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CONNEXIONS BETWEEN A MOVEMENT-DETECTING VISUAL INTERNEURONE AND FLIGHT MOTONEURONES OF A LOCUST

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SUMMARY

Both of the descending contralateral movement detector (DCMD) neurones of *Schistocerca americana gregaria*, which respond to stimulation of the contralateral eye or to loud noises, mediate excitatory postsynaptic potentials in most ipsilateral flight motoneurones.

INTRODUCTION

In the ventral nerve cord of a locust, the largest axons which run between the brain and the thoracic ganglia are those of a pair of neurones called the descending contralateral movement detectors (DCMDs), each of which responds with a vigorous burst of spikes when a small object moves suddenly in the visual field of the compound eye contralateral to its axon (Rowell, 1971). Spikes are also elicited in a DCMD by loud noises (O'Shea, 1975) or a sudden decrease in the intensity of light incident upon any of the three ocelli (P. Simmons, in preparation).

Burrows and Rowell (1973) found that a DCMD mediates excitatory postsynaptic potentials (EPSPs) in the fast motoneurone which innervates the extensor tibiae muscle of each hind leg. They suggested that the DCMDs are involved in initiating the jumps that locusts often make when startled. The types of stimuli which excite a DCMD, and the relatively high conduction velocity of a DCMD axon are consistent with such a function. There are branches from the axon of a DCMD in all three thoracic ganglia (O'Shea, Rowell & Williams, 1974), and it is reasonable to enquire whether a DCMD connects with motoneurones other than those involved in jumping. Pearson and Goodman (1979) have found that a DCMD mediates EPSPs in some unidentified flight motoneurones, as well as with motoneurones which innervate extensor and flexor muscles of the hind legs. In this paper, connexions made by the DCMDs to flight motoneurones of one species of locust are described in detail. The connexions are appropriate for causing rapid alterations in the flight course of a locust, which could prevent collision with nearby objects. The DCMDs may also play a role in triggering the opening of the wings, which often occurs when a startled locust jumps.

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MATERIALS AND METHODS

Experiments were performed on adult male and female *Schistocerca americana gregaria* (Dirsh), obtained from a crowded laboratory culture. A locust was mounted upright on a block of plasticene and an incision made along its dorsal midline from the third abdominal segment to the head. The wings were pulled laterally and secured with plasticene. The three thoracic ganglia and the connectives between them were exposed by removing the gut, some small muscles and parts of the endoskeleton. A wax-coated, stainless steel platform was positioned beneath the meso- and metathoracic ganglia and pins were placed around the ganglia to stabilize them. The elevator muscles were cut through half way along their lengths so that parts of all the flight muscles were visible. Throughout an experiment, the ganglia were covered by saline of composition (mM): NaCl, 175; KCl, 9·7; $CaCl_2$, 1·5; $MgCl_2$, 2; $NaHCO_3$, 1; Na_2HPO_4, 1·7; glucose, 39.

Intracellular recordings were made from motoneurones with glass microelectrodes which were filled with 2 M-potassium acetate and had d.c. resistances of 40–80 MΩ. Often their passage through the perineurium was assisted by applying a 1% solution of Sigma Type VI Protease in saline to the ganglia for two minutes. The microelectrodes were connected to d.c. amplifiers which incorporated bridge circuits. To identify a motoneurone which had been penetrated by a microelectrode, spikes in it, heard over the audio monitor, were correlated with twitches observed in a muscle. I have found this method to be more reliable than to employ extracellular electrodes placed in flight muscles. Names and numbers of flight muscles are from Snodgrass (1929).

To record spikes from the axons of the DCMDs, a pair of platinum hook electrodes was manipulated under each pro–mesothoracic connective. Bursts of spikes occur in a DCMD in response to an appropriate stimulus, and the spikes are of sufficient amplitude to be distinguished from spikes in other axons. Usually a DCMD was stimulated by waving a pencil in front of one eye of the locust. Sometimes auditory stimuli were employed. These were clicks or hisses uttered by the experimenter.

The recordings were stored on magnetic tape and later either filmed from an oscilloscope or analysed using a Unimac 400 signal averager (Data Laboratories Ltd, London). Unless otherwise stated, each averaged signal is derived from 32 sweeps triggered from DCMD spikes.

