

Directional Hearing in the Locust *Schistocerca gregaria* Forskål (Acrididae, Orthoptera)

Lee A. Miller

Institute of Biology, Odense University, DK-5230 Odense, Denmark

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Summary. At 2 kHz, 3.5 kHz and 5 kHz the locust ear functions as a mixed pressure and pressure-gradient receiver. The ear is inherently directional at these frequencies. The directional characteristics are independent of the amount of body tissue (Figs. 6 and 7). At 15 kHz the locust ear functions mostly as a pressure receiver, and is inherently non-directional (Fig. 6d). Hearing is, however, directional at 15 kHz owing to diffraction caused by the body (Fig. 1). Auditory thresholds are influenced by the amount of body tissue at frequencies from 2 to 15 kHz (Fig. 8). At frequencies less than 6 kHz the sound conducted through the body is attenuated by 1 to 8 dB depending on the amount of body tissue. At frequencies greater than 12 kHz the sound conducted through the body is attenuated by up to 18 dB, and the attenuation is only slightly influenced by body tissue (Fig. 2). The attenuation of sound conducted through the body is independent of the direction of sound, but may be affected by the amount of tissue between the ears (Fig. 4). The tissue in the body appears to act as a 'resistive' element, which introduces a phase shift in the sound conducted through the body relative to that striking the front side of the tympanum. Body tissue can set the level of sensitivity, but does not influence the receiver characteristics of the ear.

Introduction

Acridid grasshoppers have two bilaterally symmetrical ears (tympanal organs) located in the first abdominal segment. The intact locust ear functions primarily as a pressure receiver at frequencies above about 10 kHz (Michelsen, 1971 c). This conclusion is based partly on the fact that very little sound reaches the back side of the tympanum owing to attenuation in the body. Consequently, the ear *itself* should not contribute to directionality at high frequencies. The situation below about 8 kHz is more complex. A considerable amount of sound can reach the back side of the tympanum suggesting that the ear itself might function more like a pressure-gradient receiver. To what extent the intact locust ear functions

as a pressure-gradient receiver at lower frequencies cannot be determined from existing studies (Katsuki and Suga, 1960; Autrum et al., 1961; Michelsen, 1971 c; Römer, 1976). (For a detailed account of the physiological and biophysical aspects of insect hearing see Michelsen and Nocke, 1974). The amount of tissue in the locust body greatly affects the auditory threshold, with sensitivity being inversely proportional to tissue weight at frequencies below about 10 kHz (Michelsen, 1971 c; Römer, 1976). Michelsen (1971 c) suggests that the low sensitivity is due to internal dampening, which is probably caused by large amounts of tissue in bodies of fat animals. Body tissues, then, may influence the directional characteristics of the ear at frequencies below 10 kHz.

In this paper I describe hearing in the desert locust (*Schistocerca gregaria* Forskål) as a function of angle of incidence, body tissues, and frequency. I also describe the diffraction of sound caused by the body and the attenuation of sound conducted through the body as a function of body tissue, angle of incidence, and frequency.

General Methods

Experiments were performed in a sound tunnel located in a small room, which was insulated with 10 cm of mineral wool. The sound tunnel and sound generating apparatus were identical to that described by Michelsen (1971 a). Sound pressure levels (SPL) are given in dB values relative to 2×10^{-5} Newtons/m² if not otherwise stated.

A holder was designed to rotate the animal in the sound field. It consisted of a fork composed of two hypodermic needles 2 mm in diameter and 15 mm long mounted 15 mm apart in a brass block measuring 25 mm by 8 mm by 5 mm. The brass block was mounted on a brass rod 8 mm in diameter and 153 mm in length. The holder could be rotated continuously through 360°. The holder was grounded and served as the reference electrode in physiological experiments.

Adult *Schistocerca gregaria* (Forskål) 2 to 11 weeks after the final moult were used in these studies. In some cases individuals were starved for up to 28 days to reduce fatty tissues in the abdomen. In all cases a period of 12 h elapsed between the last feeding and experimentation.

The animals were prepared for experimentation by first removing the head, legs and wings. The gut was not removed. The insects were then impaled on the holder ventral side up through the mesothorax and the second or third abdominal segment. At 0° the ear (or microphone that replaced the ear) faced the sound source, which was placed 70 cm from the preparation. The preparations were rotated counter clockwise when right ears were examined and clockwise when left ears were examined (see inset in Fig. 5b).

The tissue located between the ears was weighed following each directional hearing and conduction experiment. The animals were arbitrarily divided into four weight groups (WG) based on the amount of tissue between the ears.

The sound field was calibrated with a 1/8 inch microphone (free-field) and accessory apparatus (Brüel & Kjaer). The microphone cartridge was mounted on a right angle adaptor such that the preamplifier was located about 10 cm below the preparation. The microphone (together with the right angle adaptor and preamplifier) was omnidirectional to within ± 3 dB up to 60 kHz. The sound field around the preparation was uniform to within ± 0.5 dB at 5 kHz, and ± 1 dB at 15 kHz. dB values are relative to the sound pressure level in the undisturbed sound field at 0°.

An IBM 360/65 digital computer using a standard IBM Fortran IV G level compiler and the Statistical Analysis System (University of Kentucky Computing Center) was used to perform analyses of variance, including two and three-way analyses, on the data. The homogeneity of variances was confirmed using the F_{\max} test (Sokal and Rohlf, 1969). Several analyses of variance models were tested on the data to obtain the P values presented below. P represents the chance for obtaining an F-value greater than that given by the test.

