

## Wing resonances in the Australian field cricket *Teleogryllus oceanicus*

H. C. Bennet-Clark

Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

(e-mail: henry.bennet-clark@zoo.ox.ac.uk)

Accepted 5 February 2003

### Summary

The anatomy and mechanics of the fore-wings of the Australian cricket *Teleogryllus oceanicus* were examined to study how resonances of the wings were excited, to model the interactions between the two wings during sound production, to account for the frequency changes that occur within the pulses and to determine the variation in sound amplitude during the pulses.

Sound is produced after raising the wings by closing the right wing over the left; the plectrum of the left wing engages and releases teeth on the file on the underside of the right wing. The mean number of teeth on the right file is 252; the teeth are more closely spaced in the posterior part of the file, which is engaged at the start of the song pulses. The anterior part of the file is separated from the base of the harp by a short flexible region. The dorsal field of the wing, in which the harp is situated, is largely mechanically isolated from the driving veins of the lateral field, except for a cross vein at the apex of the harp. The harps of the two wings did not differ significantly in area but the plectrum of the left wing was significantly longer and wider than that of the right wing. The posterior edge of the plectrum has a radius of approximately  $0.5\ \mu\text{m}$ , which allows it to engage the  $20\ \mu\text{m}$ -tall teeth of the file. The plectrum is separated from the wing by a  $0.5\ \mu\text{m}$ -thick crescent that allows it to twist lengthways and thus disengage the file teeth. The sigmoid shape of the file allows the plectrum to engage teeth over most of the length of the file.

The calling song of *T. oceanicus* consists of a chirp of four similar pulses followed by a trill of pairs of pulses. The dominant frequency of all pulses is approximately 4.8 kHz but cycle-by-cycle analysis suggests that the different types of pulse are produced by wing-closing movements through different arcs. Free resonances of the left wing occurred at 4.56 kHz [quality factor ( $Q$ )=25.1] and of the right wing at 4.21 kHz ( $Q$ =23.9). Driven by loud sound, maximum vibration of the harp was seen at approximately 4.5 kHz; at lower sound levels, the vibration was confined to the cross-veins of the harp that

extend distally from the file. Resonances of the left wing driven by vibration of the same wing, either at the plectrum or on the anal area, occurred at similar frequencies to those of the songs and had similar  $Q$ s but were approximately anti-phase, demonstrating that movement of the plectrum (e.g. by the file teeth) causes an opposite movement of the harp. When the right wing was driven directly on the file, the resonant frequency was 5.88 kHz but, when driven on the file *via* a length of the left file and the left plectrum, it was 4.83 kHz. The amplitude of the vibration increased from the posterior end of the file to the middle then fell towards the anterior end of the file. Pushing a left plectrum across the middle of the right file produced trains of damped sound pulses at 4.82 kHz ( $Q$ =23.4). Clicks excited from the anterior end of the file had lower frequencies. The resonances excited from both the left wing *via* its plectrum and from the right wing when driven *via* the left plectrum were similar in frequency to that of the song.

The resonance of the dorsal field persisted after ablation of the harp but the mean resonant frequency increased 1.12-fold with a similar  $Q$  to the intact wing. Droplets of water on the distal end of the harp or proximal part of the dorsal field raised the resonant frequency. The resonant frequency was lowered by the addition of weights to the harp or the file; the factor of the decrease suggested that the mass of the resonant system was approximately 1.4 mg, which accords with the mass of the harp plus file plus anal area of the wing (left wing, 1.27 mg; right wing, 1.15 mg) but is far heavier than the harp (0.22 mg). An earlier suggestion that the harp is the resonator is not supported; instead, it is proposed that the major elastic component of the resonant system is the file plus 1st anal vein and that the mass component is the combined mass of the file, anal area and harp.

Key words: *Teleogryllus oceanicus*, cricket, fore-wing, sound production, resonance, harp, file-and-plectrum.

## Introduction

Male crickets produce musical songs by closing their raised fore-wings. A plectrum (or scraper) on the posterior edge of the left wing engages with file teeth on the underside of the Cubitus 2 (Cu2) vein of the right wing. Capture, then release, of successive file teeth by the plectrum provides a phasic excitation that results in vibration of both wings and the production of nearly pure-tone sound (for a review, see Bennet-Clark, 1989). This mechanism has been likened to a mechanical clock in which resonant regions of the wing act as the regulator and the file-and-plectrum act as an escapement that provides a cycle-by-cycle excitation that maintains the vibration (Elliott and Koch, 1985; Koch et al., 1988). More recent analysis of the sounds made during normal and anomalous sound production by crickets provides further evidence for the mode of action of this escapement (Bennet-Clark and Bailey, 2002).

The resonant structures that act as regulators or determinants of the song frequency are thought to be the harp areas of the wings, which are bounded proximally by the file and distally by the Cubitus 1 (Cu1) vein: when driven by sound close to the song frequency, the harp vibrates with a greater amplitude than do other regions of the fore-wing (Nocke, 1971; Bennet-Clark, 1987). Both wings are involved in sound production: circumstantial evidence is provided by the similarity between the resonant frequencies of the left and right wings (Nocke, 1971) and more directly by the halving of the sound output power of the mole cricket *Scapteriscus acletus* when the harp of one wing was painted to damp out its vibration (Bennet-Clark, 1987).

Although the songs sound musical and appear to be tonally pure, there is a fall in frequency or 'glissando' within the song pulse of many cricket species (Leroy, 1966; Simmons and Ritchie, 1996; Bennet-Clark and Bailey, 2002). This suggests that, although the harp of the cricket wing has been modelled as a simple resonator (e.g. Nocke, 1971), the mechanics of the resonant regions of the wings must be changing during the wing-closing movement.

Further, although the two fore-wings of grylline crickets appear similar, in species such as *Gryllus campestris* the harps of the left wings are smaller than those of the right wings (Simmons and Ritchie, 1996), and harp ablation experiments suggest that the properties of the left wing control the frequency of the first third or half of the song pulse and those of the right wing control the later part of the pulse.

Both wings must be set in vibration by the action of the file-and-plectrum mechanism. The engagement, then release, of a file tooth causes the left plectrum to move downwards and the right file to move upwards; thus, the mechanism should cause the two wings to move in opposite directions (or anti-phase) but, because there do not appear to be discontinuities or lack of coherence of the waveform during a sound pulse, it appears that the file-and-plectrum mechanism activates the sound-producing regions of both wings so that they vibrate in phase with each other. Although there is circumstantial evidence in

bush crickets that the downward movement of the plectrum is inverted in phase to cause upward movement of the resonant region of the wing (fig. 6 in Bailey, 1970) and a model of how this may occur in mole crickets and crickets has been proposed (Bennet-Clark, 1970, 1989, 1999a), there is no direct evidence to support this idea. Indeed, the whole problem of how the file-and-plectrum mechanism interacts with other parts of the wing to produce sound pulses has received little attention.

In many cricket species, the amplitude of the song pulse builds up slowly to a maximum and then decays slowly but, in songs consisting of chirps made up of several pulses, as in those of *Gryllus campestris*, earlier pulses are quieter than later ones. In most examples, the build-up and decay are not exponential, suggesting that the drive to the sound-producing structures cannot be described in terms of the simple build-up and decay of the vibration of a resonant system. The earlier pulses appear to be produced by shorter wing-closing movements that start near the middle of the file, and the louder later pulses use more of the file; however, all pulses show a closely similar glissando, suggesting that the glissando is caused by the mechanical properties of the wings (Bennet-Clark and Bailey, 2002).

The present paper attempts to describe various aspects of sound production by crickets: how the left plectrum excites vibrations of the left wing; the mechanics of the left plectrum and how its action on the right file causes vibration of the right wing; the cause of the glissando in the song pulse; the slow build-up and decay of typical sound pulses; and the mechanical elements of the resonant system.

## Materials and methods

### Materials

Male *Teleogryllus oceanicus* (Le Guillou) from a laboratory culture in the Department of Zoology, University of Western Australia were used for all experiments. The culture had been started from wild stock caught in the previous spring (2000) near Carnarvon, Western Australia. The crickets were used between two and four weeks after the final moult.

Before experiments, the insects were decapitated but the fore-wings were left on the thorax until they were required and were then tested within the next 20 min to minimise any effects of drying. Wing dimensions were measured either with a graticule eyepiece on an Olympus stereo microscope or with a Malies curtain measuring eyepiece on a Watson Bactil microscope. Scanning electron micrographs (SEMs) of wings were made at the Centre for Microscopy and Microanalysis, University of Western Australia. Wings and parts of wings were weighed to the nearest 0.01 mg using a Mettler Toledo electronic balance.

The nomenclature of the veins and enclosed wing areas (Fig. 1) follows the Comstock–Needham system (Comstock, 1918; Snodgrass, 1935) and has been established for cricket wings by Ragge (1955; see Table 1); veins are identified hereafter by the established abbreviations given in Table 1.

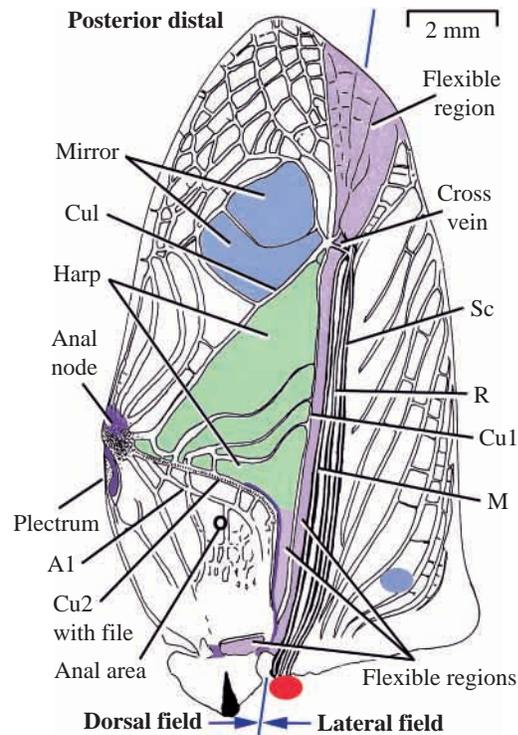


Fig. 1. Drawing of the right fore-wing of *Teleogryllus oceanicus* made from a photograph. The wing is viewed from below. The nomenclature of the venation and fields of the wing follow those given in Table 1. Areas implicated in sound production are the harp (green) and mirror (blue). The flexible regions separating the lateral field from the wing base and lateral field are shown as purple areas, and additional flexible regions are highlighted by purple lines. For free vibration tests, the wing was waxed to the vibration probe (see Fig. 2) at the base of the lateral field (blue spot). For tests in which vibration was applied to the file, plectrum or anal area, the wing was glued to a steel rod at the bases of the Sc, R and M veins (red spot). Vibration *via* the anal area was applied at the position of the circle at the end of the 'anal area' label line.

The sound recordings analysed here had been made in the field in 1996 by L. W. Simmons using a Sony Professional Walkman cassette recorder and a Tandy cardioid microphone.

These recordings were also made near Carnarvon, Western Australia.

#### Excitation of vibrations of the wing

Vibrations of the wing were driven mechanically by a piezo-electric vibration transducer, similar to that described in Young and Bennet-Clark (1995); this was fitted with a 5 mm-long, 0.5 mm-diameter probe rod; this rod was ground to give a 400  $\mu\text{m}$ -wide by 50  $\mu\text{m}$ -thick tip. The resonant frequency of the probe was 34 kHz and there were no measurable resonances between 1 kHz and 10 kHz. The transducer was driven by 50 V peak-to-peak tone bursts from a Pioneer SA-6300 audio amplifier driven by a Hewlett Packard 8111A function generator gated by square waves from a BWD 141 sine and square wave generator. Frequencies were set to the nearest 10 Hz. Excitation when the transducer was pushed against parts of the wing is termed 'probe rod vibration'.

