ASYMMETRY OF TYMBAL ACTION AND STRUCTURE IN A CICADA: A POSSIBLE ROLE IN THE PRODUCTION OF COMPLEX SONGS

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Summary

The type 1 echeme of the song of the small European cicada *Tympanistalna gastrica* consists of a pair of loud IN–OUT pulses followed by a train of soft IN–OUT pulses. In all nine insects investigated, the right and left tymbals buckled inwards and outwards alternately, but the echeme started with the buckling of the right tymbal. Both the inward and the outward buckling movements produced single discrete sound pulses.

The loud IN pulses were produced with the tymbal tensor muscle relaxed. They were approximately 10 dB louder than the loud OUT pulses and than the soft IN and OUT pulses. The period between the right loud IN and OUT pulses (3.75±0.31 ms) (mean ± S.D.) was significantly shorter than between the left loud IN and OUT pulses (4.09±0.28 ms). The period between the loud IN and OUT pulses was significantly shorter than the period between the soft IN and OUT pulses, which was similar on both sides (mean for the right tymbal 5.54±0.20 ms, mean for the left tymbal 5.30±0.51 ms).

Measured at the tymbal, the power spectrum of the right loud IN pulses showed major components between 4 and 8 kHz as well as around 11.7 kHz. That of the left loud IN pulse had approximately 10 dB less power at 4 kHz and similar power at 7–8 kHz, with a further louder peak at around 10.8 kHz. The loud OUT pulses and all subsequent IN and OUT soft pulses showed very little power at 4 and 8 kHz, but all showed a spectral peak at approximately 13 kHz. The soft OUT pulses had similar pulse envelopes to the preceding IN pulses, which they closely mirrored.

Measured at the fourth abdominal sternite, only the right loud IN pulse produced peak power at 4 kHz. The transfer function between the tymbal sound and that at sternite 4 was maximal at 4 kHz for the right loud IN pulse and showed a peak at this frequency for both loud and soft IN and OUT pulses. The 4 kHz components of all pulses, and particularly that of the right loud IN pulse, which has the loudest 4 kHz component, excited sympathetic sound radiation from the abdominal sternite region.

Measured at the tympanal opercula, both loud IN pulses produced peaks at 7–8 kHz of similar power. The transfer functions between the tymbal sound and that at the tympanal opercula showed peaks of power at this frequency range for both loud and soft IN and OUT pulses, suggesting that this component excites sympathetic radiation *via* the tympana.

Components of the sound pulses produced by one tymbal are also transmitted *via* the contralateral tymbal. The pulses transmitted during both loud IN pulses had ragged envelopes, but the soft IN pulses and all OUT pulses were transmitted as clean coherent pulses with slow build-up and slow decay, suggesting that the ipsilateral tymbal excited a sympathetic resonance in the contralateral one.

The tymbals of *T. gastrica* have two unusual features. At the dorsal end of rib 2, there is a horizontal bar that extends anteriorly over rib 3 and posteriorly over rib 1 to the dorsal end of the tymbal plate. This bar appears to couple the three ribs so that they buckle in unison. The resilin sheet at the ventral ends of ribs 1, 2 and 3 was significantly wider, dorso-ventrally, in the right tymbal than in the left in eight insects that were measured (mean right-to-left ratio, 1.37).

The asymmetry between the right and left loud IN pulses correlates with the morphological asymmetry of the tymbals. The complexities of the song in *T. gastrica* appear to result from the preferential excitation of sound radiation from the abdomen surface or *via* the tympana by components of the distinct pulses produced by the asymmetrical tymbals and from the tymbals themselves.

Moribund or fatigued insects were successively unable to produce the right loud pulse and then the left loud pulse. The complex song may in this way act as an honest signal of male fitness.

Key words: cicada, *Tympanistalna gastrica,* sound radiation, asymmetry, complex songs, tymbal.

Introduction

The calling songs of male cicadas are species-specific, with a wide variety of sound patterns. In some species the songs are tonally pure, with a relatively simple modulation pattern, while in others the songs have more or less complex, but still stereotyped, patterns with rapid amplitude and/or frequency modulation (e.g. Pringle, 1954; Popov, 1990; Fonseca, 1991). Such contrasts may be seen by comparing the songs of the Australian cicada *Cyclochila australasiae* with those of the Portuguese cicada *Tympanistalna gastrica.*

In *C. australasiae*, the sound power in the song is centred in a narrow band at 4.3 kHz, with components at other frequencies at least 30 dB quieter (or at less than 1/1000th of the power) and the song has a simple and constant modulation pattern at 230 pulses s^{-1} (Young, 1990). The primary sound-producing mechanism is the paired tymbals, which buckle to produce one or several clicks (this is a general feature of cicada sound production, see Pringle, 1954), but the sound in this species is largely radiated through the thin acoustically transparent tympana. The large internal sound pressures produced by the inward buckling of the tymbals excite a Helmholtz-type resonance in the abdominal air sac, opening *via* the tympana, to produce the pure-tone song of this species (Bennet-Clark and Young, 1992; Young and Bennet-Clark, 1995). In addition, the outward buckling of the tymbal of this species is almost silent, partly because it produces sounds at approximately 6 kHz, which are not well radiated by the abdominal air sac resonator (Young and Bennet-Clark, 1995) and also because the energy released by the outward buckling of the tymbal is far less than that released during the noisy inward buckling (Bennet-Clark, 1997).

The song of *T. gastrica* is more complex (Fonseca, 1994, 1996; Fonseca and Popov, 1994). The type 1 echemes of the calling song (Fonseca and Popov, 1994) start with a pair of loud IN–OUT pulses of both tymbals followed by a train of soft IN–OUT pulses from both tymbals; there are important differences between the loud and the soft pulses. In the loud pulses, there are major components at between 4 and 5 kHz and at 7–8 kHz, but these components are 6–15 dB quieter relative to the peak power at approximately 11 kHz. In the succeeding soft pulses, the spectral peak occurs at 12–13 kHz and the pulses contain much less energy at lower frequencies (Fonseca and Popov, 1994).

The basic song modulation into loud and soft pulses is controlled by the action of the tymbal tensor muscle (Fonseca and Hennig, 1996). The tensor muscle is inactive and the unbuckled tymbal is more convex at the start of the type 1 echeme when the pair of loud pulses is produced. The subsequent train of soft pulses is produced after activation of the tensor muscle, which causes flattening of the tymbal. In this condition, the force required to buckle the tymbal is reduced and the sound that is produced is softer (Fonseca and Hennig, 1996).

The 11–13 kHz component of the song of *T. gastrica* is radiated mainly from the tymbals but the 4–5 kHz and 7–8 kHz components, which are major components of the loud pulses are, from measurements with probe microphones, radiated mainly from, respectively, the ventral and lateral parts of the abdomen or *via* the tympana. Damping the sound radiation from these regions of the abdomen dramatically reduces the sound radiation at these frequencies (Fonseca and Popov, 1994).

Since Fonseca and Popov (1994) have shown that the sound production of *T. gastrica* does not fit the model of cicada sound production proposed by Bennet-Clark and Young (1992) and because earlier work with *T. gastrica* does not explain the very different character of the various components of the song, we have re-examined the role of the different elements of the sound-radiating system to try to relate them to the different components of the song. We also attempt to explain the differences between the complex song of *T. gastrica* and the far simpler song of *C. australasiae*.

Materials and methods

Males of *Tympanistalna gastrica* Stål were collected at Albarraque, near Lisbon, Portugal, in July 1995. Insects were subsequently kept on twigs of *Quercus coccifera* in net bags at 5–10 °C. Out of 11 insects kept thus, only one insect died during the subsequent 10 days and another individual did not sing normally when used for experimental work. *T. gastrica* is a small cicada: the body length of the males from the vertex to the tip of the abdomen is 15.3±0.6 mm (mean ± S.D., *N*=8).

Physiological preparations

Animals were prepared for experiments by removing both pairs of wings and all the legs at the coxo-trochanteral articulation. Insects were attached by insect wax on the pro- and mesonotum to a 3 mm brass rod and were then held during experiments with the ventral surface upwards (Fig. 1A).

Singing was induced by pulsed electrical stimulation of the brain *via* a pair of 0.1 mm diameter stainless-steel insect pins inserted laterally in the vertex close to the internal edge of the compound eyes (Fig. 1A), using a 1 ms stimulus of 5–10 V at 30–50 Hz. This stimulus induces several apparently normal echemes of type 1 song (Fonseca and Hennig, 1996).

In some insects, the tymbal muscles were stimulated *via* the auditory nerves, which were exposed by ventral dissection. The auditory nerves were hooked with 50 μm silver wire electrodes and stimulated using single 5 V, 1 ms pulses at 1–3 Hz from a Phipps & Bird Inc. stimulator (model 611) *via* a Grass stimulus isolation unit (type SIU5).

