

ACOUSTICS OF SOUND PRODUCTION AND OF HEARING IN THE BLADDER CICADA *CYSTOSOMA SAUNDERSII* (WESTWOOD)

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SUMMARY

The male cicada of the species *Cystosoma saundersii* has a grossly enlarged, hollow abdomen and emits a loud calling song with a fundamental frequency of about 800 Hz. At the song frequency, its hearing is non-directional. The female of *C. saundersii* lacks sound producing organs, has no enlargement of the abdomen, but possesses an abdominal air sac and has well developed directional hearing at the frequency of the species' song.

Physical mechanisms are proposed that explain these observations in semi-quantitative detail using the standard method of electrical network analogues. The abdomen in the male, with its enclosed air, is found to act as a system resonant at the song frequency, thus contributing a large gain in radiated sound intensity. Coupling between this resonator and the auditory tympana accounts for the observed hearing sensitivity in the male, but destroys directionality. In the female, the abdominal cavity acts in association with the two auditory tympana as part of a phase shift network which results in appreciable directionality of hearing at the unusually low frequency of the male song.

INTRODUCTION

The Australian bladder cicada *Cystosoma saundersii* (Westwood) is a remarkable insect in that the male produces a calling song which consists of a train of brief tone bursts of approximately 800 Hz sound repeated about 40 times per second.

This insect and its associated acoustical and behavioural questions have only recently been studied (Young, 1972; Young & Hill, 1977). The most striking feature of the male is its grossly enlarged, hollow, abdomen (Fig. 1), which enhances radiation of sound (Young, 1972), and also affects hearing in the male, rendering the auditory system non-directional to the song frequency (Young & Hill, 1977). In the female of *C. saundersii* the abdomen is not enlarged, but it contains an air sac associated with the auditory tympana, and the hearing of the female is directional at the frequency of the male song (Young & Hill, 1977).

Organs specialized for sound production are limited to the male in *C. saundersii*. Each sound pulse in the calling song is generated by the buckling of two tymbals, which consist of flexible cuticular membranes braced by a series of seven stiffer, parallel ribs. Each tymbal is approximately triangular in shape, about 20 mm² in area, and is convex outwards in the resting state (Young, 1972). The mechanics of tymbal buckling and its neuromuscular control are complex and are the subject of a paper in preparation by P. J. Simmons and D. Young.

Briefly, during production of the calling song the tymbal is held in outward tension by the tensor muscle, contraction of the large tymbal muscle overcomes this tension and the tymbal buckles inward (see also Young, 1972), generating a pulse of sound. As about six of the ribs are bent as the tymbal buckles, a series of shocks associated with sequential bending of the ribs may correspond with the 800 Hz carrier frequency of the song produced.

The enlarged abdomen of the male appears to be essential for effective sound radiation. During production of the calling song, the male abdomen is extended, possibly as the result of an increase in static internal air pressure. The singing behaviour of *C. saundersii* during pair formation is the subject of a paper in preparation by K. G. Hill and C. E. Hill.

The sound pressure of the emitted signal falls if the abdomen is removed (Young, 1972). The size of the male abdomen severely limits the insect's flight speed and agility. However, concentration of sound energy into a narrow frequency band and efficient radiation into the air medium are essential characteristics of the sound producing organs of terrestrial insects if communication signals are to be propagated over appreciable distances (Bennet-Clark, 1971; Michelsen & Nocke, 1974). In the acoustical analysis which follows, we show that the male abdomen in *C. saundersii* acts as a resonator to amplify the song and stabilize its frequency, and optimizes radiation efficiency of the signal. Although *C. saundersii* may represent an extreme case acoustically, the principles discussed may have general applicability in insects.

As with most quantitative acoustic discussions, the most convenient methods of analysis are those based on analogues derived from the more familiar field of electric circuit theory. The bases of these analogies are discussed in standard texts (Morse, 1948; Olson, 1957; Skudrzyk, 1968) which should be consulted for details. For the present we simply state some of the concepts involved in our later discussions.

Acoustics is concerned with fluctuations in atmospheric pressure and with the oscillatory flow of volumes of air through pipes and apertures, sometimes impeded by flexible membranes. Electric circuits, on the other hand, are concerned with currents and voltages and with the way in which current flow is impeded by inductances, capacitances and resistances. The most fruitful analogy for our present purpose identifies acoustic pressure with electrical potential and acoustic volume flow with electrical current. In such a system of analogies, mass-like acoustic impedances are identified with inductances, spring-like acoustic compliances with capacitances, and viscous or other similar resistances with electrical resistances. We shall discuss these analogies in greater detail as we proceed but point out that, since we are concerned with oscillatory quantities, it is customary to use angular frequencies $\omega = 2\pi\nu$ rather than the common frequencies ν expressed in hertz, and that the

