

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

I. THE TEGMINAL GENERATOR

By W. J. BAILEY

Department of Zoology, University of Newcastle upon Tyne, England

(Received 28 October 1969)

INTRODUCTION

The production of sound by bush crickets is an established phenomenon, and reviews of the stridulatory mechanics and associated behaviour are numerous, the most recent by Haskell (1964) and Alexander (1967). The fact that many bush crickets emit ultrasonic frequency components in their song is also well known, and the mechanisms behind this are discussed by Pierce (1948), Busnel (1953), Pasquinely & Busnel (1955), Broughton (1963, 1964), Suga (1966), Morris & Pipher (1967), and Bailey (1967). Pierce (1948) was the first to give any systematic evidence on the actual mechanism involved, and it has been his hypothesis that has held the dominant position over the past two decades. He suggested that the area of thin membrane bounded by the cubital complex on the right tegmen—the so-called mirror—acted as a sound-producing disk, which was forced into vibration by the plectrum (the anal margin of the same tegmen) striking on the teeth of the file on the cubital vein on the left tegmen. In some cases he suggested that the disk vibrated in resonance with the tooth impact rate.

This hypothesis was first criticized by Broughton (1964), who questioned the validity of Pierce's use of certain physical criteria in connexion with the mirror membrane. Broughton established that, at least in *Metrioptera roeselii* (Hagenb.), when this membrane was damped with a film of latex, the predominant ultrasonic frequency component was not always changed. Such a finding was confirmed by me (Bailey, 1967) with *Conocephalus discolor* (Thunb.); however, with the related *Homorocoryphus nitidulus nitidulus* (Scopoli) I found that a change invariably occurred but not as great as would have been expected if the mirror membrane alone was responsible for the production of the main frequency peak. I suggested that the latex was having a secondary influence on the mirror frame (that part of the cubital complex surrounding the mirror membrane). This was concurrently confirmed by Morris & Pipher (1967) working on *Conocephalus nigropleurum* (Bruner). They punctured the mirror membrane in various places and found that there was no substantial frequency change in the total frequency spectrum of the treated insect. They went further and suggested that the mirror frame was acting as a cantilever with its rotational axis about the vestigial file. They arrived at this conclusion after comparing the predominant frequency, and the mirror frame length, of two genera, *C. nigropleurum* and *Orchelimum gladiator* (Bruner); and they applied a formula extracted from Rayleigh (1894) to demonstrate that the two parameters were comparable and had a direct relationship with each other.

The present paper attempts a new approach to the problem by examining the tegmen in isolation, in the first case by artificially rubbing the right tegmen across the left, using a mechanical actuator, and in the second by causing the right tegmen to radiate in resonance with a contact transducer. These techniques were used to find which part of the cubital complex is responsible for the radiation of the predominant frequency peak. A subsequent paper (Bailey & Broughton, 1970) deals with the way in which this part of the tegmen is brought into vibration.

MATERIAL AND METHODS

(1) *Insects*

The insect used throughout these experiments was *Homorocoryphus nitidulus vicinus* (Walker), originally from Uganda, and at present cultured in the laboratory (Hartley, 1967). The insect was chosen following preliminary experiments on the European subspecies *H. n. nitidulus* (Scopoli) (Bailey, 1967).

(2) *Recording and analysing*

For recording the live insect, an Akai X-300 tape recorder was used, modified in circuitry at 15 i.p.s. to respond within ± 2 dB. to the frequency range 200 Hz. to 28,000 Hz. A $\frac{1}{4}$ in. Brüel and Kjaer condenser microphone, type 4135, was used in conjunction with the pre-amplifier type 2604 which had a flat frequency range up to 90,000 Hz. (± 2 dB.). Little attention was paid to the intensity of the song of the living insect as no serious attempt was made to maintain a uniform insect/microphone distance (which, however, seldom exceeded 20 cm.—see also Bailey & Broughton, 1970). The song, recorded on magnetic tape, was analysed by the Brüel and Kjaer frequency analyser type 2107, and registered on the B. and K. level recorder, type 2305. Oscillographic analyses of the low-order components were made with either a Cossor 1049 Mk. IV oscilloscope or in more detail, including the distribution of some of the higher frequency components, by the Kay Sona-graph.

