J. exp. Biol. **102**, 273–284, 1983
Printed in Great Britain © *Company of Biologists Limited 1983*

THE ROLE OF AN IDENTIFIED BRAIN NEURONE IN MEDIATING OPTOMOTOR MOVEMENTS IN A MOTH

BY F. CLAIRE RIND*

Zoology Department, Downing Street, Cambridge, England

(*Received 4 June 1982—Accepted 3 September 1982*)

SUMMARY

1. Completely unrestrained moths show an optomotor turning response to horizontal movement during pre-flight warm up or flight.

2. As the moth warms up there is a sequential recruitment of first neck, then abdominal, leg and finally some wing muscles, into the optomotor turning response.

3. Extracellular motoneurone spikes were recorded from neck muscles during optomotor stimulation. As the stimulus is oscillated from side to side, motoneurones on the ipsilateral side are excited. The latency of this response increases greatly in dim light.

4. Flight motoneurones were not observed to spike in response to movements of the optomotor stimulus, but subthreshold oscillations of 5–10 mV, in phase with the response of the identified optomotor interneurone D1, were observed. Three motoneurones, the second pleuroaxillary, the subalar and the dorsal longitudinal to the more medial, ventral fibre bundle, showed depolarizations in phase with the response of the ipsilateral D1 interneurone. Synaptic potentials in these motoneurones followed action potentials in D1, suggesting that D1 provides a direct, excitatory input to them.

5. An excitatory postsynaptic potential (EPSP) from D1 sums with a steady depolarization of all three directly postsynaptic motoneurones to produce an action potential.

INTRODUCTION

Within the visual systems of both vertebrate and invertebrate animals, neurones have been identified which are selectively responsive to one direction of movement: the directionally selective movement detectors (DSMDs).

In arthropods the morphologies of some of these neurones have been determined as well as their responses (McCann & Foster, 1971; Pierantoni, 1973, 1976; Dvorak, Bishop & Eckert, 1975*a*,*b*; Hausen, 1976; Eckert, 1978, 1980; Eckert & Bishop, 1978; Rind, 1983*b*). The activity of the DSMDs is thought to underlie the optomotor response whereby an animal keeps the image of the real world in a fixed position on its retina. Evidence for this supposition has, so far, been indirect: (i) the response of the DSMDs matches the optomotor response in the crab (Sandeman, Erber & Kien, 1975*a*,*b*), the fly (Reichardt, 1965; McCann & Foster, 1971; Eckert, 1980) and the

* Present address: Zoology Department, The University, Newcastle upon Tyne, NE1 7RU, England.
Key words: Moth, optomotor, interneurone.

locust (Kien, 1974*a*,*b*); (ii) extracellular electrical stimulation of these DSMD neurones in the optic lobe induces an optomotor response (Blondeau, 1981); and (iii) in mutant or laser treated animals lacking particular DSMD neurones, the optomotor responses are impaired (Heisenberg, Wonneberger & Wolf, 1978; Geiger & Nässel, 1981).

DSMD neurones have been found in the moth (Collett & Blest, 1966; Rind, 1983*b*). One neurone in particular, the descending interneurone, D1 (Rind, 1983*b*) has been shown to respond to optomotor stimuli and has extensive arborizations in areas of the thoracic neuropile where many flight motoneurones also have their dendrites (Rind, 1983*a*). In this paper the optomotor behaviour of the moth *Manduca sexta* is described, first in terms of behaviour and then in terms of the activity of individual participating motoneurones. The role of any direct connections, made by D1 with these motoneurones, in producing this behaviour is assessed by simultaneous recordings from D1 and identified flight motoneurones during optomotor turning behaviour. It is shown that a DSMD neurone has the appropriate output connections to mediate an optomotor response.

MATERIALS AND METHODS

Adult *Manduca sexta* (Johannson), were reared on artificial diet (B. Ballard, in preparation). Observations were made of optomotor movements performed by a completely unrestrained moth in response to a vertically striped card: 100 by 135 mm in size, striped with 12·5 mm black tape at 12·5 mm intervals. The card was moved in the frontal part of the visual field of the moth when the moth was either preparing for flight, hovering, or flying forwards immediately after leaving the ground.

Spikes and synaptic activity were recorded in the motoneurones to the muscles of the neck, thorax and abdomen of a restrained and dissected moth in response to optomotor stimuli. The activity of the motoneurones was measured extracellularly using pairs of 30 μm diameter steel wires, insulated except for their tips. The wires were implanted into muscles visible after the dissection (Rind, 1983*a*). The moth was prepared for intracellular recording, and flight motoneurones identified as described in the first paper of this series (Rind, 1983*a*). Stimulus presentation was as described in the second paper (Rind, 1983*b*). Briefly, a 5 by 9 cm card of vertical stripes, subtending 16° at the eye, was moved through 36° at velocities between 5–154°/s. The stimulus was moved back and forth in front of the moth and illuminated by a Barr and Stroud waveguide and light source. Light intensity was 5000 lux, unless stated otherwise.

RESULTS

The completely unrestrained moth would only turn to follow movement of the stimulus if vibrating its wings during pre-flight warm up or if it was airborne. The resting moth did not show any overt optomotor reactions when presented with the optomotor stimulus. As the moth warmed up prior to flight a number of optomotor responses appeared sequentially. At first the moth followed the movement of the stimulus by turning its head. As it tucked its meta-, meso-, and then prothoracic legs under its body and became increasingly airborne, the wings, assisted by movement

of those legs still in contact with the substrate, manoeuvred the whole body to follow the optomotor stimulus. When the optomotor stimulus was moved in front of a hovering moth the moth was seen to track the motion of the stimulus precisely.

