Visual Cortex in Primates

John Allman and EveLynn McGuinness

Division of Biology, California Institute of Technology, Pasadena, California 91125

EVOLUTION OF THE VISUAL SYSTEM IN PRIMATES

Fossil remains of the earliest primates that bear a close resemblance to living primates have been recovered from early Eocene deposits 55 million years old [Simons, 1972]. The skull and cranial endocast of one of these early primates, *Tetonius homunculus*, are illustrated in Figure 1. *Tetonius* possessed large bony orbits that completely encircled its eyes and a cranium containing a large brain compared with its similarly sized contemporaries. The large size and position of the orbits in *Tetonius* closely resemble living nocturnal prosimians (see Fig. 2). The cranial endocasts of *Tetonius* and other Eocene primates reveal that their brains possessed a conspicuous enlargement of the neocortex of the occipital and temporal lobes [Radinsky, 1967, 1970; Gurche, 1982]. The studies in living primates to be reviewed in this chapter indicate that all of the occipital lobe and much of the temporal lobe are devoted to the processing of visual information.

The large bony orbits and expanded occipital and temporal lobes in the early primates probably were parts of an adaptive complex that included 1) frontally directed eyes; 2) an area of high acuity in the central retina; 3) a large-field of binocular overlap; 4) a large ipsilateral projection from the retina to the lateral geniculate nucleus and the optic tectum; 5) the expansion of the representation of the central visual field in thalamic, tectal, and cortical visual structures; 6) a laminated lateral geniculate nucleus in which the inputs from the two eyes were segregated in several sets of layers; 7) a representation in the optic tectum restricted to the contralateral half of the visual field; 8) the expansion and functional differentation of primary visual cortex; 9) the expansion of extrastriate cortical visual areas and the probable elaboration of new visual areas; 10) the shift of the foramen magnum from a posterior to a more ventral position in the skull; 11) prehensile hands; 12) eye-hand coordination; 13) binocular convergence and accommodative focusing; 14) fine-grained stereopsis [see reviews, Allman, 1977, 1982]. Since most of these features are characteristic of all living primates, it is likely that they were present in the most recent common ancestors of the living primates.

Two theories have been advanced to explain this basic set of primate adaptations. In the first, Martin [1979] has suggested that the early primates, like the smaller living prosimians they closely resemble and the small arboreal marsupials of Australia and South America, adapted to a "fine-branch niche"; the prehensile hands and feet found in these animals developed to grasp the fine terminal branches of trees. Most arboreal mammals, such as squirrels, run on the trunk and larger branches but are unable to grasp the finer branches. The second theory is based on the observation that, outside of the order Primates, animals with large, frontally directed eyes (owls and felids) are nocturnal, visually directed predators, which led Cartmill [1972] to propose that visually directed predation was the ecological specialization linked to this set of developments in the early primates. Cartmill's visual predation hypothesis is supported by the fact that the tarsier, the living primate that most closely resembles the early primates of the Eocene, is exclusively a predator (see Fig. 3).

Comparative Primate Biology, Volume 4: Neurosciences, pages 279–326

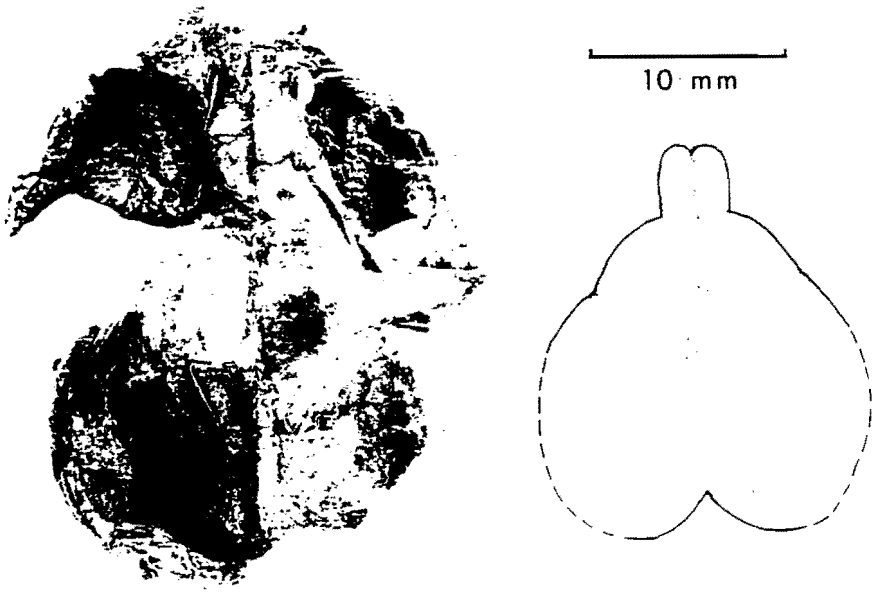


Fig. 1. Left: dorsal view of the skull of *Tetonius homunculus*. A.M.N.H.No. 4194. Right: dorsal view of Radinsky's cranial endocast of *Tetonius*. From Radinsky [1967], with permission.

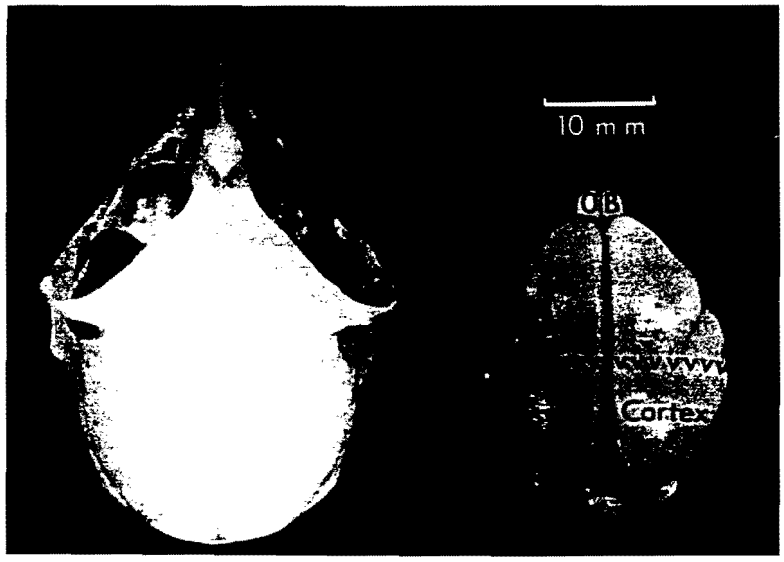


Fig. 2. Left: dorsal view of the skull of *Galago senegalensis*. Right: dorsal view of the brain of *Galago senegalensis*. The visual cortex corresponds to approximately the posterior half of the neocortex. The Vs demarcate the anterior border of visual cortex. OB, olfactory bulbs. From Allman. [1977], with permission.

Fig. 3. Tarsier seizing a lizard. The tarsier is exclusively a predator; it eats no fruit or vegetable matter. Of the living primates, the tarsier most closely resembles the early primates living in the Eocene. Photo by Dr. Johannes Tigges. From Allman [1977], with permission.

Both hypotheses may be correct. It is probable that the early primates did invade the "fine-branch niche" where they gained access to a rich array of insect and small vertebrate prey.

The early primates probably were small, nocturnal predators living in the fine branches; some primates have retained this mode of life, but most have become larger diurnal folivores or frugivores. The development of the capacity for color discrimination is probably linked to a selective adaptation for identifying ripe, and therefore digestible, fruit [Polyak, 1957]. Frugivorous diet is correlated positively with brain size [Clutton-Brock and Harvey, 1980] and the amount of neocortex relative to body size in primates [Stephan and Andy, 1970]. This association between frugivorous diet and enlarged brain and neocortex may be related to the special demands imposed because a fruit eater's food supply is not constant since different plants bear fruit at different times and at different locations in the complex matrix of the tropical forest. An animal that is guided by the accurate memory of the locations of fruit-bearing trees can more effectively exploit the available fruit resources than would otherwise be possible. Thus natural selection would have especially favored the development of visuo-spatial memory in frugivorous primates.

Another, even more significant behavioral specialization, is the development of complex systems of social organization in many primate species. The neural substrate for the mediation of social communication is bound to be an important focus of evolutionary change in the brains of primates. The order Primates is divided into the strepsirhines (lorises, galagos, lemurs), which tend to have relatively simple forms of social organization, and the haplorhines (tarsiers, monkeys, apes, humans) in which social organization tends to be more complex. In strepsirhines, as in most mammals, the rhinarium (the space between the upper lip and the nostrils) is a furless, moist mucosal tissue that is tightly bound to the underlying maxillary bone and is bisected along the midline by a deep cleft (see Fig. 4). Since strepsirhines share this type of rhinarium with most other mammals, it is very likely to have been the primitive condition in primates. By contrast, haplorhines possess a furry rhinarium and a mobile upper lip that is more capable of participating in facial expression. Strepsirhines,

Fig. 4. Left: a strepsirhine, *Galago senegalensis*. Photo by J. Allman. Right: a haplorhine, *Tarsius syrichta*. Photo by R. Garrison. Reproduced from Allman, [1977], with permission.

like most primitive mammals, have scent glands and scent-marking behaviors that play a very important role in their social communication, and while haplorhines use olfactory cues to some extent, they rely much more heavily on the use of visually perceived facial expressions and gestures, which allow much more rapid and finely differentiated communication. Strepsirhines also tend to have much larger olfactory bulbs than do haplorhines [Stephan and Andy, 1970]. As complex systems of social organization evolved in haplorhine primates, social communication was increasingly mediated by the visual channel at the expense of the olfactory channel. One expression of this evolutionary development is the sensory input to the amygdala, which is implicated in memory formation and is linked to the neuroendocrine functions of the hypothalamus and thus to the emotions. Primitively, the main input to the amygdala was from the olfactory bulb, but in haplorhines the amygdala has major reciprocal connections with some of the higher cortical areas [Aggleton et al., 1980; Amaral and Price, 1984; Turner et al., 1980; Whitlock and Nauta, 1956]. The role of these structures in the visual mediation of social signals is indicated by the presence of neurons that are selectively responsive to the images of faces and facial expressions in the amygdala and inferior temporal cortex [Bruce et al., 1981; Desimone et al., 1984; Gross et al., 1972; Leonard et al., 1985; Perrett et al., 1982, 1984, 1985a,b; Sanghera et al., 1979]. The evolutionary development of this system in higher primates is thus linked to their expanded capacity for the visual mediation of social signals and memory of past social interactions.

GENICULOSTRIATE PROJECTIONS: PARALLEL ASCENDING SYSTEMS

The parallel ascending systems arising in the retina and projecting to the lateral geniculate nucleus of the thalamus are described in the chapters by Rodieck and Kaas in this volume. In his pioneering study of comparative primate brain anatomy, Gratiolet [Leuret and Gratiolet, 1857] discovered the system of fibers forming the optic radiation that projects from the lateral geniculate nucleus to the occipital lobe (see Fig. 5). This projection terminates heavily in layer IV of striate cortex (= area 17 of Brodmann [1909] = primary visual cortex = V-I = V1). There are three distinct parallel ascending fiber systems within the geniculostriate projection; the first of these arises from the magnocellular laminae, the second arises from the parvocellular laminae, and the third arises from neurons in the interlaminar zones, including the S-laminae, and in strepsirhines from the koniocellular laminae.

Before reviewing these three ascending systems in detail, some details concerning the structure of layer IV of striate cortex must be considered. Brodmann [1909] subdivided layer IV of area 17 in primates into three sublaminae: two cell-rich layers, IVa and IVc, separated by a cell-poor layer IVb, which corresponds to the dense fiber plexus known as the stria of Gennari. Brodmann [1909]

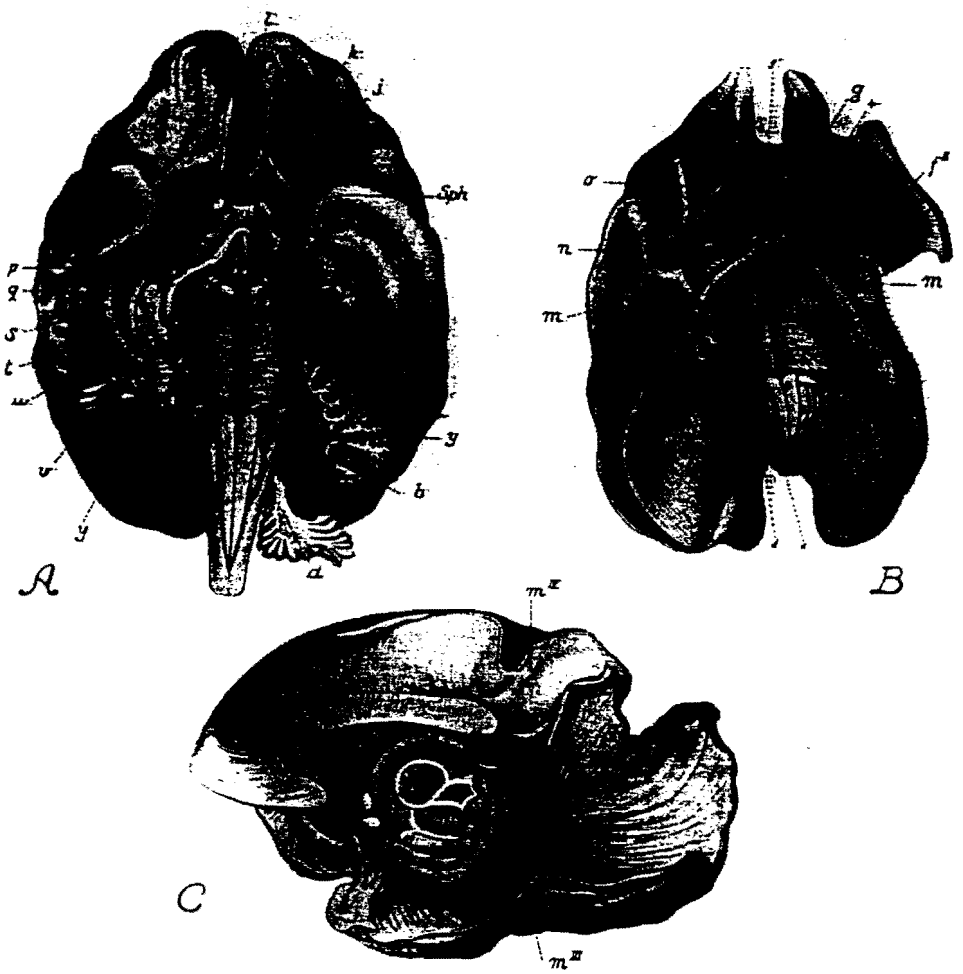


Fig. 5. Visual pathway of baboon *Papio* and of capuchin monkey, dissected by Gratiolet [Leuret and Gratiolet, 1857]. In this work, for the first time, a connection was shown between subcortical visual centers and cerebral cortex, the so-called "visual or optic radiation of Gratiolet", and the importance of the cortex as the uppermost level in the cerebral hierarchy was anatomically demonstrated. Labeling: *A*, view of the brain from below, with a part of the right temporal lobe removed to show the entry of optic tract *o* into subcortical visual centers: lateral geniculate nucleus (*s*) and pulvinar of thalamus (t); *B*, basal view of the dissected visual system of both hemispheres showing junction of optic nerves in the chiasma (*h*), external and internal "roots" of optic nerve (*i*,*j*), external or lateral geniculate nucleus (*k*), and the apparent continuation of optic nerve as a "visual radiation" (l) to the occipital lobe; *C*, medial view of right hemisphere showing visual pathway after removal of obstructing parts: the optic tract (*m*), inner and outer root of the same ($m^{I,mII}$), the latter enveloping the external geniculate nucleus, with fiber fan of visual radiation (m^{III}) streaming toward the occipital lobe at right; m^{IV}, anterior fibers of radiation mingling with callosal fibers. From a specimen "teased" or dissected with needles, after a preliminary maceration. From Leuret and Gratiolet, *Anatomie comparée du systeme nerveux (atlas)*, 1857, Pls. 26 and 27. Reproduced from Polyak, [1957], with permission.

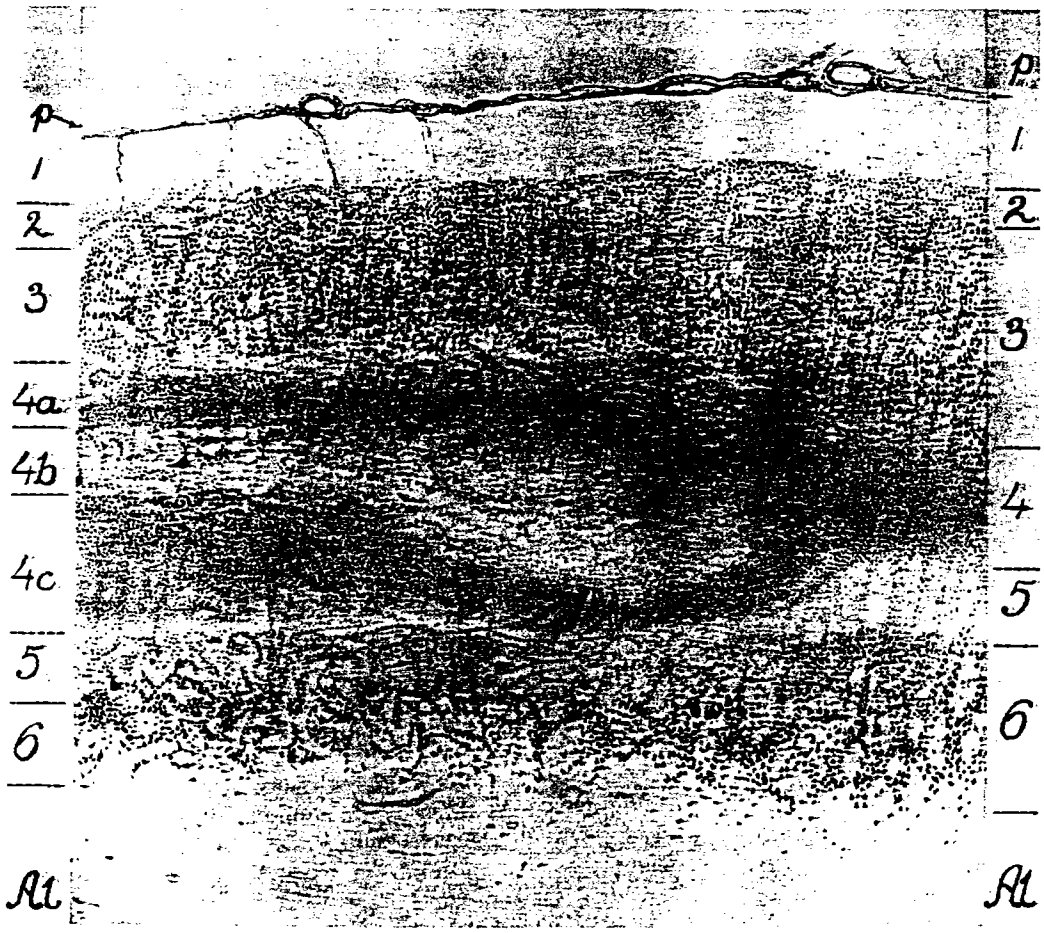


Fig. 6. Cell arrangement in the marginal portion of human striate cortex stained with Nissl-toluidine blue method (Lenhossëk's modification), showing the merging of the three sublayers of the inner granular layer of the striate area (4a, 4b, 4c) into a single layer 4 in the parastriate area at the right end of the figure. Reproduced from Polyak, [1957], with permission.

and Polyak [1957] noted that layers IVa and IVc fuse at the margin of area 17 and are continuous with layer IV in area 18 (see Fig. 6). Other anatomists have restricted their definition of layer IV of primate striate cortex to the layer corresponding to IVc of Brodmann [Hassler, 1967; Diamond et al, 1985; see also von Bonin, 1942, for discussion]. The layer corresponding to IVa of Brodmann receives a projection from the parvocellular laminae of the lateral geniculate nucleus in *Macaca* [Hubel and Wiesel, 1972] and *Saimiri* [Fitzpatrick et al, 1983], but there is no evidence of a similar projection in *Galago* and *Aotus* [Diamond et al, 1985]. This evidence suggests that the parvocellular projection to Brodmann's layer IVa may be a specialization restricted to diurnal primates. However, the cytoarchitectural distinctiveness of Brodmann's layer IVa is not associated with diurnality. For example, while it is very difficult to distinguish layers corresponding to Brodmann's IVa and IVb in *Galago* [von Bonin, 1945], they can be seen easily in *Aotus*. Moreover, Brodmann's layer IVa is especially well developed in *Tarsius*, and it is separated by a cell-poor layer (IVb) from another dense layer (IVc), as in other haplorhine primates (see Fig. 7). Moreover, layers IVa, IVb,

Fig. 7. Cresyl-violet stained parasagittal section through primary visual cortex in the calcarine sulcus in *Tarsius bancanus* from our collection.

and IVc are continuous with layer IV of the adjoining extrastriate cortex in *Tarsius*.

The magnocellular laminae project to the upper half of layer IVc of striate cortex. This has been termed layer IVc-alpha in studies in *Macaca* [Hubel and Wiesel, 1972] and layer IV-alpha in studies in *Saimiri*, *Aotus*, and *Galago* [Fitzpatrick et al, 1983; Diamond et al, 1985] (see Fig. 8). The main ascending connections of the magnocellular system are illustrated in Figure 9. Fiber conduction in the magnocellular system is faster than in other systems [Sherman et al, 1976; Dreher et al, 1976; Schiller and Malpeli, 1978; Mitzdorf and Singer, 1979; Maunsell and Schiller, 1984], which correlates with the dense myelination of Brodmann's layer IVb in striate cortex and the deeper layers of the middle temporal visual area (MT). The neurons in layer IVb of striate cortex are highly sensitive to the direction of stimulus motion [Dow, 1974; Poggio, 1984; Livingstone and Hubel, 1984; Movshon and Newsome, 1984], as are the neurons in area MT [Zeki, 1974; Baker et al, 1981; Maunsell and Van Essen, 1983a; Albright, 1984]. Neurons in the magnocellular laminae of the lateral geniculate nucleus are much more sensitive to low-contrast stimuli than are the neurons in the parvocellular laminae [Kaplan and Shapley, 1982; Hicks et al, 1983; Derrington and Lennie, 1984]. In summary, the magnocellular system is fast, sensitive to low-contrast stimuli, and probably subserves the perception of visual motion.

The parvocellular laminae occupy a much larger portion of the lateral geniculate nucleus and have a much more complex pattern of sublamination in diurnal, as compared to nocturnal, primates [Hassler, 1967; Kaas et al, 1978]. The parvocellular laminae project to the lower half of layer IVc of striate cortex. This has been termed layer IVc-beta in studies in *Macaca* [Hubel and Wiesel, 1972] and layer IV-beta in studies in *Saimiri*, *Aotus*, and *Galago* [Fitzpatrick et al, 1983; Diamond et al, 1985]. In contrast to the magnocellular system, the parvocellular system is slower, insensitive to low-contrast stimuli, and probably subserves the perception of fine detail and, in diurnal primates, color [Wiesel and Hubel, 1966; Sherman et al, 1976; Dreher et al, 1976; Schiller and Malpeli, 1978; Kaplan and Shapley, 1982; Hicks et al, 1983; Derrington and Lennie, 1984; Derrington et al, 1984].

