

## TYMBAL MECHANICS AND THE CONTROL OF SONG FREQUENCY IN THE *CICADA CYCLOCHILA AUSTRALASIAE*

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### Summary

The anatomy of the tymbal of *Cyclochila australasiae* was re-described and the mass of the tymbal plate, ribs and resilin pad was measured.

The four ribs of the tymbal buckle inwards in sequence from posterior to anterior. Sound pulses were produced by pulling the tymbal apodeme to cause the tymbal to buckle inwards. A train of four sound pulses, each corresponding to the inward buckling of one rib, could be produced by each inward pull of the apodeme, followed by a single pulse as the tymbal buckled outwards after the release of the apodeme. Each preparation produced a consistent sequence of pulses.

Each of the pulses produced had its maximum amplitude during the first cycle of vibration. The waveform started with an initial inward-going rarefaction followed by a larger outward compression, followed by an approximately exponential decay, as is typical of a resonant system. The mean dominant frequencies of the pulses produced during the inward movement were 4.37, 4.19, 3.92 and 3.17 kHz respectively. The pulse produced during the outward movement had a mean resonant frequency of 6.54 kHz. This suggests that the mass-to-stiffness ratio that determines the resonant frequencies of the various pulses differs from pulse to pulse.

If succeeding pulses followed rapidly, the next pulse tended to start on the inward-going half-cycle of its predecessor and to produce a coherent waveform. Coherence was lost if the preceding pulse had decayed to below approximately one-tenth of its peak amplitude.

When the tymbal plate was loaded by a 380 µg wire weight, the resonant frequency of all sound pulses was reduced. Pulses produced later in the inward buckling sequence were less affected by the loading than earlier ones. This suggests that the effective mass determining the resonance in the later pulses is greater than that in the

earlier pulses. The frequency of the pulses produced in the outward movement was affected most, suggesting that the mass involved was less than that in any of the pulses produced by the inward movement.

The quality factor,  $Q$ , of the pulses produced by the inward buckling of the unloaded tymbal was approximately 10. For the outward buckling,  $Q$  was approximately 6. The  $Q$  of loaded tymbals was higher than that of unloaded tymbals. The  $Q$  of the resonances varied approximately as the reciprocal of the resonant frequency.

Experimental removal of parts of the tymbal showed that the thick dorsal resilin pad was an important elastic determinant of the resonant frequency, but that the mass and elasticity of the tymbal ribs were also determinants of the resonant frequency. The major element of mass is the tymbal plate. The integrity of the tymbal ribs was essential if the buckling movement were to occur.

The force required to cause inward buckling of the tymbal was approximately 0.25 N. The force required to hold the tymbal in the buckled-in position was approximately 0.05 N. This asymmetry in the tymbal compliance, together with the different masses involved in inward and outward buckling, may account for the difference between the resonant frequencies of the inward-going and outward-going clicks.

The tymbal appears to act as an energy storage mechanism that releases energy as the tymbal ribs buckle inwards in sequence. Each pulse provides a large initial impulse to the abdominal resonator, followed by a sustaining resonant vibration at, or close to, the song frequency. Subsequent pulses maintain the coherent resonance of the song pulse.

Key words: insect, song, cicada, *Cyclochila australasiae*, resonance, energy storage, biomechanics.

### Introduction

Many cicadas, such as the Australian species *Cyclochila australasiae*, produce piercingly loud sounds in which the

main sound energy is confined to a narrow band of frequencies.

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In male cicadas, the abdomen is specialised for sound production. Paired tymbals on either side of the first abdominal tergite are buckled rapidly by large muscles which run from the sternum of the second abdominal segment to a flexible apodeme at the dorsal end of the tymbal plate (Pringle, 1954). As the tymbals buckle inwards, the inward movement occurs in a series of steps as successive ribs on the tymbal buckle in sequence from posterior to anterior (Pringle, 1954; Simmons and Young, 1978; Young and Bennet-Clark, 1995).

In *C. australasiae* and other large cicadas, tymbal buckling causes large air pressure changes within the abdomen. The abdomen appears to act as a Helmholtz resonator, the elements of which are the large abdominal air sac and the large, thin, acoustically transparent tympana or eardrums (Young, 1990; Bennet-Clark and Young, 1992). The effective sound source in cicadas such as *C. australasiae* is the tympana or eardrums, which extend across most of the ventral surface of the anterior part of the abdomen (Young, 1990).

A recent model of cicada sound production suggested that the role of the tymbal was to provide a series of sound pulses that were tuned to the resonant frequency of the abdomen from which the sound was then radiated (Bennet-Clark and Young, 1992). This model suggested that the tymbal resonates at the dominant frequency of the song and that the buckling of the successive tymbal ribs provides a coherent sequence of pulses that sustains the resonance of the abdomen. Experiments with *C. australasiae* demonstrated that in the absence of a tuned load, such as that of the insect's abdomen, the tymbal produced a damped series of resonant vibrations at or near to the song frequency as it was buckled inwards by the contraction of its muscle and another resonant pulse, at a higher frequency, as it buckled outwards following the relaxation of the muscle (Young and Bennet-Clark, 1995).

When the tymbal was vibrated mechanically, a resonance at the song frequency, 4.3 kHz, could be excited after the tymbal had been buckled in, but the tymbal in its resting buckled-out position resonated at approximately 5.5 kHz, which is the frequency of the sound pulses produced as the tymbal buckles outwards (Young and Bennet-Clark, 1995).

Thus, the tymbal of *C. australasiae* can be made to resonate in two distinct ways. During the muscle-driven inward buckling, the resonant frequency is appropriate for driving the abdominal resonator and thus for the production of the pure-tone song; the energy in this vibration, too, is large, so the sound it produces is loud. During the outward buckling, the resonant frequency of the tymbal is not consonant with that of the abdomen and the amplitude of the vibration is smaller than that of the inward buckling, so the sound it produces is quiet.

A simple resonator has two elements, (1) the mass  $m$  of the system interacting with (2) its compliance  $C$  (the reciprocal of stiffness  $S$ ). The resonant frequency  $F_0$  is given by:

$$F_0 = \frac{1}{2\pi} \sqrt{\left(\frac{1}{m \times C}\right)} = \frac{1}{2\pi} \sqrt{\left(\frac{S}{m}\right)}. \quad (1)$$

In an earlier study (Young and Bennet-Clark, 1995),

although it was shown that the tymbal could be made to vibrate at a frequency and amplitude appropriate for the production of the song, the elements of the resonant system that control its resonant frequency were not described, nor was an explanation given for the observed change in the resonant frequency as the tymbal buckled inwards then outwards.

The present paper addresses these aspects of frequency determination in cicada sound production as well as the nature of the sound pulses that the tymbal produces.

## Materials and methods

### *Insects*

Male *Cyclochila australasiae* Donovan were collected just after they had emerged as adults on trees in parkland in Melbourne, Australia. They were maintained in the laboratory on eucalyptus saplings and used for experiments between 3 days and 2 weeks after eclosion. For some experiments, recently killed and moribund insects were used.

Insects were prepared for experiments by waxing them by the tergites of the pterothorax to 150 mm  $\times$  long 6 mm diameter metal rods. The wings and legs were removed. The anterior abdominal segments were immobilised by waxing the tympanal opercula to the first abdominal sternite and the first tergite to the metanotum. The posterior part of the abdomen was cut away immediately behind the tympana and tymbals, giving access to the tymbal muscle and apodeme as well as destroying the abdominal Helmholtz resonator. To allow access to the exterior surface of the tymbals, the external tymbal covers were cut away.

This preparation was similar to the previously described 'abdomenless cicada' (Fig. 1C in Young and Bennet-Clark, 1995).

### *Tymbal preparations*

Preparations and probes were mounted on Prior micromanipulators which were held with magnetic stands onto a steel base plate.

Tymbal vibrations were excited in four main ways. (1) By pulling inwards on the disc-shaped expansion of the tymbal apodeme with forceps. This caused the tymbal to buckle inwards in a step-wise fashion and, on release, to buckle outwards. These are termed apodeme pulls. (2) By pushing inwards with a blunt-tipped rod at the apodeme pit along the main trajectory of the tymbal muscle fibres. This also caused the tymbal to buckle inwards and then outwards. These are termed apodeme pit pushes. (3) By pushing inwards with the tip of the vibration force transducer (see below) at the apodeme pit. Tymbal vibrations were then excited at various stages of the inward and outward buckling of the tymbal. These are termed forced vibrations. In 1, 2 and 3, care was taken to apply the force along the main trajectory of the tymbal muscle fibres. (4) With operated tymbals, vibrations of the tymbal plate were excited by pushing the plate inwards with forceps and then allowing the forceps to slide off the free edge of the tymbal plate so that the tymbal plate could

return freely outwards to its original position. These are termed free vibrations.

