J. exp. Biol. **103**, 265–288 (1983)
Printed in Great Britain © Company of Biologists Limited 1983

OCELLAR INPUT TO THE FLIGHT MOTOR SYSTEM OF THE LOCUST: STRUCTURE AND FUNCTION

BY C. H. F. ROWELL

Zoologisches Institut der Universität, Rheinsprung 9, CH-4051 Basel

AND K. G. PEARSON

Department of Physiology, University of Alberta, Edmonton, Alberta, Canada

(*Received 5 April 1982—Accepted 23 September 1982*)

SUMMARY

1. This paper deals with the physiology, anatomy and function of the following classes of neurones in the locust *Schistocerca*: (a) neurones carrying ocellar information to the pterothorax (Descending Ocellar Neurones, DONs), (b) mesothoracic Flight Motor Neurones (FMNs), (c) a heterogenous class of inter- and intraganglionic thoracic interneurones which receive input from the DONs, here called Thoracic Ocellar Interneurones (TONs) without prejudice to their other possible inputs and functions.

2. The thoracic arborizations of five different DONs are characterized. All project unilaterally to the pterothorax, four out of five to the ipsilateral mesothoracic or meso- and metathoracic ganglia. All are phasic OFF units, responding to stimulation either of one lateral ocellus or of the medial ocellus or of both, but none responded to the cephalic wind-hairs. Four of the five DONs showed no response decrement at stimulus frequencies up to 80 Hz. One showed habituation, recovery during a rest interval, and dishabituation in response to mechanical stimulation of a leg. There are more than six DONs, probably more than ten, in each connective.

3. All types of recorded mesothoracic FMNs receive monosynaptic EPSPs from the DONs and/or delayed IPSPs (presumably via TONs) in at least some animals. The pattern of connection is compatible with the hypothesis that a roll or downward pitch deviation induces compensating movements of the wings to correct the deviation. Many of these DON/FMN connections were, however, only occasionally recorded. None of the ocellar EPSPs recorded in the FMNs elicited spikes.

4. Most TONs receive monosynaptic EPSPs from one or more DONs, sometimes causing them to spike. Two receive delayed IPSPs, presumably via other TONs. At least one third of the recorded TONs spike in phase with either elevator or depressor FMNs during stimulated flight. *Intraganglionic* TONs in the mesothorax are all unilateral. Their anatomy suggests that they distribute input from DONs to various combinations of ipsilateral FMNs. *Interganglionic* TONs can be either unilateral or bilateral in the mesothoracic ganglion, and project unilaterally to the metathoracic (or rarely the prothoracic) ganglion, where at least one makes inhibitory synapses with a FMN.

Key words: Ocelli, interneurones, flight motor system.

5. Phasic ocellar information reaches the FMNs by two routes. One produces fast subthreshold PSPs in the FMNs directly. The other produces spikes and PSPs in thoracic interneurones, at least some of which are phasically active during flight and are presynaptic to FMNs. The roles of the two pathways are discussed.

INTRODUCTION

Hesse (1908) and Wilson (1978) proposed that one of the functions of the ocelli of flying insects is to mediate stability around the roll and pitch axes in flight. The retina of the ocellus does not receive a focussed image (Parry, 1947; Cornwell, 1955; Wilson, 1978) and cannot 'see' the horizon as such. If, however, as the consequence of roll or pitch, the centre of the field of a lateral or median ocellus dips below the horizon, the ocellus receives less total illumination; conversely, if the ocellus rotates skywards it receives more light. There are optical and neural reasons why such a system would be advantageous for flight stabilization (Wilson, 1978; Taylor, 1981*a*; C. P. Taylor & C. H. F. Rowell in preparation) relative to the information obtainable from the compound eye.

This hypothesis of ocellar function has been investigated experimentally by two groups of workers. Stange & Howard (1979) and Stange (1981) showed that when the lateral ocelli of dragonflies (Odonata, Anisoptera) are differentially illuminated, a tethered flying insect will roll its head so as to equalize the illumination to them. It is known in dragonflies and locusts that mismatch between the position of head and prothorax is detected by proprioceptors, and in flies that flight torque is then altered so as to realign the thorax and head (L. Goodman, 1959, 1965; Liske, 1977; Mittelstaedt, 1950); hence, head rolling is part of a flight correction system, and the occurrence of this response supports the Hesse/Wilson hypothesis. Taylor (1981*a*,*b*) investigated the response of locusts (Orthoptera, Acrididae), hoverflies (Diptera, Syrphidae), and dragonflies (Odonata, Zygoptera) to simulated roll using an artificial horizon in a wind-tunnel. He too showed compensatory head rolling, even in non-flying insects. In flight, head rolling increased in amplitude, and was supplemented by changes in wing-beat pattern, rudderlike motions of the abdomen and legs, and flexion of the pterothoracic/prothoracic articulation. The changes in wing-beat pattern in locusts were reflected in positive and negative phase shifts in the timing of action potentials in the first basalar and first tergosternal flight muscles (the only two investigated); changes in the time of firing of these two muscles changes the downstroke of the wing (Möhl & Zarnack, 1977) and would be expected to cause correcting torque around the roll axis.

Taylor demonstrated that either the compound eyes or the ocelli alone could mediate this behaviour. Steering responses to ocellar stimulation persisted at reduced amplitude when proprioceptive information was eliminated surgically, or when the head was prevented from rolling. This result indicated that the ocellar information is transmitted directly to the thoracic flight motor centres, as opposed to merely influencing them indirectly via the head-turning response. Taylor's work establishes the Hesse/Wilson hypothesis; it does not, of course, exclude other further functions for ocellar input.

The anatomy of the ocellar pathway and the flight motor system has been best studied in the locust *Schistocerca*. The retinula cells synapse with 17 large second order neurones (L cells, C. Goodman, 1976) and are connected to 61 pairs of smaller neurones of unknown function (C. Goodman & Williams, 1976). The L cells interact with each other (L. Goodman, Mobbs & Guy, 1977; Taylor, 1981*c*; P. Simmons, 1982) and at least some synapse in the posterior protocerebrum with a number of interneurones which descend to the thoracic ganglia (Williams, 1975; C. Goodman, 1976; Guy, L. Goodman & Mobbs, 1977; Simmons, 1981). It has long been known (e.g. Parry, 1947) that action potentials can be recorded from the thoracic nerve cord in response to illumination changes at the ocelli (review, L. Goodman, 1970), and a number of the descending ocellar neurones (DONs) have been partially characterized, either anatomically (above) or physiologically (e.g. Guy *et al.* 1977). One DON (O_3 of Williams, 1975) has been studied in detail (Simmons, 1980) and shown to make direct synaptic connections with two of the flight motor neurones of both pterothoracic ganglia.

In this paper we report on studies of DONs and other neurones of the pterothoracic ganglia which receive ocellar information, as a further step towards elucidating the circuitry responsible for the flight correction behaviour described by Taylor. We have confined our attention to the flight motor system and have ignored the elements responsible for movements of the head, and for the rudder-like use of abdomen and legs (Gettrup & Wilson, 1964; Camhi, 1970; Taylor, 1981*a*). We have concentrated on the mesothoracic ganglion, as the forewings appear to play the larger part in flight correction (Wilson, 1963). We find that DONs synapse monosynaptically with most or all of the flight motor neurones, and also with a variety of previously undescribed interneurones (both intra- and interganglionic), of which at least some are also active during flight, and synapse with flight motor neurones.

METHODS

Experiments were performed on *Schistocerca gregaria* (Forskål) and *Schistocerca americana* (Drury) of either sex. Both came from crowded laboratory culture. The culture of *gregaria* (at the Department of Zoology, University of British Columbia) has been inbred for many generations; the culture of *americana* (Department of Zoology, University of California at Berkeley) was derived from insects caught in the wild in Texas in the summer of 1979, and at the time of our experiments was in only its third captive generation. The results reported were obtained from 207 penetrations of units responding to ocellar stimulation in 46 animals. A larger number of animals yielded extracellular data.

Insects were restrained by the extended legs with pins and Plasticene. The head was stabilized by two pins in the genae. The thoracic pleura were pinned out horizontally after cutting through the terga in the midline. The inner layer of flight muscles was transected dorsally so as to expose the underlying layer; in this way all the flight muscles could be seen and checked for contraction in response to stimulation of motor neurones. The gut and the muscles attaching to the mesothoracic spina were removed and the mesothoracic sternal apophyses cut out, exposing the meso- and metathoracic ganglia and their nerve roots. The ganglia were stabilized by a steel platform which

also served as electrical ground. The tracheae running from the ganglia to the ma[illegible] longitudinal tracheae were left intact, and the preparation was continuously perfused with saline at room temperature (24 °C). A 10 mm diameter tube was positioned close to the insect so that air could be blown frontally over the head. A slightly modified procedure (Robertson & Pearson, 1982) allows the insect to produce the motor output corresponding to flight in response to air on the head ('simulated flight').

The anterior border of each compound eye was painted with several coats of thick red nail-varnish, to prevent accidental stimulation of the compound eye with stray light from the light pipes which were used to stimulate the ocelli. In most preparations the middle and posterior parts of the eye remained uncovered; they saw an invariant scene of intensity 1–10 cd/m^2. In some preparations the antennae were cut short, to prevent them from moving the light pipes. Plastic light pipes (Dupont 'Crofon') 50 mm long, of a diameter slightly less than that of the ocellus lens, were placed in contact with each of the three ocelli. Each light pipe was cemented to a green light-emitting diode (Hewlett-Packard 5082-4190, peak emission 565 nm). The L cells, and presumably therefore the ocellar retinula cells of *Schistocerca* are maximally sensitive in the u.v. (λ max = 366 nm) and have a broad secondary peak in the yellow green (λ max = 516 nm) (Wilson, 1978). A current of 24 mA in the LEDs was used to provide background illumination and allowed a dynamic stimulus range of $\pm$ 1 $\log_{10}$ unit, over which light emission was linearly related to current. Stimuli used were either 100 ms, 1 $\log_{10}$ unit square-wave pulses of increased illumination (ON stimuli) or decreased illumination (OFF stimuli) relative to normal intensity, or a sinusoidal modulation (2 $\log_{10}$ units peak-peak) about background intensity at 1–100 Hz. Stimuli could be applied to any combination of ocelli in any phase relation. Stimuli affecting only the median ocellus approximate to the input the flying animal would experience as the result of movement around the pitch axis; stimuli which affect both lateral ocelli in antiphase (or a single lateral ocellus, see Results), correspond to the effect of movement around the roll axis. The waveforms which produced these ocellar stimuli were derived from a triggered generator. Stimuli were monitored as the voltage output of a miniature silicon photocell which was cemented to the rear face of each LED. Over the range of intensities used, this voltage varied linearly with LED light output. The complex of lightguide, LED and photocell was given several coats of opaque varnish after cementing together, so that stimulating light came only from the end of the light pipe.

