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Sound Production and Hearing in the Cicada, *Cicadetta sinuatipennis* Osh. (Homoptera, Cicadidae)

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Summary. 1. The spontaneous song of *Cicadetta sinuatipennis* males consists of alternating tymbal sound production and wing-clicking (Fig. 1). The temporal and spectral characteristics of tymbal and wing sounds are unalike (Table 1, Fig. 7).

2. Wing-clicking is the result of sudden lateral movements of the forewings. A click is generated by the outward buckling of a specialized caudal margin of a forewing which is locked in a narrow groove on the scutellum before sound production (Fig. 2).

3. Central projections of auditory and motor fibres with axons in the tympanal and tensor nerves were shown with the help of axonal cobalt iontophoresis (Figs. 3–5). The anatomy of the large tymbal motor neuron and three tensor motor neurons with ventral cell bodies is described.

4. Stimulus thresholds for the summed response of primary auditory fibres were measured for different sound frequencies. The resulting hearing curves show that the auditory organs have a sharp peak of sensitivity near 6–6.5 kHz. When stimulated by the natural spontaneous song of a male, the ear gives clear "on"-responses to each click of a wing sound with thresholds of about 21–31 dB SPL and very weak asynchronous reaction to tymbal sounds with thresholds of about 70 dB SPL. This is a result of the different spectral content of these sounds (Fig. 6, 7). It is suggested that wing sounds are used for long-range communication between males and females. Tymbal sounds can be used only for short-range communication or have another, possibly repellent function.

Introduction

Some singing cicadas possess, in addition to the well-known tymbal mechanism of sound production (Leston and Pringle 1964; Pringle 1954; Popov 1969, 1975; Young 1972; Fletcher and Hill 1978; Simmons and Young 1978), an accessory sound-producing apparatus which generates short clicks and is used by males during calling and/or courtship and sometimes by females responding to calling males (Myers and Myers 1924; Myers 1929; Dugdale and Flemming 1969). The precise mechanism of click production is unknown although it is known that clicks appear during rapid lateral movements of the forewings (so called wing-flapping, wing-clicking or wing-banging of different authors). Wing-clicking is widespread in the New Zealand and Australian species of *Cicadetta* (=*Melampsalta*, subfamily Tibicininae) and *Amphipsalta*. The male tymbal song is often accompanied by wing-clicking, and "females produce similar rhythmic clicks, thus permitting a two-way communication between the sexes during courtship" (Dugdale and Flemming 1969).

The acoustic behavior of 6 species of *Cicadetta* inhabiting the southern regions of the USSR has been studied (Popov 1975); only in *C. sinuatipennis* Osh., a common species of southern Turkmenistan, was wing-clicking found. This paper describes 1) the physical characteristics of tymbal and wing sounds produced by males of *C. sinuatipennis* during spontaneous singing (=calling), 2) the mechanism of wing-clicking, 3) central projections of auditory and efferent fibres with axons in the tympanal and tensor nerves, 4) the response of primary auditory fibres to pure tone and natural sounds. It is suggested that wing sounds of males are used in this species for long range communication between males and females, whereas tymbal sounds of the spontaneous song can be used only for short range communication or they even act as a repellent to bird predators.

Methods

1. Recording and Analysis of Sounds. All observations reported here were made in the course of field work in south Turkmenistan during May-June 1979. Recordings were made using a Brüel and Kjaer condenser microphone (type 4135) and Nagra-IV-S tape re-

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Abbreviations: TS tymbal sound; *WS* wing sound

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corder at a tape speed of 38.1 cm/s. All recordings of spontaneous songs of males were made from freely singing individuals in their natural environment. The microphone was placed at a distance of about 15 cm from the animal. The taped material was analysed with the aid of oscilloscope OK-17 and Brüel and Kjaer Real-time Analyser Type 3347/3348. To analyse the spectrum of short clicks of wing sound the analyser was used in combination with a Digital Event Recorder 7502 (Brüel and Kjaer).

2. Axonal Cobalt Iontophoresis. Central projections of auditory fibres and the anatomy of motor neurons with axons in the tympanal and tensor nerves were studied with the help of axonal cobalt iontophoresis (Rehbein et al. 1974). The tympanal nerve was cut as close to the tympanal organ as possible (in most cases 0.5–0.8 mm behind the sternal canal); the tensor nerve was cut close to the tensor muscle. Cut ends of the nerves were placed in a 6% cobaltous chloride solution. The isolated central nervous system was placed in a neighboring compartment of a Plexiglas apparatus filled with insect saline (Fielden 1960). The part of the nerve between the compartments was covered by Vaseline. Direct currents of 4–20 μA were passed through the nerves. The staining times were between 0.5–1.5 h. Immediately after iontophoresis the cobalt that had migrated into the axons was precipitated with a $(NH_4)_2S$ solution (1 drop of concentrated ammonium sulphide per 10 ml of water) leaving a black CoS deposit. Then the tissue was rinsed in insect saline for 5–10 min, fixed in Carnoy's acetic-alcohol fluid, dehydrated in alcohol, cleared in xylene and embedded in Canada balsam. Camera lucida drawings were made of the stained neurons and bundles of fibres in dorso-ventral projection.

