

Sexual differences in auditory sensitivity: mismatch of hearing threshold and call frequency in a tettigoniid (Orthoptera, Tettigoniidae: Zaprochilinae)

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Summary. Sexual dimorphism of the ear of an undescribed species of zaprochiline tettigoniid is described. The internal trachea, dedicated to hearing in other tettigoniids, is unmodified in the male but fully developed in the female. The external auditory spiracle is also lost in the male. In contrast, there is no difference between the sexes in the number of sensilla within the hearing organ. The male is 10 dB less sensitive than the female. The characteristic frequency of the hearing organ at 35 kHz does not match the carrier frequency of the male's call at 51 kHz. As a result of this mismatch the female is remarkably insensitive to the male's call (threshold at 75 dB SPL), and the male is even less sensitive (threshold ≥ 80 dB SPL). In nature this provides a maximum hearing range of the male of less than 50 cm.

Key words: Tettigoniidae – Auditory sensitivity – Sexual dimorphism

Introduction

If auditory receptors were singularly adapted for the reception of signals associated with mating, we would predict (i) that sexual differences in calling and searching roles would be reflected in the anatomy and physiology of these organs and (ii) that the most sensitive frequencies of the receptors would be those at which the sexual signal was produced. However, in those insects that have been studied so far, the ear also functions for the reception of sound made by predators (Hoy 1989), and if both sexes were exposed to the same predators the ear would remain similar with regard to this function in both sexes (Bailey 1991). Any sexual dimorphism in the structure of the ear, or its sensitivity, could then be ascribed either to sexual differences in calling and searching or to differences in their exposure to predators.

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Sexual dimorphism of hearing structures and sexual differences in hearing sensitivity appear to be rare in insects, but examples are becoming more apparent. For example, in one subfamily of porthetine grasshoppers the male has well-developed tympana compared with the female in which they are small and sclerotized (Mason 1968). In the gypsy moth, *Lymantria dispar*, the ear is more variable and less tuned in the female than in the male (Cardone and Fullard 1988). More recently, Yager (1990) described sexual differences in hearing in praying mantises, with the females having reduced sensitivity to ultrasonic frequencies compared with the males. As in the gypsy moth, these hearing differences are very likely associated with differences between the sexes in their exposure to predation (Yager et al. 1990).

In the ensiferan Orthoptera, reported differences in hearing between the sexes are also rare and confined to the Phaneropterinae (Stumpner and Heller; Dobler, personal communication). In this subfamily of the Tettigoniidae there is good evidence of differences in the anatomy of the auditory system (Bailey 1991) which may result in a difference in the sensitivity or tuning of the ear.

In this paper we describe a male/female difference in hearing threshold and give evidence of a mismatch between calling song frequency and auditory sensitivity in an undescribed genus of zaprochiline tettigoniid. The physiological data we present together with the observed sexual dimorphism in the external auditory structures of this species may explain the low level of behavioural response by the male to the calls of his conspecific neighbours.

Materials and methods

The insect. The species of tettigoniid used in the experiments is Gen. Nov. 22 sp. 1 (Gwynne and Bailey 1988), an undescribed genus of the subfamily Zaprochilinae and currently under review (Rentz, un-

published) and a species endemic to Western Australia (specimens of material collected from the same population are housed at the Australian National insect collection, Canberra). Throughout this paper zaprochiline refers specifically to Gen. Nov. 22 sp. 1. Insects were collected from King's Park, an area of natural bushland close to the center of Perth between October and November 1989.

Neurophysiology. Each animal was anaesthetized with CO₂ and mounted ventral side up on a small, thin metal sheet with the forelegs oriented perpendicular to the long axis of the body. A small flap of cuticle covering the cervical connectives was removed, and one of the exposed connectives was hooked by an electrolytically sharpened electrode. Both connectives were severed posterior to the suboesophageal ganglion, and the operating hole was filled with petroleum jelly to prevent desiccation of the nervous tissue. By using this procedure we obtained recordings of spike responses of a large T-fibre-like auditory interneuron. This interneuron mediates auditory information to the brain and to the abdominal ganglia (for similar findings in other tettigoniids see Suga and Katsuki 1961; Kalmring et al. 1979; Rheinlaender and Römer 1980). In 3 control experiments an electrolytically sharpened tungsten electrode was inserted into the prothoracic ganglion, and multi-unit recordings were made from the axons of tympanic nerve fibres entering the auditory neuropil (Römer et al. 1988).

