

RESONATORS IN INSECT SOUND PRODUCTION: HOW INSECTS PRODUCE LOUD PURE-TONE SONGS

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Summary

In a resonant vibration, two reactive elements, such as a mass and a spring, interact: the resonant frequency depends on the magnitude of these two elements. The build-up and decay of the vibration depend on the way the resonator is driven and on the damping in the system.

The evidence for the existence of resonators in insect sound production is assessed. The mechanics of different types of sound-producing system found in insects is described. Mechanical frequency-multiplier mechanisms, which convert the relatively slow contraction of muscles to the higher frequency of the sound, are commonly used to convert the comparatively slow muscle contraction rate to the higher frequency of the sound. The phasing and rate of mechanical excitation may also affect the frequency and duration of the sound that is produced.

Although in many insects the song may appear to be

produced by the excitation of a simple resonator, the song frequency may not be constant, suggesting that other factors, such as the mechanism of excitation, or variation of the effective mass or elasticity of the system during sound production, may be additional determinants of the song frequency.

Loud, and hence efficient, transduction of the energy of a mechanical resonator into sound may involve a second stage of transduction which, by damping the resonator, may compromise tonal purity. Some insect singers resolve this problem by tuning both stages of transduction to the same frequency, thereby maintaining tonal purity.

Key words: insect, sound production, bioacoustics, resonator, cicada, cricket.

Introduction

The songs of insects may be shrill, raucous or musical, brief or sustained but, whether loud or quiet, they tend to convey information within a narrow band of sound frequencies. The narrow frequency band implies that the sound-producing system is in some way tuned. In this review, I shall address the mechanisms by which sharply tuned sounds are produced by insects and explore the acoustical and biomechanical mechanisms by which insects produce narrow-band sound signals. I shall also examine the transduction chains involved in the conversion of muscle power to sound power.

What is a resonator?

Resonators occur in many everyday forms such as whistles and bells, pipes and drums, the pendulum of a clock, the balance spring-and-wheel or the quartz crystal of a watch. All these resonant systems are employed for similar reasons: they vibrate at or near a single frequency, whether that is a musical note or is used as a basic timing mechanism; their vibration can be excited by an impulse, whether by a puff of air, a mechanical impact or an electrical pulse; and their vibration can be sustained by continued excitation, by supplying appropriately phased acoustic, electrical or mechanical

power, as occurs in a trumpet mouthpiece or a clock escapement.

Simple resonators rely on the interplay between two reactive elements. Consider the simple case of a mass swinging on a spring (Fig. 1): at the extreme of the swing of the mass, it has zero velocity and thus zero kinetic energy, but the strain energy in the spring is maximal; as the mass swings through the centre of its arc, its velocity is maximal so its kinetic energy is maximal, but the stored or strain energy in the straight spring is zero; the mass then decelerates to zero velocity as its kinetic energy is absorbed by the spring; the mass then re-accelerates in the opposite direction and so on.

The frequency of the vibration or resonant frequency, F_0 , determined by the mass and the compliance of the spring, is given by:

$$F_0 = \frac{1}{2\pi} \sqrt{\left(\frac{1}{m \times c}\right)} = \frac{1}{2\pi} \sqrt{\left(\frac{s}{m}\right)}, \quad (1)$$

where m is the mass, c is the compliance and s is the stiffness (the compliance of a spring is the reciprocal of its stiffness).

A similar process of transfer of energy between two components occurs in the simple electrical series resonant

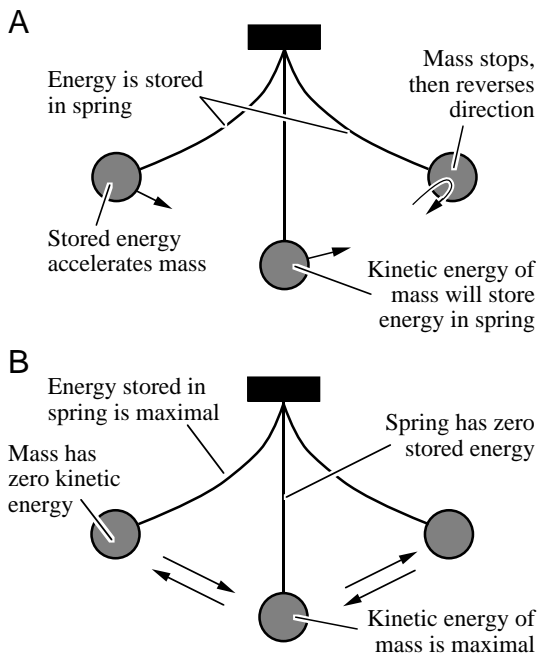


Fig. 1. Diagrams of a simple resonator composed of a mass and spring. (A) The kinetics of the system showing how elastic strain energy in the spring accelerates the mass and the kinetic energy of the mass is converted into strain energy in the spring. (B) How energy is transferred from the spring to the mass and *vice versa*.

circuit shown in Fig. 2A, in which the capacitor acts compliantly, in a manner analogous to a spring, and the inductor behaves inertially, in a manner analogous to a mass. Likewise, in an acoustic resonator, such as the Helmholtz resonator in Fig. 2B, the two reactive elements that determine the resonant frequency are analogues of a compliance or spring and an inductance or mass.

A practical resonator, vibrating freely, will come to rest because the energy of vibration is lost by friction, as heat, or is otherwise dissipated, for instance as sound. Ways in which this energy loss might occur are shown in the model systems of Fig. 2. If very little of the energy of vibration of the system is lost, the vibration will, by Newton's first law, persist; this will occur because the resistive damping is small. In a heavily damped system, the vibration will decay rapidly. In either case, the amplitude of vibration tends to decay exponentially.

A useful dimensionless index of the damping of a resonant system is the quality factor, Q , which can be measured in various related ways (Morse, 1948; Fletcher, 1992).

The Q of any of the resonators described above can be obtained by measuring the amplitude of successive cycles of the free decay following a driven oscillation. Q is then given by the slope of a plot of the natural logarithm of the amplitude per cycle during the decay (known as the \log_e decrement):

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

This method of measurement of Q has been used in a biological context to describe the resonators on cricket wings (Nocke, 1971) or those involved in cicada sound production (Bennet-Clark and Young, 1992; Young and Bennet-Clark, 1995).

