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A DIRECTIONALLY SENSITIVE MOTION DETECTING NEURONE IN THE BRAIN OF A MOTH

BY F. CLAIRE RIND*

Zoology Department, Downing Street, Cambridge, England

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SUMMARY

1. In the moth, *Manduca sexta*, a pair of neurones, one on each side of the brain, were characterized morphologically and physiologically as descending interneurones, selective for horizontal motion over a large area of the moth's visual field.

2. Their cell bodies and dendritic processes are located in the protocerebrum of the brain. Their axons, 12–15 μm in diameter, project down the ipsilateral connective, branching profusely on the ipsilateral side of the suboesophageal, prothoracic and pterothoracic ganglia.

3. Each neurone responds to movement over either retina. Their preferred directions are from front to back across the ipsilateral eye and back to front over the contralateral one. Movement in the opposite direction supresses their usual 'resting' discharge. The neurones are particularly sensitive to movements within the frontal, ventral visual field.

4. Each neurone responds repeatedly, for up to 5 h, to a stimulus oscillating back and forth across the retinae. The response is not diminished during concurrent wing flapping.

5. An increase in the velocity of stimulus movement produces a proportional increase in firing frequency. For stripes of 2·5 cm wavelength and subtending 32° at the eye, the maximum response occurs at a velocity of 3 cm/s which gives a contrast frequency of 1·2 Hz.

6. The latency of the neurone's response, measured from its axon as it enters the pterothoracic ganglion, depends on at least two factors: light intensity and the speed of stimulus movement.

7. The neurone gives a directional response to stripes of period 6·4° in bright light. The response falls to 16° in dim light.

8. At night, in dim light, the latency of response is much reduced and the threshold light intensity, necessary for a directional response, decreases by two orders of magnitude.

INTRODUCTION

When an animal is placed in the centre of a rotating striped drum it may turn its head to follow the rotations of the drum, a reaction which ensures that the image of the stripes is kept in the same position on its retinae. This reaction is termed an 'optomotor reaction' and the stripes an 'optomotor stimulus'. This optomotor reaction is important in nature as it represents a means whereby an animal can maintain a fixed

* Present address: Zoology Department, The University, Newcastle upon tyne, NE1 7RU England.
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position relative to its visual surroundings. In the moth, *Manduca sexta*, which feeds from the nectaries of the tobacco flower, entirely on the wing, like a humming bird, such a reaction is particularly important. Unlike a humming bird the moth has a flexible 5 cm long proboscis which it must first manoeuvre into the nectary before hovering motionless below the flower to feed. Neurones which are responsive to optomotor stimuli have been described in the brain and optic lobes of a closely related moth, *Sphinx ligustri* (Collett & Blest, 1966), with a similar feeding habit. The responses of these neurones to stripes moving across the eyes make them ideal candidates for controlling the moth's optomotor reactions (Collett & Blest, 1966). For instance, they were found to be responsive to stimuli moved over large parts of both eyes, so they could detect movements of the animal's entire surroundings or more probably movements of the animal relative to its surroundings. In addition they were found to be excited by either horizontal or vertical stripe movement in one direction (the preferred direction) and inhibited by movement in the other (the null direction). It was found that six out of the nine neurones recorded in the prothorax had preferred directions from front to back across the ipsilateral eye and from back to front over the contralateral eye. This means that the neurones are particularly suited to detecting movement in the visual field, such as that caused by movements of the moth, and could provide the information necessary for the moth to maintain a stationary feeding position. The aim of the present study was to investigate in *Manduca*, the properties of neurones, analogous to those in *Sphinx ligustri*, which would suit them to a role in optomotor behaviour.

MATERIALS AND METHODS

Adult *Manduca sexta* (Johannson), reared on an artificial diet, (B. Ballard, in preparation) were kept under a lighting regime of 12 h light, then 5 h dim light followed by 7 h darkness. The 12 h light periods were synchronized with natural daylight. The moths were prepared for intracellular recording following the procedure outlined in the preceding paper (Rind, 1983). In brief, moths at least three days old were immobilized by cold, mounted dorsal side up, and a dorsal midline incision made in order to expose the pterothoracic ganglion which was mounted on a stainless steel, plastic-coated platform. The microelectrodes used had resistances of 20–50 MΩ when filled with 2M-potassium acetate and tested in saline. These electrodes were either filled with 2M-potassium acetate for recording or 10% (w/v) cobalt chloride for recording and marking. Recordings from the neurones were made from the axon, as it entered the pterothoracic ganglion. The processes of the neurone in the thoracic ganglia were revealed by injecting stain into the neurone from this same position. A different approach was employed to stain the processes in the brain. The moth was mounted ventral side up and an incision made in the neck. The connectives were manipulated onto a small stainless steel platform and the neurone impaled as it emerged from the suboesophageal ganglion. In both cases 15 nA d.c. pulses, 250 ms long, were given once per second for 2–5 h. The nervous system was then dissected out, the cobalt precipitated using ammonium sulphide and the ganglia fixed, dehydrated in a graded series of alcohols, left overnight in 70% alcohol and then intensified (Bacon & Altman, 1977) the next day. The ganglia were then dehydrated.

■eared and drawn. A small length of the cervical connectives was mounted in Spurrs resin, sectioned and the 2·5 μm thick sections stained with 1% toluidine blue in borax. The cross section of the connectives and the cobalt filled axon was drawn.

The optomotor stimulus was a white 5 by 9 cm card on which 'Letrafilm Pantone' black stripes were stuck. Four cards were constructed with an equal sized black and white stripe having a period of 25·5, 12·6, 5 or 2·5 mm. The cards were placed 2·5 cm in front of the moth with stripes orientated vertically so that they subtended, respectively, 32, 16, 6·4 or 3·2° at the moth's eye. The whole card subtended approximately 90° at the moth's eye. The card was mounted on an arm attached to a Ling Dynamic System vibrator. The vibrator was driven either by single ramps so the card was moved in one direction and held there or by repetitive ramps (triangular waves). The card was moved 28 mm through an arc of 36° at velocities between 0·4 cm (5·1°)/s and 12 cm (153·6°)/s. A background against which the card was moved was constructed using the same white cardboard as the white stripes. The arm of the vibrator projected through this background and the card was then attached thus hiding the arm from the view of the moth.

The card was illuminated using either a Barr and Stroud light source and glass fibre guide, or a Zeiss mercury vapour lamp with a heat filter and a Zeiss interference filter which passed green light of wavelength 546 nm (bandwidth 2 nm). The second provided dim light of known energy. A series of Zeiss neutral density filters could be interposed to further attenuate the light source and to give illumination from $2{\cdot}13 \times 10^{-1}$ mW/cm^2 to $6{\cdot}12 \times 10^{-5}$ mW/cm^2. The response of the interneurone to the optomotor stimulus was stored on magnetic tape to be filmed and analysed later. A North Star Horizon computer was programmed to calculate mean interspike intervals from data fed into it from a digitizing board. In all cases experiments reported in this paper gave consistent results on at least three separate occasions.

