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"The Subcortical Visual System of Primates"

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The Subcortical Visual System of Primates

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INTRODUCTION

In this chapter we review aspects of organization and function of some of the many subcortical structures that can be considered as parts of the visual system in primates (Fig. 1). The task is enormous, and we have necessarily limited the review. We describe visual structures in a range of primate species, but information is commonly often available for only the primates typically used in experimental investigations. Thus, most is known from research on a few species of macaque monkeys and from more limited work in squirrel monkeys. The review considers morphological and physiological aspects of a number of visual structures, but much of the review is concerned with the lateral geniculate nucleus, the superior colliculus, and the pulvinar complex, since these major visual structures are involved in complex visual behavior, including object vision and visual attention. We also discuss the visual structures with direct retinal inputs that mediate more "automatic" aspects of visual function, describe a number of structures that have connections with the clearly visual nuclei of the brainstem, and briefly describe visuomotor centers.

THE LATERAL GENICULATE NUCLEUS

Introduction

In primates, the lateral geniculate nucleus (the dorsal lateral geniculate nucleus) is the major target of the retina, and it is the primary source of input to visual cortex. As such, the LGN is considered a relay nucleus, but it is important to stress that LGN neurons not only relay but modify retinal input. In this section, we describe the laminar organization of the nucleus, connections, and neuron properties. We start by considering two notable aspects of the LGN in primates, the conspicuous lamination of the nucleus and the marked variability in the laminar pattern across primate species.

The Laminar Pattern

The lateral geniculate nucleus of all primates is laminated—ie, cells are grouped into slabs or layers that are stacked like slices of bread (Fig. 2). Layers are often, but not always, separated by narrow, cell-poor, interlaminar zones. The main layers occur in pairs, with each pair differing from other pairs by the sizes, connections, and response properties of the constituent neurons. One member of each pair receives input from the contralateral eye, and the other member is activated from the ipsilateral eye. A simplified LGN is shown in Figure 2. This schematic LGN closely corresponds to the rather simple pattern found in the New World owl monkey (*Aotus*), but the curvatures and the true proportions of the layers are not accurately portrayed by the illustration. In owl monkeys, the nucleus consists of two layers of medium-size cells (the parvocellular layers), two of large cells (the magnocellular layers), and two thin, poorly separated layers of small, pale-staining cells (the frequently ignored superficial or "S" layers). Subdivisions of the parvocellular layers complicate the laminar structure in anthropoid primates, while most prosimians have two additional layers of small cells, the koniocellular layers inserted between the parvocellular layers, and lack superficial layers. Each layer has the three-dimensional form of an oval slab. In monkeys, apes, and

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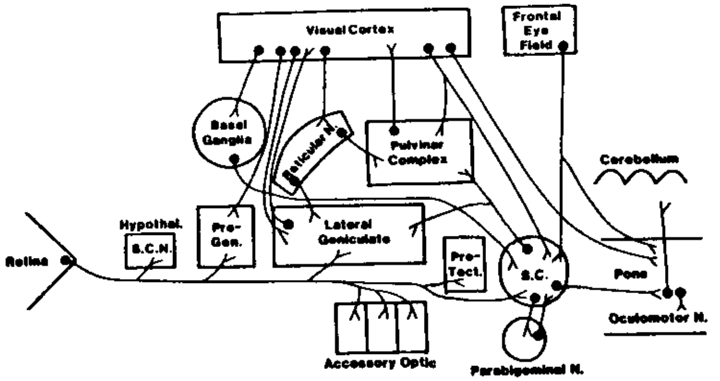

Fig. 1. An overview of some of the structures in the subcortical visual system of primates. The major retinal projection is to the (dorsal) lateral geniculate nucleus (LGN), and the next most significant target is to the superior colliculus (S.C.). The retina also projects to the suprachiasmatic nucleus (S.C.N.) of the hypothalamus, four pretectal nuclei, three nuclei that make up the accessory optic system, the pregeniculate (or ventral lateral geniculate) nucleus, and sometimes to part of the pulvinar complex. Connections with these structures and visual cortex involve parts of the basal ganglia, the pulvinar complex, parts of the thalamic reticular nucleus, the parabigeminal nucleus, parts of the pons, oculomotor nuclei, and ultimately part of the cerebellum in the subcortical visual system. The greatly simplified scheme of connections shown is for structures, and single neurons may not branch as shown. See text.

humans, the stack of layers is wrapped around a ventromedially located hilus, whereas in prosimians, the stack of layers is arranged more flatly.

The geniculate layers are distinguished by the types of input they receive from the retina (Fig. 2). The X-like ganglion cells, important in form vision (see below), project to the parvocellular layers; the Y-like ganglion cells, important in visual attention, project to the magnocellular layers; and small, W-like cells, of uncertain function, project to the interlaminar zones, the S layers, and the koniocellular layers. In addition, the three types of layers and the cells in the interlaminar zones project to distinct sublayers of cells in primary visual cortex (Fig. 7). Thus, the lamination and projections of the lateral geniculate nucleus segregate different types of retinal information (X, Y, and W) up to the cortical level.

The laminar pattern of the LGN varies considerably across primate families (Fig. 3). The lateral geniculate nucleus of all primates can be assumed to have evolved from a more generalized nucleus where cells of different types were mixed and where the only type of lamination was from the partial segregation of inputs from the ipsilateral eye in the middle of the nucleus from surrounding inputs from the contralateral eye; such a laminar pattern is apparent in a range of species of mammals with poorly developed visual systems [Kaas et al, 1972, 1978; Brauer, 1978]. This simple pattern gave rise to more complex patterns seen in the close relations of primates, the visual bats, flying lemurs, and tree shrews, and in the various primates, but the intermediate steps in the evolution of more complex laminar patterns are uncertain.

Much of the variability in laminar patterns in primates relates to differences in the parvocellular layers. The laminar pattern of the New World tamarins, marmosets, and owl monkeys includes two single parvocellular layers. However, in some individual marmosets, there is a slight tendency for parts of the external parvocellular layer to protrude into the internal parvocellular layer and vice versa. This tendency is much more pronounced in most other New World monkeys, so that the parvocellular layers partially divide and interdigitate. It has been common to consider these major protrusions as true layers, ignore the existence of the narrow S layers, and describe four parvocellular and two magnocellular layers for a total of six in the LGN of New World monkeys.

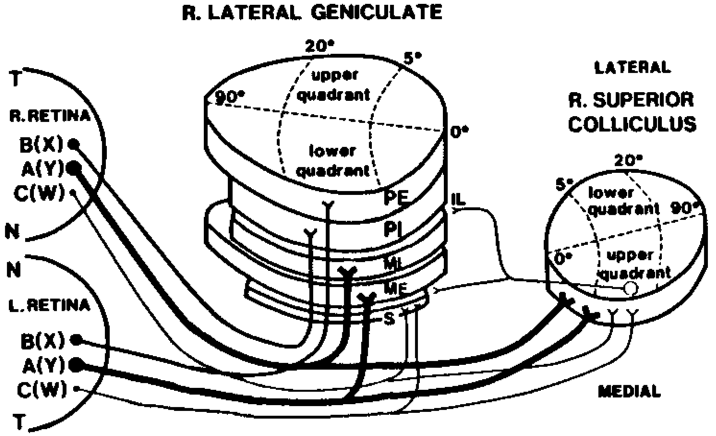

Fig. 2. A simplified schematic of the lateral geniculate nucleus of a monkey. Stacked layers represent the contralateral visual hemifield via projections from the ipsilateral or the contralateral eye. Much of each layer is devoted to central vision. (Note polar coordinates 5° and 20° from gaze.) The zero horizontal meridian (0–90°) separates the lateral representation of the upper quadrant from the medial representation of the lower quadrant. Most of the outer margins of the layers correspond to the zero vertical meridian through gaze (the line of retinal decussation). Layers with inputs from the contralateral eye extend somewhat more rostrally to represent the monocular crescent of the contralateral hemifield. The bulk of the nucleus consists of "internal" and "external" parvocellular layers (PI and PE) with inputs from the "primate beta" or "X-like" retinal ganglion cells with medium-size axons and conduction velocities. In most monkeys, the parvocellular layers subdivide and interdigitate in the caudal half of the nucleus. The smaller internal and external magnocellular layers (MI and ME) receive inputs from the "primate alpha" or "Y-like" ganglion cells with thick axons and fast conduction velocities. The superficial (S) layers and interlaminar zones of small cells receive "primate C" or "W-like" inputs via thin axons. The interlaminar zones also receive an indirect W-cell relay from the superior colliculus. Some, but apparently not all, of the Y-like input, and perhaps some of the W-like input to the superior colliculus, is via collaterals.

Because these protrusions are not complete layers but are clearly extensions of layers, we prefer to distinguish them as leaflets of layers rather than as layers [Kaas et al, 1972, 1978]. The significance of these leaflets or incomplete layers is uncertain. The parvocellular leaflets could have different functional roles [see Schiller and Malpeli, 1978] or they could simply reflect a developmental compromise between opposing tendencies of neurons from the same eye to terminate together and to terminate in specific locations [see Constantine-Paton, 1982, for general discussion]. The branching and interdigitation of the parvocellular mass is more extensive in some Old World monkeys, chimps, gorillas, and humans, so that up to eight parvocellular "leaflets" can be counted. A simpler pattern without subdivisions and interdigitation of the parvocellular layers is found in gibbons and tarsiers. The prosimian galagos, lorises, and lemurs have the simpler "monkey" pattern, so that two parvocellular layers without leaflets are found, but they have added two layers that are not found in other primates. Two layers of extremely small cells, the koniocellular layers, are inserted between the parvocellular layers. These layers appear to have the functional role of the interlaminar zones of monkeys in that they relate to the W-cell system (see below).

Diurnal primates have proportionately more of the LGN devoted to parvocellular layers [Hassler, 1966]. The bulk of the expansion of the parvocellular layers is in the part of the nucleus represent-

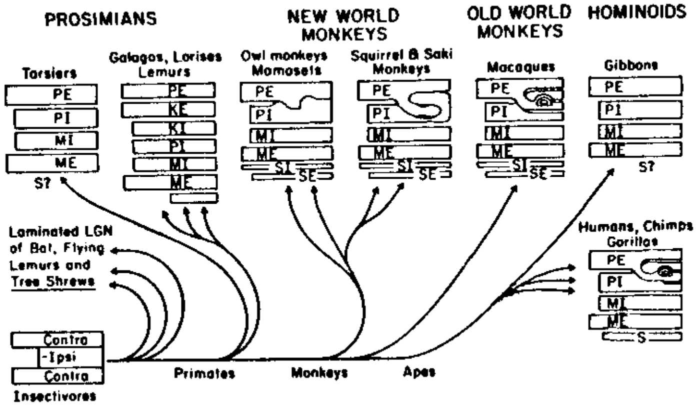

Fig. 3. The patterns of lateral geniculate nucleus lamination in extant primates and the probable course of evolution. The schematic layers are in cross section along the representation of the zero horizontal meridian (see Fig. 2) [modified from Kaas et al, 1978]. PE and PI, external and internal parvocellular layers; ME and MI, external and internal magnocellular layers; for galagos, the rectangle under ME is dMI, displaced segment of the internal magnocellular layer; KE and KI, external and internal koniocellular layers.

ing central and paracentral vision. This greater devotion to central vision is accomplished, in part, by a gradual thickening of the parvocellular layers as they extend from the representation of peripheral to central vision. However, in most monkeys and in hominids, the expansion of parvocellular regions devoted to central vision is considerable, and it is accompanied by the formation of leaflets.

Prosimians. The laminar patterns of the LGN in prosimians reflect their phylogenetic relationships. Prosimians have long been divided into two suborders, Lemuroidea and Tarsioidea [eg, Straus, 1949]. Of the two suborders, tarsiers may be more closely related to simians [eg, Petter and Petter-Rousseaux, 1979; Goodman et al, 1983], and the LGN of tarsiers more closely resembles that of simians. Lemuroidea include lemuriforms and lorisiforms, and lorisiforms are further divided into the lorises and galagos.

The lateral geniculate nucleus of lorisiforms (lorises and galagos) and lemuriforms consists of six complete layers and one incomplete and variable fragment of a layer next to the optic tract [Chacko, 1954; Hassler, 1966; Ionescu and Hassler, 1968; Kanagasuntheram et al, 1969; Giolli and Tigges, 1970; Laemle and Noback, 1970; Compos-Ortega and Hayhow, 1970; Tigges et al, 1970; Kaas et al, 1978; Weller and Kaas, 1982; Casagrande and DeBruyn, 1982]. The basic pattern seen in galagos (Fig. 4) is typical of prosimians. Thus, two thin magnocellular (MI and ME) layers are found ventrally. In addition, a superficial band of cells in the position of the S layers is found between the magnocellular layers and the optic tract in some individuals. This layer is not an S layer, but rather it is a displaced portion of the internal magnocellular layer [Casagrande and Joseph, 1980; Casagrande and DeBruyn, 1982]. The main MI layer is correspondingly thin where the displaced part of the MI layer occurs, and we suggest the term "dMI" for the displaced segment of MI. The dMI has large cells, as in MI and ME, and receives input from the ipsilateral eye, as does MI. However, the dMI does not appear to be continuous with MI. More dorsally in the nucleus, the internal parvocellular layer and the external parvocellular layer are separated by two narrow layers of small cells termed the koniocellular layers [see Kaas et al, 1978]. Cell-poor zones separate all of the layers, but this separation is least apparent between the koniocellular layers, since these layers and the cell-poor zones contain small, pale-staining neurons. Measurements of neuron sizes [Casagrande and Joseph, 1980] indicate that all layers contain a range of cell sizes, but the koniocellular neurons are, on the average, the smallest, the parvocellular neurons somewhat larger, and the magnocellular neurons the largest.

Fig. 4. A parasagittal section through the lateral geniculate nucleus of a galago (*Galago crassicaudatus*). Rostral and ventral lateral geniculate nucleus (pregeniculate nucleus) are on the right. Note that the two relatively thin parvocellular layers (PI and PE) are separated by two koniocellular layers (KI and KE) and that the cells in the magnocellular layers (MI and ME) are markedly different in size from those in the parvocellular layers.

There have been no experimental studies of the lateral geniculate nucleus of members of tarsiers, but observations on the normal laminar pattern of the LGN in tarsiers [Le Gros Clark, 1930; Chacko, 1954; Hassler, 1966; Kaas et al, 1978; Simmons, 1982] reveal that the pattern differs from that found in members of Lemuroidea. As in other prosimians, the LGN of the tarsier has a ventrally located pair of large-celled, magnocellular layers (ME and MI) and a more dorsally situated pair of parvocellular layers (PE and PI). However, the nucleus lacks the koniocellular layers found in members of Lemuroidea. There are many small, pale-staining cells in the broad interlaminar zone between PI and MI in addition to a diffuse concentration of small cells between PE and PI. It is possible that a similar sparse population of small cells between PE and PI preceded the small-celled koniocellular layers in the evolution of Lemuroidea. In the tarsier LGN, there is also a group of cells that lies ventral to ME. Although similar in location to dMI of *Galago*, the ventrally located cells in the tarsier are small and pale-staining, thus resembling the ventrally situated cells that comprise the more extensive superficial or "S" layers in anthropoid primates (see below).

Despite the lack of experimental material, the retinal projections in tarsiers appear to distribute contralaterally to PE and ME and ipsilaterally to PI and MI. This conclusion is based on the observation that, like contralaterally innervated layers in other mammals, PE and ME are more extensive than PI and MI [Kaas et al, 1978]. In addition, PE has a cell-sparse discontinuity that, as in other primates, corresponds to the blind spot of the contralateral retina [Kaas et al, 1972, 1978].

New World Monkeys. The New World monkeys have been traditionally subdivided into two major families—Callithricidae, which include marmosets and tamarins, and Cebidae, which include several subfamilies and owl, squirrel, cebus, saki, and spider monkeys.

The basic laminar pattern of the LGN in New World monkeys is apparent in a somewhat simplified form in nocturnal owl monkeys (*Aotus*), a member of Cebidae. The nucleus (Fig. 5) consists of three pairs of layers: the ventralmost, superficial

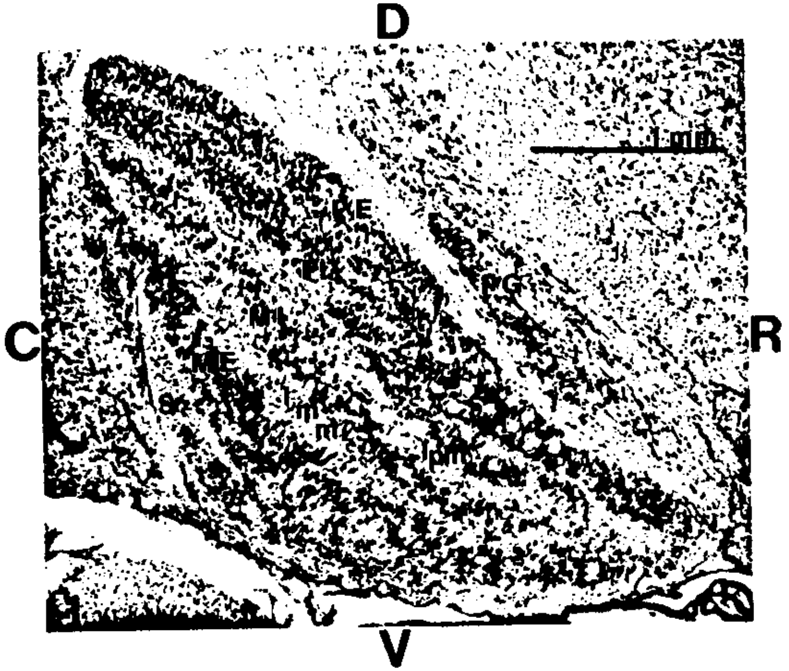

Fig. 5. A parasagittal section through the lateral geniculate nucleus of an owl monkey (*Aotus trivirgatus*). There are no koniocellular layers, but many small cells occur in the interlaminar regions, especially between the parvocellular and magnocellular layers. The superficial layers (S) are also composed of small cells. The pregeniculate nucleus (PG) is more dorsocaudal than in prosimians. Marker bar = 1 mm. Rostral is right.

Fig. 6. A frontal section through the lateral geniculate nucleus of a mandrill baboon (*Mandrillus sphinx*). The parvocellular region is extremely large and complexly subdivided into sublayers. Small cells are in the interlaminar and S layer regions. The large column of cellular degeneration, the result of a restricted cortical lesion, shows the sharpness of the geniculostriate projections and the orientation of the projection column. Note how many more parvocellular than magnocellular neurons project to the same region of cortex. The arrow marks the end of a second column of degeneration related to a second lesion. From Kaas et al [1972]. Medial, left.

or "S" layers, comprising small cells; the more dorsal, magnocellular layers, comprising large cells, and the dorsalmost parvocellular layers, comprising medium-size cells [see Norden and Kaas, 1978, for measurements]. Interlaminar zones, sparsely populated by small cells, separate most of the layers, except the S layers and the rostral part of the parvocellular layers, which appear fused. As in other primates, each member of each pair receives either ipsilateral or contralateral retinal inputs. Contralateral retinal fibers distribute to external parvocellular (PE), external magnocellular (ME), and internal S (SI) layers; the ipsilateral retina innervates PI, MI, and SE [Kaas et al, 1978]. The interlaminar zones are binocularly innervated [Kaas et al, 1978]. X-like retinal information is channeled to the parvocellular layers, and Y-like information to the magnocellular layers in owl monkeys [Sherman et al, 1976]. The response properties of the small cells in the interlaminar zones and S layers have not been studied extensively, but it is likely that they receive W-cell information [see Weber et al, 1983; Sherman et al, 1976]. In contrast to most other monkeys, the parvocellular layers of owl monkeys are simple, showing little thickening toward the representation of central vision and few signs of protrusions of PE into PI or vice versa. Also, unlike other monkeys, the interlaminar zones between MI and PI and the S layers are densely populated with neurons. Since the interlaminar zones and S layers are associated with the W-cell system, the W-cell pathways may be more important for nocturnal primates.

The laminar pattern has been studied in several other New World monkeys. Squirrel monkeys differ from most other monkeys by having a large parvocellular mass without visible lamination [Le Gros Clark, 1941a; Walls, 1953; Chacko, 1954; Hassler, 1966]. However, studies of retinal projections have revealed two parvocellular layers that subdivide so that the most caudal section of the nucleus has four parvocellular leaflets of alternating ocular input [Campos-Ortega and Glees, 1967; Tigges and O'Steen, 1974; Kaas et al, 1978]. In addition to S layers of small cells, Fitzpatrick et al [1983] noted that a displaced portion of MI is sometimes found ventral to ME in squirrel monkeys. Laminar patterns of the LGN of two other diurnal Cebidae, the spider monkey (*Ateles*) and the saki monkey (*Pithecia*), are generally similar to that of squirrel monkeys. Weak interlaminar zones are apparent in parts of the parvocellular mass, but retinal projections reveal two basic layers with large leaflets in the caudal half of the nucleus [Kaas et al, 1978; Florence et al, 1986].

The LGN of marmosets, members of Callithricidae, has been described by Le Gros Clark [1941], Chacko [1954], and Kaas et al [1978]. The organization of the LGN of marmosets is generally similar to that described for squirrel monkeys, except that the amount of interdigitation of leaflets of PI and PE is not as extensive. In the S layers, only the retinal input from the contralateral retina is distinct [Kaas et al, 1978].

Old World Monkeys. These monkeys are usually divided into two subfamilies—the Cercopithecinae including macaques, baboons, patos monkeys, and others, and the Semnopithecinae, including langurs, proboscis monkeys, and colobus monkeys. Most reports on laminar organization have been limited to members of a single genus, *Macaca* [Le Gros Clark, 1932, 1941b; Le Gros Clark and Penman, 1934; Chacko, 1948; Matthews et al, 1960; Kanagasuntheram et al, 1969; Campos-Ortega and Hayhow, 1970; Giolli and Tigges, 1970; Hendrickson et al, 1970; Hubel et al, 1977; Kaas et al, 1978]. The LGN of macaque monkeys resembles that of squirrel monkeys, except that interlaminar zones are distinct between the parvocellular layers and the two parvocellular layers interdigitate to a much greater degree. At some levels, the two interdigitating layers appear as four laminae. In fact, the macaque's LGN has traditionally been described as having four parvocellular layers. Although Le Gros Clark [1941b] and Chacko [1948] realized that the four parvocellular layers fused rostrally to become two layers, the two layers were regarded as composites of four, rather than subdivisions of two, probably because this number of layers was essential for Le Gros Clark's [1941a] theory of color vision. The parvocellular leaflets often, but not always, subdivide further to form smaller interdigitating protrusions or subleaflets [Kaas et al, 1978] that Le Gros Clark and Penman [1934] recognized as subsidiary layers. Parvocellular leaflets and subleaflets are also apparent in the parvocellular mass of baboons (Fig. 6) [Kaas et al, 1972; Campos-Ortega and Hayhow, 1970] and grivet monkeys [Kanagasuntheram et al, 1969]. In each of these monkeys, the leaflets and subleaflets are separated by narrow, but quite distinct, cell-poor interlaminar zones. The PI–MI interlaminar zone is typically broad, and it contains a scattering of lightly staining neurons, whereas the S region is indistinct and has only a few cells. However, separate groups of S cells with ipsilateral or with contralateral retinal inputs can be identified [Kaas et al, 1978].

Apes and Humans. Besides humans, the hominoids include our close relatives, the chimpanzees and gorillas; our more distant relatives, the orangutans; and our even more distant relatives, the gibbons and siamangs. Gibbons and siamangs have simple lamination patterns in the LGN, without interdigitation of parvocellular layers, whereas other hominoids have more complex patterns. Armstrong [1979] compared the numbers of neurons in the LGN of various hominoids and found that humans and great apes do not differ significantly in number (around 2 million), whereas gibbons have about half as many neurons. Thus, it appears that some time after the divergence of the line leading to gibbons, there was a stabilization of the retinogeniculate system and the relay of visual information to higher brain centers.

