

Receptor and Interneuron Light-adaptation in the Dragonfly Visual System

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Intracellular recordings show that the receptors and second-order interneurons of the dragonfly compound eye change their sensitivity in response to maintained illumination. Comparison of receptor with interneuron shows that neural mechanisms act to ensure that the modulation of interneuron membrane potential that is set up by contrast changes is independent of background intensity.

The large monopolar cells (LMC's) of the insect lamina are directly post-synaptic to the photoreceptor terminals¹ and respond to illumination of the receptors with a graded triphasic hyperpolarisation whose amplitude and waveform depends upon light intensity². The dark-adapted LMC's of the dragonfly lamina integrate the receptor signal by amplifying the voltage signal resulting from a change in intensity in such a way as to improve the signal to noise ratio³. Amplification increases the contrast efficiency which is defined as the voltage change of visual signal that results from a fixed change in contrast (relative intensity). Contrast efficiency is simply measured as the slope of the receptor or interneuron intensity/response function and is expressed as mV's/log unit intensity.

Amplification not only increases LMC contrast efficiency but decreases the dark-adapted dynamic range of the LMC's to 2 log units of intensity (Fig. 1). Despite the existence of lateral inhibition in fly lamina⁴, initial experiments report that their LMC's are unable to light-adapt⁵. It seems improbable that a neural system of considerable size and complexity should operate over such a small intensity range and the experiments reported here set out to show that LMC's light-adapt. In addition the light-adaptation of receptors under identical stimulus conditions is examined in order to demonstrate that neural interactions in the lamina play an important role in adjusting LMC sensitivity.

The techniques used for recording intracellularly from the retina and lamina of the dragonfly *Hemicordulia tau* have already been described³. Two monochromatic point sources were used for light stimuli, an adapting source (542 nm) and a test source (524 nm). Both sources subtended 40' at

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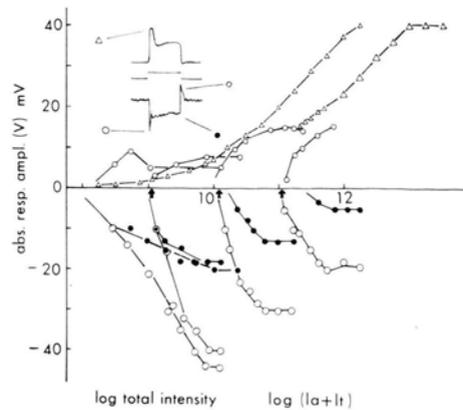


Fig. 1. Light- and dark-adapted intensity/response functions derived by intracellular recording from a single retinula cell and a single LMC. As shown in the inset only the initial peak retinula response amplitude is plotted ($-\triangle-$) whereas all three LMC response components, the hyperpolarising 'on' transient ($-\circ-$), the sustained plateau ($-\bullet-$), and the depolarising 'off' transient ($-\circ-$) are given. Absolute response amplitude is plotted against total adapting intensity expressed as corneal irradiance in 524 nm quanta/cm²/s. The three adapting intensities are marked by arrows but for clarity only the dark-adapted and the most light-adapted retinula intensity/response functions are shown.

the eye and were mounted at a centre to centre spacing of 1.0° upon a Cardan arm manipulator. This apparatus allowed both sources to be symmetrically positioned upon a vertical meridian passing through the centre of each unit's visual field. It is recognised that a restricted point source is an inadequate and unnatural background light source for interneurons showing lateral interactions⁶ but it proves sufficient to demonstrate several important properties of light-adaptation.

Complete adaptation experiments were performed upon 4 retinula and 4 large monopolar cells. Each experimental run was initiated and terminated with a neutral density series of test flashes of increasing intensity and this was used to obtain the dark-adapted intensity/response function of the unit. All test flashes were of 250 ms duration and were delivered at 2.5 s intervals. The initial determination was followed by a neutral density series performed with the adapting light source. The unit's responses to the adapting light were used to derive the effective adapting intensity, I_a , from the dark-adapted intensity/response function. This gave I_a in terms of the test light intensity, I_t . The unit was then light adapted, usually at three different adapting intensities over a range of three log units above dark-adapted threshold. During light-adaptation constant intensity test flashes were delivered to check that adaptation reached a stable equilibrium. When equilibrium was obtained (30–150 s, depending on I_a)



a full test source neutral density series was performed to obtain the light-adapted intensity/response function (Fig. 1).

