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Graded Potentials and Action Potentials in the Large Ocellar Interneurons of the Bee

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Summary. The response characteristics to light stimuli of first order ocellar interneurons in the bee (*Apis mellifera carnica*) were analysed with intracellular recordings. The neurons were identified using intracellular dye injection (Lucifer yellow).

The responses of L-(large) neurons can vary. They range from transient graded hyperpolarizations in response to light-On and -Off, (sometimes accompanied by tonic hyperpolarization during the light stimulus), to spontaneous tonic action potentials which are inhibited by light. Some neurons show both hyperpolarizations and action potentials.

The varying responses to light stimuli are dependent only on the state of the L-neuron and are not correlated systematically with particular types of L-neurons.

The experiments demonstrate that the action potentials are generated within the L-neurons and are not conducted antidromically from other neurons. The amplitude and frequency of the action potentials depend on the membrane potential of the L-neuron.

With light stimulation, or application of hyperpolarizing current, spikes can be generated within some of the L-neurons. Presumably non-spiking L-neurons are refractory due to maintained depolarization. They have membrane potentials of about −40 mV.

Action potentials in L-neurons were recorded only with high resistance microelectrodes. The vitality of the animal can not be correlated with the occurrence of spikes.

Functional significance of spontaneous tonic spike discharges in L-neurons is discussed in the context of behavioural experiments in the bee.

It is possible, that a given L-neuron uses either spiking or non-spiking signal transmission depending on the behavioural situation.

Although very fine microcapillary electrodes were used, no successful recordings or stainings of S-(small) neurons in the ocellar nerve were achieved. Therefore, results of non-identified ocellar interneurons which have been attributed to S-neurons should be critically reviewed.

Introduction

Very little is known about the ocellar system of insects compared to the large amount of detailed knowledge about the function and signal processing of the compound eyes. In the last few years the small number of large ocellar first order interneurons (L-neurons) have been used to analyse the characteristics of the ocellar visual system. These neurons are some of the largest cells in the insect brain. Their structure is well known from anatomical investigations (Goodman L.J. et al. 1975; Goodman C.S. 1976; Pan and Goodman 1977; Guy et al. 1977; Chappell et al. 1978; Guy et al. 1979). The dendritic arborizations are in direct contact with the axons of the photoreceptors. They project to both sides of the oesophagus in the posterior part of the protocerebrum (posterior slope region). Some of the neurons project as far as the thoracic ganglia. In addition to L-neurons in the ocellar tract there are interneurons of smaller axon diameter, the so called S-neurons. 30 L-neurons were identified in the honeybee, 12 of them are units of the median ocellus, and 9 units belong to each of the lateral ocelli (Pan and Goodman 1977; P. Mobbs, personal communication). Of the 9 L-neurons in the lateral ocelli 5 project into the thoracic ganglia. The total number of S-neurons in the ocellar nerve is approximately 80.

Intracellular recordings of interneurons from the ocellar nerve in different insect species revealed that the basic responses to light are graded potentials which have been ascribed to the L-neurons (dragonfly: Chappell and Dowling 1972, Patterson and Chap-

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pell 1980; locust: Patterson and Goodman 1974, Wilson 1978a, b, c; bee: Guy et al. 1979). Tonic spike discharges which were apparent in some of the recordings were attributed, without identification, to S-neurons (Wilson 1978a; Guy et al. 1979).

Graded signal transmission in non-spiking interneurons has been demonstrated repeatedly in insects and has been interpreted as being a basic mechanism of signal processing in the CNS (Burrows and Siegler 1976; Pearson 1976). Hengstenberg (1977) was able to show, that the so called non-spiking visual interneurons of the fly can produce action potentials under certain experimental conditions. Several authors using intracellular recording techniques have observed action potentials in ocellar interneurons (Chappell and Dowling 1972; Wilson 1978a, b; Guy et al. 1979; Patterson and Chappell 1980). It remains open to question whether L-neurons of the ocelli are truly non-spiking neurons or whether they are able to produce action potentials.

