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Laminar, columnar and topographic aspects of ocular dominance in the primary visual cortex of *Cebus* monkeys

M.G.P. Rosa*, R. Gattass, M. Fiorani Jr., and J.G.M. Soares

Departamento de Neurobiologia, Instituto de Biofísica Carlos Chagas Filho, Universidade Federal do Rio de Janeiro, Cidade Universitária- CCS- Bloco G- Ilha do Fundão, Rio de Janeiro RJ 21941, Brazil

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Summary. The representation of the two eyes in striate cortex (V1) of *Cebus* monkeys was studied by electrophysiological single-unit recordings in normal animals and by morphometric analysis of the pattern of ocular dominance (OD) stripes, as revealed by cytochrome oxidase histochemistry in V1 flat-mounts of enucleated animals. Single-unit recordings revealed that the large majority of V1 neurons respond to the stimulation of either eye but are more strongly activated by one of them. As in other species of monkey, neurons with preference for the stimulation of the same eye are grouped in columns 300–400 μm wide, spanning all cortical layers. Monocular neurons are clustered in layer IVc, specially in its deeper half (IVc-beta), and constitute less than 10% of the population of other layers. Neurons with equal responses to each eye are more commonly found in layer V than elsewhere in V1. In the supragranular layers and in granular layer IVc-alpha neurons strongly dominated by one of the eyes tend to be broadly tuned for orientation, while binocularly balanced neurons tend to be sharply tuned for this parameter. No such correlation was detected in the infragranular layers, and most neurons in layer IVc-beta responded regardless of stimulus orientation. Ocular dominance stripes are present throughout most of V1 as long, parallel or bifurcating bands alternately dominated by the ipsi- or the contralateral eye. They are absent from the cortical representations of the blind spot and the monocular crescent. The domains of each eye occupy nearly equal portions of the surface of binocular V1, except for the representation of the periphery, where the contralateral eye has a larger domain, and a narrow strip along the border of V1 with V2, where either eye may predominate. The orderliness of the pattern of stripes and the relationship between stripe arrangement and the representation of the visual meridians vary with eccentricity and polar angle but follow the same rules in different animals. These results demonstrate that the laminar, columnar and topographic distribution of neurons with different degrees of OD in V1 is qualitatively similar in New- and Old World monkeys of similar sizes and suggest that common ancestry, rather than parallel evolution, may account for the OD phenotypes of contemporaneous simians.

Key words: Striate cortex – Modular organization – Orientation selectivity – Primates – Platyrrhini – Evolution

Introduction

Simiiform primates have a high degree of binocular overlap. Among Catarrhines (Old World simians), visual information gathered by each retina is conveyed to separate layers of the dorsal lateral geniculate nucleus (GLd) and from there to tangentially segregated, 300–600 μm wide, patches in layer IVc in striate cortex (V1) (Hubel and Wiesel 1972; Hendrickson et al. 1978). This tangential segregation, together with the vertical, translaminar cortical intrinsic connections (Blasdel et al. 1985; Fitzpatrick et al. 1985) form the anatomical substrate of the physiologically identified ocular dominance (OD) columns (Hubel and Wiesel 1968). Patches of layer IVc innervated by afferents from a given eye are so aligned as to form long OD stripes, which run uninterruptedly for several millimeters. Therefore, OD columns have in fact the form of slabs, and slabs dominated by either eye are intrincately interlaced.

Among Platyrrhines (New World monkeys), some species seem to show only a modest degree of segregation of ocular inputs into layer IVc of V1, variable even among individuals (Kaas et al. 1976; Hendrickson et al. 1978; Rowe et al. 1978; Diamond et al. 1985). Correspondingly, in these species physiological OD columns are less obvious (Hubel and Wiesel 1978). In *Callithrix*, OD stripes are demonstrable in the first months of postnatal life but disappear upon maturity (Spatz 1979, 1989). It is presently unknown whether this regression of the stripe pattern also occurs in other genera which lack

* *Present address:* Vision, Touch and Hearing Research Centre, University of Queensland, St. Lucia, 4072, Australia

Offprint requests to: M.G.P. Rosa

OD stripes as adults. Finally, in the spider monkey *(Ateles ater)* and in the tufted capuchin monkey *(Cebus apella)* OD stripes stand out clearly in the adult (Hubel and Wiesel 1968; Florence et al. 1986; Hess and Edwards 1987; Rosa et al. 1988b, 1991). The phenotypical variability with regards to OD columns among Platyrrini contrasts with the relative structural constancy of V1 observed among Catarrhini, therefore raising a question: Among those New World monkeys that have OD columns, are these columns homologous to those of Old World monkeys? Or do they represent a case of parallel evolution? An answer to this question is rendered difficult by the paucity of systematic studies of OD among Platyrrhines, and by the diversity of these monkeys with regards to size and visual habits. A systematic description of the pattern of OD stripes in a New World monkey seemed desirable to provide a basis for comparisons with Catarrhine monkeys. The *Cebus* is well suited for such a comparison, since it is similar to the extensively studied Old World *Macaca fascicularis* in size, brain sulcal pattern and some aspects of visual cortical organization and visual behavior (Fleagle 1988; Rosa et al. 1988c; Fiorani Jr. et al. 1989; Gattass et al. 1990; Sousa et al. 1991). The aim of this study is twofold. Firstly, to explore in the *Cebus* monkey the columnar and laminar distribution of OD within V1, as determined by single-unit recordings. We will show that in the *Cebus* responses are well graded in OD terms in layers outside IVc and that OD columns span all cortical layers. In addition, the distribution of orientation-selective neurons and its relationship with the degree of OD will be presented. Secondly, experiments involving anatomical techniques and morphometric analyses of the pattern of OD stripes will be described, to give an account of the orderliness of the pattern of stripes and to show the relationship of these stripes with visual topography. Preliminary accounts of these data were published elsewhere (Rosa et al. 1988a, b).

Material and methods

Electrophysiological studies

Animal care and preparation. Four adult male *Cebus apella* monkeys were used for the electrophysiological experiments. The animals were prepared for chronic recordings by implanting a stainless steel recording chamber and a bolt for holding the head in the stereotaxic apparatus, under general anesthesia (Ketamine hydrochloride 30 mg/kg, Alphaxalone 10 mg/kg, Alphadolone 3 mg/kg and benzodiazepine 2 mg/kg) and aseptic conditions.

Each monkey underwent two recording sessions a week during a one- to four-week period. Initially, the animal was anesthetized with Halothane (2.5%) in a 7:3 N_2O/O_2 mixture, intubated, placed on a soft cushion and covered by a thermostatically controlled heating blanket. After interruption of Halothane anesthesia, no potentially painful procedures were conducted. During the recording sessions, neuromuscular paralysis was achieved by a continuous infusion of pancuronium bromide (0.1 mg/kg/hr). The animals were artificially ventilated by means of a respiratory pump with a 7:3 N_2O/O_2 mixture. Electrocardiogram, rectal temperature and the percentage of CO_2 in the expired air were continuously monitored. Mydriasis and cycloplegia were induced by topic application of Atropine (1%) and Phenylephrine (2%). Both eyes were focussed on a tangent screen placed at 115 cm by means of appropriate contact lenses. The positions of the foveae and the limits of the optic discs were projected on the screen by a reversible ophthalmoscope.

At the end of each recording session (which lasted about 12 hr), the animals were allowed to recover spontaneous breathing under anaesthesia and received an injection of antibiotics (Penicillin G-benzathine 250 000 U.I.) before returning to their cages.

Recording procedure. Varnish-coated tungsten electrodes were inserted through the dura mater at variable angles relative to the cortical surface. Electrode impedances were between 1 and 2 MΩ at 1 kHz. The recorded activity was amplified and monitored both on an oscilloscope and through an audio system. In one animal, a double-barrel guide tube was used to allow the simultaneous penetration of two electrodes (e.g. Fig. 3). Typically, at each recording site, white and colored bars and spots were moved and flashed on the tangent screen to determine the location of the multiunit receptive field for each eye separately. The most prominent unit was then isolated by means of an amplitude discriminator, and eye dominance was assessed using the neuron's preferred orientation and direction of movement. In order to normalize presentation during the qualitative analysis, the length of the oriented stimuli was kept equal to that of the multiunit receptive field, unless a clear preference for small spots was observed. Owing to the electrode characteristics, in about 10% of the recording sites we were unable to resolve the activity of a single neuron, and therefore studied the combined responses of pairs and occasional triplets of neurons. Some aspects of the OD organization, as the continuity of columns across cortical layers, were the object of specific experiments in which only the multiunit activity was systematically analysed (e.g. Fig. 4). At a background of 9 cd/m² for the tangent screen, stimulus luminance varied from 15 to 40 cd/m² depending on the neuronal response.

The response to stimulation of each eye was subjectively classified following Hubel and Wiesel's (1968) 7-point scale, the grades of "1" or "7" being attributed when the cell responded exclusively to the contra- or the ipsilateral eye, respectively; group "4" includes cells with equal responses to either eye, and groups "2", "3", "5" and "6" represent intermediate categories. Orientation selectivity was examined and classified as weak (for cells with good responses to all orientations, even if there was some bias towards some orientations) or strong (cells which had a clear preference for a restricted range of orientations and inconsistent or no responses in the "null" orientation). As explained in *Results,* cells with no trace of orientation selectivity were seldom observed outside layer IVc; when present, they were included in the former group. A sample of well-isolated units was also studied objectively, by means of stimulus presentation/data acquisition software custom-developed for the IBM-AT. The results of this analysis will be presented in full in a separate report (Fiorani Jr. et al., in prep.), and will be mentioned here only as far as they concern ocular dominance. Several electrolytic lesions (4 μA, 5–10 s) were placed along each penetration, to aid in post-mortem track reconstruction and identification of the recording sites.

