Biophys. Struct. Mech. 7, 205–208 (1981)

Biophysics of Structure and Mechanism

Short Communications

Adaptation Properties of the ERG in the Grasshopper, *Romalea microptera*

R. M. Bruckler and T. P. Williams

Institute of Molecular Biophysics Florida State University, Tallahassee, Florida 32306, USA

Abstract. The grasshopper ERG displays a rapid recovery of responsivity following the onset of a background light. Although observed earlier in skate and frog, this phenomenon has not previously been seen in an invertebrate. Furthermore, a period of hyperresponsivity exists in early dark adaptation and resembles that found in skate and frog. Thus, recovery in the light and hyperresponsivity in the dark seem to be corollaries of each other. Finally, spectral sensitivity of the ERG is determined and two peaks are found: one at 510 nm and the other at 360 nm. The former appears to be a rhodopsin-mediated sensitivity but the latter does not and they are not clearly separated by chromatic adaptation.

Key words: Grasshopper – Electroretinogram – Adaptation – Spectral sensitivity

During light-adaptation the responsivity of the grasshopper ERG undergoes a depression and partial recovery as shown in Fig. 1. Initially, the background light (500 nm) depresses the responsivity of the eye and the response to a flash of fixed

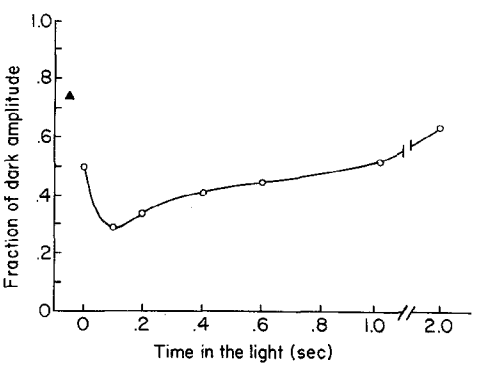

Fig. 1. Temporal changes in responsivity during light adaptation. The open circles represent the response amplitude to a test flash as a fraction of the amplitude of the response elicited by the test flash in the dark adapted eye. The filled symbol to the left of time zero is the amplitude of the response elicited by the onset of the background

0340-1057/81/0007/0205/$ 01.00

intensity reaches a minimum in 0.1 s. The eye rapidly regains a portion of its responsivity durig the first second of the background exposure then the recovery continues at a slower rate. This recovery process, occurs with a mean half-time of 0.8 s ± 0.16 s and is always "partial", i.e., the responsivity never returns to the dark-adapted value while the background is on.

The skate (Dowling and Ripps 1972) and the frog (Hemilä 1977) are unusual in that they also exhibit this "recovery in the light". Furthermore, they both display a hyperresponsivity during early dark-adaptation. If these two phenomena are related, one might expect hyperresponsivity also to occur in the grasshopper visual system. We have found that such hyperresponsivity, in fact, is present: following the offset of a 20 s exposure, the response amplitude to the test flash rapidly approached and surpassed the fully dark-adapted value. Within the first 5 s of dark-adaptation the responsivity overshot its dark-adapted value and remained above it (though dropping slightly) for more than 30 s. Then after 40 s of dark-adaptation the response amplitude returned to its original dark-adapted value. Thus, the grasshopper joins skate and frog in displaying recovery in the light and hyperresponsivity in the dark.

R. microptera has peak sensitivities in two regions of the spectrum, as shown in curve A of Fig. 2. A broad spectral peak was found in the visible region at around 510 nm and a larger (but much narrower) peak occurred in the ultraviolet region at 360 nm. The 510 peak matched Dartnall's (1953) nomogram fairly well but the UV-peak was much too narrow. Therefore, the 510 peak is probably due to absorption by the usual sort of visual pigment. However, the UV-peak may be either due to a) a visual pigment whose spectrum is being distorted (e.g., by screening with an inert pigment); or b) a non-rhodopsin, but physiologically active, "sensitizer".

