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"Principles of Organization of Sensory-Perceptual Systems in Mammals"

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Principles of Organization of Sensory–Perceptual Systems in Mammals

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I. Introduction

A common view of the functional organization of the brain, as elaborated from the early proposals by Bolton (1900), Campbell (1905), Brodmann (1909), Elliot-Smith (1906), and others (Mott, 1907; Woolard, 1925), is that sensory input is relayed over a few subcortical stations to a single cortical receiving area, the "primary sensory cortex" with elementary sensory functions, is then sent to an adjacent cortical band of "secondary sensory" or "psychic" cortex with more complex sensory and perceptual functions, and is next relayed to multimodal "association areas" for higher order abilities requiring integration of sensory information. In this view, the "association areas" are the sources of highest level perception, and their resultant outputs can also direct activation of motor cortex to initiate appropriate behaviors. The main point of the present article is that recent electrophysiological, anatomical, and ablation-behavioral studies clearly indicate that a major revision in this traditional viewpoint is required. These studies have revealed that the auditory, somatic, and visual sensory systems all have a number of topographically ordered and complexly interconnected cortical "representations" of sensory surfaces that occupy most of the classical "psychic" and "association" cortex. In addition, interfield connections are too complex to be consistent with a simple hierarchical system of organization. Furthermore, in all three sensory systems, traditional fields have been redefined. Finally, projecting systems delivering information to cortical neurons and to newly defined cortical fields are themselves subdivisible into multiple-component parallel processing systems.

II. Some Traditional Concepts of Forebrain Organization Relevant to the Genesis of Perception

A. THERE ARE ONLY A FEW DIVISIONS OF THE FOREBRAIN OF FUNCTIONAL SIGNIFICANCE FOR EACH SENSORY MODALITY, AND THESE DIVISIONS FORM A SERIAL SENSATION-TO-PERCEPTION PROCESSING SEQUENCE, WITH SUCCESSIVE FIELDS PERFORMING SUCCESSIVELY "HIGHER" FUNCTIONS

This concept is most easily related to the visual system. In the traditional view of visual cortex, there are only two or three cortical divisions of functional significance. This view stemmed from early studies of experimental and pathological cases, showing that lesions in caudal occipital cortex resulted in profound disturbances of vision (described as blindness) while more rostral lesions usually produced milder changes (considered to be disruptions of "psychic" or "perceptual" functions; see Bolton, 1900, for review). At about the same time investigators, attempting to subdivide the brain on the basis of differences in histological structure, identified two or three subdivisions of occipital cortex, and, influenced by neurological findings, ascribed either "sensory" or "psychic" functions to different cytoarchitectonically delimited areas. A "sensory" area was regarded as a waystation to a "psychic" area. Thus, Bolton (1900) and Campbell (1905) described a "primary" "visuosensory" area identified by the line of Gennari, and a "secondary" "visuopsychic" area occupying the remaining occipital cortex. Brodmann (1909) and Elliot-Smith (1906) both divided the "visuopsychic" region (somewhat differently) into two bands which they related to increasingly "higher" functions, i.e., the "occipital" and "preoccipital" areas (Areas 18 and 19) of Brodmann and the "parastriate" and "peristriate" areas of Elliot-Smith. Later investigators generally accepted the proposed existence of two hierarchically related "visuopsychic" areas, and the terminology and subdivisions of Brodmann were usually adopted.

With less justification from observations on the consequences of restricted brain damage, early neuroanatomists extended the concept of a few hierarchically related functional divisions of sensory cortex to the auditory and somatosensory systems. Thus, for example, Campbell (1905) spoke of "auditosensory" and "auditopsychic" areas, as well as "somatosensory" and "somatopsychic" areas.

The early viewpoint that each sensory modality was represented by only two or three cortical areas of successively higher levels of function later received strong support from neurophysiological investigators. Most notably, Penfield and colleagues (1952, 1954) interpreted results of extensive human brain stimulation studies as revealing the locations of "sensory," "psychic," and "interpretive" regions. Although the boundaries of these regions did not clearly coincide with the architectonic subdivisions of earlier investigators, the concept of a few hierarchically related regions was strongly reinforced. Similarly, Woolsey (Woolsey and Fairman, 1946; Woolsey, 1958) concluded from evoked potential mapping studies in primates and other mammals that there were two topographic representations in each sensory system, a "primary" and "secondary" area (i.e., AI and AII, SI and SII, V-I and V-II), and, in primates, very large adjoining regions of "association" cortex. Again, these studies reinforced the concept of a tripartite low-to-high level sensory-to-perceptual cortical hierarchy.

Finally, the elegant single unit experiments of Hubel and Wiesel (1965) were interpreted within the framework of a three-level hierarchy of visual areas (V-I, V-II, and V-III). Together with the clear evidence from the studies of Klüver and Bucy (1939) that the temporal lobes of monkeys are important in vision, the view that a three- or four-element hierarchial processing series exists in the visual system became commonly accepted.

B. ORDERLY REPRESENTATIONS OF RECEPTOR SURFACES ARE IMPORTANT IN THE EARLY STAGES OF SENSORY PROCESSING, BUT ARE NOT NECESSARY IN LATER STAGES WHICH DEAL WITH ABSTRACTIONS AND HIGHER ORDER FUNCTIONS

A widespread presumption has been that orderly representations of sensory epithelia are limited to a few brain stem structures and to cortical areas "early" in the sensory-perceptual processing chain. Other cortical areas have been presumed to be nonrepresentational or only crudely representational (perhaps as a vestigial trait) since topological organization did not seem to have any bearing on the presumed higher and more abstract functions of these areas. In this vein, an apparent lack of topographic order was and is sometimes interpreted as evidence of higher level processing of information. Thus, an earlier viewpoint was that "at the level of Area 18 and beyond . . . all topological organization in the visual process seems to have disappeared" (Hebb, 1949), and one still commonly finds such opinions as "the topographic map is strictly conserved . . . in 'lower' optic centers" such as the superior colliculus, "but as the coding system becomes more refined, wider departures from strict isomorphism are found" (Young, 1962) and "it would be astonishing if this topological organization were not gradually eroded" (from lower to higher levels) (Zeki, 1971). Recent investigators concluded that there was at best a very "weak" tonotopic organization in even primary auditory cortex (Evans *et al.*, 1965; Goldstein *et al.*, 1970). Tonotopic organization was not considered to be necessarily relevant for the presumed "higher" functions of cortical stations and more complex cortical processing algorithims were sought (e.g., see Swarbrick and Whitfield, 1972; Newman and Wollberg, 1973; Winter and Funkenstein, 1973).

The concept that higher level cortex is nonrepresentational received early support from the electrical stimulation studies of Penfield and colleagues (1952, 1954) which suggested that complex perceptions were in some sense site-specific in "psychic" areas of cortex. The interpretation that a spatially complex perception could arise from activity in one or a few neurons (whose response was specific to that given complex input) was further supported by experiments that sought object-specific or vocalization-specific neurons (e.g., see Gross *et al.*, 1972; Winter and Funkenstein, 1973).

C. ENTRANCE INTO THE "SENSORY" LEVEL OF THIS HIERARCHICAL PROCESSING SYSTEM IS FROM A LARGE, SINGLE REPRESENTATION OF THE SENSORY EPITHELIUM WITHIN THE THALAMUS

Of fundamental importance to the concept of serial hierarchical processing was the view that a single nucleus for each sensory system was the basic source of sensory information "relayed" from the periphery to sensory cortex. Furthermore, the relay was thought to be restricted to the "first" or "primary" cortical sensory representation. Thus, the medial geniculate nucleus was considered the relay nucleus for AI, the ventroposterior nucleus for SI, and the lateral geniculate nucleus for V-I. Minor modifications of this view were necessary to accommodate evidence that (*a*) the medial geniculate nucleus contained subdivisions with different cortical targets; (*b*) the lateral geniculate nucleus projects to extrastriate cortex in cats; and (*c*) there are other thalamic zones or nuclei with sensory input from the periphery. However, these early modifications have had relatively little impact on the basic idea of a single, primary thalamic relay nucleus providing input to primary sensory cortex and to the first stage of the cortical hierarchical processing system.

D. THERE ARE LARGE REGIONS OF MULTIMODAL "ASSOCIATION CORTEX" IN ADVANCED MAMMALS

It is obvious by comparing the amount of cortex occupied by the "primary" and "secondary" sensory areas in a range of mammals that these sensory representations occupy a greatly varying proportion of cortex. Thus, mammals with little neocortex, such as rats or hedgehogs, have much of the cortex devoted to the primary and secondary sensory representations and little additional sensory cortex, while progressive mammals with greatly expanded neocortex, such as cats, monkeys, and humans, have large regions of cortex outside the primary and secondary representations. Much of this additional cortex has been considered to be nonrepresentational "psychic" or "association" cortex indirectly devoted to more than one modality via cortical connections. It followed that the expansion of "psychic" or "association" cortex was the major advance in the phylogenetic development of mammalian brains.

The idea that large areas of cortex are utilized in associating inputs from two or more sensory systems has a long history. This viewpoint was extensively developed by Flechsig (1896), who concluded that large regions between the visual, auditory, and somatic sensory areas in man received limited or no direct input from the thalamus, and therefore were engaged in the association of information first relayed to the different sensory areas. These very large association regions were three in number and located in the frontal, occipital-temporal, and parietal lobes. Flechsig concluded that association centers were absent in rodents, present in carnivores, well developed in monkeys, and occupied two-thirds of the cortex in humans. Differences in the amount of association cortex were used to account for species differences in "intellectual" ability. The basic theory of Flechsig has been retained (with the exception of early recognition of thalamic input to "association" cortex) in current thinking as well as in standard textbook considerations of neocortex (e.g., see Thompson, 1975). It is also worth noting that the concept of a few "association areas" that expand in phylogeny and relate to a single dimension of increasing intelligence has been subject to a long history of criticism ranging from the early comments of Rámon y Cajal (1911) to a more recent discussion by Diamond and Hall (1969).

III. Summary of Some Recent Studies of Forebrain Organization

Studies over the past decade provide an understanding of forebrain organization that is inconsistent with many of the classical concepts of the role of the forebrain in the genesis of perception. Several basic features of organization are common to different sensory systems and appear relevant to considerations of the genesis of perception within the brain. These basic features are outlined below and their implications for the classical model of hierarchical processing systems generating sensation-to-perception serial transformations are then discussed.

