AUDITORY THRESHOLD CHANGE IN SINGING CICADAS

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Summary

The hearing sensitivity in singing cicadas is reduced during sound production by a folding of the tympanal membranes. Using electrophysiological recording and nerve stimulation techniques, we have shown an effect of the folded tympanum on the auditory threshold of two species of cicadas, *Tibicen linnei* and *Okanagana rimosa*. Auditory thresholds of both species increased by about 20 dB when the tympana folded during singing. In *T. linnei* the increase in threshold affected the whole frequency range, from 1 to 16 kHz, in a similar way. Electrical stimulation of one or both auditory nerves resulted in a folding of both tympanal membranes in a way very similar to that seen in singing animals. We have demonstrated that a cicada male is able to adjust its auditory threshold within a range of about 20 dB by the tympanal folding mechanism.

Introduction

In cicadas and many other insects, an intraspecific acoustic communication system has evolved which enhances reproduction. Cicada males produce songs which a female can recognize on the basis of their time pattern and frequency content, and these enable the female to localize the conspecific male (Huber *et al.* 1990). The males of most species produce their song by means of paired, dorsolaterally located tymbals – membranes stiffened by several ribs – which are part of the first evident abdominal segment. The tympanal membranes in cicadas are located ventrally, also in the first evident abdominal segment. In cicada males, the sound-producing tymbals and the sound-receiving tympanal membranes are directly coupled acoustically because they are both backed by the large abdominal tracheal air chamber. Thus, the male's own song provides a strong mechanical stimulus for its tympana as well as an intense stimulus for its neural auditory pathway.

Pringle (1954) described a folding of the tympana in singing cicada males. Since the folds seemed to indicate that the tympanum was relaxed, he suggested that the folding served to protect the tympana from mechanical overloading and possible damage. There

is evidence that cicadas radiate sound through the auditory tympana during singing (Young, 1990). Thus, there is a need for male cicadas to prevent overloading of their auditory system.

The hearing ability of cicadas appears to play a role in song recognition and sender localization and also in the detection of potential predators (especially birds). The two largest peripheral sensory elaborations of the cicada are the ears and eyes. For whatever reason, cicadas have evolved auditory organs with 2000 receptor cells, most of which are most sensitive to frequencies between 1 and 4 kHz (Popov *et al.* 1986; Popov, 1990; Huber *et al.* 1990). This frequency range is not matched by the maximum energy band of the male's song for many species. This suggests that the adaptive function of hearing may not be calling song recognition and localization alone, but also the detection of predators (Popov *et al.* 1986; Popov, 1990). Hence, the question arises as to whether a cicada male is able to perceive external sound with the tympana folded and during its own singing activity. Also, males that synchronize songs over long periods of chorusing, as in some periodical cicadas, must be able to hear other male's songs while they themselves are singing. Furthermore, if the folding of the tympana results in a changed auditory threshold, this mechanism might also be employed by silent males to adjust their hearing threshold selectively to the sound level around them, in a manner somewhat similar to that of the visual system adapting to the surrounding light intensity, in order to improve signal resolution.

The experiments described here show that the auditory threshold is increased by about 20 dB by the tympanal folds and that the cicadas, in principle, are able to adjust their hearing threshold within this range.

Materials and methods

Animals

Males of *Tibicen linnei* Smith & Grossbeck were collected in an apple orchard near Bangor, Van Buren County, Michigan. Individuals of *Okanagana rimosa* Say from an abundant population were caught in a scrub poplar forest regrowth area near Grayling, Oscoda County, Michigan. The animals were placed on screened shrubs and kept in the dark in a refrigerator at about 15 °C until tested. All animals tested were used for experiments within 7 days of collection. The results presented here are based on data from 18 males of *T. linnei* and 7 males of *O. rimosa.*

Recording and stimulation

Dissection

The males were fixed by pins to a small styrofoam platform with their ventral side upwards. Both pairs of wings and all the legs were removed. In some experiments, a small section of the opercula, which ventrally cover the openings to the tympana, was removed for direct visual observation of tympanal folding. For auditory nerve recording and stimulation, the meso- and metacoxae and parts of the metasternal cuticle were removed to expose the nerves exiting from the metathoracic–abdominal ganglion complex. The

preparation was kept moist with insect Ringer (in mmol l^{-1}: NaCl, 140; KCl, 10; $CaCl_2$, 7; $MgCl_2$, 1; $NaHCO_3$, 4; Tes, 5; trehalose, 4; pH 7.4) which allowed reproducible results to be collected for several hours.

