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RESEARCH ARTICLE

Marcello G .P. Rosa · Maria Carmen Piñon
Ricardo Gattass · Aglai P. B. Sousa

"Third tier" ventral extrastriate cortex in the New World monkey, *Cebus apella*

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Abstract The ventral extrastriate cortex adjacent to the second visual area was studied in the New World monkey *Cebus apella*, using anaesthetised preparations. The visuotopic organisation and myeloarchitecture of this region demonstrate the existence of a distinct strip of cortex, 3–4 mm wide, with an ordered representation of the contralateral upper visual quadrant, up to 60° eccentricity. This upper-quadrant representation is probably homologous to the ventral subdivision of the third visual complex (V3v) of Old World monkeys, also known as the ventral posterior area. The representation of the horizontal meridian in V3v forms its posterior and medial border with V2, while the upper vertical meridian is represented anterior and laterally, forming a congruent border with the fourth visual area (V4). Central visual fields are represented in posterior and lateral portions of V3v, in the inferior occipital sulcus, while the periphery of the visual field is represented anteriorly, on the tentorial surface. Cortex anterior to V3v, at the ventral occipitotemporal transition, had neurones that had poor visual responses. No representation of the lower quadrant was found adjacent to V3v in ventral cortex. However, we observed cells with perifoveal receptive fields centred in the lower quadrant immediately dorsal to V3v, around the junction of the inferior occipital and lunate sulci. These observations argue against the idea that V3v is an area restricted to the ventral cortex in New World monkeys and support the conclusions of previous anatomical studies in *Cebus* that showed a continuity of myeloarchitecture and connectional patterns between ventral and lateral extrastriate cortices. Together, these data suggest that V3v may be part of a larger area that extends into dorsolateral extrastriate cortex, overlapping to some extent with the caudal subdivision of the dorsolateral area described in other New World monkeys.

Key words Primates · Visuotopy · Cortical magnification factor · Ventral stream · Myeloarchitecture

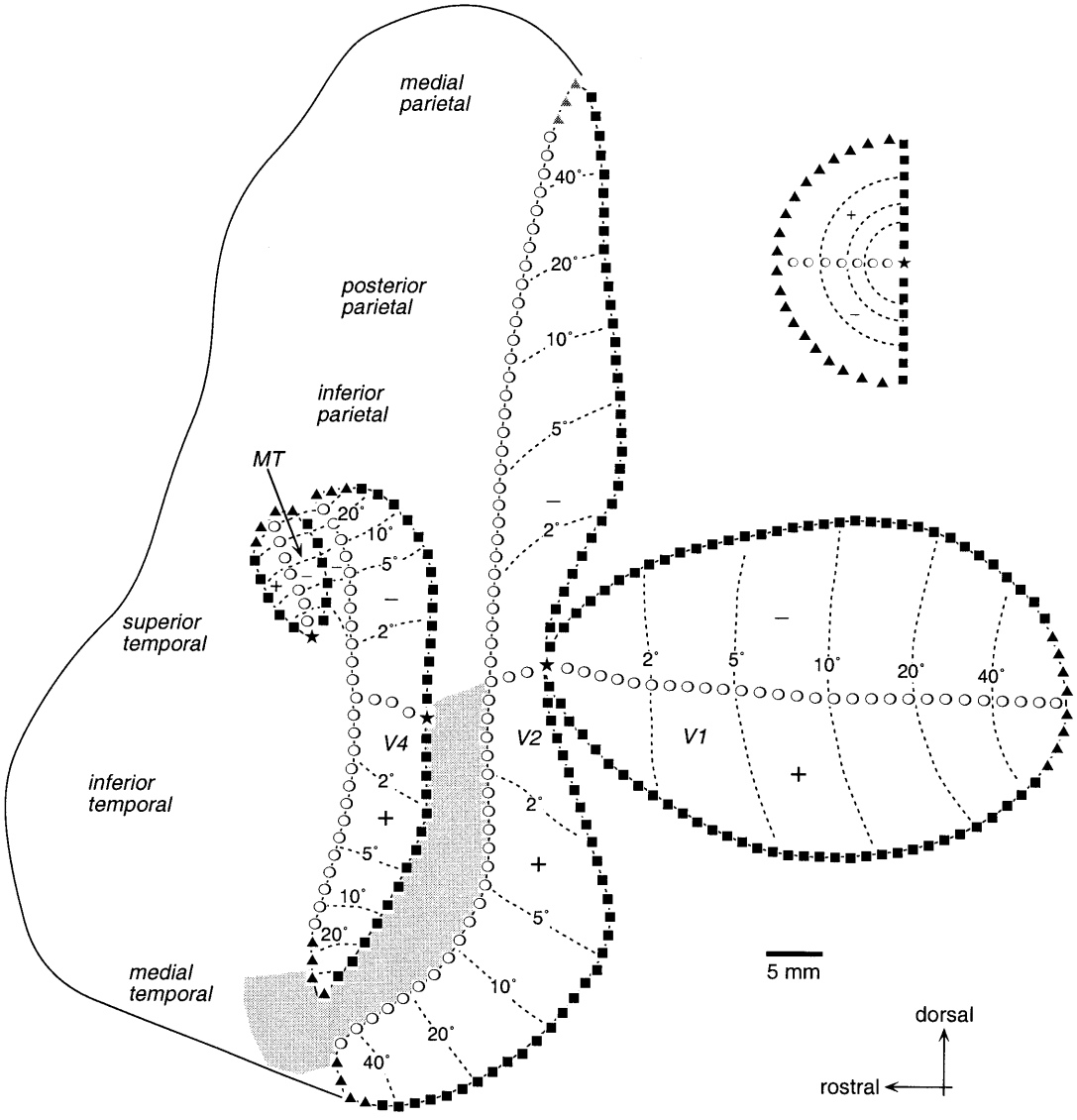
M.G.P. Rosa
Vision, Touch and Hearing Research Centre,
Department of Physiology and Pharmacology,
The University of Queensland, QLD 4072, Australia

M.C. Piñon · R. Gattass · A.P.B. Sousa
Laboratório de Fisiologia da Cognição,
Instituto de Biofísica Carlos Chagas Filho,
Universidade Federal do Rio de Janeiro,
Rio de Janeiro 21941-900, Brazil

M.G.P. Rosa (✉)
Department of Physiology, Momash University,
Clayton, VIC 3800, Australia
Tel.: 61-3-99052522, Fax: 61-3-99052547

Introduction

The existence of a representation of the upper visual quadrant adjacent to that of the second visual area (V2), in ventral prestriate cortex, was first suggested by Cragg and Ainsworth (1969) and Zeki (1969) after anatomical tracing experiments in Old World (macaque) monkeys. This region was considered to be part of a "third visual area" (V3), which wrapped around V2 both dorsally and ventrally. In later years, the organisation of the macaque "third tier areas" (i.e. the group of areas that directly adjoins V2 along its rostral border; Allman and Kaas 1975) became the subject of intense scrutiny, which revealed significant anatomical and physiological differences between the proposed dorsal (lower quadrant representation) and ventral (upper quadrant representation) subdivisions of the original "V3" (Burkhalter and Van Essen 1986; Newsome et al. 1986; Van Essen et al. 1986; Felleman and Van Essen 1987; Krubitzer and Kaas 1993; Beck and Kaas 1999). This has resulted in the hypothesis that, in Old World monkeys, the ventral and dorsal parts of the original "V3" are best regarded as separate areas, each containing an incomplete representation of the visual field (e.g. Felleman and Van Essen 1991). According to this proposal, the name "V3" or "dorsal V3" (V3d) has been retained to designate the dorsal (lower quadrant) representation only, while the upper quadrant representation has been renamed the "ventral posterior area" (VP), or "ventral V3" (V3v). Because, as we argue be-



low, it is unclear whether or not V3v/VP represents the entire extent of a visual area, we will use the abbreviation V3v to designate the ventralmost subdivision of the "third tier" complex of areas.

The name VP was coined on the basis of an anatomical study of interhemispheric connections in New World (owl) monkeys, which observed a conspicuous strip of callosal terminals in the ventral cortex anterior to V2 (Newsome and Allman 1980). A small sample of receptive fields studied in the same species demonstrated the existence of a representation of the upper vertical meridian in the corresponding region, suggesting that this region forms a mirror-image of the visuotopic map of the upper quadrant representation in V2. However, the existence of a lower quadrant representation completing the visuotopic map was not ruled out (Newsome and Allman 1980; see also Sereno et al. 1987; Kaas 1997). A similar band of callosal terminations has since been observed in the ventral cortex of Old World monkeys (Van Essen et al. 1982; Boussaoud et al. 1991), supporting the homology of V3v (VP) in both groups of simians. Nonetheless, electrophysiological recordings and anatomical tracer studies in macaques have revealed that cortex between V2 and this band contains a near-complete map of the upper visual quadrant, but no lower quadrant representation (Newsome et al. 1986; Gattass et al. 1988, 1997).

Fig. 1 Visuotopic organisation of cortical areas of the *Cebus* monkey. Graphically "unfolded" view of the posterior neocortex of the left hemisphere of a *Cebus* monkey, showing the extent and visuotopic organisation of four visual areas already mapped in this New World monkey species (*V1* first visual area, *V2* second visual area, *V4* fourth visual area, *MT* middle temporal area). The region shaded in *grey*, interposed between V2 and V4 in ventral cortex, is the subject of the present report. To create this representation, the map of V1 had to be artificially separated from extrastriate cortex. This is necessary due to the high intrinsic curvature of the caudal neocortex (Van Essen and Maunsell 1980; Rosa et al. 1993). The visuotopic organisation of cortical areas is illustrated according to the following symbols, which are also summarised in the *insert* (top left): ★ representation of the centre of the fovea, ■ representation of the vertical meridian, ○ representation of the horizontal meridian, ▲ representation of the far periphery of the visual field, *thin dashed lines* isoeccentricity lines, + representation of the upper quadrant; – representation of the lower quadrant

To summarise the present situation, there is widespread agreement that, in Old World monkeys, V3v is a strip-like systematic representation of the upper quadrant. There is disagreement, however, as to whether or not this area extends beyond the ventral cortex (so as to include a lower quadrant representation), and, if it does, where this representation is located (for reviews, see Kaas 1997; Rosa 1997). In New World monkeys, the situation regarding the ventral cortex is more uncertain. No study has followed up on Newsome and Allman's (1980) original report, so to date there is still no electrophysiological map of the ventral cortex immediately anterior to V2 in any New World monkey. Thus, it is possible that V3v (VP) forms a complete representation of the visual field in itself, distinct from that found in dorsolateral and dorsal areas (e.g. Kaas 1997). This is an important issue in understanding the organisation of the cortex anterior to V2 and the homologies between species. In particular, demonstration of substantial lower quadrant representation in V3v would support the distinction between this and other fields located dorsal to it. This distinction has recently been questioned both by studies that propose that V3v continues dorsally, to include part of the dorsolateral cortex interposed between V2 and the middle temporal area (MT; Rosa 1997; Rosa et al. 1997), and by those which propose that it is part of a much larger area which, like the original "V3", includes the dorsomedial cortex anterior to V2 (Zeki 1969, 1977; Gattass et al. 1985, 1988).

The present report describes the organisation of ventral extrastriate cortex of a New World monkey, *Cebus apella*. Previous work has detailed the organisation of V2 and V4 (the fourth visual area) in the ventral cortex of this species (Rosa et al. 1988; Piñon et al. 1998), so that the cortices posterior and anterior to the presumptive ventral V3 are already known to contain only upper quadrant representations (Fig. 1). Studies in which anatomical tracers have been used suggested that V3v contains a topographic representation of the upper quadrant of the contralateral hemifield (Sousa et al. 1991; Rosa et al. 1993). However, in view of the relative imprecision of the anatomical method for the assessment of visuotopy, a lower quadrant representation still cannot be ruled out. We have used electrophysiological techniques to map the entire extent of the ventral cortex between V2 and V4. As detailed below, the results demonstrate that V3v forms a single systematic representation of the upper quadrant, and that, as in Old World monkeys, the only lower quadrant representation adjacent to V3v is located dorsally, in the lunate sulcus.

Materials and methods

The visual topography of the ventral extrastriate cortex was studied in three adult *Cebus* monkeys (2–3.5 kg) by means of multiunit recordings, which explored the ventral cortex lateral to the calcarine sulcus, from the occipital pole to the temporal cortex. Less extensive recording data from three other animals were also used. These experiments followed the animal experimentation guidelines enforced by the Instituto de Biofísica Carlos Chagas Filho Ethics Committee. The animals were monitored by a veterinarian throughout the course of the project.

Prior to the first recording session, each animal was fitted with a cranial prosthesis consisting of a stainless steel recording chamber and a bolt for holding the head in the stereotaxic apparatus. Following the induction of anaesthesia (ketamine, 50 $mg \cdot kg^{-1}$; diazepam, 2 $mg \cdot kg^{-1}$, i.m.), the bone in the region circumscribed by the chamber was removed, leaving the dura mater intact. Stereotaxic coordinates of the main sulci visible on the dorsal surface of the brain were also measured to allow planning of the positions of electrode penetrations. The monkeys were then administered antibiotics and returned to their cages after regaining consciousness. Analgesics (buprenorphine hydrochloride, 0.01 $mg \cdot kg^{-1}$, i.m.) were given whenever deemed necessary, under veterinarian advice. An interval of 7 days was allowed before the first recording session.

