

SOUND PRODUCTION IN CRICKETS

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Summary

The calls of male *Gryllus bimaculatus* were digitally recorded under four different conditions: in air; in 80% He/20% O₂; with the tympana occluded with wax in air and finally in the helium/oxygen mixture. The principal frequency component, usually referred to as the carrier frequency, was analysed in a large sample of chirps recorded in the four conditions. In all four recording conditions, the principal frequency component was found to vary from chirp to chirp. The mean of the distribution of the principal frequency component was different in the four recording conditions. Insects with occluded tympana produced in air a greater dispersion of the principal frequency component than insects with normal functioning ears.

The spectrum of an individual chirp generally contained two frequency components, the principal component, which was related to the plectrum–file strike rate, and a

second component, which was related to the free vibration of the wings. The subalar air space volume is shown to act as an acoustic resonator and is important in the filtering and amplification of the sound signal. These observations were confirmed by a model stridulatory system. The model system shows that the resonant frequency of the subalar space is dependent upon the square root of the effective volume of the space.

The results suggest that song generation in crickets is a dynamic process involving an auditory feedback control loop. The singing insects appear to be able to control the plectrum–file strike rate as well as the resonant frequency of the subalar space by changing the relative position of the wings and the abdomen, hence varying the volume.

Key words: *Gryllus bimaculatus*, cricket, stridulation, song production, feedback control, resonance.

Introduction

Many sound-producing insects generate sound by mechanical means, rasping one cuticular structure against another. In the Ensifera (Tettigoniidae and Gryllidae), tegminal stridulation is the rule; a file on one forewing is struck by a plectrum on the other, causing the wings to vibrate. The currently accepted view is that the frequency of the call is entirely determined by the mechanical properties of the wings. This interpretation is not without problems. If both tegmina radiate sound, then they must be equally balanced and vibrate synchronously to prevent interference. They are also small with reference to the volume of sound generated.

As a means of synchronising and regulating the movement of the wings, the passage of the plectrum across the file system has been likened to the escapement mechanism of a clock, with the resonant properties of the tegmina acting as a pendulum (Elliott and Koch, 1985; Koch *et al.* 1988; Bennet-Clark, 1989).

Bailey and Broughton (1970) thought that the subtegmental air space might also act as a resonator in the bush cricket *Ruspolia nitidula* (at that time known as *Homorocoryphus nitidula*). This idea does not seem to have been further pursued and indeed Nocke (1971) denied any such function in *Gryllus*

bimaculatus, although Bennet-Clark (1970, 1987) has shown the importance of the tuned burrow in sound production and amplification in mole crickets. In mole crickets, the subtegmental air space opens directly into the acoustic horn of the burrow. Additionally, it was shown that some tree crickets (Oecanthinae) construct special baffles from the leaves where they stridulate, thereby increasing sound power output (Prozesky-Schulze *et al.* 1975; Forrest, 1982).

The tegmina of most stridulating Ensifera are frequently modified in shape or held in such a way as to partially enclose an air space between them and the body of the insect when stridulating. In some species with reduced wings, the design is such that the stridulatory part of the wing, the region posterior to the radius with thickened veins, forms a domed area flanged on the sides and posteriorly by the softer precostal and distal parts. When these insects stridulate, the wings are raised slightly but the precostal flap maintains a partially enclosed air space below the tegmina, a feature noted by Ewing (1989). This is very definitely so in *Gryllus bimaculatus*, where the precostal region is sharply bent downwards so as to enclose the air space over the body, as can be easily seen when the insect stridulates. Bennet-Clark

(1989), in his comprehensive review of sound production in crickets, suggested that this may restrict interference between the two sides of the tegmina, on the assumption that tegmina are radiators. Oecanthines that use leaf baffles do not have this wing configuration; in these crickets the wings tend to be flat.

If, as apparent from the oecanthines, the use of baffles is important in sound production, then sound production becomes a problem involving complex impedances. It is, therefore, necessary to give consideration to the acoustic impedance of the system. We discuss this aspect in conjunction with a series of experiments on sound production in *Gryllus bimaculatus* and with a model sound generator, which shows that sound amplification is dependent upon the subalar air space and that the carrier frequency of a call is dynamically controlled by the singing insect.

Materials and methods

Insects and equipment

Male crickets of the species *Gryllus bimaculatus* taken from laboratory cultures were used in this study. For song recording, a single test male accompanied by a muted male was placed in a light polyurethane foam cage with a nylon gauze top. The male was muted by cutting its plectrum ridge in several places, which made it incapable of stridulation. The test insects produced aggressive or calling songs readily under this regime, and the cage had no measurable distorting effect on the song. Whenever possible, recordings were made in a relatively sound-proof room, 3 m × 3 m × 3 m. Over 30 different males were used.

All sounds were detected with a Bruel & Kjaer (B & K) 0.5 inch (12.5 mm) (type 4133) microphone and amplified with a B & K microphone pre-amplifier (type 2639) and a B & K measuring amplifier (type 2636). The amplified signals were displayed on a Nicolet Pro 10 digital oscilloscope and stored on 3.5 inch floppy disks for subsequent analysis. The oscilloscope could be triggered by the cricket calls, and a 5 ms pre-trigger interval was used to ensure that the calls were situated centrally in the 20 ms sweep time window. This was to minimise 'end effects' in subsequent Fast Fourier Transform (FFT) analysis of the signals. The Nicolet was set in auto mode so that a preset number of consecutive calls triggering the oscilloscope could be recorded. In any recording sequence, a maximum of 100 separate chirps were stored. A B & K 2032 signal analyser was used for further sound manipulation or analysis.

The recorded calls could be analysed by (FFT) either on the Nicolet Pro 10 oscilloscope or by a commercial signal analysis package, FAMOS. This package, which runs on a PC, is designed to process data recorded on Nicolet equipment. In both cases the frequency resolution was 25 Hz with a frequency span of 25 kHz. For clarity of presentation, the FFT spectra have an overall frequency span of 10.5 kHz, but with the frequency resolution remaining at the original 25 Hz.

Experimental procedures

Changing the physical properties of one forewing

After recording the normal song of a cricket, its upper forewing was painted with typist's correction fluid (Tipp-Ex). This produced a quick-drying thick coat that adhered well.

Measurement of the free vibration of an isolated forewing

In order to stimulate mechanical excitation of the wing, as would occur through normal plectrum-file stridulation, a mechanical impulser was constructed as shown in Fig. 1. The impulser was activated by a 10 V square electrical pulse of 500 μ s duration, which generated a single in-out movement of the pin. The amplitude of this movement was approximately 1 mm. The grass stalk, to which the pin was attached, continued to vibrate, generating sound for about 20 ms after the impulse, but there was no forward movement.

Wings used for the experiment were taken from male crickets killed in a deep freeze shortly beforehand. The head was removed and the pronotum attached to a rod with an adhesive wax (a compound of beeswax and resin which, when applied molten, securely held the preparation on cooling). The abdomen, legs, hindwings and the lower forewing were also removed, leaving the remaining wing attached by its cuticular hinge and musculature to the thorax. This assembly was fixed in a micromanipulator that enabled the wing to be positioned close to the impulse pin, being so arranged that the pin just struck the wing on its outer surface directly over the file vein.

The B & K microphone was positioned about 10 mm from the wing. Sound signals detected by the microphone consisted of sound generated by the impulser and that generated by the vibrating wing. The problem was to separate these two signals. This was achieved by storing the signal-averaged response of 50 impacts of the pin against the wing in the B & K 2032 signal analyser, used in its signal enhancement mode. The wing assembly was then moved just clear of the pin and the signal

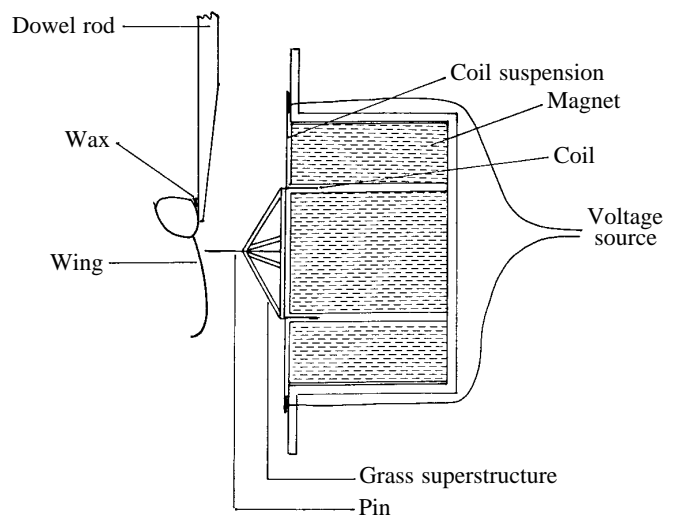


Fig. 1. Electro-mechanical impulser used to excite free vibrations in isolated wings.

from a further 50 impulses recorded. These signals, without the wing-generated component, were first inverted on the B & K 2032 and then averaged with the previously recorded signal. The resulting signal should be that attributable only to the impact and subsequent vibration of the wing.