Other parts of the lateral geniculate nucleus project to layers I, II, and III of striate cortex. With horseradish peroxidase (HRP) injections restricted to cortical layers I and II in *Galago*, Carey et al [1979] found retrograde filling of neurons in the interlaminar zones including laminae S, which lies adjacent to the optic tract, as well as in the koniocellular laminae, which are intercalated between the two parvocellular laminae in strepsirhine primates. Livingstone and Hubel [1982] demonstrated in *Macaca* and *Saimiri* that the lateral geniculate nucleus projects to the cytochrome oxidase-rich structures, variously known as "puffs," "blobs," or "patches," in striate layer III that were originally discovered by Wong-Riley [see Livingstone and Hubel, 1982, 1984]. Fitzpatrick et al [1983] found in *Saimiri* that the interlaminar zones surrounding the magnocellular laminae, including the S laminae, project to the cytochrome oxidase-rich structures in layer III and to layer I of striate cortex. Diamond et al [1985] demonstrated these projections for the interlaminar zones in *Aotus* and *Galago* and found in *Galago* that the koniocellular laminae project to these targets as well. The interlaminar zones, the S laminae, and the koniocellular laminae all receive input from the retina [Kaas et al, 1978]. The optic tectum also projects to the interlaminar zones, including the S laminae in *Saimiri* [Harting et al, 1980] and inter-

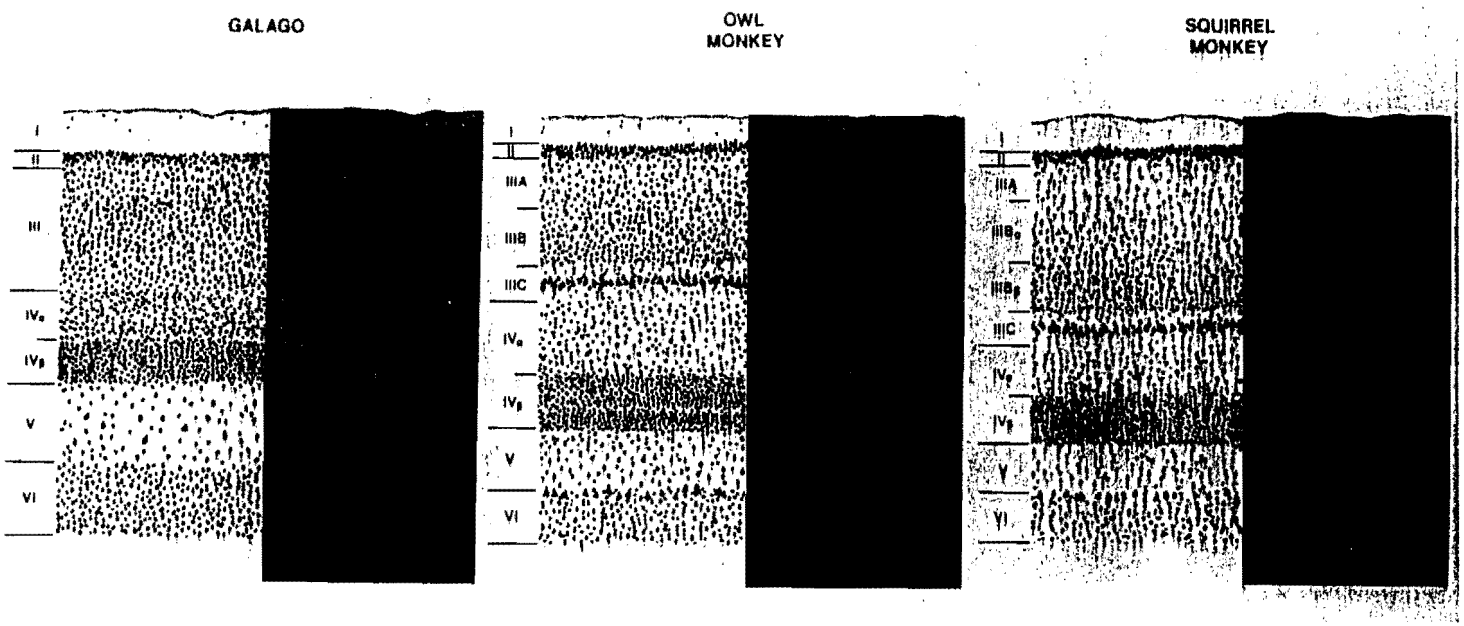


Fig. 8. Diagram to depict the relation between the laminar organization of the striate cortex and the projections of the lateral geniculate nucleus in *Galago*, *Aotus*, and *Saimiri*. Reproduced from Diamond, et al [1985], with permission.

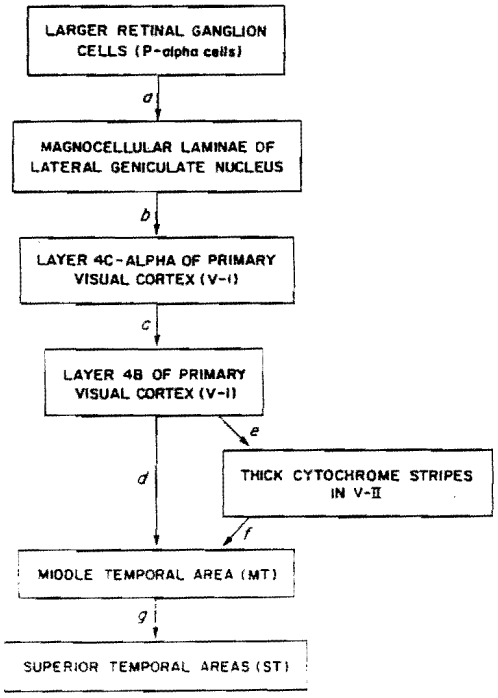


Fig. 9. The main ascending connections of the magnocellular system. The evidence for these connections by level comes from (*a*) Perry et al. [1984]; (*b*) Hubel and Wiesel [1972]; (*c*) Fitzpatrick et al. [1985]; Mitzdorf and Singer [1979]; (*d*) Spatz [1977]; Lund et al. [1975] (*e*) Hubel, personal communication; (*f*) DeYoe and Van Essen [1985]; Shipp and Zeki [1985]; (*g*) Weller et al. [1984]; Ungerleider and Desimone [1985].

laminar zones and koniocellular laminae in *Galago* [Fitzpatrick et al, 1980]. Thus the interlaminar system constitutes a third parallel ascending pathway whereby retinal and tectal input is relayed to striate cortex.

OCULAR DOMINANCE SYSTEMS AND VISUAL BEHAVIOR

In *Macaca*, *Ateles*, *Cercopithecus*, *Erythrocebus*, *Papio*, *Pan*, *Homo*, and *Galago*, the inputs from the contralaterally and ipsilaterally receptive geniculate laminae are horizontally segregated in layer IV, which is the anatomical basis of Hubel and Wiesel's [1968] ocular dominance columns [Hubel and Wiesel, 1972; Florence et al, 1986; Hendrickson et al, 1978; Hendrickson and Tigges, 1985; Tigges and Tigges, 1979; Hitchcock and Hickey, 1980; Horton and Hedley-Whyte, 1984; Glendenning et al, 1976; Casagrande and Skeen, 1980]. This horizontal segregation of ocular inputs to layer IV of striate cortex is poorly developed or absent in *Aotus*, *Callithrix*, *Saimiri*, *Pithecia*, and *Cebus*, all of which are New World monkeys [Kaas et al, 1976; Spatz, 1979; DeBruyn and Casagrande, 1981; Hubel and Wiesel, 1978; Hendrickson and Tigges, 1985; Kaas, personal communication; Rowe et al, 1978]. The ocular segregation in input has been found in all Old World primates tested thus far, including the strepsirhine, *Galago*, various monkeys, chimpanzees, and humans, plus one New World primate, the spider monkey, *Ateles*. This distribution is strongly negatively correlated with a distinctive visual behavior, "head cocking," which has been studied in 40 primate species by Menzel [1980]. When most New World monkeys look at an object they cock their heads from side to side (see Fig. 10). Head cocking is particularly notable in young animals and follows a definite ontogenetic course [Menzel, 1980]. By contrast, spider monkeys, galagos, all Old World monkeys (except *Miopithecus*), apes, and humans rarely head cock when regarding an object (see Fig. 11). *Miopithecus*, the smallest Old World monkey, various *Lemur* species, *Hapalemur*, and *Propithecus* head cock, but the input to layer IV of striate cortex is unknown in these primates.

Did the ocular dominance system evolve independently at least three times in galagos, in spider monkeys, and in Old World monkeys, apes, and humans? Or was this system present in the earliest true primates and lost in most New World monkeys, as has been suggested by Florence et al [1986]? (see Fig. 12). It is an intriguing possibility that head cocking represents a specialized form of visual scanning that is somehow incompatible with the ocular dominance system of primary visual cortex. While ocular dominance systems tend to occur in larger primates and head cocking occurs in smaller ones, it should not be concluded that it is necessarily related to interocular distance for binocular parallax for stereopsis, since the ocular dominance system is present in small galagos and head cocking is not. Furthermore, it has sometimes been suggested that the ocular dominance system is required for stereopsis. This appears not to be true since *Aotus* readily discriminates ran-

Fig. 10. Head cocking in *Aotus trivirgatus*. Reproduced from Menzel, [1980], with permission.

dom-dot stereograms with no monocular depth cues and thus possesses stereoscopic perception (Miezin and Allman, unpublished observations).

CORTICOGENICULATE FEEDBACK: A POSSIBLE SPECIALIZATION IN NIGHT-ACTIVE PRIMATES

Layer VI of striate cortex projects back upon the lateral geniculate nucleus in *Macaca*, *Galago*, and *Aotus* [Lund et al, 1975; Horton, 1984; Diamond et al, 1985]. There is evidence in *Galago* that a component of this corticogeniculate feedback projection that terminates in the parvocellular laminae is rich in acetylcholinesterase. Fitzpatrick and Diamond [1980] found in *Galago* that the parvocellular laminae are much richer in acetylcholinesterase than are the koniocellular or magnocellular laminae. In an elegant series of experiments, they demonstrated that the dense acetylcholinesterase staining in the parvocellular laminae in *Galago* was not reduced by eliminating the retinal input. Similarly, they found that kainic acid injections in the lateral geniculate nucleus, which produced severe cellular destruction, did not reduce acetylcholinesterase staining in the parvocellular laminae. However, they found that striate cortex lesions greatly reduced the staining in the visuotopically corresponding parts of the parvocellular laminae (see Fig. 13). In addition, they found acetylcholinesterase-positive neurons in layer VI of striate cortex. Fitzpatrick and Diamond [1980] also found that the parvocellular laminae were more densely stained than the magnocellular laminae in *Aotus*.

In contrast, Hess and Rockland [1983] discovered that acetylcholinesterase staining was denser in the magnocellular laminae than in the parvocellular laminae in *Saimiri*, and they suggested that the difference in laminar distribution was related to the diurnal activity pattern of *Saimiri* as compared to the nocturnality of *Galago* and *Aotus*. In other diurnal primates as well, including *Macaca* [Graybiel and Ragsdale, 1982], *Callithrix*, and *Homo* (McGuinness, McDonald, and Allman, unpublished observations), the magnocellular laminae are more densely stained for acetylcholinesterase than the parvocellular laminae. In addition to *Galago* and *Aotus*, the parvocellular laminae are more densely stained than the magnocellular laminae in the nocturnal *Tarsius* [Mc-

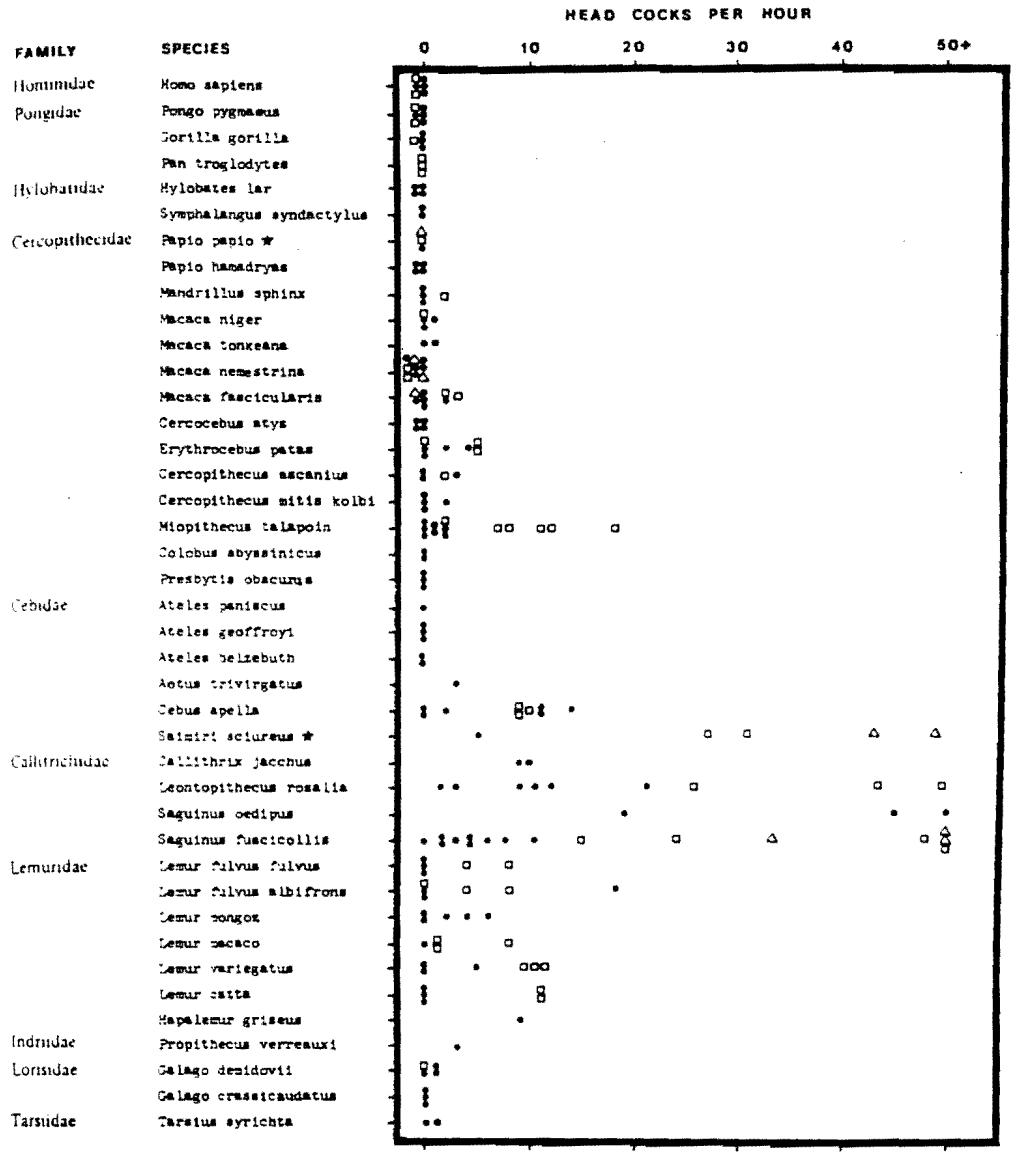


Fig. 11. Distribution of head cocking across 40 primate species. Each point is a single subject (n = 229); circles, adults; squares, juveniles; triangles, infants carried by adults. Reproduced from Menzel, [1980], with permission.

Guinness and Allman, 1985]. In *Lemur fulvus albifrons*, the parvocellular laminae also were more densely stained than the magnocellular laminae [McDonald et al, 1985], which was the first apparent exception to the correlation between dense parvocellular staining and nocturnality. *Lemur fulvus* has often been considered to be diurnal, but the *albifrons* subspecies is active at night as well and has a "round-the-clock" or *diel* activity pattern [Conley, 1975; Tattersall, 1982], and thus they must use their visual system in conditions of low illumination as do nocturnal animals. It remains to be determined whether the parvocellular laminae are rich in acetylcholinesterase in all strepsirhine

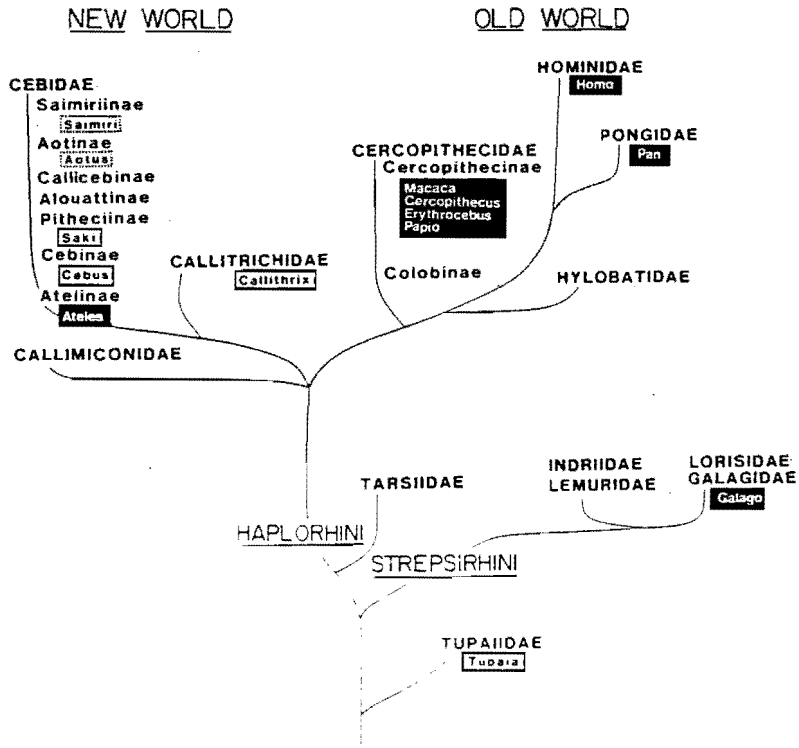


Fig. 12. A phylogenetic tree of primates indicating those genera in which clear ocular segregation (black), no ocular segregation (black outline), or weak segregation (dotted outline) has been demonstrated in normal adults. Adapted from Hershkovitz [1977]. Data for ocular segregation were taken from the following references: Casagrande and Harting [1975] (*Tupaia*); Casagrande and Skeen, [1980] (*Galago*); Conley et al. [1984] (*Tupaia*); DeBruyn and Casagrande [1981] (*Callithrix*); Florence and Casagrande [1978], and Florence et al. [1986] (*Ateles*); Glendenning et al. [1976] (*Galago*); Harting et al. [1973] (*Tupaia*); Hendrickson and Wilson [1979] (*Macaca*, *Saimiri*); Hendrickson et al. [1978] (*Macaca*), *Cercopithecus*, *Erythrocebus*, *Papio*); Hitchcock and Hickey [1980] (*Homo*); Hubel [1975] (*Tupaia*); Hubel and Wiesel [1968, 1972] (*Macaca*, *Ateles*); Hubel and Wiesel [1978] (*Saimiri*); Hubel et al [1976] (*Macaca*, *Galago*); Kaas, personal communication (*Saki*); LeVay et al. [1975, 1980, 1985] (*Macaca*); Rowe et al. [1978] (*Aotus*); Spatz, [1979] (*Callithrix*); Tigges and Tigges [1979] (*Pan*); Wiesel et al. [1974] (*Macaca*). Reproduced from Florence et al [1986], with permission.

primates or whether there are any strepsirhines that are limited to a diurnal activity pattern. The present evidence does suggest that the parvocellular laminae are rich in acetylcholinesterase in primates that are active at night and thus adapted to function in a dimly illuminated environment.

In contrast to the findings in *Galago*, Hess and Rockland [1983] found in *Macaca* and *Saimiri* that striate cortex lesions did *not* affect the pattern of acetylcholinesterase staining in the lateral geniculate nucleus, and thus the acetylcholinesterase-rich striate feedback pathway appears to be absent in diurnal primates. There are likely to be additional sources of acetylcholinesterase input to the lateral geniculate nucleus that account for the background staining throughout the nucleus and perhaps denser staining in the magnocellular laminae in diurnal primates. These may arise from the brainstem reticular formation and mediate a general enhancement of geniculate responses [Sherman and Koch, 1985].

These findings suggest that in night-active primates there is an acetylcholinesterase-rich projection feeding back from the striate cortex to the

Fig. 13. A parasagittal section through the lateral geniculate body of a *Galago* that had a small piece of the striate cortex extirpated nine days prior to death. The chief point of the photomicrograph is the presence of a break or gap in the dark bands corresponding to layers 3 and 6. These gaps are pointed out by arrowheads. ×50. Reproduced from Fitzpatrick and Diamond [1980], with permission.

parvocellular laminae that is not present in diurnal primates. A possible functional role for this system is suggested by findings in the rabbit retina, where acetylcholine enhances responses to slowly moving stimuli [Masland et al, 1984]. Alternatively, acetylcholinesterase may regulate or amplify the effects of other neurotransmitter systems [Brzin et al, 1982]. In diurnal primates, the parvocellular laminae are insensitive to low-contrast stimuli [Kaplan and Shapley, 1982; Hicks et al, 1983; Derrington and Lennie, 1984]. In primates that are active in a dimly illuminated environment, the acetylcholinesterase-rich feedback projection may serve to enhance the neural responses to low-contrast or slowly moving stimuli in the parvocellular laminae.

THE REPRESENTATION OF THE VISUAL FIELD IN STRIATE CORTEX

Gratiolet's [Leuret and Gratiolet, 1857] dissection of the optic radiation traced the visual pathway to the occipital lobe. In 1881, Munk confirmed the location of visual cortex in the occipital lobe by making a series of selective lesions in *Macaca* and observing postoperative deficits in behavior. Munk proposed a scheme for the representation of the retina in the occipital lobe, which proved to be incorrect. Schaefer [1888] established that unilateral removal of the occipital lobe produced a visual deficit in the contralateral half of the visual field. However, Schaefer [1889] was unable to determine further aspects of the map because "the difficulty of arriving at reliable conclusions from localised extirpations of the visual area is enormous. For the animals soon acquire the habit of compensating for local deficits in the visual field, by rapid movements of the eyes, so as to baffle all attempts to determine the existence of such defects. I believe, indeed, that to arrive at detailed conclusions we must await the results of perimetric observations in cases of cerebral lesions in the human subject" [Schaefer, 1889, p. 6]. Schaefer's prediction was correct. The first accurate mappings of the representation of the contralateral visual hemifield in striate cortex were achieved by Inouye [1909] and Holmes [1918], who related visual field defects to the sites of visual cortex lesions in soldiers who had been injured in the Russo-Japanese and First World Wars, respectively (see Fig. 14). The advent of positron emission tomography (PET scanning) has made possible the study of cortical organization in normal human subjects, and initial findings with this method have confirmed and extended the early observations [Kushner et al, 1982; Fox et al, 1986].

The development of amplifiers and oscilloscopes made possible the electrophysiological study of the responses of visual cortex. By recording visually evoked potentials, Talbot and Marshall [1941] mapped the representation of the central visual field in the striate cortex on the lateral aspect of the occipital lobe in *Macaca*. Daniel and Whitteridge [1961] mapped more extensive portions of striate cortex in *Macaca* and *Papio*, as did Cowey [1964] in *Saimiri*. Using microelectrode recording techniques, Allman and Kaas [1971b] produced a relatively complete map of striate cortex in *Aotus* (see Fig. 15). Myerson et al [1977] demonstrated

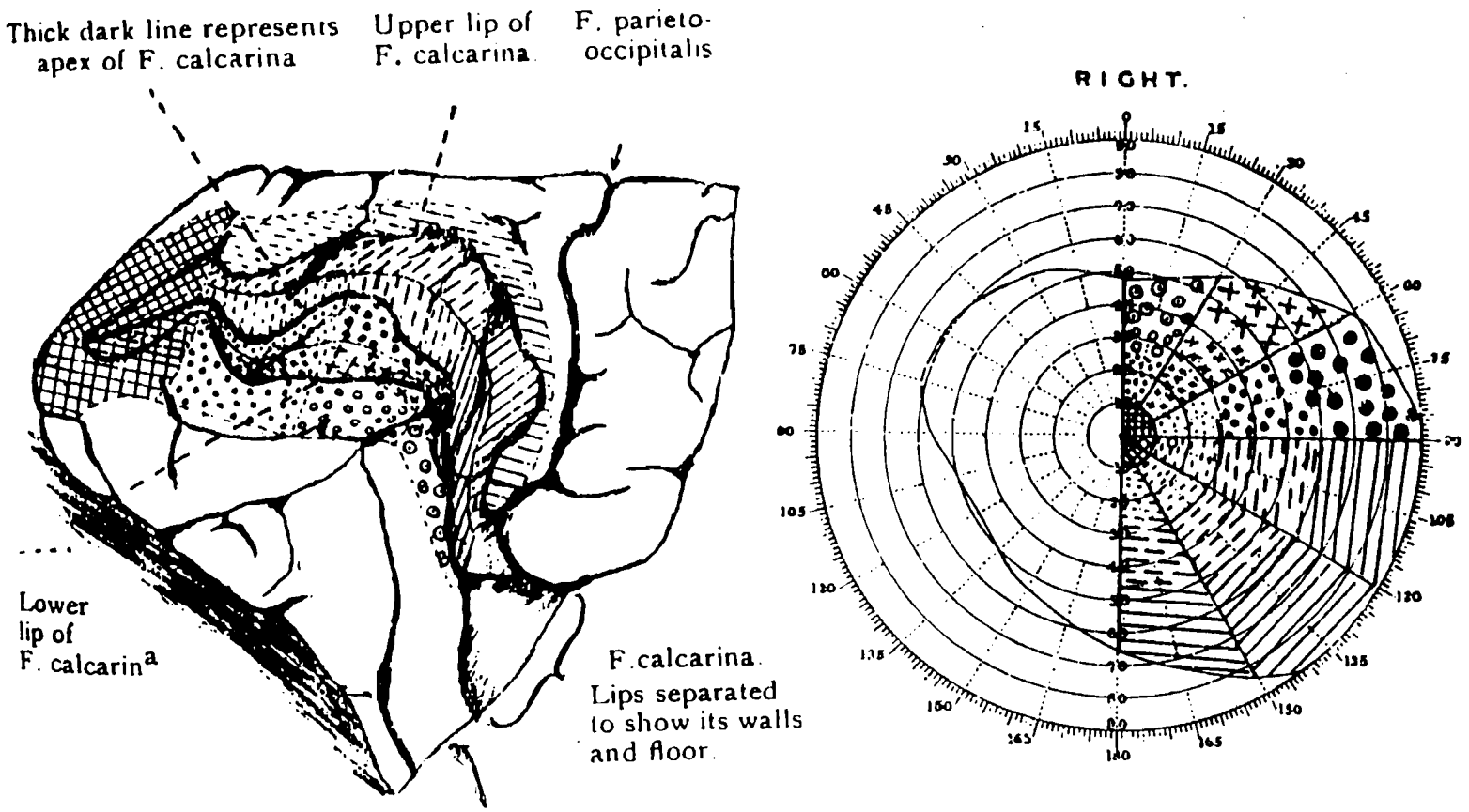


Fig. 14. A diagram of the probable representation of the different portions of the visual fields in the calcarine cortex. On the left is a drawing of the mesial surface of the left occipital lobe with the lips of the calcarine fissure separated so that its walls and floor are visible. The markings on the various portions of the visual cortex which is thus exposed correspond with those shown on the chart of the right half of the field of vision. From Holmes [1918].

