

Cortical visual areas in monkeys: location, topography, connections, columns, plasticity and cortical dynamics

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The visual system is constantly challenged to organize the retinal pattern of stimulation into coherent percepts. This task is achieved by the cortical visual system, which is composed by topographically organized analytic areas and by synthetic areas of the temporal lobe that have more holistic processing. Additional visual areas of the parietal lobe are related to motion perception and visuomotor control. V1 and V2 represent the entire visual field. MT represents only the binocular field, and V4 only the central 30°–40°. The parietal areas represent more of the periphery. For any eccentricity, the receptive field grows at each step of processing, more at anterior areas in the temporal lobe. Minimal point image size increases towards the temporal lobe, but remains fairly constant toward the parietal lobe. Patterns of projection show asymmetries. Central V2 and V4 project mainly to the temporal lobe, while peripherals V2 (more than 30°) and V4 (more than 10°) also project to the parietal lobe. Visual information that arrives at V1 projects to V2, MT and PO, which then project to other areas. Local lateral propagation and recursive loops corroborate to perceptual completion and filling in. Priority connections to temporal, parietal and parieto-temporal cortices help construct crude early representations of objects, trajectories and movements.

Keywords: topography; connections; immunohistochemistry; single-units; columns; monkey

1. INTRODUCTION

One aspect of the organization of the visual cortex in primates is the presence of multiple representations of the visual field. Although the existence of these visuotopic maps has been known for more than 60 years (Talbot & Marshall 1940; Talbot 1942), there are still many open issues regarding their meaning and organization. The processing of visual information takes place in the occipital, temporal and parietal cortices, which contain a large number of visual areas (Zeki 1969, 1971, 1973, 1974, 1978; Gattass & Gross 1981; Gattass *et al.* 1981, 1986, 1987, 1990; Rosa *et al.* 1988*b*, 1991; Fiorani *et al.* 1989; Felleman & Van Essen 1991; Rosa *et al.* 1993; Neuenschwander *et al.* 1994; Colby *et al.* 1988; Piñón *et al.* 1998). Descriptions of the number, boundaries and visuotopic organization of cortical visual areas vary not only among primates, but also between studies in the same species by different groups.

In primates, the main target of the projections of the lateral geniculate nucleus is the striate cortex, also named as primary visual cortex, area 17 of Brodmann,

area OC of von Bonin & Bailey (1947) or visual area 1 (V1). The primary visual cortex is the first of a series of visual areas located in the posterior and medial portions of the occipital cortex. Daniel & Whitteridge (1961) studied its topographic organization and described in the macaque monkey a systematic representation of the retinal surface, with large emphasis on the representation of the fovea, with the representation of the vertical meridian located at the V1/V2 border, and that of the horizontal meridian running across the area, from the opercular surface to the depth of the calcarine fissure. Area V2 is the major cortical projection target of V1 (Kuypers *et al.* 1965; Cragg & Ainsworth 1969; Zeki 1969, 1971, 1976; Jones & Powell 1970; Zeki & Sandeman 1976; Rockland & Pandya 1979, 1981; Weller & Kaas 1983; Van Essen *et al.* 1986; Shiwa 1987; Lund *et al.* 1991). It was studied in the *Saimiri* by Cowey (1964) who showed that the central representation of this area shares the representation of the vertical meridian with V1. The entire retinotopic organization of V2 was described by Allman & Kaas (1974) in the owl monkey *Aotus trivirgatus*. These authors showed an organization for V2, which they referred to as a second-order transformation of the visual field that has the representation of the vertical meridian at its posterior border

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One contribution of 12 to a Theme Issue 'Cerebral cartography 1905–2005'.

and the horizontal meridian at its anterior border. Allman and Kaas extended their studies to more anterior regions relative to V2 and described a number of additional visual areas (Allman & Kaas 1971, 1974; Allman *et al.* 1972). In the macaque, pioneer anatomical and electrophysiological studies on the central representation of the extrastriate areas completed by Zeki established a basic framework for the cortical organization of visual areas V2, V3 and V4 as concentric rings around area V1 (Zeki 1969, 1971, 1976). In his studies, Zeki used the regularity of the progressions of receptive field centres in oblique penetrations to the cortical layers as criteria to evaluate the topographic organization or re-representations of the retinal projections onto these areas. The observation of re-representations along oblique penetrations in the prelunate gyrus led Zeki to describe the V4 complex as having multiple representations of the visual field. Similarly, using the same method and the observation of a large overlap of V1 projections to the superior temporal sulcus (sts), Zeki described the 'movement area' of the superior temporal sulcus as a non-topographically organized visual area. This area was later named area MT by other authors (Gattass & Gross 1981; Van Essen *et al.* 1981; Desimone & Ungerleider 1986) to acknowledge its homology in location and topographic organization with the visual area located in the middle temporal lobe of New World monkeys named MT by Allman & Kaas (1971). Gattass and his colleagues extended Zeki's observations to more anterior and medial areas in the extrastriate cortex, describing the locations, topographic organizations and extent of the visual field representation of areas V2, V3, V4 and MT (Gattass & Gross 1981; Gattass *et al.* 1981, 1988a,b).

In the past 30 years, *Macaca* and *Cebus* have been used as experimental models, inasmuch as they are diurnal monkeys similar in brain size, sulcal pattern as well as in certain aspects of visual behaviour. In the *Macaca*, the visuotopic organization of visual areas V2, V3, V4 and MT (Daniel & Whitteridge 1961; Gattass & Gross 1981; Gattass *et al.* 1981, 1988a,b), as well as the projections of V2 and the connections of V4 have been described (Gattass *et al.* 1986, 1997; Ungerleider *et al.* 2005). In the *Cebus*, we have defined the location and the topographic organization of areas V1, V2, V4, MT (V5), PO and POd (Gattass *et al.* 1987; Rosa *et al.* 1988b; Fiorani *et al.* 1989; Neuenschwander *et al.* 1994; Piñón *et al.* 1998). In both animals, these areas contain partial or complete representations of the contralateral visual hemi-field in each corresponding hemisphere.

Our studies of V1 and V2 in the *Cebus* revealed that these areas contain the representation of the entire visual field, whereas area MT (V5) contains only the representation of the binocular portion of the visual field (Gattass *et al.* 1987, 1990; Rosa *et al.* 1988b; Fiorani *et al.* 1989). The study of V4 in both *Cebus* and *Macaca* revealed that this area has an even more restricted representation of the visual field, extending to only 30° to 40° eccentricity (Gattass 1988a,b; Piñón *et al.* 1998). We found that the representations of V1 and V2 were anisotropic, predicting the arrangement of cortical modules (columns) orthogonal to the long axis

of the anisotropies (Gattass *et al.* 1987; Rosa *et al.* 1988b). We have also studied the feedback cortical connections to visual area V1 (Sousa *et al.* 1991). More recently, the areas of the temporal and parietal lobes were divided based on the connections of areas V2 and V4 of the macaque (Gattass *et al.* 1997; Ungerleider *et al.* 2005). We also subdivided the intraparietal and superior temporal sulcus of the *Cebus* into multiple areas based on several criteria such as: afferent and efferent connections, cytoarchitecture, myeloarchitecture, histochemistry for cytochrome *c* oxidase (CytOx) and for NADPH-diaphorase, and immunohistochemistry for neurofilaments and for calcium-binding proteins (Mariani & Gattass 1996; Nascimento-Silva 2004). The study of single-unit responses and visual topography, connections and architecture of the posterior superior temporal sulcus in *Cebus* revealed that the area defined by Newsome & Wurtz (1981) and Maunsell & Van Essen (1983) as MST was composed of at least three areas (Nascimento-Silva 2004). Figure 1 shows the location of the cortical visual areas described in *Cebus* and *Macaca*. These areas were grouped based on the set of criteria that defined the areas. We also analysed the connection pattern of functionally distinct modules of V2, such as those revealed by CytOx histochemistry, by injecting retrograde fluorescent tracers in V4, MT and PO areas of different streams of visual information processing. The results suggested that different sets of modules of V2 participate in different networks of visual information processing (Nascimento-Silva *et al.* 2003).

In this paper, we review the organization of cortical visual areas in *Macaca* and *Cebus* monkeys, focusing on their location, visual topography, connections, columnar organization, cortical plasticity and cortical dynamics. First, we discuss the concept of a cortical visual area and the limitations of each method used to study the areas. Then, we review the organization of the visual areas described by electrophysiological mapping, by connective methods and by immunohistochemical, myeloarchitectural and cytoarchitectural methods. In this process, we discuss the types of visual map present in each area. Then, studying the maps in more detail, we focus our attention to local representations in cortical modules, some of them revealed by cytochrome oxidase histochemistry. We also address the contribution of local, feed-forward and feedback connections. Finally, we present a view of the visual system as a topographically organized distributed network.

2. CONCEPTUAL AND METHODOLOGICAL CONSIDERATIONS

(a) *Definition of cortical visual areas*

The definition of a cortical visual area takes into account combined evidences obtained by different experimental paradigms. Anatomical, electrophysiological and behavioural methods can contribute to definition of a cortical visual area. In our view, the method that offers the most complete and precise description of the visuotopic organization of cortical areas is that of systematic electrophysiological mapping

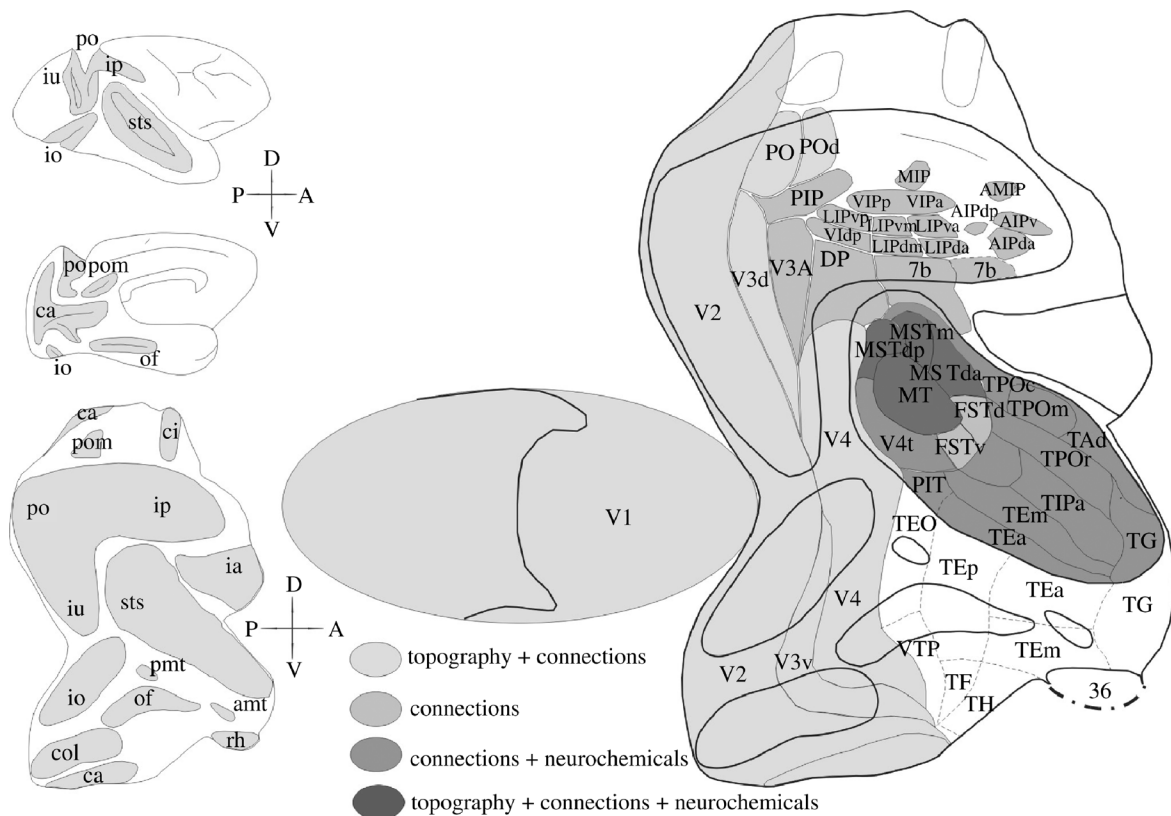


Figure 1. Two-dimensional reconstruction of the monkey cortex, showing the location of the extrastriate visual areas found in *Macaca* and in *Cebus*. The flattened map of V1 was separated from the extrastriate cortex to allow physical flattening of the 3D model of the posterior portion of the hemisphere. Heavy lines indicate the boundaries of the sulci; thin lines indicate the boundaries of the visual, visuomotor and polysensory areas. The dashed lines indicate the boundaries of the temporal areas defined in the macaque, based on cortical connections. The dot-dash lines indicate the boundaries between the neocortex and allocortex. Different grey densities label areas defined by different combination of methods. The grey area on the lateral and medial views of the hemisphere (upper right) and indicated on the 2D reconstruction (lower right) indicate cortex within sulci. Different patterns illustrate the criteria used to define the borders of the areas. White areas in the temporal lobe were defined only in the *Macaca*. d, dorsal; v, ventral; p, posterior; a, anterior. For names of areas and sulci, see glossary.

of neural responses to visual stimulation. This method was first applied to primate extrastriate areas more than 40 years ago (Cowey 1964; Hubel & Wiesel 1970; Allman & Kaas 1971; Dubner & Zeki 1971; Gross *et al.* 1972). Electrophysiological mapping has proven to be an adequate method to reveal many retinotopically organized cortical visual areas in the primate brain (Van Essen & Zeki 1978; Gattass & Gross 1981; Gattass *et al.* 1981, 1987, 1988a, 1990; Burchhalter & Van Essen 1983; Maunsell & Van Essen 1983; Felleman & Van Essen 1984; Ungerleider & Desimone 1986b; Rosa *et al.* 1988b, 1993; Fiorani *et al.* 1989; Boussaoud *et al.* 1990; Neuenschwander *et al.* 1994; Piñón *et al.* 1998).

