universe between koinomatter and antimatter indicates that there must be equal quantities of the two kinds of matter in every galaxy. From this it seems likely that a galaxy is born as an ambiplasma body, which releases a great deal of energy by annihilation. Separation of the ambiplasma into koinomatter and antimatter in reasonably stable configurations, and the burning out of the nonseparated ambiplasma, should be the main processes which govern the evolution from protogalaxies and quasi-stellar objects to ordinary galaxies.

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Organization of the Visual Pathways

Evidence is discussed concerning parallel pathways from the eye to the brain.

Mitchell Glickstein

Light rays which arise from objects and impinge upon the eye of a mammal are refracted by the cornea and lens to form a fairly accurate spatial representation of the visual world on the retina. The process of image formation is similar to that in a camera; the image is small and inverted, and both eye and camera can typically focus between infinity and some specific near point. However, the transformation from patterns of light and shadow on the retina into neural messages is more complex and subtle than a photographic process. Eyes operate over a far greater range of light intensities than a photographic film does, and the central pathways do not transmit a simple pictorial representation to the brain.

In this article I review the spatial organization of the retina and central visual structures in terms of certain questions. If the optics of the eye form a single, spatially ordered image on the retina, to what extent are the spatial organization and uniqueness of the visual image maintained along the route from receptors to visual centers in the brain? There is a functional corollary to this question: If the visual fields are represented in the brain more than once and in parallel, is some aspect of visual function being segregated by the independent maps? Earlier answers to these questions appear to have oversimplified the problem. Here I discuss some aspects of the comparative anatomy of the mammalian visual system and consider a few recent anatomical and behavioral experiments which may point the way to a more satisfactory view of structure and function in vision.

Review of Retinal Structures

The retina of mammals is a complex structure in which receptors, neurons, and their processes are arranged in orderly layers. One example of the mammalian retina is illustrated in Fig. 1, a low-power photomicrograph of the cat retina near the area centralis. The darkly stained area at the top of Fig. 1 is the choroid (*ch*), a highly vascular, deeply pigmented region which, although not a part of the retina proper, carries blood vessels supplying the receptors. Below the choroid, staining orange, is the tapetum lucidum (*t*), a reflective layer found in the eye of many nocturnal mammals; by reflecting light which has not been absorbed by receptors, the tapetum serves to increase overall sensitivity of the retina and is also the anatomical basis for the reflected shine often seen when eyes are illuminated at night. Below the tapetum lucidum is a single line of pigment epithelium cells (*pe*), which, in the cat retina, do not contain the large amount of melanin pigment seen in more strongly diurnal mammals. The areas below the pigment epithelium, stained pale blue and bright blue, are the densely packed outer segment (*os*) and inner segment (*is*) of the rods and cones; at the low magnification shown here, individual receptors are not resolved. It is the outer segments of the rods and cones that contain the photosensitive pigments responsible for transduction of light into neural activity and hence initiate the sequence of steps which results in vision. Note, incidentally, that the retina seems to be facing backward; that is, light must traverse all of the layers of the retina below the recep-

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tors before reaching these outer segments. Nuclei of the rods and cones are in the outer nuclear layer (*onl*) just below the outer limiting membrane; each receptor cell extends from the tip of the outer segment above to the outer plexiform layer (*opl*) below, where synaptic contacts are made with cells of the inner nuclear layer (*in*).

In addition to bipolar cells, traditionally described as linking receptors with ganglion cells (*1*), the inner nuclear layer contains horizontal and amacrine cells, which lie on either side of the bipolar cells. Each of these cell types was originally differentiated from the others through the use of special techniques which stain only a small percentage of cells and their processes (*1*). On the basis of the staining technique used in the work described here, horizontal, bipolar, and amacrine cell bodies are best distinguished on the basis of their successively greater depth within the inner nuclear layer. The dark blue radial lines traversing the inner plexiform layer (*ip*) and curving around ganglion cells are fibrous processes of the Müller cells whose irregularly shaped cell bodies also lie in the inner nuclear layer, and whose processes project both toward the pigment epithelium above and toward the vitreous humor below. The shape of the Müller cells is similar to that of a rivet; the trumpet-shaped endings of Müller cells form the inner and outer limiting membranes of the retina and play a major supportive role. Most of the synaptic contacts from cells in the inner nuclear layer onto retinal ganglion cells are made in the inner plexiform layer.

There are three cellular layers in the retina: an outer nuclear layer, which contains rod and cone nuclei; an inner

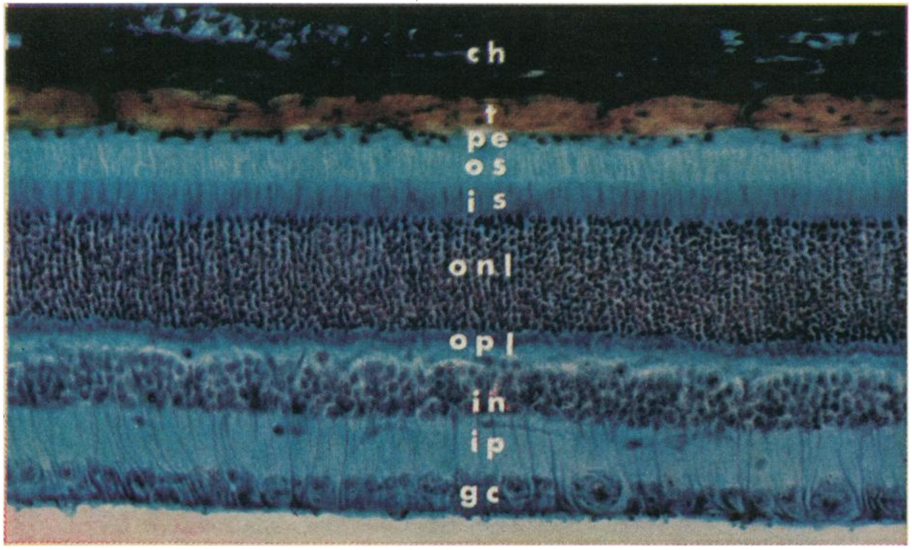


Fig. 1 (top). Cat retina (Susa fixation; embedded in low-viscosity nitrocellulose; Cason's Mallory stain; 10-micron section near the area centralis): (*ch*) choroid; (*t*) tapetum; (*pe*) pigment epithelium; (*os*) outer segments of receptors; (*is*) inner segments; (*onl*) outer nuclear layer; (*opl*) outer plexiform layer; (*in*) inner nuclear layer; (*ip*) inner plexiform layer; (*gc*) ganglion cell layer (about × 230).

