Casagrande, **V.A.** and J.H. Kaas (1994) The afferent, intrinsic, and efferent connections of primary visual cortex in primates. In: *Cerebral Cortex,* Vol. 10, *Primary Visual Cortex of Primates.* **A.** Peters and K. Rockland, Eds. Plenum Press, N.Y., **pp.** 201-259.

5

The Afferent, Intrinsic, and Efferent Connections of Primary Visual Cortex in Primates

VIVIEN **A,** CASAGRANDE and JON H. **KAAS**

1. Introduction

Because of its distinctive architecture, connections, and functions, primary visual cortex, area **17** or V1 of primates, can be easily identified in most mammals (Kaas, **1987).** V1 (also referred to as striate cortex) is particularly distinctive in primates, and, as a result, it was the first cortical area identified histologically (see Gennari, **1782,** in Fulton, **1937).** V1 of most, if not all, primates has a number of conspicuous features that distinguish this structure from its homologue in other mammals. Unlike carnivores, such as cats and ferrets, almost all of the visual input relayed from the lateral geniculate nucleus (LGN) of primates terminates in V1 (Benevento and Standage, **1982;** Bullier and Kennedy, **1983;** see Henry, **1991,** for review), and lesions of V1 produce a severe deficit known as cortical blindness (e.g., Cowey and Stoerig, **1989).** In addition, visual cortex of all primates is activated by physiologically and morphologically distinguishable streams, or channels, of inputs that are relayed from the retina to V1 in a

VIVIEN A. CASAGRANDE • Department of Cell Biology, Vanderbilt University Medical School, Nashville, Tennessee 37232. JON H. KAAS • Department of Psychology, Vanderbilt University, Nashville, Tennessee 37232.

Cerebral Cortex, Volume 10, edited by Alan Peters and Kathleen S. Rockland. Plenum Press, New York, 1994.

manner unique to primates (Kaas and Huerta, **1988;** Casagrande and Norton, **1991).** Furthermore, the intrinsic connections of V1 in primates exhibit both vertical (laminar) and areal (modular) distinctions that appear designed to create new output channels from input channels via features of internal circuitry. Finally, the output streams project **to** visual areas that seem to be organized in a manner unique to primates. In particular, the major cortical target of V1, the second visual area, V2, is composed of three morphologically distinct modules that are differentially activated from V1, and at least one other major target of V1, the middle temporal visual area or MT, appears to be a unique specialization of primates (Kaas and Preuss, **1993).** These common features of visual cortex in primates are of particular interest because these specializations relate to vision in humans as well as other primates. In this review, we focus on common features that have been described for V1 across a variety of primate species, and therefore are most likely to be present in most or all primates. In addition, we describe differences in V1 organization across primate groups, since these differences may relate to functional specializations and adaptations in the greatly varied primate order. Features that vary across taxa, when related to behavioral niches, may provide clues as to the significance of variations. Finally, this review briefly compares V1 in primates with V1 in some nonprimates to emphasize the distinctiveness of V1 in primates.

2. Architecture: Defining Layers and Compartments

Our understanding of the functional subdivisions, connections, and microarchitecture of V1 has increased enormously in the past 20 years. However, a difficulty in discussing this understanding is that all published papers do not relate to a common anatomical frame of reference. In order to review the connections of V1, it is useful to consider the general issue of how this area has been subdivided into layers and modules, or compartments. We begin with a discussion of traditional concepts and controversies concerning cortical lamination in primates. We then consider how the landscape of V1 is divided based on staining for the mitochondrial enzyme cytochrome oxidase.

2.1. Cortical Lamination

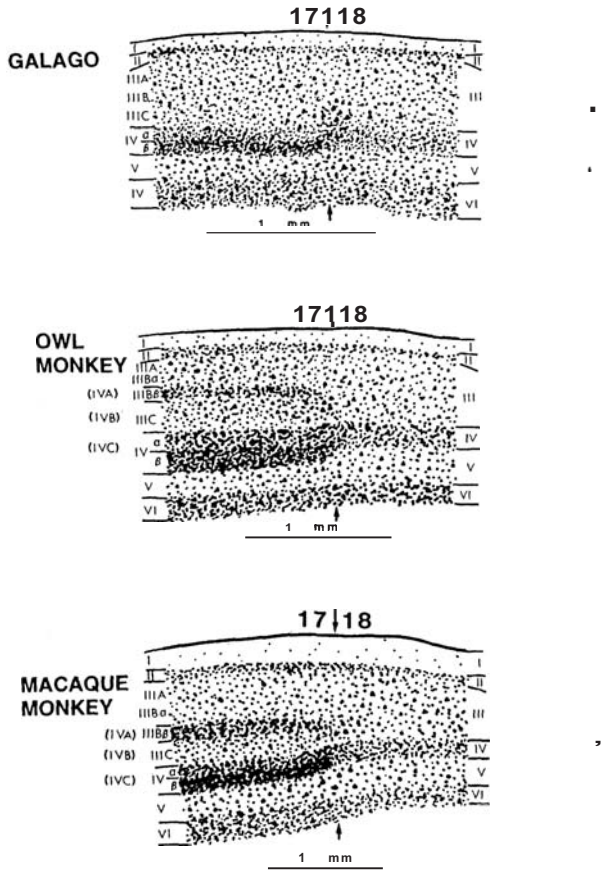
A description of laminar patterns of afferents in primate V1 is currently complicated by the use of different interpretations of cytoarchitectonically defined layers in Nissl stains for cell bodies.* There has been the widespread adoption of the framework of six layers as proposed by Brodmann **(1909)** over schemes with more layers, but variations of the six-layer framework exist (for review, see Garey, **1971;** Billings-Gagliardi *et al.,* **1974;** Braak, **1984;** Henry, **1991;** and Peters, this volume). In particular, Hassler **(1967)** and others (e.g., Weller and Kaas, **1982;** Diamond *et al.,* **1985;** Lachica *et* **al., 1993)** have argued that sublayers defined by Brodmann **as** part of layer **IV** in primate V1 are actually parts of layer III. Such differences in interpretation obviously compli-

***We use the terms area 17 or V1 and area 18 or V2 interchangeably throughout this chapter.**

cate comparisons of laminar differences and similarities across primate and nonprimate taxa, as well as comparisons across cortical areas within primates Descriptions of laminar patterns of neuron types, neurotransmitter receptor distributions (e.g., Shaw and Cynader, 1986), and connections can be misleading if homologous layers and sublayers are not correctly identified.

The architectonic observation that leads to ambiguity is that two sheets of cells in V1 of some simian primates have the appearance of layer IV in that the cells are small and densely packed. These two sheets are separated by a zone of less densely packed, larger neurons (Fig. 1). Brodmann interpreted the two sheets of small granular cells as upper and lower tiers of layer IV (termed IVA and IVC), separated by a middle tier of larger cells (termed IVB). These three "sublayers" of Brodmann's layer IV were thought to merge into a thinner, and more typical layer IV at the border of visual area 18 (V2), and indeed they often appear to do so. This view was clearly summarized by Clark (1925) with his statement that "two layers of granules have been derived from an original single layer. . . that, at the junction between the visuo-sensory and visuo-psychic areas . . . run together and connect up to form a single lamina granularis interna." On the other hand, from careful analysis of serial sections in several planes of cut, it is clear that sublayer IVB of Brodmann's area 17 merges with sublayer IIIC of area 18 (e.g., Colonnier and Sas, 1978), with IVA having no clear equivalent in area 18. This observation is more consistent with Hassler's interpretation that only IVC of Brodmann is equivalent to layer IV in "higher" primates, and that sublayers IVA and IVB of Brodmann are, instead, sublayers of layer III.

While it may appear difficult to resolve the issue of defining layers and sublayers in area 17 of primates, the bulk of the evidence clearly supports Hässler's interpretation. First, if the lamination patterns of V1 are compared across primates, it becomes apparent that layers IVA and IVB of Brodmann are less developed sublayers of layer III in most New World monkeys and hardly apparent as sublayers of layer III in prosimian primates such as galagos. Hassler (1967) used such comparisons across primate groups to support his theory of cortical lamination, and further comparisons fortify his view (e.g., Weller and Kaas, 1982; Diamond *et al.,* 1985; Lachica *et al.,* 1993). Second, layer IIIC neurons, according to Hassler's concept of layers, project to extrastriate cortex in all primate taxa examined (see below), as do layer III cells in nonprimates. According to Brodmann's scheme, these projections would originate in layer IVB of simians (e.g., macaque monkeys) and layer IIIC of prosimians (e.g., lorisids and lemurs). Clearly, Hassler's interpretation of layers allows for a simpler explanation of laminar patterns of connections, while Brodrnann's interpretation calls for explanations of how layer IV became a source of projections to extrastriate cortex in higher primates, and how a major difference in prosimian and simian primates evolved. Third, large pyramidal cells are found in Brodmann's layer IVB of monkeys (e.g., Lund *et al.,* 1979), and large pyramidal cells are not typically found in layer IV. Furthermore, as Colonnier and Sas (1978) stress, this pyramidal cell layer of area 17 merges with the IIIC pyramidal cell layer of area 18. Thus, we use a modified version of Hassler's designations for layers in the present report. For convenience we have compared the laminar designations used in this chapter with those proposed by Brodmann (parentheses) in Fig. 1. The most relevant differences between Brodmann's designations and those used here are as follows: IIIBβ (IVA), IIIC (IVB), IVα (IVCα), and IVβ (IVCβ).



2.2. Cytochrome Oxidase Modules

Primary visual cortex of primates is distinguished not only by characteristic laminar patterns in Nissl-stained sections, but **also** by the presence of a distinct, periodic pattern of light and dark staining perhaps best demonstrated using the mitochondrial enzyme cytochrome oxidase (CO) (see Fig. **2).** This staining pattern was first recognized in 1978 when Margaret Wong-Riley (see Horton, 1984) noted that CO staining was darker in some layers than in others (e.g., geniculate recipient layer IV; see also below) and that there were "puffs" of increased CO activity centered in layer III. Subsequently, it became apparent that these "puffs"—which have **also** been called dots, patches, spots, and splotches, but which **are** now popularly referred to **as** CO blobs (Livingstone and Hubel, 1984a)—marked functionally distinct modules or subdivisions of primate V1 (see Condo and Casagrande, 1990, for review). We describe the organization and variation in the appearance of CO blobs here since these blobs are ubiquitous enough to be considered **a** basic feature of primate cortex (see also Wong-Riley, this volume). Blobs appear to exist in area 17 of most, although possibly not **all,** primates (see McGuiness *et al.,* 1986; however, see Preuss *et al.,* 1993). Moreover, there is evidence from macaque monkeys, squirrel monkeys, and galagos linking CO blobs and interblobs with differences in receptive field properties and connections (see DeBruyn *et al.,* 1993, for review; see also below).

CO blobs have generally not been found in nonprimates, although two preliminary reports have suggested that similar structures can be revealed in striate cortex of cats and ferrets using special fixation procedures (Cresho *et al.,* 1992; Murphy *et al.,* 1991; however, see Kageyama and Wong-Riley, 1986). In all mammals, however, CO appears to stain those layers within area 17 that receive direct thalamic input more darkly than layers that do not receive such direct input. Thus, layer IV and to **a** lesser extent layer VI always exhibit more dense staining than layers III and V (Horton, 1984). In primates the smallest class of LGN cells (W cells) also provide **a** patchy input that colocalizes with the CO blobs. It may be that high CO activity in blobs generally corresponds to zones of dense LGN input. In fact, the borders of layer IV defined in **a** CO stain appear to match the full extent of LGN arbor terminals in layer IV. This relationship has led some investigators to define cortical laminar borders based on CO stain rather than Nissl stain; borders of layers defined in **a** Nissl stain do not exactly match those defined in **a** CO stain (e.g., layer IV appears narrower in **a** Nissl stain) (see Fitzpatrick *et al.,* 1985). Other aspects of the relative distribution of CO, however, such **as** an uneven CO staining in layer IVα in some primates, suggest that relative levels of CO do not simply reflect thalamic input (Carroll and Wong-Riley, 1984; Condo and Casagrande, 1990). More important, defining

Figure 1. The laminar organization of neurons in areas 17 and 18. The sublayers of layer III are more differentiated in monkeys than galagos. The layers and sublayers are numbered arcording to Hassler (1967), but Brodmann's (1909) numbers are given in parentheses. The use of Brodmann's terminology assumes that a broad region of sublayers in area 17 merges at the 17/18 border (arrows) to form a narrow layer IV in area 18. The use of Hässler's terminology assumes instead that only layer IVC of Brodmann is continuous with layer IV of area 18. The transition between areas is simpler in galagos, suggesting that Hassler's view is more valid. Because of such comparative and other evidence (see text), we use Hässler's terminology. Figure adapted from Weller and Kaas (1982) with permission.

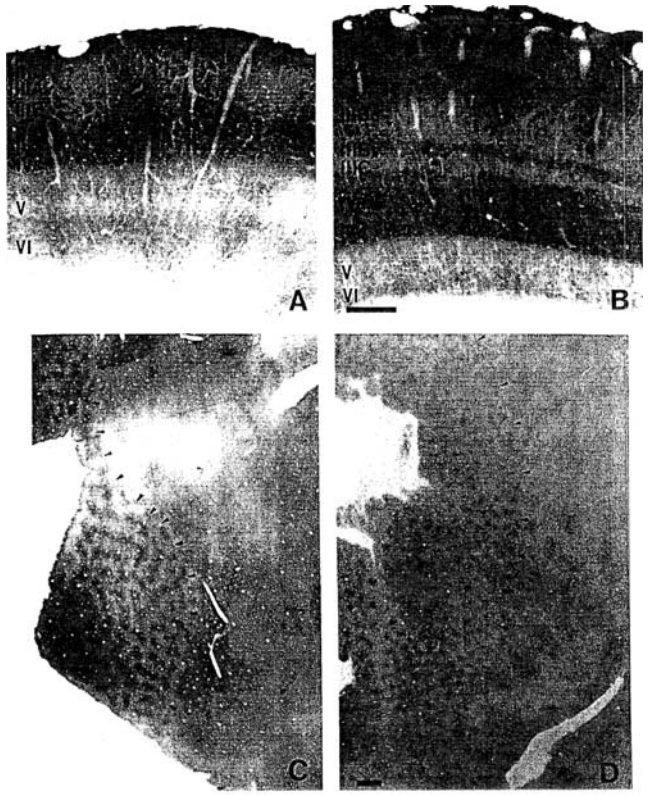


Figure 2. Cytochrome oxidase (CO)-stained sections of the striate cortex in galagos (A,C) and squirrel monkeys (B,D). Sections in A and B were cut coronal to the cortex and sections in C and D were cut tangential to the cortex after it had been unfolded and flattened. The top panels show the appearance of CO blobs in relationship to the cortical layers indicated by Roman numerals. The bottom panels show the overall distribution of the CO blobs in layer IIIB. Arrowheads indicate the border between striate cortex (i.e., area 17 and V1) and area 18 (V2). Bars = 250 μm (A, B) and 500 μm (C, D). From Lachica *et al.* (1993) with permission from the publisher.

layers with CO and/or the myriad of other markers has the potential for adding enormous confusion to the existing problem of comparing cortical layers in the same species as well as across species.

Across primates the basic pattern of CO staining is largely similar. In all primates, layer IV is densely CO positive, and CO-positive blobs appear centered in layer IIIB; weaker periodic staining aligned with these blobs occurs directly above and below the blobs as well as within the infragranular layers (Horton, 1984). A few phyletic differences in details of CO staining have also been reported. Some differences appear to be a direct reflection of differences in LGN input. Thus, as discussed in more detail below, some simian primates (e.g., macaque monkeys and squirrel monkeys) exhibit direct input from the LGN layers to a subdivision of layer 111, IIIBβ. The CO staining in IIIBβ exhibits a unique honeycomb pattern that exactly matches the variation in thalamic input to this layer in these species (Humphrey and Hendrickson, 1983; see also Peters and Sethares, 1991a, for review of the structure of IIIBβ). Primates that do not have thalamic input to IIIBβ (e.g., galagos and owl monkeys) likewise show no selective increase in CO staining of this sublayer (Tootell *et al.*, 1985; Condo and Casagrande, 1990; see **also** Fig. 3). It is likely that humans also lack thalamic input to IIIBβ, since there is no evidence of differential CO staining of IIIBβ in human striate cortex (Horton and Hedley-Whyte, 1984; Wong-Riley *et al.*, 1993). CO blobs also appear to be centered on ocular dominance columns, in those species that exhibit ocular segregation, and variations in patterns of ocular segregation correlate with the arrangement of CO blobs (Horton and Hubel, 1981; Hess and Edwards, 1987; Rosa *et al.*, 1991). Thus, in macaque monkeys the CO blobs form elliptical patches elongated with the long axis of ocular dominance columns; in squirrel monkeys, which lack ocular dominance columns, the blobs appear round and are not arranged in elongated groups (Horton and Hubel, 1981; Humphrey and Hendrickson, 1983). Other evolved differences in CO

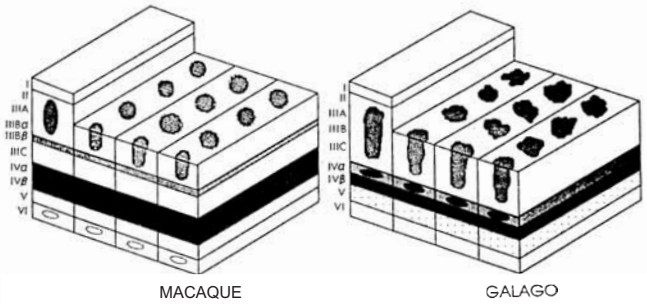


Figure 3. Schematic drawings showing the differences between the organization of CO activity in the striate cortex of the macaque monkey (left) and galago (right). Blocks indicate ocular dominance columns. Darkened layers and patches indicate high CO activity. From Condo and Casagrande (1990) with permission from the publisher. See text for details.

staining patterns are less clearly linked to LGN input. In macaque monkeys and galagos the relative size and density of CO blobs vary with eccentricity (Livingstone and Hubel, 1984a; Condo and Casagrande, 1990); blobs are both larger and less frequent in the area of V1 representing central vision than in zones representing peripheral vision. Surprisingly, the opposite **has** been reported for owl monkeys (Tootell *et al.*, 1985). Phyletic differences have also been reported in the size and number of **CO** blobs. In nocturnal galagos CO blobs appear **to** occupy relatively more tangential cortical space in the region of central vision (39 versus 35%) than in macaque monkeys (Condo and Casagrande, 1990). ,This result does not fit with arguments that blobs play **a** unique role in color vision (Livingstone and Hubel, 1988); galagos are nocturnal and thus typically operate under conditions where color is not useful.

The number of blobs increases roughly linearly with estimated size of striate cortex. Thus, species with **a** larger V1 also have more **CO** blobs (Condo and Casagrande, 1990). There are exceptions, however, in that humans appear to have fewer and larger, more widely spaced blobs than do macaque monkeys (see Horton and Hedley-Whyte, 1984; Fig. 11 of Condo and Casagrande, 1990; Wong-Riley *et al.*, 1993). Beyond these quantitative evolved differences, other qualitative phyletic differences in CO patterns have been reported. For example, in owl monkeys, galagos, and humans, layer IVα shows periodic staining which aligns with the blobs in layer III; periodic staining in IVα has not been reported in squirrel monkeys (Carroll and Wong-Riley, 1984; Horton, 1984). Moreover, weak periodic staining of large pyramidal cell bodies in layer V has been observed in macaque monkeys but not in other species, and periodicity in the neuropil of layer VI has been seen in several species (see Condo and Casagrande, 1990, for review).

3. Thalamic Control: Subcortical Inputs

The major inputs to area V1 in primates and other mammals are from the (dorsal) LGN and, to a lesser extent, the nuclei of the pulvinar complex (see **Kaas** and Huerta, 1988). The activation of V1 appears to completely depend on the inputs from the LGN, since inactivation of the geniculate neurons also blocks visually evoked responses in V1 neurons (Malpeli *et al.*, 1981). The significance of the inputs from the pulvinar complex is unknown, but pulvinar inputs may modulate the activites of V1 neurons and alter receptive field properties relative to attention and other behavioral states (see Desimone *et al.*, 1990). Relationships with the pulvinar complex are considered briefly in **a** later section. Other modulating inputs originate from **a** number of subcortical structures reviewed recently by Tigges and Tigges (1985), and they will not be considered in detail here. Briefly, these inputs include direct serotonergic inputs from the raphe nuclei, noradrenergic connections from the locus coeruleus of the brain stem, cholinergic projections from nucleus basalis of Meynert and nucleus of the diagonal band of Broca, and inputs from a few neurons in the hypothalamus, nucleus basalis lateralis of the amygdala, and intralaminar nuclei of the thalamus. In addition, **a** circumscribed portion of the claustrum is reciprocally connected with V1, and activation of claustral inputs has been shown to reduce spontaneous activity and alter neuron response characteristics of V1 neurons in

cats (e.g., Sherk and LeVay, 1983). This section focuses on the major input patterns from the LGN.

