THE MECHANICS OF STRIDULATION IN BUSH CRICKETS (TETTIGONIOIDEA, ORTHOPTERA)

II. CONDITIONS FOR RESONANCE IN THE TEGMINAL GENERATOR

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INTRODUCTION

The earlier of these two papers (Bailey, 1970) proposed that, at least in the genus *Homorocoryphus*, the predominant or peak frequency in the sound spectrum is radiated by the frame of the so-called mirror of the right tegmen. Pasquinelly & Busnel (1955) pointed out that in general there are four principal mechanical methods for throwing any sound emitter into vibration.

(1) Each stimulation may throw the emitter into vibration at its natural frequency of free vibration, so that it produces a pulse, or train of waves at this frequency, decaying more or less rapidly before the next stimulation (here the number of stimulations per second appears as a pulse repetition rate, not a spectral frequency). This was illustrated in their paper by the songs of *Ephippiger* and *Platycleis* (Tettigonioidea) and is similarly illustrated in this paper by *Conocephalus discolor* (Thunberg) (Fig. 1).
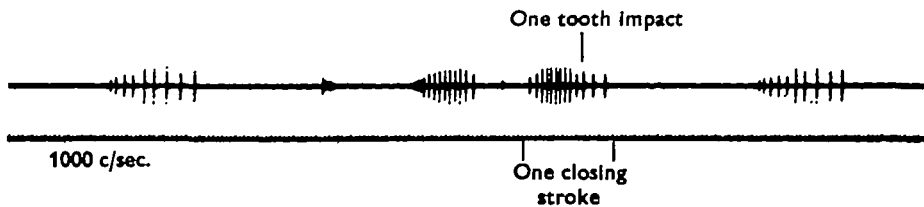

Fig. 1. The song of *Conocephalus discolor*, showing the closing stroke of thirteen discrete tooth impacts.

(2) The stimulating mechanism, if regularly periodic, may drive the emitter into forced vibration at a frequency equal to the number of stimulations per second, and unrelated to the emitter's own natural frequency of free vibration.

(3) A combination of the above two cases. The number of stimulations per second almost coincides with the natural frequency of the emitter, so that each stimulation now evokes one wave, reinforced by the next before any decay can set in; this has the effect of greatly amplifying the total energy emitted, through the virtual elimination of the damping effect of acoustic impedance. The condition is resonance, and the frequency of the resonant vibration is marginally higher than that of free vibration (for discussion see Broughton, 1963*b*, p. 848); each wave is a monocyclic pulse (Broughton, 1963*a*),

but the whole series of monocyclic pulses now simulates a simple homogeneous wave-train or the conventional pulse. Such a condition can arise in a strigilating insect (Leston & Pringle, 1963) if the plectrum sweeps a regular series of teeth at the right rate; the whole stroke of the plectrum then generates a more or less homogeneous wave-train of this type. Because the true resonance phenomenon tends to produce smoothly rising and decaying 'pulses', lacking in initial or final transients, the sound has a more musical quality than type (1) described above (which is rich in transients). This is the case in most grylloids (Pasquinelly & Busnel, 1955, fig. 2) and many tettigonioids, illustrated for *Homorocoryphus* by Fig. 2.
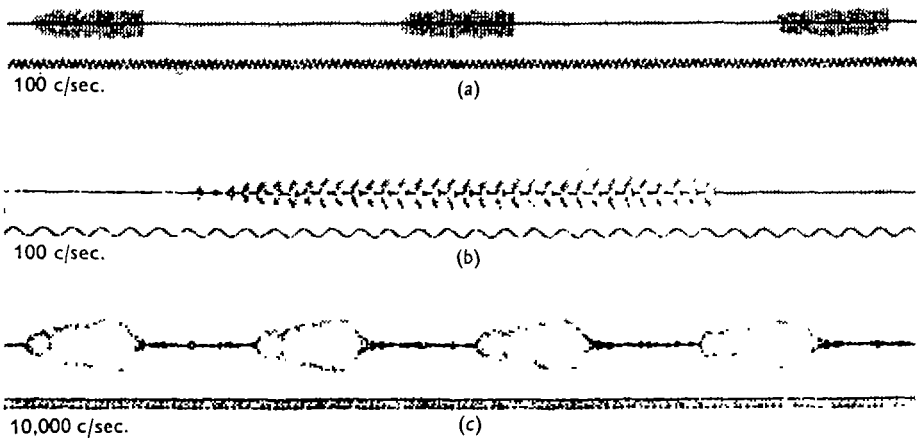