Activity in the pro-mesothoracic connectives was recorded conventionally with silver hook electrodes and AC amplification. Some animals showed little extracellular response in the connective to ocellar stimulation, and experience showed that in such animals little ocellar response could be found intracellularly in the thorax. Subsequently, only animals with a good extracellular response were accepted for experimentation. The experimental population was thus a selected one. Intracellular records were made from the neuropil of the mesothoracic ganglion with microelectrodes with tip resistances of 70–100 MΩ when filled with 3M-potassium acetate. The tips of the electrodes were routinely filled with 3 % Lucifer yellow and the shank with 3M-lithium chloride; they had high initial impedances but were usually broken to around 100 MΩ when penetrating the sheath of the ganglion. Activity was recorded either directly or via an on-line digital signal averager. When the averag[illegible]

was used, between 10 and 50 sweeps were usually averaged; occasional exceptions are noted in the figure legends. After recording, penetrated neurones were filled with Lucifer Yellow using a direct current of 1–10 nA for up to 40 min. The ganglion was then dissected out, fixed for 30 min in buffered (pH 7·2) 4% paraformaldehyde solution, dehydrated rapidly in ethyl alcohol, cleared in methyl salicylate, and examined by fluorescence microscopy. Drawings and photographs were completed within 2 h of filling the cell. This procedure produced reliable fills of structures in both the meso- and metathoracic ganglia, but the dye did not diffuse further.

RESULTS

Descending ocellar neurones (DONs)

We have filled and characterized physiologically five descending units; these are summarized in Table 1. None of our fills extended into the brain, so we cannot yet homologize our units with the nomenclature of Williams (1975) which is based on cerebral morphology. O_3 and O_4, described by Simmons (1980, 1981) were not found by us (see Discussion), but represent two further known DONs. There are certainly a number of other DONs which we have seen in extracellular recordings which we have not characterized intracellularly. We estimate a total of at least 10 DONs in each connective. As we never filled more than one DON per animal, it is not excluded that some units we describe as different entities are in fact variants of the same neurone, but we do not think this to be so. Extracellular recordings under favourable conditions clearly show that a considerable number of units are present simultaneously.

Anatomy

Dye fills of DONs invariably showed an axon running through the mesothoracic ganglion and usually into the metathoracic ganglion, but with no soma in these ganglia. Other workers have found DON somata in the brain, and the close correspondence in physiology and thoracic anatomy between these and our units suggests that the latter too originate in the brain. Usually the axon terminates in the metathorax, but on one occasion was seen to enter the abdominal connectives [a similar pattern has been seen in DCMD (Pearson & C. Goodman, 1979) and O_3 (Simmons, 1980)]. The majority of DONs, even when clearly different in their physiology, have similar morphologies (Fig. 1A–E). They have numerous branches medially and laterally within the ipsilateral hemiganglion, especially in the area of the neuropil of the flight motor neurones (FMNs) (Tyrer & Altman, 1974). The medial branches do not cross the midline. Axon and processes all lie within the dorsal 100 μm of the ganglion. Two of the six known DONs have different morphologies. The Slow I/M/(C) unit (for terminology see Table 1), which is also exceptional physiologically, fits the above description but terminates in the mesothoracic ganglion. The fast M unit has only a single branch in the mesothoracic ganglion, and this extends across the midline to branch in the contralateral FMN area: there were no branches within the ipsilateral hemiganglion.

Physiology

Intracellular records of DONs in the ganglia showed action potentials rising directly from the baseline; no synaptic activity was seen. The AP invariably correlated with

slightly preceding extracellular spike (latency ≤ 1 ms) in the pro/mesothoracic connective (Fig. 2A, B). We have no evidence suggesting that any of the DONs are too small to be recorded extracellularly, though some gave very small spikes (approx. 50 μV). This is true not only for units we penetrated, but also for those known to exist only on the basis of short-latency postsynaptic potentials in FMNs or thoracic interneurones.

All of the five different DONs we filled gave a spike or burst of spikes at light OFF to one or more ocelli. There was never any response to light ON. Responses became

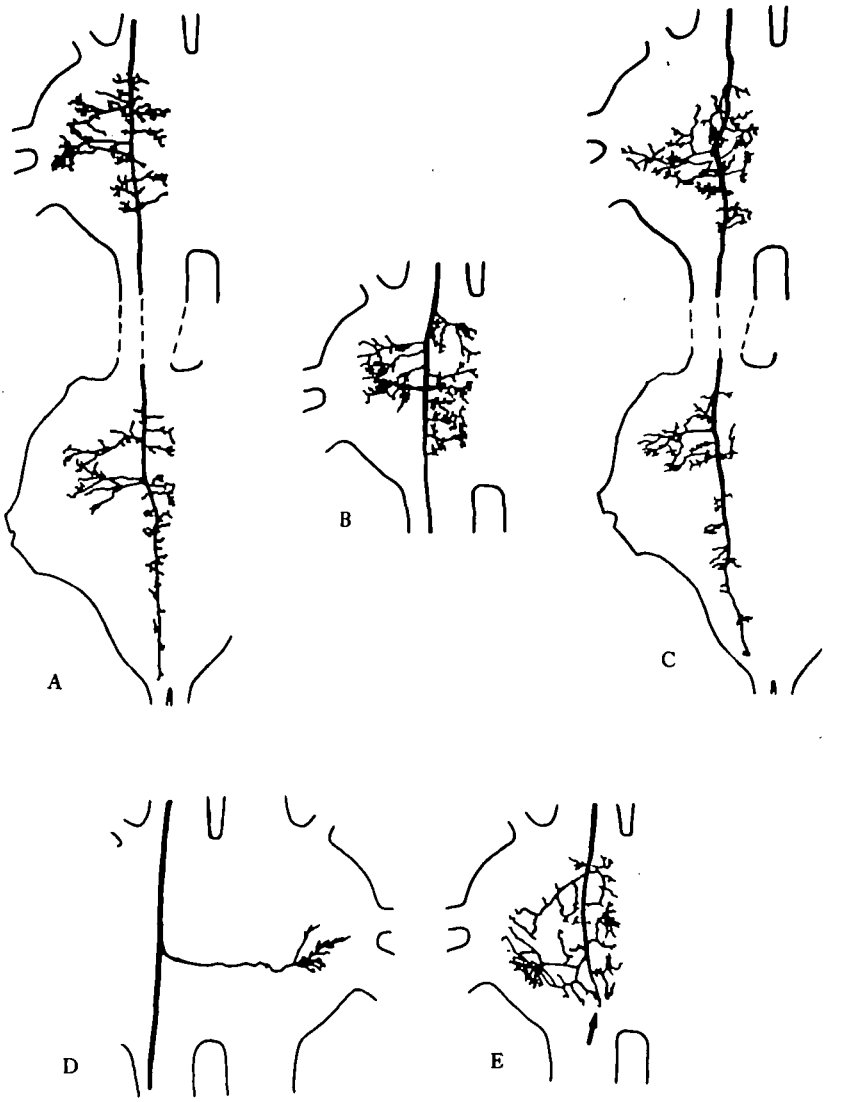

Fig. 1. Thoracic anatomy of the five descending ocellar neurones listed in Table 1, derived from fills with Lucifer yellow. A. Fast ipsi DON. B. Fast ipsi (medial) DON. C. Fast contra DON. D. Fast medial DON. E. Slow ipsi medial (contra) DON – the neurone terminates in the mesothoracic ganglion (arrow). The metathoracic projections of B and D are unknown. Scale: the mesothoracic ganglion is 1 mm wide at its widest point.