Methods for Diffraction Studies. In these studies one of the ears was replaced by the microphone cartridge such that the membrane of the microphone was flush with the surface of the body in a manner similar to that described by Michelsen (1971 c). The change in sound pressure caused by diffraction was then measured at frequencies of 2, 3.5, 5 and 15 kHz; 90 dB SPL. Diffraction was measured at angles of 0°, 30°, 45°, 60°, 90°, 120°, 135°, 150°, 180°, 225°, 240°, 270°, 300°, 315°, and 330°. Following each experiment the amount of diffraction was re-checked at 0° for 5 and 15 kHz. There was no statistical difference between the two measurements at 0°. Ten insects were examined, 5 males and 5 females. In 5 experiments the right ear was replaced by the microphone while in the remaining experiments the left ear was replaced.

Methods for Conduction Studies. The conduction studies were designed to measure the sound pressure at the inside surface of the tympanum for various frequencies and angles of incidence. One tympanic membrane was surgically removed. The microphone cartridge, with the membrane occupying the position of the tympanic membrane (but not in the same plane as the tympanic membrane), was waxed at right angles to the body of the insect in a manner similar to that described by Michelsen (1971 c). Sound frequencies of 2, 3.5, 5, 8, 10, 12, 15, 20, and 30 kHz and sound intensities of from 80 to 100 dB were used. Measurements were taken at 45° intervals from 0° to 180°. At the end of each experiment the intensity was re-measured at 0°, giving variations greater than 4 dB in only 3 of the 260 trials. The data from 13 (7 females and 6 males) of 19 experiments were analysed.

Methods for Directional Hearing Studies. A small square of cuticle overlying the metathoracic ganglion was removed from the sternum after the insect had been mounted on the holder. The first tergal nerve on one side of the animal was cut near the metathoracic ganglion. The cut nerve, which contains axons from the auditory organ, was then sucked up into a PVC suction electrode filled with locust saline. The suction electrode was mounted on a brass rod which was attached to a Leitz micromanipulator. The electrical activity from the tergal nerve was amplified (Tektronix type 122 preamplifier), monitored (Brüel & Kjaer type 2606 measuring amplifier), and displayed on an oscilloscope (Tektronix type 565), and filmed (Tönnies Recordine). Stimuli consisted of 80 ms sound pulses having a rise-fall time of from 3 to 5 ms at intensities that ranged from 10 to 70 dB SPL. Frequencies of 2, 3.5, 5 and 15 kHz were used in directional hearing studies. The choice of frequencies was based on the physiological properties of single cells in the auditory organ (Michelsen, 1966, 1968, 1971 a) and on vibrational patterns of the locust tympanal membrane (Michelsen, 1971 b). Recordings were made at 45° intervals from 0° to 180°. Six responses were recorded at each combination of frequency, intensity, and direction. A 30 to 60 s pause between stimuli was employed to avoid possible sensory adaptation. Spontaneous activity was recorded from 30 to 125 times during an experiment.

A typical directional hearing experiment started by gathering data for sensitivity plots at 0° using from 3 to 5 intensities at 5 dB intervals for each of the four frequencies. All intensities were chosen such that individual spikes could be counted in the manner described by Michelsen (1971 c). The animal was then rotated through 180° and data was gathered at two intensities 5 to 10 dB apart for each frequency and angle. At the end of each experiment the sensitivity at 0° was re-checked. Results were not included in the analyses if the sensitivity had changed by more than ± 4 dB at 0°, or if the spontaneous activity had changed by more than about 20%. The results from 29 animals out of a total of 51 animals could be used. The results from 17 animals were used to analyse directional hearing.

The raw data for the statistical analyses consisted of the number of spikes per 80 ms stimulus, or per 80 ms of silence in the case of spontaneous activity (Michelsen, 1971 c). From 500,000 to 1 million spikes were counted in these studies. Each data point in sensitivity and directional plots is an average of from 4 to 6 responses (responses containing non-stimulus related activity were disregarded). The mean spontaneous activity served as a base line for all plots. The variation was expressed as a 90% confidence interval. The slope of the response in sensitivity plots was determined by linear regression based on all points whose confidence intervals did not overlap that of the spontaneous activity (Fig. 5 a, the arrow indicates the first data point used in the regression analysis). The intercept with average spontaneous activity was arbitrarily defined as threshold (Michelsen, 1971 c). Directional plots were generated at a specific intensity for each frequency (Fig. 5 b). Intensities were chosen such that decreases in sensitivity with angle would not fall into the spontaneous activity. It was often difficult to determine a priori which intensity would be most suitable for a particular frequency and direction. It was necessary in 30 of 620 frequency-intensity measurements to determine an unmeasured response at a particular direction. This was accomplished by extrapolation using two or more measured responses at the same

direction. In addition, each directional plot is provided with a dB scale based on the slope (in spikes/dB) at 0° for that particular frequency. It was thereby possible to translate changes in sensitivity from mean spikes/80 ms to dB (Fig. 5b). Figure 5 is representative of the 309 computer generated sensitivity and directional plots.

