

## THE FUNCTION OF THE INSECT OCELLUS

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## INTRODUCTION

Many insects possess two types of eye: a compound eye and a simple eye or dorsal ocellus. Much work has been done on the powers of vision in insects, and it is known that these are almost entirely due to the presence and form of the compound eye. The perception of form and colour, and the appreciation of movement in the visual field, are its recognized functions.

No such clearly defined functions have yet been assigned to the dorsal ocellus. The optical system of this organ is such that no image can be formed on the retina. Its occurrence within the class is extremely erratic and bears no apparent relation to the mode of life or the systematic position of those insects in which it occurs. On the other hand, insects deprived of their ocelli show certain peculiarities of behaviour, which suggest that the ocellus *is* in some way concerned in the response of the animal to light.

The object of the present research was to obtain more knowledge of the function of the ocellus, primarily by recording the nervous response to ocellar stimulation. The migratory locust (*Locusta migratoria migratoroides*) provides a preparation just large enough for electrodes to be placed on the ocellar nerve and electrical changes occurring there to be amplified and recorded. It has also proved possible to record from the circum-oesophageal commissure and thus to investigate, at a point nearer the motor system, the effects of stimulating the ocellus and cutting the ocellar nerves.

Information has also been obtained on the distribution of the ocellus among insects, the optical system of the ocellus, and the histology of the ocellar nerve.

## THE OCCURRENCE OF THE OCELLUS

An examination of the literature and of museum collections was made to determine the occurrence of the ocellus within the class of insects, as it was hoped that this would throw some light on the function of the organ. In fact its distribution seemed quite anomalous, and emphasized, rather than helped to solve, the problem. The following list summarizes the facts.

ORTHOPTERA: always present in Acrididae and Gryllidae; sometimes present in Blattidae, Mantidae, Tettigoniidae; not present in Grylloblattidae. DERMAPTERA: absent. PLECOPTERA: two or three present. ISOPTERA: present. EMBIOPTERA: absent. PSOCOPTERA: sometimes present. ANOPLURA: absent. EPHEMEROPTERA: present. ODONATA: usually present. THYSANOPTERA: present. HEMIPTERA: great variation. Some families separated on the presence or absence of ocelli. Several families in which some genera possess ocelli and some do not. NEUROPTERA: conspicuous in some families, absent in others. MECOPTERA: some genera with ocelli, others without. TRICHOPTERA: some families with ocelli, others



without. One family including six genera with ocelli and two without. LEPIDOPTERA: sometimes present. COLEOPTERA: absent except in a few species not all in the same family. STREPSIPTERA: absent. HYMENOPTERA: usually present, but sometimes absent in the Vespoidea. DIPTERA: sometimes present. APHANIPTERA: uncertain.

This list shows the general irregularity of the distribution. From a more detailed analysis of the orders (especially Orthoptera and Hemiptera) it frequently appeared that of two insects, very closely related systematically and with apparently exactly the same habits, one may possess well-developed ocelli and the other have lost them altogether.

#### THE STRUCTURE AND OPTICAL SYSTEM OF THE OCELLUS

There is little variation in the structure of the ocellus throughout the class. The lens is part of the exoskeleton. The corneagen layer is a transparent area of the hypodermis underlying, and secreting, the lens. The retina consists of pigment cells and sense cells, the latter grouped together to form rhabdomes. In some ocelli the retina is a regular columnar epithelium, while in others, as in the typical orthopteran ocellus, its constituent cells are more irregularly arranged. The sense cells bear only short processes extending to the synaptic region immediately behind the retina.

The close proximity of lens and retina precludes the possibility of image perception. Homann (1924) investigated living and prepared ocelli of many insects and showed that although the lens was sufficiently well formed to produce an image, this would fall a considerable distance behind the retina. Homann did not study *L. migratoria*, but his general conclusion was confirmed by a determination of the distance of the principal focus and the retina from the front surface of the lens, which was made during the present work.