Operations to cut or remove parts of the tymbal were made using either fine scissors or a fine scalpel. Small weights were attached to the tymbal plate using stirrup-shaped lengths of 0.14 mm diameter copper wire, stuck in place with cyanoacrylate adhesive (see Fig. 8E). The standard load was a 2 mm length of copper wire which, with adhesive, weighed 380  $\mu\text{g}$ .

The mass of parts of the tymbal and tymbal loads was measured using a Cahn 29 electronic microbalance. As the aim was to assess the relative distribution of the mass of the tymbal, no attempt was made to make detailed measurements of the masses and the following procedure was adopted. The whole tymbal was excised and weighed within 1 min of excision; the tymbal plate was then separated and weighed as quickly as possible. All regions were then allowed to dry for 1 h in room conditions (about 23 °C), dissected into their components and weighed.

In the description of tymbal kinematics that follows, the following terminology is used. (1) 'Buckling' refers to a rapid step-wise movement and 'pulse' to a discrete burst of sound produced by the buckling movement. (2) The sense of a movement is given as inwards or outwards, the condition of the tymbal following such a movement is termed IN or OUT and the sound produced by such a movement is termed an IN pulse or an OUT pulse

#### *Acoustic measurements*

Sounds produced by the tymbal were recorded *via* a purpose-built probe microphone made from a Realistic Electret tiepin microphone (Tandy Corporation catalogue no. 33-1052). A similar microphone has been described in Young and Bennet-Clark (1995). The dynamic range extended from a basic noise level of +60 dB to 10% distortion at +138 dB relative to  $2 \times 10^{-5}$  Pa at 4 kHz. The records used here were made at sound pressure levels of less than 130 dB.

As the microphone produces a negative voltage with compression, all oscillograms shown here have been inverted so that compression is shown as an upward-going component of the oscillogram.

For measurements of the loud sounds produced by tymbal pulses, the microphone was placed 5 mm away from the outer surface of the tymbal. For measurements of the quiet sounds excited by the vibration transducer or free vibrations, the microphone was placed between 1 and 2 mm away from the centre of the tymbal plate. In these positions, an acoustic compression is produced by outward movement of the tymbal. The microphone output was fed to an Analog Digital Instruments MacLab 4 data acquisition system using MacScope 3.2 signal acquisition and data analysis software. This system allows single-channel analysis at  $10^5$  samples  $\text{s}^{-1}$ , giving 12-bit analog-to-digital conversion (or over 70 dB dynamic range) with samples every 10  $\mu\text{s}$ .

The instantaneous frequency of waveforms and the dominant or resonant frequency ( $F_0$ ) of vibrations were

normally measured from the timebase of Scope oscillograms of the waveform. A single cycle of a 4 kHz waveform (period 250  $\mu\text{s}$ ) could be measured to  $\pm 10 \mu\text{s}$ , giving its frequency to  $\pm 170$  Hz, with commensurately higher precision over longer measurement periods.

The signal-to-noise ratio of most records exceeded 40 dB. Sounds were brief events measured at very short source-to-microphone distances relative to the nearest sound-reflective structures, so echoes were undetectably small.

With driven vibrations, the driving frequency was set to a value that gave the largest peak amplitude of the driven waveform and the frequency was measured from oscillograms of the decaying waveform as described above.

The quality factor ( $Q$ ) is a measure of the sharpness of tuning or the resistive damping of a vibration. Throughout this work,  $Q$  was calculated by measuring the amplitude of successive cycles of the decay of vibrations from oscillograms. The natural logarithm,  $\ln$ , of the amplitude values was calculated, and a linear regression was plotted to give the slope of the  $\ln(\text{decrement})$ .  $Q$  is given by:

$$Q = \frac{\pi}{\ln(\text{decrement})} \quad (2)$$

The significance of the quality factor is discussed in detail elsewhere (Bennet-Clark and Young, 1992; Young and Bennet-Clark, 1995). As reported earlier, the repeatability of successive measurements or comparisons of  $Q$  was better than  $\pm 10\%$ . The value calculated using equation 2 is sometimes known as  $Q_{3\text{dB}}$ .

#### *Vibration force transducer*

The vibration transducer used here, made from a TDK RU40K ultrasonic acoustic transducer, has been described in detail previously (Young and Bennet-Clark, 1995).

#### *Tymbal force–distance measurements*

Preliminary measurements of the force–distance relationships of the tymbal were made using a simple spring force transducer (Fig. 1). This used a pair of 0.35 mm diameter tempered steel insect pins as springs, giving nearly parallel movement of a probe rod over small deflections. It was calibrated in the vertical position using weights attached to a loop at one end. The deflection was linear up to loads of 0.5 N and the compliance was 6  $\text{mm N}^{-1}$ . Force was applied to the tymbal by applying the probe tip of the transducer to the tymbal apodeme pit and advancing it using a micromanipulator.

Using a stiff wire probe mounted on a micromanipulator, initial measurements were made of the distance moved at the tymbal pit in order to buckle the tymbal and at which the tymbal ribs buckled outwards. Further measurements were then made using the same tymbal by applying force with the spring force transducer, and the distance moved by the tip of the force transducer was measured by reference to a fixed index adjacent to the transducer. The applied force was then calculated from the compliance of the transducer and the distance moved by its tip. The precision and repeatability of

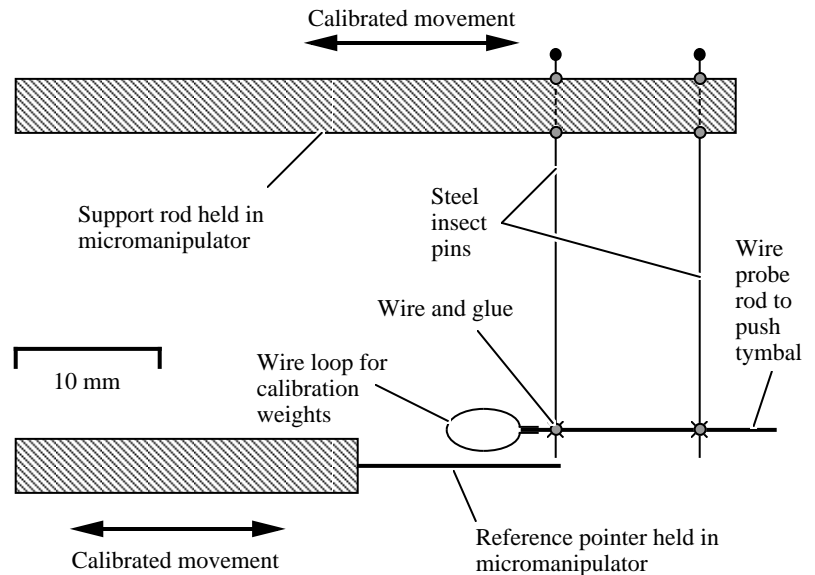


Fig. 1. Diagram of the simple force transducer used to measure the force required to buckle the tymbal. The compliance was measured using weights hung on the wire loop with the probe rod vertical. The distances moved by the base and tip of the transducer were obtained from the two micromanipulators.

the readings were approximately  $\pm 10\%$ , with a resolution to approximately 0.01 N.

#### Electrical test signals

Steady-state test signals were generated by a Tektronix function generator (type FG 501). Tone bursts were produced by triggering the FG 501 from a Tektronix pulse generator (type PG505). The carrier frequencies of these tone bursts were set to the nearest 10 Hz using a Testlab TL 3400 multimeter. Tone bursts were fed through a 0–59 dB, 600  $\Omega$  attenuator and amplified using a Toshiba SB-M30 power amplifier. The combined output of the function generator and amplifier were measured as being flat to  $\pm 1$  dB from 15 Hz to over 20 kHz with the power levels and load impedances used here.

## Results

### Anatomy and kinematics of the tymbal

The anatomy of the tymbal of *C. australasiae* has already been described, as have the kinematics of its buckling (Young and Bennet-Clark, 1995), but brief re-descriptions are necessary here (Fig. 2). The domed surface bears a series of sclerites. The posterior tymbal plate is moved inwards at its dorsal end by the large tymbal muscle. A series of four sclerotised tymbal ribs run anterior to the tymbal plate; these long ribs run dorso-ventrally, and are narrower and more highly sclerotised at their centres. Between long ribs 1 and 2, 2 and 3 and 3 and 4, there are small pear-shaped sclerites, the short ribs. As the tymbal plate is pulled inwards, the tymbal ribs buckle inwards into a V shape at their sclerotised mid-regions (Fig. 2, line A – A), in a step-wise fashion starting at the posterior rib 1 nearest to the tymbal plate and, in normal song, proceeding to the buckling of rib 3. In abnormal conditions, as in protest song or in the inward movement of the tymbal of cicadas in which the abdomen has been removed, all four long ribs buckle (Young and Bennet-Clark,

1995). As the tymbal moves back to its resting position, the ribs buckle outwards in the reverse sequence, from anterior to posterior.