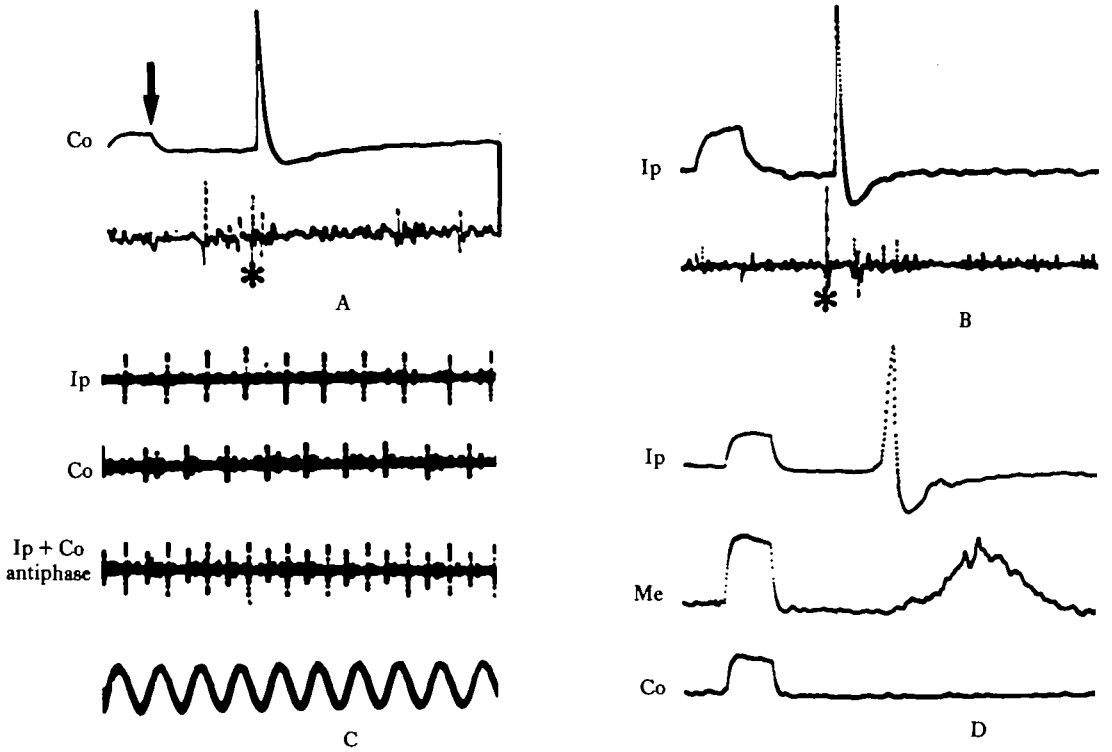

Fig. 2. Examples of recordings from fast DONs. A, B: Intracellular records from the mesothoracic axon and extracellular records (starred) from the pro-mesothoracic connective of the fast contra and fast ipsi DONs respectively. Calibration pulse, 2 mV and 10 ms. OFF stimulus was a one $\log_{10}$ unit decrease in ocellar illumination, simultaneous with the end of the calibration pulse (arrow in A). The letters Ip, Me or Co by a trace indicates which ocellus was stimulated. C: Extracellular recordings from the pro/mesothoracic connective. Stimulus (bottom trace) is $\pm$ 1 $\log_{10}$ unit sine wave modulation of light intensity at 20 Hz. Upper trace, stimulus to the ipsi ocellus only, eliciting the fast ipsi DON; second trace, stimulus to the contra ocellus only, eliciting the fast contra DON; third trace, stimulus to the contra and ipsi ocellus simultaneously in antiphase (simulated roll), which merely summates the two previous recordings. No potentiating effect of the ON stimulus at the opposite ocellus is seen. D: Averaged intracellular responses from the fast ipsi (medial) DON. Top trace, OFF to ipsi ocellus (100 stimuli) produces a highly reliable action potential of fixed latency: middle trace, OFF to medial ocellus (1000 stimuli) has a low probability of producing an action potential with a longer and much more variable latency: lower trace, OFF to contra ocellus (500 stimuli) never produces an action potential. Stimulus and calibration as in A and B.

erratic with sinewave modulation of light intensity at 0·2 Hz or slower, but reliability was restored if the stimulus risetime was shortened (e.g. square wave modulation instead of sine wave). No OFF response was ever influenced by a simultaneous ON stimulus to another ocellus. Consequently, the experimental abstraction of light OFF to one lateral ocellus appears to be a valid simplification of the antiphase OFF/ON which actually affects the two lateral ocelli during roll by a flying animal (Fig. 2C). The pattern of ocellar connection varied (Table 1); DONs responded to either one of the lateral ocelli, or to the median ocellus, or to the combination of one lateral and the medial. When two ocelli were effective, usually one was much more so than the other. The second ocellus evoked a spike only with low probability and with a variable latency, presumably indicating a longer synaptic pathway than between the DON and the main activating ocellus (Fig. 2D).

None of our DONs responded to wind on the head or body, or to light stimuli to the compound eyes. This distinguishes them from O_3 and O_4 (Simmons, 1980, 1981). The Fast Ipsi and the Fast Contra units (Table 1, Figs 1A, C; 2A, B) are the most conspicuous ocellar units in extracellular cord records, and can usually be recognized from one preparation to another by their large amplitude, short latency and response to particular ocelli. In extracellular recordings it sometimes seemed as if continuous frontal wind on the head increased the probability of doublets and triplets in the OFF response of these two units, but we were unable to confirm this in intracellular records where the possibility of confusing different units was excluded.

Four of the five recorded DONs gave 1–2–(3) spikes at OFF, and showed no response decrement in response to prolonged stimulation at up to 80 Hz. All these units were 'fast' in terms of Table 1 – latency of the spike in the mesothoracic ganglion to light OFF at the ocellus was 20–30 ms. This value was markedly temperature dependent. The remaining DON we filled had quite different properties. This unit (the Slow I/M/(C) unit) responded to either the ipsi or the median ocellus; its reliability was increased when both ipsi and median ocelli were stimulated simultaneously. There was a long latency, low probability response to the contra ocellus too. It gave an initial burst of 5–6 spikes to ipsi or median OFF, immediately decrementing to one spike for the second and subsequent stimuli at an ISI of 0·7 Hz in an unaroused animal. Recovery required 1–2 min rest. Responsiveness was restored without a rest interval (dishabituation) by touching either metathoracic tarsus, and decrement to repeated stimuli proceeded less slowly than usual while tarsal stimulus was maintained (Fig. 3). Other mechanical stimuli, including wind on the head, were ineffective in dishabituating the unit.

Flight motor neurones

We have recorded from motor neurones innervating all but two (nos 103, Tergotrochantal, and 85, Pleuroaxillary) of the mesothoracic flight muscles. In addition, we have a few records from metathoracic flight motor neurones. Simple or compound EPSPs and IPSPs are seen in the FMNs in response to OFF stimuli to the various ocelli. No PSPs are seen after ON stimuli to the ocelli. Often, but not always, the various components of compound PSPs can be correlated with the spikes of successive DONs of differing latency in the cord. Whenever EPSPs have been causally associated with particular spikes recorded in the pro-mesothoracic connectives their latency has been approx. 1 ms. They therefore appear to be monosynaptically derived from DONs. The fastest IPSPs have longer latencies, 6·5–10 ms longer than EPSPs recorded from the same cells. We presume that they are derived from DONs via thoracic interneurones (below). The IPSPs can be reversed by hyperpolarization: on some occasions hyperpolarization reveals two components, one with a reversal potential near resting potential (presumably Cl^- mediated). The amplitude of these fast PSPs typically remains stable even when stimulated at high frequency. In no FMN did the EPSP derived from ocellar input ever cause the cell to spike. Many of these characteristics are illustrated in Fig. 4A–D. The FMNs receive a great deal of synaptic input from unknown sources, and the majority of the records in Fig. 4 have been averaged to minimize this 'noise' signal over 10–50 sweeps.

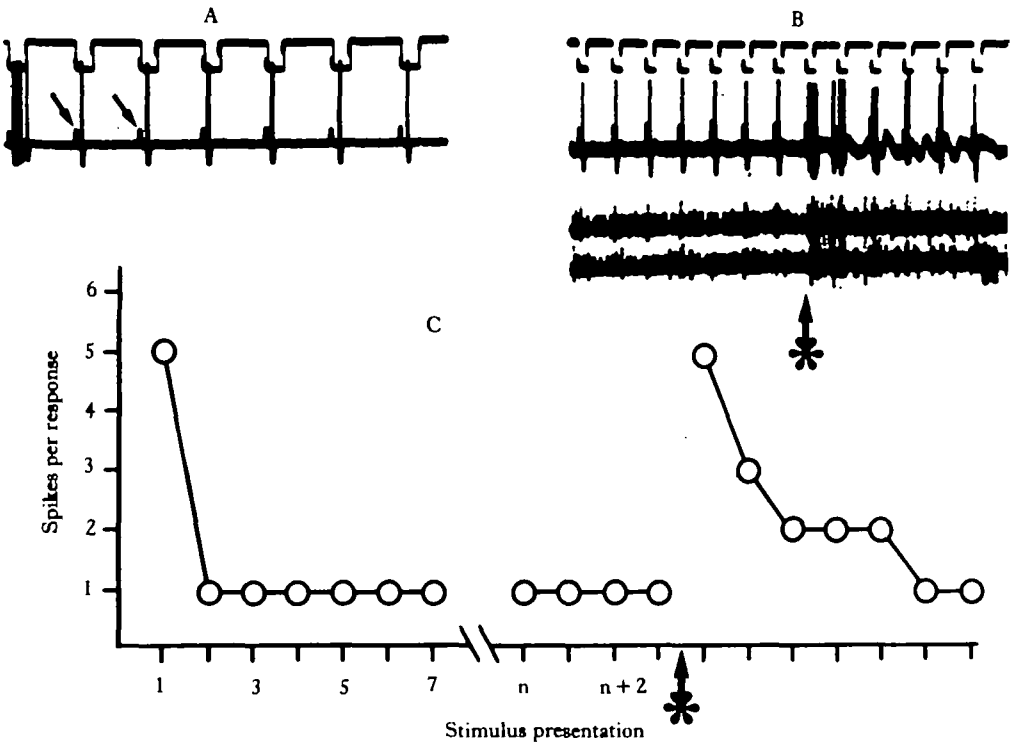

Fig. 3. Recordings from the slow ipsi/medial/(contra) DON. A: Upper trace, stimulus analogue: OFF pulses (1 $\log_{10}$ decrease in illumination) to ipsi ocellus at ISI = 700 ms. Lower trace, intracellular recording from DON; arrows indicate 2 mV, 10 ms calibration pulses. B: as A, except (i) record commences after a series of previous stimulus presentations (ii) lower traces show extracellular record from the connectives and (iii) sweep speed is decreased. After the seventh stimulus (star) the ipsilateral mesothoracic tarsus was touched with a fine paintbrush, resulting in increased neural activity in the connectives. C: The data of A and B plotted graphically as response amplitude (number of action potentials) against stimulus presentation number, to show habituation and dishabituation of the response. Similar behaviour is seen in descending visual units driven by the compound eye (e.g. Rowell, 1971).

For an understanding of the effect of ocellar input on flight behaviour, it is important to see what pattern of inputs is produced in the different functional groups of flight muscles (elevators, depressors, and the wing-rotating supinators and pronators) by the visual consequences of roll and pitch. As explained above, roll simplifies down to an OFF signal to the ocellus on the downward side, and downward pitch to OFF to the medial ocellus, as ON signals to the ocelli have no effect at the level of the DONs. (The mechanical operation of the different muscle groups is summarized in the Discussion.) With this background, the nature of the synaptic input to the mesothoracic flight motor neurones in response to OFF signals to the three ocelli is shown in Table 2. For the sake of subsequent discussion, the data of Simmons (1980) are also included. The results can be summarized as follows.

