The Projection of the Opossum's Visual Field on the Cerebral Cortex [1]

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ABSTRACT   The visual cortex of the opossum was studied by means of evoked potential and multi-unit recordings, and a map of the visual field in V_I was constructed: Evoked responses were observed in regions extending beyond the boundaries of striate cortex. Different patterns of response were obtained depending on the cortical region undergoing exploration: in a posteromedial region, coincident with striate area, complex waveforms were obtained, contrasting with the simpler forms observed in a region localized anterolaterally. V_I, which corresponds to cytoarchitectonic area 17, has a topography of projections similar to that found in other mammals: the upper visual field represented posteriorly, the temporal field represented medially, the lower field represented anteriorly and the nasal part laterally. A large proportion of V_I is devoted to the region of binocular representation, which covers approximately 100° at the level of the horizontal meridian. The cortical representation of the vertical meridian extends to approximately 60° above and below the center of gaze, suggesting that the cortical representation of the visual field is more restricted than the visual field available to the contralateral hemiretina. Our results suggest that the extreme periphery of the field is not represented in V_I. In its lateral border the projection does not end at the vertical meridian, it extends 5° into the ipsilateral hemifield of vision, so that approximately 10° of visual field is represented in both hemispheres. There is a reversal of representation along the lateral border of V_I, in a region which coincides with the cytoarchitectonic boundaries of striate and peristriate areas, suggesting the existence of at least a second representation of the visual field in the neocortex of the opossum, corresponding to V_{II} of other animals.

The magnification factor in V_I varied from 7°/mm observed at the cortical representation of the center of gaze, to 30°/mm at the extreme periphery of the field, along the horizontal meridian. A comparable decrease was also observed along the vertical meridian, towards the upper and lower limits of the visual field.

The use of marsupials as experimental animals can be of great value for comparative studies on the anatomy, physiology and ontogenesis of the nervous system. Due to the fact that the marsupials, more specifically the *Didelphidae* present a primitive nervous system as well as characteristics of generalized mammals, several investigators had already pointed out the great interest in using these animals for comparative studies. The opossum, being a marsupial, offers advantages for the study of developmental neurobiology since at the moment of birth the young are imma-ture with their nervous system in a primitive stage of development as shown by McCrady ('38) and Ulinski ('71). The pouch young opossums, easily accessible for experimental manipulation, offer a unique opportunity for the study of the development of neural connections, a field of study which is usually restricted to non-mammalian species.

There are at present no data on the retino-

topic organization of the striate cortex of a metatherian mammal and the present investigation was undertaken to provide comparative information in this respect. The opossum *Didelphis marsupialis aurita* was chosen for this purpose.

Retinotopic organization of mammalian visual cortex has been the subject of intensive investigation in a number of laboratories. Representatives of various orders have been studied in this respect, including hedgehog (Kaas et al., '70), tree shrew (Kaas et al., '72b), rabbit (Thompson et al., '50; Hughes, '71), mouse (Dräger, '75), rat (Adams and Forrester, '68; Montero et al., '73b), hamster (Tiao and Blakemore, '76b), grey squirrel (Kaas et al., '72a), cat (Bilge et al., '67), sheep (Clarke and Whitteridge, '76) and monkeys (Daniel and Whitteridge, '61; Cowey, '64).

The extent of the cortical sensory receiving areas in the opossum was investigated by Lende ('63); the visual area was delimited by means of gross photic stimulation. Using similar techniques Magalhães Castro and Saraiva ('71) studied the cortical sensory areas in a closely related species, *D. azarae azarae.*

The present report will describe part of the results obtained in a series of experiments aiming at the determination of the functional organization of the visual system of the opossum.

Specifically this paper deals with the determination of the total extent of cortex activated by visual stimuli and with the topographic representation of the visual field in V_I. In addition, it compares some aspects of the visual system of the opossum with those of other species commonly used in experimental work.

MATERIAL AND METHODS

The functional organization of visual projections in the opossum was determined by two series of experiments. In the first series, cortical responses to gross photic stimulation were recorded through surface electrodes in order to determine the total extent of the visually activated areas. In the second series the results were obtained by recording the activity of small clusters of neurons with microelectrodes in order to reveal the topographic representation in the primary visual cortex.

Animal preparation

The present experiments were performed in 29 adult specimens of *D. marsupialis aurita.* Of these 22 were employed for determining the topographic representation in V_I. All animals were initially anesthetised by intraperitoneal injection of sodium nembuthal (35 mg/kg, Fontoura Wyeth, S.A.). A stable anesthetic level was obtained by intravenous injections of a 1% solution of alpha-chloralose (Merck). Body core temperature was kept around the normal value (34°C) by means of radiant heat. As a rule tracheostomy and phlebotomy were carried out. The venous cannula was used for the administration of maintenance doses of anesthetic and of neuromuscular blocking agents.

The animals were secured in a headholder especially designed in order to minimize obstruction of the visual field. Wide craniotomy was performed and the opening was surrounded by a dam of dental impression compound. The dura was reflected and the exposed cortical surface protected with warm mineral oil or saline. The cortical surface was photographed and prints prepared in order to permit a precise demarcation of the recording sites. Two sets of photographs were obtained: in the first the optical axis of the photographic equipment was placed at a right angle with the Horsley Clarke horizontal plane; in the second the camera was tilted to 45° in order to achieve a better coverage of the lateral aspect of the cortex.

Atropine and phenilephrine were applied to the conjunctival sac to promote cycloplegia, mydriasis and exophthalmia, a condition normally observed in alert opossums. Protection of the corneal surface was achieved by application of a thin layer of silicone fluid (Dow Corning 200/350) in the macroelectrode series, and by means of individually selected contact lenses from a series especially developed for this species (Solótica Industria e Comércio Ltda) in the microelectrode series.

In order to prevent eye movement a mixture of tri-metil-ethil-gallamine (Flaxedil, Rhodia, 10 mg/ml) and toxipherine (Alloferine, Roche, 2.5 mg/ml) (Pettigrew, '74), was infused through the venous cannula at a rate of 1.8-2.5 ml/hour. After paralysis the animals were artificially ventilated.

At the end of the experiments reference markers were inserted into the cortex and their position registered in the photographs of the cortical surface. The animals were perfused through the aorta with warm saline followed by formaline. The brains were processed and Nissl stained serial sections for micro-

scopic analysis prepared. Identification of recording sites and their correlation with the cytoarchitectural areas was facilitated by the presence of the reference marks.

Macroelectrode experiments

Evoked slow-wave potentials were monopolarly led off from the cortical surface by means of a 300 μm ball tipped silver wire. The activity was amplified and displayed by conventional means and recorded in 35 mm film for further analysis.

Gross photic stimulation was obtained by directing to the eyes the collimated beams of two independent glow modulator tubes (Sylvania 1130B). The optical axis of the stimulating system was adjusted so as to coincide with the optical axis of the eyes, as determined by the Purkinje images. Flash duration was 5 ms with an intensity 4 log units above background illumination which was adjusted to 0.343 candles/m² (0.1 ft L.). Stimuli were delivered every five seconds in order to prevent response interaction.

Microelectrode experiments

Activity of small clusters of neurons was recorded by means of tungsten microelectrodes held by a MM3 Narishige micropositioner. The angle of penetration was either normal to the horizontal plane or tilted at an angle of 45°. The electrode was connected to a FET input probe and the electric activity was further amplified by two independent channels which were used to display slow wave and MU activity in a dual beam oscilloscope. MU activity was also fed to an audio monitor system.

In the microelectrode series the headholder was attached to a supporting system which could be adjusted in three orthogonal planes, allowing the eyes to be centered with respect to the arms of a Landolt type perimeter.

The headholder and the microdriver used to orient the penetrations were mounted in a common base allowing lateral displacements in such a way that each eye could be brought to the center of the perimeter, thus enabling the study of the visual field of both eyes for each recording site.

Stimulation was carried out by means of a light source which could be positioned at any point in a hemisphere with a radius of 27 cm, by the combined displacement of the light source along the arms of the perimeter and rotation of the arms around the axis of the perimeter. The light source consisted of a tungsten filament lamp (Chicago Miniature 1705, 14 V, 80 mA), a collimating lens and a ground glass acting as a diffuser. In front of this ground glass a calibrated iris diaphragm permitted adjustments of the dimension of the light spot, covering a range from 30′ to 6°, as viewed by the animal.

In order to improve the latency of incandescence inherent in filament type light sources a positive bias voltage (11 VDC) was applied producing only a slight red glow. Light flashes were obtained adding rectangular positive pulses (50 ms-50 mV) to the bias current.

