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FUNCTION OF THE TENSOR MUSCLE IN THE CICADA *TIBICEN LINNEI*

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Summary

The calling song and the disturbance squawk of the cicada *Tibicen linnei* (Insecta: Homoptera) are described in terms of their physical parameters. The calling song is composed of quiet parts, which are very similar to the disturbance squawk, and loud parts, which are amplitude- and rate-modulated. The role of the tensor muscle acting on the tymbal frame in modulating the sound pulse amplitude was investigated. We demonstrate by tensor nerve recordings, by mechanical mimicking of the tensor muscle action and by electrical stimulation of the tensor nerve, that the contraction of the tensor muscle is responsible for (a) initiating sound production and (b) modulating the sound pulse amplitude. These results allow us to construct a model which suggests that the tensor shifts the tymbal into a mechanical working range that enables sound production and modulation of the sound pulse amplitude.

Introduction

Male cicadas possess an elaborate long-distance acoustical broadcasting system which they use for communication. In addition to the stereotypic calling song which serves to attract females and males, many cicadas produce an irregular disturbance squawk or protest song (Simmons and Young, 1978) when handled. Sound in most cicadas is generated by the tymbals, a pair of stiffened membranes in the first abdominal segment, upon which the paired tymbal muscles act. Sound is amplified and radiated by the abdominal cavity, the tympanal openings and the opercula, which are thoracic cuticular flaps (Young, 1990; Bennet-Clark and Young, 1992).

The physical parameters of cicada songs are described by the sound pulse rate, the amplitude of the sound pulses and the frequency spectrum. A distinct and usually species-specific feature is the stereotypic modulation of these physical parameters. The mechanisms and structures that generate these modulations are difficult to separate experimentally. One candidate, the tensor muscle, acting upon the tymbal frame, has been

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the subject of several investigations of the amplitude, the rate or timing of the sound pulses and the frequency spectrum. Investigators are not in agreement as to the effects of the tensor muscle contraction. Pringle (1954*a*) provides a valuable account of the literature to that time and gives a detailed description of the tensor muscle insertion, as do later investigators (Hagiwara, 1956; Vasvary, 1966; Simmons and Young, 1978). Even for different and not closely related cicada species, the same basic pattern appears to apply: the tensor muscle inserts dorsolaterally on the anterior frame of the tymbal and arises more ventrally at a metathoracic apodeme. The tensor muscle is innervated by at least three motoneurones (Wohlers *et al.* 1979; Popov, 1981; Weber *et al.* 1987) and the electromyogram (EMG) of the tensor muscle shows discharge frequencies between 10 and 100Hz (Hagiwara, 1956; Simmons and Young, 1978).

The most commonly reported effect of tensor muscle contraction is an increase in amplitude of the sound pulses (Pringle, 1954*a*; Simmons and Young, 1978; Fonseca, 1991). However, Weber *et al.* (1987) report in other species a reduction in the amplitude of the sound pulses upon contraction of the tensor muscle. The change in amplitude appears to result from a change in the elastic properties of the tymbal when the tymbal frame is distorted by the tensor muscle. The time interval between consecutive sound pulses generated by one tymbal may be shorter when the tensor muscle is contracted (Pringle, 1954*b*; Simmons and Young, 1978), although Pringle (1954*a*) described an increase in the sound pulse interval. The frequency spectrum of the sound pulses may also be affected by contraction of the tensor muscle (Hagiwara, 1956; Simmons and Young, 1978).

Thus, there are three known effects of tensor muscle contraction on the sound pulses produced by a tymbal: changes in amplitude, in time interval or in frequency spectrum, all of which are likely to play an important role in sound signalling for phonotactically orientating males and females. This study shows that a contraction of the tensor muscle leads first to sound production and then to sound pulse amplitude modulation.

Materials and methods

Animals

Male *Tibicen linnei* Smith & Grossbeck were caught in an orchard near Bangor, Van Buren County, Michigan. Sound recordings were made in the field. Experiments were performed in Ann Arbor, Michigan, in a sound laboratory within 7 days of capture. The animals were kept in the dark on a live shrub placed in a refrigerator at about 15˚C until tested.

Morphology

Drawings of the morphology of the insertions of the tymbal and tensor muscles and the tymbal structures were made from males immediately after death. Animals were also preserved in 70% ethanol for later morphological analysis.

