Physical models for the analysis of acoustical systems in biology

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1. INTRODUCTION

One of the important problems of biophysics is to understand in detail the mechanisms by which animals produce acoustic signals, and the ways in which other animals, of the same or different species, detect and process these signals, through the masking effects of ambient noise, to extract their information content. At a primitive level this information relates simply to the presence of the other animal and perhaps to its proximity and direction. At the next level we find some sort of coding in the acoustic signal which identifies the species and perhaps the sex, and finally there is the whole range of information content and emotional overtone contained in a complex sound like human speech or music.

The auditory chain involved in this process has at least three links of which we shall discuss here only the first – the acoustical and mechanical processes by which the various components of the auditory system are made to vibrate under the influence of an external acoustic pressure signal, and the characteristics of their response to that signal. The next link is at the level of neurobiology, and concerns the manner in which these mechanical vibrations are transduced into nerve impulses, and the way these impulses are combined into a more refined set of signals to be presented to the animal's brain. The third link, which is generally called psychophysics, deals with the way in which the brain itself processes these signals and relates them back to the original acoustic stimulus.

The primary acoustical–mechanical link in this chain is in every way the easiest to deal with. Its analysis is founded on the well-understood principles of classical physics, and straightforward mathematical techniques can be used to predict behaviour in a precise quantitative manner. More than this, all the auditory systems with which we deal are, at this level, linear, by which remark we imply that the mechanical response to two acoustic stimuli applied simultaneously is simply the sum of the responses when each stimulus is applied separately. All these remarks,

as we shall see later, are only approximately true, but the approximation is sufficiently good to serve as a starting point which can later be refined.

In contrast, the neurobiological link rests upon biochemical and biophysical principles which are by no means fully understood. The response of individual neurons is stochastic and the firing rate is not simply proportional to the applied stimulus, so that the system is quite non-linear. In addition there may be correlatory or inhibitory features in the neural network which further complicate its behaviour.

The psychophysical domain is even further removed from detailed understanding, and even the principles upon which the human brain works are in many ways still only guessed at, despite the progress that has been made.

The sound-producing chain is in many ways similar to the auditory chain considered in reverse, but with one important difference. The final link in the chain, which is now the mechanical–acoustical sound production apparatus, can no longer be treated as though it is strictly linear. Some of its components, to be sure, do behave in a nearly linear manner, but there is always at least one highly non-linear element whose behaviour is responsible, in large measure, for the general behaviour of the system in terms of sound output and harmonic structure.

Our purpose in the present review will be to examine, in a general way, the mechanical and acoustical behaviour of auditory and sound-producing systems of rather simple types. The methods used are by no means novel and the physical principles have been understood in detail since they were first studied systematically by Lord Rayleigh more than 100 years ago. Even the method of electrical network analogies has been familiar in other branches of acoustics and vibration theory for 50 years. What does seem to be unfamiliar to most biophysicists is the application of these methods in quantitative detail to the study of the acoustic systems of insects and simple animals, most discussions so far having been qualitative (Michelsen & Nocke, 1974).

The methods are indeed powerful and, once initial difficulties of comprehension have been overcome, remarkably simple to apply. With this in mind, the present article is frankly tutorial in nature; our objective is to show what can be done rather than to describe what has been done already.

2. SOUND WAVES

Sound is a propagating pressure disturbance in a compressible medium and we shall confine the present discussion to sound in air, the problems of sound propagation and detection in water being similar in nature but quantitatively very different because of the similarity in density between water and biological material.

For a general sound wave, the pressure p at a given point is some complicated function $p(t)$ of the time. We know, however, that we can represent any function $p(t)$ by the sum of an infinite number of sinusoidal functions of the form $a \cos (2\pi ft + \phi)$ of all possible frequencies f. We have already said that the auditory systems with which we shall deal are very nearly linear, unless the pressure amplitude is too large, so that we are led to examine the behaviour of such a system under the action of a single pressure component of frequency f. In fact the usual experimental situation is one in which the sound propagates as a single plane wave, either in the free air or in an anechoic chamber, so that the sound pressure $p(x, t)$ at position x and time t can be written

$$p(x, t) = p_0 \cos [2\pi f(t - x/c)], \tag{1}$$

where p_0 is the pressure amplitude and c is the velocity of sound in air (about 344 m s^{-1} under ordinary conditions).

For our later analysis it is convenient to make two changes to this representation. The first is to introduce the angular frequency ω defined by $\omega = 2\pi f$ and measured in radians per second rather than hertz. The second is to introduce complex notation in terms of $j = \sqrt{-1}$ and to write

$$p(x, t) = p_0 \exp [j\omega(t - x/c)] \tag{2}$$

with the interpretation that, though we retain both real and imaginary parts throughout all our manipulations, we ultimately take the real parts of all the physical quantities to present their actual values. This use of the complex exponential function, common in physics and electrical engineering, avoids the introduction of sine terms similar to (1) or the use of complicating phase terms. [See, for example, Morse (1948, pp. 1–17), but note that he uses $i = -j$ so that quantities vary as $e^{-i\omega t}$ rather than as $e^{j\omega t}$.]

In all the subsequent discussion we shall use S.I. units so that pressures are measured in pascals (1 Pa = 1 N m^{-2} = 10 dyn cm^{-2}). When sound

pressure levels are referred to, they are measured in decibels relative to the nominal threshold of human hearing, 20 μPa (r.m.s.). Because our system is linear, we shall normally calculate its response for a pressure amplitude of 1 Pa, which corresponds to a sound pressure level of 91 dB.

3. ELECTRICAL ANALOGIES

Although the anatomy of a typical auditory system is complex, it is not hard to see that it can usually be represented fairly well by a similar system with the irregularities smoothed out. Indeed, if the smoothing process has not been too grossly carried out we should expect the acoustical behaviour of the idealized model to approximate quite closely that of the original system. Such a model system will generally consist of a combination of recognizable elements of which the most important are the air-filled cavity, the uniform tube, the tapered tube or horn and the flexible diaphragm. In most auditory systems the neural transducer (which is where our present analysis stops) is connected to some form of flexible diaphragm, either directly or through a system of levers. If, then, we can understand the behaviour of these acoustical and mechanical elements, we might reasonably hope to understand the system as a whole.

The physical and mathematical background for this understanding was laid by Rayleigh (1896) and is well documented in standard modern texts (e.g. Morse, 1948; Kinsler & Frey, 1962; Morse & Ingard, 1968). Fortunately for our present purposes little of this detail is required and we can treat most of the system elements in a quite elementary way. Much more important is the interaction between them.

To treat this interaction in a general way we shall make use of the method of electrical network analogies and, since this is perhaps not generally familiar, we first set it out in some detail. The references listed above give an outline of the procedures, and particularly good accounts are given by Olson (1957) and, for the mechanical rather than the acoustical case, by Skudrzyk (1968).

Classical mechanics gives a complete description of the behaviour of bodies at ordinary speeds. For example, if a body of mass m is acted on by a force F then

$$F = ma = m \, du/dt, \tag{3}$$

where a is the acceleration and u the velocity of the particle. Similarly if the force F acts on the end of a spring of modulus k, the displacement x is given by

$$F = kx = k \int u \, dt, \tag{4}$$

where we have also written x as the integral of the velocity. Finally if the force F acts on a viscous liquid flowing through a narrow tube or on a body being pulled through such a viscous liquid, then

$$F = ru, \tag{5}$$

where r is the viscous resistance.

If one is familiar with electrical circuits, then these equations immediately suggest an analogy which turns out to be fruitful. Suppose we take electrical potential difference E to be the analog of mechanical force F, and electrical current I to be the analog of velocity u. Then (3) is immediately seen to be the analog of the equation

$$E = L \, dI/dt, \tag{6}$$

where an inductance L appears as the analog of the mass m. Similarly the analog of (4) is

$$E = C^{-1} \int I \, dt, \tag{7}$$

where the electrical capacitance C is the analog of the compliance k^{-1} of the spring, and the spring displacement x has as its analog the charge on the capacitor. Finally (5) is nothing more than the simple Ohm's law equation

$$E = RI. \tag{8}$$

These analogies are indicated in Fig. 1.

When we consider acoustical systems, force and velocity are no longer the most convenient quantities to use for the description. Rather, we should like to employ pressure p and volume flow U. These are related to force and velocity simply through the area S involved, so that

$$p = F/S, \quad U = uS. \tag{9}$$

If we take p and U as the acoustical analogs of the electrical voltage and current respectively, then the other analogs can be easily worked out when we have seen to what acoustical elements they apply.
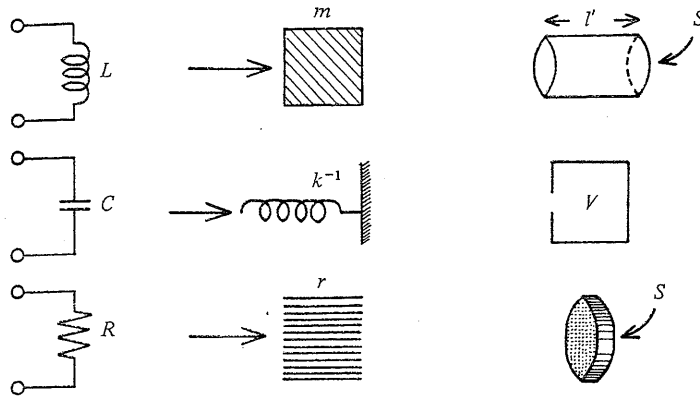
Fig. 1. Electrical, mechanical and acoustical analogs.

A free piston of mass m and area S sliding smoothly in a short cylinder is the acoustical analog of inductance and we see immediately that

$$L \leftrightarrow m/S^2. \tag{10}$$

Indeed, even in the absence of a rigid piston, the air in the pipe (together with that involved in the 'end correction' at either end) acts as a mass-like load with

$$L = \rho l'/S, \tag{11}$$

where ρ is the density of air and l', the effective length of the pipe, is given in terms of its geometrical length l by

$$l' \approx l+0\cdot 8S^{\frac{1}{2}}, \tag{12}$$

When L is an acoustical analog, as here, it is often referred to as an inertance.

The acoustic analog of a spring is a cavity full of air. The acoustic compliance of the air in the cavity is, from the analogous relation (7), simply the flow into the cavity for a small change in external pressure and, since the bulk modulus of a gas has the value ρc^2, where ρ is its density and c is the velocity of sound, we find

$$C = V/\rho c^2, \tag{13}$$

where V is the volume of the cavity.

