

CORTICAL STREAMS OF VISUAL INFORMATION PROCESSING IN PRIMATES

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1. The topographic organization of the cortical visual areas in the *Cebus* monkey and their anatomical connections support the subdivision of the visual pathways into ventral and dorsal streams of visual information processing.

2. We propose that the dorsal stream, as defined by Ungerleider and Mishkin (In: Ingle DJ, Goodale MA and Mansfield RJW (Editors), *Analysis of Visual Behavior*. MIT Press, Boston, 1982), be subdivided into dorsolateral and dorsomedial streams, which are concerned with different aspects of the processing of motion and spatial perception.

3. The data support the hypothesis of concurrent, modular processing of visual attributes in cortical visual areas in the different streams, and highlight some features of the visual field representation in each area which may reflect functional specialization of these streams.

4. The visual topography is locally disrupted in some cortical areas by the existence of functionally different modules. However, a global visuotopic organization is preserved in most areas.

5. The visuotopic organization may provide the address of space coordinates to integrate information concerning the same retinotopic locus across different visual areas.

Key words: visuotopic organization, connections, anisotropy, cytochrome oxidase, *Cebus apella*.

Introduction

The visual cortex of primates can be subdivided into multiple areas based on cytoarchitecture, myeloarchitecture, visual topography, afferent and efferent connections, single-unit responses and histochemistry (Van Essen, 1985; Gattass et al., 1986). Some of these areas are visuotopically organized, containing complete or partial representations of the visual field. Recently, several lines of evidence have suggested that each of these areas may be further subdivided into functionally distinct modules such as those revealed by cytochrome oxidase (CO) histochemistry (Tootell et al., 1985; Zeki and Shipp, 1988).

A wealth of data on the connections of the visual areas with subcortical structures and among themselves has become available in the last two decades. In spite of the enormous complexity of the pattern of connections, models have been proposed to explain visual processing from a global perspective, forming a theoretical framework based on anatomical and behavioral grounds (Ungerleider and Mishkin, 1982; Van Essen, 1985; Barlow, 1986;

Research supported by FINEP, CNPq and CEPG/UFRJ.

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Livingstone and Hubel, 1987). Among these models, we shall focus on that of Ungerleider and Mishkin (1982). These authors recognized the existence of two functional streams, a ventral one channeling visual information about shape, color and texture to the inferior temporal cortex, and a dorsal one processing movement and spatial relationships and projecting to the posterior parietal cortex (Ungerleider, 1985). The generality of this model among primates has been recognized (Weller, 1988) and the concept of parallel pathways has provided important insights for psychophysical work on the nature of visual processing in humans (Livingstone and Hubel, 1987). Recent anatomical evidence led us to suggest a subdivision of the dorsal pathway into two streams: a dorsomedial stream involving the parietooccipital visual area (PO) in the anterior bank of the parietooccipital sulcus and precuneate gyrus, and the cytoarchitectonic area PG (Von Bonin and Bailey, 1947) in the inferior parietal lobule, and a dorsolateral stream involving the middle temporal area (MT), the medial superior temporal area (MST) and the lateral intraparietal areas (Goldman-Rakic, 1987; Colby et al., 1988; Neuenschwander, 1989). As discussed below, the dorsomedial and dorsolateral streams may be involved in different aspects of motion and spatial vision processing.

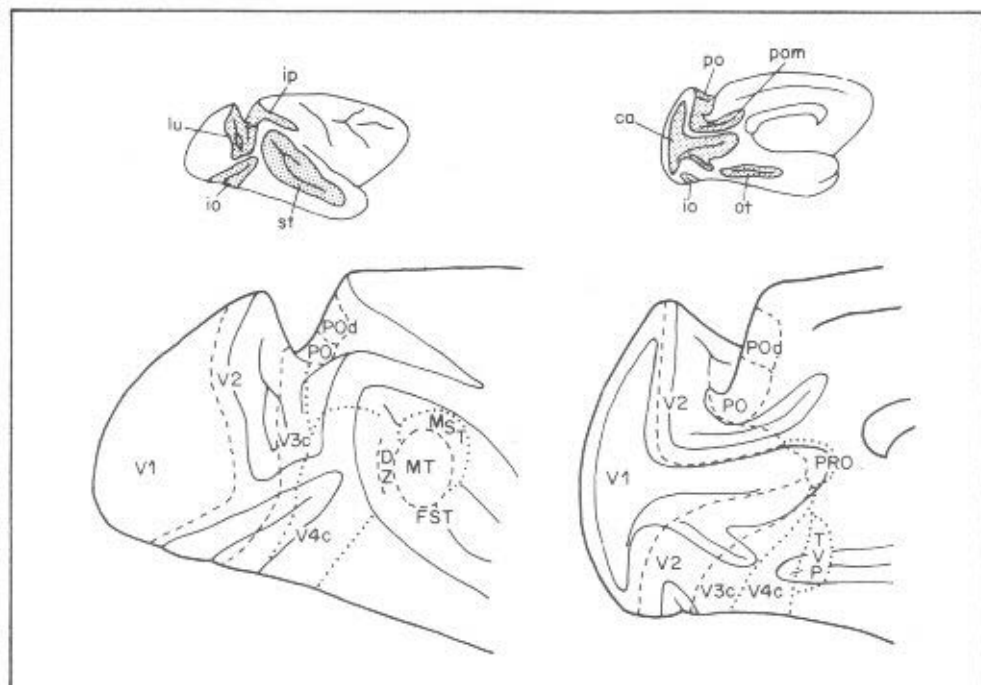


Figure 1 - Cortical visual areas in *Cebus*. The drawings are based on photographs of a brain in which sulci were partially opened. Physiologically defined areas are outlined by dashed lines, and the borders of the cortical regions defined by myeloarchitecture and by cortical connections with V1 are indicated by dotted lines. Left, lateral views; right, medial views. Ca, calcarine sulcus; io, inferior occipital sulcus; ip, intraparietal sulcus; lu, lunate sulcus; ot, occipito-temporal sulcus; po, parieto-occipital sulcus; pom, medial parietal-occipital sulcus; st, superior temporal sulcus.

In the last few years we have been studying the visual areas (Figure 1) in *Cebus apella*, a diurnal New World monkey. Several aspects of the organization of the visual areas of this New World monkey have proven to be similar to those of Old World primates (Gattass et al., 1987; Rosa et al., 1988a,c; Fiorani Jr. et al., 1989; Neuenschwander, 1989). In this paper, we will compare some characteristics of the visual areas corresponding to the early stages of visual processing in the ventral, dorsolateral and dorsomedial pathways and will report on differences in visual topography and connections among these areas.

