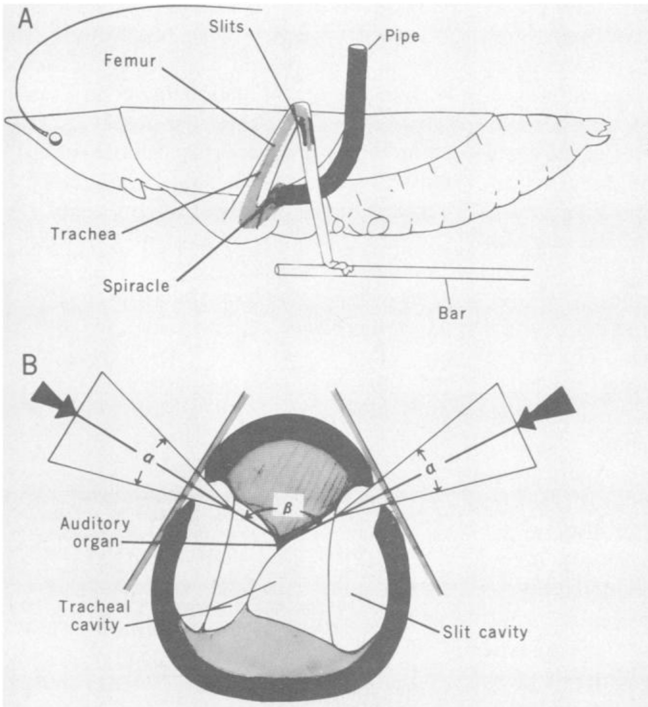
Directionality and Auditory Slit Function: A Theory of Hearing in Bushcrickets

Abstract. *Female bushcrickets locate their mates by sound. Auditory acuity is mediated by the complex anatomy of the tympanal slits, associated trachea, and spiracle. By manipulating the acoustic properties of this system and measuring the neural output, a bilobed, highly directional mechanism associated with the slits is observed, confirming Autrum's original hypothesis.*

Sound is the primary means whereby female bushcrickets (Tettigoniidae) locate singing males. A feature of this sound localization is the high degree of auditory acuity exhibited by the searching female in complex three-dimensional habitats. The detection of the sound is mediated through auditory receptors in the tibia of the forelegs beneath the knee (Fig. 1A). A schematic section (Fig. 1B) typical of the anatomy of most tettigoniids and in particular the member of the family Copiphorinae used in this experiment shows the auditory receptors situated behind the two tympanic membranes, which themselves form the inner walls of two small cavities opening to the exterior through two narrow slits. Internal to these membranes is a third partially divided cavity, which opens to the exterior via the large trachea in the femur and the auditory spiracle at the base of the foreleg. The spiracle, unlike that in crickets (Grylloidea), has no closing mechanism; its principal function appears to be auditory (*1*, *2*).

Historically the explanation of the mechanism responsible for the observed acuity has been equivocal. Autrum (*3*) speculated from a consideration of the anatomical configuration of the slits that each could act as a direction finder operating along the axis of the slit opening, in the manner suggested in Fig. 1B. However, more recent authors (*1*, *2*, *4*) testing this hypothesis with electrophysiological techniques have been unable to demonstrate the lobed function expected by Autrum. Plots of threshold neural response classically expressed in decibels against the angle of incidence of the sound have shown almost omnidirectional patterns on the ipsilateral side of the insect (compare with Fig. 2A).

The conclusions from such experiments have placed considerable emphasis on the auditory trachea and its associated spiracle and have had the slits play a minimal role (*1*, *2*). Michelsen and Nocke (*5*) argue that the dimensions of the foreleg (diameter ~ 1 mm) are small, compared to the wavelength of the principal Fourier component in the male's stridulatory call [for the species used in these experiments 11 kHz ($\lambda \sim 3$ cm)], and hence that the sound pressure around the leg will be uniform. In addition, the admittance of the sound through the slits would be independent of the direction of incidence. However, it can be shown mathematically (*6*) that (i) admittance must be a function of the direction of incidence, particularly at frequencies where there is a resonance (not necessarily in the cavity) and (ii) at resonance the amplitude of the wave inside the cavity rises sharply. The theoretically expected response pattern for the tettigoniid slit system for a constant sound-pressure source rotated around the animal should be a four-lobed figure with the lobes lying normal to the slits, both in the forward and backward directions, as Autrum predicted. Thus if Autrum's hypothesis is to be entirely rejected, at least two facts need some explanation. The first is that in most tettigoniids there are highly developed cuticular folds around the tympanic membrane forming slits, which must have a functional role other than the protection of the delicate membranes beneath. The second arises from behavioral observations in the field and the laboratory of two distinct response patterns to sound. When the insect is stationary (resting, feeding, or calling), any disturbance such as a high transient click causes the insect to freeze