With new improvements, it is now possible to use multiple electrodes to sample a much larger area in a single animal, therefore reducing the error involved in pooling topographical data obtained in different experimental sessions and in different individuals into a single 'representative' map for a given area. In principle, it is possible to combine high-resolution topographic mapping of visual responses with single-unit analysis of response properties, thereby yielding a much more reliable definition of boundaries between areas. In practice, however, one is still confronted with the opposing alternatives of mapping a few simple parameters, such as receptive field size and position, across a large extent of cortex, or conducting

quantitative analysis of cell response properties at fewer sites. Long-term chronic preparations, while allowing a detailed study of large populations of single-units, suffer from limited precision regarding the location of the recording sites, especially within the sulci. As high-resolution neural imaging techniques *in vivo* become more accessible to research laboratories, the precise three-dimensional (3D) reconstruction of recording sites during experimental sessions may become possible. This development will allow the combination of topographic and functional analyses of large populations of neurons in single animals.

(b) Data interpolation, back-transformed maps and topographical sign analyses

In the last two decades, techniques have also been developed for automatic interpretation of electrophysiological data, providing 'bias-free' maps of cortical visual topography within a pre-defined area. One such technique involves the use of computer routines to interpolate visuotopic coordinates between points sampled by electrode penetrations within a single area, based on digitized grids of recording sites and receptive field coordinates (Maunsell & Van Essen 1987; Fiorani *et al.* 1989). This technique allows quantification of certain visuotopic parameters that do not become evident through the analysis of

individual receptive fields. However, it does not address the possibility of ambiguous boundaries between areas, and its optimal use requires that the boundaries of the area under study be determined prior to the application of the interpolation algorithm (Neuenschwander *et al.* 1994). Otherwise, contamination of the data matrix with samples taken from adjacent areas may result in an unreal impression of complex topography, involving duplications or discontinuities. In contrast, the more recently described method of Sereno *et al.* (1994) does not require predetermination of the boundaries of the areas. This technique, which is based on the interpolation of coordinates across the entire dataset, uses local visual field sign as a criterion for automatic subdivision of the cortex into areas. Visual field sign is a local measure of chirality: whether the visuotopic map, as seen from the cortical surface, forms a mirror- or non-mirror image of the animal's visual field. The assumption behind this technique is that the entire cortex belonging to a single area represents the visual field according to the same field sign; therefore, transitions in field sign should correspond to borders between areas. The main merit of this approach is that it generates an impartial hypothesis regarding both the area boundary and the visual topography, based on the same dataset. However, the 'human factor' has not been totally removed, as the exact final configuration of the maps is dependent on parameters used by the interpolation algorithm that are subjectively chosen by the experimenter. Moreover, fine-scale transitions of visual field sign have been reported within a single area, such as V2 (Roe & Ts'o 1995), as a consequence of segregation of function in stripe-like compartments. Another potential problem, which is common to all of the current 'bias-free' methods, is that the algorithms assume local continuity of the maps and cannot be used in areas where discontinuities may be a real feature of the visuotopic map.

(c) *Area definition by anatomical methods*

The visuotopic organization of one area can also be inferred by tracing the connections to and from another area, for which the visual topography has already been determined (e.g. Cragg & Ainsworth 1969; Zeki 1969; Spatz *et al.* 1970; Ungerleider & Mishkin 1979; Maunsell & Van Essen 1983; Weller & Kaas 1983; Weller *et al.* 1984; Newsome *et al.* 1986; Perkel *et al.* 1986; Van Essen *et al.* 1986; Colby *et al.* 1988; Cusick & Kaas 1988; Rosa *et al.* 1988b, 1993; Krubitzer & Kaas 1990; Sousa *et al.* 1991; Steele *et al.* 1991). This method relies on the observation that cortico-cortical connections preferentially link cells that represent the same region of the visual field (Cowey 1964). The definition of the boundaries of the cortical visual areas based on anatomical connections has limitations related to the paucity of data in each cortical area and in each animal. The connective data, however, have an important role on the definition of the basic framework of the organization of the cortical areas. Connective data are adequate to show upper and lower field representations in several extrastriate visual areas.

One important assumption that has been used to define borders of a cortical area is the demonstration of coherent patterns of connections with other parts of the brain: different portions of a same area should receive or project to a similar set of areas. The inputs and outputs of an area would remain constant throughout its extension, a rule that we will discuss later in this review. However, for the purposes of a first definition of visuotopic organization, the picture provided by studying connections alone is, at best, coarse. This imprecision stems, in part, from the fact that cortico-cortical connections may also integrate representations of portions of the visual field that are not exactly matching (for a review, see Salin & Bullier 1995). In addition, because adjacent areas often share inputs (or outputs), the possibilities of erroneous interpretations are many.

Finally, metabolic mapping methods such as 2-deoxyglucose, *in vivo* imaging of intrinsic signals, and functional nuclear magnetic resonance imaging can also be used to study visuotopic representations. To date, these methods have been an important tool for analysis of the visuotopy of the areas already described in non-human primates (Tootell *et al.* 1982, 1988; DeYoe *et al.* 1994; Frostig 1994; Grinvald *et al.* 1994) using traditional electrophysiology, but allowing simultaneous determination of visuotopy, functional response properties and connections in extrastriate cortex, without the need of prohibitively long experiments (Tootell & Hamilton 1989; Malach *et al.* 1994; Malonek *et al.* 1994; Sereno *et al.* 1995).

(d) *The use of 2D reconstructions of the visual cortex*

In the absence of unequivocal anatomical limits to the cortical visual areas, many authors adopted the use of bi-dimensional reconstructions of the cortical surface to assign recording sites or projections zones to a given site. The assumption of this method is that the organization of the cortical visual areas is fixed and that the location of the areas in relation to the V1/V2 border is stable. We have been using two-dimensional (2D) reconstructions on our electrophysiological mapping and connective studies, in addition to the use of other anatomical and/or physiological criteria, to define the borders of each visual area (Gattass *et al.* 1987).

(e) *Definition of borders of visuotopically organized areas*

The myeloarchitectonic and the electrophysiological transitions were used to define the borders of the cortical visual areas. Myeloarchitectonic borders were defined at the transitions between two distinct myeloarchitectonic patterns, whereas electrophysiological borders were defined in regions where reversals of receptive field progressions occurred. Figure 2 shows visuotopically organized cortical areas with their boundaries in a flattened representation of occipital, parietal and temporal cortices. Represented in the figure are the visual topography of the first (V1) and second (V2) visual areas, of the ventral and dorsal portions of the third visual area (V3), of the 'colour area' of the prelunate sulcus (V4), of the area of

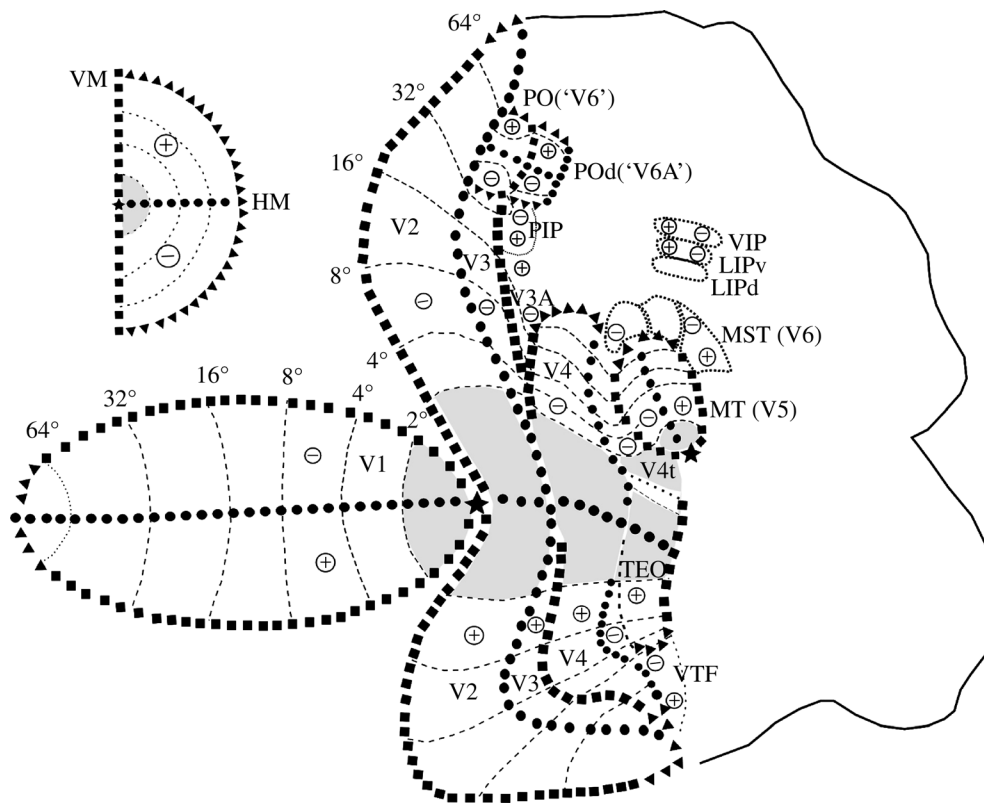


Figure 2. Visuotopic organization of the cortical visual areas shown on a 2D reconstruction of a monkey cortex. The vertical meridian is represented by black squares, the horizontal meridian by black circles, the eccentricity lines by dashed lines, the visual field periphery by black triangles. A star illustrates the representation of the fovea. + and - show upper and lower fields, respectively. Insert illustrates the contralateral visual hemi-field. For names of areas, see Glossary.

the occipitotemporal transition (TEO), of the temporal ventral posterior region (TVP), of the areas of the posterior bank of the superior temporal sulcus, the 'movement area' (MT or V5) and its adjacent dorsal zone (V4t or DZ), and of area MST, originally studied by Dubner & Zeki (1971) and later defined by Newsome & Wurtz (1981) and Maunsell & Van Essen (1983). At the anterior bank of the parietal occipital sulcus there are two topographically organized areas now named area PO (or 'V6' of Galletti *et al.* 1996, 1999) and the adjacent parieto-occipital dorsal area POd (or 'V6A'). In the parietal region are represented the areas VIP, at the fundus of the intraparietal sulcus, and LIP, on the lateral bank.

