

## ANTENNAL REFLEXES IN THE DESERT LOCUST *SCHISTOCERCA GREGARIA*

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### Summary

The control of horizontal motion of the locust antenna was studied by behavioural and electrophysiological investigations. Deflection of the flagellum and the pedicel induced by air currents or a needle were used as mechanical stimuli. The forces at this needle during imposed movements were measured with a semiconductor force transducer. The antennal movements were recorded with a capacitive movement transducer, and myograms were recorded simultaneously from the lateral and median scape muscle.

Each scape muscle is innervated by at least three excitatory motoneurons. Reflex movements of the scape–pedicel joint are triggered by several sense organs of the locust, e.g. antennal sensilla. Touching a flagellum of a resting locust normally evokes either an *avoidance reflex*, which removes the antenna from the stimulus source, or reflex chains, during which the antenna oscillates against the stimulus source. Air-current stimuli induce synchronous phasic–tonic responses in both scape muscles and a stereotyped movement of the antenna (flight-start reaction). This reaction occurs synchronously with the onset of flight muscle activity, and is the beginning of the antennal-positioning reaction that leads to the antennal flight posture. This posture is held constant during steady flight within a range of  $\pm 1^\circ$ . Sudden deflections of the antenna of a flying locust by air-current modulations or by a solid object cause phasic–tonic responses similar to those during the start of flight. Force measurements indicate these responses to be *resistance reflexes*. Experiments in which one antennal joint was immobilized at a time show the following. (1) Stimulation of only the sensilla of the pedicel–flagellum joint triggers transient avoidance reflexes in resting locusts and sustained resistance reflexes in flying ones. (2) Stimulation of the sensilla of the scape–pedicel joint alone causes avoidance and resistance reflexes in resting locusts, and resistance reflexes in flying ones.

### Introduction

The insect antenna is a complex, multimodal sense organ which monitors movement in space as well as the physical and chemical conditions of the environment. The locust antenna, for example, carries several types of sensilla:

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chordotonal organs and hair fields at the scape–pedicel joint, Johnston's organ and campaniform sensilla at the pedicel–flagellum joint, and mechano- and chemo-sensitive sensilla on the flagellum (Gewecke, 1972a). The sensory mechanisms of the antennal sensilla are integral parts of specific behaviours: mechanoreceptors control gravity orientation in flies and crickets (Horn and Kessler, 1975; Horn and Bischof, 1983), flight speed in bees (Heran, 1959) and locusts (Gewecke, 1975), and they enable mate-finding in mosquitoes (Tischner and Schief, 1955) and flies (Bennet-Clark and Ewing, 1970). In moths the latter function is performed by chemoreceptors (Kennedy and Marsh, 1974).

The perception of environmental parameters is strongly connected with an exact positioning of the sense organs of the antenna within the stimulation field (Gewecke and Heinzl, 1980). Reflex circuits serve to protect the antenna from extreme stimulus intensities and from damage. Normally, avoidance reflexes (assistance reflexes; Bässler, 1976; synergistic reflexes; Clarac and Vedel, 1975) cause removal of the antenna from the stimulus source. In flying insects, however, these avoidance reflexes are inhibited. The antennal position is held nearly constant for control of flight speed with respect to the air. Under these circumstances the antennae are moved against the direction of stimulation (Gewecke, 1972b).

The anatomy of the movement apparatus and the sensilla of the locust antenna has been investigated by Albrecht (1953), McFarlane (1953) and Gewecke (1972a). In *Locusta migratoria* the antenna consists of the basal scape, the pedicel and 24 segments of the flagellum. Only the two proximal joints are moved actively. The antenna can be raised or lowered (each up to 60°) from the horizontal position about the horizontal axis of the head–scape joint, and the pedicel with the flagellum can be turned laterally or medially within a range of approximately 90° about the vertical axis of the scape–pedicel joint (Fig. 1). These active antennal movements are performed by two pairs of muscles: the head–scape muscles (which are innervated by the lateral tegumentary nerve of the deutocerebrum) and the two scape muscles (which receive branches of the antennal nerve). The flagellum itself can only be moved passively by external forces, and the middle flagellar joints are flexible enough to allow the flagellum to be bent without damage. Gewecke (1972a) supposed that the active movements of the pedicel are controlled by two hair fields of the pedicel and by two chordotonal organs of the scape, whereas passive movements of the pedicel–flagellum joint are monitored by campaniform sensilla and the Johnston's organ of the pedicel (Fig. 1).

The present paper describes the behaviour of the antennomotor system in resting and flying locusts, and the performance and function of the antagonistic reflexes (avoidance/resistance) in the scape–pedicel joint.

### Materials and methods

Adult *Schistocerca gregaria* (Forsk.) of both sexes, 1–4 weeks after the imaginal moult, from the culture of the Institute were used in the experiments.

The head of the locust was glued ventrally to a holder which also supported the abdomen by a metal spring. The eyes were covered with graphite to reduce optical evoked reflexes. The antennal movements were measured *via* a capacitive position-measuring device (Sandeman, 1968). After glueing the scape to the head capsule in a horizontal position, the antennal angle  $\gamma$  (angle between longitudinal body axis and flagellum; Gewecke, 1972*b*) could be measured by two brass wires of the transducer over a range of  $90^\circ$  (Fig. 2, inset). The transducer signal was linear in the range  $20^\circ < \gamma < 70^\circ$ . To lead the signal of the transmitter to the flagellum, a  $20\ \mu\text{m}$  flexible stainless-steel wire was connected to the second or third flagellar segment and through this to a coat of graphite applied to the next 10 segments (Fig. 2; graphite has a good conductance, a low specific gravity, and does not increase the aerodynamic drag of the flagellum). The transducer signal was synchronously stored with the myograms on FM tape.

