought.

B. Layers and Sublayers

Cortical areas and at least some sensory nuclei are divided into layers and sublayers. Various numbers of layers have been proposed for cortex (see Sholl, 1956; Brazier, 1978), but the six layers of Brodmann (1909) have been generally accepted, and various sublayers of these six layers have come into use. The issue of the number of cortical layers is not easily resolved because the criteria for distinguishing a layer from a sublayer are not clear. Brodmann (1909) used appearance, species differences and similarities, and the embryonic development of human cortex to argue for six basic layers. The validity of his system has been supported to some extent by subsequent studies revealing patterns of connections, neuronal response properties, distributions of enzymes and pigments, and levels of metabolic activity. It is probably reasonable to recognize layers as subdivisions that are distinguishable on the bases of appearance, connections, and neuronal properties across a wide range of species, since this will allow the formulation of a basic mammalian plan of lamination. Clearly designated sublayers can be as distinct or more distinct than layers [e.g., the sublayers of striate cortex in the tarsier (Hassler, 1977)], but such sublayers may not be apparent in many regions of cortex or in the cortex of many species. However, the six layer system of Brodmann is both supportable and conventional, and it is unlikely that any other formulation will come into general use. Debate over the limits of these six layers

7.

and the proper subdivisions of these layers in various regions and species will remain (see, e.g., Billings-Gagliard *et al.*, 1979; Braak, 1976, for reviews of opinions on lamination and sublamination in striate cortex of monkeys).

Layers also subdivide thalamic nuclei and other subcortical structures such as the superior colliculus. It is important to distinguish layers from other types of subdivisions in nuclei. Layers in nuclei as well as in cortex are the grouping of neurons into functionally distinct arrays along lines perpendicular to lines of "isorepresentation" (Kaas *et al.*, 1972). Layers in thalamic nuclei should have the following characteristics.

1. All Layers within a Nucleus Should Have a Common Cortical Area as a Target and Be in Topological Register in Projections to That Target

Adjoining locations in separate layers should project to the same location in cortex (thereby demonstrating isorepresentation lines). However, some layers may not project to all parts of a cortical area. Thus, the lateral geniculate layers with input from the ipsilateral eye project only to the binocular segment of striate cortex. Also, the projections from separate layers might terminate separately in the local region in cortex, either in different layers or columns. Finally, in addition to a common target area or areas, some layers in a nucleus may have cortical areas as targets not shared by other layers in the nucleus. Thus, the C layers of the lateral geniculate nucleus of cats project to area 19 and more lateral subdivisions of extrastriate cortex, whereas the A layers do not (see Graybiel and Berson, 1981).

2. Layers Should Have Different Inputs

Inputs can be from different but matched receptor surfaces (the ipsilateral and contralateral retina to different geniculate layers), distinct sets of input neurons from the same receptor surface (the X and Y cells of the retina to parvocellular and magnocellular geniculate layers in primates), or from different structures (input to the magnocellular but not the parvocellular layers of the lateral geniculate nucleus from the MT of monkeys).

3. Layers Are Often Architectonically Distinct, and Layers Sometimes, but Not Always, Are Separated by Cell-Poor Interlaminar Zones

The interlaminar zones appear to separate groups of cells with conflicting inputs. Artificial "interlaminar zones" occur in the A1 layers of the lateral geniculate nucleus of Siamese cats where they separate misdirected input from the contralateral eye from normal input from the ipsilateral eye (Guillery and Kaas, 1971). In tree shrews (Brunso-Bechtold and Casagrande, 1981) and probably other mammals, interlaminar zones in the lateral geniculate nucleus fail to

8.

develop in the absence of retinal input, even though the layers still can be distinguished architectonically. In the lateral geniculate nucleus of some primates, some layers partially separate into interdigitating leaflets (Kaas *et al.*, 1972, 1978). Leaflets are distinguished from layers by relating only to limited parts of sensory surfaces, and by clearly being protrusions of complete layers.

C. Columns, Modules, Hypercolumns, and Bands

In 1957, Mountcastle proposed that somatosensory cortex of cats is divided into separate "elementary functional units" in the shape of narrow columns extending from white matter to the cortical surface and including all cortical layers. The concept of the cortical column was supported by the electrophysiological observations that vertical microelectrode penetrations coursing perpendicular to cortical layers encountered arrays of neurons with nearly identical receptive field locations, and with other response properties in common (neurons were classified as responsive to "cutaneous" or "deep" body receptors), while angled electrode penetrations encountered points of change in these response properties (submodalities) and in receptive field locations. The points of change were considered to be the boundaries of columnar processing units, and columns on the order of 500 μm to 1 mm in diameter were postulated. The concept of narrow, vertical cortical columns was consistent with the earlier anatomical observations of Lorente de Nó (1938) that the major intrinsic connections of cortex are vertical rather than horizontal.

Since the original proposal by Mountcastle, the use of the term "cortical column" has become common, and the term "module" has been used as an equivalent (Mountcastle, 1978), especially for subcortical structures (Szentágothai, 1975). More recently, Mountcastle (1978) has proposed that a smaller "basic modular unit" of cortex is the minicolumn, which is composed of a single row of cells from white matter to surface (typically, about 110 cells; Rockel *et al.*, 1974). The term "macrocolumn" was used as a replacement for the term "column" to distinguish it from the minicolumn. Also, the concept of the hypercolumn has been introduced (Hubel and Wiesel, 1974) as the complete set of columns dealing with the processing of information from a given region of a receptor surface. When the units of cortex and nuclei that have been termed columns or modules are considered, however, it is clear that the terms have been broadened beyond the original definitions. Or, put in another way, the same term apparently has been applied to a number of brain subdivisions, thereby blurring possibly significant distinctions.

1. COLUMNS

A precise and rather rigid definition of a cortical column might serve as a useful starting point for discussion. A "traditional" column not only contains

9.

neurons throughout all layers that are united by having response properties in common and having overlapping receptive fields varying about the same center point, but it also has sharp boundaries on all sides where there is a sudden transition to a new receptive field location or a new response property. One column does not gradually merge into another. After reviewing the presently available evidence, it is necessary to conclude that such cortical columns have not been clearly demonstrated. In the somatosensory system, for example, evidence has been presented, originally by Mountcastle (1957), that rows of neurons along an angled electrode tract sometimes change abruptly in submodality or receptive field location. However, such observations do not constitute a demonstration that the abrupt changes are associated with three-dimensional structures in the shape of cylinders. The abrupt changes could instead signify transitions across larger units of cortex (bands, blocks, or areas) or across discontinuities in somatotopic representation (Merzenich *et al.*, 1978; Kaas *et al.*, 1981). Perhaps the closest approximation to the prototypical column in the somatosensory system is the "barrel" field for the mystacial vibrissae found in some rodents and a few other mammals (Woolsey and Van der Loos, 1970; Woolsey *et al.*, 1975). Each vibrissa activates neurons in a barrel of cells seen as a ring in layer IV. The barrel of cells is not found above and below this layer, but cells above and below the barrel remain activated largely by a single hair. Adjacent barrels are activated by adjacent hairs (Welker, 1976). Thus, there are abrupt changes in receptive field locations from barrel to barrel, but there is no submodality change.

The evidence for traditional columns is even weaker in auditory cortex. Although primary auditory cortex in cats is divided into alternating "excitatory–excitatory" and "excitatory–inhibitory" bands related to the interactions of the inputs from the contralateral and ipsilateral ears (Imig and Adrian, 1977; Middlebrooks *et al.*, 1980), there is no evidence of discrete columns related to submodality and receptive field location along the cochlear sensory epithelium.

In primary visual cortex, two major types of columns have been described: the ocular dominance columns and the orientation columns (see Hubel and Wiesel, 1977). Neither conforms to the classical concept of the column. The ocular dominance columns are actually long bands of alternating ocular input in layer IV of striate cortex of cats and some monkeys. In any particular band, neurons in layer IV are activated by a particular eye, and the band, in layer IV, has sharp boundaries on each side. However, there is no evidence that the lengths of the bands are divided into discrete columns by either submodality or receptive field position. Rows of neurons along the bands might represent a continuous shift in receptive field location, rather than a stepwise progression. The columns are also not traditional in that they lose their ocular dominance (in a sense, their "submodality") above and below layer IV where neurons become more or less binocular.

10.

The orientation column of neurons preferring stimuli of a given orientation differs from the traditional column in several ways. First, orientation columns, like ocular dominance columns, are bands and there is no evidence that they are divided in a stepwise manner by receptive field location. Second, it is not obvious that even the orientation bands have definable boundaries. Rather, the evidence suggests "a continuous distribution of orientation sensitivity across the cortical surface with considerable superimposed scatter" (Lee *et al.*, 1977). Third, like ocular dominance columns, orientation columns do not involve all cortical layers. Fourth, the orientation column is not the result of the segregation of thalamic input. The cells dominated by thalamic input in layer IV have no orientation preference (at least in primates), but such preferences are created in cortex above and below layer IV by local circuits.

In addition to orientation and ocular dominance columns, Michael (1981) has reported that striate cortex of macaque monkeys has "color columns." Since the columns were described as "slablike," they would be larger subdivisions than columns. In addition, at least one sublayer in the color slabs would have non-color inputs from the magnocellular layers of the lateral geniculate nucleus (Schiller and Malpel, 1978).

The lack of compelling evidence for traditional columns does not mean that they do not exist. One problem in demonstrating classical columns is that border changes in adjoining columns representing the same submodality may be difficult to detect because the only postulated change, one of receptive field location, would be so small. This problem might be solved in the somatosensory system by experimentally inducing errors in the regeneration of peripheral nerves, in order to produce adjoining cortical columns with receptive field locations which have been artificially separated (Merzenich *et al.*, 1981; Kaas *et al.*, 1981). Given this approach, there is some evidence for columns (or minicolumns; Mountcastle, 1978) on the order of 40–60 μm in diameter. Another difficulty in demonstrating columns is that sharp borders may depend on "pericolumnar inhibition" (Mountcastle, 1978), and, therefore, borders may not be revealed by recordings under some conditions and by anatomical methods. Whether or not traditional columns can be clearly demonstrated, it is apparent that cortical areas and nuclei are divided in ways not necessarily encompassed by the traditional concept.

2. BLOCKS, SUBNUCLEI, AND SECTORS

As noted elsewhere (Sur *et al.*, 1980; Merzenich *et al.*, 1981), the representation of the body surface in somatosensory cortex of primates seems to be subdivided into four or more associated regions or blocks, each devoted to representing a given portion of the body. There are lines of discontinuity in the somatotopic map partially but not completely separating the face from the hand representation, the hand representation from that of the trunk, and the trunk from

II.

the foot representation. The independence of these blocks is so great that the trunk block is reversed in somatopic orientation in some primates (Sur *et al.*, 1982; Felleman *et al.*, 1979) without affecting the orientation of other blocks. In the gray squirrel, the hand blocks seem to have been independently replicated, so that there are two hand representations within S-I (Sur *et al.*, 1978).

The equivalent of the cortical block in the thalamus is the subnucleus. Subnuclei may form when a sensory representation is discontinuous. The separation of the representation of the face from the rest of the body by a fiber band in the ventroposterior nucleus has long been recognized, but fiber bands also partially separate trunk, foot, and hand regions into subnuclei (Kaas, 1982; Nelson and Kaas, 1981; Johnson, 1980).

Sensory representations can also be divided into "sectors" or "segments" receiving somewhat different inputs. For example, binocular and monocular segments of the lateral geniculate nucleus, striate cortex, and other visual structures can be distinguished (Kaas *et al.*, 1972; Guillery and Stelzner, 1970). The barrel field (Woolsey and Van der Loos, 1970) of S-I of rodents might be considered a sector or segment devoted to the specialized sinus hair receptors. A sector differs from a block in that it is an architectonically distinct portion of a single area.

