## Ametropic Efficiency of Visual Pathway Neurons

Emphasis is now commonly placed on responsiveness to 'trigger features', i.e., distinctive combinations and/or sequences of stimulus events, to describe the operative missions of visual pathway neurons 1, 2.

But how dependent is trigger feature tuning on optimum stimulus conditions? Here, the effects of one common class of stimulus degradations, the ametropias (i.e., refractive errors), is used to explore that question.

Examples cited are from amongst a cummulative sample of nearly 300 neurons within the rabbit mesencephalon now studied. The animals were maintained under light urethane anesthesia (5.5 ml/kg body weight of a 20% solution in saline, a dosage level found from earlier work to be no more detrimental to cell responsiveness than 'encéphale isolé' techniques). This was supplemented with 3.3 mg/kg body wt./h of gallamine triethiodide to prevent eye and body movements, the animal being artificially respirated during that period.

The animals were supported stereotaxically, the stimulated eye in each case being refracted and fitted with a contact lens to protect the cornea from drying and to bring the retina into conjugacy with the 1m distant testing plane. Stainless steel microelectrodes (average resistance, 40 megohms) were introduced into the superior colliculus trough an agar sealed skull aperture.

Once localized in visual space, the receptive field of each cell was mapped through the neutralizing refractive correction for that axis in space, using the most commonly optimal stimulus conditions (a flashing 1 sec on, 1 sec off 1/2° diameter 4.1 cd/m² light spot against a 0.03 cd/m² background). Occasionally, when as described in the results, a cell responded best to other stimuli, e.g.,

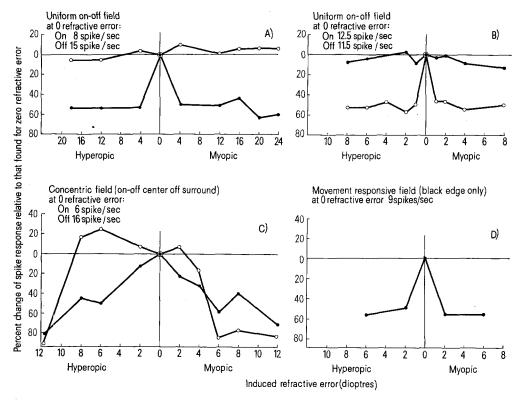
movement of an edge, those more optimal stimuli were used to map the field. The receptive field was then replotted for each of a series of spherical (plus power to induce myopia; minus power to induce hyperopia) refractive errors by centering the inducing lenses on the receptive field axis.

Recording sites within the superior colliculus were later confirmed by Prussian blue marks localized in frozen sections made of each brain.

The Figure shows examples of 4 common responses (measured for the most responsive center of each field) to dioptrically induced stimulus degradation. The percentage changes of the ordinate scales are spike count means of 6 determinations made per dioptric condition, as summed by a Beckman model 6240 EPUTmeter.

The Table summarizes the changes in response efficiency of 20 sample cells, including uniform on, uniform off, movement responsive (only), as well as several types of concentric field geometries. The effect of inducing one diopter of refractive error (averaged for hyperopia and myopia) was found to reduce the percent responsiveness of these cells by as little as 13% up to as much as 76%, the mode value lying in the 20 to 30% range. Occasionally (see example 2 of the Table), when spike numbers are small, the scatter of light by blurring appears to have a

- J. Y. LETTVIN, H. R. MATURANA, W. S. McCulloch and W. H. PITTS, Proc. Instn Radio Engrs Aust. 47, 1940 (1959).
- <sup>2</sup> H. B. Barlow, R. M. Hill and W. Levick, J. Physiol., Lond. 173, 377 (1964).



Percent change of spike response per sec with induced refractive error, relative to the spike response produced with zero refractive error. Each point is the mean of 6 or more observations at that refractive condition. Filled circles represent off responses; open circles represent on responses.