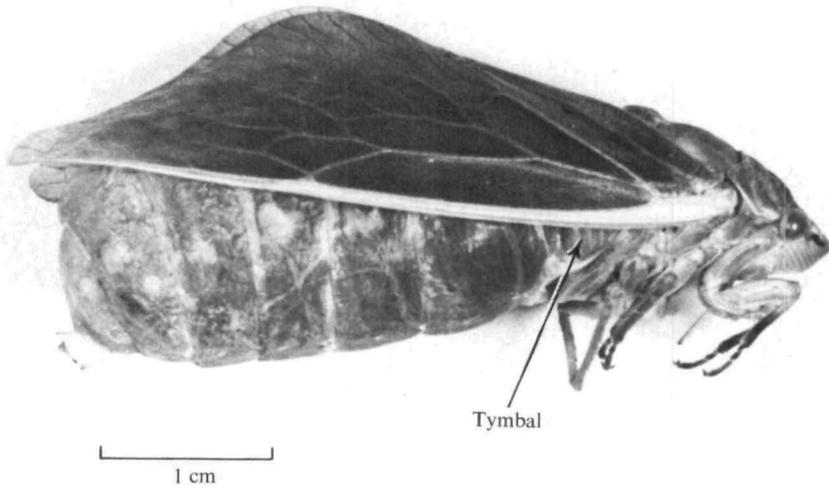


Fig. 1. The male of the species *Cystosoma saundersii*. Note the enlarged abdomen. The tymbals are on the first abdominal segment communicating directly with the air cavity. The tympana are in folds ventrally in the second abdominal segment and are not visible in the photograph.

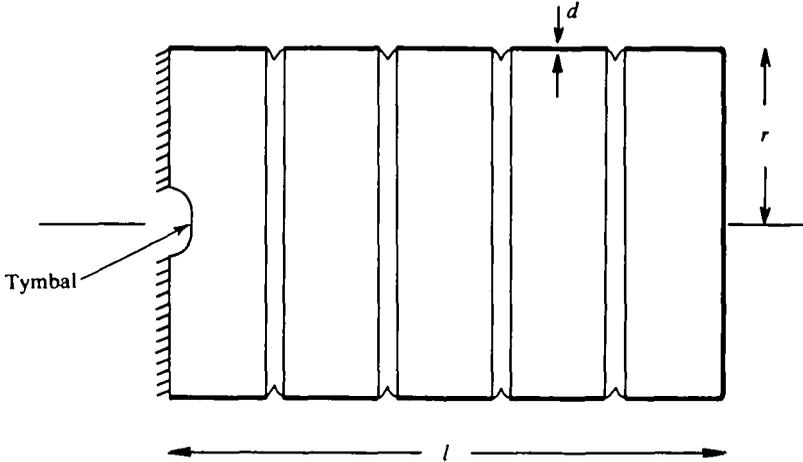


Fig. 2. Idealized model of the male abdomen. It is roughly cylindrical and consists of rather rigid ring sections joined by light flexible membrane which is stretched when the insect is singing.

oscillatory quantities are represented through a factor $\exp(j\omega t)$ where $j = \sqrt{-1}$. Details of this approach are given in the references listed above or can be found in standard texts on electric circuits.

SOUND PRODUCTION

The resonant abdomen

The abdomen in the male of *C. saundersii* is segmented (Fig. 1), and segments 3–7 may be considered as stiff rings joined together by lighter, flexible membrane (schematically illustrated in Fig. 2). The internal air cavity (an enlarged tracheal air sac) communicates with the exterior through a narrow, closable spiracle situated on the metathorax (Young & Hill, 1977). At ordinary sound frequencies, therefore, the abdomen may be considered sealed. During calling song production, the abdomen is extended so that the intersegmental membranes are in tension. The two tymbals in the first abdominal segment form part of the wall of the abdominal cavity (Young & Hill, 1977).

The acoustic circuit has three elements. The tymbals, being relatively stiff and driven by powerful muscles, act together always to displace a certain volume of air, almost irrespective of the acoustic pressure acting on them. They are thus represented by a high-impedance (constant-current) generator G as shown in Fig. 3.

The air inside the abdominal cavity, the volume V_B of which is typically about 7 cm^3 , acts as a simple springy compliance. The analogous capacitance C_B is given by standard methods (Morse, 1948) as

$$C_B = V_B / \rho_a c^2, \quad (1)$$

where ρ_a is the density of air ($\rho_a \approx 1.2 \times 10^{-3} \text{ g cm}^{-3}$) and c is the velocity of sound in air ($c \approx 3.4 \times 10^4 \text{ cm s}^{-1}$). Thus for a typical insect

$$C_B \approx 5 \times 10^{-6}, \quad (2)$$

where we use c.g.s. units for all the analogue quantities.

Motion of the abdomen wall in the mode of lowest frequency probably consists of a simple lengthening of the abdomen by a slight stretching of the membranes between the nearly rigid segments. A radial expansion would result in a much stiffer and therefore higher-frequency mode. If the bladder is idealized as a cylinder of radius r and length l capable of lengthwise expansion in the manner outlined above with one end fixed, then it is easy to show that its motion presents very nearly a mass-like load whose analogous inductance L_B has the possible range of values

$$\rho_m d / \pi r^2 < L_B < \rho_m d (r + \frac{2}{3}l) / \pi r^2 \quad (3)$$

depending on the elasticity of the membrane and hence the exact nature of the motion.