Results

1. Diffraction of Sound by the Locust Body

An understanding of directional hearing is aided by an analysis of the physical parameters involved. How the insect's body interferes with the sound field is one such parameter.

The relationship between the body size and the wave length of sound plays an important role in determining the amount of diffraction causing pressure variations at the ear. (Diffraction caused by the holder and brass block is negligible.) For frequencies of 2 and 3.5 kHz there is no measurable pressure variation at the ear as a function of angle of incidence. However, at 5 and 15 kHz the pressure variations at the ear are significant, and are affected by the angle of incidence, the sex, and the geometry of the body.

At 5 kHz the average maximum difference in sound pressure at the ear is from 2 to 3 dB. The maximum over-pressure occurs when the ear is towards the sound source (0°) while the maximum under-pressure occurs when the ear points away from the sound source (180°). The diffraction is significant when analysed for both sexes, the two ears (right and left), and all angles (Probability (P) = 0.0006 to 0.0001).

Figure 1 shows the average pressure variations at the right and left ears as a function of angle of incidence at 15 kHz. The average maximum difference in sound pressure at the ear is from 6 to 8 dB. The maximum over-pressure for right ears occurs at 30° while the maximum over-pressure for left ears occurs at 330° (Fig. 1). The maximum under-pressure for both ears occurs at 180° . (In animals that respired heavily, one can measure variations in diffraction of about ± 1 dB.) Diffraction is highly significant when analysed for both sexes, the two ears, and all angles as well as for the statistical interactions of ear vs. angle ($P = 0.0023$ to 0.0001). However, the statistical interaction of sex vs. angle is just significant ($P = 0.0247$). The $\pm 30^\circ$ shift in the maximum over-pressure shown in Figure 1 is not obvious when the data for sex and angle are plotted. Consequently, the shift in maximum over-pressure is attributed mostly to the geometry of the locust body and not to size, which is sex dependent. (Females are significantly larger than males, $P = 0.001$.) There is no change in diffraction when all but the first two segments of the abdomen are removed. Thus, the portion of the body disturbing the sound field at the ear consists of the three thoracic segments and the first two abdominal segments.

2. Conduction of Sound through the Locust Body

The intensity of sound passing through the body and impinging on the inside surface of the tympanic membrane can be determined by replacing one of the

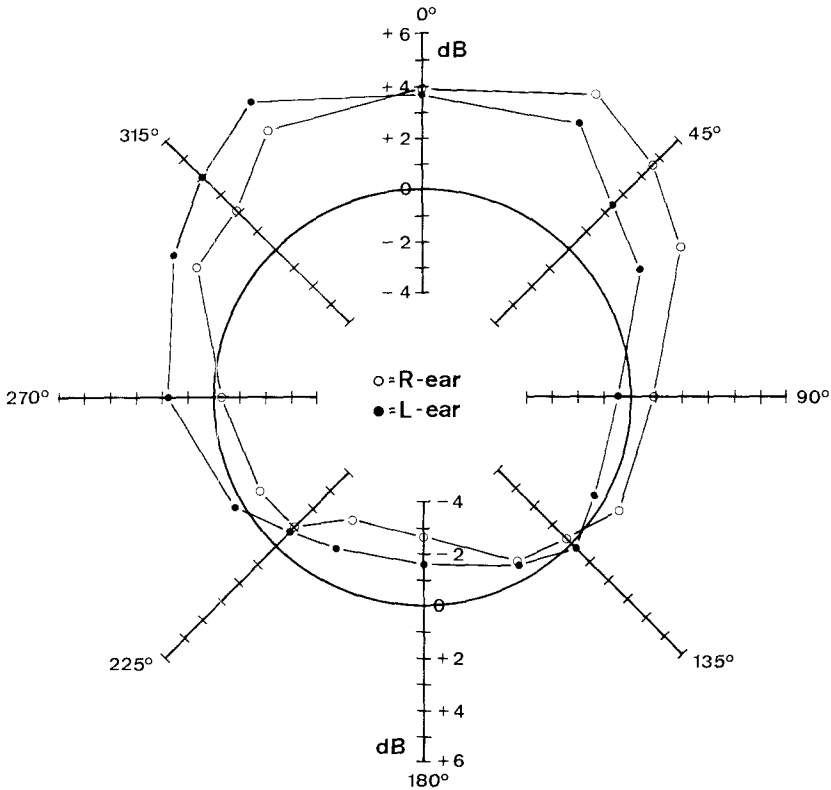


Fig. 1. Diffraction caused by the body at 15 kHz. A small condenser microphone replaced the right or left ear and the sound pressure was measured as a function of angle of incidence. Variations in sound pressure are given in dB relative to the sound pressure in the undisturbed sound field. Note that the curves are shifted to the right for right ears and to the left for left ears. $n = 10$

tympanic membranes with a microphone. The more sound being conducted through the body the more one might expect the ear to function as a pressure-gradient receiver. Parameters that might be expected to affect the conduction of sound through the body are the amount of tissue in the body, especially that located between the ears, the tracheal air sacs, the body cavity, the contralateral tympanic membrane, and the wave length (frequency) of sound. The results presented in this section provide information useful in interpreting directional hearing.

Of the animals studied, 7 fell into weight group (WG) 3 with the average amount of tissue being 24.0 ± 10.0 mg. WG4 contained 5 animals having an average of 94.6 ± 11.7 mg of tissue between the ears.