The myograms of the scape muscles were recorded through two  $20\ \mu\text{m}$  non-insulated stainless-steel wires implanted dorsally in each muscle (Fig. 2), a  $70\ \mu\text{m}$  stainless-steel wire implanted in the head for grounding and by differential bandpass amplifiers.

Two different stimulation procedures were used in the experiments: air-current stimulation was applied either from a small wind tunnel (jet diameter 41 mm; air speed measured by a thermistor anemometer) which evoked flight periods of up to 15 min, or by direct displacement of the antenna with a needle which was coupled *via* a force transducer (Akers, 801A) to an electrodynamic driver (the needle was

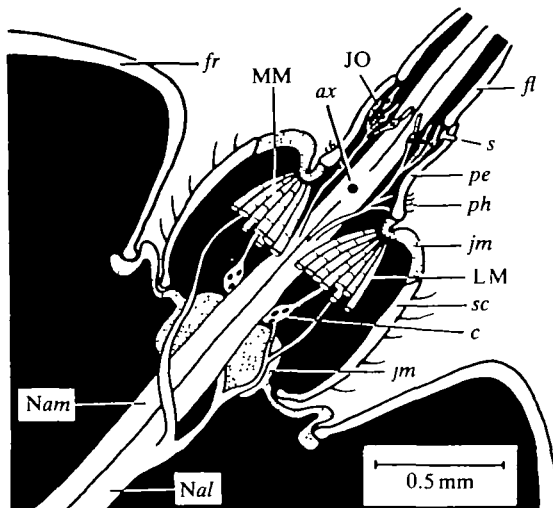


Fig. 1. Dorsal view into the proximal segments of a locust antenna (after Gewecke, 1972*a*). *ax*, vertical axis of the scape-pedicel joint; *c*, chordotonal organ; *fl*, flagellum; *fr*, frons; *JO*, Johnston organ; *jm*, joint membrane; *LM* (*MM*), lateral (median) scape muscle; *Nal* (*Nam*), nervus antennalis lateralis (medianus); *pe*, pedicel; *ph*, hair fields of the pedicel; *s*, campaniform sensilla; *sc*, scape.

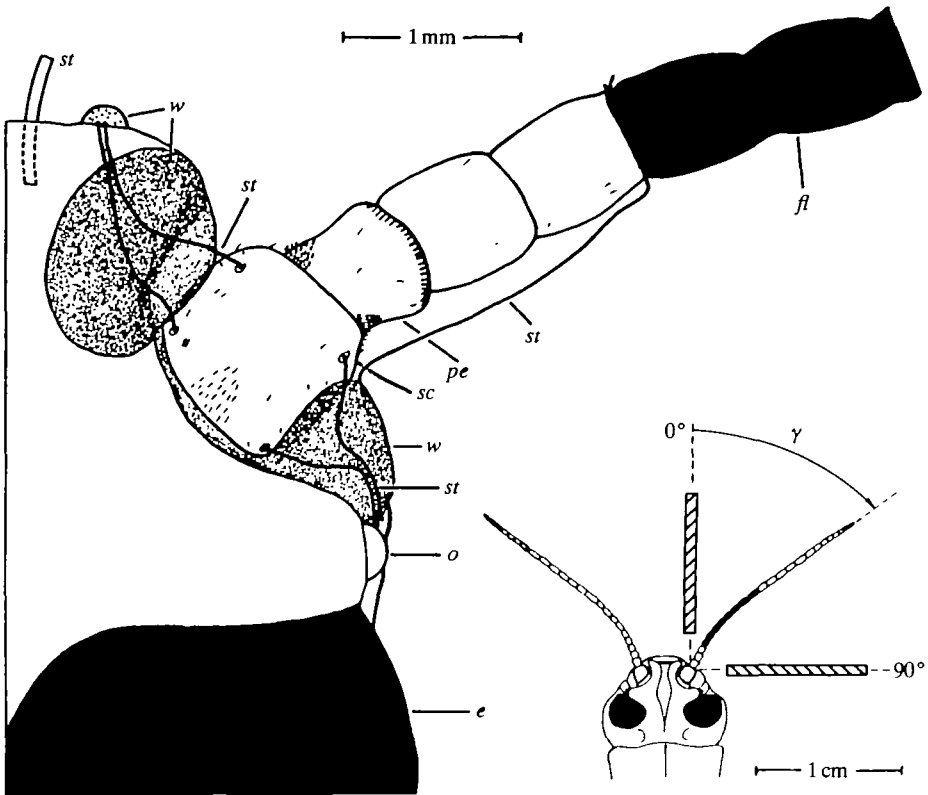


Fig. 2. Dorsal view of an antennal preparation. Inset shows the head and the position of the two receiver antennae (striped bars) of the capacitive movement transducer. The eyes (*e*) and parts of the flagellum (*fl*) are painted with graphite (black). *o*, ocellus; *pe*, pedicel; *sc*, scape; *st*, flexible steel wire; *w*, wax;  $\gamma$ , antennal angle.

not glued to the flagellum). The driver could move the flagellum in the range  $0.05\text{--}60^\circ$  (peak to peak) whilst the force transducer indicated the imposed forces.

Post-stimulus-time histograms and averaged amplitude graphs (see Fig. 4) were produced by a time histogram analyser (Ortec).