3. BANDS, STRIPS, AND CLUSTERS

When ocular dominance or orientation columns are anatomically demonstrated in visual cortex, they are actually seen as joining and diverging "bands" or strips of cortex. Similarily, area 3b of somatosensory cortex of monkeys appears to be divided into alternating strips of cortex devoted to input from either slowly adapting (SA) or rapidly adapting (RA) receptors (Sur *et al.*, 1981). The ventroposterior nucleus is equivalently divided into "clusters" of cells activated by slowly adapting or rapidly adapting receptors (Dykes *et al.*, 1981). The bands and clusters differ from columns not only in shape, but in that each one represents a region of a sensory surface, rather than a single location. For this reason, it is useful to distinguish bands and clusters from columns. Ocular dominance and RA–SA bands have definable boundaries, at least in layer IV, but it is uncertain whether orientation bands exist as discrete units or gradients of change (Hubel and Wiesel, 1977; Lee *et al.*, 1977).

4. THE HYPERCOLUMN

Hubel and Wiesel (1974, 1977) introduced the concept of a hypercolumn as a subdivision of striate cortex containing a pair of ocular dominance columns or a full set of orientation columns. Ocular dominance bands are about 0.5 mm in width, and a full 180° is covered in about 1 mm of movement across the orientation bands. Thus, since the two types of hypercolumns superimpose, a processing unit of about 1 mm^2 deals with all information from a given location

12.

have considered the superior pulvinar complex as a group of nuclei (Lin and Kaas, 1979; Graham *et al.*, 1979).

At the cortical level, some term is needed to refer to a group of functionally associated cortical areas within a single modality. Diamond (1979) has used the terms "field" and "constellation" for such a concept, but the term "field" has the disadvantage of having a number of current uses including being a synonym for "area."

According to Diamond, a "constellation" of areas is functionally unified by the sensory projections of one modality. In addition, one thalamic division or complex may project to all or most of the subdivisions of the constellation. For example, the pulvinar complex appears to project to all visual areas, and the magnocellular nucleus of the medial geniculate "complex" projects to most of auditory cortex. Diamond (1979) also argued that each constellation has a "core" area, i.e., area 17, area 3b, and A1 for the three major systems, that receives a unique projection from the thalamus and is characterized by a maximum development of layer IV.

Sometimes two representations seem to have a special relationship to each other where one area sends input to the first stage (layer IV) of local processing of the other area, while the return projection is to layers V and I, presumably largely on the apical and basal dendrites of layer V pyramidal cells providing output to distant structures. Thus, the second area seems to further process information in order to modulate other outputs of the first area. Such an anatomical relationship is seen between V-I and V-II of the visual system, the dorsolateral and posterior parietal areas of the visual system, and the areas 3b and 1 representations of the somatosensory system. We have previously referred to the secondary processing area providing the modulating feedback as an "adjunct" to the first area (Allman and Kaas, 1974; Kaas *et al.*, 1977).

III. METHODS OF DETERMINING SUBDIVISIONS

It is one problem to develop concepts of types of subdivisions in the brain, and another to list and evaluate methods of subdividing. The traditional approach has been to use appearance in histological sections, the architectonic method. Electrophysiological mapping and studies of connections have greatly supplemented this traditional method. Each approach has its strengths and weaknesses, and reliable conclusions are likely only when results from all three approaches are consistent.

A. The Architectonic Method

Traditionally, the brain has been subdivided by its appearance in stained and even unstained (Smith, 1906) brain sections. Structurally different regions have

---

been gi
distinct
informat
tions, b
architec
distinct
tunities
limited.
matter c
accordir
1925),
1978).
the arch
1956; K
signific
trophys
come a
criteria

1. T
exampl
activate
activate
ner and
been s
(1909)
in squi
separat
ally c
nucleu
2. A
import
structu
used.
strate
gators
and C
includ
(V-II)
and or
sions
3.
identi

in space, via both eyes, and for all stimulus orientations. Although the approximate size of the processing unit can be specified, the boundaries are not completely determined. Two sides of the square could be delimited by the edges of the ocular dominance columns, but the locations of the other two sides may be arbitrary, since changes to a new receptive field location or a new set of orientation bands may be gradual rather than abrupt. Of course, new information could lead to a hypercolumn with completely defined boundaries.

Since a hypercolumn is the basic processing unit within an area for all information from a given location on a receptor surface, the construct can be used outside of visual cortex, or in other sensory systems, such as area 3b of somatosensory cortex, even when specific boundaries for hypercolumns are not determined (Sur *et al.*, 1980a). Because of the inverse relationship between cortical magnification and receptive field size in area 3b [as well as striate cortex (Hubel and Wiesel, 1974)], a receptive field anywhere on the body surface relates to about the same amount of cortex. For area 3b of owl monkeys, all neurons within a region of cortex about 1.2–1.5 mm in diameter will have overlapping receptive fields (except for regions of discontinuity in the map). We have argued that the region of cortex included by overlapping receptive fields can be construed as a hypercolumn, even though boundaries are not specified. This principle can be applied to all sensory areas and nuclei, when fixed hypercolumn boundaries either do not exist, or the natures of the columnar subunits are unknown. However, for area 3b of monkeys, at least, it is now possible to fix two boundaries of proposed hypercolumns at the edges of SA and RA bands (Sur *et al.*, 1981).

D. Complexes, Constellations, and Adjuncts

It is logical to assume that areas and nuclei within a sensory system can be grouped into several types of subsystems of functional significance, and there is some evidence supporting this view. As yet, however, such types of subsystems have been only loosely defined. A few terms in current use are discussed here. However, it is clear that more specific definitions and probably further concepts will be needed as our understanding of the relationships of areas and nuclei develops.

A "complex" refers to a group of closely related nuclei where histological distinctions between adjacent nuclei are sometimes made only with difficulty. The term ventrobasal complex has been widely used to refer to the combined ventroposterolateral and ventroposteromedial nuclei, but it is now obvious that these are subnuclei of a single ventroposterior nucleus. We have presented anatomical evidence that the inferior pulvinar "nucleus" of monkeys actually consists of three separate nuclei, and prefer the term inferior pulvinar complex when referring to the complete structure (Lin and Kaas, 1979, 1980). Likewise, we

13.

been given names and the assumption has been made that these regions have distinct functions. In many cases the assumptions have been supported by limited information from lesion studies, clinical cases, or an understanding of connections, but the basic method has been to subdivide on histological appearance or architecture. The major problems with this method are that few divisions are so distinct in appearance that they are universally recognized, and that the opportunities to evaluate the significance of the proposed subdivisions have been limited. Thus, the number or locations of many subdivisions have largely been a matter of opinion, with the cortex and thalamus consisting of many subdivisions according to some investigators (i.e., Beck, 1925; Von Economo and Koskinas, 1925), and few according to others (i.e., Lashley and Clark, 1946; Kuhlenbeck, 1978). Such differences in opinion led to serious questions over the usefulness of the architectonic method (Lashley and Clark, 1946; Le Gros Clark, 1952; Sholl, 1956; Kuhlenbeck, 1978). More recently, as a result of experimental tests of the significance of proposed architectonic subdivisions, largely from electrophysiological mapping studies and investigations of connections, it has become apparent that three types of errors may commonly occur when architectonic criteria are used alone.

1. The significance of clear architectonic change can be misinterpreted. For example, striate cortex of mammals typically has two distinct parts, a larger part activated by both eyes, the binocular segment, and a smaller monocular segment activated only by the contralateral eye. Because the monocular segment is thinner and less developed than the binocular segment, the monocular segment has been sometimes mistaken for a separate cortical area [e.g., both Brodmann (1909) and Volkmann (1926), identified the monocular segment of striate cortex in squirrels as area 18]. A similar error has been made in the thalamus, where the separate "nuclei," ventroposterior medialis and ventroposterior lateralis, actually correspond to subnuclei representing the face or body within a single nucleus.
2. Another common problem is that the architectonic differences between important subdivisions of the brain may not be detected, either because the structural distinctions are not marked, or because an appropriate stain was not used. Using cytoarchitectonic differences alone, it has been difficult to demonstrate subdivisions of extrastriate visual cortex in monkeys, and several investigators have questioned the reasonableness of attempting to do so (e.g., Lashley and Clark, 1946; Zeki, 1978). However, the boundaries of several visual areas including the MT, the dorsomedial visual area (DM), and the second visual area (V-II) are obvious when appropriate fiber stains are used for myeloarchitecture, and one of these areas, the MT, appears as one of the most conspicuous subdivisions of the cortex (Allman and Kaas, 1971, 1974, 1975; see Fig. 2).
3. A third type of common error in architectonic studies of the brain is that identified subdivisions are incorrectly homologized across species. This is partly

15.

due to the temptation to find the same subdivisions in all species, and partly due to the fact that the same structure can differ markedly in appearance and position from species to species. Even the most conspicuous subdivisions of the brain can be misidentified, for Mott (1907) mistook the well-developed limbic cortex in insectivores for striate cortex. As a result, the same region of the brain might have different names in different species and different regions of the brain might have the same name. As an example of a most confusing use of terms, the "pulvinar" and "lateral posterior nucleus" are sometimes used interchangeably for the same structure in the same species, sometimes used to denote quite different structures in different species, and are both used for different structures in the same species. A related complication is that a single subdivision might be correctly recognized in some species, and incorrectly thought to include several subdivisions in others. For example, areas 3b, 1, and 2, as indicated in monkeys (Brodmann, 1909), are valid areas each corresponding to a somatosensory representation (Merzenich *et al.*, 1978; Kaas *et al.*, 1981), whereas all of these areas have been placed in single representation in rats (Krieg, 1946). Probably no other type of error has led to as much confusion.

Given these problems, it is obvious that brain subdivisions, when hypothesized from architectonic criteria alone, should be considered with caution. This is not to deny, however, that some brain areas are so distinctive in appearance that they are recognized almost universally, or that architectonic differences can be recognized and used to support conclusions based on other methods. It is this latter use that is the forte of the architectonic method.

B. Electrophysiological Maps

With the introduction of amplifying systems and the oscilloscope, electrophysiological mapping methods, either with surface recordings and evoked slow waves as favored by Woolsey (1958) or with depth recordings with multiunit microelectrodes as introduced by Adrian (1943), became a powerful tool for subdividing the brain. This procedure was used extensively for investigating the organization of sensory cortex and even thalamus during the 1940s and 1950s, especially by Woolsey and colleagues, and the resulting summary diagrams are frequently found in current textbooks and review articles. Because the method provided new information in such detail, it appeared automatically to indicate the "correct" subdivisions, as well as the extent, boundaries, and internal organization of these subdivisions. It appeared that all basic questions about the organization of sensory systems would soon be answered. Instead, and somewhat surprisingly, the method has been applied and reapplied to the same brain regions, e.g., auditory cortex of the cat, with continued revisions of concepts, and continued increases in understanding (see Merzenich and Kaas, 1980). Clearly the mapping method is not as straightforward as it once appeared.