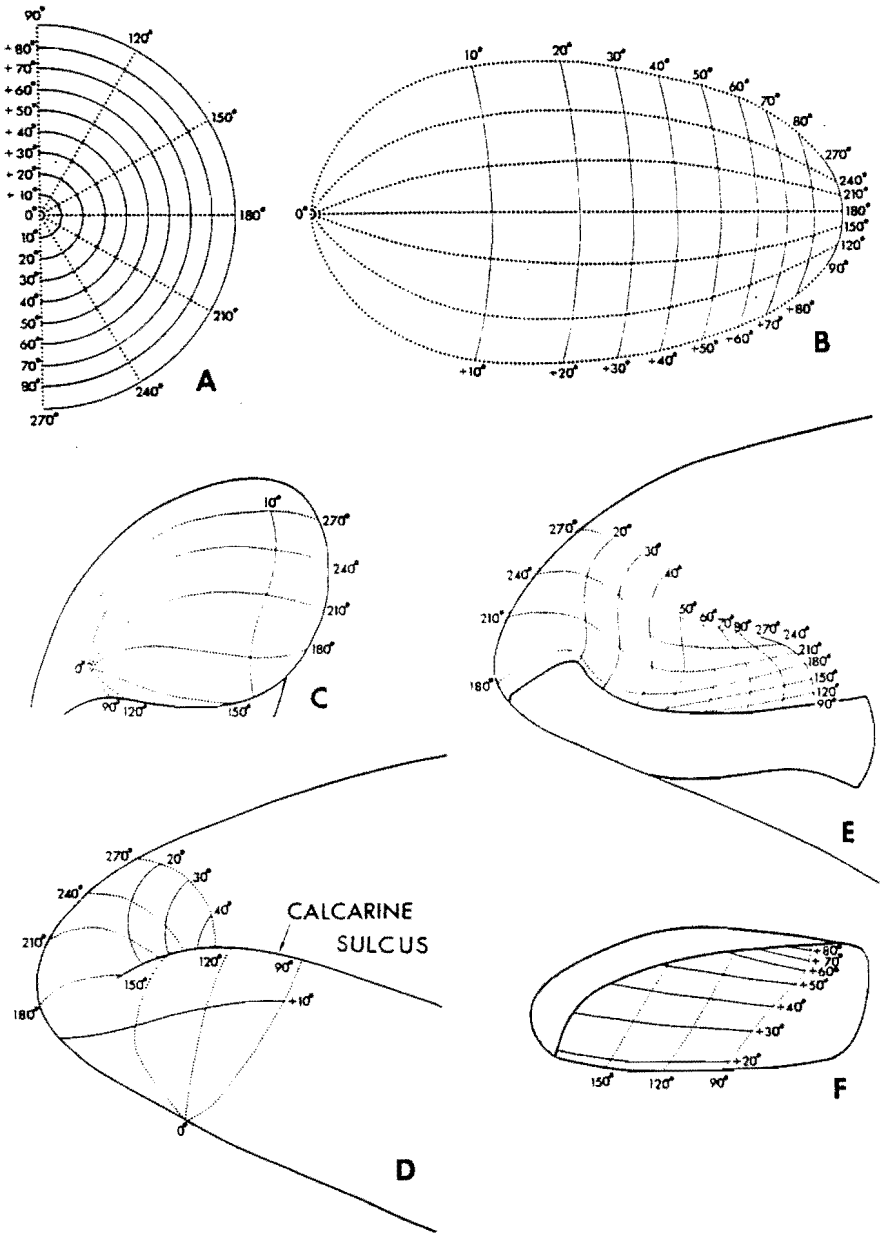


Fig. 15. Representation of the visual field in striate cortex of owl monkey. Diagram A is a planar representation of the contralateral half of the visual field, which may be thought of as a quarter of a sphere. Diagram B is a planar representation of unfolded striate cortex which is approximately one-half of an ellipsoid. The organization and location of striate cortex is shown in four views of the occipital lobe in stages of dissection below (C–F). Diagram C is a posterior view and D is a ventromedial view of the occipital lobe; in ventromedial view E, the lower bank of the calcarine fissure has been removed to expose the upper bank. The gray area indicates the brain cut made to remove the lower bank of the calcarine fissure. In F, the lower bank of the calcarine fissure, which has been removed from the brain, is viewed dorsally. Reproduced from Allman and Kaas, [1971b], with permission.

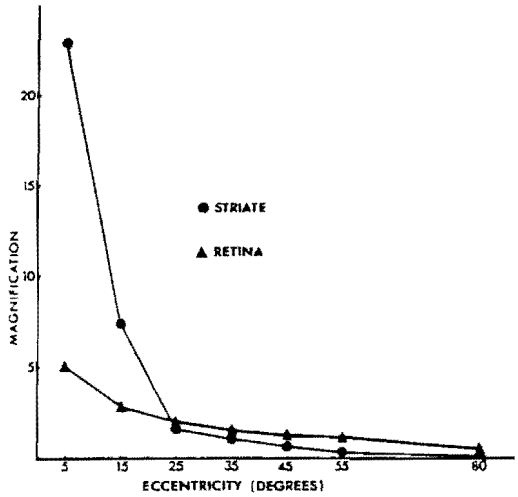


Fig. 16. Magnification in striate cortex and the retinal ganglion cell layer as a function of eccentricity. Values shown are for portions of retina and striate cortex corresponding to representations of concentric zones, each 10 degrees wide, in the visual field from 0 to 60 degrees and of the remainder of the visual field, the zone from 60 to 100 degrees. Reproduced from Myerson, [1977], with permission.

in *Aotus* that the proportion of cells in striate cortex devoted to the representation of the central visual field is much larger than the comparable proportion of retinal ganglion cells (see Fig. 16). These results, together with comparable observations for *Macaca* [Malpeli and Baker, 1975; Perry and Cowey, 1985], indicate that the relative representation of the central visual field expands in the asending pathway from the retina to the striate cortex. The representation of the fovea in *Macaca* has recently been mapped in considerable detail by Dow et al [1985] and for the entire visual field by Van Essen et al [1984].

THE REPRESENTATION OF THE VISUAL FIELD IN THE SECOND VISUAL AREA

Early electrophysiological recordings revealed the existence of a second visual area (V-II = V2) adjacent to the representation of the vertical meridian representation in the primary area in cats [Talbot, 1941] and rabbits [Thompson et al, 1950]. Cowey [1964] found electrophysiological evidence for V-II in *Saimiri*. Anatomical evidence indicated a topographically organized projection from striate cortex to the second visual area in *Macaca* [Kuypers et al, 1965; Cragg and Ainsworth, 1969; Zeki, 1969] and in *Saimiri* [Spatz et al, 1970]. The visuotopic organization of V-II was mapped in detail with microelectrodes in *Aotus* (see Fig. 17) [Allman and Kaas, 1971b, 1974a] and in *Macaca* [Gattass et al, 1984]. V-II is an elongated strip of cortex that nearly surrounds V-I. The most distinctive feature of the visuotopic organization of V-II in primates is that a few degrees out from the center of gaze the representation of the horizontal meridian splits to form most of the anterior border of the area. Allman and Kaas [1974a] termed this type of map a "second order transformation of the visual hemifield" to contrast it with the topologically simpler "first order transformation" found in V-I.

FUNCTIONAL ARCHITECTURE OF V-I AND V-II

The distribution of the mitochondrial enzyme, cytochrome oxidase, has provided an important guide to the functional architecture of visual cortex. Staining for cytochrome oxidase activity reveals dense concentrations in Brodmann's layers IVa, IVc, and VI in striate cortex, and a horizontally repeating pattern most noticeable in layer III (see Fig. 18). This pattern is most striking in tangential sections through layer III of flattened cortices. Figures 19 and 20 illustrate this pattern for *Saimiri* and *Aotus* [Tootell et al, 1983, 1985]. The pattern in striate cortex is a relatively regular array of spots of high cytochrome oxidase activity separated by a lattice of lower activity. The pattern in the adjacent area V-II is a series of thick stripes and thin stripes of high cytochrome oxidase activity separated by interstripes of lower activity that extend across the width of this beltlike area. The thin stripes are much more prominent in *Saimiri* than in *Aotus*. In experiments conducted primarily in *Macaca*, this pattern has been linked to functional architecture. In metabolic studies using ^{14}C-2-deoxyglucose (2DG) as a functional marker, Tootell et al [1982] found that stimulation with low spatial frequency gratings resulted in high 2DG uptake in the spots while stimulation with high spatial frequency gratings resulted in high uptake

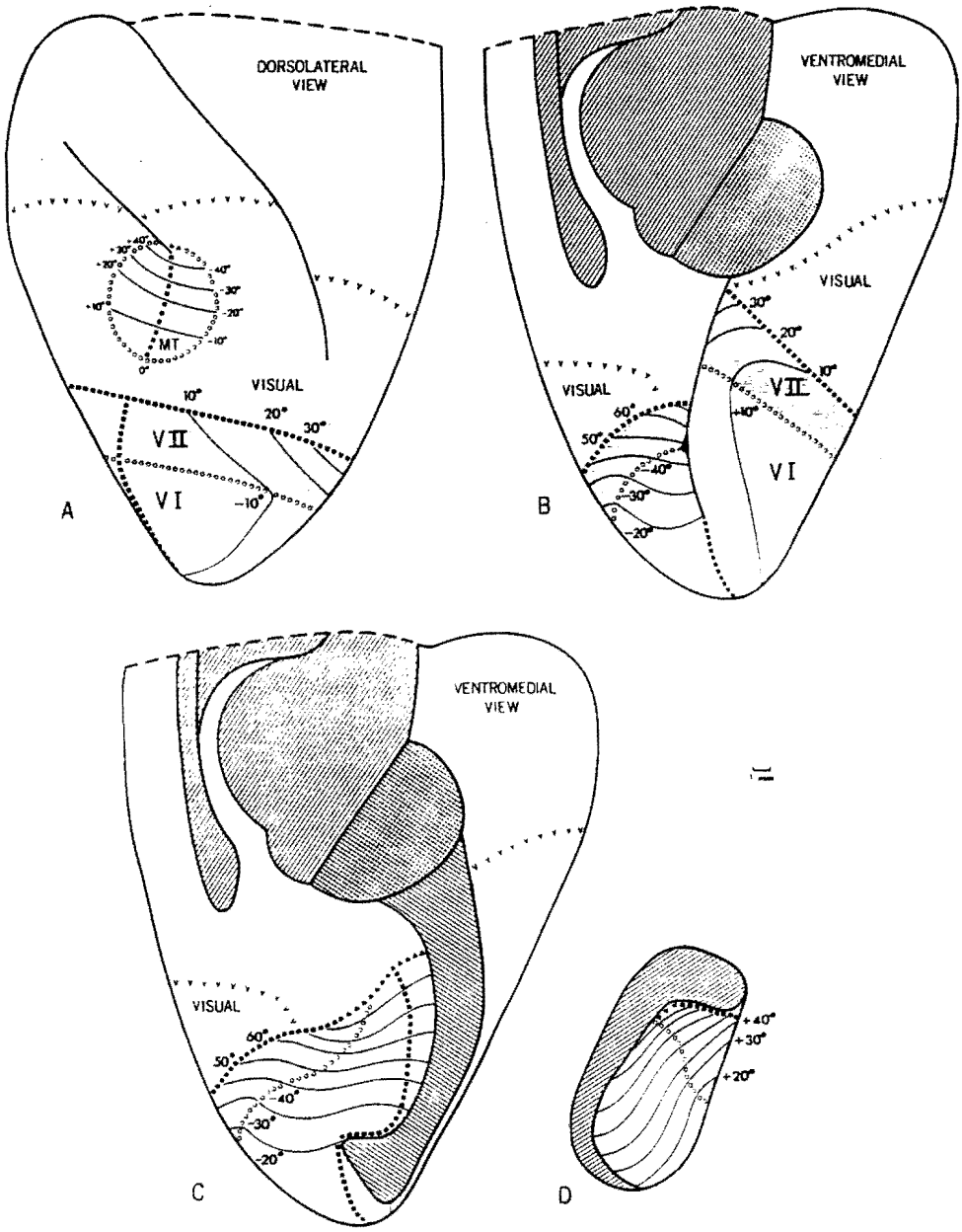


Fig. 17. Summary diagram illustrating the representations of the visual field in V-I, V-II, and MT in the owl monkey. Diagram A is a dorsolateral view of the posterior two-thirds of the left cerebral hemisphere. Diagram B is a ventromedial view of the posterior two-thirds of the left cerebral hemisphere in which the brainstem and cerebellum have been removed to expose the ventral or tentorial surface of the occipital lobe. Diagram C is a similar ventromedial view in which the lower bank of the calcarine sulcus has been removed to expose visual cortex on the upper bank of the calcarine sulcus. Diagram D is a dorsal view of the lower bank of the calcarine sulcus which has been removed from the brain. The small circles indicate the representation of the vertical meridian of the visual field; the black squares indicate the representation of the horizontal meridian of the contralateral hemifield; the black triangles indicate the representation of the temporal periphery of the contralateral hemifield. The rows of VVVVV indicate the anterior limits of visual cortex. Anterior is up in all of the diagrams. Reproduced from Allman and Kaas, [1974a], with permission.

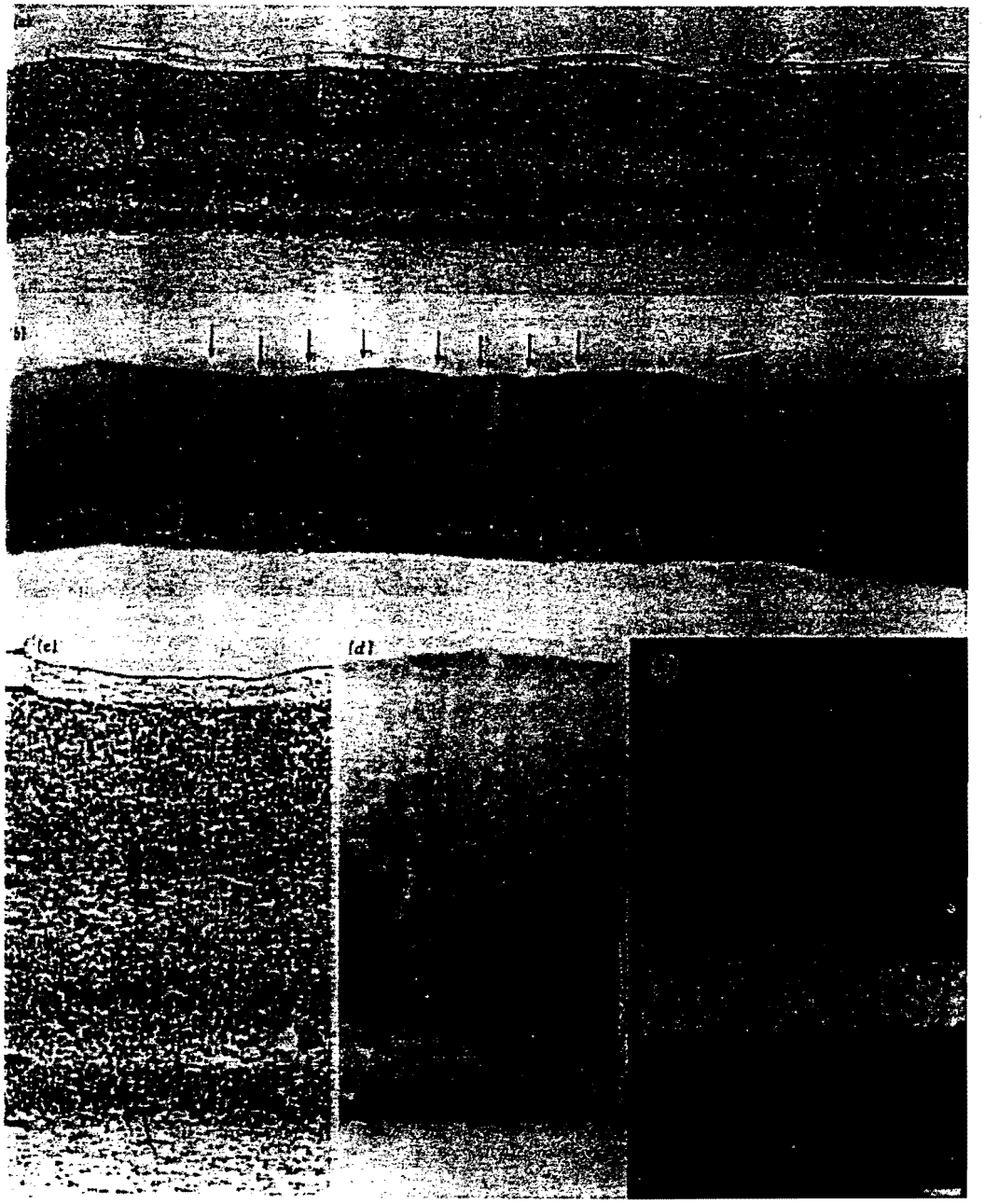


Fig. 18. Laminar pattern of cytochrome oxidase activity compared with Nissl stain and cortical projection from lateral geniculate nucleus labelled by transneuronal radioautography. (a) Coronal section through striate cortex (area 17, primary visual cortex, V1) from a normal macaque monkey stained with cresyl violet. Arrow marks a thin layer of cell bodies at interface between layers I and II, which stains lightly for cytochrome oxidase activity (see corresponding in *b*). Scale = 1 mm. (*b*) An adjacent section processed for cytochrome oxidase histochemistry shows regular columns of enhanced enzyme activity spaced about 350 μm apart (arrows). Columns are most obvious in layer III, but are also visible in layers II and IVb in this section. Nissl (*c*) and cytochrome oxidase (*d*) stains compared with geniculate projection to cortex labeled by eye injection with [^{3}H]proline (*e*). Darkest cytochrome oxidase staining is visible in layers VI, IVc, and IVa, all layers that receive a direct input from the lateral geniculate. Note that sharp lower border of layer IVc in the cytochrome oxidase stain matches the lower extent of proline label. Scale = 100 μm. Reproduced from Horton, [1984], with permission.

Fig. 19. Section through layer III of a flat-mounted occipital lobe stained for cytochrome oxidase activity in *Saimiri sciureus*. Reproduced from Tootell et al [1983], with permission.

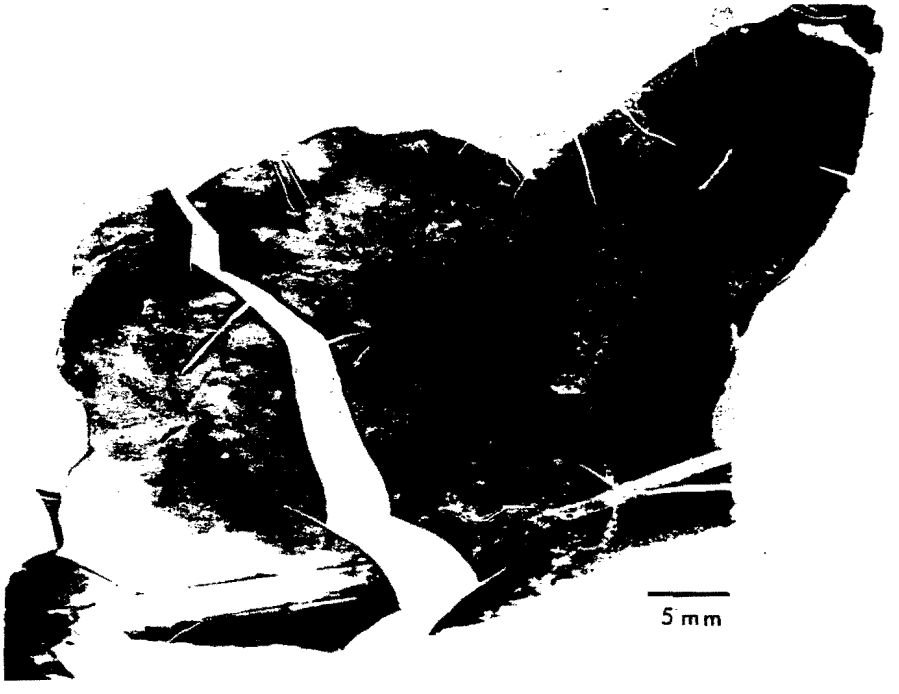


Fig. 20. Section through layer III of flat-mounted cerebral cortex of *Aotus trivirgatus* stained for cytochrome oxidase activity. Reproduced from Tootell, et al [1985], with permission.

in the surrounding lattice in striate cortex. Livingstone and Hubel [1984] found that the neurons in the cytochrome oxidase-rich spots in striate cortex, which they term "blobs," lack orientation selectivity (see Fig. 21), are rich in opponent-color mechanisms, and project to the thin stripes of cytochrome oxidase activity in area V-II. By contrast, they found that the neurons in the "interblob" lattice in striate cortex are orientation selective and project to interstripes of low cytochrome oxidase activity in area V-II. The thin stripes and interstripes in turn project to area V4 [DeYoe and Van Essen, 1985; Shipp and Zeki, 1985]. The thick stripes of high cytochrome oxidase activity in area V-II project to MT [DeYoe and Van Essen, 1985; Shipp and Zeki, 1985].

The spot-lattice pattern of cytochrome oxidase activity has also been found in the striate cortex of *Galago*, *Papio*, and *Homo* [Horton, 1984; Horton and Hedley-Whyte, 1984; Cusick et al, 1984]. It appears to be absent in *Tarsius*, *Hapalemur*, and *Cheirogaleus* [McGuinness et al, 1986]. It has thus far not been identified in any nonprimate tested, including *Rattus*, *Mus*, *Citellus*, *Felis*, *Tupaia*, *Oryctolagus*, and *Mustela* [Horton, 1984]. The stripe pattern in area V-II has thus far been identified in *Saimiri*, *Aotus*, *Macaca*, and *Homo* [Tootell et al, 1982, 1985; Livingstone and Hubel, 1984; DeYoe and Van Essen, 1985; Shipp and Zeki, 1985; Tootell and Hockfield, personal communication]. Livingstone and Hubel [1984] and Tootell [1985] have found evidence that the spots of high cytochrome oxidase activity in striate cortex are involved in the analysis of color in *Macaca*, but the presence of well-defined spot-lattice systems in the nocturnal genera, *Aotus* and *Galago*, suggests that the spots must be linked to functions other than color vision. As of yet there have been no studies of the functional correlates of the cytochrome oxidase-defined structures in nocturnal primates. However, the findings in *Macaca* that the spots are sensitive to low spatial frequency and low-contrast stimuli [Tootell et al, 1982; Tootell, 1985], together with their lack of orientation selectivity [Livingstone and Hubel, 1984], suggest that they may be linked to analysis of luminosity or possibly brightness constancy.