Anatomical preparations

Tymbals were prepared by cutting them from the surrounding cuticle and then dissecting the muscle and other tissues away from the inside surface under water. Prepared tymbals were stained for resilin (Weis-Fogh, 1960; Andersen and Weis-Fogh, 1964) using a very dilute solution of Methylene Blue for 12–24 h at 4 °C to stain the resilin brilliant sapphire-blue (the same method was used by Young and Bennet-Clark, 1995). Scale drawings were made using a Carl
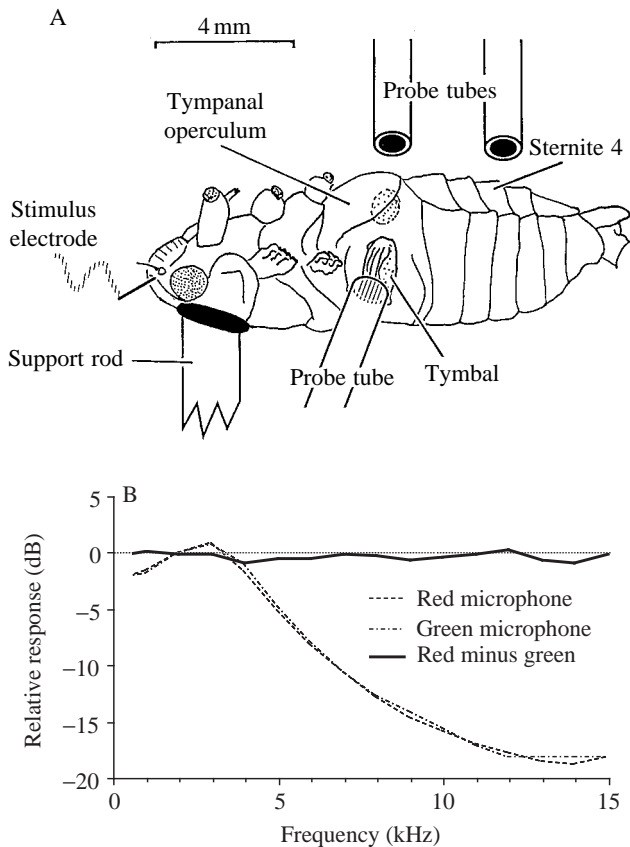
Fig. 1. (A) View of the right side of the body of a male *Tympanistalna gastrica* to show the method of preparation for acoustic measurements. After removal of wings and legs, the insect was waxed onto a support rod with its ventral surface upwards. The drawing shows the tips of the probe microphones in three positions: 1 mm from the tymbal surface, 1 mm from the surface of the tympanal opercula and 1 mm from the fourth abdominal sternite. (B) Graphs of the frequency responses of the probe microphones, colour-coded red (– – – –) and green (– · – · –) relative to their responses at 2 kHz, calibrated in a closed field against a Bruel and Kjaer type 4134 microphone. The difference between the frequency responses of the two microphones is also plotted (——).

Zeiss *camera lucida* and a Carl Zeiss monocular microscope with 6.3× objective.

Measurements of tymbals were made using a Zeiss a* objective or a Watson ×3 objective and a Malies Curtain Micrometer Eyepiece. These combinations allowed tymbal height and width to be measured to ±5 μm and the width of the ventral strip of resilin to be measured to ±2 μm.

Probe microphones

A pair of probe microphones (similar to that described in Young and Bennet-Clark, 1995) were constructed using Realistic Electret Tie Clip Microphones (Tandy catalogue 33-1052). The probe tubes were 5 mm long with 1.25 mm external and 0.8 mm internal diameter. The microphones were mounted on micromanipulators. The microphones gave matched responses within ±0.6 dB from 500 Hz to 15 kHz (Fig. 1B) and

with less than 2 μs time difference. The polarity of the microphones was such that rarefaction in the sound wave gave a positive-going voltage.

The two microphones were colour-coded red and green. Normally, the red microphone was placed on the left side of the insect and the green on its right. Tests in which the red microphone was used to record first from the left and then from the right side of a singing insect (and with the green first on the right and then on the left) showed that the spectra they produced were matched to within 1 dB from 2 kHz to 15 kHz.

The tips of the probe microphones were placed at a distance of 1 mm from the following structures: the left tymbal, the right tymbal, the fourth abdominal sternite at the mid line, and the external opening of the extra-tympanal cavity, at the mid-line closely behind the opercula (recordings from the latter are termed sound from the tympanum in Figs 6, 7). We also obtained measurements with the probe microphone at the mid dorsal surface of the abdomen and posterior to the animal, but only present data from the first-listed positions as they were shown previously by Fonseca and Popov (1994) to be the most important for sound radiation. In a typical experiment, the pair of sounds were measured with a probe microphone at the left tymbal, while the other microphone was placed successively at the other regions. The second microphone was then placed at the right tymbal, while the first microphone was placed successively at the other regions. At these close ranges, the sound records were dominated by radiation from the part of the body against which the microphone was placed (this was also shown by Fonseca and Popov, 1994).

The frequency response of one probe microphone was measured by calculating the transfer function, using a 1/4 inch B&K microphone (type 4135) and B&K preamplifier (type 2639T) as a reference. The transfer function was averaged 25 times and the coherence function of the measurements was found to be close to 1.0 in the frequency range from 500 Hz to more than 15 kHz. The sound signal exciting the probe and reference microphones at the same point (to within 1 mm), in a nearly free sound field in the frequency range used in this study, consisted of a noise pulse created as a file in a computer and down-loaded from the computer using the D/A section of a data translation board at a rate of 100 kHz. This noise pulse was delivered through a Dynaudio D28-2 loudspeaker; the frequency response of the amplifier and loudspeaker was measured and found to be within 15 dB from 500 Hz to more than 30 kHz (below 500 Hz, the values obtained have been disregarded because they were not reliable). The frequency response of the probe microphone was then used to correct the spectra shown in Figs 3, 5, 6 and 7.

Signal recording and analysis

Electrical signals were recorded on two channels of a TEAC RD-120TE DAT data recorder, which gave a flat frequency response ±1 dB from d.c. to 20 kHz. We also made checks with simultaneous 5 kHz square-wave inputs and with single-cycle 10 kHz tone bursts with gaps of 20–100 μs to establish that the DAT recorder reproduced these with amplitude matching

Fig. 2. Oscillograms showing the structure of the type 1 echeme of the calling song of *Tympanistalna gastriaca*. (A) A complete echeme of the song to show the normal sequence as recorded 20 cm away from the insect. A pair of loud IN and OUT pulses is followed by a long train consisting of a variable number of soft IN and OUT pulses. (B) A detail of the start of a type 1 echeme, measured with two probe microphones placed (upper trace) 1 mm from the right tymbal and (lower trace) 1 mm from the left tymbal. The first loud and soft IN pulses in the sequence are produced by the right tymbal. Each tymbal produces a sound pulse as it buckles inwards (IN) and then when it buckles outwards (OUT). The records also show the sound that is transmitted to and radiated by the contralateral tymbal (tr) (see also Fig. 9).
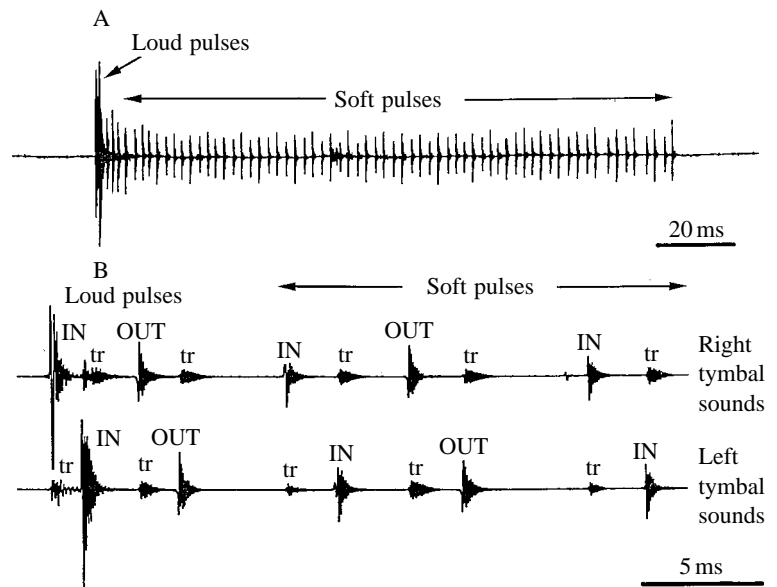
better than ±0.5 dB and interchannel phase matching better than 5 μs. During experiments, signals were monitored on a Kikusui 2 beam oscilloscope type COS 5020.

Records were digitised using a Data Translation DT 2821-F-8DI 12-bit analogue-to-digital converter at 160 kilosamples per second. On one channel, this allows a bandwidth of 80 kHz and a time resolution of ±6 μs, or 40 kHz bandwidth and ±12 μs resolution when the input is multiplexed to give two-channel conversion. The instantaneous frequency of single cycles of the sound pulses was measured from printed records of oscillograms (similar to those shown as insets in Fig. 3). The 160 kHz sampling rate allows frequency resolution of the period of a single cycle to ±3 μs which, at 10 kHz (with 100 μs period), is equivalent to ±300 Hz. The frequency resolution becomes proportionately higher over longer sampling periods. The digital signals were analysed using a purpose-built signal analyser and software written for a personal computer. The analyser produced oscillograms from which instantaneous time and amplitude could be measured to the limits of resolution of the A/D converter as well as frequency spectra by fast-Fourier transform (FFT) with a dynamic range of up to 72 dB.