In other experiments, a newly excised section of the left wing, including the file and plectrum, was waxed along the length of the file to the probe rod (Fig. 2). This was used in two ways. First, where the left plectrum was pushed against the right wing and vibrated by activating the piezo-electric probe: this excitation is termed 'probe rod vibration through the left plectrum'. Second, where the plectrum was pushed over the right file: this is termed 'push using the left plectrum'. Loads were made from 6–10 mm lengths of 0.1 mm-diameter copper wire rolled into a 1 mm-diameter ball; these could be attached reversibly to various parts of the wing with petroleum jelly or cellulose varnish. In certain experiments, parts of the wing were damped or loaded either by touching with a 0.2 mm-diameter probe rod, by adding droplets of water or by painting with cellulose varnish: with all these treatments, the effect was reversible. Parts of the wing were damped by local application of insect wax.

Wings were mounted in one of two standard ways: (1) either the wing was glued by the bases of the Sc, R and M veins (red spot on Fig. 1) to a 6 mm-diameter steel rod with cyanoacrylate glue (care was taken to ensure that no part of the lateral field was glued to the rod) or (2) the wing was waxed with its plane normal to the tip of the piezo-electric

Table 1. Nomenclature of the veins of the fore-wing of *Teleogryllus oceanicus*

Name of vein	Abbreviation	Description
Costa	C	Anterior edge
Subcosta	Sc	Strong vein with branches towards anterior edge of wing
Radius	R	Strong vein between Sc and M
Media	M	With Sc and R forms the lever that drives wing opening and closing
Cubitus 1	Cu1	Its ascending and descending branches form the distal edges of the harp
Cubitus 2	Cu2	Forms the proximal edge or base of the harp and bears the file on its underside
Anal 1	A1	Runs parallel to and adjacent to Cu2, fusing with Cu2 near the anal node
Anal 2, 3	A2, A3	Veins traversing the anal area and meeting at or near the anal node

Nomenclature follows the Comstock–Needham system (Comstock, 1918; Snodgrass, 1935) and the description given by Ragge (1955). The veins are named in order from the anterior to the posterior edge; Fig. 1 follows this usage. The C, Sc, R and M veins form the lateral or anterior field of the wing; The anal veins are somewhat ill-defined – that part of the wing is termed the anal area; the region in which Cu1, Cu2 and the anal veins run is the dorsal or posterior field of the wing.

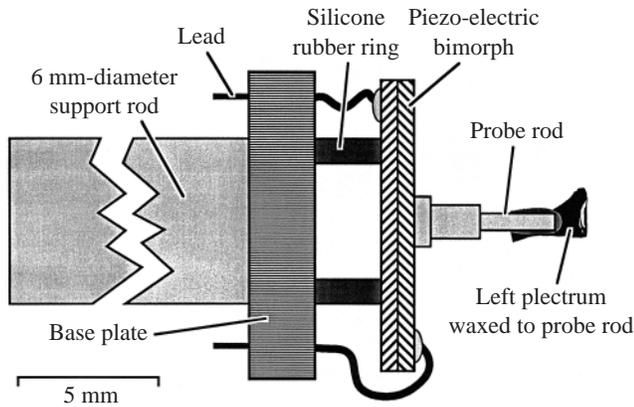


Fig. 2. Diagram of the piezo-electric vibrator used to excite wing resonances. Excitation was applied either by the probe rod or after waxing a left plectrum with a 2 mm length of the left file, as shown, to the tip of the probe rod.

vibration transducer (see above) at the base of the lateral field (blue spot on Fig. 1).

All probes, including the probe microphone (see below), were mounted on 6 mm-diameter aluminium alloy rods on separate micro-manipulators, and the wing preparation was mounted on another micro-manipulator; all micro-manipulators were mounted on magnetic stands on a 10 mm-thick steel base plate.

Vibrations were also excited acoustically by mounting a wing above a Motorola KSN 1041A piezo-electric loudspeaker. The loudspeaker was driven by the same electronic chain as the piezo-electric vibration transducer. The sound pressure level at the wing could be adjusted to a maximum of approximately 130 dB. Vibrations were observed through a dissecting microscope after sprinkling lycopodium powder on parts of the wing; areas where vibration occurs are shown by movement of the powder (Faraday, 1831).

#### *Recording and analysis of sounds produced by vibrating wings*

Sounds produced by vibrations of the cricket wings were recorded using a probe microphone similar to that described in Young and Bennet-Clark (1995) made from a Realistic Electret Tie Pin Microphone (Tandy catalogue 33-1052) with a 5 mm-long probe tube of 1.25 mm external and 0.8 mm internal diameter. The response was free of resonances and flat  $\pm 1$  dB from 100 Hz to 5 kHz and fell by 12 dB per octave above this frequency; the usable response extended to above 25 kHz. The microphone was powered and its output was amplified by a purpose-built amplifier with a flat response  $\pm 1$  dB from below 100 Hz to above 25 kHz. Because the microphone was placed less than 2 mm from the preparation, echoes were unmeasurably small. The loud clicks produced by pushes using the left plectrum were recorded at 50 mm from the preparation, and echoes were eliminated by sheets of acoustic foam placed around the preparation and microphone.

The microphone output was fed into an Apple Macintosh Powerbook 3400C and digitised at 44.1 kilosamples  $s^{-1}$  using

Canary 1.2.1 analysis software (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Frequency spectra were normally made with a filter bandwidth of 87.42 Hz, a frame length and grid length of 2048 points, a grid resolution of 10.77 Hz and a frame length of 4096 points with a Hamming window. Software was used to filter out noise below 1 kHz. For finer frequency resolution, short sections of recording were pasted into the middle of a 0.5 s duration blank recording and analysed with a filter bandwidth of 10.93 Hz and grid resolution of 2.692 Hz.

Cycle-by-cycle measurements of frequency used zero-crossing analysis of Canary text files by a program ZC v. 5 developed by K. N. Prestwich ([www.holycross.edu/departments/biology/kprestwi/ZC/](http://www.holycross.edu/departments/biology/kprestwi/ZC/); see, for example, Bennet-Clark and Bailey, 2002). This program gives a frequency resolution better than  $\pm 10$  Hz at 5 kHz from signals where the signal-to-noise ratio is greater than 30 dB. The program also calculates the root mean square (rms) voltage of a waveform.

#### *Analysis of the songs of Teleogryllus oceanicus*

The song recordings chosen for detailed analysis had a signal-to-noise ratio of greater than 30 dB and were re-recorded as Canary files and then subjected to zero-crossing analysis. Cycle-by-cycle plots of frequency against time were plotted for the different types of pulse starting at an initial level 20 dB below the peak in the pulse and ending when the level had decayed again to 20 dB below the peak. For comparisons, these plots were superimposed by eye, and the relative start and end times were measured from the superimposed plots.

#### *Properties of resonant systems, terminology and statistics*

The resonant frequency,  $f_0$ , of a typical resonant system, in which a mass and a spring interact, is given by:

$$f_0 = \frac{1}{2\pi} \times \sqrt{\left( \frac{1}{\text{mass} \times \text{compliance}} \right)} = \frac{1}{2\pi} \times \sqrt{\left( \frac{\text{stiffness}}{\text{mass}} \right)}. \quad (1)$$

Hence, a decrease in  $f_0$  implies that the mass of the system has increased and/or that its stiffness has decreased, and, in the case where only one has changed, the factor by which either the mass or stiffness has changed can be calculated from equation 1.

The rate of build-up of a resonance and its free decay can be described by the quality factor,  $Q$ , a dimensionless parameter that indicates the sharpness of the resonance: the higher the  $Q$ , the sharper the resonance. In most cases,  $Q$  has been calculated from the natural logarithm of the amplitude of the waveform during the free decay after the end of the drive or excitation (the  $\log_e$  decrement).  $Q$  is given by:

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

In practice,  $Q$  was calculated from the natural logarithm of the

rms voltage of the waveform given by the zero-crossing analysis program; tests in which the value of  $Q$  obtained using the amplitude of the waveform was compared with tests in which  $Q$  was obtained from the rms voltage showed that the two methods gave closely similar results. As confirmation, certain  $Q$  values were calculated from the resonant frequency divided by the bandwidth at 3 dB below the peak, using the highest frequency resolution obtainable from the Canary software (see above); this method gave similar results to those obtained using the  $\log_e$  decrement of the waveform. These methods are described more fully in Bennet-Clark (1999b).

The frequency at which maximum power of a sound or vibration occurs is termed the dominant frequency,  $f_D$ ; this term is used here as a simple descriptor of sound pulses that show modulations or changes in frequency over time. With sounds or vibrations in which the frequency of oscillation did not vary appreciably over time and which decayed exponentially, the frequency of vibration or of maximum amplitude of vibration is termed the resonant frequency,  $f_o$ .

In power spectra, the relative power is given in decibels (dB) relative to the peak power, where 10 dB is a 10-fold change in power. The amplitude of the response after, for example, certain experimental treatments is, in some cases, expressed in decibels (dB), where 20 dB is a 10-fold change in amplitude.

Statistical comparisons between means were made using Student's  $t$ -test.

## Results

### Anatomy of the fore-wings

The fore-wings are divided into two principal fields (Fig. 1). The lateral (or anterior) field lies against the side of the abdomen when the wings are folded, and the dorsal (or posterior) field lies above the abdomen, with the right wing folded over the left. The structures that are implicated in sound production – the harp, mirror, file and plectrum – are found in the dorsal field (Fig. 1).

The harp is an approximately triangular area surrounded distally by the V-shaped Cu1 vein and proximally by the file-bearing Cu2 vein. The anterior ascending part of Cu1 is narrower and weaker than the posterior descending region. The file-bearing Cu2 is similar in width but thicker than Cu1; it is joined by a series of short cross-veins to the robust A1 vein along the distal edge of the anal area. The whole of the anal area is slightly domed upwards. In *T. oceanicus*, the harp is traversed by three sinuous cross-veins that run from the anterior part of Cu1 to Cu2; they become thicker as they approach Cu2 and are positive veins – they are raised above the plane of the harp membrane. In the sample of seven insects that were measured, the harps of the left and right wings were similar in area (Table 2), in contrast to the finding of Simmons and Ritchie (1996) that the left harps of *Gryllus campestris* tended to be smaller than the right harps.

The files borne on the Cu2 veins of the two wings were similar in length (Table 2) and followed a sinuous curve at the proximal edge of the harp. The teeth on the under surface of

Table 2. Dimensions of different regions (mean  $\pm$  s.d.) of the fore-wings of male *Teleogryllus oceanicus*

Variable	Left wing (N)	Right wing (N)	P
Length of file (mm)	4.21 $\pm$ 0.23 (8)	4.20 $\pm$ 0.23 (8)	0.95
Length of flexible region at the anterior end of the file (mm)	0.78 $\pm$ 0.19 (8)	0.58 $\pm$ 0.33 (8)	0.08
Total length of plectrum (mm)	1.18 $\pm$ 0.027 (7)	1.00 $\pm$ 0.080 (7)	0.001
Width of plectrum including flexible region (mm)	0.28 $\pm$ 0.014 (7)	0.24 $\pm$ 0.012 (7)	0.001
Area of harp (mm <sup>2</sup> )	7.17 $\pm$ 0.44 (7)	7.18 $\pm$ 0.42 (7)	0.95

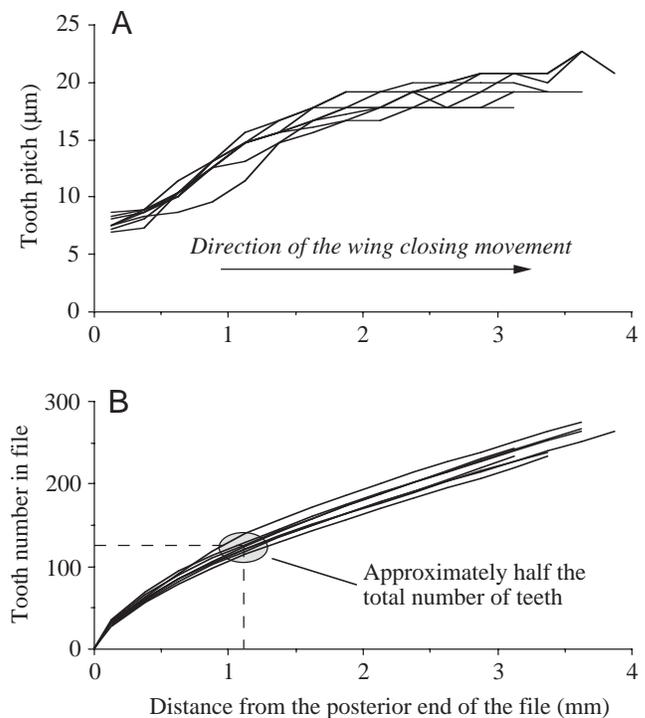


Fig. 3. (A) Graph showing the tooth pitch on the right files of five *Teleogryllus oceanicus* fore-wings, showing that the tooth spacing increases along the active length of the file: during sound production, the plectrum moves from the posterior to anterior on the file, as shown by the arrow. (B) Graph showing the cumulative number of teeth versus distance along the file for six right files of *T. oceanicus* fore-wings. Note that approximately half the teeth are situated on the distal third of the file.