THE MIDDLE TEMPORAL VISUAL AREA: AN AREA SPECIALIZED FOR THE ANALYSIS OF DIRECTION OF MOTION

The middle temporal visual area (MT) is a highly distinctive, densely myelinated region that was first identified and mapped in *Aotus* (see Figs. 22, 31, 33) [Allman and Kaas, 1971a]. In the cytochrome oxidase-stained section of flattened owl monkey cortex illustrated in Figure 20, area MT appears as a densely stained oval that corresponds to the myeloarchitecturally defined MT [Tootell et al, 1985]. Area MT has also been mapped with both anatomical and physiological methods in *Galago* (see Fig. 23) [Allman et al, 1973; Tigges et al, 1973; Symonds and Kaas, 1978], *Callithrix* [Spatz, 1977], and *Macaca* [Ungerleider and Mishkin, 1979; Gattass and Gross, 1981; Van Essen et al, 1981; Weller and Kaas, 1983]. Area MT contains a representation of the contralateral hemifield, although the representation of the far peripheral visual field extends beyond the zone of dense myelination [Allman et al, 1973; Gattass and Gross, 1981; Desimone and Ungerleider, 1986]. The striate input to area MT arises from Brodmann's layer IVb and large cells located deep in layer V in *Callithrix* [Spatz, 1975, 1977], *Saimiri* [Tigges et al, 1981], *Aotus* [Diamond et al, 1985], and *Macaca* [Lund et al, 1975]. Brodmann's layer IVb corresponds to the densely myelinated stria of Gennari, which contains many horizontally oriented fibers, some of which travel for a considerable distance [Polyak, 1957; Fisken et al, 1975; Fitzpatrick et al, 1985]. Layer IVb receives its input from the magnocellular recipient layer IVc-alpha [Fitzpatrick et al, 1985]. The neurons in layer IVb in monkeys are highly sensitive to the direction of stimulus motion [Dow, 1974; Poggio, 1984; Livingstone and Hubel, 1984; Movshon and Newsome, 1984], as are the neurons in area MT [Zeki, 1974; Baker et al, 1981; Maunsell and Van Essen, 1983a; Albright, 1984]. In *Galago*, Brodmann's layer IVb is not distinguishable, but neurons in the deeper part of layer III and in layer V project to MT [Diamond et al, 1985]. It would be interesting to determine the functional properties of this system in *Galago*, which lacks the well-

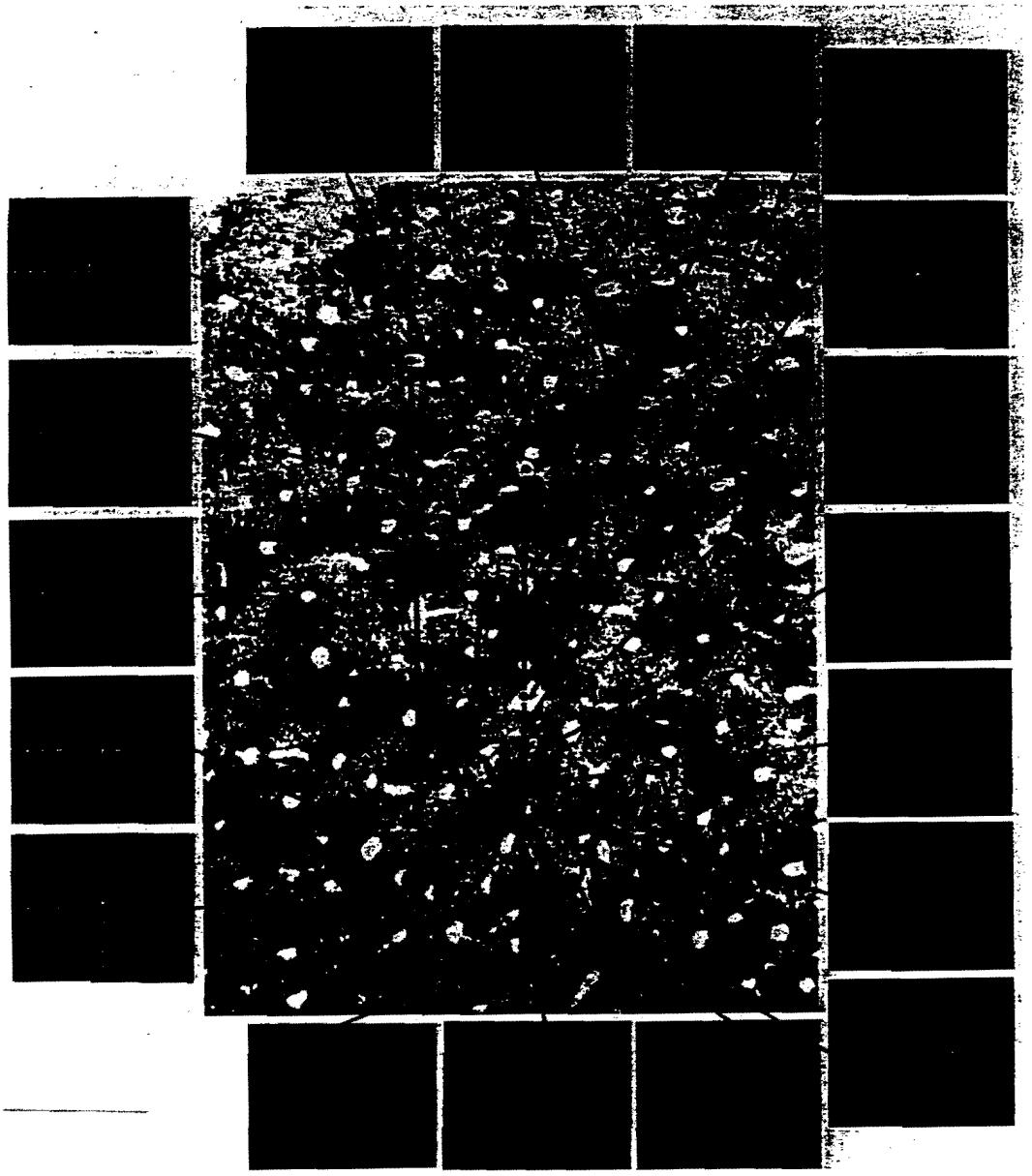


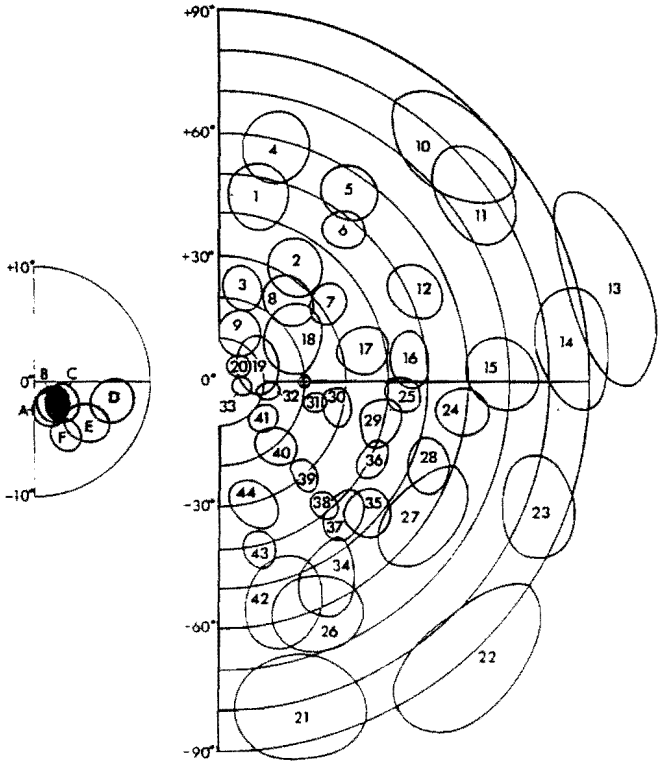
Fig. 21. Two parallel penetrations in layers 2 and 3 of macaque parafoveal striate cortex. The section was stained for cytochrome oxidase. The lesions have been emphasized with *dots*. Polar histograms of 18 of the units encountered in these two penetrations. The penetrations go from bottom to top. Reproduced from Livingstone and Hubel [1984], with permission.

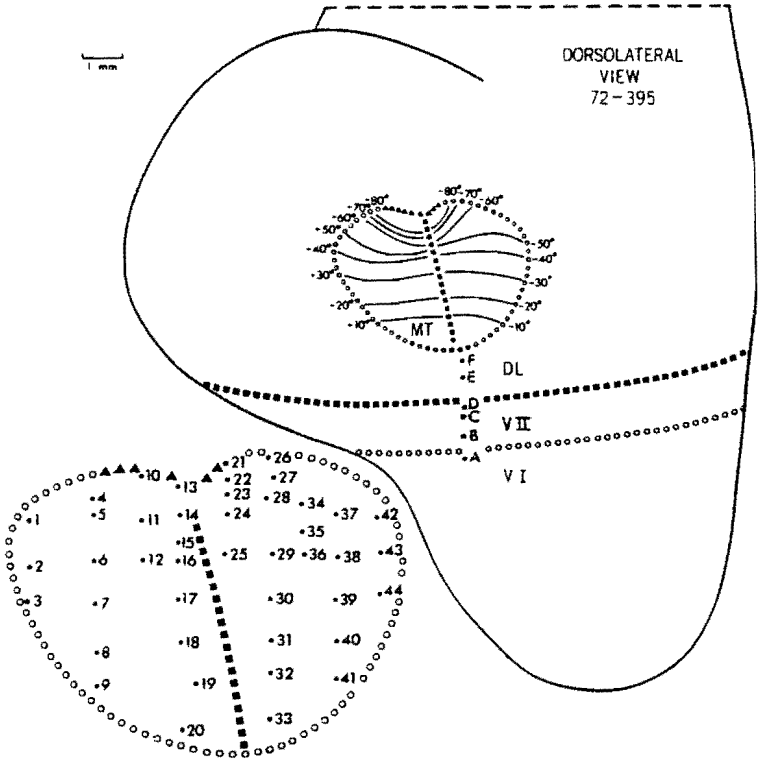
Fig. 22. Photomicrographs of two adjacent coronal sections through the middle temporal visual area (MT) in *Aotus*. The upper photomicrograph was taken of a section stained with hematoxylin for myelin. The lower photomicrograph was taken of the adjacent coronal section stained with thionin. Scale bar = 1 mm.

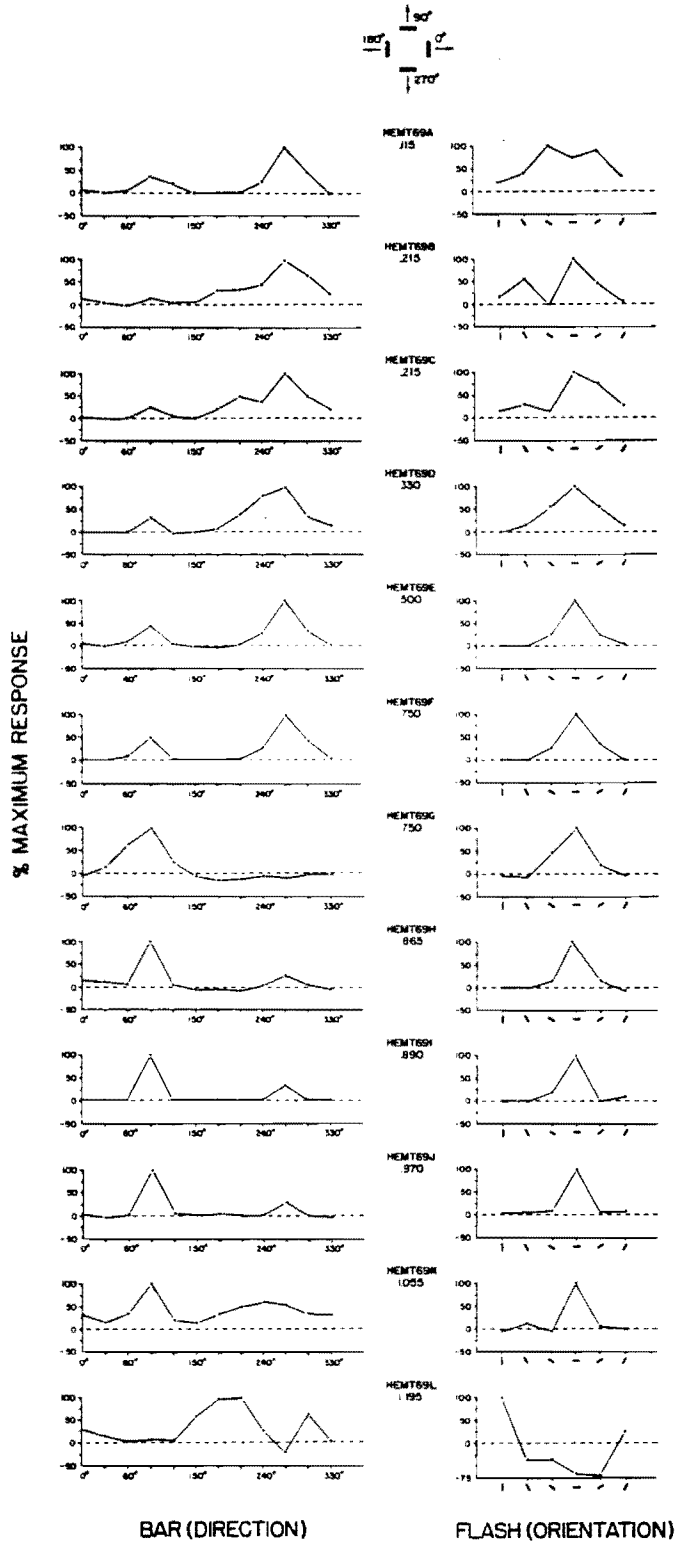
developed horizontal fiber system in the stria of Gennari.

Neurons in MT have very transient responses with average latencies of 33 milliseconds in *Aotus* [Miezin et al, 1986] and 39 milliseconds in *Macaca* [Maunsell, 1986]. The relatively short latencies and transient responses reflect the magnocellular input relayed through V-I and V-II to MT. As the microelectrode advances through MT there is a systematic shift in the directional preference of successively recorded neurons in *Macaca* [Zeki, 1974; Albright et al, 1984] and *Aotus* [Baker et al, 1981]. The system of directional preferences is linked to an orientation-selective system, since in most MT neurons the directional preference tends to be orthogonal to the orientation preference

Fig. 23. The topological transformation of the contralateral half of the visual field in MT in the bushbaby. The lower diagram is a drawing of a dorsolateral view of the caudal two-thirds of the left hemisphere. The small circles indicate the representation of the vertical meridian, the black triangles indicate the extreme temporal periphery, and the black squares indicate the horizontal meridian. The surface locations or recording sites 1–44 are shown in the enlarged view of MT, which is outlined by small circles and black triangles and lies below the drawing of the brain. Receptive fields were mapping at various depths from near the pial surface to a maximum depth of 1,350 μm. The average recording site was approximately 360 μm beneath the pial surface. The receptive fields for recording sites 1–44 in MT are illustrated in the large perimeter chart of the contralateral half of the visual field. The receptive fields for recording sites A through F in V II and the interstitial zone between V II and MT are shown in the small perimeter chart for the central 10° of the contralateral half of the visual field. The extent of V II exposed on the dorsolateral surface of the brain and the receptive fields mapped from recording sites in V II are shaded. Scale = 1 mm. Reproduced from Allman et al [1973], with permission.


+90°
+60°
+30°
0°
-30°
-60°
-90°
+10°
0°
-10°
A
B
C
D
E
F


1 mm
DORSOLATERAL
VIEW
72-395
MT
DL
VII
VI


90°
180°
0°
270°
% MAXIMUM RESPONSE
BAR (DIRECTION)
FLASH (ORIENTATION)

[Baker et al, 1981; Albright et al, 1984]. In some penetrations there are abrupt 180° shifts in preferred direction as the electrode passes through populations of neurons sharing the same orientation preference (see Fig. 24). Orientation selectivity is the basis of the columnar system in striate cortex [Hubel and Wiesel, 1968] and is an ubiquitous property of neurons in many extrastriate areas [Baker et al, 1981]. In the evolution of the functional organization of MT, the columnar system for directional selectivity may have developed out of a preexisting system for orientation selectivity. Albright et al [1984] have found a systematic columnar representation of the axis of movement in area MT (see Fig. 25), which would be orthogonal to the orientation preferences of the majority of MT neurons. In this system, adjacent columns sharing the same axis of motion have opposite preferred directions. Twenty-five percent of MT neurons respond to the apparent motion of complex grating patterns (pattern direction-selective), whereas most MT neurons and all striate layer IVb neurons respond to the actual direction of motion of the components of the grating stimulus (component direction-selective), which can be quite different from the apparent direction of motion of the whole pattern (see Figs. 26, 27) [Movshon et al, 1985; Movshon and Newsome, 1984]. The pattern direction-selective neurons may correspond to the population of MT neurons described by Albright [1984] that have preferred orientations roughly parallel to their preferred orientation. Pattern direction selectivity appears to emerge from the orientation-selective system within MT, although their exact relationship to the columnar system remains to be determined. The pattern direction-selective MT neurons match perception and constitute a significant elaboration of function beyond that found in striate cortex. The role of MT in the perception of direction of moving stimuli is also suggested by the effects of small lesions in this area, which produce deficits in the monkey's ability to make smooth pursuit eye movements that

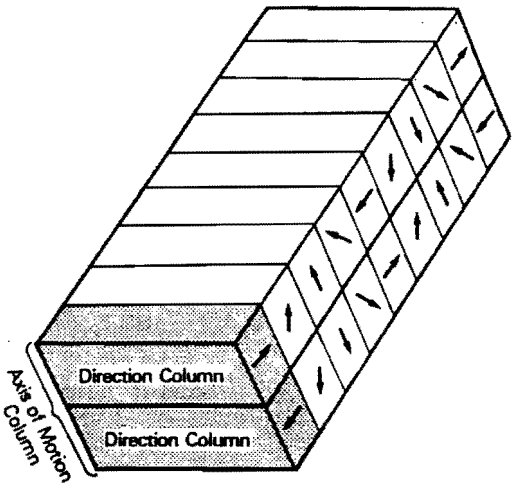


Fig. 25. Three-dimensional depiction of a block of cortical tissue containing one configuration of axis and direction of motion columns that is consistent with our data. The vertical dimension represents cortical depth. The long axis of the figure may be viewed as two complete revolutions of axis of motion columns. Moving in this dimension, one would encounter gradual changes in preferred direction. Within each axis of motion column (along the short axis of the figure), the two opposite directions of motion along that axis of motion are represented as adjacent columns. Moving in this dimension, one would encounter frequent 180° reversals in preferred direction, with no change in preferred axis of motion. Reproduced from Albright, [1984], with permission.

Fig. 24. Direction and orientation selectivity for a series of neurons recorded in a single penetration nearly perpendicular to the surface of MT. A pair of graphs is illustrated for each unit (HEMT69A–L). The depth beneath the surface at which each cell was recorded is given beneath each identifying number. An electrolytic lesion was made at the bottom of the microelectrode track. Histological reconstruction indicated that the penetration was perpendicular to the surface of MT and nearly parallel to the radial fibers. Cells A–J were located in layers II and III; cells K and L were located in layer IV. Graphs on the left illustrate the average response of each cell to five presentations of a 20 × 1° light bar at 12 different angles. HEMT69A–F preferred 270°; HEMT69G–K preferred 90°. Graphs on the right illustrate the average response of the cells to ten presentations of a flashed bar at the orientations shown. All cells except the last preferred the horizontal orientation; the last was inhibited by horizontal bars. The direction of movement was 90° to the bar orientation, thus the preferred directions of 270° (down) and 90° (up) are consistent with the preferred horizontal orientation. The receptive-field centers were located an average of 16.6° below the horizontal meridian with a standard deviation of 0.9° and an average of 6.7° temporal to the vertical meridian with a standard deviation of 3.3°. Reproduced from Baker et al [1981], with permission.

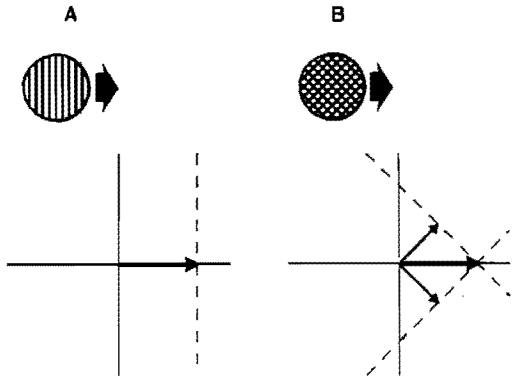


Fig. 26. A single grating (A) and a 90° plaid (B), and the representation of their motions in velocity space. Both patterns move directly to the right, but have different orientations and 1-D motions. The dashed lines indicate the families of possible motions for each component. Reproduced from Movshon, et al [1985], with permission.

track moving objects [Newsome et al. 1985]. In contrast, eye movements to stationary targets presented in the same position in the visual field were unimpaired.

While area MT contains a visuotopic map as determined by conventional receptive-field mapping techniques, 90% of its neurons are also influenced by the direction and velocity of stimuli presented simultaneously outside of the classical receptive field (see Figs. 28, 29) [Allman et al, 1985a,b]. In spite of the obvious orientation selectivity present in most MT neurons, they also respond very well to moving random-dot patterns. When mapped with moving sheets of random dots presented simultaneously within and outside the classical receptive field, the total receptive fields of MT neurons typically are 50 to 100 times the size of the classical receptive fields. Thus MT neurons are capable of integrating information about movement within their classical receptive fields with more global information about movement occurring elsewhere. The analysis of differential movement performed by these neurons may contribute to figure-ground discrimination and depth perception based on motion parallax. The anatomical basis of these global mechanisms may result from intrinsic connections within MT [Maunsell and Van Essen, 1983b], or they may result from feedback from the superior temporal visual area (ST) where the neurons also are directionally selective but have much larger classical receptive fields [Sereno et al, 1986; Weller et al, 1984]. Figure 30 illustrates a pattern of intrinsic connections extending over a large portion of area MT in *Aotus* [Weller et al, 1984].

The efferent cortical connections of area MT have been studied in *Callithrix* [Spatz and Tigges, 1972], *Galago* [Wall et al, 1982], *Aotus* [Weller et al, 1984], *Saimiri* [Tigges et al, 1981], and *Macaca* [Maunsell and Van Essen, 1983b; Ungerleider and Desimone, 1986]. Area MT's main ascending projection is to the superior temporal area (ST), which is located immediately anterior to MT in *Aotus* [Weller et al, 1984], and may correspond to the medial superior temporal area (MST), which also receives a major input from MT in *Macaca* [Maunsell and Van Essen, 1983b]. The location of these and other extrastriate areas are illustrated in Figure 31 for *Aotus* and Figure 32 for *Macaca*. Area MT projects back upon striate layers, from which it receives input. It also projects to the adjoining cortical area, termed DL in *Aotus*, and the V4 complex in *Macaca*.

THE DORSOLATERAL AREA AND THE V4 COMPLEX

In *Aotus*, the dorsolateral area (DL) wraps around MT in much the same way that area V-II forms an elongated belt nearly surrounding area V-I (see Fig. 33). Like area V-II, DL contains a representation of the horizontal meridian that splits to form most of the outer border of the area and is thus a second-order transformation of the visual field. A larger portion of DL is devoted to the representation of the central visual field than in any other cortical area in *Aotus*. DL receives its main input from area V-II [Kaas and Lin, 1977] and projects to caudal inferior temporal cortex (IT_C) [Weller and Kaas, 1985]. DL neurons have much longer average latencies (63 vs 33 milliseconds) and have much more sustained responses than MT neurons [Miezin et al, 1986], which may reflect a predominantly parvocellular system input via V-I and V-II to DL. DL neurons are highly selective for the size and shape of visual stimuli, irrespective of their position with the classical receptive field [Petersen et al, 1980]. Most DL neurons have a definite preferred size, while most

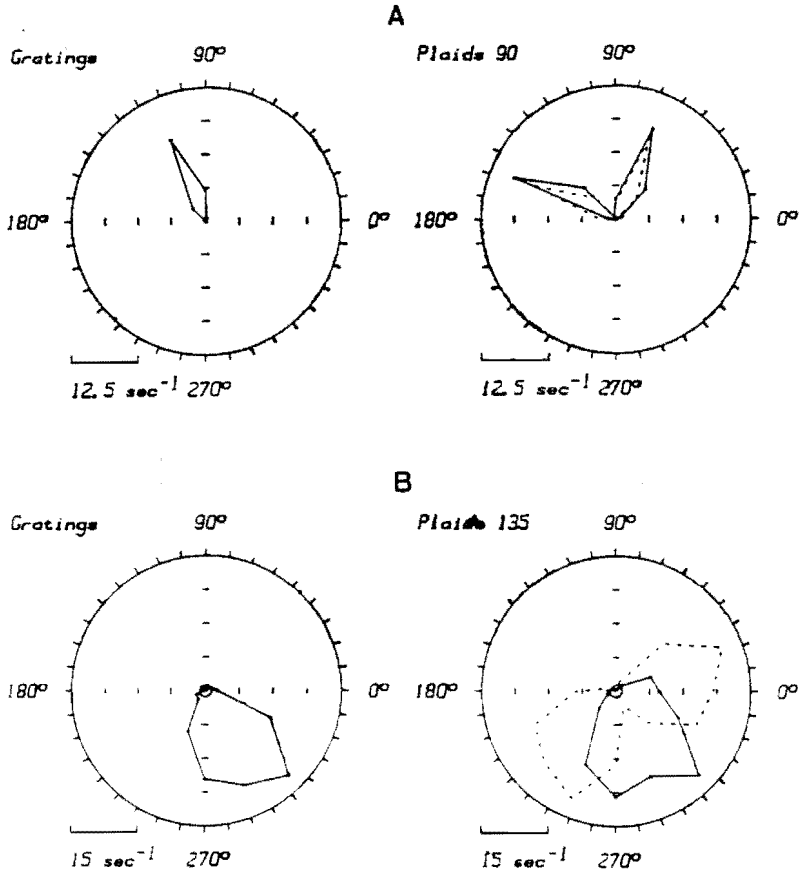


Fig. 27. Directional selectivity of two neurons from MT. A. Spatial frequency 3.6 c/deg, drift rate 4 Hz, component correlation 0.991, pattern correlation 0.092 (n = 16). B. Spatial frequency 2.7 c/deg, drift rate 4 Hz, component correlation 0.349, pattern correlation 0.940 (n = 16). Reproduced from Movshon, et al [1985], with permission.

neurons in other areas (MT, DM, and M) tend to increase their responses with increasing stimulus length, width, or diameter up to the maximum dimension tested, which corresponds to the size of the classical receptive field (see Fig. 34). The dimensional selectivity of DL neurons suggests that DL contributes to size and shape perception, which is consistent with the area's expanded representation of the central visual field and its status as the principal source of input to inferior temporal cortex. DL also is present in *Galago*, where it has a relatively expanded representation of the central visual field [Allman and McGuinness, 1983] and projects to inferior temporal cortex [Weller, 1982]. In *Callithrix*, MT projects to separate dorsal and ventral foci, which correspond in location to the dorsal and ventral wings of DL in owl monkeys [Spatz and Tigges, 1972]. In *Saimiri*, MT and V-II project to the presumptive location of DL [Tigges et al, 1974, 1981; Wong-Riley, 1979], which in turn projects to the posterior part of inferior temporal cortex [Weller, 1982].