Chacko [1954b] provided the first detailed description of the LGN of gibbons. More recent descriptions include those of Kanagasuntheram et al [1969] and Kanagasuntheram and Krishnamurti [1970] on the LGN of gibbons and siamangs. The nucleus consists of two undivided parvocellular layers, with PE receiving input from the contralateral eye as in other primates, and two magnocellular layers. In places, the magnocellular layers appear to subdivide. Chacko [1954c] illustrates a brain section through the LGN of a gibbon where ocular input was demonstrated by degeneration after eye removal and where a ventral group of large cells was related to the ipsilateral eye. Thus, a portion of MI appeared to be displaced so that it was ventral to ME. Smaller scattered cells ventral to ME could represent greatly reduced S layers, but this is uncertain. Kanagasuntheram et al [1969] noted a narrow rim of cells over part of PE in gibbons, and these cells, with demonstrated inputs from the ipsilateral eye, could be a small leaflet as displacement from the PI layer. However, except for these minor complications, the LGN of gibbons is one of the simplest in laminar structure.

Of the great apes, the chimpanzee has been most studied. Chacko [1954b] gave a detailed description and reviewed earlier studies. More recently, Tigges et al [1977] labeled retinal termination from one eye with an injection of radioactive proline and provided an excellent series of photomicrographs of autoradiograms of sections through the LGN. The two layers, PI and PE, subdivide to form large leaflets that interdigitate to form leaflets and subleaflets of alternating ocular input. The interlaminar zones are narrow in the parvocellular mass but wider in the magnocellular region, where they contain many small cells. Scattered cells ventral to ME suggest an S region, and patterns of retinal input suggest discontinuous, poorly developed SE and SI layers with ipsilateral or contralateral inputs.

The human lateral geniculate nucleus has been described by Balado and Frank [1937], Chacko [1948], and Hassler [1959]. More recently, Hickey and Guillery [1979] have illustrated the variability that occurs in the laminar patterns, and Hitchcock and Hickey [1980] have outlined the prenatal development of the laminar pattern. There are two magnocellular layers and two parvocellular layers that subdivide into leaflets and subleaflets that interdigitate. The caudal half of the nucleus has four parvocellular leaflets, which sometimes further subdivide to produce up to six leaflets and subleaflets. The interlaminar zones are distinct and narrow in the parvocellular mass. The interlaminar zones are generally wider in the magnocellular region, where they contain a population of small cells. A scattering of small cells ventral to the magnocellular suggests a poorly developed S region.

Histochemistry

The concept that the parvocellular layers, the magnocellular layers, and the very small interlaminar zones and S layers constitute three functionally distinct populations of cells is supported by the histochemical distinctiveness of these groups. Thus, laminar differences in the distribution of acetylcholinesterase, AchE (which hydrolyzes the neurotransmitter, acetylcholine, and presumably is distributed with cholinergic synapses), and the activity-related mitochondrial enzyme, cytochrome oxidase (CO), have been reported, but the relationship is not a simple one. Diurnal monkeys, both New World (squirrel monkeys) and Old World (macaque monkeys), have higher levels of AchE activity in magnocellular than parvocellular layers, whereas nocturnal New World owl monkeys, nocturnal prosimian galagos, and nocturnal tarsiers have denser levels of AchE in the parvocellular layers [Fitzpatrick and Diamond, 1980; Graybiel and Ragsdale, 1982; Hess and Rockland, 1983; McGuinness and Allman, 1985]. The AchE label appears to be in the neuropil and not somata, suggesting that it relates to an Ach input that potentiates activity. Pseudocholinesterase (of uncertain function) is most densely distributed in the parvocellular layers of at least macaque monkeys [Graybiel and Ragsdale, 1982]. Finally, studies of the distribution of cytochrome oxidase (CO) in the LGN layers suggest that the magnocellular layers have the highest level of maintained activity, the parvocellular layers have the next highest, and the S layers and interlaminar zones have the lowest. Thus, in both squirrel and macaque monkeys, the magnocellular layers stain the most densely for CO, the parvocellular stain less densely, and the interlaminar zones and the S layers show little reactivity for CO [Hess and Rockland, 1985; Kageyama and Wong-Riley, 1984; Kennedy, 1985].

Retinal Inputs

The laminar patterns of projections from each eye are summarized in Figure 3. In brief, the internal magnocellular and internal parvocellular layers receive inputs from the ipsilateral eye, and the external magnocellular and external parvocellular layers receive inputs from the contralateral eye in all primates. Leaflets and subleaflets stemming from these parent layers receive inputs from the same eye as the parent layer. In prosimians with koniocellular layers, KE receives contralateral and KI receives ipsilateral inputs. When laminar patterns of retinal input to the S region are apparent, the contralateral input is internal (SI) to the ipsilateral input (SE). Other retinal inputs terminate in the interlaminar zones. This is most obvious for the inputs from the contralateral retina in the interlaminar zone between the magnocellular and parvocellular regions (Ipm) of both New World and Old World monkeys [Kaas et al, 1978; Fitzpatrick et al, 1983]. However, sparser inputs from the ipsilateral retina also terminate in Ipm.

It appears that inputs from three major classes of ganglion cells are segregated in different laminar regions of the LGN [see Rodieck, this volume, for a detailed discussion of ganglion cell classes]. In galagos [Itoh et al, 1982], monkeys [Leventhal et al, 1981; Perry et al, 1984; Fitzpatrick et al, 1983], and most probably all primates, larger cells with thick axons project to the magnocellular layers, smaller cells with thinner axons project to the parvocellular layers, and the smallest cells with the thinnest axons project to the interlaminar zones and koniocellular layers. The large cells projecting to the magnocellular layers have been called primate Y or alpha cells after their apparent homology with Y cells or alpha cells of the cat retina (among the many types of evidence to support this hypothesis, a monoclonal antibody that binds the cells with alpha cell input in the LGN of cats also binds to the magnocellular cells in monkeys [see Hendry et al, 1984]). Rodieck (this volume) refers to Y ganglion as parasol cells, and in macaque monkeys they constitute about 10% of the ganglion cells [Perry et al, 1984]. The Y cells also project to the superior colliculus [eg, Perry and Cowey, 1984], apparently often by collateral branches (Fig. 2) [see Weller and Kaas, 1984]. Likewise, the medium-size cells projecting to the parvocellular layers have been called primate X or beta cells after X or beta cells in cats. Rodieck refers to these X cells as midget ganglion cells. They appear to project exclusively to the parvocellular layers and make up 80% of the ganglion cells in the retina of macaque monkeys. Small cells in the retina project to the koniocellular layers in galagos [Itoh et al, 1982] and, judging from the caliber of terminals, probably to the interlaminar zones of monkeys and other primates. These cells have been called W cells or C cells after a somewhat heterogeneous group of cells in the cat retina.

The distribution patterns of individual axons in the lateral geniculate nucleus have been most extensively studied in macaque monkeys. While axons may branch before reaching the zone of termination, only single zones of terminal arbors are formed [M. Conley and D. Fitzpatrick, personal communication]. Arbors in the thin magnocellular layers generally fill most of the thickness of the layer while being confined to the layer. Arbors in the interlaminar zones appear to be confined to those zones. Arbors in the parvocellular layers are typically restricted to part of the thickness of a layer and even to part of the thickness of a leaflet. All retinal inputs, judging from the restricted terminal arbors, would appear to be capable of activating only a small local population of cells. Retinal inputs are presumed to be excitatory, and they appear to provide the major driving input to the LGN.

Other Inputs

In terms of numbers of projecting neurons, the major input to the LGN is from visual cortex. This input arises almost exclusively from neurons of layer VI [eg, Lund et al, 1975] of primary visual cortex, area 17, or area V-I [see Kaas, 1978; Weller and Kaas, 1981; Allman, this volume, for details on cortical visual areas]. Neurons in layer VI of area 17 have complex receptive field properties, large receptive fields, orientation specificity, and often direction selectivity [eg, Dow, 1974]. In macaque monkeys, pyramidal cells in the upper half of layer VI project to the parvocellular layers, whereas pyramidal cells in the deeper half of layer VI project to the magnocellular layers [Lund et al, 1975]. Terminations from area 17 are concentrated in the parvocellular and magnocellular layers in monkeys, but they are also found in the interlaminar zones and S layers [Lin and Kaas, 1977; Hollander and Martinez-Millan, 1975; Hollander, 1974]. In galagos, terminations are dense in all layers and in the interlaminar zones [Symonds and Kaas, 1978; Raczkowski and Diamond, 1978a]. The input to LGN from area 17 appears to be excitatory, but synapses on inhibitory neurons indirectly produce inhibitory effects [see Marrocco and McClurkin, 1985]. The cortical inputs appear to modulate the activity of LGN neurons and to contribute to excitatory and inhibitory surrounds of receptive fields [Marrocco and McClurkin, 1985].

Other cortical inputs to the LGN may include area 18 (V-II) and the middle temporal visual area (MT). Lin and Kaas [1977; also see Graham et al, 1979] reported that in owl monkeys, sparse projections from area 18 and MT were distributed over the magnocellular and S layers and the adjoining interlaminar zones. Projections from prestriate cortex to the LGN have also been noted in macaque monkeys [Wong-Riley, 1977; Hendrickson et al, 1978], and injections of horseradish peroxidase in the LGN of macaque monkeys labeled a few cells in the region of MT [Hendrickson et al, 1978]. However, projections from MT to the LGN were not seen in galagos [Wall et al, 1982] or in a recent study of MT projections in macaque monkeys [Underleider et al, 1984].

Ascending inputs from the brainstem to the LGN have been regarded as the substrate for modulation of excitability associated with eye movements and attention. Subcortical extraretinal inputs to the LGN have not been extensively studied in primates, but they have been reviewed for mammals in general by Burke and Cole [1978] and described in cats by Hughes and Mullikin [1984]. Important visual inputs are from the superior colliculus and pretectum. The projections from the superior colliculus are of fine caliber and terminate in the interlaminar zones and S layers in monkeys and in the koniocellular layers and interlaminar zones in galagos [Fitzpatrick et al, 1980; Partlow et al, 1977; Harting et al, 1978, 1986; Huerta and Harting, 1984]. Since the superior colliculus layers projecting to the LGN receive retinal input (see below), the superior colliculus as well as the direct retinal projections could be providing W-cell information to the LGN [see Weber et al, 1983]. Projections from the pretectum are concentrated in the parvocellular layers in galagos [Harting et al, 1986]. The nucleus of the optic tract provides a major source of pretectal inputs, at least in cats [Hughes and Mullikin, 1984]. Inputs from the parabigeminal nucleus, a visuomotor structure (see below), are largely to the interlaminar zones and koniocellular layers of galagos [Harting et al, 1986]. Inputs from the parabigeminal nucleus could provide information about motor signals producing eye movements. Neurons in the parabigeminal nucleus are positive for choline acetyltransferase [Fitzpatrick et al, 1985], and they appear to be the major source of lateral geniculate terminations using acetylcholine as a transmitter [see Fitzpatrick and Diamond, 1980].

Another subcortical input is from the visual portion of the reticular nucleus of the thalamus (see subsequent section for further description). These neurons receive inputs from visual cortex and inhibit LGN neurons by releasing the inhibitory neurotransmitter, GABA [Hendrickson et al, 1983].

Other inputs to the LGN are from structures that project broadly in the brainstem and are not strictly visual. Neurons from the locus coeruleus, using norepinephrine as a transmitter, project to the LGN [Fitzpatrick et al, 1985] and to other brainstem and cortical structures. Other inputs include the raphe nuclei and pontine reticular formation neurons that are part of a widely projecting serotonergic system [Fitzpatrick et al, 1985].

Cortical Projections

The bulk of the neurons in the LGN of primates project to primary visual cortex, area 17, or striate cortex. A few neurons have projections to extrastriate cortex, at least in macaque monkeys, and a small percent of the neurons do not project to cortex, but are intrinsic neurons (see below). The details of the projection patterns have been determined for galagos, several species of New World monkeys, and macaque monkeys. Most features of

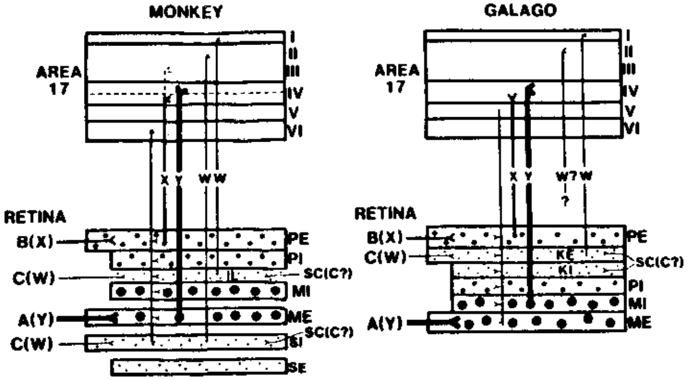

Fig. 7. Projection patterns from the lateral geniculate nucleus to cortex. The pattern shown for galagos may apply to lorises and lemurs as well, and the pattern shown for monkeys may also apply to apes and humans. Layers in striate cortex have been named differently by various investigators, so terminations in lower layer III have been described in the upper sublayer of layer IV by some authors. For reasons outlined elsewhere [eg, Weber et al, 1983], we use Hassler's [1969] terminology rather than Brodmann's [1909] for layers of cortex. Note that the projections of the different types of layers are segregated in cortex and that the terminations of the koniocellular layers of galagos resemble those of the S layers and interlaminar zones of monkeys. SC, superior colliculus inputs. Other conventions as in Figures 2 and 3.

these projection patterns probably apply to other primates as well.

The two basic projection patterns from the LGN to cortex are shown in Figure 7. In galagos [Glendenning et al, 1976; Casagrande and DeBruyn, 1982; Diamond et al, 1986] and monkeys [Hendrickson et al, 1978; Winfield et al, 1981; Hubel and Wiesel, 1972; Livingstone and Hubel, 1982; Weber at al, 1983; Fitzpatrick et al, 1983; Diamond et al, 1986], the parvocellular layers, the magnocellular layers, and the interlaminar zones, together with the S layers and koniocellular layers, all relay to different laminar levels in striate cortex (Fig. 7). The parvocellular layers project to the inner half of layer IV, less densely to inner layer III in monkeys, and lightly to the inner part of layer VI. The magnocellular layers project to the outer half of layer IV and possibly in a minor way to the outer half of layer VI. The interlaminar zones, the S layers, and the koniocellular layers contribute terminations to layer I and parts of layer III. Thus, the parvocellular X-like, the magnocellular Y-like, and the koniocellular W-like inputs are segregated in striate cortex.

Although the segregation of functionally distinct pathways to cortex seems to be a feature of the geniculocortical relay in galagos, New World monkeys, Old World monkeys, and probably all primates, the details of how these inputs terminate in cortex vary according to species. The most notable variation is in the areal distribution of inputs from the magnocellular and parvocellular layers in cortical layers III and IV. In some primates, these inputs are sharply segregated according to the ocular inputs of the projecting geniculate layers. Cells relaying information from the right eye project to distinctively different groups of cells from cells relaying information from the left eye. In macaque monkeys, for example, inputs from the left eye terminate in narrow, 0.5-mm-wide bands of layer IV cells that alternate with similar bands of terminations related to the right eye. This ocular segregation is the anatomical basis of the well-known "ocular dominance columns" of cells most activated by one eye or the other in the cortex of many primates and cats [for review, see Hubel and Wiesel, 1977]. The ocular input patterns to area 17 can be easily and clearly demonstrated by geniculate or eye injections of certain tracers such as tritiated amino acids or wheat germ agglutinin. In typical frontal or parasagittal brain sections, these alternating inputs often appear as "columns," but a complex arrangement of alternating bands of right and left eye inputs is apparent in brain sections cut parallel to the surface and through layer IV. All Old World monkeys, apes, and humans apparently have such strongly segregated inputs in layer IV [see Florence et al, 1986, for review]. In contrast, ocular inputs from the lateral geniculate overlap extensively in most New World monkeys. At best, only a weak tendency for ocular inputs to partially segregate and form bands is apparent. An exception is that New World spider monkeys demonstrate a modest tendency for ocular bands to form, especially in regard to the inputs related to the ipsilateral eye. These columns, less than 0.4 mm in width, are somewhat less wide than those in macaque monkeys. In other New World monkeys, weak ocular bands can be produced by disrupting the normal ocular balance by rearing with one eye closed, thus suggesting that a weak tendency toward ocular segregation may normally exist [see Florence et al, 1986, for further discussion]. Finally, a moderate amount of segregation is found in the ocular inputs to striate cortex of galagos. Overall, these findings suggest that the potential or tendency for the segregation of ocular inputs is a primate characteristic and that ocular bands in cortex evolved independently in several lines of descent. The separation of inputs into ocular dominance columns may not be related to function in a simple way but may be the result of general adjustments in the development of the visual system [see Constantine-Paton, 1982; Kaas, 1986].

Species differences also have been noted in the input from the W-cell relay to layer III. Inputs to layer III in galagos [Casagrande and DeBruyn, 1982], squirrel monkeys [Weber et al, 1983; Fitzpatrick et al, 1983], and macaque monkeys [Livingstone and Hubel, 1982] produce patches or "puffs" of inputs to layer III. Each patch is surrounded by cortex without this input, and each patch overlaps a region of high metabolic activity that can be revealed by the presence of high amounts of the enzyme cytochrome oxidase (the CO patches). The major feature of species difference is that these patches show no systematic relationship to layer IV inputs in galagos and New World monkeys, whereas they are arranged in rows along the junctions of the ocular dominance bands in macaque monkeys [see Carroll and Wong-Riley, 1984, for review].

In addition to neurons projecting to striate cortex, the LGN of macaque monkeys, and perhaps other primates, has a few neurons projecting to extrastriate cortex, including the second visual area (V-II), and cortex immediately rostral to V-II [Benevento and Yoshida, 1981; Fries, 1981; Yukie and Iwai, 1981; Bullier and Kennedy, 1983]. Although a few of these scattered neurons with extrastriate connections are found in the parvocellular and magnocellular layers, the vast majority are located in the interlaminar zones. Some of these neurons also appear to project via collaterals to striate cortex [Bullier and Kennedy, 1983]. Given that the input to interlaminar zones is directly or indirectly from W-like cells, the projections to extrastriate cortex from the LGN appear to relay largely W-cell information.

Morphological and Physiological Characteristics of Neurons

Neurons in the different sets of layers in the LGN are morphologically and physiologically distinct. One traditional distinguishing feature is cell size. The magnocellular and parvocellular layers reflect the easily recognized difference in neuron size in these layers. In addition, Le Gros Clark [1941] and others also noted that the cells in the interlaminar zones of monkeys are typically even smaller than those in the main layers. Likewise, neurons in the two layers inserted between the parvocellular layers in prosimians have been described as smaller than in other layers [eg, Hassler, 1967]. Because these layers consisted of cells smaller than the parvocellular layers, we introduced the term koniocellular layers [Kaas et al, 1978], since the koniocellular divisions of cortex are those with the smallest (powderlike) neurons. Measurements have confirmed the observations that layers have neurons of different sizes. The laminar differences in average neuron size are typically pronounced regardless of species [see Casagrande and Joseph, 1980; Norden and Kaas, 1978]. In squirrel monkeys, for example, magnocellular neurons have a mean soma area of 154 μm^2; parvocellular layers, 119 μm^2; and interlaminar neurons, 76 μm^2 [Fitzpatrick et al, 1983]. In galagos, the proportionate differences are similar, though the overall sizes of cells may be somewhat larger (processing and measuring differences across studies can contribute to such apparent species differences). Thus, reported values for galagos are: magnocellular layers, about 450 μm^2; parvocellular layers, about 360 μm^2; koniocellular layers, about 180 μm^2 [Casagrande and Joseph, 1980].

Neurons in the parvocellular layers, magnocellular layers, and interlaminar zones plus koniocellular layers have distinctly different properties [see Wiesel and Hubel, 1966; Dreher et al, 1976; Sherman et al, 1976; Norton and Casagrande, 1982; Perrington and Lennie, 1984; Irvin et al, 1986] in response to sensory stimuli, and these properties are consistent with the evidence that they are activated by X-like, Y-like, or W-like retinal ganglion cells, respectively (see Table 1). In the parvocellular layers, most cells have a sustained discharge to standing contrast (Fig. 8). In addition, the responses of almost every parvocellular neuron show linear spatial summation for visual stimuli, a large majority of parvocellular neurons in at least diurnal monkeys are color selective (color-opponent), and parvocellular neurons have the smallest receptive fields for given visual field locations. The cells in the magnocellular layers are predominantly phasic in response to standing contrast, exclusively broad-band in spectral sensitivity, sensitive to rapidly moving stimuli and stimuli of low contrast, have large receptive fields, and, because they are activated by large-diameter Y-cell axons and project over large-diameter axons to cortex, have the shortest response latencies to electrical stimulation of the optic tract or visual radiations. Because there are few cells in the interlaminar zones and in the S layers, the responses of these neurons have not been extensively studied [see Sherman et al, 1976]. The response properties of the neurons in koniocellular layers and, to a lesser extent, the interlaminar zones have been studied in galagos, and they have "W-like" properties [Irvin et al, 1986; Norton and Casagrande, 1982]. Whereas the W-cell geniculate neurons are heterogeneous in terms of many physiological properties, W-cells are distinguished by long latencies to stimulation of the optic tract and optic radiations (this is consistent with having input from ganglion cells with thin axons and projecting to cortex over thin axons), large receptive fields, low maintained discharge rates, long response latencies to light, and low peak firing rates. All or nearly all of these W-like neurons in galagos appear to be influenced by nonvisual (auditory and tactile) stimuli, whereas only about half of the neurons in the parvocellular and magnocellular layers are affected by nonvisual stimuli.

Because W cells of the LGN project to pufflike zones of layer III of cortex where the neurons lack orientation selectivity and are highly selective for color-spatial interactions in macaque monkeys

TABLE 1. Properties of Lateral Geniculate Relay Cells [see Kaas, 1986, for references]

	Anatomical	Physiological
Parvo B (X-like)[a]	Medium-size soma Medium axons and restricted terminal arbors in striate cortex Restricted dendrites sometimes elongated in the plane of isorepresentation	Most spectrally dependent and color opponent Sustained response to standing contrast Smaller receptive fields Medium latency to optic chiasm shock Poor activation by fast-moving bars Poor contrast sensitivity Linear spatial summation No suppression to nondominant eye Monophasic response to moving bar Medium latency to optic chiasm shock Medium velocity conducting axons to cortex
Magno A (Y-like)	Large soma Radially symmetric dendrites in galago More variety in dendritic arbors and many translaminar dendrites Large axons and terminal arbors in striate cortex	Spectrally broad-band Transient response to standing contrast Large receptive fields Short latency to optic chiasm shock Vigorous response to fast-moving bars Fast-conducting axons to cortex Biphasic (excitation *and* suppression) to moving bar with suppression from nondominant eye Both linear and nonlinear spatial summation High-contrast sensitivity
Konio C (W-like)	Small soma Thin dendrites and few branches	Long to medium optic chiasm shock latencies Large receptive fields, heterogeneous response properties, brisk to sluggish responsiveness, many nonconcentric receptive fields
Interlaminar +S	Small soma	

[a] The cells in the parvocellular, magnocellular, and interlaminar-koniocellular layers clearly differ, but opinions vary on how to classify these neurons and if the parvocellular and magnocellular neurons in primates are homologous with X and Y neurons of cats, respectively (for an alternative opinion, see Kaplan and Shapley [1982]; see Stone [1983] for an extensive discussion of the X, Y, and W classification).

[Livingston and Hubel, 1984], it is tempting to infer that the W cells relate only to color vision. However, Irvin et al [1986] stress that color is unlikely to play a major role in the vision of nocturnal galagos in which the W-cell system and the cortical puff regions are well developed. The properties of the neurons in the puff regions differ greatly from those of W cells, and the direct W-cell inputs apparently only modulate neurons apparently activated by X-cell influences relayed from cortical neurons outside the puffs. Although neurons in the puff regions appear to be color-dominated in diurnal monkeys, this may not be the case in nocturnal monkeys and prosimians.