Two modes of stimulation were employed to activate cortical neurons: static stimuli which consisted of pulses of light delivered at a repetition rate of 0.1 to 1 pulse per second, with the light source stationary in the visual field, and moving stimuli obtained by manual displacement of the light source, which was kept at a continuous luminance.

Stimulus luminance in both modes of operation was 109.8 candles/m² (32 ft L) and the background illumination was kept at a level of approximately 0.343 candles/m² (0.1 ft L).

Experimental procedure

Electrodes were oriented to the desired cortical site by means of anteroposterior and mediolateral adjustments of the micromanipulator; the penetration site being recorded on the previously prepared photographs of the cortical surface. Readings from the micromanipulator scales were employed to determine the separation between different recording sites. After establishing contact with the cortical surface the electrode was slowly advanced until a clear response to visual stimuli could be obtained.

Using static or moving stimuli the location and extent of a region of the visual field within which the stimulus evoked a response for a given electrode site was systematically determined. This region will be called the receptive field. A protocol of the various points defining the borders of the receptive fields was kept in polar coordinates. In the same protocol the positions of the blind spot, as determined by means of a reversible opthalmoscope, of the visual axis, as determined by the Purkinje images, and also of the nasal border of the visual field of each eye, determined by the presence of the corneal reflex of the light source, were also recorded.

For the final presentation of our experimental results Lambert's equatorial area azi-

muthal projection system was used. Graphic construction was carried out following the descriptions of Steers (1970) and Roblin ('71).

Taking into consideration that the position of the animal's head during the recording sessions differed from its normal posture, correction factors were introduced in order to make the horizontal meridian of the adopted coordinate system coincident with the horizontal meridian of the animal. In its normal posture the blind spot of this species lies, in average, 4.5° above the line of the horizon, making an angle of 26.7° with the midline (Sousa et al., '77). Therefore, in the present study the vertical meridian (VM) was defined as a plane, parallel to the midline, passing through the center of the eye and the horizontal meridian (HM), as a plane normal to VM situated 4.5° below the projection of the optic nerve head.

The conversion from polar to azimuthal coordinates and the adjustment of each individual experiment in relation to the average position of the blind spots in the visual field was achieved by means of programs using the algorithms derived by Gattass and Gattass ('75).

RESULTS

Results obtained in experiments using macro- and microelectrodes indicate that a wide extension of the posterior pole of the neocortex of the opossum is activated by visual stimulation.

Functional properties of responses recorded in this region indicate that part of the active region exhibits properties which justify the identification of a primary visual area coincident with the striate area, as described by Benevento and Ebner ('71) for this species. Visual responses were also obtained in a belt region surrounding the striate area, extending even beyond the boundaries of the peristriate areas defined by these authors.

Some morphological features of striate area described in previous studies (Benevento and Ebner, '71; Sousa, '75) may be of interest in order to establish a correlation between the representation of the visual field with cortical structure.

Macroscopic observation of the brain of *D. marsupialis aurita* showed that its external configuration is identical to that described by Gray ('24) and by Loo ('30) for *D. marsupialis virginiana*. In fresh material close observation of the dorsolateral cortical surface in the occipital region indicates the presence of a fissure, which is more easily identified in fixed material. Gray ('24) mentioned briefly the presence of this fissure, in some specimens, and suggested its possible relation with the lateral border of the striate area. In a previous publication (Sousa, '75) it was shown that

this fissure is present in the great majority of the specimens studied and that it can be used as a landmark to locate the lateral border of the striate area.

In a cytoarchitectonic study of the cortex of the opossum Gray ('24) described the striate area which is surrounded, in its lateral aspect, by the peristriate area. Recently, Benevento and Ebner ('71) presented a more detailed description of the visual areas of the opossum, based not only on cytoarchitectonic criteria but also on anterograde degeneration studies. Using Nissl stained serial sections of a large number of brains of the South American sub-species, it has been shown (Sousa, '75) that the cytoarchitectonic subdivisions of the visual areas are identical in both the North and South American sub-species.

The most striking feature observed in striate area was the presence of a well developed layer IV, this characteristic being more accentuated along its lateral edge. The borders of striate area were more easily identified through the observation of fiber stained sections, where the presence of fiber bundles at the level of layer IV became evident. Analysis of these sections revealed a greater density of fibers along the lateral border of striate area, decreasing gradually towards its medial portions. Using alternate series of fiber and Nissl stained sections it was possible to show a good agreement on the limits of the striate area as described based on cyto- and myeloarchitectonic criteria.

The peristriate areas consist of a belt that surrounds the striate area. This belt originates at the interhemispheric surface as a slender band that gradually widens reaching its maximum extent in the dorsolateral surface of the cortex. Medial to striate area, on the medial wall of the hemisphere above cingulate cortex a band of peristriate cortex designated by Benevento and Ebner ('71) medial peristriate (PS_m) is identified. When compared to striate area, in Nissl preparations, this area has a greatly reduced thickness, especially in layers IV and V and a layer I which is much wider relative to total cortical thickness.

Lateral to the striate border is central peristriate cortex, which is divided into a medial (PS_{cm}) and a lateral (PS_{cl}) portion, based on its cytoarchitecture.

The centro-medial peristriate cortex is characterized by a marked reduction in thickness of layer IV. In this area layer IV represents only 16% of the total cortical thickness, while in striate area it corresponds to 30% of the total cortical thickness. Central-medial peristriate is also characterized by a slightly wider layer I than striate.

In centro-lateral peristriate area there is a further reduction in the width of layer IV, which now corresponds to only 13.5% of the total cortical thickness. This region is also characterized by the greater density of layer I and by the presence of large pyramidal cells in layer V.

In both PS_{cm} and PS_{cl} the granular cells of layer IV are smaller than those found in layer IV of striate area.

The cortex localized along the anterior margin of Gray's peristriate corresponds to the anterior peristriate area (PS_a). This area presents a reduced layer IV and a layer V which is intermediate in width between that of PS_{cm} and PS_{cl}.

On the lateral surface of the hemisphere, posterior to the temporal cortex and dorsal to the rhinal fissure the posterolateral peristriate area (PS_{pl}) can be identified. This area shows a somewhat narrower total thickness due mainly to a reduction in layers V and VI. When compared to the central peristriate area PS_{pl} presents a poorly defined layer IV.

Extension of visually activated cortical areas

Evoked slow wave responses in cortical visual areas

Responses to brief visual stimuli were recorded in the dorsolateral aspect of the cortical surface. The waveform of the evoked activity showed considerable variation, depending on the cortical region under exploration and on whether the stimulus was delivered to the contralateral or ipsilateral eye. Complex polymorphic waves varying in shape from one experiment to another and also with the anesthetic level, were obtained in the posteromedial portion of the active areas. In the same experiment, responses in this area varied with the eye undergoing stimulation. Figure 1 shows a region responding only to contralateral stimulation along the postero-medial edge of the hemispheres.

In a region localized antero-laterally to that which displayed polymorphic responses, a different pattern of evoked activity was observed. Responses in this anterolateral region were simpler in form, showing an initial positive phase followed by a longer lasting negativity and occasionally by a later positive wave. In contrast to the polymorphic activity recorded in the posterior region, these responses showed similar waveforms after stimulation of either the contralateral or ipsilateral eye, as illustrated in figure 1.

Latencies of initiation of both types of responses were similar, being of the order of 25 ms for supramaximal stimuli. As a rule responses of greater amplitude were observed in the anterolateral portion of the active area.

