

glycogen levels drop during winter and early spring, the highest levels being attained by fall⁹.

During dormancy, the loss of certain ions, as observed in *Strophocheilus*, may be explained at least in part, as due to elimination with faeces and urine right at the beginning of estivation or hibernation; it is also possible that some ions may be lost with the mucus produced by the animals, as noticed by DEXHEIMER¹⁰ in relation to calcium incorporated in the mucus produced by *Helix*.

Résumé. Pendant l'hibernation, le *Strophocheilus* (Pulmoné, Mollusque) perd de l'eau, du sodium, du calcium, du magnésium, du soufre, du cuivre, du fer et des carbohydrates totaux, mais son taux de potassium et d'iode augmente. En état d'estivation, il y en a perte

d'eau, de sodium, de magnésium, de cuivre, de fer et de carbohydrates totaux, mais accumulation de calcium.

F. B. DE JORGE, J. A. PETERSEN
and A. S. F. DITADI

*Department of General and Animal Physiology,
Faculty of Philosophy, Sciences and Letters
and Department of Physiology,
School of Medicine, University of São Paulo
C.P. 6868, São Paulo (Brazil), 13 March 1969.*

⁹ O. W. THIELE, Z. vergl. Physiol. 42, 484 (1959).

¹⁰ L. DEXHEIMER, Zool. Jahrb. Neapel 63, 129 (1951).

Receptive Fields of Single Cells of a Marsupial Visual Cortex of *Didelphis virginiana*

Investigations of mammalian visual cortices have revealed a wide variety of response properties, ranging from the rather limited repertoire of the rabbit^{1,2} to the relatively sophisticated or at least selective discriminations found for cat³ and monkey⁴. These species, however, are all placental mammals. The marsupial or pouch-bearing mammals, on the other hand, offer a more primitive neocortex, even to the absence of a corpus callosum. How, then, have the sensory discrimination properties of this parallel, but more slowly evolving mammalian visual cortex developed?

Materials and methods. To explore this question, the receptive field and associated response properties of 100 single cells from the visual cortex of *Didelphis virginiana*, the American opossum, were studied. During testing, the animals, 12 young adults, were maintained under light urethane anesthesia in a stereotaxic frame. The pupils were dilated and the corneas were fitted with corrective contact lenses.

An aperture made directly over the left posterior pole of the cortex and resealed with 4% agar gel, gave passage to stainless steel or tungsten microelectrodes (1–40 mΩ) used to record from and to mark single cell response sites. These sites (all in layer IV or shallower) were later localized histologically.

The receptive field of each cell was mapped using a 1°, 85 candle/m² spot against a 3.5 candle/m² background. Response to additional visual stimuli, diffuse and discrete, light and shadow and of various edge geometries and areas were also measured.

Results and discussion. The receptive fields of 99 of the 100 cell samples studied here could be categorized into 3 geometric classes: (1) 'on' fields; those responding throughout their extent only to the onset of light; (2) 'off' fields; those responding throughout their extent only to the cessation of light; and (3) 'on-off' fields; those

responding throughout their extent to both onset and cessation of light. The remaining cell responded only to moving dark edges, uniformly in all directions, but could not be plotted by the flashing stimulus method used for the others. The frequency distribution of these classes, together with their diameters and eccentricities from the reference axis, appear in Table I. The Figure shows the distribution of these classes when projected into visual space relative to the optic nerve head center. No significant relationship was found for any of the groups between receptive field diameter and eccentricity from the reference axis in any meridian, nor were significant differences of field geometry or general response properties between cells of the upper tapetized and lower non-tapetized retina evident.

Among the unique characteristics of this cortical receptive field population was the absence of mutually inhibiting response zones within a given receptive field. Neither the concentric organization, as occurs in the rabbit visual cortex¹, nor the linear division of zones, as in the 'simple' fields reported by HUBEL and WIESEL^{3,4} for the cat and monkey visual cortices were found. The presence of antagonistic zones within these fields was tested by comparing local field responses under different retinal adaptation states and by stimulating the periphery of the field while saturating the field center. In all cases the homogeneity of response throughout these fields remained. In addition, area-response determinations showed only simple summation, i.e. as stimulus area was in-

¹ G. B. ARDEN, H. IKEDA and R. M. HILL, Nature 214, 909 (1967).

² A. HUGHES, J. Physiol. 198, 120 (1968).

³ D. H. HUBEL and T. N. WIESEL, J. Physiol. 160, 106 (1962).

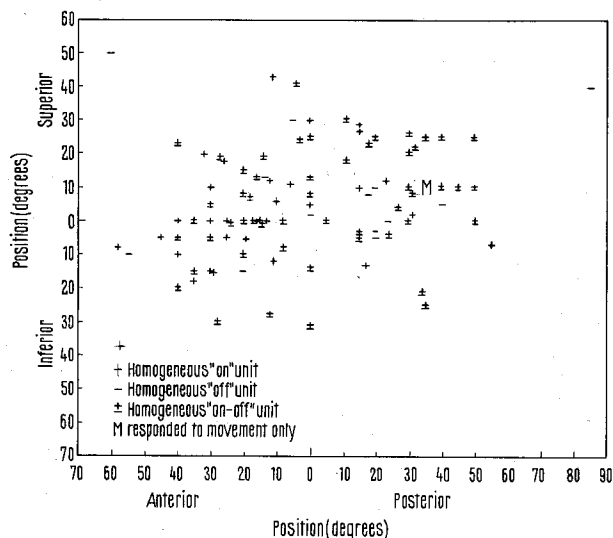
⁴ D. H. HUBEL and T. N. WIESEL, J. Physiol. 195, 215 (1968).