Each animal was studied in 4–7 chronic experimental sessions of about 8 h each during a period of up to 4 weeks. At the beginning of each session, the animal was pre-medicated with ketamine (25 $mg \cdot kg^{-1}$ i.m.) and diazepam (1 $mg \cdot kg^{-1}$, i.m.) and given atropine (0.2 $mg \cdot kg^{-1}$, i.m.). Deep anaesthesia was achieved with halothane (2% in oxygen), which was gradually substituted by a mixture of nitrous oxide and oxygen (70% N_2O:30% O_2). A nicotinic blocker (pancuronium bromide, 0.05 $mg \cdot kg^{-1} \cdot h^{-1}$) and an anaesthetic (sufentanil citrate, 2–3 $\mu g \cdot kg^{-1} \cdot h^{-1}$ in saline) were given by intravenous infusion during the recordings. The animal was artificially ventilated via a tracheal tube, and the percentage of CO_2 in the expired air, as well as the electrocardiogram and the rectal temperature, were continuously monitored. The combination of N_2O and sufentanil produced adequate anaesthesia during the recording sessions, as indicated by the lack of an electrocardiographic response to noxious stimulation and by the low level of cortical spontaneous activity.

For the mapping of receptive fields, the right eye was fitted with a hard contact lens of appropriate curvature to bring the focus to the surface of a 57.3-cm diameter, transparent hemisphere placed in front of the animal. The blind spot and the centre of the fovea were projected onto the hemisphere by means of a reversible ophthalmoscope. An electrode was then inserted in the representation of the centre of the fovea in V1, which is located just posterior to the confluence of the lunate and inferior occipital sulci (Gattass et al. 1987). The receptive field recorded at that location was repeatedly checked during the experimental session and used to correct the displacements of the fovea due to slow eye drifts. The horizontal meridian (HM) of the visual field was defined as a line passing through the fovea and the centre of the blind spot, while the vertical meridian (VM) was defined as a line perpendicular to the HM passing through the centre of the fovea.

Varnish-coated tungsten electrodes, with impedances of about 0.5 MΩ at 1 KHz, were used to record from small clusters of neurones. Vertical and oblique penetrations, 1.5–2.0 mm apart, were made following either coronal or parasagittal planes. In each penetration, recording sites were typically 500 µm apart. The neuronal activity at the tip of the electrode was monitored by listening to a loudspeaker, which was connected to an amplification system. Visual receptive fields were plotted by moving white and coloured bars in front of the hemisphere under photopic conditions and correlating increments of neuronal activity with stimulation in specific parts of the monkey's visual field. Electrolytic lesions (4 µA for 10 s) were placed at different depths in several of the electrode tracks to mark points of transition and other sites of interest. After 6–7 h, the intravenous injection of pancuronium was discontinued and substituted by saline with glucose. The animal was allowed to regain spontaneous breathing and was then returned to its cage.

After the last session, the monkey received a lethal dose of pentobarbital and was perfused through the aorta with saline, followed by formaldehyde (4% in saline). After fixation, the brain was allowed to sink in formaldehyde solution with increasing concentrations of sucrose (up to 30%) and was then frozen-sectioned at 40 µm. Alternate sections were stained for cell bodies with cresyl violet, and for myelin with the method of Heidenhain-Wöelcke (Gattass and Gross 1981). The positions of the recording sites were reconstructed based on the histological reconstruction of

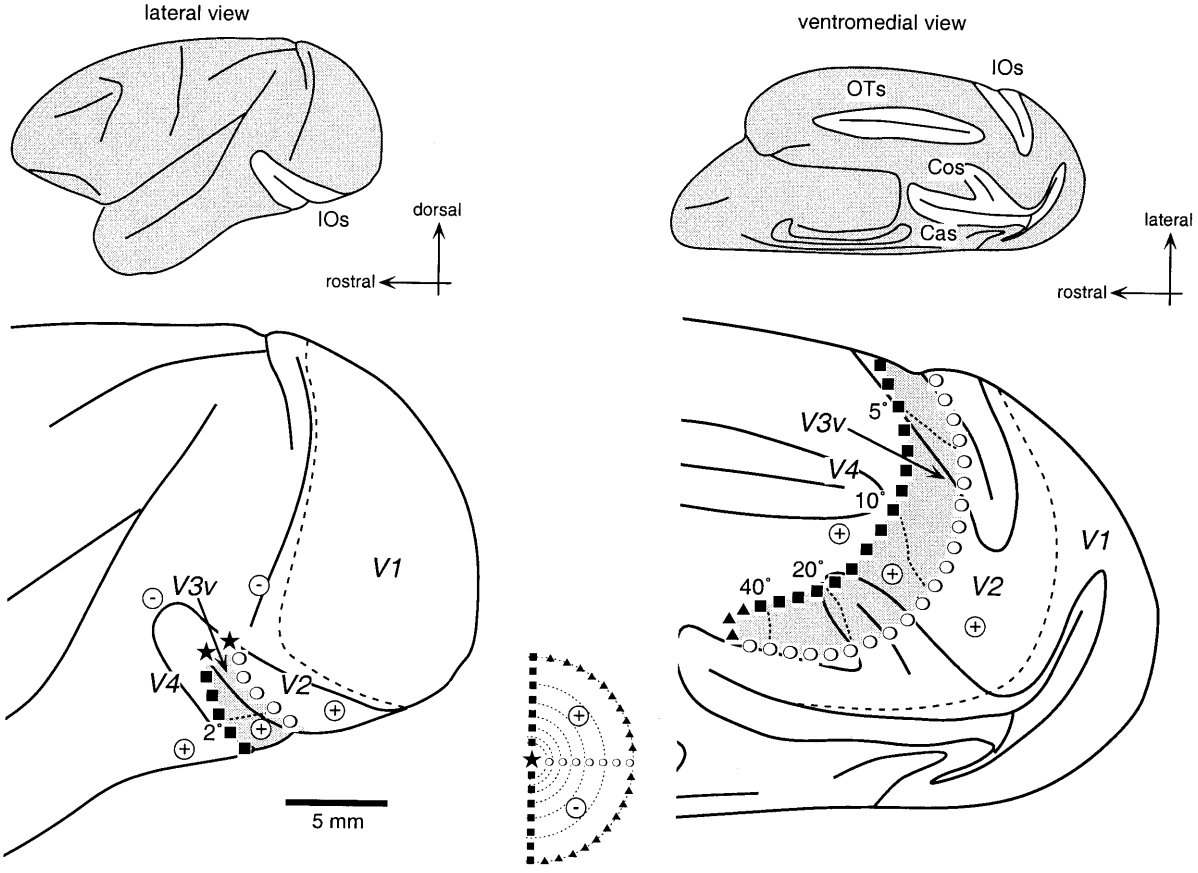


Fig. 2 Summary of the visuotopy and extent of ventrol V3 (*V3v*). *Top* lateral (left) and ventromedial (right) views of a left hemisphere of the brain of a *Cebus* monkey, in which the banks of several sulci have been pried open in order to reveal the cortex (*white*) that is normally hidden from view (*Cas* calcarine sulcus, *Cos* collateral sulcus, *IOs* inferior occipital sulcus, *OTs* occipitotemporal sulcus). The posterior half of the brain is illustrated at a higher magnification at the *bottom*, with the location of V3v highlighted in *grey*. The visuotopic organisation of V3v is indicated according to the symbols defined for Fig. 1 (summarised in the *insert*). The location of the first/second visual-area (*V1/V2*) border is indicated by the *coarse dashed line*, and the locations of upper- and lower-quadrant representations in cortex adjacent to V3v are indicated by the "+" and "–" signs, respectively. *Numbers* adjacent to the isoeccentricity lines indicate eccentricity in degrees of visual angle. *V4* Fourth visual area, *MT* middle temporal area

electrode tracks, electrolytic lesions, and transitions between grey and white matter. Shrinkage due to histological processing was estimated by comparing the distances between the electrode tracks in the sections with microdrive readings. Two-dimensional reconstructions of the ventral cortical surface were obtained by tracing and graphically "unfolding" contours of layer 4 in such a way as to retain the neighbourhood relationships between and within sections (Van Essen and Maunsell 1980; Rosa et al. 1993). The recording sites were projected to the nearest location in layer 4 and transferred, together with myeloarchitectural borders, to the "unfolded" reconstructions.

Results

In the first part of the results, we will describe the visual field representation in V3v, which will be illustrated in serial sections and in two-dimensional reconstructions. The electrophysiological and myeloarchitectural criteria used to define the borders of V3v with other visual areas, and the visuotopy of cortex surrounding V3v, will also be illustrated. Subsequent parts of the results will deal with comparisons of the cortical magnification factor and receptive-field size in V3v and neighbouring areas.

Overview of the location, extent and visuotopy of V3v

V3v is a continuous strip of cortex, about 4 mm across at its point of maximum width, which borders the upper visual quadrant representation of V2 anteriorly and laterally (Fig. 2). The representation of the fovea is located on the anterior bank and fundus of the inferior occipital sulcus. The horizontal meridian, and a small (1–2°) invasion in the lower visual quadrant, are represented along the border with V2. The upper vertical meridian, together with a slight invasion of the ipsilateral hemifield, is represented anteriorly and laterally, near the border between V3v and the upper quadrant representation in area V4 (Piñon et al. 1998). The far periphery is represented in the most anterior portion of V3v, medially in posterior temporal cortex. Other than the slight invasion of the lower quadrant by receptive fields near the V2/V3v border, no lower quadrant representation was observed in V3v, or in adjoining ventral cortex. However, neurones with receptive fields of similar size, representing the lower quadrant, were found immediately dorsal to the

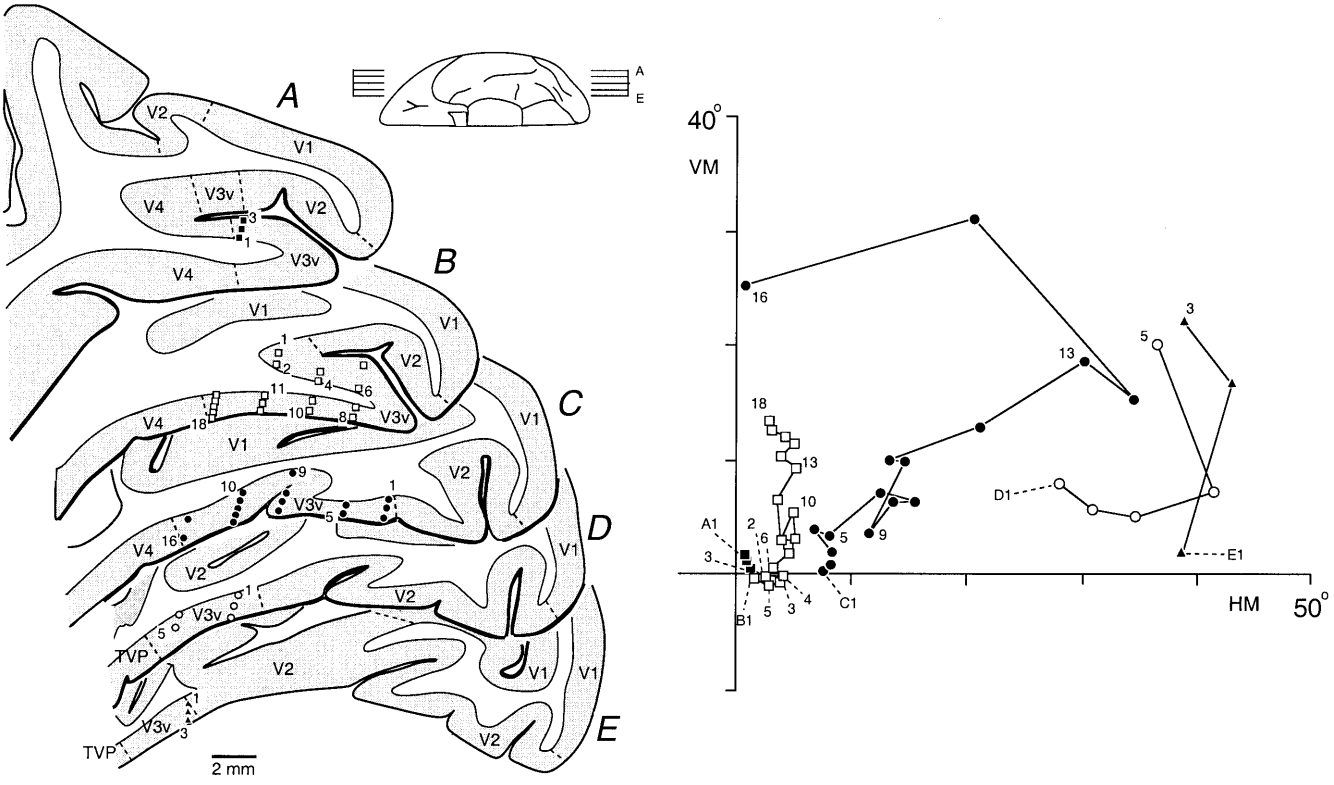


Fig. 3 Recording sites and receptive field centres in the ventral subdivision of the third visual complex (*V3v*) (case 1). *A–E* Five parasagittal sections through the posterior cortex, indicating the myeloarchitectural borders of the first visual area (*V1*), second visual area (*V2*) and V3v (*dashed lines*) and the location of recording sites in one animal (different *symbols* are used to indicate recording sites obtained at different parasagittal levels). The planes of section are indicated in a ventral view of the left hemisphere (*top*). The geometric centres of the receptive fields corresponding to these recording sites are illustrated on the right. *HM* horizontal meridian, *VM* vertical meridian, *TVP* temporal ventral posterior area, *V4* fourth visual area

foveal representation of V3v in the lunate sulcus. Different parts of the visual field are not uniformly represented, and there is a great emphasis on the representation of central vision.