As for other parts of the thalamus, neurons in the LGN can be classified as interneurons with connections confined to the LGN and relay (or projection) neurons with axons that course to cortex. Relay neurons, of course, relay information to cortex, whereas interneurons presumably modulate and alter the outputs of relay neurons. The percentages of relay and interneurons in the LGN have been a matter of debate, and estimates have been confounded by using indirect criteria such as neuron size to indicate cell types. Interneurons tend to be smaller than relay neurons, but some of the smallest neurons in the LGN project to cortex [Norden and Kaas, 1978]. Relay (or projection) neurons can be most reliably identified by a clear demonstration that they project to cortex. Thus, injections of retrogradely transported tracers into visual cortex have been commonly used to identify

Fig. 8. Responses typical of parvocellular (P) and magnocellular (M) neurons in the lateral geniculate nucleus. The responses to flashed bars of light are shown in the "response plane" format on the left and in the contour plane format on the right. The lower trace indicates the onset and offset of a 1-sec flash of a bar of light, and each subsequent trace, from lower to upper, indicates the averaged (25 trials) responses of a neuron relative to the stimulus. The first response trace is for a stimulus location starting outside the receptive field, and subsequent traces are for subsequent positions moved into and across the receptive field [see Felleman and Kaas, 1984, for details]. The contour plane shows only the locations of the peak responses relative to the stimulus. The parvocellular neuron (upper) responded to the stimulus onset and continued to respond at a reduced level throughout the duration of the stimulus. The magnocellular neuron (lower) responded only at the stimulus onset and offset and had a larger receptive field. [From Felleman and Kaas, unpublished experiments. See Sherman et al, 1976, for similar results from owl monkeys.]

projection neurons. In owl monkeys, macaque monkeys, and galagos, it appears that as many as 90–95% of the neurons in the parvocellular and magnocellular layers project to striate cortex [Norden, 1979; Norden and Kaas, 1978; Casagrande and DeBruyn, 1982]. The percentages in the koniocellular layers and interlaminar zones are also high, but they may be somewhat less. Since projection neurons also show degenerative changes after cortical lesions, degeneration methods have also been used to estimate numbers of projection neurons. In macaque monkeys, such procedures suggest that 95% of the parvocellular neurons are projection neurons but that only 85% of the magnocellular neurons are projection neurons [Hamori et al, 1983]. However, another way of estimating proportions of relay and intrinsic neurons is to identify neurons using the inhibitory neurotransmitter gamma-aminobutyric acid (GABA). Projection neurons are regarded as providing excitatory relays to cortex, whereas intrinsic (local circuit) neurons are viewed as providing inhibition in the thalamus. The distribution of neurons that are immunoreactive for glutamic acid decarboxylase (GAD), the synthesizing enzyme for GABA, or for GABA probably represents most or all of the distribution of intrinsic neurons. In agreement with conclusions based on cortical injections, the vast majority of neurons in the LGN of monkeys [Hendrickson et al, 1983] and galagos [Fitzpatrick et al, 1982] appear to be relay neurons on the basis of not being GAD-positive. However, as many as 25% of neurons may be GABA-positive, suggesting a higher proportion of intrinsic neurons than other procedures. Another observation is that GAD-positive terminations are denser in the magnocellular than in the parvocellular layers [Hendrickson et al, 1983; Montero and Zemple, 1986], and this observation agrees with the evidence for more inhibitory activity in the magnocellular layers [Rodieck and Dreher, 1979] and more interneurons [Hamori et al, 1983].

In keeping with their proposed role as intrinsic neurons, the GAD-immunoreactive neurons tend to be smaller than non-GAD neurons, and they generally have fewer primary dendrites. In galagos, the orientations of dendrites of GAD-positive neurons depend on the geniculate layer [Fitzpatrick et al, 1982]. In the magnocellular layers, GAD-positive neurons have radially arranged or oblique dendrites, the dendrites of such neurons are perpendicular to the layers and along lines of projection in the parvocellular layers, and the GAD dendrites are oriented parallel to layers in the koniocellular layers. Thus, basic features of dendrites of presumptive interneurons vary according to layer.

Attempts have also been made to identify relay and intrinsic neurons in Golgi and ultrastructure studies. In Golgi preparations of LGN cells in primates and other mammals, it is common to distinguish medium to large neurons with many branching dendrites as type I neurons, and small neurons with a few, smoothly contoured, and sparsely branching dendrites as type II neurons [see Conley et al, 1985]. Ultrastructurally, type I neurons are characterized by a rich rough endoplasmic reticulum, abundant polyribosomes, large mitochondria, and numerous lysosomes, whereas type II neurons feature pale cytoplasm, few organelles, and small dense mitochondria [eg, Hamori et al, 1983]. Type I neurons are thought to be relay neurons, and type II neurons are thought to be intrinsic neurons. Using differences in lipofuscin pigment to identify type I and type II neurons, Braak and Bachmann [1985] estimated that over 90% of the neurons in the human LGN were type I "projection" neurons.

Retinotopic Organization

The lateral geniculate nucleus of primates, as for other mammals [Kaas et al, 1972], represents the contralateral visual hemifield in a systematic manner. The LGN contains a first-order [Allman and Kaas, 1971b] or topographic representation, in that adjoining locations in the visual hemifield are adjacent in the representation. Thus, there are no "breaks" or "discontinuities" in the representation. However, in all primates the representation of the hemifield is greatly distorted so that relatively large amounts of tissue are devoted to central vision rather than peripheral vision. This is especially true of diurnal primates with a fovea.

The right and left visual hemifields (Fig. 9) are separated by a vertical line through the point of fixation in the visual field. During fixation, the area centralis or fovea of the retina of each eye is centered on the fixation point, and the vertical line through fixation (the zero vertical meridian) corresponds to a line on each retina that divides neurons in the temporal retina projecting to the ipsilateral LGN from neurons in the nasal retina projecting to the contralateral LGN (the line of decussation of the retina). However, the dividing line is not precise, and ganglion cells in a narrow 1° or so strip along the "line" can project ipsilaterally or contralaterally [eg, Bunt et al, 1977].

Each layer of the lateral geniculate receives a topographically organized input from the nasal contralateral retina or the temporal ipsilateral retina (Fig. 2), so that a systematic map of the retina is formed, with the length of each layer corresponding to the progression from central to peripheral vision, the width of the layer corresponding to the progression from upper to lower field (see Fig. 2), and the depth or thickness of the layer representing the same retinal locations (isorepresentation). Matched visual field locations from the two eyes are precisely aligned in adjoining LGN layers [see Kaas et al, 1972]. To form the retinotopic map of the visual hemifield in striate cortex, neurons along "projection lines" coursing perpendicular to the geniculate layers project to single locations in striate cortex. Projection lines or columns are easily revealed by placing small lesions in striate cortex and noting the resulting column of degenerated neurons in the LGN (Fig. 6) [Kaas et al, 1972]. Because the nasal retina sees all of the contralateral hemifield, including the peripheral monocular field (Fig. 10), the maps in the geniculate layers with input from the contralateral eye (nasal retina) are more extensive than those for the ipsilateral eye. Since the maps for inputs from each eye are aligned, the larger maps from the contralateral eye are not matched by maps from the ipsilateral eye in the portion of the LGN devoted to the monocular field (Figs. 2, 11).

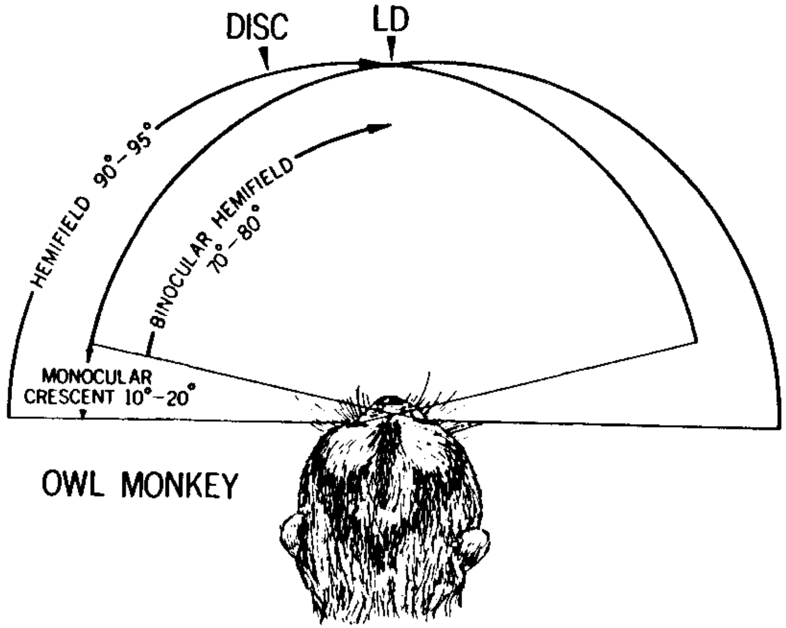

Fig. 9. The visual field of an owl monkey as determined from recordings in the geniculostriate system. The line of decussation (LD) of the retina corresponds to the zero vertical meridian through the center of gaze. The visual blind spot, 20° from gaze in owl monkeys, corresponds to the optic disk (DISC) of the nasal retina. As in other primates, most of the hemifield is binocular. Modified from Kaas et al [1972].

The basic retinotopic pattern in the LGN is similar in all primates (Figs. 2, 11). Peripheral vision is rostral, central vision caudal, the lower quadrant medial, and the upper quadrant lateral in the representation in the nucleus. The major variation is that the LGN of prosimians is less rotated from the generalized or primitive mammalian position. Thus, the portion of the geniculate devoted to central vision is dorsal and medial to the portion devoted to peripheral vision. Another difference is that more of the geniculate represents central vision in diurnal primates than in nocturnal primates (Fig. 11).

The most detailed maps of the retinotopic organization of the LGN of primates are those that have been obtained for macaque monkeys [Connolly and Van Essen, 1984; Malpeli and Baker, 1975; also see Kaas et al, 1972]. These maps indicate that the layers with contralateral input represent about 90° of horizontal visual field, with about half of the layer devoted to the first 15°, and the layers with ipsilateral inputs represent about 70–80°. In the parvocellular layers, about 110,000 cells exist within the portion devoted to the first 2.5°, and an additional 1,000,000 cells represent the other 87.5° or so of visual hemifield [Connolly and Van Essen, 1984] to central vision. In the magnocellular layers, proportionately fewer cells are devoted to central vision, so that 3,100 neurons represent the first 2.5° and 140,000 represent the next 87.5°. Thus, roughly one-tenth of parvocellular and one-fiftieth of magnocellular neurons are devoted to central vision. This difference in the

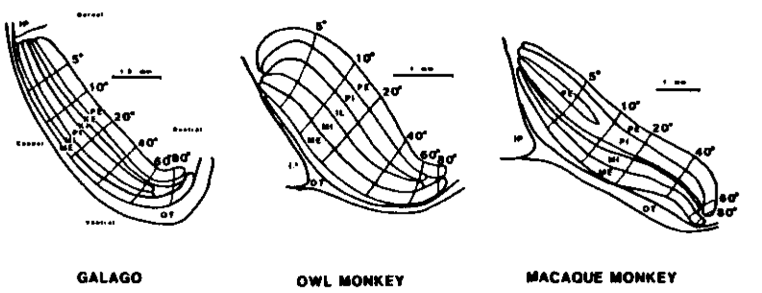

Fig. 10. The retinotopic (visuotopic) organization of the lateral geniculate nucleus in galagos, owl monkeys, and macaque monkeys. The lateral geniculate nuclei are shown in parasagittal section. Lines perpendicular to the layers in the lateral geniculate nuclei mark projection lines where neurons have receptive fields centered 5°, 10°, 20°, 40°, 50°, or 80° from the center of gaze and roughly along the zero horizontal meridian. In each geniculate, the upper visual quadrant is medial and the lower visual quadrant is lateral, as in Figure 2. Conventions for layers are as in Figure 3. Modified from Weller and Kaas [1982].

emphasis of central vision is increased further in cortex. In the projection to the map in striate cortex, each parvocellular neuron terminates on as many as an estimated 2,400 target cells for central vision to as few as 30 for peripheral vision. For comparison, each magnocellular neuron may terminate on as many as 7,000 neurons for central vision and as few as 45 for peripheral vision.

Development

Compared to many mammals, the visual systems of all primates are fairly well developed at birth, so much of the development occurs prenatally. Primates are born with their eyes open and with at least basic visual function. The lateral geniculate nucleus is fully laminated, and the major postnatal change seems to be an increase in geniculate volume. In macaque monkeys, the volume of the LGN increases by 17% after birth, but these changes are complete by 4 weeks and depend completely on growth of the parvocellular layers [Gottlieb et al, 1985]. Most of this growth in volume results from an increase in the amount of neuropil, since there is no apparent postnatal growth of the cell bodies of parvocellular neurons and little of magnocellular neurons [Headon et al, 1985], and there is an actual postnatal decrease, following a prenatal increase, of length of dendrites [Leuba and Gary, 1984]. For different primates, the time course of such postnatal changes, of course, varies with rates of maturation, since humans, apes, and some monkeys take years to reach adult size and sexual maturity, whereas some monkeys such as marmosets and prosimians in general are mature in about 1 year. Lateral geniculate neurons are mature in morphological appearance in Golgi preparations by two postnatal months in macaque monkey, and by 9 months in humans [Courten and Gary, 1982].

Experimental studies of the prenatal development of the LGN of primates have largely been based on macaque monkeys, whereas valuable observations on the prenatal development of the human lateral geniculate nucleus have been made on normal material. The developmental sequences in humans and macaque monkeys appear to be quite similar [for review, see Hitchcock and Hickey, 1980; Rakic, 1977]. Early in prenatal development, the LGN of these primates is completely unlaminated and is in a dorsoventrally oriented position in the lateral thalamus along the optic tract. This position and orientation correspond to those retained in adult forms of many generalized mammals, but in monkeys and humans there is a progressive rotation, so the dorsal pole moves ventrally, laterally, and caudally while the ventral pole moves dorsally, medially, and rostrally. Lines of projection change from a more rostrocaudal orientation to a more dorsoventral orientation, and the representation of the lower visual quadrant changes from ventral to medial in the nucleus. Layers start to appear at about 90 days in macaque monkeys and at about 140 days in humans, and they fully differentiate over a 3-week period. In macaque monkeys, the retinal inputs from the two eyes initially overlap, but these inputs become segregated as the layers differentiate. The restriction of ocular input to the individual layers depends on the presence of input from both eyes [Rakic, 1981]. Thus, after removing retinal input from one eye early in development, magnocellular and parvocellular regions appear, but all regions receive input from the remaining eye. It appears from related studies on tree shrews that layers of different cell types, but not the interlaminar spaces, develop even if retinal input is completely removed [Brunso-Bechtold and Casagrande, 1981].

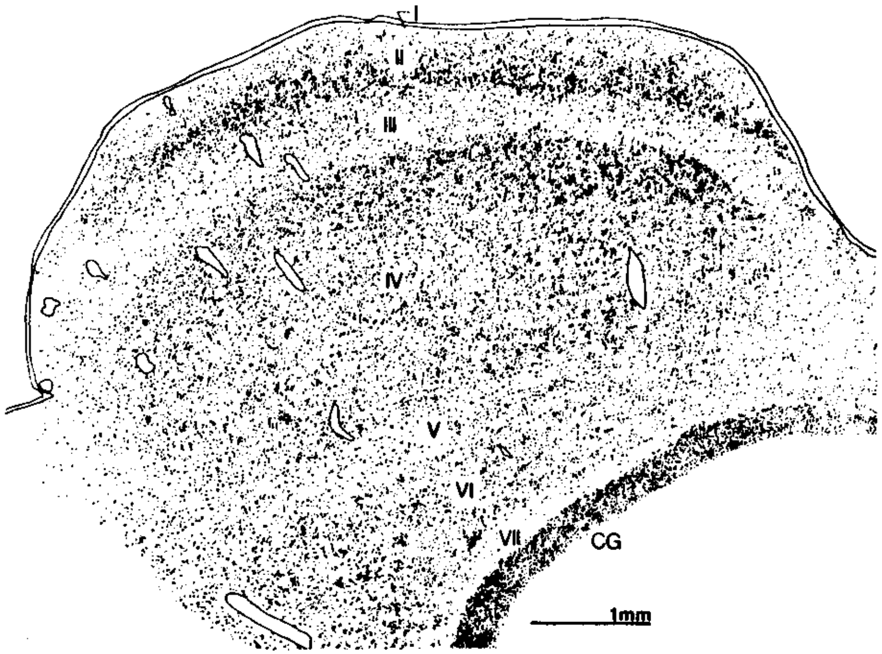

Fig. 11. Drawing of a Nissl-stained frontal section through the superior colliculus of a macaque monkey. Seven collicular layers (I-VII) and central gray (CG) are indicated. Note sublayers in layers II and IV. Medial is to the right, and dorsal to the top.

Functional Significance

The lateral geniculate nucleus is the major source of visual information to cortex. Almost all of the relay is to one visual area, the primary field, and this field is directly or indirectly responsible for activating almost all of the extensive array of extrastriate visual areas [see Allman, this volume]. The geniculate relay includes all or nearly all of the output of the retinal X cells, the W-cell influence from both the retina and superior colliculus, and most of the Y cells of the retina. Some Y-cell and W-cell information, first projected to the superior colliculus, may reach cortex via the superior colliculus projections to the pulvinar. However, disrupting the geniculocortical pathway eliminates all X-cell information, perhaps all or nearly all of the W-cell information, and most of the Y-cell information from visual cortex.

Given the dependence of the cortical visual system on the geniculostriate pathway, it is not surprising that striate cortex or LGN lesions have severe effects on visual behavior. Although little is known about the behavioral consequences of lesioning the geniculostriate system in prosimians and New World monkeys, the impairments produced by such lesions in macaque monkeys and humans appear to be quite similar. In both humans and monkeys, object or form vision, as it is normally understood, is lost. Humans, at least, have no awareness of seeing anything. Since some visually guided behavior is possible, the vision of such patients has been referred to as "blindsight." However, some investigators believe that some of the abilities attributed to blindsight are attributable to light scatter and the functions of spared parts of the geniculostriate [see Campion et al, 1983].

Systematic studies on macaque monkeys indicate that a few visual functions clearly remain after complete removal of the geniculostriate system [see Pasik and Pasik, 1982, 1983]: 1) Pupillary constriction to light remains, apparently as a function of the pretectum. 2) Blinks to increase in illumination remain as a function of the pretectum. 3) Optokinetic nystagmus recovers as a probable function of the accessory optic system. 4) Some spatial localization recovers, apparently as a function of the superior colliculus. 5) The capacity for discrimination of targets differing in brightness and total luminous flux recovers, apparently as a function of the accessory optic system. 6) Discriminations of targets equated for total luminance flux, but differing in brightness and area or total amount of contour, recover, apparently owing to information relayed from the superior colliculus to the pulvinar and thereby to cortex. Although the relay of retinal information is a major function of the LGN, another, less understood function is to modify the information in the transfer process. Brainstem inputs to the geniculate may modify the transfer with changes in oculomotor behavior, alertness, and attention, and direct and indirect cortical feedback may selectively enhance or inhibit subsets of geniculate neurons.

THE SUPERIOR COLLICULUS

Introduction

The superior colliculus is a laminated structure that occupies the rostral tectum of the midbrain and plays a dual role in vision: participating in the transmission of visual information to thalamic structures associated with perception, and participating in the transformation of visual and other types of information into signals controlling eye and head movements. To some extent, these two roles are compartmentalized within the superior colliculus, so that the superficial layers may have a role in perception and attention while deeper layers mediate visuomotor functions. Although the primate superior colliculus has not been studied as extensively as the lateral geniculate nucleus, evidence to date suggests that its structure, connections, and functions are generally similar across primates and across other mammals. The interspecies differences that are apparent are discussed below.

The Laminar Pattern and Histochemistry

Seven layers are traditionally recognized within the superior colliculus of primates and other mammals (Fig. 11). These layers are arranged concentrically around the dorsolateral aspects of the central gray and are consecutively numbered from the superficial (layer I) to the deep (layer VII) aspect of the tectum. Layers predominantly composed of fibers alternate with more cellular layers. Thus, layers I, III, V, and VII are fibrous, and layers II, IV, and VI are cellular. Some collicular layers can be further subdivided on the basis of cytoarchitecture, histochemical characteristics, and connections. The layers can be grouped into the superficial layers (I–III), intermediate layers (IV and V), and deep layers (VI and VII). Nevertheless, because of apparent connectional and functional similarities, the intermediate and deep layers are often considered together and can be referred to as the deeper layers [Huerta and Harting, 1984].

Layer I (Stratum Zonale, or SZ). Layer I lies immediately beneath the pial surface, varies in thickness from 20 to 50 μm, and is primarily composed of myelinated axons [Lund, 1972] that terminate deeper in the tectum. Most of these axons course from rostrolateral to caudomedial across the superior colliculus and are the processes of corticotectal cells [Wilson and Toyne, 1970; Lund, 1972; Hubel et al, 1975]. Layer I also contains dendrites of neurons arising in deeper layers (mainly layer II), a few small neurons in the range of 10 μm in diameter, axon terminals, presynaptic dendrites, and glial cells [Tigges and Tigges, 1975; Tigges et al, 1973, 1977].

Layer II (Stratum Griseum Superficiale, or SGS). Layer II is a 250- to 400-μm thick layer of densely packed small cells just under layer I. Typically, two sublayers are apparent, although the distinction is more obvious in some primates than others. Specifically, in galagos, lorises, marmosets, squirrel monkeys, and macaque monkeys, the dorsal one-half to two-thirds of the SGS is populated by closely packed, round cells which stain darkly for Nissl substance; the ventral one-third to one-half of the SGS is populated by somewhat larger, often oval-shaped neurons which stain more lightly for Nissl substance [Tigges and Tigges, 1970; Huerta and Harting, 1983].

Stains for cytochrome oxidase, an enzyme associated with high levels of neural activity [see Wong-Riley and Carroll, 1984], usefully identify the SGS as a layer with a high concentration of the enzyme with the superficial sublayer staining more densely than the deeper sublayer. In macaque monkeys and humans, at least, the layer II also stains densely for acetylcholinesterase [Graybiel, 1978b, 1979; Stampalija and Kostovic, 1981].

The types of cells in the superficial gray layer are largely known from studies on nonprimate mammals. Ramon y Cajal [1911] called the layer the zone of horizontal cells, and many of the neurons within the layer have dendrites that are oriented in the plane parallel to the layers. Many of the neurons have restricted dendritic arbors, often oriented vertically, whereas others have dendrites that extend in all directions [see Huerta and Harting, 1984, for review]. Neurons include a scattering of GABA-accumulating types that presumably are inhibitory in function [Mize et al, 1982]. Some of the neurons appear to be intrinsic, with axonal connections within and below the SGS, and many are projection neurons with thalamic connections (see below).

Layer III (Stratum Opticum, or SO). The stratum opticum is so named because it consists mostly of axons of the retinal ganglion cells that course from rostrolateral to caudomedial in the superior colliculus to terminate in SGS. Because axons have to terminate along the way, the stratum opticum is thicker rostrolaterally. The thickness of the layer ranges from 200 μm in small prosimians and monkeys to 500 μm in larger monkeys, apes, and humans. The stratum opticum contains relatively few neurons, and these are typically of medium size. The stratum opticum stains very lightly for cytochrome oxidase.

Layer IV (Stratum Griseum Intermediale, or SGI). Layer IV is the thickest layer of the primate superior colliculus, ranging in thickness from 800 μm in galagos to 1,300 μm in macaque monkeys. The SGI contains a mixture of small to large neurons that are more densely packed in a dorsal than in a ventral sublayer. The sublayers are also reflected by denser cytochrome oxidase staining in the dorsal sublayer. The lower cell packing and lower level of cytochrome oxidase activity in the ventral sublayer are at least in part due to the mixture of axon fascicles with the neurons. In macaque monkeys and humans, at least, stains for acetylcholinesterase reveal dense patches of activity within layer IV [Graybiel, 1978b, 1979; Ishii and Friede, 1967]. Possibly, these patches reflect the uneven distribution of one of the many afferents that distribute in a patchy manner in this layer [Huerta and Harting, 1984].

Layer V (Stratum Album Intermediale, or SAI). Layer V is one of three deeper layers that tend to merge architectonically and that are therefore somewhat difficult to separate. Together, they are about as thick as layer IV. Layer V is characterized by axons of cells in layer IV that descend and course laterally to brainstem targets. Thus, layer V is thicker and more distinct laterally than medially. Neurons are loosely packed in layer V.