The rubber-like protein resilin (Weis-Fogh, 1960; Andersen and Weis-Fogh, 1964) was reported in the tymbal by Scott

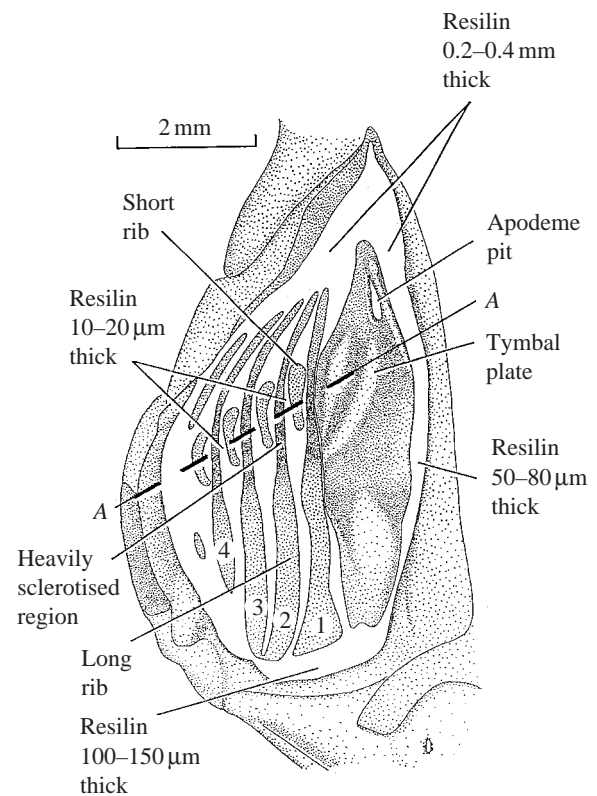


Fig. 2. Drawing of the tymbal to show its anatomy and the distribution of sclerotised cuticle and resilin. The dashed line A – A passes through the centres of the long ribs (1–4) in the region at which maximum buckling occurs.

(1970). In *C. australasiae*, the sclerotised ribs and tymbal plate are supported and inter-connected by resilin. There is a thick triangular resilin pad at the dorsal ends of the ribs and tymbal plate, and a thinner sheet around their ventral ends and along the posterior edge of the tymbal plate. Between the tymbal ribs, the resilin is much thinner (Fig. 2), and in this region the cuticle is flexible and highly deformable (Young and Bennet-Clark, 1995).

When in the OUT position, the bands of resilin between the dorsal and ventral lightly sclerotised parts of the tymbal plate and rib 1, as well as those between the lengths of all ribs, are taut. As each rib buckles inwards into its V shape, the strip of resilin between it and the region immediately anterior becomes slack along the line of the short ribs (Fig. 2, dashed line A – A) (Young and Bennet-Clark, 1995). Observations of the movement of *Lycopodium* powder placed on the tymbal showed that the maximum amplitude of the inward buckling of each rib occurs along the line (Fig. 2, dashed line A – A) that is the inner apex of the V into which each rib deforms (Young and Bennet-Clark, 1995). It thus appears that the central part of each rib is decoupled from its predecessor as it buckles inwards.

The tymbal apodeme originates at the tymbal plate on the apodeme pit; it runs inwards to the disc-shaped expansion of the insertion of the large tymbal muscle. The narrow strap-like region between the apodeme pit and the muscle insertion is remarkably flexible, particularly in the region closest to the tymbal plate: when the tymbal apodeme disc is pushed outwards, this flexible region buckles readily and does not move the tymbal plate but, when pulled inwards, tension in the apodeme causes the tymbal plate to move inwards.

The masses of the different parts of the tymbal are given in Table 1. From the differences between the initial masses and those measured after 1 h, the masses in the living insect are

Table 1. Masses of the different regions of the tymbal of *Cyclochila australasiae*

	Mass ( $\mu\text{g}$ )	<i>N</i>
Whole tymbal, wet	1780 $\pm$ 250	6
Tymbal plate, wet	553 $\pm$ 82	6
Tymbal plate, dry	484 $\pm$ 53	6
Dorsal resilin pad, dry	250 $\pm$ 13	6
All ribs, with resilin, dry	536 $\pm$ 59	6
Rib 1 entire, dry	90 $\pm$ 14	5
Rib 1, ventral region, dry	63 $\pm$ 7.8	5
Rib 2 entire, dry	75.6 $\pm$ 10.2	5
Rib 2, ventral region, dry	49.4 $\pm$ 6.2	5
Rib 3 entire, dry	71.6 $\pm$ 11.9	5
Rib 3, ventral region, dry	37.8 $\pm$ 8.0	5
Rib 4 entire, dry	50.4 $\pm$ 14.7	5
Rib 4, ventral region, dry	12.6 $\pm$ 2.5	5

Values are mean  $\pm$  S.D.

The wet masses were measured as rapidly as possible after excision of the tymbal and the dry masses were measured 1 h later.

The ventral regions of the ribs are taken as the regions ventral to the dashed line A – A in Fig. 2.

likely to be 15–20% higher than the dry masses given here. The sclerotised tymbal ribs were dissected from their resilin surrounds. These resilin sheets account for approximately half the mass of the rib region. The tymbal plate accounts for approximately one-third and the thick triangular dorsal resilin pad (Fig. 2) for approximately one-sixth of the total mass of the tymbal; the mass of each rib is less than one-fifth of that of the tymbal plate.

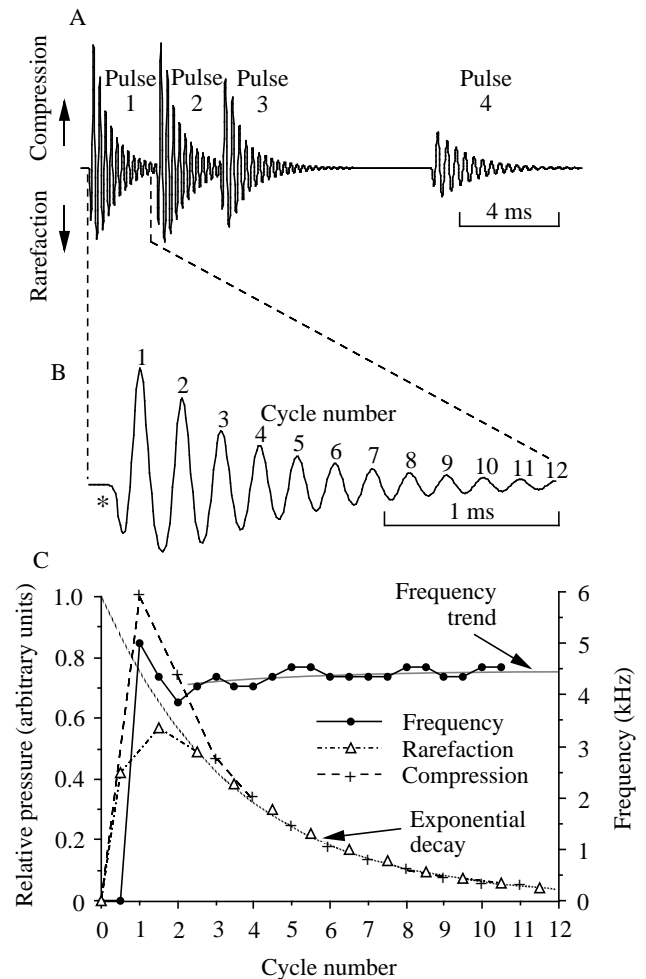


Fig. 3. The IN pulses produced by tymbal buckling. (A) Oscillogram of the sound pulses produced by the buckling inwards of the four long ribs caused by pulling the tymbal apodeme. The vertical arrows show the sense of the sound pressure outside the tymbal. (B) Pulse 1 shown on an expanded time scale to demonstrate details of the rapid build-up (\*) and long decay (cycles 1–12) of the sound pulse amplitude. (C) The pulse amplitude relative to the peak (left-hand scale) and instantaneous frequency (right-hand scale) of pulse 1 plotted against the number of cycles from the start of the pulse. The dotted line on the amplitude plot shows where the points should lie if the pulse amplitude had decayed exponentially from the start; there is evidence of non-linearity in the first three cycles from both the decay amplitude and the frequency of the pulse. Frequency was measured as the reciprocal of the period of the waveform: the limiting resolution was 10  $\mu\text{s}$ , corresponding to 170 Hz at 4 kHz. The line labelled frequency trend is explained in the text.