This paper shows that L-neurons of the honeybee can respond to visual stimulation with action potentials and graded hyperpolarizations.

Materials and Methods

Worker bees (*Apis mellifera carnica*) were caught at the hive entrance, immobilized by cooling and mounted in small metal holders (Erber and Menzel 1977). The back of the bee's head was fixed to the metal holder. The cuticula of the head capsule between the compound eyes, the bases of the antennae and the median ocellus was removed. Glands and tracheae were partly removed in order to expose the median part of the brain. The antennae, the mandibles and the proboscis were left intact and were able to move freely.

The electrode was moved into the brain with a micromanipulator while the depth of the electrode tip relative to the surface of the brain was measured continuously. The alpha-lobes of the mushroom modies were used as landmarks and most of the recordings were made in the axonal part of the L-neurons in the median protocerebrum (Fig. 1). The indifferent electrode was a silver wire introduced into the thorax of the bee. The electrophysiological recordings were made in a dim laboratory at a temperature of approximately 25 °C. The tips of the glasscapillaries were filled with a 3% aqueous solution of the fluorescent dye Lucifer yellow. The rest of the electrode was filled with 0.1 mol LiCl solution. The electrode resistance in the preparation was between 80 and 300 MOhm. Recordings of the signals were amplified with a WPI M 701 amplifier. The data were stored and analysed with conventional electrophysiological methods.

At the end of the electrophysiological recording the dye was injected into the cells by applying negative DC-current (approximately 10 nA over 5 min). The brain was dissected from the head capsule, fixed and processed histologically (Stewart 1978). The whole mount preparation of the bee brain was photographed under a fluorescence microscope. Marked neurons were reconstructed by using colour slides (Fig. 1).

A 450 W Xenon lamp (Osram XBO 450) was used as a light source for the light stimuli. With two condensors it was possible to stimulate ocelli and compound eyes independently. UV transmitting light guides were used to bring the light to the animal. To prevent stimulation of the compound eyes when the ocelli were illuminated, a small metal tube was mounted at the end of the light guide. The background light used in some of the experiments was generated by a 150 W Halogen-lamp (Schott KL 150B) and could be seen by the compound eyes also. The wavelength and intensity of the light stimulus was varied by using interference and quartz neutral density filters. Stimulus duration was controlled by an electronic shutter system.

Results

51 neurons in the protocerebrum of the bee brain were recorded from and injected with marker dye. Among these were 31 L-neurons. 7 L-cells responded with graded responses only, the remaining 24 displayed spike- and graded responses. 9 of these showed spontaneous action potentials.

The graded reaction to light stimulation of the ocelli consists of a rapid hyperpolarizing component at the onset of the stimulus (On-effect), a variable hyperpolarizing plateau during light stimulation and in most cases a hyperpolarizing component after the end of the light stimulus (Off-effect) (Fig. 2a). In many cases the membrane potential oscillate during the On- and Off-effects. In some recordings an increase of low frequency noise is observed during the light stimulus. Latencies are intensity dependent. The shortest latency for the On-effect was found to be 10 ms, and 17 ms for the Off-effect. The response of a single cell can vary markedly to identical stimuli presented at different times. Baseline deflection during penetration of a cell with a microelectrode was used to estimate the membrane potential of non-spiking L-neurons and was found to be approximately −40 mV. Combined with the graded responses to light, single or multiple spikes following the On- or Off-effect can be recorded (Fig. 2b, c, d). L-cells with spontaneously generated action potentials are shown in Fig. 2e, f. Inhibition of the spike rate during light stimulation is intensity dependent. Sometimes postinhibitory excitation of the spike rate is observed (Fig. 2f).

Figure 2 summarizes the most common responses of the L-neurons. The different types of reactions can not be correlated with particular L-cells. The L-neuron of the median ocellus shown in Fig. 1, for example, was recorded and marked five times. In different recordings the four response patterns shown in Fig. 2 were apparent (Fig. 2a, b, c, e).

The occurrence of spikes can not be correlated with the vitality of the animal nor with the duration between preparation and recording. It is dependent on the quality (resistance) of the microelectrode. With relatively low resistance electrodes (e.g. 30 MOhm) only graded responses were recorded.

