7 Cortical Visual Areas in Mammals

Martin I. Sereno and John M. Allman

Introduction

The neocortex of all mammals consists primarily of a mosaic of visual, auditory, somatosensory and motor areas. In many mammals, visual cortex constitutes the largest of these four main subdivisions. In monkeys, visual areas occupy half of the total area of neocortex, including much of what had previously been labelled polymodal association cortex (Merzenich and Kaas, 1980; Allman, 1977; Maunsell and Newsome, 1987; Sereno, 1988; Felleman and Van Essen, 1989). The aim of this chapter is to provide an overview of the layout and topographic organization of cortical visual areas in rodents, cats, prosimian primates and New and Old World monkeys – the best-studied cortices to date. First, the criteria for defining a visual area are examined. Second, we discuss cortical areas in those groups, ending with recent attempts to explore human visual cortex. In the last section, we consider patterns of evolution of cortical areas in mammals.

Definition

Cortical areas are best defined and recognized across different species on the basis of multiple converging criteria (Allman and Kaas, 1971; Van Essen, 1985). We focus here on visual areas, but analogous considerations apply to auditory and somatosensory areas. The main criteria for defining and recognizing a visual area are (a) visuotopic organization, (b) architectonic features, (c) connection patterns, and (d) physiological properties.

Many visual areas show a degree of retinotopic order and a representation of a substantial part of the contralateral visual hemifield. The details of this retinotopy provide many characters for distinguishing areas. Perhaps most basic is the handedness of the visual field representation. V1, for example, contains a mirror-image representa-

tion of the visual hemifield when viewed from the cortical surface, while V2 contains a non-mirror-image representation. Receptive field size and receptive field scatter vary somewhat independently from area to area (see also Orban, chapter 8; LeVay and Nelson, chapter 11; Spear, chapter 13). The identity and handedness of contiguous areas constitute additional features. Areas often exhibit a characteristic pattern of discontinuities in the representation of the visual hemifield. The most common pattern is a discontinuity at the horizontal meridian (Allman and Kaas, 1974); other areas have additional discontinuities along isoeccentricity lines (Sereno et al., 1987). Some areas have substantial representations of the ipsilateral visual field (Gross, 1973). Finally, a few cortical regions appear to lack retinotopy altogether (despite containing neurones with well-defined retinal receptive fields); these regions are divided into areas using the other three criteria.

Visual areas were actually first recognized by their tangential and laminar architectonic features. Many areas can be distinguished by the pattern of intracortical myelination and by cell packing densities and sizes in particular cortical layers (see also Henry, chapter 9). There are many recently recognized histological features that vary from one cortical area to another, for example, density and pattern of cytochrome oxidase, the CAT-301 antigen, calcium-binding proteins, lectin binding sites (e.g. Tootell et al., 1985; DeYoe et al., 1985).

Each area is also characterized by the set of input and output regions in the neocortex, hippocampus, amygdala, striatum, dorsal thalamus, pretectum, layers of the superior colliculus and pontine nuclei. Each corticocortical connection is characterized by its laminar origins and its laminar targets (see also Henry, chapter 9). Corticocortical projection patterns are broadly divisible into feedforward connections whose main laminar target is layer 4 and feedback connections that avoid contacting cells in layer 4 (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983). Many intermediate patterns exist.

Finally, areas are recognized by their single-unit properties. For example, area MT in monkeys, area PMLS in cats, and area LL in rats all contain a higher portion of direction-selective cells than are found in the cortex between those areas and primary visual cortex. Other areas are distinguished by degree of attention-related modulation of response, presence of eye position signals, sensitivity to true pattern direction and speed, sensitivity to rotation and expansion, sensitivity to stimulus shape, colouring, structure, and so on (see also Spear, chapter 13 and Schall, chapter 15).

Areas differ radically in the degree to which these criteria have been explored. V1 (primary visual cortex) and MT (middle temporal visual area in primates) are distinct, well-studied areas that are convergently identified by most of these criteria.

Visual Cortical Areas of Different Mammal Groups

Rodents

Rodents have at least 13 visual areas. There are three groups of rodents – murines (e.g. rats, mice, hamsters), sciurumorphs (e.g. squirrels) and cavies (e.g. guinea pigs, *Octodon*). In all, V1 is the largest visual area, accounting for about 15% of the total neocortex. As a result of the lateral placement of the eyes, the binocular portion of V1 accounts for less than half of its total area. Deoxyglucose experiments in rats reveal functional ocular dominance patches in binocular V1 (Thurlow and Cooper, 1988).

In rats, there are multiple extrastriate visual areas adjoining both the vertical meridian representation of V1 (lateral), as well as the representation of the periphery (medial) (Fig. 7.1). Interpretation of connection patterns in the cortex is complicated by the tendency for projections from areas without discontinuities to areas with discontinuities to bifurcate near the discontinuity. The use of multiple tracers and explicit electrophysiological mapping confirm that substantial parts of the visual field are in fact re-represented from area to area in rats (Montero *et al.*, 1973; Olavarria and Montero, 1984; Thomas and Espinoza, 1987). Six areas adjoin V1 laterally – rostrolateral (RL), anterolateral (AL), lateromedial (LM), posterolateral (PL), posterior 1 and 2 (P1, P2). Three areas adjoin V1 medially – anterior (A), anteromedial (AM), and medial (M). Finally, there is a second tier of lateral areas – laterointermediate (LI), laterolateral (LL), and laterolateral anterior (LLa). There appears to be a hierarchy of visual areas in rats based on patterns of laminar origins and targets of corticocortical projections, as was originally described in primates. The first tier of lateral areas appear
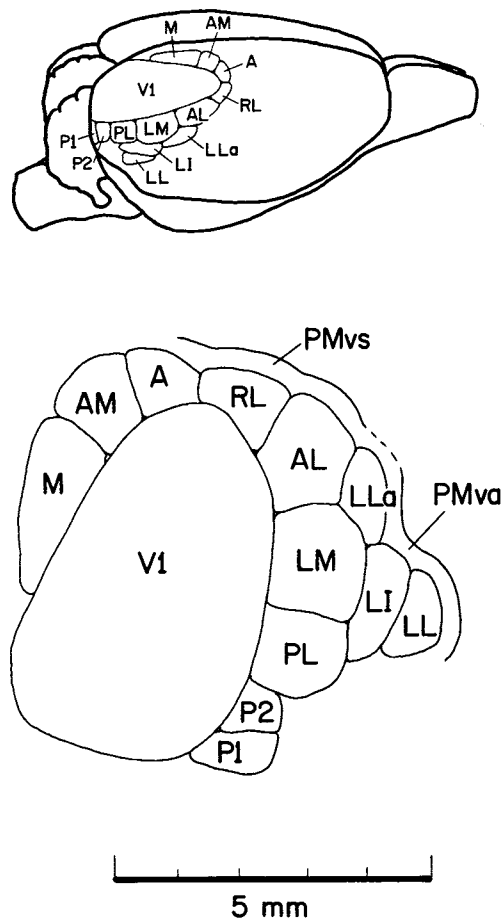