Threshold determination of the responses of the auditory interneuron were made according to a procedure described in detail by Rheinlaender and Römer (1980), and the threshold of the auditory receptor fibres was determined by monitoring the multi-unit spike responses via earphones. The mean values for auditory thresholds obtained with both kinds of recordings did not deviate by more than 3 dB at frequencies above 10 kHz, whereas at 5 kHz the threshold of the interneuron was usually about 10 dB higher compared with that for the auditory receptors (Hardt 1988).

Sound pulses with different pure tone carriers or noise of variable bandwidth were generated digitally through a 12-bit D/A converter with a sampling rate of 125 kHz. All signals were filtered by a custom-made low-pass filter, amplified (Akustischer Stimulator II, Burchard), and attenuated in 10 or 1 dB steps (Hatfield). To establish tuning curves, pure tone pulses (duration 50 ms, rise and fall time 1 ms, rate 1/s) were used. The speaker (Technics EAS-10 TH400A) was mounted at a distance of 1 m ipsilateral to the preparation. The experiments were conducted in an anechoic chamber held at a constant temperature of 20° ± 1 °C.

The prothoracic auditory spiracle of the female and the homologous respiratory spiracle of the male (see Fig. 2C, D) was blocked with soft petroleum jelly to determine the contribution of each input to the threshold response.

Morphology. Adult males and females were dissected and the configuration of the trachea of the thorax drawn with a camera lucida. Selected specimens were dried and coated for scan electron microscopy. The external spiracular morphology was examined under SEM.

The number of sensilla forming the *crista acustica* of the tympanal organ beneath the knee of the foreleg was counted in both sexes. The sensilla were readily visible by transmission microscopy after removing the anterior tympanum and staining in a Ringer's solution saturated with neutral red for about 10 min. The sensilla were photographed in vitro.

Results

Morphology

Consistent with the observations of the anatomy of the external auditory spiracle shown previously (Bailey and Simmons 1991; Fig. 2C, D), the associated trachea of the female shows the usual tettigoniid plan with the dedi-

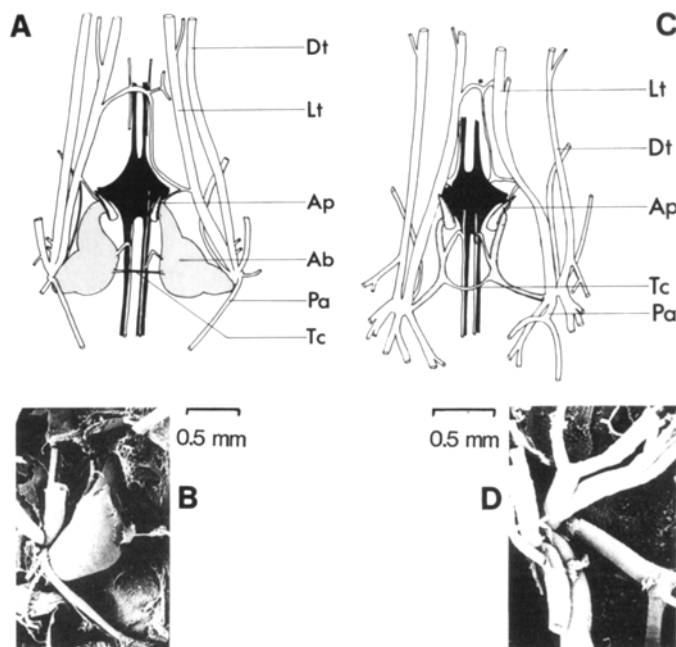


Fig. 1A–D. The anatomy of the tracheal system of a female (A, B) zaprochiline tettigoniid (Gen. Nov. 22 sp. 1) and a male (C, D). *Ap* apodeme; *Ab* auditory bulla; *Dt* dorsal trunc; *Lt* lateral trunk; *Pa* posterior alaris; *Tc* transverse connective

cated acoustic tracheal opening posterior to the ventilatory prothoracic spiracle and enlarging into an auditory bulla (Fig. 1A, B). The trachea forming the bulla continues unbranched to the prothoracic leg, dividing into two branches beneath the knee. The bullae in the female are connected by two slender tracheae that appear to be closed in the adult insect.

In addition, a feature of the pterothoracic tracheal anatomy in the male is that the tracheae serving the wing muscles are well developed (Fig. 1C, D), forming numerous branching small tracheae, whereas in the female, which is apterous, these tracheae are reduced. In the male, the homologous trachea to the auditory bulla opens with the other ventilatory tracheae serving the head, pro- and pterothorax, and legs. The main leg trachea continues unexpanded to the coxa and femur of the foreleg, serving the femur in exactly the same manner as that found in the female (Fig. 1A, B). There is one cross connection between the two leg tracheae, and a second branch opens to the trachea running lateral to the ventral nerve cord.