RESULTS

Morphology

A neurone in the brain was found to be sensitive to horizontal movement of stripes anywhere in the moth's visual field. In bright light even without stimulus movement the neurone spiked occasionally (Fig. 1A). This discharge increased when the stimulus was moved backwards over the ipsilateral and/or forwards over the contralateral eye (Fig. 1B, C). The resting discharge stopped if the stimulus was moved in the opposite direction. By contrast, vertical movements of horizontal stripes produced only a very weak response in the neurone. These responses categorize the neurone as a horizontal directionally selective, motion detector. Non-visual stimuli, such as blowing on the head, touching the moth's antennae, legs or body of the moth, hissing or presenting the moth with an olfactory stimulus (1, 1·1 Trichloroethane) were no more effective in producing a response in the neurone than the hand movements necessary to deliver the stimuli. The neurone was further characterized by a continued response during active wing flapping and also an undiminished response to back and forward stimulus movements for up to 5 h. Neurones having the above characteristics were always found to have the same morphology (in more than 25 fills). One such neurone was found on each side of the moth nervous system with its cell

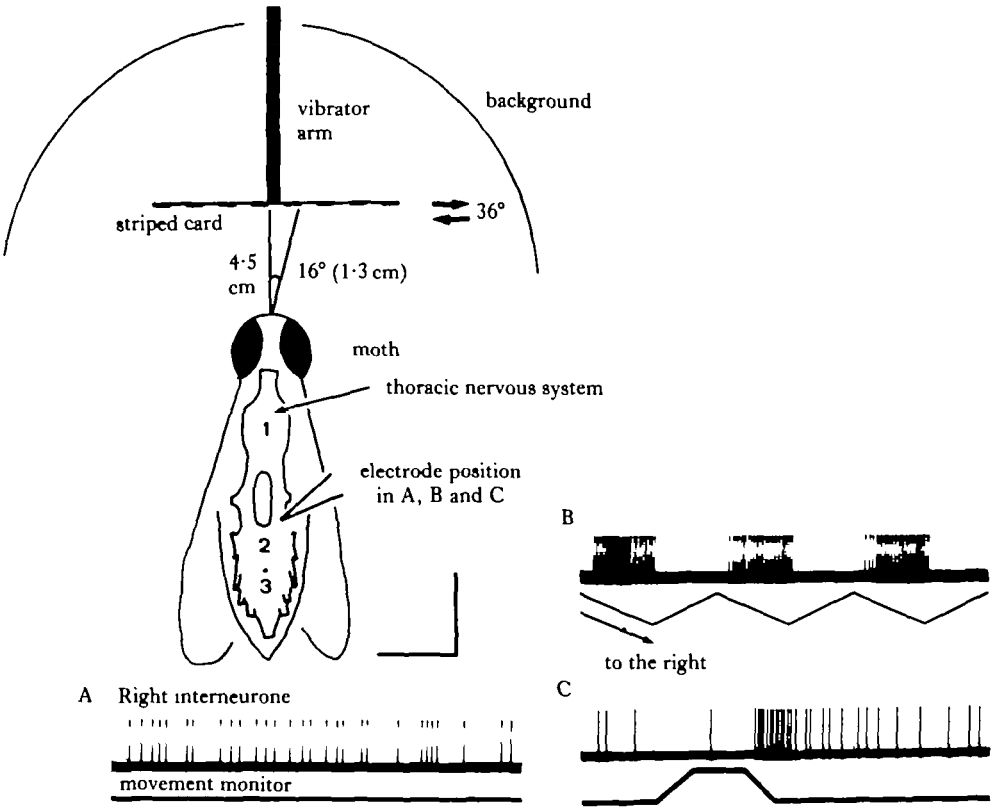

Fig. 1. Diagrammatic illustration of the optomotor stimulus and the recording position. The thoracic nervous system has been enlarged relative to the moth's body. A–C. The response of the right D1 neurone to a brightly illuminated (5000 lux) stimulus (A) to a stationary stimulus; (B) to repeated right and left motion of the stimulus; and (C) to single movements of the stimulus (ramp and hold). Parts of the thoracic nervous system are labelled: 1, prothoracic ganglion; 2, mesothoracic ganglion; 3, metathoracic ganglion.

body and dendrites in the brain, and the axon projecting down into the ipsilateral thoracic nervous system. The neurone was named 'D1' as it was the first of a population of descending interneurones to be identified.

The 30 μm cell body of D1 lies just beneath the perineurium (Fig. 2) at the posterior of the protocerebrum (Fig. 3). This location is most clearly seen when the brain is viewed from its ventral surface, as in Fig. 2. The suboesophageal ganglion is fused to the extreme ventral surface of the brain, leaving only a small hole through which the gut passes (Figs 2, 3). From the cell body the primary neurite emerges dorsally and projects forwards before making a dorsally directed forward loop of 150 μm before continuing ventrally and giving rise to 4–5 lateral branches, all of which are restricted to the side of the brain ipsilateral to the cell body. Two branches with an initial diameter of between 4–10 μm project 2–300 μm towards the optic lobes giving off many fine side branches, so that the whole projection has a fuzzy appearance when viewed with the light microscope. These branches end in a region of the protocerebrum where large diameter fibres coming from the lobula complex were also seen to terminate. Two other large diameter laterally directed processes of a simila-

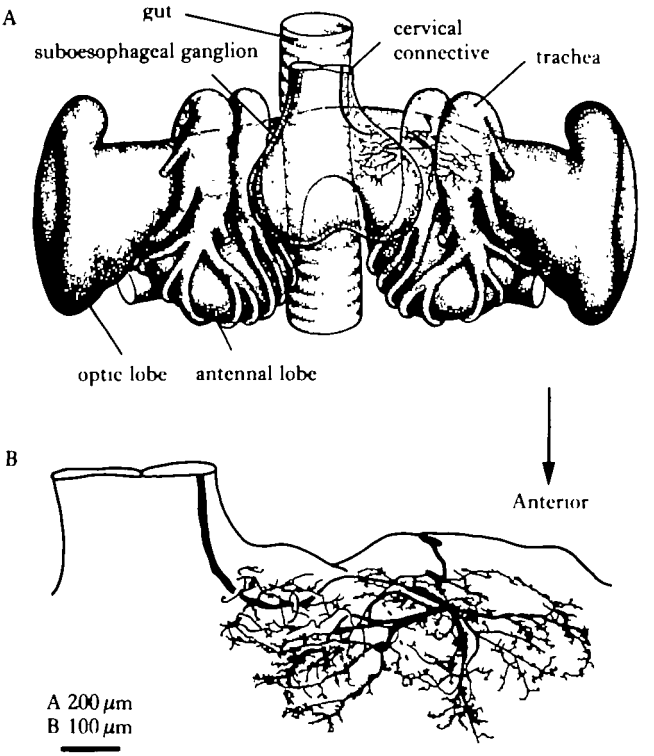

Fig. 2. Ventral view of the fused suboesophageal and supraoesophageal ganglia with a stained D1 neurone. (A) View of entire brain and the tracheal system; (B) enlarged view of the stained D1 neurone. Anterior is downward.

fuzzy appearance arise from D1's primary neurite at the same level and project in the opposite direction to the first two processes described. These two processes have many fine processes which terminate close to where the gut passes through the brain, at the posterior lateral perioesophageal region. The 5th and most major branch leaves the primary neurite after the other four, just before the neurite tapers to project laterally into the suboesophageal ganglion. The 5th branch is between 7–13 μm in diameter and follows the course of the primary neurite, but lies anterior and ventral to it, terminating just above the suboesophageal ganglion in the perioesophageal region but more ventral to the terminations of the 3rd and 4th branches. It also has the fuzzy appearance of the previous four major branches. After first tapering the neurite then expands to become the axon as it dips ventrally into the ipsilateral side of the suboesophageal ganglion. The axon has a diameter of 5–10 μm in the suboesophageal ganglion where it gives rise to about eight processes of 30–100 μm in length and 2–3 μm in diameter. These are smooth, in contrast to D1's processes in the brain. The contrast in diameter is most marked at their terminations. In the suboesophageal ganglion, even at their terminations, the processes are 1–2 μm in diameter. These processes have definite ends, which contrast sharply with the surrounding non-stained neuronal processes rather than show a gradual lightening of stain. This indicates that rather than being an artifact of an incompletely stained neurone they are in fact terminations. In the suboesophageal and all subsequent