Fig. 2. The song of *Homorocoryphus nitidulus vicinus* showing (a) three chirps of (b) 33 syllables (closing stroke only is visible). (c) is part of (b) expanded to show the homogeneous wave form within each syllable.

(4) A fourth system is possible, in which the tegminal emitter has no particular natural frequency of vibration of its own but emits a damped pulse of something approaching 'white' noise at each impact. The total sound energy would thus be distributed over a wide band of frequencies instead of being concentrated into a single frequency and so would be expected to have a smaller topographic range. The single-frequency principle would seem to have more selective advantage in an animal depending on its singing efficiency.

But in all cases a greater or lesser area of the tegmen as a whole could act as a broad-band sounding board, amplifying unselectively the particular frequencies that happen to be generated by the narrow-band principal emitting structures such as the mirror frame.

It is difficult to vary the properties of the stable acoustic system of the stridulatory apparatus in the live insect, but isolation of the tegmina by the technique described in the previous paper (Bailey, 1970) overcomes most of these difficulties. The present paper considers the effect of varying some of these properties upon the position of the spectral frequency peak, upon the intensities in this region, and upon the homogeneity of the wave-form—essentially the contrast between resonant and non-resonant conditions.

METHODS

(1) *Recording and analysing*

The principal techniques used throughout these experiments have been described in the previous paper (Bailey, 1970); however, in some of the experiments cited in this paper the Brüel and Kjaer octave filters (Type 1612) have also been used. This is a system of band-pass filters capable of selecting single or one-third-octave bands of the sound emitted by the tegmen, and excluding all others. In these experiments the band from 11·05 to 13·95 kHz., centred on 12·5 kHz., was selected; this is the region which
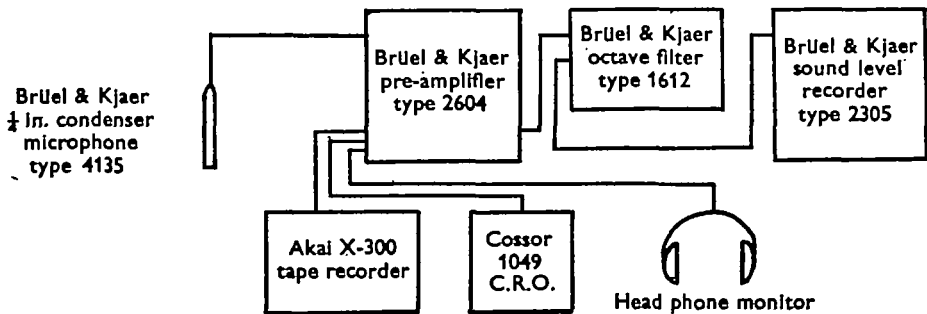

Fig. 3. The experimental arrangement for recording the sound-pressure levels from the actuated tegmen whilst the parameters controlling the tooth impact rate are being varied.
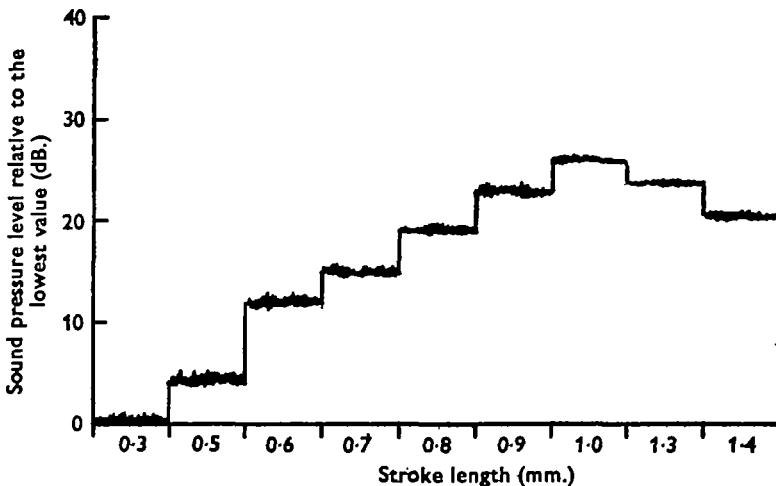

