

# Ticking of the clockwork cricket: the role of the escapement mechanism

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## Summary

The ‘clockwork cricket’ model for cricket sound production suggests that the catch-and-release of the file of one forewing by the plectrum on the opposite wing act as an ‘escapement’ to provide the phasic impulses that initiate and sustain the vibration of the resonant regions of the wings from which the sounds are produced. The action of the escapement produces the familiar ticking sound of clocks.

The higher-frequency components of the songs of twelve species of cricket were analysed after removing the dominant low-frequency components and amplifying the remaining higher-frequency components. In normal song pulses of all species, the higher-frequency components showed a close phase-locking to the waveform of the dominant frequency, but the amplitude of the higher-

frequency components did not correlate with that at the dominant frequency.

Anomalous pulses occurred spontaneously in the songs of several species: multimodal, interrupted or curtailed pulses are described. In all of these, the anomalous pulse envelope was associated with changes in the amplitude and/or instantaneous frequency of the higher-frequency components of the sound.

A model of the escapement suggests that the frequency of the residual components of the song depends on the symmetry of action of the plectrum on the teeth of the file.

Key words: cricket, Gryllidae, sound production, escapement, file and plectrum, high-frequency sound, resonator.

## Introduction

The ticking sound of a mechanical clock is produced by the action of the escapement as it delivers power to sustain the vibration of the pendulum. An escapement, in the context of time-keeping, has been defined as a mechanism ‘which intervenes between the motive power and regulator, and which alternately checks and releases the (*gear*) train, thus causing an intermittent impulse to be given to the regulator’ (Onions, 1933). Parallels between the mechanisms involved in cricket sound production and clocks were highlighted by Elliott and Koch (1985) in their work entitled ‘The clockwork cricket’.

The forewings of male crickets (Orthoptera: Ensifera: Grylloidea) are specialised for sound production: the underside of one wing bears a row of hooked teeth, which engage a blade-like plectrum at the posterior edge of the opposing wing. Sound is produced during the closing of the raised forewings. The opening stroke is usually silent because the plectrum does not engage the file teeth. In the action of this ‘escapement’ during the sound-producing closing stroke, each cycle of catch-and-release of a file tooth corresponds with a single cycle of the song waveform (Pierce, 1948; Pasquinely and Busnel, 1955; Koch et al., 1988) (for reviews, see Bennet-Clark, 1989, 1999).

Using miniature detectors to record relative wing angle, Koch (1980) showed that small steps were superimposed on the wing-closing movement in *Gryllus campestris* and that

each step corresponded with one cycle of sound within the song pulse. If a number of file teeth were removed, the wing-closing accelerated across the gap and then resumed at the original rate when the plectrum encountered further file teeth (Elliott and Koch, 1985; Koch et al., 1988). This synchronous and controlled stepwise wing-closing led them to propose their ‘clockwork cricket’ model in which they likened the catch-and-release of the file teeth to the action of the escapement of a mechanical clock or watch. Implicit in this model are, first, that there should be an escapement as defined above and, second, a ‘regulator’ which, by its oscillation, determines the successive times at which the impulses are delivered by the ‘train’ or mechanism through which the mechanical power is supplied. The regulator in a clock may be the pendulum or in a watch the balance wheel and hairspring.

In crickets, the harp region on each forewing (Fig. 1), which is surrounded distally by the cubitus 1 (Cu1) vein and proximally by the file-bearing cubitus 2 (Cu2) vein, and also is connected to the plectrum at the anal node on the contralateral forewing (Ragge, 1955), has been shown to resonate at frequencies similar to those of the cricket’s song (Nocke, 1971; Bennet-Clark, 1987). In the ‘clockwork cricket’ model, the file-and-plectrum escapement gives impulse to the harp through the file, after which the plectrum is released by a

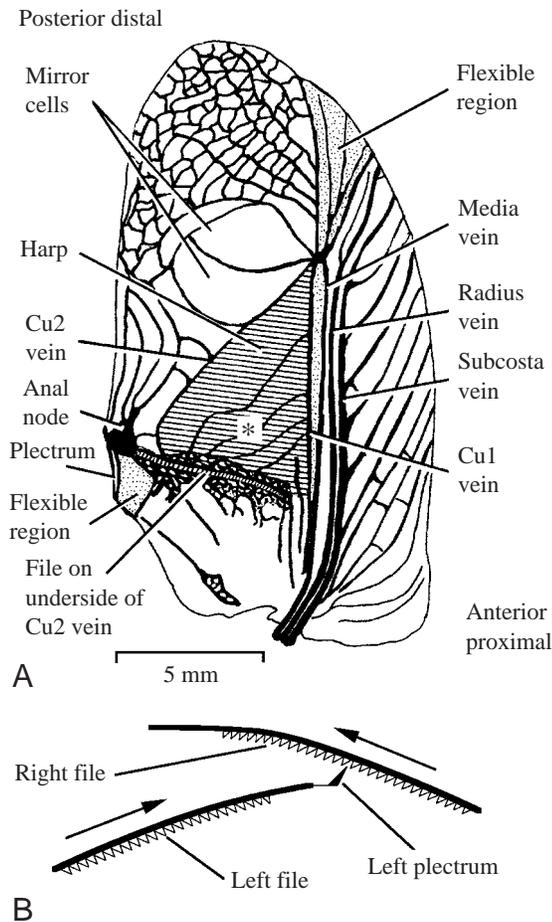


Fig. 1. (A) Drawing of the underside of the right forewing of a male *Gryllus campestris*. The harp, shown hatched, is a resonant plate that is set into vibration by the interaction during wing-closing between the file on the cubitus 2 (Cu2) vein and the contralateral plectrum. The position of the maximal amplitude of vibration of the harp, as reported by Nocke (1971) and from personal observation, is shown by an asterisk. The nomenclature of the veins follows Ragge (1955). Note the flexible regions that separate the plectrum from the file and cubitus 1 (Cu1) vein from the media vein. (B) Diagram of a section of both forewings of a typical gryllid showing the interaction between the file and plectrum during the sound-producing wing-closing stroke. The arrows show the directions in which the two wings move.

file tooth. This 'intermittent impulse' appears to cause an upward buckling of both harps (Bennet-Clark, 1970, 1989, 1999). The frequency produced by the 'clock' escapement, or in cricket terms the release of the plectrum by successive file teeth, depends on the frequency of oscillation of the 'regulator'. In this regard, Elliott and Koch (1985) demonstrated that adding to the mass of the harp reduced the speed of action of the file-and-plectrum escapement, thereby further implicating the harp as the 'regulator' and major determinant of the song frequency.

In common with certain types of clock escapement, the system was able to run either at the normal rate of one tooth per cycle of sound or at twice this rate. Further, if the harps

were destroyed, the speed of wing-closing tended to be far faster and the 'escapement' appeared to run erratically (Koch et al., 1988). The same effect would be observed after the removal of the pendulum of a clock.

The escapement in a clock, after release, moves silently then hits and captures the next tooth of the escapement, making the 'tick' sound. Analysis of these sounds may be used to diagnose faults and to monitor the accuracy of the escapement mechanism (de Carle, 1964). By analogy with a clock, the sounds made by the 'clockwork cricket' should have two components: first, the sound made by the oscillation of the regulator, believed to be the harp and, second, the ticking sound made by the escapement, believed to be the file and plectrum. In nature, the file and plectrum are likely to have irregularities, and from the 'faults' in their action one may learn how the system depends on the regular action of the file and plectrum to maintain the pulse structure of the song.

If the 'clockwork cricket' model is valid, it should be possible to analyse the 'ticking' sounds made by the 'escapement' and examine the relationship between them and the dominant sounds produced by the harp 'regulator' when driven by the escapement. Elliott and Koch's 'clockwork cricket' simplified our understanding of cricket musical songs, but it told us little about how the mechanism starts, runs and stops. We extend their ideas by analysing how the mechanism initiates and sustains the pulse structure of the song of crickets, molecrickets and bushcrickets. Elliott and Koch (1985) and Koch et al. (1988) did not consider the consistent decrease in frequency that occurs during the song pulse of many species of cricket. This effectively produces a glissando (Leroy, 1966; Simmons and Ritchie, 1996; Bennet-Clark, 1999) (all three with crickets) (Bailey and Broughton, 1970) (with a bushcricket). The present paper reports the results of such analyses.

## Materials and methods

### *Cricket wings and song analysis*

The wings of various ensiferan species were examined during the course of this and previous work on cricket sound production; these species are listed in Table 1. We have included the musical calls of the Australian bushcricket *Tympanophora similis* as this affords an example of a nearly pure tone song that has evolved independently of the Gryllidae and Gryllotalpidae. This tettigoniid species appears to have achieved the same task as many musical crickets using a similar clock mechanism. Within the crickets (*sensu lato*), we have included three species in which sound production depends both on the action of the wings and on an 'acoustic' burrow: the European *Gryllotalpa gryllotalpa*, the North American *Scapteriscus acletus* and an undescribed species of burrowing cricket from Australia *Rufoccephalus* sp. (Bailey et al., 2001).