The decaying transient that follows impulsive excitation of a resonance is found in many sound-producing systems, such as bells or the succession of pulses that make up the songs of many bush crickets. However, many biological and musical sounds are produced as driven resonances, in which the vibration is sustained by regular re-excitation at an appropriate frequency and phase. An everyday example of this is the maintenance of the swing of a clock pendulum using packets of energy liberated at an appropriate phase by the escapement, which is coupled to the pendulum (Gazeley, 1956). The

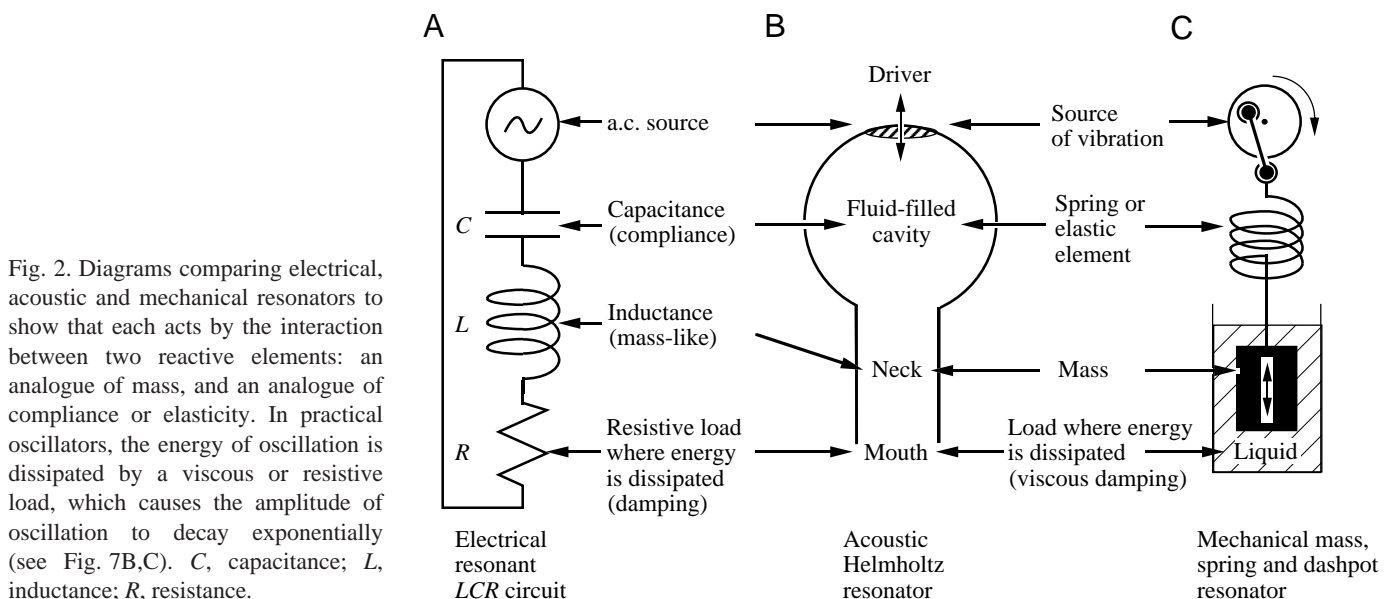


Fig. 2. Diagrams comparing electrical, acoustic and mechanical resonators to show that each acts by the interaction between two reactive elements: an analogue of mass, and an analogue of compliance or elasticity. In practical oscillators, the energy of oscillation is dissipated by a viscous or resistive load, which causes the amplitude of oscillation to decay exponentially (see Fig. 7B,C). C , capacitance; L , inductance; R , resistance.

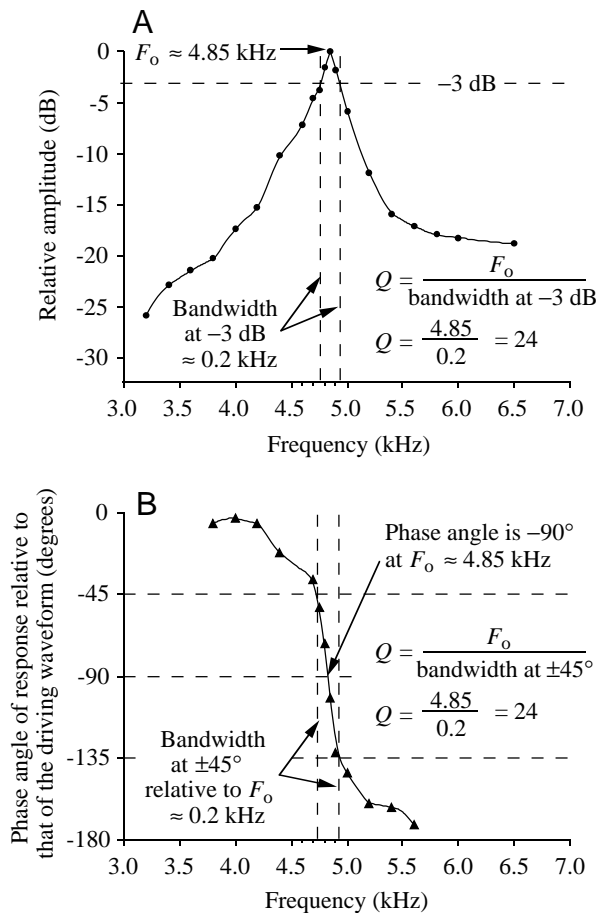


Fig. 3. Resonant properties of the harp area of a forewing of *Gryllus campestris* (see Fig. 6A) when driven by sound. (A) Graph of the amplitude of oscillation when driven by a constant sound pressure level against the frequency of the driving sound. (B) Graph of the phase angle of the oscillation of the response relative to that of the driving sound against the frequency of the driving sound. The insets show the methods by which the quality factor, Q , of the driven resonance were calculated from equation 3. F_0 is the resonant frequency. Drawn from data taken from figures in Nocke (1971).

frequency of these vibrations is not constant but can typically be driven over a range of frequencies, depending once more on the quality factor, Q , of the resonator.

This was shown elegantly by Nocke (1971), who measured the amplitude of vibration of the resonant region of the wings of crickets when driven by sound at different frequencies (Fig. 3A) and also the phase of the vibration relative to that of the pressure of the driving waveform (Fig. 3B). Q in these cases is given by:

$$Q = \frac{\text{resonant frequency}}{\text{bandwidth at } -3 \text{ dB}} = \frac{\text{resonant frequency}}{\text{bandwidth at } \pm 45^\circ} \quad (3)$$

(-3 dB is half peak power).

Such measurements provide further useful tools for studying the properties of vibrating systems: if, for instance, the amplitude of a forced vibration shows a peak at a single

frequency or the phase of a forced vibration lags that of the driving force by 90° , a simple resonator may be implicated. In practice, it is easier to measure amplitude than phase so the phase information tends to be ignored.