Cu2 ran from approximately 0.8 mm from the posterior end, near the anal node, to beyond the bend where Cu2 runs nearly parallel to the proximal end of Cu1 (Fig. 1). During sound production, the left plectrum engages the teeth on the right file: the teeth of the right file are more closely spaced near the anal node, where the teeth are engaged at the start of the sound pulse, and the tooth pitch (i.e. the distance along the file between the tips of successive file teeth) increases

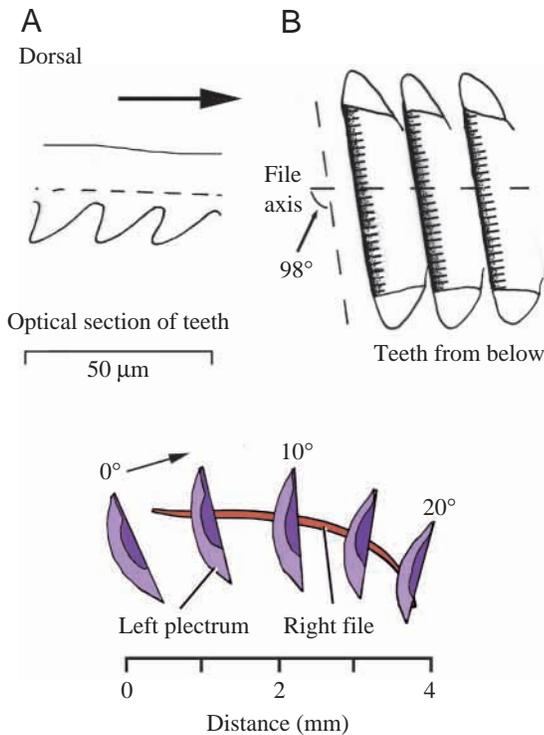


Fig. 4. (A,B) Drawings of three file teeth of *Teleogryllus oceanicus* near the middle of the right file. (A) Optical section near the middle of the teeth; the arrow shows the direction of movement of the plectrum during the wing-closing movement. (B) Plan view of the teeth from the underside of the wing showing the sclerotised edge and the angle of the teeth relative to the axis of the file. (C) Diagram showing the engagement of the plectrum with the file, based on a geometric model in which the fore-wings are separated by the 5 mm distance between the wing bases and travel through complementary arcs: the arrow shows the direction of movement of the left plectrum. The right file is drawn as if it were stationary but in the model both wings closed in opposite directions through the same angle, which is shown by the degree scale above the drawings of the left plectrum. Note that the centre of the plectrum engages with the centre of the file over most of the length of the file and that the angle made by the edge of the plectrum to the axis of the file is slightly greater than the angle of the teeth to the file axis shown in B.

systematically along the length of the file towards its proximal end (Fig. 3A). Half the total number of file teeth are situated in the distal third of the file (Fig. 3B); in other words, approximately half the file teeth are likely to be engaged in the first third of the wing-closing movement. The mean number of teeth on the right file was  $252 \pm 15$  (mean  $\pm$  S.D.,  $N=8$ ), which accords with the number given by Leroy (1966). The file teeth are asymmetrical in section, being hooked towards the posterior edge (Fig. 4A) so that they are engaged positively by the angular edge of the plectrum. The edges of the teeth do not run at right angles to the axis of the file (Fig. 4B; where the value is given as  $98^\circ$ ), and this relative angle does not vary by more than  $2^\circ$  throughout the length of the file.

The plectrum of the left wing was longer and wider than that of the right wing in each of the seven insects that were

Table 3. Mean mass ( $\pm$ S.D.) of different parts of the fore-wings of *Teleogryllus oceanicus*

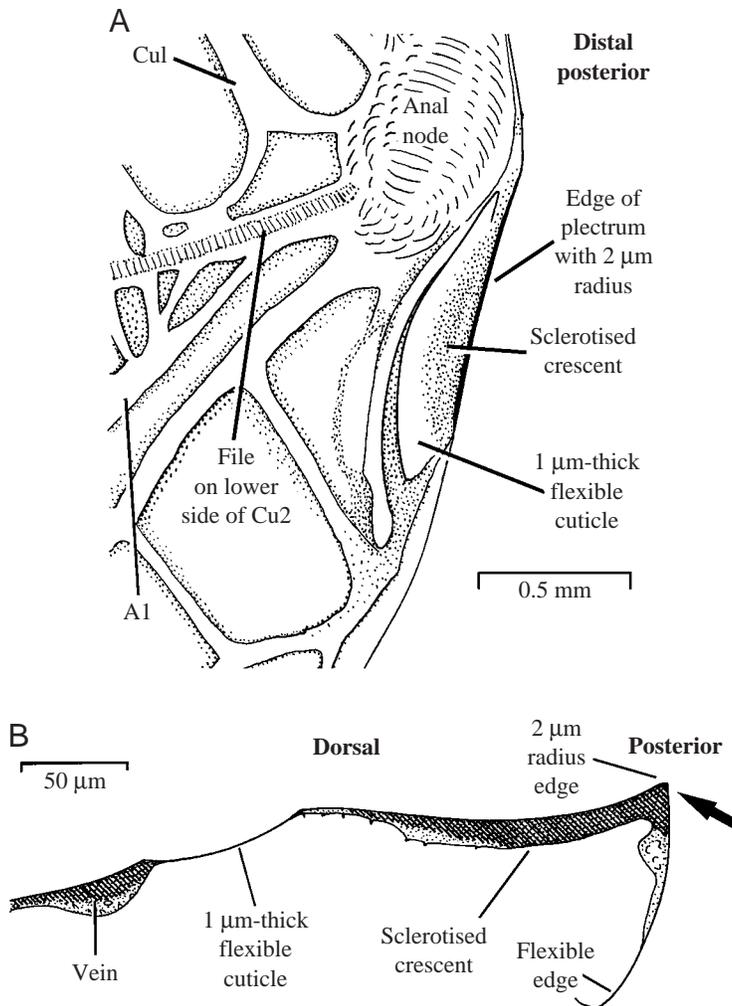
Region	Left wing (N)	Right wing (N)
Intact wing (mg)	$4.44 \pm 0.61$ (10)	$4.24 \pm 0.57$ (10)
Dorsal field (mg)	$2.02 \pm 0.26$ (10)	$1.85 \pm 0.36$ (10)
Harp and anal area (mg)	$1.27 \pm 0.20$ (10)	$1.15 \pm 0.23$ (10)
Anal area and file (mg)	$1.05 \pm 0.20$ (10)	$0.99 \pm 0.18$ (9)
Harp (mg)	$0.22 \pm 0.05$ (10)	$0.22 \pm 0.05$ (9)

measured (Table 2). The left plectrum that engages the right file has a nearly straight sclerotised posterior edge approximately 0.8 mm long (Fig. 5A) backed by a crescent-shaped area of sclerotised cuticle approximately 0.2 mm wide and 20  $\mu$ m thick (Fig. 5B). This part of the plectrum, which engages the file, is separated from the rest of the wing by a 1  $\mu$ m-thick crescent of flexible cuticle (Fig. 5B). The edge of the plectrum has a tip radius of 2  $\mu$ m that allows it to engage the file teeth, which are approximately 20  $\mu$ m deep (Fig. 4A). The plectrum can be bent along its length towards the anterior part of the wing and also twisted along its length in a dorsal direction.

The engagement of the plectrum with the file teeth was modelled by rotating tracings of the left and right wings, spaced at their bases by the mean width of the mesothorax between the bases of the fore-wings, 5.0 mm. This model suggested that for the major part of the wing-closing movement, through an angle of over  $15^\circ$  for each wing, each file tooth engages the middle of the plectrum but at the more acute angle of approximately  $110^\circ$  (Fig. 4C). This implies that engagement of the edge of the plectrum along the whole width of a file tooth can only occur after the proximal end of the edge of the plectrum has bent approximately  $10^\circ$  towards the anterior edge of the wing.

The muscle-powered closing movement of the wing is driven *via* the robust Sc, R and M veins. One major flexible region separates the lateral and dorsal fields (Fig. 1) and allows the wing to be folded alongside the abdomen or opened and extended into a flat sheet; this flexible region is traversed by the cross vein at the distal end of the harp (Fig. 1). Other flexible regions separate the proximal end of the dorsal field from the base of the wing and the insect's body (Fig. 1). The posterior end of Cu2 enters the thick but flexible anal node and, at its anterior end, Cu2 is separated from the harp by a short flexible region (Fig. 1). When pushed at its anterior end, Cu2 could be bent dorsad for a short distance before the adjacent region of the harp bent; in other words, the anterior end of Cu2 is partly decoupled from the harp. The length of this flexible region had a higher coefficient of variance than the length of the file (for data, see Table 2).

Masses of various parts of the fore-wing are given in Table 3. The lateral field is heavier than the dorsal field even though it is smaller in area (Fig. 1); the harp, although similar in area to the file and anal area (Fig. 1), is less than one fifth of their mass (Table 3).



#### The song of *T. oceanicus*

The stereotyped calling song of *T. oceanicus* consists of echemes in which a chirp of four similar loud long pulses is followed by a trill consisting of a train of pairs of pulses, each of which is quieter and briefer than the pulses of the chirp (Hoy, 1974; Fig. 6A). The mean duration of the long pulses of the chirp is 40.3 ms (Table 4A) centred on a frequency of approximately 4.6 kHz (Fig. 6C), which suggests that approximately 200 of the 252 file teeth are engaged in the production of these pulses. The cycle-by-cycle frequency falls during all the song pulses. The cycle-by-cycle frequencies of the first and second pulses in the trill show different patterns, and both types of pulse can be superimposed on the plot of the cycle-by-cycle frequency of the pulses in the chirp (Fig. 6C). The pulses in the trill are approximately 0.7 times as long as those in the chirp (Table 4A), which is significantly briefer ( $P < 0.001$ ), but the first and second of the paired pulses did not differ significantly in duration ( $P = 0.18$ ).

Plots of the cycle-by-cycle frequency of the pulses in the chirps can be superimposed closely on each other (Fig. 6C), showing a similar glissando. The cycle-by-cycle frequency plots of the first and second of the paired pulses in the trill can also be superimposed on those of the pulses of the chirps but

Fig. 5. Details of the left plectrum. (A) Drawing of the left plectrum from below. (B) Drawing based on a scanning electron micrograph of a transverse section of the left plectrum cut approximately halfway along its length. The arrow shows the direction of the push used to elicit clicks of the plectrum and also the approximate line of engagement with the teeth of the file.

that of the first paired pulse corresponds to a significantly earlier part of the pulses in the chirps than the second paired pulse; the effective start of all three types of pulse was significantly different (Table 4A:  $P < 0.005$  in all cases). The envelopes of all three types of pulses differed, and all of the fourteen different song records showed a similar pattern: the pulses in the chirp built up and decayed slowly; those in the first of the paired pulses of the trill built up slowly and decayed more rapidly; and those of the second of the paired pulses of the trill built up rapidly and decayed with a similar slope to the decay of the pulses of the chirp (Fig. 6B).