Relative amplitude and phase of the sounds produced by different parts of the insect were obtained by calculating the transfer functions using standard FFT methods. The transfer function, also referred to as the frequency response function of a system, is the ratio of a system's output to its input. The result is a spectrum that shows both the magnitude and the phase components as a function of frequency. We calculated the transfer function as follows. The signal recorded by one probe microphone close to the tymbal, considered to be the system's input (exciter or source), was compared with the signal simultaneously recorded as the output of the second probe microphone, which was placed close to each one of the structures studied (excited). The transfer function was then calculated as the ratio from the cross-spectrum of both signals to the power spectrum of the signal recorded close to the tymbal

(source or exciter). Since the transfer functions were calculated using the signals recorded by two microphones that were closely matched in amplitude and phase, the transfer functions give absolute values and do not need further corrections.

The significance of the phase measurements is as follows. Far below the resonant frequency of a simple driven resonant system, the phases of the driving and driven vibrations are closely similar. At the resonant frequency of the driven system, its response lags the driving waveform by 90°, and the amplitude of the response is maximal. Far above the resonant frequency of the driven system, the response decays rapidly, and the phase lag of the response with respect to the driving vibration increases towards 180°. Thus, the measurement of the relative phase of two waveforms can give a simple qualitative indication of the relationship between the drive to a system and its response (Morse, 1948).

The Q factor, which is a measure of the sharpness of tuning of resonances, was calculated from the rate of decay of the sound pulses. For methods of calculating Q, see Morse (1948) or Bennet-Clark and Young (1992).

Terminology

The song component studied here has, in previous work on *T. gastrica*, been termed the type 1 echeme (e.g. Fonseca, 1996). Echeme has been defined by Broughton (1976) and it is used throughout this paper, following previous usage on the song of this species. A complete type 1 echeme is illustrated in Fig. 2A.

The two types of sound pulse in the type 1 song echeme (Fig. 2) are termed loud and soft, following Fonseca and Popov (1994). The inward tymbal buckling movement, brought about by the contraction of the ipsilateral tymbal muscle, is termed inward, and the pulse of sound that this buckling produces is termed the IN pulse. The outward buckling movement of the tymbal that follows tymbal muscle relaxation is termed outward, and the pulse of sound that this buckling produces is

termed the OUT pulse. We also distinguish the first IN pulse of an echeme from the second IN pulse, etc., and the side of the animal (right or left) from which the sound pulse was produced.

Values are presented as means ± S.D.

Results

The song pattern

A type 1 echeme of the calling song of *T. gastrica* starts with a pair of loud IN–OUT pulses followed by a train of a variable number of soft IN–OUT pulses (Fonseca, 1996) (Fig. 2A). The peak amplitudes of the loud IN pulses were typically 8–12 dB louder than those of the soft pulses (and see Fonseca and Hennig, 1996). The separate loud IN pulses were produced by contraction of one tymbal muscle causing the inward buckling of the the ipsilateral tymbal, closely followed by contraction of the contralateral tymbal muscle causing the inward buckling of the contralateral tymbal to produce a second loud IN pulse. Relaxation of the tymbal muscles, allowing the tymbals to buckle outwards in the same sequence, produced a pair of loud OUT pulses with a peak amplitude approximately 12 dB below that of the preceding IN pulse of the same tymbal (Fig. 2B) and similar in amplitude to the soft IN and OUT pulses (see Fonseca and Hennig, 1996).

In all of our nine animals, examined with a probe microphone placed adjacent to each tymbal, the first loud pulse was produced by the right tymbal (Fig. 2B). In most songs, the sequence of pulses was right IN, left IN, right OUT, left OUT, but in a few song sequences the loud IN pulses of both tymbals occurred almost simultaneously.

The soft pulses followed in the same sequence, with the right tymbal movements preceding those of the left tymbal and with both inward and outward buckling of the tymbals producing sound pulses (Fig. 2B). The amplitude of the soft IN pulses was similar to that of the soft OUT pulses (Fig. 2, see also Fig. 9B), in contrast to marked IN–OUT asymmetry in the loud pulses (Fig. 2B, see also Fig. 9A).

There was also asymmetry in the time that elapsed between the IN and OUT pulses produced by the two tymbals (Table 1). The time between the loud IN and OUT pulses of the right (first) tymbal (3.75±0.31 ms) was significantly shorter than that between the loud IN and OUT pulses of the left (second) tymbal (approximately 4.09±0.28 ms). The time between the soft left and right IN and OUT pulses, although slightly asymmetrical, did not differ significantly. The time between the soft IN and OUT pulses was 30–50 % longer than the IN–OUT time of the loud pulses. The significance of these asymmetries and differences is discussed below.

On occasion, particularly at the end of a long run of experiments, animals failed to produce normal song. These abnormal animals failed to produce first the loud right IN pulse and then the left loud IN pulse, even though they were able to contract the tymbal tensor muscle and to produce trains of soft pulses.

Table 1. *Time between the start of IN and OUT pulses for the song of* Tympanistalna gastrica, *measured as means of five pairs of pulses from each of six insects*

	Song type		
	Right pulse	Left pulse	Ratio (left/right)
IN-to-OUT time for loud pulses (ms)	3.75±0.31	4.09±0.275	1.10
IN-to-OUT time for soft pulses (ms)	5.54±0.20	5.30±0.51	0.95

Values are means ± S.D.

Significant differences between the IN-to-OUT times for the different types of pulse are as follows (Student's *t*-test): right loud to left loud, $P=0.01$; right loud to right soft, $P=0.0002$; right loud to left soft, $P=0.0002$; left loud to right soft, $P=0.0002$; left loud to left soft, $P=0.01$; right soft to left soft, not significant ($P=0.26$).

### *Sound radiation from the tymbals during the loud pulses*

The waveform of the loud IN pulses recorded at the tymbal had a stereotyped pattern (Fig. 3A,C, insets). The first half-cycle was a large initial rarefaction (shown here as a positive voltage) followed by a larger compression half-cycle, after which the amplitude decayed more or less exponentially. This implies that initially there was a large-amplitude inward movement of the tymbal, followed by a larger outward rebound leading to a damped vibration. The waveforms of the OUT pulses followed the inverse pattern of a compression followed by somewhat larger rarefaction, etc. (Fig. 3B,D, insets). Sound pulses with similar changes in amplitude with time have been described for the tymbal clicks of *C. australasiae* (Bennet-Clark, 1997).

The sound produced by the loud right IN pulse that starts the echeme has a different waveform from that produced by the succeeding loud left IN pulse. This can be seen both in oscillograms of the two pulses and in their frequency spectra (Fig. 3A,C). A plot of the instantaneous frequency during typical left loud and right loud IN pulses from one insect shows that the first cycles of both pulses, during the build-up of the sound pulse, are at a lower frequency than are the later parts of the pulse, in which the amplitude decays (Fig. 4). The instantaneous frequency of the right loud IN pulse rose from about 5 kHz during the first cycle to 10 kHz during the second cycle and reached a steady value of between 11 and 13 kHz during the decay of the sound pulse. The instantaneous frequency of the left loud IN pulse increased from approximately 8–9 kHz during the first cycle to 10–11 kHz during the second cycle to reach a steady value of between 11 and 13 kHz during the decay of the sound pulse. Similar patterns were found in four other insects.

From the insets in Fig. 3A,C, it can be seen that the pulse amplitude increases during the first cycle and thereafter decays approximately exponentially, especially in the pulse from the left tymbal. A plot of the instantaneous power (calculated as the square of the pulse amplitude) in the right and left loud IN

Fig. 3. Oscillograms (insets) and power spectra (main graphs) of loud pulses recorded 1 mm from the outer surface of the tymbal. All graphs show the averaged power spectrum for four pulses from one insect. Insets show oscillograms of the waveform of one of the sound pulses used in each case. The arrows show (in italic type) the spectral peaks corresponding to the frequency during the decay of the waveform in kHz. The symbols show the positions of the 4 kHz (*), the 7 kHz (◇) and the 11–13 kHz (●) peaks (see also Figs 6, 7). (A) Right loud IN pulse. (B) Right loud OUT pulse. (C) Left loud IN pulse. (D) Left loud OUT pulse.
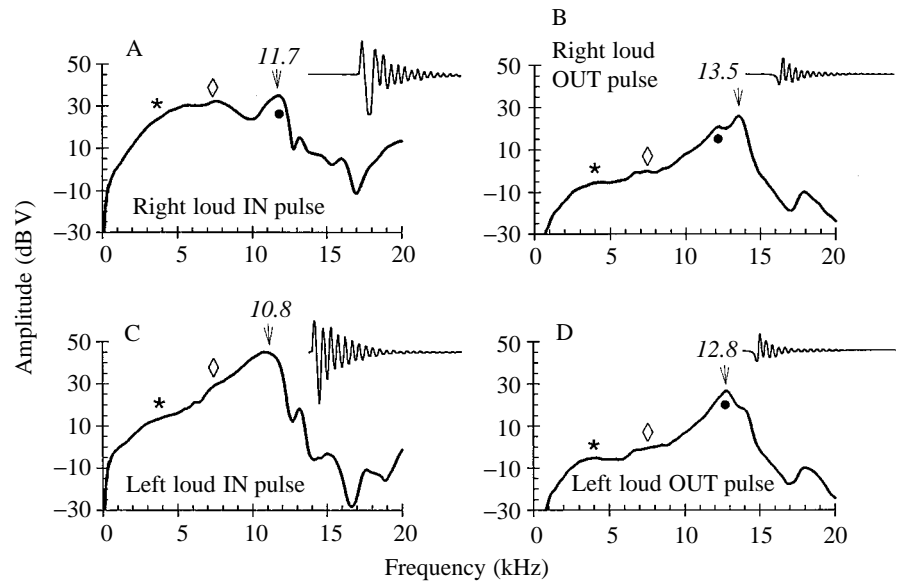
pulses (Fig. 4), shows that approximately half the total sound power was produced during the first 1–1.5 cycles of the pulse, while the pulse amplitude was building up and as it began to decay.