Fig. 7.1 *Visual cortical areas in the rat. Areal boundaries are based on maps* from Montero et al. (1973), Thomas and Espinoza (1987), and Sereno and Olavarria (unpublished). *They were drawn using the flat-mounted cortex (with striate cortex efferents and callosal connections labelled)* from Olavarria and Montero (1985, Fig. 3) *as a template. See Wagor et al. (1980) for a different interpretation of the lateral extrastriate areas. Abbreviations: A, anterior; AL, anterolateral, AM, anteromedial; LI, laterointermediate; LM, lateromedial; LL, laterolateral; LLa, laterolateral anterior; M, medial; PL, posterolateral; P1, posterior 1; P2, posterior 2; RL, rostrolateral; V1, striate cortex.*

to be one step above V1 and the medial areas appear to be one step above the first lateral tier (Coogan and Burkhalter, 1988). Receptive field size increases at each stage in the hierarchy, but there do not appear to be any non-retinotopic areas.

Many of the extrastriate areas in rodents are visually driven in the absence of V1 (Olavarria and Torrealba, 1978). There are extensive projections to rodent extrastriate visual areas from visual thalamic areas in the pulvinar (e.g. Takahashi, 1985), some of which receive input

from the superior colliculus. There is also a strong projection from the colliculus to the lateral geniculate. Small lesions in lateral extrastriate areas produce much larger deficits in difficult visuospatial tasks than do lesions in V1, again suggesting that extrastriate areas receive information in parallel with V1 in rodents (McDaniel *et al.*, 1982).

The rostral tip of visual area RL in rodents contains units with restricted visual receptive fields that also respond to stimulation of particular vibrissae; that is, both inputs are receptotopic. Laterally and posteriorly, there is a zone of visual-auditory overlap. These restricted overlap zones, observed both anatomically and physiologically, are about 500 μm wide. *Octodon degus*, a fossorial (digging) South American rodent (a cavy), appears very similar to the rat (Olavarria and Mende, 1979).

The large, well differentiated extrastriate visual cortex of the diurnal grey squirrel has not yet been electrophysiologically mapped in detail. Squirrels apparently have a single area adjoining much of the vertical meridan representation of V1 (Hall *et al.*, 1971). These mapping experiments also hinted that there is an additional area bordering the rostral part of the V1 vertical meridian, similar to rat area AL.

Hamsters and mice show a tendency for one elongated area (RL) to adjoin much of the lower field V1 vertical meridian (RL is small and ovoid in rats). It is as if RL has inserted itself in between the anterior part of AL and V1. This may be related to the origin of the single representation of the lower field (lower field V2) that adjoins the lower field vertical meridan representation of V1 in cats and primates (J. Olavarria, personal communication). A similar transition between an ovoid and an elongated shape for an area apparently occurred with area DM/V3 in New and Old World monkeys. Recently, it was pointed out that the lower visual field predominates in anterolateral areas in rats, while the upper field predominates in the posterolateral areas (Malach, 1989). In carnivores, primates, and perhaps squirrels, the underrepresented anterior upper fields and posterior lower fields may have been lost in the areas nearest V1.

Lagomorphs

The organization of visual areas in rabbits is quite similar to that in rodents. There is a binocular strip in V1 and multiple extrastriate areas adjoining both the vertical meridian and periphery of V1 (Woolsey *et al.*, 1973; Montero, 1981; Olavarria *et al.*, 1987). There appears to be only one extrastriate area adjoining much of the rostrally located lower field vertical meridian representation of V1; this differs from the situation in rats and *Octodon*, but is similar to that in mice, hamsters and squirrels.

Recordings from the binocular region of V1 in rabbits

with the eyes set in the 'freeze' position (Hughes and Vaney, 1982) result in receptive fields recorded through one eye that are displaced up to 20° horizontally from those recorded through the other eye. This suggests that rabbits (and perhaps rodents, sheep and many other mammals, but not carnivores and primates) have two functionally distinct viewing strategies. In the divergent 'freeze' position, the portion of the visual field seen by one eye hardly overlaps the portion seen by the other eye, while in the 'forward fixation' position, the eyes converge, so that the receptive fields for binocularly driven cells overlap. The binocular receptive fields in rabbits, rats, and other mammals may be generated in part by callosal connections (in additon to non-decussating axons in the optic tract as occurs in carnivores and primates).

Carnivores

Cats have several more visual areas than rodents – at least 19 (Fig. 7.2) (Rosenquist, 1985; Updyke, 1986). Extrastriate areas in cats also occupy a proportionally greater area of the total neocortex than in rodents. Unlike rodents, cats have a single visual area (area 18) adjoining the laterally placed vertical meridian representation of V1. However, the upper and lower field representations of 18 and 19 in cats are quite asymmetrical; the lower field representations are quite elongated, and show a tendency to exhibit secondary discontinuities (Tusa *et al.*, 1979) as well as several fingers of callosal inputs that pass through both areas (Olavarria and Van Sluyters, 1989). The periphery of the visual field beyond 50° eccentricity is represented in upper field area 19 but not in its lower field, or in either the upper or lower fields of area 18. These differences may possibly reflect the different evolutionary origins of the upper and lower field representations in V2/area 18. As with rodents, there are visual areas medial to V1, adjoining the representation of the periphery. The dorsally located lower field periphery of V1 is adjoined by area 21a. Cat area 18 is adjoined rostrally by a single area (area 19) in contrast to both rodents and primates (see below).