Layer VI (Stratum Griseum Profundum, or SGP). Layer VI is composed of loosely packed neurons of a range of sizes intermingled with myelinated fibers. The layer is higher in cytochrome oxidase activity than adjoining layers.

Layer VII (Stratum Album Profundum, or SAP). The deepest layer, the SAP, is adjacent to the periaqueductal gray and largely consists of myelinated axons coursing mediolaterally along the outer margin of the periaqueductal gray, together with a sparse scattering of neurons of various sizes.

Connections of the Superficial Layers

Retinal Inputs. Ganglion cells of the retina provide the major input to the superficial layers of the superior colliculus in primates and other mammals. The inputs have a characteristic distribution in the superficial layers that is somewhat variable among species (Fig. 13). Patterns of retinal terminations in the superficial layers have been described for several prosimian primates (*Galago* [Tigges and Tigges, 1970; Laemle and Noback, 1970; Weller and Kaas, 1982; Huerta and Harting, 1984], *Perodicticus potto* [Giolli and Tigges, 1970], *Nyctice-*

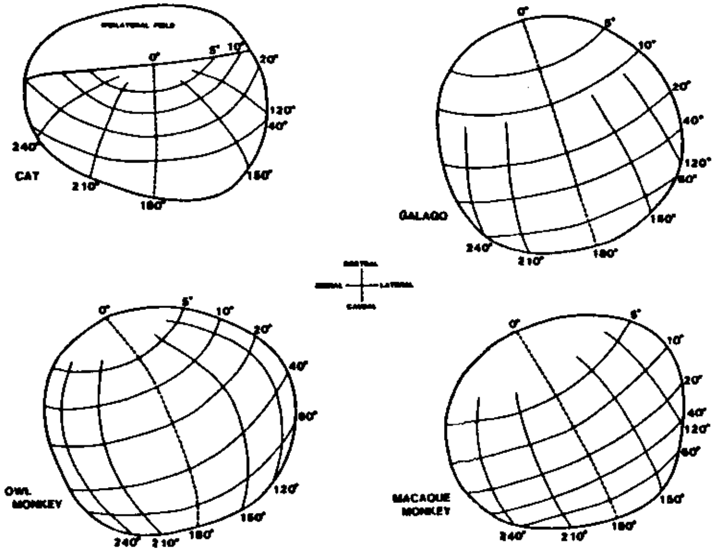

Fig. 12. Retinotopy of the contralateral superior colliculi of cat, galago, owl monkey, and macaque monkey based on recording of neural activity. Lines mark polar coordinates from the point of fixation.

bus coucang [Laemle and Noback, 1970]), a range of species of New World monkeys (*Aotus trivirgatus* [Weller and Kaas, 1982; Huerta and Harting, 1984], *Saimiri sciureus* [Tigges and Tigges, 1981; Huerta and Harting, 1984], *Ateles ater* [Florence et al, 1986], *Pithecia pithecia* [unpublished observations], *Saguinus oedipus* [unpublished observations]), Old World monkeys (*Macaca* [Wilson and Toyne, 1970; Hubel et al, 1975; Pollack and Hickey, 1979; Cowey and Perry, 1980; Weller and Kaas, 1982; Perry and Cowey, 1984]), and an anthropoid ape (*Pan troglodytes* [Tigges et al, 1977]). In all these primates, the superior colliculus receives input from both eyes, and the distribution from the ipsilateral eye differs from that from the contralateral eye. Typically, the input from the ipsilateral eye terminates deeper in the colliculus, is less dense, and is more discontinuous in distribution (Fig. 13). The ipsilateral input, of course, does not terminate in the caudomedial pole of the colliculus, where the monocular visual field is represented via projections from the contralateral eye (ipsilateral retinal input does, however, reach the rostrolateral pole, where the vertical meridian is represented; Fig. 12). In addition, a small, oval-shaped region centered in the colliculus has no terminations from the contralateral eye. This oval corresponds to the optic disk of the nasal retina, which, of course, has no ganglion cells.

The major species differences in the patterns of terminations are shown in Figure 13. In all prosimians examined, the contralateral input forms a fairly uniform distribution throughout the most superficial third of the superficial gray (layer II). The ipsilateral input, which is less continuous, terminates in a sublayer just under the contralateral input. This strict segregation of inputs in different levels of the superficial gray is not seen in other primates. The patterns of terminations from the retina in New World monkeys, Old World monkeys, and apes appear to be roughly similar in that both the ipsilateral and contralateral inputs are discontinuous, although the ipsilateral inputs are more so, and the ipsilateral terminations tend to be deeper but not completely segregated at a deeper level from the contralateral inputs. The rostrolateral colliculus, where central vision is represented, tends to have very sparse retinal terminations, but this feature is less marked in the nocturnal owl monkey than in diurnal monkeys with foveal vision. The inputs to the rostrolateral colliculus are so reduced in macaque monkeys, for example, that the first studies with relatively insensitive techniques failed to reveal any retinal terminations in the representation of foveal vision. This relative sparseness of retinal input relates to an expansion of central vision in the tectum that is greater than the increase in retinotectal projecting cells in the central retina (see below).

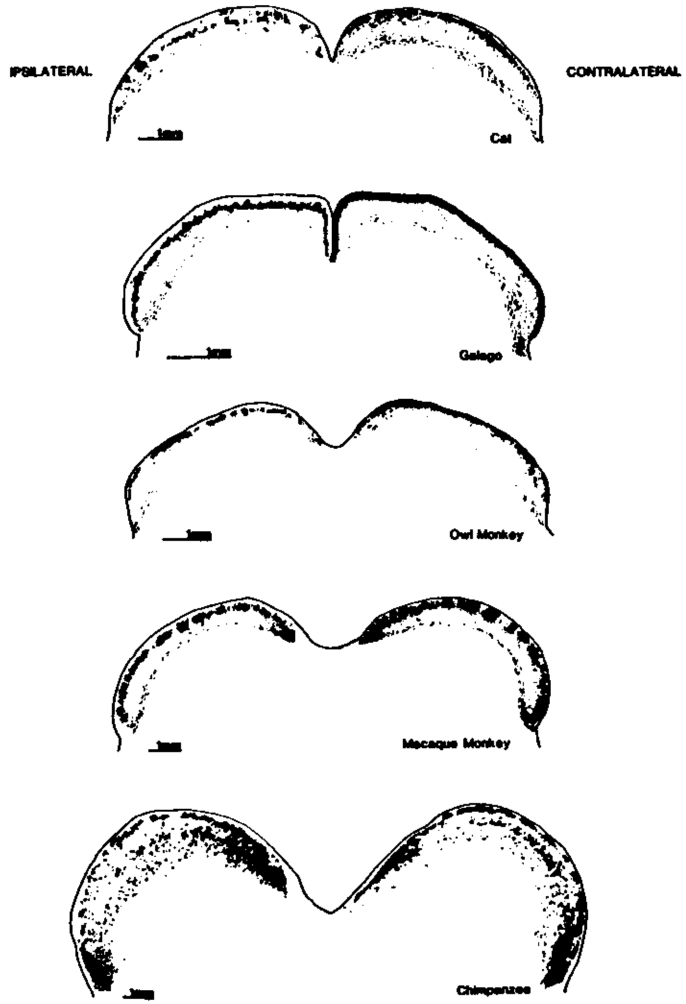

Fig. 13. Schematic representation of distribution of retinal projections to binocular portions of the colliculi of the cat, galago, owl monkey, macaque monkey, and chimpanzee. Drawing of chimpanzee material is after autoradiogram (level 699) in Tigges et al [1977].

Injections of retrogradely transported tracers into the superior colliculus reveal that for galagos [unpublished observations], squirrel monkeys [unpub-

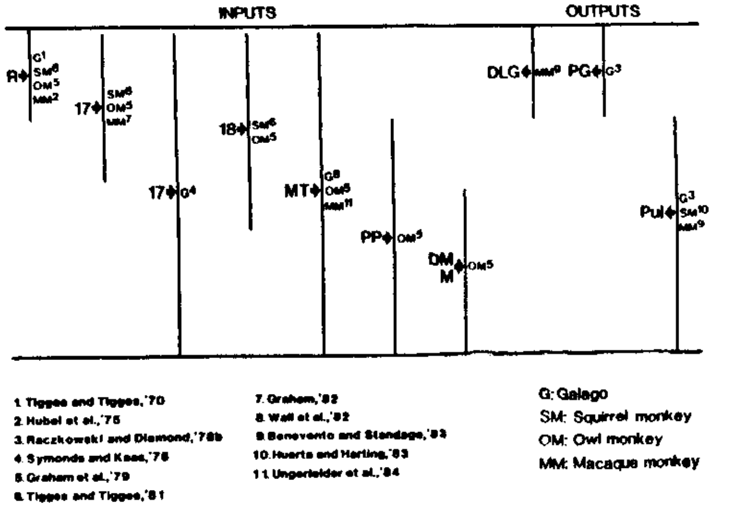

Fig. 14. Schematic representation of sublaminar arrangement of inputs and outputs of superficial layers in a varicty of primates. R, retina. See Fig. 16 for 17, 18, MT, PP, and DM. PG, pregeniculate; Pul, pulvinar, DLG, dorsal lateral geniculate.

lished observations], macaque monkeys [Perry and Cowey, 1984], and presumably all primates, the projection to the superior colliculus is confined to the nasal hemiretina of the contralateral eye and the temporal retina of the ipsilateral eye, with a line of decussation through the fovea or area centralis. However, along the line of decussation there is a narrow strip of retina where cells projecting to one side of the brain or the other are mixed. These studies also indicate that only a minority of ganglion cells project to the superior colliculus, and that the cells are only of certain classes. In macaque monkeys, for example, Perry and Cowey [1984] estimate that only 10% of the ganglion cells (about 110,000 from each eye) innervate the superior colliculus. Most of the retinal ganglion cells (80% or more) belong to the X-like class, and this class projects exclusively to the parvocellular layers of the lateral geniculate nucleus (see LGN section). However, ganglion cells in the Y-like class project to both the lateral geniculate nucleus and superior colliculus, in part via collaterals. The heterogeneous W-like "class" also provides inputs to both the lateral geniculate nucleus and the superior colliculus. Since the X-like cells rapidly increase in both numbers and proportions toward central vision, the relative projections of the Y and W classes are reduced. Since the proportion of the superior colliculus devoted to central vision is roughly comparable to that of the LGN, retinal terminations in the representation of central vision in the rostrolateral colliculus are sparser than elsewhere.

Cortical Inputs. Injections of retrogradely transported tracers into the superior colliculus indicate that most areas of neocortex project to the superior colliculus, and injections of anterogradely transported tracers into cortical fields demonstrate that many of the projections are to the superficial layers of cortex. In general, the projections are from neurons in cortical layer V, ipsilateral, topographically organized, uniformly distributed across the horizontal dimension of the colliculus, and related to different depths in the superficial gray according to cortical field. The major cortical inputs to the superficial colliculus layers are from the subdivisions of visual cortex.

Visual inputs

A large extent of the posterior half of neocortex is visual in function [see Allman, this volume], and apparently all of this cortex projects to the superior colliculus. In macaque monkeys, for example, large injections of horseradish peroxidase in the superior colliculus label neurons throughout all known visual areas [Fries, 1984], and injections in various subdivisions of visual cortex in owl monkeys [Graham et al, 1979] all demonstrate terminations in the superficial layers of the colliculus (Fig. 14). Most of the input is from ipsilateral visual areas, but some input is from contralateral cortex [eg, Distel and Fries, 1982].

Collicular projections from primary visual cortex have been well established in a number of primate species. In prosimians [Tigges et al, 1973; Symonds and Kaas, 1978], New World monkeys [Spatz et al, 1970; Graham et al, 1979; Tigges and Tigges, 1981], and Old World monkeys [Wilson and Toyne, 1970; Ogren and Hendrickson, 1976], this projection is homotopic and overlaps the retinal terminations in the stratum griseum superficiale. Cells projecting to the superior colliculus are largely layer V pyramidal cells with some layer VI cells [eg, Fries, 1984]. The layer VI cells projecting to the superior colliculus include the large Meynert cells, which also project to the middle temporal visual area (Fig. 16) [see Allman, this volume; Kaas, 1986]. At least half of the Meynert cells project via collaterals the same information to MT and the superior colliculus [Fries et al, 1985]. Since layer V cells also project to the pulvinar [eg, Lund et al, 1975] and to the region of the pons projecting to the cerebellum [Glickstein et al, 1980], neurons projecting to these targets may have axons that also branch to the superior colliculus. Apparently all of the information projected to the superior colliculus from area 17 is from cells dominated by Y-like retinal ganglion cell influences and with orientation-selective and often direction-selective receptive fields [Finlay et al, 1978; Schiller et al, 1979].

Projections from area 18 (V-II) to the superior colliculus have been described for New World and Old World monkeys [Graham et al, 1979; Tigges and Tigges, 1981; Fries, 1984] and probably exist for all primates. The inputs from V-II are homotopic (retinotopic), originate from layer V cells, and terminate slightly deeper in the superficial gray than the inputs from VI (Fig. 14).

The middle temporal area (MT) is the only other visual area that has been identified with certainty in a range of primate species. Projections from MT to the superior colliculus have been demonstrated for galagos [Wall et al, 1982], New World monkeys [Spatz and Tigges, 1973; Graham et al, 1979], and Old World monkeys [Ungerleider et al, 1984]. The projections are in topographic register with the retinotopic organization of the superior colliculus, originate from layer V cells, and terminate deep in the superficial gray. Neurons providing this input, judging from the response characteristics of 95% of the neurons in MT [see Kaas, 1986; Allman, this volume, for review], are orientation- and direction-selective, are not color-coded, and appear to represent a higher level of processing of Y-like ganglion cell information.

Less is known about the contributions of other areas of visual cortex to the superior colliculus. Apparently, layer V cells in all parts of visual cortex provide some input [eg, Fries, 1984]. In addition, inputs of extrastriate visual areas terminate deeper in the superficial gray than do the inputs from V-II and V-I [Graham et al, 1979] (Fig. 14).

Auditory, somatosensory, motor, and other inputs

In macaque monkeys, there is evidence that both primary and other auditory fields project to the superior colliculus [see Fries, 1984]. Anterior parietal cortex, including somatosensory fields 3a, 3b, 1, and 2, does not appear to project to the superior colliculus, but some layer V cells in the region of the second and other somatosensory areas in the lateral fissure do. Other inputs are from motor and premotor areas and frontal eye fields. However, the contribution of the motor areas and frontal eye fields is largely or completely to the deep layers of the colliculus (see below), and the auditory and somatosensory inputs are probably largely or completely to the deeper layers as well.

Other Inputs. Other inputs to the superficial layers have not been well documented in primates. Data from work in cats indicate that pretectal nuclei and the parabigeminal nucleus project specifically to the superficial layers [see Huerta and Harting, 1984, for review]. A pretectocollicular projection has been reported in the rhesus monkey [Benevento et al, 1977], and our unpublished preliminary results indicate that pretectal nuclei and the parabigeminal nucleus also innervate the superior colliculus of the galago, but our work does not reveal which layers receive these afferents.

In summary, the superficial collicular layers receive afferents from the retina, a variety of visual cortical areas, the parabigeminal nucleus, and the pretectal nuclei. Many of these projections occupy a particular zone (which may cross laminar bound-

TABLE II. Connections of the Superior Colliculus

Afferents	Efferents
Vision	Superficial layers (I–III)
Retina	Vision
Parabigeminal nucleus	Dorsal lateral geniculate nucleus
Pretectum	Ventral (pre-) geniculate nucleus
Ventral lateral geniculate nucleus	Inferior pulvinar
Audition	Lateral pulvinar
Inferior colliculus	Parabigeminal nucleus
Periolivary nucleus	Pretectum
Trapezoid body	Selective attention
Ventral nucleus of lateral leminiscus[a]	Inferior pulvinar
Somatosensation	Lateral pulvinar
Principal trigeminal nucleus[a]	Deeper layers (IV–VII)
Spinal trigeminal nucleus	Vision
Dorsal column nucleus	Medial pulvinar
Lateral cervical nucleus[a]	Lateral pulvinar
Spinal cord (dorsal horn)	Selective attention
Eye movements	Ventral anterior nucleus, magnocellular part
Nucleus posterior commissure	Lateral dorsal nucleus
Substantia nigra	Mediodorsal nucleus, paralamellar part
Pontine reticular formation	Parafascicular nucleus
Contralateral layer IV, superior colliculus	Medial pulvinar
Mesencephalic reticular formation	Suprageniculate-limitans complex
Miscellaneous	Paracentral nucleus
Zona incerta	Oral pulvinar
Reticular nucleus of thalamus	Central lateral nucleus
Sagulum	Lateral posterior nucleus
Locus coeruleus	Lateral pulvinar
Dorsal raphe nucleus	Eye movements
Lateral parabrachial nucleus	Rostral interstitial nucleus of MLF
Deep cerebellar nucleus[a]	Interstitial nucleus of Cajal
Medullary reticular formation	Supraoculomotor zone
Medial vestibular nucleus[a]	Paramedian pontine reticular formation
Perihypoglossal nucleus[a]	Medial accessory nucleus
	Mesenphalic reticular formation
	Nucleus of the posterior commissure
	Dorsolateral pons
	Nuclear reticularis teg. pont.
	Abducens nucleus
	Head and other movements
	Ventral anterior nucleus
	Substantia nigra
	Cuneiform nucleus
	Nucleus reticularis pontis oralis
	Ventral and intermediate horns of cervical spinal cord
	Ventral lateral nucleus
	Paralemniscal zone
	Miscellaneous
	Central latocellular nucleus
	Central densocellular nucleus
	Lateral hypothalamic area
	External medullary lamina
	Central superior nucleus
	Edinger-Westphal nucleus
	Tegmentum medial to parabigeminal nucleus
	Capsule of inferior colliculus
	Dorsal hypothalamic area
	Nucleus reuniens
	Zona incerta
	Central gray

[a] Connection demonstrated in cats.

aries; Fig. 14), and, except for the apparently interdigitating inputs from contralateral and ipsilateral retinae in simians, most distribute uniformly throughout sublamina. It is likely that all of these inputs are topographically organized.

Outputs. The efferent connections of the superficial layers appear to be generally similar in species studied so far (Table 2; Fig. 14). The superficial layers ipsilaterally innervate the parabigeminal nucleus, pretectal nuclei, inferior pulvinar complex, dorsal lateral geniculate nucleus, and ventral lateral geniculate nucleus (the pregeniculate nucleus) in prosimians [Glendenning et al, 1975; Fitzpatrick et al, 1980; Harting et al, 1986], New World monkeys [Lin and Kaas, 1979; Mathers, 1971], and Old World monkeys [Harting et al, 1978, 1980; Partlow et al, 1977; Benevento and Fallon, 1975; Huerta and Harting, 1984]. Sparse projections to the lateral pulvinar have been noted in some studies on monkeys [Harting et al, 1980].

Cells of origin of some of the efferent connections of the superior colliculus are largely restricted to sublayers (Fig. 14), so neurons projecting to the lateral geniculate nucleus occupy the dorsal half of layer II, and those projecting to the inferior pulvinar are situated in the ventral half of layer II [Raczkowski and Diamond, 1978b; Benevento and Standage, 1983; Huerta and Harting, 1983]. Projections to the interlaminar zones and S layers of the lateral geniculate nucleus in simians and the interlaminar zones and koniocellular layers in prosimians are via thin axons that appear to reflect a relay of W-like ganglion cell information (see Lateral Geniculate section). Projections to the pulvinar complex seem likely to relay Y-cell information (see Pulvinar section).

In summary, the efferent connections of the superficial layers appear generally similar across the primate species studied thus far (Table 2; Fig. 14). These layers innervate pretectal nuclei, the dorsal and ventral lateral geniculate nuclei, the parabigeminal nucleus, parts of the inferior pulvinar complex, and, in some primates at least, part of the lateral pulvinar. Cells of origin of particular superficial tectofugal pathways are often restricted to specific sublaminae (Fig. 14).

Connections of the Deeper Layers

Inputs. The deeper layers (IV–VII) of the superior colliculus comprise an important center for visuomotor integration [Wurtz and Albano, 1980; Stein, 1984; Schiller, 1984]. Despite their importance, vastly less is known about the afferents to the deeper layers than is known about inputs to the superficial layers in primates. In fact, a comprehensive list of subcortical inputs has not yet been published for any primate. Nevertheless, recent preliminary (unpublished) studies in our laboratory reveal that most of the deeper collicular afferents described for the cat [Edwards et al, 1979] are also present in the galago. As depicted in Table 2, the deeper collicular layers receive input from a large number of subcortical structures which are functionally diverse [also see Beckstead and Frankfurter, 1982, 1983; Hikosaka and Wurtz, 1983a–d]. Such inputs may provide visual, auditory, and somatosensory as well as motor-related information to the deeper layers.

Several studies have shown that the prearcuate cortex, including the frontal eye field and area 8 of Brodmann [1905], projects heavily, and in a mottled manner, to layer IV and, to lesser extents, to the remaining deep collicular layers of macaque monkeys, squirrel monkeys, and owl monkeys [Kunzle et al, 1976; Leichnetz et al, 1981; Lynch et al, 1985; Komatsu and Suzuki, 1985; Astruc, 1971; Kunzle and Akert, 1977; Huerta et al, 1986]. A similar projection arises from the inferior bank of the intraparietal sulcus in macaque monkeys [Lynch et al, 1985]. Like prearcuate cortex, this cortical region has also been implicated in visuomotor function [eg, Hyvärinen, 1982; Mountcastle, 1981].

Other cortical inputs to the superior colliculus are best known for macaque monkeys. The auditory, posterior parietal, inferior temporal, and frontal premotor areas of cortex appear to project to the deeper layers of the superior colliculus [Fries, 1984]. These cortical areas are thought to be involved in selective attention, visuomotor and motor functions, "spatial" and "object" vision, audition, and somatosensation [see Fries, 1984, for discussion]. Virtually all of the cortical cells that innervate the deeper layers occupy layer V of their respective cortical areas [Fries, 1984]. In summary, a large number of cortical and subcortical structures carry a great variety of types of information to the deep layers of the superior colliculus (Table 2).

Outputs. The outputs of the deep layers have been studied in prosimian galagos and Old World monkeys. In galagos, layers IV and V have been reported to project to the contralateral brainstem tegmentum via the predorsal bundle [Glendenning et al, 1975]. Ipsilateral projections from layers IV and V reach the mesencephalic reticular formation, intralaminar nuclei, nuclei of the posterior group, nucleus limitans, and zona incerta [Glendenning et al, 1975]. It appears that the deeper layers in the galago also project to the lateral portion of the medial dorsal nucleus, subthalamic regions medial to the zona incerta, and, very sparsely, the lateral pulvinar [Glendenning et al, 1975].

In macaque monkeys, the efferent connections have been studied in more detail. Descending tectofugal axons from the deeper layers reach much of the brainstem tegmental reticular formation via two major bundles. The first courses along the lateral extent of the central gray, crosses the midline in the dorsal tegmental decussation, and travels ventrocaudally in the predorsal bundle (or tectospinal tract) just off the midline [Harting, 1977]. From this bundle axons distribute to the paramedian pontine reticular formation (ie, medial portions of nuclei reticularis pontis oralis and caudalis) and to nucleus reticularis tegmenti pontis. Further caudally, deep collicular fibers exit the predorsal bundle to project to subnucleus b of the medial accessory olive [Harting, 1977]. The second major bundle of descending tectofugal fibers travels in the lateral portion of the ipsilateral tegmentum, distributing to the mesencephalic reticular formation, rostrolateral portions of nucleus reticularis pontis oralis, the capsule of the inferior colliculus, the cuneiform nucleus, the dorsolateral pontine gray, and nucleus reticularis tegmenti pontis [Harting, 1977]. Many of these targets relay to the cerebellum; others have connections with oculomotor nuclei [see Fuchs et al, 1985; Brodal, 1982].