Recordings of the songs of the European crickets used in this study were obtained from a compact disc published by Ragge and Reynolds (1998a) which contained representative songs of more than 10 cricket species. The songs had been recorded

Table 1. *The crickets and bushcricket studied and the characteristics of their songs*

Species	Family and distribution	Wings studied	Type of song	Dominant song frequency, $F_D$ (kHz)	Fall in $F_D$ during pulse (kHz)	Percentage change in $F_D$
<i>Gryllus campestris</i> L.	Gryllidae, Europe	+	Three- to four-pulse chirp	5	0.5	10
<i>Gryllus bimaculatus</i> de Geer	Gryllidae, Europe	+	Three- to five-pulse chirp	4.7	0.5	10.6
<i>Modicogryllus bordigalensis</i> (Latreille)	Gryllidae, Europe		Short trills	5	0.8	16
<i>Acheta domestica</i> (L)	Gryllidae, Europe		Two- to three-pulse chirp	4.5	0.6	13
<i>Nemobius sylvestris</i> (Bosc)	Gryllidae, Europe		Variable short trills	4	0.4	10
<i>Eugryllodes pipiens</i> (Dufour)	Gryllidae, Europe		Single pulses and trills	3.2	0.15	4.7
<i>Oecanthus pellucens</i> (Fischer)	Oecanthidae, Europe		Regular trills	3	0.4	13
<i>Gryllotalpa gryllotalpa</i> (L)	Gryllotalpidae, Europe	+	Long trill	1.7	<0.1	<6
<i>Gryllotalpa vineae</i> Bennet-Clark	Gryllotalpidae, Europe	+	Long trill	3.4	0.2	6
<i>Scapteriscus acletus</i> Rehn & Hebard	Gryllotalpidae, N. America	+	Long trill	2.7	0.2	7.5
<i>Rufoccephalus</i> sp.	Gryllidae, Australia		Variable trills	3.2	0–0.05	0–1.6
<i>Tympanophora similis</i> Reik	Tettigoniidae, Australia		Variable chirps	6.5	0.5	7.7

using high-quality microphones with a bandwidth from 800 Hz to over 15 kHz on either Uher Report or Nagra IV reel-to-reel tape recorders (Ragge and Reynolds, 1998b). For each of the European species (Table 1), a 5 s section of the recordings was re-recorded at 44.1 kilosamples  $s^{-1}$  onto an Apple Macintosh Powerbook 3400c. Songs of the small burrowing Australian cricket (Bailey et al., 2001) *Rufoccephalus* sp. were recorded by us in the field using a Tandy tie-clip microphone (Catalogue No. 33-1052) with a measured frequency response of  $\pm 2$  dB between 1 and 20 kHz into one channel of a Sony TCD-D8 digital audio tape recorder and recorded at 12 dB below peak level. The measured signal-to-noise ratio of all these recordings was greater than 45 dB. The tettigoniid *Tympanophora similis* was recorded in the field using a Bruel and Kjaer microphone (type 4133) onto a Racal reel-to-reel recorder at 76  $cm s^{-1}$ , giving an overall bandwidth from below 100 Hz to 40 kHz, and played back at 19  $cm s^{-1}$  to lower the frequency of all components by a factor of four.

Because the bandwidth of all the recording apparatus extends far beyond the highest frequencies that have been analysed, we have assumed that the relative phase of all sound components has not been greatly altered by the recording processes.

#### *Analysis of cricket songs*

Analyses were made either of the broad-band song waveforms or of the same signals after filtering out the dominant frequency, leaving the higher-frequency components due to the file and plectrum. Compact disc or tape recordings were re-recorded onto an Apple Macintosh Powerbook 3400c using Canary 1.2.1 software at 44.1 kilosamples  $s^{-1}$ . Recordings were initially filtered by the Canary software to remove direct-current and low-frequency components below 500 Hz. Additional software filtering was applied to remove

components around the dominant frequency; for this, the filter frequency was set half-way between the wanted and unwanted frequencies; in other words, if a 5 kHz peak were to be excluded while retaining a 10 kHz harmonic, all frequencies below 7.5 kHz were filtered out. The filtering built into the Canary software acts after computation of the spectrum and introduces filtration artefacts at the lower frequency of the chosen pass band: these artefacts appear as an oscillatory build-up at the start and an oscillatory decay at the end of the filtered signal; the frequency of these oscillations is close to the filter cut-off frequency, but their maximum amplitude is approximately one-third that of the signal and these artefacts are easily distinguished from the signal (for an example, see Fig. 2B). After filtering out the dominant frequency, the signal-to-noise ratio of the remaining higher-frequency components was always above 20 dB.

The cycle-by-cycle frequency of signals was measured by zero-crossing analysis using ZeroCrossing v.3 software written by K. N. Prestwich for use with the Canary software. ZeroCrossing v.3 was tested with both sinusoidal and asymmetric waveforms generated by a Tektronix FG 501A function generator gated to produce tone bursts by pulses from a Digitimer DS9A stimulator. Pure sinusoidal signals were resolved to less than  $\pm 1.5$  Hz below 1 kHz, rising to  $\pm 20$  Hz at 6 kHz and  $\pm 200$  Hz at 10 kHz. Because direct-current components introduced errors, all measurements of cycle-by-cycle frequency were made after filtering out components below 500 Hz from the song recordings. Noise in the signals introduced errors in the measurement of frequency, so results from waveforms with signal-to-noise ratios below 20 dB were viewed with caution. However, because frequency was measured as the reciprocal of the average period of both half-cycles of the waveform, the measurements were less sensitive to harmonic distortion (Fig. 2). To compare the relationship of

cycle-by-cycle frequency between broad-band and without- $F_D$  signals (the song pulse after filtering out the peak at the dominant frequency  $F_D$  of the song pulse is termed the without- $F_D$  waveform), the abscissa of the broad-band frequency has been placed at the left of these graphs while that for the without- $F_D$  frequency is to the right and at twice the scale range.

Because song recordings and analyses were made at a sampling rate of 44.1 kilosamples  $s^{-1}$ , the harmonics of 5 kHz songs were only defined by four (second harmonic) and fewer than three (third harmonic) data points per cycle. In all the songs analysed here, the peak amplitude of the second harmonic was 3.5–8 times that of the third harmonic, so the major effect of sampling errors is seen in the phasing of the second harmonic relative to the broad-band waveform. This sampling error is equivalent to a phasing error between the broad-band signal and its second harmonic of  $\pm 20^\circ$  at the 5 kHz dominant frequency.

### Terminology

The rate of decay at the end of sound pulses was measured and, where this was exponential, it was assumed that this represented the free decay of a resonant system. The sharpness of the resonance is quoted as the  $Q$  (or quality factor), given by  $\pi/\ln(\text{decrement of the exponential decay})$  (Morse, 1948).

When describing sinusoidal oscillations from peak to trough, we describe the upward-going mean point as  $0^\circ$ , the peak as  $90^\circ$ , the downward-going mean point as  $180^\circ$  and the trough or minimum as  $270^\circ$  (Fig. 2 inset). The dominant frequency found in a song pulse is termed  $F_D$ ; in the songs analysed here, this frequency tends to change during the pulse. Song components at multiples of this frequency are treated as if they were harmonics and are termed the second harmonic, third harmonic, etc. The frequency within a pulse measured by zero crossing analysis is termed the cycle-by-cycle frequency.

We show oscillograms of the unfiltered song pulse (termed broad-band waveform) and of the song pulse after filtering out the peak at the dominant frequency of the song (termed without- $F_D$  waveform). Because the higher-frequency waveforms were usually small in amplitude, oscillograms of these were amplified relative to the unfiltered broad-band waveforms; the amplification of the without- $F_D$  waveform relative to that of the broad-band waveform is shown in the figures and indicated in the figure legends.

