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Evolution of Neocortex

Early views of the origin of cortex and recent studies of visual cortex in hedgehogs and tree shrews are discussed.

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Historically, the first goal of comparative neurology was to determine which parts of the brain are common to all vertebrates and thereby to establish which structures expanded or arose anew in the course of vertebrate evolution. This initial phase of the inquiry was achieved around the turn of the century by the investigations of Elliot Smith in England, Ariens Kappers in Holland, and Herrick in this country. The plan of the vertebrate brain, which is easiest to recognize in species resembling the prototypical vertebrates, consists of a number of subdivisions each of which can be identified mainly with one type of sensory input—olfactory, visual, labyrinthine, or visceral. Motor centers are found as a rule in the ventral portion of each subdivision; this results in a degree of autonomy among divisions, although they are interconnected by a network of fibers. Of the major subdivisions of the brain, the olfactory forebrain expanded the most in the evolution of higher vertebrates. Under the increasing influence of nonolfactory sensory systems, the changes in the olfactory forebrain culminated with mammals in the origin of neocortex.

Below reptiles, in the evolutionary scale, there is no cortex and the cerebral hemispheres are dominated by fibers from the olfactory organs. In modern reptiles the cerebral hemispheres show a concentration of neurons on the surface, but this cortex consists of a single layer of cells and may represent a very primitive state of cortical development. In contrast, in even the most primitive mammals the cortex is comparatively well developed, with layer upon layer of neurons. The appearance of the layers varies from region to region, with the result that clear morphological distinctions can be drawn, the most obvious of which is a threefold subdivision between the lateral, medial, and dorsal walls. The significance of this subdivision was recognized by Elliot Smith (*1*), who showed that the medial wall, or hippocampus, and the lateral wall, or pyriform area, have homologs in the cerebral hemispheres of lower vertebrates. This leaves the dorsal region of cortex as a unique feature of mammals, and accordingly it was termed neocortex.

The importance of the distinction between new and old cortex is shown by the fact that further evolutionary advancement in the brains of mammals takes place chiefly in neocortex (*2*). Of course the "old" parts of the cortex must have been functionally altered with the appearance of the new cortex, and in fact their absolute size also increases, but these changes are overshadowed by the expansion and differentiation of neocortex.

Elliot Smith's studies also showed the significance of the thalamus, which lies in the fact that the nonolfactory sensory impulses to the cortex relay in the thalamus. The neocortex can be subdivided into a number of areas on the basis of its neural connections with the thalamus, and the relative position of each neocortical area is determined by the location of its relay nucleus in the thalamus. Figure 1 shows how the fibers from each thalamic nucleus in a primitive mammal take the most direct route to the cortex and thereby establish a topographic organization which can be found throughout mammals. The visual area, receiving fibers from the lateral geniculate nucleus, lies at the back of the cerebral hemisphere; the auditory area, receiving projections from the medial geniculate nucleus, lies between the visual area and the pyriform cortex; and the somatosensory-motor cortex, the target of projections from the ventroposterior and ventrolateral nuclei, lies in front (*3*).

The subdivision of neocortex into regions which can be identified in all mammals raises the question: Did the various areas of the neocortex evolve at the same rate? This too was answered by the studies of Elliot Smith. In a mammal such as the Virginia opossum, a common North American marsupial which is primitive in the sense that it has acquired relatively little neocortex, almost all of the cortex is accounted for by the motor area and the cortical targets of the thalamic sensory nuclei (see Fig. 1). In contrast, the greater part of the neocortex in man is devoted to association area, the cortical regions intercalated between the sensory and motor zones. The primary locus of evolutionary advancement in mammals thus can be further narrowed from neocortex to a particular subdivision of the neocortex, the association cortex.

Neural Model for Sensation and Perception

The expansion of association cortex fit the view prevailing in psychology in the early 1900's that integration between sensory modalities requires a complex neurological process which is

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dependent on having the neural counterpart of modality-specific sensation already available. Since sensory cortex receives fibers from the receptors relayed through the dorsal thalamus, it seemed to follow that sensory cortex is the substrate for sensations—hot, cold, blue, C sharp—while the combining of sensations to form perceptions of objects and ideas is accomplished by the corticocortical fibers known to project from sensory to association cortex (*4*). By definition the association areas do *not* receive projections from subcortical relays, but later it was discovered that association cortex does receive fibers from the thalamus. In particular, the pulvinar nucleus of higher primates projects to most of the association areas in the temporal lobe and to extensive regions of the adjacent parietal and occipital lobes (*5*). Still, the idea that convergence from sensory systems transforms simple sensations into complex perceptions could be preserved; there was no known sensory projection to the pulvinar, and axons from the thalamic relay nuclei to the pulvinar might mimic the functions of corticocortical pathways. Thus, when the facts of comparative neurology and the prevailing neuropsychology were put together, it appeared that association cortex arose in response to "association" connections from sensory cortex, and, further, that the evolutionary expansion of association cortex is explainable as the result of the selective advantage of increased opportunities for cross-modality integration.

Species Differences in Capacity for Sensation and Association

The identification of sensory cortex with "sensation" and association cortex with "perception," as these terms are used in classic psychology, has implications for the nature of individual and species differences. Since, by definition, there is no way to alter a sensation—an element can combine only with other elements—individual or species differences can consist only in differences in the number of elements and not in differences in the fundamental mechanisms for sensory discrimination. A limitation in the kind of receptors may restrict one species to sensations of yellow and blue while a closely related species has the capacity for sensing red and green as well, and such eccentricities in range and acuity might be reflected in the sensory cortex. But peculiarities of the sensory cortex corresponding to differences in sensory range, continues the argument, cannot account for the evolution of behavior in mammals. To explain this trend toward greater behavioral complexity, neuropsychology looked to the association areas. There are marked differences, between higher and lower species, in the size of association cortex and therefore in the number of potential connections between the neural counterparts of stimuli and response. Indeed, the argument leads to the conclusion that species differences in intellectual capacity consist just in this quantitative potential for forming associations (*6*). It is important to note that, if the association cortex differs *only* in the number of potential connections, it remains essentially *one* organ common to all species.

The discoveries made possible by new techniques for recording cortical potentials evoked by sensory stimuli supported the synthesis outlined above. The finding of topographic projections of receptor surface in all species and in all three neocortical modalities seemed to provide the sought-after universal mechanism for sensory discrimination (*7*). Even such deviations as the outsized representation of the snout in the cortex of the pig make sense in terms of the sensory eccentricities of the species. At this point in the inquiry everyone expected that behavioral ablation studies would support the apparent significance of topographic projection to sensory cortex. It therefore came as a surprise when the removal of auditory cortex in cats failed to disrupt simple sensory discriminations such as pitch and loudness (*8*). Eventually behavioral defects were uncovered by Neff and his co-workers, but the functions these defects implied were much more complex than "sensory" in the traditional sense. For example, cats whose auditory cortex had been removed were found to have great difficulty in identifying the locus of a brief sound, yet they could detect a change in locus from one side of the head to the other (*9*).

A question naturally arises: Is the auditory cortex of cats unique? To answer this question we decided to study the visual cortex in a "primitive" species—the hedgehog. Vision was selected as the object of inquiry because the evidence from brain damage in man and higher primates supports the idea that visual cortex is the basis for sensation, and that a loss of sensation would result from a loss of visual cortex. If similar sensory losses could be shown in a prototypical mammal, the stability of the visual neocortex throughout the class Mammalia would be demonstrated. On the other hand, a failure to find simple visual sensory losses in lower mammals would weaken the strongest link in the case for the traditional view of sensory neocortex.

Once the question of possible species differences is raised, a comparative approach becomes mandatory. Thus, we decided to study the evolution of sensory neocortex as soon as it appeared that the neocortex of the cat was not necessarily representative of the mammalian neocortex in all important respects; but that was not the only reason for choosing an evolutionary approach. It has become increasingly clear that the account of cortical and behavioral evolution outlined above is correct only as a first approximation. The concept that the size of association cortex is correlated with performance on simple learning tasks was not supported by experimental studies, which showed that all species, regardless of the size of their association cortex, formed simple associations at about the same rate (*10*). Further, the view that association cortex is the site of new pathways formed in learning and conditioning was refuted by ablation studies (*11*). As the consequence of these disappointing results, comparative psychologists in general turned away from neural models of intelligence and learning to concentrate on discovering behavioral tasks which would reveal qualitative species differences in learning ability. One school of thought even rejected the notion that diverse species could be compared on a common scale in favor of the concept that intelligence, like instinct, is species-specific (*12*). The net effect of these developments has been that comparative psychology, with some notable exceptions [see, for example, Warren (*10*)], has lost its close connection with neurology—a connection originally envisioned by anatomists and psychologists alike (*13*).

But the conviction that evolution is characterized by a progressive increase in the complexity of behavior is too strong to permit abandonment of all hope for a single science of comparative neurology and psychology. Therefore, several years ago we sought a fresh starting point within the framework provided by classical comparative neurology and psychology. Our purpose here is to report this attempt.

