

THE PHYSIOLOGY OF THE TETTIGONIID EAR

IV. A NEW HYPOTHESIS FOR ACOUSTIC ORIENTATION BEHAVIOUR

By D. B. LEWIS

Animal Acoustics Unit, City of London Polytechnic

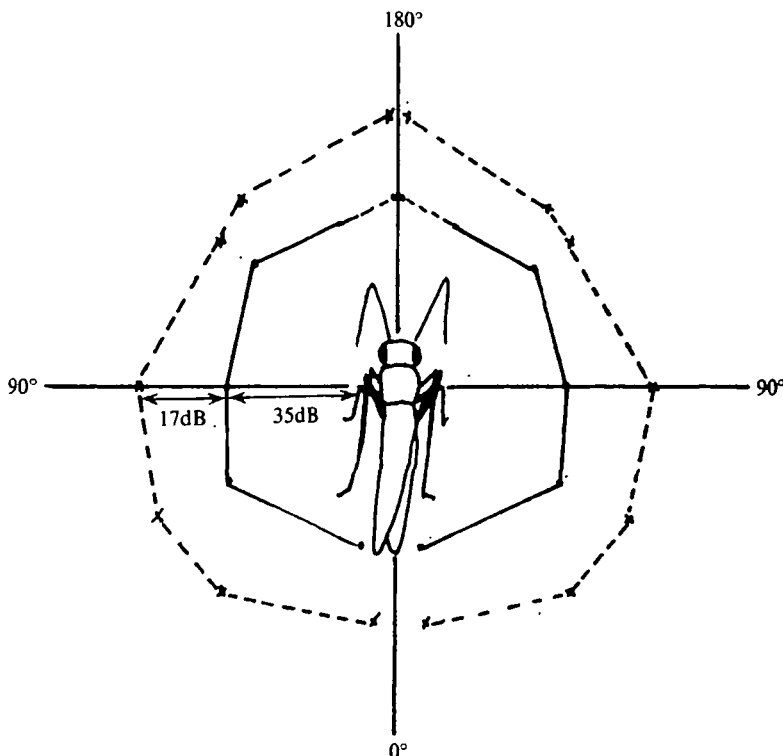
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INTRODUCTION

Sound receivers have been divided into two classes, pressure receivers and pressure-gradient receivers. A pressure microphone is backed by a closed cavity, but in a pressure-gradient microphone both sides of the membrane are exposed to the sound wave and so will respond to the difference in sound pressure on each side of the membrane, the resultant being a function of the phase difference and the intensity difference, which themselves depend on the effective distance between the two sides. A good example of a symmetrical pressure-gradient receiver is the ribbon microphone, while the Tettigoniid ear may be considered along with the locust ear (at least in small animals at low frequencies) to be an asymmetrical pressure-gradient receptor (Michelsen, 1971; Autrum, 1941; Pumphrey, 1940). The situation is likely to be more complex at very high frequencies, and perhaps at low intensities, because of the differences in threshold of the ear to spiracular and tympanal slit inputs. Since the force acting on a pressure gradient receiver is a vector quantity, the directional sensitivity of insect ears has been ascribed to the variation in the angle of incidence of sound upon the tympanal membranes. In Tettigoniids, the pressure gradient has been assumed to arise as a result of sound entry via the anterior and posterior tympanal slits, and to act across the central membrane whose resultant movement is transduced by the sensory cells (Autrum, 1942). It has been shown in a previous paper however (Lewis, 1974*b*) that the central membrane is non-vibratory.

Autrum (1940) also investigated the directional characteristics of the tympanal organ of *Tettigonia viridissima* and showed the existence of a rather skewed hemispherical field of reception about the tympanal slits, which were presumed to be the receptive fields of the whole organ system. From the consideration of the ear as a pressure-gradient receiver and from his data on the receptive fields Autrum (1942) then presented an hypothesis which suggested the existence of 'sound corridors' radiating outwards from the tympanal slits at angles of approximately 60° to each other. Since these regions of high intensity were constant to each other and to the tibia, the environment could be scanned by moving the leg fore and aft. By this means the sound source could be located.