Here ρ_m is the density of the material in the walls, which is close to 1 g cm^{-3} , and d is the average wall thickness, which we can estimate to be a few tenths of a millimetre. For a typical insect (Young & Hill, 1977, Fig. 1) $l \simeq 3 \text{ cm}$ and $r \simeq 1 \text{ cm}$ so that, again in c.g.s. units,

$$L_B \simeq 0.01 \text{ to } 0.03. \quad (4)$$

This mass-like load is in series with the elastic stiffness of the membrane between the abdominal segments, represented by an analogous capacitance C_M and an associated loss component R_M . We have no direct knowledge of the magnitudes of R_M and C_M but we shall see later that the acoustic effectiveness of the abdomen as a sound radiator requires that $C_M > C_B$ so that most of the stiffness (which is inversely proportional to C) is contributed by the internal air volume rather than by the mechanical properties of the membrane. This is in accord with the observation that the cicada can collapse its abdomen to some extent when not singing.

There is a further loading of the abdomen by the outside air. From standard discussions (Olson, 1957) this load has both a mass-like component L_A , caused by bodily motion of the air near the bladder wall, and a resistive component R_A contributed by sound radiation. Since the maximum dimension of the bladder is very much less than the sound wavelength at the song frequency ($\simeq 40 \text{ cm}$), exact calculation is unnecessary for it is only the change in volume that is important and the pulsating abdomen behaves acoustically very much like a pulsating sphere of the same volume. In particular the sound radiation should be nearly uniformly distributed in angle, as has been confirmed by K. G. Hill and C. E. Hill (in preparation). If r' is the radius of the equivalent sphere, then the actual analogue values at angular frequency ω are

$$L_A \simeq \rho_a / 4\pi r', \quad (5)$$

$$R_A \simeq \rho_a \omega^2 / 4\pi c. \quad (6)$$

Inserting typical values near 800 Hz we find

$$L_A \simeq 8 \times 10^{-5}, \quad R_A \simeq 7 \times 10^{-3}. \quad (7)$$

Note that R_A is independent of r' for such small spheres.

The analogue circuit

The topology of the analogue circuit, which is shown in Fig. 3, is determined by considerations of pressure transmission and volume flow through the various acoustic elements. If the impedances of the two tympana, represented by Z_T , are large enough

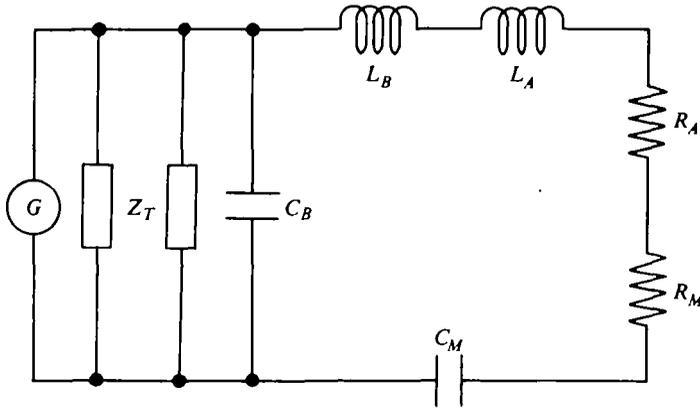


Fig. 3. Analogous electrical circuit for the tymbals and abdominal bladder. The tymbals are represented by a high impedance current generator G , the air inside the bladder by capacitance C_B , the moving mass of the bladder wall by inductance L_B , the co-moving air mass by L_A , the sound radiation resistance by R_A , the compliance of the membrane links by C_M and the resistive losses in them by R_M . The large impedances Z_T are those of the tympana, which can be neglected in the analysis of singing behaviour.

that the acoustic volume flow through them can be neglected, and if the membrane compliance C_M is greater than that of the enclosed air C_B , then the circuit approximates a parallel resonant system fed from a constant-current generator G . The radiated sound power is represented by the power dissipated in the radiation resistance R_A , which is a maximum at the resonance frequency.

Again neglecting the acoustic flow through the tympana and denoting by i_T the acoustic current at frequency ω generated by the combined action of the tymbals, it is easy to show that the magnitude of the acoustic flow i_A through the radiation resistance R_A is given by

$$|i_A/i_T| = \{[1 - (L_B + L_A) C_B \omega^2 + C_B/C_M]^2 + [(R_A + R_M) C_B \omega]^2\}^{-\frac{1}{2}} \quad (8)$$

This current is a maximum at the resonance frequency $\nu_B^* = \omega_B^*/2\pi$ given by

$$\omega_B^* = [1 + C_B/C_M]^{\frac{1}{2}} [(L_B + L_A) C_B]^{-\frac{1}{2}} \quad (9)$$

and the radiated acoustic power P_A at resonance has the magnitude

$$P_A = R_A i_A^2 = R_A i_T^2 Q_B^2, \quad (10)$$

where the Q value for the resonant circuit is given, from (8), by

$$Q_B = [(R_M + R_A) C_B \omega_B^*]^{-1}. \quad (11)$$

A bare tymbal in the absence of the abdomen would be a dipole source which would not radiate efficiently, but even without this effect it is clear from (10) that the resonant effect of the abdomen increases the radiated sound power by a factor Q_B^2 which, as we see presently, amounts to at least 10 dB.

