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OCELLAR EXCITATION OF THE DCMD: AN IDENTIFIED LOCUST INTERNEURONE

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Locusts, like most other insects, possess three ocelli, or simple eyes, in addition to two large compound eyes. Focussed images are not formed on the retinae of the ocelli (Parry, 1947; Wilson, 1978*a*) and ocellar neurones are influenced by changes in light intensity occurring over wide areas of the visual field. Some of the second-order neurones which extend from the retina of each ocellus to the brain have large axons – amongst the largest found in the locust central nervous system. They are expected to convey information about changes in light intensity to the brain with some urgency. At least two different ways in which these large second-order ocellar neurones (L-neurones) could influence the behaviour of a locust have been suggested. First, by monitoring changes in the orientation of the visual horizon they could contribute to the stability of flight (Wilson, 1978*a*; Stange & Howard, 1979; Simmons, 1980*a*). Second, they could facilitate the responses of some central neurones, such as those driven by the compound eyes, when light intensity is reduced (Parry, 1947) – for instance, when a shadow falls over the locust. The observations reported here show that the L-neurones boost the responsiveness of a pair of well-characterized central neurones when the overall light intensity is rapidly decreased.

Recordings were made from the 'descending contralateral movement detectors' (DCMDs) of adult locusts (*Schistocerca americana gregaria*, Dirsh). There is one DCMD axon in each side of the ventral nerve cord. DCMD axons are the widest in the thoracic nerve cord, and each descends the cord contralateral to its cell body in the protocerebrum of the brain (O'Shea, Rowell & Williams, 1974). The nature of the stimuli which excite a DCMD, and the pattern of synpatic connexions a DCMD makes with motoneurones suggest it serves an alarm function. A DCMD is excited by novel abrupt movement of an object across a small area of the visual field of the compound eye ipsilateral to the DCMD cell body (Rowell, 1971), and by sudden, loud noises (O'Shea, 1976). Both DCMDs make connexions with motoneurones that control muscles of the hind legs (Burrows & Rowell, 1973; Pearson & Goodman, 1979) and the wings (Simmons, 1980*b*) and may be involved in triggering responses such as jumping to avoid a predator, or changing flight direction to avoid a collision. Two techniques were employed to test whether the ocelli influence activity in a locust's DCMDs. In the first of these, one microelectrode was used to inject current into an L-neurone, while a second recorded potential changes in a DCMD cell body. The

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second technique, described later, involved determining whether stimulation of an ocellus with light influenced the number of spikes a DCMD produces in response to stimulation of a compound eye. Intracellular recordings were made from the cell bodies of DCMDs and from the axons of L-neurones with glass microelectrodes which were filled with 2 M-potassium acetate and had d.c. resistances of 40–60 MΩ. The brain was exposed dorsally prior to recording, and was supported on a stainless steel platform over which saline flowed. One end of a plastic light guide ('Croton', du Pont, London) of diameter 0·5 mm was placed on each ocellar lens. The three light guides were illuminated individually by 2·2 V lens-end torch bulbs, and the time of illumination of each guide was controlled by a separate mechanical shutter. This method of illuminating the ocelli allows stimulation of all three ocelli simultaneously, and is convenient and inexpensive. A disadvantage is that no ultraviolet light, to which L-neurones are particularly sensitive (Wilson, 1978*a*) is delivered. However, it is most likely that the responses elicited in L-neurones by this method were of similar amplitude to those which occur in a free-living locust in a natural environment. Amplitudes of response similar to those elicited by this method were caused by waving a pencil 10 cm away from a locust's head, interrupting the illumination from the laboratory window.