Auditory nerve recordings, electrical nerve stimulation and electromyograms

Auditory nerve recordings were obtained by placing the nerve on double silver wire hook electrodes (diameter 50 μm), insulated from the Ringer with a Vaseline/oil mixture, and amplifying the nerve signal differentially. Usually the activity of both auditory nerves was recorded simultaneously. The same hooks were used for electrical stimulation of the auditory nerve(s). The stimulation signal was produced by a pulse-train generator with a pulse duration of 0.5–1.0 ms and the amplitude set between 0.5 and 2.0 V by a battery-driven stimulus isolation unit which delivered the stimulus pulse. For electromyograms (EMGs) of tymbal muscles, lacquer-coated (except for the tip; diameter 30 μm) steel electrode wire was inserted into the tymbal muscles through small holes in the midsternal chitinous V to monitor singing activity.

To determine changes in auditory thresholds of singing male cicadas, we took advantage of the fact that many males showed unequivocal singing activity, yet mostly without sound production. Singing activity was evident from the regular contraction rhythm at a constant phase relationship between the left and right tymbal muscles, a slight flexion of the abdomen, and a folding of the tympanal membranes exactly as seen during sound production. Results were obtained on such soundlessly 'singing' males unless otherwise indicated. Conventional electronic equipment was used for signal recording and amplification, signal visualization and data storage on magnetic tape.

Auditory threshold determination

Sound stimuli were delivered either as clicks (1.3 ms duration, frequency spectrum 2–12 kHz), which mimicked very well the duration and frequency spectrum of the sound pulses generated by tymbal buckling in both species, or as sine-wave sound pulses for the results presented in Fig. 3. For determination of the auditory threshold in *T. linnei*, a smooth sound pulse envelope (duration 80 ms) was filled with a given sine-wave signal and broadcast by a Piezo loudspeaker (PCT 1000). Absolute auditory thresholds were determined for a given frequency by judging the threshold first in a quiescent male and then in a 'singing' male that showed folding of the tympana. This method of threshold determination was only possible for *T. linnei*, in which the tymbal motoneurone runs in a nerve other than the auditory nerve. Judging the auditory threshold from auditory nerve responses in 'singing' males of *O. rimosa*, other than by loudspeaker clicks, was not possible, because the activity of the tymbal motoneurone, which runs in the auditory nerve, masked the auditory response for the human ear.

Experiments were performed in a Faraday cage lined with sound-absorbing material (illsonic). Because of the presence of the animal holder, micromanipulators and microscope in the sound field, echoes could not be avoided; however, calibration of the intensity of the sound signals (both clicks and sine-wave pulses) showed intensity differences of only 2–5 dB measured within 3 cm of the preparation. A Brüel and Kjaer

sound level meter (type 2230) was used for acoustic calibration. Sound recordings were made with a condensor microphone (AKG type C567).

The recordings were analyzed from chart records and digitized data. The auditory nerve response to the click stimulus delivered from a loudspeaker was averaged by digitizing 30–50 responses with a SAM 68 K computer, evaluating both amplitude and latency of the responses to sound stimuli of various intensities.

Induced singing activity

Sound production in cicadas can be induced by touching the male on its abdomen, head or antennae. Even though the tympana usually also fold during the disturbance squawk or protest song (Simmons and Young, 1978), the irregularity of this singing response proved too unreliable. Regular singing was therefore induced by d.c. electrical stimulation of the brain delivered by a suction electrode (i.d. 200–500 μm) filled with insect Ringer (Hennig 1989; Hennig *et al.* 1994). Stimulated that way, the cicadas showed unequivocal singing activity which lasted for as long as the brain stimulus was applied (30–60 s).