Since spiracular sound entry is so important in Tettigoniids, Autrum's (1942) hypothesis must be reviewed. Although the pressure gradient cannot be effective across the central membrane, such a gradient does exist across each of the external membranes as a result of sound entering via the spiracle and via the tympanal slits (Lewis, 1974*a*). These sound waves will also have a phase interaction and the complexity



Text-fig. 1. The threshold values for the spiracle (●—●) and tympanal slits (x—x) to a 15 kHz, 8 msec signal drawn on a polar diagram. (dB rel 0.0002 dyne/cm².)

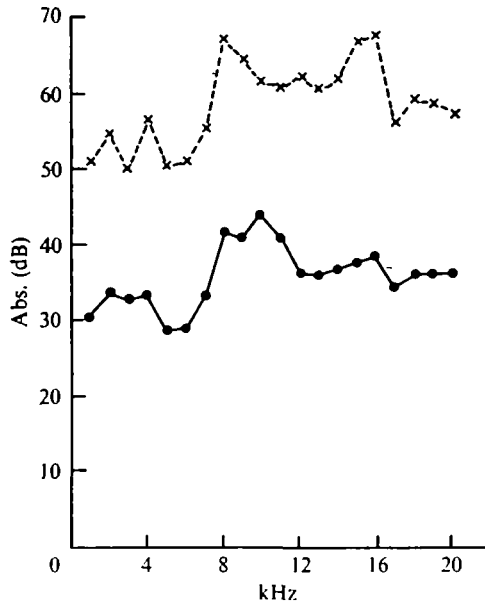
of the resultant has already been considered (Lewis, 1974c). The purpose of this paper is to consider the directionality characteristics of both the spiracle and the tympanal slits, and the ipsilateral and contralateral whole-organ responses with a view to developing a new hypothesis for acoustic orientation in Tettigoniids.

METHODS

The methods of determining the acoustic threshold of the tympanal organ to a lateral sound source has already been described (Lewis, 1974c).

The threshold of the spiracle and the tympanal slits was determined at a variety of angles as the emitter microphone with 1 mm probe attachment was moved through 180° relative to the long axis of the body. The preparation was set up in the anechoic conditions described in Paper I of this series (Lewis, 1974a), where the details of intensity calibration are also described. The stimulus used was a 15 kHz pulsed clipped sine wave of 8 msec duration, at a rate of 5 pulses sec⁻¹.

To check on any possible spiracular movements, the dimensions of the acoustic spiracle during sound emission were investigated using video-tape recordings of an individual *Platypleis intermedia* producing a long series of disyllabic chirps. This tape recording was then analysed frame by frame, and each frame was photographed. The photographic reproduction of the television picture is not as good as one would wish, but the dimensions of the spiracle can easily be determined.



Text-fig. 2. The threshold curves for the ipsilateral (●—●) and contralateral (×—×) tympanal organs.

RESULTS

The position of the legs having been fixed at right angles to the long axis of the body, the threshold values for the spiracle and the tympanal slits at a variety of angles to these structures are drawn on a polar diagram in Text-fig. 1. The spiracular threshold is shown to be around 20 dB lower than that obtained for the tympanal slits, and the receptive fields of both are roughly hemispherical about the long axis of the insect body.

The threshold curves for both the ipsilateral and contralateral tympanal organs to a lateral sound source, 30 cm from the preparation are drawn for comparison in Text-fig. 2. A clear difference of threshold sensitivity of approximately 25 dB is apparent although the forms of the curves are similar.

The single-frame exposures of the spiracular region during a single disyllabic chirp emission in *P. intermedia* are shown in Plate 1. Clearly there is no change in the dimensions of the spiracle during sound production.

DISCUSSION

Since Autrum's (1942, 1963) hypothesis for orientation behaviour in the Tettigoniids took no cognizance of the spiracular sound entry, that hypothesis must be incomplete. The existence of a receptive field which is roughly hemispherical about the spiracle and about the tympanal slits does not correspond too well with Autrum's (1940) findings. The whole-organ response may differ from the responses obtained by the use of a probe tip by up to 6 dB as a result of diffraction phenomena and this may explain the difference between these results and those of Autrum (1940).