When analysing the signal from the actuator (*q.v.*), magnetic tape was seldom used, as it was found more convenient to record direct on the level recorder, from the microphone via the frequency analyser.

(3) *Actuation and latex damping of the mirror region*

Examination of the action of the tegmen of bush crickets is hindered by the inaccessible position of the stridulatory organ whilst in motion and by the fact that most bush crickets do not sing continuously, especially under experimental conditions. The technique of isolating the tegmina allows full accessibility and therefore a completely new examination of the stridulatory mechanics. Further, all parameters affecting the production and radiation of sound may be controlled and their effects examined.

The relative motion of the tegmina, during stridulation, is approximately a simple harmonic motion. Actuation replaces muscular activity by an audio-generator fed into a device moving one tegmen against the other in as near a natural manner as possible.

The right, plectrum-bearing, tegmen is held against the left, file-bearing, tegmen (Fig. 1*D*), which is mounted on a reciprocating rod (*a*). This rod, attached to the

periphery of the coil of a loud speaker (*c*), is driven by the amplified signal from the signal generator. A peak-to-peak travel of 1.4 mm. at 140 Hz. can be produced, which ensures that most of the file traverses the stationary spectrum in a single stroke. Calibration of the stroke length is made by mounting a thin pin perpendicularly on the rod, between the bearings (*d*) and parallel to the mounting table (*f*). Beneath this is a suitable graticule (*b*), on which may be measured the distance between the two lines formed optically by the limits of the stroke of the fast-moving pin. The complete action of the tegmina, stroboscopically illuminated, is viewed under a binocular microscope.

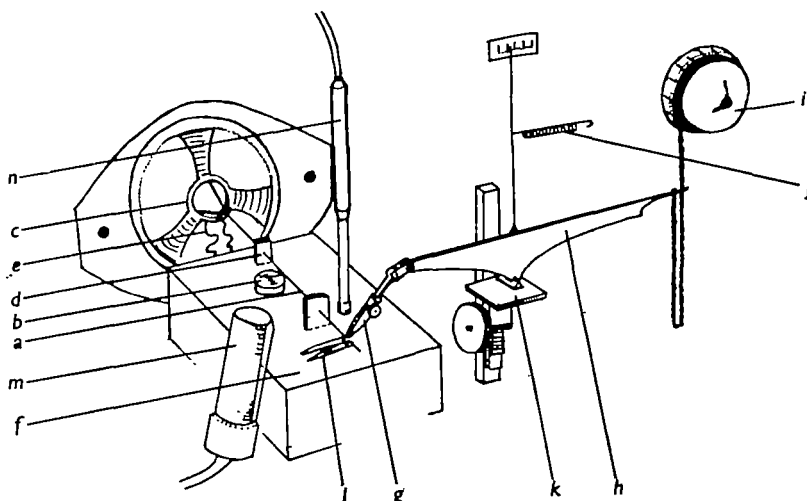


Fig. 1. Actuator and balance manipulator. (*a*) Stainless steel rod; (*b*) graticule; (*c*) loudspeaker; (*d*) bearing for rod; (*e*) coiled wire leads from attenuator to speech coil; (*f*) cork platform; (*g*) screw forceps; (*h*) chain balance arm; (*i*) calibrated drum; (*j*) damping spring; (*k*) rack-and-pinion controlling stage; (*l*) tegmina; (*m*) stroboscope lamp; (*n*) Br  el and Kjaer $\frac{1}{4}$ in. microphone.