The songs of many insects, such as crickets (Elliott and Koch, 1985; Koch et al., 1988), some bush crickets (Bailey, 1970) and certain cicadas (Bennet-Clark and Young, 1992), appear to be produced as forced vibrations of comparatively simple resonators (Table 1). For detailed treatments of different types of resonators, their parameters and how their resonant frequencies scale, see, for example, Fletcher, 1992; Morse, 1948; Olson, 1957.

Types of resonators implicated in insect sound production

There have been comparatively few formal studies of the reactive elements that determine the frequency in insect sound-producing mechanisms. Because biological structures rarely have a simple geometry with discrete disposition of the mass and compliance (or its acoustic analogues), the studies that exist have resorted to models based on known types of mechanical or acoustic resonator.

There is abundant evidence in a few cases for the existence of a resonator, such as the detailed and elegant analysis of the vibrations of the harp area of the forewings of male *Gryllus campestris* by Nocke (1971). In many other cases, the evidence is patchier (see Table 1) and may be based on such factors as the way in which the song frequency scales with the dimensions of the putative resonator.

Probably the simplest type of resonator, conceptually, is the cicada tymbal, which appears to behave rather like the simple mass-and-spring shown in Fig. 1. The principal reactive elements are the mass of the sclerotised tymbal plate and the stiffness of its dorsal support (see Fig. 5A), which is a pad of the elastic protein resilin (Weis-Fogh, 1960; Jensen and Weis-Fogh, 1962). Adding mass to the tymbal plate decreases its resonant frequency, as does removal of parts of the resilin pad, which increases the compliance of the tymbal, both of which are predicted by equation 1. Also, free vibrations of the tymbal decay exponentially in accordance with equation 2 (Bennet-Clark, 1997), and the song in the cicada *Cyclochila australasiae* is confined to a narrow frequency band (Young, 1990), consistent with the measured resonances of the tymbal (Bennet-Clark, 1997).

In many insects, such as mole crickets and many species of cicada, the sound-producing mechanism appears to involve a driving or primary resonator coupled to a secondary resonator, tuned to the same frequency, from which sound is radiated. In the cases that have been described (see, for example, Bennet-Clark, 1995; Bennet-Clark and Young, 1998), the primary resonator depends on the mechanical vibration of parts of the skeleton and the secondary resonator depends on the acoustic properties of a volume of the fluid medium (Table 1). The advantages and properties of systems of coupled resonators are considered in the section on sound production involving coupled resonators.

Table 1. *Types of resonator involved in insect sound production*

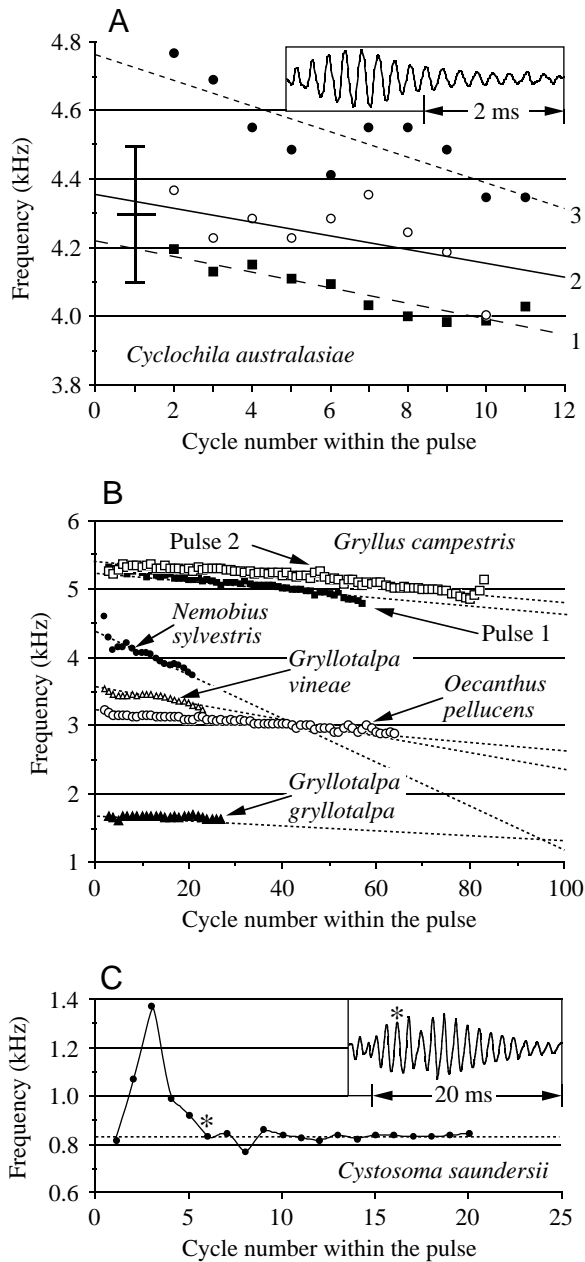
Type of resonator	Inertial element	Major compliant element	Examples	Evidence for resonator	Reference
Mass and spring (mechanical) (primary)	Mass of hinged vibrating plate	Resilin spring (? plus sclerotised cuticle of ribs)	Cicada tymbals (Fig. 5A)	Frequency/energy spectrum, exponential decay, effect of increasing mass or compliance on frequency	Bennet-Clark (1997)
Clamped plate (mechanical) (primary)	Mass of vibrating plate	Elasticity of sclerotised cuticle of plate	Cricket harp (Fig. 6A) (mole crickets)	Frequency/energy spectrum, frequency-dependent phase shift, exponential decay, effect of increasing mass on frequency	Nocke (1971)
Tuning fork (mechanical) (primary)	Length of fork	Elasticity of sclerotised cuticle of fork	Bush crickets	Frequency/energy spectrum, position of vibrating areas Song scaling	Bailey (1970) Sales and Pye (1978)
Helmholtz (acoustic) (secondary)	Length and diameter of apertures	Volume of cavity	Typical cicadas (Fig. 8A)	Frequency/energy spectrum, exponential decay, effect of altering gas on frequency Song scaling	Bennet-Clark and Young (1992) Bennet-Clark and Young (1994)
Balloon or bladder (mechano-acoustic) (secondary)	Mass of cuticle of walls of bladder	Volume of bladder	Bladder cicadas (Fig. 8B)	Frequency/energy spectrum, exponential decay, effect of increasing mass or increasing volume on frequency	Bennet-Clark and Young (1998)
Horn (acoustic) (secondary)	Length and rate of flare of horn	Cavity length and volume of bulb at throat of horn	Mole crickets	Frequency/energy spectrum, exponential decay Effect of source position	Bennet-Clark (1987) Daws et al. (1996)

A *primary* type of resonator indicates the primary determinant of the song frequency; a *secondary* resonator is tuned to the frequency of the primary resonator and driven by it; for further details see the text.

