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A MODEL OF THE MECHANISM OF SOUND PRODUCTION IN CICADAS

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Summary

1. Dried cicada bodies of the species *Cyclochila australasiae* and model cicadas made from a miniature earphone driving a plastic cavity were used to study the acoustics of sound production in male cicadas.

2. A model cicada with shape and dimensions similar to those of the abdomen of a male *C. australasiae* resonates at the natural song frequency of the species (4.3 kHz). The abdominal air sac of *C. australasiae* also resonates at frequencies close to the natural song frequency when excited by external sounds. In an atmosphere of chlorofluorocarbon (CFC) gas, the resonant frequency is lowered in keeping with the decrease in velocity of sound in the CFC gas.

3. At the model's resonant frequency, the driving earphone dissipates more electrical power with the cavity attached than without the cavity. The cavity of the model cicada acts as a narrow-band acoustic acceptance filter, tuned to the natural song frequency.

4. When the miniature earphone emits brief clicks, mimicking those produced by the natural tymbal mechanism, the model cicada produces sound pulses that vary in duration and shape according to the number and timing of the clicks. A coherent train of two or three resonant clicks results in a long slowly-decaying sound pulse similar to that in the natural song.

5. The natural song frequency can be predicted from the dimensions of the abdominal cavity and the tympana in *C. australasiae* using a simple equation for the resonant frequency of a Helmholtz resonator. This equation also predicts the song frequency of *Macrotristria angularis* and *Magicicada cassini*, but it fails with the low-frequency song of *Magicicada septendecim*. This discrepancy can be accounted for by the unusually thick tympana of *M. septendecim*, which tend to lower the resonant frequency of the system.

6. We conclude that the abdomen of male cicadas forms a Helmholtz resonator, the components of which are the large air sac as the cavity and the tympana as the neck of the resonator. We suggest that cicada sound production depends on the coupling of two resonators, that of the tymbal and that of the abdominal air sac, from which sound is radiated through the tympana. The coupled resonator system would produce the long sound pulses required for stimulating a sensitive sharply tuned auditory organ.

Key words: cicada, sound production, (Helmholtz) resonator, tympanum, *Cyclochila*, *Magicicada*.

Introduction

Cicadas produce the loudest songs so far measured from any insect (Young, 1990). These sounds are produced only by the males, which do so by means of the specialized structures shown in Fig. 1 (Myers, 1929; Pringle, 1954; Young, 1990). These structures include a bilateral pair of stiff membranes, the tymbals, situated dorsolaterally on the first abdominal segment. The tymbals click inwards when pulled by the large tymbal muscles and thus act as sound-producing structures.

A large air sac is associated with the tymbals and tymbal muscles within the abdomens of male cicadas. Some of the early workers (e.g. Carlet, 1877) suggested that this chamber acts as a resonator, but it was Pringle (1954) who demonstrated experimentally

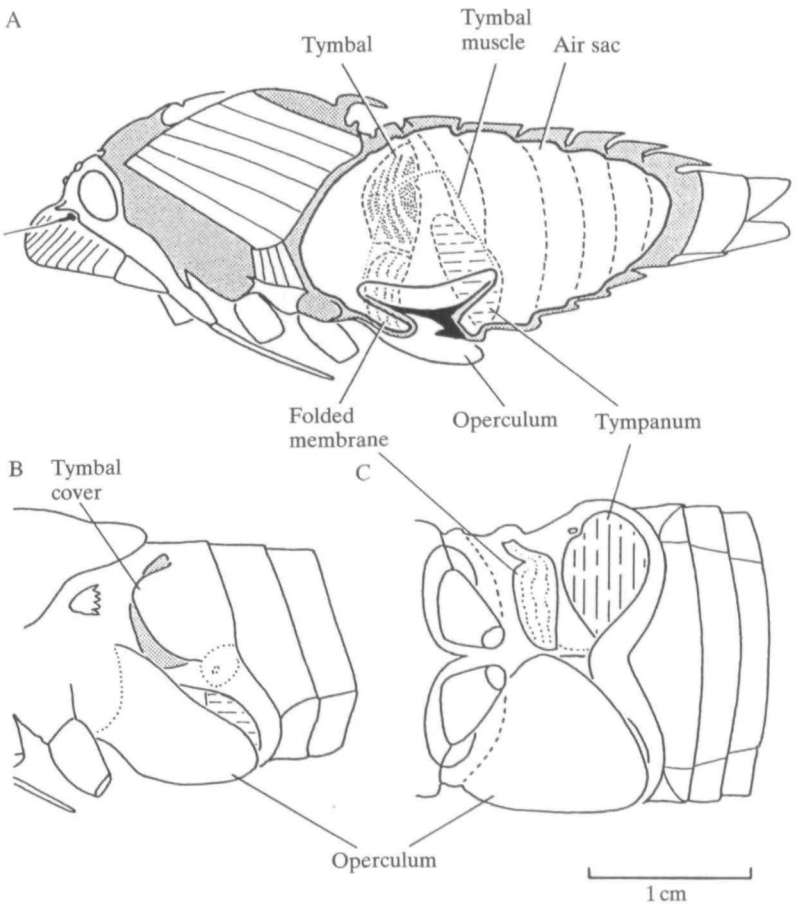

Fig. 1. Sound-producing structures in the abdomen of males of the cicada *Cyclochila australasiae*. (A) The insect has been cut open along the mid line to show the large air sac and its relationships to the tymbals, tympana and opercula. (B) Lateral view of the posterior part of the thorax and anterior part of the abdomen to show the position of the tymbal and cover and tympanum and operculum. (C) Ventral view of the posterior part of the thorax and anterior part of the abdomen to show the tympana; the left operculum has been removed. The scale bar applies to all drawings.

that the large abdominal air sac resonates at the frequencies present in the cicadas' song. Nevertheless, Pringle did not say exactly what the components of this air-sac resonator are, nor did he deal with the question of how the sound is radiated into the surrounding air.

In a review, Michelsen and Nocke (1974) stated the traditional view that sound is radiated by the tymbals but they did not consider the role of the air sac. More recently, Young (1990) has shown that the paired tympana, which form part of the auditory system and are situated ventrally on the second abdominal segment (Fig. 1), vibrate vigorously during singing and that the loudest sound is produced in their vicinity. Furthermore, the loudness of the sound can be controlled experimentally by opening or closing the opercular covers of the tympana. It thus appears that the tympanal apertures, rather than the tymbals, are the major sound radiators. Measurements of the volume of the abdominal air sac and of the area of the tympana are compatible with the suggestion that together these act as a Helmholtz resonator (Young, 1990).

A typical resonator has two components which react dynamically with each other in antiphase: a simple mechanical example consists of a spring and a mass coupled together. In the case of a Helmholtz acoustic resonator the two reactive components are the compliance of the air in the cavity (corresponding to the spring) and the inertance of the air in the hole or neck of the cavity (corresponding to the mass) (Helmholtz, 1885; Rayleigh, 1896; for a simpler account, see Seto, 1971). In the earlier cicada model, the abdominal air sac represents the cavity and the two tympanal apertures were taken to represent the 'hole' of the resonator (Young, 1990). Resonance is excited by the buckling of the tymbal and sound is radiated from the tympanal apertures.

The general equation for the resonant frequency, f_0, of a bottle-shaped resonator is:

$$f_0 = \frac{c}{2\pi}\sqrt{\left(\frac{A}{LV}\right)}, \tag{1}$$

where c is the speed of sound in the fluid, taken as $340\,\mathrm{m\,s^{-1}}$ for air, A is the area of the neck, L is the length of the neck and V is the volume of the cavity. Where the resonator has two holes, these terms should be somewhat modified: A is the combined area of the two holes, L is $16r/3\pi$ ($\approx 1.7r$) for a simple hole in a thin-walled vessel and r is the radius of one hole (Seto, 1971). These modifications to equation 1, which include corrections for the acoustic end-effect at either side of a simple hole in the wall of a vessel, have been used throughout the present paper, but equation 1 in its simple form was used, with a less appropriate estimate of the neck length L, by Young (1990) (see Results).

The effective increase in the amplitude of vibration at resonance and the rapidity with which changes occur are both indicated by the quality factor or Q value of the resonator. Like the resonant frequency, the Q value of a Helmholtz resonator also depends on the neck dimensions and cavity volume (Seto, 1971) and relates to the loss of energy from the oscillating fluid through the hole in the cavity. Q is given by:

$$Q = 2\pi\sqrt{\left(\frac{L^3V}{A^3}\right)}, \tag{2}$$

where, as above, A is the combined area of the two holes, L is $16r/3\pi$ ($\approx 1.7r$) for a simple hole in a thin-walled vessel and r is the radius of one hole.

In this paper, we have examined both the resonant frequency and the quality factor in experiments on the acoustic resonance of cicada bodies and of model cicadas of different dimensions to see how well such models predict the frequency and tonal purity of the natural cicada sounds.

During natural sound production, each tymbal buckles inwards, producing a clicking sound. Although the tymbals are ribbed, so that one muscle contraction is potentially capable of producing a train of as many clicks as there are tymbal ribs (Young and Josephson, 1983), it seems likely that the tymbal buckles in only two or three steps in many of the louder cicada species (Simmons and Young, 1978). In such a system, each step will produce an acoustic impulse. When a large part of the abdominal resonator is removed, tymbal-generated sound still contains the resonant frequency, f_0, but the intensity of other frequencies increases (Simmons and Young, 1978; Young, 1990). It appears from this that tymbal buckling produces damped sound waves at approximately the resonant frequency. In the natural song, these sound waves must then excite a sympathetic resonance in the abdominal cavity, from which the sound is radiated through the tympana.

To test this interpretation, we have also examined the acoustic effects of artificial clicks, such as might be produced by the tymbal mechanism, when used to drive model Helmholtz resonators of similar dimensions to a real cicada. From these experiments, we are able to see how well such acoustic models predict the pulse duration and envelope of observed cicada songs.

Materials and methods

Male cicadas of the species *Cyclochila australasiae* Donovan and *Macrotristria angularis* Germar were collected respectively near Melbourne, Victoria, and near Brisbane, Queensland, in Australia. Collections were made during the summer months and their dried bodies were kept for work during the winter. Measurements of certain parameters of the body and some acoustic experiments were carried out with the dried bodies. Recordings of the songs of *Cyclochila australasiae* and *Macrotristria angularis* made in the field have been used here to describe additional song parameters. Sound recordings were made with a Sennheiser MKH 816 directional microphone and a Nagra IVs tape recorder at a tape speed of $19\,\mathrm{cm\,s^{-1}}$.

Males of the North American cicadas *Magicicada septendecim* Linnaeus and *M. cassini* Fisher were collected near Lawrence, Kansas, in the United States during the emergence of 1981. Their dried bodies were kept and used for measurements of certain body parameters.

Most of the experiments were done in Melbourne but some were done in Oxford, using slightly different equipment; where experiments were repeated or extended using different apparatus in Oxford, this is shown by the abbreviation *(Oxf)*.

Physical dimensions of cicada bodies

The volume of the abdominal air sac was measured by cutting dried cicadas in half

sagittally and filling each half-abdomen with finely powdered table salt (sodium chloride) which was then levelled off. The volume of the salt was then measured by pouring it into a 2 ml hypodermic syringe. Successive measurements using this technique were consistent to within about 5 % or about 0.1 ml.

The dimensions of the tympana in *Magicicada* were measured from drawings prepared using a dissecting microscope with a squared graticule in the eyepiece and drawing paper with corresponding squares on it. The area of each tympanum was calculated from these drawings using a Zeiss MOP. Dimensions of the tympana in *Cyclochila* and *Macrotristria* (Table 1) are taken from Young (1990).

Acoustics of cicada bodies

Only dried insect bodies were available. Using a soldering iron, a small hole was bored mid-dorsally in the fourth or fifth abdominal segment, so that the tip of a probe microphone (see below) could be inserted into the body and sealed in place with BluTack or modelling clay. For measurements inside the insect body, the body was arranged with its mid-ventral surface facing the sound source. Measurements of the acoustic response of the microphone to pure tones or tone bursts were made either with the microphone in the insect body or with the body removed.