A. THERE ARE MULTIPLE REPRESENTATIONS OF SENSORY EPITHELIA WITHIN THE CORTEX OF MONKEYS IN ALL SENSORY SYSTEMS

Recent studies have revealed the existence of multiple representations of sensory epithelia within visual, auditory, and somatosensory cortex in primates, carnivores, and at least some other mammals. Some of these studies are reviewed in the following.

1. Visual Cortical Fields

There are many topographically ("retinotopically") organized fields within primate cortex. In fact, recent studies have revealed that a strict topography is preserved within fields occupying all or nearly all of cortex that was formerly classified as visual "sensory" and visual "psychic" cortex. In the most completely studied primate species, the owl monkey, topographic representations of the retina have been mapped in detail within six visual fields (Allman and Kaas, 1976; Kaas, 1978; see Fig. 1). The first visual representation, V-I, is coincident with the classical Area 17; the second representation, V-II, corresponds to Area 18 as defined in New World monkeys. The four other fully or partly mapped fields, DM, DL, MT, and M, lie completely or partly within the classical Area 19 (V-III of many formulations) of New World monkeys. Within all six mapped fields, there is a highly ordered and complete representation of the retina. In the unmapped regions between

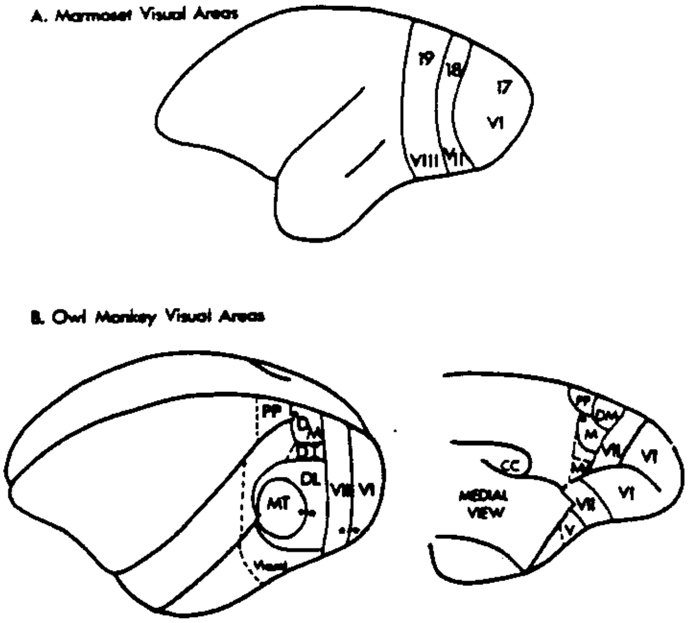


FIG. 1. Traditional (A) and current (B) views on the organization of visual cortex in New World monkeys. Areas 17, 18, and 19 of Brodmann (A) have commonly been considered to be three separate representations of the visual hemifield. In B, the first (V-I) and second (V-II) visual areas are shown, corresponding to Areas 17 and 18 of Brodmann. "Area 19" and adjoining regions of cortex consist of a number of visual areas. Asterisks mark the approximate location of the center of gaze in those visual areas where systematic representations of the visual hemifield have been fully determined. The dorsolateral (DL), dorsointermediate (DI), dorsomedial (DM), medial (M), middle temporal (MT), and posterior parietal (PP) visual areas are from Allman and Kaas (1975). Evidence for a ventral (V) visual area is from unpublished studies of Allman and Kaas. The location of a medial ventral (MV) visual area is suggested by patterns of cortical projections (Wagor *et al.*, 1975). CC, corpus callosum.

and around these fields, the visually responsive cortex also appears to be topographically organized, i.e., in rows of penetrations crossing these regions, successively defined visual fields shift systematically. In particular, a region bordering Area 18 on the ventral surface of the brain has been extensively mapped and a nearly complete representation of the visual hemifield has been revealed (J. M. Allman and J. H. Kaas, unpublished experiments; the Ventral Visual Area, Fig. 1). Other rather extensive mapping data exist for the Dorsal Intermediate Visual Area (Fig. 1). In other words, while the details of internal organization of several fields are not completely defined, evidence suggests that in the owl monkey *all* or nearly all of the caudal visually responsive cortex including all of the classic "visuopsychic area" is occupied by retinotopically organized fields, and that there are, overall, as many as 10 or more topographically organized fields in this species.

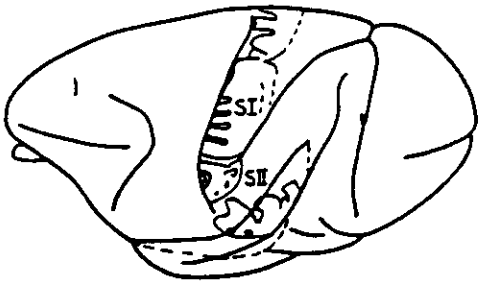
While no other primate species has been studied in corresponding detail, evidence in macaque monkeys is consistent with the existence of at least some homologous fields (e.g., see Van Essen, 1979; Weller and Kaas, 1978). In macaques, as in owl monkeys, it would appear that at least most of the "visuopsychic" cortical region is occupied by retinotopically organized fields (e.g., see Van Essen, 1979).

2. *Somatosensory Cortical Fields*

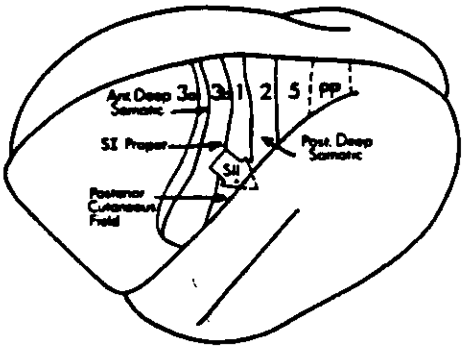
Recent studies of somatosensory cortex have, again, revealed the existence of a number of topographically ("somatotopically") organized fields. Classically, it has been contended that in higher primates, there was a single representation of the body surface in the parietal cortex occupying Brodmann's cytoarchitectonic Areas 3 (3b and 3a), 1 and 2 (Woolsey *et al.*, 1942; Penfield and Boldrey, 1937). This "single" primate representation spanning four distinct cytoarchitectonic fields has long been termed "SI" (Woolsey and Fairman, 1946). A second representation was defined in the dorsal aspect of the Sylvian fissure ("SII") (Woolsey and Fairman, 1946). On the basis of more complete microelectrode mapping studies, the classical view of "SI" organization in primates has been revised (see Fig. 2). "SI" has been found to contain four orderly representations, with Areas 3b and 1 (and in some species Area 2) each containing complete representations of the skin surface (Merzenich *et al.*, 1978; Kaas *et al.*, 1979), and Areas 3a and 2 each containing representations of "deep" receptors in muscles and joints. A narrow strip-like representation of the skin was seen, additionally, between Areas 1 and 2 (Merzenich *et al.*, 1978). Finally, there is the possibility of at least a crude representation of joint and/or muscle receptors caudal to Area 2 within Area 5 (Mountcastle *et al.*, 1975; Sakata *et al.*, 1973; Duffy and Burchfiel, 1971). Similarly, the "SII" region of monkeys has recently been found to be comprised of at least three distinct fields, probably individually topographically organized (Burton and Robinson, 1978). Thus, in a primate like a macaque or owl monkey, there are as many as seven or more somatosensory areas, most of which appear to constitute complete, orderly representations of the body surface or deep body tissues.

3. *Auditory Cortical Fields*

In auditory cortex, classical evoked potential mapping studies provided evidence for only two large fields ("AI" and "AII") in macaque monkeys (Woolsey and Walzl, 1944; Walzl, 1947; see Fig. 3). However,