Following Homann, the principal focus was found by examining the ocellus through a microscope to the tube of which was secured a horizontal cross-piece bearing a point source of light at either end. The images of these lights were reflected in the front surface of the lens, and their distance apart could be measured by a micrometer. Knowing the actual distance between the lights, and the vertical distance between them and the ocellar lens, the radius of curvature of the latter was calculated. The position of the principal focus was then worked out, knowing the refractive index of the lens. The value thus obtained took no account of refraction at the inner surface of the lens, but as the refractive index of lens and corneagen layer cannot be very different, this simplification will not introduce serious error. The radius of curvature of the front surface of the lens was 0.23 mm., and the principal focus therefore at a point 0.44 mm. behind this surface (see Fig. 1).

The position of the retina was found directly. The animal was mounted below a microscope and a bright light thrown into the ocellus by a vertical illuminator. The lens and retina were brought into focus in turn and the distance between them measured by a micrometer. As the retina has a highly diffusing surface it was not very easy to focus, but among a large number of determinations the distance between the front of the lens and the retina was never found to reach the value of 0.09 mm. The principal focus was thus five times as far behind the lens as the retina, and so the possibility of image perception by the ocellus of *Locusta* may be excluded.

## EXPERIMENTAL WORK

*Previous work on the ocellus*

The methods previously used to determine the function of the ocellus have all involved observing the effect of blinding upon the behaviour of the animal. Early investigators (Plateau, 1887-8; Homann, 1924; etc.) found that insects with their compound eyes painted over behaved as though blind whether they possessed ocelli or not. More recently, however, it has been shown that certain differences can be produced in the reactions of an insect towards light by painting over the ocelli, the compound eyes being left free. Thus *Drosophila* reacts more rapidly to a sudden exposure to light when the ocelli are free than when they are painted over (Bozler,

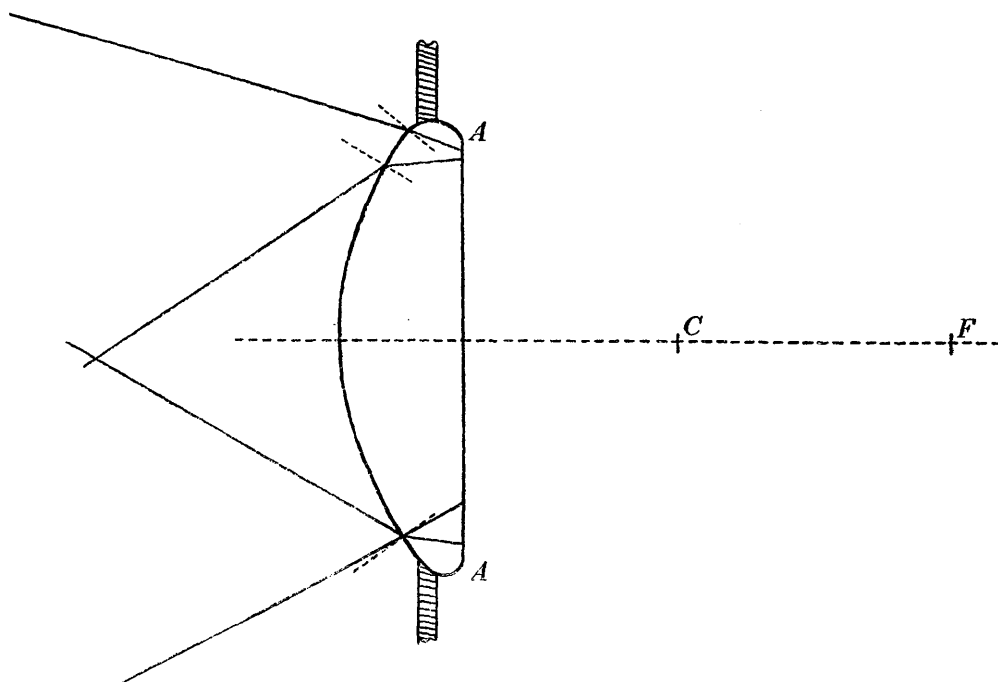


Fig. 1. Scale diagram of the ocellus. Light is shown incident on the lens from two distant point sources, and it is seen that the retina is uniformly illuminated by each except at its extreme edge. *AA*, outer face of retina; *C*, centre of curvature of outer face of lens; *F*, principal focus.

