

## THE PHYSIOLOGY OF THE TETTIGONIID EAR

### II. THE RESPONSE CHARACTERISTICS OF THE EAR TO DIFFERENTIAL INPUTS: LESION AND BLOCKING EXPERIMENTS

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#### INTRODUCTION

It was shown in the first paper of this series (Lewis, 1974) that in the frequency range 1–20 kHz, the tympanal organ of *Homorocoryphus nitidulus vicinus* and probably of other Tettigoniids is far more sensitive to sound directed at the large prothoracic spiracle than at the tympanal slits, and that the preferential entry for sound is likely to be via the spiracle. On the basis of this and other information it was suggested that the mechanism for hearing in Tettigoniids warrants a reassessment of the roles of the various structures associated with the sensory cells and a reconsideration of the mechanisms of transduction by the tympanal organ.

The anatomy of the tympanal region of Tettigoniids differs from that of the Gryllids most obviously in the presence of cuticular folds protecting the external membranes (Schwabe, 1906), which are absent from Gryllids. Sound access to the external tympanal membranes has therefore been severely restricted in the Tettigoniids. The question arises whether the closure is correlated with high-frequency sensitivity and sound production in the same way as reducing the size of one membrane in Gryllids confers a high-frequency response characteristic upon that membrane (Nocke, 1972). If the cuticular folds are associated with high-frequency sound reception then they presumably evolved in conjunction with the tracheal horn (v. Siebold, 1844; Carpentier, 1924, 1927; Zeuner, 1936) and with the evolution of the crista acoustica (Zeuner, 1936; Pumphrey, 1940; Howse, 1968; Schumacher, 1973). There is no apparent change, however, in the presence and arrangement of the three tympanal membranes. The sensory cells are associated with the larger of the tympanal air spaces and therefore with the larger (anterior) membrane, and only indirectly with the smaller (posterior) membrane *via* the central membrane and the haemocoelic space. On the basis of the anatomy, and in order to suggest a function for all three membranes, Autrum (1942, 1963) proposed an hypothesis that the tympanal organ was a pressure-gradient transducer, the pressure gradient being effective across the central membrane. The effective stimulus was therefore the resultant of the anterior and posterior membrane vibrations.

This paper investigates the role of the tympanal slits, cuticular folds and the anterior, posterior and central membranes in sound reception in the Tettigoniids.

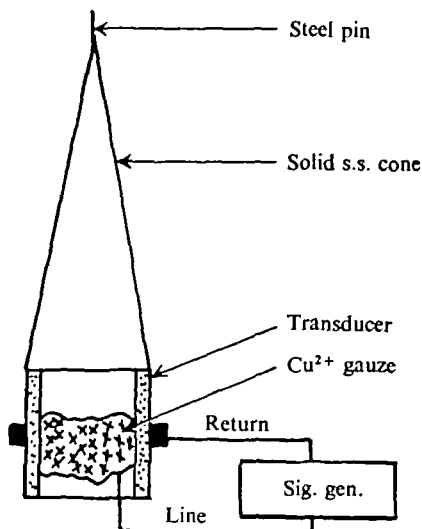


Fig. 1. A diagrammatic representation of the piezoelectric transducer.

#### METHODS

The methods used for producing a local sound stimulus and its calibration and for the recording of neural responses have been described in the first paper of this series (Lewis, 1974).

The roles of the cuticular flaps and the tympanal slits were investigated by blocking the anterior or posterior slits with Copydex and by the removal of the folds. The tympanal membranes were investigated by selectively lesioning the anterior or posterior external membranes. In each case, threshold curves were drawn for both the spiracular and the tympanal slits input. The activity of the central membrane could not be investigated in this way, since its destruction necessitated the removal of one or other of the external membranes. Experiments were therefore performed to investigate the effects of contact-mechanical vibration of the membranes, and a piezo-electric transducer (Mason, 1951) was constructed for this purpose (Fig. 1).

The piezo-electric cylinder used was lead-zirconate-titanate (p.z.t.) (Vernitron Ltd., Southampton, England). The transducer was made as previously described by Bailey (1968), who used the system for the mechanical vibration of the tegmen.

A 1-inch p.z.t. cylinder with a manufacturer's stated resonance peak at 25 kHz was used. In order that the cone should not alter the stated resonance, the cone length had to be half the wavelength as determined by the formula,

$$\frac{\lambda}{2} = \frac{v}{2f},$$

where  $\lambda$  is the wavelength,  $v$  is the velocity of sound in stainless steel ( $5.74 \times 10^5$  cm sec<sup>-2</sup>) and  $f$  is the cylinder length resonance frequency (the other resonances being outside the experimental range). At the tip of the stainless steel cone a size-20 entomological pin was sunk into a drilled hole and secured with 'Araldite'.