The effect of gas density on the free vibration of the wing

Any changes in chirp frequency observed in the different gas mixtures (see below) could be due either to the presence of a volume resonator created by the wings or to a change in the loading on the wings by the surrounding gas, altering their vibration frequency. This was investigated by comparing the free vibration of the wing in air and in an atmosphere of 100% CO₂. The previous experiment was repeated with the isolated wing, impulser and microphone contained in a large clear polythene bag which could be filled either with air or with CO₂.

Measurement of the resonance of the wings with the wing-body space

As shown in Fig. 2, a freshly killed male *Gryllus bimaculatus* with its legs removed was fixed to a 10 cm length of 0.7 cm diameter wooden dowel. The wings were raised into the singing position and secured in this position by a small bead of adhesive wax applied to the basal articulation. A vibrator consisting of a 5 mm cactus spine glued to the end of a piezoelectric bimorph element was placed in contact with the file vein of the upper wing. The bimorph element was then excited with a frequency-limited (maximum 6.4 kHz) white noise signal generated by the B & K 2032 analyser. Sounds generated were detected by the B & K microphone placed 2 cm from the preparation.

The frequency response of the whole system was recorded on the B & K 2032 analyser, and the response was stored. The cactus spine was moved just clear of the wings and the frequency response was again measured, stored and processed as above. The resulting difference spectrum should be just that of the wings and the wing-body cavity. However, it is possible that the difference spectrum could be generated by the bimorph element and wings forming a resonant system and nothing to do with the wing-body air space. In an attempt to eliminate this possibility, the following experiment was conducted. The bimorph element was connected to a charge amplifier. A load applied to the bimorph will generate a transient voltage proportional to the displacement of the bimorph by the load. The cactus spine was repeatedly applied to and removed from the wings. No voltage was detected when the spine either touched or left the wings. From this, it was concluded that the bimorph element was very stiff compared with the wing loading, that the wings probably did not affect the frequency response of the vibrating bimorph and, therefore, that the response measured arose from the wings and wing-body air space system.

The effect of interference with the hearing system of the cricket

Immediately after the normal song had been recorded from a cricket, the tympana were covered with adhesive wax. The wax,

which was applied in a molten state with a warmed needle, set firmly to produce a thick coating around the leg and over both tympana. The insect was returned to the recording arena and a further 100 chirps recorded. Most insects sang again within a few minutes of the manipulative treatment, any failing to sing within 10 min were discarded. At the end of the experiment, the insect was checked again to confirm that the tympana were still covered with wax. Covering the ears with wax seriously interferes with the insect's hearing (Patton *et al.* 1977) so, for convenience, these are referred to as deafened insects.

The effect of lower density gas mixture on the song structure

The effect of gas density on the song structure of the crickets was determined by enclosing the cage and microphone in a light clear polythene bag, as shown in Fig. 3. The bag was found to produce no material change in the song structure in that songs recorded when the bag was filled with air were indistinguishable from songs recorded freely in air. Also enclosed within the bag was a small whistle connected by a length of rubber tubing to an external rubber bulb. Repeatedly squeezing the bulb drew gas from the bag through the whistle, which thus could be made to produce a pure tone using the gas from within the bag. In this way, the effect of different gas densities on any acoustic resonator associated with song generation could be compared with changes observed in the whistle frequency.

The gas mixture used was medical-grade heliox (79% He; 21% O₂). Initially the bag was inflated with air to the point at which it just filled out, the bag remaining slightly flaccid. This was to ensure there were no increased pressure effects and that the bag itself did not vibrate; any vibration of the bag in its flaccid state would have been at very low frequency and certainly not in the frequency range of *Gryllus bimaculatus*.

With air in the bag, recordings of the whistle and 100 individual chirps of a male *Gryllus bimaculatus* were made and stored on disk. The bag was collapsed and as much air as possible removed. It was then reinflated with heliox to the same extent as before. Recordings of the whistle and more than 100 chirps, produced in the helium gas mixture, were made and stored, followed by further recordings of the whistle. In most

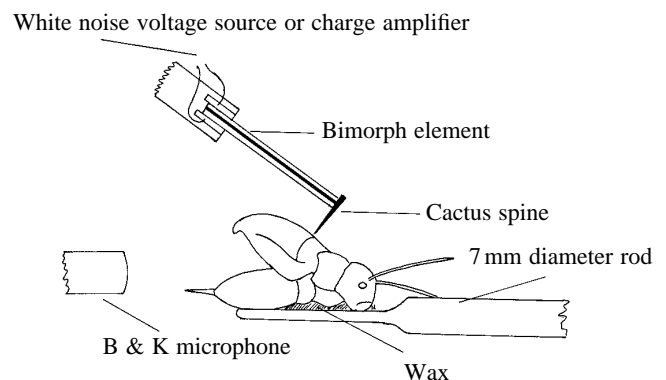


Fig. 2. Diagrammatic representation of the cricket and piezoelectric vibrator used to excite the subalar air volume.

experimental runs, the 100 chirps were produced within 20 min and no measurable change in the whistle frequency was detected.

The whistle using gas from the experimental chamber produced a resonant frequency proportional to the velocity of sound in that gas. Assuming a velocity of sound in air of 331 ms^{-1} , the velocity of sound in the heliox in which the cricket was singing, calculated from the ratio of whistle frequencies, was 465 ms^{-1} .

Crickets with waxed tympana were usually tested in heliox as described above. Such crickets would normally be recorded in air and in heliox before being waxed.

Data analysis

The frequency spectrum of a single chirp is a convolution of the principal frequency component of the chirp and the spectrum of the envelope of the oscillatory component. Many of the results given here involve comparison of the chirp spectrum before and after some perturbation of the insect's sound-producing apparatus. After such perturbation the chirps generally changed quite significantly. The prime interest of this paper is the mechanism responsible for the generation of the principal frequency component (the carrier frequency). Investigation of this component of the chirp alone would require deconvolution of the analogue signals. Generally this process is only possible if the spectra of the frequency component and the envelope are substantially different. For the chirps in question this is not the situation. Therefore, the spectra of single chirps before and after perturbation of the sound-generating mechanism have been compared. Consequently, considerable care was taken to select only those chirps having a similar overall envelope form.

Model stridulator

To examine the properties of an air space under the wings, a

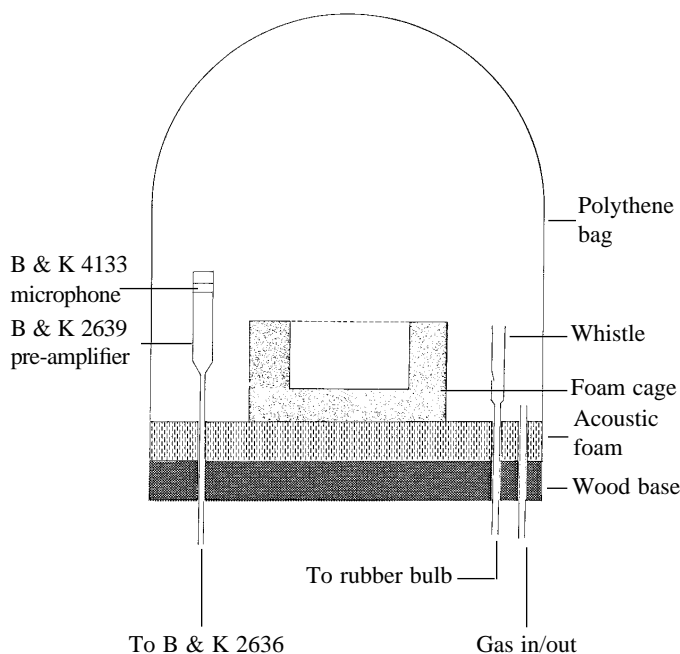


Fig. 3. The apparatus used to record insect calls in heliox.

model stridulator was constructed as shown in Fig. 4. The two wings were represented by two identical piezoelectric discs each bonded onto a circular brass shim disc of 20 mm diameter. Each 'wing' was soldered to the end of a 50 mm brass rod 3 mm in diameter. The other ends of the rods were held 6 mm apart in the end of a 12 mm diameter plastic rod. The two piezoelectric elements were connected in parallel to an oscillating voltage source. This pair of 'wings' was mounted just in front of a small Perspex cavity of variable volume. The cavity was made from a 20 mm length of 25 mm internal diameter Perspex tube fitted with a piston attached to a 1 mm pitch screw, thus enabling fine adjustment of the volume of the cavity.