3. Physiological Methods. Recordings were made in a quiet room at 20–24 °C using a single hook electrode made from fine tungsten wire. The response of the auditory system to natural sounds and pure tones was monitored by recording the activity of primary auditory fibres in the tympanal nerve. A cicada was pinned ventral side down. The legs, wings and dorsal wall of the thorax were removed to expose the nerves and the metathoracic-abdominal ganglionic complex. After the nerve was lifted on to an electrode, the cut surface of the animal was covered with filter paper moistened in insect saline to prevent the preparation from drying out. An indifferent electrode was put on the abdomen. Better long lasting summed responses with lower thresholds were obtained when a tungsten microelectrode was placed into the acoustic neuropile of the metathoracic neuromere. The electrode resistance was 1–6 MOhm. The response of the nerve or the ganglion and the stimulus applied were registered on tape. Natural continuous song of a male taped in the field at the same temperature as during the experiment and pure-tone pulses of 60 ms duration with rise and decay times of 2.5 ms were used for stimulation. Auditory thresholds in the range 2–20 kHz were judged by monitoring the amplified neural response with headphones and an oscilloscope. The loudspeaker (MSD-100, Japan) was placed 35 cm from the animal on the ipsilateral side. The acoustic field of the preparation was monitored with a B. a. K. condenser microphone (type 4145) placed in the same position (angle of incidence 0°).

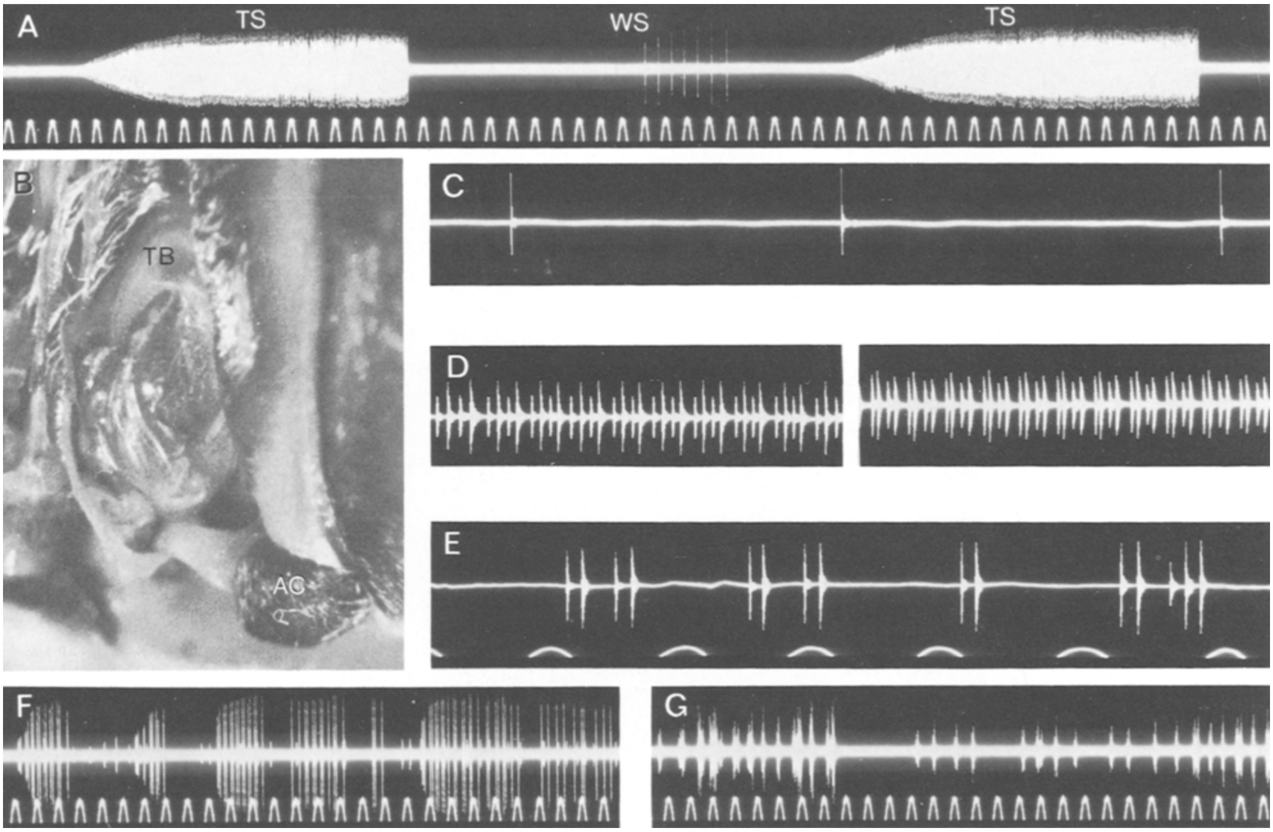

Fig. 1A–G. Sounds produced by *Cicadetta sinuatipennis* males. **A** Part of the spontaneous song. **B** The tymbal. Mean dimensions of a tymbal are: Height –3.0 mm; width –1.4 mm; total area –3.9 mm^2. **C** Part of the wing sound. **D** Part of the tymbal sound recorded from the side (left) or from above (right) the animal. **E** Part of the tymbal sound after ablation of one tymbal. **F** Supposed aggressive song. **G** Supposed courtship song. Calibration on **A**, **F** and **G** –20 Hz; calibration on **C**, **D**, **E** is equal to 100 Hz. *AC* auditory capsule; *TB* tymbal; *TS* and *WS* tymbal and wing sounds

Results

1. Temporal Characteristics of Tymbal and Wing Sounds

Spontaneous singing of *C. sinuatipennis* males in natural conditions was most frequent during the first half of the day, from 9–9.30 to 12–13 o'clock. The song consisted of regularly repeated bursts of tymbal sound (TS) alternating with bursts of wing sound (WS) (Fig. 1A). Some temporal characteristics of the song are presented in Table 1.