A. Somatic Sensory Cortex

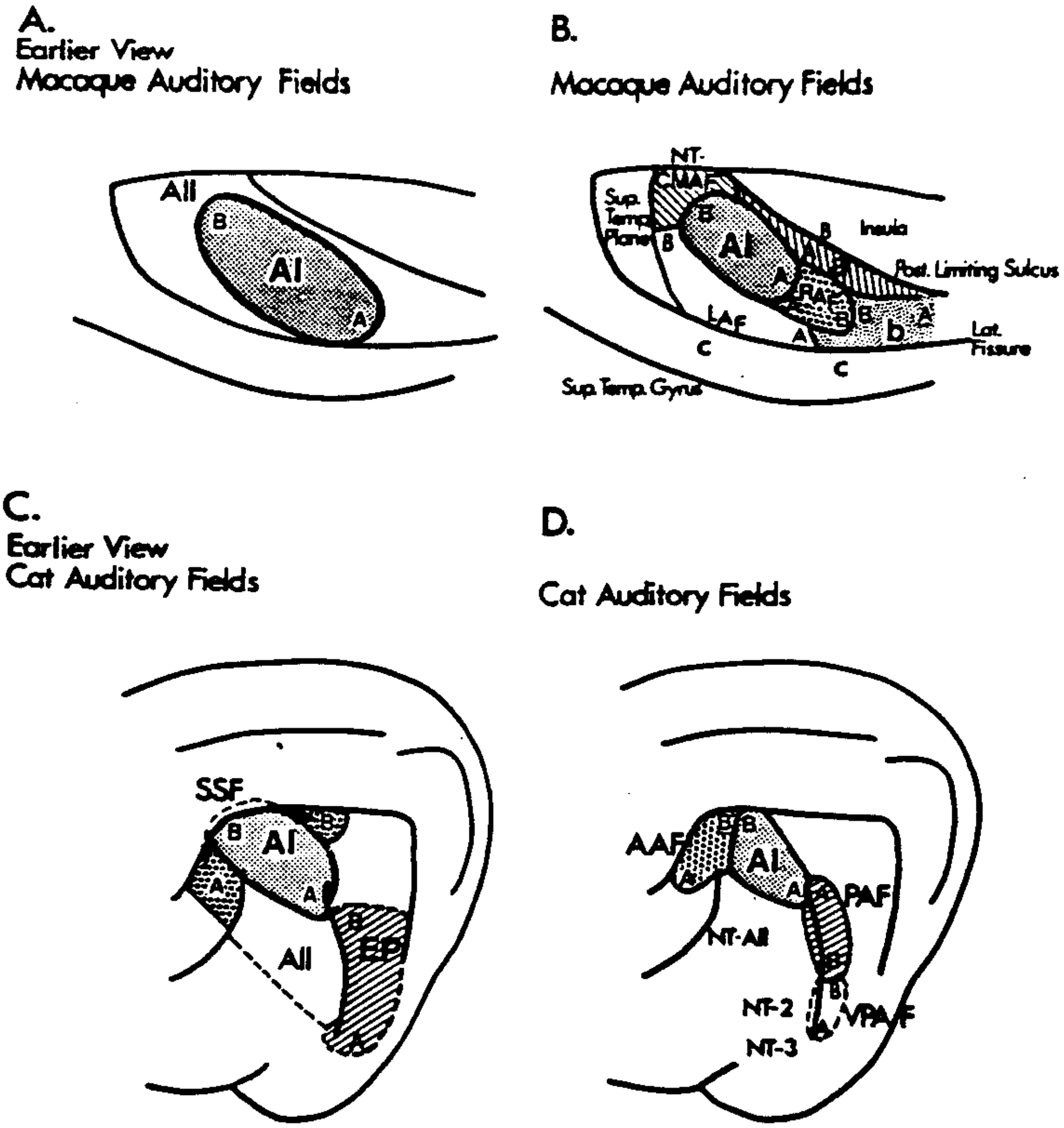


B. Owl Monkey Somatosensory Areas

Fig. 2. Traditional (A) and current (B) views of the subdivisions of parietal somatosensory cortex in monkeys. Traditionally, somatosensory cortex has been thought of as containing two divisions, the first (SI) and second (SII) somatosensory areas. (A) is redrawn from Woolsey (1958). In (B), the anterior deep somatic field (3a), SI proper (3b), posterior cutaneous field (Area 1), and the posterior deep somatic fields (Area 2) are separate representations of the body as described in Merzenich *et al.* (1978). The region of "Area 5" and posterior parietal cortex (PP) may also be involved in somatosensory processes, and both may contain subdivisions. The report of Burton and Robinson (1978) suggests the existence of additional somatosensory areas on the upper bank of the lateral fissure adjacent to or within the classical "SII."

recent studies have revealed that there are at least six topographically ("cochleotopically" or "tonotopically") organized representations within the auditory cortex of macaque monkeys (Fig. 3B), and at least four topographically organized representations within the auditory cortex of owl monkeys (Fig. 4). In both of these primates, a single non-topographically (or weakly topographically) organized field has also been identified.

Domestic cats have been studied in special detail, and four cochleotopically organized fields have been defined (Fig. 3D). In addition, there appear to be at least three other auditory fields without ap-



A. Earlier View Macaque Auditory Fields

B. Macaque Auditory Fields

C. Earlier View Cat Auditory Fields

D. Cat Auditory Fields

FIG. 3. Traditional (A and C) and current (B and D) views of the organization of auditory cortex in monkeys and carnivores. In all figures, the representation of the cochlear apex (A) and base (B) are indicated in those fields where cochleotopic organization has been described. The traditional view of auditory cortex in the monkey (A) is based on Walzl (1947) and Kennedy (1955). Only primary (AI) and secondary (AII) auditory fields were described. Later, AI was redefined and five additional auditory fields with distinct architectonic and electrophysiological characteristics were described (Merzenich and Brugge, 1973). AI, primary auditory cortex; LAF, lateral auditory field; RAF, rostrolateral auditory field; a, b, and c, other topographically organized fields; NT-CMAF, nontopographic caudomedial auditory field. Fields in A and B are shown on a view of the surface of the superior temporal plane and dorsolateral surface of the superior temporal gyrus. For the location of the auditory fields in owl monkeys, see Imig *et al.*

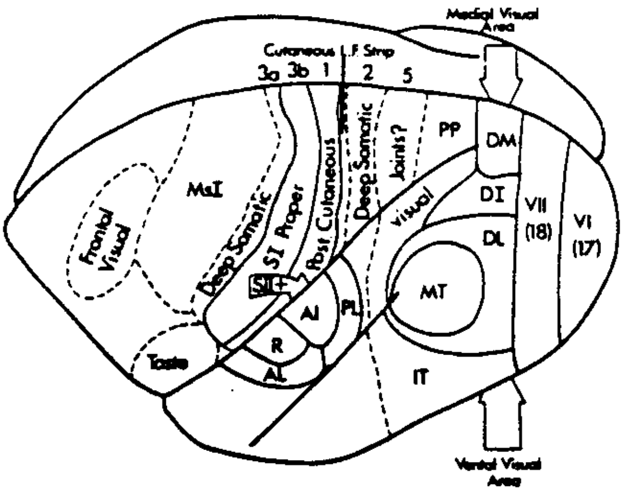


FIG. 4. A summary of the subdivisions of neocortex in a New World monkey as currently understood. Many of these subdivisions are within cortex previously considered "association cortex" (for example, see Thompson, 1975). R, rostral auditory field; AL, anterior lateral auditory field; PL, posterior lateral auditory field; MsI, motor-sensory area I; other abbreviations as in other figures.

parent tonotopic organization. Thus, in the auditory systems of cats and monkeys there is a significant region of sensory cortex that appears to be "nonrepresentational" for the sensory epithelium.

B. THERE HAVE BEEN IMPORTANT REDEFINITIONS OF SENSORY FIELDS IN ALL THREE SENSORY SYSTEMS

In some instances, the classical terms for sensory representations have been retained, although the areas have been redefined with different boundaries and extents. Unfortunately, these corrected definitions have not yet been widely adopted by neurobiologists, and it is not always clear from the use of a term if the old or new definition is intended. The major changes in definitions are noted in the following.

As illustrated in Fig. 1, the classical Area 19 or V-III of primates has been found to correspond to a number of functionally distinct subdivi-

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(1977) and Fig. 4. The traditional auditory fields of the cat have been redrawn from Woolsey (1960). The fields included AI, AII, the suprasylvian fringe (SSF) and the posterior ectosylvian area (EP). The current auditory areas of the cat are based on Merzenich and colleagues (Merzenich *et al.*, 1977; Andersen, 1979, unpublished studies) and on Reale and Imig (1977 and personal communication). Subdivisions redefined with microelectrode mapping methods include a smaller primary field, AI, at least three other cochleotopic fields (the anterior auditory field, AAF; the posterior auditory field, PAF; the ventroposterior field, VPAF), a nontopographic and redefined AII (NT-AII), and at least two other nontopographic fields (NT-2 and NT-3).

sions rather than one. While Area 18 of New World monkeys and prosimians has been found to correspond to a second systematic representation of the visual field, V-II, Area 18 as classically defined in Old World monkeys (and almost certainly in apes and humans) is far too wide and includes much more than V-II. Since a V-II appears to exist in most if not all mammals, and the architectonic zone that is coextensive with V-II has often been identified as Area 18, we have suggested that Area 18 be defined as the cortex devoted to V-II in all species (Kaas, 1978). The classical use of the term Area 18 in advanced primates presently has uncertain meaning and should be redefined as the cortex that is coextensive with V-II, as Zeki (1969) has done. However, as an added complication, Zeki (1969) has introduced the term V-III for a region of cortex that is largely within the classical Area 18 of macaque monkeys. The studies by Zeki helped define the rostral border of V-II (and thereby the true border of Area 18), but we regard the use of the term V-III or Area 19 for the cortex bordering V-II as unfortunate since there has been no demonstration that a single visual area forms the rostral border of V-II with a retinotopic organization mirroring that of V-II as would be required by the traditional concept of Area 19 and V-III. In fact, there is clear evidence of several visual areas bordering V-II of macaque monkeys (Van Essen, 1979), as in New World monkeys.

In auditory cortex, a number of distinct fields have been found to be partly or completely within the classically defined "AI" of primates as identified by Woolsey and Walzl (1944) and Kennedy (1955). The subdivision "AI" of the auditory cortex in the cat has also been redefined as occupying only part of its former area (Merzenich *et al.*, 1975, 1977; Knight, 1977). In both cats and monkeys, the classically defined boundaries of AI were apparently extended by inability of surface recordings to detect precisely reversals of topographic order. Thus, when Woolsey and colleagues stimulated the basal end of the cochlea representing highest frequencies, they must have excited cortex along the lines of reversal in the representation of highest frequencies both in AI and the bordering field. Apparently, all of this relatively continuous responsive zone was included within AI. The same complication arose at low-frequency field boundaries (e.g., in the cat, the border of AI with the field posterior to it; or in the monkey, with the field anterior to AI). All regions in which there were such reversals in representation of frequency across the boundaries of auditory fields were interpreted to be within one field. Because AI included parts of adjoining fields, the interpretation of the organization and boundaries of adjoining fields was also incorrect.

The consequence of recent detailed microelectrode mapping studies of auditory cortex has been a complete redefinition of the organization of the traditional subdivisions (Merzenich and Brugge, 1973; Merzenich *et al.*, 1975, 1977; Knight, 1977; Imig and Reale, 1977). By these new definitions, AI in cats and in monkeys is much smaller than defined by Woolsey and colleagues, large topographically organized fields are found rostral and caudal to AI, and a fourth field is situated ventral to the caudal "posterior auditory field" (Fig. 3). There are reversals (not discontinuities, as defined classically) in the sequence of representation across all of the shared borders of these fields.

In somatosensory cortex, "SI" of monkeys has been redefined with the appreciation that the classical single representation actually contains four or five complete representations. These representations occupy cytoarchitectonically delimitable subdivisions. Area 3b of primates is probably homologous with "SI" of other mammals, and hence has been renamed "SI proper" (Merzenich *et al.*, 1978). The several representations that were previously included in the classical "SI" now have been collectively termed the "parietal somatosensory strip." A similar need for redefining "SII" in primates has recently become apparent with the evidence that the region considered to be a single body surface representation may contain several body surface representations (see Burton and Robinson, 1978).

C. MOST POSTCENTRAL NEOCORTEX CONTAINS SENSORY REPRESENTATIONS

Contrary to the classical view of somatosensory, visual, and auditory cortical fields occupying narrow core areas separated by large regions of nonrepresentational "association" or "psychic" cortex, most of the cortex caudal to motor cortex and excluding the middle and anterior temporal cortex appears to be occupied by retinotopically, cochleotopically, or somatotopically organized fields. In New World monkeys, many of these representations have been fully defined, and these areas are shown in Fig. 4. In addition, there is incomplete evidence for other sensory representations, and the general conclusion that most of the caudal neocortex responsive to sensory stimuli is occupied by sensory representations appears valid. In some limited regions of cortex, careful investigations have failed to reveal any systematic representations of sensory surfaces. For example, there are at least three cortical fields that are strongly driven by auditory stimuli in cats, but are without any clear cochleotopic organization (Merzenich *et al.*, 1977; Andersen, 1979). At least one such cortical field appears to exist in monkeys (Merzenich and Brugge, 1972; Imig *et al.*, 1977). In addition, there is evidence for a narrow region between auditory, visual, and somatosensory cortex without any clear representation of any of these modalities in the rhesus monkey (Merzenich and Brugge, 1978) and in the owl monkey (Imig *et al.*, 1977). (The possibility of vestibular representation has not been ruled out.) But overall, these "nonrepresentational" cortical regions occupy only a small fraction of the parietal, posterior temporal and occipital cortex, and most of what has long been regarded as the "integrative" or "psychic" cortex is actually occupied by topographically organized fields (Fig. 4).

