Analysis of the L-Type S-Potential by means of the Stiles-Crawford Effect in the Carp Retina

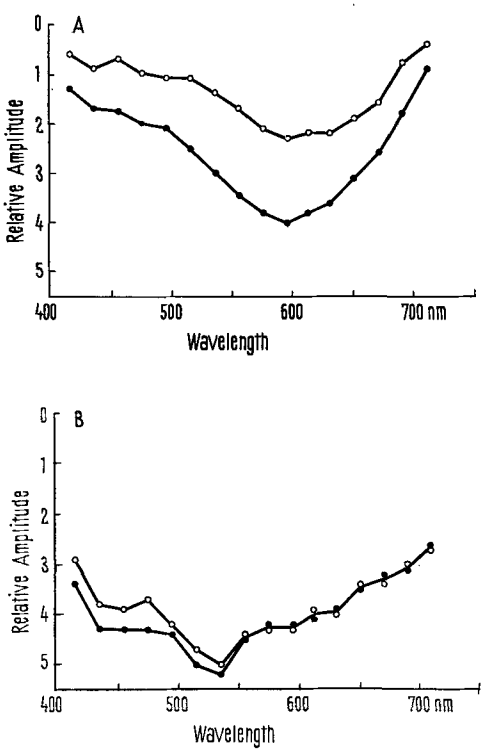
Attempts have been made to relate the function of the luminosity (L-type) S-potential, which is presumably generated by the horizontal cell of the retina, to processes of light and dark adaptation[1,2]. For the L-type S-potential to be functional in the dark adapted state, it is likely that the rod photoreceptors would participate in its generation. However, there is still some question as to whether the retinal rods contribute to the production of the L-type S-potential. Anatomical evidence, although not conclusive, indicates that the horizontal cell only makes contact with the cone photoreceptors[3,4]. In addition to the question of the rod photoreceptor function, the contribution to the generation of the L-type S-potential by a class of cone photoreceptors with a maximum sensitivity in the blue region of the spectrum has not been definitely established[5].

The Stiles-Crawford effect which refers to the directional sensitivity of photoreceptors to the angle of incident illumination provides a means to distinguish between the rod and cone contribution to the production of the L-type S-potential. The rods are relatively insensitive to the angle of incident light whereas the cones reveal a marked directional sensitivity. Therefore, by increasing the angle of incident light the signal strength of the rod receptor activity would be essentially unchanged but the signals generated by the cones would be considerably diminished. The Stiles-Crawford effect has been employed with measurements at the ganglion cell level to differentiate the relative photoreceptor activities in the frog retina[6]. It has also been shown that the S-potential is a sensitive indicant of the Stiles-Crawford effect[7].

Method. In the present study, the L-type S-potentials were recorded from the carp retina. Spectral response curves of these S-potentials were obtained with the stimulating light incident at angles of 0° and 37°. Retinas which had a controlled history of either light or dark adaptation were employed. The preparation was essentially a semi-eyecup in which the edges had been trimmed to form a reasonably flat surface. The spectral responses were obtained in the sequence of 0°, 37°, 0° and repeated as many times as possible with any one S-potential. Over 50 S-potentials were studied. The light was led from a photostimulator by means of fiber optics and fixed at 0° and 37° in a plane perpendicular to the preparation. The rays of light were rendered nearly parallel, but not collimated, by a lens system. The intensity was equated to within 2% at the site of the preparation by means of a neutral density filter. The light emerging from the fiber optics was adjusted for equal quantum by means of a previously calibrated photodiode. Micropipettes with a tip diameter of less than 0.1 μ and filled with 2*M* KCl were used as recording electrodes. The visible spectrum was scanned from 420 to 720 nm in steps of 20 nm.

Results. As shown in the Figure A, the S-potential from the light adapted retina has a maximal response at about 600 nm and exhibits a general reduction in amplitude when the angle of stimulation is changed from 0° to 37°. Most S-potentials from the dark adapted retina have a maximal response in the region of 530 nm. Since the response to this region of the spectrum was relatively insensitive to the angle of incidence, it is likely that the rods are functional in the production of the S-potential in the dark adapted condition. Although spectral sensitivity curves have not been obtained, the occurrence of the maximal response in the region of 530 nm would at least be consistent with the absorption characteristics of the porphyropsin pigment found in the rods of the carp retina.

It should also be noted that in the data presented in the Figure B the greatest reduction in amplitude occurs in response to angular stimulation with wavelengths from the blue end of the spectrum. This confirms the existence of a class of blue-sensitive cones whose signals are manifest in the S-potential of the dark adapted retina. Other S-potentials also exhibited a reduction in amplitude in response to stimulation by the longer wavelengths. This variation probably represents a change in the state of adaptation which occurred during the probing for an S-potential and/or reflects a regional difference in the receptive field organization. The point to be emphasized, is that directional sensitivity was most apparent in response to stimulation by the blue and red regions of the spectrum whereas the maximal response, which was elicited by



Spectral response curves of L-type S-potentials found in the carp retina. The data is presented such that a point below the 0 baseline corresponds to a negative potential at the recording electrode. The amplitudes are plotted on an arbitrary scale. The solid dots represent responses obtained at a 0° angle of stimulation. The circles correspond to the responses measured at a 37° angle of stimulation. (A) Luminosity S-potential from a light adapted retina. The points represented by the solid dots are the average of 2 recordings taken before and after the angular stimulation. (B) Luminosity S-potential from a dark adapted retina. The points represented by the solid dots are an average of 3 recordings and the circles an average of 2 recordings.