Visuotopic organisation

The main features of the visuotopic organisation of V3v are illustrated in Figs. 3 and 4. In the left portion of Fig. 3, recording sites obtained at each of five parasagittal levels, labelled A-E from lateral to medial, are indicated with different symbols. The geometric centres of the corresponding neuronal receptive fields are illustrated in the right portion of this figure. Analysis of the receptive-field sequences reveals that the most lateral portion of V3v, in the inferior occipital sulcus, represents the central visual fields (e.g. section A, sites 1–3; section B, sites 1–6). As one considers successively more anterior and medial parts of V3v (sections C, D, E), it is possible to observe a displacement of the sequences of receptive-field centres towards the periphery of the upper visual quadrant. At every mediolateral level, the receptive fields of neurones sampled near the V2/V3v border are located close to the horizontal meridian (e.g. section B, sites 1–2; section C, sites 1–3; section D, sites 1–3), while receptive fields near the V3v/V4 border are located near the vertical meridian (e.g. section A, site 1; section B, site 18; section C, site 16).

A clearer view of the visual topography in V3v is shown in Fig. 4, which illustrates "unfolded" reconstructions of extrastriate cortex of the same animal. The positions of the recording sites shown in Fig. 3 are projected onto the reconstruction (Fig. 4B), as well as the myeloarchitectural transitions (indicated in grey; see below). Finally, in Fig. 4C, the representations of the visual field meridians and the isoeccentricity lines were interpolated in order to provide the visual field map in V3v. Although no receptive fields near the centre of the fovea were observed in this animal, data from other cases in which the inferior occipital sulcus was studied more extensively (e.g. Fig. 5, sites A1–3, B1–4) confirm that a foveal representation exists in V3v, and that this representation is located in the region indicated in grey in Fig. 4C.

Figure 6 illustrates the organisation of V3v in coronal sections. In this case, as in those illustrated in Figs. 3, 4 and 5, moving postero-anteriorly from section A to E yields increasingly eccentric sequences; moreover, receptive field centres move towards the vertical meridian as one approaches the lateral border of V3v. As in the case illustrated in Figs. 3, 4 and 5, it is clear that the rep-

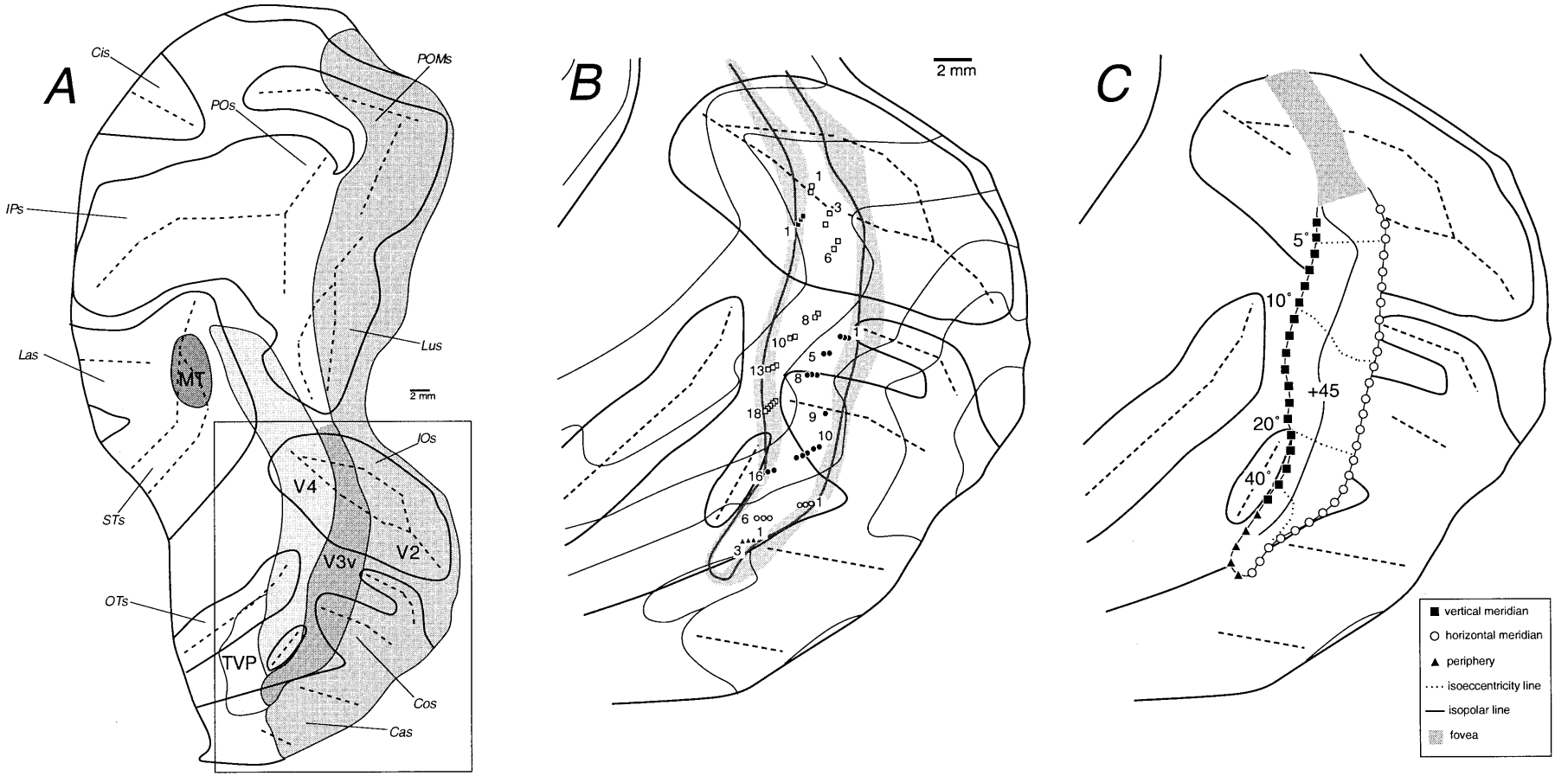


Fig. 4A–C Summary maps of the organisation of the ventral subdivision of the third visual complex (*V3v*) (case 1). **A** Two-dimensional, "unfolded" map (Van Essen and Maunsell 1980) of the caudal half of the left hemisphere of the same animal in which the data illustrated in Fig. 3 were obtained. Dorsal is towards the *top*, and anterior to the *left*. The *thick continuous lines* indicate the lips of the sulci, and the *dashed lines* the fundi and the main folds. On this representation, the extent of areas V2 (second visual area), V3v, V4 (forth visual area), MT (middle temporal area) and TVP (temporal ventral posterior area; Sousa et al. 1991) were drawn, using the cortical myeloarchitecture as a guide (Rosa et al. 1993; see also Fig. 11 and accompanying text for details). The region included in the *box* is illustrated at a higher magnification in the middle and right panels (**B, C**). **B** Map of the ventral surface of extrastriate cortex, showing the location of the same recording sites illustrated in Fig. 3. The *thin dashed lines* in this figure correspond to the layer 4 contours of individual parasagittal sections used to construct the map. The *light-grey zone* reflects the uncertainty of the myeloarchitectural determination of the borders of V3v, according to repeated estimations by different observers. The *dark-grey line* indicates the electrophysiological estimate of the borders of V3v (i.e. the mid-point between the projections of the last recording site deemed to be in V3v and the first site deemed to be in the adjacent area, according to criteria explained in the main text and Figs. 8 and 9). **C** Interpolated map of the visual field in V3v of this animal, taking into consideration the receptive field coordinates illustrated in Fig. 3. In this animal, there were no recordings in the region including the foveal representation, which is therefore estimated (*grey*) only on the basis of myeloarchitecture and recordings in other cases. *Cas* Calcarine sulcus, *Cis* cingulate sulcus, *Cos* collateral sulcus, *IOs* inferior occipital sulcus, *IPs* intraparietal sulcus, *Las* lateral sulcus, *Lus* lunate sulcus, *OTs* occipitotemporal sulcus, *POs* parietooccipital sulcus, *POMs* parietooccipital medial sulcus, *STs* superior temporal sulcus

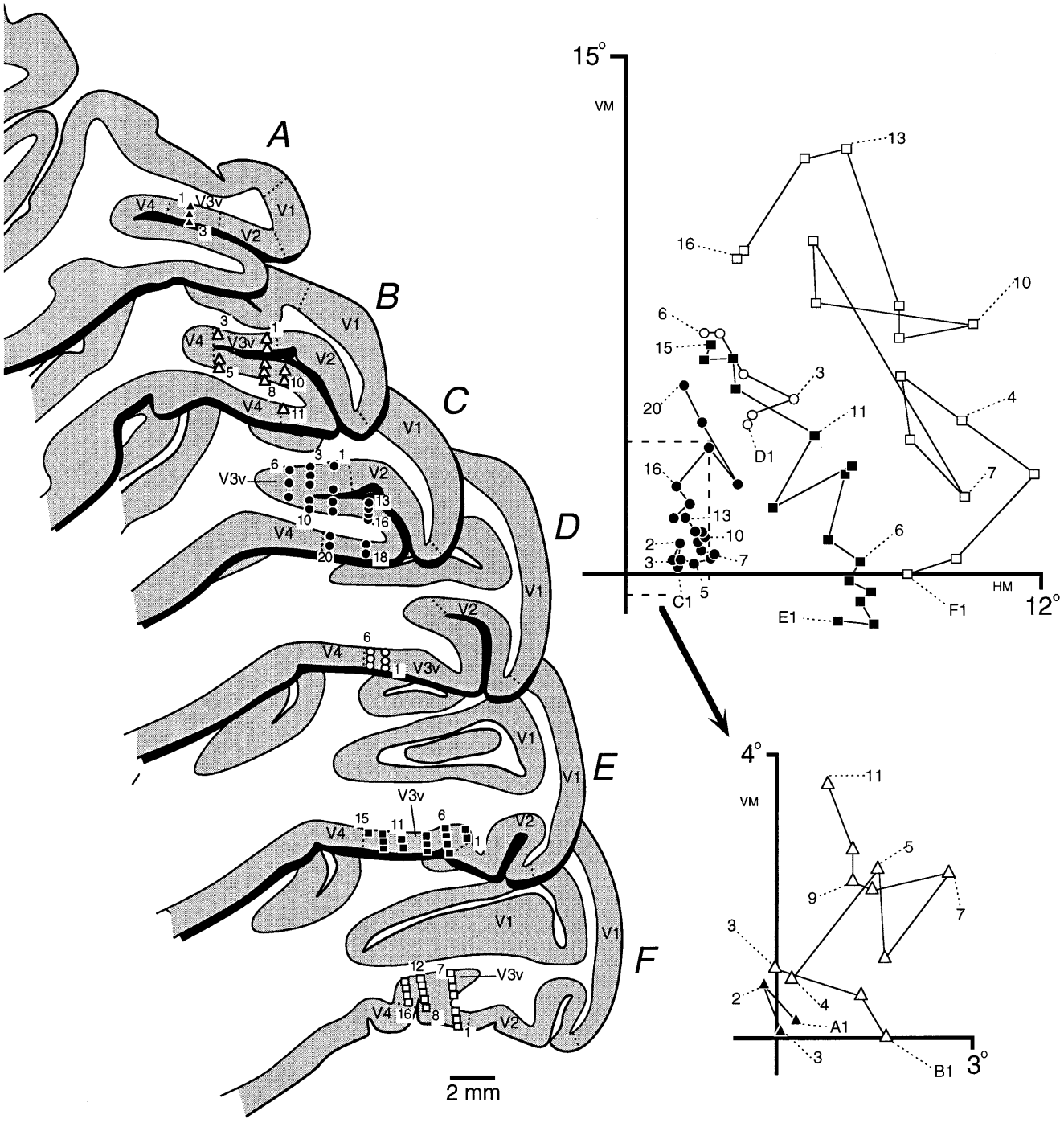


Fig. 5 Recording sites and receptive-field centres in the ventral subdivision of the third visual complex (*V3v*) (case 2). *A–F* Six parasagittal sections through the posterior cortex, indicating the myeloarchitectural borders of *V1* (first visual area), *V2* (second visual area) and V3v (*dotted lines*) and the location of recording sites in one animal (different *symbols* are used to indicate recording sites obtained at different parasagittal levels). The geometric centres of the receptive fields corresponding to these recording sites are illustrated on the *right*. The central region of the visual field (*dashed box* in top, right) is shown at a higher magnification in the *bottom right insert*. Other abbreviations as in Fig. 3

resentation of the visual field is not as precise as that in striate cortex: in some cases, a small displacement between two recording sites yielded considerable distance between receptive-field centres (e.g. Fig. 6, sites B7–8, D1–2), while in others much greater distance yielded receptive fields in the same region of the visual field (sites C2 and D1).

