

THE ACOUSTICAL IMPEDANCE
OF THE GUINEA-PIG MIDDLE EAR
AND THE EFFECTS OF THE MIDDLE-EAR MUSCLES

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Chapter 1

INTRODUCTION

The middle ear, and the middle-ear muscles, have received a good deal of attention in the past, both because of their important role in the study of evolution and phylogenetic classification, and because of the growing importance of reconstructive surgery of the middle ear. There has also been quite a bit of interest in taking advantage of the middle-ear muscles for protection against potentially damaging noise such as gun-fire.

One promising approach to the study of middle-ear function has been the construction of analogous electrical circuit models, but little progress has been made in this field since the important work of Zwislocki (1957b, 1962, 1963), Onchi (1961) and Møller (1961). As far as the muscles are concerned, some modelling has been done of the acoustic-reflex loop (Dallos, 1964; Tietze, 1969; Borg, 1971), but practically no quantitative work has been done on modelling the actual effects of the middle-ear muscles.

For the above reasons, it was thought to be appropriate to undertake a study which would aim at quantitatively modelling the middle ear and its muscles, and at understanding their functional significance. There remains a great deal of work to be done before this aim is realized: this thesis presents only the beginning. I have developed a useful experimental technique, and with it have obtained some interesting results.

There is presumably a great deal to be learned about the middle ear from studying its variations from species to species. For this reason, the review of middle-ear anatomy in Chapter 2 considers not only the guinea pig, with which I am concerned directly, but also the similarities and differences among the middle ears of other mammalian species. It is important to recognize that the guinea-pig middle ear is in many respects unusual.

After reviewing the anatomical background of this study, I compare, in Chapter 3, a number of possible experimental approaches to investigating middle-ear function. Then, based on the anatomical knowledge outlined in Chapter 2 and on data that earlier researchers have obtained using the experimental methods treated in Chapter 3, I discuss what is known about middle-ear function in Chapter 4. Simultaneously an electrical circuit model is assembled, which in fact turns out to be similar to that of Zwislocki (1963) but which has been rearranged somewhat, the better to show the relations among different parts of the ear.

The experimental approach that I have chosen is to measure the acoustical impedance at the eardrum, as a measure of middle-ear function, and to observe spontaneous muscle contractions, as a measure of middle-ear-muscle function. This choice is justified at the end of Chapter 3. The method itself is described in Chapter 5. Also described in that Chapter is the procedure that I use for preparing castings of the middle-ear cavities, using silicone rubber. These castings are valuable both for measuring the volumes of the cavities, and for visualizing their shapes.

The results that I have obtained are presented in Chapter 6. These results include impedance measurements in eight animals, observations of muscle contractions in three animals, and cavity-volume measurements in 15 animals. These results are related to the middle-ear model, and it is shown that the model can account fairly well for the effects of the muscle contractions at different frequencies. In Chapter 7, I discuss a number of directions in which this work should be extended.

Chapter 2

REVIEW OF ANATOMY

2.1 Introduction

This chapter will be concerned with the anatomy, both gross and microscopic, of the mammalian middle ear. Although my main interest in this thesis is the guinea pig, I shall also describe the ears of other species. The ears of the cat and human are of particular interest since much experimental and theoretical work has been done on both of them. (I shall not consider aquatic mammals at all, since their middle ears are very different from those of terrestrial mammals.)

The bony structure of the middle-ear cavities will be described first, followed by sections dealing with the tympanic membrane; the malleus and incus, and their articular and suspensory ligaments; the stapes; and the two middle-ear muscles. I shall not discuss the blood supply of the middle ear, nor the nature of its epithelial lining, since these are not relevant to the present work.

2.2 Bony Cavities

2.2.1 Introduction. The bony cavities of the middle ear are bounded mainly by three bones: the petrosal, the mastoid, and the tympanic. Roughly speaking, the petrosal bone forms the medial wall of the middle ear, the mastoid bone forms the roof, and the tympanic bone forms the lateral wall and the floor (see Fig. 1).

In all mammals the petrosal and mastoid bones are completely fused together to form the petrotic bone. In some mammals the petrotic and

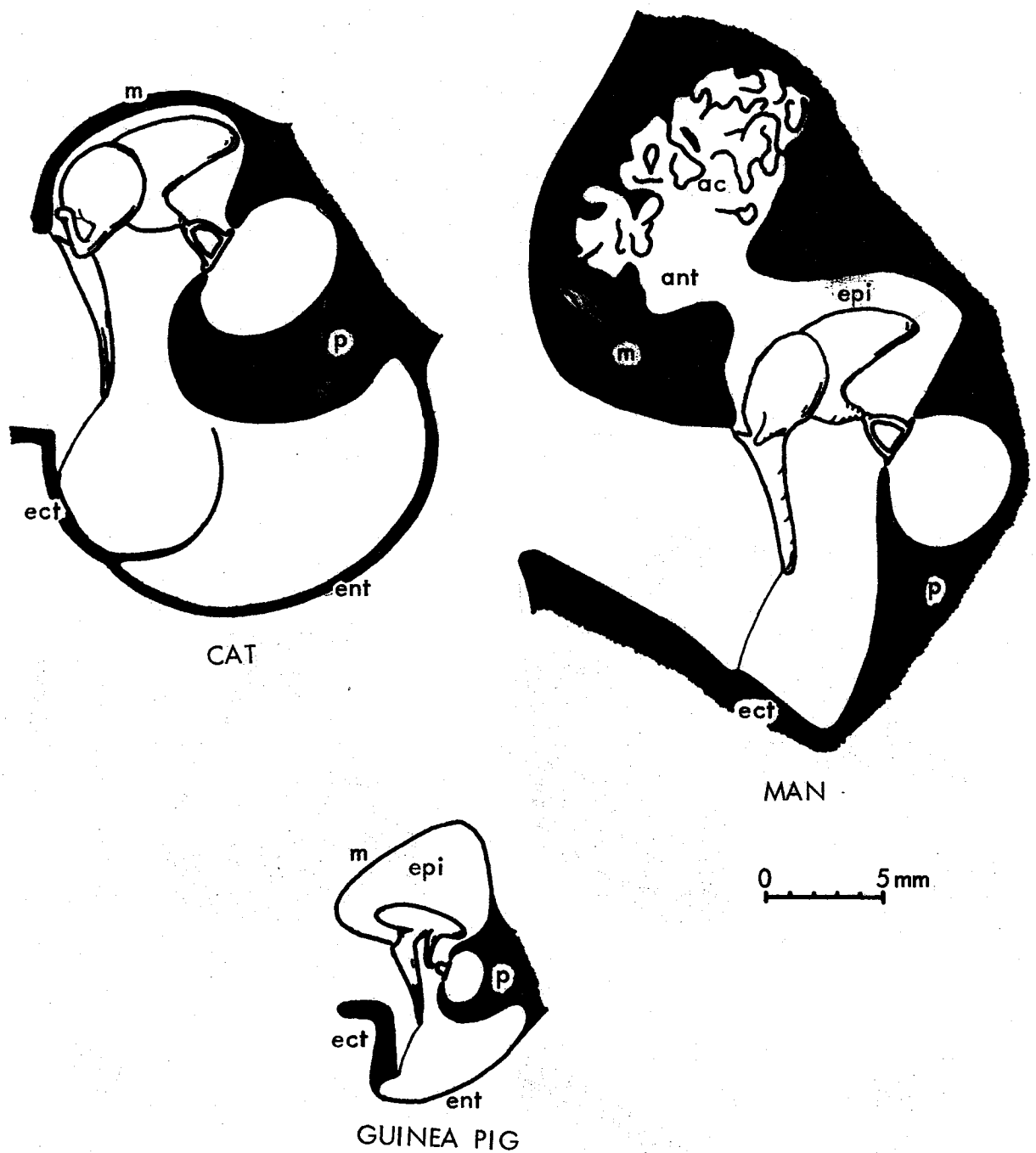


Fig. 1. Middle-ear bones and cavities of cat, man and guinea pig. For each species is shown, highly schematically, the anterior view of a section through the right ear. The scale shown is only approximate. ac=air cells of mastoid bone; ant=antrum; ect=ectotympanic bone; ent=entotympanic bone; epi=epitympanum; m=mastoid bone; p=petrosal bone.

tympanic bones are fused together and to the squamosal bone to form the temporal bone. It makes little difference, however, whether or not the various bones are actually fused in a particular species: the bones are in any case very close to one another in the living animal, so that they may be considered to function as a single unit. For the purposes of description, however, it is convenient to discuss them separately.

2.2.2 Petrosal. The petrosal (or petrous) bone is an extremely dense, hard bone which contains the cochlea and the vestibular system. It does not change very much from one mammalian species to another. Perhaps the most obvious variation is in the extent to which the cochlea protrudes into the middle-ear space. As shown in Fig. 1, the guinea-pig cochlea is almost completely exposed, while in the human the cochlea is practically completely buried in the petrosal bone. The number of turns in the cochlear spiral, and the relative sizes of the different turns, also vary from species to species.

2.2.3 Mastoid. The mastoid bone is not clearly differentiated from the petrosal bone in mammals, and varies greatly in form. Howell (1932) has suggested the following general account of the comparative anatomy of the mammalian mastoid. In animals with a large paraflocculus* the mastoid is a hard thin shell, and forms a distinct recess to hold the paraflocculus. The mastoid may become markedly cancellous, or porous, when the paraflocculus is reduced or the mastoid is enlarged. Even an enlarged mastoid bone may not be cancellous, however, as in species where it has expanded to form a large mastoid bulla.

In the guinea pig the mastoid bone is a thin shell forming two cavities.

* The paraflocculus is a part of the cerebellum, concerned with postural reflexes. It is particularly well developed in species that use a long tail for balancing.

The posterior one opens widely into the tympanic cavity. It is partially divided by a septum containing the facial canal, through which the facial nerve leaves the skull (see Fig. 20). The anterior mastoid cavity is the epitympanum, the floor of which opens into the tympanic cavity. This opening is largely blocked by the malleus and incus, whose bodies are in the epitympanum. In certain rodents with specialized ears, such as jerboas and kangaroo rats, the mastoid is greatly expanded to form a mastoid bulla. This bulla may be divided by bony septa into two or three chambers, each of which communicates with the middle ear. In some jerboas the mastoid bulla actually opens into the external ear canal, being separated from it by only a thin membrane in the living animal (Howell, 1932).

The mastoid of the cat forms a small epitympanum just large enough to hold the malleus and incus. There is a large cancellous part of the mastoid bone but this does not communicate with the middle-ear spaces.

In man the mastoid bone forms an enlarged epitympanum (or attic), as in the guinea pig. In addition, however, there is a large cancellous portion of the mastoid which communicates with the epitympanum through a restricted opening. The cancellous area consists of a central volume, the antrum, which is more or less clear, surrounded by the mastoid air cells (see Fig. 1b). The volume of air added to the middle ear by this region varies greatly, ranging from 0 to about 30 cm^3 in different individuals (Diamant, 1940; Flisberg, 1965).

In man the interior of the attic and antrum are crossed by many very delicate mucosal membranes, strands and folds. Proctor (1971), for example, has pointed out that the opening between the attic and the tympanic cavity is almost completely closed by mucosal folds. I have not been able to find any descriptions of such things in other species.

2.2.4 Tympanic. Ontogenetically and phylogenetically, the mammalian tympanic bone is considered to have two parts, the ectotympanic and the entotympanic. As a general rule, the ectotympanic part forms the bony portion of the external auditory meatus, and supports the circumference of the tympanic membrane, while the entotympanic part forms a large bulla. The form of the guinea-pig tympanic bone agrees with this description. In the cat, however, the ectotympanic bone forms a bulla of its own; a bony septum separates the ectotympanic and entotympanic cavities, and only a small opening is left between them. In man there is no bulla at all: the entotympanic bone is missing, and the ectotympanic encloses only a small volume of air in the middle ear (see Fig. 1).

2.3 Tympanic Membrane

The mammalian tympanic membrane is a shallow cone with the apex pointing inwards. It is composed of three layers: an outer epidermal layer, continuous with the epidermis of the external ear; the lamina propria; and an inner mucosal layer, continuous with the mucous lining of the middle ear. In the pars tensa, which includes most of the tympanic membrane, the lamina propria consists of four layers: a subepidermal layer of loose connective tissue; a layer of radial fibres; a layer of circular fibres; and a submucosal layer of loose connective tissue (Lim, 1968a; see Fig. 2). There are very few circular fibres near the centre of the drum. There are also, in addition to the radial and circular fibres, some "transverse" and "parabolic" fibres (Shimada and Lim, 1971) but these are relatively scarce.

In the pars flaccida, an area on the superior border of the drum (see Fig. 3), the lamina propria does not contain the regular arrays of fibres found in the pars tensa. The size and shape of the pars flaccida varies considerably

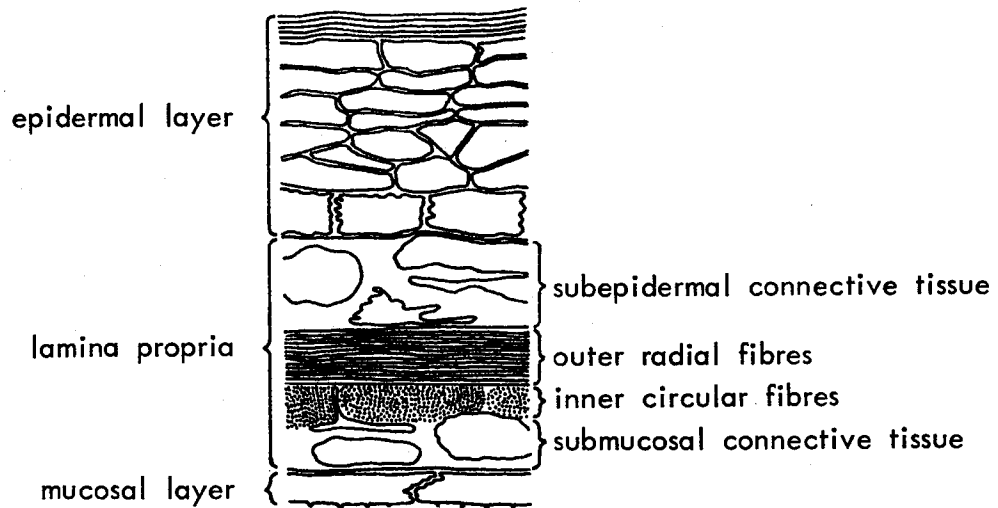


Fig. 2. Cross-sectional view of the tympanic membrane (pars tensa) of the squirrel monkey, schematically represented. (After Lim, 1968a)

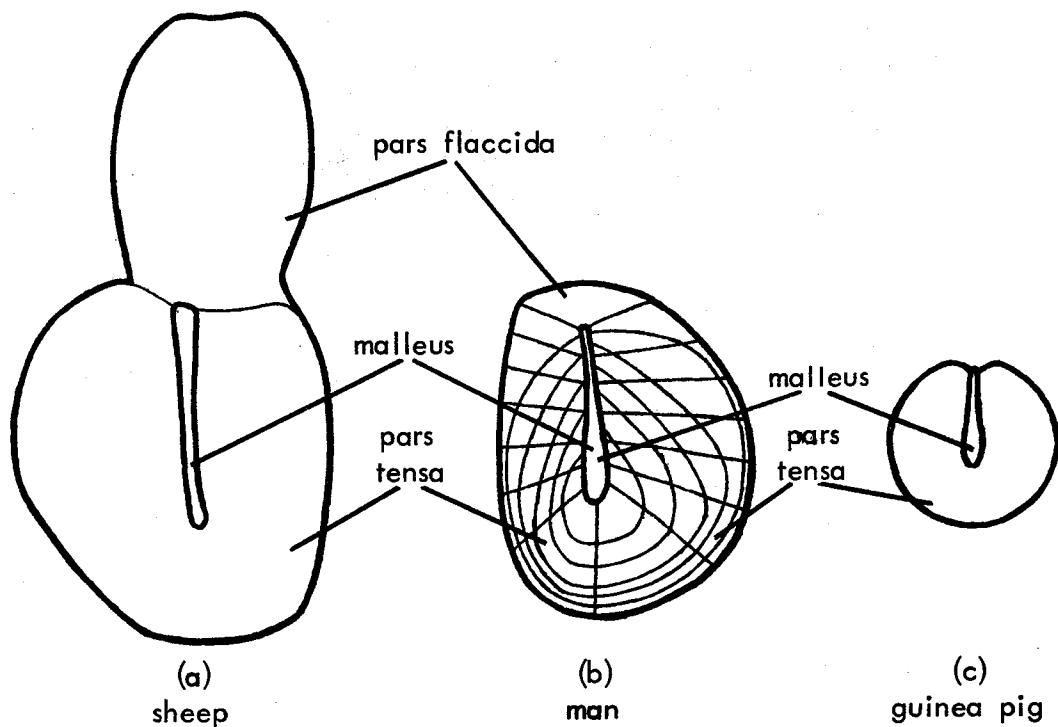


Fig. 3. Schematic drawings of the tympanic membranes of sheep, man and guinea pig. Note the variation in the size of the pars flaccida: it is very large in the sheep, smaller in man, and completely missing in guinea pig. Also indicated, in b, are the radial and circular fibres of the lamina propria. (a after Lim, 1968b; b after Filogamo, 1949)

between species (Lim, 1968b). In the guinea pig it is practically non-existent. In the cat, squirrel monkey, and man, it is a small triangular area between the superior border of the bony tympanic ring and the short process of the malleus. In the rabbit and sheep it is a large area with the shape of part of an ellipse (see Fig.3).

The pars flaccida apparently contains both collagenous and elastic fibres. Most of the fibres of the pars tensa of the cat and squirrel monkey present an ultramicroscopic appearance like that of collagen, although there is also an admixture of finer fibrils of uncertain nature. In the guinea pig there are only the finer fibrils (Lim, 1968a). Johnson *et al.* (1968) found that the fibrils in the guinea pig seem to be of a specialized protein having similarities to both collagen and elastin.

Békésy (1960, p. 194) has said that the eardrum of the calf consists of a very thick, gelatinous film. However, in a study of 20 mammalian species, Filogamo (1949) did not make note of any unusual characteristics of the bovine tympanic membrane.

2.4 Malleus and Incus

The typical mammalian malleus and incus are two separate ossicles (see Fig.4), their articular surfaces having the shapes of two matching saddles. The only known exceptions (Kobayashi, 1955a,b,c) are the guinea pig and the coypu, both being South-American rodents, in which the malleus and the incus are fused together.