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stimulation with wavelengths in the region of 530 nm of the spectrum, was not significantly altered by the angle of incidence.

Since it is known that a class of cones containing a pigment with maximum sensitivity at 540 nm exists in the cyprinidae retina, it could be argued that they are dominant in the production of the S-potential in the dark adapted state. For this to be true, the class of cones in question would have to be unique in that they did not exhibit a marked directional sensitivity.

Conclusion. By means of the Stiles-Crawford effect it has been possible to demonstrate the existence of a class of cones which are sensitive to the blue end of the spectrum and contribute to the S-potential measured in the dark adapted state. It has also been shown that either the rods are dominant in the production of the S-potential in the dark adapted retina or there exists a class of cones with a similar spectral sensitivity which are not directionally sensitive[8].

Zusammenfassung. Mit Hilfe des «Stiles-Crawford»-Effektes gelingt es, die Existenz blau-empfindlicher Zäpfchen in der Fischretina nachzuweisen, die teilweise für die S-Potentiale verantwortlich sind.

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Neuronal Properties of the Neurosecretory Cells in the Fly *Sarcophaga bullata*

Neurosecretory cells (NSC) are specialized neurons which function as endocrine glands. They retain the general morphology of neurons, but end blindly in swollen termini serving as storage and release organs for the hormones produced in the cell bodies. In several poikilotherms the NSC have been found to spontaneously produce action potentials of long duration[1–7]. However, despite much histological and endocrinological interest in the neurosecretory system in insects[8,9] there has appeared only one report of an electrophysiological examination[10].

In *Sarcophaga* the perikarya of the protocerebral NSC are located just under the neurilemma in the dorsal midline of the brain. The axons decussate before leaving the brain posteriorly to end in the corpus cardiacum located in the neck region. To gain access to the brain the head capsule was cut open and the 2 large tracheal branches which pass over the brain were removed. The perikarya of the NSC appear now as 2 small whitish clusters of cells (somata 20 μ in diameter) on either side of the midline of the brain at the base of the ocellar nerve. Intracellular recordings were made with 3*M* KCl filled micropipettes having resistances between 8 and 35 $M\Omega$. Activity was recorded with a Grass P-6 amplifier at unity gain and Hewlett Packard Model 132 oscilloscope direct coupled. In all figures, unless otherwise noted, upward deflections are positive.

The resting potentials of NSC recorded on initial penetration varied from 2–40 mV (inside negative) but mostly were about 20 mV. Action potentials recorded from the perikarya varied in amplitude from 1–40 mV (Figure 1), but were never greater in amplitude than the resting potential of the cell. In all except a few cases the cells were endogenously active. Action potentials recorded from the NSC characteristically were of a duration of

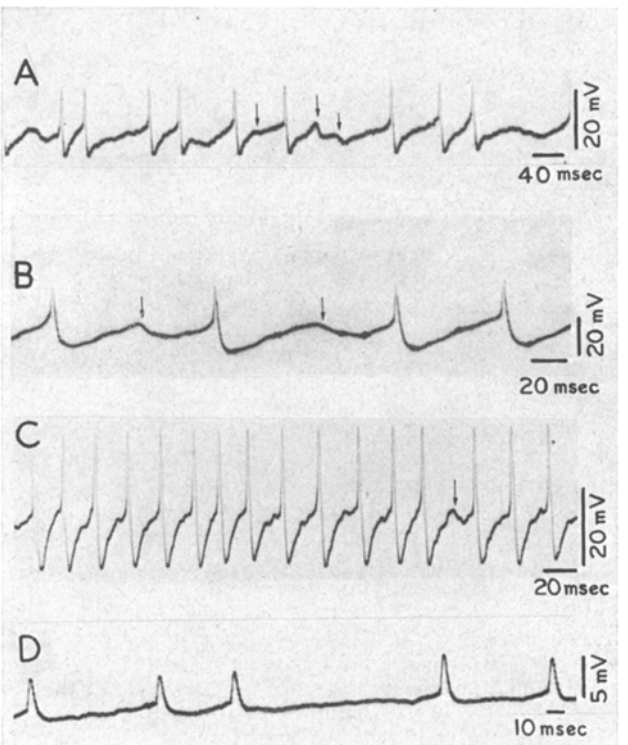

Fig. 1. Intracellular recordings of action potentials from the perikarya of NSC. (A) to (C) show spikes rising from endogenous waves of depolarization and followed by negative afterpotentials. IPSP's (arrows) were frequently seen in these records. (D) Intracellular recording of low amplitude spikes showing no synaptic activity.

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