Visual topography

Visual areas

A common feature in the early stages of processing in sensory systems is the existence of ordered (topographic) representations of the receptor surface in neural structures. This feature is depicted in Figure 2 which shows some of the visuotopically organized cortical areas of *Cebus apella*. Our studies (Gattass et al., 1987; Rosa et al., 1988c; Fiorani Jr. et al., 1989; Neuenschwander, 1989) have described in detail the boundaries and the visual topography of the first and second visual areas (V1 and V2), of MT and of an adjacent dorsal zone (DZ), of PO and of the adjacent parietooccipital dorsal area (POd). Other areas, such as MST and prostriata, have been delimited only on architectonic grounds. The boundaries of the third visual area (V3) are still a matter of controversy; some authors consider V3 of the macaque to be a single area containing the representation of both the upper and lower quadrants, although recognizing the existence of differences between dorsal and ventral V3 (Gattass et al., 1988a). On the other hand, other investigators consider these differences to be compelling enough to subdivide the third complex into two areas: V3 containing the representation of the lower quadrant and a ventral posterior area (VP) with the representation of the upper quadrant (Van Essen, 1985). In our re-investigation of the third visual area in the genus *Cebus*, we have seen no reason to separate the representation of the central 10 degrees of the lower quadrant, in the lunate sulcus, from that of the upper quadrant representation on the ventral surface (Gattass et al., 1988b). Additional experiments are in progress to clarify to what extent the lower peripheral V3 is similar to the remaining portions of the area. Therefore in this paper we shall use the term ventral V3 (V3v) for that portion of the third visual area representing the upper quadrant plus the central 10 degrees of the lower quadrant, in order to distinguish it from the densely myelinated V3 of the macaque (Van Essen, 1985). Figures 1 and 2 also illustrate other areas defined by anatomical connections (A.P.B. Sousa, M.C.G. Piñon, R. Gattass and M.G.P. Rosa, unpublished data) for which the topography and boundaries have not been established in *Cebus*. These areas include the fourth visual area (V4) and an area adjoining it anteriorly and ventrally, here called the temporal ventral posterior region (TVP), which are likely to be members of the occipitotemporal or ventral stream (see below).

How much of the visual field is represented in each area?

There is a large degree of variability in the topographic organization and in the amount of the visual field represented in the various visual areas. V1 and V2, areas which

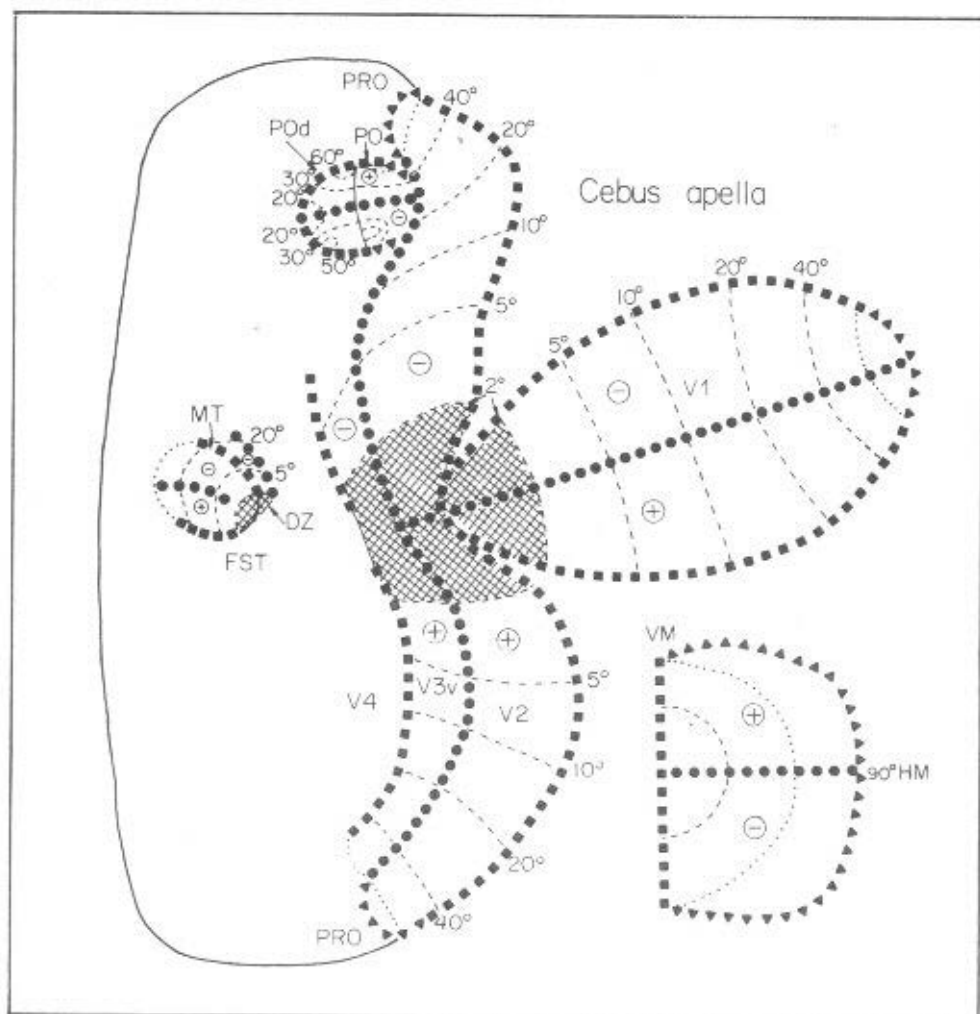


Figure 2 - Visual topography of areas V1, V2, V3v, DZ, MT, PO and POD in the *Cebus* monkey, illustrated in an unfolded map of caudal cerebral cortex. A discontinuity was introduced at the V1/V2 border to avoid distortions. The squares indicate the vertical meridian (VM), the filled circles the horizontal meridian (HM), the triangles the periphery, the dashed lines the isoeccentricity lines, the dotted lines the limit of the binocular visual field, and the hatched region the center of gaze. The thin solid lines represent estimated myeloarchitectonic borders. The inset at lower right is a representation of the upper (+) and lower (-) contralateral visual quadrants.