3.1. Geniculostriate Termination Patterns

In important ways, the geniculostriate projection pattern of primates reflects a more general mammalian pattern. In most or all mammals investigated, the major geniculostriate terminations are in layer IV, although sparser terminations have been described in the supra- and infragranular layers (e.g., cat: LeVay and Gilbert, 1976; Ferster and LeVay, 1978; mouse: Drager, 1974; rat: Ribak and Peters, 1975; squirrel: Webcr *et al.,* 1977; opossum: Sanderson *et al.,* 1980; tree shrew: Harting *et al.,* 1973; Casagrande and Harting, 1975; Hubel, 1975; Conley *et al.,* 1984; Raczkowski and Fitzpatrick, 1990). The layer IV projections originate from medium- to large-sized neurons, the physiologically defined **X** and Y neurons, respectively, of cats and the parvocellular, P (X-like), and the magnocellular, M (Y-like), neurons of primates. Terminations in layers **I,** II, and III originate from small geniculate neurons located either in layers of small cells, the koniocellular (K) layers or in intercalated **(I)** layers, layers of mixed small and larger cells, the superficial **(S)** layers, or interlaminar zones (see Casagrande and Norton, 1991, for review). These smaller LGN relay neurons typically receive inputs from the superior colliculus as well as the retina (Harting *et al.,* 1978; Lachica and Casagrande, 1993). In cats these small cells have been classified physiologically as W cells. This category is **a** heterogeneous population of cells grouped together mainly because of their tendency to have slower conduction velocities from the retina and larger receptive field sizes. Similar, but not identical, W-like cells have been identified in several mammalian species including tree shrews, opossums, and ferrets (see Stone, 1983; Casagrande and Norton, 1991, for review). In primates these smaller cells have only been studied in galagos, where they exhibit W-like receptive field properties (Norton and Casagrande, 1982; Irvin *et al.,* 1986; Norton *et al.,* 1988). Based on similarities in connections, it is likely that this class of small LGN cells will also be found to have W-like properties in other primate species (see Lachica and Casagrande, 1993). In part for convenience, we refer to the classes of geniculate relay neurons in primates **as P** (X-like), M (Y-like), and K (W-like). This nomenclature has the further advantage of neutrality in the difficult issue of whether cats, tree shrews, primates, and perhaps other mammals inherited X, Y, and W classes from **a** common ancestor, or evolved similar classes of retinal and geniculate neurons independently (see **Kaas,** 1986).

3.2. Laminar Terminations

The laminar patterns of terminations in V1 of primates have been revealed in several ways, including the use of eye injections of tracers to indirectly label geniculocortical axons via transneuronal transport, direct geniculate injections of various tracers, and by injections of horseradish peroxidase (HRP) in the white matter just beneath the cortex to label single axons and small groups of axons. The methods complement each other and provide a reasonably detailed picture of termination patterns in prosimian galagos, New World squirrel and

owl monkeys, and Old World macaque monkeys. Only limited information is available for hominoids (apes and humans), but the patterns seem to be similar across primate taxa, so that supportable inferences can be made for hominoid primates. We begin here with **a** description of the general pattern of LGN projections to layers of cortex, and in **a** later section consider the details of axon arbor morphology.

The basic laminar patterns of geniculate terminations for prosimians and New and Old World simians are illustrated in Fig. **4.** In galagos, geniculate axons terminate in layers IV, VI, III, and I (Glendenning *et al.,* 1976; Casagrande and DeBruyn, 1982; Florence *et al.,* 1983; Diamond *et al.,* 1985; Florence and Casagrande, 1987, 1990; Lachica and Casagrande, 1992). The projections to layer IV are the most obvious. They include M cell inputs to layer IVα where they spill over somewhat into inner layer IIIC, perhaps to terminate on the dendrites of neurons in layer IVα that extend into layer IIIC, or directly on layer IIIC neurons. P cells terminate in layer IVβ and K cells terminate in the CO blobs of layer III and in layer **I.** Some M and P cells also send a minor projection to layer VI.

In New World monkeys, laminar patterns of geniculate inputs into V1 have been studied in squirrel monkeys (e.g., Tigges *et al.,* 1977; Hendrickson *et al.,* 1978; Rowe *et al.,* 1978; Livingstone and Hubel, 1982; Fitzpatrick *et al.,* 1983; Weber *et al.,* 1983), cebus and spider monkeys (Hendrickson *et al.,* 1978; Florence *et al.,* 1986), owl monkeys **(Kaas** *et al.,* 1976; Rowe *et al.,* 1978; Diamond *et al.,* 1985; Pospical *et al.,* 1993), and marmosets (Spatz, 1979, 1989; DeBruyn and Casagrande, 1981). Laminar patterns of terminations appear to be quite similar in **all** of these primates. In squirrel monkeys, which have been studied more extensively, geniculate inputs are most dense in layer IV. Sparser terminations

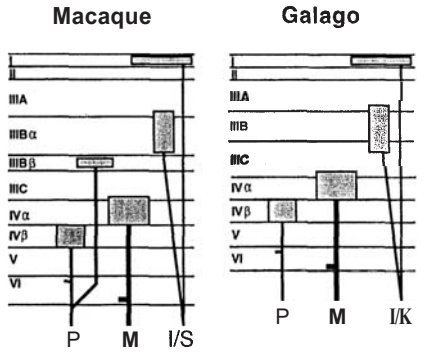


Figure 4. Schematic illustrations of the patterns of LGN axon terminations within the cortical layers of a diurnal Old World simian (macaque monkey) and a nocturnal prosimian (galago). The cortical layers are indicated using a modification of Hässler's nomenclature. The LGN relay cell pathways to cortex are indicated by: K, koniocellular [this designation includes the intercalated interlaminar (I). and superficial (S) layer cells]; M, magnocellular; P, parvocellular.

are coextensive with the CO blobs in layer III, and in layer I. As in galagos, the P geniculate cells terminate in layer IVβ, the M cells in layer IVα, and the K (interlaminar) cells in the CO blobs of layer III and layer I. In addition, and unlike galago, there is a clear projection of P cells to the inner part of layer IIIB (referred to here as layer IIIBβ). Terminations in layer VI have not been conclusively demonstrated or ruled out.

Geniculate projection patterns in other diurnal New World monkeys have not been fully studied, but they appear to be similar to those in squirrel monkeys. These projections have been more extensively investigated in the nocturnal owl monkeys, where there is again the pattern of P cell inputs to layer IVβ, M cell inputs to layer IVα, and K cell inputs to layer III blobs and layer I. A difference, however, is that there is no obvious P cell input to layer IIIBβ, which also does not appear as clear as a sublayer in Nissl preparations as it does in diurnal squirrel monkeys (Diamond *et al.,* 1985). Thus, the P cell terminations in layer IIIBβ are a feature of some, but not all, New World monkeys.

Most of what is known about geniculate termination patterns in Old World monkeys depends on studies of macaque monkeys (e.g., Hubel and Wiesel, 1972; Wiesel *et al.,* 1974; Hendrickson *et al.,* 1978; Livingstone and Hubel, 1982; Blasdel and Lund, 1983; Freund *et al.,* 1989). Again, M cells terminate in layer IVα, P cells in layer IVβ, and K cells in layer III blobs and layer I. In addition, P cells terminate densely in layer IIIBβ and some M cells and a few P cells appear to produce collateral branches that terminate sparsely in layer VI. As in galagos, the majority of direct input to layer VI appears to come from the M cell pathway.

While it has been difficult to obtain information on geniculate terminations in hominoid primates, Tigges and Tigges (1979) managed to make an eye injection and use transneuronal transport methods to determine laminar patterns of geniculate terminations in a chimpanzee that had suffered a massive stroke and had to be euthanized. Dense projections were found in layer IV, and some labeling was present in layer VI. No terminations were apparent in layers III or I, which could reflect technical difficulties, and thus the existence of such inputs in chimpanzees is still uncertain. In humans, thalamocortical terminations have been revealed in layer IV of area 17 by using silver stains in the brains of patients who died after lesions of the thalamus (Miklossy, 1992). Taken together, these results reinforce the view that there are basic similarities in the geniculate termination patterns across primate taxa. Yet, in hominoids there is no certain evidence that M and P cells terminate in different subdivisions of layer IV, or that terminations consistently exist in any of the other layers.

3.3. Ocular Dominance Columns

In many primates (see Florence *et al.,* 1986; Florence and Kaas, 1992, for review) geniculocortical inputs activated by one eye are largely separate from those activated by the other eye, forming bandlike termination zones that have been referred to as ocular dominance columns. These zones of input are more appropriately called ocular dominance bands in keeping with their shapes as viewed from the brain surface (Fig. 5). Ocular dominance bands do not occur in all primates. Moreover, they do not reflect the ancestral condition, since they are not found in other archono mammals such as tree shrews (Casagrande and Harting, 1975; Hubel, 1975; Kaas and Preuss, 1993) or most other mammals,

including those with well-developed visual systems such as squirrels (Weber *et al.,* 1977). However, ocular dominance bands are found in carnivores such as cats (e.g., Löwel and Singer, 1987; Anderson *et al.,* 1988), ferrets (Redies *et al.,* 1990), and mink (LeVay *et al.,* 1987), and weakly in sheep (Clarke and Whitteridge, 1976; Clarke *et al.,* 1976; Pettigrew *et al.,* 1984) and they may exist in other unexamined taxa. The general lack of ocular dominance bands in mammals, and the presence of such bands in members of the primate, carnivore, and artiodactyl orders indicates that bands have evolved independently in at least three groups. It also appears from the distribution of such bands across primates that distinct bands have evolved, perhaps from a weak tendency, in both New World and Old World monkeys.

Ocular dominance bands are clearly expressed in all Old World monkeys examined. They have been most extensively studied in macaque monkeys, where they were described originally using physiological techniques (Hubel and Wiesel, 1968). Subsequently, they have been revealed by a number of techniques including transneuronal transport of ^{3}H-labeled amino acids injected in the eye, fiber stains and changes in the relative density of CO staining following blockade of activity from one eye (see Florence and Kaas, 1992, for review). Most recently, they have been revealed by looking at the down-regulation of immediate early gene expression following enucleation (Chaudhuri *et al.,* 1992) and by various

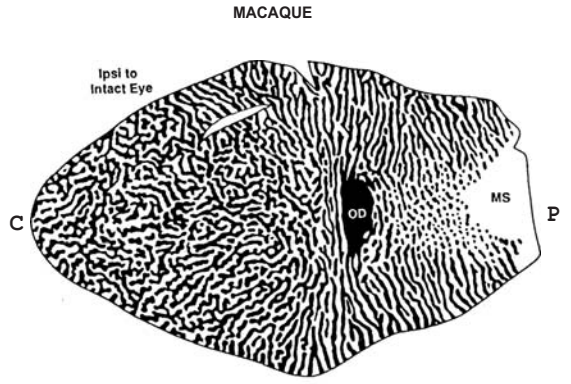
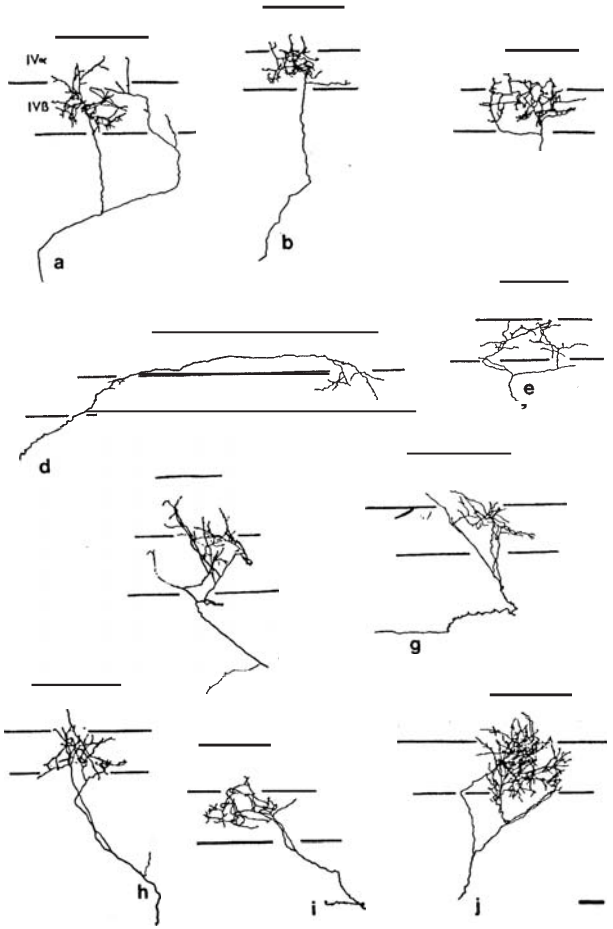


Figure 5. The complete pattern of ocular dominance bands in area 17 of a macaque monkey (*Macaca fascicularis*). The dark cytochrome oxidase regions relate to the intact ipsilateral eye (black) and light CO regions (white) relate to the suppressed contralateral eye. The figure is based on a complete reconstruction of area 17 from artifically flattened cortex cut parallel to the surface. The black oval corresponds to the projection of ipsilateral retina matched by the retina-free optic disk in the contralateral eye. The large, white area on the right corresponds to the monocular field with input only from suppressed contralateral eye. Central vision is on the left. Bar = 1 mm. Modified from Florence and Kaas (1992) with permission.

optical imaging techniques (Frostig, 1993). Although the patterns are not revealed in equal detail by each technique, the basic features revealed are very similar. Most of these features are clearly appreciated on **a** reconstructed representation of **a** flattened surface view of layer IV of V1 (e.g., LeVay *et al.,* 1985; Fig. 5). The segregation of ocular inputs in these preparations demonstrates **a** number of typical features: (1) The segregations occur in short bandlike segments that fuse, branch, and terminate in an irregular pattern that is similar, but nevertheless varies in detail from hemisphere to hemisphere in the same animal, and across animals. (2) The segregation involves both M and P pathways to IVα and IVβ, and the P pathway to IIIBβ. Since CO blobs are aligned with ocular dominance bands (see earlier), K inputs to blobs may demonstrate ocular segregation as well. (3) Rands are more nearly parallel and branchless in parts of V1 representing central rather than peripheral vision. The bands break down into **a** pattern of dots for the ipsilateral eye and larger surrounds for the contralateral eye in cortex devoted to peripheral vision, **(4)**Bands vary in width from central to peripheral vision with **a** slight decrease in average band width, and **a** progression from equal bands to larger bands and then surrounds for the contralateral eye. (5) Bands vary in width in different species, with the smallest bands for the small Old World talapoin monkeys and the largest bands for humans. This would suggest **a** relationship between body, or brain size, and band width, but since galagos (which have smaller brains) have larger ocular bands on average than talapoin monkeys, the relationship does not appear to hold across all species (see also above discussion on CO blobs, and Condo and Casagrande, 1990).

A frequent, although debatable assumption is that band width is related to the sizes of functionally significant processing units in cortex, such as hypercolumn size (see Florence and Kaas, 1992, for review). One might thus infer that processing units would vary in size across visual cortex and across species. On the other hand, this is still only inference because the arrangement of bands may be related to an original balance of developmental factors that do not relate directly to adult function (Kaas, 1988; Purves and LaMantia, 1990).

Ocular dominance bands seem to be **a** basic feature of all higher primates. They have been reported for humans (Hitchcock and Hickey, 1980; Horton and Hedley-Whyte, 1984; Wong-Riley *et al.,* 1993), chimpanzees (Tigges and Tigges, 1979), and all Old World monkeys examined (see Florence and **Kaas,** 1992, for review). There are no anatomical signs of ocular dominance bands in normal squirrel monkeys, although weak ocular periodicity has been reported from **a** physiological study in normal adult squirrel monkeys (Hubel and Wiesel, 1968) and there appears to be **a** slight tendency for anatomically defined ocular segregation after monocular rearing in this species (Tigges *et al.,* 1984). Owl monkeys and marmosets have only **a** weak tendency for ocular segregation **(Kaas** *et al.,* 1976; Rowe *et al.,* 1978; DeBruyn and Casagrande, 1981; Diamond *et al.,* 1985; Spatz, 1989), while larger New World monkeys such as *Cebus* (Hess and Edwards, 1987; Rosa *et al.,* 1988) and *Ateles* (Florence *et al.,* 1986) have obvious ocular dominance bands. Among prosimian primates, only galagos have been studied, and only **a** weak ocular periodicity has been demonstrated anatomically (Glendenning *et al.,* 1976; Casagrande and DeBruyn, 1982). However, recent physiological investigation of galago V1 suggests **a** much stronger ocular segregation (DeBruyn *et al.,* 1993). This difference raises **a** note of caution given that many studies of ocular segregation have used transneuronal transport of tracers that could diffuse across LGN layers, especially in species with narrow



LGN layers. Such technical artifacts probably do not account for major phyletic differences in ocular segregation, but more subtle differences should be verified with more than one method. The tendency for LGN axons to segregate into ocular dominance bands may be directly related to brain size (see Rosa *et al.,* 1988) or other factors indirectly related to size such as eye separation and ocular disparity (see Florence *et al.,* 1986). This issue is complicated by a surprising lack of data on what ocular dominance columns actually contribute to visual function, and the fact, as mentioned above, that several species, such as tree shrews and squirrels, have excellent visual performance without ocular dominance columns.

3.4. Axon Arbors

In general, across mammals, axon arbors that terminate in layer IV constitute the majority of inputs to area V1. They originate from the larger geniculate cells with thicker axons, and they branch profusely in layer IV forming a dense array of synaptic swellings or boutons. In cats (Humphrey *et al.,* 1985b) and tree shrews (Muly and Fitzpatrick, 1992; Usrey *et al.,* 1992), these larger LGN cells can generally be subdivided in two groups that exhibit either small, single, more compact arbors (the X class in cats) or larger sprawling arbors that sometimes terminate in separate patches (the Y class in cats). These arbors may extend into layer III, and both classes may have branches that terminate in layer VI. In cats the arbors of X and Y cells overlap extensively in layer IV (Humphrey *et al.,* 1985a). Moreover, in cats Y axons project outside of area 17, particularly to area 18 (Humphrey *et al.,* 1985a); M axon arbors in primates do not appear to innervate extrastriate areas (however, see Benevento and Yoshida, 1981). Axons from the smallest LGN relay cell class (the W cells in cats) are thinner. As in primates, some of these thin axons terminate in layers III and I. However, the details of terminations of these W cells in area 17 in cats and tree shrews differ from those found in primates in several ways which are described in more detail below in the context of intrinsic cortical connectivity.

The main characteristics of geniculostriate axon arbors of the primate visual system are similar to those of cat and tree shrew. Arbors of individual axons have been described for several species including prosimian galago (Florence and Casagrande, 1987; Lachica and Casagrande, 1992), New World owl monkey (Pospical *et al.,* 1993), and Old World macaque monkey (Blasdel and Lund, 1983; Freund *et al.,* 1989). Detailed analysis of arbors of all three LGN classes has only been done in galagos. Other studies, however, have reported that, at least for P and M cells, the basic morphological characteristics of the arbors are similar. In galagos, the P cell axons produce small, single, dense terminal fields largely or exclusively restricted to layer IVβ. In both macaques and galagos, differences

Figure 6. Composite of P axons serially reconstructed from the calcarine fissure of striate cortex in lesser galagos showing the differences in their morphology. These axons ramify primarily in layer IVβ and occasionally (see f and h) project to layer VI. The axon designated d is unusual in that the axon trunk runs parallel to the cortical layers for a considerable distance before branching at the terminal focus. Comparison of the terminal arbor size of these axons with M axons in the same cortical area (Fig. 7) demonstrates a significant size difference. From Florence and Casagrande (1987) with permission.

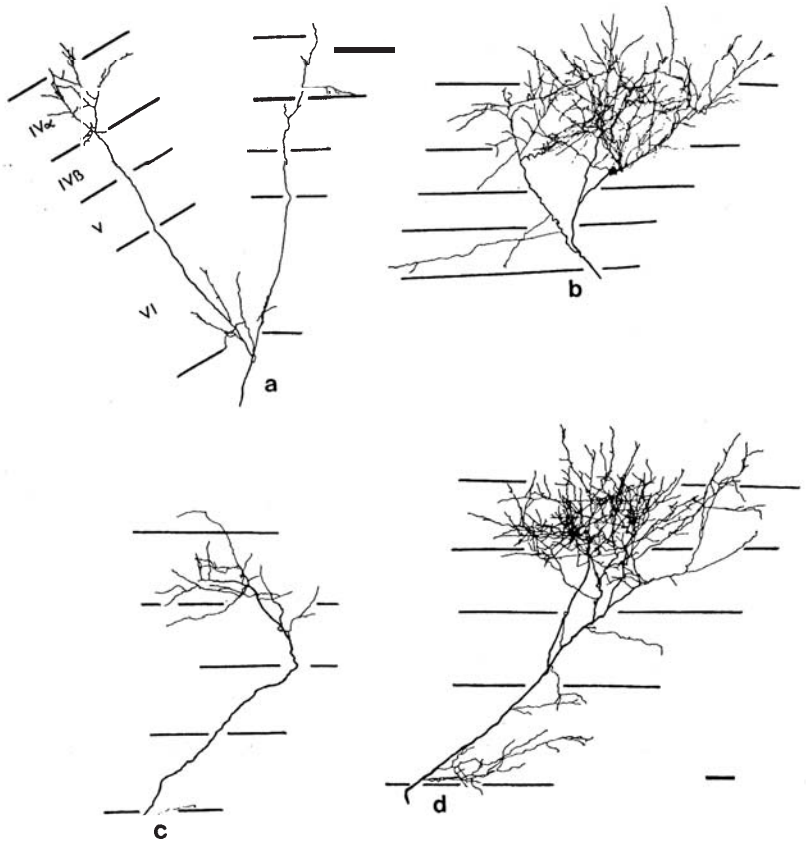
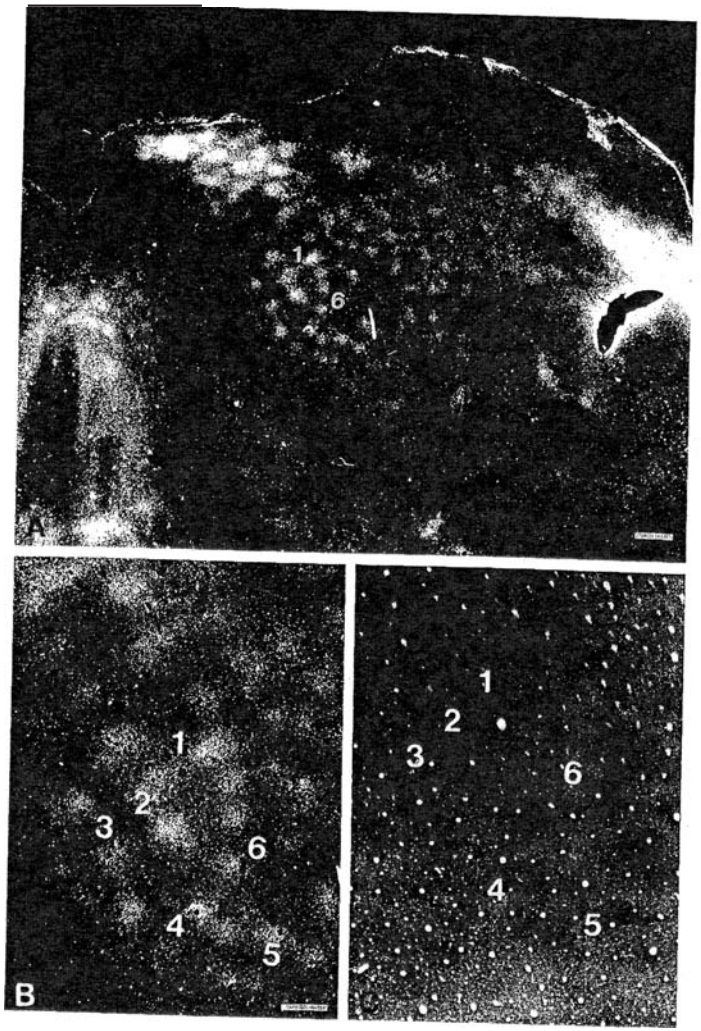


Figure 7. Composite of M arbors serially reconstructed from the dorsal surface of striate cortex showing the extent of their variation in lesser galagos. Solid lines indicate borders of cortical layers; Roman numerals identify layers according to Hässler's nomenclature. Note that all axons arborize primarily in IVα but also project to layer III and to layer VI. In some cases, the course of the axon after reaching the white matter has not been illustrated to conserve space. Bar = 50 μm. From Florence and Casagrande (1987) with permission.

have been reported in P cell arbors terminating in layer IV, but these differences prohably reflect within-class variation (see Fig. 6). In macaque monkey, however, a separate type of P axon terminates in IIIBβ (Blasdel and Lund, 1983). This type of axon, which has a distinct morphology with a narrowly focused tangentially spreading arbor, is unique to those species which exhibit geniculate terminations in layer IIIBβ (Blasdel and Lund, 1983). In both galago and macaque monkey, the M arbors exhibit a more variable morphology than the P arbors and are, on average, significantly larger in area (Blasdel and Lund, 1983; Florence and Casagrande, 1987). Some M arbors spread broadly and extend branches into lower IIIC as well as occasionally into IVβ. Other M arbors are more narrowly confined to IVα. Still others bifurcate and terminate in two patches which are generally smaller in size than M arbors that terminate in a single patch (see Fig. 7). It is unclear whether these differences reflect actual subclasses or variation within a class (see Lund, 1988). Some M and occasional P axon arbors extend a few branches into layer VI. These branches appear to be restricted such that M arbors terminate primarily on cells in the lower half of layer VI, whereas P collaterals, when present, are restricted to the upper half of layer VI. Note that, unlike galago and macaque monkey, no collaterals were found to project to layer VI in owl monkey (Pospical *et al.,* 1993). However, in galago and macaque monkey the arrangement of the projections to layer VI fits with the observation that projections to P and M layers tend to arise from cells in the upper and lower divisions of layer VI, respectively (Lund *et al.,* 1975; Lachica *et al.,* 1987).