### Results

Under natural conditions, resting locusts hold their antennae in a constant position for minutes, or move them in a saccadic manner. Sometimes one antenna is directed straight towards a moving object or to other locusts, but antennal tracking, as seen in crickets (Honegger, 1981), has never been observed. During walking, the antennae are used as tactile or olfactory sensors and, therefore, are moved to feel the ground or obstacles. If an antenna touches an object, or if an antenna is touched by an object, either an avoidance reflex or a reflex chain occurs (Fig. 3). The reflex chain is composed of an active movement towards the object, short resistance reflex and a subsequent avoidance reflex, another active move-

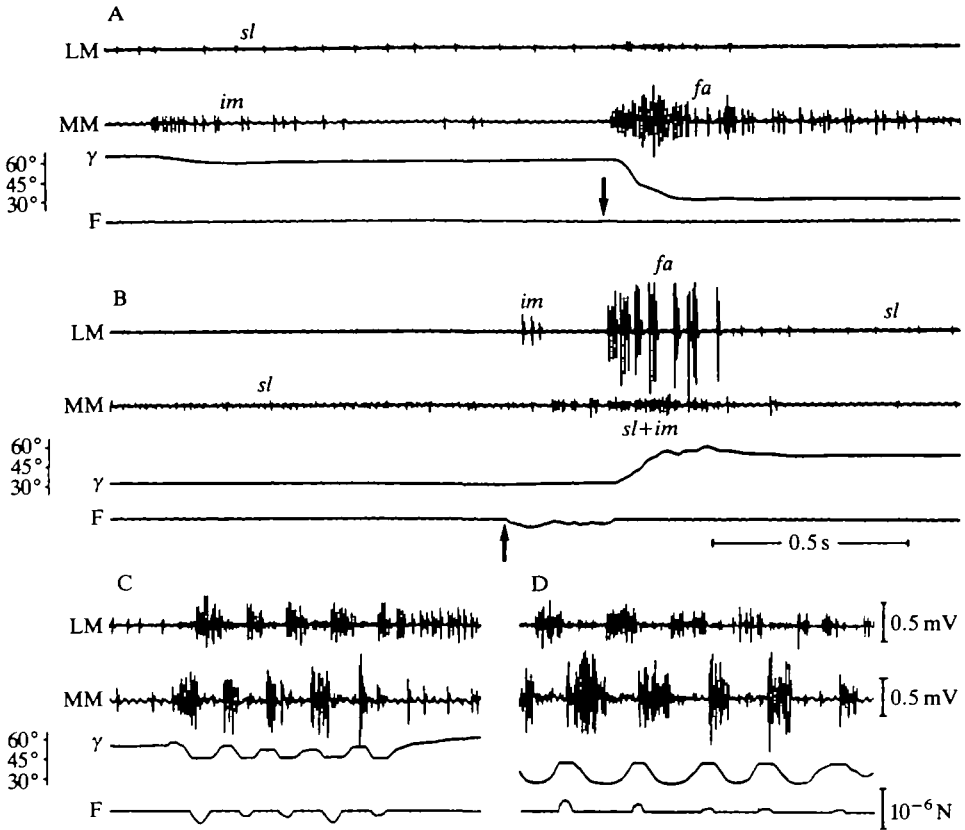


Fig. 3. Myograms of the lateral and median scape muscles (LM, MM), antennal angle ( $\gamma$ , 30–60°), and signal of the force transducer (F) during a mediad (A) and a laterad (B) antennal avoidance reflex and reflex chains (C,D). Arrows indicate timing and direction of stimulation, i.e. touching the flagellum with a needle. In C the needle was on the median side of the flagellum, and in D on the lateral one (position corresponding to  $\gamma=45^\circ$ ). *fa* (*im*, *sl*) action potentials of fast (intermediate, slow) motor units.

ment towards the object and so on. This oscillation can last several seconds with an amplitude of up to 20°. The contralateral antenna remains passive or is moved independently of the oscillating one. Antennal movements are also not coupled to those of the legs, as they are in crayfish (Sandeman and Wilkens, 1983). During walking, the antennae are moved without any rhythmic pattern. Short periods of simultaneous movements of both antennae in non-flying locusts were only observed in mating animals.

If a locust is stimulated by an air current, however, it starts to fly and both antennae are synchronously turned medially. The resulting antennal flight position can be changed by air turbulence or visual stimulation. After disturbance the previous antennal position is immediately re-adjusted. Other observations and measurements show that the antennae oscillate during flight with an amplitude of

up to  $\pm 1^\circ$  depending on wing beat, head nodding and air turbulence (Heinzel, 1983; Heinzel and Gewecke, 1987).

#### *Motor units of the scape muscles*

The myograms of the scape muscles show single or summed action potentials, depending on the activity of the motoneurons. During low muscle activity in most locusts 2–3 (occasionally 3–4) different action potentials per muscle can be distinguished by their size and shape, and by their contribution to the antennal movement. Using intracellular muscle recordings it was shown that each scape muscle is innervated by five motoneurons of the slow, intermediate, fast and inhibitory types (Bauer, 1988).

In the myogram the slow unit (*sl*) is characterized by small potentials (0.1–0.2 mV) and tonic activity that does not evoke single twitches (Fig. 3). There are probably two intermediate units (*im*), characterized by larger potentials (0.2–0.6 mV) which, if impulse frequency is low, trigger small single twitches (Fig. 3A); they trigger tetanic contractions if impulse frequency is high. The fast unit (*fa*) is characterized by the largest potentials (0.5–2 mV) which cause large single twitches. Fast units are different in the two scape muscles. In the lateral muscle (LM), fast units show very large and short action potentials ( $\leq 1$  ms) without complete tetanus, whereas fast units of the median muscle (MM) are more similar to an intermediate unit: the action potentials are smaller, last longer ( $> 1$  ms) than the ones of the lateral muscle, and cause complete tetanus at high impulse frequencies. In addition, all units show summation with increased activity. Therefore, the analysis of single motor units during flight by extracellular recording is restricted. (The size of the spikes depends on the recording conditions, e.g. on electrode position and resistance, not on the size relationships between the different units.)

#### *Antennal reflexes in intact animals*

##### *Behaviour of resting locusts*

Mechanical stimulation of an antenna of a resting locust with a needle produces avoidance reflexes or reflex chains (Fig. 3). The antennal oscillations during a reflex chain have a frequency of  $10 \pm 4$  Hz and last for 2–10 cycles. Spontaneous antennal oscillations, which are occasionally performed by very active locusts, have frequencies in the same range (8–12 Hz). In stimulated locusts which start to fly spontaneously, or in animals that have stopped flying, resistance reflexes can also occur. But these resistance reflexes last only for a short time, and are interrupted by avoidance reflexes.