The existence of a 25 dB difference in threshold between the ipsilateral and the

contralateral sides (Text-fig. 2) allows the insect to determine easily the side from which the sound comes, but it is a very difficult task to explain the reason for such a considerable difference in sensitivity. It is unlikely that the effect is due to shadow phenomena at the contralateral spiracle since the wavelengths of the sound stimuli used are not small enough. Michelsen (1971) indicated that shadow effects were unlikely to occur in *Schistocerca*, a bigger insect than *Homorocoryphus*, up to a frequency of about 40 kHz. However, the fact that the spiracle is facing away from the sound source and is partially covered by the pronotum may considerably alter the threshold of the contralateral ear.

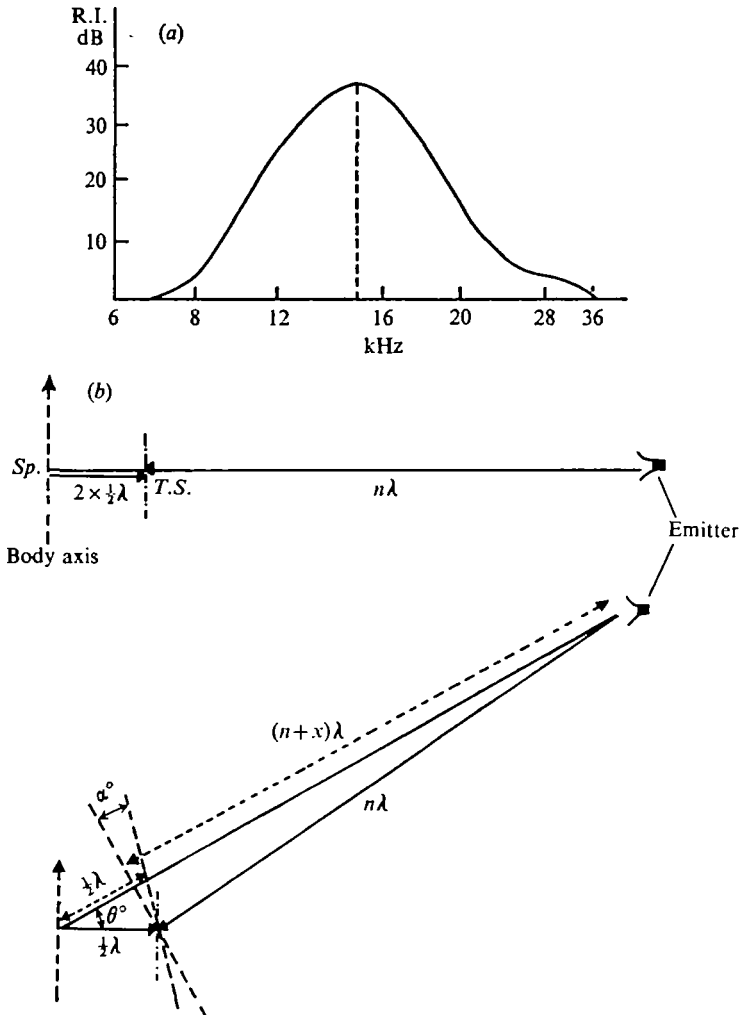
One other possibility for reducing the sensitivity of the tympanal organ is that the dorso-ventral song musculature of the thorax could cause the mesothoracic wall to abut against the pronotal flap thus effectively reducing the size of the horn mouth. No direct evidence exists but indirect evidence is supplied by the fact that during sound production (when the dorso-ventral musculature is known to contract) in *P. intermedia* at least (Plate 1) the dimensions of the pronotal flap-mesothoracic wall opening do not change. The spiracle is clearly visible throughout the whole sequence of the chirp. If the spiracle is not closed during active contraction of the dorso-ventral musculature it might be considered unlikely that the spiracle is closed in this way when the individual is not singing. It is still possible that the spiracular sound pathway is closed, because contraction of the song musculature may appose the tracheal walls within the thorax. Whatever the means used to reduce the sensitivity of the contralateral ear, right-left orientation must be possible.

Michelsen (1971) has discussed the physics of an asymmetric sound receiver and has shown that the phase angle between p_f (sound pressure acting on the front of the membrane) and p_b (sound pressure acting on the back of the membrane) due to the effective distance Δl between them is given by $2\pi\Delta l/\lambda$. In an asymmetric sound receiver such as the Tettigoniid ear the effective distance Δl may be divided into l' (the effective distance from the knee to the spiracle) and l'' (the effective distance from the spiracle down the trachea). The angle of incidence, Φ , will only affect l' .

