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Variations in Visual Cortex Organization in Primates

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Abstract. There exist significant variations in the organization of the cortical visual areas in different primate species that may be related to behavioral specializations for nocturnality, diurnality, visual scanning, the perception of color and texture, and visual guidance of object manipulation.

PRIMATE EVOLUTION

The fossil remains of the earliest primates bearing a close resemblance to living primates have been recovered from early Eocene deposits 55 million years old (Simons 1972). These early primates possessed large bony orbits that completely encircled the eyes and a cranium containing a large brain compared to its similarly-sized contemporaries. The large size and position of the orbits in the early primates closely resemble living nocturnal prosimians. 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 1970). Studies in living primates 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 were probably parts of an adaptive complex that included: (a) frontally directed eyes; (b) an area of high acuity in the central retina; (c) a large field of binocular overlap; (d) a large ipsilateral projection from the retina to the lateral geniculate nucleus and the optic tectum; (e) the expansion of the representation of the central visual field in thalamic, tectal and cortical visual structures; (f) a laminated lateral geniculate nucleus in which the inputs from the two eyes are segregated in several sets of layers; (g) a representation in the optic tectum restricted to the contralateral half of the visual field; (h) the expansion and functional differentiation of primary visual cortex; (i) the expansion of extrastriate cortical visual areas and the probable elaboration of new visual areas; (j) the shift of the foramen magnum from a posterior to a more ventral position in the skull; (k) prehensile hands; (l) eye-hand coordination; (m) binocular convergence and accommodative focusing; and (n) fine-grained stereopsis (Allman 1977). 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.

The early primates were nocturnal or crepuscular and thus lived in a dimly illuminated environment (Allman 1977). At later stages in evolution primates began to fill diurnal niches and developed the capacity for color vision. Diurnal primates also tend to have much more complex systems of social organization than do nocturnal species. In diurnal primates, the visual system is particularly involved in the detection of the complex social signals imbedded in facial expressions, gestures, and postures that serve as the basis for much of primate social communication.

OCULAR DOMINANCE SYSTEMS AND VISUAL BEHAVIOR

One of the most striking variations in the organization of visual cortex in primates is the different patterns of input to layer IV of primary visual cortex. In galagos, spider monkeys, macaques, guenons, patas monkeys, baboons, chimpanzees, and humans, 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 ocular dominance columns (Florence et al. 1986, Kaas et al. 1978). The horizontal segregation of ocular inputs to layer IV of striate cortex is poorly developed or absent in owl monkeys, marmosets, squirrel monkeys, saki monkeys, and capuchins, all of which are New World monkeys (Florence et al. 1986). The ocular segregation in input has been found in all Old World primates tested thus far: in galagos, various monkeys, chimpanzees and humans, plus one New World primate, the spider monkey (Florence et al. 1986). 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. Head-cocking is particularly notable in young animals and follows a definite ontogenetic course. By contrast, galagos, spider monkeys, all Old World monkeys (except talapoins), apes, and humans rarely head-cock when regarding an object. Talapoins, the smallest Old World monkey, and various lemuroids 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)? 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 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 owl monkeys readily discriminate random dot stereograms with no monocular depth cues and thus possess 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 galagos, which are nocturnal, a component of this corticogeniculate feedback projection that terminates in the parvocellular laminae is rich in acetylcholinesterase. Fitzpatrick and Diamond (1980) found in galagos 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 galagos was not reduced by eliminating the retinal input. Similarly, they found that kainic acid injections into 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. In addition, they found acetylcholinesterase positive neurons in layer VI of striate cortex in galagos. Fitzpatrick and Diamond (1980) also found that the parvocellular laminae were more densely stained than the magnocellular laminae in owl monkeys, which also are nocturnal. The parvocellular laminae are also more densely stained than the magnocellular laminae in the nocturnal tarsiers (McGuinness and Allman 1985).