The human ossicles have been studied more than those of other species. Two interesting points have emerged. The first is that these ossicles have some of the characteristics of both long and aerolar bones, combining both strength and lightness, particularly in the regions bearing the greatest mechanical

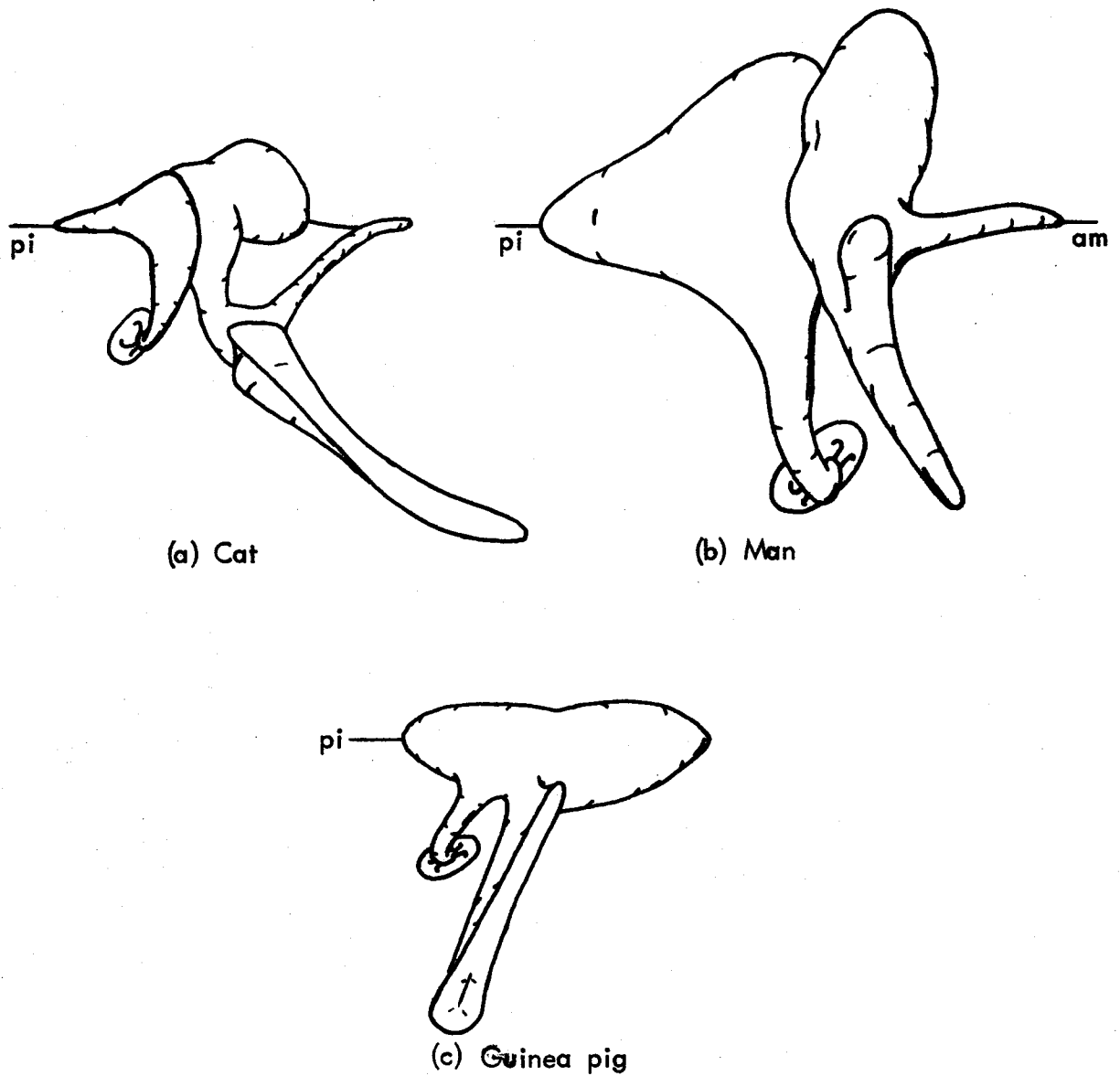


Fig. 4. Ossicles of cat, man and guinea pig (right ear, lateral view). Also indicated are the positions of the posterior incudal (pi) and anterior malleal (am) ligaments. (a after Jayne, 1898; b after Nager & Nager, 1953)

strain (Galioto and Marley, 1965). The second point is that there is often a distinct notch in the posterior process of the incus. This notch is sometimes so deep that it completely divides the tip of the process from the rest of the incus (Arensburg and Nathan, 1971).

The malleoincudal joint capsule (as well as the middle-ear-muscle tendons, the stapedial annular ligament, and the incudostapedial joint capsule) is "made up of elastic fibres, which is exceptional compared to other joints." (Myrhaug, 1963).

In most mammals the only true suspensory ligament of the malleoincudal complex is the posterior incudal ligament, which anchors the incus in the fossa incudis of the petrotic bone (Kobayashi, 1955a,b,c). In the horse and goat this ligament is missing, the incus being firmly fixed in place by cartilage and connective tissue. When the ligament does exist, it generally consists of an external and an internal bundle, as in the cat and human, but in some species there is only the external bundle. In still other species, including the guinea pig, the ligament is a broad fan-shaped structure (see Fig. 5).

In the human, in addition to the posterior incudal ligament, there are an anterior malleal ligament and a lateral malleal ligament (Kobayashi, 1955a,b,c). The former joins the anterior malleal process to the wall of the middle-ear cavity. In young mammals this process extends right to the wall, where it is fixed rigidly in the petrotympanic fissure. As the animal matures the process is partially resorbed (Legoux, 1961, p. 564). It is usually quite long even in the adult, but in man only a stump persists (see Fig. 4).

(It is frequently said that, in addition to the ligaments mentioned above, there exist also superior malleal and superior incudal ligaments. Kobayashi (1955a,b,c) found that these either did not occur at all, or were not true ligaments.)

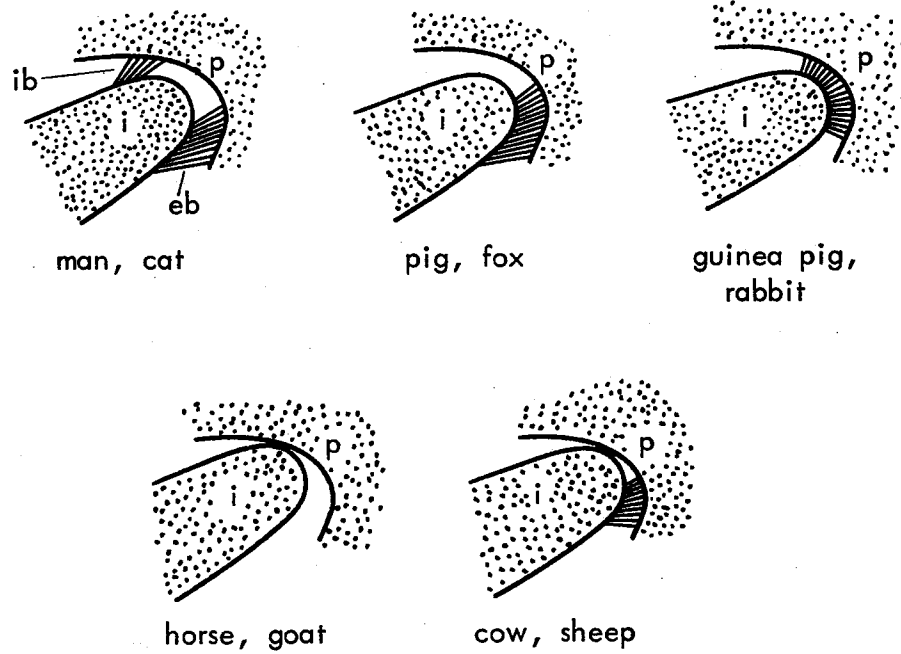


Fig. 5. Posterior incudal ligaments of various species, schematically represented. eb=external bundle of ligament; ib=internal bundle; i=incus; p=periotic bone. (Based on descriptions by Kobayashi, 1955)

2.5 Stapes

The stapes is relatively constant in form among mammals, consisting of a more or less oval footplate surmounted by an arch-like pair of crura.

The footplate is generally flat, but in gophers and kangaroo rats it bulges into the cochlear vestibule, sometimes being almost hemispherical (Howell, 1932).

The incudostapedial articulation is always a true joint (Kobayashi, 1955).

The footplate is usually held in the oval window by an annular ligament. The only known exception to this is the guinea pig, in which the articular surfaces are faced with cartilage, with no ligament between them (Kobayashi, 1955b). When the annular ligament occurs, it is generally wider on the superior border than on the inferior border. Both it and the incudostapedial joint capsule contain elastic fibres (Myrhaug, 1963).

2.6 Tensor Tympani Muscle

The main body of the tensor tympani muscle is buried in the petrosal bone. The tendon leaves the bone through a small canal, crosses the middle-ear cavity, and is inserted on the neck of the malleus (see Fig. 6). The body of the muscle consists of two portions: a cylindrical part inserted on the auditory (or Eustachian) tube, and a round part inserted on the petrosal bone. Only the auditory-tube portion is well developed in primates, whereas in ungulates and carnivores the auditory-tube part is completely missing. Rodents present a transitional situation (Kobayashi, 1956b). The ultramicroscopic structures of the two parts are different.

The tensor tympani is innervated by the mandibular branch of the trigeminal (fifth) nerve, through the otic ganglion. It also receives a few fibres from the tympanic plexus and from both the lesser and greater superficial

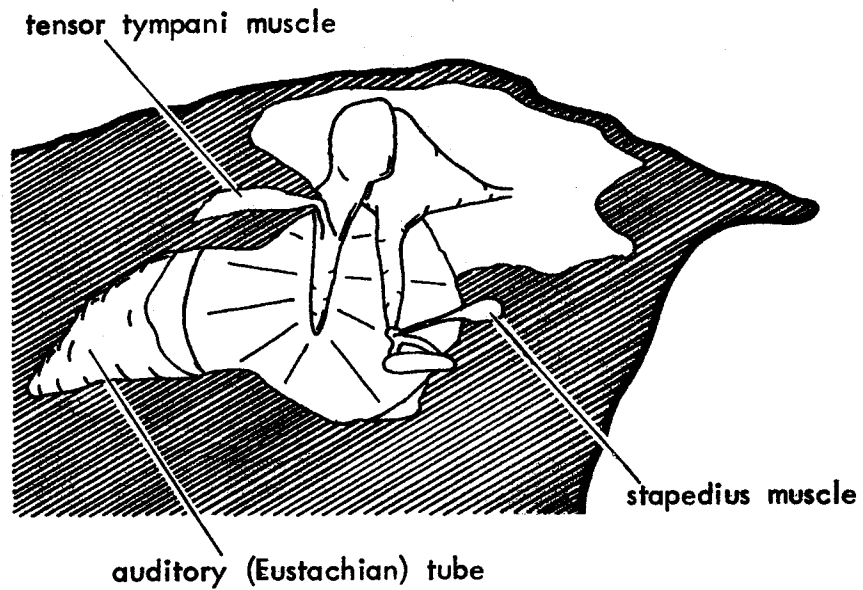


Fig. 6 . Medial view of a section of the right middle ear (human), showing the middle-ear muscles in their respective recesses in the petrosal bone. (After Deaver, 1900)

petrosal nerves (Filogamo et al., 1965, pp. 21-22).

Slow extrafusal muscle fibres have been reported to occur in the tensor tympani muscles of the cat and guinea pig (Hess, 1970; Seiden, 1971). The extraocular muscles are the only other mammalian skeletal muscles of which this may be said. Many fibres in the tensor tympani contain "atypical" (spiral and annular) fibrils; this also is as in the extraocular muscles (Filogamo et al., 1965).

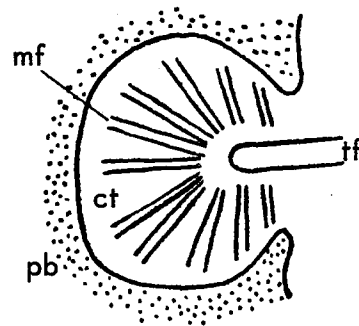
The human tensor tympani contains a few typical neuromuscular spindles, but this is apparently not the case in other species. There are structures which may be primitive proprioceptors (Filogamo et al., 1965). However, Seiden (1971) feels that some of these structures, for which sensory roles have been suggested, may rather be slow muscle fibres.

The tensor tympani muscle apparently shares a few muscle fibres with the tensor palati (Lupin, 1969). These two muscles are both synergetic with the jaw-closing muscles (Myrhaug, 1963), and are both innervated by the same branch of the mandibular nerve (Filogamo et al., 1965, p. 21).

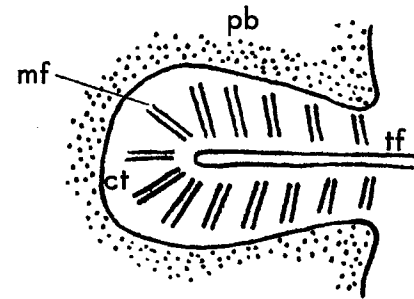
2.7 Stapedius Muscle

In most species the stapedius muscle lies in a recess in the wall of the middle-ear cavity. In the guinea pig, however, it sits on a small pedestal (Kobayashi, 1956a). Even in other species the shape of the body of the muscle varies somewhat (see Fig. 7). The tendon of the stapedius is inserted at the neck of the stapes (see Fig. 6).

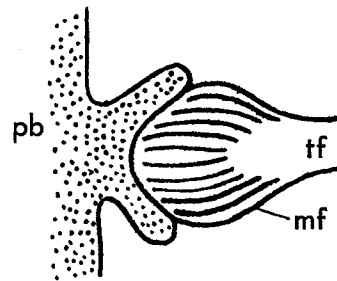
The stapedius muscle is innervated by the first motor branch of the facial (seventh) nerve. It often also receives a few fibres from the auricular branch of the vagus (Filogamo et al., 1965, p. 22). The muscle probably does not contain typical spindles, even in man, although there may be structures that serve a similar purpose.



cat, dog, etc.



man, monkey, sheep, etc.



guinea pig

Fig. 7. Stapedius muscles of various species, showing the different shapes of the muscles and the different methods of attachment to the petrosal bone. The insertion of the tendon onto the stapes is not shown. ct= connective tissues surrounding the exterior of the muscle; mf=muscle fibres; pb=petrosal bone; tf=tendinous fibres. (After Kobayashi, 1956a)

2.8 Conclusions

Two interesting points emerge from the preceding brief review of the anatomy of the middle ear. The first point, which may be significant in any consideration of the roles of the middle-ear muscles, concerns the similarities between the tympanic muscles and the extraocular muscles. As pointed out above, slow extrafusal fibres and atypical fibrils have been found in both cases. The tympanic muscles are also closer to the extraocular muscles than to ordinary skeletal muscle with regard to size of motor unit*, speed, and reaction to depolarizing drugs (Wersäll, 1958). It is possible that this similarity between the tympanic and extraocular muscles may correspond to some analogy between their functions.

The second point, which must be kept in mind when comparing studies of the middle ear in different species, concerns interspecific variations of the ear. In particular, the guinea pig is atypical in possessing neither a pars flaccida of the tympanic membrane, nor typical collagenous fibres in the tympanic membrane, nor a malleoincudal joint, nor a true annular ligament; and also in the method of anchoring the stapedius muscle to the petrosal bone. The human is atypical in the existence of the mastoid air cells communicating with the middle ear, in the existence of lateral malleal and anterior malleal ligaments, in the small size of the anterior malleal process, and in the existence of spindles in the tensor tympani muscle. The cat is atypical in possessing the large septum in its tympanic bulla. These species also differ in the gross structures of the posterior incudal ligament, of the tensor tympani, and of the stapedius muscle.

* The motor unit size is the number of muscle fibres per nerve fibre. It may be estimated from either anatomical or electromyographical data.

Chapter 3

REVIEW OF EXPERIMENTAL METHODS

3.1 Introduction

In this chapter I shall review some of the experimental methods which have been used to study the functioning of the middle ear. The methods to be discussed include: acoustical impedance measurements, which provide data about the input characteristics of the middle ear; displacement measurements, which can provide data about both the input and output of the middle ear; and cochlear-potential measurements, which provide data about the output characteristics of the system. I shall also discuss methods that have been used to stimulate the middle-ear muscles in order to study their effects. In Section 3.6 I shall present the reasoning behind the choice of experimental methods used in the present work.

3.2 Impedance Measurements

3.2.1 Introduction. Methods for measuring acoustical impedance have been divided by Beranek (1949, Chapter 7) into three categories: surface methods, transmission-line methods, and comparison methods. The surface methods involve measuring the sound pressure produced at a surface by a known volume velocity; they are discussed in Section 3.2.2. The transmission-line methods, involving analysis of standing-wave patterns or resonances, are tedious and time-consuming, and are not suitable for measuring constantly varying impedances like those of the middle ear. These methods have found little or no application in middle-ear research, and therefore I shall not

discuss them further. The comparison methods, treated in Section 3.2.3, include the use of acoustic or electroacoustic bridges.

A class of indirect impedance-measurement methods, which utilize anatomical knowledge about the middle ear, may be added to Beranek's three categories. Two such indirect methods are described in Section 3.2.4.

3.2.2 Surface methods. A fundamental method of measuring the acoustical impedance at a surface is to force a known volume velocity through it and measure the resulting sound pressure. This requires a high-impedance acoustic source and a high-impedance microphone. Møller (1965) used a half-inch condenser microphone for the acoustic driver and another for the pressure measurement; a rigid-walled tube coupled the two microphones to the ear. The characteristics of this tube were obtained by filling the middle ear with liquid; the impedance measurements then had to be corrected for the transmission-line behaviour of the tube.

Zwislocki (1957a) and Pinto and Dallos (1968) used two low-impedance transducers, with heavily damped narrow tubes in front of them; these tubes raised the effective transducer impedances enough to prevent loading of the acoustical source by the eardrum. This method does not require the time-consuming transmission-line corrections involved in Møller's method. Pinto and Dallos used their set-up as an electroacoustic bridge, balancing out the resting impedance of the ear using a variable phase shifter and a variable attenuator. They measured both components of the complex impedance, by means of a 90-degree phase shifter and two phase-sensitive demodulators.

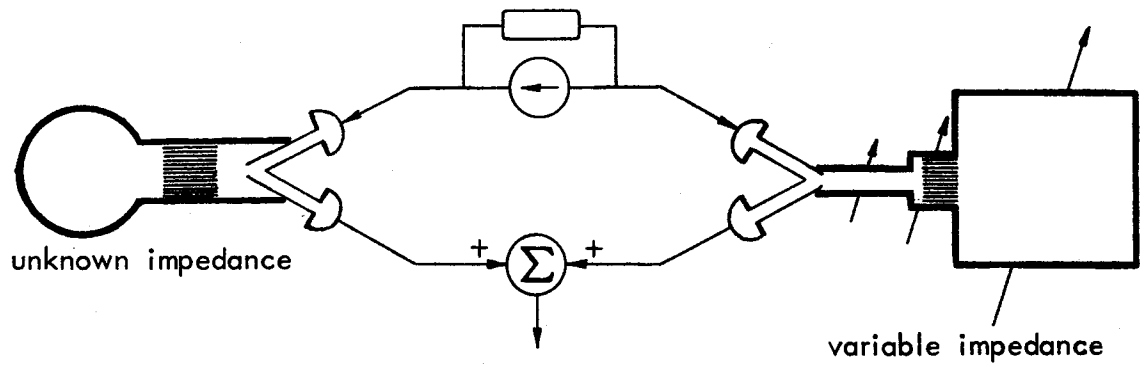
This method of measuring acoustical impedance, using two high-impedance transducers or their equivalent, is simple, requires no adjustments while the measurements are being made, can easily measure transient impedance changes, and can be computerized with little trouble.

3.2.3 Comparison methods. Bridges for measuring acoustical impedance may be either acoustic or electroacoustic bridges. An acoustic bridge compares the impedance to be measured with the impedances of variable acoustic elements such as cavities and tubes, while in an electroacoustic bridge the variable elements are electrical or electronic (see Fig. 8). An example of an acoustic bridge is the one designed by Zwislocki (1961) and manufactured by Grason-Stadler (model 3). This bridge provides both components of the complex impedance, but a calibration chart must be used to obtain the real (resistive) component. The bridge can be used only at low frequencies.

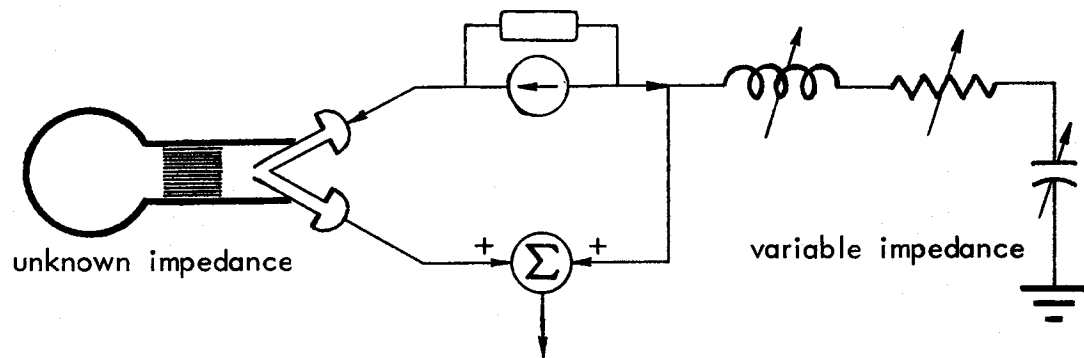
An example of an electroacoustic bridge is the one designed by Terkildsen and Nielsen (1960); it was manufactured by Madsen (model ZO61) and later modified (model ZO70). This bridge provides only the magnitude of the impedance, and can be operated at only one frequency (220 Hz). A more recent example of an electroacoustic bridge is the one described by Arguimbau and Grason (1971) and manufactured by Grason-Stadler (model 1720). This bridge is calibrated for both susceptance and conductance. It can only be used at two frequencies (230 and 690 Hz).

Zwislocki (1957a) measured impedance with a psychoacoustic bridge, in which the subject's auditory system was the detector. The method had the advantage of providing the impedance exactly in the plane of the eardrum, but was unreliable and tedious.