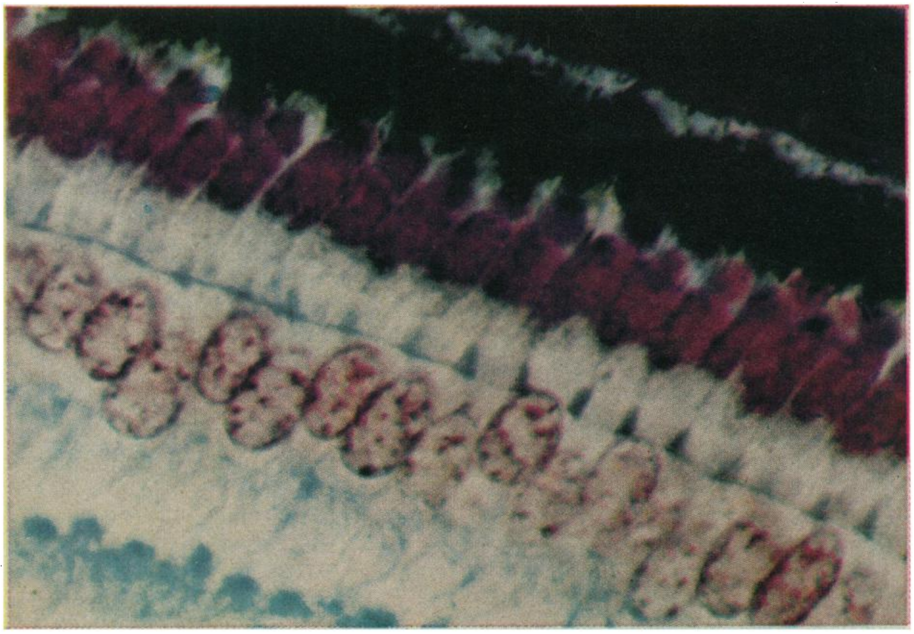


Fig. 2 (center). Tree shrew retina: pigment epithelium, cone inner segments, nuclei, and pedicles. Bouin's fixative; embedding, sectioning, and staining as in Fig. 1 (about × 2300).

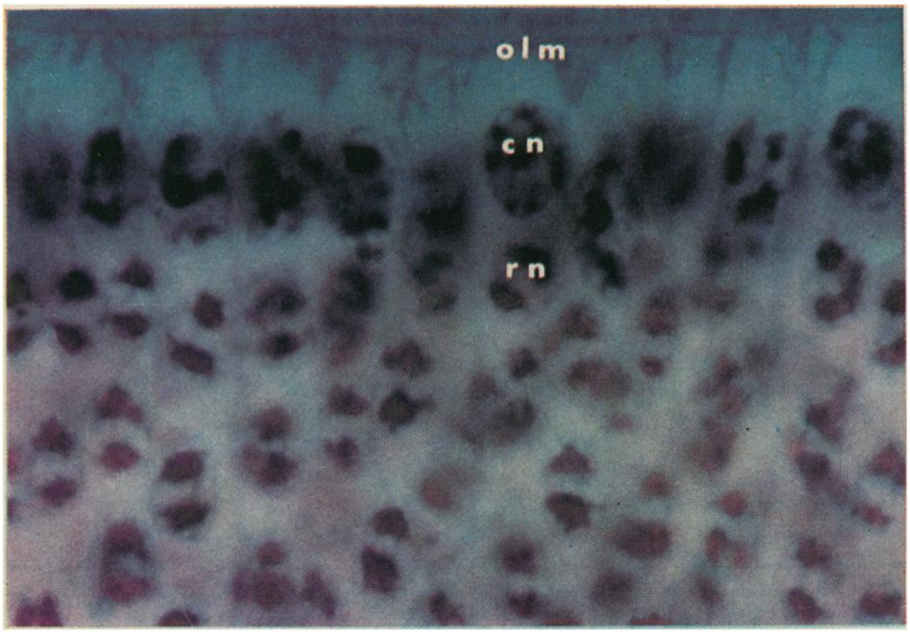


Fig. 3 (bottom). Leopard retina: (*olm*) outer limiting membrane; (*cn*) cone nucleus; (*rn*) rod nucleus. Histological techniques as in Fig. 1 (about × 2300).

nuclear layer, which contains the cell bodies of bipolar, horizontal, Müller, and amacrine cells; and a ganglion cell (*gc*) layer. The number and packing density of cells in all three layers vary greatly among species. Especially prominent are the differences between the retinas of diurnal and nocturnal mammals (*2*).

The tree shrew (*Tupaia glis*), a diurnal mammal (*3*), shows a uniquely simple arrangement of its receptors and their nuclei (Fig. 2). Almost all of the receptors in the retina of this species appear to be cones (*4*). Cone outer segments in Fig. 2 are optically isolated and screened from excess illumination by a shroud of densely concentrated pigment granules; the large dark-red-staining ovals below the mass of black pigment are the ellipsoids, a part of the inner segments of the cones. Below the ellipsoids is a single row of large nuclei, the outer nuclear layer. Note how each cone nucleus is associated with a single cone ellipsoid in the inner segment. At the bottom left in Fig. 2 the cone pedicles, the point of synaptic contact onto cells in the inner nuclear layer, are seen, staining blue.

The retina of the tree shrew, then, shows a relatively simple plan of receptor organization. There is a mosaic of cones, and below the inner segments of these cones there is a single layer of nuclei. If one were to imagine rods placed within the same retina, filling the interspaces in the cone mosaic, and if the position of the cone nuclei were fixed relative to the outer limiting membrane, then the nuclei of the rods would have to arrange themselves below the layer of cone nuclei. Such a situation is found in the retina of many mammals —for example, the leopard, *Pantherus pardus* (*5*) (Fig. 3). The outer nuclear layer has a single line of cone nuclei (*cn*) just below the outer limiting membrane (*olm*) and a larger number of rod nuclei (*rn*) below the cone nuclei. Such an arrangement of receptor nuclei is typical of the retinas of basically noctural animals which can also see in daylight, such as the great and small cats (Fig. 1) and other species of carnivore. The arrangement is also seen a few degrees away from the center of gaze in the retinas of most of the Old World primates.

Most mammalian retinas do not have equal numbers of receptors in all regions. The retina of man and of many monkeys, for example, possesses a zone of extreme receptor density, the fovea, in which there are a great number of slender cones and no rods. Below the fovea, the inner nuclear and ganglion cells, as well as blood vessels and nerve fibers, are displaced and hence do not lie in the path of the light which strikes these central receptors. A pure cone fovea is characteristic of animals with a high degree of visual acuity.