We found no evidence of dimorphism in the number of sensilla forming the *crista acustica*. In both sexes there were 18 ± 1 (male, *n* = 5; female, *n* = 6).

Auditory sensitivity

The hearing organ of the female zaprochiline is most sensitive to high frequencies between 30 kHz and 40 kHz with a characteristic frequency (CF) of 35 kHz (Fig. 2A, solid line). The threshold of 65 dB SPL at this CF is rather high when compared with other tettigoniid spe-

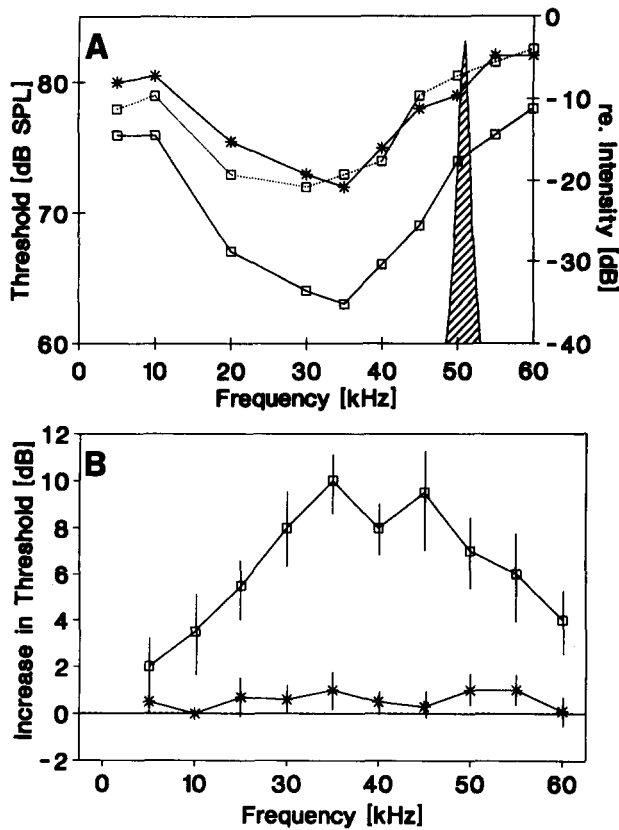
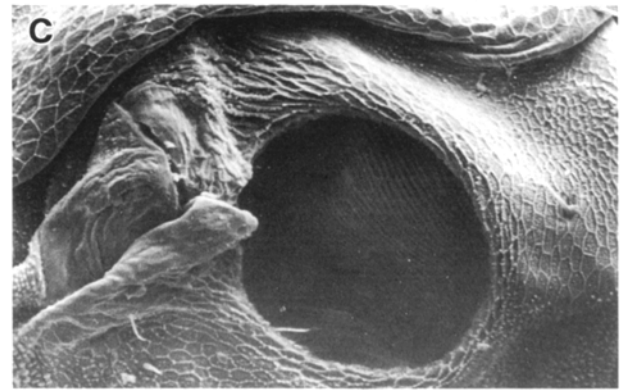


Fig. 2A–D. **A** Hearing threshold of the auditory interneuron (T-fibre) of male (*-*) and female (□-□) zaprochiline tettigoniids. Solid line is the averaged threshold value of 8 females and 6 males of the intact system. The broken line is the average threshold curve of 7 females after blocking the auditory spiracle with



petroleum jelly. The spectrum of the male calling song is shown by the dashed area. **B** Increase in neuronal threshold after blocking the acoustic tracheal system in both males ($n=6$) and females ($n=7$). Vertical bars: standard deviation. The spiracular opening of the acoustic trachea is shown in (C) for the female and in (D) for a male

cies. Similarly, the auditory system of zaprochiline males shows the highest sensitivity at 35 kHz (Fig. 2A, dashed line), and in this sex the absolute sensitivity at the CF is 10 dB less than that in the female. In both sexes there is a mismatch between the CF of the hearing organ and the carrier frequency of the male call which is almost a pure tone of $51 \text{ kHz} \pm 4 \text{ kHz}$ (see spectrum in Fig. 2; Gwynne and Bailey 1988). As a result of this mismatch, as well as of the overall reduced sensitivity of the hearing organ, the threshold for the conspecific calling song is remarkably high in females (75 dB SPL) and more so in the male (> 80 dB SPL).