Visual observations were made while exciting the cicada body with sound at 120–130 dB, using a Radioshack 40-1381 piezo-electric loudspeaker, driven directly from a Tektronix type 501A function generator. Observations of tympanal membrane vibrations were made by sprinkling cork powder directly onto the tympana (see Faraday, 1831; Bennet-Clark, 1987; Young, 1990).

Some measurements were made in an atmosphere of a commercial CFC refrigerant, for convenience termed CFC gas. The velocity of sound in a gas can be calculated from its pressure, P, density, ρ, and molar heat capacity, γ, by:

$$c = \sqrt{\left(\frac{\gamma P}{\rho}\right)}. \tag{3}$$

The density was measured by filling a plastic bag inside a 1 l beaker with CFC gas, weighing this, then re-weighing the beaker and bag when filled with air ($\rho \approx 1.2\,\mathrm{kg\,m^{-3}}$ at 20 °C). A series of five such measurements gave a mean density for the CFC gas of $3.94 \pm 0.17\,\mathrm{kg\,m^{-3}}$ (±S.D.). The molar heat capacity, γ, for typical polyatomic gases is 1.3, so at an atmospheric pressure of 10^5 Pa, the velocity of sound can be calculated as $180\,\mathrm{m\,s^{-1}}$.

Experiments with CFC gas were carried out inside a thin-walled plastic bag which was filled by a fine tube connected to the gas cylinder but it was not possible to ensure that the atmosphere was pure or to avoid some echoes from the wall of the bag. Other experiments using this method with a model cicada are reported in the Results.

Model cicadas

Two types of models were used, both made from polycarbonate disposable hypodermic syringes and driven by an Aiwa GT Sound miniature earphone, 14 mm in diameter.

The electrical impedance of the earphone was measured by measuring the voltage

across the earphone and across a 24 Ω resistor in series with the earphone, using a Fluke 8060A multimeter. These measurements also allowed the power dissipated by the earphone to be calculated (see Results). There was a weak electrical resonance at about 150 Hz and another even weaker resonance at 2.3 kHz but, at all frequencies from 50 Hz to 20 kHz, the impedance was largely resistive and between 16.4 Ω and 17.6 Ω.

The pressure response of the earphone was measured by using it to drive a Bruel & Kjaer type 4134 microphone *via* a 0.5 ml cavity 5 mm long. Since all measurements using it were comparisons between two conditions, the absolute frequency response of the earphone is not important but the measurements showed that the earphone response did not have any large or sharp resonances (see Figs 11B, 12A for examples of its response). Its pressure response at 10 kHz was some 20 dB below that at 1 kHz but it had a good transient response (see e.g. Figs 11B, 12A).

The first type of model was a series of variable-volume resonators made from 2 ml, 5 ml or 20 ml syringes, drilled with a pair of holes, which ranged from 5 mm to 2.5 mm diameter for the 2 ml syringes, from 7 mm to 2.5 mm for the 5 ml syringes and from 10 mm to 3.5 mm for the 20 ml syringes (one example is shown in Fig. 2). This series of models was used to measure the relationship between the shape of the cavity and its acoustic properties.

The other model had a fixed 15 mm long, 1.8 ml volume chamber with two adjacent 7.1 mm diameter holes, similar to the volume of the abdominal air sac and tympanal dimensions of *Cyclochila* (Fig. 3) (data from Young, 1990, and Results and Table 1). For some experiments, the sound-radiating face of the earphone was partially occluded by a polycarbonate cone with a 3 mm×7 mm oblong slot at its apex (Fig. 3A), corresponding in size to one tymbal of a male *Cyclochila* (Josephson and Young, 1981). The earphone with 'tymbal' was then sealed to the chamber with Plasticine or BluTack. In other experiments, the ventral opercula that cover the outside of the tympana of *Cyclochila* were modelled by a sheet of 0.5 mm thick aluminium sheet bent and attached to fit closely over the two holes in the wall of the chamber (Fig. 3B): the 'opercula' could be lifted to open or adpressed to occlude the two holes. In one series of experiments, the chamber was divided approximately in half by a transverse semicircle of 0.5 mm thick aluminium sheet.

Acoustic measuring apparatus

A block diagram of the electrical system used to make test signals and to observe the performance of model cicadas is shown in Fig. 4.

Most laboratory measurements of free-field sound pressure levels were made using a Bruel & Kjaer sound level meter type 2209 with 1/3-octave filter set type 1616, 1/2 inch microphone type 4134, input stage ZC0200 and flexible lead AO 0027. All measurements of transient events were made with the external filter at the 'Lin' setting to obtain the best transient response over the flat bandwidth from 20 Hz to 25 kHz. The calibration of the chain was tested and adjusted regularly using a Bruel & Kjaer type 4230 calibrator.

Relative sound pressure measurements inside cicada bodies were made using a purpose-built probe microphone (Fig. 5) consisting of a 10 mm long stainless-steel probe

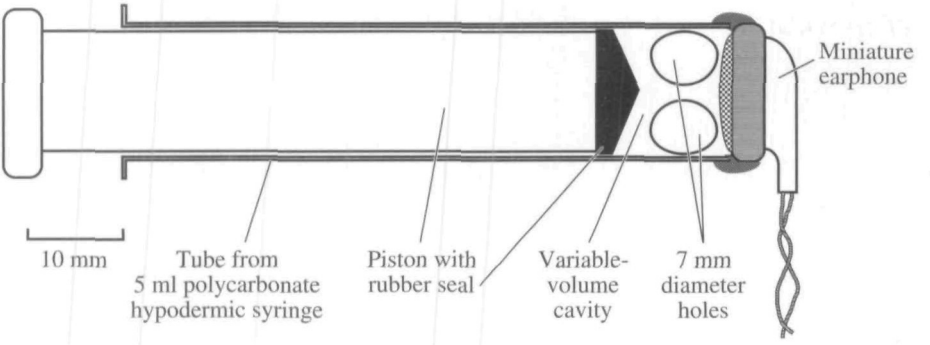

Fig. 2. Diagram of a variable-volume model cicada. The barrel and piston were made from a 5 ml polycarbonate hypodermic syringe. Two 7 mm diameter holes were bored near the needle end of the syringe. The needle end of the syringe was cut off and the Aiwa miniature earphone was sealed onto the cut end of the tube. Other models used different diameter syringes and/or had different sized holes.

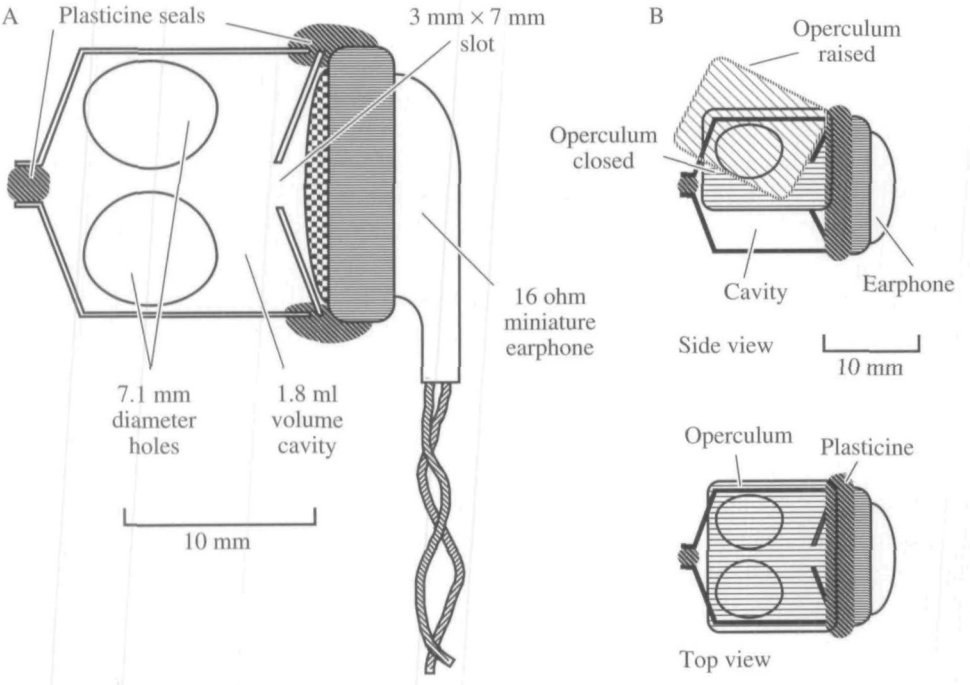

Fig. 3. Diagram of the 1.8 ml fixed-volume model cicada made from a cut-down 5 ml hypodermic syringe. (A) A general view of the model. Note that the aperture of the earphone has been partially occluded by a 3 mm by 7 mm slot similar in size to one tymbal of *Cyclochila*. (B) The sheet aluminium cover fitted over the holes in the syringe to simulate the ventral opercula that cover the tympana in *Cyclochila*. The opercular cover can be lifted and/or bent to open or occlude the holes in the cavity.

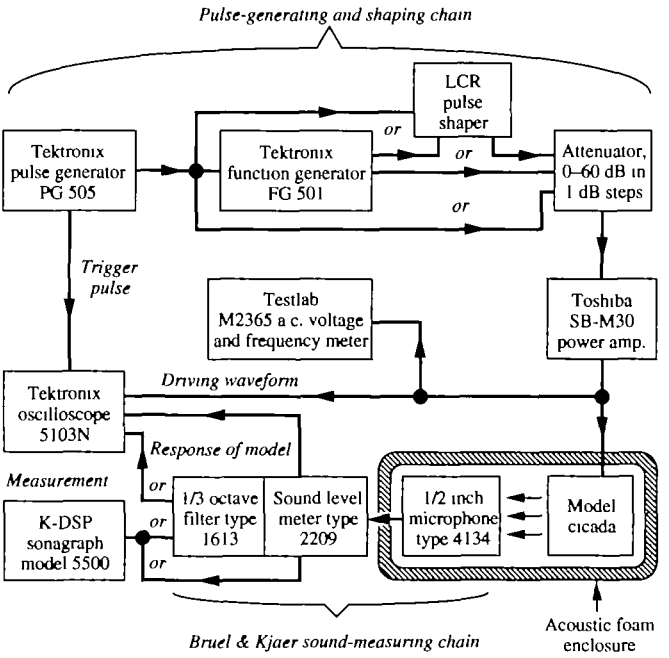

Fig. 4. Block diagram of the pulse-generating and sound-measuring chain used in most of the experiments with the model cicadas illustrated in Figs 2 and 3. amp., amplifier.

tube with a tip of 2.8 mm outside and 2.1 mm inside diameter connected to a close-fitting enclosure around a Tandy electret microphone element catalogue 270-090. This microphone drove a purpose-built preamplifier. Because of the short length of the probe tube, the response was apparently free from resonances, or effectively aperiodic, between 500 Hz and 10 kHz. No attempt was made to achieve an absolute calibration for this microphone as it was always used to measure comparisons between experimental situations.

All acoustic measurements were made inside an 0.3 m×0.3 m×0.5 m enclosure made of Sonex or Illform *(Oxf)* acoustic anechoic foam 85 mm thick. Clamps and other devices used to hold microphones and models were less than 25 mm across and support rods were less than 12.5 mm in diameter. Tests were made for the presence of echoes by use of 0.25 ms duration tone bursts which showed that echoes were typically 30–40 dB below the level of the signals under examination.

Because the sound sources and models used here can be regarded as monopoles, the sound pressure decays linearly with distance (6 dB per doubling of distance) (Olson, 1957) and it is appropriate to make comparative sound pressure measurements at distances of 20 mm. However, most measurements were made at a fixed source-to-microphone range of 50 or 200 mm. Measurements of sound pressure level against microphone-to-source distance showed that the inverse square law was obeyed with the model cicadas to within 1 dB between 10 and 250 mm and that pulse form remained unchanged over this range of distances.