Histology. After the last recording session, the monkeys were deeply anesthetized with sodium pentobarbital (50 mg/kg, I.V.) and intracardially perfused with saline followed by 4% formaldehyde in saline. The brains were then removed from the skull and allowed to sink in fixative solutions with increasing concentrations of sucrose (up to 30%), quickly frozen with dried ice and sectioned at 40 μm. Every section was saved and consecutive sections were reacted for cytochrome oxidase (cytox; Wong-Riley 1979, as modified by Silverman and Tootell 1987), stained for myelin, with the Heidenhain-Woelcke stain (as modified by Gattass and Gross 1981) or stained for cell bodies with cresyl violet. Assignement of cortical layers to recording sites was based on Blasdel and Fitzpatrick (1984) and Hess and Edwards (1987). The laminar reconstruction of the position of the recording sites was based on the localization of the electrolytic lesions and transitions between the cortex and the white matter.

Metabolic mapping

Surgery and histological preparation. In two other monkeys, long-term metabolic mapping was performed by means of cytox histochemistry after monocular enucleation (Wong-Riley 1979). The enucleation surgery was performed under general anaesthesia (the same as in the prothesis implantation described above) and aseptic conditions (For details, see Rosa et al. 1991). Four (CO6) or seven (CO5) months later, the monkey was deeply anesthetized with an IV injection of sodium pentobarbital (50 mg/kg) and intracardially perfused with a 10% sucrose in phosphate butter 0.1 M, pH 7.4 solution. The brain was removed from the skull, and the cortex posterior to the splenium of the corpus callosum was flat-mounted following the guidelines described by Olavarria and Van Sluyters (1985) and by Tootell and Silverman (1985). Briefly, after removing the pia-mater overlying the sulci, cotton swabs were used to dissect most of the white matter until all gyral and sulcal cortex were laid flat on a glass plate. Fixation was attained by storing the flattened block between two parafilm-covered glass slides in a 2.5% glutaraldehyde/10% sucrose in phosphate buffer solution. Two days later, the cortex in and around V1 was quickly frozen and sectioned parallel to the cortical surface at 40 µm. The sections were immediately mounted in gelatinized slides, dried on a hot plate and, in the following day, reacted for cytox as described by Silverman and Tootell (1987).

Quantitative analysis and assignment of retinotopic coordinates. Distortions resulting from the histological methods were evaluated by inserting, prior to the flattening procedure, triplets of marking pins perpendicular to the surface of the brain with the sulci gently opened, and comparing the original distances with those measured in the flat-mount. For most of V1, linear distortion was found to be below 5% (see Rosa et al. 1991 for details).

Prints of each section crossing layer IVc, enlarged 21 times, were combined to obtain full reconstructions of the pattern of OD stripes. Measurements were performed in negative and positive prints of the montages, with the aid of a graphic tablet linked to an Apple II microcomputer.

The eccentricity and polar angle of the sectors of V1 were estimated based on methods previously described (Rosa et al. 1991). Polar angles were attributed by considering the distance from the point under study to the border of V1, as measured in the flat-

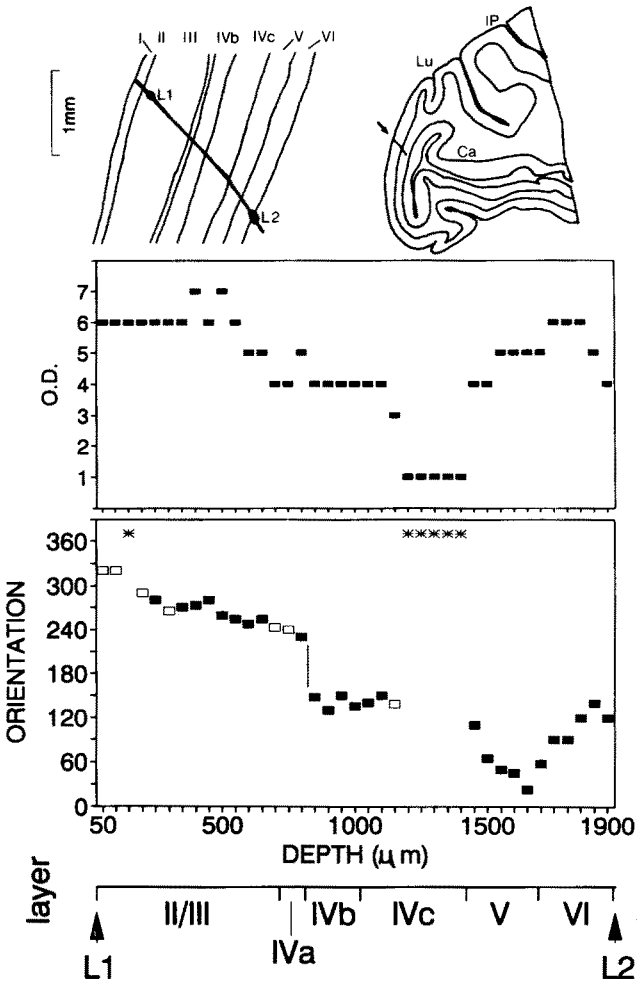

Fig. 1. Ocular dominance and orientation selectivity in a penetration through central V1. The penetration site is shown by the small arrow in the section (insert). *Upper left:* histological reconstruction of the penetration track, showing the laminar boundaries and the location of 2 lesions (L1 and L2). The *upper box* shows the OD selectivity of sites 50 µm apart. The *lower box* shows the cells' preferred orientation at these sites following the trigonometric convention as viewed by the animal (e.g., 0°, 180° and 360° correspond to horizontal bars, 90° and 270° to vertical bars). In this and in figures 2–3 the filled markers indicate strongly orientational responses, open markers indicate weakly orientational responses and asterisks indicate cells without apparent orientation bias. The vertical dashed lines indicate sites where a discontinuity in the sequence of orientations (greater than 40°/50 µm) occured. The *lower scale* is a summary of the histology, indicating laminar boundaries and the position of marking lesions. Abbreviations: calcarine sulcus; IP-intraparietal sulcus; Lu- lunate sulcus

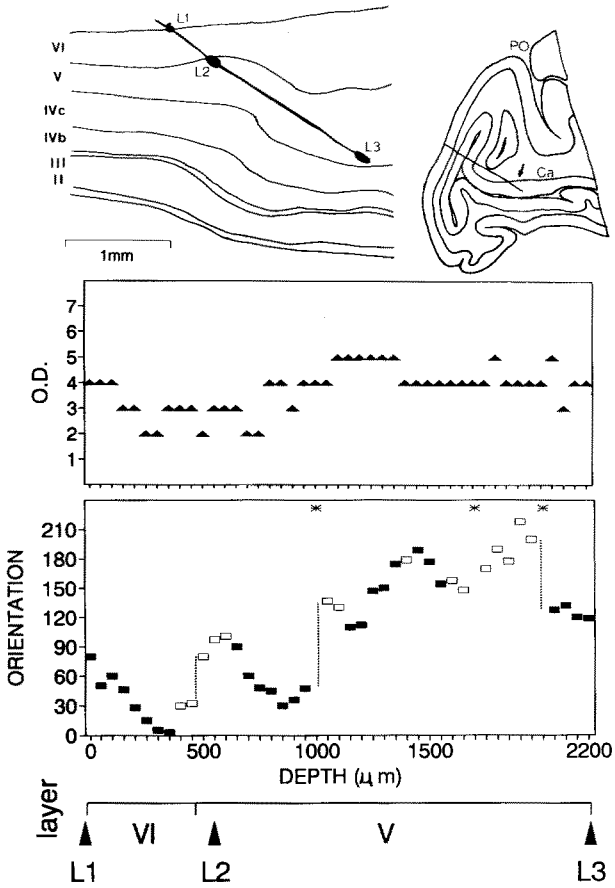

Fig. 2. OD and orientation selectivity in a penetration through the infragranular layers in peripheral V1. Lesion 2 was made 50 µm after a sequence of 6 direction-selective neurons. See also legend to Fig. 1. PO-parietooccipital sulcus

mounted slides, and referring to the visuotopic map of V1 in the *Cebus* described by Gattass et al. (1987). Isoeccentricity lines were drawn by integrating the function of isopolar cortical magnification factor vs. eccentricity of V1.

Results

Part I. Electrophysiological analysis of OD columns

Overall organization

Seven hundred and one units were examined for a qualitative appraisal of OD in V1, at eccentricities ranging from 3 to 50 degrees; of these, 58 were further studied quantitatively. Figures 1–3 show the results of penetrations through the occipital operculum and the calcarine cortex. The main results concerning the distribution of OD in V1 can be described as follows:

– Tangent or oblique penetrations through layers II, III and IVb showed a marked alternance between binocular balanced regions and regions dominated by one eye. Only a few monocular neurons were observed in these layers (Figs. 1 and 3).

– Layer IVa, characterized by an enhancement of background activity, yielded only a few recorded neurons. In most cases, multiunit activity was elicited by stimulation of either eye. Two out of 7 well-isolated units, however, were monocular (e.g., in Fig. 3).

– Layer IVc, as a whole, was also characterized by a rich spontaneous activity. In accordance with the fact that this is the main GLd-recipient layer, IVc showed the largest incidence of strictly monocular and/or strongly OD-biased responses. Recordings revealed a difference as regards the distribution of OD in the upper (IVc-alpha) and the lower (IVc-beta) tiers of this layer. While in IVc-alpha monocular neurons were a minority, in IVc-beta they predominated (e.g., Fig. 1).

