Acoustical analysis of the auditory system of the cricket *Teleogryllus commodus* (Walker)

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The basic auditory physiology of crickets, and particularly of *Teleogryllus commodus* (Walker) is examined and its behavior simulated by electrical analog networks, beginning from the simplest possible model and progressing by stages to the full system found in the real insect. It is found that the attenuation of sound in the auditory trachea plays a crucial role in the mechanism for directional hearing in even the simplest model and that the tracheal diameter is in fact appropriate to produce the desired attenuation. In a more complex model in which it is recognized that the auditory system probably responds to pressure changes in the tracheal sacs underlying the tympana rather than simply to tympanic motion, it is found that the phase shift produced by the combined effects of the central septum and the adjoining cavities leading to the spiracles is also important to hearing directionality. The final model which includes both tympana and spiracles is able to simulate both the hearing directionality and, in part, the frequency selectivity of the system. It appears, however, that a large measure of the observed frequency selectivity is due to some form of selectivity in the neural transducers themselves rather than in the simple acoustic components of the system.

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INTRODUCTION

The auditory anatomy and physiological response to sound in members of the cricket family (Gryllidae) have been the subjects of considerable detailed study particularly in recent years (Zeuner, 1963; Michelsen and Nocke, 1974; Young and Ball, 1974; Dragsten *et al.*, 1974; Nocke, 1975; Hill and Boyan, 1976; 1977; Paton *et al.*, 1977; Ball and Hill, 1978; Michelsen *et al.*, 1978). Among these studies we shall be concerned particularly with those devoted to elucidation of the mechanisms giving rise to directionality of hearing and, within this limited group, especially those relating to the cricket *Teleogryllus commodus* (Walker), though many of our models have a wider application.

Our particular concern will be to set up detailed models for the acoustical system from which can be calculated specific numerical results for frequency response, directional discrimination and other related quantities, provided that the necessary physical parameters of the auditory system are available. In order that our discussion may be of more general use, however, and because many of the physical parameters are not yet known with sufficient reliability, we shall begin by considering extreme idealizations of the auditory system and then progressively add the anatomical complications found in real insects.

Our method of proceeding will be that of electrical analogs which we have used previously in discussion of the auditory and sound producing system of the cicada *Cystosoma saundersii* (Westwood) (Fletcher and Hill, 1978). This cicada represented a particularly simple case, however, since its song frequency (800 Hz) is sufficiently low that the insect dimensions are small compared with the sound wavelength involved. In the crickets the song frequency (~ 4 kHz) is much higher and the insect dimensions are comparable with one-quarter of the sound wavelength, so that a more complex analysis is necessary.

Basic information on the application of electrical analogs to acoustical systems is available in standard texts on acoustics and vibrations (Morse, 1948; Olson, 1957; Skudrzyk, 1968), and we have recently compiled an extensive review of the treatment of bioacoustic systems by this means (Fletcher and Thwaites, 1979).

I. A SIMPLIFIED MODEL

The gross auditory anatomy of *Teleogryllus commodus* (Walker) is shown in Fig. 1. A thin tympanum on each prothoracic leg allows sound entry to a tracheal tube which connects to a spiracle. The tracheae from the two sides of the insect communicate through a thin septum on the midplane of the insect. There are refinements to the anatomy of this system which we shall discuss later.

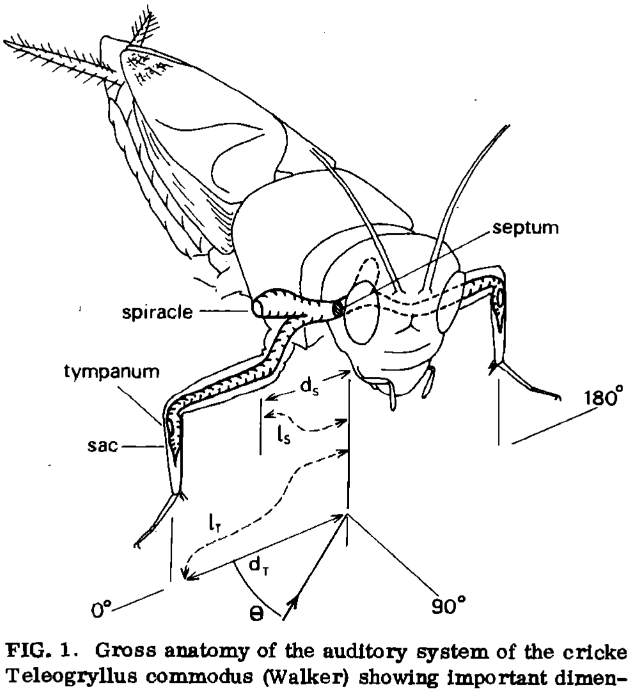

FIG. 1. Gross anatomy of the auditory system of the cricket Teleogryllus commodus (Walker) showing important dimensions. [Modified from Hill and Boyan (1976)].