Rostral to area 19, there are a large number of smaller visual areas. One adjoins area 19's extreme lower field representation in the anterior part of the medial bank of the lateral sulcus (ALG), one extends onto the posterior part of the suprasylvian gyrus (area 7), one adjoins the centre of gaze of area 19 (area 21a), eight more extend into the suprasylian sulcus – posteriomedial lateral suprasylvian, rostral and caudal subdivisions (PMLSr, PMLSc), posterolateral lateral suprasylvian, rostral and caudal subdivisions (PLLSr, PLLSc), anteromedial lateral suprasylvian (AMLS), anterolateral lateral suprasylvian (ALLS), dorsal lateral suprasylvian (DLS) and ventral lateral suprasylvian (VLS) – and four more extend out onto the small inferotemporal region (areas 20a, 20b, 21b).
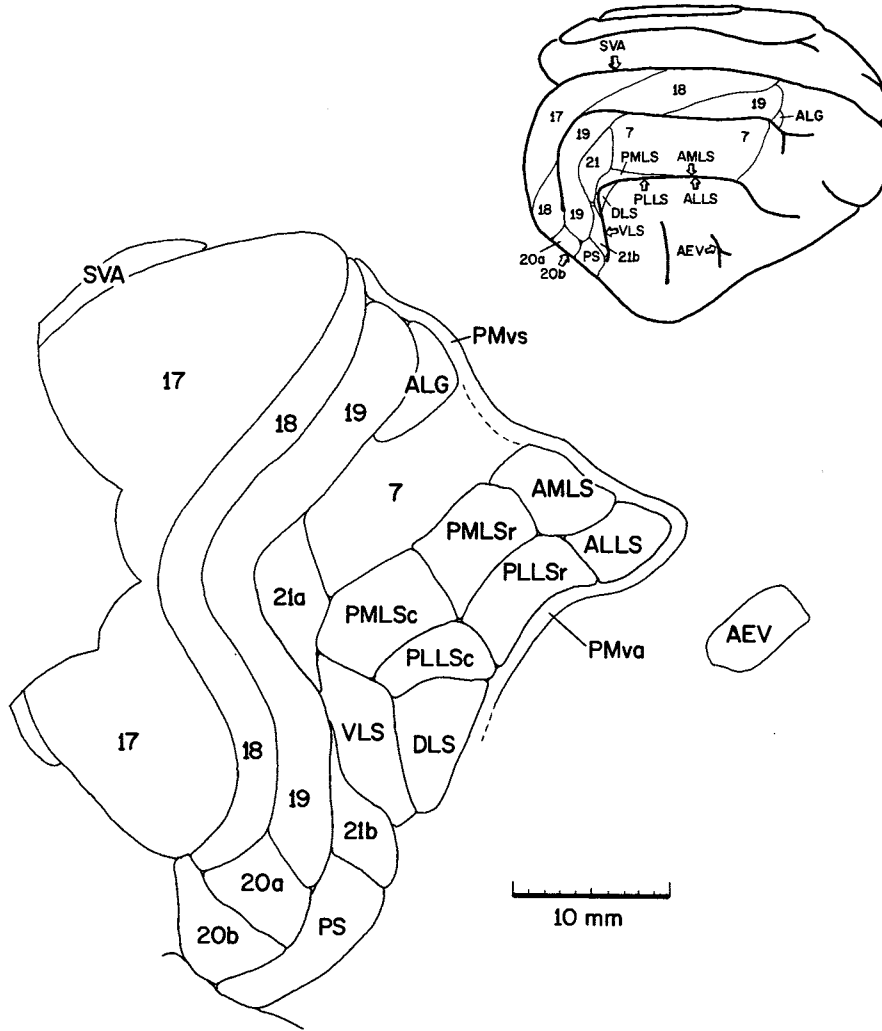
Fig. 7.2 *Visual cortical areas in the cat. Areal boundaries are based on maps* from Palmer *et al.* (1978), Tusa *et al.* (1979), Tusa and Palmer (1980), and Updyke (1986). *They were drawn using the myelin-stained flat-mounted cortex illustrated in Olavarria and Van Sluyters (1985, Fig. 3A) as a template. A cut was made in area 17 to allow the cortex to lie flat.* See Sherk (1986) *for a different interpretation of the lateral suprasylvian areas. Abbreviations: AEV, anterior ectosylvian visual; ALG, anterior lateral gyrus; ALLS, anterolateral lateral suprasylvian; AMLS, anteromedial lateral suprasylvian; PMva, polymodal visual-auditory; PMvs, polymodal visual-somatosensory; PLLS, posterolateral lateral suprasylvian (c and r, caudal and rostral subdivisions); PMLS, posteromedial lateral suprasylvian (c and r, caudal and rostral subdivisions); PS, posterior suprasylvian; SVA, splenial visual areas; VLS, ventral lateral suprasylvian; 17, striate cortex.*

Finally, there is a small visual area located in the anterior ectosylvian region (AEV), rostral to auditory areas, and near the face representation in primary somatosensory cortex. Unlike all other visual cortical areas, AEV is surrounded entirely by non-visual cortical areas. Whether there is a visual area in a homologous position in other mammals is an open question. Receptive field size generally increases in the more rostral visual areas, but as with rodents, there are few non-retinotopic areas; only area 7 appears to lack any topography. As in rodents, the zone of

overlap between modalities (e.g. the lateral border of AMLS overlaps auditory cortex) is small; multi-modal cells in this zone have restricted excitatory receptive fields (Palmer *et al.*, 1978).