RESULTS

Most intracellular recordings from flight motoneurones were made from their axons at the edge of the neuropile. Here an experimenter can be reasonably sure of recording from an equivalent position in different motoneurones, and from the same position in a particular motoneurone in different locusts. In recordings from cell bodies, EPSPs mediated by a DCMD were found only in the mesothoracic second tergosternal motoneurone (no. 84). EPSPs in this motoneurone were of comparatively large amplitude in all recordings made from the neuropile. In neuropile recordings from two other flight motoneurones, the first basalars in the mesothorax (no. 97) and

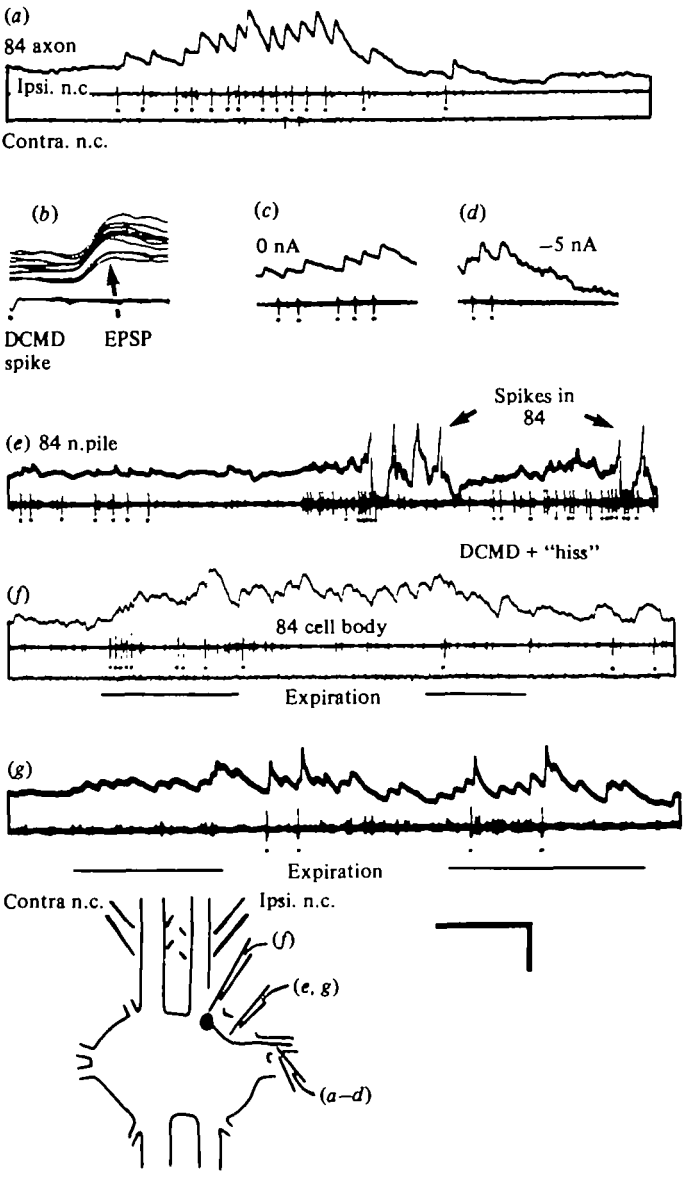

Fig. 1. EPSPs mediated by a right DCMD axon in the motoneurone of the right mesothoracic second tergosternal muscle (no. 84) of a locust. (*a*, *b*) Each spike in the DCMD (dotted here and in all other records) is followed 1·4 ms later by an EPSP in the axon of the motoneurone at the edge of the neuropile. The EPSPs are 4–5 mV in amplitude in this recording, and summate. (*b*) Ten multiple sweeps, triggered from DCMD spikes. (*c*, *d*) In another locust, hyperpolarising the right motoneurone 84 increases the amplitude of the EPSPs from 1·5 to 2 mV. (*e*) EPSPs mediated by a DCMD summate with EPSPs mediated by auditory neurones in the nerve cord, and cause this motoneurone 84 to spike. (*f*) in the cell body, EPSPs caused by spikes in the DCMD are 1 mV in amplitude and individual EPSPs of the rhythm which occurs in time with ventilation may reach 5 mV in amplitude. (*g*) In the neuropile of a different locust, EPSPs caused by the DCMD in the second tergosternal motoneurone are 6–8 mV in amplitude. Individual EPSPs of the rhythm which occurs in time with ventilation are 2–4 mV in amplitude. The drawing of the mesothoracic ganglion indicate where the recordings in each part of the figure were made. The structure of the motoneurone in the neuropile is complex, and the exact location of the electrode in recordings (*e*) and (*g*) is unknown. Calibrations: (*a*) 50 ms, 20 mV; (*b*) 2 ms, 20 mV; (*c*, *d*) 33 ms, 5 mV; (*e*) 200 ms, 10 mV; (*f*, *g*) 100 ms, 10 mV.