No attempt was made in these experiments to calibrate the intensity of the mechanical energy output of the piezo-electric transducer with the sound energy

Table 1. *A summary of the graphical treatment of the results obtained under the varying experimental conditions*

Spiracle normal							
		Blocking of slits		Removal of folds		Membrane lesion	
		Ant.	Post.	Ant.	Post.	Ant.	Post.
Stimulus at	Spiracle	× -- × in Fig. 2	× -- × in Fig. 3	○ -- ○ in Fig. 2	○ -- ○ in Fig. 3	↑ in Fig. 8	× -- × in Fig. 8
	Tympanal slit normal						
	Tympanal slit	× -- × in Fig. 4	× -- × in Fig. 5	○ -- ○ in Fig. 5	○ -- ○ in Fig. 4	↑ in Fig. 9	× -- × in Fig. 9

output of the microphone emitter except in so far as the dB input to both types of transducer was measured on the B and K Frequency Analyser Type 2107 Amplifier scale. The input energies were comparable, and the piezo-electric transducer is likely to be more efficient.

Neural recordings were made from the tympanal nerve as described for an acoustic source. The point-contact vibrator was held in a micromanipulator so that the transducer could be moved in 0.1 mm steps until the tip of the pin touched the structure under investigation. For the investigation of the central membrane, either the anterior or the posterior membrane was removed and the probe tip was moved through the opening so formed until it touched the central membrane. The stimulus used for the vibration studies was the same as that used for the acoustic investigations (8 msec pulses at 5 pulses per sec) but centred only at 16 kHz. The input intensity was monitored on the B and K Amplifier scale.

## RESULTS

Because of the many variables under investigation, and in order to avoid confusion in the reading of the results, the graphical treatment of the results is summarized in Table 1.

### 1. *Acoustic threshold curves for the tympanal organ after blocking the tympanal slits*

By blocking the tympanal slits with Copydex, the extent to which the anterior and posterior tympanal slits were effectively closed could be investigated. As in the previous paper, the sound stimulus was delivered via an Akai X-IV microphone and probe attachment, placed 1 mm from the structure under investigation.

The threshold curve for spiracular sound entry with the anterior slit blocked is compared with the normal spiracular curve in Fig. 2. The blocking procedure lowered the threshold marginally, but this increase in sensitivity is only just significant at the 5% level (*Q*-test) at 3, 8, 11, 12 and 18 kHz. The spiracular curve for the tympanal organ with the posterior slit blocked is compared with the normal curve in Fig. 3. There is a significant increase in sensitivity only at 1 and 2 kHz. It might be reason-

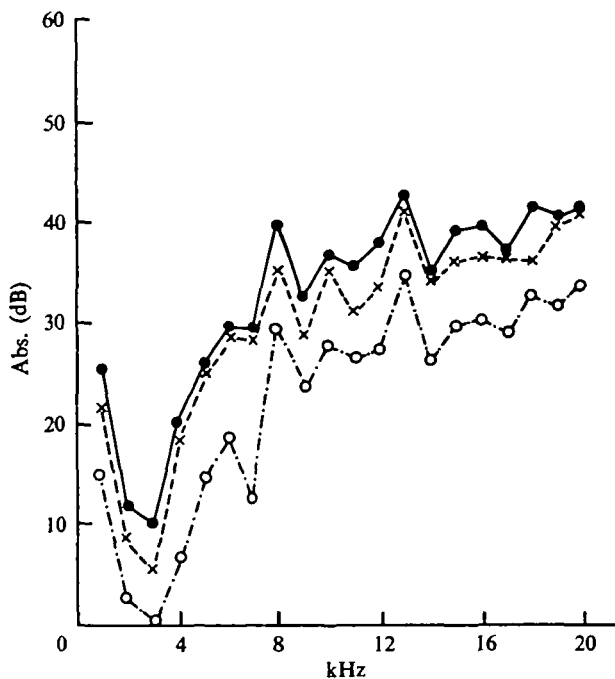


Fig. 2. Threshold curves for the spiracle under normal conditions (●—●), with anterior slit blocked (x--x), and with the anterior cuticular fold removed (○-·-·-○).

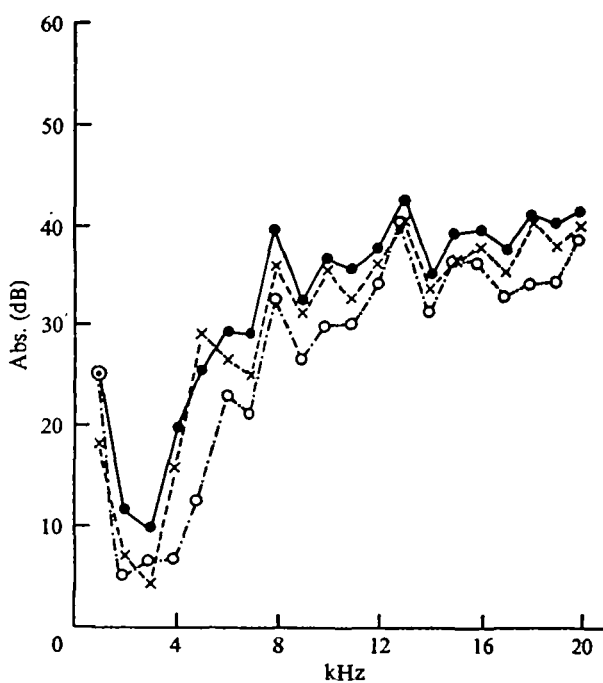


Fig. 3. Threshold curves for the spiracle under normal conditions (●—●), with the posterior slit blocked (x--x), and with the posterior cuticular fold removed (○-·-·-○).