## Results

### Mechanics of cricket wings

The harp of each wing resonates at a frequency close to that of the insect's song (Nocke, 1971; Bennet-Clark, 1987), but the resonant frequency of the left wing is usually somewhat higher than that of the right wing (Nocke, 1971; Simmons and

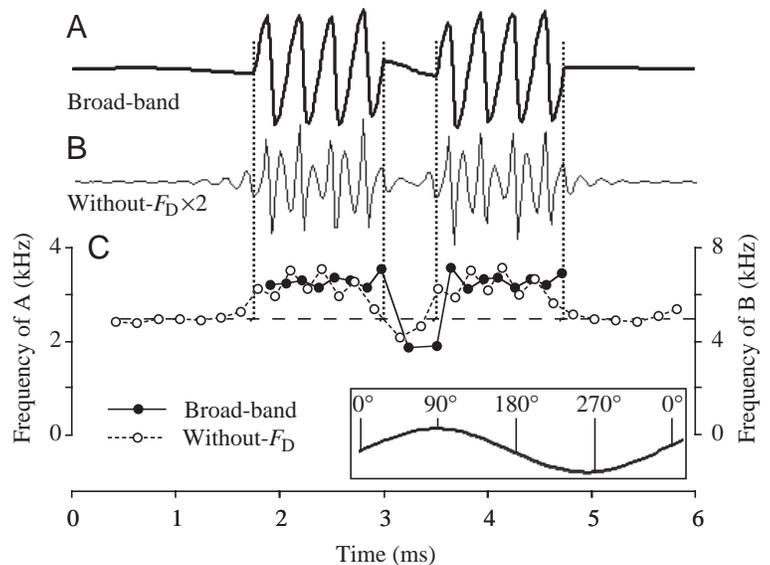


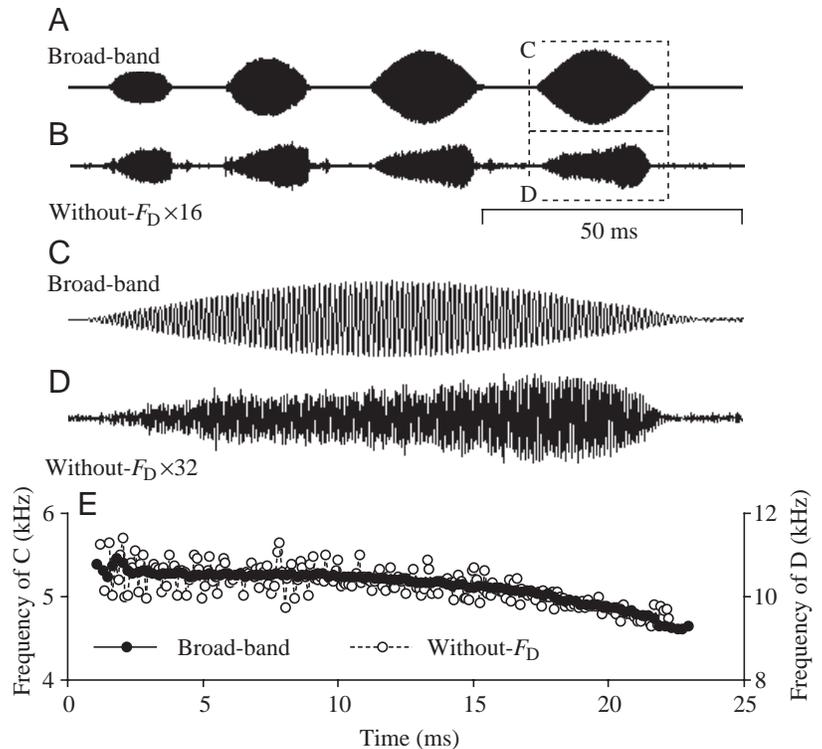
Fig. 2. (A) Oscillogram of two 3.2 kHz tone bursts, each of four cycles duration. An asymmetric waveform was generated so as to introduce second and third harmonic distortion. (B) Oscillogram to show the effect of electronic filtering by Canary software on the waveform shown in A. Frequencies below 5 kHz were filtered out; an oscillation at this frequency built up before the start of the broad-band waveform and decayed after it had ended. The vertical dotted lines show the beginnings and ends of the two four-cycle tone bursts used as a test signal. (C) Graphs of the cycle-by-cycle frequency of the waveforms in A and B plotted by zero-crossing analysis. The frequencies remained approximately constant within the tone bursts but that of the broad-band waveform fell during the gap between the first and second tone bursts (left-hand scale and filled circles). The frequency of the without- $F_D$  waveform (the song pulse after filtering out the peak at the dominant frequency  $F_D$  of the song pulse) was approximately twice that of the broad-band waveform within the tone bursts (right-hand scale and open circles). Before and after the tone bursts, the plot shows the 5 kHz frequency at which the signal was filtered. The inset shows the convention used to define the phase of a sine wave.

Ritchie, 1996). The closing movement of the file against the plectrum is driven from the wing base along the strong subcosta (Sc), radius (R) and media (M) veins and then, *via* a cross-vein traversing a region of flexible cuticle, to the tip of the cubitus 1 vein at the distal apex of the harp (Fig. 1). In *Gryllotalpa vineae*, the posterior region of the wing, bearing the file and plectrum, is thus flexibly coupled to the driving Sc, R and M veins (Bennet-Clark, 1970). We presume that a similar system holds true for other gryllids, although perhaps not for *Tympanophora similis*. The plectrum is separated from the rest of the wing by an area of flexible cuticle (Fig. 1). Hence, we assume that, when the edge of the plectrum is pushed towards the anterior edge of the wing, it buckles in the plane of the wing and also twists along its length. Similarly, when the plectrum is pushed against a file tooth, the file buckles upwards and releases the plectrum (Fig. 1B).

### Analyses of normal cricket songs

The normal song of *Gryllus campestris* consists of a series of chirps, each containing 3–4 pulses of increasing amplitude

Fig. 3. The normal song of *Gryllus campestris*. (A) Oscillogram of a chirp consisting of four pulses of increasing duration and amplitude. (B) Oscillogram of the chirp shown in A after filtering to remove frequencies below 7.5 kHz; this waveform has been amplified 16-fold relative to that in A. A and B use the same time scale. (C) Oscillogram of the fourth pulse of the chirp shown in A on an expanded time scale. (D) Oscillogram of the fourth pulse shown in B after filtering to remove frequencies below 7.5 kHz; this waveform has been amplified 32-fold relative to that shown in (C). (E) Plot of the cycle-by-cycle frequencies of the broad-band waveform shown in C (filled circles) and of the without- $F_D$  (the song pulse after filtering out the peak at the dominant frequency  $F_D$  of the song pulse) waveform shown in D (open circles). The frequency scale for the broad-band waveform is on the left and that for the without- $F_D$  waveform is on the right. C, D and E use the same time scale.



and duration. An example of a four-pulse chirp is shown in Fig. 3A,B, where the upper trace is that of the broad-band signal while the lower trace is the signal with the dominant frequency removed (without- $F_D$ ). Comparing successive pulses, it can be seen that the amplitude of the without- $F_D$  waveform reaches a similar peak value (the difference is less than 2 dB) in every pulse, despite a twofold increase in peak amplitude of the broad-band waveform between pulse 1 and pulse 4, equivalent to a 6 dB increase (cf. Fig. 3A,B noting that trace B has been amplified 16 times relative to trace A; see legend and above). Also, in all four pulses, the without- $F_D$  waveform built up in the first 5 ms of the pulse, mirroring the amplitude of the broad-band waveform, but, thereafter, the amplitude of the broad-band waveform continued to rise, even though the amplitude of the without- $F_D$  waveform stayed approximately constant (cf. Fig. 3C,D between 5 and 10 ms). As the amplitude of the broad-band waveform started to fall, the amplitude of the without- $F_D$  waveform continued to rise (cf. Fig. 3C,D between 13 and 18 ms).

The frequency of the without- $F_D$  components is close to twice that of the broad-band waveform for the majority of the pulse duration (Fig. 3E). At the end of the pulse, the without- $F_D$  waveform decayed more rapidly than the broad-band waveform.

The time course of the cycle-by-cycle frequency in pulses in successive chirps was closely similar. In Fig. 4B, five consecutive fourth pulses (as in Fig. 4A) from a series of chirps are overlaid; the difference in frequency between the corresponding regions of different pulses is less than 20 Hz over most of the pulse duration, even though the  $F_D$  falls by approximately 500 Hz during every pulse. Differences between

the pulses are greatest at the start and end of the pulses (Fig. 4B, in the first 2 ms and last 4 ms). Similarly, the cycle-by-cycle frequencies of all pulses in a chirp show closely similar time courses: in Fig. 4B, the first pulse of the four-pulse chirp shown in Fig. 3A is overlaid on the plots for five fourth pulses. Because the cycle-by-cycle frequency coincides with that of the fourth pulses after 8 ms, it appears that these short first pulses are started approximately one-third of the distance along the file.