The amplitude ( $\gamma$ ) and angular speed of the antennal reflex movements and their releasing thresholds are variable and depend on the animals' agitation or flight motivation. The maximum values measured were about  $50^\circ$  for amplitude and about  $2000^\circ \text{ s}^{-1}$  for angular speed. The releasing threshold of avoidance reflexes evoked by step function stimulation, lies between  $0.05^\circ$  and  $0.1^\circ$ . Interactions

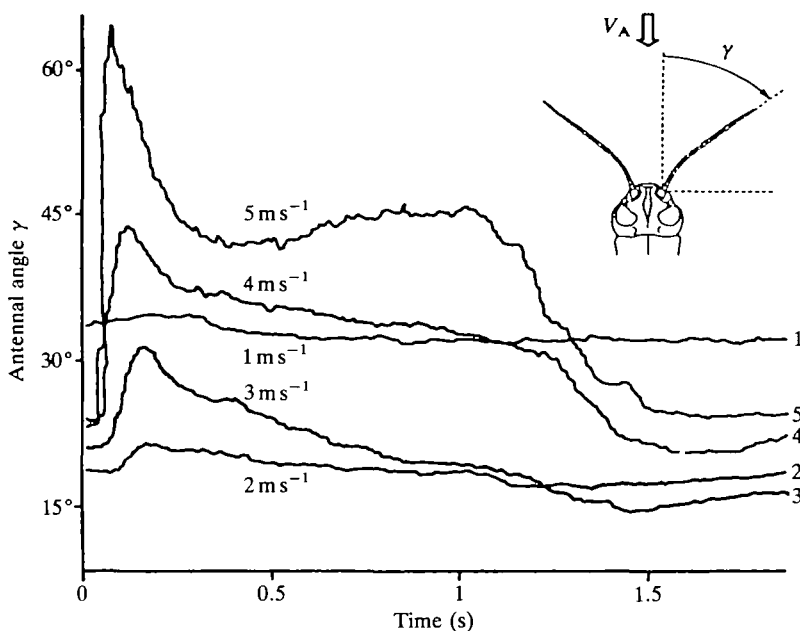


Fig. 4. Averaged amplitude graphs (each of eight successive stimulus periods; binwidth 10 ms) of antennal angle ( $\gamma$ , inset) during the first seconds of stimulation by frontal air currents of different speeds ( $V_A$ ; measured with a thermistor anemometer). The air-current front reaches the locust's head at 0.05–0.1 s, depending on the air speed, and the antennae are bent passively backwards. This movement is accompanied by an active movement (avoidance reflex). Simultaneously with the start of the flight motor (at 0.1–0.2 s), the avoidance reflex changes to a resistance reflex, by which the antenna is moved into the final flight position within about 1 min.

between the right and left antennae have never been seen in resting locusts, whereas in tethered flying locusts transient mediad deflection of one antenna with a needle causes transient lateral movement of the other.

#### *Behaviour of flying locusts*

If a locust is motivated to fly, a frontal air-current stimulation triggers a characteristic stereotyped flight-start reaction of the antennae (Fig. 4). This begins after a passive laterad deflection of the flagellum (i.e. an increase of antennal angle  $\gamma$ ) as an avoidance reflex that, by the activity of the LM, at first enlarges the antennal angle for some milliseconds. About 100 ms after the onset of stimulation the activity of the MM increases synchronously with the activation of the flight muscles. As a result the antenna is moved by a resistance reflex against the direction of the air current (i.e.  $\gamma$  decreases) into the flight posture. This flight-start reaction of the antenna lasts only a few seconds (Fig. 4). The fine adjustment of the antennal flight position, however, can last for minutes (Fig. 5).

After the start of flight, the activity of MM remains higher than that of LM. The torque in the scape–pedicel joint, and thus the positions of pedicel and flagellum,