Fig. 4. A specimen analysis of sound-pressure levels from the actuated tegmen operated at 120 syllables per second and varied in stroke from 0·3 to 1·4 mm. The sound-pressure levels are relative to that at the lowest stroke length (0·3 mm.).

includes the predominant fequency peak of the actuated, as distinct from the natural preparation. The sound was picked up by the Brüel and Kjaer ¼ in. microphone (type 4135) placed 2·5 cm. from, and vertically above, the tegmen, and amplified through the Brüel and Kjaer pre-amplifier (type 2604), before passing through the octave filter set (Fig. 3). The sound-pressure level was then recorded on the Brüel and Kjaer level

recorder (type 2305) which gave a graphic representation of the sound level at each of the selected tooth impact rates (Fig. 4); the signal could be monitored both by earphones and by an oscilloscope. The unfiltered sound was also recorded on magnetic tape by an Akai X-300 tape recorder at 15 i.p.s. (upper frequency limit of 28 kHz.) and subsequently analysed by oscillography or by slow playback on the Kay sonagraph

(2) *Changing the parameters of movement*

It was established in the previous paper and by Bailey (1967) and Morris & Pipher (1967) that the frame acts as the tegminal generator; this paper describes the effect of altering the parameters of the generator driving system, in this case the passage of the plectrum across the file. This is readily achieved with the actuator described (Bailey, 1970) both by changing the stroke length at a constant syllable repetition rate, and *vice versa*; both in effect alter the rate at which the plectrum passes over the file, and hence the tooth-impact rate. However, in practice a difficulty was experienced in that when either parameter was altered the complete stroke position tended to move toward the anal field, because the coil of the loudspeaker was being drawn in over the soft iron core. This factor presented no difficulty in the routine 'mirror frame' experiments but became important when the number of teeth swept by the plectrum had to be estimated. It was overcome by increasing the stroke length at a constant repetition rate, as this value was subject to least change, and any change taking place could be observed by stroboscopic illumination. Movement of the median of the stroke when the syllable repetition rate was increased from 70 to 190 per second was no more than 0·2 mm. as observed on the calibration graticule.

The analysis of the effects involved the following procedures: (1) The syllable repetition rate was selected for the given series and the plectrum was centred on the file by the method described in Bailey (1970), ensuring that at the upper limits it did not ride over either end of the file. (2) The smallest stroke length was measured by the calibration graticule and the sound-pressure level was recorded on the Brüel and Kjaer level recorder. (3) The stroke length was increased, measured, and the sound-pressure level was recorded for each increment up to the maximum stroke length. The syllable repetition rate was then increased and the whole procedure was repeated. Thus for each syllable repetition rate a step-wise trace (Fig. 4) was obtained showing the increments of sound-pressure level against increments of stroke length; and the whole assemblage of step-wise traces gave an overall indication from which the optimum rate of tooth impact (i.e. that producing the maximum sound-pressure level) could be determined.

The reason for measuring the sound energy in a whole band rather than the one peak frequency was to avoid falsification of results by phenomena of reflexion, absorption and phase interference of partials. At the wavelengths concerned (2·5–3·0 cm. in the region of 12 kHz.) a single-frequency determination would be far more susceptible to this kind of error than is a whole band, and this applies equally to the actuated preparation and to the live insect.