It was not possible to cleanly separate these two peak sensitivities by chromatic adaption. The data presented in Fig. 2, curve B, represent the spectral sensitivity of the grasshopper eye during exposure to a yellow background. It can be seen that the sensitivity at each peak has been depressed significantly but the

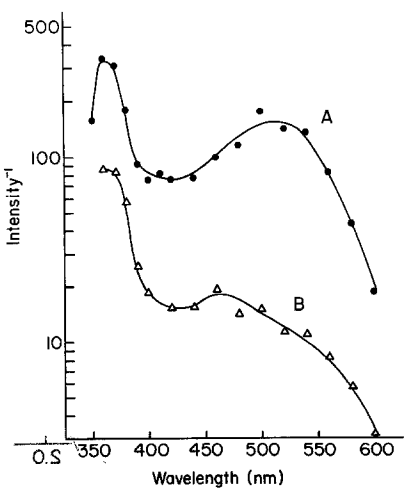

Fig. 2. The spectral sensitivity of the grasshopper eye in the dark adapted state (curve A-filled circles) and under conditions of long wavelength adaptation (curve B-open triangles). The units of intensity are (10^{14} photons/s-cm^2)

ratio of the two peaks has changed only slightly, from 2.5/1 (360/510) to 6/1. Following blue adaptation a similar change in ratios was observed: from 2.5/1 in the dark to 5/1 in the light. And during violet adaptation almost no change at all occurred in the ratio of the peaks: from 2.5/1 in darkness to 3/1 in the light. These results make it unlikely that the two pigments are present in separate receptors, unless such receptors are strongly coupled (cf. Chappel and DeVoe 1975) and thus support the idea that they exist in the same receptor. The presence of two visual pigments in the same receptor has also been suggested as an explanation for the dual sensitivity and ineffectiveness of chromatic adaptation in the eye of the wolf spider (DeVoe 1972). However, a novel hypothesis, offered by Kirschfeld et al. (1977) (cf. Kirschfeld 1979; Minke and Kirschfeld 1979) in the case of the fly's dual sensitivity may also help explain some of these results.

This hypothesis, involving a UV-absorbing (photostable) sensitizing pigment, is consistent with most of the spectral data we have collected. It can explain the narrowness of the UV-peak since the spectrum of this sensitizing pigment need not fit the spectrum of a visual pigment. It can also explain the ineffectiveness of chromatic adaptation since light absorption by either the sensitizing pigment or the rhodopsin would depress the sensitivity of the whole cell, both pigments being in that cell. If further work sustains Kirchfeld's hypothesis, the case for a photostable sensitizer in grasshopper will also be strengthened.

One set of data which is not easily explained by this hypothesis is that of long wavelength chromatic adaptation. Adaptation to a yellow background resulted in a small (ca. 2.5 times) but consistent increase in the sensitivity ratio of the ultraviolet to the visible peak. Since the data were plotted on an inverse intensity scale, this is actually a decrease in the ratio of the number of UV to long wavelength photons necessary to excite the criterion number of rhodopsin molecules. The yellow background presumably decreased (by photolysis) the number of rhodopsin molecules available to receive energy from the sensitizing pigment. Hence, if Kirschfeld's hypothesis is to explain this result it is necessary to postulate that the sensitizing pigment becomes more efficient in transferring energy to rhodopsin even though there are fewer of them present. Although this seems unlikely, it is not impossible. One way in which this might occur is that the "bleached" molecules themselves could act as sensitizing pigments. That is, the metarhodopsin of the 510 pigment may absorb at short wavelengths and act as an agent for transferring absorbed energy directly to the rhodopsin. Or, it could be that such a meta might act as an intermediate in a transfer chain, accepting energy from the UV-pigment and donating it to the rhodopsin.

Acknowledgements. This work was supported in part by National Science Foundation grant BNS24-24655.

References

Chappel RL, DeVoe RD (1975) Action spectra and chromatic mechanisms of cells in the median ocelli of dragonflies. J Gen Physiol 65: 399

Dartnall HJA (1953) The interpretation of spectral sensitivity curves. Br Med Bull 9: 24–30

DeVoe RD (1972) Dual sensitivities of cells in wolf spider eyes at ultraviolet and visible wavelengths of light. J Gen Physiol 59: 247–269

Dowling JE, Ripps H (1972) Adaptation in skate photoreceptors. J Gen Physiol 60: 698–719

Hemilä S (1977) Background adaptation in the rods of the frog's retina. J Physiol 265: 721–719

Kirschfeld K (1979) The function of photostable pigments in fly photoreceptors. Biophys Struct Mech 5: 117–128

Kirschfeld K, Franceschini N, Minke B (1977) Evidence for a sensitizing pigment in fly photoreceptors. Nature 269: 386–390

Minke B, Kirschfeld K (1979) The contribution of a sensitizing pigment to the photosensitivity spectra of fly rhodopsin and metarhodopsin. J Gen Physiol 73: 517–540

Received August 5, 1980/Accepted February 5, 1981