(i) All recorded *elevator* MNs receive a rather reliable EPSP in response to an OFF to the contralateral ocellus. An OFF to the ipsilateral ocellus produces usually no effect, sometimes an IPSP or a very small EPSP. Consequently, the flight muscles contralateral to the stimulated ocellus receive nett excitation relative to their (ipsilater

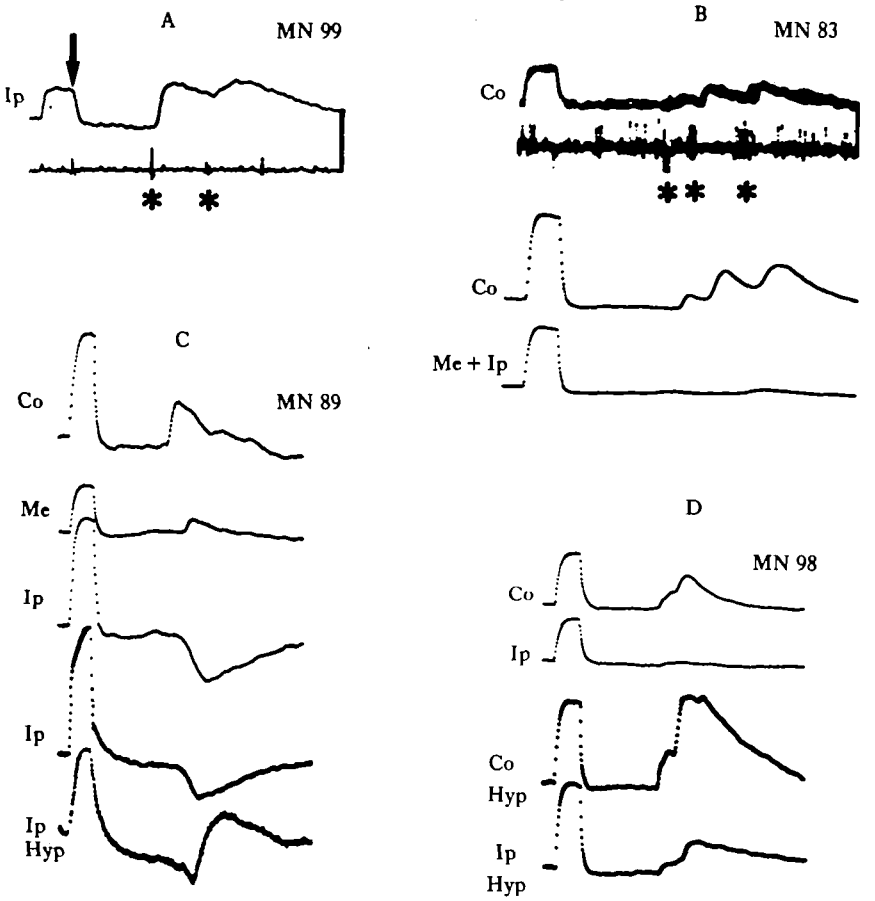

Fig. 4. Examples of synaptic potentials seen in mesothoracic flight motor neurones in response to ocellar stimulation. All the intracellular records (except the first trace in B) are averaged. Calibration 10 ms and 2 mV throughout. Stimulus, 1 $\log_{10}$ unit illumination decrease to the indicated ocellus, simultaneous with end of calibration pulse (arrow in A). A: MN of subalar muscle (no. 99). Compound EPSP (top trace) derived from two DONs of differing latency (bottom trace, starred) in the ipsilateral connective. B: MN of tergosternal muscle (no. 83). Compound EPSP (top trace) deriving from three different DONs firing in the ipsi connective (second trace) in response to an OFF to the contralateral ocellus. The two slower contra DONs seen here have not been characterized intracellularly, the fastest one is the fast contralateral DON. Third trace, same as top trace, but response averaged. Fourth trace, averaged response to simultaneous stimulation of medial and ipsi ocelli, to show absence of PSPs. C: MN of anterior tergocoxal muscle (no. 89). Top three traces: Stimulation of each of the three ocelli leads to a different pattern of EPSPs or IPSPs in the FMN, each with differing latencies. Fourth, fifth traces: the same neurone in a different preparation – note similarity of third and fourth traces. The IPSP in response to stimulation of the ipsi ocellus consists of two components, the slower of which is reversed by injection of hyperpolarizing current (fifth trace, Hyp). D: MN of 2nd basalar muscle (no. 98). Another example of differing patterns of PSPs in response to the two lateral ocelli (first two traces). Here both give EPSPs, but as in C above, during a roll the muscle contralateral to the darkened ocellus will receive more excitation than the ipsilateral. Third and fourth traces: hyperpolarizing the MN slightly shows that each EPSP is derived from several components.

homologues. Almost all these elevator MNs also receive an EPSP in response to OFF to the medial ocellus.

(ii) The *simple depressor MNs* (nos 81 and 98) respond to stimulation of the lateral ocelli in the same way as the elevator MNs: that is, the units contralateral to the

Table 2. *Nature of PSPs received by mesothoracic flight motor neurones in response to light decreases at each of the three ocelli*

Corresponding flight muscle: name, number and function, and number of times positively identified			Response to ocellar stimulation, and number of times the PSP was seen		
			Ipsi	Medial	Contra
83 1st Tergosternal	Indirect elevator	(3)	EPSP (1)	EPSP (1)	EPSP (3)
84 2nd Tergosternal	Indirect elevator	(1)	nil	nil	EPSP (1)
89 Anterior tergocoxal	Direct elevator (+ coxal promotor)	(3)	IPSP (2)	EPSP (2)	EPSP (2)
*90 + 91 1st and 2nd Posterior tergocoxals	Direct elevators (+ coxal remotors)	(7)	EPSP (2)	EPSP (4)	EPSP (6)
103 Tergotrochanteral	Direct elevator (+ trochantal depressor)			not recorded	
81 Dorsal longitudinal	Indirect depressor	(1)	nil (1)	nil (1) (Spike, Simmons, 1980)	EPSP (1)
98 2nd Basalar	Direct depressor	(8)	(EPSP) (1)	IPSP (1)	EPSP (1)
97 1st Basalar	Pronator-depressor	(5)	IPSP (1)	IPSP (1)	EPSP (3)
99 Subalar	Supinator-depressor	(2)	EPSP (2)	nil (2) (EPSP, Simmons, 1980)	nil (2)
85 Pleuroaxillary	Supinator			not recorded	

* not distinguished from each other with surety
( ) = very weak PSP.

stimulated ocellus receive nett excitation relative to their (ipsilateral) homologes. To an OFF to the medial ocellus, the MN of 98 sometimes receives an IPSP, and Simmons (1980) reports that those of 81 receive an EPSP.

(iii) The *pronators and supinators* (nos 97 and 99, which also function incidentally as depressors) respond to the lateral ocelli in respectively opposite ways. An OFF to the ipsilateral ocellus causes an EPSP in the MN of 99, and either nothing or an IPSP

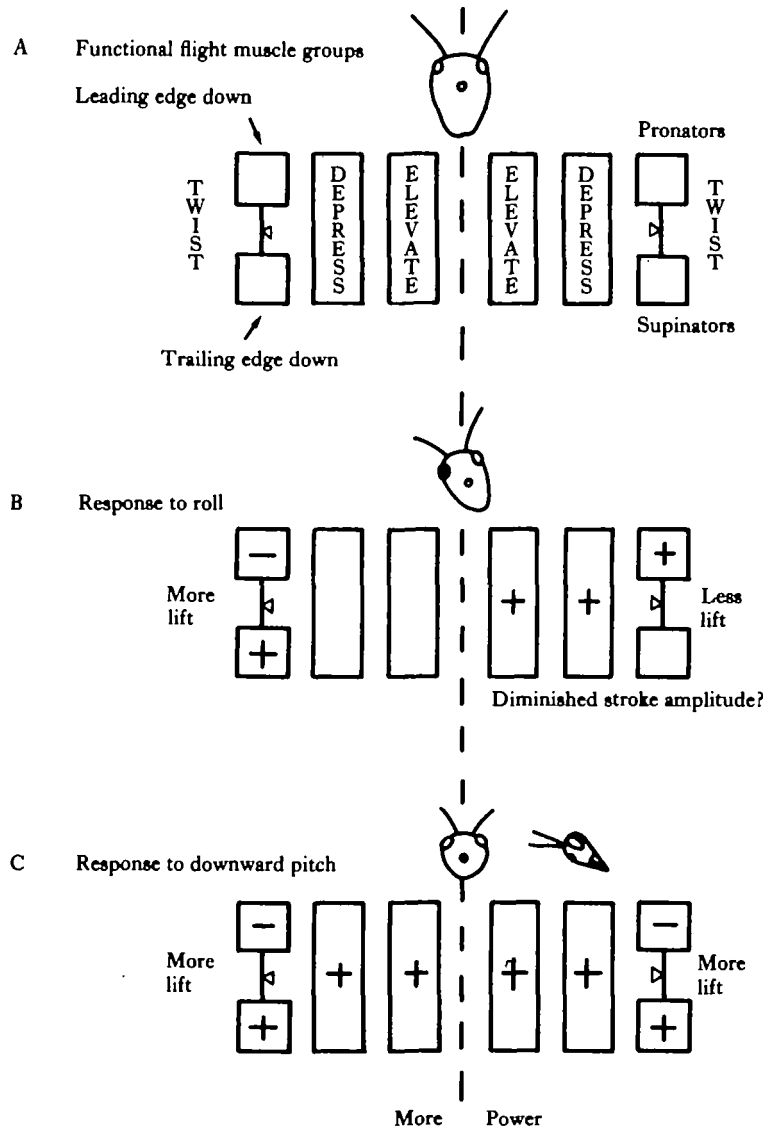

Fig. 5. Diagrammatic representation of the results shown in Table 2. The upper sketch (A) shows the functional grouping of the different flight muscles. Sketches B and C indicate the nett changes in activity in these groups expected on the basis of the PSPs generated by the ocelli in the FMNs in response to roll and downward pitch respectively, and the probable aerodynamic results. Pronation of the wing decreases the angle of attack, reducing lift, and supination has the reverse effect. Roll results in the darkening of one lateral ocellus, and downward pitch in the darkening of the medial ocellus. Further explanation in Discussion.

in 97: the nett effect will be towards supinating the wing. An OFF to the contralateral ocellus produces no effect in 99, and sometimes an EPSP in 97. Any nett effect will be towards pronating the wing. An OFF to the medial ocellus produces an IPSP in 97, and (according to Simmons, 1980) an EPSP in 99: this will tend to supinate the wing.