Cytoarchitectonic correlation

It was observed that the complex polymorphic responses were all obtained in a region coincident with the striate area. Direct correlation between the activity evoked outside the striate area and the various subdivisions of the peristriate area as defined by Benevento and Ebner ('71) is more difficult because the description of these areas does not rely entirely on cytoarchitectonic criteria, depending primarily on the pattern of thalamic and cortico-cortical connections. Indirect correlation was achieved based on the fact that in a previous study (Sousa, '75) it had been shown that the proportional coordinate system developed by Ebner and Walsh (personal communication) for the North American species is also valid for *D. marsupialis aurita*. The principles involved in the establishment of the proportional coordinate system were described in figure 2 of Walsh and Ebner's ('70) study on the sensory-motor cortex of the opossum. By establishing the borders of the various peristriate areas, as described by Benevento and Ebner ('71), by means of the proportional system, it became evident that large amplitude simple visual responses can be recorded from PScm, PScl, the active region extending beyond the rostral border of PSa. There was a gradual fall in response amplitude towards the mesial portions of PScl and PSa. No visual

A

B
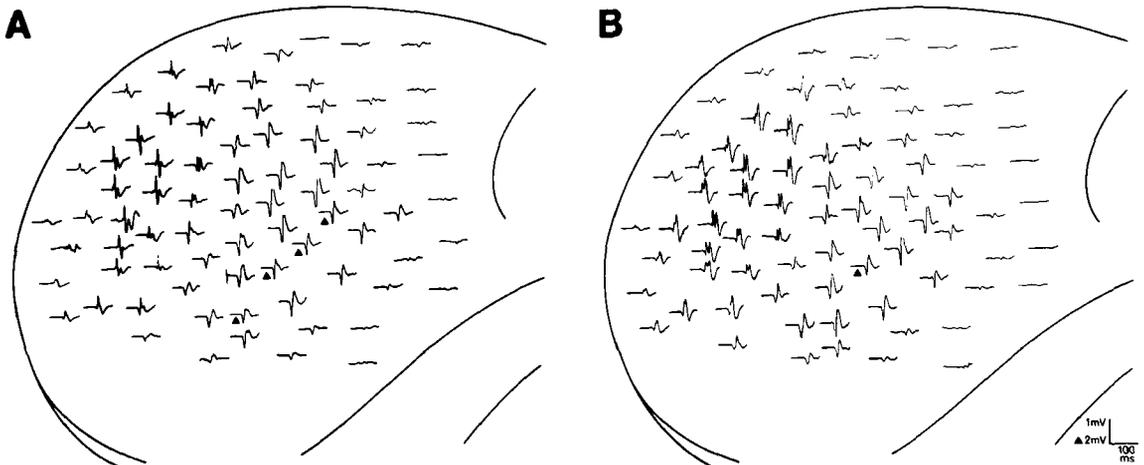
Fig. 1 Cortical responses to gross contralateral (A) and ipsilateral (B) photic stimulation, in the opossum. Examples of typical responses are presented on a 45° view of the right hemisphere. Responses recorded in striate area are characterized by their complex waveform, contrasting with the simpler type of activity recorded in the anterolateral portion of the active area. Responses tagged by triangles were recorded with lower amplification.

evoked responses could be obtained in PSpl.

Multi-unit response characteristics in V_I and V_{II}

The receptive field corresponding to each recording site was determined using simultaneous recording of slow wave and MU activity. Receptive fields corresponding to loci within the boundaries of the primary visual area were more easily defined listening to the discharge of the MU activity through the audiomonitor system. The "hash" or "swish" was clearly identified above background discharge when the stimulus was moved in and out of the receptive field.

Neurons in this area also responded with brisk discharge to on and off stimuli, of small dimensions, presented within the receptive field. Slow wave records obtained in V_I showed a wider distribution, rapidly declining in amplitude with displacement of the stimulus towards the borders of the receptive fields. A more precise definition of receptive field borders was obtained by means of moving stimuli, and this was the technique adopted as routine.

Using discrete stimuli with diameters of 30′, receptive fields as small as 2° in diameter could be easily defined, larger receptive fields with diameters of 30° or more, were found in the mesial border of V_I. As a rule, in all receptive fields, independent of its size, a region could be identified where stimuli evoked brisker responses of greater magnitude. This region generally coincided with the geometrical center of the receptive field and thus was considered as corresponding to the point of the visual space represented at the recording site.

In penetrations normal to the cortical surface response magnitude showed a gradual increase as the electrode was advanced through the cortical mantle, attaining maximum amplitude at a depth of 400-600 μm, which corresponds to the region of termination of thalamo-cortical projections. Further advancement of the electrode resulted in reduction of the amplitude of the evoked activity usually associated with a reversal of the polarity of the slow wave activity. During the descent of the electrode there was no appreciable shift of receptive field location.

Electrical activity evoked in the peristriate areas showed several characteristics different from those observed in the primary visual area. MU activity recorded in this region was always less intense than that observed in V_I, the brisk responses obtained by presenting small diameter stimuli to the center of the receptive fields were never observed. The most effective stimuli were larger spots (4°-6°) moving across the receptive field, and static stimuli were rather ineffective.

When defining receptive fields corresponding to points outside V_I slow wave activity was also taken into consideration, due to the paucity of MU discharges in these regions. However, under our experimental conditions a systematic analysis of the topography of visual projections in peri-striate areas was not possible because of the difficulties encountered in defining the receptive fields and also owing to the large size of the fields observed.

Topographic organization in V_I

For the purpose of establishing the topographic representation of the visual field in V_I 310 penetrations were made, distributed throughout the whole extent of striate area. In the majority of the experiments penetrations were made in rows oriented approximately along the frontal plane in order to facilitate the correlation between recording sites and cortical cytoarchitectonics.

The receptive fields corresponding to eight recording sites along one row are illustrated in figure 2. In this figure the position of the points of entry of these penetrations are indicated on a dorsal view of the posterior portion of the right hemisphere as well as a surface projection of the striate-peristriate border obtained from reconstruction based on serial sections (fig. 2B). As these penetrations were made normal to the horizontal plane, and as

Fig. 2   Representation of the visual field of the left eye in striate cortex of the opossum.

A   Semi-schematic drawing of a frontal section passing through the plane of the eight penetrations illustrated in figure 2B, showing the location of their corresponding recording sites (dots). Due to the columnar arrangement in cortical projections the surface representation corresponding to a recording site located in deeper layers can be determined by a line normal to the cortical surface passing through the recording site (dashed lines). The arrows indicate the borders of striate area.

B   Locations of microelectrode penetration sites are shown by dots on a dorsal view of the posterior aspect of the right cerebral hemisphere.

C   The visual field is represented by an equatorial azimuthal projection of an internal view of a hemisphere. Thus the hemisphere is shown from the animal's view rather than the observer's view. Receptive fields are numbered according to their corresponding recording sites. Parallel zero corresponds to the horizontal meridian with the animal in its normal posture, and the zero meridian corresponds to the assumed line of decussation. A continuous line in the nasal field delimits the region of the visual field which is obstructed by the rhinarium.
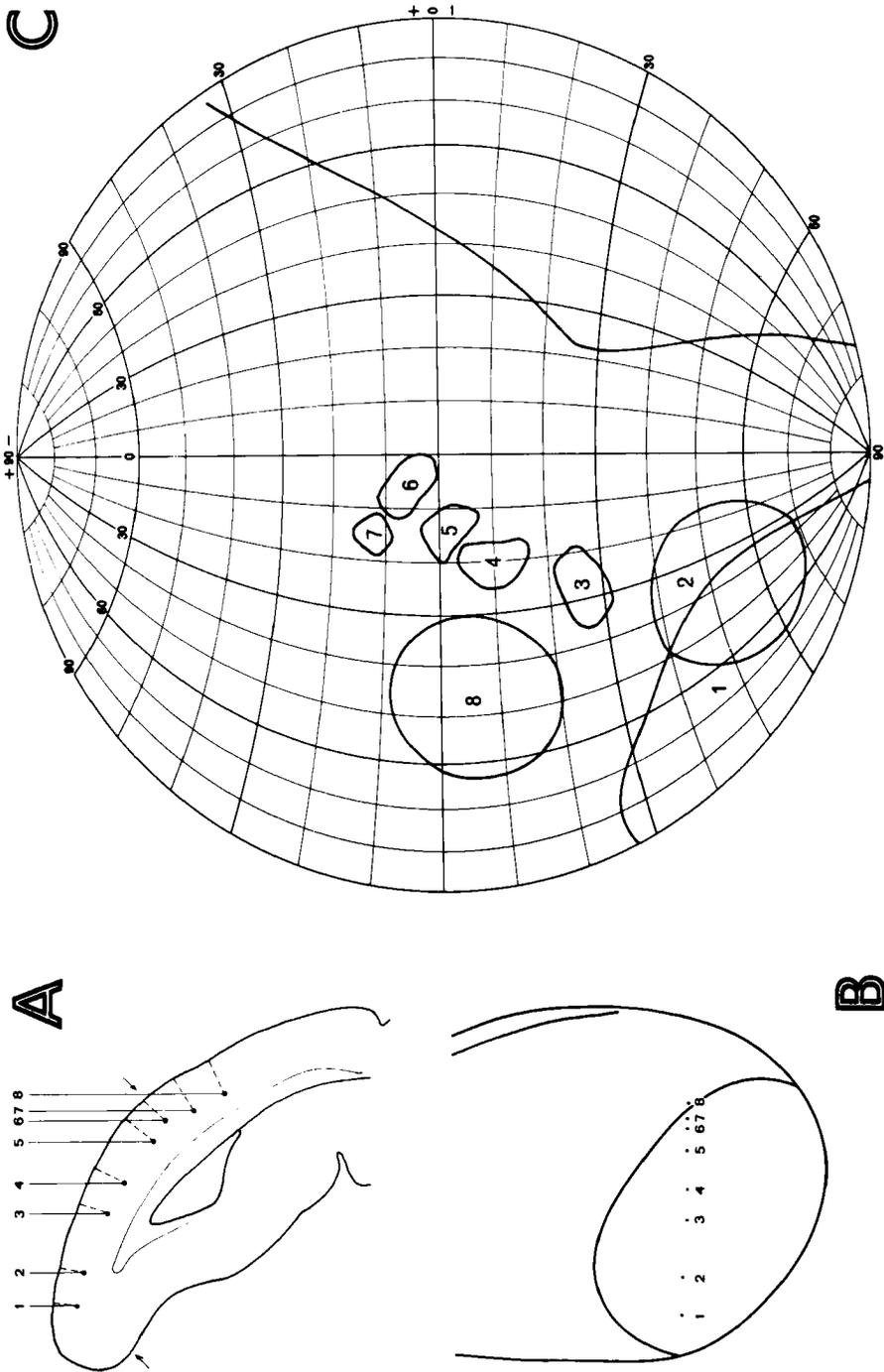
Figure 2

