THE PHYSIOLOGY OF THE TETTIGONIID EAR

III. THE RESPONSE CHARACTERISTICS OF THE INTACT EAR AND SOME BIOPHYSICAL CONSIDERATIONS

BY D. B. LEWIS

Animal Acoustics Unit, City of London Polytechnic

INTRODUCTION

The fact that sound may be effective on both surfaces of the external membranes (Lewis, 1974*a, b*) requires the consideration of the type of receptor or microphone which the organ most closely resembles. Autrum (1942) considered the tympanal organ to be a pressure-gradient receiver, the pressure gradient existing across the central membrane. Since the central membrane has been shown in an earlier paper in this series to be non-vibratory, the situation is more complex. Indeed the problem is a far more basic one in that no complete understanding of the mode of activity of the tympanal organ system can be achieved without the understanding of the physics of the system, and this has been stated recently by Michelsen (1971) for the locust ear.

The extent to which horn theory for example can be used for the understanding of structures of the dimensions of the acoustic trachea is only one problem. Richardson (1953) found that there is a stagnant layer of air about 1 mm in thickness next to the wall of a tube when the remainder of the air is vibrating, so that the effective diameter of the air column is slightly less than that of the tube. This layer, which varies in thickness with the physical conditions, is of little consequence in organ pipes, but for pipes of less than about 1 cm in diameter it becomes a considerable proportion, and in tubes of about 1 mm diameter and less, the vibrations are soon damped out. The radius of the Tettigoniid trachea is of the order of 0·15–0·20 mm and it might be expected that the vibrations of the air would be damped out within a very short distance. But it has been shown in previous papers in this series that the acoustic threshold for the spiracle is lower than for the tympanal slits and the tube condition is probably over-ridden in an exponential horn. The sound vibrations cannot be damped out before reaching the sensory cells.

Another problem in the consideration of the physics of the whole organ is that each portion of the system tends to be considered in isolation whereas of course the intact ear functions as a whole. That its consideration in this way is difficult is no reason to avoid the issue since it may provide further insight into the functioning of the insect ear.

This paper attempts to consider some of the biophysical principles of hearing in Tettigoniids, as well as the response characteristics of the whole organ. This whole-organ response is compared with the spiracular and tympanal slits response, and

confirms that the resultant stimulus at the receptor must be a complex interaction of the various inputs. If the organ acts as a pressure-gradient transducer, that pressure gradient must act across each of the external membranes.

METHODS

The principles of sound production and calibration, and the recording of neural responses were described in a previous paper (Lewis, 1974a). The threshold curve for the whole-organ response was determined using a sound signal emitted by an Akai X-IV microphone at a distance of 30 cm from the preparation. No differences were observed as between the right and left ears.

Since the spiracle is an effective site of entry for sound its proximity (3·5 mm) to the sound source during male stridulation poses the question of how much of the sound produced enters the prothoracic spiracular opening and is thus heard by the tympanal organ. This was investigated by point-contact vibration of the tegmen. The method of setting the tegmen into vibration by means of piezo-electric stimulation has been described by Bailey (1968) for *Homorocoryphus nitidulus*, where he showed that the frequency spectrum of the sound produced artificially is very similar to that produced during normal stridulation. The right tegmen was held by means of pins in a position approximating to that taken up during sound production. The tip of the contact transducer was held against the hard edge of the plectrum of the right tegmen, parallel with the plane of the tegmen and in line with the vestigial file. The B and K ¼-inch condenser microphone with 1 mm probe attachment was held perpendicular to the tegmen at a distance equal to the distance of the spiracular opening from the sound source (3·5 mm). The normal emission frequency of 16 kHz only was used and the sound output from the system was linked to the B and K microphone pre-amplifier and to the Tektronix 502A oscilloscope for the voltage deflexion. Once a recording of the tegminal vibration had been taken, contact between the probe tip and the plectrum was *just* broken and intensity readings were taken again. This ensured that any intensity values measured were the result of tegminal vibration and not due to sound emission by the probe, or to any other cause.