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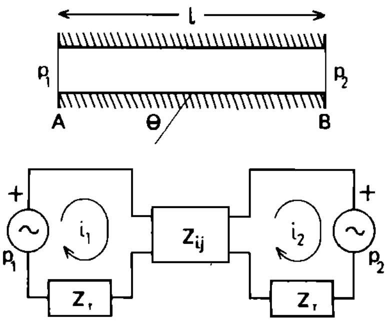

FIG. 2. (a) Grossly simplified model for the auditory system of *T. commodus* in the form of a simple tube closed by two diaphragms. p_1 and p_2 are the external sound pressures for a wave incident at angle θ; (b) Electric analog network for the acoustic system.

Experiments (Hill and Boyan, 1977) show unambiguously that for *T. Commodus* the auditory directionality is not greatly affected by blocking off the spiracles. It therefore seems reasonable to adopt as a first model one which simply neglects the tracheal branches leading to the spiracles. The auditory system then reduces to a simple tube with a tympanum at each end and a septum in the middle. Provided the septum is thin, its effect is small, so that we can further idealize the system to that shown in Fig. 2(a), in which the bends in the trachea have also been neglected.

At this stage we must emphasize that this model is specific to *T. commodus*. In other species the first approximation may be quite different and indeed Nocke (1975); and Michelsen *et al.* (1978), have shown that for the Tettigoniids the spiracles rather than the tympana are of prime importance, while the septum is sufficiently thick largely to isolate the two sides of the auditory system from each other.

In essence, the system of Fig. 2(a) is that discussed by Hill and Boyan (1976, 1977). They observed that in their specimens of *T. commodus* the tube length l is quite closely one-quarter of the sound wavelength λ so that, they argued, for ipsilateral presentation to tympanum $A(\theta = 0°)$, the path length to the inside of A is $2l = \lambda/2$ and thus the inside pressure is out of phase with that outside, giving a maximum amplitude to the motion of the tympanum. For the contralateral ear B, on the other hand, the inside and outside pressures are in phase so that there is no pressure difference across the tympanum and hence no motion.

In order to make the model behave in the required manner it is necessary to introduce both the impedence of the tympana and, even more importantly, the sound attentuation in the narrow trachea. The acoustic behavior of tympana, whether they be membranes under tension or, as is more appropriate in the present case, thin elastic plates, is examined in detail by Morse (1948, pp. 172–216). Although such a system has an infinite series of vibrational modes, the second symmetrical mode for a plate is at about four times the frequency of the fundamental and does not couple efficiently to a plane sound wave. The asymmetric modes are not coupled at all to a plane wave. Thus, we expect the motion of the tympanum to be primarily that of the simple fundamental mode, as is indeed observed (Dragsten *et al*, 1974; Michelsen *et al*, 1978). Failure to observe directly any displacement pattern characteristic of the second mode may be due to the fact that the tympanum is not a uniform circular plate.

For such a tympanum the acoustic impedence z_T has the form appropriate to a simple series-resonant circuit

$$Z_T = R_T + L_T\omega j + 1/C_T\omega j\,, \tag{1}$$

where $j = \sqrt{-1}$, the acoustic inertance L_T is associated with the membrane mass, the compliance C_T with the elastic compliance of the membrane, and the resistance R_T with viscous losses within its material. In (1) ω is the angular frequency ($\omega = 2\pi f$) and we can write the sound pressure in the external acoustic field as

$$p(x,t) = p\exp[j\omega(t - x/c)] \tag{2}$$

for a wave propagating in the x direction, with the normal sound velocity c.

To describe a tracheal tube of length l requires a set of four impedances $Z_{ij}(i,j = 1,2)$ of which only two are independent. This is analogous to the case of an electrical transmission line and allows for waves propagating in both directions. As shown, for example, by Slater [(1942); but note that his equation 4.69 has an error in sign]

$$Z_{11} = Z_{22} = Z_0 \coth\gamma l\,, \tag{3}$$

$$Z_{12} = Z_{21} = -Z_0 \operatorname{csch}\gamma l\,, \tag{4}$$

where Z_0, which is nearly real, is the characteristic impedance of the tube and $\gamma = \alpha + j\beta$ is the complex propagation constant. More explicitly, and to a sufficient approximation,

$$Z_0 \simeq \rho c/A\,, \tag{5}$$

where ρ is the density of air and A is the cross-sectional area of the tube; $\beta = \omega/c'$, where c' is the phase velocity in the tube, which is close to but rather less than the sound velocity c in free air, and α, which is positive, represents the attenuation coefficient due to wall losses in the tube. These matters are treated in detail by Benade (1968).