the curvature of the cortical mantle steepens towards its lateral aspect, when projecting the recording sites to a surface view of the cortex these factors have to be taken into consideration (fig. 2A). Therefore, as penetrations 1, 2, 3 and 4 are localized in a less inclined region the position of the projection of their recording sites to the surface does not differ significantly from the point of entry. However the recording sites corresponding to penetrations 5, 6, 7 and 8 are displaced laterally in relation to the point of entry. Therefore, recording site 6, at the bottom of the penetration, actually corresponds to a point located close to the V_I-V_{II} border. Likewise penetration 7, with its point of entry localized on the striate side of the V_I-V_{II} border, when reaching the level of layer IV is well within the peristriate area, as observed in the corresponding histological section.

The areas of the receptive fields become smaller as the recording sites approach the lateral border of V_I, increasing again as the recording sites move across V_{II} (fig. 2C). This figure also shows that there is a gradual displacement towards the nasal field as the recording sites approach the lateral border of V_I. The temporal field is represented medially and the nasal field laterally. When the V_I-V_{II} border is reached a reversal of the representation of the visual space occurs. The receptive field corresponding to recording site 7, localized in V_{II}, is displaced temporally suggesting the existence of a reversal of the sequence of representation of the visual field at the V_I-V_{II} border.

Due to the orientation of this row of penetrations it can be seen that besides this temporo-nasal displacement there is a gradual shift of the receptive fields from the lower to the upper portion of the visual field. The results obtained indicate that the plane in which these penetrations were made makes a steep angle with the cortical representation of the vertical and horizontal meridians. Similar results are shown in the five rows of penetrations depicted in figure 3. From this figure it becomes evident that the rostral portion of V_I is related to the lower visual field, the upper field being represented caudally.

Cytoarchitectonic evidences indicate that the striate area (Benevento and Ebner, '71; Sousa, '75) is not restricted to the dorsolateral aspect of the posterior pole of the neocortex. Its rostral portion extends to the mesial and ventro-mesial interhemispheric surface, and in its caudal aspect it extends to the ventral surface. In order to determine the topography of projection of the visual field to those regions which were not directly accessible to surface recording, receptive fields were plotted at different depths in some penetrations. When correlating recording site with receptive field location, the columnar organization across the cortical mantle was taken into consideration. Thus, the representation at the mesio-ventral cortical surface was determined by drawing a line normal to the cortical surface and passing through the recording site. Examples of results obtained in three such experiments are shown in figure 4 which include the receptive fields observed at different depths in five penetrations along the mesial border of V_I. Analysis of this figure revealed that recording sites in the ventromesial portion of the cortical surface were related to receptive fields located at the far periphery of the temporal visual field.

Extension of binocular representation

Five rows of penetrations carried out in four different experiments depicted in figure 3 illustrate the extent of cortical representation of the binocular field. For each recording site the eyes were independently centered in the campimetric system and the corresponding receptive fields determined. This procedure compensated for the discrepancy in the localization of the receptive fields of each eye due to interpupillary distance. Under these conditions there was, within the limits of the method, an overlap of the centers of the contralateral and ipsilateral receptive fields. The results indicated that, under neuromuscular block the nasal far periphery of the uniocular fields is obstructed by the bridge of the rhinarium. Thus the extent of its binocular field is limited by extraocular structures and not by the partial decussation of optic fibers at the chiasm. The binocular field covers an extension of approximately 100° at the level of the horizontal meridian, being restricted at the lower visual field by the rhinarium.

Vertical and horizontal meridians

The decussation line or vertical meridian (VM) is represented along the lateral border of V_I, as shown by points 1 to 9 in figure 5. Electrical activity was recorded from a series of points along this border and the centers of their receptive fields determined. From these results it also became clear that the cortical representation of the vertical meridian extends approximately 60° above and below the center of gaze.
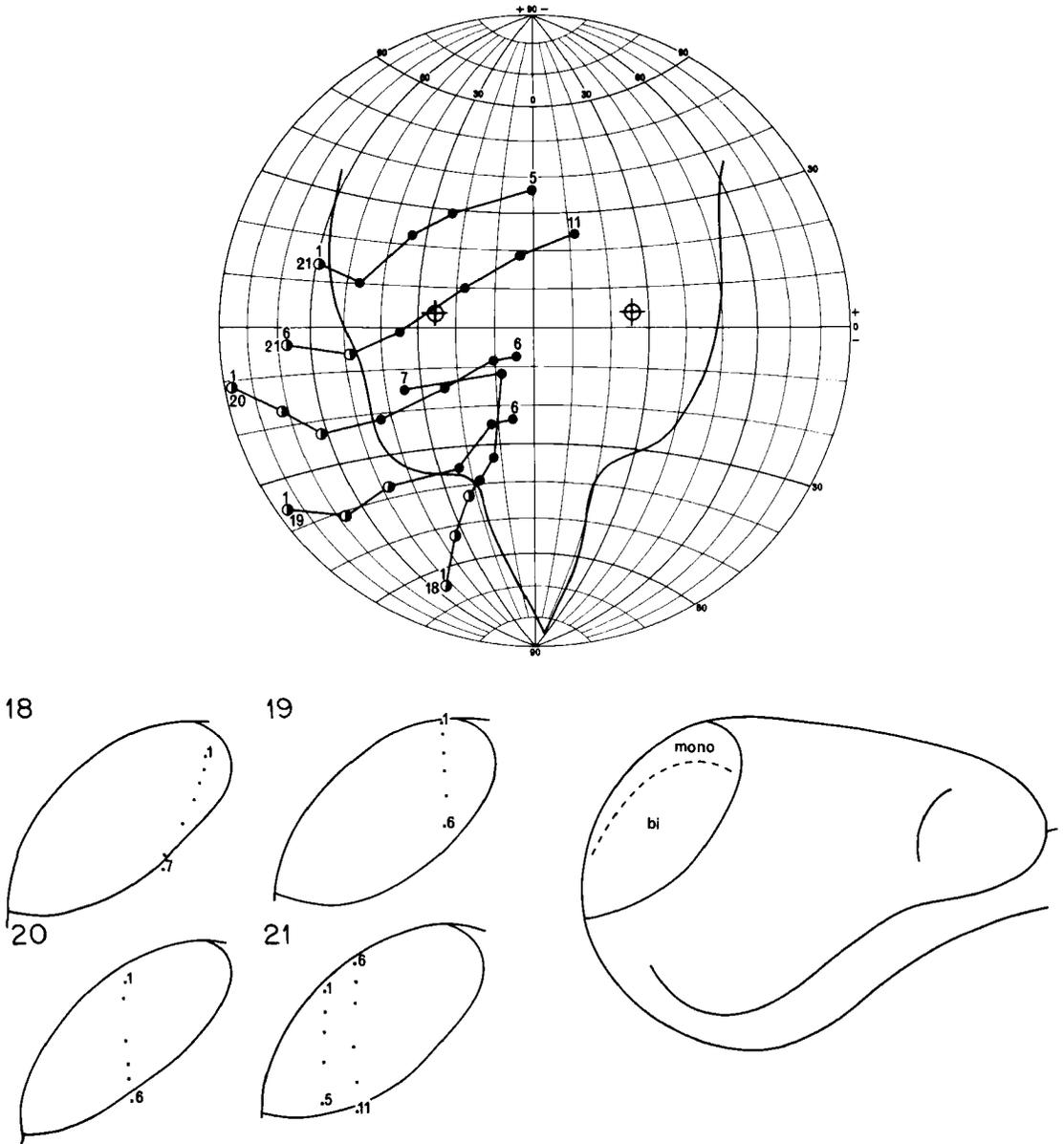
Fig. 3 Extension of monocular and binocular representation in V_I. The center of receptive fields obtained in five rows of penetrations in four different animals are indicated. Filled circles indicate receptive fields activated by binocular stimulation, while those partially filled indicate fields activated only by contralateral stimulation. Position of the blind spots, indicated here and in other figures by crossed circles, correspond to the average of the four animals. The nasal limit of the ipsilateral visual field, represented by a continuous line on the left half of the hemisphere is the average of the four animals. In the lower half of the figure the position of the recording sites, in four experiments, are indicated in 45° views of striate area. The approximate extent of binocular representation in the striate area is indicated by a dashed line in the schematic view of the opossum's brain.