In summary, the organisation of V3v is consistent between animals, both in terms of the size and shape of this area and the relationship between visuotopy and sulcal landmarks. V3v contains, in each hemisphere, a complete representation of the binocular segment of the contralat-

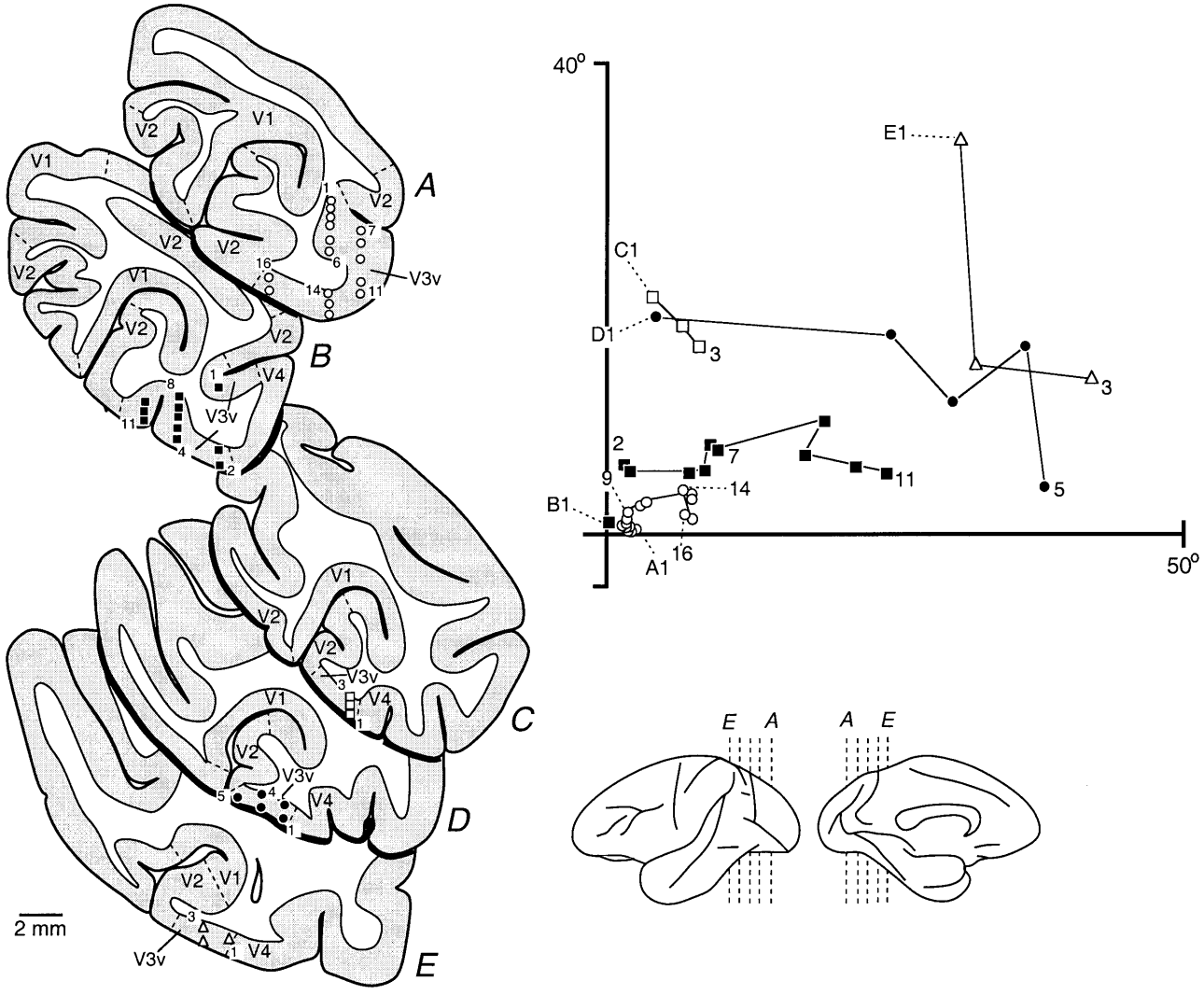


Fig. 6 Recording sites and receptive-field centres in the ventral subdivision of the third visual complex (*V3v*) (case 3). *A–E* Five coronal sections through the posterior cortex, indicating the myeloarchitectural borders of *V1* (first visual area), *V2* (second visual area) and V3v (*dashed lines*) and the location of recording sites in one animal (different *symbols* are used to indicate recording sites obtained at different anteroposterior levels). The planes of section are indicated in lateral and medial views of the left hemisphere (*bottom, right*). The geometric centres of the receptive fields corresponding to these recording sites are illustrated in the *top right diagram*. Other abbreviations as in Fig. 3

eral upper visual quadrant, with only a small invasion of the upper ipsilateral and lower quadrants. While receptive field borders were found to invade the monocular crescent, very few receptive field centres were observed in this region. Figure 7 illustrates a composite view of all receptive field borders obtained in six animals.

Physiological determination of the borders of V3v

The perimeter of V3v illustrated in Figs. 3, 4, 5, and 6 was primarily derived on the basis of electrophysiological criteria, such as reversals in receptive field sequences, changes in receptive field size and changes in multiunit response characteristics. For most of its extent, V3v is bordered by visually responsive cortex, corresponding to areas V2 and V4 mapped in previous studies (Rosa et al. 1988; Piñon et al. 1998; see Fig. 1). The level of responsiveness of V3v cell clusters to the type of stimulus used (coloured bars moved by hand) was not obviously different from that of V2 or V4 cell clusters, and receptive fields tended to have sharply defined borders. Thus, reversals in the direction of receptive field centre drift (the "field sign"; Sereno et al. 1994) and receptive field sizes are the most useful criteria to determine these boundaries. On the other hand, the most anterior border of V3v, with the anatomically defined "temporal ventral posterior area" (TVP, Sousa et al. 1991; Rosa et al. 1993), was characterised by a clear change in response characteristics: moving from posterior to anterior, recording sites yielding clearly defined peripheral receptive fields in V3v gave way to sites yielding no visual responses to the stimuli employed or, less commonly, receptive fields with ill-defined borders that may include the central 30–40° of the visual field. As detailed below,

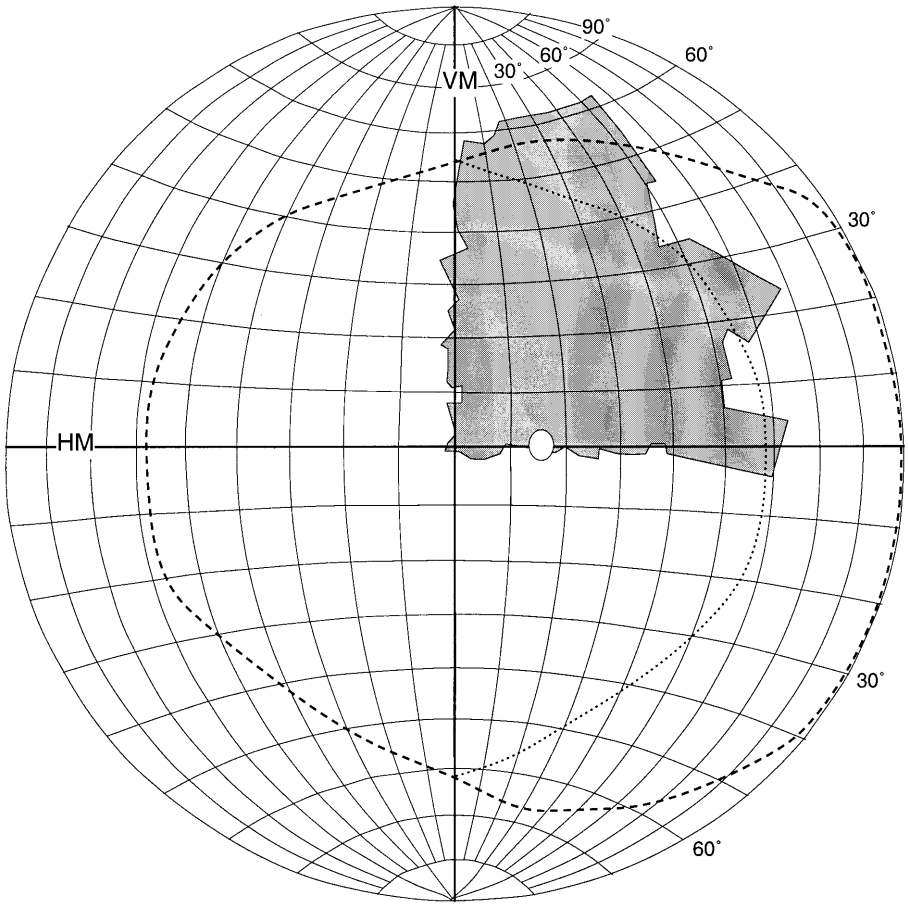


Fig. 7 Extent of the visual field represented by receptive fields recorded in the ventral subdivision of the third visual complex (*V3v*). Diagram of the visual field of a *Cebus* monkey, showing a composite view of all receptive fields recorded in V3v of six monkeys (*grey*). Each division of the chart corresponds to 10° of azimuth or elevation. The *dashed line* corresponds to the field of vision of the contralateral eye, and the *dotted line* is an estimate of the temporal limit of the binocular field of vision (Rosa et al. 1988). The location of the optic disc is indicated by the *white oval* overlying the horizontal meridian (*HM*). *VM* Vertical meridian

these transitions were also marked by changes in the cortical myeloarchitecture.

Examples of receptive-field sequences through V3v and adjacent areas are illustrated in Figs. 8 and 9. Figure 8 illustrates a parasagittal row of recording sites. Successively more anterior recording sites in V2 resulted in a sequence of receptive fields that gradually moved towards the horizontal meridian, and even invaded the lower quadrant to a slight extent (Fig. 8, sites 1–10). The border between V2 and V3v (sites 10–11) was marked by an increase in receptive-field size; moreover, in V3v, an anterior displacement of the recording electrode resulted in receptive fields that gradually moved away from the horizontal meridian and towards the vertical meridian in the upper visual field (Fig. 8, sites 11–30). The anterior border of V3v, with V4, corresponded to the representation of the upper vertical meridian representation (Fig. 8, sites 30 and 31). Beyond this point, receptive fields started to move away from the vertical meridian as the electrode was moved anteriorly (sites 31–42). The receptive field eccentricity tended to increase gradually from posterior to anterior in the cortex.

Figure 9 illustrates the borders of V3v in the peripheral representation, in a coronal section. As in the example above, sites near the V2/V3v border corresponded to receptive fields near the horizontal meridian (e.g. site 11). This border was also characterised by an increase in receptive field size, even though the receptive fields mapped in V3v clusters were less eccentric than those in V2. As one crossed the lateral border of V3v, with V4, receptive fields began to move back toward the horizontal meridian. Although an increase in receptive field size was also observed at the V3v/ V4 border in this case, a population analysis (detailed below) revealed that, on average, there was no change in receptive field size between the upper quadrant representations of areas V3v and V4.

Cortex immediately dorsal to V3v, near the junction of the lunate and inferior occipital sulci, contained a representation of the central part of the lower visual field. The transition between V3v and this region is illustrated in detail in Fig. 10. These recordings were obtained in an animal (case 4) in which the lunate and inferior occipital sulci were fused immediately rostral to the foveal representation of V2 (Fig. 10, upper left), a variant observed in about one-third of the adult *Cebus* population (e.g. Falk 1980). As in other cases, the representation of the centre of the fovea in V3v was located around the fundus of the inferior occipital sulcus (near recording site B13). Receptive fields of neurones studied at sites dorsal to this point progressively moved into the lower visual field (fields A1–5, B1–9 and C1–11). As in V3v, the visuotopic organisation of the dorsal region was such that receptive-field centres gradually approached the vertical meridian as the electrode was displaced rostrally.