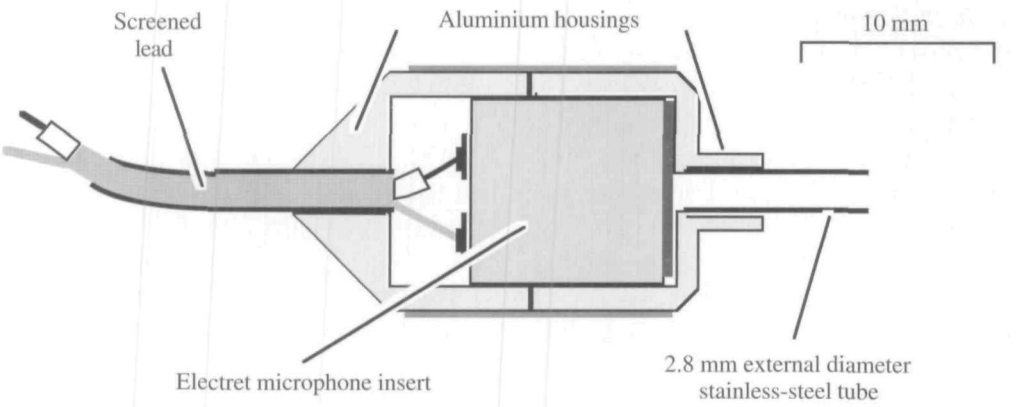

Fig. 5. Diagram of the construction of a probe microphone used to measure the acoustic response of small cavities such as the body of *Cyclochila*. The electret microphone insert is a Tandy 270-090.

Electrical test signals and electrical models of tymbal clicks

Tone bursts were generated by triggering a Tektronix function generator type FG 501 or a type 501A *(Oxf)* with pulses from a Tektronix pulse generator type PG505 or a PG501 *(Oxf)*. In this way, bursts of one or more complete cycles of sinusoidal or other types of waveforms were produced. Other pulse trains or single pulses were obtained directly from the PG501 or PG505. Waveforms were monitored on a Tektronix oscilloscope type 5103N or Telequipment D53A *(Oxf)* and carrier frequencies were set to the nearest 10 Hz between 500 Hz and 20 kHz using a Testlab M2365 multimeter (which in turn was checked for accuracy against a Tektronix DC 503 universal counter).

Square-wave pulses were, in certain experiments, passed through a pulse shaper consisting of a 10 mH inductor in parallel with a 120 nF capacitor (adjusted to resonate at 4.3 kHz) with a series variable 20 kΩ resistor by which the Q of the pulse shaper could be adjusted from below 1 to over 20 (examples of the damped 4.3 kHz oscillation produced are shown in Figs 15B and 16B).

Shaped or unshaped tone bursts were fed through a 0–59 dB 600 Ω attenuator and amplified by a Toshiba SB-M30 power amplifier. The combined output of the function generator and amplifier was measured as being flat to ±0.5 dB from 15 Hz to 45 kHz with the power levels and load impedances used here. This power amplifier introduced a constant delay of 3 μs corresponding to a phase delay of 22° at 20 kHz. A Marantz PM 230 power amplifier of similar specification was also used *(Oxf)*.

Recording and analysis of responses

Transient waveforms, such as the acoustic response of an insect body or a model to a pulse or toneburst, were observed on the screen of the oscilloscope and the amplitude, wavelength, relative phase and other parameters of the waveform were measured directly from the screen. Other measurements were made from oscillograms. Oscillograms were photographed on Polaroid film and the original positive prints were scanned into an Apple

Macintosh computer, reversed digitally and edited to remove the scale lines from the original oscillograms.

Frequency–energy spectra of the response of cicada bodies were plotted using a Radiometer wave analyser model FRA 2B.

Oscillograms of the waveforms and frequency–energy spectra of cicada songs and of the response of model cicadas were calculated and plotted by a Kay DSP Sonagraph model 5500. The transform size was set to 600 Hz to remove spiky components at 200–500 Hz due to the tymbal muscle contraction frequency of the natural cicada songs. This pulse repetition rate was imitated in the electrical models described above. For songs, the duration of the analysis was set to include a single pulse and, for signals produced by the models described above, the duration of the analysis was set at 0.1 s.

When a signal is modulated, its frequency–energy spectrum shows a peak at the carrier frequency and subsidiary peaks at either side that are related to the modulation frequency and the shape of the modulation envelope. Similarly, the energy in transient signals may show a series of peaks that depend on the duration of the signal, T. In this case the spectrum of the envelope $W(f)$ is given by:

$$W(f) = \frac{T\sin(\pi Tf)}{\pi Tf}, \tag{4}$$

where f is the frequency (for a detailed discussion see Randall, 1977). This gives a spectrum with minima at $f_0-(1/T)$, $f_0-(2/T)$, $f_0+(1/T)$, $f_0+(2/T)$ etc. and maxima at f_0, $f_0-(1/2T)$, $f_0-(3/2T)$, $f_0+(1/2T)$, $f_0+(3/2T)$ etc. Similar effects result from the periodicity within a changeable signal. Thus, by examining the power *vs* frequency spectrum of a signal, it is possible to assess its time course and/or to use the power–frequency spectrum of a signal of known temporal pattern to assess the temporal structure of another signal: this latter approach is used here.

Measurement of the acoustic properties of resonators

Two properties of a resonant system are considered here: the resonant frequency and the Q or quality factor.

Resonant frequency can be measured in various ways. The simplest is to observe the frequency at which the amplitude of the response is maximal: below this frequency, the amplitude of the response tends to equal that of the driving waveform, and above this frequency, the amplitude of the response tends to decrease by 12 dB per octave. With simple resonators at resonance, the amplitude of the response is Q times the response at frequencies well below resonance. In the present case, the response also depends on the properties of the resonator as a sound radiator: this problem is considered further below but, since the radiation resistance of small sound sources, such as that of the cicada, is markedly dependent on the ratio of source size to sound wavelength, the absolute value of the response at resonance may differ from that predicted for a simple resonator.

The resonant frequency may also be observed from the phase of the response. Far below the resonant frequency, the response is in phase with the driving waveform; at resonance, the response lags by 90° and far above resonance the response lags by 180° on the driving waveform. Practical measurement of the phase in an acoustic system of the

type described here requires that due account be taken of the finite passage time of the sound wave between the source and the measuring instrument: in a probe microphone, this time includes the passage time between the tip of the probe tube and the transducer of the microphone.

At resonance, as indicated above, the effective gain of the response is maximal: this can be observed on an oscilloscope trace of the response of the resonator to a tone burst where, at resonance, the decay of the oscillation is most persistent when the resonator is driven at its resonant frequency.

Since both the cicada and model resonators described here tend to show several resonances, all three of the methods described above have been used to characterise these resonances. The accuracy and repeatability of measurements of the resonant frequency was approximately ±3 %.

Q can also be measured in several ways. The simplest is to measure the effective gain in the amplitude of the response at resonance compared with that at a frequency far below the resonant frequency but, for this measurement to be valid, it is important to have a standard against which the response of the resonator can be compared. As indicated above, the properties of the resonator as a sound radiator will tend adversely to affect measurements made in this way with low-Q systems.

Q can also be measured from the change of amplitude or of phase with frequency using:

$$Q = \frac{\text{bandwidth at } -3\,\text{dB}}{\text{resonant frequency}} = \frac{\text{bandwidth at } -45 \text{ to } -135\,^\circ}{\text{resonant frequency}}, \tag{5}$$

where -3 dB is half peak power.

The most reliable estimate of Q for resonators of the type used here is obtained by measuring the amplitude of successive cycles of the build-up at the start or free decay following a driven oscillation. Q is then given by the slope of a plot of ln increment or ln decrement per cycle:

$$Q = \frac{\pi}{\text{ln increment}} = \frac{\pi}{\text{ln decrement}}. \tag{6}$$

Where the data made this possible, Q values that are quoted have been calculated from the ln decrement of the free decay at the end of a tone burst (see Fig. 6 for examples of this method): however, all three of the methods described above have been used here to evaluate Q so that results from different experiments or procedures may be compared. The repeatability of successive measurements or comparisons of Q was about ±10 %.

Results

The sound-producing mechanisms and songs of *Cyclochila australasiae* and *Macrotristria angularis* are described in Young (1990). Relevant details are summarised here in Fig. 1 and Table 1.

Body dimensions and song characteristics of cicadas

The average volume of the large abdominal air sac of the male cicadas was found to be

1.93 cm^3 (range 1.8–2.1 cm^3, N=3) for *C. australasiae* and 1.67 cm^3 (range 1.5–1.8 cm^3, N=3) for *M. angularis*. From Table 1, the average area of both tympana is 86 mm^2 for *C. australasiae* and 56 mm^2 for *M. angularis*. In calculating (equation 1) the resonant frequency, f_0, of a resonator with simple holes, it is necessary to estimate the effective source radius from which the effective neck length can be obtained (see Introduction). Following Rayleigh (1896), we have calculated the equivalent radius for a circle of the same area as that of the tympanum (Table 1): this approximation is valid for a small amount of eccentricity in the shape of the aperture. Using the values shown in Table 1, f_0 is calculated to be 4.56 kHz for *C. australasiae* and 4.41 kHz for *M. angularis*.

These values agree adequately with the observed values of 4.3 kHz and 4.0 kHz, respectively, for the carrier frequencies of the song of these two species (Young, 1990). Young (1990) calculated a f_0 of 5.1 kHz for the abdominal air sac of *Cyclochila*, but this earlier calculation was based on inaccurate estimates of 5 mm for the neck length term, L, and of 1.8 ml for the volume term, V, in equation 1.

When singing, *Cyclochila* males extend their abdomens (Young, 1990), which will have the effect of enlarging the volume of the abdominal cavity and hence reducing its resonant frequency to a lower value than that calculated here and one that is likely to be close to the insect song carrier frequency.

Based on the dimensions given above and in Table 1, and using equation 2, the calculated Q value of the air sac and tympana of *C. australasiae* is 5.5 and that of *M. angularis* is 7.0.

These values may be compared with estimates of the Q value made from field recordings of the songs of both species. There is considerable natural variability in the type of pulse produced by *C. australasiae*. In many songs, the pulses build up rapidly and decay slowly (Fig. 6A,B). The ln decrement for the free decay of sound pulses of this type has a mean value of 0.213 (range 0.165–0.26, N=4) (Fig. 6C shows an example in which the ln decrement was 0.20). Using equation 6, the mean Q for this type of song was calculated to be 15.2 (range 12.1–19.2, N=4). In other songs from other insects, parts of

Table 1. *Body dimensions of males in two cicada species*

	Cyclochila australasiae	*Macrotristria angularis*
*Body length (mm)	45.3	44.5
*Body width (mm)	17.6	16.8
*Tympanal width (mm)	8.37	7.0
*Area of one tympanum, A (mm^2)	43.3	28.2
*Tympanal thickness (μm)	1–2	–
Volume of abdominal air sac, V (cm^3)	1.93	1.67
Equivalent hole radius from area, $=\sqrt{A/\pi}$ (mm)	3.70	3.0
Effective neck length (L), $=16r/3\pi$ (mm)	6.3	5.1
Calculated resonant frequency, f_0, equation 1 (kHz)	4.56	4.41
*Song carrier frequency (kHz)	4.3	4.0

* These data are taken from Young (1990).