In some cases L-neurons varied their membrane potentials spontaneously during recording, exhibiting

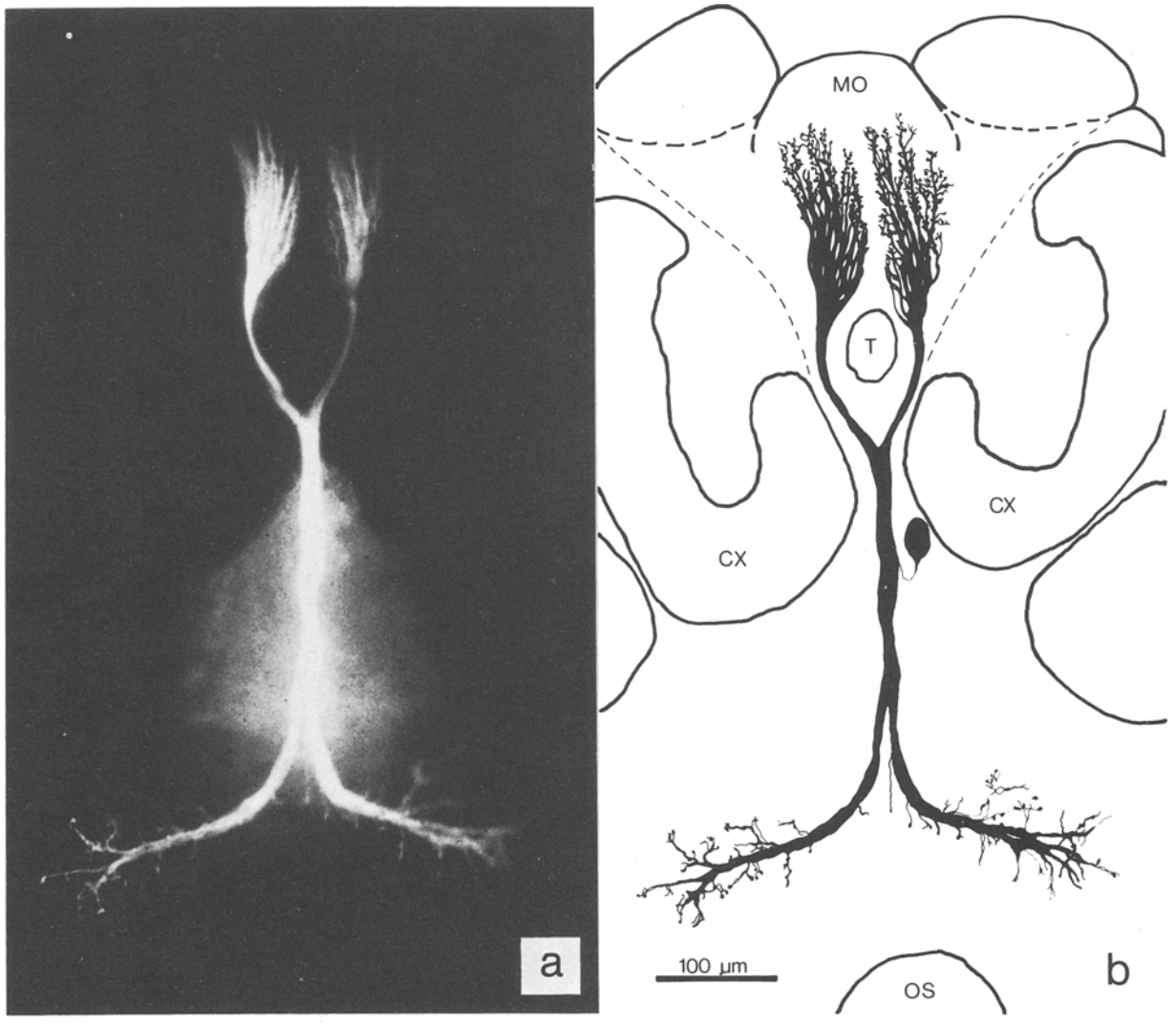

Fig. 1a, b. Intracellular stained L-neuron of the median ocellus of the bee. **a** Picture of the dye-injected cell (Lucifer yellow) in whole mount preparation. **b** Drawing of the reconstructed neuron. *MO* median ocellus; *OS* oesophageal foramen, *CX* calyces; *T* central trachea. The neuron is shown from the anterior. The two input arborizations in the retina each form projections which descend beside the central trachea and then join to form a single axon. This axon divides again above the oesophageal foramen into two branches which lead into the output arborizations in the posterior slope region of the median protocerebrum. (Compare with neuron MOC 7, Guy et al. 1979). – The response of this neuron to light stimulation is shown in Fig. 2c

changes between response patterns as shown in Fig. 2. An example is shown in Fig. 3. At the beginning of the recording the neuron shows no spontaneous activity and responds to white light with On- and Off-transients followed by spikes and with a hyperpolarizing plateau during light-On. After the end of the stimulus the membrane potential shifts to more negative values. Low frequency noise is apparent (Fig. 3a). When the membrane potential hyperpolarizes further, the noise increases until the neuron starts to spike spontaneously (Fig. 3b, c, d). A light stimulus now leads to an inhibition of the spike rate. With the passage of time the quality of the recording reduces. The cell then shows only graded reactions followed by On- and Off-spikes. This was the most common response in all L-neuron recordings (Fig. 3e).