Each burst of tymbal sound lasted about 700 ms. During the first part of the burst the sound level rose steadily and then remained constant. The tymbal sound consisted of short (0.3–0.6 ms) pulses rising from inward and outward bucklings of the tymbals. When the sound was recorded from the side of the animal the amplitude of the pulses from each tymbal was different; when recorded from above the animal

Table 1. Temporal characteristics of wing and tymbal sounds in the spontaneous song of *Cicadetta sinuatipennis* Osh. males

	t_1 (ms)	t_2 (ms)	t_3 (ms)	t_4 (ms)	t_5 (ms)	F_{cl} (Hz)	t_6 (ms)	F_t (Hz)	T °C
1	680±20	459±47	1,626±115	151±14.2	31±0.8	32.2	0.79±0.1	322	33
	C=3.7	C=12.5	C=8.5	C=11.3	C=6.7		C=29.9	C=2.3	
	625–712	381–550	1,450–1,800	125–169	27–35		0.48–1.2	303–333	
2	728±22.5	512±6.4	1,650±22.5	181±7.2	31±0.4	32.2	0.93±0.2	278	41
	C=7.8	C=4.6	C=3.3	C=7.9	C=9.6		C=3.3	C=8.0	
	512–775	469–550	1,525–1,725	161–200	27–34		0.6–1.5	232–303	

For each parameter the following data are given: mean value with standard error; variability coefficient ($C=\frac{\sigma \cdot 100}{\bar{x}}$) and limits of variation. Data for 2 males are presented. t_1 tymbal sound duration; t_2 interval between tymbal and wing sounds; t_3 tymbal sound repetition period; t_4 wing sound duration; t_5 repetition period of clicks in the wing sound; t_6 pulse repetition period in the tymbal sound; F_{cl} click repetition frequency in the wing sound; F_t repetition frequency of tymbal action; T °C temperature of air at the position of the animal

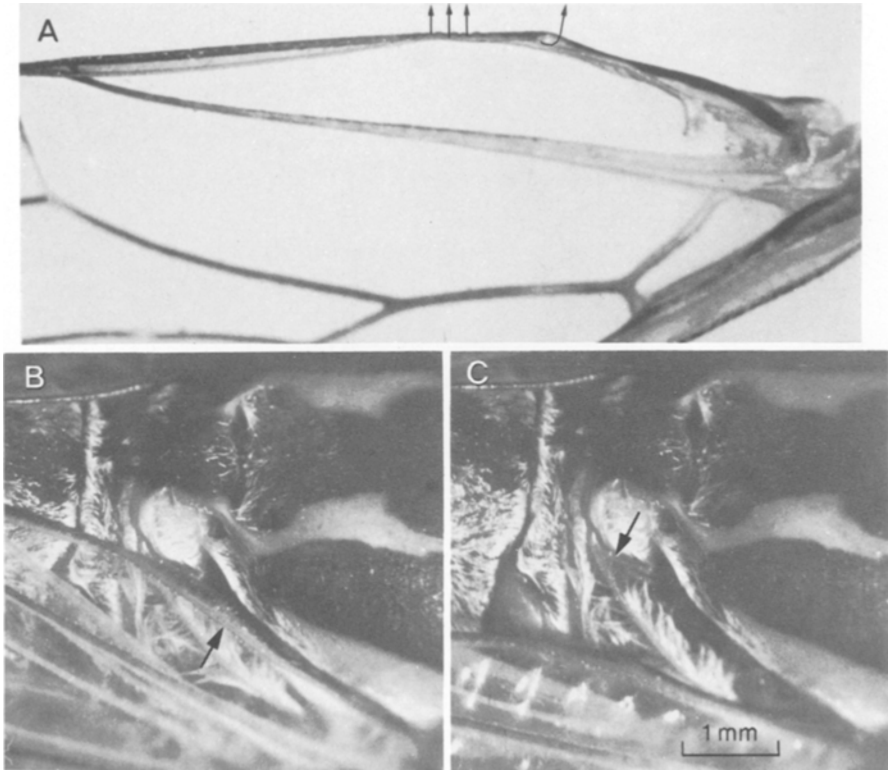

Fig. 2 A–C. Part of a forewing (**A**) and its position before (**B**) and after (**C**) click production. **A** Ventral view of a forewing. The anal edge which is curved ventrally moves outwards (in the direction of arrows) during click production. **B** Forewing in start position. The robust caudal margin marked by an arrow is locked in a wing locking groove. **C** Forewing position after click production. Arrow marks a wing locking groove on the scutellum

the pulses from both tymbals were equal (Fig. 1 D). Experiments in which one tymbal was ablated showed that "in"- and "out"-pulses of each tymbal are nearly equal and follow each other with a period of 1.6–1.7 ms (Fig. 1 E). Such pairs of pulses recurred in natural song with a frequency of about 300/s which corresponds to the frequency of tymbal action. When both tymbals were intact the sequence of sound pulses was as follows 'in'$_1$–'in'$_2$–'out'$_1$–'out'$_2$, i.e., tymbals are working in alternation with phase shift of about 0.8–0.9 ms. The mean pulse repetition frequency in the tymbal sound reached 1,000–1,260/s. The tymbal sound repetition period was a rather stable characteristic of the song.

The tymbals of *C. sinuatipennis* males are similar to those of other species of *Cicadetta* (Popov, 1975). Each has a wide distal field, 2 long and 2 short poorly pigmented and sclerotised ribs (Fig. 1 B).

Each burst of wing sound consisted of 5–7 very short (about 150 μs) clicks following each other with rather stable intervals (Fig. 1 C). Click repetition frequency was similar in the songs of different males and was not temperature dependent, at least in the range of 30–44 °C. The interval between tymbal and wing sounds can either be stable or rather variable in the songs of different males.

