

DESCENDING INTERNEURONES OF THE LOCUST REPORTING DEVIATION FROM FLIGHT COURSE: WHAT IS THEIR ROLE IN STEERING?

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Summary

Some descending interneurones (DNs) in insects encode deviation from flight course. Intracellular recording reveals their inputs (from eyes, wind hairs, proprioceptive information from the neck and in some cases ocelli). Intracellular stimulation during flight reveals their motor effects. All components of steering (modification of wing stroke, ruddering with the hind legs, ruddering with the abdomen and head rotation) can be initiated by single DNs. Steering in flight involves the concerted action of at least 10 pairs of DNs synapsing with motor neurones and premotor interneurones. The whole system forms an autopilot, well suited for corrective steering. It is modulated principally by head movements, which have both optical and proprioceptive effects: compensatory head movements increase the accuracy of correctional steering by reducing overshoot, and disable the autopilot during turns evoked by directional pulsed ultrasound for purposes of bat-evasion. DNs responding specifically to visual flow fields are also known, but appear to be related to control of velocity rather than to steering.

Introduction

It has been known for a considerable time that the arthropod ventral nerve cord contains numerous descending axons carrying information originating from the sense organs of the head. Such units were studied extensively in decapod crustaceans by Wiersma and his colleagues in the 1960s and subsequently by many other authors, using extracellular single-unit techniques. Stimulation experiments (usually accomplished with teased-out bundles) indicate that the information is used for both postural control (e.g. of the abdomen or telson) and for various aspects of locomotion: the most dramatic example of the latter is the medial giant unit of crayfish, which can alone trigger a backwardly directed tail-flip evasion response. In many cases, however, stimulation of individual fibres led to no detectable response, or only to partial or rudimentary movements, and this was explained by the concept of synergism: several fibres must be active, simultaneously or in sequence, to produce behavioural output. A considerable body of literature, including that grouped around the 'command fibre' concept, arose from this work.

■ Key words: interneurone, flight, locust, steering.

Although comparable descending neurones (DNs) were demonstrated very early in insects (e.g. Parry, 1947), our knowledge of their information content and behavioural function has progressed diffusely and relatively slowly, largely because the insect nervous system is not as well suited to the techniques of extracellular recording and stimulation of single units as that of the Crustacea. With a few exceptions (e.g. Suga & Katsuki, 1962; Collett & Blest, 1966; Palka, 1967; Horn & Rowell, 1968; Elsner, 1970) the characterization of DNs in insects has come about only since the general adoption of intracellular techniques for recording, dye-filling and stimulation.

Since the application of these techniques, one category of descending unit has become very prominent over the past decade. These are the descending neurones which bring sensory information relevant to flight, especially to steering in flight, to the thoracic motor centres. Like most successful preparations, they owe their popularity primarily to the relative ease with which they can be recorded and/or selectively stimulated. Not only are they themselves often of large diameter, consistent with the need for rapid transmission of regulatory information to the flight motor, but they are often postsynaptic to large fan-shaped optic lobe units or to large electrotonically propagating ocellar interneurones. The large size facilitates penetration and recording. A second reason lies in the relatively well-developed understanding of flight in insects: both the aerodynamics and neural components of the flight motor have been intensively investigated, which greatly facilitates recognition and analysis of the effects of the descending interneurones.

There are now quite substantial bodies of published work on descending neurones of this general nature in dragonflies (e.g. Olberg, 1981*a,b*), grasshoppers (references given below), flies (e.g. Hengstenberg, 1973; Strausfeld & Seyan, 1985; Strausfeld & Bassemir, 1985; Strausfeld *et al.* 1987), moths (e.g. Collett & Blest, 1966; Rind, 1983*a,b*) and bees (e.g. Fletcher *et al.* 1984; Goodman *et al.* 1987; M. R. Ibbotson & L. J. Goodman, in preparation). Although detailed homologies between the flight-related DNs have not yet been sought, there are obvious similarities in their structure and function in all these orders, despite their phylogenetic remoteness. This is to be expected, given that flight (and therefore presumably also its sensory control mechanisms) is a primitive characteristic in insects. The resemblances are therefore probably due to homology, subsequently obscured by the evolution of individual modifications (e.g. the split between the Palaeoptera and the Neoptera in respect of wing musculature and mechanics).

My laboratory has specialized in the nervous system of the acridid grasshopper ('locust'); this is also the animal in which the greatest number of flight DNs have been characterized, and in which the most detailed studies of insect flight mechanisms have been made. Most of this article will therefore be drawn from the example of the grasshopper.

The functional identification of DNs concerned with flight

In principle, one can expect that descending sensory information will have al

variety of effects on the flight system. Two functions that are adequately documented for DNs are (i) starting, maintaining and terminating flight, and (ii) steering. There are probably others, too: flow-field-sensitive DNs (see below) seem to affect primarily wingbeat frequency and so probably flight speed. At least one well-characterized DN, the DCMD of locusts, synapses with flight motor neurones (Simmons, 1980*b*), but seems to play no role in either flight maintenance or steering (C. H. F. Rowell, unpublished observations).

The most satisfactory way to demonstrate the functional role of these neurones is to induce behavioural modification by experimental activation of individual neurones. When it can also be shown that these are activated by sensory inputs occurring in flight, one can be fairly certain that one is dealing with a behaviourally significant element. Merely demonstrating synaptic connection between the DN and neurones of the flight circuit, or demonstrating appropriate sensory responses in the DN with no data on its output connections or functions, does not prove behavioural involvement.