Area V4 in *Macaca* was originally identified by Zeki [1971] as a major recipient of input from the second visual area. The extent of this region in *Macaca* has yet to be determined and it may contain several visual areas; for these reasons it has been termed the *V4 complex*. Possible subdivisions

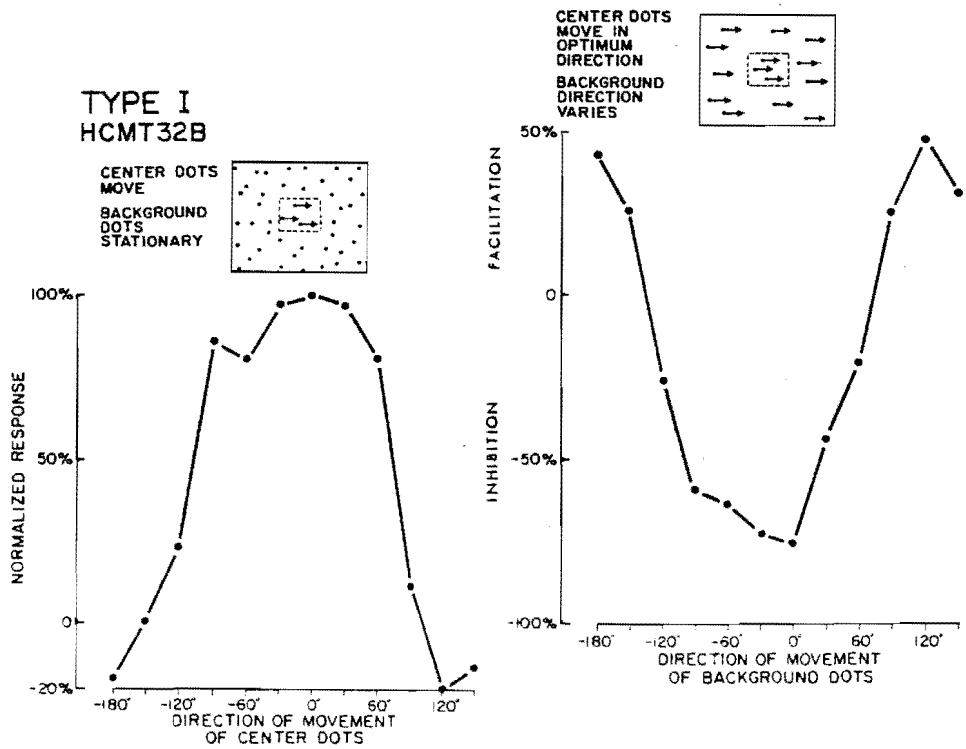


Fig. 28. Response properties of a Type I neuron (antagonistic direction-selective surround). The left graph depicts the response of the cell, HCMT32B, to 12 directions of movement of an array of random dots coextensive with its classical receptive field (crf). The response is normalized so that 0% is equal to the average level of spontaneous activity sampled for 2 second periods before each presentation. Negative percentages in the left graph indicate inhibition relative to the level of spontaneous activity. The response in the optimum direction is 100%. The right graph depicts the response of the cell to different directions of movement in the surround while the crf was simultaneously stimulated with an array moving in the cell's preferred direction. In the right graph the crf was stimulated by the array moving in the optimum direction during the 2 second sample periods preceding background movements; thus a response of 100% in the left graph is equivalent to 0% in the right graph. A value of − 100% in the right graph indicates that the movement in the surround reduced the neuron's firing rate to zero. The stimulus conditions are depicted schematically above each graph. In the experiment the dots were much denser and the background much larger relative to the center than depicted schematically. Reproduced from Allman, et al [1985a], with permission.

of the V4 complex have been suggested on the basis of connections, neural response properties, and visuotopic organization [Zeki, 1971, 1977, 1983a; Maguire and Balzer, 1984]. Like area DL in *Aotus*, the V4 complex is the major source of input to inferior temporal cortex [Desimone et al, 1980]. Similarly like DL, V4 neurons are very selective for the size and shape of stimuli [Desimone and Schein, 1987]. Also like DL, V4 neurons have longer latencies and much more sustained responses than MT neurons [Maunsell, 1987], which presumably reflects a predominately parvocellular system input from the thin stripes and interstripes in the second visual area [DeYoe and Van Essen, 1985; Shipp and Zeki, 1985]. The formidable complexity of this region in *Macaca* may be related to the similarities between macaques and humans in color perception and spatial contrast sensitivity [DeValois et al, 1974a,b]. This complexity parallels the expansion of the parvocel-

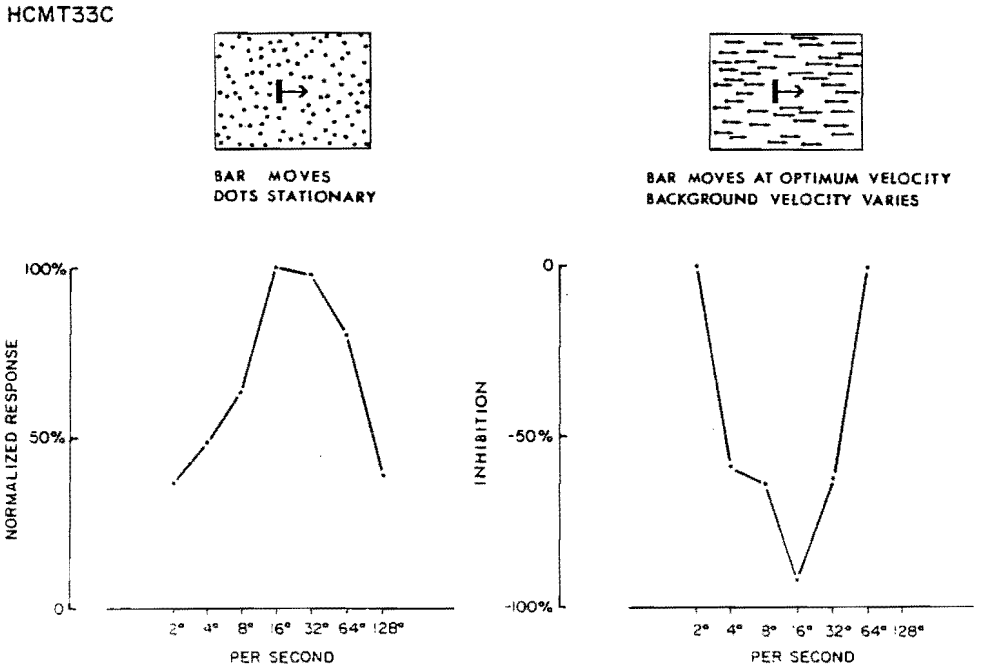


Fig. 29. The effect of bar and background velocity on neuron HCMT33C. The left graph is a velocity tuning curve for a bar moving in the optimum direction with the background stationary. The right graph is a velocity tuning curve for background movement in the same direction while simultaneously presenting the bar moving at the optimum velocity (16° sec^{-1}). The stimulus conditions are depicted schematically above the graphs, but in the experiment the dots were much denser and the surround larger. Reproduced from Allman, et al [1985a], with permission.

lular geniculate laminae relative to the magnocellular laminae and the formation of anatomically and functionally differentiated leaflets within the parvocellular laminae in *Macaca* and most other diurnal higher primates, including humans [Kaas et al, 1972, 1978; Schiller and Malpeli, 1978].

Recent recordings from neurons in the V4 complex in *Macaca* have revealed broad surround regions tuned for orientation, spatial frequency, and color [Desimone and Schein, 1987]. Moran et al [1983] found that while the classical receptive fields for V4 cells located near the vertical meridian extended an average of only 0.6° into the ipsilateral hemifield, the inhibitory surrounds extended at least 16° into the ipsilateral hemifield. The suppression resulting from stimulation in the ipsilateral hemifield was greatly reduced by section of the corpus callosum. Zeki [1983a,b] reported two types of neurons in macaque V4: wavelength selective and color coded. The responses of the first type were highly dependent on the wavelength of light illuminating the classical receptive field while the color-coded cells exhibited color constancy over a certain range of illumination conditions. The response of the color-coded cells depended on the color of objects located outside the classical receptive field, which indicated that they possess surround mechanisms with complex and as yet undetermined properties [Zeki, 1983b]. The influence of the surround on the color of an object was limited to the ipsilateral hemifield in a corpus callosum-sectioned human subject [Land et al, 1983], which restricts the locus of the "retinex" effect to the cortex, but regions other than the V4 complex, particularly area V-II and the ventral posterior area (VP) and inferior temporal cortex, may be involved in these color constancy effects as well [Allman et al, 1985a].

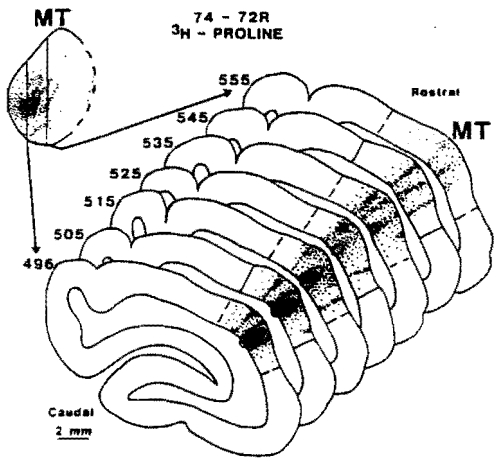


Fig. 30. Intrinsic connections in MT. An injection of ^{3}H-proline in MT of owl monkey 74-72 resulted in a densely labeled injection site (black) with a less densely labeled surround (shaded). Other concentrations of label (dots) tended to form spaced columns from white matter to cortical surface in frontal brain sections (50= μm sections numbered caudorostrally). In a surface view of MT (upper left), the columns joined to form bands. The boundaries of MT were architectonically determined from fiber-stained sections. The fiber-stained sections varied in quality and dashed lines indicate less certain estimates of the position of the boundaries. Reproduced from Weller, et al [1984], with permission.

Recent investigations have also demonstrated important attentional and nonvisual inputs to the V4 complex in *Macaca*. Moran and Desimone [1985] have found in trained monkeys that the spatial location of focal attention gates visual processing by filtering out irrelevant visual information within the classical receptive fields of neurons in V4 and IT. Haenny et al [1987] have trained macaques to match the orientation of a visually presented grating with a tactually presented grating and recorded the responses of V4 neurons during this task. Sixty percent of the V4 cells were influenced by the orientation of the tactile gratings, which were not visible to the monkey; some of these responses were very specific and are likely to have developed as a consequence of the animal's training. It is not clear how these influences are relayed to the visuotopically mapped areas; however one possible route involves the amygdala, which is strongly implicated in memory processes [Mishkin, 1982]. The inferior temporal visual cortex, as well as higher somatosensory and auditory cortices, projects to the amygdala [Whitlock and Nauta, 1956; Aggleton et al, 1980; Turner et al, 1980]. The amygdala in turn is reciprocally connected with the neuroendocrine centers of the hypothalamus [Price and Amaral, 1981]. The amygdala projects to the visual cortex [Tigges et al, 1981, 1982; Mizuno et al, 1981], particularly to the junction between layers I and II in V4 and other cortical visual areas [Amaral and Price, 1984]. These connections provide avenues for influences for other sensory modalities, as well as motivation and memory, to mediate responses within the visuotopically organized cortical areas.

INFERIOR TEMPORAL CORTEX

Lesions of inferior temporal cortex greatly diminish a monkey's ability to learn new visual discriminations [Gross, 1973]. In humans, damage to the ventromedial aspect of the occipito-temporal cortex produces a syndrome known as *prosopagnosia*, or the inability to recognize the faces of familiar individuals [Meadows, 1974a]. Such lesions may also affect the patient's ability to recognize other familiar objects such as animals. It has been suggested that the main deficit in prosopagnosia is an inability to sort out an individual from a large array of similar objects [Damasio et al, 1982].

Many neurons in the inferior temporal cortex in *Macaca* respond selectively to complex stimuli, particularly those with special biological relevance, such as the image of hands and faces in different orientations (see Fig. 35) [Gross et al, 1972; Desimone et al, 1984]. The preferred orientation for the image of the hand usually corresponded to the way in which the monkey would see its own hand. The neurons selectively responsive to faces are particularly common in the depths of the superior temporal sulcus [Bruce et al, 1981; Perrett et al, 1982]. This region also contains neurons responsive to facial expressions and particularly to whether the eyes are gazing at the subject or not, which is an important social signal in *Macaca* [Perrett et al, 1984]. This area also contains neurons selectively responsive to views of body movement, such as a person walking toward or away from the monkey [Perrett et al, 1985a]. These highly selective visual neurons in the depths of the

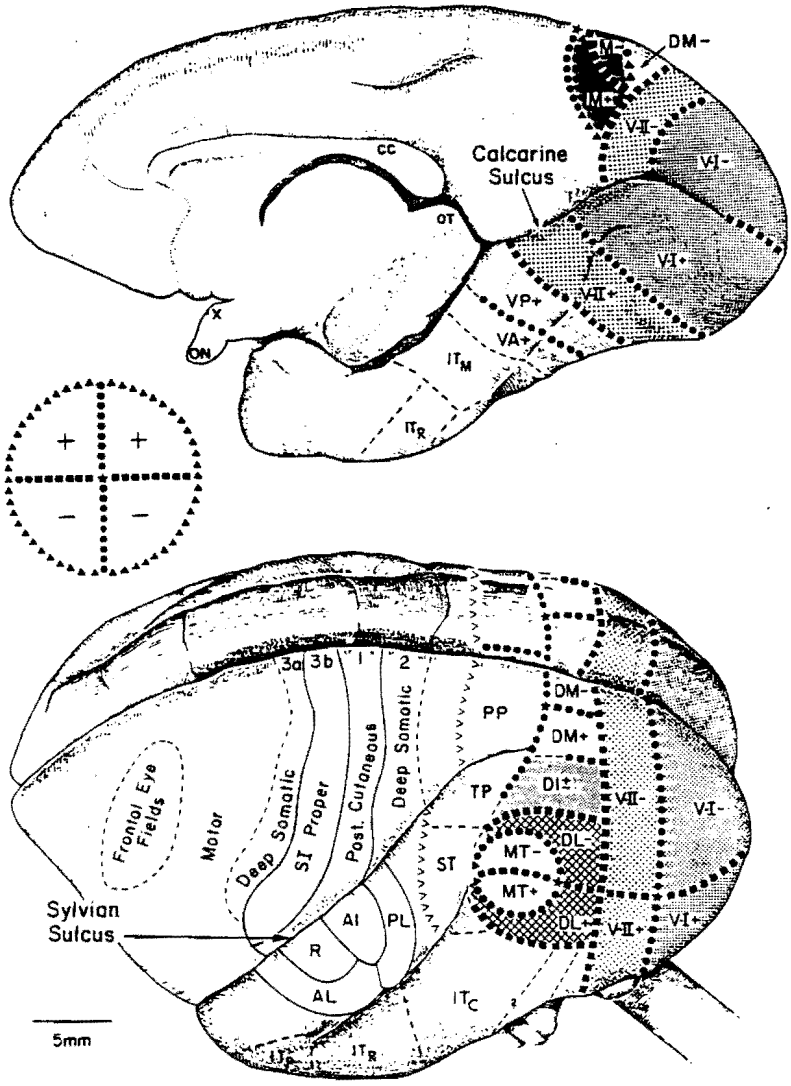


Fig. 31. The cortical areas of the owl monkey based on microelectrode mapping and architectonic and connectional studies. Above is a ventromedial view; below is a dorsolateral view. On the left is a perimeter chart of the visual field. The pluses indicate upper quadrant representations; minuses indicate lower quadrants. The row of Vs indicate the approximate border of visually responsive cortex. AI, first auditory area; AL, anterolateral auditory area; CC, corpus callosum; DI, dorsointermediate visual area; DL, dorsolateral crescent; DM, dorsomedial visual area; IT_C, inferotemporal-caudal; IT_M, inferotemporal-medial; IT_R, inferotemporal-rostral; M, medial visual area; MT, middle temporal visual area; ON, optic nerve; OT, optic tectum; PL, posterolateral auditory area; PP, posterior parietal visual cortex; R, rostral auditory area; ST, superior temporal visual cortex; TP, temporal parietal visual cortex; V-I, first visual area; V-II, second visual area; VA, ventral anterior visual area; VP, ventral posterior visual area; X, optic chiasm. The cortical visual areas were mapped by Allman and Kaas [1971a,b; 1974a,b; 1975; 1976] and Newsome and Allman [1980]; the somatosensory areas by Merzenich et al [1978]; the auditory areas by Imig et al [1977]. The subdivisions of superior temporal and inferotemporal cortex are based on the connectional studies of Weller [1983], Weller et al [1984], and Weller and Kaas [1985]. Scale =5mm.

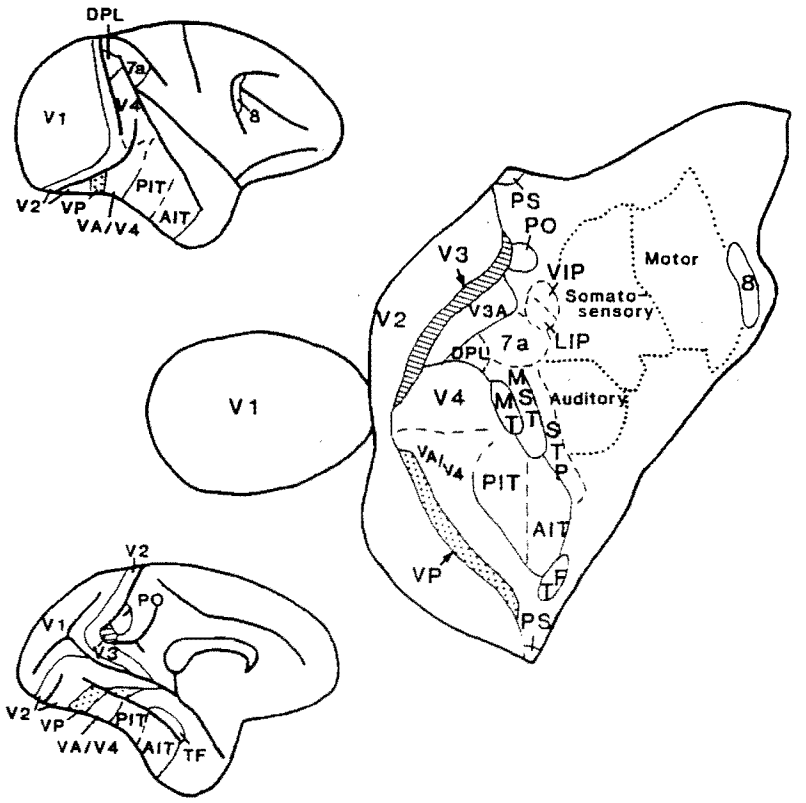


Fig. 32. The cortical areas of the macaque monkey based on microelectrode mapping and architectonic and connectional studies [see review by Van Essen, 1985]. In the upper left is a lateral view of the cortex of the right hemisphere in the macaque monkey. In the lower right this cortex is unfolded. The cortex has been cut along the upper and lower borders between the first and second visual areas. AIT, anterior inferotemporal cortex; MST, medial superior temporal visual cortex; MT, middle temporal visual area; PIT, posterior inferotemporal cortex; PO, parietal occipital visual area; PS, prostriata; VIP, ventral intraparietal cortex; V1, first visual area; V2, second visual area; V3, third visual area; V3A, third visual area (accessory); V4, fourth visual area; VA, ventral anterior area; VP, ventral posterior area. Courtesy of David Van Essen.

superior temporal sulcus are mixed with neurons responsive to auditory and somesthetic stimulation [Bruce et al, 1981; Perrett et al, 1982]. It would be interesting to determine whether the auditory cells in this area respond selectively to specific macaque vocalizations or whether there is any relationship between cells responsive to the image of the hand and somesthetic stimulation, as would occur in visuo-tactile exploration. Inferior temporal cortex projects to the amygdala, which also contains neurons selectively responsive to faces and facial expression [Sanghera et al, 1979; Leonard et al, 1986], as well as to entorhinal cortex and portions of the frontal lobe [Weller, 1982].

THE MEDIAL VISUAL AREA AND PARIETOOCCIPITAL AREA

The medial visual area (M) is unique among all the cortical visual areas in *Aotus* in that it has a proportionally large representation of the peripheral visual field (see Fig. 36) [Allman and Kaas, 1976]. Only 4% of area M is devoted to the representation of the central 10° of the visual field. In *Macaca* there is an area in the same location with a similar visuotopic organization and emphasis of the peripheral visual field representation that has been termed the parieto-occipital area (PO) [Covey et al, 1983]. In *Macaca* this area receives a strong

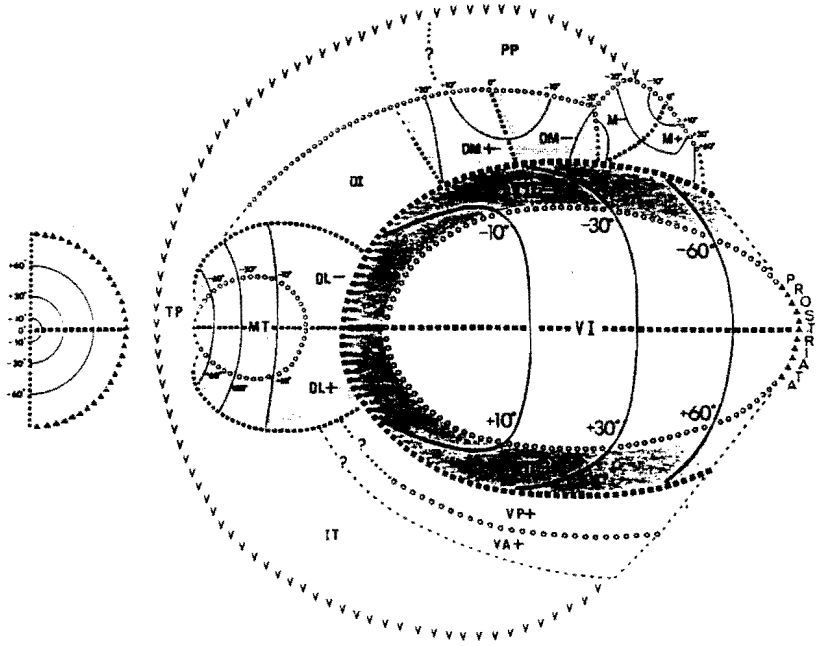


Fig. 33. A schematic unfolding of the visual cortex of the left hemisphere in the owl monkey. The visual cortex corresponds to approximately the posterior third of the entire neocortex. The unfolded visual cortex is approximately a hemispherical surface, which is viewed from above in this diagram. The perimeter chart on the left shows the contralateral (right) half of the visual field. The "prostriata" is histologically and physiologically distinct from V-II. Symbols are the same as in Figure 31. [Sanides, 1970; Allman and Kaas, 1971b]. Reproduced from Allman, [1982], with permission.

input from area V-II, with lesser inputs from striate cortex, V3, V3A, VP, and parts of posterior parietal cortex [Colby et al, 1983; 1987]. In *Saimiri* there is a region in the same location on the medial wall that receives input from the peripheral visual field representation of striate cortex in a pattern corresponding to the visuotopic organization in area M [Martinez-Millan and Hollander, 1975; Allman and Kaas, 1976]. Area M has been reported not to receive input from striate cortex or area V-II in *Aotus*, but it does receive input from DM and posterior parietal cortex [Weller and Kaas, 1981]. Area M may be homologous with the "dorsal" area in *Galago*, which is located anterior to the lower field peripheral representation in V-II, and possesses a similar visuotopic organization and emphasis on periphery [Allman et al, 1979].

Medial area neurons have very transient responses, which suggests that this area may be related to the magnocellular system [Miezin et al, 1986]. Medial area neurons have average latencies that are slightly longer than in area MT (42 vs 33 milliseconds), which suggests that contrary to existing anatomical evidence there may be inputs from V-I and V-II in *Aotus*. Area M is unusual among cortical areas tested in *Aotus* in that most of its neurons respond preferentially to rapidly moving stimuli (>50° per second) [Baker et al, 1981]. Finally, area M is unique in that all of its outgoing projections terminate in cortical layers I, V, and VI [Graham et al, 1979], which are usually *feedback* connections (see Fig. 38, and below). Thus it appears that the main function of area M may be to modulate the activity of other areas, such as DM and posterior parietal cortex (PP). We hypothesize that area M may detect suddent movements in the periphery of the visual field and facilitate the corresponding parts of the visual field representation in other cortical areas resulting in a shift of attention to the novel stimulus. Neurons in posterior parietal cortex in *Macaca* are specifically facilitated when visual stimuli are presented in a position in the visual field upon which the monkey's attention has been directed [Robinson et al, 1978]. Lesions in this locality in humans produce visual neglect and the inaccurate localization of visual stimuli [Holmes and Horrax, 1919; Critchley, 1953].

