J Comp Physiol (1983) 152:197–207

Journal
of Comparative
Physiology · A

Pure-tone songs in cicadas with special reference to the genus *Magicicada*

D. Young[1] and R.K. Josephson[2]

[1] Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia
[2] Department of Psychobiology, University of California, Irvine, California 92717, USA

Accepted March 25, 1983

Summary. 1. The calling song of *Magicicada cassini* consists of complex pulses of sound, each pulse being subdivided into about 9 sub-pulses, and is broadly tuned ($Q_{3\,\mathrm{dB}} = 5$) around a peak frequency near 6 kHz. The calling song of *M. septendecim* consists of a modulated pure tone, not divided into pulses or sub-pulses, and is sharply tuned ($Q_{3\,\mathrm{dB}} = 25$) at a peak frequency of 1.3 kHz (Figs. 2, 3).

2. In both *M. cassini* and *M. septendecim* the sound-producing tymbal consists of a membrane bearing 12 stiffening ribs anteriorly and an irregularly shaped tymbal plate posteriorly. The tymbal of *M. cassini* has a much higher resting stiffness than that of *M. septendecim.*

3. The tymbal muscles of both species produce single twitches in response to electrical stimulation and contract more rapidly as muscle temperature increases (Fig. 6). The tymbal muscle of *M. cassini* is relatively more powerful than that of *M. septendecim.*

4. In *M. cassini*, each cycle of tymbal movement produces one complex pulse, the succession of 9 sub-pulses being correlated with the successive buckling of 9 ribs. In *M. septendecim*, each tymbal movement produces one simple pulse, an unbroken train of sound waves, not obviously correlated with rib buckling (Fig. 5).

5. If, in *M. septendecim*, the rib buckling frequency determines the fundamental sound frequency, then the latter should increase with rising muscle temperature but this effect is not observed. It is more likely that sound is generated by the tymbal buckling in only 3 or 4 distinct stages, each generating a few oscillations at the fundamental sound frequency. This interpretation is also applicable to the pure-tone song of *Chlorocysta viridis.*

6. It is suggested that pure-tone songs in cicadas are made possible by a reduction in the stiffness of the tymbal. This permits the precise time of buckling of each rib to be influenced by the phase of oscillation in the abdominal resonator, thereby creating a coherent and continuous train of sound waves from one tymbal cycle to another.

Introduction

Detailed studies of eleven species of cicada (Homoptera: Cicadidae) have revealed a great diversity in the sound patterns that are generated by their tymbal mechanisms (Simmons and Young 1978; Josephson and Young 1981; Young and Josephson 1983). In the majority of species, the sound produced is basically sinusoidal but a wide range of frequencies is necessarily introduced by the pulsed structure of the songs. The more complex the pulses are, the wider must be the bandwidth of the overall sound. However, in one species, *Chlorocysta viridis*, there are no distinct pulses and the calling song is a modulated pure tone (Young and Josephson 1983). This kind of song was first noticed by Moulds (1975) in *Lembeja brunneosa* from North Queensland, Australia. This species produces a calling song that is indistinguishable to the human ear from the output of an electronic sine-wave generator. Thus, within the family Cicadidae, there is a range of song patterns from pure tones to those with wide bandwidths.

A similar diversity of sounds has long been recognised in the orthopteran families, Gryllidae and Tettigoniidae. In these families, the extremes of variation in sound pattern are associated with differences in the file and scraper mechanism by which the sound is produced. These differences are summarised by Bailey and Broughton (1970), Sales and Pye (1974, pp. 100–105) and by Bennet-Clark (1975, Fig. 2).

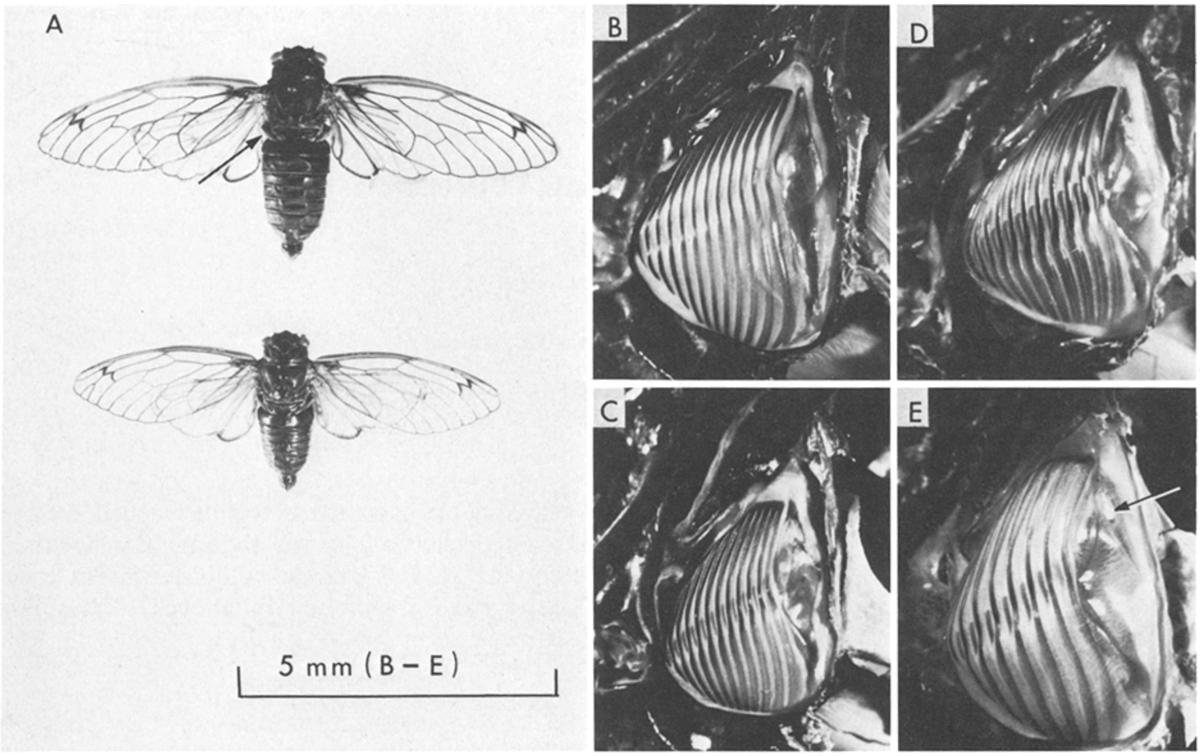

Fig. 1. **A** Mounted specimens of *Magicicada cassini* (*below*) and *M. septendecim* (*above*), approximately natural size. *Arrow* shows the location of the sound-producing tymbal and also indicates the approximate angle from which photographs in **B**–**E** were taken. **B**–**E** Tymbals in four species of cicadas; all are at the same degree of magnification. *Arrow* in **E**, point of insertion of the tymbal muscle. **B** *M. septendecim;* **C** *M. cassini*; **D** *Abricta curvicosta*; **E** *Chlorocysta viridis*

In species of Gryllidae and Tettigoniidae with relatively pure-tone songs, each tooth impact generates a single sound wave that does not decay before the next tooth impact. Consequently each cycle of wing movement produces one continuous train of sound waves at the tooth impact frequency, i.e. a single pulse of long duration. The wing membrane acts as a resonator, sharply tuned (high Q) to the tooth impact frequency, and the file and scraper mechanism acts as a source driving the wing membrane at its resonant frequency. In species with wide bandwidth songs, each tooth impact generates a damped train of sound waves that decay before the onset of the next tooth impact. Thus each cycle of wing movement produces many such trains of sound waves, i.e. many pulses. The wing membrane that is excited by the tooth impacts is very broadly tuned (low Q) to amplify the wide range of frequencies produced and the system as a whole is effectively non-resonant.