3. IRREGULARITIES IN THE VISUAL MAPS

In both V1 and V2 of *Cebus*, we have observed that at a given eccentricity the cortical magnification factor (CMF) is higher when measured between points located along an isopolar rather than along an iso-centric line. This anisotropy in visual representation is less pronounced in V1 than in V2, where the isopolar CMF is usually 50% higher than the iso-centric CMF. This anisotropy in the cortical magnification factor is reflected by the oval shape of the minimum point image size (MPIS), calculated as the product of cortical magnification factor by multiunit receptive field size. More recently, we have been studying the regularity of visual maps in other areas of the *Cebus apella*. In ventral V3 (V3v), for example, we observed an anisotropy that is even more pronounced than that of V2: isopolar CMF in V3v is at least twice as large as

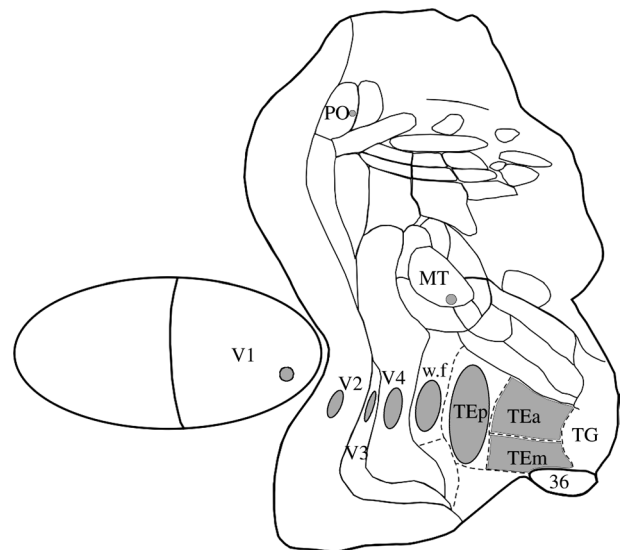


Figure 3. Anisotropies in cortical visual maps illustrated by the asymmetries of the minimal point image size in different visual areas, shown on a 2D reconstruction of a monkey cortex.

the iso-centric CMF (Rosa *et al.* 2000). There is also evidence for a similar amount of anisotropy in the portion of ventral V3 located at the anterior bank of the lunate sulcus and in the ventral portion of V4 (Piñón *et al.* 1998).

While areas corresponding to the first stages of the ventral pathway are all characterized by anisotropies, a similar analysis carried out in MT did not yield any evidence for anisotropy in its visual map (figure 3). In the areas of the dorsomedial pathway, PO and POd, we found a different type of irregularity in the visual

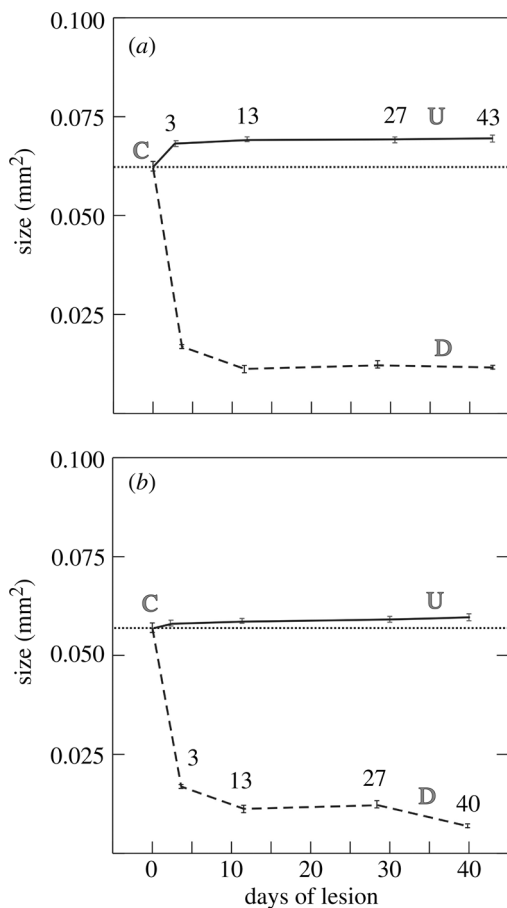


Figure 4. Changes in blob cross-sectional area in V1 after massive (a) and focal (b) retinal laser lesions at different times, from 3 to 43 days. Undeprived blob sizes (continuous lines) increase after massive retinal lesions. Deprived blob sizes (dashed lines) decrease drastically in both cases. Bars, standard error of the mean; C, control (non-lesioned area).

map: it was always possible to define the representations of isopolar lines, but not those of the isoecentric lines. At present, we have no direct evidence regarding the functional significance of the observed 'order in the isopolar' versus 'disorder in the isoecentric domain' in these areas. One may speculate that centrifugal and centripetal organizations of directionality, such as those observed in area PG, which is connected to PO, demand interactions between neurons that analyse regions of space sharing a similar polar angle but with different eccentricities. It may be that the intermixing of eccentricities of receptive fields in adjacent columns in PO and POd allow these interactions to occur at local circuits. This arrangement would be considered a 'non-visuotopic' map, but nonetheless a topographically organized isopolar functional map. It would not be surprising to find a similar type of organization at other levels of the central nervous system as, for example, at the oculomotor system. The use of large electrode arrays progressing systematically through the cortical layers may reveal other types of organization in areas of the anaectant gyrus and neighbouring regions of the intraparietal and parieto-occipital sulci.

4. MODULAR ORGANIZATION

The anisotropies in V1, V2 and V3v in the *Cebus* have motivated studies on the intrinsic organization of these

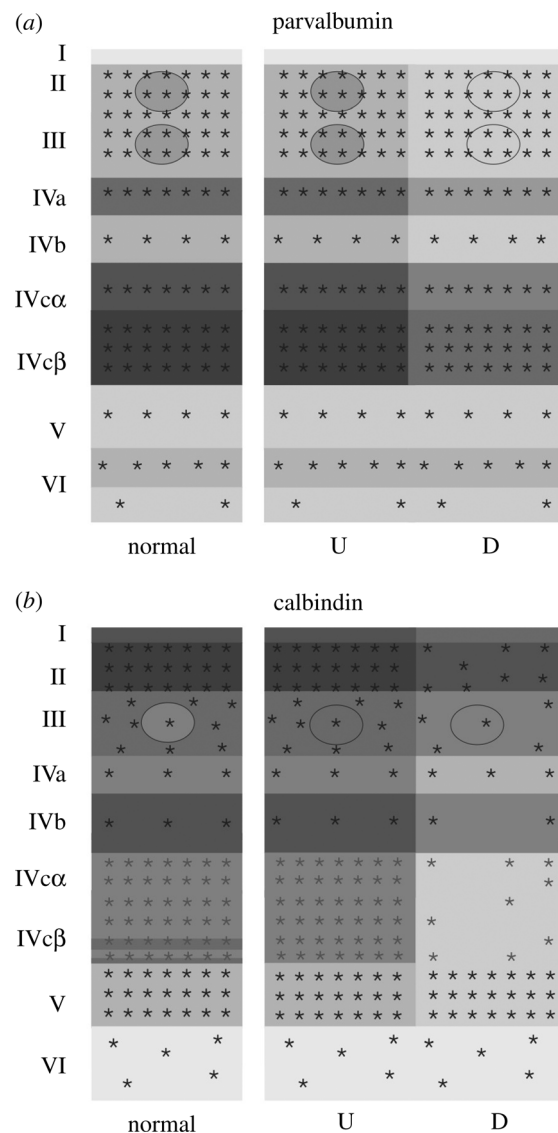


Figure 5. Schematic of the laminar distribution of cell bodies (asterisks) and neuropils (greys) in coronal sections of V1, stained for parvalbumin (a) and calbindin (b), after massive retinal laser lesions. Schematics of the stains are illustrated for normal and for deprived (D) and undeprived (U) columns.

areas. Tangential sections of the striate cortex of Simiiform primates stained for CytOx showed a periodic pattern of heavily stained, oval-shaped 'blobs' in a matrix of less reactive 'interblob' regions (Horton & Hubel 1981; Wong-Riley & Carrol 1984). To evaluate the regularity of the modular organization of V1 in primates, we studied the distribution of CytOx blobs in flattened preparation of V1 (Rosa *et al.* 1993; Farias *et al.* 1997). Blobs are present throughout V1 in all already-studied primate species. Another aspect of the modular organization of V1 is the existence of ocular dominance (OD) columns. In the macaque, the observed anisotropy of V1 has been interpreted as a result of the orientation of the OD stripes. The CMF would be greater along the axis perpendicular to the stripes owing to the need of representing twice the same region of the visual field, once for each eye. In *Cebus* (Rosa *et al.* 1988a; Gattass *et al.* 1988), the study of the distribution of OD stripes revealed that their orientation would account for the anisotropy in the

representation of the visual field in V1. These results are consistent with the notion that the visual map of V1 may be made up of two partially overlapping visual maps, one for each eye (Gattass *et al.* 1987).

In V2, modules as revealed by CytOx histochemistry are also stripe-like, running from the anterior border of V2 to its border with striate cortex. Three types of stripes are currently recognized in V2, namely the thin and thick CytOx-rich stripes as well as the CytOx-poor interstripes, which differ in neuronal response properties and connections (Tootell *et al.* 1982; Livingstone & Hubel 1983; DeYoe & Van Essen 1985; Shipp & Zeki 1985, 1989; Rosa *et al.* 1988a; Levitt *et al.* 1994; Roe & Ts'o 1995; Gattass *et al.* 1997; Olavarria & Van Essen 1997). Both the thin stripes and the CytOx-poor interstripes, through their connections with V4, seem to be related to the ventral stream, whereas the thick stripes, by way of their connections with MT, seem to be related to the dorsolateral stream of visual processing. In the *Cebus*, to evaluate whether there is a segregation of the streams of visual information processing in CytOx modules of V2, we injected fluorescent retrograde tracers into V4, MT and PO and studied the distribution of the labelled cells in these modules. The distribution of labelled cells provided evidence for three streams of visual processing with origins in different CytOx modules in area V2, with the subdivision of the dorsal stream of visual information processing into a dorsomedial and a dorsolateral component (Nascimento-Silva *et al.* 2003). We have, therefore, reasoned that the same portion of the visual field should be represented multiple times in V2 in stripes of different kinds (Rosa *et al.* 1988b). Taking into consideration the periodical arrangement and orientation of the stripes and assuming little or no overlap between neighbouring modules, one would expect a ratio of isopolar-to-isoeccentric anisotropy in V2 of 3–4 : 1, in comparison with the observed anisotropy ratio of 3 : 2. We have, therefore, suggested that heterogeneous sub-modules should form each stripe (Rosa *et al.* 1988a). In a later study using sections stained for CytOx in V2 of *Cebus* monkeys (Gattass *et al.* 1990), we demonstrated that the thin bands are composed of a series of equally spaced puffs. Studies in enucleated animals suggest that the thick bands may be similarly organized.

Regarding area MT, CytOx-stained tangential sections did not reveal a modular organization. In the owl monkey, area MT shows a dark oval region with fuzzy, randomly distributed light sub-regions. In MT of the *Cebus*, we found no evidence for modularity using the same histochemical method. This finding is coherent with our current interpretation of the data inasmuch as no anisotropies were observed in this area for the *Cebus*.

5. ADULT BLOBS PLASTICITY

The plastic changes in V1 blobs of adult primates depend on the severity of visual deprivation and on the amount of time of deprivation. Restricted lesions, produced by small laser shots, and massive retinal lesions, produced by laser lesions at the border of the blind spot, induce different degree reorganization on CytOx-rich layer III blobs, with different time courses.

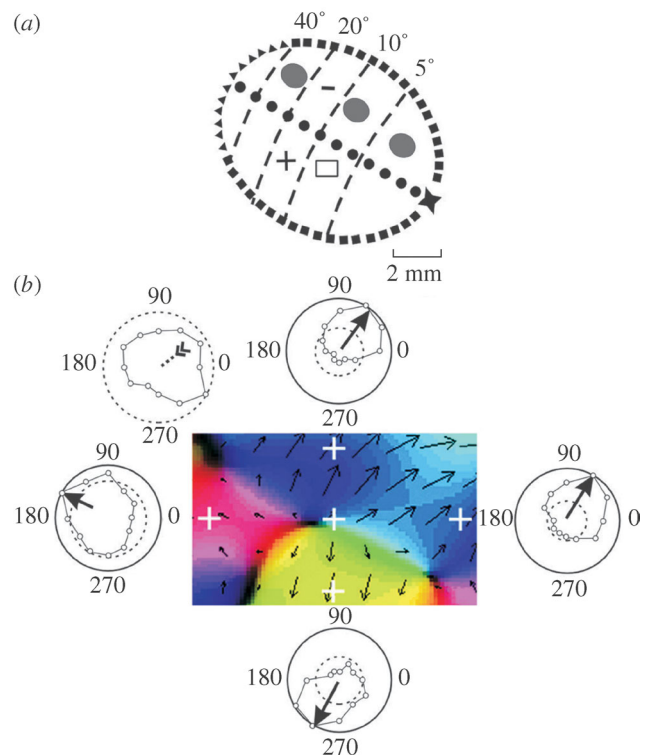


Figure 6. Direction map and single-unit in MT: illustration of neuronal responses that gave rise to a pinwheel map formation. (a) Visual topography of MT showing the location of map region highlighted in panel b. Three minimal point image sizes in MT are illustrated at different eccentricities. (b) Magnified view of a rectangular region of cortex showing a portion of the direction map with a pair of directional singularities (at centre and lower right) with corresponding pinwheel formations, which are linked by a fracture. Each pinwheel is composed of a half-rotation (180°) and a fracture. White crosshairs indicate the locations of five recording sites, which include a site near the pinwheel centre and four sites around the perimeter. The central site exhibited a weak form of directional tuning that was entirely shaped by inhibition. The remaining sites were excitatory and uni-directional. Dashed circle, spontaneous firing rate; external circle, maximum firing rate at the recording site.