constitute the primary source of all streams, contain the representation of the entire visual hemifield (Gattass et al., 1987; Rosa et al., 1988c), while only a few of the areas anterior to them do so. In the macaque, V3 and V4 contain representations of only the centralmost 30 to 40 degrees (Gattass et al., 1988a) and the cytoarchitectonic area TEO, the next area in the ventral stream, seems to contain an even more restricted central representation (Fenstemaker

et al., 1985). On the other hand, the ventral V3 of *Cebus* may contain the representation of the whole binocular portion of the upper quadrant (Gattass et al., 1988b). However, in neither species has a representation of the far periphery (monocular crescent) been detected in these areas. In addition, we have to be aware that one could have overlooked the representation of the monocular crescent in these areas because of its low magnification factor. In agreement with these observations, receptive fields of neurons in the inferotemporal cortex all include the fovea, and do not extend into the monocular periphery of the visual field (Desimone and Gross, 1979). In contrast, the areas corresponding to the early stages in the dorsomedial pathway, such as PO and POd, contain representations of both the binocular and monocular visual fields (Neuenschwander, 1989). A particularly interesting aspect of these areas is the virtual absence of receptive fields including the fovea. Note that receptive fields in area PG, a later stage of the dorsomedial pathway, often extend to the far periphery of the visual field and represent the fovea sparingly (Motter and Mountcastle, 1981; Steinmetz et al., 1987).

Finally, areas of the dorsolateral pathway vary in the extent of visual field representation. While most studies fail to show a representation of the monocular crescent in MT (Desimone and Ungerleider, 1986; Maunsell and Van Essen, 1987; Fiorani Jr. et al., 1989), MST, a later stage of the dorsolateral stream, was shown to contain a representation of the visual field which includes the monocular crescent as well (Desimone and Ungerleider 1986; Saito et al., 1986; Fiorani Jr. et al., 1989). This representation is likely to be relayed to MST by area PO, to which MST is interconnected (Boussaoud et al., 1987; Colby et al., 1988).

Emphasis on central vision representation

Another aspect of visual topography, which is intimately linked with the extent of the visual field representation, is that of the ratio of central vs peripheral representation. The amount of cortex devoted to the visual field periphery (more than 20 degrees) for each area is illustrated in Figure 3 (shaded area). In the source of all pathways (V1 and V2), as well as in the areas of the ventral stream (V3, V4, TEO, TVP), there is a large magnification of central vision representation (Fenstemaker et al., 1985; Gattass et al., 1987, 1988a; Rosa et al., 1988c; A.P.B. Sousa, M.C.G. Piñon, R. Gattass and M.G.P. Rosa, unpublished data). MT, an area of the dorsolateral stream, likewise has an expanded representation of central vision, which, however, is less pronounced than that found in areas of the ventral stream (Fiorani Jr. et al., 1989). The most intriguing observation, however, is that in PO virtually no receptive field centers were found below 20 degrees of eccentricity, and only a few were found in POd (Neuenschwander, 1989). These differences in the emphasis on central vs peripheral vision in distinct visual areas, as well as in the extent of visual field representation, are likely to be related to the different roles performed by the ventral, dorsolateral and dorsomedial streams. Areas of the ventral stream, with large central representations, may be related to form, texture and color processing (Ungerleider, 1985). The differences between the dorsolateral and dorsomedial streams might also be related to different aspects of motion and spatial processing. Psychophysical experiments point to the existence of two distinct mechanisms responsible for this type of analysis, one of them prevailing at the central and the other at the

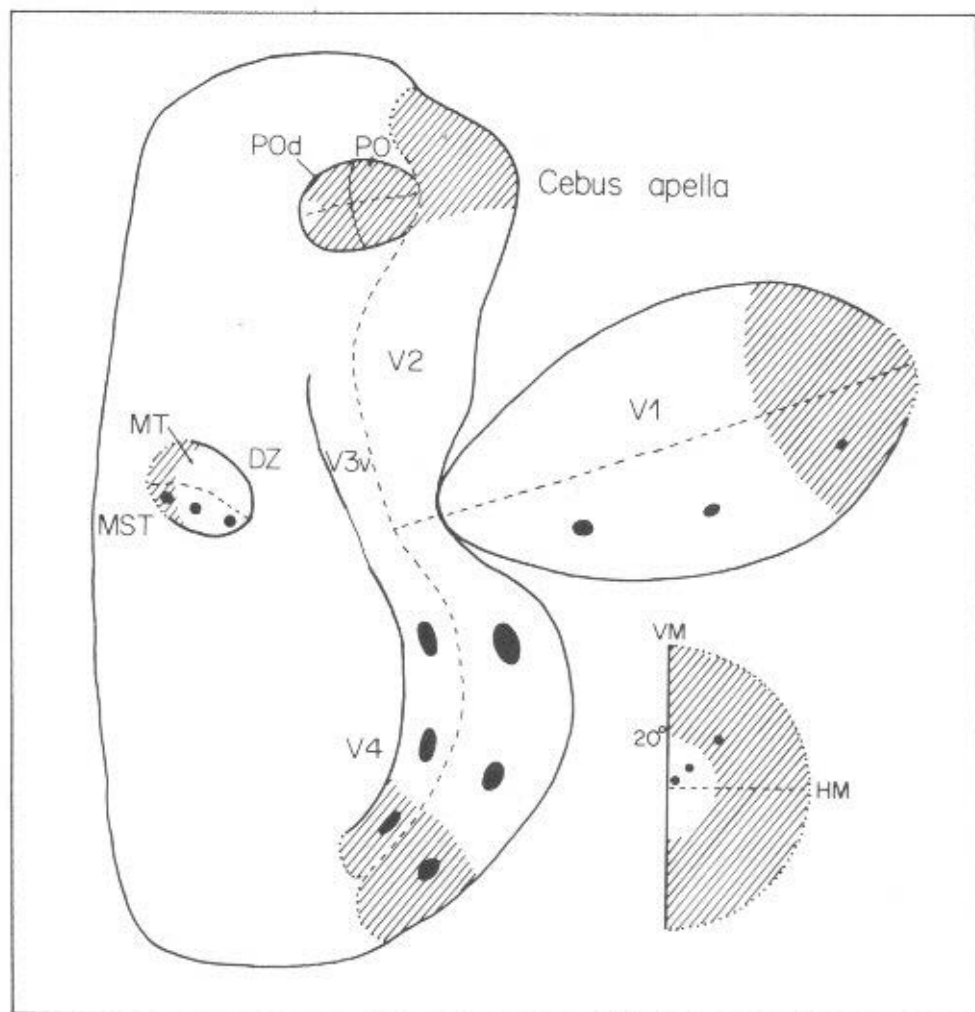


Figure 3 - Point-images and representations of the visual field periphery, beyond 20 degrees, in cortical visual areas. The point images at 3, 10 and 30 degrees eccentricity are illustrated in black and the periphery as hatched areas. Thick solid lines indicate the vertical meridian (VM), the dashed lines the horizontal meridian (HM) and dotted lines the limit of the peripheral visual field representation in the areas. Due to the nature of the visual topography in PO and POd we were unable to determine point-images in these areas. For details, see text.