Evidence that the expansion and differentiation of neocortex proceeded independently in the major mammalian lines of descent provided a clue to the direction this fresh start should take. Since most orders of mammals diverged from the common ancestor at about the same time in evolution, a cat, a monkey, and a wallaby, for example, must have acquired their enlarged cortex independently (*14*). Now we can ask whether the evolution of cortex converged or diverged in different lines of descent.

Such an inquiry must be founded on the prototypical organization, and therefore our first step was to select a suitable species; our next was to make an intensive study of the organization of the neocortex in the species selected. In the next section of this article we undertake to refine the traditional view of the evolution of neocortex, presenting evidence that association cortex may have arisen as a primitive sensory area and that the classical sensory areas are not stable in the evolution of some groups. Further, we show that removal of the visual cortex does not produce simple sensory loss. We also argue that the expansion of sensory cortex is divergent in primates and carnivores, showing that the association cortex

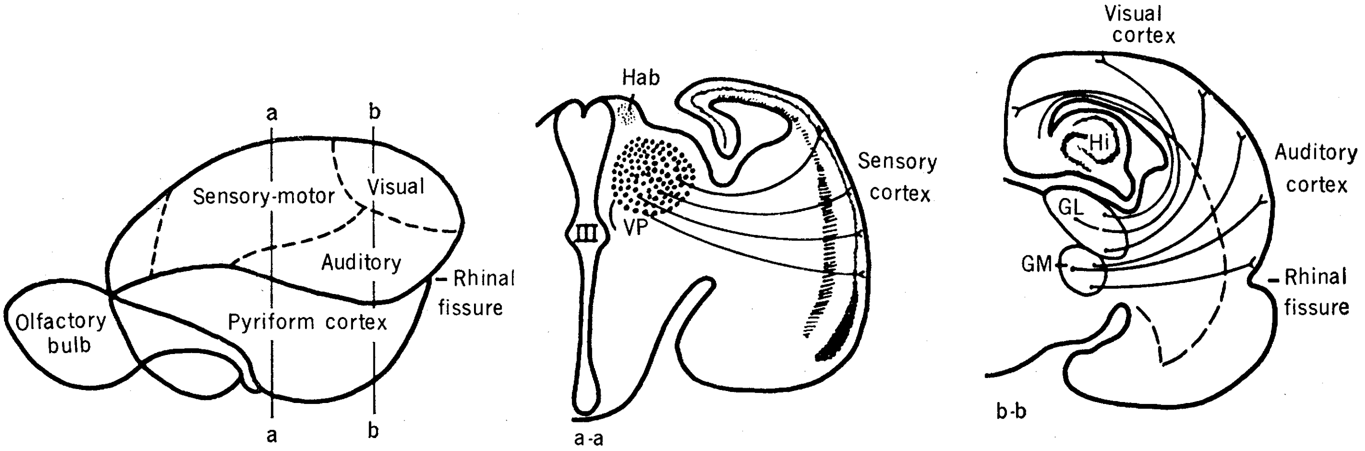
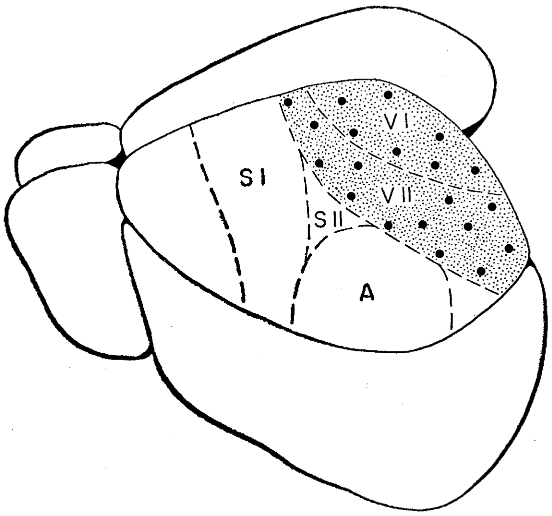


Fig. 1. A map of the cortical areas in a primitive mammal. The frontal section through the cerebral hemispheres at plane *a-a* shows the direct route taken by the thalamic fibers from the sensory relay nucleus of the thalamus to the somatic cortex in a fetal platypus. The platypus has a large sensory bill, and the trigeminal nerves and centers are greatly enlarged. Frontal section at plane *b-b* shows the direct route taken by visual and auditory fibers to the cortex in a primitive mammal such as the opossum. [Adapted from Elliot Smith (*1*)]



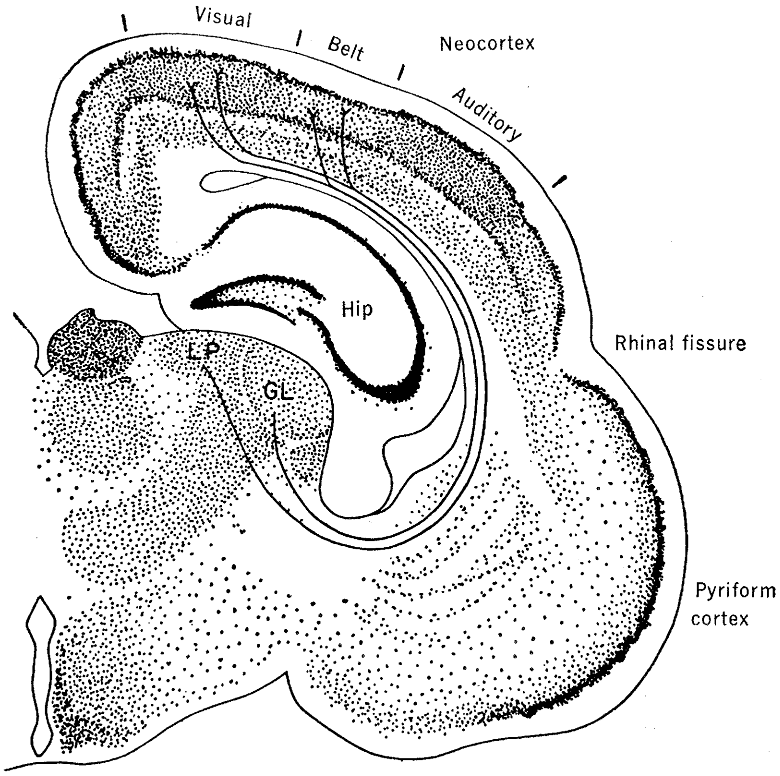


Fig. 2 (above). Thalamic projections in the hedgehog from LP (circles) and GL (stippled area) in relation to cortical subdivisions defined by evoked potentials and architectonics (for abbreviations, see *30*). Both visual areas received projections from both GL and LP. The auditory cortex lies adjacent to V II, so there is no additional zone between the projections from GL and GM. Fig. 3 (right). Diagram of pathways from the visual thalamus to the visual cortex in the hedgehog. Axons leaving GL and LP enter the internal capsule and travel through the white matter underlying the cortex. In drawing the cortex an attempt was made to suggest the increased granular layer characteristic of the visual area and the auditory area. Between these two sensory zones is a belt of cortex. In the diagram each thalamic fiber sends one collateral to the belt and one to the visual cortex; in order to produce severe retrograde degeneration, both branches must be severed.

most characteristic of higher primates cannot even be identified in carnivores and, further, that in carnivores the most striking evolutionary changes took place in sensory cortex. Finally we present evidence that similar cortical organization is achieved independently in response to similar ecological niches.

The Prototypical Organization

The same comparative-anatomical methods which lead to a concept of ancestral species suggest that the brains of some living species have departed very little from the archetype. The brain of the hedgehog merits this description. Of those species readily available for laboratory experiments, none of the others possesses a neocortex so small in proportion to the total cortex. Further, there is very little differentiation within the neocortex; only a few subdivisions can be identified, and they are not well defined. The lack of distinct boundaries between nuclei is even more apparent in the thalamus, where most of the cells look alike. The classical sensory relay nuclei can be identified, but the boundaries between them are often uncertain. All these features establish the hedgehog as a baseline from which the course of development of neocortex in different mammalian lines can be traced, and for that reason we selected the hedgehog for a program of anatomical and behavioral research.