The power spectra (Fig. 3A,B) and instantaneous frequency and power graphs (Fig. 4) show that the right loud IN pulse provides broad-band sound power between 4 and 8 kHz and a further peak at 11.7 kHz, whereas the left loud IN pulse provides approximately 10 dB less power than the right IN pulse at 4 kHz, similar power at 8 kHz but a broad-band louder peak at approximately 10.8 kHz.

The amplitude of the loud OUT pulses is largest in the first cycle and is followed by an approximately exponential decay (Fig. 3B,D). The major sound power is radiated between 12.5 kHz and 14 kHz (Fig. 3B,D) for both tymbals. The spectra of the sound produced by the right and left tymbals do not differ as markedly as in the IN pulses and there is very little sound power below 10 kHz.

When the tymbal muscles were stimulated directly (see Materials and methods), both the right and left tymbals could

be made to produce a train of IN and OUT loud pulses. For each pulse, the spectra did not differ in amplitude by more than 1 dB from those produced by the same animal after stimulation of the brain. Thus, the differences between the left and right loud IN pulses do not result from the order of contraction of the tymbal muscles, from distortion of the abdominal cuticle or from residual stress in the contralateral tymbal muscle.

Sound radiation from the tymbals during the soft pulses

All soft pulses recorded from the ipsilateral tymbal had similar waveforms, both in terms of initial amplitude and in terms of the rate of decay of the pulse, but those of the OUT pulses were inversions of the preceding IN pulses (Figs 2B, 5, insets). In contrast to the loud IN pulses, and particularly to the right loud IN pulse, there was little energy below 10 kHz but there was a single relatively sharp peak at approximately 13 kHz for all four types of soft pulse (Fig. 5) and their spectra were closely similar. Thus, the major right:left asymmetry seen in the loud pulses was not found in the soft pulses.
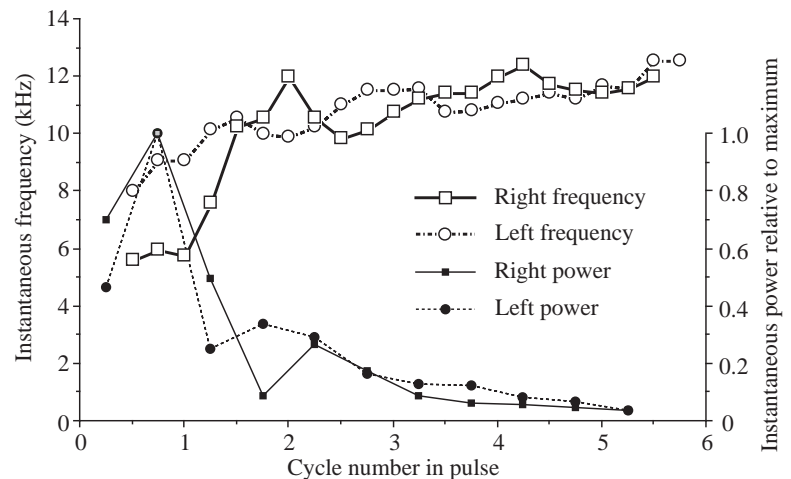

Fig. 4. Instantaneous frequency and power (calculated as the square of amplitude) *versus* cycle number for single right and left loud IN pulses from the same insect.

Fig. 5. Oscillograms (insets) and power spectra (main graphs) of soft pulses recorded 1 mm from the outer surface of the tymbal. All graphs show the averaged power spectrum for four pulses from one insect. Insets show oscillograms of the waveform of one of the sound pulses used in each case. The arrows show the frequency of peak energy of the pulse in kHz (value is shown in italics). (A) Right soft IN pulse. (B) Right soft OUT pulse. (C) Left soft IN pulse. (D) Left soft OUT pulse.
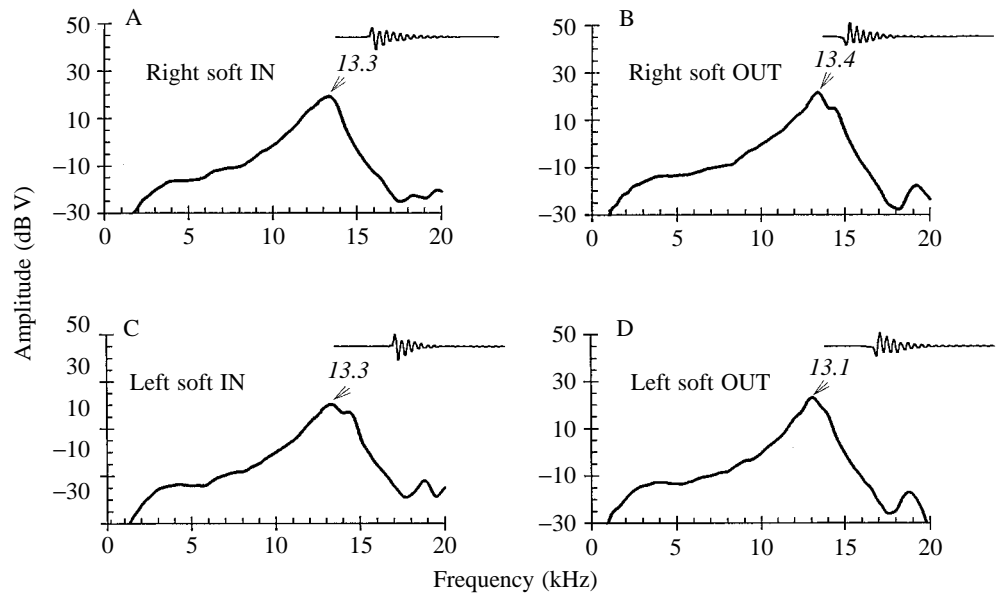
Sound radiation from sternite 4 and via *the tympana*

The sounds radiated from the ventral surface of the abdomen, measured using a probe microphone placed on the mid-line, 1 mm away from sternite 4, reflected the asymmetry of the loud tymbal sounds. Measured at sternite 4, the right loud IN pulse contained discrete energy peaks at approximately 4 kHz, at 7–8 kHz and at 11–13 kHz (Fig. 6A). The 4 kHz peak of the left loud IN pulse was more than 20 dB quieter than that from the right loud IN pulse and there was broad-band radiation between 7 and 11 kHz in the left loud IN pulse (Fig. 6B).

The sounds radiated *via* the tympana, measured using a probe microphone placed on the mid-line, 1 mm away from the posterior edge of the opercula, also showed right *versus* left asymmetry in the sound patterns. The right loud IN pulse had spectral peaks at 4 kHz, at 7–8 kHz and at 11–13 kHz (Fig. 6C),

but their relative amplitudes varied relative to those at sternite 4: the amplitude of the 4 kHz peak was approximately 20 dB less than that from sternite 4 but the 7–8 kHz peak was similar in amplitude (compare Fig. 6A and 6C). The power spectrum and oscillogram of the waveform measured close to the tympana for left loud IN pulses were similar to those recorded from sternite 4, but the 4 kHz peak was approximately 6 dB lower and the energy at 7–8 kHz was slightly higher (compare Fig. 6B and 6D).