metathorax (no. 127), EPSPs mediated by a DCMD were also of sufficient amplitude to be seen clearly on the oscilloscope screen during an experiment. To detect EPSPs mediated by a DCMD in other flight motoneurones, signal averaging was employed.

Inputs from a DCMD to wing elevator motoneurones

The mesothoracic second tergosternal motoneurone

In the mesothorax, the tergosternal muscle consists of two distinct blocks of fibres, each of which is innervated by a separate fast motoneurone. The first tergosternal muscle (no. 83) is the anterior block, and the second tergosternal muscle (no. 84) is the posterior. The tergosternal muscles elevate and do not appear to twist their forewing.

In the metathorax there is one tergosternal muscle (no. 113) with a single fast motoneurone.

A spike in the right DCMD axon was consistently followed by an EPSP in the right motoneurone 84 (Fig. 1). Recorded from the axon of the motoneurone, at the edge of the neuropile, this EPSP rose sharply to a peak of 4–10 mV (Figs 1*a*, *b*). There was a latency of 1·4 ms between the arrival of a DCMD spike at the hook electrodes anterior to the mesothoracic ganglion and the start of the EPSP in the motoneurone (Fig. 1*b*). A DCMD axon in the thorax has been shown to conduct spikes at 3·1 m/s (Burrows and Rowell, 1973), so less than 1 ms would be required for the spike to travel from the electrodes to the ganglion. When the motoneurone was hyperpolarized by passing current through the electrode, the amplitude of the EPSP could be increased (Figs 1*c*, *d*). These observations are consistent with the hypothesis that there is a chemical synapse between a DCMD and a motoneurone 84, although they do not prove it.

The EPSPs caused by a burst of spikes in a DCMD summated, but not sufficiently to cause the motoneurone to spike (Figs 1*a*, *e*). EPSPs mediated by other interneurones summed with those from a DCMD and could give rise to motoneurone spikes. For instance, producing a 'hiss' activates auditory interneurones in the nerve cord. When activated alone, these interneurones did not cause a tergosternal motoneurone to spike, but when the experimenter hissed and optically stimulated a DCMD at the same time, the motoneurone could spike (Fig. 1*e*).

Recordings from a motoneurone 84 clearly showed the bursts of EPSPs which occur synchronously with the expiratory phase of ventilation (Burrows, 1975*b*). In the cell body these EPSPs were of greater amplitude than those mediated by a DCMD (Fig. 1*f*), but in all the recordings from the neuropile the DCMD-mediated EPSPs were of greater amplitude than the rhythmical EPSPs (Fig. 1*g*). These observations indicate that the two types of interneurone have separate sites of input onto the motoneurone; the synapses from the rhythmically spiking interneurones must be nearer to the cell body than those from the DCMD.

Other wing elevator motoneurones

Intracellular recordings were made from motoneurones of all but two of the wing elevator muscles (Table 1). In these recordings a small EPSP followed each spike in the DCMD axon ipsilateral to the motoneurone (Fig. 2). In the recording from a right mesothoracic first tergosternal motoneurone (no. 83), an EPSP of amplitude