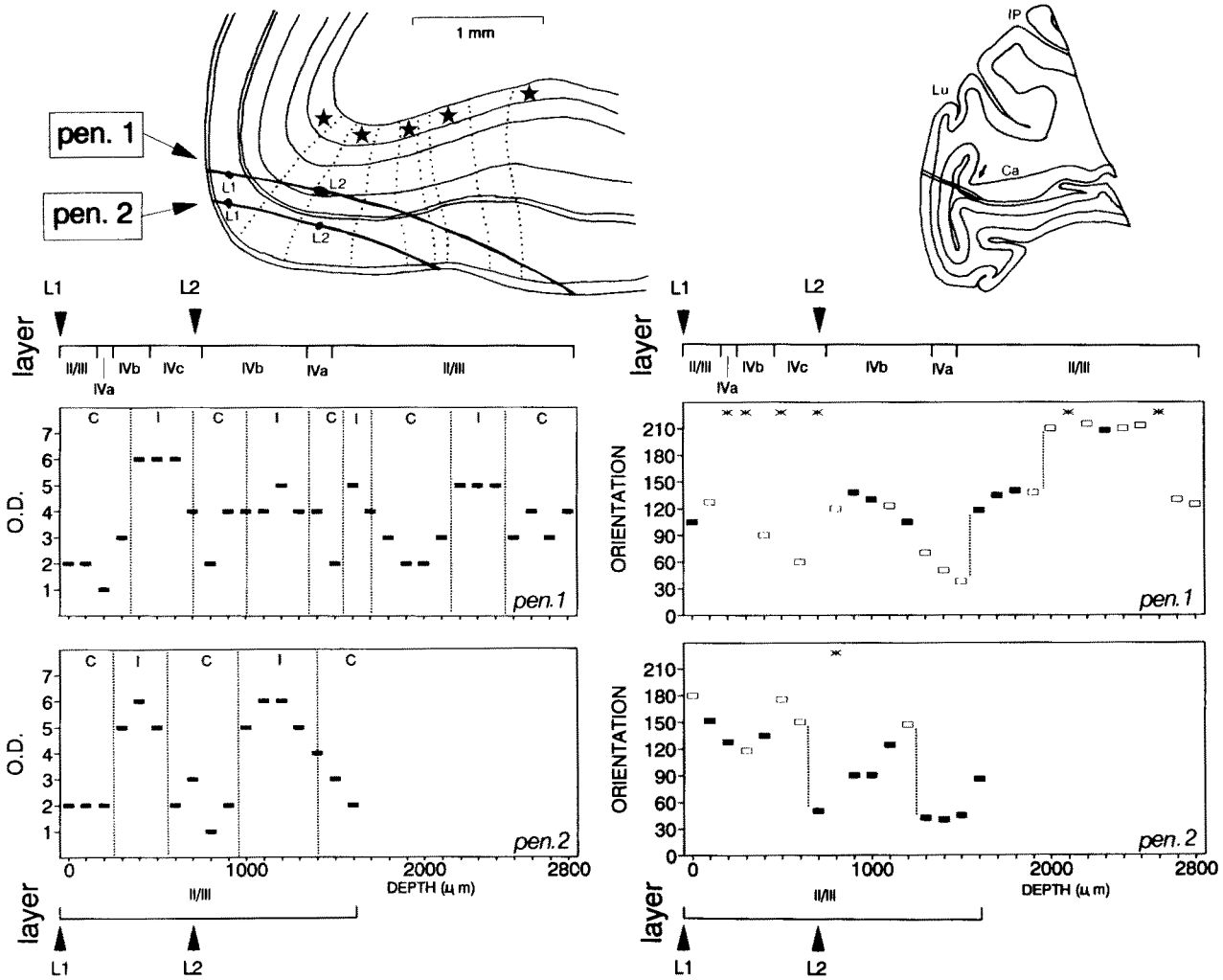

Fig. 3. Ocular dominance and orientation selectivity in a pair of parallel penetrations through the calcarine sulcus. Receptive fields were 20° eccentric in the lower visual field. In the histological reconstruction shown in the *upper left*, the layout of OD columns is drawn based on the depth where reversals in eye preference occured and in the shape of cell fascicles revealed by Nissl staining (dotted lines). Columns dominated by the contralateral eye are labeled by stars. The *left boxes* show OD selectivity in these tracks, with the proposed columnar boundaries indicated by dotted lines ("C" showing contralateral eye preference, "I" showing ipsilateral eye preference). The right boxes show orientation selectivity. The *upper boxes and laminar scales* refer to penetration 1 (pen. 1), and the *lower boxes and scales* to pen. 2. See legend to Fig. 1 for details

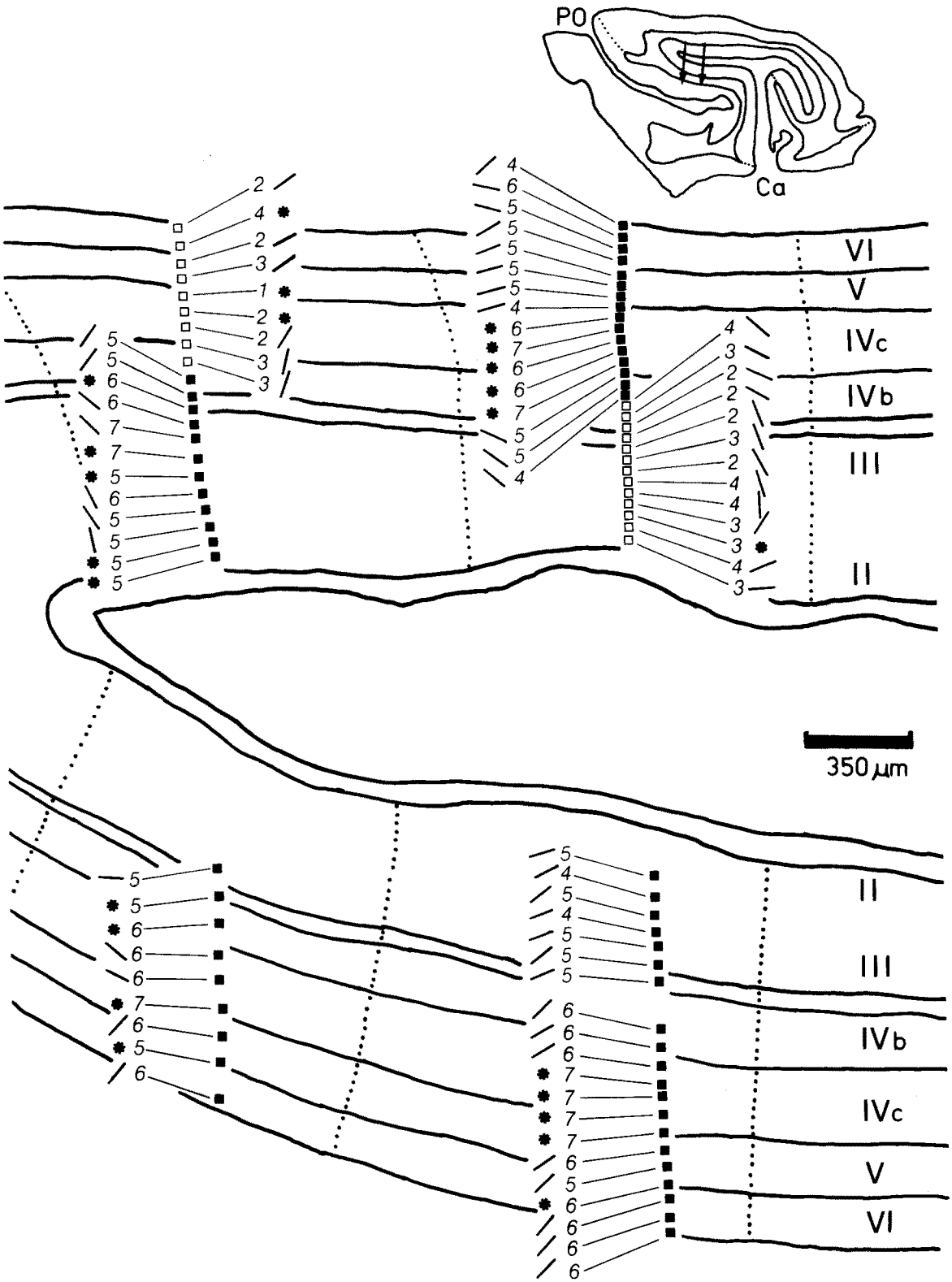

Fig. 4. Penetrations nearly perpendicular to the layers in V1 yield long strings of sites with similar eye preference. Scoring of OD at each site, based on multiunit activity, is shown by the adjacent numbers. From top to bottom, the penetration crossed the roof and the upper bank of the calcarine sulcus (see arrows in the insert). Orientation selectivity of cell clusters is shown by line segments, and asterisks indicate sites without apparent orientation bias. Open squares show sites in columns dominated by the contralateral eye, and filled squares by the ipsilateral eye. The dotted lines show the approximate orientation of the radial cell fascicles and blood vessels. Scale bar shows the typical width of OD stripes

– In both layers V and VI, alternation of the OD with the progression of the electrode was also observed. However, specially in layer V, the OD fluctuations about group 4 were of a relatively small amplitude when compared to those at the granular and supragranular layers. The large majority of responses was either weakly biased towards one eye or responded equally to both eyes (Fig. 2).

Although the data summarized above establish the existence of regions dominated by each eye in the supra- and infragranular layers of V1 in *Cebus*, it does not directly address the issue of columnar organization. Figure 3 illustrates the results of a pair of parallel penetrations 250 μm apart through the upper bank of the calcarine sulcus, with the electrode tips in register. As expected in a truly columnar organization, the sequence of ipsi- and contralateral eye-dominated regions is in register for both electrodes, approximately following the radial fascicles of cells revealed by Nissl staining (dotted lines in the section of Fig. 3). While penetrations similar to those shown in Fig. 3 found several reversals in eye preference, running at a shallow angle relative to the cortical layers, more oblique penetrations. (Figs. 1,4) crossed long sequences of cells with the same eye preference and, in some cases, yielded responses with dominance to one of the eyes only (Fig. 4). These results converge to support the existence of OD columns in *Cebus* monkeys. The width of the electrophysiologically-determined columns is, however, variable, since it depends on such factors as the orientation of the penetrations relative to that of OD stripes (see below) and the portion of V1 under study. For example, in Fig. 2 a long sequence of sites yielding binocularly balanced and contralaterally-biased neurons is interrupted by a few short groups of ipsilaterally-biased neurons. This is to be expected by the observation that OD stripes are wider for the contralateral eye in peripheral V1 (see PART II).

