

THE AUDITORY BEHAVIOUR OF FLYING LOCUSTS

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Summary

The auditory behaviour of tethered locusts flying in a wind tunnel was investigated under controlled acoustic conditions.

1. Reflection, attenuation and diffraction of ultrasound evoked by the locust's physical presence caused pronounced distortions of the acoustic field. Interaural pressure variations were observed that account for directional hearing at high frequencies.

2. Sound field measurements indicated only a minor influence of flight posture or wing position on the interaural pressure gradient.

3. The locusts steered away from pulsed ultrasounds that simulated bat echolocation signals. The phonotactic response was measured as ruddering by the abdomen and hind legs, resulting in a yaw torque directed away from the sound source. Wingbeat frequency increased by 15% in response to ultrasonic stimulation. This behaviour is considered to be analogous to the bat avoidance behaviour of flying crickets.

4. The avoidance response was observed for carrier frequencies higher than 10 kHz and for sound pressure levels (on average) higher than 45 dB SPL. Low-frequency stimuli (<10 kHz) failed to elicit any phonotactic steering at any intensity used (up to 100 dB SPL). Because of its relatively low threshold of reaction, this steering behaviour is thought to be part of an early-warning system adapted to the acoustic detection of echolocating predators.

5. The avoidance response was suppressed when a 30 kHz (normally effective) tone was combined with a 5 kHz tone (which is ineffective alone). Two-tone suppression only occurred when the low-frequency component was 10–15 dB SPL higher than the high-frequency tone. The biological significance of two-tone suppression is discussed.

6. The intensity–response characteristics, the frequency sensitivity and the two-tone suppression of the avoidance behaviour are discussed with respect to the auditory physiology of *Locusta migratoria*. The involvement of some identified auditory ascending interneurons in the avoidance behaviour is considered.

Introduction

The very rich literature on the biophysical and neurophysiological aspects of
Key words: locust, flight steering, acoustic behaviour, ultrasound avoidance.

acoustic communication and orientation of flying or walking insects (see Kalmring & Elsner, 1985) suggests that the acoustic ecology of these animals is adapted to two main functions. First, the recognition of complex conspecific acoustic signals (mainly studied in orthopterans) is of significance for reproductive behaviour (Regen, 1924, and many subsequent authors). Second, the acoustic detection of predators, such as echolocating bats, provides the basis of a predator avoidance system. Such behaviour was first described by Roeder for moth–bat interactions (e.g. Roeder & Treat, 1957; Roeder, 1967*a,b*). Green lacewings have an acoustic alerting system that produces an increased survival rate and thus, in turn, a selective advantage (Miller & Olesen, 1979). An acoustic warning system has also been reported in the praying mantis (Yager & Hoy, 1986), in bushcrickets (Bellwood & Morris, 1987) and in coleopterans (Spangler, 1988). Among orthopterans, avoidance steering in response to artificial bat cries has been described in flying crickets (Moiseff *et al.* 1978; Nolen & Hoy, 1986*a,b*).

Locusts and many (but not all, see Mason, 1969) other acridid grasshoppers possess sophisticated ears that have attracted much scientific attention. The sensitivity range of the ear, the response characteristics of the receptor cells and the biomechanics of the tympana have been described in detail (Michelsen, 1971*a,b,c*; Miller, 1977; Römer, 1976). Furthermore, neurophysiological studies on the auditory pathway of *Locusta* have yielded much detailed information; e.g. the synaptology of auditory neurones, processing of synthetic and natural sounds (Kalmring, 1975*a,b*), structure and function of metathoracic interneurones (Rehbein, 1976; Römer & Marquart, 1984), auditory input to the flight system (Boyan, 1985), differential processing of pure tones and complex model songs by auditory ascending interneurones (Boyan, 1986; Römer & Seikowsky, 1985), to mention only a few.

The behavioural consequences of stridulation have been intensively studied. Much less work has been devoted to the behavioural role of the auditory sense in flying grasshoppers. Haskell (1957) described a take-off tendency for resting *Schistocerca*, and Yinon *et al.* (1971) reported a delayed initiation of flight in quiescent *Schistocerca* exposed to wingbeat noise. More recently, Boyan (1985) has shown that sound can initiate rhythmic activity in flight muscles and flight interneurones, but did not mention any phonotactic effects.

However, phonotaxis may well be important in locust flight. Hearing is directional over the whole auditory range (*Schistocerca*, Miller, 1977; *Locusta*, Römer, 1976). At frequencies higher than 10 kHz, directional information relies on sound diffraction and attenuation by the locust body (non-inherent directional hearing, Michelsen, 1971*c*; Miller, 1977). This causes distortions of the sound field that produce an interaural acoustic pressure gradient. This gradient is considered to be the source of directional information at high frequencies. In addition, there is direct physiological evidence of binaural and directional processing at the level of auditory interneurones (Römer & Dronse, 1982; Römer & Seikowsky, 1985; Römer *et al.* 1981; Rowell & McKay, 1969).

In this paper I report that tethered flying locusts detect and steer away from

sources of ultrasonic pulses resembling bat cries. This response is similar to the bat avoidance steering response of flying crickets (Moiseff *et al.* 1978; Nolen & Hoy, 1986*a,b*). The intensity–response curve, the frequency sensitivity and the two-tone suppression of this avoidance behaviour are measured, and they are discussed in the light of neurophysiological studies on the auditory pathway of the locust.

Materials and methods

Animals

Adult *Locusta migratoria* (L.) of either sex were used in all experiments. They were obtained from a crowded laboratory colony kept at 26–28°C and on a 16 h:8 h light:dark cycle.

Experimental set-up

Intact locusts were tethered dorsally at the pronotum to the axle of a torque meter (Fig. 1A) that monitored the force produced by the animal around its vertical (yaw) axis. The yaw torque signal was generated by the translation of a small magnet over a Hall-effect sensor (Texas Instruments TL 173) as the locust turned. The freedom of rotation of the spring-loaded axle was $\pm 0.2^\circ$ (for details,

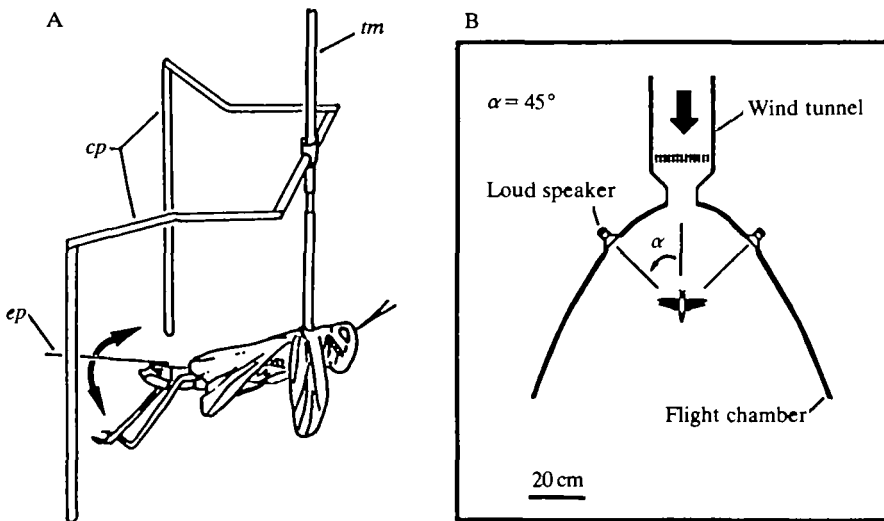


Fig. 1. (A) Configuration of the capacitive detector (*cp*) monitoring ruddering with the abdomen (arrow) and, due to capacitive coupling, the hindlegs, of a locust tethered to the torque meter (*tm*). This configuration interferes neither with the sound waves (see Results) nor with the aerodynamics of the flying locust. The locust also cannot touch the detectors (*cp*) with its hind legs or with the antenna of the capacitive detector (*ep*). (B) Top view of the flight chamber. The flying locust (not to scale) is positioned in the middle of the linear airstream. The angle of incidence (α) of the sound stimulus is 45° to the flight direction. The loudspeakers are mounted at the locust's height (11 cm from the ground; total height of flight chamber 55 cm).

see Robert, 1988). Sustained flight behaviour was elicited by the laminar air flow of a propulsion-type wind tunnel (Fig. 1B). Wind was set at the usual flight speed of 3 m s^{-1} (Gewecke & Philippen, 1978). All experiments were performed in the dark.