Table I. Distribution of photically responding cells of a marsupial (*D. virginiana*) visual cortex by receptive field geometry

Receptive field type	No.	%	Mean diameter	Standard deviation	Range	Mean eccentricities	Standard deviation	Range
On	31	31	20.16°	8.74°	5°–44°	29.24°	12.81°	5°–45°
Off	15	15	19.87°	9.26°	4°–40°	32.93°	23.83°	2°–94°
On-Off	53	53	17.75°	8.73°	5°–50°	29.28°	12.31°	5°–56°
Unclassed	1	1						
	100							

creased the number of spikes resulting per stimulus increased regularly to the field boundary as well, further supporting the absence of mutually inhibitory internal zones.

Table II shows the distributions of cells which could be stimulated by either retina or just one. The relative dominance, i.e. the eye requiring the minimum stimulation to give a response, is also shown. The contralateral predominance among the monocularly driven cells would be expected based on the high percentage of optic nerve fibers (about 80%) crossing at the optic chiasm. The grouping of cells of the same dominance seen successively within a single penetration suggests a vertical columnar organization similar, for example, to the columnar



Distribution in visual space of receptive fields of cells of the visual cortex of the marsupial *D. virginiana*.

Table II. Distributions of monocularly and binocularly responding cells from a marsupial (*D. virginiana*) visual cortex by receptive field geometry and dominance

	Monocular cells		Binocular cells		
	Right eye only ^a	Left eye only ^b	Right eye dominant ^a	Left eye dominant ^b	Equal
On	12	2	3	5	9
Off	11	2	—	1	1
On-Off	28	6	5	4	10
Unclassed	1				

^a Contralateral eye. ^b Ipsilateral eye.

organization found for orientation of simple fields of cells of the cat cortex⁵. Summation between the 2 monocular field of a single cell, when stimulated simultaneously, could be seen as well.

Comparing the cortical visual response repertoire of this animal with that of his superior colliculus⁶, more differences than similarities are noted; e.g. (1) the presence of 3 basic geometrical field organizations at the cortex compared with 8 or more at the mesencephalic level; (2) the virtual absence of mutual inhibitory zones within a cortical receptive field; although similar homogeneous fields were found for some cells of the superior colliculus, many concentric, as well as asymmetric, antagonistic zones were found too; (3) the higher number of binocularly driven cells found at the cortical level, often with additive, i.e. right plus left eye summation characteristics; such binocular summation was less readily demonstrated at the mesencephalic level; (4) short-term habituation to repetitive stimulation was much more common at the collicular level⁷. In terms of similarity, however, cells at both the cortical and midbrain levels were seldom found selective to meridional or direction characteristics of the stimulus; cells at both levels, on the other hand, frequently demonstrated discrete ranges of velocity response and often had optimum velocities for maximum excitation.

This marsupial visual cortex then appears to offer in primitive, or at least early, form a wide variety of geometric and response properties found in more sophisticated stages of development among the higher placental mammals, suggesting this neo-cortex as an unique neurophysiological, anatomical model of inter-order, as well as synaptic level, development among the mammals⁸.

Zusammenfassung. Etwa 40% von 100 Zellen vom visuellen Kortex des Beuteltieres *Didelphis virginiana* konnten entweder von der rechten oder linken Retina gereizt werden. In der Regel war eine Retina dominant. Areale Summation innerhalb und zwischen den monokulären Feldern war vorhanden, obschon gegenseitige Hemmung innerhalb eines rezeptiven Feldes nicht beobachtet wurde.

J. L. CHRISTENSEN and R. M. HILL

Physiology Laboratory, College of Optometry,
The Ohio State University,
Columbus (Ohio 43210, USA), 21 August 1969.

⁵ D. H. HUBEL and T. N. WIESEL, *J. Neurophysiol.* 28, 231 (1965).

⁶ R. M. HILL, *Experientia* 24, 559 (1968).

⁷ G. HORN and R. M. HILL, *Expl. Neurol.* 14, 199 (1966).

⁸ This work was supported by U.S.P.H.S. Grants Nos. NB 06983 and NB 05416.

Electron Microscopic Observations on the Innervation of the Intestinal Inner Muscle Layer

The inner muscle layer of mammalian small intestine is richly supplied with nerve fibres ('plexus interfasciculaires et plexus terminaux', CAJAL¹). Ultrastructural observations on intramuscular nerve fibres have been provided by RICHARDSON² and TAXI³. It has recently been shown that these include adrenergic nerve fibres: fibres rich in adrenergic-type vesicles⁴ have been detected by electron microscopy⁵; fluorescence microscopy (method of FALCK and HILLARP) has demonstrated the presence

of catecholamine containing fibres⁶. The present paper reports a more detailed analysis of the ultrastructural features of the intramuscular plexus.

For this purpose, samples of small intestine from 4–6-month-old albino rats (*Epimys norvegicus*, var. *albina*, Erxl.) were fixed in 4% glutaraldehyde in 0.1M phosphate buffer (pH 7.4) post-fixed in osmium, dehydrated in alcohol and embedded in Araldite (CIBA). Ultra-thin sections were stained with uranyl acetate and lead citrate,