8 The Organization of Extrastriate Visual Cortex

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Introduction

With the probable exception of nearly blind species, a large portion of posterior cortex in mammals is likely to be visual. Yet, for most mammals, little or nothing is known about the organization and connections of visual cortex. This is not surprising since architectonic studies are difficult, experimental investigations take considerable time and effort, and there are roughly 12 000–15 000 species of mammals distributed across 19 orders (Walker, 1964). Rodents alone include 35 families and over 350 genera, and there can be major morphological divergences within an order as well. In primates, for example, brain size and other obvious features of brains vary enormously. Thus, there are good *a priori* reasons to believe that features of visual cortex organization are variable as well. In fact, this assumption is supported by the results of the many studies on visual cortex organization that have been published, even though these studies have concentrated on only a few species of mammals. Thus, there can be a fascinating future of discovering and describing species differences in the organization of visual cortex and determining how these differences relate to differences in visual abilities.

Our more limited goal in this chapter is to outline for a few select mammals what is known about visual cortex organization and connections in an effort to illustrate several basic principles. In most or all mammals, visual processing is mediated by a network of cortical areas or representations that are interconnected in a semi-hierarchical manner. All visual mammals apparently have a primary visual area, striate cortex (area 17 or V-I), in common and probably several other visual areas, including the second visual area, V-II (which constitutes part, or all of cytoarchitectonic area 18) (see Kaas, 1980). V-I receives inputs directly from the major thalamic target of the retina, the dorsal lateral geniculate nucleus, and distributes to V-II, occipital-temporal cortex lateral or rostral to

V-II, and sometimes to other targets such as limbic cortex. In addition, in some mammals, especially cats and monkeys, other cortical areas areas have been identified as visual by being responsive to visual stimuli and having connections with other subdivisions of visual cortex. Some of these areas access motor and visuomotor areas of the frontal lobe, lateral limbic structures (entorhinal cortex, the amygdaloid complex, and the hippocampus) important in learning and memory and hence object recognition (see Mishkin, 1982), and medial limbic cortex important for motivation and attention (see Mesulam, 1981). Finally, each visual area projects to a number of subcortical structures (see Graham *et al.*, 1979; Dreher, 1986), presumably to modulate the inflow of visual information, indirectly influence other visual areas via pulvinar connections, and mediate visuomotor and motor functions.

Comparative studies provide clear evidence that mammals vary, not only in brain size and amount of cortex devoted to processing of visual information, but in number of visual areas (see Kaas, 1989a). Visual areas, or Brodmann's (1909) 'organs of the brain', are functionally distinct processing stations that are often distinguished by having a systematic representation of visual space (a retinotopic or visuotopic organization). Differences in connections with other structures and areas, and often specializations in local circuitry, reflected in histological structure, provide the anatomical framework for the distinct functional roles of cortical areas. Such differences can be used to distinguish cortical areas, especially where simple retinotopic maps do not exist.

Although it is difficult to unambiguously determine how cortex is subdivided in any species, some conclusions are justified (Kaas, 1987a,b; 1989a,b). Mammals with little neocortex and small brains have only a few visual areas (of the order of five to ten). Other mammals with expanded neocortex may have many more processing stations. Since mammals with large brains evolved from mammals with

little neocortex (see Kaas, 1987b), the numbers of visual areas have increased in some lines of descent. This has undoubtedly happened independently in at least the carnivore and primate lines. The visual areas that evolved later appear to have been inserted between the early processing stations, V-I and V-II, and the 'highest' effector stations, the limbic and visuomotor areas. While the connection patterns leading to the cortical endstations are partially understood for some mammalian species, the access routes are not yet known for most investigated species. Yet because these endstations mediate critical functions, such pathways must exist for most mammals. Thus, mammals with few visual areas must have more direct inputs from earlier stations to endstations in processing hierarchies than mammals with more areas. It also follows that in mammals with fewer areas, these areas must be more general in function and less specialized, since a range of basic visual capabilities seem to exist in most mammals.

Another general conclusion is that some visual areas, perhaps most or all, are functionally heterogeneous. That is, functionally similar neurones are segregated in small groups that are scattered across the area and separated by other groups. This is known as the columnar or modular organization of cortex (Szentágothai, 1975; Mountcastle, 1978) in contrast to the more obvious laminar segregation of function. Because functionally distinct groups of neurones come in various shapes including bands and blobs, we prefer to call such subdivisions modules. Modules have been most clearly demonstrated in V-I and V-II of monkeys (see Livingstone and Hubel, 1988). However, experimental studies consistently reveal that connections between and within visual areas are unevenly distributed, and this suggests that modules exist throughout visual cortex (see Kaas, 1990). Indeed experimental studies in all mammals consistently reveal that associational connections *between* visual areas are patchy (Gilbert and Kelly, 1975; Wong-Riley, 1979; Montero, 1981b; Bullier *et al.*, 1984; Livingstone and Hubel, 1984; Symonds and Rosenquist, 1984; Shipp and Zeki, 1985, 1989a,b; Sherk, 1984a; Zeki and Shipp, 1989) and this in turn suggests that modules are a common feature of all mammalian visual cortex (see for reviews LeVay, 1988; Gilbert and Wiesel, 1989; Kennedy *et al.*, Chapter 9).

Given this framework, we describe subdivisions and connections of visual cortex in mice, squirrels, tree shrews, domestic cats and several species of primates. We start with mice because they have very little neocortex in both relative and absolute terms. Although there are other extant mammals with proportionately less neocortex, such as hedgehogs (Kaas *et al.*, 1970), mice and rats are more common experimental animals and more is known about their cortical organization. Mice illustrate that some mammals (and by implication early mammals) have only a few visual areas. Squirrels and tree shrews are included

because they are highly visual mammals with somewhat expanded occipital and temporal regions of neocortex. They have proportionally more visual cortex, and possibly more visual areas than mice and other less visual mammals. Some of the visual areas in squirrels and tree shrews have been defined, and some of the connections are known. There is also evidence for modular organization within some of their visual areas. Next, we consider the organization of visual cortex in cats, because they have a more complex visual system than most mammals outside the order of Primates. Finally, we consider the organization of visual cortex in prosimian primates, New World monkeys, and Old World monkeys. Both New World and Old World monkeys have expanded, complex visual systems that include some 20–30 cortical visual areas or more (Van Essen, 1985; Maunsell and Newsome, 1987; Kaas, 1989a), and at least some of this complexity is apparent in prosimians as well (Weller and Kaas, 1982). Because much of our research has been on New World owl monkeys, which offer the technical advantage of a relatively unfissured brain with most of the visual areas accessible on the surface, visual cortex is described most extensively for this primate.

Simple Brains: Visual Cortex in Mice and Rats

An important question is how visual cortex is organized and connected in mammals with relatively little neocortex, since the system is likely to be least complex and more easily understood in these mammals. Previously, we have illustrated visual and other sensory and motor areas in the brains of hedgehogs (Kaas, 1987a,b), insectivores with proportionately less neocortex than almost any other extant mammal (except for other insectivores). Hedgehogs have both V-I and V-II (Kaas *et al.*, 1970), and since these fields border auditory and somatosensory cortex, there is little cortical space for other visual areas. Thus, hedgehogs, having about the same amount of neocortex as the first mammals (Jerison, 1973) nearly 200 million years ago, have at least two visual areas, but probably no more than three to four. Since hedgehogs are not generally available for experimental studies, we consider here other small brained mammals that are more commonly studied, such as mice and rats. Fig. 8.1 illustrates some of the proposed subdivisions of neocortex in mice. Like other mammals with little neocortex, mice and rats appear to have few visual areas. However, it has been argued on the basis of the laminar distributions of association neurones and terminals in area V-I and in patches of cortex within cytoarchitectonic areas 18a and 18b flanking rat's area V-I (cf. Montero *et al.*, 1973a,b; Olavarria and Montero, 1981;

Espinoza and Thomas, 1983; Thomas and Espinoza, 1987) that at least some of these patches constitute separate visual areas (Coogan and Burkhalter, 1990; Sanderson *et al.*, 1991). Indeed, some investigators concluded that extrastriate cortex of rats and mice includes several visual areas (e.g. Montero 1981b, Olavarria and Montero, 1984, 1989). Furthermore, a semi-hierarchy (for the explanation of the concept of hierarchy of visual areas see sections concerning tree shrews, cats and primates) of visual areas in rat's visual cortex has been proposed (Coogan and Burkhalter, 1990; Sanderson *et al.*, 1991).

Our summary of cortical areas in mice (Fig. 8.1) is based on brain sections cut from cortex separated from the rest of the brain, manually flattened, and sectioned parallel to the flattened surface. The sections were stained for cells or fibres. In both sets of sections, several obvious subdivisions of cortex were identified and used as landmarks to locate other fields. These included primary visual cortex, V-I, auditory cortex (probably A-I; see Luethke *et al.*, 1988) and S-I (where even details of the somatotopic patterns are apparent; see Dawson and Killackey, 1987).

Injections of tracers in V-I of mice (e.g. Olavarria and Montero, 1989) demonstrate patchy projections to cortex on the lateral border of V-I in a region identified in physiological experiments as area V-II (Dräger, 1975; Wagor *et al.*, 1980). Although as mentioned above each patch in the projection pattern can be interpreted as a separate visual area (e.g. Olavarria and Montero, 1989), we do not favour this interpretation because projections from area V-I to area V-II in other mammals, where V-II has been established by multiple criteria, are always patchy (see Figs. 8.2, 8.4 and 8.13). Instead, the patches might represent modules within V-II (see Malach, 1989 for exposition of this argument for the rat visual cortex). Other projections are to cortex just lateral to V-II indicating the presence of at least one and probably several addi-
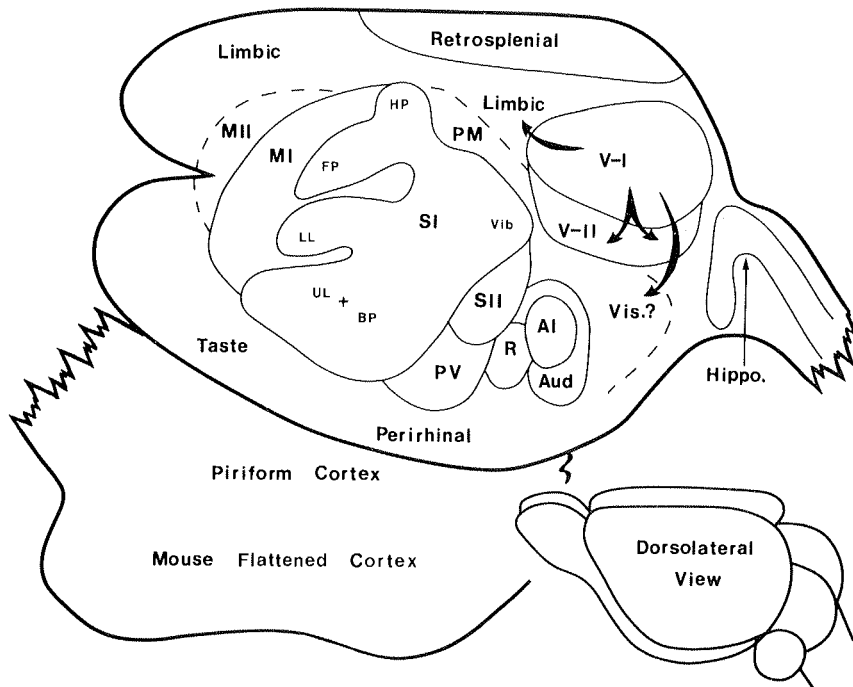