Quite often males separated by a few meters produced wing sounds in clear alternation. Such alternation of tymbal sounds was not observed. Sometimes tymbal sound production was absent altogether and

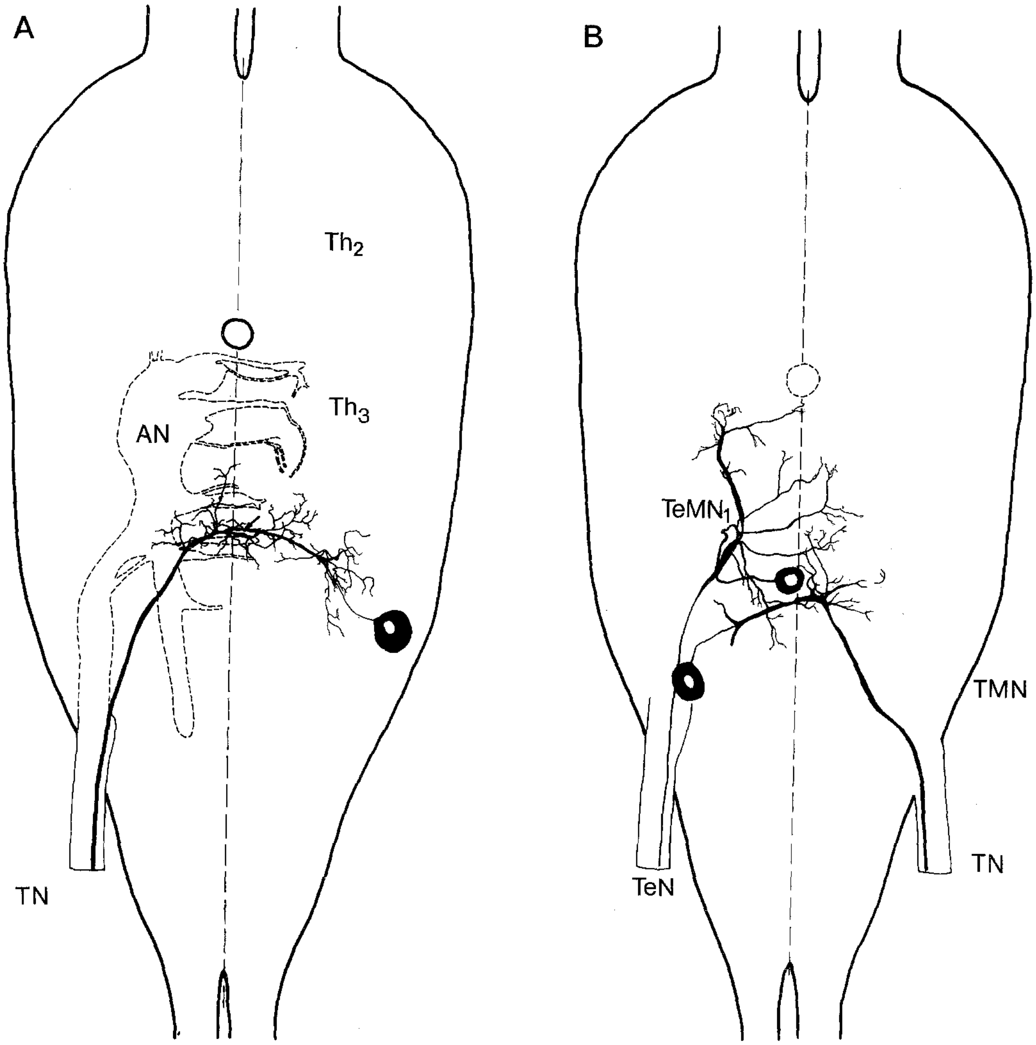

Fig. 3A, B. Efferent neurons with axons in the tympanal (*TN*) and tensor (*TeN*) nerves. **A** Large tymbal motor neuron. **B** One of the tensor motor neurons ($TeMN_1$). *AN* acoustic neuropile (marked by a dashed line). Th_2 and Th_3 meso- and metathoracic neuromeres. *TMN* Large tymbal motor neuron males produced only wing sounds. Wing-clicking in females, characteristic for *Amphipsalta* (Myers, 1929; Dugdale and Flemming 1969), was never observed in *C. sinuatipennis.*

The peak amplitude of tymbal sound at a distance of 15 cm from the animal was about 71–72 dB SPL. The corresponding value for wing sound was always 3–5 dB higher.

When several males and one female were put in a small cage together they produced two other types of sounds which were interpreted as songs of aggression and courtship. Both songs were produced by tymbals only and their amplitude modulation pattern differed greatly from that of the spontaneous song (Fig. 1F, G).

2. *The Mechanism of Wing-Clicking*

During clicking the forewings of the males changed their position from roof-like to nearly parallel to the dorsal surface of the body; they made sudden lateral movements. Similar clicks can be evoked by artificial lateral movement of a forewing held in the same position. Such artificial wing-clicking was easy to evoke only in living, anesthetized or freshly killed males, but not in dry specimens, evidently because of the loss of natural elasticity of the wings. Each lateral jerking of a forewing produced one click just at the moment when the robust caudal margin of the forewing leaves the wing locking groove on the scutellum (Fig. 2B, C). Examination of the forewings during