Preparation

For all experiments, a male was pinned ventral side up on a small styrofoam platform, with the legs and wings removed. EMG wires (30mm diameter, insulated except at the tip) were inserted ventrally into the tymbal muscles. The opercula were left intact. In this preparation, the tensor action could be mimicked by mechanical manipulation of the tymbal frame with forceps.

Recording and electrical stimulation of the tensor nerve

The ventral cuticle was removed, exposing the nerves exiting from the metathoracic-abdominal ganglionic 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; pH7.4). Identification of the tensor nerve was based on (1) anatomical descriptions (Vasvary, 1966; Wohlers *et al.* 1979), (2) relating nerve recordings and the EMG of the tensor muscle and (3) nerve stimulation and correlated tensor muscle contraction in a dissected preparation. For recording and stimulation, the tensor nerve was placed on double silver hook electrodes (50mm diameter) insulated from the Ringer’s solution with a Vaseline/oil mixture. The stimuli were pulses of 0.5ms duration and 1–2V amplitude applied at frequencies of 10–100Hz. Custom-made amplifiers were used for extracellular recordings and battery-driven stimulation units (WPI 850 A) for nerve stimulation. The data were stored on magnetic tape (Racal Store 4DS). Sound recordings were made by a condensor microphone (AKG type C567). The data were evaluated by analyzing chart records and digitized data.

Eliciting singing

The disturbance squawk was elicited by touching the abdomen, head or antennae or by electrical stimulation of the brain. The patterns elicited by the two methods were indistinguishable. We were not successful in eliciting the calling song. Cicada males commonly became silent after some time during an experiment, despite regular and normal tymbal muscle activity indicated by the EMG of the tymbal muscles.

Results

Description of the calling song and the disturbance squawk of Tibicen linnei

The calling song of *T. linnei* consisted of quiet and loud parts, both of which were of variable duration (10–20s each, Fig. 1A). The beginning and ending were both quiet and showed the greatest variation in duration. The inward buckling of each tymbal appeared to involve 2–3 ribs producing one sound pulse, as shown by the sound pulse envelope, and a pulse of lower amplitude when the ribs moved out (Hennig *et al.* 1992). Sections of the calling song in Fig. 1A are shown on an expanded time scale in Fig. 1Bi–vi. At the beginning of the song, the sound pulses were quiet and grouped in fours (Fig. 1Bi). As the amplitude of the sound pulses slowly increased, the rate of the sound pulses also increased (Fig. 1Bii) until the grouping disappeared (Fig. 1Biii). The loud part of the calling song then started; this also showed distinct amplitude- and rate-modulation (Fig. 1Biv, see Fig. 2 for details). Towards the end of the loud section (Fig. 1Bv), the regular modulation ended, the grouping of sound pulses into fours reappeared and the amplitude and rate slowly decreased (Fig. 1Bvi) until the same pattern as at the beginning of the song reappeared (Fig. 1Bi). Towards the end of a call, the left/right relationship of