The right tegmen is clamped by forceps mounted on a balance manipulator (Fig. 1). This consists of a chain balance, modified to take a universal-jointed clamp forceps (*g*). The contact pressure is controlled by winding the chain on the drum (*i*), which is calibrated in grams weight. To avoid an uncontrolled oscillation, the beam is spring-loaded by a helical spring (*j*) acting on the pointer. During actuation the equilibrium is displaced slightly to the left. Coarse adjustment is effected by mounting the whole balance manipulator on a rack-and-pinion-controlled stage (*k*). A simpler arrangement, with the fixed (right) tegmen held by a micromanipulator, was tried but it was found too rigid. The balance manipulator, although apparently cumbersome, did allow the contact pressure to be measured and the right tegmen to be 'rejected' by the left during any one stroke by bouncing off the file.

With the tegmina isolated and mounted ventral surface uppermost it was possible to experiment on the stationary, mirror-bearing, right tegmen. The principal experiments consisted of applying small spots of latex across the mirror region, thus damping selected parts of the supposed sound emitter. Experimental procedure was as follows: (1) record the insect's natural song on magnetic tape; (2) remove the tegmina and

mount on the actuator as described, after first dipping the cut in latex to avoid excess dehydration from the veins; (3) adjust the position of the tegmina and the audio-generator frequency so that the signal produced is constant; (4) record on magnetic tape for subsequent oscillography; (5) analyse the signal direct on the spectrum analyser and level recorder; (6) apply the latex spot; (7) re-analyse; (8) remove the latex and analyse again. Such a routine allowed a comparison of the natural song with the artificial actuated signal and a determination of the effect of successive applications of latex to various parts of the mirror region. The time and temperature were noted after each application, and throughout each series of experiments similar-sized latex spots were used.

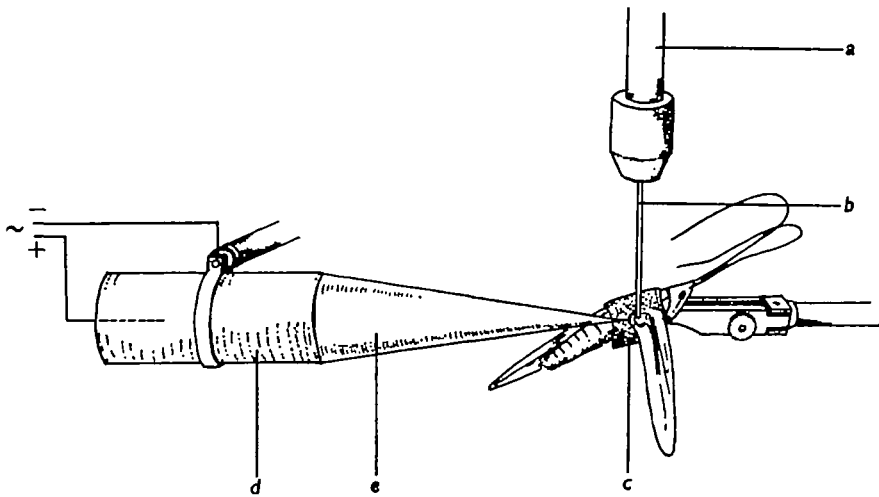


Fig. 2. The probe microphone and piezo-electric transducer being used to detect the sound pressure level at various sites across the mirror region of *Homorocoryphus nitidulus*. (a) Brüel and Kjaer $\frac{1}{4}$ in. microphone; (b) steel probe tube; (c) insect in Plasticine saddle; (d) lead zirconate titanate cylinder resin-bonded to a stainless steel cone (e).

(4) Mapping the sound-radiating areas of the right tegmen

In order to check the results obtained with the latex damping technique, a system was devised whereby the right tegmen of a living insect was made to resonate to contact stimulation. Its vibration was detected by a fine probe microphone held over the mirror region of the tegmen (Fig. 2). The probe consisted of a tube, 4.3 cm. long and with a 1 mm. bore, held perpendicularly to the face of the microphone diaphragm by a brass sleeve fitting over the end of the microphone. This facilitated the measurement of the relative sound pressure level at particular points on the surface of the tegmen.