As in rats, there appears to be a rough hierarchy of areas; this is complicated by the partly orthogonal separation of information into X, Y and W cell streams (Stone, 1983). Area 17 receives X, Y and W input via the A and C laminae of the dLGN, area 18 receives Y input via the A laminae, some W inputs via the C laminae, and input from

MIN, and area 19 and the lateral suprasylvian areas receive mostly input from several classes of W cells via the C laminae and the geniculate wing. Receptive fields in area 19 are smaller than those in area 18, also arguing against a straightforward 17→18→19 hierarchy. Areas 20a, 20b, 21a, 21b and AEV, however, receive much weaker direct input from the dLGN, suggesting that they may be at a higher level in a processing hierarchy. There is a dorsally located, heavily myelinated area (PMLS) that contains many direction-selective cells (Spear and Baumann, 1975). Finally, as in rats, much of extrastriate cortex remains active in the absence of V1 (Dreher and Cottee, 1975).

Primates

Prosimians

The first primates were probably nocturnal, judging from the large size of their orbits (Allman, 1977; see also Szalay and Delson, 1979; Schwartz, 1986). The primates living today that are most closely related to these early primates are mostly nocturnal or crepuscular, and most have a tapetum. In the galago, the only prosimian primate examined in detail, there are at least 14 visual area (Allman and McGuinness, 1983; unpublished studies). V1 projects directly only to V2 and MT (Symonds and Kaas, 1978). There are multiple areas adjoining the anterior border of V1 (V2 upper and lower field, and a small area intercalated into the upper field representation of V2 that contains both upper and lower fields). Galagos have a clearly defined, heavily myelinated MT with a non-mirror-image hemifield representation oriented so that the representation of the fovea is the most posterior. There appear to be three additional areas in between the dorsal, lower visual field representation in V2 and area MT. As in rodents and cats, all visual areas in galagos exhibit a substantial degree of retinotopic organization, including areas in anterior inferotemporal cortex. The border between the different modalities appears to be as sharp in galagos as in rats — there is a diminuitive strip on the anterior border of visual cortex less than 1 mm wide that responds to visual and somatosensory stimuli dorsally, and visual and auditory stimuli ventrally.

Recent evidence (Krubitzer and Kaas, 1988) suggests that the subdivision of information into parallel streams, signified in V1 by the presence of cytochrome oxidase blobs (see below), may be present in subsequent corticocortical projections in galagos, despite the lack of obvious cytochrome oxidase stripes in galago V2. Other prosimian primates (e.g. tarsiers and lemurs) even lack cytochrome oxidase blobs in V1 (McGuinness *et al.*, 1986); but it is not yet known whether this signifies a lack of functional streams in V1 in these animals.

New World Monkeys

Monkeys (anthropoids) are thought to have diverged from the ancestors of galagos at least 40 million years ago (Szalay and Delson, 1979). All but one of the anthropoids are diurnal (a derived character for primates) suggesting that day-living habits evolved early in the monkey lineage. The only nocturnal monkey, the New World owl monkey, lacks a cellular tapetum like that found in many prosimians, suggesting that its ancestors had diurnal habits. Fig. 7.3 shows a summary map of 24 postcentral visual areas in the owl monkey (Allman, 1977; Sereno *et al.*, 1986, 1987; Weller *et al.*, 1984; Weller and Kaas, 1985, 1987; Sereno *et al.*, unpublished studies). V1 is adjoined by a single, continuous visual area, V2. Upper and lower field V1 projects directly to V2 and MT, but lower field V1 also projects to a second, densely myelinated area directly adjoining the eccentric lower field representation in V2 (area DM) (Lin *et al.*, 1982). There are three areas between the central lower field representation in V2 and area MT (dorsolateral posterior (DLp), dorsolateral intermediate (DLi) and dorsolateral anterior (DLa)).

There appear to be at least three somewhat separate streams of information passing through V1 and V2 (the magnocellular, parvocellular interblob and parvocellular blob streams) that remain somewhat separated as one moves on to higher areas, as originally described in the macaque monkey (Ungerleider and Mishkin, 1982; Livingstone, and Hubel, 1984; Fitzpatrick *et al.*, 1985; DeYoe and Van Essen, 1988; Zeki and Shipp, 1988; Felleman and Van Essen, 1989; LeVay and Nelson, chapter 11; Dow, chapter 12). The first pathway passes through layer 4Cα, to layer 4B, to the thick stripes in V2. The second pathway passes through layer 4Cβ, to layer 4A and the interblobs, to the interstripes in V2. The third pathway passes through 4Cβ to the blobs, to the thin stripes in V2. In contrast to the situation with other mammals, inactivation of V1 decreases (Rodman *et al.*, 1989) or abolishes (Schiller and Malpeli, 1977) the visual responsiveness of extrastriate cortical areas in monkeys.