Ocular dominance distribution

Table 1 summarizes the incidence of OD groups in different layers of V1. No distribution is shown for layer IVa because of the small sample of single units recorded therein. Briefly, more than 70% of the responses in layers II, III and IVb were dominated by one of the eyes, but only a few were monocular. Layer IVc-alpha showed a predominance of units strongly dominated by one eye (47%), and a high percentage of monocular responses (31%); the same was true for IVc-beta, although monocular units were twice as common as compared with IVc-alpha. Finally, both layers V and VI showed a predominance of units weakly biased towards one eye and binocularly balanced neurons, the latter being more common in layer V than elsewhere. The results obtained with quantitative methods support the differences between the supragranular, granular and infragranular layers, as far as only 1 out of 11 monocular cells was found outside layer IVc. Moreover, 10 out of 16 cells responding equally to both eyes were located in layers V and VI. We would like to point out that none of the units subjectively classified as monocular (1/7) proved to respond significantly ($P<0.05$) to the stimulation of the non-dominant eye when quantitative tests were applied. However, group 4 includes some neurons with a slight bias towards one of the eyes, and therefore the percentage of binocularly balanced neurons shown in Table I and Fig. 5 may be, in fact, an overestimate.

Table 1. Ocular dominance in different layers of V1

LAYER	n[a]	GROUP 1/7[b]	GROUP 2/6[b]	GROUP 3/5[b]	GROUP 4
II/III	316	3.5%	35.8%	38.6%	22.1%
IVb	106	6.6%	32.1%	34.9%	26.4%
IVc alpha	70	31.5%	47.1%	10.0%	11.4%
IVc beta	57	66.7%	19.3%	10.5%	3.5%
V	76	2.6%	15.8%	36.8%	44.8%
VI	69	2.9%	23.2%	39.1%	34.8%

[a] Number of cells recorded in each layer
[b] Cells with a similar degree of ocular bias were grouped together regardless of the dominant eye

No statistically significant difference was seen between the number of cells dominated by the ipsi- or contralateral eyes in the occipital operculum ($n=249$, $\chi^2=1.91$, $0.15<P<0.2$). An overall comparison of the incidence of ipsi- and contralaterally-dominated cells in the calcarine cortex likewise shows no significant difference ($n=452$, $\chi^2=2.47$, $0.1<P<0.15$). This may be, however, misleading since only one penetration recorded from the representation of the far periphery in V1 (Fig. 2).

Orientation selectivity

The percentage of responses classified as "weak" with respect to orientation selectivity was higher in the opercular (50%) than in the calcarine striate cortex (33%). This observation suggests that, as in the macaque (Poggio et al. 1975; Zeki 1983; Livingstone and Hubel 1984), orientation selectivity in V1 of *Cebus* increases with increasing eccentricity.

In spite of the difficulty in separating truly non-selective neurons from those weakly tuned for orientation based on a subjective examination, the data revealed that in the striate cortex of *Cebus* the vast majority of the neurons outside layer IVc showed, in fact, a variable degree of bias towards some orientations. As in Old World monkeys (Livingstone and Hubel 1984), neurons with robust orientation selectivity tended to receive more balanced ocular inputs than neurons with poor orientation selectivity. This fact is illustrated in Fig. 5, which compares OD distribution for the weakly- and strongly orientation selective responses. This relationship holds for layers II/III, IVb and IVc-alpha, although not for the infragranular layers. Only 6 strongly orientation-selective neurons were recorded from layer IVc-beta, out of a total sample of 57. With one exception, they were strongly dominated by one of the eyes (groups 1, 2 and 6).

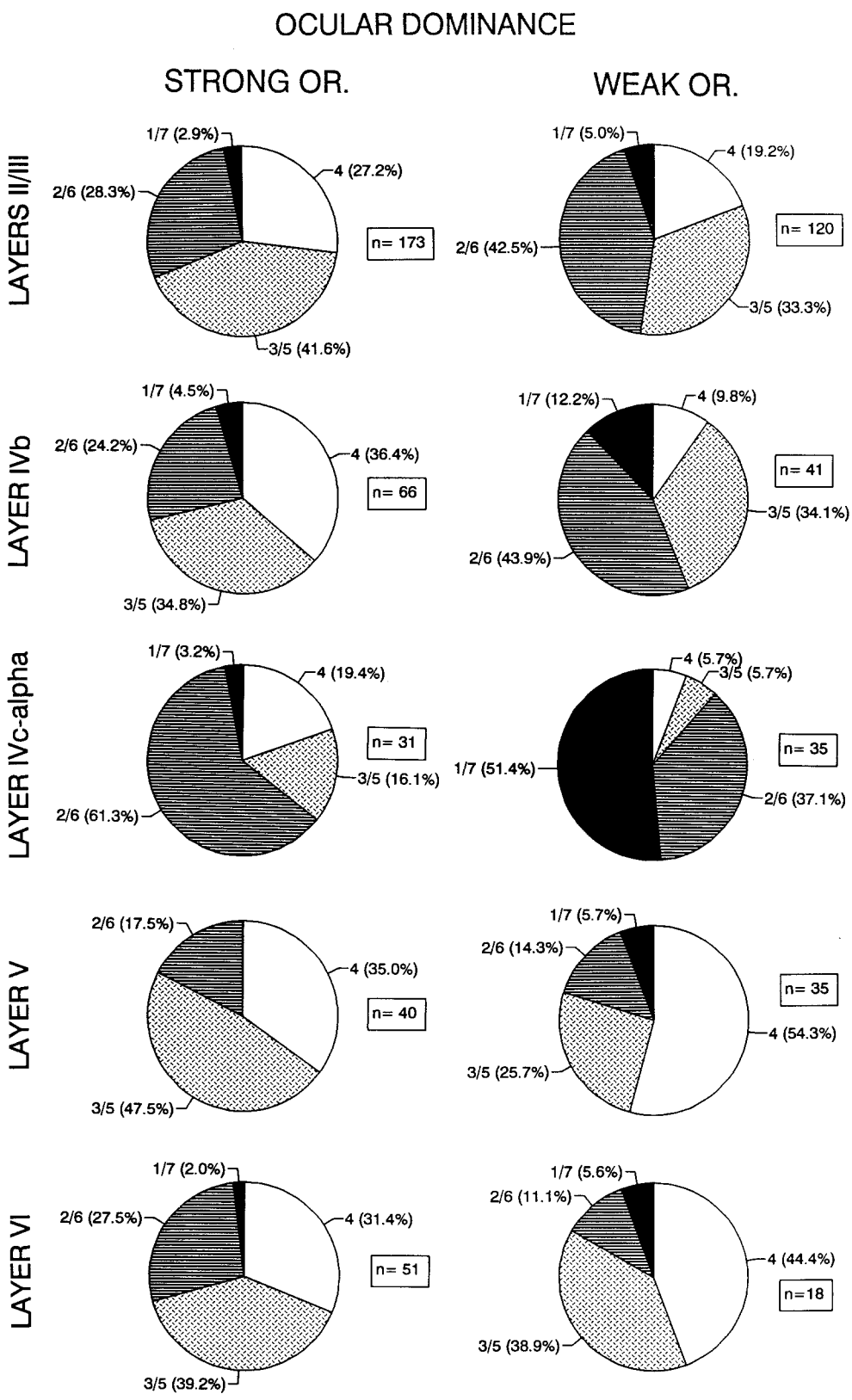

Fig. 5. Comparison of OD properties of strongly orientation selective *(left column)* and weakly orientation selective *(right column)* cells in different cortical layers. The percentage of recordings in each category is shown adjacent to the respective pie segment, and the number of recordings in shown in the box to the right of each pie

Noted here briefly is the incidence of direction-selective neurons in layers IVb and IVc-alpha. In IVb, these neurons correspond to more than half of the sample. This kind of selectivity was also common in layer VI, allowing in many cases the physiological determination of the layer V/VI border (see legend to Fig. 2).

Orientation hypercolumns

As shown in Figs. 1–4, changes of the preferred orientation of neurons recorded along a penetration were gradual. In some penetrations, however, sequences of orientations were interrupted by "fractures" 400–700 μm

apart, where changes of 45–90° were observed between adjacent sites. Taking into consideration the "smooth" segments of each sequence ($n=25$) we obtained a mean estimate of 914 μm (+/− 516 μm) for the tangential dimension of a cycle of orientations encompassing 180°, the orientation hypercolumn.

Part II. Morphological study of OD columns

Laminar organization

In normal *Cebus* monkeys tangential sections of layer IVc reacted for cytox show rich and uniform labeling (Rosa et al. 1991). In contrast, in long-term monocularly enucleated monkeys this layer shows alternating stripes, about 350 μm wide, lightly and heavily stained by the cytox reaction (Fig. 6). As previously established (Horton 1984) the dark bands are dominated by the intact eye, and the light bands by the enucleated eye. Ocular dominance stripes are absent from two regions of V1, corresponding to the representations of the optic disk and of the monocular crescent (Fig. 7). The pattern of alternately light and dark continuous stripes characterizes both tiers of layer IVc, as well as layer IVa, which are the main geniculate-recipient layers in *Cebus* (Hendrickson et al. 1978). In all other layers, the regions dominated by the intact eye have a characteristic "beaded" aspect, due to the patchy cytox architecture (Fig. 6). Although continuous OD stripes are present in layers IVa, IVc alpha and beta, they are not equally well defined. Stripes are clearest in IVc beta and fuzziest in IVa. The difference in the sharpness of stripe boundaries correlates with the frequency of monocular neurons in different layers: the highly monocular layer IVc-beta shows clear limits between the domains of each eye, while IVc-alpha, with a larger number of binocular neurons, shows a less defined pattern. Moreover, in the supragranular layers cytox-rich patches are visible along deprived stripes even after several months of enucleation (Fig. 6A). The existence of monocular units among the few recorded neurons in IVa and the fuzziness of the stripes in this layer suggest a degree of monocularity intermediate between that of IVc-alpha and of the supragranular layers.