In contrast, Hess and Rockland (1983) discovered that acetylcholinesterase staining was denser in the magnocellular laminae than in the parvocellular laminae in squirrel monkeys, and suggested that the difference in laminar distribution was related to the diurnal activity pattern of this species as compared to the nocturnality of galagos and owl monkeys. In other diurnal primates as well, including macaques (Graybiel and Ragsdale 1982), marmosets, and humans (McGuinness, McDonald and Allman, unpublished observations), the magnocellular laminae are more densely stained for acetylcholinesterase than are the parvocellular laminae. The present evidence strongly suggests that the parvocellular laminae are rich in acetylcholinesterase in primates active at night and thus adapted to function in a dimly illuminated environment.

In contrast to the findings in galagos, Hess and Rockland (1983) found in macaques and squirrel monkeys that striate cortex lesions did *not* effect 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, which account for the background staining throughout the nucleus and perhaps denser staining in the magnocellular laminae in diurnal primates. These may arise from the brain stem 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 which 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). In primates 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.

VARIATIONS IN THE PATTERNS OF CYTOCHROME OXIDASE ACTIVITY IN THE FIRST AND SECOND VISUAL AREAS

The distribution of the mitochondrial enzyme, cytochrome oxidase, has provided an important guide to the functional architecture of visual cortex in primates. Staining for cytochrome oxidase activity reveals dense concentrations in Brodmann's layers IVa, IVc and VI in striate cortex, and a horizontally repeating pattern in layers II, III, V and VI (Horton 1984). This repeating pattern is most easily seen in tangential sections through the cortex that has been dissected away from the underlying white matter and flattened. The pattern in striate cortex is a relatively regular array of spots of high cytochrome oxidase activity, separated by a lattice of lower activity. In primates possessing ocular dominance stripes in striate cortex, such as macaque monkeys, the spots are centered on the stripes for each eye

(Horton 1984). The pattern in the second visual area (V-II) in tangential sections of flattened cortex is a series of thick stripes and thin stripes of high cytochrome oxidase activity, separated by pale stripes of lower activity that extend across the width of this belt-like area (Tootell et al. 1983). The thin stripes appear to be more prominent in diurnal squirrel monkeys than in nocturnal owl monkeys (Tootell et al. 1983, 1985).

In experiments conducted in macaque monkeys, the cytochrome oxidase pattern has been linked to functional architecture. In studies using ^{14}C-2-deoxyglucose (2DG) as a functional marker, Tootell (1985) found that stimulation with low spatial frequencies resulted in high 2DG uptake in the spots, while stimulation with high spatial frequencies resulted in high uptake in the surrounding lattice in striate cortex. This result has recently been confirmed and extended with optical recording techniques (Tootell and Blasdel 1987). Livingstone and Hubel (1984) found that the neurons in the cytochrome oxidase rich spots, which they term "blobs", lack orientation selectivity and project to the thin stripes of high cytochrome oxidase activity in V-II. By contrast, they found that the neurons in the "interblob" lattice are orientation selective and project to the pale stripes in area V-II. Both the electrophysiological recordings of Livingstone and Hubel and the 2DG studies of Tootell have found that the cytochrome oxidase rich spots are preferentially involved in color processing. Recently, Ts'o, Gilbert and Wiesel (1986) have found that individual cytochrome oxidase rich spots are dominated by cells of one particular opponent color class, either red-green or blue-yellow.

The spot-lattice pattern of cytochrome oxidase activity has also been found in the striate cortex of baboons and humans (Horton 1984). It appears to be absent in many prosimian primates including tarsiers, hapalemurs and dwarf lemurs (McGuinness et al. 1986), but is present in prosimian galagos (Horton 1984; McGuinness et al. 1986). It has thus far not been identified in any nonprimate tested including, rats, mice, ground squirrels, cats, tree shrews, rabbits, and mink (Horton 1984). 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 macaque monkeys, but the presence of well-defined spot-lattice systems in nocturnal primates such as galagos and owl monkeys indicates that the spots must be linked to functions other than color vision in these animals.