In order to establish the contribution of the auditory trachea of the female to the insect's overall sensitivity, we blocked the auditory spiracle in the female and the prothoracic spiracle in the male. When the auditory spiracle in females (see Fig. 2C) was blocked with petroleum jelly, the sensitivity of the hearing system was reduced to values approaching those for the male – there was no observable difference between the blocked female's sensitivity and that of the intact male at any frequency (Fig. 2A, dotted line). The loss in sensitivity was frequency-dependent and highest around the CF of the system (Fig. 2B). In contrast, when the homologous prothoracic spiracle of the male (Fig. 2D) was blocked, we observed no significant effect on the auditory sensitivity. This

suggests that there is no auditory input through this trachea.

Discussion

This is the first report of a physiological difference in the hearing sensitivity of an ensiferan orthopteran. Reduced sensitivity in the male is the result of a severe reduction in the tracheal apparatus associated with the ear. However, despite this reduction of the input to the male's hearing organ there appears to be no difference in either the number of sensory cells within the crista acustica or in the external morphology of the tympanal organ. We demonstrate that the male is still able to hear, albeit with a reduced sensitivity of 10 dB, so confirming the findings of Bailey and Simmons (1991), who point out differences in external spiracular morphology of the zaprochiline tettigoniid and report that males show little behavioural evidence of hearing their conspecifics' call compared with females. These authors demonstrate that where males occur in aggregations, inter-male distances were close (between 0.5 and 1.5 m, in some circumstances much closer than this). Sound intensities of a calling male fall to 75 dB SPL within 1 m (Bailey and Simmons 1991). Thus, due to the reduced hearing sensitivity at the calling song frequency for males, the active range of the con-

specific call will be about 50 cm or even less. Although there is no evidence that the aggregating behaviour of the males is dependent on sound, this very small active range of the signal would constitute a limit of auditory reception for males within an aggregation. For females, the active range for a male's call may be twice this distance, a situation similar to that in the spring peeper, *Hyla crucifer*, in which the thresholds of units of the basilar papilla to the male advertisement call differ by 11 dB between male and female. This results in large sexual differences in the active range of the signal (Wilczynski 1986).

In the zaprochiline species used in this investigation, we showed that the trachea of the female, with its separate spiracular opening, contributes 10 dB to the overall sensitivity of the hearing system and 6–8 dB to its frequency tuning (Fig. 2B). These findings support the generally held hypothesis that the spiracular input to the hearing organ emphasises sound in a restricted frequency range (see review by Bailey 1990). That the trachea provides only 10 dB to the ear's sensitivity compared with 20–30 dB in other species (e.g. Lewis 1974; Nocke 1974; Hill and Oldfield 1981) may be attributed to the extremely small size of the spiracular opening (diameter 0.5 mm; Fig. 2C).

There is, however, no adequate explanation for the mismatch between the tuning of the ear and the carrier frequency of the male's call. Our findings add to a limited number of descriptions of a signal/hearing mismatch. In cicadas the female locates the call for mating, and there are differences in hearing sensitivity between the sexes, undoubtedly influenced in many species by the large abdominal resonators associated with the male sound-producing organ (Young and Hill 1977). Popov and Sergeeva (1987) describe how the female cicada (*Cicadetta yezoensis*) is 10 dB more sensitive than the male between 3 and 4 kHz. Further, there is a mismatch between the male's call with a frequency close to 9.5 kHz and the best sensitivity of the female hearing system at 3–4 kHz. At the call's carrier frequency, the hearing threshold is 40 dB higher.

A similar mismatch has been described for other cicadas by Huber et al. (1990). In *Cyphoderris monstrosa*, a haglid cricket, the mismatch results in a reduction of sensitivity in both sexes to the male calling song by 20 dB (Mason 1991). The mismatch may have evolved through the hearing organ's primary function in the detection of non-social signals – perhaps those of predators. Woodside and Taylor (1985) describe a number of Australian bats that have peak frequencies in their echo-locating calls between 20 and 50 kHz. However, both males and females of our zaprochiline do not fly and are therefore not susceptible to aerial attacks from bats. Hence, one may argue that we are looking at vestigial ears. Surprisingly, however, behavioural experiments show that females are sensitive to small changes in the carrier frequency of the male's call (Gwynne and Bailey 1988). Therefore, despite the reduced hearing sensitivity of the female, and to a greater extent in the male, it would appear that sound still plays some role in social communication in this species, perhaps at close range.

Plasticity in the development of structures associated with the ear is not uncommon in the Ensifera. For example, a loss of hearing in certain crickets is associated with a parallel loss in the use of sound in social communication (Otte and Alexander 1983) – in some species of Nemobiinae, the tympana are severely reduced and in others, lost altogether. Hence, we may infer that the production of sound and its reception are costly in terms of both metabolism, energetic costs of producing sound, and development. In the species of tettigoniid used in this study, for which sound plays a lesser role in male-male behaviour (Simmons and Bailey 1990), the cost of the development of structures enhancing sound reception may be reflected in the loss of the trachea in the male.

