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A LOCUST WIND AND OCELLAR BRAIN NEURONE

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SUMMARY

1. One of the large descending brain neurones in each half of the central nervous system of a locust is probably important in regulating the attitude of the locust's flight in the pitch plane. This function is suggested by a consideration of the stimuli which excite the interneurones, and of the muscles whose motoneurones they excite.

2. Each of these interneurones has its cell body in the protocerebrum and its axon descends the ipsilateral connective and has branches in all of the thoracic ganglia.

3. The interneurones are excited by currents of air directed at the front of the head. An increase in the intensity of light falling on the median ocellus causes a reduction in the frequency of spikes produced by stimulation of the wind-sensitive hairs, and a reduction in the intensity of this light causes an increase in the frequency of these spikes.

4. Each interneurone makes excitatory connexions with motoneurones of the subalar and dorsal longitudinal flight muscles ipsilateral to it.

INTRODUCTION

Although the structures of a few of the largest neurones in the brains of locusts have been described (Williams, 1975) the functions of most of them are unknown. Approaches which may be employed to establish a function for a particular brain neurone are to list the sensory stimuli which excite it; to search for output connexions from it to other identified neurones such as motoneurones; and to observe how it responds when a locust is allowed to move in different behavioural situations. These approaches have been applied to two large descending brain neurones, the descending contralateral movement detector (DCMD) and the tritocerebral commisure giant (TCG). A DCMD is excited by an abrupt movement of a small object in front of one compound eye and by a loud noise (Rowell, 1971; O'Shea, 1975), and it makes excitatory connexions to some of the motoneurones which move the hind legs and the fore- and hind wings (Burrows & Rowell, 1973; Pearson & Goodman, 1979; Simmons, 1980). Burrows & Rowell (1973) have suggested that it plays a role in the initiation of a jump, and it may also help to extend the wings prior to a jump and to execute rapid changes in flight course to avoid collisions (Simmons, 1980). A TCG is excited by mechanical stimulation of some of the wind-sensitive hairs on the head or

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of an antenna and by alterations in light intensity (Bacon & Tyrer, 1978) and it makes excitatory connexions with some flight motoneurones (Bacon and Tyrer, 1979).

This paper deals with the stimuli which influence the frequency of spikes in another of the large descending brain interneurones in one side of the nervous system of a locust, and with the output connexions which it makes with some of the thoracic motoneurones. It is excited by a current of air flowing over the head and by a reduction in the intensity of light falling on the median ocellus. An increase in the intensity of light falling on the median ocellus causes a reduction in the frequency of wind-induced spikes.

The pathway that the interneurone provides between an ocellus and flight motoneurones is interesting because ocelli have been thought for some time to be associated with the control of flight (e.g. Demoll & Scheuring, 1912; Link, 1909; Kalmus, 1945), and M. Wilson (1978*a*) has suggested that they help to stabilize flight by monitoring changes in the orientation of the visual horizon. He points out that a number of features make the large second-order neurones of ocelli suitable for detecting changes in the orientation of the horizon. These features are: (1) they are very sensitive to ultra violet light, which makes them well able to detect a change in the position of the border between the sky and the land; (2) their large axons ensure the rapid transmission with little attenuation of signals from the receptors of an ocellus into the brain; (3) they have very large spatial sensitivity; and (4) the three ocelli of a locust are disposed in a way that allows them to detect the horizon right around the animal. Changes in the intensity of light reaching the median ocellus of a flying locust would signal changes in orientation in the pitch plane. The connexions that the interneurone described here makes with flight motoneurones are suitable for altering the angle of pitch of a locust's flight course, and I shall suggest that one of its functions is to ensure the stability of flight in this plane.

MATERIAL AND METHODS

Experiments were performed on 65 adult *Schistocerca americana gregaria* (Dirsh), of both sexes, taken from cultures. An incision was made along the middle of the dorsal surface of a locust from the second abdominal segment to the head. The wings were gently pulled sideways and secured with plasticene to spread the thorax laterally. The gut, fat, some small muscles and parts of the endoskeleton which lie over the thoracic central nervous system were removed. A stainless steel, plastic-coated platform was placed beneath the meso- and metathoracic ganglia by manipulating it through the abdominal connectives. In some experiments the prothoracic ganglion was stabilized in a similar manner. Hook electrodes placed beneath each pro-meso-thoracic connective recorded extracellular spikes from some interneurones.

Microelectrodes for recording from central neurones were filled with 2 M potassium acetate and had d.c. resistances of 50–80 MΩ. In most experiments the perineurium of ganglia and connectives was softened by applying a 1% solution of protease in saline for 2 min. No differences were found between animals which were treated in this way and those which were not. The identity of a flight motoneurone penetrated by a microelectrode was established by correlating spikes in it, induced by applying a depolarizing current, with twitches seen in a muscle. By cutting through the elevato

muscles halfway along their lengths, parts of all the flight muscles were made visible. This method proved more reliable than employing extracellular leads to record from and stimulate motoneurone terminals in flight muscles. Most intracellular recordings from motoneurones were made in the regions of nerve roots, where the most likely neuronal process for an electrode to penetrate is the axon of a motoneurone or sensory neurone. The muscles are named and numbered from Snodgrass (1929).

To stain interneurones electrodes were filled with 1 M cobalt nitrate, and 500 ms pulses of positive current not exceeding 15 nA were applied for up to 2 h at 1 Hz. After treatment in 2% ammonium sulphide in saline and fixation for 30 min in buffered 10% formalin ganglia were intensified as whole mounts (Bacon & Altman, 1977).