The behavioural response of the locusts was recorded both as yaw torque and as ruddering movements of the hind legs and abdomen. Yaw torque production and abdomen bending are clear indicators of steering efforts (Dugard, 1967; Camhi, 1970; Gewecke & Philippen, 1978; Taylor, 1981; Robert, 1988). Ruddering (this expression is used for the movements of both abdomen and hind legs) was monitored by means of a capacitive position transducer (modified after Forman & Brumbley, 1980) (Fig. 1A). The recordings were low-pass filtered (cut-off frequency 15 Hz) to remove signals at wingbeat frequency. The unfiltered signals were used to determine wingbeat frequency. Measurements were made only on animals displaying the full flight posture for at least 15 min after flight initiation. 53% of the animals tested ($N = 42$) responded during the first acoustic experiment. Most of the remaining 47% responded in subsequent tests performed a few hours or days later.

The flight chamber

The design of the flight chamber was adapted to the requirements of acoustic experiments. The flight chamber had a parabolic configuration and the locust was placed posterior to the focus of the parabola (Fig. 1B). The chamber was lined with soft white felt on the wall, and cotton wool on the floor. This configuration offered several advantages. First, the sound emitted by the loudspeakers was not reflected off the wall of the chamber on to the animal. Consequently, any echoes experienced by the animal were caused only by reflection of sound waves already reflected (and thus attenuated) off the animal itself. Moreover, the rear opening of the chamber took advantage of the high spatial attenuation of ultrasound and eliminated any echo from behind, where there was no hard structure orthogonally oriented to the sound waves within 3 m. Furthermore, the locust's flight location was not at the focal point of the parabola, thus preventing possible amplification effects. The flight chamber also provided good protection against sound field disturbances caused by the experimenter and apparatus. The fairly flat distribution of the sound pressure shown in Fig. 2 (for 15 and 30 kHz) attests that the experiments were performed under controlled acoustic conditions. There were two loudspeakers, one at 45° left of the longitudinal axis of the animal, the other at 45° to the right of this axis (Fig. 2). The sound field was homogeneous up to 35 kHz, irrespective of which of the sources was used.

Synthesis of the acoustic stimuli

Sound pressure levels were calibrated with 6.4 mm (B & K type 4135) and 3.2 mm (B & K type 4138) microphones, preamplifier (B & K type 2639) and measuring amplifier (B & K type 2609). If not otherwise stated, sound pressure levels are given in dB SPL re $20 \mu\text{Pa rms}$ ($2 \times 10^{-5} \text{ N m}^{-2}$). Means and standard

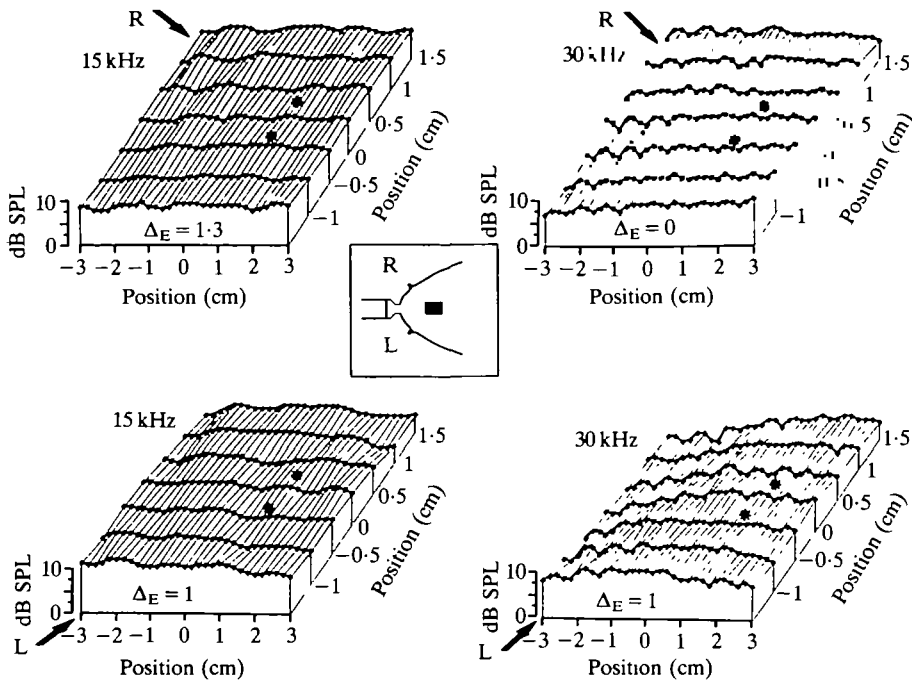


Fig. 2. Spatial distribution of the sound field in the presence of the fixation rod and the capacitive detectors (omitted for clarity), but without animal. Inset: orientation of the horizontal measurement area in the flight chamber, seen from above. Sound pressure is given in dB (SPL re 90 dB), for two frequencies (15 and 30 kHz) and two angles of incidence of the stimulus ($\pm 45^\circ$; L and R arrows). The asterisks show the virtual location of the locust ears. Δ_E is the sound pressure gradient calculated from the SPL values at the asterisk positions. The field is homogeneous within ± 2 dB over all frequencies tested (up to 35 kHz). This indicates no consistent bias in the experimental arrangement.

deviations of sound pressure levels were calculated from the values in pascals and reconverted into dB SPL. Sound pulses were synthesized by gating the output of a function generator (HP 3310B) with a custom-made trapezoidal pulse shaper with integrated broadband amplifier. Duration of the pulses was 20 ms and pulse repetition rate was 10 pulses s^{-1} . The rise/fall time of the envelope (linear and symmetrical) was set at 1 ms. Train length was 1 s. Constant-frequency tones with carrier frequencies ranging from 5 to 35 kHz were then produced with two horn tweeters (ACR Swiss type FT 15H), mounted symmetrically at the animal's height (Fig. 1). The sound pressure levels ranged from 40 to 100 dB at the animal, which was mounted 19 cm from the loudspeakers. The ultrasonic pulses resemble the echolocation cries of hunting bats.

To perform two-tone experiments, the sinusoidal signals of two function generators were mixed with a differential amplifier before being fed to the pulse shaper. Two-tone signals had the same temporal structure as single tones.

Acoustic field measurements

Since sound pressure gradients play a key role in acoustic orientation, it was necessary to assess how the sound field was distributed in the space around the flying animals. Sound pressures were measured systematically within a 3 cm × 6 cm horizontal plane centred on the animal's tethering point and at the height of the ears (for orientation, see inset of Fig. 2). The spatial distribution of the sound field in the presence of the holding rod and the capacitative detectors (but without the animal) is shown in Fig. 2. For all carrier frequencies used, the sound field in this area was homogeneous to within 4 dB. The pressure difference at the virtual position of the ears (interaural gradient Δ_E) (asterisks in Fig. 2) did not exceed 1.3 dB. The diffraction caused by the measuring devices was thus negligible.