It is likely that the earliest primates lacked a differentiated spot-lattice system in striate cortex, since the system appears to be absent in a number of living prosimians and in all nonprimates tested thus far. The differentiated system probably developed in primitive members of the anthropoidea (ancestors of monkeys, apes and humans) in the early Oligocene period (ca. 40,000,000 years ago), since the system is present in all members of the anthropoidea tested thus far. It also appears to have developed independently in one group of prosimians: the galagos. The presence of the spot-lattice system in nocturnal species suggests that the basic functional differentation is not between streams of neural processing devoted to color and noncolor respectively, but rather between low and high spatial frequency or more simply between coarse and fine grained vision. The physiological evidence suggests that the spot system is devoted to perception of the coarse outlines of objects and shading, like a "rough sketch" of the retinal image done in charcoal. The lattice system is devoted to the perception of the fine grained detail, like that present in textured surfaces. Most of the time the system probably operates mainly in the coarse mode, emphasizing the information passing through the spots, but can shift to the fine grained detail of the lattice system; thus, the spots are metabolically more active and more densely stained for cytochrome oxidase activity. In diurnal primates, functions related to the perception of color are grafted onto a preexisting system devoted to shading that resides in the spots.

VARIATIONS IN THE ORGANIZATION OF HIGHER CORTICAL AREAS

The visual cortex anterior to the second area contains a large array of visual areas defined on the bases of visuotopic organization, connections, and functional specializations. Two of these areas, the middle temporal (MT) and the medial (M), are present in all primates tested thus far and appear to be relatively conservative in evolution. The neural responses in both of these areas are very transient and may represent higher levels in the system that involves the *magnocellular* laminae of the lateral geniculate nucleus, which is characterized by sensitivity to low contrast and fast conducting transient responses, and also appears to be relatively conservative in evolution. By contrast, the organization of higher cortical areas, apparently related to the stream of information relayed through the *parvocellular* laminae of the lateral geniculate nucleus, are much more variable. The parvocellular laminae are characterized by requiring higher contrast stimulation, and by slower and more sustained responses, which is also characteristic of area DL in New World monkeys and V4 in Old World monkeys. The variability in the organization of the parvocellular–dominated cortical areas such as DL and V4 parallels the considerable variability in the organization of the parvocellular laminae, which are related to the more phylogenetically advanced systems of color and fine detail (Hassler 1967; Kaas et al. 1978).

Middle temporal visual area. Area MT is a highly distinctive, densely myelinated region characterized by fast conducting, transient responses, sensitivity to low contrast stimuli, and a high proportion of directionally selective neurons (Allman and Kaas 1971; Baker et al. 1981; Miezin et al. 1987; Tootell 1985; Zeki 1974). The magnocellular laminae of the lateral geniculate nucleus project to layer IVc-alpha of striate cortex, which in turn projects to the adjacent layer IVb, which in turn projects to MT. An interesting difference in the organization of MT is revealed when visuotopic organization of this structure is projected back upon the visual field (Maunsell 1987). In galagos and owl monkeys this back projection is unremarkable; however, in macaque monkeys the back projection reveals a strikingly enlarged representation of the portion of the visual field extending from the center of gaze along 45° axes in the lower visual field, which corresponds to the position of the arms in the visual field when the hands are manipulating an object. Macaque monkeys manipulate objects with a precision grip utilizing the thumb and forefinger; galagos and owl monkeys lack the precision grip and grasp objects with the entire hand. Thus it is possible that this specialization in the visuotopic organization of MT in macaque monkeys is related to the visual guidance of the precision grip in object manipulation.

Medial visual area. The medial visual area (M) is unique among the cortical visual areas in owl monkeys in that it has a proportionally large representation of the peripheral visual field (Allman and Kaas 1976). Only 4% of area M is devoted to the representation of the central 10° of the visual field. In macaques 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 parietooccipital area (PO) (Covey et al. 1982). Area M is probably homologous with the "dorsal" area in galagos, 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. 1987). Area M is unusual among cortical areas tested in owl monkeys 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. 1980), which are usually *feedback* connections. 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 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 macaques are specifically facilitated when visual stimuli are presented in a position in the visual field upon which the monkeys's attention has been directed (Robinson et al. 1978). In other posterior parietal neurons, responses in the periphery of the visual field are facilitated when the monkey fixates straight ahead (Andersen and Mountcastle 1983). Lesions in this locality in humans produce visual neglect and the inaccurate localization of visual stimuli (Holmes and Horrax 1919).