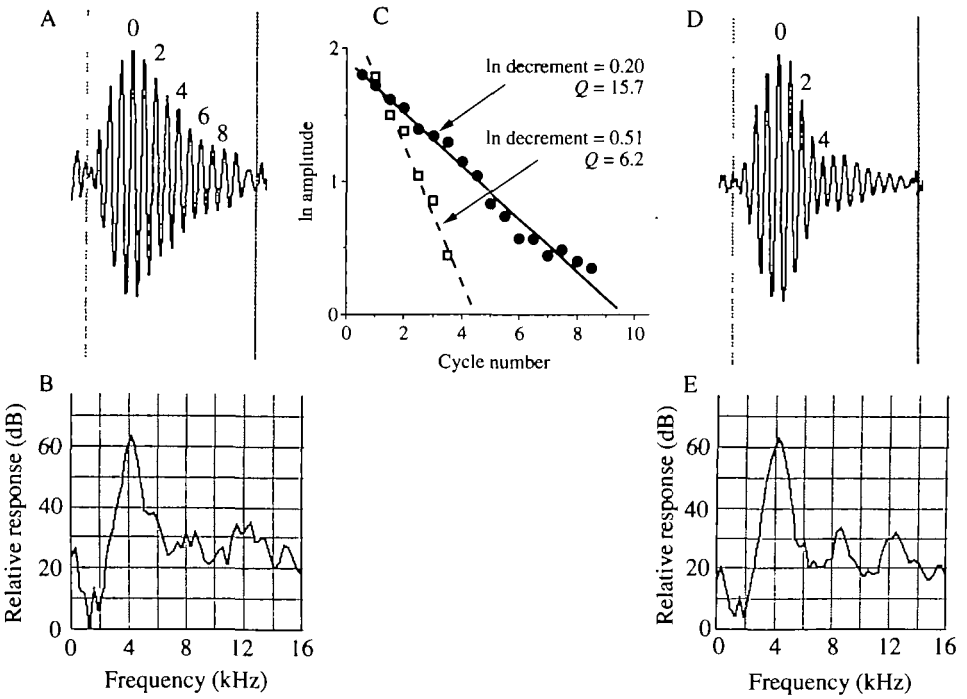

Fig. 6. Records and analyses of single pulses of the song of *Cyclochila australasiae* made in the field. (A,B) One type of pulse, with rapid build-up and slow decay. (D,E) Another type of pulse in which the amplitude decays more rapidly within the pulse. (A,D) Oscillograms of single pulses of the song. (B,E) Power *versus* frequency spectra of the pulses shown in A and D. (C) Plots of ln decrement against cycle number for the two pulses shown here; (●) from the pulse at the left and (□) from the pulse at the right. The cycles that were measured are numbered on the oscillograms: measurements of amplitude were made at every half-cycle. Q is calculated from equation 6.

the pulse both build up and decay rapidly (Fig. 6D,E). The ln decrement of the rapid decay of the pulse amplitude in this type of song (the region indicated on Fig. 6D) had a mean value of 0.505 (range 0.45–0.58, N=4) (Fig. 6C shows an example in which the ln decrement was 0.51). We calculate a mean Q for this second type of song of 6.29 (range 5.4–7.0, N=4).

The song spectrum for the rapidly-decaying song pulse (Fig. 6E) shows a f_0 of 4.2 kHz, minima at about 6.5 and 10.5 kHz and maxima at 8.5 and 12.5 kHz. These spectra will be compared with those of artificial signals.

Only a single recording was available of the song of *M. angularis* for which a ln decrement of 0.34 was calculated, giving a Q value of 9.2 for this species.

The Q value for rapidly-decaying pulses of *Cyclochila* song (Fig. 6D,E) is similar to that calculated above from the dimensions of the body and reported from the acoustic responses of the cicada bodies (see below). A possible explanation of the far higher value of Q measured from the slowly-decaying pulses (Fig. 6A,B) is given below.

Acoustics of cicada bodies

Acoustic measurements were made on four male *C. australasiae* bodies using the probe microphone (see Materials and methods). For each insect, the apparent gain of the abdominal air sac was measured by comparing the response within the insect body to the free-field response of the microphone alone.

All insect abdomens resonated at between 3.6 and 5.3 kHz (which may be compared with the calculated values of 4.28–4.58 kHz: see above), with an apparent gain of between 6 and 11 dB. The results from one insect body are shown in more detail in Fig. 7. The gain of the intact body, which had both opercula raised by about 1.5 mm, was 10 dB at a resonant frequency, f_0, of about 4.6 kHz. Removal of the right operculum raised f_0 to about 5.1 kHz and reduced the apparent gain to 6 dB, but removal of the other operculum had little further effect. With another insect body in which the opercula were more tightly shut, leaving a gap of 0.5 mm between their edge and the posterior rim of the tympana, f_0 changed from 3.75 kHz in the intact insect to 4.25 kHz after removal of the left operculum and to 4.75 kHz after removal of both opercula. When the opercula were stuck back in place with wax, leaving a gap of 0.5 mm, f_0 returned to 3.7 kHz and when they were subsequently raised to increase the gap to 5 mm, f_0 increased to 4.7 kHz.

The Q value was measured in three *C. australasiae* bodies from the ln decrement of the decay of the acoustic response to a tone burst (equation 6 and see Fig. 6). The Q value of the intact bodies was between 7.6 and 5.5 (average 6.4, N=3). These values are similar to those calculated for dimensions of the insect body or for the rapidly-decaying song pulses (Fig. 6D,E) described above. Removal of the opercula had little effect with one body and lowered the Q of the other two from 7.6 to 5.4 and from 6.1 to 4.2.

The apparent gain of the insect body at resonance is between 6 and 11 dB (Fig. 7). The theoretical sound pressure gain for a resonator with a Q of 5.5 is 14.8 dB (Seto, 1971). The discrepancy may be partly explained as follows. Below 2 kHz the apparent gain is −4 to −14 dB. This reduction in gain may be due to the lower acoustic admittance of the small tympana to sound at lower frequencies, particularly when occluded by the opercula, and such factors may reduce the effective gain that can be observed in our experimental set-up. Above 6 kHz, the gain is also negative. Negative gain is expected from a Helmholtz resonator, which approximates to a low-pass filter with a cut-off frequency at $2f_0$ (Morse, 1947).

Thus, the measurements of resonant frequency and Q are also broadly compatible with the suggestion that the abdominal cavity of *Cyclochila* acts as a Helmholtz resonator.

When a *C. australasiae* body was excited by sound in an atmosphere of CFC gas (see Materials and methods), in which the velocity of sound is about 180 m s^{-1}, its resonant frequency dropped from 5.3 kHz in air to 3.0 kHz in the CFC. From equation 1, the resonant frequency is proportional to the velocity of sound, c, in the fluid, so the resonant frequency should have fallen to 2.8 kHz, but the rather crude experimental conditions did not make it possible to obtain a pure atmosphere of CFC. Even so, the experiment demonstrated that the air-sac resonance depended in an appropriate way on the velocity of sound in the gas.

When the *C. australasiae* bodies were sprinkled with cork powder and then excited by loud continuous pure-tone external sounds (see Materials and methods), the only regions

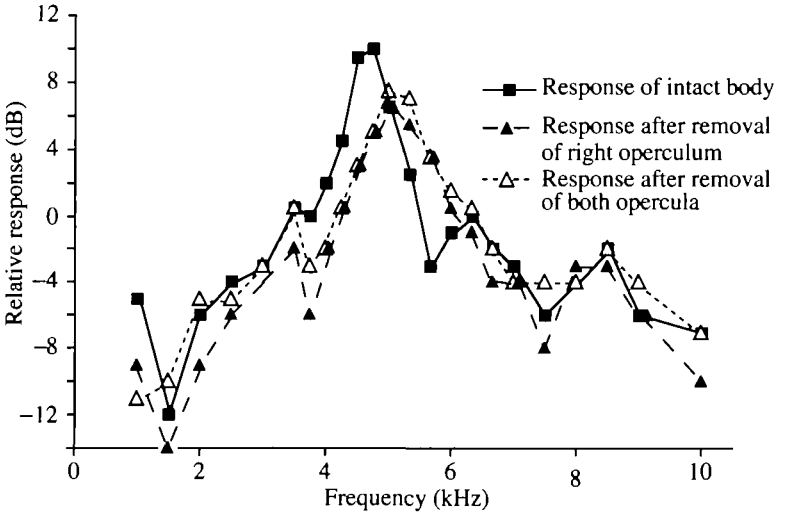

Fig. 7. Graph of the acoustic response inside the body of a male *Cyclochila versus* frequency. The graphs plot the change in the free-field sound pressure response when the intact cicada body was placed over the probe microphone shown in Fig. 4 and the effects of the subsequent effect of removal of one or both of the opercula that cover the ventral tympana.

in which vibration could be seen were the tympana, which vibrated vigorously, and in a simple manner with maximal amplitude at the centre of the tympanum without nodal lines, but only at frequencies similar to those previously measured for the air-sac resonance. This experiment provides further supporting evidence for the suggestion that the tympana are acoustically transparent and are the major acoustic apertures of the abdominal air sac (Young, 1990) (and see Discussion).

Acoustics of model cicadas

Effect of varying the shape of the cavity and of altering hole size

The series of variable-volume resonators (Fig. 2) was used to measure how resonant frequency and Q varied with cavity volume, hole size and cavity length. In addition to measurements of the fundamental resonance, the frequencies at which higher resonances (not necessarily harmonics) occurred were measured.

With all models, there was a close agreement between the theoretical (equation 1) and measured resonant frequency when the piston in the syringe was pushed far in, so that the cavity length and diameter were similar. When the holes were large relative to the diameter of the tube, as with 5 mm diameter holes in a 2 ml syringe (Fig. 8A) compared with 5 mm holes in a 20 ml syringe, or when the piston was withdrawn making a long narrow cavity, the measured resonant frequency decreased more rapidly than simple theory predicts (Fig. 8B).

From equation 1, the resonant frequency should scale as cavity volume$^{-0.5}$ and as hole diameter$^{0.5}$. The exponents of f_0 against hole diameter were close to the theoretical 0.5 with short wide tubes of all three diameters but in all cases fell to values of between 0.32

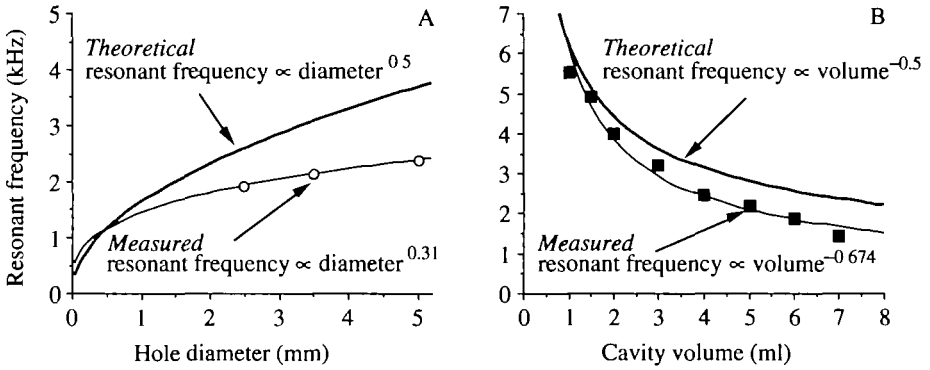

Fig. 8. Plots of the frequency of the fundamental resonances of model cicadas of the type shown in Fig. 2. (A) The effect of changing the diameter of the two holes of a model made from a 2 ml syringe, at a volume of 2 ml. As the holes increase in diameter, the measured resonant frequency becomes progressively lower than the calculated value, shown as a dotted line where $f_0 \propto$ hole diameter$^{0.5}$: at a volume of 2 ml, the internal length of the cavity is 31 mm and its diameter is 9 mm. (B) The effect of varying the volume, by withdrawing the piston, of a model made from a 5 ml syringe with paired 7 mm diameter holes. The resonant frequency calculated from equation 1 is shown as a dotted line where $f_0 \propto$ cavity volume$^{-0.5}$. The measured resonant frequency is similar to the calculated value with short, small-volume cavities but becomes markedly lower that the calculated value with the longer cavities: at a volume of 7 ml, the internal length of the cavity is 54 mm and its diameter is 13 mm.

and 0.29 with the longest tubes (see Fig. 8A). With the variable-volume models, the exponents of f_0 against volume were between −0.79 and −0.85 with the longest tubes with the largest holes and only approached the theoretical exponent of −0.5 with long thin tubes with small holes when exponents of −0.55 were observed (see Fig. 8B). This suggests that the longer tubes are behaving more like pipes, where f_0 varies as length^{-1}, than as Helmholtz resonators. Helmholtz (1885) reports similar findings with non-spherical resonators and with resonators with a large hole.