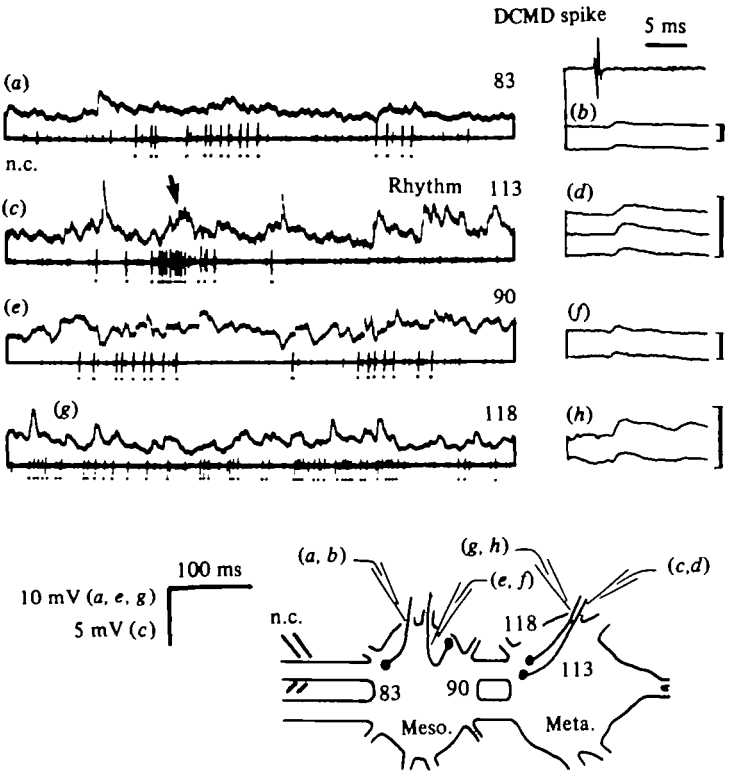

Fig. 2. EPSPs mediated by the right DCMD axon in four different right elevator motoneurones, revealed by signal averaging. Each of the four motoneurones was recorded in a different locust. On the left are shown continuous films of the recordings, and on the right, averaged signals made from the same recordings. (*a*) EPSPs associated with DCMD spikes are 0·25–0·5 mV in amplitude in the axon of this mesothoracic first tergosternal motoneurone. (*b*) Two EPSPs, revealed by averaging, in the mesothoracic second tergosternal motoneurone. The EPSPs have a latency of 1·4 ms. Since there is summation between EPSPs which occur successively in the motoneurone, the averaged EPSPs take more than 10 ms to decay. To the right of each set of averaged recordings is a 1 mV calibration bar. (*c*) Individual EPSPs from the DCMD cannot be distinguished in this recording from the right metathoracic tergosternal motoneurone of a locust. Arrowed is a potential of 3 mV amplitude which occurs in the motoneurone when there is a burst of spikes in the right DCMD axon. Summation of EPSPs caused by this burst probably contribute to this potential. (*d*) Averaged EPSPs from the metathoracic tergosternal motoneurone. (*e, f*) From a recording from a mesothoracic first posterior coxoalar motoneurone. (*g, h*) From a recording from a metathoracic anterior coxoalar motoneurone.

Table 1. *Motoneurones of wing elevator muscles which receive EPSPs from the ipsilateral DCMD axon*

Name	No.	EPSP found	Total No. of recordings made
Tergosternal	Meso: 83	✓	6
	84	✓	12
	Meta: 113	✓	5
Anterior tergocoxal	Meso: 89	—	2
	Meta: 118	✓	2
First posterior tergocoxal	Meso: 90	✓	6
	Meta: 119	✓	3
Second posterior tergocoxal	Meso: 91	—	—
	Meta: 120	—	—
Tergotrochanteral	Meso: 103	—	1
	Meta: 133	✓	1