The contact transducer was designed on the lines of that invented by Mason (1951). A straight-sided stainless steel cone was mounted on a piezo-electric cylinder made of lead zirconate titanate; this cylinder, when driven by a sine-wave generator, transmits the signal by compression and extension of its length to the steel cone (Fig. 2) which concentrates at its tip the sound energy generated by the cylinder.

One transducer, whose response was flat to 40 kHz., was placed in contact with the plectrum of the extended right tegmen of a living insect held in a plasticine saddle.

This produced low-level forced vibration of the tegmen throughout the entire frequency compass, except in the region of 15 kHz., where a marked increase in sound-pressure level showed that the tegmen was resonating. Once it had been established that the tegmen would resonate at this frequency a second transducer, with its own resonance in the 15 kHz. region for increased efficiency, was used to produce maximal vibration of the tegmen at the tegmental resonant frequency during scanning by the probe microphone. By means of a micromanipulator the probe microphone was systematically moved over the surface of the mirror region in both horizontal and vertical planes, at a height 1 mm. above the surface; a three-dimensional picture of the sound-pressure level was obtained in this way by separate examinations of both the ventral and dorsal surfaces.

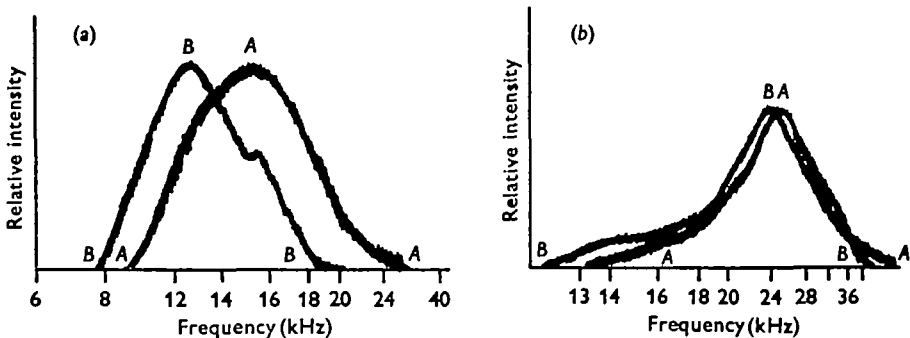


Fig. 3a, b. Frequency analysis of the natural song (A) and that produced by the actuated tegmina (B) in *Homorocoryphus nitidulus* (a) and *Metrioptera roeselii* (b).

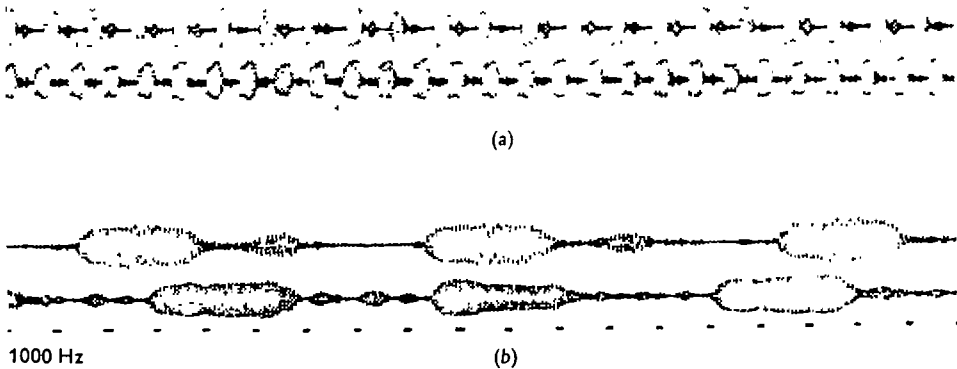


Fig. 4. (a) Oscillographic analysis of the actuated signal (upper trace) and natural song (lower trace) of *Homorocoryphus nitidulus vicinus*. (b) The same recording, extended to show the wave components of both traces.