The 'wings' were excited with a square-wave voltage at a frequency of 5.9 kHz, a resonant frequency of the discs. The sound generated was detected through a 2 mm diameter probe tube, attached to the B & K microphone, placed 50 mm in front of the 'wings'.

Acoustic impedance of the stridulatory apparatus

The total acoustic impedance of the stridulatory apparatus $Z(s)$ can be written as the sum of two components: (i) the acoustic impedance of the wing structures $Z(Ws)$; and (ii) the acoustic impedance of wings vibrating in air (or any other gas mixture) $Z(W)$.

Combining these gives:

$$Z(s) = Z(Ws) + Z(W). \quad (1)$$

This total acoustic impedance has both resistive and reactive components. Generally it can be written as a complex number $Z(s) = R(s) + jI(s)$, where $j = \sqrt{-1}$. The real component $R(s)$ comprises the resistive part and generally is independent of frequency. The imaginary component $I(s)$ is associated with the reactive part of the overall impedance and is frequency-dependent. The frequencies at which the reactive component becomes equal to zero are associated with the resonances of the system. The total resistive component of $Z(s)$, $R(s)$, is the sum of the resistive component of $Z(Ws)$ and $Z(W)$,

$$R(s) = R(Ws) + R(W). \quad (2)$$

$R(Ws)$ arises from the frictional forces within the wing structure as it vibrates. $R(W)$ is equal to the total radiation resistance of the wings as they vibrate in the air radiating sound waves. The total reactive component can, in the same way, be considered as the sum of two reactive components:

$$I(s) = I(Ws) + I(W). \quad (3)$$

Zero values of $I(Ws)$ are associated with the resonant frequencies of the free vibration of the wings; for example, the resonant frequency of the mirror membrane. It may be surprising that the acoustic impedance of the wings vibrating in air has a reactive component. Sound waves are generated by both the upper and lower surfaces of the wings as they vibrate. The sound waves generated by the upper surface propagate away from the insect into free space, those from the underside are affected by the presence of the abdomen and the volume of air lying between the abdomen and the underside of the wings. If V is the volume

of the semi-enclosed air space lying between the wings and the body and x is the amplitude of the wing vibration, then the pressure in the enclosed air space will change by:

$$dp = \frac{\partial p}{\partial V} dV = -\frac{B}{V} dV, \quad (4)$$

where B is the bulk modulus of the gas. The bulk modulus can be expressed in terms of the density ρ and the velocity of sound c in the gas:

$$B = \rho c^2. \quad (5)$$

If A is the area of the vibrating wing, which defines V , then the change in volume dV of the trapped gas as the wing vibrates will be:

$$dV = Ax. \quad (6)$$

The force F exerted on the wing by the air in the wing-body cavity is:

$$F = pA, \quad (7)$$

where p is the instantaneous pressure in the volume V . Differentiating equation 7 with respect to V :

$$dp = \frac{F}{A} dV. \quad (8)$$

Now substituting equations 4, 5 and 6 into equation 8 gives:

$$\frac{F}{x} = \rho \frac{c^2 A^2}{V}. \quad (9)$$

The quantity F/x is the mechanical stiffness of the air volume. The acoustic compliance of the air space between the body and the wings can then be calculated by dividing the square of the effective wing area by the mechanical stiffness. The compliance $c(\omega)$ so obtained will be a function of the frequency f (note $f=2\pi\omega$) of the sound waves generated in the air space:

$$\begin{aligned} c(\omega) &= \frac{x}{F} A^2 \\ &= -\frac{V}{\rho c^2}. \end{aligned} \quad (10)$$

If M is the mass of the wings, then the total acoustic impedance of the wings is equal to:

$$Z(W) = R(W) + j\omega M - j\frac{\rho c^2}{\omega V}, \quad (11)$$

where ω is the angular frequency of the wing vibration. The resonant frequency of the wings f_0 ($\omega_0=2\pi f_0$) vibrating against the volume V of air (or gas) is obtained by equating the imaginary component of equation 11 to zero, i.e.

$$\begin{aligned} M\omega_0 - \frac{\rho c^2}{\omega_0 V} &= 0 \\ \text{or} \quad f_0 &= \frac{c}{2\pi} \left(\frac{\rho}{MV} \right)^{\frac{1}{2}}. \end{aligned} \quad (12)$$

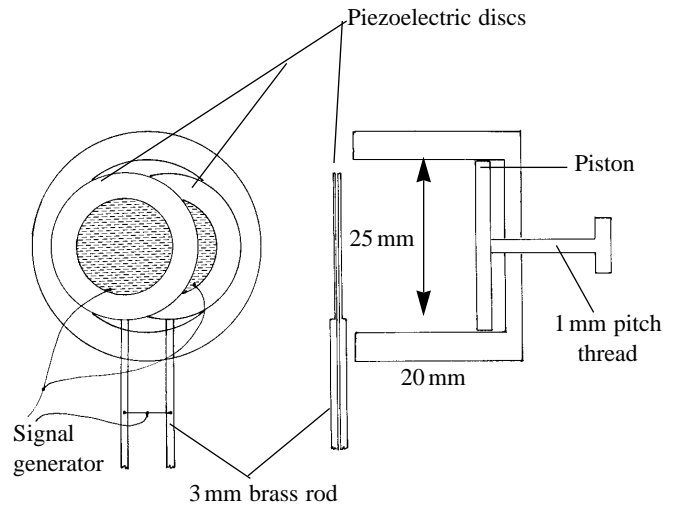


Fig. 4. Two diagrammatic sketches of the model stridulatory apparatus from different angles.

This calculation indicates that the wings coupled to the wing-body air cavity act as a resonant system. In many respects, the system behaves like a Helmholtz resonator.

The physical effects predicted above were clearly demonstrated with the model stridulator.

Model stridulator

Fig. 5A is a recording of the sound generated by the synthetic wings alone without the cavity. The resulting waveform has frequency components at 2.45, 5.9 and 11.8 kHz. The cavity was then placed just behind the 'wings' and then, by tuning the cavity to its resonant volume, it was possible to generate the almost pure sine-wave signal shown in Fig. 5B. A plot of the acoustic gain of the 5.9 kHz component in dB against the square root of cavity volume is shown in Fig. 5C, with the cavity of the apparatus now fixed at the position of best gain for the 5.9 kHz component. Fig. 5D shows the amplitude response to difference frequencies. Fig. 5C,D clearly shows the highly selective response of the tuned baffle amplifier.

Results

All recordings were of aggressive or calling chirps. Courtship songs were excluded. The following terms are consistently used in the results and discussion. (i) Plectrum-file impulse (P.F.I.) rate. This is the rate at which the plectrum passes across the file during a closing wing stroke. It may vary during the closing wing motion if the velocity of the wings changes as they close. (ii) Principal frequency component. This is the frequency component in the Fourier spectrum of a single call which has the largest amplitude. This component may in some instances be equivalent to what is loosely referred to in the literature as the carrier frequency or stridulation frequency.

Normal chirps

Fig. 6A illustrates the analogue signal of a single chirp of a male *Gryllus bimaculatus*. This call, recorded in free space, is a modulated harmonic pulse. The frequency spectrum of this

chirp, shown in Fig. 6B, contains a principal frequency component at 4.75 kHz and a second component at 5.6 kHz. The difference between these two frequencies, 0.8 kHz, should be the modulation frequency observed in Fig. 6A. A small peak at the expected modulation frequency of 0.8 kHz is indicated by the arrow on Fig. 6B. Recordings made from other singing male *Gryllus bimaculatus* showed spectra with similar characteristics.

Fig. 7 illustrates the Fourier spectra of two consecutively recorded chirps of *Gryllus bimaculatus* showing a slight shift in the principal frequency between the two chirps. Examination of a sequence of over 100 comparable chirps produced within a 1 h period reveals that there is a consistent slight variation in the modal frequency from chirp to chirp. This is shown in Fig. 8 ($N=92$, mean frequency= 4.65 ± 0.062 kHz).

An immediately obvious and important point arising from the above results is that the frequency is varying from chirp to chirp. If the carrier frequency (principal frequency component) of the chirp were determined by the modal vibration of the wings alone, then consecutive calls would have to be of the same frequency, the only changes possible being those that could occur as a result of changes in the mechanical properties of the wings over a period of time.