Fig. 8.1 *Proposed subdivisions of neocortex in mice. Visual cortex includes first (V-I) and second (V-II) visual areas, and projections from V-I identify parts of occipital-temporal cortex as visual. V-I also projects to limbic cortex medially. Most of the rest of cortex is occupied by somatosensory, auditory, motor or limbic areas. Thus, mice have little visual cortex and few visual areas. Somatosensory cortex includes the first area, S-I, where the hindpaw (HP), forepaw (FP), facial vibrissae (Vib), upper lip (UL), lower lip (LL) and buccal pad (BP) are represented. We also define a second area (S-II), a parietal ventral field (PV) and a posterior medial field (PM). Auditory cortex includes a first area (A-I) and a rostral area (R) as well as other auditory cortex. In frontal cortex, there is evidence for a first motor area (M-I) and a premotor region (PM or M-II). Conclusions are based on cytoarchitectonic distinctions in brain sections cut from cortex that has been separated from the rest of the brain, flattened and cut parallel to the surface. See Krubitzer* et al. *(1986),* Luethke et al. *(1988),* Kaas et al. *(1989)* Li et al. *(1990) for reviews on somatosensory, auditory, visual and motor cortices of rodents respectively.*

tional visual areas in occipital-temporal cortex (cf. reciprocal connections between rat's area 17 and area 36 in the temporal lobe as well as area 13/35 located along the rhinal sulcus: Miller and Vogt, 1984; Zilles and Wree, 1985; Dreher *et al.*, 1990; Sanderson *et al.*, 1991). Indeed, such projections to cortex just lateral to area V-II are common to a wide range of studied mammals (see Kaas, 1980). Other projections of area V-I of nocturnal murid rodents are to cortex medial and rostromedial to V-I. This cortex may be part of limbic cortex (Vogt and Miller, 1983; Zilles and Wree, 1985; Dreher *et al.*, 1990; Sanderson *et azl.*, 1991). Thus, in some mammals area 17 appears to directly access the limbic system (see also Vogt *et al.*, 1986 for the direct connections between area 17 and retrosplenial limbic area 29d of rabbit). In rats, there is even evidence for direct projections from area V-I (as well as from some extrastriate areas) to oculomotor fields in frontal cortex (Miller and Vogt, 1984; Torrealba *et al.*, 1984; Sukekawa, 1988; Dreher *et al.*, 1990; Sanderson *et al.*, 1991). Overall, in both mice and rats there is little neocortex, much of the neocortex is occupied by known sensory and motor fields, and there is a small amount of poorly understood cortex that could contain additional and yet undiscovered visual areas. Thus, these nocturnal rodents and probably other mammals with little neocortex have only a few visual areas, and these areas appear to directly relate to limbic and motor structures.

Moderately Expanded Visual Cortex: Squirrels and Tree Shrews

When compared with most other rodents, including mice and rats, squirrels have expanded occipital and temporal regions of cortex (Fig. 8.2). Most of this cortex is probably visual. V-I (area 17) is large, cytoarchitectonically distinct, and contains an orderly map of the contralateral visual hemifield (Hall *et al.*, 1971). Just lateral to V-I, a strip-like bordering region, V-II, is cytoarchitectonically distinct, contains an orderly map of the contralateral visual hemifield with the lower quadrant represented rostrally and the zero vertical meridian medially as in other mammals, and has a topological pattern of inputs from V-I (Hall *et al.*, 1971; Kaas *et al.*, 1989). However, as in other mammals, the projection from any single small region in V-I is to several separate, nearby locations in V-II, providing evidence for repeating subsets of functionally and connectionally distinct processing modules in V-II.

Other projections of V-I are to occipital-temporal cortex just lateral to V-II (Fig. 8.2(b)). The projection pattern suggests that this cortex contains at least three presumptive areas, which we term here (modifying our previous terms from Kaas *et al.*, 1989), the rostral, middle and caudal occipital-temporal areas (OTr, OTm and OTc). V-I projects densely in two distinct patterns to OTr and OTm, and sparsely to OTc. V-I may also project sparsely to limbic cortex (Cusick *et al.*, 1980). V-II projects to limbic cortex, as well as to OTr and OTm (Kaas *et al.*, 1989). In addition, V-II projects lateral to OT to cortex in the upper temporal lobe, providing evidence for further subdivisions of visual cortex. Much more than mice and rats, squirrels have a large region of caudal temporal cortex that does not appear to be auditory (Luethke *et al.*, 1988), and could be visual. Thus, even among different rodents, where there is a tendency to think of the brains as more or less alike, there is considerable variability in the amount of visual cortex, and possibly in the number of visual areas.

Tree shrews are small, highly visual mammals that are squirrel-like in appearance, but more closely related to primates (Cronin and Sarich, 1980). Like squirrels, tree shrews have moderately expanded occipital and temporal regions of neocortex, and much of this cortex is responsive to visual stimuli (Kaas *et al.*, 1972) and is involved in visual behaviour (Killackey *et al.*, 1971). V-I projects in a patchy but topographic pattern to V-II (Sesma *et al.*, 1984), which is architectonically distinct and contains an orderly representation of the contralateral hemifield (Kaas *et al.*, 1972). V-I also projects to a region of occipital-temporal cortex that we term here by location, the OTm, although it is not certain if this is the same field (homologous) as OTm in squirrels. The projection patterns indicate that the lower visual field is represented rostrally and the peripheral visual field is represented laterally in OTm. V-I projects sparsely to caudal occipital-temporal cortex and to limbic cortex. V-II projects most densely to OTm and occipital parietal cortex (OP). OTm projects to OP, OTc, limbic cortex and locations more lateral in the temporal lobe (Sesma *et al.*, 1984). The evidence suggests that tree shrews have at least six visual areas, and probably more, given the large amount of temporal cortex of uncertain function.

Studies conducted on tree shrews also usefully demonstrate some general features of connection patterns. First, connections are almost invariably reciprocal. Areas receiving inputs from a given area also send back inputs. In monkeys, 'feedforward' and 'feedback' laminar patterns between areas within processing hierarchies have been described, with feedforward projections terminating largely on the 'receptive cells' of layer IV and feedback projections terminating on cells in other layers (e.g. Rockland and Pandya, 1979; Weller and Kaas, 1981; Maunsell and Van Essen, 1983). In mice and rats, the differences between laminar patterns are less pronounced (Coogan and Burkhalter, 1990; Dreher *et al.*, 1990; Sanderson *et al.*, 1991), and these mammals may reflect the more primitive or generalized mammalian plan. Limited evidence from
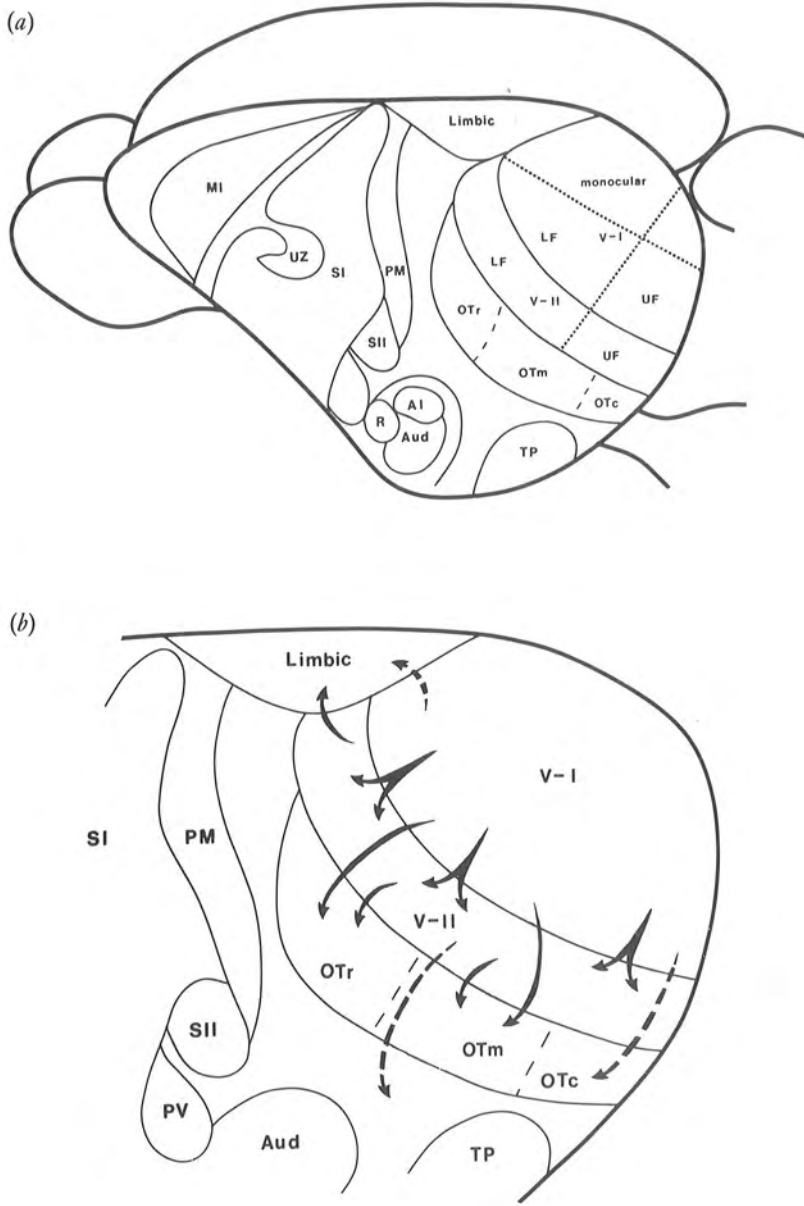
(a)