The tonal purity of insect songs

Many of the existing measurements of the frequency/energy spectra of the songs of crickets or cicadas suggest that the species' song frequency is both highly specific and confined to a narrow bandwidth (e.g. Bennet-Clark, 1971; Young, 1990). Thus, it is tempting to assume that the song frequency is determined by a simple clock-like mechanism that produces a constant frequency of vibration. This view is reinforced by the unequivocal demonstration of the resonant properties of, for example, the harp area of the forewings of crickets (Nocke, 1971) or the tymbal of cicadas (Bennet-Clark, 1997). The underlying assumption here is that the mass and compliance of the vibrating system do not change during sound production. However, during sound production, the sound-producing structures are driven and may be more or less coupled to other structures that may affect the effective mass and/or stiffness of the system and hence the frequency at which it vibrates. This may be inferred from spectrograms of cricket songs (e.g. Leroy, 1966; Simmons and Ritchie, 1996), which tend to show a decrease in sound frequency throughout the pulse, but in most cases, the bandwidth of the analysis window of typical spectrograms obscures the details of any such frequency modulation or inconstancy.

I have now measured the instantaneous frequency within the pulses of the songs of a number of individuals of the cicada *Cyclochila australasiae* (using unpublished song recordings made by David Young) and of single individuals of various cricket species (using song recordings published by Ragge and Reynolds, 1998). For each of these recordings, the frequency for every cycle of the waveform was calculated from measurements of the period and then subjected to three- or five-point smoothing. A single cycle at 5 kHz has a period of 200 μ s, so the frequency resolution at 100 kilosamples s⁻¹ or $\pm 10 \mu$ s gives a frequency resolution of ± 250 Hz. After five-point smoothing, the effective resolution for the measurement of instantaneous sound frequency becomes approximately 50 Hz at 5 kHz, and after three-point smoothing it becomes approximately 100 Hz at 5 kHz. The instantaneous song frequency during the song pulses is shown in Fig. 4A,B. The songs of the one cicada and five cricket species that were analysed show a decrease in sound frequency between the start and the end of the song pulse. This decrease in intra-pulse frequency appears to be a general feature of the songs of crickets as shown by spectrograms of 25 species of gryllids studied by Leroy (1966). There are two simple explanations for the observed shift in



frequency during the production of a sound pulse. First, from equation 1, the compliance of the system or its mass may increase. Second, the force driving the system may decrease (which is tantamount to a decrease in the stiffness of the system). Given the nature of the trigger that releases the driving impulse in cicadas (Young and Bennet-Clark, 1995; Bennet-Clark, 1997) or of the escapement mechanism that sustains the sound-producing vibration in crickets (Elliott and Koch, 1985; Koch et al., 1988; Bennet-Clark, 1989), either of which would fail to release if the driving force were to decrease greatly, it seems more likely that the effective compliant and mass elements of the system vary during the production of the sound pulse.

The song of the bladder cicada *Cystosoma saundersii* is a

Fig. 4. Plots showing instantaneous frequency during the sound pulses of various species of insect. The frequency data were obtained as the reciprocal of the period of individual cycles of the sound. (A) The song of three individuals of the cicada *Cyclochila australasiae*. The inset shows an oscillogram of one sound pulse of this species. The raw data were subjected to three-point smoothing; the lines show linear regressions of the data for each individual (for insect 1, $r^2=0.841$, $P<0.01$; for insect 2, $r^2=0.69$, $P<0.05$; for insect 3, $r^2=0.31$, $P>0.1$). The cross and bar lines at 1 ms show the mean and standard deviation ($N=10$) of the centre frequency of the song of this species reported by Young (1990) (measured from field records made in 1988 by David Young). (B) The songs of various crickets (Gryllidae). For *Gryllus campestris*, the frequency against cycle number data are shown for the first and second pulses of the same chirp; an oscillogram of a second pulse of this species is shown in Fig. 7A. The raw data for *Nemobius sylvestris* were subjected to three-point smoothing and all other raw data to five-point smoothing; the dotted lines show the trend of the frequency change for the different pulses (measured from a CD of orthopteran songs; Ragge and Reynolds, 1998). (C) The song of the bladder cicada *Cystosoma saundersii*. The inset shows an oscillogram of the sound pulse from which the frequency against cycle number data were measured; the data were not smoothed. The horizontal dotted line shows that the frequency does not vary greatly between cycle 6 (*) and the end of the pulse (measured from an original recording).

notable exception to the more usual observation that frequency falls throughout the sound pulse. After the first quarter of the pulse, which is of lower amplitude but at a higher frequency, the song frequency is effectively constant throughout the pulse (Fig. 4C) (Bennet-Clark and Young, 1998). An explanation for this special case is offered in the section on sound production involving coupled resonators.

Although sharply tuned resonators have been implicated as the primary determinants of the song frequency in various groups of insects, the song that these insects produce may appear to be less sharply tuned. Compare, for instance, the high- Q resonance of the isolated harp area of the wing of *Gryllus campestris*, which is centred on a single frequency (Fig. 3A), with the continually falling frequency (or *glissando*) that is typical of the song (see Fig. 7D). The bandwidth of the song pulse shown in Fig. 7A extends from 5.35 kHz at the start of the pulse to 4.85 kHz at the end (0.5 kHz bandwidth). This suggests either that the Q of the system during sound production is far less than that of the isolated forewing or that the frequency modulation results from changes in the excitation of the sound-producing mechanism. Even greater frequency modulation can be seen in some of the cricket songs described by Leroy (1966, 1977) or Simmons and Ritchie (1996).