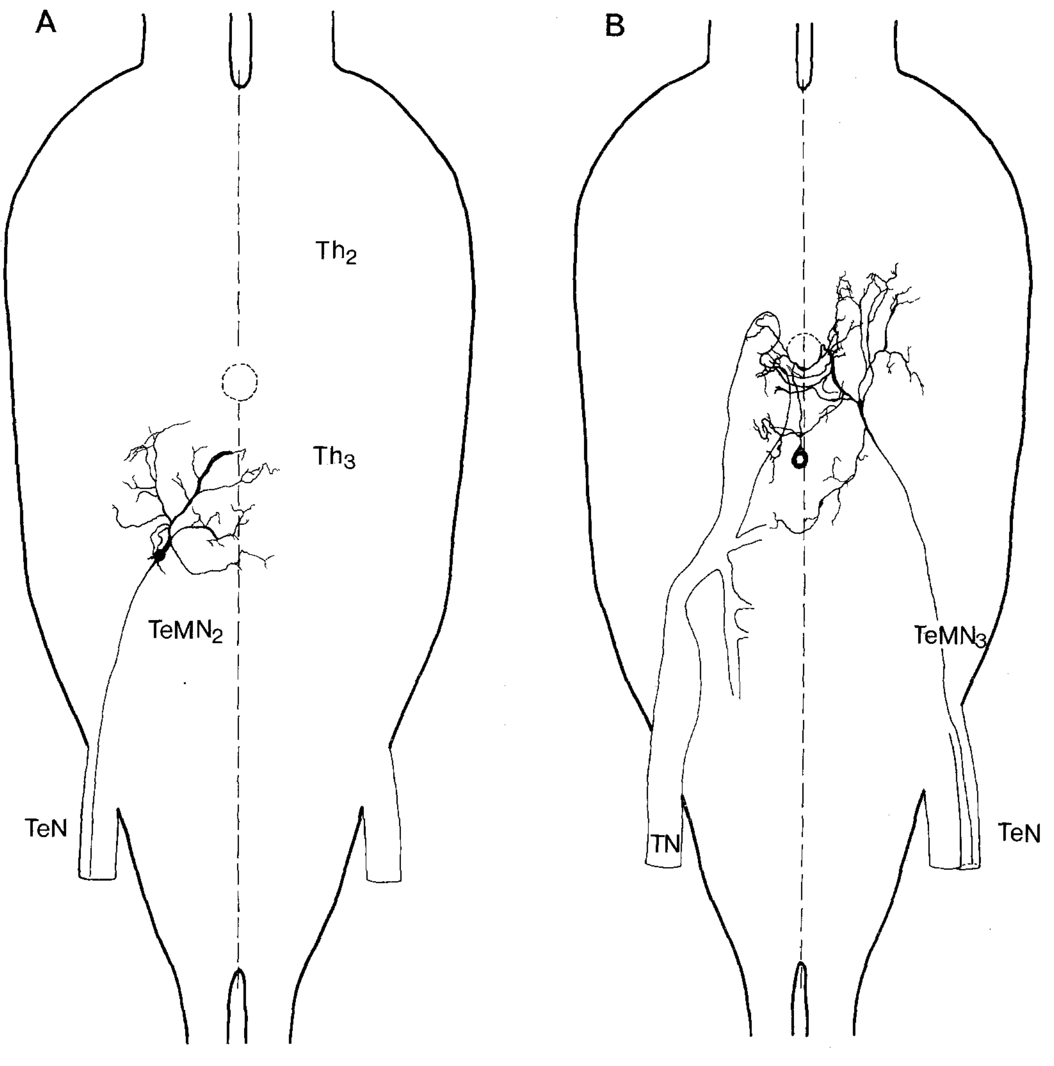

Fig. 4 A, B. Two other efferent motor neurons with axons in the tensor nerve (TeN). **A** $TeMN_2$; **B** $TeMN_3$. Central projection of the tympanal nerve sensory fibres is also shown on **B** (left side). Th_2 and Th_3 meso- and metathoracic neuromeres

artificial click production under the binocular microscope showed that the click is caused by the outward buckling of the basal part of the anal margin of a forewing (marked by arrows in Fig. 2A, B). This part of the caudal margin is curved ventrally and in start position before click production is pressed to the lateral vertical or even inclined medially wall of the wing locking groove. When force was applied moving the wing to the side, the locked anal edge buckled outwards producing a click.

3. *Efferent Neurons with Axons in the Tympanal and Tensor Nerves*

Tymbal and tensor muscles are the main muscles of the tymbal sound-producing organs of cicadas (Pringle 1954). Inward buckling of a tymbal is caused by a twitch contraction of the tymbal muscle. The form of sound pulses produced by a single tymbal is modified by the tensor muscle (for details see Simmons and Young 1978).

In *C. sinuatipennis* the tympanal nerve carries both sensory fibres from the auditory (tympanal) organ and the motor innervation to the tymbal muscle as in many other species studied (Young 1972; Simmons and Young 1978; Wohlers et al. 1979). Several efferent fibres leaving the ganglionic complex via the tympanal nerves were found in *Magicicada* suggesting polyneural innervation of the tymbal muscle at least in this species (Wohlers et al. 1979) contrary to the classic view that this muscle in cicadas is innervated by a single large motor neuron (Pringle 1957; Svidersky 1965; Simmons 1977).

In *C. sinuatipennis* we found only one large motor neuron with the axon in the tympanal nerve the spiking of which coincided in time with tymbal muscle activity. Only one motor neuron was consistently stained in the ganglionic complex through the tympanal nerve, and we interpret it to be the tymbal motor neuron.