Quantitative comparisons of the distributions of M and P axons in galago cortex show that both arbor types are significantly larger in the area of layer IV innervated in the zone of area V1 representing central vision than in cortex representing the visual periphery (Florence and Casagrande, 1987). Although such quantitative comparisons of axon area across layer VI are not available for other primate species, these size differences fit with the proposed proportional increase in magnification of the representation of central vision over peripheral vision in V1 versus in the LGN (see Florence and Casagrande, 1987, for discussion). These differences are also reflected in the relative sizes of ocular dominance columns and the average diameter of M arbors, although P arbors are on average much smaller than the width of an ocular dominance column. In addition, M and P arbors tend to be elongated parallel to ocular dominance columns in galagos. This relarionship suggests that their shape may be constrained by binocular interactions in species that have ocular dominance columns. However, given that P arbors are much smaller than ocular dominance columns, anisotropies in shapes of arbors may simply reflect anisotropies in the topography of V1 (Tootell *et al.,* 1982; Van Essen *et al.,* 1984).

The K arbors have been described only in one primate, galago (Lachica and Casagrande, 1992). In this primate, all K axons terminate within CO blobs in layer III; no axons are found that terminate within interblob zones. This relationship can be appreciated by comparing the overall pattern of input from the K cells with the location of CO blobs on adjacent stained sections (Fig. 8). In addition to inputs to CO blobs, K arbors extend collateral branches to layer I where arbors spread tangentially over a broad zone. Branches in layer I clearly extend beyond the boundaries of underlying parent arbors in the CO blobs in layer III. Thus, K arbors could have transcompartmental influence via contacts with apical dendrites extending into layer I. Within a CO blob column, the focus of most K arbors is in cortical layer IIIB. However, some K arbors are centered



in either IIIA or IIIC (see Fig. 9). Thus, the K pathway is in a position to directly influence cells in the major pathways that project to extrastriate cortex that exit via layers IIIA or IIIC (see also below). The distribution of K arbors in cortex also reinforces the view that blob and interblob columns have different functions and that these differences may extend to cells in layers above and below the blobs. This view is further supported by differences in vertical intrinsic connections in blob and interblob cortex.

4. Intrinsic Connections

The physiological properties of cells in V1 are very different from those seen at the level of the retina and LGN. Moreover, many properties seen in V1 for the first time can be identified in higher-order visual areas to which V1 projects. Therefore, it is clear that a key to understanding the functional significance of visual cortical organization lies in determining how inputs to V1 are transformed into new output streams which subserve different extrastriate visual areas. One way to begin to understand how inputs are transformed into outputs in V1 is to examine the details of its internal circuitry, or wiring. Presumably, aspects of such circuitry that are basic to all primates (as well as to other mammals) are of fundamental importance to visual cortical function. In keeping with the purposes of this chapter we begin with a review of these basic primate features of V1 circuitry. We then compare this organization with that seen in other mammals. Finally we examine features of intrinsic circuitry that appear to differ between primate groups.

4.1. Background

The intrinsic circuitry of V1 of cortex has been examined in only a few primate species. The most extensive work has been done in macaque monkeys (e.g., Lund, 1988, 1990; see also Lund, this volume). In fact, many details of V1 cell morphology and connections have been described only in macaque monkeys. Recent studies, however, have begun to provide information on intrinsic connections in three other species, namely galagos, squirrel monkeys, and owl monkeys, and some information is now available for humans (i.e., Burkhalter and Bernardo, 1989; Miklossy, 1992). Several features of intracortical circuitry which relate V1 inputs to outputs appear to exist in all four of these primates. We consider these consistent features here.

Figure 8. (A) Low-magnification (caudal to the top, medial to the left), dark-field photomicrograph of striate cortex that has been flattened, cut tangential to the surface, and reacted for TMB histochemistry to reveal the patchy pattern of K-cell geniculostriate terminations in layer III. A higher-magnification photomicrograph of a small field marked in A (by Nos. 1 and 6) is shown in B. Blood vessels in B are identified by number so that they may be easily matched with blood vessels in C, which shows an adjacent section stained for cytochrome oxidase. Bars = 1 mm (A) and, 500 pm (B, C). From Lachica and Casagrande (1992) with permission.

As described earlier, the main inputs to V1 arise from the LGN via three

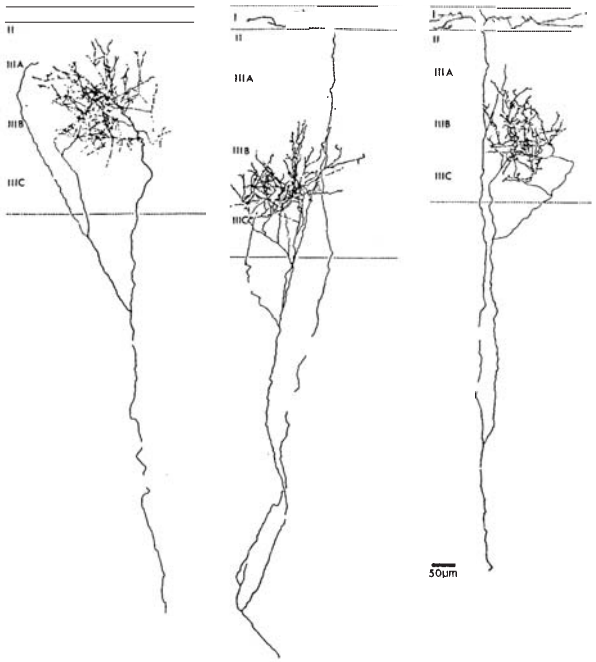


Figure 9. Reconstructions of three different varieties of PHA-L-labeled K geniculocortical axon arbors. The majority of K geniculostriateaxons terminated in layer IIIB, and had collateral branches that arborized in layer I. Modified from Lachica and Casagrande (1992) with permission.

and interblobs, respectively, and each projects to separate zones within V2 (Rockland and Pandya, 1979; Tigges *et al.,* 1981; Livingstone and Hubel, 1984b, 1987; Krubitzer and Kaas, 1990b; Van Essen *et al.,* 1990; Rockland, 1992; see Lachica *et al.,* 1993, for review). There are **also** several major pathways to subcortical areas and these arise from infragranular layers V and VI, which project to several distinct zones in the thalamus, midbrain, and pons (see Kaas and Huerta, 1988).

4.2. Basic Primate Plan

The intrinsic connections between the input and output pathways within primate V1 are exceedingly complex, as illustrated in the many elegant studies of Lund and colleagues in macaque monkeys (e.g., Lund, 1988, 1990; see Lund, this volume). Since the details of projections of individual classes of cells have been reviewed in detail recently (Lund, 1990; Henry, 1991), they will not be considered here. There are three major features of internal connections that have been consistently observed across primate species. First, most layers in V1 send and receive heavy vertical projections from several other layers **as** well as inputs from outside V1. Thus, the direction of flow of information is not strictly serial. For example, in macaque monkeys layer **IV** receives input from layers V and VI **as** well **as** from the LGN; layer IV, in turn, sends projections back to layer V1 (itself an LGN target) and also to layers IIIB and IIIC, which themselves get input from layers V and VI (Blasdel *et al.,* 1985; Fitzpatrick *et al.,* 1985; Lund, 1987, 1990; Lachica *et al.,* 1992, 1993). In spite of these complexities, a consistent suborder can be discerned in specific circuits, particularly those that relate to the output pathways. Layer IIIC, which, **as** mentioned above, sends the largest projection to extrastriate area MT, receives its major projection directly from M-recipient layer IVα (see Fig. 10 and Fitzpatrick *et al,* 1985; Lachica *et al.,* 1993). In contrast, layer **IIIA,** which provides the major output to area V2, does not appear to get any direct input from M- and P-recipient IVα and IVβ; instead, signals from both M- and P-recipient divisions of layer IV appear to be initially relayed to IIIB, **IIIC,** and other layers before reaching IIIA (see Fig. 11 and 12 and Fitzpatrick *et al.,* 1985; Lachica *et al.,* 1992, 1993). This arrangement suggests that cells in IIIB may function **as a** set of interneurons specifically for the construction of new output signals in **IIIA** (Fitzpatrick *et al.,* 1985; Lachica *et al.,* 1992, 1993). Since layers IIIC and **IIIA** form the initial substrates for information entering the two proposed major processing streams for analysis of object location (or "where") and object identification (or "what"), respectively (Ungerleider and Mishkin, 1982), the differences in intrinsic wiring of cells in **IIIC** and **IIIA** may offer clues concerning the initial coding of information for these basic visual functions. The lower layers also show some sublaminar specialization in **all** primates. Layer **V** exhibits a distinct thin subdivision at its upper border termed Va by Lund and colleagues (Lund, 1987). Layer **VA** appears to be particularly well developed in simian primates and has been described in macaque monkeys as **a** set of interneurons (Lund, 1987). This zone, unlike the remainder of layer V, shows connections with IVα (Lund, 1987; Lachica *et al.,* 1993) and also exhibits distinct connections with the remaining layers (Lund, 1987; Lachica *et al.,* 1993). **Our** data suggest that, in simian primates, the cells in the upper and lower halves of layer V show differences in connections with the CO blob and

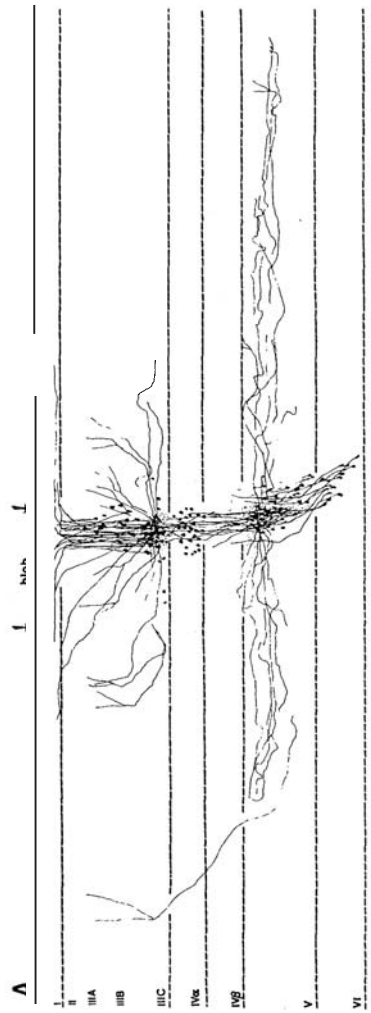


Figure 10. Camera lucida reconstructions showing labeled cells and axons following injections into blob (A) and nonblob (B) layer IIIC in galago. Note labeled cells are absent from layer IVβ following all injections into IIIC. Roman that numerals indicate layers according to a modification of the nomenclature of Hässler, Reproduced from Lachica *et al.* (1993) with permission. See text for details.

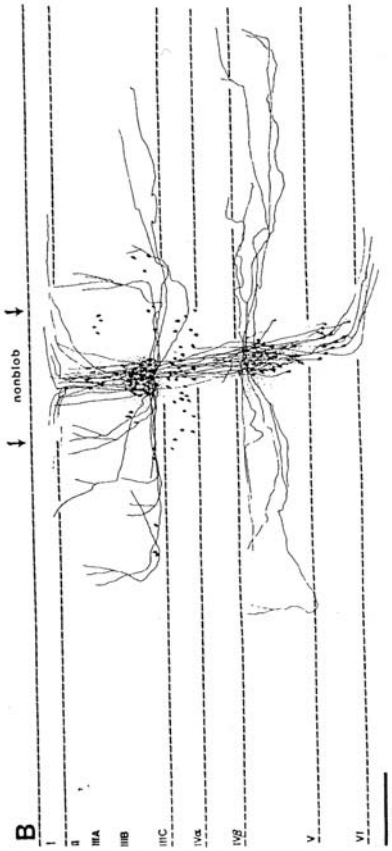


Figure 10. (*Continued*)

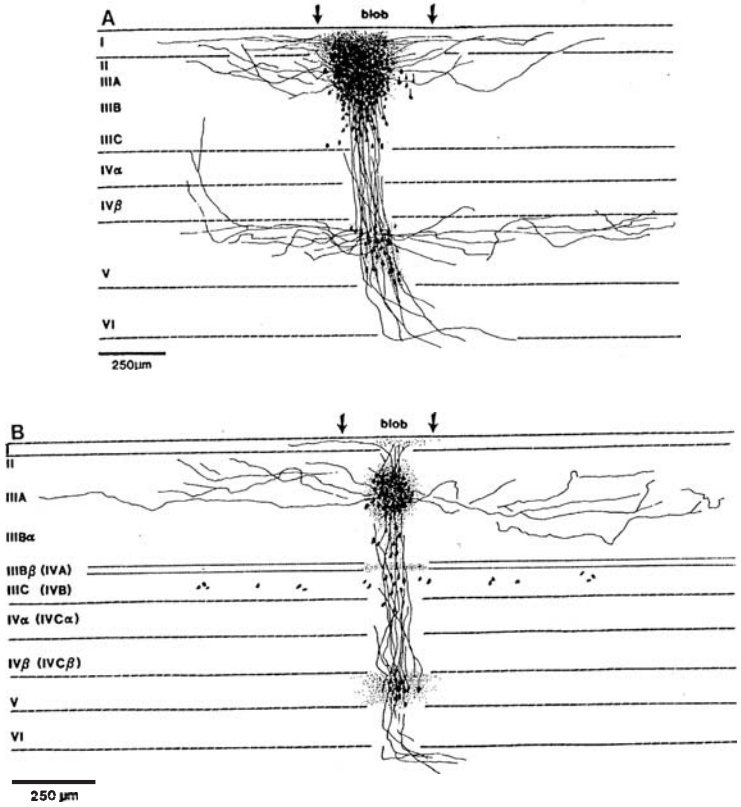


Figure 11. Camera lucida reconstructions showing labeled cells and axons following injections into blob IIIA in a galago (A) and a squirrel monkey (B). Arrows indicate the edges of a blob. Roman numerals indicate layers according to a modification of the nomenclature of Hässler with Brodmann nomenclature in parentheses. Reproduced from Lachica *et al.* (1993) with permission.

interblob compartments and with the substrata of layer III (Casagrande *et al.,* 1992; Lachica *etal.,* 1992, 1993). Examples are shown in Figs. 12 and 15. Layer VI shows a clear division in all primates examined such that the lower division sends and receives input from the **M** LGN layers and its target layer IVα, while the upper division relates in a similar manner to the P pathway (Lund *et al.,* 1975, 1988; Blasdel and Lund, 1983; Swadlow, 1983; Florence and Casagrande, 1987). Each division of layer VI shows somewhat different patterns of vertical connections with the supragranular layers and CO compartments (Blasdel *et al.,* 1985; Lund *et al.,* 1988; Lachica *et al.,* 1992, 1993).

A third related feature found consistently in primate V1 is the existence of different intrinsic connections of modules identified by CO staining. Within layer III the CO blob and interblob compartments exhibit differences in patterns of vertical connectivity with other layers or sublayers. For example, within IIIB the CO blobs receive indirect input via layer **IV** from ***both M and P*** LGN pathways as well as a direct input from the **K** LGN axons (see Figs. 12–14). Thus, the cells in the CO blobs in layer **IIIB** are in a position to integrate signals from ***all*** LGN relay cell classes. In contrast, cells in the IIIB interblobs appear to receive a more restricted input, mainly via layer IV from one relay cell class (either M or P depending on the primate species), and there is no direct input from the K pathway (unless on dendrites extending into layer 1). Examples of patterns of retrogradely labeled cells in different cortical layers following injections into interblobs are shown in Figs. 12 and 15. This pattern of connections does not mean that interblobs are solely influenced by one LGN channel. In fact, physiological studies in which input from either the M or P pathway was blocked pharmacologically at the level of the LGN suggest that interblob cells do get input from both M and P pathways in macaque monkeys (Nealey and Maunsell, 1991; Maunsell *et al.,* 1992). What our anatomical studies suggest is that interblob cells must get this input via a different route than do blob cells, either via cortical layers

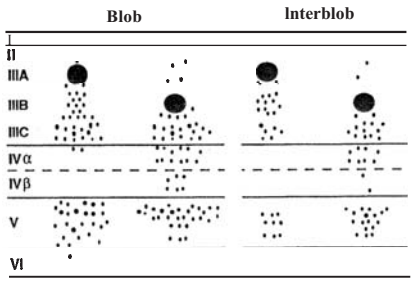


Figure 12. Schematic summary of the differences in patterns of retrogradely labeled cells seen following injections of tracers (biocytin or HRP) into layer IIIA or IIIB blobs and interblobs in an owl monkey. Note that IIIB blobs get input from both M- and P-recipient IVα and IVβ, respectively. Layer IIIB interblobs get input primarily from IVα in this nocturnal primate. Roman numerals indicate layers according to a modification of the nomenclature of Hassler. From Casagrande *et al.* (1993).

below **IV** or via interconnections with cells in more superficial layers (Fitzpatrick *et al.,* 1985; Blasdel *et al.,* 1985; Casagrande *et al.,* 1992; Lachica *et al.,* 1992, 1993). Note that cells in layers **IIIA** and **IIIC** that lie directly above or below the centers of the IIIB CO-rich and -poor compartments also connect with distinct divisions of layers V and **VI** (Lachica *et al.,* 1992, 1993). In other words, CO blob and interblob differences in intrinsic connections appear to extend beyond the center of blobs and interblobs in layer IIIB to include cell groups within the same vertical cortical domain (see Fig. 11; also compare the patterns shown in Figs. 14 and 15).

These modular differences in wiring reinforce the view that compartments defined by relative ***CO*** staining provide substrates for creating separate output pathways. This proposal is further supported by physiological data showing that, as reported for the diurnal simians (macaque monkeys and squirrel monkeys), CO blobs and interblobs can be distinguished in nocturnal prosimians (galagos) (Livingstone and Hubel, 1984a, 1987; Silverman *et al.,* 1989; Hubel and Livingstone, 1990; Born and Tootell, 1991a,b; DeBruyn *et al.,* 1993).

Finally, V1 of primates is characterized not only by elaborate vertical connections, but also by periodic tangential connections that connect cell groups within layer III and within layer **V** (Rockland and Lund, 1983; Livingstone and Hubel, 1984b; **Ts'o** *et al.,* 1986; Cusick and Kaas, 1988b; Ts'o and Gilbert, 1988; Gilbert and Wiesel, 1989). These tangential connections are not diffuse, but

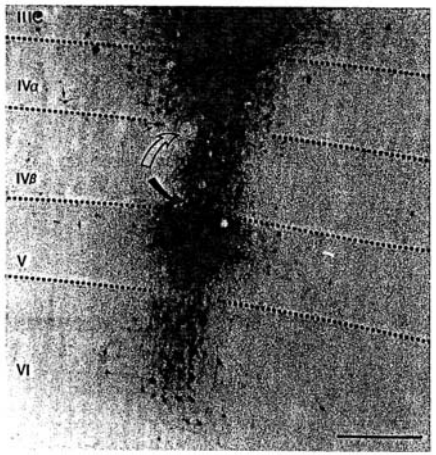


Figure 13. A photomicrograph illustrating the pattern of retrogradely labeled cells following a biocytin injection and into a blob in layer IIIBα of a squirrel monkey. Note that layers IVα, IVβ, and V can be defined solely on the basis of the distribution of labeled cells. Labeled cells are much more widely distributed in layer IVα, some lying well away from the projection column (small arrow). The top (open arrow) and bottom (closed arrow) borders of the narrow column of labeled cells in IVβ are easily defined. Bar = 100 pm. Reproduced from Lachica *et al.* (1993) with permission.