A restrained and dissected moth could be induced to produce turning responses to an optomotor stimulus by cutting the leg nerves and so depriving the moth of the sensory information from its legs. In a preparation showing turning responses, the first muscles to become recruited into the response were the neck muscles. Then, sequentially, came the abdominal muscles of the first two abdominal segments; three wing depressor muscles, namely the dorsal longitudinal, the second pleuroaxillary and the subalar; and finally the other wing muscles. The metathoracic muscles and the leg muscles were not visible. This sequence of activity meant that it was easiest to record optomotor responses, in terms of extracellularly monitored motoneurone spikes, from the neck muscles. As will be seen later, using intracellular recordings from flight motoneurones, this does not mean that there was no activity in other motoneurones in response to the optomotor stimulus but rather that, in a quiescent moth, the activity does not manifest itself as spikes which could be recorded extracellularly.

The extracellular recordings from the neck muscles (Fig. 1A) show that the motoneurones to the right muscle are excited when the stimulus moves to the right

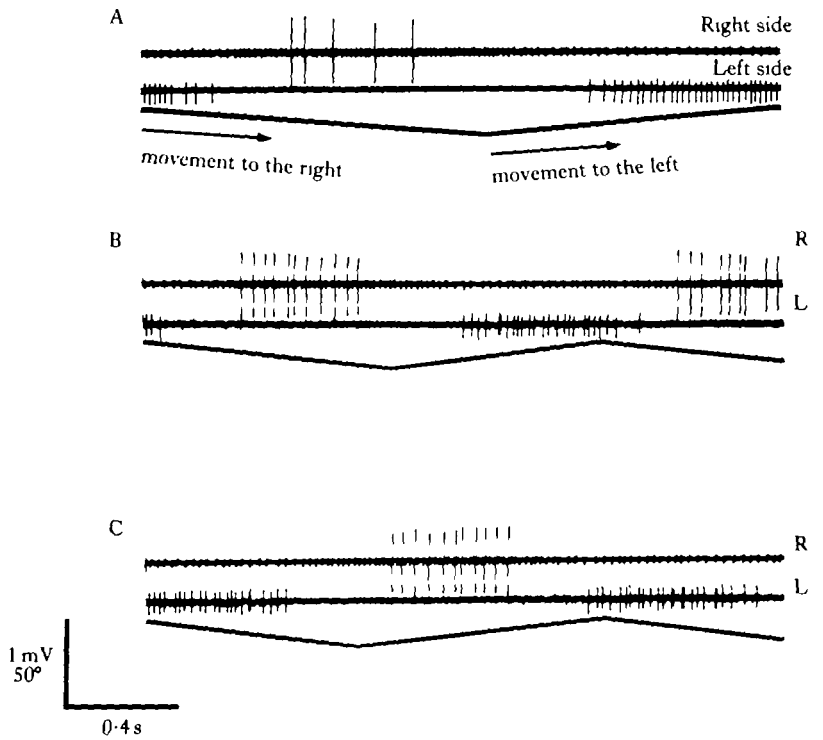

Fig. 1. A, Extracellularly recorded activity in a right and left neck muscle in response to alternating right and left movement of the optomotor stimulus. B, The velocity of stimulus movement is increased. C, The light intensity is decreased. The stimulus had a stripe period subtending 32° at the moth's eye.

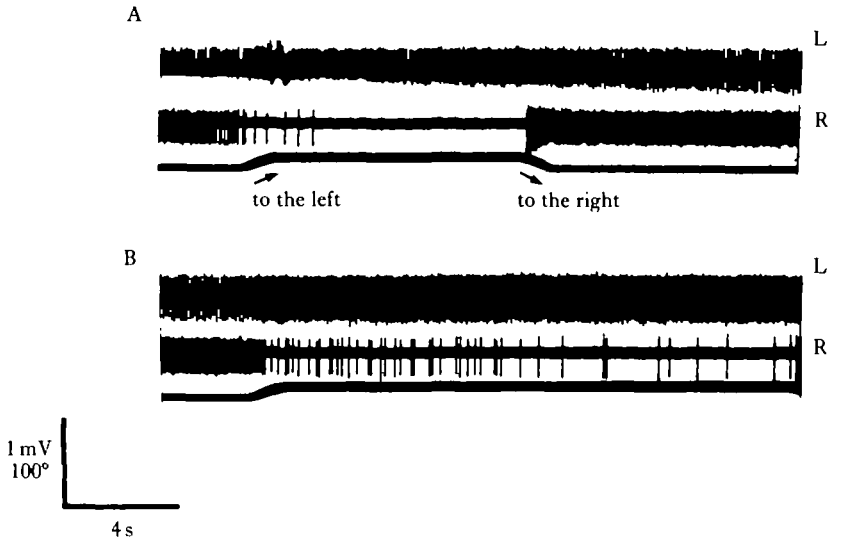

Fig. 2. A and B. As in Fig. 1 except movements are single left or right ramps of stimulus movement. The stimulus is then held in the new position for up to 16 s.

and inhibited when it moves to the left. Those to the left muscle are excited when the stimulus moves towards the left. Recordings from the descending interneurones D1 showed a similar pattern: the right D1 was excited by movement towards the right and the left D1 by movement to the left (e.g. Fig. 3).