(b)

Fig. 8.2 *Visual cortex in squirrels. Squirrels are highly visual rodents with expanded occipital and temporal regions of visual cortex.
(a) Proposed visual, auditory, somatosensory and motor areas are indicated on a dorsolateral view of the brain. Area 17 or V–I has a
monocular (17m) and binocular (17b) portion. Both V–I and V–II (area 18) contain systematic representations of the visual hemifield
(Hall et al., 1971) with the lower field (LF) projected to cortex rostral to that of the upper field (UF). Occipital–temporal cortex has
rostral (OTr), middle (OTm) and caudal (OTc) divisions that differ in connection patterns. TP (temporal posterior) is a densely
myelinated region of cortex with uncertain but possibly visual functions. Auditory, somatosensory and motor areas as in Fig. 8.1. (b)
Some of the feedforward connections of visual cortex in squirrels. V–I projects in a patchy but topological manner to V–II, with rostral
V–I projecting to rostral V–II. Other patchy connections are to OTm, and somewhat less densely to OTr. Limbic cortex and OTc
receive sparse inputs. Projections from V–II implicate cortex lateral to OTm in visual functions. Connections are summarized from
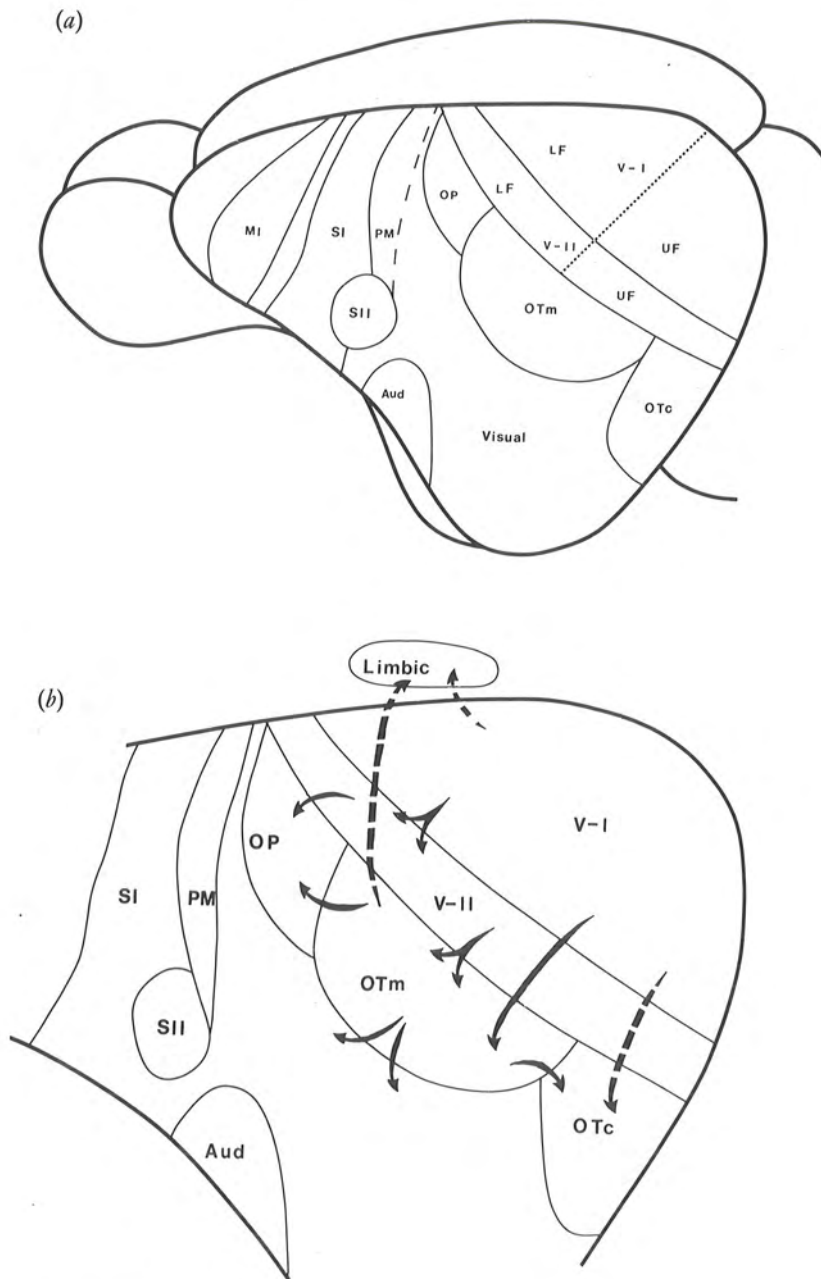Cusick et al. 1980 and Kaas et al., 1989.*

Fig. 8.3 *Visual cortex in tree shrews. Tree shrews are highly visual squirrel-like mammals that, as members of the archonta radiation, are close relatives of primates. (a) Area 17 or V–I and area 18 or V–II are cytoarchitectonically distinct representations of the visual hemifield with the lower field (LF) rostral and upper field (UF) caudal. (b) V–II and the middle occipital temporal region, OTm, receives topographically organized projections from V–I. Connection patterns also define a caudal occipital–temporal region, OTc, and an occipital–parietal region OP. Cortex lateral to OTm receives inputs from OTm. Thus, tree shrews have at least six visual areas. Auditory (Aud), first motor (M–I), first (S–I) and second (S–II) somatosensory areas and a parietal medial field (PM) are also indicated. (Based on (a) Sesma et al., 1984 and (b) Sur et al., 1981.)*
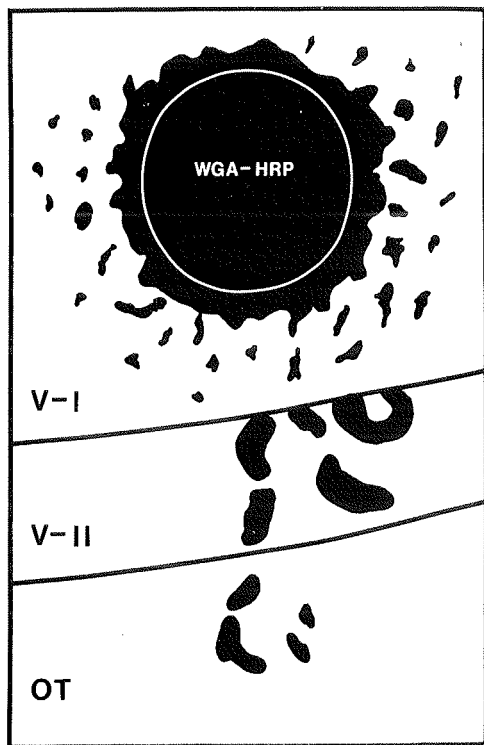
Fig. 8.4 *Modular connections of area 17 in tree shrews. An injection of wheat germ agglutinin conjugated with horseradish peroxidase (WGA-HRP) produces a pinwheel of patchy labelled neurones and terminals in area 17, and bands of patches in area 18 and occipital-temporal cortex (OT). The discontinuous distributions of interconnected locations suggest a modular or uneven distribution of function within these fields. (Based on Sesma et al., 1984.)*

squirrels and tree shrews suggests that laminar patterns are more like those in primates.

A second notable feature of the connection pattern in tree shrews is its patchy and discontinuous nature. Injections of tracers in V-I reveal both intrinsic and extrinsic cortical connections that are patchy (Fig. 8.4; also see Rockland and Lund, 1982; Sesma *et al.*, 1984). Within area 17, injections of tracers produce a pinwheel of periodic foci of labelled terminals and cells. Thus, neurones separated by several mm of cortex can influence each other directly. What is not now known is if the interconnected labelled sets of cells correspond to a specific subset of neurones, like the specialized cytochrome oxidase blobs in V-I of primates (see below), or if the cells in all locations have widespread connections. In V-II, the transported label forms clumps that sometimes merge to form bands crossing the width of the field. Finally, less dense clumps of label are found in OT. The obvious implication of such patchy connections is that these extrastriate areas are func-

tionally heterogeneous, with a given location in V-I connecting to only certain classes of modular groups of neurones in extrastriate cortex. The nature of this presumed modular organization is not yet known but three types of modules have been demonstrated in V-II of monkeys (see below).

The uneven distribution of interhemispheric connections is another feature of the connection patterns that suggests the existence of functionally distinct zones within cortical areas. When horseradish peroxidase injections into one hemisphere are used to reveal the distribution of callosally projecting neurones and terminations in the other hemisphere of tree shrews (Fig. 8.5), only the lateral third of area 17 representing frontal vision is labelled (Cusick *et al.*, 1985). Area 18 or V-II demonstrates dense areas of callosal connections surrounding 'holes' of sparse connections. The 'holes' are also apparent as myelin-poor patches in sections stained for myelin. Much of the centre of OTm area has sparse connections (compare with Fig. 8.3), and more temporal visual cortex has regions of dense and sparse connections. This pattern of uneven connections is typical of a number of studied mammals (Cusick and Kaas, 1986) including rats and mice (e.g. see Olavarria and Montero, 1989). In general, callosal connections are dense but not restricted to the lateral border of
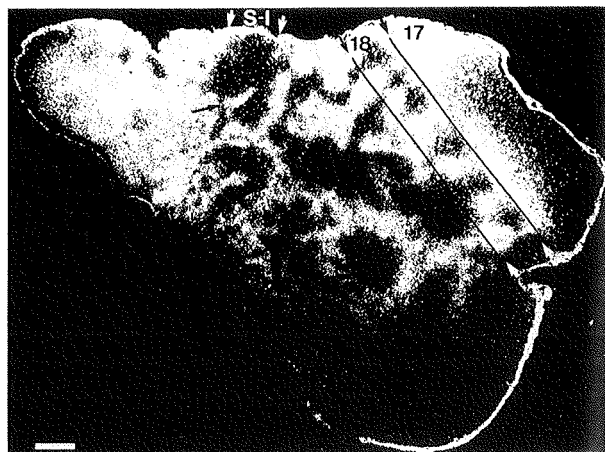

Fig. 8.5 *Interhemispheric connections in tree shrews. The right cerebral hemisphere has been injected with the tracer horseradish peroxidase and the left hemisphere has been flattened and cut parallel to the surface. The reacted section above shows the uneven distribution that characterizes the callosal connection pattern of many mammals. Note especially the connection-poor callosal 'holes' in area 18 (V-II). Because injections were not placed in the lower temporal lobe, label is sparse in that region. Arrows mark the border of area 18 and the location of S-I. A single arrow indicates a strip of callosally connected cortex that separates the hand and face representations in S-I. Compare with Fig. 8.3. Scale bar = 1 mm. (From Cusick et al., 1985.)*

V-I, corresponding to the line of decussation of the retina (zero vertical meridian). Area 18 or V-II has a series of alternating regions of dense and sparse callosal connections. More laterally located regions of visual cortex also have heterogenous patterns of callosal connections, suggesting that these regions have modular organizations.