There is a rough subdivision of the more rostral visual areas into a parietal group (e.g. MT, temporoparietal (TP), superior temporal (ST)) receiving primarily magnocellular stream input, and an inferotemporal group (e.g. dorsal and ventral divisions of caudal inferotemporal (ITcd, ITcv), intermediate and rostral inferotemporal (ITi, ITr)) receiving input primarily from the parvocellular blob and interblob streams. Some areas appear to receive mixed inputs (e.g. dorsomedial area (DM)) (Petersen *et al.*, 1988). The border between different modalities is as sharp as in rodents, carnivores and galagos; the auditory-visual overlap zone is a little less than 1 mm wide.
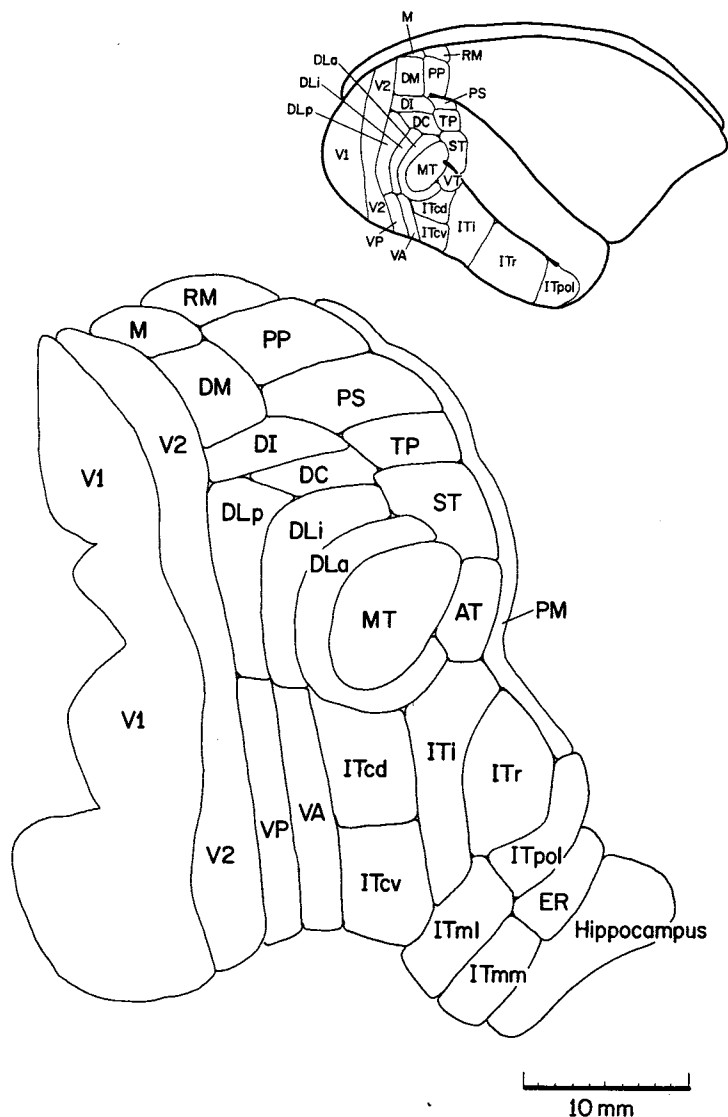
Though the organization of extrastriate cortex in the

Fig. 7.3 *Visual cortical areas in the owl monkey. Areal boundaries are based on* Allman and Kaas (1971, 1974, 1975, 1976), Weller and Kaas (1985, 1987), and Sereno et al. (1986, 1987). *They were drawn using a cytochrome oxidase-stained flat-mounted hemisphere as a template. A cut was made in V1 in depths of the calcarine sulcus to allow the cortex to lie flat. Abbreviations: AT, anterior temporal; DC, dorsocentral; DI, dorsointermediate; DLa, dorsolateral anterior; DLi, dorsolasteral intermediate; DLp, dorsolateral posterior; DM, dorsomedial; ER, entorhinal; ITcd, caudal inferotemporal – dorsal division, ITcv, caudal inferotemporal – ventral division; ITi, intermediate inferotemporal; ITml, medial inferotemporal – lateral division; ITmm, medial inferotemporal – medial divison; ITpol, polar inferotemporal; ITr, rostral inferotemporal; MT, middle temporal; PM, polymodal; PP, posterior parietal; PS, posterior sylvian; RM, rostromedial; ST, superior temporal; TP, temporoparietal; VA, ventroanterior; VP, ventroposterior; V1, striate cortex, V2, second visual area.*

squirrel monkey and the cebus monkey is less well known, it appears to be quite similar to that of the owl monkey (e.g. Cusick and Kaas, 1989). Squirrel monkeys and cebus monkeys both have a well developed fovea. In line with this, the multiple representations of the centre of gaze situated between foveal V1 and MT are much larger than

their counterparts in owl monkeys. Area DM in squirrel monkeys (based on its connections and myelin pattern) appears much more elongated than in owl monkeys (Kaas and Krubitzer, 1988); in this respect, it resembles the similarly situated area V3 in the Old World macaque monkey (Van Essen *et al.*, 1986).
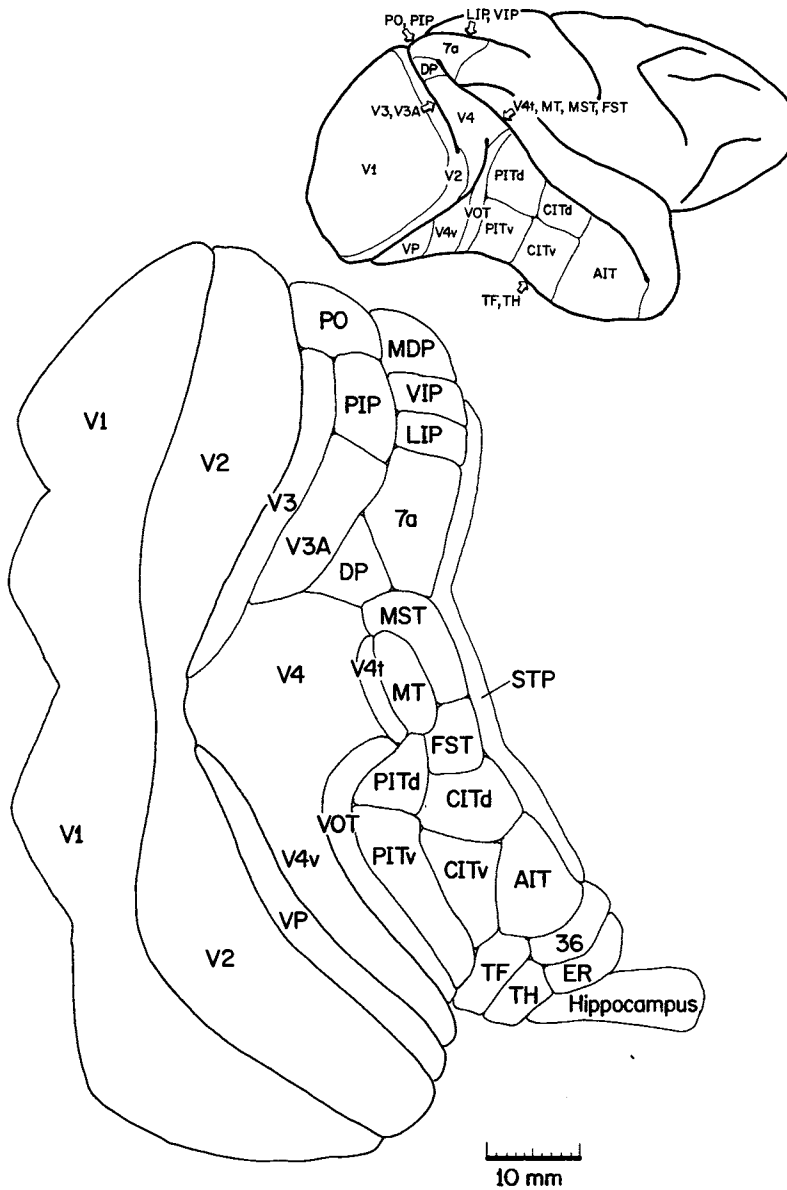
Fig. 7.4 *Visual cortical areas in the macaque monkey. Areal boundaries are based on* Van Essen (1985), Van Essen *et al.* (1986), Felleman *et al.* (1986, 1987) Colby *et al.* (1988) and Felleman (personal communication). *They were drawn using the graphically flattened cortex summary* from Van Essen (1985) *as a model. V1 has been cut along the fundus of the calcarine sulcus.* See Seltzer and Pandya (1978) *for a different interpretation of the inferotemporal areas. Abbreviations: AIT, anterior inferotemporal; CITd, central inferotemporal – dorsal division; CITv, central inferotemporal – ventral division; DP, dorsal prelunate; ER, entorhinal; FST, fundus of the superior temporal sulcus; LIP, lateral intraparietal; MDP, medial dorsal parietal; MST, medial superior temporal; MT, middle temporal; PIP, posterior intraparietal; PITd, posterior inferotemporal – dorsal division, PITv, posterior inferotemporal – ventral division; PO, parieto-occiptal; STP, superior temporal polysensory; TF, temporal field F; TH, temporal field H; VIP, ventral intraparietal; VP, ventroposterior; VOT, ventral occipitotemporal; V1, striate cortex, V2, second visual area; V3, third visual area; V3A, third visual area – accessory; V4, fourth visual area; V4t, V4-transitional; V4v, V4-ventral. Two areas distinguished by Colby* et al. *(1988) are not illustrated – PP, posterior parietal, and MIP, medial intraparietal.*