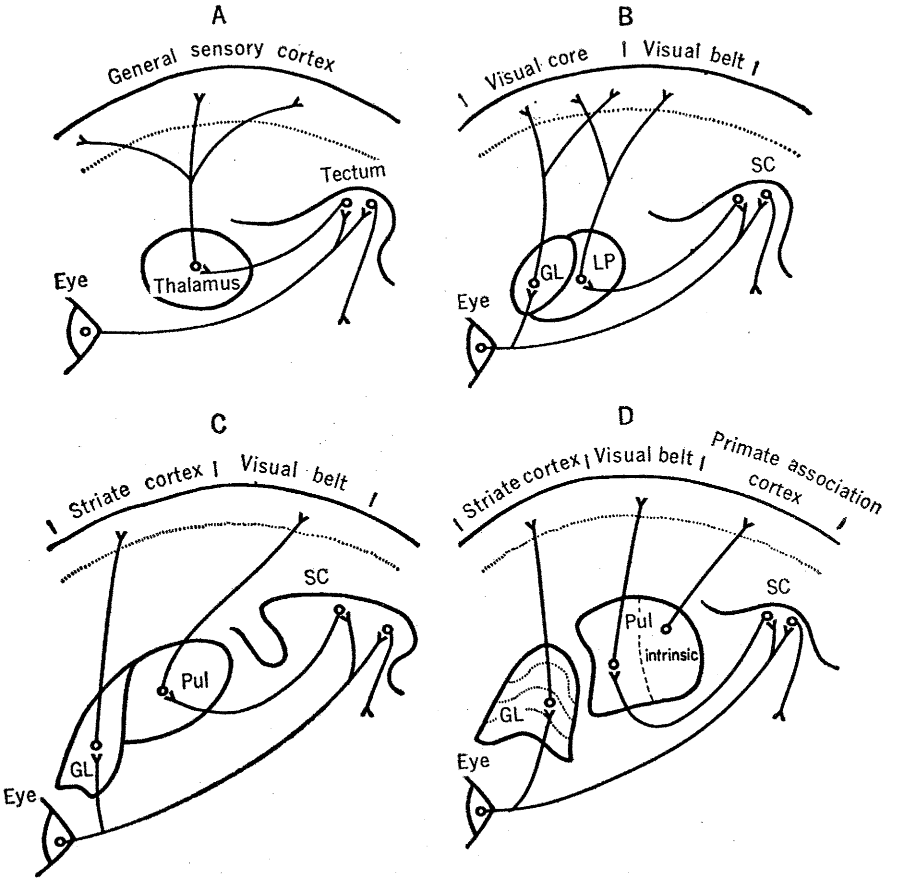


Fig. 4. Schematic representation of the four main steps in the evolution of thalamic and cortical visual areas from a hypothetical reptile-like mammalian ancestor to higher primates. The first stage (A) is represented by a reptile-like ancestral type, envisioned by Herrick, in which the thalamus relays tectal impulses diffusely into the general sensory cortex. Only the visual path is shown, but Herrick postulated that auditory and somatic tectal fibers ended upon the same thalamic cells. In the second stage (B), represented by early mammals and approximately by the hedgehog, a portion of the thalamus receives fibers directly from the optic tract, which may have provided the basis for the distinction between the lateral geniculate on the one hand and the lateral group (including LP and Pul) on the other hand. The projections from LP and GL, however, still overlap in the visual cortex. In the third stage (C), which may be represented by the tree shrew, the lateroposterior nucleus has become more like a primate pulvinar and projects to the temporal cortex. The lateral geniculate projects entirely to the striate area. The fourth stage (D) is represented by a higher primate such as the monkey. This stage (not discussed in the text) differs from the third stage in that there is further elaboration and subdivision of the pulvinar. Only a portion of the pulvinar now receives visual fibers from the tectum and a new "intrinsic" part projects to the true primate association cortex.

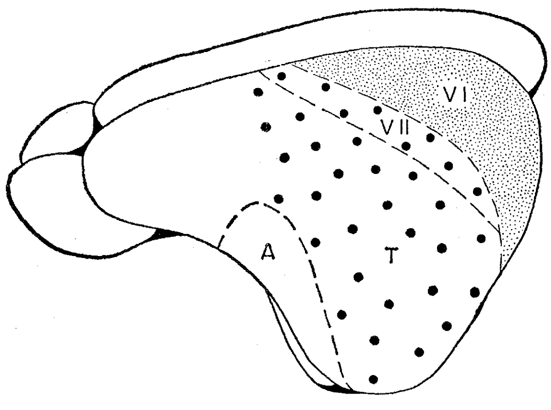
Elliot Smith's picture of cortical areas in a primitive mammal (Fig. 1) is supported by our studies in a general way, but the qualifications and refinements carry far-reaching implications. When the sensory areas are defined by the method of thalamic retrograde degeneration, then it is found that projections from the lateral geniculate body, medial geniculate body, and ventroposterior nucleus meet each other and may even overlap (*15*). Similarly, the method of evoked potentials shows that few if any silent areas are intercalated between regions responsive to sensory stimulation (*16*, *17*). Both methods yield a map of sensory cortex similar to Fig. 1. However, each of the sensory areas so far studied can be subdivided further. For example, the use of small spots of light as stimuli reveals a double representation of the retina (see Fig. 2), with the vertical meridian represented along the border between the two maps (*16*). Since similarly organized visual areas I and II are found in so many mammalian species, the areas are probably homologous—that is, they can be attributed to a common ancestor. The boundaries of visual area I correspond precisely with an architectonic field that we had already identified as sensory cortex by means of the usual criteria, such as increased thickness of the fourth granular layer (see Figs. 2 and 3) (*15*). Visual area II occupies a belt of cortex intercalated between two architectonic sensory areas—visual and auditory. Thus, visual area II might once have been called association cortex, and this old classification is not without some relevance to the present argument. Figure 3 is an attempt to show the relation of the belt to the two sensory areas on either side; it also depicts the thalamic projections described next.

The key to the significance of the two visual areas lies in the organization of thalamic projections. Instead of one visual relay nucleus, the lateral geniculate, we now have evidence of two visual projections to the neocortex, with the second relaying by way of the lateroposterior nucleus (see Fig. 3). The first relay, and the only one traditionally recognized as a visual pathway to cortex, receives fibers from the optic tract, but recent studies in several mammalian species have demonstrated a second pathway to the thalamus from the visual tectum (*18, 19*). Specifically, the tectum projects to the lateroposterior nucleus. Since the tectum is the target of the optic tract in all vertebrates, it must have been the major visual center prior to the evolution of the dorsal thalamus and neocortex. In mammals only the smallest fibers of the optic nerve continue to project to the tectum, a fact which can be taken as a sign of its older phyletic origin.

Here we might digress to point out that both small- and large-fiber pathways are characteristic of the auditory and somatic systems as well as of the visual. As a result of the classical studies of Erlanger, Gasser, and Bishop, the significance of fiber size in peripheral nerves has been interpreted in terms of the correlation between axon diameter and modality—touch, pain, and temperature (*20*). However, this type of subdivision does not apply as readily to the visual or auditory systems, so Bishop has recently sought a more general organizing concept (*21*). He noted that, in general, small fibers project to phyletically older targets in the midbrain and brain stem, while large-fiber tracts bypass older centers, passing directly to new targets in the dorsal thalamus. Bishop therefore postulated an evolutionary trend toward increasing fiber diameter, with the provision that the older tracts are never lost with advent of the new. In the light of Bishop's ideas we can imagine a stage in evolution in which the only pathway visual impulses could take to reach the dorsal thalamus was through the tectum (see Fig. 4). Further, on the basis of Herrick's study of amphibians, it is tempting to view the thalamus in such a hypothetical reptile-mammal ancestor as polysensory and as projecting diffusely to a general sensory cortex (*22*). Indeed, we have obtained evidence (*23*), using the method of evoking responses in single cells of the thalamus, that the auditory and somatic relay nuclei of the hedgehog are incompletely differentiated and that neither is modality-specific.

This line of reasoning leads us to postulate that the lateral geniculate became differentiated from some older thalamic area in response to the direct projections of the optic tract and that the lateroposterior nucleus in the hedgehog is the remnant of that older region. It is not surprising that we found the cortical projections of the lateroposterior nucleus and the lateral geniculate body extensively overlapping in the hedgehog, since that species may represent an early phase in the evolution of the lateral geniculate (*15*). This is not to say that the organization of the projections to visual core and belt in the hedgehog are identical. Insofar as the lateral geniculate body has *essential* projections [as distinguished from *sustaining* projections (*24*)], they are almost certainly confined to visual area I. At the same time, if the lateroposterior nucleus sends any essential projections at all to the cortex, they are certainly *not* to visual area I. Still, the overlap between the lateral geniculate body and the lateroposterior nucleus means that the organization of visual area II is not necessarily the result of the secondary system's relaying through the lateroposterior nucleus, although the simplicity of such a scheme is compelling.