These data suggest two independent plastic mechanisms for blob plasticity: one for the decrease of blob size on deprived columns and another for the increase of blob size on non-deprived columns.

Blob cross-sectional area and spatial density were analysed in CytOx-reacted tangential sections of flat mount preparations of V1 in *Cebus* with focal and massive retinal laser lesions. In cases with focal retinal lesions, the cross-sectional area and spatial density of deprived blobs decrease after 3 days of lesion. There is no variation in cross-sectional area, spatial density or the total area occupied by non-deprived blobs when compared with the control ones. In cases with massive lesions, blob cross-sectional area, blob spatial density and the total area occupied by deprived blobs decrease after 1 day of lesion. The cross-sectional area and the total area occupied by non-deprived blobs increases after 5 days of lesion (Farias 2002). Figure 4a shows a decrease in mean blob size of deprived blobs, with time, in an animal that received focal and restricted laser lesions at different times, whereas figure 4b shows an

additional increase of blob size of undeprived blobs, after massive retinal lesions at different times. In both cases there is a significant decrease in blob size of deprived columns (Farias 2002).

Normal *Cebus* monkeys showed a complementary labelling in V1 of calbindin (Cb) and parvalbumin (Pv). Layers II, IVb, the superior third of layer IVc α and the inferior third of layer IVc β are intensely labelled by Cb. Layer V shows stronger labelling than layer VI. In layer III, the interblobs are more densely labelled than the blobs. By contrast, Pv stained preferentially the blobs and layers IVa, IVc and VI. Figure 5 shows the distribution of Cb and Pv in V1, 28 days after a series of laser lesions around the optic disc of one eye. The distributions of Cb and PV were differentially altered. The deprived ocular dominance columns showed a reduction of Cb neuropil (layers I–V) and labelled cell bodies (layers II, III, IVb and IVc). By contrast, the Pv decreased in deprived ocular dominance columns only at the neuropil in layers III, IVa and IVc (Botelho 2004).

In humans with retinal lesions blob size changes drastically in the region corresponding to lesion, although its spatial density remains constant throughout the binocular field representation in V1. The regions showing conspicuous OD columns showed different degrees of variability of blob plasticity. In the region representing the retinal lesion, blobs are larger and darker above the undeprived OD stripes than in the alternative deprived stripes. Although deprived blobs are on average smaller than those from normal regions, this difference was not significant. Our results suggest that plasticity in V1 after retinal lesions caused by chronic diseases in adult humans is different from that described after acute retinal lesions in non-human primates. In humans, the size increase of undeprived blobs prevails over the decrease of deprived blob sizes. These results suggest the existence of additional mechanisms to regulate blob size other than simple competitive interactions between CytOx-rich blobs (Marcondes 1997).

6. DIRECTIONAL COLUMNS IN MT

To study the directional columns in MT, we recorded neuronal activity from multielectrode arrays as they were stepped through the area, at a plane parallel to the cortical layers. At each recording site, we determined the preferred direction of motion. Responses recorded at successive locations from the same electrode in the array revealed gradual changes in preferred direction, along with occasional directional reversals. Systematic comparisons of responses from adjacent electrodes, at successive locations, allowed the reconstruction of the 2D pattern of preferred directions across the cortex (Diogo *et al.* 2002). The data were obtained using the 11 electrode array and 12 sampling nodes, at 200 μ m intervals. Between these discrete nodes we interpolated responses to visual motion and then used the interpolated responses to construct 2D maps of preferred direction. We then constructed a set of 12 2D maps of normalized neuronal activity—one for each of the 12 tested directions of motion. Next, each of the 12 conditional activity matrices was multiplied by a unit

vector, the direction of which corresponded to the stimulus motion used to obtain the measured neuronal responses for that matrix. These multiplications yielded a new set of 12 matrices, in which each element was a vector of direction corresponding to the stimulus motion and of length proportional to firing rate (measured or interpolated) at that map location. Finally, a matrix representing preferred direction at each map location was obtained by summing the 12 vectorial matrices. The direction and length of the resulting vector sum at each map location reflect, respectively, the neuronal preferred direction and strength of selectivity at that location. This vector-sum matrix was used to produce a 2D map of directionality, in which the preferred direction at each map location was represented by a colour code. The electrophysiological imaging demonstrates a systematic organization for directionality in area MT of the New World *Cebus* monkey, which is similar to that known to exist in the Old World macaque monkey (Albright 1984). The tangential organization of directional selectivity is characterized by slow continuous changes in directional preference, as well as by the presence of lines (fractures) and points (singularities) that fragment continuous regions into patches (figure 6). These electrophysiological methods also allowed a direct investigation of neuronal selectivity that gives rise to map features. In particular, our results suggest that inhibitory mechanisms may be involved in the generation of fractures and singularities (Diogo *et al.* 2003).

7. CORTICAL VISUAL AREAS

(a) *Areas defined by electrophysiological mapping and connections*

(i) *Area V1*

In the macaque, Daniel & Whitteridge (1961) described a systematic representation of the retinal surface, with large magnification of the fovea representation in the primary visual area, or V1. Their model for V1 established a relation between the representation of the retinal surface or of the 'cortical map' with a functional area in the cortex. The studies of Hubel & Wiesel (1967, 1968, 1972) on single-unit properties of V1 established the basis for a hierarchical model and the notion that single-unit properties would become gradually more complex at successive stages of visual processing. They also described functional modules in V1 capable of decoding ocular dominance and orientation of the visual stimuli. We studied the topographic representation of V1 in the *Cebus* and we found a small anisotropy along the isopolar domain at the peripheral representation of V1. This anisotropy could be related to the orientation of the OD columns of peripheral V1 (Gattass *et al.* 1987).

We have also addressed the contextual and surrounding influences contributing to the dynamics of receptive-field properties in V1. We found that at the representation of the blind spot, as well as throughout the extension of V1, inputs from large and relatively distant portions of the retina may sometimes influence the response of single cells. This dynamic property of the cell response was characterized as 'perceptual

completion of oriented lines' and showed that the map of V1 was visuotopic (Fiorani *et al.* 1992). More recent findings from our group have demonstrated that visuotopic representation of V1 predicts well the receptive field location, but sometimes fails to predict stimulus orientation or direction (Azzi 2004).

(ii) Area V2

In macaques, the major cortical projection target of area V1 is area V2 (Kuypers *et al.* 1965; Cragg & Ainsworth 1969; Zeki 1969, 1971, 1976; Jones & Powell 1970; Zeki & Sandeman 1976; Rockland & Pandya 1979, 1981; Weller & Kaas 1983; Van Essen *et al.* 1986; Shiwa 1987; Lund *et al.* 1991). V2 is located within area 18 of Brodmann and corresponds to area OB of von Bonin & Bailey (1947). The visual map of V2 (Gattass *et al.* 1981; Rosa *et al.* 1988b) corresponds to a second-order transformation of the visual field with the representation of the vertical meridian at the posterior border of the area. The horizontal meridian splits at about 0.5° and forms the anterior border of the area. The lower field is represented dorsally whereas the upper field is represented ventrally (Allman & Kaas 1971; Gattass *et al.* 1981; Rosa *et al.* 1988b). Although a number of studies have described projections from V2 back to V1 and feed-forward projections from V2 to several visuotopically organized extrastriate areas, including V3, V4, MT and PO, these reports were based almost entirely on injections of retrograde tracers outside of V2 (Rockland & Pandya 1981; Felleman & Van Essen 1983, 1984; Maunsell & Van Essen 1983; Festemaker *et al.* 1984; DeYoe & Van Essen 1985; Kennedy & Bullier 1985; Shipp & Zeki 1985, 1989; Burkhalter *et al.* 1986; Ungerleider & Desimone 1986b; Colby *et al.* 1988; Zeki & Shipp 1989; Boussaoud *et al.* 1991; Nakamura *et al.* 1993). The only exception is a report by Zeki (1971) describing anterograde degeneration in V3, V4 and MT after small lesions in V2, and, in that study, the only part of V2 examined was the representation of the lower half of the central visual field. We studied the projection of V2 in the macaque (Gattass *et al.* 1997) and found that all V2 sites project topographically back to V1 and forward to V3, V4, and MT. There is also a topographically organized projection from V2 to V4t, but this projection is limited to the lower visual field representation. Thus, V2 appears to project to virtually all visual areas within the occipital lobe. In addition to projections to occipital visual areas, V2 sites representing eccentricities of about 30° and greater project to three visual areas in parietal cortex, namely the medial superior temporal (MST), parieto-occipital (PO) and ventral intraparietal (VIP) areas. This peripheral field representation of V2 also projects to area VTF, a visual area located in area TF on the posterior parahippocampal gyrus.

(iii) Area V3

Currently there are still two different views regarding the organization of V3 in macaques. Based on electrophysiological mapping studies, Gattass and his colleagues (Gattass *et al.* 1988b) have argued that the entire region bordering V2 anteriorly is a single visual area, which contains a representation of the visual field up to 30° to 40° eccentricities in both the upper (V3v) and

lower (V3d) visual quadrants. By contrast, Van Essen and his colleagues have argued that V3d and V3v are different visual areas based on differences in projections from V1, myeloarchitecture, and neural response properties (Burkhalter *et al.* 1986; Newsome *et al.* 1986; Van Essen *et al.* 1986). These investigators have termed the upper and lower visual field representations anterior to V2 as areas V3 and VP, respectively. V1 may project asymmetrically to V3, but V2 does not. Whereas the upper field representation of V2 projects to V3v, the lower field representation of V2 projects to V3d. Further, central field representations of V2 project laterally within both V3v and V3d, while more peripheral field representations project more medially. Our results also show that the visual field representation within V3 may extend beyond 40° eccentricity but does not extend to 70°. Thus, there is a reduction in the extent of the visual field represented as one moves from V2 to V3, consistent with the findings from electrophysiology (Gattass *et al.* 1981; Gattass 1988a,b). Finally, the results in the macaque show that V3d shares the representation of the vertical meridian with areas V4 and PO, which is again consistent with findings from electrophysiology. There was a large inter-animal variability in the visual topography of V3d, with reflections in the organization of V3A (Gattass 1988a,b).

A representation of the upper visual quadrant adjacent to the second visual area (V2) in ventral prestriate cortex was suggested by Cragg & 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 organization of the macaque 'third tier areas' (Allman & 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 *et al.* 1986; Newsome *et al.* 1986; Van Essen *et al.* 1986; Felleman & Van Essen 1987; Krubitzer & Kaas 1993; Beck & Kaas 1999). This has resulted in the hypothesis that, in Old World monkeys, the ventral and dorsal parts of the original 'V3' are regarded as separate areas, each containing an incomplete representation of the visual field (e.g. Felleman & Van Essen 1991). This hypothesis does not find support on the connections of dorsal and ventral V2, which projects to V3d and V3v, respectively (Gattass *et al.* 1987). The width of the middle portion of V3d varies from animal to animal. Some of the discrepancy based on anatomical data of the projection of V1 may be related to such variability.