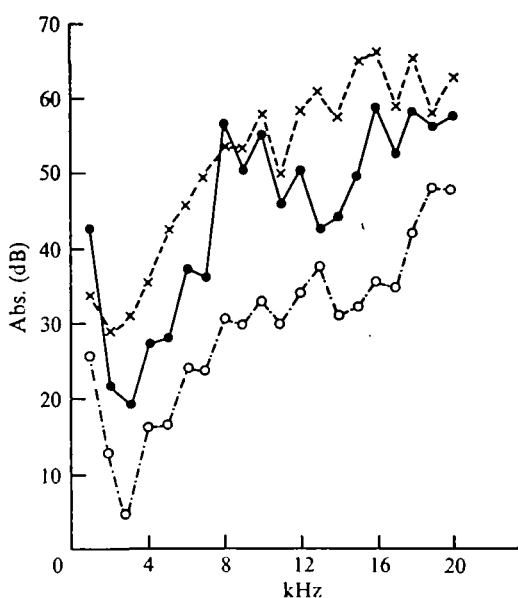


Fig. 4

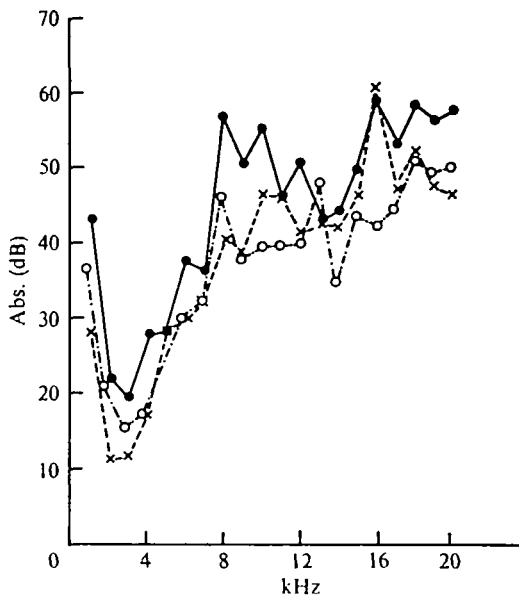


Fig. 5

Fig. 4. Threshold curves for the tympanal slits under normal conditions (●—●), with the anterior slit blocked (×—×), and with the anterior cuticular fold removed (○—○).

Fig. 5. Threshold curves for the tympanal slits under normal conditions (●—●), with the posterior slit blocked (×—×), and with the posterior cuticular fold removed (○—○).

able to conclude that, for spiracular sound input, the anterior and posterior tympanal slits are effectively closed; such a slight change in sensitivity might be associated with the equalization of pressure.

A comparison of the threshold curves for the tympanal slit sound entry under normal and anterior blocked conditions (Fig. 4) shows curves that are sufficiently different to be significant except between 8 and 12 kHz, at the 5% level. The differences are greatest between 2 and 8 kHz, the range of the intermediate organ (Zhantiev, 1970) and 12–16 kHz, the dominant frequency of the species song. The equivalent curves with the posterior slits blocked are given in Fig. 5. The tympanal slit threshold curve is significantly *lowered* at all frequencies except at 5 and 11 kHz and between 13 and 16 kHz, again the dominant frequency of the species song. The greatest differences occur in the frequency bands 8–11 kHz and 16–20 kHz, the frequency bands not covered by the anterior tympanal slits.

## 2. Acoustic threshold curves for the tympanal organ after removal of the cuticular folds

The existence of anterior, posterior and central membranes poses problems regarding the extent to which each structure contributes to the responses of the sensory cells. Since the effects of membrane lesion could not be determined without first removing the cuticular folds, and since the cuticular folds may be important in themselves during sound reception, the effects of removal of these folds was determined.

The frequency-intensity data for the spiracle with the anterior cuticular folds

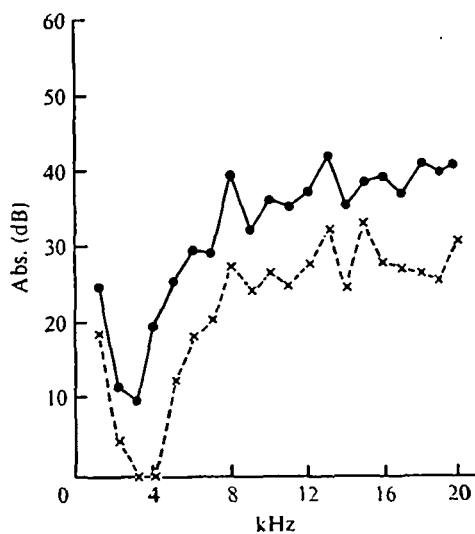


Fig. 6

Fig. 6. The effects of removing both cuticular folds ( $\times - - \times$ ) on the normal spiracular threshold curve ( $\bullet - \bullet$ ).