1925). Bees, walking along a path between two lights of equal intensity, may be caused to deviate towards one or other of the lights by painting the median and one lateral ocellus. The deviation occurs towards the side of the blinded ocellus (Müller, 1931). Bees which are normally negatively phototactic, at a temperature below 14° C., become positively so when the ocelli are painted over (Gotze, 1927; Müller, 1931).

In general it appears that ocelli are not capable of evoking a motor response by themselves, but only do so when working in co-operation with the compound eyes. They seem to 'prepare' the nervous system for the reception of stimuli from the more specific sense organs. This view has been elaborated by Wolsky (1930, 1931,

1933). He considers that whereas most sense organs possess a specific function in evoking certain motor responses and also have a general stimulating effect on the nervous system, the ocelli possess only the latter property.

#### METHODS

Almost all the present work was done on *Locusta migratoria*; the preparations used will be described in the appropriate sections. The amplifier was a three-stage directly coupled instrument with a balanced input and separate power stage driving a Matthews oscillograph. A fourth, condenser-coupled stage, could be switched into the circuit at will. During all this work a loud-speaker was continuously in use.

The fine platinum electrodes were moved into position by means of a Zeiss micromanipulator, without the use of which the investigation of these small preparations would be impossible.

As the ocellus is incapable of forming an image, its response to a simple on-off stimulation from a flash-lamp or dissection lamp was investigated.

#### RESULTS

##### (i) *The ocellar response*

The preparation consisted of the isolated head of the locust mounted, ventral side uppermost, in plaster of Paris. The mouthparts and tentorium were removed and the brain exposed. The ocellar nerves, which are about 1 mm. long, were then freed from the membranes which support them. This must be done with great care, as any tension produced in the nerves tends to pull the retina of the ocellus away from the lens. It was necessary to take precautions against desiccation, otherwise the nerves dried up within about 3 min. The ordinary type of moist chamber could not be used in conjunction with the micromanipulator, and the frequent use of Ringer was inconvenient. Good preservation of the nerve was first obtained by raising the humidity of the laboratory to a high value, but later it was found possible to immerse the whole preparation in medicinal paraffin saturated with oxygenated Ringer. The nerve would live for at least an hour under these conditions.

The preparation was mounted on a paraffin block beneath a binocular microscope and fine hook electrodes used to make contact with the tissues. Fig. 2A shows a typical preparation and response. When the light was switched *on*, the electrode nearer the eye became positive to the one nearer the cut end of the nerve; when the light was switched *off*, this potential disappeared after an 'overswing' of varying size. As the nerve near the cut will be depolarized, it follows that light stimulation is accompanied by increased polarization at the ocellus, and darkness by decreased polarization.

These results were repeated (Fig. 2B) with one electrode on the cut nerve and one on any tissue in the head. The latter then acts as though in contact with the ocellus. The same form of response was also obtained with electrodes on the intact nerve, but this preparation is unsatisfactory owing to the uncertainty of the electrical connexions within the tissues.

The potential changes just described were never accompanied by nerve impulses, even when the condenser-coupled amplifier with a gain of  $10^5$  was in use. This may