To assess the importance of sound diffraction caused by the locust body, freshly anaesthetized animals were tethered to the torque meter. Mimicking two different typical flight postures, the wings were waxed at their hinge (i) in a midstroke position and (ii) in an upstroke position (see insets of Figs 3, 4). In addition, the legs were also waxed in the typical flight position. The postures were taken from drawings by Baker & Cooter (1979) and flash photographs of tethered flying animals by Thüring (1986) and the author. Sound pressures were then remeasured as described above. The 3.2 mm microphone was positioned vertically for convenience of manoeuvrability and to minimize the diffraction it caused.

Orientation of the acoustic stimulus

The angle of incidence of the sound stimulus was 45° right or left from the flight direction (Fig. 1B). This orientation was coherent with the acoustics and geometry of the flight chamber. The interaural sound pressure gradient has also been reported to be optimal at this angle of incidence (Miller, 1977; Römer, 1976).

Results

In locusts, directional hearing at high frequencies relies on interaural pressure variations (see Introduction). The first experiments were thus made to assess the pressure gradient between the two ears. Two natural factors could distort such a gradient; insufficient sound diffraction by the locust's body, and postural interference. These factors are investigated below.

Sound diffraction by the locust body

The diffraction caused by the presence of an object in a sound field is influenced by the size of the object and the wavelength of the sound (Yost & Nielsen, 1977). Here, the wavelength is of the same order of magnitude as the body size; between 3.44 cm (10 kHz) and 0.98 cm (35 kHz). Thus, diffraction is expected to cause pressure variations in the sound field surrounding the locust.

Sound field measurements showed that the side of the locust facing the sound source was submitted to a sound overpressure whereas the side opposite showed slight underpressure (Fig. 3). The sound shadowing effect was illustrated by a zone

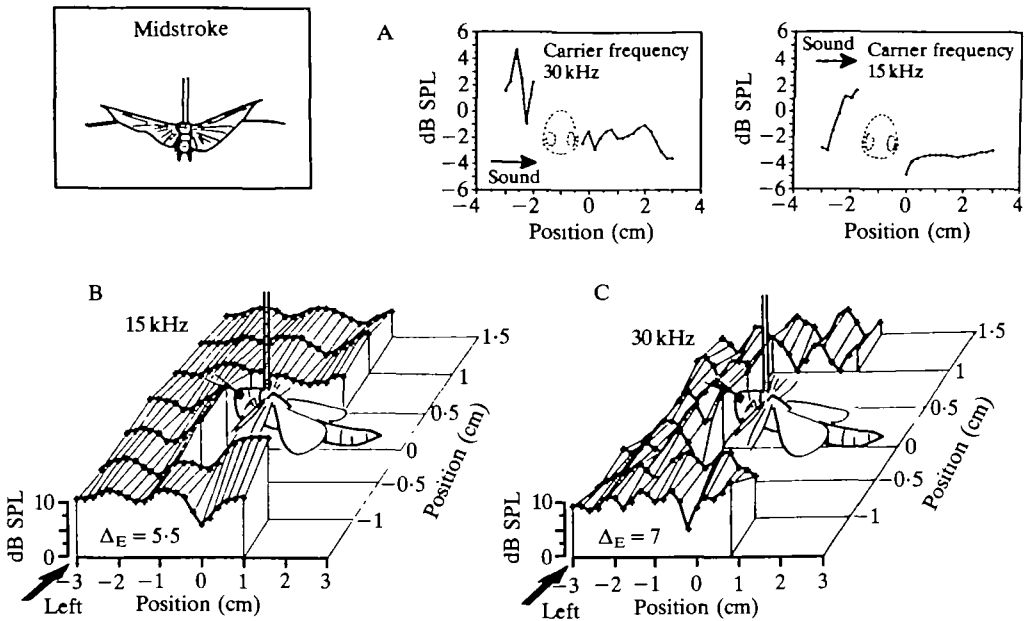


Fig. 3. Sound pressure distribution around a freshly anaesthetized locust. Sound pressure is given in dB SPL relative to 90 dB. Inset: caudal view of the fixed flight posture of the tethered animal. (A) Asymmetrical distribution of the acoustic pressure resulting from a sound stimulus 45° from the left. Measurements at the level of the ears, along the transverse (pitch) axis of the animal at 30 and 15 kHz. (B,C) Spatial distribution of the sound pressure around the animal. Conventions and abbreviations as in Fig. 2. Sound from the left (arrow). Note the more distorted distribution at 30 kHz (C).

of reduced sound energy on the right-hand side of the animal (Fig. 4). The mean interaural gradient of acoustic pressure, 8.2 dB (s.d. = $+2.2$, -3 dB; $N = 10$), is significantly different from zero. The spatial reconstructions of Figs 3 and 4 show the non-homogeneous distribution of sound pressure in the presence of a freshly anaesthetized locust fixed in midstroke flight posture. Since the free-field conditions were homogeneous (Fig. 2), the perturbations observed here are caused by sound diffraction, attenuation and reflection from the animal itself. Distortion was greater at 30 kHz than at 15 kHz, as shown in Fig. 3. In this set of measurements, the interaural gradients (Δ_E) were 5.5 dB for 15 kHz, and 7 dB for 30 kHz (Fig. 3B,C).

Importance of posture and wingbeat

At high frequencies, the position of the hind legs strongly influences the acoustic pressure at the eardrum (Adam, 1983). Similarly, the wings of a flying locust could cause sound pressure variations. Therefore, the pressure distribution (around the anaesthetized animals) was measured for two flight postures at 15 and 30 kHz

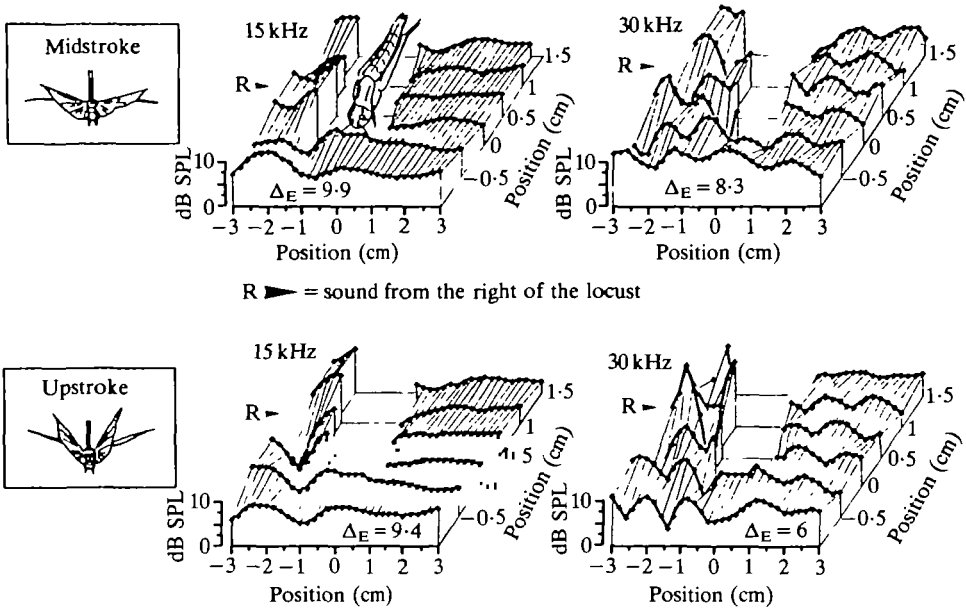


Fig. 4. Sound pressure distribution for different flight postures and carrier frequencies. Insets: caudal views of the flight postures. Upper diagrams: midstroke, lower diagrams: upstroke. The position of the animal (wings not drawn) relative to the measured area is shown in the upper left plot and then omitted for clarity. Sound is from the right of the animal (given in dB SPL re 90 dB). Note the zone of higher acoustic pressure on the side of the animal facing the sound source.