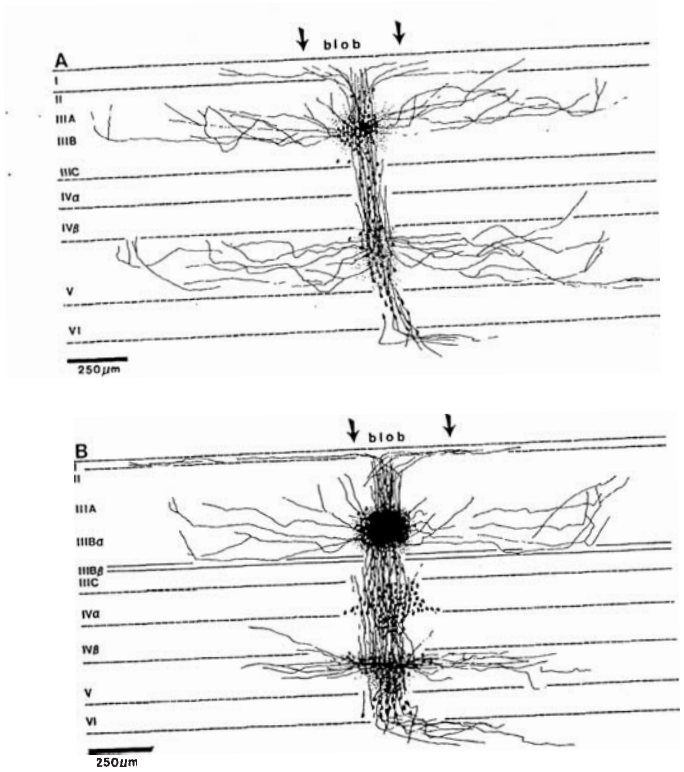


Figure 14. Camera lucida reconstructions showing labeled cells and axons following injections into CO blobs in IIIB in a galago **(A)** and IIIBα in a squirrel monkey (B). Roman numerals indicate layers according to a modification of the nomenclature of Hassler. Reproduced from Lachica et al. (1993) with permission. See text for details.

form highly organized lattices of periodic connections principally, but not exclusively (see Malach *et al.*, 1992), between cells that occupy anatomically and physiologically similar compartments (e.g., connections between CO blobs in III; Rockland and Lund, 1983; Livingstone and Hubel, 1984b; Ts'o *et al.*, 1986; Cusick and Kaas, 1988b; LeVay, 1988). At present, it is still unclear what purpose these lateral interconnections serve. It has been suggested that they may form substrates for feature-linking (Gilbert *et al.*, 1991). Regardless, the presence of periodic tangential interconnections is a feature that has not been described at earlier stages of processing (i.e., the retina or LGN), but appears to be ubiquitous in V1 and other visual cortical areas to which V1 projects.

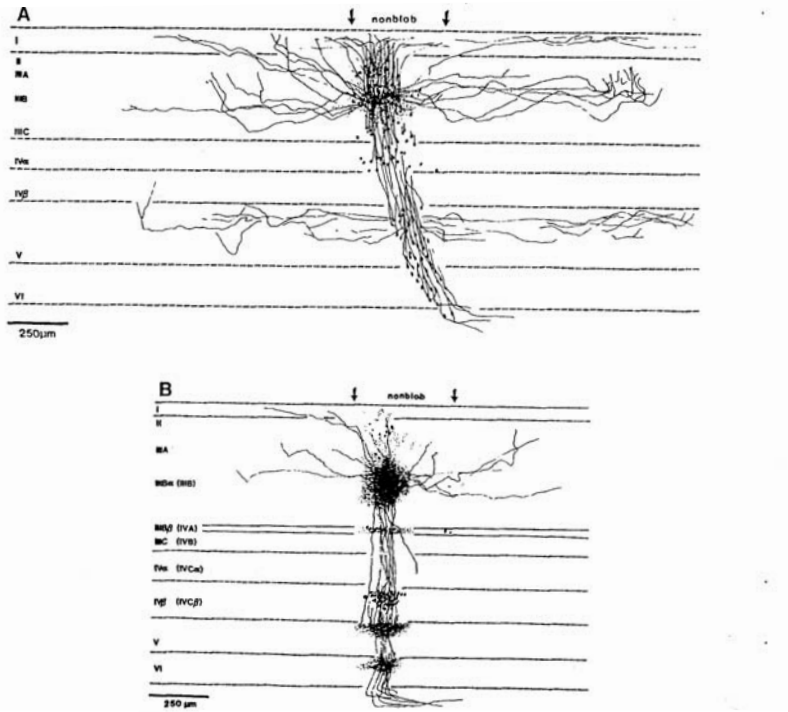


Figure 15. Camera lucida reconstructions showing labeled cells and axons following injections into nonblob IIIB in a galago **(A)** and nonblob IIIBα in a squirrel monkey (B). Roman numerals indicate layers according to a modification of the nomenclature of Hassler. Reproduced from Lachica et al. (1993) with permission. See text for details.

4.3. Nonprimate Pattern

Details of intrinsic cortical connections have only been described for area 17 or V1 of a few mammals. It is not our purpose here to provide an extensive review of detailed similarities and differences. Rather, in this section we examine some of the main features of patterns that other mammals share with primates as well as key points of difference. We restrict our review here primarily to cats and tree shrews.

All mammals appear to share several basic features of V1 organization with primates. Thus, as in primates, inputs from the LGN terminate principally in layer IV (see earlier). In addition, LGN inputs to layers VI and **I** as well as a portion of layer III have been widely described (e.g., Hendrickson *et al.,* 1978; Diamond *et al.,* 1985). However, there are clear species differences in the detailed organization of LGN inputs to cortex. Two examples make this point.

In cats, LGN cells have been classified in **X,** Y, and W cell types. However, as described earlier, **X** and Y cells project in an overlapping fashion to layer IV of area 17 (Humphrey *et al.,* 1985a). W cells appear to project to separate strata in cats, but unlike their counterparts in primates, these cells in cats project both to the upper half of layer V (Gilbert and Wiesel, 1981) and to layer **I.** In addition, a large number of LGN cells in cats send projections to visual areas outside of area 17 (see Sherman and Spear, 1982). The same appears to be true of other carnivores (e.g., ferrets and mink). Thus, unlike in primates, area 18 in carnivores gets a substantial projection from Y and W LGN cells, and W LGN cells also send axons to a number of visual areas beyond area 18 that are themselves targets of area 17 and/or 18 (e.g., Humphrey *et al.,* 1985b).

In tree shrews, as in primates, area 17 appears to be the major or almost exclusive target of LGN cell axons (Harting *et al.,* 1973; Casagrande and Harting, 1975; Hubel, 1975; Conley *et al.,* 1984; Usrey *et al.,* 1992). However, the organization of LGN layers and their projections to area 17 differ for tree shrews and primates. In tree shrews, **X** and Y cells have been described in the LGN (Sherman *et al.,* 1975). However, a unique feature of the LGN of tree shrews is the segregation of neurons that respond to the onset and offset of light in the centers of their receptive fields (ON-center versus OFF-center cells) (see Conway and Schiller, 1983; Holdefer and Norton, 1986). The tree shrew LGN has pairs of layers, one innervated by each eye, with layers for ON-center cells (layers 1 and 2) and layers for OFF-center cells (layers 4 and 5) as well as two contralaterally innervated layers **(3** and **6)** with physiologically distinct W-like cells. Projections of tree shrew LGN cells to cortex maintain the segregation of ON, OFF, and W-like cells. Unlike primates, the upper and lower divisions of layer IV receive separate projections from the ON- and OFF-center LGN layers, respectively, while the W-like layers each show a unique pattern of projections to a combination of layers including III and I (Conley *et al.,* 1984; Usrey *et al.,* 1992). Tree shrew geniculocortical projections to cortex also show a species-unique horizontally stratified pattern of ocular inputs such that ipsilateral inputs end in restricted bands at the top and bottom of layer IV and contralateral inputs extend throughout layer IV (Casagrande and Harting, 1975; Hubel, 1975; Conley *et al.,* 1984; Usrey *et al.,* 1992).

As with LGN inputs, there are features of area 17 intrinsic organization that appear to be common to primates and other mammals as well as features that are not found in primates. **As** in primates, area 17 of other mammals is organized such that the supragranular layers provide major projections to extrastriate cortical areas and the infragranular layers send major projections out of cortex to sites in the thalamus, midbrain, and hindbrain (e.g., Henry, 1991). The latter projections appear to consistently involve a major pathway from cells in layer **V** to the superior colliculus and a major reciprocal pathway form layer VI to the LGN (see Swadlow, 1983, for review). Within the cortex itself, several intrinsic patterns have been reported in both primates and other mammals. Thus, layers IV and **VI** appear to connect; both are also direct targets of the main layers of the LGN. **Also,** layers V and III have heavy interconnections (see Henry, 1991). Finally, tangential periodic connections appear to be a characteristic feature of V1 in at least some primate and most nonprimate mammals (Rockland *et al.,* 1982; Sesma *et al.,* 1984; Burkhalter and Charles, 1990).

Since one function of area 17 is to combine information from parallel LGN inputs to construct appropriate output channels, the differences in intrinsic circuitry appear to relate to differences in the organization of output pathways. For example, in tree shrews the projections from layer IV to layer III have three separate tiers of innervation within layer III (see Muly and Fitzpatrick, 1992). However, this organization is very different from that just described for primates. In tree shrews, the projections of layer IV to layer III reflect the segregation of ocular dominance and the segregation of ON- and OFF-center cells within layer IV. Muly and Fitzpatrick (1992) have postulated that the differential projections from layer IV to layer **III** may help to combine ON- and OFF-center pathways in a way that preserves ocular bias. The only similarity to primate organization is that in both tree shrews and primates, stratification in layer IV is reflected in differential patterns of projections within layer III. It is unclear whether the same rule applies to cats where projections from different cell types largely overlap in layer IV. However, it does appear that in cats, cells in the lower portion of layer III project heavily to area 18, while output cells that lie in the more superficial portion of layer III send projections to separate extrastriate visual areas (Symonds and Rosenquist, 1984). The latter observation suggests that functionally relevant stratification may commonly exist in layer **III** and that its organization may reflect specializations both in the input and in the output pathways.

4.4. Primate Variations

As might be expected from the diversity and behavioral adaptations in primates, some species differences in the intrinsic connections of V1 have been reported. Although only a few studies have addressed the issue of primate species differences in intrinsic circuitry, three observations stand out. First, comparisons of organization of **V i** in prosimian galagos (*Galago*) with that of the New and **Old** World simians, squirrel monkeys, owl monkeys, and macaque monkeys (*Saimiri, Aotw, and Macaca*), suggest that V1 in galagos is less differentiated and compartmentalized. In Nissl-stained sections, laminar boundaries appear less distinct in galagos than in the three simian primates (see Fig. 1). Cells giving rise to the major output pathways in galagos also appear slightly less precisely confined to subdivisions in layer III than do output cells in simians. In

addition, sublaminar distinctions of intrinsic connections of layers V and VI with substrata and CO compartments of layer III appear quite distinct in macaque monkeys and squirrel monkeys even though these connections appear only as gradients in galagos (Blasdel *et al.*, 1985; Lachica and Casagrande, 1992, 1993). These species differences may also reflect nocturnal–diurnal adaptations since the intrinsic connections of subdivisions of layers V and VI in the nocturnal simian owl monkeys are also less sharp than those of their diurnal New World squirrel monkey cousins (Casagrande *et al.*, 1992; see also Fig. 12).

Nocturnal–diurnal specializations appear to correlate with a second difference in intrinsic V1 connectivity in primates. In the diurnal macaque monkeys and squirrel monkeys, cells in the CO-poor interblob zones receive connections indirectly via IVβ from the LGN P pathway, whereas in nocturnal owl monkeys and galagos these zones receive connections indirectly mainly via IVα from the M LGN pathway (see Figs. 12 and 15 and Lachica *et al.*, 1992, 1993). Note that differences in the relative strength of input and output pathways have also been found to correlate with nocturnal–diurnal niche specialization. Thus, the ratio of P to M LGN cells in areas of the LGN devoted to central vision is lower for nocturnal primates [e.g., 40 to 1 for macaque monkey and 4 to 1 for galago (Connolly and Van Essen, 1984; Florence and Casagrande, 1987)]. Differences may simply reflect acuity differences between nocturnal and diurnal species (Langston *et al.*, 1986). However, species differences are also seen in the proportion of tissue devoted to homologous extrastriate areas (see next section). Relevant to the present argument is the fact that nocturnal primates have proportionately larger amounts of tissue devoted to the middle temporal visual area (MT) than do diurnal primates (Krubitzer and Kaas, 1990b). Since area MT receives M-dominated input via layer IVα, it may be that M-pathway signals provide information that is particularly important to vision in dim illumination (see also discussion of this point in Lachica *et al.*, 1993). Alternatively, it may be more appropriate to conclude that the P pathways are expanded and more important in diurnal primates.

A third species difference in V1 intrinsic connectivity relates to differences in cortical laminar specialization. In the diurnal catarrhine simians (e.g., macaque monkeys and other Old World monkeys), as well as some diurnal platyrrhine simians (e.g., squirrel monkeys), a thin subdivision of layer IIIB, IIIBβ, receives a specialized input from the P layers of the LGN. As discussed earlier, IIIBP is absent in prosimian primates. It is weakly evident in some species even when LGN input is lacking, as is the case in the owl monkey (see Fig. 1). In any case, in species that possess a distinct IIIBβ that receive P LGN input (squirrel monkeys and macaque monkeys), it is clear that this sublayer has intrinsic connection patterns with other cortical layers that are distinct from the connections of the remaining sublayers of layer III (IIIC, IIIBα, and IIIA) (see Lund and Yoshioka, 1991; Peters and Sethares, 1991b). At present, it is unclear why some simians possess a weli-deveioped layer IIIBβ, while others do not. No differences in the LGN laminar location of P cells that innervate IIIBP versus IVβ have been identified. Physiological studies suggest that cells in IIIBβ of macaque monkeys reflect P inputs from the LGN as do cells in IVβ, yet again no distinctions between these two layers have been reported that would help to identify why the P LGN cells split their input to V1 to two layers in some primate species and not others.

5. Ipsilateral Cortical Connections

In all primates examined, V1 projects to several extrastriate areas that are similar in location and which presumably constitute homologous visual areas across primate taxa (see Fig. 16). However, this conclusion is not straightforward, since the terminologies used by different investigators vary and schemes for subdividing extrastriate cortex in primates vary across species. The major cortical target of V1 is the second visual area, V2 or area 18, a visual area present in most or all mammals. A second target is the middle temporal visual area, MT, also known as the superior temporal area or V5. A third target is the dorsomedial area, DM, also known as dorsal V3 and V3a. A fourth target is the

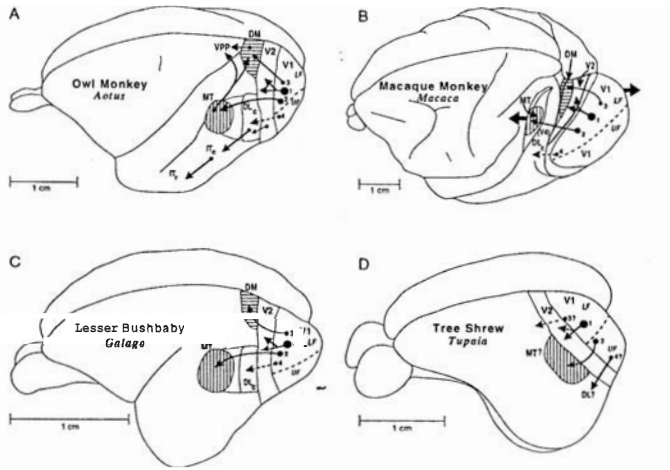


Figure 16. Projections of V1 to other visual areas in primates and tree shrews. All primates appear to have projections to the second visual area, V2, the middle temporal visual area, MT, and the dorsomedial visual area, DM (solid arrows 1–3 with dot size and arrow thickness reflecting the proportions of the projections). In B the large filled arrows indicate where sulci are opened to reveal areas which are normally buried from view within sulci (e.g., MT). The lateral part of V1 representing central vision also projects to the caudal division of the dorsolateral complex, DL, (dashed arrow 4). Tree shrews (D) are close relatives of primates and they have some of the primate patterns of V1 projections. As in all mammals, V1 projects directly to V2 of tree shrews (projection 1). Other projections (2) are to a lateral field that adjoins V2, but may be the primitive location of the precursor of MT (see Kaas and Preuss, 1993). Other projections are to cortex that may correspond to DM (3) and DL (4) in primates. In V1 of A–D, a dashed line divides the representation of the lower field (LF) from the upper field (UF) in V1. In A (owl monkey), additional projections from MT to DM and ventral posterior parietal cortex (VPP) are shown to illustrate parts of the dorsal stream (Ungerleider and Mishkin, 1982) of processing, while projections from DL, to caudal (IT,) and then to rostral (IT,) divisions of inferior temporal cortex reflect parts of the ventral stream (Weller and Kaas, 1987). These streams appear to exist in all primates.

caudal division of the dorsolateral complex **or** DL_c, also known **as** V4. Other targets have been inconsistently reported and may be species-variable, individually variable, or artifactually-labeled false positives.

5.1. Connections with V2

In all primates studied, the majority of the cortical projections of V1, perhaps 80% **or** more, are to the second visual area, V2. The architectonic equivalent of V2 is often considered to be area 18 of Brodmann (1909), but since Brodmann distinguished area 18 **as** a field that varied in extent across species, from closely corresponding to V2 in a New World monkey to being nearly twice **as** large in an Old World monkey, the identification of area 18 with V2 can be misleading. Here we define area 18, in contrast to the historical area 18, **as** the field that is coextensive with **a** systematic, second-order representation of the contralateral visual hemifield or V2 (Allman and Kaas, 1974).

A complication that may have hindered earlier attempts at an architectonic description of V2 is that the field is not structurally homogeneous. In many mammals, V2 appears to be modularly organized ***so*** that the density of myelination and connections with V1 and with the other hemisphere are unevenly distributed (e.g., Kaas *et al.,* 1979; Sesma *et al.,* 1984; Cusick and Kaas, 1986b). However, this modular specialization seems more pronounced in simian primates. The architectonic manifestations of the modular organization of V2 are most apparent in brain sections from cortex that have been stained for CO **or** myelin (Fig. **17;** Krubitzer and Kaas, 1989). In such preparations, V2 can be identified by **a** series of dense CO bands separated by light CO bands, the CO interbands. The bands are roughly perpendicular to the V1/V2 boundary and they span the width of V2. When V2 is characterized by these bands, the area can be seen as **a** long, narrow belt along approximately 90% of the outer border of V1 and occupying **a** surface area less than V1 (Krubitzer and Kaas, 1990b). The bands shorten and the field narrows in the middle of the belt in the portion representing central vision, and toward the ends of the belt, representing the extremes of peripheral vision of the upper and lower quadrants (see Allman and Kaas, 1974; Gattass *et al.,* 1981). Although it is difficult to obtain brain sections where all the bands are evident, it appears that owl monkeys have roughly 30–40 CO-dense bands and the same number of interbands (e.g., Kaas and Morel, 1993) while macaque monkeys have about 56 CO-dense bands (Van Essen *et al.,* 1990). The interbands are further distinguished by dense myelination, ***so*** that ***CO*** and myelin procedures reveal patterns of dense staining (Fig. 17; Krubitzer and Kaas, 1990a).

The CO-dense bands have been subdivided into two alternating types. One set of bands projects to MT (e.g., Weller *et al.,* 1984; DeYoe and Van Essen, 1985; Ship and Zeki, 1985) and another set **of** bands projects to caudal DL (DL_c) or caudal V4 (DeYoe and Van Essen, 1985; Shipp and Zeki, 1985; Cusick and Kaas, 1988a). In macaque monkeys, the set of bands projecting to MT have been called "thick" bands, and the set projecting to DL, ($V4_c$) "thin" bands (Livingstone and Hubel, 1982), but the widths of the bands do not seem to reliably indicate the type of projection in macaque monkeys (e.g., Van Essen *et al.,* 1990). In macaque monkeys and apparently humans (Hockfield *et al.,* 1983), the monoclonal antibody Cat-301 preferentially labels bands projecting to MT (Hockfield *et al.,*

1983; DeYoe *et al.,* 1990). In some New World monkeys, the thinner bands appear to project to MT, whereas in other New World simians the bands are not notably different in width (see Fig. 17 and Krubitzer and Kaas, 1990b). Thus, we define the bands projecting to MT as MT bands or dorsal stream bands, because they send information to MT and subsequently into the parietal lobe, and the bands projecting to DL_c–$V4_c$ as ventral stream bands because information from DL_c–V4 is sent into **a** hierarchy of visual areas in the temporal lobe (Ungerleider and Mishkin, 1982). We avoid the terms M bands and **P** bands (see DeYoe and Van Essen, 1985) to refer to these zones in V2 since the terms M and **P** imply that LGN input pathways can be equated with specific V1 output pathways or their functions. As discussed previously, cells in the output streams leaving V1 have very different properties from the M, **P,** or **K** input cells of the LGN, and this difference undoubtedly reflects the complex intrinsic circuitry of V1. The CO-dense bands have an internal structure, ***so*** that at high magnifications they may

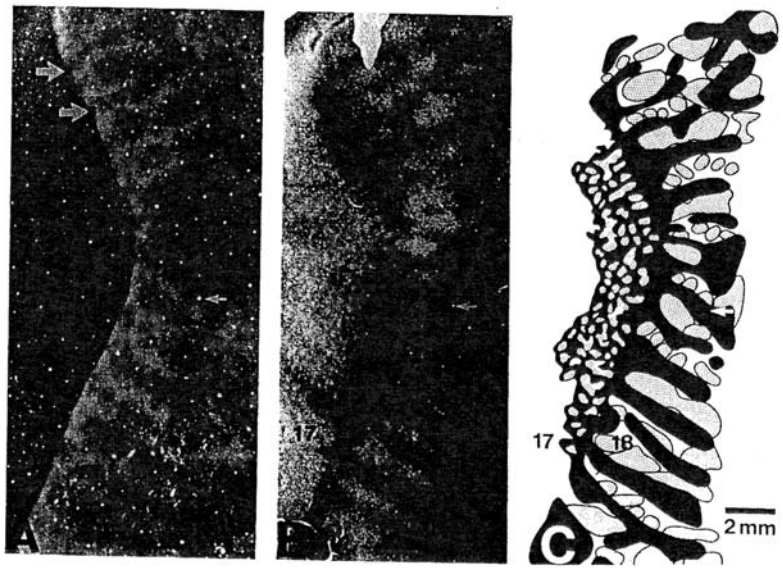


Figure 17. Pattern of cytochrome oxidase (CO)- and myelin-dense regions in areas 17 and 18 of squirrel monkeys. (A) A section stained for CO cut at the level of layer IV parallel to the surface of flattened cortex. Layer IV stains densely in area 17, while alternating CO-dense and -light bands characterize area 18. Large arrows mark two CO-dense bands. (B) A slightly more superficial section stained for myelin. In area 17, denser myelination surrounds and outlines CO blobs of adjacent sections. the myelin-dense bands in area 18 correspond to the CO-light or interbands of panel A. (C) A schematic with the CO-dark (shaded) and myelin-dark (black) regions superimposed. A small arrow in A–C marks one of the blood vessels used to align brain sections. From Krubitzer and Kaas (1989) with permission.

appear as rows of CO-dense patches that nearly fuse (Carroll and Wong-Riley, 1984; Cusick and Kaas, 1988a; Tootell and Hamilton, 1989; Krubitzer and Kaas, 1990b). Finally, CO-dense stripes in V2 appear to be absent or poorly developed in prosimians (Condo and Casagrande, 1990; Krubitzer and Kaas, 1990b; Preuss *et al.,* 1993), although bandlike patterns of connections indicate that V2 is functionally organized in a similar manner in both simian and prosimian primates.