The representation of the vertical meridian does not occur along the whole extent of the lateral border of V_I. Activity recorded in penetrations along the mesio rostral border of V_I, beyond point 9 of figure 5, does not correspond to receptive fields located along the vertical meridian. The receptive fields obtained for penetrations carried out along the antero-me-
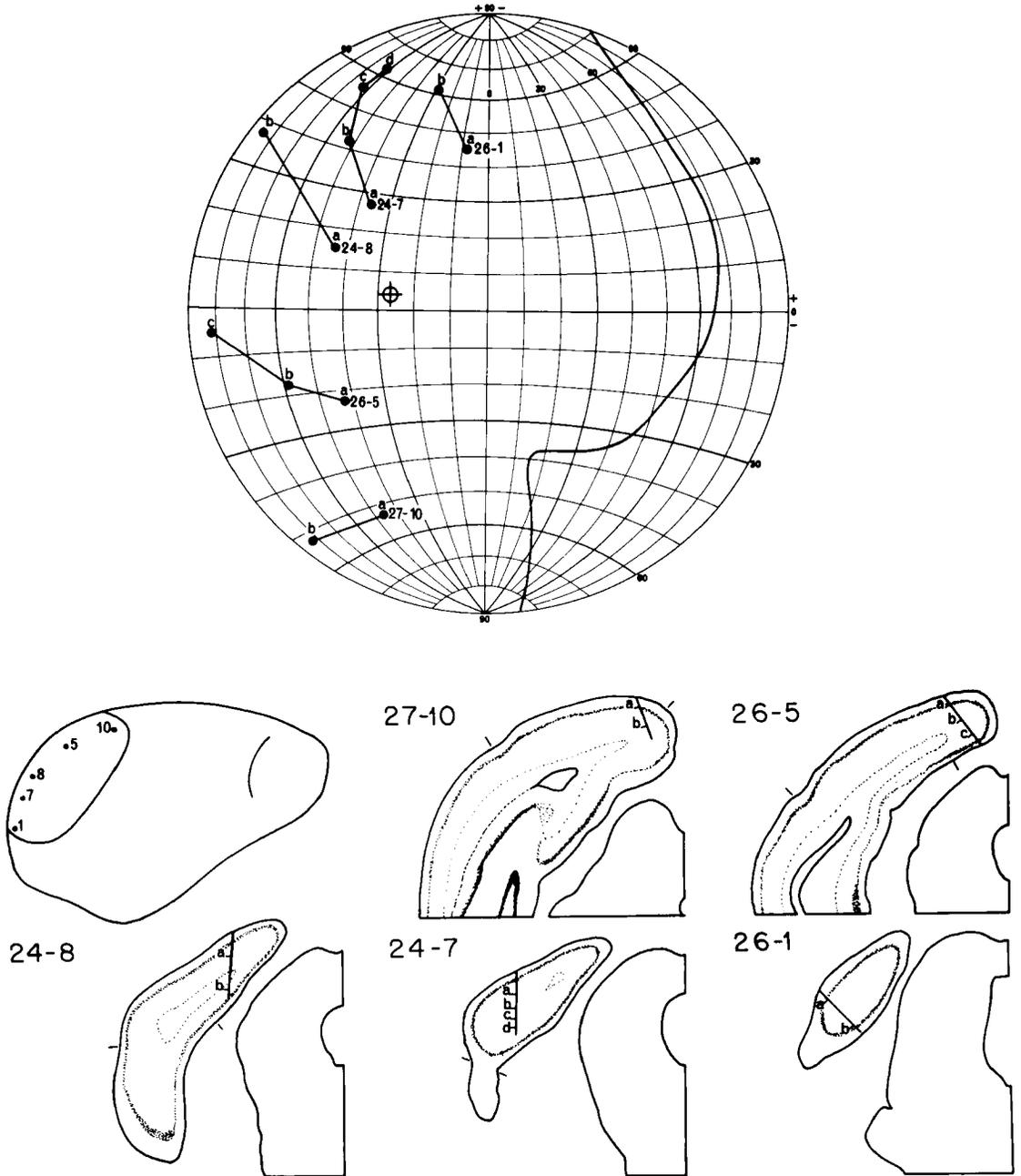
Fig. 4   Receptive fields at different depths along the mesial border of V_I. The upper part of the figure shows the center of receptive fields observed at different depths in five penetrations along the mesial border of V_I, obtained in three different animals. Penetration tracks are shown in the schematic drawings in the lower portion of the figure. The recording sites are indicated by small letters along the tracks. The position of the blind spot and the portion of the visual field obstructed by the rhinarium correspond to the average positions in the three animals. Small bars, normal to the pial surface indicate the borders of striate area.
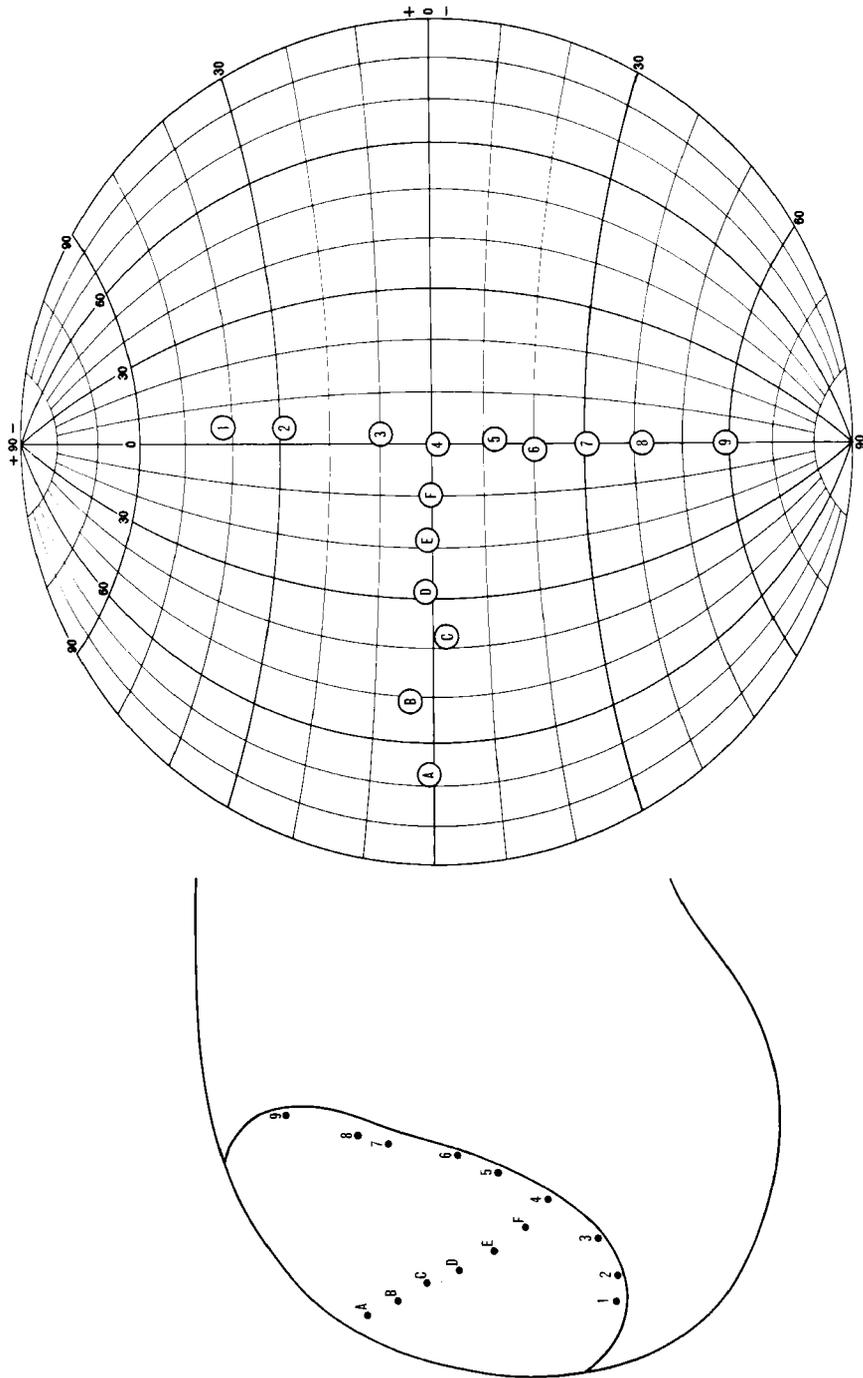
Fig. 5 Representation of the horizontal and vertical meridians. Localization in the cortical surface of recording sites corresponding to receptive fields located along the decussation line, indicated by numbers, and along the horizontal meridian, indicated by letters. This figure is a synthesis of results obtained in three animals.