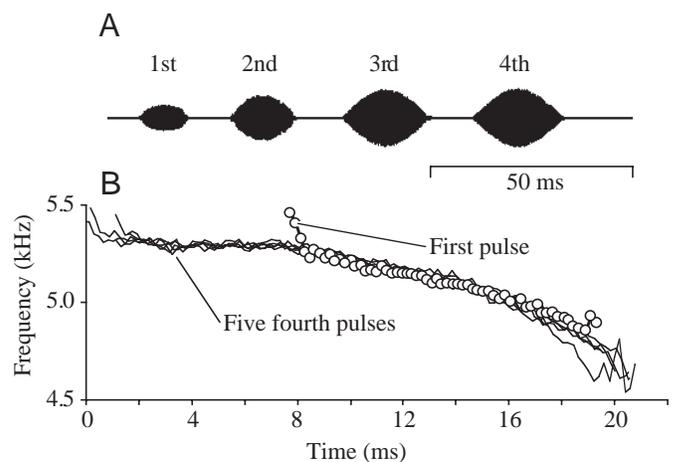
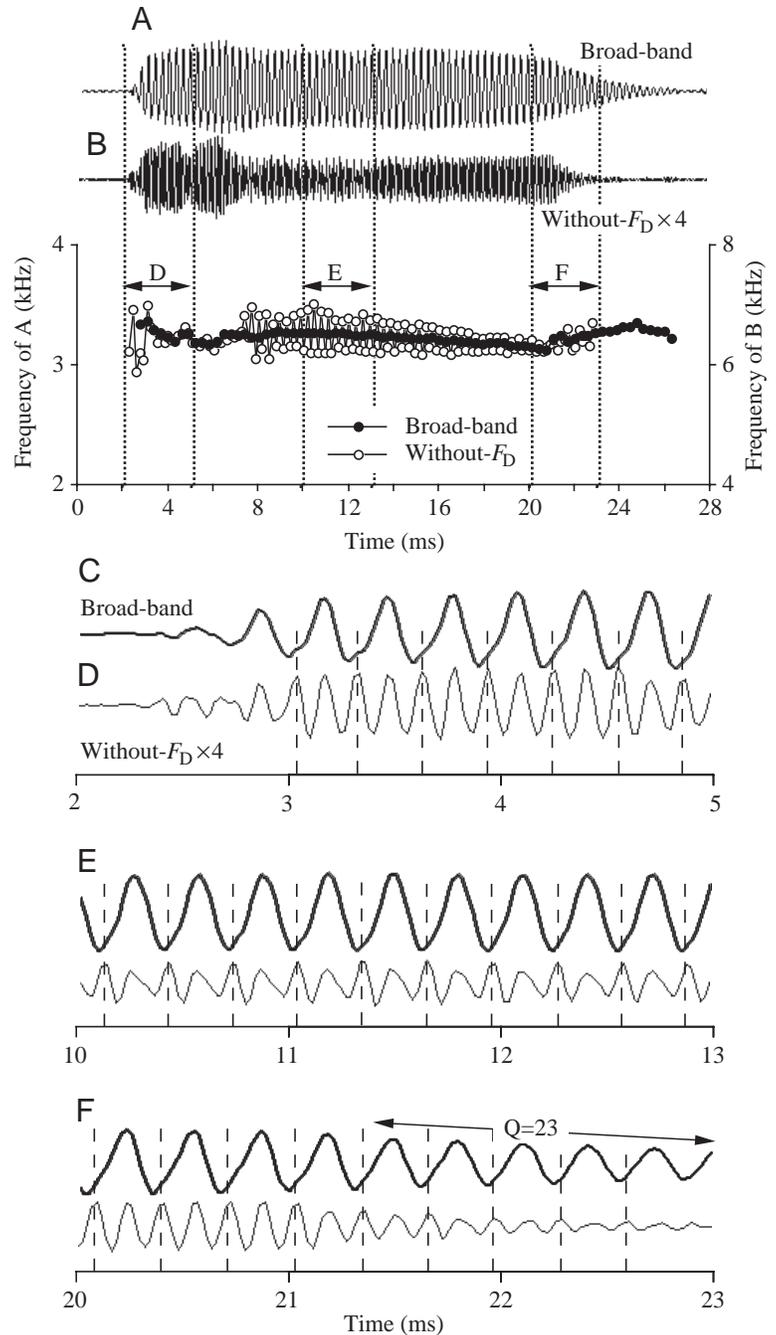


Fig. 4. (A) Oscillogram of the four pulses in a typical chirp of *Gryllus campestris*. (B) Graph of the cycle-by-cycle frequency against time of five consecutive *G. campestris* fourth song pulses to show that they are closely similar (thin lines and no data points). In addition, data for pulse 1 from Fig. 3A are superimposed (thick line and open circles).

Fig. 5. The song of *Eugryllodes pipiens*. (A) Oscillogram of a single normal pulse within a multiple-pulse sequence. (B) Oscillogram of the pulse shown in A after filtering to remove frequencies below 4.5 kHz; this waveform has been amplified fourfold relative to that shown in A. (C) Plot of the cycle-by-cycle frequencies of the broad-band waveform shown in A (filled circles) and the without- $F_D$  waveform (the song pulse after filtering out the peak at the dominant frequency  $F_D$  of the song pulse) shown in B (open circles); the frequency scale for the broad-band waveform is on the left and that for the without- $F_D$  waveform is on the right. A, B and C use the same time scale. D, E and F show 3 ms sections (shown in A, B and C by vertical dotted lines and labels) of the waveforms shown in A and B: D from the start of the pulse, E in the middle of the pulse and F from the end of the pulse. For each, the thick line shows the broad-band waveform and the thin line shows the without- $F_D$  waveform, amplified fourfold relative to the broad-band waveform. The time scales in D–F show the regions of the pulse that have been amplified. The vertical dashed lines in D–F show that the relative phasing of the broad-band and without- $F_D$  waveforms remains nearly constant throughout the pulse. In F, the decay of the pulse after 21.5 ms is close to exponential with a quality factor (Q) of 23.



There are two important aspects to this observation. First, the shape of the envelope over the middle part of the pulse varies only slowly because it is driven in a nearly constant manner by the drive of the plectrum moving across the file. This suggests that the escapement (or file-and-plectrum drive) is providing power to the regulator at the same rate as power is being dissipated as loss from the regulators (or harps). At the start of the pulse, when the plectrum engages and then disengages from the file, the force leads to a tripping of the escapement – rather like the first push of a swing. We infer from this recording that in *G. campestris* there is a slow build-up of the driving force over the entire pulse (Fig. 3D), while in *Eugryllodes pipiens* the initial driving force of the system rises rapidly (Fig. 5B). This is reflected in the steep slope of the initial section of the pulse envelope of both the without- $F_D$  and broad-band waveforms (Fig. 5A,B,D).

Second, the fall in frequency throughout the pulse (Fig. 4B) appears typical of most grylloid species (see Leroy, 1966) and has been observed in the musical songs of the tettigoniid *Ruspolia differens* (Bailey and Broughton, 1970). We have observed a similar glissando effect in all but one of the species examined in this study (Table 1). In field crickets, the frequency falls by 4.7–16% of  $F_D$ ; in mole crickets, the frequency falls by between less than 6 and 7.5% of  $F_D$ , but in the burrowing cricket *Rufoccephalus* sp.,  $F_D$  is almost constant throughout the pulse (Table 1). In the bushcricket *Tympanophora similis*, which has a different sound-producing mechanism, the fall in frequency is 7.7% of  $F_D$ .

We examined the phase relationship between broad-band

and without- $F_D$  waveforms in the song of *Eugryllodes pipiens* (Fig. 5A), which has an  $F_D$  of approximately 3.2 kHz. We used *E. pipiens* for this task because the without- $F_D$  waveform of *E. pipiens* has relatively more power than the without- $F_D$  waveform of *G. campestris* (note that the without- $F_D$  waveform is amplified only four times compared with 16 times in *G. campestris*; cf. Fig. 3A,B and Fig. 5A,B). Further, examining the relative phase of these two components is easier with a lower-frequency song: 3.2 kHz compared with 5 kHz for *G. campestris* (Table 1) (see *Analysis of cricket songs*).

As in the song of *G. campestris*, the dominant frequency of the without- $F_D$  components in the song of *E. pipiens* is close

to twice the  $F_D$  (Fig. 5C) and, at the start of the pulse, both the broad-band and the without- $F_D$  waveforms build up rapidly and their relative amplitudes are closely similar (Fig. 5D). As in the song of *G. campestris*, the without- $F_D$  and broad-band waveforms are phase-locked for the majority of the duration of the pulse (Fig. 5D–F). In the song of *E. pipiens*, the amplitude of the without- $F_D$  components is large enough to cause considerable distortion of the broad-band waveform (Fig. 5D,E).

Towards the middle of the pulse, the character of the without- $F_D$  waveform changes from a regular sine wave (Fig. 5D) at twice  $F_D$  to an irregular waveform of lower relative amplitude that alternates between above and below twice  $F_D$  (Fig. 5E). In a clock with a regular tick, the tick sound occurs at a constant phase of the oscillation of the pendulum or regulator. The phase relationship between the broad-band and without- $F_D$  waveforms of *E. pipiens* suggests that the broad-band waveform is close to one extreme of its oscillation (in the furthest downward-going parts or at  $270^\circ$  in the cycles shown in Fig. 5D) when the without- $F_D$  waveform shows upward-going maxima at  $90^\circ$  (vertical dashed lines in Fig. 5D). The irregularity in the middle section of the without- $F_D$  waveform of *E. pipiens* (Fig. 5E) shows that the first, shorter-wavelength or higher-frequency peaks occur close to  $270^\circ$  on the broad-band waveform and that the second, lower frequency peaks occur close to  $90^\circ$  on the broad-band waveform. This suggests that, with regard to the broad-band waveform,  $90^\circ$  is close to the driving point of the system by the escapement.