(iv) Area V4

Zeki first studied the prelunate gyrus in the macaque in 1969 and described it as an area that receives projections from V2 and V3 and represents the central portion of the visual field. Based on these criteria he divided the prelunate gyrus into areas V4, located in the anterior bank of the lunate sulcus, and V4A, located in the prelunate gyrus. Van Essen & Zeki (1978) studied the prelunate gyrus and named this region as 'V4 complex' because a single point of the visual space

was represented multiple times in this area. The region they studied only contained the representation of the first 10° of the inferior quadrant of the visual field and probably included a large part of area TEO. Zeki (1978) extended his recordings to the superior temporal sulcus in an area lateral to area MT and found a topographic organized area that was later named area V4t (Maguire & Baizer 1984). Maguire & Baizer (1984), studying the visual topography of the prelunate in the awake-behaving macaque monkeys, divided this gyrus into four areas: anterior lateral (AL), posterior medial (PM), dorso-posterior (DP) and V4 transitional or V4t. According to their data, area PM corresponds to area V4 and area AL might correspond to area V4A defined by Zeki (1969). Areas AL and PM have a crude representation of the 30° of the inferior quadrant. Area AL includes the prelunate gyrus and the posterior part of superior temporal sulcus whereas area PM includes the prelunate gyrus and the anterior portion of the lunate sulcus. Dorsal to these two areas is area DP containing large receptive fields. Between MT and AL is V4t, with a distinct and pale myeloarchitecture. Although V4 was originally described as being located on the prelunate gyrus (Zeki 1973; Van Essen & Zeki 1978), it is now clear from more extensive mapping studies that this area extends ventrally into the occipitotemporal cortex. Gattass *et al.* (1985, 1988*a,b*) extended Zeki's electrophysiological recordings to the ventral aspect of the cortex, and defined area V4 as a dorsoventral strip of cortex, containing the representation of 30° to 40° of the visual field. This area has the lower visual field represented dorsally in the hemisphere and the upper visual field represented ventrally (Gattass 1988*a,b*; Piñón *et al.* 1998). Consistent with these electrophysiological findings, we found projections to both upper and lower visual field representations of V4 from V2 sites representing eccentricities of up to but not greater than 46° eccentricity. In addition, the vertical meridian representation of V2 projects to the V3/V4 border, where the vertical meridian is again represented (Gattass *et al.* 1987; Piñón *et al.* 1998). Dorsally in the hemisphere, the representation of the horizontal meridian of V2 projects anteriorly to the V4/V4t border, which also contains a horizontal meridian representation (Desimone & Ungerleider 1986). Ventrally, however, the horizontal meridian of V2 does not appear to project to the V4/TEO border, but rather projects to a region within V4 itself. This anatomical finding agrees with the observation of Gattass *et al.* (1987) that the horizontal meridian representation of ventral V4 is usually located caudal to the area's anterior border, and it is consistent with the lower field representation of V4 bordering the lower field of VTF (Gattass *et al.* 1985, 1987; Piñón *et al.* 1998). We studied the cortical connections of area V4 in the macaque (Ungerleider *et al.* 2005) and we found that all parts of V4 are connected with V2, V3, V3A, V4t, MT, FST, TEO, TE and the frontal eye field (FEF), confirming prior reports (Zeki 1971; Rockland & Pandya 1981; Maunsell & Van Essen 1983; Festemaker *et al.* 1984; Kennedy & Bullier 1985; Burkhalter *et al.* 1986; Ungerleider & Desimone 1986*a,b*; Shipp & Zeki 1989; Boussaoud *et al.* 1991; Nakamura *et al.* 1993). Based on the distribution of

labelled cells and of terminals, the projections to V2 and V3 are defined as feedback, those to V3A, V4t and the FEF as intermediate, and those to MT, FST, TEO and TE as feed-forward. Injections in the representation of the fovea in V4 revealed connections from and to V1, confirming previous anatomical findings (Zeki 1971; Rockland & Pandya 1981; Maunsell & Van Essen 1983; Festemaker *et al.* 1984; Kennedy & Bullier 1985; Burkhalter *et al.* 1986; Ungerleider & Desimone 1986*b*; Shipp & Zeki 1989; Boussaoud *et al.* 1991; Sousa *et al.* 1991; Nakamura *et al.* 1993). Injections of anterograde tracers in peripheral V4 did not reveal connections to V1, although injections of retrograde tracers revealed projections in one out of five cases (Ungerleider *et al.* 2005).

(v) Area V4t

Area V4t has been defined as the region lying between V4 and MT on the lateral bank of the superior temporal sulcus. Injections in V2 and V4 also revealed topographically organized projections from and to V4t (Zeki 1980; Maguire & Baizer 1984; Desimone & Ungerleider 1986; Gattass 1988*a,b*). Physiological evidence indicates that this area contains a representation of the lower visual field only (Schein *et al.* 1982; Desimone & Ungerleider 1986; Ungerleider & Desimone 1986*a,b*; Gattass 1988*a,b*). We observed projections to V4t from the lower field representations of V2 up to 46° eccentricity, with some evidence for a crude central to peripheral field organization as one progresses from lateral to medial within the area. Frequently, the projection to V4t from lower field V2 was continuous with the projections to V4 and MT (Piñón *et al.* 1998). This area was named DZ in the *Cebus* monkey (Fiorani *et al.* 1989).

(vi) Area MT

Dubner & Zeki (1971) first described the existence of a visual area with directionally selective neurons located in the superior temporal sulcus in macaques. This area has been named MT (Gattass & Gross 1981; Van Essen *et al.* 1981; Desimone & Ungerleider 1986) to acknowledge its homology with a visual area located in the middle temporal lobe of a New World monkey, the owl monkey (Allman & Kaas 1971). Area MT occupies the lower bank and the floor of the posterior superior temporal sulcus. It contains the representation of the contralateral binocular visual hemi-field, with the vertical meridian represented at the border of the area while the representation of the horizontal meridian runs across the lower bank and floor of the area. It corresponds to area OAa of Seltzer & Pandya (1989). Central field injections (those centred at eccentricities less than 30°) in V2 produced labelled terminals in the heavily myelinated part of MT, whereas peripheral field injections (those centred at eccentricities 30° and greater) produced labelled terminals medial to the heavily myelinated part of MT, i.e. within MTp (Desimone & Ungerleider 1986). A crude central to peripheral field trend and an upper versus lower field segregation was observed in the projections, which is in keeping with the visuotopic map reported for this area (Ungerleider & Mishkin 1979; Gattass & Gross 1981; Van Essen *et al.* 1981; Desimone & Ungerleider 1986).

(vii) *Area TEO*

In the macaque, representations of both the lower and upper quadrants were found in the area that occupies the lateral and ventrolateral aspects of the occipito-temporal transition, between area V4 and the non-topographically organized IT complex. This area was named ITC (Weller & Kaas 1985) TEO (Gattass 1988a,b; Boussaoud *et al.* 1991) because it roughly corresponds to the cytoarchitectonic area defined TEO by Von Bonin & Bailey (1947). It also corresponds to area TEO defined by myeloarchitecture and pattern of connections by Webster *et al.* (1991). Complete representations of both visual quadrants were observed, although the magnification factor of the upper-quadrant representation was found to be greater than that of the lower-quadrant representation (Boussaoud *et al.* 1991). The receptive fields in this area are often large and encompass portions of both the vertical and the horizontal meridians. No systematic map-discontinuities were observed within its coarse visual topography. The visual map in this area may be regarded as having a gradient of eccentricities that grows from lateral to medial on the ventrolateral surface, with the upper quadrant represented caudally and the lower quadrant rostrally. Based on anatomical connections other investigators have suggested that the caudal part of TEO should be considered as an additional visual area, VOT (ventral occipitotemporal area; Van Essen *et al.* 1990; Felleman & Van Essen 1991), located between areas V4 and TEO, which only contains the representation of the upper quadrant. Systematic studies, using additional criteria and high-density sampling, would be needed to support this proposal.

Lesions of area TEO in monkeys produce a severe impairment in visual pattern discrimination. Area TEO receives feed-forward input from prestriate areas V2, V3, V3A, V4, V4t and it sends feedback projections to all these areas, both being topographically organized. Further inputs derive from STS areas MT, FST and areas PP, PITd, TEM, TEa and TIPa (IPa of Seltzer & Pandya 1989). These connections are also reciprocal. Connections with DP, MST and STP could not consistently be demonstrated. Furthermore, TEO receives feedback projections from temporal areas TE, TH, TG, 36 and 35, and intermediate ones from parietal area LIP, parahippocampal area TF, as well as from FEF in the frontal lobe. With the exception of areas TG, 36 and 35, these areas receive in turn a projection from TEO (Webster *et al.* 1991).

(viii) *Area PO*

Area PO has been defined as a myeloarchitectonically distinct area, containing a complex visuotopic map with a de-emphasis on the central field representation (Covey *et al.* 1982; Gattass *et al.* 1986; Neuenchwander 1989; Neuenchwander *et al.* 1994). Peripheral field injections in V2 at eccentricities of 30° and greater showed projections to area PO. While upper field cases showed projections medially in PO, lower field cases showed projections laterally, which is consistent with the visuotopic organization described for PO (Covey *et al.* 1982; Gattass *et al.* 1986; Colby *et al.* 1988; Neuenchwander 1989; Neuenchwander *et al.* 1994).

The absence of projections to PO after injections in more central portions of the visual field representation of V2 may be related to the difference in cortical magnification in these two visual areas (Gattass *et al.* 1986); however, it is unlikely to be related to some technical factor, as Colby *et al.* (1988) also found projections to PO from peripheral but not central field representation of V2 using retrograde tracers. In *Cebus*, Neuenchwander *et al.* (1994) have described two distinct areas in the anterior bank of parieto-occipital sulcus, based on visual topography, receptive field size and myeloarchitecture, and named them PO and POd. Area POd has larger receptive fields and a distinct myeloarchitecture, when compared with area PO. The organization of PO, with emphasis in the isopolar domain, is quite different from that of dorsal V3, which preserves the isoecentric domain (Neuenchwander *et al.* 1994).

Adding diversity to the nomenclature, more recently Galletti *et al.* (1996, 1999) proposed the name of 'V6' to visual area PO of the macaque. More recently, POd was also renamed as 'V6A' by Galletti and collaborators (2001). There are reasonable arguments to find these names inadequate: the label for visual area PO (PO) can be confused with the label of the parieto-occipital cleft (*po*), but the name V6 should be reserved for area MST, originally studied with MT (V5), by Dubner & Zeki (1971) in the macaque.

(ix) *Area VTF*

In *Cebus* monkeys, the occipitotemporal transition has been subdivided into two areas, on the basis of anatomical connections: a medial area (temporal ventral posterior area, TVP) that projects to both V1 and MT, and a lateral area (TEO) that does not (Sousa *et al.* 1991; Rosa *et al.* 1993). The connections between TVP, V1 and MT follow a central-peripheral gradient of eccentricities, from lateral to medial, respectively. In the macaque, the area located medial to TEO, adjacent to the rostral tip of the calcarine fissure, is less understood. In a brief report, Gattass and collaborators (1985) found receptive fields representing the upper and lower quadrant in the ventromedial aspect of the caudal temporal lobe, in a region that they named VF (by analogy with cytoarchitectonic area TF), which encompassed the recording sites in the occipital temporal sulcus. In a study of area TEO, Boussaoud *et al.* (1991) found evidence for a visual area on the parahippocampal gyrus anterior to V2 and V3v and medial to V4 and TEO. They termed this area VTF because it was the portion of architectonic area TF (von Bonin & Bailey 1947) that was visually responsive. Although occupying the position of the temporal ventral posterior area (area TVP) reported in *Cebus* (Gattass *et al.* 1985; Sousa *et al.* 1991), VTF appears to be located farther medially in the hemisphere. We found projections to VTF from the far peripheral upper field representation of V2 (Sousa *et al.* 1991). Although it might be argued that this region would be part of ventral V4, VTF and V4 have a markedly different appearance both in cyto- and in myeloarchitecture.

(b) Areas defined by single-unit recordings and anatomical connections**(i) Area MST**

Area MST is located in the upper bank of the posterior superior temporal sulcus and contains cells sensitive to direction of motion either in the frontal plane, in depth, or in both (Dubner & Zeki 1971; Van Essen *et al.* 1981; Maunsell & Van Essen 1983; Saito *et al.* 1986; Tanaka *et al.* 1986). It also contains cells that appear to play a role in visuomotor control (Komatsu & Wurtz 1988). Using myeloarchitecture it is not possible to precisely define area MST, an area medial to MT in the superior temporal sulcus. However, the medial portion of the area is characterized by a densely myelinated zone (DMZ; Desimone & Ungerleider 1986). We saw projections within DMZ after peripheral field injections (more than 45°) in V2. The projection within DMZ was separate from the one located medial to MT, i.e. within MTp. Thus, the far peripheral field representation of V2 projects directly to MST and this projection appears to be additional to the one to the far peripheral representation of MTp. MST and MT are reciprocally connected to V4, thus providing the necessary information to extract form information from motion. Anatomical and electrophysiological studies in *Cebus* suggest that MST is composed of three areas, with crude visual topography (see figures 1 and 2).

(ii) Area VIP

In the present review, and in keeping with the studies by Blatt *et al.* (1990), Colby & Duhamel (1991) and Colby *et al.* (1993), we have defined VIP as the area at the fundus of the intraparietal sulcus ventral to the heavily myelinated zone (LIPv) on the lateral bank. Cells in this area present directional property similar to those found in area MT. We saw projections to VIP after peripheral V2 injections (more than 30°) or after peripheral V4 injections (more than 10°). In some cases the projection extended laterally to include a small portion of LIPv after V2 injections. By contrast, they always extended to LIPv and LIPd after peripheral V4 injections (Ungerleider *et al.* 2005). These results are consistent with those of Cavada & Goldman-Rakic (1989), who observed retrogradely labelled cells in peripheral field V2 following injections that included the ventral portion of the lateral bank of the intraparietal sulcus.