These differences suggest that the pulses of the chirp are produced when the wing closes through a larger arc than for pulses in the trill and that the first of the paired pulses in the trill is produced from a more posterior part of the file than the second pulse of the pair (Fig. 6C).

The dominant frequencies,  $f_D$ , of the echemes and different pulses of the song are shown in Table 4B. Because each type of pulse showed a considerable glissando, it was hard to define the  $f_D$  and it was not possible to distinguish the different types of pulse from this parameter: these data are included here to highlight the difference between the song pulses and the free resonances of the left and right fore-wings (as shown in Table 4C; Fig. 7).

#### Free resonances of the left and right fore-wing

To ensure that the vibration of the dorsal field of the wing was not influenced by direct contact with the probe, resonances were excited by probe rod vibration with the probe rod waxed near to the base of the lateral field of the fore-wing (blue spot on Fig. 1). Resonances were driven by a 12.5 ms-duration tone burst and measured by the probe microphone 2 mm away from the geometrical centre of the harp. Sharp resonances were recorded from both wings of seven insects and, in all, the resonant frequency of the left wing was significantly higher ( $P < 0.002$ ) than that of the right wing (Fig. 7). The mean frequencies  $\pm$  s.d. are given in Table 4C. The values of  $Q$  found here (Table 4C) were similar to those reported for *Gryllus campestris* by Nocke (1971).

Wing vibration excited by high intensity sound, as visualised by the movement of lycopodium powder, was observed between 2.5 kHz and 7 kHz and over a range of sound intensities. The frequency resolution of this method was poor and did not allow distinctions between the left and right wings; similar vibration patterns were observed for both wings. The largest vibrations were seen on the harp, confirming the observations of Nocke (1971). Changing the sound frequency

Table 4.

A. Start and end points of pulses in the chirp relative to the duration of the pulses in the trill of the song of *Teleogryllus oceanicus* (see Fig. 6 and text)

Variable	Mean $\pm$ S.D. (N)
Start of first paired trill pulse (S1/duration of chirp pulse)	0.14 $\pm$ 0.06 (9)
Start of second paired trill pulse (S2/duration of chirp pulse)	0.25 $\pm$ 0.05 (9)
End of first paired trill pulse (E1/duration of chirp pulse)	0.87 $\pm$ 0.04 (9)
End of second paired trill pulse (E2/duration of chirp pulse)	0.97 $\pm$ 0.03 (9)
Relative duration of first paired trill pulse and chirp pulse	0.69 $\pm$ 0.05 to 1 (9)
Relative duration of second paired trill pulse and chirp pulse	0.72 $\pm$ 0.05 to 1 (9)

N is the number of different insects whose songs were measured.

B. Dominant frequencies ( $f_D$ ) of different components of the song of *T. oceanicus*

Variable	Mean $\pm$ S.D. (N)
$f_D$ of a complete echeme of song (kHz)	4.83 $\pm$ 0.13 (15)
$f_D$ of pulses in chirp (kHz)	4.79 $\pm$ 0.21 (14)
$f_D$ of first of paired pulses in trill (kHz)	4.85 $\pm$ 0.10 (14)
$f_D$ of second of paired pulses in trill (kHz)	4.78 $\pm$ 0.15 (14)

N is the number of different insects whose songs were measured.

C. Free resonant frequency ( $f_o$ ) and quality factor (Q) of the wings of *T. oceanicus*

Variable	Mean $\pm$ S.D. (N)
$f_o$ of left fore-wing (kHz)	4.56 $\pm$ 0.20 (8)
Q of left wing	25.1 $\pm$ 7.7 (8)
$f_o$ of right fore-wing (kHz)	4.21 $\pm$ 0.16 (8)
Q of right wing	23.9 $\pm$ 7.1 (8)

N is the number of wings that were measured.

caused the area of maximal vibration to shift from the middle of the anterior edge of the harp at 3 kHz to the centre of the harp between 4 kHz and 5 kHz (as shown in Fig. 8) and up towards the distal apex of the harp at 6 kHz. At 4.5 kHz, the region of maximal vibration was centred over the middle of the first cross-vein of the harp (Fig. 8). Viewed with the wing inverted, so that the harp formed a slightly concave surface, at lower sound intensities and with light dustings of lycopodium powder, the vibration at 4.5 kHz was confined to the grooves formed by the cross veins (orange in Fig. 8), but raising the sound intensity caused the vibration to extend across the adjacent harp membrane. Similar vibrations were seen on four left and four right wings.

*Excitation of the left wing*

This series of experiments examined the way in which the left wing, which is driven *via* its plectrum, vibrates when driven either at the plectrum or on the anal field. Isolated left wings were attached to a support rod at the base of the Sc, R and M veins (at the red spot on Fig. 1) with cyanoacrylate glue and driven with probe rod vibration either *via* the plectrum or with the probe rod pushed against the middle of the file, normal to the plane of the harp or normal to the anal area (at the end of the 'anal area' label line on Fig. 1). For vibration *via* the

plectrum, the vibration probe rod was angled so that the direction of its action approximated to that of the contralateral file: approximately 20° below the plane of the left harp (along the arrow in Fig. 5B) and approximately normal to the line of the edge of the plectrum.

In all eight wings tested this way, sharp resonances were excited when the wing was driven either *via* its plectrum or on its anal area; at either site, the frequency of maximal vibration amplitude was similar. Subsequent recordings for analysis were made with the same driving frequency at both sites. The mean values for  $f_o$  and Q at either site of excitation are shown in Table 5, and representative sound pulses are shown in Fig. 9A. The mean values for  $f_o$  and Q did not differ significantly ( $P=0.44$  and  $0.48$ , respectively) from those obtained from the free vibration of the left fore-wing when vibrated on the lateral field (Table 4) nor did the Q of the resonance observed when the system is driven *via* its plectrum differ significantly from the Q when driven at its anal area ( $P=0.60$ ).

The relative phasing of the sound waveforms was established by referring the phase of both responses to that of the driving waveform. The relative phasing of sounds when a wing was excited *via* its plectrum or at its anal area depended on two factors: first, the position and angle of incidence of the

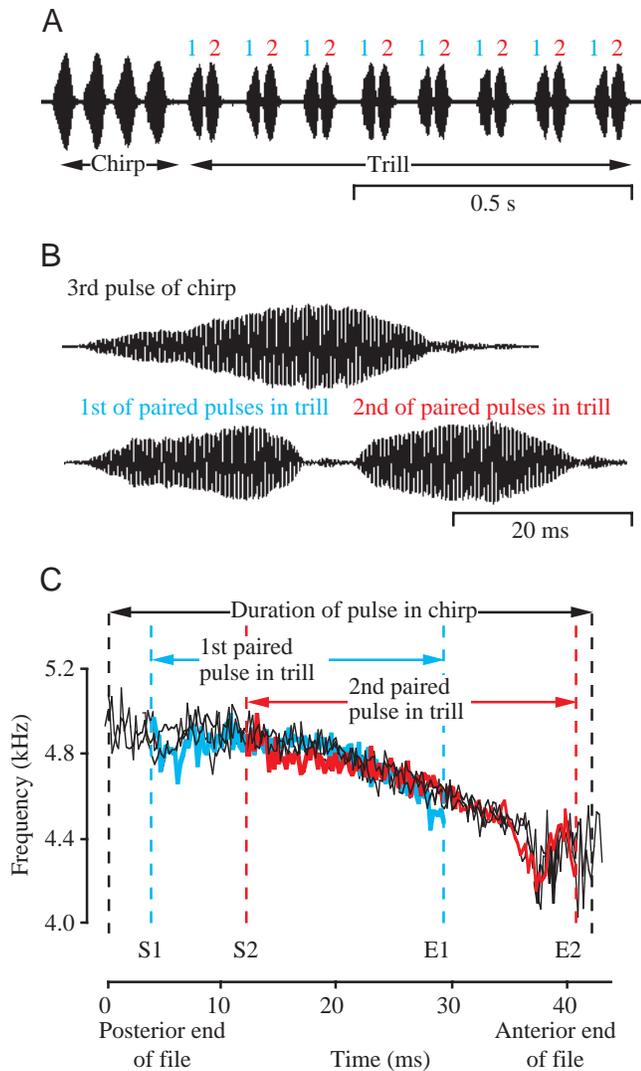


Fig. 6. The calling song of *Teleogryllus oceanicus* taken from a recording made in the field at Carnarvon, Western Australia. (A) Oscillogram of one song echeme, showing the chirp of four pulses and a trill of paired pulses. (B) Oscillograms of the third pulse of the chirp shown in A and the first and second of the first of the pair of pulses of the trill shown in A. (C) Graph of the cycle-by-cycle frequency of the four pulses of the chirp shown in A (black lines) and the first (blue line) and second (red line) pulse of the paired pulses of the trill shown in A. The frequency against time plots have been superimposed by eye and the starts (S1 and S2) and ends (E1 and E2) of the paired pulses in the trill are shown by vertical, broken lines. Note that these data suggest that the 1st and 2nd of the paired pulses of the trill are produced by different parts of the file.

vibration probe on the plectrum; second, on the frequency of the driving waveform. In the former case, differences may be ascribed to the differences in the geometry of the action of the plectrum on the resonant system acting through the veins adjacent to the plectrum. In the latter case, small changes in phase can be ascribed to the high  $Q$  of the resonance, where, with a  $Q$  of 25 at 4.5 kHz, a change of phase of  $45^\circ$  between the driving waveform and the resultant vibration will occur

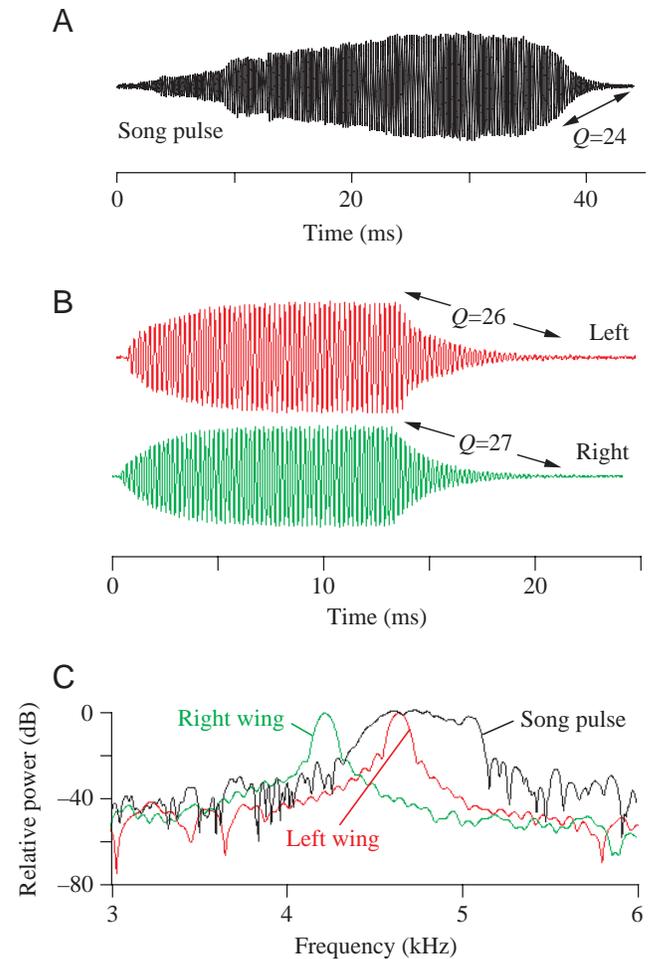


Fig. 7. Comparison of the waveform and frequency spectrum of a typical song pulse with those of free vibrations of the left and right wings of *Teleogryllus oceanicus*. (A) Oscillogram of a pulse from a chirp of the song. (B) Oscillograms of the sound recorded from free vibrations of the left (red) and right (green) wings driven by 12.5-ms duration tone-bursts at their resonant frequencies. In A and B, the quality factor ( $Q$ ) of the exponential decay of the vibrations is shown. (C) Frequency-energy spectra of the song pulse shown in A (black) and of the free vibrations of the left (red) and right (green) wing.