The experiments to establish the connexions that an interneurone makes with motoneurones were performed in Cambridge. Here the ocelli were illuminated by light from 2·2 V lens-end torch bulbs powered by 3 V batteries. Switching of lights was achieved manually, by relays operated from a pulse generator, or by a rotor spun by an electric motor. A light-sensitive transistor was used to monitor the switching. Light was led to each ocellus by a plastic light guide (of 'Croton', du Pont). Each light guide had a diameter the same as the lens of an ocellus, and was positioned with its end less than 1 mm from its ocellus lens. This method of illumination is inexpensive, but delivers no ultra violet light. Puffs of air were delivered to the locust's head from a glass tube with diameter 3 mm, using either a compressed air supply or a rubber pipette bulb.

The experiments which established the stimuli which excite the interneurone and how they interact were performed in Berlin. Here the light source was a 900 W Xenon Arc Lamp, and the light path contained quartz optical elements. Interference and neutral density filters were used to vary the colour and intensity of the light beam. It was restricted to the median ocellus by a hypodermic tube which just fitted over its lens. Air was delivered to the whole head by a tube of internal bore slightly greater than it and placed 5 cm from it. By employing two solenoid-operated valves to switch between the stimulating jet and an exhaust jet, an almost constant velocity of air was achieved during a stimulus.

RESULTS

The interneurone described in this paper has an axon which is one of the largest in the nerve cord and occupies a dorso-lateral position within it. Spikes are recorded from it both in response to currents of air directed over the head and to a reduction in the intensity of light falling on the median ocellus. During this study, no other neurone with its axon in the dorso-lateral part of the nerve cord was found to spike in response to both of these stimuli. From its anatomy in the brain, it is most likely that the interneurone is the neurone termed '03' by Williams (1975 – see also C. S. Goodman, 1976), and it will be referred to as 03 throughout this paper.

The structure of an 03 neurone

An 03 neurone has its cell body on the posterior face of the protocerebrum, adjacent to that of a DCMD (O'Shea, Rowell & Williams, 1974), near to where one of the major tracheal trunks enters the brain (Fig. 1). From the cell body, a neurite runs to

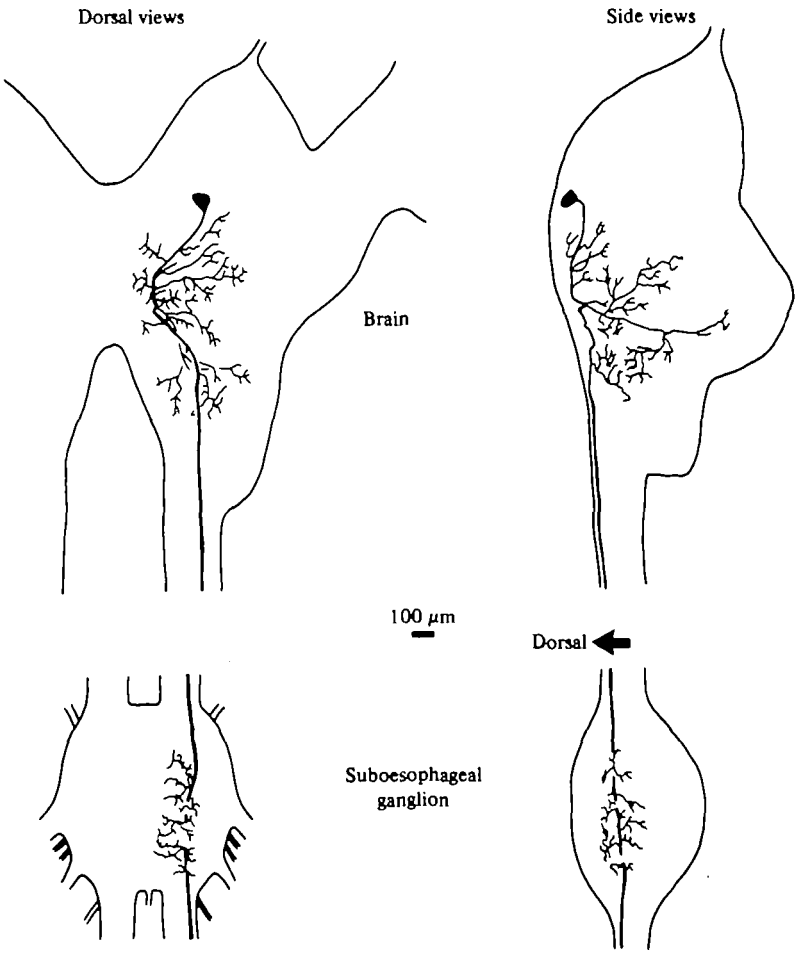
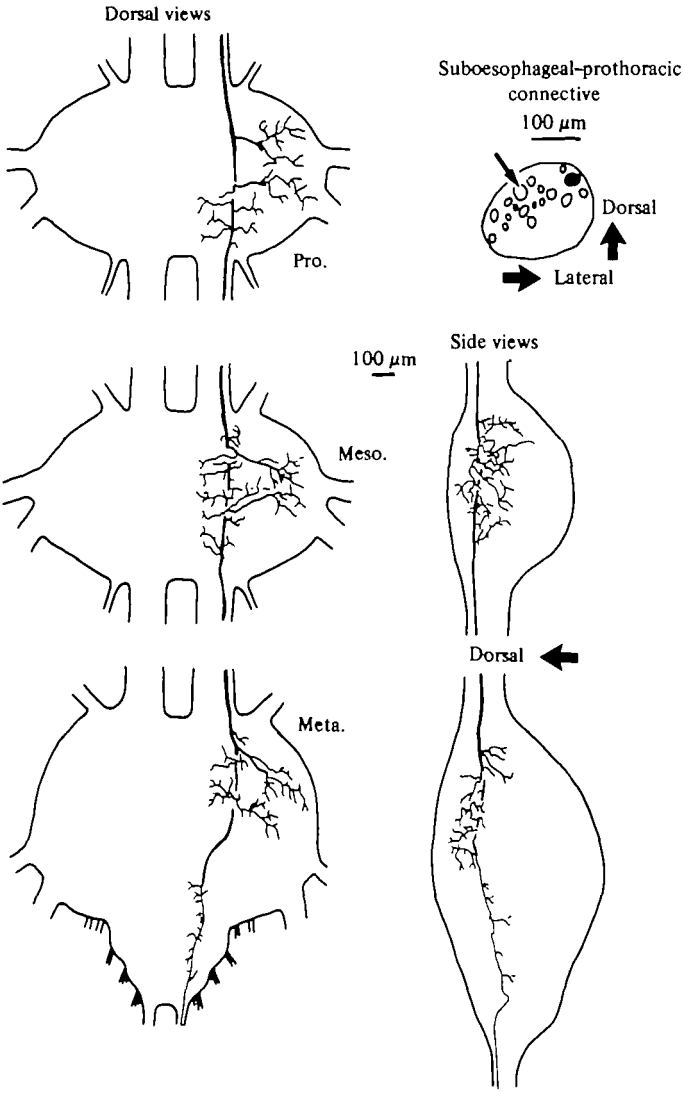