(iii) Area LIPv and LIPd

Areas LIPv and LIPd are located in the lateral bank of the intraparietal sulcus, dorsal to area VIP (Colby *et al.* 1993). LIPv corresponds to the heavily myelinated region in the lateral bank. At the level of LIPv at more dorsal location in the lateral bank there is a less myelinated region named LIPd. Cells in these areas present re-mapping properties of the location of their visual receptive field depending on oculomotor signals. Injections in peripheral V2 and V4 (Gattass *et al.* 1997; Ungerleider *et al.* 2005) show projections to the lower bank of the intraparietal sulcus, which includes two visual areas that have been termed the ventral intraparietal area, or VIP (Maunsell & Van Essen 1983; Ungerleider & Desimone 1986a), and the lateral intraparietal area, or LIP (Andersen *et al.* 1985, 1990). These two areas largely fall within the

cytoarchitecturally defined area POae of Seltzer & Pandya (1980), although some injections were close enough to the cortical surface that areas 7a and 7b may have been minimally involved as well (see Andersen *et al.* 1985; Cavada & Goldman-Rakic 1989).

(c) Other areas defined by architectural and connective studies

Based on the anatomical connections of visual area V2 and V4 we define groups of areas in the superior temporal sulcus, and in the parietal and temporal lobes. More recently, using the histochemistry for CytOx, immunohistochemistry for neurofilaments, neurotransmitter, calcium binding proteins and components of the extracellular matrix, we proposed subdivisions for the superior temporal sulcus and for the intraparietal sulcus.

(i) Areas of the superior temporal sulcus

Areas MT, MST and FST all contain many cells sensitive to the direction of motion of the stimulus either in the frontal plane, in depth, or in both (Dubner & Zeki 1971; Bruce *et al.* 1981; Van Essen *et al.* 1981; Maunsell & Van Essen 1983; Albright 1984; Desimone & Ungerleider 1986; Saito *et al.* 1986; Tanaka *et al.* 1986). Cells in some of these areas are also known to be sensitive to binocular disparity (Zeki 1974; Newsome & Wurtz 1981; Maunsell & Van Essen 1983), and cells in different portions of MST play a role in visuomotor processing (Komatsu & Wurtz 1988; Newsome *et al.* 1988; Fiorani *et al.* 1989; Baizer *et al.* 1991; Boussaoud *et al.* 1992; Kaas & Morel 1993; Cusick *et al.* 1995; Stepniewska & Kaas 1996; Felleman *et al.* 1997; Maioli *et al.* 1998). Areas MT and MST are reciprocally connected to more peripheral portions of V2 and V4, thus providing the necessary information to extract form information from motion (Gattass *et al.* 1997; Ungerleider *et al.* 2005). In addition, area FST has reciprocal connections with V4 (Ungerleider *et al.* 2005).

In more anterior portions of the sulcus, labelled cells were located predominantly in the upper bank but they also spread across the floor of the sulcus into the lower bank. The upper bank contains the superior temporal polysensory area (STP of Bruce *et al.* 1981; or TPO of Seltzer & Pandya 1989) where we did not find projection from either V2 or V4. More recently, using anatomical methods and immunohistochemical markers we found evidence for the existence of several areas (figure 1) in the superior temporal sulcus (STS) and in the intraparietal sulcus (IP; Nascimento-Silva 2004). Table 1 summarizes the anatomical criteria used to delimit these areas. With the exception of one area (IPa, here named TIPa), we labelled the STS-areas using the nomenclature of Seltzer & Pandya (1978). The location and the borders of these areas coincide with the cytoarchitectonic borders determined by using lectin histochemistry (Nascimento-Silva 2004). The distribution of connections shown in table 2 suggests a segregation of the areas of the posterior STS, more related to early (V1, V2 and V4) stages of visual processing, from those of the anterior portion of STS, that are more related to connections of late stages of form perception processing (V4 and TEO).

Table 1. Density of labelled cells in the intraparietal zones after injections in areas V4, TEO, PO and MT. (p, posterior; m, medial; a, anterior; +, isolated cells; ++, sparse; +++, dense; + + + +, very dense projections.)

	V4		TEO		PO		MT
	superficial	deep	superficial	deep	superficial	deep	
V3A (DM)	++	+++		+	+		
7A					++	+++	+
LIPv-p			+++		+++	+	
LIPv-m							
LIPv-a	++	+++	+++	+++	++	++	+
LIPd-p			+++	++	+++	+++	
LIPd-m	+++	++					++
LIPd-a	+++	+++	++++	+++	+	++	+
AIPv	++	+		+++	++		
AIPd-p	++	+				++	++
AIPd-a							+
VIP-p	+	+					++
VIP-a							++
5b-p	+						

Table 2. Immunohistochemistry density reaction and density of labelled cells in the STS zones, after injections in areas V2, LIP and TEO.

	histochemistry				connections		
	SMI-32	CAT-301	PV	CO	V2	LIP	TEO
Ipa	++++	++++	++++	++++			++
TPOc	++++	++++	++++	++	++++	++++	++
TAa	++++	++++	++	++++			++++
TPOr	++	++	++	++	++		++
V4t	++++	++++	++		++++		++++
MSTdp	+	++++	++	+++	++++	++++	+
MSTda	++	++	++	++++	++++	+++	
FSTd		+	+	+++	++	++	
FSTv	++		++	+	++	++	+
MT		++++	++	++	++++	++	
Pga	++++		++++	++++	++++		++
TG	++++	++++					
TEa	++++		++++	++++			
MSTm		++++	+				
PIT	++++			++++	++++		++
TEm		++			++		++
TPOm						++	++++

The connection to areas V2, LIP and TEO confirm the subdivisions obtained with the immunohistochemistry. Table 1 suggests the criteria used to subdivide the intraparietal areas. The laminar distribution of the connections to areas V4, TEO, PO and MT were used to segregate the areas. These areas were labelled using topographical landmarks, and they coincide with the nomenclature used by several authors (Seltzer & Pandya 1980; Rockland & Pandya 1981; Felleman & Van Essen 1983; Andersen *et al.* 1990).

(ii) Areas of the temporal lobe

Central and peripheral V2 and V4 are reciprocally connected to visual area TEO (Gattass *et al.* 1997; Ungerleider *et al.* 2005), also named caudal infero-temporal cortex (ITc) while mostly central V4 has additional connections with different portions of cytoarchitectonic area TE (TEp, TEa, TEm), including the portions of TE located within the superior

temporal sulcus. Other temporal-lobe areas such as area TG, at the temporal pole, areas TF and TH on the parahippocampal gyrus and the presubiculum are also connected with central V4 (Ungerleider *et al.* 2005). Connections of the regions of representations of the lower field of V2 and V4 were found within areas TEO, TEp and TEm, while connections from areas V1, V2 and V4 also avoid area TG in the upper bank of STS in the anterior portion of the temporal pole (Desimone & Gross 1979). In the terminology of Seltzer & Pandya (1978), the connections in the anterior portion of the sulcus roughly spanned architectonic areas TAa, TPO, PGa, TIPa (IPa) and TEa, although the labelled region was not sharply demarcated and did not seem to follow any known areal boundary. Projections were also found ventromedially in the temporal lobe both on the parahippocampal gyrus, in area TF, and in the presubiculum. Early horseradish peroxidase (HRP) studies of the projections to area TE showed a more

restricted region of input, with labelled cells located in V4 and TEO but not in V2 or V3 (Desimone *et al.* 1980; Shiwa 1987). The difference between those studies and the more recent ones is probably accounted for by the fact that our dye injections encroached on area TEO (Morel & Bullier 1990), whereas the HRP injections in the earlier studies were limited to TE. Consistent with this explanation, several reports have described direct projections from V2 and V3 to TEO (Festemaker *et al.* 1984; Shiwa 1987; Morel & Bullier 1990). A further difference may be the greater sensitivity of fluorescent dyes used in the more recent studies (Webster *et al.* 1991; Ungerleider *et al.* 2005) compared with HRP, especially as employed by Desimone *et al.* (1980) without tetramethyl benzidine as chromogene.

The multimodal region in the upper bank (area TPO) is divisible into four rostral-to-caudal architectonic sectors, exhibiting increasing degrees of laminar differentiation and cellularity as one proceeds caudally (Nascimento-Silva 2004). In addition, each rostro-caudal sector of area TPO has reciprocal connections with the laterally adjacent area TAA, at the upper rim of the sulcus, and with the medially adjacent areas PGA and TIPa (IPa), near the depth (Seltzer & Pandya 1989).

The properties of neurons in areas projecting to inferior temporal cortex are consistent with the role of the temporal lobe in object recognition. In addition to area TEO, the primary source of inputs to TE from prestriate cortex is area V4. Cells in V4 are sensitive to many visual features relevant to object perception, including colour, spatial frequency, orientation, length and width (e.g. Zeki 1973; Desimone & Schein 1987*a,b*; Schein & Desimone 1990; Youakim & Baizer 1990). Moreover, lesions of area V4 produce impairments in both form and colour vision (Wild *et al.* 1985; Heywood & Cowey 1987; Desimone *et al.* 1990). Area TE is non-topographically organized, has cells selective to stimulus shape and their receptive field always includes the fovea (Gross *et al.* 1972). Area TE is subdivided into three areas; one located anteriorly (TEa), another posteriorly (TEp) and another medially (TEm). Area TEa also has reciprocal connections with adjacent segments of area TEm laterally, at the lower rim of the sulcus, and area TIPa (IPa), medially, in the depth. In both the upper and the lower bank, caudal-to-rostral forward connections begin in supra-granular layers of cortex and terminate in and around layer IV (Seltzer & Pandya 1989).

(iii) *Areas of the parietal lobe*

Projections from several visual areas to the intraparietal sulcus have been previously described. A projection from the prelunate portion of V4 to area LIP is well established (Seltzer & Pandya 1980; Rockland & Pandya 1981; Felleman & Van Essen 1983; Andersen *et al.* 1990), as are the projections from V4 to VIP (Maunsell & Van Essen 1983; Ungerleider & Desimone 1986*a*) and from V4 to both VIP and LIP (Andersen *et al.* 1990; also see Colby *et al.* 1988). More recently, Boussaoud *et al.* (1990) reported projections from areas MST and FST in the superior temporal sulcus to areas VIP and LIP, and several

studies have described a projection from V3 to the intraparietal sulcus (Burchhalter & Van Essen 1983; Felleman & Van Essen 1984; Andersen *et al.* 1990; Morel & Bullier 1990). In cases of injections into peripheral V4, projections were found in dorsal parieto-occipital cortex, including areas PO, V3A, PIP and DP. Projections from the peripheral representation of V2 to the intraparietal sulcus have also been noted in preliminary reports (Ungerleider *et al.* 1983; Van Essen 1985) and were more clearly demonstrated by Gattass *et al.* (1997). More recently, Ungerleider *et al.* (2005) showed that the peripheral representation of V4 has reciprocal connections with the middle portion of areas LIPv and LIPd, as shown in figure 1. The results also demonstrate that the peripheral field representations of V4 project to a number of other visual areas located in occipitoparietal cortex, including DP, VIP, LIPd and LIPv, PIP, MST and PO, as well as to a portion of area TF located on the posterior parahippocampal gyrus. V4 projections to DP, VIP and PIP are of the intermediate type, whereas those to LIPd and LIPv, MST, and TF are of feed-forward type.

8. UPPER AND LOWER FIELD REPRESENTATIONS REVEALED BY ANATOMICAL CONNECTIONS

Projections of V2 and V4 allowed to reveal upper and lower field representations in VIP, LIPv, PIP and V3A and confirm the location of upper and lower field representations in V2 (Gattass *et al.* 1981; Rosa *et al.* 1988*b*), V3 (Gattass 1988*a,b*), PO (Neuenschwander *et al.* 1994), MT (Gattass & Gross 1981; Ungerleider & Desimone 1986*a,b*) and TEO (Boussaoud *et al.* 1990). V4 connectional data were adequate to show superimposed upper and lower field representations in areas VF, TH, TEp and TEa. Although no one has yet reported electrophysiological mapping of VIP or LIP, the connectional results suggest an upper versus lower field segregation within these areas (figure 2). Anatomical and electrophysiological mapping also suggest crude topographical organization in areas MSTm, MSTda and MSTdp.