Table 5. Resonant frequency ( $f_0$ ) and quality factor ( $Q$ ) of the left and right fore-wings of *Teleogryllus oceanicus*

Variable	Left wing <sup>a</sup>	Right wing <sup>b</sup>
$f_0$ (kHz)	4.63±0.16 (8)	4.83±0.29 (7)
$Q$ when driven <i>via</i> plectrum	22.4±6.1 (8)	14.15±6.5 (7)
$Q$ when driven on anal area	24.9±10.2 (8)	–

Values are means ± s.d. The number of wings that were measured are given in parentheses.

<sup>a</sup>Measurements for the left fore-wing were driven by probe rod vibration *via* the left plectrum or on the left anal area.

<sup>b</sup>Measurements of the right wing were driven by probe rod vibration through the left plectrum applied at the middle of the right file.

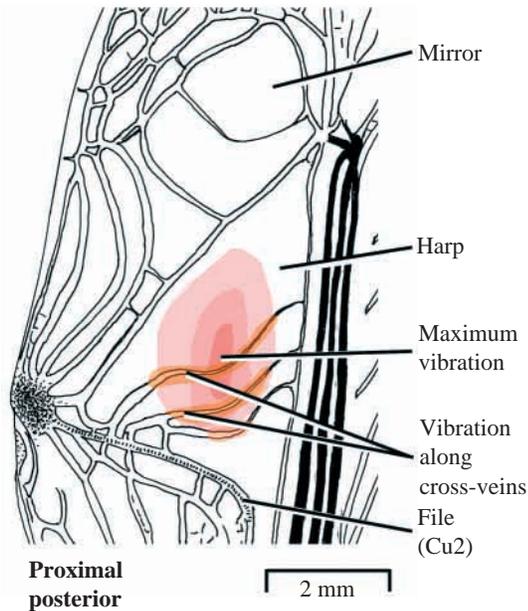


Fig. 8. Drawing showing the areas of maximum vibration of the harp when driven by loud sound at 4.5 kHz, visualised with lycopodium powder placed on the underside of the right harp. At lower sound intensities, the visible vibration is confined to the cross-veins of the harp (shown by orange lines).

with a change of driving frequency of 180 Hz close to  $f_0$ . With five wings, excited *via* the plectrum and then at the same frequency on the anal area, phase differences of between  $150^\circ$  and  $210^\circ$  were observed: an example is shown in Fig. 9B.

The results of this series of experiments show that, although the resonances that were excited at the plectrum and anal area were closely similar in both  $f_0$  and  $Q$ , the waveforms are approximately anti-phase. This provides evidence that the vibration at the left plectrum can excite a resonance of the ipsilateral wing but that, in so doing, the plectrum acts so that the push at its edge is converted into an upward movement in the region of the file and harp; it should be noted that when the plectrum pushes against the right file, it causes the right file to move upwards also; this mechanism ensures that the harps of both wings vibrate in the same phase. When pushed along the plane of the wing with a probe placed against the edge of the left plectrum, the left file and harp could be seen to move upwards, providing direct evidence for the effect of the plectrum on the ipsilateral wing.

When excited by probe rod vibration on the centre of the file, the resonances that were excited were typically of lower  $Q$  and higher in frequency than those excited *via* either the plectrum or the anal area; similar results for the right wing are reported in the section 'Excitation of the right wing'.

The sound emitted by the click of the left plectrum was measured with the probe microphone less than 1 mm away from the surface of the plectrum. The cuticle surrounding the plectrum was covered with insect wax (Fig. 10A) to damp vibrations of these areas. A probe rod was pushed past the edge of the plectrum in the direction shown by the arrows in Figs 4B

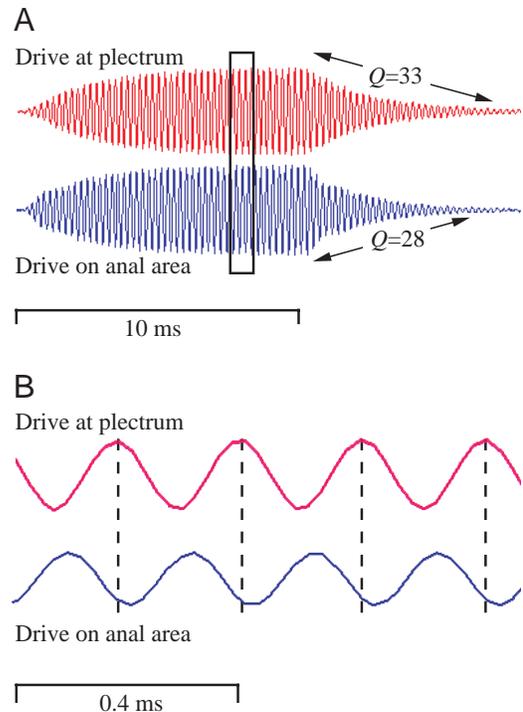


Fig. 9. Comparison of the resonances of a left fore-wing of *Teleogryllus oceanicus* when driven by the vibration probe applied either at the plectrum or on the anal area. (A) Waveforms of the sounds produced by 10-ms duration tone-bursts at the resonant frequency: red, when driven at the plectrum; blue, when driven at the same frequency on the anal area. The quality factor ( $Q$ ) of the decays of the vibration are similar. (B) Detail of A showing the region in the black box on an expanded time-scale to show the relative phase of the vibration when driven at the two positions.

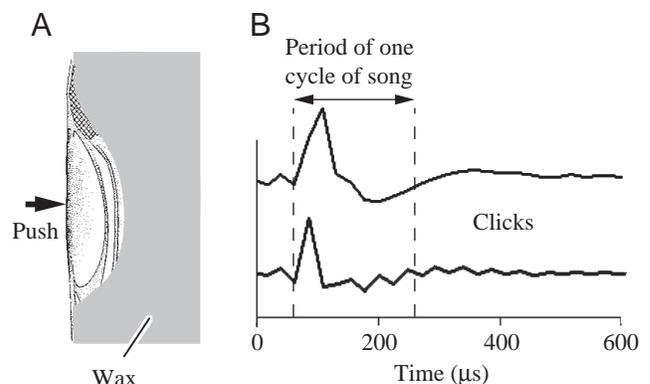


Fig. 10. (A) Diagram of the plectrum preparation from which the clicks shown in B were excited by pushing a probe rod past the edge of the plectrum at the position shown by the arrow. (B) Plectrum clicks produced by two different preparations; the fast component of the click is far briefer than the period of one cycle of the insect's song.

and 10A, so that the plectrum was initially buckled and then released by the rod. Examples of the clicks produced by two different plectra are shown in Fig. 10B; these highly damped

sounds are briefer than the 200–220  $\mu$ s duration of single cycles of the insect's song.

#### Excitation of the right wing

The right wing is excited *via* its file by interaction with the left plectrum; accordingly, experiments were directed to the way in which resonances could be excited by mechanical action on the file. Right wings were attached to support rods by the base of the Sc, R and M veins with glue (red spot on Fig. 1). The wings were driven either by probe rod vibration through the left plectrum or by push *via* the left plectrum acting on the right file. These drives were applied at various positions along the length of the file or adjacent areas of the wing. In most experiments, sounds were measured with the probe microphone positioned 2 mm away from the dorsal surface of the centre of the harp, but, with pushes *via* the left plectrum, the sounds were so loud that the probe microphone was placed 50 mm away from the dorsal surface of the harp.

An initial series of experiments, made with probe rod vibration directly onto the right file, excited resonances with a mean  $f_0$  of  $5.88 \pm 0.66$  kHz ( $N=6$ ) and a mean  $Q$  of  $14.0 \pm 5.5$  ( $N=6$ ). As both the  $f_0$ s and the  $Q$ s that were measured were significantly different from the  $f_0$  of free resonances of the right fore-wing and the  $f_D$ s of song pulses ( $P < 0.05$  in all cases), it was clear that this type of excitation differed from that effected during natural sound production, so these experiments were discontinued in favour of a more life-like excitation using the left plectrum driving on the right file.

Later experiments examined interactions between the newly excised left file (plus plectrum attached to the vibration probe; Fig. 2) and the right file; this allowed excitation at different distances along the file either by probe rod vibration through the left plectrum or by pushes using the left plectrum.

Measurements made with vibration through the left plectrum applied approximately halfway along the length of the right file (at the origin of the most anterior cross-vein of the harp; Fig. 1) gave the mean values of  $f_0$  shown in Table 5; these values are significantly lower ( $P=0.015$ ) than those obtained from the probe rod vibration cited in the preceding paragraph but are significantly higher ( $P < 0.005$ ) than the  $f_0$  obtained for the free vibration of the right wing (c.f. Table 4). Note, however, that, the  $f_0$  obtained by probe rod vibration through the left plectrum is similar to the  $f_D$  of the song pulses (Table 4) but that the  $Q$  of these resonances is lower than those of the free vibrations of either wing (Table 4). These results suggest that vibration through the left plectrum provides similar excitation of the right wing to that occurring in natural sound production.

Vibration through the left plectrum applied at the anterior end of the right file, at the bend in Cu2 (Fig. 1), excited resonances, but in all of the six preparations,  $f_0$  was lower than that of the same wing when excited halfway along the file; the mean decrease of  $f_0$  was  $0.24 \pm 0.11$  kHz. The amplitude of the acoustic response measured at the centre of the harp also varied with the position at which the vibration was applied: the maximum amplitude occurred when vibration was applied at the centre of the file and decreased when applied either towards the anterior

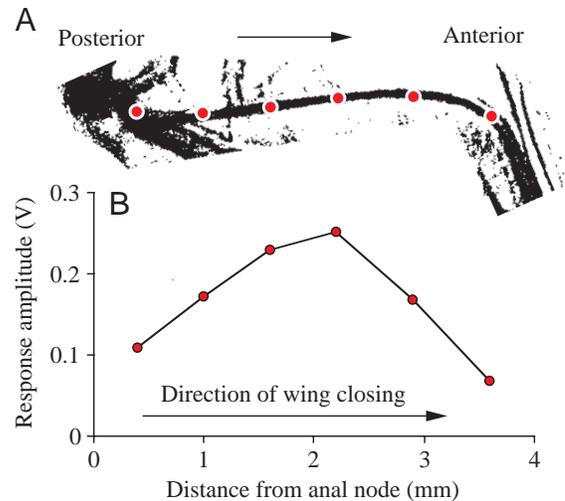


Fig. 11. (A) Diagram of the right file from below showing the points (red circles) at which resonances were excited by vibration applied *via* the left plectrum. (B) Graph of the amplitude of the sound measured at the centre of the harp against the distance from the anal node at which the vibration was applied to the file. The red circles on the graph correspond to the points shown on A above.

end, near the bend in the file, or towards the posterior anal node (Fig. 11). This variation in amplitude resembles the increase then decrease in amplitude that occurs during the production of song pulses by the singing insect (Fig. 6).

To examine the sounds produced by the catch and release of file teeth by the plectrum, clicks from the right wing were produced by pushing the left plectrum across the right file. It was difficult to excite clicks when the plectrum was pushed against the posterior 1–1.5 mm of the file, between the anal node and the first cross vein of the harp (Fig. 1), but clicks were easily excited when the plectrum was pushed across the anterior half of the file. These sounds were far louder than those excited by probe rod vibration *via* the plectrum. Typically, the clicks took the form of a transient that built up rapidly and decayed exponentially with a high  $Q$  (Fig. 12A). Throughout the waveform, the frequency remained nearly constant (Fig. 12B). The mean  $f_0$  of clicks excited from the middle of the file was  $4.82 \pm 0.55$  kHz ( $N=5$ ), which is comparable with the values obtained by probe rod vibration through the left plectrum (Table 5), but their mean  $Q$  of  $23.4 \pm 5.9$  ( $N=5$ ) is higher than those values (Table 4B). From any one preparation, it was possible to excite trains of clicks that varied in amplitude and that were repeated more or less rapidly; this seemed to depend on the speed at which the plectrum was pushed against the right file and the pressure applied during the push. There was also evidence, from sudden increases in amplitude within the clicks (arrows in Fig. 12A), that the excitation was caused by the catch and release of more than one file tooth in succession, but this did not appear to be associated with great changes in the cycle-by-cycle frequency of the sound (Fig. 12B).