The probe of the B and K microphone was then pushed through the preparation to emerge at the correct angle through the right spiracle. The probe position was set until its opening was flush with the spiracular surface and the tegmen was again set into vibration. The intensity values were taken and a control test was carried out as before. In this way the differences in sound intensity at source and at the spiracle could be measured.

RESULTS

The spiracular and tympanal slit curves were obtained with the emitter probe 1 mm from the relevant structure as described in previous papers. The whole-organ response curve is that curve obtained with a lateral sound source, using the Akai X-IV microphone without probe attachment.

The threshold curve obtained for the ipsilateral tympanal organ is given in Fig. 1. The curve is so clearly different from the curves obtained for the spiracle and for the tympanal slits (shown in the same figure) that the interactions postulated earlier between the anterior and posterior membrane responses, between the anterior and
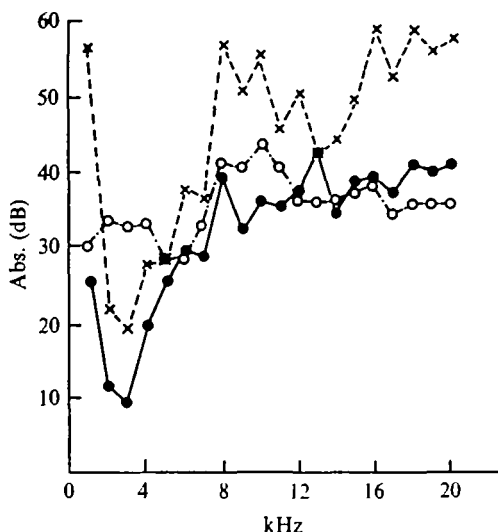
Fig. 1. The threshold curve for the ipsilateral whole organ (O—·—·—O) is compared with the spiracular (●—●) and tympanal slit (×– –×) curves determined by means of the probe emitter.

posterior air spaces and between the spiracular and tympanal slits inputs gain some support.

Two other factors may be contributing to the differences between these curves in addition to those mentioned above. First, the spiracular and tympanal slits curves were obtained with a sound source only 1 mm from the appropriate structure and these structures are therefore in a spherical wave. The whole-organ response curve was obtained using a sound source 30 cm lateral to the insect which would therefore be approaching a plane wave system. However, since the intensity values 1 mm from the emitter probe tip were calibrated using a B and K ¼-inch microphone with a brass probe 6·5 cm long and with a tip diameter equal to that of the emitter probe tip, and comparable to the spiracular opening, the sound intensity measured with this B and K probe is therefore a fair approximation to the actual intensity at the spiracle. The sound intensity during the whole-organ response was calibrated using the B and K ¼-inch microphone without probe, set at the position of the insect during recording.