(Fig. 4). The results show that wing position has little effect on either the pressure distribution around the animal or on the interaural gradient Δ_E (Fig. 4).

However, the situation could be different during active flight in the wind tunnel. Sound recordings made close (2–4 mm) to the tympanum of a tethered flying animal indicated variations in sound pressure of 2 dB, which is small compared to the diffraction effect (8.2 dB mean attenuation). Wing movements modulated the sound pressure almost sinusoidally at the flight frequency (17–22 Hz), but on both sides simultaneously. The contribution of the wings – a thin soft material – to the modulation of sound seems to be of little importance, at least for high frequencies. Further, as both ears were affected equally and simultaneously, there was little effect on the interaural gradient.

Reaction to high-frequency pulses

High-frequency pulses (carrier frequency: 15 kHz, pulse length: 20 ms, pulse repetition rate: 10 pulses⁻¹, 64 dB SPL) delivered alternately from the right and the left of a tethered flying locust elicited ruddering (Fig. 5). Ruddering was correlated with the production of yaw torque (Fig. 5). For instance, stimulation from the left provoked abdomen bending and yaw torque, both to the right. Similarly structured ultrasonic pulses of 30 kHz carrier frequency (84 dB SPL)

were also effective in eliciting this behavioural response (Fig. 5). In response to ultrasonic stimulation, locusts thus alter their flight course and attempt to fly away from the sound source. Notably, different ultrasonic stimulation regimes [e.g. high intensity (>90 dB SPL) or repetition rates up to 200 pulses s^{-1}] elicited avoidance steering responses similar to those shown in Fig. 5.

After stimulus onset, there was an interval of 65 ± 10 ms before ruddering and 63 ± 17 ms before yaw torque. The reaction time shortened slightly as stimulus intensity increased (see Fig. 7). Moreover, wingbeat frequency increased by 15% in response to ultrasonic stimulation (from 17.6 ± 1.5 Hz to 20.3 ± 1 Hz, $N = 99$).

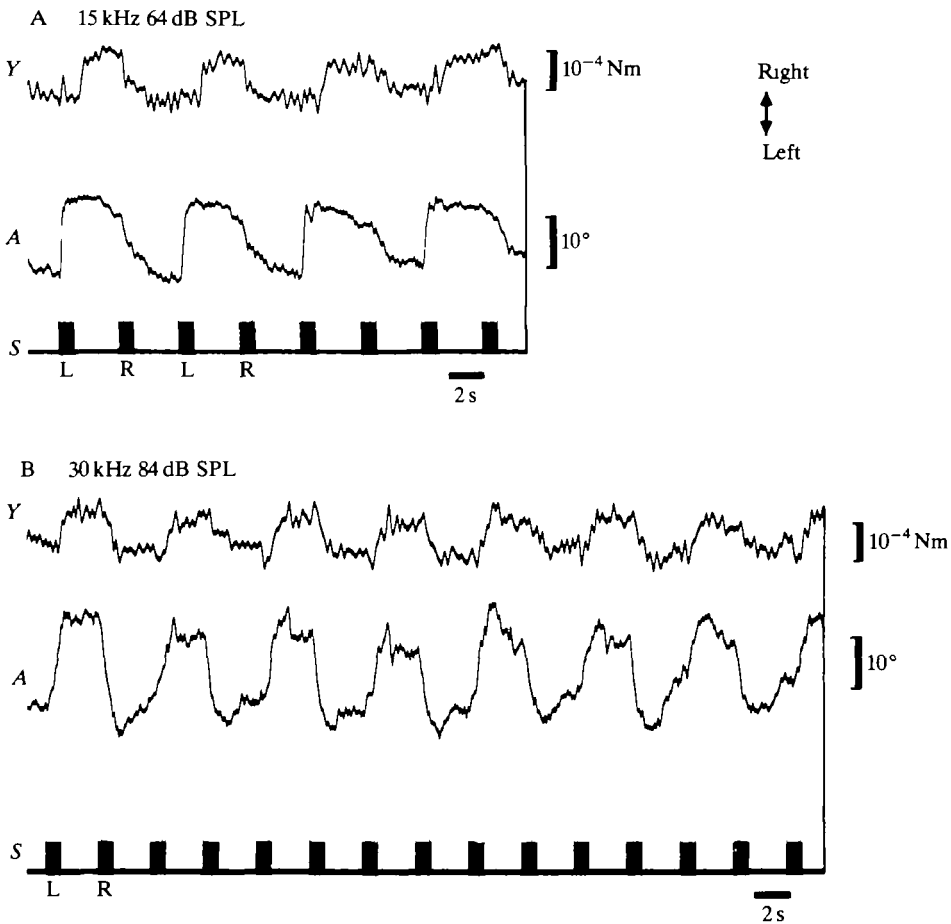


Fig. 5. Behavioural reactions of a steadily flying locust to pulsed ultrasounds. Pulse length 20 ms. Repetition rate 10 pulses s^{-1} . (A) 15 kHz, 64 dB SPL. (B) 30 kHz, 84 dB SPL. (S) Sound stimulus, given alternately from the left and the right. (A) Abdominal ruddering. (Y) Yaw torque. Abdominal ruddering and yaw torque are positively correlated and directed away from the sound source. The apparent phase lag between Y and A is due to different low-pass filtering of these traces.

(Wingbeat frequency also increases during visually induced steering, Schmidt & Zarnack, 1987.)

Above threshold intensity (mean 45.8 dB SPL at 15 kHz), the behavioural response was clearly directional; the animal bent its abdomen away from the ultrasonic source (Fig. 6). The amplitude of the steering response also depended on the intensity of the acoustic stimulus (Figs 6, 7). This non-linear, saturating type of intensity–response relationship has previously been related to the binaural processing of acoustic information (Pollack & Plourde, 1982) (see Discussion).

The frequency sensitivity of the avoidance behaviour is shown in Fig. 8. The threshold of reaction is defined as the minimal sound pressure level eliciting a clear

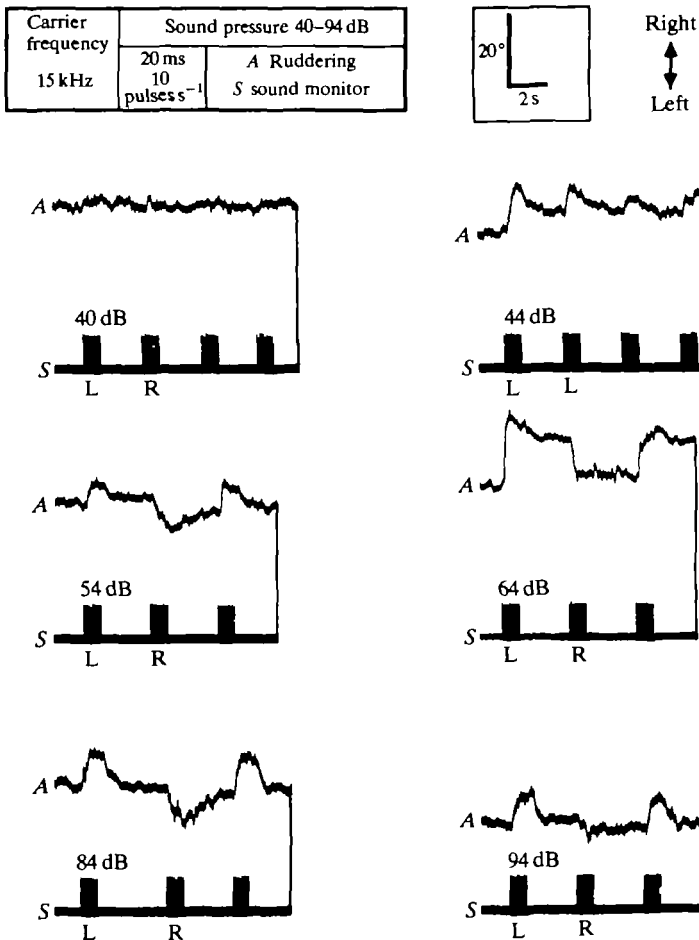


Fig. 6. Recordings of the ultrasound avoidance response of a flying locust for 15 kHz at different stimulus intensities. (A) Abdominal steering movements are used to monitor the steering response. (S) Sound stimulus given alternately from the right (R) and the left (L) (except for the 44 dB SPL recording). Stimulation conditions are given in the inset.