*Tymbal sounds produced by buckling the intact tymbal*

When buckled inwards by a single movement at an appropriate speed through an appropriate distance, either by apodeme pulls or by apodeme pit pushes (see above), the tymbal produces a train of four discrete IN pulses (Fig. 3A). Each pulse starts with a rarefaction followed by a larger compression and then decays as a damped oscillation. (The compression and rarefaction described here are relative to the external surface of the tymbal; the sound pressures that drive the Helmholtz resonator are those within the abdomen, which are reversed in sign.)

The sense of the sound pressure during the first cycle of each sound pulse is compatible with an initial rapid inward movement of the tymbal plate as the first tymbal rib buckles, followed by a larger-amplitude outward rebound of the tymbal plate (Fig. 3B). After the first one or two cycles, the sound amplitude decays more-or-less exponentially (Fig. 3C).

At the start of an IN pulse (Fig. 3B, marked with an asterisk), the first half-cycle builds up over approximately 20  $\mu$ s into the rapid first rarefaction as the tymbal plate buckles inwards, followed by the compression of the rebound of the outward movement; in most preparations, this first cycle also showed considerable frequency and amplitude distortion. The inward-moving half-cycle occurred more rapidly than the following outward-going half-cycle, and the amplitude of the rarefaction was smaller than that of the immediately succeeding compression. In this first cycle or in the first two cycles, the pulse is highly asymmetrical, with the amplitudes of successive compressions exceeding those of the rarefactions (Fig. 3B); as the pulse decays, the waveform becomes more symmetrical and its instantaneous frequency also rises by 150–350 Hz between the start and the end of the pulse (frequency trend in Fig. 3C). Both these observations suggest that the vibration is initially non-linear when the amplitude of vibration is largest but that it becomes more linear as the pulse decays. Plots of the pulse amplitude against time show that, after the first two or three cycles, the amplitude decays nearly exponentially (typically  $r^2 > 0.98$ ,  $d.f. > 20$ ), suggesting that the resonance in this region is determined by the simple interaction between linear mass, compliance and damping elements.

The asymmetry of the waveform suggests that the amplitude of the initial inward movement is smaller than that of the subsequent outward rebound. The geometry of tymbal buckling (Fig. 8 in Young and Bennet-Clark, 1995) suggests that the inward movement of the tymbal plate and rib 1 will be constrained by the resilin sheet that couples it to the next, unbuckled, rib. The outward rebound, however, will not be constrained in this way.

The IN pulses produced by successive tymbal apodeme pulls are closely similar. Fig. 4 shows superimposed groups of five repetitions of each of the four IN pulses from the same tymbal. For IN pulses 1 and 2, the peak amplitude varies by less than 1 dB, the rate of decay of the pulse and  $Q$  are closely similar, and the frequency of oscillation during the decay does not vary by more than 50 Hz. IN pulses 3 and 4 become successively more variable, possibly because of the difficulty of pulling the

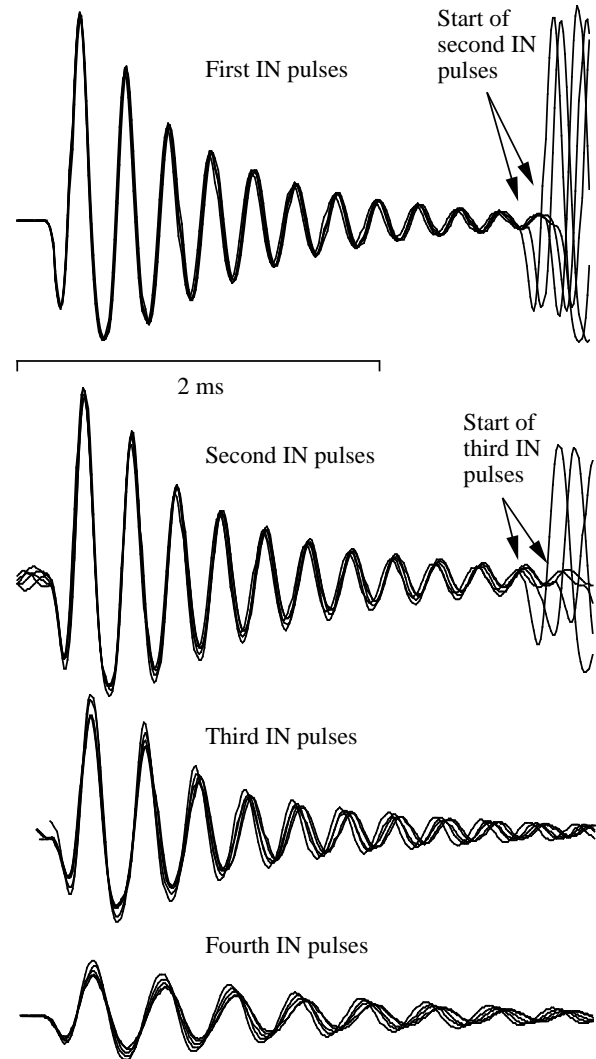


Fig. 4. Superimposed oscillograms of five IN pulses, produced by the successive buckling of each of the four tymbal ribs, to show the repeatability of the pulse structure. The IN pulses were all obtained from the same tymbal preparation by pulling on the tymbal apodeme.

apodeme in exactly the same direction each time. However, IN pulses 1 and 2 are sufficiently repeatable for successive and comparative measures to be made.

A single rapid apodeme pull produced pulses that followed one another closely, and a slower pull produced pulses that were spaced more widely apart. If an IN pulse followed its predecessor rapidly, before the preceding pulse amplitude had decayed greatly, the waveform tended to be coherent throughout the waveform of the pulse train; in other words, the phase of a succeeding pulse was locked to that of a preceding pulse (Fig. 5A). If, however, the preceding pulse amplitude had decayed to less than approximately one-quarter of its peak amplitude, the phase-locking tended to break down (Fig. 5B). This suggests that a rib buckles inwards more easily if the start of its movement coincides with the inward phase of the existing vibration of its predecessor.

Between the first IN pulse, produced by the buckling of

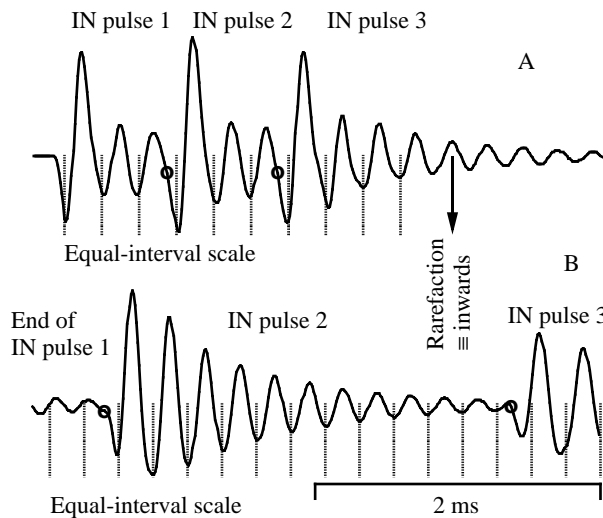


Fig. 5. Oscillograms of sequences of three IN pulses produced by apodeme pulls on two different preparations. (A) A rapid apodeme pull that produces closely spaced pulses that decay to approximately one-third of peak amplitude before the next pulse starts. The equal-interval scale aligned with the peak rarefactions of IN pulse 1 shows that the waveform during all three pulses is closely coherent in phase and that succeeding pulses appear to be initiated at a constant phase and amplitude on the inward-going half-cycle of the preceding pulse (○). (B) A slower apodeme pull that produces more widely separated pulses which have decayed to approximately one-tenth of peak amplitude before the start of the next pulse. The equal-interval scale is aligned with the peak rarefactions of IN pulse 2 and shows that pulse 2 is not phase-locked to either IN pulse 1 or IN pulse 3. Succeeding pulses do not start at a constant phase relative to that of preceding pulses (○).

tymbal rib 1, and the fourth IN pulse produced by rib 4, the dominant frequency of each pulse fell (Table 2).  $Q$  for the decay of the vibration increased between IN pulse 1 and IN pulse 4 with the decreasing frequency of the vibration (Fig. 6A,B). The peak amplitudes of the first two pulses were usually similar; the peak amplitudes of the third and fourth pulses were usually approximately 2 dB and over 6 dB, respectively, less than that of the first pulse (Table 2).