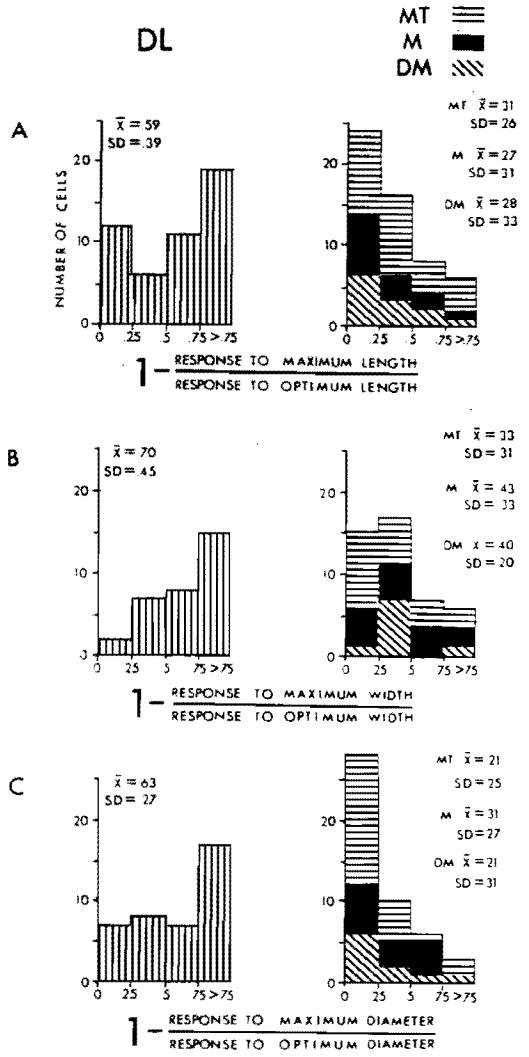
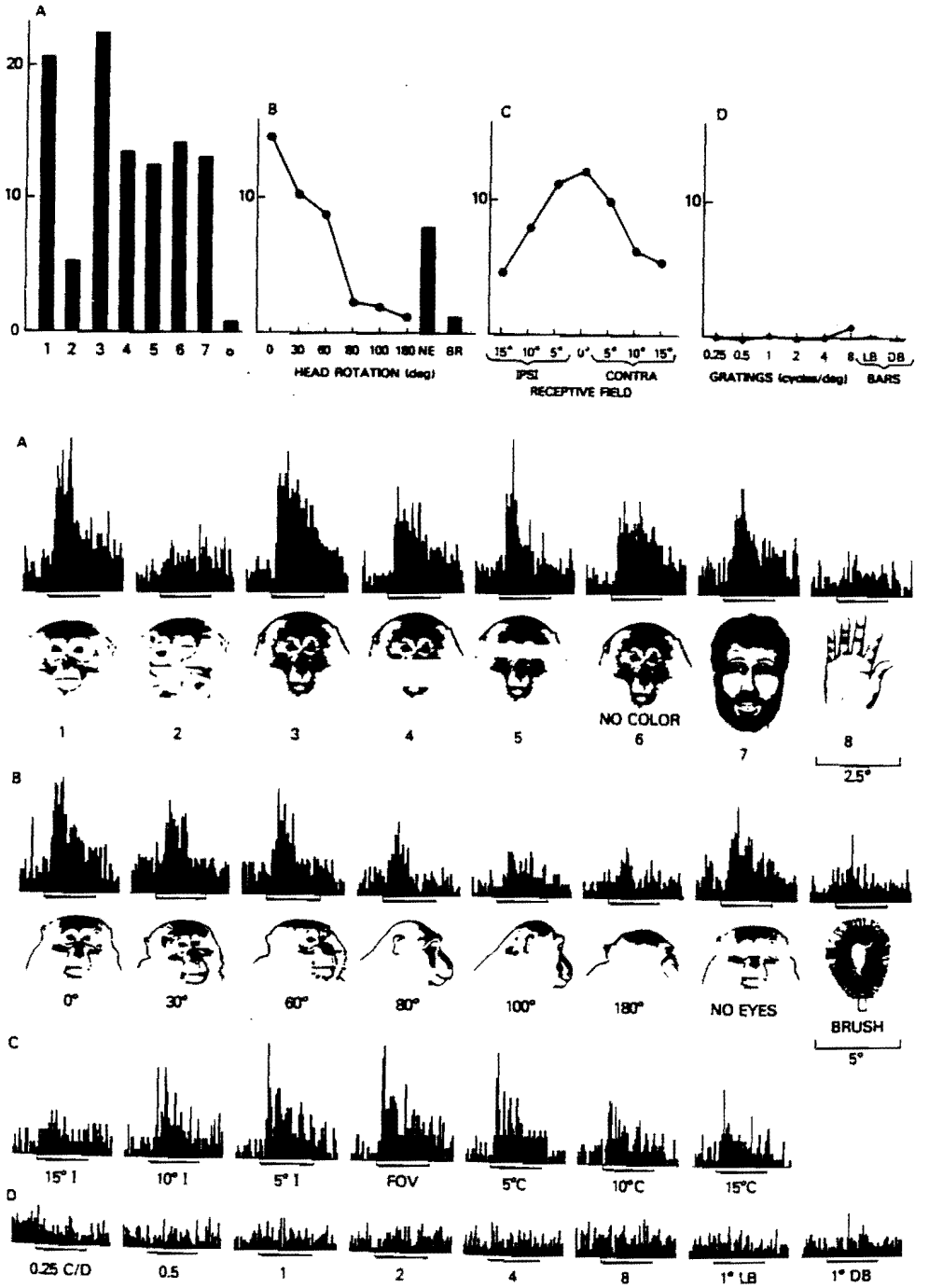


Fig. 34. Distributions of stimulus dimension selectivity indices for length (A), width (B), and spot diameter (C). The distributions for DL cells are on the left, and the distributions for MT, M, and DM cells are on the right. Statistics comparing these distributions; df for length = 3.94; width = 3.66; spot diameter = 3.81. S-values for length, width, and spot diameter selectivity, respectively: DL vs MT = 3.42,* 3.91,* 8.66*; DL vs M = 3.14,*1.53, 3.44*; DL vs DM = 2.76,*1.55,4.94*; MT vs M = 0.05, 0.21, 0.29; MT vs DM = 0.03, 0.07, 0.01; M vs DM = 0.01, 0.02, 0.21. *, $P < 0.05$. Reproduced from Petersen, et al [1980], with permission.

THE DORSOMEDIAL VISUAL AREA AND THIRD VISUAL AREA

The dorsomedial visual area (DM), like area MT, is a highly distinctive, densely myelinated zone in *Aotus* [Allman and Kaas, 1975]. DM receives input from striate cortex, area MT, and area M and projects to posterior parietal cortex [Lin et al, 1982; Wagor et al, 1975]. The responses of DM neurons are more sustained than neurons in areas MT and M, but more transient than in DL

Fig. 35. Responses of a unit that responded more strongly to faces than to any other stimulus tested. A) Comparison of responses to faces, to faces with components removed, and to a hand. Stimuli were photographic slides, presented for 2.5 sec, indicated by the bar under each histogram. All stimuli were centered on the fovea. Drawings under each histogram were traced from stimuli. 1, Monkey face in natural color; 2, same monkey face with components rearranged (four pieces); 3, second monkey face in color; 4, same monkey face with snout removed; 5, eyes removed; 6, color removed; 7, human face; 8, hand. The bar graph at top left indicates summed responses to each stimulus. Responses were computed from the firing rate of the unit during the stimulus presentation minus the average firing rate before the stimulus presentation. 0 represents the base line firing rate. Removing any component of the face reduced the response, while scrambling the components eliminated the response. B) Responses to a monkey face in different degrees of rotation. All stimuli were colored slides; other conditions were the same as in A. Responses decreased as the face was rotated from frontal to profile view. As in A, removing the eyes from the frontal view reduced the response. C) Responses to faces in different locations within receptive field. The stimulus was the same as in B (frontal view of face). The stimulus was centered on the horizontal meridian of the visual field. I, Ipsilateral visual field; C, contralateral visual field; FOV, fovea. The best response was to the stimulus positioned over the fovea. D) Responses to sine-wave gratings and bars. Gratings ranged from 0.25 to 8 cycles/degree, and bars were 0.1° wide. All stimuli had a vertical orientation. Gratings were drifted at 1 cycle/sec for 5 sec, and bars were moved at 1°/sec. Stimuli were generated on a 10° diameter CRT display. LB, Light bar; DB, dark bar. There was no response to either bars or gratings of any frequency. Reproduced from Desimone et al [1984], with permission.


A
20
10
0
1 2 3 4 5 6 7 o
B
10
0 30 60 80 100 180 NE BR
HEAD ROTATION (deg)
C
10
15° 10° 5° 0° 5° 10° 15°
IPSI
CONTRA
RECEPTIVE FIELD
D
10
0.25 0.5 1 2 4 8 LB DB
GRATINGS (cycles/deg)
BARS
A
1
2
3
4
5
NO COLOR
6
7
8
2.5°
B
0°
30°
60°
80°
100°
180°
NO EYES
BRUSH
5°
C
15° I
10° I
5° I
FOV
5°C
10°C
15°C
D
0.25 C/D
0.5
1
2
4
8
1° LB
1° DB

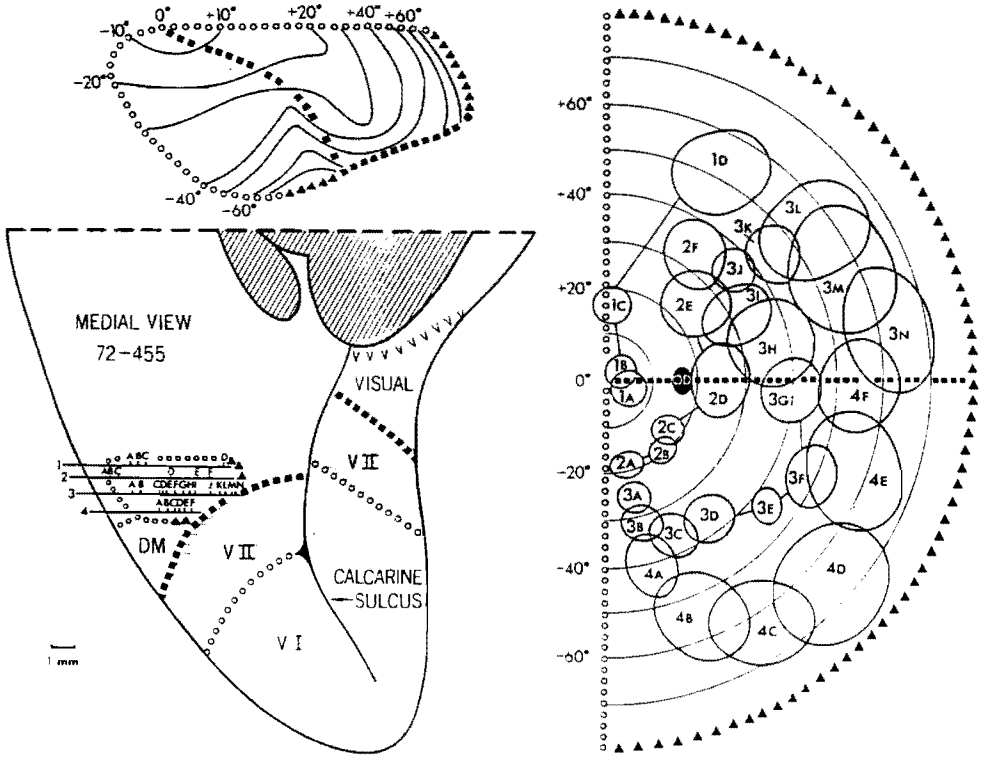


Fig. 36. Microelectrode recording penetrations and receptive field data for the medial visual area in owl monkey 72-455. The diagram on the lower left is a view of the posterior half of the medial wall of cerebral cortex of the left hemisphere with the brainstem and cerebellum removed. Anterior is up and dorsal is to the left in this diagram. Microelectrode penetrations are numbered, and recording sites are indicated by short bars denoted by letters. Scale = 1 mm. The corresponding receptive fields are shown in the perimeter chart on the right. In the upper left is an expanded map of the visuotopic organization of the medial area. The circles indicate the representation of the vertical meridian (midline) of the visual field; the squares indicate the horizontal meridian of the contralateral half of the visual field; the triangles indicate the temporal periphery of the contralateral hemifield. V I is the first visual area; V II is the second visual area; DM is the dorsomedial visual area. OD indicates the projection of the optic disk or blind spot. Reproduced from Allman and Kaas [1976], with permission.

[Petersen et al, 1986]. The average latencies of DM neurons are the same (42 milliseconds) as in area M [Miezin et al, 1986]. DM neurons are more sharply tuned for stimulus orientation than neurons in area MT, M, or DL. In *Macaca*, the third visual area (V3) is located in a similar position, is densely myelinated, and receives input from striate cortex [Felleman and Van Essen, 1986]. Area V3 differs from DM in that its visual field map is restricted to the lower visual field and its shape is more stretched out along its common border with the second visual area (see Fig. 32). Area V3's dense myelination and input from Brodmann's layer 4B in striate cortex links this area with the magnocellular system [Van Essen, 1985]. Adjacent to V3 is another area termed V3A [Van Essen and Zeki, 1978] that contains both an upper and lower visual field representation and may correspond to the dorso-intermediate visual area (DI) in *Aotus*. V3 was originally considered to extend along the entire anterior border of the second visual area in *Macaca* on the basis of striate projections [Zeki, 1969], but this is no longer consistent with available data [Van Essen, 1985].

THE VENTRAL AREAS

Following corpus callosum section in *Aotus* there is a clear-cut band of degeneration extending across the ventral surface of the anterior occipital lobe that corresponds to the vertical meridian representation separating the ventral posterior (VP) from the ventral anterior (VA) visual areas (see Figs. 31, 33, 37) [Newsome and Allman, 1980]. In the original studies of this region, all of the receptive fields were located in the upper field; however, in

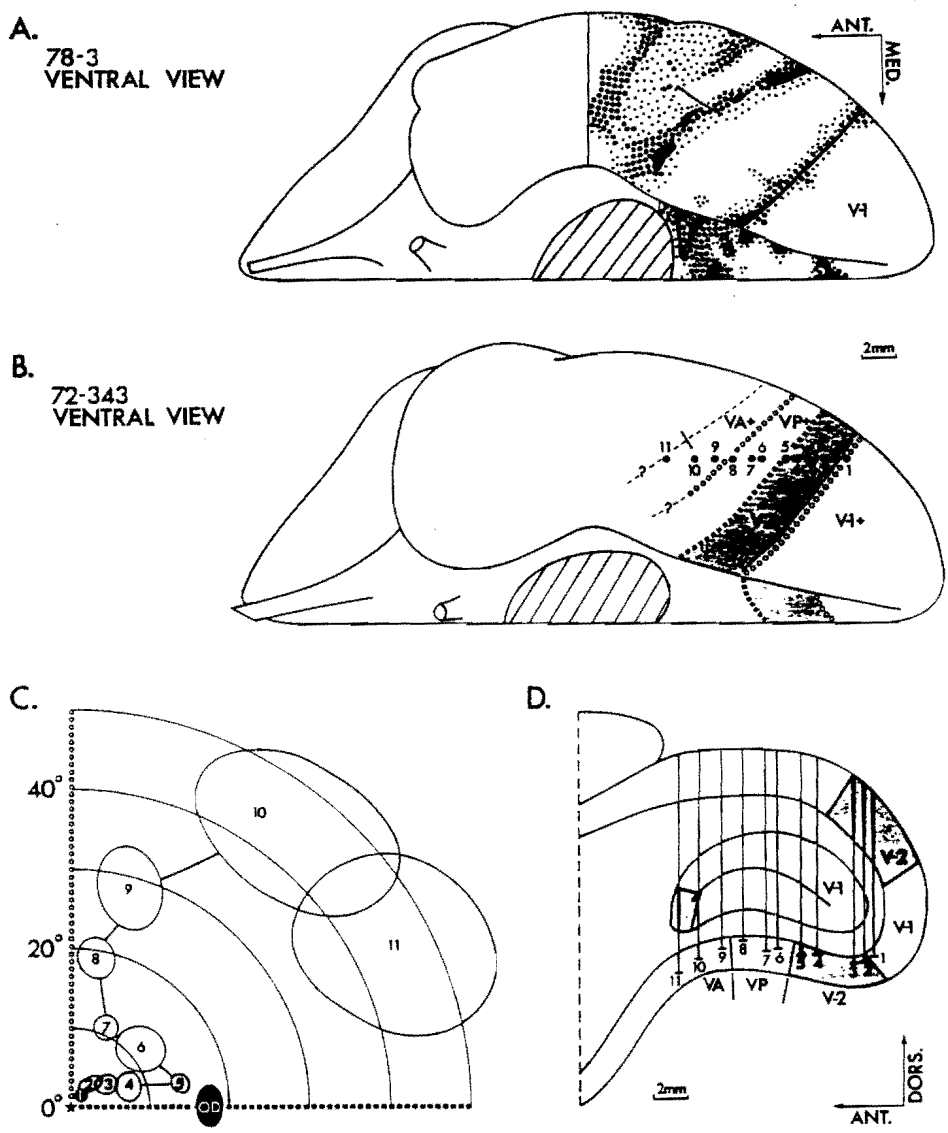


Fig. 37. Comparison of anatomical results with physiological data for the ventral surface of owl monkey visual cortex. A. The pattern of degeneration on the ventral surface of owl monkey 78-3. Heavy degeneration is solid black, moderate degeneration is represented by the large dots, and light degeneration by the small dots. B. Electrophysiological recording sites (1–14) on the ventral surface of owl monkey 72-343 (Allman and Kaas, unpublished observations). The location of the recording sites is based on a histological reconstruction of the electrode tracks superimposed on a photograph of the ventral surface taken postmortem. Open circles denote the vertical meridian representations and the solid squares signify the horizontal meridian representation. Dashed lines represent uncertain boundaries. Scale in A and B = 2 mm. C. Receptive fields for recording sites 1–11. The black receptive field is in VI, the gray-shaded receptive fields are in V2, and the unshaded receptive fields are in VP and VA. Note the progression of receptive fields from the horizontal meridian (recording site 5) at the V2- VP border to the vertical meridian (recording site 8) at the VP-VA border. D. Receptive fields for recording sites 12–14. Note the change in scale between C and D. Recording site 12, near the VP-VA boundary, yielded a receptive field very near the vertical meridian. The physiological representations of the vertical meridian illustrated in B appear remarkably similar to the distinct bands of callosal degeneration in A (solid arrows). The data of C and D also illustrate the progression from representation of the center-of-gaze laterally to representation of the periphery medially. OD, optic disk; VA, ventral anterior area; VP, ventral posterior area; V1, first visual area, or striate cortex; V2, second visual area. Reproduced from Newsome and Allman [1980], with permission.

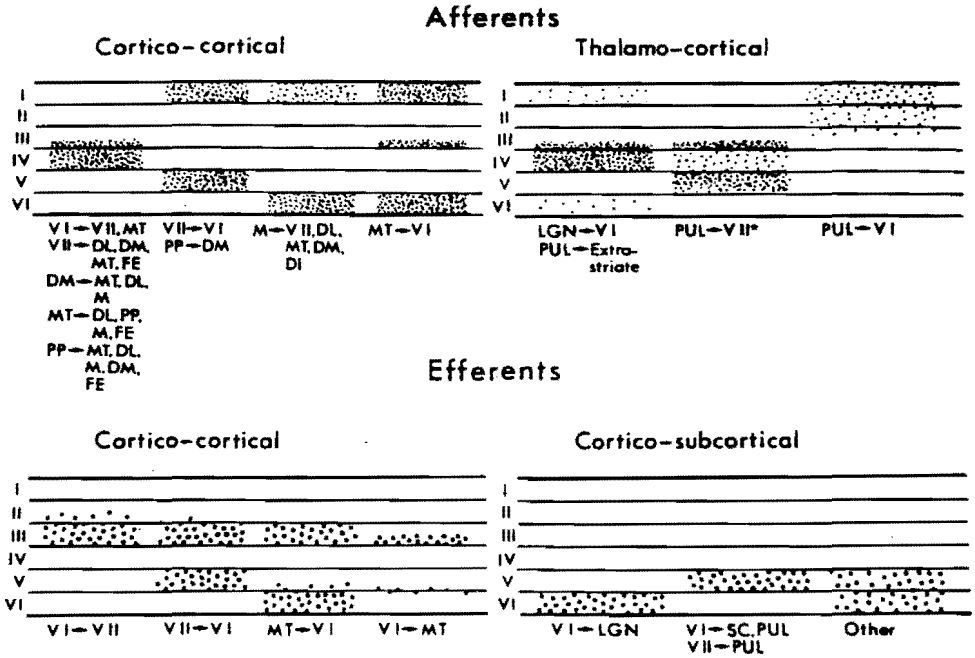


Fig. 38. Laminar patterns of afferent terminations and efferent neurons for visual areas of cortex. Small dots indicate projections into cortex; larger dots represent efferent cells of origin. Reproduced from Weller and Kaas [1981], with permission.

a more extensive mapping study in progress in our laboratory, there is evidence for a considerable region of lower field representation on the ventral surface [Sereno et al, 1986]. Following corpus callosum section in *Macaca* there also is a clear-cut line of degeneration extending across that lobe with a similarly organized ventral posterior area [Newsome et al, 1986]. It is not clear at present whether area VA is a separate representation or a ventral extension of the V4 complex.

Area VP, which has been considered to be a detached ventral part of V3 by some authors [Gattass et al, 1984; Ungerleider et al, 1983], differs from V3 in a number of significant respects [Van Essen, 1985]. First, V3 recives an input from striate cortex; VP does not [Burkhalter and Van Essen, 1983; Burkhalter et al, 1986]. Second, V3 is densely myelinated; VP is not [Van Essen, 1985; Felleman and Van Essen, 1986]. Third, corpus callosum connections crisply define the anterior border of VP, but not V3 [Van Essen, 1985]. Fourth, in quantitative studies of response properties, the incidence of color-selective neurons is three times as high (60%) in VP as in V3 (21%) [Burkhalter and Van Essen, 1982]; conversely the incidence of directionally selective cells is three times as high (40%) in V3 as in VP (13%) [Felleman and Van Essen, 1987].

The discovery of a high incidence of color-selective neurons in VP is particularly interesting in view of color-vision deficits resulting from ventral occipital lesions in humans. Damasio et al [1980] described a very carefully documented case of *hemiachromatopsia* resulting from such a lesion. Their patient "was unable to recognize or name any color in any portion of the left field of either eye, including bright reds, blues, greens and yellows. As soon as any portion of the colored object crossed the vertical meridian, he was able to recognize and accurately name its color. When an object such as a large red flashlight was held so that it was bisected by the vertical meridian, he reported that the hue of the right half appeared normal while the left half was gray. Except for the achromatopsia, he noted no other disturbance in the appearance of objects (i.e. objects did not change in size or shape, did not move abnormally, and appeared in correct perspective). Depth per-

ception in the colorless field was normal. The visual acuity was 20/20 in each eye." The patient had a small left upper visual field scotoma, but apart from this, had no other neurological abnormality. A CAT scan revealed a well-defined lesion due to a stroke in the ventral part of the right occipital lobe, primarily in extrastriate cortex. A similar case of hemiachromatopsia was reported by Verrey [1888] that resulted from a contralateral ventral occipital lesion confirmed by autopsy. Damasio et al [1980] concluded: "judging from case 1 and in Verrey's case, one single area in each hemisphere controls color processing of the entire hemifield. This is so regardless of the fact that such an area is eccentrically located, in the lower visual association cortex, classically related to *upper quadrant* processing only. The remarkable finding further supports the view that visual processing is organized in parallel, proceeding through specific and preassigned structures. The classic concept of a concentrically organized visual association cortex no longer appears tenable." Since a ventral lesion is unlikely to have damaged the lower field representation in V-II, it is probable that it affected an area containing both an upper and lower field representation anterior to V-II. These results suggest that one or more of the ventral areas contains a complete map of the visual field and is involved in the perception of color in humans.

THE LAMINAR CONNECTIONS OF ASCENDING AND DESCENDING SYSTEMS

Many authors have noted that the apparent direction of information flow in visual cortex is correlated with the lamina of origin of the neurons and the lamina of termination in the target area [Tigges et al, 1977; Rockland and Pandya, 1979; Weller and Kaas, 1981; Maunsell and Van Essen, 1983b]. In general, ascending projections originate in layers II and III and terminate in layer IV of the target area; feedback projections tend to avoid layer IV and prefer layers I and VI; layer V projects subcortically; layer VI is the source of feedback to lower areas (see Fig. 38). [The connections of area MT are a partial exception to these rules in that the projection arises from Brodmann's layer IVb and the deeper part of layer V and feedback from MT returns to these layers. This may reflect the anatomical and functional discreteness of this system. Some authors consider Brodmann's layer IVb to actually be part of layer III (Hasler, 1967; Spatz, 1975, 1977; Tigges et al, 1977; Weller and Kaas, 1981, and see Fig. 38; Diamond et al, 1985).] The visual cortex treats the amygdala as a higher cortical area; the projections from the inferior temporal cortex arise largely from layer III and the amygdalar projections back onto visual cortex terminate at the border between layers I and II [Amaral and Price, 1984].