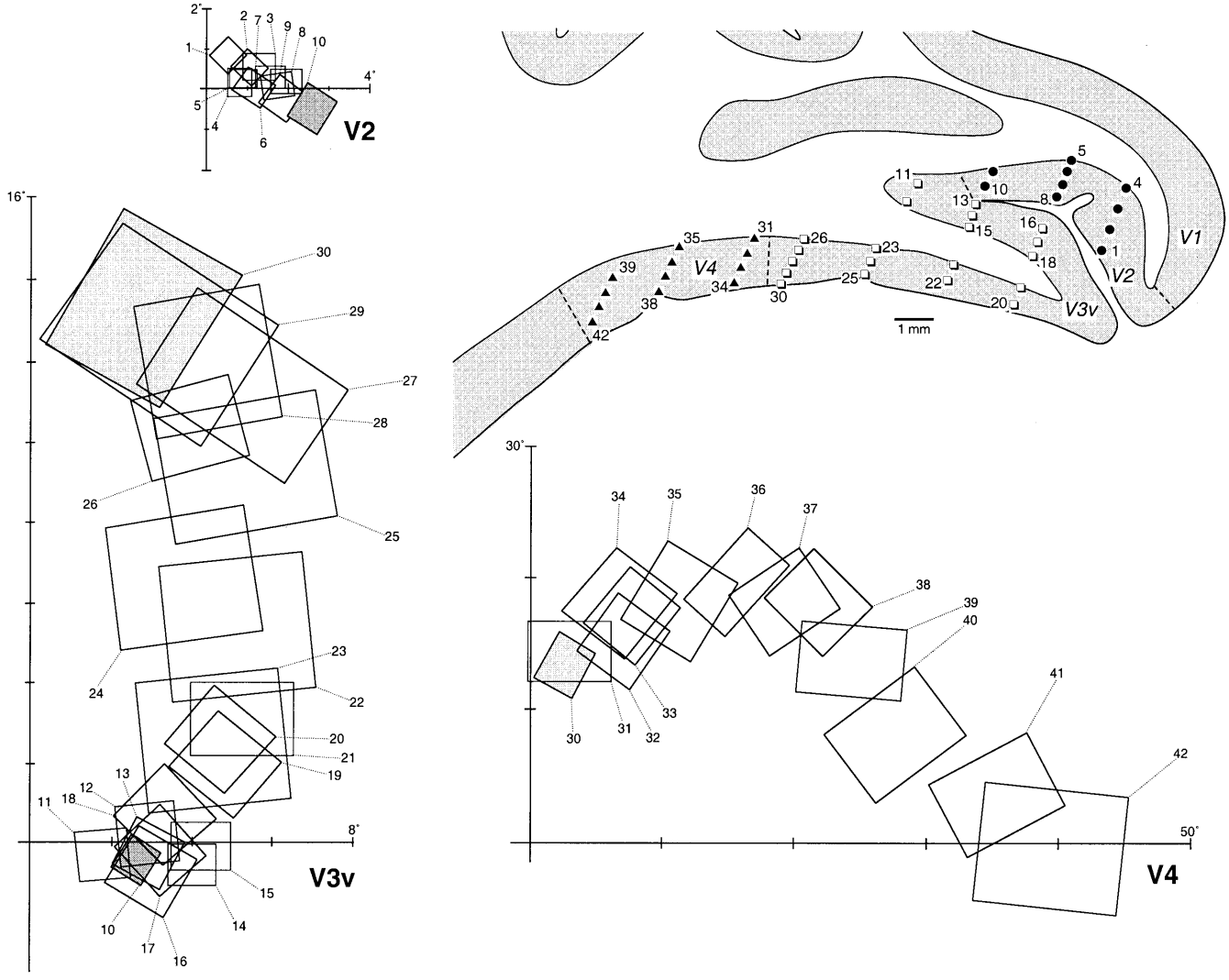


Fig. 8 Electrophysiological borders of the ventral subdivision of the third visual complex (*V3v*) (case 1). *Top right* Parasagittal section through the caudal half of a *Cebus* monkey brain, showing the myeloarchitectural boundaries of *V1* (first visual area), *V2* (second visual area), V3v and V4 (fourth visual area, *dashed lines*) as well as forty-two recording sites (●: V2, □:V3v, ▲: V4). The corresponding receptive fields are illustrated in the *top-left* (V2), *bottom-left* (V3v) and *bottom-right* (V4) diagrams. The V4 receptive fields are illustrated on a different scale from that used for V2 and V3v receptive fields. Receptive fields 10 and 30 (*grey*), which are near the borders of V2/V3v and V3v/V4, respectively, each appear in two diagrams, to convey an impression of the continuity in visuotopic progression

Myeloarchitecture of V3v and surrounding areas

For most of its extent, ventral V3 can be distinguished from surrounding cortex on the basis of myeloarchitecture. Figure 11 illustrates Heidenhain-Wöelcke-stained parasagittal sections through V2, V3v, V4 and TVP. In contrast with V2, in which cortex from the bottom of layer 3 to the white matter shows a near-homogenous appearance in myelin-stained sections (Rosa et al. 1988, 1997), V3v had a well-defined outer band of Baillarger, separated from the lower layers by a slightly less stained band. In V4, the stratification of cortex became even more conspicuous, with the inner and outer bands of Baillarger becoming clearly separated by a lightly stained, myelin-poor band. V3v could be further distinguished by the fact that the supragranular layers were relatively thicker than in either V2 or V4. Thus, V3v was characterised by a broad myelin-light upper stratum, encompassing layers 1 to 3, and by the apparent "compression" of the bands of Baillarger towards the white matter (Piñon et al. 1998). As described previously (Rosa et al. 1993), this pattern also characterises the rostral bank of the lunate sulcus, where a representation of the central lower quadrant was found (Fig. 10). Area TVP, in posterior temporal cortex, was more lightly myelinated than either V3v or V4, and had well-separated inner and outer bands of Baillarger.

Cortical magnification factor and receptive-field size

The cortical magnification factor (CMF) was calculated as the ratio of the distance in the cortex between two re-

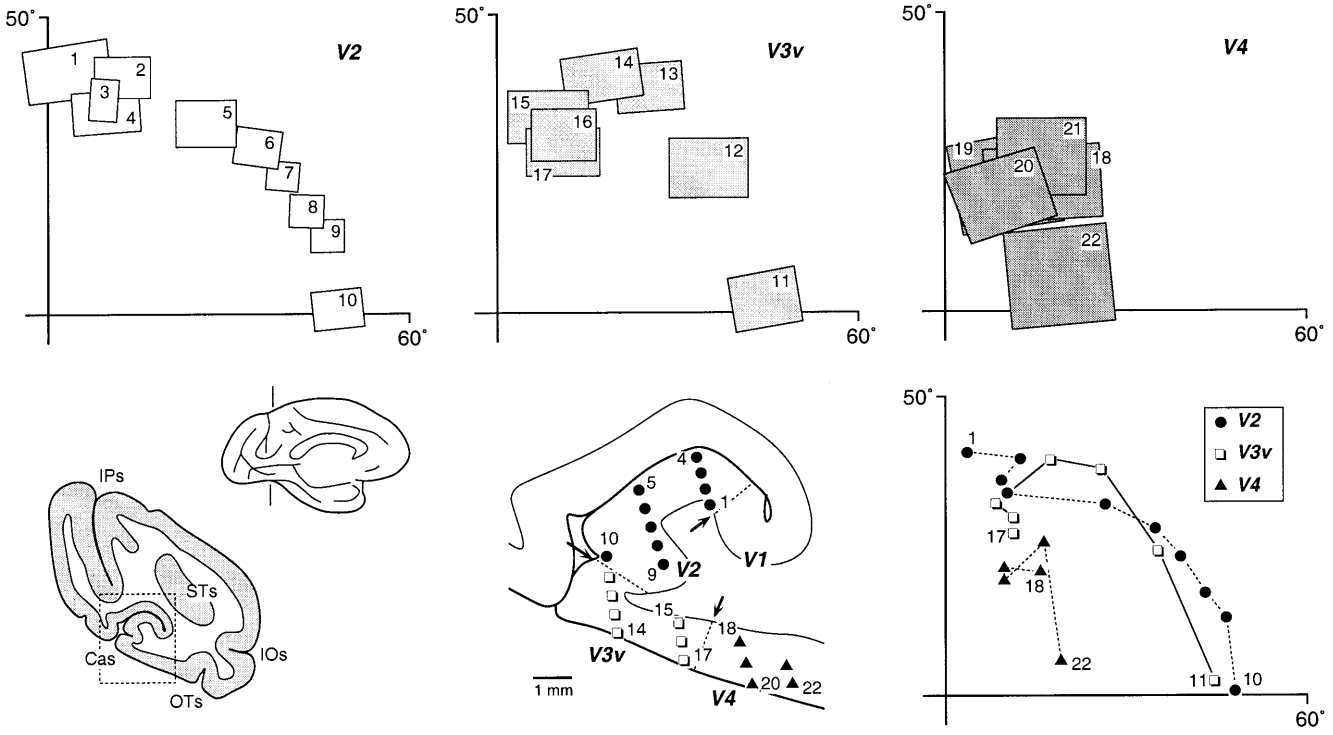


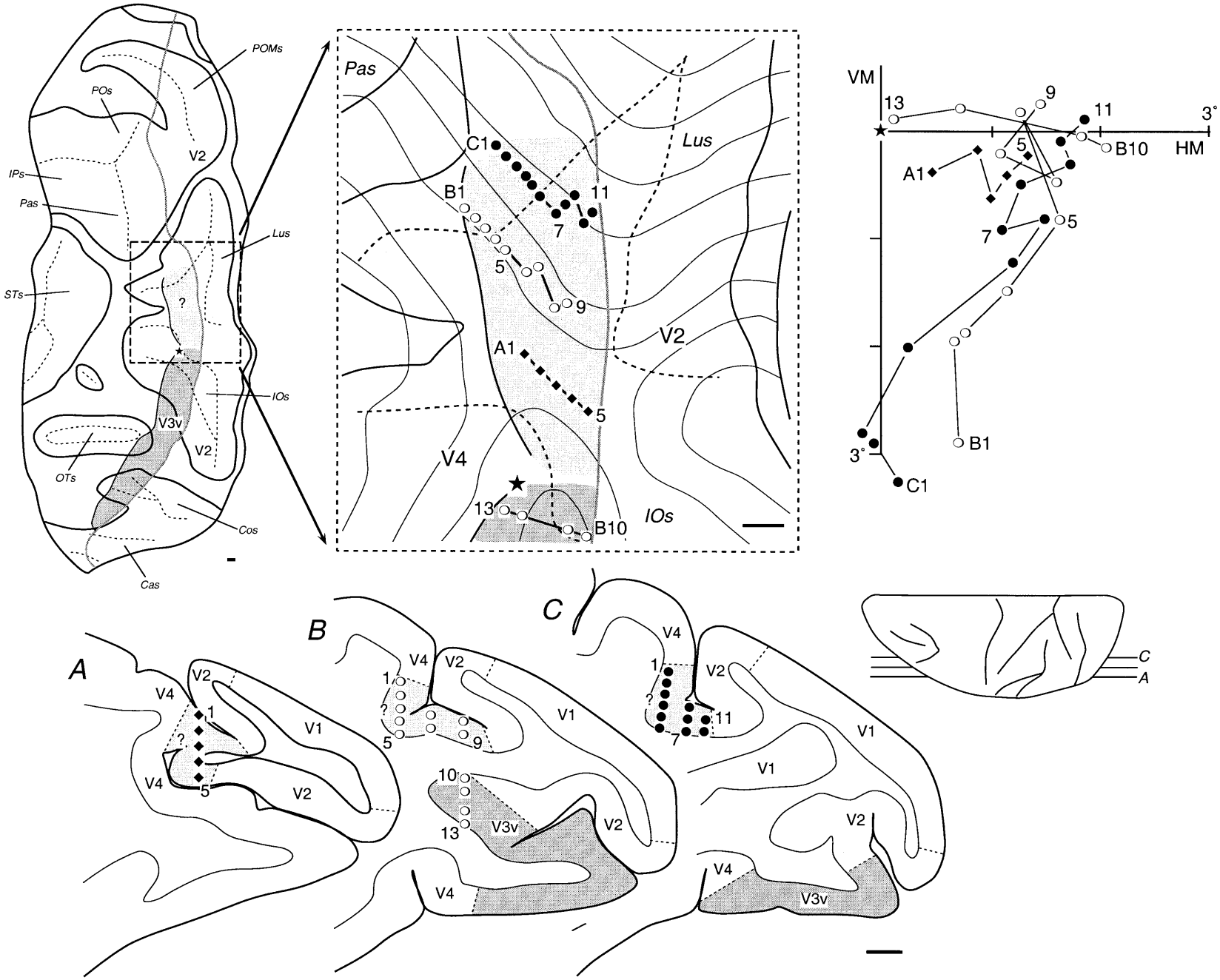
Fig. 9 Electrophysiological borders of the ventral subdivision of the third visual area (*V3v*) (case 6). *Bottom middle* Coronal section through the ventral occipitotemporal cortex of a *Cebus* monkey, at a level indicated in the *bottom left inserts*. The myeloarchitectural boundaries of *V1* (first visual area), *V2* (second visual area), V3v and V4 (fourth visual area; *arrows* and *dashed lines*), as well as twenty-two recording sites (●: V2, □:V3v, ▲: V4) are illustrated. The corresponding receptive fields are depicted in the *top-left* (V2), *top-middle* (V3v) and *top-right* (V4) diagrams, and the receptive field centres are illustrated in the *bottom right* diagram. *Cas* Calcarine sulcus, *IOs* inferior occipital sulcus, *IPs* intraparietal sulcus, *OTs* occipitotemporal sulcus, *STs* superior temporal sulcus

cording sites, in millimetres, to the distance in the visual field between the centres of the receptive fields there recorded, in degrees. The CMF was calculated separately for pairs of sites located along lines parallel (CMF_{pl}) and perpendicular (CMF_{pd}) to the longer axis of V3v (Rosa et al. 1997). Results of this analysis, based on three animals, are shown in Fig. 12 (top and middle). Both CMF_{pl} and CMF_{pd} decreased monotonically with increasing eccentricity, approximately following power functions. However, for any given eccentricity, the CMF_{pl} was typically twice as large as the CMF_{pd} (Fig. 12). The representation of the upper visual quadrant in V3v was, therefore, anisotropic in a way similar to that observed in V2 and V4 (Rosa et al. 1997; Piñon et al. 1998). As a separate measure of the relative emphasis on the representation of central vision, which is independent of the direction of measurement, we measured the areal cortical magnification factor (ACMF, Tusa et al. 1979) for different ranges of eccentricities in V3v and other visual areas. The ACMF was calculated by dividing the area of the cortical surface between two isoeccentricity lines (in mm^2) by the area of the segment of the visual field represented therein (in $degrees^2$). The square root of the ACMF was taken as a measure of the "average" CMF for a given range of eccentricities. This analysis (Fig. 12, bottom) revealed that, in absolute terms, the average CMF for a given eccentricity in V3v was lower than that in areas V1 and V2 (data obtained as part of the studies of Gattass et al. 1987 and Rosa et al. 1988, respectively), but higher than that in the middle temporal area (MT; Fiorani et al. 1989).