We can now cite two reasons for considering the visual belt itself—that is, visual area II—as representing a more primitive level of organization than visual area I. (i) In comparing the architectonics of visual areas I and II, we find that the layers in area II are less distinct and less well developed than those in area I, and that the fibers projecting to and from visual area II are small and poorly myelinated (*15*). (ii) The receptive fields of neurons in visual area II are larger, presumably



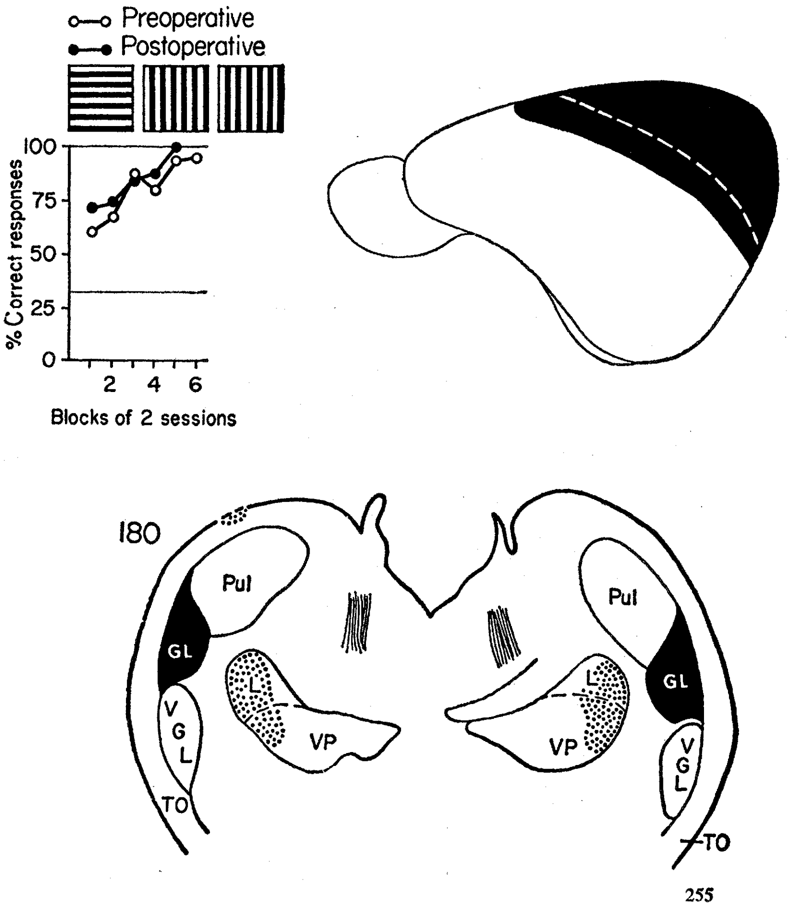


Fig. 5 (above). Projections of GL (strippled area) and Pul (circles) to the posterior neocortex of the tree shrew. The projections of GL are entirely confined to the striate area, whose boundary is indicated by the same broken line that defines the limit of V I. The projections from Pul cover the region from V I to the auditory cortex and include V II. Fig. 6 (right). Cortical lesion in a tree shrew, Tupaia 110, and record of the animal's performance on a pattern-discrimination test. (Top left) The behavioral record, showing that the habit of selecting the horizontal stripes was quickly relearned after surgery. (Upper right) The lesion, shown in black on a standard view of cortex. The boundary of the striate area is shown by a dashed white line; it is clear that all of this area was ablated. (Bottom) A section through the thalamus, showing that all of the lateral geniculate is degenerated (black designates complete cell loss). The stippled area in L and in VP is a sign of partial degeneration.

reflecting a less precise topographic projection of the retina (*16*).

The effects on simple pattern discrimination of ablating the visual areas confirms the idea that both areas have visual functions. After complete removal of the core, or visual area I, hedgehogs never regain their preoperative level of performance, but neither is their performance at a chance level. We have interpreted this deficit in terms similar to our interpretation of the localization deficit found in cats after removal of the auditory cortex. That is, we believe the hedgehogs without visual area I can detect a difference between patterns but find it impossible to identify a pattern. As yet we do not have enough hedgehogs with complete ablation of visual areas I and II to warrant a general conclusion about the effects of removing both areas. However, on the basis of partial lesions of varying sizes, we can say with assurance that visual area II plays a role in pattern vision.

To sum up, the sensory areas in the hedgehog account for most and probably all of the posterior neocortex. Each area can be further subdivided, and, in particular, the visual area consists of an architectonic core and belt corresponding to visual areas I and II as defined by evoked potentials. We regard the belt as representing a more primitive level of organization, on the following grounds. (i) The belt is the chief target of a second and older visual projection system proceeding from the tectum by way of the lateroposterior nucleus. (ii) The topographic projection of the retina to the belt is less precise than the projection to the core. (iii) The architecture of the belt appears primitive. Since the lateroposterior nucleus seems to be the precursor of the pulvinar nucleus, which expands so much in primate evolution, the obvious question posed by these conclusions is whether the belt is the precursor to the association cortex of primates. Whatever the answer, the two projection systems in the hedgehog are incompletely separated at the cortical level inasmuch as the radiations of lateral geniculate body and lateroposterior nucleus overlap. We show below that in the tree shrew the lateral geniculate body does not project to the belt and the degree of separation between striate cortex and belt found in higher primates is thus achieved.

Studies of the Visual System in the Tree Shrew

An opportunity to study the structural changes marking the origin of primates is provided by the tree shrew (*Tupaia glis*), a small squirrel-like inhabitant of southeast Asia. Although the precise taxonomic position of *T. glis* is still uncertain, its brain shows many similarities to that of the primate while, at the same time, retaining many primitive features found in the hedgehog. For example, its cortex has neither