It is natural to ask whether a corresponding difference in mechanism might account for the great differences found in cicada songs. Rather unexpectedly, we found that it was possible to study extreme examples from the range of variation within a single genus of cicadas, the North American genus *Magicicada. Magicicada cassini* and *M. septendecim* are the two principal species in a complex of 3 species having 17 year life-cycles (Alexander and Moore 1958, 1962). *M. cassini* and *M. septendecim* are very similar in overall appearance and bodily proportions but differ considerably in size (Fig. 1A). In spite of their close relationship, we found that these two species have very different song patterns. The study of these differences was facilitated by our being able to induce males of both species to produce their calling songs while tethered in the laboratory, with electrodes implanted in their muscles. Hitherto, the only species of cicada in which this has been achieved is *Cystosoma saundersii* (Simmons and Young 1978; Josephson and Young 1979).

Materials and methods

All observations were made on Brood IV of the periodical cicada in June 1981 and attention was confined to two species, *Magicicada cassini* and *M. septendecim.* Field observations were made near Lawrence, Kansas, at the Rice Biological Reserve belonging to the University of Kansas. Specimens were also collected at this reserve and taken to Kansas University's Department of Entomology at Lawrence for experimental study. Some observations made on two Australian species, *Abricta curvicosta* and *Chlorocysta viridis*, are also included in this paper. Pertinent details on these two species will be found in our previous paper (Young and Josephson 1983).

Tape recordings of the calling songs of individual specimens of the two species of *Magicicada* were made at Rice Biological Reserve on warm, sunny days. The recordings were made at a tape speed of $7^1/_2$ inches/s on a Nagra IVS tape recorder with a Sennheiser MKH 816 directional microphone. Sound and electrophysiological recordings were made in the laboratory using the same experimental methods as in our previous paper (Young and Josephson 1983).

In addition to the experiments on the protest songs, electrophysiological recordings were also obtained from tethered individuals that produced their calling songs in the laboratory. A myogram electrode of 50 μm insulated silver wire was inserted into one tymbal muscle through its ventral attachment (the chitinous V) and secured with wax. A reference electrode of bare silver wire was inserted into the posterior abdomen. The cicada was waxed to a holder and given a styrofoam ball to walk upon (this method is illustrated in Simmons and Young 1978, and Josephson and Young 1979). A thermometer was placed near the cicada, which was warmed with a lamp until the thermometer recorded about 30 °C. A cage containing several males of the same species was placed near the experimental animal, with the whole set-up being near a large window but not subject to direct sunlight. These experiments were run at those times of day that each species prefers to sing in the field: in the morning for *M. septendecim* and in the afternoon for *M. cassini* (Alexander and Moore 1962). Under these circumstances, the tethered cicadas would produce their calling songs occasionally in response to calls of the caged individuals. The sound and myogram from the tethered insect were then recorded on tape.

The contraction kinetics of the tymbal muscles were examined using the same methods as in our previous studies (Josephson and Young 1979, 1981). The lengths of experimental muscles were measured with a graduated scale held against the muscles while they were maintained at the lengths used in the kinetic measurements. At the end of each experiment, the animals were preserved in 70% alcohol. Later, the experimental muscle was dissected out, cleaned of adhering tissue, rehydrated in insect saline and weighed. Tettigoniid muscles have been found to lose about 12% of their wet weight when they are fixed in 70% alcohol and later rehydrated (M. Ready, unpublished). We have assumed that there is a similar weight loss in cicada muscles and have corrected for it in determining muscle mass. Muscle cross-sectional area was determined from the ratio of muscle mass to length.

Experiments on protest songs at different temperatures were carried out with individuals tethered to holders as for the electrophysiological experiments. A thermistor probe was inserted into the abdomen near the tymbal muscles in order to measure temperature. After each desired temperature had been reached, 5 min was allowed for equilibration before eliciting protest song. Low temperatures (20 °C) were obtained by surrounding the insect with a box containing blocks of ice and high temperatures (up to 35 °C) were obtained by warming the insect with a lamp. The protest songs elicited at different temperatures were recorded on tape.

The illustrations of cicada tymbals (Fig. 1, B–E) were obtained by dissecting preserved (dried) specimens so as to show the full extent of the tymbal membrane. To do this it was usually necessary to remove all of the abdomen posterior to the tymbal, cutting along a line as close as possible to the posterior edge of the tymbal. The photographs were taken using a Zeiss Tessovar.

Results

The song patterns

Males of *M. cassini* produce their calling songs in dense choruses during the day. The calls of many individuals may be synchronised (Alexander and Moore 1958, 1962), which makes recording difficult. However, individual males may be heard calling in relative isolation in the late afternoon and clear recordings of individual songs can then be obtained (Fig. 2A–C). The calling song consists of a regularly repeated phrase (Fig. 2A), each of which is separated from the next by a silent interval of up of 1 s. Each phrase has an initial portion with a very low pulse repetition frequency of 15–30 Hz, followed by a final portion with a high pulse repetition frequency of 170–200 Hz ($\bar{x}=180$; S.D.$=13.5$; $n=5$). The individual pulses have a compound structure that remains the same in both the initial and the final portions (Fig. 2B, C). Each compound pulse is divided into about 9 sub-pulses and each sub-pulse consists of a train of sound waves that rise and fall sharply in amplitude (Fig. 2C).

Males of *M. septendecim* also call in dense choruses (Alexander and Moore 1958, 1962) but it is not difficult to approach members of this species closely without them flying away. Therefore, recordings of individual calling songs are readily obtained (Fig. 2D–F). The pattern of sound in *M. septendecim* is quite different from that found in *M. cassini.* The calling song consists of a phrase that is repeated about three times, with a silent interval of about 1 s between phrases. Each phrase (Fig. 2D) consists of a continuous burst of song lasting 2–3 s, with a drop in both amplitude and frequency at the conclusion of the phrase (Alexander and Moore 1958; Moore and Alexander 1958). The sound within each phrase (Fig. 2E) is not divided into distinct pulses, still less into sub-pulses, but there are amplitude modulations at a constant frequency of 120–150 Hz ($\bar{x}=136$; S.D.$=10$; $n=7$). The sound wave continues without interruption or change of phase from one amplitude peak to the next so that the sound pattern is a modulated pure tone (Fig. 2F). In this respect, the calling song of *M. septendecim* is very similar to that of *Chlorocysta viridis* (Young and Josephson 1983, Fig. 3).