The second factor affecting the whole-organ response is likely to be far more important. Michelsen (1971) has considered the importance of diffraction of sound by an obstacle, such as the locust body, in relation to the operation of the ear. He estimates that the surplus sound pressure arising from diffraction for an intact ear on the side facing the sound source will increase from 0 dB at 2–3 kHz to about 8 dB at 40 kHz. He also predicts that the surplus pressure will vary around 6 dB in an oscillatory manner above 40 kHz. This phenomenon may be unimportant in a locust whose sensitivity above 40 kHz is very low, but in *H. n. vicinus* perhaps, and certainly in the majority of bush-crickets, it could be extremely important in reinforcing frequency-dependent responses. This diffraction effect may be added to in Tettigoniids by interference effects due to reflected high-frequency waves returning from the side of the body past the tympanal slits. Since the leg was in a fixed position the distance from the thoracic wall to the tympanal slits was constant in the prepara-
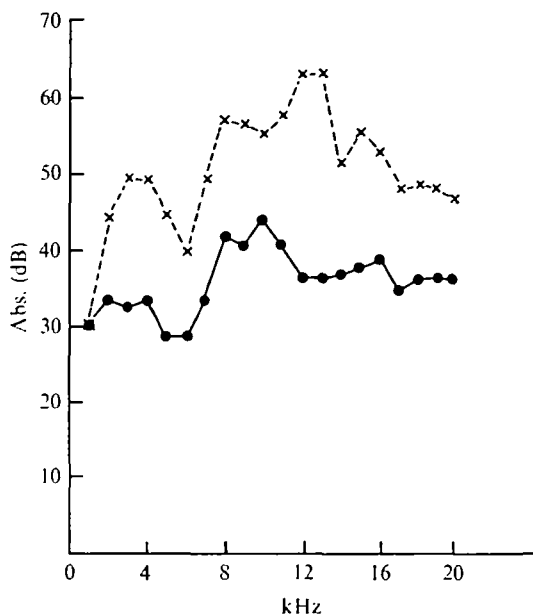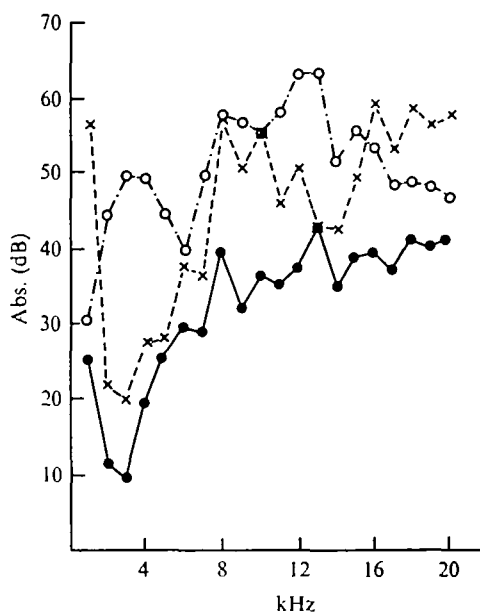
Fig. 2. A comparison of the threshold curves of the whole organ (●—●) with that of the whole organ with the spiracle blocked (× — — ×) using a lateral sound source.

Fig. 3. A comparison of the threshold curve of the whole organ with the spiracle blocked (O-·-·-O), with the spiracular (●—●) and tympanal slit (×--×) curves determined with the probe emitter.

tion so that the effect will have been frequency-dependent. To this extent, the separate curves obtained for the spiracle and tympanal slits using the emitter probe are artificial, and the whole-organ response is likely to be far more representative of the natural situation.

Some idea of the importance of diffraction phenomena in the response of the whole-organ system is shown in Fig. 2, where the response of the whole organ (with the spiracle blocked) to a lateral sound source has been drawn with the normal whole-organ response. The most obvious feature is that the threshold curve with the spiracle blocked is markedly raised to the intensities associated with the tympanal slits (Fig. 3). The curves, however, are different in shape (Fig. 3) and this difference is probably largely due to diffraction and reflexion phenomena, but there is also the possibility that even when the spiracle was blocked sound may have passed through the external cuticle and into the trachea. The threshold for the spiracle at 16 kHz is 38 dB. The acoustic insulation properties of the Copydex was investigated at an intensity of 50 dB (Lewis, 1974a) and found capable of reducing this intensity to less than 10 dB. If therefore sound does pass into the tracheal horn through the body wall, at an incident sound intensity of 52 dB, then the horn sound intensity must be very low, and below the threshold level for the open spiracle. Its effect is thus likely to be small compared to the effects of diffraction.

