J. exp. Biol. **165**, 137–160 (1992)
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THE PERCEPTION OF THE VISUAL FLOW FIELD BY FLYING LOCUSTS: A BEHAVIOURAL AND NEURONAL ANALYSIS

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Accepted 13 December 1991

Summary

1. Tethered locusts (*Locusta migratoria*) were stimulated with an artificial flow field (FF) device, which produced the visual effect of forward motion ('progressive flow field') or backward motion ('regressive flow field'). Progressive FFs (contrast frequencies, CF, of 2–10 Hz and angular period of pattern, λ, of 33° or 42°) can initiate and maintain flight, even without frontal wind. Regressive FFs inhibit flight. The locusts adjust their wingbeat frequency (and thus probably their flight speed) in response to a gradually changing FF contrast frequency; they fly faster when the FF motion is faster and *vice versa*. Sudden decelerations of FF motion, however, are transiently counteracted by increases in wingbeat frequency.

2. Rotational movements of the entire flow field device, simulating yaw and/or roll deviations during progressive flight, elicit compensatory steering responses of the head and abdomen. Corrective steering behaviour and simultaneously presented FF stimuli do not influence each other.

3. A descending interneurone (FFDN1) is described which reports the progressive visual FF. It receives input from both compound eyes, prefers FFs on the ventral retina, and responds over the range of contrast frequencies of 1–20 Hz. Its response is tonic and adapts only weakly to maintained FF stimuli. It follows changing FF velocities but tends to counteract sudden decelerations. In addition, FFDN1 is excited by frontal and contralateral wind and inhibited by ipsilateral wind. It is also excited by the flight motor and sometimes by light-off at the ocelli. The neurone is generally insensitive to simulated roll and yaw deviations. Electrical stimulation of the cell can result in lifting of the abdomen, inhibition of dorsal neck muscle activity, and occasional flight muscle spikes. FFDN1 is probably a sister cell of the previously described DNM neurone, but the two could be one neurone with very variable responses.

4. At least one further descending interneurone responding selectively to progressive flow fields, but with a different morphology, is present in the central

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Key words: locust, flow field, descending neurone, flight control, multimodal integration, vision, *Locusta migratoria*.

nervous system. Additionally, two different thoracic interneurones have been found with properties suggesting that they are postsynaptic to FFDNs and presynaptic to the flight circuitry.

5. The possible role of the visual flow field in the regulation of flight activity of locusts and other insects is discussed.

Introduction

Flying insects perceive various patterns of movements. One important type of stimulus originates from the relative motion of the insect and the stationary surroundings. In the anterior half of the field of view this visual flow field has the form of a radially expanding pattern. It is characterized by a pole (the point towards which the animal is heading, which forms the focus of outflow) and an increasing angular speed as the radial distance from the pole increases. The flow field, which is a reafference (von Holst and Mittelstaedt, 1950) for the flying animal, must be distinguished from other visual stimuli: specific objects in the visual field, for example, may or may not lead to context-specific intentional steering manoeuvres (approach, avoidance, landing, etc.), while stimuli signalling unintended deviations from a straight flight path must elicit compensatory steering to avoid disorientation or even a crash.

Involuntary deviations from course are mainly caused by wind turbulence or by the animal's own motor error. The visual movements produced by these deviations are mostly rotational, and visual interneurones sensitive to this input have been found in many groups of flying insects. The mechanisms underlying this sort of steering behaviour in locusts have been studied in detail (for a review, see Rowell, 1988). Large descending deviation detector neurones receive exteroceptive (e.g. from compound eyes, ocelli, wind-sensitive hairs) and proprioceptive (e.g. from neck receptor) signals (Simmons, 1980; Möhl and Bacon, 1983; Reichert *et al.* 1985; Rowell and Reichert, 1986; Hensler, 1988, 1989). Their outputs summate with rhythmic information from the flight oscillator and are applied to flight, neck and abdominal motor neurones, either directly or *via* intercalated thoracic interneurones (Reichert and Rowell, 1985; Baader, 1990*a*,*b*, 1991*b*; Rowell and Reichert, 1991; Rowell, 1991). Correctional ruddering of the hindlegs and abdomen and differential movement of the wings then follow and are accompanied by partially compensatory head movements.

The visual flow field is also known to be important for the orientation of flying insects. There is evidence that, for example, flying moths alter their lift and thrust when a spiral pattern rotates beneath them (Preiss and Kramer, 1983), and in flies certain geometrical parameters of patterns approaching the animal trigger a landing response (e.g. Perez De Talens and Taddei Ferretti, 1970; Wehrhahn *et al.* 1981; Wagner, 1982; Borst and Bahde, 1988). Neural elements responding to horizontal, progressive motion have been studied in flies (Chillemi and Taddei Ferretti, 1981; Hausen, 1982), in bees (De Voe *et al.* 1982; Ibbotson, 1991) and in dragonflies (Olberg, 1981*a*). No specialised translational movement detectors have been previously described in grasshoppers. The direction-sensitive neurones

previously described from locusts (Kien, 1974; Osorio, 1986; Rowell and Reichert, 1986; Rind, 1990*a*,*b*) respond primarily to visual effects of rotation, and not, so far as is known, to translation. Consequently, one of the questions that can be addressed is whether information about flow fields and about rotational movement is coded in the same descending neurones or in different subpopulations.

Locusts and other grasshoppers can fly at very high altitude (up to 2000 m) or as close as 1 m above ground (Uvarov, 1977). The flow fields affecting the eyes therefore have a very wide range of velocities. Even slow temporal patterns (angular speed of $0.1–50°\,s^{-1}$) resulting from wind drift are detected by high-flying locusts (Riley *et al.* 1988), leading to complex compensatory steering responses (Preiss and Gewecke, 1988).

This study reports the effects of fast flow field stimuli (simulating visual near-field conditions) on the fictive flight of locusts. It will be shown that flight activity is modulated to some extent by the progressive flow field. Additionally, some neurones that may be involved in these effects are described. A preliminary note has appeared previously (Baader, 1988).

Materials and methods

Preparation

Experiments were performed using adult *Locusta migratoria* (L.) of either sex obtained from laboratory culture or from a commercial supplier. The wings and legs were removed and the pterothorax was cut open along the dorsal midline. The animal was then pinned dorsal side up onto a support of balsa wood, leaving the head and the abdomen free to move. The gut was removed and either the connectives between the prothoracic and mesothoracic ganglia or the metathoracic ganglion itself were exposed and stabilized with a metal spoon. The positions of the head and the abdomen were monitored by means of capacitative transducers (Sandeman, 1968), the antennae of which were fixed with beeswax to the frons and to the fourth abdominal segment. This allowed the simultaneous registration of rolling of the head and of horizontal and vertical deflections of the abdomen. Fictive flight activity was monitored by inserting wire electrodes into the right and/or left direct depressor muscle m97 (mesothoracic first basalar muscle). The temperature in the laboratory was 20–23 °C during experiments.

Stimulation apparatus

The stimulation device could produce the visual effects of both rotation and translation and also provided a jet of non-laminar wind. Its construction and functional properties have been described in detail elsewhere (Baader, 1991*a*). In brief, the head of the animal was positioned in the centre of a hemi-ellipsoid formed by 380 green light-emitting diodes (LEDs). Periodic concentric patterns could be generated by activating circles of LEDs. In addition, the mechanical movement of the hemi-ellipsoid about the roll and yaw axes produced rotational stimuli. These simulated involuntary course deviations and induced optomotor

responses in the animals with amplitudes similar to those obtained previously with an artificial horizon (Rowell and Reichert, 1986).

The flow field was simulated by electronically moving the concentric pattern forwards or backwards over the hemisphere, generating visual contrast frequencies (CF) of up to 80 Hz. The contrast frequency was monitored by a photodiode. Contrast ($\Delta I/I$, where I is intensity) of the pattern was 0.84 and the maximum intensity was 400 mW m^{-2}, measured at the head of the animal when all LEDs were activated.

The flow field device produces not only the visual effect of translation but also a periodic modulation of the total light intensity reaching the retina (for explanation and discussion, see Baader, 1991*a*). This intensity component (flicker) stimulates many neurones that do not respond to translation *per se*. In this article, we attribute effects to the translational component only when they are directionally selective (i.e. occur only in response to progressive motion): the intensity modulation component is identical in both progressive and regressive modes.

Recording and anatomical visualisation

For physiological studies, intracellular recordings were made from the connectives between the prothoracic and mesothoracic ganglia and from the meso- and metathoracic ganglia. Thick-walled glass microelectrodes were filled with 5 % Lucifer Yellow dye in distilled water and backfilled with 0.1 mol l^{-1} lithium acetate. They had final resistances ranging from 80 to 200 MΩ. Data were stored on magnetic tape for subsequent analysis. After the recording, the dye was injected by negative direct current of up to 15 nA for 5–20 min. The ganglia were dissected, fixed in 4 % paraformaldehyde, dehydrated and cleared in methyl salicylate. Whole mounts were viewed under a fluorescence microscope and neurones were drawn directly or photographed and subsequently traced from colour slides.

Using Lucifer Yellow and a thoracic penetration site we were never able to stain the FF-sensitive descending neurone in more than the three thoracic ganglia. Attempts to find and fill the flow field neurone in the head ganglia were defeated by its sensitivity to dissection of this region. Preliminary attempts to display the cerebral anatomy of the neurone using Lucifer-labelled dextrins of medium molecular weight injected electrophoretically into the thoracic axon were also unsuccessful. We finally succeeded in repeatably filling the entire neurone from thoracic penetrations using a modification of the biocytin/avidin method of Horikawa and Armstrong (1988). The detailed procedure is given below.