9. PREFERRED FLOW OF INFORMATION: FEED-FORWARD AND FEEDBACK PROJECTIONS

Using the laminar distribution of labelled cells and terminals as criteria, many authors (Kuypers *et al.* 1965; Spatz & Tigges 1972; Tigges *et al.* 1973, 1974; Wong-Riley 1978; Rockland & Pandya 1979; Wall *et al.* 1982; Maunsell & Van Essen 1983; Weller *et al.* 1984; Kennedy & Bullier 1985; Weller & Kaas 1985; Ungerleider & Desimone 1986*a,b*; Boussaoud *et al.* 1990; Felleman & Van Essen 1991) distinguished feed-forward projections, originating from cells in superficial layers and terminating in layer IV of a higher-order target areas, from feedback projections, which originate from cells in infragranular layers and terminate mostly outside layer IV of lower-order target areas. Equally strong labelling of cells in layers III and V/VI and rather homogeneous terminal labelling in all cortical laminae indicate an intermediate type or undetermined relative position of two areas in the cortical hierarchy. Using

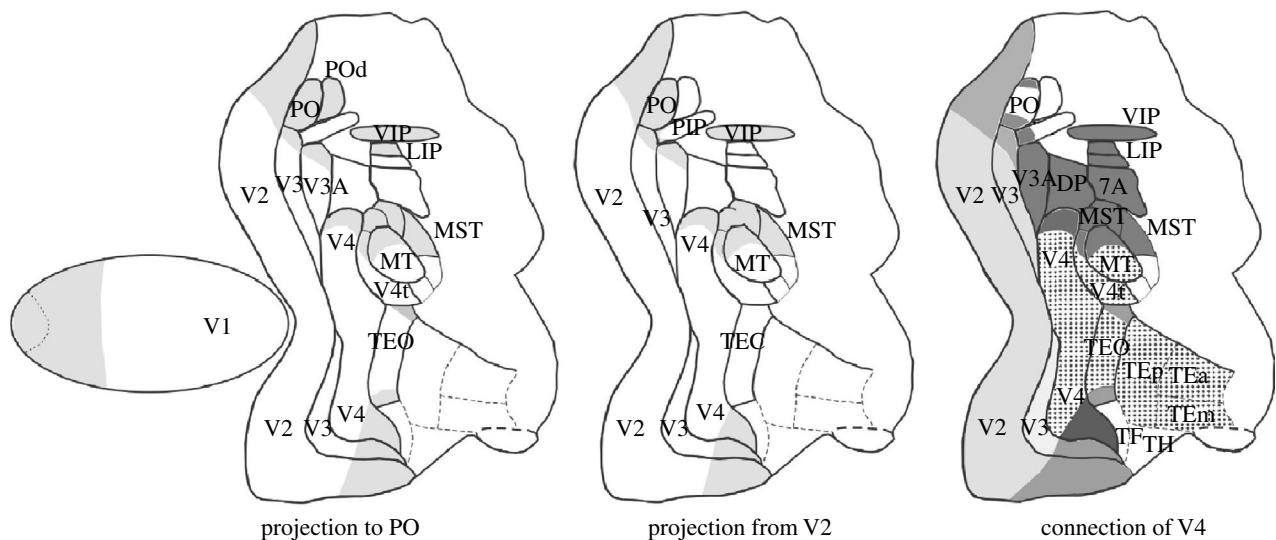


Figure 7. Projections to visual area PO (left), projection from peripheral V2 (middle) and connections from central and peripheral V4 (right) represented onto a 2D reconstruction of the monkey visual cortex. The connections to area PO arise from the peripheral representation of areas V1, V2, V3, V3A, V4, V4t, TEO, MT, MST, VIP, LIP and POd; the projection from peripheral V2 encompass areas V1 (not shown), V2, V3, V3A, V4, V4t, MT, MST and VIP; the connection of the central V4 feedback to areas V2 and V3 and project forward to MT, V4t, and to the temporal lobe areas (TEO, TEm, TEa), while the connection from peripheral V4 projects also to the parietal areas (PO, PIP, V3A, DP, MST, VIP, LIP and 7a).

these criteria, we found feedback projections of area TEO to posterior prestriate areas V2, V3, V3A and V4 and caudal STS areas V4t and MT. Mainly feed-forward projections were identified to rostral STS areas TEm, TEa and TIPa and to temporal lobe areas TE and TH. The input from posterior prestriate areas and from V4t and MT was, in turn, classified as feed-forward. The input from temporal areas TE, TH, TG, 36 and 35 had solely feedback characteristics. The connections of TEO with FST and PITd in caudal STS, with the parietal areas, and with the parahippocampal area TF appeared to be of intermediate or undetermined type. By contrast, the laminar distribution of labelled neurons revealed by PITd injection indicated that PITd receives feed-forward input from area V4 and from LIP, and feedback input from MT, FST and TE. The connections with TEO, TEm and TEa were of intermediate nature. A rich pattern of projections interconnects areas of different streams of information processing, at different hierarchical levels, to constitute specific cortical circuit loops. In spite of the multiplicity of connections among visual areas, we favour the notion that direct feed-forward connections relay important information to target areas for the construction of a first crude representation of the object, object trajectory or egocentric motion.

10. CENTRAL AND PERIPHERAL TOPOGRAPHICALLY DISTRIBUTED NETWORKS

There is accumulating evidence for differences in the cortical projections of central and peripheral visual field representations in extrastriate cortex. Zeki (1969) first noted that the fovea representation of V1, but not the remainder of the area, projects directly to V4, a finding later replicated by Nakamura *et al.* (1993). In addition, Zeki (1980) reported that peripheral V1 but not central V1 projects to V3A (see also Ungerleider & Mishkin 1982). Moreover, Ungerleider & Desimone (1986a) found that V3A receives a projection from peripheral

but not central MT. In addition, Colby *et al.* (1988) demonstrated direct input to PO from peripheral but not central field representations of V1 and V2. Gattass *et al.* (1997) also found that peripheral but not central field V2 projects directly to area PO. Injections placed at eccentricities of 30° or greater produced label in PO, but those placed at lesser eccentricities did not. In addition, Gattass *et al.* (1997) found that peripheral but not central field V2 projects to areas MST, VIP and VTF. These projections also arose from the portions of V2 representing eccentricities of 30° or greater. More recently, Ungerleider *et al.* (2005) found that central field of V4 projects mainly to temporal areas, whereas peripheral field V4 projects mainly to parietal areas. Contrasting from the V2 connections, the parietal projections arise from the portions of V4 representing eccentricities of 10° or greater.

The difference between peripheral and central field inputs may be related to the visual processing requirements of an area. Which areas of the lateral occipito-temporal cortex receive preferential inputs from central field representations is consistent with the role of these areas in object vision (Ungerleider & Mishkin 1982). By contrast, those within occipitoparietal cortex receive preferential inputs from peripheral field representations, which is consistent with the role of these areas in spatial vision (Gattass *et al.* 1990, 1999). The projections from peripheral field V4 to parietal areas PO, VIP, LIP, DP and area 7 support this notion.

Figure 7 illustrates the connections of area PO, and the segregated projections of central and peripheral representations of V2 and V4. The direct projection from the peripheral representations of V1, V2, V3, V4, MT and MST to the parietal lobe would be equivalent to the direct projection from central V1, V2, V3 and V4 to the temporal lobe. The bypass of the information from the early stages of processing (V1 and V2, for example) would contribute to advance information about the stimulus, and might aid in constructing,

within area TE, the initial representation of the overall shape and colour of an object, with the fine-grained information arriving later to fill in the important details. Similarly, the projections from peripheral V2 and V4 to parietal areas could provide a direct route for information about the periphery to quickly reach parietal cortex and thereby rapidly activate circuits for spatial vision and spatial attention.

The study of the connections of the visual areas reveals several interconnections between multiple maps for a particular modality, with each map being of a more or less specialized nature. This arrangement may reflect advantages of modular design proposed by Marr (1976) for the question of computer pattern recognition. Essentially, large computational problems are most easily dealt with through the division of the problem into smaller sub-problems, which are as nearly independent of each other as possible. This allows small changes in one part of the problem not to disrupt other parts of the problem, making the problem as a whole easier to solve, whether by human design or natural selection and mutation. For the visual system, implementing such an approach would be greatly facilitated by an arrangement that could easily reintegrate the visual information once divided among areas. An interconnecting network, which preserves information about position of the stimulus in the visual field and allows different computations of attributes of the stimulus, is an important component of this system. We thus propose two or more classes of central-peripheral segregated, topographically distributed networks, with intrinsic, feed-forward and feedback interactions, as the neuronal basis underlying either visual perception or oculomotor processing. Figure 8 illustrates three of such networks that work in parallel, one with emphasis on central vision, another with emphasis on object trajectory and another with emphasis on peripheral vision.

To evaluate the contribution of the feedback projection at different nodes of the network we chemically inactivate visual areas MT and V4 (Jansen 2002) and the lateral pulvinar (Soares *et al.* 2004) while recording neurons in V2. The inactivation of visual area MT, with different amounts of GABA, while studying topographically corresponding areas of V2 neurons produces a general decrease in the excitability of the neurons, which includes a decrease of the spontaneous and driven activities. The inactivation of MT is also followed by changes in orientation and direction selectivity of V2 neurons. The changes in direction selectivity are towards gain or loss of selectivity. Thus, feedback connections arising from MT may change receptive field properties of neurons in V2. These feedback projections are capable of not only modulating the spontaneous and driven activity of V2 neurons, but also of modifying V2 receptive field properties, such as its direction selectivity (Jansen *et al.* 2004). Figure 9 illustrates the change in direction selectivity of a neuron of V2 after GABA inactivation in MT.

11. THE VISUOTOPIC MAP OF V1

In the process of mapping visual area V1 in *Cebus*, we noticed unequivocal responses at the representation

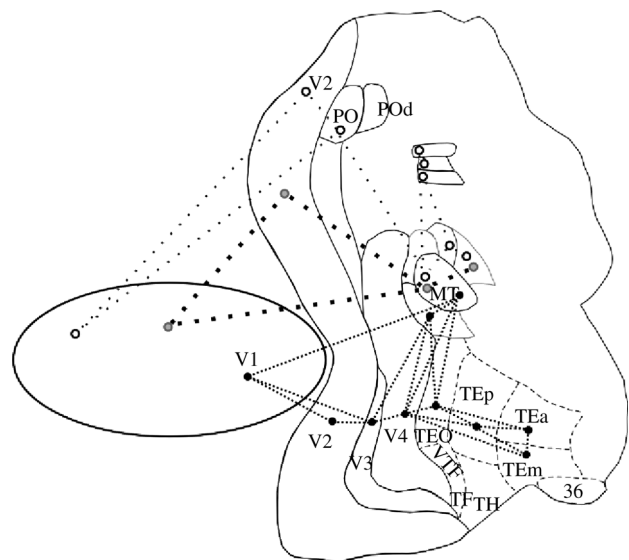


Figure 8. Topographically organized networks in different streams of visual information processing. Three topographically organized networks link different cortical visual areas, at different eccentricities. These networks process the visual information in parallel, one with emphasis on central or object vision (black circle), another with emphasis on object trajectory or object motion (grey circle) and another with emphasis on peripheral vision or forward egocentric motion (white circle).

of the blind spot of the contralateral eye. We were using long moving bars on the surface of a transparent globe placed in front of the animal with the representation of the fovea and that of the blind spot drawn onto the surface of the hemisphere. This finding motivated us to do a quantitative study of single-units of V1 in *Cebus* that constituted the first description of a mechanism of completion of shape in V1 (Fiorani *et al.* 1992). Also, the automated quantitative mapping of the blind spot region with long moving bars showed a precise organization (see figure 10) that suggests that the visual representation in V1 is visuotopic, rather than retinotopic, i.e. V1 has a continuous representation of the visual field instead of the discontinuous retinal one (Fiorani *et al.* 2001; Azzi 2004). We propose that distinct forms of perceptual filling-in engage different portions of a wide distributed processing network. The automatic mapping of receptive field in V1 revealed that the orientation selectivity of the 'blind' eye is statistically different from that of the other eye, showing the influence of long range iso-orientational connections (Azzi 2004). Figure 10 shows the regularity of the progressions of receptive field centres for both eyes and the difference in orientation selectivity of the cell at the representation of the blind spot, for inputs of the 'blind' eye. At the same time, boundary completion associated with illusory contour stimuli probably involve V2 circuits as revealed by the studies of von der Heydt & Peterhans (1989). These two forms of boundary completion should be contrasted with feature completion, such as brightness and texture filling-in. The De Weerd *et al.* (1995) study strongly suggests that V2 and V3 (but not V1) mediate texture filling-in. Brightness filling-in seems, at least in part, to involve the striate cortex (Rossi & Paradiso 1996). However, the view we advance here is not that of

