Auditory Function in Tettigoniidae (Orthoptera: Ensifera)

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Accepted December 8, 1980

Summary. 1. An ascending, auditory unit has been extracellularly recorded from the cervical connective in specimens of two tettigoniid species. Spike potentials arising from unilateral afferent input were monitored in response to airborne sounds in the frequency range 6.3-40 kHz and incident from different directions. Recordings were also obtained of the massed auditory response in the tympanal nerve in a third species.

2. Frequency sensitivities of auditory organs were measured at threshold and suprathreshold levels. Optimum frequencies generally corresponded with energy peaks in relevant song spectra (Figs. 3, 4). Intensity characteristics of the ascending unit were obtained near the corresponding frequency optimum (Fig. 5). Directional sensitivities of the auditory organs near the frequency optima were measured at 15° intervals around the preparation at threshold and suprathreshold levels of stimulation (Fig. 6). Threshold sensitivities to ipsilateral and contralateral stimulation were compared over the range 6.3-40 kHz.

3. Directional sensitivity of the ascending unit generally increased with increasing sound frequency. Maximum differences of from 8–25 dB were observed between sensitivities to ipsilateral and contralateral sound presentation in the frequency range 6.3–40 kHz (Fig. 8). Similar results were obtained for the massed primary response.

4. The frequency sensitivity and the directional sensitivity of the auditory organs, for sound frequencies higher than 8–10 kHz (depending on species) and at threshold and suprathreshold levels, were found to be independent of pressure-gradient effects at the auditory tympana (Figs. 7, 8).

5. The gross morphology of the prothoracic spiracle and associated trachea to the level of the tympanic membranes has been examined in each species. In the thorax, the trachea abruptly reduces in cross-sectional area by about a factor of five. From the coxa to the distal femur the trachea undergoes a further three to four-fold reduction in cross section (Fig. 2).

6. Physiological experiments and direct measurements using miniature probe microphones indicate that, in the frequency range 8–40 kHz (depending on species) the acoustic gain of the trachea leading from the prothoracic spiracle to the auditory tympana is 10–30 dB (Figs. 9, 10). The shape of the hearing threshold curve, however, only partially matches the gain curve of the trachea.

7. Near the frequency optimum of the auditory organ, the sound pressure measured by a probe microphone in the thoracic tracheal vesicle adjacent to the prothoracic spiracle changes by 10–16 dB as a function of the direction of the incident sound (Fig. 12A).

8. Simultaneous measurements using two probe microphones show that relative sound pressure in the thoracic tracheal vesicle changes by 10–16 dB, whereas that in the trachea distal in the femur may change by 8–24 dB for different directions of sound (Fig. 12C). Directional sensitivities measured neurophysiologically are, therefore, fully explained by the relative sound pressure level in the fore-leg trachea leading to the auditory tympana.

9. Dissimilarities sometimes observed between the directivity patterns of the sound pressures measured in the thoracic vesicle and in the femoral trachea possibly are due to the effects of sound entering the trachea along the length of the leg.

10. These results are discussed in relation to the properties of acoustic horns and to other recent studies of auditory function in tettigoniids.

1. Introduction

Stimulation of ensiferan auditory receptors depends on the vibrations induced in the fore-tibial tympanic membranes by acoustic pressures in the surrounding...
air medium and/or in the tracheal air spaces in the leg behind the tympana (e.g. Lewis 1974a; Nocke 1975; Hill and Boyan 1977; Field et al. 1980). Certain aspects of the response properties of the receptors (e.g. coding of sound pressure amplitude modulation, coding of sound source location) may be attributed to the relative amplitudes of vibration of the tympana under the particular conditions of stimulation. The frequency sensitivity of ensiferan auditory receptors, however, appears to depend on some additional phenomena other than the frequency response of the tympanic membranes themselves (Ball and Hill 1978; Kalmring et al. 1978; Hill 1980).