Results

Morphology

The tympana in cicadas cover the frontal ventral half of the tracheal air chamber in the first evident abdominal segment, in which the sound-producing tymbals and tymbal muscles are also situated (Fig. 1A). The tympana of male and female cicadas of each species investigated show a considerable difference in area, the male tympana being much larger. In both species, the tympana are almost completely covered ventrally by metathoracic cuticular flaps, the opercula (not shown). In a quiescent cicada, the tympana are usually planar (Fig. 1B) and clearly under some tension. During singing (Fig. 1C), the tympana relax as a result of a movement of both the tympanal rim and the abdomen, probably caused by contraction of the detensor tympani muscles and ventral longitudinal muscles (Fig. 1A; see also Pringle, 1954). The photographs (Fig. 1B,C) were taken of the left tympanum of *Tibicen linnei* in a quiescent and 'singing' male. The appearance of the tympanal folds was always associated with the beginning of singing activity induced by electrical brain stimulation or with natural disturbance squawks. Tympanal folding was a comparatively slow process, requiring about 0.5 s for completion, and was then maintained for as long as sound production continued. During folding, several folds appeared; the number of folds did not change as folding progressed. The number of folds was not constant between animals and the folds in the ventral half of the tympanum appeared to be of greater amplitude. These observations were consistent for both species.

Auditory nerve response

Auditory nerve recordings from both species document changes in auditory threshold associated with relaxation of the tympana during singing. The acoustic stimulus consisted either of a brief click from a loudspeaker, very similar in duration and frequency content to the sound-pulse from a single rib in a buckling tymbal, or a sine-wave pulse.

Determination of the auditory nerve responses was only possible because many of the male cicadas used here did not produce sound despite showing 'singing' activity. Otherwise the auditory nerve response to external sound would have been completely masked by the response to the sound pulses produced by the buckling of the tymbal.
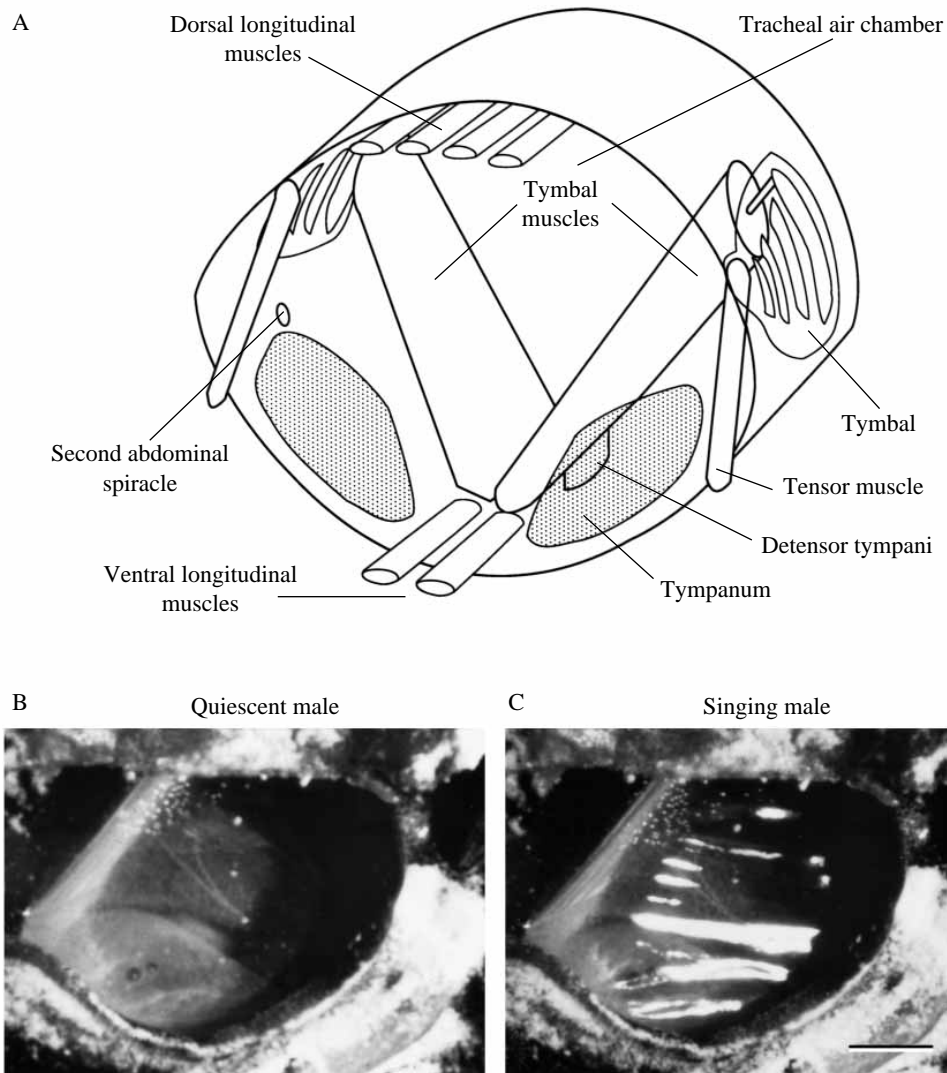