The anatomy of the large tymbal motor neuron was described by Simmons (1977) in *Cystosoma saundersii* and by Wohlers et al. (1979) in *Magicicada septendecim*. Our data result from the analysis of 6 successful stainings of this neuron in males of *C. sinuatipennis*. Figure 3A shows a typical branching pattern of this neuron within the ganglionic complex. The large cell body (60–70 µm) is situated close to the lateral border of the ganglion at the level of the roots of the tensor and tympanal nerves. Dendritic branches one found in the ipsilateral, medial and contralateral dorsal regions of the ganglionic complex on the border of abdominal and metathoracic neuromeres. The main process runs ventrally on the cell-body side sending out branches to the dorsal neuropile. Close to the midline of the ganglionic complex the main process turns sharply dorsally (at the point of an arrow, Fig. 3A) then passes across the contralateral side on this level sending out side branches, and continues as an axon into the contralateral tympanal nerve. There is a bilaterally symmetrical pair of such neurons whose main processes come into close contact at the midline of the ganglionic complex. Dendritic fields of these neurons overlap to a large extent. A clear predominance of branching contralateral to the soma, characteristic for homologous neurons of *Magicicada* (Wohlers et al. 1979), was not observed in *C. sinuatipennis*.

The tensor nerve is also a mixed nerve. According to Simmons and Young (1978) in *C. saundersii* it innervates the tensor muscle, the dorsal muscle, the spiracle muscle and a small muscle below the spiracle.

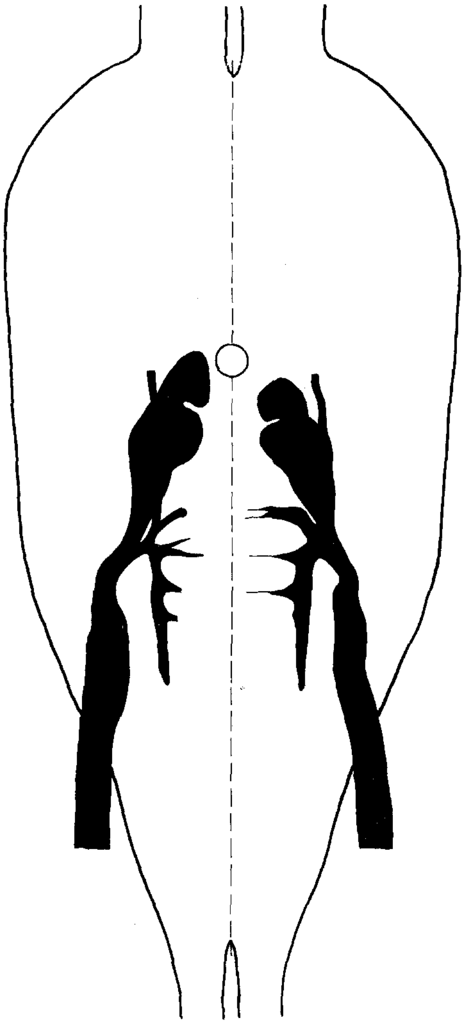

Fig. 5. Central projections of tympanal nerves in the metathoracic-abdominal ganglionic complex

Sensory branches innervate hairs situated close to the insertion point of the tensor muscle, tymbal and tensor chordotonal organs described by Young (1975).

Three motor neurons in the ganglionic complex of *C. sinuatipennis* were stained through the tensor nerve which was cut as close to the tensor muscle as possible. Since in *C. saundersii* the tensor muscle is innervated by 3 axons (Simmons and Young 1978), we believe that our neurons are tensor motor neurons, though additional evidence is desirable. Wohlers et al. (1979) described at least 4 types of motor neurons with axons in the tensor nerve of *Magicicada* but none of them can be homologized with neurons found in *C. sinuatipennis,* either because there are different kinds of motor neurons innervating different kinds of muscles, or because the homologous neurons are very different in different cicadas.

The largest of the three (TeMN$_1$) has a large (50–60 μm) soma situated near the midline of the ganglionic complex on the ventral side (Fig. 3B). A single cell process runs to the dorsal neuropile where it connects to a thick integrating segment and profusely branching dendritic tree. The integrating segment tapers gradually and continues as an axon into the ipsilateral tensor nerve. At least five large dendritic branches are connected to the integrating segment. They terminate in different regions of the dorso-medial neuropile of the metathoracic and first abdominal neuromeres on both sides. Ipsilateral branching clearly predominates over contralateral branching. Two caudal branches come into close contact with the dendritic tree of the large tymbal motor neuron, which was stained through the contralateral tympanal nerve on the same preparation (Fig. 3B).

The second motor neuron (TeMN$_2$) has a small cell body (25–30 μm) positioned also on the ventral side but more laterally (above or slightly behind the projection of its integrating segment) (Fig. 4A). The axon and main dendritic branches are ipsilateral to the soma. The dendritic tree consists of four main branches terminating in the dorso-medial and dorsolateral regions of the ipsilateral metathoracic neuromere. There are only a few contralateral projections. The most caudal branch overlaps with the dendritic tree of the large tymbal motor neuron.

The third motor neuron (TeMN$_3$) has a cell body 40–50 μm in diameter positioned exactly on the midline of the ganglionic complex on the ventral side.