dial border of V_1 show a gradual displacement towards the temporal visual field, indicating that the lower most parallel of the visual field is represented at the antero-medial border of striate area. A similar transition of representation was also found in the latero-caudal border of V_1, in the region of projection of the upper limit of the visual field.

Occasionally receptive fields extending beyond the VM were observed (see receptive field 21-11 in figure 3), suggesting the presence of a 10° wide strip in the visual field which projects to both hemispheres and lies along the retinal decussation line.

The approximate localization of the cortical representation of the horizontal meridian (HM) is illustrated in figure 5 by the position of recording sites 4 and A to F, since the centers of their corresponding receptive fields were located within 6° of this reference line. Figure 5 also shows that the center of gaze, which corresponds to the intersection of the vertical and horizontal meridians, is located in the caudal third of V_1. Also, the portion of the horizontal meridian lying on the dorsal surface of the striate area is concerned with the representation of 70° of visual space, starting from the line of decussation. Recording from the ventral surface of the cortex indicated that a total of approximately 110° of visual space is represented along the horizontal meridian.

Magnification factor

The cortical magnification factor was defined by Daniel and Whitteridge ('61) as an expression relating the linear extension of cortical tissue, expressed in millimeters, with the representation of 1° of visual field. We adopted the reverse relation, degrees of visual field per millimeter of cortex, as suggested by Talbot and Marshall ('41) due to the small dimension of V_1 in the opossum. This relation was calculated from data obtained in 73 penetrations. The distance separating the recording sites was determined by trigonometry and correlated with the angular separation between the center of the corresponding receptive fields. The lowest value, of the order of 7°/mm, was observed at the cortical representation of the center of gaze. Along the HM, in a region 60° from the center of gaze values of the order of 20°/mm were obtained, while values of 30°/mm were found at the extreme periphery. A comparable decrease of cortical representation is also observed as one moves

from the center of gaze towards the upper or lower limits of the visual fields.

A map of the visual field in V_1

Due to the large number of recording sites necessary to establish a detailed topography of the visual projections in V_1 it was not possible to make a complete exploration of the primary visual area in a single experiment.

Figure 6 is a cartographic representation of the visual field in the dorsal (A) and ventral (B) surfaces of striate area, based on approximately 220 points obtained in a total of 22 experiments. For each experiment the positions of the penetrations were projected to a horizontal plane as well as to a plane making a 45° angle with the midline. By means of the proportional coordinate system suggested by Walsh and Ebner ('70) these positions were transposed to a dorsal and to a dorsolateral view of a standard striate area. The limits of the standard striate area were determined using the proportional coordinate system, based on a brain with a hemisphere length of 19.7 mm. This figure represents a projection of the striate area on a plane making an angle of 45° with the sagittal plane. The lower visual field, extending to parallel −60° is represented in the anterior portion of the primary visual area. In the posterolateral portion of this area the VM is related to the first 45° of the upper visual field; the upper extreme of the visual field being represented in the posteroventral surface of V_1 as shown in figure 6B. The central portion of the visual field has a more extensive cortical representation when compared with the peripheral representation.

DISCUSSION

In recent years an increasing number of publications, using both the North and South American opossum have appeared in the literature (Johnson, '77). Correlation of results obtained in both sub-species depend on the demonstration that they are alike from the point of view of neural organization. Although recent evidences, based on the chromosomal pattern of New World marsupials (Gardner, '73 in Jurgelski, '74) suggest that the North American opossum, *D. marsupialis virginiana* and the South American variety are members of two distinct species, the cytoarchitectonic organization of subcortical nuclei (Oswaldo-Cruz and Rocha-Miranda, '68) as well as of cortical areas (Sousa, '75) were shown to be alike in both forms. Surface reconstructions of
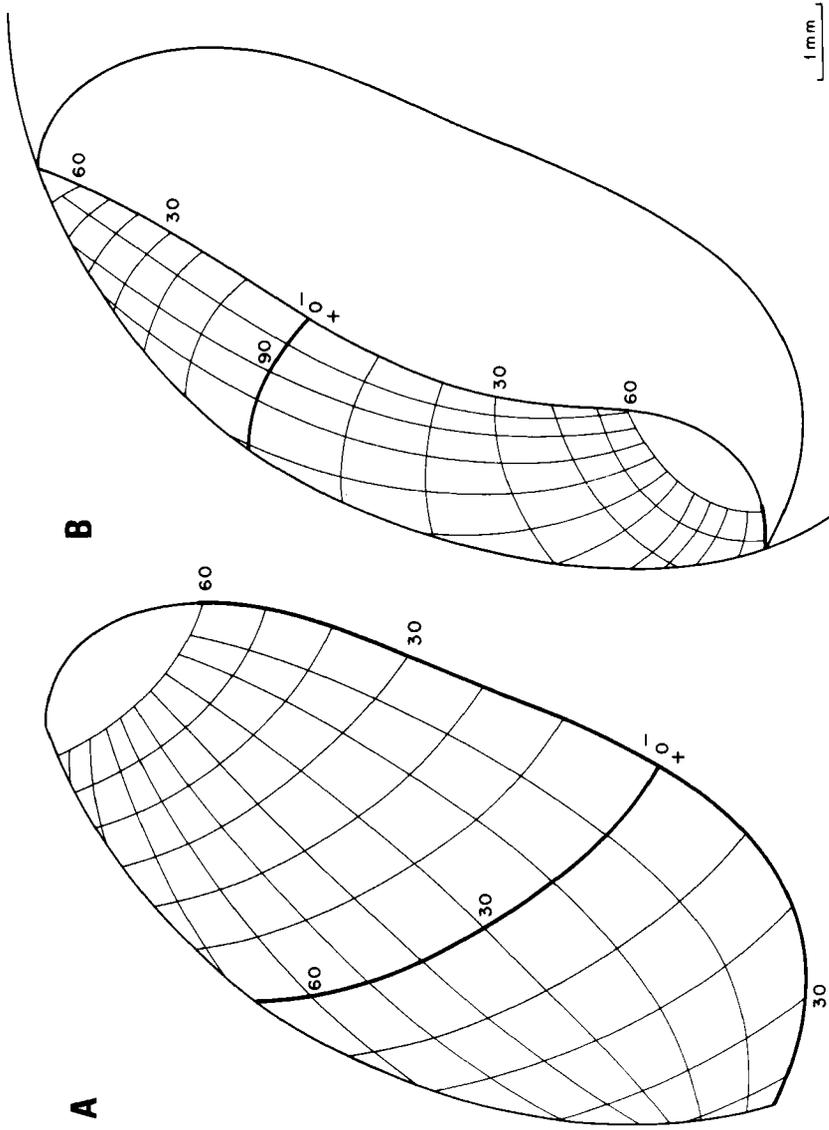
Fig. 6 Topography of projections of the visual field in V_I. A, dorsolateral view; B, ventral surface, as viewed from the same angle. Parallels and meridians are drawn at 10° intervals, the horizontal and vertical meridians being represented by a heavier line.

cortical areas carried out in both the North American (Ebner and Walsh, personal communication) and South American sub-species (Sousa, '75) indicate that the proportional coordinate system developed by Ebner and Walsh (personal communication) is applicable to both forms.