The variation of multi-unit receptive-field size in V3v, calculated as the square root of the receptive field area, is shown in Fig. 13 (data pooled from six animals). The data illustrated in the insert of Fig. 13 confirm that, on average, the receptive fields of V3v multi-unit clusters were larger than those of V1 and V2 clusters, but were not different from those of V4 (Piñon et al. 1998). By comparison, receptive fields in MT, a visual area of the "dorsal stream", are much larger (Fiorani et al. 1989).

Discussion

We have studied the visuotopic organisation of the "third tier" visual cortex on the ventral surface of the occipital and posterior temporal lobes in a diurnal New World monkey, the tufted capuchin *(Cebus apella)*. Unlike the dorsal cortex anterior to V2, where there is evidence for multiple visual-field representations, in both New World and Old World monkeys (for reviews, see Felleman and Van Essen 1991; Kaas 1997), the entire strip of cortex inserted between the ventral subdivisions of V2 and V4 forms a single, systematic representation of the upper contralateral quadrant. This region (for which we adopted the designation V3v) is also distinct from adjacent ar-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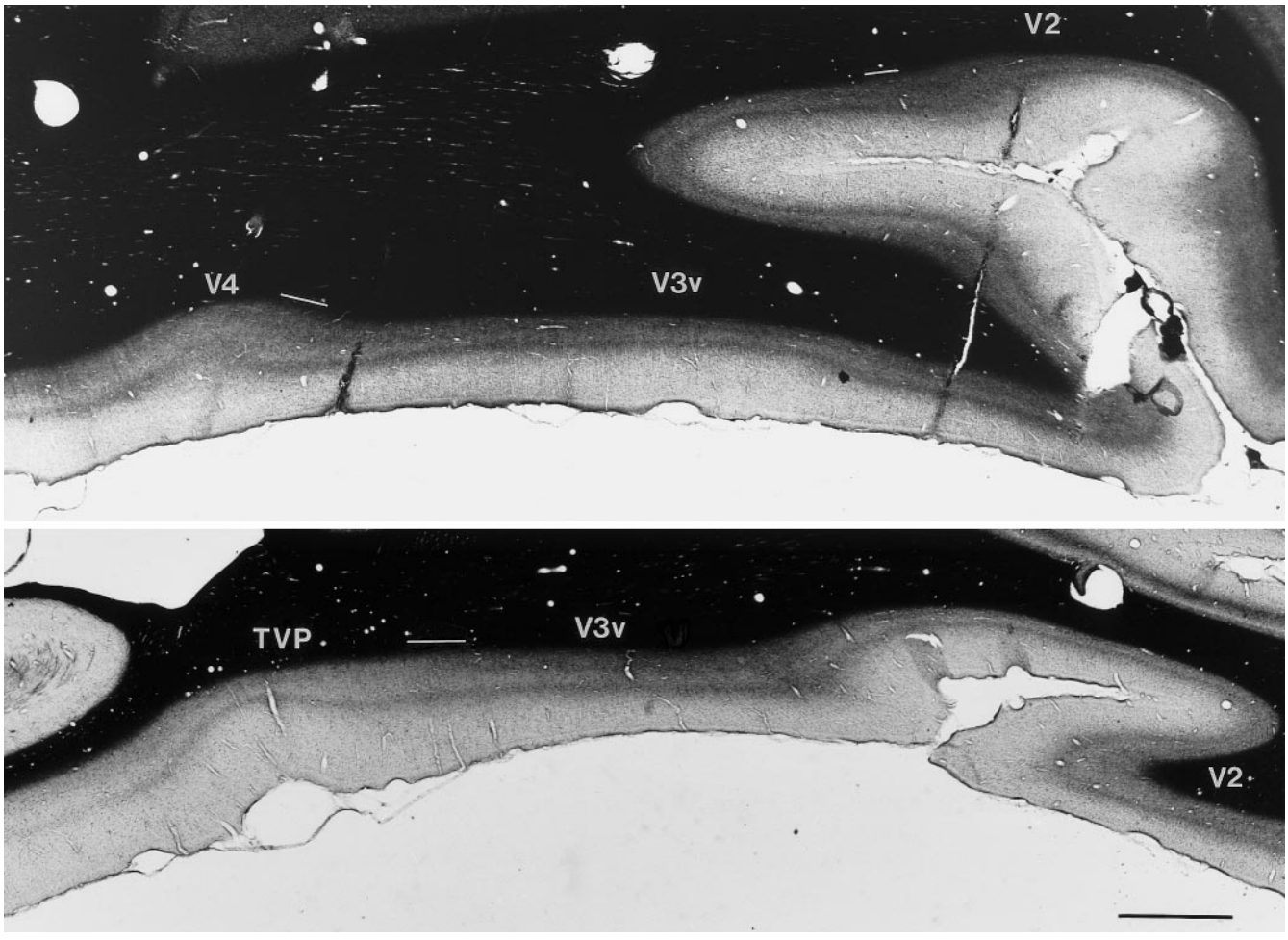

◀ **Fig. 10** Visuotopy of cortex immediately dorsal to the ventral subdivision of the third visual complex (*V3v*) (case 4). *Top left* "Unfolded" map of the caudal half of the left hemisphere. Dorsal is towards the top, and anterior to the left. The *thick continuous lines* indicate the lips of the sulci, and the *dotted lines* the fundi and the main folds. On this representation, the extent of *V2* (second visual area) and V3v (*dark grey*) were drawn using electrophysiological and myeloarchitectural data as guides. The *light-grey zone* encompasses a region (?) immediately dorsal to V3v, which includes a representation of the central lower quadrant. The region included in the *box (dashed)* is illustrated at a higher magnification in the *top, middle panel*. *Top middle* Map of the lateral extrastriate cortex around the junction of the lunate and inferior occipital sulci, showing the location of recording sites, obtained at different parasagittal levels (*bottom*), relative to the sulci. The *thin dashed lines* in this figure correspond to layer 4 contours of individual parasagittal sections used to construct the map. The *star* indicates an electrophysiological estimate of the foveal representation in V3v. *Top right* Diagram of the central visual field, showing the location of receptive field centres relative to the vertical and horizontal meridians (*VM* and *HM*, respectively). *Pas* Paraoccipital sulcus; other abbreviations as in Fig. 4. *Scale bars* (bottom right of each panel): 1 mm

Fig. 11 Myeloarchitectural determination of the borders of the ventral subdivision of the third visual complex (*V3v*). *Top and bottom* Parasagittal sections showing the myeloarchitectural characteristics of V3v and surrounding areas (Heidenhain-Wöelcke stain). The *white lines* overlying layer 6 indicate zones of transition between one myeloarchitectural pattern and another. In the *bottom panel*, the compression of the cortical layers around the fundus of the occipitotemporal sulcus hinders the visualisation of the exact location of the V2/V3v border. Several electrode tracks are visible in the *top panel*. *Scale bar* (bottom right): 2 mm. *V2* Second visual area, *V4* fourth visual area, *TVP* temporal ventral posterior area

eas in terms of myeloarchitecture and neuronal receptive field size.

With the exception of a slight invasion at the V2/V3v border, no lower quadrant representations were observed in V3v or in surrounding ventral cortex. Thus, two possibilities exist: either V3v is an area which contains only a representation of the upper half of the visual field (as suggested for Old World monkeys by Newsome et al. 1986) or V3v constitutes part of a larger area, which encompasses a representation of the lower quadrant in dorsal or dorsolateral extrastriate cortex. This lower quadrant representation could be continuous with the upper quadrant representation (as suggested by the present data and the anatomical results of Rosa et al. 1993) or be located in a segregated "island" of cortex, as suggested by Gattass et al. (1988) for the macaque. We have difficulty accepting the concept of a visual area that only represents the upper (or lower) half of the visual field, as this would probably imply that some neuronal operations are

performed only on inputs arising from the lower or upper parts of the retina, resulting in a sharp functional or perceptual transition between quadrants. Moreover, as reviewed below, there is currently no compelling reason for ruling out a dorsal extension of V3v, although the exact extent of this area remains the subject of debate. Thus, it is more likely that V3v will prove to be part of a larger visual area. Although some of the cat visual areas have been considered to represent only one quadrant of the visual field (e.g. area 21a; Tusa and Palmer 1980), there are alternative ways of interpreting the same data, preserving complete or nearly complete maps of visual space (Sherk 1986; Grant and Shipp 1991; Payne 1993; Sherk and Mulligan 1993). As argued previously (see Rosa and Schmid 1995 for a review), these "improbable" (Kaas 1997) areas with representations restricted to one quadrant often prove, under close scrutiny, to be based on only one of many possible interpretations of the experimental evidence.

Visuotopic organisation of V3v

The present study has yielded the first complete map of the visual field representation in the "third tier" ventral cortex of a New World monkey. The present observations complement those of previous studies (Rosa et al. 1988; Piñon et al. 1998) in rendering a complete and accurate view of the visuotopically organised cortex on the ventral surface of the primate brain. The visual topographies of ventral visual areas in general, and V3v in particular, are similar in the New World monkey *Cebus* and the Old World monkey *Macaca* (Newsome et al. 1986; Gattass et al. 1988). Moreover, the visuotopic maps of ventral cortex obtained by microelectrode maps in these species are both compatible with those obtained in humans by means of functional magnetic resonance imaging (Sereno et al. 1995). These similarities argue in favour of the existence of a highly stereotyped organisation of ventral extrastriate cortex, which has been inherited from common ancestors throughout the simian/humanoid lineage.

In all three species, the horizontal meridian is represented posteriorly and medially in V3v, and the upper sector of the vertical meridian is represented anteriorly and laterally. In addition, the central visual fields are rep-

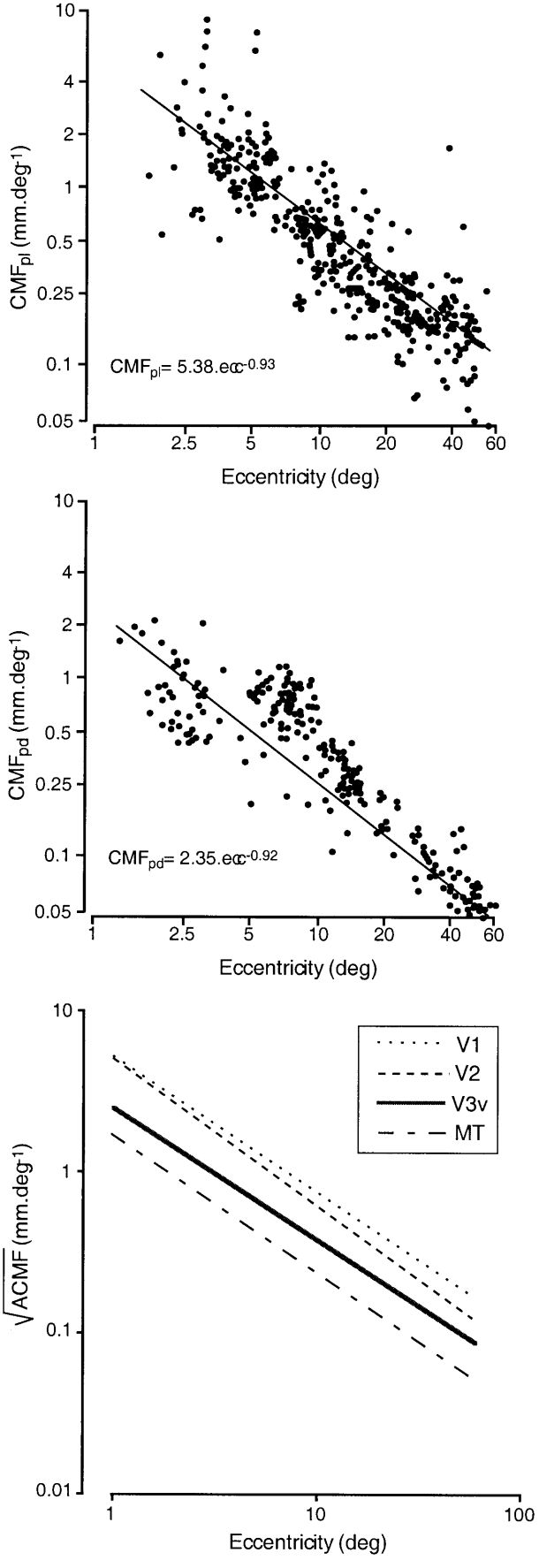

Fig. 12 Cortical magnification factor (*CMF*) as a function of eccentricity in the ventral subdivision of the third visual complex (*V3v*). Two different sets of data, representing the CMF parallel (CMF_{pl}) or perpendicular (CMF_{pd}) to the V2/V3v border, are illustrated (*top* and *middle graphs*, respectively). The data set derives from the pool of recordings in the three best-studied animals (cases 1–3). The best-fitting power functions are indicated by the *thin continuous lines*. *Bottom* Comparison of the square root of the areal cortical magnification factor (*ACMF*) between four visual areas of the *Cebus* monkey. Data from V1, V2 and V3v are all from the same pool of individuals (cases 1–3), while the data from middle temporal area (*MT*) are from a different pool of four animals (Fiorani et al. 1989). *V1* First visual area, *V2* second visual area