Fig. 1. Location of the tympana in cicadas. (A) Schematic representation of the first evident abdominal segment showing the tympana, which lie in close proximity to the sound-producing apparatus (tymbals, tymbal muscles and tensor muscles). The detensor tympani muscles are intersegmental muscles inserting at the tympanal rim; the tensor muscles arise in the metathorax and insert on the tymbal rim. (B) The tympanum of *Tibicen linnei*, showing a quiescent male without folds and (C) the same tympanum of a brain-stimulated 'singing' male with typical transverse folds. Scale bar, 1 mm.

Nevertheless, the results presented here for a singing animal were always recorded from males with clear tympanal folds which did not depend on whether sound was produced.

Auditory nerve recordings from quiescent males of *T. linnei* showed a prominent response to a click stimulus presented at peak values greater than 30 dB SPL (Fig. 2A). In a singing male the auditory nerve response to the same stimulus was greatly reduced (Fig. 2B). The EMGs of tymbal muscles shown are typical for a quiescent (Fig. 2A) and a 'singing' (Fig. 2B) male. Averaging the auditory responses, as shown in Fig. 2A at different click intensities, showed that there was no response to peak intensities below
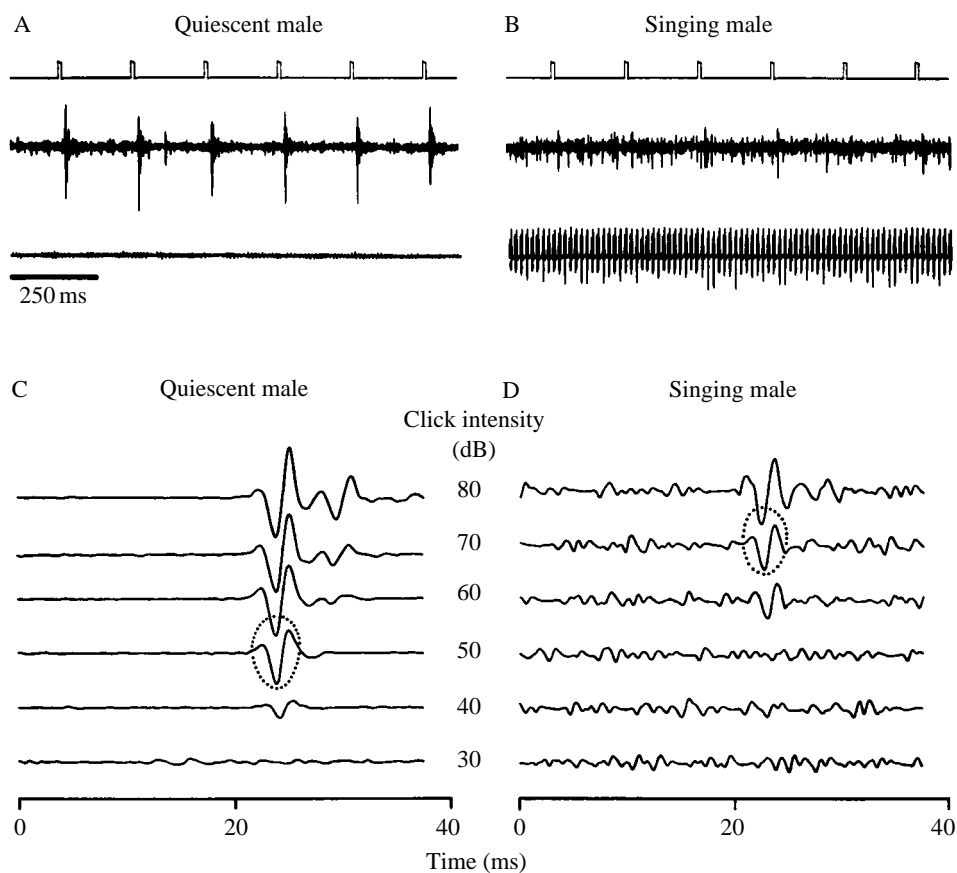

Fig. 2. Change in auditory thresholds due to folded tympana. (A,B) Auditory nerve recording in *Tibicen linnei* during acoustic stimulation by brief clicks (70 dB SPL, frequency spectrum 2–12 kHz) in a quiescent (A) and a silently 'singing' male (B); singing activity was monitored by recording the tymbal muscle (upper trace, clicks from loudspeaker; middle trace, auditory nerve recording; bottom trace, tymbal muscle EMG). (C,D) Averaged auditory nerve responses (N=30) to peak click intensities between 30 and 80 dB SPL from the recordings shown in A and B. (C) Quiescent male; (D) silently 'singing' male. Each trace is triggered by a click stimulus (upper trace in A, B). The dotted circles in C and D show the same response magnitude under both conditions. During singing activity (B and D), there was also a general increase in nerve activity.