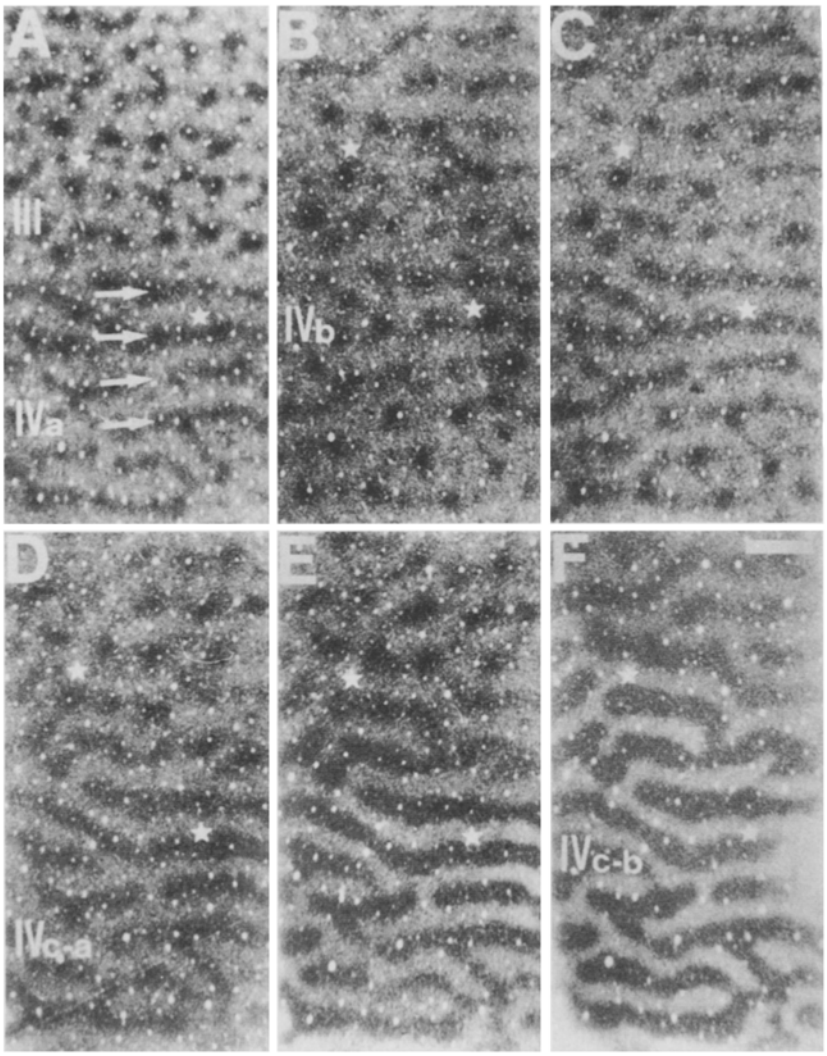

Fig. 6A–F. Series of tangential sections through central lower field V1 showing the variation in the appearance of OD stripes at different laminar depths (case CO5L). A pair of blood vessels is indicated by stars in all sections to aid in localization. **A** This section illustrates the transition from the patchy cytox architecture, in layer III (upper portion) and the pattern of fuzzy OD stripes is layer IVa (lower portion). Four stripes dominated by the spared eye are indicated by arrows. In contrast with layer III, there is little or no labeling along enucleated eye-stripes in layer IVa. **B** At a deeper level, the patchy cytox architecture reappears, in layer IVb. The upper right portion of this panel shows a portion of layer IVa. **C–E** Sections through the interface between layers IVb and IVc-alpha. At the outermost portion of layer IVc-alpha (region around the lower star in **C**) continuous OD stripes reappear fuzzily, but they become sharper at deeper levels of this layer (lower portion of **D** and **E**). In **E**, a small piece of layer IVc beta is visible to the right of the lower star. **F**: A section mostly from layer IVc-beta, where OD stripes appear in high contrast. The upper portion of this panel shows layer IVc-alpha, and small portions of layer V (light regions) are likewise visible. Scale (in **F**) = 1 mm

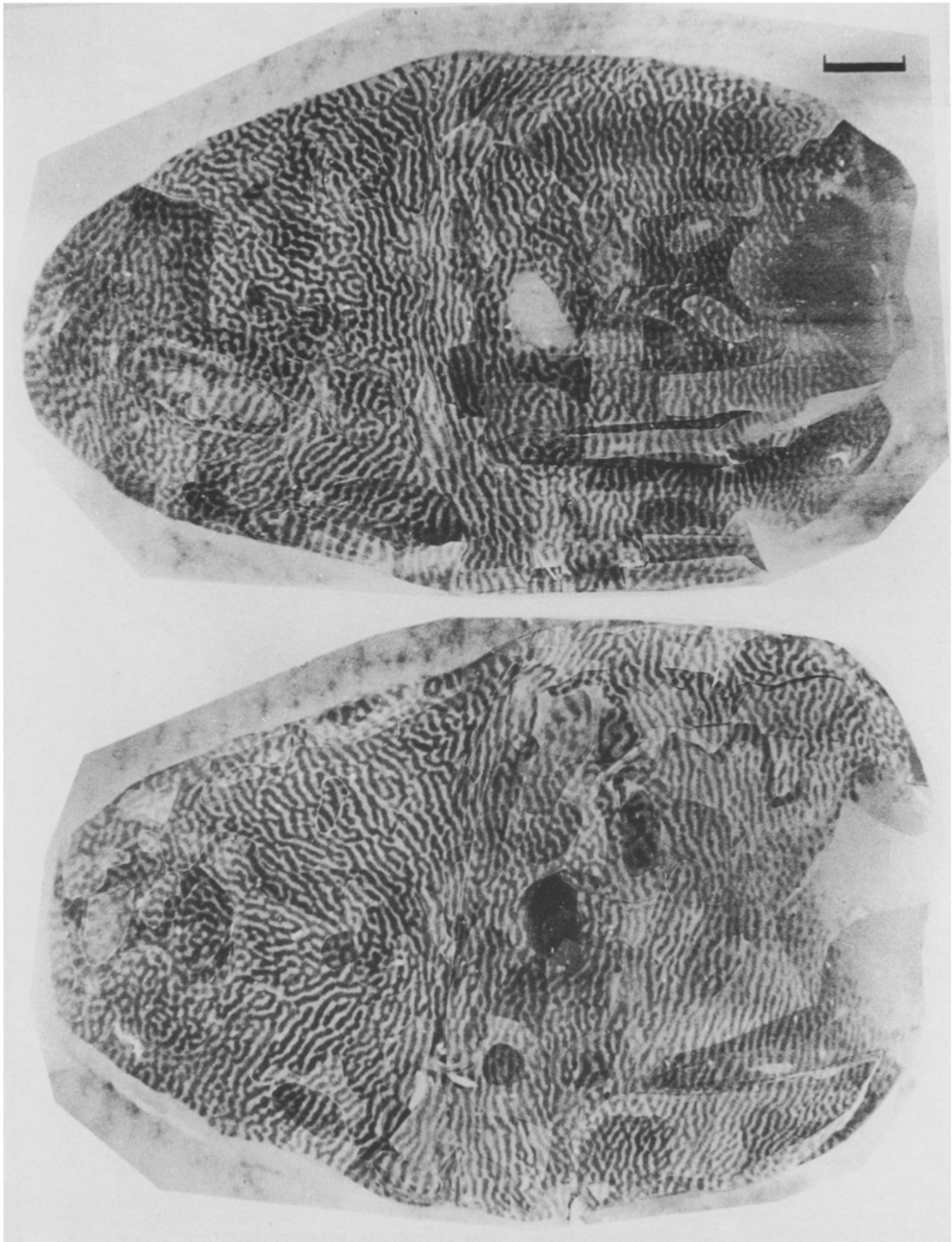

Fig. 7. Montages showing the pattern of OD stripes in layer IVc in 2 hemispheres of a single animal. *Upper:* CO6L, hemisphere ipsilateral to the enucleated eye; *Lower:* CO6R, contralateral to the enucleated eye. The reconstruction of right hemisphere (lower) was printed inverted to better allow for comparison across cases. In both cases, portions of area V2 are visible around V1. Scale bar = 5 mm

Correlation between the pattern of OD stripes and visuotopy

The bidimensional distribution of the OD stripes in V1 is not random: adjacent stripes tend to run in similar orientations relative to the representation of the visual field meridians. However, the precise relationship between stripe orientation and visual topography varies in different regions of V1. To a large extent, the main orientation of stripes is similar in different hemispheres (Fig. 7).