Effect of loading one wing

Painting one wing with Tipp-Ex produced no measurable change in the results obtained above for the intact cricket. Changing any resonant property of a wing should have produced an imbalance between the wings, but no significant change in the frequency spectrum was found. The absence of any clear effect of painting or mutilating the tegmina in various bush crickets was previously reported by Bailey (1970), who also quoted a number of other authors.

Free vibration of a single wing

The efficacy of the averaging method in eliminating extraneous sound was tested by a control run without the insect when two sets of 50 impulses were recorded, averaged and the ensembled signal stored. The first set was in normal and the second set in inverted mode. When the two ensembled averaged signals were combined, the resultant trace was practically flat.

The free vibration frequency of all the 10 wings tested varied from specimen to specimen between 5.4 and 5.6 kHz. Fig. 9A shows a signal-enhanced analogue trace of the free vibration of an isolated wing of male *Gryllus bimaculatus* obtained by this difference method. The frequency of the observed vibration, determined from the periodicity of the analogue trace, is 5.6 kHz. Fig. 9B shows the signal-enhanced analogue trace of the same wing now recorded in an atmosphere of 100% CO₂. Apart from a slight distortion, produced by the polythene bag, the signal generated by the isolated wing in CO₂ was not measurably different from that produced in air. This was to be expected since the free vibration of a stiff and, in comparison with the surrounding

gas, dense structure will be independent of the density of the medium in which it vibrates.

Measurement of the resonance of the wings with the wing-body air space

Fig. 10 shows the frequency response of the wings, raised into the singing position, vibrating against the air space lying between the wings and the abdomen. The centre frequency, 4.9 kHz, of the resonance agrees well with the mean principal frequency component measured in normal singing animals. This resonant response disappeared after the abdomen had been removed.

Chirps generated under different experimental conditions

Fig. 11A–D illustrates the distribution of the principal frequency component of 100 chirps recorded from one of the *Gryllus bimaculatus* males in each of the four different situations. The total number of calls analysed was usually less than 100 since it was not possible to analyse some of the calls. In air (Fig. 11A), the mean modal calling frequency was 4.86 ± 0.071 kHz (s.d.; $N=91$). Replacing the air with heliox (Fig. 11B) caused the mean modal frequency to rise to 5.15 ± 0.068 kHz ($N=89$). Re-recording from the insect in air gave results that did not significantly differ from the first sequence in air. When this insect was deafened and recorded in air (Fig. 11C), the frequency of the chirps varied widely and apparently at random, resulting in a mean modal frequency of 4.96 ± 0.105 kHz ($N=87$). The same deafened insect in heliox (Fig. 11D) now produced a much narrower frequency spread, clearly non-Gaussian, with a mean modal frequency of 5.36 kHz ($N=80$).

The changes in mean modal calling frequency and the standard deviation of the call frequency distributions presented above have been examined statistically. The changes in the mean frequency of chirps from normal insects in heliox, deafened insects in air and deafened insects in heliox have been compared with the mean calling frequency in air of the normal cricket using the Fisher–Behrens distribution. In all three cases, the change in mean frequency is significant at the 99% confidence level. The variances of the distributions in the three modified calling situations have also been compared with the variance in air using the variance ratio distribution F . The change in variance of the undeafened cricket in heliox is not significant at the 95% confidence level.

Deafening the cricket does produce (at the 95% confidence level) a significant increase in variance of the call frequency. The variance of the calls of deafened crickets in heliox was not compared with that in air since Fig. 11D so clearly does not have a Gaussian distribution. Examples of the spectra of individual calls recorded under these four conditions are shown in Fig. 12A–E. The spectrum (Fig. 12A) from a chirp recorded in air showed the same frequency structure as Fig. 6B, albeit the principal frequency component for this chirp was 4.95 kHz. The higher-frequency component, presumably that generated by the free vibration of the wing at 5.45 kHz, was only just visible in this example.

In the three following experimental procedures it should be noted that the intensity of the chirps was less than for the

normal insect in air. However, intensities could not be quantified as the position of the cricket and its distance from the microphone were not controlled. With the air replaced by heliox, a spectrum (Fig. 12B) was generated with frequency peaks at 4.9 kHz and 5.45 kHz. Since the overall power of the chirp was lower, the 5.45 kHz component appears to be larger. An example of the spectrum of a chirp produced by the deafened insect (Fig. 12C) has peaks at 5.05 kHz and 5.45 kHz. Most of the spectra generated by the deafened insect in heliox (Fig. 12D) showed only a single frequency component at 5.45 kHz. However, in some calls a lower-frequency component was also visible (Fig. 12E).

These results show that the cricket must be able, in some

way, to control its wing speed so as to produce the correct tooth strike rate. The greatest variation in frequency occurred when the deafened cricket sang in air. Since the only difference from the intact insect is that the insect is now deafened, it must be that the insect hearing its call frequency is stridulating only within a certain range of wing movements in an attempt to produce the chirp it is expecting to hear.

Discussion

It has been a long-held belief that the carrier frequency, the principal frequency component, of ensiferan song was uniquely determined by the modes of free vibration of the wing structures. The excitation of these wing structures results from

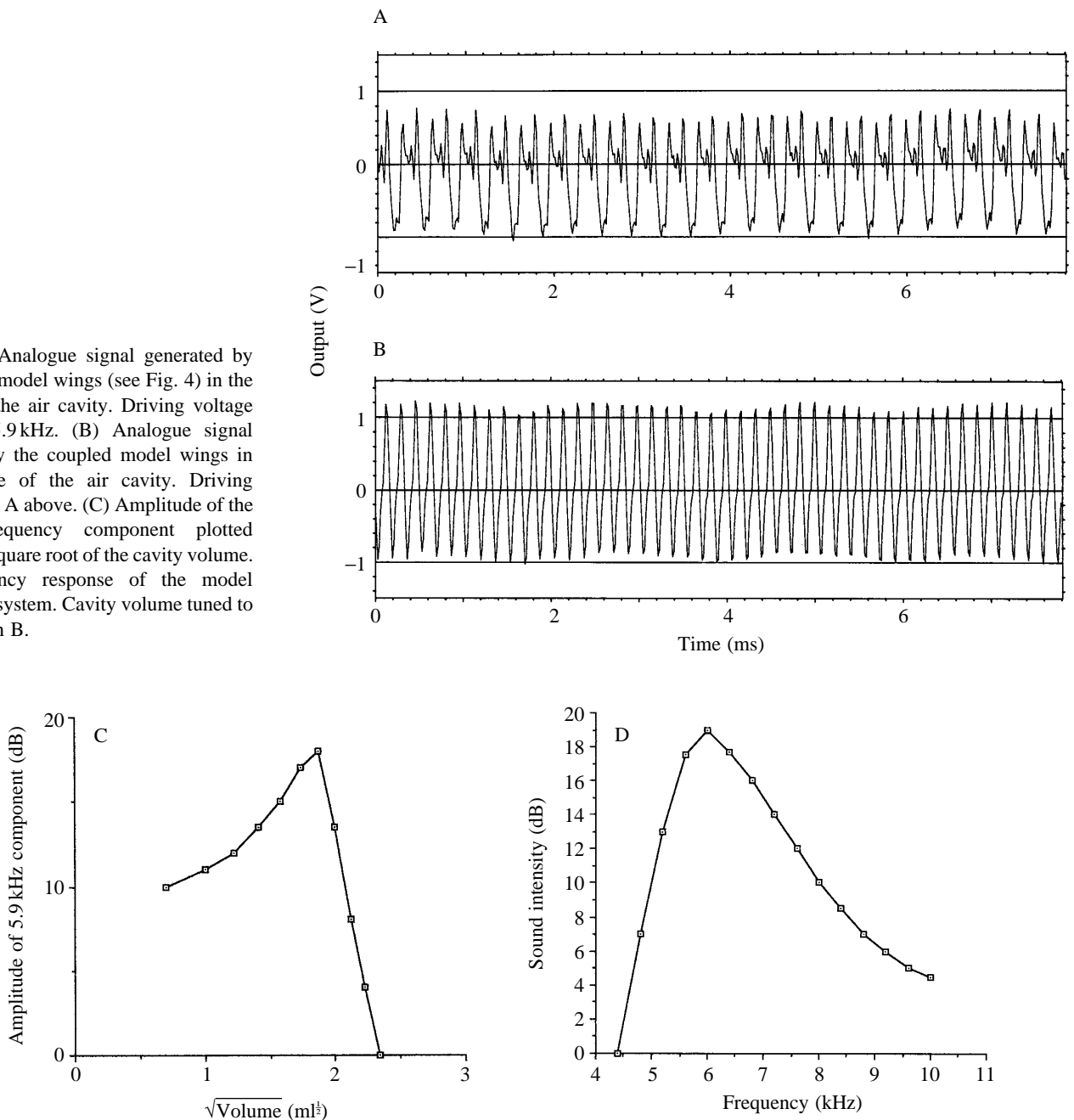


Fig. 5. (A) Analogue signal generated by the coupled model wings (see Fig. 4) in the absence of the air cavity. Driving voltage frequency 5.9 kHz. (B) Analogue signal generated by the coupled model wings in the presence of the air cavity. Driving voltage as in A above. (C) Amplitude of the 5.9 kHz frequency component plotted against the square root of the cavity volume. (D) Frequency response of the model stridulatory system. Cavity volume tuned to 5.9 kHz as in B.

the action of the plectrum on the file. There is no doubt that vibration of the wings is the source of sound. What is in contention is how insects such as gryllids are able to generate a relatively pure sinusoidal sound signal. If the observed sinusoidal waveform is indeed generated by a modal vibration of the wings, then it is necessary for this vibration to be synchronous with the P.F.I. rate. Elliott and Koch (1983) showed a one-to-one relationship between P.F.I. rate and the principal harmonic component of the call in gryllids, as was inferred previously by Nocke (1971). To explain this observed synchronisation between P.F.I. rate and wing vibration, Elliott and Koch (1983, 1985) compared the action of the plectrum

on the file with the escapement of a clock. This model was further refined by Bennet-Clark (1989).