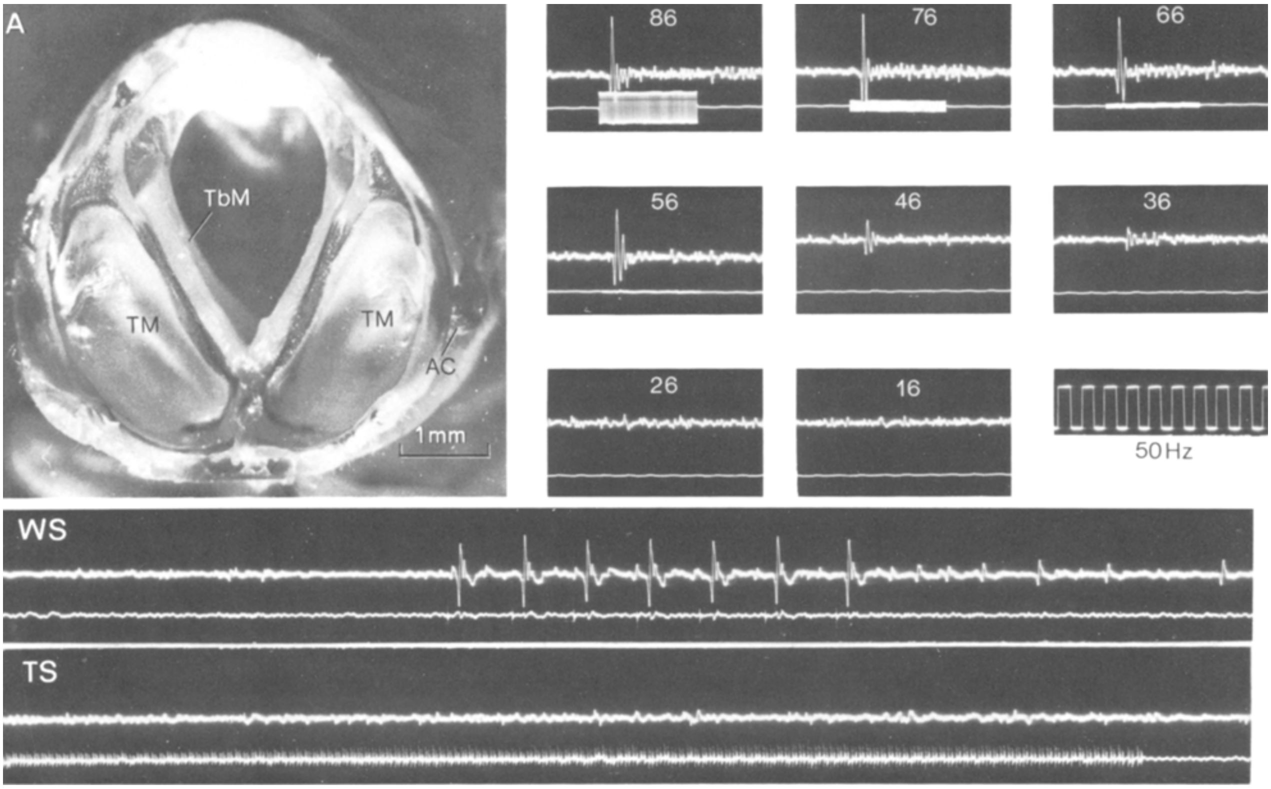

Fig. 6. Tympanal membranes (*A*) and tympanal nerve response to pure tone 6.5 kHz (right oscillograms) and natural sounds (2 lower oscillograms). Intensity of the pure tone in dB SPL is indicated above each oscillogram. *TS* and *WS* tymbal and wing sound stimulation, respectively. Peak intensity of these sounds was 61 and 65 dB SPL, respectively. The response of the nerve is on the first trace, the stimulus on the second trace. *AC* auditory capsule. *TbM* tymbal muscle. *TM* tympanal membrane

A very long cellular process first runs anteriorly to the border between the mesothoracic ganglion and the metathoracic neuromere gradually approaching the dorsal half of the neuropile where it connects to the large dendritic tree (Fig. 4B). All dendritic projections are dorsal. They occupy the medial regions of the mesothoracic and metathoracic neuropiles on both sides. Projections ipsilateral to the axon predominate. The main dendritic branches fuse forming an integrating segment which gradually tapers and continues as an axon into the tensor nerve.

4. *Central Projections of Tympanal Nerve Fibres*

Several sensory structures are innervated by the tympanal nerve in cicadas: the tympanal organ, the detensor tympani-chordotonal organ (Young 1975) and body hairs (Wohlers et al 1979). In order to stain predominantly auditory fibres the tympanal nerve was cut as close to the tympanal organ as possible. Projections thus obtained (Fig. 5) are very similar to those described by Wohlers et al. (1979) in *Magicicada*. They are present in an intermediate neuropile of the metathoracic and several abdominal neuromeres of the ganglionic complex. Metathoracic projections are more dense and are subdivided into three lobes, the intermediate lobe being more extensive. A small bundle of fibres passing more ventrally continues to the mesothoracic ganglion (only partly shown in the figure). Abdominal projections have 2–3 finger-like, thin arborizations to the midline (six such arborizations in *Magicicada* were described by Wohlers et al. 1979). Most sensory projections are strictly ipsilateral. Only few fibres project also to the contralateral side. Such fibres were stained only in one preparation (Fig. 3A).