If we insert into (9) values of C_B , L_B and L_A from (2), (4) and (7) and recall from our discussion that $C_M > C_B$, then we find

$$500 \text{ Hz} < \nu_B^* < 1000 \text{ Hz} \quad (12)$$

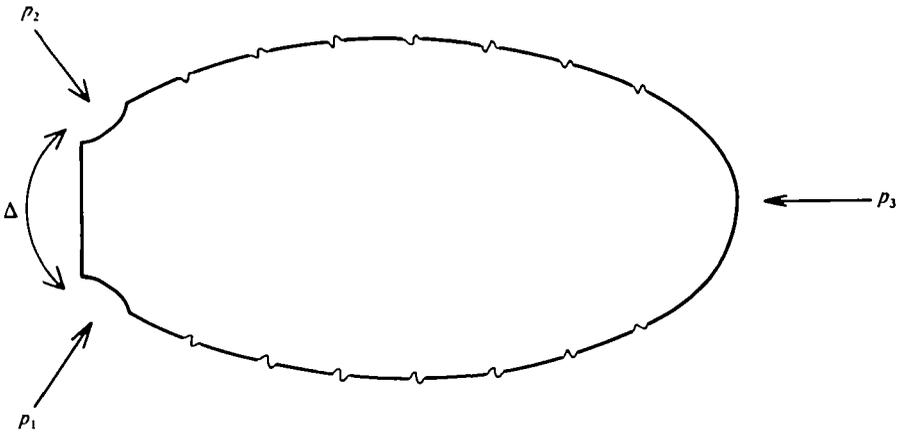


Fig. 4. Schematic representation of the relation between the tympana and the abdominal bladder. p_i are the pressures acting on the system and Δ is the acoustic path length between the tympana for lateral sound incidence.

Table 1. *Analogous impedances (c.g.s. units) and related quantities used in the calculations*

	Symbol	Male	Female
Abdominal cavity compliance	C_B	6×10^{-8}	2×10^{-7}
Abdominal wall inertance	L_B	0.01	(∞)
Abdominal membrane compliance	C_M	1×10^{-3}	(0)
Abdominal membrane resistance	R_M	3	—
Q for abdominal resonance	Q_B	10	—
Tymbal impedance	—	$\gg 100$	—
Tympanum inertance	L_T	1	0.05
Tympanum compliance	C_T	1×10^{-7}	7×10^{-7}
Tympanum resistance	R_T	1000	150
Q for tympanum resonance	Q_T	3	3
Acoustic path length	Δ	2	2

as the extreme range for the estimated resonance frequency. The best estimate is near the mid-point of this range which is acceptably close to the song frequency of 800 Hz.

If the membrane joining the abdominal segments were perfectly elastic ($R_M = 0$) so that damping was entirely by radiation, then numerical values inserted in (11) would give $Q_B \approx 200$. It is likely, however, that $R_M \gg R_A$ so that the internal friction of the membrane constitutes the major damping mechanism, and indeed most biological compliances have $Q < 10$.

Independent evidence is available on this point from the work of Young (1972), who observed a decrease of 8–10 dB in sound pressure level in the distress call when the abdominal sac was removed, and from Young & Hill (1977) who measured a 24 dB decrease in auditory sensitivity at 800 Hz under similar conditions. Interpretation is not simple because the bare tymbals and tympana are exposed on both surfaces and so act as dipoles. More direct is the observation of Young and Hill that the sound pressure at 800 Hz inside the male abdomen is about 11 dB higher than in the free field. Again, as we see later, interpretation is not simple but the implication of

all these results is that Q_B is between about 3 and 10. In a more normal situation oscillograms of the free song (Fig. 5*a* of Young 1972) show that each tone burst has an exponential decay with a characteristic decay time for sound pressure of about 8 ms. This implies $Q_B \simeq 18$, which may be an overestimate since there may be some energy input from the tymbals. It is probably not too far from correct to suggest $Q_B \simeq 10$, giving a 20 dB gain in radiated power and implying $R_M \simeq 3$ c.g.s. acoustic ohms.

For ease of reference and comparison, values of analogous impedances for both male and female are collected in Table 1.

HEARING IN THE MALE

The two auditory tympana in the male form part of the wall of the abdominal cavity as shown schematically in Fig. 4. Each tympanum is about 4 mm² in area and has two large masses of amorphous material attached to it. A cuticular bar connects the tympanum to the receptors located laterally in the auditory capsule (Young and Hill, 1977). When the animal is singing, tension in the tympanum is removed by the detensor tympani muscle (Young, 1975).

