

Research Note

Complete pattern of ocular dominance stripes in V1 of a New World monkey, *Cebus apella*

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**Summary.** The presence of ocular dominance (OD) stripes in layer IVc of striate cortex (V1) is characteristic of all Old World simians so far studied. In contrast, some species of New World monkeys do not have ocular dominance stripes, and in those that do, the pattern of stripes may be different from that shown in Old World monkeys. This difference has led to the suggestion that OD stripes evolved independently in both groups. We have mapped the entire system of OD stripes in the New World monkey *Cebus*, by means of cytochrome oxidase histochemistry after monocular enucleation. A striking similarity was found between the patterns in *Cebus* and *Macaca*, which is suggestive of common ancestry, rather than parallel evolution.

**Key words:** Striate cortex – Ocular dominance – Cytochrome oxidase – Evolution – Platyrrhini

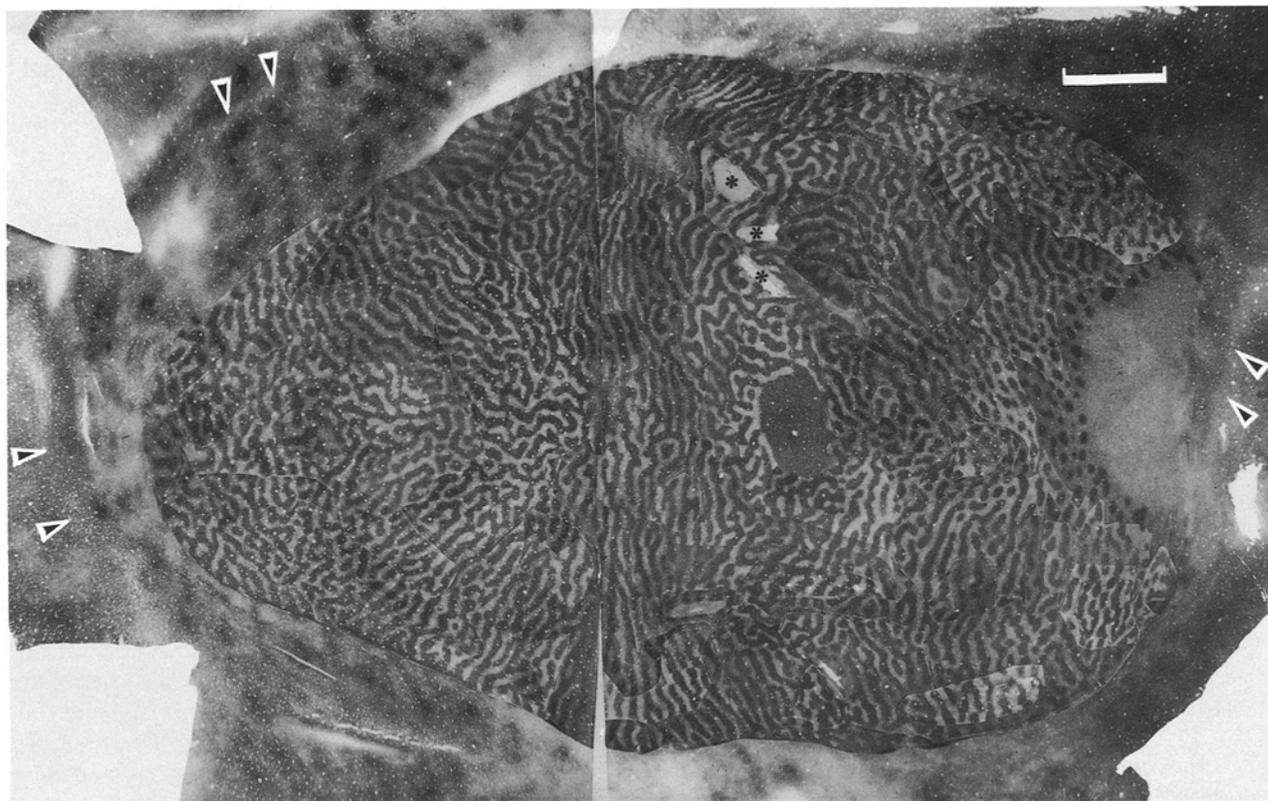
Introduction

In layer IV of primary visual cortex (V1) of Old World simians, axons carrying information from each eye terminate in alternating stripes (Le Vay et al. 1975; Le Vay et al. 1985). In contrast, while some genera of New World monkeys present OD stripes in V1 (Florence et al. 1986; Hess and Edwards 1987), several have either weak OD stripes or no ocular segregation (Hendrickson et al. 1978; Rowe et al. 1978; Spatz 1979). These results were interpreted as suggesting that the cortical circuitry of V1 was not fully differentiated in ancestral Simiiforms and that OD stripes evolved independently in several primate lines (Spatz 1979).

Bi-dimensional reconstructions of “unfolded” layer IV have been used to describe, in the macaque, the complete pattern of OD stripes in V1 (Le Vay et al. 1975, 1985). Although the fine details of the pattern are variable among individuals, there are features which are constant among animals, and thus seem to be characteristic of the genus. For example, stripes tend to run in similar orientations and have similar widths at corresponding parts of the visual field representation in different monkeys (Le Vay et al. 1975, 1985). In this paper, we have shown that the tangential distribution of OD stripes in the New World genus *Cebus* is remarkably similar to that of similar-sized Old World monkeys.