Broughton in 1965 (personal communication) made a rough measure of the sound intensity during stridulation in *Homorocoryphus* and found it to be in the region of

120 dB near the sound source, and about 90 dB at the region of the spiracle. However, the true measure of the intensity at the spiracle can only be obtained by a probe microphone in the position of the spiracle, and more important, in the plane of the spiracular opening and facing in the same direction. The intensity of the sound produced by the tegminal vibration was 124 dB at a distance 3·5 mm above the mirror region, and 54 dB with the B and K microphone probe tip in the plane and position of the spiracle. The noise level when the vibrator was not in contact with the tegmen was less than 10 dB in each case.

DISCUSSION

Zhantiev (1970) has considered the response characteristics of the tympanal organs of three Tettigoniid species, using split tympanal nerve preparations. He agrees with Autrum (1941) that the subgenual organ does not respond to airborne sound and further states that the intermediate organ responds to the range 1–15 kHz with an optimum at 4–7 kHz. Both the spiracular and tympanal slit curves (Fig. 1) show a peak sensitivity at 3 kHz. In the whole-organ response (Fig. 1) this peak has disappeared, the low threshold appearing at 5–6 kHz. This sensitivity peak is still within Zhantiev's optimum response band of the intermediate organ. Zhantiev's (1970) data show a crista acoustica response band between 2 and 100 kHz with an optimum at 12–30 kHz. In *Homorocoryphus*, the spiracular curve shows what may be a number of sensitivity peaks whereas the tympanal slit curve shows a second peak at 13 kHz. The whole-organ threshold falls sharply beyond 10 kHz without showing a significant peak up to 20 kHz. Zhantiev's optimum band starts at 12 kHz so that the response above 12 kHz may be due primarily to the crista acoustica.

Whatever the characteristics of the Tettigoniid hearing organ are ultimately determined to be, they are likely to be closely related to the song structure. The existence of non-steady-state phenomena (i.e. sounds of very short time-course) in their songs makes the physics of the hearing organ even more complicated, and this may be part of the reason for the difference between the calculated and observed cut-off frequency for the tracheal horn, since the calculation is based on sine-waves of long duration (Lewis, 1974*a*). Calculation of the behaviour of short pulses in horns of general shape is difficult because of the behaviour of the impedance function (Morse, 1948). In simple horns, for example conical horns, part of the wave has the same 'shape' as the 'velocity shape' of the motion at the mouth of the horn. Behind this wave, however, is a 'wake' which dies out exponentially. The original pulse moves into the horn with a velocity c and with amplitude diminishing as $(x+x_0)^{-1}$ where x = the length of the horn and x_0 is the distance back from the throat to where the apex of the cone would be. This constant, x_0, is of course, a function of the rate of flare of the horn. After the sharp pulse comes a negative pressure wave which dies out exponentially. The smaller x_0 is, the more rapidly does this wake die out. The effective force on the internal surfaces of the membranes may therefore be a positive pressure wave which is not followed by a succeeding negative wave, or a negative wave of much smaller intensity; while on the outer surface, in the absence of a horn, both positive and negative waves will be incident on the membranes. Such a situation could well go a long way towards explaining the complicated interactions of the spiracular and tympanal slits threshold curves to produce the whole-organ response (Fig. 1).

Having discussed the importance of non-steady-state phenomena, it may seem equivocal to now consider whether the whole or any part of the organ has any resonant characteristics. However, since the dominant frequency of the songs is not constant throughout the Tettigoniids, the importance of such a dominant frequency could lie in some part of the organ system being particularly responsive to this frequency and its harmonics. Since insect songs tend to have a more numerous series of upper than of lower side-bands (Bennet-Clark, personal communication), the proper emphasis of these harmonics may be an important factor.

The dominant frequency of the insect song may be emphasized as a result of the fact that the horn is small compared to the wavelength of the component at that frequency, so that the trachea approximates to many wood-wind instruments which are approximately exponential or catenoidal horns, but having mouths which are designed to be small enough to ensure resonance inside the horn. The equation for the resonance frequencies (v_n) of such wood-wind instruments is (Morse, 1948),

$$ v_n \simeq \left(\frac{c}{2l_p}\right)\sqrt{\left(n^2+\left(\frac{l_p}{\pi h}\right)^2\right)}, $$

where c is the speed of sound in air; l_p is the end correction and is $\simeq l+0\cdot6a$ for a small flange, where l is the length and a the radius of the horn; n 1, 2, 3, etc., are the resonance frequencies; h is the scale factor.