Motoneurone activity followed movement of the stimulus at all speeds (5–154 °/s), and firing rate increased with the rate of movement (Fig. 1B). The large fast unit increased its firing rate more than the tonically active motoneurone to the same muscle. The latency, as measured from the onset of stimulus movement in the excitatory direction, to a spike or an increase in spike rate, was different in all three motoneurones. The large unit has the longest latency and the tonically active unit the shortest. In dim light the latency of response of all the motoneurones was considerably increased (Fig. 1C), mimicking the response of D1 to decreased illumination (Rind, 1983*b*). The response of the motoneurones in dim light was almost 180° out of phase with the stimulus movement. The exact relationship between the response of the motoneurones and the phase of stimulus movement depended on stimulus illumination and on the speed of stimulus movement.

The response of tonically active neck motoneurones to ramp and hold movements

Fig. 3. Membrane potential fluctuations recorded in various flight motoneurones concurrently with the response of D1 to both right and left movements of the optomotor stimulus. A, the right second pleuroaxillary motoneurone; B, the right subalar motoneurone and C, the left motoneurone to fibres of the most medial, ventral bundle of the left dorsal longitudinal muscle are all recorded concurrently with the right D1 interneurone. D, Simultaneous recording of the same motoneurone as C and the left D1 neurone. Note the phase difference between the motoneurone and the left and right D1. E, recording as in A from the right second pleuroaxillary motoneurone concurrently with the right D1 interneurone. The motoneurone has been depolarized by the injection of a steady 5 nA of current and spikes in phase with the response of D1. F, recording from the right second basalar motoneurone to show the absence of membrane potential fluctuations in phase with the response of the right D1. Calibrations: Vertical, upper trace A, B, C, D and F, 12 mV; E, 20 mV; middle trace 80 mV A–F; bottom trace 160° A–F. Horizontal, A, B, C, E and F, 1 s; D, 2 s.

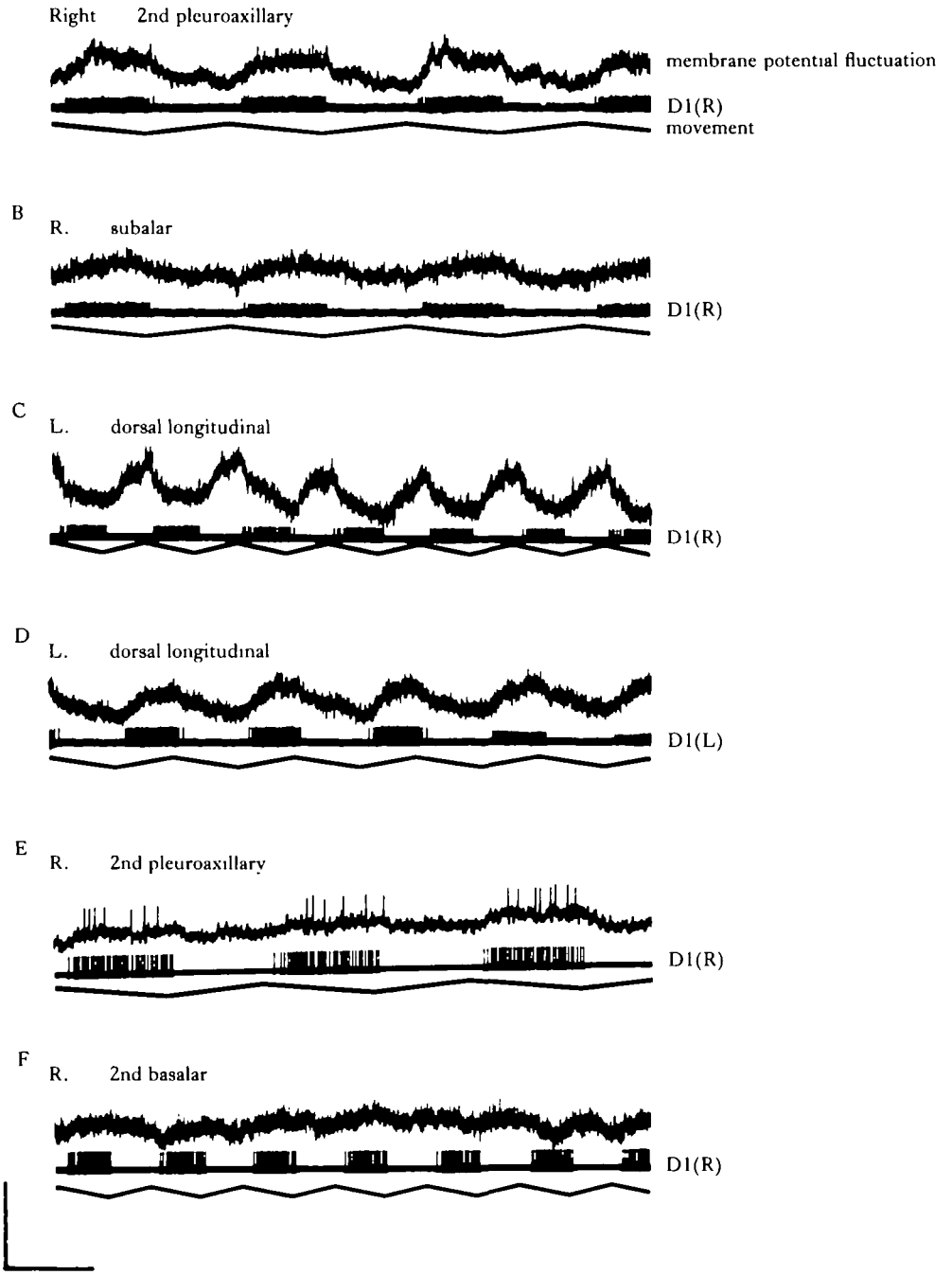
Right 2nd pleuroaxillary
membrane potential fluctuation
D1(R)
movement
B
R. subalar
D1(R)
C
L. dorsal longitudinal
D1(R)
D
L. dorsal longitudinal
D1(L)
E
R. 2nd pleuroaxillary
D1(R)
F
R. 2nd basalar
D1(R)

