

## Mechanical phase shifters for coherent acoustic radiation in the stridulating wings of crickets: the plectrum mechanism

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### SUMMARY

**Male crickets produce stridulatory songs using engaged tegmina (forewings): a plectrum on the left sweeps along a tooth row on the right. During stridulation, the plectrum moves across the teeth and vibrations are amplified by the surrounding cells and veins, resonating at the frequency of tooth impacts. The advance of the plectrum on the file is controlled by an escapement mechanism so that passing each single tooth generates one wave of a highly tonal signal. Both tegmina must oscillate in phase to avoid destructive interference. But as each plectrum-tooth contact begins, the right and left tegmina react in opposite oscillatory directions. A mechanical phase shifter is part of the left tegmen and compensates to achieve wing oscillation synchrony. We use a new technique to simulate plectrum-on-file interactions: in combination with laser vibrometry, this technique assessed plectrum mechanics in the cricket *Gryllus bimaculatus*. Using an excised teneral file, shaped like a partial gear and moved by a motor, and a microscan Doppler laser vibrometer, plectrum and left-tegmen mechanics were explored. The results show that plectrum and harp oscillate with a phase difference of ca. 156 deg., a shift rather than a complete phase inversion (180 deg.). This phase shift occurs at the site of a large wing vein (possibly A3). Plectrum and harp vibrate with similar fundamental frequency, therefore, plectrum torsion resonant frequency is important for maintaining vibration coherence. The mechanical aspects involved in this partial phase inversion are discussed with respect to the escapement mechanism. The plectrum mechanics and its implications in katydid stridulation are also considered.**

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Key words: biomechanics, stridulation, phase shifter, bioacoustics, Gryllidae, Orthoptera.

### INTRODUCTION

Male crickets produce calling songs by stridulation, using their forewings or tegmina: a plectrum or scraper on the left tegmen is swept along a row of teeth (the file) on the right tegmen. Therefore, this mechanism, also known as tegminal stridulation, consists of two major components: the stridulatory file (SF) or ‘pars stridens’ and the plectrum (Sales and Pye, 1974).

The SF is part of the vein A1, which has developed on the underside tegminal surface to form a series of teeth. The plectrum is formed by a more sclerotised projecting part in the tegminal anal region and may also correspond to a modified anal vein (Figs 1 and 2). The file-bearing tegmen (FBT) overlaps the plectrum-bearing tegmen (PBT) so that the plectrum moves and engages with SF teeth on the ventral side of the contralateral tegmen; hence, the two forewings have adapted to different tasks (Forrest, 1987). An SF and plectrum occur in both tegmina, which suggests that crickets can stridulate using either wing overlapping but males of this family tend to stridulate with the right tegmen on top (i.e. there is usually a preferred plectrum and a preferred SF). In crickets, the PBT is the left tegmen (Fig. 1), which, in most cases, is overlapped by a right tegmen (also) with a plectrum. In some species, however, individuals with either tegminal overlapping can be found in equal proportions (Kavanagh and Young, 1989; Masaki et al., 1987). In any case, it is not clear whether crickets voluntarily switch tegminal

overlapping during stridulation (the sound produced with either overlapping is not statistically different) as observed in hump-back crickets (Morris et al., 2002; Morris and Gwynne, 1978).

During stridulation, the tegmina open and close, and the major components of the sound are generated during the closing stroke (Bennet-Clark, 1999a). The plectrum is driven across the SF teeth and vibrations produced by SF-plectrum impacts are amplified by the surrounding wing cells, especially by a triangular area called the harp (Fig. 1), which resonates at the frequency of tooth impacts (Nocke, 1971). The motion of the plectrum over the SF is controlled mostly by the resonant vibration of the FBT: the passage of a single tooth generates one sound oscillation (Bennet-Clark and Bailey, 2002; Elliott and Koch, 1985). This 1:1 correspondence is achieved by an escapement mechanism similar to a clock, where the harps represent the pendulum and the SF-plectrum represent the energy supplier (Koch et al., 1988). The result is a low frequency (range 2–8 kHz) sinusoidal (tonal) signal, functioning to attract females. This mechanism has been analysed and discussed in detail in only a few species of Gryllidae and Gryllotalpidae (Bennet-Clark, 1970; Bennet-Clark, 2003; Bennet-Clark and Bailey, 2002; Koch et al., 1988; Prestwich et al., 2000; Prestwich and O’Sullivan, 2005).

Cricket pure-tone stridulation requires two features: (1) that the main sound radiators of both tegmina vibrate in phase at the same frequency [otherwise the output is affected by destructive

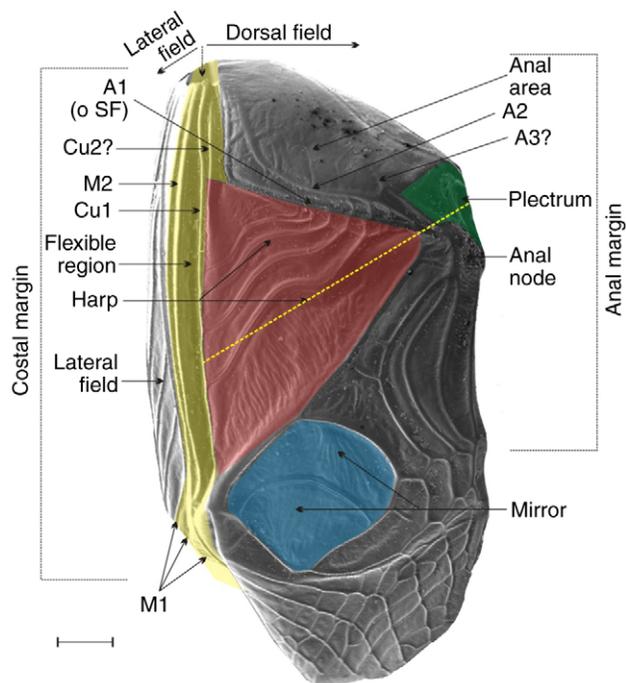


Fig. 1. Left tegmen of *G. bimaculatus*, showing the main areas involved in sound production. The plectrum (green) and the harp (red) were the main regions analysed with a microscan Doppler laser vibrometer during plectrum stimulation with an excised file used as a gear. Nomenclature of wing venation follows Desutter-Grandcolas (Desutter-Grandcolas, 2003). M, medial veins; Cu, cubital veins; A, anal veins; SF, stridulatory file. Broken yellow line crossing the plectrum and harp shows the tegmen region used in phase shift analysis. Scale bar, 1 mm.

interference (Bennet-Clark, 2003)]; and (2) that the functional file be transversely flexible so as to bend when vibrating at the resonant frequency ( $f_0$ ) with enough amplitude to produce catches and releases of the plectrum during every cycle of the oscillation (Bennet-Clark, 2003; Bennet-Clark and Bailey, 2002; Prestwich and O'Sullivan, 2005). Additionally, Ensifera species singing below 40 kHz tend to exhibit a systematic distribution of the file teeth: inter-tooth space gradually increases in the same direction as the plectrum closing movement (Montealegre-Z, 2005); crickets are not an exception to this rule (Bennet-Clark, 1987; Prestwich and O'Sullivan, 2005) (Fig. 3). Thus, tooth spacing could help to determine the relative velocities of the tegmina at plectrum-tooth impact (Koch et al., 1988; Montealegre-Z and Mason, 2005; Prestwich and O'Sullivan, 2005), i.e. the tegminal velocity should gradually increase during the closing stroke.

Bennet-Clark analysed the mechanical interaction of the right and left tegmina in *Teleogryllus oceanicus* pointing out that the two should be phase-locked to generate a coherent pulse (Bennet-Clark, 2003). Theoretically, when the plectrum engages a file tooth, the tooth and rest of the FBT moves away from the resting position making a high pressure (condensation) on its upper face (90 deg. phase), while the plectrum and the rest of the PBT, receiving the opposite push, would make a low pressure (rarefaction) on its lower face (270 deg.). Both tegmina would then be oscillating out of phase by 180 deg. and destructive interference would result in reduced sound production.

The sinusoidal waveform of the sound pulse, which is built upon the vibration of both tegmina, does not, however, show

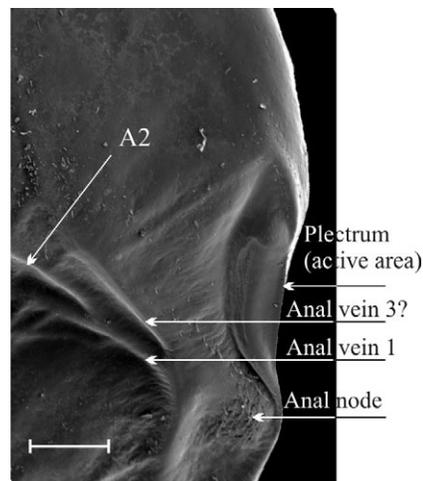


Fig. 2. Close view of the left plectrum area in a recently emerged adult *G. bimaculatus* (dorsal aspect). The anal vein 1 bears the nonfunctional stridulatory file (ventrally modified with a series of teeth). Scale bar, 0.5 mm.

discontinuities or lack of coherence, which suggests that the file-and-plectrum mechanism activates the sound radiating regions of both tegmina so that they vibrate in phase with each other. Using probe microphones, Bennet-Clark measured the vibration of isolated tegmina from different plectrum-wing regions, in response to vibration generated by a piezo-electric actuator (Bennet-Clark, 2003). He observed phase differences between 150 deg. and 210 deg. when the PBT was driven through the plectrum and through the anal area (see Fig. 1 for location of this area). With this, Bennet-Clark (Bennet-Clark, 2003) provided evidence that the vibration at the left plectrum can excite a resonance of the ipsilateral tegmen 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. This phase shift explains how the tegmina maintain a proper constructive phase relationship and make a coherent tonal pulse in crickets.