Fig. 1. The structure of 03, revealed by injection of cobalt and intensification. The drawings indicate the extent of branches from the interneurone, but no attempt is made to convey their density, which cannot be done accurately at this scale. Cobalt never travelled the length of the axon from the brain to the metathoracic ganglion, and rarely could details in more than two ganglia be seen. The drawings of the meso- and metathoracic ganglion are from one

meet the thickest process of 03 in the brain, which runs for 200 μm, parallel to the midline of the brain and 150 μm away from it. From this process, most branches of 03 within the brain originate. None of them cross the midline. Some extend laterally, towards the optic lobe. One very extensive branch extends anteriorly, almost reaching the antennal lobe, and ventrally as far as the tritocerebrum. Ramifications from it intermingle with those from some branches which originate in the tritocerebrum. The thickest process of 03 runs close to some large, second order neurones of the



preparation, and each of the other ganglia are from separate preparations. The section was from the prothoracic ganglion drawn here (8 μm in wax). In the section, the injected 03 interneurone is drawn black, and the DCMD is arrowed. The interneurone was filled successfully three times in the brain, three times in the suboesophageal ganglion, four times in the prothoracic ganglion and five times in the meso- and metathoracic ganglia.

median and ipsilateral ocellus, and primary wind-sensitive neurones have branches near those of 03 in the tritocerebrum (Bacon & Tyrer, 1978).

The axon of an 03 passes down the connective ipsilateral to its cell body and has processes in the ipsilateral sides of the suboesophageal and all three thoracic ganglia (Fig. 1). It extends as far as the abdomen, but its projections here have not been traced. In each connective it is one of the largest axons and occupies a dorso-lateral position. It runs in the latero-dorsal tract in each ganglion (Gregory, 1974).

In the suboesophageal ganglion there are five or six major branches from each 03 axon, all originating posterior to nerve 2. In the pro- and mesothoracic ganglia, the structure of an 03 is similar. There are two major branches, one originating level with the root of nerve 3 and passing postero-laterally, and the other originating just posterior to the root of nerve 5 and passing antero-laterally. Other branches extend laterally and medially from the axon. There are also two major branches within the metathoracic ganglion, both anterior to the root of nerve 3.

The Excitation of 03

In a well-lit laboratory, in still air, the axon of an 03 is normally silent. It responds, usually with a single spike, to a reduction in the intensity of light falling on the median ocellus (Fig. 2*a*). A spike from an 03 induced by this, or any other stimulus cannot be recognized in extracellular recordings from a whole connective unless accompanied by an intracellularly-recorded spike, as in Fig. 2(*b*). Most recordings from 03s in different locusts were made just anterior to the mesothoracic ganglion, and their spikes reach this position 25–30 ms after a reduction in the intensity of light to the median ocellus.

In response to an air current flowing over the whole of the front of a locust's head, an 03 spikes continually (Figs. 2*c*, *d*). These spikes continue for as long as an air current is applied. The optimal direction for an air current to elicit spikes is from directly in front of the head. When an air current is directed at a small area of the head from a jet of internal diameter 1 mm and positioned 5 mm from it an 03 usually responds only with a brief burst of spikes, implying that it is excited from wind-sensitive hairs situated on widely separated locations over the head.

Increasing the intensity of light falling on the median ocellus causes a decrease in the frequency of spikes induced by an air current (Fig. 2*d*). When the light applied to the median ocellus is switched off there is usually a transient increase in the frequency of these spikes.

Occasionally a spike is recorded from an 03 axon when a bright light applied to the ocellus ipsilateral to it is switched off. The intensity change required is several log. units greater than that required for light applied to the median ocellus. The possibility that light applied to the ipsilateral ocellus stimulates receptors of the median ocellus due to scattering within the head capsule cannot be ruled out, but stimulation of the ocellus contralateral to an 03 axon has never been found to elicit spikes in it. No spikes have been recorded from an 03 axon in response to stimuli applied to the compound eyes, antennae, ears, wings or legs.

The Conduction Velocity of the Axon of 03

An 03 conducted spikes with a velocity of 2·3 m/s between two electrodes placed in its axon 1·54 mm apart and either side of the mesothoracic ganglion. Measurement of the conduction velocity between hook electrodes placed beneath a connective and a microelectrode placed in various locations along the axon did not show any difference in the velocity of spikes travelling along a connective and spikes travelling through a ganglion. For comparison, Burrows & Rowell (1973) report that a DCMD axon has a conduction velocity of 3·1 m/s. The slower conduction velocity of an 03 axon is consistent with its smaller diameter.