RESULTS

(1) Performance of the actuator

A comparison between the artificial, actuated, signal and the natural song is shown in Figs. 3 and 4. Fig. 3a and b shows that in the freshly mounted preparation the predominant frequency of the actuated preparation is lower than in the natural song. Constant observation of the position of the predominant frequency of the actuated

signal, over periods often in excess of 8 hr. after mounting, showed that it moves to higher frequencies with the increase of time. The sudden drop in peak frequency at the time of mounting may be explained by the loss of control over the endocuticle either nervously or mechanically (Maddrell, 1966) due to the tegmen being isolated. This probably affects the water content of both the veins and cuticle, the latter probably absorbing water after denervation; both would render the vibrating system less rigid. Subsequent recovery of the peak frequency would be accounted for by the increased stiffness through the tegmen drying out.

Fig. 4 shows the oscillographic analyses, where, in comparison with the natural song, the actuated signal shows a loss of homogeneity in its envelope form. This loss is fully discussed in a following paper (Bailey & Broughton, 1970).

Fig. 3*b*, of *Metrioptera roeselii* (Hagenb.), shows that the song of other bush crickets can be replicated in a similar way; aurally similar results were obtained with *Pholidoptera griseoptera* (Degeer).

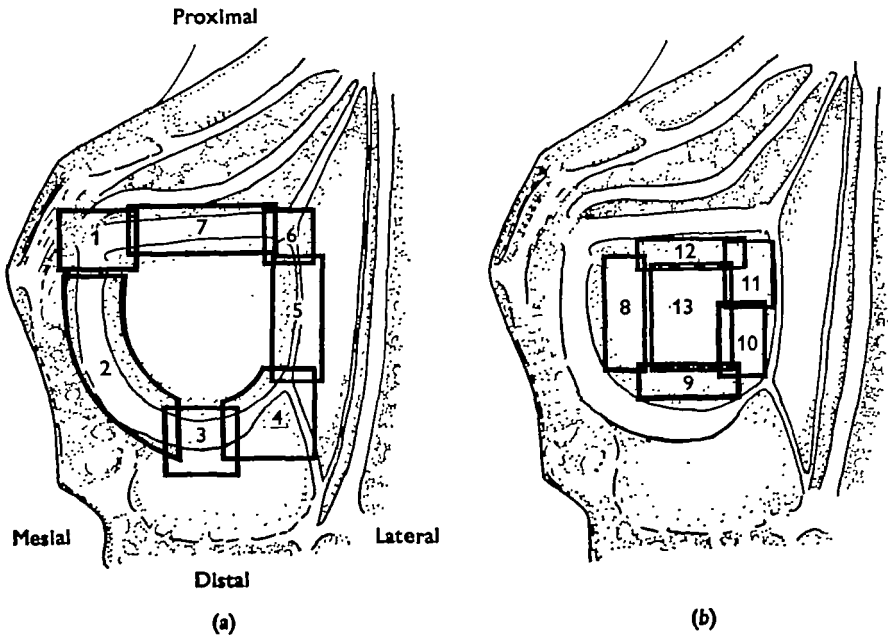


Fig. 5. Ventral surface of the mirror region of *Homorocoryphus nitidulus* showing the numerical classification of the areas tested with latex. (a) Areas including the frame; (b) areas including the membrane.

(2) Damping the vibration of the mirror region with latex.

The results of the observed changes in frequency and intensity, due to 341 random applications of small spots of latex over the mirror region, were divided into two major categories, those applied on the mirror frame, and those confined to the mirror membrane. Each of these regions was subdivided into areas shown in Fig. 5.

In considering the mirror frame (1-7, Fig. 5*a*), an analysis of variance on the change, if any, of the peak frequency and its intensity compared to the preceding control spectrum, showed a significant between-area difference ($P < 0.01$) for both para-

meters. When the between-area differences were subjected to Tukey's test (Snedecor, 1956), the following comparison resulted:

Intensity	Area 4 more affected by latex than areas 1, 2, 7 Areas, 5, 6 more affected by latex than areas 1, 2
Frequency	Areas 4, 5 more affected by latex than areas 1, 2, 3, 7 Area 6 more affected by latex than areas 1, 2, 7

$P < 0.01$

Latex applied to area 3 does not produce a significant change of intensity ($P < 0.01$) as compared to the adjacent areas.