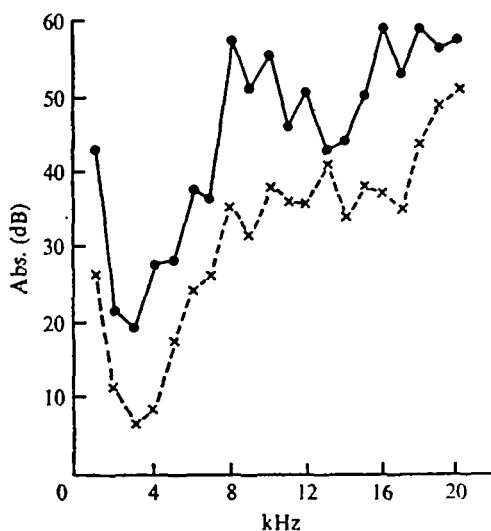


Fig. 7

Fig. 7. The effects of removing both cuticular folds ( $\times - - \times$ ) on the normal tympanal slit threshold curve ( $\bullet - \bullet$ ).

removed is compared with the normal condition and the results of blocking in Fig. 2. Clearly removal of the anterior fold lowers the threshold of the spiracular sound input, but the form of the curve has not been changed.

The threshold curves for the spiracle under normal conditions and with posterior fold removed are compared in Fig. 3. As with the removal of the anterior fold, posterior fold removal produces a lowering of the threshold curve, though this drop is not as great as with anterior fold removal. The form of the curve compares well with the normal condition. When the posterior-fold-removed curve is compared with the posterior-slit-blocked curve, the result is less clear (Fig. 3) since the curves overlap at two frequency bands, notably 1–4 kHz and 13–16 kHz.

The threshold curve for the tympanal slits with anterior folds removed is compared with the normal condition in Fig. 4. There is a marked lowering of threshold in the frequency band 1–20 kHz with perhaps some modification at 13 kHz and 19 kHz. This lowering of the threshold can be compared with the effect of blocking the anterior slit. The shape of the curve with anterior slit blocked compares well with the curve with anterior fold removed. It may be that, due to the cuticular fold, the anterior membrane is in some way especially tuned at 13 kHz.

The effect of removing the posterior cuticular fold compared with the normal condition (Fig. 5) is not as marked as removing the anterior fold. Indeed in the lower frequency band, 1–8 kHz, the effect is less than that of blocking the posterior slit. This perhaps suggests that the posterior membrane is more concerned with high frequencies and that the small aperture is important for the correct functioning of the membrane.

The effects of these operational procedures are clearly complex and the results will

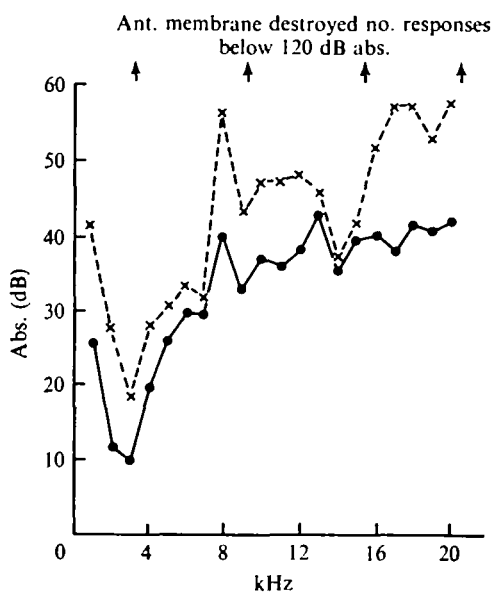


Fig. 8

Fig. 8. The effects of destruction of the anterior ( $\uparrow$ ) and posterior ( $\times - \times$ ) membranes on the normal spiracular threshold curve ( $\bullet - \bullet$ ).