These effects are summarized in Fig. 5, and their functional consequences are treated in the Discussion. In general, the observed pattern is compatible with the hypothesis that any alteration in wing movements produced by the ocellar inputs would tend towards correction of flight deviations.

It should be noted that the connections described above are not always found. In this there is extensive individual variation, even though the experimental population was preselected (see Methods) for animals with prominent extracellular DON discharges. This is especially true for the inputs to MNs from the ipsilateral ocellus; Table 2 shows that the described ipsilateral inputs were actually seen in respectively 1/3, 2/3, 2/7, 1/5, 1/8 and 2/2 penetrations (sum, 9/28). MNs of muscle 98 were penetrated eight times, but on only 3 of a possible 24 occasions was an ocellar PSP seen. Similarly, in our few penetrations of the relevant MNs we did not see the PSPs mediated by O_3 described by Simmons (1980) (the PSPs that were recorded from these FMNs (e.g. Fig. 4A) were apparently derived from DONs with different properties from O_3). This point is returned to in the Discussion.

Rarely, PSPs with longer latencies (20 ms or so after the fastest EPSPs) were seen (not included in Table 2). These may derive from the slow, rare responses of some DONs to auxiliary ocellar input (Table 1).

Thoracic ocellar neurones

In addition to the DONs and FMNs, we have recorded from numerous other units in the mesothorax which receive synaptic input from the DONs. All which have been filled have been interneurones.

Anatomy

All these 'thoracic ocellar' neurones (TONs) are effectively planar, lying in the same dorsal sheet of neuropil as the FMNs. Their branching is concentrated in two areas, the lateral flight motor neuropil, and in a longitudinal strip lateral to the ganglion midline, approximately coinciding with the dorsal longitudinal axon tracts. Their morphology is illustrated on Figs 6 and 7,corresponding to two main groups.

(i) Mesothoracic intraganglionic interneurones. All of this category are unilateral only. Typically they extend to two or all of the anterior, intermediate or posterior areas of the lateral flight motor neuropil and also to the lateral edge of the dorsal longitudinal tract, which includes the DONs (Fig. 6).

(ii) Interganglionic interneurones. These fall into three types: unilateral projection in mesothorax, axon projecting to ipsilateral prothoracic ganglion; unilateral projection in mesothorax, axon projecting to ipsilateral metathoracic ganglion; bilateral projection in mesothorax, axon projecting unilaterally to metathoracic ganglion. The cell bodies of all these neurones lie in the mesothorax, and can be ipsilateral or contralateral to the axon running in the connective (Fig. 7). The interganglionic interneurones as a class differ from the intraganglionic in that their ramifications in the vicinity of the DONs can be either or both ipsi- and contralateral relative to th

[redacted]n axon. They also have unilateral or bilateral projections to the FMN areas of the mesothoracic ganglion. Within the metathoracic ganglion, those cells that have been filled all project unilaterally to the FMN area.

We do not know, as yet, how many of these TONs occur in the mesothoracic ganglion, but a total of twenty pairs seems a conservative estimate. We recognize as distinct at least the 14 neurones listed in Table 3. Some have been filled more than once, and then are recognizably of the same morphology and have the same physiological characteristics. Some morphologically similar cells are clearly different from one another in detail or show quite different physiological responses. Some physiologically distinctive cells have not yet been filled.

Physiology

The physiological responses of the TONs are summarized in Table 3 and Fig. 8.

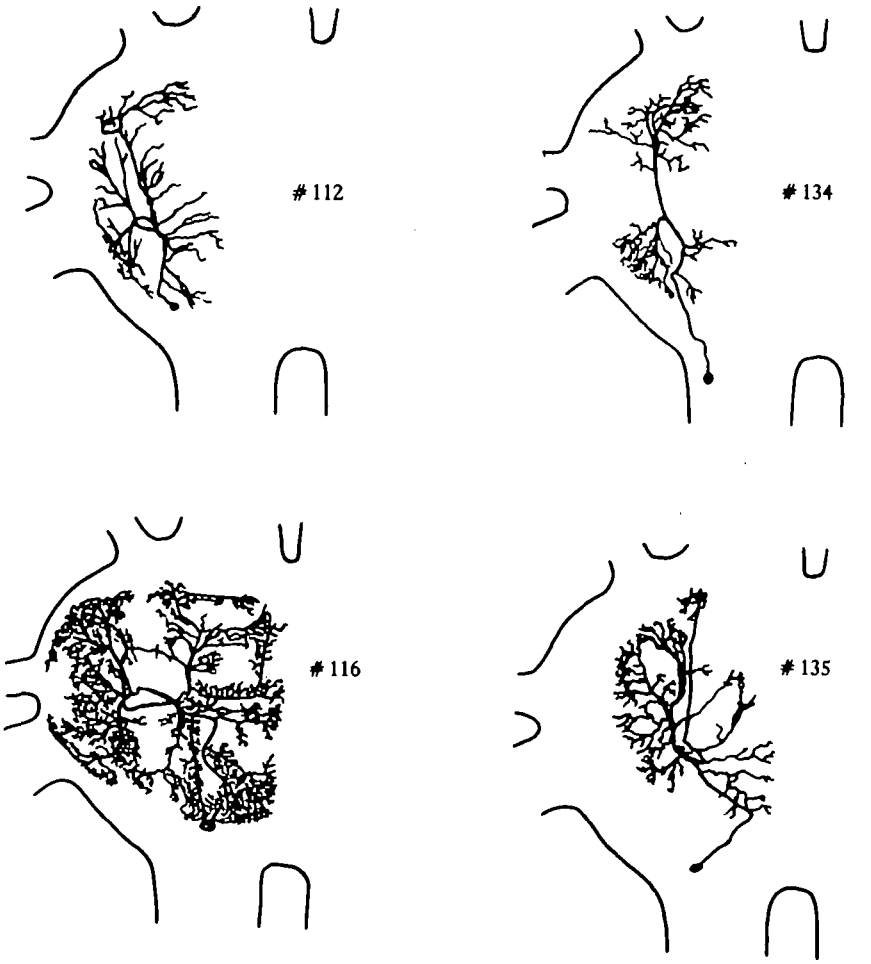

Fig. 6

Fig. 6. Drawings of Lucifer yellow fills of some of the mesothoracic intraganglionic interneurones which receive ocellar input, listed in Table 3. Of those not figured, #120 bears a general resemblance to #112, #109 to #116, and #136 to #135, though all are undoubtedly distinct. Scale as in Fig. 1.

Fig. 7

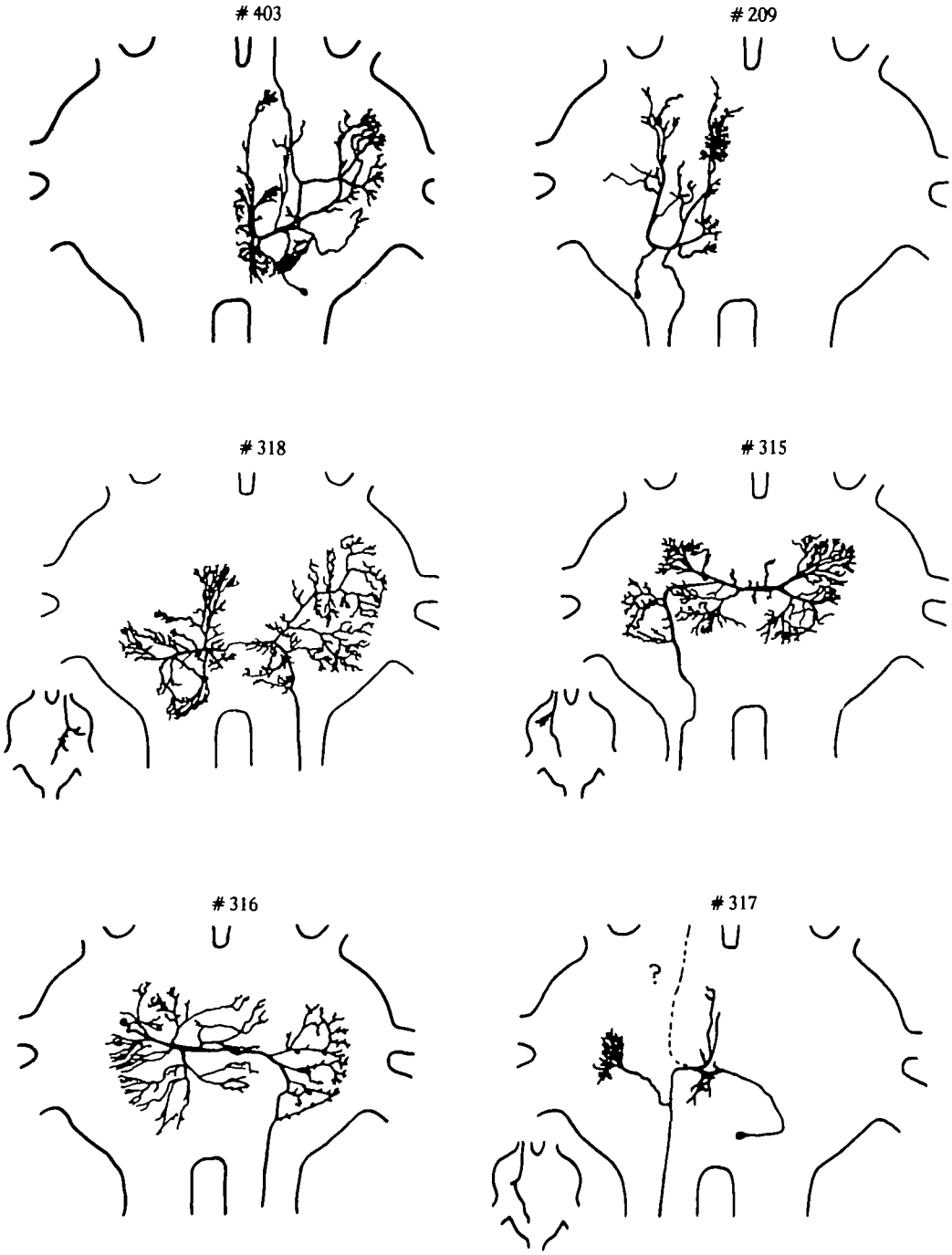

Fig. 7. The morphology of some of the mesothoracic interganglionic interneurones which receive ocellar input, listed in Table 3. #302, not figured here, is similar in general morphology to #318. The small inset sketches show the axonal projection in the metathoracic ganglion. Scale as in Fig. 1.