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References

- Bailey WJ (1990) The ear of the bushcricket. In: Bailey WJ, Rentz DCF (eds) *The Tettigoniidae: biology, systematics, evolution*. Crawford House Press, Bathurst, pp 217–247
- Bailey WJ (1991) The acoustic behaviour of insects – an evolutionary perspective. Chapman and Hall, London
- Bailey WJ, Simmons LW (1991) Male-male interactions and sexual dimorphism in the ear of a zaprochiline tettigoniid. *J Insect Behav* 4:51–64
- Cardone B, Fullard JH (1988) Auditory characteristics and sexual dimorphism in the gypsy moth. *Physiol Entomol* 13:9–14
- Gwynne DT, Bailey WJ (1988) Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). *Behaviour* 105:202–223
- Hardt M (1988) Zur Phonotaxis von Laubheuschrecken: eine vergleichende verhaltensphysiologische und neurophysiologische/neuroanatomische Untersuchung. PhD Thesis, Universität Bochum
- Hill KG, Oldfield BP (1981) Auditory function in Tettigoniidae (Orthoptera: Ensifera). *J Comp Physiol* 142:169–180
- Hoy RR (1989) Startle, categorial response, and attention in acoustic behaviour of insects. *Annu Rev Neurosci* 12:355–375
- Huber F, Kleindienst H-U, Moore TE, Schildberger K, Weber T (1990) Acoustic communication in periodical cicadas: neuronal responses to songs of sympatric species. In: Gribakin FG, Wiese K, Popov AV (eds) *Sensory systems and communication in arthropods*. Birkhäuser, Basel, pp 217–228
- Kalmring K, Rehbein H, Kühne R (1979) An auditory giant neuron in the ventral cord of *Decticus verrucivorus* (Tettigoniidae). *J Comp Physiol* 132:225–234
- Lewis DB (1974) The physiology of the tettigoniid ear. *J Exp Biol* 60:821–869
- Mason JB (1968) The tympanal organ of Acridomorpha (Orthoptera). *Eos Madr* 44:267–355
- Mason A (1991) Hearing in a primitive ensiferan: the auditory system of *Cyphoderris monstrosa* (Orthoptera: Haglidae). *J Comp Physiol A* 168:351–363
- Nocke H (1974) The tympanal trachea as an integral part of the ear in *Acripeza reticulata* Gukrin (Orthoptera: Tettigoniidae). *Z Naturforsch* 29:652–654
- Otte D, Alexander RD (1983) The Australian crickets (Orthoptera: Gryllidae). *Acad Nat Sci Philadelphia, Monogr* 22, p 477
- Popov AV, Sergeeva MV (1987) Sound signalling and hearing in the Baikal cicada, *Cicadetta yezoensis*, Homoptera, Cicadidae. *Zool Zh* 66:681–691 (in Russian)

- Rheinlaender J, Römer H (1980) Bilateral coding of sound direction in the CNS of the bushcricket *Tettigonia viridissima* (Orthoptera, Tettigoniidae). *J Comp Physiol* 140:101–111
- Römer H, Marquart V, Hardt M (1988) Organization of a sensory neuropile in the auditory pathway of two groups of Orthoptera. *J Comp Neurol* 275:201–215
- Römer H, Bailey WJ (1986) Insect hearing in the field. II. Male spacing behaviour and correlated acoustic cues in the bushcricket *Mygalopsis marki*. *J Comp Physiol A* 159:627–638
- Simmons LW, Bailey WJ (1990) Resource influenced mating sex roles of zaprochiline tettigoniids. *Evolution* 44:1853–1868
- Suga N, Katsuki Y (1961) Central mechanisms of hearing in insects. *J Exp Biol* 38:545–558
- Wilczynski W (1986) Sexual differences in neural tuning and their effect on active space. *Brain Behav Evol* 28:83–94
- Woodside DP, Taylor KJ (1985) Echolocation calls of fourteen bats from eastern New South Wales. *Austr Mammal* 8:279–297
- Yager DD (1990) Sexual dimorphism of auditory function and structure in praying mantises (Mantoidea; Dictyoptera). *J Zool (Lond)* 221:517–537
- Yager DD, May ML, Fenton MB (1990) Ultrasonic-triggered, flight-gated, evasive maneuvers in the praying mantis *Parasphendale agrionia*. I. Free flight. *J Exp Biol* 152:17–39
- Young D, Hill KG (1977) Structure and function of the auditory system of the cicada, *Cystosoma saundersii*. *J Comp Physiol* 117:23–45