In Figs 1*a*, *b* the responses of a DCMD and of an L-neurone to a 500 ms pulse of (light delivered to the right ocellus are shown. The origin of the responses of an L-neurone to increases and decreases in illumination has been described by Wilson, 1978*b*). Upon illumination of the ocellus, the L-neurone hyperpolarizes, and it remains hyperpolarized throughout the light pulse. There is no corresponding maintained change in the membrane potential of the DCMD, although there is a reduction in the frequency of EPSPs. When the light is switched off, the L-neurone spikes and there is a series of EPSPs in the DCMD. Injection of depolarizing current into the L-neurone also causes a series of EPSPs in the DCMD, showing that the EPSPs are mediated by the ocelli rather than resulting from light scattered within the head capsule stimulating photoreceptors of the compound eyes. It is not possible to tell whether the EPSPs originate within the DCMD itself, or within the 'lobula giant movement detector' (LGMD) with which it makes an electrical synapse (O'Shea & Rowell, 1975; Rowell & O'Shea, 1980). Because it is not necessary for an L-neurone to spike for the EPSPs to occur (Fig. 1*c*), there must be another neurone in the pathway.

In 13 locusts of the 15 from which intracellular recordings were made, no L-neurone of any ocellus was found which did not evoke EPSPs in a DCMD. No differences between the EPSPs mediated by the three ocelli of one locust have been found, and stimulation of all three ocelli together does not produce any greater effect than stimulation of one ocellus alone. It is, however, difficult to compare the responses mediated by the different ocelli, since the responses in a DCMD to repeated, identical stimuli delivered to one ocellus vary in the frequency, summation and duration of EPSPs (Fig. 1*a*).

To test whether the ocellar-mediated EPSPs influence the spiking output of a DCMD, extracellular spikes were recorded in minimally dissected locusts. The spikes were recorded with hook electrodes placed under a pro-mesothoracic con-