Lamination of the Outer Nuclear Layer

Color and size differences of cone and rod nuclei may give the outer nuclear layer a laminar appearance (Fig. 3). A single line of cone nuclei forms the top layer; a larger number of rod nuclei forms the lower one. Lamination in this instance is associated with a major functional difference between cell types in the two laminae. Rods and cones function under greatly differing conditions of illumination and differ in their degree of convergence onto cells in the inner nuclear layer. Depending on the intensity of the ambient light, one or another array of receptors plays a role in the transmission of a spatially ordered map of the visual world. At the level of the receptors, then, rods and cones operate in parallel to map the visual fields. However, parallel maps along the visual pathway may reconverge. There is definite evidence (*6*) that both rods and cones often are connected functionally to the same ganglion cell.

Central Connections of the Retina: Origin of Crossed and Uncrossed Fibers

Figure 4 is a highly schematic diagram of the central visual pathways in a monkey. The axons of the ganglion cells within each eye unite at the optic disk and pass through the sclera to emerge as the optic nerve. The nerves

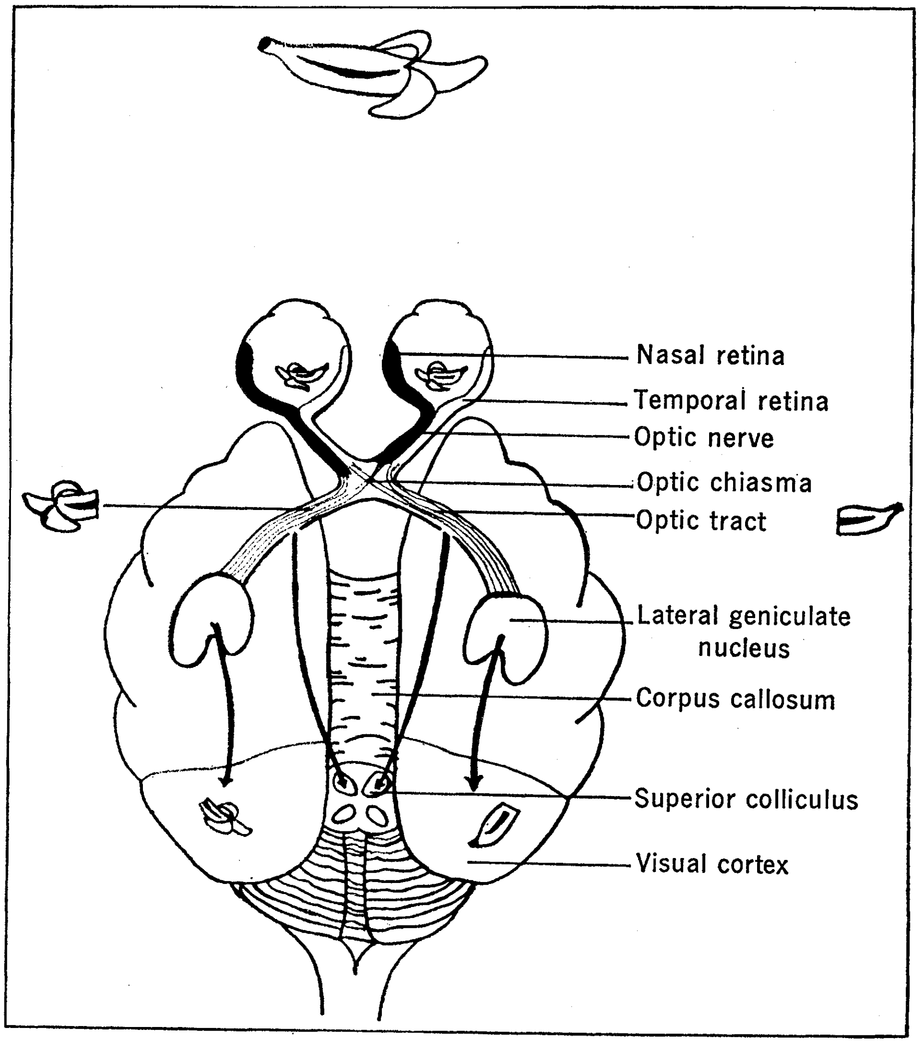


Fig. 4. Highly schematic diagram of optic pathways in a monkey. Note inversion of the image on the retina, the crossing of nasal retinal fibers, and the representation of one half of the visual field in each hemisphere. Only the two major terminations of the optic tract are diagramed.

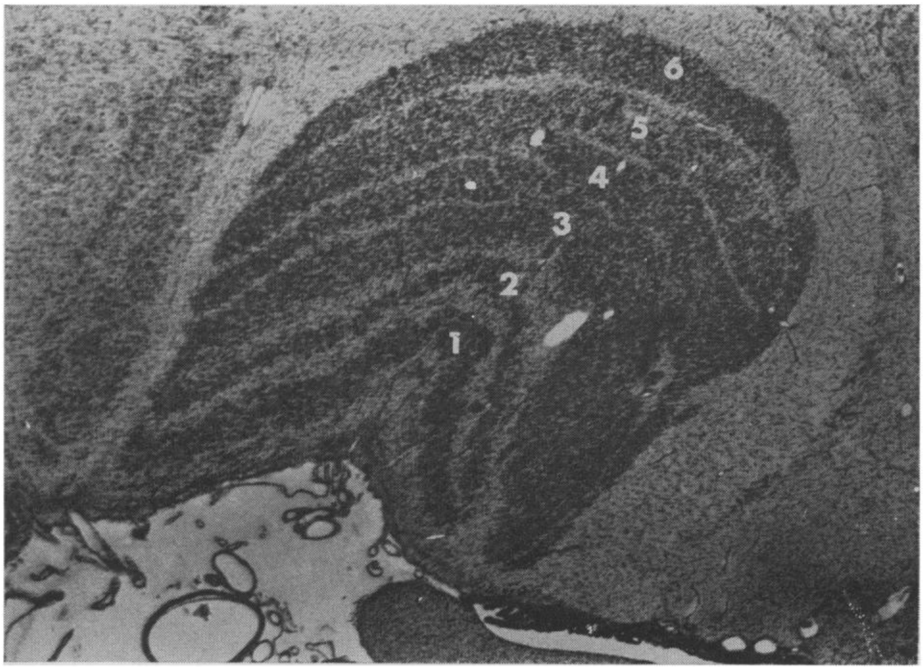


Fig. 5. Lateral geniculate nucleus of the monkey (*Macaca mulatta*) (celloidin-embedded; cresyl stain). Note the six cellular layers with interdigitating layers of fibers. Each of the six cellular layers contains an independent map of one half of the visual fields (about × 18).

from the two eyes then course medially and posteriorly to unite in an X-shaped structure, the optic chiasma. In lower vertebrates there is said to be complete crossing of the optic nerves at the optic chiasma, with fibers from a given eye proceeding to the opposite side of the brain. In mammals the percentage of crossed and uncrossed fibers is a function of the degree of overlap of the visual fields of the two eyes (*2*). The rat, whose eyes are placed far to the side of the head, has few uncrossed fibers. Man and monkey, with almost completely overlapping visual fields, have about 50 percent uncrossed fibers (*2*).