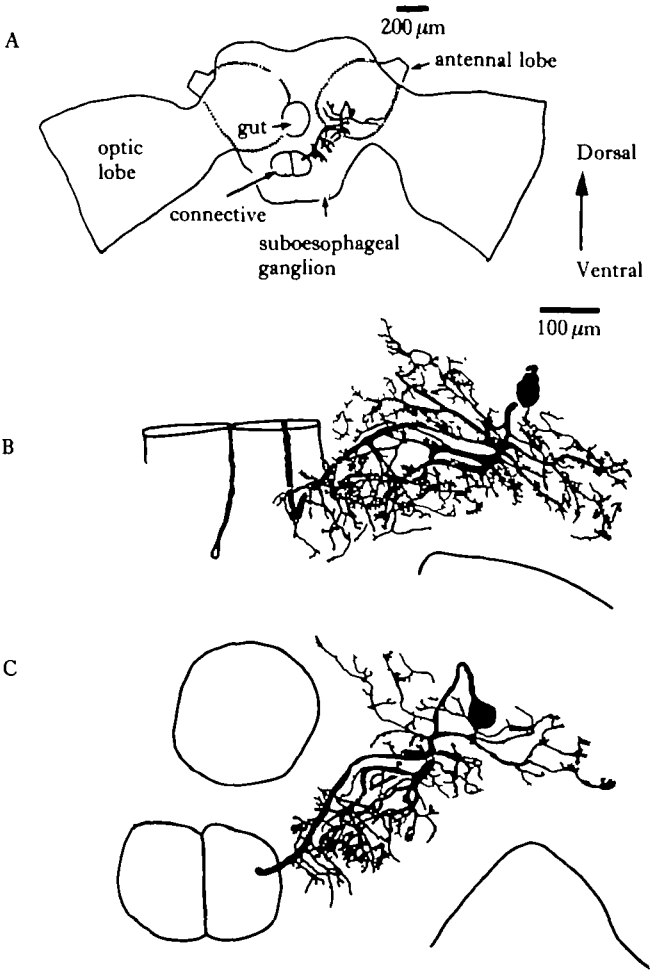

Fig. 3. Posterior view of the suboesophageal and supraoesophageal ganglia in which a D1 neurone has been stained. (A) View of entire brain; (B) enlarged view of D1; (C) enlarged view of D1 from a second moth.

thoracic and abdominal ganglia all the processes of D1 are restricted to the same side of the nervous system as its cell body and dendrites. As the axon emerges from the suboesophageal ganglion in the cervical connectives it turns ventrally and posteriorly. At this point the axon of D1 is 13 μm in diameter and lies in the dorso-lateral quadrant of the fused left and right connectives. The axons of D1 neurones from the right side of two moths are shown in cross-section in Fig. 4A, B. The axon of D1 is one of the largest in the connective. There is no consistently recognizable pattern of axons from left to right connective in the same animal or between animals (compare Fig. 4A and 4B). In the prothoracic and pterothoracic ganglia the axon of D1 follows the same path through the ganglia as other large diameter (10–15 μm) interganglionic interneurones. The axon and all the processes are restricted to the dorsal half of the nervous system (Figs 5A, 6A). Within 100–200 μm of entering a ganglion the axon branches to give 50–100 μm medially directed branches (Figs 5, 6A, B) and 300–350 μm laterally

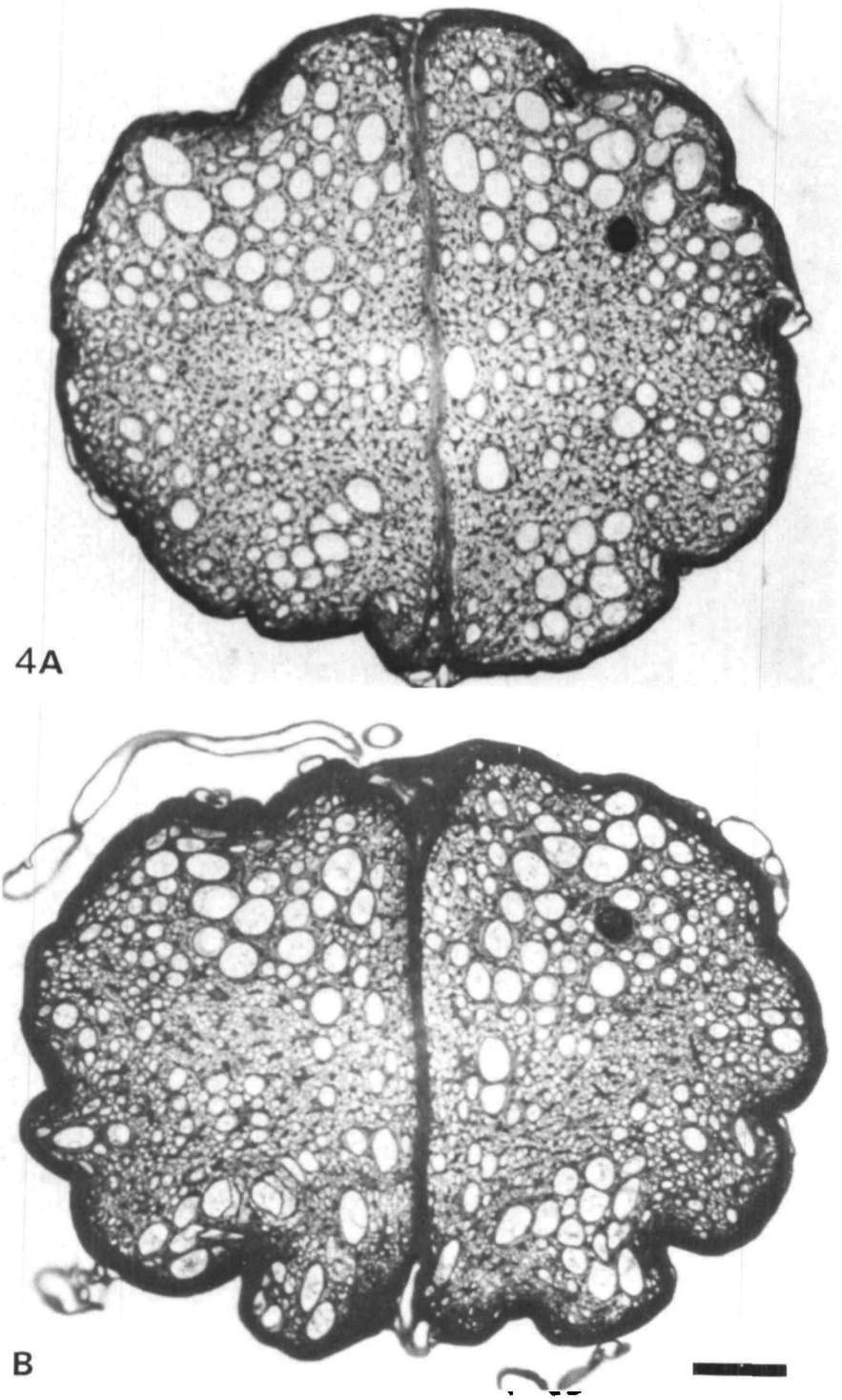

Fig. 4. Cross sections of the left and right cervical connectives from two moths (A) and (B) in which the right D1 neurone had been stained. The darkened rounded profiles are the axons of the stained D1 neurones. Scale bar measures 25 μm.