Although the PBT obviously receives energy through a single region (the plectrum), it is as yet unknown whether the phase of vibration remains uniform in all regions of this tegmen and how energy spreads from the plectrum to the rest of the wing after a tooth impact.

The aim of this paper is to explore the plectrum mechanism in *Gryllus bimaculatus* De Greer stridulation in more detail and to test the phase shifter idea first formulated by Bennet-Clark (Bennet-Clark, 2003). We analyse how energy propagates from the plectrum to the rest of the PBT resonant areas and provide measurements of plectrum and harp motion during repetitive tooth impacts. Additionally, we propose a new method to study the mechanism of tegminal stridulation. In contrast to previously used methods, it does not require removal of the tegmen under experimentation from the specimen. Instead, the plectrum is stimulated *in situ* by a real SF and with tooth impact rates that mimic those used in natural conditions [as opposed to piezo-transducer stimulation (e.g. Bennet-Clark, 2003; Montealegre-Z and Mason, 2005)].

## MATERIALS AND METHODS

### Species

All experiments used adult males of *Gryllus bimaculatus* obtained from a provider (Peregrine Live Foods Ltd, Ongar, UK) or from a colony maintained in the Department of Biological Sciences at the

University of Bristol. In all experiments, we used only young males (selected two weeks after their final moult). Males were recorded before experimentation. We evaluated male sound quality by analysing the carrier frequency ( $f_c$ ), purity of the sound (i.e. the  $Q$  factor), pulse envelope and intensity from these sound recordings:  $f_c$  was normally  $4.8 \pm 0.3$  kHz, pulse duration was normally  $20 \pm 0.4$  ms, and  $Q$  values ranged from 12 to 15. Males with call parameters that significantly differed from the normal average of the lab population were avoided. A total of 14 males were used in the experiments.

#### Analysis of pars stridens anatomy

Morphology of the plectrum and of the file tooth distribution was analysed by scanning electronic microscope (SEM). For the stridulatory file, the right tegmen was removed from some freshly killed specimens; it was mounted on a stub and left to dry in a desiccator with silica gel. The detailed anatomy of the plectrum was studied using transverse sections with a microtome, according to the process described by Di Sant'Agnes and De Mesy Jensen (Di Sant'Agnes and De Mesy Jensen, 1984). Microtome sections were mounted on slides and examined in a light transmission microscope (JEOL, 1200 EX, Tokyo, Japan) at the University of Bristol. Specimens mounted on stubs were gold-coated and studied by SEM using a Philips 501B (Netherlands, Eindhoven). SEM images were digitized with a Keithley DAS 1202 plug-in card (Keithley Instruments, Tauton, MA, USA), and the software SEM 1.2 (A. Gebert and G. Preiss, Medical School, Lab. of Cell and Electron Microscopy, Hannover, Germany). For five specimens, we obtained lateral-view pictures at high magnification of the file that allowed the accurate determination of tooth depth and inter-tooth distances (Fig. 3B). Specimens were scanned and measured twice on two different days. Analysis of the file morphology was performed on digitised SEM photographs using the dimension tool of a drawing program (Corel Draw 13, Corel Inc. 2005). Data for a single specimen represent the average measured from two different sets of SEMs. Inter-tooth distances were measured from the edge of the cusp of one tooth, and tooth depth as shown in Fig. 3B. File morphology is described for comparative purposes: as we describe a new method for *in situ* wing stimulation, which requires an excised file mounted on a wheel, it is important to show how file morphology changes after this procedure.

#### Recordings of sound

We recorded calling sounds from each male used in the experiment using a 1/8" condenser microphone Brüel & Kjaer Type 4138, connected to a Brüel & Kjaer 2633 preamplifier (Brüel & Kjaer, Nærum, Denmark). The microphone was positioned dorsal to the specimen. Instantaneous frequency of pulses obtained from sound recordings and pulses obtained from artificial stimulation (see below), were analysed with the Zero-crossing module for Canary 1.2.4 software (Cornell University, Laboratory of Ornithology, Ithaca, NY, USA). Zero-crossing v. 5 was provided by K. N. Prestwich (<http://www.holycross.edu/departments/biology/kprestwi/ZC/>).

#### Experiments

We induced vibrations of the left tegmen by stimulating its plectrum with an excised 'file as gear' system (referred to here as the 'cog-cricket'), driven by a motor (Fig. 4). Experimental animals were anaesthetised using CO<sub>2</sub>, then mounted in a holder affixed with commercial wax (Boxing Wax Sticks, KERR Co., Romulus, MI, USA), with the left tegmen maintained extended normal to the body (Fig. 4). The tegmen was gripped at the hinge (axillary sclerites and

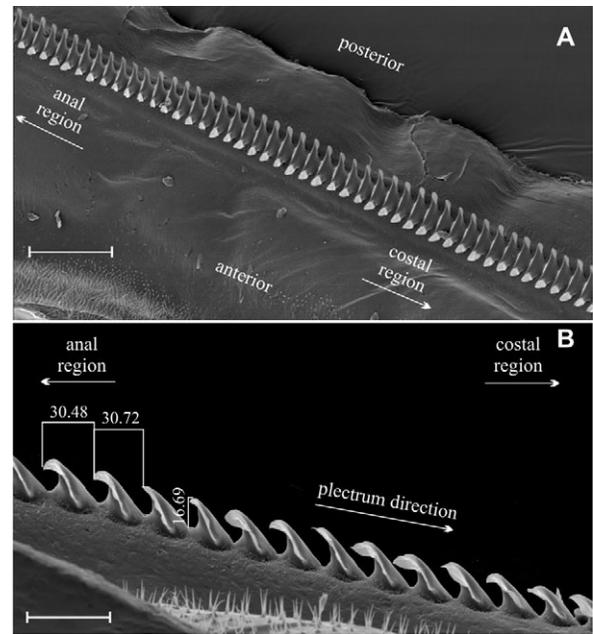


Fig. 3. Close views of the stridulatory file of a newly emerged adult of *G. bimaculatus*. (A) Mid-region of the file showing tooth shape and tooth distribution. Scale bar, 200  $\mu$ m. (B) Lateral aspect of file teeth (file focused anteriorly in relation to body coordinates), illustrating measurement of inter-tooth distances and tooth depth. Scale bar, 50  $\mu$ m.

folded axillary membranes) with wax (previous recordings with the micro-scan laser vibrometer showed that in this region vibrations are low or almost absent, and that the structures associated with the wing hinge do not resonate at a particular frequency). This tegmen, by remaining attached to the body and unwounded, retained its resonant properties unaffected by blood-loss dehydration. The complete preparation was mounted as shown in Fig. 4B.

#### Mounting a dissected stridulatory file on a plastic ring

The 'cog-cricket' machine used a natural SF that was carefully excised from a teneral specimen and inversely bent and glued around a plastic ring fitted on the shaft of a motor. This preparation incorporates: (1) a plastic cylinder LEGO<sup>TM</sup> (4.8 mm external diameter, 3 mm internal diameter and 4 mm long) with a thin protruding rib (thickness, 0.6 mm; length, 0.8 mm) extending on one of the edges (Fig. 4A); (2) a Mabuchi Motor FA-30RA-2270 (Matsudo, Japan), flat type (length, 25.0 mm; height, 15.1 mm; diameter, 20.1 mm; shaft size, 9.4 mm; shaft diameter, 2.0 mm) (Fig. 4B). Driven at 1.5 V, the shaft of the motor rotates with a speed of 9100 rpm but it also ran smoothly at voltages down to 0.1 V; and (3) a SF removed from the right tegmen of a teneral male *G. bimaculatus*. The right tegmina of several newly moulted males were carefully removed under a dissecting microscope, using razor blades and No. 5 forceps. Tegmina of recently moulted males were used because, although teneral, they are flexible enough to tolerate the bending and gluing processes (see below). Males were separated and kept in individual cages for approximately five days after their last moult and then the SF excised from their right tegmen as explained above. The dissected file was glued to the external rim of the plastic ring (Fig. 4A).

The SF of crickets is not rectilinear: the anal and proximal parts curve (see Fig. 1), the excised part included only the straightest central file region. A normal SF of *G. bimaculatus* includes