If one imagines a line drawn along the vertical meridian of the eye through the center of the fovea in man, all fibers nasal to the vertical meridian, it is thought, would cross and all fibers temporal to that meridian would remain uncrossed (*7*). Recent evidence suggests that there may not be strict meridional segregation of crossed and uncrossed fibers in all mammals. Stone (*8*) found a central region along the vertical meridian of the cat retina in which projections are bilateral. Within this small band, ganglion cells send their axons into either optic tract irrespective of their precise nasotemporal position. Stone also discovered that a percentage of fibers from the entire temporal retina of the cat crosses and enters the contralateral optic tract.

These discoveries raise a question as to whether there might be some overlap of ganglion cells with crossed and uncrossed fibers along the vertical meridian of the retina of man and higher primates. A small area of bilateral projection along both sides of the vertical meridian may have been overlooked by the earlier anatomists and would be of potential functional importance. As early as 1900, Heine (*9*) pointed out that the image of points directly in front of or behind a fixation point must project to independent hemispheres, yet such points fuse in binocular vision to yield a single point seen in depth. For example, a point within the fusional area closer than the fixation point would be imaged on the temporal retina of each eye.

According to classical anatomical teachings, the images would be projected independently to the left and right hemispheres. If this were the case, interaction between the neural representation of these points would have to be effected by way of connections from striate to prestriate cortex and thence through the corpus callosum. And yet, Bridgman and Smith (*10*) reported no disturbance in binocular depth perception, in maintenance and recovery of binocular fusion, or in apparent movement across the vertical meridian in patients who had undergone section of the corpus callosum. It seems worth while to reconsider the possibility that the primate retina has a region of bilateral projection from a narrow area along the vertical meridian, since such an anatomical arrangement would provide, within a single hemisphere, the structural basis for binocular fusion.

Lateral Geniculate and Superior Colliculus

Optic fibers make synaptic connections with several structures in the brain. In mammals these fibers go principally to the dorsal lateral geniculate nucleus and the superior colliculus; in lower vertebrates the fibers mainly connect with the optic tectum, the homolog of the superior colliculus. In some mammalian eyes the more primitive retinocollicular pathway is still a dominant one. For example, the tree shrew, although it has a visual cortex, also has a very large superior colliculus which receives the majority of the optic nerve fibers (*11, 12*).

Traditionally, the fibers going to the superior colliculus in man are said to mediate purely reflex functions of the visual system. On the other hand, "conscious vision," especially form perception and color vision, is said to be mediated by the striate cortex, which receives its input from the dorsal lateral geniculate nucleus (*7*). This general conclusion about the differential organization of the visual pathways cannot be valid for all mammals. Lashley (*13*) had shown quite early that rats deprived of striate cortex, although they had impaired form vision, were capable of solving problems based on brightness differences. Moreover, Snyder, Hall, and Diamond (*14*) have recently demonstrated that the tree shrew is capable of excellent form discrimination after total ablation of the striate cortex and complete retrograde degeneration of the dorsal lateral geniculate nucleus. Presumably the superior colliculus and its central connections are adequate for mediation of form vision in this species.

These data pose the problem of the differential role of midbrain and cortical structures in vision. It seems probable that some aspect of visual function is being segregated by the division between collicular and geniculocortical maps, but such functional segregation cannot be equivalent in all mammals. For a complete understanding of the differential role of cortex and midbrain in vision, the great differences in visual projections among mammalian species must be taken into account.

Lamination of the Dorsal Lateral Geniculate Nucleus

The dorsal lateral geniculate nucleus (*15*) is the major visual thalamic relay nucleus of mammals. It receives a massive input from the optic tract, and the neurons in the lateral geniculate nucleus project their axons to the cerebral cortex. While in many species the dorsal lateral geniculate nucleus resembles other thalamic nuclei in that it consists of a cellular mass without obvious subdivisions, in primates (*16–18*), carnivores (*18, 19*), and some marsupials (*20*) the lateral geniculate has a conspicuous laminar structure. In the lateral geniculate nucleus of man and monkey (Fig. 5) there are six layers of cells with interdigitating layers of nerve fibers.

In the animals with laminated geniculate nuclei so far studied, electrophysiological analysis of unit responses suggests that each geniculate layer typically receives direct input from only one eye. Few cells in the lateral geniculate nucleus can be binocularly activated by visual stimuli (*21*), although there may be binocular inhibitory effects, presumably involving a cortical relay (*22*).

In addition to the study of unit responses, study of the pattern of transneuronal atrophy reveals that the connections to almost all geniculate cells are monocular. In humans or macaque monkeys (*Macaca mulatta*) that have lost one eye, the contralateral lateral geniculate body eventually shows atrophy sharply restricted to layers 1, 4, and 6, and the ipsilateral lateral geniculate body shows similar atrophy in layers 2, 3, and 5 (*18, 23*). Crossed and uncrossed fibers, then, terminate in independent layers in the lateral geniculate nucleus. Figure 6 shows an example of transneuronal atrophy in the dorsal lateral geniculate of a macaque monkey. Layers 1, 4, and 6 underwent severe transneuronal atrophy after input from the crossed eye was cut at the optic chiasma.

Fig. 6. Lateral geniculate nucleus of monkey killed 2 years after section of the optic chiasma. Histological techniques and magnification as in Fig. 5. Transneuronal atrophy of layers 1, 4, and 6 is revealed as a difference in the grain of these layers; compare Fig. 5.

In some species, laminar organization of the lateral geniculate may be covert in normal animals and not completely revealed by simple staining procedures. In such cases, study of transneuronal atrophy can clarify the ocular connections to the lateral geniculate, and can also help in determining the number of layers present. The lateral geniculate nucleus of the squirrel monkey, *Saimiri sciureus*, consists of a pair of large-celled layers in the ventral area and, in the dorsal area, of a single unlaminated mass in which the cells are somewhat smaller. When a squirrel monkey was killed 1 year after removal of one eye, hidden lamination of the parvocellular mass was revealed. Layers 1, 4, and 6 were atrophied on the side opposite the enucleated eye; layers 2, 3, and 5, on the same side as the enucleated eye (*16*). This pattern of geniculate lamination in this New World species is identical to that of man and the Old World primates.