After removal of all of the lateral field of the wing except

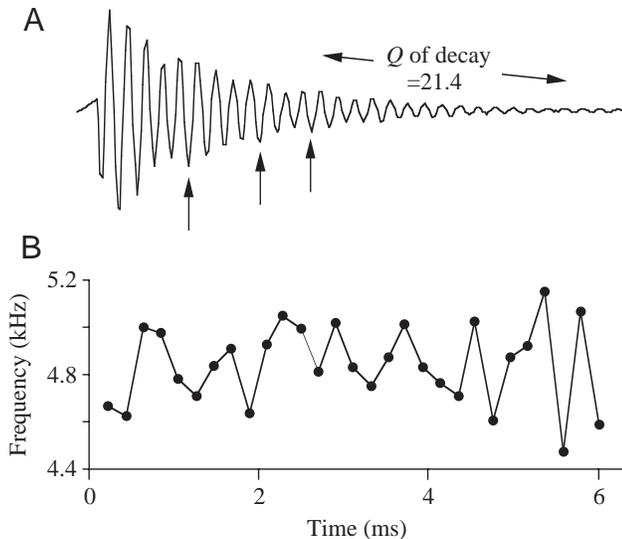


Fig. 12. Click produced by pushing the left plectrum across the file on the underside of the right fore-wing. (A) Oscillogram of the click; the arrows show points at which the amplitude has increased, probably due to impact of the plectrum on an adjacent file tooth. (B) Plot of cycle-by-cycle frequency of the pulse shown in A.

the basal 1 mm by which it was attached to the support rod, including the more distal parts of the Sc, R and M veins (see Fig. 1), the dorsal field became so flexible that it was impossible to excite vibrations by pushing the file with the left plectrum.

#### *The effects of removal of parts of the wing, loading and damping*

These experiments were designed to examine what the elastic and mass components of the resonant system of the wing were, by ablation and/or by altering the properties of the system.

In the first set of experiments, wings were driven by probe rod vibration with the probe rod attached to the lateral field of the fore-wing (blue spot on Fig. 1). The resonant frequency,  $f_0$ , was recorded with the intact wing, after which as much of the harp as possible was cut away with a fine scalpel blade, leaving the Cu1 and Cu2 veins intact, and the wing was re-excited. The  $f_0$  and  $Q$  of the vibration of the region adjacent to the file were then measured. A total of three right wings and two left wings were used.

In all cases, sharp resonances were recorded from the intact wings, with similar  $f_0$ s to those described earlier (Table 4C). The sound produced after removal of the harp was always far quieter than that from the intact wing but had similar values of  $Q$ . In all cases, the  $f_0$  rose after removal of the harp. The mean  $f_0$  increased by a factor of  $1.12 \pm 0.075$  ( $N=5$ ). The properties of the resonant system of the fore-wing were further examined by putting a load on different parts of the dorsal field, and resonances were excited by probe rod vibration on the lateral field. The load weighed 1.65 mg and was attached with a small quantity of petroleum jelly. With an intact right wing,  $f_0$  was

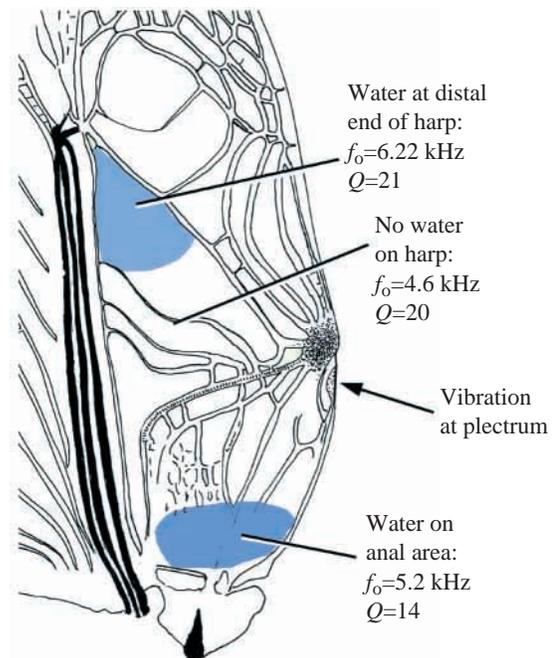


Fig. 13. Drawing of part of the left wing of *Teleogryllus oceanicus* to show the effect on the resonant frequency of placing droplets of water (blue areas) on either the distal end of the harp or the proximal end of the anal area (for terminology, see Fig. 1). Vibration of the harp was excited by probe rod vibration applied at the plectrum.  $Q$ , quality factor;  $f_0$ , resonant frequency.

4.29 kHz and, after placing the load on the middle of the file,  $f_0$  became 2.89 kHz; the same load placed on the centre of the harp lowered  $f_0$  to 3.24 kHz and, after removal of the load,  $f_0$  reverted to 4.28 kHz. With a left wing, the unloaded  $f_0$  was 4.63 kHz and, after loading at the middle of the file,  $f_0$  became 2.88 kHz.

Water droplets added to the harp or to the anal area did not abolish the resonance. In one of a series of experiments, a left wing was excited by vibration *via* its plectrum and the  $f_0$  and  $Q$  of the untreated wing were measured with the probe microphone at the dorsal side of the centre of the harp. A water droplet was then placed on the distal corner of the ventral surface of the harp and the measurements were repeated. The water was absorbed with paper towelling and the measurements were repeated. Then, a droplet of water was placed on the ventral surface of the anal area and the measurements were repeated. Finally, the droplet was removed and the measurements were repeated. The  $f_0$  and  $Q$  of the untreated wing were similar to that after absorption of the successive water droplets. Fig. 13 shows the approximate area and position of the water droplets and the  $f_0$ s and  $Q$ s that were measured. With another wing, when a smaller droplet was added to the distal corner of the harp covering only one fifth of its length,  $f_0$  increased from an unwetted value of 4.8 kHz to 5.5 kHz, then to 6.5 kHz when more water was added to extend the droplet over the distal one-third of the length of the harp, and finally to 7.5 kHz when the droplet covered all but

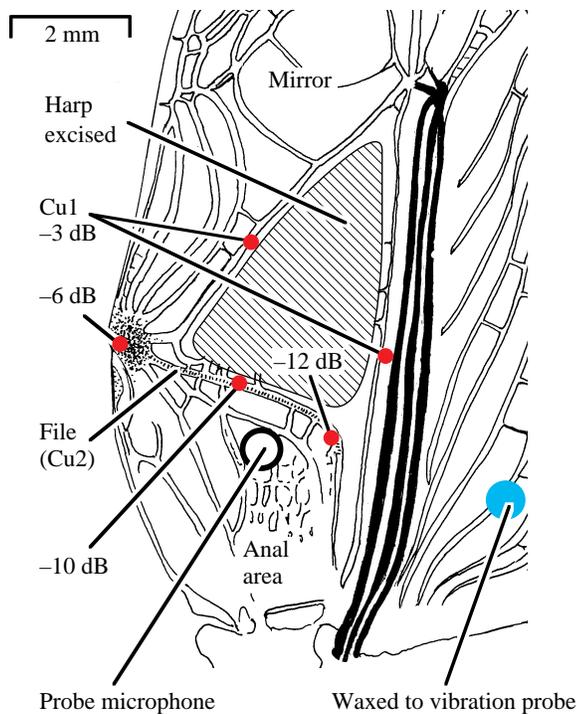


Fig. 14. Drawing of part of the right wing of *Teleogryllus oceanicus* to show the effect on the loudness of the sound produced by applying damping with a sharply pointed rod at the points shown as red circles. The wing was driven by the vibration probe attached to the lateral field (blue circle) after excision of the harp at its resonant frequency ( $f_0$ ; 5.15 kHz). The sound output, made with the probe microphone at the anal area, is expressed in dB relative to the sound output of the undamped wing.

the proximal one-third of the harp. A droplet of water placed on the file abolished the resonance, as did painting the file with cellulose varnish.

In another experiment, a right wing that was driven on its file by vibration *via* the left plectrum had an initial  $f_0$  of 4.85 kHz and a  $Q$  of 30. Successively, thin films of wax were added to the wing, first on the proximal edge of the anal area, giving an  $f_0$  of 5.15 kHz and  $Q$  of 30, then along the posterior edge of Cu1 distal to the anal node, giving an unaltered  $f_0$  of 5.15 kHz but a  $Q$  of 22.6, then along the anterior of Cu1, raising  $f_0$  to 6.15 kHz and lowering  $Q$  further to 13.7. Finally, waxing over the anal area to within 1 mm of the file lowered  $f_0$  to 4.3 kHz with a  $Q$  of only 6.

Damping was applied more locally by applying a sharply pointed rod to freely vibrating wings from which the harp had been excised and which were driven from the proximal end of the lateral field (blue spot on Fig. 14). The probe microphone was placed 2 mm away from the anal area, approximately at the circle on Fig. 14. The effect of damping at different points on the sound produced by vibration of the anal area for a right wing is shown in Fig. 14. The greatest effect was observed with the damping applied to the file (Cu2), particularly at the anterior end, but damping applied to either side of the harp frame, on Cu1, had only a small

effect. It should be noted that the damping did not completely abolish the resonance, suggesting that the A1 vein of the anal area, which runs parallel to Cu2, may be a component of the resonant system. Damping applied to either the lateral field or the distal end of the dorsal field had no discernible effect. Similar effects were seen with two left wings and with another right wing.

#### *Resonance of the mirror*

The observations reported here are incidental to the main thrust of this paper and were not pursued in detail. Mirror resonances were difficult to excite from either wing when vibrated on the file but could be excited by free vibration with the wing attached onto the vibration probe by the lateral field (at the blue spot on Fig. 1). Sounds were recorded from the fore-wings of five insects with the probe microphone 2 mm away from the geometric centre of the mirror (Fig. 1). The mean  $f_0$  from a total of three left and three right wings was  $7.00 \pm 0.42$  kHz and the mean  $Q$  was  $19.6 \pm 7.5$ . These resonances were localised at the mirror and did not appear to excite any sympathetic vibration of the harp. They were heavily damped by a probe rod touching the centre of the mirror, but touching the dorsal field distal to the mirror had no discernible effect. Further experiments to try to find the mechanism by which the resonances were determined or excited were not carried out.

## Discussion

### *Confirmation of earlier work*

The results of the experiments reported here confirm the majority of the results reported by previous workers on this topic. The harps of both fore-wings are areas that show maximal vibration at similar frequencies and vibrate with similar sharpness (or  $Q$ ) to those reported by Nocke (1971). The role of the file-and-plectrum as the escapement mechanism that excites and sustains the vibration of the sound-producing mechanism proposed by Elliott and Koch (1985) and Koch et al. (1988) is compatible with the recordings made here on the right wing with pushes using the left plectrum. Experimental support is given to the previously suggested role of the plectrum as the exciter of the resonance of the left wing, as well as its role as a phase-inverting mechanism that causes both wings to vibrate in phase with each other (Bennet-Clark, 1970, 1989; and inferred from Bailey, 1970).

### *Sounds of the escapement mechanism*

The sounds produced by the release of the plectrum are highly damped brief clicks (Fig. 10B). The duration of the first half cycle of the click is less than half the period of one cycle of the insect's song (see Fig. 10B), which suggests that, after the plectrum has been released by a file tooth, it can return sufficiently quickly to capture the next tooth of the file. However, analyses of the songs of several cricket species (Bennet-Clark and Bailey, 2002) showed that the high-frequency song components, attributed there to the action of

the plectrum-and-file escapement mechanism, are far quieter than that the dominant song component produced by vibration of the harp, which suggests that the energy loss in the escapement mechanism is relatively small.