D. THE NUMBER OF CORTICAL FIELDS (AND OVERALL CORTEX DEVOTED TO TOPOGRAPHICALLY ORGANIZED CORTEX) HAS INCREASED IN SEVERAL LINES OF MAMMALIAN PHYLOGENY

While modern mapping methods have revealed many sensory representations in advanced mammals with expanded cortex like cats and the various monkeys, fewer representations have been demonstrated in smooth-brained mammals with relatively little neocortex. Perhaps the strongest evidence for the conclusion that the number of sensory representations has increased in phylogeny comes from sensory mapping studies on the hedgehog (Kaas *et al.*, 1970), which is a small insectivore with proportionally less neocortex than almost any extant mammal. While no attempt has been made to subdivide auditory cortex in this species, it appears that there are only two visual representations, and only two somatosensory representations (Fig. 5). Since the visual areas directly adjoin the somatosensory areas, there is no room for "undiscovered" additional representations and the conclusion seems inescapable that, although most of the neocortex of the hedgehog is sensory, there are only a few subdivisions of sensory cortex. Because all present day eutherian mammals evolved from insectivore-like ancestors with little neocortex and an external brain morphology similar to that of the hedgehog (see Kaas *et al.*, 1970), it is reasonable to conclude from studies of the hedgehog that the first mammals had few subdivisions of cortex. Furthermore, this conclusion is supported by similar results on other mammals (such as oposums and rats) with little neocortex. Here too, there seem to be few sensory representations. Thus, small smooth forebrains with few sensory representations is a generalized condition and therefore most likely ancestral, while large forebrains with fissures and many sensory representations has been a product of several parallel lines of evolution.

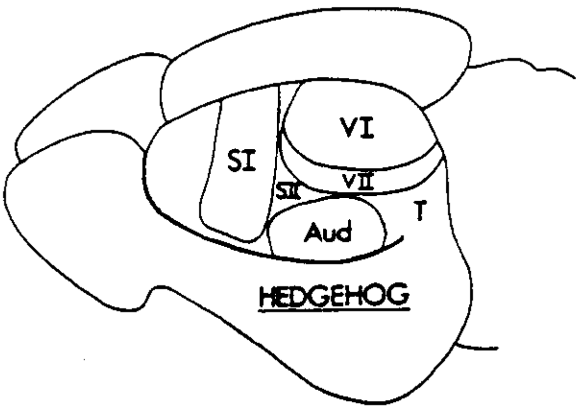

FIG. 5. Subdivisions of neocortex in the hedgehog, an insectivore with little neocortex. Note that there are few subdivisions, and that most of the defined subdivisions are sensory representations. No attempts have been made to divide auditory cortex. After Kaas *et al.* (1970).

If species of mammals differing in amount of neocortical expansion are considered, there is evidence that cortical expansion is related to an increase in the *number* of sensory representations. Thus, two topographic cortical representations of the cochlea have been found in a rodent with a slight expansion of neocortex, the squirrel (Merzenich *et al.*, 1976), at least three auditory representations exist in the tree shrew (Oliver *et al.*, 1976), which has an expanded temporal cortex, while owl monkeys (Imig *et al.*, 1977) have at least four and rhesus monkeys (Merzenich and Brugge, 1973) have at least six auditory representations. All mammals appear to have two somatosensory representations, SI and SII, although opposums do not seem to have a "motor" representation separate from SI (Lende, 1963). However, more somatosensory representations clearly exist in monkeys, although it is not yet certain if New and Old World monkeys vary in numbers of areas, or if prosimians have fewer representations than monkeys, as recent studies suggest (Sur *et al.*, 1979). In the visual system, there is evidence for four or fewer representations in a range of small smooth brained mammals, while cats (Palmer *et al.*, 1978) and monkeys (Kaas, 1978) have 10 or more representations.

E. INFORMATION IS DELIVERED TO THE THALAMUS AND THEN TO THE CORTEX OVER A NUMBER OF FUNCTIONALLY DISTINCT PARALLEL PATHWAYS

Classically, descriptions of sensory projection systems have focused on simple, serial "main-line" large-fiber systems complemented in minor ways by "secondary" small-fiber systems (see Rose and Mountcastle, 1959; Bishop, 1959). It is now evident that (*a*) each "mainline" system is actually a composite of several input classes projecting in parallel; (*b*) there are multiple projection systems outside the "main-line" system; and (*c*) most if not all sensory representations have direct thalamic inputs.

The "main-line" projection system in the visual system of primates differs from those of the somatic and auditory systems in that only one sensory representation, V-I, receives the most direct visual information (however, the lateral geniculate nucleus and the medial interlaminar nucleus relay direct retinal projections to several cortical fields in cats). Recently, major advances have been made in the understanding of the functional organization of the "main-line" projection system from the retina. The main-line projection system can be considered to constitute the "X," "Y," and some of the "W" ganglion cell populations projecting to the lateral geniculate nucleus (see Rowe and Stone, 1977, for review). The X cells are considered important in form vision, respond in a sustained manner to static stimuli, are largely color-opponent types in primates, and are concentrated in the central retina. The Y cells are thought to be important in visual attention, respond to stimulus changes, are "broad-band" in response to color, conduct information rapidly to the thalamus over large axons, and are more evenly distributed over the retina. The W cells form a heterogeneous group with a range of response properties, slowly conducting axons, and probably several functional types. It now appears that the X cells project solely or almost solely to the parvocellular layers of the lateral geniculate nucleus of primates, while the Y cells project to the magnocellular layers of the lateral geniculate nucleus and via collaterals to the superior colliculus (Schiller and Malpeli, 1977; Weller *et al.*, 1979). The W cells project to the superior colliculus and possibly to parts of the lateral geniculate nucleus such as the interlaminar zones and the superficial S layers. The segregation of input types in the magnocellular and parvocellular layers is maintained at the next level since these layers project to different layers of cortex. There is also evidence that interlaminar cells project separately to layer I (Carey *et al.*, 1979). Thus, there is evidence for at least three parallel projection systems relaying through the lateral geniculate nucleus and terminating in separate layers of striate cortex.

In addition to the lateral geniculate nucleus as a subdivisible "main-line" structure delivering visual information to cortex, there are at least five separate topographically organized subdivisions of the pulvinar complex, each with its own pattern of projections to cortical visual areas (see Graham *et al.*, 1979; Lin and Kaas, 1979; Symonds and Kaas, 1978). Two of these subdivisions receive topologically ordered projections from the superior colliculus (Fig. 6). Other visual input to the pulvinar complex and other nuclei is from targets of the retina in the pretectum (Benevento *et al.*, 1977).

In the "main-line" somatosensory system (the "lemniscal system"; see Mountcastle, 1974), inputs from populations of neurons innervating different mechanoreceptor types are handled largely in parallel from the skin to the cortex. Thus, in the input layers of somatosensory cortex, response characteristics of neurons can be very much like those of primary afferent fibers (see Mountcastle *et al.*, 1969). Moreover, in the squirrel monkey there is evidence of a segregated processing of information from deep and pacinian, cutaneous quickly adapting, and cutaneous slowly adapting receptor populations within strictly delimited sectors of the ventrobasal thalamus (J. Kaas, M. Sur, R. Nelson, R. Dykes, and M. Merzenich, unpublished results). From the ventroposterior nucleus of the thalamus there is parallel input to both SI proper (Area 3b) and the posterior cutaneous field (Area 1) (see Fig. 7; also Lin *et al.*, 1979; Jones *et al.*, 1979). Some of the input to each area appears to originate in separate sets of thalamic neurons, while some thalamic neurons appear to project to both fields. There is further evidence that a thalamic region dorsal to the ventroposterior nucleus projects to the posterior representation of deep body tissues (Area 2), while sensory information

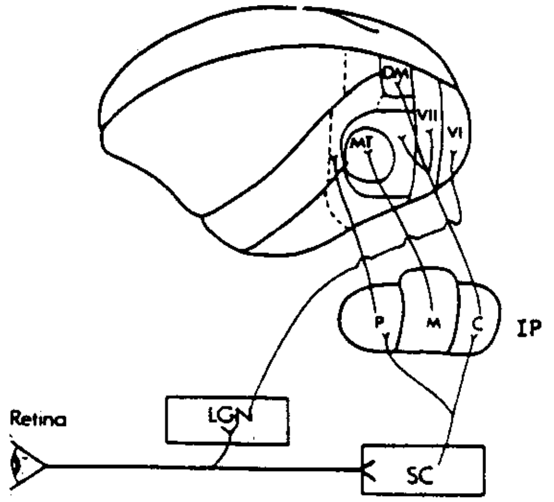

FIG. 6. Some of the thalamocortical connections of the visual system in monkeys. Connections are topographic and reciprocal. Posterior (P), medial (M), and central (C) divisions of the inferior pulvinar complex (IP) are shown. LGN, lateral geniculate nucleus; SC, superior colliculus. Other abbreviations as in Fig. 1. Separate parallel pathways of the X, Y, and W ganglion cell systems through the LGN to V-I, as well as connections with the superior pulvinar complex, are not shown. Based on Lin and Kaas (1979).

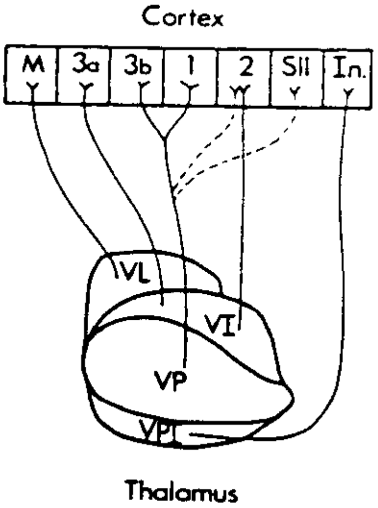

FIG. 7. Some of the thalamocortical connections of the somatosensory system in monkeys. Dashed lines indicate less pronounced connections. Probably all connections are topographic and reciprocal. The approximate spatial relationships of the ventroposterior (VP), the ventroposteroinferior (VPI), ventralis intermedius (VI), and ventralis lateralis (VL) nuclei are indicated. M, motor cortex; In, insular cortex. Other abbreviations as in Fig. 4. Based on Lin *et al.* (1979) and Jones *et al.* (1979, and unpublished studies).

from muscle afferents is relayed from the ventrolateral thalamus to Area 3a (Tanji, 1975; Heath *et al.*, 1976).