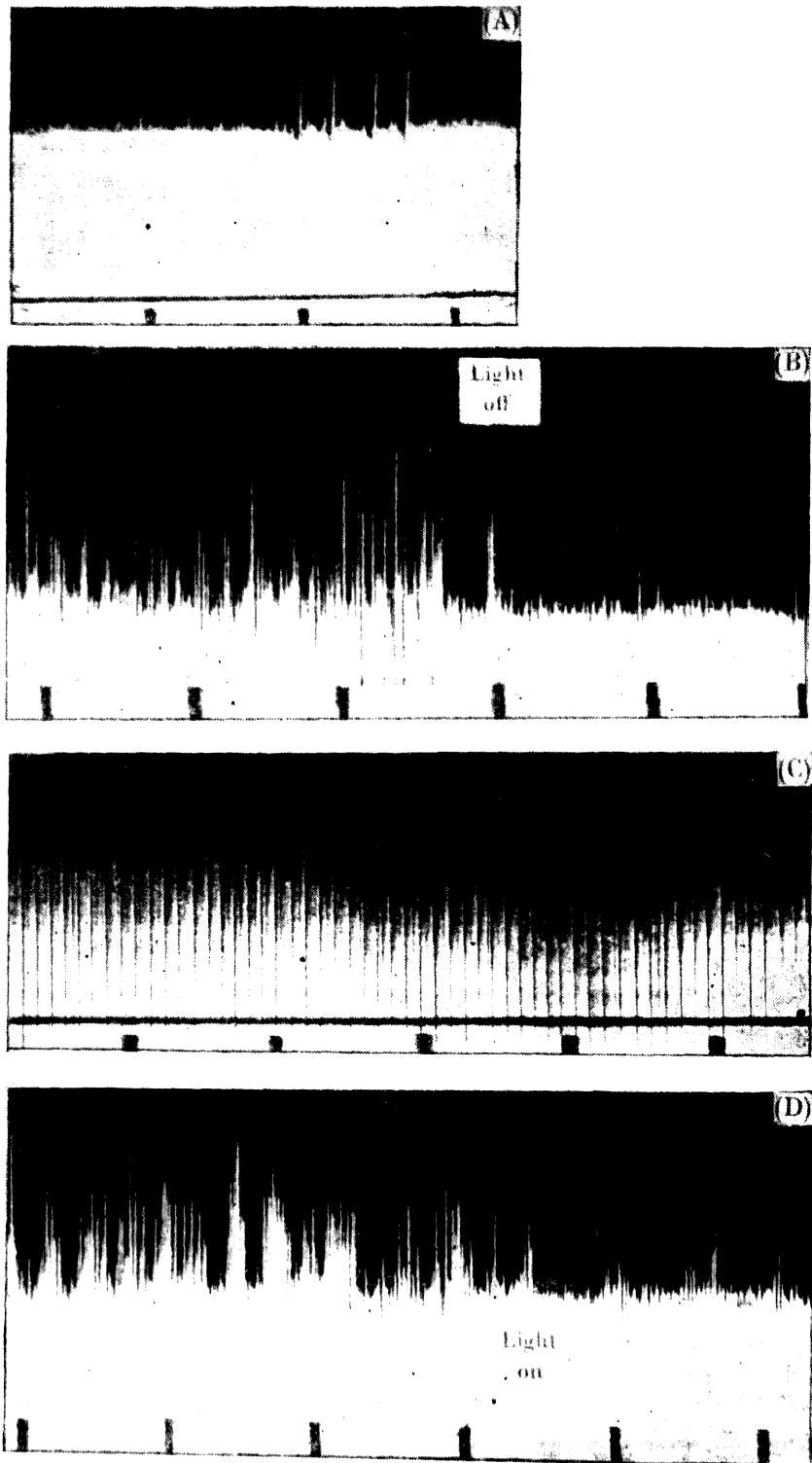


Fig. 3. Explanation in text. Records read from right to left. Time marks every  $\frac{1}{10}$ th sec.

gradually dying away. If, however, the light was switched on before this time, the discharge immediately ceased.

The maintained discharge just described will be referred to as the 'darkness' effect, and the response to movement in the visual field as the 'movement' effect.

(b) *Optic lobes cut.* In such a preparation the movement effect was absent, while the darkness effect was as well marked as in the previous preparation.

(c) *Ocellar nerves cut.* The effect of cutting the ocellar nerves was very marked and surprising. It was the same whether the optic nerves were previously cut or not. Severing the frontal ocellar nerve had no effect beyond an 'injury' discharge of a few seconds, and possibly an increase in the darkness effect due to the intact lateral ocelli. When the latter were cut, however, there occurred, sometimes after a silent period of up to half a minute, a series of impulses of gradually increasing frequency, at first individually discernible but after a minute producing a low note. Fig 3 C shows this discharge after it has become fully developed. It was unaffected by light and was maintained for several minutes before gradually dying away. When it had done so, there was no darkness effect whether the optic lobes were intact or not. If they were intact, a darkening of the field produced a short burst of impulses which was almost certainly the 'movement' effect due to the change of intensity as the lamp filament cooled. The short burst was repeated when the lamp was turned on, and can be explained in the same way. Fig. 3 D shows this response, while at the beginning of the record can be seen all that remains of the discharge produced when the lateral nerves were cut.