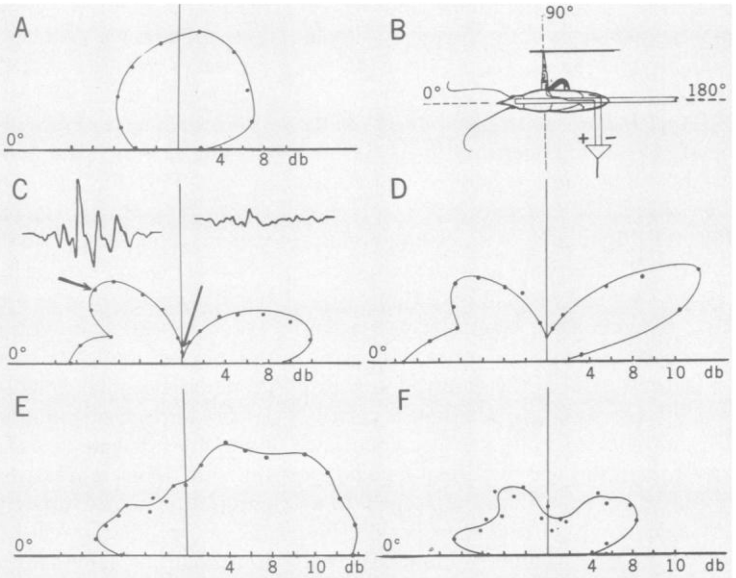


Fig. 1 (left). Schematic representation of the tettigoniid acoustic system. (A) The insect *Mygalopsis* showing the relative positions of the tympanal slits on the foreleg (middle and hind legs are removed) and the auditory trachea (shaded) passing through the leg. The polypropylene pipe is waxed into the spiracular opening. (B) The relative positions of the auditory organ to the three acoustic cavities seen in cross section through the slit region.

Fig. 2 (right). Polar plots expressed as decibels on radial axes with the spiracle as the center of the goniometer. (A) Response without the polypropylene tube. (B) Geometrical orientation of the insect at the center of the goniometer with respect to the sound source (tube marked in black). (C and D) The lobed pattern with the tube inserted showing two examples of the averaged response pattern [arrow in (C)]. (E) Effect on polar pattern (C) of raising the sound source above the horizontal axis by 10°. (F) Effect on polar pattern (D) of beveling the end of the tube at an angle of 45° to the direction of the speaker.

(predator avoidance response); however, once the insect has initiated orientation locomotor activity directed toward the call of a conspecific, similar noises have little effect.

Nocke (*2*), in a series of elegant experiments, showed that the spiracle and auditory trachea formed a resonant cavity at the call frequency. Since the spiracle is the largest auditory orifice, the admittance through this structure will dominate at the call frequency. It is then perhaps not surprising that polar plots derived from intact insects reflect this aspect to a large degree. Hence, if the admittance via the spiracle could be maintained constant in phase and amplitude for all directions of incidence, the contribution to directionality of the slits would be revealed. If we assume that the response of the auditory sensila at the point of attachment (Fig. 1B) is determined by the vector sum of the acoustic pressures in the three cavities—those behind the slits and that in the trachea—and if the pressure in the trachea is constant, differences between the slit components should be observable. To this end we inserted a polypropylene tube (internal diameter 0.6 mm, length 28 mm) into the spiracle opening. The external aperture of the tube was above the insect in the plane of the speaker and placed at the center of rotation of the sound source. The admittance of sound to this tube in this particular geometry is expected to be a minimum and to remain constant in both phase and amplitude in relation to the rotation of the speaker.