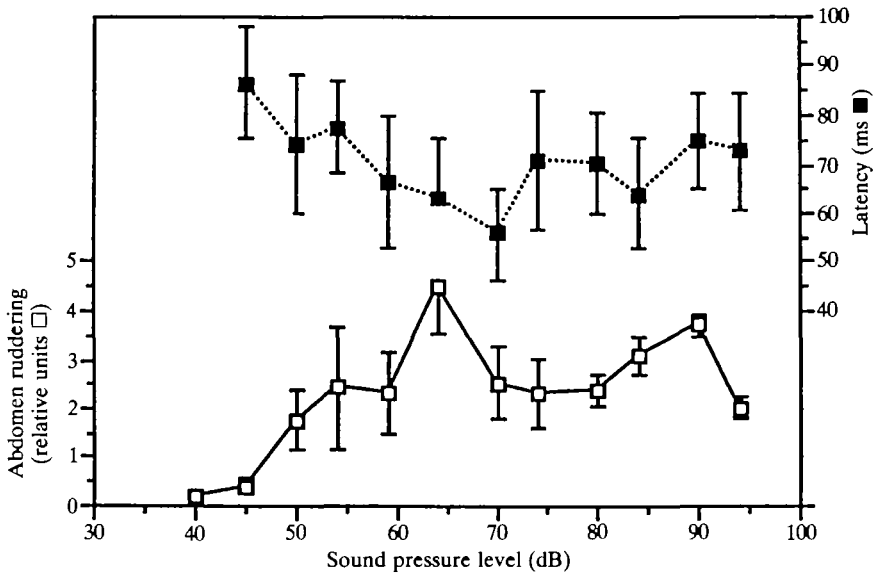


Fig. 7. Intensity and latency of the ultrasound steering reaction as a function of stimulus intensity. Acoustic stimulation 15 kHz, pulse length 20 ms, repetition rate 10 pulses s^{-1} , intensity range 40–95 dB SPL. Each point of the intensity curve (open squares) is the mean (\pm s.e.m.) of 4–9 events. Each value of the latency curve (filled squares) is the mean (\pm s.d.) of 7–13 events ($N = 105$).

directional avoidance steering response (measured as ruddering). All sound pulses were 20 ms long and were delivered at 10 pulses s^{-1} repetition rate (train length 1 s). Threshold did not vary much between 15 and 30 kHz, but was noticeably higher for 10 kHz (56.9 dB SPL, s.d. = +3.5, -4.7) and was infinite (i.e. no reaction) at 5 kHz (Fig. 8, arrow).

Reaction to low-frequency pulses

Neither positive nor negative phonotaxis was observed following 5 kHz pulsed tones (20 ms, 10 pulses s^{-1}) over an intensity range of 64–100 dB SPL (Fig. 9). The 15 kHz 64 dB SPL control performed immediately after the trial at 5 kHz 100 dB SPL demonstrated the continuing good responsiveness of the animal. 5 kHz pulses delivered at different pulse lengths (1–50 ms) and repetition rates (200–4 pulses s^{-1} , respectively), or as continuous tones of 1 s duration also failed to provoke steering reactions (not shown).

Two-tone suppression

The two-tone experiments described here show that the negative phonotaxis elicited by a high-frequency (15 kHz) stimulus can be suppressed by the simultaneous delivery of an identically pulsed low-frequency tone (5 kHz).

Single- and two-tone sequential tests were performed with the same steadily flying animal (Fig. 10). First, as a control, the high-frequency tone alone elicited

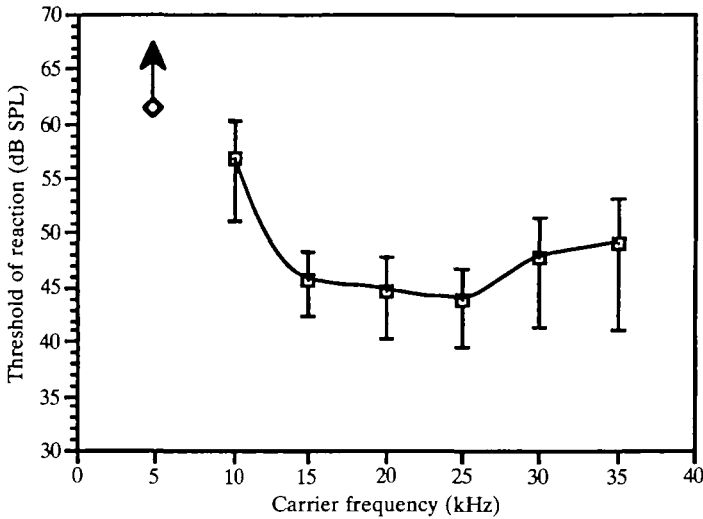


Fig. 8. Behavioural audiogram showing the threshold tuning curve of the avoidance steering response. Threshold of reaction is defined as the minimal sound pressure level eliciting a clear directional avoidance response (measured as the amplitude of abdominal steering). Each value is the mean (\pm s.d.) of nine animals. Means and standard deviations are calculated from values in pascals. Sound pulses 20 ms long at 10 pulses s^{-1} (train length 1 s). Since 5 kHz sonic pulses do not elicit any steering behaviour, the corresponding threshold is infinitely large (arrow).

the avoidance response (ruddering is shown) (Fig. 10A). For suppression to occur, the low-frequency tone had to be louder than the high-frequency tone (respectively 65 and 85 dB SPL), as shown in Fig. 10B,C. The low-frequency component alone did not induce any steering reaction (Fig. 10D), whereas a control 15 kHz pulse did, showing that the absence of response was not due to fatigue (Fig. 10E). In Fig. 10B, ruddering to the left marked by the arrowhead is not related to any acoustic stimulus. Spontaneous steering manoeuvres sometimes appeared when the animals were flying in the dark; this did not, however, influence their responsiveness.

The low-frequency sound pressure at which the suppression occurred depended on the high-frequency sound pressure. Accordingly, two-tone suppression curves were determined for different high-frequency sound pressures (Fig. 11). It appears that the intensity difference (low-frequency minus high-frequency) required for suppression is 10–15 dB.