Restricted injections of tracers into given areas (e.g. Sesma *et al.*, 1984) demonstrate other typical features of interhemispheric connections. Locations in one hemisphere usually project to a scattering of patches in the matched location in the other hemisphere, plus additional locations in one to three visual areas. For example, the major callosal connections of rostral locations in area 17 are to rostral locations in area 17 and 18 of the opposite hemisphere. Thus, interhemispheric connections of a given area are not restricted to the matched area, but include areas that are adjacent in the putative processing hierarchy. Because the homologous visual areas of the two cortical hemispheres represent different halves of the entire visual field, callosal connections, other than those related to the zero vertical meridian, connect mismatched parts of the visual field representations.

Expanded Visual Cortex in Non-primates: Domestic Cats

The visual cortex of domestic cats (Fig. 8.6) is of special interest in that cats have been used extensively in investigations of the organization and connections of visual cortex, and evidence is available for the existence of over 15 visual areas (for review, see Tusa *et al.*, 1981; Symonds and Rosenquist, 1984; Rosenquist, 1985; Dreher, 1986). As other mammals, cats have first (V-I) and second (V-II) representations of the contralateral visual hemifield in cytoarchitectonically distinct regions of the cortex, areas 17 and 18, respectively. Area 18 of cat's visual cortex resembles primary visual cortex in that it receives its principal thalamic input from the dorsal lateral geniculate nucleus – LGNd (see for review Garey *et al.*, Chapter 5). Indeed, unlike monkeys (see below), the only significant effect of the removal (Dreher and Cottee, 1975) or reversible inactivation (Sherk, 1978) of cat area V-I (area 17) is a substantial reduction of responsiveness of area V-II (area 18) neurones to slowly moving stimuli. This effect is probably related to the fact that area V-II unlike area V-I receives its principal geniculate input from Y-type relay cells, while the X-type geniculate neurones with their good responsiveness to slowly moving visual stimuli activate V-II via the association neurones in area V-I (see Stone *et al.*, 1979; Dreher, 1986; cf. Garey *et al.*, Chapter 5; Valverde, Chapter 6). Other subdivisions of visual cortex include a third representation of the contra-
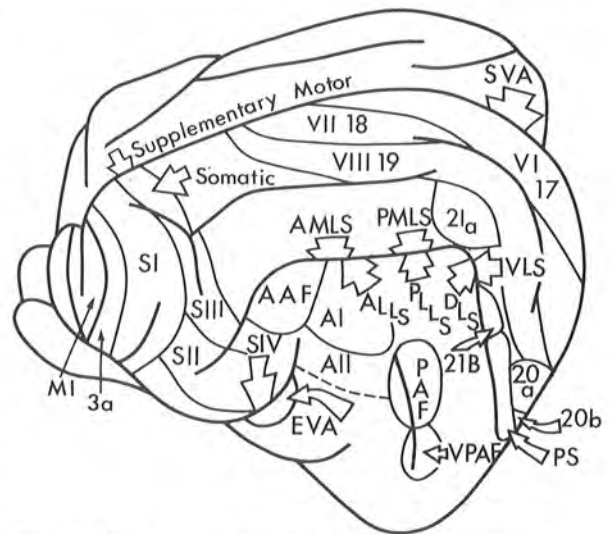

Fig. 8.6 *Visual and other sensory areas in cats. Visual cortex includes the now traditional area V-I (area 17), area V-II (area 18) and area V-III (area 19). Other presumptive areas are those from the electrophysiological mapping studies of Tusa, Palmer and Rosenquist (see Rosenquist, 1985). They include the anteromedial and anterolateral lateral suprasylvian areas (AMLS and ALLS), the posteromedial lateral suprasylvian and posterolateral syprasylvian areas (PMLS and PLLS), and the dorsal (DLS) and ventral (VLS) lateral suprasylvian areas. Other proposed visual areas are the splenial visual area (SVA), the visual area of the anterior lateral gyrus (ALG), visual areas in cytoarchitectonic areas 20a, 20b, 21a, and 21b, the ectosylvian visual area (EVA), and the posterior suprasylvian area (PS). See text, as well as Rosenquist (1985) and Dreher (1986) for further details. Auditory fields include the traditional first (A-I) and second (A-II) areas, the anterior auditory field (AAF), the posterior auditory areas (PAF), and the ventral posterior auditory field (VPAF). Somatosensory areas are numbered and with the exception of area 3a cytoarchitectonic boundaries of these areas are not indicated (for details on somatosensory areas see Kaas, 1983).*

lateral hemifield, area V-III which coincides with cytoarchitectonic 'area 19', just lateral to V-II, and which has been recognized since the landmark study of Hubel and Wiesel (1965). Cortex along the laterocaudal border of area 19 is also visual, and several cytoarchitectonic zones (areas 20a, 20b, 21a and 21b) appear to contain separate, albeit only incomplete representations of the contralateral visual hemifield (Tusa and Palmer, 1980). Six other visual areas in the medial and lateral banks of the lateral suprasylvian sulcus have been described (for another point of view, see Sherk, 1986b) and named by location (e.g. the anterolateral lateral suprasylvian area, ALLS; Fig. 8.6). Furthermore, a partial representation of the lower contralateral visual hemifield has been described along the rostrolateral border of area 19, in the area located in the

anterior lateral gyrus (ALG) and Updyke (1986) has described the posterior suprasylvian area (PS area) located in cortex rostrolateral to area 20a which also contains an incomplete representation of the contralateral visual hemifield. An additional visual area occupies the cortex in the depth of the caudal two-thirds of the anterior ectosylvian sulcus. This so called ectosylvian visual area (EVA) contain neurones responsive to visual stimuli but its retinotopic organization is very loose, as indicated by a substantial scatter of the receptive field positions of neurones recorded from adjacent locations (see Mucke et al., 1982; Olson and Graybiel, 1983, 1987). There is also limited evidence, based mainly on clustering of the neurones responsive to visual stimuli, which suggests the existence of another visual area, along the ventral bank of the rostralmost part of the anterior ectosylvian sulcus and adjoining aspects of the anterior sylvian gyrus (Benedek et al., 1986; Hicks et al., 1988). Again the retinotopic organization of this area appears to be very diffuse (Benedek et al., 1986: Hicks et al., 1988). Finally, according to one unconfirmed report (Kalia and Whitteridge, 1973) limbic cortex located along the medioventral border of area 17, the splenial visual area (SVA), is responsive to visual stimuli and contains a single representation of the contralateral visual hemifield. It is important to point out that in most visuotopically organized cortical areas the disproportionate amount of each area contains a representation of the high resolution retinal area: area centralis (see Tusa et al., 1981; Rosenquist, 1985). However, the area centralis is not overrepresented in AMLS, ALLS and area 20a.

In addition to the above mentioned visuotopically organized cortical areas there are polysensory cortical areas which have visual inputs and therefore should be considered in the present context. Polysensory area 7 (or area 7p) located in the parietal region along the crown of the middle suprasylvian gyrus (Heath and Jones, 1971; Olson and Lawler, 1987) is considered to be visual because it receives thalamic input from the pulvinar and has associational interconnections with several of the visuotopically organized cortical areas mentioned above (see for review Rosenquist, 1985). Similarly, another area, referred to as the visual belt of the posterior ectosylvian gyrus (EPp), is classified as visual, so far exclusively on hodological (rather than functional) grounds. In particular, the visual belt of EPp receives substantial associational input from several extrastriate visuotopically organized areas – ALLS, PLLS, DLS, VLS and areas 19, 21a, 21b, 20a and 20b (Bowman and Olson, 1988b). Furthermore, the visual belt of EPp receives thalamic input from two of the retinotopically organized components of the lateral posterior nucleus as well as from the central intralaminar nucleus (Bowman and Olson, 1988a; cf. Garey et al., Chapter 5).

The visuotopically organized cortical areas which are located medially and receive the majority of their thalamic afferents from the LGNd complex (visual cortex areas 17 and 18) or receive a substantial proportion (but not the majority) of their thalamic afferents from the retinorecipient parts of the thalamus (e.g. area 19) tend to send associational information to the more laterally located visual areas (receiving a smaller proportion of their afferents from the retinorecipient part of the ipsilateral thalamus, see for review Garey et al., Chapter 5) via associational neurones located in supragranular layers 2 and 3. By contrast, more laterally located visuotopically organized cortical areas which receive only a small proportion of their afferents from the retinorecipient parts of the thalamus (e.g. PMLS area) tend to send associational information to medially located areas via neurones located in infragranular layers 5 and 6 (for reviews see Rosenquist, 1985; Dreher, 1986).

In other words the 'lower' visual areas located more medially and receiving their principal thalamic input from the retinorecipient parts of the thalamus appear to send feedforward or ascending associational projections to the 'higher' visual areas located more laterally. By contrast, the higher areas tend to send feedback or descending projections to the lower areas. The trend extends to the ectosylvian visual area (EVA) since EVA appears to receive almost exclusively feedforward associational inputs from the lateral suprasylvian areas and sends predominantly feedback type projections back to these areas (Olson and Graybiel, 1987). In particular, associational projections from the lateral suprasylvian areas to EVA originate almost exclusively in supragranular layer 3 and terminate mainly in layer 4 (Mucke et al., 1982; Miceli et al., 1985; Norita et al., 1986; Olson and Graybiel, 1987). Conversely, the associational projections from EVA to the lateral suprasylvian areas originate predominantly in infragranular layer 6 and terminate in layer 1 (Miceli et al., 1985; Olson and Graybiel, 1987). With this information in mind one could argue that of the cortical areas which are purely visual rather than polysensory or visuomotor, EVA constitutes the highest level of the hierarchy.

It is important to point out in this context that a similar semi-hierarchy with feedforward (ascending) projections and feedback (descending) projections is apparent in the cat's heterotopic commissural (callosal) interconnections (see Rosenquist, 1985; Dreher, 1986; Kennedy et al., Chapter 9).