The differences in song patterns between *M. cassini* and *M. septendecim* are also brought out

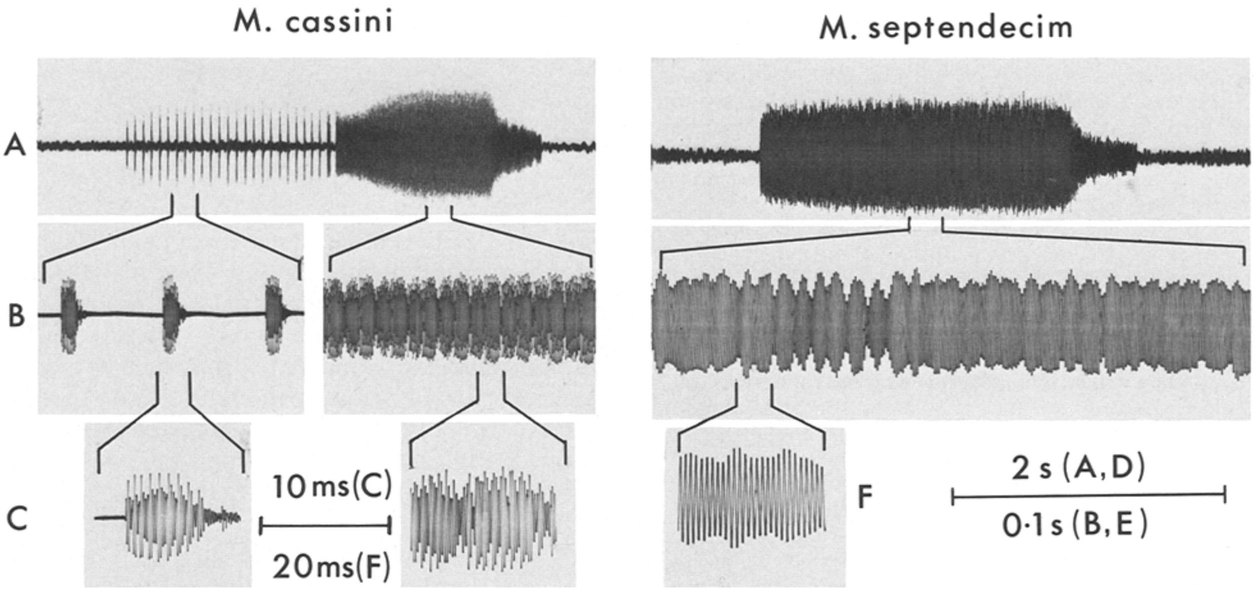

Fig. 2. **A–C** Oscillograms of the calling song of *Magicicada cassini*. **A** Low speed film record of an entire song phrase; **B** high speed film records from the initial portion (*left*) and the final portion (*right*); **C** single sweep records of a single pulse from the initial portion (*left*) and of part of the final portion (*right*). **D–F** Oscillograms of the calling song of *Magicicada septendecim*. **D** low speed film record; **E** high speed film record; **F** single sweep record showing how the sound waves continue from one amplitude peak to the next

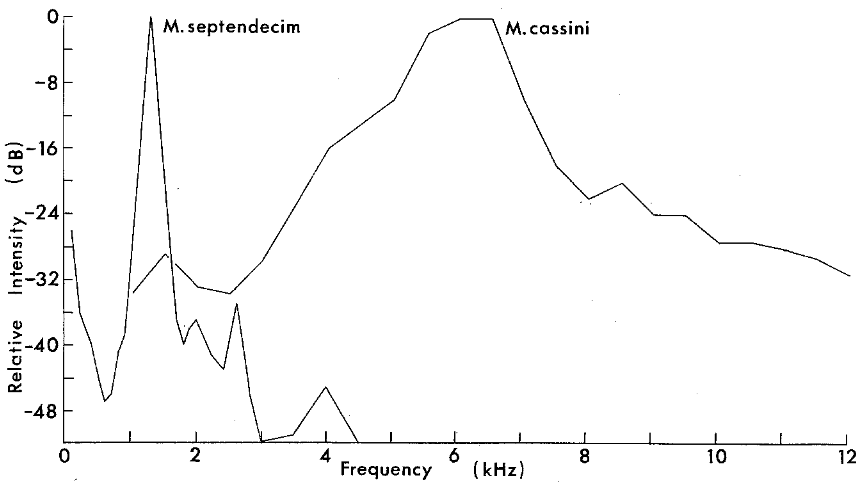

Fig. 3. Frequency-power spectra for the calling songs of *Magicicada cassini* and *M. septendecim*. Curves show intensity in dB relative to peak value in each species

by examining the sound frequencies present in their calling songs. Some information on the frequency content of the calling songs of these two species is provided by Alexander and Moore (1958), Moore and Alexander (1958) and Simmons et al. (1971). Further information may be obtained by analysis of the sound spectrum of small portions of individual calls (Fig. 3). In our samples, these analyses yielded dominant frequencies around 6 kHz for *M. cassini* and close to 1.3 kHz for *M. septendecim*.

More importantly, the sound spectra show great differences between the two species in the shape of the curve. In *M. cassini*, there is a broad peak with a relatively gentle slope on either side so that the bandwidth is about 5 kHz at 20 dB below the peak (Fig. 3). Dividing the peak frequency by the bandwidth 3 dB down yields a measure of the sharpness of tuning (Q) with a value of about 5. There is a small but consistent peak around 1kHz that probably represents the subpulse repetition frequency. In *M. septendecim*, the sound is sharply tuned around the peak frequency and the bandwidth at 20 dB down is 0.5 kHz or less (Fig. 3). Measurement of the major peak gives Q values close to 25. A first harmonic is consistently discernable at about 2.6 kHz but this is always 30 dB or more below the main peak. A