peripheral visual field (Dichgans and Brandt, 1974; Bonnet, 1977). Steinmetz et al. (1987) have already called attention to the relation between the peripheral fields of area PG and one of these mechanisms, the one related to flow-field perception during animal locomotion, in which the images on that part of the retina corresponding to midline frontal vision show little angular displacement. It is, therefore, likely that PO and POd, with a homogeneous representation of the visual field periphery, provide the essential inputs mediating this kind of

analysis. In addition, stimulation of the visual field periphery was shown to dominate the perception of self-motion, even when antagonistic moving images are presented at center of gaze (Dichgans and Brandt, 1974). Therefore, one could suggest that the areas of the dorsomedial stream are involved in visuomotor integration and perception of global spatial relationships. Interestingly, PO, POd and PG were shown to project to the pontine nuclei, which relay information to the part of the cerebellum involved in motor planning (Brodal, 1978). The movement-sensitive areas of the dorsolateral stream, with large central field representations, on the other hand, may provide the characteristics for the centrally prevailing motion mechanism. Their projections to the lateral intraparietal subdivision of the parietal lobe (Ungerleider, 1985; Blatt et al., 1987; Boussaoud et al., 1987; Goldman-Rakic, 1987) as well as lesion experiments (Newsome et al., 1985) point to the participation of these areas in the processing of movement and object location essential for the control of eye movements.

How large is the local integration in visual areas?

A gradual increase in multiunit receptive field size is observed in progressively later stages of the ventral and dorsolateral streams. In some of these areas, receptive field sizes increase with increasing eccentricities. For a given eccentricity, receptive fields are larger in areas corresponding to the later stages of processing than in those corresponding to the early stages (Gattass et al., 1986; Komatsu and Wurtz, 1988). For example, in V4 receptive fields are larger than those in V3 and V2, which in turn are larger than those in V1 (Gattass et al., 1986). Cells of striate cortex, because of the small sizes of their receptive fields, are not suitable for a global analysis of visual stimuli. Under normal conditions, the receptive field sizes are too small to allow the extraction of form or color. These features of the visual image demand comparisons of line orientations and intersections or wavelengths in the context of a background, over a wider aperture. In contrast, the sizes of receptive fields in V4, TEO or the inferotemporal cortex and the filtering mechanisms associated with selective attention (Desimone et al., 1985; Moran and Desimone, 1985) may be adequate for the extraction of figure from ground and color from wavelength. This argument based on the notion of processing centered in the activity of single cells also applies to the distributed processing of the activity of an ensemble of cells, such as that proposed by Gross and collaborators (1985) for the inferotemporal cortex. Thus, the gradual increase in receptive field size in the chain of areas belonging to these streams is consistent with the larger local integration necessary for the processing of form, color or movement. In contrast, areas of the dorsomedial stream, such as PO and POd, show a small representation of the central visual field and an invariance of field size with eccentricity (Neuenschwander, 1989). The homogeneous representation of the visual field and the constancy in field size with eccentricity in PO and POd are consistent with the characteristics of spatial vision throughout the visual field. These properties parallel human psychophysical ability to detect continuously moving targets, which is relatively invariant throughout the visual field (Bonnet, 1977; Steinmetz et al., 1987).

How precise are the representations?

The representation of the visual field inferred from the topographic distribution of

receptive field centers may be misleading. Inasmuch as receptive fields have finite sizes and their sizes increase with increasing eccentricities, the topography inferred from receptive field centers in MT, for example, would not show a representation of the vertical meridian beyond 15 degrees eccentricity (Fiorani Jr. et al., 1989). However, this meridian would be represented throughout its extent in a map that took into account the receptive field borders.

Nevertheless, there are differences among the areas in the three streams that cannot be attributed to such shortcomings in the method of interpolating the visuotopic maps. For example, the visuotopic organization derived from receptive field centers for an area at a more advanced stage is not as precise as that found for one at an earlier stage of processing. In the ventral pathway, the visuotopic maps are somewhat coarser in V3 and V4 than in V2 (Gattass et al., 1988a); they are very coarse in TEO (Fenstermaker et al., 1985); and no visuotopic organization could be described at a farther station, the inferior temporal cortex (Desimone and Gross, 1979). The decrease in the precision of visual field representation, i.e., the increase in the amount of scatter in receptive field position, has been usually related to the increase in receptive field size in these areas (Hubel and Wiesel, 1974; Gattass and Gross, 1981). However, the variety of irregularities in addition to the scatter found in the visuotopic maps has not been fully evaluated. Thus, it is possible that these irregularities may be of different natures in different areas.

We have observed that, at a given eccentricity, the cortical magnification factor (CMF) is higher when measured between points located along lines of the same polar angle (isopolar lines) than along lines of similar eccentricity (isoeccentric lines), in both V1 (Gattass et al., 1987) and V2 (Rosa et al., 1988c) of *Cebus*. This anisotropy in visual representation is less pronounced in V1 than in V2, where the isopolar CMF is usually 50% higher than the isoeccentric one. This anisotropy in the cortical magnification factor is reflected by the oval shape of the minimum point image size (MPIS) (Rosa et al., 1988c), calculated as the product of cortical magnification factor by multi-unit receptive field size (Figure 3). Moreover, while in V1 the overall isopolar/isoeccentric anisotropy increases towards the peripheral representation, such tendency was not observed in V2. We have also observed that in crossing V2 along the isopolar dimension receptive field eccentricities change in a discrete way. For example, the electrode position may be moved as much as 4 mm without a predictable change in receptive field eccentricity, while an additional 0.5 mm displacement may result in a considerable change in receptive field eccentricity (Rosa et al., 1988c). This loss of topographic order along a particular dimension of the map is another characteristic of V2 and probably of other highly anisotropic areas. These irregularities in visual maps may reflect the existence of functionally different regions crossing these areas (see below).

More recently, we have also been studying the regularity of visual maps in other areas of *Cebus apella*. In V3v, for example, we observed an anisotropy that was even more pronounced than that observed in V2: the isopolar CMF in ventral V3 was at least twice the isoeccentric CMF (Gattass et al., 1988b). 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 (M.C.G. Piñon, R. Gattass, A.P.B. Sousa and M.G.P. Rosa, unpublished results).