In a sound pressure field of amplitude p we are concerned with three external sound pressures acting on the insect – the pressures p_1 and p_2 applied to the external surfaces of the tympana and the resultant pressure p_3 interacting with the fundamental resonant mode of the abdomen through its external surface. Each of these pressures is supplied from a low impedance source – the sound wave, which fixes pressure but not volume flow – and so is represented by an analogous electrical voltage generator. In complex notation these three potentials can be written

$$p_i = p \exp[j\omega(t + \delta_i)], \quad (13)$$

where ω is the angular frequency and the δ_i are time delays caused by the differing path lengths of the sound wave to the action points considered. If Δ is the external acoustical path length between the two tympana, then, with sound incident from one side of the insect, we can write

$$\delta_{1,2} = \pm \Delta/2c, \quad \delta_3 = 0, \quad (14)$$

where + refers to the ipsilateral and – to the contralateral tympanum and c is the velocity of sound.

In terms of electrical analogues each tympanum is represented by a series resonant circuit. The inductance is associated with the tympanum mass and has the value

$$L_T = \rho_m d/A_T, \quad (15)$$

where A_T is the area and d the effective thickness of the tympanum and ρ_m the density of its material. The anatomical detail given by Young & Hill (1977) shows that the tympanum in the male consists of a membrane about 2 μ m thick at its centre and loaded, except near the central part, by as much as 0.5 mm thickness of amorphous material. The central region, about 0.1 mm² in area, is loaded by a ridge that transmits its motion to the neural transducers. If only the central portion of the tympanum vibrates then probably $L_T \sim 1$, though a value of not much greater magnitude is obtained if it is assumed that the entire tympanum with its attached amorphous material moves.

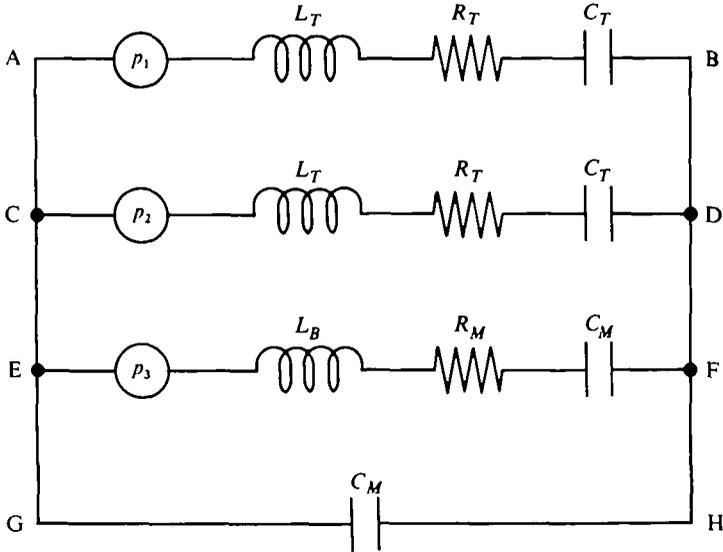


Fig. 5. Network representing the acoustical behaviour of the male auditory system shown in Fig. 4. L_T , R_T and C_T refer to the tympana, L_B , C_B , R_M and C_M to the abdomen (the smaller quantities L_A and R_A are neglected). p_i are the external pressures shown in Fig. 4.

The stiffness of the tympanum is provided by the elasticity of its membrane, together with some contribution from the amorphous material. It is difficult to decide unambiguously on the mode of motion of the tympanum until more is known about the elastic properties of the amorphous loading material. The most likely vibration is one in which the whole tympanum moves with most of its stiffness being provided by the tympanic membrane rather than by the amorphous load. By comparison with the female tympanum, which we discuss later, it is likely then that $C_T \approx 1 \times 10^{-7}$ which implies a resonance frequency near 500 Hz, or well below the song frequency. If the Q for the tympanum resonance has a rather low value, say 3, because of damping in the load, then $R_T \approx 1000$ c.g.s. units. From these values, which are not critical in our later analysis, it is clear that the impedance of the tympana at the song frequency is at least a factor of 100 greater than that of the abdomen, thus justifying the assumption made in the previous section.

Consideration of the paths of action of the acoustic pressures and the relationships between the acoustic flows now leads to the analogue circuit shown in Fig. 5. Note that there are some changes from the circuit in Fig. 3 because one of the excitations, p_3 , is now applied as a pressure acting on the outside of the abdomen rather than as a volume flow to its interior.