Excitation of sound-producing resonant structures

Some insect songs, such as those of many tettigoniid bush crickets, appear to be produced by successive impacts on the sound-producing mechanism, each of which produces a brief transient sound that decays more or less rapidly, but the mechanism of production of these signals has not been

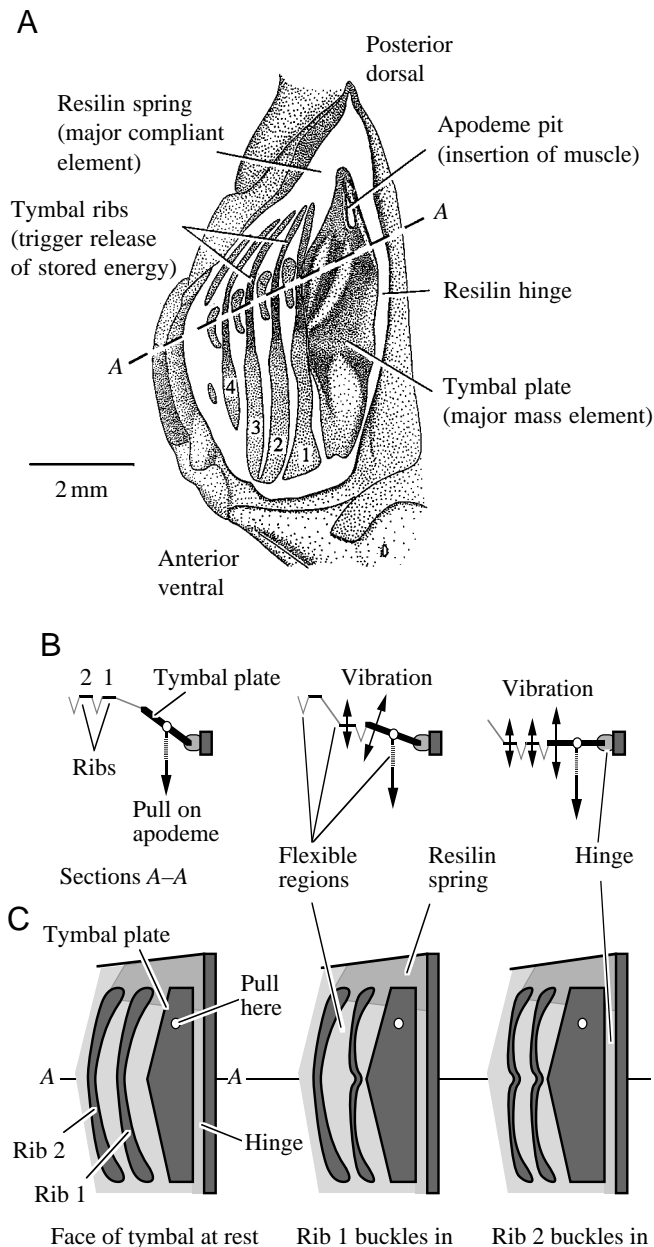


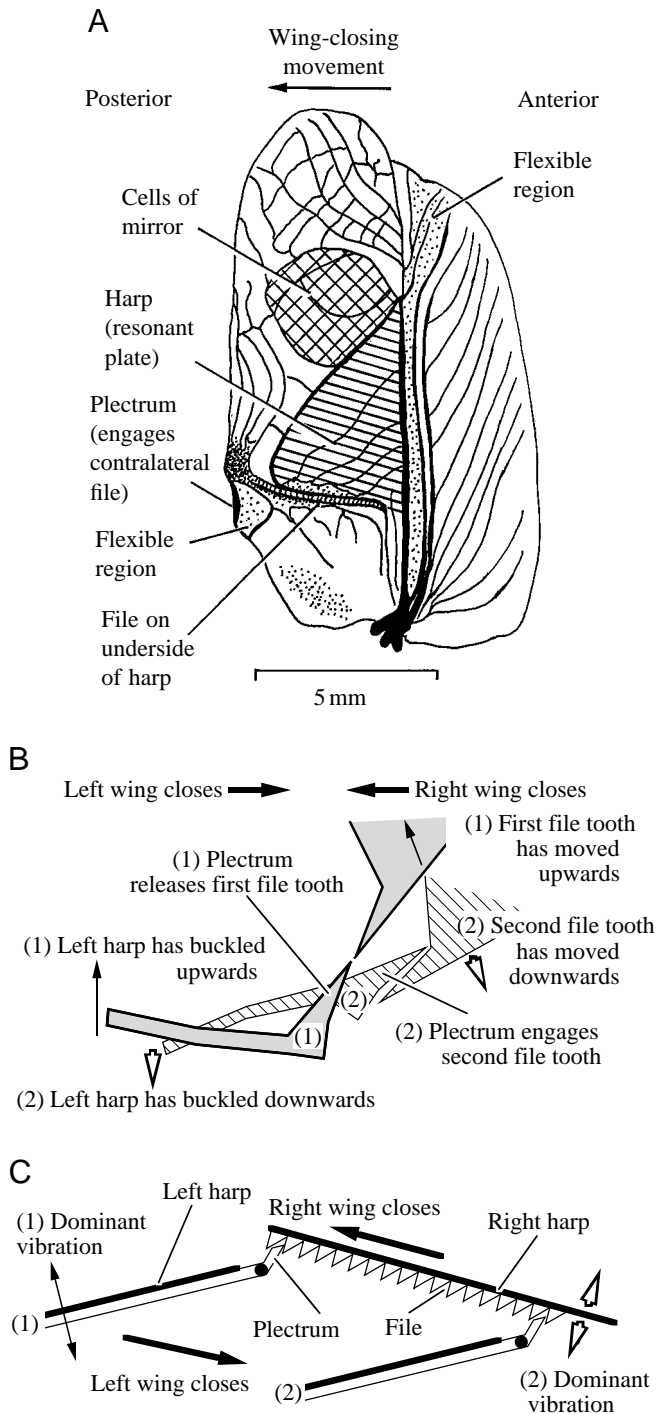
Fig. 5. (A) Drawing of the tymbal of the cicada *Cyclochila australasiae* to show the principal elements of the resonator. The tymbal ribs act as a series of triggers that release elastic strain energy that has been previously stored in the resilin spring; the ribs buckle in the region shown by the line A–A. (B,C) Diagrams of the mode of excitation of resonances in cicada tymbals. Left: inward movement of the tymbal plate is brought about by contraction of the tymbal muscle pulling on the apodeme. Initially, the movement is constrained by the bow-shaped tymbal ribs (shown in A). Right and centre: as each tymbal rib buckles inwards along the line A–A and becomes V-shaped, previously stored energy in the resilin spring is released, allowing the tymbal plate to move rapidly inwards and then vibrate. Although the tymbal ribs are partially decoupled from the tymbal plate by flexible regions of resilin-containing cuticle, it is likely that they contribute in turn to the mass and stiffness of the vibrating region (B,C, centre and right).

analysed in the same detail as the longer coherent pulses produced by gryllid crickets or cicadas. To produce these longer pulses, packets of energy are delivered to the sound-producing mechanism throughout the pulse, first initiating and then sustaining the sound-producing vibration *via* a frequency-multiplier mechanism.