60 dB in 'singing' males, while a response was clearly present in quiescent males at 40 dB SPL (Fig. 2C). Thus, in order to obtain the same nerve response magnitude in a 'singing' male as in a quiescent male, the level of the sound stimulus had to be increased by 18±4 dB in *Okanagana rimosa* (data from five males) and by 23±5 dB in *T. linnei* (data from six males). Despite considerable differences in the size and the morphology of the two species investigated (and thus in the size and shape of the respective tympana, *O. rimosa* being an exposed-tymbal cicada while *T. linnei* is a concealed-tymbal cicada), they both showed the same increase of about 20 dB in auditory threshold during singing. The recording of the auditory nerve during singing (Fig. 2A) as well as the averaged recording signal (Fig. 2B) showed that there was an increase in nerve activity during 'singing'. The nerve activity recorded probably includes activity in efferent as well as afferent fibres.

The acoustic stimulation with a broad-band click stimulus does not reveal whether the folding of the tympana reduces the auditory response equally over the whole frequency range of the auditory receptors or whether certain frequencies are more affected than others. In order to test this, we determined the auditory threshold of quiescent and singing males of *T. linnei* (Fig. 3). This species showed the best responses to frequencies between 3 and 5 kHz, with maximum sensitivity at about 30–35 dB SPL. During 'singing', the auditory response diminished over the frequency range tested (1–16 kHz), except that responses could not be elicited in 'singing' males at frequencies below 1.5 or above 12.5 kHz (Fig. 3), owing to the limitations of the stimulation set-up.

Electrical stimulation of the auditory nerve

The complete action of tympanal folding, involving movement of both the abdomen and the tympanal rim, can be induced by electrical stimulation of either or both auditory
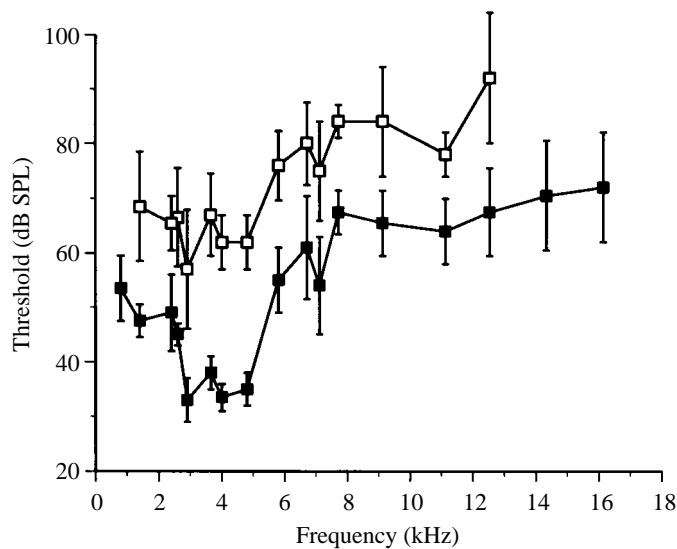

Fig. 3. Auditory thresholds in quiescent (■) and singing (□) *Tibicen linnei* males. Mean values with standard deviations; data from eight auditory nerve recordings from four males.

nerves. This allowed us to address the question of whether the reduction in response amplitude due to tympanal folding is gradual or abrupt. A gradual effect would allow cicadas to adjust their dynamic hearing ranges according to the surrounding sound levels.

The auditory nerve response to a sound click (60 dB SPL) was investigated under various degrees of folding controlled by electrical stimulation of the auditory nerve. There was a clear reduction in auditory response amplitude with increasing folding that was induced by increasing stimulation frequencies in *T. linnei* (Fig. 4A). This effect occurred at electrical stimulation frequencies between 10 and 34 Hz. The magnitude of the amplitude reduction between stimulation frequencies of 20 and 34 Hz was equivalent to a sensitivity loss of 20 dB, as described previously (see Fig. 2).