The tips of thin-walled microelectrodes were filled with 5 % biocytin (Molecular Probes) in 0.5 mol l^{-1} KCl/50 mmol l^{-1} Tris base, pH 8.5. Resistance varied from 5 to 20 MΩ depending on the condition of the microelectrode after it had passed through the ganglion sheath. Biocytin was pressure-ejected (Picospritzer) using constant pressure of up to 0.8 MPa (approximately 8 atmospheres), sometimes assisted by hyperpolarising current pulses (4–6 nA, 500 ms, 1 Hz) to reduce clogging. The duration of successful fills varied from a few minutes to more than

1 h. Fixation was then delayed for 4 h to allow the biocytin to reach all parts of the neurone.

The ganglia were fixed in buffered 4 % paraformaldehyde (pH 7.5) for 2 h at room temperature and transferred to PBS (10 mmol l^{-1} PO_4^{3-}, 0.9 % NaCl, pH 7.5). After 1–7 days in the refrigerator the ganglia were immersed in 70 % ethanol (30–60 min at room temperature, approximately 23 °C) to remove lipids and endogenous peroxidase activity. After a further period of 1–4 days in PBS at 4 °C, the ganglia were incubated in avidin/horseradish peroxidase complex (Vectastain ABC Elite kit from Vector Laboratories) using 4 μl of solution A and 4 μl of solution B in 1 ml of PBS/1 % Tween 20. The incubation was carried out on a shaker in the refrigerator for 40 h to allow the reagent to reach the innermost parts of the ganglion. The ganglia were then rinsed in PBS/0.1 % Tween for 6 h and incubated for 1 h at 4 °C in 0.07 % diaminobenzidine in PBS/0.1 % Tween with 0.02 % $NiCl_2$ as intensifier. The colour reaction was carried out under visual control in 1 ml of PBS/0.1 % Tween to which was added 10 μl of 0.35 % H_2O_2, and took 5–15 min at room temperature. $NiCl_2$ was omitted from this step to avoid darkening the ganglion sheath. The preparation was then washed in PBS, dehydrated in an alcohol series and cleared in methyl salicylate. After viewing in whole mount and drawing, some preparations were embedded in paraffin and sectioned.

The terms ipsi- and contralateral are used in this article as perceived by the animal or with respect to the axon of the penetrated cell.

Results

Behavioural responses to flow field stimulation

In these experiments each animal's wings and legs were removed but the animal was otherwise left intact. The locust was then positioned in front of the flow field simulator. Stimulation with wind at more than 2 m s^{-1} usually induced fictive flight. The duration of the flight sequences varied between several seconds and 4 min. Fig. 1A shows a typical example. The animal has stopped flying after a wind-triggered flight sequence (not shown); when progressive flow field stimuli (CF=5 Hz) are given, flight is reinitiated. The head and abdomen are moved into the flight position, i.e. the head is moved somewhat forward and downward and the abdomen is lifted and positioned horizontally. Both vibrate slightly in flight rhythm. Flight activity, induced by the flow field and simultaneous wind, can be terminated either by switching off the pattern or by reversing its direction: the latter result indicates that flight activity is dependent on the translational component of the visual stimulus (see Materials and methods). Regressive flow fields result in two types of behaviour (Fig. 1A): either the animals do not start flying at all or the flight burst stops after a few cycles. In some preparations, progressive FF stimulation in the absence of wind is sufficient to elicit flight behaviour. Initiation and maintenance of flight activity by the FF is dependent upon the contrast frequency of the progressive moving stimulus. The strongest

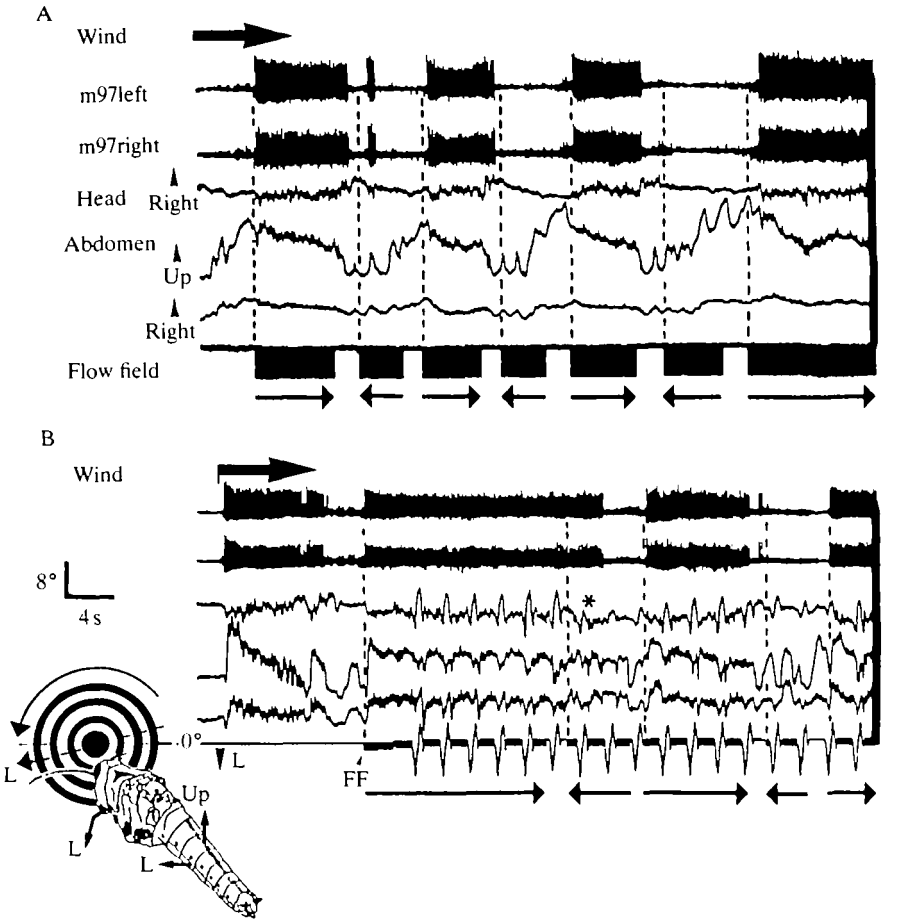


Fig. 1. Fictive flight activity of tethered locusts in the flow field, monitored as activity of the right and left mesothoracic first basalar (m97) muscles (top traces). (A) A flight sequence is triggered by progressive pattern motion (contrast frequency CF=5 Hz, spatial period λ=42°, arrows under the flow field trace pointing right). Regressive motion (arrows pointing left) induces a short burst of muscle spikes or no response. During flight, the abdomen is lifted and moved horizontally. It makes ventilatory movements when the animal is not flying. (B) Simultaneous flow fields and simulated yaw and roll. Flight is initiated by the onset of frontal wind (vertical arrowhead beneath bottom trace) and subsequently by progressive flow fields, as in A. The bottom trace shows the flow field as in A (note reduced vertical scale) and also sinusoidal movements of the horizon around its axes. These, consisting of first 25° to the left (L) and counterclockwise, then 50° to the right and clockwise, and finally back to the horizontal position (=0°), simulate deviations of the animal. It responds with compensatory head turns and lateral abdomen bending during flight sequences induced by the flow field (FF). The behaviour is diminished when the direction of the pattern is reversed (asterisk) or when the locust does not fly. Vertical bar, 8° for head and abdomen movement. The traces are in the same order as in A.

flight sequences are achieved with contrast frequencies ranging from 2 to 10 Hz. Patterns with spatial angular periods (λ) of 33° or 42° both produce the sort of effects described above and are equally effective, but broad single stripes (λ=85°) trigger an entirely distinct behaviour: the head and abdomen jerk up and down in phase with each stripe, the legs are retracted in the same rhythm, and flight becomes erratic and stops.

The hemisphere of LEDs provides a visual pattern sufficient to elicit correctional steering responses when the whole environment is rotated, regardless of whether FFs are present or not. In Fig. 1B an 8 s flight sequence is initiated by wind alone. After this sequence, flight is triggered again by the progressive FF (CF=5 Hz) and then simultaneous yaw and roll deviations are simulated by rotating the whole hemisphere ±25° about both the respective axes. The locust responds with tracking head movements and abdominal ruddering. The latter are neither potentiated nor diminished significantly by the FF. However, after the FF has been turned off or reversed (e.g. at the asterisk in Fig. 1B), flight activity ceases. Without flight activity, movements of the head become very small, as shown previously (e.g. Taylor, 1981); they increase again when flight is reinitiated.

Flying locusts adjust their wingbeat frequency to the changing contrast frequency of a flow field. The average wingbeat frequency recorded in the left basalar forewing muscle (m97) during six flight sequences of two animals is shown in Fig. 2A. Since the animals had different inherent wingbeat frequencies, the maximum values of each sequence are normalized to an arbitrary value of 15 Hz.