When the angle of incidence is in line with both the spiracle and the tympanal slits (the condition of no parallax, Text-fig. 3) Φ is zero and the phase difference is entirely dependent upon the distance $l' + l''$. In the condition where Φ is greater than zero then the phase difference is the result of both the effective distance and the angle of incidence, so that,

$$\alpha = \frac{2\pi(l' \cos \Phi + l'')}{\lambda}.$$

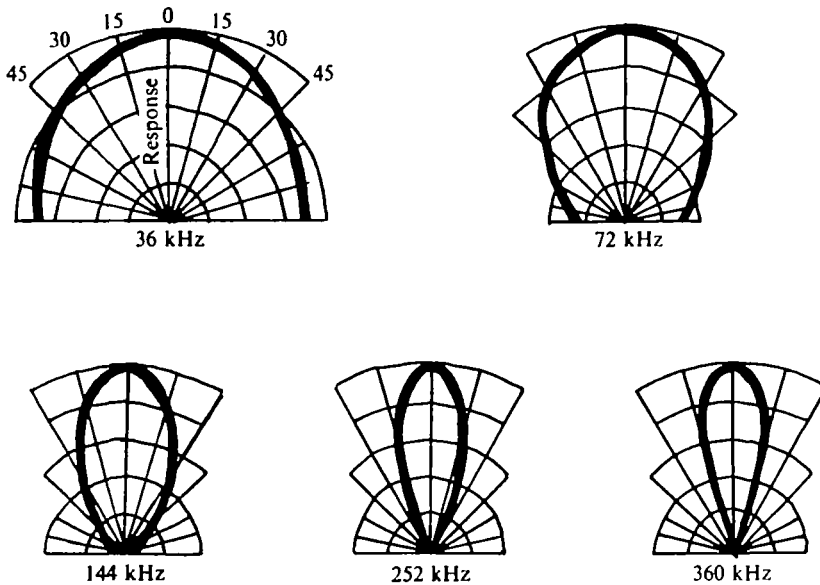
Measurement of the distance l' in *Homorocoryphus* gives a value of about 1.2 cm, and for l'' a value of 1.4 cm. The total distance in the condition of no parallax is therefore 2.6 cm corresponding to a frequency around 16 kHz (Text-fig. 3). Therefore in this condition and at this frequency the sound incident on the two surfaces of the membrane will be in phase, and the displacement of the tympanal membranes should be minimal (zero, if the inputs are equal). Text-fig. 2, however, shows that the threshold for the whole-organ system at 15–16 kHz is low, i.e. sensitivity is high. This result may be due to two factors. First, even with no phase differences, there will still be sensitivity differences due to the lower threshold of the spiracle; secondly, this intensity difference will be emphasized because of the resonant



Text-fig. 3. (a) The frequency spectrum of *Homorocoryphus* (redrawn from Bailey (1968)), and (b) the importance of the angle of incidence of sound upon the activity of the tympanal organ (*Sp.* = spiracle; *T.S.* = tympanal slits). Further explanation in text.

function of the horn shown in a previous paper (Lewis, 1974*c*) to be 16 kHz. When the angle of incidence is greater than zero, the distance l' will change and the 15–16 kHz sound on each side of the membrane will be out of phase. The resultant response will thus be a function not only of intensity differences but also of phase differences, and the maximal response will be obtained when the incident sound is maximally out of phase (i.e. 180° out of phase). It is also true of course, that in a parallax situation, although 15 kHz sound will be out of phase, some other frequency will be in phase.

These factors suggest an hypothesis for acoustic orientation behaviour in Tettigoniids. Autrum (1955) suggested a directionality characteristic for the tympanal slits of Tettigoniids in such a way that there were regions of high sensitivity in line with each slit, with an area of low sensitivity between them. But due to their size, such