In a clock or watch, the rate or time-keeping is determined by the frequency of oscillation of a pendulum or a balance wheel. In the case of a pendulum, the restoring force is generated by the effect of gravity on the pendulum weight (bob); with a balance wheel oscillator, the restoring force is generated by the balance spring. In either case the frequency of oscillation is uniquely determined by the moment of inertia of the pendulum, or the balance wheel plus balance spring, about its centre of rotation, and the restoring force, gravity for a pendulum and the spring constant of the balance spring for a balance wheel.

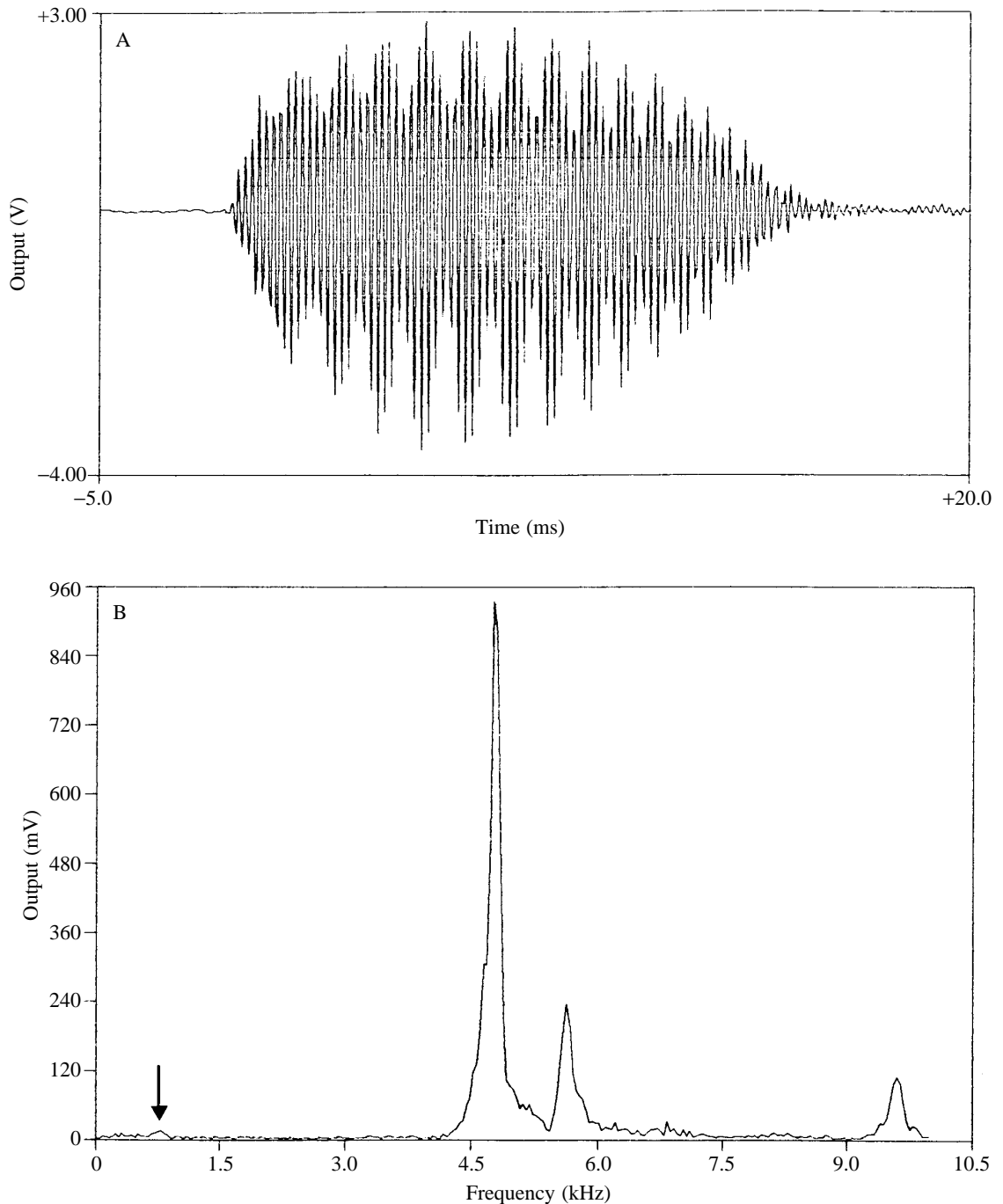


Fig. 6. (A) Analogue signal of a single chirp recorded in free space. (B) Frequency spectrum of A. The modulation frequency observed in A is indicated by the arrow at 0.8 kHz.

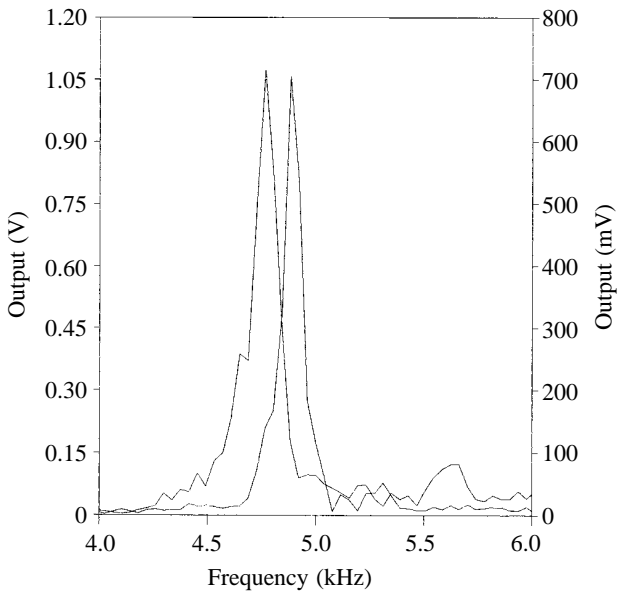


Fig. 7. The spectra of two consecutive chirps of a male *Gryllus bimaculatus* recorded in free space. The scale on the right applies to the chirp with the lower principal frequency.

The action of the escapement is to deliver a force, with the correct phase relationship relative to the motion of the oscillator (pendulum or balance) to maintain the oscillation at the set frequency. Variation of this applied force causes a second-order change in the rate by altering the amplitude of the oscillation. Increasing the force increases the amplitude and reduces the rate, whereas reducing the force reduces the amplitude and increases the rate. The tolerances allowed in any escapement are a matter of a few thousandths of a millimetre between one that will function and one that will not, irrespective of the driving force applied.

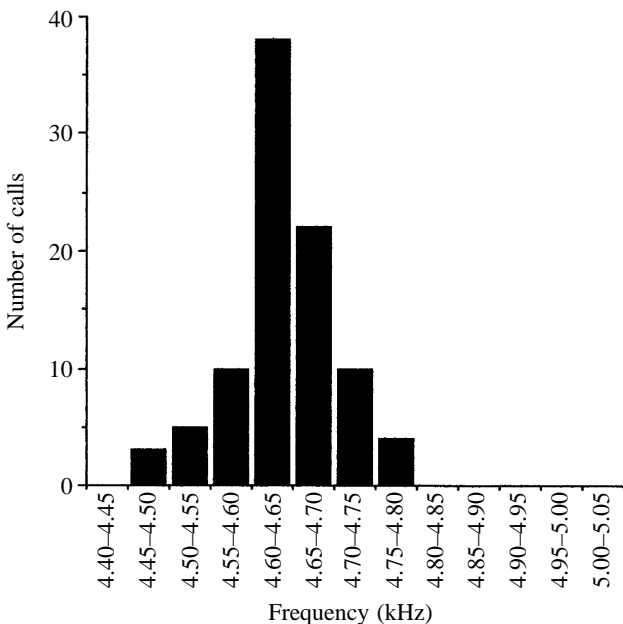


Fig. 8. The frequency distribution of the 92 chirps recorded, two examples of which are given in Fig. 7.