In order to quantify the tendency of stripes to run in specific orientations we used a modification of the method described by Anderson et al. (1988). Points about 400 μm apart were drawn centered along the stripes dominated by the contralateral eye of two hemispheres of different monkeys. These points were used to define a series of line segments, which provided a rough description of the whole pattern of stripes. The angle between each line segment and the orientation of the nearby isopolar lines was then measured, and the relative frequency of segments with specific orientations was computed within sectors defined by isoeccentricity and isopolar lines, to a total of 80–130 measurements per sector. Figure 8 compares the orientation of stripes in 2 monkeys. We have arbitrarily chosen to attribute a specific angle of stripe orientation to a sector only if more than 50% of the measured angles clustered within a 60° range (the whole spectrum of possible orientations encompasses 180°); in this case, the attributed angle corresponded to the weighed mean of the angles within this range. Otherwise, the sector was considered not to present a specific stripe orientation. The relative orientation of stripes in a given portion of V1 of a monkey is usually within 30–40° of that observed in the other monkey. Perhaps more significant, in view of the imprecision of the attribution of retinotopic coordinates, the tendency for variation of stripe orientation along a given isopolar line is the same in both monkeys. Noteworthy is the fact that some stripe orientations are underrepresented in the overall population. In particular, stripes nearly parallel to isopolar lines were rare.

In order to allow a clearer picture of the relationship between OD stripes and V1 visuotopy, we projected the pattern of stripes on a polar representation of the visual hemifield (Fig. 9), following the back-transformation technique previously employed by Hubel and Freeman

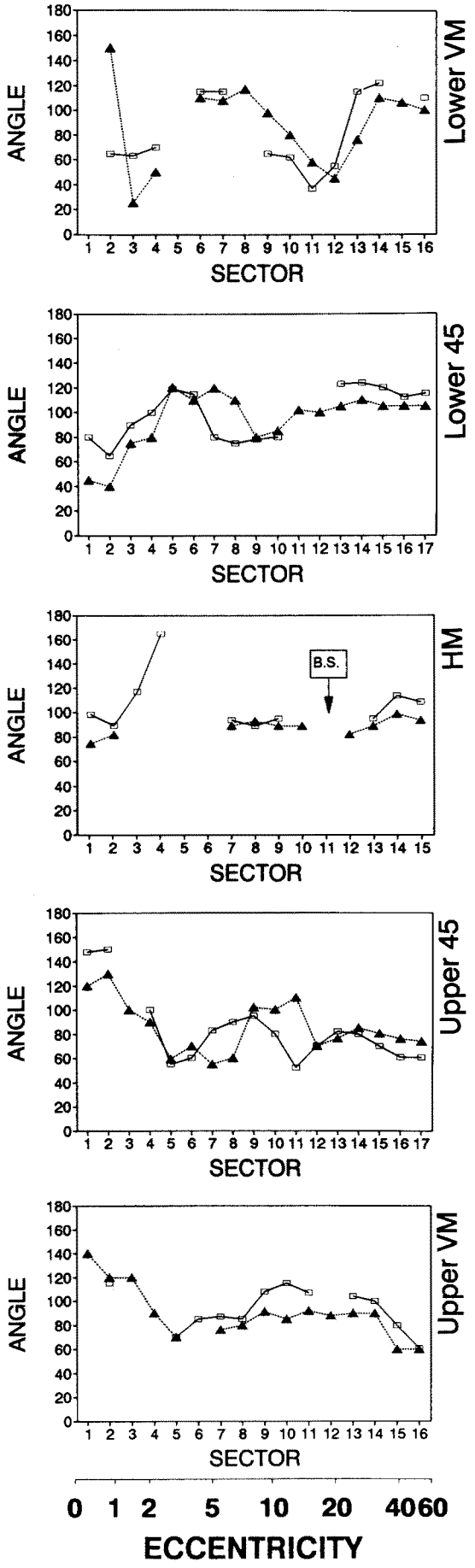

Fig. 8. Orientation of stripes along 5 isopolar lines in V1 of two monkeys. *Empty rectangles* and *continuous lines* represent data from CO5L (case illustrated in Rosa et al. 1988b) while *filled triangles* and *dotted lines* are from CO6L (upper reconstruction in Fig. 7). In the convention used to express stripe angles, 0° represents stripes parallel, and 90° stripes perpendicular to isopolar lines; angles between 0° and 90° represent stripes tilted towards the periphery, and angles between 90° and 180° stripes tilted towards the fovea, in reconstructions such as those shown in Fig. 7. The lower scale shows the approximate relationship between the sectors and eccentricity. *Abbreviations.* VM: vertical meridian; HM: horizontal meridian; 45: isopolar line equidistant from the VM and HM

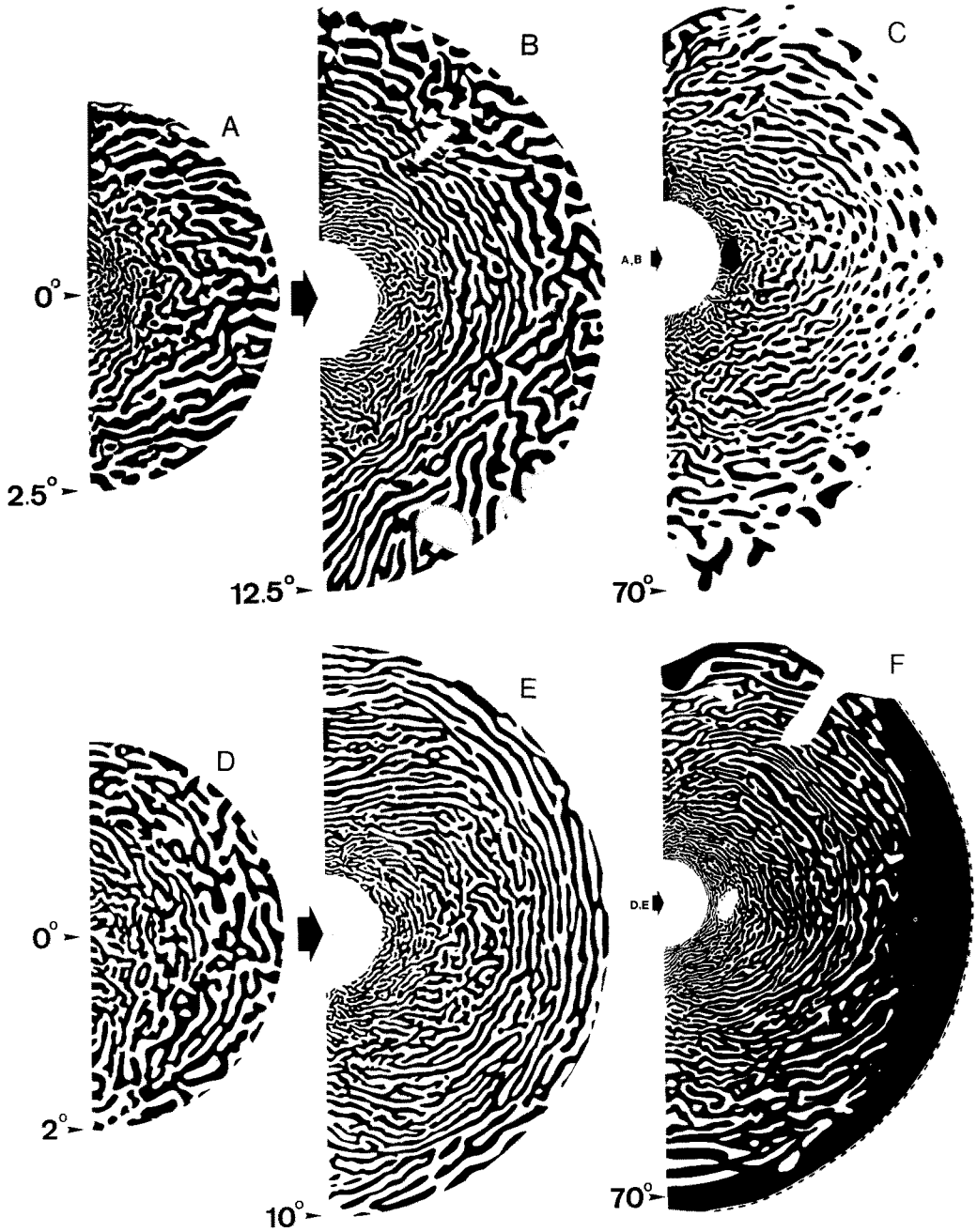

Fig. 9A–F. Result of a back-transformation of the pattern of OD stripes into a polar representation of the visual hemifield. In each case, the vertical meridian is to the left, and the upper quadrant above. **A–C** Correspond to case CO5L, and **D–F** to CO6L. In both cases, it was necessary to use different magnifications to illustrate the pattern of stripes in the central (**A, D**), intermediary (**B, E**) and peripheral (**C, F**) regions of the visual field. The interruptions were made in slightly different regions in each case, so that the interrupted regions of one reconstruction are shown continuous in the other. In **F**, the dashed line corresponds to an interruption along the monocular crescent

(1977) and Le Vay and colleagues (see Le Vay et al. 1985 for a discussion on the advantages and limitations of this technique). The result of the back-transformation (Fig. 9) shows that, in both animals:

– The large decrement of the cortical magnification factor with increasing eccentricity in V1 of *Cebus* (Gattass et al. 1987) results in an expansion of the stripes as projected onto the visual field. If one assumes the existence of a continuous and ordered map of the visual field in V1, the width of the region of the visual field represented in a pair of adjacent stripes (i.e., in an OD hypercolumn) varies from a 4′ arc, at the center of the fovea, to about 6° at the peripheral border of the binocular field;

– The pattern of OD stripes tends to be less organized at the foveal representation (Fig. 9A, D) than elsewhere, with no apparent specific orientations. This may be in part derived from the fact that the stripes are more fragmented in this region and have a large number of bifurcations and blind endings.

– At the posteromedial portion of the occipital operculum the OD stripes are so organized as to approach the dorsal and ventral borders of V1 nearly perpendicularly, converging towards the representation of the horizontal meridian and turning towards the midline. In the back-transformation, the net result of this arrangement is the organization of nearly horizontal lines in the portions of the visual field close to the vertical meridian, at eccentricities between 2 and 6° (Fig 9A, B, D, E). This tendency becomes less marked as the stripes move away from the border of V1. A tendency of the stripes in the operculum to follow the representation of the horizontal meridian,

as reported for *M. fascicularis* (Le Vay et al. 1975, 1985) was observed in one case (CO5L; Fig. 1 of Rosa et al. 1988b), but is far less marked in the other (Fig. 7).