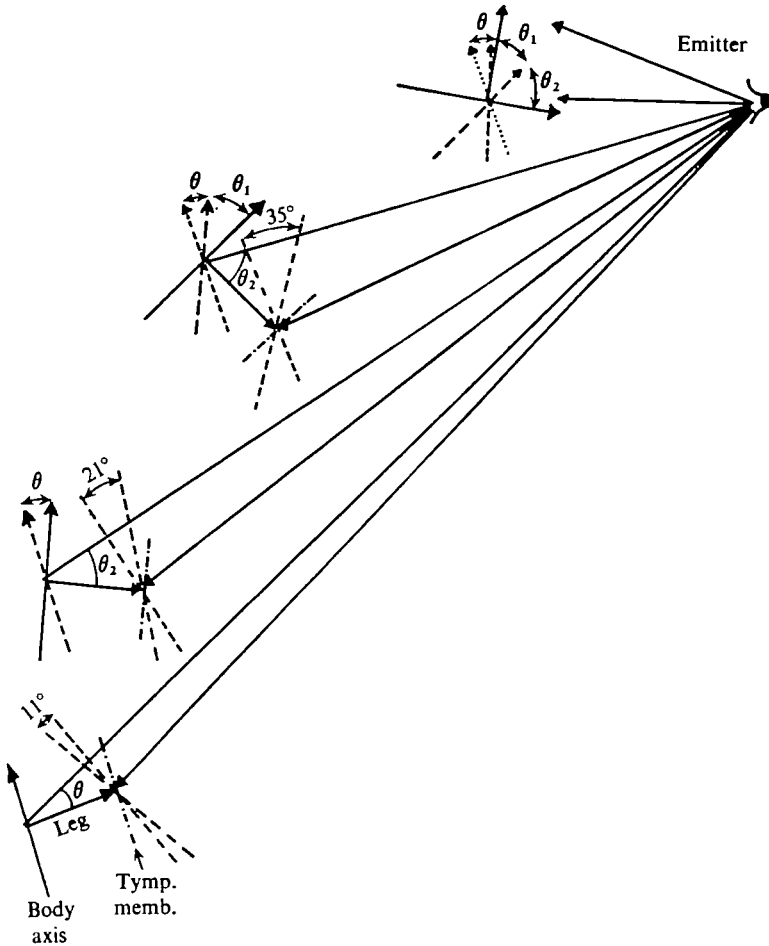


Text-fig. 4. Directional characteristics of a small exponential horn of circular cross-section and of the dimensions of the acoustic trachea. The polar graphs show the sound level at a fixed distance as a function of the angle of incidence. The direction 0° is the axis of the horn. (Redrawn and recalculated from Olson, 1967.)

structures are unlikely to have such a clearly defined acoustic corridor and indeed poor directionality for both the spiracle and the tympanal slits has been shown for *Homorocoryphus* (Text-fig. 1) using a probe emitter. A broad symmetrical receptive field is also suggested from physical considerations (see also Lewis, 1974c). Text-fig. 4 is redrawn and recalculated from Olson (1967). It can be seen that for an emitter or receiver of the dimensions of the spiracle and trachea, some degree of directionality is only attained at about 70 kHz. For the tympanal slits the value will be even higher because they are smaller. For directionality similar to that postulated by Autrum (1955), frequencies in excess of 250 kHz would be required. These structures alone cannot provide directional information.

The existence of a large difference in threshold between the ipsilateral and contralateral tympanal organs allows the insect to determine easily the side from which the sound comes and this may be further emphasized by means of central nervous factors (McKay, 1969; Suga & Katsuki, 1961; Rheinlander & Kalmar, 1973). Presumably the neural network is such that the animal will turn towards that side where the response is greatest.

If the sound has an angle of incidence (Φ) greater than zero, some frequency will be in phase as determined by the above equation, and its effect will therefore be diminished. All other frequencies will be out of phase, and their effects will be the result of both phase and intensity differences across the membranes; the overall intensity of sound at 15–16 kHz will be increased as described above (Text-fig. 3). If it was not for the effect of the resonant factor of the horn, the responses to these other out-of-phase-frequencies would be comparable to those for 15–16 kHz. But in addition to the horn function, the song emitted by *Homorocoryphus* and many other Tetti-



Text-fig. 5. A proposed hypothesis for acoustic orientation behaviour in Tettigoniids. Further details in text.

goniids, is reasonably sharply peaked (Bailey, 1970; Bennet-Clark, 1971) (Text-fig. 3), so that at frequencies above or below 15–16 kHz the song intensity falls off sharply, and this decrease in intensity will be correlated with the angle of incidence.