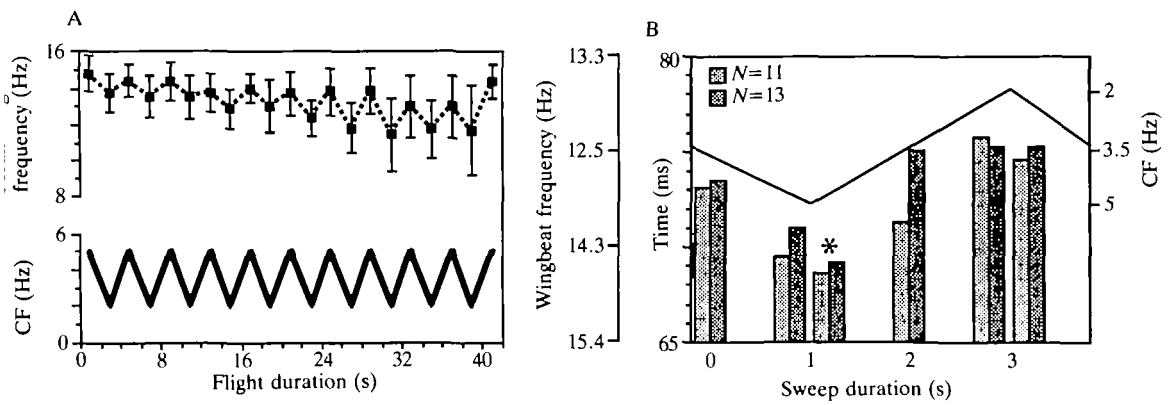


Fig. 2. (A) Modulation of wingbeat frequency (monitored in depressor muscle m97, upper trace) by a changing contrast frequency of the progressive flow field (CF=2–5 Hz, λ=42°, lower trace). Flight activity was measured at CF=2 Hz and 5 Hz in each stimulus period. Mean values±S.D. of six flight sequences for each of two animals. (B) Activity in flight muscle m97, in two animals, measured as time between successive spikes, at different contrast frequencies of the pattern. Each of the two types of bar represents one animal. The two flight sequences contained 11 and 13 stimulus periods. The spike rate follows the change of pattern velocity as in A, except for the point where CF decreases (asterisk).

The contrast frequency of the progressive flow field is modulated between 2 and 5 Hz by a triangular function (period length 4 s). Wingbeat frequency was counted successively within each second. The average frequency diminishes with time, but is also modulated by approximately ±1 Hz according to the changing contrast frequency of the flow field; a high contrast frequency produces a high wingbeat frequency and *vice versa*. This effect increases with the duration of the performed flight sequences. In Fig. 2B the flight sequences of two animals are analyzed in more detail. The intervals between the spikes were counted and averaged within a 400 ms window directly before and after the flow field speed increased and decreased (it varied between extreme values of 2 and 5 Hz) and, as a control, spikes were counted in a 400 ms window at an intermediate value (3.5 Hz). For convenience, the corresponding wingbeat frequency is shown on a parallel ordinate. As in Fig. 2A, in both animals the interval between two consecutive spikes shortens with an increasing stimulus velocity.

Interestingly, when the pattern slows down, the flight frequency unexpectedly increases over the next 400 ms (asterisk in Fig. 2B) before it too diminishes. A comparable effect is not seen when the pattern accelerates: flight motor activity follows the modulation immediately. These results indicate that locusts tend to adjust their wingbeat frequency to a gradually changing flow field, but abrupt decelerations are initially counteracted. This phenomenon will be returned to in the Discussion.

Characterization of a flow-field-sensitive interneurone

We have recorded and filled at least two different protocerebral descending neurones that respond selectively and positively to progressive flow fields (FFDN1 and FFDN2). Though their cerebral anatomy is similar, they have very different thoracic morphologies, FFDN1 being bilateral and FFDN2 strictly unilateral in its projections. FFDN1 has been relatively intensively studied and its characterization is given below.

Morphology and responses to rotational and static inputs

The neurone FFDN1 was recorded and dye-filled by all three authors independently in a total of 14 different preparations and showed only little variation between individuals. Its anatomy is shown in Fig. 3. The soma and an extensive unilateral network of dendrites lie dorsally in the anterior protocerebrum. The zone of dendritic branching is confined to the ispilateral protocerebrum. The largest dendrite runs to the tritocerebrum and crosses the axon ventrally. The axon descends in the ipsilateral connective and runs dorsally and superficially in the dorsal medial tract of the thoracic ganglia (Tyrer and Gregory, 1982; the revision by Pflüger *et al.* 1988, shows an anatomy closer to that observed by us). The axon usually extends into the abdominal cord, but appears not to reach the first free abdominal ganglion (i.e. the fourth abdominal neuromere). It passes through the suboesophageal ganglion with few branches but has a characteristic and complex bilateral branching pattern in the dorsal flight neuropile of all three thoracic

ganglia and in the first three abdominal neuromeres of the metathoracic ganglion. There are 0–1 major contralateral projections in the suboesophageal ganglion, 2 in the prothoracic, 2–3 in the mesothoracic, and 5–6 in the fused metathoracic ganglion. The largest contralateral projection in the mesothoracic ganglion runs in dorsal commissure II (Tyrer and Gregory, 1982). All processes arising from the axon lie laterally or ventrally to it.

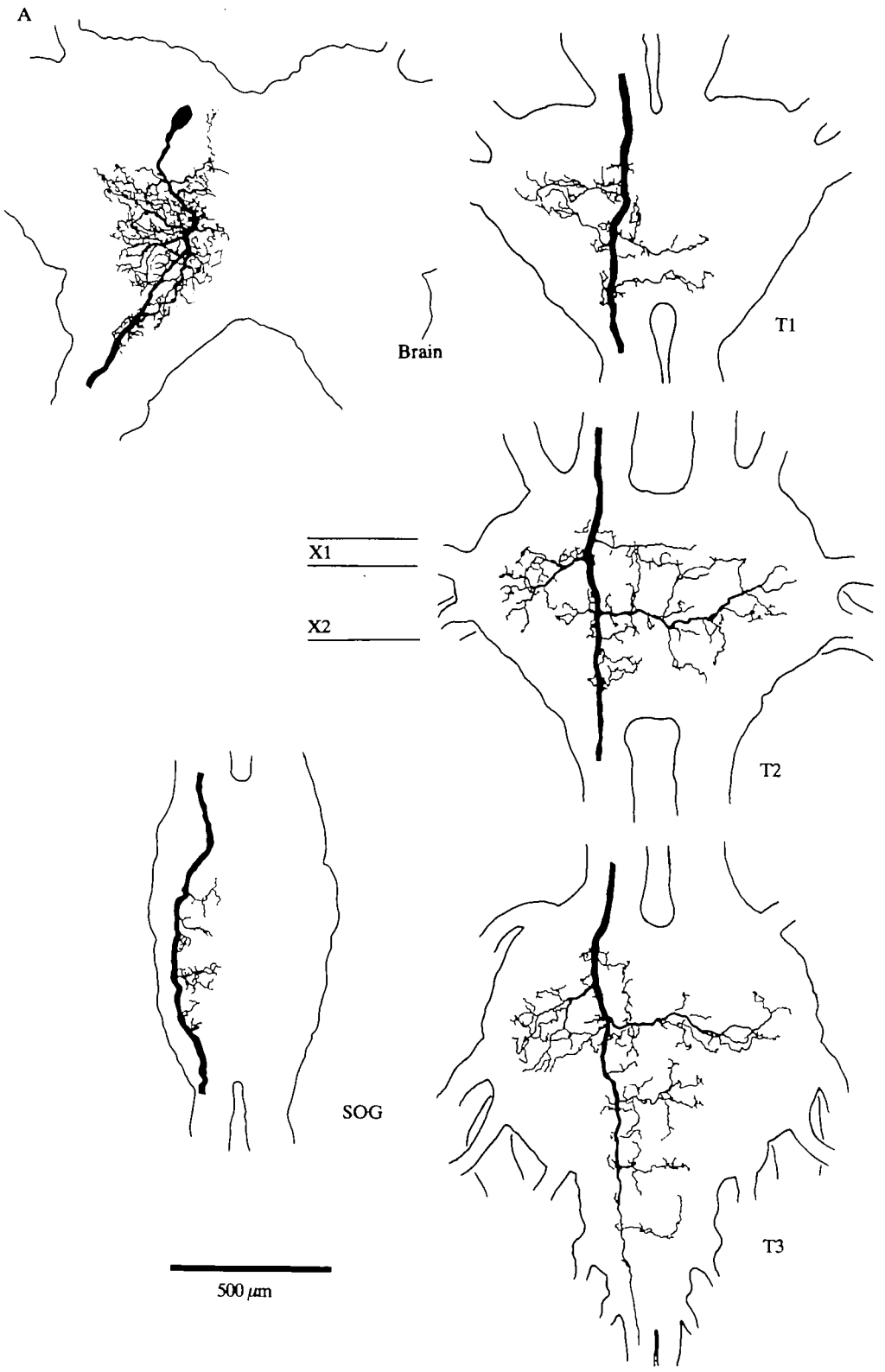
The neurone responds to stationary whole-field light pulses with off-spikes. The same kind of response can often be obtained when the ocelli are selectively stimulated with 1 mm diameter light guides attached to green LEDs (for further details of the ocellar stimulation method see Rowell and Reichert, 1986). In the latter case, the off-spikes occur with a relatively constant latency (see Discussion). What at first sight appear to be occasional light-on spikes prove, on analysis, to have no fixed temporal relationship to the stimulus and are therefore probably spontaneous activity. The ocellar response is rather weak and variable: a reliable spiking response usually requires simultaneous stimulation of all three ocelli and is only seen after some minutes of adaptation to dim light. A substantial minority of individuals give no response at all to any combination of ocellar stimuli. Stimulation of single ocelli rarely produces a spike in FFDN1, but the median ocellus is the most likely to do so.