Table 2. Resonant frequency, frequency ratio and relative peak amplitude of the pulses or sound pulses produced by successive tymbal rib buckling produced by apodeme pulls

Source of sound pulse	Resonant frequency during the decay of the pulse (kHz)		Frequency ratio, loaded:unloaded	Peak amplitude of sound pulses relative to maximum for IN pulse 1
	Tymbal unloaded	Tymbal plate loaded with 380 $\mu$ g		
Rib 1 IN	4.37 $\pm$ 0.13 kHz (8)	3.23 $\pm$ 0.25 kHz (7)	0.74	1
Rib 2 IN	4.19 $\pm$ 0.37 kHz (8)	3.04 $\pm$ 0.33 kHz (7)	0.73	1.01 $\pm$ 0.31 (7)
Rib 3 IN	3.92 $\pm$ 0.32 kHz (7)	3.03 $\pm$ 0.30 kHz (6)	0.77	0.83 $\pm$ 0.20 (7)
Rib 4 IN	3.17 $\pm$ 0.36 kHz (5)	2.61 $\pm$ 0.27 kHz (4)	0.82	0.39 $\pm$ 0.22 (5)
Tymbal OUT	6.54 $\pm$ 0.27 kHz (7)	4.43 $\pm$ 0.55 kHz (5)	0.68	0.34 $\pm$ 0.16 (6)

The amplitude of the OUT pulse has been corrected for the 6 dB decrease in the microphone response at 6 kHz relative to that at 4 kHz. The table shows means  $\pm$  S.D. of measurements from different preparations ( $N$ ).

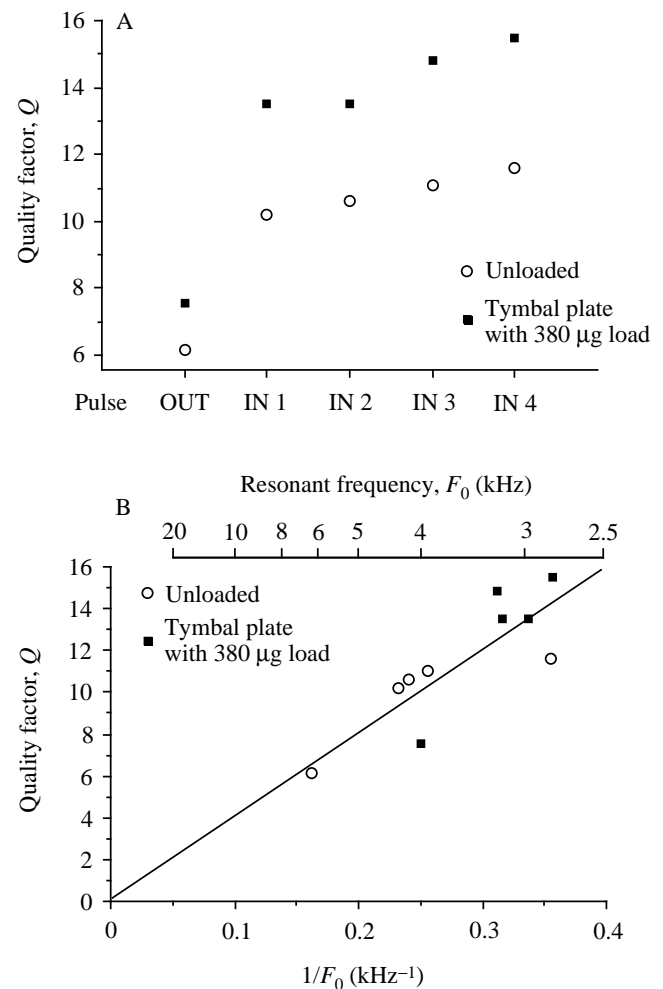


Fig. 6. (A) The quality factor ( $Q$ ) of the decay of IN and OUT pulses of a tymbal loaded with a 380  $\mu$ g weight and after the load has been removed. (B) The quality factor ( $Q$ ) plotted against the reciprocal of the resonant frequency ( $1/F_0$ ) for the IN and OUT pulses of the same tymbal as in A.

The dominant frequencies of the first two IN pulses are typically slightly above and slightly below, respectively, the

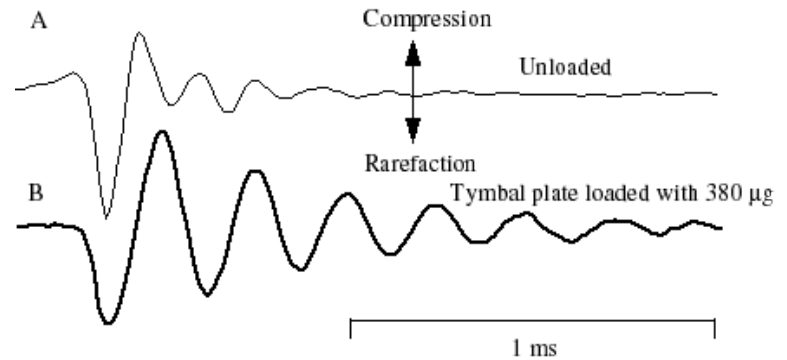


Fig. 7. OUT pulses produced by the buckling outwards of the tymbal after release of the tymbal apodeme. (A) A pulse from an unloaded tymbal; (B) a pulse from the same tymbal with a 380  $\mu\text{g}$  load glued onto the tymbal plate.

4.3 kHz dominant frequency of the insect's calling song (Table 2). The 3.9 kHz frequency of the third IN pulse and the 3.2 kHz of the fourth IN pulse are lower than that of the song. Normally, during singing, only the first two, or sometimes the first three, ribs buckle (Young and Bennet-Clark, 1995).

When the concave (buckled-in) tymbal buckled outwards to regain its convex rest position, the movement produced a single short OUT pulse (Fig. 7A). This brief pulse has been described previously (Young and Bennet-Clark, 1995); the dominant frequency was between 6 and 7 kHz (Table 2) and the waveform was often highly asymmetrical (Fig. 7A) with a small initial compression followed by a larger rarefaction. In *C. australasiae*, the amplitude of the OUT pulses (Table 2) was typically approximately 10 dB lower than that of the corresponding IN pulses, and  $Q$  (Fig. 6A) was also lower than those of the IN pulses. This is in contrast to the relatively loud tymbal OUT pulses of some other cicadas, such as *Tympanistalna gastrica* (Fonseca and Popov, 1994).

#### Tymbal sounds produced by buckling the loaded tymbal

Tymbal pulses were produced by pulling the tymbal apodeme after loading the tymbal plate with a 380  $\mu\text{g}$  weight glued into a concavity 2–2.5 mm ventral to the apodeme pit (Fig. 8E). Trains of four IN pulses similar in character and with similar pulse envelopes to those produced by the unloaded tymbal (cf. Fig. 8A,B), but always of far lower resonant frequency (cf. Fig. 8C,D) and with higher  $Q$  (Fig. 6A), were produced.

In the unloaded tymbal,  $F_0$  decreased systematically from IN pulse 1 to IN pulse 4, but  $F_0$  for the different IN pulses differs far less in the loaded tymbal (Table 2); the resonant frequency of IN pulse 1 was reduced to 0.74 times that of the unloaded tymbal, but that of IN pulse 4 was reduced to 0.82 times that of the unloaded tymbal. This change in relative resonant frequency implies that the ratio between the mass and the stiffness of the vibrating system alters as successive ribs buckle (equation 1). For the unloaded tymbal, the successive rib bucklings cause a reduction in the product of the mass and