The sounds radiated *via* sternite 4 and the tympana during the loud OUT pulses showed far less left *versus* right asymmetry than those produced by the loud IN pulses (Fig. 7). The sounds radiated *via* sternite 4 still had a peak at 4 kHz (Fig. 7A,B), but the sounds radiated *via* the tympana had a minimum at 4 kHz (Figs 7C,D). All records had peaks at between 11 and

Fig. 6. Oscillograms (insets) and power spectra (main graphs) of loud IN pulses recorded at two points on the surface of the abdomen. Measurements were made at 1 mm distance from either the centre of sternite 4 or the tympanal opercula. All graphs show the averaged power spectrum for four pulses from one insect. Insets show an oscillogram of the waveform of one of the pulses used in each case. The symbols show the positions of the 4 kHz (*), the 7–8 kHz (◇) and the 11–13 kHz (●) peaks also highlighted in Fig. 3. (A) Right loud IN pulse at sternite 4. (B) Left loud IN pulse at sternite 4. (C) Right loud IN pulse at the tympanal opercula. (D) Left loud IN pulse at the tympanal opercula.
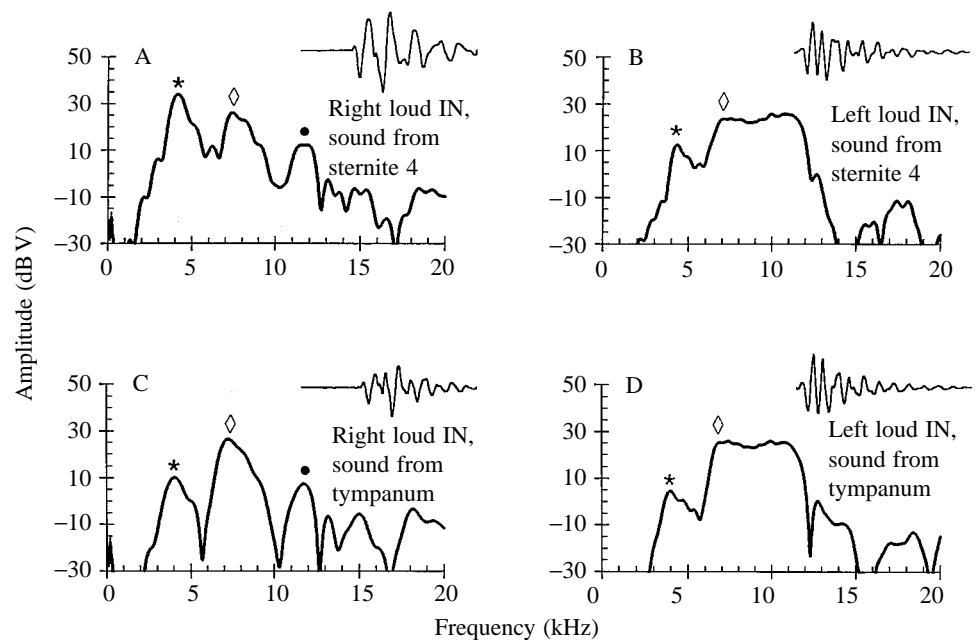
Fig. 7. Oscillograms (insets) and power spectra (main graphs) of loud OUT pulses at two points on the surface of the abdomen. Measurements were made at 1 mm distance from either the centre of sternite 4 or the tympanal opercula. All graphs show the averaged power spectrum for four pulses from one insect. Insets show an oscillogram of the waveform of one of the pulses used in each case. The symbols show the positions of the 4 kHz (*), the 7–8 kHz (◇) and the 11–13 kHz (●) peaks also highlighted in Fig. 3. (A) Right loud OUT pulse at sternite 4. (B) Left loud OUT pulse at sternite 4. (C) Right loud OUT pulse at the tympanal opercula. (D) Left loud OUT pulse at the tympanal opercula.
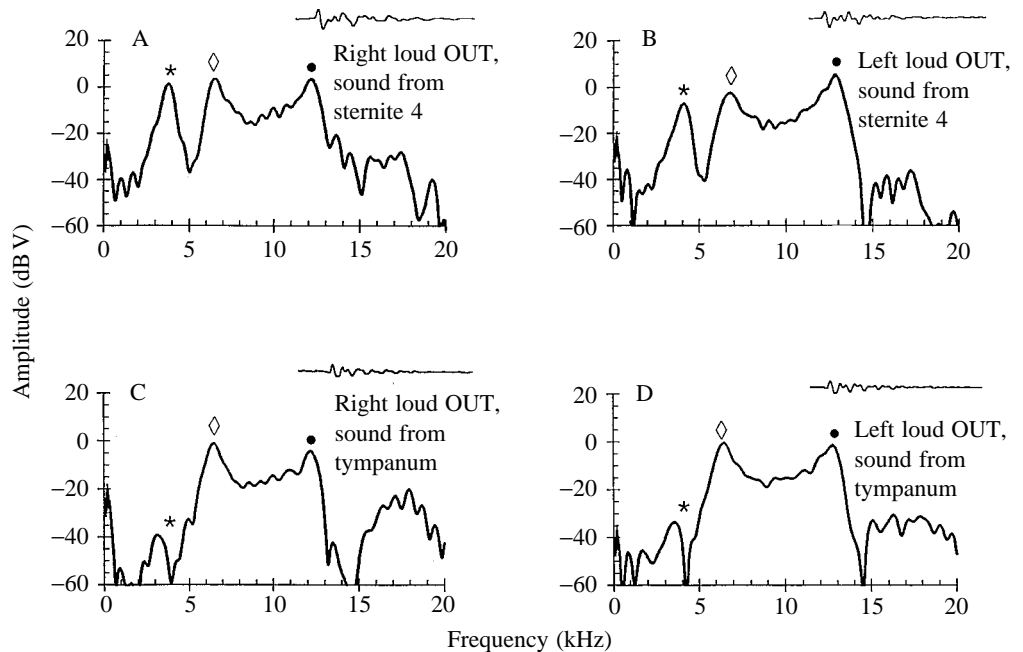
13 kHz. Not only were the loud IN pulses recorded at the tymbal approximately 10 dB louder than the loud OUT pulses but they had relatively more energy at low frequencies (Fig. 3). These differences are reflected in the sounds radiated *via* sternite 4 and *via* the tympana (Figs 6, 7).

The apparent excitation of sympathetic vibration and thence of sound radiation from sternite 4 and *via* the tympana by components of the tymbal sound pulses was investigated by calculating the transfer function between the tymbal sound and the sounds from sternite 4 and the tympana (Fig. 8).

The transfer function of the right loud IN tymbal pulse to sternite 4 was maximal at 4–5 kHz, with a subsidiary peak at 7–8 kHz, but the transfer function from the tymbal to the tympana was maximal at 7–8 kHz (Fig. 8A).

With all other pulses (loud and soft, IN and OUT), good transfer was shown from the tymbal pulses to sternite 4 at 4 kHz and also at 7–8 kHz (Fig. 8). Transfer from the left loud IN pulse from the tymbal to sternite 4 at 4 kHz was less than that from the right loud IN pulse [note that the absolute amplitude of the spectrum at 4 kHz was approximately 10 dB lower from the left than from the right tymbal (Fig. 3) but that there was relatively good transfer from the tymbal to the tympana in the left loud IN pulse (Fig. 8B)]. In all cases, the transfer from the tymbal to the tympana was relatively poor at 4 kHz and there was also poor transfer to both sternite 4 and the tympana around 12 kHz (Fig. 8).

The average phase of the tymbal sound relative to that at sternite 4 at the 4 kHz peak and between the tymbal sound and the sound at the tympana at the 7–8 kHz peak was calculated (Fig. 8). The phase at the 4 kHz peak from sternite 4 lags by between 88 ° and 121 ° relative to that at the tymbal. The phase at the 7–8 kHz peak from the tympana lags by between 66 ° and 136 ° relative to that from the tymbal. These two series of measurements do not rule out the hypothesis that the sounds

from sternite 4 or from the tympana result from distinct resonances that have been excited by consonant components of the tymbal pulses. However, the ragged shapes of the pulse envelopes and the presence of components at higher frequencies suggest that, if there are driven resonances of the sternites or *via* the tympana, neither is sharply tuned.

Comparison between loud and soft pulses

The major frequency during the decay of the right loud pulses is 11.7 kHz for the IN pulse and 13.5 kHz for the OUT pulse (Fig. 3, and measured from oscillograms); similar values for the left loud IN and OUT pulses are 10.8 and 12.8 kHz, respectively, so there is a difference of approximately 2 kHz in this component between the IN and OUT pulses. However, the spectral peaks of all soft IN and OUT pulses occur at 13–13.5 kHz and do not show major left:right or IN:OUT differences (Fig. 5). (These values were measured from one male; measurements made with a further four males showed the same trend but with peak frequencies differing by up to 0.5 kHz relative to the values given above.)