FFDN1 responds only weakly or not at all to yaw or roll deviations of the animal. In Fig. 4 the average spike rate during visually simulated turns was calculated every 0.2 s. The black bars show the mean response of a representative FFDN1 during five horizon movements in each direction; similar responses were seen in five other preparations. Slight excitation at the onset of horizon movement is not directional (compare upper and lower diagrams). In one preparation only (hatched bars), the response to contralateral deviations was stronger than that to ipsilateral deviations. Unfortunately, the design of the flow field apparatus, which was essential for the physiological identification of the neurone, did not allow simulated pitch to be tested.

Spontaneous spikes occur only occasionally in FFDN1. Stimulation with frontal wind, however, results in a tonic excitation that is further enhanced when the animal starts flying (Fig. 5). The response to wind is dependent on both direction and intensity (Fig. 6). Wind from the ipsilateral side tends to inhibit the response, while that from the contralateral side tends to increase it in some preparations (Fig. 6A). The example in Fig. 6B shows the spike activity of one FFDN1 at different wind speeds. Similar responses were seen in three other animals. The mean activity of five cells at constant wind speed ($3\,m\,s^{-1}$) is 6.8 ± 1.6 Hz ($\pm$S.D.). In all cases it increases with increasing wind speed up to $4\,m\,s^{-1}$. Above $4\,m\,s^{-1}$ the responses saturate or, in three of the five neurones tested in this manner, decrease. None of the cells responds to acoustic stimuli.

Responses to the visual flow field

FFDN1 is tonically excited by progressive FFs (Fig. 7A, arrows pointing to the right). In contrast, regressive motion is not effective, indicating that the response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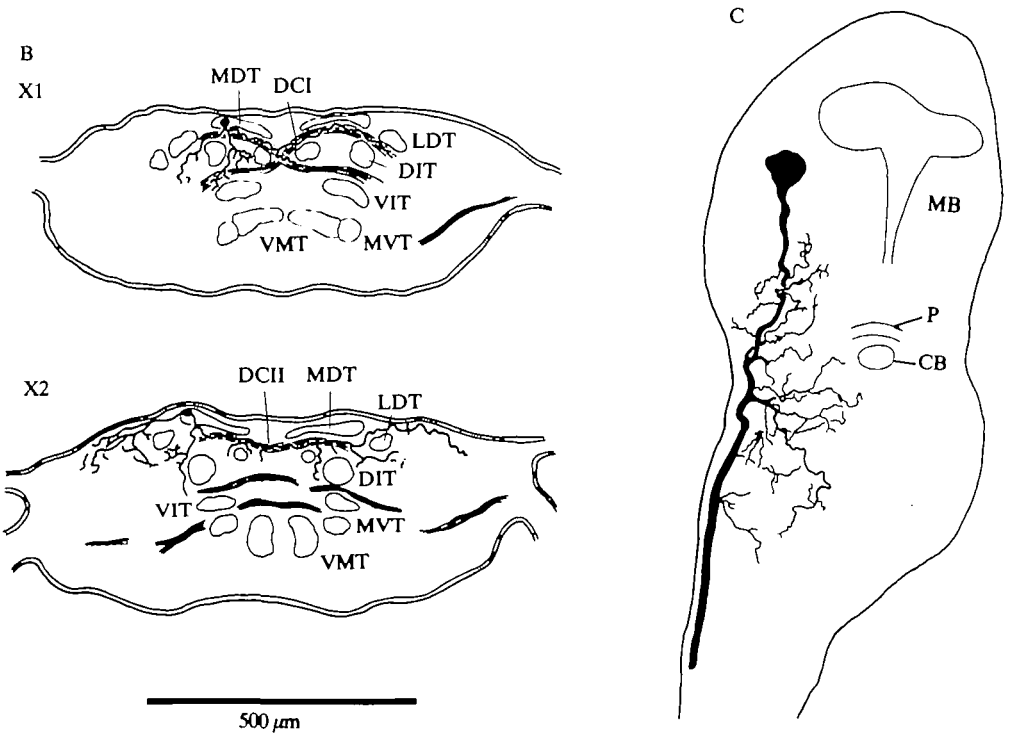

Fig. 3. (A–C) Morphology of FFDN1. (A) Structure of FFDN from the dorsal aspect. The drawing is made from a single biocytin fill. X1 and X2 indicate the zones of the mesothoracic ganglion from which the cross sections shown in B were reconstructed. (B) Transverse sections of a mesothoracic ganglion from a different preparation to show the course of the main dendrites. X1 is based on 6, and X2 on 14, 15 μm serial sections. Labelling is according to Tyrer and Gregory (1982). MDT, medial dorsal tract; DCI, DCII, dorsal commissures I and II; LDT, lateral dorsal tract; DIT, dorsal intermediate tract; VIT, ventral intermediate tract; MVT, medial ventral tract; VMT, ventral medial tract; MDT, medial dorsal tract. (C) Whole-mount drawing of the brain projection of the preparation shown in A, seen after sagittal section. The light profiles indicate the approximate positions of central body (CB), pons (P) and mushroom body calyx (MB). Their positions were determined by comparing preparation C with stained serial sagittal sections of the brain. SOG, suboesophageal ganglion; T1, T2, T3, pro-, meso- and metathoracic ganglia, respectively.

is not simply elicited by the intensity modulation component of the moving pattern. In Fig. 7B spike activity of the FFDN is evaluated during a 50 s stimulation with a progressive flow field (CF=9 Hz). The response is shown from the beginning of FF stimulation. The response fluctuates but, in general, adaptation is weak. When the left and the right halves of the visual field are stimulated successively (Fig. 8, fourth and fifth bars), no significant change in the strength of the response can be recorded, indicating that the cell receives equal binocular inputs. However, in the preparation shown in Fig. 8 (one of three

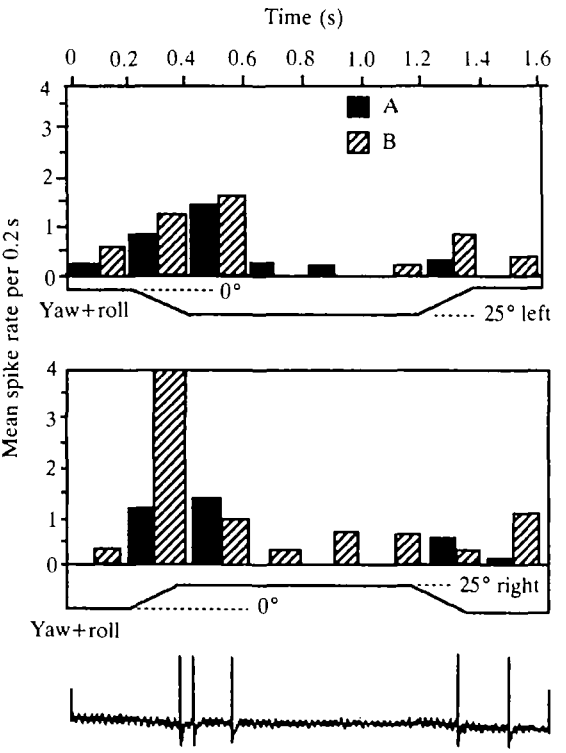

Fig. 4. Responses of left-side FFDN1 neurones to simulation of yaw and roll (±25°) to the ipsilateral (upper diagram) and contralateral (lower diagram) sides. Averaged spike frequency, calculated every 0.2 s, N=5 trials. (A) Example of the response of one neurone representing the usual response of FFDN1 neurones (black bars); that is, weak excitation in response to movement of the horizon in either direction. (B) The only example seen that showed a preference for contralateral deviations. The oscilloscope trace at the bottom shows a single representative response. Time scale as in the diagrams; the action potentials (approximately 70 mV) have been retouched.

tested) a significant difference (t-test, $P<0.05$) between the responses to dorsal and ventral stimulation could be observed (see second and third bars in Fig. 8). The animal was successively stimulated with the patterns indicated from left to right. Ventral FF (second bar) induces a somewhat stronger response than that to whole-field FF (first and last bars), while the response to dorsal FF stimulation (third bar) is the weakest.

The amplitude of the FFDN response is a function of the contrast frequency of the pattern. In Fig. 9A the CF was increased gradually, eliciting spikes in the neurone up to a certain upper cut-off frequency. Fig. 9B illustrates this effect for six individual preparations. FFDN is not sensitive to slow visual patterns with the test apparatus used here ($\leq$1 Hz at CF=42°s^{-1}, but see Discussion) but responds strongly to faster FFs up to a value that varies with individuals between 10 and

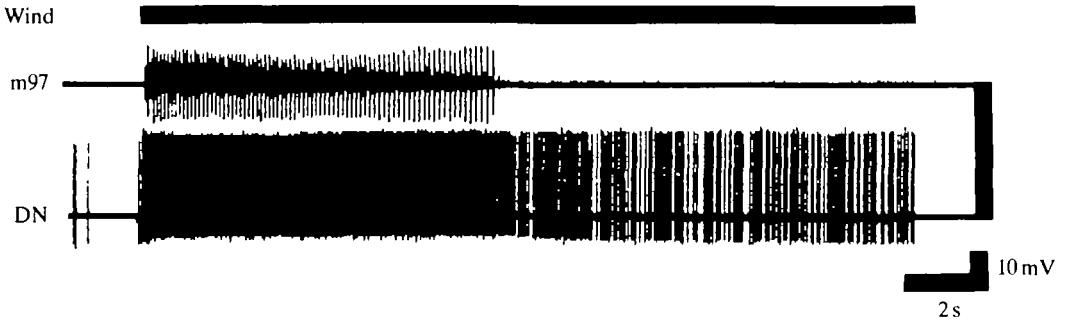

Fig. 5. Spike activity in FFDN1 (DN) during stimulation with frontal wind at $3\,m\,s^{-1}$ and during flight (m97). Both excite the cell tonically.