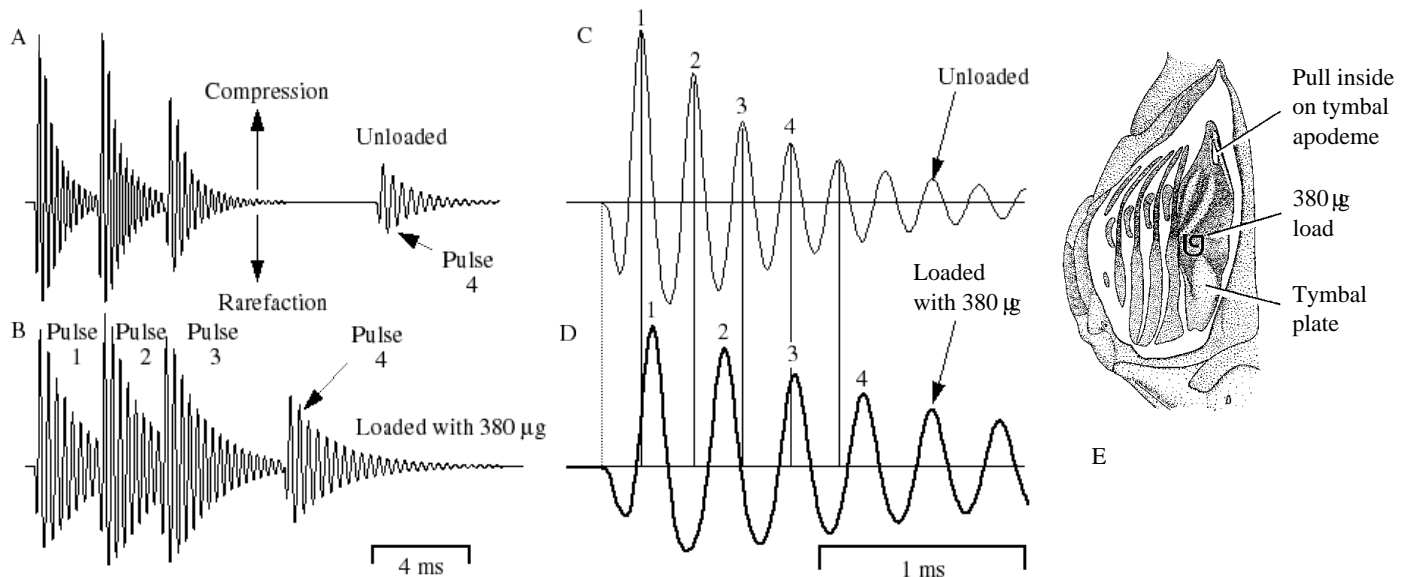


Fig. 8. IN pulses produced by the same tymbal when loaded and unloaded. (A) The train of four IN pulses produced by pulling on the apodeme of an unloaded tymbal; (B) the train of four IN pulses produced by the same tymbal when loaded with a 380  $\mu\text{g}$  wire weight. (C) The first IN pulse of the unloaded tymbal, on an expanded time scale; (D) the first IN pulse of the loaded tymbal on the same time scale as C. In C and D, the first four cycles of the pulse are numbered to allow the waveforms to be compared. (E) Diagram of the tymbal to show the position on the tymbal plate of the 380  $\mu\text{g}$  wire weight.



the stiffness so that the resonant frequency falls steadily; as the buckling of rib 4 only involves a very small change in mass, the stiffness of the system must fall considerably as this rib buckles inwards. For the loaded tymbal, the resonant frequency of successive IN pulses remains more nearly constant, implying that, as the ribs buckle inwards, any successive changes in the vibrating mass are more nearly matched by the changes in stiffness.

The wet mass of the tymbal plate was approximately 550  $\mu\text{g}$  and that of rib 1 approximately 100  $\mu\text{g}$  (Table 1), so the vibrating mass of the tymbal plate + rib 1 (after rib 1 has buckled inwards) is approximately 650  $\mu\text{g}$ . The standard load used here was 380  $\mu\text{g}$ , giving a total mass for the loaded tymbal plate + rib 1 of approximately 1030  $\mu\text{g}$ . If the resonant system were a simple mass and compliance, the resonant frequency after loading would be expected to fall by  $\sqrt{(650/1020)}$  or to 0.8 times the unloaded value. The resonant frequency of pulse 1 of the loaded tymbal was 0.74 times that of the unloaded tymbal, which is a reasonable, but not very close, approximation to the expected value. However, in a hinged system of the type studied here, it would be hard to ensure that any load has been applied at the effective centre of mass of the vibrating system.

$F_0$  for IN pulses 2, 3 and 4 was also reduced following loading, but to a decreasing extent (Table 2). This is the expected result if a standard load is applied to a series of resonant systems of increasing mass. A result of this type would be expected if the masses of successive buckled-in ribs were to be added to the vibrating system.

The OUT pulses of the loaded tymbal (Fig. 7B) were also lower in frequency, to 0.68 times that of the unloaded tymbal (Table 2); this effect on the resonant frequency is greater than that for the IN pulses, suggesting either that a smaller vibrating mass, such as that of the tymbal plate alone, is involved or, less likely, that the compliance involved in this resonance has decreased.

In the abdomenless cicada preparation used here, the damping of the tymbal due to the acoustic load of the abdominal Helmholtz resonator is greatly reduced. The  $Q$  values measured here, for both the unloaded and the loaded tymbal, far exceed those found in the intact animal (as reported by Young and Bennet-Clark, 1995), in which the tymbal vibration is damped by the acoustic load. The  $Q$  values for the acoustically loaded tymbal in the intact insect (data from Young and Bennet-Clark, 1995) are always approximately half those found here for the corresponding IN pulses of the unloaded tymbal. A plot of  $Q$  factor against the reciprocal of resonant frequency ( $1/F_0$ ) (Fig. 6B) suggests that damping increases with increasing frequency. This is what is expected if the damping is mainly due to internal viscous losses in the tymbal and its surrounds.

During rapid apodeme pulls with loaded tymbals, a coherent train of IN pulses, similar to those shown in Fig. 5A, was produced. This suggests that a similar mechanism maintains the coherence of the waveform even though the dominant frequency is significantly lower.

#### Driven resonances of the tymbal

When the intact tymbal was excited by the vibration probe, several distinct resonances were observed. The frequency at which these occurred was measured by first observing the frequency at which the amplitude of the response was maximal and then observing the frequency at which the build-up of the pulse envelope was most gradual.

With light pressure on the apodeme pit, causing a 25–100  $\mu\text{m}$  inward displacement of the tymbal plate but no rib buckling, the resonance occurred between 5.4 and 7 kHz, corresponding to the dominant frequency of the OUT pulses.

When the vibration probe was advanced further, ribs 1 and 2 tended to buckle inwards together, followed by the buckling of rib 3 then rib 4. By then withdrawing the probe rod, the successive resonances were observed to be at 2.7–3.5 kHz with rib 4 IN, 3–4 kHz with rib 3 IN, 3.3–4.5 kHz with rib 2 IN and 3.5–4.7 kHz with only rib 1 IN. The frequencies observed were very sensitive to both the trajectory of the push and the precise point on the tymbal at which the probe was applied.

These measurements are essentially similar to those described by Young and Bennet-Clark (1995); the difference is that the range of resonant frequencies observed with the tymbal ribs IN is now ascribed to the state of each of the different ribs.

#### Effects of removal of parts of the tymbal

The regions that were removed from the tymbal and the cuts

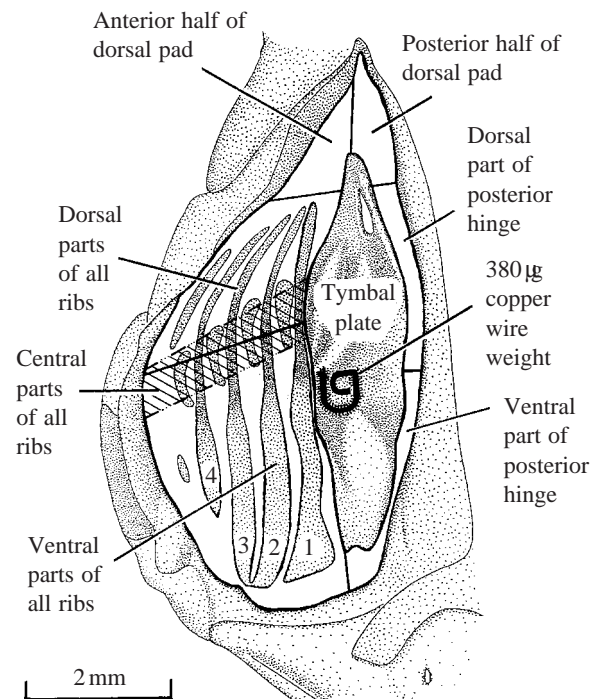


Fig. 9. Drawing of the tymbal to show the parts that were removed for the tests described in the text and Table 3. The long ribs are numbered as in Fig. 2. The position on the tymbal of the 380  $\mu\text{g}$  wire weight is also shown.

Table 3. *Effect of successive removal of parts of the tymbal (see Fig. 9) on the presence (+) of a rib 1 IN pulse and on the resonant frequency ( $F_0$ )*

Parts cut or removed	Drive	IN Pulse	$F_0$ (kHz)
<b>Tymbal A</b>			
Intact, first IN pulse	Apodeme pull	+	3.63
Dorsal parts of all ribs	Free vibration	–	3.23
Ventral parts of ribs 3 and 4	” ”	–	2.56
Ventral parts of ribs 2, 3 and 4	” ”	–	2.05
Ventral parts of all ribs (all ribs removed)	” ”	–	2.58
Anterior half of dorsal pad	” ”	–	1.56
<b>Tymbal B</b>			
Intact, first IN pulse	Apodeme pit push	+	4.24
Dorsal pad	” ”	+	3.23
Centres of all ribs	Free vibration	–	2.67
Dorsal parts of all ribs	” ”	–	2.30
Dorso-ventral cut anterior to rib 4	” ”	–	2.34
Ventral parts of ribs of 3 and 4	” ”	–	1.68
Ventral parts of ribs of 2, 3 and 4	” ”	–	1.22
Ventral parts of all ribs	” ”	–	1.56

See Materials and methods for a description of the different methods used to drive the tymbal.  
Tymbals A and B were from different animals.

or operations that were made are shown in Fig. 9. The effects of these treatments are shown in Table 3.