Change of spike response induced by Refractive Error Average for refactive errors of plus and minus 1 diopter

Example No.	Field type	Spike change per diopter	Response change per diopter (%) a	Example No.	Field type	Spike change per diopter	Response change per diopter (%)
1	on	1.5	-15	12	off	0.6	-22
2	on	2.0	+28	13	on	10.0	76
3	on-	0	0 27	14	off °	1.7	
4	off b on-	4.0 0	0	15	on-	0	0
	off c	2.7	-17		off	0	0
5	off	2.0	28	16	off a	8.5	-30
6	on-	0	0	17	on-	5.0	-40
	off	1.0	-25		off	0	0
7	on-	0	0	18	on-	0	0
	off	3.5	-37		off	2.5	-21
8	off₫	2.3	-24	19	on-	2.5	-13
					off f	0	0
9	on-	0	0	20	on-	1.2	-17
	off b	0.7	23		off	0.8	<b>—16</b>
10	offa	1.8	-20				
11	off	7.0	-58				

<sup>&</sup>lt;sup>a</sup> A (+) sign indicates an increase in spike frequency, a (-) sign indicates a decrease. <sup>b</sup> These fields were giving on-off responses uniformally throughout. <sup>c</sup> This field had an on-off center and an off surround. <sup>d</sup> Response to an encreaching black edge only. <sup>c</sup> This field had an off center and an off surround. <sup>t</sup> This field had an on-off center and an off surround.

recruiting effect on the near-by surround; most commoly, however (all other cases shown in the Table) the opposite is true, suggesting that surround inhibition is being activated by the enlarging blur circle, in combination with a less strongly stimulated center area.

Dioptric degradation of the retinal image then can have a significant detrimental effect on the responsiveness of individual visual pathway neurons and such effects can vary over a wide range depending on the particular cell. Also, it should be noted that on and off response mechanisms of a cell can lose their response efficiencies independently of one another, suggesting controlled blur as one possible means of isolating the responses of the two, and perhaps more clearly identifying the individual missions of each.

Zusammenfassung. Bestimmung der Auswirkung von artefiziellen Refraktionsanomalien auf die Aktivität von Neuren in primären Sehzentren.

J. M. LEE and R. M. HILL<sup>3</sup>

College of Optometry, The Ohio State University, Columbus (Ohio 43210, USA), 31 January 1972.

## Electrical Responses of Cardiac Muscle in Na-Free High-Ca Solution

Frog atrial muscle immersed in Na-free high Ca solution relaxes completely after a transient contracture and then responds to electrical stimuli with strong twitches, which may be 'all or none' (BOZLER<sup>I</sup>). In the present work the changes in the membrane potential associated with these twitches were recorded using glass microelectrodes. Modified Ringer solution contained in mM: NaCl 115; KCl 3; CaCl<sub>2</sub> 1.5; Tris chloride (pH 7.2) 2. In Na-free high-Ca solution, all Na was replaced by 83 mM Ca. Rings of the atrium of the frog (Rana pipiens) were used.

In the Na-free High-Ca solution conducted action potentials could be obtained, most readily after epinephrine  $(5.10^{-6}M)$  was added. These action potentials have a large overshoot (membrane potential reversal), reaching an amplitude of 65 to 90 mV, as compared to 25–30 mV in Ringer solution. Including the resting potential, which was increased by the solution used, the total depolarization was as large as 185 mV. The potentials were not influenced by TTX ( $10^{-7}$  g/ml) and their duration was about half of that in Ringer solution. In the absence of epine-

phrine responses were generally local. If they were conducted, the drug increased the amplitude and the duration of the plateau.

These results strongly support views regarding the role of Ca in cardiac activity based on recent electro physiological studies. Voltage clamp experiments have indicated an influx of Ca during the cardiac action potential (Reuter<sup>2,3</sup>, Rougier et al.<sup>4</sup>), although these results have been questioned by Johnson and Lieberman<sup>5</sup>. The action potentials in Na-free solution reported here clearly demonstrate an influx of Ca during responses of cardiac muscle and show that the influx can be strong enough for con-

<sup>&</sup>lt;sup>3</sup> This work was supported by U.S.P.H.S. Grant No. EY00576.

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<sup>&</sup>lt;sup>2</sup> H. REUTER, Arch. ges. Physiol. 287, 357 (1966).

<sup>&</sup>lt;sup>3</sup> H. Reuter, J. Physiol., Lond. 192, 479 (1967).

<sup>&</sup>lt;sup>4</sup> O. Rougier, G. Vassort, D. Garnier, Y. M. Gargouil and E. Coraboeuf, Arch. ges. Physiol. 308, 91 (1969).

<sup>&</sup>lt;sup>5</sup> E. A. Johnson and M. Lieberman, A. Rev. Physiol. 33, 479 (1971).