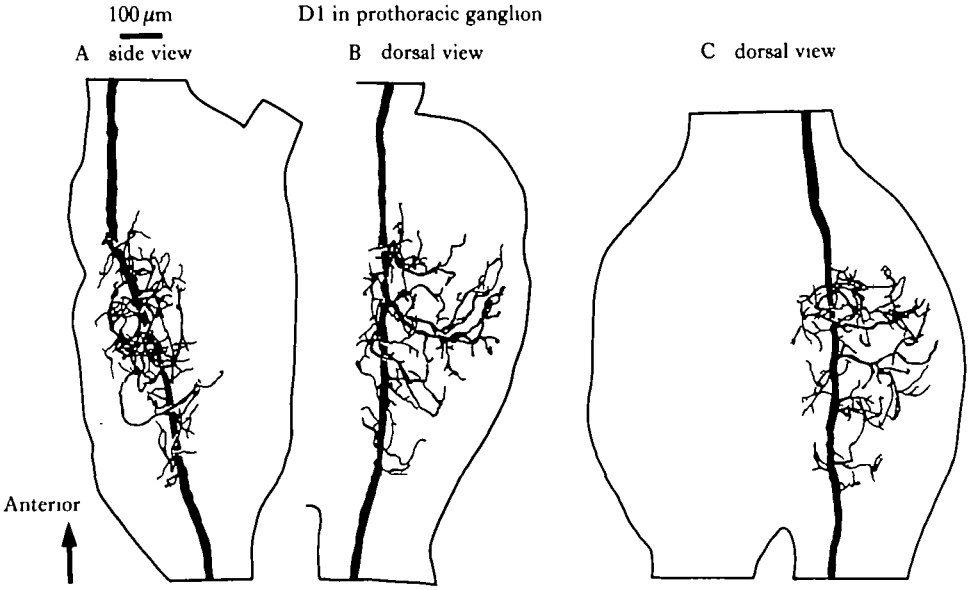

Fig. 5. Branching pattern of two D1 neurones stained in two different moths. (A) and (B) are the side and dorsal view of the branches of one D1 neurone in the prothoracic ganglion (C) is the dorsal view of the branching pattern of a second D1 neurone also in the prothoracic ganglion.

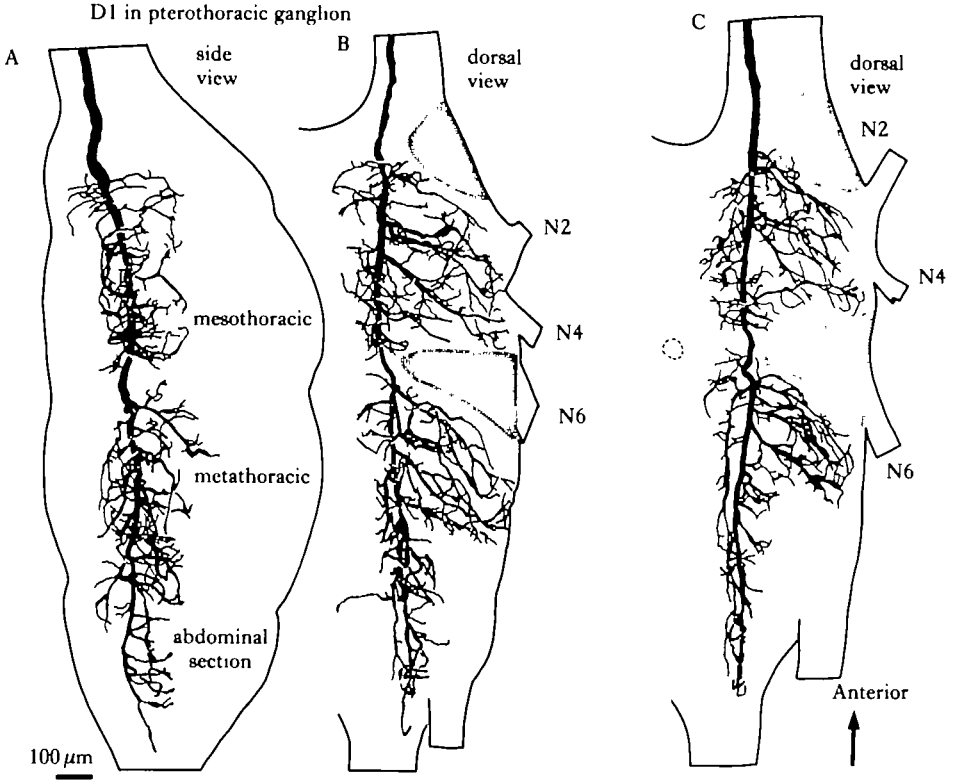

Fig. 6. As for Fig. 5 except the branching pattern of two D1's in the pterothoracic ganglion is shown.

directed ones. In the meso- and metathoracic segments of the pterothoracic ganglia these branches project to the same area of neuropile as the dendritic processes of the flight motoneurones (Rind, 1983). Within the pterothoracic ganglion there are very few branches into the anterior and posterior groups of flight motoneurone cell bodies. No process of D1 extended beyond the pterothoracic ganglion into the abdominal connectives.

Response to optomotor stimuli

The input onto D1 came from both eyes. Both were equally effective in either exciting D1 when the optomotor stimulus was moving in the preferred direction (backward over the ipsilateral eye, forward over the contralateral) or inhibiting D1 when it was moving in the opposite direction. Temporarily blinding the ipsilateral eye had the same effect as temporarily blinding the contralateral (Fig. 7), which was to reduce both the excitatory response to the preferred direction and the inhibitory response in the null direction. Thus, both eyes seem to contribute to both phases of the response.

Not all regions of the eye contributed equally to the response. The facets in the ventral frontal quadrant are significantly larger in diameter than those in the dorsal posterior one. The response of D1 to movement in the preferred direction was reduced by up to one half when a barrier was placed in front of the moth preventing the image of the stimulus from falling on the frontal ventral region of the two eyes. Fig. 8 shows this response, in terms of the mean interspike interval, to optomotor stimuli travelling at different velocities presented before and after placement of the barrier prevented vision of the stimulus by these frontal ventral facets. Resting discharge in the absence of stimulus movement was also lowered, indicating the role of light falling on those frontal ventral facets in its maintenance.

The following three experiments were conducted to test D1's 'attention' under conditions that simulate those a freely moving moth would encounter. First, to test the persistance of D1's response over a length of time the optomotor was moved back and forth for up to 5 h. The response of D1 to movement in the preferred and the null direction was kept up throughout the 5 h (Fig. 9A). Second, as during these experiments the moth was not able to move its head in response to the optomotor stimulus, I tested whether proprioceptive information from a head movement would inhibit the response of D1, by turning the moth's head in front of a stationary striped pattern (Fig. 9B). The response was the same as when the card was moved relative to a stationary moth, ruling out the possibility that the response of D1 is switched off by proprioceptive information from head turning movements. It does not rule out the possibility that the response of D1 may be inhibited when the moth itself turns its head or performs any other movement. Finally, to test this, I recorded intracellularly both the response of D1 to stimulus movement and the activity of motoneurones to the wing muscles, for example, the motoneurone to a muscle which elevates the wing (Fig. 9C, upper trace). In the absence of any wing flapping (first 3 traces) D1 shows a typical response to movement of the stimulus in the preferred and then the null direction. The response of D1 was unchanged even when the wing was flapping vigorously and the elevator motoneurone was producing action potentials.