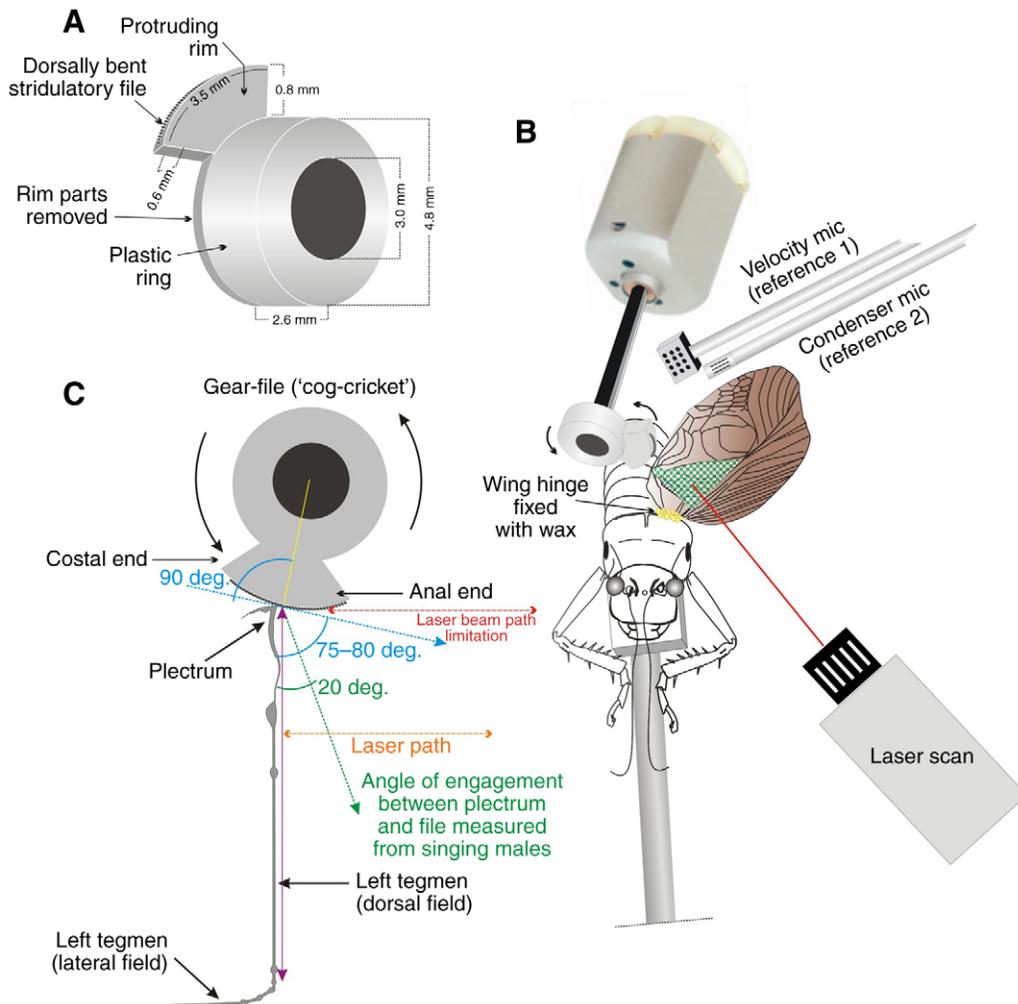


Fig. 4. Preparation used for plectrum stimulation. (A) The gear-file system. The dorsal surface of a file segment was glued to the curved rim; most of the rim was removed after this procedure, leaving only the part containing the file. (B) Setup of the preparation. The insect was mounted in a holder and fixed to a special platform with wax, while its plectrum wing was maintained extended by fixing the wing hinge (axillary sclerites and folded membranes) with wax. The motor speed was controlled by applying different voltages to obtain the desired impact rate. The rotating file teeth produced impacts on the plectrum. Vibrations were recorded with a laser Doppler vibrometer and sound monitored with a velocity (Reference 1) and a pressure microphone (Reference 2). Reference 1 was used as a trigger during recordings. The cross-hatched green area depicts the scanned region of the wing, although a close-up view of the plectrum region was also scanned in the same preparation. (C) Cross section of the 'cog-cricket' system and left tegmen, showing the angle of tooth-plectrum engagement used during experiments. Broken blue line depicts the imaginary tangential line that touches the circumference, formed by the gear-file rotation, at the point of plectrum contact. The broken yellow line represents an imaginary radius perpendicular to the blue tangent.

approximately 130–140 teeth and the exclusion of the curved ends left only ca. 70–80 teeth (Fig. 3A shows part of this straight segment). From high-speed video recordings of 13 different males (F.M.-Z, unpublished observations), we observed that sound pulses made by a healthy singing male require hitting 90–105 teeth of the file, the last 10–15 of which occur in the curved proximal region. Therefore, all 70–80 teeth in the excised straight segment of the file mounted on the wheel are part of those normally used during stridulation.

A drop of cyanoacrylate gel superglue (Henkel Loctite, Winsford, Cheshire, UK) was applied to the edge of the ring's rim and was left exposed to the air for a few seconds until it became tacky. Then the dorsal part of the file was gently pressed against the spread glue, pushed down first at one of its ends, then progressively along the rim's circumference. Light pressure was applied until the adhesive completely stabilised (approx. 1 min). Once the file was affixed and shaped to the rim's circumference contour, the excess portions of the rim were removed with a razor blade (Fig. 4A,C); thus only the region bearing the file contacted the plectrum during each cycle of rotation. The length of the retained arc bearing the file was ca. 3.5 mm (Fig. 4A,C). The preparation was left to dry for about 48 h to allow cuticular hardening. A total of two excised files from teneral specimens were used in the experiments incorporated in this paper. The effects of bending the SF on tooth distribution and removing its curved parts are presented in the results.

Unlike actual file teeth, those on our preparation did not deviate from a straight line; this was necessary because all were required to hit the plectrum during the rotation of the gear (under natural conditions, several of the teeth from the curved parts of the file are hit because the tegmina close at an angle [see fig. 4C in Bennet-Clark (Bennet-Clark, 2003)]. The process of gluing the SF to a rigid surface will change its mechanical properties (elasticity, hardness, Poisson's ratio, etc.) but we are interested here only in the mechanics of the PBT: in other words, the process of stimulating the plectrum with a damped file can provide information only on PBT vibration and not on two resonating wing structures vibrating simultaneously.

The 'cog-cricket' system was inserted on the motor shaft (Fig. 4B). The motor was driven at different voltages (from 0.1 to 1.0 V) using a stabilised TTi power supply (EL302, 18V, 3.3A, Thurlby Thandar Instruments Ltd, Cambridgeshire, UK). Voltage resolution was controlled and observed with a Digital multimeter (ISO-TECH IDM93N, RS Components Ltd, Northants, UK) connected between the power supply and the motor. For calibration, the rotational speed of the 'cog-cricket' system was measured at different voltages using a high-speed video camera (HSV-500c3, NAC Image Technology, Simi Valley, California, USA), which allowed us to select the range of voltages that generated a tooth-passage rate of 4700–5000 teeth mm<sup>-1</sup>. This span of appropriate tooth-passage rate was obtained with voltages in the range of ca. 170–190 mV.

### Plectrum stimulation with a 'cog-cricket' system

With the insect mounted, its left tegmen extended, the areas and density of points on the tegminal surface to scan by laser Doppler vibrometer were chosen. The plectrum was then stimulated at different rates of tooth passage. Practically the motor powering the 'cog-cricket' was set into motion, usually starting at 300–400 mV. The spinning file was carefully positioned close to the plectrum so that tooth impacts engaged the plectrum ventrally, such that SF engagements occurred from the anal end toward the costal end, as in a real closing stroke (Fig. 4C). The frequency response was monitored in real time with a frequency analyser.

Although in a singing individual the angle adopted during the closing stroke between PBT and FBT is ca. 15–20 deg. (Fig. 4C), the 'cog-cricket' system allowed us to achieve 75–80 deg. This angle was measured against the tangential line that touches the circumference of SF (cog-cricket) rotation at the plectrum contact point (Fig. 4C). The tangential line was traced with a laser pointer mounted on a protractor. A smaller angle of engagement could have been obtained but at angles <75 deg., the ring's rim blocked the beam path of the laser Doppler vibrometer and interfered with proper recording, especially in the plectrum scanned area (see Fig. 4C). However, with an angle of engagement of 20 deg. it is possible to scan most of the harp surface. The harp vibration response to cog-cricket stimulation was recorded, adopting both angles of engagement (20 deg. and 80 deg.) and a constant angular speed. We found no differences in the frequency (paired Wilcoxon test  $P=0.92$ ; means  $\pm$  standard deviation:  $4.97\pm 0.36$  kHz at 20 deg., and  $4.95\pm 0.33$  at 80 deg.,  $N=6$ ).

The voltage driving the motor was gradually adjusted from an initial setting (300–400 mV) into the range producing optimal velocities, until a maximum amplitude peak was observed. At this stage, it was also possible to appreciate by ear, a reduction in pitch and an increase in the quality of the output sound as seen in Movie 1 in the supplementary material. This peak amplitude value was compared with the  $f_0$  of the tegmen (obtained by stimulating the wing with periodic chirps, see below), and experiments were carried out with whichever voltage had provided that tooth-strike rate. Although the  $f_0$  of the PBT in crickets is close to  $f_c$  of the calling song, the PBT  $f_0$  differs among individuals (Bennet-Clark, 2003). For this reason, the rotational speed in all experiments was adjusted for every specimen, until a peak with optimal amplitude, close to the mean  $f_0$ , was observed in the fast Fourier Transform (FFT) analyser windows.

### Recordings of tegminal vibrations

Tegminal vibrations were examined in response to sympathetic vibration and artificial tooth strikes using the 'cog-cricket' system. Vibration velocities were measured by a micro-scanning laser Doppler vibrometer with an OFV-056 scanning head fitted with a close-up attachment; the latter allowed the laser beam (ca. 5  $\mu$ m diameter) to be positioned with an accuracy of 1  $\mu$ m. The laser spot location on the tegmen membrane was monitored by live video feed to the vibrometer's controlling computer. The vibrometer allows accurate measurement of the topography of surface motion in a contact-free way, without requiring the use of a reflective medium (Windmill et al., 2007).