Analysis of the latex applications to the mirror membrane (8–13, Fig. 5*b*) revealed that only in frequency change was the between-area difference significant ($P < 0.05$), and not in intensity. Tukey's test on this difference showed that areas 10 and 11 are significantly more affected than areas 8 and 12 ($P < 0.01$) but not than areas 9 and 13.

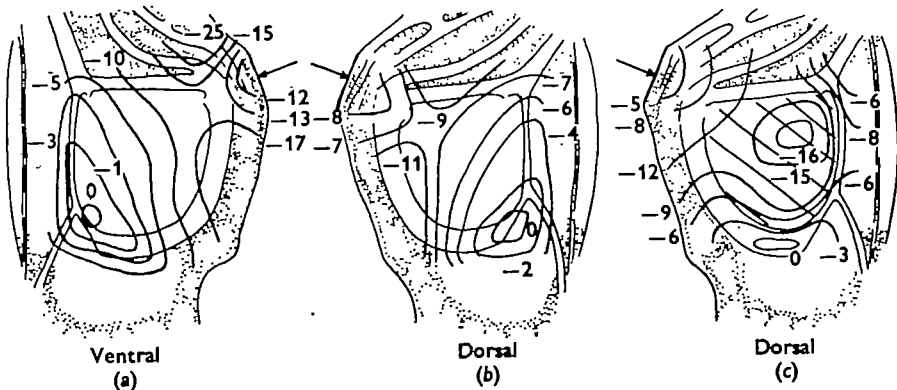


Fig. 6. The sound maps of the mirror region of *Homorocoryphus nitidulus vicinus* using a probe microphone on the tegmen activated by a 15.5 kHz. signal from the point-contact transducer placed against the plectrum (arrowed). (a) The ventral surface, and (b) the dorsal surface of the same tegmen. (c) The dorsal surface of a tegmen from which the mirror membrane has been ablated (cross hatched). Values are expressed in decibels relative to the highest value recorded in each experiment, indicated as zero.

When the two sets of figures are compared by 2×2 contingency tests it is found that:

- Area 4 (frame) differs from areas 8, 12 (membrane) ($P < 0.01$)
- Area 4 (frame) differs from area 9 (membrane) ($P < 0.05$)
- Area 5 (frame) differs from area 8 (membrane) ($P < 0.05$)

with respect to the change in frequency.

Such a comparative treatment of the results both with regard to different areas on the frame and on the membrane, and to those within each group, demonstrates that the damping effect of the small latex spot is most effective in that region towards the lateral distal part of the mirror region (see Fig. 5*a*).

(3) *Sound maps of the mirror region*

Fig. 6*a* and *b* shows the sound-pressure level, expressed in dB. relative to the highest value recorded (all values appearing negative to this), on both the ventral and dorsal surfaces of the tegmen. It is clear that there is an antinode of vibration over the distal lateral part of the mirror frame (an antinode, in a vibrating system, being that part with the maximum amplitude). There is some indication of another antinode, over the plectrum, but the antinode over the frame was consistently the stronger.

Fig. 6*c* shows how the sound-pressure level is affected by the complete removal of the mirror membrane. The main antinode appears more mesial (higher up the frame arm), and that over the plectrum more pronounced. The node at -16 dB. indicates that the action of the frame arm is not in the plane of the tegmen but perpendicular to it; for if it were the former an antinode would be expected within the mirror region (cf. a tuning fork).

Experiments of the same nature on the actuated tegmen produced comparable results.

DISCUSSION

Mirror membrane

Classical opinion on the role of the mirror membrane of bush crickets in sound production has been criticized by previous authors (Broughton, 1964; Morris & Pipher, 1967; Bailey, 1967) and from the results given in this paper it would appear not to have the 'resonance' function attributed to it by Pierce (1948). However, where it has been interfered with, either by cautery (Morris & Pipher, 1967; Bailey, 1968) or loading with a damping substance (Broughton, 1964; Bailey, 1967, 1968) there has been a reduction in the sound intensity, and in the case of the damping experiments an occasional displacement in the predominant peak frequency.