As has been reported previously, the buckling of the tymbal depends on the integrity of the long ribs (Young and Bennet-Clark, 1995). However, if part or all of the dorsal resilin pad was removed without damaging the ribs, the tymbal could still be buckled in, producing a pulse of sound, but removal of or cuts to the long ribs, starting at rib 4 and working towards rib 1, successively weakened and ultimately destroyed the buckling and IN pulses during inward apodeme pit pushes.

When the anterior half of the dorsal resilin pad was cut away, the resonant frequency of the tymbal plate fell; it fell further after removal of the posterior half of the dorsal pad when the tymbal was made to buckle in by apodeme pit pushes (Table 3) and after it had buckled in when driven by forced vibrations. It was difficult to ensure that the same amount of the pad had been removed, causing the effect to vary between preparations.

The effects of successive removal of various regions of the tymbal (Fig. 9) are shown in Table 3. The general finding was that removal of either the ribs or parts of the dorsal resilin pad lowered the resonant frequency of the tymbal plate in free vibration. This implies that there are two major compliant elements in the resonant system: the dorsal resilin pad, which

also restores the buckled-in tymbal to its resting buckled-out position, together with the long ribs which, with their resilin surrounds, provide extra stiffness. One exception is that removal of the ventral halves of rib 1, after previous removal of the other ribs, caused the resonant frequency to increase slightly, implying that the overall mass of the system had been reduced with little change of stiffness.

The high-frequency OUT resonance was little affected by cutting along the anterior edge of the tymbal between rib 4 and the frame, but after this operation, the amplitude of the IN pulses was greatly reduced. After complete removal of ribs 2–4, the OUT resonance remained but the amplitude and  $Q$  of the IN pulse were reduced still further. However, after inward buckling of the remaining ribs or rib, the lower-frequency IN resonance was still found, but always at a lower frequency than was observed with the same tymbal before the operation. After removal of all ribs (Fig. 9), buckling the tymbal inwards was impossible. Only a single resonance of the tymbal plate could be observed, usually at approximately 3 kHz, which is rather lower than the typical IN resonances of the intact tymbal. Thus, the asymmetry between the OUT and IN resonance seems to require the integrity of at least one rib adjacent to the tymbal plate. The IN resonant frequency appears to be partly determined by the participation of the intact ribs and their resilin surrounds with the tymbal plate.

Loading the tymbal plate of a tymbal that had all the ribs cut away lowered the resonant frequency of the free vibration of the tymbal plate from 1.46 kHz to 930 Hz. This loaded:unloaded ratio of 0.64 is similar to the ratio of 0.68 measured for the effect of loading on the frequency of the OUT pulse of intact tymbals, suggesting that a similar combination of mass and stiffness determine both resonances.

#### *The force–distance relationships of the tymbal*

The tymbal was buckled IN by pushing on the apodeme pit along the axis of pull of the tymbal apodeme. The force required to buckle rib 1 inwards was approximately 0.25 N (values of 0.22, 0.25 and 0.3 N were obtained from three different preparations). After it had been buckled in, the force required to hold rib 1 IN was approximately 0.05 N. Unfortunately, it was not possible to carry out detailed measurements of changes in the force as the tymbal plate was moved inwards and outwards.

The force required to buckle the tymbal increased as the tymbal plate was pushed inwards. From rest, the distance moved until rib 1 buckled IN was approximately 300  $\mu\text{m}$  (Young and Bennet-Clark, 1995), but over the last 100–150  $\mu\text{m}$  the force was approximately 0.25 N. During the outward movement, the force was 0.03–0.05 N during the first 100–150  $\mu\text{m}$  of the movement.

## Discussion

### *The resonant tymbal as a determinant of the insect's song frequency*

By external manipulation, the tymbal of *C. australasiae* can

be made to produce a train of pulses in a similar manner to those produced by the action of the insect's tymbal muscle, but on a slower and more manageable time scale. Each of these artificially driven pulses is a vibration with a rapid initial build-up followed by a slower exponential decay, producing a sound pulse as a hammer blow might excite a vibration in a bell or a piano string. The resonant frequency of the tymbal vibration is nearly constant throughout each pulse, suggesting that a simple mass-and-compliance mechanism is responsible for the resonance, but asymmetry in the waveform at the start of the pulse indicates that non-linear deformation may occur during the initial rapid release of stored energy as each rib buckles. The non-linearity occurs during the rarefaction or inward-moving half-cycle, suggesting that the initial large-amplitude inward movement is being constrained by adjacent regions of the tymbal, such as the succeeding rib, which remains in the OUT position, but that a similar constraint is not imposed during the outward movement. This interpretation is compatible with an earlier reconstruction of the mode of buckling of the tymbal based on its anatomy (Fig. 8 in Young and Bennet-Clark).

The resonant frequencies of the pulses produced by the buckling of the first two long ribs are close to the frequency of peak power of the insect song. This is consistent with an earlier model of the role of the tymbal as the primary resonator in cicada sound production (Bennet-Clark and Young, 1992; Bennet-Clark, 1995). The  $Q$  values of the tymbal resonances described here are higher than the  $Q$  value normally measured from the intact insect's song pulses, supporting the suggestion that the tymbal pulses of the intact singing insect are damped by the abdominal resonator during the transduction of the high-pressure tymbal sound pulses that allows the dissipation of energy as sound (Young and Bennet-Clark, 1995).

The four successive tymbal IN pulses produce sound pulses with peak energy at decreasing frequencies (Table 2), suggesting that the stiffness of the system is decreasing and/or that the mass of the system is increasing. The former effect is likely to be more important because rib 4 is the smallest (Fig. 2) and its mass is least (Table 1), but the change in peak frequency between IN pulse 3 and IN pulse 4 is greatest (Table 2). The effect of an applied load on the tymbal plate on the resonant frequency of the pulses differs from rib to rib: with the unloaded tymbal, there is a steady decrease in the  $F_0$  values between IN pulses 1, 2 and 3, but with the loaded tymbal, there is little difference between the  $F_0$  values of IN pulses 2 and 3 (Table 2), suggesting that comparatively minor changes in the mass:compliance ratios of the elements of the tymbal might be used to adjust the relative frequency of successive IN pulses.

#### *The tymbal as a frequency-multiplying driver*

Earlier work suggested that the long song pulses of *C. australasiae* are driven by two or three IN pulses produced by the buckling of a series of tymbal ribs (Young and Bennet-Clark, 1995). Tests using a model showed that such song pulses could only be produced if the successive IN pulses were coherent (Figs 13–14 in Bennet-Clark and Young, 1992) but

did not suggest a mechanism by which coherence might be ensured or provide other than circumstantial evidence that it occurred. Further evidence that the train of IN pulses is normally coherent is given in Young and Bennet-Clark (1995; their Fig. 10).

Fig. 5 shows that if the successive bucklings occur rapidly enough, while the amplitudes of the preceding pulses are large, the waveform of a series of three IN pulses can be closely coherent, but if the preceding pulse has decayed greatly before the start of the next pulse, coherence may be lost.

When the tymbal is buckled by its muscle during singing, the ribs buckle IN at intervals of 2–3 cycles (approximately 0.5–0.7 ms), as in Fig. 5A where all three pulses are coherent. It appears that the tymbal buckling mechanism offers good coupling between the vibrations of the ribs so that the rapidly excited tymbal inevitably produces a coherent waveform. A given rib is most likely to buckle inwards when the preceding rib is at the inward phase of its vibration.

Analogous mechanisms for producing long coherent waveforms by a succession of impulses have been modelled in bush crickets (*Homorocoryphus*) (Bailey and Broughton, 1970) and described in crickets (*Gryllus*) (Elliott and Koch, 1985). These mechanisms are likely to be found in any insect sound-producing mechanism that produces long sustained sound pulses.

#### *The tymbal resonant frequencies and the asymmetry between the IN and OUT pulses*

Given approximate values for the mass and stiffness of different parts of the tymbal, an estimate of the tymbal resonant frequency in the IN and OUT conditions can be made using equation 1.