There is growing evidence that associational interconnections within and between different areas of cerebral cortex are excitatory (see for reviews LeVay, 1988; Gilbert and Wiesel, 1989) and the main neurotransmitter involved is an excitatory amino acid, either glutamate or aspartate (see for reviews Fonnum, 1984; Hicks, 1987; Mayer and Westbrook, 1987). However, not much is known about the

functional role of the associational feedforward or feedback projections (for reviews see Dreher, 1986; Kennedy *et al.*, Chapter 9).

Finally, several extrastriate areas located along the lateral suprasylvian sulcus (AMLS, ALLS, PLLS) and EVA project directly to cortical area 6m, which is located on the medial aspect of the frontal lobe of the cerebral hemisphere in the vicinity of the cruciate sulcus (Olson and Jeffers, 1987). This area appears to constitute a part of cat's frontal eye field (Hassler, 1966a; Dreher *et al.*, 1970; Schlag and Schlag-Ray, 1970; Guitton and Mandl, 1987a,b). However, unlike in the rat, the frontal eye field in cats does not receive direct associational input from the primary visual cortex (Olson and Jeffers, 1987). The lack of direct connections between the primary visual cortex and the visuomotor frontal eye field (one of the presumed cortical endstations) is consistent with the idea that during mammalian evolution new visual areas have been inserted between the primary cortex and the cortex at the top of the processing hierarchy.

While uncertainties about how cat's visual cortex is subdivided and interconnected remain, it is clear that cat visual cortex contains a relatively large number of functionally distinct subdivisions, only a few of which are clearly homologous with those in rodents, tree shrews and primates (see below). Thus, cats have a complex visual system that resembles that of monkeys by having a large number of cortical visual areas. But many of these visual areas apparently evolved independently in the carnivore line. Studies on cats, therefore, provide strong evidence that the number of cortical visual areas has increased independently in different lines of mammalian evolution.

Visual Areas in Owl Monkeys

Owl monkeys are nocturnal New World monkeys that have a greatly expanded cortical visual system. We have used owl monkeys in experimental studies of the visual system because, as New World monkeys, they are likely to have a cortical organization that reflects the basic features of simian neocortex. Furthermore, as monkeys with relatively few cortical fissures, they are easier to investigate, and as nocturnal primates, they are less specialized for central (foveal) vision and therefore retinotopic patterns of organization in cortical fields can be more apparent in microelectrode mapping experiments. Another advantage of owl monkeys is that a number of somatosensory, motor and auditory regions of cortex have been experimentally defined so less cortex of uncertain function remains. Our studies indicate that the neocortex of owl monkeys contains roughly 20 visual and visuomotor areas (Kaas, 1986, 1988, 1989a). Some of these proposed subdivisions

(Fig. 8.7) have been well-defined by multiple criteria while others are based on more limited evidence. Future studies will undoubtedly redefine some regions by altering boundaries, adding new subdivisions, and perhaps even by eliminating some of the presently proposed fields.

In owl monkeys, V-I and V-II constitute easily defined distinct areas (Allman and Kaas, 1971b, 1974b; Tootell *et al.*, 1985; Krubitzer and Kaas, 1990c) which are probably homologous to those in most or all mammals. The middle temporal visual area, MT, of owl monkeys (Allman and Kaas, 1971a) is densely myelinated, receives major inputs from both areas 17 and 18, and projects directly and indirectly to posterior parietal cortex (Kaas and Lin, 1977; Lin *et al.*, 1982; Weller *et al.*, 1984). Because MT has been demonstrated in prosimian galagos and a number of other monkeys (see Krubitzer and Kaas, 1990c), it is likely to be common to all primates. MT has not been identified with certainty in any non-primate mammals, but there is some evidence, largely from connection patterns, that area OTm (Fig. 8.3) of tree shrews is a homologue of MT (Sesma *et al.*, 1984). If so, MT appears to have been displaced from a more primitive position along the outer border of V-II into the temporal lobe by the evolution and expansion of the dorsolateral visual area (DL) in primates.

In owl monkeys and other primates, and probably most mammals, almost all of the geniculate relay of visual information is to V-I (Kaas and Huerta, 1988). Area 17 or V-I, in turn, projects directly to all parts of three visual areas. Most of the outputs ($\sim 90\%$) are to V-II and MT. Most of the remaining outputs (Lin *et al.*, 1982; Krubitzer and Kaas, 1990b) are to a visual area on the border of the dorsomedial part of V-II, the dorsomedial area, DM (Allman and Kaas, 1975). DM contains a complete and systematic representation of the contralateral visual hemifield, is densely myelinated, receives additional inputs from V-II, and relays largely to MT and the ventral portion of posterior parietal cortex, VPP (Wagor *et al.*, 1975; Krubitzer and Kaas, 1990c). A projection from area 17 to the location corresponding to that of DM has been demonstrated in a range of primates, including galagos and several species of New and Old World monkeys (see Krubitzer and Kaas, 1990b). This projection has been assumed to be in the dorsal portion of the proposed visual area, V3, in macaque monkeys (see Burkhalter *et al.*, 1986), but we propose that the projection to this location in all primates is to DM (see below).

The part of V-I representing central vision projects to part of a fourth visual area, the dorsolateral visual area, DL, which represents the lower visual quadrant medially and the upper visual quadrant laterally (Allman and Kaas, 1974b). Only the caudal half of DL receives dense inputs from V-II (Cusick and Kaas, 1988a). This argues that caudal DL (DLc) and rostral DL (DLr) constitute two separate areas. Since receptive fields are large for neurones
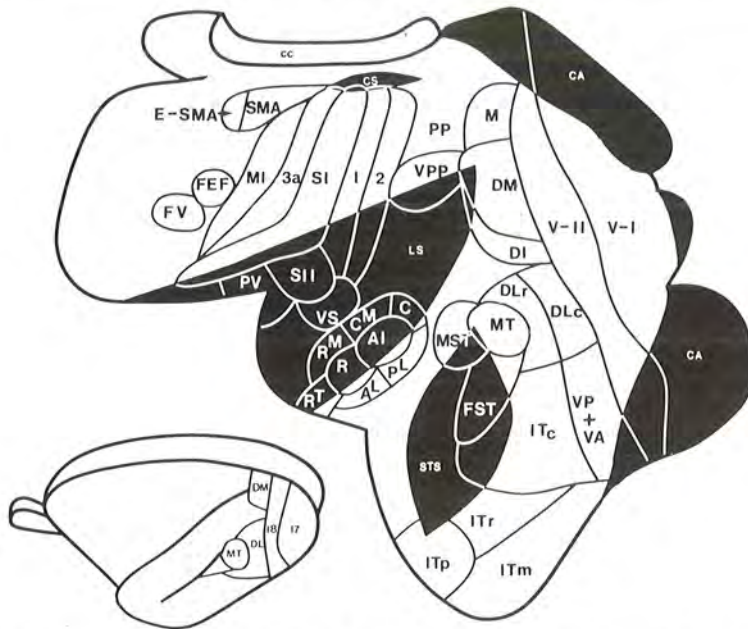
Fig. 8.7 *Visual cortex in owl monkeys. Owl monkeys are New World monkeys with the advantage of few brain fissures. Cortical areas are indicated on the upper right on a dorsolateral view of the brain on the lower left and on the surface view of the unfolded and flattened cortex. Proposed subdivisions have been established with varying degrees of certainty (see text). They include the first and second visual areas, V-I and V-II or areas 17 and 18, rostral and caudal divisions of the dorsolateral complex, DLc and DLr, the dorsointermediate area, DI, dorsomedial area, DM, the medial area, M, the middle temporal area, MT, the middle superior temporal area, MST, the fundal superior temporal area, FST, the ventral posterior parietal area, VPP, the posterior parietal region, PP, the ventroposterior and ventral anterior complex, VP+VA, the temporal-parietal region, TP, caudal, rostral, medial and polar subdivisions of inferotemporal cortex, IT, the frontal eye field, FEF, frontal visual area, FV, and the eye portion of the supplementary motor area, E-SMA. The prostriata area, PS, is part of limbic cortex. CC, corpus callosum. For details on visual areas, see text. For somatosensory areas (3a, S-I or 3b, 1, 2, S-II, PV and VS) see Kaas et al., 1979; Cusick et al., 1989 and Krubitzer and Kaas, 1990a. For auditory areas see Morel et al., 1989.*

in DL, the electrophysiological evidence is largely consistent with the possibility of two parallel representations of the visual hemifield, one in DLc and one in DLr. In macaque monkeys, cortex in the same region has been called V4 or the V4 complex, but the locations of boundaries and subdivisions are presently uncertain (for example compare V4 in Van Essen, 1985 and Ungerleider and Desimone, 1986; however, see Gattass et al., 1988).

The medial area, M, is the only other visual area that has been completely mapped with microelectrodes in owl monkeys (Allman and Kaas, 1976). The representation of central vision in area M is relatively smaller than that in the other mapped areas. The probable homologue of area M has been called area PO in macaque monkeys (e.g. Colby et al., 1988). Recordings have been obtained from the dorsointermediate area, DI, but its organization has not been fully determined. Recordings have also demonstrated that cortex on the ventral surface of the cerebral hemisphere, just rostral to V-II, is retinotopically organized, but the details are not yet known. Limited

results, however, suggest the presence of separate ventroanterior and ventroposterior fields.

The middle superior temporal area, MST, and the fundal area of the superior temporal sulcus, FST, are projection targets of MT that were formerly included within the superior temporal region, ST (Weller et al., 1984). More recent experiments, where cortex was processed after flattening, revealed two separate projection zones in two ovals of cortex of moderately dense myelination (Krubitzer and Kaas, 1990c). Since these two subdivisions were first defined by MT projections in macaque monkeys (Ungerleider and Desimone, 1986), we use terms introduced for macaque monkeys. The VPP is an oval of moderately myelinated cortex within the posterior parietal cortex that receives the major outputs of DM (Krubitzer and Kaas, 1990b). The caudal, rostral, medial and polar regions of inferior temporal cortex are subdivisions defined by patterns of connections and architectonic differences (Weller and Kaas, 1985, 1987). Finally, the temporal parietal region, TP, is responsive to visual stimuli

and has connections with other subdivisions of visual cortex.

Besides areas of predominantly visual functions in the occipital, temporal and parietal lobes, at least three regions of frontal cortex are visual or visuomotor in function. These include the well-known frontal eye field, which exists in owl monkeys and probably all primates (see Huerta *et al.*, 1987). In addition, the rostral part of the supplementary motor area (E-SMA) is involved in producing eye movements (Gould *et al.*, 1986; Schlag and Schlag-Rey, 1987; Huerta and Kaas, 1990). Finally, the frontal ventral area, FV, just ventral to FEF, receives inputs from a number of visual areas including MT (Kaas and Krubitzer, 1988). FEF, FV and E-SMA are interconnected with each other and probably have a close functional relationship.