Before presenting the results of a calculation on this circuit it is helpful to analyse it qualitatively. From our discussion above and the numerical values summarized in Table 1 it is clear that the impedance of the branches AB and CD (> 1000 acoustic Ω) is greater than that of EF and GH (~ 30 acoustic Ω) so that to a first approximation we can consider just the low-impedance circuit EFGH. From the viewpoint of the pressure generator p_3 this is a series circuit resonant at the song frequency and the resonance leads to an enhanced pressure $\propto Q_B p_3$ across C_B , where $\alpha = C_M / (C_M + C_B)$ lies between $\frac{1}{2}$ and 1. This is the enhanced pressure inside the abdomen measured by

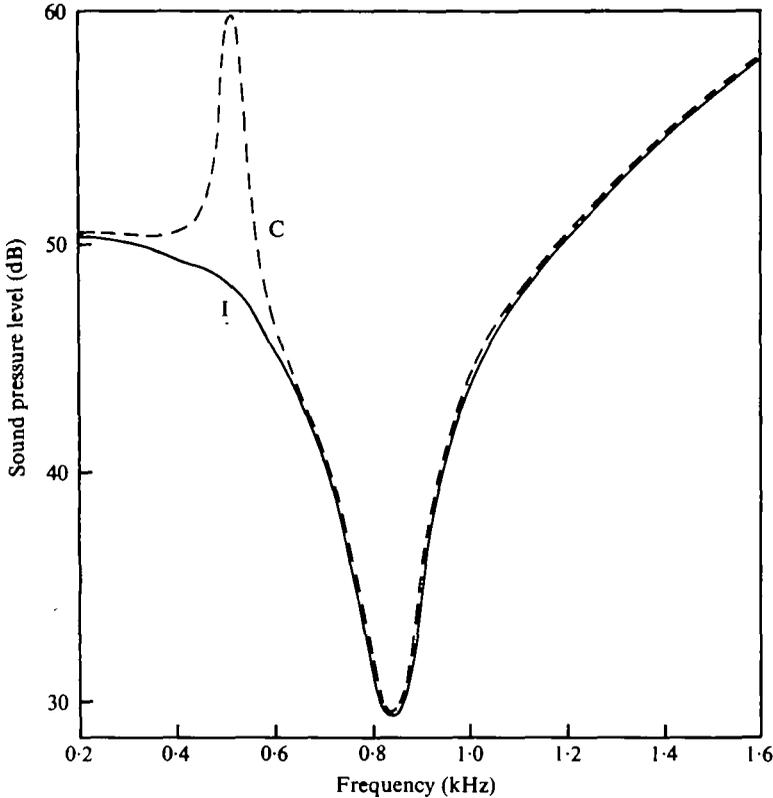


Fig. 6. Calculated sound pressure level (in dB relative to $0.0002 \mu\text{bar}$) required to produce 10 \AA vibration amplitude at the ipsilateral (I) and contralateral (C) tympana of the male cicada. A change in SPL of 20 dB is required to change the vibration amplitude by a factor of 10.

Young & Hill (1977). The phase of the abdominal pressure is, however, in quadrature with the external pressure p_3 and hence, since the phase shifts $\omega\delta_i$ are small, essentially in quadrature with p_1 and p_2 as well.

Considering now the branches AB and CD connected across the low-impedance circuit EFHG, we can see that the driving pressures in these branches are essentially $[(\alpha Q_B p_3)^2 + p_1^2]^{\frac{1}{2}}$ and $[(\alpha Q_B p_3)^2 + p_2^2]^{\frac{1}{2}}$ respectively. If $Q_B \approx 10$ then these are both nearly equal to $\alpha Q_B p_3$ irrespective of details of the phase shifts δ_i , and the tympanum displacements at resonance are

$$x^* \approx \alpha Q_B p / \omega_B^* A_T R_T. \quad (16)$$

With the values given in Table 1 this gives a displacement of about 10 \AA (10^{-7} cm) at the observed (Young & Hill, 1977) threshold sound pressure level of 40 dB relative to the normal reference level of $0.0002 \mu\text{bar}$ (1 bar = 10^5 Pa).

This analysis thus accounts for the non-directionality of hearing sensitivity in the male and provides an estimate that seems not too unrealistic for the absolute value of the deflection of the tympanum. To complete the analysis involves straightforward calculation of the currents in the branches AB and CD of Fig. 5 and their integration to give tympanum displacement as a function of frequency. The results of such a calculation, using the values given in Table 1, are shown in Fig. 6. For easy

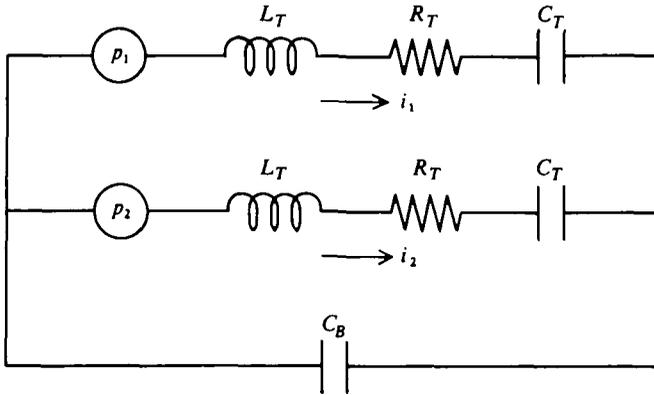


Fig. 7. Network representing the acoustical behaviour of the female auditory system. L_T , R_T and C_T refer to the tympana and C_B to the body cavity. p_1 and p_2 are external sound pressures acting on the tympana.

comparison with published experimental results (e.g. Young & Hill, 1977) the results are given as a threshold sensitivity curve assuming that a tympanum displacement of 10 \AA is required at the auditory threshold. The curve can be simply shifted up or down for different assumed thresholds or inverted to give tympanum deflexion for a given sound pressure level.