The degree of folding induced by electrical stimulation of the auditory nerve in *T. linnei* could also be observed under a binocular microscope. At low stimulation frequencies (below 15 Hz), which had a clear effect on the auditory threshold (Fig. 4A), there was no apparent change in abdominal posture and no tympanal folds were seen (Fig. 4B). With increasing stimulation frequencies, there was first a weak lifting of the abdomen at stimulation frequencies up to 25 Hz, followed by the development of folds
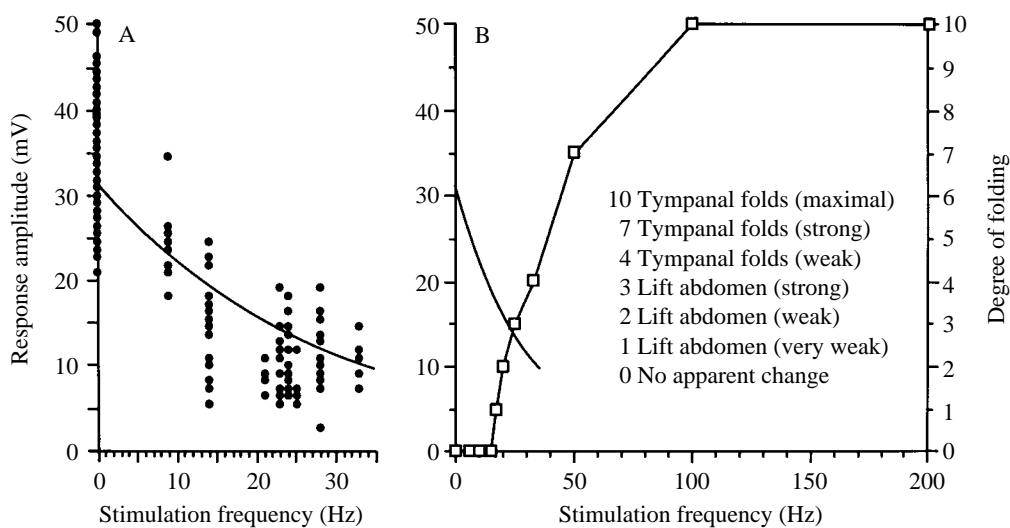

Fig. 4. Electrical stimulation of an auditory nerve of *Tibicen linnei* inducing folding of a tympanum and thus a change in the auditory threshold. (A) Amplitude of auditory nerve response to external clicks (60 dB SPL) related to frequency of electrical stimulation of the auditory nerve (stimulation and recording electrodes were placed on the same nerve). All measurements are shown; the curve indicates the best exponential fit. Data from one male; each data point represents the average response to at least 30 acoustic stimulations. (B) Qualitative description derived from visual inspection of the folding of the tympana caused by electrical stimulation of the auditory nerve (same individual as in A). Inset, assigned arbitrary values for degree of folding. The electrical stimulation frequency during the maximum reduction of the nerve response seen in A (here shown as a line) corresponded to a weak lifting of the abdomen at 20–34 Hz, and thus relaxation (but not yet folding) of the tympana. The reduction of the auditory response was already maximal at stimulation frequencies well below those causing tympanal folds typical of those during singing activity.

and an increase in their magnitude (Fig. 4B). From this observation, it appears very likely that threshold changes of the auditory receptors occur in response to very small changes in the tension of the tympanum. Furthermore, it seems likely that cicada males can selectively adjust their dynamic hearing range up to 20 dB.

Discussion

The neuromuscular basis of tympanal folding

The role of individual muscles and innervation patterns participating in tympanal folding is not clear and needs further investigation. Although the detensor tympani muscles are true intersegmental muscles (Pringle, 1954), it seems possible from visual observations that contraction of the ventral longitudinal muscles as well as a tonic component in the tymbal muscle contraction during singing also contribute to the folding effect. Electrical stimulation of the auditory nerve alone had the effect of folding of the tympanum. This implies that the auditory nerve not only innervates the auditory organ (and the tymbal muscle in *O. rimosa*) but also innervates the detensor tympani muscles and some ventral longitudinal muscles. The peripheral targets of the various motoneurones other than the tymbal motoneurones described within the auditory nerve (Wohlers *et al.* 1979) are as yet unknown.

What can be achieved by peripheral modulation of auditory sensitivity?