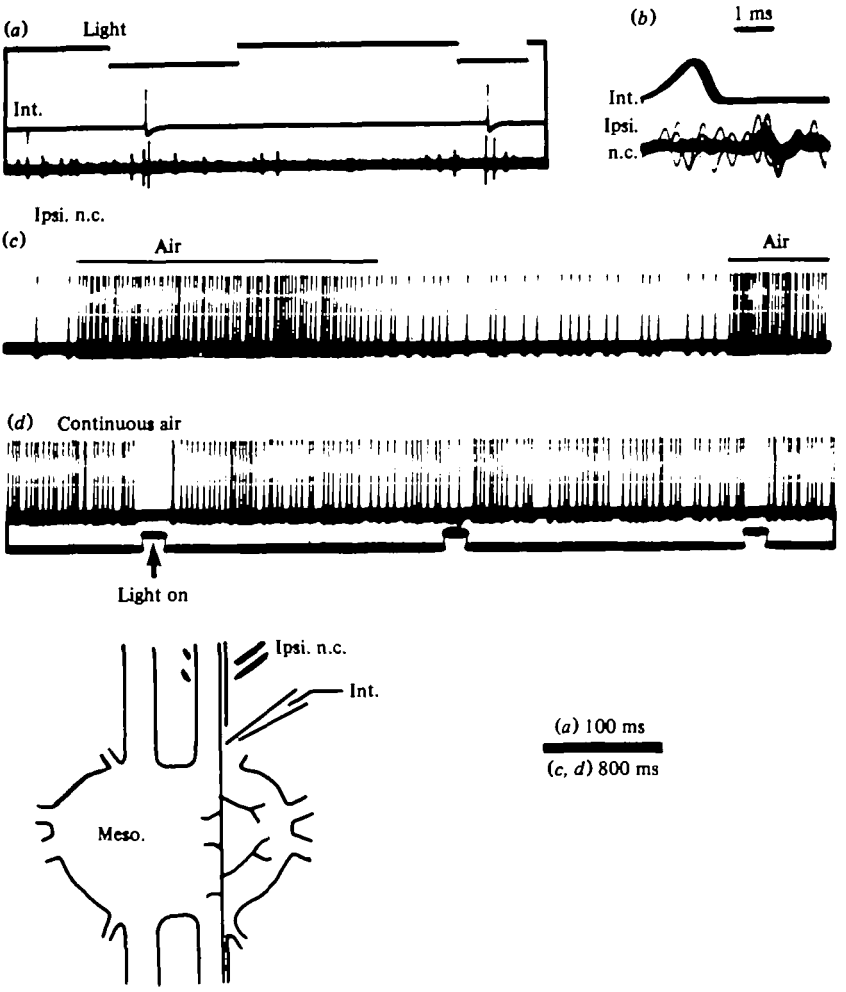


Fig. 2. The excitation of 03.

(*a*) Reduction in the intensity of light to the median ocellus (downward deflexion on the top trace) is followed, after 25–30 ms, by a spike in the interneurone as it enters the meso-thoracic ganglion. Other interneurones, seen in the extracellular recording from the nerve cord, are also excited by this stimulus.

(*b*) The spike in the 03, recorded by hook electrodes around the connective, is revealed by multiple sweeps triggered from intracellularly-recorded spikes. Time runs backwards in this recording since the microelectrode was posterior to the hook electrodes and the tape recorder was replayed backwards.

(*c*) Currents of air, directed at the front of the head, excite the interneurone.

(*d*) A current of air directed over the head continually elicits spikes in the interneurone. Increasing the intensity of light to the median ocellus reduces the frequency of spikes, and reducing the intensity of this light causes a transient increase in spike frequency. The amplitude of the interneurone spike, recorded intracellularly, was 70 mV in (*a*) and (*b*) and 80 mV in (*c*) and (*d*).

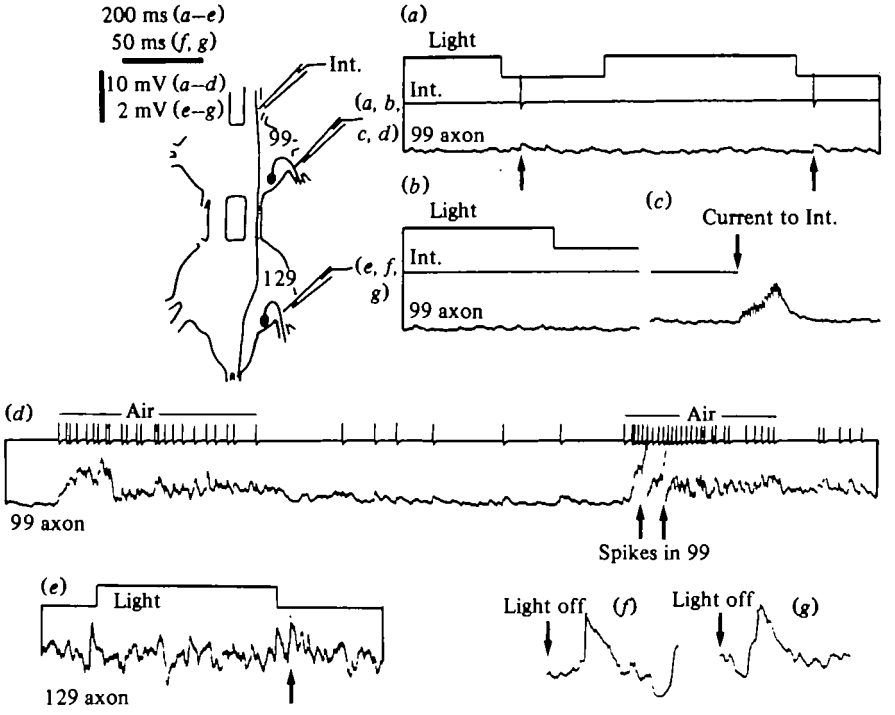


Fig. 3. Connexions from an 03 to subalar motoneurones. The light was applied to the median ocellus, and upward deflexion indicates switching on, downward deflexion indicates switching off. (*a*) Spikes in the right 03 of a locust are accompanied by EPSPs (arrowed), 1·5 mV in amplitude, in the axon of a right mesothoracic subalar motoneurone. (*b*) When the interneurone spike fails, so does the EPSP in the motoneurone. (*c*) Injection of positive current into the interneurone causes a series of summating EPSPs in the motoneurone. Spikes in the interneurone are evident as artifacts in the recording from the motoneurone. (*d*) An air current to the head causes spikes in the interneurone and many PSPs, not all mediated by the 03, in the motoneurone. The motoneurone spikes during the second application of air. (*e–g*). Dimming of the light to the median ocellus is followed by an EPSP in a hindwing subalar motoneurone. This EPSP is distinguishable from others by its latency from the switching of the light. The amplitude of the interneurone spike is 80 mV in (*a*) and (*d*).