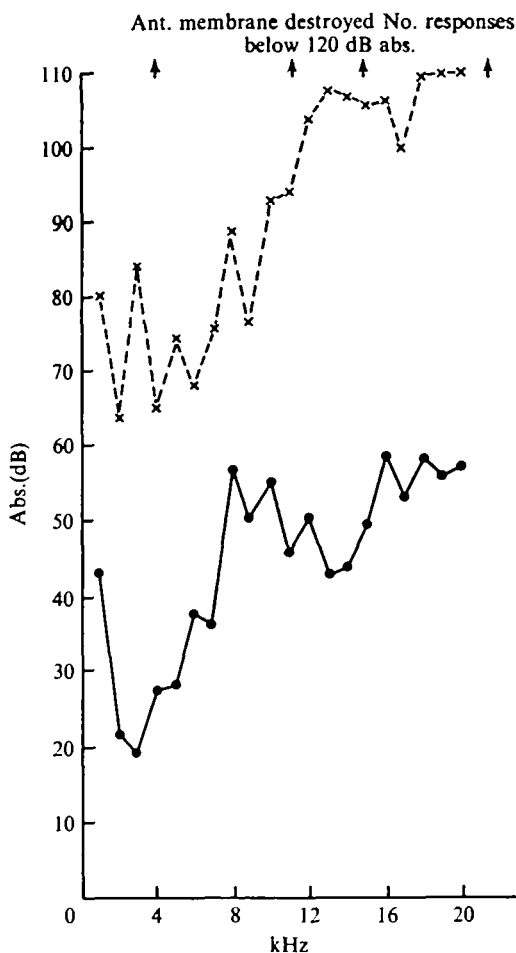


Fig. 9

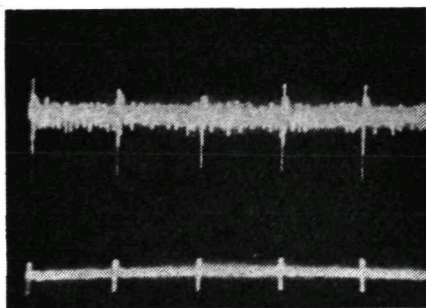
Fig. 9. The effect of destruction of the anterior ( $\uparrow$ ) and posterior ( $\times - \times$ ) membranes on the normal tympanal slit threshold curve ( $\bullet - \bullet$ ).

be considered further in the discussion. However, it is probably worth emphasizing that where specific effects have been noticed these have been centred around the dominant frequency of the species song, and it may be argued that all these structures have evolved in order to emphasize this frequency.

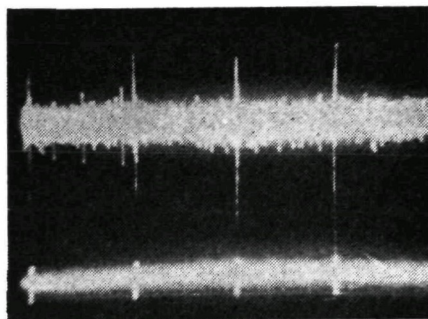
The effects of removal of both cuticular folds on spiracular sound entry are given in Fig. 6, and on tympanal slit sound entry in Fig. 7.

### 3. Acoustic threshold curves for the tympanal organ after membrane lesion

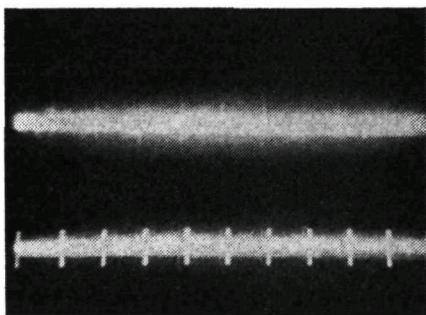
Destruction of the anterior tympanal membrane eliminated all responses to sound in the frequency band 1–20 kHz, even at intensities greater than 120 dB, for each of two attempts in three separate preparations. It may therefore be concluded that the anterior membrane is of prime importance in sound reception, both to spiracular and



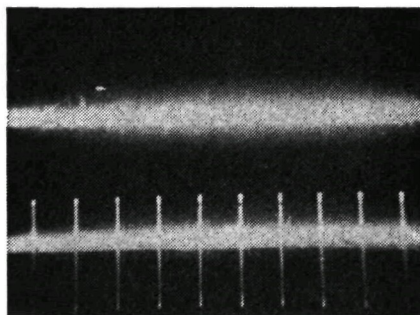
(a) Ant. membrane  
95 dB



(b) Post. membrane  
95 dB



95 dB



(c) Central membrane

125 dB

Fig. 10. The responses obtained to point-contact vibration of the three tympanic membranes. 8 msec, 16 kHz stimulus delivered at 5 pulses sec<sup>-1</sup>. (dB values are input intensities; see text.)

to tympanal slit sound entry. It could be argued that the effect of membrane lesion was a direct one on the sensory cells. However, there was no haemocoelic loss in any of the preparations where readings were taken. This would be expected if the anterior haemocoelic space and possibly therefore the cells had been destroyed.

Destruction of the posterior membrane produced the spiracular curve drawn with the normal curve in Fig. 8. The shape of the curve has been radically changed. They approach each other at 7 and 14 kHz. Removal of the posterior membrane may allow the remaining membranes to respond in an harmonic fashion. On each side of these frequencies the effect of posterior membrane lesion is to raise the threshold markedly.

The effect of the removal of the posterior membrane on tympanal slit input is drawn in Fig. 9. Again, the removal of the membrane has profoundly affected the shape of the curve, and the increase in threshold is clearly shown. While the anterior membrane is effective over the entire range of frequencies investigated, the posterior membrane exerts an increasing effect at higher frequencies, and its maximal effect may well be beyond 20 kHz. This will be investigated in future experiments.



#### 4. Piezo-electric stimulation of anterior, posterior and central membranes

Since the tuning of the receptor to airborne sound is dependent upon the coupling of the impinging sound waves to movements of the ear drum, as well as to the transformation of tympanal membrane movements into distortions of the transduction region (Adams, 1972), the data obtained by point-contact vibration should provide some information about the first component as well as about the vibration of the central membrane.