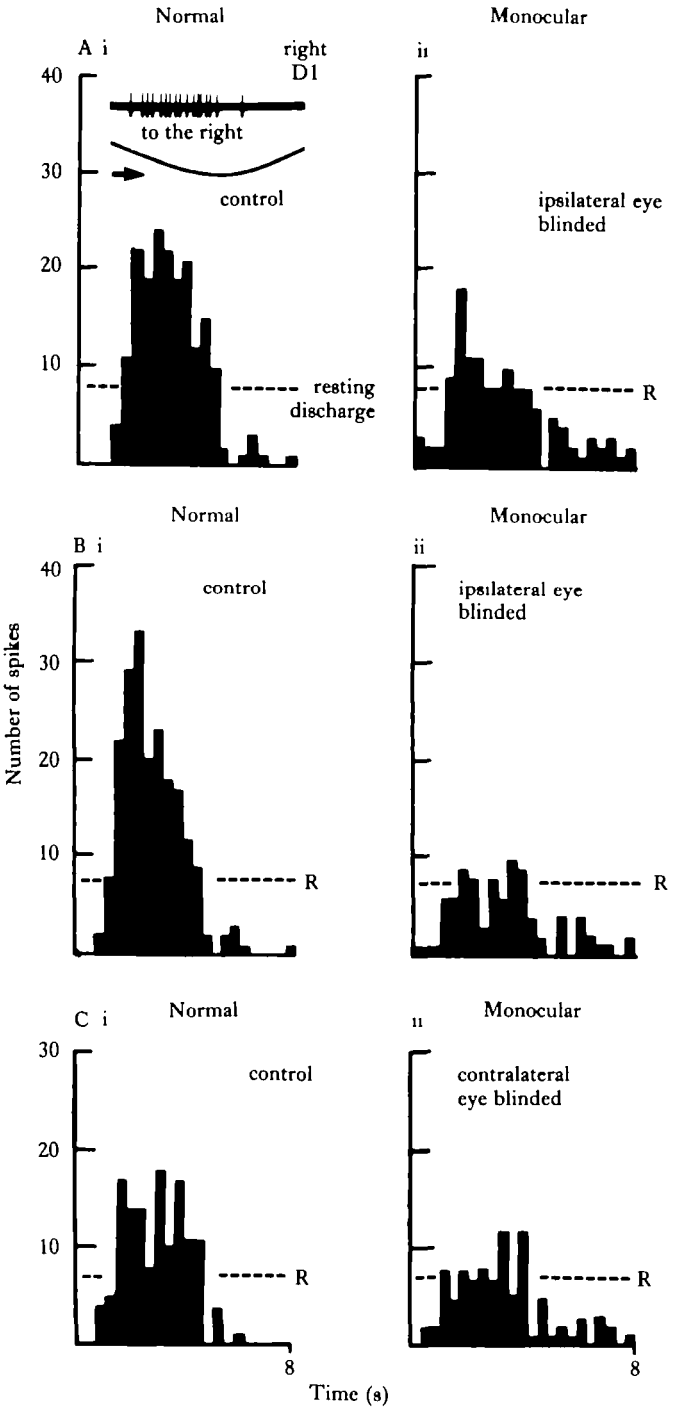

Fig. 7. Response of the optomotor interneurone to sinusoidal oscillations of the stimulus pattern before and after temporary monocular blinding. An inset in Fig. 8A (i) shows a typical response of the visual interneurone. The neurone is excited during intervals 3–15 (down on the movement trace) and inhibited during 15–23 (up on the movement trace). 23 intervals = 8 s. The histogram intervals show in which part of the stimulus movement the spikes were counted. The height of each bar is determined by the number of spikes occurring during that interval over seven complete oscillations. The experiment was performed in daylight (1000 lux) with a stimulus wavelength of 32° (25·2 mm).

The excitatory response of D1 to movement of the optomotor stimulus in the preferred direction is affected by the speed of that movement (Figs 10, 11). The greater the velocity of movement the greater the rate of spike production. The rate of spike production is roughly proportional to velocity of movement up to stimulus velocities of 3 cm/s (Fig. 11). Further increases in velocity of stimulus movement did not lead to increases in spike rate. The wavelength of stripe was 2·5 cm so this represents a maximum spike frequency at a contrast frequency (velocity/wavelength) 3/2·5 cm/s or 1·2 Hz.

Manduca is active in dim light at night but so far all the measurements have been made from D1 in bright light. To be a candidate for optomotor control of flight the neurone must also work effectively in dim light. The following experiments compare the latency of response, and the acuity of D1 in both bright and dim light during the day.

The time taken from the onset of stimulus motion in the preferred direction to an

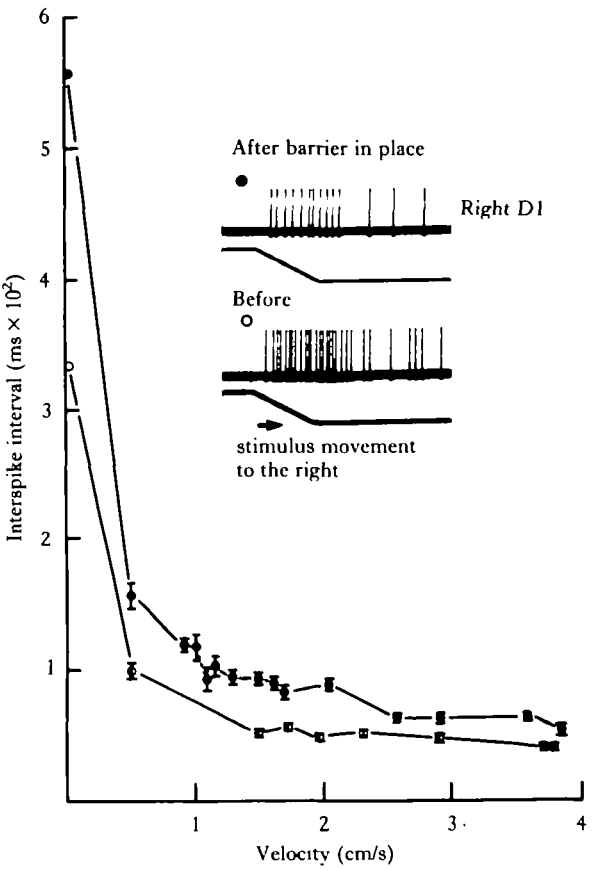

Fig. 8. Response of the optomotor interneurone to single ramp movements of the pattern at different velocities before and after the placement of a barrier in front of the moth's head between the two eyes. The experiment was performed in bright light (5000 lux) with a stimulus wavelength of 12·6 mm (16°). Mean interspike interval (ms) is shown before (○) and after (●) placement of the barrier. Standard error bars are given. For each point n is from 12–110. The inset shows the response to stimulus movements at 1·7 cm/s before and after placement of the barrier.