In the electrical analog circuit of Fig. 2(b); p_1 and p_2 represent the acoustic pressures acting on the outsides of the tympana at A and B, respectively, so that, for a sound incidence angle θ as defined in Figs. 1 and 2(a), we can write

$$p_1 = p\exp j\omega t\,, \tag{6}$$

$$p_2 = p\exp[j\omega(t - l\cos\theta/c)]\,, \tag{7}$$

these pressures being applied in the sense defined by the +signs in the figure. Similarly i_1 and i_2, in the senses shown, represent the acoustic volume flows through the tympana A and B and are thus proportional to the displacement velocities of those tympana.

It is now a simple matter to follow the standard methods of circuit analysis to set up equations for the network of Fig. 2(b). This set of equations is easily solved for either i_1 or i_2, giving

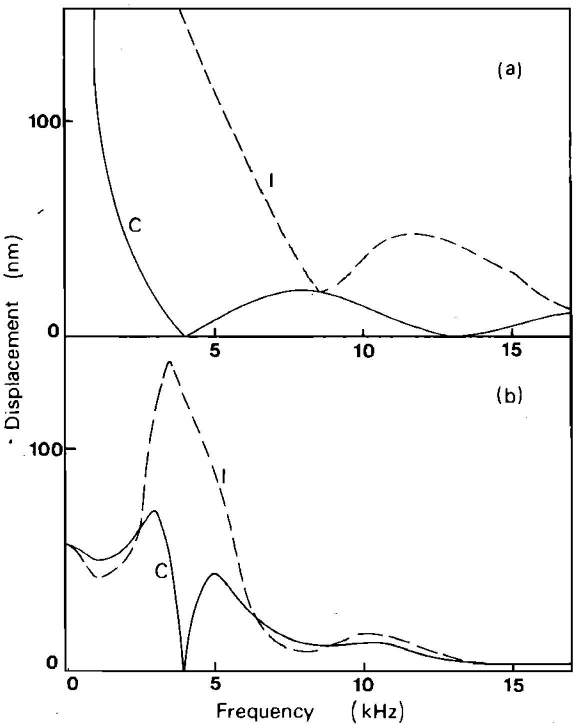

FIG. 3. Calculated response of the tympana in the model of Fig. 2 for the case of (a) tympana of infinitesimal thickness, and (b) tympana of thickness 20 μm. Other parameters are given in Table I.

$$i_1=\frac{p_1(Z_T+Z_{11})+p_2Z_{12}}{(Z_T+Z_{11})^2-Z_{12}^2}\,. \qquad (8)$$

We need not write the equation for i_2 because of the symmetry of the problem.

It is interesting as a first step to examine the behavior of this expression for ipsilateral ($I, \theta=0$) and contralateral ($C, \theta=180°$) stimulation of ear A in the limiting case of very light tympana ($Z_T \ll Z_0$). If the tube is exactly $\lambda/4$ in length at the frequency considered then from (3)–(7) we find for the vibration amplitude x_T of the tympanum

$$x_T=i_1/A_T\omega=(p/Z_0A_T\omega)\,\mathrm{sech}\,\alpha l(\sinh\alpha l\pm1)\,, \qquad (9)$$

where the +sign applies to ipsilateral and the −sign to contralateral stimulation. Clearly, to achieve zero response in the contralateral ear we require an attenuation coefficient α such that $\sinh\alpha l=1$. Since $l\simeq20$ mm for this species, this means that $\alpha\simeq40\ \mathrm{m}^{-1}$ for the tracheal tube, which is consistent with a tube of radius $a\simeq50\ \mu$m if the tube walls are ideally smooth and stiff or with a tube radius of perhaps twice this value for more realistic wall conditions (Benade, 1968; Kinsler and Frey, 1962, p. 241). This is quite close to the average anatomical value found by Young and Ball (1974).