Cortical cytoarchitectonics of striate and peristriate areas in the North and South American opossums were shown to be identical; in addition, it was shown that the striate area can also be characterized by the presence of radially oriented fiber bundles, at the level of layer IV. The difference in the myeloarchitectonic pattern between striate and peristriate areas probably reflects the larger diameter of the specific thalamo-cortical projections, as shown in the mouse by Ramon y Cajal ('55) and in the hedgehog by Kaas et al. ('70). The possibility of delimitating the striate area based on myeloarchitectonic grounds has already been reported in other species, such as the cat (Hubel and Wiesel, '65) the hedgehog (Hall and Diamond, '68), the squirrel (Hall et al., '71, Kaas et al., '72a) and the tree shrew (Diamond et al., '70).

The thickness of striate area in the opossum is not uniform in its whole extent, attaining its maximum development at its lateral border, a fact which possibly reflects the greater density of innervation corresponding to the region of representation of central vision. A similar variation between central and peripheral density of innervation was also reported by Hokoç and Oswaldo-Cruz ('78), at retinal levels, in this species.

This variation in thickness can also be attributed to the representation of binocular vision; however in the opossum the structural differences between the binocular and uniocular regions of representation are not as marked as those reported in other species (Hall et al., '71; Kaas et al., '72a,b); the transition being indicated by a sudden increase in the taper observed in layer IV, as well as by a decrease in total cortical thickness.

The extension of cortical surface activated by global photic stimulation was similar to that described by Lende ('63) in his study of the cortical sensory projection areas in the North American subspecies. The waveform of the primary visual response, as observed for other species (Doty, '58; Cowey, '64), present a higher degree of complexity than that evoked on the peristriate areas. Responses recorded outside the borders of the primary visual area

present, as a rule, higher amplitude and simpler waveform; similar findings being also reported in the cat (Doty, '58) and rat (Adams and Forrester, '68). This difference in response pattern could be attributed to the fact that activation of the peristriate area is probably carried out by means of cortico-cortical connections linking the striate and peristriate areas. These connections have been shown in various species by anatomical (Montero et al., '73a) as well as electrophysiological methods (Cowey, '64). In the opossum Benevento and Ebner ('71) have shown that the peristriate areas receive ipsi- and contralateral projections from the striate area. In addition the peristriate areas receive projections from the latero-posterior thalamic nuclei (Bodian, '42). Evoked responses, showing complex waveform were recorded from a region coincident with the striate area, as defined on cytoarchitectonic grounds. A sharp transition in the response waveform was observed at the level of the lateral border of the striate area, indicating a good correlation between the two methods.

Similar results were obtained at the transition between visual and auditory areas; activity evoked by clicks and flashes, recorded from closely spaced cortical points permitted the establishment of the mesial border of the temporal area. The results obtained by this method are in close agreement with the cytoarchitectonic borders of the temporal area in this animal.

Thus, in spite of the limitations introduced by electrotonic spread in a volume conductor, the cortical surface evoked response is a useful tool for the delimitation of functionally distinct areas, the resolution achieved by this method being better than one millimeter. Thus even allowing for the electrotonic spread of the large amplitude responses recorded in the antero-lateral region of the peristriate area, it was shown that the cortical surface activated by visual stimuli extends beyond the rostral limits of the anterior peristriate area, as defined by Benevento and Ebner ('71). Visual responses outside the limits of striate and peristriate areas have also been reported in various species: in the so-called "poly-sensory" or "association" areas of carnivores (Albe-Fessard and Besson, '73), and edentata (Meulders et al., '66) and also at the medio- and infero-temporal areas of primates (Allman and Kaas, '71; Allman et al., '73; Gross et al., '72). On the other hand the absence of

visual responses in the postero-lateral peri-striate area of the opossum, a region receiving cortical afferents from other visual areas, may reflect more rigid requirements of the trigger features of its neurons not present in the simple types of stimuli used in this experimental series, or a greater susceptibility to the anesthetic agent employed.

Although surface recorded evoked responses can be used to determine the topography of sensory projections, the use of microelectrodes for recording the activity of small clusters of neurons was shown to be of great advantage for the detailed analysis of the topography of projections in the central nervous system (Daniel and Whitteridge, '61; Welker, '71).

In general the size of multi-unit receptive fields in the primary visual cortex of the opossum does not differ from that described under similar experimental conditions in the visual areas of eutherian mammals. Taking into consideration the area of single unit receptive fields (Rocha-Miranda et al., '76), one may suggest that the extent of multi-unit receptive fields reflects the average size of the receptive fields of the isolated units which comprise the population under study. Thus, as described for single units, the area of the receptive fields is a function of its retinal eccentricity, smaller receptive fields being observed at the center of gaze. This finding indicated that the cortical representation of the visual field in this species is not homogeneous, the center of gaze being represented with a finer grain. A preferential representation of the center of gaze is also supported by the findings of Hokoç and Oswaldo-Cruz ('78) which showed that retinal ganglion cell density at the level of intersection between the vertical and horizontal meridians is five times higher than at the periphery. Commenting on the paper by Whitteridge and Daniel ('61) Glees compared the retina to a photographic plate with a grain which varies from one region to the other: the central region, with a finer grain permitting a greater enlargement of its representation. The "cortical enlargement" is apparently adjusted in such a way as to represent with the most effective resolution the various regions of the visual field. All these parameters are intimately related to the cortical magnification factor, which will be considered in more details later.

In the course of a penetration normal to the cortical surface, variations in the magnitude of the responses as well as in the temporal pattern of discharge could be observed. Also visual activity was always obtained with maximum amplitude in response to stimuli presented for the same region of the visual field. This may indicate the existence of a radial arrangement of cortical elements, similar to the columnar organization described in higher mammals. However, as already stressed by Hughes ('71), a true columnar organization requires uniformity of other functional criteria, in addition to the constancy in spacial location. In single unit studies Rocha-Miranda et al. ('76) did not investigate this aspect of functional organization in the visual cortex of the opossum.

The primary visual area of the opossum, as in all mammals so far studied, can be defined by a single orderly representation of the visual field. A region of the visual field covering approximately 10° around the line of decussation projects to both hemispheres; similar findings have also been reported for other species. The extent of bilateral representation varies from approximately 2° in the cat (Leicester, '68) to 20° in the mouse (Dräger, '75) and in the hamster (Tiao and Blakemore, '76b). This bilateral representation could be attributed to a projection of a vertical strip of retina to each lateral geniculate body, as shown in the cat by Stone ('66), as well as to interhemispheric connections. An interesting finding is that the extent of the VM representation along the lateral border of striate area, closely coincides with the zone showing the greatest density of intercortical connections (Benevento and Ebner, '71).

We were surprised with the extent of the binocular field in the opossum which, at the level of the HM covers an angle of 110° degrees, larger than that found in the cat (Hughes, '76). As a consequence a greater proportion of the cortical primary visual area is devoted to the binocular representation of the visual field. In a single unit analysis of the visual cortex of the opossum Rocha-Miranda et al. ('76) found that of a group of units tested for ocular dominance 85% were binocularly driven. Although the opossum's interpupillary distance (circa 25 mm) is smaller than that of the cat and of the monkey, large angular disparities would result when the animal is visually exploring its immediate surroundings. Compensatory vergent movements of the eyes are certainly possible, for this species possesses fairly well developed extra-ocular musculature, with a pattern of insertion simi-

lar to that observed in higher mammals (Oswaldo-Cruz et al., '77). The existence of units activated by disparity in the receptive fields has not been demonstrated in the opossum, however, we believe that the above mentioned findings favor the existence of true stereoscopic vision in this animal. Stereoscopic vision would probably be of great functional significance for coping with the 3-dimensional complexities of its arboreal habitat.

Values obtained for the cortical magnification factor at the region of representation of the center of gaze, in the opossum, are lower than those observed in monkeys (Daniel and Whitteridge, '61) and in the cat (Bilge et al., '67). They are, however, of the same order of magnitude of those reported for the hamster (Tiao and Blakemore, '76b), rat (Adams and Forrester, '68) and mouse (Dräger, '75). When correlating cortical magnification factor with eccentricity the results obtained are not as clear as those reported in the monkey (Daniel and Whitteridge, '61). They show a larger scatter, similar to that found in the hamster (Tiao and Blakemore, '76b). Nevertheless, it is evident that there is a disproportionate representation of the center of gaze at the expenses of the periphery of the visual field. This predominance of central representation is confirmed by the presence of a region of increased ganglion cell density which corresponds to the center of gaze, as shown by Hokoç and Oswaldo-Cruz ('78), in flat mounted opossum retinas.