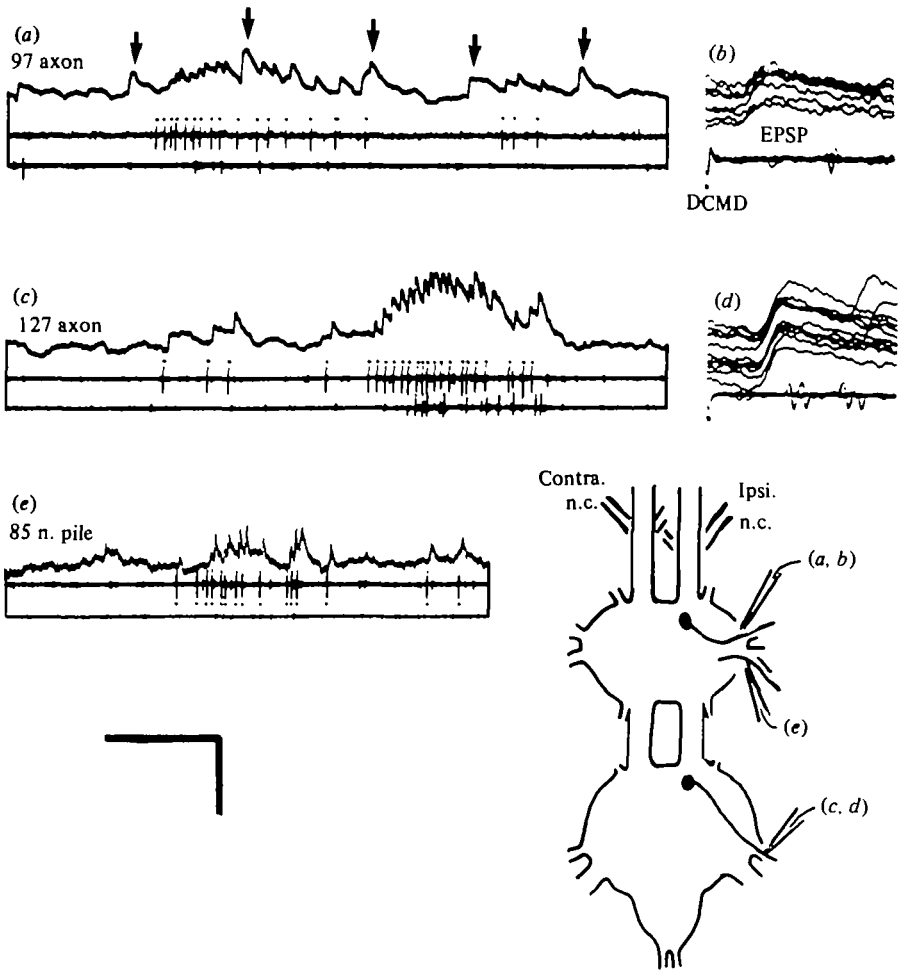

Fig. 3. EPSPs mediated by a right DCMD axon in motoneurones of right first basalar muscles of the meso- and metathorax, and in a pleuroaxillary motoneurone. (*a*) Each spike in the DCMD is followed by an EPSP in this right mesothoracic first basalar motoneurone. EPSPs mediated by the right forewing stretch receptor (arrowed, see Burrows, 1975*a*) are much larger in amplitude and have a longer duration than the EPSPs mediated by the DCMD. Recordings from nerve 1 of the mesothoracic ganglion (not shown) demonstrate that the larger EPSPs arise from the stretch receptor. (*b*) Eight multiple sweeps, triggered from DCMD spikes, show that the latencies of the EPSPs they cause in the motoneurone of (*a*) are 1·4 ms. (*c*) Spikes in the right DCMD of the same locust as (*a*) cause summating EPSPs in the motoneurone of the metathoracic first basalar muscle. (*d*) Single sweeps from the same recording as (*c*). (*e*) EPSPs mediated by the right DCMD in a fast motoneurone of the right mesothoracic pleuroaxillary muscle. Calibrations: (*a*) 100 ms, 5 mV; (*b*) 5 ms, 2 mV; (*c*) 100 ms, 2 mV; (*d*) 5 ms, 1 mV; (*e*) 100 ms, 2 mV.

0·25 to 0·5 mV was associated with each spike in the right DCMD axon (Fig. 2*a*). The presence of this EPSP was confirmed with the signal averager (Fig. 2*b*). The EPSP had a latency of 1·4 ms from the DCMD spike, as had the EPSP in motoneurone 84.

In recordings from other flight motoneurones it was impossible to distinguish

Table 2. *Motoneurones of wing depressor muscles which receive EPSPs from the ipsilateral DCMD axon*

Name	No.	EPSP found	Total No. of recordings made
Dorsal longitudinal	Meso: 81	—	6
	Meta: 112	—	5
First basalar	Meso: 97	✓	7
	Meta: 127	✓	3
Second basalar	Meso: 98	✓	7
	Meta: 128	✓	2
Subalar	Meso: 99	✓	8
	Meta: 129	✓	3
Pleuroaxillary	Meso: 85	✓	3
	Meta: 114		1

by visual inspection the EPSP that followed each ipsilateral DCMD axon spike (Figs 2*c*, *e*, *g*). However, in all recordings from wing elevator motoneurones where, on the basis of the amplitudes and shapes of spikes and EPSPs, the electrode was judged to have sealed well into the motoneurone membrane, signal averaging revealed an EPSP following a spike in the ipsilateral DCMD axon (Figs 2*d*, *f*, *h*).