The response characteristic predicted from (9) with $Z_T \ll Z_0$ is shown in Fig. 3(a) with other parameters as in Table I. Clearly the model is unsatisfactory in relation to frequency response and this is obviously attributable to omission of the resonant behavior of the tympanum. In fact, since the tympanic membrane is typically 20–30 μm in thickness, and the Q value for biological tissue is unlikely to exceed about 10, Z_T is comparable to Z_0 at the tympanum resonance frequency $f_T=\omega_T/2\pi$ and exceeds Z_0 increasingly at frequencies above or below f_T. The motion of the ipsilateral tympanum thus closely follows the resonance curve of the tympanum itself, and it would be surprising if the peak response were not close to the song frequency so that $f_T\simeq4000$ Hz. This is closely the behavior measured by Paton *et al.* (1977).

If we assume this resonance frequency and the other physical dimensions given in Table I, then we find that the value of the tracheal attenuation coefficient α necessary to achieve a contralateral null response varies between about 35–15 for values of the quality factor Q_T ranging from 10–3. These possibilities are all anatomically reasonable and we might presume that evolutionary processes would have developed an optimal combination. The calculated response curves for ipsilateral and contralateral stimulation are now as shown in Fig. 3(b). The results are in very encouraging agreement with both the measured tympanic displacement response found by Paton *et al.* (1977) or by Michelsen *et al.* (1978), though actual amplitudes are larger by about a factor three, and with the neural response curves of Hill and Boyan (1977), though the neural response is much more sharply tuned than is the tympanic motion.

TABLE I. Assumed parameters for calculation with the simplified model. (For ease of calculation the frequency variation of Z_0, α, and c' has been ignored.)

Length of trachea	$l=20$ mm
Characteristic impedance (real)	$Z_0=120\ a^{-2}\ \mathrm{Pa\,m^{-3}s}$
Sound velocity in trachea	$c'=c=340\ \mathrm{ms^{-1}}$
Density of tympanum material	$\rho_T=1000\ \mathrm{kg\,m^{-3}}$
Resonance frequency of tympanum	$\omega_T/2\pi=4000$ Hz
Sound pressure amplitude (SPL≈91 dB)	$p=1$ Pa
Q factor of tympanum resonance	$Q_T=5$
First case:	
Tympanum thickness	$h_T=0$
Attenuation coefficient	$\alpha=44\ \mathrm{m}^{-1}$
Second case:	
Tympanum thickness	$h_T=20\ \mu$m
Attenuation coefficient	$\alpha=28\ \mathrm{m}^{-1}$

Apart from selecting an appropriate combination of α and Q_T values, our model is relatively insensitive to the other physical quantities.

The directional response pattern predicted by (8) has also been calculated at various frequencies, though we shall not bother to plot it here. The response has a cardioid pattern at frequencies close to 4000 Hz, and becomes more nearly nondirectional at lower and higher frequencies.

II. AN EXTENDED MODEL

In our simplified model we have tacitly assumed that motion of the tympanum is the important thing and that this motion is somehow converted into nerve impulses. However, a study of the anatomy of the auditory system (Young and Ball, 1974) shows no direct connection between the tympanum and the neural transducers. On the contrary, these are connected to a complex double-tube sac lying immediately under the main tympanum in the leg. It seems more likely, indeed, that these neural transducers respond not to tympanic motion, but rather to distortions induced by changes of pressure in this sac.

With this possibility in mind we can extend our physical model of the auditory system by including air sacs as shown in Fig. 4(a). These sacs may be assigned an effective volume V_T which is equal to the actual volume if the sac walls are rigid, but is rather larger than the actual volume if the walls are somewhat compliant as, of course, they are in the real situation. Such air-filled cavities act as acoustic compliances, given by $C_T = V_T/\rho c^2$, where ρ is the density of air. The cavities therefore present a shunt impedance

$$Z_C = 1/C_T\omega j\,, \tag{10}$$

at frequency ω and, by adding stiffness, effectively raise the resonance frequency of the tympanic system above its bare value ω_T.

We can now construct the electrical analog network for the auditory system as shown in Fig. 4(b). Solution of the network is quite straight forward, but we shall not trouble to write this down since it turns out that it is not possible to achieve a null in the sac pressure for contralateral stimulation. The system can, in fact, be made satisfactorily directional but the null in sac pressure occurs for ipsilateral stimulation, which is clearly not the situation revealed by neurophysiological response measurements.

