Discrimination Characteristics of the Turtle's Retinal Ganglion Cells

The functional properties of populations of retinal ganglion cells and their associated neural networks have been studied in mammals[1], amphibia[2,3], birds[4], and teleosts[5], but little is known of ganglion cell behavior in the case of reptiles[6,7]. The present work examined the processing of information at this neuronal level in the eastern box turtle, *Emys blandings*.

A platinum microelectrode detected extracellularly the action potentials from the ganglion cell's axon in the isolated eye cup. Images of light and shadow stimuli in an object plane were projected onto the retina by a lens system. In a total of 22 retinas, 109 cells were tested.

The great majority (91%) of the cells when light adapted responded to reduction of light flux to their receptive fields, produced either by a reduction in the test light's intensity or by encroachment of a dark image onto the receptive field. A smaller proportion of the cells responded to an increase of light flux to their receptive fields; this proportion increasing (to 76%) with dark adaptation. See Table I.

An encroaching dark edge proved to be a generally effective stimulus (i.e., for 93 (97%) of the 96 cells tested, and over a broad adaptation range, 4.6 $\log_{10}$ units). In this population of cells effective velocities of encroachment ranged from 15 μm/sec to greater than 470,000 μm/sec. The effective ranges for individual cells were more limited (e.g. 75 μm/sec to 600 μm/sec) and many cells responded maximally to a particular velocity. For the population these optimal velocities ranged from 75 μm/sec to 2250 μm/sec.

Fifteen cells of 88 tested (17%) responded most strongly to a dark line or dark edge when it encroached from a particular direction. This directional selectivity occurred in 3 patterns. In one (7 cells), the response occurred only for angles within a limited deviation from the preferred direction. In the second (3 cells), the response was absent or markedly reduced for a particular direction of encroachment and increased with deviation from that direction. In the third (5 cells), the response was weak or absent except for movements along a particular meridian, and was stronger for one of the directions along that meridian. In addition, 5 other cells showed this meridional selectivity for a dark edge without any accompanying directional selectivity.

Thirty-six cells responded both to an encroaching light edge and to a dark edge. These included 4 of the cells having directional selectivity and 1 of the cells having only meridional selectivity. A very few cells (5) responded to an encroaching light, but not dark, edge. None of them was directionally or meridionally selective.

Abrupt changes of light intensity, i.e., onset or cessation of either diffuse or local illumination, also proved to be effective stimuli for 100% of the 106 tested cells. The distribution of responses is given in Table I. Many cells (28) also discharged in response to small changes in the level of diffuse illumination. Changes as small as 0.02 $\log_{10}$ intensity were effective.

The receptive fields for response to a moving edge were circular in 72 out of 78 cells measured, the remaining 6 fields being elliptical. The circular field diameters ranged from 75 μm to 450 μm with an average diameter of 206 μm for response to a dark edge (70 cells) and of 186 μm for response to a light edge (24 cells).

Most of the cells were fired by a moving dark line (92 cells) or light line (40 cells) or by both (36 cells). Under conditions of optimal velocity, intensity, and direction for each cell, responses were commonly obtained for dark line widths of less than 40 μm (but more than 12 μm) and for light line widths of 25 μm and less.

When tested by dark and light moving edges or flashes, the type of response (ON, OFF, or ON/OFF) was found to be the same throughout the receptive field of each cell (95 cells) with the exception of 5 cells which evidenced a center-surround organization. See Table II.

Table I. Detection of flashes and moving edges

Stimulus type	Cells responding to diffuse flashes No. tested	 No. responding	Cells responding to localized flashes No. tested	 No. responding	Cells responding to both kinds of flashes No. tested	 No. responding
Flash on	78	59 (76%)	47	30 (64%)	30	15 (50%)
Flash off	95	88 (93%)	67	54 (81%)	65	52 (80%)
Flash on/off	71	46 (65%)	44	24 (55%)	38	20 (53%)

Stimulus type: Encroachment by	All cells responding to movement No.	 % Total pop.	Cells showing only directional selectivity to movement No.	 % Total pop.	Cells showing both directional and meridional selectivity No.	 % Total pop.	Cells showing only meridional selectivity to movement No.	 % Total pop.
Dark edge only	56	58	8	8	11	11	4	4
Dark or light edges	36	37	2	2	4	4	1	1
Light edge only	5	5	0	0	0	0	0	0
No. of cells tested	97	100	10	10	15	15	5	5

---

[1] S. W. KUFFLER, J. Neurophysiol. *16*, 37 (1953).

[2] H. K. HARTLINE, Am. J. Physiol. *121*, 400 (1938).

[3] J. Y. LETTVIN, H. R. MATURANA, W. S. MCCULLOCH and W. H. PITTS, Proc. Instn. Radio Engrs. U.S.A. *47*, 1940 (1959).

[4] H. R. MATURANA, Science *142*, 977 (1963).

[5] H. G. WAGNER, E. F. MACNICHOL JR. and M. L. WOLBARSHT, J. gen. Physiol. *43*, 45 (1960).

[6] R. GRANIT, Acta physiol. scand. *2*, 334 (1941).

[7] T. M. HERIC and L. KRUGER, J. comp. Neurol. *124*, 101 (1965).