In the case of many cicadas such as *Cyclochila australasiae*, the primary sound-producing structure is a tymbal (Fig. 5A), which bears on its convex surface a posterior large tymbal plate anterior to which runs a row of thin vertical ribs. Contraction of the tymbal muscle initially stores energy in the dorsal resilin pad until, at a critical force, rib 1 buckles and releases the stored energy (Bennet-Clark, 1997; Bennet-Clark and Daws, 1999); this is followed by the buckling of ribs 2 and 3 over a period of approximately 2 ms, which releases further packets of energy (Young and Bennet-Clark, 1995).

As each rib buckles, the energy that is released sets up a resonant vibration of the tymbal plate, initially at approximately 4.4 kHz for rib 1 then at approximately 4.2 kHz for rib 2 and then at approximately 3.9 kHz as rib 3 buckles (Bennet-Clark, 1997). This is seen in the insects' songs as a steady decrease in frequency during the pulse (Fig. 4A). This decrease may be explained by the sequential nature of the excitation of the vibration: as rib 1 buckles, it will become coplanar with and partially coupled to the tymbal plate (Fig. 5B,C), adding a component of its mass to that of the tymbal plate; then as rib 2 buckles, its mass will be added to that of the tymbal, etc. Assuming that the compliance of the system remains constant (for which there is no evidence), this type of sequential excitation, with sequential addition to the mass of the vibrating system, will lead to the stepwise decrease in the resonant frequency reported earlier (Bennet-Clark, 1997) and account for the decrease in frequency observed in the song (Fig. 4A), but the stepwise nature of this decrease in the natural song is obscured by smoothing due to the secondary resonator (see Bennet-Clark and Young, 1992, and the section on sound production involving coupled resonators).

In crickets, which typically produce long coherent song pulses, the sound pulse is produced by a closing movement of the forewings which, in *Gryllus campestris*, is right wing over left. A plectrum or scraper on the posterior edge of the lower (left) wing engages with ratchet teeth on the file, which is part of the Cu2 vein (Ragge, 1955) of the upper (right) wing (Fig. 6A), to multiply the 30 Hz wing-closing frequency to the song frequency of 4.5–5 kHz. As the wings are closed, successive catch–release cycles of the plectrum on the file provide a cycle-by-cycle drive to the adjacent harp resonators on both wings. The mechanism is thought to provide direct excitation, *via* the file, to the harp of the right wing and, *via* a phase inverter, to the harp of the left wing (Bennet-Clark, 1970, 1989) (Fig. 6B), which sets up in-phase resonances of the harps of both wings. A complication, so far little understood, is that the group of cells on the wing known as the mirror (Fig. 6A) can be set in resonance at approximately 6.5 kHz (Nocke, 1971), but this does not appear to be excited by the normal action of the plectrum on the file.



Although this mechanism excites both wings, they show some independence: if the harp of the left (plectrum-activated) wing is destroyed, only the last two-thirds of the pulse is at the normal song frequency; if the harp of the right (file-activated) wing is destroyed, only the first third of the pulse occurs at normal song frequency. This suggests that the plectrum-and-file mechanism excites the two wings differently at different stages of the wing-closing movement. In either case, the anomalous part of the pulse occurs at a far higher frequency than that of the normal song (Simmons and Ritchie, 1996): this

Fig. 6. (A) Drawing of the underside of the right forewing of the cricket *Gryllus campestris* to show the harp (the principal resonant structure, shown hatched) and the mirror (a subsidiary resonant structure, shown cross-hatched). Vibration of the harp is excited and sustained by cycles of release and engagement between the plectrum of the left wing and the teeth of the file on the right wing. The vein bearing the file is termed Cu2. (B) Diagram showing how both harps are set in vibration by the plectrum-file mechanism. In stage 1 (shown by stippling), the V-shaped plectrum on the posterior edge of the left wing buckles to release a tooth of the file on the underside of the right wing; before release, the buckling of the plectrum and file causes upward movement of both harps (arrows). Prior to stage 2 (shown by cross-hatching), both harps are free to buckle downwards (arrowheads), so the plectrum is able to engage the next file tooth. (C) Diagram showing how excitation of the resonant harp regions of the two wings may occur (1) at the start of the wing-closing movement (shown by arrows) and (2) when the plectrum is engaging teeth in the middle of the file (shown by arrowheads). The coupling between the two harps and/or their relative contribution to the overall resonance of the pair of wings is likely to change during the production of the sound pulse.

is expected if the mass of the system has been dramatically reduced (equation 1).

The dominant frequency of the songs of *Gryllus campestris* is significantly lower in insects with larger-area harps, and the frequency modulation of the song pulses that occurs is associated with bilateral asymmetry in the area of the harps, being greater in crickets in which the right harp is the larger (Simmons and Ritchie, 1996). However, even in crickets with apparently symmetrical harps, or in those in which the left harp is larger than the right, a fall in frequency during the song pulse can be seen (as in all the species of cricket described by Leroy, 1966; see also Fig. 4B).

From the harp-ablation experiments of Simmons and Ritchie (1996), it appears that the resonances of the two wings are excited at different phases of the sound-producing wing-closing movement.

At the start of the wing-closing movement, the left plectrum engages the posterior end of the right file (Fig. 6C). At this stage, the catch-and-release of the plectrum may depend more on the properties of the left wing than on those of the right wing because the tooth engagement only occurs at the posterior end of the file. By the middle of the stroke (Fig. 6C), the plectrum engages along the mid-line of the right harp, on which it is likely to have a more direct effect; also, the influence on the right harp of any additional mass-like component due to the left wing is likely to be greater when the wings are fully closed than at the start of the wing-closing stroke.

As yet, the evidence for interactions of this type is thin. However, Fig. 7B shows an anomalous song recording in which the closing movement appears to have ceased half-way through the pulse, after which the sound decays exponentially with a similar Q to that of isolated wings (c.f. Figs 3 and 7C). In this case, the instantaneous frequency during the decay is virtually constant, suggesting that the vibration is decaying freely. The decay occurs at a markedly higher frequency than that of the same stage of a normal pulse, suggesting that some