Calculation of the fundamental resonant frequency of the *H. n. vicinus* trachea gives a value approximately 16 kHz, which is the dominant frequency of the species song.

The understanding of the function of the anterior and posterior tympanal air cavities is more difficult, since the cavity cannot be considered to have a neck of short effective length, and neither can it be considered a neckless resonator. It is probably these factors which are to a large extent responsible for the extremely high value obtained for the fundamental frequencies of these cavities. Indeed the values are so high (127 kHz for the anterior, and 174 kHz for the posterior cavity) that the cavities cannot in themselves act as resonators.

Since the horn may have a resonant function as well as a general amplification function, and since the mouth of the horn is smaller than the incident wavelength, it is important to consider the physical basis of directionality of such a structure. The measured directionality function of the spiracle will be discussed in a subsequent paper, but it is important at this stage to point out that the directional characteristics of a horn depend on shape, mouth opening and frequency. Where the wavelength is greater than the mouth diameter it is the mouth of the horn which plays a major role in determining the directional characteristics (Olson, 1960). In the case of a symmetrical horn the response is maximal on the axis, where all disturbances incident upon the plane of the mouth are in one phase. In oblique directions the intensity is less, but does not fall materially short of maximum until the obliquity is such that the phase difference of disturbances at the nearest and furthest points on the mouth amount to about half a wavelength (Rayleigh, 1895). The advantage of having a relatively small opening is that the sound-intensity level would not be greatly diminished because of the lateral direction of the horn mouth. If, however, the directional characteristic of the spiracle is low, then it might be expected that the sound emitted when the insect is itself singing would be at an extremely high intensity value at this point,

since the opening is only 3·5 mm away from the sound source. The measured intensity values of 124 dB at source and 54 dB at the spiracle show that such is not the case. This intensity drop is probably mainly a feature of the sound-emitter apparatus and not the sound receiver, for Nocke (1971) has shown that in *Gryllus* sound is produced from a modified doublet source and that the sound is loudest behind the insect, but that there is a null at right angles to the sagittal plane (see also Bennet-Clark, 1971). The same is probably true of the Tettigoniids, though the doublet source will there be modified not only by the position of the wings and the substratum, but also by the pronotal overlap. The net effect seems to be to reduce the sound intensity at the spiracle so that the animal is not deafened during its own song (an important consideration in continuous singers with an emission intensity of around 120 dB). Moreover, the fact that the sound intensity level is higher than the spiracular threshold at that frequency means that it is capable of monitoring its own song as well as the songs of other individuals, such that the acoustic alternation or synchrony known to occur in Tettigoniid populations can be explained even if there were no other feedback involved.

This brief consideration of some of the biophysical aspects of the Tettigoniid ear must, of course, be very incomplete if only because the various structures have been considered in isolation. It is hoped, however, that these possible interpretations of function on a physical basis may provide further insight into the insect ear and stimulate research into the physical basis of insect hearing.

SUMMARY

1. The threshold curve obtained for the whole organ, with a lateral sound source 30 cm from the insect, indicates the degree of interaction that occurs between the spiracular and tympanal slits inputs.

2. The threshold curve for the whole organ with the spiracle blocked shows an increase in threshold to the level of the tympanal slits, and suggests that diffraction phenomena may be important during sound reception.

3. Measurement of the sound intensity emitted by mechanical vibration of the tegmen shows that there is a fall in sound intensity from 124 dB at source to 54 dB at the spiracle; the spiracular intensity is still above the spiracular threshold, however.

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