Experiments were conducted under nearly free-field conditions in a large laboratory with minimal background noise. The insect, *Mygalopsis* sp. (Copiphorinae, Tettigoniidae) was mounted in the center of a three-dimensional goniometer (radius 70 cm) on a light wire frame (Fig. 2B). The recording electrode was a fine Diamel-coated silver wire waxed firmly to the cuticle with the electrode tip just beneath the surface of the femur cuticle. The stability of both the electrode and the preparation was such that a constant response to sound was observed from any direction over a 12-hour period. Polar points from different animals varied in magnitude against sound pressure; however, they remained similar in general shape (Fig. 2, C and D). The stimulus was a 50-msec pure tone pulse of 11 kHz with an interpulse interval of 200 msec. This frequency is close to the carrier frequency of the song as well as the optimum threshold response of the tympanal system. The response to echo was avoided by recording the averaged response of 256 sound presentations in such a way that the sample interval included only the first 25 msec of the response. The observed echo occurred at the preparation well after this interval.

A typical averaged response pattern is shown in the inset of Fig. 2C. These polar plots show for what we believe to be the first time the change in neural response for sound intensities above threshold—a more realistic consideration than previously published threshold measurements. The total neural response was characterized by measuring with an opisometer the total length of the trace, which gave a quantifiable measure of power output from the receptors. The values so obtained were expressed in decibels through the use of a set of input-output curves. Polar plots are shown only over the ipsilateral half circle to avoid shadowing effects produced by the body of the insect. Such an effect is without doubt important in the whole animal's behavior, but of little relevance to the unilateral study of the directional characteristics of the single receptor system.

Figure 2, C and D, shows typical polar plots from different experiments expressed as the averaged neural response to a constant sound source of 10 dB and 5 dB, respectively, above the threshold. The threshold value taken as the just-observable averaged response was that measured at 30° in the horizontal plane. The remarkable features of both plots are the two distinct lobes representing an increase in neural response, that is, sensitivity along the normals subtended by the slits, (β) 40° and 160° (Fig. 2C) and 50° and 150° (Fig. 2D). The direction between 0° and 30° increases from the backward expected lobe of the rear slit. These lobes are similar in shape, and the angular half-width is about 20° ($^1/_2\ \alpha$), which agrees again with the geometrical anatomy of the leg (Fig. 1B). The neural response becomes small when the angular admittance of sound is equal through both slits, that is, at the angle bisecting the slits. This represents a sound pressure fall of approximately 10 dB in Fig. 2C, a considerably greater differential from that normally obtained from a control polar plot (Fig. 2A) dominated by the spiracle. These plots were recorded when the distal opening of the pipe was parallel with the direction of the incident sound. Raising the angle of the source of the sound out of the horizontal plane or beveling the end of the tube should alter the admittance of sound into the tracheal system and hence alter the observed polar response. Figure 2, E and F, shows the effect of such changes in terms of magnitude of the neural response and directionality of the ear.

This evidence of slit function, at least in a manipulated situation (*7*), justifies Autrum's original hypotheses. The pattern derived from the unmanipulated insect (Fig. 2A) confirms those of previous workers and probably indicates a wide-spectrum omnidirectional receiver, an advantage to a prey species. Thus, the auditory system could have two separate functions, the first mediated by the spiracle and tracheal system, which produces a highly sensitive nondirectional auditory receiver, and the second mediated by the slits, giving rise to a highly directional receiver. Our results confirm the hypothesis that the neural response is determined by the sum of the three acoustic pressures. Clearly each individual pressure will be a function of frequency and angle of incidence. The cusps in Fig. 2, C and D, occur when the acoustic pressures through each slit balance. In particular in Fig. 2C we have the unique situation where all three forces are in balance, and the response falls to zero at this angle. If these two situations occur and are controllable, the insect must be able to switch between these two functions. This could be achieved by controlling the resonant properties of the trachea during locomotive orientation. The bushcricket while singing, resting, or feeding is prone to be attacked. Under these conditions it would be expected that the auditory response is omnidirectional and very sensitive; however, once the insect is responding to a conspecific call; directionality becomes of first importance, perhaps to the detriment of sensitivity.

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References and Notes

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5. A. Michelsen and H. Nocke, *Adv. Insect Physiol.* **10**, 285 (1974).
6. P. Morse and H. Feshbach, in *Methods of Theoretical Physics* (McGraw-Hill, New York, 1953), p. 1380.
7. At the proof stage of this report, we have achieved similar lobed patterns in the unmanipulated insect (genus *Tympanophora*).
8. Supported by the Australian Research Grants Committee.

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