3.2.4 Indirect methods. Both Onchi (1961) and Mundie (1962) exploited the fact that part of the impedance of the middle ear is contributed by cavities whose volumes can be measured. Mundie simply measured the sound-pressure levels just outside the eardrum and inside the bulla (of the guinea pig). The latter measurement, along with the assumption that the middle-ear cavity acts as a pure compliance, gave a measure of the volume-velocity entering the



(a) Acoustic bridge



(b) Electroacoustic bridge

Fig. 8. Comparison of acoustic and electroacoustic bridges. In each case the variable impedance elements are adjusted until the output of the summer is zero.

cavity, at least at low frequencies. This volume velocity, in combination with the sound pressure just outside the eardrum, provided the input impedance.

Using the same principle in human temporal bones, Onchi first blocked the passage between the mastoid antrum and the epitympanum (cf. Fig. 1). This left only the tympanic cavity to affect the measurement, and permitted the assumption that the cavity acted as a pure compliance at all frequencies of interest. The impedance of the entire ear could then be obtained by a second measurement after unblocking the entrance to the antrum.

This method requires care to avoid damage when inserting probes into the middle-ear cavity. It also requires a fair amount of calculation to arrive at the actual impedance.

3.3 Displacement Measurements

3.3.1 Introduction. Many methods of measuring displacements have been used, or proposed, for studying the middle ear. In the following paragraphs I shall briefly discuss capacitive probes; direct observation under stroboscopic illumination; measurement of light reflection; two methods using coherent light, namely interferometry and time-averaged holography; and the use of the Mössbauer effect.

3.3.2 Capacitive probes. Many researchers have used capacitive probes in studying middle-ear vibrations (Békésy, 1960, pp. 53 ff.; Møller, 1963; Hoeft et al., 1964; Fischler et al., 1964, 1967; Tonndorf et al., 1966). The principle is to use the vibrating surface as one plate of a capacitor, the other plate being a small probe fixed with respect to the skull. The capacitance changes as a function of the distance between the plates, and can

be used to modulate a carrier signal, which in turn can be demodulated to provide a voltage proportional to the distance. Fischler et al. (1964) were able to measure displacements as small as 1 nm with this method. Both phase and amplitude data can be measured with a capacitive probe.

3.3.3 Direct observation. Vibratory displacements of the ossicles have been measured by direct microscopic observation (Mach and Kessel, 1874; Guinan and Peake, 1967). Small reflective silver particles were sprayed onto the ossicles to aid visualization. The use of stroboscopic illumination simplifies the displacement measurements, and also permits phase determination (Békésy, 1960, pp. 37 ff.; Guinan and Peake, 1967). Guinan and Peake achieved a resolution on the order of tens or hundreds of nanometres. The method is time-consuming and difficult.

3.3.4 Reflection of light. Jako et al. (1966) and Brask (1969) studied displacements in the middle ear by measuring the amount of light back-scattered from the structures of interest. The light was guided to and from the middle ear through fibre optics (see Fig. 9a). The curve of displacement against the amount of reflected light is linear in two separate regions. One of these regions ("C" in Fig. 9b) permits the measurement of displacements down to about 1000 nm (Brask, 1969); by using the other region ("A") one can resolve to about 20 nm (Jako et al., 1966).

3.3.5 Laser interferometry. Interferometry using coherent light from lasers is a popular method for measuring very small displacements. It has been applied to studies of the middle ear by Frei et al. (1966) and by Tonndorf and Khanna (1968). The set-up used by Frei et al. had frequency-sensitive characteristics; they obtained a sensitivity of 1 nm at 1 kHz. The

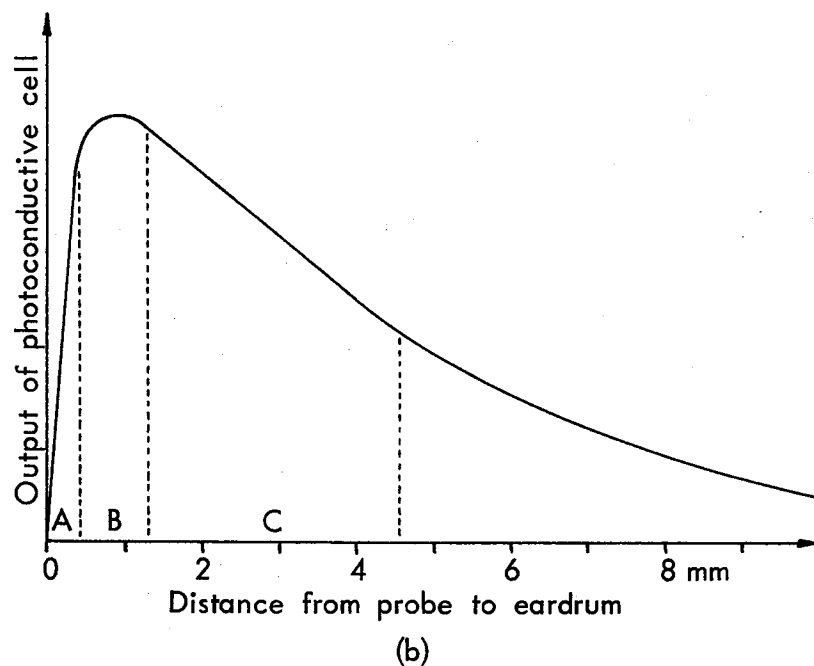
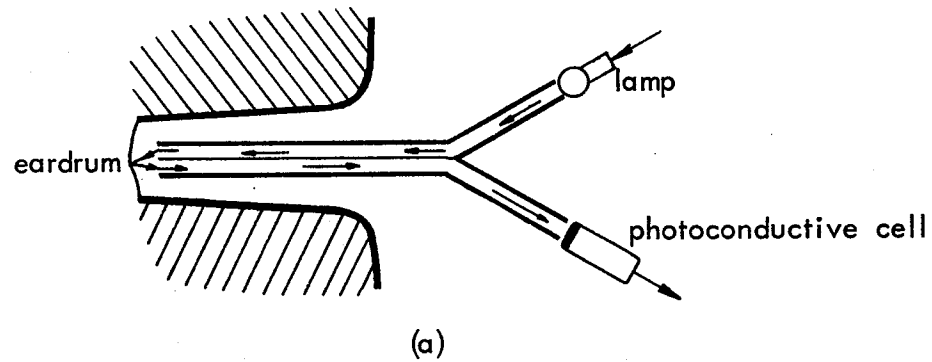


Fig. 9. Displacement measurement by reflected light. (a) schematic diagram of set-up, showing the fibre-optic probe inserted into the ear canal. (b) Plot of photo-cell output against displacement, showing the two linear regions A and C, discussed in the text. (After Brask, 1969)

method of Tonndorf and Khanna permitted a sensitivity of 0.003 nm, independent of frequency. This method can be used for nonsinusoidal vibrations, provides phase information, and can easily be calibrated absolutely (Khanna et al., 1968).

3.3.6 Time-averaged holography. If an object is vibrating sinusoidally while a hologram is being made of it, then the reconstructed image will show iso-amplitude contours. This effect has been used to study the vibration patterns of the tympanic membrane (Tonndorf and Khanna, 1970) and of the round-window membrane (Khanna and Tonndorf, 1971). The resolving power depends on the wavelength of the light used: the helium-neon laser used by Khanna and Tonndorf can resolve to about 100 nm. Time-averaged holography, "in its present form", does not provide direct phase information (Tonndorf and Khanna, 1971).

3.3.7 Mössbauer effect. Under certain conditions a radioactive source can emit gamma rays without recoil, so that the frequency of the radiation is fixed; the gamma rays can then be detected by a resonant absorber. Any motion of the source toward or away from the detector will produce a Doppler shift in the radiation frequency, and will reduce the efficiency of absorption. This effect, discovered by Mössbauer, has been used by several researchers to study the middle ear (Gilad et al., 1967; Taylor and Johnstone, 1970; Rhode, 1970). The method can measure velocities as small as 0.1 nm sec^{-1} (Rhode, 1970). Gilad et al. (1967) achieved a displacement resolution of about 0.2 nm at 1 kHz, but this required a detection time of 5 minutes.

3.4 Cochlear-Potential Measurements

The electrical output of the inner ear, in particular the cochlear microphonic potential, may be used as a measure of the mechanical output of the middle ear. To eliminate the uncertainties due to the internal characteristics of the cochlea itself, the method may only be used to measure changes in middle-ear function. Even then, care must be taken to avoid the nonlinear region of operation of the cochlea, and to ensure that the response characteristics of the cochlea remain constant with time; Guinan and Peake (1967) have discussed these matters in more detail.

3.5 Muscle Stimulation

3.5.1 Introduction. In order to study the effects of contractions of the middle-ear muscles, one can either apply mechanical forces directly to the muscles, or stimulate them to contract. Muscle contractions can be induced using drugs or electrical stimulation, or by eliciting either acoustic or non-acoustic reflexes. Alternatively, one can simply wait for spontaneous muscle contractions to occur.

3.5.2 Application of mechanical forces. Onchi (1961), Neergaard et al. (1963) and Cancura (1970) have applied small weights (up to 50 g) directly to the muscles, in order to measure the effect on middle-ear transmission. This procedure requires care, and necessarily involves opening the middle-ear cavities. In addition, it is difficult to correlate the results quantitatively with the normal behaviour of the muscles.

3.5.3 Drugs. The muscles may be made to contract by the intravenous use of drugs (Wersäll, 1958), but the effects depend on many factors, and are extremely variable. If one wished to measure cochlear potentials at the same time, the effects of the drugs on the cochlea itself would be a problem. It might be possible to avoid the problem by applying the drug directly onto the muscles, but this would involve considerable disruption of the middle ear, and great care would be needed to ensure that the cochlea was not affected (Vanderbeek, 1952).

3.5.4 Electrical stimulation. Electrical stimulation of the motor nerves supplying the muscles, or even of the muscles themselves, can be used to elicit contractions. It is quite difficult to reach appropriate places for stimulation, however; Wersäll (1958), for example, removed practically the entire middle ear in his experiments.

3.5.5 Acoustic reflexes. Perhaps the most obvious way of stimulating the middle-ear muscles is to utilize the acoustic reflex. Although a great deal of work has been done this way, especially in humans, most of it is only qualitative as far as concerns the effects of the muscles. The variables to be considered include the subject's hearing threshold and reflex threshold; whether the reflex being observed is ipsilateral or contralateral; and difference between species. In particular, the guinea pig appears not to have an acoustic middle-ear-muscle reflex (Perlman, 1960).

3.5.6 Nonacoustic reflexes. Middle-ear-muscle contractions can be elicited by nonacoustic stimuli, such as touching the external ear or puffing air at the eyes. Such methods are even more difficult to quantify than are methods involving acoustic reflexes.

3.5.7 Spontaneous[†] contractions. Spontaneous* contractions of the middle-ear muscles have been observed in unanaesthetized cats (Carmel and Starr, 1962; Simmons and Beatty, 1962). They have also been observed in guinea pigs, either anaesthetized or awake, but never in man (Perlman, 1960).

3.6 Conclusions

In choosing among the experimental methods discussed in Sections 3.2 to 3.4 above, the main requirements for the present project were that the technique should (1) disturb the middle ear as little as possible; (2) supply phase information, to back up the amplitude data; (3) lend itself to computerization; and (4) permit the measurement of the time courses of transient changes, with a view to studying muscle and reflex dynamics in the future. Impedance measurements using a high-impedance source meet these requirements, and also are easy to calibrate and use.

For investigating the effects of the middle-ear muscles, it was decided to take advantage of spontaneous muscle contractions since this does not involve disruption of the middle-ear cavities. Acoustic reflexes are not available in the guinea pig. The use of intravenous drugs, or the eliciting of nonacoustic reflexes, are just as difficult to quantify as are spontaneous contractions, and so offer nothing to offset their greater complexity.

* The contractions were spontaneous in the sense of not being responses to any obvious external stimuli. They were often associated with subsequent body movements or vocalizations.

Chapter 4

REVIEW OF MIDDLE-EAR FUNCTION

4.1 Introduction

After summarizing the over-all characteristics of the middle ear, I shall discuss the functioning of its various parts, following roughly the plan of Chapter 2. For each of these anatomical units I shall arrive at an analogous electrical circuit, based on the electroacoustic impedance analogy. According to this analogy, acoustical sound pressure (or mechanical force) corresponds to electrical voltage, while acoustical volume velocity (or mechanical displacement velocity) corresponds to electrical current (Olson, 1958).

The interconnections of the various anatomical units may be represented as in Fig. 10. The first block stands for the portion of the external ear which lies between the sound source and the middle ear itself. The current (or volume velocity) leaving this block must pass through the eardrum into the middle-ear cavities. In the process some of the current enters the malleo-incudal complex; thence it passes, with some losses in the incudostapedial joint, to the stapes and cochlea.

There are several places in this model where it would be strictly proper to put ideal transformers, both to represent the transitions between an acoustical system and a mechanical one, and to make explicit the various lever mechanisms of the middle ear. I have omitted these transformers, however, preferring at this stage of development of the model to absorb their effects into the parameter values.

Since I shall be discussing middle-ear function in terms of analogous lumped electrical circuits, it is important to know over what frequency range it is

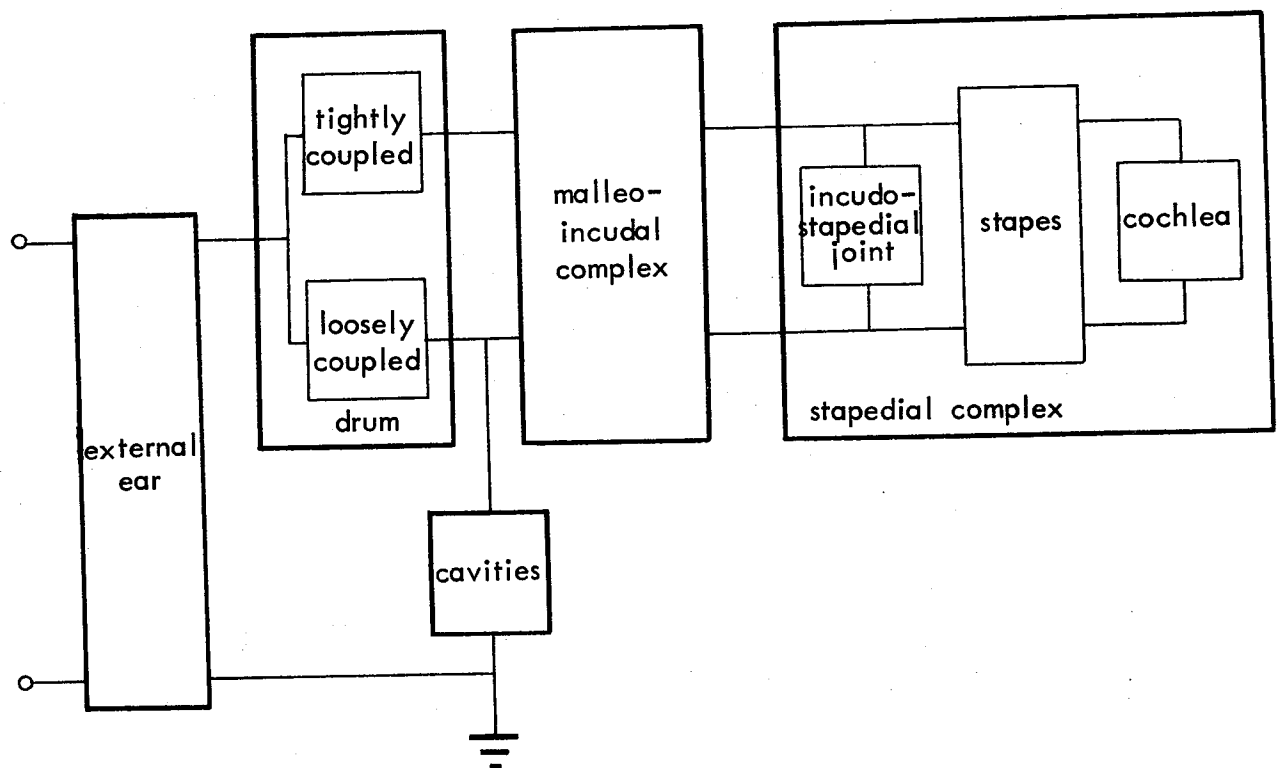


Fig. 10. Block diagram of the middle ear. See text for discussion.

legitimate to use lumped-parameter models. For example, Beranek (1954) says that for a closed tube to be modelled by a capacitor, the length (in metres) must be less than $30/f$ (where f is the frequency in Hz) for an accuracy of 5%. For a length of, say, 1 cm, which is typical of the guinea-pig middle ear, this constraint corresponds to an upper frequency limit of 3 kHz, which is rather low. Note, however, that an error of 5% corresponds to only 0.5 dB. If one can accept an error at the highest frequency of 1 dB, the upper frequency limit can be extended to over 10 kHz. An acceptable error of 2 dB means an upper limit of almost 15 kHz.

4.2 Over-all Characteristics

In Fig. 11 are shown representative input impedance data for man (Onchi, 1961), cat (Møller, 1965) and guinea pig (Mundie, 1962). (It should be remembered that there are considerable variations among individuals of the same species, as well as among species.) Note that at low frequencies the input impedance is essentially that of the middle-ear cavities: the impedance magnitude decreases at about 6 dB per octave, and the phase is constant at about -90° . At higher frequencies the mass and friction of the other structures become relatively more important. Some of the resonances and antiresonances are due to the shapes of the middle-ear cavities, while others are presumably due to the ossicular chain itself.

In Fig. 12 are shown measurements of the transfer characteristics of the cat middle ear (Guinan and Peake, 1967). The data were obtained by direct observation under stroboscopic illumination (see Section 3.3.3). The curves represent stapes volume displacement for constant sound-pressure level at the eardrum. The cochlea was intact for these measurements, and correction was made for the opening of the bulla. Similar data were obtained in the squirrel monkey using the Mössbauer effect (Rhode, 1971). The shapes of the curves at low

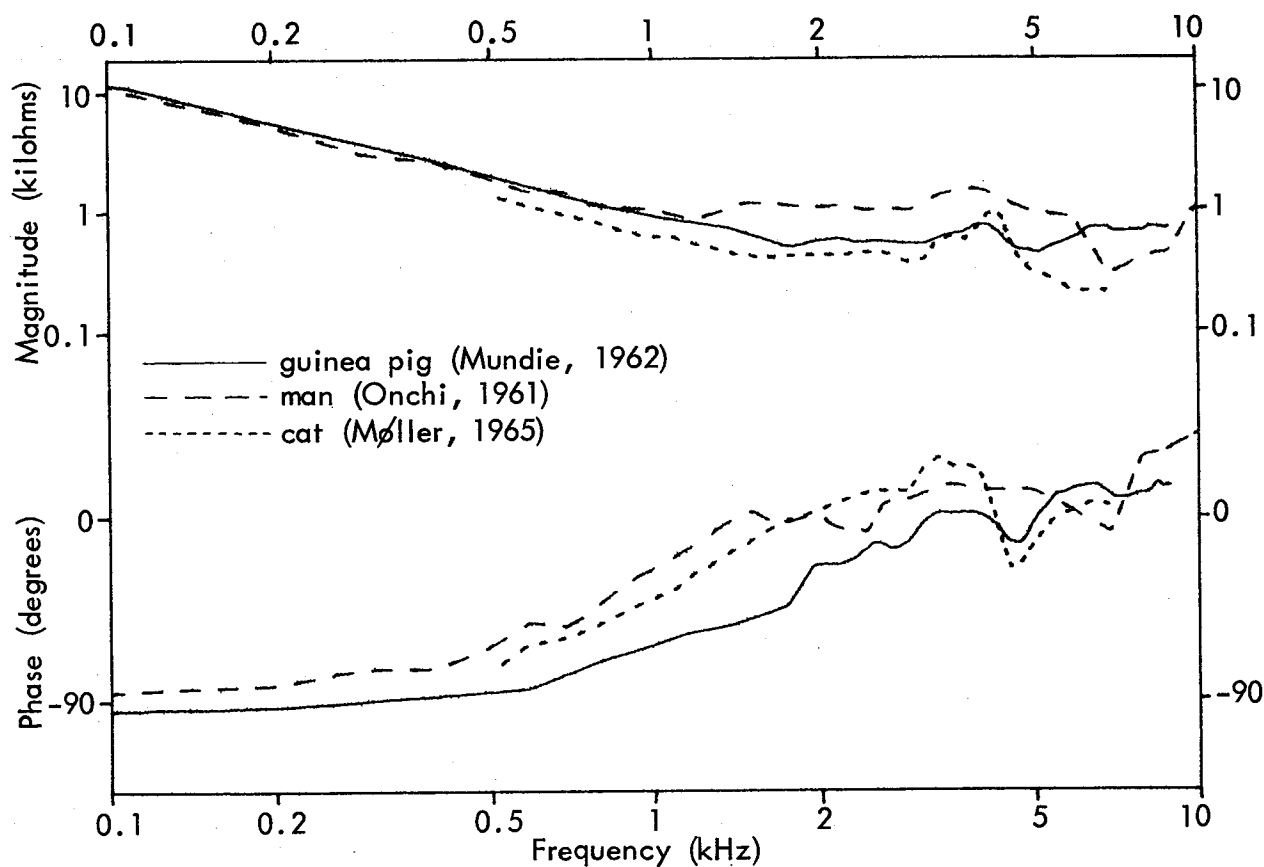


Fig. 11 . Acoustical input impedance of typical normal middle ears of guinea pig, man and cat.