<center>RESULTS</center>

Fig. 5 summarizes five series of experimental determinations of the changes in sound-pressure level resulting from variation of the tooth-impact rate. Each value is the maximum of a series obtained by varying stroke length at a given fixed syllable repetition rate, so the whole plot indicates how syllable repetition rate has to vary with stroke length so as to give maximum sound pressure level. The line drawn in the
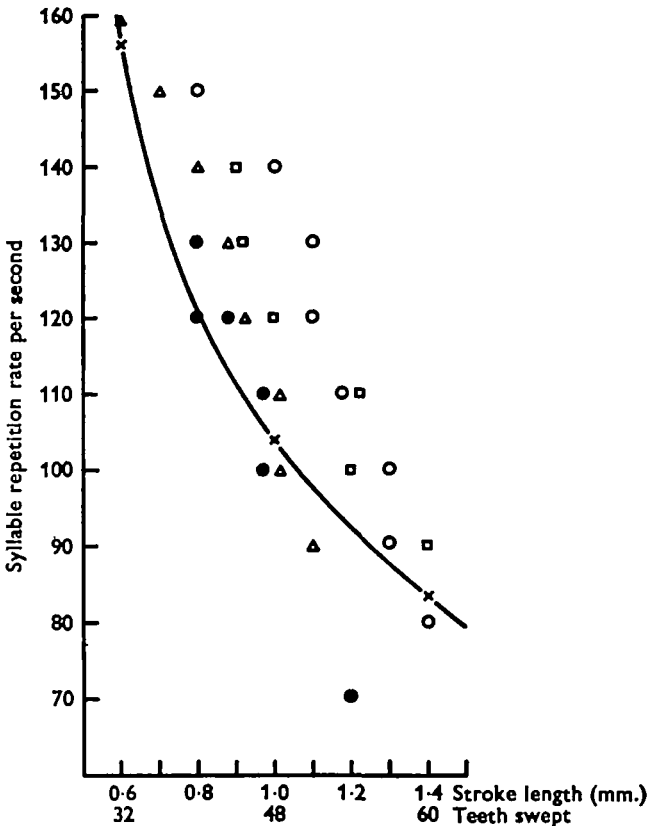

Fig. 5. Five experiments where the parameters controlling the tooth impact rate have been altered. Each symbol represents that tooth-impact rate (a function of syllable repetition rate and stroke length) which produces the highest sound-pressure level in its own stepwise trace (Fig. 4) in the frequency band 11·05–13·95 kHz. The solid line indicates the expected syllable repetition rate and stroke length of a (corrected) tooth-impact rate of 12,500 per second. The tooth numbers have been estimated from photomicrographs.

figure is part of the hyperbola representing the relation between syllable repetition rate and stroke length (expressed in number of teeth swept, for a fixed tooth-impact rate of about 12,500 tooth impacts per second; for the method of arriving at this figure see below).

The calculation of the mean tooth-impact rate is quite straightforward; at a syllable repetition rate of s syllables per second (equal to audio-generator frequency) one to-and-fro movement is executed in $1/s$ sec. The number of teeth (n) included in the given stroke length is swept in each half of this period, i.e. in $1/2s$ sec.; therefore in

1 sec. $2ns$ teeth are swept and this is the mean tooth-impact rate; but it requires to be multiplied by a correction factor discussed below.