Fig. 3

of the stimulus was sustained for as long as the stimulus was held in the same position (Fig. 2A, B). This response does not reflect that of D1 to the same movements (Rind, 1983*b*).

Intracellular recordings from the motoneurones to several flight muscles showed that even when no action potentials were produced in response to motion of the striped card there were subthreshold oscillations in membrane potential. These were of the same period in the different neurones, and, for similar stimulus conditions, showed a constant phase relationship with movements of the optomotor stimulus and also the response of D1 (Fig. 3A–F). Membrane potential fluctuations which followed optomotor stimulus movement occurred in the second pleuroaxillary (Fig. 3A, E), in the subalar (Fig. 3B) and the dorsal longitudinal (Fig. 3C, D) motoneurones. When one of these three motoneurones was depolarized by the injection of a steady d.c. current, this nonspecific depolarization summed with the previously subthreshold oscillations to produce action potentials which had a fixed phase relationship to optomotor stimulus movements. Membrane potential fluctuations in phase with the stimulus were never observed in the basalar motoneurones (Fig. 3F).

In motoneurones which showed these membrane potential fluctuations, the membrane was depolarized when the stimulus moved to the ipsilateral side. At the same time, there was excitation of the D1 cell body on the ipsilateral side, i.e. in the D1 cell body at the same side as dendrites of the depolarized motoneurone. For example, Fig. 4 shows that both the onset and termination of the depolarization in a right, second pleuroaxillary motoneurone occur at the same time as the onset or termination of

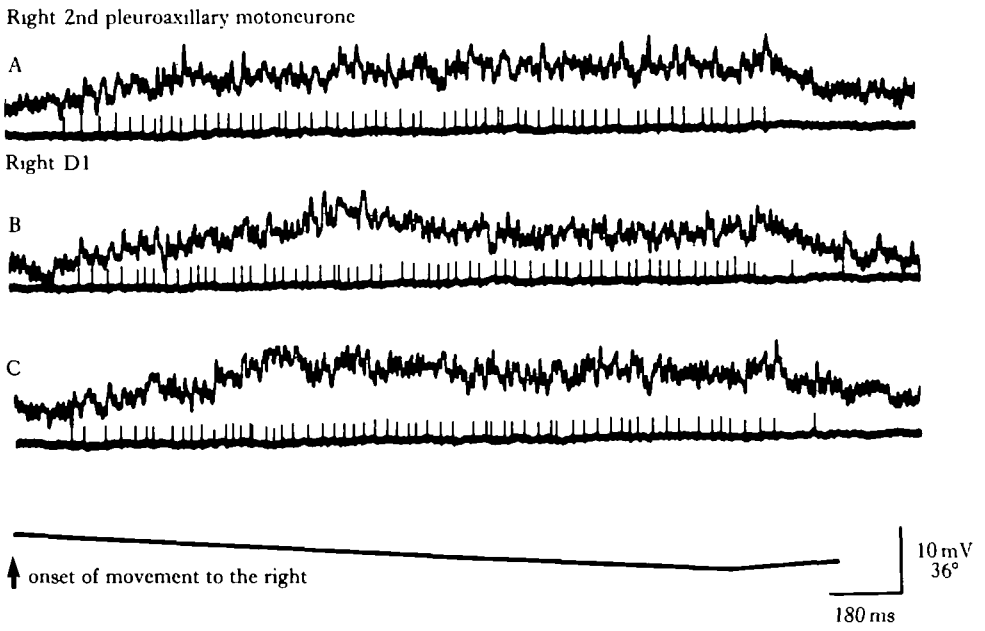

Fig. 4. A–C. Membrane potential fluctuations and their constituent PSPs on an expanded time scale. The membrane potential of the second pleuroaxillary motoneurone is recorded concurrently with the response of D1 to stimulus movement towards the right. Three successive movements are shown.