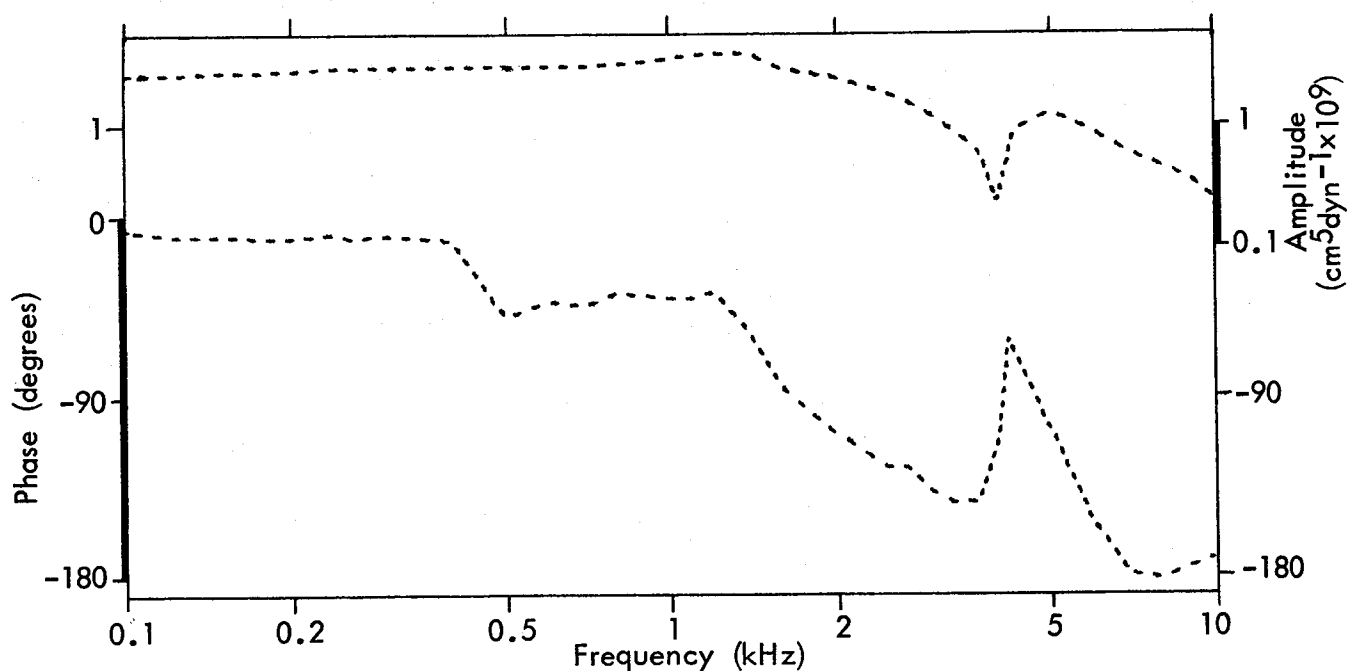


Fig. 12 . Transmission characteristics of a typical normal cat middle ear. The output is taken to be the volume displacement of the stapes (cm^3), the input is taken to be the sound-pressure level at the eardrum (dyn cm^{-2}). (Guinan & Peake, 1967)

frequencies is what would be predicted from the impedance data under the assumption that the drum and ossicles all vibrate in phase with each other. It is difficult to compare the transmission and impedance curves at high frequencies because of the great variability between individuals.

Taylor and Johnstone (1970) have reported Mössbauer-effect measurements of the transfer characteristics of guinea-pig, cat and frog middle ears. Their data do not agree with other such measurements, but until the details of their work are published it is difficult to explain the discrepancy.

The middle ear is linear up to sound pressures of at least 120 or 130 dB SPL (Mundie, 1962; Guinan and Peake, 1967). The resistance is more sensitive to sound-pressure level than is the reactance (Mundie, 1962).

4.3 Bony Cavities

The modelling of the cavities for any given species is straightforward: identify distinct chambers with capacitors, and the passages between the chambers with series R-L branches, as in Fig.13. The capacitance values

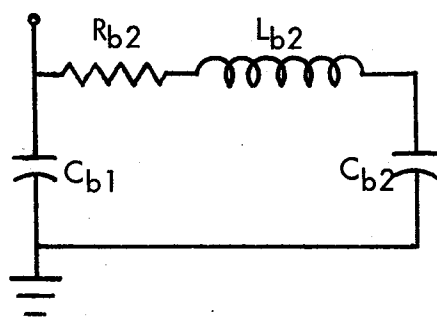


Fig. 13. Electrical circuit model of the middle-ear cavities. See text for explanation.

can be calculated from the chamber volumes. The resistance and Inductance values must be determined from measured frequency characteristics, since the inter-cavity passages are too irregular to permit calculating R and L.

For the human, C_{b1} represents the tympanum and epitympanum, while C_{b2} represents the mastoid antrum and air cells. Although the air cells have a complex form and could be more accurately modelled (Onchi, 1961), it is probably sufficient

simply to include their volume with that of the antrum since at high frequencies, where their form is more critical, the increasing reactance of L_{b2} will tend to isolate them from the tympanum (Zwislocki, 1962).

In the cat, C_{b1} and C_{b2} represent the ectotympanic and entotympanic cavities, respectively. In the guinea pig, they represent the tympanum and epitympanum, respectively. The posterior mastoid cavity of the guinea pig (see Section 2.2.3) is included in C_{b1} , since it opens very widely into the tympanic cavity.

As an example of the effects of the resonance and antiresonance introduced by the middle-ear cavities, Fig. 14 shows transmission characteristics calculated using the model of Peake and Guinan (1967) for the cat. The solid lines indicate the normal characteristics, while the dashed curves show what would happen if the bullar septum (see Fig. 1) could be removed without otherwise altering the middle-ear cavities. It can be seen that the existence of the septum has markedly decreased the transmission at 4 kHz, while raising it slightly at higher frequencies. (Note that these curves represent the transmission characteristics of the middle ear itself. As pointed out below, in Section 7.1.1, it would be necessary to take into account the impedance of the external ear before drawing conclusions about the effect on hearing of removing the bullar septum.)

In the living animal the middle-ear cavities are criss-crossed by mucosal strands and folds, some of them carrying blood vessels or nerves. Their possible acoustical effects have never been investigated. I shall follow past practice by ignoring them in this work.

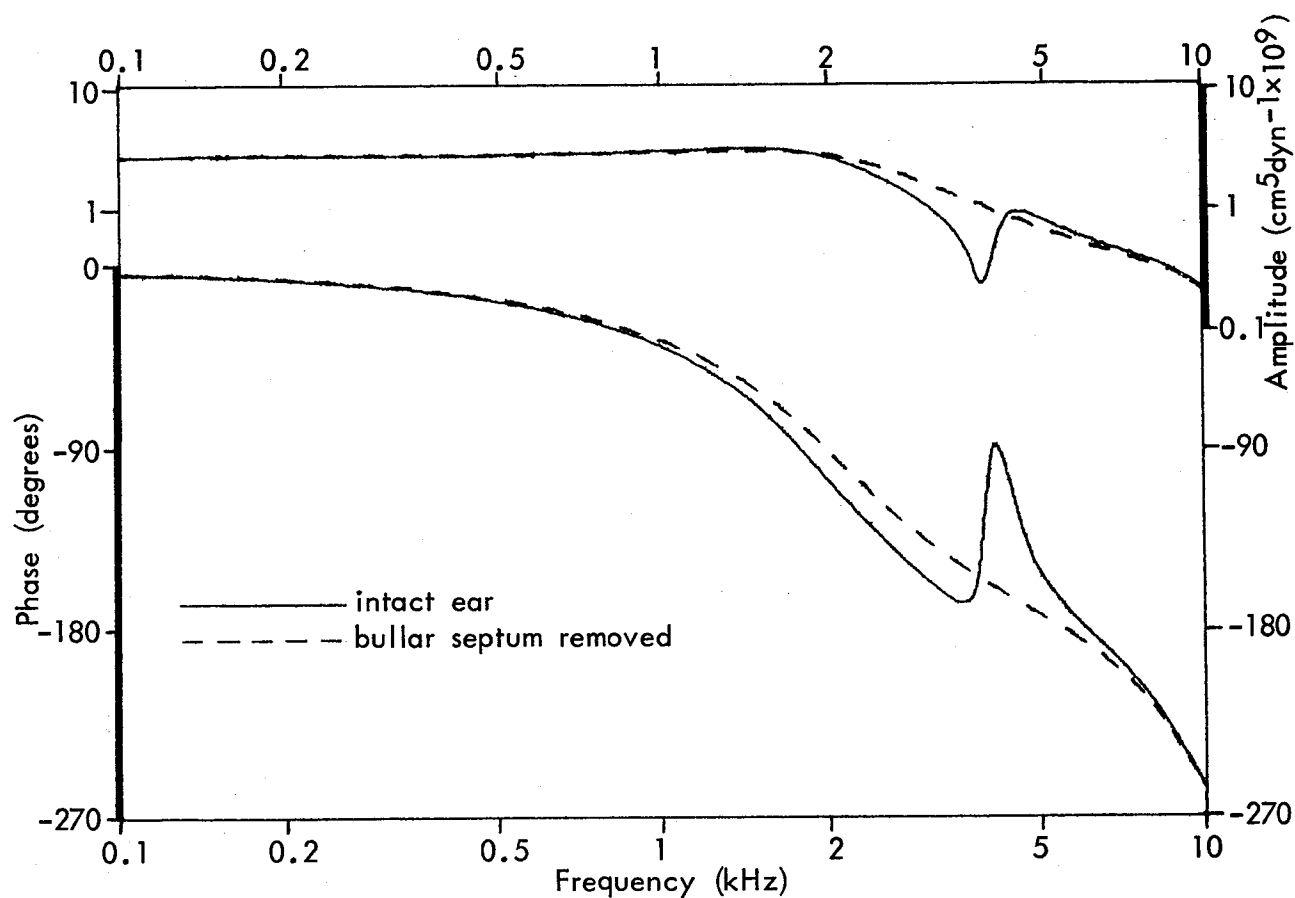


Fig. 14 . Transmission characteristics of the cat middle-ear model of Peake and Guinan (1967); cf. Fig. 12. The output is volume displacement, the input is sound-pressure level. The solid curves represent an intact ear, while the dashed curves represent the same ear but with the bullar septum removed, as described in the text.

4.4 Tympanic Membrane

At low frequencies the entire surface of the tympanic membrane vibrates in phase. Tonndorf and Khanna (1970) found that in the cat this pattern occurs at frequencies below about 1.5 kHz. Above that frequency the vibration pattern becomes more complicated, and above 3 kHz the malleus appears to be driven directly by the sound pressure, the drum acting more or less as a baffle. McArdle and Tonndorf (1968) found that below about 3 kHz parts of the membrane near the base of the manubrium are more closely coupled to the ossicular chain than are parts nearer the tip of the manubrium.

Onchi (1961), Møller (1961) and Zwislocki (1962, 1963) have all modelled the tympanic membrane in two parts: one part tightly coupled to the malleus, and one part less tightly coupled, through which energy may enter the middle-ear cavities directly, bypassing the ossicles. Only Peake and Guinan (1967), in their model for the cat, did not find it necessary to include the possibility of shunting energy past the ossicles. It is important to remember that there may well be species differences in this respect, particularly in view of the statements of Békésy (1960, pp. 192-197) concerning differences between the tympanic membrane of man and those of calves and sheep (see Section 2.3 above).

Helmholtz (1868) suggested that the curvature (Fig.15) of the tympanic

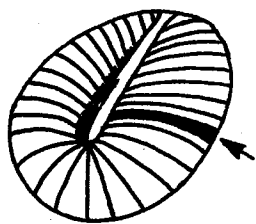


Fig.15. Lateral view of left tympanic membrane of the cat, showing its curvature (arrow). (After Tonndorf & Khanna, 1970)

membrane contributes to the lever ratio of the middle ear. Esser (1947) developed the idea, mathematically analyzing such a system. Békésy (1960, p.96) discounted the hypothesis, based on his own observations of the elasticity of the drum. Wever and

Lawrence (1954) tried to repeat the experiment that Helmholtz used to support his idea, and they obtained different results. Hartman (1971) feels that the discrepancy was due to a computational error by Helmholtz.

Although all of this appears to discredit Helmholtz' hypothesis, Tonndorf and Khanna (1970) have found reason in their holographic observations of the cat tympanic membrane to revive the curved-membrane hypothesis. For the present purposes, however, it matters little since the mechanisms of the middle-ear lever are not being made explicit in the model.

4.5 Malleoincudal Complex

The malleus and incus appear to rotate about an axis joining the anterior malleal and posterior incudal processes (see Fig. 4). There is some evidence that, at least in the cat, the malleus and incus do not always vibrate as a rigid body, due either to movement of the malleoincudal joint or to flexibility of the bones themselves (Tonndorf and Khanna, 1967; Guinan and Peake, 1967). In the guinea pig, however, Gilad *et al.* (1967) found no relative motion of the malleus and incus; certainly there can be no flexion of the malleoincudal joint since the two bones are fused together.

The guinea-pig malleoincudal complex may thus be modelled as a series R-L-C branch, following Zwislocki (1963). The inductance represents the moment of inertia of the pair of ossicles, while the resistance and capacitance represent the frictional and elastic forces in the suspensory ligaments and in the tensor tympani muscle.

4.6 Stapedial Complex

Many authors have considered the stapes to rotate about the inferior border of the footplate, as is suggested by the anatomy of the annular ligament; Møller (1961) treats it this way in his model of the human ear. More recent experimental data have suggested that the stapes vibrates like a piston in the oval window (Guinan and Peake, 1967; Dankbaar, 1970). In either case the stapes may be modelled as a series R-L-C branch, with the inductance representing its mass (or moment of inertia, if it rotates), and the resistance and capacitance representing the combined effects of the annular ligament and stapedius muscle.

The incudostapedial joint appears anatomically to be fairly flexible. Experimental work seems to indicate, however, that there is no slippage at the joint (Guinan and Peake, 1967; Rhode, 1970). Therefore, following Zwislocki (1962), I shall not include the incudostapedial joint in the model of the guinea-pig middle ear.

The load presented by the cochlea is considered by Zwislocki (1962) to have both resistive and reactive components, but to be mainly resistive. In any case it can be combined with the model for the stapes, so that the whole stapedial complex may be modelled as a single series R-L-C branch.

4.7 Muscles

It is difficult to compare quantitatively the results of different researchers on the effects of the middle-ear muscles. The difficulty is due to differences of experimental technique, to the problems of stimulating the muscles reproducibly, and to the differences among species and individuals. It may be said, however, that at low frequencies a contraction of either muscle will increase

the input impedance and decrease the efficiency of transmission; the tensor tympani generally seems to have less effect than the stapedius. At higher frequencies the effects are less, and the input impedance can increase or decrease; the same is true for the transmission efficiency.

Neergaard et al. (1963), by applying weights to the muscles, found that the stapedius tends to produce a positive phase shift in the middle-ear transmission (that is, a change in the direction of increased stiffness), while the tensor tympani produces little phase shift. I am not aware of any other published data concerning the phase effects of the individual muscles.

Onchi (1961) found, in the human, a fibrous fixation of the tendon where the tensor tympani leaves its bony canal. He suggested that the tensor tympani serves only to provide stiffness to the ossicular chain, since the fixation of its tendon to the surrounding bone would seem to prevent it from changing the characteristics of the chain. However, later authors have described impedance changes due to contractions of the tensor tympani in man (Djupesland, 1969).

Perlman (1960) felt that the muscles in the human have no effect on middle-ear transmission when they are at rest, but Simmons (1959) found in the cat that they increased the stiffness of the ossicular chain, as compared to the stiffness of the chain when the muscles were completely relaxed due to anaesthesia.

In the middle-ear model the effects of the tensor tympani and stapedius muscles can be represented by changes in the elasticities and resistances of the branches representing the malleoincudal complex and the stapedial complex. Although it is possible that the muscles affect the effective masses of the ossicles, perhaps by modifying the rotational axes of the ossicular chain, such effects are probably secondary to the changes of elasticity and resistance.

4.8 Conclusions

In light of the above discussion, the guinea-pig middle ear may be modelled as shown in Fig.16a.(cf. Fig.10). By combining the four R-L-C branches corresponding to the part of the drum coupled to the ossicles, the malleoincudal complex, the stapes, and the cochlea, one obtains the simplified circuit of Fig.16b. This is adequate for the present purposes since my experimental impedance data does not provide means of separating the effects of these four blocks.

In the final model, C_e corresponds to the volume of the external ear canal between the acoustic driver and the tympanic membrane. C_{b1} represents the volume of the tympanic bulla, while C_{b2} represents the volume of the epitympanum; R_{b2} and L_{b2} stand for the passage between these two cavities. R_d , L_d and C_d represent the part of the drum that is not tightly coupled to the ossicles, while R_o , L_o and C_o represent the ossicular chain itself. The effects of the muscles are represented by the variability of R_o and C_o .

The middle-ear model presented here is essentially the same as that of Zwislocki (1963), except that his cochlear resistance (R_c) has been absorbed into R_o , and R_o and C_o have been made variable to account for the muscles. The topology of the model has been rearranged to better suit the actual mechanoacoustical system, but this does not affect the behaviour of the model.