Acoustic resistance is often provided by a structure such as a fine mesh cloth. For a given pressure difference across the cloth, the volume

flow is proportional to area S, so that in this case the acoustic resistance R varies as S^{-1}.

These acoustical elements are also shown in Fig. 1 along with their electrical analogs. Note that the electrical analogs are all 'two-terminal devices', which are the simplest kind possible. We shall see later that certain more complex situations, particularly at high frequencies, require the use of four-terminal analogs but, before adding this complication, we shall see what can be done with the apparatus we have assembled thus far.

4. NETWORK ANALYSIS

In the sort of acoustical system with which we shall deal we are presented with one or more acoustic pressure inputs to the system and we want then to calculate the acoustical flows and mechanical motions in various elements of the system. This leads naturally to the concept of impedance as the quotient of these two quantities. Using our acoustical notation in which p is the analog of electrical potential and U the analog of electrical current, we define the acoustic impedance Z between a particular pair of input terminals by the relation

$$Z = p/U, \tag{14}$$

where, since the behaviour of the system generally depends on frequency, p and U are small quantities with a particular frequency ω. Since, from (2) for a fixed x, p has a complex form like $p_0 \exp [j\omega(t - \phi)]$, where ϕ is a constant, Z will generally be a complex quantity. In fact we see immediately from the analog equations (6)–(8) that for the case where the two terminals are those of a simple inertance L, compliance C or resistance R, the impedance Z at frequency ω has the values

$$Z \rightarrow L\omega j, \quad 1/C\omega j, \quad R \tag{15}$$

respectively, as we recall from elementary circuit theory. As in electrical theory, impedances in series can simply be added together.

Also of use for some of our calculations will be the admittance Y, which is simply the reciprocal of the impedance Z,

$$Y = Z^{-1}. \tag{16}$$

Again, as in elementary theory, admittances in parallel can be simply added together.
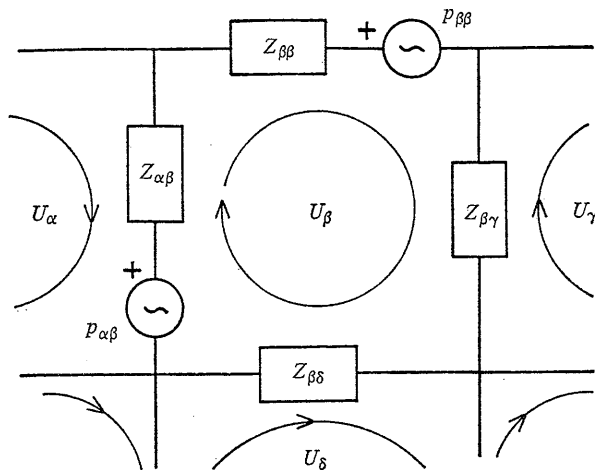
Fig. 2 Section of a general electrical network consisting of impedances $Z_{\alpha\beta}$ and generators $p_{\alpha\beta}$ having the polarities indicated. Mesh currents U_{α}, U_{β}, ... have been drawn so that at least one current passes through each branch of the circuit.

These notions of impedance and admittance apply equally, of course, to electrical, mechanical and acoustical elements and circuits and indeed we can often define both a mechanical and an acoustical impedance for the same physical structure. The units for the different analogs are, however, entirely incompatible and we must be careful not to mix them in the one calculation unless we know exactly what we are doing.

We shall see in the next section how we go about constructing an electrical analog network for a given acoustical system. Here we examine the formalities of solving such a network to find the currents (acoustic flows) in all its branches so that this technique is available to us when it is required.

Fig. 2 shows part of a general network involving a number of impedances $Z_{\alpha\beta}$ and a number of externally applied acoustic pressures $p_{\alpha\beta}$. There is nothing special about the geometry, but each of the pressure generators is labelled with a + to show in which direction its pressure is applied. We draw a current loop U_{α}, U_{β}, ...in each mesh of the circuit and, for convenience, take these all to flow clockwise unless the topology of the network makes this impossible. The impedances common to two meshes are given appropriate subscripts. In drawing the currents the exact paths are not important as along as at least one

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current flows in every link of the network and we have used the minimum possible number of current loops.

Now concentrate on one mesh of the circuit, say that defined by the current U_β. We write down the product of each impedance with the current flowing through it and set this equal to the algebraic sum of the pressure generators in the mesh. For the particular case illustrated in Fig. 2 we have

$$Z_{\alpha\beta}(U_\beta - U_\alpha) + Z_{\beta\beta}U_\beta + Z_{\beta\gamma}(U_\beta - U_\gamma) + Z_{\beta\delta}(U_\beta - U_\delta) = p_{\alpha\beta} - p_{\beta\beta} \quad (17)$$

or, rearranging the terms,

$$-Z_{\alpha\beta}U_\alpha + (Z_{\alpha\beta} + Z_{\beta\beta} + Z_{\beta\gamma} + Z_{\beta\delta})\, U_\beta - Z_{\beta\gamma}U_\gamma - Z_{\beta\delta}U_\delta = p_{\alpha\beta} - p_{\beta\beta}. \quad (18)$$

We derive one of these equations for each mesh of the circuit and they have the general form

$$\left. \begin{aligned} Z_{11}U_1 + Z_{12}U_2 + \ldots + Z_{1n}U_n &= p_1, \\ Z_{21}U_1 + Z_{22}U_2 + \ldots + Z_{2n}U_n &= p_2, \\ \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot & \\ Z_{n1}U_1 + Z_{n2}U_2 + \ldots + Z_{nn}U_n &= p_n, \end{aligned} \right\} \quad (19)$$

where Z_{ii} is the total impedance in mesh i, Z_{ij} is the impedance linking it to mesh j (with appropriate sign) and p_i is the net driving pressure in mesh i.

A formal solution to these equations that is useful for small meshes can be obtained in the form

$$U_i = \Delta_i / \Delta, \quad (20)$$

where Δ is the determinant of the matrix Z_{ij} and Δ_i is the determinant of the matrix obtained by replacing the ith column by the column vector p_j from the right-hand side. The physical implication of this set of equations is most easily seen by omitting the common factor exp $(j\omega t)$ from all the p_j and U_j in (19) and then considering simply the amplitude and phase of the complex quantity U_i given by (20).

Although in physically interesting cases many of the Z_{ij} in (19) are zero so that the matrix is rather sparse, it is often advisable to use numerical methods to solve the equation set (19) rather than simply evaluating the formal solution (20). Most desk-top computers have

programs available to perform this task for the relatively small number of equations (rarely more than 10 × 10) encountered in the analysis of typical biological systems.

Knowledge of the acoustic currents U_i, either from (20) or from a numerical solution using a computer, tells us all we need to know about the system, for from them we can deduce directly the amplitudes and phases of the motion of its mechanical parts together with the pressures in all of its cavities. The main part of this exposition will show how this is done.

5. LOW-FREQUENCY AUDITORY SYSTEMS

The simplest auditory systems to analyse are those in which all the system dimensions are less than about one tenth of the sound wavelength considered, for in such cases simple two-terminal electrical analogs suffice to a good degree of approximation. In this section, therefore, we examine the behaviour of several typical systems in this approximation, with the dual aims of seeing how the analog networks are constructed and analyzed, and of understanding several biologically important cases. The techniques, and indeed the systems themselves, are all closely similar to those employed in various types of microphones (Olson, 1957, pp. 246–339), a circumstance which should perhaps not surprise us.

(a) The diaphragm

An important element of most auditory systems is a tympanum or diaphragm blocking off one of the tubes or cavities, and it is very often the motion of this diaphragm which is conveyed to the neural transduction mechanism. We therefore consider first the behaviour of such a diaphragm, set in an infinite baffle as in Fig. 3(a), when one of its surfaces is exposed to an acoustic pressure field of amplitude p and angular frequency ω. The diaphragm then vibrates backwards and forwards about its flat position as a smoothly bell-shaped surface whose form is related to the zeroth-order Bessel function.

The diaphragm has both mass and stiffness and resists motion under the applied pressure for both these reasons. In addition all materials, and biological materials in particular, have internal losses which are often of viscous type and which become apparent when they are strained elastically. The total acoustic impedance Z of the diaphragm thus has
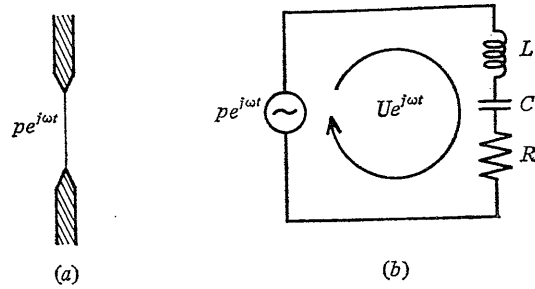
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Fig. 3. (a) The mechanical configuration and (b) the analog electrical network representation for a flexible diaphragm surrounded by a baffle and acted upon by an acoustic pressure on one side. In the analog circuit, L, represents the diaphragm mass, C, its elastic compliance and R viscous losses within its material.

an inertance L, a compliance C and a resistance R in series as shown in the analog circuit of Fig. 3(b), and, from (15)

$$Z = L\omega j + (1/C\omega j) + R. \qquad (21)$$

If the area of the diaphragm is S, its thickness d and the density of its material ρ_B, then, because the diaphragm flexes rather than moving as a rigid piston, the result (10) is modified by a factor closely equal to 4/3 (Morse, 1948, p. 202) so that

$$L \approx 4\rho_B d/3S. \qquad (22)$$

The effective compliance C of the diaphragm depends on its stiffness and the tension under which it is held, and R similarly depends on these parameters and upon the material of the diaphragm. Although both C and R could be determined from a sufficient knowledge of these quantities, there is fortunately an easier way by which to proceed.