FIG. 2.
boundaries o
brain section
of the MT ar
with striate
sensitive to
and Kaas, 1

What a
why does
Mapping
judgment
ing site.
recording
The m
used ext
from the
the acti
would b
generate
a partic
the reco
evoked

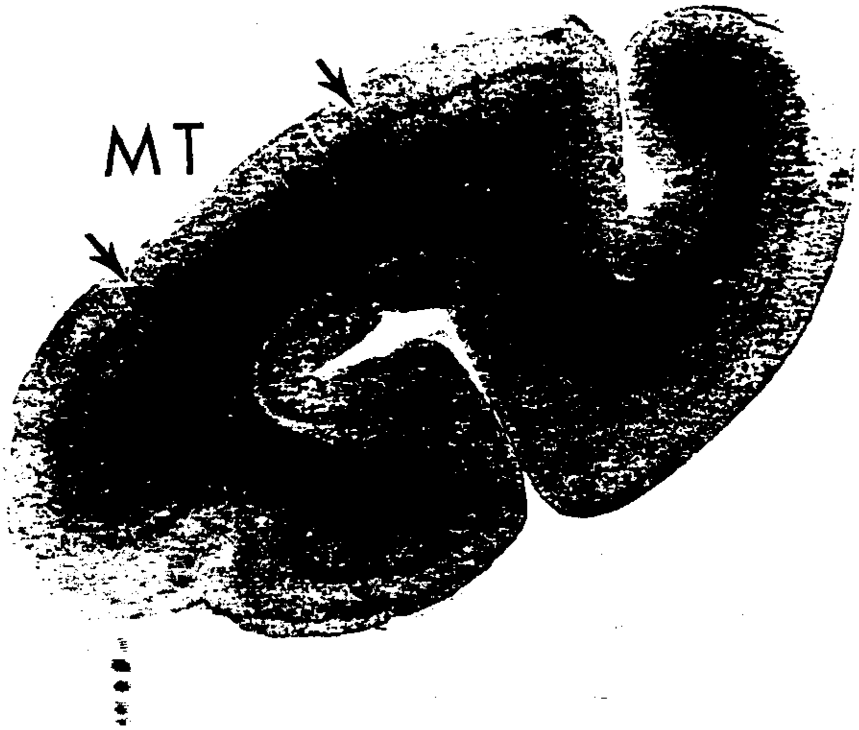

FIG. 2. The myeloarchitecture of the middle temporal visual area (MT). Arrows mark the boundaries of the MT. Note that the MT is densely myelinated, and that the borders are sharp. Frontal brain section of an owl monkey stained with a hematoxylin procedure. Other distinguishing features of the MT are a first-order representation of the contralateral visual hemifield, reciprocal connections with striate cortex and the medial nucleus of the inferior pulvinar, and a population of neurons sensitive to direction of stimulus movement (see Baker *et al.*, 1981; Van Essen *et al.*, 1981; Weller and Kaas, 1981).

What are the problems with the electrophysiological mapping method, and why doesn't it "automatically" indicate the "proper" subdivisions of the brain? Mapping methods generate data, but the data need interpretation. The need for judgment starts with the identification of a "receptive field" for a given recording site. A complication at this point is that there are three different methods of recording, each with its own problems for identifying receptive fields.

The method of recording evoked slow waves with surface electrodes has been used extensively. A problem with this approach is that neural activity distant from the recording electrode can contribute to the slow wave. In fact, if much of the activity is normally generated in cortical layer IV, the recording electrode would be about 1 mm from the major generating site. In principle, activity generated anywhere in the brain would be reflected in the recorded slow wave at a particular site, but in practice neural activity from more than 1 mm or so from the recording site gets lost in the noise of the fluctuating activity. Because the evoked potential is from a 1-mm or so region of tissue, the receptive field for a surface recording is typically larger than receptive fields for single neurons in that same region, since the individual receptive fields vary somewhat in location. With computer averaging of responses, where the effects of noise are reduced, the amount of tissue contributing to the evoked potential above the noise increases, and the size of the receptive field increases correspondingly. The sizes of receptive fields in evoked potential studies can also be increased by the need to precisely time-lock the activity of a large number of neurons to a single stimulus. Thus, sudden strong stimuli such as a tap, a tone burst, or a flashed spot of light are often used, and the possibility of stimulus-spread activating receptors outside the intended receptor surface is introduced. Finally, judging receptive field limits can be very time consuming in evoked potential studies, since there are no real limits. The effectiveness of a stimulus decreases from a maximum as it is moved across a receptive surface, and the receptive field is defined as the region of the receptive surface where the response level is above the noise level, or some arbitrary level such as 50% of the maximum. Obviously it is difficult and time consuming to make this judgment at all borders of the receptive field. These factors indicate that there are three general weaknesses with the evoked potential method: (1) Precise borders and detailed organizations of areas cannot be obtained because recordings are from an unspecified amount of tissue; (2) receptive fields are large, so that patterns of organization across recording sites are less apparent; and (3) determinations of receptive field boundaries are difficult and time consuming, so that fewer recording sites can be explored in a given time.

Another approach in mapping studies has been to record receptive fields for single neurons (units). This approach allows detailed information to be gathered, and precise borders can be determined, but there are several disadvantages. The most serious problem is that it takes time to isolate the potentials of single neurons and, because the stimulus requirements may be rather specific, to determine receptive fields. This problem can drastically limit the number of recording sites in a single experiment. Another potential problem is that recordings could be from a neuronal element that does not reflect the receptive fields of the local population of neurons. It is possible, for example, to record from axons coursing through cortex where the cell body of the axon is at some distance.

The multiunit microelectrode mapping method, which is the most common procedure, has the advantage of precision, since information is gathered from a few adjacent neurons, and the advantage of speed, since it is not necessary to carefully isolate a single neuron and the stimulus requirements of a group of neurons are likely to be less specific than those of single neurons in the group. In addition, recordings in cortical mapping experiments are generally made in layer IV, where the neurons are most easily activated by simple stimuli.

Whatever the mapping method, the data obtained need interpretation. First, it must be remembered that the receptive fields obtained usually do not reflect the total inputs impinging on the neurons. Typically, the excitatory response to nearthreshold stimuli in anesthetized animals is used to determine the receptive field. This information is the most useful in revealing topological patterns of representation of receptor surfaces, but it should not lead to the conclusion that neurons in designated locations in the resulting map are influenced only by the designated receptor surface. Inhibitory and modulatory influences usually are not reflected in the map, and thus only part of the organization of cortex, the short-latency excitatory framework, is revealed.

With mapping methods, the brain subdivisions are mainly indicated by changes in spatial patterns of representation, with other data such as receptive field size and neuron response characteristics sometimes serving as a guide. The more recording sites and the greater portion of a representation explored, the more likely a clear pattern will be revealed. There are two major factors that complicate the interpretation of mapping data: (1) there are several topological types of sensory representations (Kaas, 1977); and (2) the regions where two representations border each other commonly represent similar portions of the sensory surface.

It is relatively easy to recognize a representation from the pattern of receptive field locations when it is complete and topological so that adjacent locations on the receptor surface always relate to adjacent locations in the representation. This simple pattern has been called a "first-order transformation" (Allman and Kaas, 1974). Some representations also have splits and discontinuities (second-order transformations), extra parts, duplications, or are incomplete, or are complex in other ways such as the "point-to-line" or "line-to-area" representations in regions of extrastriate cortex of the cat (higher order transformations) (Palmer *et al.*, 1978). Such complications clearly increase the possibility that mapping data will be misinterpreted and that proposed subdivisions will incorrectly include or exclude parts of the subdivisions. Because of the difficulty in interpreting data for higher order visual representations in the cat, for example, Palmer *et al.* (1978) cautioned that "division of cortex based on retinotopy alone must remain speculative."

The second complication for the interpretation of mapping data is that the representations commonly have what we have called congruent borders (Allman and Kaas, 1975; Kaas, 1977). That is, adjoining recording sites on each side of the border between two representations typically have nearly identical receptive fields. Usually there is a mirror reversal of organization along the border. Thus, a progression of receptive fields for a row of recording sites from the first visual area, V-I, into the second visual area, V-II, reverses from moving toward the vertical meridian to moving away from it as the border between the two areas is crossed. Because the receptive fields for recording sites on both sides of the border are so similar, it is easy to include parts of adjoining areas in a single map. Of course, the more limited the mapping data, the more likely it is that this error is made. Previous examples of this mistake are the inclusion of separate, parallel

19.

body representations in areas 3b, 1, and 2 of postcentral somatosensory cortex in a single "S-I" representation (see Kaas *et al.*, 1981, for review), the inclusions of much of V-III in V-II of the cat (Woolsey, 1971), the inclusion of apparently three divisions of the inferior pulvinar complex (Lin and Kaas, 1979, 1980) in a single representation (Allman *et al.*, 1972), and the inclusion of parts of the anterior auditory field and posterior auditory field (Merzenich *et al.*, 1977) in primary auditory cortex (A-I) of the cat (Woolsey, 1960).

Given these two major problems, mapping data are most likely to be interpreted correctly when they are detailed and complete enough so that complete patterns and changes in patterns can be seen. For example, borders between areas can be quite accurately determined when careful attention is paid to reversals of receptive field progressions in repeated rows of closely spaced recording sites across the borders.

C. Patterns of Connections

With the advent of the newer anatomical tracing techniques, patterns of connections have become more useful in revealing subdivisions of the brain. The use of patterns of connections to determine brain subdivisions relies on the assumption that subdivisions have only extremely local connections within themselves. Thus, it is usual to assume that distinct projection zones indicate separate areas or nuclei. The usual approach is to use the connections of well-identified parts of the brain to identify the locations, extents, and internal organizations of other parts. The great ability of the newer methods to reveal connections is an advantage of the approach. A disadvantage is that usually the connections of only one site in a subdivision are investigated in a single animal. In addition, tracers are often centered or placed in a particularly accessible location in a subdivision, so that even across animals the connections of only a limited part of the subdivision are determined.

There are several difficulties in interpreting anatomical tracing data.

1. Because information on the total pattern of connections between two parts is likely to be limited, anatomical data are far less likely than mapping data to distinguish between several theoretical frameworks. We have pointed out, for example, that the projections of the central part of area 18 (V-II) in owl monkeys (Lin and Kaas, 1977) produce a pattern of connections that is consistent with both the traditional concept of V-III and the concept of another visual area with a quite different total shape, location, and organization, the dorsolateral visual area (DL). It is the connection patterns with other parts of area 18 that support the hypothesized organization of the DL and conflict with the concept of V-III.

2. Connections may incorrectly suggest a greater number of sensory areas. A generally valid assumption is that each separate zone of connections from an

---

injection
least two
more tha
split alon
represent
horizonta
the split r
1981). S
discontin
and it is
subunits
some ar
"area"
this may
projectio
striate c
3. An
connecti
to indic
tions ha
represen
same sc
pected.
isorepre
nuclei.
band of
(Symor
and Ka
produc
nucleus

D. Ot

Whi
had le
advanc
contrib
limite
tion h
Penfie
possib
motor

injection site indicates a separate area. However, this is not the case under at least two circumstances. First, parts of a first-order representation project to more than one location in a second-order representation. For example, V-II is split along most of the horizontal meridian in monkeys to form a second-order representation, while V-I is not split. Tracers injected on the representation of the horizontal meridian in V-I, therefore, produce two zones of terminations along the split representation of the horizontal meridian in V-II (see Weller and Kaas, 1981). Second, it is also common for projections from one area to another to be discontinuous, probably due to the arrangement of subunits or modules in areas, and it is sometimes difficult to determine if a discontinuous projection indicates subunits in the area, or separate areas. Finally, there is some possibility that some areas project discontinuously within themselves. The posterior parietal "area" of owl monkeys seems to project within itself (Wagor *et al.*, 1975), but this may simply indicate that is is not a single area. More significantly, patch-like projections to locations around the injection site have recently been reported for striate cortex of tree shrews (Rockland and Lund, 1982).

3. Another problem with anatomical tracing methods is that a single zone of connections might extend from one area or nucleus to the next, and thereby fail to indicate separate subdivisions. This problem is a result of sensory representations having congruent borders so that similar regions of sensory surfaces are represented across borders. If two adjacent areas or nuclei receive input from the same source, a single continuous projection zone at the border would be expected. This problem is especially pronounced in the thalamus where lines of isorepresentation (Kaas *et al.*, 1972) often course uninterrupted through adjacent nuclei. Thus, a single injection of a tracer in striate cortex can produce a single band of label through two adjacent nuclei of the pulvinar complex in prosimians (Symonds and Kaas, 1978) and monkeys (Ogren and Hendrickson, 1976; Lin and Kaas, 1979). Similarily, a single injection in primary auditory cortex of cats produces a continuous band of label extending through more than one auditory nucleus in the thalamus (Anderson *et al.*, 1980).