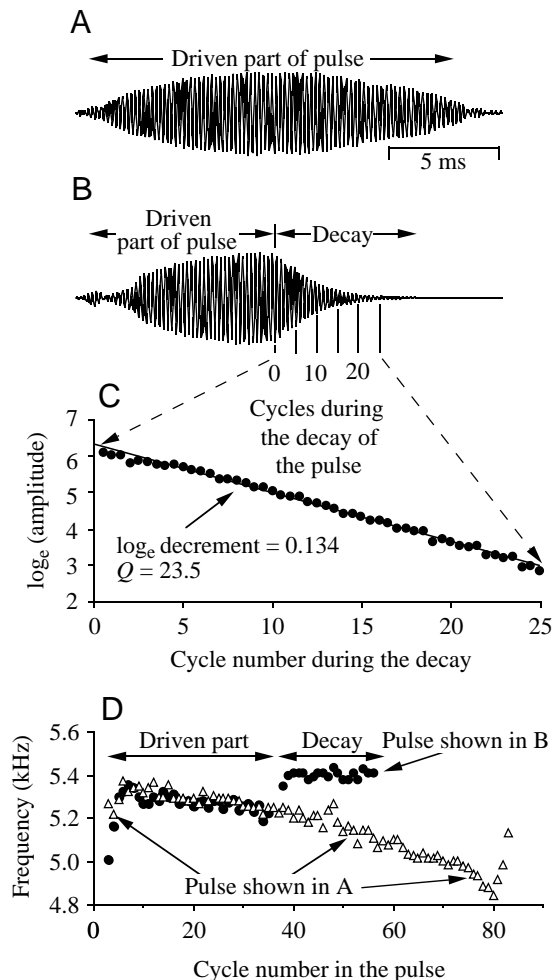


Fig. 7. Resonances in song pulses of the cricket *Gryllus campestris*. (A) Oscillogram of a typical second pulse. (B) Oscillogram of an anomalous second pulse produced by the same insect in the same recording. The duration of the driven part of this pulse is approximately half that of the normal pulse. (C) Graph of the natural logarithm (\log_e) of the amplitude against the cycle number in the decaying part of the pulse shown in B, as indicated by the arrows, showing that the decay is exponential. The quality factor, Q , is calculated from the slope of the plot of \log_e of the amplitude of the waveform (\log_e decrement) against the cycle number (see equation 2). (D) Plots of the instantaneous frequency against cycle number for the pulses shown in A (Δ) and B (\bullet). The frequency in the driven parts of both pulses is closely similar but, in the exponentially decaying region of the anomalous pulse, the frequency is far higher than that in the corresponding part of the normal pulse. The raw data in D were subjected to five-point smoothing. Oscillograms and measurements were made from a CD recording of orthopteran songs; Ragge and Reynolds (1998).

previous addition to the effective mass of the system has been removed.

The conclusion of this section is that, although many sound-producing systems appear to be simple resonators, the biological desirability may be to produce a long sustained pulse of sound, which requires successive excitations of the primary

resonator. The requirement for repetitive excitation during a single cycle of muscle contraction, as a part of the typical frequency-multiplication process that is involved, may substantially affect one or more elements of the resonant system and hence lead to changes in the frequency at which the system resonates.

Sound production involving coupled resonators

Small body size precludes efficient sound radiation (Bennet-Clark, 1971, 1995). In particular, the dimensions of the sound-producing structures may be small relative to the wavelength of the sound and, consequently, there may be an impedance mismatch between the insect and the surrounding air (Bennet-Clark, 1995, 1998). For good impedance-matching, the diameter of the sound source should be greater than one-third of the sound wavelength (see, for example, Olson, 1957; Fletcher, 1992); the insect sound-producing resonators discussed above, such as the tymbal of cicadas or the harp of crickets, are usually smaller than this optimum (Table 2).

In many of the insects producing louder sounds, transduction of muscle energy into sound energy is a two-stage process. Stage one uses muscle power to drive a small mechanical resonator, such as the tymbal or harp described above, which acts as the frequency-multiplier that determines the song frequency; I term this the primary resonator. This may then drive a second larger acoustic resonator from which the sound is radiated with better impedance-matching to the surrounding air. Some examples of these are given in Table 1, with their dimensions in Table 2, which shows that this second stage of transduction can greatly increase the effective area of the sound source.

Cicadas seem to have exploited this general principle with several different anatomical configurations. The tymbals of typical cicadas, such as *Cyclochila australasiae*, drive a secondary abdominal resonator, which can be modelled as a Helmholtz resonator (Fig. 2B) (Young, 1990; Bennet-Clark and Young, 1992) in which the two frequency-determining reactive elements are the compliance of the large volume of the abdominal air sac and the inertance of the large, acoustically transparent tympana or eardrums (Fig. 8A) through which the sound is radiated (Young, 1990). In the Australian bladder cicada *Cystosoma saundersii*, the tymbals drive a secondary resonator in the vast thin-walled abdomen, in which the compliant element is the volume of the air sac and the mass element is made up of thin flat areas of cuticle on the sides and ventral surface of the abdomen (Fig. 8B) (Bennet-Clark and Young, 1998). In yet other cicadas, such as the 'double drummers' *Arunta perulata* and *Thopha saccata*, each of the paired tymbals drives an exterior cuticular Helmholtz resonator, from the mouths of which the sound is radiated (Daws, 1996; H. C. Bennet-Clark, unpublished observations).

Among Orthoptera, the only examples of secondary sound radiators for which resonant properties have been established and tested using equation 2 occur in mole crickets (Bennet-Clark, 1987; Daws et al., 1996). All mole crickets so far studied

Table 2. Dimensions and properties of resonators involved in insect sound production

Insect	Typical cicada <i>Cyclochila australasiae</i>	Bladder cicada <i>Cystosoma saundersii</i>	Mole cricket <i>Scapteriscus acletus</i>
Song frequency (kHz)	4.3	830	2.7
Song wavelength (mm)	79	410	126
Optimal source diameter (mm)	25	130	40
Primary resonator (see Table 1 for elements)	Tymbal	Tymbal	Harp
Unloaded Q of primary resonator*	12	15	Not known
Size of primary resonator (mm)	5×3	6×5	4×3
Secondary resonator (see Table 1 for elements)	Helmholtz resonator	Thin-walled bladder	Horn-shaped burrow
Q of secondary resonator	6	9	≈ 2.5
Acoustic output from secondary resonator	Thin tympana	Thin wall of abdomen	Mouth of horn
Dimensions of secondary sound source (mm)	10×22	Two 10 mm diameter plus one 15×10	30×40

For details of the different types of resonators, see the text and Table 1.

*The values of the quality factor, Q , for the primary resonators were obtained after removal of the acoustic loading due to the secondary resonator; when loaded, far lower values of Q are likely.

For references, see the text.

radiate sound from a similar-shaped burrow (Bennet-Clark, 1970, 1987; Daws, 1996; Nickerson et al., 1979) in which the insect sings at the throat of a horn-shaped tunnel that has a large opening or openings to the surface (the dimensions for one species are given in Table 2); tuning depends on the length

and volume of a bulbous cavity at the throat of the horn and on the dimensions and shape of the horn (Daws et al., 1996). It appears that the insect tests and tunes its burrow while it is being dug (Bennet-Clark, 1987).