The net result of these factors will be that in the no-parallax situation the intensity of the carrier frequency of the song of *Homorocoryphus* will be minimal. As the sound moves to a more anterior position, or as the animal turns to bring the sound anterior, the 15–16 kHz frequency will become progressively out of phase and will approach a maximal phase difference when the sound is directly ahead. The animal should therefore turn and move towards the sound source.

Moving the leg through an angle θ° by scanning or walking will produce a new no-parallax situation, and minimal sound reception. If there is a proprioceptive input from the leg, and it seems reasonable to suppose there is, then the extent of the input will be dependent upon the position of the leg relative to the long axis of the body. The position of the leg at *minimum* sound intensity level will therefore indicate the angle of incidence of the sound relative to the long axis of the body. Text-fig. 5 takes this

argument a stage further. If the insect can compute the angle θ° , then the body must move through this angle in order to face the sound source and thus maximize the input. If the insect moves forwards at the same time as the body is turned, however, by the time the turn of θ° has been accomplished, the sound source is still at an angle of incidence greater than 0° . Indeed the angle of incidence has increased due to the fact that the animal is now closer to the sound source. The environment must therefore be 'scanned' by the leg yet again for the minimal sound intensity and this time comes to rest at an angle θ_1^0 . The body is now moved forwards through an angle of θ_1^0 , by which time the insect is nearer the sound source, but at a greater angle of incidence. This procedure can be repeated until the receiver is within sight of the emitter when localization by vision can occur. Should the insect turn through to greater an angle than θ_n^0 , then the sound will be more intense on the opposite side of the body and a corrective movement can occur. Near the sound source, it is expected that corrective movements will constantly occur as the body is moved through too great an angle.

Although this is probably a crude hypothesis for the basis of orientation in Tettigoniids, some support for this 'angular homing' system comes, perhaps surprisingly in view of the differences in the tympanal organ structures, from the Gryllids. Murphey & Zaretsky (1972) and Zaretsky (1972) showed similar orientation behaviour in *S. marginatus*, and that movement was made in short bursts of activity, between the chirps of the emitter. There are certain to be differences, however, since *S. marginatus* is a discontinuous singer while *Homorocoryphus* is a continuous one. Movement in *Homorocoryphus* may appear to be much more smooth and continuous than in Gryllids. Further work is in progress to investigate the behavioural and neurophysiological basis of orientation in bush-crickets.

SUMMARY

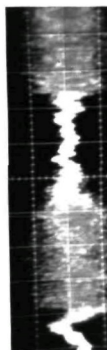
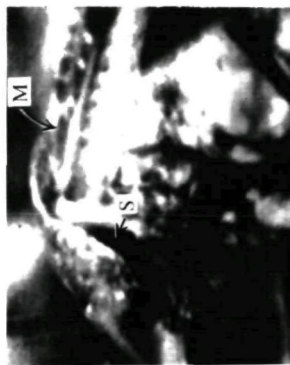
1. The thresholds for the spiracle and for the tympanal slits have been determined at a variety of angles to the body axis and show little directionality.
2. A difference in threshold levels of 20 dB exist between the ipsilateral and contralateral whole organs in the frequency range 1–20 kHz.
3. Single-frame exposures of a video-tape recording show that the spiracular dimensions do not change during stridulation.
4. In the light of the evidence, a new hypothesis for acoustic orientation behaviour is advanced.

REFERENCES

- AUTRUM, H. (1940). Über Lautäusserungen und Schallwahrnehmung bei Arthropoden. II. Das Richtungshören von Locusta und Versuch einer Hörtheorie für Tympanalorgane vom Locustidentyp. *Z. vergl. Physiol.* **28**, 326–52.
- AUTRUM, H. (1941). Über Gehör und Erschütterungssinn bei Locustiden. *Z. vergl. Physiol.* **28**, 580–637.
- AUTRUM, H. (1942). Schallempfang bei Tier und Mensch. *Naturwissenschaften* **30**, 69–85.
- AUTRUM, H. (1955). Analyse physiologique de la réception des sons chez le Orthoptères. *Annls inst. natn. Rech. agron. Paris*, Ser. C. *Ann. epiphyt.*, fascicule special: L'acoustique des Orthoptères. **6**, 338–55.
- AUTRUM, H. (1963). Anatomy and physiology of sound receptors in invertebrates. In *Acoustic Behaviour of Animals* (ed. R. G. Busnel). Elsevier.
- BAILEY, W. J. (1968). Studies in the Mechanics of Sound Production in *Homorocoryphus nitidulus* (Scopoli) (Orthoptera, Tettigoniodea) and Allied Species. Ph.D. Thesis. University of London.