Discussion

The biophysical basis of acoustic orientation

The biophysical basis of directional hearing (and thus acoustic orientation) in the locust has been established by Michelsen (1971a,b,c). Directional hearing at high frequencies is principally based on sound diffraction, reflection and attenu-

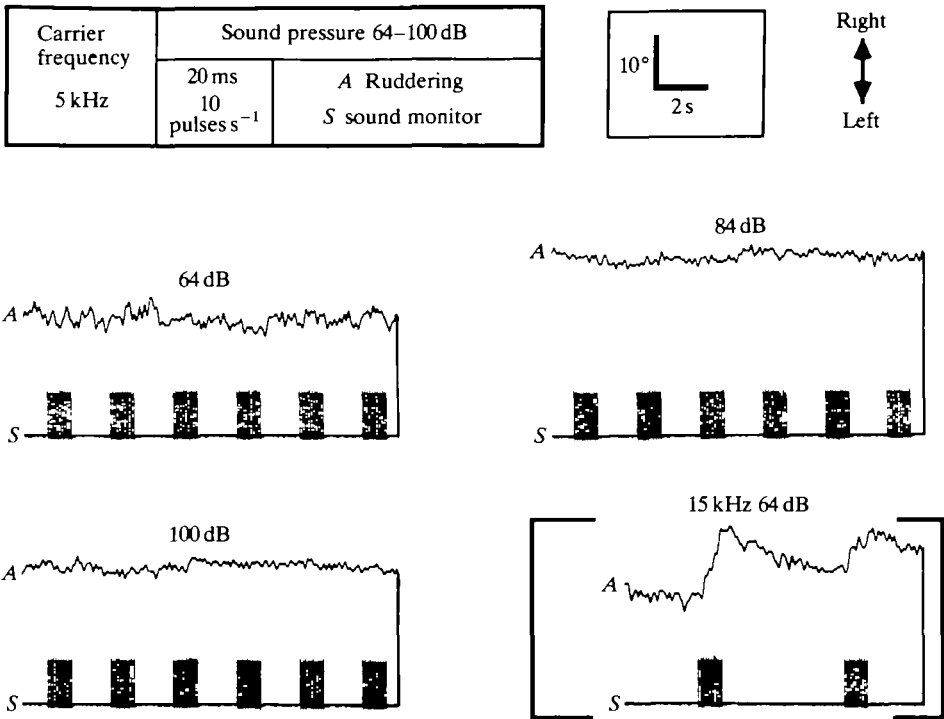


Fig. 9. Sonic stimulations at 5 kHz (see inset) of various intensities. Specifications in the inset. Framed traces 15 kHz 64 dB SPL control performed 15 s after the trial at 5 kHz 100 dB SPL. Tones were given exclusively from the left.

ation by the locust body (Michelsen, 1971c; Miller, 1977; Römer, 1976) so that, at frequencies higher than 10 kHz, the ears are working as pressure receivers. Because of this property, the interaural gradient seems to be the unique source of the directional information that can be extracted from ultrasonic stimuli.

The present results show that the physical presence of an intact locust – in a typical flight posture – alters the sound field in accordance with the measurements and expectations of Michelsen (1971c). The locust's side facing the sound source experiences an overpressure, whereas the far side is in the 'sound shadow' (Figs 3, 4). The mean pressure gradient (Δ_E) of 8.2 dB SPL (s.d. = +2.2; -3) reported here corroborates the measurements of Adam (1983; 8–12 dB) and Miller (1977; 8 dB).

Postural influence

Adam's measurements (1983) describe the influence of the hind femora on the sound pressure in the tympanal aperture of *Locusta*. His results show that, at high frequency (20 kHz), femoral diffraction only influences the frontal/caudal sound gradient. According to Adam, this effect would help to solve the delicate problem of frontal/caudal stimulus ambiguity but in no way contribute to the formation of

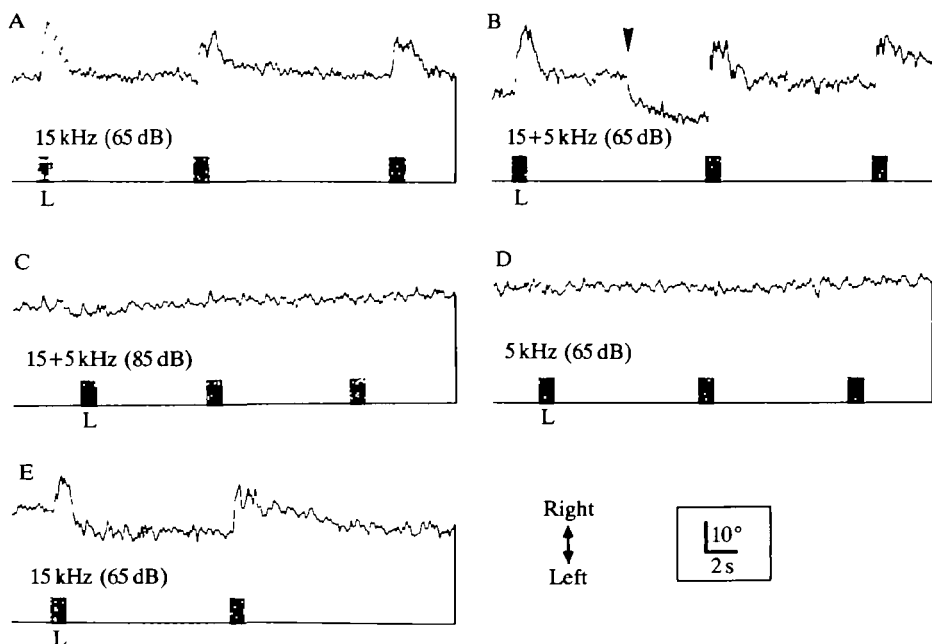


Fig. 10. Two-tone suppression of the avoidance steering response. Sound stimulation from the left. Upper trace: abdominal steering. Lower trace: sound monitor. Pulses 20 ms at 10 pulses s^{-1} . (A) 15 kHz ultrasonic stimulus eliciting avoidance steering. (B) Two-tone stimulus ($15+5\text{ kHz}$) with both frequencies at low intensity (65 dB). Arrowhead: spontaneous ruddering to the left. (C) Two-tone suppression caused by simultaneous presentation of high-frequency (65 dB) and low-frequency (85 dB) pure tones. (D) Low-frequency tone alone. (E) 15 kHz control stimulus attesting the locust's responsiveness.

interaural pressure difference. Abdominal bending and hind-leg yawing would then have no effect on directional hearing.

Similarly, the present results do not indicate any dependence of the interaural pressure gradient Δ_E on wing position (Fig. 4). The beating wings modulate the acoustic pressure bilaterally only to a small extent (2 dB). It can therefore be concluded that the locust's directional sensitivity to ultrasound does not depend physically on wingbeat.

However, the present evidence does not exclude the possibility that wingbeat can affect the hearing process in other ways. Indeed, peripheral modulation of auditory receptor activity has recently been reported to occur during flight activity (Hedwig, 1988).

Acoustic behaviour of flying locusts

The only behaviour of *Locusta* that has previously been related to acoustic stimulation is flight initiation elicited by a broadband (white) noise (Haskell, 1959; Yinon *et al.* 1971). It has been reported that low (5 kHz) and high ($15, 30\text{ kHz}$)

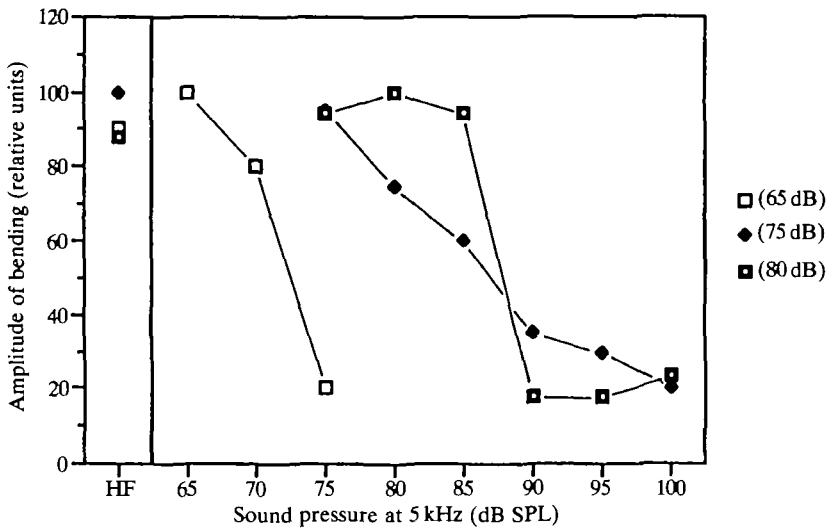


Fig. 11. Two-tone suppression curves. Amplitude of abdominal bending as a function of the intensity composition of the two-tone stimulus. Abscissa, amplitude of reaction for high-frequency (HF) pure tones alone. Suppression of the steering reaction takes place at low-frequency sound levels 10–15 dB louder than that of the high-frequency component.