Visual Cortex in Other Primates

Our basic contention is that primates have a number of visual areas in common. Fig. 8.8 illustrates the locations of several proposed subdivisions of cortex on dorsolateral views of the brains of prosimian galagos, marmosets (as representatives of the most primitive branch of New World monkeys – Callitrichidae), and squirrel monkeys, a member of the larger ceboid radiation of New World monkeys. We conclude that all of these primates have visual areas V-I, V-II, DL, MT, DI, DM, MST and FST (Krubitzer and Kaas, 1990b). The evidence for these fields is based on architectonic similarities and on patterns of connections. In all of these primates, V-I projects to V-II, MT, DM and part of DL. V-II projects mainly to caudal DL and to MT and DM. MT receives inputs from modules of neurones (see below) in V-I and V-II and projects to MST and FST.

Together, these eight visual areas occupy 30–40% of neocortex in owl monkeys, squirrel monkeys, marmosets and galagos (Fig. 8.9). V-I is obviously the largest visual area, constituting about 15% of neocortex. V-II is about half the size of V-I. DL is somewhat difficult to delimit, but it is the next largest visual area. The other visual areas are relatively small. The eight visual areas occupy slightly more of the neocortex in the diurnal primates (marmosets and squirrel monkeys) than in the noctural primates (owl monkeys and galagos), and striate cortex, area 18, and DL account for most of this difference. These areas are critical stations in the processing of object vision (Ungerleider and Mishkin, 1982). The proportional sizes of the visual areas presumably involved in visual attention and tracking (MT, MST, FST and DM) are similar in the nocturnal and diurnal primates.

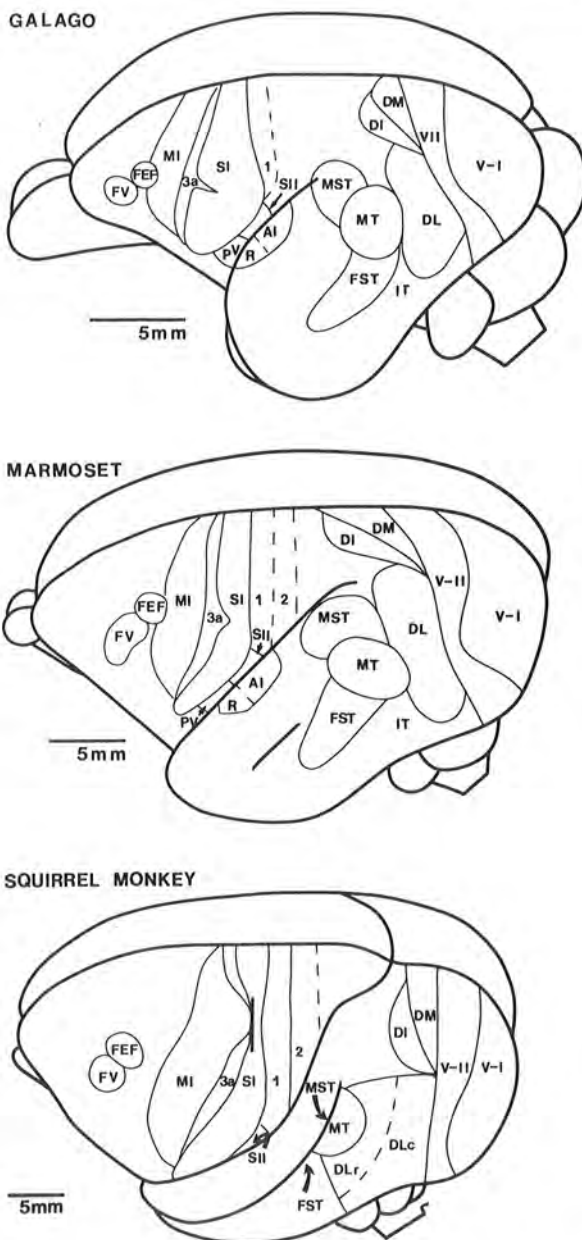Besides the eight visual areas identified, these and other

Fig. 8.8 *Some of the visual areas in prosimian galagos and New World marmosets and squirrel monkeys. Areas were identified by myeloarchitecture and connection patterns (see Krubitzer and Kaas, 1990c). All these primates appear to have first (V-I) and second (V-II) visual areas, dorsolateral (DL), dorsointermediate (DI), and dorsomedial (DM) visual areas, and middle temporal (MT), medial superior temporal (MST) and fundal superior temporal (FST) visual areas. Note also the frontal eye field (FEF) and the frontal visual area (FV). Auditory (AI and R), somatosensory (3a, SI or 3b, 1 and 2) and motor (M-I) areas are also indicated (see Sur et al., 1980, 1982; Luethke et al., 1989; Krubitzer and Kaas, 1990c).*
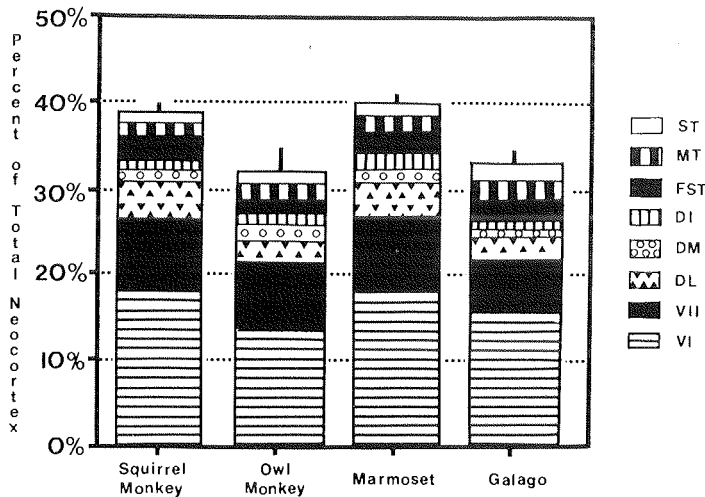
Fig. 8.9 *The surface of proposed subdivisions of visual cortex as percentages of the total surface area of cortex. Even though the four primate species considered occupy different behavioural niches (diurnal squirrel and marmoset monkeys; nocturnal owl monkeys and galagos), and both prosimian and different simian branches of primate evolution, the relative sizes of visual areas are remarkably constant. Values are based on measurements taken from cytoarchitectonic fields in brain sections from manually flattened cortex. ST corresponds to area MST of Krubitzer and Kaas, 1990c.*

primates probably share other visual areas as well. For example, projections to the caudal part of inferotemporal cortex suggest that ITc is basic to these primates, and MT projects to part of posterior parietal cortex that appears to be VPP. In addition, all these primates have a frontal eye field, a frontal visual area, and probably an eye movement portion of the supplementary motor area.

Comparisons of visual cortex organization in Old World monkeys with New World monkeys have been complicated by the difficulty of determining the relative positions of proposed subdivisions in cortex of the more fissured brains of Old World monkeys. It can be difficult to compare results across species or even across cases of the same species when data are portrayed on brain sections of various planes and angles. This problem has been greatly reduced by efforts to illustrate data on surface-views of unfolded cortex as reconstructed from serial brain sections (e.g. see Van Essen, 1985; Ungerleider and Desimone, 1986). However, such reconstructions may produce considerable distortion in spatial relationships, especially in local details. An alternative is to manually flatten cortex. This produces little distortion, but splits are often necessary to achieve a flat surface. While it is obviously more difficult to manually flatten the cortex of a large brain with many fissures, we have been able to do so with the brains of Old World talapoin and macaque monkeys. In these primates, we have used cytoarchitectonic distinctions and connectional patterns in the brains we flatten so that the shape and spatial arrangements of proposed fields can be most accurately determined and compared with other pri-

mates. Results for a talapoin monkey are shown in Fig. 8.10. We find the arrangement of areas in the flattened cortex of macaque monkeys to be very similar to that of talapoin monkeys.

As in other primates, V-I, or area 17, and V-II, or area 18, are very distinct and easily identified on cytoarchitectonic grounds in both talapoin and macaque monkeys. MT is also apparent as a densely myelinated oval of cortex. As in other primates, in talapoins (Kaas and Krubitzer, 1990) and macaque monkeys (e.g. Weller and Kaas, 1983; see Perkel *et al.*, 1986 for a description of other cortical connections of V-I in macaques) most of the outputs of V-I are to V-II and MT. Other projections of V-I in both talapoins and macaque monkeys are to a wedge of myelinated cortex on the dorsomedial border of V-II that we identify as DM. The usual interpretation of this projection of V-I in macaque monkeys is that it is to 'V3', a visual area originally postulated (e.g. Cragg, 1969; Zeki, 1969) to border most or all of 'V2' (V-II). V3 was thought to be retinotopically organized as a mirror image of the representation in 'V2'. Subsequent studies failed to demonstrate connection patterns that are compatible with the concept of V3, and instead a 'dorsal V3', with input from V-I, and ventral V3 or a ventroposterior area (VP), without input from V-I have been proposed (see Burkhalter *et al.*, 1986; however, see Gattass *et al.*, 1988).