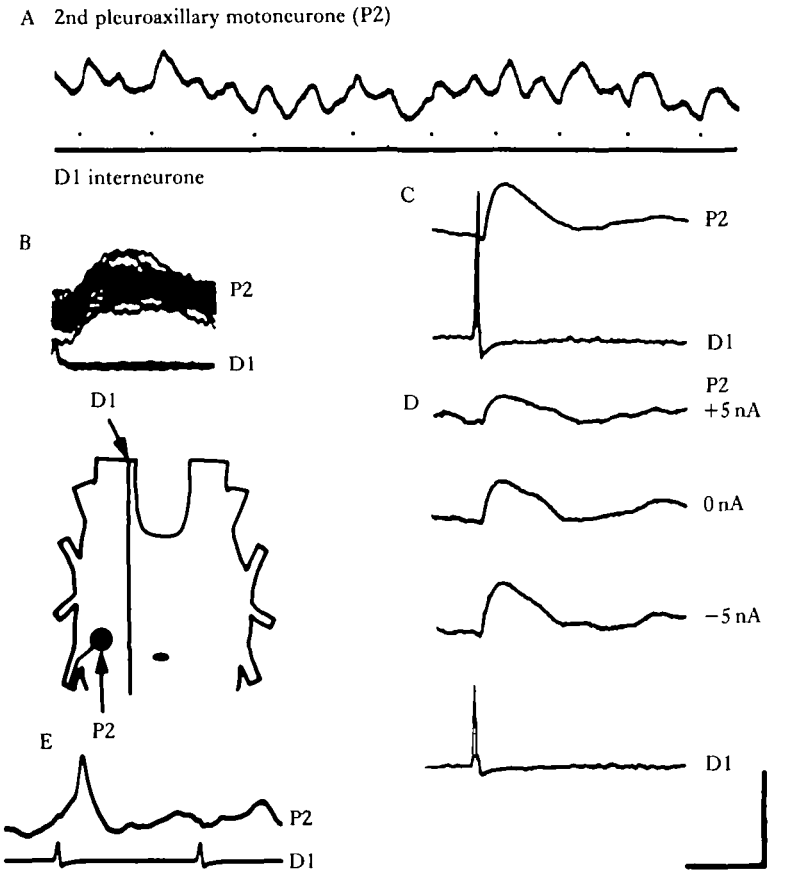

Fig. 5. An example using the 2nd pleuroaxillary motoneurone showing the synaptic potentials generated by D1 in motoneurones to flight muscles. A, Recording from the motoneurone to the right, 2nd pleuroaxillary muscle (upper trace) simultaneously with the right D1. Spikes in D1 are indicated by a dot above the lower trace. Synaptic potentials are seen to follow each spike in D1. B, Multiple single sweeps (upper trace) show that a PSP does follow each D1 spike (lower trace) with a constant latency. C, The shape and duration of the PSP (upper trace) is shown when 257 PSPs following a spike on D1 (lower trace) are averaged. D, The PSP is probably a chemically mediated EPSP. Its amplitude depends on the membrane potential of the motoneurone. Injection of depolarizing current (1st trace) decreases the normal size of the PSP (2nd trace). Hyperpolarizing current increases the size of the PSP (3rd trace). Each trace is the average of 64 sweeps triggered by a spike in D1 (4th trace). E, The PSP is excitatory as it can bring the membrane potential to the threshold necessary for spike production. Calibrations: Vertical, A, upper trace 6 mV, lower trace 10 mV; B, upper trace 3 mV, lower trace 15 mV; C, upper trace 3 mV, lower trace 2·5 mV; D, 1st, 2nd and 3rd traces 3 mV, 4th trace 5 mV; E, upper trace 5 mV, lower trace 15 mV. Horizontal, A, 30 ms; B, 7 ms; C and D, 16 ms; E, 75 ms.

spikes in D1. Depolarizing postsynaptic potentials of several millivolts appear to follow each spike in D1.

The detailed temporal relationship between a spike in D1 and a subsequent synaptic potential is illustrated in Fig. 5 for the second pleuroaxillary motoneurone. A spike in D1, shown as a dot in the lower trace of Fig. 5A, is correlated with a sharp depolarization in the motoneurone membrane potential (upper trace, Fig. 5A). Successive superimposed sweeps on a faster time base show that this membrane depolarization follows a spike, recorded from the axon of D1 at its entry into the

pterothoracic ganglion, with a short but constant 1·8 ms delay (Fig. 5B). The shape of the postsynaptic potential (PSP) is more clearly revealed by signal averaging when it can be seen that the synaptic potential lasts about 15 ms (Fig. 5C). The synaptic delay and also the fact that the size of the PSP can be altered by passing hyperpolarizing or depolarizing current into the motoneurone (Fig. 5D) indicate that there is a chemical synapse between D1 and the flight motoneurone. The effect of the PSP is excitatory, causing a spike in the second pleuroaxillary motoneurone (Fig. 5E).

Excitatory postsynaptic potentials (EPSPs) following a spike in D1 were found in two other motoneurones to flight muscles, the dorsal longitudinal and the subalar (Figs 6, 7).

The EPSPs in the second pleuroaxillary, the dorsal longitudinal and the subalar muscle motoneurones occurred, respectively, 1·8 ms, 1·6 ms and 2·1 ms after a spike in the axon of D1 as it enters the pterothoracic ganglion. Conduction velocity of an action potential in D1 was measured once, at 17 °C, between intracellular electrodes placed 0·5 mm apart in the pro-mesothoracic connective. The conduction velocity was estimated to be 0·7 m/s. This means that it would take an action potential in D1 about 0·9 ms to be conducted from an electrode in the pro-mesothoracic connectives to an electrode in any process of a motoneurone. Electrotonic conduction of a PSP from the synaptic site to the recording electrode in the motoneurone will probably not be at the same velocity as an action potential in D1 so at best this is only an approximation of the delay due to conduction velocity between the two electrodes. However, taking the conduction delay of 0·9 ms from the latencies gives a synaptic delay of 0·9 ms, 0·7 ms, and 1·2 ms in the second pleuroaxillary, dorsal longitudinal and subalar motoneurones respectively. This synaptic delay is commensurate with a monosynaptic connection between D1 and these motoneurones.

