The Tympanal Trachea as an Integral Part of the Ear in *Acripeza reticulata* Guérin (Orthoptera, Tettigonioidea)

Harald Nocke

Department of Neurobiology *, Research School of Biological Sciences, Australian National University

(Z. Naturforsch. **29 c**, 652–654 [1974]; received June 4, 1974)

Tettigonioidea, Ear, Function Tympanal Trachea

The functional role of the large trachea which runs from a spiracle in the thorax down the leg (tympanal trachea) was analysed in relation to the tympanal organ. The tympanal trachea not only tunes the tympanal organ to a certain frequency (Fig. 1) but is important for the directional sense of hearing in the whole animal. The directional sensitivity of the ear depends only on the relative positions of the spiracle of the tympanal trachea and the direction of sound (Fig. 2), irrespective of the foreleg walking position.

In the vertebrate ear only one air-conduction-pathway for sound is important functionally: That inward the outer ear and the front side of the ear-drum. This "vertebrate-model" has greatly influenced the present view on Tettigoniid hearing. Based on anatomical studies it was suggested, however, as early as 1876 by Graber [1] that sound might reach the sensory structures of the tibial TO [2], located in both forelegs of many Tettigoniids, not only via the outer side of the two tympani on each leg, but also *via* the TT [3] which runs from a spiracle in the thorax to the TO.

Autrum [4] was the first to study the physiology and to develop a "hearing theory for the TO of the Tettigoniid type". This theory, however, which has generally been accepted, does not take a possible sound pathway *via* the TT into account. The functional significance of the TT of the Australian Tettigoniid *Acripeza reticulata* Guérin was therefore analysed.

The anatomy of the TT system found in *Acripeza* is typical of many Tettigoniids with hearing organs. It is anatomically very similar to that of the European species *Tettigonia viridissima* Lin. (see Carpentier [5], Zeuner [6], Ander [7]) which Autrum [4] used in his experiments.

Many possible acoustic functions have been suggested for the TT (or for parts of it), including resonator and horn (Zeuner [6]). Recently Lewis [8] suggested that the TT of *Homorocoryphus* functions as an exponential horn which for physical reasons could increase the sensitivity of the TO considerably (Beranek [9]). A possible horn function of the TT in *Acripeza* will at first be considered from a physical point of view. This must take into account the physical dimensions of the TT and the carrier wavelength λ of the *Acripeza* song ($\lambda \cong 41$ mm) which is transmitted down to the horn throat. In this paper only the ratio between the circumference C of the horn mouth (= spiracle) and the wavelength λ will be considered. For $C/\lambda > 3$, the horn would behave approximately like an exponential horn of infinite length. For ratios of $C/\lambda < 0.5$, however, the hornlike structure looses the physical properties characteristic of an exponential horn and resonates like a cylindrical tube of approximately the same length (Beranek [9]). In *Acripeza* $C/\lambda \cong 0.16$ and therefore we have the condition for resonance. Since the TT is open at the stigma and not rigidly closed where it terminates at the two tympani, its first resonance is to be expected at a frequency where the length of the TT equals one half wavelength (Beranek [9]). The acoustic length of the TT of one side in *Acripeza*, measured using acoustic interference (Nocke [10]), is near 19.5 mm, which is close to one half wavelength ($\lambda/2 \cong 20.5$ mm) of the carrier frequency ($\cong 8$ kHz) of *Acripeza* sound communication.

The following experiments were carried out in an anechoic room (cut off frequency 430 Hz) with a background noise level (0.315 – 31.5 kHz) ≤ 0 dB. During the experiments the animal holder with the animal was the only object projecting into the sound field. The recording technique and the determination of the hearing threshold curve follows essentially that given by Nocke [11]. For a more detailed description of the experimental technique see Nocke [10]. All sound pressure levels will be given below in RMS values re 2×10^{-5} N/m^2.

The physical considerations above suggest that the TT tunes the TO to the carrier frequency of the song and possibly increases its sensitivity by means of the tube resonance. If this is correct we can expect that the tube length has an influence on the "tuning" of the hearing threshold curve of this ear and must consequently change with the effective length of the TT. The physical laws pertaining to the resonance of open tubes also imply that the optimum or best frequency of the hearing threshold curve decreases if the TT is extended. The hearing threshold curve of *Acripeza* has a best frequency of 8.2 kHz in the intact animal (Fig. 1). This best frequency shifts to 3.8 kHz (Fig. 1) if the TT is extended by a 18 mm long piece of tubing. The best frequency can be lowered further by increasing the length of the extension. The diameter of the ex-

---

* I am grateful to Prof. Dr. G. A. Horridge for discussions and for reading and criticising the manuscript.

Requests for reprints should be sent to Dr. H. Nocke, P.O. Box 4, 2606 Chifley, *Canberra* (ACT), Australien.