The clockwork model likens the oscillator of a clock to the free vibration of the wing structures. As a consequence, the song should be characterised by a single frequency, determined by the elastic properties (equivalent to the balance spring) and mass (inertia) of the wing. The frequency so generated should be relatively constant; changes in muscular effort during the movement of the plectrum across the file can, as pointed out above, cause only second-order changes in frequency. Increased muscular effort will reduce the frequency generated but will be associated with an increase in the intensity of the call. Reduction in muscular effort will cause precisely the reverse to occur. The constant action of the plectrum scraping across the file will cause wear on both plectrum and file (Hartley and Stephen, 1989). Such wear will affect the escapement action of the plectrum and file teeth.

The observations and results of this study do not support the clockwork model. First, the spectrum of the song of the cricket is characterised by two frequency components, one at approximately 4.75 kHz and a second at approximately 5.6 kHz (see Fig. 6B). It is impossible for a clock escapement to run at two different rates at the same time. Second, the principal frequency component of the song is not constant. Fig. 8 shows that the principal frequency component of 92 consecutive calls is distributed with a normal distribution around a mean value of 4.65 kHz. The maximum percentage variation in frequency of the series of calls shown in Fig. 8 is 4.5%. For a spring-powered clock, the driving force applied to the escapement will change by a factor of approximately three as the spring unwinds. As the clock runs over a typical 7 day period, the rate will change by approximately 3 min over this period. This value gives a percentage change in rate of 0.03%. It is thus extremely unlikely that the variation in the principal frequency component observed in Fig. 8 could be ascribed to changes in muscular effort during calling. Further, no relationship between changes in call frequency and call intensity was observed, as should have been the case if the clockwork model were applicable. Third, the measured frequency of free vibration of an isolated gryllid wing was found to be at approximately 5.6 kHz and not at the call carrier (principal frequency component) frequency of approximately 4.75 kHz. *Gryllus bimaculatus* also generates courtship song with a frequency in the region of 16 kHz. The clockwork model as expounded by Elliott and Koch (1983) cannot generate calls of this frequency. It is most unlikely that gryllids employ two entirely different mechanisms for generating calling and courtship song. The acoustic model developed in this paper accommodates, without difficulty, the generation of both types of call. It is therefore concluded that, in the light of the results presented in this paper, the clockwork model of stridulation is without foundation.

The acoustic model of stridulation

The spectrum of the call of freely singing male *Gryllus bimaculatus* has been shown to contain two frequency components, a principal component (the carrier frequency) at a frequency of approximately 4.75 kHz and a higher-frequency component at approximately 5.6 kHz. The 4.75 kHz component

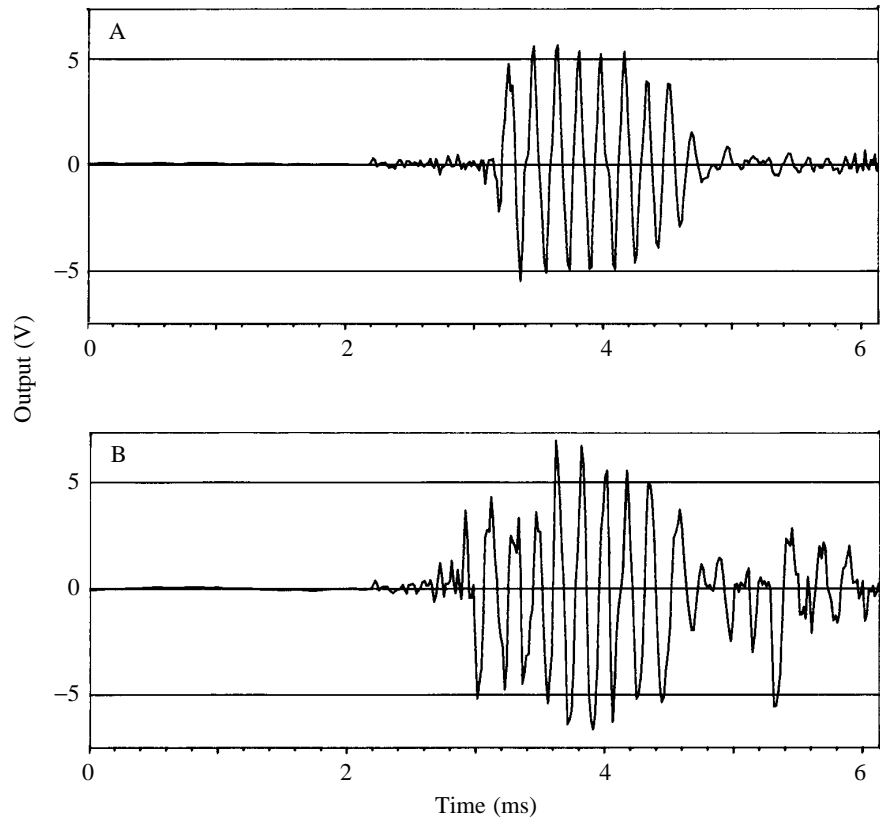


Fig. 9. (A) The enhanced time signal of the free vibration of an isolated wing excited using the electro-mechanical impulser. The background sound from the impulser has been subtracted. (B) The enhanced time signal of the free vibration of the wing recorded in 100% CO₂.

is generated by the P.F.I. rate. The finding that this frequency is not constant is in accordance with this conclusion. At the start of each call, the wing velocity increases from zero to the observed rate for that call. It is almost inconceivable that the velocity of the wings in each and every call could have precisely the same value. A normal distribution of strike rates about a mean value would be expected, as is indeed observed (Fig. 8). The 5.6 kHz component has been associated with the free vibration of the wings. This frequency should remain constant from call to call. This has also been observed to occur.

The calculation of the acoustic impedance of the vibrating wings shows that the air (or any other gas) in the subalar space acts as a resonant load on the wings. The wings and the resonant load behave like a conventional Helmholtz resonator. It is important to note that this subalar volume need not be completely closed for the air in it to act as a resonant load. This point is clearly demonstrated by the model stridulatory system. The quality factor Q (defined as resonant frequency/bandwidth at -3 dB) of the resulting resonant system will depend on the degree of coupling between the air load and the vibrating wings. This, in turn, will depend on how effectively the wings enclose the cavity. This resonant system will also act as an effective acoustic filter. The action of the plectrum scraping across the file will generate a complex frequency waveform with a fundamental period equal to the P.F.I. rate. This waveform will be filtered and amplified by the resonant air load. This filtering and amplification of a complex waveform has been demonstrated with the model stridulatory system (Fig. 5A,B). The component of the complex waveform generated by the plectrum-file impulses that is filtered will depend

on the frequency relationship between the resonant frequency of the air load and the frequency components of this complex waveform. This point will be further considered in the discussion of the heliox experiments.

This resonant frequency depends on the square root of the subalar volume (see equation 12). During stridulation, this volume will decrease as the wings close. This will cause the resonance curve to shift to a higher frequency. In the

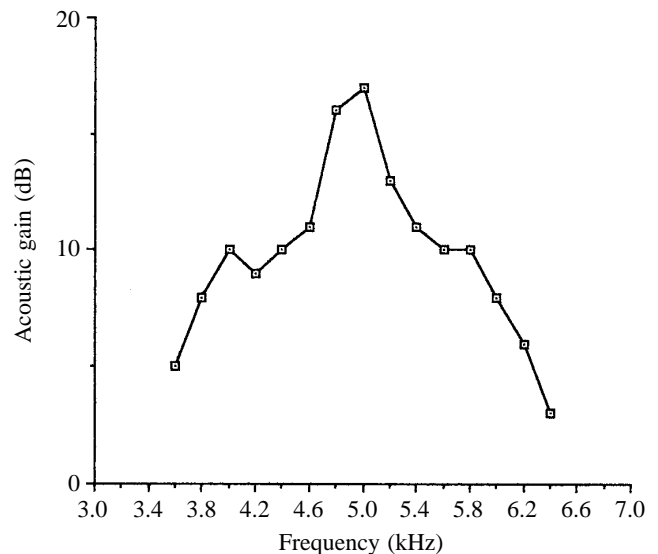


Fig. 10. The frequency response of the wing plus subalar volume measured using white noise.