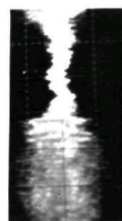
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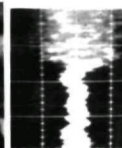
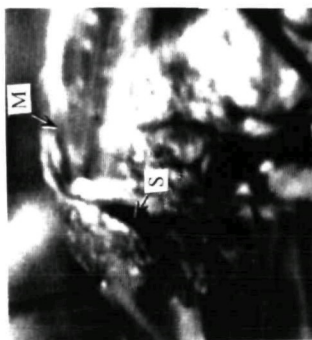
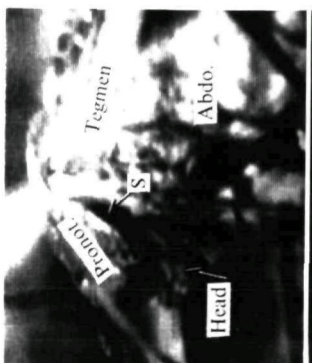
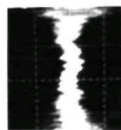
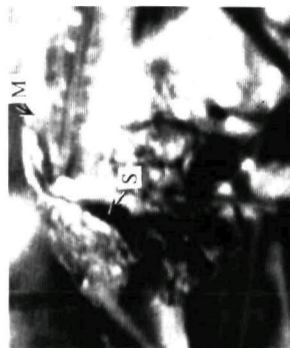
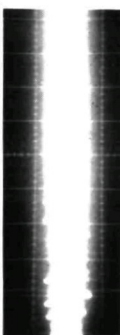
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- BAILEY, W. J. (1970). The mechanics of stridulation in the bush-crickets (Tettigoniodea, Orthoptera). I. The tegminal generator. *J. exp. Biol.* **52**, 495-505.
- BENNET-CLARK, H. C. (1971). The acoustics of insect song. *Nature, Lond.* **234**, 255-9.
- LEWIS, D. B. (1974a). 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.
- LEWIS, D. B. (1974b). The physiology of the tettigoniid ear. II. The response characteristics of the ear to differential inputs: lesion and blocking experiments. *J. exp. Biol.* **60**, 839-51.
- LEWIS, D. B. (1974c). The physiology of the tettigoniid ear. III. The response characteristics of the intact ear and some biophysical considerations. *J. exp. Biol.* **60**, 853-9.
- MICHELSSEN, A. (1971). The physiology of the locust ear. *Z. vergl. Physiol.* **71**, 49-128.
- MCCAY, J. M. (1969). The auditory system of *Homorocoryphus* (Tettigoniodea, Orthoptera). *J. exp. Biol.* **51**, 787-802.
- MURPHEY, R. K. & ZARETSKY, M. D. (1972). Orientation to calling song by female crickets, *Scapsipodus marginatus* (Gryllidae). *J. exp. Biol.* **56**, 335-52.
- OLSON, H. F. (1967). *Music, Physics and Engineering*. 2nd ed. New York: Dover.
- PUMPHREY, R. J. (1940). Hearing in insects. *Biol. Rev.* **15**, 107-32.
- RHEINLAENDER, J. & KALMRING, K. (1973). Die afferente Hörbahn im Bereich des Zentralnervensystems von *Decticus verrucivorus* (Tettigoniidae). *J. comp. Physiol.* **85**, 361-410.
- SUGA, N. & KATSUKI, Y. (1961). Central mechanisms of hearing in Insects. *J. exp. Biol.* **38**, 545-58.
- ZARETSKY, M. D. (1972). Specificity of the calling song and short term changes in the phonotactic response by female crickets *Scapsipodus marginatus* (Gryllidae). *J. comp. Physiol.* **79**, 153-72.

EXPLANATION OF PLATE

Single-frame exposures of the spiracular region of *P. intermedia* during a video-tape recording of a single disyllabic chirp.