– For most of the buried portion of V1, in the calcarine sulcus, OD stripes run nearly perpendicular to the border of V1. The stripes cross from the dorsal to the ventral border of striate cortex with relatively few interruptions, as compared with opercular V1. In the back-transformation, this organization results in nearly isoeccentric stripes in the peripheral visual field. In fact, the isoeccentric tendency in the far periphery is somewhat exaggerated (Fig. 9C, F) by the polar projection. It is usually observed that the intersection of the stripes with the horizontal meridian occurs at a greater eccentricity than the intersection with the vertical meridian. Nonetheless, at more central locations (eccentricities between 7° and 13°, still in calcarine cortex), the precise isoeccentric arrangement is not artifactual.

– The transition between the regions of monocular and binocular representation is gradual. The stripes corresponding to the ipsilateral eye become gradually thinner and shorter as compared with contralateral eye stripes, as successively more peripheral regions are considered (Fig. 9C, F). This tendency is particularly clear along the representation of the horizontal meridian (see below).

Morphometric analysis

The width of a given OD stripe is not constant along its length. For this reason, in order to estimate the width of OD stripes we adopted a random sampling strategy. A grid of points 500 μm apart was superimposed on the reconstructions of layer IVc, and stripe width at each point was measured perpendicular to the local orientation of the overlaid stripe. As shown in Table 2, the width of the OD hypercolumn varies little in V1. The only consistent tendency observed in 4 flatmounted hemispheres of 2 monkeys was the narrowing of stripes dominated by the ipsilateral eye with increasing eccentricity,

Table 2. Width of OD stripes in different portions of V1[a,b]

	central[c]	intermediary[d]	peripheral[e]
Case CO5[f]			
ipsi eye	369 (+/−79)	354 (+/−68)	327 (+/−67)
contra eye	368 (+/−73)	333 (+/−62)	382 (+/−68)
hypercolumn	737	687	709
Case CO6[g]			
ipsi eye	327 (+/−62)	313 (+/−55)	262 (+/−44)
contra eye	330 (+/−66)	318 (+/−61)	343 (+/−65)
hypercolumn	657	631	605

[a] Measurements performed on left hemispheres
[b] Figures correspond to means and standard deviations (parentheses) in micrometers of 500 measurements
[c] From the center of the fovea to 5° eccentricity
[d] From 5° to 20° eccentricity
[e] From 20° eccentricity to the border of the binocular field
[f] Contralateral eye enucleated
[g] Ipsilateral eye enucleated

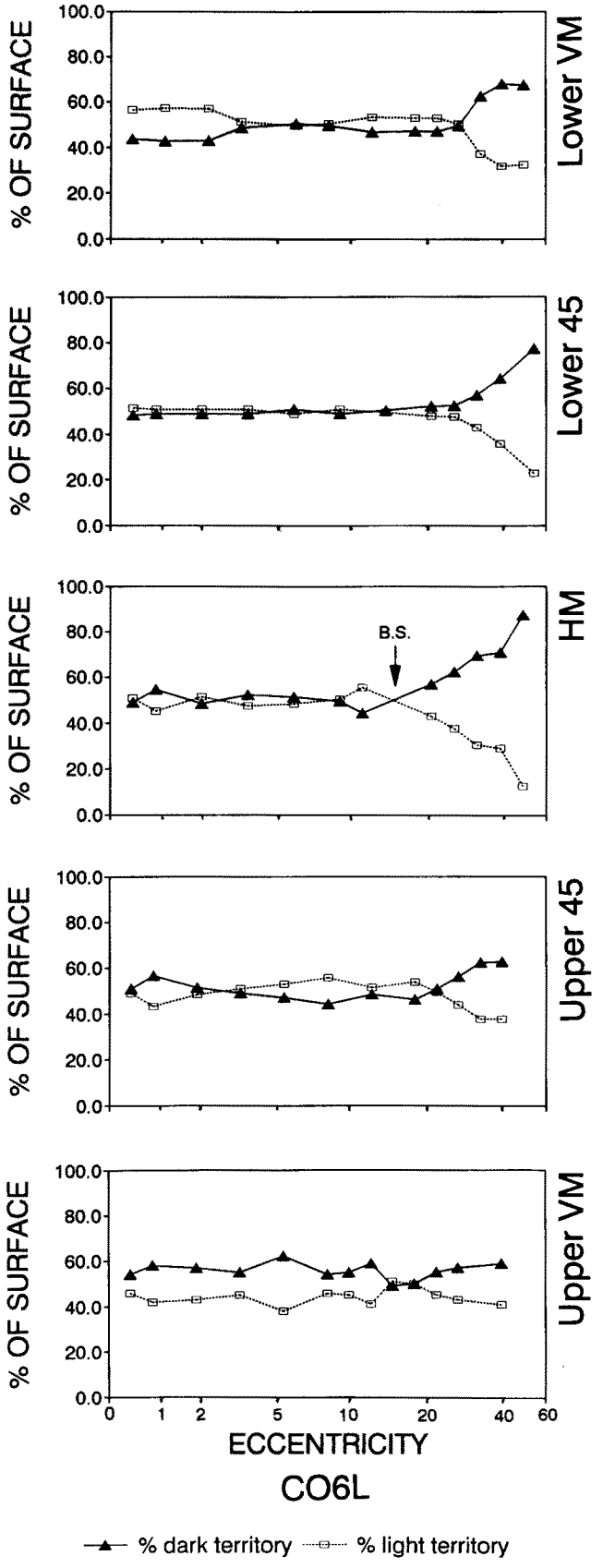

Fig. 10. Proportion of the cortical surface of layer IVc dominated by dark and light stripes along five isopolar sectors in hemisphere CO6L. In this case, dark stripes correspond to the contralateral eye. The approximate eccentricity at each site is indicated by the scale at the bottom panel. See also legend to Fig. 8

mainly at the peripheral representation. The decrement of ipsilateral eye stripe width is, to a large extent, counterbalanced by an increment of contralateral eye stripe width. For most of V1, the proportion of layer IVc dominated by the ipsi- or the contralateral eye is close to 50% (Fig. 10). The exception is the peripheral representation, where the territory of contralateral eye representation gradually overwhelms that of ipsilateral eye representation. Also noteworthy is the fact that in every studied hemisphere a narrow region immediately adjoining the border of V1 showed an imbalance regarding the relative extent of the representations of each eye. For example, in both hemispheres of CO6 (Fig. 7) the dorsal border of V1 shows a larger representation of the ipsilateral eye.

Discussion

Electrophysiological studies: ocular dominance

Ocular dominance and orientation selectivity have been investigated in many Catarrhine species (Hubel and Wiesel 1968; Baker et al. 1974; Dow 1974; Poggio et al. 1975; Schiller et al. 1976; Blakemore et al. 1978; Bullier and Henry 1980; Vita-Durand and Blakemore 1981; Zeki 1983; Blasdel and Fitzpatrick 1984; Hawken and Parker 1984; Livingstone and Hubel 1984; Kennedy et al. 1985; Michael 1985; Creutzfeldt et al. 1987). A review of the literature on these properties reveals, however, wide variations as regards classification and quantification of cell types in V1, as well as their laminar distribution. Several factors may account for these discrepancies, individual and interspecific variations aside. Differences in the preparation (anesthetised, unanesthetised and paralysed or behaving), in the procedure for visual stimulation, and in the electrode characteristics are among the most obvious methodological ones. Moreover, variations in the response scoring and even in the criterion for assigning a cell to a specific class can both contribute to the discrepant results. As will become apparent as we proceed in this section, the degree of similarity of *Cebus* to the Old World monkeys cannot be straightforwardly established. In fact, for results in any given layer there are examples of Old World monkey studies which fully agree with our observations, while others report different results.

An important issue in our study is the proportion of monocular cells in V1. For this reason, units with strong OD were the object of a careful search for weak responses from the non-dominant eye. As a whole, 12% of the studied neurons were found to be monocular, and these were strongly clustered in layer IVc. The overall number of monocular neurons in V1 of *Cebus* is lower than that reported for Old World monkeys (40%, Hubel and Wiesel 1968; 23%, Baker et al. 1974; 57%, Poggio et al. 1975; 28%, Schiller et al. 1976; 37%, Kennedy et al. 1985). On the other hand, Creutzfeldt et al. (1987) found that only 4% of the neurons in V1 could be classified in OD groups 1 and 7 in awake macaques, and that even those units had a very weak input from the non-dominant eye. With this exception, the above figures suggest that monocular segregation is weaker in *Cebus* than in Catarrhine monkeys. However, a consideration of the laminar distribution of OD in the previous studies reveals the fact that technical factors may be the cause of much of this discrepancy, as will be argued below.

Hubel and Wiesel (1968) reported that 10% of the cells in layers II and III in anesthetized macaques were monocular. Later, Livingstone and Hubel (1984) reported a figure of 23%. While both estimates are higher than the one we found in *Cebus* (less than 4%), it is important to have in mind that Livingstone and Hubel (1984) also classified as monocular units 16% of the layer II/III neurons in the squirrel monkey, a New World species in which OD segregation was found to be either weak or non-existent even in layer IVc (Hendrickson et al. 1978; Hubel and Wiesel 1978; Rowe et al. 1978). Thus, apart from effects of different anesthetics and from the ever-present possibility that slightly different electrodes may lead to sampling biases, it could well be that we have been too strict in assigning a cell to categories 1 and 7. The same arguments could apply to other layers as well. For example, Hubel and Wiesel (1968) and Blakemore et al. (1978) emphasized the almost complete preponderance of monocular cells in layer IVc, while Hawken and Parker (1984), Livingstone and Hubel (1984) and ourselves observed a significant proportion of binocular cells in this layer as well, especially in the upper tier (IVc-alpha). Interestingly, Tootell et al. (1988), using the 2-deoxyglucose metabolic mapping, also found evidence for binocular interactions in layer IVc-alpha. As regards layer IVb, some studies report that monocular cells represent half or more of the population (Poggio et al. 1975; Livingstone and Hubel 1984). Hawken and Parker (1984), however, found a much lower proportion of monocular cells in the macaque, similar to the one we report for *Cebus*. Finally, in *Cebus* the large majority of neurons in the infragranular layers was binocular, as reported by Vital-Durand and Blakemore (1981), Livingstone and Hubel (1984) and by Blasdel and Fitzpatrick (1984) in Old World primates.