Figure 2 shows the average attenuation of sound in dB conducted through the body. The attenuation is averaged for all angles and plotted as a function of frequency and weight of tissue between the ears. The amount of tissue between the ears significantly affects the attenuation of sound by the body ($P = 0.0001$). The magnitude of attenuation increases at about 4 to 6 dB per octave from 3.5 kHz

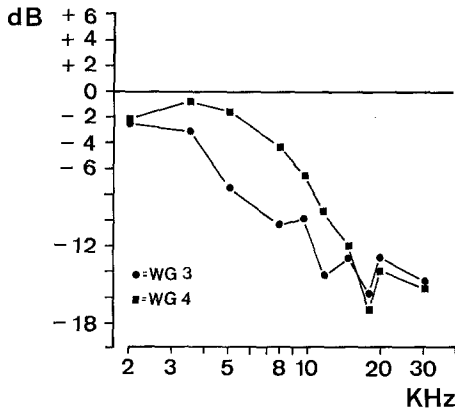


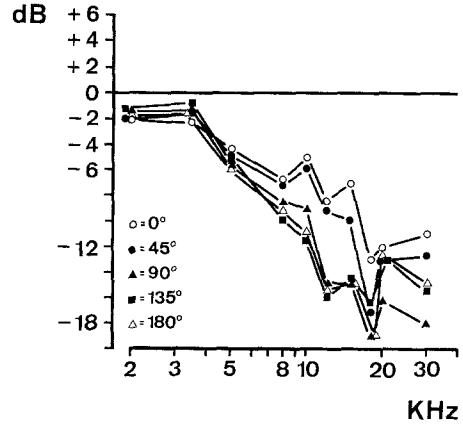
Fig. 2. Sound conducted through the body as a function of the weight of tissue between the ears and frequency (averaged for all angles). The results are expressed in dB relative to the sound pressure in the undisturbed sound field. Weight group 3 = 24.0 mg ($n = 7$). Weight group 4 = 94.6 mg ($n = 5$)

to 18 kHz. The attenuation is greatest (16 to 18 dB) at 18 kHz (Fig. 2). Variations in attenuation for a given animal are from 2 to 5 dB at frequencies greater than about 10 kHz. Such variations probably result from respiratory activity.

The attenuation of sound is inversely proportional to the amount of tissue between the ears for frequencies from 3.5 kHz to about 12 kHz. At frequencies above 12 kHz, the attenuation is essentially unaffected by the weight of tissue between the ears (Fig. 2). This suggests that parameters other than body weight influence the attenuation of sound conducted through the body at higher frequencies. One such parameter is the body cavity. To elucidate how the body cavity affects the attenuation of sound a series of experiments was performed on 5 insects in the heaviest weight group (WG 4, average weight of tissue = 84.2 mg). The attenuation was measured before and after removing the tissue from between the ears. Removing the tissue destroys the integrity of the tracheal air sacs and the contralateral tympanic membrane. The results from operated animals are probably not comparable to what one would expect from meager animals. The attenuation of sound in operated animals is similar to that in intact animals at frequencies from 2 to about 8 kHz (averaged for all angles). However, at frequencies greater than 8 kHz the attenuation of sound is greater for operated animals than for intact animals. The maximum attenuation occurs at 18 kHz in operated insects, which is identical to that of intact insects. Apparently, the acoustic properties of the body cavity in the vicinity of the ears determines the frequency at which maximum attenuation occurs. The magnitude of attenuation is determined in part by the body cavity, but also by other parameters of which body tissue plays a rather minor role at frequencies greater than 12 kHz. At frequencies from 2 to 12 kHz the acoustic properties of the body cavity have a limited influence on the attenuation of sound. However, body tissue together with the undetermined effects of the tracheal air sacs and the contralateral tympanic membrane determine the magnitude of attenuation at frequencies from 2 to 12 kHz.

Figure 3 is similar to Figure 2 except that the attenuation of sound is averaged for all weight groups and plotted as a function of frequency and angle. The values are not corrected for diffraction partly because diffraction was not studied above

Fig. 3. Sound conducted through the body as a function of angle of incidence and frequency (averaged for all weight groups). The results are expressed in dB relative to the sound pressure in the undisturbed sound field. The results are not corrected for diffraction (see text)



15 kHz. The attenuation increases at about 5 to 6 dB per octave from 3.5 kHz to about 8 kHz for all angles of incidence. From 8 kHz to about 18 kHz the attenuation is less at 0° and 45° than at other angles (Fig. 3). This is probably due to increased sound pressure caused by diffraction at 0° and 45° for high frequencies (Fig. 1). If corrections for diffraction are made at 15 kHz for 0° and 45° the magnitude of attenuation nearly equals that at 90°, 135°, and 180°. These results indicate that the attenuation of sound conducted through the body is not influenced by the angle of incidence.