From Fig. 6 it is clear that the model reproduces the general features of the behaviour measured by Young & Hill (1977). The auditory system is most sensitive near the song frequency of 800 Hz, where it shows no distinction between ipsilateral and contralateral stimulation and is thus completely insensitive to sound direction. At frequencies near 500 Hz the system shows appreciable directional discrimination. This frequency is not determined by the tympanum resonance but rather by a series resonance in the circuit branch EF, while the extent of the discrimination is influenced by the membrane resistance R_M . The small directionality noted by Young & Hill (1977) at other frequencies away from 800 Hz may possibly be due to a diffraction effect making p_2 not quite equal to p_1 .

HEARING IN THE FEMALE

In the female of the species, as we have already pointed out, the abdominal cavity is smaller than in the male, only about 0.2 cm^3 , and the abdominal walls are relatively massive (Young & Hill, 1977). This implies a very large value for the inductance L_B in Fig. 5 so that the pressure p_3 is effectively insulated from action on the system. The analogous circuit thus reduces to the simpler network shown in Fig. 7. The capacitance C_B representing the cavity volume is, from (1), approximately

$$C_B \simeq 2 \times 10^{-7} \text{ c.g.s. units.}$$

The female tympanum is generally similar to that of the male except that the amount of amorphous material is greatly reduced and the tympanal membrane ranges from 1 to $5 \mu\text{m}$ in thickness. The total tympanal area is about 3.9 mm^2 , similar to the area in the male, and the thin central region is about 0.5 mm^2 . Again the tympanum is loaded by a rib conveying its vibrations to the neutral transducers (Young & Hill

1977). These dimensions suggest an inertance L_T in the range 10^{-2} – 10^{-1} for the bare tympanum and we estimate $L_T \simeq 0.05$ as a reasonable value, allowing for the rib loading.

As we shall see presently, the bare tympanum is probably resonant near the song frequency which implies $C_T \simeq 7 \times 10^{-7}$. A loaded Q value near 5 is probably about right for the membrane, although this could be less because of the ridging and the layer of amorphous material noted by Young & Hill (1977). This implies $R_T \simeq 50$ though it might be 100 or a little more. Here, as before, c.g.s. units are implied. (Later we shall see that we need to assume $R_T \simeq 150$ in order to achieve sufficient directional discrimination. This is within the uncertainty of our estimates.)

We consider a situation in which a sound wave is incident in the horizontal plane at an angle θ to the symmetry plane of the insect. We can write

$$\begin{aligned} p_1 &= p \exp[j\omega(t+\delta)], \\ p_2 &= p \exp[j\omega(t-\delta)], \end{aligned} \quad (17)$$

where

$$\delta = \Delta \sin \theta / 2c \quad (18)$$

and Δ is the separation between the two tympana and c the velocity of sound.

Analysis of the network in Fig. 7 is straightforward and the results are simplified when we remember that Δ is much less than the sound wavelength at frequencies of concern, so that $\omega\delta \ll 1$. With this simplification, the current through the branch representing tympanum 1 at frequency ω is

$$|i(\theta)| \simeq pB \left\{ \left[L_T \omega - \frac{1}{C_T \omega} \right]^2 + \left[R_T + \frac{\Delta}{c} \left(\frac{1}{C_B} + \frac{1}{2C_T} \right) \sin \theta \right]^2 \right\}^{\frac{1}{2}}, \quad (19)$$

where

$$B = \left[\left(R_T^2 - K^2 + \frac{1}{C_B^2 \omega^2} \right)^2 + 4R_T^2 K^2 \right]^{-\frac{1}{2}} \quad (20)$$

and

$$K = L_T \omega - \frac{1}{C_T \omega} - \frac{1}{C_B \omega}. \quad (21)$$

In (19), $\theta = 90^\circ$ implies ipsilateral and $\theta = -90^\circ$ contralateral stimulation.

The factor in braces in (19) determines the directional response. This discrimination is a maximum at the resonance frequency of the bare tympanum, for then $L_T \omega = 1/C_T \omega$ and the factor reduces to

$$\left\{ R_T + \frac{\Delta}{c} \left(\frac{1}{C_B} + \frac{1}{2C_T} \right) \sin \theta \right\}. \quad (22)$$

This gives a cardioid directional response which can be made to have zero sensitivity in the contralateral direction if

$$R_T = \frac{\Delta}{c} \left(\frac{1}{C_B} + \frac{1}{2C_T} \right). \quad (23)$$

If $\Delta \simeq 2$ cm this requires $R_T = 300$ which is rather higher than expected, but even $R_T \simeq 150$ gives 10 dB discrimination between ipsilateral and contralateral incidence. The true value of Δ may perhaps be less than 2 cm and closer to the geometrical value of about 1.2 cm. In any case the degree of discrimination is almost certainly limited by sound conduction through the body tissue of the insect.