As noted above, in man and monkey the outermost geniculate laminae (layers 1 and 6) are connected to the contralateral eye. In the cat, also, the outermost layers of the geniculate are connected to the contralateral eye (*24*). In some species the pattern of ocular connections may be quite different.

When the tree shrew was studied after one eye had been removed, an unusual but orderly pattern of geniculate lamination was found (*25*). The ipsilateral eye was found to be connected to two of the outer layers of the lateral geniculate body (layers 1 and 5). The contralateral retina was observed to be connected to internal layers within the geniculate (layers 2 and 4). The middlemost layer, layer 3, and an external layer next to the optic tract, layer S, appeared not to receive a major connection from either eye.

The eyes of the tree shrew are placed far to the side of its head, and the great majority of the fibers from each eye cross at the chiasma. Even though the optic fibers which cross outnumber those which do not cross by about 20 to 1 (*11*), crossed and uncrossed fibers from a single eye appear to be connected to about the same number of cells in the lateral geniculate nuclei. One possible explanation for this apparent paradox is that the lateral geniculate nucleus in the tree shrew may receive most of its input from retinal ganglion cells whose receptive fields lie in the small binocular portion of the visual fields.

If this should be the case, then a number of interesting consequences would follow. The striate cortex in this animal should then disproportionately represent the binocular portion of the visual fields. If the geniculocortical system of *Tupaia* were predominantly binocular, this might suggest one clue to the evolution of the lateral geniculate nucleus and striate cortex: the geniculostriate system in this animal may have evolved in parallel with the evolution of binocular vision. Perhaps the system functions to organize the input of cortical units which respond to slight disparity between the two retinas (*26*). Hence, although few cells in the geniculate have direct binocular connections, the geniculate may play an indirect role in stereoscopic depth perception.

The possible functional correlates of geniculate lamination are still poorly understood. In man and monkey, one half of each visual field is mapped and remapped onto six stacked layers of the lateral geniculate nucleus, so that a point in space is represented as a radial line through all six layers (*27*). This multiple mapping of the visual fields suggests that some aspect of vision is being segregated in the individual laminae. As Gordon Walls wrote (*17*), "The whole organization of the human LGN [lateral geniculate nucleus] cries aloud that something is being segregated. The question before us is simply: *What*?" As a first guess, LeGros Clark (*28*) suggested that trichromatic vision was mediated by the three paired layers of the lateral geniculate. While detailed criticism (*17*) reveals this to be a grossly oversimplified view, analysis of the receptive-field properties of geniculate cells has begun to reveal differences in receptive-field organization and chromatic sensitivity of cells in large and small cell layers (*29*). There is as yet, however, no compelling functional interpretation of laminar structure; Walls's question remains unanswered.

Organization and Singularity of the Geniculocortical Projections

Traditional anatomy of the visual system holds that, even in animals with laminated lateral geniculates, the projections to cortex reunite the laminae, so that the visual fields are mapped onto the cortex in a unique and point-for-point manner (*7, 30*). The map may be distorted in that foveal portions of the visual fields are represented in a relatively large area of cortex (*31, 32*), but the fields are thought to be mapped once and only once from the retina onto the cortex, with neighboring points in the visual fields projecting onto neighboring points in the cortex.

A number of clinical, anatomical, and physiological studies support the view that the visual fields are mapped in an orderly fashion onto the visual cortex. Small lesions placed in the striate cortex of monkeys lead to correspondingly small regions of retrograde degeneration within all six layers of the ipsilateral geniculate (*7*). Patients with circumscribed lesions of visual cortex have corresponding regions of blindness—scotomas—in predictable portions of the visual fields (*7, 33*). Small, focused spots of light projected onto the retina evoke localized potentials on the cortical surface and impulses in the underlying nerve cells. These electrical signals reveal that the visual fields are indeed mapped in an ordered way (*31, 32, 34, 35*).

Although there is abundant evidence for spatial ordering of the retinocortical map, the evidence for uniqueness of the map has been less clear. Talbot and Marshall (*32*) mapped potentials on the cat cortex that were evoked by small, focused spots of light. In their initial work they reported a single organized map of the visual fields, which, in their rough sketch, included parts of cortical areas later termed areas 17, 18, and 19 by Otsuka and Hassler (*36*). Talbot subsequently described (*37*) a second visual area, visual II, located laterally, which appeared to map the visual fields a second time. The map was ordered, but ordered as if it were a mirror image of the projection of primary visual cortex. The spatial organization of visual areas I and II was confirmed in studies of single-unit responses by Hubel and Wiesel (*35*), who identified these areas as coextensive with areas 17 and 18, respectively, as described by Otsuka and Hassler (*36*).

Hubel and Wiesel (*35*) presented anatomical evidence for connections from visual area I to visual II, and in their theoretical treatment regarded visual II as a region whose input is derived from a series connection with primary visual cortex. However, visual II itself behaves in some respects like a primary sensory area (*38*), perhaps receiving an independent and *parallel* input from the lateral geniculate. When the entire visual field of a cat is stimulated by a bright flash (*39*), gross evoked potentials can be recorded from both visual I and visual II. The potentials recorded in visual II are equivalent in latency to those recorded in visual I and actually of higher amplitude (*40*).

In an attempt to clarify visual projections to the cat's cortex, stereotaxic lesions were made in the lateral geniculate nucleus and degeneration was mapped on the surface of the cat brain after varying survival periods (*41, 42*). In order to rule out spurious effects due to lesions outside the lateral geniculate nucleus, the direction by which the electrode was angled toward the geniculate was varied in different animals, and different portions of the geniculate were destroyed in different cases. Figure 7 is representative of the findings from that study. In this case, a lesion was placed in the anterior portion of the lateral geniculate nucleus, by means of an electrode track which was angled toward the geniculate from the forward direction. After 21 days the cat was killed, and degenerating fibers in the cortex were studied by means of a modified Nauta method. In this and all other cases, projections from the lateral geniculate nucleus to the cortex of the cat were found to extend beyond area 17. In addition to projections to area 17 (coextensive with visual I), there is a projection, equally dense, to area 18, a region coextensive with visual II. The location of these two cortical regions is shown in one of the cross-sectional diagrams of Fig. 7 (section 43). Both areas extend for a considerable distance anteriorly and posteriorly, but they are not labeled in the other diagrams.

When these anatomical findings of a direct geniculate projection to visual II are considered along with the results of physiological studies (*37*), they suggest that the visual fields are mapped in parallel at least twice onto the surface of the cat brain directly from the lateral geniculate nucleus. Unit responses which can be recorded in visual II of the cat are not necessarily driven by way of a series input from visual I but may be activated directly from the lateral geniculate nucleus.