Most of the published literature belongs to this latter class, providing suggestive, but not conclusive, evidence for a role of the descending neurones in flight behaviour. Two exceptions are provided by the work of Möhl & Bacon (1983) (the wind-sensitive TCG neurone of locusts) and of Olberg (1981*a,b*) (multimodal DNs in the dragonfly). Stimulation of the first of these neurones produces steering behaviour in a wind-tunnel, and of the second, wing and abdominal movements in non-flying insects. Selective stimulation of the tritocerebral commissure giant neurone (TCG) can also sometimes induce flight (Bicker & Pearson, 1983). Additionally, both sets of neurones respond to sensory inputs in a manner appropriate to a role in flight steering: the TCG is directionally wind-sensitive (Bacon & Tyrer, 1978), and the dragonfly units respond in a directionally sensitive manner to moving visual patterns, wind on the head and movements of head and abdomen.

My laboratory has concerned itself with steering in flight for a decade, and by 1985 had characterized three DNs which have sensory properties suggestive of an involvement in flight steering; they respond optimally to specific aerodynamic situations (Griss & Rowell, 1986; Rowell & Reichert, 1986). We had also established the general outline of the thoracic neural circuitry responsible for the modulation of the wingbeat which occurs in steering manoeuvres (Reichert & Rowell, 1985; Reichert *et al.* 1985; Rowell & Reichert, 1989). Finally, we and others (Simmons, 1980*a*; Tyrer, 1981; Rowell & Pearson, 1983; Reichert *et al.* 1985; C. H. F. Rowell & H. Reichert, in preparation) had shown that the DNs commonly made synaptic connections with elements of the thoracic flight circuit. These three sets of findings are strong presumptive evidence for a causal role of the DNs in flight steering, but – as pointed out above – do not actually prove it. The observed inputs of the DNs on the thoracic interneurones might not, in fact, be sufficient to bring about the behaviour.

Accordingly, in parallel with the identification and characterization of further DNs putatively involved in steering (Hensler, 1988; and in preparation; A.

Baader, in preparation), we have tested these and other candidate DNs with intracellular stimulation techniques for effects on fictive or tethered flight and on related steering motor patterns. As will be shown below, we find that most of the DNs have demonstrable effects on steering behaviour, and that all aspects of steering behaviour can be influenced or initiated by stimulation of single DNs. First, however, it is necessary to summarize some background material on steering behaviour and the DNs which are putatively involved in it.

Flight behaviour and putative flight-associated DNs

Steering behaviour in locusts

This has been extensively described. A comprehensive list of references is given by Rowell (1988). In common with other flying insects, grasshoppers steer largely by modifying the wing stroke, thus producing asymmetries in lift and thrust. The proximate events responsible for the steering modulation of wing movements consist of shifts in the timing of the discharge of effectively all flight motor neurones within the wingbeat cycle (Möhl & Zarnack, 1975, 1977; and many subsequent authors). Grasshoppers (Dugard, 1967; Camhi, 1970a) and some other insects supplement this basic method by ruddering with the hind legs and/or the abdomen – these manoeuvres not only produce asymmetrical streaming resistance, like the steering surfaces of boats and aircraft, but also shift the centre of gravity laterally. Additionally, characteristic movements of the head relative to the prothorax (i.e. at the neck) and, to a lesser extent, of the prothorax relative to the pterothorax, occur, which have no obvious aerodynamic significance. This, too, occurs regularly in other insects; see, for example, Land (1973) and Hengstenberg (1988) for similar movements in flies.

Sensory inputs inducing steering behaviour

Wing movements in flight are extensively modified by proprioceptive feedback (reviewed by Altman, 1982: see also Möhl, 1985, 1988; Wolf & Pearson, 1988; Reye & Pearson, 1988; references contained therein), but it is not clear that this can be regarded as steering. Steering behaviour can, however, be elicited by almost any exteroceptive input which simulates deviation from course in flight: asymmetrical illumination of the compound eyes (Goodman, 1965) or of the ocelli (Taylor, 1981), movement of the horizon or other elements of visual pattern (Waldron, 1967; and subsequent authors) or asymmetrical stimulation of wind receptors on the head; these include hairs of frons and vertex (Camhi, 1970b), antennae (Saager & Gewecke, 1985; Arbas, 1986) cerci (Altman, 1983; Arbas, 1986; Boyan *et al.* 1986) and possibly other parts of the body (Pflüger, 1984). A combination of these stimuli is especially effective.

DNs responding to sensory inputs inducing steering

Special interest naturally attaches to neurones which respond specifically to the

stimuli or combination of stimuli listed above. These are numerous, and fall into the following categories.

(a) Directional wind-sensitive neurones, with little or no input from other modalities [e.g. TCG (Bacon & Tyrer, 1978) and several others (A. Baader, in preparation)].

(b) Visually sensitive units, with little or no input from other modalities. These are rare and not so far known to influence steering [e.g. DCMD (Rowell, 1971; and subsequent authors)].

(c) Visual and wind units, with either or both modalities directionally sensitive [e.g. PI(2)5 (Hensler, 1988) and other neurones (K. Hensler, in preparation; A. Baader, in preparation)]. The visual response of these units is typically to large-field movement, but some neurones responding to small objects moving in the visual field are also known, both in insects known to undertake visual chases (dragonflies, flies) and in grasshoppers (C. H. F. Rowell & H. Reichert, in preparation).

(d) As type c, with additionally directionally sensitive input from the ocelli [e.g. DNI, DNM, DNC (Rowell & Reichert, 1986)].

(e) DNs of types a, b, and d often additionally receive directionally sensitive input from neck proprioceptors (K. Hensler, in preparation). There may also be neurones which carry only proprioceptive information.

(f) Units which are responsive to visual and/or wind inputs, but without much directional sensitivity. They receive their directional properties from input from neck receptors and, thus, convey steering information to the thorax only when the head is rolled as part of steering behaviour (K. Hensler, in preparation).

There are at least 12 pairs of such units in the nerve cord of grasshoppers. This number also holds approximately for bees and moths. On morphological criteria, Altman & Kien (1985) estimated that about 70 pairs of DNs originate in the grasshopper brain and run in the neck connectives – this sets a theoretical upper limit, but probably only a fraction of these have a function in flight steering.

