Visual Cortex in Primates

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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, *Tetomius homunculus*, are illustrated in Figure 1. *Tetomius* 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 *Tetomius* closely resemble living nocturnal prosimians (see Fig. 2). The cranial endocasts of *Tetomius* 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 differentiation 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).
Fig. 1. Left: dorsal view of the skull of *Teronius homunculus*. A.M.N.H. No. 4194. Right: dorsal view of Radinsky’s cranial endocast of *Teronius*. 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.
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.
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 = VI). 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. Brodman [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. Brodman [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 *a* 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*, *m*), the latter enveloping the external geniculate nucleus, with fiber fan of visual radiation (*m*) streaming toward the occipital lobe at right; *m*, 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 système nerveux (saisas)*, 1857. Pls. 26 and 27. Reproduced from Polyak, [1957], with permission.
Allman and McGuinness.

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. 6. Cell arrangement in the marginal portion of human striate cortex stained with Nissl-toluidine blue method (Lenhossek'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 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 Maupelli. 1979; 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 parvo-cellar 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 Maupelli. 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-

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

...visual behavior...
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 [McC-
**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 albibrons*, 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 *albibrons* 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 Hanmg [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, Cercopithecus, Atus); Spatz, [1979] (Callithrix); Tigges et al. [1979] (Pant); 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
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.

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.
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 ascending 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 14C-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, VI) 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 [3H]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 "inter-blob" 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, Felix, Tupai a, Or vicolagus, 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 [Tigges et al. 1981; 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; Fiskcn 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.

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.

developed horizontal fiber system in the stra 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.
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...
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 (ITd) [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
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.
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.

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-11 and the ventral posterior area (VP) and inferior temporal cortex, may be involved in these color constancy effects as well [Allman et al., 1985a].
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, 1974]. 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; ITc, inferotemporal-caudal; ITM, inferotemporal-medial; ITR, 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 PARIETO-OCCIPITAL 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
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 Holland, 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 target sudden 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].
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. 1. 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.
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 [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 V1, 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.
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 recieves 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 hemisphere. 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-IV, it is probable that it affected an area containing both an upper and lower field representation anterior to V-IV. 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 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.

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