As a further complication, a field very much like DM in terms of location and retinotopic organization, area 'V3a', has been described as just rostral to dorsal 'V3'. The area V3a was first described as outside the V-I projection zone
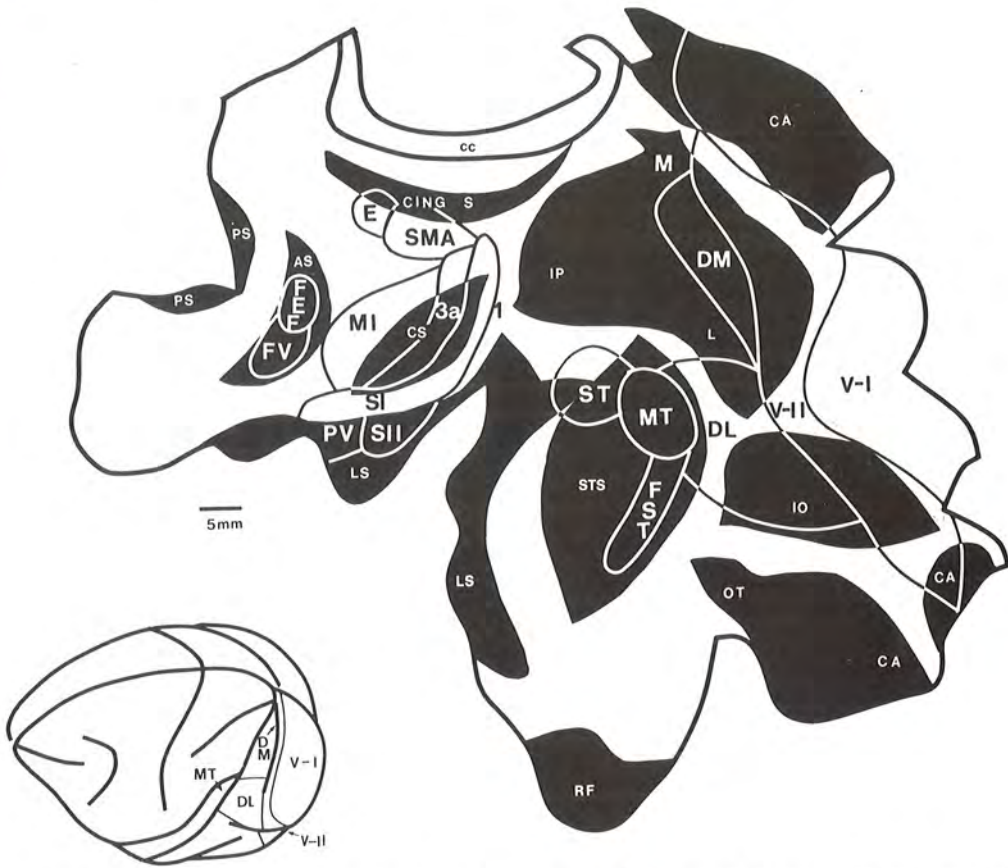
Fig. 8.10 *Some visual areas in the small Old World talapoin monkey. The small brain, with relatively shallow fissures, is easier to flatten than brains of most Old World monkeys. A dorsolateral view of the brain on the lower left has several fissures. On the upper right, fissures have been opened and cortex has been flattened by splitting V–I and surrounding cortex. Black regions indicate cortex normally buried in fissures. Visual areas were located by cytoarchitecture and connections. Borders of DL are approximate. Sulci are as follows: AS, arcuate sulcus; CA, calcarine sulcus; CS, central sulcus; Cing. S, cingulate sulcus, IO, inferior occipital sulcus; IP, intraparietal sulcus, lunate sulcus; LS, lateral sulcus; OT, occipitotemporal sulcus; PS, principal sulcus; CC, corpus callosum. See Figs. 8.5 and 8.6 for other visual areas. (Based on Kaas and Krubitzer, 1990).*

(Zeki, 1978), but was later included within the V–I projection zone (Zeki, 1980; Van Essen *et al.*, 1986). To us, the more supportable and parsimonious hypothesis is that DM is a visual area common to a wide range of primates, including Old World monkeys, and that much or all of the dorsal V3 and V3a regions in macaque monkeys are parts of DM. If so, it should be possible to demonstrate additional similarities in the DM region across primates.

There is evidence that other visual areas of New World monkeys and prosimians have homologues in Old World monkeys. The 'V4' area of macaque monkeys (cortex with inputs from V2 (Zeki, 1971)) is in the position corresponding to area DL, and DLc has dense inputs from V–II and provides the major visual inputs to caudal inferotemporal cortex (Cusick and Kaas, 1988a). However, the full extent and location of 'V4' and the components of the 'V4 com-

plex' (Van Essen and Zeki, 1978) are uncertain, and the proposed extent varies considerably (for example, compare V4 in Van Essen, 1985; Ungerleider and Desimone, 1986 and Gattass *et al.*, 1988). Our definition of DL in talapoin monkeys is based on myeloarchitecture and it corresponds in location to DL in New World monkeys, where borders have been experimentally identified (Allman and Kaas, 1974a; Cusick and Kaas, 1988a; Krubitzer and Kaas, 1990b). V–II projections are to caudal DL in talapoin, providing evidence for caudal and rostral subdivisions. However, further efforts are needed to delimit these fields. Areas MST and FST, as distinguished in macaque monkeys by Ungerleider and Desimone (1986), can be identified in talapoins, as well as other primates, and the area described as PO in macaques is likely to be a homologue of area M (see Colby *et al.*, 1988).

Finally, Old World monkeys have frontal eye fields, a frontal ventral area and an eye movement portion of the supplementary motor area (see Huerta *et al.*, 1987; Huerta and Kaas, 1990), and these are likely to be visual areas in parietal and temporal cortex which are homologous with those in New World monkeys. Further research is needed to identify valid subdivisions of visual cortex in all primates and to establish probable homologues.

We are less certain how primate species differ. The number of proposed extrastriate visual areas for macaque monkeys has increased over the last several years up to a recent count of about 30, with roughly 235 interconnections (Felleman and Van Essen, 1989). Given the relatively large size of neocortex and the complexity of visual behaviour in Old World monkeys, it is likely that they do indeed possess more visual areas than their New World cousins. However, the experimental evidence for the existence of most proposed cortical fields is presently limited.

Processing Hierarchies

The concept of serial processing across subdivisions of the visual system is longstanding, going back to early ideas of a primary or sensory field feeding into a psychic or perceptual field or fields and then to association cortex (e.g. Campbell, 1905). This concept was based on evidence that lesions of area 17 in humans have devastating effects on object vision, while extrastriate lesions alter vision in more subtle ways. A complication revealed by modern techniques is that connections between cortical areas are commonly reciprocal and thus information flows both ways. In addition, laminar patterns of cells of origin and termination have been found to vary. In particular, the output of area 17 largely originates from layer 3 neurones and terminates largely in layer 4 of other fields, while projections from the target fields originate from neurones both above and below layer 4 and terminate both above, largely in layer 1, and below layer 4 in area 17. The general significance of these differences in laminar patterns was stressed by Rockland and Pandya (1979) when they postulated that the rostrally directed pattern 'may relay sensory information from the primary cortical region to successively higher order sensory areas, while feedback modulation may be provided by the caudally directed system'. This general principle received experimental support from studies showing that neurones in V-II of monkeys are dependent on inputs from V-I, while the response properties of neurones in V-I are only altered but not abolished by deactivating V-II (Schiller and Malpeli, 1977; Sandell and Schiller, 1982; Girard and Bullier, 1989). More recently, evidence has been presented that neurones in MT depend on inputs from V-I for activation (Krubitzer and Kaas,

1989c; Maunsell *et al.*, 1990; however see Rodman *et al.*, 1989). Thus, there is value in following the lead of Maunsell and Van Essen (1983) in constructing processing hierarchies of visual areas using feedforward projections to determine the level of each area. Such a hierarchy is shown for visual areas in owl monkeys in Fig. 8.11. The proposed network incorporates some of the modular components of the LGNd, V-I and V-II, recognizes obvious sequences such as V-I, V-II, DL and IT, and reflects components of the 'two cortical visual systems' of Ungerleider and Mishkin (1982; also see Morel and Bullier, 1990). The construction of hierarchical models is useful because it
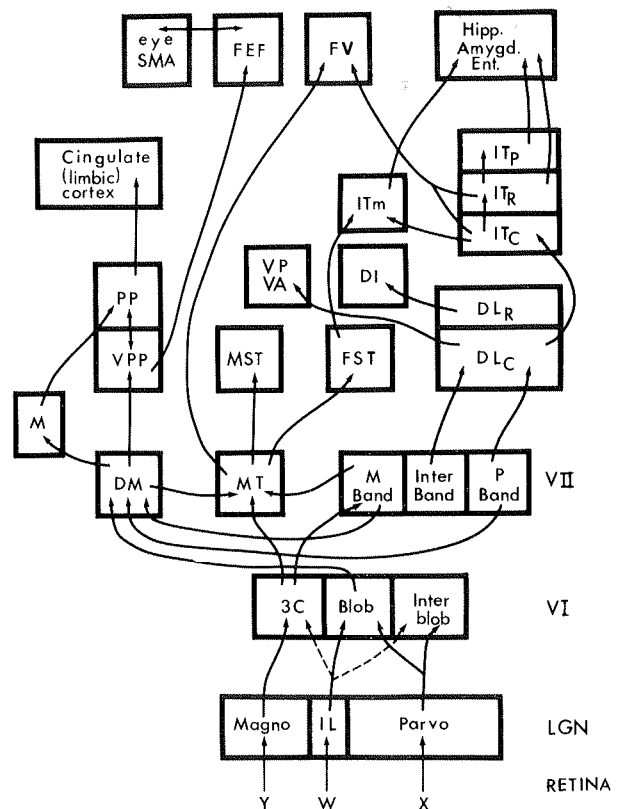

Fig. 8.11 *A processing hierarchy for visual areas in owl monkeys. This greatly simplified outline emphasizes major feedforward connections, but does not include many other known connections, and the total connection pattern has not been adequately investigated. Separate Y, W and X streams, originating from distinct classes of ganglion cells in the retina, terminate in magnocellular, interlaminar or parvocellular regions of the lateral geniculate nucleus, and, after a relay in layer IV, activate layer 3c (of Hassler, 1966), cytochrome oxidase blobs, or both blob and interblob regions (see Kaas and Huerta, 1988 for review). References for subsequent cortical relays are provided in the text. See Fig. 8.7 for areas and abbreviations.*

summarizes conclusions and suggests experiments (such as determining the effects of removing MT on neurones in MST and FST). However, the hierarchy is potentially misleading in that it fails to represent the full complexity of the system, and it implies that our understanding of functional relationships between areas is fairly predictable from the connection patterns.

The summary in Fig. 8.11 is a simplification in that only a small fraction of the total connections are included. First, the connections of some areas have not been adequately determined. Second, to avoid providing a complicated maze, only major pathways are included. Most areas connect densely with two to five areas of the same hemisphere and two to three of the opposite hemisphere. Many more sparse connections exist. Each area also projects subcortically to parts of the pulvinar complex (Graham *et al.*, 1979) which in turn relay to cortical fields, providing other routes of interaction. Third, higher fields typically have inputs from several earlier levels, making it difficult to determine, without experimental evidence, the impact of each input. For example, should MT be placed at a second level, as in Fig. 8.11, because it has direct input from V-I, at a third level, as placed by Maunsell and Van Essen (1983), because it has input from V-II, or at a higher level, because it has inputs from DLr and DM? The answer is not obvious from the connection patterns alone, and studies on the contributions of various inputs to a cortical area are needed (see Garraghty *et al.*, 1990 for review). Finally, connection patterns between fields reflect a range of laminar arrangements (e.g. Weller and Kaas, 1982), so that 'intermediate' rather than feedforward and feedback patterns are common. This obviously complicates attempts to deduce function from patterns of connections.