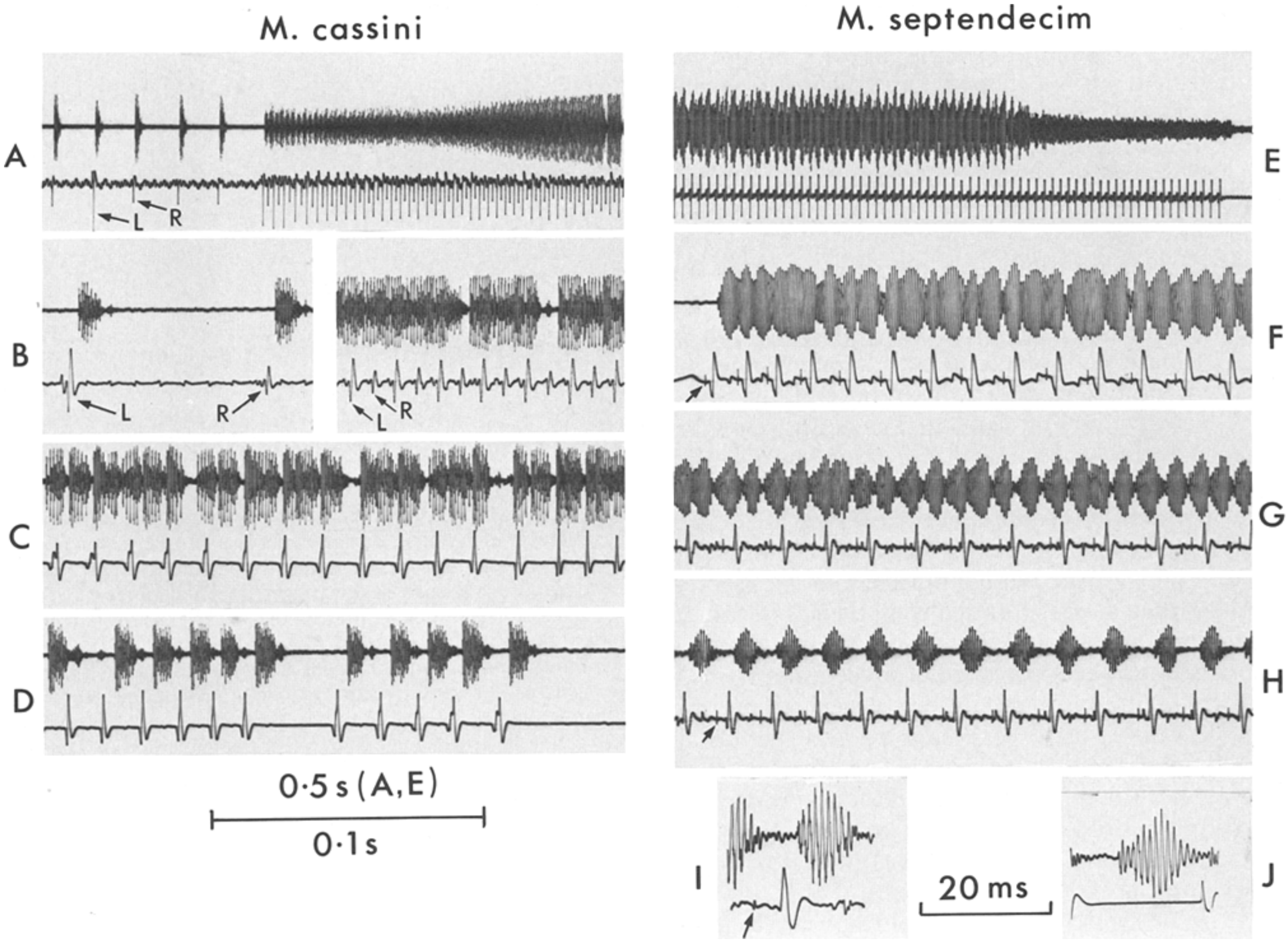

Fig. 4. A–D Laboratory recordings of sound output and tymbal muscle action potentials in *Magicicada cassini*. **A, B** Calling song in a specimen with implanted electrodes, showing sound (*upper trace*) from both tymbals and myograms (*lower trace*) from left (*L*) and right (*R*) tymbal muscles (although myogram electrodes were implanted in left tymbal muscle, they have also picked up the muscle action potentials from right tymbal muscle and these are distinguishable by their smaller amplitude): **A** low speed film record at the transition from the initial to the final portion; **B** high speed film records of the initial (*left*) and of the final portion (*right*). **C, D** Protest song in a specimen with implanted electrodes: **C** sound (*upper trace*) from both tymbals and myogram (*lower trace*) from left tymbal muscle only; **D** same insect as in **C** after destruction of right tymbal, showing sound and myogram from the left side only. **E–J** Laboratory recordings from *Magicicada septendecim*. **E, F** Calling song in a specimen with implanted electrodes, showing sound (*upper trace*) from both tymbals and myogram (*lower trace*) from the left tymbal muscle only: **E** low speed record at conclusion of song phrase; **F** high speed film record at onset of song (*arrow* indicates motor neuron impulse). **G, H** Protest song in an animal with implanted electrodes: **G** sound (*upper trace*) from both tymbals and myogram (*lower trace*) from the left tymbal muscle only; **H** same insect as in **G** after destruction of the right tymbal, showing sound and myogram from the left side only. **I** Single sweep record of protest song with sound (*upper trace*) and tymbal muscle myogram (*lower trace*) from left side only (expanded time-scale from record **H**; *arrow* indicates motor neuron impulse). **J** A single sound pulse (*upper trace*) initiated by electrical stimulation (*lower trace*) applied to the tymbal muscle

peak is also observable at about 100 Hz and this probably represents the amplitude modulation frequency of the calling song.

The mechanism of sound production

In *M. cassini*, Moore and Sawyer (1966) and Reid (1971) have interpreted each compound pulse as the result of a single contraction in one tymbal muscle. The sub-pulses are due to the consecutive buckling of the several stiff ribs on the tymbal as it is drawn inwards by the contracting muscle. The outward movement of the tymbal is ineffective in producing sound but a continuous burst of sound is achieved by contracting the left and right muscles alternately. A similar mechanism appears to operate in *Abricta curvicosta*, which has a similar pulse structure in its song (Young 1972; Young and Josephson 1983).

Our results confirm this interpretation for *M.*

cassini. Myograms recorded from tethered insects, producing their calling song in the laboratory, show directly that each compound pulse is preceded by a contraction in one tymbal muscle (Fig. 4A, B). During the final portion of the song, the left and right tymbal muscles contract alternately at a constant frequency that is half the pulse repetition frequency of the song, i.e. 90 Hz. This frequency does not change during changes in volume of the emitted song (Fig. 4A). Similarly the relatively isolated pulses of the initial portion of the song are each preceded by a single muscle action potential (Fig. 4B) and so must be the result of a single tymbal movement. The contraction frequency of the tymbal muscles is much lower during this initial portion of the song and the strict alternation of left and right is not observed (Fig. 4A).