Synaptic connections of DNs

Some of the DNs described above have been demonstrated by direct stimulation and recording techniques to be presynaptic to thoracic interneurones, including premotor interneurones, and to flight motor neurones. All monosynaptic connections described so far have been excitatory; polysynaptic connections between DNs and both the other classes of neurone, however, are frequently inhibitory (see references cited above). No connections have been demonstrated between DNs and flight oscillator interneurones, defined as those which reset the flight rhythm when stimulated by current injection in a preparation devoid of proprioceptive feedback (Reichert & Rowell, 1989).

Behavioural effects of stimulation of DNs

Effects on steering behaviour

Some DNs can be stimulated selectively by appropriate sensory inputs (e.g. the

ocellar responding neurones DNI, DNM and DNC, which appear to be the only descending units in the locust responding to ocellar Off-stimuli). After ablation of all other directional inputs, locusts will make steering responses with head, wings and abdomen (Taylor, 1981) and develop appropriate turning torques (Thüring, 1986) in response to ocellar inputs, even though these alone generate only small changes in activity in the DNs. The TCG unit can be stimulated selectively by extracellular techniques. It produces alterations in the firing pattern of the flight motor neurones similar to those seen during corrective yaw behaviour (Möhl & Bacon, 1983).

Most of the DNs, however, can be stimulated selectively only by the use of intracellular current injection. Applying this technique to an orthodox preparation, dissected from the dorsal side to expose the pterothoracic nervous system, it can be shown that stimulation of many DNs produces steering movements of the abdomen and/or rolling movements of the head (the effects on wingstroke cannot be investigated behaviourally in this preparation). A. Baader (unpublished results) has correlated the sensory properties and the behavioural effects of a large number of these neurones.

(a) DNs which are exclusively or largely wind-sensitive usually elicit steering movements of the abdomen, and in some cases also head movements. Units which are most responsive to frontal wind (i.e. whose activity is reduced by simulated yaw) produce no steering behaviour. Those which are maximally stimulated by simulated yaw to one side produce steering movements of the abdomen, always consisting of bending to the side ipsilateral to the DN axon. TCG (Fig. 1), previously (see above) shown to have effects on wing stroke, belongs to this group; it also produces ruddering of the hind leg (data not shown). In general, the spike activity of these wind-sensitive DNs increases with wind velocity up to the maximum flight speed of about 4 m s^{-1} , and is somewhat greater during fictive flight than when the insect is passive. The abdominal movements produced by these neurones are typically compatible with correctional steering (thus, for example, a DN which is excited by simulated yaw to the left will cause abdominal ruddering which would produce yaw to the right in a free-flying animal). There are, however, some exceptions to this generalization.

(b) DNs with multimodal inputs (compound eyes and wind, sometimes additionally ocelli and tympana) typically produce head movements, and in some cases also evoke abdominal and antennal movements. Usually the head movements are those seen during correctional steering by intact animals: the animal yaws and rolls its head towards the side to which it is steering [in locusts, in contrast to flies, yaw movements are always associated with roll ('banked turns'), which allows a more intuitive understanding of this behaviour]. Previously described DNs falling into this class include DNC and PI(2)5: both evoke head rolling (and also correctional steering by the wings, see below), but neither causes abdominal movements when selectively stimulated. Several multimodal units depart from this pattern, in that they cause movements of abdomen and head which are not congruent with normal correctional steering: the head is rolled in the