Other cortical areas besides areas 17 and 18 appear to receive direct input from the lateral geniculate nucleus of the cat. When Marshall, Talbot, and Ades (*39*) mapped potentials on the cat cortex that were evoked by full-field flash, they observed that, in addition to visual I and visual II, a region on the medial bank of the suprasylvian sulcus showed short-latency evoked potentials. Vastola (*43*) later showed that potentials evoked in this area by stimulation of the optic nerve persist after cutting of all pathways that connect this region with primary visual cortex in the lateral gyrus. Our own data supported Vastola's suggestion of a direct geniculate pathway to suprasylvian cortex. In addition to the dense projections observed in areas 17 and 18 ipsilateral to the lesion, medium-to-dense degeneration was found on both banks of the suprasylvian fissure, lending support to the idea that this region receives an independent and parallel direct projection from the lateral geniculate nucleus. The case presented in Fig. 7 does not prove the existence of a suprasylvian projection, since in this case the electrode track itself probably caused fiber degeneration in suprasylvian cortex. However, in all cases the same distribution of degenerating fibers in suprasylvian cortex was seen after geniculate lesion, and this distribution was independent of the angle of the electrode as it passed though the brain. Our observations suggested that the region from which Vas-

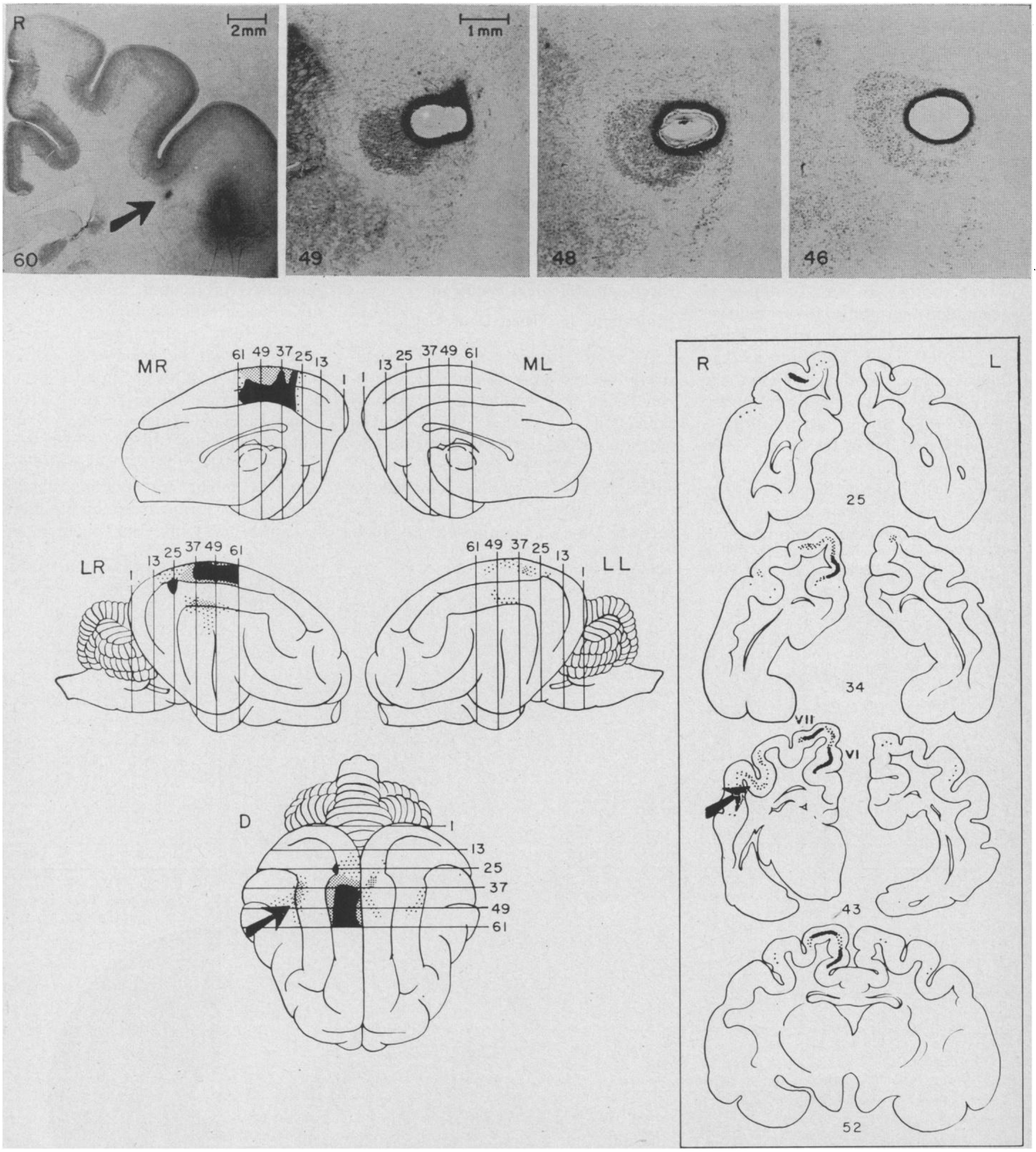


Fig. 7. Photomicrographs and cortical maps of cat A.T. 21, from a study (*41, 42*) described in the text. (Top) Photomicrographs showing electrode track and right lateral geniculate lesion. (Bottom) Cortical maps of degenerating fibers and representative cross sections. Section through the brain at the level of slide 60 (top left) illustrates the electrode track just below the suprasylvian sulcus (arrow). (Solid areas) Heavy degeneration; (dense stippling) medium degeneration; (less dense stippling) light degeneration. The degeneration is equivalent in areas VI and VII (section 43). For example, degeneration on the medial face of the hemisphere in section 43 is largely in visual I (area VI); equally dense degeneration on the dorsal surface of the lateral gyrus is in visual II (area VII). In the cat, these two areas (VI and VII) are coextensive with areas 17 and 18 (*36*). The arrow (D and section 43) points to the region of degeneration found on the banks of the suprasylvian sulcus. (MR) Medial view, right hemisphere; (ML) medial view, left hemisphere; (LR) lateral view, right hemisphere; (LL) lateral view, left hemisphere; (D) dorsal view, both hemispheres.

tola recorded evoked potentials may be the medial edge of a wider system arising in the lateral geniculate and projecting to both banks of the suprasylvian sulcus.