Other somatosensory thalamic inputs are to "Area 5" and the SII region. There is evidence for separate anterior and posterior fields within "Area 5" with inputs from the pulvinar and lateral posterior nucleus, respectively (Jones *et al.*, 1979). The ventroposterior nucleus and nuclei of the posterior group project to separate fields in the SII region (Burton and Jones, 1976).

Multiple parallel sensory pathways have been most fully demonstrated for the auditory system of cats (Figs. 8 and 9). While different classes of ganglion cells send distinct types of information centrally in the somatic and visual system, the auditory system has its own way to accomplish the same end. From a relatively homogeneous input from the cochlea, information is distributed to a series of different response-specific neuron populations that, by virtue of different synaptology, extract very different information from this common input. Subsequently, information from the two ears is combined in several binaural "comparator" nuclei apparently abstracting information relevant to the localization of sound sources. Information from the two ears is added in other neuron populations; this adding of information from the two ears results in a two-ear excitatory-excitatory product. Thus, while information from the somatosensory and visual systems at the level of the thalamus is very

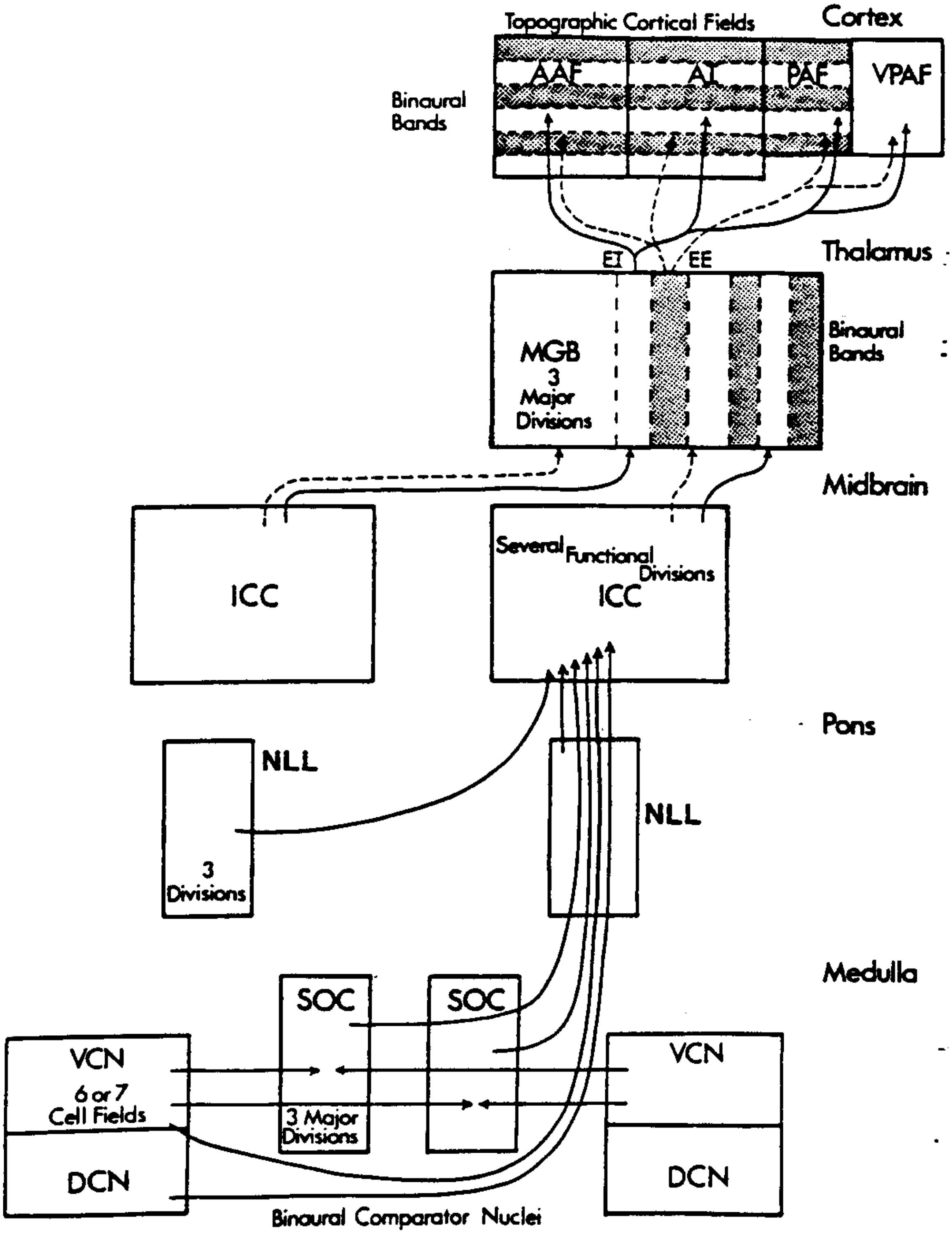

FIG. 8. The basic organization of the main-line auditory system in the cat. Inputs from specific cell fields of the right and left ventral cochlear nulcei (VCN) converge on the binaural comparator nuclei of the superior olivary complex (SOC). Neurons of the ventral and dorsal cochlear nuclei and neurons of subdivisions of the superior olivary complex

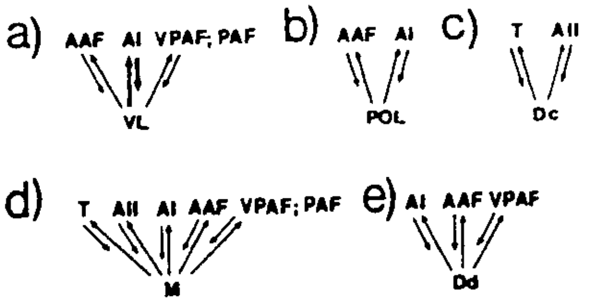

FIG. 9. Some of the thalamocortical connections of the auditory system of the cat. (a) The ventrolateral thalamus (VL) is topographically interconnected with four auditory cortical areas (see Fig. 3 for abbreviations). (b) The lateral "nucleus" of the posterior group (POL) is topographically interconnected with two auditory fields. (c) The caudal part of the dorsal division of the medial geniculate complex (Dc) is interconnected with nontopographic AII and other temporal auditory fields (T). (d) The medial division of the medial geniculate complex (M) is interconnected with all studied auditory fields. (e) The deep dorsal division of the medial geniculate complex (Dd) is topographically interconnected with three auditory fields. Redrawn from Andersen (1979) with reference to Fitzpatrick *et al.* (1977), Winer *et al.* (1977), and Colwell and Merzenich (1980).

like information recorded at the level of the peripheral sensory neurons and the ganglion cells, there is a profound *second-level abstraction of information* in the auditory system. Neuron populations in different subdivisions of the cochlear nuclear complex (there are on the order of six or seven functionally and morphologically distinct classes of projecting neurons), superior olivary complex (three major divisions), and nuclei of the lateral lemnisci (there are three principle projecting nuclei) all have different source-specific response characteristics. Thus, in the sensory system with the most homogeneous input from the sensory epithelium, many response classes of neurons are *created* as a consequence of the second level of abstraction of information in the system. As in the visual and somatosensory systems, once class-specific auditory information is derived, it is delivered forward in parallel over at least largely separate

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project to the three nuclei of the lateral lemnisci (NLL). Subdivisions of all these nuclear groups (VCN, DCN, SOC, NLL) project to the principal midbrain auditory center, the central nucleus of the inferior colliculus (ICC). These inputs are segregated into at least four subdivisions of the ICC. The ICC projects bilaterally to the three major thalamic subdivisions of the main-line system, the medial nucleus, the ventral nucleus, and the deep part of the dorsal nucleus of the medial geniculate body (MGB). Details of how information from different midbrain nuclei project are lacking, but it appears that there are alternating slabs of excitatory-excititory and excitatory-inhibitory neurons in at least part of the large ventral nucleus. The main-line thalamic nuclei project to at least four topographically organized cortical fields; abbreviations as in Fig. 3D. Three of these fields (AI, AAF, and PAF, see Fig. 9) are known to contain alternating excitatory-excititory and excitatory-inhibitory binaural bands (see text for further description).

pathways from the midbrain to cortical fields (Roth *et al.*, 1978; Imig and Adrian, 1978; Morest, 1964). That is, inputs from different nuclei in the pons are delivered to different, segregated neuronal populations within the principal midbrain nucleus (the central nucleus of the inferior colliculus), and relayed to subdivisions of the auditory thalamus. Each subdivision of auditory cortex receives input from one or more of the component nuclei or subnuclei of the ventral, dorsal, and medial divisions of the medial geniculate complex (Colwell and Merzenich, 1980; Andersen *et al.*, 1977; Andersen, 1979). Thus, for example, the anterior auditory field receives its principal input from the deep dorsal nucleus of the medial geniculate body and not from the lateral part of the ventral nucleus (which provides the most powerful input to "AI") (Merzenich *et al.*, 1977; Andersen *et al.*, 1977; Andersen, 1979). There are at least seven projecting subdivisions of the medial geniculate body, projecting in a variety of different field-specific combinations to different auditory cortical fields (see Colwell and Merzenich, 1980; Andersen, 1979). Cortical fields that are topographic receive thalamic input from a different group of thalamic nuclei than do the cortical fields without obvious topographic organization.

Thus, rather than the early concept of a simple single thalamic nucleus for each sensory system, it is now apparent that the "main-line" thalamic region for each system is actually a complex of segregated neuron populations with input relayed from different classes of peripheral or second-level neurons. Even the "main-line" systems, then, are multiple-component parallel projection systems, feeding information in different mixes to different cortical representational fields. Rather than a simple serial relay from the thalamus to "primary" sensory cortex, most if not all representations have direct thalamic inputs. This allows each cortical representation to be simultaneously or nearly simultaneously activated by direct thalamic projections as well as by cortical connections.