The effect of the loading experiments has been explained elsewhere (Bailey, 1967). It was stated to be a secondary effect on the surrounding frame caused by a relatively large quantity of latex on the mirror membrane. Such a conclusion formulated by experiments on the live insect is substantiated by the more rigorous tests on the isolated actuated tegmina. Cautery removes or damages the mirror membrane (a situation not uncommon in the field); this could either modify any control the membrane has on other vibrating structures (i.e. similar to the removal of the cone of a loudspeaker, allowing undamped freedom to the coil), or could impair its function if it were a radiating surface.

In bush crickets such as *C. discolor* the difference in thickness between membrane and frame is small, so that the membrane can have a much heavier damping effect on the frame, and this probably accounts for at least part of the discreteness of each tooth-pulse. In *H. nitidulus*, where the membrane is extremely thin relative to the frame, membrane cautery had little effect, both in the live insect and in the actuated tegmen. Fig. 6 (*c*) illustrates such effect as it has on the overall sound maps; in figs. 6(*a*) and (*b*) the dB. contours crossing the membrane indicate a weak passive transduction of the vibration from the main antinode, a condition destroyed in Fig. 6 (*c*), where the membrane area has become virtually silent.

Thus in the *Homorocoryphus* type (thick frame and comparatively thin membrane) there is probably little or no damping and only a little radiation by the membrane as a weak sounding-board without resonances; in the *Conocephalus* type (thin frame, comparatively thick membrane), there is clearly heavy damping and probably more radiation by the membrane, but again, only as a passive sounding-board, without resonances.

Mirror frame

In the experiments using the damping function of latex on the mirror region (Fig. 5) the area indicated as being responsible for maximum vibration was the area at the end of the mirror frame, including the small cross-vein connexion of the cubital. The

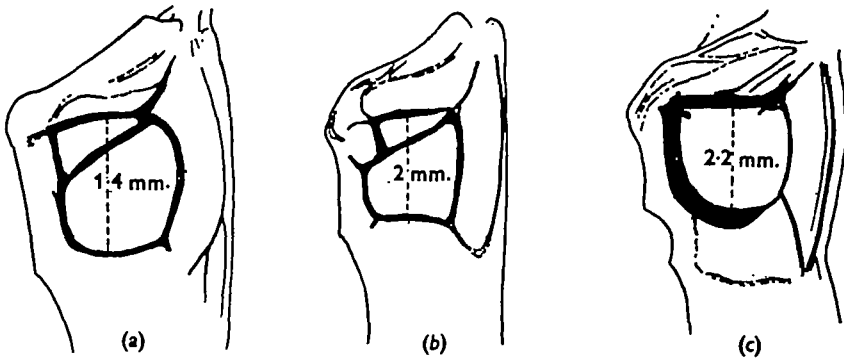


Fig. 7. Diagrammatic comparison between three genera of bush cricket to show the variation in cantilever size and shape. (a) *Conocephalus nigropleurum*; (b) *Orchelimum gladiator* (both redrawn after Morris and Pipher (1967)); (c) *Homorocoryphus nitidulus*.

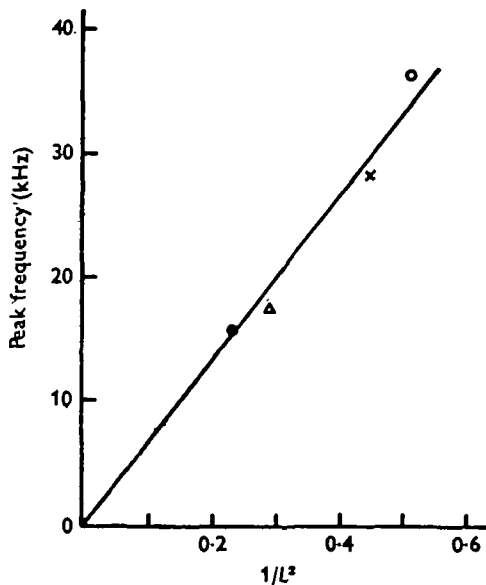


Fig. 8. Plot suggesting the feasibility of a cantilever model. Points for *Conocephalus nigropleurum* (○) and *Orchelimum gladiator* (Δ) (Morris & Pipher, 1967) and *Homorocoryphus nitidulus* (●) and *Conocephalus discolor* (×).