The circuit of Fig. 3 (b) is known as a series resonant circuit and, if we write the acoustic volume current as $U \exp(j\omega t)$, then from (14) or equivalently from (17),

$$U = p/Z = p/[R + j(L\omega - 1/C\omega)]. \qquad (23)$$

Since we are not concerned with phase but only with amplitude, we can take the absolute value to get

$$|U| = |p|/[R^2 + (L\omega - 1/C\omega)^2]^{\frac{1}{2}}. \qquad (24)$$

This expression, which is known as a resonance curve, is plotted in Fig. 4(a). The velocity response is a maximum at the resonance frequency ω^* given by $\qquad \omega^* = (LC)^{-\frac{1}{2}}. \qquad (25)$
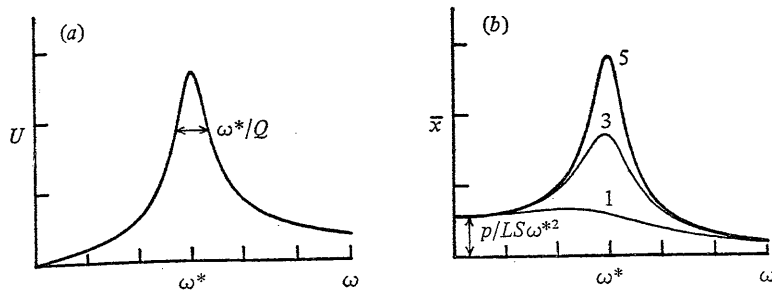
Fig. 4. Response in terms of (a) acoustic flow U, and (b) average displacement $\bar{x}$ for the membrane of Fig 3 considered as a series resonant circuit. Q is the quality factor of the resonance, shown as a parameter in (b).

The height of the peak is simply p/R and the width of the peak between two points at $1/2^{\frac{1}{2}}$ of its peak height is ω^*/Q, where Q, which is called the quality factor of the resonance, is given by

$$Q = L\omega^*/R. \tag{26}$$

To relate the acoustic flow $U \exp(j\omega t)$ to a more useful quantity, the average displacement amplitude $\bar{x}$ of the diaphragm, we note that, when only magnitudes are considered,

$$\bar{x} = U/\omega S \tag{27}$$

so that $\bar{x}$ has the form shown in Fig. 4(b) as a function of frequency. Provided Q is greater than unity, which is usually the case, the peak in $\bar{x}$ is very nearly at the resonance frequency ω^* and the displacement amplitude at resonance is very nearly Q times the low-frequency displacement amplitude $pC/S = p/LS\omega^{*2}$.

A more sophisticated discussion of the behaviour of a diaphragm (e.g. Morse, 1948, pp. 172–213) shows that it has an infinite number of resonant vibration modes of which the one we have considered is the lowest-frequency or fundamental mode. In fact the non-symmetrical higher modes of a circular or elliptic membrane cannot be excited by a simple acoustic pressure, and even the second symmetrical mode, whose frequency is between two and three times that of the fundamental depending upon the stiffness of the diaphragm, couples rather inefficiently to the sound wave. For our present purposes we can therefore neglect these higher vibration modes.
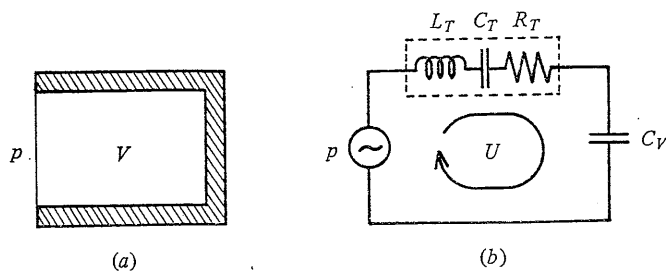
Fig. 5. (a) A simple omni-directional ear consisting of a thin tympanum over a closed cavity V. (b) The analog electrical circuit; L_T, C_T and R_T refer to the bare tympanum and C_V to the enclosed air volume.

(b) The simplest ear

Perhaps the simplest ear of which we can conceive consists of a tympanum or diaphragm closing an air-filled cavity as shown in Fig. 5(a), the diaphragm being flush with the outside of the animal's body. Since part of the external pressure is supported by the diaphragm and part by the resilience of the air in the cavity, the analog circuit is as shown in Fig. 5(b). If the diaphragm is defined by its area S, thickness d, bare resonance frequency ω_T^* and Q value and if the cavity volume is V, then the response peak of the whole ear is at the resonance frequency

$$\omega^* = \omega_T^*(1 + C_T/C_V)^{\frac{1}{2}}, \tag{28}$$

where C_V is given by (13) and C_T by (22) and (25). Clearly the extra resilience contributed by the enclosed air raises the resonance frequency so that $\omega^* > \omega_T^*$, and this frequency shift is large if the cavity volume, and hence C_V, is small.

From our discussion of the simple diaphragm, the low-frequency displacement response is

$$\bar{x}_0 = p/L_T S \omega^{*2} \approx p/\rho_B d\omega^{*2} \tag{29}$$

and the resonant response is Q times this value, as in Fig. 5(b).

The performance of such an ear, which is essentially identical to a simple condenser microphone, can be optimized in various ways. If Q is made close to unity, for example by deposition of lossy material around the edge of the diaphragm, or by filling the cavity with fibrous material, then the response can be made essentially uniform from low frequencies up to an upper limit near ω^*. The actual response, from

(29), varies, however, as ω^{*-2}, so that the product (gain) × (bandwidth)^2 remains constant as the tension of the membrane or the size of the cavity is varied to change ω^*.

Another possibility, which is more likely for a simple ear, is to optimize auditory sensitivity, and thus signal-to-noise ratio, at a particular frequency corresponding to a mating call or the cry of a predator. In this case ω^* is set to the desired frequency and Q is made as large as possible. The limit for biological material is probably not much more than 10 for Q, which represents a 20 dB improvement in threshold near ω^* and a 3 dB frequency discrimination bandwidth of $0 \cdot 1 \omega^*$. Much finer frequency selectivity than this is achieved by many animals with quite simple ears, but this must be as a result of further signal processing at a neural level. A sharply tuned neural transducer, if such a thing exists, would effectively multiply the Q of the basic resonance, but it seems likely that the real mechanism is more sophisticated than this.

Finally, we note from (29) that $\bar{x}$ increases as the diaphragm thickness d is decreased. There is, however, a limit to what can be done in this direction, not only because the diaphragm must be strong enough to resist mechanical damage, but also because d is really an effective thickness which takes into account the moving mass of the neural transduction apparatus connected to the tympanum. This mass, and its associated losses which tend to reduce Q, cannot be made negligibly small, so that there is a limit below which d cannot reasonably be reduced even for very small and suitably protected ears. Note that the area S of the tympanum does not enter directly into the final expression in (29) but is important indirectly because of the interdependence of ω_T^*, d and S for a diaphragm of stiff biological material.

To gain some idea of the magnitudes involved for a typical insect in a sound pressure field of 1 Pa, we note $\rho_B \approx 1 \text{ kg m}^{-3}$ and typically $d \sim 10 \,\mu\text{m}$, $\omega^* \sim 10^4 \text{ rad s}^{-1}$ so that $\bar{x}_0 \sim 1 \,\mu\text{m}$. These values can, of course, vary quite considerably.

Finally we note that, provided the tympanum is small in diameter compared with the sound wavelength involved, this ear is completely non-directional and it is usual to say that it has an acoustic pressure response.

(c) A bi-directional ear

The next form of ear to be considered consists of a diaphragm open to the influence of sound pressure on both sides, as shown in the idealization
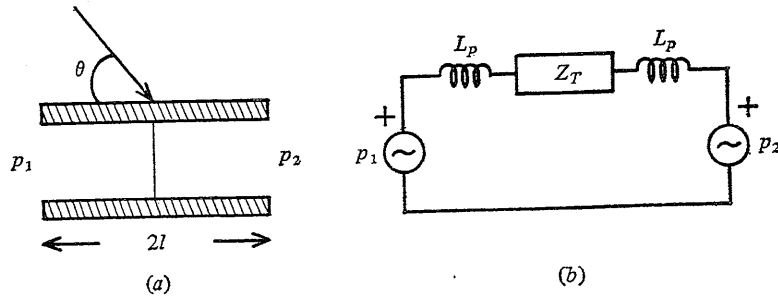
Fig. 6. (a) This idealized bi-directional ear consists of a tympanum mounted centrally in a short pipe. The direction θ of sound incidence is shown. (b) The electrical analog network; Z_T is the tympanum impedance and L_p the inertance of one of the half-lengths of pipe.

of Fig. 6(a). No biological examples having the exact symmetry of Fig. 6(a) are known but there are less symmetrical examples which operate on similar principles. This system has two ports through which sound pressures p_1 and p_2 act. If we take the centre of the system as geometrical reference and suppose that a plane sound wave arrives from a direction θ as shown, then from (2) we have

$$p_1 = p \exp \left[j\omega(t + (l/c) \cos \theta) \right], \tag{30}$$

$$p_2 = p \exp \left[j\omega(t - (l/c) \cos \theta) \right]. \tag{31}$$

Once again the inertances $L_p = \rho l/S$ of the two pipe sections are acoustically in series with the diaphragm impedance Z_T, as shown in Fig. 6(b), and the driving pressures p_1 and p_2 act in opposition to give a net forcing pressure $p_1 - p_2$.

The network of Fig. 6(b) is again trivially simple to solve and we find

$$U = p(e^{j\delta} - e^{-j\delta})/(Z_T + 2L_p \omega j), \tag{32}$$

where we have dropped the factor $e^{j\omega t}$ from U and p and have written

$$\delta = (\omega l/c) \cos \theta. \tag{33}$$

Since $\delta \ll 1$ because the auditory system is small compared with the sound wavelength, $(e^{j\delta} - e^{-j\delta}) \approx 2j\delta$ so that, taking absolute values,

$$|U| = 2|p \cos \theta|(\omega l/c)[R_T^2 + (L_T \omega + 2L_p \omega - 1/C_T \omega)^2]^{-\frac{1}{2}} \tag{34}$$

and again the diaphragm displacement $\bar{x}$ can be found by dividing by ωS, as specified by (27).
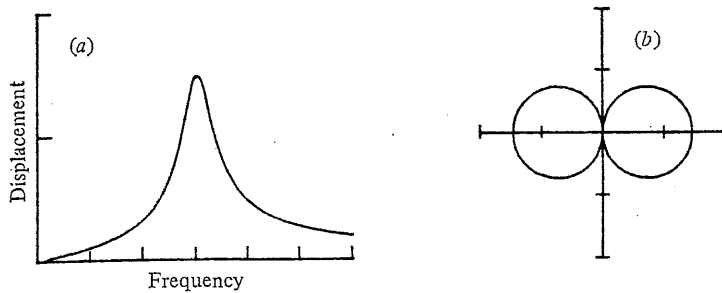
Fig. 7. (a) The frequency response and (b) the directional response of the simple bi-directional ear of Fig. 6. No units are given since this ear is not biologically realistic.

For any given angle θ, the displacement response $\bar{x}$ has a resonance curve like that shown in Fig. 7(a), going to zero at both low and high frequencies and with a peak at

$$\omega^* = [C_T(L_T + 2L_p)]^{-\frac{1}{2}}, \tag{35}$$

which is a somewhat lower frequency than that of the bare tympanum resonance, because of the mass load of the air in the tubes.