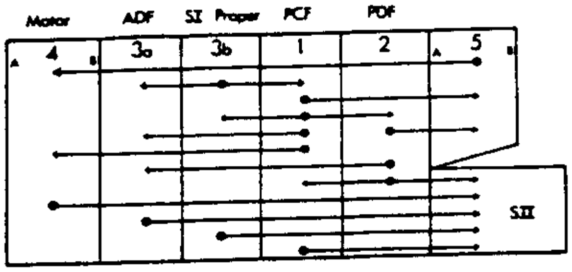
F. TOPOGRAPHICALLY ORGANIZED CORTICAL FIELDS ARE MULTIPLY INTERCONNECTED. INTERCONNECTIONS ARE OFTEN RECIPROCAL

Our present understanding of the connections of the topographically organized cortical fields is far from complete. Many subdivisions of sensory cortex have been only recently defined, the significance of some previously described architectonic fields has only been recently determined, and all of the subdivisions of sensory cortex are not yet known for any mammalian brain. Yet, enough is known to allow some general statements about connections. First, the ipsilateral connections invariably appear to be homotopic in that they relate similar parts of sensory surfaces in separate representations (although they may spread to include more than the homotopic site in at least some somatosensory fields; see Jones *et al.*, 1978). Second, multiple interconnections occur for most (if not all) representations (Fig. 10). Third, reciprocal interconnections between areas are common (Fig. 10). However, "reciprocal" interconnections often differ in the magnitude of the connection and in the laminar termination pattern. Thus, there are anatomical reasons for suggesting that "reciprocal" interconnections are not equivalent in function. Fourth, corpus callosum interhemispheric connections add to the complexity of the system by being of at least three types (Kaas, 1978). One type is homotopic or nearly so and relates the margins of representations in the two hemispheres where they are devoted to adjoining or overlapping parts of the same sensory surface (i.e., along the line of decussation of the retina or along the dorsal midline of the body surface). Another type is homoregional and connects other parts of matched representations of the two hemispheres. A third type is heteroregional and connects a representation on one side of the brain with one or more different representations on the other side of the brain. Fifth, most cortical areas project to other representations within the same sensory domain. Sensory representations of different modalities are not significantly interconnected. When these generalizations about cortical connections are considered, it is obvious that the concept of a hierarchical cortico-cortical sequence of processing is an oversimplification.

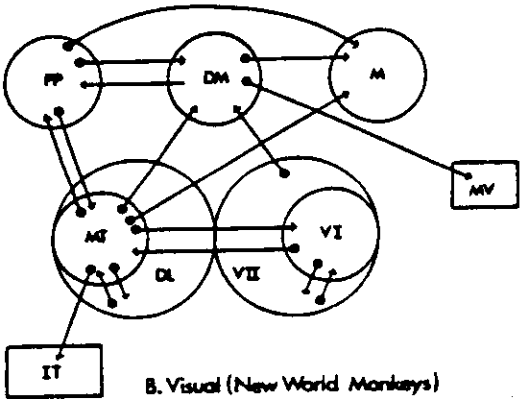
G. SENSORY REPRESENTATIONS VARY IN INTERNAL ORGANIZATION. FEW REPRESENTATIONS ARE ACTUALLY TOPOLOGICALLY EQUIVALENT TO A SENSORY SURFACE

There are a number of significantly different ways in which sensory surfaces are represented in neocortex. These differences are seen in all three sensory systems (Kaas, 1977). They suggest that functional considerations have an important role in determining the organization of sensory representations.

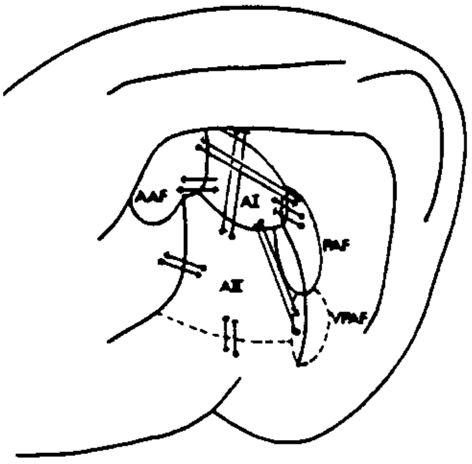
In the visual system, a most obvious difference between representations is in the proportions of tissue devoted to different portions of the hemiretina or hemifield (Fig. 10A). For example, in the owl monkey, the Medial Area devotes little cortex (about 5%) to the central 10° of the visual field while most of the Dorsolateral Area (about 75%) is devoted to the central 10° (Allman and Kaas, 1976). There are also several quite



A. Somatic (Old World Monkeys)



B. Visual (New World Monkeys)



C. Auditory (Cat)

FIG. 10. Some of the ipsilateral corticocortical connections of sensory areas of cortex. Connections between topographically organized fields appear to be homotopic. The complex transcallosal interfield connections are not drawn. (A) Connections of somatosensory areas based on Vogt and Pandya (1978) and Jones *et al.* (1978). Connections with the supplementary motor area are not shown. Cortical areas as in Fig. 2. (B) Some of the known connections of visual cortical areas of New World monkeys as summarized by Kaas (1978). The connections of only a few of the visual areas have been fully established and connections with frontal cortex are not shown. The extents and boundaries and possible subdivisions of inferotemporal (IT) and medioventral (MV) cortex are unknown. Other abbreviations as in Fig. 1. (C) Connections of auditory cortex in the cat based on Reale and Imig (1977); Andersen (1979, unpublished observations). Abbreviations as in other figures.

different types of representations or transformations of the hemifield in visual cortical fields. In primates, V-I and MT are basically simple topological transformations of the visual hemifield, or first-order transformations (Allman and Kaas, 1974), if one ignores the complication of rerepresentation of visual space in layer IV of adjoining ocular dominance columns in some primates (see Hubel and Wiesel, 1977). Another type of representation is found in V-II, DL, DM, and M (Fig. 11). In these representations, the hemifield is largely or almost completely split along the zero horizontal meridian. This second-order transformation (Allman and Kaas, 1974) is topological in the representa-

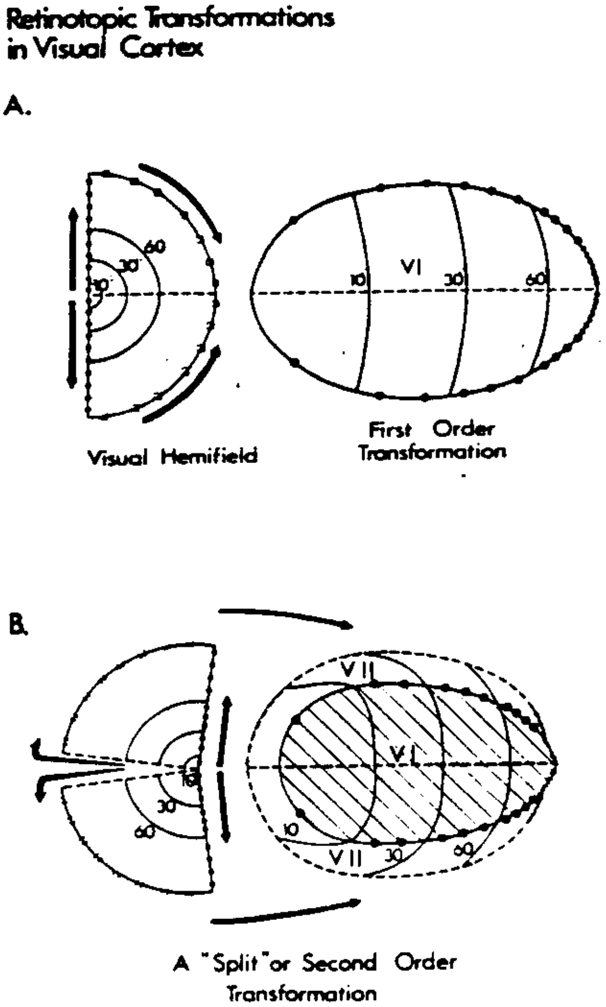


FIG. 11. Two basic types of visual hemifield representation in monkeys. (A) In the first-order transformation, found in V-I and MT, the visual hemifield is distorted but not split in the representation. (B) In the second-order transformation found in V-II, DL, DM, and M, the visual hemifield is distorted and split. Visual areas also differ considerably in the ways they distort the visual hemifield. After definitions of Allman and Kaas (1974).

tion of the upper and lower visual quadrants, but because of the split it is not topological overall. The split in the representation allows a second-order representation (such as V-II or DL) to wrap around a first-order transformation (such as the adjoining V-I or MT) with minimal distortion and matched or congruent borders. This arrangement also permits short interconnections between paired representations. For other areas, the split allows partially matched borders along the horizontal meridian of V-II. Only these two types of representations have so far been found in primates. However, "extended representations" including part of the ipsilateral hemifield have been found in the visual cortex of sheep, and they may occur elsewhere. More complicated "point-to-line" transformations have been described for visual areas of the suprasylvian sulcus of cats (Palmer *et al.*, 1978), but again, this type of representation has not yet been found elsewhere. As more is understood about the organizations of visual areas, less obvious differences in the internal organizations of separate areas no doubt will be revealed. For example, the division of V-I into "ocular dominance" and "orientation" columns or bands (Hubel and Wiesel, 1977) apparently does not occur, at least in the same way, in other visual fields.

In the somatosensory cortex, recent studies have revealed that the separate representations of the skin surface in the parietal somatosensory strip differ in topography in several ways. For example, there are differences in the proportional area of cortex dedicated to specific skin surfaces in the different fields (Merzenich *et al.*, 1978; Kaas *et al.*, 1979; Nelson *et al.*, 1979). Moreover, discontinuities in the representation of the skin surface relate to different skin locations in the separate cortical representations. A striking example is illustrated in Fig. 12, in which the very different schema for representing the dorsal surfaces of the fingers in Areas 3b and 1 of the owl monkey are shown. Another example of an important variation in organization is seen in "SII" in which ipsilateral and contralateral body surface representations are overlying and in register. Important differences in the microorganizations of somatosensory fields can be expected to be revealed by further study. For example, there is evidence that at least part of Area 3b is divided into "columns" or strips devoted to slowly adapting or rapidly adapting receptor inputs (Sur, 1978), much like the ocular dominance "columns" and orientation "columns" divide V-I. A corresponding organization is not yet apparent in Area 1.