probe microphone experiments resulting in the sound maps confirmed this view, and more specifically implicated the distal part of the thickened frame as vibrating perpendicularly to the plane of the tegmen (Fig. 6). Thus the frame resembles not so much a tuning fork as a horseshoe clamped along one arm and struck at the mid-point; such a model would account for the usual antinodes.

The *Conocephalus* type of frame (Fig. 7*a, b*) studied by Morris & Pipher (1967) differs from the *Homorocoryphus* type in being a complete rectangle of hardened material, so that for the distal arm to vibrate maximally the frame would have to rotate about the whole axis of the vestigial file, as they suggested. In *Homorocoryphus*, the whole axis of the file need not be implicated, because there is no rigid link between its far end and the opposite end of the 'horseshoe'. The transfer of energy from the plectrum must be rather more complicated in that the rocking of the free part of the frame would be about a pivot which is a single point or a very short length of frame near the plectrum.

In spite of this difference an attempt was made to fit the data from this study to Morris & Pipher's plot for *C. nigropleurum* and *O. gladiator* (Fig. 8). They measured the frame length from the vestigial file direct to the distal part of the frame (Fig. 7*a, b*) in these two insects and also the predominant peak frequencies; these were compared between genera by applying the formula:

$$f = K/L^2,$$

where f is the predominant frequency, L is the length of the frame and K is a constant derived from the thickness, density and Young's modulus of the frame (they considered that in the two species they examined this constant would be the same, as the structural comparison was close). It was found (Fig. 8) that the *Homorocoryphus* type (Fig. 7*c*) still fitted this plot despite the fact that it differed substantially from the *Conocephalus* type (Fig. 7*a*). Perhaps the differences in these respects are compensated for in other details, and in this context it is worth remembering that Pierce's mirror-membrane hypothesis has stood for two decades for exactly this reason, that is, when a system is compared across genera using only a limited number of criteria, it is not unlikely that comparable results will be obtained. However, it is felt that with the tests applied in this work there is ample justification for thinking that the hypothesis presented is near the truth.

SUMMARY

1. A method has been devised by which the isolated tegmina of bush crickets can be actuated in such a manner as to simulate the insect's natural song.
2. The actuator was used to make a detailed analysis of the mechanics of sound production, with particular reference to the emission of the more or less pure tone at 15 kHz., characteristic of *Homorocoryphus nitidulus*.
3. Results involving damping and cautery indicated that the area of the right tegmen responsible for the radiation of this sound was the mirror frame, the vein enclosing the classical mirror membrane.
4. Further experiments involving transduced sound and a probe microphone led to the construction of sound radiation maps of the right tegmen which supported the above view.

5. The cantilever hypothesis, involving the mirror frame with the axis of the vestigial file as the cantilever's rotational axis, was considered in the light of the *Homorocoryphus* type.

6. The *Homorocoryphus* type differed from the *Conocephalus* type (on which the cantilever hypothesis was based) in that a simpler cantilever is formed in a line direct from the plectrum to the tip of the frame arm.

I am indebted to Mr W. B. Broughton for his close supervision throughout this work, which constituted part of a Ph.D. thesis submitted to the University of London and was carried out at the Animal Acoustics Unit, Sir John Cass College, London; to Dr J. C. Hartley for providing and re-stocking the culture of *H. n. vicinus*. Also to Dr E. T. Burt and Dr H. C. Bennett-Clark for their criticism of this manuscript; any errors, however, are my own responsibility.

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