Table 3. *PSPs received by mesothoracic interneurones in response to light decrease at the ocelli*

Morphological type and no. of neurone	No. of fills	Response to ocellar OFF: Ipsi	Medial	Contra	Comments
Intraganglionic, unilateral:					
112	1	Spike, dIPSP	/	IPSP	
120	2	/	EPSP	(EPSP)	Discharges with depressors
136	1	EPSP	/	Spike	
134	1	dEPSP	/	dEPSP	
109	2	Spike	(EPSP)	/	Discharges with depressors
116	1	EPSP	(EPSP)	/	
135	1	/	EPSP	(EPSP)	Cephalic wind-hair input
Interganglionic, meso-prothoracic, unilateral:					
403	2	EPSP	EPSP	EPSP	Discharges with depressors
Interganglionic, meso-metathoracic, unilateral:					
209	2	EPSP	/	/	
Interganglionic, meso-metathoracic, bilateral:					
302	2	EPSP	/	/	Discharges with depressors; inhibits metathoracic elevator
318	1	Spike	Spike	dEPSP	
315	1	EPSP	/	EPSP	Leg mechanoreceptor input
316	1	EPSP	/	EPSP	
317	1	/	dIPSP	/	

Symbols: d = delayed response
/ = no response
( ) = very weak response

All penetrations were made in the neuropil, and none were from either cell body or from areas of spike-sustaining membrane, though spikes generated elsewhere in the cell were clearly visible. By definition, all TONs receive PSPs from OFF stimulation of one or more ocelli. EPSPs are normally of short latency (1–3 ms) with respect to the associated DON spike in the cord (e.g. Fig. 8A–C), and appear to derive monosynaptically from DONs. Compound EPSPs are usually derived from more than one DON (of different latencies) converging on the recorded interneurone (Fig. 8B). IPSPs are 5–20 ms later, and presumably derive from DONs via TONs. Sometimes delayed EPSPs are also seen. EPSPs are much commoner than IPSPs (Fig. 8E), and 4 of the 13 neurones receiving EPSPs are driven to spike reliably by the ocellar input (e.g. Fig. 8A). Decrement in response to repeated stimulation occurs in some but by no means all of the TONs (Fig. 8D). Most of these TONs are not obviously multimodal. Only one (135) received input from cephalic wind-hairs, and one (315) received powerful mechanoreceptive excitatory input from the ipsilateral mesothoracic tarsus.

In the four cases in which the experiment has been possible (Table 3) the TONs

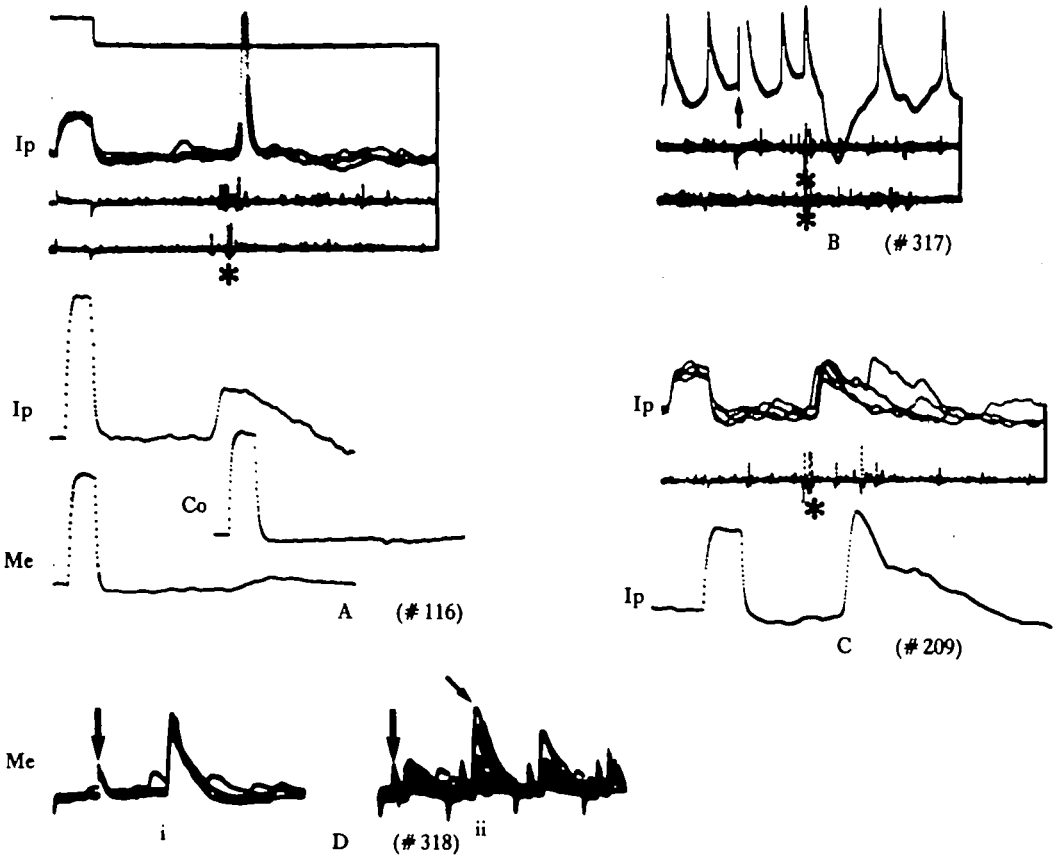

Fig. 8. Recordings from TONs. A, C, Calibration pulse 2 mV, 10 ms; stimulus coincident with trailing edge of calibration pulse. B, D, see legend. A: Intraganglionic TON #116. Top four traces: the fast ipsi DON (starred, 4th trace) elicits an EPSP leading to spiking in the TON (2nd trace). Fifth trace, averaged record of the same EPSP after hyperpolarization to prevent spiking. Sixth and seventh traces: averaged records showing that the contra ocellus has no input to this TON, and that the median ocellus elicits a very small EPSP of longer latency. B: Interganglionic interneurone #317. IPSP produced in response to stimulation (arrow) of medial ocellus. The cell is damaged by the penetration and is spiking repetitively: the spikes are not associated with the stimulus. Scale: the IPSP is 7 mV, the latency of the DON with respect to the stimulus is 25 ms. C: Interganglionic interneurone #209. Compound EPSP (1st and 3rd, averaged, traces) in response to stimulation of ipsi ocellus. The first component of the EPSP is associated with the fast ipsi DON (second trace, starred): the second component could not be associated with any observed DON and is probably derived from an interneurone (TON). D: Interganglionic interneurone #318. Decrement of EPSP recorded in response to stimulation of median ocellus (large arrow) at frequencies higher than 10/s. Unit hyperpolarized to prevent spiking. In D(i) the ISI is 1 s, and no response decrement is seen (five superimposed traces). In D(ii) the ISI is 0·05 s; the 1st, 5th, 9th, 13th, etc. responses (small arrow) to the stimulus (large arrow) show obvious decrement. Initial amplitude of EPSP is 10 mV, and its latency is 28 ms.

have been found to fire bursts of action potentials in phase with either depressor or elevator FMNs during simulated flight (Robertson & Pearson, 1982). One interneurone (302), which discharged in phase with the mesothoracic depressors, was shown (Fig. 9) to inhibit a metathoracic elevator FMN.

Despite specific search, we have so far found no non-spiking interneurones which receive ocellar input.

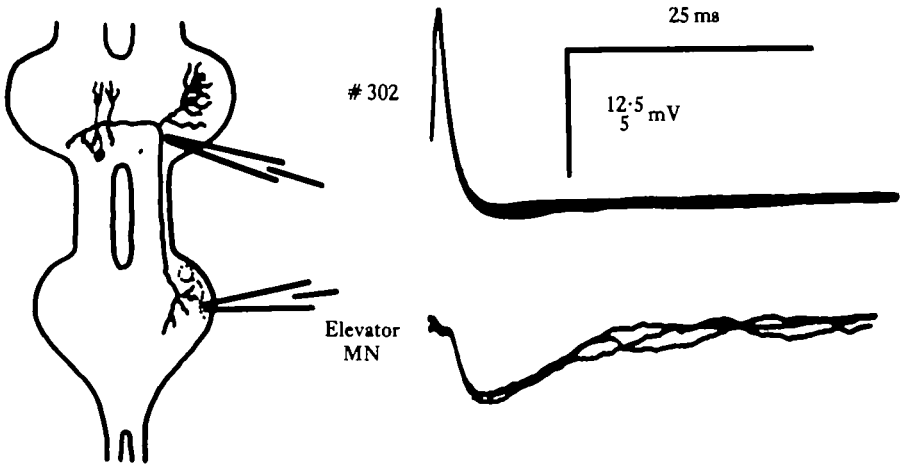

Fig. 9. Simultaneous recordings from interganglionic thoracic ocellar neurone #302 and an unidentified metathoracic elevator motorneurone. The interneurone discharges in bursts of action potentials (upper trace) during the depression phase of simulated flight, and produces an IPSP in the elevator motoneurone (lower trace). See also Fig. 10 of Robinson & Pearson (1982). This recording is from the homologous neurone in *Locusta*.