For the experiments, we scanned the plectrum and harp area (including the SF and anal vein 2) of the PBT using a lattice of 130–200 measurement points (Fig. 5A). The plectrum area, including a small harp region, was also subsequently scanned at higher resolution using 300–400 measurement points (Fig. 5B). Before the experiments were carried out, tegminal vibrations were examined

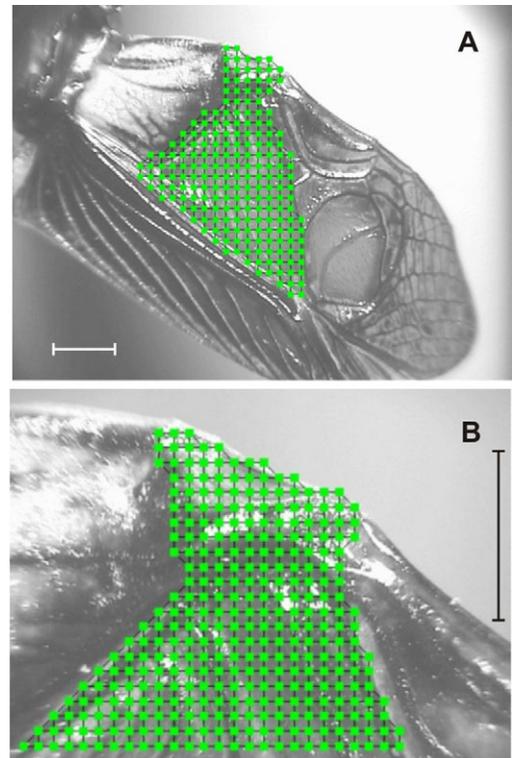


Fig. 5. Capture of the video image from the laser Doppler vibrometer illustrating the plectrum-bearing wing during measurements and the lattice of laser scanning points. (A) Entire tegmen ( $N$ , 200 points; scanning mesh size, 170  $\mu$ m; dot-positioning accuracy, ca. 1  $\mu$ m), scale bar, 1 mm. (B) High-resolution scan of the plectrum region ( $N$ , 320 points; scanning mesh size, 85  $\mu$ m; dot positioning accuracy, ca. 1  $\mu$ m), scale bar, 1 mm.

in the frequency domain in response to acoustic stimulation with periodic (chirp) signals, using a bandwidth of 20 kHz (range 1–20 kHz), 3200 FFT lines and a frequency resolution of 6.25 Hz. The acoustic signals were generated by the PSV 300 internal data acquisition board (National Instruments PCI-4451; Austin, TX, USA), amplified (Sony amplifier model TAFE570; Tokyo, Japan) and passed to a loudspeaker (ESS AMT-1; ESS Laboratory, Inc., Sacramento, CA, USA) positioned 20 cm from the specimen. These recordings allowed us to determine in advance the  $f_0$  of the tegmen under study, so that for the following experiment (cog-cricket stimulation) the frequency at which a particular tegmen should resonate was known.

We recorded sound pressure levels from the 'cog-cricket' system on the plectrum, using a 1/8" condenser microphone Brüel & Kjaer Type 4138 and a Brüel & Kjaer 2633 preamplifier (Brüel & Kjaer). Calibration values provided by the company for gains of 30 and 40 dB were accounted for in the laser vibrometer acquisition settings. In addition to the pressure microphone, a particle velocity microphone was used as a trigger. Particle velocity microphones provide a localised measurement of acoustic radiation and therefore also a reliable trigger signal.

Laser and microphone signals were sampled at rates of up to 204.8 kHz. Measurements resulted from an average of 10–20 measurements at each point and were transformed to the frequency domain using a FFT (rectangular window, frequency resolution, 12.5 Hz).

All experiments were carried out on a vibration isolation table (TMC 784-443-12R; Technical Manufacturing Corp., Peabody, MA, USA) at room temperature (25–27°C) and relative humidity of 50–62%. The vibration isolation table with the specimen and the laser vibrometry measurement head were located in an acoustic isolation chamber (IAC series 1204A; internal dimensions: length, 4.50 m; width, 2.25 m; height, 1.98 m; Industrial Acoustics, Bronx, NY, USA). In synchrony with the mechanical measurements, the microphones were positioned next to the preparation.

Frequency spectra of the laser signal were normalised to those of the microphone signal by the computation of transfer functions, calculated as the cross-power spectrum of the laser and the microphone signals divided by the auto-power spectrum of the latter (Windmill et al., 2005). The magnitude-squared coherence between the vibrometer and microphone signals was also computed for each data point, to assess data quality for the entire dataset and so estimate the amount of unrelated noise (Windmill et al., 2007). Coherence values can range between zero and one, with a value of one indicating the absence of external, unrelated noise. Data were considered of sufficient quality when coherence exceeded 85%. From the FFT data, phase angles were obtained for every point scanned with the laser vibrometer.

#### Individual resonances of the plectrum and harp

From the tegminal areas scanned shown in Fig. 5, we selected specific points to measure local frequency of vibration, individually for the plectrum (ca. 30 points) and for the harp (ca. 150 points). Frequency was estimated as the average spectrum from all selected points in each area. The quality factor,  $Q$ , measures a resonant system's internal-to-external damping and also the rate at which such a system reaches maximum amplitude or decays (Prestwich and O'Sullivan, 2005). For comparative purposes,  $Q$  was measured from calling song recordings of 11 specimens and from pulses produced by 'cog-cricket' stimulation using the method proposed by Bennet-Clark (Bennet-Clark, 1999b).  $Q$  was calculated from the free decay of a pulse, i.e. from those oscillations free from the driving force after plectrum-file disengagement. We detected that stridulation had ceased using Zero-Crossing analysis. The abrupt jumps in instantaneous frequency late in the pulses are believed to be associated with the disengagement of file and plectrum (Bennet-Clark and Bailey, 2002; Bennet-Clark, 2003; Prestwich and O'Sullivan, 2005).

#### Statistical analysis

From the FFT data, phase angles were obtained for every (single) point scanned with the laser Doppler vibrometer. For statistical analysis, phase data were chosen from scanned points aligned in a straight line extended from the plectrum central region to the harp as shown in Fig. 1. Before proceeding with further statistical analysis, phase vectors were normalised with respect to the lowest phase value for every specimen. From these angular data representations, a mean vector was calculated trigonometrically by using the formulae given for grouped data in Batschelet (Batschelet, 1981). Circular standard deviation and standard error of mean were also estimated. Plectrum and harp resonances were compared using a Wilcoxon test for two related samples. Inter-tooth distances from the SF of five intact males and those of the two SF used in the experiments (i.e. bent files) were compared in a two-way analysis of variance (ANOVA). The same test was used for  $Q$ -value comparison. Statistical analyses were carried out using the program Oriana 2.02e (Kovach-Computing-Services, Anglesey, UK) for circular statistics and the R software (v. 2.7.1, www.r-project.org).

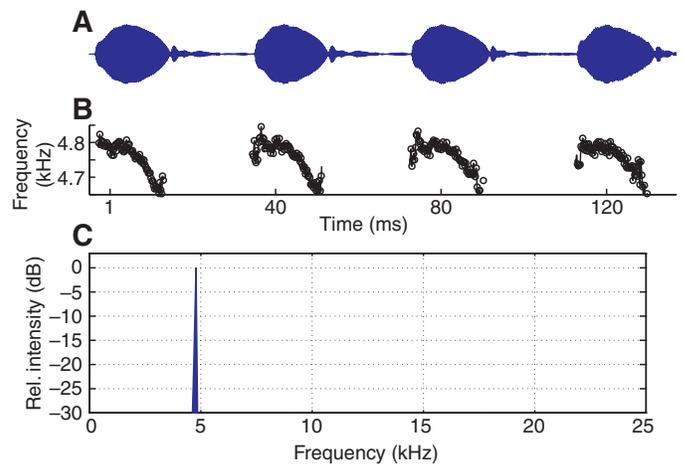


Fig. 6. Acoustic features of *Gryllus bimaculatus*. (A) A single chirp made of four phonotomes. (B) Zero-crossing analysis of the song sequence shown in A, depicting instantaneous frequency. (C) Spectral analysis of the pulses in A.

Acoustic analyses and plots were generated using Matlab software v. 7.6 (The MathWorks, Natick, MA, USA).

## RESULTS

### Calling song description

The calling song of *G. bimaculatus* consists of series of repeated chirps, which are themselves composed of three to five (normally four) sound pulses (Fig. 6A,B). The mean duration of each pulse in the chirp was  $22.0 \pm 1.3$  ms ( $N=20$ ) centred on a frequency of  $4.7 \pm 0.2$  kHz ( $N=20$ ) (Fig. 6C). As with most crickets for which the song has been analysed (Leroy, 1966; Simmons and Ritchie, 1996), pulses present frequency modulation (FM), the fundamental frequency and overtones fall during the last half of all the song pulses (Fig. 6B) (see also Simmons, 1988).

### File and plectrum morphology

Fig. 7A shows that tooth spacing gradually increases (linearly) from the anal to the costal region, reaching a maximum spacing ( $\sim 40 \mu\text{m}$ ) between teeth numbered 85–90. Thereafter, the spacing gradually decreases. Tooth-space increments occur in the same direction as plectrum movement, a common feature in singing ensiferans that generate pure tones (reviewed by Montealegre-Z, 2005). Teeth are also inclined at a 45–47 deg. angle, leaning into the approaching plectrum (Fig. 3). Individual tooth morphology in *G. bimaculatus* is typical of several cricket species (Walker and Carlysle, 1975): the tooth basal area is small in relation to the cusp area, the latter being expanded into lateral flaps curved towards the file anal region (Fig. 3A,B). This tooth morphology seems to help maximise the plectrum contact region, while at the same time providing basal flexibility for local bending during file vibration. The asymmetrical tooth shape and tilted orientation may maximise friction between plectrum and file, creating an appropriate engagement of both structures.