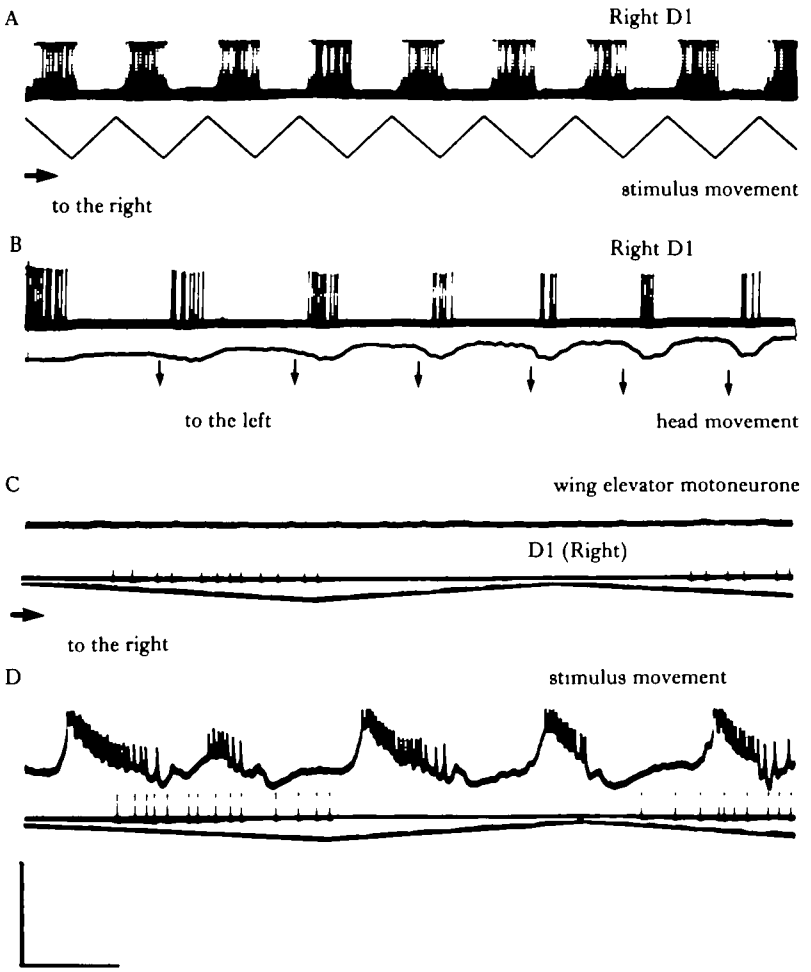

Fig. 9. A, Response of the interneurone to oscillatory stimuli, at a constant velocity over 14 s (stripe period = 16°, 12·6 mm; velocity = 2·9 cm/s, light itensity = 5000 lux). B, Response of the optomotor interneurone to gentle 2–3 mm movements, of the moth's head while the stimulus remained stationary. Stimulus and lighting conditions were as above. The interneurone was on the left side of the moth. Head movements toward the right (downward deflection on the lower trace) excite the neurone, while movements towards the left inhibit it. Comparison of the response of the optomotor interneurone to an oscillating stimulus during rest (C) and during strong voluntary movement (D). Upper trace: Intracellular recording from a flight motoneurone; Middle trace: Intracellular recording from D1 interneurone; Bottom trace: Stimulus movement. Calibration: Vertical A, top trace 50 mV, lower trace 80 mm, B, top trace 30 mV, lower trace 12 mm; C and D, top trace 15 mV, lower trace 80 mV, bottom trace 16°. Horizontal, A, 2 s. B, C and D, 400 ms.

excitatory response, measured as action potentials in the axon of D1 as it enters the pterothoracic ganglion, was found to depend on both the light intensity and the velocity of stimulus movement (Figs 10, 12). Points for both Figs 10 and 12 were taken from the same D1 interneurone. As the light intensity or velocity of stimulus movement decreased so D1's latency of response increased. In bright light (5000 lux) the minimum latency was 80 and the maximum 420 ms. This compares with a minimum of 210 and a maximum of 1450 ms in dim light (100 lux). The relationship

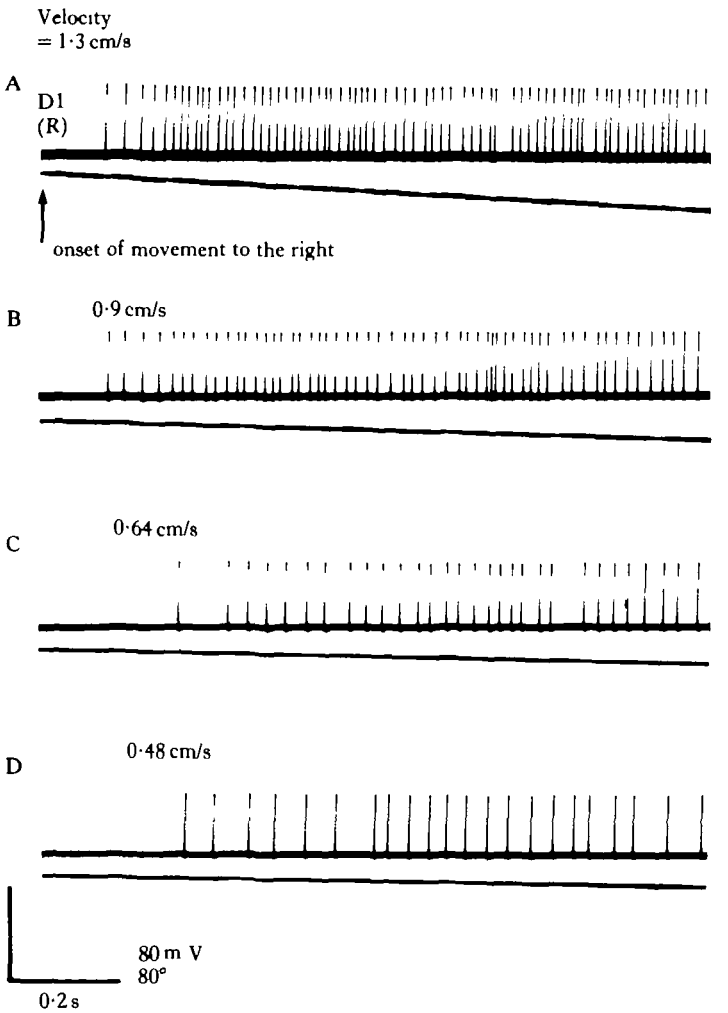

Fig. 10. Response of D1, recorded as in Fig. 1, to four different velocities of stripe movement. The latency and the interspike interval increase with slower stripe movements. The experiment was performed in bright light (5000 lux) with a slowly oscillating stimulus of spatial wavelength 32° (25·2 mm).

of latency of response to level of illumination was investigated more accurately using monochromatic green light (wavelength, 546 nm). The overall illumination was low, which means that latencies are longer than those measured in bright light. Within the range tested the relationship of latency, in ms, plotted against the log of the light intensity, was approximately linear, with a 10-fold increase in light giving a 50 ms decrease in latency (Fig. 13).

The differential response of D1 to motion of stripes in the preferred versus the null direction can be used to test the ability of D1 to resolve stripes of different wavelengths, that is, the acuity of D1. Four cards with a stripe period respectively of 32° (2·5 cm), 16° (1·3 cm), 6·4° (0·5 cm) or 3·2° (0·25 cm) were used as the optomotor stimulus and moved in front of the moth while the response of D1 was monitored (Fig. 14). The solid circles represent the response of D1 to movement in

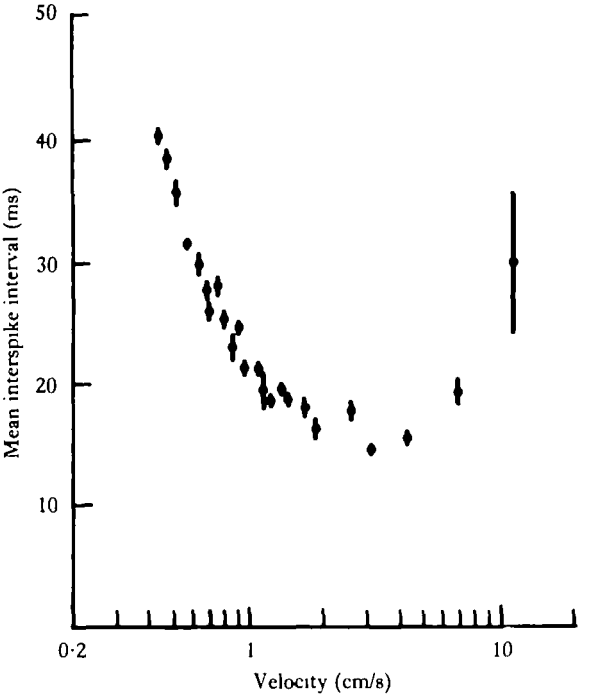

Fig. 11. The mean and standard error of the interspike interval during the excitatory respose of D1 to different velocities of pattern movement. For each point, n is from 15–150.