Auditory function in Tettigoniidae is the subject of several recent physiological and biophysical studies (see below), in which a variety of experimental procedures have been employed. No consensus has been reached, however, about the biophysical characteristics of the tettigoniid auditory system and the mechanisms of its frequency and directional sensitivity. The most important question outstanding on the subject of tettigoniid auditory function concerns the nature of the acoustic waveguide formed by the prothoracic trachea that extends from the large, open spiracle to the tympanic membranes of the fore-tibia. Nocke (1975) concluded that this acoustic trachea behaves as a lightly-damped, tube resonator and that it strongly amplifies the sound pressure reaching the inner surfaces of the tympana in a narrow frequency band, thereby conferring a sharply-tuned response characteristic on the population of auditory receptors. Directional sensitivity was then tentatively assumed to depend on a change in the amplitude of the sound pressure at the prothoracic spiracle as a function of the direction of incident sound, since the pressure in the trachea would dominate the response of the ear. In contrast, Seymour et al. (1978) concluded that the trachea does not have a sharply-tuned resonance, but rather, that it behaves as a horn-like waveguide with a broad band-pass characteristic and very low efficiency. They estimated that the amplitude of the sound pressure conducted to the inside of the tympana would equal the external sound pressure in the range 1–3 kHz and that the internal pressure would only about double the external pressure at higher frequencies. Directionality could, therefore, largely depend on the interaction between the external and internal sound pressures at the tympana and the shape of the hearing threshold curve would depend on mechanisms other than acoustic resonance in the trachea. Further confusion was added to this picture when Bailey and Stephen (1978) claimed a function for the cuticular tibial slits (through which the outer surfaces of the tympana communicate with the exterior in some tettigoniid species) in directional sensitivity. We have examined the structure and function of the auditory system in certain tettigoniid species, with and without slits in front of the tympana, in order to elucidate its general properties and, if possible, to resolve some of the current controversies concerning tettigoniid hearing.

II. Materials and Methods

A. Physiological Recording

Experiments were conducted on wild male and female Tettigoniidae of the following species, *Mygalopsis marki* (Bailey 1979) (Phyllophorinae), *Acriseps reticulata* (Guerin) and *Caecidia longipennis* (Brunner) (Phaneropterae). *M. marki* were collected near Perth, Western Australia, *A. reticulata* in the Brindabella mountains near Canberra and *C. longipennis* were caught on vegetation in Canberra.

Most neurophysiological recordings were made from a cervical connective using a thin silver, tungsten or platinum wire hook electrode. The cuticle covering the prothoracic ganglion and cervical connectives was removed, cricket *Ringer* (Eibl 1976) applied, and the ventral connectives were cut immediately posterior to the suboesophageal ganglion and the prothoracic ganglion. One of the cervical connectives was placed on the recording electrode and when auditory responses were obtained with satisfactory signal to noise ratio, the contralateral tympanal nerve was cut. To prevent desiccation, the dissected prothoracic and oesophageal region were covered with vaseline. Other recordings were made from the tympanic nerve within the femur opened mid-way along its length, after severing the nerve central to the recording electrode.

Insects were mounted either ventral side up on a thin wire support, 20 cm high and 1 mm diameter, or in the case of simultaneous physiological and relative sound pressure measurements (see below), preparations were mounted dorsal side up on a 1 mm diameter glass probe tube extending 10–15 cm from a 1/4" Briel and Kjaer microphone held vertically in the sound field. In all preparations, the forelegs were held in a natural position by waxing the tarsi to a thin wire support attached to the insect's head. Other legs and wings were removed.

The animal on its stand was placed on a turntable (360° rotation) in an anechoic chamber, the acoustic properties of which have been described elsewhere (Nocke 1975; Hill and Boyan 1977; Boyan 1979). The anechoic chamber, situated inside a double-shelled isolated concrete building, consists of a chipboard box, lined on the inside with rockwool wedges (calculated cut-off frequency 0.43 kHz). The loud speakers (Altec-Lansing 807/8A-811 B, Realistic 40–1310) were mounted at the closed end of the box, 1.65 m from the preparation. At the sound frequencies used, the sound field was ±1 dB within 2 cm of the position of the preparation.

Sound stimuli were produced in a similar manner to that described by Nocke (1975). Pure-tone pulses of 200 ms duration and 5 ms rise and decay times were produced at a rate of 0.5 Hz by modulating (Schönenmann 1972/04) the sine wave output of an audio oscillator (General Radio 1309). Sound pressure levels were adjusted in 1 dB steps (Hatfield 2120) and monitored near the preparation using a Briel and Kjaer measuring amplifier (type 2607), passband filter (type 1614) and 1" condenser microphone (type 4145). The free-field response of the microphone (protective grid in place, 0° sound incidence) was corrected according to Briel and Kjaer specifications. The reduced sensitivity of the 1" microphone to sound frequencies above 20 kHz was calibrated against the corrected, free-field response of a 1/4" Briel and Kjaer microphone (type 4136). Neural recordings were amplified (Grass...