D. Other Methods

While there are other methods for subdividing the brain, these methods have had less impact. The arguments against cerebral equipotentiality were greatly advanced by the results of electrically stimulating the brain, starting with the contribution of Fritsch and Hitzig in the 1870s, but this method has had only limited use in sensory systems. However, in awake humans, electrical stimulation has been valuable because verbal reports of sensations are possible (see Penfield and Rasmussen, 1952; Libet, 1973; Pollen, 1975). In addition, it is also possible to generate motor maps for some sensorimotor systems. Thus, a rough motor map can be generated by higher levels of stimulation for S-I as well as motor cortex (Woolsey, 1958), and eye movement maps have been obtained for the frontal eye fields (Robinson and Fuchs, 1969) and the superior colliculus (see Goldberg and Robinson, 1978). Ablation behavior studies have also been used to suggest subdivisions of the brain such as subdivisions of inferotemporal cortex (Iwai and Mishkin, 1969). More recently, the 2-deoxy-D-glucose method and measures of local blood flow have been used to map areas and subareas of increased metabolic activity under conditions of restricted sensory stimulation (see, e.g., Durham *et al.*, 1981; Roland *et al.*, 1981).

IV. SPECIES VARY IN NUMBERS OF SUBDIVISIONS; SIMILAR SUBDIVISIONS HAVE BEEN INDEPENDENTLY ACQUIRED

Modern mammals evolved from early mammals with small brains and very little neocortex (Diamond and Hall, 1969; Jerison, 1973). Some modern mammals still have very small brains with little neocortex, and a few of these have been used as models for the early stages of forebrain evolution in mammals. In particular, the hedgehog (e.g., Lende and Sadler, 1967; Kaas *et al.*, 1970; Ebner, 1969; Gould and Ebner, 1978; Gould *et al.*, 1978) and the opossum (e.g., Lende, 1969; Ebner, 1969) have been used to represent the brains of early eutherian and metatherian mammals, respectively. These studies indicate that there is not only very little neocortex in these mammals, but neocortex is subdivided into very few sensory representations (Fig. 4A). The hedgehog, for example, appears to have no more than two visual and two somatosensory representations, and its auditory cortex is small and unlikely to contain more than a few representations (Kaas *et al.*, 1970). In contrast, monkeys and cats have large brains with much neocortex containing many sensory representations. Some of these representations are shown for the domestic cat and a New World monkey, the owl monkey, in Figs. 3B and C. The owl monkey has at least 10 visual areas (Allman and Kaas, 1975; Kaas, 1978), 6 somatosensory areas, including 2 in the S-II region (Kaas *et al.*, 1981; Cusick *et al.*, 1981), 4 auditory areas (Imig *et al.*, 1977), and 2 or more motor-somatic representations, judging from work on squirrel monkeys (Strick and Preston, 1978). Old World monkeys have at least as many subdivisions (Van Essen, 1979; Kaas *et al.*, 1981; Merzenich and Brugge: 1973). Cats have at least 13 visual areas (Tusa and Palmer, 1980), 5 somatosentory areas (Clemo and Stein, 1982), and 7 auditory areas (see Merzenich and Kaas, 1980). The total number of cortical sensory representations in each of these mammals is obviously considerable, but the exact numbers are unknown. Most of the illustrated areas have been recently discovered, at least some are tentative, and the organization of much of the sensory responsive cortex is unknown. It also appears that the thalamus of monkeys and cats contains more nuclei than that of hedgehogs and opossums (e.g., consider the subdivisions of the lateralis posterior–pulvinar complex in monkeys and cats). Although all of the mentioned sensory representations are not firmly established, the conclusion seems inescapable that cats and monkeys have more sensory areas than hedgehogs. It follows that the number of sensory nuclei and areas in the forebrain has increased in the evolution of advanced mammals. Furthermore, since cats and monkeys independently evolved from mammals that must have been very much like hedgehogs in forebrain organization, multiple sensory areas must have evolved independently in several lines of descent.

If sensory representations increased in numbers in several lines of evolution, then it also may be likely that quite similar patterns of forebrain organizations would develop independently. Thus, sensory areas that appear to have many features in common in cats and monkeys, for example, (or even in New and Old World monkeys), may not be homologous in the sense of being present in a common ancestor, but they may have replicated or differentiated from the same "parent" representation (see below). The new structures in the separate lines can be said to be similar as the result of parallel or convergent evolution because they were subject to similar selection pressures, and because the common ancestor had the appropriate precursor state. If the early mammals had only a few sensory representations, then it is likely that similar solutions, e.g., the creation of V3, have reoccurred.

V. THE EVOLUTION OF SUBDIVISIONS

A. Multiple Representations

A wealth of data, reviewed in part above, indicate that the number of sensory representations has increased in mammalian evolution. Advanced mammals clearly have great numbers of sensory representations, and it seems impossible that all of these representations were hidden in some diminutive state in early primitive mammals, as if waiting for some future expansion and development. It is not known how increases in the numbers of sensory areas and nuclei were accomplished. There seem to be only two logical possibilities: (1) already existing subdivisions of the brain have gradually formed new subdivisions, or (2) new subdivisions have been suddenly created.

The view that single areas of cortex gradually become two or more areas, thereby leading to an increase in number has been expressed a number of times. A common opinion has been that brains of "lower" mammals are not fully differentiated into separate fields, and that the evolution from primitive to advanced cortical organization proceeded by the gradual separation and differentia-

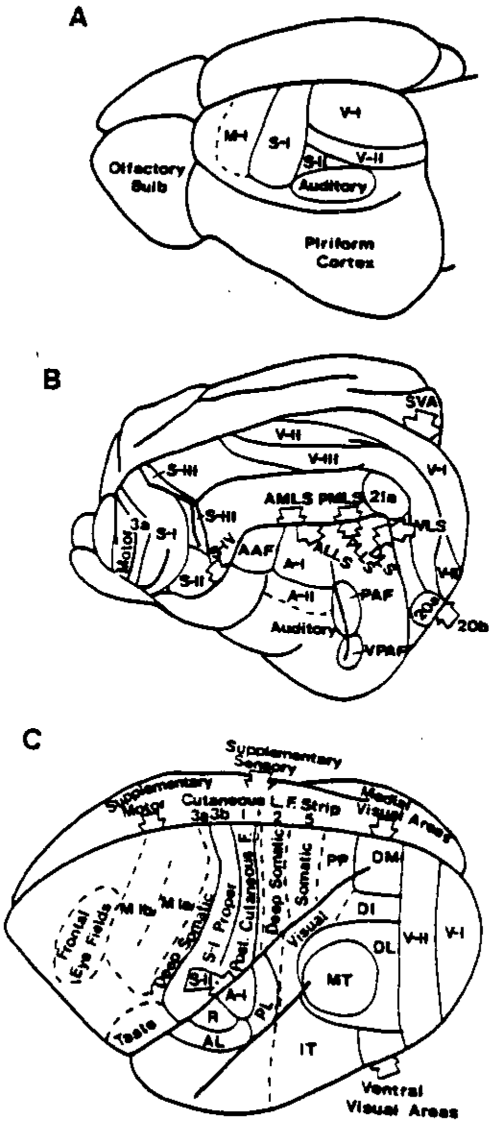

FIG. 3. Sensory and motor–sensory areas of cortex in (A) a prototypical mammal, the hedgehog, and two moderately advanced mammals (B) the domestic cat and (C) a New World monkey, the owl monkey. The hedgehog appears to have only a few areas (Kaas *et al.*, 1970): the primary motor (M-I), primary and secondary somatic (S-I and S-II), primary and secondary visual (V-I and V-II), and auditory (Aud.) fields. The cat and owl monkey have both independently acquired a greater number of sensory areas. Proposed subdivisions for the cat include four somatosensory fields, S-I, S-II, S-III, and S-IV (see Clemo and Stein, 1982); the anterior auditory field (AAF); the posterior auditory field (PAF); the ventral posterior field (VPAF); the primary auditory field (A-I); and a nontopographic second auditory field (A-II) (see Merzenich and Kaas, 1980). Visual areas for the cat are from Tusa and Palmer (1980) and include the traditional first (V-I), second (V-II), and third (V-III) visual areas: four representations identified by Brodmann's numbers, 20a and b and 21a and b; and six retinotopically organized suprasylvian visual areas [the posteromedial (PMLS), posterolateral (PLLS), anteromedial (AMLS), anterolateral (ALLS), dorsal (DLS), and ventral (VLS) lateral suprasylvian areas]. The splenial visual area (SVA) is from Graybiel and Berson (1981). The somatosensory areas in monkeys include separate representations in the 3a, 3b, 1, and 2 fields of Brodmann (see Mer-

tion of
1977). A
the repo
especial
brained
mediate
by any
lap, whi
to be th

Perha
presente
argumer
stimulat
motor (
ping pri
advance
complet
nuclei,
and par
areas in
single r
mechan
mamma
not son

How
overlap
based o
Becaus
judged
Lende
simply
Striate
in man
tion of
evidenc
region

---

zenich a
sensory
(R); ante
dorsome
inferoter

tion of originally overlapping fields (e.g., Luria, 1966; Lende, 1969; Jerison, 1977). A particular version of this theory is shown in Fig. 4A, which is based on the report of Lende (1969). The argument was made that visual, auditory, and especially somatic and motor areas of cortex are highly overlapping in small-brained mammals such as hedgehogs and opossums and thus reflect an intermediate stage of cortical evolution in mammals. An earlier stage, not represented by any extant mammals, was thought to be characterized by even greater overlap, while the complete separation recognized in monkeys and cats was thought to be the consequence of gradual separation.

Perhaps the strongest case for such a mechanism for increasing areas has been presented by Donoghue *et al.* (1979) and Donoghue and Ebner (1981). The argument is made, stemming in part from the electrophysiological mapping and stimulation studies of Lende (1963), that the primary somatosensory (S-I) and motor (M-I) fields are completely overlapping in opossums, partially overlapping principally in the foot representation in rats, and completely separate in advanced mammals such as cats and monkeys (Fig. 4B). The evidence for complete and partial overlap includes patterns of connections with thalamic nuclei, as well as sensory and motor maps. The point is that if complete overlap and partial overlap are found in some species of what are clearly two separate areas in other species, then it is logical to assume that the gradual separation of single representations into two complete representations has been a common mechanism for the evolution of multiple sensory representations in advanced mammals. If motor and somatic representations can gradually drift apart, why not somatic from somatic, visual from visual, and auditory from auditory?

However, there are two difficulties with the theory of gradual separation of overlapping representations. First, for the most part the evidence for overlap is based on recording and stimulating methods that fail to give precise boundaries. Because of a typical error of 1 mm or so, the smaller the brain the greater was the judged overlap. The overlap of visual, auditory, and somatic fields reported by Lende (1963) using surface electrodes for the very small-brained hedgehogs simply was not found with microelectrode mapping methods (Kaas *et al.*, 1970). Striate cortex, for example, is architectonically less distinct in the hedgehog than in many other mammals, but the boundaries of the area are sharp, the representation of the visual field within the area is retinotopically organized, and there is no evidence for overlap by other fields. It is perhaps instructive that the proposed region of overlap of somatic and motor fields in the rat is for the very narrow

---

zenich and Kaas, 1980) and several areas in the S-II region (Cusick *et al.*, 1981). Separate motor–sensory representations are from Strick and Preston (1978). For auditory fields [primary (A-I); rostral (R); anterior lateral (AL); and posterior lateral (PL)] and visual areas [V-I, V-II, dorsolateral (DL); dorsomedial (DM); dorsointermediate (DI); middle temporal (MT); posterior parietal (PP); and inferotemporal (IT)], see Merzenich and Kaas (1980). Also see text.

25.

representation of the foot where the resolution of both electrophysiological and anatomical methods is approached. It appears that those sensory areas that are present in primitive mammals are just as segregated as those found in advanced mammals.

A second problem for the theory of gradual separation is that adjoining sensory representations have different internal retinotopic, somatotopic, or tonotopic organizations. Typically, adjoining representations of the same modality are roughly mirror reversals of each other (Kaas, 1977). How could a sensory representation with one intrinsic organization gradually separate from a "parent" representation with a quite different intrinsic organization? An example of this problem is given in Fig. 4B. The overlapping somatic and motor representations found in the opossum have the same somatotopic organization. The organization is that of S-I of other mammals, not that proposed for M-I, which is said to have a mirror-image organization. Since S-I of mammals normally has a motor component, and electrical stimulation of S-I evokes movements in the same pattern as the sensory map, one interpretation of the data for opossums is simply that the representation is S-I with an increased motor component, and that M-I does not exist. In any case, if the somatotopic order in S-I is a–b–c, it is difficult to see how an opposite motor order of c–b–a could result from gradual separation (Fig. 4B).