Connexions from an 03 *to Subalar Motoneurones*

A spike in an 03 axon mediates a unitary excitatory postsynaptic potential (EPSP) in the motoneurones of the ipsilateral mesothoracic subalar muscle (no. 99), and probably also in those of the ipsilateral metathoracic subalar muscle (no. 129) (Fig. 3). The following observations establish the existence of the connexion to a right mesothoracic subalar motoneurone. First, following the extinction of a light applied to the median ocellus there is a one-to-one correspondence between a spike in the axon of the right 03 axon and an EPSP in the motoneurone (Fig. 3*a*), and when the interneurone spike fails so does the EPSP in the motoneurone (Fig. 3*b*). Second, when a pulse of current applied to the axon of an 03 elicits a burst of spikes in it, a series of summating EPSPs is recorded from the interneurone (Fig. 3*c*). A stream of air applied to the locust's head elicits spikes in the 03 and EPSPs in the motoneurone (Fig. 3*d*). Some of these EPSPs are probably mediated by other wind-sensitive, descending brain interneurones.

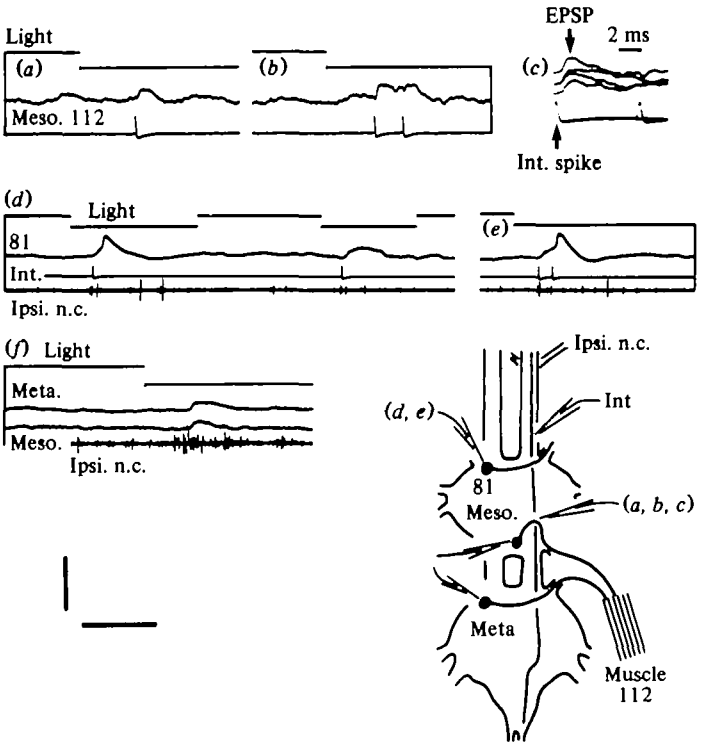


Fig. 4. Connexions from right 03s to motoneurones of the right dorsal longitudinal muscles of locusts. Spikes in the interneurone were elicited by switching off a light applied to the median ocellus, indicated by downward deflexions on the upper traces.

(*a*, *b*) Each spike in the interneurone is followed by an EPSP in process of a dorsal longitudinal motoneurone in the neuropile of the mesothoracic ganglion. The motoneurone innervates the middle block of fibres of the right hindwing dorsal longitudinal muscle.

(*c*) There is a latency of 1 ms between the arrival of the interneurone spike at the mesothoracic ganglion and the start of the EPSP shown in (*a*) and (*b*).

(*d*, *e*) In another locust, each interneurone spike is followed by an EPSP which can be recorded from the cell body of the right forewing dorsal longitudinal motoneurone in the mesothoracic ganglion. In (*d*), the first spike in the interneurone causes an EPSP which gives rise to a spike in the motoneurone. In (*e*), there are two spikes in the interneurone, and they cause EPSPs which summate and trigger a spike in the motoneurone.

(*f*) An EPSP is recorded from each cell body of two motoneurones of the right hindwing dorsal longitudinal muscle of another locust. The EPSPs occur 30 ms after the light to the median ocellus is switched off. One cell body is in the mesothoracic ganglion, and its neurone innervates the central block of muscle fibres. The other cell body is in the metathoracic ganglion, and its neurone innervates the most ventral group of muscle fibres.

Calibrations: (*a*, *b*): 50 ms; 5 mV (motoneurone); interneurone spike, 20 mV. (*c*): 2 ms; 5 mV (*d*, *e*): 100 ms; 10 mV (motoneurone); interneurone spike, 50 mV. (*f*): 50 ms; 5 mV.

In a metathoracic subalar motoneurone, an EPSP follows extinction of a light applied to the median ocellus by 30 ms, about the time required for a spike in an 03 to reach this ganglion (Figs. 3*e–g*). In a recording from the axon of the motoneurone at the edge of the neuropile this EPSP does not always stand out clearly from other EPSPs, some of which may be mediated by interneurones other than 03 which are excited from the median ocellus.

Each subalar muscle is innervated by two motoneurones, which can be dis-

tinguished because one of them innervates the anterior part and the other the posterior part. In one experiment I made recordings successively from both motoneurones of a right mesothoracic subalar muscle, and found that they both received an EPSP 30 ms after extinction of a light applied to the median ocellus.