The last part of the broad-band waveform pulse of *E. pipiens*, after 22 ms, shows an extended and exponential decay with a Q of 23 (Fig. 5F). At this stage, the driving without- $F_D$  waveform has effectively disappeared. The broad-band waveform represents the exponential decay of the oscillation of the regulator at its natural frequency, either after the escapement has disengaged or when the driving force has ceased. The wing of *Gryllus campestris* has a characteristic natural vibration frequency, and its free oscillation has been shown to decay in a similar exponential manner with a similar Q (Nocke, 1971).

Similar observations have been made in five other chirps or pulses for *Gryllus campestris* and *Eugryllodes pipiens*, as well as for song pulses of *Gryllus bimaculatus*, *Acheta domestica*, *Rufoccephalus* sp., *Oecanthus pellucens* among the Grylloidea and for *Tympanophora similis* among the Tettigoniodea. Although the pattern was similar in all species, there was considerable variation in the relative amplitudes of the broad-band and without- $F_D$  waveforms: in *E. pipiens*, the amplitude of the without- $F_D$  waveform was approximately 0.1–0.2 times that of the broad-band waveform, but in *G. campestris* and *Rufoccephalus* sp. the without- $F_D$  waveforms were far less intense, at between 0.1 and 0.03 times those of the broad-band waveforms (Fig. 3C,D).

The components of normal cricket song pulses can be summarised as follows. At the start of a pulse, the amplitude builds up; the amplitude of the without- $F_D$  components is

relatively large and the  $F_D$  may vary rapidly. In the middle of the pulse, the broad-band amplitude varies slowly, and the without- $F_D$  components may have an asymmetrical waveform that is closely phase-locked to that of the broad-band components. At the end of the pulse, the relative amplitude of the without- $F_D$  components may increase and then decay rapidly, after which the amplitude of the broad-band waveform decays at a slower rate, often exponentially. The lack of a consistent correlation between the amplitudes of the broad-band and without- $F_D$  waveforms is strong evidence that the without- $F_D$  waveform cannot be a simple or constant-level harmonic distortion of the broad-band waveform. Such an observation is crucial to the development of the hypothesis that the without- $F_D$  waveform reflects the *modus operandi* of the escapement; the system makes sounds both as the plectrum engages and then as it disengages from each tooth of the file.

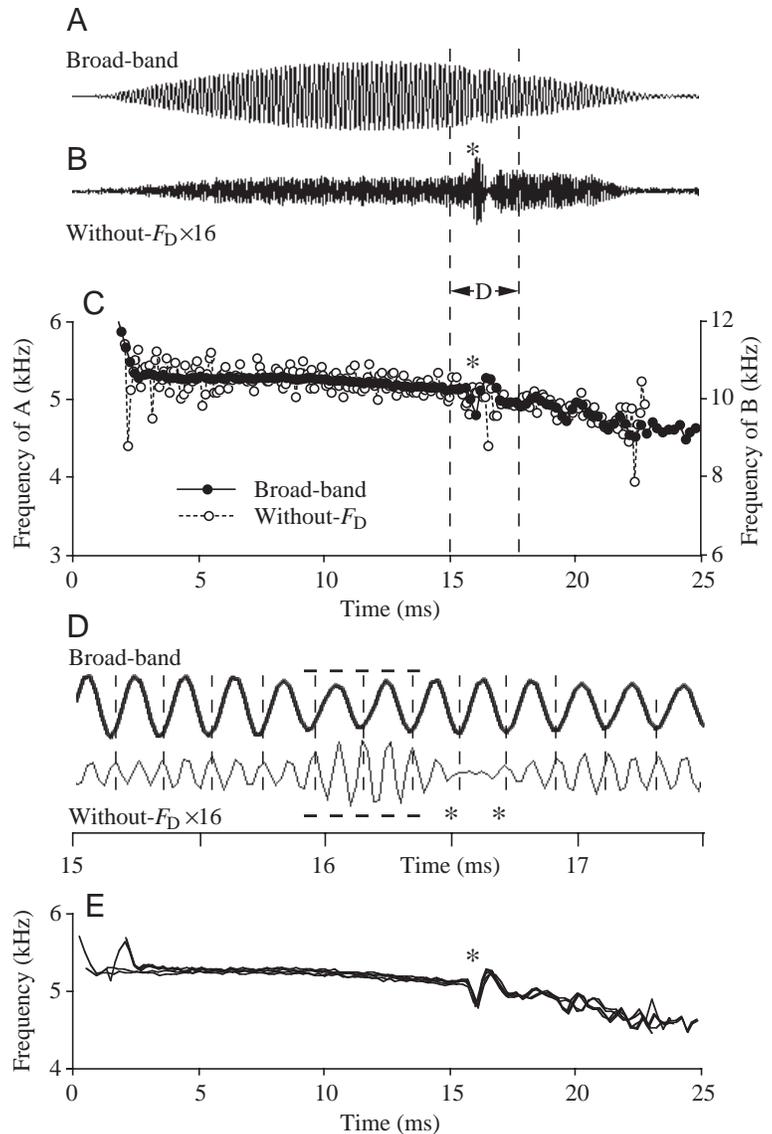
#### Anomalous cricket song pulses

The structure of the songs of some individual insects and the pulses within otherwise normal songs occasionally differed from the normal pattern described above. Within these songs, some pulses were bimodal or multimodal, others showed rapid amplitude modulation within the pulse and yet others were of anomalous duration.

For example, 10 out of 24 fourth song pulses of *Gryllus campestris* showed irregularities during the course of pulses that had an otherwise smooth envelope. An example is shown in Fig. 6A. For the first two-thirds of the pulse, the waveforms of both the broad-band and without- $F_D$  components and their relative phase were all closely similar to those within the normal pulse shown in Fig. 3; the cycle-by-cycle frequency of the broad-band waveform closely tracked that of the without- $F_D$  components (Fig. 6C). However, between 15.8 and 16.8 ms (Fig. 6D), there was an abrupt increase in the amplitude of the without- $F_D$  components associated with a decrease in the amplitude of the broad-band waveform (Fig. 6A) and an irregularity in the cycle-by-cycle frequency (Fig. 6C). Following the increase in amplitude of the without- $F_D$  waveform at 16 ms, there was a period from 16.5 to 16.7 ms in which the without- $F_D$  component almost disappeared (between the asterisks in Fig. 6E), after which it built up to its earlier level and with the same phase as in the earlier parts of the pulse (vertical dashed lines in Fig. 6D). Irregularities of this type have also been seen in individual song pulses of *Gryllotalpa gryllotalpa*, *Rufoccephalus* sp. and *Nemobius sylvestris* with similar effects on the structure of both the waveforms and their phase relationships.

This anomaly is most likely to have occurred where the plectrum impacts first with more force against one or more file teeth (shown by horizontal dashed lines between 15.9 and 16.4 ms in Fig. 6D) and then, with less force, jumping over one or more file teeth (shown by asterisks between 16.5 and 16.7 ms in Fig. 6D). Evidence for the increase in driving force at 15.9 ms can be summarised as follows: the amplitude of the broad-band waveform approximately halved (Fig. 6D upper trace) at the same time as the amplitude of the without- $F_D$

Fig. 6. (A–D) An anomalous pulse from the song of the same *Gryllus campestris* as in Fig. 3. (A) Oscillogram of a single pulse of a chirp of the song. (B) An oscillogram of the pulse shown in A after filtering to remove frequencies below 7.5 kHz; this waveform has been amplified 16-fold relative to that shown in A. (C) Plot of the cycle-by-cycle frequencies of the broad-band waveform shown in A (filled circles) and the without- $F_D$  (the song pulse after filtering out the peak at the dominant frequency  $F_D$  of the song pulse) waveform shown in B (open circles); the frequency scale for the broad-band waveform is on the left and that for the without- $F_D$  waveform is on the right. A, B and C use the same time scale; the asterisks show the regions at which the waveforms and frequency became irregular. (D) A 2.5 ms section of the waveforms shown in A and B from the region around the irregularities in the waveforms. The thick line shows the broad-band waveform and the thin line shows the without- $F_D$  waveform amplified 16-fold relative to the broad-band waveform. The time scale in D shows the regions of the pulse that have been amplified, the vertical dashed lines show the relative phasing of the broad-band and without- $F_D$  waveforms and the asterisks shows the region of the pulse in which the without- $F_D$  waveform became small in amplitude. This was preceded by an irregularity in the broad-band waveform and an increase in amplitude of the without- $F_D$  waveform (horizontal dashed lines). (E) Plot of the cycle-by-cycle frequencies of the broad-band waveforms of five pulses that show similar pulse envelopes to that shown in A. The anomaly appears at the same place in each pulse, shown by an asterisk which corresponds with the asterisk in A and B.



waveform approximately doubled (Fig. 6D lower trace), and the cycle-by-cycle frequency fell at this time (asterisk in Fig. 6C), possibly as a result of an associated increase in the effective mass of the system (see Bennet-Clark, 1999). Further evidence for the brief decrease in driving force at 16.5 ms is the sudden increase in cycle-by-cycle frequency that occurs at that time (Fig. 6C).