The relationship between compound pulses and contractions of the tymbal muscle that is observed in the calling song is found also in the protest song. Myogram recording from one tymbal muscle shows that an action potential precedes every second pulse in the intact insect, except where the tymbal fails (Fig. 4C). Following destruction of one tymbal, the pulse repetition frequency is halved and the relation of muscle action potentials to sound pulses becomes one to one (Fig. 4D). This indicates that each muscle contraction is followed by one compound pulse and that the left and right tymbal muscles contract alternately. Where myogram recordings have been confined to the protest songs, as is usual in cicada work (e.g. Reid 1971; Young and Josephson 1983), the assumption has been made that the resulting interpretations may be extended to the calling songs. The above results show that, in *M. cassini*, this assumption is valid.

In the calling song of a tethered specimen of *M. septendecim*, the amplitude modulations are more pronounced than they are in songs produced freely in the field. When myogram recordings are made from one tymbal muscle in such a specimen (Fig. 4E, F), two amplitude modulations are seen to follow each muscle action potential. The situation is particularly clear at the onset of a phrase especially as it was sometimes possible to detect the motor neuron impulse preceding each muscle action potential (Fig. 4F). This result suggests that each amplitude peak results from a single contraction of one tymbal muscle and that the two tymbal muscles contract alternately. The contraction frequency of each tymbal muscle is thus half the amplitude modulation frequency seen in the calling song, i.e. 68 Hz. This interpretation is confirmed by reference to the protest song, where the amplitude modulations are so marked as to rank as distinct pulses (Fig. 4G). Here also, every second modulation is preceded by an action potential in one of the tymbal muscles. Following the destruction of one tymbal, the repetition frequency of the modulations is halved, giving a one-to-one relationship between muscle action potentials and sound pulses (Fig. 4H). In such a unilateral preparation, the amplitude modulations appear as entirely distinct pulses.

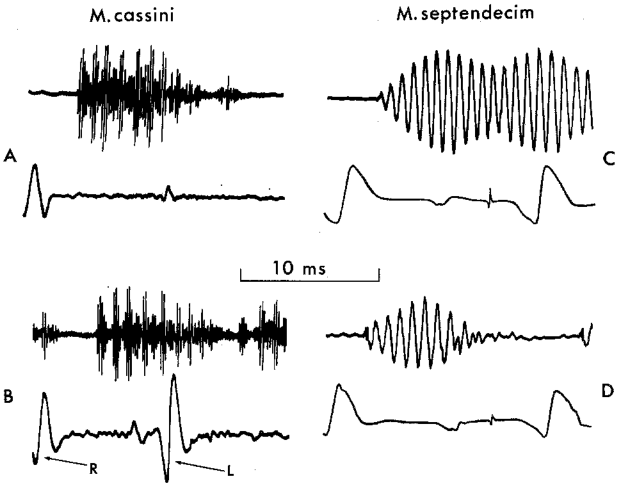

Fig. 5A–D. Laboratory recordings on an expanded time-scale to show, in each case, the relation between muscle action potentials (myogram, *lower trace*) and sound pulses (*upper trace*). Each record is a single sweep triggered off the initial deflection of a muscle action potential in the lower trace. All records share the same time-scale. **A** *M. cassini* calling song: a single compound pulse from the initial portion of the song. **B** Protest song from the same specimen as in **A**. Myogram electrodes were implanted in left (*L*) tymbal muscle but have also picked up action potentials from right (*R*) tymbal muscle. **C** *M. septendecim* calling song, showing the situation at onset of a burst of song. Myogram is from left tymbal muscle only. **D** Protest song from the same specimen as in **C**, after destruction of the right tymbal, showing sound and myogram from the left side only

When the distinct pulses from Fig. 4H are examined more closely, each is seen to consist of a continuous train of sound waves (Fig. 4I) of a frequency similar to that found in the calling song (Fig. 2F). It was confirmed that each of these pulses results from a single contraction of a tymbal muscle by electrical stimulation of the muscle via the myogram electrode. Each stimulus is followed by a pulse similar to that seen in the protest song (Fig. 4J).

The differing outcomes, in these two species, of a single cycle of tymbal action are summarised in Fig. 5. In *M. cassini*, each contraction of the tymbal muscle is followed by a compound pulse, divided into 8 or 9 sub-pulses. The pulses produced during protest song are very similar to those seen

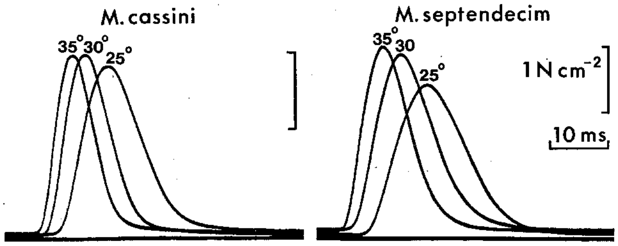

Fig. 6. Mechanical recordings of single twitches of tymbal muscles of *M. cassini* (*left*) and *M. septendecim* (*right*) at 3 different temperatures. Time calibration is identical for both records but tension calibration differs slightly as indicated by the two *vertical scale-bars*

Table 1. Contraction kinetics of tymbal muscles in *Magicicada cassini* and *M. septendecim* (means ± standard error)

Species	Muscle temperature (°C)	Twitch tension (Ncm^{-2})	Twitch rise-time (ms)	Twitch duration onset −90% relaxation (ms)
M. cassini ($n=6$)	25	2.69 ± 0.48	7.6 ± 0.5	17.8 ± 0.8
	30	2.67 ± 0.46	6.0 ± 0.3	13.7 ± 1.0
	35	2.73 ± 0.45	5.2 ± 0.4	10.8 ± 0.8
M. septendecim ($n=5$)	25	2.04 ± 0.61	9.2 ± 0.5	21.1 ± 2.1
	30	2.29 ± 0.72	7.3 ± 0.5	16.2 ± 1.7
	35	2.43 ± 0.82	6.4 ± 0.4	14.0 ± 1.3

Table 2. Tymbal muscle size in *Magicicada cassini* and *M. septendecim* (means ± standard error)

Species	Muscle length (mm)	Muscle weight (mg)	Cross-sectional area (cm^2)
M cassini ($n=6$)	4.4 ± 0.1	12.0 ± 0.6	0.027 ± 0.001
M. septendecim ($n=5$)	4.7 ± 0.2	11.7 ± 0.7	0.025 ± 0.001

in calling song (Fig. 5A, B). In a unilateral preparation of *M. septendecim*, each contraction of the tymbal muscle is followed by a simple pulse, consisting of an uninterrupted train of sine-waves (Fig. 5D). In the calling song, the same is evidently true but the pulses from left and right tymbals are amplified and smoothed out to give the pattern of sound seen in Fig. 5C.