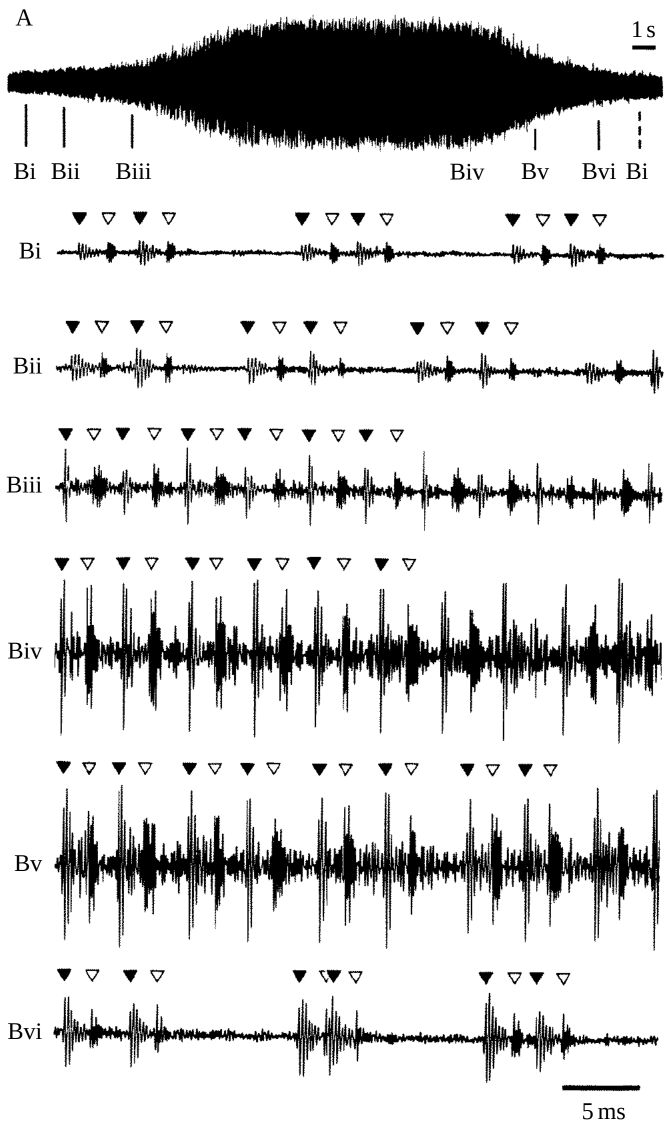

Fig. 1. Analysis of the calling song pattern of *Tibicen linnei*. (A) Oscillogram of the calling song, which commences with pulses of low amplitude, increases in amplitude and finally becomes quiet again. (B) Expanded sections (Bi–Bvi) of the calling song from A at respective points indicated below the record. Both tymbals were intact. In-pulses are indicated by a filled triangle, out-pulses by an open triangle. Records in Bi, Bii, Bv and Bvi correspond to the sound pulse pattern also seen during the disturbance squawk of this species.

the two tymbals became irregular (Fig. 1Bvi) such that the out-pulse of one tymbal overlapped the in-pulse of the other. Overlapping of sound pulses was not seen during the loud parts of the song. This irregular sound pulse pattern during the calling song is identical to the sound pulse pattern observed during the disturbance squawk.

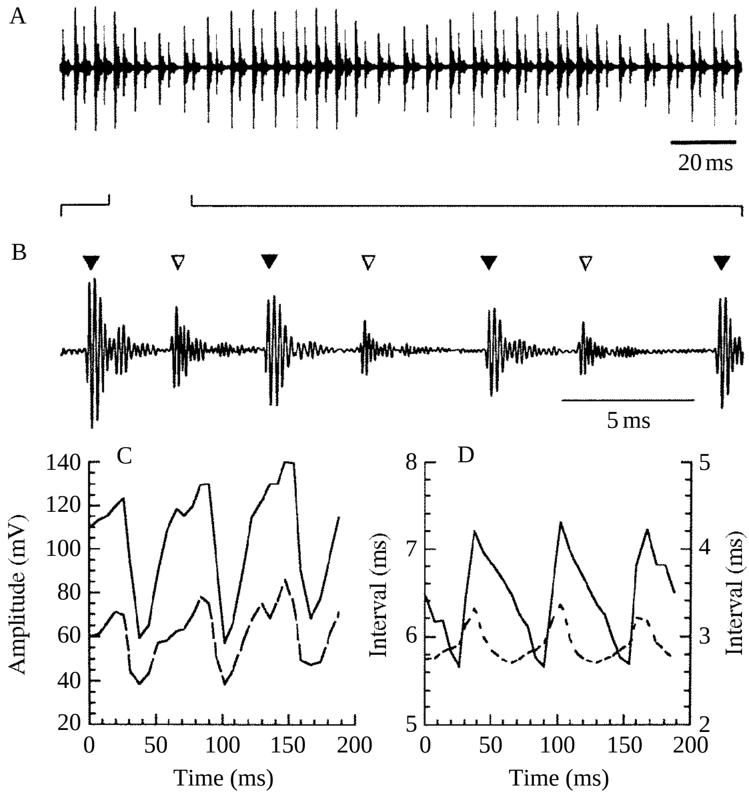

Fig. 2. Analysis of the calling song pattern of *Tibicen linnei* with only one tymbal intact. (A) Sound pulse sequence from the middle section of the calling song (as in Fig. 1A). The typical amplitude modulation of the sound pulses is associated with abdominal movements. (B) Series of three consecutive in and out sound pulses from the sequence shown in A. In-pulses are marked by filled triangles, out-pulses by open triangles. The three selected cycles show the modulation in amplitude and intervals of the sound pulses. (C) Quantification of the change in sound pulse amplitude during full singing activity (upper, solid curve) and at the beginning of the song (lower, dashed curve). (D) The time interval from in-pulse to in-pulse of the same tymbal (solid line, left-hand ordinate) and from in-pulse to out-pulse (dashed line, right-hand ordinate) during full singing activity. There is a periodic modulation of both intervals as well as of amplitude (C). The rate of the periodic modulation in C and D changes only very little (13–17Hz). Each interval, however, follows a different time course of modulation.