In making these calculations (Table 4), I have made various assumptions. First, that the effective compliance in the IN

Table 4. *The asymmetry of the tymbal resonance for inward and outward movements*

IN resonance	
Force required to hold rib 1 after it has buckled inwards (N)	0.05
Distance moved ( $\mu\text{m}$ )	100
Compliance ( $\text{mN}^{-1}$ )	$2 \times 10^{-3}$
Effective mass when buckled IN (=mass of tymbal plate + 1, 2 or 3 ribs) ( $\mu\text{g}$ )	650–900
Calculated $F_0$ when IN (kHz)	4.4–3.8
Measured $F_0$ of IN pulses (kHz)	4.4, 4.2, 3.9 and 3.2
OUT resonance	
Force required to move tymbal inwards after rib 1 has buckled outwards (N)	0.13
Distance moved ( $\mu\text{m}$ )	150
Compliance ( $\text{mN}^{-1}$ )	$1.2 \times 10^{-3}$
Effective mass when buckled OUT (=mass of tymbal plate alone) ( $\mu\text{g}$ )	550
Calculated $F_0$ when OUT (kHz)	6.2
Measured mean $F_0$ of OUT pulses (kHz)	6.5

resonance is that observed as the tymbal moves outwards from the buckled IN to the OUT position *before* the outward buckling has occurred, and that the effective compliance in the OUT resonance is that measured as the tymbal moves inward from the OUT to the buckled IN position *after* buckling has occurred. Second, that the effective mass in the IN resonance is that of the tymbal plate plus one or more tymbal ribs, and that the effective mass in the OUT resonance is that of the tymbal plate; these assumptions are based on measurements of the effects of loading the tymbal plate described above. Third, in the calculation of the tymbal compliances, that the force acting on the tymbal system during the inward movement is approximately half the maximum force required to buckle rib 1 and acts over half the 300  $\mu\text{m}$  distance that the apodeme pit moved before rib 1 buckled IN. After the tymbal has buckled IN, the force is assumed to be constant over the 100  $\mu\text{m}$  movement during which the resonant frequency of a driven tymbal is known to be more-or-less constant (Fig. 13 in Young and Bennet-Clark, 1995).

These assumptions are, of course, over-simplifications. However, using these assumptions, the frequencies calculated for the IN and OUT resonant frequencies are reasonably close to the values measured from tymbal pulses (Table 4). In particular, the asymmetry between the outward compliance and the inward compliance provides an explanation for the observed differences between the IN and OUT resonant frequencies.

This model is only offered tentatively but it suggests that more detailed data might give a better understanding of the factors determining the resonant frequencies.

#### *The tymbal as an energy store and muscle-power amplifier*

From the experiments described above, it is likely that the resilin surrounding the tymbal plate and the ribs, together with the dorsal pad, act as major elastic elements in the tymbal. The role of these elements in tymbal buckling cycle is now considered.

Initial muscle contraction causes deformation of the tymbal, accompanied by a rise in the force required for deformation, which together store energy in the resilin. This energy continues to be stored because the unbuckled long rib restricts the distance through which the tymbal plate can move inwards.

When the rib buckles at its centre, the tymbal plate moves inwards rapidly. This movement is accompanied by a rapid reduction in the stiffness of the tymbal as the stored energy is suddenly released. This rapid release of energy accounts for the shape of the envelope of the pulse produced by each rib, which reaches a peak amplitude during the first cycle of vibration (Fig. 3A). During the subsequent outward movement in which the tymbal returns to its resting OUT position, the stiffness of the tymbal mechanism is far lower than during the inward movement so the amount of energy available for release as the ribs finally buckle outwards is far smaller than during the inward movement. The OUT pulse is therefore far quieter than the IN pulse (Table 2).

Typical  $Q$  values for IN pulses were greater than 10

(Fig. 6A) but, for two tymbals,  $Q$  values of greater than 14 were measured for pulses of the unloaded tymbal. For a  $Q$  of 10, the natural logarithm of the decrement of the vibration is  $-0.314$ , so the amplitude per cycle decreases by  $e^{-0.314}$  or at a rate of 0.73-fold per cycle; the power per cycle is proportional to the square of the decrease in amplitude ( $=1-0.73^2$ ) so the power loss per cycle is 0.47-fold, or 0.22-fold per half-cycle. This corresponds to an elastic efficiency per half-cycle of 0.78. This value can be compared with the loss factor of 2.5 % per half-cycle reported by Jensen and Weis-Fogh (1962) for locust resilin wing hinges, which they equated with an elastic efficiency of 0.96–0.97. Although the efficiency of locust wing hinge resilin is far higher than the values obtained in the present study, Jensen and Weis-Fogh's (1962) measurements were made with small-amplitude strains and at frequencies below 200 Hz, whereas the present measurements have been made at approximately 4 kHz and with large strains that show some non-linearity (Fig. 3A,B); it is not known what effects other damping, such as that due to air-sac membranes etc., may have had on the overall vibration of the system. However, since resilin appears to be a major elastic component in the system, the present findings show that this remarkable elastic protein is capable of the storage and release of energy with comparatively high efficiency, even at 4 kHz and without a balance sheet of the other losses in the system.

As in the jump of the flea (Bennet-Clark and Lucey, 1967) and many other insect energy-storage systems (reviewed by Gronenberg, 1996), resilin acts as an energy store in which muscle work is stored comparatively slowly (perhaps during the first 2–4 ms of contraction) and is then released rapidly by the sudden buckling of the tymbal ribs over a period of one cycle or 230  $\mu\text{s}$ . Even allowing for losses, this sudden release gives an effective mechanical power amplification of approximately tenfold, which is used to provide a sound pressure impulse to the inside of the abdominal resonator of the cicada. The type of sound pulse that such impulses excite may be compared with the slow build-up of the sound pulses that is seen in the songs of crickets, tree crickets, mole crickets, etc. (e.g. Leroy, 1966; Dumortier, 1963; Bennet-Clark, 1970), in which the song is produced cycle-by-cycle by a file-and-scraper mechanism that acts as a sort of escapement, supplying energy to the resonant system at an appropriate phase in each cycle of the pulse (Elliott and Koch, 1985).

#### *The roles of the different parts of the tymbal*

The results of the experiments described here show that the tymbal acts in a complex way to produce trains of sound pulses. It is clear that there is no single and simple element of mass or compliance in the tymbal. The cuticular ribs provide mass to the system, but also show some compliance. Similarly, the resilin structures function mainly as compliant elements, but also have inherent mass. Further, the compliance of different structures varies with the state of the tymbal. However, the results do suggest specific functions for the various parts of the tymbal. These are discussed below.

*Tymbal plate*

The tymbal plate acts as a large-area rigid plate, driven by the tymbal muscle. When each long rib buckles, the tymbal plate moves inwards rapidly and is set into resonance, thereby producing a high-pressure sound pulse within the abdomen. It acts as a major mass determinant of  $F_0$ .

*Long ribs*

In the OUT position, the long ribs act as the unstable catch that allows energy to be stored in the elastic elements of the inward-moving tymbal. As each rib buckles at its narrow flexible centre, the stored energy is released to initiate each of the train of tymbal IN pulses. The asymmetry in the forces and distances over which the inward and outward buckling occur results in asymmetry in both the amplitude and frequency of the IN and OUT pulses. The mass and elasticity of the ribs and the resilin that surrounds them are both determinants of  $F_0$ . The long ribs and their surrounds also act as energy stores.

*Short ribs*

The short ribs allow independent buckling of the long ribs at their centres, permitting the tymbal plate to vibrate freely as successive long ribs buckle inwards.

*Dorsal pad*

The dorsal pad is a major elastic antagonist to the tymbal muscle. It acts as an energy store during the inward movement and as an elastic restoring force to move the tymbal plate outwards. It is a major elastic determinant of  $F_0$ .

*Posterior resilin hinge*

This determines the locus of the tymbal plate movement. It is only a minor elastic determinant of  $F_0$ .

*The tymbal as a mechanical system*

The tymbal of *C. australasiae* is anatomically complex and, despite the present attempts to describe the masses and compliances that determine its resonant behaviour, remains difficult to reduce to simple components. It does not have any single definable mass or any single discrete compliant element: the various structures are coupled so that they interact, and the interactions vary with the state of the tymbal ribs; the different structures all appear to have individual masses and compliances that interact on the resonant properties of the whole.

Tymbals with a similar basic structure are found throughout the Cicadidae. Differences in the body size, the song frequency (Bennet-Clark and Young, 1994), the number of tymbal ribs (Young and Josephson, 1983b; Fonseca, 1994), the rate of muscle contraction (Young and Josephson, 1983a) and the effect of the tymbal tensor muscle have been described for a variety of cicadas and are known to be factors that affect the quality of their songs (Fonseca and Hennig, 1996), but it is likely that, in all cicadas, the tymbal has the same general role as an energy-storing determinant of the song frequency.

Once again, it is a pleasure to acknowledge my gratitude to the University of Melbourne for hospitality, a Visiting Scholar's grant and facilities during a period spent in Melbourne during my sabbatical leave from Oxford University and St Catherine's College, Oxford. Financial support was also provided by a grant from the Australian Research Council to Dr David Young. My thanks go, too, to many members of the Department of Zoology, University of Melbourne, for once more making me so welcome during this recent visit. It is a special pleasure to acknowledge the assistance and advice of Dr David Young and Dr Alisdair Daws throughout this work, and to Alisdair Daws and an anonymous referee for their comments on the manuscript.

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