The situation is somewhat more complicated in auditory cortex where there are two unique features of organization. First, auditory cortical fields necessarily have a fundamentally different kind of representation of the sensory epithelium (see Merzenich *et al.*, 1977). The auditory sen-

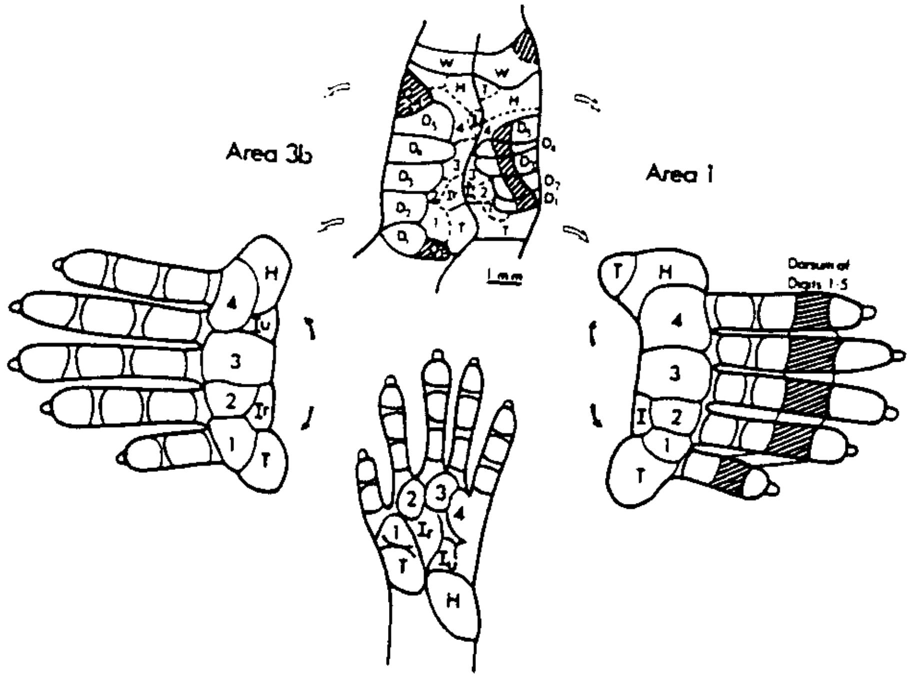
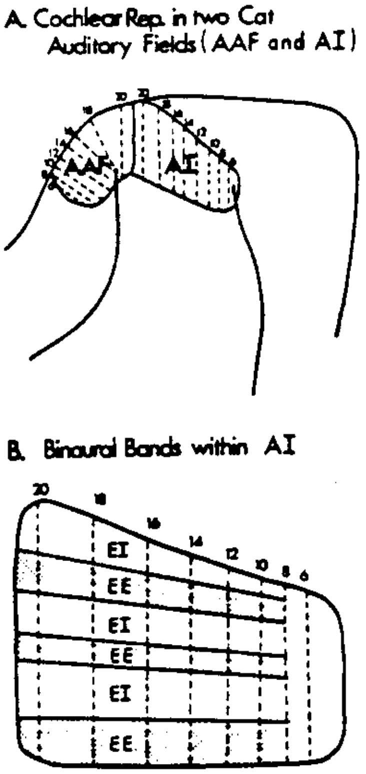


FIG. 12. Differences in the representations of the hand in Area 3b (SI proper) and Area 1 (the posterior cutaneous field) in owl monkeys. Basically, the palmar hand (below) is split (right and left) between the pads of the palm and distorted to form two roughly mirror image representations in Areas 3b and 1 (above). However, major differences in the two representations exist in the proportions of cortex devoted to different parts of the hand and the detailed arrangement of the parts. To point out two clear distinctions, (*a*) there is a greater proportion of representation of the glabrous surfaces of the fingers in Area 3b than in Area 1; and (*b*) the dorsum of the digits (shaded) is centered in the representation of the glabrous digits in Area 1 and split out to dorsal and ventral cortex in Area 3. Many such distinctions are found in the internal topography of these two large representations in this and other primates. Based on Merzenich *et al.* (1978).

sory epithelium, the organ of Corti, is a *line* of cells of insignificant width (3000 or so hair cells long, and one or four hair cells wide). If represented topographically within a cortical field like the point-to-point representations of visual and somatosensory sensory epithelia (which are surfaces), the organ of Corti would occupy a strip of cortex of insignificant width. Of course auditory cortex has an additional dimension, and, in this dimension, the cochlea is rerepresented, i.e., any given short sector of the cochlea is represented across a band of cortex of approximately constant width that extends across AI (or other cortical fields) from edge to edge (Fig. 13) (Tunturi, 1950; Merzenich *et al.*, 1975). Second, recent studies have revealed that there are a series of response-specific bands within AI that are oriented orthogonal to cortical lines of isorepresentation ("isofrequency contour"). Thus, each isofrequency



A. Cochlear Rep. in two Cat Auditory Fields (AAF and AI)

B. Binaural Bands within AI

FIG. 13. (A) Cochleotopic representation within two auditory fields (AAF and AI) in the cat. Numbers represent locations along the cochlear sensory epithelium measured from the cochlear apex. When these two fields are unfolded, they are seen to be topographic mirror images of about equal size, with a reversal in the representation of the extreme cochlear base along the border between the two fields. Note that the cochlear sensory epithelium is rerepresented across one axis (the axis of "isofrequency" contours) of cochleotopically organized fields; this axis of rerepresentation is indicated by the broken lines in this schematic drawing. After Merzenich *et al.* (1975); Knight (1977). (B) Highly schematized drawing of the internal organization of AI. This field is marked by a series of alternating functional binaural bands, orthogonal to the isofrequency contours of the field. Within a given binaural band, all neurons are excited by stimulation of both ears (EE bands), or excited by stimulation of the contralateral ear and inhibited by stimulation of the ipsilateral ear (EI bands). The lowest frequency part of AI (at the right) has not been studied in sufficient detail to determine its internal binaural organization. After Middlebrooks *et al.* (1979).

contour crosses five or six major AI subdivisions (Brugge and Imig, 1978; Imig and Adrian, 1977; Imig and Brugge, 1978; Middlebrooks *et al.*, 1978, 1979). In each of these subdivisions, binaural response properties of neurons are similar, and they differ from those of neurons in adjacent bands. At least three (probably four) auditory cortical fields in the cat (the cochleotopically organized fields) appear to have similar subdivisions. However, the several apparently "nontopographic" fields in the cat do not have this organization. These fields not only lack a clearly delineable topographic order, but they also appear to lack the binaural response bands of AI and other topographic fields.

The organization of AI raises a basic question about how to subdivide auditory cortex. Is "AI" the functional unit? Or are the individual bands of AI actually individual representational areas, ultimately processing input from different brainstem sources? Some evidence supports both views (see Middlebrooks *et al.*, 1979; Andersen, 1979). If the individual bands are separate representations, there would actually be on the order of 20 representations of the auditory sensory epithelium within auditory cortex in cats and probably more in primates.

From these examples, it is evident that in all three sensory systems there are different types of sensory representations, and that representations commonly differ from each other in important features of their detailed topography.

H. NEURONS IN SENSORY REPRESENTATIONS HAVE FIELD-SPECIFIC RESPONSE PROPERTIES, PRESUMABLY REFLECTING DIFFERENT INPUTS AND PROCESSING

While several sensory areas of the same modality may contain neurons that respond similarly to a particular sensory stimulus, there is evidence to support the view that all sensory representations differ in the overall response properties of populations of contained neurons, and, in some cases at least, have clear, field-specific classes of neurons. These differences argue that each sensory representational area is mediating distinct aspects of perception.

In the somatosensory cortex, many field-specific differences in overall response properties have been established. There is evidence, for example, that Area 3b has more neurons activated by slowly adapting peripheral neurons than do Areas 1 or 2 (Paul *et al.*, 1972a). Area 1 has neurons related to quickly adapting Pacinian receptors, while such input is not seen in Area 3b (Paul *et al.*, 1972a; Merzenich *et al.*, 1978; Sur *et al.*, 1978). Furthermore, neurons in Area 3b have a homogeneous receptive field organization, while many cells in Area 1 have a center-surround receptive field organization (Sur, 1978). Area 2 has joint and other "deep" receptor inputs without obvious cutaneous receptor inputs in the anesthetized owl monkey (Merzenich *et al.*, 1978), but in macaque monkeys both deep and cutaneous inputs were apparent in similar recordings (see Nelson *et al.*, 1979). Area 3a is predominantly activated by the stimulation of afferents from muscle (Tanji, 1975; Heath *et al.*, 1976). Finally, neurons in Area 1 have larger receptive fields than do those of Area 3b. There is evidence that these larger receptive fields are a consequence of greater convergence of inputs to Area 1 "columns" (Sur, 1978; Paul *et al.*, 1972b; M. M. Merzenich, J. H. Kaas, Sur and, R. A. Nelson, unpublished).

Differences in response characteristics are less clearly understood in the topographically organized auditory cortical fields, but detailed temporal response characteristics and susceptibility to anesthesia are clearly to some extent field-specific (see Merzenich *et al.*, 1975; Knight, 1977; Andersen, 1979). Of course, response properties are very different in nontopographic and topographic cortical fields (e.g., see Merzenich *et al.*, 1975).

In the visual system, Hubel and Wiesel (1965) noted striking field-specific response characteristics in the visual cortex of cats. They found that a class of neurons, the "simple" cells, were common in V-I but were absent in "V-II" and "V-III." Similarly, "simple" cells and "circularly symmetric" cells appeared to be confined to V-I in monkeys (Hubel and Wiesel, 1968). In further studies of macaque monkeys, Hubel and Wiesel (1970) later described "binocular depth" cells in V-II of a type not found in V-I (also, see Poggio and Fischer, 1977). In more recent investigations, a high proportion of neurons in Area MT of the owl monkey (Newsome *et al.*, 1978) and in the probable homolog in macaque monkeys (Zeki, 1974) have a preference for stimuli moving in a particular direction. Zeki (1977) has also described an area of the superior temporal sulcus of macaque monkeys with a concentration of "color-coded" neurons. Finally, neurons in the various visual areas have different receptive field sizes, again suggesting differing degrees of convergence and/or different sources of inputs.