The precise sound pulse pattern for each of the two tymbals was determined by recording the calling songs with only one tymbal intact. The loud part of the song (Fig. 2A) was amplitude- and rate-modulated (120–180 Hz). Since the phase relationship between the left and right tymbal in this part of the calling song was approximately 0.5, the rate of sound pulses in an intact singing male was 240–360 Hz. The amplitude- and rate-modulation had a cycle frequency of 13–17 Hz (Fig. 2C,D). Fig. 2B illustrates the modulation of the period and the amplitude of the in- and out-pulses during three cycles.

Fig. 2C shows the amplitude-modulation (up to 50 %) of the in-pulses determined from three modulatory cycles at the beginning of the calling song and during the loud part of the calling song. The amplitude of the out-pulses is modulated correspondingly (Fig. 2B). Modulation of the time interval from in- to out-pulses and in- to in-pulses followed different time courses (Fig. 2D). The tymbal rate, determined by the tymbal muscle action, showed a sudden drop within two contraction periods of one tymbal muscle; this occurred almost simultaneously with the decrease in amplitude (Fig. 2B,D). The in- to out-intervals were also maximal when the in- to in-interval was maximal: however, the in- to out-interval had already increased, when the in- to in-interval was still decreasing (Fig. 2D). This indicates that the two intervals may be governed by two different mechanisms.

The disturbance squawk of *T. linnei* consisted of a continuous sequence of sound pulses with an irregular pattern (Fig. 1Bvi). There was no periodic amplitude- or rate-modulation of the sound pulses. The sound pulses resulting from tymbal buckling were essentially the same as those observed in the calling song: an in-pulse was followed by an out-pulse with a somewhat higher frequency band. However, the phase relationship between left and right tymbal muscles was usually shifted towards a phase of 0.1–0.3 (compared with 0.5 in the loud part of the calling song), which resulted in the grouping of the sound pulses in fours. This phase shift could be attributed to a constant latency between the left and right tymbal action and to an extended interval between the actions of the same tymbal.

Thus, the basic events of a tymbal cycle are similar for the calling song and the disturbance squawk, both consisting of an in-pulse with the acoustic contribution of 2–3 ribs and an out-pulse. The sound pulse pattern during the quiet parts of the calling song was essentially the same as that seen during the disturbance squawk. However, there are distinct differences between the calling song and the disturbance squawk in the rate, the phase relationship between the two tymbals and the regularity of the amplitude-modulation during the loud part of the calling song. Since the calling song could not be elicited under experimental conditions, the experimental results described here are necessarily based on disturbance squawks.

Sound-generating apparatus of Tibicen linnei

The sound pulse modulations in the calling song of *T. linnei* are rather complex and involve the amplitude and rate of the sound pulses and the sound pulse envelope (Fig. 2B). We investigated the role of the tensor muscle in inducing amplitude modulations. The general morphology of the tymbal, the tymbal frame and the associated musculature is similar in all tymballing cicadas (Fig. 3). During sound production in cicadas, the tymbal muscle buckles the tymbal inwards and it springs back outwards by stored elastic force. There are no muscles directly opposing the action of the tymbal muscle. The tensor muscle distorts the tymbal frame and is thus likely to change the elastic properties of the tymbal by changing the tymbal tension.

Tensor nerve recordings and correlated sound production

Recordings from the tensor nerve showed increased activity of small units correlated with bouts of sound production (Fig. 4, arrowheads). In most cases, however, there was no