The role of the tymbal muscles

In response to electrical stimulation, the tymbal muscles of both *M. cassini* and *M. septendecim* give all-or-nothing twitches with a single, sharp threshold (Fig. 6). This result is consistent with reports that the cicada tymbal muscle is innervated by a single, excitatory motor neuron, the tymbal motor neuron (Hagiwara 1955; Pringle 1954; Simmons 1977). Wohlers et al. (1979) and Wohlers and Bacon (1980) have published anatomical evidence from *M. cassini* and *M. septendecim* suggesting that up to 5 additional neurons may innervate the tymbal muscle. However, there is no hint of multiple innervation in our tension measurements on these two species (Fig. 6), a result that is consistent with other species of cicada that we have examined (Josephson and Young 1979, 1981). If additional neurons do innervate the tymbal muscle, they do not appear to play any detectable role in muscle contraction.

The tension measurements show that the tymbal muscles contract more rapidly and more strongly with increasing muscle temperature (Fig. 6; Table 1). At a given temperature, the tymbal muscles of *M. cassini* are capable of developing greater twitch tension than those of *M. septendecim*. Anatomical measurements show that the tymbal muscles are of similar size in the two species, those of *M. cassini* being slightly shorter but also slightly greater in cross-sectional area than those of *M. septendecim* (Table 2). When allowance is made for the considerable difference in overall body size between these two species (Fig. 1A), these results indicate that *M. cassini* has proportionately more powerful tymbal muscles than *M. septendecim*.

The tymbal muscles of *M. cassini* are also capable of contracting and relaxing more rapidly than those of *M. septendecim* (Table 1). This difference is correlated with the higher contraction frequency during singing in the former species (Young and Josephson 1983).

The role of the tymbal

Despite the differences in sound pattern between these two species, their tymbals are very similar in structure (Fig. 1B, C). In both species, the tymbal consists of a cuticular membrane bearing 11 or 12 long ribs. These ribs are arranged parallel to one another but converge somewhat toward the dorsal edge of the tymbal. They are sclerotized and raised distinctly above the level of the membrane, especially in the dorsal part of the tymbal. Interspersed between the long ribs are an equal number of short ribs that lie along the line of buckling of the tymbal. The short ribs are not raised noticeably above the tymbal membrane. Posteriorly the tymbal membrane turns sharply inwards and bears an irregularly shaped, sclerotized region, the tymbal plate (terminology of Simmons and Young 1978). The apodeme of the tymbal muscle inserts dorsally on the tymbal plate, where the point of attachment can be seen as a small indentation on the external surface. Reid (1971) includes photographs of the tymbal of *M. cassini* but these do not show the tymbal plate and one of them (his Fig. 1C) is printed upside-down. The tymbals of *M. cassini* and *M. septendecim* differ in size, in proportion to the difference in overall size between the two species.

Thus there are no obvious differences in structure that might account for the quite different patterns of sound produced by the tymbals in these two species. The same is true for the tymbals of *Chlorocysta viridis* (Fig. 1E) and *Cystosoma saundersii* (Simmons and Young 1978, their Fig. 4). The tymbal of *Abricta curvicosta* (Fig. 1D) does closely resemble that of the two *Magicicada* species and *A. curvicosta* produces a song with compound pulses that are divided into sub-pulses even more markedly than is the case in *M. cassini* (Young 1972; Young and Josephson 1983). Evidently, there is no tymbal configuration uniquely associated with the production of pure-tone songs.

Nevertheless, as soon as one begins to experiment on *M. cassini* and *M. septendecim*, it is evident that there is a striking difference in the behaviour of their tymbals. The action of the tymbal muscle can be mimicked by pushing inward at the point of the muscle attachment on the tymbal plate with fine forceps or sharp pencil. The tymbal of *M. cassini* feels quite stiff and always produces a distinctly audible sound when buckled by hand, even after removal of the abdomen. By contrast, the tymbal of *M. septendecim* feels relatively sloppy and, when buckled by hand, the sound that it produces is barely audible. In qualitative terms, it is evident that the tymbal of *M. cassini* has a much higher resting stiffness than that of *M. septendecim*. We did not make quantitative measurements on the differences in tension required to buckle the tymbal in the two species.

However, an estimate of the relative stiffness of the tymbals in the two species may be obtained by examining myogram recordings on an expanded time-scale (Fig. 5). There is a delay between the muscle action potential, which marks the onset of muscle contraction, and the beginning of the sound pulse, which marks the onset of tymbal buckling. The length of this delay must reflect both the stiffness of the tymbal and the contraction kinetics of the tymbal muscle. Since the contraction kinetics of the tymbal muscles are known (Table 1), an estimate of the relative stiffness of the tymbals can be obtained from measurements of this delay. The time-course of the muscle action potentials is faster in *M. cassini* than in *M. septendecim* but the overall delay from the onset of the muscle action potential to the onset of the sound pulse is similar in the two species, averaging about 5 ms in *M. cassini* and about 4.5 ms in *M. septendecim* (Fig. 5).

The tension developed by the tymbal muscles in these lengths of time at 30 °C (the approximate temperature of the laboratory during these experiments) can be estimated from Table 1, taking into account the shape of the curves in Fig. 6. Since the rising phases of the curves in Fig. 6 approximate to straight lines over most of their length, the tension developed in the above times may be obtained simply by dividing the twitch tension by the fraction of the rise time that has elapsed. In *M. cassini*, the average value is about 2.23 $\mathrm{N\,cm^{-2}}$ in 5 ms and, in *M. septendecim*, it is about 1.41 $\mathrm{N\,cm^{-2}}$ in 4.5 ms. These values assume a negligible delay between the onset of electrical activity in the muscle membrane and the onset of contraction in the muscle fibrils. If this delay is not negligible, the values given must be reduced on account of the reduced time available for contraction but their mutual proportion will not change significantly. Thus these estimates indicate that, by the time the tymbal buckles, the tymbal muscles of *M. cassini* have developed 50% more tension than those of *M. septendecim*. This difference must reflect a corresponding difference in the stiffness of the tymbals to which the muscles are attached.

There are two ways in which such similar tymbals might, in the process of buckling, produce the observed differences in song pattern. On the one hand, each rib in the tymbal of *M. septendecim* might produce only a single oscillation in contrast to the several oscillations making up each subpulse in *M. cassini*. That is to say, the rib-buckling frequency would equal the fundamental sound frequency in *M. septendecim*. In this case, each sound pulse should contain a number of oscillations up to, but not greater than, the number of ribs. This requirement holds true in the calling and protest songs of *M. septendecim*. On the other hand, the buckling of each rib might produce several oscillations in *M. septendecim*, just as it does in *M. cassini*, but only a small number of ribs would be effective in producing sound. This appears to be the case in the pure-tone song produced by *Chlorocysta viridis* (Young and Josephson 1983).