Material and methods

Territories of innervation of each eye were delimited by long-term metabolic mapping with cytochrome oxidase histochemistry (Horton 1984). An adult *Cebus apella* monkey was anaesthetised with ketamine hydrochloride (50 mg/kg im) and pentobarbitone sodium (10 mg/kg iv), and monocularly enucleated under aseptic conditions. After 7 months of survival, it was intracardially perfused with 0.1 M phosphate buffer, pH 7.4. In order to minimize the ambiguities in the process of reconstructing the stripes pattern, we took advantage of a recently described method for flat-mounting large portions of convoluted cortex (Tootell et al. 1985). Sections cut parallel to the pial surface were processed for cytochrome oxidase as described by Tootell et al. (1985). Sections from a second, non-enucleated monkey were processed following the same protocol and used as control. Reconstruction of the stripes pattern was accomplished by aligning corresponding blood vessels in adjacent sections. Inasmuch as in this protocol the tissue is flattened in a relatively unfixed state, we inserted pairs of marking pins prior to the flattening, in order to evaluate distortions, which were found to occur only in regions of high curvature, such as the stem of the calcarine sulcus and the medial surface. Although these regions are reconstructed in Fig. 1, they were not used for quantitative analysis. Measurements were made onto enlarged (20×) high-contrast negative and positive prints with the aid of a digitizer and a microcomputer.



**Fig. 1.** Photographic montage showing the pattern of ocular dominance stripes in the lower half of layer IVc of V1 of a *Cebus* monkey. Lower visual field is represented in the upper portion, and upper visual field in the lower portion of the figure. Asterisks show lesions in the cortical tissue, due to damage during the flattening procedure. Arrows point to cytochrome oxidase stripes in V2, which can be seen from central (left) to monocular peripheral representation (right). Note that V1 was divided in two blocks of tissue, in order to accommodate the sections in the slides. Scale bar = 5 mm