Comparisons with other Platyrrhines are more limited. Coherently with reports of absence of OD stripes in layer IVc (Hendrickson et al. 1978; Rowe et al. 1978), studies in *Saimiri* (squirrel monkey) point to a lesser degree of ocular segregation (Hubel and Wiesel 1978). However, as mentioned above, Livingstone and Hubel (1984) found that 16% of layer II/III neurons were monocular, and that 45% were strongly dominated by one of the eyes (groups 1–2 and 6–7). The latter figure is similar to our result in *Cebus* (39%). With regard to the *Ateles*, an illustrated penetration (Fig. 10, Hubel and Wiesel 1968) suggests that this large New World monkey may resemble *Cebus* with regard to its OD laminar distribution: only 2 out of 24 cells found outside layer IVc, and 4 out of 9 cells in layer IVc were monocular.

Orientation selectivity

Several studies in Catarrhines emphasize the paucity of neurons with non-oriented receptive fields outside layer

IVc (Hubel and Wiesel 1968; Baker et al. 1974; Blakemore et al. 1978; Michael 1985). However, several other studies reported weakly- or non-oriented neurons in the supra- and infragranular layers as well (Dow 1974; Poggio et al. 1975; Bullier and Henry 1980; Zeki 1983; Livingstone and Hubel 1984; Kennedy et al. 1985; Creutzfeldt et al. 1987). This discrepancy is likely to reflect the criteria of classification. Here, we found it easy to classify neurons as weakly or strongly orientational by using the response in the "null" orientation as a criterion. However, nearly all of the weakly oriented neurons outside IVc-beta had, in fact, a bias towards some orientations. Thus, the discrepancy appears to be due to different thresholds for assigning "orientation selectivity" to a given response. Weakly orientational cells outside layer IVc-beta are presently believed to lie in columns which coincide with cytox-rich patches in both New and Old World monkeys (Livingstone and Hubel 1984). Unfortunately, the plane of sectioning employed in our study does not favor a histological confirmation of this point. With regards to layer IVc, our results confirm the existence of a large proportion of orientation selective neurons, which are concentrated in its upper tier, IVc-alpha (Schiller et al. 1976; Henry and Bullier 1980; Blasdel and Fitzpatrick 1984; Hawken and Parker 1984; Livingstone and Hubel 1984; Kennedy et al. 1985; Michael 1985; see Blakemore et al. 1978 for a conflicting view). The small proportion of orientation-selective cells in layer IVc-beta was similar to that reported by Michael (1985), but lower than those reported by Schiller et al. (1976) and by Hawken and Parker (1984). Both Blasdel and Fitzpatrick (1984) and Livingstone and Hubel (1984) were unable to find any such cells in IVc-beta, thus lending some support to Blakemore et al. (1978), who suggested that the occasional orientational neurons may represent recordings from cells in adjacent layers. Differences in electrode characteristics may account for this discrepancy.

Directional selectivity was often observed to occur in small cell clusters, which were verified to coincide with layers IVb, IVc-alpha and VI. This laminar distribution matches exactly that reported by Hawken et al. (1988) for Old World monkeys.

Pattern of OD stripes

Prior to this study, the Old World *Macaca fascicularis* was the only primate in which the organization of OD stripes had been studied in detail. In this species, Le Vay and colleagues (1975, 1985) described both the pattern of stripes and its relationship with the representation of the visual field in V1. The main trends of the pattern of stripes described by Le Vay were largely confirmed by Horton (1984) and by Tootell et al. (1988), who used the flat-mount technique to obtain partial reconstructions of this pattern in several macaque species. In addition, though, these studies revealed more complexity in the local domain of stripes. Tootell et al. (1988) also compared patterns in both hemispheres of single individuals and across individuals of the same species and concluded, as we did, that the general orientation of the stripes at a given point of V1 is consistent for a given species, while the fine pattern varies.

The comparison of our results with those of previous studies reveal similarites between *C. apella* and *M. fascicularis:* a) no consistent trend in the pattern of stripes in the foveal projection; b) stripes converge and stream medially in the parafoveal occipital operculum; c) stripes run nearly isoeccentrically in peripheral V1; d) the width of individual stripes in the central representation is about 340 μm (Tootell et al. 1988; Trusk et al. 1990). The main difference between these species relies on the fact that there may exist a larger variation in stripe width from the central to the peripheral representation in the macaque (Le Vay et al. 1985) than in *Cebus*. In addition, larger species of macaques have wider stripes arranged in what appears to be a more regularly organized pattern (Tootell et. al. 1988). Taken together, these observations indicate that there may exist a common genetic basic for the expression of OD stripes during development in both Infraorders of monkeys, so that stripes tend to assume some orientations and avoid others. The laminar distribution of stripes and the effects of monocular enucleation on supra- and infragranular layers are also similar in *Cebus* and *Macaca* (Horton 1984; Rosa et al. 1991). The similarity between these species of monkey is even more significant when they are compared with non-primates such as the cat, which lacks any obvious order in the pattern of OD columns (Anderson et al. 1988), and the ferret, which has stripes of unequal width for the ipsi- and contralateral eye which are regularly organized along iso-elevation lines (Law et al. 1988). The differences between closely related species of Old World monkey (Tootell et al. 1988) suggest that epigenetic factors, such as those related to growth, intraspecific and interspecific allometry (Fleagle 1988) may play an important role in determining the fine pattern of stripes in primates.

Hess and Edwards (1987) described the pattern of OD stripes in V1 of *Cebus* as "less orderly, or more discontinuous and mosaic, than in the macaque". Our results, and those of Tootell et al. (1988) caution against such a generalization, for an investigation on this point may yield different results depending on the region of V1, on the macaque species and even on the individuals used for comparison. Hess and Edwards (1987) also emphasized the difference between the area corresponding to dark vs. light stripes, and suggested that this may indicate an incomplete ocular segregation in *Cebus,* as contrasted with macaque. Trusk et al. (1990) also found evidence for a diminished domain for the enucleated eye in the macaque, but suggested that this should be a consequence of cellular atrophy rather than incomplete segregation. Although in our data the mean width of dark stripes tended to be slightly higher than that of light stripes in both monkeys, the large variance of stripe width (Table 2) does not allow statistical significance to be attributed to this result. Our results and those of Tootell et al. (1988), in the normal macaque, show that the differences in the areas dominated by either eye are variable between portions of V1 and between individuals. Once again, we

found no evidence for systematic differences between capuchins and macaques; rather, the same results could be attributed to biological variability.

Different degrees of ocular segregation in New World monkeys

The Infraorders of simians, Platyrrhini and Catarrhini, have been separated from each other by about 30 million years, i.e., nearly half of the whole history of the order Primates (Fleagle 1988). Nonetheless, the laminar and, to a large extent, the tangential patterns of OD stripes are similar in representatives of New- and Old World monkeys with similar sizes and sulcal patterns. We regard as of low probability that such a similarity could have arisen by independent mutational events on a common ancestral situation in which OD stripes were absent (Spatz 1979), and that the situation seen in *C. apella* and *M. fascicularis* would represent a case of synapomorphy. On the contrary, both Infraorders may have evolved from a group which already had the genetic information coding the formation of OD stripes. A problem with this hypothesis is how to explain the absence of stripes in adult representatives of several contemporaneous New World species, including *Aotus, Saimiri* and *Callithrix* (Kaas et al. 1976; Hendrickson et al. 1978; Rowe et al. 1978; Spatz 1979). Based on the observation of the regression of the OD stripes during postnatal development, Spatz (1989) suggested that the formation of stripes and their maintenance during adult life are controlled by different genetic mechanisms. According to this hypothesis, only the first mechanism (the formation of stripes) would have been present in the common ancestor of all monkeys, while the mechanism which stabilizes the stripes would have appeared several times in primate evolution. This hypothesis, however, involves too many unlikely steps, in view of current evolutionary scenarios of simian relationships. For example, *Cebus* and *Saimiri* are usually regarded as close relatives (Fleagle 1988), but only the former show stripes; in contrast, stripes are present in genera as far apart as *Ateles* and most (if not all) Catarrhines. Moreover, it would be hard to justify how, among various possibilities (see, for example, Anderson et al. 1988; Law et al. 1988), the stripes would come to show similar arrangements in *Cebus* and in some Old World species, in contrast to others (as the larger macaques). A more parsimonious hypothesis that would account for these observations postulates a single mechanism which interacts with epigenetic factors to produce the whole array of phenotypes observed among simians. As discussed above, interspecific allometry is likely to be one of the epigenetic factors which would determine the final condition of stripes in striate cortex. This hypothesis takes into account the model of competitive interactions involving opposing "retinotopic" and "segregative" forces, which would occur during the pre- and postnatal development, leading to the formation of OD stripes in Old World monkeys (Le Vay et al. 1975, 1985; Hubel et al. 1977). Factors likely to play a role in this context are the surface area of V1 (as discussed by Rosa et al. 1988b), the number of ganglion cells and optic nerve fibers, as well as the ratio of convergence/divergence in the retino-geniculo-striate pathway.

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