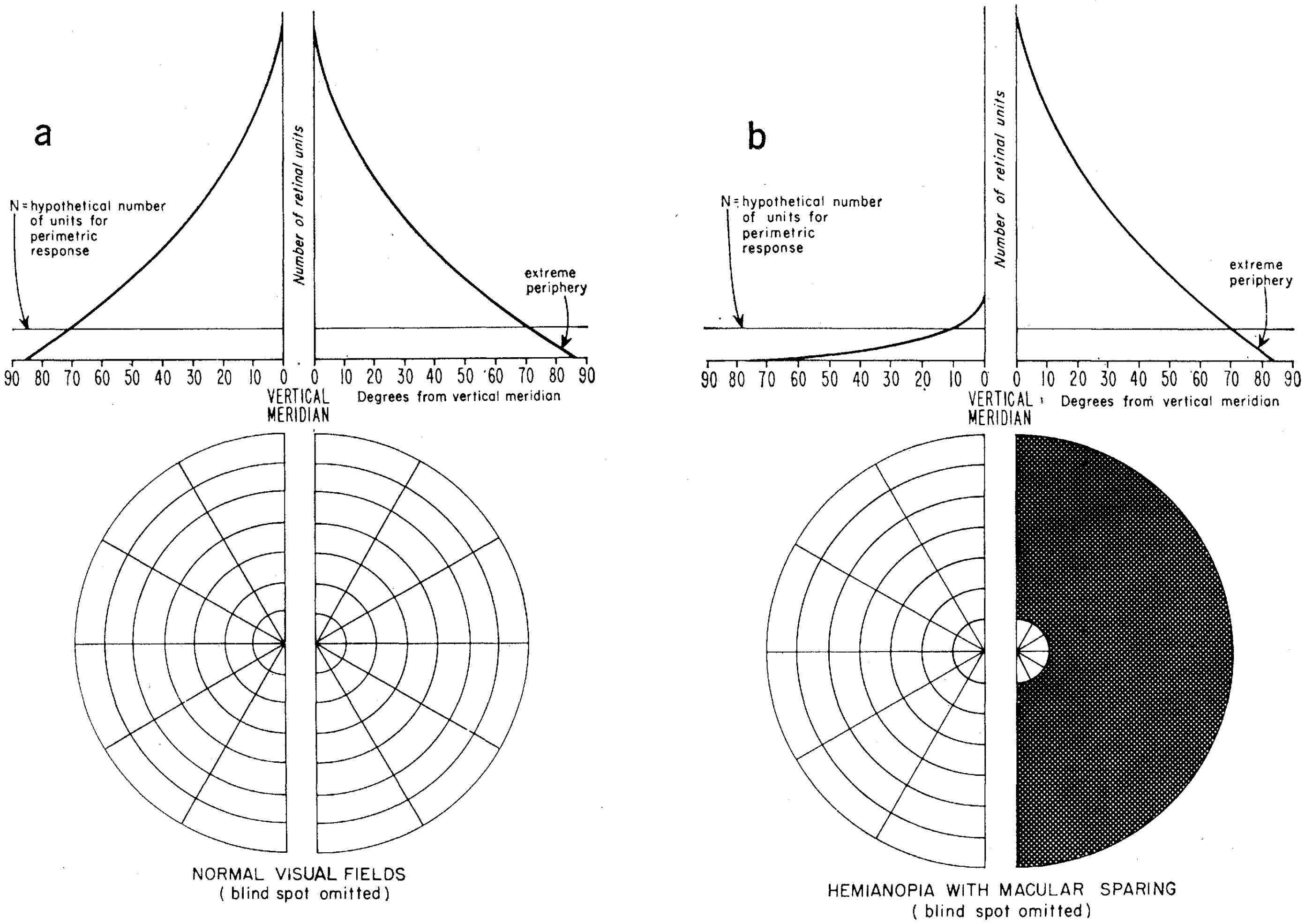
Degenerating fibers were also found in still other cortical areas. Most interesting is the somewhat controversial finding of a crossed pathway to the opposite lateral gyrus (*42, 44*). In all cats we saw evidence of degenerating axons in the contralateral hemisphere, although the density of degeneration varied widely. The focus of degeneration in the contralateral visual areas was not contiguous with commissural degeneration resulting from damage caused by the electrode track. Moreover, while fewer in number than the projections mentioned above, the crossed fibers show a tendency toward coherent organization. Cats with lesions of anterior portions of the lateral geniculate showed degeneration more anteriorly on the opposite hemisphere than cats with more posterior lesions.

Despite independent confirmation of the presence of projections from the lateral geniculate to visual I and visual II and the suprasylvian gyrus, Wilson and Cragg (*45*) could not confirm the presence of a crossed pathway to the opposite hemisphere, hence, the presence of such a pathway must remain in doubt. Discrepancies in results may have been due to relatively more or less sensitive techniques of staining degenerated fibers in the two studies or to fortuitous commissural damage that may have occurred in our study.

Electrophysiological Study of Projections to Visual II of Cats

As another attempt to show conclusively that the input to visual II is independent of and parallel to the primary projection to visual I, visual evoked potentials were recorded from the cortex of cats (*46*). In one experiment the entire lateral gyrus was removed on one side and the corpus callosum was sectioned, then a large lesion was made in visual I of the contralateral hemisphere. Despite the absence of the commissural input and the presence of a massive lesion in area 17, the photic evoked potentials in area 18 were relatively unaffected in amplitude or distribution. In contrast, when stereotaxic lesions were made directly in the lateral geniculate nucleus on the side from which we recorded, the amplitude of evoked potentials was severely diminished at many points in area 18. The points at which the amplitude of the evoked potential was diminished corresponded closely to regions of lateral geniculate projections as revealed by silver degeneration-staining.

These data support once more the conclusion that the visual fields are represented at least twice on the surface of the cat brain. However, the question of the functional interpretation of such multiple mapping of the visual fields remains. Walls (*17*) had suggested that visual II might not function directly as an area of form perception but might be concerned with visual fixation and



NORMAL VISUAL FIELDS
(blind spot omitted)

HEMIANOPIA WITH MACULAR SPARING
(blind spot omitted)

Fig. 8. Theoretical interpretation of macular sparing. (a) Distribution of receptors and central connections in the normal case yields the observed visual fields. (b) If only one-eighth of the receptors retained a functional connection with an extrastriate region of the brain, the results might resemble sparing of macular vision.

field-holding reflexes. The exquisite sensitivity of cells in visual II in response to movement (*35*) lends some support to this view, although it is far from being established.

Clues to the functional interpretation of parallel visual maps can come from several sources. Because of the difficulty of making isolated laminar lesions in the lateral geniculate nucleus, analysis of receptive-field properties of cells in the various laminae must remain the major means of obtaining data for this area. In the case of cortex, other techniques can supplement analysis of receptive-field properties. For example, lesions might be placed in visual I and their effects compared to the effects of lesions in visual II. By appropriate behavioral techniques the differential visual deficit caused by damage to these two areas might be explored.