While areas corresponding to the first stages of the ventral pathway are all characterized by anisotropies, a similar analysis carried out in MT (Fiorani Jr. et al., 1989)

did not provide any evidence for anisotropy in the visual map (Figure 3). In the areas of the dorsomedial pathway, PO and POd, the topographic irregularities are far more complex. Here it is always possible to define the representation of isopolar lines, such as the horizontal meridian, but the interpolation is more difficult when defining the isoeccentric lines (Neuenschwander, 1989). At present, we have no direct evidence regarding the functional significance of the observed order in the isopolar domain vs disorder in the isoeccentric lines present in PO and POd. One may speculate, however, by taking into account the receptive field characteristics of area PG, which is connected with PO (Colby et al., 1988). Centrifugal and centripetal organizations of directionality, such as those observed in area PG (Motter and Mountcastle, 1981; Steinmetz et al., 1987), demand interactions between neurons which analyze 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 by local circuits. This arrangement would resemble what Barlow (1986) called a "non-topographic" functional map. Thus, the visual maps of PO and POd may be the consequence of different computational strategies performed by these areas.

Modular organization as revealed by cytochrome oxidase

Neurons in different cortical modules vary in their content of cytochrome oxidase (CO), a mitochondrial enzyme of oxidative metabolism (Horton and Hubel, 1981). The concentration of CO also reflects long term changes in neuronal activity, such as those occurring after deafferentation (Horton, 1984; Rosa et al., 1988a; Wong-Riley et al., 1989).

The anisotropies in V1, V2 and V3v of *Cebus* have motivated studies of the intrinsic organization of these areas. These studies, carried out in normal and monocularly enucleated primates, were based on the analysis of sections tangential to the pial surface stained by a method that reveals the enzyme cytochrome oxidase. Tangential sections of striate cortex of Simiiform primates stained for CO show a periodic pattern of heavily stained, oval-shaped "blobs" in a matrix of less reactive "interblob" regions (Horton and Hubel, 1981; Horton, 1984). In order to evaluate the regularity of the modular organization of V1 we studied the distribution of CO blobs in V1 of *Cebus*. Blobs are present throughout V1 in this species. In *Cebus*, in spite of the large variation of CMF with eccentricity (Gattass et al., 1987), blob spatial density is fairly constant within the binocular representation and decreases only slightly in the monocular crescent (Rosa et al., 1988b). Blob spatial density in the binocular field representation is slightly higher in the marmoset (5.5 blobs/mm²) than in the *Cebus* (4 blobs/mm²) and much lower in men (1.2 blobs/mm²) (Gattass et al., 1990). Therefore, under the assumption that blob distribution is related to the distribution of functional modules, we conclude that these modules may be compressed in primates with smaller striate cortices. While in V1 of *Cebus* and humans, species with very different brain sizes, there is a similar number of blobs, in marmosets the further decrease in V1 size is not paralleled by a proportional increase in blob spatial density, meaning that there are fewer modules in the smaller species (Gattass et al., 1990). It may be that a minimum number of neurons is needed to perform whatever operation blobs are responsible for. Therefore, for smaller brain sizes there would be a decrease in the number of modules rather than in the number of neurons within each module.

Another aspect of modular organization in V1 is the existence of ocular dominance (OD) columns, which reflect the periodic pattern of termination of geniculate projections in layer IVc (Hendrickson et al., 1978). In the macaque, the observed anisotropy of V1 has been interpreted to be the result of the orientation of the ocular dominance stripes in such a manner that the CMF would be greater perpendicular to the stripes because of the need to represent twice the same region of the visual field, once for each eye (Tootell et al., 1988). In *Cebus*, the observation of an anisotropy in V1 was surprising, in view of earlier reports on the absence of OD stripes in New World monkeys, including *Cebus* (Hendrickson et al., 1978, Gattass et al., 1987). In a recent re-investigation of this subject we were able to demonstrate the existence of these stripes in this genus by means of CO-histochemistry after long-term monocular enucleation (Rosa et al., 1988a). The study of the distribution of OD stripes revealed that their orientation would account for the anisotropy in the local measurements of CMF in V1 (Gattass et al., 1987; Rosa et al., 1988a). These results are consistent with the notion that the visual map of V1 may be made of two partially overlapping visual maps, one for each eye.

In V2, as revealed by CO-histochemistry, modules are stripe-like, running from the anterior border of V2 to its border with the striate cortex (Tootell et al., 1983; Rosa et al., 1988a). Three types of stripes are currently recognized in V2, namely the thin and thick CO-rich stripes and the CO-poor interstripes, which differ in neuronal properties and connections (De Yoe and Van Essen, 1985; Hubel and Livingstone, 1987). Both the thin stripes and the CO-poor stripes seem to be related to the ventral stream through their connections with V4, while the thick stripes seem to be related to the dorsolateral stream by way of their connections with MT (De Yoe and Van Essen, 1985; Zeki and Shipp, 1988). We have, therefore, reasoned that the same portion of the visual field should be represented many times in V2, in stripes of different kinds (Rosa et al., 1988c). In *Cebus*, the study of V2 sections tangential to the cortical surface revealed a pattern similar to that described for other monkeys (Rosa et al., 1988a; Gattass et al., 1990). Taking into consideration the periodical arrangement and orientation of the stripes and assuming little or no overlap between neighboring modules, one would expect an anisotropy of about 3-4:1 in V2, in comparison with the observed anisotropy of 3:2. Thus, we have suggested that each stripe should be formed by heterogeneous sub-modules (Rosa et al., 1988c). Recently, the study of the sections stained for CO in V2 of *Cebus* confirmed the existence of such heterogeneities along the thin bands, in normal animals (Figure 4), which are composed by a series of equally spaced puffs (Gattass et al., 1990; M.G.P. Rosa and R. Gattass, unpublished results). Studies in enucleated animals suggest that the thick bands may be similarly organized (M.G.P. Rosa, M. Fiorani Jr. and R. Gattass, unpublished results). In summary, the mosaic arrangement of functionally different modules in V2 may account for the distortion of the visuotopic map of this area discussed in the previous section. These discrete regions in V2 may be involved with local processing of the visual information and we suggest that they independently represent small portions of the visual field (Rosa et al., 1988c).