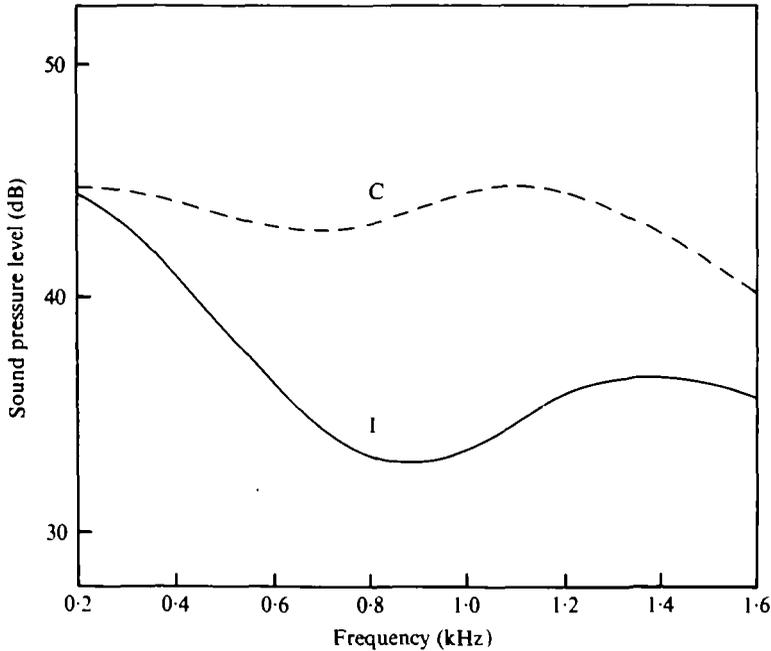


Fig. 8. Calculated sound pressure level (in dB relative to $0.0002 \mu\text{bar}$) required to produce 10 \AA vibration amplitude at the ipsilateral (I) and contralateral (C) tympana of the female cicada.

The factor B in (19) affects the general shape of the response curve and has a maximum near the frequency for which $K = 0$. This cannot be brought to coincidence with the song frequency except by assuming that the tympanum is much heavier than seems possible. In fact this peak frequency seems likely to lie above 2000 Hz for the dimensional values discussed above.

Evolutionary processes have presumably optimized the parameters of the acoustic system for the female cicada. Our calculations, shown in Fig. 8, display ipsilateral and contralateral behaviour for one such set of parameters consistent with our limited knowledge of the system, the values being those given in Table 1. As before, the results have been plotted as threshold sound pressure level for a deflexion of 10 \AA at the tympanum.

From Fig. 8 it is clear that our model is incomplete. There is, certainly, a discrimination of about 10 dB between ipsilateral and contralateral sound at the song frequency and this discrimination, which has a cardioid pattern, reduces at higher or lower frequencies. The ipsilateral response, too, is peaked near the song frequency, but this sensitivity is very much less prominent than the neurophysiologically measured peak.

Several mechanisms might be proposed to account for this discrepancy. The simplest is to suggest that the lever system connecting the tympanum to the auditory capsule is mechanically resonant at a frequency near 800 Hz . Alternatively it is possible that the auditory capsule behaves like a mass load coupled in such a way as to reduce its high-frequency response, while the spiracle vents may constitute a resistive path to the abdominal cavity of such a magnitude as to reduce the low-frequency response. Some auxiliary mechanism such as this seems necessary since

it is not possible, by reasonable variation of the available parameters, to reproduce accurately both the frequency response and directional discrimination of the system.

DISCUSSION

We have examined an acoustic model for sound production and for hearing in *C. saundersii* and shown, in general terms, that it is capable of giving a semi-quantitative account of the measured behaviour. Agreement with experiment is not good in some features. These defects in the treatment can be attributed to uncertainties in some of the physical quantities involved, to oversimplifications in the mechanical models for sub-systems like the tympana, or to effects arising from the neglect of the physical dimensions of some of the elements compared with the wavelength of sound. It also seems probable that some secondary resonant system is interposed between the tympana and the neural transducers in the female cicada, and possibly also in the male, or that the transducers themselves exhibit a response that is sharply peaked near the song frequency of 800 Hz.

Despite these discrepancies, the general agreement between theory and experiment is sufficiently good that the treatment may be accepted as broadly correct. This then allows us to appreciate the acoustical functions of the various anatomical features that have been described, and to see how the magnitudes of the acoustical impedances with which they are associated affect the performance of the whole system.

C. saundersii is an insect unusually well suited for the sort of analysis present above, for its song is low enough in frequency that simple lumped-parameter electrical analogues can be used to elucidate its acoustic behaviour. For many insects with songs of higher frequency such simplifications will no longer be possible, but clues to the function of various system elements can perhaps be found by analogy with the present study.

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