The outputs of V1 are related very clearly to the banding pattern in V2. Small injections of tracers into the blob regions of V1 label neurons and terminals in the ventral stream bands of V2 while injections in the interblob regions label the pale interbands (Livingstone and Hubel, 1984a). Output neurons to V2 originate in layer IIIA of V1 (Rockland and Pandya, 1979; Lund *et al.,* 1981; Tigges *et al.,* 1981; Rockland, 1992) and from a few neurons in layers V and VI, at least in macaques (Kennedy and Bullier, 1985). Small injections in V2 indicate that neurons in these locations project to the ventral stream bands and interbands (Livingstone and Hubel, 1987). In contrast, injections in the dorsal stream bands of V2 label neurons in IIIC of V1 (Livingstone and Hubel, 1987). As a result of these patterns of connections, randomly placed injections in V2 can label different modules in V1 depending on the bands affected by the injections (Cusick and Kaas, 1988a). Thus, sections parallel to the brain surface and through layer III of V1 can reveal zones of labeled neurons and fine processes in CO blobs or interblob regions in a pattern that reflects the involvement of ventral stream bands or interbands (Fig. 18).

Because of the modular nature of V2, the terminal patterns of the projections of V1 to V2 can be quite patchy (see Weller *et al.,* 1979; Wong-Riley, 1979; Lin *et al.,* 1982; Cusick and Kaas, 1988b), reflecting both the matching of modular output zones and target zones, and the patchy nature of the bands. In addition, the fact that V2 is a "second order" representation, split along the horizontal meridian (see Allman and Kaas, 1974), means that injections placed along the representation of the horizontal meridian in V1 label separate locations in the dorsal and ventral wings of V2.

5.2. Connections with MT

The other major target of V1 is the middle temporal visual area (MT), a small oval of densely myelinated cortex in the upper temporal lobe that contains a systematic representation of the contralateral visual hemifield (Allman and Kaas, 1971). Unlike V2, MT is a visual area that has only been definitely identified in primates. Yet, all mammals have projection targets in cortex rostral or lateral to V1, and one of these targets may represent a less specialized homologue of MT (see Kaas, 1993; Kaas and Preuss, 1993). Cortex in the region now identified as MT has been known to receive inputs from V1 (Kuypers *et al.,* 1965; Myers, 1965) since well before MT was identified as a visual area by its other characteristics. Subsequently, evidence from a range of primate species, including humans (Clark and Miklossy, 1990; Kaas, 1992), has indicated that MT is part of the basic primate plan of cortical organization, and likely exists in all primates (see Kaas and Krubitzer, 1992; Preuss *et al.,* 1993).

In simians, the projections to MT originate from IIIC neurons and from a scattering of different types, depending on species, in layer V along the layer VI border and variably in layer VI (e.g., Lund *et al.,* 1975; Tigges *et al.,* 1981; Shipp and Zeki, 1985). In prosimian galagos, the neurons projecting to MT are more widely distributed, such that although the majority are in IIIC, some are also located in upper sublayers of layer III (Diamond *et al.,* 1985). Thus, IIIC, as an output layer to MT, seems to be more differentiated and specialized in simians than in prosimians. Nevertheless, cells in the inner part of layer III are the major source of MT projections from V1 in all primates. The projections to MT are topographic, in that retinotopic locations in the two representations are interconnected (e.g., Symonds and Kaas, 1978; Spatz, 1979; Lin *et al.,* 1982; Weller and Kaas, 1983). However, the projections from any location in V1 to MT are patchy (e.g., Montero, 1980), suggesting the existence of separate classes of processing modules in MT (Fig. 19; see Kaas, 1986). The projections of V1 to MT terminate in layer IV, where they constitute the major source of activation (Kaas and Krubitzer, 1992; Maunsell *et al.,* 1992), but not the only one, since in macaque monkeys there is evidence that many neurons in MT remain responsive to visual stimuli after the inactivation of V1 (Rodman *et al.,* 1990; see Bullier, this volume). As a major component of the dorsal stream of visual processing for visual attention and spatial aspects of vision (Ungerleider and Mishkin, 1982; Goodale and

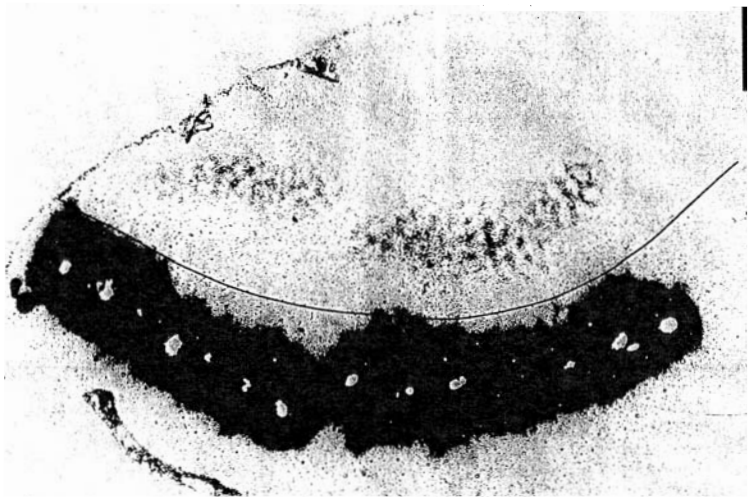


Figure 18. A row of injection sites in area 18 of a squirrel monkey and labeling in area 17. The effective injection sites (around the holes) are smaller than the dense band of label in area 18 so that bands and interbands were randomly involved. As a result, label in area 17 was sometimes concentrated in interblob surrounds in upper and lower 17 and sometimes in blobs (middle 17). Cortex was flattened before sectioning, and processed for HRP. Bar = 2 mm. From Cusick and Kaas (1988) with permission.

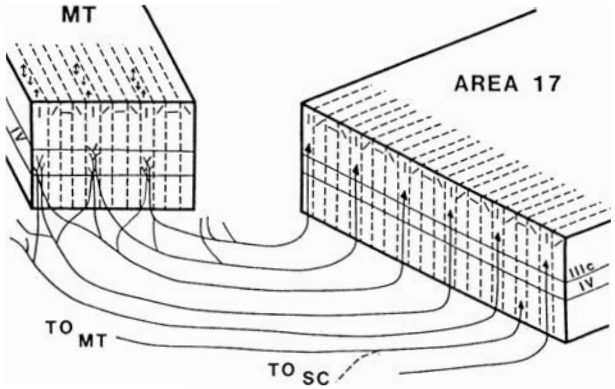


Figure 19. Proposed patterns of divergence and convergence of projections from area 17 and MT. Neurons of specific orientation and direction of movement selectivity in area 17 project to reveal groups of neurons with similar selectivity in MT. Likewise, each group of neurons in MT receives from several matched groups of neurons in area 17. These features of connectivity would account for the anatomical patterns of connections actually observed (e.g., Krubitzer and Kaas, 1990). From Kaas (1986) with permission.

Milner, 1992), the outputs of MT are directed to posterior parietal cortex and to DM (see below), which relays directly to posterior parietal cortex (see Krubitzer and Kaas, 1990a).

5.3. Connections with DM (Dorsal V3)

A third target of V1, that appears to exist in all primates, is located in the dorsomedial cortex just rostral to V2 (Krubitzer and Kaas, 1993). In owl monkeys this cortex has been called the dorsomedial visual area (DM) (Allman and Kaas, 1975), and it contains a systematic, but split or second-order, representation of the contralateral visual hemifield. Injections of tracers in V1 (Fig. 20) label reciprocal connections with area DM (Lin *et al.*, 1982; Krubitzer and Kaas, 1990a, 1993). V1 projections to DM terminate in layer IV and thus may constitute the feedforward or major visual drive for cells in this area, although it is unclear whether the less direct inputs from MT and V2, which are **also** dense, actually provide the main visual drive for DM cells. The projections from V1 to DM originate from a scattering of neurons that are located primarily within CO blobs. These projections probably constitute less than 5% of the total output of area V1. Feedback projections from DM to V1 originate mainly in layer V neurons, with a few originating from cells in layer III; these projections terminate in supragranular layers of V1.

DM likely exists in all primates since V1 sends axons to cortex in the location of DM in **all** investigated primates. However, DM has been established as a visual area by additional morphological and physiological criteria only in owl monkeys. In Old World macaque monkeys, cortex in the region of DM has long been

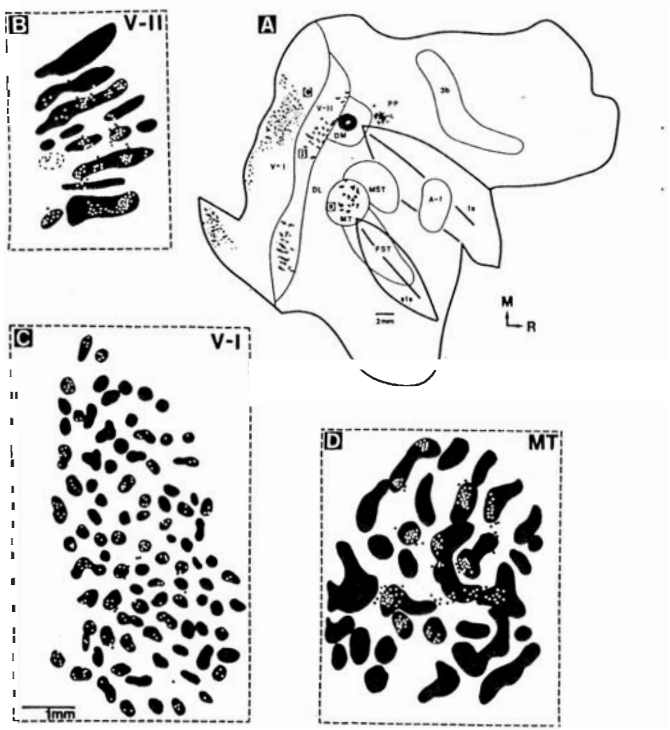


Figure 20. Connections of VI, VII, and MT with the dorsomedial area (DM) in owl monkeys. (A) The connection pattern on cortex that has been separated from the brain, flattened, and cut parallel to the surface. VI, VII. DM, the middle temporal visual area (MT), the fundal superior temporal area (FST), the middle superior temporal area (MST), auditory cortex (A1), and somatosensory cortex (area 3b) were determined architectonically. The dark circle indicates the injection of WGA-HRP in DM, and black dots indicate labeled neurons and terminations in other areas. (B) Projections from VII originated from neurons (dots) that were largely in the CO-dense bands (black). (C) Projections from VI were from neurons largely in CO-dense blobs. (D) Projections from MT were from neurons largely in CO-dense bands. From Krubitzer and Kaas (1990) with permission.

considered to be part of a visual beltlike region, V3, bordering V2 (e.g., Myers, 1965; Cragg, 1969; Zeki, 1969), but the concept of a single beltlike V3 with direct inputs from V1 is inconsistent with the evidence given that the dorsal and ventral parts of V3 have different characteristics (Burkhalter *et al.,* 1986; Van Essen *et al.,* 1986). In particular, ventral "V3" lacks a projection from V1. However, the region defined as dorsal "V3" in macaque monkeys differs from DM in that DM constitutes a complete representation of the contralateral hemifield, whereas dorsal V3 represents only the lower visual quadrant. Nevertheless, cortex adjoining dorsal V3, termed V3a by Zeki (Zeki, 1980a), also receives inputs from V1, is densely myelinated like DM (and like dorsal V3), and represents the upper visual quadrant (Gattass *et al.,* 1988). Thus, dorsal V3 and V3a of macaque monkeys, together, may be homologous to DM in owl monkeys (see Krubitzer and Kaas, 1993). Projections to a densely myelinated area in the expected location of DM have been found in other Old World monkeys (talapoins), New World squirrel monkeys and marmosets, and prosimian galagos (Cusick and Kaas, 1988b; Weller *et al.,* 1991; Krubitzer and Kaas, 1993). It seems unlikely that the dorsomedial target of V1 projections represents different visual areas in different primates. Rather, it seems more parsimonious to conclude that the projections are to DM, a single area common to all primate groups.

DM appears to be linked by its inputs from MT and its projections to posterior parietal cortex (Fig. 20), to the dorsal stream of visual processing concerned with visual attention and localization (Ungerleider and Mishkin, 1982). Yet, direct inputs from the CO blobs of V1, as well as both the dorsal and ventral stream bands in V2 indicate that DM has inputs associated with the ventral as well as the dorsal stream. The ventral stream is critical for object recognition (Ungerleider and Mishkin, 1982). Thus, DM is a visual area with access to both streams of information processing, and it may play a central role in providing ventral stream information to posterior parietal cortex.

5.4. Connections with Dorsolateral Cortex (DL or V4)

V1 also projects to a cortical region that lies between V2 and MT called the dorsal lateral area (DL) in owl monkeys (Allman and Kaas, 1974) and in most other primates (see Steele *et al.,* 1991, for review), and V4 in macaque monkeys (Zeki, 1971). The main output of DL–$V4_c$ is to the inferior temporal cortex (see Steele *et al.,* 1991, for review). It has been difficult to define the exact borders of this region, and uncertainties remain, but it now appears that the region contains three visual areas, each with a crude representation of the visual field. In brief these areas are: (1) a caudal division, DL_c, which is more densely myelinated, expresses more CO activity (Cusick and Kaas, 1988b; Steele *et al.,* 1991; Preuss *et al.,* 1993), and receives the majority of forward projections of V2 (Cusick and Kaas, 1988b); (2) a more rostral division, DL_r, which has connections that associate it with the dorsal rather than the ventral stream of processing (Cusick and Kaas, 1988b; Steele *et al.,* 1991; Weller *et al.,* 1991); and (3) a narrow ringlike area around most of MT that has been called the MT crescent or MT, (Kaas and Morel, 1993). The region termed "V4t" of macaque monkeys (Ungerleider and Desimone, 1986) appears to correspond to MT, of owl monkeys. Evidence for these three visual areas, or subdivisions thereof, within the DL or V4 complex largely depends on research in New World monkeys (e.g., Steele *et al.,* 1991), but there is

evidence for these areas also in Old World monkeys (see Perkel *et al.,* 1986); in prosimians (e.g., Preuss *et al.,* 1993) there is evidence for DL, and DL, but not yet for MT_r. While the major input to DL, is from V2, a moderate input is from V1 (e.g., Steele *et al.* 1991; for review: Zeki, 1978; Lin *et al.,* 1982; Cusick and Kaas, 1988a; Krubitzer and Kaas, 1993). This layer VI input originates mainly from the part of V1 that represents the central few degrees of vision, but since receptive fields for DL neurons are large, this input terminates over much of the middle portion of DL_c. The input to DL, **is** from a scattering of supragranular cells throughout V1, and the major feedforward output of DL, is to caudal inferior temporal cortex, although DL, and MT also receive minor inputs.

The connections of DL, have been less fully described (see Cusick and Kaas, 1988b; Steele *et al.,* 1991). The inputs from V2 are sparse, in contrast to DL_c, and the inputs from V1 are very weak, if present (however, see Preuss *et al.,* 1993). Little is known about the connections of MT, (see Kaas and Morel, 1993). Cortex in the region of MT_r, however, has been described as having connections with V1 in *Cebus* (Sousa *et al.,* 1991) and macaque monkeys (Perkel *et al.,* 1986).

5.5. Connections with Other Fields

In addition to the connections of V1 described above, other connections have been reported occasionally (Perkel *et al.,* 1986; Sousa *et al.,* 1991; Rockland, this volume). Extremely sparse and variable connections between V1 and posterior parietal cortex as well as cortex medial to DM have been described (Perkel *et al.,* 1986; Sousa *et al.,* 1991). These areas include area M (Allman and Kaas, 1976), also referred to as PO (Colby *et al.,* 1988), the inferior temporal cortex, and the medial superior temporal area (MST) just rostral to MT. To the extent that such connections exist, they would seem to play an extremely minor role in visual processing.

5.6. Feedback Connections

All of the major targets of V1 also project back to V1, and thus these connections are reciprocal. **As** first stressed by Wong-Riley (1979), Rockland and Pandya (1979), and Tigges *et al.* (1981), and subsequently by others (e.g., Maunsell and Van Essen, 1983; Burkhalter and Bernardo, 1989), the feedback connections to V1 have different laminar origins and terminations than feedforward projections from V1. Feedforward projections originate largely in layer III of V1 and terminate largely in layer IV of V2, MT, DM, and DL_c, while in these same areas neurons in layers V, VI, and to a lesser extent layer III project back to supragranular and infragranular layers of V1 (see Rockland, this volume). Feedback from both areas V2 and MT terminates in the supragranular layers. However, feedback from these areas to the infragranular layers differs such that V2 projects to layer V and also layer IIIC of area V1; MT projects to layer VI. There are area-specific differences in the laminar patterns of feedback as well as feedforward connections. In addition, feedback connections have the general feature of being less topographically specific than feedforward connections. Most notably, the feedback connections from MT to V1 are broadly distributed in a manner that suggests that the feedback from orientation and direction of movement columns in MT include mismatched **as** well as matched columns in V1 (Shipp and Zeki, 1985; Krubitzer and Kaas, 1989). **Also,** the feedback connections from MT to V1

are denser in the interblob regions of layer III, although cells in both blobs and interblobs appear to get input from MT. Thus, feedback from MT as well as other targets of V1 has the potential to influence the neurons that provide their own inputs from V1 as well as outputs to other areas.

6. Callosal Connections of V1

The general impression of many investigators is that V1 of primates is completely devoid of callosal connections. This incorrect impression stems, in part, from the results of early studies of V1 in macaque monkeys, using less sensitive degeneration methods, which failed to find evidence for callosal connections (e.g., Myers, 1965), and, in part, from subsequent reports where only the outer margin of V1 was found to have callosal connections (e.g., Kennedy *et al.,* 1985). With more information the picture has changed. The use of more sensitive axonal-transport tracing procedures, coupled with studies of a greater range of species, have led to the general conclusion that area 17 in all mammals investigated, including primates, has callosal connections. The extent and magnitude of these connections are quite variable across species. Nevertheless, a consistent feature of this pathway is that connections are always concentrated along the V1–V2 border (see Cusick and Kaas, 1986b, for review).

In most mammals, area 17 has rather extensive callosal connections. Even in opossums, which lack a corpus callosum, most of area 17 contributes to strong interhemispheric pathways which travel through an anterior commissure (Cusick and Kaas, 1986b). Tree shrews, generally regarded as close relatives of primates, demonstrate the typical pattern with the majority of callosally projecting neurons densely packed within 0.5–1.0 mm of the 17/18 border, but with some cells also projecting callosally from more peripheral regions of area 17 (Cusick *et al.,* 1984). The callosally projecting neurons in most mammals originate in layer IIIC and in layer V, and terminations are concentrated in the same layers. Weyland and Swadlow (1980) first demonstrated that the callosal connections of V1 in prosimians (galagos) can be substantial when they showed that labeled cells extend several millimeters into V1 after HRP injections in the other hemisphere. Subsequent studies have shown that the callosal pattern in primates is quite variable. Several aspects of the species differences in callosal connection patterns of V1 are apparent in Fig. 21 (Cusick *et al.,* 1984; Cusick and Kaas, 1986b). First, as described by Weyland and Swadlow (1980), callosal connections of V1 in galagos do extend inward with decreasing density several millimeters from the border. Moreover, away from the border, the connections have a patchy pattern that matches the pattern of CO blobs. The projecting neurons and terminations are concentrated in layer IIIC and in layer V. This pattern further reinforces the view that CO blob and interblob compartments are not limited to layer IIIB but may involve all cortical layers within a vertical column.