#### *Interaction between the two wings*

The present work highlights the notion that cricket sound production involves interaction of both wings and that the mechanical properties of one wing may affect those of the contralateral wing. In the case of the left wing, which is driven *via* its plectrum by the right file, the  $f_o$  of the free resonance of the wing is close to the  $f_D$  of the insects' song (Table 4B,C), although somewhat lower in frequency: this suggests that the interaction of the plectrum on the file in sound production may add stiffness to the resonant system of the left wing (by reference to equation 1). In the case of the right wing, the effect is more striking: the  $f_o$  of the free resonance was far lower than the  $f_D$  of the song, and the  $f_o$  of the resonance when driven on the file was far higher than the  $f_D$  of the song; however, when driven at the middle of the file, either by vibration through the left plectrum or with pushes using the left plectrum, the  $f_o$  of the resonances was closely similar to the  $f_D$  of the song. This can be explained as follows: the plectrum adds sufficient stiffness to the right wing system to raise its  $f_o$  to near to the  $f_D$  of the song and the  $f_o$  of the left wing, but excitation *via* the vibration probe directly on the right file raises the stiffness of the resonant system of the right wing to more than that occurring while the wings are interacting during sound production. It would appear that the effective vibration frequencies of the two wings during sound production are due to the effect on their own free  $f_o$ s of the stiffness that is added either to the left wing by its plectrum and the right file or to the right wing by the left plectrum.

The experiments by Simmons and Ritchie (1996) with harp ablation suggest that the left wing makes a major contribution to the first third of the pulse, and the right wing becomes more important in the latter part of the pulse. The vibration of the left wing is driven *via* its plectrum by excitation from the release of the teeth of the right file. In the early part of the wing-closing movement, the closely spaced teeth of the right file will provide adequate drive to the left wing but little drive to the right wing (Fig. 11), but, later, as the left plectrum reaches the middle of the right file, the release of the escapement is likely to be more affected by the increased amplitude of vibration of the right file, which, in the absence of the right harp, will tend to release at an anomalous and higher frequency. By contrast, ablation of the left harp will affect the first part of the pulse but, towards the middle of the file (and pulse), as the amplitude of vibration of the right harp increases, the mechanics of the right wing will tend to dominate the resultant sound.

In normal sound production, there is, of course, the effect of the escapement (Elliott and Koch, 1985), which will tend to couple the wings together and hence smooth out minor differences in their vibration frequencies (see Bennet-Clark and Bailey, 2002).

#### *Factors affecting the frequency and amplitude of the song pulses*

The glissando that is typical of cricket song pulses (Leroy, 1966; Simmons and Ritchie, 1996) appears, in part, to be associated with the flexible region adjacent to the file that is distal to the anterior end of the harp (Fig. 1; Table 2); the  $f_o$  of the resonance when driven in this region is lower than that when the resonance is driven near the middle of the file, probably because this part of the file is less stiff than its centre. This cannot, however, explain all the glissando, which typically starts about halfway through the sound pulse (Fig. 6), because the more flexible region of the file only includes the last quarter or fifth of the total number of file teeth involved in sound production. Thus, the present work can only provide a partial explanation of the glissando and cannot explain the variability of the glissando from insect to insect that has been reported by Simmons and Ritchie (1996). It is possible that the asymmetry of the wings has an optimal value for the production of pulses with little glissando and that greater asymmetry increases any mismatch between the  $f_o$ s of the two wings and hence brings about a greater change in the frequency as the pulse progresses.

The slow build-up and fall of the pulse envelope that is typical of cricket song pulses appears in part to be due to the effect of excitation at different points on the file on the amplitude of the sound produced by the right harp (Fig. 11); in *T. oceanicus*, maximal vibration of the right harp occurs when the vibration is applied approximately halfway along the file. The possible effect of this on the amplitude of the sound pulses is modelled in Fig. 15, which superimposes diagrams of the sound pulses against a linear scale showing the tooth number on the file, counting from its posterior end in the direction of the wing-closing movement. The upper scale, showing the distance along the file, reflects the fact that the file teeth are more widely spaced at the anterior end of the file (Fig. 3A). Based on the number of cycles of tone in the long sound pulses of the chirp (calculated from Fig. 6C), this model suggests that the amplitude should build up to maximum halfway along the file, at approximately tooth number 170, more than halfway through the pulse. The paired pulses in the trill have differently shaped envelopes: in the first, the amplitude is maximal towards the end of the pulse, but with the second the amplitude is maximal in the middle of the pulse (Fig. 6B); these briefer paired pulses appear to be produced from engagement of the plectrum with different parts of the file (Fig. 6C), with the first of the paired pulses starting nearer the anal node and just passing over the centre of the file and the second paired pulse being produced symmetrically either side of the centre of the file, as modelled in Fig. 15. In addition, it is likely that the build-up at the start of all these pulses is slow because the escapement action of the file-and-plectrum at this stage provides a steady flow of small impulses to the sharply tuned resonant system (evidence for this is given in Bennet-Clark and Bailey, 2002) rather than an abrupt 'kick start', as occurs with the cicada tymbal (Young and Bennet-Clark, 1995; Bennet-Clark, 1997), and that at the end of the

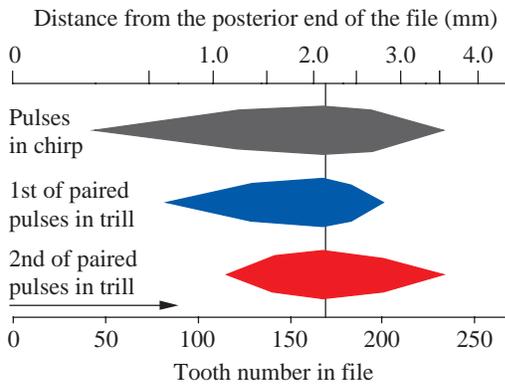


Fig. 15. Diagrammatic representation of the shape of the envelope of the different types of song pulses produced by *Teleogryllus oceanicus*. The lower horizontal scale shows the number of teeth along the length of the file. Each tooth equates with one cycle of sound in each pulse. The upper scale shows the distance along the file corresponding to particular file teeth. The long pulses of the chirp consist of approximately 180 cycles of sound and are assumed to be produced by the middle 180 teeth of the file. The first of the paired short pulses of the trill (blue) appears from Fig. 6C to be produced from a more posterior part of the file than the second of the paired pulses (red). The vertical line at tooth number 170, 2.2 mm from the posterior end of the file, is the point at which excitation of the right file produces maximal sound radiation by the harp (see Fig. 11). The horizontal arrow shows the direction of the wing-closing movement.

pulses the decay of the vibration is also slow, again reflecting the decay of the resonant vibration of the system.

It should be noted that the considerable change in tooth pitch that occurs along the length of the right file (Fig. 3) is not correlated with the small changes in the cycle-by-cycle frequency of the song (c.f. Figs 3, 6C). What apparently occurs is that the velocity of the plectrum over the contralateral file increases steadily as the first 1.5 mm of the file is traversed (see Fig. 3) but then remains more or less constant; a similar change in wing-closing velocity is seen during sound production by another cricket, *Gryllus campestris* (Koch et al., 1988; Fig. 3A). The force produced by muscle twitches typically rises smoothly over the first third of the total twitch duration, then falls towards the end of the twitch (e.g. Neville and Weis-Fogh, 1963; reviewed by Kutsch and Huber, 1989). It is possible that the file tooth spacing is tailored to exploit this property of the muscle motor: the release of the closely spaced file teeth at the start of the pulse can occur relatively easily, allowing the wing to accelerate as the muscle force rises in the initial phase of the muscle twitch. In the second half of the pulse, tooth release can be sustained by the inertia of the now-rapidly moving wing. This is also consistent with the steady increase in sound amplitude that occurs in the early part of the pulse.

#### *The primary resonator*

Previous work has asserted that "... the harp is a uniform and linear resonance system. The harp frame has no resonator

function." (Nocke, 1971; p. 222). In the present work, it has been shown that the maximal amplitude of vibration when the fore-wing is excited, either with sound or by mechanical vibration, occurs at the centre of the harp, but the experiments on the effects of removal of the harp membrane, leaving the Cu1 and Cu2 veins of the frame and file intact, showed that the resonance persists, albeit at a higher frequency. This suggests that the harp frame, and particularly the region including the file, is a major component of the resonator and that the harp acts merely as a lightweight sound-radiating surface, driven from the vibration of the file *via* the cross veins (Figs 1, 8) in contradiction of Nocke's (1971) assertion.

The following interpretation is offered: the resonant system is made up of the file, associated with the closely linked A1 vein of the anal area, as the major elastic component, loaded by the mass of the file plus anal area plus harp, which have a total mean mass of 1.27 mg (Table 3). The effect of ablation or loading on the  $f_0$  can be compared with the effects predicted from equation 1. After removal of the 0.22 mg mass of the harp membrane leaving an effective mass of 1.05 mg, the  $f_0$  should rise by  $\sqrt{(1.27/1.05)}$  or to 1.1-fold the value for the intact system, which is similar to the measured mean increase of 1.12-fold in the resonant frequency after removal of the harp membrane. The experiments in which the file was loaded by 1.65 mg, causing a drop in  $f_0$  to approximately 0.65 of its original value, suggest that the mass of the system had increased to approximately 2.2-fold its original value and thus that the original mass of the resonant system is approximately 1.38 mg; this also approximately accords with the mean measured masses of the harp plus file plus anal area of 1.27 mg or 1.15 mg (left and right wings, respectively: Table 3) but differs greatly from the 0.22 mg mass of the harp alone (Table 3).

The somewhat unexpected finding that adding droplets of water to the distal end of the harp did not abolish the resonance but instead raised its  $f_0$  (Fig. 13) suggests that the water droplet may have provided a heavy base from which the remainder of the harp membrane acted as a short wide spring, adding to the stiffness of the file (possibly plus A1) as the spring in the resonant system. This effect is hard to quantify.

In his study of the sound-producing system in the bush cricket *Homorocoryphus nitidulus vicinus*, Bailey (1970) showed that the veins of the right 'mirror' frame acted as the resonator when vibrated *via* the ipsilateral plectrum; despite a different tradition of popular nomenclature, it appears that these veins are homologous to the Cu1 and Cu2 veins in field crickets. The proposition that these veins were analogous to a tuning fork was borne out by studies of the scaling of  $f_0$ , which Bailey showed was shown to be proportional to  $1/(\text{length of the mirror})^2$  for four bush cricket species; this was later supported by measurements from a total of 19 bush cricket species by Sales and Pye (1974). So far, there does not appear to have been any comparable attempt to correlate the song frequency in field crickets with the dimensions of the file.

A tuning fork can be regarded as two similar bars, clamped together at one end and arranged so that the free ends of the

bars vibrate together-and-apart in the plane of the fork (Morse, 1948), in contrast with the bush cricket example in which the bars appear to beat up-and-down normal to the plane of the fork (and wing) and in phase (Bailey, 1970); in both, the amplitude of vibration is greatest at the free ends of the bars. Neither of these models applies in the field cricket because the cricket resonator appears to comprise a single bar, Cu2 (+ A1), which, from the loudness of the sound produced when it is excited at different distances along its length (Fig. 11), vibrates maximally in the middle, corresponding to the behaviour of an elastic bar that is either fixed at both ends or free at both ends (Morse, 1948).

The mechanical design of the dorsal field of the fore-wings has various hitherto-undescribed flexible regions (Fig. 1). The effect of these is to allow parts of the dorsal field to vibrate freely and largely independently from the rest of the wing, as shown by the high  $Q$  values for the resonances that are reported here; experiments in which this mechanical decoupling was reduced by touching with a probe rod or by application of cellulose varnish led to a decrease in the  $Q$  value.