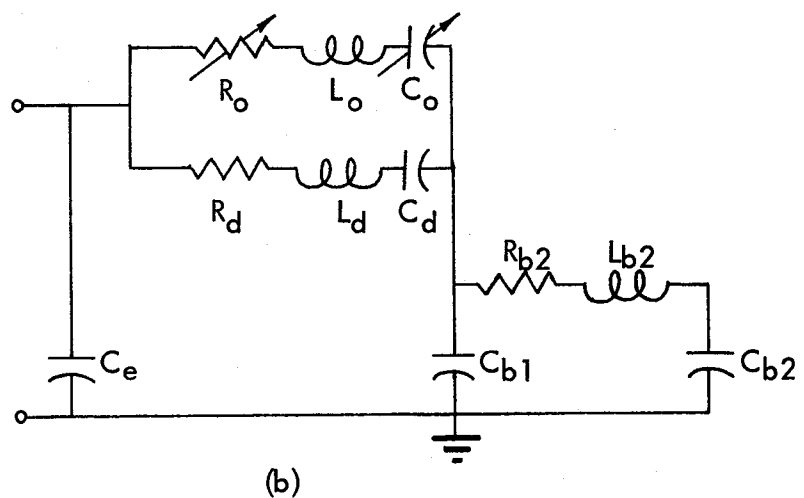
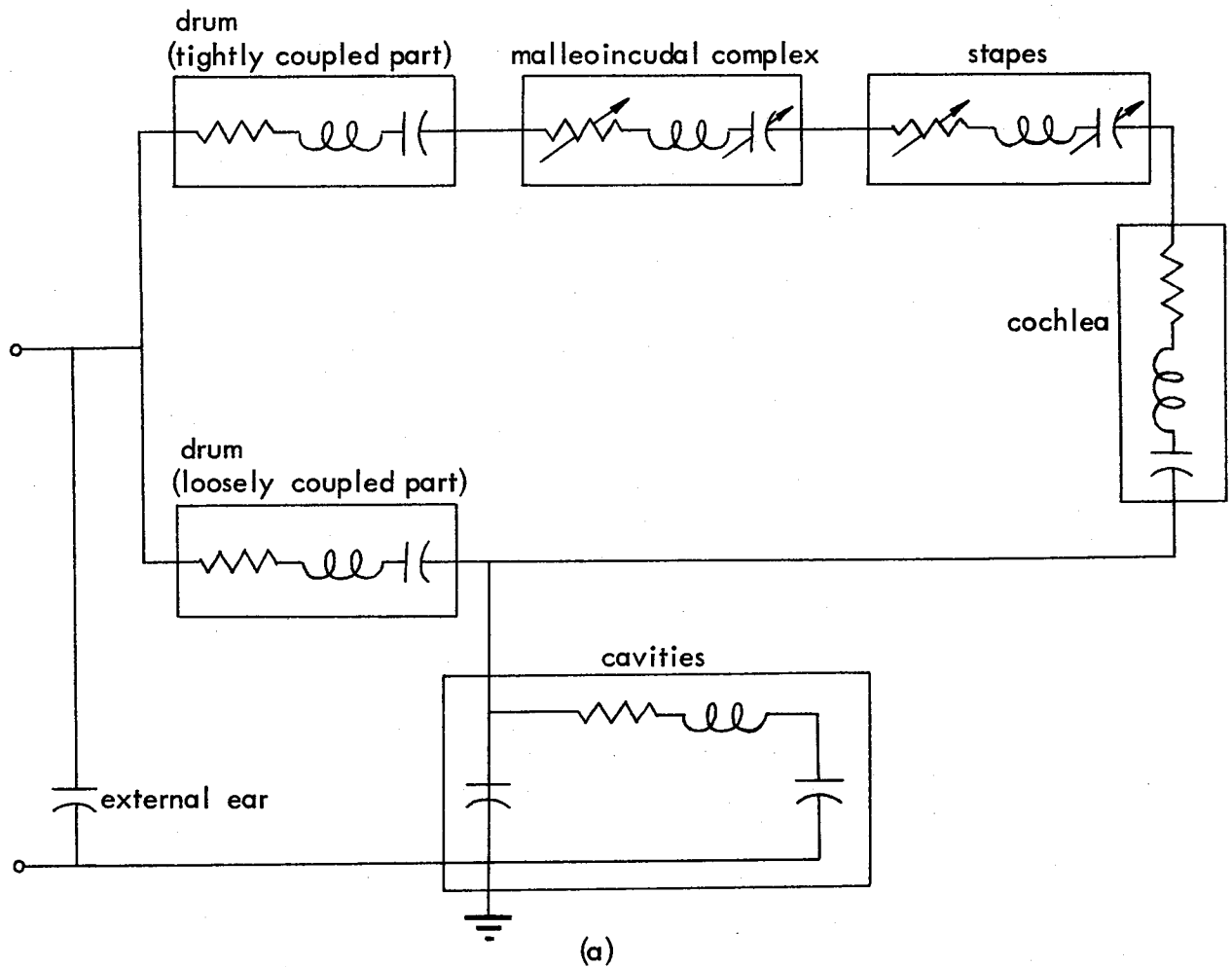


Fig. 16. Electrical circuit models of the middle ear. a shows the model arrived at in the review of middle-ear function. b shows the same model but with the four R-L-C branches corresponding to the cochlea, the ossicles and part of the drum combined into one R-L-C branch. The variable elements represent the effects of muscle contractions, as discussed in the text.

Chapter 5

EXPERIMENTAL METHOD

5.1 General Description

As pointed out in Section 3.6 above, I have chosen to measure the acoustical impedance of the guinea-pig ear using a high-impedance driver and a high-impedance microphone. A block diagram of the over-all set-up is shown in Fig.17.

The sinusoidal signal is generated by an oscillator with discretely variable frequency (Hewlett-Packard 4204A), fed through adjustable attenuators (0-111 dB in 0.1-dB steps), and amplified (McIntosh MC75). The signal is then applied, along with a 200-VDC polarizing voltage, to a half-inch condenser microphone cartridge (Brüel & Kjaer 4134). The mounting, testing and use of this cartridge as a high-impedance acoustic driver are discussed in Section 5.2.

The sound-pressure level just outside the animal's tympanic membrane is monitored using a half-inch condenser microphone (Brüel & Kjaer 4134), with a plastic-and-metal probe tube attached. A 2-cm length of cotton thread is put inside the probe tube for damping. The probe tube is placed in a hole drilled in the guinea pig's tympanic bulla after exposing the bulla surgically (Laszlo, 1970).

The microphone output is amplified by a third-octave spectrum analyzer (Brüel & Kjaer 2111). (The third-octave filters are only used for the measurement of transient impedance changes, the spectrum analyzer being used as an ordinary amplifier most of the time.) The amplifier output, and the reference signal, are then sampled and analyzed by the computer (DEC PDP-12) as described in Section 5.3.

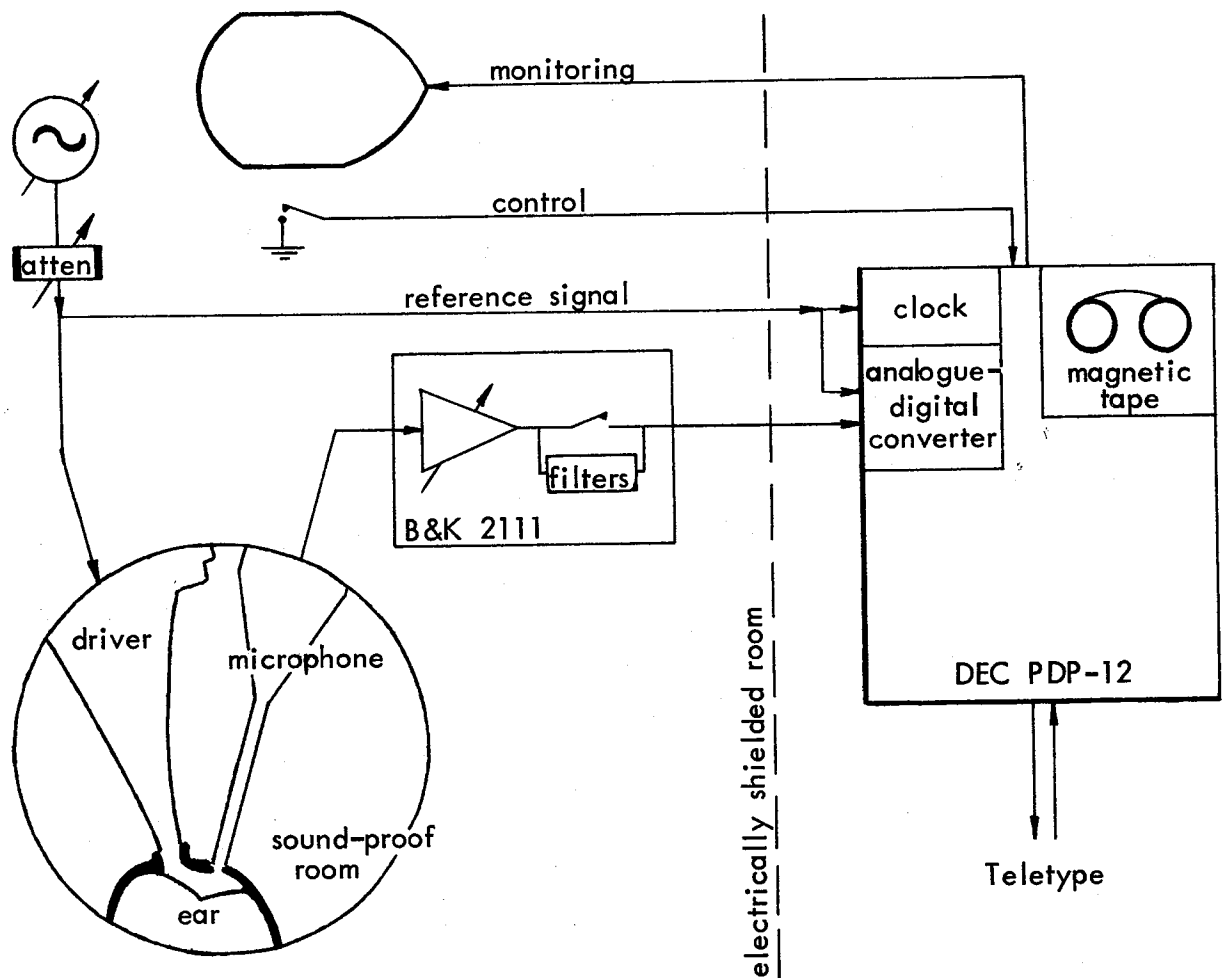


Fig. 17. Impedance-measurement instrumentation, as described in the text.

The usual experimental procedure starts with the exposure of the right tympanic bulla, and removal of the pinna and concha. This is done under Nembutal (Abbott) anaesthesia ($0.7 \text{ cm}^3 \text{ kg}^{-1}$ initial dose, intraperitoneal). The animal's rectal temperature is monitored throughout the surgery and the measurements by an electric thermometer (Yellow Springs 43TF). A hot-water bottle is used to keep the temperature between 37 and 38.5°C .

When the surgery is complete the animal is removed to the sound-proof room, the acoustical driver and microphone are clamped into place, and a curve of impedance against frequency is measured. Transient impedance changes are then observed at various frequencies. Periodically the frequency characteristic is remeasured throughout the course of the experiment. At the end of the experiment the tympanic membrane is destroyed and removed as much as possible, and another frequency response is obtained. This response includes only the effects of the middle-ear cavities themselves, and permits the calculation of their volumes (see Section 6.2.2).

After the last impedance measurements the animal is killed with an overdose of Nembutal, and the ears are dissected out and left to dry in the air. At a later date castings are made of the middle-ear cavities, as described in Section 5.4. This permits an independent measure of the volumes of the cavities.

It should be noted that the acoustical impedance measured with the above procedure is not that of the middle ear alone, but includes also the effect of the small volume between the end of the acoustical driver and the eardrum. This volume is on the order of 0.04 cm^3 , and must be taken into account before comparing the data with published middle-ear impedance measurements. Note that the indirect impedance-measuring method of Onchi (1961) and Mundie (1962), described in Section 3.2.4 above, avoids this problem of needing to know the volume between the source and the eardrum, but the

price is that one must know the volume of the tympanic cavity itself. The indirect method is also more difficult to carry out than the method used here, and entails a greater risk of changing the characteristics of the middle ear through damage or fluid seepage.

A considerable amount of programming effort has been necessary in developing the set-up used in these experiments. It may be worth noting that many of the resulting programmes are of general usefulness beyond their immediate application in this project. This applies particularly to the amplitude-and-phase-measurement programme, which may be used for measuring many types of signal besides acoustical impedance, and to various utility programmes that have been developed or modified (such as Funnell, 1971, 1972a,b).

5.2 High-Impedance Driver

The driver used in this study is a half-inch condenser microphone cartridge (Brüel & Kjaer 4134) feeding into a small-bore plastic tube. Cotton thread in the tube provides acoustical damping. The plastic tube is coupled to the cartridge by a standard 2-mm probe adaptor (Brüel & Kjaer DB0242). The electrical connection to the cartridge is by a spring-loaded brass contact in an aluminium holder, patterned after the standard microphone-preamplifier connection.

The behaviour of a condenser microphone cartridge is such that the volume displacement of its diaphragm is directly proportional to the applied voltage. Thus in the present experiment, in which the amplitude of the applied voltage is independent of frequency, the driver actually acts as a constant-volume-displacement source rather than as a constant-volume-velocity source. This is not a problem, however, since volume velocity can be calculated from volume displacement simply by multiplying by $j\omega$ ($=j2\pi f$).

To ensure that the driver will actually act as a constant-volume-displacement source under the present conditions, it is necessary to determine whether its internal impedance is sufficiently high compared to the impedance of the load that will be used. According to the manufacturer the microphone cartridge has an acoustical impedance equivalent to an air volume of about 0.01 cm^3 . To this must be added about 0.02 cm^3 , representing the volume of air enclosed in front of the diaphragm by the probe adaptor and plastic tube,

less the volume of the cotton thread in the tube. Thus the internal impedance of the driver has a capacitive component equivalent to less than 0.03 cm^3 , plus resistive and inductive components due to the tube and its damping. This equivalent volume is small compared to a typical guinea-pig middle-ear volume of 0.25 cm^3 (Mundie, 1962). At high frequencies the effective volume of the middle ear may drop by a factor of ten or more, but there will also be an increase of the driver impedance due to the inductance of the tube.

It would thus appear that the internal impedance of the driver may be sufficiently high to qualify the driver as a constant-volume-displacement source for this application. To check this further I measured the sound-pressure levels produced by the driver in cavities of various sizes. If the cavities act as ideal capacitors, then the driver should produce sound-pressure levels which are independent of frequency but inversely proportional to the cavity volumes. In Fig. 18 is shown the sound-pressure level as a function of frequency for a 0.39-cm^3 cavity. The curve is everywhere within 5 dB of the straight line representing an ideal volume-displacement source. The departures from a straight line are characteristic of the source itself, and are not due to interactions with the load. This was shown by measuring the sound pressures produced in three other cavities. One of the three had the same volume as the one mentioned above (0.39 cm^3) but a different shape; the other two had smaller volumes (0.24 and 0.13 cm^3). The sound pressures produced in these three cavities, relative to that produced in the original 0.39-cm^3 cavity, are shown in Fig. 19. These curves are very flat, demonstrating that the volume-displacement output of the driver is not dependent on the load. The sound pressures at high frequencies are within a fraction of 1 dB of the pressures predicted from the cavity volumes. The curves depart more noticeably from the predicted straight lines at low frequencies, where the inductive reactance of the driver tube is small, and at very high frequencies,

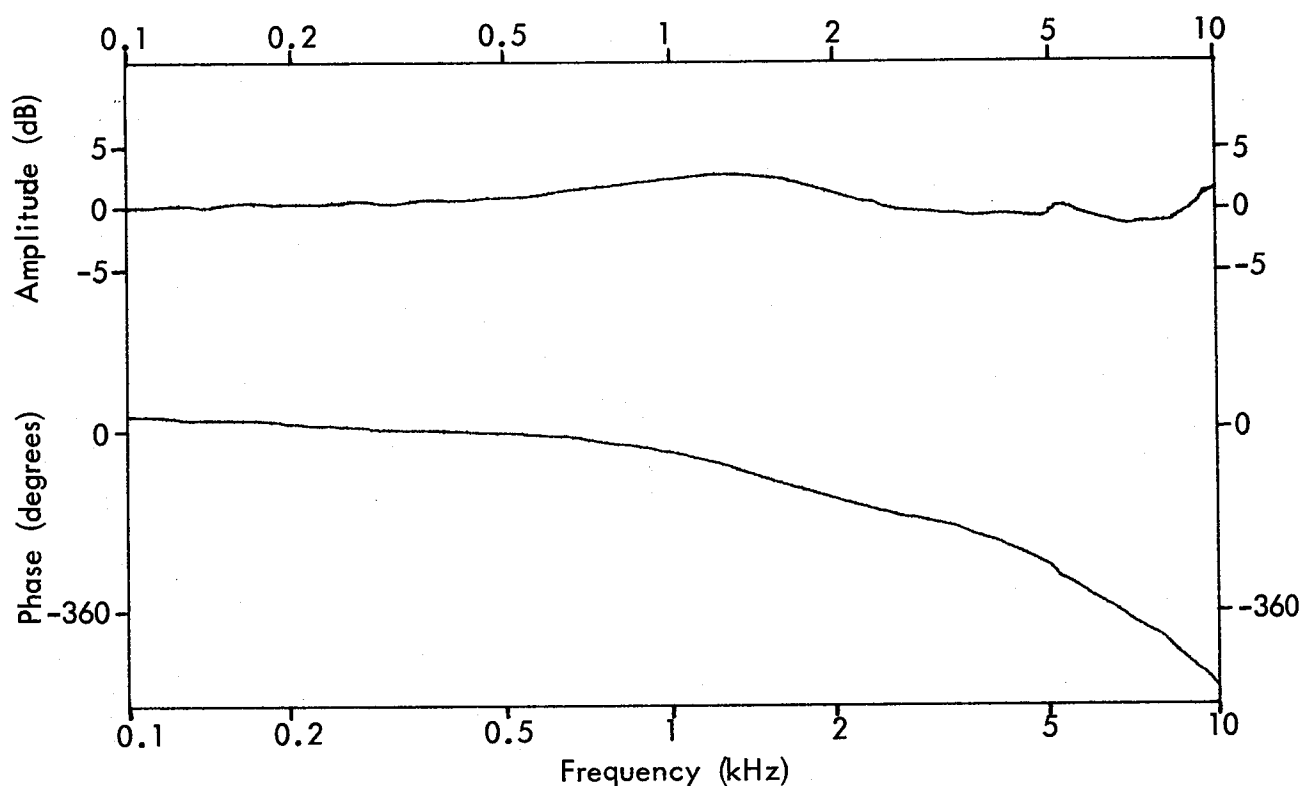


Fig. 18. Sound-pressure level produced in 0.39-cm³ reference cavity by the high-impedance acoustic driver described in the text. The zero-dB level for the sound-pressure amplitude is arbitrary.

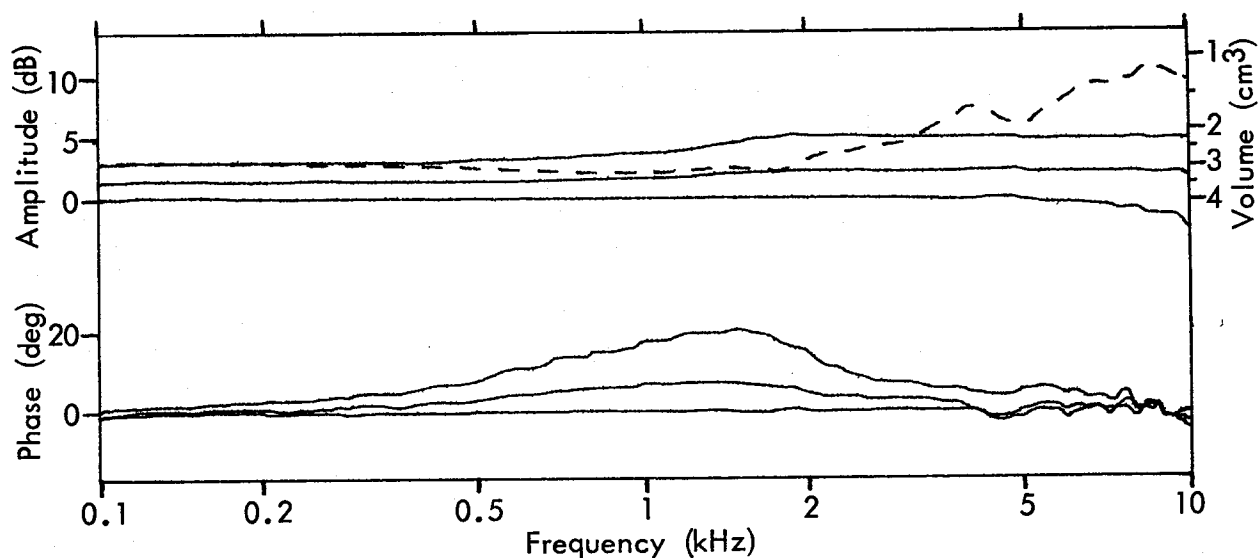


Fig. 19. Sound-pressure levels produced in three test cavities, relative to the sound-pressure in the reference cavity. The scale on the right shows the range of volumes equivalent to these measured sound pressures. The test-cavity volumes are 0.39, 0.24 and 0.13 cm³. The dashed line represents the impedance of a normal guinea-pig ear (Mundie, 1962).

where the cavities no longer act as ideal capacitors.

Also shown in Fig. 19, as a dashed line, is the equivalent volume of a typical guinea pig (based on data from Mundie, 1962). At low frequencies this volume is about 0.25 cm^3 ; the driver's behaviour was within 1 or 2 dB of ideal for a test cavity of almost the same volume. At higher frequencies the equivalent volume of the middle ear decreases, but it is in this region that the driver comes closest to the ideal. It would thus appear that the acoustical driver being used produces a volume-displacement which is within a few decibels of being independent of the load impedance, over the range of impedances measured in this work. The frequency characteristics of the driver (and also of the probe tube and microphone used for measuring the sound-pressure level in front of the eardrum) are corrected for by measuring the behaviour of the driver with the 0.39-cm^3 cavity, and subtracting this from the raw sound-pressure-level data measured with the animal. Dividing by $j2\pi f$ then corrects for the constant-volume-displacement nature of condenser microphones (as mentioned above), and adding 131.3 dB to the data accounts for the volume of the reference cavity and converts to impedance in acoustical ohms. The last correction corresponds to dividing by 0.39 cm^3 , and then multiplying by $\rho_0 c^2$ ($=1.43 \times 10^6$), where ρ_0 is the density of air and c is the speed of sound in air (Beranek, 1954, p. 35).