The deeper collicular layers in macaque monkeys project to a large number of rostral targets, many of which receive inputs from the frontal eye fields and are known or thought to participate in visuomotor activity [see Huerta et al, 1986; Schlag-Rey and Schlag, 1984; Schlag and Schlag-Rey, 1984]. These include the medial, lateral, and anterior subdivisions of the pulvinar; the nucleus limitans-suprageniculate complex; lateral portions of the medial dorsal nucleus; the parafascicular nucleus; the nucleus of the posterior commissure; the zona incerta; the rostral interstitial nucleus of the medial longitudinal fasciculus; the paracentral nucleus; and the magnocellular part of the ventral anterior nucleus [Benevento and Fallon, 1975; Partlow et al, 1977; Benevento and Standage, 1983]. In recent unpublished studies, we have found that the ascending and descending projections of the deeper collicular layers of the squirrel monkey strongly resemble those of macaque monkeys.

In summary, the deeper collicular layers project to a large number of rostral and caudal targets, many of which participate in visuomotor function (Table 2). These include parts of the pons that in turn project to cerebellar zones implicated in eye movement functions, parts of the pons and midbrain with connections with oculomotor nuclei, and thalamic nuclei thought to have visuomotor functions.

Morphological and Physiological Characteristics of Neurons

The superior colliculus of primates contains neurons of several morphological and physiological types. The morphological types of neurons in the primate superior colliculus have not been extensively studied outside the reports of Laemle [1981, 1983], but it appears from the studies on humans, macaque monkeys, and squirrel monkeys that these primates differ little in the basic types of neurons and that the neuron types are those also found in other, more commonly studied mammals such as cats and rats. Common neurons are stellate or multipolar cells with primary dendrites lacking specific orientation. Stellate neurons are distributed throughout both superficial and deep layers, but they tend to be much smaller in the superficial layers, where they are sometimes referred to as granule cells. Both projection neurons and local circuit neurons are thought to be of the stellate morphology. They are suited to gather information locally over a limited space. Vertical or spindle-shaped neurons differ by having dendritic orientations perpendicular to the layers. They, too, are thought to be both projection and local-circuit neurons. Vertical cells gather information over a limited retinotopic zone and are found in both superficial and deep layers. Large multipolar neurons with vertically and horizontally oriented dendrites occur in the deeper layer, where they have been called pyramidal neurons. They gather information over larger portions of the colliculus and are likely to contribute to descending projections. Finally, horizontal cells are characterized by a soma that is fusiform and orientated parallel to the layers. Dendrites originate from each pole and extend 500 μm or more along the layers. They are found in both superficial and deep layers, and they are likely to be inhibitory interneurons, since they have flat synaptic vesicles [Tigges and Tigges, 1975] and contain GABA in cats at least [Mize et al, 1982].

The response properties of neurons in the superior colliculus have been studied rather extensively [for review, see Goldberg and Robinson, 1978; Wurtz and Albano, 1980; Sparks and Mays, 1983a; Schiller, 1984; Chalupa, 1984; Stein, 1984]. Most of the information comes from studies on macaque monkeys, and there is little comparative information on species differences.

Superficial Layers. Neurons throughout layers I–III are responsive to visual input, and the responses are basically consistent with the properties of the Y-like or "broad-band" and W-like or "poorly responding" retinal ganglion cells that are known to project to the colliculus [Schiller and Malpeli, 1977; Marrocco and Li, 1971]. In keeping with the Y-like inputs, neurons typically are not color-selective [however, see Kadoya et al, 1971b], have a relatively short latency to visual stimulation, and respond in a transient manner to stimulus onset or offset.

The receptive fields of superficial collicular neurons are larger than their retinal or dorsal lateral geniculate nucleus counterparts. As in other visual structures, the size of the receptive field varies as a function of location in the representation of visual space, being smaller near the representation of central space and larger near the representation of the periphery [eg, Cynader and Berman, 1972; Lane et al, 1974]. In addition, cells deeper in the superficial layers have larger receptive fields than do cells in less deep parts, even though the receptive field center occupies the same point in space.

The typical receptive field of a neuron in the superficial layers has a center from which visual stimuli evoke responses at onset and/or offset and a suppressive surround or flank which, when stimulated in conjunction with the center, decreases the response but which, when stimulated alone, does not produce a response [Schiller and Koerner, 1971; Goldberg and Wurtz, 1972a; Cynader and Berman, 1972; Updyke, 1974; Schiller and Malpeli, 1977]. In the squirrel monkey, receptive fields with segregated "on" and "off" regions have also been reported [Kadoya et al, 1971a]. Moreover, these units are concentrated in a specific intermediate sublamina of layer II [Kadoya et al, 1971a]. In addition, neurons respond to moving stimuli. In macaque monkeys, one-fifth or less of the neurons demonstrate some preference for a particular direction of movement [Cynader and Berman, 1972; Goldberg and Wurtz, 1972a; Marrocco and Li, 1977; Schiller and Stryker, 1972; Schiller and Koerner, 1971]. In squirrel monkeys [Kadoya et al, 1971a,b], there may be a somewhat stronger tendency for collicular cells to be selective for the direction of stimulus movement; in the latter monkey, units that respond to stationary stimuli are concentrated in the upper part of layer II, whereas those responding to moving stimuli are most prevalent in the lower part of layer II and in layer III [Kadoya et al, 1971a,b].

The majority of superficial collicular neurons respond to stimuli presented to either eye, with one eye usually being more effective than the other in driving responses [Schiller and Koerner, 1971; Updyke, 1974; Marrocco and Li, 1977]. Since the contralateral and ipsilateral retinal projections appear to be somewhat segregated in the superficial layers, it might be expected that this binocularity is conferred upon the superficial neurons by the afferents from striate cortical neurons (which are binocular) [Finlay et al, 1978]. The binocularity of neurons in the superior colliculus of cats, in fact, does depend on visual cortex [Wickelgren and Sterling, 1969]. Despite this expectation, inactivation or abolition of striate cortical input has little effect on most properties of superficial collicular cells, including their binocularity [Schiller et al, 1974]. However, it seems possible that the property of direction selectivity, which is present in cortical cells projecting to the superior colliculus [Finlay et al, 1978] and not in ganglion cells, is dependent on cortical inputs. In cats, the direction-selective properties of neurons in the superior colliculus depend on visual cortex [Wickelgren and Sterling, 1969].

In addition to "passive" physiological properties such as those described above, the responses of superficial collicular neurons to visual stimuli are also modulated by the behavior of the animal. Superficial cells either exhibit an increased (enhanced) or a decreased (suppressed) response to visual stimuli in relation to saccades. The enhancement is spatially and temporally specific, whereas the suppression is not spatially specific and may be the product of corollary discharge [Goldberg and Wurtz, 1972a,b; Richmond and Wurtz, 1977]. Thus, the visual response is enhanced when an eye movement is made to the location of the neuron's receptive field, whereas the activity of superficial cells decreases when the animal makes a saccade of any size or direction [Goldberg and Wurtz, 1972a].

Deeper Layers. As might be expected from the diversity of cortical and subcortical inputs, the deeper collicular layers are multimodal. Individual neurons in these layers respond to auditory, somatosensory, or visual stimuli either alone or in various combinations [eg, Cynader and Berman, 1972; Stein, 1984; Updyke, 1974]. These inputs are represented topographically, with the map of visual space being the same as that present in the superficial layers and with the size of visual receptive fields positively correlated to depth in the superior colliculus [eg, Updyke, 1984; Stein, 1984; Cynader and Berman, 1972]. Unlike those of the superficial layers, visual responses of neurons in the deeper collicular layers are dependent on cortical input [Schiller et al, 1974].

Although the intermodal relationships have been studied more extensively in nonprimates [see Meredith and Stein, 1986, for review], the activity of deep collicular neurons in relation to eye movements has been stressed in primates. In studies using awake, behaving rhesus monkeys, deeper collicular neurons respond prior to saccadic eye movements of particular sizes and directions [Mohler and Wurtz, 1976a; Schiller and Koerner, 1971; Schiller and Stryker, 1972; Mays and Sparks, 1980a,b; Wurtz and Goldberg, 1972a]. Such cells usually have a visual receptive field, and the location of the receptive field is related to the saccade-related discharge. Specifically, a neuron will discharge prior to an eye movement if the saccade is made to the region of visual space where the visual receptive field of that cell is located; this is called the cell's "movement field." Moreover, electrical stimulation in the region of a particular neuron will elicit a conjugate saccade to the region of visual space that contains the neuron's visual receptive field [eg, Schiller and Stryker, 1972]. Thus, movement fields are topographically organized similar to the map of visual space [Wurtz and Goldberg, 1972a; Mohler and Wurtz, 1976a; Schiller and Koerner, 1971; Schiller and Stryker, 1972], although a relationship between saccades and visuotopic organization is not a simple one [Jay and Sparks, 1984; Harris et al, 1980; Sparks and Mays, 1983a,b; Mays and Sparks, 1980a,b; Sparks and Porter, 1983]. The timing of collicular activity in relation to saccadic eye movements is related to the depth of the cell in the superior colliculus. Typically, cells located in superficial parts of the deeper layers (eg, in the dorsal part of layer IV) discharge tens of milliseconds prior to an eye movement. Neurons located more deeply discharge hundreds of milliseconds before the saccade. Such evidence has led some to suggest that the efferent eye movement signals arise from the superficially located cells of the deep layers [eg, Mohler and Wurtz, 1976a].

The eye movement-related activity of deeper collicular neurons is consistent with the known patterns of outputs and inputs. The deeper layers project to numerous structures that are known, or thought, to be involved with eye movements. In addition, visuomotor cortical areas in prefrontal cortex (eg, the frontal eye field) and parietal cortex (the inferior bank of the intraparietal sulcus) also innervate the deeper collicular layers [eg, Lynch et al, 1985; Leichnetz et al, 1981; Komatsu and Suzuki, 1985; Kunzle et al, 1976; Huerta et al, 1986].

Retinotopic Organization

The organization of the visual input in the superior colliculus has been studied in a number of primates including prosimians (*Galago* [Lane et al, 1973]), New World monkeys (*Saimiri* [Kadoya et al, 1971a], *Aotus* [Lane et al, 1973], *Cebus* [Updyke, 1974]), and Old World monkeys (*Macaca* [Cynader and Berman, 1972]). In all of these primates, the superior colliculus contains a topographic representation of the contralateral visual hemifield via both eyes (see Fig. 12 for galago, owl monkey, and macaque monkey). Central or foveal vision is represented at the rostrolateral pole of the superior colliculus, and successively more peripheral parts of the contralateral visual hemifield are represented in a caudalward progression across the colliculus. The upper visual quadrant is represented medially, and the lower visual quadrant projects laterally. As in other visual structures, the representation of central and paracentral vision is proportionately expanded in the superior colliculus so that much of the rostral pole is devoted to the central 5° of vision. This feature is species-variable, so diurnal monkeys with a well-developed fovea have more of the superior colliculus devoted to the central few degrees of vision than nocturnal monkeys and prosimians (Fig. 12). Because of the expansion of central vision, most of the outer boundary of the superior colliculus corresponds to the zero vertical meridian through gaze (the line of decussation of the retina), and only the caudal pole corresponds to the extreme periphery, the 10° or so of the contralateral visual hemifield that is seen only by the contralateral eye. This portion of the superior colliculus, of course, is activated by only the contralateral eye. The same orderly representation of visual space that is found in the superficial layers is also present in the deeper collicular layers, except that receptive fields are larger and the topography is therefore coarser [eg, Updyke, 1974; Stein, 1984a; Cynader and Berman, 1972].

As stressed above, the superior colliculus of primates, like the lateral geniculate nucleus, represents only the contralateral visual hemifield and does so via both eyes. This type of organization was long thought to be present in the superior colliculus of all mammals. Surprisingly, this has not proved to be the case. The superior colliculus of most mammals receives input from all parts of the retina of the contralateral eye and represents the whole visual field of the contralateral eye, including the portion of the ipsilateral hemifield that is seen by that eye [see Lane et al, 1974; Kaas et al, 1974, for review]. The inputs from the contralateral eye typically dominate the sparser or even absent inputs from the ipsilateral eye. Thus, in nonprimate mammals, the line of decussation of the retina relates to the retinogeniculate rather than the extended retinocollicular projection. An exception may be the megachiropteran bats, where the superior colliculus appears to represent only the contralateral hemifield, as in primates [Pettigrew, 1986]. The significance of this similarity is uncertain, but bats are generally thought to be more closely related to primates than most mammals [see Kaas et al, 1978; Pettigrew, 1986].

Auditory, Somatosensory, and Motor Maps

Whereas the superficial layers (I–III) are exclusively visual, the deeper collicular layers (IV–VII) receive visual, auditory, and somatosensory inputs and contain neurons related to eye and head movements. The visual, auditory, somatosensory, and motor modalities are represented topographically within the deep layers, and these representations are in spatial register with each other [eg, Cynader and Berman, 1972; Stein, 1984; Updyke, 1974; Mays and Sparks, 1980a,b]. Thus, the rostral pole of the superior colliculus is activated by visual stimuli in the center of the visual field, auditory stimuli originating from sources near the midline, and somatosensory stimuli on the face. Electrical stimulation (used to reveal motor topography) of the rostral pole of the colliculus results in almost no eye movement when the animal is already fixating on central visual space. In contrast, the caudomedial pole of the deeper collicular layers contains neurons that are activated by visual and auditory stimuli presented in the contralateral periphery and by somatosensory stimuli on the hind limb, and electrical stimulation of the caudomedial pole results in rather large eye movements directed toward the contralateral periphery.

Development

The embryonic development of the superior colliculus has been extensively studied only in macaque monkeys [Cooper and Rakic, 1981, 1983]. In macaque monkeys, which have a gestation period of 165 days, the cells of the superior colliculus are generated from embryonic days 30 to 56; 90% of the cells are generated between embryonic days 36 and 48, and over half of the collicular neurons are born between embryonic days 38 and 43. There are only slight differences in when cells for different layers are generated. Specifically, neurons for deeper layers of the superior colliculus begin being generated at embryonic day 30, whereas neurons of layer II begin generating somewhat later, after embryonic day 36. In addition, whereas neurons born from embryonic days 30 to 40 are uniformly distributed rostrocaudally, there are more neurons born caudally than rostrally during embryonic days 43–56.

Despite the relatively homogeneous neurogenesis of the rhesus monkey's superior colliculus, lamination is apparent in the rostral tectum by embryonic day 41. A darkly stained ventricular zone and central gray and a more lightly stained superior colliculus can be discerned in Nissl-stained material. Within the superior colliculus proper, three zones are apparent [Cooper and Rakic, 1981]. The most superficial is extremely thin, void of cell bodies, and may correspond to layer I of the adult. Subjacent to this fiber zone is a layer of small neurons that stain darkly and that may contribute mostly to layers II and III of the adult. The remaining, deeper part of the superior colliculus is populated by larger, pale-staining, round cells. One week later, at about embryonic day 54 or 55, the superior colliculus has thickened considerably, and the ventricular zone has thinned considerably. In addition, a cell-sparse zone, which corresponds to layer VII, is obvious just superficial to the central gray, and layer VI is becoming distinct from the overlying layer V. Also at this time, the superficially situated band of darkly staining cells is becoming cytoarchitectonically differentiated. Specifically, at rostral levels, the medial and lateralmost regions of the band remain composed of small, darkly stained neurons, whereas a region between these regions is composed of larger neurons which stain more faintly and which are more loosely packed. The differentiation of the superficial band of cells (which will form layer II and contribute cells to layer III) continues caudally, medially, and laterally, so that by embryonic day 81, most of the superficial band is composed of large, loosely packed, relatively pale-staining neurons. Also by embryonic day 81, all of the layers present in the adult can be distinguished in Nissl-stained material [Cooper and Rakic, 1983].

Although there is no experimental information, the superior colliculus of the human appears to develop similarly to that of macaque monkeys. However, the human development is delayed compared to that of monkeys. Thus, at 9 weeks' gestation the superior colliculus of the human resembles that of the rhesus monkey at embryonic day 47 [Stampalija and Kostovic, 1981; Cooper and Rakic, 1983]. Specifically, in the 9-week fetus there is an acellular "marginal zone" superficially; beneath this zone is a densely and uniformly packed "cellular plate," and the deepest region is composed of a "transitional layer" that comprises less densely packed cells [Stampalija and Kostovic, 1981]. At 15 weeks' gestation, the marginal zone has widened, the cellular plate has differentiated into a dark layer and a light layer, and cells have aggregated into islands within the transitional layer [Stampalija and Kostovic, 1981]. Such an aggregation of cells has not been reported in the rhesus monkey [Cooper and Rakic, 1981, 1983]. One to two weeks later, a cellular layer II and a fibrous layer III are apparent, as are a "deep cellular layer," which contains cell-dense and cell-sparse islands and which probably corresponds to layer IV; a "transitional layer," which may correspond to layers V and VI; and a "layer of commissural fibers," which may correspond to layer VII [Stampalija and Kostovic, 1981]. By gestation week 24, the adult pattern of lamination, with seven clearly defined layers, is present in the superior colliculus of the humans [Stampalija and Kostovic, 1981].

The postnatal development of the superior colliculus has not been well studied in primates. Stein [1984b] has recently reviewed the postnatal development of the superior colliculus in mammals, where much of the relevant data have been collected from cats and rodents. Several general conclusions are likely to apply to primates, which have well-developed visual systems at birth. 1) Adultlike patterns of retinal inputs and hence retinotopic maps are typically present at birth. These patterns include adultlike segregation of ipsilateral and contralateral retinal inputs (nonprimates with long postnatal periods of development before eyes open may be exceptions [see Cusick et al, 1982]). Prenatally, retinal projections are widespread and thus restrict to form the proper retinotopic maps. 2) Efferents responsible for eye movements are largely or completely in place by birth. 3) The response properties of neurons are probably immature, especially in regard to those imposed by cortical inputs, and they gradually mature.

Functional Significance

The two basic types of outputs of the superior colliculus suggest a dual role in visual behavior. The predominant ascending projections of the superficial layers of the colliculus are to the lateral geniculate nucleus and the inferior pulvinar complex, and these structures, via interconnection with visual cortex, are critical for object vision, perception, and visual attention. Thus, the superficial layers could have a role in perception and attention. The deeper layers of the colliculus, in contrast, project largely to brainstem centers involved in generating signals for eye and head movements. Thus, the deeper layers of the colliculus are important in visuomotor behavior. The role of the superficial layers in vision is less certain than the role of the deeper layers, but other types of evidence further support and elaborate both roles.

The superficial layers of the colliculus receive inputs from visual cortex and from the retina, and the neurons appear to be exclusively or nearly exclusively visual. Basic response features of the neurons appear to be more dependent on the direct visual input from the retina than the indirect visual input from the cortex, but the cortical input may add important response features such as directional selectivity. The retinal inputs are from the Y-like and the W-like classes of ganglion cells. The input from striate cortex, at least, appears to be from neurons exclusively influenced by the relay of Y-like ganglion cell information to striate cortex by the magnocellular layers of the lateral geniculate nucleus. The overall properties of Y-like neurons, with rapidly conducting axons and high sensitivity to contrast change, suggest a role in visual attention and the localization of moving and changing objects in the environment [eg, see Kaas, 1986]. The sluggish responses of W cells would seem to limit their possible role in attention to rapid change, but they could have a role in persisting changes in levels of attention or other aspects of vision [see Stone, 1983, for review of hypotheses]. The relay of the superficial layers of the superior colliculus to the lateral geniculate nucleus is from neurons with thin axons, as for W cells of the retina, and is to portions of the geniculate nucleus with direct W-cell inputs. It thus seems likely that the superior colliculus provides a second, perhaps modified source of W-cell information to the lateral geniculate nucleus. The significance of the subsequent role of the relay of W-cell inputs to the cytochrome oxidase "puffs" and layer I of striate cortex is unclear, but it seems likely (see section on the lateral geniculate nucleus) that these inputs modulate the responses of cells in the object vision subsystem related to X-like cells of the retina.

The projection of the superior colliculus to the pulvinar complex may depend more on the Y-cell inputs from the retina and projections from striate cortex from Y-cell-dominated layer V neurons. The superior colliculus inputs to the pulvinar complex appear to modulate neurons projecting to wide regions of striate and extrastriate cortex. The Y-cell system is thought to be important in visual attention [eg, Stone, 1983; Kaas, 1986], and thus the projection of the superficial layers to the pulvinar could have a role in visual attention. Lesions of the superior colliculus produce some deficits that are consistent with possible roles in visual perception and attention. Thus, such lesions produce a decrease in the frequency of saccades to behaviorally irrelevant stimuli in the peripheral visual space [Albano et al, 1982], a decrease in the detection of visual stimuli briefly presented in peripheral vision [Butter et al, 1978], and an increase in the time it takes to find a visual target hidden in visual noise [Latto, 1978].

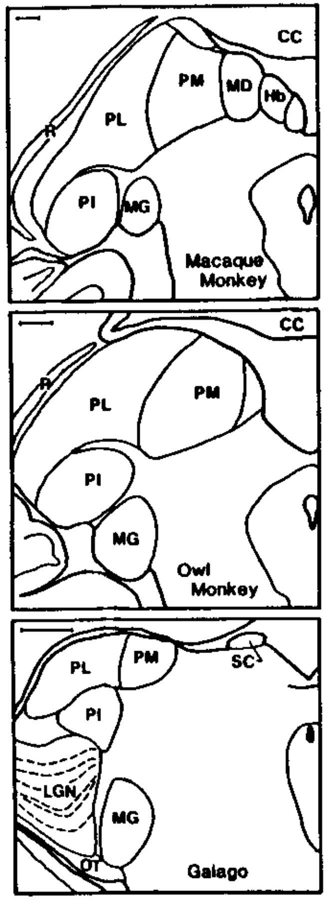

Fig. 15. Major subdivisions of the pulvinar complex. Drawings from frontal brain sections show the relative positions of the lateral (PL), medial (PM), and inferior (PI) divisions of the pulvinar in a macaque monkey (*Macaca fuscata;* Horsley-Clarke plane A8), an owl monkey (*Aotus trivirgatus*), and a galago (*Galago senegalensis*). The cytoarchitectonic border of PL with PM is not distinct and is only approximate in the figures. The anterior or oral division of the pulvinar is anterior to the thalamic levels shown. Other abbreviations are CC, corpus callosum; Hb, habenula; LG, lateral geniculate; MG, medial geniculate; R, reticular nucleus; SC, superior colliculus. Medial is right.

The role of the superior colliculus in visuomotor behavior is better understood. The deeper layers of the superior colliculus receive visual information, in part apparently from the superficial layers, auditory inputs, and somatosensory inputs that indicate where objects worthy of visual attention are located. This information is integrated by neurons in the deep layers that project to brainstem structures that generate the outputs essential for eye and head movements that allow the foveation of attention-getting objects (the target localization or foveation hypotheses [see Schiller, 1984, 1972; Robinson, 1972, for review]). An alternative pathway with the ability to partially compensate for damage to the superior colliculus appears to be from the frontal eye fields to some of the same brainstem structures innervated by the superior colliculus [Schiller et al, 1980]. In support of the foveation hypotheses, lesions of the superior colliculus produce a general decrease in the frequency of eye movements [Anderson and Symmes, 1969; Rosvold et al, 1958; Schiller et al, 1980] and decreases in saccade velocity, size, and fixation accuracy [Pasik et al, 1966; Anderson and Symmes, 1969; Wurtz and Goldberg, 1972b; Keating, 1974; Mohler and Wurtz, 1976b; Kurtz and Butter, 1980; Schiller et al, 1980]. Deficits in eye movements are most pronounced immediately after inactivating the superior colliculus, showing that other structures rapidly compensate for damage [Hikosaka and Wurtz, 1985, 1986].

THE PULVINAR COMPLEX

Introduction

"Pulvinar" is an old term, first applied to the large protrusion from the posterior surface of the human thalamus [see Jones, 1985, for review]. Most modern workers recognize four divisions (Fig. 15), or "nuclei," within the pulvinar complex of at least macaque monkeys—the anterior (or oral) pulvinar, the medial pulvinar, the lateral pulvinar, and the inferior pulvinar [eg, Olszewski, 1952]. Since the anterior pulvinar seems to merge with the medial pulvinar, some investigators have not separated the two, and other investigators have simply distinguished superior (including medial, lateral, and anterior "nuclei") and inferior divisions of the complex. In nonprimates, it is common to call some part or most of the pulvinar complex the "lateral posterior" nucleus. However, in primates, the lateral posterior nucleus is another thalamic region that is basically somatosensory in function. Experimental evidence from studies of connections and electrophysiological mapping studies have greatly added to an understanding of the pulvinar complex, and it is now clear that at least some of the four main "nuclei" should be regarded as divisions rather than nuclei, since at least the inferior and lateral pulvinars appear to contain functionally distinct subdivisions that qualify as nuclei. However, our discussion is organized around the four traditional divisions. Because information is limited, we do not discuss the development of the pulvinar complex. However, Rakic [1974] has described the development of the human pulvinar.