The possibility of one representation gradually becoming two seems more likely in the thalamus where a single nucleus might gradually differentiate along lines of isorepresentation. Indeed, it is almost possible to argue that separate sets of layers in the lateral geniculate nucleus of some mammals form separate nuclei. The parvocellular and magnocellular layers of the lateral geniculate nucleus of primates, e.g., receive inputs from different classes of ganglion cells in the retina (Sherman *et al.*, 1976; Dreher *et al.*, 1976), magnocellular layers project above the parvocellular layers in cortex (see Kaas, 1978), and the magnocellular layers but not the parvocellular layers receive inputs from the MT (Lin *et al.*, 1977) and the superior colliculus (Harting *et al.*, 1978). Since separate nuclei in the pulvinar complex (see Weller and Kaas, 1981) and medial geniculate complex (Anderson *et al.*, 1980) join along lines of isorepresentation, separate nuclei could have evolved by a gradual segregation of connections of a single nucleus along lines of isorepresentation.

Another possibility is the duplication of existing structures (Fig. 4C). We have suggested elsewhere that it is likely that the number of cortical areas and subcortical nuclei increased by the sudden duplication of existing areas and nuclei (Allman and Kaas, 1971; Kaas, 1977, 1978). Such a mechanism seems to be common in evolution, leading to the serial replication of appendages in the ancestors of lobsters, e.g., followed by the gradual differentiation and specialization of function in the replicated parts (Gregory, 1935). For the brain, some

FIG.
has bee
would
separat
reports
in othe
increas
differe
denly c
initiall
and fu
explan

inher
repre
Hc
selec
dupl
presc
A ar
mem
pear
and
It

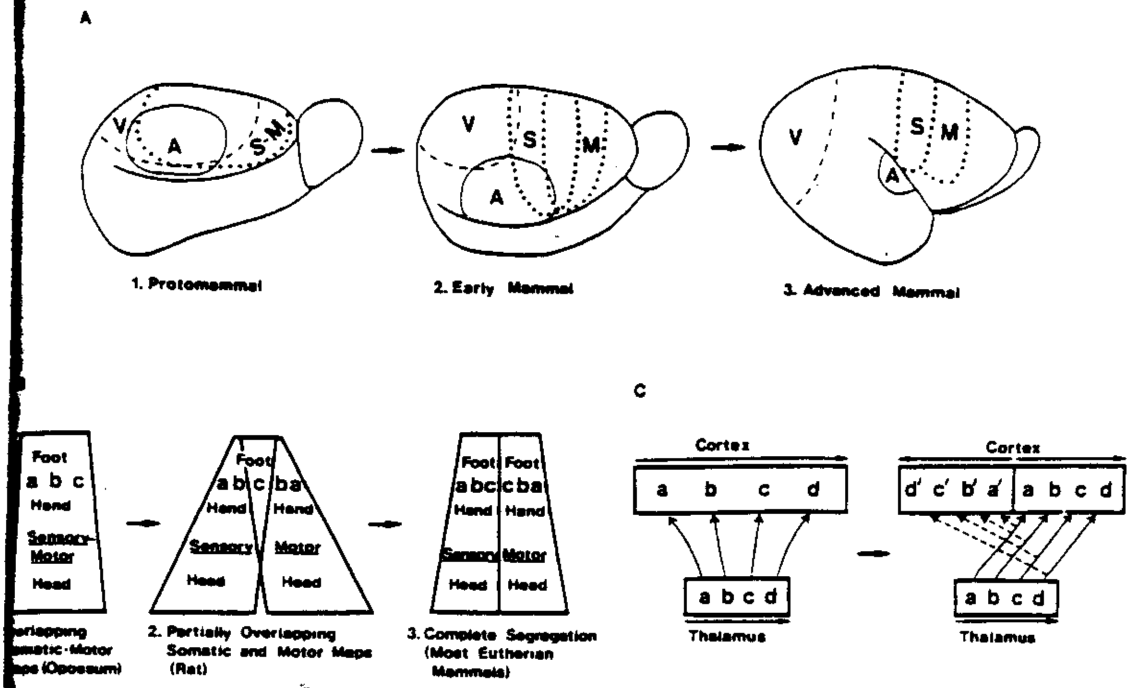

FIG. 4. Concepts of cortical evolution. (A) Segregation of overlapping areas. A common view has been that overlapping sensory and motor regions gradually separated. An extension of this view would have the evolution of the many representations within each modality resulting from gradual separation. (B) Gradual segregation. Evidence for gradual separation of cortical areas stems from reports of complete overlap of primary sensory and motor field in some mammals, partial separation in others, and complete separation in others. (C) Sudden replication. Another mechanism for the increase in numbers of sensory representations is that due to some mutation, a single representation differentiated during development into two mirror-image representations instead of one. This suddenly created new representation would attract a similar or identical set of connections, and would be initially redundant in function, but the gradual evolutionary differentiation of structure, connections, and functions of the two representations would be possible and expected. See text for further explanation.

inheritable accident could lead to the duplication of a given sensory representation.

However, such a duplication would not often be obvious, since there would be selective pressure for the rapid functional and morphological divergence of the duplicated structure, and a fossil record of the stages of transition would not be preserved. Yet, as a curious example of clear duplication in the brain, the single A and A1 layers of the lateral geniculate nucleus of carnivores have doubled in members of the weasel family, and there is no apparent difference in the appearance and connections of the duplicated layers (Sanderson, 1974; Sanderson and Kaas, 1974).

It is not known what factors would lead to the duplication of a sensory representation but some suggestions are possible. Adjoining sensory representations commonly approximate mirror reversals of each other, and mirror reversal duplications of the optic tectum have been induced in frog embryos by surgically rotating part of the thalamic precursor into the middle of the tectal precursor (Chung and Cooke, 1975, 1978). Apparently the thalamic cells induce the formation of an orderly retinal map in the tectum relative to the thalamic cells. Misplacing the thalamic cells can result in two orderly mirror-image maps rather than one. In a similar manner, mirror-reduplicated retinotectal maps have been produced in tadpoles by removing half of an eye in early larval stages (Feldman and Gaze, 1975). It is not clear why the maps duplicate, but the fact that they do so suggests mirror-image duplications can be induced in mammals as well. The duplication of a cortical representation could be as simple as acquiring a mutation that induces the development of maps in two directions instead of one. Since the retina projects to both of the duplicated tectal structures in frogs, it can be expected that any duplicated cortical area in mammals would be completely duplicated in connections as well. One of the two areas would be redundant, and could gradually, over many generations, acquire new connections and functions, or the two areas could share the original functions in some way, each giving up some, and each gradually acquiring new functions.

As a specific example of how cortical duplication might work, the single sensory and motor map as seen in opossums (Lende, 1963) with input from both somatic and motor nuclei in the thalamus (Killackey and Ebner, 1973; Donoghue and Ebner, 1981) could replicate by the somatotopic order being induced in two directions instead of one. This would yield two mirror-image sensorimotor maps which would attract the same connections from the thalamus (Fig. 4C). Gradually over later stages of evolution, the rostral cortical map would specialize for motor activities and lose thalamic somatosensory connections while the caudal map could specialize for sensory activities and lose the cerebellar relay via the ventral anterior thalamic nucleus to motor cortex. This speculation is offered as an alternative to the gradual separation view illustrated in Fig. 4B.

There is evidence from studies of Siamese cats (Guillery and Kaas, 1971; Guillery and Casagrande, 1976), where some of the axons from retinal ganglion cells are misdirected to the wrong side of the brain, that changes (errors) in the formation of connections are inheritable. Furthermore, changes in connections at one stage in a system lead to an avalanche of alterations and compensations throughout the system. Thus, with limited genetic modification, the organizations of sensory systems may be profoundly altered.

Whatever the mechanism, the acquisition of new sensory representation in any line of evolution would have great potential for increasing behavioral capability. By comparison, the specializations, differentiations, and expansions of already existing brain parts would have much less potential.

B. Modules and Layers

It is obvious from studies of the lateral geniculate nucleus of mammals that distinct layers have differentiated out of relatively uniform structures in terms of cell types, in a number of lines of descent (Walls, 1953; Kaas *et al.*, 1972; Robson and Hall, 1976). Likewise, the superior colliculus has become highly differentiated and laminated several times, e.g., in the independent lines of evolution leading to squirrels and tree shrews (Robson and Hall, 1976; Graham and Casagrande, 1980). The same can be said for the laminar development of striate cortex, and other sensory areas. Less is known about the species differences in cortical columns or modules, but it is likely that ocular dominance bands evolved independently in cats and primates. Most mammals that have been investigated do not have obvious segregation of ocular inputs in cortex (see De Bruyn and Casagrande, 1981). Such columns of input are highly segregated in Old World monkeys, but are weakly developed in prosimians and weakly developed or absent in New World monkeys. From this comparative evidence it appears that the common ancestors of cats and monkeys did not have ocular dominance bands, and they developed independently in two (perhaps more) evolutionary lines.

Like the replication of cortical areas, the segregation of inputs into columns or bands within areas could be a rather direct consequence of a few genetic changes. Constantine-Paton (1981) has studied the patterns of retinal projections to the tectum of three-eyed frogs, the extra eye achieved by adding a third eye primordium from a donor to a young frog embryo. In these frogs, two of the three eyes abnormally innervate a single tectal lobe, and ocular dominance can be studied in a structure that is normally monocular. After an initial state of overlap, the tectal inputs segregate into interdigitating eye-specific bands that are strikingly similar to the ocular dominance bands of cat and monkey visual cortex. It is highly unlikely that a genetic code exists for banding in the tectum per se since banding of direct retinal inputs never occurs in normal frogs. Rather, Constantine-Paton suggests that such banding is the general outcome of distinct inputs competing for the same space. A hypothesized "need" for axons from the same source to group, countered by a "need" for neurons to distribute topographically within a map results in the solution of alternating bands, the width of which is determined by the relative importance of the two factors (Constantine-Paton, 1981; Law and Constantine-Paton, 1981). Judging from the prevalence of discontinuous inputs to cortical areas, these two factors may commonly operate, often leading to banding of functionally distinct sets of cells.

Thus, it seems likely that marked changes in the subdivision of areas and nuclei into layers and modules can follow alterations in inputs. The segregation of function within subdivisions of areas and nuclei apparently has occurred repeatedly and independently, both as a result of changes of input, and probably other factors such as alterations of neuronal migration during development (Rakic, 1981).

VI. WHAT IS THE FUNCTIONAL SIGNIFICANCE OF SUBDIVIDING?

The capacity of the brains of advanced mammals to mediate a greater variety of tasks or functions than the brains of simpler mammals appears to have been accomplished mainly by increasing the numbers and internal differentiations of cortical areas and thalamic nuclei for sensory systems rather than by simply enlarging existing subdivisions. If the goal is to increase the range of behavior, the solution of simply increasing the size of a sensory area does not seem sufficient. Apparently new functions can not be added indefinitely to an existing area or nucleus.

One reason why areas and nuclei may not be able to continually add functions by growth is that the functions of an area depend on local groups of interconnection neurons or local circuits (e.g., Creutzfeldt *et al.*, 1975: Szentágothai, 1975, 1979; Mountcastle, 1978). Adding more neurons related to new functions would spread out the neurons for any existing local circuit, or if the local circuits are in modules or columns, spread out the classes of modules. Neurons interact with each other through synapses of axons on dendrites and cell bodies, dendrites on dendrites, and even axons on axons (see Peters *et al.*, 1976). The limit on the possible distance between interacting neurons is not necessarily from the axon, since they are capable of traversing long distances, and even within a single area such as striate cortex they may travel several millimeters to synapse (Gilbert and Wiesel, 1981). There may be problems in maintaining enough axon branches and finding all the appropriate targets if the target cells of axons are not grouped, but interactions over long distances are theoretically possible. Rather a major limit of distance seems to be imposed by dendrites, where the graded effects of synaptic contacts rapidly diminish with distance (Eccles, 1957). Dendritic fields of neurons are typically confined within a distance of 500 μm from the cell, although the apical dendrites of cortical pyramidal cells extend further (Lund, 1981). Contacts between dendrites appear to be a highly important form of interaction between neurons (e.g., Ralston, 1971, 1979; Scheibel and Scheibel, 1975; Graubard and Calvin, 1979), and dendrodendritic synapses have been found for both sensory nuclei (Ralston, 1971) and sensory areas of cortex (Shanks and Powell, 1981).