5.3 Frequency, Amplitude and Phase Measurements by Computer

5.3.1 Introduction. It is necessary for this work to measure continuously the varying amplitude and phase of sinusoidal signals over a frequency range of two decades (100 to 10 000 Hz). One approach to this problem would have been to buy or build specialized electronic hardware; Pinto and Dallos (1968), for example, used variable phase shifters and phase-sensitive demodulators (see Section 3.2.2 above). The computer would then need only to sample the relatively slowly varying demodulator outputs. Instead, I decided to use the computer in place of the specialized hardware. Using the clock and two of the analogue-to-digital channels of the PDP-12, I measure the frequency of a reference signal, and the amplitude and phase of another signal relative to the reference. In the following paragraphs I shall compare various ways of carrying out these tasks, and describe the methods I have chosen.

5.3.2 Frequency. The frequency of a sinusoidal signal can be measured either by measuring the length of a specified number of periods of the sine wave, or by counting the number of cycles in a given length of time. Applying either one of these methods over a wide frequency range leads either to inaccuracy (when measuring the lengths of short periods) or to long measuring times (when counting cycles at low frequencies). Therefore I have applied a combination of the two methods: I measure the time interval (\underline{I}) required for an integral number of cycles (\underline{n}), with the constraint that \underline{I} must be greater than some minimum. For low frequencies only one or two cycles will be measured, while for high frequencies the measurement time will be only slightly longer than the minimum. This minimum is chosen so that an uncertainty of ± 1 clock count represents a small percentage error.

5.3.3 Amplitude and phase. To measure the amplitude of a sinusoidal signal one could simply sample as rapidly as possible for some time and then pick out the largest sampled voltage as representing the peak of the sine wave. Unfortunately this method is sensitive to high-frequency noise: a positive noise spike on top of the peak of the sine wave will make the peak look higher, but a negative spike will just be ignored. Thus, high-frequency noise will always tend to increase the amplitude estimate and cannot be averaged out. The method is also limited by the sampling rate: the shortest sampling interval of the PDP-12 corresponds to a phase change of more than 65° at 10 kHz, so that one is not guaranteed of having any sample fall near the peak of the sine wave. Another way of measuring amplitude, if the frequency of the signal is known, is to detect a zero-crossing, then sample after a delay equal to one quarter of the period. This method is relatively unaffected by the timing limitations of the clock since an error of, say, 10° corresponds to an error of less than 0.2 dB, due to the flatness of the peak of a sine wave. However, the method does require the clock's Schmitt trigger to be set somewhere near the centre of the sine wave, and would be affected by a large DC component in the signal.

The most direct way of measuring the relative phase of two sinusoidal signals of known frequency would be to measure the time between a zero-crossing of one signal and a zero-crossing of the other. However, this requires an accurate adjustment of the thresholds of the Schmitt triggers used to detect zero-crossings, and is sensitive to any superfluous DC components in the signals. The method is also limited by the counting rate of the clock: for the standard PDP-12 clock the shortest clock-pulse interval corresponds to a phase of more than 9° at 10 kHz (the highest frequency of concern here).

The method that I have chosen for measuring amplitude and phase involves taking three evenly spaced samples within one cycle of the sine wave. From these samples (which are triggered by the clock) one can calculate the amplitude, phase and DC component of the signal. The calculation is simplest if the samples are exactly one third of a period apart, but at high frequencies

this condition cannot always be satisfied precisely because of the limited counting rate of the clock. The sampling interval is thus taken as an integral multiple of the clock interpulse interval; in the calculations one may compensate for the difference between the sampling interval and one third of the period.

This method avoids the problems of the other methods discussed above, since no Schmitt trigger is used, and since the precision of the timing is limited only by the stability of the clock and not by its rate. The main disadvantage of the method is its speed, which is limited by the computation time. At the moment my set-up requires at least 30 ms to take one measurement of amplitude and phase; at frequencies below about 600 Hz it takes longer because of the time required to collect the three samples. It should be possible to decrease the computation time by using arithmetic routines that are less general and more efficient.

5.4 Middle-Ear Castings

In preparing castings of the middle-ear cavities it is desirable to use a moulding material which is as fluid as possible before setting and which does not require heat to make it fluid. These two conditions are to prevent rupture or dessication of the membranes of the ear, in particular the tympanic and round-window membranes: the integrity of each of these is required to delimit the middle-ear cavities. It is also desirable that the moulding material be fairly elastic after setting, to facilitate removal of the bone surrounding the casting. The material that I have chosen is silicone rubber (Dow-Corning Silastic RTV). I am using the most fluid grade available (type A), further thinned by the addition of one part thinner to ten parts base. This is the most thinner that can be added without degrading the quality of the

cured rubber. The resultant material, although described as "highly pourable", cannot be poured into a mould as small as that formed by the middle-ear bones. Therefore I inject it into the cavities using a number 19 needle on a syringe, more for the purpose of guiding it than of applying pressure.

There are three types of catalyst available for this silicone rubber, giving working times of 10 minutes, 2.5 hours or 5 hours. I use the one giving a 2.5-hour working time (type 1). The curing time of six hours is not excessive, and the long working time permits careful weighing of the base, thinner and catalyst, and unhurried stirring and casting of the mixture. Too much haste in these later steps causes larger numbers of air bubbles in the mixture and lowers the quality of the final mould.

In the procedure I have developed to obtain high-quality moulds of the middle-ear cavities, the first step of the actual casting is to inject the rubber through the external ear canal onto the eardrum. No pressure is applied, and the drum should be neither damaged nor noticeably distorted. After the external ear has thus been filled, the moulding material is injected into the main middle-ear cavity through a hole (about 1 mm diameter) drilled at the anterior end of the tympanic bulla, near the opening for the auditory tube (see Fig.20). Small relief holes (about 0.5 mm diameter) have earlier been drilled at the posterior end of the posterior mastoid cavity, both inferior and superior to the facial canal. The epitympanum is filled separately through a hole at its anterior end, with a relief hole at the posterior end.

Once the rubber has set, the bone is carefully chipped away from the casting using forceps. Careful note is made of any large bubbles which may appear on the surface of the casting due to air having been trapped against the walls of the mould. In a good casting there will be only a few very small bubbles (less than 1 mm^3) visible anywhere.

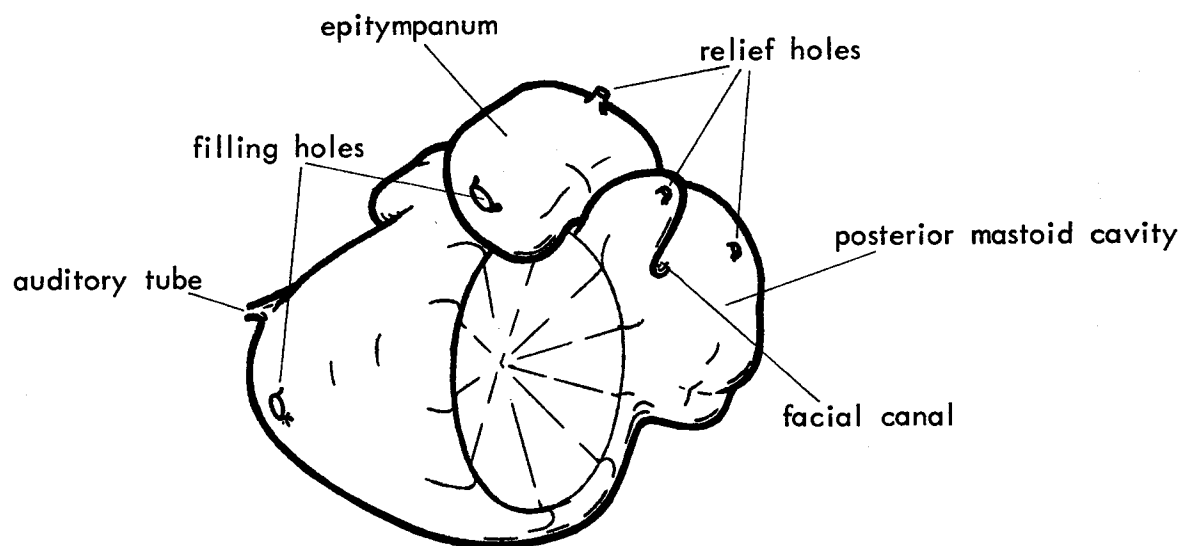


Fig. 20 . Typical casting of the middle-ear cavities of the guinea pig, including the marks left by the two filling holes and three relief holes. The part of the casting corresponding to the external ear has been removed.

The part of the casting corresponding to the external-ear cavity can easily be separated from the rest of the casting since the eardrum is intact. The part corresponding to the epitympanum is cut from the rest of the casting, and the incus can be lifted out. The stapes is left embedded in the casting.

The volumes of the various parts of the casting are measured using a specific-gravity bottle and distilled water. The bottle is supposed always to enclose the same volume; thus the volume of a piece of the casting may be obtained by (1) weighing the piece (W_c); (2) filling the bottle with water and weighing (W_{bw}); and (3) putting the piece into the bottle, filling with water and reweighing ($W_{bw'c}$). The volume of the piece of the casting is then given by

$$V_c = \frac{1}{\rho} (W_c - W_{bw'c} + W_{bw}),$$

where ρ is the density of the water.

The main sources of error in this volume determination are bubbles on the surface of the casting, air bubbles around the casting when it is put into the water, and the uncertainty of the volume enclosed in the bottle. With care the volumes can be determined to within less than 0.01 cm^3 .

See Zs.-NAGY + 75 re a volumetry technique \approx similar precision, less trouble.

Chapter 6

EXPERIMENTAL RESULTS

6.1 Introduction

For the work reported in this thesis, 21 animals were used. Measurements were taken on only 10 of these. Most of the 11 failures were due to difficulties in anaesthetizing the guinea pigs. In the first two of the ten animals for which impedance data were obtained, the tympanic membranes were accidentally torn during the drilling of the holes for the microphone probe tube. Although it would be very interesting to study the effects of such tears, this is beyond the scope of the present effort and the data from these two animals will not be reported here.

There are thus eight animals for which I shall present impedance data (Section 6.2). The effects of muscle contractions were measured in the last three of these experiments (Section 6.3). Although periodic drum retractions were observed during surgery in some of the earlier animals, they did not persist long enough to permit the measurement of their effects on the impedance. In this connection it is important to monitor and closely control the animal's temperature. Although the muscle contractions are very sensitive to the physiological state of the animal, it is possible to observe them consistently if sufficient attention is given to the animal's condition.

As described in Section 5.4, at the end of each experiment the ears were dissected out and saved, and castings were made later. The volumes measured from these castings are presented in Section 6.4, along with incudal weights measured at the same time.

6.2 Frequency Characteristics

6.2.1 Introduction. In Fig. 21 are presented curves of impedance versus frequency for the eight animals for which data were obtained. Each of these animals was alive at the time the measurements were taken. The solid curves show the impedance (magnitude and phase) of normal ears, with intact tympanic membranes. The dashed curves show the impedance after the eardrums had been removed, so that the drums and ossicles no longer contributed to the impedance. Note that all of these curves include the effects of the external-ear volume, V_e^* , for which no correction has been made.

6.2.2 No-drum impedance. All of the dashed curves (representing the "no-drum" impedance) show the behaviour described by Mundie (1962): as the frequency increases an impedance minimum (resonance) occurs, followed by a maximum (antiresonance). At frequencies above the antiresonance frequency (f_2) the effective volume of the middle ear is the sum of the external-ear and tympanic-bulla volumes ($V_e + V_{b1}$), while at frequencies below the resonance frequency (f_1) the epitympanic volume is added (V_{b2}). Note that at the highest frequencies the impedance sometimes departs from the expected behaviour. This may simply be due to the difficulties of measuring the impedance at very high frequencies, or perhaps the irregularities of the middle-ear cavities may be having a noticeable effect.

From the frequency characteristics of the no-drum impedance one may derive the following parameters of the middle-ear model: $(C_e + C_{b1})$, C_{b2} , L_{b2} and R_{b2} . This may be done by an automatic curve-fitting procedure

* The subscripts used here are those defined in Fig. 16, which shows the middle-ear model. "V" will be used in place of "C" when I am referring to a volume rather than the equivalent capacitance.

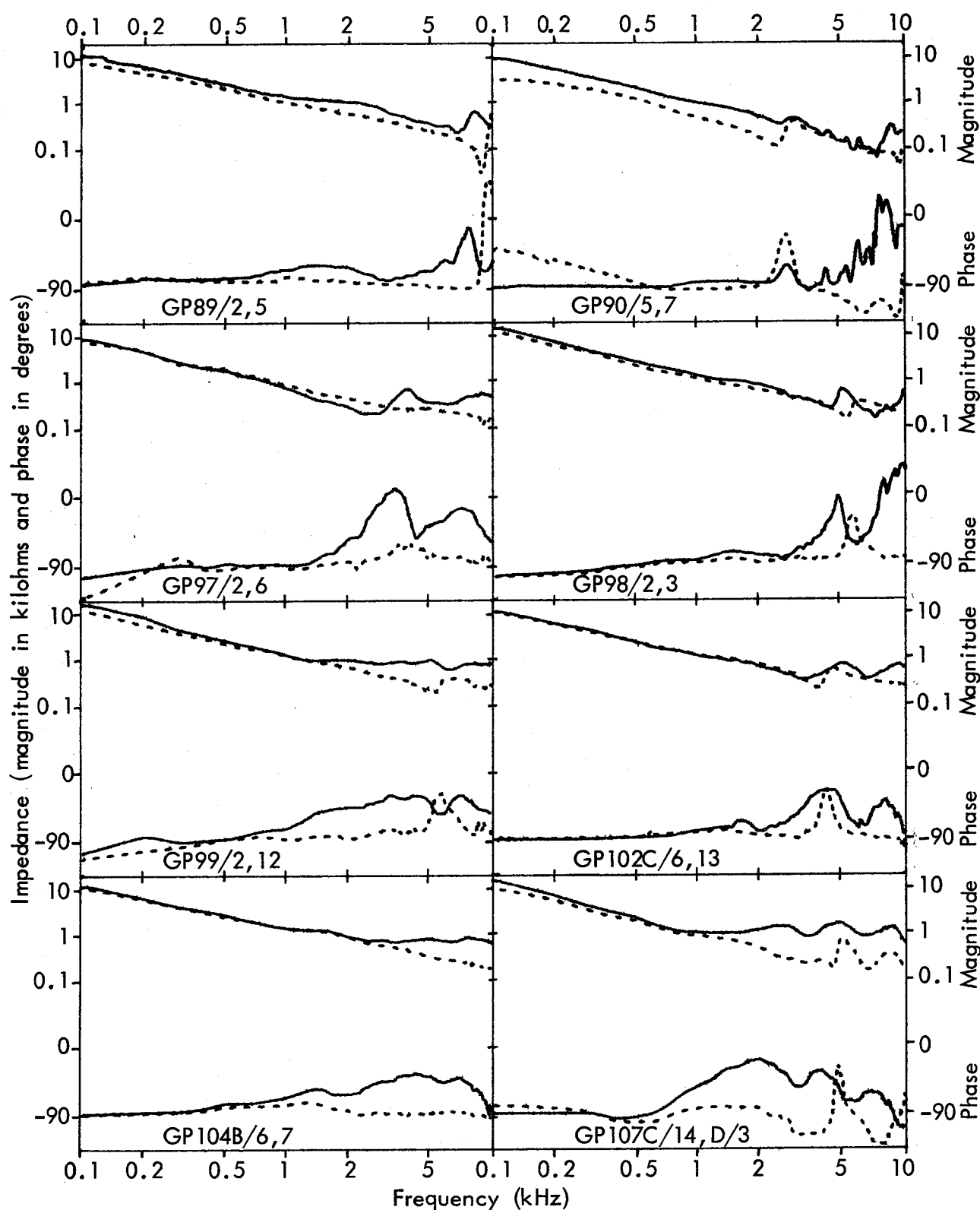


Fig. 21. Acoustical input impedance of eight guinea-pig ears. The solid curves represent normal ears, the dashed curves represent the no-drum condition. None of these curves has been corrected for the presence of the small external-ear volume.

with four degrees of freedom, or, as I have chosen to do, by calculating the parameters based on certain features of the curves. The four features that I have selected are the low-frequency equivalent capacitance (C_1), the resonance and antiresonance frequencies (f_1 and f_2), and the difference in magnitude between the impedances at the antiresonance and resonance (ΔZ). C_1 is obtained by noting the magnitude of the measured impedance relative to the 0.39-cm³ reference volume (see Section 5.2), while f_1 , f_2 and ΔZ can be read directly from the curves (see Fig. 22).

Under the initial assumption that $R_{b2}=0$, it can be shown (see Appendix) that

$$\left\{ \begin{array}{l} C_e + C_{b1} = \left(\frac{f_1}{f_2}\right)^2 C_1 \\ C_{b2} = \left[1 - \left(\frac{f_1}{f_2}\right)^2\right] C_1 \\ L_{b2} = \left(\frac{f_2}{f_1}\right)^2 / \left[4\pi^2 (f_2^2 - f_1^2) C_1\right]. \end{array} \right.$$

One can now obtain R_{b2} by trying different values until the ΔZ of the model equals the ΔZ of the measured curve. Unfortunately, as R_{b2} is increased the resonance and antiresonance frequencies separate, f_1 decreasing slightly and f_2 increasing slightly. For most of the animals presented here R_{b2} is small enough that the frequency shifts are small, but it is occasionally necessary to revise one's estimate of f_1 and f_2 and to recalculate the model parameters based on the new estimates.

The results of applying the above analysis to each animal are presented in Table 1. Note that in two cases R_{b2} and L_{b2} have not been calculated: for these two animals the resonance-antiresonance part of the curve is very flat, making it difficult to specify f_1 and f_2 . Thus C_{b2} was obtained directly from the equivalent capacitance (C_2) of the middle ear above the antiresonance. This is not usually feasible because the high frequency of the antiresonance

Animal number	Body weight	$C_e + C_{b1}$ (μF)	C_{b2} (μF)	R_{b2} (ohm)	L_{b2} (mH)
GP87*	1042	0.25	0.04	20	8
GP89	976	0.14	0.04	17	8
GP90	1206	0.21	0.12	150	37
GP97	506	0.14	0.07		
GP98	277	0.12	0.03	190	29
GP99	336	0.12	0.03	220	27
GP102	385	0.15	0.02	200	76
GP104	316	0.12	0.05		
GP107	440	0.15	0.03	120	35

Table 1. Parameter values for the middle-ear cavities, calculated from the no-drum impedance data. (* No impedance data for the normal ear was obtained in this animal, but a no-drum curve was obtained.)

makes it difficult to determine C_2 exactly. For these two animals, however, f_1 and f_2 are both quite low.

Included in Table 1 are the body weights of the animals. The variations of the different parameters with body weight will be discussed in Section 6.4.1.

The degree of agreement between the measured no-drum data and the characteristics of the model is indicated for a typical animal in Fig. 22, in which the solid curve represents the experimental data and the dashed curve has been calculated using parameter values derived by the above method. It will be seen that the main discrepancy is that the model impedance is somewhat low in the upper half of the frequency range. One possible contributing factor is the loading of the acoustical driver by small volumes, as discussed in Section 5.2. The effect of this loading would be in the right direction to explain the observed disagreement, but apparently would not be large enough to account for it fully. It is possible that another factor contributing to the discrepancy is that the model is oversimplified, but it is difficult to see at this time in just what way it should be improved.