Oscillograms of the sound from the actuator show that the time occupied by the signal is a fraction of the total syllable time (see, for example, upper trace, fig. 4b, Bailey, 1970); the silent intervals (not so apparent in the live insect's song) account for about $\frac{1}{5}$ of the syllable time. This effectively makes the tooth impact rate $\frac{5}{4}$ $(2ns)$ seconds.
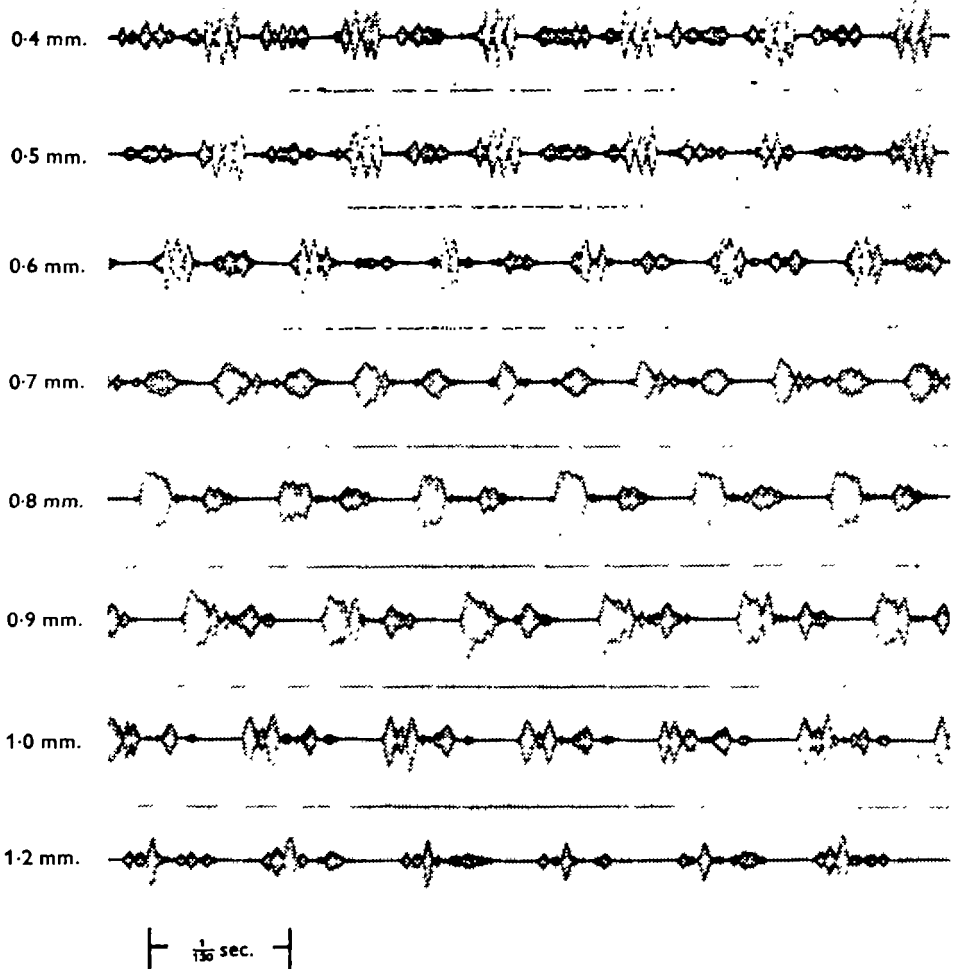

Fig. 6. Oscillographic analyses of the effect on the homogeneity of the signal produced by increasing the stroke length from 0·3 to 1·2 mm. when the actuator frequency is constant at 130 syllables per second.

The stepwise analysis and the oscillograms (Fig. 6) show that when the tooth-impact rate and the natural frequency of the tegmen coincide the sound energy is greatest and the wave-form most pure. In Fig. 6 the homogeneity of the half-syllable becomes evident when the stroke length approaches 0·8 mm. at 130 syllables per second. At this point the value of the tooth-impact rate, calculated from the above