The important thing about this analysis is the angular variation of the response, which behaves like $|\cos \theta|$, giving the figure-8 patterns shown in Fig. 7(b). The basic reason for this behaviour is easily appreciated for the diaphragm responds to the difference in pressure acting on its two surfaces and thus to the gradient of acoustic pressure, or acoustic phase shift, along the length of the tube. Any ear which has ports allowing very nearly equal entry of acoustic pressure to each side of a diaphragm will behave in a rather similar manner.

(d) A directional ear

The essential feature leading to directionality in the ear considered in the previous section was the existence of two sound ports. This feature must always be present in directional auditory systems whose overall dimensions are small compared with the sound wavelength involved. In the present section we discuss an ear with a unidirectional response characteristic and which is in many ways an elementary prototype for all the more complex auditory systems to follow.

Fig. 8(a) shows the essential features of the system which is similar to the primitive pressure-response ear of Fig. 5(a) except for the
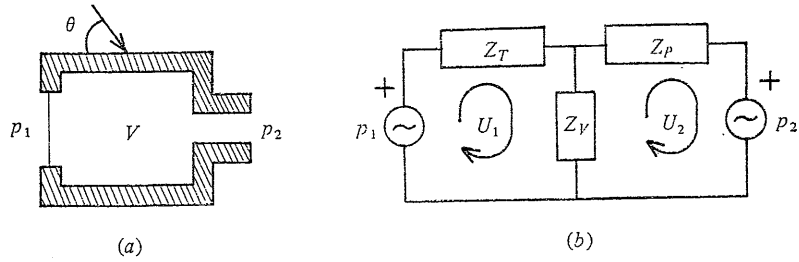
Fig. 8. (a) A simple directional ear consisting of a tympanum closing a cavity which possesses an additional venting port. The direction θ of sound incidence shown. (b) The electrical analog network; Z_T is the impedance of the tympanum, Z_P that of the port and Z_V that of the cavity. p_1 and p_2 are external acoustic pressures at the tympanum and port; U_1 and U_2 are acoustic volume flows through tympanum and port respectively.

presence of an additional constricted port. Two pressures, p_1 and p_2, given once again by (30) and (31), act on the outside of the diaphragm and at the entry to the second port respectively.

Construction of the analog network for the system, as shown in Fig. (8b), involves the observation that both ports allow acoustic pressure to enter the cavity and that the prime function of the cavity is as an acoustically compliant reservoir rather than as a pipe connecting the two ports. In fact these two aspects must both be taken into account when the cavity dimensions are no longer small compared with the sound wavelength, as we shall see later. The network now has the two-mesh form shown and, to simplify the algebra, we denote by Z_T the impedance of the tympanum, by Z_V that of the cavity, and by Z_P that of the second port which can be represented as an inertance and a resistance in series. This inertance is provided by the port itself and the resistance either by the narrow dimensions of the port or by obstructions within it.

Following the methods outlined in section 4 above we arrive at the appropriate special case of the system of equations (19) in the form

$$(Z_T + Z_V)U_1 - Z_V U_2 = p_1,$$

$$-Z_V U_1 + (P_P + Z_V)U_2 = -p_2. \tag{36}$$

We are concerned with the motion of the diaphragm and hence with U_1 which from (20) is given by

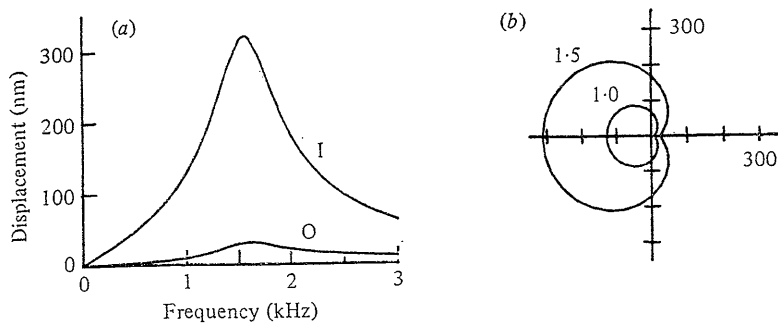$$U_1 = \frac{p_1(Z_P + Z_V) - p_2 Z_V}{(Z_T + Z_V)(Z_P + Z_V) - Z_V^2}. \tag{37}$$

Fig. 9. (a) Frequency response for ipsilateral (I) and contralateral (C) stimulation, and (b) directional response for the left ear at 1·0 and 1·5 kHz of the auditory system of Fig. 8 as calculated using the parameters in Table 1 for a sound pressure level of 91 dB.

Using (30), (31) and (33) we find, to first order in δ,

$$U_1 \approx \frac{p[Z_P + (Z_P + 2Z_V)j\omega l \cos \theta/c]}{Z_T Z_P + Z_V(Z_T + Z_P)}. \tag{38}$$

It is clear that, in a general way, the angular response pattern is determined by the numerator while the frequency response has peaks near the minima of the denominator.

If we write $Z_P = L_P\omega j + R_P$ and $Z_V = 1/C_V\omega j$ in the numerator of (30) then it takes the form

$$[R_P + (2/C_V - L_P\omega^2)\, l \cos \theta/c] + j\omega[L_P + R_P l \cos \theta/c]. \tag{39}$$

The behaviour of this expression depends on the values of the parameters involved but if ω is small so that $L_P\omega^2 \ll 2/C_V$ and the second term of (39) is much smaller than the first, then an approximate null can be obtained for sound incident from the direction of the port ($\theta = 180°$) if

$$R_P = 2l/cC_V. \tag{40}$$

The response is then maximal for $\theta = 0$ and the ear is usefully directional.

To give an indication of the complete performance of an auditory system with this configuration, which is not unlike that used in some directional condenser microphones, we show in Fig. 9(a) the frequency response for $\theta = 0$ and 180° and in Fig. 9(b) the polar response at several frequencies for an ear having the physical parameters given in Table 1. These are chosen to be of reasonable magnitude for the ear of a small insect, though perhaps no ear with just this configuration has

TABLE I. *Assumed parameters for directional ear*

Tympanum area	$S_T = 10^{-5}\,\text{m}^2$
Tympanum thickness	$d = 100\,\mu\text{m}$
Tympanum resonance	$\omega_T^*/2\pi = 1500\,\text{Hz}$
Tympanum Q value	$Q = 5$
Cavity volume	$V = 4 \times 10^{-7}\,\text{m}^3$
Port area	$S_p = 10^{-5}\,\text{m}^2$
Port resistance	$R = 2 \times 10^7\,\text{Pa s m}^{-3}$
Port separation	$2l = 20\,\text{mm}$
Port length	$l_p = 3\,\text{mm}$

evolved. Once again we have calculated the average displacement amplitude $\bar{x}$ of the tympanum using (27), and the accurate result (37) is used rather than the approximate form (38).

From Fig. 9(a) we see that the response for the ear is peaked near the resonance frequency of the diaphragm and that the response falls to zero at low frequencies rather than remaining finite as in the simple pressure-response ear. The frequency ω_0 below which this fall-off becomes pronounced is determined by the transmission of acoustic pressure to the cavity through the port, and is given by

$$\omega_0 \approx 1/R_P C_V. \qquad (41)$$

The height of the resonance peak is determined largely by the Q value of the diaphragm but is reduced somewhat by losses in the port resistance.

From Fig. 9(b) we see that the polar response curve is cardioid in shape with a reasonably sharp null for sound coming from the direction of the port and a broad maximum for sound falling directly upon the tympanum. This is a useful directionality for biological purposes, but it is clear that the animal can locate a sound source only by moving a single ear or by using more sophisticated neural processing and an array of two or more ears.

In many ways this directional ear can be considered as a combination of the omnidirectional ear of Fig. 5 with the figure-8 response of the pressure-gradient ear of Fig. 6. Indeed, if the port is made small so that the value of R_P is much larger than the value given by (40), the present ear shows an omnidirectional response while, if the port is large so that R_P is much smaller than the value given by (40), the response is of figure-8 form. The optimum R_P value effectively adjusts these two types
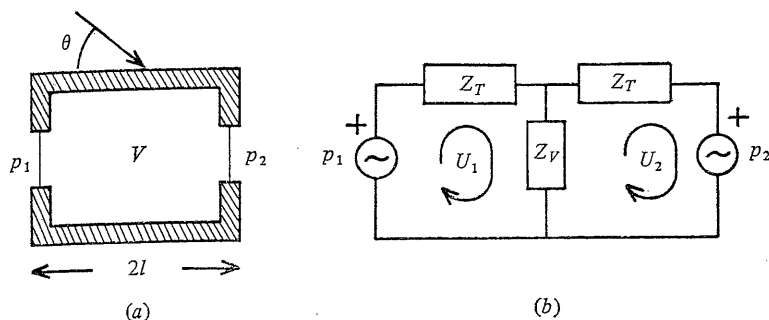
Fig. 10. (*a*) A simple coupled ear pair consisting of two identical tympana communicating with a closed cavity. (*b*) The electrical analog network; Z_T is the tympanum impedance and Z_V that of the cavity.

of response to comparable magnitude so that for sound from the front of the ear the two motions add while for sound from the direction of the port they tend to cancel.

Another way of viewing the behaviour, which is in fact more generally applicable, is to note that the combination of a port and cavity introduces a phase shift in the wave reaching the inside of the diaphragm. By appropriate adjustment of port, resistance and cavity size this phase shift tends to make the phases of internal and external pressure similar for sound from the direction of the port, leading to minimal diaphragm motion. For sound from other directions the phase relations are different and the pressure difference across the diaphragm is greater, giving more movement.

(*e*) Two coupled ears

Most animals have bilateral symmetry and one or more pairs of ears which interact acoustically with one another through a system of cavities, tubes and septa. If the central septum is thick and heavy, the two ears of a pair are effectively isolated and can be treated separately, though their outputs may be combined at a higher neural level. If the central septum is thin or non-existent, then direct acoustical interaction between the two ears may have a dominant effect on their response.