Pursuing this point, the higher resonances of a variable-volume model with paired 7 mm diameter holes were measured. The results are summarised in Fig. 9, which both shows the frequencies at which resonances occurred and indicates the amplitude of the sound output at these resonances relative to the output of the fundamental. With cavity volumes of 1.5 and 2 ml, the first two higher resonances were quite weak, with sound outputs some 15 dB below that of the fundamental. Only the fourth resonance produced a comparable output to that of the fundamental. With the larger – and longer – cavities, the output at the second, fourth and higher resonances was comparable or even greatly in excess of that at the fundamental resonance. In other words, the longer cavities tend to be more capable of being excited at a variety of frequencies and/or of introducing considerable tonal impurity to the output of the resonant system.

The resonant frequency of one model was measured in air and in CFC gas (see Materials and methods) over a volume range of 1–6 ml. In all cases, the resonant frequency in CFC gas was between 0.5 and 0.6 of the resonant frequency in air. This is consistent with the measurements made with a cicada body (see above).

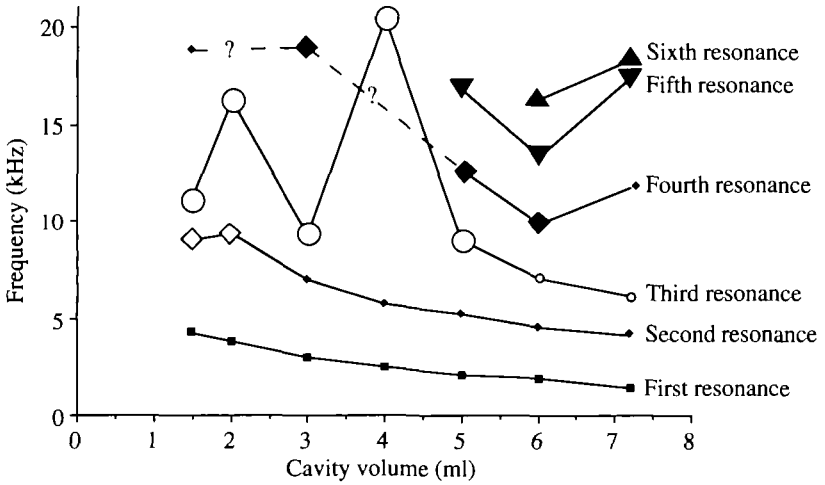

Fig. 9. Plots of the fundamental and higher resonances of the model made from a 5 ml syringe with paired 7 mm diameter holes illustrated in Fig. 2. The graphs show the frequencies at which the resonances were observed against cavity volume and also indicate the relative loudness of the sound output at these frequencies. Small filled symbols show sound outputs within ±5 dB of the first resonance, large filled symbols show outputs greater than +5 dB, small open symbols show outputs from −5 dB to −10 dB and large open symbols show outputs more than −10 dB relative to that of the first resonance at a particular volume. Small short cavities tend to have weak higher resonances and larger longer cavities tend to have stronger higher resonances.

Acoustics of the 1.8 ml model cicada

Since the abdominal air sac of male *Cyclochila* approximates to an ellipsoid about 20 mm long, 12 mm high and 15 mm wide, with large tympanal apertures, it is likely that the resonant frequency of this cavity will be adequately modelled by equation 1 and that a model with similar dimensions to those of the air sac will have a similar acoustic performance. Therefore, the acoustic behaviour of the model cicada shown in Fig. 3 was examined in greater detail.

Measurements were made of the acoustic output of the earphone in response to a continuous sinusoidal input of constant voltage, either alone or with the model cicada in place as in Fig. 3A. Measurements made between 1 and 15 kHz are shown in Fig. 10.

The acoustic response when the model cicada is driven by a constant 104 mV shows a resonance at 4.3 kHz and apparent anti-resonances at 6 and 13 kHz (Fig. 10A). The increase in the sound output at 4.3 kHz is 9.3 dB, which is comparable to the increase in sound pressure inside the body of *Cyclochila* reported above. There was some evidence of weak resonances at 7.5 and 9 kHz, similar to those shown with the variable-volume model in Fig. 8A. As measurements were not extended above 15 kHz, the expected higher resonance at about 19 kHz was not observed.

The electrical response (Fig. 10B) shows the extra power dissipated by the earphone when driving into the model cicada (see Materials and methods). The output of the amplifer was set to give a constant voltage of 240 mV across the earphone and 24 Ω series resistor, giving about 102 mV across the earphone, so the total electrical power dissipated

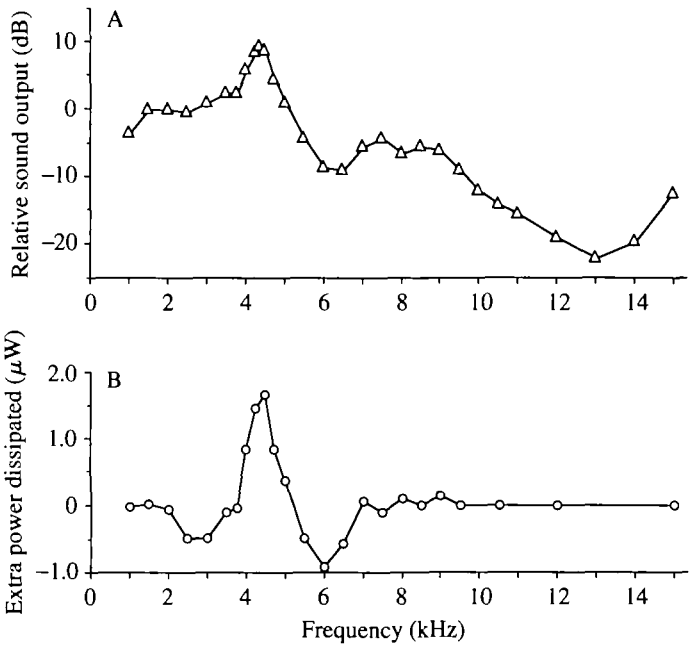

Fig. 10. Plots of the excess sound pressure output and extra electrical power dissipation against frequency of the fixed-volume model (Fig. 3A). Measurements were made as comparisons from the model with the Helmholtz resonator *in situ* or removed. (A) The increase in sound pressure level, expressed as decibels gain, against frequency. (B) The change in electrical power dissipated is expressed in microwatts change *versus* frequency. Positive values indicate that the model dissipated more power, as at the fundamental resonant frequency 4.3 kHz: at either side of this frequency, the model dissipated less power, suggesting that there are anti-resonances at 3 and 6 kHz.

by the earphone was about 600 μW in this experiment. When the model cicada was attached, the power dissipated increased by only 1.7 μW at 4.25 kHz. However, the response curve of the *extra* power dissipated shows similar features to the graph in Fig. 10A. There is a sharp resonance peaking at between 4.25 and 4.5 kHz, with a strong anti-resonance at 6 kHz and a weaker one at 3 kHz.

This shows that when the model cicada is attached the earphone dissipates more power at the resonant frequency of the Helmholtz resonator. In other words, power dissipation from the driver is influenced by the resonant load, which acts as an acceptance circuit at the resonant frequency, thereby restricting the frequency range over which the system absorbs power and then radiates it as sound power (seen as increased sound radiation in Fig, 10A). Note, too, that the extra electrical power dissipation is reduced at the anti-resonances on either side of the 4.3 kHz peak, so that power inputs at these frequencies are rejected by the resonant load. The Q value of the electrical resonance shown in Fig. 10B can be calculated from the −3dB or half-power bandwidth (equation 5), about 800 Hz, and the resonant frequency, about 4.3 kHz, which gives a value for Q of about 5.4, which is similar to that described below for the acoustic resonance.

The Q value of the acoustic response of the Helmholtz resonator was obtained by

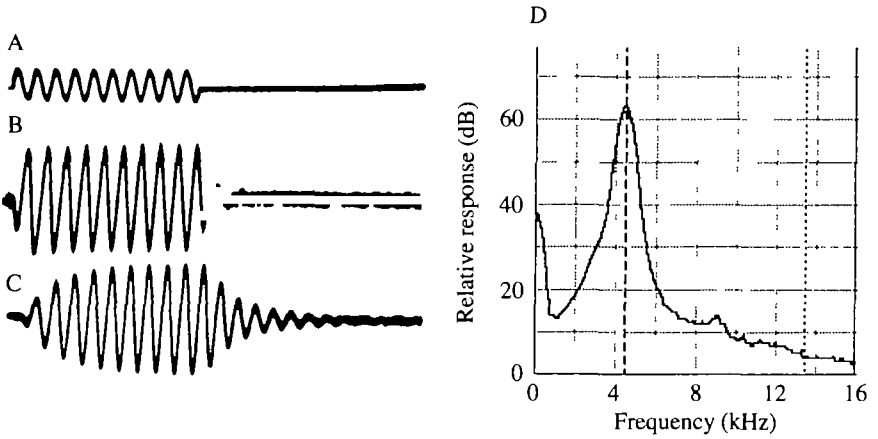

Fig. 11. Acoustic response of the fixed-volume model cicada (Fig. 3A) when excited by a 10-cycle 4.3 kHz sine-wave tone burst. (A) Oscillogram of the electrical drive to the earphone. (B) Oscillogram of the sound output of the earphone alone. (C) Oscillogram of the sound output of the model cicada. (D) Power *versus* frequency spectrum of the response shown in C. On the oscillograms, the trace length is 5 ms. On the power spectrum, the dashed vertical line shows the 4.4 kHz fundamental and the dotted vertical line shows where the 13.2 kHz third harmonic might occur.

driving the model cicada with a tone burst of 10 coherent sinusoidal cycles at 4.3 kHz (Fig. 11A, top). The acoustic response of the earphone alone (Fig. 11B) is essentially non-resonant, but that of the model cicada (Fig. 11C) shows the exponential build-up and decay characteristic of a resonant system. The ln decrement of the decay of the response is 0.44, giving a Q of 7.1 for the resonator, which is similar to that measured for the body of *Cyclochila* and for rapidly-decaying song pulses of the insect (Fig. 6D,E). The power spectrum of the response of the model to this type of excitation shows a major peak at the driving frequency, 4.3 kHz, and a tiny resonance 50 dB below the peak at about 9 kHz (Fig. 11D). This may be compared with similar spectra for the calling songs of *Cyclochila* and *Macrotristria*, which show a range of subsidiary peaks at 30–50 dB below the carrier frequency (Fig. 2 in Young, 1990).

The ability of the model to act as a tuned acoustic filter is shown by comparing the output of the earphone alone with that of the model when driven by a train of 10 square pulses at 4.4 kHz. The results are shown in Fig. 12, which shows that the pulse produced by the earphone alone builds up and decays over one and a half cycles (Fig. 12A). With this test signal, the pulse duration is 2.3 ms, giving $1/T$ of 440 Hz (see equation 4).

The power spectrum shows two series of subsidiary peaks. The 4.4 kHz carrier frequency shows subsidiary peaks at approximately 3 and 5.7 kHz, or at ±1.4 kHz, which can be attributed to the third harmonic of the pulse duration (3×440 Hz $\approx$ 1.3 kHz). The sharp peak at 13.2 kHz may be attributed to the third harmonic of the carrier frequency, 4.4 kHz, that is present in the square-wave drive to the earphone (Fig. 12B).