In contrast to galagos, dense callosal connections extend only a short distance into V1 of New World owl monkeys, and hardly at all into V1 of macaque monkeys. Again, the callosally projecting cells are located in both layer IIIC and layer V, although the majority are in layer IIIC. Terminations of callosal axons are found in the same layers, but terminations seem to be more widely distributed than projecting cells, suggesting that individual callosal projection neurons have large axon arbors (see also Newsome and Allman, 1980; Kennedy *et al.,* 1986;

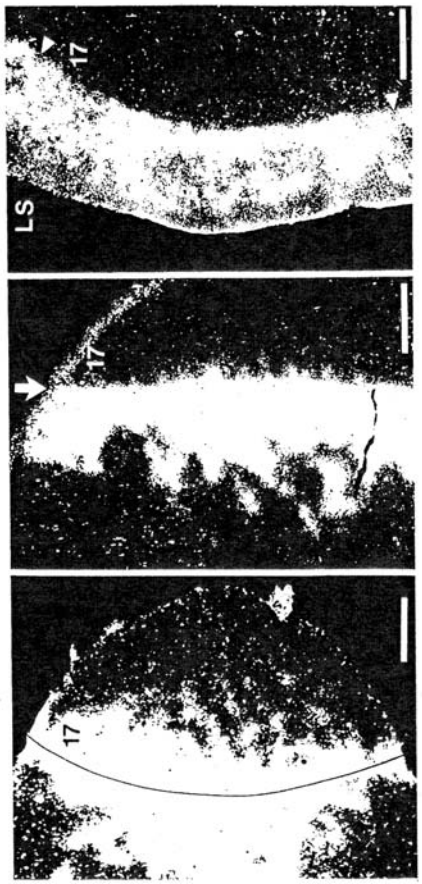


Figure 21. Callosal connections of area 17 in primates. The dark-field photomicrographs are of cortex cut parallel to the surface after injections of HRP in the opposite hemisphere. The 17/18 border is marked in each section by a line or arrow. The label extends from the 17/18 border into area 17 for several millimeters in prosimian galagos (left), only slightly in owl monkeys (middle), and hardly at all in macaque monkeys (right). Bars = 1 mm. LS, lunate sulcus. From Cusick and Kaas (1986a) with permission.

Gould *et al.,* 1987; Kennedy and Dehay, 1988). In owl monkeys, patches of connections are periodically spaced along the V1 border. Diurnal New World monkeys such as squirrel monkeys (Gould *et al.,* 1987) and marmosets (Cusick *et al.,* 1984) appear to have a more restricted pattern than nocturnal New World owl monkeys, so that they more closely resemble diurnal Old World monkeys.

Callosal connections in V1 of primates may subserve some of the basic functions of intrinsic connections for parts of V1 near the border where the horizontal spread of intrinsic connections would be truncated. Nocturnal primates with lower visual acuity and larger receptive fields in V1 apparently have more widespread intrinsic connections in V1 (see Cusick and Kaas, 1988b), and more widespread callosal connections would complement the widespread intrinsic system. Thus, the patterns of callosal connections of V1 in primates closely reflect the patterns of intrinsic connections, and thus they are likely to mediate similar functions.

7. Subcortical Connections

Area 17 projects to a variety of subcortical targets. In all mammals examined, these projections have been described as arising from cells in layers V and VI. As a rule, projections from layer V target a variety of zones in the thalamus, midbrain, and pons, with a strong projection to the superior colliculus being a consistent feature. In contrast, the subcortical targets of cells in layer VI are principally limited to the thalamus and always include a feedback pathway to the LGN.

In primates, cells in layer V of area V1 project to a number of targets, the main ones being the pulvinar, superior colliculus, pretectum, and pons (see Kaas and Huerta, 1988, for review). In galagos and macaque monkeys, similar pyramidal cells in layer V appear to send projections to both the inferior pulvinar and the superficial layers of the superior colliculus (Trojanowski and Jacobson, 1976; Raczkowski and Diamond, 1980), although double-label studies have not been performed to prove this point. However, double-label studies have shown clearly that the large Meynert cells at the lower border of layer V project to both cortical area MT and the superior colliculus (Fries *et al.* 1985). Thus, area 17 pyramidal cells in layer V can innervate multiple targets via collaterals (see also O'Leary and Stanfield, 1985).

Projections to the superior colliculus are retinotopically organized. The corticocollicular projection, however, terminates within the deepest zone of the superficial gray layer and within the upper portion of the stratum opticum, only partially overlapping the projection from the retina (e.g., Huerta and Harting, 1984). In macaque monkeys, it has been argued that the V1 pathway to the colliculus relates most strongly to the M layers of the LGN since silencing the M layers of the macaque LGN or cooling V1 also inactivates cells in the deep layers (i.e., below the stratum opticum; Schiller *et al.,* 1974). Because V1 does not project directly to the deep collicular layers, it is not entirely clear how the information from the M LGN layers and V1 influence the deep collicular neurons. Moreover, in macaque monkeys, galagos, and squirrel monkeys, it is clear that colliculogeniculate projections avoid the M layers and end in the interlaminar zones and the K layers and their equivalents (see Lachica and Casagrande, 1993). Thus, the superior colliculus does not appear to directly modulate M layer activity that is relayed to V1.

Projections from V1 to the pulvinar are also complex and appear to involve zones that get input from cells in the superior colliculus that, themselves, are innervated by projections from V1. At least two divisions of the pulvinar complex have reciprocal connections with V1. The pulvinar is commonly divided into inferior, lateral, medial, and anterior divisions or "nuclei" although each division may actually include several nuclei (see Kaas and Huerta, 1988). Both the central nucleus of the inferior pulvinar and the lateral nucleus of the lateral pulvinar project to V1 and receive topographically organized projections from V1 (Benevento and Rezak, 1976; Ogren and Hendrickson, 1977; Symonds and Kaas, 1978; Carey *et al.,* 1979; Graham *et al.,* 1979; Lin and Kaas, 1979; Rezak and Benevento, 1979; Raczkowski and Diamond, 1980; Graham, 1982; Ungerleider *et al.,* 1983; Dick *et al.,* 1991). Two points are noteworthy regarding inputs to the primate pulvinar. First, it has been demonstrated for macaque monkeys that in regions where projections from V1 and the colliculus overlap (e.g., the inferior pulvinar) in the pulvinar, the main drive for cells in the pulvinar is from the cortex, **not** the colliculus (Bender, 1983); cells in the inferior pulvinar do not respond to visual stimulation in the absence of input from V1. However, this dependence on V1 may not be the case for other mammals, such as tree shrews, that are able to see well without striate cortex, but not without the temporal lobe target of the pulvinar (Snyder and Diamond, 1968). Second, in macaque monkeys the pulvinar also sends patchy input back to layers I and II of V1 (Ogren and Hendrickson, 1977; Rezak and Benevento, 1979). The pulvinar also projects back to V1 in other primates, but it is not clear if the patterns are identical (see Kaas and Huerta, 1988, for review).

In addition to projections to the colliculus and pulvinar, cells in layer V of primate V1 show projections to several pretectal nuclei (Graham *et al.,* 1979; Hoffman *et al.,* 1991), and to a set of specific zones in the pons. In macaque monkeys, projections from V1 to the pons terminate in several eye-movement-related nuclei (Glickstein *et al.,* 1980).

As mentioned earlier, the major subcortical projection of the cells in layer VI of area V1 is to the LGN. In macaque monkeys and galagos, it has been shown that separate tiers of layer VI project to specific classes of LGN cells from which they also receive a minor direct LGN projection. Preliminary data in galagos indicate that the projections back to the LGN from cortex may be even more complex with some axons innervating pairs of LGN layers as well as the reticular nucleus, and others innervating a single layer, or several interlaminar zones (Lachica *et al.,* 1987, and unpublished). Patterns of projections from layer VI to the LGN in other mammals suggest that considerable variability exists across species (e.g., Swadlow, 1983). Thus, in ferrets single axons have been shown to innervate functionally distinct components of the LGN (e.g., the C layers, A layers, and the interlaminar zones) as well as the perigeniculate nucleus (Claps and Casagrande, 1990). In other species such as tree shrews, V1 projections to the LGN appear to mainly concentrate in the interlaminar zones (Brunso-Bechtold *et al.,* 1983).

Layer VI also sends a projection to the thalamic reticular formation (e.g., Symonds and Kaas, 1978). The latter appears to be part of a loop involving the LGN. Thus, the "visual" portion of the thalamic reticular formation projects heavily to and receives from the LGN. This loop forms a portion of the inhibitory circuitry that regulates the flow of information through LGN relay cells (see

Casagrande and Norton, 1991). Projections from V1 to the LGN and reticular nucleus provide a means by which the cortex can regulate its own input by engaging this inhibitory circuitry or by projecting directly back to cells that send information to layer IV.

8. Conclusions

In humans and other primates, V1 appears to be critical for object recognition and conscious perception (Weiskrantz, 1986; Bullier, this volume). In contrast, some nonprimate species, such as tree shrews, retain good object recognition and spatial localization despite the complete removal of area 17 and subsequent complete degeneration of the LGN (Snyder and Diamond, 1968). The relative importance of V1 to primate vision is also reflected by the size of this area, which occupies nearly 20% of neocortex in both prosimians and New and Old World simians (Felleman and Van Essen, 1991; Krubitzer and Kaas, 1990b). In primates, V1 also represents the main link between visual signals from the eye, via the LGN, to all other visual cortical areas. Thus, primate V1 represents the first staging area for the reorganization of perceptually relevant visual information to be distributed and utilized for perception in subsequent target visual areas. There are across-species similarities in the way parallel inputs and outputs of V1 are organized and relate to intrinsic circuitry in primates. The intrinsic circuitry allows new output pathways to be created from the parallel inputs to V1 in order to support further analysis by higher visual areas located in the dorsal and ventral streams (see Martin, 1992; Merigan and Maunsell, 1993; DeBruyn *et al.*, 1993). In this review we focused on the anatomical framework for the transformation and distribution of signals in V1 of primates, highlighting those features that are common across primate taxa. Several conclusions can be drawn from such comparisons. Some of the connections described earlier are also summarized in Fig. 22.

1. The widespread use of Brodmann's nomenclature for cortical layers, defined in Nissl stain, in V1 of primates generates confusion and error, and this terminology should be replaced with one compatible with both traditional architectonic and current experimental observations. In brief, the evidence indicates that Brodmann included two sublayers of layer III (IIIC and IIIBβ) in layer IV (IVB and IVA) of primates. Thus, comparisons of layers and sublayers of area V1 with layers in other areas in the same species are invalid because the homologies have been evaluated incorrectly. Comparisons across species for area 17 also are invalid because the direct homologies are in error. We use a modified version of Hassler's nomenclature. This system retains the distinctions for the unique primate specializations of layer IV (IVα and IVβ) and also defines the layer III specialization of some simian primates (e.g., IIIBβ).
2. An architectonic feature of area V1 that appears to be universal or nearly so among primates is the distinct periodic pattern of elevated metabolic activity that is revealed by staining for CO. The CO dark (blob) and light (interblob) regions mark zones of distinct vertical connectivity within V1 and connectivity between V1 and other areas. Thus, blobs and interblobs

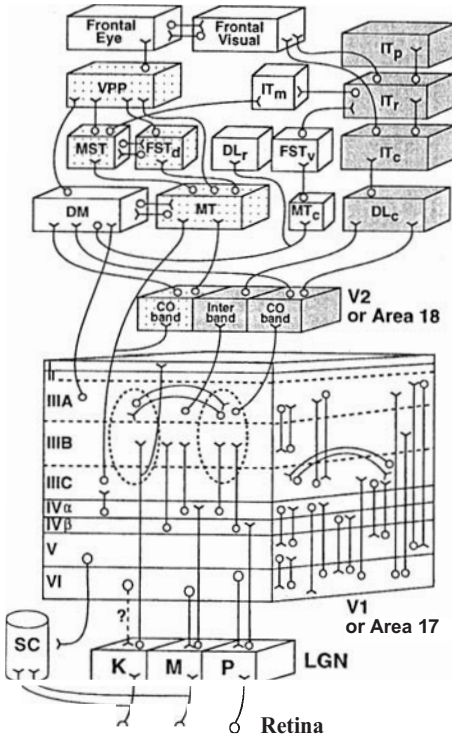


Figure 22. A schematic indicating some of the main intrinsic and extrinsic connections of V1 in primates as described in the text. No effort was made to define the strength of connections, or to indicate true axon collaterals or species-unique features. The major input to V1 is from the lateral geniculate nucleus (LGN) which arrives via three pathways, the koniocellular (K), magnocellular (M), and parvocellular (P) pathways. The retina also projects to other targets, one of which, the superior colliculus (SC), is shown. Within V1, cell layers are heavily interconnected, not only by some of the axonal pathways shown but also via dendritic arbors (not shown). The main ipsilateral connections to extrastriate cortex exit from layers IIIA and IIIC. Within IIIA, the cells within cytochrome oxidase (CO)-rich blobs, indicated by dotted ovals, and CO-poor interblobs send information to different target cells within bands in V2. These three output pathways project into dorsal (light stipple) and ventral (dense stipple) streams. Visual areas within each stream may represent functional clusters; however, visual areas within these streams are also heavily interconnected. Many of these areas also send feedback connections to VI (not shown). Areas are as follows: DL_c, caudal dorsolateral ($V4_c$); DL_r, rostral dorsolateral; DM, dorsornedial ($V3_d$); FST_d, dorsal subdivision of superior temporal; **FST**, ventral subdivision of superior temporal; MT, middle temporal; MT_c, crescent of middle temporal ($V4_t$); MST, medial superior temporal; IT, inferior temporal (c, caudal: r, rostral; p, posterior; m, medial); **VPP**, ventral posterior parietal.

mark functionally distinct subdivisions of V1 that are basically similar across primate taxa. While it has been common to relate blobs to **a** subsystem subserving color vision, blobs are equally prominent and occupy proportionately as much, or more, of V1 in nocturnal primates with limited color vision (e.g., galagos and owl monkeys) as in diurnal primates with well-developed color vision (e.g., squirrel and macaque monkeys). Thus, blobs are likely to participate in functions other than color vision, and they may help mediate a broad range of functions.

3. In some primates, although not all, ocular-specific inputs (via the LGN) are highly segregated into diverging and merging bands that gradually change to a dot and surround pattern in the portion of area V1 devoted to peripheral vision. All catarrhine (Old World) simian primates have ocular dominance bands, but they are well segregated in only the larger platyrrhine (New World) simian primates. Other platyrrhine primates have little or no tendency to exhibit ocular dominance bands, and bands, defined anatomically, are only weakly expressed in prosimian galagos. There are no known functional correlates of bands, although roles in functions such as stereoscopic vision have been postulated. For reasons that are as yet unclear, the ocular dominance bands also appear to have an organizing influence on CO blobs because blobs, or vice versa, are centered on bands.
4. In all primates, the LGN sends major inputs to area V1 over three anatomically and physiologically distinct parallel pathways via the neurons located in magnocellular, parvocellular, and interlaminar or koniocellular LGN layers (M, P, and K). These three LGN pathways terminate, by and large, separately in layers IVα (M), IVβ (P), and the CO blobs of layer III and in layer I (K), respectively. Differences in the physiological characteristics and response properties of neurons in the M and P pathways have been used to support arguments that the M pathway is especially important in providing inputs used in motion perception, and the P pathway in detailed object and color perception. However, given the overlap in the spatial and temporal resolution of P and M LGN cells and the anatomical substrates that provide for mixing of information (see below), it seems unlikely that both of these pathways contribute directly to higher-order perceptual attributes (see Casagrande and Norton, 1991; Merigan and Maunsell, 1993, for discussion). At present, it is not clear what contribution the K pathway makes to the integration of visual processes in V1. In primates the physiological properties of K cells have only been examined in galagos, where studies indicate that these cells are physiologically heterogeneous and resemble W cells in cats. A strong projection of W **or** W-like retinal ganglion cells to the superior colliculus has suggested to some that this pathway is more primitive and may be associated with general orientation in space and "ambient vision" (Stone, 1983). The strong collicular input to this class of cells in primates and their highly specific output to the CO blobs **also** hint at a role for this pathway in local modulation of activity (perhaps physiological priming for shifts of local attention) in V1 of primates.
5. In all primates studied, there are major vertical intrinsic connections in V1. Since **all** layers send and receive vertical interconnections from several other layers, the direction of flow of information cannot be defined anatomically into strict serial steps. Major input from the LGN enters V1

within layer IV, which itself is influenced by projections from the deeper layers. From this point information can travel to both the superficial and deep layers. Within the superficial layers, layer III consists of at least three main sublayers; IIIA, which sends projections to V2, IIIC, which sends projections to MT and the other hemisphere, and IIIB, which appears to act mainly as an interneuronal pool. The subdivisions of layer III have heavy interconnections with other layers, especially layer V. Layer III is also divided tangentially into the CO blob and interblob zones which themselves show differences in vertical connectivity and project to different ventral stream bands of V2. Although there are differences in the details of connections among species, CO blobs in layer IIIB in all species appear to receive not only **a** direct projection from **K** LGN cells, but also indirect inputs, via projections from layers IVα and IVβ, from both LGN M and P cells. The interblobs appear to get more restricted inputs but, at least in some species (e.g., owl monkeys), they also get indirect input from both M-recipient IVα and P-recipient IVβ. Thus, there is **a** mixing and integration of LGN streams in these cortical modules. Layer IIIC receives **a** heavy projection from M-recipient layer IVα, in addition to projections from both deep and superficial layers. Whereas layer IIIC cells may be dominated more by input from LGN M cells via layer IVα, inputs from infra- and supragranular layers would be subject to P and **K** influences. The deeper cortical layers V and VI also show sublaminar differences in connections. Within layer V, the most superficial strip, layer VA, may act as **a** set of interneurons, while layer VB sends major projections to subcortical targets (e.g., pulvinar and superior colliculus). The upper subdivision of layer VI appears to project mainly to P LGN layers and it receives **a** minor projection from them as well. The lower division of layer VI sends **a** projection mainly to M LGN layers and it also receives a minor projection from them. Layer VI also has connections with virtually all other cortical layers including layer IV.

6. In all primates studied, lateral or horizontal intrinsic connections within VI are pronounced in layers III and V, and they are extensive for CO blob modules. These connections unite groups of neurons of matched response properties, and they provide **a** potential substrate for more global processing not found within subcortical levels of the visual system.
7. In all primates studied, three major output pathways distribute information from V1 to other areas of cortex.

   a. Direction-selective neurons in layer IIIC and in layer VB provide output to MT in all investigated primates. MT is a major station in the dorsal stream of visual processing directed to posterior parietal cortex that is important in localizing objects, visual tracking, other spatial aspects of vision, and visual attention.

   b. Layer IIIC cells also provide inputs to the dorsal stream bands of V2. These dorsal stream bands relay to MT, DM, and ventral subdivision of superior temporal (FST,), visual areas associated with the dorsal stream. Layer **IIIA** cells in the **CO** blob modules project to the ventral stream bands, which then relay largely to DL, and then to inferior temporal cortex. Layer **IIIA** cells in the interblob modules project to the interbands of V2, which then also relay to DL,.

c. Layer IIIA cells, largely associated with the blob modules, project to DM, thereby providing an input usually associated with the ventral stream to a dorsal stream area. Other inputs to DM are from both sets of CO-dense bands in V2. DM further relays to posterior parietal cortex.

8. The callosal connections of V1 appear to subserve the functions of the intrinsic connections for portions of V1 near the border. Thus, they are most dense along the margin of the area where they span all layers and resemble the dense vertical intrinsic connections. Other connections extend with decreasing density up to several millimeters away from the border, especially in layer III and more notably in the CO blob modules, both subdivisions of V1 that have the most extensive horizontal intrinsic connections. These more widespread callosal connections are species variable, being very limited in diurnal simians and most prevalent in nocturnal prosimians (i.e., galagos), where V1 is also characterized by widespread intrinsic connections.
9. Subcortical connections follow the general mammalian pattern with layer VI cells projecting to the LGN and claustrum, and layer V cells projecting to nuclei of the pulvinar and the superficial layers of the superior colliculus. These connections allow feedback to modulate the relay of visual information to cortex. Thus, area 17 projections to the LGN can directly modulate the major inputs to area 17 and projections *to* the pulvinar and claustrum activate feedback that also modulates area 17 neurons as well as neurons in other visual fields. More indirect feedback loops may involve the projections to the striatum, superior colliculus, and brain-stem structures, especially the visual pons.

In summary, the organization of V1 inputs, intrinsic connections, and output targets is remarkably similar across primate species. Some of the features, but by no means all, are present in nonprimate mammals. The similarities among priinates are somewhat surprising, given that the primate order is one of the most varied in body features, and varies enormously in body size and brain size from the mouse lemur to the gorilla and large-brained human. The reassuring implication of this basic similarity is that much of visual processing and distribution of visual functions are similar across primates, and generalizations based on findings limited to a few species are likely to apply to other species including humans.

ACKNOWLEDGMENTS. This work was supported by NIH grants EY01778 (V. A. C.) and EY02686 (J. H. K.) and core grants HD15052 and EY08126. We thank Kathy Rockland, John Allison, and Roz Weller for helpful comments on the manuscript, Barbara Westendorf for help with the figures, Thea Williams for word processing, and Julia Mavity-Hudson for help an all phases of preparation of the manuscript.

9. References

Allman, J. M., and Kaas, J. H., 1971, A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*), *Brain Res.* 31:85–105.

Allman, J. M., and Kaas, J. H., 1974, The organization of the second visual area (VII) in the owl monkey: A second order transformation of the visual field, Brain *Res.* 76:247–265.

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

Allman, J. M., and Kaas, J. H., 1976, Representation of the visual field on the medial wall of occipital–parietal cortex in the owl monkey, *Science* 191:572–576.

Anderson, P. A., Olavarria, J., and Van Sluyters, R. C., 1988, The overall pattern of ocular dominance bands in cat visual cortex, *J. Neurosci.* 8:2183–2200.

Bender, D. B., 1983, Visual activation of neurons in primate pulvinar depends on cortex but not colliculus, *Brain Res.* 279:258–261.

Benevento, L. A., and Rezak, M., 1976, The cortical projections of the inferior pulvinar and adjacent lateral pulvinar in the rhesus monkey (*Macaca mulatta*), *Brain Res.*, 108:1–24.

Benevento, L. A., and Standage, G. P., 1982, Demonstration of lack of dorsal lateral geniculate nucleus input to extrastriate areas MT and visual 2 in themacaque monkey, *Brain Res.* 252:161–166.

Benevento, L. A., and Yoshido, K., 1981, The afferent and efferent organization of the lateral geniculoprestriate pathways in the macaque monkey, *J. Comp. Neurol.* 203:455–474.

Billings-Gagliardi, S., Chan-Palay, V., and Palay, S. L., 1974, A review of lamination in area 17 of the visual cortex of *Macaca mulatta*, *J. Neurocytol.* 3:619–629.

Blasdel, G. G., and Lund, J. S., 1983, Termination of afferent axons in macaque striate cortex, *J. Neurosci.* 3:1389–1413.