formula, is ($\frac{5}{4} \times 2 \times 130 \times 40 =$) 13,000 teeth per second, which agrees well with the experimentally determined natural frequency of the actuated tegmen at 12–14 kHz. (e.g. Fig. 3(a) B in Bailey, 1970). The number of teeth swept (40—see Fig. 5) is derived from photomicrograph estimates. The situation becomes less clear when, in the values on either side of the optimum in Fig. 6, the sound envelope does not break up completely. Fig. 7 is a sonagram of the natural song of the subspecies *H. n. nitidulus* which differs from *H. n. vicinus* (W. J. Bailey, in preparation) in certain features but not essentially in its mechanism of sound production. Here the harmonics of the song are evident where the recording (initially on an Ampex 307 modified instrument
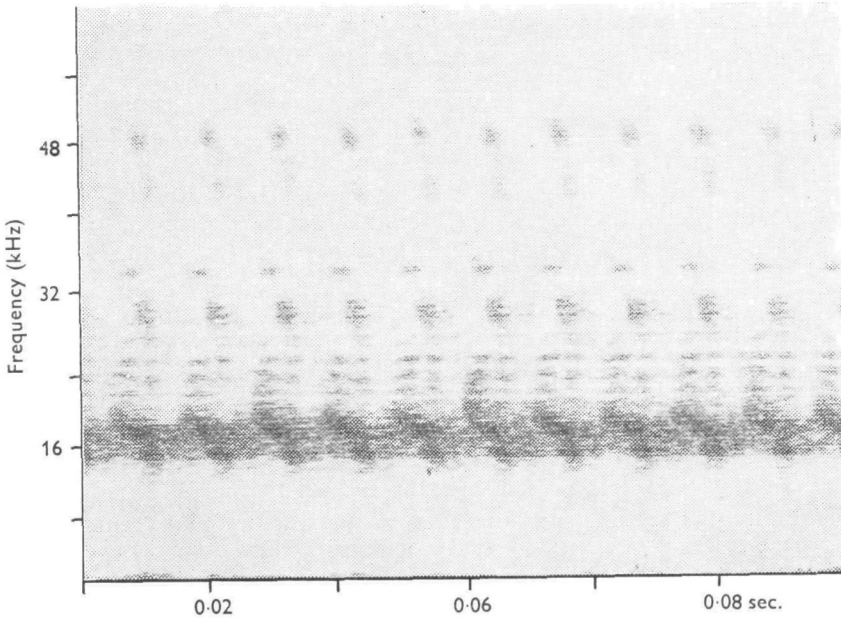

Fig. 7. A sonagram of the continuous song of *Homorocoryphus nitidulus vicinus* showing the glissando effect in each syllable, and the presence of harmonics above the 16 kHz. fundamental.

recorder with Brüel and Kjaer condenser microphone and pre-amplification giving an upper frequency limit of 60 kHz.), has been greatly reduced in play-back speed to accommodate the upper frequency limits imposed by the sonagraph. Sonagrams of *H. n. vicinus* at comparable refinement have not yet been made. The fundamental is here clearly seen as a glissando starting at 17 kHz. and slipping down to something in the region of 14 kHz. Partials at about the position of second and third harmonics are present, the latter being close to 48 kHz.; also present are a number of other partials.

DISCUSSION

Resonance and free vibration

From the definition of resonance (B.S. 661/1022) it is clear that not only must there be a structure capable of free vibration but also a system to drive this element at its resonant frequency.

The area responsible for sound propagation has been established (Bailey, 1970) as

the frame of the right tegmen; it was also shown that this has a natural vibration frequency close to that determined by frequency analysis of the recorded song. These studies, and those of Morris & Pipher (1967) showed that the direction of movement of this piece of cuticle is perpendicular to the surface of the tegmen; it may act as cantilever with an axis of rotation or a simple pivot near the vestigial file (Fig. 8, point *a*).

The driving frequency in *H. nitidulus* is the tooth-impact rate during the closing stroke of the tegmina. (A fact very easily established by provoking the insect to make some stridulatory movement whilst its tegmina are covered in 'wet' latex, the action being thus slowed down to resolvable speeds.) Resonance clearly does not occur in *C. discolor* where each tooth impact merely sets the tegmen vibrating at its natural frequency, the pulse quickly decaying before the next impact.

Tooth-impact rate

If the tooth-impact rate fails to coincide with the natural frequency of the mirror frame for any substantial part of the stroke, resonance will be impaired. Structural irregularities in the file will, unless compensated for, impair resonance in this way. The teeth are in fact farther apart towards the lateral end of the file, but the direction of movement is towards this end of the file, since in the natural song it is the closing stroke that produces the main sound. If the situation is comparable to that in the Grylloidea (Bentley & Kutsch, 1966) the muscle power is presumably mostly used in the closing stroke, and a repetition rate of 130 movements per second (period 8 msec.) is high enough to suggest the likelihood of some click mechanism. If this were the case (the problem is now being studied) the velocity would increase towards the end of the stroke, compensating for the increased separation of the teeth.

Thus the differential spacing of the teeth need not impair the efficiency of resonance; in fact the glissandos in Fig. 7 show that despite any compensating velocity changes that may occur the frequency of the system does fall towards the end of each stroke, to the extent of a few thousand cycles. On the other hand, the frequency spectrum of the natural song (fig. 3(*a*) *A*, Bailey, 1970) has a broad peak, which would be consistent with the system's being a resonator of low 'Q', capable of resonating to all these frequencies.