EVOLUTION OF CORTICAL VISUAL AREAS

It has been proposed that new cortical areas resulted from major genetic mutations that produced replicas of preexisting areas, which was followed in subsequent generations by a series of minor mutations that produced the gradual divergence of structure and function of the replicated areas [Allman and Kaas, 1971a; see Allman, 1987, for review]. This general idea of genetic replications as a source of evolutionary novelty was first advanced by Bridges in 1918 as a result of gene mapping experiments in the giant chromosomes of *Drosophila*. Bridges [1935] later remarked: "In my first report on duplications at the 1918 meeting of the A.A.A.S., I emphasized the point that the main interest in duplications lay in their offering a method for evolutionary increase in lengths of chromosomes with identical genes which could subsequently mutate separated and diversify their effects." Lewis [1951] and Ohno [1970] extended this concept by pointing out that duplicated genes escape the pressure of natural selection operating on the original gene and thereby can accumulate mutations that enable the new gene to perform previously nonexistent functions, while the old gene continues to perform its original and presumably vital functions. It is now well documented that gene duplication is probably the most important mechanism for generating new genes and new biochemical processes [Britten and Kohne, 1968; Li, 1983]. It is likely that analogous processes have occurred in the evolution of the cortical visual areas. A number of cortical structures share similar anatomical location, connections, and visuotopic organization in different primate species and therefore are very likely to be homologous; nevertheless they may be functionally quite different. For example, in *Macaca* the cytochrome oxidase "blobs" and area VP are rich in color-selective processes, yet both structures are present in the nocturnal *Aotus*, where the color mecha-

nisms are unlikely to be well developed. A careful comparative examination of the response properties of neurons in these structures could reveal which functions these structures have in common and which have emerged since these structures originally developed in their common ancestor.

NEW METHODS FOR THE STUDY OF VISUAL CORTEX

Recently several powerful new methods, monoclonal antibody technology and positron emission tomography, have been applied to the study of the organization of visual cortex. These new methods promise to be particularly useful in studying the visual cortex in our own species.

Hockfield and colleagues [1983] have developed a monoclonal antibody (Cat-301) that binds to neurons at various levels in the magnocellular system in macaque monkeys, including the magnocellular laminae in the lateral geniculate nucleus, layer IVb in striate cortex, the thick stripes in the second visual area, and area MT [De Yoe et al, 1986]. Tootell and Hockfield [personal communication] have used Cat-301 binding in conjunction with staining for cytochrome oxidase activity and fibers to map the organization and extent of the thick stripes in V-II in human visual cortex obtained from autopsies.

McDonald, Thai, and Allman [1986] have developed monoclonal antibodies that selectively bind to fiber pathways associated with area MT in the owl monkey. These monoclonal antibodies were generated by using a differential immunosuppressive technique [Matthew and Patterson, 1983] in which mice were immunized with frontal cortex, followed by immunosuppression with cyclophosphamide, and then immunized with tissue from area MT. This approach suppressed common brain antigens and allowed for the selection of antigens specific to area MT. One particularly interesting monoclonal antibody (2E10) appears to be associated with the fiber pathway connecting MT with the ventral visual areas VP and VA. It is intriguing that thus far this differential immunosuppressive method has yielded only monoclonal antibodies that appear to bind mainly to fiber pathways rather than cortical neurons. This may be due to technical factors; however, it may also be that what is unique about a particular cortical area is its set of connections with other brain structures. Monoclonal antibodies potentially provide a powerful new way to map homologous systems of connections among cortical visual areas in different primate species, including our own.

Finally, the ability to map stimulus-evoked changes in local cerebral blood flow with positron emission tomography (PET scanning) has opened many new possibilities in the study of human visual cortex. An important feature of this technique is that local cerebral blood flow changes resulting from different stimulus conditions, as well as unstimulated control conditions recorded in the same experimental session, can be compared quantitatively. In an initial study of the retinotopic organization of primary visual cortex, a resolution of about 3 millimeters was achieved and the data revealed remarkable consistency in the cortical locations activated by retinotopic stimuli in all six subjects tested [Fox et al, 1986]. In this study macular stimulation also resulted in activation of a region on the lateral aspect of the occipital lobe, possibly corresponding to the conjunction of areas V4 and MT, and an additional focus in posterior parietal cortex that may be related to visual fixation [Fox et al, 1987]. A new scanner now being tested at Washington University may provide a significant improvement in resolution, possibly to the range of 1 to 2 millimeters. Thus it appears to be possible to map the retinotopic and functional organization of visual cortex in our own species.

ACKNOWLEDGMENTS

This work was supported by NIH grants EY-03851 and RR-07003.

REFERENCES

Aggleton, J.P.; Burton, M.J.; Passingham, R.E. Cortical and subcortical afferents to the amygdala of the rhesus monkey (*Macaca mulatta*). BRAIN RESEARCH 190:347–368, 1980.

Albright, T.D. Direction and orientation selectivity of neurons in visual area MT of the macque. JOURNAL OF NEUROPHYSIOLOGY 52:1106–1130, 1984.

Allman, J. Evolution of the visual system in the early primates. PROGRESS IN PSYCHOBIOLOGY AND PHYSIOLOGICAL PSYCHOLOGY 7:1–53, 1977.

Allman, J. Reconstructing the evolution of the brain in primates through the use of comparative neurophysiological and neuroanatomical data. Pp. 13–28 in PRIMATE BRAIN EVOLUTION. E. Armstrong; D. Falk, eds. New York, Plenum Press, 1982.

Allman, J. Maps in context: Some analogies between visual cortical and genetic maps. Pp. 369–393 in MATTERS OF INTELLIGENCE. L. Vaina, ed. Nihjot, Riedel, 1987.

Allman, J.M.; Campbell, C.B.G.; McGuinness, E. The dorsal third tier area in *Galago senegalensis*. BRAIN RESEARCH 179:355–361, 1979.

Allman, J.M.; Kaas, J.H. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). BRAIN RESEARCH 31:84–105, 1971a.

Allman, J.M.; Kaas, J.H. Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*). BRAIN RESEARCH 35:89–106, 1971b.

Allman, J.M.; Kaas, J.H. The organization of the second visual area (V-II) in the owl monkey: A second order transformation of the visual hemifield. BRAIN RESEARCH 76:247–265, 1974a.

Allman, J.M.; Kaas, J.H. A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). BRAIN RESEARCH 81:199–213, 1974b.

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

Allman, J.M.; Kaas, J.H. Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. SCIENCE 191:572–575, 1976.

Allman, J.M.; Kaas, J.H.; Lane, R.H. The middle temporal visual area (MT) in the bushbaby (*Galago senegalensis*). BRAIN RESEARCH 57:197–202, 1973.

Allman, J.; McGuinness, E. The organization of cortical visual areas in a strepsirhine primate, *Galago senegalensis*. SOCIETY FOR NEUROSCIENCE ABSTRACTS 9:957, 1983.

Allman, J.M.; Miezin, F.M.; McGuinness, E. Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). PERCEPTION 14:105–126, 1985.

Allman, J.M.; Miezin, F.M.; McGuinness, E. Stimulus selective responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. ANNUAL REVIEW OF NEUROSCIENCE 8:407–430, 1985b.

Amaral, D.G.; Price, J.L. Amygdalo-cortical projections in the monkey (*Macaca fascicularis*). JOURNAL OF COMPARATIVE NEUROLOGY 230: 465–496, 1984.

Baker, J.F.; Petersen, S.E.; Newsome, W.T.; Allman, J.M. Response properties in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*): A quantitative comparison of medial, dorsomedial, dorsolateral, and middle temporal areas. JOURNAL OF NEUROPHYSIOLOGY 45:397–416, 1981.

Bridges, C. B. Salivary chromosome maps. JOURNAL OF HEREDITY 26:60–64, 1935.

Britten, R.J.; Kohne, D.E. Repeated sequences in DNA. SCIENCE 161:529–540, 1968.

Brodmann, K. VERGLEICHENDE LOKALISATIONSLEHRE DER GROSSHIRNRINDE. Leipzig, Barth Press, 1909.

Bruce, C.; Desimone, R.; Gross, C. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. JOURNAL OF NEUROPHYSIOLOGY 46:369–384, 1981.

Brzin, M.; Sketelj, J.; Klinar, B. Cholinesterases. Pp. 251–292 in HANDBOOK OF NEUROCHEMISTRY. A. Lajtha, ed. New York, Plenum Press, 1982.

Burkhalter, A.; Van Essen, D.C. Processing of color, form, and disparity in visual areas V2 and VP of ventral extrastriate cortex in the macaque. SOCIETY FOR NEUROSCIENCE ABSTRACTS 8:811, 1982.

Burkhalter, A.; Van Essen, D.C. The connections of the ventral posterior area (VP) in the macaque monkey. SOCIETY FOR NEUROSCIENCE ABSTRACTS 9:153, 1983.

Burkhalter, A.; Felleman, D.J.; Newsome, W.T.; Van Essen, D.C. Anatomical and physiological asymmetries related to visual area V3 and VP in macaque extrastriate cortex. VISION RESEARCH 26:63–80, 1986.

Carey, R.; Fitzpatrick, D.; Diamond, I.D. Layer 1 of striate cortex of *Tupaia glis* and *Galago senegalensis*: Projections from thalamus and claustrum revealed by retrograde transport of horeseradish peroxidase. JOURNAL OF COMPARATIVE NEUROLOGY 186:393–438, 1979.

Cartmill, M. Arboreal adaptations and the origin of the order Primates. Pp. 97–212 in THE FUNCTIONAL AND EVOLUTIONARY BIOLOGY OF PRIMATES. R. H. Tuttle, ed. Chicago, Aldine, Atherton Press, 1972.

Casagrande, V.A.; Harting, J.K. Transneuronal transport of tritiated fucose and proline in the visual pathways of the tree shrew, *Tupaia glis*. BRAIN RESEARCH 96:367–372, 1975.

Casagrande, V.A.; Skeen, L.C. Organization of ocular dominance columns in galago demonstrated by autoradiographic and deoxyglucose methods. SOCIETY FOR NEUROSCIENCE ABSTRACTS 6:315, 1980.

Clutton-Brock, T.H.; Harvey, P.H. Primates, brains and ecology. JOURNAL OF ZOOLOGY (LONDON) 190:309–321, 1980.

Colby, C.L.; Gattass, R.; Olson, C.R.; Gross, C.G. Cortical afferents to visual area PO in the macaque. SOCIETY FOR NEUROSCIENCE ABSTRACTS 9:152, 1983.

Colby, C.L.; Gattass, R.; Olson, C.R.; Gross, C.G.

Topographic organization of cortical afferents to extrastriate visual area PO in macaque: A dual tracer study. In press in JOURNAL OF COMPARATIVE NEUROLOGY, 1987.

Conley, J.M. Notes on the activity pattern of *Lemur fulvus*. JOURNAL OF MAMMALOGY 56:712–715, 1975.

Conley, M.; Fitzpatrick, D.; Diamond, I.T. The laminar organization of the lateral geniculate body and the striate cortex in the tree shrew (*Tupaia glis*). JOURNAL OF NEUROSCIENCE 4:171–198, 1984.

Covey, E.; Gattass, R.; and Gross, C.G. A new visual area in the parieto-occipital sulcus of the macaque. SOCIETY FOR NEUROSCIENCE ABSTRACTS 9:152, 1983.

Cowey, A. Projection of the retina onto striate and prestriate cortex in the squirrel monkey, *Saimiri sciureus*. JOURNAL OF NEUROPHYSIOLOGY 27:366–696, 1964.

Cragg, B.G.; Ainsworth, A. The topography of the afferent projections in circumstriate visual cortex of the monkey studied by the Nauta method. VISION RESEARCH 9:733–747, 1969.

Critchley, M. THE PARIETAL LOBES. E. Arnold & Co., London, 1953.

Cusick, C.G.; Gould H.J. III; Kaas, J.H. Interhemispheric connections of visual cortex of owl monkeys (*Aotus trivirgatus*), marmosets (*Callithrix jacchus*), and galagos (*Galago crassicaudatus*). JOURNAL OF COMPARATIVE NEUROLOGY 230:311–336, 1984.

Damasio, A.R.; Damasio, H.; Van Hoesen, G.W. Prosopagnosisa: Anatomic basis and behavioral mechanisms. NEUROLOGY 32:331–341, 1982.

Damasio, A.; Yamada, T.; Damasio, H.; Corbett, J.; McKee, J. Central achromatopsia: Behavioral, anatomic, and physiologic aspects. NEUROLOGY 30:1064–1071, 1980.

Daniel, P.M.; Whitteridge, D. The representation of the visual field on the cerebral cortex in monkeys. JOURNAL OF PHYSIOLOGY (LONDON) 159:203–221, 1961.

DeBruyn, E.J.; Casagrande, V.A. Demonstration of ocular dominance columns in a new world primate by means of monocular deprivation. BRAIN RESEARCH 207:453–458, 1981.

Derrington, A.M.; Krauskopf, J.; Lennie, P. Chromatic mechanisms in lateral geniculate nucleus of macaque. JOURNAL OF PHYSIOLOGY 357:241–265, 1984.

Derrington, A.M., Lennie, P. Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. JOURNAL OF PHYSIOLOGY 357:219–240, 1984.

Desimone, R.; Albright, T.D.; Gross, C.G.; Bruce, C. Stimulus-selective properties of inferior temporal neurons in the macaque. JOURNAL OF NEUROSCIENCE 4:2051–2062, 1984.

Desimone, R.; Fleming, J.; Gross, C.G. Prestriate afferents to inferior temporal cortex: An HRP study. BRAIN RESEARCH 184:41–55, 1980.

Desimone, R.; Schein, S.J. Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. JOURNAL OF NEUROPHYSIOLOGY 57:835–868, 1987.

Desimone, R.; Ungerleider, L. Multiple visual areas in the caudal superior temporal sulcus of the macaque. JOURNAL OF COMPARATIVE NEUROLOGY 248:164–189, 1986.

De Valois, R.L.; Morgan, H.C.; Polson, M.C.; Mead, W.R.; Hull, E.M. Psychophysical studies of monkey vision. I. Macaque luminosity and color vision tests. VISION RESEARCH 14:53–67, 1974a.

De Valois, R.L.; Morgan, H.C.; Snodderly, M. Psychophysical studies of monkey vision. III. Spatial luminance contrast sensitivity tests of macaque and human observers. VISION RESEARCH 14:75–81, 1974b.

DeYoe, E.A.; Garren, H.; Hockfield, S.; Van Essen, D.C. CAT-301 antibody identified distinct areas and subdivisions in macaque extrastriate cortex. SOCIETY FOR NEUROSCIENCE ABSTRACTS 12:130, 1986.

DeYoe, E.A.; Van Essen, D.C. Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. NATURE 317:58–61, 1985.

Diamond, M.T.; Conley, M.; Itoh, K.; Fitzpatrick, D. Laminar organization of geniculocortical projections in *Galago senegalensis* and *Aotus trivirgatus*. JOURNAL OF COMPARATIVE NEUROLOGY 242:610, 1985.

Dow, B.M. Functional classes of cells and their laminar distribution in monkey visual cortex. JOURNAL OF NEUROPHYSIOLOGY 37:927–946, 1974.

Dow, B.M.; Vautin, R.G.; Bauer, RA. The mapping of visual space onto foveal striate cortex in the macaque monkey. JOURNAL OF NEUROSCIENCE 5:890–902, 1985.

Dreher, B.; Fukada, Y.; Rodieck, R.W. Identification, classification and anatomical segregation of cells with X-like and Y-like properties in the lateral geniculate nucleus of old-world primates. JOURNAL OF PHYSIOLOGY 258:433–452, 1976.

Felleman, D.J.; Van Essen, D.C. Cortical connections of area V3 in macaque extrastriate cortex. SOCIETY FOR NEUROSCIENCE ABSTRACTS 10:933, 1984.

Felleman, D.J.; Van Essen, D.C. Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. JOURNAL OF NEUROPHYSIOLOGY 57:889–920, 1987.

Fisken, R.A.; Garey, L.J.; Powell, T.P.S. Patterns of degeneration after intrinsic lesions of the visual cortex (area 17) of the monkey. BRAIN RESEARCH 53:208–213, 1973.

Fitzpatrick, D.; Carey, R.G.; Diamond, I.T. The pro-

jection of the superior colliculus upon the lateral geniculate nucleus in *Tupaia glis* and *Galago senegalensis*. BRAIN RESEARCH 194:494–499, 1980.

Fitzpatrick, D.; Diamond, I.T. Distribution of acetylcholinesterase in the geniculo-striate system of *Galago senegalensis* and *Aotus trivirgatus*: Evidence for the origin of the reaction product in the lateral geniculate body. JOURNAL OF COMPARATIVE NEUROLOGY 194:703–719, 1980.

Fitzpatrick, D.; Itoh, K.; Diamond, I.T. The laminar organization of the lateral geniculate body and the striate cortex in the squirrel monkey *Saimiri sciureus*. JOURNAL OF NEUROSCIENCE 3:673–702, 1983.

Fitzpatrick, D.; Lund, J.S.; Blasdel, G.G. Intrinsic connections of macaque striate cortex: Afferent and efferent connections of lamina 4C. JOURNAL OF NEUROSCIENCE 5:3329–3349,1985.

Florence, S.L.; Casagrande, V.A. A note on the evolution of ocular dominance columns in primates. INVESTIGATIVE OPHTHALMOLOGY SUPPLEMENT, pp. 291–292, 1978.

Florence, S.L.; Conley, M.; Casagrande, V.A. Ocular dominance columns and retinal projections in the New World spider monkey, *Ateles ater*. JOURNAL OF COMPARATIVE NEUROLOGY 243:234–248, 1986.

Fox, P.; Miezin, F.; Allman, J.; Van Essen, D.; Raichle, M. Retinotopic organization of human visual cortex mapped with positron emission tomography. JOURNAL OF NEUROSCIENCE 7:913–922, 1987.

Fox, P.; Miezin, F.; Raichle, M.; Allman, J. Superior parietal cortical activation during visual and oculomotor tasks measured with averaged PET images. ARVO ABSTRACTS, SUPPLEMENT TO INVESTIGATIVE OPHTHALMOLOGY 28(3):315, 1987.

Gattass, R.; Gross, C.G. Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the macaque. JOURNAL OF NEUROPHYSIOLOGY 46:621–638, 1981.

Gattass, R.; Sousa, A.P.B.; Covey, E. Cortical visual areas of the macaque: Possible substrates of pattern recognition mechanisms. Pp. 1–20 in PATTERN RECOGNITION MECHANISMS. C. Chagas; R. Gattass; C. Gross, eds. Vatican City, Pontificiae Academiae Scientiarum Scripta Varia, 1984.

Glendenning, K.K.; Kofron, E.A.; Diamond, I.T. Laminar organization of projections of the lateral geniculate nucleus to the striate cortex in *Galago*. BRAIN RESEARCH 105:538–546, 1976.

Graham, J.; Wall, J.; Kaas, J.H. Cortical projections of the medial visual area in the owl monkey. NEUROSCIENCE LETTERS 15:109–114, 1979.

Graybiel, A.M.; C.W. Ragsdale Jr. Pseudocholinesterase staining in the primary visual pathway of the macaque monkey. NATURE 299:439–442, 1982.

Gross, C.G. Inferotemporal cortex and vision. PROGRESS IN PHYSIOLOGICAL PSYCHOLOGY 5:77–115, 1973.

Gross, C.G.; Rocha-Miranda, C.E.; Bender, D.B. Visual properties of neurons in inferotemporal cortex of the macaque. JOURNAL OF NEUROPHYSIOLOGY 35:96–111, 1972.

Gurche, J.A. Early primate brain evolution. Pp. 227–246 in PRIMATE BRAIN EVOLUTION. E. Armstrong; D. Falk, eds. New York, Plenum Press, 1982.

Haenny, P.E.; Maunsell, J.H.R.; Schiller, P. State dependent activity in monkey visual cortex: II Retinal and extraretinal factors in V4. EXPERIMENTAL BRAIN RESEARCH, submitted.

Harting, J.K.; Diamond, I.T.; Hall, W.C. Anterograde degeneration study of the cortical projection of the lateral geniculate and pulvinar nuclei in the tree shrew (*Tupaia glis*). JOURNAL OF COMPARATIVE NEUROLOGY 148:361–386, 1973.

Harting J.K.; Huerta, M.F.; Franfurter, A.J.; Strominger, N.L.; Royce, G.J. Ascending pathways from the monkey superior colliculus: An autoradiograhic analysis. JOURNAL OF COMPARATIVE NEUROLOGY 192:853–882, 1980.

Hassler, R. Comparative anatomy of the central visual systems in day- and night-active primates. Pp. 410–434 in EVOLUTION OF THE FOREBRAIN. R. Hassler; H. Stephan, eds. New York, Plenum Press, 1967.

Hendrickson, A.E.; Tigges, M. Enucleation demonstrates ocular dominance columns in Old World macaque but not in New World squirrel monkey visual cortex. BRAIN RESEARCH 333:340–344, 1985.

Hendrickson, A.E.; Wilson, J.R. A difference in ^{14}C deoxyglucose and autoradiographic patterns in striate cortex between *Macaca* and *Saimiri* monkeys following monocular stimulation. BRAIN RESEARCH 170:353–358, 1979.

Hendrickson, A.E.; Wilson, J.R.; Ogren, M.P. The neuroanatomical organization of pathways between the dorsal lateral geniculate nucleus and visual cortex in New and Old World primates. JOURNAL OF COMPARATIVE NEUROLOGY 182:123–136, 1978.

Hershkovitz, P. LIVING NEW WORLD MONKEYS (PLATYRHINI). University of Chicago Press, 1977.

Hess, D.T.; Rockland, K.S. The distribution of cholinesterase and cytochrome oxidase within the dorsal lateral geniculate nucleus of the squirrel monkey. BRAIN RESEARCH 289:322–325, 1983.

Hicks, T.P.; Lee, B.B.; Vidyasagar, T.R. The responses of cells in macaque lateral geniculate nucleus to sinusoidal gratings. JOURNAL OF PHYSIOLOGY 337:183–200, 1983.

Hitchcock, P.F.; Hickey, I.L. Ocular dominance columns: Evidence for their presence in humans. BRAIN RESEARCH 182:176–179,1980.

Hockfield, S.; McKay, R.D.; Hendry, S.H.C.; Jones,

E.G. A surface antigen that identifies ocular dominance columns in the visual cortex and laminar features of the lateral geniculate nucleus. COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY 48:877–889, 1983.

Holmes, G. Disturbances of vision by cerebral lesions. BRITISH JOURNAL OF OPHTHALMOLOGY 2:826, 1918.

Horton J.C. Cytochromes oxidase patches: A new cytoarchitectonic feature of monkey visual cortex. PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF LONDON B 304:199–253, 1984.

Horton, J.C.; Hedley-Whyte, E.T. Mapping of cytochrome oxidase patches and ocular dominance columns in human visual cortex. PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF LONDON B 304:255–262, 1984.

Hubel, D.H. An autoradiographic study of the retinocortical projections in the tree shrew (*Tupaia glis*). BRAIN RESEARCH 96:41–50, 1975.

Hubel, D.H., Wiesel, T.N.; LeVay, S. Functional architecture of area 17 in normal and monocularly deprived macaque monkeys. COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY 40:581–589, 1976.

Hubel, D.H.; Wiesel, T.N. Receptive fields and functional architecture of monkey striate cortex. JOURNAL OF PHYSIOLOGY (LONDON) 195:215–243, 1968.

Hubel, D.H.; Wiesel, T.N. Laminar and columnar distribution of geniculo-cortical fibers in the macaque monkey. JOURNAL OF COMPARATIVE NEUROLOGY 146:421–450, 1972.

Hubel, D.H.; Wiesel, T.N. Distribution of inputs from the two eyes to striate cortex of squirrel monkeys. SOCIETY FOR NEUROSCIENCE ABSTRACTS 4:632, 1978.

Imig, T.; Roggero, M.; Kitzes, L.; Javel, E.; Brugge, J. Organization of auditory cortex in the owl monkey (*Aotus trivirgatus*). JOURNAL OF COMPARATIVE NEUROLOGY 171:111–128, 1977.

Inouye, T. DIE SEHSTORUNGEN BEI SCHUSSVERLETZUNGEN DER KORTIKALEN SEHSPARE, NACH BEOBACHTUNGEN AN VERWUNDETEN DER LETZTEN JAPANISCHEN KRIEGE. Leipzig, W. Engelmann, 1909.

Kaas, J.H.; Guillery, R.W.; Allman, J.M. Some principles of organization in the dorsal lateral geniculate nucleus. BRAIN, BEHAVIOR AND EVOLUTION 6:253–299, 1972.

Kaas, J.; Heurta M.F.; Weber, J.T.; Harting, J.K. Patterns of retinal terminations and laminar organization of the lateral geniculate nucleus of primates. JOURNAL OF COMPARATIVE NEUROLOGY 182:517–554, 1978.

Kaas, J.H.; Lin, C.-S. Cortical connections of area 18 in owl monkeys. VISION RESEARCH 17:739–741, 1977.

Kaas, J.H.; Lin, C.S.; Casagrande, V.A. The relay of ipsilateral and contralateral retinal input from the lateral geniculate nucleus to striate cortex in the owl monkey: A transneuronal transport study. BRAIN RESEARCH106:371–378, 1976.