The existence of multiple representation of the visual field at the cortical level has been demonstrated in a wide variety of mammals, ranging from insectivores to primates. The common feature in all species so far studied is the coincidence of the V_I-V_{II} border with the representation of the line of decussation, and the mirror-like reversal of the topological organization observed in these two areas. In a study of the cortical visual areas in the hedgehog Kaas et al., ('70) reported a single reversal in the representation of the visual field, which corresponds to visual areas I and II, in this primitive mammal. In the opossum a similar reversal of representation was also observed. Although a systematic search for other representations of the visual field was not carried out, the presence of two cytoarchitectonically distinct peristriate areas, such as described by Benevento and Ebner ('71), may suggest the existence of an area homologous to V_{III} described in other mammals. In the mesial border V_I is contiguous with the medial peristriate area, which, as defined by Benevento and Ebner ('71), receives projections arising from other visual areas. The medial peristriate area could be considered homologous to area 18a reported in the cat by Kalia and Whitteridge ('73), in the mouse by Dräger ('75) and in the hamster by Tiao and Blakemore ('76b). By means of gross photic stimulation visually evoked activity was also observed in the region corresponding to the anterior peristriate area defined by Benevento and Ebner ('71). However a detailed study of the topography of projections in this area was not carried out. Nevertheless we may tentatively suggest that this area may be equivalent to the vision projections observed in the parietotemporal region of higher mammals. Other evidences are needed in order to affirm that the opossum, although a primitive mammal, presents the same general characteristics of cortical organization of the visual areas as higher mammals.

The performance of the visual system of a given species is determined by several factors. Some of these are determined by the characteristics of peripheral elements of the visual system, such as: the optics of the eye; type, dimension, number and distribution of receptors; intrinsic retinal synaptic organization and total number and fiber spectrum of the optic nerve. Others depend upon the central organization of the visual information processing system.

In order to make an interspecies comparison data relative to some of these determinant factors were gathered, and the information obtained is summarized in table 1.

At this time we may profitably discuss some of the data previously presented. The primary visual area in the level of representation of the horizontal meridian, varies from 1.4 mm near the representation of the vertical meridian, to 1.3 mm at the limit of the region of binocular representation. Cortical neuronal density was estimated to be of the order of 44.5 × 10^3 neurons/mm^3, based on the fact that neuronal density can be correlated to body weight in non-primate species (Cragg, '67). Cortical magnification factor is of the order of 7°/mm at the center of gaze and 20°/mm for the meridian 60° temporal to the center of gaze.

Using these figures it is possible to determine the extension of cortical surface corresponding to one degree [2] of the visual field. The value obtained, multiplied by the corre-

TABLE 1

Species	Region	Area 17 surface (mm²)	Area 17 thickness (mm)	Area 17 neurons/mm³	Cortical magnification mm²/sq deg	Cortical neurons/ sq deg	Ganglion cell/ sq deg	Acuity
Macaca (M)	Center	1,320	2.0	113 × 10³	30.0	6,780,000	3,250	0.67'
	Periphery				0.1	22,000	100	
Saimiri (S)	Center	720	2.0	113 × 10³	26.0	5,814,000	3,000	0.74'
	Periphery				0.1	22,000	100	
Cat (C)	Center	320	1.8	42 × 10³	4.0	300,000	300	5.5'
	Periphery				0.03	2,300	24	
Rabbit (R)	Center	80	1.8	44× 10³	0.1	8,000	125	17'
	Periphery		1.5		0.02	1,300	150	
Opossum (O)	Center	55	1.4	44.5 × 10³	0.02	1,271	31	11'-10.8'
	Periphery		1.3		0.002	116	4.4	
Rat (Rt)	Center	15	1.5	45 × 10³	0.002	140	24	25'
Hamster (H)	Center	13	1.1	45 × 10³	0.014	713	11	18'
Mouse (Mo)	Center	3	.9	92 × 10³	0.002	141	10	19'

Explanatory text to table 1

Information relative to the opossum included in this table is mainly derived from our experimental work; the surface of area 17 was calculated based on drawings supplied by Ebner and Walsh. Information for other species has been taken from figures quoted in text or measured from diagrams, and from data previously analysed by Hughes ('71). Figures quoted for central vision correspond to the center of gaze, i.e., to the fovea, *area centralis* or to the temporal portion of the visual streak. Values quoted for the periphery correspond to a region 60° temporal to the center of gaze.

1. *Surface of area 17.* (M) Daniel and Whitteridge, '61; Rolls and Cowey, '70. (S) Rolls and Cowey, '70. (C) Tusa, '75, (R) Hughes, '71. (O) Ebner and Walsh, personal communication. (H) Tiao and Blakemore, '76b. (Rt) Montero et al., '73b. (Mo) Dräger, '75.

2. *Area 17 thickness.* (*values corrected for shrinkage). (M)* Hubel and Wiesel, '68. (S) Rolls and Cowey, '70. (C)* Hubel and Wiesel, '65. (R)* Hughes, '71. (O)* Oswaldo-Cruz and Rocha-Miranda, '68. (H) Smith and Bodemer, '63. (Rt) Adams and Forrester, '68. (Mo) Woolsey, '67.

3. *Neuron density in area 17.* (M), (C), (R), (Rt) and (Mo) Cragg, '67, absolute values corrected for shrinkage. (S) Rolls and Cowey, '70. (O), (H) values based on arguments presented by Cragg, '67.

4. *Cortical magnification mm²/sq deg.* (M) Daniel and Whitteridge, '61; Rolls and Cowey, '70. (S) Rolls and Cowey, '70. (C) Bilge et al., '63; Hughes, '71. (R) Hughes, '71. (O) this paper. (H) Tiao and Blakemore, '76b. (Rt) Adams and Forrester, '68. (Mo) Dräger, '75.

5. *Cortical neurons/sq deg of visual field.* Figures calculated from data in columns 2, 3 and 4.

6. *Ganglion cell count/sq deg.* (M), (S) Rolls and Cowey, '70. (C) Hughes, '76. (R) Hughes, '71. (O) Hokoç and Oswaldo-Cruz, manuscript in preparation, and this paper. (H) Tiao and Blakemore, '76a. (Rt) Hughes, '71. (Mo) unpublished observations from this laboratory, results from counts in flat mounted retinas.

7. *Acuity.* (M), (S) Rolls and Cowey, '70. (C) Blake et al., '74. (R) Hughes, '71. (O) 11'-Duke Elder, '58; 10.8'-this paper.* (Rt) Lashley, '32. (H) Tiao and Blakemore, '76a.* (Mo) this laboratory, unpublished results.*

(*—based on Shannon's sampling theorem).

sponding cortical thickness and the neuronal density gives the number of cortical neurons activated by a one-degree² stimulus. Thus a one-degree² stimulus presented at the center of gaze will activate 1,271 cells in the region of representation of the center of gaze in V_I of the opossum. In the macaque a stimulus with the same dimension and positioned at the center of gaze will activate approximately 7 × 10⁶ cortical neurons; while in the rat such stimulus would activate only 140 neurons, as shown in table 1.

An important factor in evaluating the visual performance of an animal is the determination of the resolving power of the system. In the absence of behavioral data, visual acuity in the opossum was estimated using Shannon's sampling theory.

In other species results obtained by this method are in close agreement with those ob-

tained using behavioral and electrophysiological techniques.

Retinal ganglion cell density at the center of gaze is of the order of 3,950 cells/mm² (Hokoç and Oswaldo-Cruz, '78). The image of a one-degree stimulus in the retina corresponds to a linear extension of 89 μm (Oswaldo-Cruz et al., '77). Thus a one-degree² stimulus will fall upon 31 ganglion cells and a linear stimulus measuring 1° will impinge upon $\sqrt{31}$ cells. We may thus estimate the visual acuity of the opossum applying Shannon's sampling theorem. According to this theorem the sampling density of a system is double the maximum frequency that a system can transmit. Thus the estimated cut-off frequency for the opossum is $\sqrt{31}/2$ = 2.8 cycles/degree, which corresponds to a grating with a minimum resolvable bar width of 10.8'.

When comparing this value with those ob-

tained for other species it becomes evident that the opossum has a visual acuity inferior to that of the monkey and cat, but comparable to that of the rabbit and of the hamster.

ACKNOWLEDGMENTS

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