Spike rate and spike amplitude are functions of membrane polarization, as can be clearly seen for the Off-effect in Fig. 3c and d. Assuming a membrane potential of approximately -40 mV for the non-spiking state, the relationship between membrane potential and spike amplitude and rate were analysed (Fig. 4).

Spike amplitude increased with increasing hyperpolarization. Spike rate also increased until approximately -56 mV and then fell. With a membrane po-

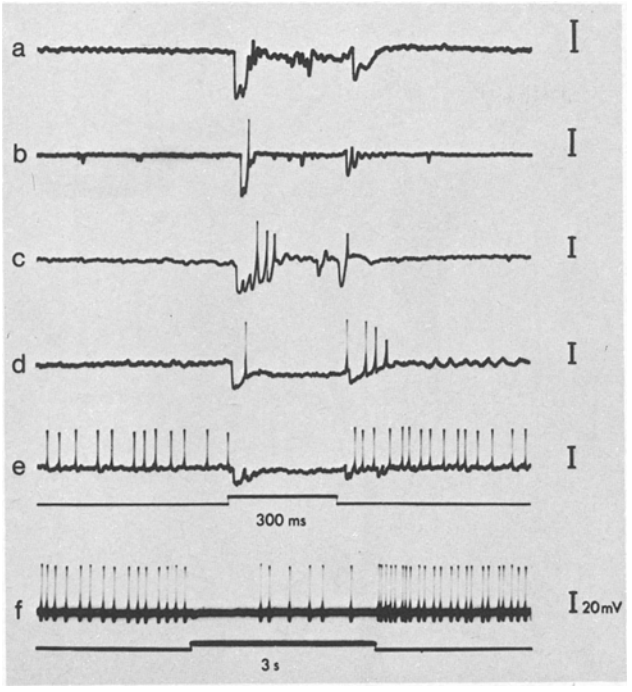

Fig. 2a–f. Response patterns of identified L-neurons to stimulation with white light. **a** Graded On- and Off-reactions, some 'noise' during stimulation. **b** On-effect together with one spike, oscillations during Off-effect, no hyperpolarizing plateau can be observed during stimulation. **c** On-effect with superimposed oscillations and spikes, Off-effect plus a single spike. **d** On- and Off-effects accompanied by spikes, a hyperpolarizing plateau appears during stimulation. **e** Spontaneous spike discharges, graded On- and Off-effects, inhibition of spike rate during stimulation. **f** Spontaneous discharge of action potentials, inhibition by illumination, postinhibitory excitation after the end of the stimulus. Only a small graded response to light-On can be seen. – Horizontal bars: stimulus duration; vertical bars: amplitude = 20 mV

tential of −60 mV the amplitude of the action potentials reached 67 mV. Under these conditions there was a positive overshoot of the membrane potential during a spike. The duration and form of action potentials in spontaneous spiking L-neurons is not apparently different from signals in other nerve cells of the bee brain. The phase of repolarization is fast. A correlation between the amplitude of spikes and the recording site along the axon was not observed.