After attaching the resonator, the response of the model builds up over the duration of the pulse and then decays slowly (Fig. 12C). In this case, the power spectrum shows that

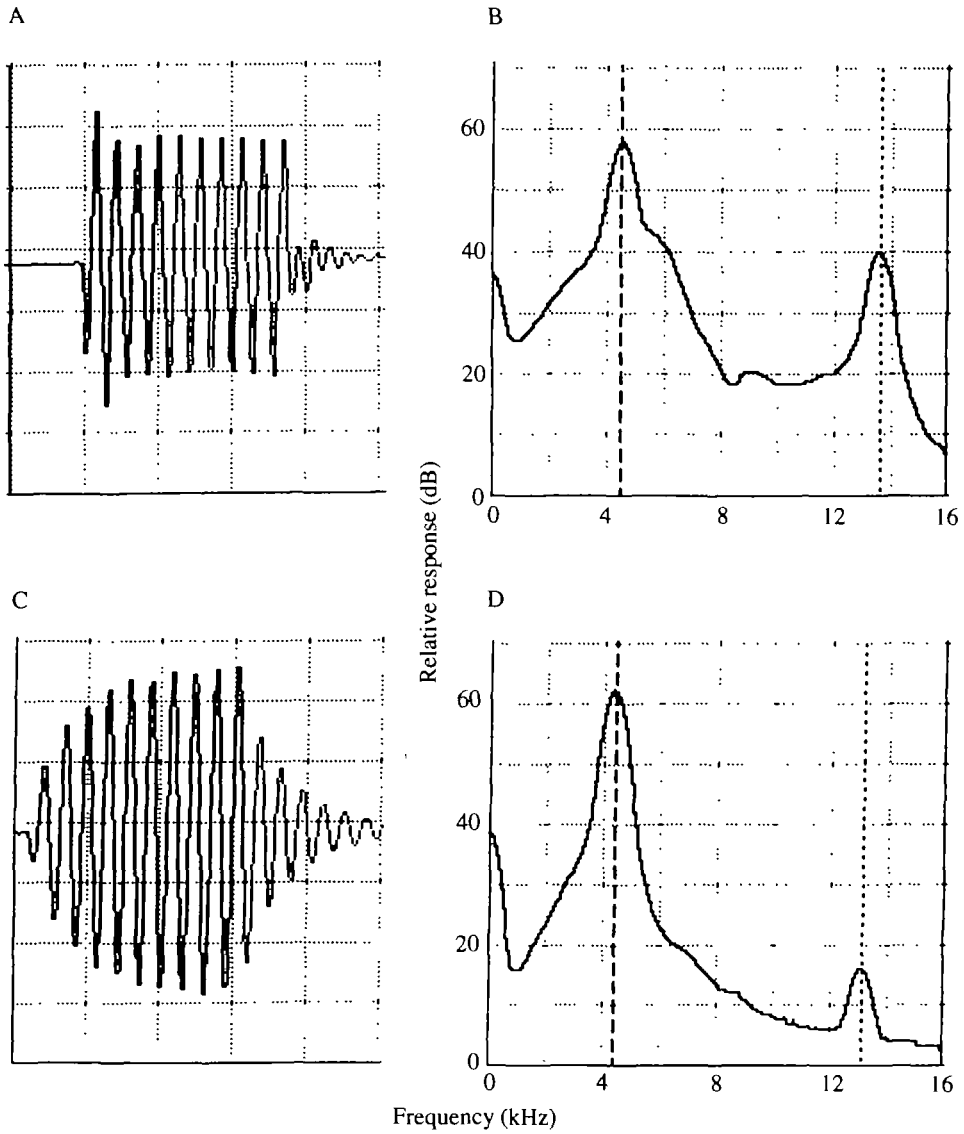

Fig. 12. Acoustic response of the fixed-volume model cicada (Fig. 3A) when excited by a 10-cycle 4.4 kHz square-wave tone burst. The plots were made by the K/DSP 5000 signal analyser. (A,B) The response of the earphone alone. (A) Oscillogram of the sound output and (B) its power *versus* frequency spectrum. (C,D) The response of the model cicada. (C) Oscillogram of the sound output and (D) its power *versus* frequency spectrum. On the oscillograms, the horizontal time axis increases in units of 0.78 ms. On the power spectra, the dashed vertical lines show the 4.4 kHz fundamental and the dotted vertical lines show the 13.2 kHz third harmonic of the carrier frequency.

the level of the fundamental is increased, the subsidiary peaks are shifted outwards and reduced in power, and the power of the third harmonic is greatly reduced (Fig. 12D).

This change in response is consistent with the change in the shape of the pulse

envelope. The gradual and exponential build-up of the pulse reduces the effective pulse duration (compare Fig. 12A and C), so the frequency difference between the carrier and the subsidiary peaks will increase. In addition, the amplitude of the harmonics of the pulse envelope will be reduced, so the power in these subsidiary peaks will be reduced: there will, of course, still be subsidiary peaks due to the 440 Hz fundamental of the pulse duration (equation 4) but these are obscured by the 600 Hz analysis window used here (see Materials and methods).

In different experiments using this model, the resonant frequency varied between 4.2 and 4.4 kHz and Q values varied between 6.5 and 7.8. These differences may be due to small differences in the way the model was assembled and to the quality of the seal between the earphone and the hypodermic syringe.

Since the abdominal air sac of cicadas is obstructed internally by a large V-shaped structure formed by the tymbal muscles and their apodemes, we measured the effect of putting a semicircular partition across the inside of the model between the earphone and the tympanal holes. The effect varied with the size and position of the partition and with the type of pulses used to drive the model. Generally, the response with the partition in place showed less tonal purity. This suggests that the some of the tonal impurity observed in the songs of cicadas (Fig. 6) may be due to higher-order cavity resonances caused by internal intrusions into the abdominal air sac.

Modelling tymbal action in the excitation of the Helmholtz resonator

Typical song pulses of *Cyclochila* consist of 10–12 cycles of tone which build up and then decay slowly (Fig. 6A,B). Somewhat similar pulses have been produced by the model, as shown in Fig. 11C, when excited by a coherent 10-cycle tone burst. This is not how cicada songs are excited (see Introduction). Note, too, that the power spectrum of the model sound output (Fig. 11D) is effectively confined to a single peak, whereas that of the insect song has a series of high- and low-frequency modulation components (Fig. 6).

To obtain a form of excitation that approximates to the natural one, a series of click trains was produced. These click trains were used to drive the fixed-volume model cicada (Fig. 3) either as a direct square-wave drive to the earphone or *via* the resonant pulse shaper described in Materials and methods, set to a mean Q value 5.6.

The effect of multiple excitation of the model cicada was examined using trains of square pulses of differing duration and period, and examples of the effects are shown in Fig. 13. A train of three square pulses of 450 μs period and 110 μs pulse width, fed directly to the earphone, produced a train of three discrete sound pulses from the earphone alone. With the model cicada attached, the output was a long pulse of sound, superficially similar to a cicada song pulse but with a more ragged pulse envelope (Fig. 13Aiii). When a train of three square pulses of 620 ms period was fed through the pulse shaper to produce damped oscillations to drive the earphone, the pulse envelope of the model's sound output became cleaner and longer (Fig. 13Biv) and more closely resembled a slowly-decaying pulse of *Cyclochila* song (Fig. 6A).

The effect of single or multiple excitation was examined by feeding one or more similar pulses *via* the pulse shaper to the model. A single click or damped oscillatory excitation of the model cicada produced a brief asymmetric sound pulse with a relatively

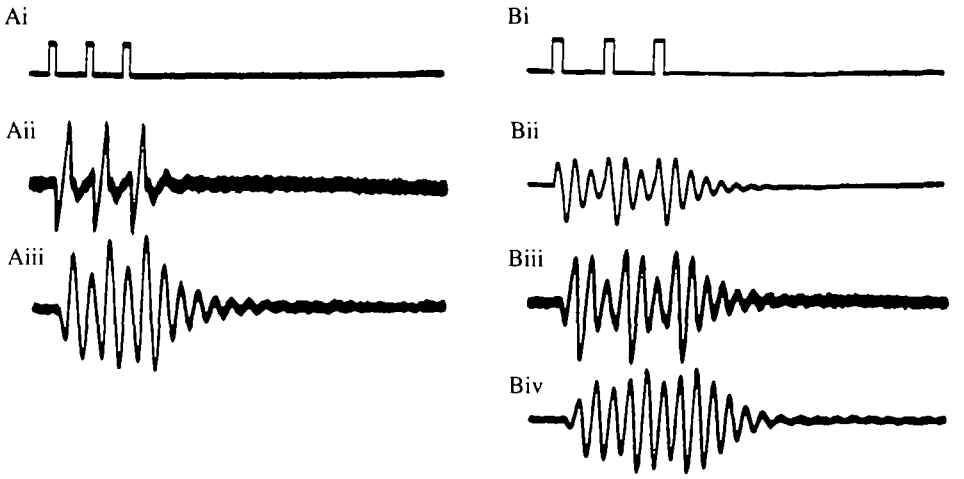

Fig. 13. Acoustic response of the model cicada (Fig. 3A) when excited by square-wave tone bursts of different periods. (A) Drive to the model of three square waves of 450 μs period and 110 μs pulse width. (Ai) Drive to earphone; (Aii) output of earphone alone; (Aiii) sound output of the model. (B) Drive to the model of three square pulses of 620 ms period fed through the pulse shaper to produce damped oscillatory pulses into the earphone. (Bi) Drive to pulse shaper; (Bii) output of pulse shaper; (Biii) output of earphone alone. (Biv) Sound output of the model cicada. In all, the trace duration is 5 ms.

rapid build-up and a slower decay (Fig. 14C, left). By introducing a second or even a third coherent sinusoidal click, with an inter-pulse period of 450 μs, the duration of the sound pulse produced by the model cicada can be greatly increased while maintaining a smooth pulse envelope (Fig. 14C, centre and right).

In the experiments shown in Fig. 14, the Q of the exciting electrical pulse was 5.6. The sound pulse produced by the Helmholtz resonator (shown as oscillograms in Fig. 14C) when driven by this damped oscillation decays more slowly than those produced by discrete tone bursts. The Q measured from the right-hand trace in Fig. 14C is 13. This Q value is similar to that measured from slowly-decaying pulses of *Cyclochila* song (Fig. 6A) and approximates to the the sum of the Q values for the exciting pulse (approximately 6) and the response of the Helmholtz resonator (approximately 7). This implies that in certain samples of *Cyclochila* song the exciting pulse due to the tymbal is tuned to the same frequency as the resonance of the abdominal cavity.

The importance of the coherence of successive excitations of the model cicada was shown by excitation with square waves of varying pulse lengths. Square voltage pulses were adjusted continuously to give constructive excitation of the model's resonances at pulse durations of 0.5λ, 1.5λ, 2.5λ etc. and destructive excitation at durations of λ, 2λ, 3λ etc. Examples of the effects seen are shown in Fig. 15. Feeding the model with two cycles of a 960 Hz symmetrical square wave through the pulse shaper, at $f_0/5$ of the model cicada (or 2.5λ), produced a very long sound pulse, which was sustained by the in-phase excitation every 2.5 cycles (Fig. 15, left), but non-coherent excitation by two square pulses at 760 μs period gave antiphase excitation after 3.5 cycles and produced a double-

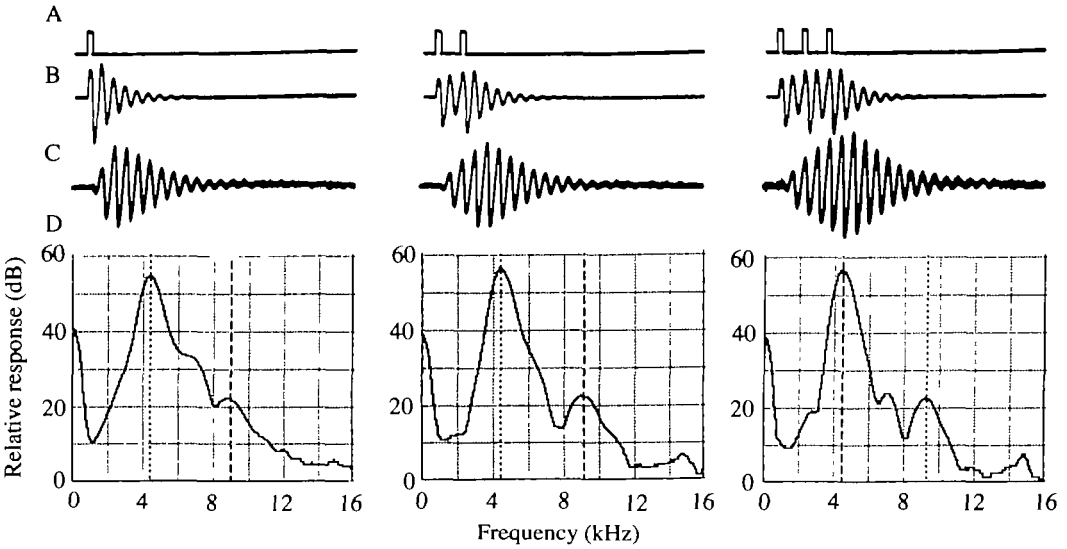

Fig. 14. Oscillograms of the electrical drive and acoustic response of the model cicada (Fig. 3A) to one or more clicks of excitation. In all, the trace duration is 5 ms. (A) Drive to pulse shaper. (B) Output of pulse shaper. (C) Sound output of the model cicada. (D) Power *versus* frequency spectrum. Left: response to a single pulse of duration 75 μs. Centre: response to two pulses of 75 μs duration and 450 μs period. Right: response to three pulses of 75 μs duration and 450 μs period.