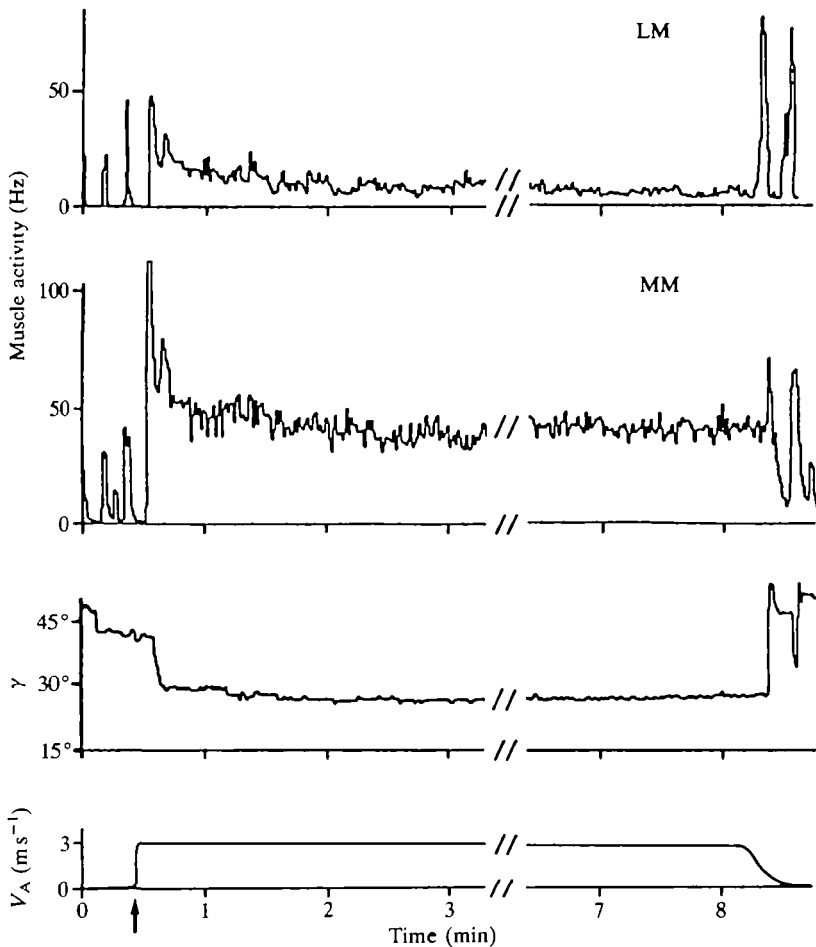


Fig. 5. Example of scape-muscle activity (of all motor units, Hz; binwidth 1 s) and control of antennal angle ( $\gamma$ ) before, during and after flight. The scape-muscle activity is increased phasic-tonically at the onset of an air current ( $V_A$ ) and at the start of flight (arrow). When the air current stops (at 8.2 min) and flight ceases,  $\gamma$  is increased to its original size. The activity of the median scape muscle (MM) remains high at about 50 Hz during flight, whereas that of the lateral one (LM) decreases to about 10 Hz.

is held constant by a balance between the forces of the two scape muscles and the aerodynamic forces ( $\gamma = \text{constant} \pm 1^\circ$ ; Fig. 5). The level of activity of both muscles controls the stiffness of the scape-pedicle joint. The stiffness decreases from its maximal value during the first few seconds of flight to a lower level. Each change in the aerodynamic conditions produces passive antennal deflection which triggers phasic-tonic responses of the muscle activity (Fig. 6). As a result, the stiffness of the scape-pedicle joint increases, and the antennal angle is re-adjusted.

Fig. 7 demonstrates the dependence of the antennal reflexes on flight activity. Only during flight is the sinusoidal modulation of  $\gamma$  counteracted by a resistance



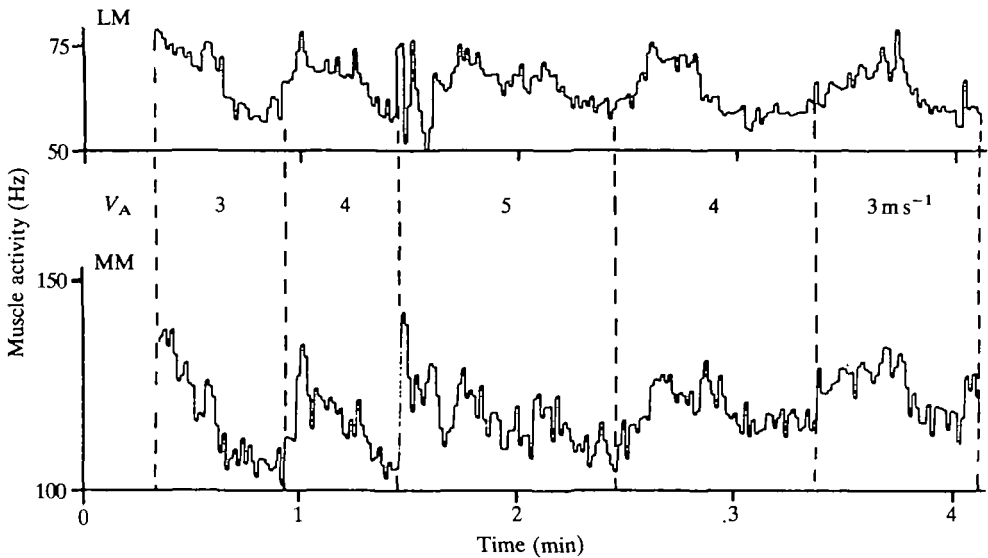


Fig. 6. Activity histograms (of all motor units, Hz; binwidth 1 s) of the scape muscles (LM, MM) during continuous flight with changing air speed ( $V_A$ ). When air speed is increased, phasic-tonic responses occur in both muscles. Decreasing steps in air speed are also followed by an increase in muscle activity, but without the phasic component. Each change of air speed produces a stiffening of the scape-pedicel joint brought about by increased activity of both muscles.

reflex by which the flagellum is pressed frontally against the stimulating needle (left part of Fig. 7A). At the end of flight the activity of MM is reduced ( $t_1$ ; end of resistance reflex). As a result, the flagellum only touches the needle gently and does not follow its sinusoidal movements any longer (right part of Fig. 7A). Fig. 7B shows the change from an avoidance reflex of a resting locust (the flagellum is not pressed against the moving needle) to a resistance reflex after the spontaneous start of flight ( $t_2$ ). During the last two stimulus periods, only tonic activity of MM counteracts the force of the needle.

#### *Elimination experiments*

To decide which group of antennal mechanoreceptors is responsible for the different reflexes, the scape-pedicel joint, the pedicel-flagellum joint or both were immobilized with wax. By these (reversible) operations, defined groups of joint sensors were deprived of mechanical stimulation. For these experiments, locusts with high flight motivation (demonstrated by spontaneous flight starts) were used; these locusts also occasionally show resistance reflexes during rest.