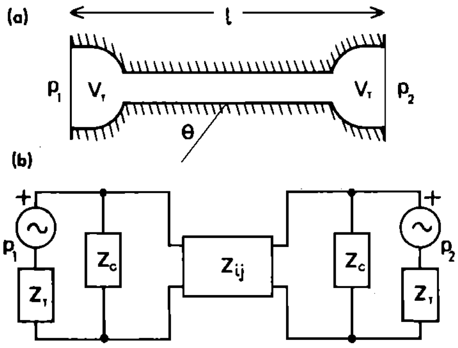

FIG. 4. (a) Simplified model including the tympanic air sacs of volume V_T; (b) Electric analog network for the acoustic system.

It is easy to see, from Fig. 4, how this comes about. For the contralateral ear, independently of tube length and of any phase delays in the tympana, the total phase delay to the tympanic sac is very nearly the same for the external path and for the path through the trachea so that pressure amplitude is maximal. For the ipsilateral ear the phase delay in the path through the contralateral ear and trachea is about $2\omega l/c$ greater than that through the ipsilateral tympanum so that cancellation can occur if $l \approx \lambda/4$ and the attenuation factor α has an appropriate value.

To achieve a pressure null in the contralateral tympanic sac we must somehow introduce an extra phase delay of π for propagation through the trachea. This can be achieved by either convoluting the trachea so as to increase its effective length by $\lambda/2$, or by introducing a phase-shifting element at some place in the tracheal path in the form of a cavity (compliance) in association with a membrane or narrow opening to provide either a resistance or an inertance.

In *T. commodus* a combination of these two mechanisms seems to be involved. The length of the main trachea connecting the ears is rather greater than the external distance between them and, if we assume the spiracles to be effectively closed by their cuticular covers for much of the time (Paton *et al.*, 1977), the cavities created by the short broad tracheae leading to the spiracles together with the central septum would seem capable of constituting an appropriate phase-shifting network.

A simplified physical model for this phase-shifting network is shown in Fig. 5 together with its electrical network analog. The behavior of such filter networks is described in standard works on electrical circuit theory (for example, Harnwell, 1938). To be properly matched to the rest of the system, it is desirable that the characteristic impedance Z_0' of the filter, given by

$$Z_0' = Z_P[Z_S/(2Z_P + Z_S)]^{1/2}\,, \tag{11}$$

where $Z_P = 1/C_{SP}\omega j$, should be equal to that of the tracheal tube, because then there is no unwanted reflection from the junction. If this is approximately satisfied then the performance of the filter at a given fre-

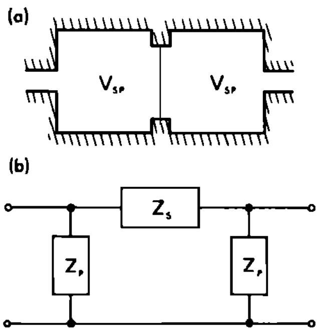

FIG. 5. (a) Acoustic filter consisting of two cavities divided by a thin septum; (b) Electric analog filter network.

quency ω is well defined.

For $\omega_S < \omega < \omega^*$, where ω_S is the septum resonance frequency and ω^* is the frequency at which $Z_S/Z_P = -2$, this being the cutoff frequency, then the filter is of the low-pass type operating in the regime where there is no attenuation and where the phase shift across the filter increases towards π at $\omega = \omega^*$. To meet the conditions of our model we therefore expect $\omega \lesssim \omega^*$ in order to introduce the necessary phase shift without excessive attenuation.

The real system with spiracles closed probably approximates these conditions fairly well if the septum is an untensioned membrane. Mismatch between Z_0 and Z_0' would introduce reflections which would degrade system performance but the effect of a finite R_S value in Z_S would be only minor. The physical dimensions of the cavities and septum are of at least roughly the correct order of magnitude to satisfy these conditions on Z_0' and ω^* but we cannot be more precise at the present time.

III. THE COMPLETE AUDITORY SYSTEM

After this preliminary discussion we are now in a position to attempt analysis of the complete auditory system of *T. commodus*. A diagram of the system, only slightly idealized, is shown in Fig. 6(a) and below it in 6(b) the electrical analog network. In the central phase-shifting network of Fig. 5(b) the two simple capacitances Z_P have been replaced by short lengths of rather wide transmission line Z_{ij}' and we have allowed for the entry of sound through the spiracles which have impedance

$$Z_{SP} \simeq L_{SP}\omega j\,, \tag{12}$$

determined by the size and geometry of the spiracle opening. The difference between the length $2l_T$ of the trachea joining the tympana and their geometrical separation $2d_T$ is recognized and other dimensions are as shown in the figure.