Dorsomedial visual area and V3. The dorsomedial visual area (DM), like area MT, is a highly distinctive, densely myelinated zone, in *Aotus* (Allman and Kaas 1976). 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 (Miezin et al. 1987). DM neurons are more sharply tuned for stimulus orientations than neurons in area MT, M or DL (Baker et al. 1981). Our mapping of DM revealed an interesting case of variability in the organization of a cortical area within a species. In a series of ten owl monkeys, area DM had the same organization in nine, but in one owl monkey, area DM possessed two representations of the upper visual field, one in the normal location and a second in the place normally occupied by the lower field representation (Allman and Kaas 1976). The position of the receptive fields in the abnormal upper quadrant representation in this owl monkey were mirror symmetrical about the horizontal meridian with the normal lower quadrant representation. It was as though distance from the horizontal and vertical meridians was correctly represented, but in the upper as opposed to the normal lower half of the visual field. In macaques, the third visual area (V3) is located in a similar position, is densely myelinated, and receives input from striate cortex (Felleman and Van Essen 1984). 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 areas. In galagos, there appears to be no area corresponding to DM or V3 (Allman et al. 1979).

Ventral visual areas (VP and VA). Following corpus callosum section in owl monkeys, 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 (Newsome and Allman 1980). Following corpus callosum section in macaques, there is also a clear–cut line of degeneration extending across the ventral surface of the anterior occipital lobe with a similarly organized ventral posterior area. 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 receives an input from striate cortex; VP does not. Second, V3 is densely myelinated; VP is not. Third, corpus callosum connections crisply define the anterior border of VP, but not V3. Fourth, in quantitative studies of response properties, the incidence of color selective neurons is three times as high in VP (60%) as in V3 (21%); conversely, the incidence of directionally selective cells is three times as high in V3 (40%) as in VP (13%). 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 perception 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 no further 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. Verrey (1888) reported a similar case of hemiachromatopsia 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 for 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.

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REFERENCES

Allman, J. 1977. Evolution of the visual system in the early primates. In: Progress in Physiological Psychology, eds. J. Sprague and A. Epstein **7**: 1–53.

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

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

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

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

Andersen, R.A., and Mountcastle, V.B. 1983. The influence of angle of gaze upon the excitability of the light sensitive neurons of the posterior parietal cortex. *J. Neurosci.* **3**: 532–548.

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

Brzin, M.; Sketelj, J.; and Klinar, B. 1982. Cholinesterases. In: Handbook of Neurochemistry, ed. A. Lajtha, pp. 251–292. New York: Plenum.

Covey, E.; Gattass, R.; and Gross, C.G. 1982. A new visual area in the parieto-occipital sulcus of the macaque. *Soc. Neurosci. Abst.* **8**: 681.

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

Felleman, D.J., and Van Essen, D.C. 1984. Cortical connections of area V3 in macaque extrastriate cortex. *Soc. Neurosci. Abst.* **10**: 933.

Fitzpatrick, D., and Diamond, I.T. 1980. 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. *J. Comp. Neurol.* **194**: 703–719.

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

Gattass, R.; Sousa, A.P.B.; and Covey, E. 1984. Cortical visual areas of the macaque: possible substrates of pattern recognition mechanisms. In: Pattern Recognition Mechanisms, eds. C. Chagas, R. Gattass, and C. Gross, pp. 1–20. Vatican: Pontificiae Academiae Scientiarum Scripta Varia.

Graham, J.; Wall, J.; and Kaas, J.H. 1980. Cortical projections of the medial visual area in the owl monkey. *Neurosci. Lett.* **15**: 109–114.

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

Hassler, R. 1967. Comparative anatomy of the central visual system in day- and night- active primates. In: Evolution of the Forebrain, eds. R. Hassler and H. Stephan, pp. 410–434. New York: Plenum.

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

Holmes, G., and Horrax, G. 1919. Disturbances of spatial orientation and visual attention, wityh loss of stereoscopic vision. *Arch. Neurol. Psychiat.* **1**: 385.

Horton, J.C. 1984. Cytochrome oxidase patches: a new cytoarchitectonic feature of monkey visual cortex. *Phil. Trans. R. Soc. Lond.* **304**: 199–253.