It is suggested, therefore, that the insect has a reasonably efficient wave generator at the plectrum, which activates the vibrating system within the frequency range of its 'Q' resonance curve, the width of the latter compensating for the lack of efficiency of the former. However, such a wide 'Q' curve makes the physical and mathematical analysis of the system practically impossible, a factor singularly recommending studies on the Grylloidea, where the 'Q' curve is remarkably narrow although the problem of phase is perhaps more complex (see later in the Discussion).

The plectrum in its passage over the file is acting as a phase inverter. The pivot (*a*) (Fig. 8) inverts the phase at the plectrum so that the vibrating end of the frame is in opposite phase to it. Thus, when the plectrum (*g*) is under tension on impact with a tooth, the arm of the mirror frame (*ac*) will be forced into the position tending to equilibrium; the period of this is half a cycle (*dcb*), i.e. 0·3 msec. Once the plectrum has left the tooth the remainder of the cycle will be completed—by the elasticity of the system, the frame springing back to the opposite position by the time the next

tooth is struck (Fig. 8, iii). The timing of this must be in phase at the resonant frequency; however, at the end of the stroke, due to the decreasing tooth-impact rate, the two elements will slowly come out of phase, thus producing a partial damping effect which may amount to complete damping when the plectrum stops for its return stroke. Part of the build-up and decay times of the signal may be attributable to this, as well as to the normal inertia of the resonant system.
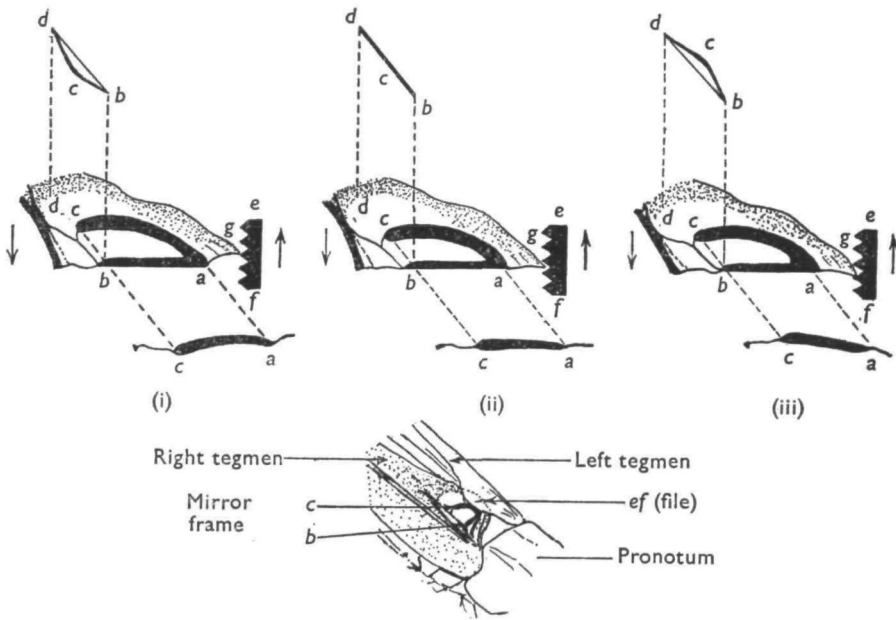

Fig. 8. Diagram showing the mode of vibration of the mirror frame of *Homorocoryphus nitidulus*. The inset below shows the position of the stridulatory apparatus relative to the insect, the right tegmen bearing the mirror frame, and the left tegmen the file. The centre three diagrams show the plectrum (*g*) moving across part of the file (*ef*); the strain on the plectrum acts about the cantilever pivot (*a*), causing the tip of the frame (*c*) to move in the opposite direction. (*c*) is therefore the point of maximum displacement of the cantilever (*ac*). The upper diagram (*dbc*) shows the vibrational mode across the mirror: (i) shows the plectrum about to leave the tooth; (ii) an intermediate stage; and (iii) just before striking the next tooth.