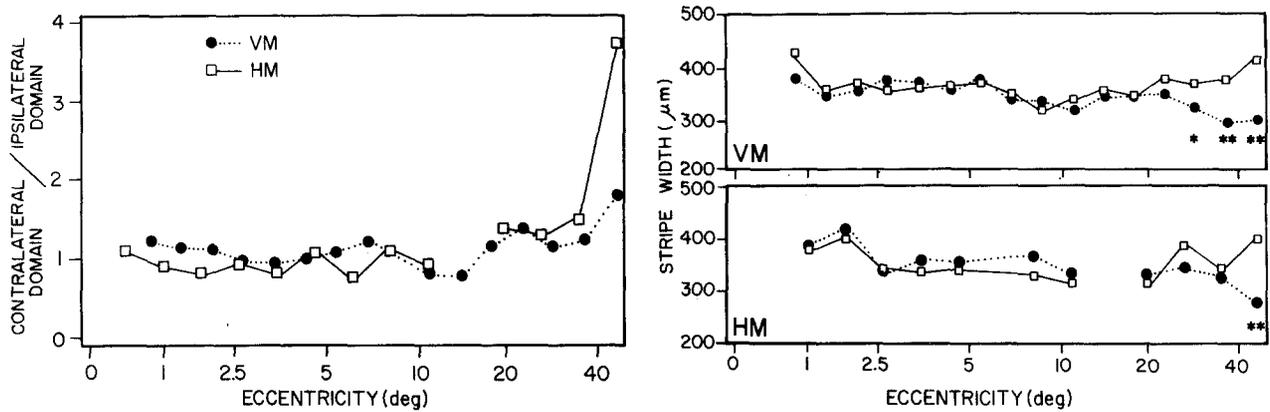
## Results

In the normal *Cebus* monkey, the laminar and tangential distribution of cytochrome oxidase activity in V1 confirmed the results of a previous report (Hess and Edwards 1987). In the enucleated monkey layer IVc presented clear ocular dominance stripes, and the cytochrome oxidase "blobs" tended to be more strongly labelled in the regions overlying the intact-eye stripes than those overlying the deprived stripes (Hess and Edwards 1987). Figure 1 illustrates a complete reconstruction of cortical layer IVc from the left striate cortex and surrounding areas of a monkey that underwent right eye enucleation. Several important features of the ocular dominance map can be readily observed:

a) The borders of striate cortex in layer IVc are sharply defined. A pattern of cytochrome oxidase stripes, characteristic of V2 (Tootell et al. 1983), can be observed bordering most of V1.

b) As in the Old World monkeys (Le Vay et al. 1985), the distribution of stripes follows a complex

pattern throughout most of V1. Locally, stripes dominated by each eye tend to run parallel to each other. Branches and varicosities are observed in an apparently random fashion. The relationship of the stripe pattern to the representation of meridians and isoeccentricity lines in V1 is complex, as judged by comparing the OD pattern with the visuotopic map described by Gattass et al. (1987). Throughout the representation of the binocular field OD stripes tend to reach the V1/V2 border nearly orthogonally, and they seldom run parallel to isopolar lines. In the occipital operculum, except at the foveal representation (where no consistent tendency can be observed), stripes leaving the V1/V2 border converge and stream medially. In comparison, for most of the cortex buried in calcarine sulcus the stripes run almost parallel to isoeccentricity lines. In the peripheral representation, and specially near the representation of the horizontal meridian, the territories innervated by ipsilateral eye tend to decrease relative to those of the contralateral eye (Fig. 2-left), and to lose the stripe-like appearance. Instead, they form strings of



**Fig. 2.** Left: Ratio of the surface areas dominated by contralateral and ipsilateral eye as a function of eccentricity. Different symbols correspond to measurements along vertical (dots) and horizontal (squares) meridians. Right: Width of OD stripes as a function of eccentricity along the vertical (upper) and horizontal (lower) meridians. Each data point corresponds to the mean of 15 measurements of stripe width (contra = squares; ipsi = dots), made in 10 mm<sup>2</sup> sectors centered along the meridians. Asterisks indicate statistical difference (t-test: \*\* =  $p < 0.01$ ; \* =  $p < 0.05$ )

elongated patches, which still seem to run along lines of isoeccentricity. Ipsi- and contralaterally dominated stripes have similar widths (about 350  $\mu\text{m}$ ) for most of V1. At far peripheral representation, ipsilateral stripes tend to narrow relative to contralateral stripes (Fig. 2-right).

c) Two large regions of homogeneous CO distribution are observed. One is a dark oval, about  $4.9 \times 3.1$  mm, lying on the roof of the calcarine sulcus. This region is entirely dominated by the intact (ipsilateral) eye, and corresponds retinotopically to the location of the blind spot of the enucleated eye. A second region, with low and homogeneous CO activity, is observed at the anteriormost portion of the calcarine sulcus. This region corresponds to the representation of the contralateral monocular crescent, a domain of the contralateral eye (enucleated).

