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Nerve Impulses from Single Receptors in the Eye of Limulus.

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One of us[1] has reported "small but definite electrical changes" in the optic nerve of *Limulus polyphemus* when the eye is exposed to light. The present communication continues this study with improved methods which have made it possible to record impulses in single fibres of that nerve, by means of a battery coupled amplifier and Matthews' oscillograph.

The compound lateral eye of *Limulus* is an admirable preparation for the study of photoreception. Each of the large and widely spaced ommatidia is supplied with one nerve fibre which runs directly to the central ganglion. In the eye itself there is no evidence of either ganglion cells or neural interconnections. The optic nerve is easily obtained and the eye, together with a centimeter or more of optic nerve attached, may be excised and will survive 8 hours or longer.

Action potentials from the whole nerve were studied in the young animal. When the eye is illuminated there is developed a succession of slow potential changes, superimposed on which are the typical rapid changes associated with the conduction of nerve impulses. In the whole nerve these impulses are quite irregular and resemble the responses recorded from the optic nerve of *Conger vulgaris* by Adrian and Matthews.[2]

A study of the discharge of impulses from a restricted number of sense cells is made possible by the circumstance that the optic nerve of *Limulus* contains little connective tissue, and hence can be separated into bundles containing only a few fibres. Moreover, in the adult animal it appears that many of the ommatidia are no longer functional, and it frequently happens that in a small bundle separated off from the whole optic nerve there is only one active fibre.

Fig. 1 is a record obtained from such a bundle. The nerve impulses demonstrated are usually large (*ca.* 0.6 millivolts), due in part, at least, to the fact that there is little short-circuiting material surrounding the active fibre. The regularity in the discharge of the

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[1] Hartline, H. K., *Am. J. Physiol.*, 1928, **83**, 466.

[2] Adrian, E. D., and Matthews, R., *J. Physiol.*, 1927, **63**, 378.

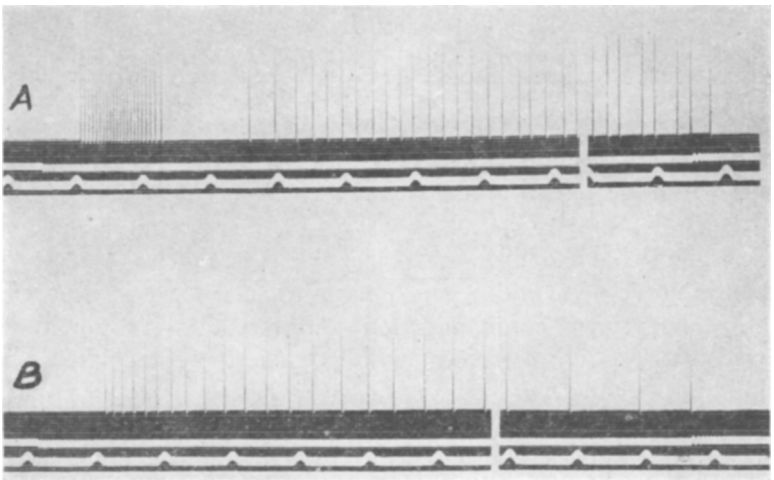

FIG. 1.

Oscillograph records of potential changes in a small bundle of fibers from the optic nerve. Leads taken from the cut end of the bundle and an uninjured point about 5 mm. distal to it. Increasing negativity of the distal lead produces a deflection of the shadow edge upwards. Time tracing (at bottom) in fifths of seconds. Deflection downwards of the signal (above time tracing) indicates the onset of illumination. Area of eye illuminated = 0.01 mm.^{2} Complete dark adaptation in both records.

A. Intensity of stimulation = 1.00 (arbitrary units). The gap in the record represents an interval of 7.2 sec. B. Intensity of stimulation = 0.014 (arbitrary units). The gap in the record represents an interval of 9.0 sec. (1 arbitrary unit of intensity equals approximately 85,000 meter candles on the surface of the eye.)

impulses and their uniformity in size indicate that only one visual element is concerned. When the bundle contains more than one active fibre, the impulses belonging to each are clearly recognizable. Aside from the fact that each one forms its own definite regular sequence, the impulses in any 2 fibres can readily be distinguished by differences in the magnitude and form of the recorded response. Moreover, the photoreceptors attached to these fibres have different thresholds and discharge impulses at different rates.

The impulse discharge from these receptors resembles that found by previous investigators from other sense cells, *e. g.*, tension receptors in muscle.[3, 4, 5] The discharge starts after a short latent period at a high frequency, falls rapidly at first, and then more slowly, tending to reach a constant value after several minutes. The impulses stop when the light is turned off. The frequency of impulses in both the initial burst and final steady discharge depends on

[3] Adrian, E. D., and Zotterman, Y., *J. Physiol.*, 1926, **61**, 151.

[4] Bronk, D. W., *J. Physiol.*, 1929, **67**, 270.

[5] Matthews, B. H. C., *J. Physiol.*, 1931, **71**, 64.

the intensity of the stimulating light (*cf.*, Fig. 1, A and B). Dark adaptation also modifies the discharge frequency, *i. e.*, the end organ responds to a stimulating light of given intensity with an initial frequency which is greater the longer the eye has been in the dark.

The short pause following the initial burst of impulses, observable in Fig. 1A, is a characteristic response of the completely dark adapted eye to light of high intensity. This "silent period" is absent if the eye is not completely dark adapted, or if the intensity of the stimulus is low. The discharge then consists of an unbroken succession of impulses regularly decreasing in frequency (*cf.*, Fig. 1B).

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Time-Intensity Relations for the Stimulation of Tissue by Electric Currents.

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Justification is felt in advancing a new analysis of the time-intensity relations for electrical stimulation as it is much simpler mathematically than any existing general analysis and therefore more useful in planning and co-relating experiments while at the same time it fits, as well or better, the experimental data of the Lapicques.

The derivations are based on the following hypotheses: (a) The rate of growth of the local excitatory process whose magnitude is designated by p is proportional to the applied voltage. (b) The tissue has a reaction toward normal at a rate proportional to p. (c) When p reaches a liminal value h excitation is accomplished.* The differential equation expressing (a) and (b) is,

$$\frac{dp}{dt} = KV - kp$$

where V is the applied voltage, K and k are constants.

For direct current a solution is,

$$kt = \log \frac{KV}{KV - kh} = \log \frac{V}{V - R}$$

when the rheobase, R, is substituted for kh. All the direct current data in Lapicque's book[3] fit the equation,

* h is probably in general a function of the voltage, *e. g.*, when C is not zero with direct currents.