And what about V3v? Its large anisotropy suggests that the cortical modules in this area are arranged side by side along the longer (isopolar) dimension of the map. Tootell et al. (1985) described these heterogeneities in the ventral extrastriate cortex of owl monkeys. We have made similar observations regarding the cortex at the anterior bank of the

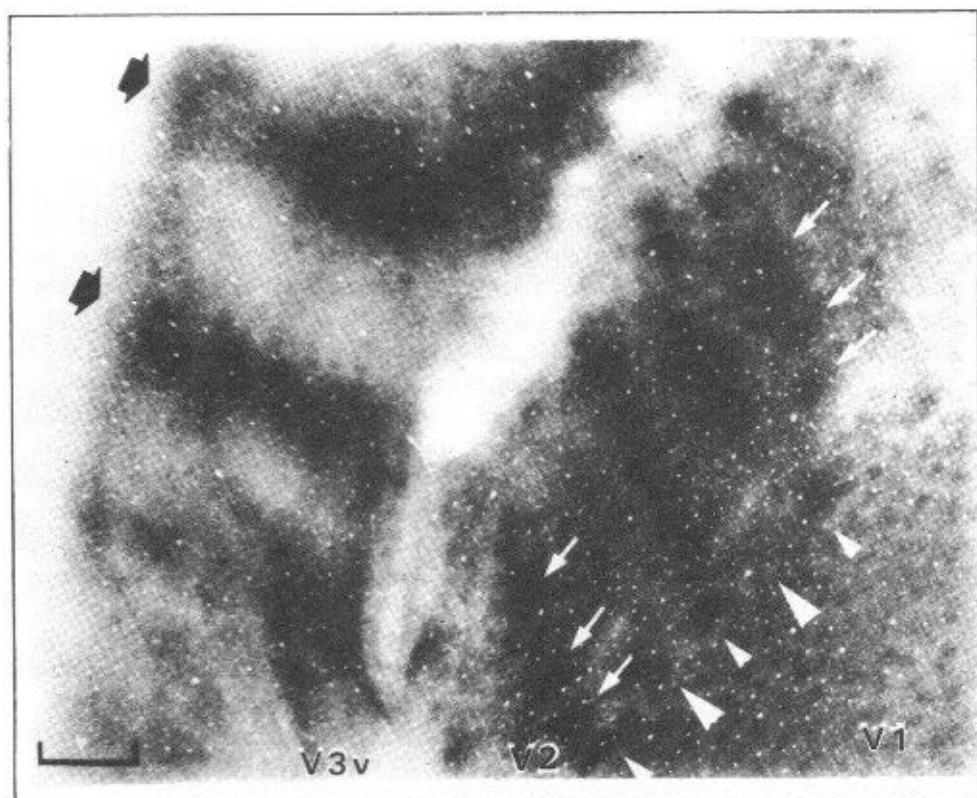


Figure 4 - Photomicrograph of cytochrome oxidase-stained section through the middle layers of V1, at the occipital operculum, and of V2 and V3 at the lunate sulcus. The small white arrowheads point to the thin bands, and the large white arrowheads point to the thick bands in V2. The fuzzy thick bands in V3v are indicated by the black arrows. The heterogeneities along the thin bands in V2 are indicated by white arrows. The strip of white matter between V2 and V3v corresponds to the fundus of lunate sulcus. Scale bar, 2 mm.

lunate sulcus of *Cebus*, where one finds the representation of the central portion of the lower visual field of V3v (Figure 4). Thus, in *Cebus*, we observed alternating fuzzy thick CO-rich and CO-poor bands located anteriorly to V2 both dorsally and ventrally (M.G.P. Rosa and R. Gattass, unpublished results). This observation strongly supports the unity of area V3v. It should be pointed out that in *Cebus*, as in the owl monkey, the stripes of the ventral prestriate cortex may extend not only to V3v but also to the anteriorly placed ventral V4 (Tootell et al., 1985). It seems, therefore, that anisotropy, elongated point-images and stripe-like modules are all characteristics of prestriate areas linked to the inferior temporal cortex. Interestingly, the pattern of termination of projections to the inferotemporal cortex is also stripe-like (Zeki and Shipp, 1988).

In CO-stained tangential sections, Tootell et al. (1985) described MT as being dark and heterogeneous in the owl monkey. In MT of *Cebus*, an area of the dorsolateral stream, we also found no evidence for stripe-like regions (M. Fiorani Jr., R. Gattass and

M.G.P. Rosa, unpublished results). This finding is coherent with our current interpretation of the data inasmuch as no anisotropies were observed in this area.

Patterns of connections in the visual cortex

It is currently accepted that patterns of connections among visual areas are organized according to general rules that apply to all primates. A central concept of this view is that of feedforward and feedback connections. As recognized by Tigges et al. (1981), the laminar source or termination of a given cortical projection depends on the hierarchical position of the areas in the visual stream. Based on this concept, Van Essen (1985) attributed hierarchical levels of processing to the visual areas within each stream. There is independent electrophysiological (Sandell and Schiller, 1982; Nakamura et al., 1986) and behavioral (Haber and Hershenson, 1973) evidence suggesting that some aspects of visual information may be processed serially; however, the importance of parallel processing should be emphasized. As described in previous sections, the existence of parallel pathways which compose the different visual streams was demonstrated by a combination of physiological, behavioral and anatomical data. Moreover, parallel pathways from subcortical structures to the visual cortex can account for some aspects of visual behavior, such as the residual visual capabilities (blindsight) of subjects with total removal of striate cortex (Covey and Stoerig, 1989).

One can speculate, therefore, that there may be independent pathways of visual processing and that hierarchy may exist within some of these pathways. Recently, however, it was shown that there is a multiplicity of connections which allow cross-talk between streams. Thus, the activity in a given stream can possibly influence the processing in other streams. The connections between streams were shown both within single areas (Rockland, 1985) and among different areas (Morel and Bullier, 1987; Zeki and Shipp, 1988).

The possibility for the presence of these integrations in *Cebus* is given, for example, by the feedback projections to V1. Sousa and collaborators (1987, and unpublished results) have shown that most of the prestriate areas, which correspond to several levels of hierarchical processing, project back to V1. Figure 5 shows a summary of the cortical afferents to V1 in the *Cebus* monkey. The afferent connections of V1 revealed the existence of a region on the ventral cortical surface, the temporal ventral posterior region (TVP), which projects primarily to the foveal and parafoveal regions of V1. Due to this emphasis on central vision representation, we are tentatively including this area in the ventral stream. These data also revealed clear topographically organized projections from the third and fourth visual complexes (V3c and V4c), areas of the ventral stream, and a crude organization in area PO of the dorsomedial stream. Among the areas of the dorsolateral stream, MT shows topography in the pattern of projections, although cruder than that observed in the areas of the ventral stream. The projections from MST show no clear topographic trend. In contrast to TVP, which projects to foveal and parafoveal regions, PO and MST project primarily to the periphery of V1.