DISCUSSION

The DONs

The present results, with those of Simmons (1980) on O_3, corroborate at the single unit level what has been previously suggested about the population of DONs by earlier workers from extracellular recording. All DONs so far recorded by us or by others (e.g. Burtt & Catton, 1954) from the thorax are phasic OFF units. DONs with other properties (e.g. tonic response, or ON units) have been reported from the circumoesophageal connectives (Guy *et al.* 1977). Taylor's (1981*a*) results show that tonic ocellar information is transmitted to the neck motor neurones. If these other DONs stop at the level of the suboesophageal or prothoracic ganglia (from which the neck muscles are driven), it would explain their absence from recordings in the pterothorax.

As both the medial ocellus and the cephalic wind-hairs signal pitch deviations, one might expect considerable convergence of these modalities in the DONs. Perhaps surprisingly, only two DONs to date are known to have wind-hair input (O_3 and O_4, Simmons, 1980, 1981). We found three other DONs with more or less important medial ocellus input, none of which is responsive to wind. Similarly, of the seven TONs found to respond to medial ocellar input, only one also responded to wind-hair input. The other properties of this TON, however, suggest that it is not driven by O_3, as it receives excitation from the contralateral and medial ocelli, whereas O_3 responds to the ipsilateral and medial.

The lateral ocelli signal roll, which leaves the wind-hairs largely unaffected (though they might respond to a rapid transient component, see Bacon & Möhl, 1979). Convergence of these two inputs in a single DON is consequently unexpected, and (except for the minor sensitivity of O_3 to ipsilateral ocellar input) is indeed not found. Another descending wind-hair unit, the tritocerebral commisure giant (TCG) has been described by Bacon & Tyrer (1978). It receives additionally visual input from the

compound eye. One would expect the visual response of the TCG to be specific yaw and pitch (the two rotations to which the wind-hairs are sensitive) but this information is not available; so far only ON/OFF stimuli have been tested.

We recorded no DON with the properties described by Simmons (1980) for O_3 and O_4, despite virtually identical stimulus regimes. The question arises as to whether any of our units could have been confused with O_3 and O_4. Both O_3 and O_4 responded strongly to wind on the head, and O_3 (which was characterized in detail) responded principally to the medial ocellus and weakly to the ipsilateral ocellus. Of our units the only one to respond principally to the medial ocellus (the Fast Medial unit, Table 1) had a totally different thoracic morphology. The Fast Ipsi (Medial) unit, with a weak, long latency (twice that of O_3) response to the medial ocellus, showed no response to wind and has a slightly different morphology. The thoracic morphology of what we call the Fast Ipsi unit is almost identical to that of O_3. We filled this unit twice and recorded it extracellularly in many preparations. It never responded to either wind on the hair or the medial ocellus. We conclude that we did not penetrate O_3. This in itself is unremarkable, as there are certainly several more DONs which we recorded extracellularly but failed to penetrate. We also failed to record responses to stimulation of the medial ocellus in the mesothoracic motor neurones postsynaptic to O_3, 99 and 81 (Table 2). Probably this simply reflects the variability between individuals seen in the strength of the synaptic inputs to the FMNs in general (see Results), combined with the effects of a very small sample of indubitable 99 and 81 MNs.

The thoracic anatomy of all the known descending neurones in the grasshopper which respond to ocellar and wind-hair inputs (and to combinations of these with other modalities) seems to be extremely similar, as would be expected if they are all doing basically the same job (mediating flight corrections) and having the same thoracic targets. The characteristic unilateral projection of the locust DONs in the pterothorax is similar to that described for analogous units in the bee (Pan & L. Goodman, 1977).

Mode of functioning of ocellar inputs to the thoracic ganglia

Short-latency inputs to the FMNs

Lift and thrust forces arise during flight because the plane of the wing lies at an angle (the angle of attack) to the plane in which the wing is moved by the elevators and depressors. The angle of attack is controlled by the rotation of the wing about its long axis: rotation decreasing the angle of attack is called pronation, and rotation increasing the angle of attack is called supination. Supination of the wing during upstroke has been thought to be entirely passive, while downstroke supination is controlled by the balance of forces exerted by the first basalar (pronator-depressor) and the subalar (supinator-depressor) (Wilson & Weis-Fogh, 1962). (It has recently been shown, Pfau & Nachtigall, 1981, that the pleuroaxillary muscle 85 also influences the angle of attack, acting as a tonic supinator; so far, no theories of flight take account of it, and no measurements of its activity in flight are available. Its inputs from the ocellar system, if any, are also unknown.) The amount of downstroke supination/pronation is critical, and is always modulated during flight corrections. In general, more downstroke supination generates more lift. The remaining motor units are also modulated during flight corrections, but only provide complementa

anges in power; thus when more lift is generated, there is increased general depressor activity, e.g. recruitment of the normally silent second basalar (Wilson & Weis-Fogh, 1962). Further details are to be found in Wilson, 1961, 1963; Gettrup & Wilson, 1964; Dugard, 1967; Waldron 1967*a*,*b*; Koch, 1967; Zarnack & Möhl, 1977 and Baker, 1979*a*,*b*. The FMNs receive from the DONs monsynaptic EPSPs and longer latency IPSPs. The data of Table 2 indicate what synaptic inputs will operate on virtually all the mesothoracic flight MNs in response to a given roll or pitch. This pattern can then be compared with what would be predicted from our current understanding of the mechanics of the system. Simmons (1980) has recently done this for the effects of one DON (O_3) on two FMNs (subalar and dorsal longitudinal). He concluded that downward pitch could generate increased lift (through an EPSP to the supinating subalars) and that upward pitch would cause ON-induced inhibition of the continuous wind-hair response which he assumed to be present in O_3 during flight. Our results extend Simmons' argument to all of the mesothoracic FMNs and DONs. Table 2 can be represented graphically by Fig. 5. This shows that the pattern of PSPs in the FMNs in response to roll could generate more lift (via greater wing supination) on the DOWN side, less lift (via greater pronation) on the UP side; the increased elevator and depressor activation on the UP side should generate more muscular power, the need for which is not obvious, but it could also cause the reduced wing stroke seen by Taylor via increased antagonism. When the animal pitches downwards the EPSP pattern would tend to supinate both forewings. Simultaneously, increased activation of all depressors and elevators should generate more power; depending on timing, a greater or lesser reduction in wingstroke might also be expected, but it is not clear to us from the literature what is actually observed under these circumstances. The overall result of pitch-down should be increased lift on both sides of the body. Hence, for both roll and pitch-down the ocellar signal would tend to produce correcting behaviour in the flight output, assuming that the subthreshold EPSPs would have some effect upon the spikes produced in the relevant MNs. A pitch-up deviation will, however, produce no OFF response from any DONs in the thorax, and unless these units are simultaneously carrying another signal (as Simmons suggested) they will not be susceptible to inhibition. Simmons' suggestion is plausible for O_3 under his conditions of a steady air stream on the head, but has some problems. The wind-hairs are actually activated phasically at wing beat frequency, not tonically (Horsmann, Heinzel & Wendler, in the press), and the TCG neurone, a typical wind-hair descending neurone which responds tonically under steady state conditions, similarly fires only once per wing beat cycle in real flight (Bacon & Möhl, 1979). O_3 might be expected to behave similarly as a wind-hair neurone; as an ocellar neurone, it will probably also fire once per wing beat cycle, due to the 5° nodding movement of the head (Taylor, 1981; Horsmann, Heinzel & Wendler, in the press). This presents a smaller substrate for inhibition than a continuous discharge. However, the phasic ocellar inputs to the thorax are only a part of a much larger sensory system, and need not be expected to explain all functions. It is quite possible that pitch-up is corrected mainly by e.g. the wind-hair input, and that the phasic ocelli units play only a minor role.

The thoracic interneurones

The designation 'thoracic ocellar neurones' follows from the fact that the units were

recognized from their response to ocellar input, but should be received with some caution. It does not imply that this is the only or even the most important input to these cells, which in several cases are known to have others. Further work on the flight oscillator and its coupling to the MNs is required before the 'TONs' can be seen in proper functional perspective. If, as seems likely, they are involved in mediating ocellar flight correction behaviour, they probably participate when this behaviour is driven by other sense organs and voluntary commands.

We know only a few facts about the connectivity of the TONs. (i). TONs are excited or (rarely) inhibited by ocellar input (Table 3; Fig. 9). (ii). Several TONs discharge rhythmically during simulated flight in phase with either elevator or depressor FMNs (Table 3; Fig. 10 of Robertson & Pearson, 1982). (iii). At least one such TON has inhibitory connections with a FMN of the opposite type (Fig. 9), and the anatomical similarity of this cell with others suggests that this will turn out to be general.

If (ii) and (iii) are indeed typical, then, during flight, FMNs will receive regular IPSP volleys between their own bursts. Additional ocellar modulation of the sources of these IPSPs could readily produce the observed phase shifts (Taylor, 1981*b*) in FMN activity. This model would produce the observed behaviour, but further work is required to establish it.

At least some interneurones must act as 'inverters' to provide the delayed IPSPs seen in the FMNs in response to DON spikes. The simple unilateral intraganglionic interneurones appear to have a suitable morphology, but only some of them spike reliably in response to DON input, which the hypothesis requires.

Integration of ocellar inputs on to the motor neurones

The fast phasic information from the ocelli reaching the thorax goes to the FMNs by at least two routes. First, there is a simple 'direct' connection, consisting of monosynaptic EPSPs and slightly delayed (probably disynaptic) IPSPs of the sort figured by Simmons (1980) and in this paper. Secondly, the ocellar signal produces PSPs or spikes in a population of thoracic interneurones, of which an as yet unknown proportion spike rhythmically during flight (Table 2) and make synaptic connection with the motor neurones (as in Fig. 9). Obviously both routes must play some role in behaviour.