Old World Monkeys

Fig. 7.4 shows a summary map for an Old World monkey, the macaque monkey (Van Essen, 1985; Desimone and Ungerleider, 1986; Felleman *et al.*, 1986, 1987; Felleman and Van Essen, 1987; Colby *et al.*, 1988). Although many of the areal names are not the same, and though the relative sizes of similar areas differ, the overall configuration of the map is quite similar to the owl monkey map. V1 is bordered by a continuous V2. V1 projects to V2, MT and V3 (input to V3 only from lower field V1). New and Old World monkeys diverged at least 30 million years ago. The main difference between the maps is the reduced size of the areas between V2 and MT in the owl monkey; for example, in macaques, areas V4 (perhaps equivalent to DLi in the owl monkey) is one of the largest extrastriate areas. Some of these differences reflect the more prominent emphasis on the centre of gaze in the retina of the diurnal macaque. Other differences involve the loss of reduced upper and lower field representations. Area V3, for example, does not contain any representation of the upper visual field, unlike its presumed counterpart in owl monkeys, area DM, which has a substantial upper field representation. Similarly, areas VP and VA in owl monkeys contain partial lower field representations that are lacking in macaque VP and V4v.

There does not appear to be any increase in the area of overlap between modalities. Furthermore, the separation between modalities is maintained in the projection of visual, auditory and somatosensory areas to the frontal cortex (Barbas, 1988). There is a zone several millimetres wide in the fundus and dorsal bank of the superior temporal sulcus that responds to more than one modality (e.g. Bruce *et al.*, 1981); this is in line with the greater overall area of V1 in the macaque compared to the owl monkey. A trend seen in both New and Old World monkeys is the development of a set of non-topographic visual areas in the rostral, temporal and parietal regions.

Our current view of the alignment between visual areas in owl monkeys and macaque monkeys is as follows (macaque areas are given in parentheses); V1 (= V1), V2 (= V2), DM (= V3) DLp (− lower field V3A), DLi (= V4), DLa (= V4t), AT (= FST), VP (= VP), VA (= V4v), M (= PO), RM (= MDP), ??? (= PIP), DI (upper field V3A), DC (= DP), ST (= MST), TP (= 7a), PP (= LIP), PS (= VIP), ??? (= VOT), ITcd (= PITd), ITcv (= PITv), ITi (= CITd,v), ITr (= AIT), ITmm (= TH), ITml (= TF), ITp (= 36).

These maps (and more fragmentary data from other species) suggest that the parcellation of extrastriate visual cortex has not changed radically during much of the evolution of the primate order. New and Old World monkeys in particular, are surprizingly similar. Furthermore, there does not seem to be any significant increase in monkeys in the regions where several modalities overlap, or any increase in the number of areas; rather, extrastriate areas have increased in size.

Humans

It has commonly been assumed that human cortex is uniquely characterized by a large, recently-evolved expanse of polymodal association cortex, or language cortex situated in between the primary areas in each of the main modalities. The evidence for this, however, has been quite indirect. The only human visual area whose borders are surely known is V1. Recent advances in anatomical techniques for monitoring activity (e.g. positron emission tomography, Miezin *et al.*, 1987) are beginning to change niques for monitoring activity (e.g. positron emmission tomography, Miezin *et al.*, 1987) are beginning to change this. Fixed-tissue injections suggest that human visual areas V1 and V2 are organized quite similarly to those of other primates (Burkhalter and Bernardo, 1989). Also, there is a heavily myelinated, ellipsoidal region located in a dorsolateral occipital sulcus (Fig. 7.5) that may correspond to human visual area MT (Sereno *et al.*, 1988). Normalized with respect to the area of V1 in macaques and humans (Frahm *et al.*, 1984), the densely myelinated area is about three to four times the size of macaque MT; and there is proportionately more cortex in humans between V1 and the putative MT than between macaque V1 and MT. If one-third to one-half of human cortex is visual as in all other mammals, then there is several times as much extrastriate cortex in humans as in monkeys. The larger size of the putative MT, and of the area between it and V1, suggest that much of the increase in non-primary cortex in humans relative to monkeys may be due simply to the larger size of human extrastriate visual areas. Lesions in left posterior inferotemporal cortex in humans cause severe deficits in language comprehension (Rubens and Kertesz, 1983); this suggests that extrastriate cortex in humans may also subserve linguistic functions (cf. Penfield and Perot, 1963; Haxby *et al.*, 1988).