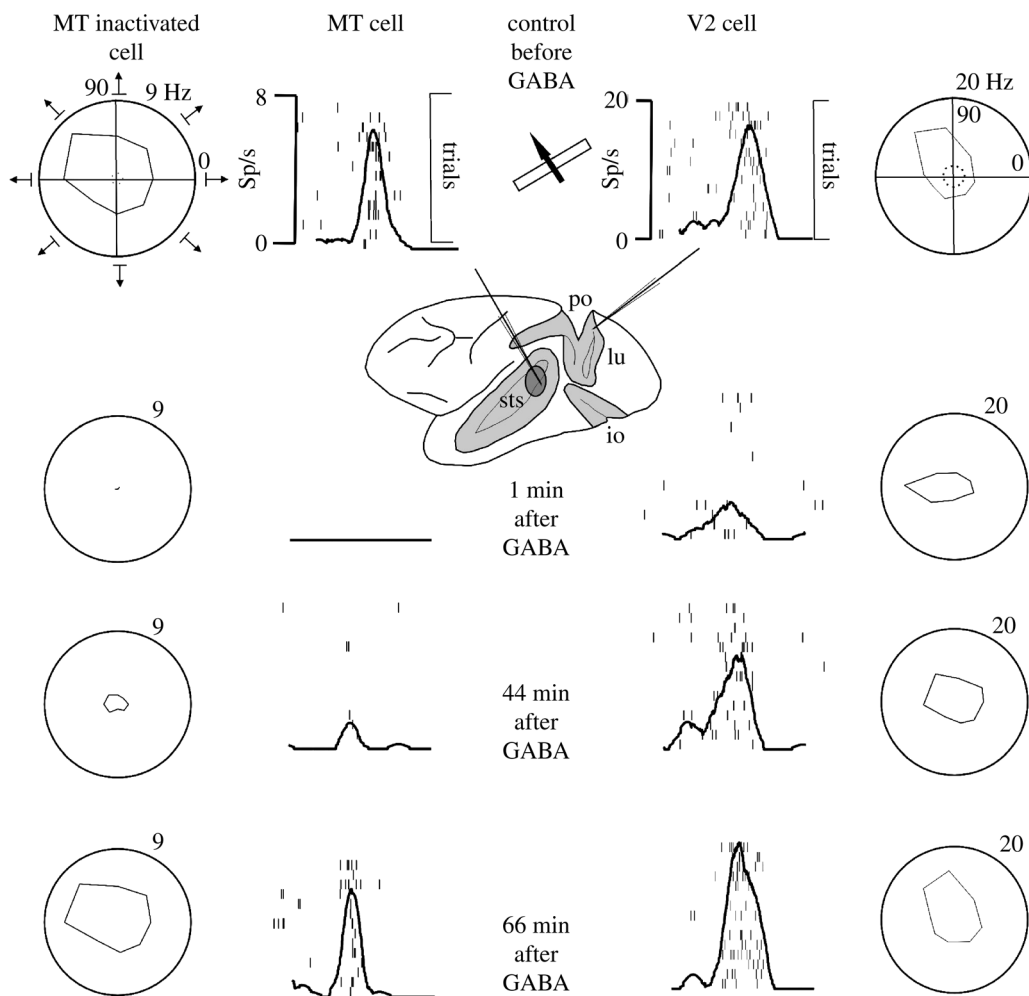


Figure 9. Changes of direction selectivity in V2 after GABA inactivation in MT. Activity of two cells at topographically corresponding locations in MT and V2, before and after GABA inactivation of MT. The directional selectivity (polargram) and the post-stimulus histogram at the preferred direction are shown for both cells 1, 44 and 66 min after GABA injections in MT. The response of the V2 neuron decreases and its direction selectivity changes while the topographically corresponding location in MT is inactivated. Solid circle, maximum spike rate of the cell; dashed circle, spontaneous spike rate.

‘one-effect-one-area’, but instead that a distributed network of topographically organized areas is involved. So, for example, V2 and V3 circuits are important for texture filling-in. Finally, although illusory contours trigger responses in V2, recent evidence suggests that other areas may also be involved (such as V4).

The visual system is constantly confronted with the problem of organizing the retinal pattern of stimulation into coherent percepts. Somehow, from the luminance pattern stimulating the eyes, the visual system must produce organized, meaningful representations of the world around us. At every instant, multiple organizations of the elementary pattern of stimulation are possible, and the visual system must generate useful representations that can guide behaviour. Therefore, we can view the behaviour of the visual system as, at every instant, recursive loops in topographically organized networks would try different converging algorithms to select the ‘best hypothesis’ consistent with the incoming stimulus. Thus, we propose a framework for understanding visual perception based on topographically organized, functionally synchronized distributed cortical networks (Gattass *et al.* 1999) that project to more anterior non-topographic shape-sensitive visual areas in the temporal lobe, while other

networks project to the parietal lobe to organize oculomotor or egocentred behaviours. Finally, we suggest that multiple representations of the stimulus engage competitive mechanisms that select the ‘most probable hypothesis’ capable of constructing a single neural representation of perceived objects.

In summary, the cortical visual system is composed of a number of specialized visual areas where different visual attributes are segregated and processed in parallel in different areas. Analytic posterior cortical visual areas are topographically organized whereas more anterior temporal areas are not, and they have a more holistic processing. The visual information relayed at the lateral geniculate nucleus projects mainly to the striate cortex, also known as the first visual area or V1. V1 projects primarily to areas V2, MT and PO, and those in turn project to a number of other areas to constitute three main streams of visual information processing. For a given eccentricity, there is an increase in receptive field size at each step of processing. In addition, in most topographically organized areas, there is a gradual increase of the receptive field size with increasing eccentricity. These increases are greater at more anterior areas in the temporal lobe or at more dorsal areas in the parietal lobe. The scatter of receptive

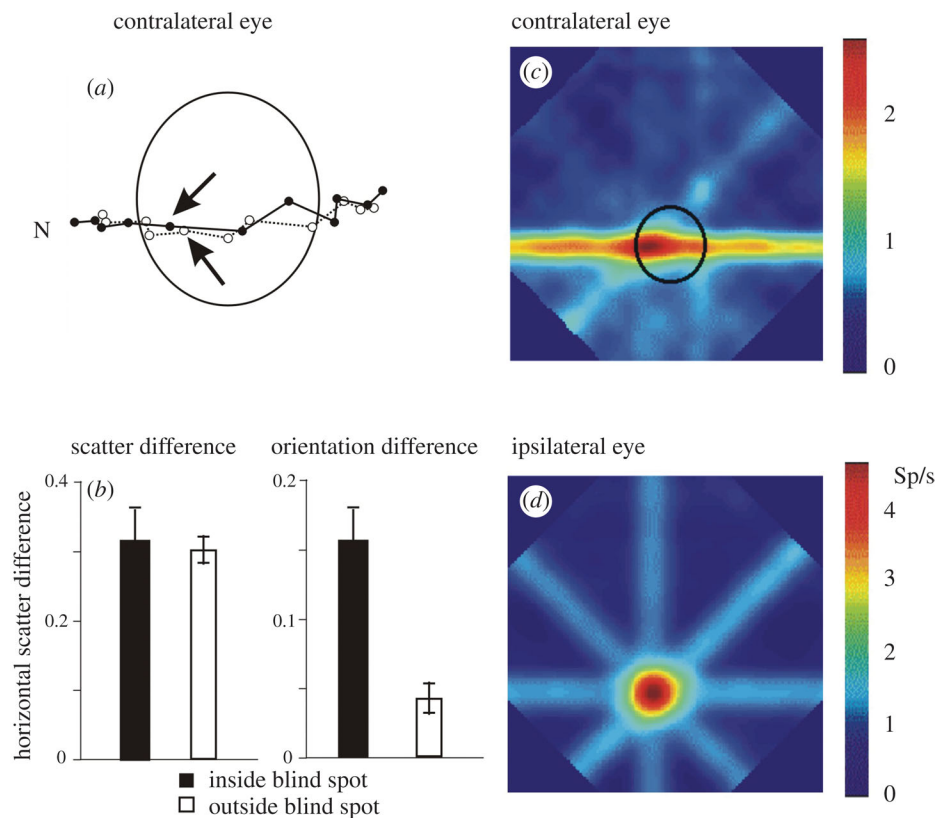


Figure 10. Precision of receptive field location and discrepancy of orientation selectivity. (a) Location of receptive field centres mapped through the contralateral (filled circles and solid line) and ipsilateral (open circles and dotted line) eyes corresponding to 11 recording sites in V1 across the representation of the contralateral optic disc, N, nasal. (b) Difference in horizontal receptive field position (scatter) and difference in direction/orientation selectivity of the receptive fields for the contralateral and ipsilateral eye, for 123 recording sites. (c,d) Representations of the receptive field response in the space domain, for the centres marked by arrows in (a), based on the single-unit responses to eight different directions. The ellipse in the contralateral eye represents the optic disc position. Spike rate for each eye is colour-coded (right: colour scale).

field location increases with increasing receptive field size. Thus, the visual topographies are progressively coarser toward the temporal and parietal lobes. The visual areas contain coexisting functional modules (columns) arranged together independently, however preserving a certain degree of overall visual topography. Other types of organization related to perception of egocentric motion or oculomotor behaviour may prevail in dorsal parietal areas. The minimal point image size, i.e. the extent of cortex devoted to the processing of a point in the visual field, increases towards the temporal lobe and remains constant or shows a slight decrease toward the parietal lobe. The concept of topographical distributed networks, connecting areas that contain organized visual maps and different functional modules for visual processing, contrasts to other types of organizations that are related to non-visually organized areas.

The extent of the visual field represented in each area is different. Areas V1 and V2 contain the representation of the entire visual field, area MT, the binocular visual field, while area V4 represents only the central 30° to 40°. Areas of the parietal lobe have larger emphasis in the representation of the periphery. There are asymmetries in the pattern of connections of central and peripheral representations, in different areas. Central V2 and central V4 project mainly to the temporal lobe, whereas peripheral V2 (more than 30°) and peripheral V4 (more than 10°) project mainly to the parietal lobe. Priority

connections targeting the temporal, parieto-temporal and parietal lobes may be important to construct crude early representations of objects, objects' trajectories and egocentric movements in the visual space.

This work would not be possible without the aid of Maria Thereza A. Monteiro and Liliane H. Pontes in the preparation of the manuscript. This work was supported by grants from FUJB, PRONEX, FINEP, CEPG and CNPq.

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GLOSSARY

CMF: cortical magnification factor
 CytOx: cytochrome oxidase
 DMZ: densely myelinated zone
 FEF: frontal eye field
 HRP: horseradish peroxidase
 OD: ocular dominance

Cortical visual areas

FST: visual area FST
 LIPd: dorsal portion of lateral intraparietal area
 LIPv: ventral portion of lateral intraparietal area
 MIP: medial intraparietal area
 MST: medial superior temporal area (V6)
 MT: visual area MT (V5)
 MTp: peripheral portion of MT
 PIP: posterior intraparietal area
 PO: parieto-occipital area
 POd: dorsal parieto-occipital area
 TEa: anterior portion of area TE
 TEm: medial portion of area TE
 TEO: posterior inferior temporal cortex
 TEp: posterior portion of area TE
 TH: cytoarchitectonic area TH
 V1: primary visual cortex
 V2: visual area 2
 V3A: a V3 visual complex part A
 V3d: dorsal portion of visual area 3
 V3v: ventral portion of visual area 3
 V4: visual area 4
 V4t: V4 transition zone
 VIP: ventral intraparietal area
 VTF: visual portion of parahippocampal TF

Cortical sulci

amt: anterior middle temporal sulcus
 ar: arcuate sulcus
 ca: calcarine fissure
 ce: central sulcus
 ci: cingulate sulcus
 co: collateral sulcus
 ec: external calcarine sulcus
 io: inferior occipital sulcus
 ip: intraparietal sulcus
 la: lateral sulcus
 lu: lunate sulcus
 orb: orbital sulcus
 ot: occipitotemporal sulcus
 p: principal sulcus
 pmt: posterior middle temporal sulcus
 pom: medial parieto-occipital sulcus
 rh: rhinal sulcus
 sp: subparietal sulcus
 st: superior temporal sulcus