Figure 4 shows the effect of removing the tissue from between the ears on the attenuation of sound conducted through the body for a given angle. The attenuation of sound is inversely proportional to the amount of tissue between the ears, but independent of angle when the values for attenuation are averaged for all frequencies ($P = 0.1806$ for a two-way analysis of variance on intact and operated insects vs. angle for all frequencies). The attenuation of sound in animals with varying amounts of body tissue (weight groups) is likewise independent of angle ($P = 0.2298$ for a two-way analysis of variance of weight groups vs. angle for all

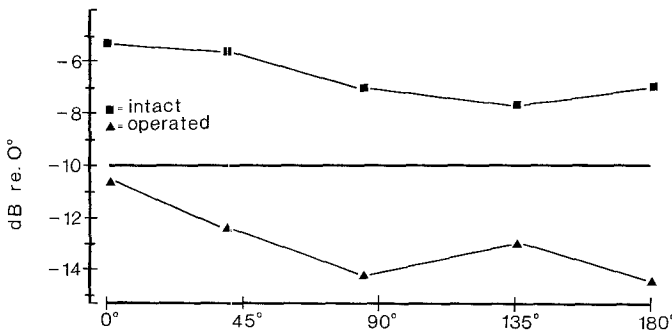


Fig. 4. Sound conducted through the body before (■) and after (▲) removal of tissue from between the ears. The results are given as a function of angle (averaged for all frequencies) and expressed in dB relative to the sound pressure in the undisturbed sound field. All animals fell into weight group 4 (84.2 mg tissue between the ears, $n = 5$). Note that the attenuation is independent of angle ($P = 0.1806$)

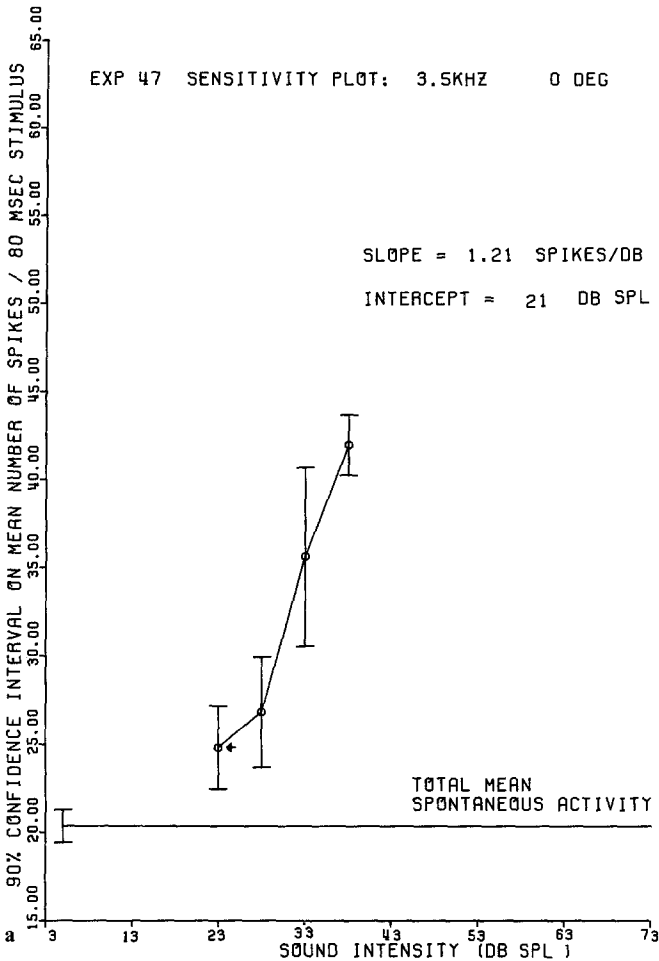
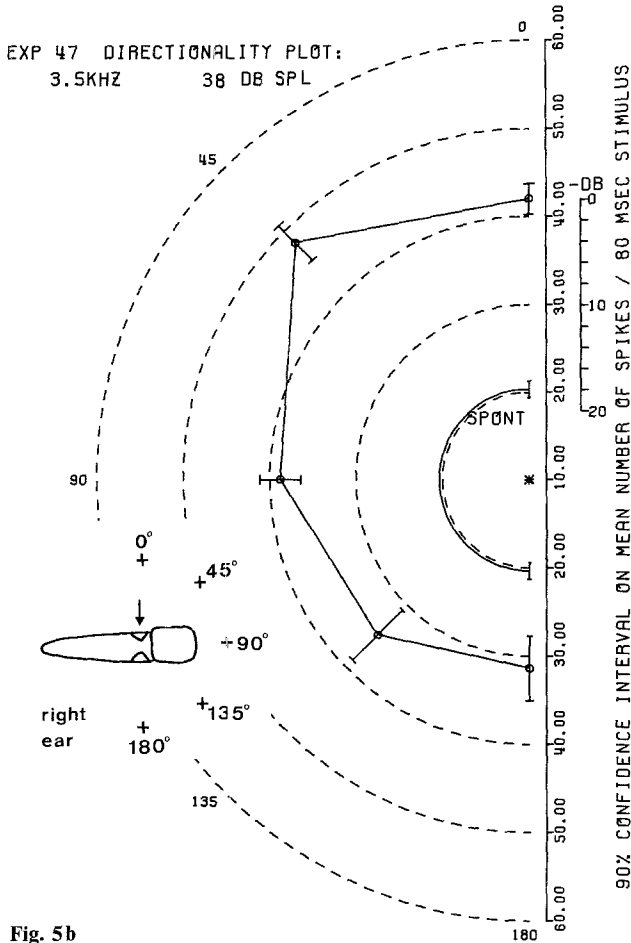


Fig. 5 a and b. Computer generated sensitivity plot (a) and directionality plot (b) at 3.5kHz from a single experiment. Each data point represents the average number of spikes recorded in the first tergal nerve for 6 sound pulses 80 ms in duration at 5 dB intervals. The arrow in a shows the first data point used in a linear regression analysis to determine the slope and intercept with the average spontaneous activity. The intercept value arbitrarily defines the auditory threshold. In this case the threshold is 21 dB SPL. The slope in a is used to convert the response in spikes/80 ms stimulus to a dB scale relative to 0° (ear towards the sound) in b. The data in b was gathered at 38 dB SPL. The inset in b shows the presentation of sound (arrow) with direction

frequencies). The results of this section imply that directional sensitivity may be independent of body tissue if the conduction of sound through the body influences hearing.