Evolution of Visual Cortical Areas

Discussion of the evolution of cortical areas has often been characterized by misunderstandings of the nature of phylogenetic reconstruction. The problem is exemplified in the pre-evolutionary rat-cat-monkey-man *scala natura*. Rats, of course did not evolve into primates; rather rodents, carnivores and primates all evolved from a primitive mammal which no longer exists. A subtler version of this fallacy is to assume that primates evolved from modern primitive mammals like hedgehogs. Modern primitive mammals, however, exhibit many specialized features. The platypus, for example, is a living member of
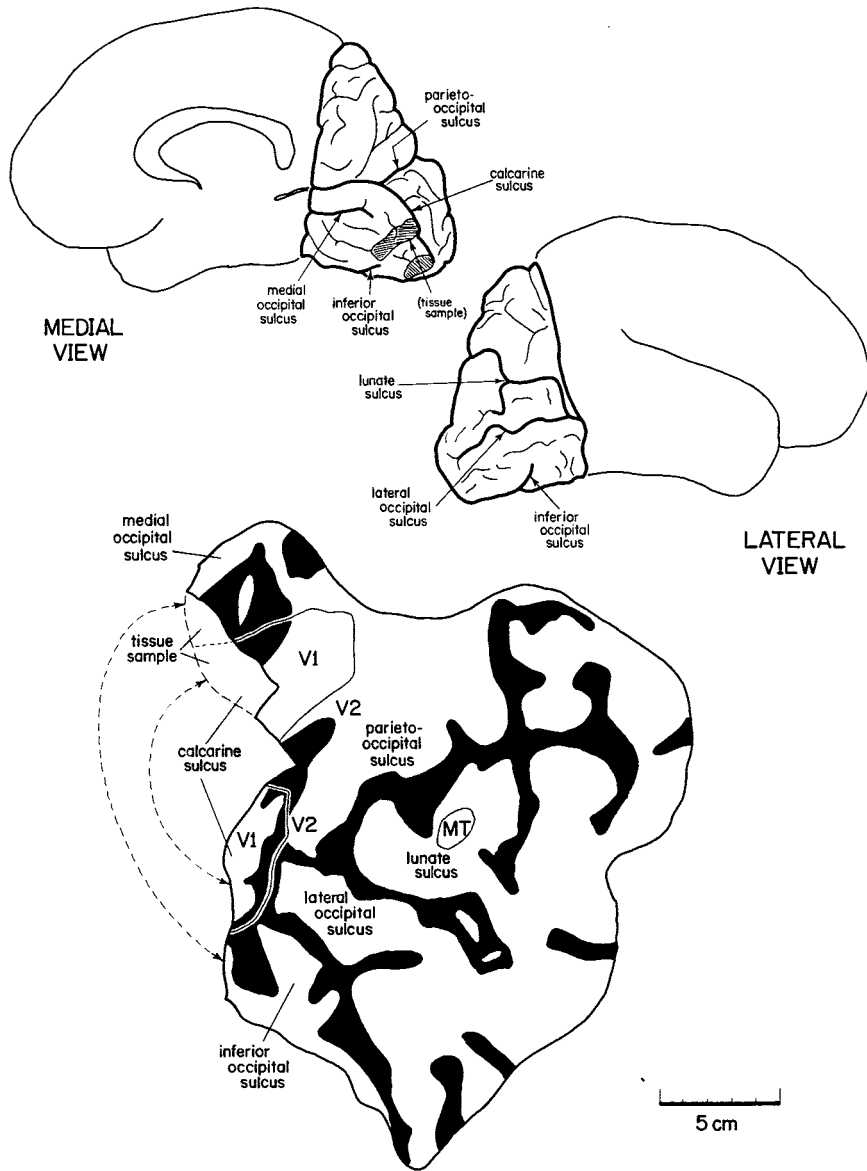
Fig. 7.5 *Visual cortical areas in the human (preliminary). A left occipital lobe (reversed here to aid comparison with previous figures) was physically flattened, sectioned parallel to the cortical laminae, and stained for myelin using the Gallyas method (Sereno et al., 1988). The exposed crowns of the gyri are coloured black in the diagram of the flat cortex (i.e. the sulci are white). The myelin stain clearly revealed V1 (darkly stained layer 4B and ocular dominance column boundaries) as well as an elliptical, densely myelinated area located in a dorsolateral (lunate) sulcus that may correspond to area MT. The pattern of deeper sulci (drawn with thicker lines in the insets at top) was quite similar in other human occipital lobes. The pattern of shallower dimples (thinner lines) was much more variable. Abbreviation: MT, middle temporal; V1, striate cotex; V2, second visual area.*

a primitive mammalian group, the monotremes, that diverged early from other mammals. It exhibits many primitive features (e.g. lack of nipples, egg-laying). However, it also exhibits many derived characters not present in primitive Mesozoic mammals (e.g. cranial characters associated with the development of a bill, an underwater electric sense). In fact, species typically show such a mosaic of primitive and derived characters. Thus, a large

expanse of neocortex is clearly a derived condition and so is a thick, laminarly differentiated cortex, both of which are present in carnivores and humans. Dolphins, however, have as very large cortical expanse, which is a derived condition, yet they have a very primitive-looking pattern of lamination and cellular differentiation (Morgane *et al.*, 1985).

Another problem has been the inappropriate concentration on the evolution of particular areas. There is a unique phylogenetic branching pattern for organisms or species that can be approximately reconstructed using fossil and modern evidence; but there is no equally unique phylogeny of cortical areas. There may not even be clear ancestor/descendant relations between areas in organisms related by descent. Thus, although it appears that one area has sometimes given rise to two (just as one species may give rise to two) there are other cases where there appear to have been wholesale reorganizations of the topography of cortex. In these cases, one may not be able to draw up a specific phylogeny of individual areas as one can always do (at least in principle) for individual organisms. As with non-neural characters (e.g. dental, skeletal, muscular characters), cortical areas within a mammalian order are much more similar to each other than between orders – we can define a rodent pattern, a carnivore pattern, a primate pattern. The greatest difficulties come in trying to bridge the large gaps between these well-defined groups. With these cautions in mind, we consider macroevolutionary patterns with respect to cortical areas.