What might be the advantages of high  $Q$  resonators in a sound-producing system of this type? Consider the physics of sound radiation from a small sound source in which the radiated sound power is proportional to the square of the amplitude of vibration of the source and its radiation resistance (Olson, 1957). The wings of crickets are small relative to the wavelength of the sound that they radiate, with a consequently small radiation resistance (see, for example, Bennet-Clark, 1971, 1998; Fletcher, 1992). However, the steady-state amplitude of vibration of a driven resonance is approximately  $Q$  times that of the driving waveform (e.g. Fletcher, 1992) so, the higher the  $Q$  of the cricket wing system, the greater the sound power that can be radiated from the small wings. In practice, the acoustic loading on the wings will damp the resonance and lower the effective  $Q$ ; in this context, it should be noted that the  $Q$  values reported here are those of single isolated wings rather than the pair of wings held above the body of a singing cricket, which will present a larger effective sound source on which the acoustic damping will be greater.

#### *The effect of air loading on the resonant frequency*

The interpretation of the nature of the resonator given in the preceding section also conflicts with the estimate of the mass of the resonant system made by Prestwich et al. (2000) as a result of measurements of the  $f_D$  of the songs of the grylline cricket *Anurogryllus arboreus* singing in air or in a helium/oxygen (heliox) mixture. They extrapolated from their findings with *A. arboreus* to the similarly sized *Gryllus campestris*, assuming that the harp was loaded with an approximately spherical air load of equivalent radius to the dimensions of the harp. They observed shifts in the  $f_D$  of the song of 1.07- to 1.14-fold, which equates to an effective mass for the resonator that agrees closely with Nocke's (1971) estimates (with *G. campestris*) of 163–190  $\mu\text{g}$ . These estimates of the mass of the harp also agree closely with the measurements reported here for the mass of the harp of *T.*

*oceanicus* (Table 3) but disagree strongly with the estimates for the mass of the resonant system given in the preceding section. Both the estimates by Nocke (1971) and Prestwich et al. (2000) of the mass of the air load on the wing depend on the assumption that the effective area of the sound-radiating surface is circular and confined to the harp. However, the mass of the air load may either be far less or far greater than these estimates suggest. This is explored further below.

Prestwich et al. (2000) calculated the mass of the resonant system using a modification of equation 1 from the present paper. Modifying their equation 9 to meet the present circumstance, the ratio of the resonant frequency in heliox ( $f_{o \text{ heliox}}$ ) to that in air ( $f_{o \text{ air}}$ ) is given by:

$$\frac{f_{o \text{ heliox}}}{f_{o \text{ air}}} = \sqrt{\left( \frac{\text{mass of resonator} + \text{mass of air load}}{\text{mass of resonator} + \text{mass of heliox load}} \right)}. \quad (3)$$

There is considerable uncertainty about the effective size of the sound source. Here, I consider the effect of air *versus* heliox loading on sources of three possible sizes. Case 1 – a source about half the width of the harp. This is justified by the observation that the area of vibration of the harp reported here (Fig. 8) appears to be considerably smaller than the area circumscribed by the harp frame (Cu1 and Cu2); the equivalent radius is taken as 1.2 mm. Case 2 – a source approximately equivalent in area to the harp, as suggested by Prestwich et al. (2000), which they took as equivalent to a circle of radius 2.2 mm. Case 3 – as the harp can be viewed as a piston vibrating in a baffle (Olson, 1957), the effective source size may be closer to that of the whole wing, which, from the dimensions of the wing of *G. campestris* (fig 2 in Bennet-Clark and Bailey, 2002) or of *T. oceanicus* (Fig. 1), appears to have an area approximately equivalent to a circle of radius 4 mm.

Table 6 shows estimates of the masses of the air or heliox loads for the three sources listed above. The observed change in  $f_o$  between air and heliox (1.07-fold to 1.14-fold; Prestwich et al., 2000) can be explained either if both the source and the resonator are the harp or if the source is the whole wing and the resonator is the harp plus file plus anal area as proposed above. This is not to say that the general conclusions of Prestwich et al. (2000) are in any way in error but to point out that their estimate of the effective mass of the vibrating system is dependent on an estimate of the mass of the air load that is hard to define.

In the calculations of the mass of the resonant system made in the preceding section, the effect of the mass of the air load on the wings was ignored. This is partly because ablation of the harp will have changed the effective source area and air load in a way that would be hard to define and, more importantly, because the magnitude of the effects of harp ablation and wing loading effectively ruled out the possibility that the harp is the primary resonator. This remains an area for further work.

#### *Conclusions*

The experiments reported here show that the production of

Table 6. Estimates of the effects of air or heliox loads on sound sources of different sizes (see Equation 3)

Sound source	Case 1 Half width of harp	Case 2 Harp	Case 3 Fore-wing
Effective source radius (mm)	1.1	2.2	4.0
Volume of equivalent sphere (m <sup>3</sup> )	5.6×10 <sup>-9</sup>	44.6×10 <sup>-9</sup>	270×10 <sup>-9</sup>
Mass of sphere of air (µg)	6.7	54	320
Mass of sphere of heliox (µg)	2.7	22	130
Effect of heliox <i>versus</i> air on resonant frequency ( $f_0$ ; Equation 3)			
If the resonator is harp	1.01	1.06	1.24
If resonator is harp + file + anal area	1.002	1.01	1.07

The following densities are used for the gases: air, 1.2 kg m<sup>-3</sup>; heliox, 480 g m<sup>-3</sup>.

The mass of the harp is taken as 0.22 mg; the mass of the harp plus file plus anal area is taken as 1.2 mg (mean of left and right wing from Table 2).

a nearly pure-tone sound by the excitation with the file-and-plectrum mechanism requires the wings to be asymmetrical because it causes vibration of both wings and involves their interaction. The vast majority of field crickets sing with the right fore-wing above the left wing and, even though they can be induced briefly to sing left-over-right, the song is far quieter and they speedily revert to the normal right-over-left wing action (Elliott and Koch, 1983). This directional asymmetry of wing action is associated with asymmetry in the neuromuscular system (reviewed by Kutsch and Huber, 1989).

Various aspects of cricket sound production are still unexplained: how the vibration of the Cu2 region of the wing is transferred to and apparently amplified as vibration of the harp; how distortion of the plectrum is transmitted to the ipsilateral file; how the variability in the glissando observed from individual crickets relates to the structure and mechanics of their wings.

The similarities between the sound-producing mechanisms of field crickets and bush crickets are greater than have previously been described: both groups use a plectrum on one wing as a phase-inverting mechanism to excite a resonance of robust veins on the ipsilateral wing, which leads to vibration of a thin sound-radiating membrane. However, in bush crickets, the file-bearing wing is silent (Bailey, 1970) whereas that of field crickets is also resonant when driven by the contralateral plectrum and, in that situation, resonates at a similar frequency to the plectrum-bearing wing. In general, bush crickets produce higher frequency sounds than field crickets so they may achieve an adequately high radiation resistance for efficient sound production (see, for example, Bennet-Clark, 1971, 1998) when using only one wing, but field crickets, producing lower frequency sounds, are under selection pressure to maximise the size of the source and achieve this by using both wings.

Once again, I am grateful to the Department of Zoology of the University of Western Australia for hospitality during the last three months of 2001 while I was doing the experimental part of this work. This work would have been impossible without the help of Prof. Leigh Simmons and Maxine

Beveridge, who provided the insects and song records, and Michael Archer, Sharon Platten and Tom Stewart, who took photographs and made SEM pictures of cricket wings. Special thanks to Prof. Win Bailey for friendship, hospitality, the loan of apparatus and also for encouragement and wise advice at critical stages of the work.

## References

- Bailey, W. J. (1970). The mechanics of stridulation in bush crickets (Tettigoniodea, Orthoptera) 1. The tegminal generator. *J. Exp. Biol.* **52**, 495-505.
- Bennet-Clark, H. C. (1970). The mechanism and efficiency of sound production in mole crickets. *J. Exp. Biol.* **52**, 619-652.
- Bennet-Clark, H. C. (1971). Acoustics of insect song. *Nature* **234**, 255-259.
- Bennet-Clark, H. C. (1987). The tuned singing burrow of mole crickets. *J. Exp. Biol.* **128**, 383-409.
- Bennet-Clark, H. C. (1989). Songs and the physics of sound production. In *Cricket Behavior and Neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), pp. 227-261. Ithaca, London: Cornell University Press.
- Bennet-Clark, H. C. (1997). Tymbal mechanics and the control of song frequency in the cicada *Cyclochila australasiae*. *J. Exp. Biol.* **200**, 1681-1694.
- Bennet-Clark, H. C. (1998). Size and scale effects as constraints in insect sound communication. *Phil. Trans. R. Soc. Lond. Ser. B* **353**, 407-419.
- Bennet-Clark, H. C. (1999a). Resonators in insect sound production: how insects produce loud pure-tone songs. *J. Exp. Biol.* **202**, 3347-3357.
- Bennet-Clark, H. C. (1999b). Which Qs to choose: questions of quality in bioacoustics? *Bioacoustics* **9**, 351-359.
- Bennet-Clark, H. C. and Bailey, W. J. (2002). Ticking of the clockwork cricket: the role of the escapement mechanism. *J. Exp. Biol.* **205**, 613-625.
- Comstock, J. H. (1918). *The Wings of Insects*. Ithaca: Comstock Publishing Company.
- Elliott, C. J. H. and Koch, U. T. (1983). Sensory feedback stabilising reliable stridulation in the field cricket *Gryllus campestris* L. *Anim. Behav.* **31**, 887-901.
- Elliott, C. J. H. and Koch, U. T. (1985). The clockwork cricket. *Naturwissenschaften* **72**, 150-153.
- Faraday, M. (1831). On a peculiar class of acoustical figures: and of certain forms assumed by groups of particles on vibrating elastic surfaces. *Phil. Trans. R. Soc. Lond.* **121**, 299-318.
- Fletcher, N. H. (1992). *Acoustic Systems in Biology*. Oxford: Oxford University Press.
- Hoy, R. R. (1974). Genetic control of acoustic behavior in crickets. *Am. Zool.* **14**, 1067-1080.
- Koch, U. T., Elliott, C. J. H., Schäffner, K.-H. and Kleindienst, H.-U. (1988). The mechanics of stridulation in the cricket *Gryllus campestris*. *J. Comp. Physiol. A* **162**, 213-223.
- Kutsch, W. and Huber, F. (1989). Neural basis of song production. In *Cricket*

- Behavior and Neurobiology* (ed. F. Huber, T. E. Moore and W. Loher), pp. 262-309. Ithaca: Cornell University Press.
- Leroy, Y.** (1966). Signaux acoustiques, comportement et systématique de quelques espèces de Gryllidae (Orthoptères, Ensifères). *Bull. Biol. Fr. Belg.* **100**, 1-134.
- Morse, P. M.** (1948). *Vibration and Sound*. New York: McGraw-Hill.
- Neville, A. C. and Weis-Fogh, T.** (1963). The effect of temperature on locust flight muscle. *J. Exp. Biol.* **40**, 111-121.
- Nocke, H.** (1971). Biophysik der Schallerzeugung durch die Vorderflügel der Grillen. *Z. Vergl. Physiol.* **74**, 272-314.
- Olson, H. F.** (1957). *Acoustical Engineering*. Princeton: Van Nostrand.
- Prestwich, K. N., Lenihan, K. M. and Martin, D. M.** (2000). The control of carrier frequency in cricket calls: a refutation of the subalar-tegmina resonance/auditory feedback model. *J. Exp. Biol.* **203**, 585-596.
- Ragge, D. R.** (1955). *The Wing Venation of the Orthoptera*. London: British Museum (Natural History).
- Sales, G. D. and Pye, J. D.** (1974). *Ultrasonic communication in animals*. London: Chapman and Hall.
- Simmons, L. W. and Ritchie, M. G.** (1996). Symmetry in the songs of crickets. *Proc. R. Soc. Lond. Ser. B* **263**, 305-311.
- Snodgrass, R. E.** (1935). *Principles of Insect Morphology*. New York: McGraw-Hill.
- Young, D. and Bennet-Clark, H. C.** (1995). The role of the tymbal in cicada sound production. *J. Exp. Biol.* **198**, 1001-1019.