The Inferior Pulvinar

Architectonic Subdivisions. The borders of the inferior pulvinar are relatively standard, since part of the border is formed by the outer margin of the thalamus, and ventral and dorsal fiber bands mark other borders. Architectonically, the division is associated with darkly stained and densely packed neurons, but a number of investigators have noted that the division is not uniform in appearance. For example, Hassler [1959] described two divisions of the inferior pulvinar in the human thalamus. Other researchers have commonly distinguished a "posterior nucleus" on the medial margin of the inferior pulvinar of monkeys [eg, Mathers, 1971], and Glendenning et al [1975] noted a separate "transitional region" within the inferior pulvinar of galagos. Our current understanding of the organization of the inferior pulvinar resulted when patterns of connections with subdivisions of visual cortex and the superior colliculus were related to thalamic architecture in owl monkeys. This research led to the conclusion that the inferior pulvinar contains three separate nuclei—the central nucleus of the inferior pulvinar (PI_C), the medial nucleus of the inferior pulvinar (PI_M), and the posterior nucleus of the inferior pulvinar (PI_P) (Fig. 16). These three nuclei are described first for New World monkeys and then for other primates.

New World monkeys

The position of the inferior pulvinar complex (PI) relative to the lateral pulvinar and other thalamic structures is shown for an owl monkey in Figure 15. PI is distinguished by the densely packed and darkly stained neurons, and fiber bands separate PI from the medial geniculate nucleus and the lateral geniculate nucleus. The fiber band separating the superior from the inferior pulvinar is less apparent, but it is reasonably clear.

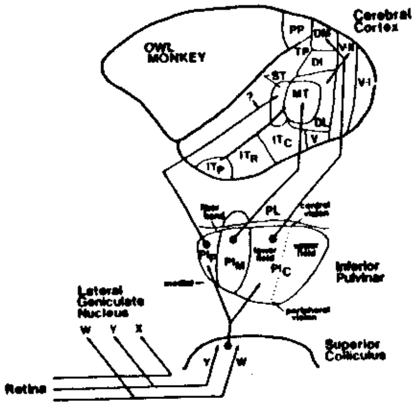

Fig. 16. Some connections of the three nuclei of the inferior pulvinar in owl monkeys. The Y-like and W-like, but not the X-like, ganglion cells of the retina project to the superior colliculus, which in turn projects to the posterior ($\mathrm{PI_P}$) and central ($\mathrm{PI_C}$) nuclei but not the medial nucleus ($\mathrm{PI_M}$) of the inferior pulvinar complex. $\mathrm{PI_C}$ relays to caudal visual areas including primary (V-I) and secondary (V-II) fields, the dorsolateral (DL) and dorsomedial (DM) areas, and probably other fields. $\mathrm{PI_M}$ relays largely to the middle temporal visual area (MT), whereas $\mathrm{PI_P}$ projects to cortex rostral to MT. Subdivisions of cortex with input from PI also project back to PI (see text). The drawing of the inferior pulvinar complex is based on a frontal section with medial to the left. $\mathrm{PI_M}$ protrudes dorsally past the encapsulating fiber band separating the inferior from the lateral pulvinar (PL). In $\mathrm{PI_C}$, central vision is represented dorsally; peripheral vision, ventrally; the lower field, medially; and the upper field, laterally. $\mathrm{PI_M}$ may have a parallel organization with central vision represented dorsally. Cortical fields include the dorsointermediate area (DI), caudal, rostral, and polar divisions of inferiotemporal cortex ($\mathrm{IT_C}$, $\mathrm{IT_R}$, $\mathrm{IT_P}$), posterior parietal cortex (PP), temporal posterior cortex (TP), and ventral visual cortex (V).

In frontal sections, three subdivisions of the inferior pulvinar are apparent (Fig. 16), especially in sections stained for fibers, since each subdivision is somewhat encapsulated by fibers [see Lin and Kaas, 1979]. Differences in connections suggest that each subdivision is a separate nucleus. The large central nucleus of the inferior pulvinar, $\mathrm{PI_C}$, occupies 70% of the complex in owl monkeys and perhaps as much as 90% in diurnal monkeys. Thus, $\mathrm{PI_C}$ is likely to be "the inferior pulvinar" of most studies. $\mathrm{PI_M}$ is distinguished from the rest of the inferior pulvinar by encapsulating fibers. In addition, the neurons in $\mathrm{PI_M}$ appear to be more densely packed, somewhat larger, and more darkly stained. A portion of $\mathrm{PI_M}$ extends above the traditional dorsal border of the inferior pulvinar, the fiber band between PI and the superior pulvinar, so that a part of $\mathrm{PI_M}$ protrudes into the lateral pulvinar. This dorsal part of $\mathrm{PI_M}$ has the same connections as other parts [Lin and Kaas, 1979], and it is necessary to complete the retinotopic map in $\mathrm{PI_M}$. In owl monkeys, $\mathrm{PI_M}$ occupies about 20% of the PI complex. $\mathrm{PI_M}$ can be identified in diurnal New World monkeys, such as squirrel monkeys, where it is clearly smaller. $\mathrm{PI_P}$ corresponds to a small group of cells on the posteromedial margin of the PI complex. $\mathrm{PI_P}$ is separated from $\mathrm{PI_M}$ by a fiber band, and $\mathrm{PI_P}$ has more scattered and less densely stained cells than $\mathrm{PI_M}$. In owl monkeys, $\mathrm{PI_P}$ occupies about 10% of the complex, but it is smaller in diurnal monkeys. Because the cells are more scattered, a number of investigators have distinguished $\mathrm{PI_P}$ in New World monkeys as the "posterior nucleus" [eg, Mathers, 1971; Spatz, 1975].

Old World monkeys

The organization of the inferior division of the pulvinar in Old World monkeys is similar to that of New World monkeys with one complication: a portion of the lateral pulvinar extends ventrally in the lateral and caudal thalamus to form part of the lateral border of the pulvinar complex (Fig. 16) [Bender, 1981; Ungerleider et al, 1983, 1984]. Most investigators have not subdivided the inferior pulvinar or have only distinguished $\mathrm{PI_P}$ as the posterior nucleus. Overall, the architectonic appearance of the PI complex is more uniform in Old World monkeys, and differences are difficult to distinguish. However, connection patterns and microelectrode mapping procedures (see below) have demonstrated the existence of $\mathrm{PI_M}$, $\mathrm{PI_C}$, and $\mathrm{PI_P}$.

$\mathrm{PI_P}$ makes up the bulk of PI in macaque monkeys. This nucleus corresponds to a systematic representation of the visual hemifield referred to as P1 by Ungerleider et al [1984]. As in owl monkeys, $\mathrm{PI_C}$ starts rostrally as the nuclear mass between the lateral geniculate nucleus and medial geniculate nucleus. More caudally, the lateral pulvinar extends along the lateral margin of $\mathrm{PI_C}$ and $\mathrm{PI_M}$ (referred to as P3 by Ungerleider et al [1984]) and is a small division just medial to $\mathrm{PI_C}$. Caudally, $\mathrm{PI_M}$ expands to replace $\mathrm{PI_C}$ and border the lateral pulvinar. As illustrated by Ungerleider et al [1984], $\mathrm{PI_M}$ (P3) is proportionately larger in macaques than in owl monkeys. As for $\mathrm{PI_M}$ of owl monkeys, Ungerleider et al [1984] note that "P3", on the basis of connection patterns, clearly extends across the brachium of the superior colliculus into the lateral pulvinar. Likewise, Standage and Benevento [1983] describe a "crescent-shaped" subdivision (our $\mathrm{PI_M}$) that is set off from the rest of the inferior pulvinar by a fiber network. As for $\mathrm{PI_M}$ of owl monkeys, this crescent extends dorsally into the lateral pulvinar. Thus, $\mathrm{PI_M}$ in macaques as well as owl monkeys extends above the fiber band usually used to delimit the inferior pulvinar. The $\mathrm{PI_P}$ nucleus, equivalent to the "posterior nucleus" of some investigators [eg, Harting et al, 1980], is a small nucleus on the medioposterior margin of $\mathrm{PI_M}$.

Prosimians

Symonds and Kaas [1978] have described $\mathrm{PI_C}$, $\mathrm{PI_M}$, and $\mathrm{PI_P}$ in galagos. The large $\mathrm{PI_C}$ occupies much of the total volume of the pulvinar complex (Fig. 18). Most of the medial border of $\mathrm{PI_C}$ is formed by the smaller $\mathrm{PI_M}$, which is distinguished by a slight increase in cell packing and slightly larger cells. At the dorsoposterior extreme of the complex, a small region, $\mathrm{PI_P}$, is most reliably distinguished by a dense input from the superior colliculus (see below) rather than any notable change in cytoarchitecture.

Connections. Some of the major visual connections of the three nuclei of the inferior pulvinar are summarized in Figure 16. At least some of these connections are found in both New World and Old World monkeys and in prosimians. An important source of visual input to PI is from the superior colliculus. The superior colliculus projects densely to $\mathrm{PI_P}$ and more diffusely to $\mathrm{PI_C}$ in galagos [Glendenning et al, 1975], New World monkeys [Lin and Kaas, 1979; Mathers, 1971], and Old World macaque monkeys [Harting et al, 1980; Benevento and Fallon, 1975]. The medial margin of $\mathrm{PI_C}$, just along the lateral geniculate nucleus, and more lateral locations, possibly in $\mathrm{PI_M}$, may receive sparse input directly from the retina in macaque monkeys [Mizuno et al, 1982; Nakagawa and Tanaka, 1984; Itaya and Van Hoesen, 1983]. Other visual inputs are from subdivisions of visual cortex (Fig. 16) [see Allman, this volume].

The thalamic projections of primary visual cortex and the middle temporal visual area (MT) have been studied in a range of primate species. In all species studied, primary cortex projects in a topographic pattern to $\mathrm{PI_C}$ (macaque monkeys [Campos-Ortega and Hayhow, 1972; Graham, 1982; Ungerleider et al, 1983], owl monkey [Lin and Kaas, 1978], squirrel monkeys [Ogren and Hendrickson, 1976], galagos [Symonds and Kaas, 1978]). Primary visual cortex (V-I) also projects in a topographic pattern to $\mathrm{PI_M}$ in galagos and owl monkeys, but a projection from V-I to $\mathrm{PI_M}$ has not been reported for macaque monkeys [see Ungerleider et al, 1983]. V-I does not appear to project to $\mathrm{PI_P}$. MT projects densely to $\mathrm{PI_M}$ and sparsely to $\mathrm{PI_C}$ in all primates studied [eg, Lin and Kaas, 1979; Symonds and Kaas, 1979; Ungerleider et al, 1984]. Other cortical inputs to the inferior pulvinar complex are known largely from studies on owl monkeys [Lin and Kaas, 1979]. A number of caudal visual areas (areas M, PP, DM, PL, V-II, and V-I; see Fig. 16) project to both $\mathrm{PI_M}$ and $\mathrm{PI_C}$. These same visual areas do not project to $\mathrm{PI_P}$, but instead $\mathrm{PI_P}$ receives input from visual areas just rostral to MT (including ST, $\mathrm{IT_C}$, and $\mathrm{IT_R}$).

The cortical projections of the PI complex have been determined only in part (Fig. 16) [Lin and Kaas, 1980]. $\mathrm{PI_C}$ projects to a number of visual areas in the occipital lobe [see Ogren and Hendrickson, 1976; Curcio and Harting, 1978; Symonds and Kaas, 1978; Benevento and Rezak, 1976; Perkel et al, 1986]. These projections appear to largely terminate in layer I of primary visual cortex and in a patchy fashion in similar layers of prestriate cortex [eg, Ogren and Hendrickson, 1977; Rezak and Benevento, 1979]. $\mathrm{PI_M}$ projects densely to MT and perhaps only to MT [Lin and Kaas, 1980; Lin et al, 1974; Standage and Benevento, 1983]. In fact, $\mathrm{PI_M}$ is most easily defined by dense reciprocal connections with MT. The thalamic extent of these connections completely supports the architectonic evidence that $\mathrm{PI_M}$ extends dorsally past the brachium of the superior colliculus into the region traditionally considered to be the lateral pulvinar. $\mathrm{PI_P}$ projects to regions of visual cortex rostral to MT [Lin and Kaas, 1980].

Retinotopic Organization. The large $\mathrm{PI_C}$ forms a rather precise map of the contralateral hemifield; a somewhat cruder map appears to exist in $\mathrm{PI_M}$. $\mathrm{PI_P}$

may have only very crude retinotopic organization or none. Most information is available for PI$_C$, which occupies most of the inferior pulvinar and can be considered to be equivalent to the inferior pulvinar in most studies of retinotopic organization. Campos-Ortega and Hayhow [1972] first discerned the retinotopic organization of PI (PI$_C$) in the macaque monkey by studying the termination pattern of projections from different locations in primary visual cortex (striate cortex). By knowing the retinotopic organization of striate cortex and assuming that connections are between matched retinotopic locations, the retinotopic organization of PI$_C$ was deduced. In a similar but less precise manner, projections from locations in the retinotopic map in the superior colliculus to PI$_C$ have revealed aspects of retinotopic organization [Benevento and Fallon, 1975; Partlow et al, 1977]. More recently, microelectrode mapping methods have been used to reveal the retinotopy of PI$_C$ more fully [Allman et al, 1972; Bender, 1981].

Anatomical studies [eg, Symonds and Kaas, 1978; Perkel et al, 1985] best reveal the lines of isorepresentation (or lines of projection). All cells in a line or column of isorepresentation coursing through PI$_C$ represent the same location in the visual field, and adjacent columns represent adjacent locations. Anatomical studies reveal that the columns of isorepresentation [see Kaas et al, 1972] course through PI$_C$ of both galagos (Fig. 16) and macaque monkeys in roughly a rostrocaudal direction. Thus, a single location in visual space is represented over a sequence of rostrocaudal locations in PI$_C$. In macaque monkeys, the lower visual quadrant is represented dorsomedially and the upper visual quadrant ventrolaterally, so that the representation of the zero horizontal meridian courses from central vision to peripheral vision through PI$_C$ from near the lateral geniculate nucleus to near the medial geniculate nucleus. PI$_C$ has a similar organization in New World owl monkeys [Allman et al, 1972] and cebus monkeys [Gattass et al, 1978]. The main difference is that in owl monkeys, PI$_C$ is rotated clockwise in the frontal plane so that the representation of the horizontal meridian is nearly dorsoventral (Fig. 17), rather than oblique. In galagos, the retinotopic organization of PI$_C$ is similar to that of monkeys, but the relationship of PI$_C$ to the LGN is somewhat different [Symonds and Kaas, 1978]. Because the LGN extends under PI$_C$ somewhat, the more caudal portions of the LGN border parts of PI$_C$ representing paracentral rather than central vision.

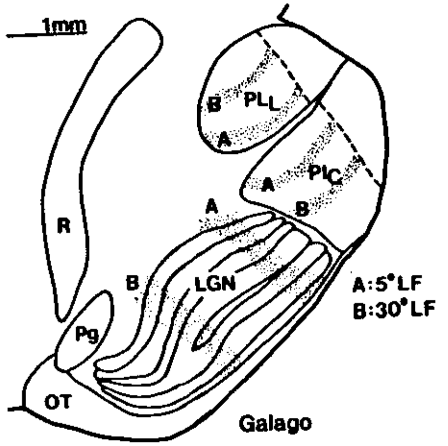

Fig. 17. A parasagittal brain section through the lateral pulvinar (PL) and inferior pulvinar (PI) of a galago. Injections of radioactive proline in primary visual cortex were placed into the representation of the visual field 5° (A) and 30° (B) from the center of gaze. The resulting bands of label in the thalamus show where 5° and 30° are represented in the lateral geniculate nucleus (LGN), the central nucleus of the inferior pulvinar (PI$_C$), and the lateral nucleus of the lateral pulvinar (PL$_L$). The lengths of the bands indicate lines of isorepresentation. Note the mirror image retinotopic organizations of PI$_C$ and PL$_L$. The caudal inferior pulvinar, without input from primary visual cortex, probably corresponds to the posterior nucleus (PI$_P$). The unlabeled caudal portion of PL is probably the medial division, PL$_M$. Based on Figure 17 of Symonds and Kaas [1978]. The ventral (B) band of label in the LGN actually occurred on a brain section adjacent to the one drawn. Other label was on the drawn section.

The organization of PI$_M$ is best known from its connection pattern with the representation of the contralateral visual hemifield in visual areas MT and primary visual cortex. Because it is difficult to restrict injections to only small parts of MT, studies of connections with MT have provided only crude information. Connection patterns in macaque monkeys led Ungerleider et al [1984] to suggest that there is a convergence of inputs to "P3" (PI$_M$) from MT and thus little or no retinotopic organization. Connection patterns in owl monkeys [Lin and Kaas, 1979, 1980] support the view that central vision is dorsal and peripheral vision ventral in PI$_M$ but provide little information on the representation of the upper and lower quadrants. In galagos [Symonds and Kaas, 1978], it also appears that central vision is represented dorsal to peripheral vision in PI$_M$.

PI$_P$ is small, and projections from the superior colliculus have not revealed any clear retinotopic organization. Cortical connections are not well established and have not been studied for retinotopic patterns.

Neuron Properties. The morphological and physiological properties of neurons in the inferior pulvinar have been studied only to a limited extent. The Golgi studies of neuron morphology [eg, Ogren and Hendrickson, 1979; Campos-Ortega and Hayhow, 1973] indicate that the inferior pulvinar contains two main types of multipolar neurons. A larger type of neuron has up to ten primary dendrites that subsequently form secondary arborizations. These are by far the most common of the two types, and they are assumed to be relay or projection neurons. A smaller type of neuron has 6–8 primary dendrites that, after an initial bifurcation, do not arborize further. However, these presumably intrinsic neurons can have very long dendrites.

Bender [1982] has reviewed the response properties of neurons in the inferior pulvinar of both New World and Old World monkeys. The vast majority of PI neurons are responsive to visual stimuli, even in anesthetized preparations. Neurons have well-defined receptive fields, ranging from a few degrees to 10° or more in diameter, with receptive fields generally being somewhat smaller for macaque than squirrel monkeys. Neurons sensitive to orientation or direction of movement are mixed with those insensitive to those variables. Most cells can be driven by either eye. Some neurons suppress visual responsiveness during eye movements [Robinson and Peterson, 1985]. There is no evidence of neurons being activated by auditory or somatic stimuli, although such stimuli could alter the pattern of spontaneous activity and responsiveness to visual stimuli.

The responsiveness of PI neurons seems largely to depend on inputs from striate cortex [Bender, 1983]. Lesions of the superior colliculus have little effect on the responses of PI neurons, though striate cortex lesions eliminate responsiveness to visual stimuli. After a recovery period of 3 weeks following striate cortex lesions, some responsiveness to visual stimuli recovers, presumably because of an enhancement of the effectiveness of superior colliculus inputs. However, there is no return of sensitivity to stimulus orientation and direction of movement, well-known properties of layer V cells of striate cortex that project to PI.

Functional Significance. The inferior pulvinar has three different nuclei, each apparently contributing to vision in its own way. PI$_C$ neurons largely reflect the properties of striate cortex neurons, although they are subject to modulation by superior colliculus inputs. Both PI$_C$ [Bender, 1983] and the prestriate visual areas with inputs from PI$_C$ [Desimone et al, 1979] depend on striate cortex for activation. The principal role of PI$_C$ appears to modulate visual processing within a number of areas of prestriate areas. In addition, PI$_C$ feedback provides information to layer I of striate cortex.

The possible functions of PI$_M$ are less clear. Neuron properties have not been specifically studied. The only visual input appears to be from visual cortex, and the major visual input is from the middle temporal visual area (MT), a processing station in the "visual attention" sequence [see Kaas, 1986]. Thus, we would expect PI$_M$ neurons to be much like MT neurons, to be insensitive to color as a variable, and to be orientation- and direction-selective. The major output of PI$_M$ is MT, so PI$_M$ can be viewed as an adjunct to MT, receiving visual input from MT and projecting back to modify visual neurons in MT.

PI$_P$ receives dense projections from the superficial layers of the superior colliculus, and presumably PI$_P$ neurons could be activated by this input. Since PI$_P$ projects to cortex rostral to MT in the general region of polysensory cortex that remains responsive to visual stimuli after lesions of striate cortex [Desimone et al, 1979], PI$_P$ could provide the major or sole source of visual information to cortex after striate cortex lesions. Pasik and Pasik [1982] provide evidence that certain visual discriminations of total amount of contour or differences in area depend on a pulvinar relay after striate cortex removal. Perhaps the pulvinar relay depends on PI$_P$. However, it is likely that this pathway would preserve little retinotopic information and would function poorly for form vision.

Lesion studies of the inferior pulvinar provide little information on its possible functions in vision. A number of such studies have reported impairments in tasks that require shifts in attention and movement of eyes. However, such impairments apparently depend on disruptions of corticotectal fibers rather than destroying neurons in the inferior pulvinar, because lesions produced by kainic acid, which leave fibers largely intact, do not produce such impairments [Nagel-Leiby et al, 1984].

The Lateral Pulvinar

The lateral pulvinar varies in size and location relative to other structures such as the inferior pulvinar in primates. Its cells are similar in size and general distribution to those of the medial pulvinar, so a dividing line between the two divisions is difficult to determine. In humans, apes, and most monkeys, the lateral pulvinar is greatly expanded, so it extends ventrally and caudally to form the caudolateral border of the thalamus and partly engulf the inferior pulvinar. Because a dense array of corticotectal and other fibers course through the lateral portion of the nucleus in these primates, the neurons are broken up into largely horizontal rows and columns of neurons. The medial part of the lateral pulvinar, by being less disrupted by fibers, has a more uniform distribution of cells.

In nocturnal owl monkeys, the lateral pulvinar is less expanded than in diurnal monkeys, and it occupies a position that is largely dorsal (superior) to the inferior pulvinar (Fig. 15). In addition, the cells are not as disrupted by bundles of fibers. Finally, it is more obvious in owl monkeys than macaque monkeys that the neurons of the lateral pulvinar stain less densely than those of the inferior pulvinar. As in other monkeys, a clear division between the medial and lateral pulvinar is not apparent in owl monkeys. Because of this lack of a clear distinction of lateral and medial divisions of the pulvinar and because of the position of the lateral pulvinar over the inferior pulvinar, it is sometimes convenient to refer to the lateral pulvinar as the superior pulvinar [eg, Allman et al, 1972], with or without an attempt to distinguish a medial pulvinar.

In galagos and lorises, the lateral pulvinar is dorsal and somewhat rostral to the inferior pulvinar (Figs. 15, 17), and thus the term "superior pulvinar" [eg, Symonds and Kaas, 1978] seems quite appropriate. As in owl monkeys, the neurons of the lateral pulvinar in these prosimians stain less densely than those of the inferior pulvinar, and there is little disruption by coursing bands of fibers. Neurons of the medial pulvinar are similar in appearance and distribution, so a clear border between the two divisions is not apparent.

Subdivisions and Retinotopic Organization. Part of the lateral pulvinar receives input from striate cortex, and part does not (eg, Fig. 17). Thus, there are at least two subdivisions or nuclei. Furthermore, the projection pattern shows that the subdivision with striate cortex input is retinotopically organized. Because this nucleus is in the lateral part of the lateral pulvinar in galagos and owl monkeys and in the lateroventral part in Old World monkeys, we use the term PL_L for lateral nucleus of the lateral pulvinar. In galagos, PL_L has been called the "central" nucleus of the superior pulvinar, PS_C [Symonds and Kaas, 1978], and in macaque monkeys PL_L has been termed "P2" [Ungerleider et al, 1984].