Maintained depolarization of L-cells which respond with graded potentials appears to prevent spike generation. Therefore application of a hyperpolarizing current should enable spike generation by shifting the membrane potential. When this was done, spikes could be generated only in those cells which already showed On- and Off-spikes in addition to the graded responses. The recordings indicate that cells showing On- and Off-spikes are less depolarized than those which show only graded responses. L-neurons which responded only with graded responses showed no

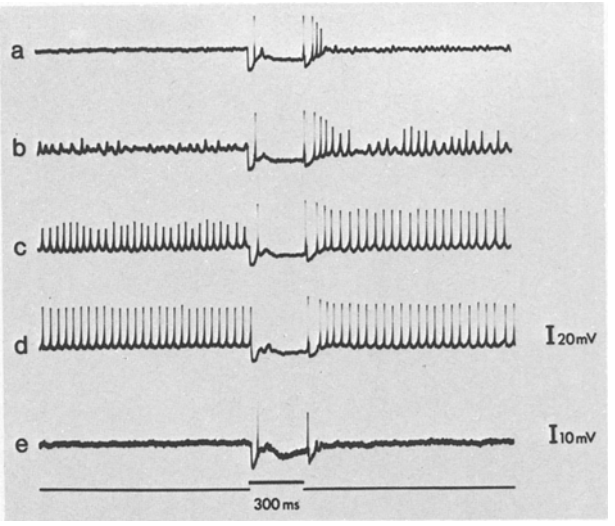

Fig. 3a–e. Alterations in response pattern of an L-neuron to light stimulation during one recording. **a** No spontaneous activity, the neuron remains slightly hyperpolarized and some 'noise' can be observed. **b** "Noise" has become stronger, after the end of the stimulus, some spontaneously generated spikes are observed. **c** Further intensified spike activity. **d** Spontaneous discharge of action potentials, inhibition by light stimulation. **e** After the quality of the recording was reduced with time no further spontaneous activity was observed and only one On- and Off-spike could be seen. Horizontal bar: light stimulus, vertical bars: amplitude. This neuron was used to prepare Fig. 4

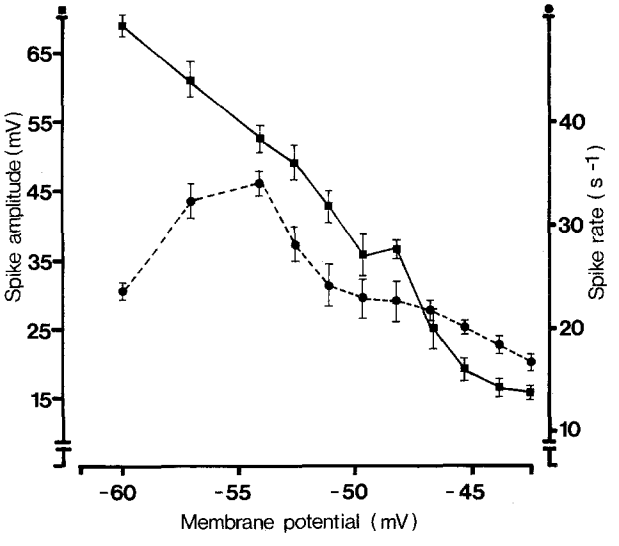

Fig. 4. Dependence of spike amplitude and frequency on membrane polarization. Spike amplitude increases with increasing hyperpolarization of the membrane potential (■). The spike frequency also increases until approximately −56 mV and then starts to fall (●). At membrane potential values more positive than −40 mV no spontaneous activity can be observed. Vertical bars: standard deviation