Step-function stimulation imposed on one flagellum of a non-flying locust produces responses in both the scape muscles of one antenna. The responses of the avoidance reflex are regular, whereas those of the resistance reflex only occur occasionally (Fig. 8A). If the scape-pedicel joint is fixed, only fast avoidance

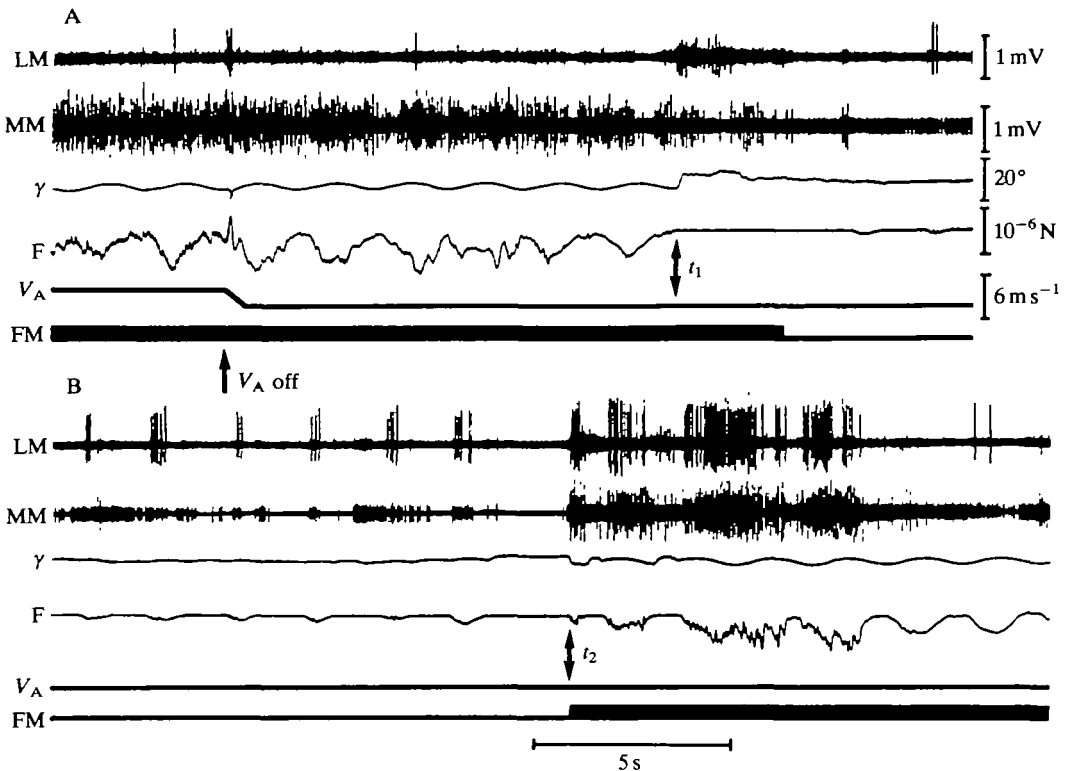


Fig. 7. Competition between avoidance and resistance reflexes. (A) Change (at  $t_1$ ) from resistance reflex of a flying locust to avoidance reflex when the air current ( $V_A$ ) is switched off. (B) The reverse change when the animal starts spontaneous flight (at  $t_2$ ). The sinusoidally vibrating needle at the force transducer (F) remains in the same average position in A and B. FM, flight muscle activity. (For abbreviations, see Fig. 3.)

reflexes are triggered (Fig. 8B). After immobilizing the pedicel–flagellum joint, both muscles show tonic activity during deflection of the antenna (resistance reflex; Fig. 8C). If both antennal joints are fixed, no stimulus responses occur (Fig. 8D).

In flying locusts the antennomotor system reacts, after the initial part of the flight-start reaction, with resistance reflexes. This is demonstrated in Fig. 9A by high activity in MM which counteracts passive lateral deflection of the flagellum at the onset of frontal air-current stimulation, and by high activity in LM (off-response) counteracting mediad flagellar deflection when the air current stops. In flying animals the sensilla of the pedicel–flagellum joint trigger not fast avoidance reflexes but sustained resistance reflexes (scape–pedicel joint immobilized; Fig. 9B), i.e. the effect of their activity on antennal motoneurons depends on the behavioural context (resting or flying). Stimulation of the scape–pedicel joint (pedicel–flagellum joint immobilized) of flying locusts produces resistance reflexes (Fig. 9C) similar to those seen in control animals.