Other fourth pulses from the same song recording showed a closely similar change in amplitude and frequency at a similar point in the pulse, suggesting that the common cause of this anomaly is some irregularity in the action of the file-and-plectrum escapement that occurs at a particular part of the file. Fig. 6E shows an overlay of the cycle-by-cycle frequency of the broad-band waveform for five such pulses.

Another type of anomalous song pulse was seen in the song of *Gryllus campestris*. Eight out of 24 of the brief quiet short first pulses of the chirp (as in Fig. 3A) and three out of 24 of the second or third pulses showed a similar pattern. An example is shown in Fig. 7A, in which the without- $F_D$  oscillation ended abruptly at 10.5 ms (Fig. 7B,E). Between 4 and 10 ms into this pulse, the phase relationships between the broad-band waveform and the without- $F_D$  components were similar to those in Fig. 3 (see Fig. 7D,E). At 10.5 ms, the frequency of the broad-band waveform jumped from 5.2 to 5.4 kHz (Fig. 7C), and this was accompanied by a rapid

decrease in the amplitude of the without- $F_D$  waveform and a phase change of over  $90^\circ$  of the without- $F_D$  relative to the broad-band waveforms (Fig. 7E, vertical dashed lines). Thereafter, the broad-band waveform decayed exponentially with a Q of 23 (Fig. 7E after 10.5 ms).

The frequency of the pulse changed as the song reached its end. Such decaying pulses have been described from the songs of *Rufoccephalus* sp. (Bailey et al., 2001), and this type of pulse, although comparatively rare in *Gryllus campestris*, occurred in five out of nine pulses in the song of *Eugryllodes pipiens*.

The pulse illustrated in Fig. 7A demonstrated another anomaly that has been seen in 24 out of 96 pulses of *G. campestris*: at the start of the pulse, at 2 ms, there was brief quiet sub-pulse, at the end of which the phase of the without- $F_D$  components lagged considerably on its normal phase relative to that of the broad-band waveform (the second vertical dashed line in Fig. 7D) and the broad-band waveform almost disappeared. After 2.8 ms, the broad-band waveform started to build up (Fig. 7A,D) and, between 2.8 and 4 ms, the

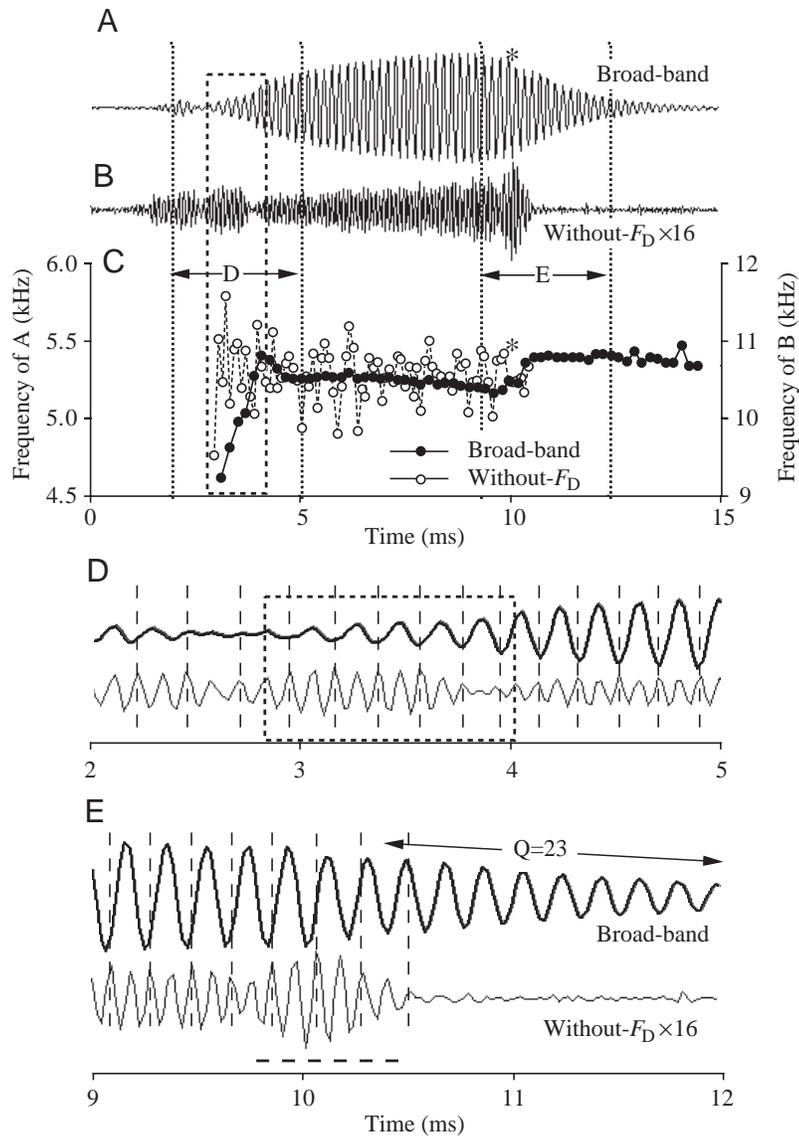


Fig. 7. Anomalous pulse from the song of the same *Gryllus campestris* as in Fig. 3. (A) Oscillogram of a single pulse of a chirp of the song. (B) An oscillogram of the pulse shown in A after filtering to remove frequencies below 7.5 kHz; this waveform has been amplified 16-fold relative to that shown in A. (C) Plot of the cycle-by-cycle frequencies of the broad-band waveform shown in A (filled circles) and the without- $F_D$  (the song pulse after filtering out the peak at the dominant frequency  $F_D$  of the song pulse) waveform shown in B (open circles). Before 3 ms, both waveforms were very irregular; after 10 ms, the without- $F_D$  amplitude became very small. The cycle-by-cycle frequency data in these regions have been deleted. The frequency scale for the broad-band waveform is on the left and that for the without- $F_D$  waveform is on the right. A, B and C use the same time scale. The asterisks show the time at which the broad-band waveform started to decay exponentially and the cycle-by-cycle frequency of the broad-band waveform rose by 0.2 kHz, thereafter remaining nearly constant. (D,E) 3 ms sections of the waveforms shown in A and B; D is from the irregular region at the start of the pulse and E is from the region around the irregularities in the waveforms. For both, the thick line shows the broad-band waveform and the thin line shows the without- $F_D$  waveform, amplified 16-fold relative to the broad-band waveform. The time scales in D and E show the regions of the pulse shown in A that have been amplified. The vertical dashed lines in D and E show the relative phasing of the broad-band and without- $F_D$  waveforms. In D, the box shows the region in which the cycle-by-cycle frequency of the broad-band waveform rose rapidly. In E, the horizontal dashed line shows the region of the pulse in which the without- $F_D$  waveform increased and then became small in amplitude; this was associated with the start of the exponential decay of the broad-band waveform. The quality factor ( $Q$ ) of the exponential decay is shown.

without- $F_D$  components became relatively large but only loosely phase-locked to the broad-band waveform (Fig. 7D). In this part of the pulse (dotted boxes on Fig. 7A–D), the frequency of the broad-band waveform rose rapidly and, after 4 ms, the without- $F_D$  waveform remained phase-locked to the broad-band waveform. Sub-pulses preceding the main song pulse have also been seen in the song of *Modicogryllus bordigalensis*.

In the case shown in Fig. 6D, the plectrum appears to have made a heavier-than-normal engagement with some teeth and then jumped over succeeding file teeth. In the example shown in Fig. 7D of the start of a pulse, the plectrum appears to have engaged and then jumped over succeeding teeth as a result of too heavy and then too light pressure between the wings. In the example shown in Fig. 7E of the end of a pulse, the plectrum appears to have made heavy contact with the file teeth and then either locked or jumped over the remaining teeth, allowing free vibration of the harp regulator.

## Discussion

### *High-frequency sounds during normal sound production*

Pure-tone songs have evolved in a range of orthopteran taxa. While the mechanisms producing a pure-tone call are undoubtedly remarkable, they are far from perfect. Our analysis of the high-frequency components produced during normal sound production and of anomalous song pulses indicates that, as in a faulty clock, these deficiencies in design can be explained within the model.

The ‘clockwork cricket’ model should have the following elements: a supply of mechanical power; a mechanism whereby the power is delivered to the escapement; an escapement that delivers impulses to the regulator; and a regulator that is set into vibration by the impulses delivered by the escapement but which, in turn, controls the locking and unlocking of the escapement. The tick of a clock can be described both by its loudness and by the frequency of the sound it makes.