frequencies promote activity of tergo-sternal muscles (M83), known to be initiators of wing opening (Boyan, 1985). But a flight initiation mechanism (or an enhancement mechanism) does not necessarily imply a need for directional hearing. Other authors, however, have emphasized the inherent (at low frequencies) as well as non-inherent (at high frequencies) directional characteristics of the locust ear (Michelsen, 1971c; Miller, 1977; Römer, 1976). Furthermore, directional processing of the acoustic information has already been observed physiologically (Römer & Dronse, 1982; Römer & Seikowsky, 1985; Rowell & McKay, 1969; von Helversen & Rheinländer, 1988), suggesting that locusts have the ability to perform some acoustic orientation tasks.

It is demonstrated here that tethered locusts flying in a laminar airstream orient with respect to a high-frequency sound source.

Physiological correlates of the avoidance behaviour

Previous studies have provided detailed information on the frequency sensitivity of the auditory receptors (Michelsen, 1971a; Römer, 1976). Remarkably, the threshold curve of the d-group (named by Gray, 1960; *Locusta*) receptor cells [Michelsen, 1971a, *Schistocerca*; Römer, 1976, *Locusta* (type 4); Inglis & Oldfield, 1988, *Valanga*] strongly resembles the audiogram of the avoidance behaviour (Fig. 12). Since only these receptors display a low threshold for the (ultra)sonic frequencies that provoke the ultrasound response, it is very tempting to infer that their activity is directly responsible for avoidance steering. The

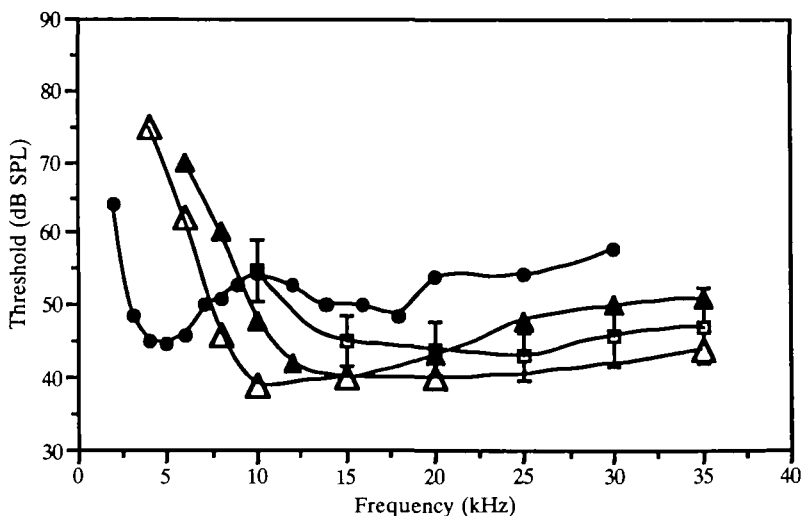


Fig. 12. Tuning curves of the ultrasound avoidance response (□), a high-frequency auditory receptor (type 4 ▲), the auditory nerve (●) and an identified interneurone (SN5) of the auditory neuropile (△). All data are obtained for *Locusta migratoria*. Data on receptor type 4 and auditory nerve from Römer (1976) and SN5 interneurone from Römer *et al.* (1988).

informational content of the ultrasonic pulse (mimicking the bat's echolocation cry) would then be conveyed exclusively by interneurons postsynaptic to the d-receptor fibres. Recently, the high-frequency afferents have been shown to branch mainly in the anterior intermediate sensory neuropile of the metathoracic ganglion (Halex *et al.* 1988; Römer *et al.* 1988). Interestingly, Marquart (1985) reports a local interneurone (UGN5, named SN5 in Römer *et al.* 1988) which branches restrictively in the area of the high-frequency terminals. Additionally, its tuning curve closely corresponds to that of the d-receptor (Fig. 12). The striking similarity between the sensory, neuronal and behavioural tuning curves strongly suggests a direct involvement of the SN5 cell type in the ultrasound avoidance behaviour. The tuning curve of the auditory nerve (from Römer, 1976) shows the additional sensitivity of the whole ear (Fig. 12) in the low-frequency range.

Involvement of identified ascending auditory interneurons in the avoidance behaviour

Several observations support the idea that ascending auditory metathoracic interneurons are involved in the ultrasound avoidance behaviour. First, intracellular investigations (A. Baader, in preparation) reveal ultrasonic-sensitive interneurons that, when electrically stimulated, cause abdomen movements away from the sound source. Second, some identified ascending auditory interneurons [531 (AN1), 533 (AN2), 539 (AN3), 541 (AN4)] are already known to be predominantly excited by high-frequency pure tones (Römer & Seikowsky, 1985; Marquart, 1985). (The synonymy of the interneurons mentioned in the present

Table 1. *Synonymy of some acridid identified auditory metathoracic interneurones (based partially on Boyan, 1986)*

Interneurone		Reference
529	AN10	Marquart (1985)
	B2	Kalrmring (1975a)
531	AN1	Römer & Marquart (1984)
	B1	Kalrmring (1975a)
	TH3-AC1	Hedwig (1986)
533	AN2	Römer & Marquart (1984)
539	AN3	Römer & Marquart (1984)
541	AN4	Marquart (1985)
714	G	Rehbein (1976)
–	SN5	Römer <i>et al.</i> (1988)
	UGN5	Marquart (1985)
139*	SN2	Römer <i>et al.</i> (1988)
	UGN2	Marquart (1985)

Numerical nomenclature after Robertson & Pearson (1983).

* After K. G. Pearson (unpublished results).

study is listed in Table 1.) For instance, 533 (AN2) shows an inhibitory reaction to low-frequency pure tones and a combined inhibition–excitation to conspecific broadband model songs, whilst it is excited by high-frequency pure tones (Römer & Seikowsky, 1985). Third, by means of anatomical criteria and calculation of synaptic delays, Römer *et al.* (1988) provide evidence that AN2 (533) receives excitatory input from SN2 (139), a local interneurone located close to branches of the high-frequency receptors. However, as these authors point out, superimposition of terminal branches is not necessarily indicative of synaptic contacts.

The intensity–response curve of the avoidance behaviour (Fig. 7) is qualitatively similar to those of ascending auditory interneurones reported by Römer & Seikowsky (1985) and Römer & Dronse (1982). These neurones have an optimum intensity range. According to Römer & Seikowsky, this is due to the combined effects of intensity-dependent inhibitory and excitatory inputs. This type of intensity coding (saturating, non-linear proportionality) has also been implicated in binaural processing of acoustic information in crickets (Pollack & Plourde, 1982) and in locusts (Römer & Dronse, 1982; Kalrmring, 1975a).

What is the effect of sonic stimulation?

Low-frequency (1–9 kHz) pure tone stimuli fail to elicit steering behaviour (Fig. 9). At first sight, it could be thought that low-frequency pure tones (at least within the limits of the temporal and spectral parameters used here) are in this context of little informational significance. However, this auditory information is

known to be coded by thoracic interneurons and conveyed by ascending interneurons to the brain (Boyan, 1983; Rehbein, 1976; Römer & Seikowsky, 1985). The absence of a low-frequency-related orientation behaviour in flight does not rule out roles in other contexts and, indeed, species-specific stridulation is dominated by low-frequency sound. Furthermore, even in the flight-steering context, low-frequency sound may have a modulatory effect on the high-frequency response.