The anal region of the left tegmen bears the active plectrum, which has a nearly straight sclerotised posterior sharp edge approximately 0.76 mm long (Fig. 2) backed by a convex area of softer cuticle approximately 0.17 mm wide and  $33 \mu\text{m}$  thick (Fig. 8). This region curves down and ends in a narrow U-shaped depression approximately  $11 \mu\text{m}$  thick. Another triangular region of flexible cuticle, rises up by

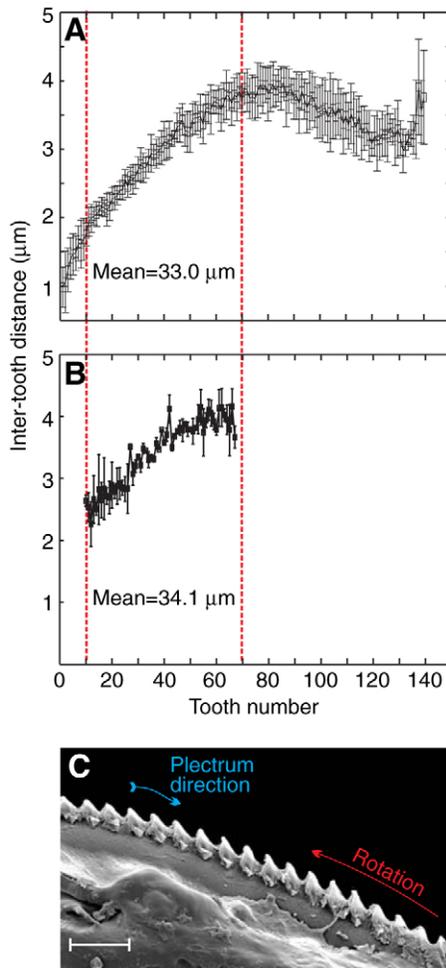


Fig. 7. Comparison between inter-tooth spacing in files of *Gryllus bimaculatus* and the files used as a gear in our driving system. (A) Mean inter-tooth spacing of five intact specimens; error bars indicate standard deviation. (B) Mean inter-tooth spacing of the two files excised from two general males used in our gear-motor system (after bending). Note that mean inter-tooth spacing significantly increases after bending. Broken lines show the excised area of the file (including ~70 teeth) used bent and glued to the plastic-ring's rim. (C) Segment of a bent file used in the 'cog-cricket' system. Scale bar, 100  $\mu\text{m}$ .

0.8 mm from the depression (Figs 2 and 8) and is backed by a thick protruding vein (believed to be A3) approximately 42  $\mu\text{m}$  in diameter. The file teeth are approximately 17–20  $\mu\text{m}$  deep (Fig. 3B), and the edge of the plectrum has an active tip, ca. 14  $\mu\text{m}$  depth, formed by the wing's dorsal layer of cuticle that bends to the anal side in an angle of ca. 107 deg. The topography of the convex area may help to facilitate the plectrum's release from a tooth because its dome-shape could work as a roller, slipping on the file as the wings are pushed in opposite directions: this might cause the plectrum to rotate ventrally and so disengage more cleanly from a tooth (Fig. 8). During tooth engagement, the plectrum and convex area should bend dorsally along its length towards the costal region of the wing, till the plectrum is released. A similar mechanism is described in Montealegre-Z [pp. 100–101 in Montealegre-Z (Montealegre-Z, 2005)].

#### Individual resonances of plectrum and harp

The mean FFT of selected scanned points in either the plectrum or the harp shows the local frequency of vibration in each area. Both

the plectrum and harp resonate at similar frequency (means  $\pm$  standard deviation: plectrum=4.86 $\pm$ 0.61 kHz harp=4.91 $\pm$ 0.61 kHz; paired Wilcoxon test,  $P=0.47$ ,  $N=24$ ).

#### Response to SF actuation using the 'cog-cricket' system

Using the SF as a gear required bending the dorsal surface of the file onto the semi-circumference of the ring-rim. After bending, mean inter-tooth spacing of the SF in two preparations, using files of two different specimens, significantly increased over the intact SF condition [intact SF mean, 0.033 ( $N=5$ ); bent file, 0.034 ( $N=2$ ); d.f.=1,  $F=11.56$ ,  $P=0.001$ ]. The bending of the file also altered the angle of attack but tooth spacing preserved the gradually increasing pattern (Fig. 7B,C).

As expected, the short SF segment (ca. 70 teeth) mounted on the ring's rim, produced a pulse shorter than that of intact individuals (Fig. 9). 'Cog-cricket' pulses varied in length between 6 and 15 ms and, in most cases, exhibited build-up followed by free decay. From time-to-time upward FM from ca. 4.5 to ca. 5.0 kHz would appear in the preparation output. With this method, the  $f_0$  of the PBT (measured with laser vibrometry and microphones) in 14 different individuals was remarkably constant and kept to the range of 4.5 to 5.0 kHz (Fig. 10). The average  $Q$ -factor for the PBT, calculated from the free decay of the three outputs (vibration, pressure and particle velocity), remained in the range of 8 to 10.6 (vibration, 10.6 $\pm$ 2.7; pressure, 8.2 $\pm$ 1.2; particle velocity, 8.6 $\pm$ 1.4,  $N=14$ ), which was significantly lower (d.f.=1,  $F=21.5$ ,  $P<0.001$ ) than the  $Q$  values calculated from of the species calling song (12.9 $\pm$ 3.7,  $N=11$ ) (Fig. 9).

#### The plectrum mechanism: phase shifter or phase inverter?

The mechanical response of the entire left tegmen was evaluated in the frequency domain, both as a gain (or magnitude response) and a phase response. The scanned dorsal surface of one of the crickets used in our study is illustrated in Fig. 11. The quality of each measured point was evaluated by estimating the magnitude-squared coherence between tegmen vibration and reference microphone across the frequency range in use, as shown in Fig. 12C. High coherence levels were observed with frequency values around  $f_0$  of the wing but decreased below 0.8 for values exceeding 5.0 kHz (Fig. 12C). High coherence at  $f_0$  shows that the amplitude and phase data used in the analysis are quite reliable and also confirms that the plectrum and harp resonant frequencies are similar. The plectrum and harp regions vibrate with phase differences of ~156 deg. (Fig. 12A). The plectrum region maintains a phase of vibration around ca. 20.0 deg. (range between 4.6 $\pm$ 2.5 deg. and 52.2 $\pm$ 12.9 deg.,  $N=14$ ) but after energy moves away from the plectrum region (toward the harp), the harp adopts a phase of vibration of ca. 167.3 deg. (range between 151.1 $\pm$ 13.7 deg. and 172.0 $\pm$ 10.2 deg., angular mean  $\pm$  standard error of mean,  $N=14$  in both cases). High-resolution scans of the plectrum area show that this sudden change occurs at the transition delineated by a large vein (possibly vein A3), which merges with A1 at the anal node area (Fig. 2 and Fig. 13A,B). The wing vibrates up and down in a cantilever manner from this region (Fig. 11B), and plectrum and harp vibrate with significant gain differences, being higher by several orders of magnitude, for the harp region (Fig. 14B,C).

## DISCUSSION

#### The 'cog-cricket' method to produce tooth-plectrum impacts

The new method of stimulation described here could be used more widely to study tegminal stridulation in Ensifera. The rotational velocity of this 'cog-cricket' as controlled by a low-voltage motor,

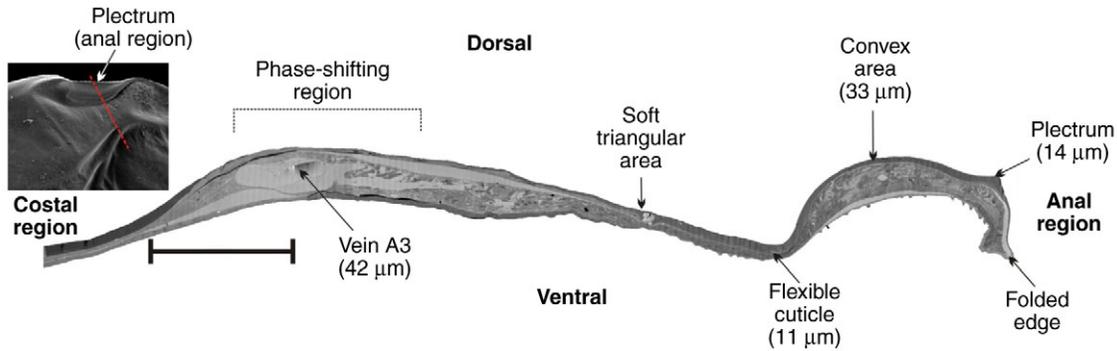


Fig. 8. Microtome section of the left plectrum of *G. bimaculatus* cut approximately one-third along length of the plectrum active area. Inside picture shows the dorsal surface of the plectrum. Note that the phase-shifting area looks broad in the microtome section as the vein A3 was sectioned through the region crossed by the red broken line. Scale bar, 100 μm.

allows the animal's sound radiating structures to be driven under different regimes. The spinning file is set in contact with a PBT in the plectrum region; such that the plectrum and the rest of the tegmen can be excited into vibration at different impact rates. Because this method does not require the removal of the activated tegmen from the insect's body, it constitutes a less invasive and more naturalistic way to set the PBT into vibration using real tooth impacts. The 'cog-cricket' technique can also be used with other singing Ensifera

(Tettigoniidae, Gryllotalpidae and Haglidae), and, therefore, represents a very practical experimental tool for physiological and biomechanical experimentation. Its application should allow insight into the diverse stridulatory mechanisms used in the family Tettigoniidae, especially those species using broadband calls but also in the study of wing resonances in a diversity of singing ensiferans.