The responses obtained to 8 msec pulses set at 16 kHz, and repeated at 5 pulses  $\text{sec}^{-1}$  are shown in Fig. 10.

#### DISCUSSION

The first paper of this series showed that the sensitivity of the tympanal organ of *H. n. vicinus* was greater when the sound was directed at the prothoracic spiracle than when the sound was incident upon the tympanal slits. It should be remembered that the curves for the spiracle and for the tympanal slits are the result of the vibration of both the anterior and the posterior membranes. Since these membranes differ in size and the cavities associated with them have different volumes, it is likely that the curves are the resultant of the mechanical activity of the two membranes. For these reasons it is important to know the part played by the membranes and also whether the central membrane integrates the responses of the external membranes.

The effect of membrane lesion is quite dramatic; removal of the anterior membrane completely eliminates the response to sound up to 120 dB, at all frequencies investigated, whether the sound is incident upon the spiracle (Fig. 8) or upon the tympanal slits (Fig. 9). Since the sensory cells are more closely associated with the anterior membrane, this membrane must be considered as of prime importance in the frequency band 1–20 kHz. Destruction of the posterior membrane does not eliminate the response in this range. The effect of removal of the posterior membrane on spiracular sound entry (Fig. 8) is to raise the threshold of the organ at all frequencies except the fundamental of 13–15 kHz and the subharmonic at 7 kHz. The posterior membrane appears to have a much greater role to play in the tympanal slit sound entry, since its removal raises the threshold considerably and also dramatically changes the shape of the threshold curve (Fig. 9). The shape of the threshold curve for the tympanal slits under unoperated conditions must therefore be the result of a complex interaction of the vibration patterns of the anterior and posterior membranes. The predominant effect must, however, still be exerted by the anterior membrane at these frequencies, and the effect of the posterior membrane upon spiracular entry may be to exert a loading function on the tracheal air column and reduce energy loss.

Loading the anterior membrane by clocking the anterior tympanal slit tends to lower the spiracular threshold marginally (Fig. 2) but this increased sensitivity is only just significant (*Q*-test) at the 5% level at 3, 8, 11, 12 and 18 kHz. Blocking the posterior tympanal slit produces a significant increase in sensitivity to spiracular sound entry only at 1 and 2 kHz (Fig. 3). It is reasonable to conclude that, for spiracular sound entry, the anterior and posterior tympanal slits are effectively almost totally closed.

As might be expected, blocking the anterior tympanal slit raises the threshold curve for tympanal slit sound entry (Fig. 4) though not significantly between 8 and 12 kHz. The shape of the curve, however, is not greatly changed and it is difficult to know what interpretation to place on this finding. Since the blocked curve is not consistently raised perhaps the cuticular folds air space has some tuned characteristic or perhaps the response between 8 and 12 kHz is a function of the posterior membrane. Blocking the posterior tympanal slit (Fig. 5) *lowers* the tympanal slit threshold curve significantly at all frequencies except the narrow band between 13 and 16 kHz. This result may be consistent with the hypothesis that in the frequency range 1–20 kHz the posterior membrane exerts a loading effect on the tympanal organ. Increased loading by blocking would enhance the effect. The band 13–16 kHz corresponds to the peak frequency of the species song in *H. n. vicinus* and loading the posterior membrane has no effect, so that for those frequencies it may be optimally loaded.

It must be remembered that interaction between spiracular and tympanal slit inputs must normally occur, since apart from the condition of anterior membrane lesion where the response is totally abolished, the effects of lesion and blocking differ and depend upon the site of sound entry.

The interaction of sound signals across and between the anterior and posterior membranes could conceivably be exerted upon the sensory cells via the central membrane, and Autrum (1942, 1963) has considered this possibility. He did not however consider the effect of sound entering via the spiracle, and the system is now seen to be very much more complex than in his interpretation. Point-contact stimulation of the central membrane was performed only at 16 kHz and must therefore be considered preliminary. Detailed investigations will follow and threshold considerations still remain to be determined. The indications, however, are consistent with preceding data.

Fig. 10 shows the responses obtained to point-contact stimulation of the three membranes. Both the anterior and the posterior membranes responded well to mechanical vibration at a B and K Amplifier input intensity equivalent to 95 dB (compared to a spiracular threshold of 74 dB and a tympanal slit threshold of 83.8 dB on the Amplifier scale to sound at 16 kHz). The central membrane, however, gave no response at this intensity nor indeed at an amplifier input intensity of 125 dB, even though the stimulus was delivered at four different positions on the membrane. It is probably reasonable to conclude that the central membrane has no vibratory function, at least at 16 kHz, and does not act as an integrator of anterior and posterior membrane responses as suggested by Autrum (1942, 1963). The fact that the central membrane is double throughout its extent, heavily cuticularized in large part, and in some positions very short, does not preclude a vibratory function since it could act as a plate rather than a membrane. It seems, however, that any interaction between the anterior and posterior membrane must be mediated not through the central membrane but through the region of the sensory cells or even in the cells themselves. The central membrane may thus have one or two functions. First, the existence of two thin external membranes may reduce the strength of the leg in this region so that a structural strut, the central membrane has developed. Secondly, the membrane may be important, not in itself, but in the fact that it separates two cavities of different

volumes, thus conferring two distinct frequency characteristics on the external membranes.