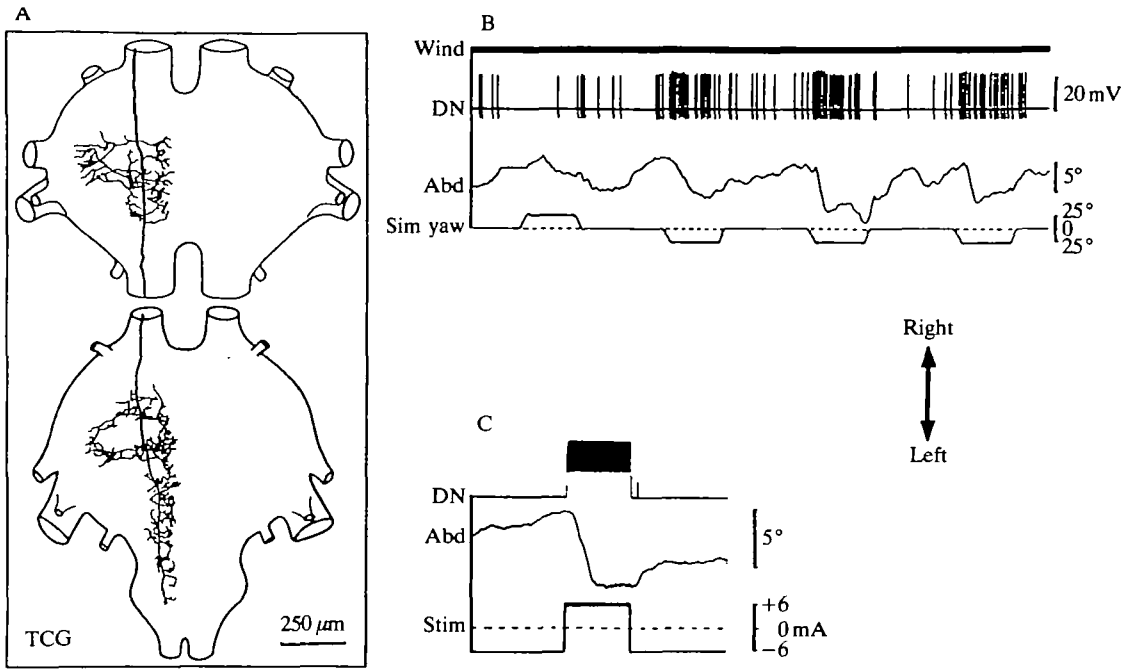


Fig. 1. Sensory response and effects of stimulation of a descending neurone directionally sensitive to wind (TCG of Bacon & Tyrer, 1978). (Data from A. Baader, unpublished results.) (A) Anatomy of penetrated cell (from a Lucifer-Yellow fill). (B) Response to simulated yaw. The animal is in darkness, exposed to a continuous frontal air stream of 3 m s^{-1} (top trace), but is not flying. The air jet is moved (bottom trace) around the yaw axis, 25° to the left or 25° to the right (thus simulating for the animal deviations from course to right and left, respectively). This elicits correctional steering from the animal, here registered (third trace) as ruddering movements of the abdomen: simulated yaw to the right elicits bending movements of the abdomen to the left and *vice versa*. The TCG (second trace) responds to simulated yaw to the side contralateral to the axon with phasotonic bursts of spikes, and ignores simulated yaw to the opposite (ipsilateral) side. This is the characteristic and previously described response of this neurone. (C) Intracellular current injection (bottom trace) into the TCG axon (top trace) elicits a dense burst of action potentials (which mimics a simulated yaw to the right). These elicit bending of the abdomen to the left (middle trace), outward rotation of the left hind leg (data not shown) and alteration of the firing pattern of the flight motor neurones (Möhl & Bacon, 1983) in a manner corresponding to steering to the left.

direction opposite to that towards which the animal is steering (Fig. 2). This pattern of movement is seen in a form of steering associated with bat-avoidance behaviour (see below), and it may therefore be of special interest that these DNs also carry acoustic information.

All the effects described above are generally of larger amplitude during fictive flight than in quiescent animals. This suggests that a convergence takes place, at the level of the neck or abdominal motor neurone or premotor interneurone,

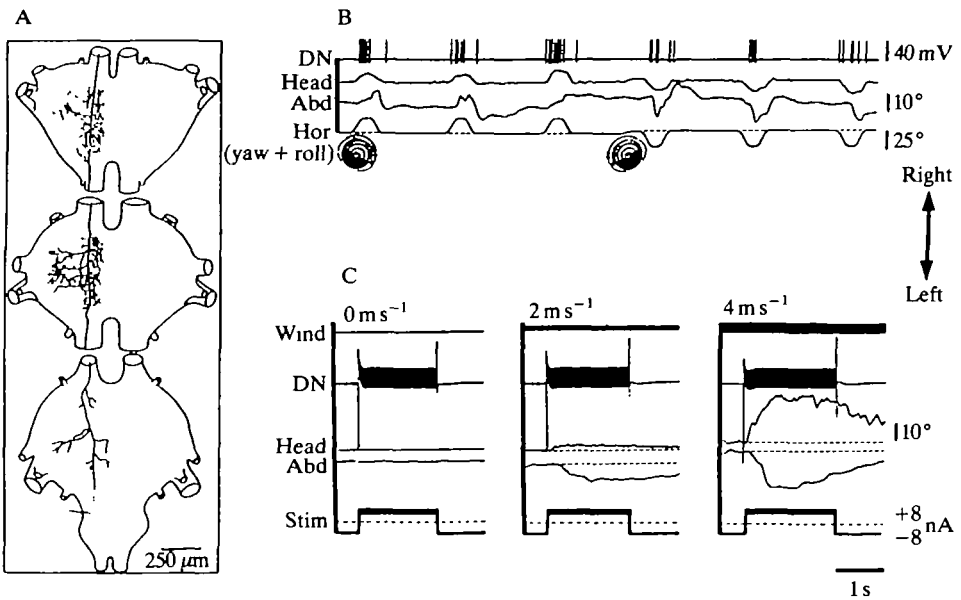


Fig. 2. Sensory response and effects of stimulation of a multimodal descending neurone (A. Baader, unpublished results). (A) Anatomy of penetrated cell (from a Lucifer-Yellow fill). (B) Response of the neurone (top trace) to simulated yaw and roll (combined) to left or right (bottom trace). Both directions elicit spikes, but the neurone responds preferentially to simulated deviations to the ipsilateral (here left) side. The stimulus also elicits correctional steering, here seen as rolling of the head (second trace) and bending of the abdomen (third trace), both in the direction opposite to that of the perceived deviation from course. The neurone also responds to auditory inputs (data not shown). (C) Depolarizing current injection (bottom trace) into the neurone (top trace) elicits a dense burst of spikes. In the absence of facilitating inputs (i.e. no other DNs activated simultaneously) these spikes have no behavioural effect. However, when coupled with frontal wind (which alone causes no steering behaviour, but tonically excites many DNs) the injected current elicits bending of the abdomen to the ipsilateral (here left) side and rolling of the head to the contralateral side. This behaviour is seen in bat-evasive turns elicited by high-frequency sound (see text and Fig. 5). Intracellular stimulation of this neurone also causes an upward movement of the ipsilateral antenna (data not shown).

between signals derived from the DN and those from the flight oscillator. Such a convergence has been documented in the mesothoracic ganglion in neurones concerned with wing movement in flight (Reichert & Rowell, 1985, 1986; C. H. F. Rowell & H. Reichert, in preparation).

A different technique has been developed by Hensler, who has penetrated descending axons in the neck connectives of otherwise intact animals. As in the more traditional preparation, the effects of sensory inputs and intracellular stimulation can then be investigated. As the animal can engage in (tethered) flight, it is also possible to examine the effects of the DNs on the flight pattern in this

preparation. Using this technique, and recording from selected flight muscles (usually the left and right basalar muscles of the meso- and metathoracic segments, which are sensitive indicators of flight steering processes), it has been possible to show that many DNs, including most of those already described in the literature, are indeed capable of modifying the flight motor pattern in a way consistent with correctional steering (K. Hensler & C. H. F. Rowell, in preparation).