In a normal cricket, stridulatory file inter-tooth spacing increases basad, toward the costal region (Fig. 2A and Fig. 7A). Because of

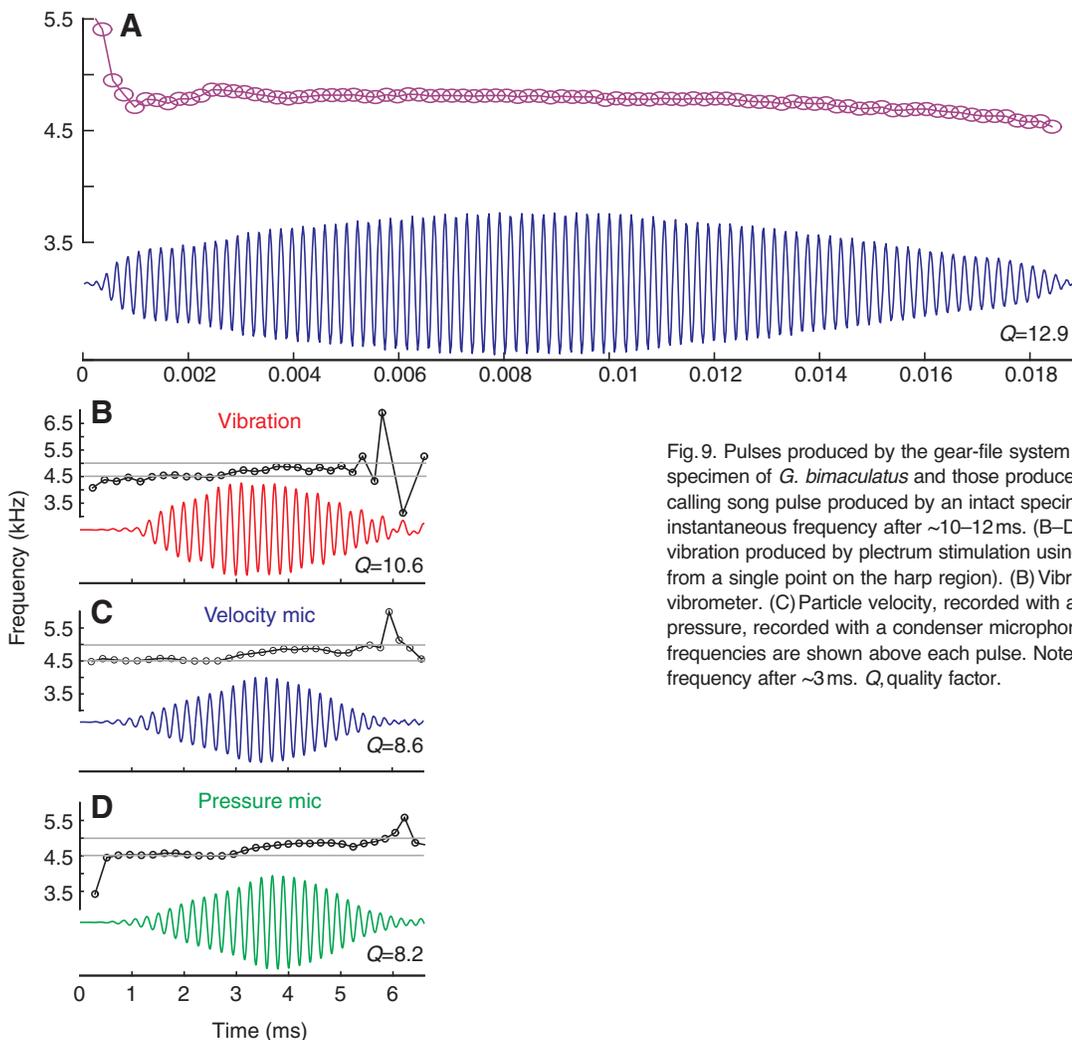


Fig. 9. Pulses produced by the gear-file system on the plectrum of a single specimen of *G. bimaculatus* and those produced by an intact specimen. (A) A calling song pulse produced by an intact specimen. Note the moderate drop in instantaneous frequency after ~10–12 ms. (B–D) Recordings of sound and vibration produced by plectrum stimulation using a gear-file system (data obtained from a single point on the harp region). (B) Vibration, recorded with a laser Doppler vibrometer. (C) Particle velocity, recorded with a velocity microphone. (D) Sound pressure, recorded with a condenser microphone. Corresponding instantaneous frequencies are shown above each pulse. Note the moderate increase in frequency after ~3 ms. *Q*, quality factor.

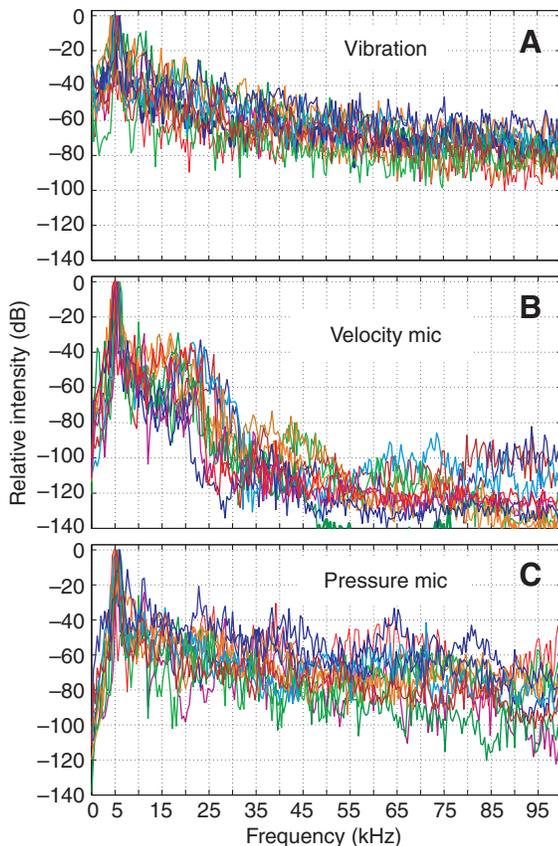


Fig. 10. Spectral analysis of the average wing frequency response to plectrum stimulation in 10 specimens (indicated by different colour traces) using the ‘cog-cricket’ motor system. (A) Vibrational response ( $4.9 \pm 0.7$  kHz). (B) Particle velocity response ( $5.2 \pm 0.4$  kHz). (C) Sound pressure response ( $5.2 \pm 0.4$  kHz).

this systematic change, it is possible to maintain a constant plectrum-on-tooth strike rate only if the velocity of the closing stroke also increases appropriately during sound production (Bennet-Clark, 2003; Koch et al., 1988; Prestwich and O’Sullivan, 2005). After placement, the excised files preserve this tooth density pattern so a potential limitation of our technique is that motor velocity is constant while inter-tooth spacing gradually increases. Tooth contact rate is a function of  $f_c$ . Therefore, gradual drops in instantaneous frequency [analogous to the Glissando effect (Bennet-Clark, 2003)] are expected when using the ‘cog-cricket’ system. Yet FM in most cases was either very moderate (ca. 500 Hz) or absent from the pulses made with the ‘cog-cricket’ system. When FM was intermittently observed, instead of exhibiting the gradual drop in instantaneous frequency, expected for a constant tooth strike rate and increasing inter-tooth-distance pattern, a gradual increment was observed (Fig. 9B–D). We have no explanation for this, although it may be related to minor variations in a motor’s rotational speed when driven at low voltages. Duration and envelope shape of the pulses generated by ‘cog-cricket’ apparently depend on orientation and forces applied to the gear with respect to the plectrum: because this was manually controlled, it was difficult to apply precisely a constant force and orientation during all experiments.

The results reported here show that the wing vibrations produced by the ‘cog-cricket’ method can be monitored with a Doppler laser vibrometer, pressure and/or velocity microphones.

### The mechanical phase shifter in the plectrum of crickets

Bennet-Clark (Bennet-Clark, 1970; Bennet-Clark, 1989; Bennet-Clark, 1999a; Bennet-Clark, 2003) suggested that the plectrum and harp (in the PBT) of crickets and mole crickets vibrate with phase differences. The present paper not only confirms this work but also identifies the anatomical location of the structures involved in the phase-shifting mechanism and provides quantitative data that can be used to explain how this phase shifter works.

Vibrations induced at the plectrum, propagating to the rest of the PBT, experience a series of discontinuities within the medium of propagation, the tegminal cuticle. With changes in geometry come discontinuities in mass, density, thickness, tension and stiffness – features inherent to ensiferan forewings that have evolved to promote effective sound radiation (Fig. 8).

A vibration travelling across a complex heterogeneous medium, as that exhibited by the plectrum region, will have a particular behaviour in regards to reflection and transmission, which depends on the material properties of both regions of the system. One important property is the characteristic impedance of the material and discontinuities in impedance (Hirose and Lonngren, 1985). The characteristic impedance of a material is the product of mass density and wave speed. Therefore, given the magnitude of the vibration in the plectrum region and harp (Fig. 14B,C), one can observe that oscillations travelling in the cricket PBT system increase in amplitude after crossing the phase shifter region. This is analogous to an incident wave travelling from a high density (low wave speed) region towards a low density (high wave speed) region. In this case, part of the energy will be reflected back from the boundary (the region where density and impedance abruptly change) and part will be transmitted across the boundary [pp. 103–108 in Hirose and Lonngren (Hirose and Lonngren, 1985)] to the rest of the sound-radiating regions of the PBT, with a gain in amplitude. Depending upon the mismatch in wave impedance between the two media, amplitudes of reflected and transmitted waves can be compared to that of the incident wave (Fletcher, 1992), and the frequency of the vibration can slightly change from one medium to the other (Hirose and Lonngren, 1985). Although not being the main purpose of this paper, our finding of dissimilar amplitudes of vibration between plectrum and harp (Fig. 14B,C) suggests that both regions exhibit different impedances and different densities. Assuming waves travelling across the plectrum can be analogised to those waves travelling from a high density region towards a low density one, the energy reflected back from the boundary (vein A3) could induce the release of the plectrum from a specific tooth. In other words, this energy might make a significant contribution to the escapement mechanism.