## Discussion

The studies so far published on the tangential distribution of OD stripes in macaques have faced difficulties with the two-dimensional reconstruction of the pattern of stripes. These problems are related either to ambiguities in "filling up" the gaps between stripes in adjacent sections (Le Vay et al. 1985) or to difficulties in reconstructing the pattern in regions with high curvature (Le Vay et al. 1975). The present method obviates these problems.

It has been suggested that anisotropies in the visuotopic map may arise from different angles of intersection of visual field lines with ocular dominance stripes (Sakitt 1982; Tootell et al. 1982). The isoeccentric orientation of the stripes for most of V1

and the global anisotropy observed in V1 of the *Cebus* by Gattass et al. (1987), with greater magnification along the isopolar dimension, support this hypothesis. However, based on this hypothesis alone, one would expect an isotropic projection of the blind spot onto V1, since only one eye is represented in this region. In fact, the blind spot sector is slightly elongated in the isoeccentric dimension, as compared with a mean blind spot of *Cebus* ( $6.0^\circ \times 4.5^\circ$ , Silveira LCL, Picanço-Diniz CW, Oswaldo-Cruz E, personal communication). The observation of an anisotropy which is inverse to that observed throughout V1 (Gattass et al. 1987) suggests that factors other than the need of representing twice the same portion of the visual field may contribute to generate distortions of the visuotopic map. As suggested by Horton (1984), a local anisotropy in the blind spot sector may arise to avoid discontinuities in the map of neighboring portions of the visual field.

The simian lineages ancestral to present-day New and Old World monkeys have been separated from each other for at least 30 million years (Fleagle et al. 1986). Even so, the map of OD stripes in V1 of New and Old World monkeys with equivalent sizes is very similar. This result contradicts a recent report by Hess and Edwards (1987), which emphasizes the lack of global order in the OD stripe pattern in *Cebus*. However, these authors reconstructed only a portion of the foveal representation, which lacks an obvious relationship between stripes and visual topography both in *Cebus* and *Macaca* (Le Vay et al. 1985). Likewise, the difference in the width of labeled and unlabeled stripes reported by these authors can be observed in some restricted portions of V1 (Fig. 2-

right), but is not statistically significant when most of the binocular field is sampled.

The remarkable similarity between Platyrrhini and Catarrhini, both relative to the stripe dimensions and to their preferred orientation at corresponding portions of V1, is unlikely to have arisen from independent mutational events. Thus, the existence in the common ancestry of all simians of a genetic machinery coding stripe formation would be the most parsimonious explanation. How would, then, the different degrees of ocular segregation observed in living monkeys arise? It is possible that some of the previous reports on absence of OD stripes in New World genera may be result of limitations inherent to the anatomical methods. For example, Hubel and Wiesel (1978) demonstrated by physiological methods the presence of eye dominance clusters in the squirrel monkey, a genus which lack anatomically-discernible OD columns. Moreover, we suggest that, among simians, there is a minimum size of V1 in which clear segregation of OD stripes will develop during ontogenesis. In small New World monkeys like the marmoset, the owl monkey and the squirrel monkey no anatomically-discernible OD columns were observed, even using methods similar to the ones we used (Hendrickson and Tigges 1985). In contrast, in the larger *Cebus* and *Ateles* and in the Old World monkeys these stripes were fully developed. In small monkey species, cortical volume may turn out to be a limiting factor, and competitive interactions such as those responsible for the formation of OD stripes in the macaque (Hubel et al. 1977) may not be strong enough to produce complete segregation. Relevant to this hypothesis are the experiments of De Bruyn and Casagrande (1981), which have shown that under abnormal conditions (early monocular deprivation) OD stripes may be demonstrated in the marmoset. The mechanisms proposed by these authors, i.e., a partial overlap, may represent a compromise between segregation imposed by competitive interactions and volume constraints. Thus, monkeys may vary on phenotypical grounds (the degree of ocular segregation), but share a basic genotype coding stripe formation.

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