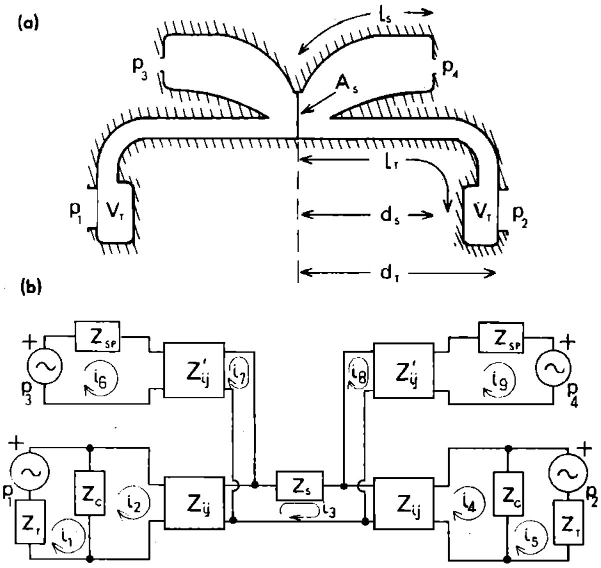

FIG. 6. (a) Complete acoustic system showing important dimensions. (b) Electric analog network.

If we neglect pressure and phase changes caused by diffraction effects around the insect body, which is probably legitimate to a sufficient approximation (Hill and Boyan, 1977), then, for sound incident at angle θ as shown, we can write

$$p_1 = p\exp(j\omega t)\,, \tag{13}$$

$$p_2 = p\exp[j\omega(t - 2d_T\cos\theta/c)]\,, \tag{14}$$

$$p_3 = p\exp\{j\omega[t - (d_T - d_S)\cos\theta/c]\}\,, \tag{15}$$

$$p_4 = p\exp\{j\omega[t - (d_T + d_S)\cos\theta/c]\}\,, \tag{16}$$

and the equations for the electrical network of Fig. 6(b) can be written

$$\begin{bmatrix} (Z_c+Z_T) & -Z_C & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -Z_C & (Z_C+Z_{11}) & Z_{12} & 0 & 0 & 0 & -Z_{12} & 0 & 0 \\ 0 & Z_{12} & (Z_S+Z_{11}) & Z_{12} & 0 & 0 & -Z_{11} & -Z_{11} & 0 \\ 0 & 0 & Z_{12} & (Z_C+Z_{11}) & -Z_C & 0 & 0 & -Z_{12} & 0 \\ 0 & 0 & 0 & -Z_C & (Z_C+Z_T) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & (Z_{11}'+Z_{SP}) & Z_{12}' & 0 & 0 \\ 0 & -Z_{12} & -Z_{11} & 0 & 0 & Z_{12}' & (Z_{11}'+Z_{11}) & 0 & 0 \\ 0 & 0 & -Z_{11} & -Z_{12} & 0 & 0 & 0 & (Z_{11}'+Z_{11}) & Z_{12}' \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & Z_{12} & (Z_{11}'+Z_{SP}) \end{bmatrix} \begin{bmatrix} i_1 & & p_1 \\ i_2 & & 0 \\ i_3 & & 0 \\ i_4 & = & 0 \\ i_5 & & -p_2 \\ i_6 & & p_3 \\ i_7 & & 0 \\ i_8 & & 0 \\ i_9 & & -p_4 \end{bmatrix}. \tag{17}$$

This set of equations can be solved to give the pressure in the tympanic sac of ear A as

$$P_T = Z_C(i_1 - i_2)\,, \tag{18}$$

while the mean displacement amplitude of the tympanum in the same ear is

$$x_T = i_1/\omega A_T\,, \tag{19}$$

where A_T is the area of the tympanum. Algebraic solution of the Eqs. (17) is possible but, since numerical values are required in any case, it is simpler to perform the solution on a desk-top computer using one of the standard algorithms.

TABLE II. Assumed physical dimensions for full auditory model calculation. Refer to Figs. 1 and 6.