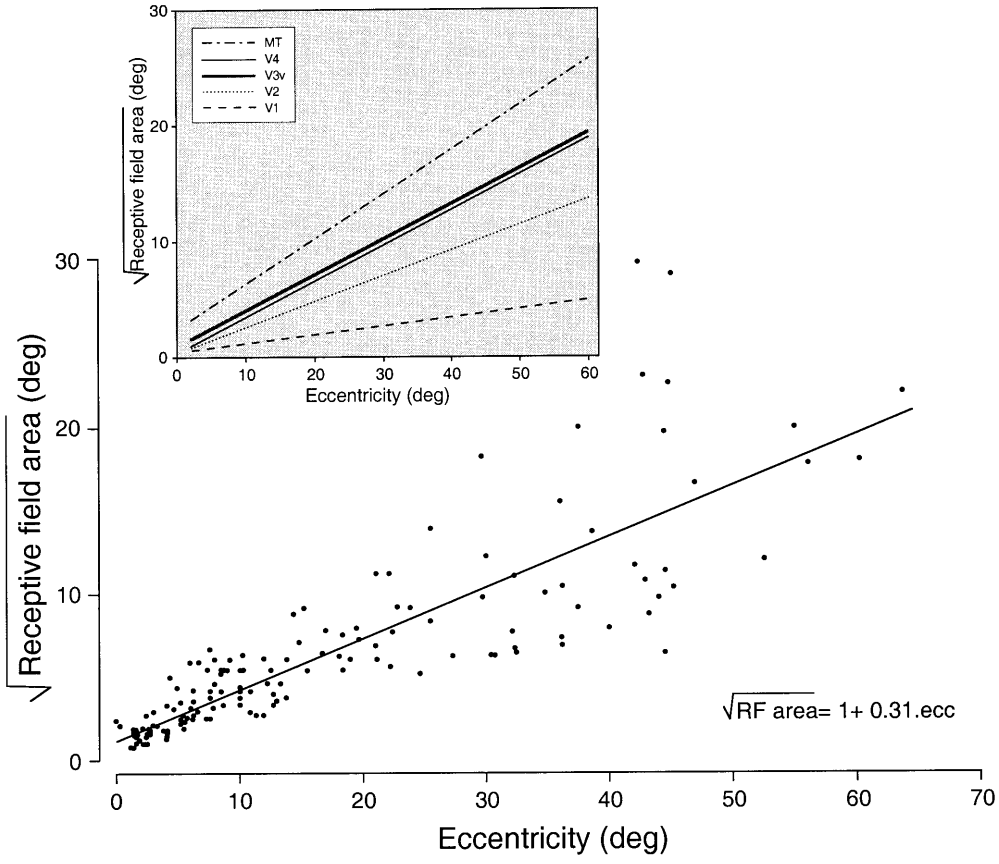

Fig. 13 Receptive-field size as a function of eccentricity in the ventral subdivision of the third visual complex (*V3v*). *Main panel* Receptive-field (*RF*) size (estimated as the square root of the receptive-field area) in V3v. The *line* represents the linear function that best fits the data (receptive fields pooled from six individuals). *Insert* Comparison of the relationship between receptive field size and eccentricity in five visual areas. Each *line* was obtained by fitting linear functions to data pools obtained from no less than four individual monkeys (Gattass et al. 1987; Rosa et al. 1988; Fiorani et al. 1989; Piñon et al. 1998; present results). With the exception of the functions obtained for V3v and the fourth visual area (*V4*), all other comparisons between areas are statistically different at a level of significance of 0.01 (*t* test for slope of linear functions). *V1* First visual area, *V2* second visual area, *MT* middle temporal area

resented laterally, in the banks of the inferior occipital sulcus, while the visual field periphery is represented anteriorly, in the occipitotemporal transition. A similar organisation has also been inferred to exist in the owl monkey (Newsome and Allman 1980), on the basis of less extensive recordings, although the existence of a lower quadrant representation in V3v (or VP) was still deemed possible (see also Sereno et al. 1987; Allman et al. 1994; Kaas 1997). The main difference between the descriptions of V3v in *Cebus* and *Macaca* is with regards to the extent of the visual field representation in V3v. While in *Macaca* the representation is reported to be restricted to the central 30–40° (Gattass et al. 1988), in *Cebus* it extends to at least 60° of eccentricity. A similar difference was observed between area V4 in *Cebus* and *Macaca* (Piñon et al. 1998). As argued previously (e.g. Rosa and Schmid 1995; Rosa et al. 1997), these should be regarded as minimum values, and it is quite possible that V3v includes a representation of the entire upper quadrant. Due to the low magnification factor and large receptive fields of peripheral representations, the "missing" part of the visual field may be represented within a few cubic millimetres of cortex, which could easily have been missed between electrode penetrations.

Receptive field sequences in V3v are often not linear, and overlapping receptive fields can be recorded from multi-unit clusters located over 2 mm apart. It is often the case that receptive field sequences crossing V3v in the centro-peripheral direction (i.e. parallel to the longer axis of this area) show examples of re-representation (e.g. Fig. 8), while sequences crossing V3v along its shorter axis (e.g. Fig. 9) are more regular. We have also observed that the CMF in V3v is greater, and shows a larger scatter in the distribution, when measured between pairs of sites located along imaginary lines approximately parallel to the V2/ V3v border as compared with perpendicular to this border. In all of these aspects, the visuotopic organisation of V3v resembles that of V2 (Rosa et al. 1988). This type of redundant mapping is correlated, in V2, with the existence of functionally distinct stripe-like modules that cross this area perpendicular to its borders with V1 and V3v (Rosa et al. 1988; Roe and Ts'o 1995). This arrangement requires each portion of the visual field to be re-represented in adjacent compartments, resulting in the CMF anisotropy (Roe and Ts'o 1995). The similarity in visuotopic organisation suggests that V3v may also be formed by stripe-like modules which cross this area perpendicular to its longer axis (see also Newsome et al. 1986). In agreement with this model, Tootell et al. (1985) have observed, using cytochrome-oxidase histochemistry in owl and squirrel monkeys, a coarse pattern of bands in the region of V3v.

Is V3v part of a larger area?

The present results argue against the idea that V3v represents the entire extent of a visual area in New World

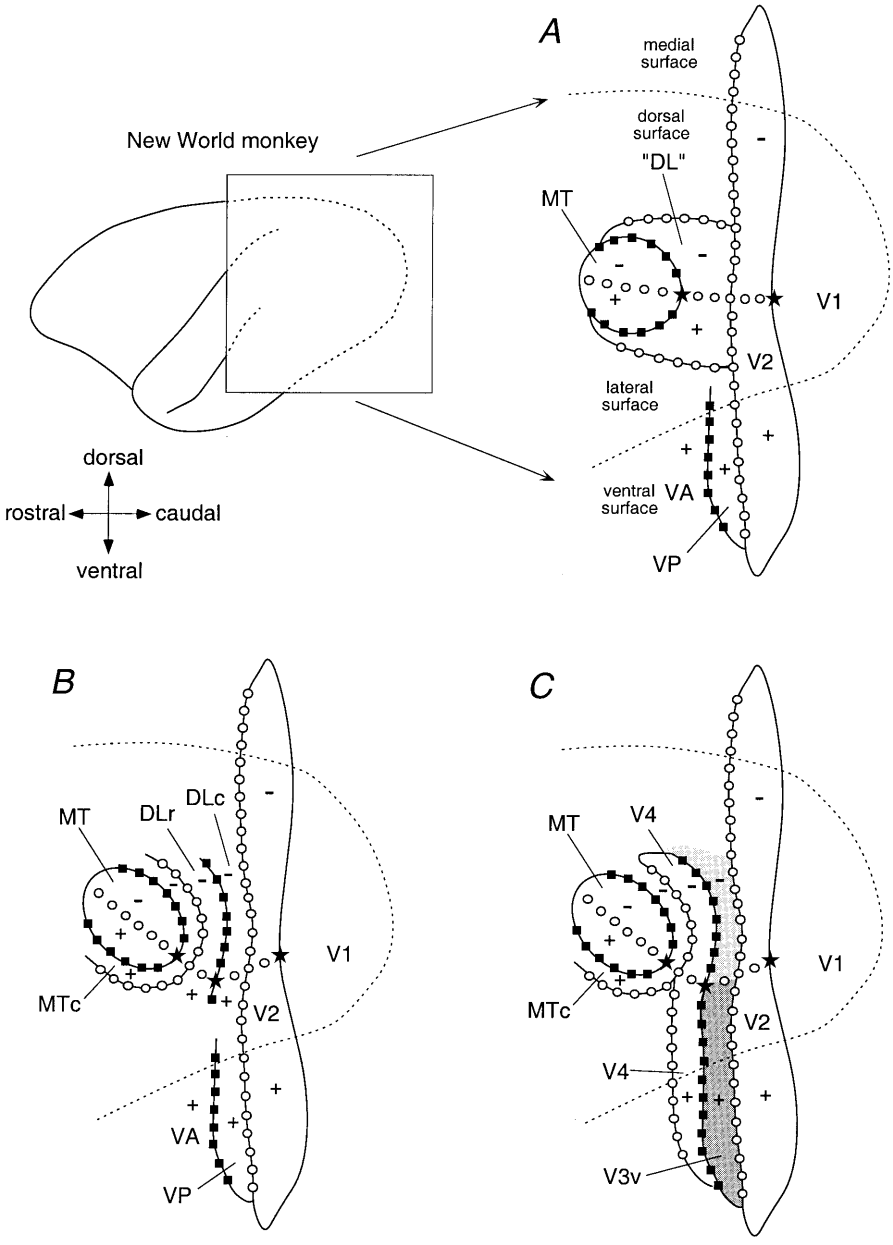

Fig. 14A–C Organisation of ventrolateral extrastriate areas in New World monkeys. *Top left* Schematic representation of a lateral view of the left hemisphere of the brain of a New World monkey, highlighting the region shown in detail in **A–C** (*dashed outline* and *box*). **A** Original view, largely based on the works of Allman and Kaas (1974) and Newsome and Allman (1980) in the owl monkey. The middle temporal area (*MT*) was deemed to be circular in shape, and a large dorsolateral area (*DL*) spanned the entire expanse of cortex between areas *V2* (second visual area) and MT. Ventral cortex included ventral anterior (*VA*) and ventral posterior (*VP*) areas, including largely upper quadrant representations, but also a "highly compressed" lower quadrant representation. *Symbols* indicating the visuotopy of cortical areas are according to Fig. 1. **B** A more recent re-interpretation, based on studies in several species of New World primate, including owl, marmoset and squirrel monkeys. Area MT appears as an elongated oval, with the representation of the horizontal meridian slanted relative to the horizontal plane. The original territory of DL is subdivided into three representations of the visual field, namely the caudal and rostral subdivisions of DL (*DLc* and *DLr*, respectively), and the *MTc*, or "middle temporal crescent" (e.g. Kaas and Morel 1993; Allman et al. 1994; Sereno et al. 1994; Rosa et al. 1997; Rosa and Elston 1998). **C** A hypothesis based on the present data and parallel studies in *Cebus* monkeys. Whereas the interpretation illustrated in **B** suggests that the dorsolateral areas have small representations of the upper quadrant, which are independent of those in ventral areas (VA and VP), in **C** these representations together form a single map of the upper quadrant. Indeed, the rostral subdivision of DL and the ventral anterior upper-quadrant representation (VA) together have been shown to form a fourth visual area (*V4*), which includes a representation of both quadrants (Rosa 1997; Piñon et al. 1998). We suggest that the upper quadrant representation *V3v* (ventral subdivision of third visual complex), mapped in the present study (*dark grey*), is also likely to extend dorsally, to encompass a lower quadrant representation originally assigned to the caudal subdivision of DL (Rosa 1997; Rosa et al. 1997; see also Fig. 10). The presumptive extent of this lower quadrant representation is indicated in *light grey*. Note that the exact extent of this lower quadrant representation is still unclear; it may not extend as far medially as to include the darkly myelinated area "V3d" or DM (Beck and Kaas 1999)

monkeys. The sector of the visual field represented in V3v largely excludes the lower quadrants (Fig. 7), with the exception of occasional receptive fields of cells near the border with V2. These receptive fields, which cover only a few degrees below the horizontal meridian, were assigned either to V2 or V3v on the basis of their size (e.g., Fig. 8). There are no other lower-quadrant representations adjacent to V3v in ventral cortex. Thus, previous references to "a highly compressed representation of the lower quadrant" (Weller and Kaas 1985; Burkhalter et al. 1986) may refer to the V2/ V3v border region. The degree of invasion of the lower quadrant by receptive field centres of cells at the V2/ V3v border is, in the vast majority of cases, within the margin of error introduced by the technique used for estimating the position of the fovea (0.5–1°) and was never found to exceed 2°. Moreover, in areas with a second-order representation of the visual field, there is usually a slight overlap between the sectors of the visual field represented on each side of the field discontinuity (for example, between the parts of the visual field represented in dorsal and ventral V2; Rosa et al. 1988, 1994, 1997). Thus, the existence of these receptive fields that invade the lower quadrant cannot be used as a valid argument in favour of V3v as a "complete" area, representing both quadrants.