Protection from mechanical overloading

In male cicadas, the tympana are directly coupled acoustically to the sound-producing apparatus with which they share the same large abdominal tracheal air chambers. There is evidence that the abdomen plays an important role in amplification and radiation of the sound signal generated by the tymbals. This suggests that the tympanal openings are part of the sound-radiating system, and very high sound levels have been recorded in their vicinity (Young, 1990; Bennet-Clark and Young, 1992). Relaxation of the tympana during singing would clearly protect the tympanal membranes and their associated chordotonal systems from possible damage by mechanical overloading (Pringle, 1954). A peripheral mechanism with an apparently similar effect has been described for bats (Suga and Jen, 1975). In these bats, a middle ear muscle reflex attenuates the self-stimulation when an echolocation call is emitted. Thus, bats are able to detect the faint echoes following echolocation calls only after a short time delay. The protection of a sensory pathway from habituation by intense self-stimulation has also been described for amphibians (Russel, 1976), fishes (Klinke and Schmidt, 1970), crustaceans (Krasne and Wine, 1977), grasshoppers (Wolf and von Helversen, 1986; Hedwig, 1990) and crickets (Hörner *et al.* 1989).

Dynamic range adjustment

The folding of the tympana during singing in cicadas reduces the sensitivity to broadcast sounds by 20 dB, but it does not completely disable sound reception. It appears unlikely that a cicada detects external sounds during its own full singing activity or that

the sensory signal generated by a cicada's own singing activity may be effective as a feedback mechanism to stabilize its own song. Nevertheless, there are cicadas with calling songs that show much lower amplitude or intermittent parts and which show clear singing responses to the songs of nearby males (e.g. *Magicicada cassini*, Alexander and Moore, 1962; *Tettigetta argentata/atra*, Fonseca, 1991). Despite the folded tympana, the males of some cicadas must still be able to detect external sound with levels higher than 60 dB SPL, which they use to synchronize their own singing activity with that of other males, as in *Magicicada cassini* and *M. tredecassini*. These periodical cicada males also congregate within about 30 cm of one another and incorporate visual cues, such as regular wing-flipping or flying, in their synchronized chorusing. During silent or low-amplitude phases of calling songs, predators might also be detected and localized on the basis of their noise, as well as by sight. Visual acuity and auditory sensitivity in cicadas may both have evolved special attributes in response to selection by predators and parasites as well as in response to species-specific interactions. In particular, the common auditory sensitivity between 1 and 4 kHz evident in hook electrode records from whole auditory nerves, even in the case of many species whose own carrier frequencies lie outside that range (Popov *et al.* 1986; Popov, 1990; Huber *et al.* 1990), may attest to such selection by general predators such as frogs, birds and mammals. Thus, it appears that cicadas employ tympanal folding during singing to adjust their dynamic hearing range both to the sounds that they themselves generate and to the sounds that surround them. This may enable cicadas to maintain maximum acoustic acuity for broadcasting sounds in response to both internal and external background sound levels. Cicadas also appear to use this mechanism while they are silent, because they have been observed to generate tympanal folds without singing activity. Many species of cicadas show very low hearing thresholds (20–30 dB SPL at 1–4 kHz, Popov *et al.* 1986), and it may therefore be advantageous to be able to adjust the hearing threshold according to the sound level by which the male is surrounded. This mechanism may not be exclusive for cicada males because females are also known to show auditory threshold modulation (Hennig *et al.* 1993), the basis of which may be the tensor tympani, the ancestral tymbal muscle and the ventral abdominal muscles (Pringle, 1954; Wohlers and Bacon, 1980). It remains to be demonstrated whether cicadas also use different receptor classes each with its own threshold, which is another way of increasing the dynamic range of hearing known to be employed by grasshoppers (Römer, 1976) and crickets (Oldfield *et al.* 1986).

References

Alexander, R. D. and Moore, T. E. (1962). The evolutionary relationships of 17-year and 13-year cicadas and three new species (Homoptera, Cicadidae, Magicicada). *Misc. Publ. Mus. Zool. Univ. Michigan* **121**, 5–59.

Bennet-Clark, H. C. and Young, D. (1992). A model of the mechanism of sound production in cicadas. *J. exp. Biol.* **173**, 123–153.

Fonseca, P. J. (1991). Characteristics of the acoustic signals in nine species of cicadas (Homoptera, Cicadidae). *Bioacoustics* **3**, 173–182.