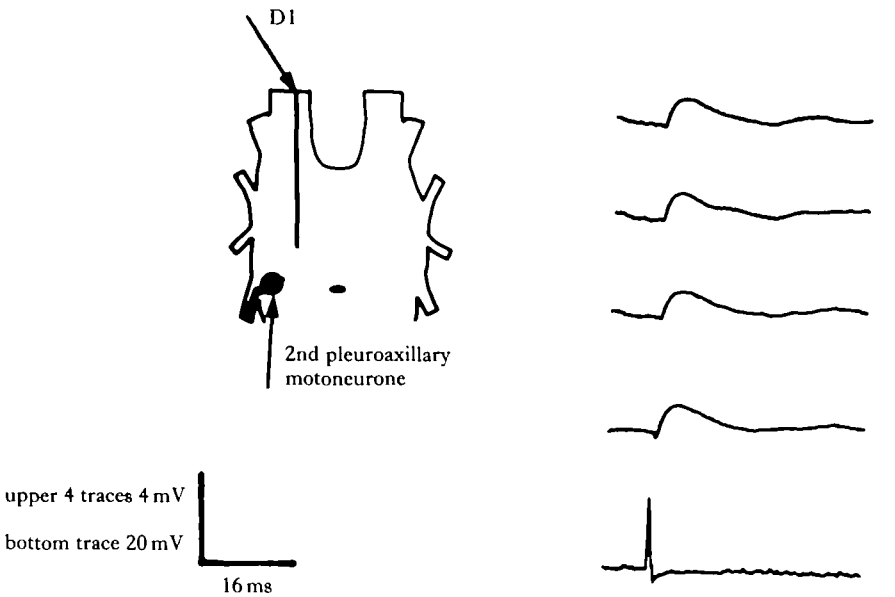

Fig. 6. Synaptic potentials in motoneurones of ipsilateral 2nd pleuroaxillary muscles following action potentials in D1. EPSPs have been revealed by signal averaging. Each trace represents 64 occurrences of a spike in the visual interneurone and shows the consistency of the EPSP in the motoneurone.

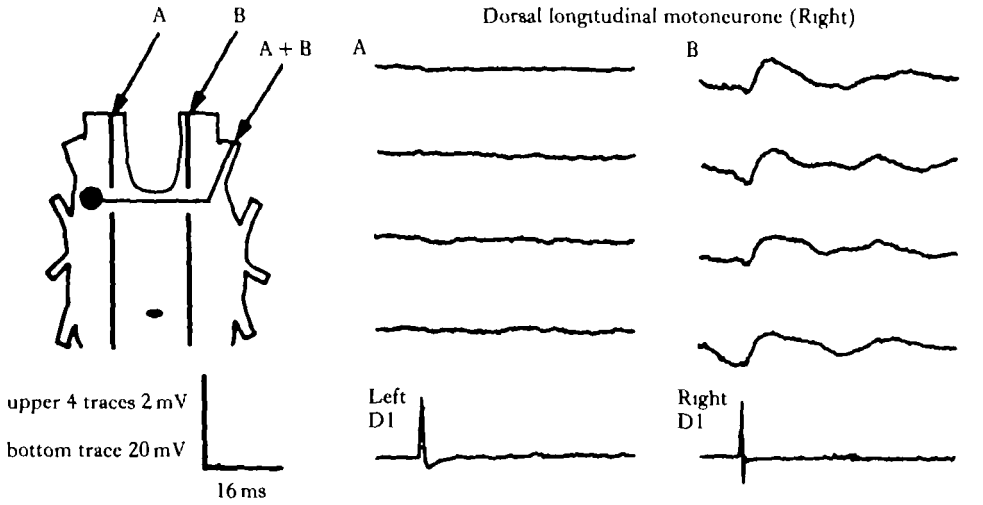

Fig. 7. Recordings from D1 in the left (A) and right (B) connective and a motoneurone to the right dorsal longitudinal muscle (D.L.1a). EPSPs follow a spike in the D1 ipsilateral to the dorsal longitudinal muscle (B) but not in the D1 contralateral to it (A). EPSPs in the motoneurones have been revealed using signal averaging, each of the upper three traces represent the average membrane potential of 64 sweeps, triggered by a spike in D1 (bottom trace).