PL_L has a somewhat simpler retinotopic organization in galagos [Symonds and Kaas, 1978] than macaque monkeys [Bender, 1981; Ungerleider et al, 1983]. In galagos, PL_L lies immediately over PI_C, and the retinotopic organization of PL_L mirrors that of PI_C (Fig. 17). Thus, central vision is represented ventrally in PL_L and dorsally in PI_C, and peripheral vision is represented dorsally in PL_L and ventrally in PI_C. In both nuclei, the lower visual quadrant is represented medially, the upper visual quadrant laterally, and lines of isorepresentation course rostrocaudally with a slight dorsalward progression (Fig. 17). This type of representation, without a split or disruption, is similar to that found in the lateral geniculate nucleus and has been referred to as a topological or "first-order" representation [Allman and Kaas, 1974b].

In macaque monkeys, the retinotopic organization of PL_L is more complex [Bender, 1981; Ungerleider et al, 1983]. The nucleus has rotated and enlarged so that it is lateral and caudal to PI_C. However, PI_C has also rotated so that the mirror-image reversal of retinotopy is maintained. Thus, central vision is represented medially in PL_L and laterally in PI_C so that the border between the two structures is retinotopically matched. The upper visual quadrant is ventral and the lower visual quadrant is dorsal in both structures. Lines of isorepresentation course mainly in the dorsocaudal direction. However, unlike PI_C in macaque monkeys, the representation of the horizontal meridian only bisects the representation of the first few degrees of central vision. For paracentral and peripheral vision, the representation in PL_L is split along the horizontal meridian so that the horizontal meridian forms the outer boundary of PL_L and locations in the lower visual quadrant but near the horizontal meridian are displaced dorsally, and matched locations for the upper visual quadrant are displaced ventrally. Thus, the representation is partly "split" along the horizontal meridian so that adjoining locations in the visual field can be quite distant in the representation. Such a split representation occurs for several cortical representations, such as V-II, and has been termed a "second-order" representation [Allman and Kaas, 1974b]. Since a "split" is not evident in PL_L of galagos, the second-order representation in PL_L of macaque monkeys may result from restraints imposed by the rotation and enlargement of the lateral pulvinar while maintaining retinotopically congruent borders with PI_C.

A representation of the contralateral visual hemifield in part of the lateral pulvinar has also been demonstrated by microelectrode mapping methods in New World cebus monkeys [Gattass et al, 1978], and connection patterns with striate cortex indicate a representation in the lateral portion of the lateral pulvinar of squirrel monkeys [Ogren and Hendrickson, 1976] and owl monkeys [Graham et al, 1979]. Thus, New World monkeys have a PL_L nucleus, and the retinotopic organization roughly matches that of macaque monkeys.

In monkeys and galagos there are parts of the lateral pulvinar that are outside of the retinotopic map and do not receive input from striate cortex. This portion of PL is largely medial to PL_L, and we refer to it as PL_M without implying that it is functionally homogeneous and a "nucleus." PL_M also extends dorsal and caudal to PL_L in both prosimians and monkeys.

Connections. In monkeys and galagos, PL_L receives a major visual input from layer V cells of striate cortex. In galagos, the inputs include those from portions of striate cortex at least as far out into the representation of peripheral vision as 40° [Symonds and Kaas, 1978]. However, Ungerleider et al [1983] were able to demonstrate such connections only from the part of striate cortex representing the first 7° in macaque monkeys. Thus, there seems to be a striking species difference in input. Other inputs to PL_L are from MT [see Wall et al, 1982; Ungerleider et al, 1983, for review]. Studies of six cortical visual areas in owl monkeys [Graham et al, 1979] indicate that the second visual area, V-II; the dorsomedial area, DM; the medial area, M; and posterior parietal visual cortex, PP, all project to PL_L. Other inputs are from the dorsolateral visual area, DL [Weller and Kaas, unpublished]. Inputs from V-II and "V4" (the dorsolateral visual area of owl monkeys) have been demonstrated in macaque monkeys [see Ungerleider et al, 1983, for review]. Thus, PL_L receives cortical input from a number of visual areas. In macaque monkeys, a sparse input to IP_L has been demonstrated from the superior colliculus [Huerta and Harting, 1983; Harting et al, 1980]. The projections of PL_L have not been fully determined. A projection to layer I of striate cortex from PL_L appears to be less dense than that from PI_C [see Ogren and Hendrickson, 1977]. Another projection of PL_L is to V-II or area 18 [Wong-Riley, 1977; Winfield et al, 1975; Curcio and Harting, 1978], where terminations in middle layers form alternating bands. Other targets are less certain, but it appears that PL_L projects broadly to a number of extrastriate visual areas. In owl monkeys, projections to areas 17, 18, DM, DI, and DL have been demonstrated [Lin and Kaas, 1980].

The connections of parts of the lateral pulvinar that are outside the retinotopic map that is coincident with the inputs from areas 17 and 18 are not well known. However, in owl monkeys, areas MT, DM, M, and PP all appear to project to both PL_L and PL_M [Graham et al, 1979]. Thus, PL_M, like PL_L, receives input from a number of visual areas. However, unlike PL_L, PL_M does not have input from areas 17 and 18. Injections in the most caudomedial portion of the lateral pulvinar result in projections to lateral "V4" and adjoining caudal portions of inferotemporal cortex in macaque monkeys [Benevento and Rezak, 1976; Benevento and Davis, 1977]. However, the labeled terminations in inferotemporal cortex may have resulted from involving the medial pulvinar in the injections [see Weller and Kaas, 1986].

Besides the connections discussed above, all parts of the lateral pulvinar appear to get inputs from the thalamic reticular nucleus and the claustrum [Trojanowski and Jacobson, 1975].

Neuron Properties. The responses of neurons in the lateral pulvinar to visual stimuli undoubtedly depend on inputs from visual cortex, since there is no other major source of visual inputs. PL_L, with inputs from striate cortex, area 18, and other visual areas, may have neurons with somewhat simpler response properties than PL_M without V-I and V-II inputs but with inputs from higher-order visual areas. Some physiological evidence supports this view. Bender [1981] found that neurons in the lateral pulvinar (PL_L) had restricted receptive fields, were typically binocular, and were often selective for orientation and direction of movement. However, neurons outside the caudal pole of the lateral pulvinar (PL_M) often had large receptive fields that included the fovea and sometimes extended into the ipsilateral visual hemifield and had complex binocular interactions [Benevento and Miller, 1981]. Other response properties, such as color sensitivity [Felsten et al, 1983], have been found for neurons throughout the lateral pulvinar. Some neurons in the lateral pulvinar are reported to be responsive to somatosensory stimuli and not to light, or to both [Mathers and Rapisardi, 1973]. The source of somatosensory activation could be from inputs from posterior parietal cortex.

Functional Significance. The major function of the lateral pulvinar appears to be to relay visual information from striate and extrastriate visual areas to other visual areas. Via direct cortical connections and indirect connections through the lateral pulvinar, each extrastriate visual area is subject to a multitude of influences from other visual areas. The lateral pulvinar has a lateral division mainly related to "lower-order" caudal visual areas and a medial division or divisions related to "higher-order" rostral visual areas. The sparse inputs from the superior colliculus and pretectum probably have minor roles in the functions of the lateral pulvinar.

The Medial and Anterior Divisions of the Pulvinar

The other two major divisions of the pulvinar complex do not appear to have simple roles in vision. Bender [1981] excluded the medial pulvinar from the visually responsive pulvinar in macaque monkeys, and Acuna et al [1983] found neurons in the anterior and medial pulvinar that were activated during eye and arm movements. Connections include sparse inputs from the deep layers of the superior colliculus and interconnections with visuomotor areas of the frontal lobe [eg, Trojanowski and Jacobson, 1974; Huerta et al, 1986], the superior temporal gyrus and polar regions of the temporal lobe [Burton and Jones, 1976; Markowitsch et al, 1985], two subdivisions of inferotemporal cortex [Weller and Kaas, 1986], insular cortex [Mufson and Mesulam, 1984], limbic cortex [Baleydier and Mauguiere, 1985], and amygdala [Jones and Burton, 1976]. The connections with the temporal lobe and the amygdala suggest that the medial pulvinar may relate to the final stages of object recognition and visual memory [see Kaas, 1986]. More specifically, the connections and neural properties of the medial pulvinar are consistent with a suggested role in mediating intentional movements toward objects of interest [Baleydier and Mauguiere, 1985].

The anterior (oral) pulvinar is a rostromedial extension of the medial pulvinar, without an obvious histological boundary. The anterior pulvinar is distinguished by connections with subdivisions of parietal cortex, including regions of posterior parietal cortex that may also have visual functions [see Pons and Kaas, 1985, for review]. The predominance of connections with cortex that is considered somatosensory in function suggests that the anterior pulvinar has no major role in visual processing.

OTHER TARGETS OF THE RETINA

Introduction

Several relatively small brainstem structures receive direct retinal input and are involved with regulatory, automatic aspects of visual behavior. These structures include the pretectal complex, which mediates the pupillary light reflex and possibly has oculomotor and other functions; the accessory optic nuclei, which are involved in oculomotor functions; the ventral lateral geniculate nucleus, which relates to visual reflexes; and the suprachiasmatic nucleus, which has pacemaker cells for a biological clock and the regulation of circadian rhythms. These three systems with retinal inputs are briefly discussed.

The Pretectum

The pretectal complex comprises several small nuclei with somewhat indistinct boundaries best defined by multiple criteria. Recently, Hutchins and Weber [1985] used cytoarchitectonic, myeloarchitectonic, and connectional features to define the pretectal nuclei in squirrel monkeys. In addition, they attempted to establish a much needed standard nomenclature for the pretectal nuclei in primates. Hutchins and Weber [1985] defined five nuclei: the anterior pretectal nucleus (sublentiform nucleus of Benevento and Standage [1983]), the posterior pretectal nucleus, nucleus of the optic tract, the pretectal olivary nucleus, and the medial pretectal nucleus (nucleus of the pretectal area of Benevento and Standage [1983]). Although the nucleus of the posterior commissure is sometimes included in the pretectal complex, it is not one of the pretectal nuclei according to Hutchins and Weber [1985]. The locations of the five pretectal nuclei in the brain of *Macaca fascicularis* are shown in Figure 18.

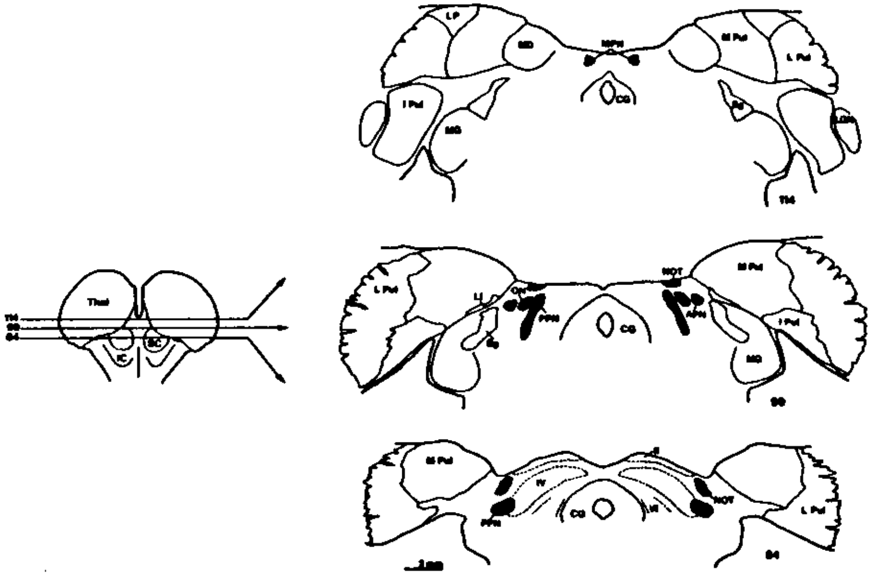

Fig. 18. The location of pretectal nuclei (blackened) in the macaque monkey as viewed in frontal sections through the mesodiencephalic junction. APN, anterior pretectal nucleus; BSC, brachium of the superior colliculus; IC, inferior colliculus; I Pul, inferior pulvinar; LGN, lateral geniculate nucleus; Li, nucleus limitans; LP, lateral posterior nucleus; L Pul, lateral pulvinar; MD, medial dorsal nucleus; MG, medial geniculate; MPN, medial pretectal nucleus; M Pul, medial pulvinar; NOT, pretectal nucleus of the optic tract; ON, olivary pretectal nucleus; PPN, posterior pretectal nucleus; SC, superior colliculus; Sg, suprageniculate nucleus; II, IV, VI, layers of the superior colliculus.

The best-documented afferents to the pretectal complex are from the retina; a retinopretectal projection has been demonstrated in all primates thus far studied, including prosimians, New World and Old World monkeys, and the chimpanzee [eg, Giolli and Tigges, 1970; Tigges and Tigges, 1970; Tigges et al, 1977; Benevento and Standage, 1983; Hutchins and Weber, 1985; unpublished observations]. The most recent evidence available for squirrel monkeys indicates that retinal axons reach all pretectal nuclei [Hutchins and Weber, 1985]. In macaque monkeys, the medial pretectal nucleus was considered to be devoid of retinal input [Benevento and Standage, 1983], but unpublished observations from our laboratory suggest that very sparse inputs from the contralateral retina exist. In both squirrel and macaque monkeys, the optic tract nucleus and the olivary nucleus receive very dense bilateral retinal afferents. Moreover, in both primates, input from each eye to the olivary nucleus is segregated into laminae that are also apparent in Nissl and myelin preparations [Benevento and Standage, 1983; Hutchins and Weber, 1985; unpublished observations]. In macaque monkeys, a particular class of large ganglion cells has been found to project to the olivary nucleus [Perry and Cowey, 1984]. The retinal innervation of the remaining pretectal nuclei is primarily contralateral and is considerably less dense than that to the olivary pretectal nucleus or the nucleus of the optic tract.

Other subcortical afferents include the superficial collicular layers which, in macaque monkeys, project heavily to the nucleus of the optic tract and the posterior pretectal nucleus and sparsely to the anterior pretectal nucleus [Harting et al, 1980]. The deep collicular layers send a moderate projection to the medial pretectal nucleus. Axons arising from the superior colliculus in macaque monkeys do not innervate the olivary pretectal nucleus [Harting et al, 1980]. Similar pathways exist in squirrel monkeys, although they have been studied less extensively [Huerta and Harting, 1983].

With regard to cortical innervation, the pretectal nuclei of owl monkeys receive axons arising from cells in at least six visual areas. Specifically, areas V-I, V-II, MT, DM, M, and PP each project to the posterior pretectal nucleus and/or the nucleus of the optic tract [Graham et al, 1979]. In contrast, the anterior pretectal nucleus receives input from only areas M and PP. Visual area MT has also been shown to project to the pretectal complex in galagos and marmosets [see Wall et al, 1982] but not in macaques [Ungerleider et al, 1984]. However, the pretectum of macaque monkeys has been shown to receive fibers from area V-4 [Dineen and Hendrickson, 1983] and the frontal eye field [Huerta et al, 1986]. The frontal eye field also innervates pretectal nuclei of owl and squirrel monkeys [Huerta et al, 1986].

The efferent connections of the pretectal complex have been studied relatively little. In accordance with its function in the pupillary light reflex, the olivary pretectal nucleus in macaque monkeys projects to the Edinger-Westphal complex, which houses the preganglionic parasympathetic neurons that innervate the ciliary ganglion of the eye [Carpenter and Pierson, 1973]. The olivary nucleus also projects to the contralateral olivary nucleus, the medial pulvinar, and accessory optic nuclei [Carpenter and Pierson, 1973]. The medial pretectal nucleus innervates the nucleus of the posterior commissure and the anterior and/or posterior pretectal nuclei [Carpenter and Pierson, 1973]. The nucleus of the optic tract and the anterior and/or posterior pretectal nuclei send axons to the nucleus of the posterior commissure, the inferior and medial pulvinar nuclei, the pregeniculate, and the dorsal lateral geniculate nucleus in macaque monkeys [Carpenter and Pierson, 1973]. Recent data from macaque monkeys reveal that the pretectum also innervates the lateral pulvinar and suggest that the pulvinar zones that receive input from the superior colliculus also receive pretectal input [Benevento and Standage, 1983].

A comprehensive analysis of the efferent connections of the pretectum has not been carried out in any primate. However, a detailed study in the tree shrew *(Tupaia)* indicates that pretectal nuclei project to structures associated with eye movements including the nucleus of the posterior commissure, the somatic cell column of the oculomotor nucleus, a zone adjacent to the trochlear nucleus, and the nuclei of Darkschewitsch and Cajal [Weber and Harting, 1980]. Pretectal nuclei also innervate precerebellar relay nuclei (the inferior olivary complex, the medial terminal nucleus, and the pontine gray) as well as the lateral nucleus and reticular nucleus, the zona incerta, and the intralaminar nuclei of the diencephalon [Weber and Harting, 1980].

The pretectum has long been thought to play a major role in the pupillary light reflex [see Weber, 1985]. There is also evidence for a role in performing eye movements and maintaining body posture [Pasik et al, 1969]. Recent lesion studies more specifically suggest that the nucleus of the optic tract represents a first relay station in the circuit for horizontal optokinetic nystagmus [Kato et al, 1986]. The diversity of targets of the pretectal complex suggest that it has other functions as well.

The Accessory Optic System

Like the pretectum, the accessory optic system comprises several small nuclei that receive retinal input [for recent reviews see Weber, 1985; Simpson, 1984; McKenna and Wallman, 1985]. In most mammals, three retinorecipient nuclei constitute the accessory optic system: the dorsal terminal nucleus, the lateral terminal nucleus, and the medial terminal nucleus [eg, Hayhow, 1959, 1966; Hayhow et al, 1960; Campbell et al, 1967; Tigges, 1966; Weber, 1985; Oyster et al, 1980; Erickson and Cotter, 1983]. In primates, however, the medial terminal nucleus is often difficult to identify, as is its retinal innervation [Campos-Ortega and Glees, 1967; Campbell, 1969; Giolli, 1963; Giolli and Tigges, 1970; Lin and Giolli, 1979; Tigges and Tigges, 1969, 1970; Tigges and O'Steen, 1974; Tigges et al, 1977]. Nevertheless, recent evidence strongly suggests that the medial terminal nucleus receives input from the retina in primates [Itaya and Van Hoesen, 1983; Cooper, 1986; Weber, 1985; Weber and Giolli, 1986; see also Gillian, 1941; Itaya and Van Hoesen, 1983].

In primates, the dorsal terminal nucleus is located in the lateral midbrain tectum just caudal to the medial geniculate nucleus and ventrolateral to the brachium of the superior colliculus [eg, Lin and Giolli, 1979]. In the slow loris, the dorsal terminal nucleus has been shown to have only contralateral retinal input; in rhesus monkeys this nucleus receives primarily contralateral input, but an ipsilateral retinal projection has also been suggested [Lin and Giolli, 1979].

The lateral terminal nucleus is wedged between the brachium of the inferior colliculus and the ventromedial aspect of the medial geniculate nucleus at the mesodiencephalic junction. This nucleus is the most obvious of the three accessory optic nuclei in primates, but it is relatively inconspicuous in nonprimate mammals [Lin and Giolli, 1979]. In the squirrel monkey and the rhesus monkey, the lateral terminal nucleus receives contralateral and, to a lesser extent, ipsilateral retinal afferents [Weber and Giolli, 1986; Lin and Giolli, 1979].

The medial terminal nucleus, which is located in the mesencephalic tegmentum just medial to the cerebral peduncle at a level immediately rostral to the exit of the oculomotor nerve [Weber and Giolli, 1986], receives sparse input from the contralateral eye in the slow loris, mouse lemur, marmoset monkey, squirrel monkey, cynomolgus monkey, and rhesus monkey [Weber and Giolli, 1986; Itaya and Van Hoesen, 1983; Cooper, 1986].

Although there are only limited data regarding efferent connections and the functions of the accessory optic system, it is thought that these nuclei participate in visuomotor activity. Specifically, in the rabbit the accessory optic nuclei innervate a portion of the inferior olivary nucleus which, in turn, innervates the flocculonodular lobe of the cerebellum [Maekawa and Simpson, 1972, 1973; Takeda and Maekawa, 1976; Maekawa and Takeda, 1979]. Other projections are to the nucleus of the optic tract and vestibular nucleus. Physiological and ablation-behavioral studies suggest that these connections function in stabilizing the retinal image [see Simpson, 1984].

The Pregeniculate Nucleus (Ventral Lateral Geniculate Nucleus)

The ventral lateral geniculate nucleus of mammals is a derivative of the ventral thalamus rather than the dorsal thalamus and is thus quite distinct from its dorsal neighbor, the dorsal lateral geniculate nucleus [Niimi et al, 1963]. The ventral lateral geniculate nucleus is commonly divided into an internal (medial) layer (or segment) of pale, small cells, and an external (lateral) layer of larger deeply staining cells. Sometimes a clump of cells separating the dorsal from the ventral lateral geniculate is described as the intergeniculate layer or nucleus. The term "ventral lateral geniculate nucleus" is usually retained for the structure in prosimian primates, but in other primates the term "pregeniculate" nucleus is used, and the nucleus is rotated relative to the dorsal lateral geniculate nucleus so that it caps the dorsorostral extent of the dorsal lateral geniculate [eg, Babb, 1980].

The ventral lateral geniculate nucleus of mammals receives inputs from a number of visual structures including the retina, areas of visual cortex, the superior colliculus, the pretectal region, and the contralateral ventral lateral geniculate nucleus. Efferent projections are to the superior colliculus, the pretectal region, the dorsal lateral geniculate nucleus, the contralateral ventral lateral geniculate nucleus, pontine nuclei, the suprachiasmatic nucleus, the lateral terminal nucleus of the accessory optic system, and the interlaminar nuclei of the thalamus [see Brauer et al, 1984]. Retinal inputs are largely segregated in the internal layer, and cortical inputs terminate in the external layer.

Patterns of retinal inputs to the pregeniculate of a number of prosimian and simian primates are illustrated by Kaas et al [1978]. Most of the internal layer receives input from the contralateral eye, but a restricted portion receives input from the ipsilateral eye [also see Tigges and Tigges, 1970; Hendrickson et al, 1970]. Projections from area 17 to the pregeniculate nucleus have been reported in some but not all studies in monkeys [see Graham et al, 1979, for review]. In owl monkeys, inputs were found from cortical areas MT, DM, M, and PP but not from areas 17 and 18 [Graham et al, 1979]. All cortical inputs were to the external geniculate layer. Judging from reports on nonprimates [see Brauer et al, 1984, for review], cortical projections originate from layer V pyramidal cells. Other afferents to the pregeniculate nucleus, probably to the external layer, have been reported from the pretectum [Benevento et al, 1977] and superficial layers of the superior colliculus [Benevento and Fallon, 1975]. Neurons in the ventral lateral geniculate of at least some mammals respond tonically to stationary spots of light, probably as a result of the direct retinal inputs [see Brauer et al, 1984, for review]. In monkeys, some but not all neurons in the pregeniculate nucleus respond to flashes of light, and the majority of neurons exhibit changes in activity in relation to eye movements [Buttner and Fuchs, 1973].

The diversity of connections of the pregeniculate nucleus suggests that it has a role in a number of functions. Polyak [1957] proposed a role in the control of pupillary light reflexes, and there is some ablation-behavioral evidence to support this viewpoint, but the mediating connections are unknown. Efferents to the suprachiasmatic nucleus may influence circadian rhythms. The sensitivity of neurons to eye movements, connections with the superior colliculus, and pons support the notion, often proposed [eg, Polyak, 1957; Graybiel, 1974; Brauer et al, 1984], of a major role in oculomotor functions. These functions appear to be under the influence of a range of visual inputs from the retina to even "higher order" visual areas of cortex. The high degree of segregation of retinal from other inputs in the external and internal subdivision, respectively, raises the possibility of quite different functions for the two parts of the pregeniculate nucleus.