3. Directional Hearing

Figure 5 shows the results obtained from a typical directional hearing experiment. Figure 5a shows an intensity-response plot taken at 3.5 kHz, 0° (ear towards



sound). Each point represents the average number of spikes for 6 sound pulses, 80 ms in duration. The slope is 1.21 spikes/dB with a threshold value of 21 dB SPL. The directionality plot (Fig. 5b) for the same experiment is expressed in mean number of spikes as well as in dB relative to 0°. The dB values are based on the slope given in Figure 5a. Consequently, the results of all directional hearing experiments can be compared irrespective of absolute levels in spikes per unit time and frequency dependent differences in slopes. To analyse peripheral auditory physiology of the locust without the complications of diffraction one must compensate for diffraction at 5 and 15 kHz.

Directional hearing as a function of frequency and the weight of tissue between the ears is shown in Figure 6. Each point represents an average of from 8 to 36 measurements taken at 45° intervals and expressed relative to 0°. The animals were placed into four weight groups (WG) based on the amount of tissue between the ears:

- WG1 = 1.3 ± 0.3 mg ($n = 2$), WG2 = 7.0 ± 2.7 mg ($n = 5$),
- WG3 = 20.7 ± 10.4 mg ($n = 6$), WG4 = 108.2 ± 66.1 mg ($n = 4$).

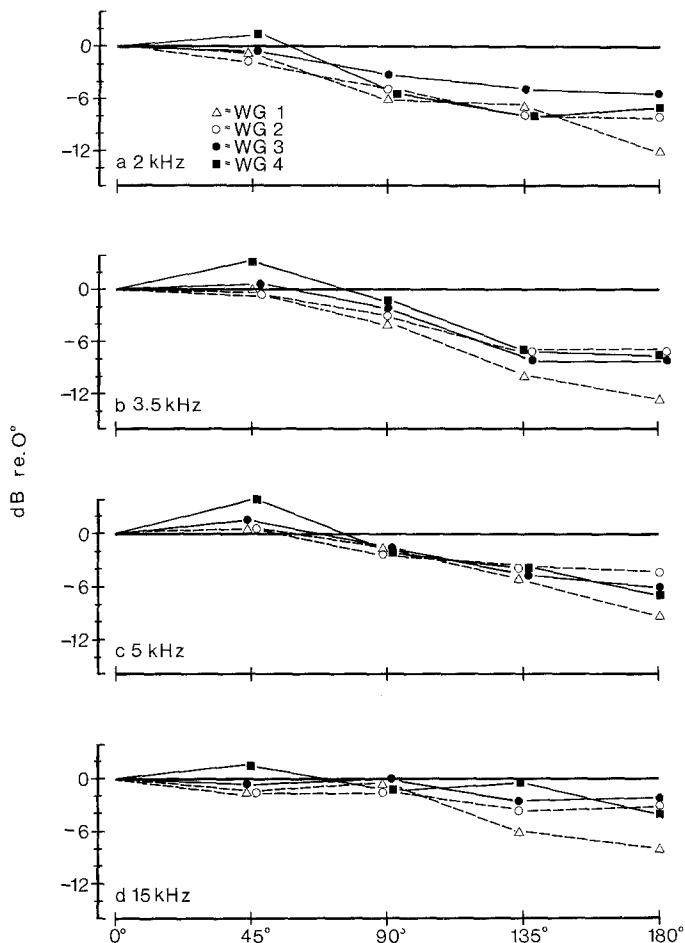


Fig. 6. Directional hearing as a function of frequency and amount of tissue between the ears (weight groups, *WG*). Each data point represents an average based on the auditory activity elicited by 8 to 36 sound pulses. The results are expressed in dB relative to the response at 0° (ear towards sound). The results at 5 kHz and 15 kHz are corrected for diffraction. WG 1 = 1.3 mg, $n = 2$; WG 2 = 7.0 mg, $n = 5$; WG 3 = 20.7 mg, $n = 6$; WG 4 = 108.2 mg, $n = 4$. The variation of sensitivity with angle is independent of the amount of tissue between the ears (see text)

All curves show attenuation with angle. The lightest animals (WG1) show the greatest attenuation, about 6 dB relative to other weight groups for all frequencies. The heaviest animals (WG4) all show an increase in sensitivity of about 3 dB relative to all other weight groups at 45° for all frequencies. Differences among weight groups are slight, being less than 1 dB at certain frequencies and angles. Directional hearing, then, appears not to be influenced by the amount of tissue located between the ears. To test this assumption regression analyses were performed on the data from each of the 16 combinations of frequency and angle. The data were arranged with weight of tissue between the ears as the independent variable and variations in sensitivity in dB relative to 0° as the dependent variable.