Effects on flight initiation

Bicker & Pearson (1983) have previously reported that fictive flight can be induced in quiescent preparations by electrical stimulation of the TCG. Our experiments have shown that this is commonly the case for the DNs as a group; the TCG is, in this respect, not unique. It is quite plausible that, as suggested by Bicker & Pearson, the DNs have input to the mechanism responsible for flight initiation. The primarily wind-sensitive and visually sensitive DNs would be well suited to respond to the exteroceptive inputs caused by the jumping take-off of the grasshopper, and thus to contribute to wing-spreading and flight initiation. The neural mechanism responsible for these activities is not understood. However, several interneurons have been described which greatly influence the probability of fictive flight when excited electrically, though they are not themselves modulated at flight frequency (Pearson *et al.* 1985; Ramirez, 1988). One of these neurones (404 of Pearson *et al.* 1985) is represented in the mesothoracic ganglia by several units of closely similar morphology. C. H. F. Rowell & H. Reichert (in preparation) have shown that whereas at least one of this cluster does not receive input from visually responsive DNs, at least one other does, and it is also modulated at flight frequency. Further work is required to establish the connectivity of these cells.

Some caution is necessary in interpreting results on flight initiation. First, DNs stimulated by sensory feedback from jumping cannot alone be primarily responsible; the latency of wing opening is too short (for a review see Pearson *et al.* 1986). Second, many insects, including some acridid grasshoppers, commonly spread the wings and vibrate them (e.g. in preflight warm-up, or as part of a defensive or sexual display) without first doing anything likely to excite the known DNs. Third, highly responsive individual grasshoppers, whether intact but tethered, or reduced to acute physiological preparations, will start to fly in response to almost any sudden stimulus, visual, acoustic, tactile, chemical or even thermal. Others (unfortunately commoner!) are totally recalcitrant, and cannot be made to fly at all. Very probably amine and/or neuropeptide modulators of the flight system are involved in the modulation of flight threshold (octopamine, serotonin and adipokinetic hormone are all vaguely implicated at the time of writing). Stimulation of individual DNs can undoubtedly trigger flight but, as these very responsive animals indicate, it may not do so over a direct pathway: it could be a secondary effect of, for example, mechanosensory feedback from muscle contraction caused by the DN activity.

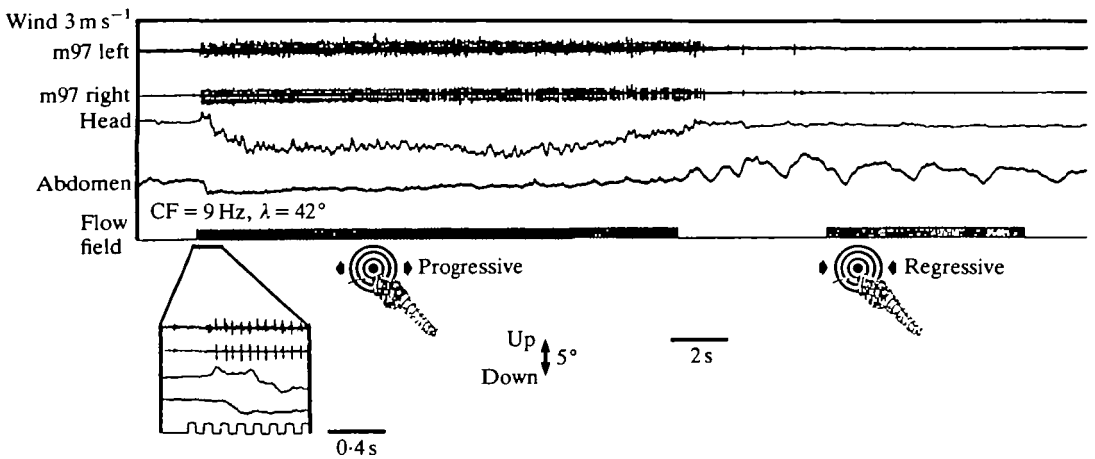


Fig. 3. Visual flow-field stimuli can contribute to the initiation and maintenance of flight. Records were made from a dissected preparation capable only of fictive flight. Continuous frontal wind at 3 m s^{-1} (top trace) is by itself insufficient to elicit flight in this individual. A striped pattern originating in the centre of the artificial horizon and propagating radially outwards mimics the visual effect of flying forward through a visually structured environment ('progressive flow field'). This stimulus (bottom trace), when paired with frontal wind, elicits and maintains flight (recorded as rhythmic activity in the left and right first basalar muscles, second and third traces). During flight the abdomen is contracted and deflected upwards, and respiratory pumping ceases (fifth trace); the head is protruded and tilted forward (fourth trace). (The sense of the voltage monitor is reversed between the fourth and fifth traces.) A 'regressive flow-field' stimulus (bottom trace, second half of record) has no effect. CF, contrast frequency; λ , wavelength of striped pattern. (Modified from Baader, 1988.).

Effects on flight maintenance

Closely associated with flight initiation is the concept of flight maintenance. It seems likely *a priori* that factors or inputs which increase the probability of flight initiation will also increase its probable length. For example, it is well known to experimenters that tethered locusts fly much longer when exposed to a frontal air current than in still air, and Weis-Fogh (1949) showed that much of this effect is due to stimulation of the wind-sensitive hairs of the head – a similar role for head hairs has also been established (Arbas & Hildebrand, 1986) for hawkmoths. These sensilla provide input for most of the flight-associated DNs so far described – very few are completely unaffected by wind – and in some produce tonic excitation. A similar chain of reasoning to that outlined above for flight initiation suggests that the DNs may then be wholly or partly responsible for the effect of wind on flight maintenance. Once again, however, proof of this proposition is lacking.