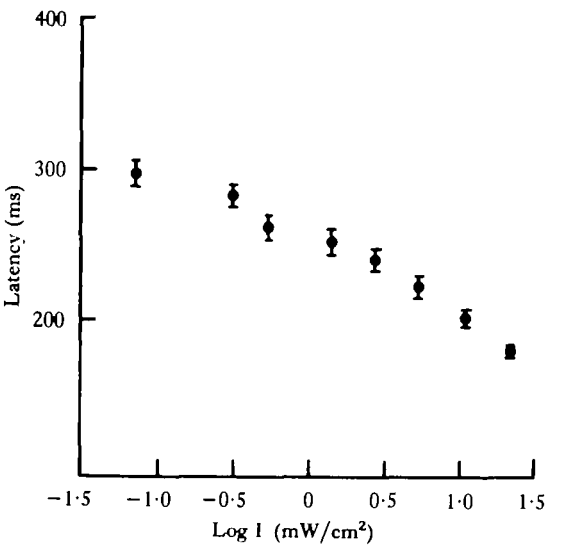

Fig. 12. Mean and standard error of the D1 response latency as a function of average light intensity at 546±2 nm wavelength. The recording situation was as in Fig. 1. Before the latency was measured the neurone was adapted to each new light intensity for 5 min. For each point $n = 20$.

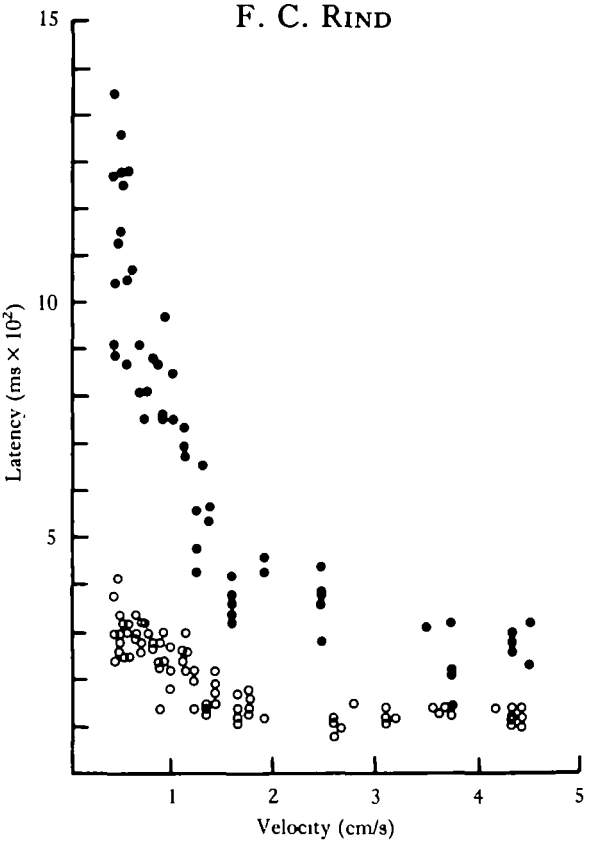

Fig. 13. Latency of response of the optomotor interneurone to different velocities of stimulus movement. The recording situation was as in Fig. 1. The results were compared at two light intensities, 100 lux (●) and 5000 lux (○).

the preferred direction and the open circles represent the response for the null direction. The dashed line is the response in the absence of stimulus movement (the resting discharge). Movement of stripes of wavelength 32°, 16° and 6·4° showed a clear separation in the response of D1 to movement in the excitatory and inhibitory directions. There was no clear separation of responses to stripes with a wavelength of 3·2°. When this experiment was repeated in dim light (Fig. 15) the acuity of D1 was reduced. With a stripe period of 6·4° (5 cm) there was no longer a separation of the response to movement in the preferred and null directions. In addition, there was no clear directional response to low velocities of movement even with the 16° wavelength stimulus. In dim light the resting discharge was extremely low – 6 spikes were recorded over a period of 5 min – and the response to all wavelengths of stimulus was reduced. Thus there is no evidence from these experiments of any spatial reorganization of the inputs to D1 in dim light.

As mentioned previously, in the wild, *Manduca* is active in the evening rather than during the day. All the previous experiments were conducted during the day. To test the influence any daily rhythms may have on the response of D1, the latency of response and the threshold light intensity necessary for a directional response to stripes of 16° wavelength were compared in the same D1 neurone at 4 p.m. and 8 p.m. (Table 1). The latencies at night were much shorter than those during the day

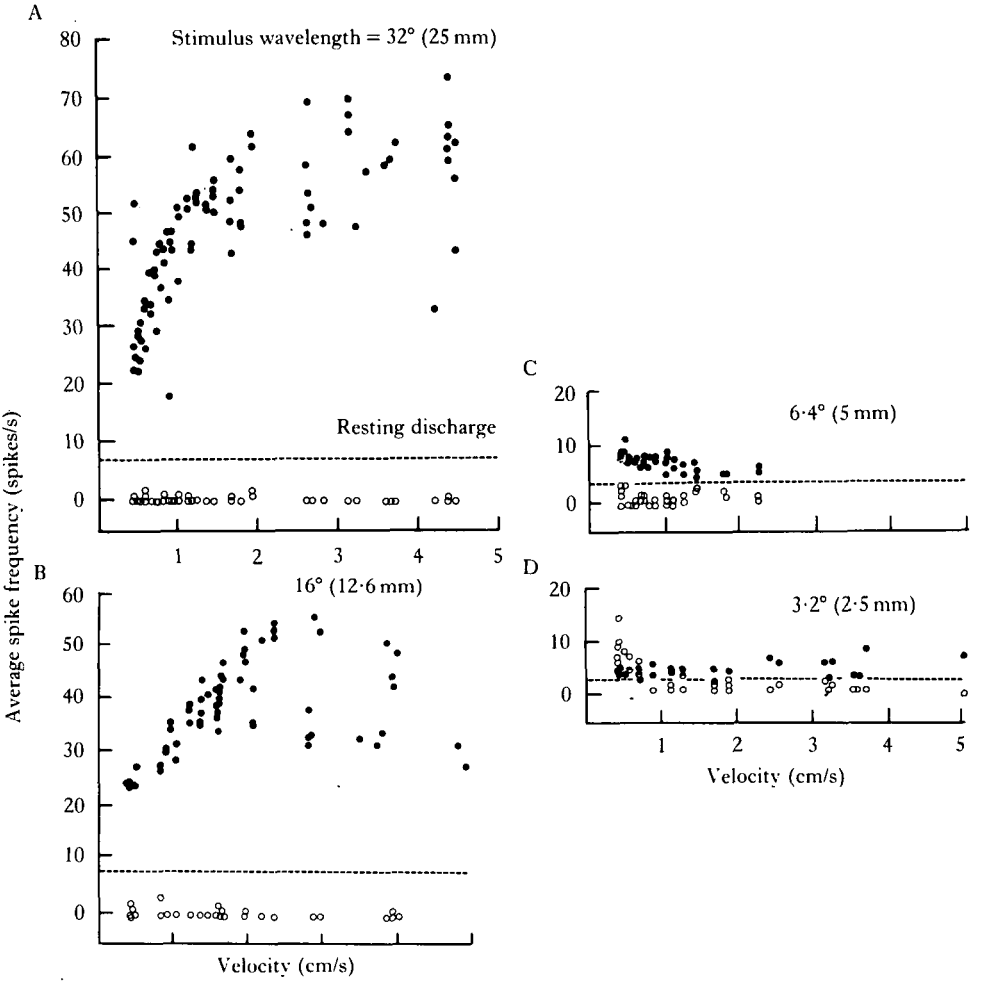

Fig. 14. Response of D1 to different spatial wavelengths in bright light. Filled circles, response of D1 to movement in the preferred direction. Open circles, response of D1 to movement in the null direction. Dotted line, response of D1 to a stationary stimulus. Spatial wavelength of stimulus is (A) 32° (B) 16° (C) 6·4° (D) 3·2°.