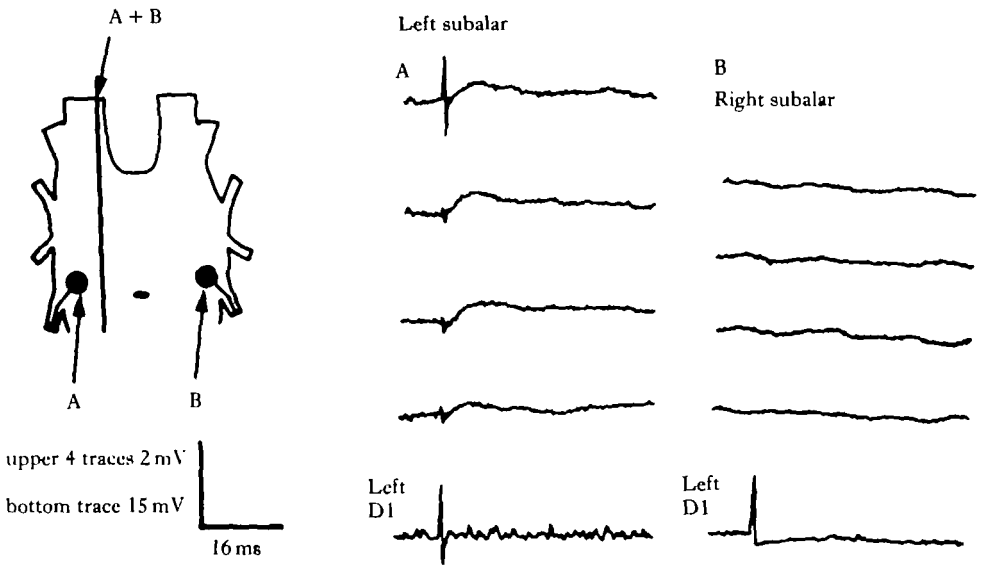

Fig. 8. Synaptic connections (revealed as in Fig. 6) made by D1 with motoneurones of (A) ipsilateral and (B) contralateral subalar muscles.

Table 1 summarizes the pattern of connections made by D1 with the motoneurones to the mesothoracic wing muscles. The criteria for establishing the existence of these connections was that in four signal averaged traces, each from 64 successive sweeps triggered from a spike in D1, there was a constant latency PSP in the simultaneously impaled motoneurone. All the connections made by D1 with flight motoneurones are excitatory, and they are all with motoneurones to muscles on the same side of the

Table 1. *D1 makes excitatory connections with motoneurones to flight muscles ipsilateral but not contralateral to its axon. No inhibitory effects of a spike in D1 was seen in any flight motoneurones*

		Motoneurones ipsilateral to D1		Motoneurones contralateral to D1	
	Muscle	No. of observations	No. of preparations	No. of observations	No. of preparations
Indirect depressor	Dorsal longitudinal 1a	2 (EPSP)	2	2 (no connection)	2
Direct depressors	Basalar 1	1 (no connection)	1	—	
	Basalar 2	3 (no connection)	2	—	
	Basalar 3	4 (no connection)	2	—	
	Basalar 4	4 (no connection)	3	—	
	Pleuroaxillary 1	5 (no connection)	4	—	
	Pleuroaxillary 2	3 (EPSP)	3	—	
	Subalar	5 (EPSP)	5	1 (no connection)	1
Elevators	Dorso–ventral 1–6	8 (no connection)	8		

moth's body as D1. Even when simultaneous recordings were made from D1 and the contralateral subalar or dorsal longitudinal motoneurone there were no indirect inhibitory potentials revealed when successive records were averaged.

Very few recordings were made from neck motoneurones simultaneously with D1, so I was not able to examine whether D1 made direct connections to these motoneurones. However, membrane potential fluctuations, often accompanied by spikes, were seen in them, giving rise to the extracellularly recorded responses to optomotor stimulus movement shown in Figs 1A and B. This pattern of activity was only seen in flight motoneurones with which D1 made direct connections. I would predict that D1 also makes direct connections with these ipsilateral neck motoneurones.

DISCUSSION

D1 is shown in the preceding paper to react to optomotor stimuli (Rind, 1983*b*) and now it is shown that PSPs which it induces in flight motoneurones are appropriate for mediating optomotor responses. This is the first report of an identified neurone which responds to optomotor stimuli and whose firing is associated with synaptic potentials in identified motoneurones.

The motoneurones only generate action potentials to optomotor stimulation when other excitatory inputs sum with the EPSPs of D1. These excitatory inputs do not need to be patterned. A nonspecific, steady depolarization superimposed on the input

of D1 is sufficient to cause the postsynaptic motoneurone to spike in response to the motion of the optomotor stimulus in the appropriate direction. The effect of this requirement is that the moth only shows overt optomotor responses when it is flying or about to fly and its flight motoneurones show depolarizations of up to 20 mV (Rind, 1983*b*).

I will now discuss how D1 could influence the direction of flight by considering: (a) the flight motoneurones in which it produces EPSPs; and (b) what is known of the mechanical effects of muscles innervated by these motoneurones. D1 makes connections with only a few ipsilateral flight motoneurones. All innervate wing depressor muscles. Two innervate direct depressor muscles, the other an indirect depressor, the dorsal longitudinal, a powerful lift producing muscle. Kammer (1971) states that the subalar wing muscle depresses and supinates the wing, increasing the angle of attack of the wing and hence its drag. The other direct depressor, the second pleuroaxillary, is thought by Kammer to remote the wing during flight. The combined actions of these muscles would lead to the moth turning, in a horizontal plane (yawing) towards the side that the three muscles are active. The moth would effectively brake with the 'stimulated' wing, which would then be on the inside of the turn. Increased activity in the powerful dorsal longitudinal muscle would counteract any concomitant tendency of the moth to roll on the 'stimulated' wing, due to contraction of the subalar, and second pleuroaxillary muscles.