Each retinula cell gave a maximum response (depolarisation) of more than 40 mV and each LMC peak hyperpolarisations of 25–45 mV and during the experiment maximum response and resting potential fluctuated by less than 5 mV. In addition the final control dark-adapted intensity/response functions showed that long term sensitivity changes and drift in receptive field position were negligible. These recording conditions allow the light- and dark-adapted intensity/response functions to be described in terms of absolute response amplitude, V , expressed as millivolts deflection from dark-adapted resting potential, and in terms of total intensity, $(I_a + I_t)$, (Fig. 1). There was a considerable total scatter in dark-adapted LMC thresholds (0.5 log units) and for comparison of LMC results (Fig. 2) the adapting intensity for each unit was normalised by expressing I_a as log units above dark-adapted threshold. Retinula cell dark-adapted sensitivities showed less than 0.1 log units total scatter so that normalisation of I_a was not required however, for comparison with the LMC results (Fig. 2) I_a was expressed as log units above the average LMC dark-adapted threshold.

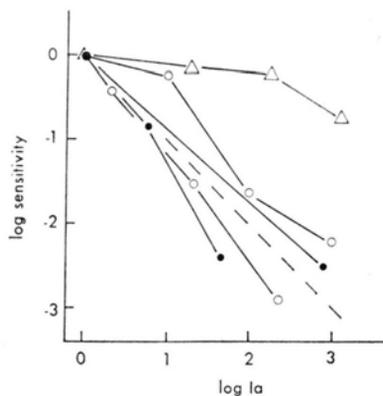


Fig. 2. A comparison of the dependencies of retinula (\triangle) and LMC (\circ , \bullet) sensitivities on adapting intensity. Log sensitivity (as defined in text) is plotted against log background for four separate LMC's whereas the average retinula sensitivity function is shown. The dashed line shows the Weber-Fechner relationship, log sensitivity \propto log background.

The changes in retinula cell intensity/response functions induced by light-adaptation (Fig. 1) are almost identical with the similar results reported from drone bee⁷ and white eyed *Calliphora*⁸. Two points are of particular importance. At any given light-adapted equilibrium the background light always maintains a significant level of receptor de-

polarisation. Secondly the process of light-adaptation displaces the intensity/response functions to higher intensities in such a way that the $V/\log I$ curves remain parallel (Fig. 1). This means that light-adaptation reduces sensitivity as defined as the reciprocal of the total light intensity ($I_a + I_t$) required to give a constant total voltage signal, V . This sensitivity decrease (Fig. 2) is equivalent to either a reduction in the quantum capture efficiency of the receptor and/or a decrease in the number of conductance channels opened by the absorption of a single quantum of light. Note that for weak background intensities the change in receptor sensitivity is small (Fig. 2).

The net result of the light adaptation of LMC's is similar to that of retinula cells in as much as the $V/\log I$ curves are displaced parallel to the log intensity axis (Fig. 1) and thus the sensitivity (as defined above) reduced (Fig. 2). Although individual units showed a significant scatter of slopes of the $V/\log I$ curves at different adapting intensities (e.g. Fig. 1), when averaged for all 4 LMC's the dark- and light-adapted contrast efficiencies were not significantly different. However, the process of interneuron light adaptation differs from receptor adaptation in three important ways. First, the hyperpolarisation set up by the maintained adapting stimulus rapidly decrements so that there is no sustained LMC signal in response to the adapting light. Secondly, the LMC response waveform changes with light-adaptation and becomes more phasic with a relative increase in the amplitude of the 'on' and 'off transients (Fig. 1). Finally, in order to avoid saturation by low adapting intensities, the initial sensitivity change in LMC's is greater than in retinula cells so that interneuron sensitivity follows the Weber-Fechner law rather well (Fig. 1).

These differences between receptor and interneuron light-adaptation characteristics show that neural interactions must play a significant role in determining interneuron sensitivity. In particular there must be a time dependent inhibition that counteracts the sustained adapting signal from the receptors and this may be related to the lateral inhibitory effects previously described⁶. Moreover, despite an increase in retinula cell contrast efficiency at low intensities (see Fig. 1) the LMC contrast efficiency remains relatively constant and this is probably achieved by a reduction in the voltage transfer gain at the level of the first synapse³.

In conclusion it is clear that LMC's do light adapt and this enables them to respond to intensity changes over a total range of average intensity of at least 4 log units. It appears that neuronal adapta-

tion mechanisms ensure that the full voltage response bandwidth of the LMC is matched to the likely change of environmental contrasts at any one background and standardise contrast efficiency for

higher order neurons. These considerations support the hypothesis³ that LMC's form the input to a system designed to detect changes in contrast.

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