In a clock, the 'tick' is produced by the action of the escapement. The louder sound occurs when a tooth on the escapement hits a pallet of the lever that transmits energy to the regulator. The equivalent in the 'clockwork cricket' model is the impact of a file tooth on the plectrum of the opposite wing. There is also a far quieter 'tick' sound produced by a clock as the escapement wheel releases the pallet which, in cricket sound production would occur as a file tooth releases the plectrum. From the evidence of the waveforms we provide (e.g. Fig. 5E), both the engagement and release of the cricket's escapement produce sound.

In clocks, the metallic tick from the escapement (the without- $F_D$  component) is at a far higher frequency than the inaudibly low-frequency of oscillation of the regulator (the  $F_D$  component). In crickets, the frequency of the tick appears to have a dominant component at or close to twice that of the  $F_D$  waveform of the song (Figs 3, 5). The close phase-locking between the broad-band and without- $F_D$  waveforms (Fig. 5D–F) is consistent with this explanation of the cause of the without- $F_D$  sound and it should be noted that phase-locking persists even though the frequency of vibration of the 'regulator' decreases during the pulse (e.g. Fig. 3E).

The ticking of a clock reflects the energy wasted by the catch-and-release of the teeth of the escapement and becomes louder if the driving force increases, independently of the depth of engagement of the escapement. The without- $F_D$  sound in cricket song appears to be produced at two phases of the action of the escapement. The first is as the plectrum impacts on a file tooth at  $270^\circ$  in the up–down oscillation of the file, and the second as the elastic plectrum is released by the tooth at or near  $90^\circ$  in the oscillation of the file (Fig. 8). However, if the depth of engagement is shallower, the impulse that the escapement gives to the regulator will be smaller than that given by a deeper engagement: this is an important aspect of the design of clock escapements (Gazeley, 1958). The loudness of the without- $F_D$  sound of the 'escapement' of the cricket probably reflects similar changes in the force driving the movement of the wings but is not reflected in the amplitude of the broad-band song pulses (cf. Fig. 3A,B). Also, if the geometry of an escapement changes, the ticking noise it makes may become louder but the impulse it delivers to the regulator may decrease. Because the file is long and curved in section (Fig. 1), changes in the driving force or coupling between the file and the harp (as the regulator) during the sound-producing wing-closing movement are to be expected and would explain changes in relative amplitudes between the broad-band and without- $F_D$  waveforms in the successive pulses of the chirp (Fig. 3A,B) or at the end of the fourth pulse of *G. campestris* (Fig. 3C,D).

There is the associated problem of controlling the shape of the pulse envelope. In *G. campestris*, the rate of rise and fall and the overall shape of the envelope differed from pulse 1 to pulse 4 (Fig. 3A) and, in this species, the amplitude of the later pulses typically rose and fell slowly, whereas in *Eugryllodes pipiens* (Fig. 5A) and *Rufoccephalus* sp., the amplitude usually rose and fell rapidly (see Bailey et al., 2001). This suggests that the depth of engagement of the file and plectrum, or the

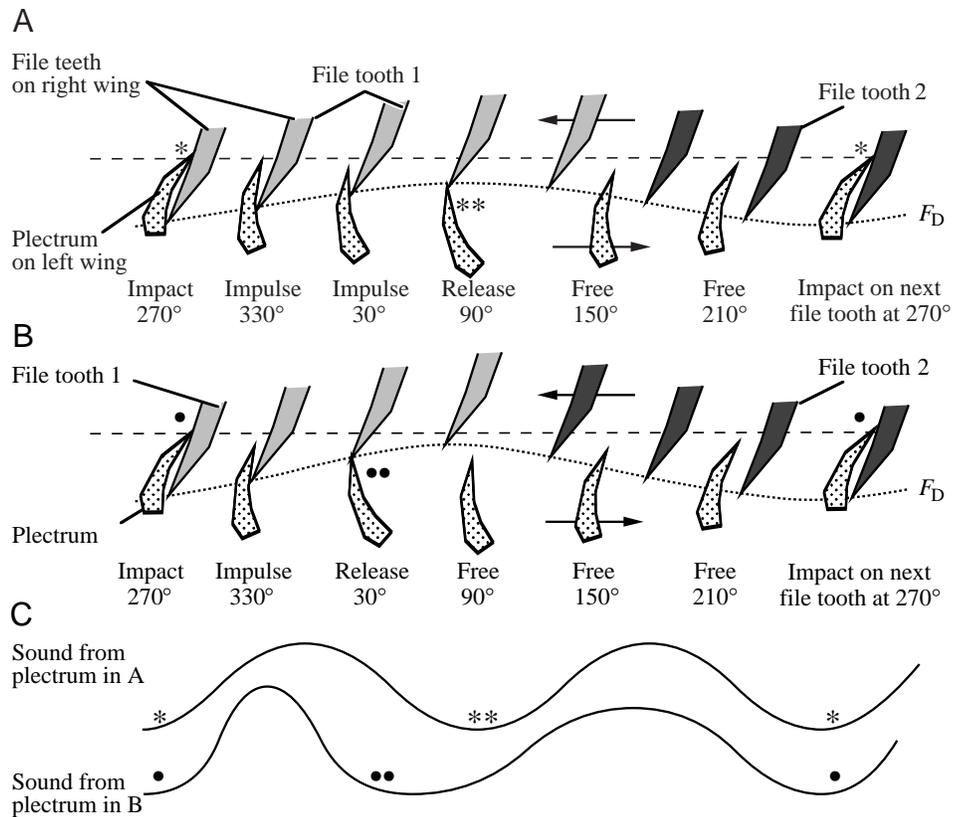
energy of the impulse delivered at each cycle of catch-and-release, can be varied and differs among species. Such variability is abhorred in mechanical clocks because it is associated with poor time-keeping but, even by the standards of the most primitive clocks, the sound-producing mechanisms of crickets are undoubtedly poor timekeepers!

The broad-band waveforms of the four pulses in a typical chirp of *G. campestris* differ in both amplitude and duration (Fig. 3A). However, the cycle-by-cycle frequencies of song pulses follow very similar time courses and they can be closely superimposed (Fig. 4). It was suggested earlier that production of the first pulse started nearer the middle of the file and that the later pulses utilise successively more of the file. This is borne out by cinematographic measurements by Pierce (1948) using *Gryllus assimilis* and measurements of wing angle by Elliott and Koch (1983) with *G. campestris* and provides further support for a clockwork cricket model in which the catch-and-release of the escapement is linked to the oscillation of the regulator.

There is an important difference between a typical pendulum clock and the 'clockwork cricket'. In a long-case (or 'grandfather') clock, the escapement acts symmetrically either side of the centre of the swing of the pendulum regulator so it can only release after the pendulum has swung through a critical angle from the central position: when stopped and re-wound, the clock can only be re-started after the pendulum has been swung through this critical angle. If the lever escapement of a watch is deliberately set to act asymmetrically, the sound from the escapement becomes an irregular tick–tick–tick–tick but the watch will start spontaneously as it is wound up. The clock escapement is, by its design, safe: it is hard to make it catch and release at rates other than that determined by the regulator.

From its geometry, the cricket's file-and-plectrum escapement cannot act symmetrically (see Fig. 1B). Both the file and the plectrum have a hooked profile. This asymmetric profile will allow a deep overlap, shown as the impact at  $270^\circ$  (asterisk in Fig. 8A and filled circle in Fig. 8B). The phasing of the impact and release of the escapement will depend on the amplitude of oscillation of the file relative to the plectrum. The escapement will 'run' regularly if the impact and release of the plectrum by the file occur  $180^\circ$  apart and the 'tick-tick' sounds will occur at exactly twice  $F_D$ , as is seen in Fig. 5D and has been modelled in Fig. 8C, upper trace. If the plectrum engages at  $270^\circ$  and disengages at  $30^\circ$  (filled circle and double filled circles, respectively, in Fig. 8B), the ticking of such an escapement will be highly irregular, with a period of one-third that of  $F_D$  between the impact and release of the plectrum and two-thirds that of  $F_D$  while the plectrum is dropping freely onto the next file tooth; this is likely to produce the sort of without- $F_D$  waveforms that are seen in Fig. 5E (modelled in Fig. 8C, lower trace). An important feature of the asymmetric cricket escapement is that it will start and run as long as the impulse given during each period of engagement between the file and plectrum is sufficient to overcome or exceed the losses in the harp regulator.