The pattern of the feedback projections from these areas to V1 called our attention to the difference in the three streams of visual information processing. While several of the areas of the ventral stream project to V1, in the dorsomedial stream, only area

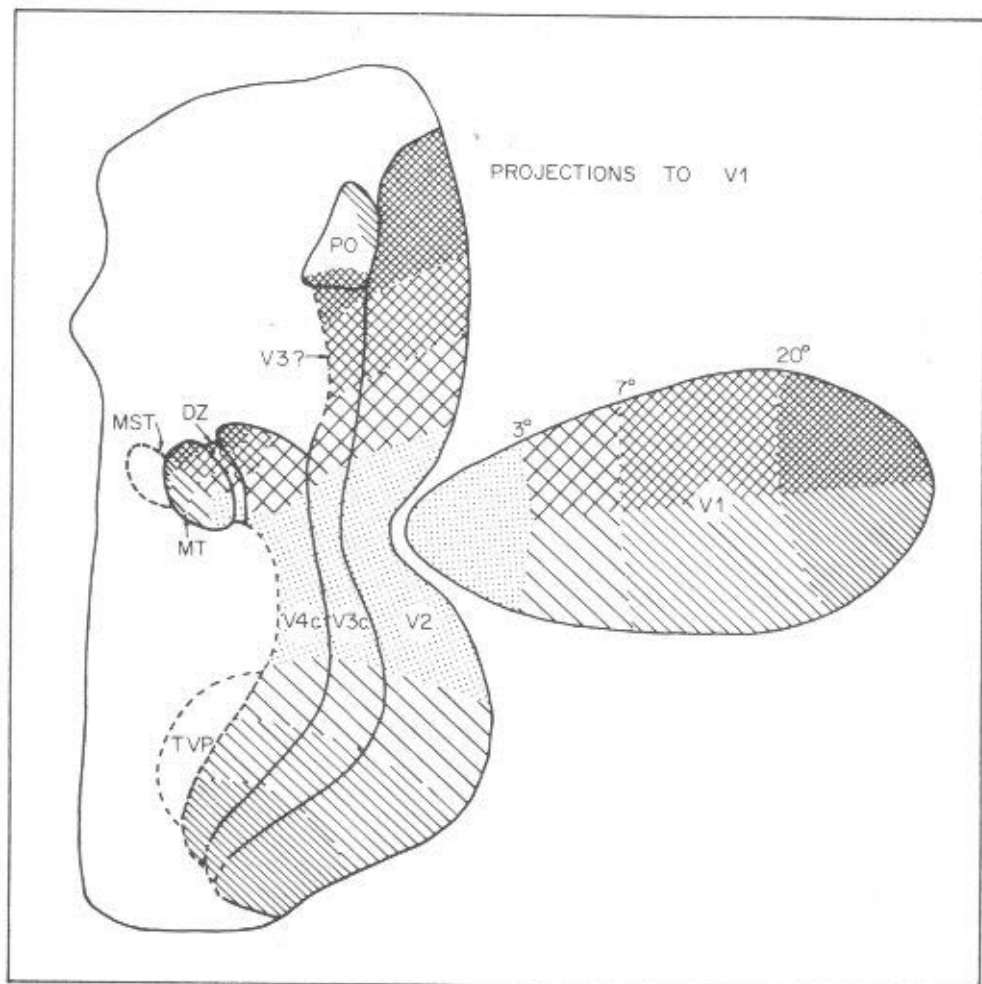


Figure 5 - Flattened map showing the pattern of connections from prestriate areas to V1 in *Cebus*, based on data from A.P.B. Sousa, M.C.G.P. Piñon, R. Gattass and M.G.P. Rosa (unpublished data). The locations of injection sites in V1 and of corresponding projection zones are shown with similar symbols. Solid lines correspond to borders defined both by electrophysiological and myeloarchitectonic methods, while dashed lines correspond to borders defined by the pattern of connections. Note that only part of MST projects back to V1. V3c and V4c stand for the third and fourth visual complexes. For details, see text.

PO, the area which receives direct projection from V1 (Colby et al., 1988), projects back to striate cortex. Area POd, which is similar to PO topographically, is not connected with V1 (Neuenschwander, 1989). In the dorsolateral stream, only area MT and part of area MST project back to V1. In summary, anatomical studies suggest that the cortical visual pathways are better described as networks, in which there is a preferential direction of information flow rather than as a multitude of hierarchically organized, independent parallel pathways (Figure 6).

A hypothesis on cortical operation

The parallel pathways of visual processing begin within the retina (Figure 7) with different classes of ganglion cells projecting to different subcortical structures, which in turn project differentially to the cortical mantle, giving rise to the dorsolateral, dorsomedial and ventral streams.

In this paper, we have suggested that each cortical visual area has a distinct topographic strategy determined by the type of neuronal processing within the area. In the ventral stream, a certain degree of visuotopy is preserved until late stages of processing. In areas within this stream, which simultaneously process several attributes of the image, the local topographic order may be broken by a mosaic of parallel processors (modules) that initially decode the image in terms of its simple components. The image may be subsequently integrated by serial (e.g. increasing integration of image features at larger and more complex receptive fields), and parallel processes (e.g. comparison of different image attributes at the same retinotopic locus). The existence of parallel representations of portions of the visual field in adjoining modules of different types is likely to optimize feature extraction by neuronal populations. In other areas, that may be composed of a more homogeneous set of modules (Albright et al., 1984), the visuotopic order may be broken at relatively early levels of processing. The large scatter found in MT and the crudely retinotopic maps found in MST (Komatsu and Wurtz, 1988) and PO (Neuenschwander, 1989) may reflect this type of functional organization, which is prevalent within areas of the dorsal streams.