The response of D1 is to horizontally moving stripes (Rind, 1983*b*), and the reaction it brings about, that is yawing, also occurs in a horizontal plane. Following this reaction through – a horizontal movement of the stripes to the right excites the right D1 interneurone which then produces EPSPs and a contraction in the right dorsal longitudinal, second pleuroaxillary and subalar muscle, which in a flying moth would cause it to yaw to the right. This can be related to movements of the moth relative to its visual surroundings by one further step. Movement of the optomotor stimulus would, in nature be correlated with deviation of the moth from a straight flight path or stationary position causing the image of the surroundings to move across its retinae. Deviation towards the left would cause the image to move to the right, across the retinae. This situation is mimicked by movement of the optomotor stimulus to the right. Thus the situation described above, of movement of the optomotor stimulus towards the right causing yawing to the right, would have been caused by an initial deviation towards the left. The response mediated by D1 is entirely appropriate for correcting unintentional deviations of the moth during straight flight or hovering, i.e. mediating an optomotor response.

Although D1 gives a response appropriate for mediating the optomotor response it is not the only neurone to do so (F. C. Rind, in preparation). Some of the sustained optomotor reactions shown by neck motoneurones could not be mediated by direct action from D1. Direct influences of other descending optomotor interneurones and indirect effects, via as yet unidentified neurones, can also be expected to contribute to the moth optomotor response.

This research was carried out in the Zoology Department, Cambridge. I would like to thank Malcolm Burrows, Melody Siegler, Peter Simmons, Juliet Hale, Alan Watson and Alan Kay for all their help and encouragement.

REFERENCES

BLONDEAU, J. (1981). Electrically evoked course control in the fly *Calliphora erythrocephala*. *J. exp. Biol.* **92**, 143–154.

COLLETT, T. S. & BLEST, A. D. (1966). Binocular, directionally selective neurones, possibly involved in the optomotor response of insects. *Nature, Lond.* **212**, 1330–1333.

DVORAK, D. R., BISHOP, L. G. & ECKERT, H. E. (1975*a*). Intracellular recording and staining of directionally selective motion detecting neurons in the fly optic lobe. *Vision Res.* **15**, 451–453.

DVORAK, D. R., BISHOP, L. G. & ECKERT, H. E. (1975*b*). On the identification of movement detectors in the fly optic lobe. *J. comp. Physiol.* **100**, 5–23.

ECKERT, H. (1978). Response properties of dipteran giant visual interneurones. *Nature, Lond.* **271**, 358–360.

ECKERT, H. (1980). Functional properties of the H1 neurone in the third optic ganglion of the blowfly, *Phaenicia*. *J. comp. Physiol.* **135**, 00–00.

ECKERT, H. & BISHOP, L. G. (1978). Anatomical and physiological properties of the vertical cells in the third optic ganglion of *Phaenicia sericata* (Diptera, Calliphoridae). *J. comp. Physiol.* **126**, 1–14.

GEIGER, G. & NÄSSEL, D. R. (1981). Visual orientation behaviour of flies after selective laser beam ablation of interneurones. *Nature, Lond.* **293**, 398–399.

HAUSEN, K. (1976). Functional characterisation and anatomical identification of motion sensitive neurones in the lobula plate of the blowfly *Calliphora erythrocephala*. *Z. Naturforsch.* **31C**, 629–633.

HEISENBERG, M., WONNEBERGER, R. & WOLF, R. (1978). Optomotor-blind H31 – a *Drosophila* mutant of the lobula plate giant neurons. *J. comp. Physiol.* **124**, 287–296.

KAMMER, A. E. (1971). The motor output during turning flight in a hawkmoth, *Manduca sexta*. *J. Insect Physiol.* **17**, 1073–1086.

KIEN, J. (1974*a*). Sensory integration in the locust optomotor system – I: behavioural analysis. *Vision Res.* **14**, 1245–1254.

KIEN, J. (1974*b*). Sensory integration in the locust optomotor system. II: direction selective neurons in the circumoesophageal connectives and the optic lobe. *Vision Res.* **14**, 1255–1268.

MCCANN, G. D. & FOSTER, S. F. (1971). Binocular interactions of motion detection fibers in the optic lobes of flies. *Kybernetik* **5**, 193–203.

PIERANTONI, R. (1973). An observation on the giant fiber posterior optic tract in the fly. Biokybernetik, Band V. IV Int. Symp. *Biokyberntik*, pp. 157–163. Keipzig.

PIERANTONI, R. (1976). A look into the cockpit of the fly. The architecture of the lobular plate. *Cell Tiss. Res.* **171**, 101–122.

REICHARDT, W. E. (1965). Detection of single quanta by the compound eye of the fly *Musca*. In *The Functional Organization of the Compound Eye*, (ed. C. D. Bernhard), pp. 267–289. Int. Symp. Ser. 7.

RIND, F. C. (1983*a*). The organisation of flight motoneurones in the moth, *Manduca sexta*. *J. exp. Biol.* **102**, 239–251.

RIND, F. C. (1983*b*). A directionally selective motion detecting neurone in the brain of a moth. *J. exp. Biol.* **102**, 253–271.

SANDEMAN, D. C., ERBER, J. & KIEN, J. (1975*a*). Optokinetic eye movements in the crab, *Carcinus maenas*. I: Eye torque. *J. comp. Physiol.* **101**, 243–258.

SANDEMAN, D. C., ERBER, J. & KIEN, J. (1975*b*). Optokinetic eye movements in the crab, *Carcinus maenas*. II: Responses of optokinetic interneurons. *J. comp. Physiol.* **101**, 259–274.