A further stimulus which both initiates and maintains flight, and also increases wingbeat frequency in previously flying animals, consists of visual flow fields, similar to those generated on the eye when the animal moves forward through a visually structured environment (Fig. 3). An interesting subclass of DNs has been

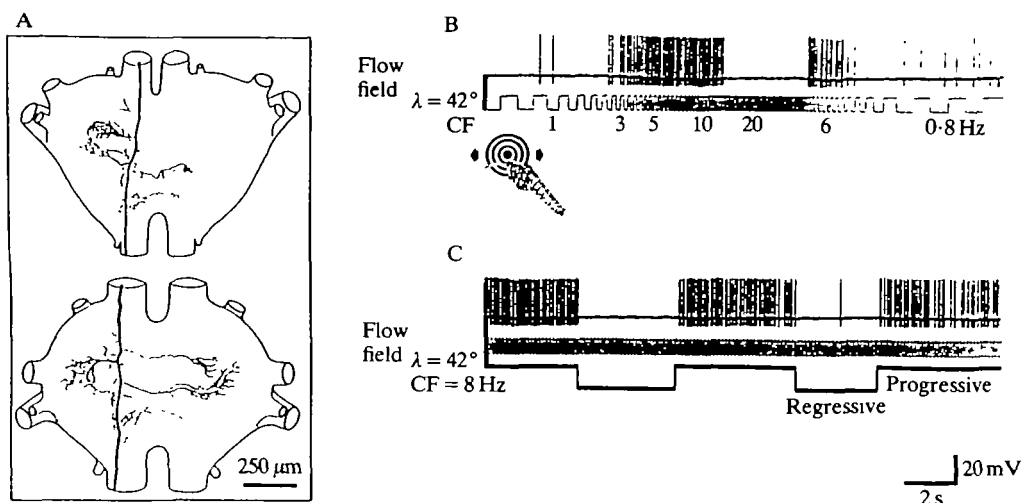
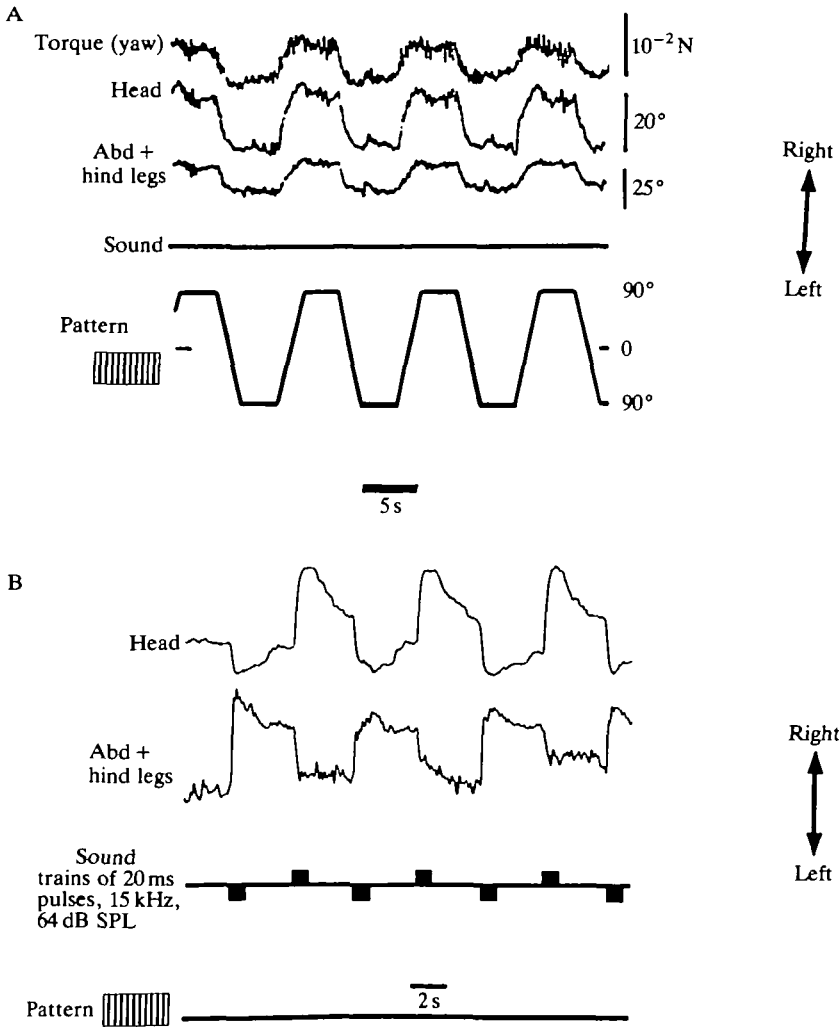


Fig. 4. A DN responding selectively to the progressive flow-field stimulus illustrated in Fig. 3 (A. Baader, unpublished results). (A) Anatomy of penetrated cell (from Lucifer-Yellow fill). (Note bilateral projection, otherwise characteristic only of DNs signalling pitch, which requires bilateral wing manoeuvres for its correction.) (B) Response of DN to a progressive flow field (for explanation see Fig. 3) of varying contrast frequency (CF). Tonic firing is elicited over the range 3–15 Hz. (C) Progressive flow fields are excitatory, regressive ones are not. The neurone does not respond to yaw or roll displacements of the artificial horizon in which the flow field is generated (data not shown). Intracellular stimulation has no behavioural consequences.

recently discovered by Baader (1988, and unpublished), which are primarily sensitive to such flow fields; they are directionally selective, in that they ignore regressive flow (corresponding to what the animal would see if flying backwards) and show a contrast frequency optimum (Fig. 4). They are not sensitive to horizon movements or to acoustic inputs, and only phasically responsive to sustained wind. Unfortunately, no behaviour has been elicited by intracellular stimulation of their axons. It seems likely that these DNs play a role in governing flight speed, which is known to be influenced by both visual and antennal inputs (Gewecke, 1975); however, this hypothesis requires postulating convergence of more than one DN to explain the absence of effect of intracellular stimulation.