The rate of decay of the tymbal vibration seems to be rather similar during IN and OUT pulses for both loud and soft pulses, with a Q value of between 9 and 13. This is compatible with the frequency response of the tymbal measured using laser vibrometry (Fonseca and Popov, 1994). In all cases, the tymbal clicks have a sharp onset with peak amplitude during the first cycle and then tend to decay exponentially. The peak amplitude of the first cycle of each pulse (IN or OUT, loud or soft) is approximately 1.4 times (or approximately 3 dB louder than) the amplitude (approximately +3 dB louder than) of the succeeding cycle of the pulse, and the amplitude of all components of the loud IN pulses is approximately three times (or approximately 10 dB louder than) the corresponding amplitudes of the soft pulses.
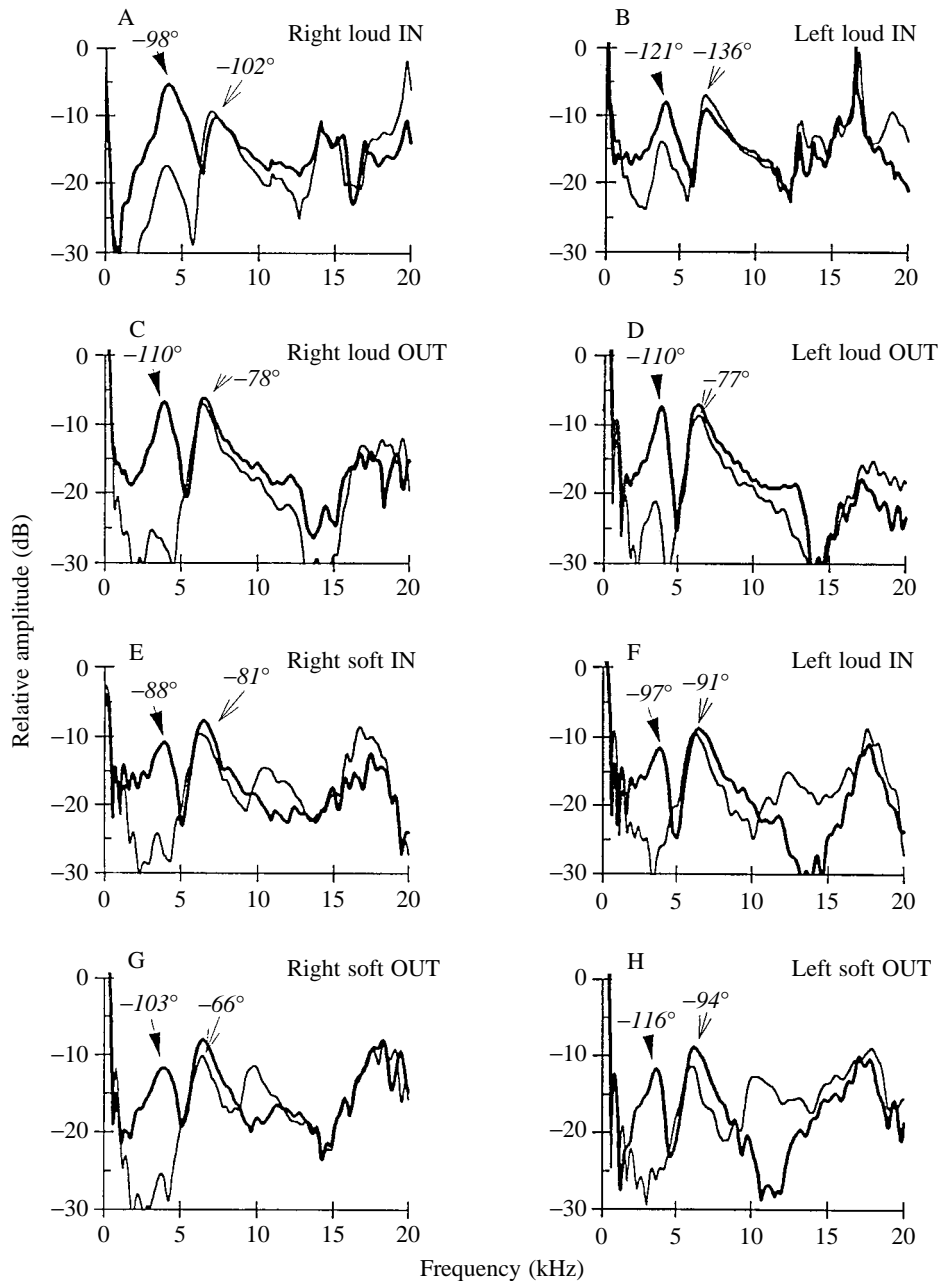
Fig. 8. Plots of the transfer function between the sound produced at the tymbal and that radiated from sternite 4 (thick lines) or from the tympanal opercula (thin lines). The solid arrows (sternite 4), thin arrows (tympanal opercula) and their associated values (in italic type) show the phase angle between the tymbal sound and the sound produced by these other regions at the peaks of their respective transfer functions. (A) Right loud IN pulse. (B) Left loud IN pulse. (C) Right loud OUT pulse. (D) Left loud OUT pulse. (E) Right soft IN pulse. (F) Left soft IN pulse. (G) Right soft OUT pulse. (H) Left soft OUT pulse.

Animals that had fatigued or were producing abnormal type 1 song typically failed to produce the right loud IN pulse at the start of the echeme, even though they were able to produce soft pulses from the right tymbal. This suggests that the right tymbal requires more muscle energy to bring about buckling during the loud pulses than it does during the soft clicks or than is required for the loud clicks of the left tymbal.

Internal transmission from tymbal to tymbal

With all pulses, there was considerable sound radiation from the contralateral tymbal (Figs 2, 9). In the loud pulses, the right IN pulse, as transmitted by the contralateral left tymbal, had a ragged and irregular waveform but the left IN pulse was transmitted with a rather smoother pulse envelope through the right tymbal (Fig. 9A). The loud right IN pulse, after transmission through the left tymbal, showed a lack of coherence from cycle to cycle. The right loud IN pulse has a broad-band spectrum and thus is unlikely to provide a coherent drive to the left tymbal. In contrast, the right and left loud OUT pulses (Fig. 9A), and all soft pulses (Fig. 9B), which have a peak in their power spectra close to those of the contralateral tymbals caused inter-tymbal transmission as coherent pulses.

During the soft pulses, all transmissions through the contralateral tymbal (at approximately 13 kHz) are fairly similar. In these transmitted pulses, the sound amplitude builds up over the first 2–4 cycles and then decays slowly, regardless of the side of the insect that is driving the contralateral tymbal or whether the buckling is IN or OUT (Fig. 9B).

A

Right loud IN

Right loud OUT

Transmitted by right

Transmitted by right

0   1   2 ms

Transmitted by left

Transmitted by left

Left loud IN

Left loud OUT

B

Right soft IN

Right soft OUT

Transmitted by right

Transmitted by right

Transmitted by left

Transmitted by left
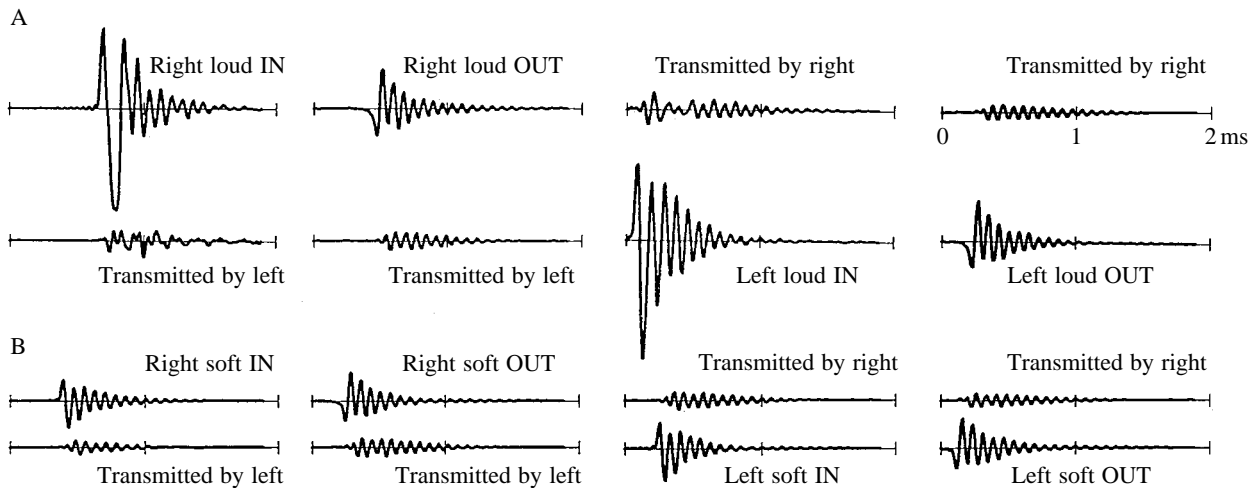
Left soft IN

Left soft OUT

Fig. 9. Oscillograms of the sound pulses measured at 1 mm from the two tymbals to show sound transmission between the two tymbals. The records show the sequence right IN, right OUT, left IN, left OUT with the sound recorded from the right tymbal shown above that from the left. All records were made with same vertical gain and have a common time scale. (A) Loud pulses. (B) Soft pulses.

It thus appears that the pulse of sound pressure caused by tymbal buckling produces a significant sympathetic vibration of the contralateral tymbal when their major frequencies of vibration are closely similar (as in the loud OUT pulses and in all soft pulses (see Figs 3B,D, 5), but not when there is a major frequency mismatch between the driving waveform and the resultant transmitted waveform, as occurs when the right loud IN pulse drives the left tymbal (Figs 9A, 3A).

The anatomy and kinematics of the tymbals

The anatomy of the tymbals of *C. australasiae* has been described previously in some detail (Young and Bennet-Clark, 1995). In the description that follows, only the major and special features of the anatomy of the tymbals of *T. gastrica* and contrasts with the tymbals of *C. australasiae* are described.