Given that at least some types of neuronal interactions require that the neurons are reasonably close together, it is impossible to continue to add functions to an area or nucleus by adding more neurons. If the functions are distributed through-

---

out th
additi
distan
altern
one le
the ne
Some
and m
limite
Intera
basic
neuro
conta
into t
relatir
1978
array
patter
nucle
statio
ences

Tr
arran
corte
is in

1.
of re
man
recei
visu
2.
stron
3.
4
have
of n
ticoc

out the area (in all parts of the sensory representation), then the continued addition of new neurons would separate the old neurons by greater and greater distances until the original neural network could no longer be maintained. The alternative is to separate neurons by functional types into layers and modules at one level, and into areas and nuclei mediating a limited number of processes at the next level. New functions are largely added by adding new areas and nuclei. Some advance is possible by increasing the segregation of neuron types in layers and modules, but the number of layers and modules within a nucleus or area is limited by the need for short distance interactions between layers and modules. Interactions between areas are possible, of course, over axonal pathways. The basic plan for brain organization and evolutionary progress, then, is to group neurons into clusters interacting over short distances compatible with dendritic contacts, and add new functions through the addition of new groups integrated into the system by axonal pathways. Areas and nuclei are arrays of such clusters relating a given set of functions to all parts of a sensory surface (see Mountcastle, 1978). Functions are added by adding new areas and nuclei, and thereby new arrays of neuronal clusters. Functions are integrated into systems via complex patterns of largely reciprocal connections between areas, and between areas and nuclei. The result is that systems are not constructed as linear series of connected stations, but as multiply interconnected stations, each subject to many influences, and influencing many others (Kaas, 1978).

VII. HOW SENSORY SYSTEMS WORK

Traditionally, sensory systems were envisioned as consisting of a few serially arranged processing stations on the way to association cortex and then to motor cortex (for review, see Merzenich and Kaas, 1980; Diamond, 1979). This model is inadequate for a number of reasons.

1. Complex sensory systems in advanced mammals consist of a large number of representations. These representations are not connected in a simple serial manner. Each representation typically projects to 10 or more other structures and receives input from a similar number (for a review of connections of the primate visual system, see Weller and Kaas, 1981).
2. The laminar patterns of the cortical connections are of several types, which strongly suggests that the functional roles of connections differ.
3. Very little cortex can be considered associational in the traditional sense.
4. Few representations have direct access to motor cortex, or even appear to have indirect cortical relays to motor cortex. Thus, the final target of the results of most sensory processing does not appear to be motor cortex through corticocortical connections.

31.

Rather than a hierarchical processing system, a network of multiple interconnections allows most of the representations in a system to be simultaneously active while processing sensory events. Each representation probably mediates several aspects of the total processing, and the output from each representation probably both provides basic information to other representations, and modulates the outputs of other representations. In addition, the many subcortical projections of most representations suggest that they provide outputs that rather directly influence behavior, and that the structures that generate behavior must be simultaneously influenced by the outputs of many cortical fields. When the subcortical projections of 6 visual areas in owl monkeys were compared, for example, a total of 16 subcortical targets were noted and each target typically received input from 4 or more of the 6 cortical areas (Graham *et al.*, 1979).

The large number of areas actively processing any sensory event, and the great number of influences on the generation of any behavior, explain why restricted cortical lesions seldom produce dramatic impairments. The lesion degrades aspects of the sensory–perceptual processing, so that the distribution of some information to other centers is lost, the modulating influence on some other structures and a portion of the inputs to behavior-generating, memory, and affective systems is lost, but multiple other inputs to these other systems remain, and the defects and changes in performance may go on largely unnoticed.

VIII. SUMMARY AND CONCLUSIONS

The basic subdivision of sensory systems is the area or nucleus. Areas and nuclei, as equivalent structures, contain systematic sensory representations, are architectonically distinct, interconnect with a number of other structures in a unique pattern, are distinguished by the response characteristics of the population of neurons, and uniquely contribute to the sensory–perceptual processing of the system. Sensory areas and nuclei have sharp boundaries, and thereby have "absolute localization." Species differ in number of areas and nuclei, and increases in numbers have occurred independently in many lines of evolution. Complex behaviors have been acquired largely by increasing the number of areas and nuclei.

Areas and nuclei are commonly differentiated along the lines of isorepresentation into layers, which allows the grouping of neurons specialized for receiving certain inputs, providing certain outputs, or mediating types of local computations. Areas and nuclei also may be differentiated in directions counter to lines of isorepresentation into processing modules devoted to classes of sensory inputs. While layers often appear to have sharp boundaries, it is not certain to what extent modules have absolute or relative boundaries. Since there is evidence for several types of modules, types with either absolute or relative localization might exist. Modules of the same type in cortex are typically joined in long bands, which bifurcate and merge at various distances. All the modules within an area processing input from a given location on a sensory surface are grouped to form a "hypercolumn." Like nuclei and areas, types of modules and layers have evolved independently a number of times. Subsets of areas and nuclei appear to be grouped into subsystems of functionally related structures, but a clear understanding of what types of subsystems exist has not yet emerged.

Mechanisms of gradual differentiation and separation of single areas and nuclei into additional areas and nuclei, and the sudden replication of areas and nuclei have been proposed for the phylogenetic increase in the numbers of these structures. Probably both mechanisms have led to the increases, but it appears likely that sudden replication has been the common mechanism for cortical areas.

Advanced mammals have many sensory representations within each major sensory system. These representations are complexly interconnected, and most must participate in the processing of a sensory event within the system. The multitude of subcortical efferent connections of each area suggests that most cortical representations influence behavior, memory, and emotion, in a rather direct manner.

ACKNOWLEDGMENTS

Research by the author has been supported by the National Science Foundation, and the National Institutes of Health. Helpful comments on this article have been made by a number of friends and colleagues including V. A. Casagrande, M. Constantine-Paton, F. F. Ebner, D. J. Felleman, M. M. Merzenich, T. P. Pons, M. K. Powers, M. Sur, L. L. Symonds, J. T. Wall, and R. E. Weller. Illustrations were drawn by R. E. Weller.

REFERENCES

Adrian, E. D. (1943). Afferent areas in the brain of ungulates. *Brain* **66**, 89–103.

Allman, J. (1977). Evolution of the visual system in early primates. *Progr. Psychol. Physiol. Psychol.* **7**, 1–53.

Allman, J. M., and Kaas, J. H. (1971). A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res.* **31**, 85–105.

Allman, J. M., and Kaas, J. H. (1974). The organization of the second visual area (V-II) in the owl monkey: A second order transformation of the visual hemifield: *Brain Res.* **81**, 199–213.

Allman, J. M., and Kaas, J. H. (1975). The dorsomedial cortical visual area: A third tier area in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Res.* **100**, 473–487.

Allman, J. M., Kaas, J. H., Lane, R. H., and Miezin, F. M. (1972). A representation of the visual field in the inferior nucleus of the pulvinar in the owl monkey (*Aotus trivirgatus*). *Brain Res.* **40**, 291–302.

Anderson, R. A., Knight, P. L., and Merzenich, M. M. (1980). The thalamocortical and corticothalamic connections of AI, AII, and the anterior auditory field (AAF) in the cat: Evidence for two largely segregrated systems of connections. *J. Comp. Neurol.* **144**, 663–701.

Baker, V. F., Petersen, S. E., Newsome, W. T., and Aldman, V. M. (1981). Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*): A quantitative composition of Medial, Dorsomedial, Dorsolateral, and Middle Temporal Areas. *J. Neurophysiol.* **45**, 397–416.

Beck, E. (1925). Zur Exaktheit der myeloarchitektonischen Felderrung des Cortex cerebri. *J. Psychol. Neurol.* **36**, 281–288.

Billings-Gagliardi, S., Chan-Palay, V., and Palay, S. L. (1979). A review of lamination in area 17 of the visual cortex in *Macaca mulatta*. *J. Neurocytol.* **3**, 619–629.

Braak, H. (1976). On the striate area of the human isocortex. A Golgi- and pigment-architectonic study. *J. Comp. Neurol.* **166**, 341–364.

Braak, H. (1978). On the pigment-architectonics of the human telencephalic cortex. *In* "Architectonics of the Cerebral Cortex" (M. A. B. Brazier and H. Petsche, eds.), pp. 137–157. Raven, New York.

Brazier, M. A. B. (1978). Architectonics of the cerebral cortex: Research in the 19th century. *In* "Architectonics of the Cerebral Cortex" (M. A. B. Brazier and H. Petsche, eds.), pp. 9–29. Raven, New York.

Brodmann, K. (1909). Vergleichende Lokalisationslehre der Grosshirnrinde, p. 324. Barth, Leipzig.

Brunso-Bechtold, J. K., and Casagrande, V. A. (1981). Effect of bilateral enucleation on the development of layers in the dorsal lateral geniculate nucleus. *Neuroscience* **6**, 2579–2586.

Chung, S.-H., and Cooke, J. (1975). Polarity of structure and of ordered nerve connections in the developing amphibian brain. *Nature (London)* **258**, 126–132.

Chung, S. H., and Cooke, J. (1978). Observations on the formation of the brain and of nerve connections following embryonic manipulation of the amphibian neural tube. *Proc. R. Soc. Lond.* **201**, 335–373.

Clemo, H. R., and Stein, B. E. (1982). Somatosensory cortex: A "new" somatotopic representation. *Brain Res.* **235**, 162–168.

Constantine-Paton, M. (1981). Induced ocular-dominance zones in tectal cortex. *In* "The Organization of Cerebral Cortex" (F. O. Schmitt, F. G. Worden, G. Adelman, and S. G. Dennis, eds.), pp. 47–67. MIT Press, Cambridge, Massachusetts.

Cowey, A. (1964). Projection of the retina on the striate cortex and prestriate cortex in the squirrel monkey. *Saimiri sciureus*. *J. Neurophysiol.* **27**, 266–393.

Creutzfeldt, O., Innocenti, G. M., and Brooks, D. (1975). Neurophysiological experiments on afferent and intrinsic connections on the visual cortex (Area 17). In "Golgi Centennial Symposium" (M. Santini, ed.), pp. 319–327. Raven, New York.

Cusick, C. G., Wall, J. T., Felleman, D. J., and Kaas, J. H. (1981). An electrophysiological and anatomical investigation of the organization of the second somatosensory area, S-II, in owl monkeys. *Anat. Rec.* **7**, 834.

De Bruyn, E. J., and Casagrande, V. A. (1981). Demonstrations of ocular dominance columns in the New World primate by means of monocular deprivation. *Brain Res.* **207**, 453–458.

Diamond, I. T. (1979). The subdivisions of neocortex: A proposal to revise the traditional view of sensory, motor, and association areas. *Prog. Psychol. Physiol. Psychol.* **8**, 1–43.

Diamond, I. T., and Hall, W. C. (1969). Evolution of neocortex. *Science* **164**, 251–262.

Donoghue, J. P., and Ebner, F. F. (1981). The organization of thalamic projections to the parietal cortex of the Virginia opossum. *J. Comp. Neurol.* **198**, 365–388.

Donoghue, J. P., Kerman, K. L., and Ebner, F. F. (1979). Evidence for two organizational plans in the somatic sensory-motor cortex of the rat. *J. Comp. Neurol.* **183**, 647–666.

Dreher, B., Fukada, Y., and Rodieck, R. (1976). Identification, classification, and anatomical segregation of cells with X-like and Y-like properties in the lateral geniculate nucleus of Old World primates. *J. Physiol. (London)* **258**, 433–452.