The practical advantage of studying the ocelli by recording from the commissure is that, whereas the locust is the only available insect with ocellar nerves long enough for electrodes to be placed on them, there are probably a number of insects with commissures long enough for this purpose. It is thus possible to verify the above results with other species and to compare them with the responses to light obtained from insects not possessing ocelli. During this research the only other insect used was a dragonfly, which possessed ocelli, and in it the movement and darkness effects were both obtained, and also a note discharge when the ocellar nerves were cut.

#### DISCUSSION

We have found that when the ocellus is darkened it becomes depolarized and at the same time there is a burst of impulses in the commissure. The condition may be maintained for several minutes if the darkness is continued, but disappears immediately the ocellus is reilluminated. When this happens the ocellus becomes polarized and the impulses in the commissure abruptly cease. Now there is a considerable amount of evidence that the passage of impulses from a ganglion is preceded by a state of depolarization in the ganglion itself, while an increase in the polarity of the ganglion is accompanied by inhibition of impulses. Adrian (1931), working on the central nervous system of *Dytiscus*, placed an electrode on one of the ventral ganglia and another on the nerve cord. Before each burst of impulses he found that the ganglion became negative to the nerve, the record consisting of a slow

potential change with impulses superimposed. Barron & Matthews (1936) showed that when motor neurones in the frog's cord are reflexly stimulated an electrotonic spread may be detected in the ventral root, which they regard as an indication of depolarization within the cord. A motor volley may accompany this, depending on the extent of the depolarization. They also found that the application of negative potentials to the cord would produce an impulse volley in the ventral root.

These results suggest the following interpretation of the action of the ocellus. When the ocellus is darkened or the ocellar nerve cut, depolarization occurs in the ocellus, which spreads electrotonically down the very short nerve and depolarizes a ganglion within the brain, with the consequent discharge of impulses down the commissure. There are two independent pieces of evidence in support of this hypothesis which can most conveniently be described here.

First, it was found that when a potential of a few microvolts was applied between the ocellar nerve and the base of the brain, the nerve being negative, a continuous discharge similar to the darkness effect was recorded from the commissure. When the nerve was made positive this discharge immediately ceased.

Secondly, the ocellar nerves are histologically unusual. They contain very few fibres (four in the frontal and five in the laterals) of exceptionally large diameter— $25\mu$  on the average—a condition also described in the bee by Kenyon (1896), and in the dragonfly and other insects by Cajal (1918). In view of the above experimental results it is interesting to note that Cajal describes the fibres from all three ocellar nerves, together with fibres from the optic lobes, forming a ganglion on the posterior face of the brain, just above the oesophagus.

It will require more evidence than is provided in the present paper finally to establish the existence of a nerve in which the usual nerve impulses are lacking. But whatever the mechanism of conduction in the nerve, the effect of varying light intensities on the ocellus is clear: darkening the ocellus (or cutting the ocellar nerve) results in discharges down the commissure, and these discharges are inhibited when the ocellus is illuminated and the nerve intact. It is known from behaviour experiments that darkening the ocellus does not by itself produce reflex activity, and therefore the results described above seem to give support to Wolsky's theory that the ocellus affects the general excitatory state of the nervous system. It might well be to an insect's advantage if certain reflexes were facilitated when the light intensity is reduced, as by a shadow; and it would be interesting to measure the threshold stimulus needed to evoke various reflexes involving the central nervous system when the ocellus is illuminated and when it is darkened.

#### SUMMARY

1. Little light is thrown on the function of the insect ocellus by blinding experiments or by a study of its distribution within the class.
2. The ocellus cannot, on optical grounds, receive an image, but can only be affected by changes in intensity of illumination.
3. The ocellar nerves are characterized by a small number of constituent fibres, and by the large diameter of the latter.



4. When the ocellus is darkened, the electrical response in the nerve consists of a decrease in potential near the ocellus, relative to the cut end of the nerve. No impulses were detected in the ocellar nerve.

5. When the ocellus is darkened, or one of the lateral ocellar nerves cut, there is a continuous discharge of nerve impulses in the commissures. This ceased as soon as the ocellus was reilluminated.

6. It is suggested that darkening the ocellus causes depolarization which spreads down the ocellar nerve and depolarizes a ganglion in the brain, thereby inducing the discharge of impulses down the commissures. It is pointed out that this might facilitate reflexes at lower centres, and so accelerate the animal's response to shadows.

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