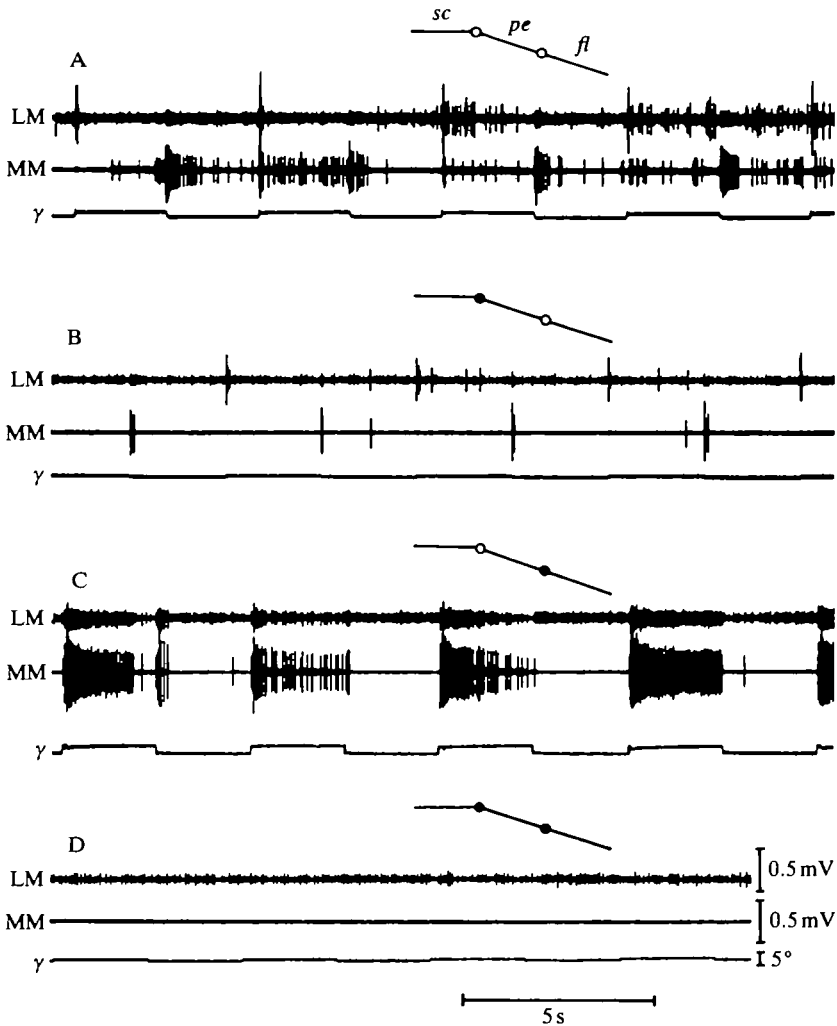


Fig. 8. Elimination experiments in a resting locust. (A) Response of an intact antenna to rectangular antennal deflections ( $\Delta\gamma$  approx.  $5^\circ$ ; median position of the stimulating needle): avoidance and resistance reflexes occur. (B) After immobilizing the active movable scape–pedicel joint (inset: ●) only the avoidance reflexes with phasic responses remain, whereas after immobilizing the pedicel–flagellum joint (C) the activities of the tonic discharges of resistance reflexes increase in MM compared with A. Immobilizing both antennal joints (D) suppresses all responses to antennal deflections. (For abbreviations, see Figs 2, 3.)

### Discussion

The relatively short antennae of locusts are less suitable as tactile sense organs than the long antennae of other arthropods, e.g. crayfish. Apart from this, there are similarities in the antennomotor systems of the two animal groups: for example, in both locusts and crayfish the antennae constitute an active tactile

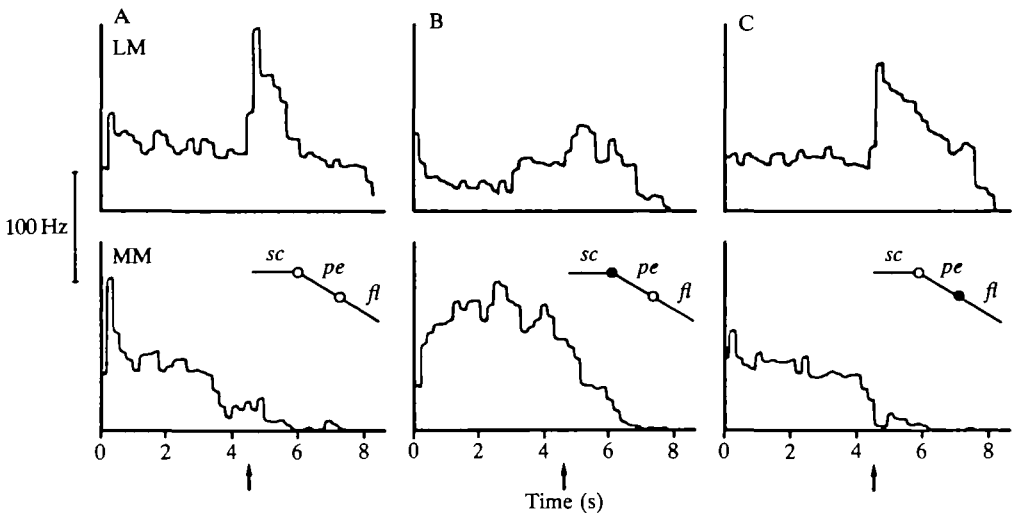


Fig. 9. Elimination experiments in a flying locust. Flight is triggered by the onset of air-current stimulation ( $V_A = 3 \text{ m s}^{-1}$ ) at 0 s; the end of flight is indicated by an arrow. Activity histograms (of all motor units of a scape muscle, Hz; binwidth 0.1 s) show averaged data for three successive stimulus periods. (A) Normal antennal-positioning reaction is performed after air-current stimulation as a result of activity of both scape muscles. (B) After immobilizing the scape–pedicel joint (inset: ●), the high activity in MM demonstrates the resistance reflex. (C) After immobilizing the pedicel–flagellum joint, the initial phasic activity is reduced in comparison with that of the control. (For abbreviations, see Figs 2, 3.)

system (Zeil *et al.* 1985) in which different antennal reflexes occur (Vedel, 1980). The phenomenon of reflex reversal in arthropods has previously been discussed by Bässler (1976, 1986), Vedel (1980) and Sandeman (1985). It is found in movement control of legs and antennae.

In the present paper it is shown that reflexes can be switched, e.g. by air-current stimulation, between the avoidance and the resistance reflexes. In resting or walking locusts mechanical deflection of one flagellum triggers (only in the same antenna) an avoidance reflex, as a defensive response, or reflex chains, by which an object could be scanned for tactile perception. In flying locusts, however, antennae are air-current sense organs. They are symmetrically projected forward in the flight position, and the attending aerodynamic forces deflect the flagella backwards (Gewecke, 1972*b*; Gewecke and Heinzl, 1980). This mechanical stimulation triggers resistance reflexes by which the flight position of both antennae is controlled. Therefore, the resistance reflexes are part of the antennal-positioning reaction which adapts the operating range for those mechanoreceptors of the pedicel that control flight speed (Gewecke, 1972*b*, 1975).

During flight the antennal muscles must contract continuously for hours. Bauer (1988) has shown that proctolin enhances tetanic contractions of the scape muscles. Therefore, it is possible that the operating range of the antennal muscles

can be shifted by proctolin or other cotransmitters to enable economic power generation. It should be tested in the preparation described above whether neurohormones or cotransmitters are involved in the modulation mechanisms underlying the antennal reflex reversal. The application of proctolin or of flight-releasing octopamine (Stevenson and Kutsch, 1986) could possibly have modulating effects on the antennomotor system.