Durham, D., Woolsey, T. A., and Kruger, L. (1981). Cellular localization of 2-[^{3}H]deoxy-D-glucose from paraffin-embedded brains. *J. Neurosci.* **1,** 519–526.

Dykes, R. W., Sur, M., Merzenich, M. M., Kaas, J. H., and Nelson, R. J. (1981). Regional segregation of neurons responding to quickly adapting, slowly adapting, deep and pacinian receptors within thalamic ventroposterior lateral and ventroposterior inferior nuclei in the squirrel monkey (*Saimiri sciureus*). *Neuroscience* **6,** 1687–1692.

Ebner, F. F. (1969). A comparison of primitive forebrain organization in metatherian and eutherian mammals. *Ann. N.Y. Acad. Sci.* **167,** 241–257.

Eccles, J. C. (1957). "The Physiology of Nerve Cells." The John Hopkins Press, Baltimore, Maryland.

Feldman, J. D., and Gaze, R. M. (1975). The development of half-eyes in xenopus tadpoles. *J. Comp. Neurol.* **162,** 13–22.

Felleman, P. J., Nelson, R. J., Sur, M., and Kaas, J. H. (1979). Organization of the somatosensory cortex in cebus monkeys. *Neurosci. Abstr.* **5,** 706.

Felleman, D. J., Wall, J. T., Cusick, C. G., and Kaas, J. H. (1981). Evidence for a single cutaneous representation within the S-I region of the cat. *Anat. Rec.* **199,** 82A.

Gilbert, C. D., and Wiesel, T. N. (1981). Laminar specialization and intracortical connections in cat primary visual cortex. *In* "The Organization of the Cerebral Cortex" (F. O. Schmitt, F. G. Worden, G. Adelman, and S. G. Dennis, eds.), pp. 163–191. MIT Press, Cambridge, Massachusetts.

Glickstein, M., Stein, J., and King, R. (1972). Visual input to the pontine nuclei. *Science* **178,** 1110–1111.

Goldberg, M. E., and Robinson, D. E. (1978). Visual system: Superior colliculus. *In* "Handbook of Behavioral Neurobiology" (R. B. Masterton, ed.), Vol. I, pp. 119–164. Plenum, New York.

Gould, H. J., and Ebner, F. F. (1978). Connections of the visual cortex in the hedgehog (*Paraechinus hypomelas*) II., Corticocortical projections. *J. Comp. Neurol.* **177,** 473–502.

Gould, H. J., Hall, W. C., and Ebner, F. F. (1978). Connections of the visual cortex in the hedgehog (*Paraechinus hypomelas*) I. Thalamocortical projections. *J. Comp. Neurol.* **177,** 445–472.

Gouras, P., and Kruger, J. (1979). Responses of cells in foveal visual cortex of the monkey to pure color contrast. *J. Neurophysiol.* **42,** 850–860.

Graham, J., and Casagrande, V. A. (1980). A light microscopic and electron microscopic study of the superficial layers of the superior colliculus of the tree shrew (*Tupaia glis*). *J. Comp. Neurol.* **191,** 133–151.

Graham, J., Lin, C.-S., and Kaas, J. H. (1979). Subcortical projections of six visual cortical areas in the owl monkey, (*Aotus trivirgatus*). *J. Comp. Neurol.* **187,** 557–580.

Graubard, K., and Calvin, W. H. (1979). Presynaptic dendrites: Implications of spikeless synaptic transmission and dendritic geometry. *In* "The Neurosciences, Fourth Study Program" (F. O. Schmitt and F. G. Worden, eds.), pp. 317–331. MIT Press, Cambridge, Massachusetts.

Graybiel, A. M., and Berson, D. M. (1981). On the relation between transthalamic and transcortical pathways in the visual system. *In* "The Organization of the Cerebral Cortex" (F. O. Schmitt, F. G. Worden, G. Adelman, and S. G. Dennis, eds.), pp. 285–319. MIT Press, Cambridge, Massachusetts.

Gregory, W. K. (1935). Reduplication in evolution. *Q. Rev. Biol.* **10,** 272–290.

Guillery, R. W., and Casagrande, V. A. (1976). Adaptive connections formed in the visual pathways in response to congenitally afferent inputs. *Cold Spring Harbor Symp. Quant. Biol.* **40,** 611–617.

Guillery, R. W., and Kaas, J. H. (1971). A study of normal and congenitally abnormal retinogeniculate projections in cats. *J. Comp. Neurol.* **143,** 73–100.

Guillery, R. W., and Stelzner, D. J. (1970). The differential effects of unilateral lid closure upon the monocular and binocular segments of the dorsal lateral geniculate nucleus in the cat. *J. Comp. Neurol.* **139**, 413–422.

Harting, J. K., Casagrande, V. A., and Weber, J. T. (1978). The projection of the primate superior colliculus upon the dorsal lateral geniculate nucleus: Autoradiographic demonstration of interlaminar distributions of tectogeniculate axons. *Brain Res.* **150**, 593–599.

Hassler, R. (1967). Comparative anatomy of the central visual systems in day and night-active primates. *In* "Evolution of the Forebrain" (R. Hassler and H. Stephan, eds.), pp. 419–434. Plenum, New York.

Hubel, D. H., and Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* **28**, 229–289.

Hubel, D. H., and Wiesel, T. N. (1974). Uniformity of monkey striate cortex: A parallel relationship between field size, scatter and magnification factor. *J. Comp. Neurol.* **158**, 295–302.

Hubel, D. H., and Wiesel, T. N. (1977). Functional architecture of macaque monkey visual cortex. *Proc. R. Soc. Lond. Ser. B.* **198**, 1–59.

Humphrey, A. L., Albano, J. E., and Norton, T. T. (1977). Organization of ocular dominance in the striate cortex of the tree shrew. *Brain Res.* **134**, 225–236.

Imig, T. J., and Adrian, H. O. (1977). Binaural columns in the primary field (A1) of cat auditory cortex. *Brain Res.* **138**, 241–257.

Imig, T. J., Ruggero, M. H., Kitzes, L. M., Javel, E., and Brugge, J. F. (1977). Organization of auditory cortex in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* **171**, 111–128.

Iwai, E., and Mishkin, M. (1969). Further evidence on the locus of the visual area in the temporal lobe in the monkey. *Exp. Neurol.* **25**, 585–594.

Jerison, H. J. (1973). "The Evolution of the Brain and Intelligence." Academic Press, New York.

Jerison, H. J. (1977). The theory of encephalization. *Ann. N.Y. Acad. Sci.* **199**, 146–160.

Johnson, J. I. (1980). Morphological correlates of specialized elaborations in somatic sensory cerebral neocortex. *In* "Comparative Neurology of the Telencephalon" (S. O. E. Ebbesson, ed.), pp. 423–447. Plenum, New York.

Kaas, J. H. (1977). Sensory representations in mammals. *In* "Function and Formation of Neural Systems" (G. S. Stent, ed.), pp. 65–80. Dahlem Konferenzen, Berlin.

Kaas, J. H. (1978). The organization of visual cortex in primates. *In* "Sensory Systems of Primates" (C. R. Noback, ed.). Plenum, New York.

Kaas, J. H. (1982). The somatosensory cortex and thalamus in *Galago*. *In* "The Lesser Bushbaby (*Galago*) as an Animal Model: Selected Topics" (E. D. Haines, ed). CRC Press, Boca Raton, Florida. In press.

Kaas, J. H., Hall, W. C., and Diamond, I. T. (1970). Cortical visual areas I and II in the hedgehog: Relation between evoked potential maps and architectonic subdivisions. *J. Neurophysiol.* **33**, 595–615.

Kaas, J. H., Guillery, R. W., and Allman, J. M. (1972). Some principles of organization in the dorsal lateral geniculate nucleus. *Brain Behav. Evol.* **6**, 253–299.

Kaas, J. H., Lin, C. S., and Wagor, E. (1977). Cortical projections of posterior parietal cortex in owl monkeys. *J. Comp. Neurol.* **171**, 387–408.

Kaas, J. H., Huerta, M. F., Weber, J. T., and Harting, J. K. (1978). Patterns of retinal terminations and laminar organization of the lateral geniculate nucleus of primates. *J. Comp. Neurol.* **182**, 517–554.

Kaas, J. H., Nelson, R. J., Sur, M., and Merzenich, M. M. (1981). Organization of somatosensory cortex in primates. *In* "The Organization of the Cerebral Cortex" (F. O. Schmitt, F. G. Worden, G. Adelman, and S. G. Dennis, eds.), pp. 237–261. MIT Press, Cambridge, Massachusetts.

Killackey, H. P., and Belford, G. R. (1979). The formation of afferent patterns in the somatosensory cortex of the neonatal rat. *J. Comp. Neurol.* **183**, 285–304.

Killackey, H. P., and Ebner, F. (1973). Convergent projection of the three separate thalamic nuclei onto a single cortical area. *Science* **179**, 283–285.

Krieg, W. J. S. (1946). Connections of the cerebral cortex, I. The albino rat. A. Topography of the cortical areas. *J. Comp. Neurol.* **84**, 221–227.

Kuhlenbeck, H. (1978). "The Central Nervous System of Vertebrates, Vol. V, Part II. Mammalian Telencephalon, Surface Morphology and Cerebral Cortex," pp. 635. Karger, Basel.

Lashley, K. S., and Clark, G. (1946). The cytoarchitecture of the cerebral cortex of Ateles: A critical examination of architectonic studies. *J. Comp. Neurol.* **85**, 223–305.

Law, M. I., and Constantine-Paton, M. (1981). Anatomy and physiology of experimentally produced striped tecta. *J. Neurosci.* **1**, 741–759.

Lee, B. B., Albus, K., Heggelund, P., Hulme, M. J., and Creutzfeldt, O. D. (1977). The depth distribution of optimal stimulus orientations for neurons in cats Area 17. *Exp. Brain Res.* **27**, 301–314.

Le Gros Clark, W. E. (1952). A note on cortical cyto-architectonics. *Brain* **75**, 96–104.

Lende, R. A. (1963). Cerebral cortex: a sensorimotor amalgam in the Marsupialia. *Science* **141**, 730–732.

Lende, R. A. (1969). A comparative approach to neocortex: Localization in monotremes, marsupials, and insectivores. *Ann. N.Y. Acad. Sci.* **167**, 262–276.

Lende, R. A., and Sadler, K. M. (1967). Sensory and motor areas in neocortex of hedgehog (Erinaceus). *Brain Res.* **5**, 390–405.

Libet, B. (1973). Electrical stimulation of cortex in human subjects and conscious sensory aspects. *In* "Handbook of Sensory Physiology, Somatosensory System" (A. Iggo, ed.), Vol. II, pp. 773–790. Springer-Verlag, Berlin and New York.

Lin, C.-S., and Kaas, J. H. (1977). Projections from cortical visual areas 17, 18, and MT onto the dorsal lateral geniculate nucleus in owl monkeys. *J. Comp. Neurol.* **173**, 457–473.

Lin, C.-S., and Kaas, J. H. (1979). The inferior pulvinar complex in owl monkeys: Architectonic subdivisions and patterns of input from the superior colliculus and subdivisions of visual cortex. *J. Comp. Neurol.* **187**, 655–678.

Lin, C.-S., and Kaas, J. H. (1980). Projections from the medial nucleus of the inferior pulvinar complex to the middle temporal area of the visual cortex. *Neuroscience* **5**, 2219–2228.

Lorente, de Nó (1938). Cerebral cortex: Architecture, intracortical connections, motor projections. *In* "Physiology of the Nervous System" (Fulton, ed.), pp. 288–312. Oxford Univ. Press, London and New York.

Luria, A. R. (1966). "Higher Cortical Functions in Man," p. 634. Basic Books, New York. [In English].

Merzenich, M. M., and Brugge, J. F. (1973). Representation of the cochlear partition on the superior temporal plane of the macaque monkey. *Brain Res.* **50**, 275–296.