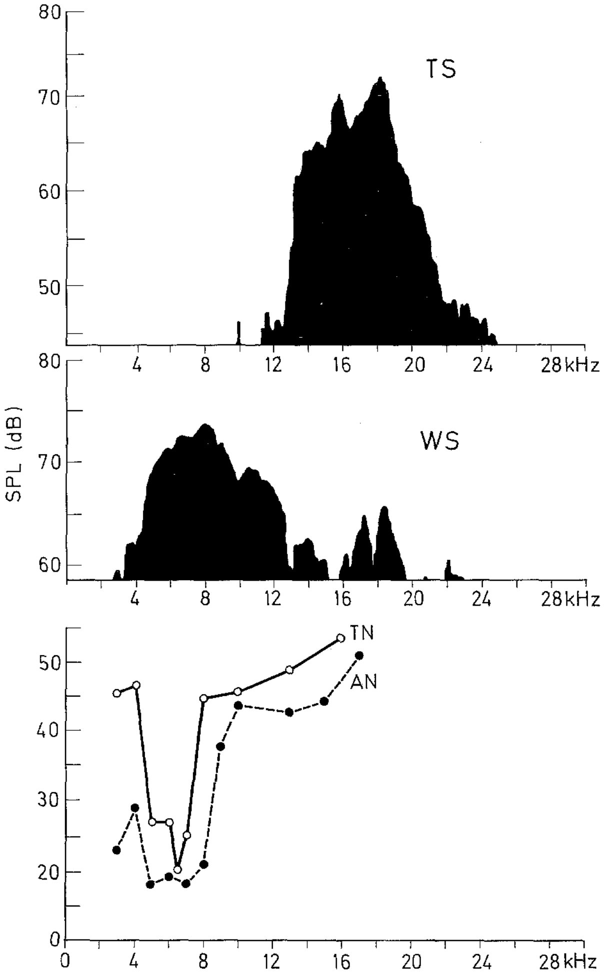

Fig. 7. Spectra of wing (*WS*) and tymbal (*TS*) sounds of the spontaneous song and typical hearing curves of *Cicadetta sinuatipennis* Osh. *AN* and *TN* typical hearing curves obtained by recording the auditory response from the acoustic neuropile in the metathoracic neuromere and from the tympanal nerve to pure tone stimulation. No consistent differences were found between hearing curves of males and females (6 insects of each sex were used). The lowest thresholds at the best frequencies varied in different preparations from 18 dB to 39 dB SPL

5. *Auditory Physiology*

The tympanal nerve response of *C. sinuatipennis* males and females to pure tone pulses contains a large amplitude 'on'-component and little asynchronous activity (Fig. 6). The amplitude of the 'on'-component decreases gradually with decreasing intensity of the signal. When stimulated by the wing sound reproduced from the tape, the auditory fibres give a clear 'on'-response to each click (Fig. 6. WS) down to an intensity level of 21–31 dB (peak value) (the loudspeaker was positioned at a distance of 35 cm from the animal on the ipsilateral side). When stimulated by the tymbal sound of the free song, the response was asynchronous and the threshold was about 70 dB SPL. This is easily understandable if one compares the hearing curves of the auditory organs with the spectra of corresponding sounds (Fig. 7). The tympanal nerve response has a very sharp peak of sensitivity near 6–6.5 kHz in most animals with thresholds of about 20–28 dB SPL. The best frequency varies from animal to animal in the range 5–7 kHz. The hearing curves obtained from recording the auditory response in the acoustic neuropile are wider (optimum 4–6 kHz) and the thresholds are lower (18–25 dB SPL; Fig. 7, a dashed curve on the lower graph). Such a difference was consistent for all preparations.

The spectrum of the tymbal sound ranged from 12 kHz to 25 kHz with clear maxima at frequencies of 15–16 kHz and near 18 kHz (Fig. 7, upper graph).

These frequencies are nearly outside the hearing range of this species. That is why the auditory threshold for this component of the song is so high.

On the contrary, the wing sound spectrum has its maximum at frequencies of 6–8 kHz (Fig. 7, middle graph) to which the auditory organs are well tuned.

Calculations based on a comparison of natural intensity of tymbal and wing sounds with corresponding hearing thresholds show that wing sounds can be perceived by these animals from a distance of at least 30–40 m, whereas tymbal sounds can be effective only at short range (not more than 0.5–1.0 m).

Discussion

The data presented in this paper show that tymbal and wing sounds of cicadas have different functions. At least in *C. sinuatipennis* only wing sounds of males ensure long-range communication between conspecific males and females over a distance greater than 10 meters. All features of wing sounds are well suited for this function. First of all, they have a species-specific amplitude modulation pattern to ensure species recognition. Secondly, they have a relatively high intensity and contain frequencies to which the auditory system of conspecific insects is highly sensitive. Thirdly, they have large transients facilitating localization of a singing male. In the field we easily localized wing-clicking males but had great difficulty in finding males producing only tymbal sounds although our mechanisms of sound localization may be different. The first reaction of a singing male to danger (e.g. an approaching person or other being) is to cease wing-clicking. The tymbal sound production often continues even in cases when a being is close and in the visual field of a male. Descriptions of alternation of wing-clicking of males separated by several meters also support the assumption that this signal is used for long-range communication. Wing-clicking described in *Amphipsalta* (Dugdale and Flemming 1969) may have a similar function.

Tymbal sounds in the spontaneous song of *C. sinuatipennis* males have nearly the same intensity as the wing sounds, but their spectrum is outside the range of maximal sensitivity of the ear. That is why they can be perceived by conspecific insects only at close range (not more than 1 m). Although the envelope of tymbal sound bursts and their repetition frequency are both species-specific and stable, their internal rhythmic structure is lost for cicadas because the pulse repetition frequency is too high to be resolved by their auditory system. That means that this signal has no large transients for cicadas and is perceived by them and by man as a continuous and hardly localizable sound. The tympanal nerve response to tymbal sounds is asynchronous as is the case with continuous tones.

A very similar situation was found in *Cicadatra hyalina* (Popov 1969, 1975). The males of this species spontaneously produce the so called "continuous song" with a spectrum which is outside the optimal range of hearing of conspecific insects.

We suggest that if tymbal sound of the spontaneous song of *C. sinuatipennis* males is used for intraspecific communication, this communication is possible only at short range. Our observations show that when males and a female are placed together in a small cage, other tymbal sounds are produced in aggressive and courtship contexts, and the role played by spontaneous song tymbal sounds for intraspecific communication is uncertain.

It is more likely that spontaneous tymbal sound of *C. sinuatipennis,* as well as the continuous song of *Cicadatra hyalina,* acts as a repellent to bird predators as was suggested by Simmons et al. (1971) for *Magicicada* although additional field work is necessary to test this hypothesis.

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