We attempted to distinguish between these two alternatives by exploiting the changes in contraction kinetics of the tymbal muscle with changing temperature. In both species, the tymbal muscle contracts more rapidly at higher temperatures (Fig. 6; Table 1) and so the tymbal must be drawn in more rapidly at higher temperatures. Hence the frequency of rib-buckling, within each cycle of tymbal movement, should rise with temperature (see Josephson and Young 1979). Accordingly, an increase in the repetition frequency of the sub-pulses, within each compound pulse, is to be expected in *M. cassini* as muscle temperature rises. In *M. septendecim*, a corresponding increase in fundamental sound frequency with temperature is to be expected if the first alternative is correct. If the second alternative is correct, the fundamental frequency should not change greatly with temperature. This is because the frequency of oscillation will be determined by physical properties, such as the mass and compliance of the tymbal and abdomen, and these properties do not change significantly over the biological range of temperature.

When protest song is elicited at different temperatures in *M. cassini*, the repetition frequency of sub-pulses increases with temperature as expected. At the lowest temperature employed, 20 °C, this frequency is about 650 Hz and at the highest temperature employed, 35 °C, the frequency rises to about 1,200 Hz (Fig. 7A). The fundamental frequency of the sound in the sub-pulses of *M. cassini* does not change with temperature. In *M. septendecim*, the fundamental sound frequency does not change over the temperature range 20 °C to 35 °C but remains constant at just over 1 kHz (Fig. 7B). To guard against the possibility that the rib-buckling frequency might be strongly influenced by the abdominal resonator in *M. septendecim* (see Discussion), we repeated this experiment with the abdomen removed. The result was rendered doubtful by the fact that it was difficult to record any sound from the tymbal under these conditions. The faint sounds obtained (Fig. 7C) show many additional frequencies but do not appear noticeably different in fundamental frequency from 20 °C to 35 °C. This result tells against the possibility that the sound frequency is equal to the rib-buckling frequency in *M. septendecim*.

If the second alternative is correct and the tymbal buckles in a small number of distinct stages, then one would expect to see signs of a small number of sub-pulses under experimental conditions. Such sub-pulses are seen in the protest song of *Chlorocysta viridis* (Young and Josephson 1983, Fig. 3) but there is little sign of them in the protest song of *M. septendecim* (Figs. 4G, H; 5). However, with direct muscle stimulation, about three sub-pulses of increasing size are distinguishable (Fig. 4J). With the abdomen removed, the faint pulses of sound produced following muscle stimulation show clear signs of subdivision (Fig. 7D) but one should be cautious in interpreting such faint sounds. Thus our results tend to support the second alternative but are not entirely conclusive.

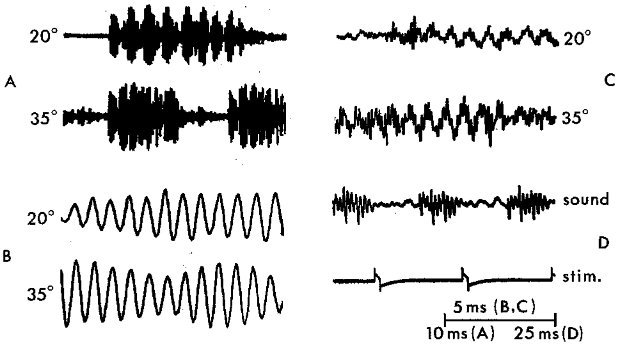

Fig. 7A–C. Oscillograms of protest songs elicited at different temperatures. **A** *Magicicada cassini.* Note that the *upper record* (at 20 °C) includes only one compound pulse whereas the *lower record* (at 35 °C) includes almost two compound pulses. This occurs because the repetition rate of the compound pulses rises with temperature as well as the repetition rate of the sub-pulses. **B** *M. septendecim* intact individual; **C** *M. septendecim*, individual with abdomen removed. **D** sound pulses (*upper trace*) initiated by electrial stimulation (*lower trace*) applied to tymbal muscle in *M. septendecim*; individual with abdomen removed

Discussion

M. cassini and *M. septendecim* differ strikingly in the sounds that result from each cycle of tymbal movement (see Fig. 5). In the former species, each cycle produces a compound pulse consisting of a train of about 9 sub-pulses, with each sub-pulse consisting of a train of sound waves that rise and decay rapidly in amplitude. In the latter species, each cycle produces a simple pulse consisting of a continuous train of sound waves that rises and decays in amplitude much more slowly. These differences must reflect differences in the action of the tymbals and the tymbal muscles.

It seems reasonably certain that, in *M. cassini*, the compound pulses are produced by about 9 ribs buckling in succession, with each rib generating a short train of sound waves (a sub-pulse) by vibrating at its natural frequency. In spite of their morphological similarity to those of *M. cassini*, the tymbals of *M. septendecim* must behave differently. One possibility is that the buckling of each rib generates only one sound wave so that the fundamental sound frequency is generated by the rib-buckling frequency. An obvious attraction of this interpretation is that it is directly comparable to the situation in the Orthoptera, where the sound frequency is generated by the tooth-impact frequency in species with relatively pure-tone songs (see Introduction). Nevertheless, the results of our experiments with songs at different temperatures appear to be inconsistent with this interpretation.

The balance of evidence from *M. septendecim*, as well as the evidence from *Chlorocysta viridis*, leads us to prefer the second interpretation: the tymbal of *M. septendecim* buckles in a small number of distinct stages, each of which generates a short train of sound waves. It is likely that each stage represents the buckling of a single rib, as it does in *M. cassini*, but one should allow for the possibility that several ribs might buckle simultaneously. In *Cystosoma saundersii*, it was shown that the tymbal buckles in two stages, each generating a train of sound waves: the first rib buckles, followed by the almost simultaneous buckling of a variable number of other ribs (Simmons and Young 1978). Provisionally, then, we adopt the view that the pure-tone songs of both *M. septendecim* and *Chlorocysta viridis* are the product of tymbals that buckle in 3 or 4 stages, each of which generates a short train of sound waves. This view fits in with the suggestion of Simmons and Young (1978) that all cicada tymbals work in essentially the same manner, with individual ribs generating short trains of sound waves (sub-pulses) as they buckle inward.

If this view is correct, then one has to explain how it is that both sub-pulses and pulses are run together to form a coherent and continuous train of sound waves in *M. septendecim* and *Chlorocysta viridis*, instead of being distinct as they are in related species such as *M. cassini* and *Cystosoma saundersii*. The following experimental evidence may be relevant to this problem. In *M. septendecim*, the tymbal is remarkable for its relative lack of stiffness, so much so that is is difficult to obtain any audible sound from it in a dissected preparation. The tymbal is activated by a muscle that is relatively less powerful than that in *M. cassini*, which is understandable in view of the tymbal's reduced stiffness. This relative lack of stiffness should make the tymbal mechanism more susceptible to external perturbations than would be the case in a very stiff tymbal, activated by a powerful muscle. If so, the tymbal in *M. septendecim* may not only serve as the source driving a resonator (the abdominal air sac) but also be influenced by the vibration of the resonator, to which it is closely coupled. The precise moment of buckling of each rib (on a scale of microseconds) may be influenced by the phase of oscillation in the resonator even though the general timing (on a scale of milliseconds) is determined by the neuromuscular system. In this way, an uninterrupted train of sound waves could be produced by a mechanism that intrinsically tends to produce pulses of sound.