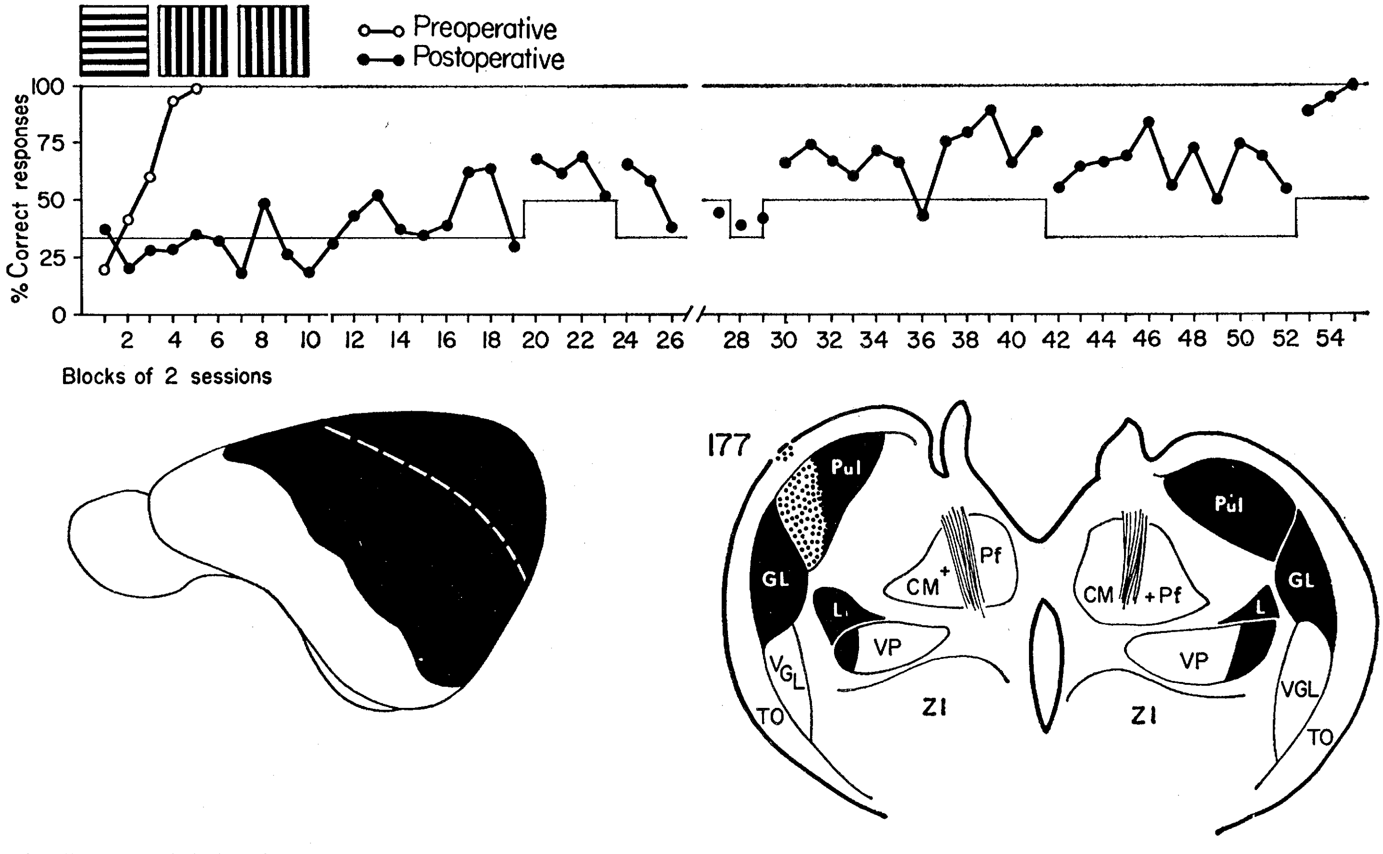


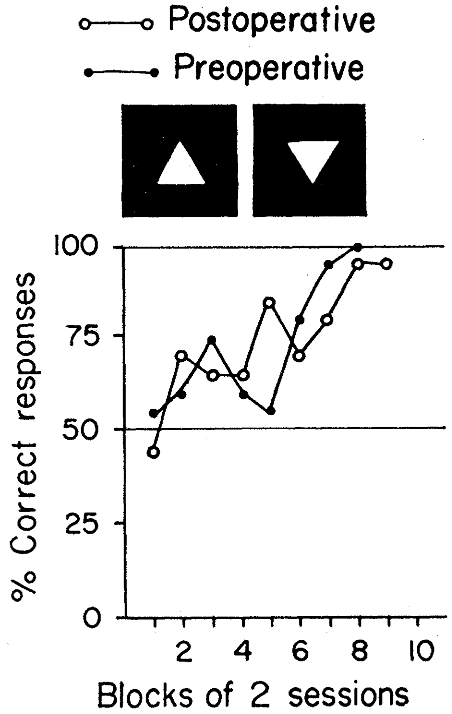
Fig. 7. Cortical lesion in a tree shrew, Tupaia 103, and record of the animal's performance on a pattern discrimination test. Unlike Tupaia 110, this animal failed to show improved performance. At the end of session 38 the discrimination task was simplified by reducing the number of alternatives from three (two incorrect, one correct) to two. This point is indicated by the change in the chance level from 33 to 50 percent. Eventually, after a period of training (indicated by a break in the abscissa) on the orientation of a single stripe, the animal achieved a learning criterion. (Bottom left) Diagram of the cortical lesion; the striate area is indicated by a dashed white line. In contrast to the lesion of Tupaia 110, a large portion of the temporal area has been ablated. (Bottom right) A thalamic section, at about the same level as the thalamic section shown for Tupaia 110 (see Fig. 6). In the case of Tupaia 103, the pulvinar shows severe degeneration.

sulci nor a large number of cytoarchitectonic subdivisions. Still, some overall expansion of neocortex beyond that seen in the hedgehog is indicated by the downward displacement of the rhinal fissure. One region in particular, the visual area, stands out as if it has precociously achieved primate status. The visual cortex of the tree shrew resembles primate striate cortex sufficiently to merit the term *striate area.* Aside from the striate area, the most conspicuous new feature is a large temporal area separating the auditory and visual areas. (As discussed above, only a narrow belt separates auditory and visual cortex in the hedgehog.)

Also, the thalamus of the tree shrew shows striking differences from that of the hedgehog, notably the expansion of the lateral geniculate and the development of distinct lamina within this nucleus. Almost as great an increase in size has taken place in the adjacent lateroposterior nucleus, which now occupies an extensive sector of the thalamus. The cortical connections of this nucleus have developed sufficiently in the primate direction to warrant the name *pulvinar.* The pulvinar projects to a wide sector of cortex extending from the boundary of the striate area to the border of the auditory cortex (see Fig. 5). Some topography is easily recognized in these projections, but the relation between size of lesion and severity of degeneration points to a rather diffuse projection of collaterals. Thus, small lesions within the temporal area produce little or no retrograde degeneration in the pulvinar, whereas large lesions produce severe degeneration. In contrast, the projections from the lateral geniculate are exquisitely precise. A small lesion of striate cortex produces total cell loss within a small region of the geniculate. Complete removal of the striate area leads to complete degeneration in the lateral geniculate, whereas lesions anywhere outside the striate area produce no degeneration in the lateral geniculate. Thus, the limits of the projections of the lateral geniculate correspond precisely with the boundaries defined by cytoarchitecture (*25*).

The striate area also corresponds exactly with visual area I, as defined by evoked potentials. Visual area II, defined as the mirror image of the retinotopic organization found in visual area I, also can be identified with an architectonic zone, a belt lying adjacent to the striate area. Since the projections of the lateral geniculate are confined to the striate area, they cannot, of course, account for visual area II, so it is natural to wonder whether visual area II depends on the tectopulvinar pathway. There is little doubt that visual area II is included in the target of the pulvinar, but we also found that all, or most, of the region between the striate and auditory cortex receives fibers from the pulvinar. These results are summarized in Fig. 5.

Finding that only a part of the pulvinar target is organized as visual area II, we expected to find that only a part of the pulvinar relays visual impulses from the tectum; but Abplanalp and Nauta discovered that all of the pulvinar receives fibers from the tectum (*18*). We cannot explain why only a portion of the pulvinar target is topographically organized as visual area II, and it may be that visual area II is unrelated to the pulvinar but depends instead upon corticocortical connections. The rest of the temporal lobe outside visual area II responds to stimulation of large areas of visual field. In the next section we present behavioral evidence that all of the second visual area—a region much larger than visual area II as defined by electrophysiology—is involved in visual functions.



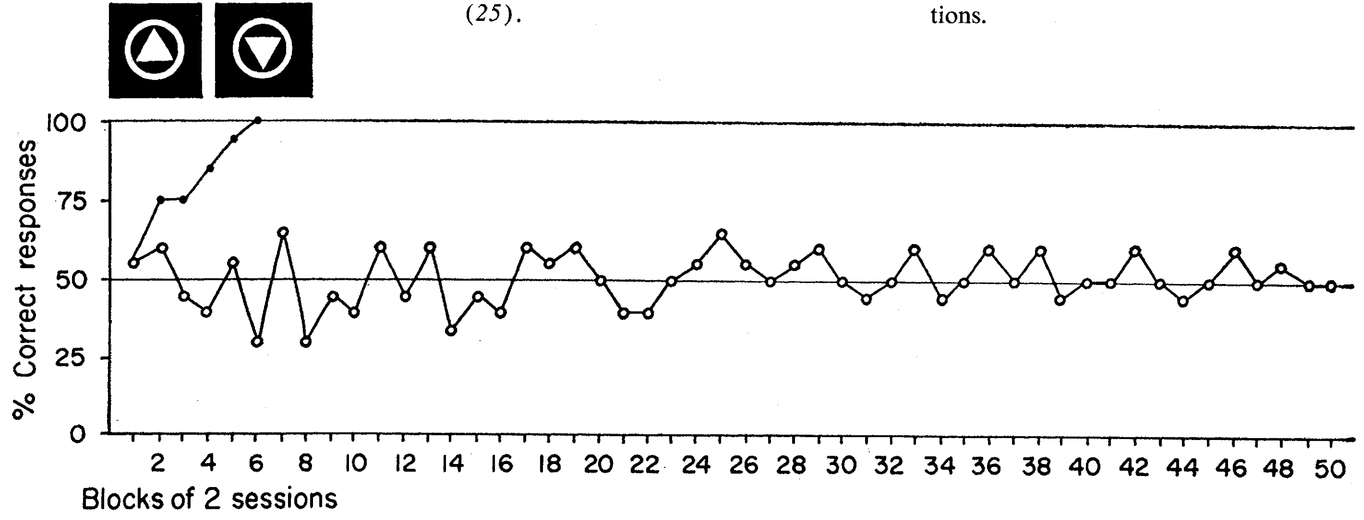


Fig. 8. Learning curves for tree shrew Tupaia 169 before and after complete removal of the striate cortex. (Top) Record showing that the animal had no difficulty after the operation in relearning to discriminate between an upright and an inverted triangle. (Bottom) Record showing that, when the triangles were encircled by a white band, the animal, after surgery, never achieved better than a chance level of performance. Before surgery the encircling of the figures provided little or no additional obstacle to discrimination.

Ablation Studies of Visual Areas in the Tree Shrew

We began our studies of the behavioral effects of removing the striate and temporal areas with simple patterns, such as horizontal and vertical stripes. After the tree shrews had been trained to discriminate with a high degree of reliability, the striate area was ablated —either alone or together with portions of the pulvinar target. The animals with more restricted lesions showed no obvious loss of ability to learn to discriminate patterns; this indicated that elaboration of the striate area was chiefly for the performance of functions more complex than simple sensory functions. Figure 6 is the behavioral record of a representative tree shrew with complete striate lesion. Not only were the animals with such lesions capable of discriminating differences in pattern but they appeared to have normal object vision, avoiding obstacles in their path and catching moving pieces of food. The animals with larger cortical lesions, represented by Tupaia 103 (Fig. 7), showed severe retardation in learning to discriminate patterns (*26*). Further studies of animals with lesions confined to the temporal cortex revealed a similar retardation in learning habits based on visual discrimination.