FFT analysis of the scanned wing regions showed that the  $f_0$  of plectrum and harp are not significantly different (plectrum =  $4.86 \pm 0.61$  kHz and harp =  $4.91 \pm 0.61$  kHz). This indicates that the plectrum torsional  $f_0$  (its angular natural vibration) matches the  $f_0$  of the whole tegmen and that such torsional  $f_0$  is critical for making the phase-shifting mechanism work. Interestingly, if the plectrum is stimulated at lower or higher tooth-strike rates, rates different to that of its own  $f_0$ , tegmen resonance is lost and thus its sound purity (see Movie 1 in supplementary material). The phase relationship observed in Figs 11 and 12 is also lost, therefore, the escapement mechanism is not at work if the tooth strike rate dramatically changes (Montealegre-Z et al. in prep).

Studying wings in isolation, Bennet-Clark showed that for *T. oceanicus* both forewings differ in  $f_0$ , this normally being higher for the PBT (PBT = 4.56 kHz, FBT = 4.21 kHz) (Bennet-Clark, 2003). This difference appears to be consistent with the subtle

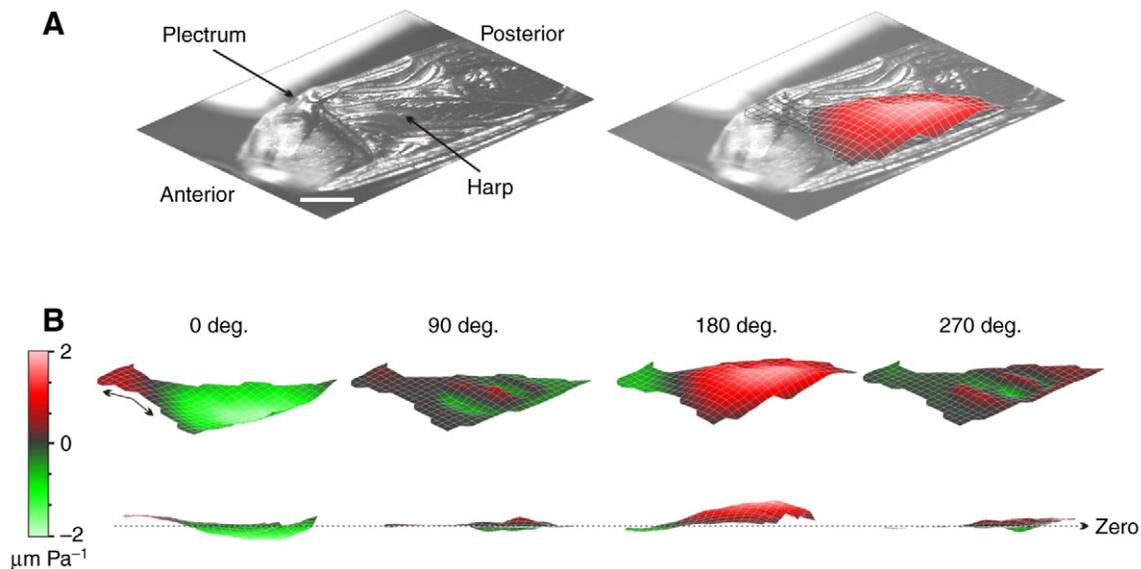


Fig. 11. Scanned area and deflection shapes of the tegmen dorsal surface (harp and plectrum) in *G. bimaculatus*. (A) Orientation image relating tegmen topography (left image) to the position of the scanning lattice (right image). (B) Area scans of tegmen-membrane deflections at  $\sim 4.8$  kHz ( $4800 \text{ teeths}^{-1}$ ). The deflections are shown each time for four different phases along the oscillation cycle. Deflections are additionally shown as profiles, looking at the tegmen from its anterior aspect. Red indicates positive displacements (or outward membrane deflections) and green indicates negative displacements (or inward membrane deflections).

morphological asymmetry of the tegmina (Bennet-Clark, 2003; Simmons and Ritchie, 1996). Similar differences in the  $f_0$  between tegmina occur in the katydid *Panacanthus pallicornis* (Montealegre-Z and Mason, 2005): the  $f_0$  is significantly higher for the PBT (5.1 kHz) than for the FBT (4.3 kHz).

The  $Q$  values calculated here from calling songs and from the PBT stimulated by the 'cog-cricket' system are lower than those reported by Bennet-Clark (Bennet-Clark, 2003) for *T. oceanicus* and by Nocke (Nocke, 1971) for *G. camprestris* ( $>20$ ). Perhaps this has to do with our method of stimulation and with the fact that the tegmina were left attached to the body. Bennet-Clark (Bennet-Clark, 2003) measured  $Q$  values of both tegmina from vibrations induced by piezo-electric actuators; and his method might provide a more accurate measurement of tegminal  $Q$  values because the structures are vibrating freely, unengaged. In our experiments,  $Q$  values measured from pulses produced by the 'cog-cricket' were lower because the PBT was engaged to a file as occurs in actual insect stridulation. Indeed, although  $Q$  values measured from sound recordings were statistically significantly higher (ca. 12.9) than those measured from the pulses produced by the 'cog-cricket' (8.2–10.6), they both can be considered similarly low when compared with  $Q$  values from free tegminal vibration. This suggests that the 'cog-cricket' method provides a reasonable way of tegminal stimulation.

The difference in  $f_0$  observed in crickets between the left and right tegmina [being higher for the PBT (Bennet-Clark, 2003)] might be related to an 'imperfect' phase inverting mechanism in the PBT. For a complete phase shift, one expects a dramatic phase change of 180 deg. between plectrum and resonator. In the present study, changes of only  $\sim 156$  deg. were observed.

Could this subtle asymmetry be a mechanism that ensures both wings though vibrating with slightly different frequencies can be phase-locked? Bennet-Clark (Bennet-Clark, 2003) suggested that the effective vibration frequencies of the two wings during sound production are due to the effect on their own free fundamental natural resonance 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 (added by the one engaging with the other). Therefore, the slight imperceptible asymmetry between the left and right tegmina in crickets (Bennet-Clark, 2003; Simmons and Ritchie, 1996) might not require a perfect phase inverting mechanism in the PBT in order to correct for the difference in  $f_0$  of both tegmina and thus reach an single  $f_c$  value. Additionally, it has been assumed that after a tooth strike the SF on the FBT will make its first vibration toward the higher pressure zone (i.e. 90 deg.) but it might be that this first movement occurs toward a different phase value. Finally, a limitation inherent to our method – the adopted angle of engagement between file and plectrum during 'cog-cricket' stimulation (75–80 deg., Fig. 4C) – might have also produced this incomplete inversion.

#### Plectrum mechanics and phase 'shifting' in other stridulating Ensifera

Katydids, crickets and haglids all share a common ancestor, haglids being the group with the most plesiomorphic conditions (Jost and Shaw, 2006). As crickets, haglids have bilaterally symmetrical tegmina (subtle symmetry might be present) and males produce pure-tone signals for intraspecific communication (Mason, 1996; Morris et al., 2002; Spooner, 1973), therefore, the production of pure-tone signals using bilaterally symmetrical tegmina is probably a plesiomorphic trait of the ancestors of extant Ensifera.

If the function of a phase-inverting mechanism is to phase-lock the vibration of two bilaterally symmetrical tegmina, which are then supposed to oscillate with similar amplitudes at nearly the same frequency, one would expect katydid, in species where their wings are bilaterally asymmetrical, not to require a mechanical phase shifter. Morphological tegminal asymmetry in katydid was presumably a derived feature from a symmetrical ancestor [inferred from Jost and Shaw (Jost and Shaw, 2006)]. But synapomorphically, although the stridulating wings are asymmetrical in katydid, katydid seem to have a mechanical phase shifter in the PBT (see Bailey, 1970) (reviewed by Bennet-Clark, 2003).

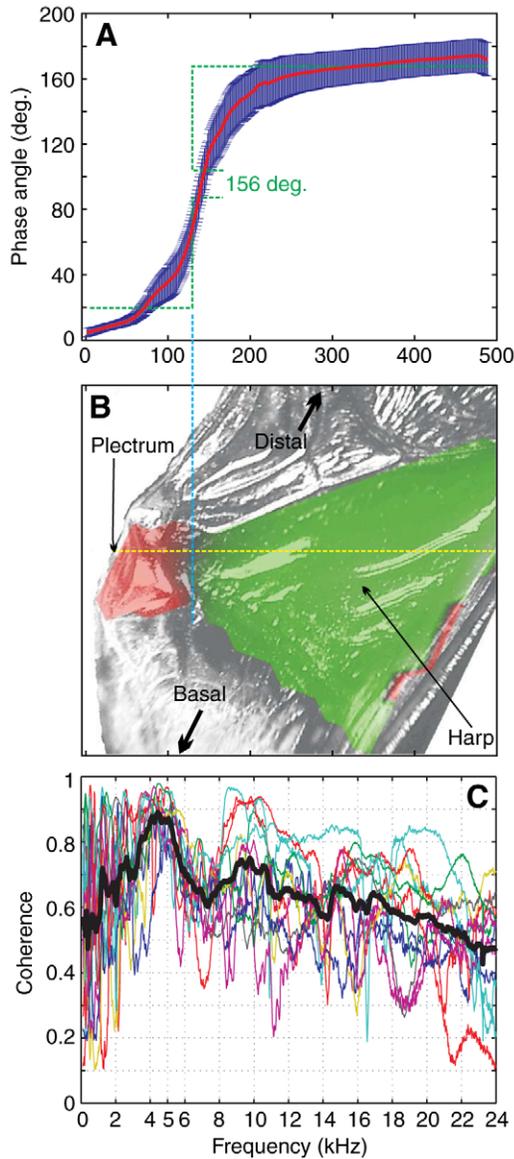


Fig. 12. Phase changes in the plectrum-bearing wing of *G. bimaculatus*. (A) Mean vector (red trace) calculated by combining each of 14 individual vectors using established methods for circular data. Error bars (in blue) represent standard error or mean. Mean phase shift shown by the red line. (B) Capture of the video image of the left tegmen illustrating the phase angle difference between plectrum area (red) and harp (green). Extrapolated vertical blue broken line associates the critical region where the phase shift occurs between data points and morphology. Horizontal yellow broken line shows the region across which phase was measured. (C) Coherence across the frequency range of the plectrum-bearing wing after gear-file stimulation. Black trace shows a mean of 14 specimens (different colours). Note high coherence levels around  $f_c$  (~4.5–5.0 kHz).