The Suprachiasmatic Nucleus

The suprachiasmatic nucleus (SCN) is a small subdivision of the hypothalamus, located on either side of the third ventricle just dorsal to the optic chiasm [see Moore, 1983, for review]. The SCN functions as a biological clock in a circadian timekeeping system that is reset on a daily basis by normal day-night environmental changes in lighting. The visual information depends on projections via the retinohypothalamic tract, which courses in the optic nerve to the SCNs of both sides. The input appears to be excitatory, so that the SCN neurons are most active during the light cycle. In macaque monkeys [Reppert et al, 1981], the nucleus is ovoid in shape and consists of small, densely packed, darkly stained cells. The ventrolateral aspect of the nucleus receives dense retinal input, with patchy input scattered more dorsally so that about half of the nucleus has retinal input. At least in rats, a second visual input to the SCN is from the ventral lateral geniculate nucleus (or pregeniculate nucleus of most primates), but the significance of this input is uncertain. The SCN projects widely to periventricular structures. The SCN also appears to project to the epithalamus, and lesions of the SCN in macaque monkeys have been shown to disrupt circadian rhythms in the production of the pineal hormone melatonin [Reppert et al, 1981]. Lesions of the SCN in monkeys also disrupt the usual entrainment of activities such as drinking to 24-hr dark-light cycles and disrupt free-running circadian rhythms [Albers et al, 1984a,b].

OTHER VISUAL STRUCTURES

Introduction

A number of additional subcortical structures are visual in that they are visuomotor in function, relay visual information, or have major connections with other structures that are recognized as part of the visual system. These parts of the visual system are briefly reviewed here.

The Reticular Nucleus of the Thalamus

The reticular nucleus of the ventral thalamus consists of a thin shell of scattered neurons along most of the lateral and rostral sides of the dorsal thalamus. The reticular nucleus receives collaterals from relay neurons projecting from the dorsal thalamus to cortex and from cortical neurons projecting to the brainstem. The inputs are excitatory, but the outputs are inhibitory, as the nucleus consists of neurons releasing the inhibitory neurotransmitter, gamma-aminobutyric acid (GABA) [see Jones, 1985, for review]. Each subdivision of neocortex appears to relate to a particular segment of the reticular nucleus and thus inhibit a particular thalamic nucleus or nuclei. Areas of visual cortex project to caudal portions of the reticular nucleus. Individual visual areas appear to project topographically to the reticular nucleus [see Graham et al, 1979, for review]. Striate cortex, for example, projects in a topographic pattern to the most caudal portion of the reticular nucleus, and this region in turn projects to the lateral geniculate nucleus. Thus, excitatory projections from striate cortex can have an excitatory effect by terminating directly on lateral geniculate neurons or an inhibitory effect by terminating on reticular nucleus neurons that project to the lateral geniculate nucleus. The inhibitory projections of the reticular nucleus are thought to terminate on the geniculate relay neurons rather than the inhibitory interneurons [see Jones, 1985].

The Parabigeminal Nucleus

The parabigeminal nucleus consists of a small group of cells on the lateral edge of the midbrain just ventral to the medial geniculate nucleus and the brachium of the inferior colliculus. In all mammals studied, including galagos [Glendenning et al, 1975] and macaque monkeys [Harting, 1977], the parabigeminal nucleus is interconnected with the superior colliculus. The superficial tectal layers project to the ipsilateral nucleus, which, in turn, sends projections back largely to the superficial layers of both the ipsilateral and contralateral colliculi. The interconnections appear to be topographic, and the inputs to the parabigeminal nucleus create a retinotopic map. Because of these connections, Graybiel [1978a] has referred to the parabigeminal nucleus as a "satellite" of the superior colliculus. In cats [Sherk, 1979], the responses of neurons in the parabigeminal nucleus to visual stimuli are very much like those in the superficial layers of the superior colliculus, as one might expect from the major connection pattern. The parabigeminal nucleus in galagos [Harting et al, 1986] also projects to koniocellular and interlaminar zones of the lateral geniculate nucleus, and similar projections probably exist in other primates and other mammals. The projections to W-cell zones of the lateral geniculate nucleus suggests that the parabigeminal nucleus functions in conjunction with the superficial collicular layers as part of the W-cell subsystem [see Harting et al, 1986].

Motor Nuclei

Visuomotor nuclei provide the final path to eye muscles that stabilize images on the retina and allow eye movements that move visual images to the part of the retina that best resolves the image (area centralis or fovea). The necessary disjunctive eye movements of convergence or divergence and conjugate slow or rapid (saccadic) movements are produced by contraction of various combinations of the extraocular muscles. The lateral rectus muscle is innervated by the abducens nucleus; the accessory lateral rectus muscle (which may be homologous to the retractor bulbi muscle of the cat) is innervated by some neurons in the abducens nucleus as well as by cells in the ventral abducens nucleus [Spencer and Porter, 1981]; the medial rectus, superior rectus, inferior oblique, and inferior rectus muscles are innervated by cells of the somatic portion of the oculomotor complex (this complex also includes a visceral portion which provides autonomic innervation of the eye); and the superior oblique muscle receives input from the trochlear nucleus. The motor neurons projecting to the extraocular muscles effect changes in eye position by providing a burst of action potentials, which initiates the eye movement, followed by a tonic level of activity, which maintains the newly obtained eye position [Fuchs et al, 1985; Schiller, 1970]. Motor nuclei contain both motoneurons and interneurons [eg, Baker and Highstein, 1985].

As the final common pathways to the muscles that produce eye movements, motor nuclei receive and combine information relevant to visual fixation, saccadic eye movements, and eye movements related to visual and vestibular stimuli. The abducens nucleus of monkeys, as a recently studied example [Langer et al, 1986], with the function of generating conjugate horizontal eye movements, receives a major bilateral input from vestibular nuclei. Other afferents are from neurons in the part of the oculomotor complex related to the medial rectus muscle. Thus, the motor center's related horizontal eye movements are interrelated. A sparse and variable input originates from the intermediate gray of the superior colliculus [Harting, 1977]. In addition, visual neurons in the reticular nucleus of the pons, that project to the cerebellum, also project to the abducens nucleus. These neurons receive visual information from cortex and the superior colliculus. Other neurons in the pons that may be a part of groups generating horizontal saccades [see Fuchs et al, 1985, for review] project to the abducens nucleus. Other inputs to motor neurons of the extraocular muscles include those from the rostral interstitial nucleus of the medial longitudinal fasciculus, the interstitial nucleus of Cajal, vestibular nuclei, and the perihypoglossal complex [Buttner-Ennever and Henn, 1976; Buttner-Ennever and Buttner, 1978; Steiger and Buttner-Ennever, 1979; Carpenter and Batton, 1980; Buttner-Ennever and Akert, 1981]. Many of these structures receive inputs from the deeper layers of the superior colliculus.

Subcortical Structures With Connections With Visual Cortex

A number of structures in the brainstem can be considered at least partly or indirectly visual in that they have connections with subdivisions of visual cortex [see Tigges and Tigges, 1985, for review]. Many of these also contain neurons that respond to visual stimuli. These structures are listed below.

The *locus coeruleus* (LC) consists of a small group of neurons in the ventral mesencephalon that produce norepinephrine as a neurotransmitter and project broadly to visual and nonvisual structures of the brainstem and cortex in all mammals including primates. In squirrel monkeys, Tigges et al [1982] have shown that neurons in LC project bilaterally to visual cortex but more densely to the ipsilateral hemisphere. Visual areas 17, 18, cortex along the rostral border of area 18 (probably DL or V4), and MT and the frontal eye field all receive inputs from LC [see Allman, this volume, for visual areas]. Connections from LC to visual cortex have also been shown in macaque monkeys [Gatter and Powell, 1977] and in the chimpanzee [Tigges et al, 1983]. The early appearance of LC projections to cortex and their widespread projection suggest that they have some sort of neurotrophic role [see Tigges and Tigges, 1985]. The presence of norepinephrine in cortex is thought to be essential in maintaining the plasticity that permits changes in connections and synaptic strength [see Pettigrew, 1982]. The LC inputs may also be important in maintaining normal cycles of sleeping and in promoting spontaneous arousal and awakening to sensory stimuli [Livingstone and Hubel, 1981].

The *raphe nuclei* and associated neurons in the pontine reticular formation project broadly to visual and nonvisual brainstem and cortical structures in all mammals and use serotonin as a neurotransmitter [see Tigges and Tigges, 1985]. The projections are mostly ipsilateral, and injections of tracers in visual cortex of primates label only a small proportion of neurons. The terminations in area 17 of monkeys are particularly dense in layer IV, where they are in a position to modulate the early processing of visual information [see Kosofsky et al, 1984].

Other neurons in the *mesencephalic reticular formation* have been shown to project to visual and other regions of cortex in monkeys [see Doty, 1983; Tigges et al, 1983; Tigges and Tigges, 1985; Huerta et al, 1986]. These neurons could have a role in the widespread activation of cortex that has been shown to follow electrical stimulation of the reticular formation.

A few neurons in the *lateral hypothalamus* (LH) project to visual and other areas of cortex [see Tigges and Tigges, 1985]. The significance of this projection is uncertain, but the pathway may be inhibitory and dependent on GABA.

The basal forebrain includes two structures that project to visual and other regions of cortex in all mammals and use acetylcholine as a neurotransmitter: the *nucleus basalis of Meynert* (NBM) and the *nucleus of the diagonal band of Broca* (NDB) [see Tigges and Tigges, 1985]. The NBM shows profound degeneration in patients afflicted with Alzheimer's disease, which results in defects in thinking and memory. Thus, the widespread inputs of a small group of neurons with acetylcholine as a transmitter may be very important in maintaining normal brain activity.

The *claustrum* is a thin sheet of neurons just under insular cortex. The claustrum is sometimes considered a cortical structure and more often a subcortical one. Neurons in the claustrum receive inputs from visual and nonvisual areas of cortex via layer VI cells and project back broadly across layers to the areas of cortex providing the inputs. Neurons in the caudoventral portion of the claustrum have been shown to be interconnected with primary visual cortex in galagos, monkeys, and apes [Carey et al, 1979; Doty, 1983; Tigges et al, 1982, 1983; Perkel et al, 1986]. These connections form a reverberating circuit of uncertain significance. Most or all visual areas may be interconnected with the claustrum [see Graham et al, 1979]. Judging from research on cats, the interconnections for different visual areas may overlap in the claustrum [LeVay and Sherk, 1981]. Connections for a given visual area appear to be topological. For example, in monkeys, connections devoted to the central visual field from area 17 are at the external border of the head of the claustrum [Perkel et al, 1986]. In cats, the response properties of visual neurons in the claustrum are very similar to the layer VI cells of visual cortex providing the source of activation [Sherk and LeVay, 1981]. The neurons in the claustrum, with binocular, bidirectional, elongated receptive fields, could modulate the activity of area 17 neurons with less specific properties.

A considerable number of neurons in the *lateral basal nucleus of the amygdala* project to visual cortex in primates [Tigges et al, 1982, 1983; Tigges and Tigges, 1985]. Tigges and Tigges [1985] suggest that this projection could provide information on behavioral (emotional and motivational) states to visual cortex. In addition, visual information that is processed for form vision in the temporal lobe is relayed to the amygdala, and this input is important in visual memory [eg, Turner et al, 1980].

The *intralaminar nuclei* of the thalamus are a source of "unspecific" or diffuse projections to visual and nonvisual areas of cortex [Jones, 1985]. Commonly, the central lateral (CL), centralis medialis (CeM), and paracentralis (Pc) are distinguished as separate nuclei. Tigges and Tigges [1985] describe projections from all three structures to occipital visual cortex in monkeys and chimpanzees and review possible functions of these connections. This projection is considered as part of a relay of activation from the mesencephalic reticular formation, and research in cats suggests roles in the control of eye movements and visual attention.

Pontine Nuclei and Cerebellum

A small region of the dorsolateral pons in mammals is referred to as the dorsolateral pontine nucleus (DLPN). This nucleus is part of a corticopontocerebellar system that is involved in oculomotor functions. In monkeys, the DLPN receives afferents from striate cortex, prestriate cortex, visual cortex of the temporal lobe, and visuomotor areas of posterior parietal cortex [Brodal, 1978; Fries, 1981; Glickstein et al, 1980; Wiesendanger et al, 1979]. Other visual inputs are from the deeper layers of the superior colliculus [Harting, 1977; Huerta and Harting, 1984] and from the pretectum [Weber and Harting, 1980]. Neurons in the DLPN respond to visual stimuli and background movement in particular directions, and one hypothesis is that the DLPN provides a cerebellar system involved in eye movements of smooth pursuit with information about the direction and velocity of target image motion on the retina [see Suzuki and Keller, 1984].

The posterior vermis of the cerebellum receives both visual and vestibular signals [eg, Suzuki and Keller, 1982; Suzuki et al, 1981; Waespe and Henn, 1981] and has a major role in oculomotor functions. One source of visual input is from the DLPN, which projects via mossy fibers to vermal lobules VI and VII and the flocculus of the cerebellum [Brodal, 1979, 1982; Noda, 1981]. In addition, in rabbits at least [Takeda and Maekawa, 1980], the dorsal cap of the inferior olive receives visual inputs from the dorsal and lateral terminal nuclei of the accessory optic tract and the nucleus of the optic tract, and projects via climbing fibers to the contralateral flocculus.

The Corpus Striatum and Substantia Nigra

The corpus striatum and substantia nigra are parts of basal ganglia and the extrapyramidal motor system and are not normally considered visual in function. Yet, inputs from visual cortex and outputs to the superior colliculus suggest a role in visuomotor behavior as well as in other motor functions. The corpus striatum [for an extensive review, see Graybiel and Ragsdale, 1979] is traditionally subdivided into the striatum (the caudate nucleus and putamen) and pallidum (or globus pallidus). The striatum is considered the input side and the pallidum the output side of the corpus striatum. In primates, motor cortex provides a major input to the putamen, and premotor and prefrontal cortex provide major inputs to the caudate nucleus. The caudate nucleus and putamen provide major inputs to the pallidum which, in turn, projects to the ventral thalamus for a relay to motor cortex. Thus, connections closely associate the corpus striatum with the motor system. However, all parts of cortex are thought to project to the corpus striatum, with different fields having specific projection regions, although the inputs from visual areas are not the most dense [see Kemp and Powell, 1971, for review]. Evidence for projections from specific areas has been presented for New World and Old World monkeys [see Graham et al, 1979, for review] and, to a lesser extent, for prosimian galagos [see Wall et al, 1982].

Projections from areas 17 and 18 to the striatum are not well established and remain questionable. In owl monkeys, inputs to the striatum have been shown for visual areas MT, DM, M, and PP. In galagos, MT has been found to project to the putamen. Further studies will undoubtedly establish the existence of other visual inputs in these and other primates.

Although a major output of the corpus striatum is to motor fields via the thalamus, another target is the substantia nigra, which provides outputs to widespread regions of the forebrain and midbrain. The most significant projection of the substantia nigra for visual functions is to the intermediate gray of the superior colliculus [Jayaraman et al, 1977; Hikosaka and Wurtz, 1983d].

In macaque monkeys, neurons in the pars reticulata of the substantia nigra, the part projecting to the superior colliculus, respond to visual and auditory stimulation, and these responses are enhanced when the stimulus is used as a target for a saccadic eye movement [Hikosaka and Wurtz, 1983a]. Visual responses can be suppressed by other visual stimuli, and responses can be dependent on remembered visual targets [Hikosaka and

Wurtz, 1983b,c]. Hikosaka and Wurtz [1983d] suggest that substantia nigra inputs to the superior colliculus provide tonic inhibition of superior colliculus neurons and that a decrease in inhibition produces a burst of spikes in the superior colliculus cells that precede and result in a saccadic eye movement.

CONCLUSIONS

The subcortical visual system contains a number of structures that are predominantly or exclusively visual in function. The visual system is associated with other subcortical structures, such as the reticular nucleus of the thalamus, that have broad functions that relate to the visual as well as other systems. Some structures, such as the suprachiasmatic nucleus and parts of the pretectum, appear to be largely regulatory in function. The lateral geniculate nucleus and perhaps parts of the pulvinar via the superficial layers of the superior colliculus are the sources of input for information processing in cortex. Visual cortex is reciprocally related to pulvinar nuclei and the claustrum, and these structures may function to modify the properties of cortical neurons. The superior colliculus accesses oculomotor nuclei in the brainstem and has a major role in attention and the direction of gaze toward novel objects. These subcortical structures and general functions are characteristic of mammals including primates. However, parts of the subcortical visual system are enlarged and more differentiated in primates than in mammals in general. In particular, the lateral geniculate nucleus is large and subdivided into functionally distinct layers, and the pulvinar complex is greatly expanded and subdivided into a number of nuclei. These changes, of course, are associated with the greatly expanded cortical visual system of primates. The massive and complex cortical visual system alters subcortical centers such as the superior colliculus, and even the pregeniculate nucleus, via an impressive subcortical projection system. Within primates, major structural differences in parts of the subcortical visual system are apparent, especially in the lateral geniculate nucleus and pulvinar complex. These species differences appear to relate to increased perceptual abilities in higher primates.

Principles

Some general conclusions regarding the functions and significance of the main subcortical visual centers are possible.

1. The lateral geniculate nucleus of primates consists of three functionally distinct regions, each with segregated inputs from each eye. The parvocellular region receives inputs from the X-like ganglion cells and functions as a relay in the object vision pathway. Separate layers exist for the ipsilateral and contralateral retinal inputs, and these layers subdivide and interdigitate to varying extents in different simian but not prosimian primates. The significance of the interdigitation is not clear, but we suggest the predominance of developmental rather than functionally related causes. The parvocellular layers constitute most of the geniculate, indicating the importance of object vision. The magnocellular layers relay Y-like ganglion cell information to cortex as part of a subsystem mediating visual attention. Two magnocellular layers, one for each eye, are found in all primates. One magnocellular layer is fractionated into a main layer and a smaller displaced segment for unknown reasons in some prosimians. The interlaminar cells and S layers of simians and the interlaminar cells and koniocellular layers of prosimians relay a relatively sparse W-cell input to cortex. This cortical relay appears to influence (modulate) neurons in the object vision pathway from area 17, especially those related to color vision in macaque monkeys. However, the W-cell relay is especially well developed in prosimians, including nocturnal prosimians, in which color vision is not highly important. Thus, the W-cell relay is likely to relate to object vision in general rather than just the color vision component.

2. The superior colliculus appears to have a dual role in vision. The superficial layers receive the Y-like and W-like ganglion cell inputs but not those from the X-like ganglion cells. Thus, a substantial role in object vision is unlikely. Instead, a major function of the superficial layers of the superior colliculus is to relay W-cell information to the W-cell region of the lateral geniculate nucleus, providing a second course of W-cell inputs for uncertain reasons, and relay Y-cell and perhaps W-cell information to parts of the pulvinar complex. Much of this relay appears to modulate only pulvinar neurons and is therefore not a second source of Y-cell activation for cortical neurons. However, a retina–superior colliculus–pulvinar relay may activate restricted regions of polysensory cortex and help mediate functions related to visual changes and novelty. Retinal and cortical inputs to the superficial layers also relate via local circuits in the colliculus to the deep layers, which have oculomotor functions via outputs to oculomotor nuclei. The major function of the deep layers appears to be to use information from visual, auditory, and somatic modalities via cortical and more direct sensory relays to provide outputs that allow the center of gaze to be directed toward locations of interest and probable importance.

3. The pulvinar complex is greatly expanded in primates and includes three large divisions. In all primates, one division, the inferior pulvinar complex, is highly visual and contains three nuclei. The most massive of the three, the central nucleus, is interconnected with primary and adjoining secondary visual areas and receives input from the superior colliculus. The smaller medial nucleus is interconnected with cortical area MT, and the small posterior nucleus may relay visual information from the superior colliculus to cortex rostral to MT. The lateral pulvinar (or lateral part of the superior pulvinar) contains two or more nuclei with interconnections with striate and extrastriate visual areas. The medial pulvinar and its rostral extension, the anterior (or oral) pulvinar, are not as well understood, but they have widespread interconnections with inferotemporal and parietal cortex and therefore have roles in higher-order visual and nonvisual functions. With the probable exception of a minor relay of visual information from the colliculus to cortex, the role of the massive pulvinar complex appears to be as an adjunct to the cortical visual system, receiving processed inputs from cortex, modifying and altering in uncertain ways these inputs, and sending the modified information back to cortex. Reciprocal connections allow for close interaction between parts of the pulvinar and specific visual areas, but connections also allow pulvinar neurons to broadly distribute information.

4. Most of the subcortical visual structures such as the nuclei of the accessory optic system, the pregeniculate, the pretectal nuclei, the suprachiasmatic nucleus, and motor nuclei of the brainstem are closely related to regulative and motor functions. Of course, primates differ from generalized mammals in having inputs from a more elaborate cortical visual system to some of these structures. Thus, higher order and less direct control over these regulatory and motor functions characterize the primate visual system.

Trends

Comparisons of the subcortical visual system of the various extant primates reveal trends associated with phylogeny so that prosimian, New World monkeys, Old World monkeys, apes, and humans represent, to some extent, successive levels of complexity and advance as recognized by Le Gros Clark [eg, 1959]. In addition, there are specializations associated with adaptations for nocturnal (actually crepuscular) or diurnal vision.

The major phylogenetic differences in the subcortical visual system undoubtedly relate to different levels of cortical expansion and subdivisions found in various primates. Since much of the cortical expansion appears to relate to the subsystem involved in object vision, the subcortical structures most closely related to object vision are the most variable across species.

In the lateral geniculate nucleus, monkeys have proportionately larger parvocellular masses than prosimians, but apes and humans show little change from Old World macaque monkeys. Much of this change is presumably related to an emphasis on foveal and detailed object vision in advanced primates, which certainly involves more complex cortical processing and expanded behavioral capacities in higher primates but little or no increase in the relay of information channels from the retina. Of course, nocturnal primates, including owl monkeys, emphasize the parvocellular component of the lateral geniculate nucleus and detailed vision less than diurnal primates. The mostly nocturnal lemuriform and lorisiform prosimians have the specialized koniocellular geniculate layers that are related to W-cell geniculate inputs, and the nocturnal owl monkey has a large interlaminar zone of W-cell function that is densely packed with cells. Thus, an adaptation for nocturnal life involves a significant relay of W-cell information that is reduced in higher primates, which are also diurnal.

The ventral lateral geniculate nucleus occupies its primitive position in prosimians but rotates to become the pregeniculate in simians. Its relative importance, probably as an oculomotor center, decreases, perhaps as a consequence of greater cortical control.

A significant and well-known trend is the expansion of the pulvinar complex in higher primates. We propose that this is largely a consequence of the close functional relationship of the pulvinar with extrastriate visual cortex and the phylogenetic expansion of extrastriate visual cortex.

The superior colliculus of primates appears to express phylogenetic changes related to an increased importance of foveal vision and an increased importance of cortical processing. The visual and visuomotor maps devote proportionately more tissue to central vision in diurnal macaque monkeys than in nocturnal prosimians and possibly even in diurnal New World monkeys. Retinal inputs apparently become less important relative to cortical inputs, so that in macaque monkeys retinal inputs are very sparse over much of the rostral colliculus devoted to central vision and are discontinuous (disrupted) throughout, especially for the sparser ipsilateral inputs, whereas they are continuous and dense from both eyes in prosimians. However, as a visual center, the superior colliculus is not more differentiated in higher primates, and hence there does not seem to be a phylogenetically increasing role for the superior colliculus. Possibly, however, motor fields in frontal cortex such as the frontal eye field may play a greater role in advanced primates by complementing some of the oculomotor functions of the superior colliculus.

Research Needs

The greatest research need, from a comparative standpoint, is to obtain more information on the subcortical system of the tarsier, the sole representative of a complete suborder of primates. Only minimal descriptions of normal material are available. Given that tarsiers are rare and endangered, it is unlikely that extensive information will be obtained. However, we are encouraged by efforts to establish breeding colonies and the possibility of obtaining critical information from various histological preparations from brains rapidly recovered after natural deaths [see Allman, this volume].

Another concern is that most studies have concentrated on the lateral geniculate nucleus, superior colliculus, and pulvinar (with much less attention being directed toward the pulvinar). Other structures should be studied more intensively.

Finally, great advances have been made in understanding the connections of the subcortical visual system, but there is little understanding of the significance of the connections. Disconnection studies with analyses of neuron properties and/or behavior are needed.

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