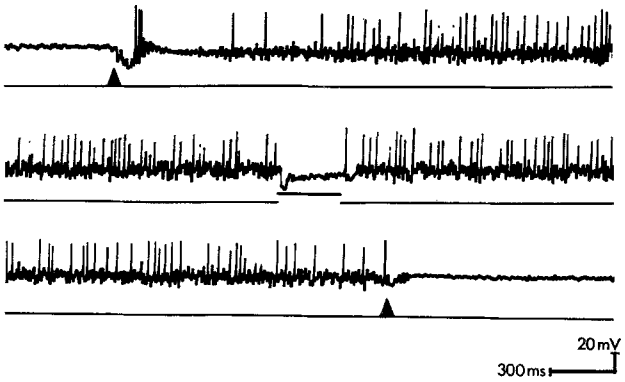

Fig. 5. Induction of spike activity in an L-neuron by visual stimulation. Switching on a background light (arrow head) produces spike activity in the L-neuron. An additional imposed flash of white light inhibits the discharges. Switching off the background light (arrow head) returns the neuron to a state in which no spontaneous activity is observed. Horizontal bar: stimulus duration, vertical bar: amplitude

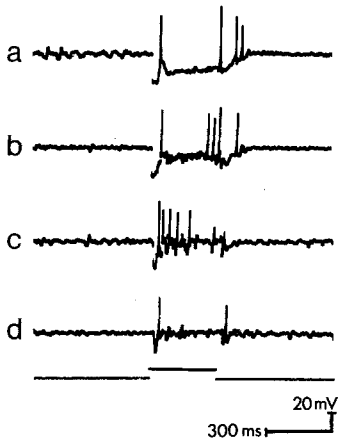

Fig. 6a–d. Intensity dependence of L-neuron response patterns to stimulation with white light. **a** At log I=0: On- and Off-effects with spikes, but no spikes during hyperpolarizing plateau. **b** log I=−0.5: plateau is reduced, some spikes in the rear of the plateau. **c** log I=−1.0: the hyperpolarizing plateau is reduced further, several spikes appear in the plateau region. **d** log I=−1.5: no plateau can be observed and the appearance of spikes is limited to the On- and Off-effect. The responses of the L-neuron in the plateau region show a relationship between the degree of hyperpolarization of the membrane potential, which is elicited here by white light stimulation, and the appearance of action potentials (compare with Fig. 4)

change during current injection. But after the prolonged hyperpolarizing current injection required for Lucifer yellow marking, On- and Off-spikes could be seen. This effect was only apparent for the first light stimulations and disappeared rapidly. With these neurons it was impossible to induce spontaneous spike discharges.

Sustained light stimulation also can lead to spike activity. As shown in Fig. 5 the L-neuron responds with action potentials to a background illumination. An additional white light flash leads to inhibition of the spike rate. After switching off the background light, the neuron again displays no activity at all. If now stimulated with flashes of white light of varying intensity, no spikes at the plateau levels for low and high intensities are observed whereas spikes are generated at an intensity of log −1 (Fig. 6). Comparing this result with the dependence of the spike rate on the membrane potential (Fig. 4), it becomes obvious that the medium light intensities hyperpolarize the membrane potential in such a way that the L-neuron is able to generate spikes, whereas low light intensities do not lead to significant hyperpolarization and cannot compensate for the maintained depolarization. The strong hyperpolarization following a light flash of high intensity inhibits spike activity in the same way as is known for normal spiking neurons.

In some experiments spiking neurons with excitatory or inhibitory light responses were found. By staining these neurons they all were identified as local higher order interneurons in the median protocerebrum. In no case were there successful recordings of S- (small) neurons. There were no responses of L-neurons to light stimulation of the compound eyes, whereas local interneurons can respond to ocellar and compound eye illumination (Milde, in preparation).