As the simplest example consider a pair of ears consisting of two tympana coupled to a common cavity as shown in Fig. 10(*a*). The analog circuit shown in Fig. 10(*b*) is similar to that of Fig. 8(*b*) but exhibits the bilateral symmetry of the acoustical system. The acoustic
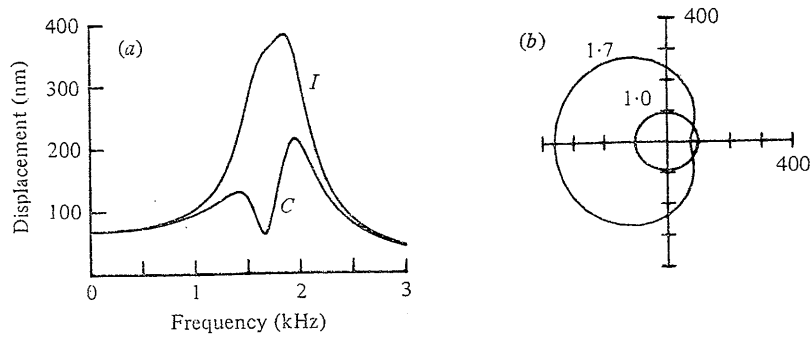
Fig. 11. (a) Frequency response for ipsilateral (I) and contralateral (C) stimulation, and (b) directional response for the left ear at 1·0 and 1·7 kHz of the auditory system of Fig. 10 as calculated using the parameters in Table 2 for a sound pressure level of 91 dB.

current U_1 through the left ear for sound incident at an angle θ as shown is given, by analogy with (37), by

$$U_1 = \frac{p_1(Z_T + Z_V) - p_2 Z_V}{Z_T(Z_T + 2Z_V)}, \qquad (42)$$

where Z_T and Z_V are the acoustic impedances of the tympanum and cavity respectively.

The response U_1 has two maxima, one at the frequency for which Z_T is a minimum and one at the frequency for which $Z_T + 2Z_V$ is a minimum. These correspond respectively to a mode in which the tympana move in the same direction (one in and one out, giving no compression of the air in the cavity) and a mode in which the tympana move in antiphase. The first mode is driven by the pressure gradient and the second by the average pressure, the resonance for the second mode always being at a rather higher frequency than that for the first, though often they overlap substantially.

The precise behaviour of the system can be found by evaluating (42) using (30) and (31) for p_1 and p_2 but we can easily see the general outline by approximate evaluation of (42) for particular situations. Thus, at frequencies well below the tympanum resonance, Z_T behaves like a compliance $1/C_T\omega j$, $p_2 \approx p_1$ and

$$U_1 \to p/(Z_T + 2Z_V) \to p\omega C_T C_V/(C_V + 2C_T) \qquad (43)$$

so that the tympanum displacement $\bar{x} = U_1/\omega S_T$ becomes constant and independent of sound direction.

TABLE 2. *Assumed parameters for simple ear pair*

Tympanum area	$S_T = 10^{-5}\ \mathrm{m^2}$
Tympanum thickness	$d = 100\ \mu\mathrm{m}$
Tympanum resonance	$\omega_T^*/2\pi = 1500\ \mathrm{Hz}$
Tympanum Q value	$Q = 4$
Cavity volume	$V = 5 \times 10^{-7}\ \mathrm{m^3}$
Separation of ears	$2l = 30\ \mathrm{mm}$

At the tympanum resonance, on the other hand, $Z_T = R_T$ and the numerator of (42) becomes, to first order,

$$p[R_T + (2l/cC_V)\cos\theta + j(\omega l R_T/c)\cos\theta]. \tag{44}$$

The real part of this expression can be made to vanish for contralateral stimulation ($\theta = 180°$) if $R_T = 2l/cC_V$ and the response for this angle is then much smaller than that for ipsilateral stimulation ($\theta = 0$). It is not possible to achieve an exact null for $\theta = 180°$ and indeed optimum cancellation occurs at a frequency slightly below the tympanum resonance.

Finally, at high frequencies Z_T becomes large and inductive and both U_1 and $\bar{x}$ fall asymptotically to zero. Fig. 11(a) shows the calculated frequency response for ipsilateral (I) and contralateral (C) stimulation for an auditory system having the detailed parameters shown in Table 2. Fig. 11(b) shows the polar response, which is seen to be cardioid near the frequency of maximum sensitivity and more nearly circular at higher and lower frequencies. For the particular system calculated, the tympanum thickness and Q value were chosen to give good directionality, since such optimization is certainly possible during the evolutionary development of the auditory system in real animals.

(f) Multi-port systems

The twin-ear system discussed above can be further generalized by the addition of further sound-entry ports, which might be physically realized in the form of nares or spiracles or by secondary tympana communicating with the central cavity. Another possible complication is the existence of a central septum as we have previously mentioned.

Fig. 12(a) shows such a system with two closely spaced nostrils entering a cavity with which the tympana also communicate, an example with minor complications being the auditory system of the frog. Since the nares are closely spaced they can be lumped together, giving the

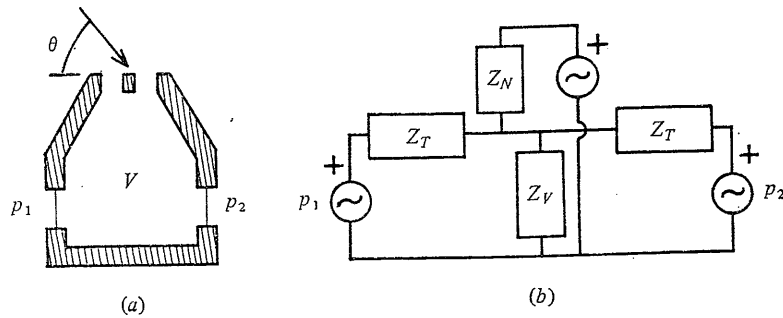(a)   (b)

Fig. 12 (a) The auditory system of a frog-like animal. Two tympana and two
closely spaced nares communicate with an otherwise closed mouth cavity.
(b) The analog network for this auditory system. The two nares have been
replaced by a single impedance because of their close spacing.

slightly simplified network shown in Fig. 12(b), which has just three
meshes. A rather similar though unrelated system is that of the male
cicada *Cystosoma saundersii* (Westwood) discussed by Fletcher & Hill
(1978), in which case the third input is through the resonant abdominal
shell rather than through the nares.

Without going into details of the solution of the frog-like system, we
note that, because the inlet to the nares is placed forward of the tympana,
the auditory system has some degree of frontal directionality in addition
to the lateral directionality conferred by the paired tympana, the nares-
tympana system operating rather like the simple directional system of
Fig. 8. With the simple system illustrated, the response is always
greatest in the rear ipsilateral quadrant so that the directions of approxi-
mate null are in frontal quadrants. This may not give the animal optimal
hearing acuity but does give optimal directional information when the
responses of the two ears are compared neurally.

To illustrate this behaviour Fig. 13 shows calculated frequency
response and directionality for a frog-like auditory system having the
physical parameters given in Table 3.

6. PIPES, HORNS AND LEVERS

We now introduce a more complex type of acoustical element which
requires for its representation a four-terminal electrical analog. This is
true of virtually all structures whose dimensions are comparable with
the sound wavelength involved and is also a necessity for certain other
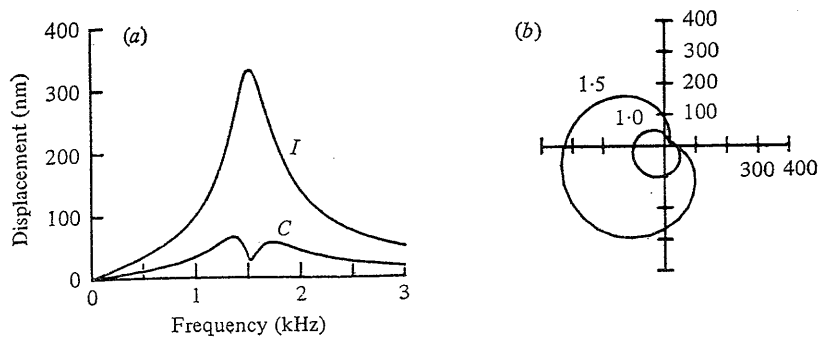structures, such as horns and levers, at all frequencies.

Fig. 13. (*a*) Frequency response for ipsilateral (*I*) and contralateral (*C*) stimulation, and (*b*) directional response for the left ear at 1·0 and 1·5 kHz of the frog-like auditory system shown in Fig. 12. System parameters are given in Table 3 and the sound pressure level is 91 dB. Note that the maximum response is in the rear ipsilateral quadrant.

TABLE 3. *Assumed parameters for frog-like system*

Tympanum area	$S_T = 10^{-5} \text{ m}^2$
Tympanum thickness	$d = 100 \ \mu\text{m}$
Tympanum resonance	$\omega_T^*/2\pi = 1500 \text{ Hz}$
Tympanum Q value	$Q = 5$
Cavity volume	$V = 10^{-6} \text{ m}^3$
Total nares cross-section	$S_N = 10^{-5} \text{ m}^2$
Nares length	$l_N = 1 \text{ mm}$
Nares resistance	$R_N = 5 \times 10^6 \text{ Pa s m}^{-3}$
Separation of ears	$2l = 20 \text{ mm}$
Forward distance of nares	$l' = 10 \text{ mm}$

(*a*) *Pipes*

As the first component to be considered, let us take a cylindrical pipe of radius *a*, cross-section $S = \pi a^2$ and length *l*. Such a tube has two inlet ports, one at each end, and it is clear that a pressure signal applied at one port may appear in modified form at the second port because of transit time delays and transmission losses in the tube. To analyse this situation we use pressures and acoustic currents as defined in Fig. 14 and write

$$p_1 = Z_{11} U_1 - Z_{12} U_2, \tag{45}$$

$$p_2 = -Z_{21} U_1 + Z_{22} U_2. \tag{46}$$

Note that both U_1 and U_2 flow clockwise and that the senses of p_1 and p_2 are opposite. (Equations (45) and (46) differ from the form often used
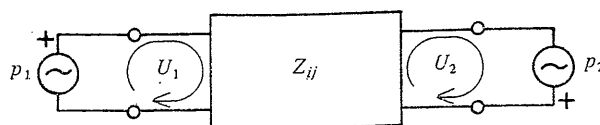
4

Fig. 14. Definition of the senses of pressures and currents for a 4-pole network analog.

in electrical engineering because of the minus signs given to Z_{12} and Z_{21} but this simplifies our subsequent discussion.)

Explicit determination of the impedance coefficients Z_{ij} involves consideration of acoustic waves propagating in both directions along the pipe. Since each wave is attenuated by wall losses if the pipe is narrow (as is usually the case in biological systems) we must generalize (2) and write, for a wave propagating in the $+x$ direction in the pipe,

$$p(x, t) = p_0 \exp (-\alpha x) \exp [j\omega(t - x/c')], \qquad (47)$$

where α is the attenuation coefficient and c' which is less than c, is the speed of sound of frequency ω inside the tube.