This situation leaves open several hypotheses: (1) the fact that some katydid species and crickets both have a phase shifter mechanism in the PBT suggests that either katydids preserve the plesiomorphic phase shifter, derived from a forewing-symmetrical ancestor, which is no longer used during their modern stridulatory behaviour; or (2) that the top-lying tegmen is not totally mute (as opposed to Bennet-Clark's (Bennet-Clark, 2003) and Bailey's (Bailey, 1970) conclusions.

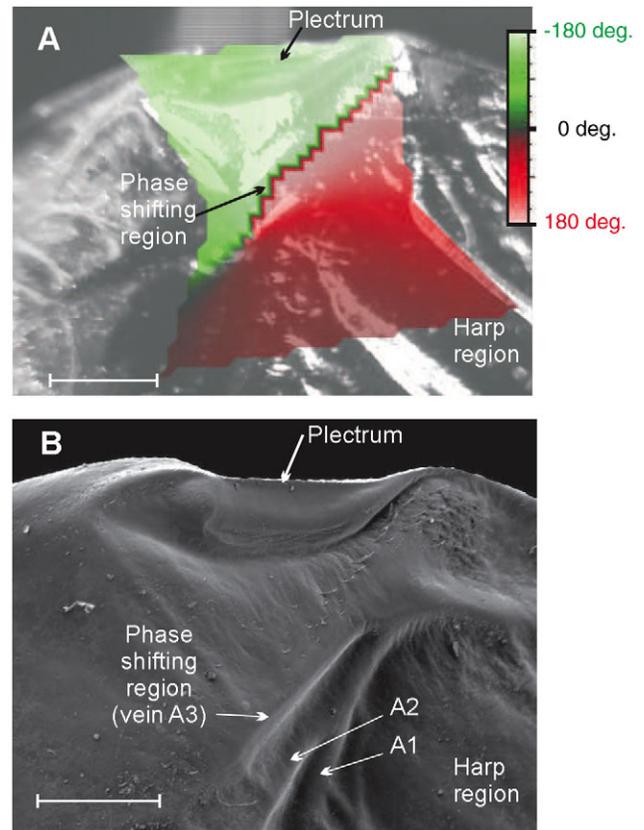


Fig. 13. The mechanical phase shifter in the plectrum of *G. bimaculatus*. (A) High resolution scan showing the critical area where the phase shift occurs. Red indicates positive phases (outward deflections) and green indicates negative phases (inward deflections). (B) SEM of the plectrum area shown in A, highlighting the critical region: a rigid vein (possibly Anal vein 3 serves as a mechanical phase shifter of the vibrations travelling from the plectrum to the harp. Scale bars, 0.5 mm.

Significant differences between the amplitude responses of both tegmina (free vibration) to sympathetic vibration in the katydid *Panacanthus pallicornis* have previously been reported (Montealegre-Z., 2005). The PBT is ca. 55% higher than the FBT. Therefore, the FBT is not totally silent. This suggests (at least in *P. pallicornis*) that the PBT plays most of the role (in terms of intensity) during sound radiation but also implies that a phase-lock mechanism might still be required to maintain the proper phase of vibration between both tegmina and thus consequent sound purity.

**Conclusion and future direction**

Crickets using an escapement mechanism employ an elaborate mechanical phase shifter to change the phase with which vibration at the plectrum region reaches the rest of the PBT. This phase shifter is necessary to phase-lock the vibration of the left and right tegmina. The mechanism is more complex than expected because it has to allow for quick mechanical identification of the FBT phase shifts (produced by the tooth impacts at different regions on a flexible file) and account for these as well.

Whereas the PBT maintains a constant input phase during a single file sweep, the FBT exhibits a different situation. The plectrum moves along the file of the FBT adding mechanical energy at successive points as it changes position. If a particular location in the main resonating region of the FBT is chosen arbitrarily, it will be seen that

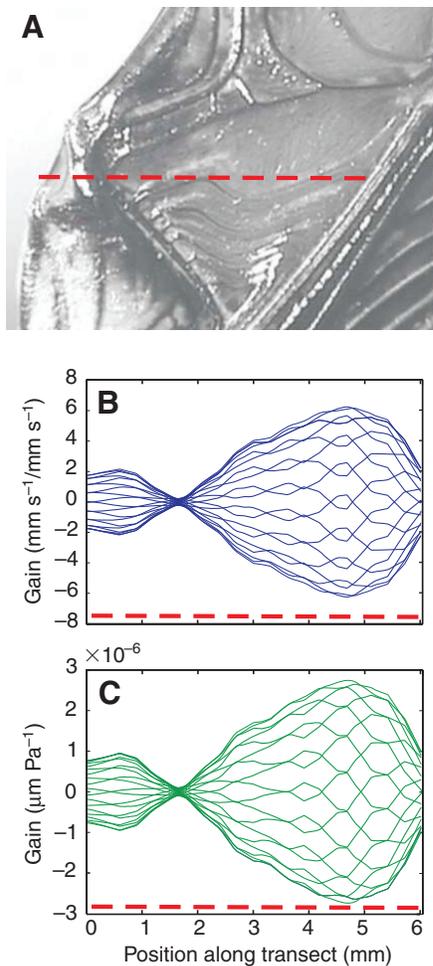


Fig. 14. Envelopes of mechanical deflections across plectrum and harp membranes in a specimen of *G. bimaculatus* along indicated transect (broken red line). The plectrum was stimulated with the 'cog-cricket' system at a rate of  $4.8 \text{ teeth s}^{-1}$ . (A) The position along the transect lines is given with a calibrated scale (broken line, 6 mm). This scale corresponds to the x axis in B and C. (B) Deflection envelopes constructed by displaying the instantaneous deflection velocities along the transect for a series of phases (in  $20 \text{ deg.}$  increments) along the full oscillation; the laser displacement relates to sound velocity. (C) Same as B but the cycle reference used was the Brüel & Kjaer condenser microphone, laser displacement relating to sound pressure.

the energy input arising with each tooth must travel different distances (along different lines of transmission) to reach that particular locus. In other words, the point of energy input for the file-bearing wing will change continually as the plectrum moves. For energy travelling variable distances to reach and set into vibration any selected area, the times of energy arrivals must also vary and presumably so will the phases of oscillations at that particular region.

If, instead of visualising a single locus, one considers all possible resonating regions of the FBT, an even more complex situation arises. The FBT will experience phase changes as the plectrum continuously moves along the file and successively strikes teeth at different file regions. While the PBT exhibits a constant phase of vibration due to a constant energy input, the FBT will experience changing phases due to a continuously changing tooth-strike region. If this is the situation, how is it that the sequential phase changes in the FBT do not seem to affect the output song produced by most

species of crickets, this being usually a precise coherent (simple sinusoidal) pulse? Answers to this question might help to understand why most katydids, using higher frequencies than crickets, evolved the conspicuous directional asymmetry of their tegmina and why crickets cannot maintain the song purity at tooth strikes rates above the normal range used by most species ( $2\text{--}8 \text{ kHz}$ ).

#### LIST OF ABBREVIATIONS

A3	third anal vein
FBT	file bearing-tegmen
$f_c$	carrier frequency, the most energetic spectral frequency
FFT	fast Fourier transform
$f_o$	the resonant frequency of an oscillator
PBT	plectrum-bearing tegmen
$Q$	quality factor
SF	stridulatory file

#### GLOSSARY

File bearing-tegmen	in crickets, it is typically the right tegmen, in katydids it is typically the left. See also definition of 'functional file.'
Functional file/ functional plectrum	the term functional refers to the stridulatory file and/or plectrum used during stridulation in those species that possess bilaterally symmetrical tegmina (i.e. that have a plectrum and a file in both wings) but that have lateral (left or right) tendency of wing overlapping, so only one plectrum and one file is used.
Glissando	frequency modulation, or the gradual fall of instantaneous frequency within the song pulses produced during the calling songs of most crickets.
Higher pressure zone	the peak of maximum amplitude of a sinusoid when a phase of $90 \text{ deg.}$ is reached. Lower pressure zone will then be the lower peak at $270 \text{ deg.}$
Plectrum-bearing tegmen	in crickets the left tegmen, in katydids the right one. See also definition of 'functional plectrum'.
Poisson's ratio	the ratio of transverse contraction strain to longitudinal extension strain in the direction of stretching force.
Pulse envelope	the shape traced out by amplitude maxima in the time domain reflecting a sound's onset, run and decay (final part).
Quality factor	it measures a resonant system's internal-to-external damping and also the rate at which such a system reaches maximum amplitude or decays (Prestwich and O'Sullivan, 2005).
Stridulatory file	a modified vein (believed to be the anal vein A1) of the tegmina of acoustic Orthoptera, Ensifera.
Tegmen (pl. tegmina)	the modified leathery mesothoracic forewings of an insect. In crickets and katydids, both tegmina exhibit remarkable adaptations for song production.
Torsional $f_o$	a torsional vibration frequency is an oscillation of angular position about a centerline and is caused by oscillating torque forces. Therefore, torsional resonant frequency is the angular natural vibration of the system around this centerline.

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