Unpublished results with transient yaw stimulation of a locust flying in front of a wind tunnel demonstrate that the resulting excitation of the antennal neurones influences the activity of the basalar flight muscles. Under natural conditions all changes of flight direction and speed result in transient stimuli for any air-current sense organ, e.g. the antenna (Saager and Gewecke, 1985). Translatory or rotatory acceleration of a flying locust produces deflections of the flagella by inertial and by aerodynamic forces (Gewecke and Heinzel, 1980). These deflections stimulate the mechanoreceptors of the antennae, and the resulting resistance reflexes re-adjust the antennal flight position. Therefore, the antennal reflexes guarantee adequate positioning for control of the animal's movement by their antennae.

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### References

- ALBRECHT, F. O. (1953). *The Anatomy of the Migratory Locust*. London: Athlone Press.
- BÄSSLER, U. (1976). Reversal of a reflex to a single motoneuron in the stick insect *Carausius morosus*. *Biol. Cybernetics* **24**, 47–49.
- BÄSSLER, U. (1986). Afferent control of walking movements in the stick insect *Cuniculina impigra*. II. Reflex reversal and the release of the swing phase in the restrained foreleg. *J. comp. Physiol. A* **158**, 351–362.
- BAUER, C. K. (1988). Neuronale Kontrolle der Antennenbewegung bei der Wanderheuschrecke *Locusta migratoria migratorioides* (Reiche & Fairmaire, 1850). Inauguraldissertation, Universität Hamburg.
- BENNET-CLARK, H. C. AND EWING, A. W. (1970). The love song of the fruit fly. *Scient. Am.* **223**, 84–92.
- CLARAC, F. AND VEDEL, J.-P. (1975). Neurophysiological study of the antennal motor patterns in the rock lobster *Palinurus vulgaris*. I. Reflex modulation of extensor and flexor motoneurone activities. *J. comp. Physiol.* **102**, 201–221.
- GEWECKE, M. (1972a). Bewegungsmechanismus und Gelenkrezeptoren der Antennen von *Locusta migratoria* L. (Insecta, Orthoptera). *Z. Morph. Tiere* **71**, 128–149.
- GEWECKE, M. (1972b). Antennen und Stirn-Scheitelhaare von *Locusta migratoria* L. als Luftströmungs-Sinnesorgane bei der Flugsteuerung. *J. comp. Physiol.* **80**, 57–94.
- GEWECKE, M. (1975). The influence of the air-current sense organs on the flight behaviour of *Locusta migratoria*. *J. comp. Physiol.* **103**, 79–95.
- GEWECKE, M. AND HEINZEL, H.-G. (1980). Aerodynamic and mechanical properties of the antennae as air-current sense organs in *Locusta migratoria*. I. Static characteristics. *J. comp. Physiol.* **139**, 357–366.
- HEINZEL, H.-G. (1983). Rezeption von Luftströmungen und ihre Bedeutung für den Flug der Wanderheuschrecke. In *Insect Flight*, vol. 2 (ed. W. Nachtigall), pp. 53–69. Stuttgart, New York: Gustav Fischer Verlag.
- HEINZEL, H.-G. AND GEWECKE, M. (1987). Aerodynamic and mechanical properties of the antennae as air-current sense organs in *Locusta migratoria*. II. Dynamic characteristics. *J. comp. Physiol. A* **161**, 671–680.

- HERAN, H. (1959). Wahrnehmung und Regelung der Flugeigengeschwindigkeit bei *Apis mellifica* L. *Z. vergl. Physiol.* **42**, 103–163.
- HONEGGER, H.-W. (1981). A preliminary note on a new optomotor response in crickets: antennal tracking of moving targets. *J. comp. Physiol.* **142**, 419–421.
- HORN, E. AND BISCHOF, H.-J. (1983). Gravity reception in crickets: the influence of cercal and antennal afferences on the head position. *J. comp. Physiol.* **150**, 93–98.
- HORN, E. AND KESSLER, W. (1975). The control of antennae lift movements and its importance on the gravity reception in the walking blowfly, *Calliphora erythrocephala*. *J. comp. Physiol.* **97**, 189–203.
- KENNEDY, J. S. AND MARSH, D. (1974). Pheromone-regulated anemotaxis in flying moths. *Science* **184**, 999–1001.
- McFARLANE, J. E. (1953). The morphology of the chordotonal organs of the antenna, mouthparts and legs of the lesser migratory grasshopper, *Melanoplus mexicanus mexicanus* (Saussure). *Can. Entomol.* **85**, 81–103.
- SAAGER, F. AND GEWECKE, M. (1985). Die Heuschreckenantenne als Beschleunigungs-Sinnesorgan. *Verh. dt. Zool. Ges.* **78**, 240.
- SANDEMAN, D. C. (1968). A sensitive position measuring device for biological systems. *Comp. Biochem. Physiol.* **24**, 635–638.
- SANDEMAN, D. C. (1985). Crayfish antennae as tactile organs: their mobility and the responses of their proprioceptors to displacement. *J. comp. Physiol. A* **157**, 363–373.
- SANDEMAN, D. C. AND WILKENS, L. A. (1983). Motor control of movements of the antennal flagellum in the Australian crayfish, *Euastacus armatus*. *J. exp. Biol.* **105**, 253–273.
- STEVENSON, P. A. AND KUTSCH, W. (1986). Basic circuitry of an adult-specific motor program completed with embryogenesis. *Naturwissenschaften* **73**, 741–743.
- TISCHNER, H. AND SCHIEF, A. (1955). Fluggeräusch und Schallwahrnehmung bei *Aedes aegypti* L. (Culicidae). *Verh. dt. Zool. Ges.* **48**, 453–460.
- VEDEL, J.-P. (1980). The antennal motor system of the rock lobster: competitive occurrence of resistance and assistance reflex patterns originating from the same proprioceptor. *J. exp. Biol.* **87**, 1–22.
- ZEIL, J., SANDEMAN, R. AND SANDEMAN, D. (1985). Tactile localisation: the function of active antennal movements in the crayfish *Cherax destructor*. *J. comp. Physiol. A* **157**, 607–617.