The propagation of such attenuated waves in pipes has been summarized in an article by Benade (1968). In general terms, $c' \approx c$ provided $\omega a^2 > 2 \times 10^{-5}$ m^2 s^{-1} but for narrower tubes or lower frequencies c' varies in proportion to $\omega^{\frac{1}{2}} a$. The attentuation coefficient α varies roughly as $\omega^{\frac{1}{2}} a^{-1}$ at all frequencies though there is a shift in the proportionality constant of about a factor 2 near $\omega a^2 \approx 2 \times 10^{-5}$ m^2 s^{-1}. Details of this behaviour for frequencies and tube sizes of biological interest are shown in Fig. 15. The attenuation in the tracheae of the acoustical systems of insects, which are often less than 100 μm in diameter and several millimetres long, will generally be quite appreciable and may be large.

To evaluate the Z_{ij} of (45) and (46) is a little complicated and the final results are given in a rather different form in most texts (e.g. Morse (1948), pp. 233–65; Olson (1957), pp. 106–108; Slater (1942), pp. 7–42). If we write $\beta = \omega/c'$ in (47) so that

$$\gamma = \alpha + j\beta = \alpha + j\omega/c' \qquad (48)$$

is a sort of complex propagation constant, then it can be shown that

$$Z_{11} = Z_{22} \approx (\rho c/S) \coth \gamma l, \qquad (49)$$

$$Z_{12} = Z_{21} \approx (\rho c/S) \operatorname{cosech} \gamma l, \qquad (50)$$
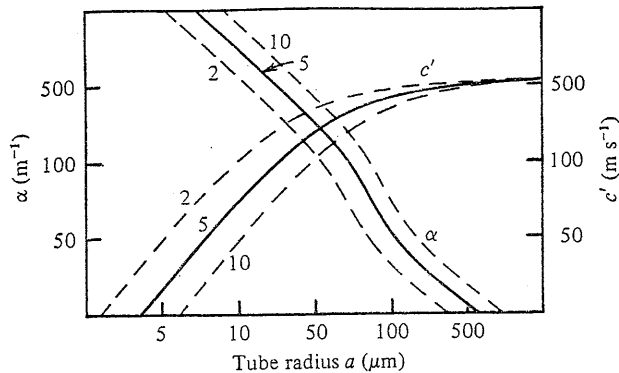
Fig. 15. The phase velocity c' and attenuation coefficient α for propagation of sound of given frequency (shown in kilohertz as a parameter) through a tube of radius a. The plotted results refer to a tube with smooth rigid walls; any deviation from this assumption will affect both c' and α.

the approximation involving the factor $\rho c/S$, which should really have a small imaginary part as well. The properties of these complex hyperbolic functions are summarized in the Appendix. It is interesting to note that if the tube is short so that $\gamma l \ll 1$, then clearly all the Z_{ij} are nearly equal and, if in addition the tube is wide enough that $\alpha \ll \beta$, then $Z_{ij} \approx \rho c/^2 Sl\omega$ which is just the two-terminal impedance of a simple cavity with volume $V = Sl$.

The relations (45), (46), (49) and (50) are easily seen to contain all the familiar information about the resonances of open and closed pipes one half or one quarter of a wavelength long but to generalize this to the discussion of lossy pipes of arbitrary length. For example, if the pipe is open at end 2 so that $p_2 \approx 0$, then from (45) and (46) we find for the input impedance at end 1

$$Z_{in} = p_1/U_1 = (\rho c/S) \tanh \gamma l \to (j\rho c/S) \tan \omega l/c, \qquad (51)$$

where the final form is appropriate if the attenuation α becomes zero. In this case the impedance of the pipe is nearly purely reactive and becomes small, which is the sounding condition for a flute-like instrument, if $\omega l/c = n\pi$ and the pipe is an integral number of half wavelengths long. Z_{in} becomes large, which is the sounding condition for a clarinet-like instrument, if $\omega l/c = (2n+1)\pi/2$ and the pipe length is an odd number of quarter wavelengths.

(b) Horns

The acoustics of horns is a good deal more complex than that of simple pipes but is treated in essentially the same way (Morse (1948), pp. 265–88; Olson (1957), pp. 100–115). We shall content ourselves with outlining the essential physics of the situation and giving some approximate results of accuracy sufficient for our present purposes.

A biological horn may be of quite complex shape but fortunately the general behaviour does not depend critically upon shape for the cases with which we shall deal. Mathematically simple horns include those in which the cross section $S(x)$ at co-ordinate x along the horn varies either as x^2 (a conical horn), x^n (a Bessel horn), e^{mx} (an exponential horn) or $\cosh^2 (\tfrac{1}{2}mx)$ (a hyperbolic or catenoidal horn). Most biological horns are not too far from exponential in shape and, since this is algebraically the simplest case to treat, we shall base our discussion upon it.

Acoustic waves will propagate inside an infinite horn provided its rate of flare (as measured by the parameter m for an exponential horn) is not too large. For frequencies below that for which the horn cross-section S changes by more than a factor e over a distance $\lambda/4\pi$, where λ is the sound wavelength, waves cannot propagate along the horn, though the enclosed air does vibrate all in phase and with an amplitude that is exponentially attenuated along the horn. This flare cut-off frequency ω_c is defined by

$$\omega_c = mc/2. \tag{52}$$

Conical horns do not show this sharp cut-off behaviour but their propagation characteristics deteriorate rapidly below a similar frequency which depends on the cone angle. If the horn is very short then this low-frequency attenuation may not be significant, but to obtain the desired action of a horn as an impedance transformer, and thus as a collector of sound energy in auditory systems, it is generally desirable that it operate above its cut-off frequency.

From the general expression given by Olson (1957, pp. 108–9) we can derive the four-pole impedance parameters Z_{ij} for the particular case of a lossless exponential horn with flare parameter m, length l and end cross-sections S_1 and S_2. Clearly

$$m = l^{-1} \ln (S_2/S_1), \tag{53}$$

which allows us to determine the cut-off frequency from (52). Provided

the horn is operated well above its cut-off frequency then we have the simple approximate results

$$Z_{ii} \approx (\rho c/S_i) \coth (\bar{\alpha}+j\omega l/c) \quad (i = 1, 2), \qquad (54)$$

$$Z_{12} = Z_{21} \approx [\rho c/(S_1 S_2)^{\frac{1}{2}}] \operatorname{cosech} (\bar{\alpha}+j\omega l/c), \qquad (55)$$

where $\bar{\alpha}$ is an average value of the wave attenuation caused by wall loss along the horn. Because of its flaring shape, the value of $\bar{\alpha}$ is usually not large but it is important in some cases that it not be taken to be zero, or resonant peaks of unreasonable heights may result.

From the form of (54) above it can be seen that a horn acts firstly as an impedance transformer, since $Z_{11}/Z_{22} = S_2/S_1$, and secondly as a resonant tube of length l with its resonances and anti-resonances determined by the factor $\cot (\omega l/c)$. Because the tube or diaphragm at the narrow end of a horn is generally of high acoustic impedance, while the free air presents a low acoustic impedance to the open end of the horn, its presence may thus aid very significantly in improving the response of the system, though with a significant expenditure of space either within the animal or in the form of external horns. For a high diaphragm impedance the pressure gain is essentially $(S_2/S_1)^{\frac{1}{2}}$. If in addition the horn is an odd number of quarter wavelengths long, a further significant increase in acoustic pressure at its throat can be achieved. Such horns, with or without the resonance feature, are a common component of auditory and vocal systems. Because of flare cut off, however, the pressure gain that can be achieved is limited to about 10 dB unless the horn is extended to an external pinna of large size.

Another aspect of horn behaviour which is sometimes important in auditory or sound production systems is the directionality conferred by the action of the horn itself, irrespective of the existence of any other ports in the system. Such directionality is reciprocal, in the sense that the polar pattern of the horn used as a sound generator coupling is the same as when it is used as an auditory system coupling. Directionality becomes appreciable only when the radius of the open end of the horn exceeds about one fifth of the sound wavelength involved, which is also the condition for the disappearance of resonances in the horn. For higher frequencies the horn becomes increasingly directional, receiving or directing sound preferentially along a direction normal to the plane of its open end which, for a bent horn, may not coincide with its axis. This directionality becomes pronounced if the horn radius exceeds half the sound wavelength.
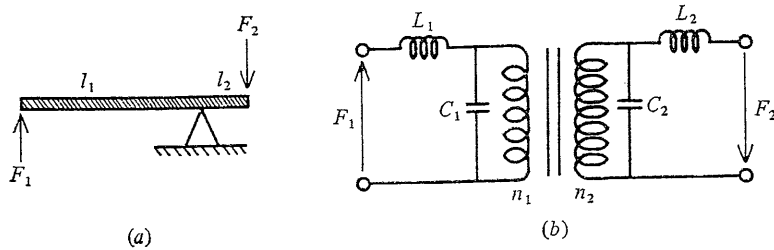
Fig. 16. (a) Physical configuration and (b) network analog for a simple lever. L_1 and L_2 represent the masses and C_1 and C_2 the elastic compliances of the lever arms. The transformer is assumed to be ideal, with $n_1/n_2 = l_2/l_1$.

If an auditory-system horn is operated well below its cut-off frequency (i.e. if its flare rate is very rapid) then essentially all $|Z_{ij}| \approx 1$ so that there is no transformer action but only a transmission phase shift for a plane wave impinging on the horn.

(c) Levers

The lever is a mechanical rather than an acoustical device and commonly occurs in auditory systems as a link between the moving tympanum and the auditory capsule containing the neural transducers. In order to treat its action we must first deduce, from the motion of the tympanum, the force that it is capable of exerting on one arm of the lever. We then treat the lever itself and the remainder of the system in terms of mechanical rather than acoustical impedances.

The mechanical arrangement of a simple lever is shown in Fig. 16(a); note that in a general case l_2 might be negative so that the force F_2 is applied on the same side of the fulcrum as F_1. An approximate four-terminal network for a real lever is shown in Fig. 16(b). L_1 and L_2 represent the masses, or rather the moments of inertia, of the two lever arms and C_1 and C_2 their springy compliances. In an ideal lever these four quantities would be zero. The ideal transformer connecting the two ports of the circuit has a turns ratio

$$n_1/n_2 = l_2/l_1 \tag{56}$$

and, in order that the transformer should respond to static forces, both n_1 and n_2 must approach infinity, giving an infinite inductance to the open-circuited transformer. The ideal transformer that is the central part of the analog network has

$$Z_{11} = \mu n_1^2 \omega j, \quad Z_{22} = \mu n_2^2 \omega j, \quad Z_{12} = Z_{21} = \mu n_1 n_2 \omega j \tag{57}$$

in the limit $\mu \to \infty$. Note that if the sign of l_2 and hence n_2 is changed by moving the fulcrum, then the signs of Z_{12} and Z_{21} are also changed.