majority of chirps, the acoustic pulse increases rapidly to a maximum and then decreases at a much slower rate. In all the calls recorded in this study, the frequency of a given call remained constant over the entire duration of the call. The observed changes in amplitude have been explained as a change in muscular effort over the duration of the wing sweep. Any change in muscular effort would have, by necessity, produced a change in the instantaneous frequency over the duration of a call. This would have occurred

irrespective of the model of stridulation assumed. The acoustics of the system presented here offer an alternative and more plausible explanation. The initial rise in amplitude will be determined by the bandwidth of the resonant system. The 3 dB bandwidth of the resonance curve shown in Fig. 10 is 350 Hz. The bandwidth of the resonant air load in a live stridulating animal can be estimated from the rise time of the call. The number of cycles n required for the call to reach a constant amplitude has been estimated from the recorded

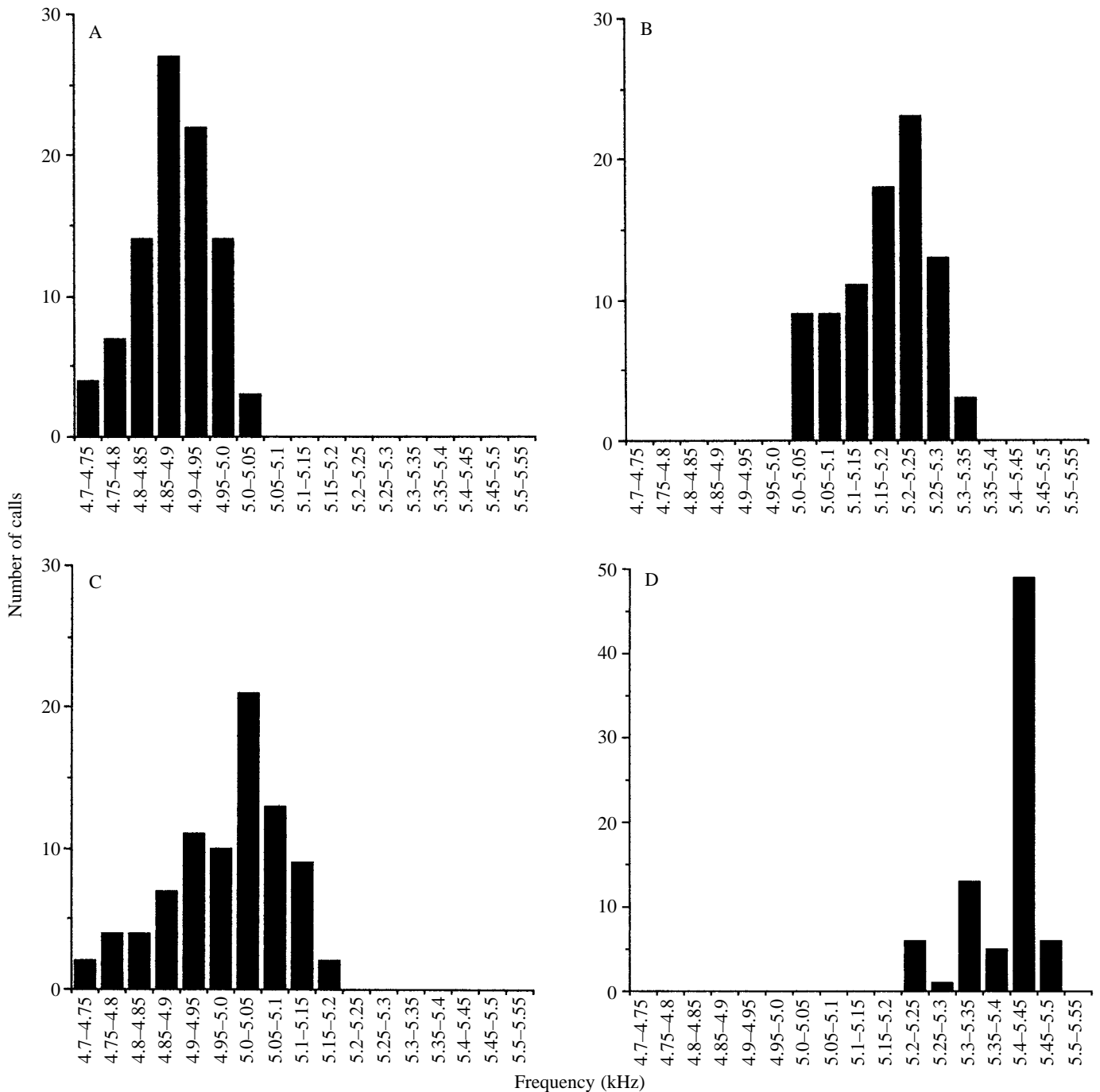


Fig. 11. (A) Frequency distribution of a series of chirps of a normal male *Gryllus bimaculatus*. Chamber filled with air. (B) As A. Chamber filled with heliox. (C) Frequency distribution of a series of chirps of the same male *Gryllus bimaculatus* shown in A after deafening by placing wax on the tympana; chamber filled with air. (D) As C, but with the chamber filled with heliox.

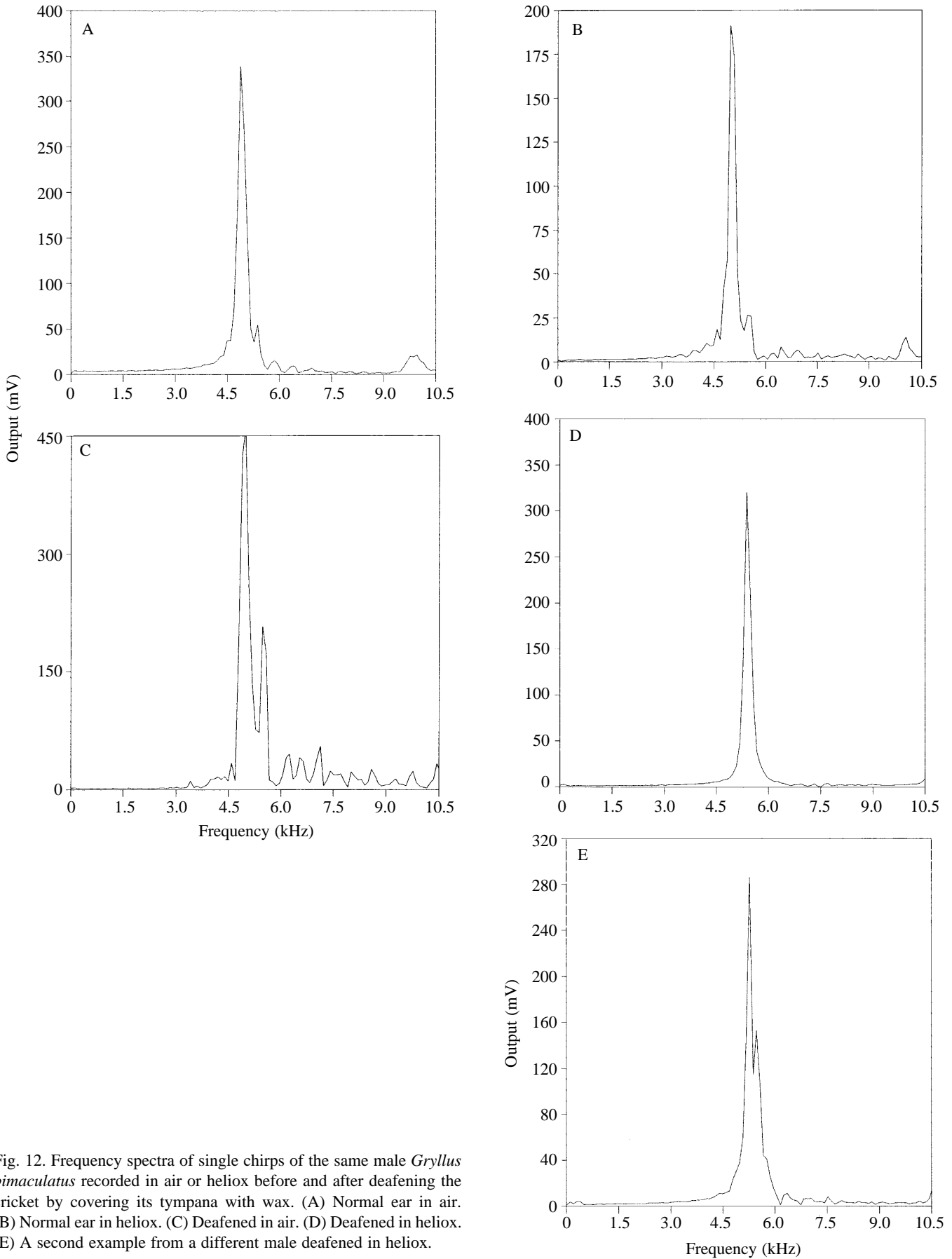


Fig. 12. Frequency spectra of single chirps of the same male *Gryllus bimaculatus* recorded in air or heliox before and after deafening the cricket by covering its tympana with wax. (A) Normal ear in air. (B) Normal ear in heliox. (C) Deafened in air. (D) Deafened in heliox. (E) A second example from a different male deafened in heliox.

calls to be approximately 15. If the bandwidth of the resonant air load is B , then:

$$(B/f_0)n = 1, \quad (13)$$

where f_0 is the resonant frequency. Using $n=15$ and $f_0=4.75$ kHz in the above relationship, the bandwidth B is equal to 316 Hz, which agrees reasonably with the value obtained from Fig. 10 of 350 Hz. Note that the spectrum of the call (e.g. Fig. 6B) cannot be used to estimate the bandwidth of the resonant element. The shape of the spectral curve at the principal frequency component is not determined by the Q of the resonance but by the frequency distribution of the complex P.F.I. waveform prior to filtering by the resonant element and by the duration of the call.