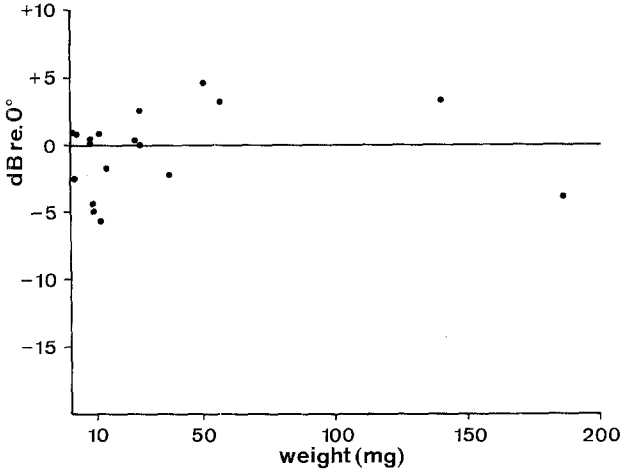


Fig. 7. The relationship between auditory sensitivity (in dB relative to the response at 0°) and weight of tissue between the ears (in mg) for 2 kHz at 45°. Each data point represents an average of the responses to 6 sound pulses. The figure shows one of the 16 frequency/angle combinations used in linear regression analyses to test the relationship between auditory sensitivity and weight. In this case, the slope is not significantly different from 0 ($P = 0.305$)

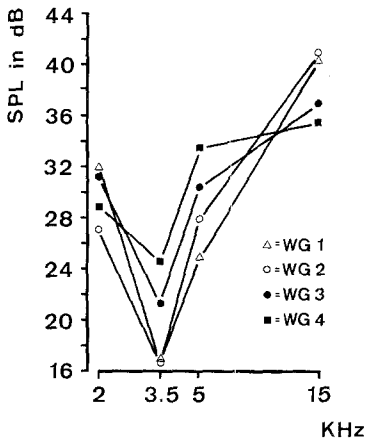


Fig. 8. Auditory thresholds measured at 0° for different weight groups (*WG*) as a function of frequency. The amount of tissue between the ears for each weight group is: WG 1 = 1.3 mg, $n = 3$; WG 2 = 6.6 mg, $n = 7$; WG 3 = 25.3 mg, $n = 14$; WG 4 = 100.1 mg, $n = 5$

Figure 7 shows the data for 2 kHz at 45°, and is typical for all but one of the 16 plots. Each of the 18 points in Figure 7 represents an average of from 4 to 6 measurements. The slope is not significantly different from zero ($P = 0.305$). In only one instance (15 kHz, 45°) did the slope deviate significantly from zero ($P = 0.009$). Therefore, directional hearing is independent of the weight of tissue between the ears. This suggests that the variation in sensitivity with direction involves a factor other than weight.

The amount of tissue between the ears significantly affects the threshold of hearing determined at 0° ($P = 0.0032$). Figure 8 shows mean threshold values in dB SPL for 4 frequencies and 4 weight groups in 29 animals (WG 1 = 1.3 ± 0.3 mg, $n = 3$; WG 2 = 6.6 ± 2.3 mg, $n = 7$; WG 3 = 25.3 ± 12.0 mg, $n = 14$; WG 4 = 100.1 ± 55.2 mg, $n = 5$). For 3.5 kHz and 5 kHz the threshold increases for increasing tissue weight, while at 15 kHz the threshold increases for decreasing tissue weight.

Discussion

At frequencies greater than 12 kHz very little sound reaches the back side of the tympanum. The sound pressure on the back side of the tympanum is about 1/10 that on the front side at 18 kHz. The magnitude of attenuation is influenced only slightly by changes in tissue weight (Fig. 2). Except for the most meager of animals, *the ear, when considered as a receiver, is essentially non-directional if the output is corrected for diffraction at 15 kHz (Fig. 6d). Thus, the locust ear functions mostly as a pressure receiver at frequencies higher than about 12 kHz, which agrees with the results of earlier studies (Michelsen, 1971 c).*

The locust body disturbs the sound field significantly at 15 kHz. Diffraction can cause pressure variations at the ear of up to 8 dB. The diffraction pattern is asymmetrical, being shifted 30° to the right for right ears and 30° to the left for left ears (Fig. 1). When the effect of diffraction is combined with the slight variations in auditory sensitivity at 15 kHz (Fig. 6d), variations of up to 12 dB can occur as the preparation is rotated through 180° . Consequently, *hearing is directional at high frequencies.*

The difference in sound pressure at the front and back sides of the tympanum is rather small at frequencies lower than about 12 kHz (Fig. 2). At frequencies of 2, 3.5, and 5 kHz, auditory sensitivity shows an overall decrease of from 4 to 14 dB as the preparation is rotated through 180° (Fig. 6a–6c). Diffraction caused by the body is insignificant at low frequencies. *The locust ear, then, is inherently directional and is functioning primarily as a combined pressure and pressure-gradient receiver at low frequencies.*