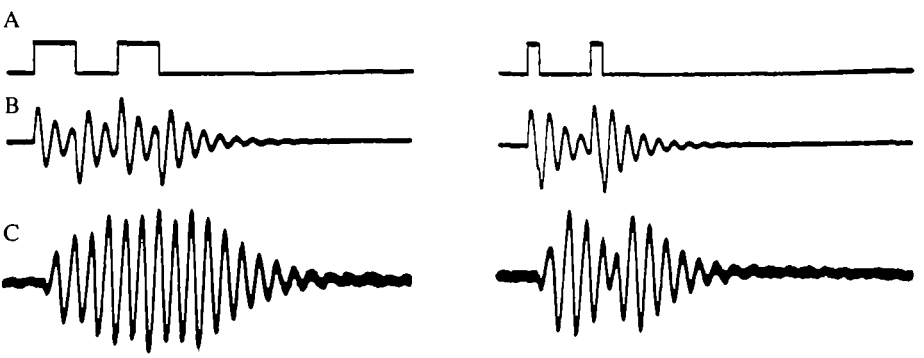

Fig. 15. Acoustic response of the model cicada (Fig. 3A) to in-phase or out-of-phase clicks of excitation. (A) Drive to pulse shaper. (B) Output of pulse shaper. (C) Sound output of the model. Left: response to two symmetrical square cycles of 960 Hz or 1.04 ms period which provide in-phase excitation every 2.5 cycles. Right: response to two pulses of duration 75 μs and 760 μs period which provide an in-phase drive at 0.5 cycles and and antiphase drive at 3.5 cycles. In all, the trace duration is 5 ms.

humped pulse envelope (Fig. 15, right), similar to that found in certain samples of *Cyclochila* song.

The power *versus* frequency spectra of this type of song model may be compared with

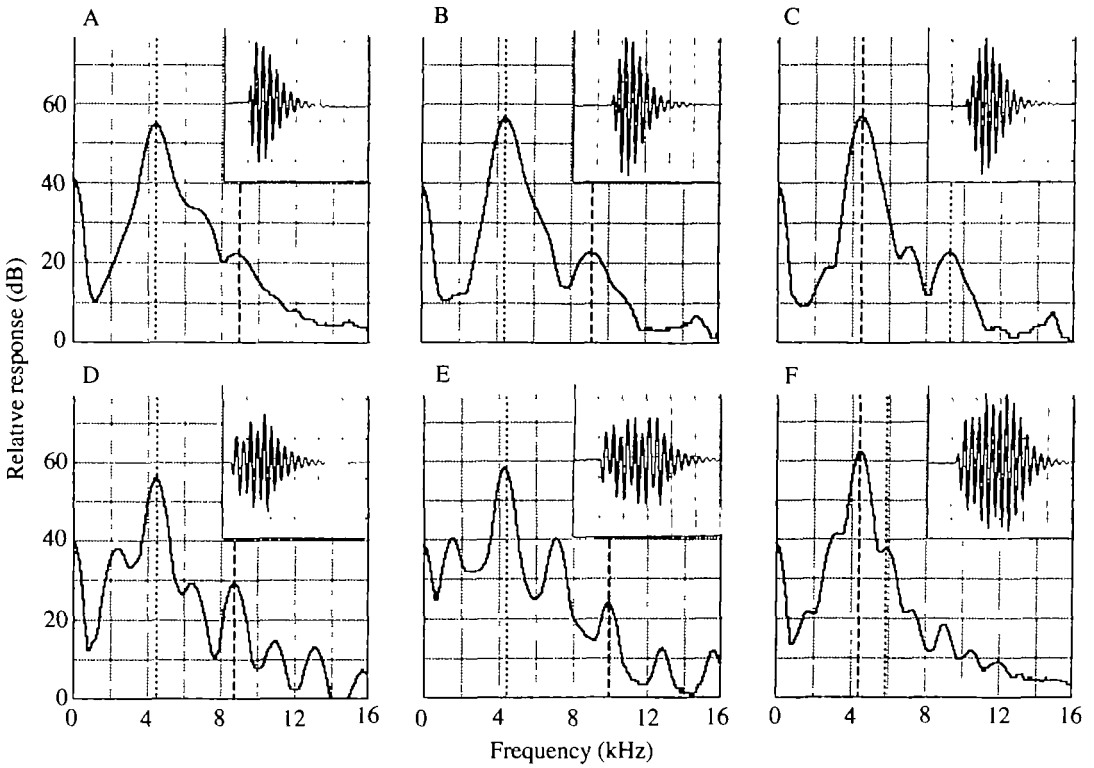

Fig. 16. Frequency *versus* energy spectra of the acoustic response of the model cicada (Fig. 3A) to one or more clicks of excitation. The insets show oscillograms of the sound pulses produced by the model, at a carrier frequency of 4.3–4.5 kHz. (A) Response to a single shaped pulse of 120 μs duration: dotted line at 4.4 kHz and dashed line at 8.96 kHz. (B) Response to two shaped pulses of 120 μs duration and 230 μs pulse period: dotted line at 4.4 kHz and dashed line at 9.12 kHz. (C) Response to three shaped pulses of 120 μs duration and 230 μs pulse period: dotted line at 4.48 kHz and dashed line at 9.28 kHz. (D) Response to three cycles of a 2.2 kHz symmetrical square-wave unshaped drive: dotted line at 4.48 kHz and dashed line at 8.72 kHz. (E) Response to three cycles of a 1.45 kHz symmetrical square-wave unshaped drive: dotted line at 4.40 kHz and dashed line at 9.92 kHz. (F) Response to three shaped pulses of duration 120 μs and 690 μs period: dashed line at 4.40 kHz and dotted line at 5.84 kHz.

those for cicada song. Fig. 16A–C shows spectra for model songs excited by one, two or three pulse-shaped clicks at 230 μs (approximately 1/4.3 kHz): all these show a clear subsidiary peak at about 9 kHz as well as a minor peak at 6.5–7 kHz.

In another series of trials, the model was driven by three cycles of a 2.2 kHz symmetrical square wave providing positive-going impulses at 0 μs, 460 μs and 920 μs and negative-going impulses at 230 μs, 690 μs and 1150 μs, giving periodic excitation coherent with the model's response alternating in phase at 230 μs intervals (approximately 1/2.2 kHz). This produced a series of subsidiary peaks in the spectrum at $f_0 \pm 2.2$ kHz, f_0+4.4 kHz, f_0+6.6 kHz etc. (Fig. 16D). When the model was driven by three cycles of a 1.45 kHz symmetrical square wave, this provided positive-going impulses at

0 μs, 690 μs and 1380 μs and negative-going impulses at 345 μs, 1035 μs and 1725 μs: this gave periodic excitation alternating in phase at 345 μs intervals (approximately 1/2.9 kHz, or at every one and a half cycles of the carrier), which produced a series of subsidiary peaks in the spectrum at f_0±2.9 kHz, f_0+5.8 kHz, f_0+8.7 kHz etc. (Fig. 16E). When driven by three 120 μs duration pulses at 690 μs period, which provided positive-going impulses at 0 μs, 690 μs and 1380 μs, giving periodic in-phase excitation at 690 μs intervals (approximately 1/1.45 kHz or at every third cycle of the carrier), the model produced a series of subsidiary peaks in the spectrum at f_0±1.45 kHz, f_0±2.9 kHz, f_0+4.35 kHz etc. (Fig. 16F).

These response curves may be compared with those measured from *Cyclochila* songs (Fig. 6). In the song illustrated in Fig. 6D,E, there are strong subsidary peaks at 8.6 and 12.9 kHz, suggesting that the tymbal clicks occurred at intervals of 1/4.3 kHz or in successive cycles of this song. In the slowly-decaying song pulses (Fig. 6A,B), the song spectrum shows a fundamental at 4.2 kHz and subsidiary peaks at about 5.8 kHz or at about 1.33f_0 and others at around 8 kHz and again around 12 kHz or at about 2f_0 and 3f_0. This implies that the tymbal clicks might have occurred with an interval of 1/f_0 and again with an interval of 3/f_0, or at cycle zero, cycle one and cycle three. Neither of these interpretations is inconsistent with the way in which the song pulse envelopes build up. Song spectra published elsewhere (Young, 1990) show similar evidence for periodic excitation of a resonance: that for *Cyclochila* shows peaks at 4.3, 5.6, 8.6 and 13 kHz (giving a similar spectrum to that shown here in Fig. 6D) and that for *Macrotristria* shows large peaks at 6 and 12 kHz, and minor peaks at 8 and 10 kHz, suggesting that this particular song might have had two pulses of excitation which were separated by two cycles of the carrier.

The acoustic role of the tympanal opercula

We have already described the effect of opening or closing the opercula of dead cicada bodies. We also examined the acoustic effect of the model opercula fitted over the holes in the fixed-volume model cicada (Fig. 3B).

The effect of the position of the opercula on the resonant frequency and sound output of the model is shown in Table 2. Closing the opercula reduces the model sound output by about 10 dB, which is similar to the 11 dB reduction in the song SPL measured by Young (1990) when he held the opercula of living cicadas closed during sound production.

The resonant frequency of the model is also reduced by closing the opercula. Closing the opercula reduces the Q of the resonance, in contrast with the effect measured with cicada bodies. Inspection of equation 2 shows that closing the opercula might either increase or decrease the value of Q, depending on whether the effective radius of the neck changes more or less rapidly than the change in its area as the opercula are closed. No attempt has been made to quantify this with the present model.

The songs of Magicicada

For comparison with the results obtained in *Cyclochila*, measurements were also made on the dried bodies of two species of the North American cicada *Magicicada*. These two species are of particular interest in the present context because one, *Magicicada*

Table 2. *Effect of the operculum on sound output of the model cicada (Fig. 4)*

	Operculum removed	5 mm gap	0.5–1 mm gap
Model resonant frequency, f_0 (kHz)	4.33	3.93	3.54
SPL 10 cm from hole (dB)	65.6	67.2	56.2
Q of the resonance	7.8	8.4	5.2

septendecim, produces a quiet whistling song at a low carrier frequency while the other, *M. cassini,* produces a louder song at a much higher carrier frequency (Young and Josephson, 1983).

Some relevant dimensions of the bodies and song parameters of *M. septendecim* and *M. cassini* are shown in Table 3. Calculation of the resonant frequency of a Helmholtz resonator with the dimensions of the abdominal air sacs and tympana in these two species gives a value of 4.4 kHz for *M. septendecim* and of 6.7 kHz for *M. cassini.* From the actual song frequencies given in Table 3, it can be seen that equation 1 adequately predicts the song frequency of *M. cassini,* but the song frequency of *M. septendecim* is nearly two octaves lower than predicted.