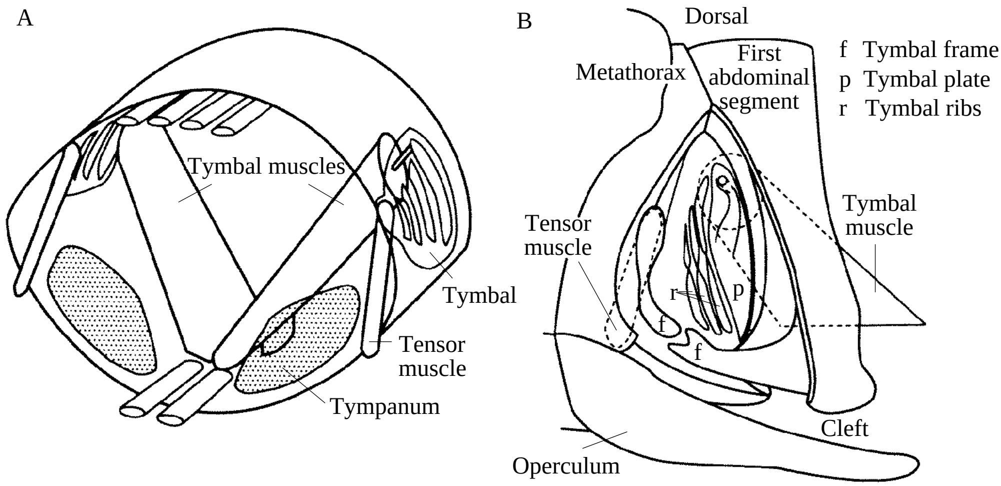

Fig. 3. Anatomy of the sound-producing apparatus in *Tibicen linnei*. (A) Schematic view of the first abdominal segment. (B) Lateral view of the tymbal (tymbal cover removed) and the insertion of the associated muscles (dashed lines). The tymbal is situated in the first abdominal segment with the tymbal muscle attached to it by a slender apodeme extending from the tymbal plate. The tensor muscle attaches dorsally to the anterior upper tymbal frame and ventrally to a stout lateral apodeme anchored in the metathorax.

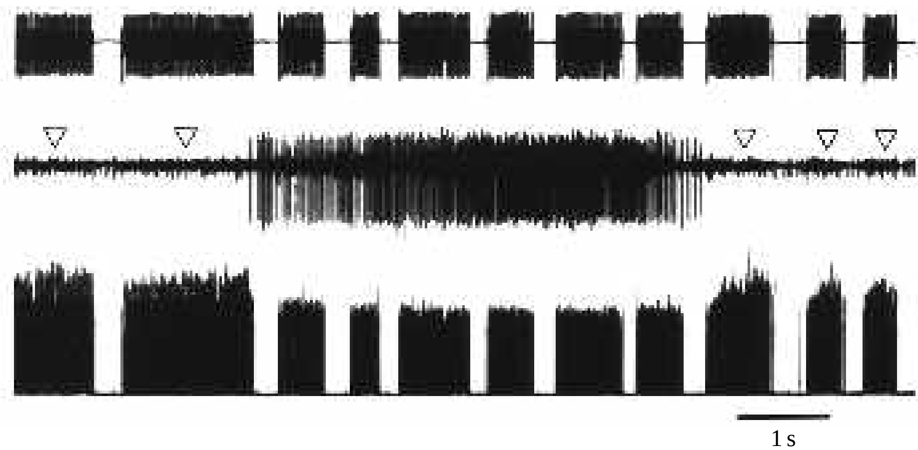

Fig. 4. Tensor nerve recording and correlated disturbance squawk production. In the tensor nerve, small motor units were recorded (arrowheads) whose activity was correlated with sound production, and also a large motor unit, whose activity was correlated with amplitude-modulation, although the tymbal muscle activity did not obviously change (upper trace, tymbal muscle EMG; middle trace, tensor nerve recording; bottom trace, rectified sound pulses).

amplitude-modulation of the sound pulses during the disturbance squawk. Sometimes a large unit appeared spontaneously in the tensor nerve recordings with a maximal discharge frequency of about 100 Hz. Correlated with the activity of that large-amplitude unit was a