Acoustic coupling

The problem of acoustic coupling is perhaps more complex and involves the mechanical-to-air transducer, i.e. the mirror region. The frame is surrounded by membrane except of course at its connexion to the vestigial file and plectrum, at which places the archedictyon tends to become increasingly dense. From the probe microphone studies (Bailey, 1970) there appeared to be an antinode over the far end of the heavy frame or rather closer to the junction of the cross vein of the cubital. The node occurs over the mirror membrane and over the distal membranous region outside the frame; this latter area is of course damped by the increasing thickness of the archedictyon. The fact that the pivot lies between the plectrum and the main antinode and divides the distance between them in the ratio of the order $\frac{1}{3}-\frac{1}{4}$ suggests that the genesis of the second and third harmonic, or both (Fig. 7), may be sought in this relationship;

but more detailed study is now required to establish this or otherwise, and is in progress.

So far only the vibration of the solid elastic system has been discussed and resonance has been implicated only as a possible feature of this system. The coupling with air, however, may or may not involve resonance of air masses. In the simplest case the ambient air will be merely thrown into vibration as a free-field system, in which all resonances found can be attributed simply to the vibrating tegminal system itself. Now, the main frequency of 15 kHz. would have a ½-wavelength of some 1·2 cm. in air; the distance between the tegmina and the dorsum of the insect is clearly much less than this, but if the length of the subtegminal air space is taken into account, the air column could be of the right order for air-column resonance to take place. The fact that resonance can be detected in the isolated tegmina, where there is no such air-column, does not necessarily exclude air-column resonance from being added to that of the solid system in the living insect. Such a dually based system of resonances would more simply account for the breadth of the frequency peak in the natural song spectrum, although this clearly is not the only factor contributing to this. H. C. Bennet-Clark (in preparation) has further shown that in Gryllotalpidae the two tegmina may act in push-pull (giving effectually two circular resonance systems mutually coupled), but this is unlikely in *H. nitidulus* because of gross differences between the tegmina. In *C. discolor*, since there appears to be no resonance but only free vibration, the loading due to the air column presumably adds to the damping.

The final problem is that of decoupling the vibrating structures from the surrounding tegmen. This is achieved in *H. nitidulus* by the membrane between the cubital complex and the median vein being thin and folded in such a way as to give maximum freedom from the heavily sclerotized, and therefore damped area of the medius and radius.

In summary then, the present study shows that the tooth-impact rate in those insects using a resonant system drives a complex transducer, which in the case of *H. nitidulus* consists of a rigid vein partially surrounded by thin cuticular membrane allowing free or resonant vibration. In those bush crickets in which resonance is not employed the vein acts merely as the passive radiator of the often ultrasonic signals; each tooth impact evokes the natural frequency of free vibration of the system, which is quickly damped by mechanical or air impedances or both.

The analysis of the physics involved would need a refined mathematical approach beyond the scope of these authors. The sound emitted from its system is not pure, but consists of a number of frequencies within a more-or-less narrow spectrum, therefore any calculation must be an analysis of a fundamental which changes rapidly as the plectrum passes along the file, and at spectral frequencies the harmonics of which, in this almost certainly non-linear system, would produce serious intermodulation preventing any accurate assessment of the detailed sound-energy distribution.

SUMMARY

1. Using isolated tegmina of the bush cricket *Homorocoryphus nitidulus vicinus* (Walker) mounted on the actuator described in a previous paper the parameters controlling tooth-impact rate have been varied.

2. Results have shown that the mirror frame can be thrown into resonant vibration at between 12 and 15 kHz. when the tooth-impact rate approaches these values.

3. The situation in the *Homorocoryphus* type of stridulation is compared with that of the *Conocephalus* type where resonance does not occur.

4. The tooth-impact rate in *H. n. vicinus* is coupled with the frequency of natural vibration of the mirror frame via a plectrum-pivot-frame system which is made to act as a cantilever with the pivot at the mesial end of the vestigial file and the plectrum as the point of excitation.

5. The problem of acoustic coupling involving mechanical and air-column systems is discussed.

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