One possible explanation for this discrepancy involves the very different appearance of the tympanal membranes in the two species. The tympana of *M. cassini* are delicate and optically transparent, as are those of *Cyclochila,* which Young (1990) has shown to be acoustically transparent. The tympana of *M. septendecim* are opaque and apparently quite thick, though their thickness has not been measured.

The thicker tympana of *M. septendecim* were modelled by covering the holes in the 1.8 ml model cicada with either stretched rubber from a surgical glove or with cigarette paper 25 μm thick. Both of these caused a considerable decrease in the resonant frequency of the model, from an initial value of 4.3 kHz down to values of between 2.4 and 1 kHz with the rubber glove, depending on the tension, and to values of between 2 and 1 kHz with the paper. These values are much closer to the observed song frequency of *M. septendecim.* Tests with the probe microphone showed that the sound was still being radiated from the holes in the model.

Table 3. *Body dimensions and song parameters of* Magicicada *males*

	M. septendecim	*M. cassini*
Tympanal width (mm)	3.86±0.25	3.9±0.21
Tympanal height (mm)	3.6±0.19	3.58±0.22
Area of one tympanum (mm^2)	8.44±0.94	8.82±0.86
Air-sac volume (ml)	0.81±0.105	0.37±0.032
Calculated cavity f_0 (kHz)	4.4	6.7
*Song carrier frequency (kHz)	1.3	6

Body dimensions are means and standard deviations from five individuals.
* Song carrier frequencies are taken from Young and Josephson (1983).

Discussion

The cicada abdomen as a Helmholtz resonator

Young (1990) suggested that the abdomen of male cicadas forms a Helmholtz resonator, the components of which are the large air sac as the cavity and the tympana as the holes through which sound is radiated from the system. The results of the various experiments described here are consistent with this interpretation.

Strong support for this suggestion comes from the model cicadas made from plastic syringes and driven by a miniature earphone. The shape and dimensions of the model shown in Fig. 3 are similar to those of the abdomen of a male *Cyclochila australasiae* and the model resonates at a similar frequency to the natural song of this species. At this resonant frequency, the sound output of the model has a power spectrum and a Q value similar to those of the rapidly-decaying pulses of natural song. Without the Helmholtz resonator attached, the output of the earphone driven by tone bursts at the same frequency has a broader power spectrum and its response is essentially non-resonant, showing that the Helmholtz resonator component of the model acts as a tuned acoustic filter.

There is the possibility that the dried bodies that we have used behave differently from those of live or newly killed insects but there does not seem to be much internal or external dimensional change after death: the air-sac walls remain intact and the acoustic performance of dried bodies of *C. australasiae* is very similar to that of the model cicadas; their performance is also consistent with the known parameters of the conspecific song. When excited by external sounds, the abdominal cavity in the insect resonates at frequencies close to the natural song frequency. And this cavity resonance depends in an appropriate way on the velocity of sound, as shown by conducting the experiment in CFC gas; this experiment also excludes the possibility that the observed resonance is due to a mechanical resonance of the elastic walls of the abdominal cavity.

The simple Helmholtz resonator model of equation 1 adequately predicts the natural song frequency of both *C. australasiae* and *Macrotristria angularis* when the dimensions of their abdominal air sacs and tympana are used in the equation. However, in the genus *Magicicada*, equation 1 predicts the song frequency of *M. cassini* but not that of *M. septendecim*, which is almost two octaves below the predicted value. Our results suggest that the low frequency produced by *M. septendecim* may be accounted for by the relatively thick tympanal membranes in this species. The effect of placing a thick compliant membrane across the neck of a Helmholtz resonator will be to increase the inertance or effective mass of the orifice, as well as possibly to reduce the effective area of the tympana, and hence to lower the resonant frequency of the system. Such an increase in the neck inertance of the resonator would also raise the Q value; and an exceptionally high Q value of 25 is reported for this species (Young and Josephson, 1983). An analogy would be to increase the mass in a simple spring-and-mass resonator, where the resonant frequency $\propto$ mass$^{-0.5}$. In the 1.8 ml cicada model, the resonant frequency is lowered significantly by covering the holes with a membrane to model the thick tympana of *M. septendecim*. So it appears that, with minor modification, the Helmholtz resonator model also holds with this species.

In the natural song of *Cyclochila*, the air sac is excited by the buckling of each tymbal

and the resulting sound output is a pulse with a rather variable rate of decay. Our experiments with the 1.8 ml model cicada show that slowly-decaying pulse envelopes can be obtained by exciting the model with a coherent train of two or three damped resonant pulses of appropriate frequency.

These observations suggest that the long-duration slowly-decaying sound pulses observed in some samples of natural cicada song (Fig. 6A,B) can be produced in the following conditions: that there are double or triple clicks of the tymbal, which resonate at the same frequency as the air sac; these clicks will then excite and sustain the resonance in the abdominal air sac, provided that successive clicks are coherent with the sympathetic resonant oscillations in the air sac; and that the clicks occur at appropriate time intervals. Hence, the Helmholtz resonator model is consistent with the actual mode of excitation of the cicada air sac, so far as this is known at present.

The effect of non-coherent excitation of the abdominal resonator and/or inappropriate time intervals between successive tymbal clicks has also been modelled, and probably explains some of the relatively irregular pulse envelopes that can be seen in certain samples of cicada song (see Josephson and Young, 1981, Fig. 2B; 1985, Fig. 6D).

The fact that the tympanal membranes are set into vibration when the air-sac resonance is excited by external sounds, as shown by dusting the bodies with cork powder, supports the conclusion of Young (1990) that the tympana are the major acoustic apertures of the abdominal air sac. Experimental observation (Young, 1990) showed that removal of the tympana had no measurable effect on the sound produced by male *Cyclochila*, and calculation (from Olson, 1957) suggests that a membrane of 1 μm thickness will transmit over 99.5 % of the incident sound – in other words, that the tympana are acoustically transparent.

Cicadas can vary the effective size of the tympanal apertures by raising or lowering the opercula covering the tympana. When producing the calling song, males of *C. australasiae* raise and extend the abdomen, thereby lifting the tympanal openings away from the opercula by some 5 mm (Young, 1990). From our results, it appears that this action has two main effects. First, it increases the effective area of the sound source, allowing greater sound power to be radiated from the resonant air sac. This is reflected in the increase of about 10 dB SPL in the sound output when the opercular gap is open rather than closed, both in the model and in the living insect (see Results; Young, 1990). Second, this action increases the effective radius of the neck of the resonator and/or decreases its effective length (see equation 1), which results in a somewhat higher resonant frequency (see Results).

The function of the abdominal Helmholtz resonator

One successful strategy for acoustic communication in insects is to have both the sound-producing and auditory systems quite sharply tuned to the same carrier frequency. This frequency is then an important species-specific parameter of the song, as is the rate of amplitude modulation of the carrier frequency.

In cicadas, a click of the type that a tymbal might produce is likely to have maximal amplitude and power in the first cycle of vibration, decaying exponentially thereafter, as in the model click illustrated in Fig. 14B, left. Such brief signals suffer from the

disadvantage that the response of a tuned receiver does not build up to its maximum value until after the exciting signal has started to decay. A single click is therefore much briefer than the response it excites in a resonant system (such as the Helmholtz resonator response shown in Fig. 14C, left). Consequently, the tymbal click is too brief to excite more than a weak sympathetic response in a tuned ear. So one important function of the Helmholtz resonator in the sound-producing system will be to lengthen the duration of the radiated sound, making it a stronger adequate stimulus for the receiving insect.

At the same time, the tymbal click on its own will be too impure for it to be worthwhile having a sharply tuned ear with a high Q value (and thus high sensitivity), and so another important function of the Helmholtz resonator will be to increase the tonal purity of the radiated sound. We have shown (see Results Fig. 10B) that a Helmholtz resonator dissipates most power at its resonant frequency and dissipates less power on either side of its resonance, in effect acting as a narrow band-pass filter (Fig. 12C,D). If such a system is driven by a closely coupled but loosely tuned exciting click, the oscillations of the exciting click are likely to be pulled into coherence with the oscillations of the resonant load. Evidence that this occurs in the song of *C. australasiae* is provided by the observation that ablation of the abdominal resonator reduces the level of the 4.3 kHz carrier frequency but greatly increases the level of higher-frequency components of the song (Young, 1990, Fig. 5).

The coherence of the succeeding clicks of the tymbal is also likely to be ensured by the resonant load, which then functions in a similar way to the escapement mechanism proposed for cricket sound production by Elliott and Koch (1985). An important distinction is that, in typical crickets, successive disengagements of the plectrum and file escapement occur at every cycle of the song, as with a pendulum clock escapement. But with the cicada tymbal, the initial click is likely to be relatively large and may not be followed in the next sound cycle by a second click, because the muscle does not contract quickly enough (Josephson and Young, 1981). In cicadas, it is likely that the next click occurs during the persisting oscillation of the abdominal Helmholtz resonator's response to the first click (as has been modelled in e.g. Fig. 14B or Fig. 16B). The tymbal in-click would then be opposed in the compression half-cycle of the sound oscillation in the air sac and facilitated in the rarefaction half-cycle, and thus be phase-locked to the air-sac sound oscillation. In some cases, this effect may be strong enough to ensure that the coherence even extends from one pulse to the next; Young and Josephson (1983) have suggested that the pure-tone songs of *Chlorocysta viridis* and *Magicicada septendecim*, in which there are no separate pulses, are produced in this way.

As has already been indicated, too brief a signal will not allow the receptor response to build up to its maximum value. An infinitely long signal, however, will allow the receptor response to build to a maximum and to saturate. So an optimum pulse length will just allow the receptor response to build to its maximum, which will only occur if the sound-producing resonator is excited to produce a pulse with a flat-topped envelope of an appropriate duration. This, of course, is achieved by the double-click or triple-click excitation of the abdominal Helmholtz resonator. The pulse envelope of the calling song of *C. australasiae* and of many other species often has such a long duration (Fig. 6).

The time course of the response to a constant-amplitude song pulse can be estimated by

reference to equation 6. Assuming that the response builds up and decays exponentially, it will build up to $1-e^{-1}$ times its maximum value (or to within 0.632, or 4 dB below the maximum amplitude) and decay to e^{-1} times the maximum (or to 0.368 of maximum amplitude, a decay of 8.7 dB) after Q/π cycles. For a Q of 8, these levels will occur after 2.5 cycles of build-up or decay. This treatment can be extended to show that for the response of a tuned receptor to build up to within 1 dB of its steady-state level, the steady state of the driving song pulse must persist for $2.22\times Q/\pi$ cycles, which is 5.5 cycles with a Q of 8. An example of a gradual build-up of this type is shown in Fig. 12. In a well-adapted song pulse, one might expect a build-up over about five cycles, then a plateau lasting five cycles (or 1.2 ms) and then a decay over five cycles. At a carrier frequency of 4.3 kHz, this gives a total pulse duration of 3.5 ms, or a pulse rate of 280 Hz.

The song of *Cyclochila* is modulated with a song pulse rate of 230 Hz (Young, 1990). The abdominal resonator has a Q between 7 and 8, giving a -3 dB bandwidth of 540–610 Hz (equation 5). The frequency at which a resonator can be modulated is similarly inversely related to its Q. The song pulse rate of 230 Hz is sufficiently slow to allow the signal to be modulated into discrete pulses (Fig. 6) but will be long enough to include the 1.2 ms plateau that a similarly tuned receptor requires in order to allow its response to build up to within 1 dB of its steady-state response.

The proposed model in which the tymbal clicks provide coherent acoustic excitation to an abdominal resonator from which sound can be radiated is thus seen as a highly specialised mechanism for the production of loud acoustic signals which are sharply tuned to a species-specific frequency.

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