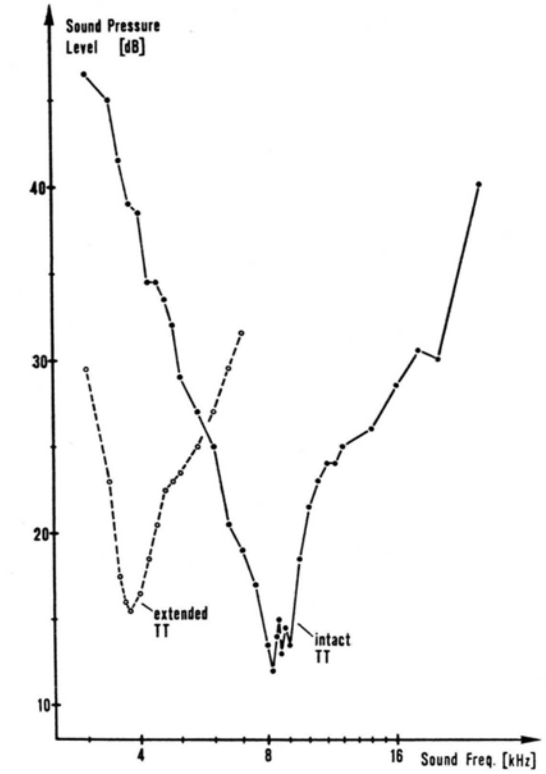

Fig. 1. *Acripeza reticulata.* Threshold curve of the tympanal nerve, for the intact ear and for the same ear with an extended TT (further explanation see text).

tension tube has no measurable influence on this frequency shift (tubes with inner diameters between 1.2 and 5 mm were used). The TT does not only effect the tuning of the *Acripeza* ear but it is important to its directionality.

Our present picture of the directionality of Tettigoniid ears has been largely determined by Autrum's experiments on *Tettigonia.* Here the TO itself is directional and its directional sensitivity depends on the position of the leg relative to the direction of the sound (Autrum [4], Figs 4, 5). However, Autrum always worked with the isolated leg, and therefore cut the TT. I find that the directional sensitivity of the *Acri*peza ear depends only on the relative positions of the opening of the TT (= spiracle) and the direction of the sound. From Fig. 2 it follows that the ear is most sensitive if the spiracle points towards the sound source (180°) and least sensitive if it points away from it (0°). This directionality disappears if the spiracle is closed artificially. Moreover, the relative position between the symmetry axis S of the directivity pattern and the longitudinal axis L of the animal (Fig. 2) does not change if the foreleg is brought into different walking positions (Fig. 2, see also Nocke [10]). This differs from *Tettigonia* where the two axes (L and S) move relative to each other when the animal is walking.

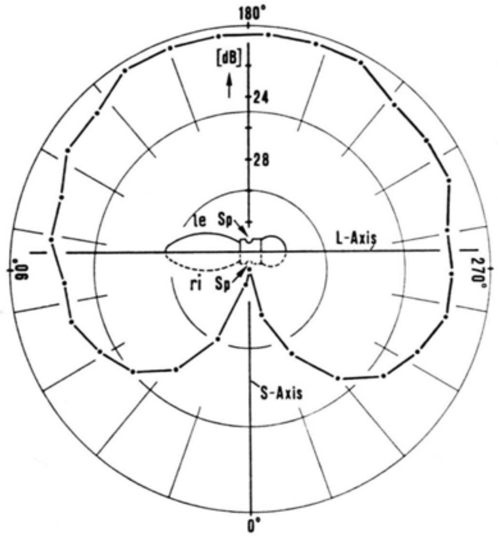

Fig. 2. *Acripeza reticulata.* Directivity pattern for the left hearing organ, showing the relative position between the animals longitudinal axis (L) and the symmetry axis (S) of the pattern. For the 8-kHz-stimulus used in this experiment the directional sensitivity difference between 0° and 180° was 15 dB. le Sp, ri Sp: anatomically left and right spiracle (further explanations, see text).

Recently Michelsen and Nocke [12] suggested that most insect ears probably function as a "combined pressure and pressure gradient receiver" (Beranek [9]). This intermediate receiver type has a cardioid directivity pattern like that of the Acripeza ear (Fig. 2), quite different from the "figure 8" type directivity pattern which follows from Autrum's theory. The measured pattern in *Tettigonia,* however, shows a residual sensitivity in the 0°-direction and only a very small decrease of sensitivity in the 180° direction (Autrum [4], Figs 4, 5), somewhat similar to *Acripeza* (Fig. 2). Curiously, the *Tettigonia* ear gave the highest sensitivity in the direction (180°) where the opening of the cut TT points to the sound source (Autrum [4], Figs 4, 5). The TO of *Acripeza* also becomes "directional", with a maximum sensitivity in the 180°-direction when the foreleg is cut off and rotated in the sound field as in the *Tettigonia* experiments. The physiological differences between the directional sensitivity of the ear in *Tettigonia* and those in *Acripeza,* with similar anatomy, are probably caused by the different experimental arrangements.

Strong evidence is already available to show that the ear of *Teleogryllus commodus* Walker similarly depends on the tracheal system.

[1] V. Graber, Denkschr. k. Akad. Wiss. Math.-Naturwiss. Cl. **Bd. 36,** Wien 1876.

[2] TO = tympanal organ.

[3] TT = tympanal trachea.

[4] H. Autrum, Z. vergl. Physiol. **28,** 326–352 [1940].

[5] F. Carpentier, Ann. Soc. scientif. de Bruxelles Sér. BT47, Louvain [1927].

[6] F. Zeuner, Proc. R. Entomological Soc. London A **1936, 11.**

[7] K. Ander, Opuscula entomologica, Berlingska Boktryckeriet, Lund 1939.

[8] B. Lewis, Nature **231,** 493 [1971] (see also Lewis in Michelsen and Nocke [12]).

[9] L. Beranek, Acoustics, McGraw-Hill Book Company, New York 1954.

[10] H. Nocke, Physical and physiological properties of the Tettigoniid ear. A new hearing theory, in preparation.

[11] H. Nocke, J. Comp. Physiol. **80,** 141–162 [1972].

[12] A. Michelsen and H. Nocke, Advances in Insect Physiology **vol. 10,** Academic Press, London and New York 1974.