The DNs, the autopilot circuitry and steering behaviour

The results outlined above provide excellent support for the view that many, probably most, of the DNs associated with flight are involved in an 'autopilot' circuit (Reichert & Rowell, 1986), in which the DNs act as highly tuned feature-detectors, reporting to the pterothorax deviations from flight course and eliciting corrective steering which compensates for the deviation. This is 'how locusts fly straight' (Rowell *et al.* 1985) – and probably other insects too. It is, however, obvious that the story cannot end here, otherwise locusts could *only* fly in straight



lines, which is self-evidently not so. The question, therefore, arises as to what happens to the autopilot circuitry when the animal changes course 'voluntarily', as this is often expressed – that is, at times unexpected by the observer. *A priori* there would seem to be two classes of possible mechanisms: in one the autopilot would be switched off or otherwise modified in function, in the other its effects would simply be swamped by a much stronger drive to the motor output system deriving from a different command structure.

Using tethered locusts flying under open- or closed-loop conditions in a visual flight simulator (for details see Robert, 1988), Robert has investigated this problem at a behavioural level. Flying locusts, like many other night-flying insects (the dispersal flights of grasshoppers, including those of locust species when in the solitary phase, are typically carried out at night) turn away from a directional source of pulsed ultrasound, presumably as part of a bat-evasion behaviour

Fig. 5. Turning behaviour elicited in tethered flying locusts by (A) rotational movement of the visual surround (optomotor response) and (B) pulsed high-frequency sound alternately from the left and right (bat-evasion response). (Data from D. Robert, unpublished results.) (A) The animal is tethered to a transducer measuring torque around the yaw axis (top trace), and is flying in a laminar-flow windstream of 3 m s^{-1} . The striped pattern surrounding the animal is moved by a servomotor driven by the waveform shown in the bottom trace. The locust attempts to follow this movement (but cannot, because of the open-loop conditions), and develops corresponding torques to the right and left alternately. These are caused by steering behaviour, here registered as ruddering of the abdomen and hind legs (third trace) and associated rolling of the head. Note that both abdomen and head are deflected in the same direction. (B) Same experimental situation as above, but here the visual surround is held stationary. Trains of pulses of 15 kHz sound are delivered alternately from 45° to the left and 45° to the right. The animal steers away from the sound (see abdomen/hind legs trace), but simultaneously turns the head in the opposite direction (i.e. towards the sound source), even though this generates an optomotor situation which should oppose this head movement.

(D. Robert, in preparation). When sound sources of this nature are incorporated into the simulator, locusts flying under visual closed-loop conditions (i.e. actively stabilizing their course) will make sudden turns away from the sound. To do this, they have to ignore the visual inputs which – *via* the autopilot circuitry – had up to that point determined their flight path. What happens to the autopilot?

It turns out that any possible effect of the autopilot is reduced, possibly eliminated, by an unexpected and very simple mechanism. During the acoustically triggered turn, the locust turns its head in the opposite direction, thus minimizing or cancelling the visual signal which would normally produce correctional steering and hold the insect on course. As stated above, locusts performing correctional steering typically turn the head into the turn: thus, a locust turning to the right after an unintentional deviation to the left would make appropriate wingbeat corrections, bend the abdomen to the right *and* turn the head to the right (Fig. 5A). The effect of this head movement is complex; it quickly reduces the amplitude of the visual signal eliciting the steering manoeuvre, so producing a better-modulated correctional response with less overshoot (K. Hensler & D. Robert, in preparation; D. Robert, in preparation) and it activates neck receptors which, in turn, feed into the visual DNs and alter their directionality and tonicity and, in part, compensate for the loss of visual signal (Hensler, 1988, and in preparation). Also, of course, it helps stabilize the visual world on the retina. Pulses of high-frequency sound from the left cause the locust to steer to the right with the wings and to bend the abdomen to the right; the head, however, is simultaneously rotated to the *left*, the opposite of what is seen in correctional steering (Fig. 5B). The effect is once again to stabilize the visual world on the retina, and the autopilot is accordingly not activated by the animal's turn – the locust can perform its bat avoidance without interference from the autopilot. This head movement is driven exclusively by the auditory input: it is not affected by either darkness or the experimental reversal of the sign of the visual feedback.

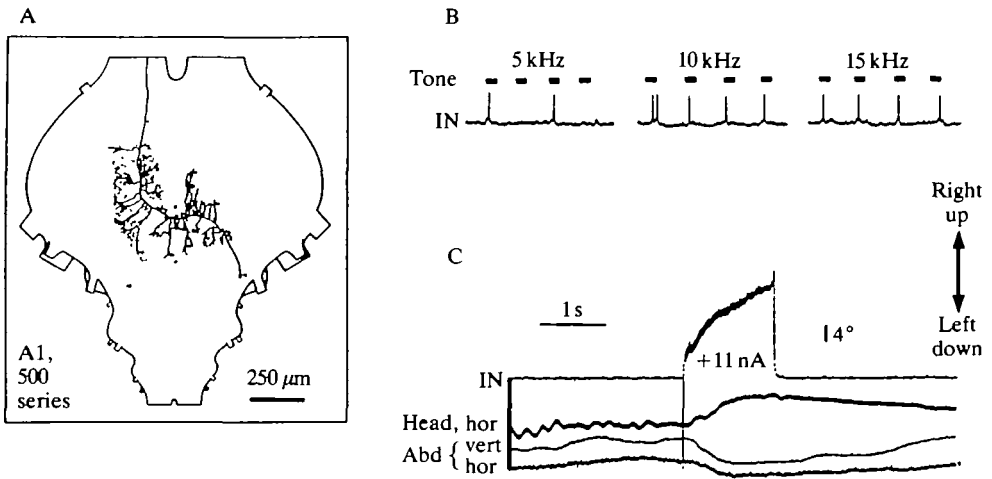


Fig. 6. Example of a candidate interneurone (IN) for participation in the bat-evasion response (see text). (Data from A. Baader, unpublished results.) (A) Anatomy of penetrated cell (from a Lucifer-Yellow fill). Its morphology is of the 500-type (Robertson & Pearson, 1983) and its soma is located in the first abdominal neuromere of the 'metathoracic' ganglion. It appears not to have been previously described. (B) Pulsed high-frequency sound elicits action potentials in the interneurone. The response is best in the range 15–20 kHz, but also extends much higher. Its acoustic directionality is not known. (C) Intracellular current injection into the interneurone (top trace) elicits bending of the abdomen to the ipsilateral side and rolling of the head (second trace) to the contralateral side (relative to the axon), the characteristic pattern for bat-evasive turns (see Fig. 5B). The third and fourth traces record the movement of the abdomen in the vertical and the horizontal (i.e. around yaw axis) planes, respectively.