Some clues as to the function of the striate cortex are provided by studies now in progress in our laboratory at Duke University. Killackey has found that tree shrews without striate cortex are unable to discriminate between an upright and a vertical triangle when each triangle is surrounded by a circle (see Fig. 8). This inability must be dependent upon the masking effect of the circle, since the same animal just before failing to discriminate between the circled triangles had succeeded in discriminating between simple upright

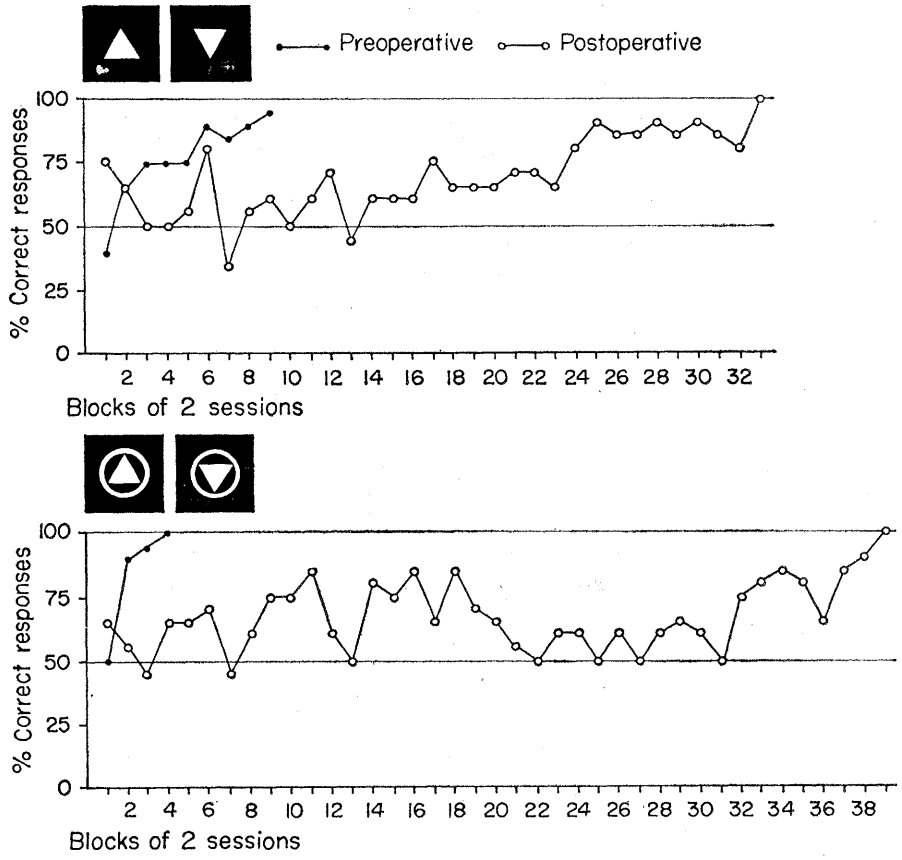


Fig. 9 (left). Learning curves for tree shrew Tupaia 162 before and after ablation of a large part of the temporal lobe. The task was the same as that of Fig. 8. The animal first learned to discriminate the orientation of the triangle, then the triangles were shown encircled by a white band. After surgery this animal showed pronounced retardation on both tasks, but criterion was eventually attained.

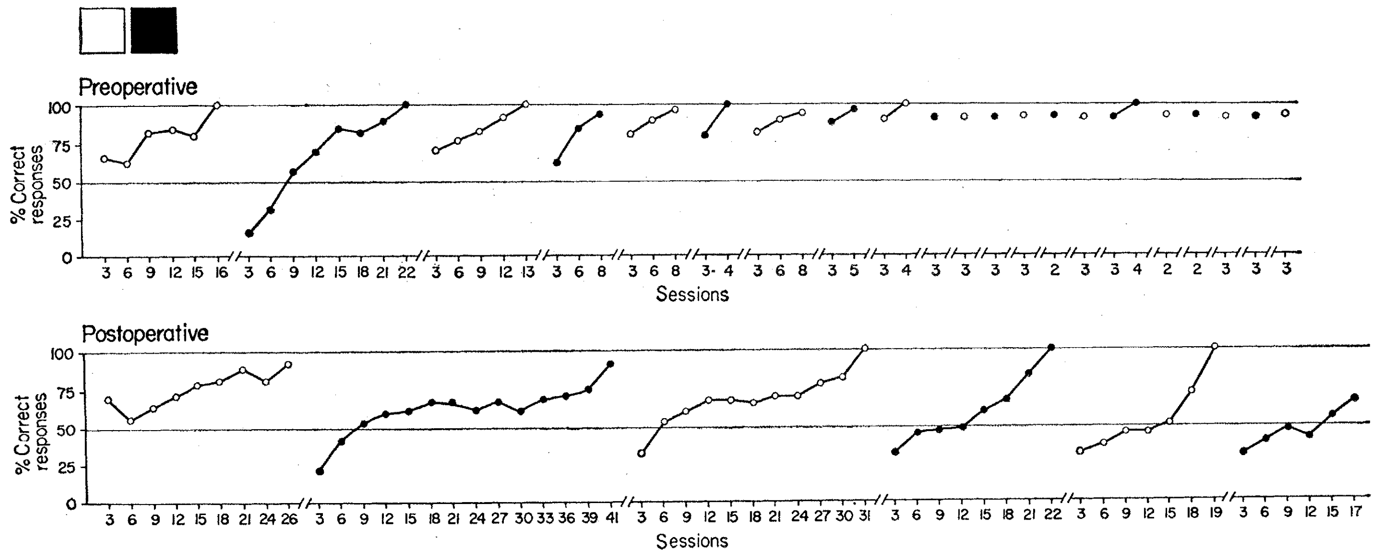


Fig. 10. Pre- and postoperative reversal learning in tree shrew Tupaia 127. The curves show successive learning of (open circles) a white positive stimulus and (solid circles) a black positive stimulus. The preoperative record shows a marked saving in learning time by the second reversal. In contrast, after surgery the animal's performance starts below the chance level on every reversal and learning is slowed down in every case. It is obvious that the animal never regains the habit of making the correct selection after the first trial with positive stimulus reversed.

and inverted triangles. Ablation of the striate cortex appears to be uniquely related to this failure, since animals with lesions of the temporal lobe learn to discriminate between encircled figures and simple patterns with equal ease (see Fig. 9).

Since the extrastriate visual area—at least the large portion of it lying in the temporal lobe adjacent to visual area II—expands with further primate evolution, one naturally wonders whether any of its functions forecast the functions of the temporal lobe in higher primates. We have some evidence that this is the case. Killackey has trained four tree shrews to choose a white card when it is paired with a black card (*27*). After the animals had attained a criterion of 15 correct responses on 15 trials in a single session, the significance of the two cards was reversed—that is, the animal was then trained to choose the black card. These reversals were continued until 20 reversals had been completed. Normal animals learned in the course of several reversals to shift the grounds for their choice, after making one or two errors. In contrast, the tree shrews with lesions of the temporal lobe had to learn the task all over again with each reversal (see Fig. 10). The lesion of animal 127 of Fig. 10 is shown in Fig. 11; it is clear that the cortical part of the lesion is restricted to the temporal area and that thalamic retrograde degeneration is almost entirely confined to the pulvinar.

From the point of view of anatomical specialization it is important to ask whether this deficit is specific to the temporal area. The available evidence indicates that it is; for example, lesions of the striate area do not abolish reversal-learning sets. Thus, two syndromes can be distinguished, each identified with removal of one of the visual cortical areas. Ablation of striate cortex alone results in a total incapacity to abstract a figure embedded in a larger pattern, but there is no loss of simple pattern discrimination. On the other hand, removal of the cortical target of the secondary visual path produces a retardation in learning visual discriminations and a complete inability to master reversal-learning sets, but camouflaging figures with additional patterns creates no further difficulties. At the risk of oversimplification, perhaps one may say that this evidence reverses the traditional view of sensory and association cortex. The temporal area, which would have been classed