Discussion

The specific criteria for non-spiking neurons as formulated by Pearson and Fourtner (1975) and Hengstenberg (1977) (as far as they were testable with the methods used in these experiments) are satisfied by the L-neurons of the bee in the non-spiking state. These neurons show (1) graded responses, (2) low membrane potentials (−40 mV), (3) no generation of action potentials during depolarization and (4) often noise-like potential fluctuations during the light stimulus. On the other hand, L-neurons in the spiking state have properties which can only be explained by a regenerative excitable membrane mechanism in that the spike rate and amplitude depend on membrane polarization. The action potentials in the L-neurons are not different in their time course from other neurons in the bee brain, they have high amplitudes and are able to depolarize the membrane potential to positive values. It is unlikely that spikes with these features could be transmitted passively across electrical synapses from postsynaptic units. The results argue for an origin of action potentials within the L-neuron itself. However, the recordings gave no

indication of a local region of regenerativeness as is the case in locust L-neurons (Wilson 1978b).

Intracellular staining clearly shows that L-neurons of the same type can either respond with graded potentials or action potentials depending on the conditions of the recording. Similar to the movement-sensitive interneurons of the fly (Hengstenberg 1977) L-neurons are refractory, and therefore non-spiking as a result of maintained depolarization. The onset of refractoriness does not seem to be a function of anoxia, because it does not correlate with the time between preparation and recording. Possible mechanisms for the maintained depolarization could be a constant synaptic input depolarizing the neuron or a leakage current of the membrane leading to depolarization (Hengstenberg 1977). The cause of the relationship between the quality of the microelectrodes and the grade of refractoriness is unknown at the moment. Blunt microcapillaries seem to affect the membrane in such a way that refractoriness is maintained.

Further evidence for this relationship comes from extracellular recordings from ocellar nerves. In these experiments the single cell membrane was not impaired, and the neurons always showed action potentials. In investigations with the dragonfly (Ruck 1961; Rosser 1974; Kondo 1978), the locust (Hoyle 1955), the fly (Metschl 1963) and the bee (Labhart 1978) tonic dark discharges of spikes were described. Stimulation of the ocelli with light inhibited this dark discharge, often leading to an excitatory effect after the cessation of the stimulus. These results were identical with those presented in Fig. 2e and f, where response patterns of intracellularly recorded L-neurons of the bee are shown. Therefore it seems probable that the extracellularly recorded reactions are also responses of the large L-neurons and are not due to the S-neurons. In the investigations of Guy et al. (1979) intracellular spike responses of ocellar interneurons of the bee, similar to those described above, were shown. As these neurons were not dye injected and identified, the authors attributed the spike responses to the S-neurons.

With intracellular recordings from the ocellar nerves of other insect species, spike responses have been reported in some cases. Chappell and Dowling (1972) found with extracellular, and some times also with intracellular, recordings from the dragonfly spontaneous impulse activity which was inhibited during the light stimulus and which was similar to the responses described in the bee. During intracellular recordings these responses could be observed for a short time only. Afterwards the cell responded in a graded manner which was attributed by the authors to cell damage. Patterson and Chappell (1980) found graded responses, and in some cases different types of spike activity ranging from Off-spikes to spontaneous spike discharges, when they recorded from ocellar interneurons in the dragonfly. The spontaneous spike discharges in these experiments were inhibited by light stimulation. Wilson (1978b) also described the appearance of spikes in L-neurons of the locust but only after cessation of a light stimulus or an injected hyperpolarizing current. He assumed, that these Off-spikes were caused by a regenerative membrane mechanism in the L-neuron which is confined to a local region in the brain. On the other hand he attributed tonic spike discharges to S-neurons (Wilson 1978a). Obviously there are indications for spike activity in ocellar interneurons (L-neurons) in other insects too.