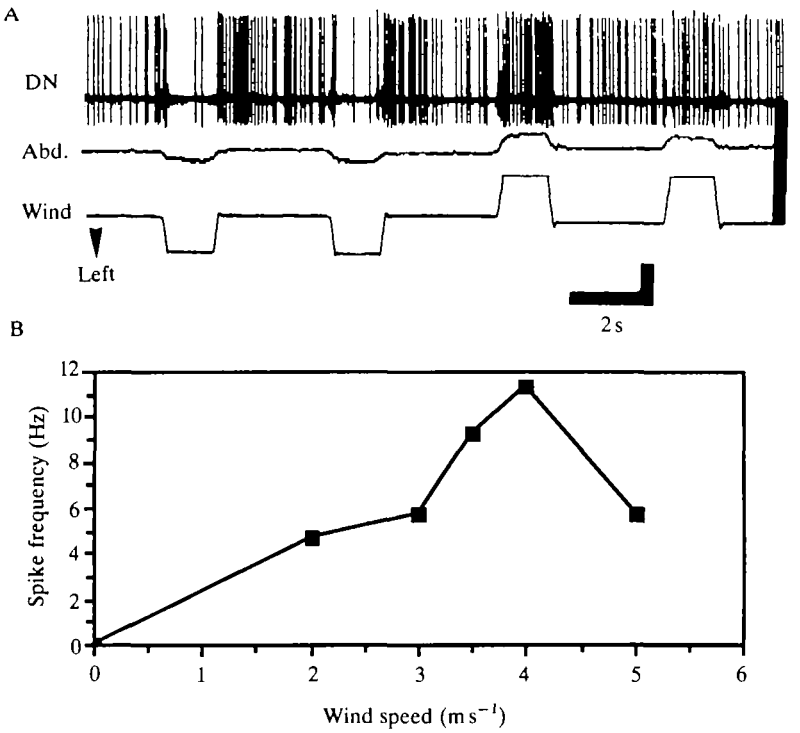

Fig. 6. (A) Directionality of the wind response: FFDN1 (DN) is less excited by wind coming from the ipsilateral side (with respect to the axon – in this example, from the left side) and more excited by contralateral wind (the latter effect seen in only three of eight preparations). The turning wind jet elicits abdominal ruddering (Abd.). Scale bar, 2 s, 10 mV, 9° for abdomen, 18° for wind jet. (B) Typical dependence on wind speed of the FFDN1 response (one animal, two sequences averaged), showing a maximum value at $4\,m\,s^{-1}$ and a subsequent decrease (seen in three out of five tested animals) in response to stronger wind.

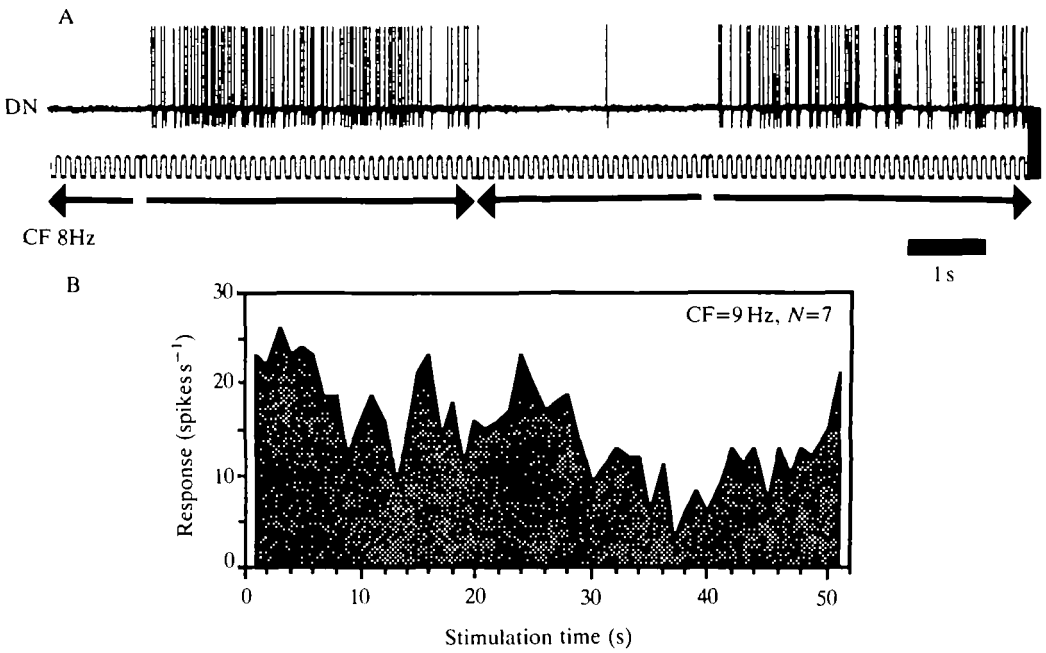

Fig. 7. (A) Response of FFDN1 (DN) to flow field stimuli (CF=8 Hz, λ=42°, continuous recording): progressive flow (arrow pointing right) produces tonic excitation, regressive flow inhibits it. (B) A continuous progressive flow field stimulus (CF=9 Hz, λ=42°) produces only weak adaptation (spikes counted each second of stimulation, one animal).

21 Hz. The response is roughly proportional to the logarithm of CF over a range of about 1–10 Hz. This is demonstrated in Fig. 10 where the sinusoidal and triangular curves represent the gradually changing CF, while the bars represent the average discharge frequency during 12 and 7 stimulus presentations, respectively. In the experiment shown in the upper graph, simultaneous wind was given at constant speed of 3 m s^{-1}. Only when the CF decelerates does the response not follow immediately (asterisk). At this point, the spike rate increases temporarily, although the CF has already passed its maximum value. In the lower graph, an FFDN was stimulated in a different preparation and without wind. Again there is an increase in discharge frequency when the CF decelerates. This behaviour is very similar to that already seen for flight frequency in Fig. 2B, and will be treated in the Discussion.

Activity in FFDN1 can be directly related to the animal's behaviour by stimulating the cell electrically. Owing to the size of the neurone, this was accomplished in only three preparations and only after a long preceding hyperpolarization. In one animal (Fig. 11) this stimulation led to an upward movement of the abdomen and to an inhibition of activity in neck muscle m59, a

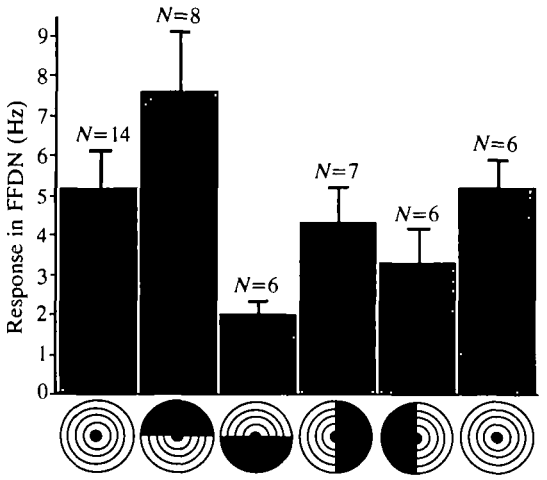

Fig. 8. Responses of one FFDN1 when selected areas of the hemi-ellipsoid are activated (see symbols: unactivated parts are dark). Columns represent mean neurone activity (+S.D.) for N stimulation sequences, each lasting 1 s. The leftmost and rightmost columns show activity of the cell at the beginning and the end of the experiment (controls). The neurone prefers ventral stimulation (second column; the difference between this and the third column is statistically significant) and shows no significant difference in activity when only the left or the right half of the visual field is stimulated (fourth and fifth columns).

muscle that is known to lift the head (Shepeard, 1974). Additionally, during two periods of stimulation, spikes were recorded in the flight muscle m97 (not shown), indicating a possible input of FFDN1 to the flight motor.

Thoracic interneurones also respond to progressive flow fields

Thoracic premotor interneurones are the functional links between descending deviation detector neurones and flight motor neurones (Reichert and Rowell, 1986). A similar pathway is likely for the flow field detectors. At least two thoracic neurones with properties suggesting that they are (a) postsynaptic to an FFDN and (b) presynaptic to elements of the flight circuitry have been recorded and dye-filled. One is a metathoracic 500-series interneurone, which projects to the mesothoracic ganglion, the other is a prothoracic 300-series neurone which projects to the metathoracic ganglion. In the interests of brevity these neurones are not described in detail. They do, however, indicate that the expected neurones, which could transfer FFDN information to the flight system, are indeed present in the thoracic ganglia. Other thoracic interneurones, though not directly postsynaptic to FFDNs, are either excited or inhibited by progressive flow field stimuli.