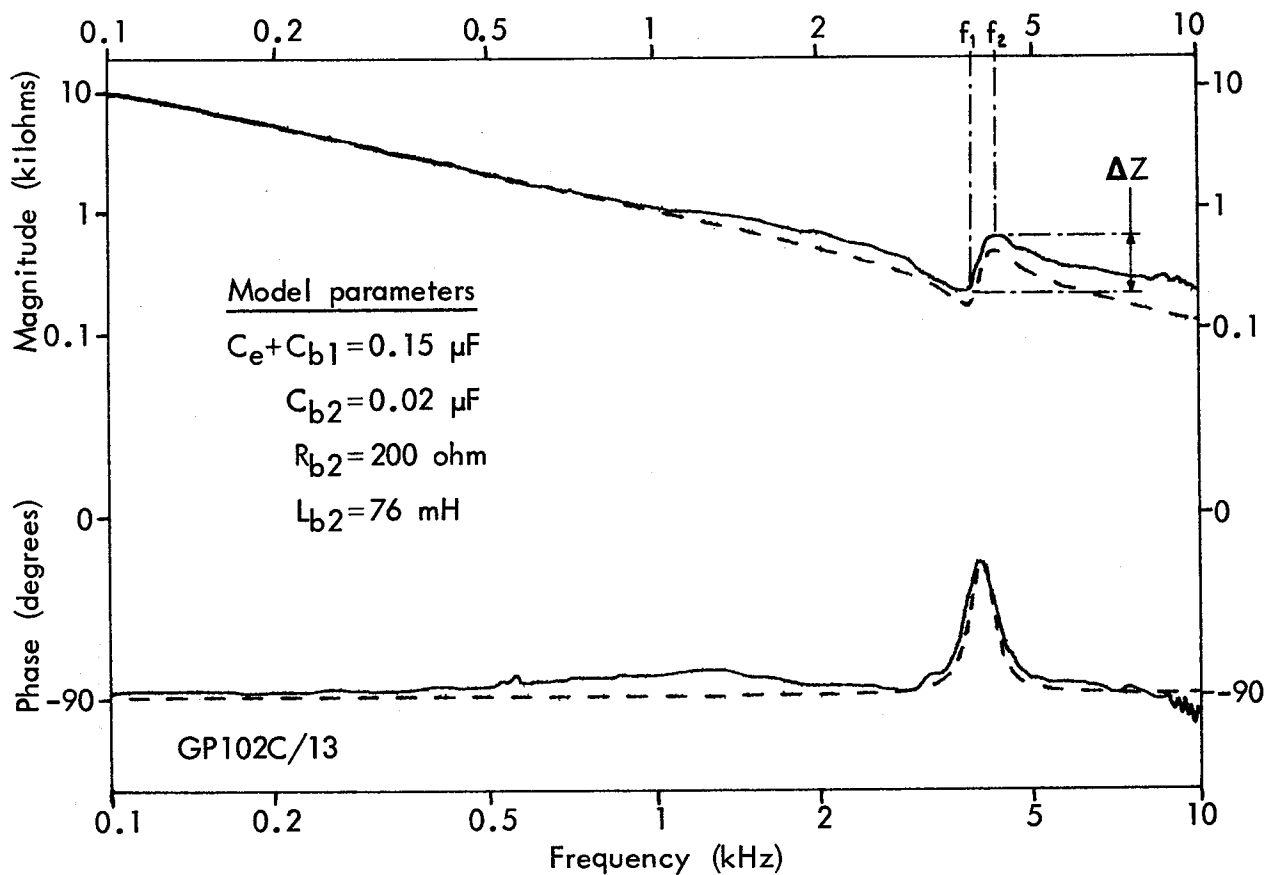


Fig. 22. Acoustical input impedance of a typical guinea-pig middle ear with the tympanic membrane removed. The solid curves are the experimentally measured data. The dashed curves were calculated from the model using the parameters shown. Also indicated on the graph are the definitions of f_1 , f_2 , and ΔZ : f_1 is the resonance frequency, f_2 is the antiresonance frequency, and $\Delta Z = |Z(f_2)| - |Z(f_1)|$.

6.2.3 Normal impedance. It can be seen from Fig. 21 that the impedance of the intact middle ear varies even more from animal to animal than does the no-drum impedance. At low frequencies the normal impedance is within a few decibels of the no-drum impedance, and is usually larger, as is to be expected since it includes the added stiffness of the eardrum and ossicles. At higher frequencies the normal impedance is often considerably higher than the no-drum impedance, and often displays a peak at or near the frequency of the antiresonance due to the middle-ear cavities.

There is some question about the variability of the middle-ear impedance of any particular animal. Figure 23 presents three normal-impedance curves from a typical animal. Two of them are very much the same, and were measured about an hour apart. The odd curve was taken about 75 minutes before the first of the two similar ones. During that 75 minutes the acoustical driver and the probe microphone were removed and replaced. It is thus possible that the change in impedance was due to variations in the placement of the driver, or to an actual change of the middle-ear characteristics. This variation, which is about 9 dB (or a factor of less than 3) at the worst frequency, is almost the greatest observed in any of the animals in the present series of experiments. It is to be compared with Mundie's statement that the impedance "sometimes varied within a short period of time by as much as a factor of 4 to 8 times" (Mundie, 1962).

Shown in Fig. 24 is an example of the agreement that can be obtained between the model and the experimental data. The solid curves represent the measured impedance, while the dashed curves represent the impedance of the model. It can be seen that the fit is qualitatively good: the main discrepancies are that (1) the mid-frequency antiresonance is at too low a frequency, and its low-frequency slope is too shallow; (2) the low-frequency slope of the high-

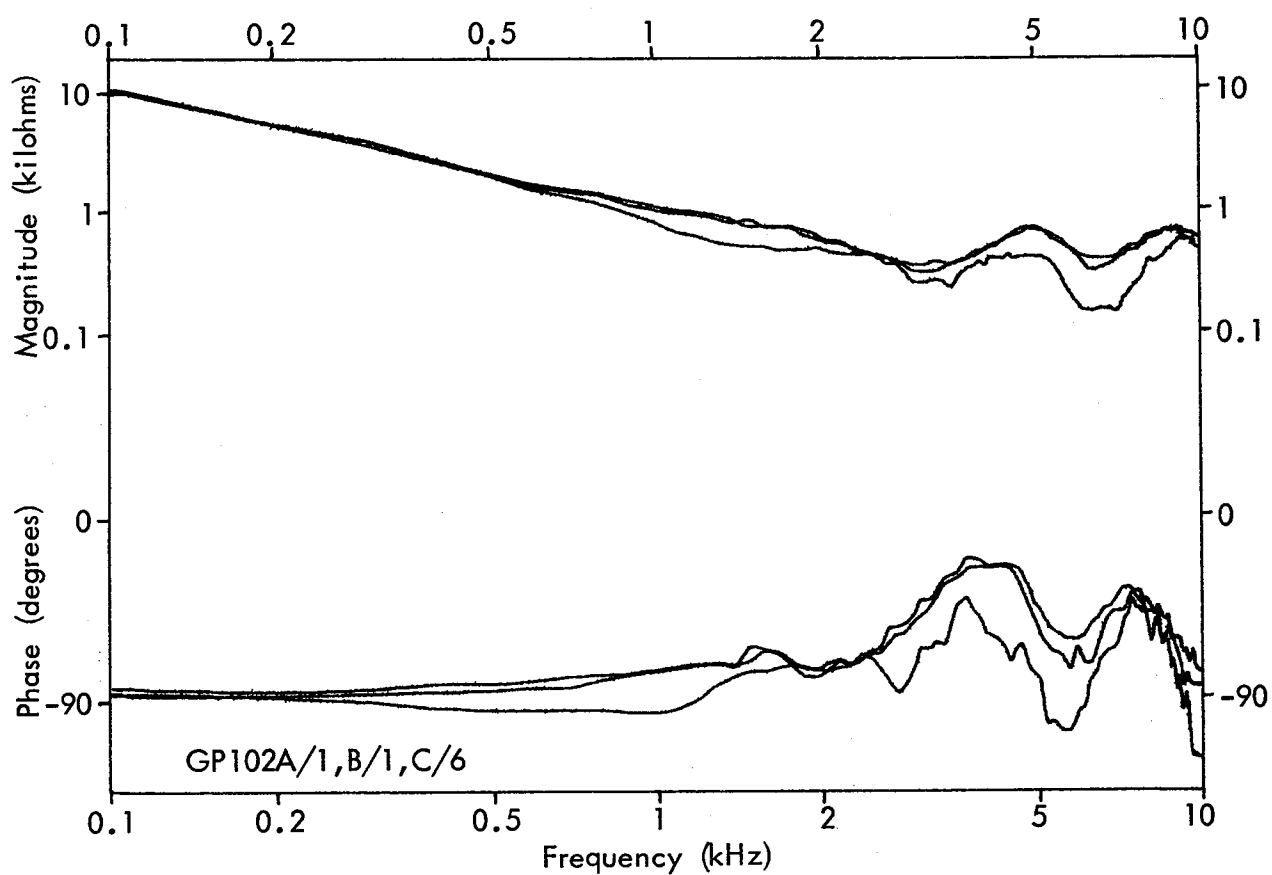


Fig. 23. Variability of the acoustical input impedance of the guinea-pig middle ear. The three sets of measurements were taken with the same animal. See text for discussion.

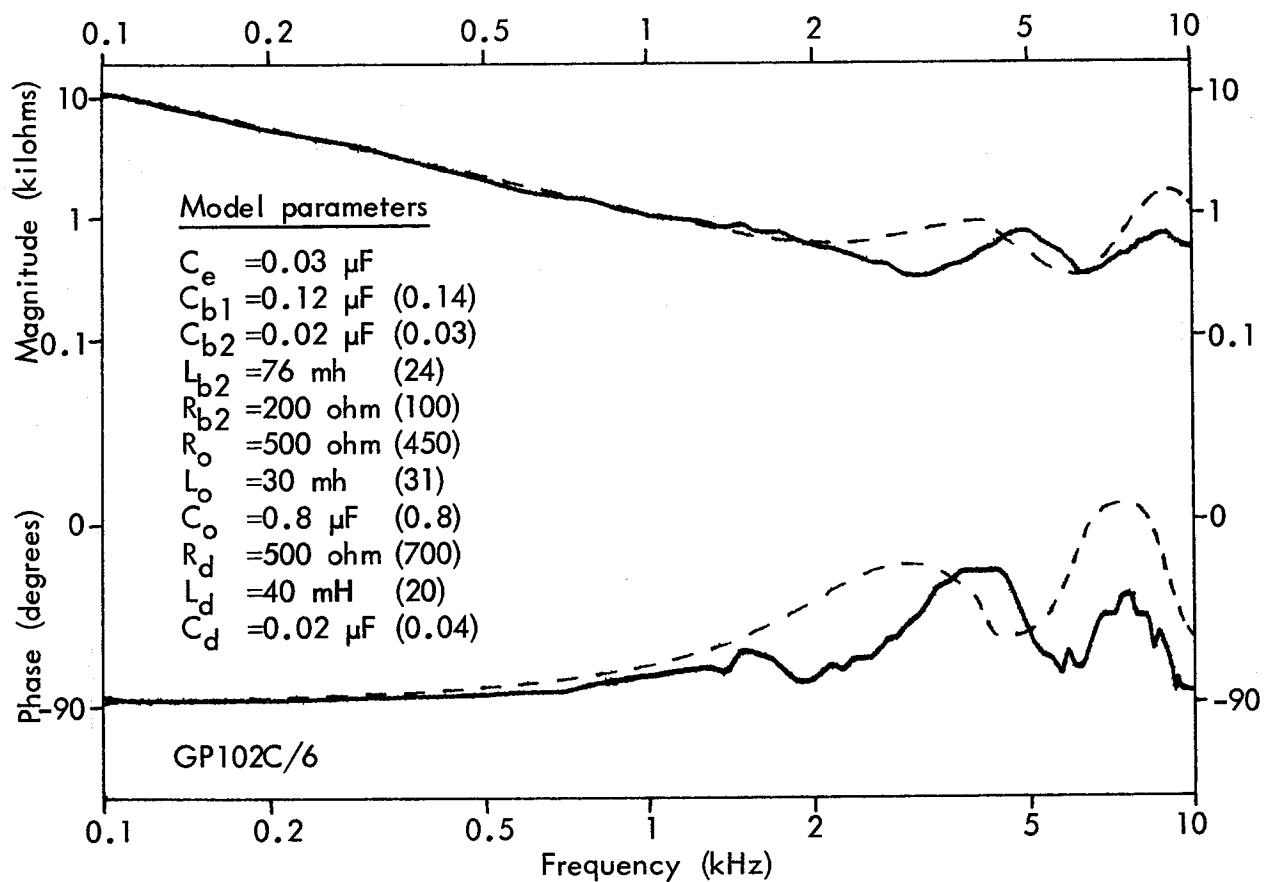


Fig. 24. Acoustical input impedance of a typical intact guinea-pig middle ear. The solid curve represents the experimental data, the dashed curve represents the model. The parameter values used are shown, with the values used by Zwislocki (1963) in parentheses. Note that my R_o is equivalent to his $(R_o + R_c)$.

frequency antiresonance is too steep; and (3) the over-all impedance level is too high at the higher frequencies. This last problem may be due in part to the factors discussed in Section 6.2.2 in relation to the no-drum curves.

No claim is made that the fit shown here is the best possible with the present model; it is simply the best fit obtained after a good deal of manual parameter variation. The parameter values were kept as close as possible to those used by Zwislocki (1963). The final values used by me are listed in Fig. 24 (with Zwislocki's values in parentheses).

6.3 Effects of Muscle Contractions

In Fig. 25 are presented a set of typical muscle contraction records; they were obtained from the same animal whose middle-ear impedance is shown in Figs. 22, 23, and 24. The waveforms and amplitudes were quite stable over a period of hours, the only significant variations occurring in the phase records at frequencies above 1 kHz. The effects of muscle contractions were observed in two other animals: in both cases the amplitudes and waveforms were similar, although these two preparations were not quite as stable as the one presented here, and in one of them impedance changes were observed at only a few frequencies. The evidence that the phenomenon that was observed is in fact the contraction of the middle-ear muscles is that (1) they occur only in animals in which regular, visible retractions of the tympanic membrane occur, and (2) they do not correspond to any visible movement of the rest of the animal.

It will be noticed that, particularly at the higher frequencies, the impedances are not single-peaked, but rather seem to include two components. The significance of this is not clear from the present data, but is discussed further in Section 7.2.2. Another feature of the data whose significance is not clear is the fact that the repetition rate of the contractions depends on the signal frequency. This also is discussed in Section 7.2.2.

In the middle-ear model that I am using, the effect of a muscle contraction is presumably to decrease C_o and increase R_o , that is, to increase both the stiffness and resistance of the ossicular chain (see Section 4.7). At very low frequencies only the change in C_o has any effect, while at higher frequencies they both have an effect. Thus one can estimate the parameter changes corresponding to the measured impedance changes in two steps: (1) find a change in C_o which causes an impedance increase at 100 Hz which is

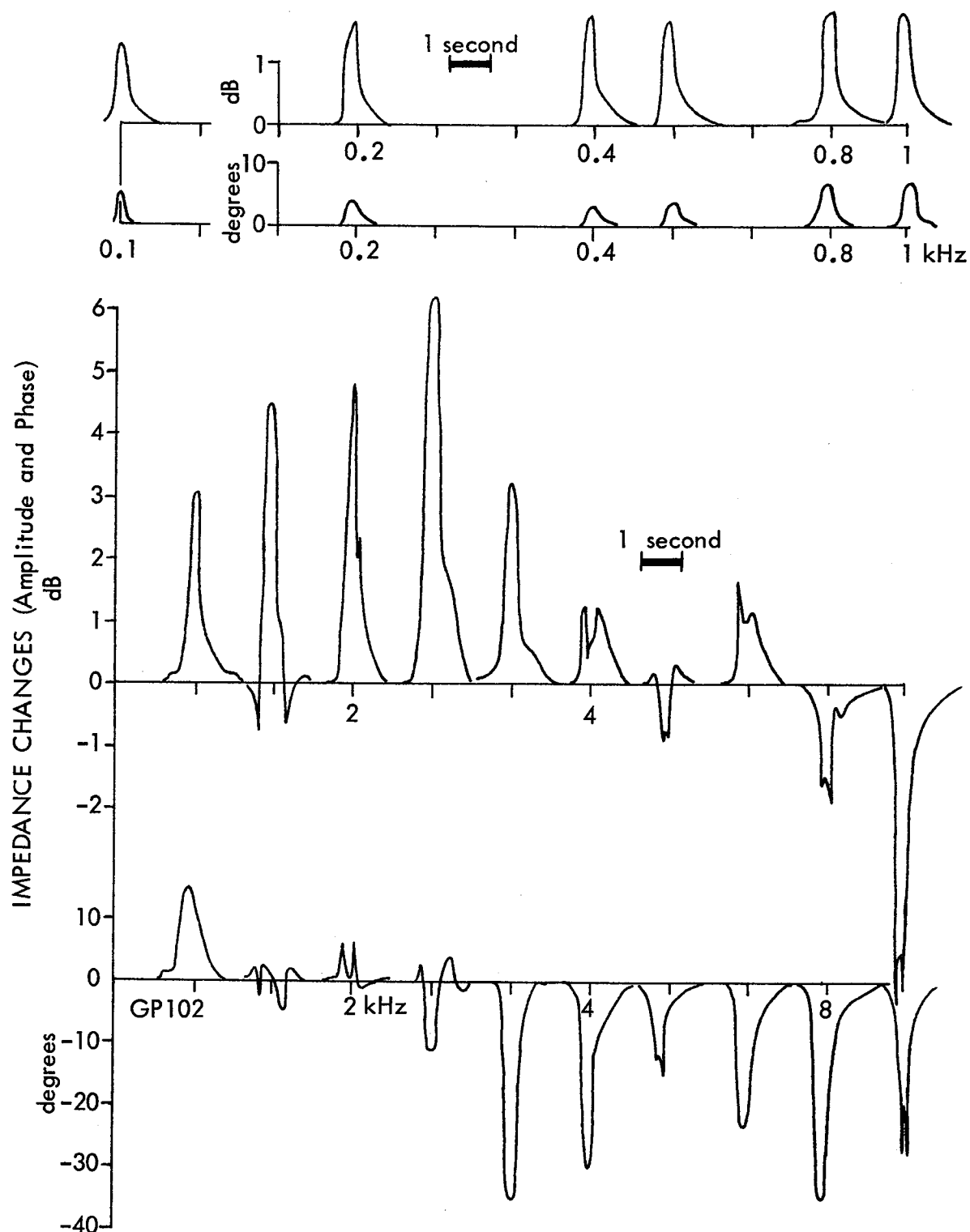


Fig. 25. Montage of muscle-contraction records, showing both amplitude and phase. The numbers along the horizontal scales are the signal frequencies (one-third-octave intervals) at which the contractions were observed. Note the di-phasic nature of the impedance changes at some frequencies.

the same as that observed experimentally; then (2) given this change in C_o , find a change in R_o such that the combined effect is a maximal mid-frequency impedance increase equal to that observed experimentally. Note that this procedure uses the measured impedance-magnitude data at only two frequencies, and does not use the phase data at all.

Applying the above procedure for the animal presented in Fig. 25 yields the result that a muscle contraction is to be simulated by decreasing C_o from 0.8 to 0.25 μF , and increasing R_o from 500 to 1500 ohms. The resultant impedance changes predicted by the model are compared to the measured data in Fig. 26. It can be seen that the agreement is quite good qualitatively. This agreement is all the more remarkable when one considers that (1) very few points were used in estimating the appropriate parameter changes; and (2) the fit of the model to the normal, resting impedance data is far from perfect.

The parameter changes calculated for the other animal in which impedance changes were measured at many frequencies, are: (1) decrease C_o from 0.8 to 0.25 μF , and (2) increase R_o from 800 to 2200 ohms. It can be seen that the results from the two animals are in excellent agreement.