Blasdel, G. G., Lund, J. S., and Fitzpatrick, P., 1985, Intrinsic connections of macaque striate cortex: Axonal projections of cells outside lamina 4C, *J. Neurosci.* 5:3350–3369.

Born, R. T., and Tootell, R. B., 1991a, Single-unit and 2-deoxyglucose studies of side inhibition in macaque striate cortex, Proc. *Natl. Acad. Sci. USA* 88:7071–7075.

Born, R. T., and Tootell, R. B., 1991b, Spatial frequency turning of single units in macaque supragranular striate cortex, *Proc. Natl. Acad. Sci. USA* 88:7066–7070.

Braak, H., 1984, Architectonics as seen by lipofuscin stains, in: *Cerebral Cortex*, Volume 1 (A. Peters and E. C. Jones, eds.), Plenum Press, New York, pp. 59–104.

Brodmann, K., 1909, *Vergleichende Lokalisationlehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*, J. A. Barth, Leipzig.

Brunso-Bechtold, J. K., Florence, S. L., and Casagrande, V. A., 1983, The role of retinogeniculate afferents in the development of connections between visual cortex and the dorsal lateral geniculate nucleus, *Dev.* Brain *Res.* 10:33–39.

Bullier, J., and Kennedy, H., 1983, Projection of the lateral geniculate nucleus onto cortical area V2 in the macaque monkey, *Exp. Brain Res.* 53:168–172.

Burkhalter, A., and Bernardo, K. L., 1989, Organization of corticocortical connections in human visual cortex, *Proc. Natl. Acad. Sci. USA* 89:1071–1075.

Burkhalter, A., and Charles, V., 1990, Organization of local axon collaterals of efferent projection neurons in rat visual cortex, *J. Comp. Neurol.* 302:920–934.

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

Carey, R. G., Fitzpatrick, D., and Diamond, I. T., 1979, Layer 1 of striate cortex of *Tupaia glis* and *Galago senegalensis:* Projections from thalamus and claustrum revealed by retrograde transport of horseradish peroxidase, *J. Comp. Neurol.* 186:393–438.

Carroll, E. W., and Wong-Riley, M. T. T., 1984, Quantitative light and electron microscopic analysis of cytochrome oxidase-rich zones in the striate cortex of the squirrel monkey, *J. Comp. Neurol.* 222:1–17.

Casagrande, V. A., and DeBruyn, E. J., 1982, The galago visual system: Aspects of normal organization and developmental plasticity, in: *The Lesser Bushbaby (Galago) as an Animal Model: Selected Topics* (D. E. Hainea, ed.), CRC Press, Boca Raton, Fla., pp. 137–168.

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

Casagrande, V. A., and Norton, J. T., 1991, Lateral geniculate nucleus: A review of its physiology and function, in: *Electrophysiology of Vision* (A. G. Leventhal, ed.), Macmillan Press, London, pp. 41–84.

Casagrande, V. A., Mavity-Hudson, J. A., and Taylor, J. G., 1992, Intrinsic connections of owl monkey cortex: Difference between cytochrome oxidase (CO) blobs and interblobs, *Soc. Neurosci. Abstr.* 18:389.

Chaudhuri, A., Dyck, A., Matsubara, J. A., and Cynader, M. S., 1992, Ocular dominance columns in monkey striate cortex revealed by activity-dependent expression of zif268, *Soc. Neurosci. Abstr.* 18:209.

Claps, A., and Casagrande, V. A., 1990, The distribution and morphology of corticogeniculate axons in ferrets, *Brain Res.* **530**:126–129.

Clark, W. E. L. G., 1925, The visual cortex of primates,/. *Anal. (London)* **59**:350–357.

Clark, S., and Miklossy, J., 1990, Occipital cortex in man: Organization of callosal connections, related myelo- and cytoarchitecture, and putative boundaries of functional visual areas, *J. Comp. Neurol* **298**:188–214

Clarke, P. G. H., and Whitteridge, D., 1976, The cortical visual areas of sheep,]. *Physiol (London)* **256**:497–508.

Clarke, P. G., Donaldson, I. M., and Whitteridge, D., 1976, Binocular visual mechanisms in cortical areas I and II of the sheep, *J. Physiol. (London)* **256**:509–526.

Colby, C. L., Gattass, R., Olson, C. R., and Gross, C. G., 1988, Topographical organization cortical afferents to extrastriate area PO in the macaque: A dual tracer study, *J. Comp. Neurol.* **269**:392–413.

Colonnier, M., and Sas, E., 1978, An anterograde degeneration study of the tangential spread of axons in cortical areas 17 and 18 of the squirrel monkey (*Saimiri sciureus*), *J. Comp. Neurol.* **179**:245–262.

Condo, G. J., and Casagrande, V. A., 1990, Organization of cytochrome oxidase staining in the visual cortex of nocturnal primates (*Galago crassicaudatus* and *Galago senegalensic):* I. Adult patterns, *J. Comp. Neurol.* **293**:632–645.

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

Connolly, M., and Van Essen, D., 1984, The representation of the visual field in parvicellular and magnocellular layers of the lateral geniculate nucleus in the macaque monkey,]. *Comp. Neurol.* **226**:544–564.

Conway, J. L., and Schiller, P. H., 1983, Laminar organization of the tree shrew lateral geniculate nucleus, *J. Neurophysiol.* 50: 1330–1342.

Cowey, A,, and Stoerig, P., 1989. Projection patterns of surviving neurons in the dorsal lateral geniculate nucleus following discrete lesions of striate cortex: Implications for residual vision, *Exp. Brain Res.* **75**:631–638.

Cragg, B. G., 1969, The topography of the afferent projections in the circumstriate visual cortex of the monkey studied by the Nauta method, *Vision Res.* **9**:733–747.

Cresho, H. S., Rasco, L. M., Rose, G. H., and Condo, G. J., 1992. Blob-like pattern of cytochrome oxidase staining in ferret visual cortex, *Soc. Neurosci. Abstr.* **18**:298.

Cusick, C. G., and Kaas, J. H., 1986a. Interhemispheric connections of cortical, sensory and motor maps in primates, in: *Two Hemispheres—One Brain* (M. P. F. Lepore and H. H. Jasper, eds.), Liss, New York, pp. 83–102.

Cusick. C. G., and Kaas, J. H., 1986b, Interhemispheric connections of cortical connections of visual cortex of owl monkeys (*Aotus trivirgatus*) marmosets (*Callithrix jacchus*), and galagos (*Galago crassicaudatus*), *J. Comp. Neurol.* **230**:311–336.

Cusick, C. G., and Kaas, J. H., 1988a, Cortical connections of area 18 and dorsolateral visual cortex in squirrel monkey, *Visual Neurosci.* **1**:211–237.

Cusick, C. G., and Kaas. J. H., 1988b, Surface view patterns of intrinsic and extrinsic cortical connections of area 17 in a prosimian primate, *Brain Res.* **458**:383–388.

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

DeBruyn, E. J., and Casagrande, V. A., 1981, Demonstration of ocular dominance columns in a New World primate by means of monocular deprivation, *Brain Res.* **207**:453–458.

DeBruyn, E. J., Casagrande. V. A., Beck, P. D., and Bonds, A. B., 1993, Visual resolution and sensitivity of single cells in the primary visual cortex (V1) of a nocturnal primate (bush baby),]. *Neurophysiol.* 69:3–1S.

Desimone, R., Wessinger, M., Thomas, L., and Schneider, W., 1990, Attentional control of visual perception: Cortical and subcortical mechanisms, *Cold Spring Harbor Symp. Quant. Biol.* **55**:963–971.

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

DeYoe, E. A., Hockfield, S., Garren, H., and Van Essen, D. C., 1990, Antibody labeling of functional subdivisions in visual cortex: Cat-301 inimunoreactivity in striate and extrastriate cortex of the macaque monkey, *Visual Neurosci.* **5**:67–81.

Diamond, I. T., Conley, M., Itoh, K., and Fitzpatrick, D., 1985, Laminar organization of geniculocortical projections in *Galago senegalensis* and *Aotus trivirgatus, J. Comp. Neurol.* **242**:584–610.

Dick, A., Kaske, A., and Creutzfeldt, O. D., 1991, Topographical and topological organization of the thalamocortical projection to the striate and prestriate cortex in the marmoset (*Callithrix jacchus*), *Exp. Brain Res.* **84**:233–253.

Drager, U. C., 1974, Autoradiography of tritiated proline and fucose transported transneuronally from the eye to the visual cortex in pigmented and albino mice, *Brain Res.* **82**:284–292.

Felleman, D. J., and Van Essen, D. C., 1991, Distributed hierarchical processing in the primate cerebral cortex, *Cereb.* Cortex **1**:1–47.

Ferster, D., and LeVay, S., 1978, The axonal arborizations of lateral geniculate neurons in the striate cortex of the cat, *J. Comp. Neurol.* **182**:923–944.

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

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

Florence, S. L., and Casagrande, V. A., 1987, The organization of individual afferent axons in layer IV of striate cortex of a primate *(Galago senegalensis). J. Neurosci.* **7**:3850–3868.

Florence, S. L., and Casagrande. V. A., 1990, The development of geniculocortical axon arbors in a primate, *Visual Neurosci.* **5**:291–311.

Florence, S. L., and Kaas, J. H., 1992. Ocular dominance columns in area 17 of Old World macaque and talapoin monkeys: Complete reconstructions and quantitative analyses, *Visual Neurosci.* **8**:449–462.

Florence, S. L., Sesma, M. A., and Casagrande, V. A., 1983, Morphology of geniculo-striate afferents in a prosimian primate, *Brain Res.* **270**:127–130.

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

Freund, T. F., Martin, K. A., Soltesz, I., Somogyi, P., and Whitteridge, D., 1989, Arborization pattern and postsynaptic targets of physiologically identified thalamocortical afferents in striate cortex of the macaque monkey, *J. Comp.* Neurol. **289**:315–336.

Fries, W., Keizer, K., and Kuypers, H. G. J. M., 1985, Large layer VI cells in macaque striate cortex (Meynert cells) project to both superior colliculus and prestriate area V5, *Exp. Brain Res.* **58**:613–616.

Fulton, J. F., 1937, A note on Francesco Gennari and the early history of cytoarchitectural studies of the cerebral cortex. Bull. *Inst. Hist. Med.* **5**:895–913.

Garey, L. J., 1971, A light and electron microscopic study of the visual cortex of the cat and monkey, *Proc. R. Soc. Londm* Ser. B **179**:21–40.

Gattass, R., Gross, C. G., and Sandell, J. H., 1981, Visual topography of V2 in the macaque,]. *Comp.* Neurol. **201**:519–539.

Gattass, R., Sousa, A. P., and Gross, C. G., 1988, Visuotopic organization and extent of V3 and V4 of the macaque,]. *Neurosci.* **8**:1831–1845.

Gilbert, C. D., and Wiesel, T. N., 1981, Laminar specialization and intracortical connections in cat primary cortex, in: *Organization of the Cerebral Cortex* (F. O. Schmitt. F. G. Worden, G. Adelman, and S. G. Dennis, eds.), MIT Press, Cambridge, Mass., pp. 163–191.

Gilbert, C. D., and Wiesel, T. N., 1989, Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex,]. Neurosci. **9**:2432–2442.

Gilbert, C. D., Hirsch. J. A., and Wiesel, T. N., 1991, Lateral interactions in visual cortex, Cold *Spring Harbor Symp. Quant. Biol.* **55**:663–677.

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

Glickstein, M., Cohen, J. L., Dixon, B., Gibson, A., Hollins, M., Labossiere, E., and Robinson, F., 1980, Corticopontine visual projections in macaque monkey, *J. Comp. Neurol.* **190**:521–541.

Goodale, M. A., and Milner, A. D., 1992, Separate visual pathways for perception and action, *Trends Neurosci.* **15**:20–25.

Gould, H. U., Weber, J. T., and Rieck, R. W., 1987, Interhemispheric connections in the visual cortex of the squirrel monkey (*Saimiri sciureus*), *J. Comp. Neurol.* **256**:14–28.

Graham, J., 1982. Some topographical connections of the striate cortex with subcortical structures in *Macaca fascicularis, Exp. Brain Res.* 47:1–14.

Graham, J., Lin, C., and Kaas, J. H., 1979, Subcortical projections of six visual cortical areas in the owl monkey (*Aotus trivirgatus*), *J. Comp. Neurol.* **187**:557–580.

Harting, J. K.. Diamond, T. T., and Hall, W. C., 1973. Anterograde degeneration study of the cortical projections of the lateral geniculate and pulvinar nuclei in the tree shrew (*Tupaia glis*), *J. Comp. Neurol.* 150:393–440.

Harting, J. K., Casagrande, V. A., and Weber, J. T., 1978, The projection of the primate superior colliculus upon the dorsal lateral geniculate nucleus: Autoradiographic demonstration of interlaminar distribution of tectogeniculate axons, *Brain Res.* 150:593–599.

Hässler, R., 1967, Comparative anatomy of the central visual systems in day- and night-active primates, in: *Evolution of the Forebrain* (R. Hässler and S. Stephen, eds.), Thieme, Stuttgart, pp. 419–434.

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

Henry, *G.* H., 1991, Afferent inputs, receptive field properties and morphological cell types in different layers, in: *Vision and Visual Dysfunction,* Volume 4 (A. C. Leventhal, ed.), Macmillan Press, London, pp. 223–240.

Hess, D. T., and Edwards, M. A,, 1987, Anatomical demonstration of ocular segregation in the retinogeniculocortical pathway of the New World capuchin monkey *(Cebus apella), J. Comp. Neurol.* 264:409–420.

Hitchcock, P. F., and Hickey, T. L., 1980, Ocular dominance columns: Evidence for their presence in humans, *Brain Res.* 182:176–179.

Hockfield, S., McKay, R. D. G., Hendry, S. H. C., and Jones, E. G., 1983, A surface antigen that identifies ocular dominance columns in the visual cortex and laminar features of the lateral geniculate nucleus, Cold Spring *Harbor Symp. Quant. Biol.* 48:877–889.

Hoffman, K.-P., Distler, C., and Erickson, R., 1991. Functional projections from striate cortex and superior temporal sulcus to the nucleus of the optic tract (NOT)and the dorsal terminal nucleus of the accessory optic (DTN) of macaque monkeys, *J. Comp. Neurol* 313:707–724.

Holdefer, R. N., and Norton, T. T., 1986, Laminar organization of receptive-field properties in the lateral geniculate nucleus of the tree shrew, *Soc.* Neurosci. *Abstr.* 12:8.

Horton, J. C., 1984, Cytochrome oxidase patches: A new cytoarchitectonic feature of monkey visual cortex, Philos. *Trans.* R. *Soc.* London *Ser. B* 304:199–253.

Horton, J. C., and Hedley-Whyte. E. T., 1984, Mapping of cytochrome oxidase patches and ocular dominance columns in human visual cortex. Philos. *Trans.* R. *Soc. London Ser. B* 304:255–272.

Horton, J. C., and Hubel, D. H., 1981, Regular patchy distribution of cytochrome oxidase staining in primary visual cortex of macaque monkey, *Nature* 292:762–764.

Hubel, D. H., 1975, An autoradiographic study of the retino-cortical projections in the tree shrew (*Tupaia glis*), *Brain Res.* 96:41–50.

Hubel, D. H., and Livingstone, M. S., 1990, Color and contrast sensitivity in the lateral geniculate body and primary visual cortex of the macaque monkey, *J. Neurosci.* 10:2223–2237.

Hubel, D. H., and Wiesel, T. N., 1978, Distribution of inputs from the two eyes to striate cortex of squirrel monkeys (abstract), *Soc.* Neurosci. 4:632.

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

Hubel, D. H., and Wiesel. T. N., 1972, Laminar and columnar distribution of geniculocortical fibers in macaque monkey, *J.* Comp. *Neurol.* 146:421–450.

Huerta, M. F., and Harting. J. K., 1984, The mammalian superior colliculus: Studies of its morphology and connections, in: *Comparative Neurology of the Optic Tectum* (H. Vanegas, ed.), Plenum Press, New York, pp. 687–773.

Humphrey, A. L., and Hendrickson, A. E., 1983, Background and stimulus-induced patterns of high metabolic activity in the visual cortex (area 17)of the squirrel and macaque monkey, *J. Neurosci.* 3:345–358.

Humphrey, A. L., Sur, M., Ulrich, D. J., 2nd Sherman, S. M., 1985a, Termination patterns of individual X- and Y-cell axons in the visual cortex of the cat: Projections to area 18, to the 17/18 border region, and to both areas 17 and 18, *J. Comp. Neurol.* 233:190–212.

Humphrey, A. L., Sur, M., Ulrich, D. J., and Sherman, S. M., 1985b, Projection patterns of individual X- and Y-cell axons from the lateral geniculate nucleus to cortical area 17 in the cat, *J. Comp. Neural.* 233:159–189.

Irvin, G. E., Norton, T. T., Sesma, M. A., and Casagrande. V. A., 1986, W-like response properties of interlaminar zone cells in the lateral geniculate nucleus of a primate (*Galago crassicaudatus*), *Brain Res.* 363:254–274.

Kaas, J. H., 1986, The structural basis for information processing in the primate visual system, in: *Visual Neuroscience* (J.D. Pettigrew and J. Sanderson. eds.), Cambridge University Press, London, pp. 315–340.

Kaas, J. H., 1987. The organization of neocortex in mammals: Implications for theories of brain function, *Annu. Rev. Psychol.* 38: 129–151.

Kaas, J. H., 1988,Development of cortical sensory maps, in: *Neurobiology of Neocortex* (P. Rakic and W. Singer, eds.), Wiley, New York, pp. 101–113.

Kaas, J. H., 1992, Do humans see what monkeys see? *Trends* Neurosci. 15:1–3.

Kaas, J. H., 1993, The organization of visual cortex in primates: Problems, conclusions, and the use of comparative studies in understanding the human brain, in: The *Functional Organization of the Human Visual Cortex* (B. Gulyas, D. Ottoson, and P. E. Roland, eds.), Pergamon Press, Oxford, pp. 1–11.

Kaas, J. H., and Huerta, M. F., 1988, Subcortical visual system of primates, in: *Comparative Primate Biology,* Volume 4 (H. P. Steklis, ed.), Liss, New York, pp. 327–391.

Kaas, J. H., and Krubitzer, L. A., 1992, Area 17 lesions deactivate area MT in owl monkeys, *Visual Neurosci.* 9:399–407.

Kaas, J. H., and Morel, A., 1993, Connections of visual areas of the upper temporal lobe of owl monkeys: The MT crescent and dorsal and ventral subdivisions of FST, *J. Neurosci.* 13:534–546.

Kaas, J. H., and Preuss, T. M., 1993. Archonton affinities as reflected in the visual system, in: *Mammal Phylogeny* (F. Szulay, M. Novacek, and M. McKenna, eds.), Springer-Verlag, New York, pp. 115–128.

Kaas, J. H., Lin, C.-S., and Casagrande. V. A., 1976, The relay of ipsilateral and contralateral retinal input from the lateral geniculate nucleus to striate cortex in the owl monkey: A transneuronal transport study, *Brain Res.* 106:371–378.

Kaas, J. H., Nelson, R. J., Sur, M., Lin. C.-S., and Merzenich, M. M., 1979, Multiple representations of the body within the primary somatosensory cortex of primates, *Science* 204:521–523.

Kageyama, *G.* H., and Wong-Riley, M.. 1986, Laminar and cellular localization of cytochrome oxidase in the cat striate cortex, *J. Comp. Neurol.* 245:137–159.

Kennedy, H., and Bullier, J. C., 1985. A double-labelling investigation of the afferent connectivity to cortical areas V1 and V2 of the macaque monkey, *J. Neurosci.* 5:2815–2830.

Kennedy, H. and Dehay. C.. 1988, Functional implications of the anatomical organization of the callosal projections of visual areas V1 and V2 in the macaque monkey. *Behav. Brain Res.* 29:225–236.

Kennedy, H.. Bullier, J., and Dehay, C., 1985, Cytochrome oxidase activity in the striate cortex and lateral geniculate nucleus of the newborn and adult macaque monkey, *Exp. Brain Res.* 61:204–209.

Kennedy, H., Dehay, C.. and Bullier, J., 1986, Organization of the callosal connections of visual areas V1 and V2 in the macaque monkey, *J. Comp. Neurol.* 247:398–415.

Krubitzer, L. A., and Kaas, J. H ., 1989, Cortical integration of parallel pathways in the visual system of primates, *Brain Res.* 478:161–165.

Krubitzer, L. A., and Kaas, J. H., 1990a, Convergence of processing channels in the extrastriate cortex of monkeys, *Visual* Neurosci. 5:609–613.

Krubitzer, L. A., and Kaas, J. H., 1990b, Cortical connections of MT in four species of primates: Areal, modular, and retinotopic patterns, *Visual Neurosci. 5:*165–204.

Krubitzer, L. A., and Kaas, J. H.. 1993, The dorsomedial visual area (DM) of owl monkeys: Connections, myeloarchitecture, and homologies in other primates,]. *Comp. Neurol.,* 334:497–528.

Kuypers, H. G., Szwarcbart, M. K., Mishkin, M., and Rosvold, H. E., 1965, Occipitotemporal corticocortical connections in the rherus monkey, *Exp. Neurol.* 11:245–262.

Lachica, E. A., and Casagrande. V. A., 1992, Direct W-like geniculate projections to the cytochrome oxidase (CO) blobs in primate visual cortex: Axon morphology, *J.* Comp. *Neurol.* 319:141–159.

Lachica, E. A., and Casagrande, V. S., 1993, The morphology of collicular and retinal axons ending on small relay (W-like) cells of the primate lateral geniculate nucleus, *Visual* Neurosci., in press.

Lachica, E. A., Hutchins, J. B., and Casagrande, V. A., 1987, Morphology of corticogeniculate axon arbors in a primate, *Soc. Neurosci. Abstr.* 13:1434.

Lachica, E. A., Beck, P., and Casagrande. V. A., 1992, Parallel pathways in macaque monkey striate cortex: Anatonomically defined columns in layer III, *Proc. Nail. Acad. Sci. USA* 89:3566–3570.