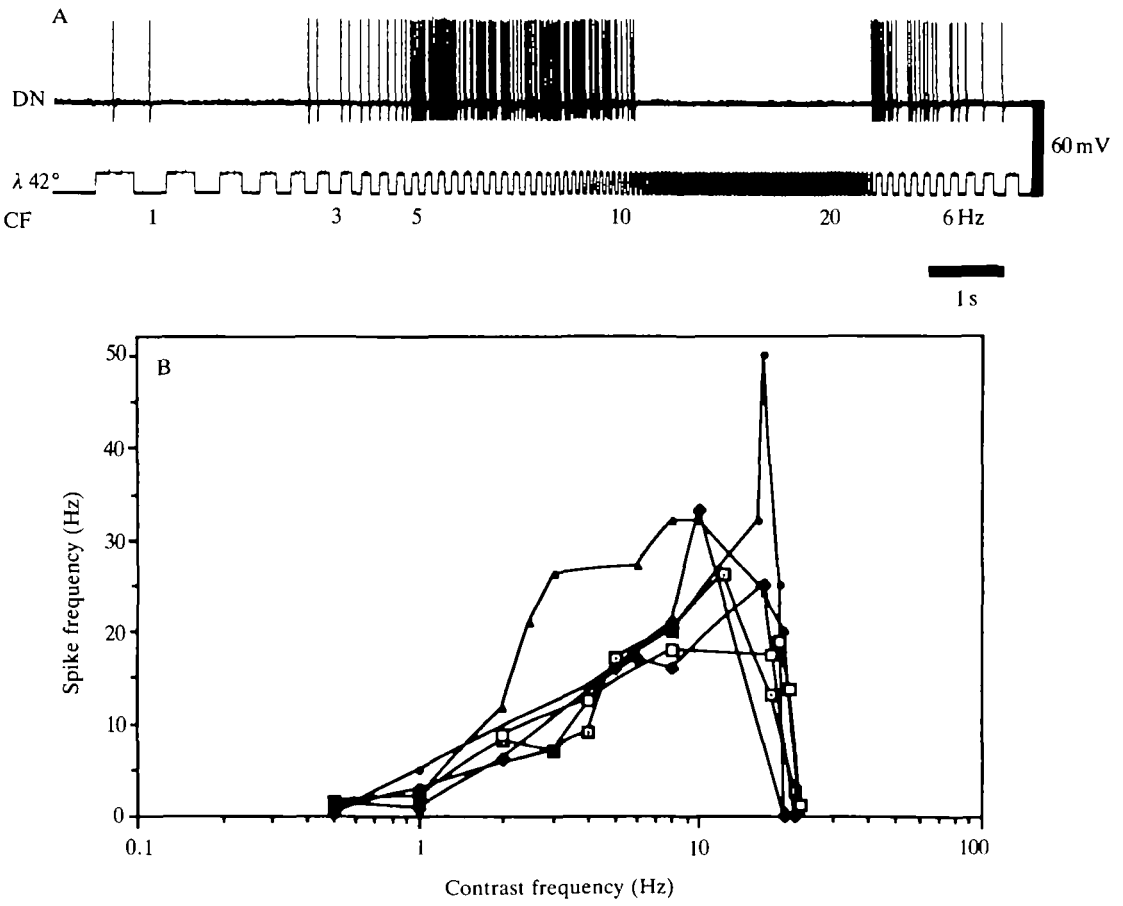

Fig. 9. FFDN1 codes for the changing contrast frequency of the flow field. (A) An example of a single cell (DN), the response of which drops off at about 13 Hz but reappears at once when the contrast frequency (CF) is lowered again. (B) Frequency response curves of six FFDN1 neurones (one trial for each neurone) responding to increasing frequencies up to their upper cut-off frequencies.

Discussion

The efficacy of the flow field pattern

Motion of the LED stripes elicits behavioural responses when the CF is within an optimum range of about 1–10 Hz, regardless of spatial period over the range λ=33–42°. Progressive patterns of this frequency are capable of eliciting flight (Fig. 1A) and shifting the wingbeat frequency (Fig. 2). This optimum range is in agreement with optomotor experiments (Robert, 1988), where tethered flying locusts showed optimal responses for similar CFs (up to 14 Hz) which were also roughly independent of spatial period between λ=20° and 50°. In the experiments of the present study, slow-motion patterns (<1 Hz) are not effective. This is due to the spatial separation of the single LEDs: jumping stripes do not provide the

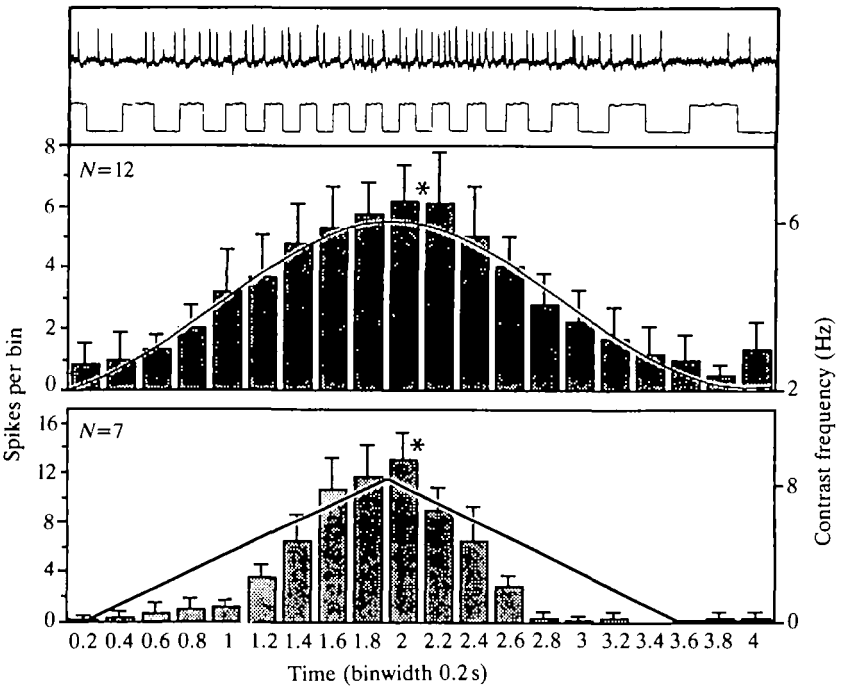

Fig. 10. Dependence on contrast frequency of FFDN1 responses in two preparations. The mean number of spikes (+S.D.) is calculated every 0.2 s. Upper graph, spike rate (bars) is proportional to CF (line: 2–7 Hz, λ=42°) which is paired with a constant wind at 3 m s^{-1}. Note that the response ceases to follow the stimulus at the point where CF slows down from its maximum value of 6 Hz (asterisk), but increases immediately when the pattern accelerates from its minimum value of 2 Hz. The panel above the upper graph shows one specimen record of FFDN1 (upper trace) and contrast frequency (lower trace); the time scale is the same as for the graph, and the action potentials are approximately 20 mV in amplitude. Without wind (lower graph, different animal) spike activity is not proportional to CF at lower values of the latter, but the same effect can be seen at the upper reversal point of the CF (asterisk).

illusion of self-movement. The same loss of responsiveness is also seen in FFDN1 (Fig. 9). In contrast, CFs of 1 Hz and higher provide FFDN and the whole animal with the illusion of a continuously moving flow field. All this implies that the lower CF limit found here is an artefact of the apparatus: the real lower cut-off frequency of FFDNs in general may be well below this value, since high-flying locusts are able to detect the speed of ground patterns down to 10^{-2}°s^{-1} (Riley *et al.* 1988).

When the CF exceeds 10 Hz flight is interrupted. This could imply that the animal has an idea 'about what the visual consequence of its intended action is going to be', as Collett (1980) has put it. The animal's expectation might, for example, be coded in a second FF-sensitive pathway, having an inhibitory effect on the flight oscillator. The activity of this and the excitatory FFDN pathway could be continuously compared and would finally stop flight at the appropriate

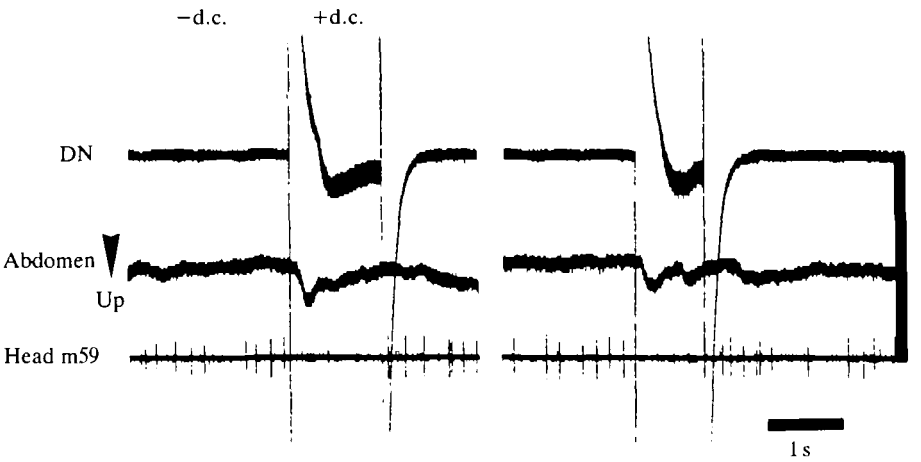

Fig. 11. Stimulation of FFDN1 (DN) with positive current (+d.c.) after a long period of hyperpolarization (−d.c.). The abdomen moves upwards and neck muscle activity (Head m59) is inhibited; there is also occasional flight activity in m97 (not shown).

frequency. The FF detectors are still functional at this speed (10 Hz), their upper cut-off frequency lying between this value and 21 Hz (Fig. 9), showing that the cessation of flight is not simply due to their saturation.