Adams (1972) considered the tuning of a receptor to be due to two components: the coupling of the impinging sound waves to movements of the ear drum, and the transformation of ear drum movements into mechanical distortions of the transduction region. The first component depends upon the acoustic properties of the membrane and associated cavities, so that in the present case the lower threshold of the anterior membrane compared to the posterior membrane at 1–20 kHz probably indicates a higher degree of coupling of the anterior membrane to sound at these frequencies.

The second component results from the mechanical properties of the receptor organ and its mode of vibration. It can be seen from Fig. 10 that the amplitude of the compound action potentials obtained from the posterior membrane is greater than that obtained from the anterior membrane. This result was consistent over six preparations and four different positions on the membranes, and is surprising in view of the fact that the sensory cells are more closely associated with the anterior air space and the anterior membrane. The posterior membrane is apparently associated with the sensory cells only via the central membrane of the anterior haemocoelic space. Since the central membrane has been shown to be inert at this frequency one is forced to consider whether the vibrations of the posterior membrane are transmitted via the anterior haemocoelic space, and if so, whether this is not also true of the anterior membrane. Recently Freidman (1972), on the basis of light-microscopical and electron-microscopical data, has suggested a similar conclusion for Gryllid hearing organs. At present, the experimental results do not allow any conclusion to be drawn, but it is a problem which warrants further investigation.

Some attempt was made in the first paper to suggest a reason for the evolution of the tracheal horn. It is much more difficult to suggest a reason for the enclosure of the external tympanal membranes by the cuticular folds since if sound stimuli produced their effects on the external surface of the membranes, these structures should by all accounts remain fully exposed. It has been suggested (Figs. 2, 3) that the slits may be effectively closed to spiracular sound entry, but open to slit entry (Figs. 4, 5), and the radiation impedance characteristics of such small openings can allow entry of sound while resisting its exit. The removal of the cuticular folds reduces the tympanal slit threshold to that of the spiracle (Fig. 11), and to a significantly lower level than the spiracular threshold at the lower frequencies. Further, removal of the cuticular folds significantly lowers the spiracular threshold at all frequencies (Fig. 6). This latter result strongly suggests that the cuticular folds exert a substantial loading function on the membranes to sound incident upon the internal or external surfaces of the membranes. The lowering of the tympanal slit threshold is perhaps of greater interest, and suggests that the open membranes of Gryllids may be as effective for sound reception as the elaborate tracheal horn and that the sensitivity of cricket ears is comparable to that of bush-crickets, although in different frequency bands. An answer to the question of why the folds and tracheal horn have developed in *Tettigoniids* may be suggested by the curves of Fig. 11. Removal of the folds lowers the tympanal slit threshold significantly below that of the spiracle in the frequency range 3–8 kHz. This is the frequency band of most of the Gryllid proclamation songs, and external sound entry may be particularly effective at these frequencies. From 8 to

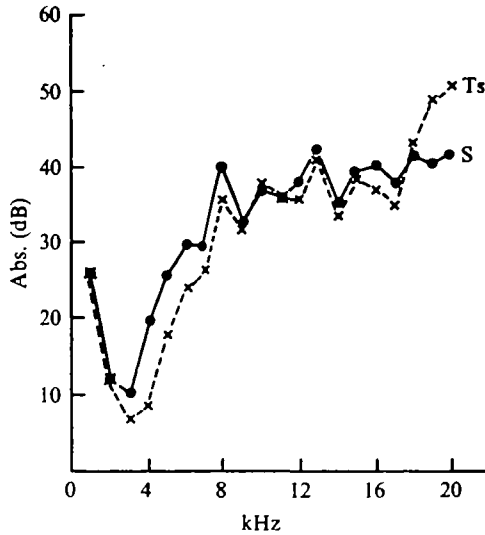


Fig. 11. The threshold curves for the spiracle under normal conditions (●—●) and for the tympanal slits with both cuticular folds removed (× — ×).

18 kHz, however, the curves are not significantly different. Sound incident upon the open external surfaces of the membranes is no more effective than sound entering via the spiracle and activating the membranes from the inside. From 8 to 18 kHz there is no disadvantage in having cuticular folds. Above 18 kHz the open tympanal membranes are significantly less effective as sound receivers than the spiracle. If this trend continues above 20 kHz, then the cuticular folds may have developed along with the exponential horn and crista acoustica, and perhaps a non-steady-state song constant, in order to maintain a sensitivity at high frequencies comparable to the sensitivity of the open membranes at low frequencies. Indeed at high frequencies the slits may lower the resistive radiation impedance and thus make the ear more sensitive (cf. Michelsen, 1971, on the intact locust ear).