Connexions from an 03 *to Dorsal Longitudinal Motoneurones*

Each spike in a right 03 mediates an EPSP in all of the motoneurones of the right dorsal longitudinal muscles of a locust (Fig. 4). This EPSP is clearly seen in recordings from cell bodies of dorsal longitudinal motoneurones (Figs. 4*d–f*) as well as from the neuropile (Figs. 4*a–c*). Its latency, following arrival of an 03 spike at the anterior of a ganglion, is 1 ms (Fig. 1*c*). This is consistent with the existence of a chemical synapse between the interneurone and motoneurones. Sometimes a single spike in an 03 can elicit a spike in a dorsal longitudinal motoneurone (Fig. 4*d*). When two spikes occur in the interneurone in response to stimulation of the medial ocellus, two EPSPs occur in a dorsal longitudinal motoneurone (Fig. 4*b*), and they may summate to produce a motoneurone spike (Fig. 4*e*).

The five motoneurones which innervate each dorsal longitudinal muscle can be distinguished because they each innervate a distinct block of fibres within it. Four of the motoneurones innervating the right metathoracic dorsal longitudinal muscle have their cell bodies in the posterior part of the right side of the mesothoracic ganglion, and the remaining motoneurone has its cell body on the left side of the metathoracic ganglion (Fig. 4). The innervation of the mesothoracic dorsal longitudinal muscle is similar. An EPSP occurs in all the motoneurones of a dorsal longitudinal muscle when there is a spike in the 03 axon ipsilateral to the muscle. When a recording is made from two motoneurones that innervate the same dorsal longitudinal muscle, an EPSP is seen in both 30 ms after light to the median ocellus is switched off (Fig. 4*f*).

In the single motoneurone in the mesothoracic ganglion which innervates the right mesothoracic dorsal longitudinal muscle, interneurones in both left and right connectives mediate EPSPs after light applied to the median ocellus is reduced (Fig. 5). When both connectives are intact, a 3 mV EPSP is recorded from the cell body of this motoneurone and from that of its contralateral partner following this stimulus (Fig. 5*a*). When the right connective is cut, the EPSP in the motoneurone to the muscle on the right is reduced to about 0·5 mV and the EPSP in the motoneurone to the muscle on the left is only slightly reduced in amplitude (Fig. 5*b*). When this experiment was repeated for the two dorsal longitudinal motoneurones which have their cell bodies in the metathoracic ganglion, the same result was obtained. The most obvious explanation for these results is that both left and right 03s connect with these four motoneurones. Further recordings are required to show whether this is so. These motoneurones have extensive branches on both sides of their ganglia, whereas the branches from other flight motoneurones are mostly restricted to one side only (Tyrer & Altman, 1974), making it most unlikely that an 03 would connect directly with other flight motoneurones contralateral to its axon.

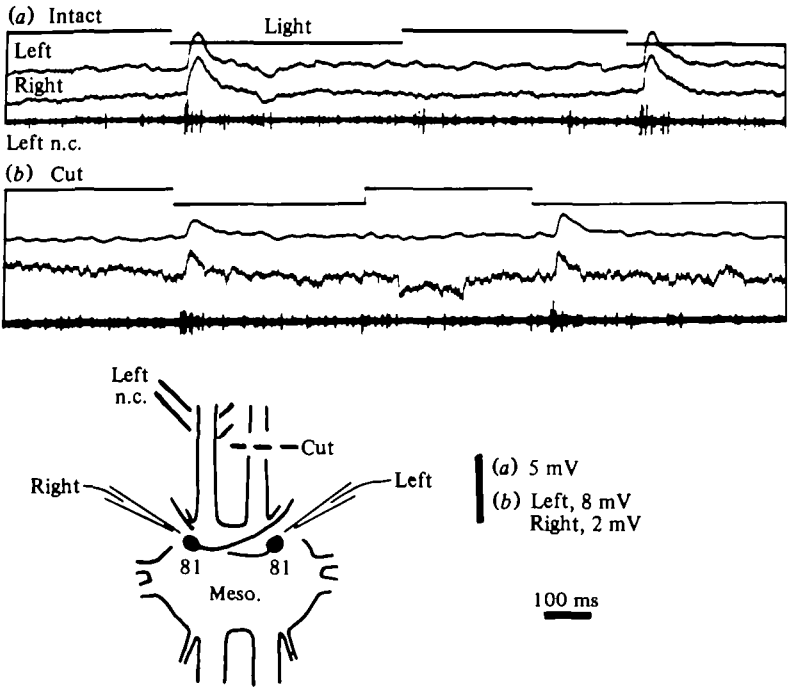


Fig. 5. The motoneurones in the mesothoracic ganglion which innervate the dorsal longitudinal muscles of the forewings receive inputs from interneurones excited by dimming of light to the median ocellus in both nerve cords. The dimming of the light to the median ocellus is indicated by downward deflexions of the top traces.

(*a*) When both connectives are intact, dimming of light to the median ocellus is followed by an EPSP 3 mV in amplitude in both cell bodies.

(*b*) When the right connective is cut, the EPSPs in the cell body of the motoneurone of the right muscle are reduced to 0·5 mV in amplitude. The cell body of this motoneurone is on the left of the ganglion. There is no obvious change in the amplitude of the EPSPs in the motoneurone of the left muscle. The operation did not affect the amplitudes of spikes recorded from the left and right motoneurones, providing evidence that these neurons were not damaged.

DISCUSSION

In order to discuss the function of an o3 in the control of a locust's behaviour it is necessary to consider how it might be excited in natural circumstances and what effects its known outputs to motoneurones have on the locust's movement. Because an o3 is excited by a current of air flowing over the head and because it connects with flight motoneurones, it is probably involved in the control of flight. The way in which the frequency of spiking in it is affected by the intensity of light falling on the median ocellus and the way in which the muscles whose motoneurones receive EPSPs from it move the wings both suggest that an o3 plays a role in regulating the angle of pitch of a flying locust. This is illustrated in Fig. 6.