Optomotor responses are not compromised by the motion of the flow field (Fig. 1B). This has already been shown for the fly *Syritta pipiens*, which uses certain parameters in its visual field to distinguish involuntary course deviations from the visual flow field (Collett, 1980). The flying animal receives a stationary retinal image at the point that sees the focus of outflow. Image motion through the focus of the FF is detected as deviation and is properly corrected. In addition, another strategy used both by moths (Preiss, 1987) and by man (Warren and Hannon, 1988) is to detect unintended and self-generated movements as motion parallax of the surroundings. As will now be shown, the results of this study imply that at least the former strategy could also be used by locusts.

The longitudinal body axis of flying locusts is often not aligned with their actual flight path through the air or with their ground course (Rainey, 1963). This has two consequences: (1) the pole of the flow field is shifted away from the frontal parts of the retinae and (2) the animal, which otherwise perceives exclusively frontal *Fahrwind*, apart from the air currents caused by its wing movements (Horsmann *et al.* 1983), now experiences a more lateral air flow. The visual response of FFDN1 is not altered when the pole of the flow field moves laterally, but lateral wind input modulates the activity in the neurone; its spike frequency decreases when the wind comes from the ipsilateral side (Fig. 6). In principle, the comparison of left and right FFDN1 activity could provide the insect with information about its orientation relative to the direction of movement. There is, however, no evidence that the information is used in this way.

The regulation of forward flight

It has been shown both during free flight and in laboratory studies that the flight speed of locusts is correlated with wingbeat frequency (Baker *et al.* 1981). This investigation presents evidence that the wingbeat frequency is to a certain degree adjusted to the contrast frequency of the FF (Fig. 2A). This indicates, in principle, that the animal uses flow field information for speed control.

In this context it is of considerable interest that the wingbeat frequency does not immediately follow the CF when the latter is suddenly decelerated (Fig. 2B), but instead it is temporarily elevated. A possible functional explanation of this could be that the animal reacts to the perceived deceleration by speeding up, in an attempt to compensate. Why is the response transitory? Presumably because under our open-loop experimental conditions no feedback information was available to the animal, unlike what would happen in nature. At the lower reversal point of the stimulus velocity (slower to faster) the locust responds immediately to the increasing pattern speed. For two reasons these results cannot be interpreted as simple neuronal delays: the effects last up to 400 ms after their respective causes and they are different at the two CF reversal points. A comparable compensatory activity for the upper velocity reversal point of a changing flow field pattern can also be seen in FFDN1 (Fig. 10).

Further evidence for regulatory activity is seen when the direction of flow was suddenly reversed during progressive flow field stimulation: flight initially speeds up to correct for the obvious error, and then, presumably since no adequate feedback signal appears, ceases.

Flight orientation or landing response

A pattern very similar to the one used in this study leads to a distinctive behaviour in flies (Goodman, 1960) and bugs (Coggshall, 1972): visual gratings moved to simulate progressive motion can elicit a landing response instead of continued flight. The original hypothesis that the landing response of the fly is driven by the flow field (Eckert, 1982; Wagner, 1982) was somewhat modified by the findings of Borst and Bahde (1988), who suggested that the landing response is elicited by the activity of direction-sensitive movement detectors which integrate the perceived motion spatio-temporally. Some of these movement detectors are known to be excited by front-to-back stimuli and inhibited by back-to-front stimuli (Wehrhahn *et al.* 1981). It is conceivable that the same visual detectors registering progressive motion are involved in both the landing response and the maintenance of flight in flies (and in locusts, if a similar perception system is assumed). One critical parameter for triggering the landing response in flies is the change of expansion speed of the progressing pattern (Wagner, 1982); this must be high enough and occupy a certain area of the animal's retina. The same mechanism may well exist in the locust, where motion of very large patterns (e.g. those subtending a visual angle of 90°) reliably elicits extension of the front legs and sometimes stops flight, whereas smaller gratings do not.

The identity of FFDN1

FFDN1 displays many physiological similarities (relatively high conduction velocity, spiking response to ocellar, and especially medial ocellar, off-stimuli, tonic response to wind, absence of directional response to visual roll and yaw) with a previously described large interneurone, the deviation detector neurone DNM (Rowell and Reichert, 1986), though DNM (as then described) responded best to wind coming from above rather then from the ipsilateral side. The anatomy of DNM (Griss and Rowell, 1986) is also extremely similar to that of FFDN1. Either the two cells are morphological 'twins' (which are of frequent occurrence in the insect CNS, usually shown by inadvertent double fills – for examples, see Rowell and Reichert, 1991) and of rather similar physiology, or they are the same cell. It has been surprisingly difficult to decide which of these alternatives is true.

Physiological arguments

The original experiments on DNM (Rowell and Reichert, 1986) did not include stimulation with flow fields (which elicit a characteristic response from FFDN1) and our current apparatus unfortunately precludes testing FFDN1 with pitch stimuli (which elicit a characteristic response from DNM). Subsequently we have tested five neurones fulfilling the normal ocellar criteria for DNM with the flow field: all responded to the flicker frequency of the flow field device, but none showed any preference for progressive flow fields, as FFDN1 does. Another possible physiological criterion lies in the ocellar off-response. Of 10 FFDN1 neurones (defined by their directionally selective response to progressive flow-fields) in which the response to all three ocelli has been tested, four gave no ocellar response at all and six responded relatively reliably to the simultaneous stimulation of all three ocelli (but only irregularly to the median ocellus alone), with modal latencies (normalised to 25 °C, for details, see Rowell and Reichert, 1986) of 35–45 ms and with considerable scatter. In contrast, all five DNM units mentioned above (showing no preference for a progressive flow field) gave a reliable response to stimulation of the median ocellus alone, with corrected latencies of 24–32 ms and virtually no scatter. All these results suggest two different neurones. However, electrical stimulation of FFDN raises some doubts. Stimulation of single deviation detectors usually elicits steering behaviour appropriate to correct the deviation that the DN signals (see Hensler and Rowell, 1990). DNM has not been tested in this way, but its sensitivity to pitch-down would suggest that it should result in the abdomen being raised and the head lowered. This is indeed what is seen when FFDN is electrically stimulated (Fig. 11).

Anatomical arguments

If DNM and FFDN are distinct neurones, it should be possible, in principle, to record and fill both in the same hemiganglion of the same preparation. This has not so far been achieved. In one preparation the electrode indeed passed (accidentally!) from an axon with the physiological characteristics of FFDN to an

immediately neighbouring axon with the characteristics of DNM, both as defined above but, unfortunately, neither recording was held long enough to fill with dye. We have also attempted to dye-fill all descending axons found in a single hemiganglion giving a response to stimulation of the medial ocellus on the grounds that FFDN1 responds to this stimulus in at least some preparations and DNM always does. If FFDN1 and DNM are different, one might expect two similar neurones to be filled, at least in some preparations, but this has not happened so far. However, Lucifer Yellow was used in these experiments, and this tends to diffuse out of filled neurones if fixation is delayed for some hours while the second unit is sought and recorded.

On balance, the evidence suggests that FFDN1 and DNM are physiologically distinct neurones of closely similar morphology, but the alternative explanation, that there is a single neurone with variable properties that are distributed bimodally, cannot be rigorously excluded by our experiments.

It is probably not a coincidence that FFDN1 appears to be very similar in architecture and probably closely related to DNM. The self-movement detectors of the locust, including DNM (e.g. Rowell and Reichert, 1986) and of the dragonfly (Olberg, 1981*a*,*b*), both of which respond to rotational stimuli, share the largest number of physiological properties with the FFDNs of this study. Like them, the self-movement detectors are not responsive to small targets, show strong responses to horizontal pattern motion with only little adaptation, and drive or influence wing movements of the animal. Additionally, wind is signalled by these cells.

The flow field neurones in insects

The flow field detectors described here have analogues, or possibly homologues, in other insect species. There is indirect evidence that they exist in *Drosophila melanogaster*, where bulk activity in the connectives is enhanced by a front-to-back moving pattern and inhibited by regressive motion (Hengstenberg, 1973). In *Musca domestica*, fibres reporting progressive motion and light-off stimuli were recorded, as well as back-to-front-sensitive light-on units (Chillemi and Taddei Ferretti, 1981). Other neurones could also be involved in flow field detection: horizontal cells of the lobula plate of *Calliphora* are sensitive to gratings (presented on both sides of the animals) that simulate progressive motion of CF=2–5 Hz (Hausen, 1982). Since the present article was first submitted, Ibbottson (1991) has described a descending neurone sensitive to progressive flow fields in the honeybee. This neurone is physiologically similar to FFDN1, but differs in morphology from both FFDN1 and FFDN2, having a contralateral soma and innervating only the ipsilateral neuropiles of the thoracic ganglia.

These examples show that neurones carrying flow field signals to the thoracic motor centres are a significant pathway in many insect species. In the locust they are capable of regulating flight activity by monitoring the motion of surroundings caused by the movement of the animal and may work independently from those

neuronal channels that report unintended rotational deviation from a straight course.

We are grateful to our Basel colleagues for discussion and for reading previous drafts of this article, and to P. Wehrli, D. Vonlanthen and I. Singh for technical assistance. Supported by a grant of the Swiss Nationalfonds to C.H.F.R.

References

BAADER, A. (1988). Activity of neck motor neurones and flow-field modulated interneurones in flying locusts. In *Sense Organs: Interfaces between Environment and Behaviour* (Proc. 16th Göttingen Neurobiology Conference) (ed. N. Elsner and F. G. Barth), p. 121. Stuttgart, New York: Thieme Verlag.