Why, then, have previous investigators concluded that V3v is an area restricted to the ventral cortex? Early studies of both the macaque and the owl monkey illustrated a V3v (or "VP") that is bordered dorsally by V4, or the dorsolateral area (DL), respectively (e.g. Newsome and Allman 1980; Van Essen 1985). In the owl monkey, electrophysiological recordings of lateral extrastriate cortex initially suggested that DL was an area that encompassed all the cortex between V2 and MT, including both a lower field representation dorsally and an upper field representation ventrally (Allman and Kaas 1974; see Fig. 14A). Thus, at the time Newsome and Allman (1980) detected the existence of VP (V3v), which included an upper quadrant representation in ventral cortex, it was logically concluded that it represented an area distinct from DL.

The organisation of DL has, however, been extensively revised in recent years, on the basis of both electrophysiological recordings (Sereno et al. 1994; Rosa 1997; Rosa and Elston 1998) and connections (Cusick and Kaas 1988; Kaas and Morel 1993; Rosa et al. 1993). The modern view is that the DL "complex" (Fig. 14B) includes at least three areas, the most posterior of which (i.e. the one in "third tier" extrastriate cortex) is referred to as the caudal subdivision of the dorsolateral area (DLc; Cusick and Kaas 1988) or the dorsolateral posterior area (DLp; Sereno et al. 1994). Important for the present argument is the fact that the re-examination of this region has failed to support the prediction that DLc includes a significant upper quadrant representation in dorsolateral cortex. For example, recent electrophysiological data extending to the lateral edge of the owl monkey's occipital lobe revealed an extensive representation of the lower field and central vision, but no upper quadrant representation (e.g. Fig. 6 of Sereno et al. 1994). Moreover, studies in the marmoset, another New World monkey, have concluded that V3v (VP) blends gradually into the posterior part of DL, without re-representation of portions of the visual field (Rosa 1997 and unpublished observations), a view compatible with the data illustrated in Fig. 10. In addition, the myeloarchitecture of ventral and dorsolateral areas is similar (Rosa et al. 1993; Piñon et al. 1998). Finally, much of the upper quadrant representation originally assigned to "DL" by Allman and Kaas (1974) has been shown to belong to an area distinct from DLc, named the "middle temporal crescent" (MTc). The MTc is very different from the remaining parts of the DL "complex" in terms of connections, architecture and response properties (Kaas and Morel 1993; Rosa and Elston 1998). Thus, in New World monkeys, the main logical impediments for considering the posterior part of DL and VP as parts of the same area have been removed (see also Rosa 1997).

In Old World monkeys, the dorsal and ventral parts of "V3", as originally proposed by Zeki (1969), have been deemed functionally different on the basis of single-unit properties (Burkhalter et al. 1986). However, the same type of investigation has emphasised the similarity in response properties between V3v (VP) and parts of the V4 complex (Burkhalter and Van Essen 1986). Both V3v and the posterior subdivision of V4, including the anterior bank of the lunate sulcus, have neurones that are highly selective for shape and colour, but are not strongly direction selective (Zeki 1983). These properties, which contrast with those found among neurones in dorsal V3 (V3d; Felleman and Van Essen 1987), and the connections of V3v with areas of the "ventral stream" (Felleman et al. 1997) suggest a role in extraction of visual features related to object recognition. These previous studies in the macaque, and the present study in the *Cebus* monkey, raise the possibility that an extended V3v is an area common to both New and Old World monkeys. In the macaque, the boundaries of this revised area may encompass both area VP and the posterior part of V4. A revision and unification of the nomenclature of these extrastriate areas may become necessary when more information becomes available. One possibility would be to adopt the designation "DM" (dorsomedial area) for the densely myelinated area that overlaps with V3d, as suggested by Krubitzer and Kaas (1993), and to refer to the revised and extended V3v as either DLc or VP (see also Rosa and Schmid 1995). A second possibility would be to maintain the designations dorsal V3 and ventral V3, in recognition of their "third tier" location, but with the understanding that the borders of V3v extend beyond the upper-quadrant representation (present results), and that V3d may also include an upper-quadrant representation (Beck and Kaas 1999). Finally, a new nomenclature may be needed, which more accurately reflects the anatomical position of these areas.

We therefore conclude, based on the present observations as well as recent studies in other species, that there is no logical reason why V3v in *Cebus* has to be regard-

ed as an area restricted to ventral cortex, or incomplete in terms of visual field representation. Neuroimaging studies in humans (e.g. Sereno et al. 1995; Tootell et al. 1997), electrophysiological and architectural data in New World monkeys (Rosa et al. 1988, 1993, 1997; present observations) and single-unit responses in macaques (Zeki 1983; Burkhalter and Van Essen 1986) all converge in support of the view that the area including V3v also encompasses a lower-quadrant representation that extends at least to dorsolateral cortex (e.g. Fig. 10). However, until extensive recording data including the entire extent of the cortex anterior to V2 (dorsally and ventrally) become available, the exact dorsal extent of this area will remain uncertain.

Note added in proof A more recent study in a different species of New World monkey has confirmed that ventral V3 is part of a larger area, which includes a representation of the lower visual field in dorsolateral cortex (Rosa and Tweedale 2000).

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References

Allman JM, Kaas JH (1974) A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). Brain Res 81:199–213

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

Allman J, Jeo R, Sereno M (1994) The functional organisation of visual cortex in owl monkeys. In: Baer JF, Weller RE, Kakoma I (eds) *Aotus:* the Owl Monkey. Academic Press, San Diego, pp 287–320

Beck PD, Kaas JH (1999) Cortical connections of the dorsomedial visual area in Old World macaque monkeys. J Comp Neurol 406:487–502

Boussaoud D, Desimone R, Ungerleider LG (1991) Visual topography of area TEO in the macaque. J Comp Neurol 306:554–575

Burkhalter A, Van Essen DC (1986) Processing of color, form and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey. J Neurosci 6:2327–2351

Burkhalter A, Felleman DJ, Newsome WT, Van Essen DC (1986) Anatomical and physiological asymmetries related to visual areas V3 and VP in macaque extrastriate cortex. Vision Res 26:63–80

Cragg BG, Ainsworth A (1969) The topography of the afferent projections in the circumstriate visual cortex of the monkey studied by the Nauta method. Vision Res 9:733–747

Cusick CG, Kaas JH (1988) Cortical connections of area 18 and dorsolateral visual cortex in squirrel monkeys. Vis Neurosci 1:211–237

Falk D (1980) Comparative study of the endocranial casts of New and Old World monkeys. In: Ciochon RL, Chiarelli AB (eds) Evolutionary biology of the New World monkeys and continental drift. Plenum Press, New York, pp 275–292

Felleman DJ, Van Essen DC (1987) Receptive field properties of neurones in area V3 of macaque monkey extrastriate cortex. J Neurophysiol 57:889–920

Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in primate cerebral cortex. Cereb Cortex 1:1–47

Felleman DJ, Burkhalter A, Van Essen DC (1997) Cortical connections of areas V3 and VP of macaque monkey extrastriate visual cortex. J Comp Neurol 379:21–47

Fiorani M, Gattass R, Rosa MGP, Sousa APB (1989) Visual area MT in the *Cebus* monkey: location, visuotopic organisation, and variability. J Comp Neurol 287:98–118

Gattass R, Gross CG (1981) Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the macaque. J Neurophysiol 46:621–638

Gattass R, Sousa APB, Covey E (1985) Cortical visual areas of the macaque: possible substrates for pattern recognition mechanisms. In: Chagas C, Gattass R, Gross CG (eds) Pattern recognition mechanisms. Pontificial Academy of Sciences, Vatican City, pp 1–20

Gattass R, Sousa APB, Rosa MGP (1987) Visual topography of V1 in the *Cebus* monkey. J Comp Neurol 259:529–548

Gattass R, Sousa APB, Gross CG (1988) Visuotopic organisation and extent of V3 and V4 of the macaque, J Neurosci 8:1831–1845

Gattass R, Sousa APB, Mishkin M, Ungerleider LG (1997) Cortical projections of area V2 in the macaque. Cereb Cortex 7:110–129

Grant S, Shipp S (1991) Visuotopic organisation of the lateral suprasylvian area and of an adjacent area of the ectosylvian gyrus of the cat cortex: a physiological and connectional study. Vis Neurosci 6:315–338

Kaas JH (1997) Theories of visual cortex organisation in primates. In: Rockland KS, Kaas JH, Peters A (eds) Cerebral cortex, vol 12. Extrastriate cortex in primates. Plenum Press, New York, pp 91–125

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

Krubitzer LA, Kaas JH (1993) The dorsomedial visual area of owl monkeys: connections, myeloarchitecture, and homologies in other primates. J Comp Neurol 334:497–528

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

Newsome WT, Maunsell JHR, Van Essen DC (1986) Ventral posterior visual area of the macaque: visual topography and areal boundaries. J Comp Neurol 252:139–153

Payne BR (1993) Evidence for visual cortical area homologs in cat and macaque monkey. Cereb Cortex 3:1–25

Piñon MC, Gattass R, Sousa APB (1998) Area V4 in *Cebus* monkey: extent and visuotopic organisation. Cereb Cortex 8:685–701

Roe A, Ts'o DY (1995) Visual topography in primate V2: multiple representation across functional stripes. J Neurosci 15:3689–3715

Rosa MGP (1997) Visuotopic organisation of primate extrastriate cortex. In: Rockland KS, Kaas JH, Peters A (eds) Cerebral cortex, vol 12. Extrastriate cortex in primates. Plenum Press, New York, pp 127–203

Rosa MGP, Elston GN (1998) Visuotopic organisation and neuronal response selectivity for direction of motion in visual areas of the caudal temporal lobe of the marmoset monkey (*Callithrix jacchus*): middle temporal area, middle temporal crescent, and surrounding cortex. J Comp Neurol 393:505–527

Rosa MGP, Schmid LM (1995) Visual areas in the dorsal and medial extrastriate cortices of the marmoset. J Comp Neurol 359:272–299

Rosa MGP, Tweedale R (2000) Visual areas in lateral and ventral extrastriate cortices of the marmoset monkey. J Comp Neurol (in press)

Rosa MGP, Sousa APB, Gattass R (1988) Representation of the visual field in the second visual area in the *Cebus* monkey. J Comp Neurol 275:326–345

Rosa MGP, Soares JGM, Fiorani M, Gattass R (1993) Cortical afferents of visual area MT in the *Cebus* monkey: possible homologies between New and Old World monkeys. Vis Neurosci 10:827–855

Rosa MGP, Schmid LM, Pettigrew JD (1994) Organisation of the second visual area in the megachiropteran bat *Pteropus*. Cereb Cortex 4:52–68

Rosa MGP, Fritsches KA, Elston GN (1997) The second visual area in the marmoset monkey: visuotopic organisation, magnification factors, architectonical boundaries, and modularity. J Comp Neurol 387:547–567

Sereno MI, McDonald CT, Allman JM (1987) Multiple visual areas between V2 and MT in the owl monkey. Soc Neurosci Abstr 13:625

Sereno MI, McDonald CT, Allman JM (1994) Analysis of retinotopic maps in extrastriate cortex. Cereb Cortex 4:601–620

Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RBH (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. Science 268:889–893

Sherk H (1986) Location and connections of visual cortical areas in the cat's suprasylvian sulcus. J Comp Neurol 247:1–31

Sherk H, Mulligan KA (1993) A reassessment of the lower visual field map in striate-recipient lateral suprasylvian cortex. Vis Neurosci 10:131–158

Sousa APB, Piñon MCGP, Gattass R, Rosa MGP (1991) Topographic organisation of cortical input to striate cortex in the *Cebus* monkey: a fluorescent tracer study. J Comp Neurol 308:665–682

Tootell RBH, Hamilton SL, Silverman MS (1985) Topography of cytochrome oxidase activity in the owl monkey. J Neurosci 5:2786–2800

Tootell RBH, Mendola JD, Hadjikhani NK, Ledden PJ, Liu AK, Reppas JB, Sereno MI, Dale AM (1997) Functional analysis of V3A and related areas in human visual cortex. J Neurosci 15:7060–7078

Tusa RJ, Palmer LA (1980) Retinotopic organisation of areas 20 and 21 in the cat. J Comp Neurol 193:147–164

Tusa RJ, Rosenquist AC, Palmer LA (1979) Retinotopic organisation of areas 18 and 19 in the cat. J Comp Neurol 185:657–678

Van Essen DC (1985) Functional organisation of primate visual cortex. In: Peters A, Jones EG (eds) Cerebral Cortex, vol 3. Visual cortex. Plenum Press, New York, pp 259–329

Van Essen DC, Maunsell JHR (1980) Two-dimensional maps of the cerebral cortex. J Comp Neurol 191:255–281

Van Essen DC, Newsome WT, Bixby JL (1982) The pattern of interhemispheric connections and its relationship to extrastriate visual areas in the macaque monkey. J Neurosci 2:265–283

Van Essen DC, Newsome WT, Maunsell JHR, Bixby JL (1986) The projections from striate cortex (V1) to areas V2 and V3 in the macaque monkey: asymmetries, areal boundaries, and patchy connections. J Comp Neurol 244:451–480

Weller RE, Kaas JH (1985) Cortical projections of the dorsolateral visual area in owl monkeys: the prestriate relay to inferior temporal cortex. J Comp Neurol 234:35–59

Zeki SM (1969) Representation of central visual fields in prestriate cortex of monkey. Brain Res 14:271–291

Zeki SM (1977) Simultaneous anatomical demonstration of the representation of the vertical and horizontal meridians in areas V2 and V3 of rhesus monkey visual cortex. Proc R Soc Lond B Biol Sci 195:517–523

Zeki SM (1983) The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. Proc R Soc Lond B Biol Sci 217:449–470