Once the call has reached its maximum amplitude, the wings are rapidly beginning to close, thus reducing the subalar volume. The rate of wing closure from measurements of Elliott and Koch (1983) and from the constancy of the stridulation frequency (P.F.I. rate) within a single call appears to be constant. This implies that the input frequency to the resonant filter remains constant while at the same time the resonance curve shifts towards higher frequencies. The gain of the system at the input frequency will then steadily decrease as the wings close. The amplitude of the call will decrease from its initial maximum value at a rate determined by the shape of the subalar resonance curve and by the rate at which the resonant frequency of the air load increases as the subalar volume decreases. The frequency of the call will remain constant and equal to the instantaneous P.F.I. rate. It is thus possible that the envelope of a gryllid call is determined more by the acoustics of the subalar air space than by changes in muscular effort or wing speed during stridulation.

Heliox experiments

The recordings of gryllids singing in heliox reveal new and interesting aspects of orthopteran auditory communication. The conclusions to be drawn rely on the model of stridulation developed above. When a gryllid stridulates, the subalar air volume resonates at the P.F.I. frequency, so filtering and amplifying this component. If the cricket were placed in heliox, and the volume of the subalar space remained the same, then the resonant frequency would increase. Taking the resonant frequency in air as 4.65 kHz (mean value from Fig. 8), then the increase in frequency can be calculated using the ratio of the frequency of the whistle in heliox and in air (a factor of 1.36). The resonant frequency of the subalar volume would be 6.5 kHz. The bandwidth of the subalar resonator is not expected to change radically in heliox. If the cricket attempts to stridulate in heliox by adopting the same wing position as in air, then in theory it should not be able to generate any sound, since the P.F.I. frequency is now decoupled from the resonating subalar volume. The observations presented show that the cricket does generate a song, albeit at an increased mean frequency without any significant change in the standard deviation of the call frequency distribution. Spectra of the calls in heliox show, as in air, two frequency components, one variable (mean at 5.15 kHz) and a second at the same frequency as in air (see Fig. 12A,B). The

latter component is the free vibration frequency of the wings and the former the now increased P.F.I. frequency. The P.F.I. frequency is being filtered and amplified in the normal way. This can only have come about if the resonant frequency of the subalar volume had been reduced. When the gryllid is placed in heliox, in addition to affecting the stridulatory apparatus, the heliox fills the auditory system. Any resonant elements within the auditory apparatus are expected to have their resonant frequencies increased, so distorting the insect's perception of sound towards higher frequencies. The effect of the heliox on the gryllid has been to cause the insect to increase the volume of its subalar space until the resonant frequency matches the increased P.F.I. frequency, these parameters being controlled by a now distorted sense of hearing.

If feedback control of stridulation *via* the auditory system does indeed operate, then deafening the insect should have an effect on song generation. Fig. 12C shows that this is the situation. The P.F.I. frequency varies widely and apparently at random around a mean value of 5 kHz. Placing the deafened insect in heliox should further decouple the feedback control system. Many of the deafened insects did not sing in heliox when earlier, before the tympana were waxed over, they sang readily in that medium. Experimental insects which did sing often only did so rather weakly. Fig. 12D shows the results of one which did sing, the frequency component most frequently being filtered and amplified by the subalar volume is the constant free-vibration frequency of the wings (5.45 kHz). The insect was only able, by chance, to match the P.F.I. frequency to the subalar volume in 40% of calls recorded.

The evidence presented above indicates the presence of a feedback control of stridulation in *Gryllus bimaculatus* *via* the auditory system. The feedback involves control of both P.F.I. rate and wing position prior to singing, which sets the resonant frequency of the subalar volume to match the P.F.I. frequency.

Gryllus bimaculatus also produce courtship song with a frequency in the region of 16 kHz. The P.F.I. waveform will contain components at this frequency. It is possible for the calling insect to generate harmonic calls of this frequency by simply reducing the subalar volume until it resonates at the required frequency. The results of the model stridulatory system confirm the possibility of this hypothesis. The waveform generated by the piezoelectric wings in the absence of the 'subalar' volume contains several different frequency components (see Fig. 5A). It was possible to filter and amplify any of these components by simply adjusting the volume of the 'subalar' cavity to match the frequency of the component.

The most important result of this investigation, that the call frequency in normal singing insects in air is not constant but varies about a mean, is a clear indication that there is both a variable-frequency resonator and a mechanism for regulating the song. The model shows that this is likely to be the subalar air space. The experiment on the free vibration of the wing reveals a fixed vibration frequency that is identifiable in all the calls.

Occluding the tympana of the insect with wax results in a very significant change in the frequency distribution of the calls (Fig. 11). This implies that the auditory system is involved in the

detection and measurement of the frequency generated. It also means that the insect needs a measure of the absolute value of the stridulation frequency if it is to attempt to regulate the frequency it generates. Covering the tympana with wax will not necessarily render the insect totally bereft of hearing, some sound can still reach the auditory receptors *via* the acoustic trachea, but it implies that the normal acoustico-mechanical functions of the tympana are essential in frequency discrimination.

The measurements in heliox support these hypotheses. The presence of the less dense gas in the auditory system will have an effect on the absolute discrimination of frequency. It appears that the insect is able to control its stridulation frequency to a considerable extent. If this were not the case, given the Q of the subalar volume resonator in heliox, the centre frequency of this resonator with the volume in air would have been 6.6 kHz. With a stridulation frequency of 4.9 kHz, the wings and subalar volume would have been effectively decoupled. The recordings in heliox of normal animals showed a slight reduction in call intensity but not to the degree expected if total decoupling had occurred. This would only be possible if the insect were able to control the volume of the cavity to maintain effective coupling between stridulation and the subalar air space. Furthermore, effective control of either stridulation or cavity volume does not occur in the deafened insect in heliox. In over 60% of the analysed calls, the only frequency present was that of the free vibration of the wings around 5.5 kHz. Great difficulty was experienced in recording an adequate number of calls from deafened insects in heliox since they appeared to be able to produce a call only when, by chance, there was an approximate match between subalar volume and tooth strike rate. Previously these insects sang well in heliox, as they did when subsequently deafened in air.

Control of song frequency obviously occurs in other orthopteran species. Oecanthines construct leaf baffles to facilitate the generation of their songs. There is no essential difference in the physics of these leaf baffles and the subalar system of *Gryllus bimaculatus*. The oecanthine will have to tune its leaf baffle resonator if it is to couple this with its stridulation. This it can only do acoustically. Similarly, mole crickets 'tune' their burrows and again this tuning can only involve an acoustic feedback. There is no reason then why *Gryllus bimaculatus* should not use acoustic feedback to control the frequency and intensity of its own song.

This paper presents a radically different picture of sound production in *Gryllus bimaculatus* from that currently accepted. However, the baffle effect responsible for the generation of the harmonic structure of the calls of this insect is not a unique physical process. It was, for example, shown by Alexander (1956) to be used by some oecanthines. The same effect occurs whenever vibrating structures are placed in enclosures. A familiar example is that of a loudspeaker in a cabinet. These cabinets can generate resonance effects arising from the process described in this paper as well as those associated with the physical dimensions of the cabinet. The resonance properties of a Helmholtz resonator are a single resonance, the Helmholtz resonance, and a series of cavity resonances harmonically

related to one another but not to the Helmholtz resonance. It would have been surprising if the effect described and observed had not occurred in either the model system or the stridulating insect. It is expected that this method of sound amplification will be widespread in insect sound production.

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