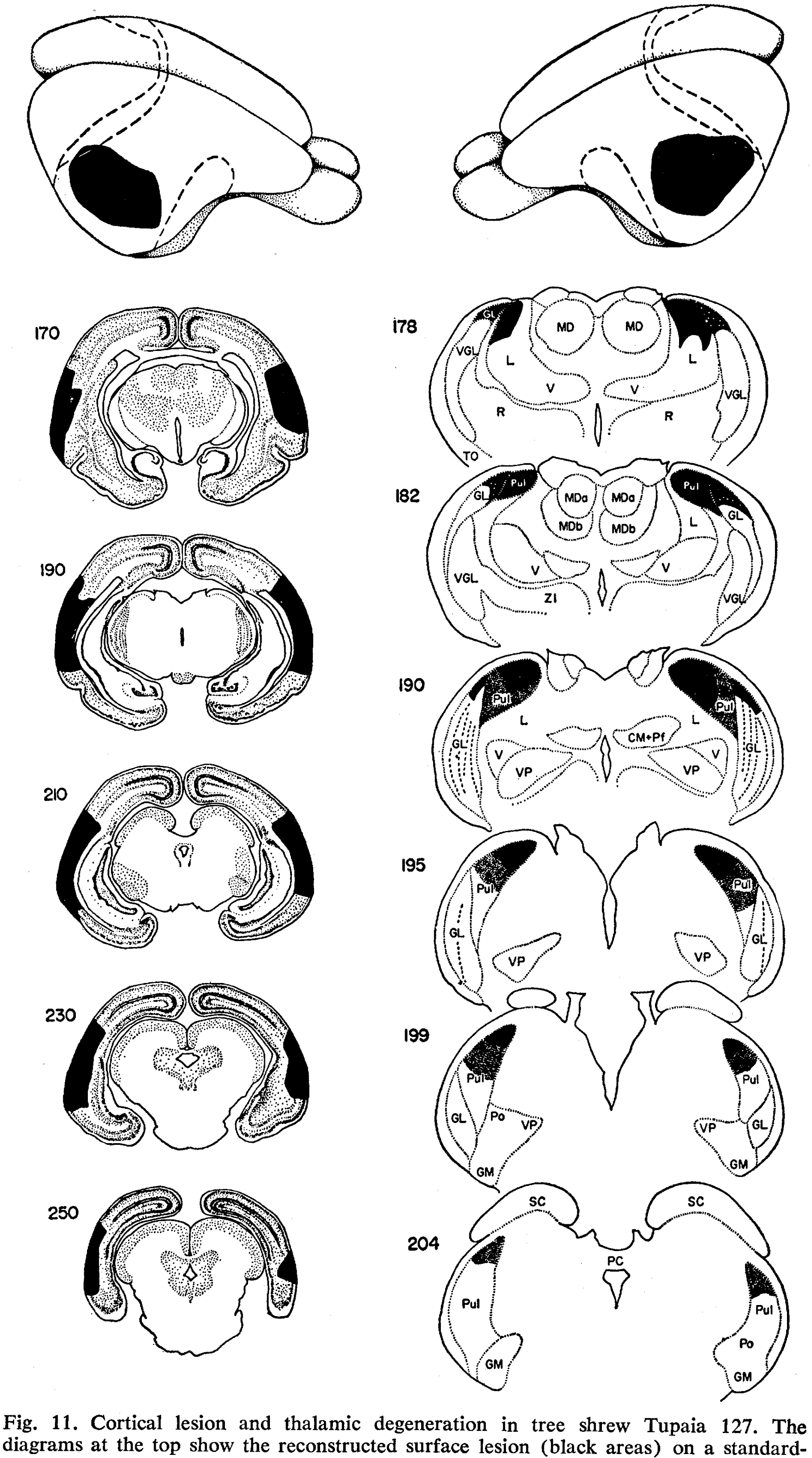


Fig. 11. Cortical lesion and thalamic degeneration in tree shrew Tupaia 127. The diagrams at the top show the reconstructed surface lesion (black areas) on a standardized view of the hemispheres. The numbered sections at left are frontal sections through the lesion; again, black represents areas where tissue has been removed. The lesion is always well below the striate area depicted by shading of the fourth layer, but in places the underlying fiber tracts are invaded and some geniculostriate fibers have been sectioned. This accounts for the small area of retrograde degeneration in the lateral geniculate, as seen in the diagrams at right. In these diagrams, black represents severe thalamic degeneration; this is confined mainly to the pulvinar nucleus. The stippled areas in the pulvinar, from sections 190 to the caudal tip, indicate moderate degeneration. The white dots in the lateral geniculate of sections 178 and 182 indicate a number of entirely preserved cells forming islands within the degenerated zone. Such a pattern can be accounted for only by postulating invasion of tracts projecting to the striate area.

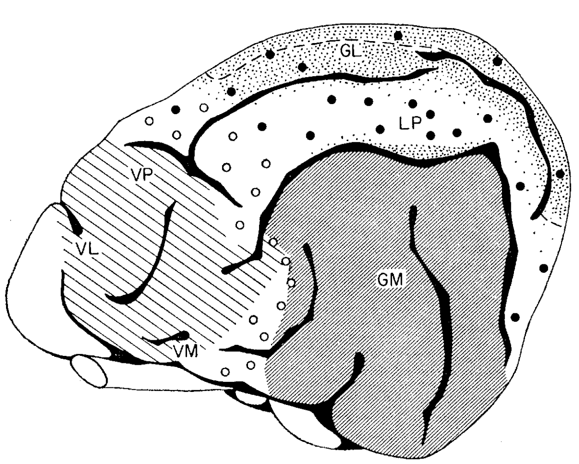


Fig. 12 (top left). Projections of thalamic nuclei to the neocortex in the cat. This diagram is an attempt to suggest the extent of the cortical target for each thalamic nucleus and the degree of overlap between their projections. There is considerable overlap between LP (a designation that includes the pulvinar nucleus as this nucleus is often defined) and GL, and only the center of the middle suprasylvian gyrus is shown as being free of lateral geniculate fibers. The targets of the ventral nuclei include the motor cortex (VL), the somatosensory areas (VP), and the taste area (VM). The temporal area is dominated by the projections from GM that extend from the rhinal fissure on the ventral surface to the suprasylvian sulci. Rostrally the fibers from GM approach, and may overlap, the projections from Po (open circles). Po is the ventral portion of a large complex, the dorsal portion of which is LP. There still remain some portions of the lateral nuclei not accounted for by these terms; this remnant is designated L. The cortical target for L and the cortical target for the posterior nuclei are both depicted by open circles. The reason for giving the same symbol to the projections of the two nuclear groups is that it is difficult to draw a sharp line between them on the basis of retrograde degeneration evidence. In general, we know that L projects between the visual and the somatosensory areas and that Po projects between the auditory and the somatosensory areas.

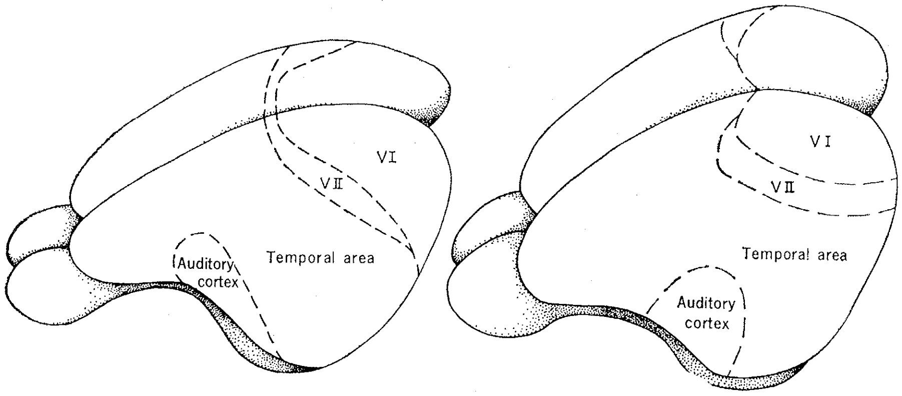


Fig. 13 (bottom left). Diagrams of the cortex in (left) the tree shrew and (right) the squirrel. The boundaries of the various subdivisions illustrate how similar the cortical organization is in these two species.

as association cortex on the basis of traditional criteria, in fact receives sensory input and has sensory functions in the broad sense of having a role in visual discrimination, while the chief function of the striate cortex is clearly not sensory in the sense in which this term was used in classical psychology.

Divergent and Convergent Evolution

By comparison with the cortex of the hedgehog, the cortex of the cat shows three marked advances: the rhinal fissure has been pushed down to the ventral surface; the formation of sulci greatly increases the total area of neocortex; and many different subdivisions can be identified on the basis of cytoarchitecture. While these changes parallel those found in the primate line, there are some obvious differences between the two lines. The most obvious is that, in the neocortex of the cat, the temporal area does not receive projections from the pulvinar; instead, most of the neocortex between the rhinal fissure and the visual area is occupied by auditory cortex (see Fig. 12). This extensive region, limited by visual and olfactory areas, contains many cytoarchitectonic subdivisions; not all of these receive equally heavy projections from the medial geniculate and not all can be shown to be auditory by the method of evoked potentials, but none can be positively eliminated as a target of the medial geniculate (*28*).

The lateral geniculate and striate cortex have also expanded and differentiated (for example, the lateral geniculate has acquired lamina—of course, entirely independently of the lamination found in the primate line), and the projections of the lateral geniculate to the striate area are more precisely topographic in the cat than in the hedgehog. However, as in the hedgehog, the projections from the lateral geniculate are not confined to the striate area. One concentrated projection lies in the middle suprasylvian sulcus, which constitutes the dorsal border of auditory cortex (*29*). If we had no idea of the prototypical organization, the relation between the lateral geniculate projection in cat and primate would be inexplicable, but, on the basis of data obtained for the hedgehog, it appears that the widespread projection of collateral fibers from the lateral geniculate in the cat is a reflection of the ancestral organization, and that the restriction of the lateral geniculate to the striate area in primates signifies a loss of the collateral projection. Our own studies of the retrograde degeneration in the lateroposterior-pulvinar complex of the cat suggest a similar widespread projection which has the result that fibers from this complex may overlap lateral geniculate fibers to a considerable extent. Once again, the visual system of the cat seems to have departed less from the prototype than the visual system of the primate.