Fig. 8. A model of the interaction between the file and plectrum of a cricket during sound production. In both A and B, the phase of the interaction between the file and the plectrum during the cycle is referred to the lowest point in the cycle of oscillation of the file, termed  $270^\circ$ . The horizontal arrows show the directions of the closing movements of the two wings. The horizontal dashed lines act as references for the relative positions of the file and plectrum at the moment of impact and the dotted lines show the up-and-down oscillation of the tips of the file teeth. In A, it is assumed that a file tooth is engaged, that an impulse is given throughout the first half-cycle ( $270\text{--}90^\circ$ ) and that the plectrum is detached from the file during the second half-cycle ( $90\text{--}0^\circ$ ). At the start of the next cycle (right-hand side), the plectrum engages with the next file tooth (shown by denser stipple). In B, where the amplitude of oscillation is larger, file teeth are engaged and an impulse is given only during the first one-third of the cycle ( $270\text{--}30^\circ$ ); during the later two-thirds of the cycle, the plectrum is detached from the file ( $30\text{--}270^\circ$ ). Sounds will be produced by the 'escapement' at both the impact and release of the plectrum (shown by asterisks in A and C or filled circles in B and C). In A, this will give rise to sounds at multiples of twice the frequency of oscillation and in B to asymmetrical waveforms of the type seen in Fig. 5E.  $F_D$  is the dominant frequency of the song pulse.



The amplitude of the without- $F_D$  waveform decreases before the end of the broad-band waveform (Figs 3C,D, 5F); the end of the without- $F_D$  waveform is often accompanied by a rapid change in the cycle-by-cycle frequency of the broad-band waveform and its subsequent exponential decay (Fig. 5C). With a typical pendulum clock, when the driving force is removed, which with a simple clock happens as it is wound, the clock stops ticking; in this condition, the regulator (pendulum) continues to oscillate but the amplitude of its vibration decays exponentially because there is no phasic impulse; this also occurs if the escapement is loosely coupled to the regulator. A different effect occurs if the escapement is locked; the oscillation of the regulator may then be brought rapidly to rest. Effects of this type may explain the brief first pulses of *G. campestris* (Fig. 3A,B) in which the amplitude of the broad-band waveform decayed more rapidly than that of the fourth pulse.

#### The production of anomalous song pulses

Faults occur in the escapements of mechanical clocks. Irregularities in the escapement or its action or damage to either the escapement wheel or the locking pallets may lead to partial malfunction (de Carle, 1964). These faults can be detected acoustically using such machines as the Vibrograf or Tickprint (see de Carle, 1964). Jamming of the escapement

due to faulty geometry leads to sudden loss of the driving impulse to the regulator and the subsequent decay of the vibration of the regulator.

Two types of anomalous song pulses of *Gryllus campestris* (Figs 6, 7) show interruptions to the typical steady supply of impulses that occurs in normal sound production. A comparison of these pulses suggests that the interruptions (Figs 6E, 7E) are of different types and may have different causes, but that both may involve some fault in the 'escapement'. In the pulse in Fig. 6, both the broad-band and without- $F_D$  waveforms are interrupted almost simultaneously (Fig. 6E, horizontal dashed lines) but, after a build-up and then decay, the without- $F_D$  waveform returns to its original level and a more-or-less normal broad-band waveform resumes. One explanation is that there is a temporary malfunction of the 'escapement' which, becomes briefly noisier at 16 ms (Fig. 6D, horizontal dashed lines), then becomes quiet at 16.5 ms (Fig. 6D, asterisks) before building up to resume at a normal amplitude. Sounds of this type would occur if the plectrum jumped one or more file teeth and was then caught noisily, held silently and then re-commenced a normal cycle of catch-and-release. The fact that the interruption occurs at the same point in other anomalous pulses from the same insect suggests that there is some failure of the escapement giving rise to this type of anomaly. Koch et al. (1988) report instances of double-

speed wing closing and irregular closing speeds following damage to the file, but it now appears that other irregularities may occur in apparently normal insects.

The anomalous pulse illustrated in Fig. 7 appears to have a different cause. First, the pulse is briefer than normal pulses (compare Fig. 3A,C with Fig. 7A). Second, the stage in the wing-closing movement at which the change occurs and events following the change differ from those in Fig. 6. In the pulse in Fig. 7A, the without- $F_D$  waveform suddenly becomes larger at 9.8 ms then decays rapidly. There is a small change in the amplitude of the broad-band waveform at 10.2 ms, and the broad-band waveform decays exponentially thereafter (Fig. 7A,E). After 10.5 ms, the without- $F_D$  waveform has effectively ceased. From the jump in the relative phase between the without- $F_D$  and broad-band waveforms and in the cycle-by-cycle frequency and the exponential decay that follows, it seems likely that the normal regular cycle of catch-and-release of the 'escapement' has ceased, allowing a free oscillation of the regulator to occur.

#### *Control of sound-production by the cricket*

The anomalous song pulses described here are unusual in that, for most of the species we have examined, most songs show a remarkably consistent waveform from trill to trill, from pulse to pulse and even within successive pulses (e.g. Fig. 4B). This regularity is surprising in view of the 'unsafe' nature of the file-and-plectrum escapement and its probable sensitivity to changes in geometry or driving force. Sensory feedback from proprioceptors such as hair plates on the forewings has been shown to be important in controlling the angle through which the wings open, and it can also be inferred that such feedback controls the force with which the wings are pressed together to engage the escapement (Elliott and Koch, 1983).

One aspect of the song over which most crickets appear to have little control is the frequency within the pulse. Although succeeding song pulses may be closely similar with regard to their within-pulse frequency, which suggests that the mechanism is excited in a very constant manner, the frequency within the pulse of the song may decrease between the start and end of the pulse by between 6 and 16% (Table 1) (see also Leroy, 1966; Bailey and Broughton, 1970; Simmons and Ritchie, 1996; Bennet-Clark, 1999). The frequency of oscillation of a simple resonator depends on the interaction between its effective mass and its stiffness: increasing the effective mass lowers and increasing the stiffness increases the resonant frequency. From the exponential decay at the end of the broad-band waveform, such as is shown in Figs 3 and 5, it appears that the region that is excited by the action of the file and plectrum has resonant properties. However, it also appears that the file and plectrum do not excite or drive a simple resonance of the harps as the regulator nor is the song produced by a free vibration but, rather, that the mass/stiffness ratio of the regulator changes during the course of the wing-closing movement. It has been argued that any observed decrease in frequency occurring during the pulse is most probably caused by the increase in the effective mass of the right harp (the

'regulator') as the plectrum traverses the right file (Bennet-Clark, 1999); the frequency and phasing of the without- $F_D$  waveforms described here suggest strongly that the 'escapement' continues to sustain the vibration of the harp despite changes in the frequency of its vibration.

The exception to the general observation that  $F_D$  changes during the pulse is interesting in itself. Bailey et al. (2001) describe how, in its normal song, *Rufoccephalus* sp. maintains its call frequency throughout the pulse with remarkable stability. However, *Rufoccephalus* sp. is the only example of the species chosen for this study that calls from within a sharply tuned burrow. By comparison, although the fall in relative frequency was lower than in non-burrow-calling crickets, the glissando of the within-pulse frequency in the mole crickets *Scapteriscus acletus*, *Gryllotalpa gryllotalpa* and *Gryllotalpa vineae* is nevertheless significant (Table 1). The burrows of these mole crickets are not as sharply tuned (Bennet-Clark, 1987) as that of *Rufoccephalus*, in which the burrow rather than the wings appears to control the frequency (Bailey et al., 2001).

#### *Concluding remarks*

It is difficult to make a clock that ticks silently. The without- $F_D$  sounds reported in the present study, imputed to the action of the file and plectrum as an escapement, are far quieter than the broad-band calling songs. A well-designed escapement delivers most of the available mechanical power to the regulator and it is tempting to assume that the relative quietness of the without- $F_D$  waveforms of cricket songs indicates efficient transfer of mechanical power from the sound-producing muscles to the vibrating surfaces. Unfortunately, the recording methods used for some of the songs described here limit the analysis of sounds to frequencies below 20 kHz. It is possible that there are louder higher-frequency sounds produced by the small structures of the file-and-plectrum escapement; if these sounds were to be recorded and analysed with accurate information about their relative phase, this would throw further light on the mechanism of excitation of the harps.

The sounds produced during normal sound production in crickets parallel those produced by mechanical clocks, suggesting analogies between the mechanisms. These analogies have already been drawn in the masterful critique of their 'clockwork cricket' model by Koch et al. (1988) but, since they were mainly concerned with the speed of wing closing and its temporal relationships with the sound pulses that were produced, they did not extend their analysis to the relationships between the catch/release of the file-and-plectrum escapement and the impulses that this mechanism delivers to the harp regulator. The present study complements and supports the earlier work (Elliott and Koch, 1985; Koch et al., 1988) but extends it to describe how the 'clockwork cricket' ticks.

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and the University of Western Australia for hospitality and laboratory space during the course of this visit. The work was continued during a reciprocal visit by W.J.B. to Oxford, where thanks to that department are also recorded. The cycle-by-cycle frequency analyses described here would have been far more tedious to make and far less accurate without the ZeroCrossing programme written by K. N. Prestwich, who discussed the design of the programme with H.C.B-C and gave it freely to us.

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