In all cases, these secondary resonators have been shown to be tuned to close to the frequency of the primary resonator and, in all cases, some fine tuning can occur by altering one or other of the reactive elements: in the case of typical cicadas, by extending the abdomen and/or adjusting the effective opening of the tympana; in the case of mole crickets, by adjusting the dimensions of the burrow or altering the position in the burrow from which the insect sings.

A secondary resonant load tuned to the same frequency as the driving resonator offers major advantages: because, at the resonant frequency, the impedance is purely resistive, the song frequency will be unaffected by the extra stage of transduction. Indeed, if the Q of the secondary resonator is high, the song energy may be confined to a narrower band; there is circumstantial evidence that this occurs in the cicada *Cyclochila australasiae* (Young and Bennet-Clark, 1995) and an extreme case is the remarkably constant frequency over

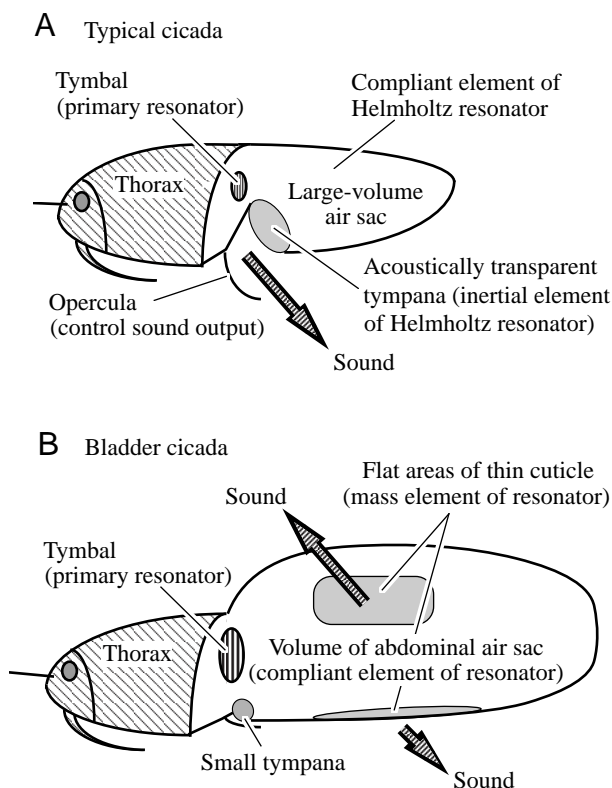


Fig. 8. Diagrams of secondary resonators used as impedance-matching mechanisms to increase the effective source size in cicadas. (A) Sound in typical cicadas is radiated from the large thin tympana, which form the inertial element of a Helmholtz resonator of which the compliant element is the large abdominal air sac (see Fig. 2B). (B) In bladder cicadas, sound is radiated from the thin-walled sides and ventral surface of the abdomen. The elements of this secondary resonator are the vibrating mass of the cuticle and the compliance due to the large-volume air sac. In both cases, the secondary resonators are driven by internal pressure changes caused by the buckling of the small tymbals.

most of the duration of the song pulses of the bladder cicada *Cystosoma saundersii* (Fig. 4C). Another effect of a secondary resonator may be to smooth the somewhat irregular amplitude of the pulse envelope produced by the primary resonator (Bennet-Clark and Young, 1992). A secondary resonator may also smooth out left-right asymmetries such as that between the two tymbals in a typical cicada (see Fig. 14 in Young and Bennet-Clark, 1995).

The two-stage transduction process has a further great advantage: because the effective source area of the secondary resonator is far larger than that of the primary resonator (Table 2), the impedance matching between the insect and the air is close to optimal. As a result, the efficiency of transduction of muscle power into sound power can be remarkably high. Transduction efficiencies of 17–34% have been estimated for the mole cricket *Gryllotalpa vineae* (Bennet-Clark, 1970), while more direct measurement suggests transduction efficiencies of 18–46% in the cicada *Cyclochila australasiae* (Bennet-Clark and Daws, 1999).

Discussion

Long-range sound communication has parallels with radio communication, which involves transmission of a tuned signal that may be detected at a distance by a receiver tuned to the same frequency. By tuning the sender and receiver to the same frequency, interference from background noise can be reduced. By confining the power in the signal within a narrow band, the signal amplitude within that band can be increased. By tuning the receiver sharply, its effective sensitivity can be increased.

There is a trade-off. If the signal is to convey complex information, it must be modulated, either in amplitude or in frequency. An amplitude-modulated signal is made up of the centre frequency and a series of side-bands at the centre frequency plus and minus the modulating frequency: a 10 kHz signal modulated by a sine wave at 1 kHz will be made up of components at 9, 10 and 11 kHz; if the modulation is not sinusoidal, the pattern of side-bands becomes more complex.

Similarly, if a signal is very brief, conversion of the time domain to the frequency domain introduces side-bands, so a 1 ms pulse (equivalent to 1 kHz) at 10 kHz has components at 9, 10 and 11 kHz; and, once again, if the modulation is not sinusoidal, the pattern of side-bands becomes more complex (see, for example, Fletcher, 1992, chapter 15; Randall, 1977).

In practice, insect song tends to require a compromise between a pure tone for range and specificity, and a broad bandwidth within which large amounts of information can be conveyed. The analogy with radio engineering is the relatively pure tone signal, with a bandwidth of only 1 kHz, that is required for Morse code signalling against a bandwidth of at least 5 MHz that is required for a television signal. Also, although extremely sharply tuned signals and receivers may be a *beau ideal*, biological reality introduces variability, with tuning errors or mismatches between the sound producers or receivers both within and between individuals.

Thus, the desirable level of tuning of both sender and

receiver is that tuning should be broad enough to provide the required bandwidth to convey the biologically meaningful signal and to take account of individual variation but narrow enough to give species-specificity.

Various questions remain. Given the biological variability of both the sending and receiving insects, is tight control of the song frequency desirable? Given the sort of variability that has been shown to occur both between conspecifics (e.g. Fig. 4A) and within the song of an individual (e.g. Fig. 7), does this variability offer cues on which female choice may be based? So far, there is direct evidence showing that female crickets prefer larger males that produce lower-frequency songs and more-symmetrical males that produce songs with less frequency modulation (Simmons and Ritchie, 1996), all of which depends on an auditory system that is capable of good frequency analysis.

Resonant sound-producing mechanisms occur in many insect groups. Some advantages of confining an acoustic signal to a narrow frequency band and some of the problems encountered in the production of narrow-band signals by insect sound-producing mechanisms have been described. It must, however, be remembered that many insect singers, such as grasshoppers and many bush crickets, produce broad-band songs in which there is little or no evidence of the excitation of a resonator and in which hearing also extends over a broad frequency band.

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