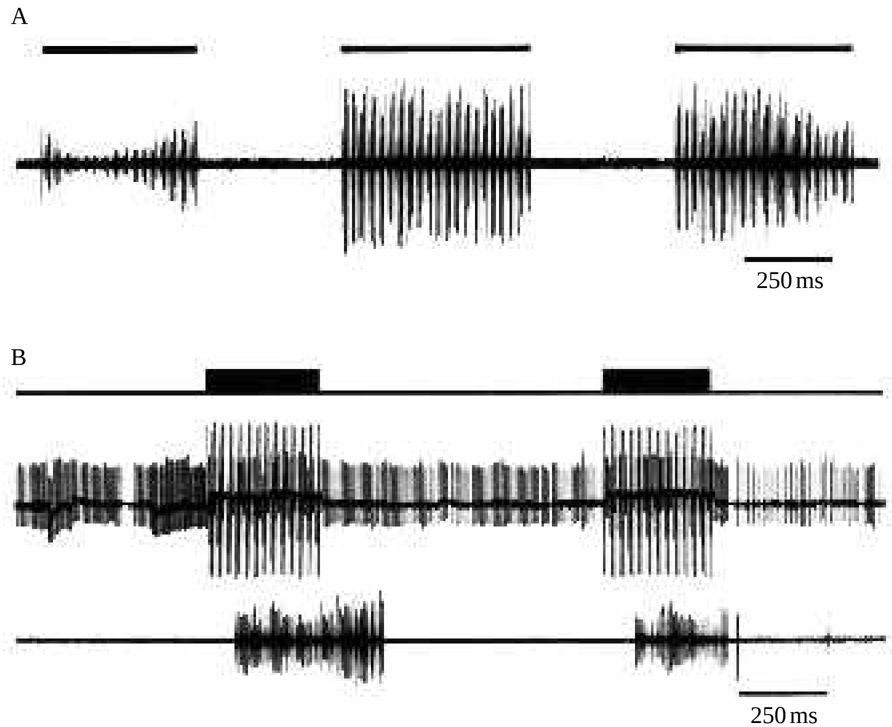

Fig. 5. Mimicking the tensor action. (A) Pushing the point of insertion of the tensor muscle at the tymbal frame in a 'silently singing' male results in sound production, when a constant force is applied, and in amplitude-modulation of the sound pulses, when the force is modulated (not monitored). Only the tymbal on the side on which force was exerted produced sound (upper trace, an indication of when the force was applied; lower trace, sound pulses). (B) Electrical stimulation of the tensor nerve leads to sound production by a tymbal whose tymbal muscle was continuously twitching (upper trace, stimulus monitor, pulse rate 100Hz; middle trace, tymbal muscle EMG with a stimulus artefact; bottom trace, sound pulses).

decrease in the sound pulse amplitude by about 20 % (Fig. 4), although there was no obvious change in tymbal muscle activity. Thus, the tensor nerve carries units whose activity is correlated with sound production and sound pulse amplitude-modulation.

Mimicking the tensor contraction mechanically

The force of the tensor muscle on the tensor sclerite of the tymbal frame may also be demonstrated mechanically using fine forceps. Under experimental conditions, it was not uncommon for *T. linnei* to show regular contractions of the two tymbal muscles, as shown by their EMGs, without any sound production (i.e. the males 'sang silently'). In these cases, a slight force applied to one tymbal frame led to sound production by that tymbal as well as to sound modulation if the applied force was modulated (Fig. 5A). Thus, one may propose that efferent innervation from the tensor nerve may be responsible for (a) sound production by the tymbal and (b) sound modulation.

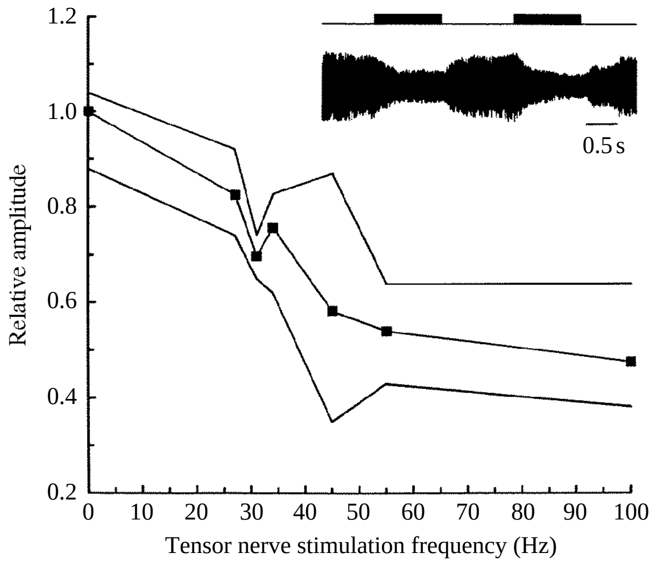

Fig. 6. Electrical stimulation of the tensor nerve during sound production led to a reduction in amplitude that was dependent on the rate of stimulation. The relative sound pulse amplitude was calculated by dividing the amplitude value during electrical stimulation by the amplitude value without electrical stimulation. Mean values (■); range of measurements indicated by lines. Data from three males. Inset: an example of a sound recording at a nerve stimulation frequency of 100Hz (upper trace, stimulus pulse monitor; lower trace, sound pulses).