The tymbals of *T. gastrica* (Fig. 10) are driven by an inward movement of the posterior tymbal plate which covers approximately one-third of the area of the tymbal and has, at its dorsal end, the apodeme pit of the large tymbal muscle. The domed anterior half of the tymbal surface bears of a row of four sclerotised ribs running dorso-ventrally, separated by bands of resilin-containing cuticle. The narrow central regions of the first three of these ribs are rather more sclerotised than the broader dorsal and ventral regions, but not as markedly so as in *C. australasiae*. In contrast with *C. australasiae,* there are no short ribs between the mid-sections of the ribs.

The dorsal, ventral, anterior and posterior cuticle surrounding the sclerotised parts of the tymbals contains resilin. As in *C. australasiae*, these resilin sheets separate and suspend the moving parts of the tymbal from the thick sclerotised tymbal frame that surrounds them. The resilin is thickest at the dorsal and ventral ends of the tymbal plate and tymbal ribs, as well as along the posterior edge of the tymbal plate, and is thinnest in the narrow dorso-ventral strips that run between the tymbal plate and the four tymbal ribs (this

distribution of resilin is similar to that described and illustrated in Young and Bennet-Clark, 1995).

Dorsally, the sclerotised dorsal end of the second rib extends posteriorly to near the dorsal end of the tymbal plate and surrounds the dorsal end of the first rib; this dorsal bar also has an anterior projection over the dorsal end of the third rib (Fig. 10). This bar appears to act as a coupler between this group of three ribs and the tymbal plate. When the tymbal plate was pushed inwards at the apodeme pit, the first three ribs appeared to buckle inwards together, instead of separately and in sequence from posterior to anterior as has been described in *C. australasiae* (Young and Bennet-Clark, 1995; Bennet-Clark, 1997).

The movements of the tymbal associated with the contraction of the tensor muscle were described by Fonseca and Hennig (1996). The tymbal tensor sclerite, forming the ventral anterior edge of the tymbal frame, appears to be hinged dorsally and has a broader ventral connection onto the rest of the tymbal frame. The tensor muscle attaches to the tensor sclerite, which is bordered anteriorly by a folded membrane on which it hinges. When the tensor muscle contracts, the posterior edge of the tensor sclerite moves inwards and anteriorly, pulling rib 4 at the anterior edge of the tymbal and thereby flattening the dome of the tymbal. The tensor muscle contracts (flattening the tymbal) just before the train of soft song pulses and relaxes (allowing the tymbal to become more highly domed) before the start of the next pair of loud pulses.

The dorsal regions, the tymbal plates and the ribs of the left and right tymbals of *T. gastrica* are superficially bilaterally symmetrical. However, the resilin pad that connects the ventral ends of the tymbal ribs to the tymbal frame is on average 1.37 times wider dorso-ventrally in the right tymbal than in the left tymbal (Table 2; Fig. 10). This highly significant left–right morphological asymmetry was measured from eight insects and has been seen on each of a further ten *T. gastrica* examined.
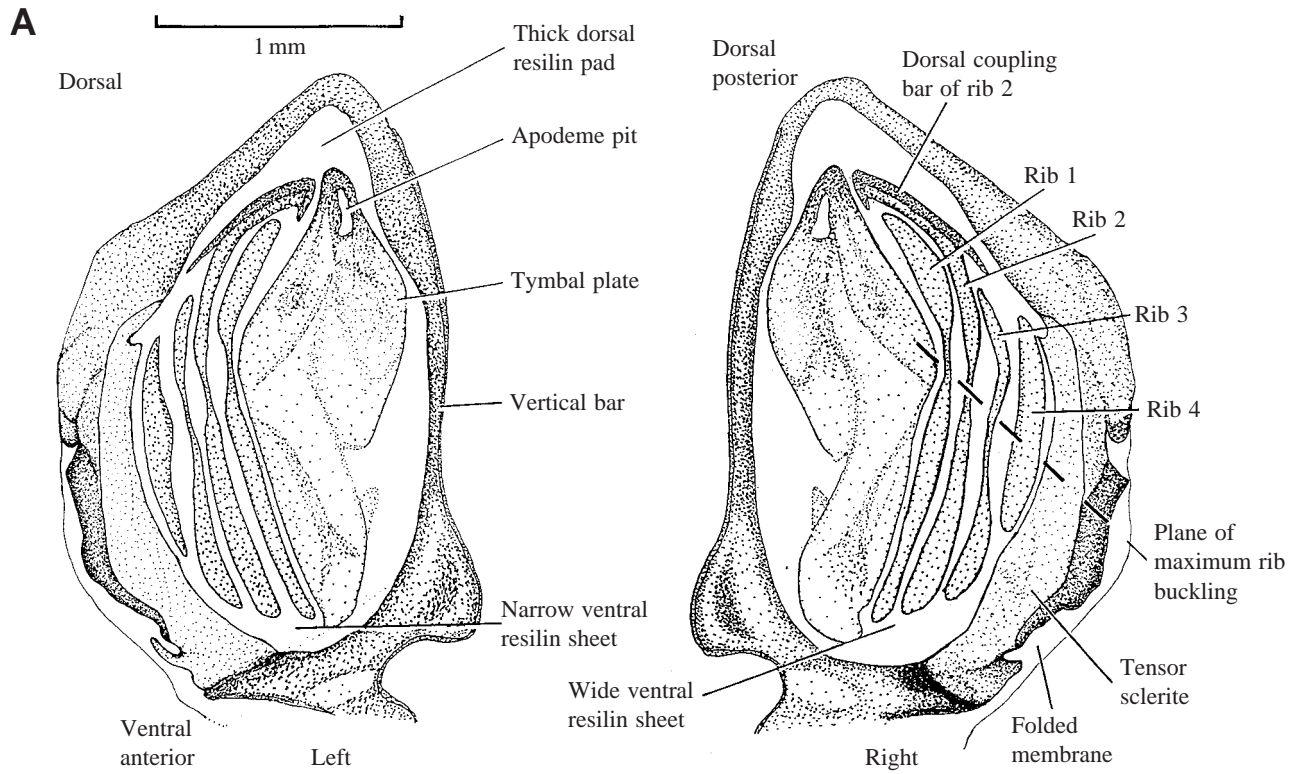
Fig. 10. (A) Drawings of the left and right tymbals of *T. gastrica*. Sclerotised cuticle is stippled and the degree of stippling indicates the relative thickness and degree of sclerotisation of the cuticle. The unstippled regions are areas of cuticle containing resilin. The area of resilin-containing cuticle at the ventral ends of the ribs is wider, dorso-ventrally, in the right tymbal than in the left. There are also differences in the anatomy and extent of sclerotisation at the ventral ends of the tensor sclerites. (B) Photographs (taken by David Paul, Department of Zoology, University of Melbourne) of the left and right tymbals.

Table 2. *Dimensions of the left and right tymbals of* Tympanistalna gastrica

	Left tymbal	Right tymbal	t	P
Dorso-ventral height of tymbal (mm)	2.19±0.093	2.21±0.082	0.9	0.4 (NS)
Anterior–posterior width of tymbal (mm)	1.32±0.057	1.35±0.077	2.14	0.07 (NS)
Dorso-ventral width of ventral resilin sheet (mm)	0.15±0.012	0.20±0.011	29.7	0.001

Values are means ± S.D. (*N*=8 males).
Comparisons between left and right mean values were made using Student's *t*-tests; NS, not significant.

There are also anatomical differences at the ventral ends of the two tensor sclerites. That on the right also appears more heavily sclerotised than that on the left (Fig. 10) but this difference has not been quantified.

There is thus a right–left asymmetry in both the loud IN pulses of the song and in the anatomy of the tymbals of *T. gastrica*.

Discussion

The loud IN pulses of the right tymbal excite sound radiation with peak power at approximately 4 kHz from the walls of the abdomen, especially the thinner flat sides of the tergites and central parts of the sternites (and see Fonseca and Popov, 1994) and also excite sound radiation at approximately 7–8 kHz measured at the opercula, probably *via* the tympana. These components accompany distinct peaks in the transfer function from the tymbal sound with a phase lag of approximately 90° between the sound radiated from sternite 4 or *via* the tympana and the driving sound pulses from the tymbals (Fig. 8); these indirectly radiated sounds appear as large components of the right loud IN pulses, but the 4 kHz component is relatively smaller in the left loud IN pulse. Both these indirectly radiated components are smaller in the loud OUT pulses and in all the soft pulses; these pulses only show peak energy of sound radiation at approximately 13 kHz (Figs 3B,D, 5).

There is, however, less difference between the right loud OUT pulse (which occurs when the right tymbal muscle relaxes while the left muscle is still contracted) and the left loud OUT pulse (which occurs when the left tymbal muscle relaxes). Also, the soft pulses all appear rather similar, with little difference between pulses from the right and left sides, and only a small difference in dominant frequency between the IN and OUT pulses. The polarity of the soft OUT pulse is opposite to that of the IN pulse but, when inverted, the envelope of the soft IN pulse is very similar to that of the soft OUT pulse (see Figs 5, 9).