In an auditory system, as we have said, a lever system is often used to connect the tympanum to the auditory capsule. The capsule itself has a mechanical impedance which is determined by the size, number and elastic properties of its constituent cells and the substrate on which they are supported. These cells presumably have a firing threshold for some particular elastic distortion and a distribution of firing thresholds allows a discrimination of stimulus level. The use of an appropriate lever allows optimal matching of the mechanical impedance of the tympanum to that of the auditory capsule.

7. HIGH-FREQUENCY AUDITORY SYSTEMS

The analysis of high-frequency auditory systems follows along exactly the same lines discussed for low-frequency systems in section 5 above. The best way to make this clear, while at the same time gaining insight into several typical real auditory systems, is to discuss some simple systems in detail.

(a) Simple doublet tube ear

The simplest possible high-frequency ear with bilateral symmetry consists of two tympana connected by a straight narrow tube as in Fig. 16(a). The electrical analog circuit is given in Fig. 16(b), with Z_{ij} being the four-pole network for a narrow tube, as defined in (49) and (50), and Z_T being the tympanum impedance given by (21). The network equations are

$$
\left.\begin{aligned}
(Z_T + Z_{11})U_1 - Z_{12}U_2 &= p_1, \\
-Z_{12}U_1 + (Z_T + Z_{22})U_2 &= -p_2,
\end{aligned}\right\} \tag{58}
$$

with p_1, p_2 given by (30) and (31). The solution for ear 1 is

$$
U_1 = \frac{p_1(Z_T + Z_{11})^2 - p_2 Z_{12}}{(Z_T + Z_{11})^2 - Z_{12}{}^2}, \tag{59}
$$

where we have used the facts that $Z_{12} = Z_{21}$ and, for a cylindrical pipe, $Z_{11} = Z_{22}$.

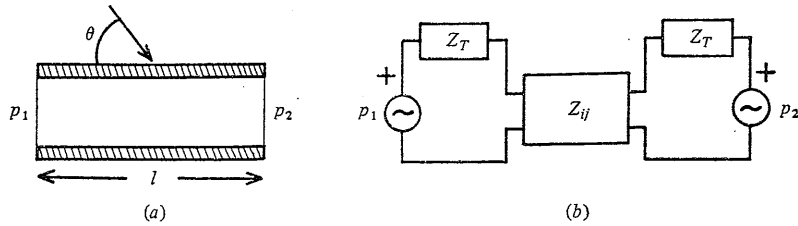The behaviour of this system is particularly simple if the tympana are

Fig. 17. (a) Physical configuration and (b) network analog for a simple doublet auditory system in which two tympana are coupled by a narrow tube. Z_T is the tympanum impedance and the 4-pole Z_{ij} represents the tube.

extremely light (much lighter than would be possible in practice) so that $Z_T \ll Z_{11}$ and if the tube length is just one quarter of a wavelength so that $\omega l / c = \pi/2$. If we calculate the displacement of tympanum 1 at this frequency for ipsilateral ($\theta = 0$) and contralateral ($\theta = 180°$) stimulation, then we find, using the results in Appendix A,

$$\bar{x} = (p/\rho c \omega) \operatorname{sech} \alpha l \, (\sinh \alpha l \pm 1), \qquad (60)$$

where the plus sign refers to the ipsilateral and minus to the contra-lateral case. Clearly if the attenuation coefficient α in the tube is of such a magnitude that $\sinh \alpha l = 1$, then there is exact cancellation for contralateral sound at this frequency. For typical insect songs with $\omega \sim 10^4$ to 10^5 rad s^{-1} and $l \sim 10$ mm this requires a tube about $100 \, \mu$m in diameter, which is close to the dimensions found.

This special case cannot serve, however, as the description of any real system because, though the behaviour is reasonable at other frequencies as shown in Fig. 18, the tympanum displacement clearly diverges at very low frequencies. To remedy this defect we must return to (59) and retain a finite impedance for the tympanum. This has been done in Fig. 19, which displays the results of a calculation for a typical case using the physical parameters shown in Table 4. The response shows a sharp peak near the tympanum resonance, and exact cancellation can be achieved for contralateral stimulation through an appropriate choice of the Q value of the tympana and the attenuation coefficient in the tube. The directional response has an approximately cardoid form.

There is, in fact, a fair measure of freedom in the selection of parameters for such a system, and the attenuation necessary for directionality can be shared in an arbitrary fashion between the tube and
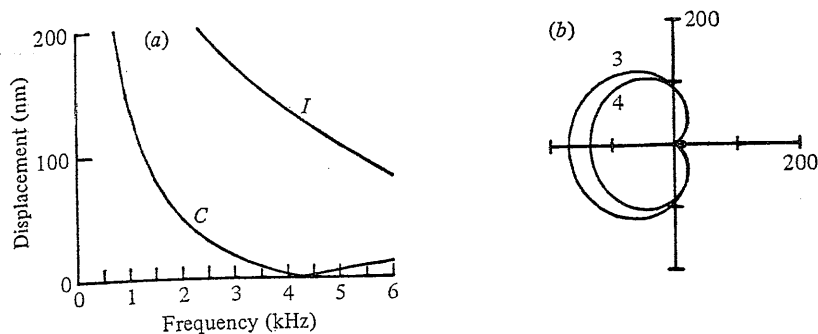
Fig. 18. (a) Frequency response for ipsilateral (*I*) and contralateral (*C*) stimulation, and (b) polar response for the left ear at 3·0 and 4·0 kHz of a tube-coupled doublet auditory system, as in Fig. 17, for the case where the tympana have negligible mass. Tube length is 20 mm, attenuation coefficient $\alpha = 44$ m^{-1} and sound pressure level is 91 dB.
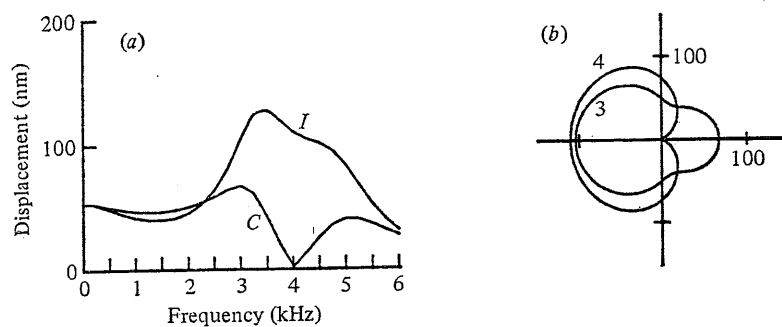

Fig. 19. (a) Frequency response for ipsilateral (*I*) and contralateral (*C*) stimulation, and (b) polar response for the left ear at 3·0 and 4·0 kHz of a tube-coupled doublet auditory system for the realistic parameter values given in Table 4. The assumed sound pressure level is 91 dB.

TABLE 4. *Assumed parameters for a doublet tube ear*

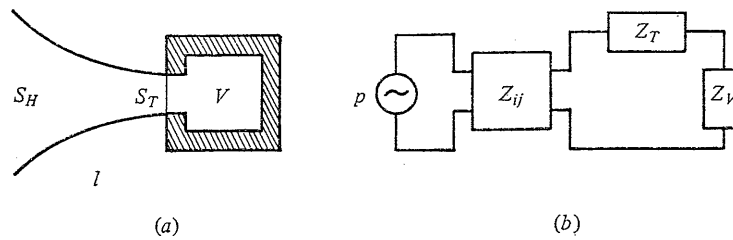|	
Tympanum area	$S_T = 7 \times 10^{-8}$ m^2
Tympanum thickness	$d = 20$ μm
Tympanum resonance	$\omega_T^*/2\pi = 4000$ Hz
Tympanum Q value	$Q = 5$
Tube radius	$a = 150$ μm
Tube length	$l = 20$ mm
Tube damping coefficient	$\alpha = 28$ m^{-1}

Fig. 20. (a) Physical arrangement and (b) analog network for a simple horn-coupled non-directional ear. Z_T is the tympanum impedance, Z_V the cavity impedance and Z_{ij} the 4-pole representing the horn.

the resistive losses of the tympana. Such a system is therefore not necessarily confined to the narrow tracheae of insects but could also be used with wider tubes in larger anaimls.

(b) Simple horn-coupled ears

Fig. 20(a) shows a prototype horn-coupled ear of the simplest possible kind. A horn of length l and open area S_H tapers to meet a tympanum of area S_T which is backed by an enclosure of volume V. The electrical analog network is shown in Fig 20(b).

If the horn is operating well below its cut-off frequency (i.e. if its flare rate is very rapid) then it has essentially no effect on the behaviour of the system, which then reduces to the simple pressure-response ear of section 5. More usefully, suppose that the horn is chosen so that it is well above its flare cut-off frequency at the resonant frequency of the diaphragm–cavity combination. Two distinct cases then arise: either the horn resonance is close to that of the tympanum, in which case the two resonances reinforce one another, or else these two resonance frequencies are well separated, in which case the horn acts simply as a non-resonant impedance transformer at the diaphragm resonance frequency and contributes a small peak of its own at its quarter-wavelength resonance.

Calculations for typical examples of these two cases are given in Fig. 21, using the physical parameters listed in Table 5. The gain in performance when the horn resonance coincides with the resonance of the tympanum is clearly apparent. It is incidentally worthy of note, however, that this performance depends to some extent on the impedance of the tympanum at resonance. If this is too low, either because the tympanum is too thin or because its Q value is too high, it is unable to
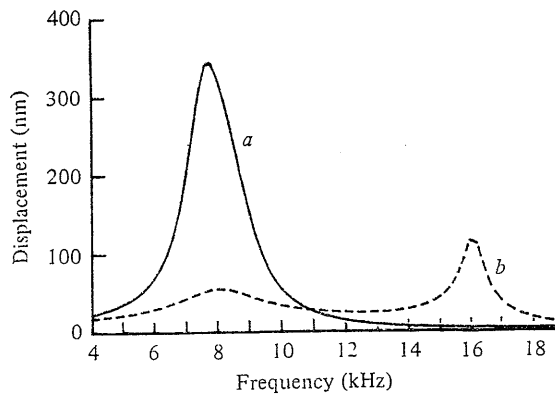
Fig. 21. Frequency response for a horn-coupled ear of the form shown in Fig. 20 for the cases where (*a*) the quarter-wave horn resonance coincides with the tympanum resonance, and (*b*) the horn is half this length but still above its flare cut-off frequency. Other parameters are given in Table 5.