Hubel, D.H., and Wiesel, T.N. 1968. Receptive fields and functional architecture of monkey striate cortex. *J. Physiol. (Lond.)* **195**: 215–243.

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

Kaplan, E., and Shapley, R.M. 1982. X and y cells in the lateral geniculate nucleus of macaque monkeys. *J. Physiol.* **330**: 125–143.

Lin, C.-S.; Weller, R.E.; and Kaas, J.H. 1982. Cortical connections of striate cortex in the owl monkey. *J. Comp. Neurol.* **211**: 165–176.

Livingstone, M.S., and Hubel, D.H. 1984. Anatomy and physiology of a color system in the primate visual cortex. *J. Neurosci.* **4**: 309–356.

Masland, R.H.; Mills, J.W.; and Cassidy, C. 1984. The functions of acetylcholine in the rabbit retina. *Proc. R. Soc. Lond. B* **223**: 121–139.

Maunsell, J.H.R. 1987. Representation of three-dimensional space in the cerebral cortex. *Can. J. Physiol. Pharmacol.*, in press.

Maunsell, J.H.R., and Schiller, P.H. 1984. Evidence for the segregation of parvo- and magnocellular channels in the visual cortex of the macaque monkey. *Soc. Neurosci. Abst.* **10**: 520.

McGuinness, E., and Allman, J.M. 1985. Organization of the visual system in tarsiers. *Am. J. Phys. Anthropol.* **66**: 200.

McGuinness, E.; McDonald, C.; Sereno, M.; and Allman, J.M. 1986. Primates without blobs: the distribution of cytochrome oxidase activity in Tarsius, Hapa lemur and Cheirogaleus. *Soc. Neurosci. Abst.* **12**: 130.

Menzel, C.R. 1980. Head-cocking and visual perception in primates. *Anim. Behav.* **28**: 151–159.

Miezin, F.M.; Petersen, S.E.; and Allman, J.M. 1987. Segregation of information flow in four extrastriate area of the owl monkey. *Arvo Abst.*, p. 124.

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

Radinsky, L.B. 1970. The fossil evidence of prosimian brain evolution. In: The Primate Brain, eds. C.R. Noback and W. Montagna, pp. 209–224. New York: Appleton-Century-Crofts.

Robinson, D.L.; Goldberg, M.E.; and Stanton, G.B. 1978. Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J. Neurophysiol.* **41**: 910–932.

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

Simons, E.L. 1972. Primate Evolution. New York: Macmillan.

Tootell, R.B.H. 1985. Functional Anatomy of Macaque Striate Cortex. Dissertation. Berkeley: Univ. of California.

Tootell, R.B.H., and Blasdel, G.G. 1987. In vivo demonstration of presumptive blob and interblob regions by manipulation of stimulus spatial frequency in macaque striate cortex. *Soc. Neurosci. Abst.* **13(1)**: 2.

Tootell, R.B.H.; Hamilton, S.L.; and Silverman, M.S. 1985. Topography of cytochrome oxidase activity in owl monkey cortex. *J. Neurosci.* **5**: 2786–2800.

Tootell, R.B.H.; Silverman, M.S.; De Valois, R.L.; and Jacobs, G.H. 1983.

Functional organization of the second cortical visual area in primates. *Science* **220**: 737–739.

Ts'o-, D.Y.; Gilbert, C.D.; and Wiesel, T.N. Relationships between color-specific cells in cytochrome oxidase rich patches of monkey striate cortex. *Soc. Neurosci. Abst.* **12**: 1497.

Ungerleider, L.G.; Gattass, R.; Sousa, A.P.B.; and Mishkin, M. 1983. Projections of area V2 in the macaque. *Soc. Neurosci. Abst.* **9**: 152.

Van Essen, D.C. 1985. Functional organization of primate visual cortex. In: Cerebral Cortex, eds. A. Peters and E.G. Jones, vol. 3, pp. 259–329. New York: Plenum.

Verrey, D. 1888. Hemiachromatopsie droite absolue. Archives de Ophthalmologie 8: 289–300.

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

Zeki, S.M. 1974. Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol. Lond.* **236**: 549–573.