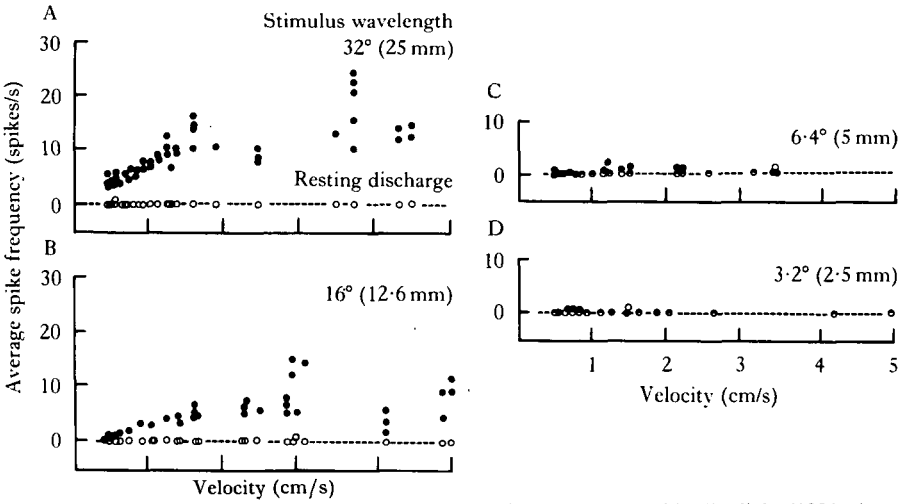

Fig. 15. As in Fig. 14 except the directional response of D1 is now tested in dim light (100 lux).

Table 1. *Latency of D1's response to stimulus movement in the preferred direction compared during the day (4 p.m.) and at night (8 p.m.). The stimulus pattern subtended 16 ° and was moved at 1 cm/s*

Light intensity mW/cm^2 in green light (546 nm)	Latency ms Day	Night
21·30	199·8	200·0
5·31	247·0	205·8
2·78	282·0	179·3
1·40	323·5	205·0
0·55	295·0	185·5

Table 2. *Latency of D1's response to stimulus movement in the preferred direction in low light intensity during the night (8 p.m.)*

Light intensity mW/cm^2 in green light (546 nm)	Latency ms Night
$3{\cdot}81 \times 10^{-2}$	132·9
$2{\cdot}54 \times 10^{-2}$	170·5
$1{\cdot}46 \times 10^{-2}$	209·0
$7{\cdot}97 \times 10^{-3}$	263·3
$3{\cdot}90 \times 10^{-3}$	297·5
Threshold at $6{\cdot}12 \times 10^{-5}$ mW/cm^{-2}	

particularly at levels of illumination below 5·31 mW/cm^2. The threshold illumination necessary for directional response by D1 occurred at $7{\cdot}1 \times 10^{-2}$ mW/cm^2 at 4 p.m. By 8 p.m. the threshold illumination had fallen to $6{\cdot}12 \times 10^{-5}$ mW/cm^2. The latency of D1's response at these dim night time illuminations close to threshold was only 300 ms (Table 2) a value comparable to the daytime value which occurred with light levels two orders of magnitude greater.

DISCUSSION

Directionally selective motion detectors have been found in the optic lobes or visual pathways in the brain of a wide range of vertebrate and invertebrate animals. Within the invertebrates, large field directionally selective motion detectors like D1 have been identified in such diverse insects as the locust (Horridge, Scholes, Shaw & Turnstall, 1965), the grasshopper (Northrop & Guignon, 1970), the cricket (Palka, 1969), the bee (Kaiser & Bishop, 1970), the butterfly (Swihart, 1968), the fly (Bishop & Keehn, 1967) and the moth (Collett & Blest, 1966). Those best studied are those of the fly lobula plate, where giant neurones sensitive to horizontal and/or vertical movement have been identified and some of their responses and the underlying synaptic relationships which give rise to their directional selectivity elucidated (Bishop & Keehn, 1967; Bishop, Keehn & McCann, 1968; McCann & Dill, 1969; McCann & Foster, 1971; Pierantoni, 1973, 1976; Dvorak, Bishop & Eckert, 1975; Hausen, 1976; Eckert & Bishop, 1978; Soohoo & Bishop, 1980; Eckert, 1980·

Hausen, Wolbur-Buchholz & Ribi, 1980). None of these lobula plate neurones project into the thoracic nervous system as D1 does. Preliminary evidence suggests that in the moth, neurones like D1 would receive their inputs from neurones in the lobula plate with similar morphologies and responses to those of the lobula plate giant neurones in the fly (Strausfeld & Blest, 1970; Collett, 1971*a*,*b*).

Optomotor stimuli are clearly effective in eliciting a response from D1. The responses of D1 to vertical stripes make it particularly suited to detect yawing movement of the moth about its vertical axis. D1 has a receptive field covering both eyes and is excited by backward movement over the ipsilateral eye and forward over the contralateral, so it will respond well to movements of the moth's entire surroundings over the eyes such as would occur in yawing movements during hovering. During hovering, in particular, the optomotor system in moths is envisaged as operating by providing an efficient velocity servo in which image motion across the retina is reduced to zero. D1 is particularly suited to detecting low velocities of stripe or image movement such as would occur when the animal has stabilized its position so that the error signal is small and the velocity of movement across the eyes is close to zero. In addition, during feeding, the hovering moth stabilizes the image of the flower on the ventrofrontal region of the eyes. D1 is particularly sensitive to movements occurring in this region.

During forward flight the situation is more complex. D1 would be responsive under these circumstances, as shown by its continuing response over several hours, during head movements and also during vigorous wing flapping. During forward flight the image of the moth's surroundings flow backwards over both its eyes. D1 gets equal input from both eyes, so that the net response to equal velocities of movement forward, in the preferred direction over the ipsilateral eye and backward, in the null direction over the contralateral eye, would be nil.

When the moth flying forwards deviates from a straight course the image movement generated by that deviation is added to that due to the forward component of the flight. The response D1 has to this deviation depends on the velocity of the forward flight compared with the turn. During forward flight the velocity of image motion is least across the frontal visual field (Collett & King, 1975; Collett, 1980). This is a fact of special significance as D1 is particularly sensitive to movements in the frontal part of the visual field. This heightens the responsiveness of D1 to image motion due to the turn and makes it likely that over part of the region of highest sensitivity there will be a net forward motion over the eye on the inside of the turn and a net backward motion over the eye on the outside of the turn. Forward motion over the eye on the inside of the turn and backward over the outside eye means excitation of the D1 on the side of the moth outside the turn. The excitation will be proportional to the velocity of the turn.

If D1 is to mediate the optomotor responses of the moth it must be able to detect motion of images across the retina in dim light. In bright light D1 gave a directional response and could therefore detect motion of stripes subtending as little as 6° at its eye. A 16° separation of stripes was necessary before D1 gave a directional response in dim light during the day. This deterioration, observed during the day, may not mimic the conditions operating during the evening. The threshold stimulus illumination necessary for a directional response in D1 declines by two orders of magnitude

in the evening and, to a lesser extent, so does the latency of response of D1. This is not the first time this has been observed in a nocturnal insect although it is the first time an identified motion detector has been shown to exhibit it. Meyer-Rochow & Horridge, (1975) found that whereas in the day the beetle *Anoplognathus* gave an optomotor response to stripes of wavelength 20° in dim light at 350 lux, in the night it is able to respond to stripes of 15° at 1·5 lux. For comparison light from the full moon gave a reading of 5 lux. Many arthropods – crayfish, crab (Nässel & Waterman, 1979; Stowe, 1980), spider (Blest, 1978), locust, praying mantis (Horridge *et al.* 1981) and fly (Williams & Blest, 1980) – show a diurnal cycle of membrane turnover in the retinula cells of the retina. The membranes are synthesized at dusk and break down around dawn. It has been proposed (Blest, 1978) that in nocturnal arthropods such as the spider *Dinopis*, more sensitive night-time photoreceptive membrane is synthesized and added to the rhabdom in the evening. This membrane is subsequently broken down again at dawn to restore the diurnal condition. A similar cycle occurring in moth rhabdoms could account for the diurnal change in the sensitivity of D1. At present there is no evidence to support such a diurnal rhythm in the moth.

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