Hedwig, B. (1990). Modulation of auditory responsiveness in stridulating grasshoppers. *J. comp. Physiol.* A **167**, 847–856.

HENNIG, R. M. (1989). Neuromuscular activity during stridulation in the cricket, *Teleogryllus commodus. J. comp. Physiol.* A **165**, 629–639.

HENNIG, R. M., WEBER, T., HUBER, F., MOORE, T. E., KLEINDIENST, H.-U. AND POPOV, A. V. (1993). A new function for an old structure: the 'timbal muscle' in cicada females. *Naturwissenschaften* **80**, 324–326.

HENNIG, R. M., WEBER, T., MOORE, T. E., HUBER, F., KLEINDIENST, H.-U. AND POPOV, A. V. (1994). Function of the tensor muscle in the cicada *Tibicen linnei. J. exp. Biol.* **187**, 33–44.

HÖRNER, M., GRAS, H. AND SCHÜRMANN, F. W. (1989). Modulation of wind sesitivity in thoracic interneurons during cricket escape behavior. *Naturwissenschaften* **76**, 534–536.

HUBER, F., KLEINDIENST, H.-U., MOORE, T. E., SCHILDBERGER, K. AND WEBER, T. (1990). Acoustic communication in periodical cicadas: neuronal responses to songs of sympatric species. In *Sensory Systems and Communication in Arthropods* (ed. F. G. Gribakin, K. Wiese and A. V. Popov), pp. 217–228. Basel, Boston, Berlin: Birkhäuser.

KLINKE, R. AND SCHMIDT, C. L. (1970). Efferent influence on the vestibular organ during active movements of the body. *Pflügers Arch.* **318**, 352–353.

KRASNE, F. B. AND WINE, J. J. (1977). Control of crayfish escape behavior. In *Identified Neurons and Behavior of Arthropods* (ed. G. Hoyle), pp. 275–292. New York: Plenum Press.

OLDFIELD, B. P., KLEINDIENST, H. U. AND HUBER, F. (1986). Physiology and tonotopic organization of auditory receptors in the cricket *Gryllus bimaculatus* DeGeer. *J. comp. Physiol.* A **159**, 457–464.

POPOV, A. V. (1990). Co-evolution of sound production and hearing in insects. In *Sensory Systems and Communication in Arthropods* (ed. F. G. Gribakin, K. Wiese and A. V. Popov), pp. 301–304. Basel, Boston, Berlin: Birkhäuser.

POPOV, A. V., ARONOV, I. B. AND SERGEEVA, M. V. (1986). Calling songs and hearing in cicadas from Soviet central Asia. English translation from *Zhurnal Evol. Biokhim. Fiziol.* **21**, 451–462.

PRINGLE, J. W. S. (1954). A physiological analysis of cicada song. *J. exp. Biol.* **31**, 525–560.

RÖMER, H. (1976). Die Informationsverarbeitung tympanaler Rezeptorelemente von *Locusta migratoria* (Acrididae, Orthoptera). *J. comp. Physiol.* **109**, 102–122.

RUSSEL, I. J. (1976). Amphibian lateral line receptors. In *Frog Neurobiology* (ed. R. Llinas and W. Precht), pp. 513–550. Berlin, Heidelberg, New York: Springer.

SIMMONS, P. AND YOUNG, D. (1978). The tymbal mechanism and song patterns of the bladder cicada, *Cystosoma saundersii. J. exp. Biol.* **76**, 27–45.

SUGA, N. AND JEN, P. H. S. (1975). Peripheral control of acoustic signals in the auditory system of echolocating bats. *J. exp. Biol.* **62**, 277–311.

WOHLERS, D. AND BACON, J. (1980). Sexual dimorphism of motoneurons: tymbal muscle innervation in male periodical cicadas and homologous structures in females. *Cell Tissue Res.* **209**, 371–382.

WOHLERS, D. W., WILLIAMS, J. L. D., HUBER, F. AND MOORE, T. E. (1979). Central projections of fibers in the auditory and tensor nerves of cicadas (Homoptera: Cicadidae). *Cell Tissue Res.* **203**, 35–51.

WOLF, H. AND VON HELVERSEN, O. (1986). 'Switching-off' of an auditory interneuron during stridulation in the acridid grasshopper *Chorthippus biguttulus* L. *J. comp. Physiol.* A **158**, 861–871.

YOUNG, D. (1990). Do cicadas radiate sound through their ear-drums? *J. exp. Biol.* **151**, 41–56.