Lachica, E. A., Beck, P. D., and Casagrande, V. A., 1993, Intrinsic connections of layer III of striate cortex in squirrel monkey and bush baby: Correlations with patterns of cytochrome oxidase, *J. Comp. Neurol.*, in press.

Langston, A. L., Casagrande, V. A., and Fox, R., 1986, Spatial resolution of the galago, *Vision Res.* 26:791–796.

LeVay. S., 1988, The patchy intrinsic projections of visual cortex, *Prog. Brain Res.* 75:147–161.

LeVay, S., and Gilbert, C. D., 1976, Laminar patterns of geniculocortical projections in the cat, *Brain Res.* 113:1–19.

LeVay, S., Connolly, M., Houde, J., and Van Essen, D. C., 1985, The complete pattern of ocular dominance stripes in the striate cortex and visual field of the macaque monkey, J. Neurosci. 5:486–501.

LeVay. S., McConnell, S. K., and Luskin, M. G., 1987, Functional organization of primary visual cortex in the mink (*Mustela vison*) and a comparison with the cat, *J. Comp. Neurol.* 257:422–441.

Lin, C.-S., and Kaas, J. H., 1979, The inferior pulvinar complex in owl monkeys: Architectonic subdivisions and patterns of input from the superior colliculus and subdivisions of visual cortex, J. Comp. Neurol. 187:655–678.

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

Livingstone, M. S., and Hubel, D. H., 1982, Thalamic inputs to cytochrome oxidase-rich regions in monkev visual cortex, *Proc. Natl. Acad. Sci. USA* 79:6098–6101.

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

Livingstone, M. S., and Hubel. D. H., 1984b, Specificity of intrinsic connections in primate primary visual cortex, *J. Neurosci.* 4:2830–2835.

Livingstone, M. S., and Hubel, D. H., 1987, Connections between layer 4B of area 17 and thick cytochronie oxidase stripes of area 18 in the squirrel monkey, J. Neurosci. 7:3371–3377.

Livingstone, M., and Hubel, D., 1988, Segregation of form, color, movement, and depth: Anatomy, physiology, and perception, *Science* 240:740–749.

Löwel, S., and Singer. W., 1987, The pattern of ocular dominance columns in flat-mounts of the cat visual cortex, *Exp. Brain Res.* 68:661–666.

Lund, J. S., 1987, Local circuit neurons of macaque monkey striate cortex: I. Neurons of laminae 4C and 5A, *J.* Comp. Neurol. 257:60–92.

Lund. J. S., 1988, Anatomical organization of macaque monkey striate visual cortex, *Annu.* Rev. Neurosci. 11:253–288.

Lund. J. S., 1990, Excitatory and inhibitory circuitry and laminar mapping strategies in the primary visual cortex of the monkey, in: *Signal and Sense. Local and Global Order in Perceptual Maps (G.* M. Edelman. W. E. Gall, and W. M. Cowan, eds), Wiley, New York, pp. 51–66.

Lund. J. S., and Yoshioka, T., 1991, Local circuit neurons of macaque monkey striate cortex: III. Neurons of laminae 4B, 4A. and 3B, *J. Comp. Neurol.* 311:234–258.

Lund, J. S., Lund, R. D., Hendrickson, A. E., Bunt, A. H., and Fuchs, A. F., 1975, The origin of afferent pathways from the primary cortex. area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase, J. *Comp. Neurol.* 164:287–304.

Lund, J. S., Henry, G. H., MacQueen, C. L., and Harvey, A. R., 1979, Anatomical organization of the primary visual cortex (area 17) of the cat. A comparison with area 17 of the macaque monkey, *J. Comp.* Neurol. 184:599–618.

Lund, J. S., Hendrickson, A. E., Ogren, M. P., and Tobin, E. A., 1981, Anatomical organization of primate visual cortex area VII, *J. Comp. Neurol. 202:* 19–45.

Lund. J. S., Hawken, M. J., and Parker, A. J., 1988, Local circuit neurons of macaque monkey striate cortex: II. Neurons of laminae 5B and 5, *J. Comp. Neurol.* 276:1–29.

McGuiness, E., McDonald, C., Sereno, M., and Allman, J. M., 1986, Primates without blobs: The distribution of cytochrome oxidase activity in *Tarsius, Hapalemur,* and *Cheirogaleus, Soc. Neurosci. Abstr.* 12:130.

Malach, P., Amin, Y., Bartfeld, E., and Grinvald. A., 1992, Biocytin injections guided by optical imaging reveal relationships between functional architecture and intrinsic connections in monkey visual cortex, *Soc. Neurosci. Abstr.* 18:389.

Malpeli, J. G., Schiller, P. H., and Colby, C. L., 1981, Response properties of single cells in monkey striate cortex during reversible inactivation of individual lateral geniculate laminae, *J. Neurophysiol.* 46:1102–1119.

Martin, K. A. C., 1992. Parallel pathways converge: Recent results raise doubts about the popular

view that different aspects of vision, such as form, colour and motion, are processed through separate, parallel pathways in the brain, *Vis.* Cortex 2:555–557.

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

Maunsell, J. H. R., and Van Essen, D. C., 1987, Topographic organization of the middle temporal visual area in the macaque monkey: Representational biases and the relationship to callosal connections and myeloarchitectonic boundaries, *J. Comp. Neurol.* 266:535–555.

Maunsell, J. H. R., Nealey, T. A., and DePriest, D. D., 1990, Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey, *J. Neurosci.* 10:3323–3334.

Maunsell. J. H. R., Nealey, T. A., and Ferrera, V. P., 1992, Magnocellularand parvocellular contributions to neuronal responses in monkey visual cortex, *Invest. Ophthalmol. Vis. Sci. Suppl.* 33:901.

Merigan, W. H., and Maunsell, J. H. R., 1993, How parallel are the primate visual pathways? *Annu. Rev. Neurosci.* 16:369–402.

Miklossy, J., 1992, Thalamocortical connections and rostral visual areas in man, in: *The Functional Organization of the Human Visual Cortex* (B. Gulyas, D. Ohoson. and P. E. Rowland, eds.), Pergamon Press, Oxford, pp. 123–136.

Montero, V. M., 1980, Patterns of connections from the striate cortex to cortical visual areas in superior temporal sulcus of macaque and middle temporal gyrus of owl monkey,]. *Comp. Neurol.* 189:45–59.

Muly, E. C., and Fitzpatrick, D., 1992, The morphological basis for binocular and ON/OFF convergence in tree shrew striate cortex,]. *Neurosci.* 12:1319–1334.

Murphy, K. M., Van Sluyters, R. C., and Jones, D. G., 1991, The organization ofcytochrome-oxidase blobs in cat visual cortex, *Soc. Neurosci. Abstr.* 18:1088.

Myers, R. E., 1965, The neocortical commissures and interhemispheric transmission of information, in: *Functions of the Corpus Callosum* (E. G. Ettinger, ed.), Little, Brown, Boston, pp. 1–17, 133–193.

Nealey, T. A.. and Maunsell, J. H. R., 1991, Magnocellular contributions to the superficial layers, *Suppl. Invest. Opthal. Vis. Sci.* 32:1117.

Newsome, W. T., and Allman, J. M., 1980, Interhemispheric connections of visual cortex in the owl monkey, *Aotus trivirgatus,* and the bushbaby *Galago senegalensis,* J. *Comp. Neurol.* 194:209–233.

Norton, T. T., and Casagrande, V. A., 1982, Laminar organization of receptive-field properties in lateral geniculate nucleus of hush baby (*Galago crassicaudatus*), *J. Neurophysiol.* 47:715–741.

Norton, T. T., Casagrande, V. A., Irvin, G. E.. Sesma, M. A., and Petry, H. M., 1988. Contrast-sensitivity functions of W-, X-, and Y-like relay cells in the lateral geniculate nucleus of bush baby, *Galago crassicaudatus, J. Neurophysiol.* 59: 1639–1656.

Ogren, M. P., and Hendrickson, A. E., 1977, The distribution of pulvinar terminals in visual areas 17 and 18 of the monkey, *Brain Res.* 137:343–350.

O'Leary, D. D.. and Stanfield, B. B., 1985, Occipital cortical neurons with transient pyramidal tract axons extend and maintain collaterals to subcortical but not intracortical targets. *Brain Res.* 336:326–333.

Perkel, D. J., Bullier, J., and Kennedy, H., 1986, Topography of the afferent connectivity of area 17 in the macaque monkey: A double-labelling study, *J.* Comp. Neurol. 253:374–402.

Peters, A., and Sethares, C., 1991a, Layer IVA of rhesus monkey primary visual cortex, *Cereb. Cortex* 1:495–462.

Peters, A., and Sethares, *C.*, 1991b, Organization of pyramidal neurons in area 17 of monkey visual cortex, *J. Comp. Neurol.* 306: 1–23.

Pettigrew, J. D., Ramachandran, V. S., and Bravo, H., 1984, Some neural connections subserving binocular vision in ungulates, *Brain Behav. Evol.* 24:65–93.

Pospical, M. W., Florence, S. L., and Kaas, J. H., 1994, The postnatal development of geniculocortical axon arbors in owl monkeys, manuscript in preparation.

Preuss, T. M., Beck, P. D., and Kaas, J. H., 1993, Areal, modular, and connectional organization of visual cortex in a prosimian primate, the slow loris, *Nycticebus coucang, Brain Behav. Evol.*, 42:237–251.

Purves, D., and LaMantia, A., 1990, Number of "blobs" in the primary visual cortex of neonatal and adult monkeys, *Proc. Natl. Acad. Sci. USA* 87:5764–5767.

Raczkowski, D., and Diamond, I. T., 1980, Cortical connections of the pulvinar nucleus in *Galago, J. Comp. Neurol.* 193:1–40.

Raczkowski, D., and Fitzpatrick, D., 1990, Terminal arbors of individual, physiologically identified geniculocortical axons in the tree shrew's striate cortex, *J. Comp. Neurol.* 302:500–514.

Redies, C., Diksic, M., and Riml, H., **1990,** Functional organization in the ferret visual cortex: A double-labeled 2-deoxyglucose study, *J. Neurosci.* **10:**2791–2803.
Rezak, M., and Benevento, L. A., **1979,** A comparison of the organization of the projections of the dorsal lateral geniculate nucleus, the inferior pulvinar and adjacent lateral pulvinar to primary visual cortex (area **17**) in the macaque monkey, *Brain Res.* **167:**19–40.
Ribak, C., and Peters, A., **1975,** An autoradiographic study of the projections from the lateral geniculate body of the rat, *Brain Res.* **92:**341–368.
Rockland, K. S., **1992,** Laminar distribution of neurons projecting from area V1 to V2 in macaque and squirrel monkeys. *Cereb. Cortex* **2:**38–47.
Rockland, K. S., and Lund, J. S., **1983,** Intrinsic laminar lattice connections in primate visual cortex, *J. Comp. Neurol.* **216:**306–318.
Rockland, K. S., and Pandya, D. K., **1979,** Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey, *Brain Res.* **179:**3–20.
Rockland, K. S., Lund, J. S., and Humphrey, A. L., **1982,** Anatomical banding of intrinsic connections in striate cortex of tree shrews (*Tupaia glis*), *J. Comp. Neurol.* **209:**41–58.
Rodman, H. R., Gross, C. G., and Albright, T. D., **1990,** Afferent basis of visual response properties in area MT of the macaque. II. Effects of superior colliculus removal, *J. Neurosci.* **10:**1154–1164.
Rosa, M. G. P., Gattass. R., and Fiorani, M., Jr., 1988, Complete pattern of ocular dominance stripes in V1 of a New World monkey, *Cebus apella, Exp. Brain Res.* **72:**645–648.
Rosa, M. G. P., Gattass, R., and Soares, J. G. M., 1991, A quantitative analysis of cytochrome oxidase-rich patches in the primary visual cortex of cebus monkeys: Topographic distribution and effects of late monocular enucleation, *Exp. Brain* Res. **84: 195–209.**
Rowe, M. H., Benevento, L. A., and Rezak, M., **1978,** Some observations on the patterns of segregated geniculate inputs to the visual cortex in New World primates: An autoradiographic study, *Brain Res.* **159:**371–378.
Sanderson, K. J., Haight, J. R., and Dearson, L. J., **1980,** Transneuronal transport of tritiated fucose and proline in the visual pathways of the brushtailed **possum,***Trichosurus vulpecula, Neurosci. Lett.* **20:**243–248.
Schiller. P. H., Stryker, M. P., Cynader, M., and Berman, N., **1974,** Response characteristics of single cells in the monkey superior colliculus following ablation or cooling of the visual cortex, *J. Neurophysiol.* **37:**181–194.
Sesma, M. A., Casagrande, V. A., and Kaas, J. H., **1984,** Cortical connections of area **17** in tree shrews, *J.* Comp. *Neurol.* **230:**337–351.
Shaw, C., and Cynader, M., 1986, Laminar distribution of receptors in monkey (*Macaca fascicularis*) geniculostriate system, *J. Comp. Neurol.* **248:**301–312.
Sherk, H., and LeVay, S., **1983,** Contribution of the cortico-claustral loop to receptive field properties in area **17** of the cat, *J. Neurosci.* **3:**2121–2127.
Sherman, S. M., and Spear, P. D., **1982,** Organization of visual pathways in normal and visually deprived cats, *Physiol. Rev.* **62:**738–855.
Sherman, S. M., Norton, T. T., and Casagrantle. V. A., **1975,** X- and Y-cells in the dorsal lateral geniculate nucleus of the tree shrew (*Tupaia glis*), *Brain Res.* **93:**152–157.
Shipp, S., and Zeki, S., **1985,** Segregation of pathways leading from area **V2** to areas **V4** and V5 of macaque monkey visual cortex, *Nature* **315:**322–324.
Silverman, M. S., Grosof, D. H., De Valois, R. L., and Elfar, S. D., **1989.** Spatial-frequency organization in primate striate cortex, *Proc. Natl. Acad. Sci. USA* **86:**711–715.
Snyder, M., and Diamond, I. T., **1968,** The organization and function of the visual cortex in the tree shrew, *Brain Behav. Evol.* **1:**244–288.
Sousa, A. P., Pinon, M. C., Gattass, R., and Rosa, M. G., 1991, Topographic organization of cortical input to striate cortex in the cebus monkey: A fluorescent tracer study, *J. Comp. Neurol.* **308:**665–682.
Spatz, W. B., **1979,** The retino-geniculo-cortical pathway in *Callithrix.* II. The geniculo-cortical projection, *Exp. Brain* Res. **36:**401–410.
Spatz, W. B., **1989,** Loss of ocular dominance columns with maturity in the monkey. *Callithrix jacchus, Brain Res.* **488:**376–380.
Steele, G. E., Weller, R. E., and Cusick, C. G., **1991,** Cortical connections of the caudal subdivision of the dorsolateral area (V4) in monkeys, *J. Comp. Neurol.* **306:**495–520.
Stone, J., **1983,** Parallel processing, in: The *Visual System: The Classification of Retinal Ganglion Cells and Its Impact on the Neurobiology of Virion.* Plenum Press, New York.
Swadlow, H. D., **1983,** Efferent systems of primary visual cortex: A review of structure and function, *Brain Res. Rev. 6:***1–24.**

Symonds, L. L., and Kaas, J. H., 1978, Connections of striate cortex in the prosimian (*Galago senegalensis*), *J. Comp. Neurol.* **181:**477–512.
Symonds, L. L., and Rosenquist, A. C., **1984,** Corticocortical connections among visual areas in the cat, *J. Comp.* Neurol. **229:**39–47.
Tigges, J., and Tigges, M., **1979,** Ocular dominance columns in the striate cortex of chimpanzee *(Pan troglodytes), Brain Res.* **166:**386–390.
Tigges, J., and Tigges, M., **1985,** Subcortical sources of direct projections to visual cortex, in: *Cerebral Cortex,* Volume **3** (A. Peters and E. G. Jones, eds.), Plenum Press, New York, pp. **351–378.**
Tigges, J., Tigges, M., and Perachio, A. A., **1977,** Complementary laminar termination of afferents to area **17** originating in area **18** and in the lateral geniculate nucleus in squirrel monkey, *J. Comp.* Neurol. **176:**87–100.
Tigges, J., Tigges, M., Anschel, S., Cross, N. A., Letbetter, W. D., and McBride, R. **L., 1981,** Area and laminar distribution of neurons interconnecting the central visual cortical areas **17,** 18, **19,** and MT in squirrel monkey (Saimiri), *J. Comp, Neurol.* **560:**539.
Tigges, M., Hendrickson, A. E., and Tigges, J., **1984,** Anatomical consequences of long-term monocular eyelid closure on lateral geniculate nucleus and striate cortex in squirrel monkey, *J. Comp.* Neurol. **227:**1–**13.**
Tootell, R. B. H., and Hamilton, S. L., **1989,** Functional anatomy of the second visual area (V2) in the macaque, *J. Neurosci.* **9:**2620–2644.
Tootell, R. B. H., Silverman, M. S., Switkes, E., and De Valois, R. L., 1982, Deoxyglucose analysis of retinotopic organization in primate striate cortex, *Science* **218:**902–904.
Tootell, R. B. H., Hamilton, S. L., and Silverman, M. S., **1985,** Topography of cytochrome oxidase activity in owl monkey cortex, *J. Neurosci.* **5:**2786–2800.
Trojanowski, J. Q., and Jacobson, S., **1976,** Areal and laminar distribution of some pulvinar cortical efferents in rhesus monkey, *J. Comp. Neurol.* **169:**371–392.
Ts'o, D. Y., and Gilbert, C. C., **1988,** The organization of chromatic and spatial interactions in the primate striate cortex, *J. Neurosci.* 8:17 **12–1727.**
Ts'o. D. Y., Gilbert, C. D., and Wiesel, T. N., **1986,** Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis, *J. Neurosci.* **6:**1160–1170.
Ungerleider, L. G., and Desimone, R., 1986, Projections to the superior temporal sulcus from the central and peripheral field representations of V1 and V2, *J. Comp. Neurol.* **248:**147–163.
Ungerleider, L. G., and Mishkin, M., 1982, Two cortical visual systems, in: *Analysis of Visual Behavior* (M. A. Goodale and R. J. W. Mansfield, eds.), MIT Press, Cambridge, Mass., pp. 549–586.
Ungerleider, L. G., Galkin, T. W., and Mishkin, M., **1983.** Visuotopic organization of projections from striate cortex to inferior and lateral pulvinar in rhesus monkey, *J. Comp. Neurol.* **217:**137–**157.**
Usrey, W. M., Muly, E. C., and Fitzpatrick, D., **1992,** Lateral geniculate projections to the superficial layers of visual cortex in the tree shrew, *J. Comp. Neurol.* **319:**159–171.
Van Essen, D. C., Newsome, W. T., and Maunsell, J. H. R., **1984,** The visual-field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies. and individual variability, *Vision Res.* **24:**429–448.
Van Essen, D. C., Newsome, W. T., Maunsell. J. H. R., and Bixby, J. L., **1986,** The projections from striate cortex (V1) to areas V2 and V3 in the macaque monkey: Asymmetries, areal boundaries, and patchy connections, *J. Comp. Neurol.* **244:**451–480.
Van Essen, D. C., Felleman. D. J., DeYoe, E. A., Olavarria, J., and Knierim, J., **1990,** Modular and hierarchical organization of extrastriate visual cortex in the macaque monkey, *Cold Spring Harbor Symp. Quant. Biol.* **55:**679–696.
Weber, J. T., Casagrande, V. A., and Harting, J. K., **1977,** Transneuronal transport of ^{3}H proline within the visual system of the grey squirrel, *Brain Res.* **129:**346–352.
Weber, J. T., Huerta, M. F., Kaas, J. H., and Harting, J. K., **1983,** The projections of the lateral geniculate nucleus of the squirrel monkey: Studies of the interlaminar zones and the S layers, *J. Comp. Neurol.* **213:135–145.**
Weiskrantz, L., **1986.** *Blindsight,* Oxford University Press (Clarendon), London.
Weller, R. E., and Kaas, J. H., **1982.** The organization of the visual system in *Galago:* Comparisons with monkeys, in: The *Lesser Bush Baby* (Galago) as an *Animal Model: Selected Topics* (D. E. Haines, ed.), CRC Press, Boca Raton, Fla., pp. 107–135.
Weller, R. E., and Kaas, J. H., **1983,** Retinotopic patterns of connections of **17** with visual areas V-II and MT in macaque monkeys, *J. Comp. Neurol.* **220:**253–279.

Weller, R. E., and Kaas, J. H., **1987.** Subdivisions and connections of inferior temporal cortex in owl monkeys, *J. Comp. Neural.* **256:**137–172.

Weller. R. E., Kaas, J. H., and Wetzel, A. B., 1979, Evidence for the loss of Y-cells of the retina after long-term ablation of visual cortex in monkeys, *Brain Res.* **160:**134–138.

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

Weller. R. E., Steele, G. E., and Cusick. C. G., **1991,** Cortical connections of dorsal cortex rostral to V II in squirrel monkeys, *J. Comp. Neural.* **306:**521–537.

Weyland, T. G., and Swadlow, H. A., **1980,** Interhemispheric striate projections in the prosimian primate, *Galago senegalensis, Brain Behav. Evol.* **17:**473–477.

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

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

Wong-Riley, M. T. T., Hevner, R. F., Cutlan, R., Earnest, M., Egan, R., Frost, J., and Nguyen, T., **1993,** Cytochrome oxidase in the human visual cortex: Distribution in the developing and the adult brain, *Visual Neurasci.* **10:**41–58.

Zeki, S. M., **1969,** Representation of central visual fields in prestriate cortex of monkey, *Brain Res.* **19:**63–75.

Zeki. S. M., **1971,** Cortical projections from two prestriate areas in the monkey, *Brain Res.* **34:**19–35.

Zeki, S. M., **1978,** The cortical projections of foveal striate cortex in the rhesus monkey, *J. Physiol. (London)* **277:**227–244.

Zeki, S. M., 1980a, A direct projection from area V1 to area V3a of the rhesus monkey visual cortex, *Prac. R. Soc. London* **270:**499–506.

Zeki, S. M., 1980b, The representation of color in the cerebral cortex, *Nature* **284:**412–418.