Half-separation between tympana	$d_T = 8$ mm
Half-separation between spiracles	$d_S = 3$ mm
Half-length of tympanic trachea	$l_T = 10$ mm
Half-length of spiracular trachea	$l_S = 4$ mm
Radius of tympanic trachea	$a_T = 120$ μm
Radius of spiracular trachea	$a_S = 120$ μm
Area of tympanum	$A_T = 0.07$ mm^2
Thickness of tympanum	$h_T = 30$ μm
Volume of tympanic sac	$V_T = 0.05$ mm^2
Resonance frequency of tympanum	$\omega_T/2\pi = 2000$ Hz
Q value of tympanic resonance	$Q_T = 5$
Effective area of open spiracle	$A_{SP} = 0.01$ mm^2
Resistance of open spiracle	$R_{SP} = 1.3 \times 10^8$ kg m^{-4}s
Area of septum	$A_S = 0.2$ mm^2
Thickness of septum	$h_S = 10$ μm
Resonance frequency of septum	$\omega_S/2\pi \approx 0$ Hz
Density of biological material	$\rho_T = 10^3$ kg m^{-3}
Sound pressure amplitude (SPL ≈ 91 dB)	$p = 1$ Pa

The internal tracheal dimensions in *T. commodus* are not well known because the tracheae tend to collapse during sectioning. In addition, the tracheae are not really simple cylindrical tubes but change somewhat in radius along their lengths. For these reasons a certain amount of optimization is permissible in the calculation, the final values used being shown in Table II. All are within the limits expected for typical specimens of *T. commodus*. The resonance frequency of the bare tympanum is necessarily below the song frequency because of the stiffening effect of the air in the tympanic sac.

In Fig. 7 are plotted the displacement responses of the ipsilateral I and contralateral C tympana together with the pressure amplitudes in the ipsilateral and contralateral tympanic sacs, as calculated for an intact specimen.

The tympanic displacement response has a simple resonant maximum near the song frequency, as observed by Dragsten *et al.* (1974) but the response of the contralateral tympanum is actually somewhat greater than that of the ipsilateral tympanum. The directionality near the song frequency is about 6 dB. The calculated amplitudes are again somewhat larger than those measured on a different species.

The pressure response in the tympanic sac, on the other hand, shows strong directionality, amounting to rather more than 10 dB just above the song frequency, and an ipsilateral response that is sharply peaked near the song frequency. The peak ipsilateral sac pressure is about three times the external sound pressure, though the precise value of this excess depends to some extent on the assumed tympanic Q value. The variation of pressure response with sound incidence angle between the ipsilateral and contralateral extremes is roughly cardioid in shape, near the song frequency as shown in Fig. 8.

Finally in Fig. 9 we show the calculated response with the spiracle openings occluded. Both response amplitude and directionality have deteriorated somewhat from their initial values, but the auditory system still functions in at least qualitative agreement with experiment.

It should be emphasized that most of the dimensions of the model are not critical to the final acoustic response behavior provided that a change in any one parameter is accompanied by an appropriate compensating change in some other parameter. Such stability would seem to be necessary from a biological viewpoint in order that small variations in size between different

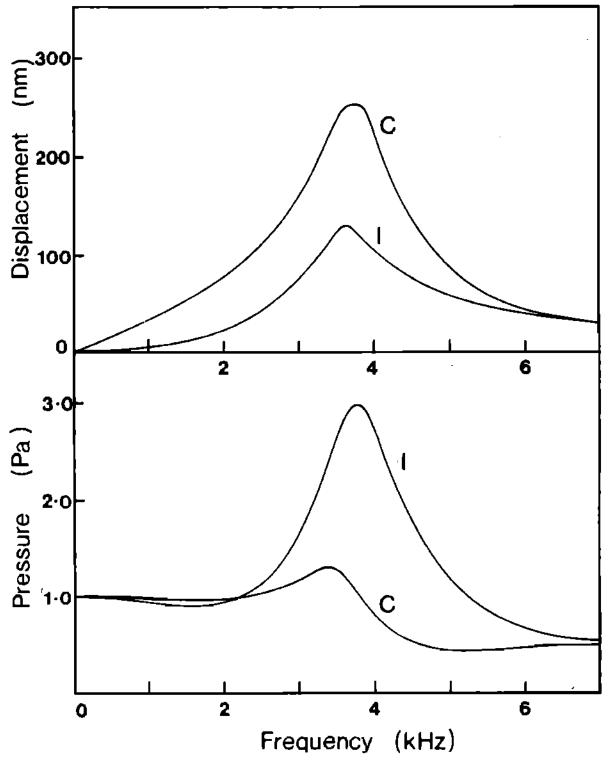

FIG. 7. Tympanum displacement and tympanic sac pressure response for ipsilateral (I) and contralateral (C) stimulation of the complete auditory system of Fig. 6. System parameters are given in Table II.