Merzenich, M. M., and Kaas, J. H. (1980). Principles of organization of sensory-perceptual systems in mammals. *Prog. Psychobiol. Physiol. Psychol.* **9**, 1–42.

Merzenich, M. M., Roth, G. L., Anderson, R. A., Knight, P. L., and Colwell, S. A. (1977). Some basic features of organization of the central auditory nervous system. *In* "Psychophysics and Physiology of Hearing" (E. F. Evans and J. P. Wilson, eds.), pp. 1–11. Academic Press, New York.

Merzenich, M. M., Kaas, J. H., Sur, M. and Lin, C.-S. (1978). Double representation of the body surface within cytoarchitectonic Areas 3b and 1 in "S-I" in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* **181**, 41–74.

Merzenich, M. M., Sur, M., Nelson, R. J., and Kaas, J. H. (1981). Organization of the SI cortex: Multiple cutaneous representations in areas 3b and 1 of the owl monkey. *In* "Cortical sensory organization, Vol. 1, multiple somatic areas" (C. N. Woolsey, ed.), pp. 47–66. Humana Press, Clifton, New Jersey.

Michael, C. R. (1981). Columnar and laminar organization of color cells in monkey striate cortex. *J. Neurophysiol.* **46,** 587–604.

Middlebrooks, J. D., Dykes, R. W., and Merzenich, M. M. (1980). Binaural response-specific bands in primary auditory cortex (A1) of the cat: Topographical organization orthogonal to isofrequency contours. *Brain Res.* **181,** 31–48.

Mott, F. W. (1907). The progressive evolution of the structure and functions of visual cortex in mammalia. *Arch. Neurol. (Mott's)* **3,** 1–117.

Mountcastle, V. B. (1957). Modality and topographic properties of single neurons of cats' somatic sensory cortex. *J. Neurophysiol.* **2,** 408–434.

Mountcastle, V. B. (1978). An organizing principle for cerebral function: The unit module and the distributed system. *In* "The Mindful Brain" (G. M. Edelman and V. B. Mountcastle, eds.), pp. 7–50. MIT Press, Cambridge, Massachusetts.

Nelson, R. J., and Kaas, J. H. (1981). Connections of the ventroposterior nucleus of the thalamus with the body surface representations in cortical Areas 3b and 1 of the cynomolgus macaque (*Macaca fascicularis*). *J. Comp. Neurol.* **199,** 29–64.

Norton, T. T., and Casagrande, V. A. (1982). Laminar organization of receptive-field properties in the lateral geniculate nucleus of bushbaby (*Galago crassicaudatis*). *J. Neurophysiol.* **47,** 715–741.

Ogren, M., and Hendrickson, A. (1976). Pathways between striate cortex and subcortical regions in *Macaca mulatta* and *Saimiri sciureus:* Evidence for a reciprocal pulvinar connection. *Exp. Neurol.* **53,** 780–800.

Palmer, L. A., Rosenquist, A. C., and Tusa, R. J. (1978). The retinotopic organization of lateral suprasylvian visual areas in the cat. *J. Comp. Neurol.* **177,** 237–256.

Penfield, W., and Rasmussen, T. (1952). "The Cerebral Cortex of Man." Macmillan, New York.

Peters, A., Palay, S. L., and Webster, H. F. (1976). "The Fine Structure of the Nervous System," p. 406. Saunders, Philadelphia, Pennsylvania.

Pollen, D. A. (1975). Some perceptual effects of electrical stimulation of the visual cortex in man. *In* "The Nervous System, the Clinical Neurosciences" (D. B. Tower, ed.), Vol. II, pp. 519–528. Raven, New York.

Ralston, H. J. (1971). Evidence for presynaptic dendrites and a proposal for their mechanism of action. *Nature (London)* **230,** 585–587.

Ralston, H. J. (1979). Neuronal circuitry of the ventrobasal thalamus: The role of presynaptic dendrites. *In* "The Neurosciences, Fourth Study Program" (F. O. Schmitt and F. G. Worden, eds.), pp. 373–379. MIT Press, Cambridge, Massachusetts.

Randolph, M., and Semmes, J. (1970). Behavioral consequences of selective subtotal ablation in the postcentral gyrus of *Macaca mulatta. Brain Res.* **70,** 55–70.

Robinson, D. A., and Fuchs, A. F. (1969). Eye movements evoked by stimulation of frontal eye fields. *J. Neurophysiol.* **32,** 637–648.

Robson, J. A., and Hall, W. C. (1976). Projections from the superior colliculus to the dorsal lateral geniculate nucleus in the grey squirrel (*Sciuvus carolinensis*). *J. Comp. Neurol.* **173,** 355–388.

Rockel, A. J., Hioms, R. W., and Powell, T. P. S. (1980). The basic uniformity in structure of the neocortex. *Brain* **103,** 221–244.

Rockland, K. S., and Lund, J. S. (1982). Widespread periodic intrinsic connections in tree shrew visual cortex (area 17). *Science* **215,** 1532–1534.

Roland, P. E., Skinhøj, E., and Lassen, N. A. (1981). Focal activation of human cerebral cortex during auditory discrimination. *J. Neurophys.* **45,** 1139–1151.

Rose, J. E., and Woolsey, C. N. (1948). Structure and relations of limbic cortex and anterior thalamic nuclei in rabbit and cat. *J. Comp. Neurol.* **89,** 279–348.

Rose, J. E., and Woolsey, C. N. (1949). The relations of the thalamic connections, cellular structure, and evocable electrical activity in the auditory region of the cat. *J. Comp. Neurol.* **91,** 441–446.

Rowe, M. H., and Stone, J. (1977). Naming of neurons. Classification and naming of the cat retinal ganglion cells. *Brain Behav. Evol.* **14,** 185–216.

Sanderson, K. J. (1974). Lamination of the dorsal lateral geniculate nucleus in carnivores of the weasel (*Mustelidae*), raccoon (*Procyonidae*) and fox (*Canidae*) families. *J. Comp. Neurol.* **153,** 239–266.

Sanderson, K. J., and Kaas, J. H. (1974). Thalamocortical interconnections of the visual system of the mink. *Brain Res.* **70,** 139–143.

Scheibel, M. E., and Scheibel, A. B. (1975). Dendrites as neuronal couplers: The dendrite bundle. *In* "Golgi Centennial Symposium" (M. Santini, ed.), pp. 347–365. Raven, New York.

Schiller, P. H., and Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *J. Neurophysiol.* **41,** 788–797.

Shanks, M. F., and Powell, T. P. S. (1981). An electron microscopic study of the termination of thalamocortical fibers in Areas 3b, 1 and 2 of the somatic sensory cortex in the monkey. *Brain Res.* **218,** 35–47.

Sherman, S., Wilson, J., Kaas, J., and Webb. S. (1976). X- and Y-cells in the dorsal lateral geniculate nucleus of the owl monkey (*Aotus trivirgatus*). *Science* **192,** 475–477.

Sholl, D. A. (1956). "The Organization of the Cerebral Cortex." Methuen, London.

Smith, G. E. (1906). A new topographic survey of human cerebral cortex, being an account of the distribution of the anatomically distinct cortical areas and their relationship to the cerebral sulci. *J. Anat. Physiol.* **42,** 237–254.

Strick, P. L., and Preston, J. B. (1978). Multiple representation in primate motor cortex. *Brain Res.* **154,** 366–370.

Sur, M., Nelson, R. J., and Kaas, J. H. (1978). The representation of the body surface in somatosensory Area I of the grey squirrel. *J. Comp. Neurol.* **179,** 425–450.

Sur, M., Merzenich, M. M., and Kaas, J. H. (1980a). Magnification, receptive-field area, and "hypercolumn" size in Areas 3b and 1 of somatosensory cortex in owl monkeys. *J. Neurophysiol.* **44,** 295–311.

Sur, M., Nelson, R. J., and Kaas, J. H. (1980b). Representation of the body surface in somatic koniocortex in the prosimian *Galago. J. Comp. Neurol.* **189,** 381–402.

Sur, M., Wall, J. T., and Kaas, J. H. (1981). Modular segregation of functional cell classes within the postcentral somatosensory cortex of monkeys. *Science* **212,** 1059–1061.

Sur, M., Nelson, R. J., and Kaas, J. H. (1982). Representation of the body surface in cortical areas 3b and 1 of squirrel monkeys: Comparisons with other primates. Submitted.

Symonds, L. L., and Kaas, J. H. (1978). Connections of striate cortex in the prosimian, *Galago senegalensis. J. Comp. Neurol.* **181,** 477–512.

Szentágothai, J. (1975). The "module concept" in cerebral cortical architecture. *Brain Res.* **95,** 475–496.

Szentágothai, J. (1979). Local neuron circuits of the neocortex. *In* "The Neurosciences, Fourth Study Program" (F. O. Schmitt and F. G. Worden, eds.), pp. 399–415. MIT Press, Cambridge, Massachusetts.

Tusa, R. J., and Palmer, L. A. (1980). Retinotopic organization of Areas 20 and 21 in the cat. *J. Comp. Neurol.* **193,** 147–164.

Tyner, C. F. (1975). The naming of neurons. Application of taxonomic theory to the study of cellular populations. *Brain Behav. Evol.* **12,** 75–96.

Van Essen, D. C. (1979). Visual areas of the mammalian cerebral cortex. *Ann. Rev. Neurosci.* **2,** 227–263.

Van Essen, D. C., Maunsell, J. H. R., and Bixby, J. L. (1981). The middle temporal visual area in

39.

the macaque: Myeloarchitecture connections, functional properties and topographic organization. *J. Comp. Neurol.* **199**, 293–326.

Volkmann, V. (1926). Vergleichende Untersuchungen an der Rinde der "Motorischen" and "Schegion" von Nagetieren. *Vehandl. Anat. Ges.* **35**, 234–243.

Von Economo, C., and Koskinas, G. N. (1925). Die Cytoarchitecktonik der Hirnrinde des erwachsenen Menschen. Springer, Vienna and Berlin.

Wagor, E., Lin, C.-S., and Kaas, J. H. (1975). Some cortical projections of the dorsomedial visual area (DM) of association cortex in the owl monkey, *Aotus trivirgatus*. *J. Comp. Neurol.* **163**, 227–250.

Walls, G. W. (1953). The lateral geniculate nucleus and visual histophysiology. *Univ. Calif. Publ. Physiol.* **9**, 1–100.

Welker, C. (1976). Receptive fields of barrels in the somatosensory neocortex of the rat. *J. Comp. Neurol.* **166**, 173–190.

Weller, R. E., and Kaas, J. H. (1981). Cortical and subcortical connections of visual cortex in primates. *In* "Cortical Sensory Organization: Multiple Visual Areas" (C. N. Woolsey, ed.), Vol. 2, pp. 121–155. Humana Press, Clifton, New Jersey.

Wong-Riley, M. T. T., Merzenich, M. M., and Leake, P. A. (1978). Changes in endogenous enzymatic reactivity to DAB induced by neuronal inactivity. *Brain Res.* **141**, 185–192.

Woolsey, C. N. (1958). Organization of somatic sensory and motor areas of the cerebral cortex. *In* "Biological and Biochemical Bases of Behavior" (H. F. Harlow and C. N. Woolsey, eds.), pp. 63–81. Univ. of Wisconsin Press, Madison.

Woolsey, C. N. (1960). Organization of cortical auditory system: A review and a synthesis. *In* "Neural Mechanisms of the Auditory and Vestibular Systems" (G. L. Rasmussen and W. Windle, eds.), pp. 165–180. Thomas, Springfield, Illinois.

Woolsey, C. N. (1971). Comparative studies on cortical representation of vision. *Vision Res. Suppl.* **3**, 365–382.

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

Woolsey, T. A., Welker, C., and Schwartz, R. (1975). Comparative anatomical studies of the SM-I face cortex with special reference to the occurence of "barrels" in layer IV. *J. Comp. Neurol.* **164**, 79–94.

Zeki, S. M., (1978). Functional specialization in the visual cortex of the rhesus monkey. *Nature (London)* **274**, 423–428.

40.