Now, if we add to the visual and auditory areas the projections of the ventral nuclei to the sensory motor cortex and the projections of the posterior nuclei which relay auditory and somatic impulses to areas intercalated between auditory and somatic cortex, then almost all of the neocortex is accounted for. Therefore, results of studies with the cat provide little support for the generalization that the chief expansion of neocortex occurs in the association areas.

In view of the very different behavioral requirements in the adaptation of early carnivores and primates (the former being night hunters and the latter occupying a semiarboreal niche), it is not surprising that the neocortex diverged in the two lines. It remains to be asked whether similar habitats might result in similar cortical organizations. The common gray squirrel offers an easy opportunity to test the prediction of convergent evolution, and the results confirm our expectations. Rather than resembling the brains of other, closely related, rodents, the brain of the common gray squirrel exhibits an elaboration of the same visual centers that we have found to be highly differentiated in the tree shrew (*25*). For example, in the squirrel the lateral geniculate is large and layered, and it projects only to the striate area, as in the tree shrew. The lateroposterior nucleus is also larger in the squirrel than in the hedgehog or in other rodents, and in the squirrel this nucleus has an extensive cortical target which includes a large temporal area intercalated between the auditory and visual areas. Once again, the resemblance to the tree shrew is unmistakable. The convergence which is apparent from a study of architectonics is confirmed by the method of evoked potentials and thalamic retrograde degeneration. Figure 13 shows, side by side, the cortex of the tree shrew and that of the squirrel, with the various areas, as defined by experimental methods, outlined.

The anatomical similarities between the brain of the squirrel and that of the tree shrew raise the further question of whether these similar structures have similar functions. The results we have obtained thus far from ablation studies of the squirrel suggest that they do. For example, removal of the striate area produces a relatively mild loss of ability to discriminate patterns, similar to the loss found in the tree shrew. To produce a severe loss of this ability it is necessary to extend the lesion to include the projection target of the lateroposterior nucleus in the temporal area. We conclude that, since the tree shrew and the squirrel have arrived at similar semiarboreal habits but show no common arboreal ancestors, ecological factors must have played a large part in the differentiation of thalamic and cortical centers.

Summary

We began by reviewing the contribution made by comparative anatomists at the turn of the century to our understanding of neocortex. In lower mammals such as the hedgehog or opossum, almost all of the neocortex is devoted to three regions—visual, auditory, and sensory-motor. Each of these cortical areas receives sensory fibers from a thalamic relay nucleus. In higher mammals—man and species closely related to man—the neocortex has greatly expanded and these three regions occupy a relatively small proportion of the whole. Most of the remaining neocortex was called association cortex since it receives "association" or corticocortical fibers from the sensory and motor areas. These results clearly defined the task of comparative psychology: to demonstrate that the function of association cortex consisted in the formation of associations. But no learning task that could measure and reflect the size of association cortex was ever invented. Further, the method of ablation failed to localize the engram or uncover the neural mechanism of learning. These disappointments led to doubts about the basic assumption that species occupying diverse niches could be compared on a common abstract scale, and ultimately led to a bifurcation of comparative neurology and psychology.

In our own experiments on the visual cortex of two "primitive" species, the hedgehog and the tree shrew, we have been able to take advantage of the considerable progress that has been made in anatomical, physiological, and behavioral ablation studies of neocortex. In particular, the continuing investigation of the thalamus has led to the conclusion that the association cortex of man and higher primates is not restricted to a reception of corticocortical fibers but, like sensory cortex, receives fibers from the thalamus. One thalamic nucleus in particular stands out—the pulvinar—both because of the extent of its cortical target and because of the degree of its internal differentiation. A precursor to the pulvinar, the lateroposterior nucleus, can be found in the lowly hedgehog, and its further development can be traced through comparisons between hedgehog and tree shrew. A clue to its function is provided by the fact that visual impulses project to it from the tectum. In the hedgehog we find that both lateral geniculate and lateroposterior nuclei relay visual impulses to an extensive posterior sector of neocortex comprised of two architectonic subdivisions—a core and a belt. The boundaries of the core coincide with visual area I as defined by evoked potentials; visual area II occupies the belt. Both cortical areas are implicated in pattern discrimination. We have concluded that the two visual projection systems may represent stages of phyletic development, arguing that the tectal-belt pathway may have come first in evolution and may have given rise to both the striate cortex and the association cortex found in advanced mammals. In the hedgehog the two visual systems have not achieved the degree of independence found in higher mammals, and we take this to be a sign of the hedgehog's primitive level of organization as well as support for our thesis.

A complete separation of the cortical projections of the lateral geniculate and pulvinar nucleus is attained in the tree shrew. The ablation method can therefore tell us something about the function of each system: the geniculostriate system is not necessary for simple sensory tasks, but the striate cortex is required for a higher level of integration. A clue to this higher function is provided by the failure of the animals with brain lesions to distinguish a figure embedded in a larger pattern. On the other hand, the pulvinar system is implicated in learning visual patterns. Further behavioral evidence—the loss of reversal-learning sets in animals with lesions of the temporal area—tempted us to speculate that the temporal lobe has begun to assume primate-like functions. In carnivores, on the other hand, the temporal area expands in response to projections from the medial geniculate, and as a result the lateral surface of the neocortex is dominated by the auditory cortex and not the cortical target of the pulvinar. We now propose that the functions of this expanded auditory cortex may be considered as contributing to the highest behavioral capacities in the carnivore repertoire. Finally, we offer evidence that the primary and secondary visual systems of the squirrel and the tree shrew have evolved along similar lines, apparently in response to similar ecological niches.

It is our hope that the continuing inquiry into the converging and diverging evolution of cortex in the several lines of mammalian descent will reunite comparative neurology and psychology—a union originally envisioned by Elliot Smith.

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30. The following abbreviations are used in the figures and figure legends: *A*, auditory area of cortex; *CM* + *Pf*, centromedian + parafascicular nuclei; *GL*, lateral geniculate nucleus; *GM*, medial geniculate nucleus; *Hab*, habenula; *Hip*, hippocampus; *L*, lateral group of nuclei; *LP*, lateroposterior nucleus; *MD*, mediodorsal nucleus; *PC*, posterior commissure; *Po*, posterior nucleus; *Pul*, pulvinar nucleus; *R*, reticular nucleus; *S I*, somatic area I; *S II*, somatic area II; *SC*, superior colliculus; *T*, temporal area of cortex; *TO*, optic tract; *V*, ventral group; *V I*, visual area I; *V II*, visual area II; *VGL*, ventral lateral geniculate; *VL*, ventrolateral nucleus; *VM*, ventromedial nucleus; *VP*, ventroposterior nucleus; *ZI*, zona incerta.
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The Strategy of Ecosystem Development

An understanding of ecological succession provides a basis for resolving man's conflict with nature.

Eugene P. Odum

The principles of ecological succession bear importantly on the relationships between man and nature. The framework of successional theory needs to be examined as a basis for resolving man's present environmental crisis. Most ideas pertaining to the development of ecological systems are based on descriptive data obtained by observing changes in biotic communities over long periods, or on highly theoretical assumptions; very few of the generally accepted hypotheses have been tested experimentally. Some of the confusion, vagueness, and lack of experimental work in this area stems from the tendency of ecologists to regard "succession" as a single straightforward idea; in actual fact, it entails an interacting complex of processes, some of which counteract one another.

As viewed here, ecological succession involves the development of ecosystems; it has many parallels in the developmental biology of organisms, and also in the development of human society. The ecosystem, or ecological system, is considered to be a unit of biological organization made up of all of the organisms in a given area (that is, "community") interacting with the physical environment so that a flow of energy leads to characteristic trophic structure and material cycles within the system. It is the purpose of this article to summarize, in the form of a tabular model, components and stages of development at the ecosystem level as a means of emphasizing those aspects of ecological succession that can be accepted on the basis of present knowledge, those that require more study, and those that have special relevance to human ecology.

Definition of Succession

Ecological succession may be defined in terms of the following three parameters (*1*). (i) It is an orderly process of community development that is reasonably directional and, therefore, predictable. (ii) It results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go. (iii) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow. In a word, the "strategy" of succession as a short-term process is basically the same as the "strategy" of long-term evolutionary development of the biosphere—namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations. As I illustrate below, the strategy of "maximum protection" (that is, trying to achieve maximum support of complex biomass structure) often conflicts with man's goal of "maximum

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The author is director of the Institute of Ecology, and Alumni Foundation Professor, at the University of Georgia, Athens. This article is based on a presidential address presented before the annual meeting of the Ecological Society of America at the University of Maryland, August 1966.