Table II. Response properties dependent on sub-unit organizations of the receptive field

Response property	No. cells tested	No. cells responding
Center-surround organization	95	5 (5%)
Directional selectivity[a]	92	18 (20%)
Meridional selectivity[a]	90	10 (11%)
Intermittent movement of:		
Dark edge	30	25 (84%)
Light edge	11	7 (64%)
Response to alternation of dark images displaced relative to each other in the receptive field	3	2 (67%)
Surround inhibition	12	7 (58%)
Difference in receptive field size for spatial vs temporal changes in the stimulus	9	8 (89%)
Difference in spectral sensitivity of center vs surround	1	1 (100%)

[a] To dark edge or light edge or both.

Evidence was found for sub-unit organizations of the receptive field for 51 cells of 99 cells tested. The tests and the proportion of cells found by each test to have these field organizations are given in Table II. The mechanisms of directional selectivity and of response to intermittent movements have been modeled in terms of such sub-unit organization[8,9]. Meridonal selectivity can similarly be modeled by sub-unit mechanisms[10].

In an initial sample of 6 retinal ganglion cells all showed a sharp decrease in spectral sensitivity at short wavelengths in correspondence to the high absorption at those wavelengths by the colored oil droplets of this retina[11].

The ganglion cell population of the turtle's retina shows a broad repertoire of discriminations. The ensembles of discriminations shown by each of the ganglion cells graded into each other rather than falling into distinct, mutually exclusive classes. This array of discriminations would seem to provide a retinal mechanism especially suited for visual detection of moving objects and shadows[12].

Zusammenfassung. Die Reaktionscharakteristiken von Ganglienzellen der Netzhaut eines Reptils (*Emys blandings*) wurden untersucht und dabei festgestellt, dass die Ganglienzellen mannigfaltige Detektionscharakteristiken aufweisen.

L. E. LIPETZ and R. M. HILL[13]

Academic Faculty of Biophysics,
College of Biological Sciences, The Ohio State University,
Columbus (Ohio 43210, USA), 12 November 1969.

[8] H. B. BARLOW, R. M. HILL and W. R. LEVICK, J. Physiol. *173*, 377 (1964).

[9] H. B. BARLOW and W. R. LEVICK, J. Physiol. *178*, 477 (1965).

[10] L. E. LIPETZ and R. M. HILL, in manuscript.

[11] L. E. LIPETZ, unpublished results.

[12] Supported in part by U.S. Public Health Service grants Nos. NB-01408, NB-05416 and NB-06983.

[13] Also, College of Optometry.

Reactivity of Juxtaglomerular Granule Cells to Changes in Sodium and Potassium Intake in the Absence of the Adrenal Bodies

The juxtaglomerular region of the mammalian kidney[1], and probably the granule cells themselves[2], are the source of renin, and the renin-angiotensin system affects the secretion of aldosterone[3] in some species at least, with angiotensin as a direct stimulant of the adrenal cortex[4]. Angiotensin is not, of course, the only stimulus to aldosterone secretion, and even after nephrectomy the latter may be increased by major surgery[5] or haemorrhage[6], for example. The converse relationship, the possible stimulation of juxtaglomerular cells through the mediation of the adrenal cortex, has received less attention. Although aldosterone does not directly stimulate the secretion of renin in dogs[7], exogenous mineralocorticoid can increase juxtaglomerular activity in rats[8].

We have therefore investigated the reaction of juxtaglomerular granule cells in the absence of the adrenals. Our earlier studies[9] showed that the juxtaglomerular granule index[10,11] was not only lowered by increasing the intake of sodium, as expected[12], but was raised when potassium intake was increased, contrary to an earlier report[13]. In order to carry out a similar experiment in the absence of the adrenals, adult rats after adrenalectomy were given sodium or potassium chloride as 2% solutions for drinking, offered ad libitum but without choice of other fluid. A preliminary experiment showed that this potassium loading killed adrenalectomized rats within 24 h. However, such animals survived if they were first given sodium chloride, as will be described.

[1] J. BING and J. KAZIMIERCAK, in *Hormones and the Kidney* (Ed. P. C. WILLIAMS; Academic Press, London 1963), p. 255.

[2] R. EDELMAN and P. M. HARTROFT, Circulation Res. *9*, 1069 (1961).

[3] J. O. DAVIS, J. T. HIGGINS JR. and J. URQUHART, in *Aldosterone* (Ed. E. E. BAULIEU and P. ROBEL; Blackwell, Oxford 1964), p. 175.

[4] J. R. BLAIR-WEST, J. P. COGHLAN, D. A. DENTON, J. R. GODING, J. A. MUNRO, R. A. PETERSON, M. WINTOUR and R. D. WRIGHT, Aust. J. Sci. *25*, 100 (1962).

[5] F. C. BARTTER, B. H. BARBOUR, A. A. CARR, C. S. DELEA and J. D. H. SLATER, Canad. med. Ass. J. *90*, 240 (1964).

[6] J. SÓLYOM, S. KOTRA, A. SALAMON and J. STURCZ, Acta Physiol. Acad. Sci. Hung. *24*, 293 (1964).

[7] G. W. GEELHOED and A. J. VANDER, Life Sci. *6*, 525 (1967).

[8] F. W. DUNIHUE, M. BLOOMFIELD and B. MACHANIC, Endocrin. *72*, 963 (1963).

[9] J. M. N. BOSS and M. KRAUS, J. Physiol. *181*, 64P (1965).

[10] P. M. HARTROFT and W. S. HARTROFT, J. exp. Med. *97*, 415 (1953).

[11] F. W. DUNIHUE and W. VAN B. ROBERTSON, Endocrinology *61*, 293 (1957).

[12] W. S. HARTROFT and P. M. HARTROFT, Fedn. Proc. *20*, 845 (1961).

[13] P. M. HARTROFT, Circulation Res. *12*, 525 (1963).