It may be premature to evaluate the relative significance of these channels, but some obvious factors need to be spelt out. The 'direct' PSPs at all our recording sites are very small (approx. 1 mV) relative to the 15–25 mV oscillation seen in the FMNs during simulated flight (Robertson & Pearson, 1982). In order for them to have any reliable effect on the timing of the FMN spike they would require precise synchronization with the wing beat cycle. It is not excluded that such a synchronization exists, either by neural feedback to the ocellus (Kondo, 1978) or by mechanical feedback via turbulence affecting wind-hairs and via head nodding (see above), but this needs to be demonstrated. We also have the impression that these synapses are unusually variable, in the sense of not being findable in many individuals (see Results); although realistic sample sizes do not allow this to be demonstrated with statistical conviction, we think this a real characteristic of the direct ocellar FMN connections. On the other hand, these connections are fast, which seems to be one of the advantages of the phasic ocellar and wind-hair neurones over other parts of the stabilization machinery, such as the descending inputs from the compound eyes or those that work via head rotation and proprioceptio

The 'indirect' connection affects the FMNs only during flight, when at least a sizeable minority of the TONs (here assumed to be generally presynaptic to the FMNs) are firing in bursts at the flight frequency. The ocellar PSPs seen in these interneurones are relatively large, they sometimes alone bring the cell to spike or are competent to shut off a previously spiking cell (Fig. 8A, B). These considerations suggest that the interneurones probably play an important role in correction behaviour; possibly the small amplitude, direct connections serve to accelerate the ultimate response in the FMN. An analogous situation seems to be found in the wing stretch receptor. Activity in this organ probably influences flight motor neurone output (though this is much less clear than in the case of the ocelli) and there are subthreshold monosynaptic connections with the FMNs (Burrows, 1975). The stretch receptor, however, also makes powerful connections with thoracic interneurones rhythmically active during flight (R. M. Robertson & K. G. Pearson in preparation) and the relative importance of the two pathways in producing behaviour is not yet clear. Parallel sensory pathways to the motor output are commonly seen in arthropods (e.g. the crayfish tail-flip, the visually-induced jump of the locust) and their relative role in refining the behavioural output is only beginning to be investigated. The flight stabilization circuitry of the locust, with its multiple sensory inputs, each with several routes to the thoracic centres, may present good material for such an investigation.

This work was supported by NSF Grant BNS 78-26785 to C. H. F. Rowell and by a grant from the Canadian Medical Research Council to K. G. Pearson. Part of this work was carried out at the Zoology Department, University of California at Berkeley. We thank Dr J. Bacon for reading and criticizing the manuscript.

REFERENCES

Baker, P. S. (1979*a*). The wing movements of flying locusts during steering behavior. *J. comp. Physiol.* **131**, 49–58.

Baker, P. S. (1979*b*). The role of forewing muscles in the control of direction in flying locusts. *J. comp. Physiol.* **131**, 59–66.

Bacon, J. & Möhl, B. (1979). Activity of an identified wind interneurone in a flying locust. *Nature, Lond.* **278**, 638–640.

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

Burrows, M. (1975). Monosynaptic connexions between wing stretch receptors and flight motoneurones of the locust. *J. exp. Biol.* **62**, 189–219.

Burtt, E. T. & Catton, W. T. (1954). Visual perception of movement in the locust. *J. Physiol., Lond.* **125**, 566–580.

Camhi, J. M. (1970). Yaw-correcting postural changes in locusts. *J. exp. Biol.* **52**, 519–532.

Cornwell, P. B. (1955). The functions of the ocelli of *Calliphora* (Diptera) and *Locusta* (Orthoptera). *J. exp. Biol.* **32**, 217–233.

Dugard, J. J. (1967). Directional change in flying locusts. *J. Insect Physiol.* **13**, 1055–1063.

Gettrup, E. & Wilson, D. M. (1964). The lift-control reaction of flying locusts. *J. exp. Biol.* **41**, 183–190.

Goodman, C. S. (1976). Anatomy of the ocellar interneurones of acridid grasshoppers. I. The large interneurones. *Cell Tiss. Res.* **175**, 166–183.

Goodman, C. S. (1978). Isogenic locusts: genetic variability in the morphology of identified neurons. *J. comp. Neurol.* **182**, 681–706.

Goodman, C. S. & Williams, J. L. D. (1976). Anatomy of locust ocellar interneurones: II. The small interneurons. *Cell Tiss. Res.* **175**, 184–203.

Goodman, L. J. (1959). Hair receptors in locusts. Hair plates on the first cervical sclerites of the Orthoptera. *Nature, Lond.* **183**, 1106–1107.

GOODMAN, L. J. (1965). The role of certain optomotor reactions in regulating stability in the rolling pl during flight in the desert locust, *Schistocerca gregaria*. *J. exp. Biol.* **42**, 385–408.

GOODMAN, L. J. (1970). The structure and function of the insect dorsal ocellus. *Advances in Insect Physiology* **7**, 97–196.

GOODMAN, L. J., MOBBS, P. G. & GUY, R. G. (1977). Information processing along the course of a visual interneuron. *Experientia* **33**, 748–750.

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

HESSE, R. (1908). Untersuchungen über die Organe der Lichtempfindung bei niederen Tieren. VII. Von den Arthropoden Augen. *Z. wiss. Zool.* **70**, 347–473.

HORSMANN, U., HEINZEL, H.-G. & WENDLER, G. (1983). The phasic influence of self-generated air current modulations on the locust flight motor. *J. comp. Physiol.* (in press).

KOCH, U. T. (1967). A miniature movement detector applied to recording of wingbeat in *Locusta*. *Fortschr. Zool.* **24**, 327–332.

KONDO, H. (1978). Efferent system of the lateral ocellus in the dragonfly: its relationships with the ocellar afferent units, the compound eyes, and the wing sensory system. *J. comp. Physiol.* **125**, 341–350.

LISKE, E. (1977). The influence of head position on the flight behaviour of the fly *Calliphora erythrocephala*. *J. Insect Physiol.* **23**, 375–379.

MITTELSTAEDT, H. (1950). Physiologie des Gleichgewichtssinnes bei fliegenden Libellen. *Z. vergl. Physiol.* **32**, 422–463.

MÖHL, B. & ZARNACK, W. (1977). Activity of the direct downstroke flight muscles of *Locusta migratoria* (L.) during steering behaviour in flight. II. Dynamics of the time shift and changes in the burst length. *J. comp. Physiol.* **118**, 235–247.

PAN, K. C. & GOODMAN, L. J. (1977). Ocellar projections within the central nervous system of the worker honey bee, *Apis mellifera*. *Cell Tiss. Res.* **176**, 505–527.

PARRY, D. A. (1947). The function of the insect ocellus. *J. exp. Biol.* **24**, 211–219.

PEARSON, K. G. & GOODMAN, C. S. (1979). Correlation of variability in structure with variability in synaptic connections of an identified interneuron in locusts. *J. comp. Neurol.* **184**, 141–165.

PFAU, H. K. & NACHTIGALL, W. (1981). Der Vorderflügel grosser Heuschrecken als Luftkrafterzeuger. II. Zusammenspiel von Muskeln und Gelenkmechanik bei der Einstellung der Flügelgeometrie. *J. comp. Physiol.* **142**, 135–140.

ROBERTSON, R. M. & PEARSON, K. G. (1982). A preparation for the intracellular analysis of neuronal activity during flight in the locust. *J. comp. Physiol.* **146**, 311–320.

ROWELL, C. H. F. (1971). Variable responsiveness of a visual interneurone in the free-moving locust, and its relation to behaviour and arousal. *J. exp. Biol.* **55**, 727–748.

SIMMONS, P. J. (1980). A locust wind and ocellar brain neurone. *J. exp. Biol.* **85**, 281–294.

SIMMONS, P. J. (1981). Synaptic transmission between second- and third-order neurones of a locust ocellus. *J. comp. Physiol.* **145**, 265–276.

SIMMONS, P. J. (1982). Transmission mediated with and without spikes at connexions between large second-order neurones of locust ocelli. *J. comp. Physiol.* **147**, 401–414.

STANGE, G. (1981). The ocellar component of flight equilibrium control in dragonflies. *J. comp. Physiol.* **141**, 335–347.

STANGE, G. & HOWARD, J. (1979). An ocellar dorsal light response in a dragonfly. *J. exp. Biol.* **83**, 351–355.

TAYLOR, C. P. (1981*a*). Contribution of compound eyes and ocelli to steering of locusts in flight. I. Behavioural analysis. *J. exp. Biol.* **93**, 1–18.

TAYLOR, C. P. (1981*b*). Contribution of compound eyes and ocelli to steering of locusts in flight. II. Timing changes in flight motor units. *J. exp. Biol.* **93**, 19–32.

TAYLOR, C. P. (1981*c*). Graded interactions between identified neurons from the simple eyes of an insect. *Brain Res.* **215**, 382–387.

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

WALDRON, I. (1967*a*). Mechanisms for the production of the motor output pattern in flying locusts. *J. exp. Biol.* **47**, 201–212.

WALDRON, I. (1967*b*). Neural mechanism by which controlling inputs influence motor output in the flying locust. *J. exp. Biol.* **47**, 213–228.

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* (Orthoptera). *J. Zool., Lond.* **176**, 67–86.

WILSON, D. M. (1961). The central nervous control of flight in a locust. *J. exp. Biol.* **38**, 471–490.

WILSON, D. M. (1963). Motor and sensory mechanisms of lift control in locust flight. Proc. XVI Int. Congr. Zool., Washington DC, 1963.

WILSON, D. M. & WEIS-FOGH, T. (1962). Patterned activity of coordinated motor units, studied in flying locusts. *J. exp. Biol.* **39**, 643–668.

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

ZARNACK, W. & MÖHL, B. (1977). Activity of the direct downstroke flight muscles of *Locusta migratoria* (L.) during steering behaviour in flight. I. Patterns of time shift. *J. comp. Physiol.* **118**, 215–233.