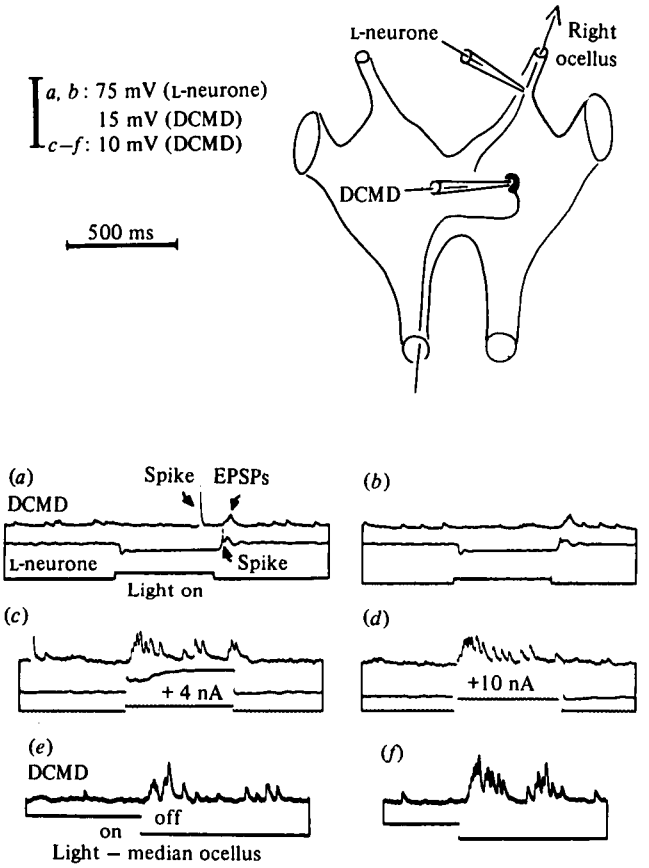

Fig. 1. EPSPs recorded from the right DCMD cell body when ocellar illumination is reduced and when depolarizing current is injected into an L-neurone. Positions of the two electrodes used are shown on the diagram of the brain, which is viewed dorsally. (*a*) The L-neurone hyperpolarizes by 10 mV when the light is applied to the right ocellus. When the light is shut off, the L-neurone spikes, and a burst of EPSPs occurs in the DCMD. Just before the light is switched off, the DCMD spikes. (*b*) A less intense pulse of light is applied to the right ocellus. The amplitudes of the hyperpolarization and of the spike in the L-neurone are smaller than in (*a*), but the duration and amplitudes of the EPSPs in the DCMD are very similar. (*c*) Injection of 4 nA depolarizing current into the L-neurone causes a series of EPSPs in the DCMD. The electrodes were connected to amplifiers, incorporating bridge circuits to allow recording of membrane potential and injection of current through the same electrode, and the recording from the L-neurone shows that it did not spike when it was depolarized. (*d*) EPSPs in the DCMD when 10 nA depolarizing current is injected into the L-neurone. In this case, there is no record from the L-neurone, but other experiments employing two electrodes in a single L-neurone, show that a positive current of at least 25 nA is normally required to elicit any regenerative response. (*e*, *f*) Two pulses of light of equl intensity applied to the median ocellus are each followed, upon termination, by a train of EPSPs in the DCMD.

nective of a locust embedded upside-down in plasticine, and the DCMD spikes were distinguished from those of other interneurones by their large amplitude. To stimulate a DMCD, the needle of a small voltmeter, positioned 25 mm to one side of the head, was driven across the visual field of a compound eye by a 500 ms pulse. The number of spikes occurring during the first 200 ms of each stimulus was counted, and the

Table 1. *Results of one experiment to test the effectiveness of change in illumination of the median ocellus in regulating spike output from a DCMD*

Number of spikes in first 200 ms of stimulus	Frequency of recording this number of spikes when compound eye stimulus is presented	
	Alone	With ocellar stimulation
2	0	0
3	0	0
4	3	0
5	2	3
6	6	0
7	1	9
8	2	4
9	2	4
10	0	3
11	0	0
12	0	0

Mean no. of spikes: Compound eye stimulus alone: 6·2.
Mean no. of spikes: Compound eye stimulus plus ocellar stimulus: 7·6. $z = 2{\cdot}9$.

stimulus was repeated every 60 s, in order to reduce the effects of habituation. Roughly half the stimuli were accompanied by a pulse of light delivered to the median ocellus (the median ocellus was used since it is difficult to illuminate either lateral ocellus separately from the compound eyes). When the median ocellus was illuminated its pulse of light started 5 s before the needle travelled across the compound eye, and terminated 100 ms after the needle began to move. The ocellar stimulation was presented at random.

This experiment was performed on five locusts, and was repeated between three and six times on each. For each experiment, between 16 and 25 stimuli presented alone to the compound eye were compared with a similar number of stimuli accompanied by a reduction in the illumination of the median ocellus. The results of one experiment are presented in Table 1. Significance of the differences between the numbers of spikes elicited by the two treatments was tested by the Mann-Witney U-Test, calculating z because of the rather large number of 'tied' values (Siegel, 1956, pp. 116–126. In all the experiments performed on four of the locusts, stimulation of the compound eye accompaned by a reduction in illumination of the median ocellus produced a greater number of spikes than that produced by stimulation of the compound eye alone ($P < 0{\cdot}01$). No significant differences between the two treatments were obtained from the fifth locust. In three locusts, a comparison was made between stimulation of a compound eye alone and stimulation of a compound eye accompanied by an increase in illumination of the median ocellus. No significant differences between the responses elicited by these two treatments were found. Stimulation of the median ocellus without stimulating the compound eye did not evoke any spikes in a DCMD.

The pathways between the ocelli and the DCMDs of a locust are part of a range of mechanisms for adjusting the responsiveness of the DCMDs to the compound eye stimuli. When a locust is allowed to adapt to ambient light intensity for at least 15 min,

The responsiveness of a DCMD is maintained over a range of light intensities, and this can be explained by the known processes of light and dark adaption which occur in the outermost neurones of a compound eye (Rowell & O'Shea, 1976). The ocellar-driven mechanism acts more immediately, to boost responsiveness when light intensity falls rapidly.

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