Although we have not specifically studied the matter, it seems very likely that the sound-producing mechanism in *M. septendecim* exhibits resonance. By this is meant that the abdominal air sac is capable of free vibration and is driven at its resonant frequency by the vibration of the tymbals. The fundamental frequency of 1.3 kHz is present in the tymbal vibrations, even without the abdomen (Fig. 7C, D), but the amplitude of vibration is greatly increased by the presence of the abdomen (Figs. 4J and 7B). At the onset of the calling song, the amplitude of the sound increases gradually over several cycles (Fig. 5C) and the same effect is seen at the onset of each pulse in protest song (Fig. 5D). This is to be expected where there is resonance since it takes time for a lightly damped system to build up to a maximum amplitude of vibration. Indeed one might reasonably take it as prima facie evidence of resonance whenever the sound pulses of cicadas are seen to rise gradually in amplitude over several cycles after onset.

Certainly, this gradual increase in amplitude is seen in the sound pulses of *Cystosoma saundersii*, a species where experimental evidence (summarised in Simmons and Young 1978) and theoretical calculations (Fletcher and Hill 1978) combine to show that resonance is important in sound production. It is seen also in the pulses of *Platypleura capitata* (Pringle 1954; Josephson and Young 1981), the first species in which evidence of resonance was provided (Pringle 1954). In these species, the calling songs are divided into distinct pulses so that their songs are necessarily less pure than those of *M. septendecim* and *Chlorocysta viridis*. The additional frequencies introduced by the pulses show up in the sound spectrum of *Cystosoma saundersii* (Young 1980) but the song of this species is still much more sharply tuned ($Q_{3\,\mathrm{dB}} = 15$) than that of *M. cassini*. In *M. cassini* and many other species, such as *Abricta curvicosta* and members of the genus *Psaltoda* (Young and Josephson 1983), the amplitude of the pulses rises and falls sharply and one would not expect them to exhibit sustained resonance as defined above. Rather, one would expect to find a broadly tuned abdominal resonator that is excited only transiently by each tymbal action.

If the suggestions made in this discussion are correct, then the evolution of pure-tone songs from pulsed songs exhibiting resonance should be relatively straightforward. There is no change involved in the pattern of sound produced by the buckling of each rib on a tymbal. The required flexibility in the precise time of buckling can be effected by a reduction in the stiffness of the tymbal. This would permit the phase of vibration in the abdominal resonator to influence the precise time of rib-buckling in a way that could hardly be achieved by purely neuro-muscular coordination. The occurrence of pure-tone songs is known so far in three species: *Chlorocysta viridis* (Young and Josephson 1983), *Lembeja brunneosa* (Moulds 1975) and *Magicicada septendecim* (this paper). It is easy to see why similar songs have not been reported in crickets (Gryllidae and Tettigoniidae). In these families, the left and right wings interact to produce sound during the closing stroke. There is necessarily a silent period during wing opening, during which resonance must decay. By contrast, the left and right tymbals of cicadas produce sound independently of each other and so continuous excitation of the resonator is possible by having the two tymbals working in antiphase.

Acknowledgements. We are specially indebted to Dr. Charles Michener and the staff of the Department of Entomology at Lawrence, Kansas, for providing facilities for our study of periodical cicadas. Dr. Bill Bell kindly made space available in his laboratory and Dr. Bill Gordon gave us the benefit of his advice and lent us equipment. The sound spectra were plotted at Oxford with the help of Dr. H.C. Bennet-Clark. Mr. Brian Carr took the photographs in Fig. 1. D.Y. was supported by a Special Studies Programme from the University of Melbourne.

References

Alexander RD, Moore TE (1958) Studies on the acoustical behavior of seventeen-year cicadas (Homoptera: Cicadidae: *Magicicada*). Ohio J Sci 58:107–127

Alexander RD, Moore TE (1962) The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Misc Publ Mus Zool Univ Mich 121:1–59

Bailey WJ, Broughton WB (1970) The mechanics of stridulation in bush crickets (Tettigonioidea, Orthoptera). II. Conditions for resonance in the tegminal generator. J Exp Biol 52:507–517

Bennet-Clark HC (1975) Sound production in insects. Sci Prog (Oxford) 62:263–283

Fletcher N, Hill KG (1978) Acoustics of sound production and of hearing in the bladder cicada, *Cystosoma saundersii.* J Exp Biol 72:43–55

Hagiwara S (1955) Neuromuscular mechanism of sound production in the cicada. Physiol Comp Oecol 4:142–153

Josephson RK, Young D (1979) Body temperature and singing in the bladder cicada, *Cystosoma saundersii.* J Exp Biol 80:69–81

Josephson RK, Young D (1981) Synchronous and asynchronous muscles in cicadas. J Exp Biol 91:219–237

Moore TE, Alexander RD (1958) The periodical cicada complex (Homoptera: Cicadidae). Proc 10th Int Entomol Congr 1:349–355

Moore TE, Sawyer RT (1966) The mechanism of cicada timbal action (Insecta: Homoptera: Cicadidae). Am Zool 5:509

Moulds MS (1975) The song of the cicada *Lembeja brunneosa* (Homoptera: Cicadidae) with notes on the behaviour and distribution of the species. J Aust Entomol Soc 14:251–254

Pringle JWS (1954) A physiological analysis of cicada song. J Exp Biol 31:525–560

Reid KH (1971) Periodical cicada: mechanism of sound production. Science 172:949–951

Sales G, Pye D (1974) Ultrasonic communication by animals. Chapman and Hall, London

Simmons PJ (1977) Neuronal generation of singing in a cicada. Nature 270:243–245

Simmons PJ, Young D (1978) The tymbal mechanism and song patterns of the bladder cicada, *Cystosoma saundersii.* J Exp Biol 76:27–45

Simmons JA, Wever EG, Pylka JM (1971) Periodical cicada: sound production and hearing. Science 171:212–213

Wohlers DW, Bacon J (1980) Sexual dimorphism of motoneurons: timbal muscle innervation in male periodical cicadas and homologous structures in females. Cell Tissue Res 209:371–382

Wohlers DW, Williams JLD, Huber F, Moore TE (1979) Central projections of fibers in the auditory and tensor nerves of cicadas (Homoptera: Cicadidae). Cell Tissue Res 203:35–51

Young D (1972) Neuromuscular mechanism of sound production in Australian cicadas. J Comp Physiol 79:343–362

Young D (1980) The calling song of the bladder cicada, *Cystosoma saundersii*: a computer analysis. J Exp Biol 88:407–411

Young D, Josephson RK (1983) Mechanisms of sound-production and muscle contraction kinetics in cicadas. J Comp Physiol 152:183–195