Simple vector analysis can be used to compare the expected variations in sensitivity with the measured variations. (See Michelsen and Larsen (1977) for a detailed explanation of how vector analysis can be applied to insect hearing.) The sound pressure at the front surface of the tympanum (P_f) is not necessarily in phase with the sound pressure on the back side of the tympanum (P_b). Assuming that the changes in auditory sensitivity reflect changes in "effective pressure" (P_e = the driving force per unit area). The resultant, \vec{P}_e , can be determined graphically (or mathematically) from the values of \vec{P}_f , \vec{P}_b and the phase angle (α) between \vec{P}_f and \vec{P}_b . The arrows indicate vector values. If α is 0° then P_e is a minimum and equal to $\vec{P}_f - \vec{P}_b$. If $\alpha = 180^\circ$, \vec{P}_e is a maximum and equal to $\vec{P}_f + \vec{P}_b$. As the preparation is rotated through 180° , α will change as a function of $(2 \cdot l'/\lambda) \times 360^\circ$ where l' is the effective distance of the sound path around the outside of the locust body (approximately 1.5 cm), and λ is the wave length of sound at a particular frequency (Michelsen, 1971 c). α will increase as the frequency increases.

Values of α can be found that give changes in \vec{P}_e equal to the measured changes in sensitivity as the preparation is rotated through 180° . Figure 2 gives values for \vec{P}_b at various frequencies and weight groups (WG3 and WG4). Changes in sensitivity with direction, frequency, and weight are obtained from Figure 6. α must lie between 35° and 120° at 2 kHz to give a change in \vec{P}_e equal to the measured change in sensitivity with direction. The corresponding values for α at 3.5 kHz are 39° and 165° while the values for α at 5 kHz are 44° and 214° . (The ranges for α presented here are greater than the minimum α values plus $(2 \cdot 1'/\lambda) \times 360^\circ$ since the results of the calculations for WG 3 and WG 4 are combined.) At 15 kHz, α will pass through $470^\circ (= (2 \cdot 1'/\lambda) \times 360^\circ)$ as the preparation is rotated through 180° . Consequently, \vec{P}_b will pass through 180° giving a maximum \vec{P}_e , which is about 1 dB less than the measured change in sensitivity with direction (Fig. 6d).

Vector analysis can also be used to determine whether or not the changes in threshold at 0° can occur within the calculated range for α at each frequency. Such calculations are possible for WG3 and WG4, where measured values of \vec{P}_b are available (Fig. 2). Changes in threshold as a function of frequency and weight at 0° are shown in Figure 8. The results of these calculations show that a change in α ($= \Delta\alpha = \alpha(\text{WG4}) - \alpha(\text{WG3})$) equal to 15° at 2 kHz can account for the measured change in threshold at 0° (ear towards sound). The corresponding $\Delta\alpha$ values for 3.5 kHz, 5 kHz, and 15 kHz are 12° , 30° , and 110° respectively. The calculated $\Delta\alpha$ values represent a constant fraction of the calculated values for α given by $(2 \cdot 1'/\lambda) \times 360^\circ$. That is, $\Delta\alpha / (2 \cdot 1'/\lambda) \times 360^\circ$ is a constant ($= 0.19$, range: 0.11 to 0.23) and independent of frequency.

Body tissue, then, appears to act as a 'resistive' element that introduces a frequency independent phase shift in the sound passing through the body. Regression analyses show that directional hearing is independent of the amount of tissue between the ears (Fig. 7). The conduction of sound through the body as a function of direction is likewise independent of the amount of tissue between the ears (Fig. 4). This is to be expected if body tissue functions as a 'resistive' element. The change in phase angle between \vec{P}_f and \vec{P}_b due to body tissue simply sets the level of sensitivity without changing the receiver characteristics. That the receiver characteristics are not influenced by body tissue can be seen in Figures 2 and 6. For example, in heavy animals (WG4) \vec{P}_b is 0.8 to $0.9 \times \vec{P}_f$ at frequencies from 2 to 5 kHz. Such large values of \vec{P}_b could, theoretically, give a nearly ideal pressure-gradient receiver (Michelsen, 1971 c). In actuality, the ear functions as a combined pressure and pressure-gradient receiver at these frequencies (Fig. 6a to 6c). Consequently, phase changes between \vec{P}_f and \vec{P}_b other than those caused by body tissue must influence the receiver properties of the ear. Phase changes introduced by the contralateral tympanic membrane, the tracheal air sacs, and the body cavity itself could influence the receiver characteristics. The results presented here, however, cannot verify such claims.

Vector analysis cannot account for the increase in sensitivity at 45° (Fig. 6) for the heaviest animals (WG4). An increased sensitivity at 45° suggests that α passes through 180° , where \vec{P}_e is a maximum. As rotation continues, α increases and \vec{P}_e becomes smaller. If one assumes that $\alpha = 180^\circ$ when the angle between the ear and the sound is 45° , the calculated values of \vec{P}_e are considerably less than the measured differences in sensitivity with direction (Fig. 6). It is likewise

not possible to determine the actual start values of α from the results presented here. Therefore, vector analysis must be regarded as a useful model for examining hearing in the locust, and not as a method for determining the actual phase values for α .

Investigations using laser vibrometry will help explain some of the problems regarding locust hearing. With laser vibrometry one can measure the actual phase shifts between the force driving the tympanum and the velocity of the resulting movement (Michelsen and Larsen, 1977). From these measurements one can calculate the phase angles between \vec{P}_f and \vec{P}_b as well as determine how single elements in the acoustic pathway contribute to phase changes.

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