In a locust flying along a horizontal course, each o3 would probably spike continually in response to the stimulation of the wind-sensitive hairs on the head. If the locust pitched upwards, the intensity of light falling on the median ocellus would increase and the frequency of the spikes in the o3s would decrease. Conversely, if

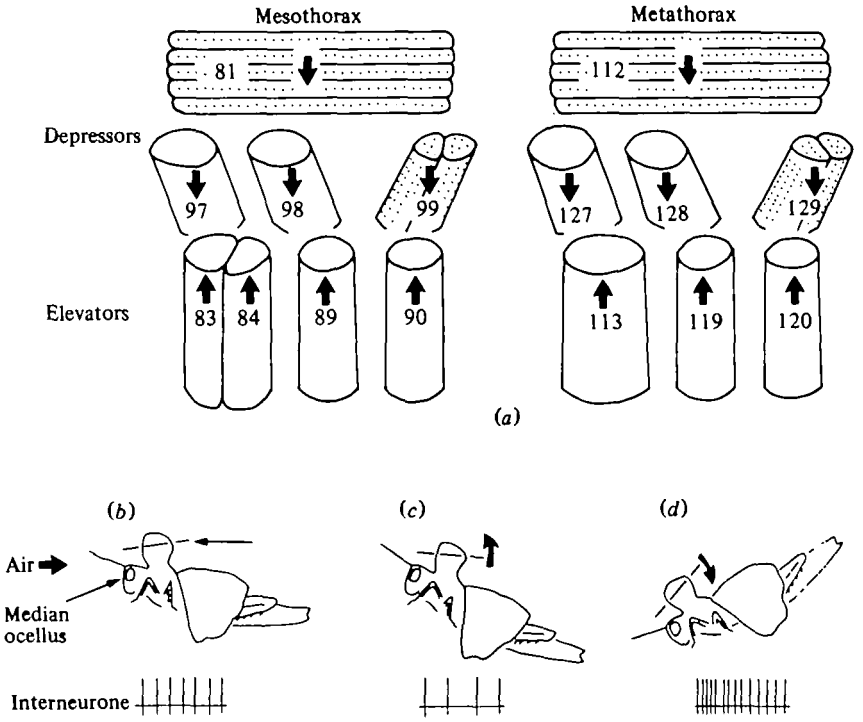


Fig. 6. Diagrams of the proposed function of an o3 in ensuring stability of flight.

(*a*) Schematic representation of the muscles of the right fore and hind wings of a locust, viewed from inside the thorax. The muscles which are stippled have motoneurones that are excited by the right o3. The up or down movement of a wing tip, caused by contraction of each muscle, is indicated by arrows on the muscles. The basalar muscles 97, 98, 127 and 128, pronate their wings during a downstroke, and the subalar muscles 99 and 129, oppose this action. The dorsal longitudinal muscles, 81 and 112, are powerful depressors of the wings. Several smaller muscles, whose motoneurones have not been found to be influenced by o3s, are omitted.

(*b*) A locust flying along a horizontal flight path. The wings have a slightly positive angle of attack – the angle between by the line drawn across the left forewing and the direction of air flow past the locust. Each of its o3s is excited by the wind flowing over the locust's head.

(*c*) The pitch of the locust has suddenly increased, due, for instance, to air turbulence. The angle of attack of the wings is now slightly negative. But the excitation of the o3s is reduced since the intensity of light falling on the median ocellus has increased. This causes the excitation of the subalar motoneurones to decrease, and the resulting decrease in force generated by the subalar muscles allows the wings to pronate towards their former angle of attack, indicated by the curved arrow.

(*d*) The pitch of the locust has suddenly decreased, and the angle of attack of the wings has increased. But the reduction of light intensity to the median ocellus causes an increase in the frequency of spikes in the o3s. This leads to increased force generated by the subalar muscles, twisting the trailing edges of the wings downwards, so that their former angle of attack is restored.

the locust pitched downwards, the intensity of light falling on the median ocellus would decrease, and the frequency of spiking in the o3s would increase.

The subalar and dorsal longitudinal muscles, whose motoneurones receive EPSPs from the o3s, are capable of regulating the lift produced by the wings and the angle of pitch of a locust. (Fig. 6*a* shows the arrangement of the flight muscles on the right side of a locust, and the subalar and dorsal longitudinal muscles are stippled.) The

lift generated by a locust wing depends upon the power applied to it and upon its angle of attack and velocity relative to the air stream moving past the body. The subalar muscles are important in regulating the twisting motions of the wings around their bases, and their angles relative to the long axis of the body (D. M. Wilson and Weis-Fogh, 1962). The dorsal longitudinal muscles are powerful depressors of the wings, and alteration of the force generated by them will alter the power delivered to the wings and the lift they generate. When a locust is flying along a horizontal flight path, the angle of attack of the wings is slightly positive (Fig. 6*b*). If the locust pitches upwards, the angle of attack of the wings (relative to the air stream) will initially increase and the locust may be in danger of stalling (Fig. 6*c*). However, the excitation of the subalar and dorsal longitudinal motoneurones from the 03s will decrease. The resulting decrease in force generated by the subalar muscles will allow the wings to twist around their hinges towards their former angles of attack. The twisting of the wings is indicated by the curved arrows in Fig. 6*c*. Reduction in the force generated by the dorsal longitudinal muscles will help reduce the danger of stalling. If a locust pitches downwards, the angles of attack of the wings will decrease, which could precipitate a nose-dive (Fig. 6*d*). The increase in frequency of spiking of the 03s will cause an increase in force generated by the subalar muscles, which will twist the wings towards their former angles of attack (Fig. 6*d*). Increased force from the dorsal longitudinal muscles will assist the locust to reattain its former flight path.