First, there appears to have been a marked increase in the number of non-primary areas. In turtles, an outgroup for mammals, there appear to be only two cortical visual areas – the pallial thickening and dorsal cortex, which both receive dLGN input (Ulinski, 1983, 1986). There is also one visual area in the dorsal ventricular ridge, a non-cortical pallial structure whose affinities with mammalian cortex remain unclear. The dorsal ventricular ridge area receives input from the thalamic nucleus rotundus, itself the recipient of a bilateral, non-topographic tectal input (Ulinski, 1983). The thalamic projections to all three of these areas are non-topographic, including the projection from the retinotopically organized turtle dLGN to dorsal cortex. The dorsal cortex projects directly into medial structures that resemble mammalian entorhinal cortex and dentate gyrus. This contrasts strongly with primates, for example, which have more than 20 visual areas, many of which are retinotopically organized, interposed between the dLGN and the hippocampus.

The total number of visual areas in primitive mammals, however, is presently not clear. Early work suggested that the small-brained hedgehog had only two visual areas (Kaas *et al.*, 1971). However, the higher visual areas in rodents are quite small; similarly-sized areas could have been missed in that early survey. If the number of areas in primitive mammals was more comparable to the number in modern rodents or lagomorphs, then the number of visual areas has doubled in some lineages. The trend seems to point to an increasingly sophisticated network of topographically organized pre-processing areas feeding into less topographic secondary areas more concerned with spatial relations, object recognition and memory. Multiple non-topographic neocortical areas, however, only reappear in primates. The non-topographic, bilateral, tectofugal pathway has been retained as a parallel route to extrastriate visual cortical areas in mammals, and several new topographic tectofugal pathways to extrageniculate thalamus and then to cortex have appeared (e.g. Takahashi, 1985; Abramson and Chalupa, 1988). the peculiarly devastating effects of V1 lesions in primates, nevertheless, suggest that the thalamofugal pathway (dLGN→V1→extrastriate cortex) has increased in importance relative to the tectofugal pathway in this group.

The trend toward more extrastriate areas is reflected in the increase in the proportional area of extrastriate visual cortex after normalizing with respect to body weight and the size of V1. V1 increases in absolute size in larger mammals; but it falls on a line when plotted against body weight on a double log scale. Total visual cortex furthermore occupies about 45–55% of the total neocortex in most mammals that have been examined. However, the proportion of the total visual cortex occupied by extrastriate areas, and hence the overall area of the cortex, increases with respect to the size of V1 in many diurnal groups. In the nocturnal rat, extrastriate cortex constitutes about 40% the total area of visual cortex, while in the diurnal squirrel, it constitutes about 50% of the total. In nocturnal owl monkeys, extrastriate cortex constitutes about 60% of visual cortex; in diurnal macaques, this number is 75%. The proportion of total visual cortex occupied by extrastriate cortex is probably even larger in apes and humans.

Second, there has been a tendency for the parallel pathways in the cortex defined by different classes of retinal ganglion cells to remain connectionally distinct further into the system. This is especially clear in primates where V1 contains three parallel streams. This is reminiscent of the tendency in other modalities for derived structures to exhibit more and clearer laminae than their primitive counterparts; streams and laminae are both primarily means for segregating different inputs, outputs and processing stages. In the gustatory system, for example, the solitary nucleus is a rather unassuming clump of cells in most mammals; its homologue in teleost fishes (the vagal lobe) is, by contrast, an enormous laminated structure containing many cell types and interlaminar connections that is comparable in size and complexity to the tectum.

Third, partial representations of the upper or lower visual fields in an area are quite labile, evidenced both by individual variation and evolutionary loss and gain. For example, in rats, the more anteriorly located lateral areas

have a predominance of the lower field. The extent to which the upper and lower fields are represented, however, varies from rat to rat. In other kinds of rodents (e.g. squirrels) the reduced upper visual field representations in these areas may have actually been lost.

Fourth, the steepness of the retinal ganglion cell density gradient strongly affects the geometry of extrastriate cortical areas since adjoining cortical areas tend to have congruent borders. As the central field representation in V1 expanded in diurnal animals, for example, it may have dragged adjoining extrastriate areas with congruent borders away from the centre of gaze. Where adjoining areas differ radically in size, there may be a sort of competition in development and evolution between the tendency for an area to represent most of the visual field, and the tendency for congruent borders to form between adjoining areas. In the process, the topology of the cortex may be altered – as areas insert or withdraw themselves from in between other areas, the pattern of neighbour relations changes. For example, in owl monkeys, a rectangular-shaped DM seems to have come partly unstuck from V2; it contains a representation of much of the visual field, but its upper field representation has to form an incongruent border with V2 (as does the near-central part of its lower field representation) (Allman and Kaas, 1975). In macaques, by contrast, V3 is greatly elongated, allowing it to form a much more congruent border with V2, but it entirely lacks an upper field representation (Van Essen *et al.*, 1986). As with RL in rats *vs* mice and hamsters, the insertion (or withdrawal) of V3/DM from in between V2 and V3A/DLp leads to new neighbour relations.

Finally, areas may coalesce or subdivide. Allman and Kaas (1974) previously suggested that areas may have been generated *de novo* by mirror-image duplication. The similarities between the callosal fingers in the unduplicated lower field representations in cat areas 18 and 19, and the callosal rings surrounding the multiple visual field representations (each containing both lower and upper fields) in this position in rodents may be traces of another process by which areas are generated – namely, the subdivision of an area into several areas, or conversely, the coalescing of several areas to form a single area (it is not clear whether the cat or the rat condition is primitive).

Progress in developmental neurobiology may eventually lead to a more mechanistic understanding of the complex intracortical and extracortical interactions in cortical development that generated the particular mosaics of cortical areas seen in the different mammalian groups.

Acknowledgements

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