I. THERE IS SOME DIRECT EVIDENCE THAT DIFFERENT TOPOGRAPHIC REPRESENTATIONS MAKE SPECIFIC CONTRIBUTIONS TO EVOKED PERCEPTIONS

Identification of field-specific contributions to perception constitutes a difficult task because there is very little information about selectively activating or inactivating individual fields. However, one clear demonstration of field-specific contributions to behavior exists in the ablation-behavioral studies of Randolph and Semmes (1974). They demonstrated that removal of the hand representation in Area 1 of somatosensory cortex of monkeys resulted in an impairment on tasks involving discriminations of "texture" while a specific deficit in form discrimination could be attributed to a lesion of the hand representation in Area 2. Thus, distinct changes in perceptual abilities were demonstrated to be field-specific and assignable to these two Areas.

The neurological literature provides numerous examples of highly specific deficits resulting from restricted cortical lesions in humans (see Hines, 1929, for classical review, and Teuber, 1960, and Luria, 1966, for more contemporary reviews). Thus, in classical neurological studies color perception has been lost without loss of form discrimination, or depth perception without pattern discrimination. In the somatosensory system, various limited combinations of losses of vibratory, temperature, pain, tactile pattern, or position sensibility have long been described consequent of different parietal lobe lesions. A wide variety of lesion-specific deficits have been described; in the words of a contemporary neurologist, "for every local lesion functional systems develop specific defects" (Luria, 1966). Unfortunately, information on lesion location and cortical field definition in humans is rarely adequate for unequivocally relating specific sensory deficits to given cortical representations.

IV. General Conclusions

A. A SUMMARY OF FINDINGS RELEVANT TO THE CLASSICAL VIEW OF FOREBRAIN ORGANIZATION

Consider again the aforementioned tenets of the classical concept of forebrain organization.

1. There are only a few divisions of the forebrain of functional significance for each sensory modality.
2. These divisions form a system for serial sensation-to-perception processing, i.e., successive fields subserve successively "higher" functions.
3. Orderly representations of receptor surfaces are important in the early stages of sensory processing, but are not necessary in later stages, which deal with abstractions and higher order functions.
4. These higher order functions are the product of large regions of "psychic" or multimodal "association" cortex.
5. Nonrepresentational "psychic" or "association" cortex expands greatly in mammalian phylogeny.
6. Entrance into the sensory level of a cortical hierarchical processing system is primarily from unitary "main-line" projection systems, i.e.,

from a single large representation of the retina, cochlea, or skin surface within the thalamus.

None of these ideas is now supportable. To the contrary:

1. There are a number of topographic representations of sensory surfaces in each sensory system. Thus, in the cortex of a macaque monkey, there are six or more representations of the organ of Corti, seven or more representations of the skin surface, and probably 10 or more representations of the retina.
2. Identification of these representations has led to a nearly complete redefinition of cortical field identity and boundaries both in primates and in carnivores.
3. Topographic representations occupy most of cortex caudal to the central sulcus in primates. There is proportionately little nontopographically organized cortex. The existence of an "association cortex" as the site of the generation of the highest level of perceptual information is in doubt.
4. Perhaps nonrepresentational cortex has expanded in primate phylogeny, but not nearly as much as has been proposed. On the other hand, the *numbers* of sensory representations clearly have increased with phylogenetic expansion of the forebrain.
5. The present understanding of cortical connections does not support the traditional concept of a serial cortical sensation-to-perception hierarchy of processing of information. Rather, each cortical field is multiply interconnected with other representations with the inclusion of parallel, serial, and recurrent components. Most connections are within a sensory domain. Parallel thalamocortical projection systems that segregate different classes of information are common.
6. The topography of different fields is field-specific and often dramatic differences are seen.
7. Different cortical fields receive different mixes of input with component-segregated information. Many response characteristics of neurons are consequently field-specific.
8. The response properties of neurons in "secondary" fields in comparison with those of neurons in "primary" fields are not consistently compatible with the concept of higher functions in the "secondary" fields.
9. Finally, some evidence from studies of the effects of lesions or damage of cortical regions indicates that different topographic representations can make field-specific contributions to perceptions.

B. SOME IMPLICATIONS FOR THE GENESIS OF PERCEPTION FROM THE FOREBRAIN

1. Perception Arises from the Nearly Simultaneous and Largely Parallel Activation of a Number of Cortical Fields

While the responses of cortical neurons are greatly dependent on specific stimulus features, it is also true that rather simple stimuli such as a moving bar of light, onset of a tone, or the depression of the skin will activate neurons in all or nearly all of the cortical representations at about the same time. Thus, a viewed object would generate concurrent topographic patterns of activity in a number of cortical fields. Because cortical areas differ in the source of their inputs, their internal topographics and intrinsic structure, and their overall neural response properties, each area must make a field-specific contribution to the resulting perception of the object. Since a spatially unified perception is generated, the cortical maps must allow the same "peripheral reference" to be established for each cortical site activated by the same stimulus.

2. There Are Potentially Complex Functional Interfield Interactions Modifying the Product of Fields; Cortical Fields Can also Potentially Modify Their Inputs (and the Inputs to Other Fields)

While the percept of an observed or felt object must be the product of the nearly simultaneous activation within most or all of the fields of cortex within the appropriate sensory domain, there are many anatomically expressed opportunities for interfield interactions that could modify that percept. Certain clusters of topographic fields are strongly interconnected. This creates tremendous *potential* for interfield interactions, although the functional significance of the complex system of interconnections has not yet been defined. Moreover, most fields have connections that would allow the direct modification of their thalamic input and thalamic input to other fields. Thus, while different cortical fields usually derive their principal inputs from parallel ascending sources, there are complex connections that allow the possibility of both the manipulation of that input and the modification of the cortical field product. As far as is known, at least most interfield and descending connections are homotopic or nearly so. Differences in how an object is perceived could result from such a complexly interconnected system. In other words, under different operational conditions such as in different states of attention or expectancy, complex interactions could produce greatly altered outputs from specific fields, and hence result in quite different perceptions of the same object.

3. *Implications for Dreaming and Remembering*

If perception is generated by the coincident activity of a number of topographic matrices that generate a unified sensation by virtue of their internal topographies, homotopic interconnections, and coincidentally assigned peripheral references, memories and dreams are likely to depend on similar mechanisms. Since memories and dreams have similar spatial referents to ongoing perceptions, it is parsimonious to hypothesize that they all arise as a consequence of the same basic neural representational mechanisms. Thus it seems plausible that a memory or a dream is somehow reintroduced across much of the same representational matrices that are normally activated during perception. Differences in the memory or the dream of an object and the actual perception of the object could be a consequence of a different mix or balance of outputs from different representational areas. In fact, there is recent evidence that regions in topographically organized visual cortex are differentially active during REM (dreaming) sleep. Whether a memory is stored in some way throughout the representational matrices, or whether there is some site-specific memory storage system is an intriguing question. In any case, without knowing how information is stored it is difficult to speculate how stored information could be replayed across representational cortical matrices.

If dreams and memories depend on the activation of a collection of sensory representations, how do we account for the observation that electrical stimulation of single cortical locations in what must be representational cortex in humans sometimes evokes complex memories (see Penfield and Rasmussen, 1952; Penfield and Jasper, 1954). One possibility is that the relatively high levels of stimulation used in such instances are capable of activating complete networks of cortical and subcortical areas, and somehow activating storage and replay mechanisms. Such memories are not commonly activated near the epileptic focus in epileptic patients where presumably cortical depression would reduce the recruitment of other brain structures. In addition, lower levels of cortical stimulation related to the development of a "visual prosthesis" resulted in only simple sensations such as points of light, stars, and small bars (Dr. Daniel Pollen, personal communication). Thus, it appears unlikely that activity restricted to a single sensory representation is capable of inducing complex memories, dreams, or perceptions.

4. *The Significance of "Association" Cortex: Is It the Highest Level Cortex for Genesis of Perception?*

One of the clear implications of recent studies of sensory cortex and thalamus is that there is actually relatively little multimodal processing in sensory systems. Yet, there still may be limited small regions of cortex between the topographic visual, auditory, and somatosensory areas that are reasonably characterized as bimodal or multimodal. Is this the "highest level" cortex from which refined aspects of perception arise, or does multimodal cortex have some other role? Since nontopographic multimodal fields would seem incapable of assigning *topographic* attributes to evoked perceptions, it would seem reasonable to hypothesize that such multimodal nontopographic regions are performing in the perceptual realm what Penfield termed "interpretative" functions. Penfield found that general perceptual attributes ("I've seen (felt, heard) this before," "I like this," "I don't want to do this," "I don't feel (or see or hear) any," etc.) were applied to any ongoing experience of the stimulated patient (see Penfield and Rasmussen, 1952; Penfield and Jasper, 1954). Such interpretative attributes are, in a sense, *lower* level attributes. They are applicable to more than one modality for the very reason that a spatial reference is irrelevant. In terms of its *perceptual* contributions, then, multimodal cortex might possibly subserve interpretative functions.

Of course, as pointed out by Mountcastle and colleagues (1974), multimodal neural integration can probably be expected to have a role in controlling an animal's decision to act. However, the command control of voluntary activity should be separated from considerations of the perception evoked from normal activation of this cortex.

C. SUMMARY OF PRINCIPLES OF A UNIFIED HYPOTHESIS ON THE GENESIS OF PERCEPTION IN THE FOREBRAIN BASED ON CONTEMPORARY RESULTS OF STUDIES OF SENSORY SYSTEMS

A hypothesis of the basic mechanism of genesis of spatial aspects of perceptions from the forebrain based on recent studies of sensory systems might contain the following principles:

1. Perception is a product of a nearly simultaneous activation of a number of topographic sensory representations.
2. Inputs to and the response properties of neurons within these topographic representations are in some respects field-specific.
3. The intrafield topographic orders establish a spatial referent for each spatially assignable perceptual attribute generated by these representational areas.
4. Differences in the perception of a given stimulus are to some extent a result of variations in the contributions of individual topographic representations to perception under different conditions of attention, expectancy, or other factors.
5. Contributions to perception are also made by "interpretative" cortical regions that may be multimodal. Perceptual attributes contributed by these cortical fields are not spatially assignable (or are only weakly so). There may be representational cortex between the topographically ordered visual and somatosensory and auditory cortical fields that are of this type.
6. Memories and dreams receive their spatial referents by the same mechanisms as do real-time perceptions. Differences between dreams, memories, and perceptions are a result of differential activations of specific subsets of topographic representations. Remembering must require a mechanism whereby stored information can in some way be replayed across topographic representations so that the memory gains its spatial referents.
7. Complex interfield connections might be involved in (*a*) the generation of a spatially unified perception, (*b*) the replaying of memories or dreams across multiple cortical topographic representations, and (*c*) the production of perceptual variety for given stimuli.

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