Because it is continually excited by air currents in a flying locust, an 03 can register both increases and decreases in the pitch of flight. It provides a rapid pathway for transmission of information from the median ocellus to flight motoneurones, enabling the locust to adjust its flight quickly to overcome disturbances. Other interneurones connected with the lateral ocelli may function in a similar way to stabilize flight in the roll plane. No doubt several different sensory pathways register changes in flight directions, but the ocelli are equipped to register changes in the orientation of the locust relative to the horizon very rapidly, as summarized in the introduction. Experiments on the flight of tethered locusts could provide useful information about their function in stabilizing flight. Experiments are also required to demonstrate the nature of air flow around a freely flying locust's head, so that we can predict more accurately than is presently possible the type of activity that occurs in wind-sensitive neurones when a locust flies and turns.

Study of the mechanisms of excitation of an 03 in the brain would be worthwhile. Some of its processes overlap processes from large second-order ocellar neurones (C. S. Goodman, 1974, 1976; L. J. Goodman, Patterson & Mobbs, 1975; Guy, Goodman & Mobbs 1977), and the second order neurones may synapse directly with it. It should be relatively easy to make intracellular recordings from the two types of neurone since they are among the largest in the brain of a locust. Such recordings would provide useful information about the processing of information by brain neurones, and about the physiology of synapses, since the large second-order ocellar neurones exhibit both graded potentials and spikes (M. Wilson, 1978*b*).

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REFERENCES

BACON, J. P. & ALTMAN, J. S. (1977). A silver intensification method for cobalt-filled neurones in wholemount preparations. *Cell Tiss. Res.* **178**, 199–219.

BACON, J. P. & TYRER, N. M. (1978). The tritocerebral commissure giant (TCG): a bimodal interneurone in the locust, *Schistocerca gregaria*. *J. comp. Physiol.* **126**, 317–325.

BACON, J. & TYRER, N. M. (1979). Wind interneurone input to flight motor neurones in the locust, *Schistocerca gregaria*. *Naturwissenschaften* **66**, 116.

BURROWS, M. & ROWELL, C. H. F. (1973). Connections between descending visual interneurones and metathoracic motoneurons in the locust. *J. comp. Physiol.* **85**, 221–234.

DEMOLL, R. & SCHEURING, L. (1912). Die Bedeutung der Ocellen der Insecten. *Zool. Jb.* (*Abt. Zool. Physiol*). **31**, 519–628.

GOODMAN, C. S. (1974). Anatomy of locust ocellar interneurons: constancy and variability. *J. comp. Physiol.* **95**, 185–201.

GOODMAN, C. S. (1976). Anatomy of the ocellar interneurons of Acridid grasshoppers. I. The large interneurons. *Cell Tissue. Res.* **175**, 184–203.

GOODMAN, L. J., PATTERSON, J. A. & MOBBS, P. G. (1975). The projection of ocellar neurons within the brain of the locust, *Schistocerca gregaria*. *Cell Tiss. Res.* **157**, 467–492.

GREGORY, G. E. (1974). Neuroanatomy of the mesothoracic ganglion of the cockroach *Periplaneta americana* (L). I. The roots of the peripheral nerves. *Phil. Trans. Roy. Soc.* B **267**, 421–465.

GUY, R. G., GOODMAN, L. J. & MOBBS, P. R. (1977). Ocellar connections with the ventral nerve cord in the locust, *Schistocerca gregaria*: electrical and anatomical characteristics. *J. comp. Physiol.* **115**, 337–350.

KALMUS, H. (1945). Correlation between flight and vision, and particularly between wings and ocelli in insects. *Proc. R. ent. Soc. Lond.* A **20**, 84–96.

LINK, E. (1909). Über die Stirnaugen der hemimetabolen Insecten. *Zool. Jb. Anat.* **27**, 281–376.

O'SHEA, M. (1975). Two sites of axonal spike initiation in a bimodal interneuron. *Brain Res.* **96**, 93–98.

O'SHEA, M., ROWELL, C. H. F. & WILLIAMS, J. L. D. (1974). The anatomy of a locust visual interneurone; the descending contralateral movement detector. *J. exp. Biol.* **60**, 1–12.

PEARSON, K. G. & GOODMAN, C. S. (1979). Correlation of variability in structure with variability in synaptic connections of an identified interneurone in locusts. *J. comp. Neurol.* **184**, 141–166.

ROWELL, C. H. F. (1971). The orthopteran descending movement detector (DMD) neurones: a characterization and review. *Z. vergl. Physiol.* **73**, 167–194.

SIMMONS, P. J. (1980). Connexions between a movement sensitive interneurone and flight motoneurones of a locust. *J. exp. Biol.* (in the press).

SNODGRASS, R. E. (1929). The thoracic mechanism of a grasshopper and its antecedents. *Smithson. misc. Collns.* **82**, (2), 1–111.

TYRER, N. M. & ALTMAN, J. S. (1974). Motor and sensory flight neurones in a locust demonstrated using cobalt chloride. *J. comp. Neurol.* **157**, 117–138.

WILLIAMS, J. L. D. (1975). Anatomical studies of the insect central nervous system: A ground-plan of the midbrain and an introduction to the central complex in the locust, *Schistocerca gregaria*. *J. Zool.* (*Lond.*) **176**, 67–86.

WILSON, D. M. & WEIS-FOGH, T. (1962). Patterned activity of co-ordinated motor units, studied in flying locusts. *J. exp. Biol.* **39**, 643–667.

WILSON, M. (1978*a*). The functional organization of locust ocelli. *J. comp. Physiol.* **124**, 297–316.

WILSON, M. (1978*b*). Generation of graded potential signals in the second order cells of locust ocellus. *J. comp. Physiol.* **124**, 317–331.