One other factor should be considered. With sound stimuli effective on both surfaces of the membranes, a differential input across the membranes may be necessary in order to produce a response, since, (1) the spiracular and slit entry may be out of phase at some frequencies; the effect would be a resultant of the phase difference and intensity difference; (2) the slit and spiracular inputs may be in phase at some frequencies and intensity differences become very important. These considerations will be discussed further in a subsequent paper.

This paper has attempted to provide some insight into the roles of the various structures of the tympanal organ of Tettigoniids, with special emphasis on *H. n. vicinus*, during sound reception. It must be emphasized, however, that the consideration of these structures alone can only provide an indication of the way in which the whole organ system works. Clearly, the anterior and posterior cuticular folds, and the three membranes, as well as the air spaces, all show individual response characteristics which interact to produce the resultant stimulus for the sensory cells. Equally, there must also be an interaction between the stimulus descending the tracheal horn and that entering externally. Thus, consideration of the function of the parts must necessarily fall short of the function of the total organ system.

## SUMMARY

1. The effects of blocking the anterior and posterior tympanal slits suggests that the slits are effectively closed to spiracular sound input, but open to tympanal slit inputs.
2. Removal of both the anterior and posterior cuticular folds significantly lowers the threshold curves for both spiracular and tympanal slit entry. The sensitivity to tympanal slit entry is increased to that of the normal spiracle.
3. Destruction of the anterior membrane eliminates all responses in the frequency range 1–20 kHz; removal of the posterior membrane reduces sensitivity.
4. Point-contact vibration of the three membranes at 16 kHz indicates that the central membrane is non-vibratory and that although the posterior membrane is poorly coupled to sound up to 20 kHz, its mechanical movements are transduced with less loss than those of the anterior membrane.

## REFERENCES

- ADAMS, W. B. (1972). Mechanical tuning of the acoustic receptor of *Prodena ridiana* (Cramer) (Noctuidae). *J. exp. Biol.* **57**, 297–304.
- AUTRUM, H. (1942). Schallempfang bei Tier und Mensch. *Naturwissenschaften* **30**, 69–85.
- AUTRUM, H. (1963). Anatomy and Physiology of sound receptors in invertebrates. In *Acoustic Behaviour of Animals* (ed. R. G. Buanell). Elsevier.
- BAILEY, W. J. (1968). Studies in the Mechanics of Sound Production in *Homorocoryphus nitidulus* (Scopoli) (Orthoptera, Tettigoniidae) and Allied Species. Ph.D. Thesis. University of London.
- CARPENTIER, F. (1924). Sur le double stigmate de quelque Orthoptères. *Bull. Soc. ent. Belg.* **6**, 123–40.
- CARPENTIER, F. (1927). Sur les trachéides de la base des pattes et des ailes de la Saut. verte. *Annls Soc. scient. Brux.* Série B **47**, 63–86.
- FREIDMAN, M. H. (1972). A light and electron microscopic study of sensory organs and associated structures in the foreleg of the cricket *Gryllus assimilis*. *J. Morph.* **138** (3), 263–334.
- HOWSE, P. E. (1968). The fine structure and functional organization of chordotonal organs. *Symp. zool. Soc. Lond.* **23**, 167–98.
- LEWIS, D. B. (1974). The physiology of the tettigoniid ear. I. The implications of the anatomy of the ear to its function in sound reception. *J. exp. Biol.* **60**, 821–37.
- MASON, W. P. (1951). *Piezo-electric Crystals and their Application to Ultrasonics*. Van Nostrand. New York.
- MICHELSSEN, A. (1971). The physiology of the locust ear. *Z. vergl. Physiol.* **71**, 49–128.
- NOCKE, H. (1972). Physiological aspects of sound communication in crickets (*Gryllus campestris* L.). *J. comp. Physiol.* **80**, 141–62.
- PUMPHREY, R. J. (1940). Hearing in Insects. *Biol. Rev.* **15**, 107–32.
- SCHUMACHER, R. (1973). Beitrag zur Kenntnis des tibialen Tympanalorgans von *Tettigonia viridissima* (L.) (Orthoptera: Tettigoniidae). *Mikroskopie*, Bd. **29**, 8–19.
- SCHWABE, J. (1906). Beiträge zur Morphologie und Histologie der tympanalen Sinnesapparate der Orthopteren. *Zoologica, Stuttg.* **50**, 1–154.
- v. SIEBOLD, C. T. E. (1844). Ueber das Stimm-und Gehörorgan der Orthopteren. *Arch. Naturgesch.* **11**, 71–86.
- ZEUNER, F. (1936). The prothoracic tracheal apparatus of Saltatoria (Orthoptera). *Proc. R. ent Soc. Lond. (A)*, **11**, 11–21.
- ZHANTIEV, R. D. (1970). (In Russian.) Frequency characteristics of tympanal organs in grasshoppers (Orthoptera, Tettigoniidae). *Zool. J. U.S.S.R. Acad. Sci.* **50**, 507–14.