Input from a DCMD to wing depressor motoneurones

The first basalar motoneurones

The first basalar muscles (no. 97 in the mesothorax and no. 127 in the metathorax) depress and pronate the wings (Wilson and Weis-Fogh, 1962). Each of these muscles is innervated by a single motoneurone. A spike in the right DCMD axon was always followed by an EPSP in the right motoneurones 97 and 127 (Figs. 3*a–d*). The latency between the spike, recorded in the pro-mesothoracic connective, and the start of the EPSP in motoneurone 97 was 1·4 ms (Fig. 3*b*), which is the same as that found for mesothoracic elevator motoneurones. The EPSPs summated, and their amplitude could be altered by passing current into the motoneurone. EPSPs mediated by a DCMD were not found in recordings from first basalar motoneurone cell bodies.

Other depressor motoneurones

EPSPs mediated by a DCMD were found in motoneurones of the second basalar, subalar and pleuroaxillary muscles, but not in those of the dorsal longitudinal muscles (Table 2). In Fig. 3*e*, each spike in the right DCMD axon is followed by an EPSP in one of the three motoneurones of the right mesothoracic pleuroaxillary muscle, no. 85. This muscle controls the degree of pronation of its wing (Pfau, 1977). In motoneurones of other depressor muscles, signal averaging was used to reveal the EPSPs which follow DCMD spikes (Fig. 4). The EPSPs were not found in averaged recordings from the cell body of any wing depressor motoneurones. In one experiment recordings were made simultaneously from the cell body and from the neuropile of one second basalar motoneurone (Fig. 4*a–d*). EPSPs from the ipsilateral DCMD axon were 0·35 mV in amplitude in the recording from the neuropile, but were not

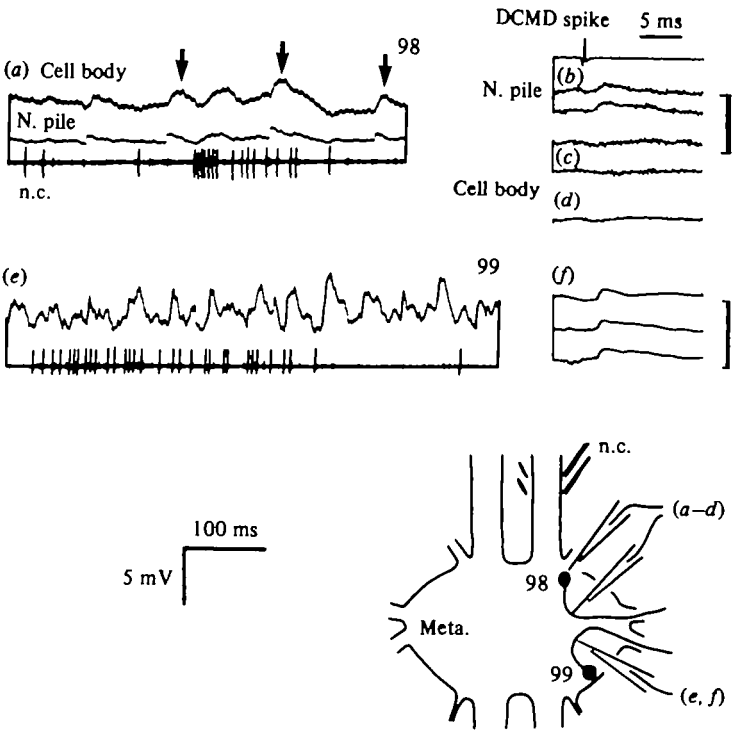

Fig. 4. EPSPs mediated by a right DCMD in motoneurones of the mesothoracic second basalar and subalar muscles, depressors of the wing. (*a*) Simultaneous recordings from the cell body and from a neuropilar process of a second basalar motoneurone. EPSPs mediated by the right forewing stretch receptor (arrowed) are clear in both. EPSPs mediated by the right DCMD can be distinguished in the recording from the neuropile, but not in the recording from the cell body. (*b*) Two averaged records from the neuropile of the second basalar motoneurone. The EPSP can be seen clearly. (*c*) Two averaged records of the recording from the cell body of the second basalar motoneurone. No sign of an EPSP is apparent. (*d*) As (*c*), but one record of 128 averaged sweeps. (*e*) Recording from a neuropilar process of one of the two motoneurones of the right mesothoracic subalar muscle. EPSPs mediated by the DCMD cannot be distinguished from other EPSPs. (*f*) Three averaged EPSPs from the same recording as (*e*). The recordings from the two motoneurones were made in different locusts.

found at all in recordings from the cell body. EPSPs in a subalar motoneurone, mediated by a DCMD, were 0·2 mV in amplitude in the axon at the edge of the neuropile (Fig. 4*f*). The recording from this motoneurone in Fig. 4*e* shows that there are PSPs from other, unidentified sources which have amplitudes 20 times as great as this.