Multiple Mapping and the Problem of Macular Sparing

The phenomenon of "macular sparing" led some earlier anatomists to question the view that the visual pathways in man are organized and unitary in character. Humans seldom lose all vision in one side of the visual field after unilateral cortical lesion. Typically, a small region of the central visual fields, corresponding to the central area of the retina, remains on the affected side. Most authors (*7, 33*) tend to regard this macular sparing as brought about by one of several causes, since no single explanation accounts for all cases. In the case of patients who have had a stroke, the double blood supply of the cortical projection of the central visual fields from middle and posterior cerebral arteries might explain preservation of a small central area of vision after vascular damage. In other cases visual fixation might become eccentric, so that chronic deviation of the eye into the sighted portion of the visual field could account for the apparent sparing of central vision.

The presence of parallel geniculocortical maps in the cat makes one wonder whether a vestige of such a system might exist in man, and suggests an interpretation for some cases of macular sparing. Rönne suggested (*47*) that all hemianopias be viewed not as complete blindness of one half of the visual field but as special cases of partial blindness or amblyopia. We might apply this idea to a hypothetical extrastriate visual area in man. If there were a surviving functional visual center spared by the lesion, the poorer functioning of such a residual visual center might give the appearance of a spared macula. Figure 8 illustrates this theory. Consider an approximation to the known distribution of cones in the eye. The distribution is maximum in the fovea and falls off toward the periphery of the retina (*1*). Let us assume that it takes *N* of these receptors, plus their central connections, in order for a person to see a test object. Now, suppose one-eighth of these receptors were functionally connected to a region outside the striate cortex—perhaps a second visual cortical area, although a subcortical area might also play such a role. Only a small part of the visual fields would have enough receptors to enable the patient to see the test object. If only the foveal area had a sufficient number of receptors, perimetric testing would give the impression of a spared macula.

This interpretation of macular sparing implies a number of consequences. For one thing, it suggests that the visual acuity in the spared macula should be very poor—on the order of the acuity of peripheral vision in a normally sighted person. It further suggests that, under varying conditions of perimetric testing, the size of the apparently spared macula could be changed. For example, with a sufficiently small test object, the macula might appear to be split. Some evidence supporting this type of interpretation was presented by Rönne, but the theory awaits testing with modern methods of stimulus presentation and eye-movement control.

The presence of a parallel functional visual area would also account for the remarkable findings of Cowey and Weiskrantz (*48*), who discovered that monkeys with lesions of the striate cortex are capable of detecting a light in a supposedly blind region of the visual field even when tested with rigorous controls for light scatter and eye movement.

In summary, it appears that the classical principle of spatial ordering of retinal projections to the striate cortex of the brain has stood the most careful clinical and experimental test. Recent evidence, however, allows one to question the accepted unique and singular role of visual cortex in form vision. In some species a collicular circuit appears capable of mediating form vision, and, in some, the visual fields appear to be projected more than once onto the cortex.

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30. The anatomical terminology in this section can be somewhat confusing. Striate cortex is so named because of the presence in layer 4 of a stripe of myelinated fibers parallel to the surface of the human cortex. This "stripe of Gennari" is less clearly visible in other species, such as the cat, although the term *striate cortex* is frequently retained and used synonymously with visual cortex. Striate cortex is also synonymous with area 17, in Brodmann's subdivisions. In the cat, both striate cortex and area 17 have become synonymous with visual I. There is, in the cat, a contiguous cortical area, visual II, which has a visual function and appears to be coextensive with area 18 (see text).
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49. I am indebted to my colleagues and students for critical discussion of the manuscript, especially, Drs. Lorrin A. Riggs and Donald S. Blough. I am grateful to Eileen LaBossiere who collaborated in developing a technique for histological preparation of retinas and did all of the histological work presented here. The research reported here was begun at the University of Washington and was supported by grants MH-06722 and and was supported by PHS grants MH-06722 and FR-00166.

Congress Meets Science: The Appropriations Process

Although legislators question the purposes and management of science programs, they play a supportive role.

Michael D. Reagan

The federal government's role as patron of science has been discussed and documented at some length in recent years (*1*). The emphasis in most writings, however, has been upon activities of departments and agencies of the executive branch. The congressional role has been little examined. This article explores one major type of confrontation between Congress and science: the legislature's overseeing of science agency programs as it is accomplished through the appropriations process.

The appropriations process is a crucial point of contact, and not only because that's where the money is. It is also the most frequent, continuing means by which the legislators attempt to exercise control over the coordinate executive branch. Congressional oversight, so-called (the function of ensuring that executive agencies fulfill their statutory mandates effectively and efficiently), is also performed by the substantive committees (the ones on agriculture, commerce, and so forth), by the committees on government operations and by ad hoc special investigations; but the appropriations process is the only vehicle of oversight that operates every year with respect to every agency.

Appropriations work is done primarily by specialized subcommittees, each handling a particular department or functional area. There is no science budget as such, just as there is no single agency engaged in science. To examine the Congress-science relationship in the appropriations arena is therefore to look at particular subcommittees dealing with particular agencies. I shall focus on the National Science Foundation (NSF) and three science-oriented bureaus in nonscience departments: the Geological Survey (GS) in the Department of the Interior, Agricultural Research Service (ARS) in the Department of Agriculture, and the National Bureau of Standards (NBS) in the Department of Commerce. In NSF, science stands "on its own" as it were; in the others, Congress sees science as embedded in the extrascientific missions of the respective departments. Covering both enables us to see whether science per se is differently handled or fares worse or better than science given the "protective coloration" of some other social mission. Each of the three science bureaus examined is the largest research-oriented component of its respective department, and each performs basic as well as applied research. Approximately half of the ARS and NBS research budgets go into basic research, taking fiscal 1967 as an example, and in GS the proportion devoted to basic research is about three-fourths. These budgetary allocations are sufficiently large so that any particular congressional biases regarding basic research would certainly become apparent in the process of making appropriations.

The format of appropriations is designed so that each major component of a department (the generic name for these components is bureau) is considered as a discrete unit. Each receives its own hearing, those covered here generally being allocated from half a day to a full day of discussion. The findings reported here are based on hearings for the period of fiscal years 1962–68.

Geological Survey

During the years covered, the appropriation for the Geological Survey increased from $50 million to $85 million. The work of the Survey was changing rapidly, with diverse new programs being added in the mapping of rare mineral and metal deposits, earthquake studies, water studies, oceanography, and the remote sensing of minerals. The traditional topographic mapping, despite its continuing importance in the agency's overall program, elicited relatively few comments because it was a long-accepted activity. Legislators would simply ask how many states remained to be covered and what uses were made of the maps as they became available. As is typical in appropriations hearings, the agency head briefly described each of his programs and

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