Kaplan, E.; Shapley, R.M. X and Y cells in the lateral geniculate nucleus of macaque monkeys. JOURNAL OF PHYSIOLOGY 330:125–143, 1982.

Kushner, M.; Rosenquist, A.; Alavi, A.; Reivich, M.; Greenberg, J.; Cobbs, W. Macular and peripheral visual field representation in the striate cortex demonstrated by positron emission tomography. ANNUAL REVIEW OF NEUROLOGY 12:89, 1982.

Kuypers, H.G.; Szwarcbart, M.K.; Mishkin, M.; Rosvold, H.E. Occipitotemporal corticocortical connections in the rhesus monkey. EXPERIMENTAL NEUROLOGY 11:245–262, 1965.

Land, E.H.; Hubel, D.H.; Livingstone, M.S.; Perry, S.H.; Burns, M.M. Colour-generating interactions across the corpus callosum. NATURE 303:616–618, 1983.

Leonard, C.M.; Rolls, E.T.; Wilson, F.A.W.; Baylis, G.C. Neurons in the amygdala of the monkey with responses selective for faces. BEHAVIORAL BRAIN RESEARCH 15:159–176, 1985.

Leuret, F.; Gratiolet, P. ANATOMIE COMPAREE DU SYSTEME NERVOUX CONSIDEREE DANS SES RAPPORTS AVEC L'INTELLIGENCE. Paris, J.B. Bailliere and Fils, 1857.

LeVay, S.; Hubel, D.H.; Wiesel, T.N. The pattern of ocular dominance columns in macaque visual cortex revealed by a reduced silver stain. JOURNAL OF COMPARATIVE NEUROLOGY 159:559–576, 1975.

LeVay, S.; Wiesel, T.N.; Hubel, D.H. The development of ocular dominance columns in normal and visually deprived monkeys. JOURNAL OF COMPARATIVE NEUROLOGY 191:1–51, 1980.

LeVay, S.; Connolly, M.; Houde, J.; Van Essen, D.C. The complete pattern of ocular dominance stripes in the striate cortex of the macaque monkey. JOURNAL OF NEUROSCIENCE 5:486–501, 1985.

Lewis, E.B. Pseudoallelism and gene evolution. COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY 16:159–174, 1951.

Li, W.H. Evolution of duplicate genes and pseudogenes. In EVOLUTION OF GENES AND PROTEINS. M. Nei; R.K Koehn, eds. Sunderland, Massachusetts, Sinauer Associates, 1983.

Lin, C.-S.; Weller, R.E.; Kaas, J.H. Cortical connections of striate cortex in the owl monkey. JOURNAL OF COMPARATIVE NEUROLOGY 211:165–176, 1982.

Livingstone, M.S.; Hubel, D.H. Thalamic inputs to cytochrome oxidase-rich regions in monkey visual cortex. PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCE USA 79:6098–6101, 1982.

Livingstone, M.S.; Hubel, D.H. Anatomy and physiology of a color system in the primate visual cortex. JOURNAL OF NEUROSCIENCE 4:309–356, 1984.

Lund, J.S.; Lund, R.D.; Hendrickson, A.E.; Bunt, A.H.; Fuchs, A.F. The origin of efferent pathways from the primary visual cortex, area 7, of the macaque monkey as shown by retrograde transport of horseradish peroxidase. JOURNAL OF COMPARATIVE NEUROLOGY 164:287–305, 1975.

Maguire, W.M.; Baizer, J.S. Visuotopic organization of the prelunate gyrus in rhesus monkey. JOURNAL OF NEUROSCIENCE 4:1690–1704, 1984.

Malpeli, J.G.; Baker, F.H. The representation of the visual field in the lateral geniculate nucleus of *Macaca mulatta*. JOURNAL OF COMPARATIVE NEUROLOGY 161:569–594, 1975.

Martin, R.D. Phylogenetic aspects of prosimian behavior. Pp. 45–77 in THE STUDY OF PROSIMIAN BEHAVIOR. G.A. Doyle; R.D. Martin, eds. New York, Academic Press. 1979.

Martinez-Milan, L.; Hollander, H. Cortical-cortical projections from striate cortex of the squirrel monkey (*Saimiri sciureus*). A radio-autographic study. BRAIN RESEARCH 83:405–417, 1975.

Masland, R.H.; Mills, J.W.; Cassidy, C. The functions of acetylcholine in the rabbit retina. PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON B 223:121–139, 1984.

Matthew, W.D.; Patterson, P.H. The production of a monoclonal antibody that blocks the action of a neurite outgrowth-promoting factor. SYMPOSIA ON-QUANTITATIVE BIOLOGY 48:625–631, 1983.

Maunsell, J.H.R. Physiological evidence for two visual subsystems. In MATTERS OF INTELLIGENCE. L. Vaina, ed. Nijhot, Riedel, 1986.

Maunsell, J.H.R.; Schiller, P.H. Evidence for the segregation of parvo- and magnocellular channels in the visual cortex of the macaque monkey. SOCIETY OF NEUROSCIENCE ABSTRACTS 10:520, 1984.

Maunsell, J.H.R.; Van Essen, D.C. Functional properties of neurons in middle temporal visual area (MT) of macaque monkey. I. Selectivity for stimulus direction, velocity and orientation. JOURNAL OF NEUROPHYSIOLOGY 49:1127–1167, 1983a.

Maunsell, J.H.R.; Van Essen, D.C. The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. JOURNAL OF NEUROSCIENCE 3:2563–2586, 1983b.

McDonald, C.; McGuinness, E.; Allman, J. Laminar distribution of acetylcholinesterase and cytochrome oxidase in the dorsal lateral geniculate nucleus of *Lemur fulvus*. INVESTIGATIVE OPHTHALMOLOGY 26:163, 1985.

McDonald, C.T.; Thai, T.; Allman, J.M. Immunocytochemical characterization of monoclonal antibodies generated against striate cortex and the visual area MT of primates. SOCIETY FOR NEUROSCIENCE ABSTRACTS: 12:131, 1986.

McGuinness, E.; Allman, J. Organization of the visual system in tarsiers. AMERICAN JOURNAL OF PHYSIAL ANTHROPOLOGY 66:200, 1985.

McGuinness, E.; McDonald, C.; Sereno, M.; Allman, J. Primates without blobs: The distribution of cytochrome oxidase activity in striate cortex in tarsius, hapalemur, and cheirogaleus. SOCIETY FOR NEUROSCIENCE ABSTRACTS: 12:130, 1986.

Meadows, J.C. The anatomical basis of prosopagnosia. JOURNAL OF NEUROLOGY, NEUROSURGERY, AND PSYCHOLOGY 37:489–501, 1974a.

Meadows, J.C. Disturbed perception of colours associated with localized cerebral lesions. BRAIN 97:615–632, 1974b.

Menzel,C.R. Head-cocking and visual perception in primates. ANIMAL BEHAVIOR 28:151–159, 1980.

Merzenich, M.; Kaas, J.; Sur, M.; Lin, C. Doulb representation of the body surface within cytoarchitectonic areas 3b and 1 in SI in the owl monkey (*Aotus trivirgatus*). JOURNAL OF COMPARATIVE NEUROLOGY 181:41–74, 1978.

Miezin, F.M.; Petersen, S.E.; Allman, J.M. Segregation of information flow in four extrastriate areas of the owl monkey. ARVO ABSTRACTS, SUPPLEMENT TO INVESTIGATIVE OPTHALMOLOGY AND VISUAL SCIENCE, 28(3):124, 1986.

Mishkin, M. A memory system in the monkey. PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF LONDON B 298:85–90, 1982.

Mitzdorf, UA.; Singer, W. Excitatory synaptic ensenble properties in the visual cortex of the macaque monkey: A current source density analysis of electrically evoked potentials. JOURNAL OF COMPARATIVE NEUROLOGY 187:71–84, 1979.

Mizuno, N.; Kuniko, U.; Nomura, S.; Nakamura, Y.; Sugimoto, T.; Uemura-Sumi, M. Extrageniculate projections to the visual cortex in the macaque monkey. An HRP study. BRAIN RESEARCH 212:454–459, 1981.

Moran, J.; Desimone, R.; Schein, S.J.; Mishkin, M. Suppression from ipsilateral visual field in area V4 of the macaque. SOCIETY FOR NEUROSCIENCE ABSTRACTS 9:957, 1983.

Moran, J.; Desimone, R. Selective attention gates visual processing in the extrastriate cortex. SCIENCE 229:782–784, 1985.

Movshon, J.A.; Newsome, W.T. Functional character-

istics of striate cortical neurons projecting to MT in the macaque. SOCIETY FOR NEUROSCIENCE ABSTRACTS 10:933, 1984.

Movshon, J.A.; Adelson, E.H.; Gizzi, M.S.; Newsome, W.T. The analysis of moving visual patterns. Pp. 117–151 in PATTERN RECOGNITION MECHANISMS. C. Chagas; R. Gattass; C. Gross, eds. New York, Springer, 1985.

Munk, H. Zur Physiologie der Grosshirnrinde. ARCH. F. PHYSIOL. (Du Bois-Reymond) p.455, 1881.

Myerson, J.; Manis, P.; Miezin, F.; Allman, J. Magnification in striate cortex and retinal ganglion cell layer of owl monkey: A quantitative comparison. SCIENCE 198:855–857, 1977.

Newsome, W.T.; Allman, J.M. The interhemispheric connections of visual cortex in the owl monkey, *Aotus trivirgatus*, and the bushbaby, *Galago senegalensis*. JOURNAL OF COMPARATIVE NEUROLOGY 194:209–234, 1980.

Newsome, W.T.; Maunsell, J.H.R.; and Van Essen, D.C. Ventral posterior visual area of the macaque: Visual topography and areal boundaries. JOURNAL OF COMPARATIVE NEUROLOGY 252:139–153, 1986.

Newsome, W.T.; Wurtz, R.H.; Dursteler, M.R.; Mikami, A. Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. JOURNAL OF NEUROSCIENCE 5:825–840, 1985.

Ohno, S. EVOLUTION BY GENE DUPLICATION. New York, Springer-Verlag, 1970.

Perrett, D.I.; Rolls, E.T.; Caan. W. Visual neurones responsive to faces in the monkey temporal cortex. EXPERIMENTAL BRAIN RESEARCH 47:329–342, 1982.

Perrett, D.I.; Smith, P.A.J.; Potter, D.D.; Mistlin, A.J.; Head, A.S.; Milner, A.D.; Jeeves, M.A. Neurons responsive to face in the temporal cortex: Studies of functional organization, sensitivity to identify, and relation to perception. HUMAN NEUROBIOLOGY 3:197–208, 1984.

Perrett, D.I.; Smith, P.A.J.; Mistlin, A.J.; Chitty, A.J.; Head, A.S.; Potter, D.D.; Broennimann, R.; Milner, A.D.; Jeeves, M.A. Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: A preliminary report. BEHAVIORAL BRAIN RESEARCH 16:153–170, 1985a.

Perrett, D.I,; Smith, P.A.J.; Potter, D.D.; Mistlin, A.J.; Head, A.S.; Milner, A.D.; Jeeves, M.A. Visual cells in the temporal cortex sensitive to face view and gaze orientation. PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON B 233:293–317, 1985b.

Perry, V.H.; Oehler, R.; Cowey, A. Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. NEUROSCIENCE 12:1101–1123, 1984.

Petersen, S.E.; Baker, J.F.; Allman, J.M. Directional selectivity of neurons in the dorsolateral visual area of the owl monkey. BRAIN RESEARCH 197:507–511, 1980.

Poggio, G. Processing of stereoscopic information in primate visual cortex. Pp. 613–625 in DYNAMIC ASPECTS OF NEOCORTICAL FUNCTION. M. Cowan, ed.————, ————,1984.

Poggio, G.F.; Motter, B.C.; Squatrito, S. Trotter, Y. Responses of neurons in visual cortex (VI and V2) of the alert macaque to dynamic random-dot stereograms. VISION RESEARCH 25; 397–406, 1985.

Polyak, S. THE VERTEBRATE VISUAL SYSTEM. Chicago, University of Chicago Press, 1957.

Price, J.L.; Amaral, D.G. An autoradiographic study of the projections of the central nucleus of the monkey amygdala. JOURNAL OF NEUROSCIENCE 1:1242–1259, 1981.

Radinsky, L.B. The oldest primate endocast. AMERICAN JOURNAL OF PHYSIOLOGY AND ANTHROPOLOGY 27:385–388, 1967.

Radinsiky, L.B. The fossil evidence of prosimian brain evolution. Pp. 209–224 in THE PRIMATE BRAIN. C.R. Noback; W. Montagna, eds. New York, Appleton-Century-Crofts,1970.

Robinson, D.L.; Goldberg, M.E.; Stanton, G.B. Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. JOURNAL OF NEUROPHYSIOLOGY 41:910–932,1978.

Rockland, K.S.; Pandya, D.N. Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. BRAIN RESEARCH :3–20, 1979.

Rowe, M.H.; Benevento, L.A.; Rezak, M. Some observations on the patterns of segregated geniculate inputs to the visual cortex in new world primates: An autoradiographic study. BRAIN RESEARCH 159:371–378, 1978.

Sanghera, M.K.; Rolls, E.T.; Roper-Hall, A. Visual responses of neurons in the dorsolateral amygdala of the alert monkey. EXPERIMENTAL NEUROLOGY 63:610–626,1979.

Sanides, F. Functional architecture of motor and sensory cortices in primates in the light of a new concept of neocortex evolution. Pp. 137–208 in THE PRIMATE BRAIN. C. Noback and W. Montagnau, eds. New York, Appleton-Century-Crofts, 1970.

Schaefer, E.A. Experiments on special sense localizations in the cortex cerebri of the monkey. BRAIN 10:362, 1888.

Schaefer, E.A. Experiments on the electrical excitation of the visual area of the cerebral cortex in the monkey. BRAIN 11:1, 1889.

Schiller, P.H.; Malpeli, J.G. Functional specialty of lateral geniculate nucleus laminae of the rhesus monkey. JOURNAL OF NEUROPHYSIOLOGY 41:788–797:1978.

Sereno, M.I.; McDonald, C.T.; Allman, J.M. Organization of extrastriate cortex in the owl monkey. SOCIETY FOR NEUROSCIENCE ABSTRACTS: 12:1181, 1986.

Sereno, M.I.; McDonald, C.T.; Allman, J.M. Multiple visual areas between V2 and MT in the owl monkey. In press in SOCIETY FOR NEUROSCIENCE ABSTRACTS 13, 1987.

Sherman, S.M.; Koch, C. The anatomy and physiology of gating retinal signals in the mammalian lateral geniculate nucleus. MIT AI LABORATORY MEMO 825, 1985.

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

Shipp, S.; Zeki, S. Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. NATURE 325:322–325, 1985.

Simons, E.L. PRIMATE EVOLUTION. New York, Macmillan, 1972.

Spatz, W.B. An efferent connection of the solitary cells of Meynert. A study with horseradish peroxidase in the marmoset *Callithrix*. BRAIN RESEARCH 92:450–455, 1975.

Spatz, W.B. DER VISUELLE BEREICH DER GROSSHIRNRINDE. Unpublished Dissertation. Frankfurt, Johann Wolfgang Goethe-Universitat, 1977.

Spatz, W.B. Topographically organized reciprocal connections between areas 17 and MT (visual area of superior temporal sulcus) in the marmoset *Callithrix jacchus*. EXPERIMENTAL BRAIN RESEARCH 27:559–572, 1977.

Spatz, W.B. The retino-geniculo-cortical pathway in *Callithrix*. II. The geniculo-cortical projection. EXPERIMENTAL BRAIN RESEARCH 36:401–410, 1979.

Spatz, W.B.; Tigges, J. Experimental-anatomical studies on the "middle temporal visual area (MT)" in primates. I. Efferent corticocortical connections in the marmoset *Callithrix jacchus*. JOURNAL OF COMPARATIVE NEUROLOGY 146:451–464, 1972.

Spatz, W.B.; Tigges, J.; Tigges, M. Subcortical projections, cortical associations, and some intrinsic interlaminar connections of the striate cortex in the squirrel monkey (*Saimiri*). JOURNAL OF COMPARATIVE NEUROLOGY 158:155–174,1970.

Stephan H.; Andy, O.J. The allocortex in primates. Pp. 109–135 in THE PRIMATE BRAIN. C.R. Noback; W. Montegna, eds. New York, Appleton-Century-Crofts, 1970.

Symonds, L.L.; Kaas, J.H. Connections of striate cortex in the prosimian, *Galago senegalensis*. JOURNAL OF COMPARATIVE NEUROLOGY 181:477–512, 1978.

Talbot, S.A. A lateral localization in cat's visual cortex. FEDERATION PROCEEDINGS 1:84, 1941.

Talbot, S.A.; Marshall, W.H. Physiological studies on neural mechanisms of visual localization and discrimination. AMERICAN JOURNAL OF OPHTHALMOLOGY 24:1255, 1941.

Tattersall, I. THE PRIMATES OF MADAGASCAR. New York, Columbia University Press, 1982.

Thompson, J.M.; Woolsey, C.N., Talbot, S.A. Visual areas I and II of cerebral of rabbit. JOURNAL OF NEUROPHYSIOLOGY 12:277–288, 1950.

Tigges, J.; Tigges, M. Ocular dominance columns in the striate cortex of chimpanzee (*Pan troglodytes*). BRAIN RESEARCH 166:386–390, 1979.

Tigges, J.; Spatz, W.B.; Tigges, M. Efferent corticocortical fiber concentrations of area 18 in the squirrel monkey (*Saimiri*). JOURNAL OF COMPARATIVE NEUROLOGY 158:219–236, 1974.

Tigges, J.; Tigges, M.; Kalaha, C.S. Efferent connections of area 17 in *Galago*. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 38:393–398, 1973.

Tigges, J.; Tigges, M.; Perachio, A.A. Complementary laminar terminations of afferents to area 17 originating in area 18 and the lateral geniculate nucleus in squirrel monkey. JOURNAL OF COMPARATIVE NEUROLOGY 176:87–100, 1977.

Tigges, J.; Walker, L.C.; Tigges, M. Subcortical projections to the occipital and parietal lobes of the chimpanzee brain. JOURNAL OF COMPARATIVE NEUROLOGY 220:106–115.

Tigges, J.; Tigges, M.; Anschel, S.; Cross, N.A.; Letbetter, W.D.; McBride, R.L. Areal and laminal distribution of neurons interconnecting the central visual cortical areas 17, 18, 19, and MT in squirrel monkey (*Saimiri*). JOURNAL OF COMPARATIVE NEUROLOGY 202:539–60, 1981.

Tigges, J.; Tigges, M.; Cross, N.A.; McBride, R.L.; Letbetter, W.D.; Anschel, S. Subcortical structures projecting to visual cortical areas in squirrel monkey. JOURNAL OF COMPARATIVE NEUROLOGY 209:29–40.

Tootell, R.B.H. FUNCTIONAL ANATOMY OF MACAQUE STRIATE CORTEX. Unpublished dissertation. Berkeley, University of California, 1985.

Tootell, R.B.H.; Hamilton, S.L.; Silverman, M.S. Topography of cytochrome oxidase activity in owl monkey cortex. JOURNAL OF NEUROSCIENCE 5:2786–2800, 1985.

Tootell, R.B.H.; Silverman, M.S.; De Valois, R.L.; Jacobs, G.H. Functional organization of the second cortical visual area in primates. SCIENCE 220:737–739, 1983.

Tootell, R.B.H.; Silverman, M.S.; Switkes, E.; De Valois, R.L. The organization of cortical modules in primate striate cortex. SOCIETY FOR NEUROSCIENCE ABSTRACTS 12:707, 1982.

Turner, B.M.; Mishkin, M.; Knapp, M. Organization

of the amygdalopetal projections from modality-specific cortical association areas in the monkey. JOURNAL OF COMPARATIVE NEUROLOGY 191:515–543, 1980.

Ungerleider, L.G.; Desimone, R. Cortical connections of visual area MT in the macaque. JOURNAL OF COMPARATIVE NEUROLOGY 248:190–222, 1986.

Ungerleider, L.G.; Gattass, R.; Sousa, A.P.B.; Mishkin, M. Projections of area V2 in the macaque. SOCIETY FOR NEUROSCIENCE ABSTRACTS 9:152, 1983.

Ungerleider, L.G.; Mishkin, M. The striate projection zone in the superior temporal sulcus of *Macaca mulatta*: Location and topographic organization. JOURNAL OF COMPARATIVE NEUROLOGY 188:347–366, 1979.

Van Essen, D.C. Functional organization of primate visual cortex, Pp. 259–329 in CEREBRAL CORTEX, VOLUME 3, A. Peters; E.G. Jones, eds. New York, Plenum Press, 1985.

Van Essen, D.C.; Maunsell, J.H.R.; Bixby, J.L. The middle temporal visual area in the macaque: Myeloarchitecture, connections, functional properties and topographic organization. JOURNAL OF COMPARATIVE NEUROLOGY 199:293- 326, 1981.

Van Essen, D.C.; Newsome, W.T.; Maunsell, J.H.R. The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability. VISION RESEARCH 24:429–448, 1984.

Van Essen, D.C; Zeki, S.M. The topographic organization of rhesus monkey prestriate cortex. JOURNAL OF PHYSIOLOGY 277:193–226, 1978.

Verrey, D. Hemiachromatopsie droite absolue. ARCHIVES DE OPHTHALMOLOGIE (Paris). 8:289–300, 1888.

Wagor, E,; Lin, C.-S.; Kaas, J.H. Some cortical projections of the dorsomedial visual area (DM) of association cortex in the owl monkey, *Aotus trivirgatus*. JOURNAL OF COMPARATIVE NEUROLOGY. 163:227–250, 1975.

Wall, J.T.; Symonds, L.L.; Kaas, J.H. Cortical and subcortical projections of the middle temporal area (MT) and adjacent cortex in Galagos. JOURNAL OF COMPARATIVE NEUROLOGY 211:193–214, 1982.

Weller, R.E. SUBDIVISIONS AND CONNECTIONS OF INFERIOR TEMPORAL CORTEX IN OWL MONKEYS. Doctoral dissertation. Nashville, Vanderbilt University, 1982.

Weller, R.E.; Kaas, J.H. Cortical and subcortical connections of visual cortex in primates. Pp. 121–155 in CORTICAL SENSORY ORGANIZATION. C.N. Woolsey, ed. Englewood Cliffs, New Jersey, Humana Press, 1981.

Weller, R.E.; Kaas, J.H. Retinotopic patterns of connections of area 17 with visual areas V-II and MT in macaque monkeys. JOURNAL OF COMPARATIVE NEUROLOGY 220:253–279, 1983.

Weller, R.E.; Kaas, J.H. Cortical projections of the dorsolateral visual area in owl monkeys: The prestriate relay to inferior temporal cortex. JOURNAL OF COMPARATIVE NEUROLOGY 234:35–59, 1985.

Weller, R.E.; Wall, J.T.; Kaas, J.H. Cortical connections of the middle temporal visual area (MT) and the superior temporal cortex in owl monkeys. JOURNAL OF COMPARATIVE NEUROLOGY 228:81–104, 1984.

Whitlock, D.G.; Nauta, W.J.H. Subcortical projections from the temporal neocortex in the *Macaca mulatta*. JOURNAL OF COMPARATIVE NEUROLOGY 106:183–212, 1956.

Wiesel, T.N.; Hubel, D.H. Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. JOURNAL OF NEUROPHYSIOLOGY 29:1115–1118, 1966.

Wiesel, T.N.; Hubel, D.H.; Lam, D.M.K. Autoradiographic demonstration of ocular dominance columns in the monkey striate cortex by means of transneuronal transport. BRAIN RESEARCH 79:273–279, 1974.

Wong-Riley, M.T.T. Changes in the visual system of monocularly sutured or enucleated cats demonstrable with cytochrome oxidase histochemistry. BRAIN RESEARCH 171:11–28, 1979.

Zeki, S.M. Representative of central visual fields in prestriate cortex of monkey. BRAIN RESEARCH 14:167–176, 1969.

Zeki, S.M. Convergent input from the striate cortex (area 17) to the cortex of the superior temporal sulcus in the rhesus monkey. BRAIN RESEARCH 28:338–340, 1971.

Zeki, S.M. Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. JOURNAL OF PHYSIOLOGY (LONDON) 236:549–573, 1974.

Zeki, S.M. Color coding in the superior temporal aulcus of rhesus monkey visual cortex. PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON B 197:195–223, 1977.

Zeki, S.M. Colour coding in the cerbral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. NEUROSCIENCE 9:741–765, 1983a.

Zeki, S.M. Colour coding in the cerebral cortex: The responses of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition. NEUROSCIENCE 9:767–781, 1983b.

The Su

Jon

Dep

In this ch
and functio
structures t
visual syste
enormous.
review. We
primate spe
available f
experiment
from resear
keys and fr
keys. The
physiologic
tures, but n
the lateral g
ulus, and th
visual struc
behavior, in
tion. We al
direct retin
matic" aspe
ber of struc
clearly visu
describe vis

THE LA

In primat
dorsal later
get of the r
input to visu
ered a relay
that LGN ne
input. In th