Electrical stimulation of the tensor nerve

In order to test these two hypotheses and to quantify the effects of tensor muscle contraction on sound pulse amplitude, we stimulated the tensor nerve. In 'silently singing' males, electrical stimulation of the tensor nerve at frequencies higher than 20Hz led to sound production by the ipsilateral tymbal (Fig. 5B). In sound-producing males, trains of electrical stimulation pulses led to a reduction of the sound pulse amplitude (Fig. 6, inset). The relationship between the amplitude of the sound pulses and the stimulation frequency was inverse, i.e. the higher the stimulation frequency, the greater was the reduction in amplitude (up to 50% at frequencies higher than 40Hz; Fig. 6). Thus, the hypothesized roles of the tensor muscle in both sound production and amplitude-modulation are confirmed. The latency was around 50–100ms from the onset/cessation of electrical stimulation to the measurable effect in either turning on sound production or modifying amplitude during sound production. This observation indicates that the tensor muscle in *T. linnei* is a tonically acting muscle, as already suggested by Pringle (1954*a*), Hagiwara (1956), Simmons and Young (1978) and Weber *et al.* (1987).

Discussion

It was shown for disturbance squawks that the tensor muscle in *Tibicen linnei* is a tonically contracting muscle which inserts dorsolaterally on the tymbal frame and acts by exerting a force on it. There are two effects produced by the tensor muscle, as demonstrated by mechanical and electrical stimulation: ‘switching on’ of sound production by the ipsilateral tymbal in ‘silently singing’ males (Fig. 5) and amplitude-modulation in sound-producing males (Figs 4 and 6). The activity of at least two correlated units may be seen in tensor nerve recordings during disturbance squawks (Fig. 4).

Implications for the calling song

The effects of tensor muscle contraction (Figs 4, 5 and 6) can only be related to the quiet parts of the calling song to which the disturbance squawk corresponds. It appears that the tensor muscle acts to modulate the sound pulse amplitude, whereas the tymbal muscle sets the rate and phase relationship. It is also possible, however, that the tensor muscle contributes to the modulations seen in the loud part of the calling song, since the magnitude of the modulation was similar both for the calling song (Fig. 2) and following electrical stimulation of the tensor nerve (Fig. 6). Weber *et al.* (1987) confirmed a role for the tensor muscle in production of courtship sounds for periodical cicadas, but not in disturbance squawks or calling song production. Sound production in cicadas involves several morphologically linked structures – a hollow abdomen (amplification and radiation), the tympana and folded membranes, and the opercula, in addition to tymbals, tymbal muscles and tensor muscles (Young, 1990). Clearly, tensor muscle contraction does affect sound pulse amplitude, but it is likely that these other structures also make a contribution. The tymbal system is clearly a delicately balanced system involving at least three motoneurones that innervate the tensor muscle (Popov, 1981) and a large number of sensillae monitoring mechanical stress (Young, 1975). Perturbations of this system introduced by experimental manipulations, such as removal of the opercula, might therefore account for the observation of ‘silent singing’.

Construction of a model on the working range of the tymbal

From the results presented here, the effects of the tensor muscle on the sound pulses produced by the tymbal may be viewed as being dependent on the strength of the tensor muscle contraction. It appears (1) that some tensor muscle contraction is required for sound production (Fig. 5), (2) that there is a range of weak tensor activity leading to maximal sound pulse amplitude (Figs 4 and 6) and (3) that progressively increased tensor contraction leads to progressively decreased amplitude (Fig. 6). This is summarized by the model in Fig. 7. It is suggested (1) that a small contraction of the tensor muscle leads to a ‘switching on’ of sound production, (2) that intermediate contraction leads to maximal sound amplitude and (3) that a strong contraction reduces the amplitude of the sound pulses. The model proposes that a tymbal with insufficient stress, i.e. without tensor muscle contraction, will produce no sound. It appears that tensor muscle contraction increases the mechanical stress on the tymbal resting in the tymbal frame. A certain amount of tymbal stress and a certain activation rate will bring the tymbal as close as possible to a resonating system. A further increase in tensor muscle contraction will lead beyond optimal conditions and, hence, modulate the amplitude of the sound pulses.