BAADER, A. (1990*a*). The posture of the abdomen during locust flight: regulation by steering and ventilatory interneurones. *J. exp. Biol.* **151**, 109–131.

BAADER, A. (1990*b*). An ascending visual neural pathway in locusts. *Naturwissenschaften* **77**, 338–340.

BAADER, A. (1991*a*). Simulation of self-motion in tethered flying insects: an optical flow field for locusts. *J. Neurosci. Meth.* **38**, 193–199.

BAADER, A. (1991*b*). The contribution of some neck and abdominal motoneurones in locust (*Locusta migratoria*) steering reactions. *J. Insect Physiol.* **37**, 689–698.

BAKER, P. S., GEWECKE, M. AND COOTER, R. J. (1981). The natural flight of the migratory locust, *Locusta migratoria* L. III. Wing-beat frequency, flight speed and attitude. *J. comp. Physiol.* A **141**, 233–237.

BORST, A. AND BAHDE, S. (1988). Spatio-temporal integration of motion. A simple strategy for safe landing in flies. *Naturwissenschaften* **75**, 265–267.

CHILLEMI, S. AND TADDEI FERRETTI, C. (1981). Landing reaction of *Musca domestica*. VI. Neurones responding to stimuli that elicit the landing response in the fly. *J. exp. Biol.* **94**, 105–118.

COGGSHALL, J. C. (1972). The landing response and visual processing in the milkweed bug, *Oncopeltus fasciatus*. *J. exp. Biol.* **57**, 401–413.

COLLETT, T. S. (1980). Some operating rules for the optomotor system of a hoverfly during voluntary flight. *J. comp. Physiol.* A **138**, 271–282.

DE VOE, R. D., KAISER, W., OHM, J. AND STONE, L. S. (1982). Horizontal movement detectors of honeybees: Directionally-selective visual neurones in the lobula and brain. *J. comp. Physiol.* A **147**, 155–170.

ECKERT, H. (1982). Radial pattern expansion drives the landing response of the blowfly, *Calliphora*. *Naturwissenschaften* **69**, 348–349.

GOODMAN, L. J. (1960). The landing responses of insects. I. The landing response of the fly, *Lucilia sericata* and other Calliphorinae. *J. exp. Biol.* **37**, 854–878.

GRISS, C. AND ROWELL, C. H. F. (1986). Three descending interneurones reporting deviation from course in the locust. I. Anatomy. *J. comp. Physiol.* A **158**, 765–774.

HAUSEN, K. (1982). Motion sensitive interneurones in the optomotor system of the fly. II. The horizontal cells: Receptive field organization and response characteristics. *Biol. Cybernetics* **46**, 67–79.

HENGSTENBERG, R. (1973). The effect of pattern movement on the impulse activity of the cervical connective of *Drosophila melanogaster*. *Z. Naturforsch.* **28**, 593–596.

HENSLER, K. (1988). The pars intercerebralis neurone PI(2)5 of locusts: convergent processing of inputs reporting head movements and deviations from straight flight. *J. exp. Biol.* **140**, 511–533.

HENSLER, K. (1989). Corrective flight steering in locusts: convergence of extero- and proprioceptive inputs in descending deviation detectors. In *Neurobiology of Sensory Systems* (ed. R. Naresh Singh and N. J. Strausfeld), pp. 531–554. London, New York: Plenum Press.

HENSLER, K. AND ROWELL, C. H. F. (1990). Control of optomotor responses by descending deviation detectors in intact flying locusts. *J. exp. Biol.* **149**, 191–205.

HORIKAWA, K. AND ARMSTRONG, W. E. (1988). A versatile means of intracellular labeling: injection of biocytin and its detection with avidin conjugates. *J. Neurosci. Meth.* **25**, 1–11.

HORSMANN, U., HEINZEL, H.-G. AND WENDLER, G. (1983). The phasic influence of self-generated air current modulations on the locust flight motor. *J. comp. Physiol.* A **150**, 427–438.

IBBOTSON, M. R. (1991). A motion-sensitive visual descending neurone in *Apis mellifera* monitoring translatory flow fields in the horizontal plane. *J. exp. Biol.* **157**, 573–578.

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

MÖHL, B. AND BACON, J. (1983). The tritocerebral commissure giant (TCG) wind-sensitive interneurone in the locust. II. Directional sensitivity and role in flight stabilisation. *J. comp. Physiol.* A **150**, 453–465.

OLBERG, R. M. (1981*a*). Object- and self-movement detectors in the ventral nerve cord of the dragonfly. *J. comp. Physiol.* A **141**, 327–334.

OLBERG, R. M. (1981*b*). Parallel encoding of direction of wind, head, abdomen, and visual pattern movement by single interneurones in the dragonfly. *J. comp. Physiol.* A **141**, 27–41.

OSORIO, D. (1986). Directionally selective cells in the locust medulla. *J. comp. Physiol.* A **159**, 841–847.

PEREZ DE TALENS, F. AND TADDEI FERRETTI, C. (1970). Landing reaction of *Musca domestica*: Dependence on dimensions and position of the stimulus. *J. exp. Biol.* **52**, 233–256.

PFLÜGER, H.-J., BRAUNIG, P. AND HUSTERT, R. (1988). The organization of mechanosensory neuropiles in locust thoracic ganglia. *Phil. Trans. R. Soc. Lond. B* **321**, 1–26.

PREISS, R. (1987). Motion parallax and figural properties of depth control flight speed in an insect. *Biol. Cybernetics* **57**, 1–9.

PREISS, R. AND GEWECKE, M. (1988). Visually induced wind compensation in the migratory flight of the desert locust, *Schistocerca gregaria*. In *Sense Organs: Interfaces between Environment and Behaviour* (Proc. 16th Göttingen Neurobiology Conference) (ed. N. Elsner and F. G. Barth), p. 38. Stuttgart, New York: Thieme Verlag.

PREISS, R. AND KRAMER, E. (1983). Stabilization of altitude and speed in tethered flying gypsy moth males: influence of (+) and (−)-disparlure. *Physiol. Ent.* **8**, 55–68.

RAINEY, R. C. (1963). Meteorology and the migration of desert locusts. Technical Note no. 54, Anti-Locust Research Centre, London.

REICHERT, H. AND ROWELL, C. H. F. (1985). Integration of nonphaselocked exteroceptive information in the control of rhythmic flight in the locust. *J. Neurophysiol.* **53**, 1216–1233.

REICHERT, H. AND ROWELL, C. H. F. (1986). Neuronal circuits controlling flight in the locust: how sensory information is processed for motor control. *Trends Neurosci.* **9**, 281–283.

REICHERT, H., ROWELL, C. H. F. AND GRISS, C. (1985). Course correction circuitry translates feature detection into behavioural action in locusts. *Nature* **315**, 142–144.

RILEY, J. R., KRUEGER, U., ADDISON, C. M. AND GEWECKE, M. (1988). Visual detection of wind-drift by high-flying insects at night: a laboratory study. *J. comp. Physiol.* A **162**, 793–798.

RIND, F. C. (1990*a*). A directionally selective motion-detecting neurone in the brain of the locust: physiological and morphological characterization. *J. exp. Biol.* **149**, 1–19.

RIND, F. C. (1990*b*). Identification of directionally selective motion-detecting neurones in the locust lobula and their synaptic connections with an identified descending neurone. *J. exp. Biol.* **149**, 21–43.

ROBERT, D. (1988). Visual steering under closed-loop conditions by flying locusts: flexibility of optomotor response and mechanisms of correctional steering. *J. comp. Physiol.* A **164**, 15–24.

ROWELL, C. H. F. (1988). Mechanism of flight steering in locusts. *Experientia* **44**, 389–395.

ROWELL, C. H. F. (1991). The organization of exteroceptive sensory inputs to interneurones of the flight neuropile in locusts. *Tissue & Cell* **23**, 271–276.

ROWELL, C. H. F. AND REICHERT, H. (1986). Three descending interneurones reporting deviation from course in locust. II. Physiology. *J. comp. Physiol.* A **158**, 775–794.

ROWELL, C. H. F. AND REICHERT, H. (1991). Mesothoracic interneurones involved in flight steering in the locust. *Tissue & Cell* **23**, 75–139.

SANDEMAN, D. C. (1968). A sensitive position-measuring device for biological systems. *Comp. Biochem. Physiol.* **24**A, 635–638.

SHEPEARD, P. (1974). Control of head movement in the locust, *Schistocerca gregaria*. *J. exp. Biol.* **60**, 735–767.

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

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

TYRER, N. M. AND GREGORY, G. E. (1982). A guide to the anatomy of locust suboesophageal and thoracic ganglia. *Phil. Trans. R. Soc. Lond. B* **297**, 91–123.

UVAROV, B. (1977). *Grasshoppers and Locusts*, vol. 2. Cambridge: Cambridge University Press. 613pp.

VON HOLST, E. AND MITTELSTAEDT, H. (1950). Das Reafferenzprinzip (Wechselwirkungen zwischen Zentralnervensystem und Peripherie). *Naturwissenschaften* **37**, 464–476.

WAGNER, H. (1982). Flow-field variables trigger landing response in flies. *Nature* **297**, 147–148.

WARREN, W. H. AND HANNON, D. J. (1988). Direction of self-motion is perceived from the optical flow. *Nature* **336**, 162–163.

WEHRHAHN, C., HAUSEN, K. AND ZANKER, J. (1981). Is the landing response of the housefly (*Musca*) driven by motion of a flow field? *Biol. Cybernetics* **41**, 91–99.