The response characteristics of ocellar interneurons showing graded hyperpolarizations were compared to those of the monopolar cells in the lamina of the insect compound eyes (Laughlin 1981; Wilson 1978b). Spike-like events from second order visual cells in invertebrate preparations have been recorded occasionally (Laughlin 1973, dragonfly; Zettler and Järvilehto 1973, fly; Erber and Sandeman 1976, crab). In barnacle I-cells, Stuart and Oertel (1978) found action potentials which are due to voltage-sensitive calcium conductance of the membrane. Shaw (1968) described some recordings from second order cells in the locust lamina with spike discharges. It is quite possible that, as with ocellar interneurons in the bee, action potentials might be found in other visual interneurons with improved recording techniques. Whereas Hengstenberg (1977) assumed that the non-spiking state in movement-sensitive neurons in the flies' lobula did not represent the natural state of these neurons but is caused by cell damage, the results shown in Fig. 3 indicate that L-neurons in the bee might switch between two different coding mechanisms. In different behavioural situations (e.g. in flight) the bee may select the optimal form of information transmission. Graded signals would enable higher temporal resolution of the visual information. Depending on the conductance properties of the axon, graded potentials might only be transmitted over shorter distances. On the other hand there may be selective synaptic mechanisms which are specific for graded potentials or action potentials and therefore transfer information specifically to particular following neurons.

Electrophysiological experiments with identified interneurons in the optic lobes of the bee revealed that visual information processing can change during the recording. In these cells the movement dependent response alters from excitation to inhibition (Hertel, pers. comm.). These response alterations could be caused by intrinsic changes of the nervous system or by extrinsic inputs from other stimulus modalities.

Experiments with multimodal neurons in the median protocerebrum of the bee have shown that stimulation with sugarwater to the proboscis or the antennae can change all multimodal response components of a cell or can modulate specific responses alone (Erber 1980). Current electrophysiological analysis on the bee L-neurons has shown that spiking L-neurons can respond to stimulus modalities other than illumination of the ocelli. In this sense they are multimodal interneurons (P. Mobbs, personal comm.; Homberg and Milde, in preparation). These other stimulus inputs could be used as a possible mechanism for realization of switching from graded signal transmission to transmission by action potentials.

More detailed interpretations about signal processing and the function of the ocelli might arise from the correlation of electrophysiological data with behavioural experiments. In a detailed analysis of the ocellar system of the locust Wilson (1978a) concluded that graded signal transmission is very suitable for coding and transmitting fast changes of light intensity. He argued that the ocelli are involved in flight control. In experiments with *Locusta,* Taylor (in preparation) was able to demonstrate that during flight the ocelli control head movements and accompanied steering movements of the wings when an artificial horizon is rotated around the body axis of the animal. This behaviour is caused by changes of light intensity in the whole visual field of the animal.

With extracellular recordings it became evident that the ocelli code intensity levels and changes of background light (Ruck 1961; Metschl 1963; Autrum and Metschl 1963). Behavioural analysis in the bee confirmed this conclusion. In experiments with ocellar-blinded bees, it was shown that the ocelli transmit information about the level of background light intensity and its changes during foraging, phototactic behaviour (Schricker 1965) and waggle dance (Gould 1975). One conclusion from these experiments was that the sensitivity of the compound eyes is controlled via ocelli. Ocellar interneurons transmitting information concerning background light intensity have not been identified. However, the expansive arborizations of L-neurons in the ocellar retina suggest that they may be well suited to such a function. On the basis of the results discussed in this paper it is difficult to understand how non-spiking L-neurons could be able to code the intensity of a steady background light. The tonic response during a maintained light stimulus is rather small, often there is no plateau at all or the hyperpolarizing response vanishes during maintained illumination. In accordance with intracellular recordings, coding of steady background light intensity could be produced by the tonic frequency of action potentials. The changes of light intensity could be coded by the graded potentials as well as by inhibition or excitation of the spike frequency. More information concerning the dependence of action potentials on light stimuli is necessary to determine whether or not the L-neurons are involved in coding background light intensities.

As S-neurons have not been identified so far in electrophysiological experiments their function in signal coding and processing remains unknown.

The experiments discussed here form the basis for future investigations analysing the factors controlling the appearance of action potentials and the mechanisms of switching between the two modes of coding. The biophysical properties of the L-neuron membrane need to be analysed in a more detailed manner. The multimodal characteristics of the L-neurons indicate that the ocelli might be involved in numerous behavioural patterns. It can be concluded that the ocellar system is certainly much more complex than has been generally assumed.

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