The presence of visuotopic organization in most areas of the ventral stream is *per se* evidence for distributed spatial processing. Throughout most of the ventral stream each point of the visual field is processed in separate regions within each area. The processing of central vision, for example, is done at the same time (in parallel) as that of peripheral portions of the visual field. Thus, the processing in the ventral stream, at least up to visual area V4, is performed by means of algorithms for local processing in contrast to the global or holistic

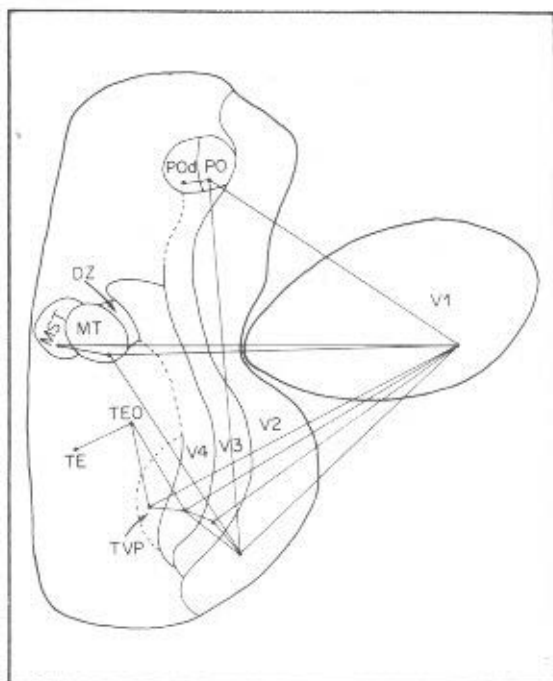


Figure 6 - Distributed network of elements representing a region in the upper visual field. Forward and backward connections may have important roles in determining the activity of each module in the network. For example, the activity of a locus in V1 may depend on the activity of several loci of extrastriate areas located anteriorly. Although DZ projects to V1 it is not included as a node in the network because, so far, no upper field representation has been described for this area.

algorithms implemented in computer vision.

Our data are compatible with a model in which neuronal ensembles engaged in the processing of a given visual parameter are spatially segregated, either in different areas or in different modules within the same area. These ensembles maintain "up-stream" connections with the corresponding ensembles in other areas, allowing serial processing, but may also be locally interconnected with neurons that analyze other image parameters (Rockland, 1985). In addition, there is a complex pattern of "down-stream" projections exemplified by the widespread prestriate projections to V1. These feedback projections do not necessarily respect boundaries between functionally different modules (Zeki and Shipp, 1988). Therefore, a multi-stage cross-correlation process may occur among different parallel chains of processing. By means of these cross-correlations, a percept may have as neural substrate the simultaneous activity of several chains of processing belonging to different streams.

A given attribute such as shape can be inferred from information present in one or more subsets of the processing stream, integrated within a common retinotopic locus. For example, the sil-

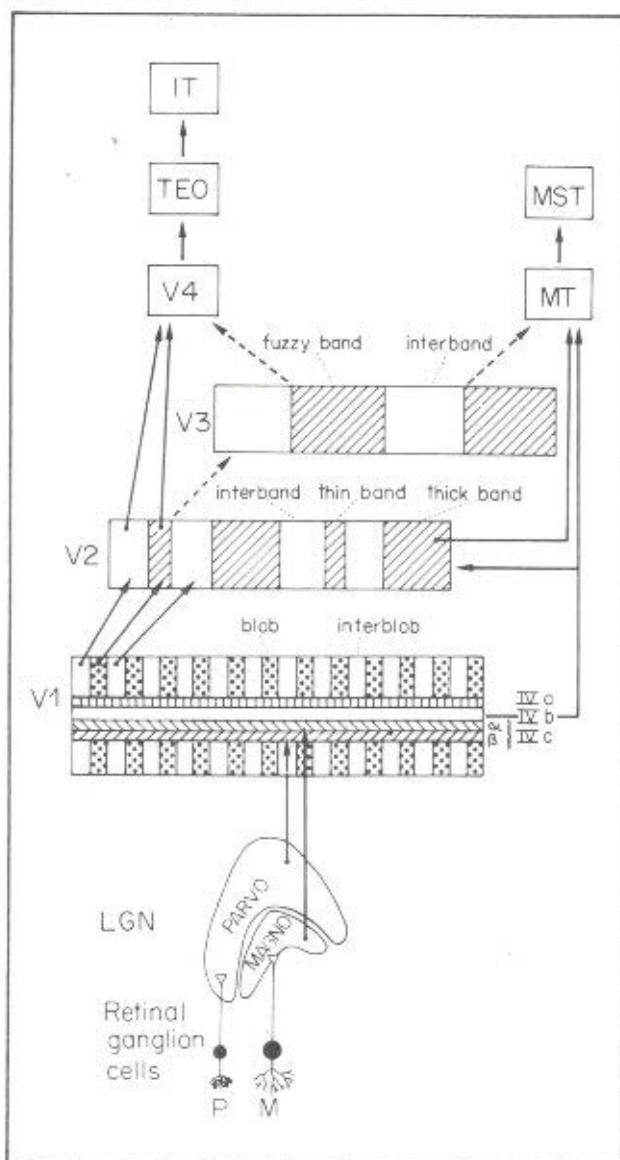


Figure 7 - Parallel pathways which begin within the retina with different classes of ganglion cells (P and M). These cells project to different subdivisions (magnocellular and parvocellular) of the lateral geniculate nucleus, which, in turn, project to different regions of layer IVc (α , β) in V1. Cells from these layers project to different cytochrome oxidase regions in V1, which, in turn, project to different CO-rich or CO-poor regions in V2 or to MT. The different CO bands in V2 possibly project (dashed arrows) to different regions in V3 and V4, and to MT.

houette of a female dancer (shape) can be inferred during a performance by information present in the form, color or movement processing stream. The system could work, for example, with a first-come prompting cue pointing to a given inferred attribute (female silhouette inferred from motion) which is accepted as a percept (3D form of a young woman) if cues concurrently decoded in other modules, at the same retinotopic locus, substantiate that attribute (silhouette inferred from contrast or contour).

Thus, one may conclude that the cortical pathways involved in visual processing may be described as a distributed, highly complex, multilayered network (Figures 6 and 7). Although the processing streams depicted in the model of Ungerleider and Mishkin (1982) truly reflect anatomical specializations present in the cortex, the evidence for interactions between adjacent, functionally distinct modules (Rockland, 1985) and between areas belonging to different streams (Morel and Bullier, 1987) cannot be overlooked. A distributed network, comparing the patterns of activity at corresponding retinotopic loci at each level of the different chains of processing might provide the hardware necessary for a systematic search of "suspicious coincidences" (Barlow, 1986) in the visual image.

Acknowledgments

We thank Drs. C.E. Rocha-Miranda and A. Cowey for helpful comments about the manuscript, Edil S. da Silva Filho for technical assistance, Virginia P.G.P. Rosa for the illustrations, and Juliana G.M. Soares for helping with data analysis. We also thank Edna M. A. da Silva and Maria Tereza Monteiro for typing the manuscript. Our thanks are also due to the Fundação Parque Zoológico de São Paulo for providing the animals used in these studies.

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Received November 21, 1989

Accepted April 4, 1990