Only unilateral connexions from a DCMD to flight motoneurones were found

Although in every successful recording from a flight motoneurone, connexions from both ipsilateral and contralateral DCMD axons were sought, no sign of a PSP mediated by the contralateral DCMD axon was found (Fig. 5). In contrast, the fast extensor tibiae motoneurone of each hind leg usually receives an EPSP from both the left and the right DCMD axons (Burrows and Rowell, 1971), but apparently not in all strains of locusts (Pearson & Goodman, 1979). These leg motoneurones also receive EPSPs from the right and left descending ipsilateral movement detectors (DIMDs). I found no evidence for input from a DIMD to any flight motoneurone (Figs 5*c*, *d*).

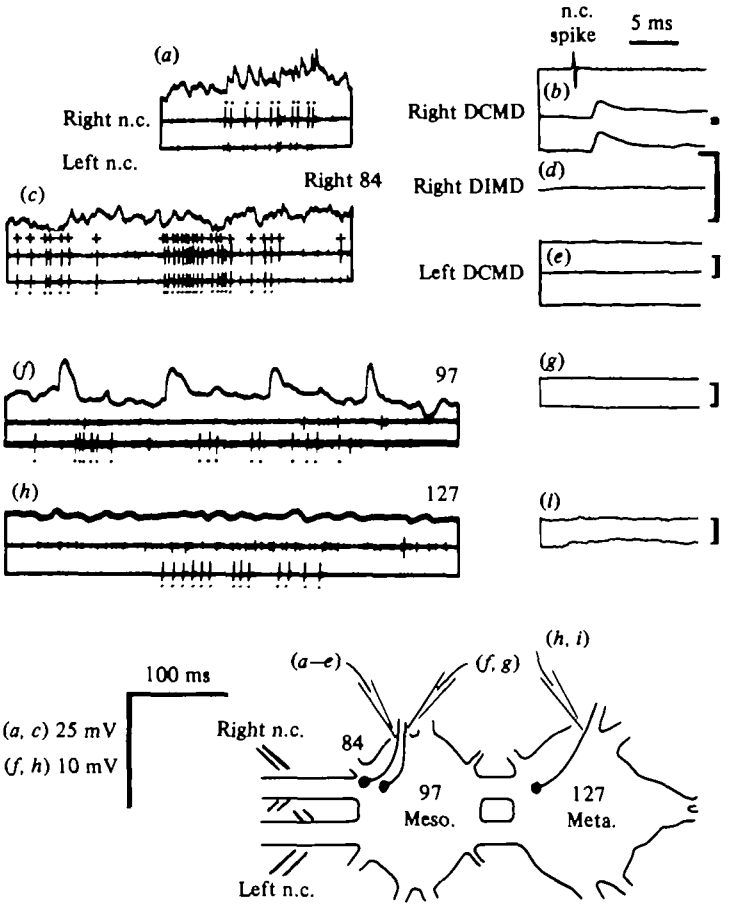

Fig. 5. No EPSPs can be found mediated by a left DCMD axon in motoneurones of flight muscles on the right. (*a*, *b*) EPSPs in a right mesothoracic second tergosternal motoneurone, mediated by a right DCMD axon. (*c*) In the same tergosternal motoneurone, no EPSPs associated with spikes in either the right DIMD (crosses) or left DCMD (dots) are apparent. (*d*) Averaged recording, triggered from the right DIMD of (*c*). (*e*) Three averaged recordings from a right mesothoracic second tergosternal motoneurone, triggered from spike in the left DCMD; (*e*) is from a different locust from (*a–d*); there is no sign of an EPSP. (*f*, *g*) A recording from a right mesothoracic first basalar motoneurone, the same neurone displayed in Fig. 3*a*. No EPSPs follow spikes in the left DCMD axon. (*h*, *i*) Recording and averaged recordings from the right metathoracic first basalar motoneurone in another locust do not show any EPSPs following spikes in the left DCMD axon.