The two-tone stimulus experiments reported above show this to be the case. As shown in Figs 10 and 11, suppression of the avoidance behaviour occurs when the low-frequency tone is some 10–15 dB louder than the high-frequency tone. This result corroborates the findings of Nolen & Hoy (1986b) on flying crickets (*Teleogryllus*). In crickets, pulsed 5 kHz pure tones delivered simultaneously at sound pressure levels 10–15 dB louder than the high-frequency ones (which normally elicit avoidance steering), completely suppressed the steering response.

Apart from the interesting finding that the auditory system of the locust (like other orthopterans: *Gryllus bimaculatus*, Boyan, 1981; *Teleogryllus bimaculatus*, Nolen & Hoy, 1986b) displays two-tone suppression effects, the present experiments show that the avoidance response is not the consequence of unspecific stimulation of the locust's auditory system. The avoidance response clearly depends on the frequency content of the signal (Fig. 10). The present results demonstrate that pure tones (mimicking hunting bats) and two-tone stimuli (which feature low- and high-frequency components) have different behavioural effects.

In an electrophysiological study on *Locusta*, Römer & Seikowsky (1985) report that identified ascending auditory interneurons (AN1, AN2, AN4) receive both excitatory and inhibitory inputs from, respectively, high-frequency (12 kHz) and low-frequency (4 kHz) tones. Further, A. Baader (personal communication) has observed two-tone suppression in locust metathoracic auditory interneurons. Moreover, the simulated stridulatory noise of *Locusta*, through its low-frequency components (some 15–20 dB louder than the high-frequency components), has an inhibitory effect on AN1 (531), which is known to be predominantly sensitive to high frequencies (Römer & Seikowsky, 1985).

Biological significance of two-tone suppression in Locusta

The biological significance of two-tone suppression in the flying locust may, however, differ from the one proposed by Nolen & Hoy (1986b) for flying crickets. In crickets, which fly while searching for a mate, the role of two-tone suppression would be to prevent the avoidance of the conspecific calls (because of their high-frequency harmonics) by a suppressive effect of the low-frequency fundamental. Do flying locusts hear sounds containing both low and high frequencies? Obviously, the stridulatory chirps of resting locusts and the wingbeat noise display the required broadband characteristics (Adam, 1969; Haskell, 1957). The limited acoustic power of stridulation (as well as spatial and spherical spreading attenuation) makes it unlikely that flying locusts hear their congeners stridulating at ground level. In the Oedipodinae (such as *Locusta*), stridulation is less complex

and does not play as vital a role in pair formation as in some other grasshopper subfamilies (e.g. Gomphocerinae) (Uvarov, 1977). Acridid grasshoppers, unlike gryllids and some tettiigonids, do not seek stridulating partners while in flight. Stridulation in acridids occurs only in situations where flight is unlikely.

Haskell (1957) analysed the frequency content of the wingbeat noise and reported that 70% of the whole sound energy is concentrated in a narrow band of 3.2–5 kHz. Consequently, only a reduced, but not negligible, sound power is found in the ultrasonic range. As pointed out by Boyan (1986), the sound pressure of the wingbeat noise at 10 cm (sound level: 62–70 dB, Haskell, 1957) would theoretically be sufficient to suppress the activity of auditory interneurons, notably of IN714 (G) (Boyan, 1986). One might then speculate that the function of suppression is to mask the high-frequency harmonics of the wingbeat noise, which would otherwise elicit the ultrasound avoidance response. Two-tone suppression would then act as a contextual filter for high frequencies and suppress acoustic responses while in flight (swarm and own flight noise). However, this hypothesis has not yet been tested with playback experiments of model wingbeat sounds.

Furthermore, it has been suggested (Boyan, 1986) that the filtering effect of suppression enhances the sensitivity to ultrasonic pure tones. In an adaptive perspective, this makes sense, since ultrasound discrimination has survival value for flying locusts.

Comparison with crickets

The striking resemblance between locusts (*Locusta*) and crickets (*Teleogryllus*) seen in the ultrasound avoidance behaviour is also reflected in the physiology of identified interneurons. The crickets' interneurone Int-1 has been described to be both sufficient and necessary for the occurrence of the avoidance behaviour (Nolen & Hoy, 1984). Furthermore, it is selectively excited by high-frequency tones, displays a suppression of its spiking activity by two-tone stimuli (Moiseff & Hoy, 1983; Nolen & Hoy, 1986b) and shows lateralization in the processing of ultrasonic stimuli (Moiseff & Hoy, 1983). It seems likely that ascending auditory interneurons (AANs) are serious candidates for the role of key neural elements in the ultrasound avoidance behaviour in *Locusta*.

Interaction between locusts and bats

The success of the avoidance response depends on several factors, such as the neural reaction time to the ultrasonic stimuli, the threshold of the reaction and the speed difference between the bat and the locust. The latency of the behavioural steering reaction ranges from 40 to 88 ms (65 ± 10 ms). The locust initiates the avoiding turn within about one wingbeat (period approx. 60 ms). Considering this short reaction time, how reasonable are the chances of a flying locust of escaping from a hunting bat?

Based on estimations of Miller (1983) for noctuid moths, one can assume that a locust, with a mean detection threshold of 46 dB SPL (s.d. = +2.4, -3) in the 15–35 kHz range, is able to detect a crying bat (84 dB SPL at 1 m, Kick, 1982) when

it still is some 20 m away (this takes into account the spatial attenuation of these ultrasounds as well as spherical spreading). With low levels of background noise, a vespertilionid bat is able to localize a prey the size of a locust at a maximum distance of about 5 m (Fullard & Thomas, 1981) (assuming that the bat has a threshold for echo-detection of 0 dB; Kick, 1982). The locust thus has a spatial safety factor of at least 4 (20 m/5 m). Under favourable conditions, the temporal safety (the time to detection) in favour of the locust probably ranges from 2 to 5 s, assuming a speed difference between the bat and the locust of 6 to 11 ms⁻¹ [hunting bat speed: 10–14 ms⁻¹ (J. Gebhard, personal communication); locust speed: 3–4 ms⁻¹].

In view of these estimates, it is likely that locusts benefit from an early-warning system against echolocating hunting bats. In this context, it is worth mentioning that some vespertilionid bats, by raising their emission carrier frequency (up to more than 100 kHz), could make their echolocation signals less detectable to insect prey (Fullard & Thomas, 1981). This, however, would have to be made at the cost of the maximum distance for target detection by the bat, since high frequencies rapidly attenuate in air.

Observations in the field

The dispersal flights of solitary-phase locusts and most other grasshoppers occur at night. Flying grasshoppers, embarrassingly abundant, ubiquitous and good-tasting (Holt, 1885), are thus potential prey for insectivorous bats. However, there is no direct evidence, similar to the elegant field observations by Roeder (1967*a,b*) on flying moths, that bats prey on locusts. But bats will prey on orthopterans (Bellwood & Morris, 1987; H. Rowell & J. Gebhard, personal observations). In a field study, Barclay (1985) reports that the African vespertilionid bat *Scotophilus* feeds on Orthoptera. This order, however, does not represent the bat's main diet, which consists of over 75 % of Coleoptera and Hemiptera.

Interestingly, it has been reported that, in Africa, some people combat small to mid-size swarms by hitting metallic pots. This deflects the swarms from their dwellings. Accordingly, wild African locusts are expected to show ultrasound avoidance behaviour.

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