Modular Organization of Visual Areas in Primates

The concept that areas are subdivided into different sets of functionally distinct processing columns or modules has dominated much of the thinking about cortical organization for the last 20 years, and yet compelling evidence to support this idea has been surprisingly limited until recently (see Kaas, 1990 for review). Now there is considerable evidence that possibly in all primates, magnocellular and parvocellular streams from the dorsal lateral geniculate nucleus remain largely segregated in V-I, and that the parvocellular stream further subdivides into two channels (see Livingstone and Hubel, 1988). In brief, the magnocellular and parvocellular inputs terminate in upper and lower sublayers of layer IV, respectively (we use Hassler's (1966b) designations of layers rather than Brodmann's (1909)), and relay to lower (3c) or upper (3b) parts

of layers III, respectively. Layer 3c neurones in the magnocullular stream project to MT and band-like modules in V-II (Fig. 8.12). Layer 3b is divided into functionally distinct regions that can be conveniently distinguished by differences in the density of cytochrome oxidase (CO) (see Horton, 1984) or myelin (Krubitzer and Kaas, 1989a). CO dense 'blobs', which are myelin poor, receive direct input from the W-cells of the interlaminar regions of the dorsal lateral geniculate nucleus (Fitzpatrick *et al.*, 1983), and contain neurones activated by the parvocellular channels that are more responsive to colour and less responsive to stimulus orientation than the neurones in the interblob regions (e.g. Livingstone and Hubel, 1984). Neurones in blobs project to DM (Krubitzer and Kaas, 1990b), and to specific CO dense bands of neurones in V-II (Livingstone and Hubel, 1984). The interblob regions, also in the parvocellular stream, project to CO light interbands in V-II. The CO blobs are also distinguished by having more widespread intrinsic connections than interblob regions (Fig. 8.13; Livingstone and Hubel, 1984; Cusick and Kaas, 1988b) and, in some primates, more widespread callosal connections (Cusick *et al.*, 1984). Thus, three types of processing and outputs are segregated in V-I in 'modules' of quite different shapes; blobs, surrounds and layers. It is likely that all primates have these modules, since the laminar segregation of magnocellular and parvocellular inputs and CO blobs are features that have been demonstrated in a wide range of species.

Segregation of neurones by preference for certain stimulus orientations, the 'orientation columns' (e.g. Hubel and Wiesel, 1977), may be a common feature of organization in area 17 (Humphrey *et al.*, 1980), while segregation by eye of dominant activation, the ocular dominance columns, is a variable feature of area 17 in primates (Florence *et al.*, 1986).

Area V-II of all primates also is modularly organized. As noted above, area V-II of monkeys contains CO and myelin dense bands that cross the width of the field and are separated by interbands that are CO light and myelin dense (see De Yoe and Van Essen, 1985, 1988; Shipp and Zeki, 1985; Livingstone and Hubel, 1988; Krubitzer and Kaas, 1989a). In macaque monkeys, every other CO dense band often appears to be thicker, and the thick CO dense bands are thought to be the ones with inputs from the magnocellular streams in V-I. The thicker bands also project to MT. The interbands and thin bands are thought to receive inputs from the interblob (Pi) and blob (Pb) parvocellular streams, respectively, and both project to DL. The difference in thickness of CO dense bands in New World monkeys is not always obvious, and the thinner bands may be the ones projecting to MT (Krubitzer and Kaas, 1989a). In galagos, CO dense bands are only weakly apparent, and yet alternating band-like strips of neurones project to MT or to DL, as in monkeys (Krubitzer and

Kaas, 1990c). Thus, all examined primates appear to have three types of modules in V–II that are band-like in shape, and alternate in a regular manner, but they might vary in thickness and in the density of the CO reaction across species.

Little is known about how other visual areas might be modularly organized. However, CO reactions and myelin stains reveal uneven densities in many fields, suggesting a mosaic of functionally distinct modules. This possibility is further supported by the patchy distribution of cortical,
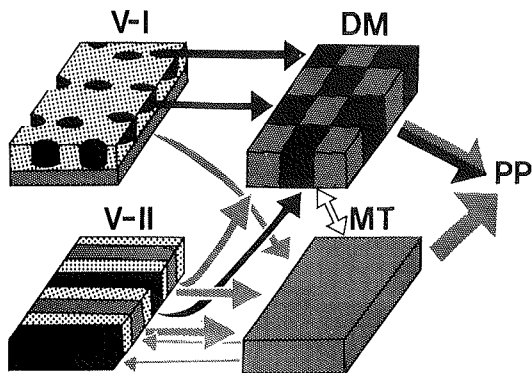

Fig. 8.12 *Some of the modular connections of visual areas V-I, V-II and DM of owl monkeys. In V-I, layer 3c of the magnocellular stream projects to MT and to one set of alternating cytochrome oxidase (CO) dense bands in V-II. CO dense blobs in V-I project to DM and to the other set of CO dense bands in V-II. The interblob regions of V-I project to the CO interbands of V-II. (Based on Krubitzer and Kaas, 1990b,c.)*
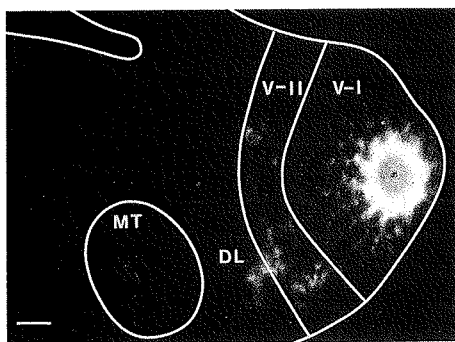
thalamic and callosal connections. Thus, it is likely that, as for V-I and V-II, many or most visual areas contain multiple, fractionated, interdigitated and functionally distinct maps of receptor surfaces.

The existence of modules in areas V-I and V-II, with distinct patterns of connections with other modules, and other visual areas, is consistent with the view that aspects of visual function are isolated and functions are computed in multiple processing streams (see De Yoe and Van Essen, 1988; Livingstone and Hubel, 1988). However, subsystems within the visual system are also interconnected in ways that allow interactions that might be important in unifying perception or creating opportunities for additional calculations. The multiple inputs each visual area receives from other visual areas provide an obvious substrate for functional integration. Another is in the merging of the outputs of different modules, such as the projections of both parvocellular and magnocellular streams from modules in V-I and V-II to DM (Krubitzer and Kaas, 1990c). A third substrate for integration is the feedback projection system, which is not only to modules providing inputs, but also to modules in addition to those providing the feedforward projections. For example, MT receives feedforward projections from one set of CO dense bands in V-II, while feedback projections terminate on both sets of CO dense bands (Krubitzer and Kaas, 1989a). Feedback projections from MT to V-I are also more broadly distributed than the output sources (Shipp and Zeki, 1989a). Thus, feedback projections influence neurones that are parts of other processing streams, and an important function of feedback connections may be to integrate information across diverging streams.

Fig. 8.13 *Some intrinsic and extrinsic connections of V-1 in a prosimian primate, galago. An injection of tracer in V-I reveals a pinwheel of foci interconnected with the injection site. The foci overlap the CO dense blobs. Patchy regions of interconnections are also found in V-II, MT and DM (not apparent). The patchy pattern of the connections suggests the segregation of functionally distinct groups of neurones (modules) in the visual areas. Cortex has been cut parallel to the flattened surface. A darkfield photomicrograph. Scale bar = 1 mm. (From studies described by Cusick and Kaas, 1988b.)*

Conclusions

The central issue of this chapter is how extrastriate cortex is subdivided in mammals. The question has not been fully answered, but modern experimental approaches are providing the beginnings of an understanding. This understanding incorporates the longstanding concept that cortex is divided into regions of distinct and differing functions, the cortical areas, and the more recent concept of smaller parts within areas, the cortical modules. In many ways, current proposals on how cortex is subdivided across species differ considerably from traditional proposals.

1. Mice and other mammals with small brains and little neocortex have only a few visual areas. These include V-I and V-II, and probably two to three other fields in temporal cortex. These few areas must be 'general purpose areas', and direct connections with motivation, memory

and motor centres are expected, and to some extent have been demonstrated.

2. Mammals with large brains and expanded cortex have larger numbers of visual areas, perhaps as many as 15 in cats and 20 or more in some primates. These include V-I and V-II and probably two to three other fields that are parts of the basic mammalian plan. Because numbers of areas have increased independently in separate lines of descent, most of the other fields in complex brains of separate lines are not homologous. However, because the mechanisms and ways of increasing numbers of fields may be limited, and useful functions may be similar, comparable organizations may have been independently acquired in different species. The organizations of the moderately expanded extrastriate visual systems of tree shrews and squirrels appear to be at least superficially similar, probably as a result of parallel elaborations of the basic mammalian organization.

3. Most of all visual areas contain functionally distinct modules, such as those demonstrated in V-I and V-II of primates. Connections between visual areas are typically uneven, with a given location in one field projecting to several closely spaced locations in other fields. If cortical areas are functionally homogeneous, a simple connection pattern would be expected. However, patchy, complex connection patterns are consistently observed and they provide evidence for modules. Nevertheless, except for V-I and V-II, more direct evidence is limited.

4. Connection patterns can be used to place areas at various levels in semi-hierarchical sequences. However, these sequences are complex in that each area is influenced by inputs from a number of other visual areas via direct feedforward, intermediate and feedback connections, and by interactions with thalamic and other subcortical structures. As a result, there can be uncertainties about the presumed significance of any set of connections, as well as the presumed level of an area in a hierarchy. To date, there have been only a few experimental attempts to evaluate the contribution of specific connections to the response properties of neurones.

5. Connections reflect both topographic and modular features of cortical areas. Thus, parts of visual areas devoted to central (frontal) vision preferentially interconnect with parts of other visual areas that are devoted to central vision. Yet, connections are topographically divergent, to a varying extent, and relate to specific subsets of grouped neurones (modules). The divergent and modular aspects of connection patterns complicate and may confound efforts to use such patterns to define cortical areas. Thus, parts of areas may be misidentified as complete areas.

6. Visual cortex of all primates is remarkably similar in a number of ways. All primates appear to have three major processing streams emerging from V-I and V-II, one reflecting the magnocellular pathway and two diverging from the parvocellular pathway. All primates appear to have area MT and subsequent stations (MST, FST and posterior parietal cortex) as major parts of the magnocellular stream and area DL (V4) and subdivisions of inferotemporal cortex as fields in the parvocellular streams.

There is evidence that area DM is also common to all or most primates, and this field may merge parvocellular and magnocellular streams. Finally, all primates appear to share visuomotor fields in the frontal lobe (FEF, FV and E-SMA).

Acknowledgements

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