Contraction of the tymbal tensor muscle in *T. gastrica* flattens the tymbal. The loud IN and OUT pulses occur while the tymbal tensor muscle is inactive and the soft pulses all occur after its contraction. The tensor sclerite can be seen to swing inwards and the tymbal to flatten as the tensor muscle is activated at the start of the soft pulses (Fonseca and Hennig, 1996).

The loud pulses occur while the tymbal is highly domed. In this condition, the buckling movements, both inward and outward, require larger forces than for the soft pulses, where the buckling occurs with a flatter tymbal (Fonseca and Hennig, 1996). During the loud inward buckling, the highly domed tymbals will require more power from the tymbal muscles and, during the loud outward buckling, there will be a larger restoring force from elastic strain energy in the distorted tymbal ribs. This difference in the configuration of the tymbal between the loud and soft pulses is consistent with the relative loudness of the two types of pulse, the shorter IN-to-OUT times of the loud pulses relative to the soft pulses (Table 1) and the greater difference between the peak frequency of decay during loud IN *versus* OUT compared with that for the soft IN and OUT pulses.

The different sounds made by the two tymbals in the loud IN pulses may be explained as follows: when the tymbal tensor muscle is inactive, the ventral resilin pad is more compliant than it is after the tensor muscle has contracted, thereby stressing it and thus increasing its stiffness; the effect is greater in the right tymbal with its wide (and initially more compliant and less stiff) ventral resilin pad than in the left tymbal with its narrower ventral resilin pad. The role of the different compliant components of the tymbal of *C. australasiae* has been discussed in Bennet-Clark (1997).

The difference in loudness of the pulses accompanies a change in the convexity of the unbuckled tymbal ribs. With the tensor relaxed and the tymbal more convex, the tymbal muscle must provide more energy before the tymbal buckles inwards than when the tymbal is flattened through the contraction of the tensor muscle (Fonseca and Hennig, 1996). Consequently, the work required to buckle the tymbal, which is then released as a sound pulse, is greater during the loud pulses when the tymbal is more convex. The role of the tymbal as an energy storage/release mechanism was addressed by Fonseca and Hennig (1996) and has been discussed for *C. australasiae* (Bennet-Clark, 1997).

The tymbals of *T. gastrica* differ from those of *C. australasiae* or *Cicada* spp. in having a dorsal sclerotised bar on rib 2 that runs from a flexible attachment to the tymbal plate across the dorsal ends of ribs 1 and 3. This bar appears to couple the first two or three ribs together, so that they tend to act in unison, in contrast to the situation in *C. australasiae* where the long ribs buckle separately and in a posterior-to-anterior sequence; the rib coupling in *T. gastrica* produces a single discrete IN pulse, with greatest amplitude at the start of the pulse, in contrast with the train of 2–4 separate pulses that are produced by the sequence of buckling of the separate ribs

of *C. australasiae* (Young and Bennet-Clark, 1995; Bennet-Clark, 1997).

In the song of *T. gastrica*, the presence of the coupling bar may also correlate with the loudness of all OUT pulses, which are relatively far louder than the OUT pulses of *C. australasiae* (Bennet-Clark, 1997) or *Tibicina quadrisignata* (Fonseca, 1991, 1996).

Small cicadas such as *T. gastrica* tend to produce higher-frequency sounds than larger species such as *C. australasiae* (Bennet-Clark and Young, 1994). But muscle contraction frequency is physiologically limited to approximately 500 Hz (e.g. Josephson and Young, 1985) (and realistically to only approximately 250 Hz in most cases; Fonseca, 1996) or a contraction-to-relaxation time of 2 ms or longer. In *C. australasiea*, the tymbal muscle buckles the three long ribs at intervals of three cycles at a frequency of 4.3 kHz tone with a period of 230 μs per cycle; thus, rib 1 buckles at 0 ms, rib 2 buckles three cycles later at 0.7 ms (3×230 μs) and rib 3 buckles at 1.4 ms (data from Young and Bennet-Clark, 1995). This pattern gives a sound pulse, including the decay period, of approximately 2–2.5 ms, a period wholly compatible with muscle kinetics. In the case of the tymbal of *T. gastrica*, which has a peak sound output above 10 kHz, the period of one cycle of the song is less than 100 μs and, if the mechanism were identical to that of *C. australasiae*, rib 2 would have to buckle at 300 μs and rib 3 at 600 μs, periods that are too brief to be consistent with the kinematics of even the fastest tymbal muscle.

In the *T. gastrica* tymbal sounds reported here, two or three tymbal ribs buckle together as a group, rather explosively, instead of in a longer-duration sequence as in *C. australasiae*, where they typically buckle every two or three cycles of the sound pulse. It has been suggested that the use of a *T. gastrica* type of brief, broad-band high-frequency transient sound pulse is more appropriate for a small insect singing through vegetation than is a longer, purer-tone low-frequency sound pulse (Bennet-Clark, 1998).

The song structure in T. *gastrica* differs from that in *C. australasiae* in two significant ways. First, the IN pulses and OUT pulses form distinct components of the song structure of *T. gastrica*, but the OUT pulses are not distinct in *C. australasiae*. The structure of the song of *T. gastrica*, in which the IN and OUT pulses are distinct and, in terms of the pulse-to-pulse pulse duration ratio, widely separated, will favour the production of loud sounds by the IN and OUT buckling of the tymbals. In contrast, the song of *C. australasiae*, in which the actions of the left and right tymbals alternate so rapidly that their pulses overlap, would be more likely to result in a quiet OUT pulse, produced at a different frequency, which will not interfere with the next loud IN pulse produced by the contralateral tymbal.

Second, the soft IN and OUT pulses of *T. gastrica* are similar in loudness, but the IN pulses of *C. australasiae* are far louder than the OUT pulses. This difference may have several causes. First, all tymbal ribs appear to act in unison during both the IN buckling and OUT buckling movements in *T. gastrica*,

so the instantaneous sound pressure at the tymbal surface will be greater in both movements. Second, there may be a lesser dependence in *T. gastrica* on the use of the abdominal air sac plus tympana as a sound-radiating system than in *C. australasiae* with its Helmholtz-type resonator (Bennet-Clark and Young, 1992). Third, the force–distance relationships of tymbal buckling are very different during the inward and outward movements of the tymbal plate in *C. australasiae* (Bennet-Clark, 1997), and this is reflected in the different loudness and frequency of the IN and OUT pulses. The similar but inverse patterns of the soft IN and OUT pulses in *T. gastrica* suggest that the mechanics of inward and outward buckling is symmetrical but inverted when the tymbal is flattened by the tymbal tensor muscle.

In many circumstances, close structural bilateral symmetry correlates well with fitness (e.g. Møller, 1992; Enquist and Arak, 1994) and appears in many cases to be recognised and used by conspecific females as a mate choice criterion (for a recent review, see Simmons and Ritchie, 1996). However, examples of functional asymmetry are common in the animal kingdom (Neville, 1976). For example, the asymmetries in the sound-producing wings of tettigoniids (Dumortier, 1963; Bailey, 1970) are related to their different mechanical roles: one wing bears the file that excites the resonance, and this passes across the underside of the other wing, which bears the plectrum and the resonator from which the sound is radiated. The asymmetry found here in the tymbals of *T. gastrica* is related the fact that the two tymbals produce different types of loud sound pulse and also that the action of the right one always precedes that of the left.

An asymmetry in the neural pattern during sound production has been recorded in many species of *Gryllus*, which typically close their wings right-over-left. Both wings produce sound, but if the wing positions are artificially reversed, the insect returns them to the usual right-over-left pattern before singing. Wing position in these crickets is detected by sensory hairs on the wing surfaces (Kutsch and Huber, 1989). In these crickets, there is also a tendency for the left harp to be slightly smaller than the right harp (Simmons and Ritchie, 1996). The resonant frequencies of the two harps also differ systematically: that of the left harp is higher than that of the right (Nocke, 1971). In *T. gastrica*, directional anatomical asymmetry (Van Valen, 1962) between the right and left tymbals is reflected in differences between the song pulses they produce. The song pattern also shows a stereotyped directional asymmetry: the action of the right tymbal always precedes that of the left.

However, only the first two loud pulses in the echeme show right:left asymmetry and IN:OUT asymmetry. The subsequent soft pulses are not only symmetrical but also occur as a long train consisting of a variable number of pulses (Fonseca, 1994).

Although morphological and functional directional asymmetry in animals is common (Neville, 1976) and may be associated with neural-pattern asymmetries (e.g. Kutsch and Huber, 1989), stereotyped right:left asymmetry of an activity sequence seems to be rare in arthropods and, indeed, would be a selective disadvantage in some circumstances (e.g. during

locomotion). In the present case, however, the stereotyped asymmetrical sequence may have two functions. First, because fatigued and moribund animals failed to produce first the right loud pulses and then the left loud pulses, the asymmetry may provide an example of an 'honest' fitness signal (Zahavi, 1975). Second, the complete type 1 echeme may provide the female with a longer, more complex, signal which may be more attractive (Tuckerman *et al.* 1993). In this species, the ability to produce a complex song may be of considerable selective advantage.

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