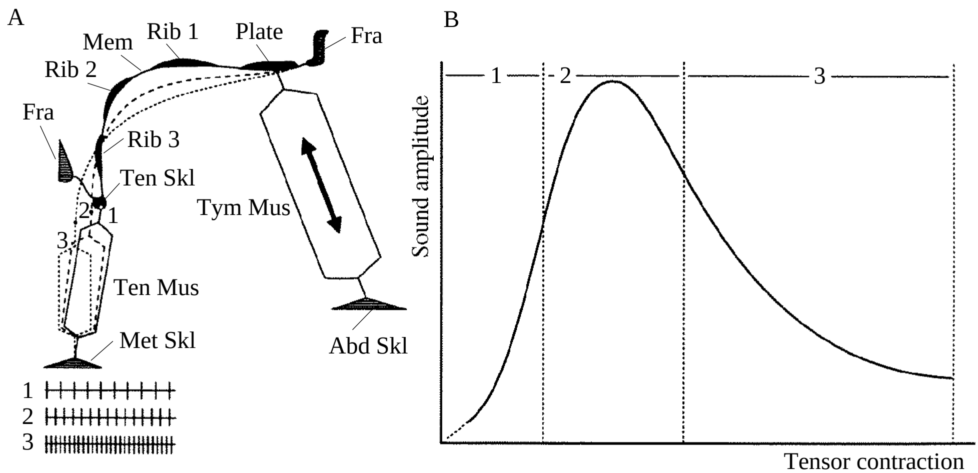

Fig. 7. Model of the mechanical working range of a tymbal in *Tibicen linnei*, as effected by its tensor muscle. (A) Schematic representation of the tensor muscle action on the tymbal frame distorting the tymbal. The tensor contraction levels were grouped into three classes according to the experimentally observed effects. The three contraction levels correspond to three frequencies of nerve discharge and are labelled 1, 2 and 3. Abd Skl, abdominal sclerite; Fra, tymbal frame; Mem, membrane; Met Skl, metathoracic sclerite; Ten Mus, tensor muscle; Ten Skl, tensor sclerite; Tym Mus, tymbal muscle. (B) The working range of the tymbal. It is suggested (1) that a low contraction level of the tensor muscle leads to the ‘switching on’ of sound production, (2) that intermediate activity leads to maximal sound amplitude and (3) that a strong contraction reduces the amplitude of the sound pulses.

The shape of the working range of the tymbal should depend on the mechanical properties of the tymbal itself, which are, however, not known. Nevertheless, the tensor muscle seems to shift the tymbal, probably by changing its elastic properties, into a mechanical working range within which it produces sound of varying intensity.

One difficulty with this interpretation is that the electrical stimulation was superimposed on the normal disturbance sounds (see Fig. 6), so some uncontrolled motor activity of the tensor may have been present already. Therefore, experiments are needed in which sound pulses are produced in a controlled way by electrical stimulation of the tymbal muscle or tymbal motoneurone.

Previous findings on the function of the tensor muscle indicate an increase in amplitude as a result of tensor muscle contraction (Pringle, 1954*a*; Simmons and Young, 1978; Fonseca, 1991), although Weber *et al.* (1987) demonstrated a decrease in amplitude and no initial tensor muscle contraction for sound production. The available data, as well as the model of the working range of tymbals based on the results obtained in *T. linnei* (Fig. 7), suggest that some tensor muscle contraction is required for sound production and that an increase in amplitude occurs only as a result of a comparatively small contraction, whereas amplitude reduction is caused by stronger tensor muscle contraction (Figs 4 and 6; Weber *et al.* 1987). It is conceivable that the seemingly contradictory effects described by others (Pringle, 1954*a*; Simmons and Young, 1978; Fonseca, 1991; Weber *et al.* 1987) are due to differences in the working range of the tymbal in different species. The working range is dependent on the mechanical properties of the tymbal and the tymbal frame. Thus, a difference between species in the mechanical properties of the sound-producing apparatus could lock the tymbal in stages 1 and 2 of the model (Fig. 7B), which would result only in an increase of the sound pulse amplitude as observed in other species (Pringle, 1954*a*; Simmons and Young, 1978). Only further comparative investigations can show how generally this model may apply to cicadas, notwithstanding the widespread similarity in basic morphological design of the tymbal/tensor system in all but the Platypleurinae, the principal group of cicadas lacking tymbals.

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