[The latter observation, and others (see Fig. 5), may indicate that the autopilot is also suppressed, but our data do not yet make this certain.] Latency measurements (see also Boyan, 1985) suggest that the auditory inputs activate the motor machinery directly, rather than after first ascending to the brain (in grasshoppers high-frequency sound is perceived *via* the group D sensilla of the paired tympana, the axons of which project to the first abdominal ganglion). Interneurones have been found in the metathoracic and first abdominal neuromeres which are sensitive to high-frequency sound and which elicit head and abdominal rotation in opposite directions, as required by the bat-avoidance turn: these are candidates for the neuronal circuit (Fig. 6). The input elements of the acoustic behaviour are thus quite different from those in visual steering. If DNs play any role in the auditory response, it is unknown and is likely to be subtle and complex – perhaps allowing the animal subsequently to realign head and body without perturbing the (new) flight path.

These two examples (corrective steering and bat-avoidance behaviour) suggest that the functioning of the DNs and the associated thoracic circuitry is modulated to a considerable extent by head movements. Although these are in part evoked directly by the DNs themselves, there are certainly other influences at work. For

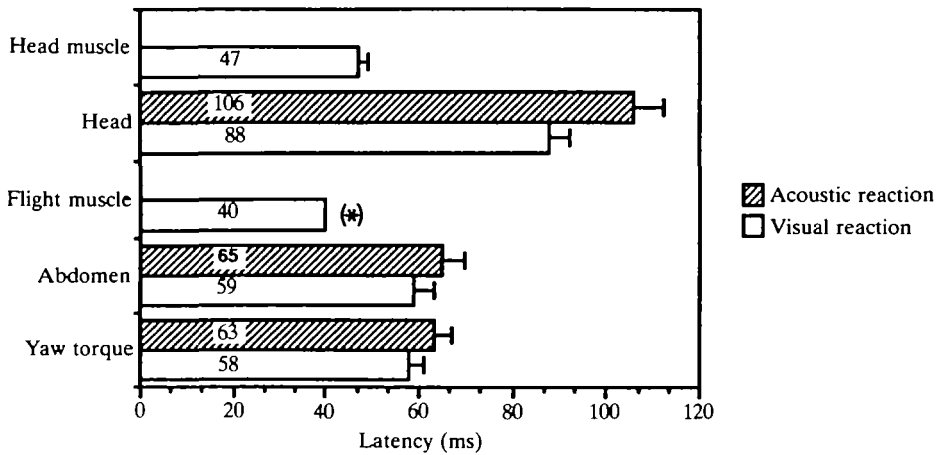


Fig. 7. Latency of various components of steering behaviour, measured under open-loop conditions during tethered flight by intact locusts. Turns are elicited as in Fig. 5: i.e. either by rotations around the yaw axis of the visual surround, or by pulsed high-frequency sound from microphones mounted 45° to the left or right of the animal's longitudinal axis. Error bars at end of the columns correspond to standard deviation. (Data collected from D. Robert, K. Hensler & C. H. F. Rowell, all unpublished results.) The value (approx. 40 ms) given for the latency of the flight muscle response (*) is derived indirectly: as the activity of the flight motor neurones is primarily determined by a periodic oscillator drive, a simple steering latency measurement cannot be made – it depends when the eliciting stimulus occurs in relation to the oscillator stimulus. However, latency shifts can sometimes be observed in the first wingbeat cycle following stimulation, and the period of this cycle is about 50 ms. At body temperatures typical of flying locusts (30°C and above), the minimum latency of PSPs derived from DN's relaying steering information recorded in the FMNs can be less than 20 ms. To this must be added conduction time to the muscle and synaptic delay at the neuromuscular junction.

example, the head nods regularly at wingbeat frequency during flight, probably moved passively as a result of the contraction of the wing musculature. Further, intracellular stimulation of local interneurons with DN input in the metathoracic ganglion can lead to directional head movements in the absence of flight (A. Baader, unpublished observation), indicating that ascending feedback loops exist. We know nothing of the function of these loops.

Head movements during steering in flight by insects have always been rather difficult to rationalize. They have no aerodynamic significance and (at least in animals like locusts with more-or-less all-round vision and without markedly foveate eyes) limited visual effects. An earlier theory, which proposed that steering manoeuvres were *initiated* by head movements (for a review see Rowell, 1988), has been eliminated experimentally – their latency is greater than that of either wing or abdominal steering (Fig. 7, and D. Robert, in preparation). It now seems likely that the modulatory effects on the DN's, probably along with partial

stabilization of the image on the retina, are the main reason for head movements in flight steering.

Finally, it is worth noting that the distinction made temporarily above between 'voluntary' and 'involuntary' turning is in all probability false, and the details of the two mechanisms summarized here support this view. Rather, both forms of turning are adaptive responses to certain stimulus situations; each has its own particular neural elements, and shares some others, for example in the final common pathway. Other stimulus situations producing turns in flight can readily be imagined: turns away from one visual stimulus (a predator, perhaps) or towards another one (a sex partner, a prey item, a desirable habitat) or turns with respect to an olfactory stimulus, such as a pheromone or a foodplant odour. The distinction between voluntary and involuntary is anthropocentric, deriving from the greater conscious awareness we have of some of the stimuli influencing our own behaviour than of others. There is no need to complicate our interpretations of insect behaviour by assuming that they suffer from a similar mental duality.

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