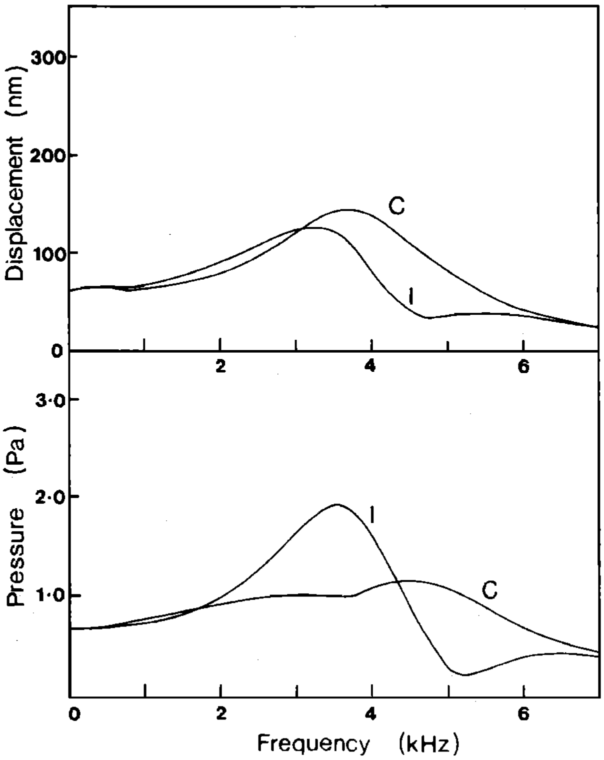

FIG. 8. Tympanum displacement and tympanic sac pressure response for ipsilateral (I) and contralateral (C) stimulation of the auditory system of Fig. 6 with spiracles blocked.

members of the same community should not be critical to auditory behavior.

Inspection of the pressure curves of Fig. 7, or indeed of any of the curves for simpler approximations, shows that in no case is the ipsilateral acoustical response tuned nearly as sharply to the song frequency as is the observed neural response. Indeed an examination of the tube sizes and coupling coefficients involved suggests that the observed slopes of about 30 dB/octave on either side of the peak (Hill and Boyan, 1976) are simply not attainable for any physically reasonable combinations of acoustic parameters. We conclude, therefore, that there must be a secondary frequency discrimination mechanism, probably either associated with the electromechanical properties of the neural transducers or else occurring at a higher neural level. Such a secondary mechanism would preserve the calculated difference in response between ipsilateral and contralateral stimulation, which is already in good agreement with experiment both in magnitude and in that maximum directionality occurs at a frequency slightly above the response maximum.

IV. CONCLUSIONS

This study was carried out with two major aims in view. The first and clearly overt aim was to understand the auditory system of the cricket *Teleogryllus commodus* (Walker), on which a great deal of careful experimental work has been done, in as detailed a manner as possible. Our model for the auditory system reproduces most of the observed physiological responses in at least reasonable semiquantitative agreement with experimental measurements. We cannot, however, be too dogmatic about details of the model since many of the physical parameters are as yet rather poorly defined and we have had to assume plausible values adjusted within the range allowed by anatomical data to give the best possible agreement with experiment. The models discussed above can be specialized in various alternative ways to serve as a background for examination of other insect auditory systems. For example, if the spiracle impedance is taken to be very small and the septum impedance rather large, the model approximates the auditory system of the Tettigoniids (Zeuner, 1936; Nocke, 1975; Michelsen *et al.*, 1978).

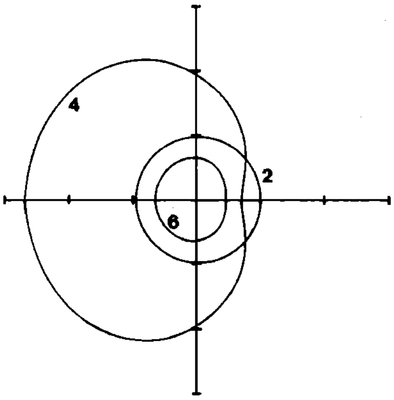

FIG. 9. Directional response of the tympanic sac pressure at three frequencies, shown in kHz as a parameter.

The other important purpose for which these analyses can be used is in the planning of physiological experiments. If the immobilization or excision of particular elements of the system is involved then the relevant impedance, Z is set to infinity or zero, respectively. If sound pressure is applied to only some of the ports of the system, then the other p_i are set equal to zero. Analysis of the results of a variety of such experiments followed by comparison with the predictions of the model allows determination of many of its parameters. In principle, such a comparison should be possible with work such as that of Michelsen *et al.* (1978, Pt. III) on *Gryllus campestris L.*, but we have not attempted this here, this set of papers not having appeared at the time the present work was done.

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