DISCUSSION

The stimuli which excite a DCMD, the rapid conduction velocity of its axon, and the direct excitatory connexions which it makes with leg and flight motoneurones are all features consistent with a role in triggering a rapid movement when a locust is startled. The possible involvement of a DCMD in initiating a jump when a locust is surprised has been discussed by Burrows and Rowell (1973), and it is reasonable for the same neurone to be employed in triggering emergency movements made with the wings. Here the possibilities that a DCMD participates in the unfolding of the wings prior to flight, and in causing a change in flight course are discussed.

Often, when a locust is startled it jumps, opens its wings, and flies, as anyone who has tried to catch one knows. If a burst of spikes in a DCMD were to trigger a jump, it would inevitably depolarize some flight motoneurones at the same time, and this could be a mechanism for co-ordinating the unfolding of the wings with the jump. Whether the EPSPs caused by a DCMD in flight motoneurones are important in triggering wing unfolding is impossible to state, for two reasons. First, the muscles involved in this action are unknown. Second, a DCMD connects only with motoneurones of flight muscles ipsilateral to its axon, whereas the wings on both sides of the body are unfolded at the same time, which implies that there are local interneurones which co-ordinate the movements on either side.

In a flying locust, a burst of spikes in a DCMD will result in increased spiking by some of the flight motoneurones ipsilateral to its axon. This will lead to a transient increase in the power applied to the wings on one side of the body, and to an alteration in flight course. Consistent with this is the apparent lack of connection between a DCMD and motoneurones of muscles 81 and 112, the dorsal longitudinals. In each segment the left and right dorsal longitudinal muscles attach to the same cuticular struts, so contraction of one of these muscles causes depression of both the left and the right wing. Each of the other flight muscles moves only the wing to the base of which it attaches.

There are four major problems in relating the EPSPs caused by a DCMD in flight motoneurones to any particular change in flight direction. (1) The effectiveness of a DCMD-mediated EPSP in triggering a spike in any flight motoneurone will vary as the membrane potential of the motoneurone changes throughout a wingbeat. (2) The DCMD-mediated EPSPs were measured at only one location in the motoneurone. It is necessary to know how the EPSP is integrated with other changes in membrane potential at the spike initiation site (the location of which is unknown). In the axon at the edge of the neuropile, the DCMD-mediated EPSP is of greater amplitude in motoneurone 84 than in any other wing elevator, and in motoneurones 97 and 127 than in any other wing depressors. Further recordings are necessary to show whether a DCMD exerts more influence over the production of spikes in these motoneurones than in other flight motoneurones. (3) Even if a DCMD is more likely to trigger spikes in motoneurones 97 and 127 than in other wing depressors, the consequences are not clear. Each of the muscles, 97 and 127, pronates its wing during the downstroke, altering the angle of attack of the wing, and the lift it generates. Unfortunately there is confusion in the literature about whether a locust yaws towards or away from the side where the wings are more strongly pronated. Dugard (1967), working with locusts tethered in a manner that allowed them to rotate in the yaw plane, correlated increased pronation on one side with yawing towards that side. Zarnack and Möhl (1977), working with locusts which could not rotate, argue for the opposite case. (4) It is unknown if the DCMDs of a flying locust respond to the same stimuli as those of a stationary locust and it is difficult to predict how they might operate. One possible function is to prevent collision with other airborne objects, such as other locusts flying in a swarm. Locusts flying in swarms maintain a distance of 1–2 m between each other (Waloff, 1972). However, locusts flying at the edge of a swarm tend to turn towards their companions, and movement of a small object in the visual field of one eye of a tethered, flying locust can induce a yaw by the locust towards that object (Cooter, 1979).

A balanced picture of the operation of a DCMD must consider other brain interneurones, which may either spike or be inhibited at the same time as the DCMD spikes, and it must also consider the inputs from a DCMD to local interneurones which connect with motoneurones. There are very few marks on our canvas so far. Besides the DCMD, two other brain neurones, with large axons in the ventral nerve cord, are known to connect with flight motoneurones (Bacon and Tryer, 1979; Simmons, 1980). Almost nothing is known about the local interneurones which co-ordinate motoneurones during flight.

I thank Malcolm Burrows for his help in carrying out this work.

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