TABLE 5. *Assumed parameters for a horn-coupled ear*

Tympanum area	$S_T = 10^{-5} \, \mathrm{m^2}$
Tympanum thickness	$d = 100 \, \mu\mathrm{m}$
Tympanum resonance	$\omega_T^*/2\pi = 8000 \, \mathrm{Hz}$
Horn opening area	$S_H = 2 \cdot 3 \times 10^{-5} \, \mathrm{m^2}$
Tympanum Q value	$Q = 3$
Cavity volume	$V = 8 \times 10^{-8} \, \mathrm{m^3}$
Horn length (non resonant)	$l = 5 \, \mathrm{mm}$
Horn length (resonant)	$l = 10 \, \mathrm{mm}$

act as an adequate termination for the horn and the combined resonance peak has a dip in its centre.

Provided the horn diameter is less than about one fifth of a wavelength, this auditory system will be essentially non-directional. For higher frequencies, as discussed before, sound from the direction of the horn mouth will predominante.

(*c*) Complex auditory systems

The auditory systems of many animals, and particularly of insects, have developed as specializations of their respiratory systems and therefore sometimes consist of a labyrinth of tubes and cavities with no obvious acoustical function. Evolution has permitted the development of these

structures, however, in such a way that they do not interfere with the auditory function and may indeed enhance it by providing extra resonances or phase shifts within the primary system.

It is not appropriate here to calculate in detail an example of such a complex auditory system, since this can only be done with the anatomy of a particular animal in mind. One case that has been so studied is that of the cricket *Teleogryllus commodus* (Walker) where the acoustical analysis seems to explain very satisfactorily the observed auditory response (Fletcher & Thwaites, 1979).

In addition to the anatomical complexities involved in real animals it is also appropriate to recognize that the external form of the animal in which the auditory system is embedded may also have an influence on system behaviour. Thus diffraction effects around the animal's body may influence not only the path lengths to the various ports of the auditory system (these lengths then becoming weak functions of the incidence angle θ) but also the magnitude of the pressure at each port (which may again be a weak function of θ). While these effects are unlikely to be important, they may well be appreciable in determining total system performance.

8. SOUND-GENERATING SYSTEMS

As we remarked in the introduction, sound-generating systems are in many ways similar in structure to auditory systems except that the auditory capsule is replaced by a mechanical vibration generator. There is, however, a considerable difference in detail between the two systems, if only because of the vast difference in power levels involved. Thus the mechanical generator in most systems is a robust, high-impedance structure driven either by heavy muscles or by a relatively high-pressure air flow. The generator is also generally highly non-linear, in the sense that, though its oscillations are driven by linear feedback from some of its vibrating parts, cubic terms in the oscillation behaviour act decisively to determine the amplitude of vibration and hence the maximum possible sound output.

Sound generators may have in-built periodicity, like the saw-teeth on one part of the body which are drawn at constant velocity across another structure, or may have an oscillation frequency that is determined by resonance, either within the mechanical structure or in other associated pipes and cavities. In many cases both these effects co-

operate to create a steady vibration with good frequency stability and large amplitude. An example of such a cooperative system is the cicada in which the primary sound producers, the tymbals, buckle progressively under the influence of muscular action to provide a train of pulses which are in resonance with a large acoustic bladder (Fletcher & Hill, 1978).

In the analysis of these systems it is important to remember that the primary sound generator is often a high-impedance source whose own resonances may completely dominate those of associated acoustic structures which serve then simply to couple the sound efficiently to the air. The analogy with musical instruments (Fletcher, 1979) is therefore fruitful only if impedances are taken quite explicitly into account in order to determine which part of the system is really responsible for its dominant behaviour. With this caveat we can apply much of the formal apparatus of analysis discussed above to this rather different class of problems. Two additional specific things must, however, be taken explicitly into account.

The first of these is sound radiation, for this generally represents only a small fraction of the total dissipation in the system. From a systems analysis point of view, which is what we are attempting here, the radiation resistance appears as a dissipative element in series with one of the components of the acoustical system. In the case of a horn-coupled vocal system as in most of the larger animals, this radiation resistance (along with an inertance load representing the 'end correction') appears across the output port of the horn network. Explicit expressions for this radiation impedance are given, for example, by Morse (1948, pp. 326–338) and by Olson (1957, pp. 97–99). If the radius of the open end of the horn is less than about one-fifth of a wavelength, which is usually the case at least for the lower-frequency components of the sound, then the acoustical resistance loading the horn is independent of its mouth size but increases proportionally to frequency, so that high-frequency sounds are more efficiently radiated than are low-frequency sounds. If the horn radius is larger than about a fifth of a wavelength then, as we have already noted, there is no reflexion from the open end and all sounds are radiated equally, though with increasing directionality at high frequencies. In this case the acoustic resistance loading the mouth of the horn is simply $\rho c/S$, where S is the mouth area.

In the case where the sound radiator is not one-sided like a horn but two-sided like a vibrating wing membrane, the radiation process is much less efficient unless the loading on the two sides of the vibrator is made

asymmetrical or unless the size of the vibrator is at least comparable with the wavelength involved (Olson, 1957, pp. 9). Insect wings in flying therefore radiate relatively little sound for the muscular effort involved, and sound generators of this type generally rely on the proximity of the body to one side of the membrane or the presence of some resonating device to couple the vibration efficiently to the air (Fletcher & Hill, 1978).

Finally we note that, since the primary sound generator is non-linear, we may expect an acoustical spectrum consisting either of a series of harmonics based on a fundamental, or sometimes of a series of sum and difference frequencies based on two or more fundamentals (Fletcher, 1978). The extent of overtone generation depends very much, however, upon details of the basic generator involved and on the presence or absence of any closely coupled resonant cavities. The human larynx, for example, is extremely non-linear and produces a train of flow pulses with very high harmonic content, while the songs of many birds and insects are very nearly sinusoidal, the generator presumably having just sufficient non-linearity at its working level to limit the amplitude of its vibrations.

9. EXPERIMENTAL ANALYSIS OF SYSTEMS

The behaviour of an auditory or sound-producing system can be said to be properly understood only if we can account quantitatively for all features of its behaviour. Leaving aside the complex non-linearities involved in muscular sound generators, this means that we must know the numerical values of all the acoustic impedance elements involved in the equivalent network at all frequencies of interest. As we have seen, once these impedances are known, we can easily deduce the system behaviour.

Part of the value of our method of analysis is that it tells us what measurements must be made to determine uniquely the impedance elements of the system. Let us see how we should proceed.

The basic measurements that can be made on the acoustical system all involve exciting the system at one or more of its ports with an acoustical pressure signal and then measuring either acoustic pressure (by means of a probe microphone) or acoustic flow (by observing the motion of a membrane) in some other part of the system. The measurement in each case involves determining both a magnitude and a phase.

Since the elements of the system are linear, we should first remark that application of two exciting signals simultaneously to different ports of the system gives no information in addition to that obtained from measurements with the two signals applied separately. It also follows that, since only the ratio of the magnitude of the observed quantity to the applied quantity and the difference in phase between them are significant, each such measurement yields exactly two pieces of information. We assume that each measurement is extended over the whole frequency range of interest.

Preliminary analysis of the acoustical system based on anatomical information now allows us to construct an electrical analog circuit and we can simplify this as much as possible by combining series elements to form lumped impedances Z. Each such impedance consists of a resistive part R and a reactive part X so that

$$Z = R + jX \tag{61}$$

both R and X depending, in general, upon frequency. Each symmetrical tube requires two impedances, Z_{11} and Z_{12}, for its specification and each horn three impedances Z_{11}, Z_{22} and Z_{12}. If the total number of impedance elements is N, then, since each involves two quantities R and X, we require $2N$ measurements for their determination. If amplitude ratio and phase difference are found for each physical measurement, we therefore require N independent physical measurements.

Measurements are in general independent if the excitation and observation points differ from one measurement to the other and are not related by symmetry. Another possible way of achieving an independent measurement is to replace one of the unknown impedances in the circuit by a different and known impedance, generally an effectively infinite impedance obtained by blocking an opening with wax or by immobilizing a tympanum by flooding it with liquid.

The exact procedure for finding all the impedance values from the experiments consists essentially of substituting the measured values into equations like (20) for the particular system configuration concerned and then solving these N equations for the unknown impedances. Provided the system is not too complex, this procedure is quite feasible on a desk-top computer, and the resulting $Z(\omega)$ values at all frequencies effectively define the system completely.

10. CONCLUSION

The analysis of auditory and sound-producing systems, even at the mechanical and acoustic level, is by no means a simple task but, as we have tried to show, formal analytical methods are available to perform this task. We would emphasize once again that this is only the beginning – acoustical considerations serve merely to define the first stage of auditory behaviour and it is to higher levels of neural sophistication that we must look to find the sharp frequency and orientation discriminations which are so vital in auditory neurophysiology.

APPENDIX

The hyperbolic functions cosh γ, sinh γ, tanh γ and their reciprocals sech γ, cosech γ and coth γ for a complex argument $\gamma = \alpha + j\beta$ are defined by analogy with the corresponding trigonometric functions through the relations

$$\cosh \gamma = \tfrac{1}{2}(e^{\gamma} + e^{-\gamma}), \tag{A 1}$$

$$\sinh \gamma = \tfrac{1}{2}(e^{\gamma} - e^{-\gamma}). \tag{A 2}$$

We then immediately find the relations

$$\cosh j\beta = \cos \beta, \tag{A 3}$$

$$\sinh j\beta = j \sin \beta, \tag{A 4}$$

for a real variable β, and the further results

$$\cosh (\alpha + j\beta) = \cosh \alpha \cos \beta + j \sinh \alpha \sin \beta, \tag{A 5}$$

$$\sinh (\alpha + j\beta) = \sinh \alpha \cos \beta + j \cosh \alpha \sin \beta, \tag{A 6}$$

which are used in manipulating the formulae in the text.

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ERRATUM

Physical Models for the Analysis of Acoustical Systems in Biology

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Figure 15 of the paper titled above (*Quart. Rev. Biophys.* **12**, 1, February 1979, page 51) contained several drafting errors. It should be replaced by the corrected version below.

Tube radius *a* (μm)