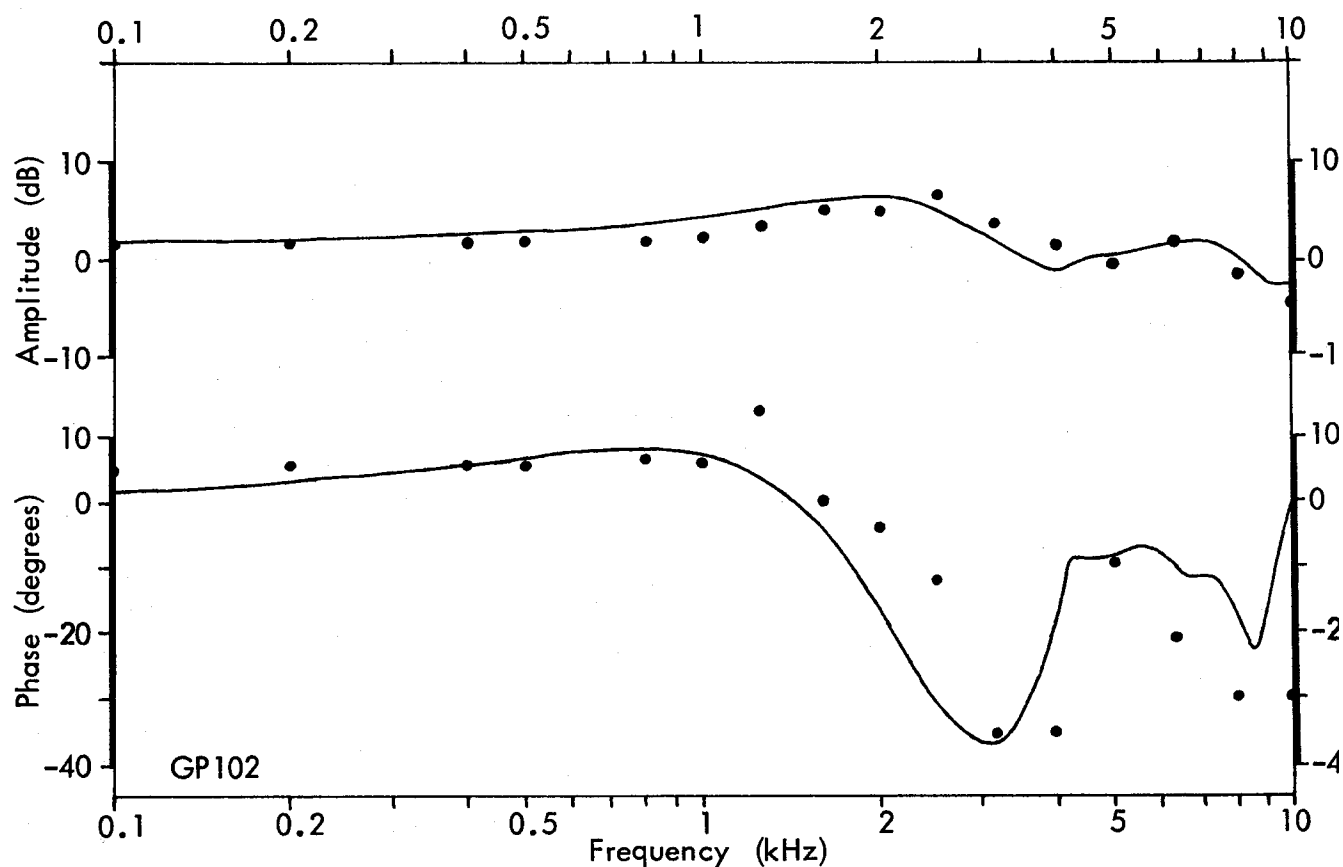


Fig. 26. Effects of muscle contractions on middle-ear impedance, showing the changes from the resting impedance. The points represent experimental data, while the curves represent the changes calculated from the middle-ear model discussed in the text.

6.4 Middle-Ear Volumes and Weights

6.4.1 Cavity volumes. Mundie (1971) was kind enough to provide me with some unpublished data on the volumes of the cavities of the guinea-pig middle ear. He measured the volumes by weighing the amount of mercury necessary to fill the cavities. In Fig. 27 and 28 I have plotted his data (filled circles) against the body weights of the animals. I have drawn in straight lines representing least-squares fits to Mundie's data. It can be seen in Fig. 27 that there is clearly a relationship between middle-ear volume and body weight. Fig. 28 shows that the fraction of the total volume taken up by the tympanic bulla remains more or less constant, that is, that the tympanic bulla and the epitympanum grow at about the same rate. Both of these conclusions are supported by my own data, which are plotted in the same figures (open circles). These volumes were measured from middle-ear castings.

I have also measured the volume of the cavity external to the eardrum, out to approximately the end of the bony ear canal. Although the measurements are not very precise, it would appear that this volume varies hardly at all with body weight: it was about 0.04 cm^3 in animals whose weights ranged from 277 to 1042 g. The reason for this behaviour is not clear, but it is convenient for my purposes, since it means that this volume will have more or less the same effect in most guinea pigs.

Acoustical theory would predict that if the over-all dimensions of the middle-ear cavities increase, then R_{b2} and L_{b2} should both decrease, since the acoustic resistance and inertance of an open tube are directly proportional to negative powers of the tube's linear dimensions (Beranek, 1954, equations 5.48 and 5.49). There is too little data in Table 1 to permit one to say whether such a variation occurs in the animals that I have measured.

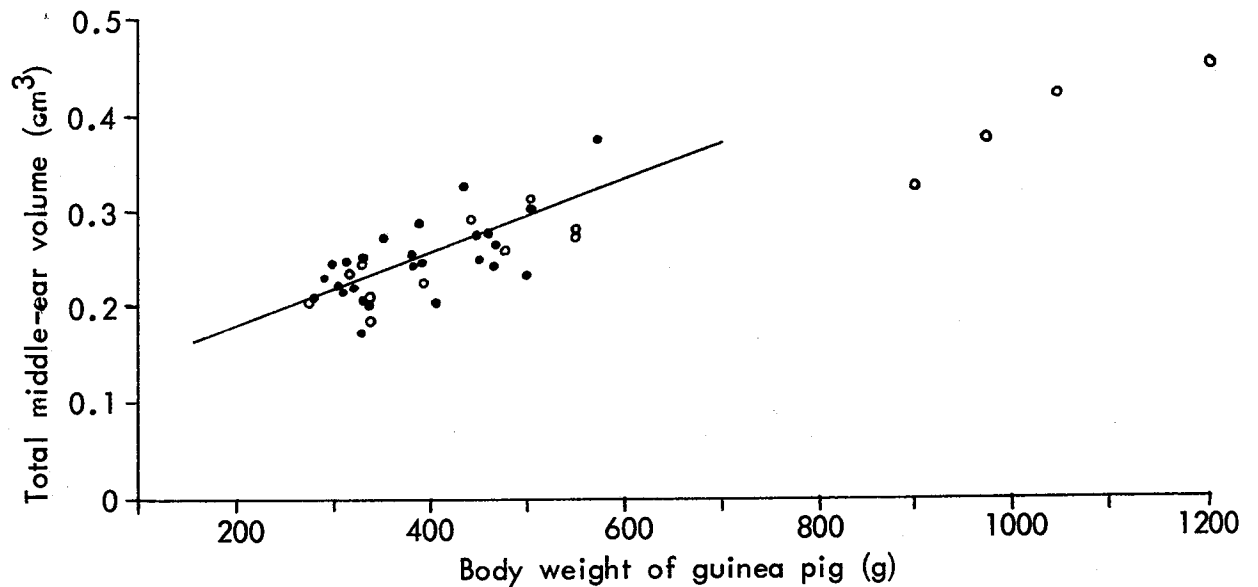


Fig. 27. Total middle-ear volume, $V_{b1}+V_{b2}$, as a function of body weight. The filled circles are data from Mundie (1971), the open circles are my data. The straight line represents a least-squares fit to Mundie's data.

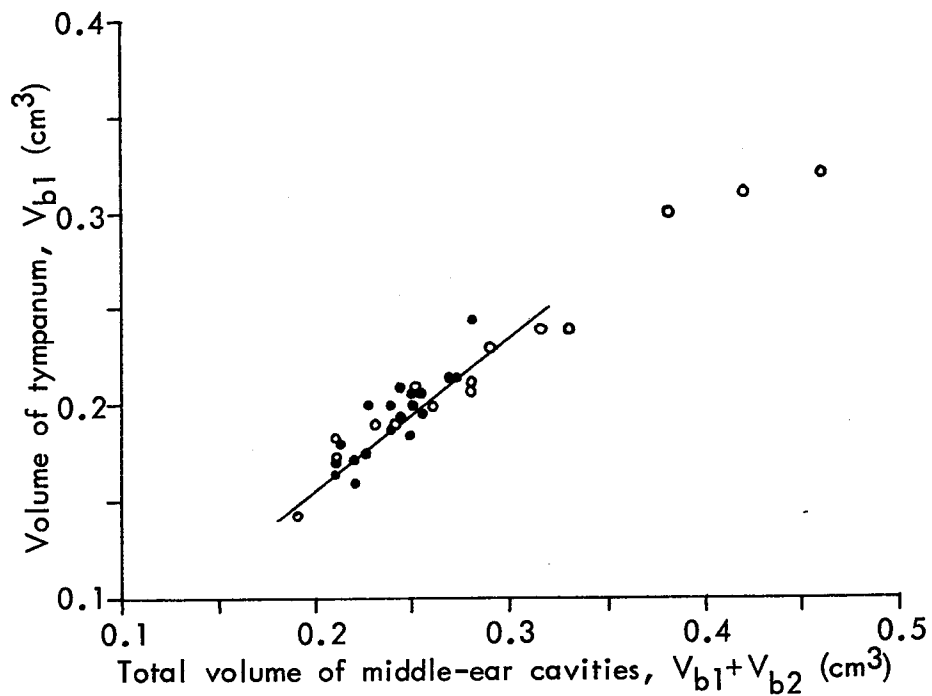


Fig. 28. Relationship between V_{b1} and $(V_{b1}+V_{b2})$. The filled circles are data from Mundie (1971), the open circles are my data. The straight line represents a least-squares fit to Mundie's data.

The measurements of the volume of the epitympanum (V_{b2}) by direct volumetry and from the impedance data are compared in Table 2. It can be seen that the agreement, while far from perfect, does indicate that the impedance analysis is reasonably accurate. One cannot expect very close agreement between these two measures because of the presence of various membranes, and possibly fluid, in the fresh middle ear.

Also shown in Table 2 are the results of calculating V_e by subtracting the volumetric measurement of ($V_{b1}+V_{b2}$) from the value of ($V_e+V_{b1}+V_{b2}$) derived from the impedance data. It is obvious that the values shown are consistently too small. Apart from experimental uncertainty, two possible reasons for this are that (1) the impedance method yields volumes which are too small; or (2) the volumetric method yields volumes which are too large. Note that the second reason, at least, might be expected, since the membranes on the walls of the cavities had dried out by the time the castings were made.

6.4.2 Ossicular weights. I have weighed the dried incudes of 15 guinea-pig ears. The incudes weighed between 4.6 and 5.8 mg, with an average weight of 5.2 mg. There appeared to be no relationship between incudal and body weights. These data are consistent with an average weight of 5.4 mg for six dried incudes weighed by Mundie (1971). Note that these incudes were separated from the attached malleal arm by breakage at a point near the body of the malleus, so that the weights reported include the bodies of the mallei as well as the incudes. It is not possible to separate the two since they are fused together in the guinea pig.

Mundie (1971) has also weighed dry malleal arms and tympanic membranes (average weight 0.49 mg) and dry stapedes (average weight 0.45 mg).

The weights of these structures are of interest because they can be related

Animal number	V_{b2} from volumetry (cm ³)	V_{b2} from impedance (cm ³)	V_e (cm ³)
GP87	0.11	0.06	0.0
GP89	0.08	0.06	-0.12
GP90	0.14	0.17	0.0
GP97	0.07	0.09	-0.02
GP98	0.03	0.03	0.01
GP99	0.04	0.03	-0.03
GP102	0.04	0.06	0.02
GP104	0.05	0.05	0.01
GP107	0.06	0.05	-0.03

Table 2. Epitympanic and external-ear volumes, based upon both impedance and volumetric data. The two centre columns show volumetric and impedance estimates for the epitympanic volume, V_{b2} . The last column shows estimates for the external-ear volume, V_e , obtained by combining both volumetric and impedance data, as described in the text. Note that these estimates are all very small, some actually being negative.

to the values of L_o and L_d in the model. In particular, L_o represents the effective mass (at the eardrum) of the stapes, the incus, the malleus and part of the drum, as well as ligaments and muscles attached to the ossicles. It is not yet possible to determine exactly what this effective mass should be, in terms of the actual masses, since not enough is known about the modes of vibration of the tympanic membrane or the ossicles. In 1963, Zwislocki estimated the effective mass of the guinea-pig ossicles to be about one quarter of the actual mass. However, his calculations involved assumptions about the vibration of the tympanic membrane which have since been questioned (Tonndorf and Khanna, 1970), and he did not attempt to calculate the moments of inertia of the ossicles. A detailed investigation of this question is beyond the scope of my present study.

Chapter 7

DISCUSSION

7.1 The Role of the Middle-Ear Muscles

7.1.1 Possible roles. The roles which have been suggested for the middle-ear muscles have been classified by Legoux (1961) as protection, accomodation, fixation, and intralabyrinthine-pressure regulation. The intralabyrinthine-pressure regulation theory supposed that by regulating the fluid pressure in the inner ear, the muscles could control the vibratory response of the basilar membrane; Legoux (1961) points out that there is evidence that the vibration of the basilar membrane is insensitive to the surrounding fluid pressures, so that there is little support for the idea that it can be controlled by the middle-ear muscles. The fixation theory suggests that the muscles are responsible for holding the ossicles in the "best" positions for sound transmission to the inner ear, and in particular for modifying the degree of coupling between the different ossicles. This theory is very closely related to the accomodation theory, according to which the muscles adjust the middle ear's characteristics to favour different frequencies according to the needs of the moment.

The protection theory states that the main function of the middle-ear muscles is to protect the ear from loud sounds, by means of the acoustic reflex. This theory has received more experimental attention than the others. The result of this experimental work has been to show that removal or paralysis of the muscles does in fact increase the amount of damage caused to the inner ear by loud noise. However, the attenuation due to the muscles is relatively small and is largely restricted to low frequencies. Other objections to the

protection theory are that (1) the muscles may actually increase the damage due to sounds at around 4 kHz, to which the human ear is particularly vulnerable anyway; (2) the tensor tympani would be more effective if it were attached to the malleus nearer the tip of the manubrium; and (3) the reflex is too slow to offer protection against impulsive sounds, but fatigues too rapidly to protect against long-continued sounds (Onchi, 1953). In reply to some of these criticisms, Tsukamoto (1953) suggested that the resting tonus of the muscles may be responsible for a degree of protection. (It is interesting to note the possible survival value of such a mechanism: a sleeping animal would effectively increase its auditory sensitivity by the relaxation of its middle-ear muscles.)

Simmons (1964) has suggested several other possible roles for the middle-ear muscles, including signal identification, masking reduction, attention maintenance, and frequency-response smoothing. The signal-identification hypothesis points out that the brain could, by contracting the muscles for a moment, distinguish externally generated sounds from sounds generated internally which are bone-conducted, and from physiological noise generated more centrally than the middle ear. The muscles might also reduce masking due to low-frequency sounds such as chewing or swallowing, thus improving the signal-to-noise ratio for important external high-frequency sounds, including speech (Lidén *et al.*, 1963). This is actually a type of accommodation theory. Another suggested function is in the maintenance of attention by the constant jitter of the muscles, by analogy with the extraocular muscles (see Section 2.8 concerning similarities between the tympanic and extraocular muscles). The fourth role suggested for the muscles is that of smoothing the frequency response of the middle ear by rapidly shifting the peaks back and forth. This would permit the ear to be relatively lightly damped, preserving sensitivity. This idea is in contrast

with the classical accommodation theory which holds that the muscles permit tuning of the middle-ear, thus exploiting the frequency-response peaks rather than minimizing their effects.

Simmons (1964) and Carmel and Starr (1964) found that cats contract their middle-ear muscles in anticipation of their vocalizations, not in response to them. The same anticipatory response has been tried as a method of reducing damage due to loud sounds (Brasher *et al.*, 1969, and others). It is possible that such conditioned reflexes have played a part in some experiments designed to investigate the protective role of the muscles, such as the studies of Taruya (1953).

A final possible role for the middle-ear muscles is in localization. (Lawrence, 1963). Legoux (1964) has pointed out that small differences of muscle activity could put the two ears out of phase.

Before one could properly use the present experimental results as a basis for discussing the roles of the middle-ear muscles, one would have to (1) make some assumptions about the cochlear load, to permit calculating the transmission characteristics of the model; and (2) model the impedance of the external ear (Sinyor, 1971) and of the surrounding air. The second point is necessary because one must consider the efficiency of energy transfer into the middle ear, as well as through the middle ear into the cochlea.

Judging by the impedance data itself (Fig. 26), without calculating the actual transmission changes, one can say that the muscle contractions will cause attenuation mainly at low frequencies, with more complex effects at high frequencies, as has been observed before. It also appears that the muscles may introduce phase shifts of up to 30 or 40° at some frequencies. This last lends credibility to the suggestion of a role for the muscles in localization.

Most of the roles that have been suggested for the middle-ear muscles involve changes of the frequency characteristics of the ear. Only the attention-maintenance

and signal-identification hypotheses concentrate on the fact that the muscles can be considered as amplitude-modulating the audio-frequency signal being transmitted by the middle ear. It is this sort of amplitude modulation that is actually measured in the present work. In the future it may be fruitful to consider this role of amplitude modulation from the point of view of engineering communication theory.

7.1.2 Significance of the resonance and antiresonance. As discussed in Sections 2.2 and 4.3 above, many mammals have middle-ear cavities that are subdivided in such a way that a resonance and an antiresonance are introduced into the frequency characteristics. Although in an animal like the guinea pig it is possible that this arrangement of cavities is necessary for the mechanical support of the ossicles, it is difficult to see what structural purpose is served by the bony septum in the cat (described in Section 2.2.4). It is tempting to speculate that the resonance and antiresonance have a purpose, which might be to permit some degree of frequency tuning by the middle-ear muscles. In other words, there may be some anatomical support for the accommodation theory discussed above. If these particular cavity arrangements have no other purpose beyond their acoustical effect, it would detract from the frequency-smoothing hypothesis which assumes that the peaks in the frequency response are undesirable.

With regard to the possible role of the cavity resonance and antiresonance in tuning of the ear, it may be relevant to mention that (as pointed out to me by Dr. M. L. Blostein of our Department of Electrical Engineering) the electrical-circuit model of the middle-ear cavities (Fig.13) is the same as that used to model the piezoelectric crystals used for frequency tuning in radio receivers (v. Dyke, 1945).

7.2 Directions for Further Study

7.2.1 Improvement of impedance-measurement technique. One improvement that would facilitate future impedance measurements would be to incorporate the microphone probe tube and the driver tube in a single unit, so that a separate hole would not have to be drilled for the probe tube. Such an arrangement was used with guinea pigs by Honrubia and Ward (1969). It would not only make the experiment easier, but would reduce the risk of damaging the tympanic membrane, and would also reduce the seepage of blood onto the tympanic membrane which sometimes now occurs.

Another desirable improvement of the experimental technique would be to increase the speed of the computations described in Section 5.3.3. This would permit finer temporal resolution of the impedance changes due to the muscle contractions, and might help clarify the significance of the biphasic waveforms that occur at some frequencies (Section 6.3). It would also be advantageous to streamline the data-collection procedure so that more muscle-contraction records could be taken in a short time.

7.2.2 More extensive studies. In addition to obtaining more data of the sort reported in this thesis, it will be desirable to measure some other variables. In particular, the cochlear potentials should be measured to provide information about the transmission characteristics of the middle ear (as discussed in Section 3.4). This would provide further data with which to improve the model, and would permit stronger conclusions to be drawn concerning the role of the middle-ear muscles.

In the present work, as well as measuring the characteristics of the normal ear, I have measured the characteristics with the tympanic membrane removed. This is a well defined intervention which provides much valuable information about para-

meter values in the model. It will be useful to perform other such manipulations, such as making large openings in the bulla, or disrupting the ossicular chain, or cementing the ossicles to each other or to the surrounding bones. Unfortunately, once one has made a fairly large opening in the bulla it is difficult to reseat it and still have the same cavity volumes enclosed. Thus it would be difficult, after performing one of these manipulations, to measure the impedance of the same ear with the tympanic membrane removed but the cavities intact. As a result, one would be gaining information about certain parameters in the model while losing information about others. It is important to gain as much information as possible about as many parameters as possible in each animal, since there is such great variability among individuals.

A particular subject requiring investigation is the mechanism of the spontaneous muscle contractions observed in this work. At some frequencies the impedance changes show fairly complex time courses (see Fig. 25). On the basis of the present data one cannot choose between the various possible explanations of this phenomenon. These explanations include (1) interactions between central inhibition and excitation, such as those observed by Baust *et al.* (1964a,b,c); (2) a time delay between the contractions of the two muscles; and (3) impedance changes in opposite directions due to the two muscles. The only previous record of diphasic impedance changes is in the observations of Flottorp and Djupesland (1970) on otosclerotic humans.

Another subject requiring further work is the observation (Section 6.3) that the rate at which the contractions occur appears to depend on the frequency of the acoustical signal. Since the sound-pressure level of the acoustical driver used in my work depends on frequency, the explanation of the phenomenon may perhaps be found in an interaction between the signal intensity and the central mechanism responsible for the contractions. A streamlined data-collection procedure, an acoustical driver that can supply a wider range of intensities, and a greater number of experiments, are all required to resolve this point.

In addition to studies on the guinea pig, there is a need for further investigations of the middle ears of other species, both common ones like cats, and species like the kangaroo rat (Legoux et al., 1954, 1955; Webster, 1962) which have peculiar anatomical arrangements of the ear (see Section 2.2.3). It is to be hoped that the results of such comparative studies can be combined with phylogenetic and ontogenetic knowledge to provide fresh insights into the functioning of the middle ear.

7.2.3 Improvement of the model. There is obviously much room for improvement in the model used in this work. In particular, there should be a closer relationship between the values of the inductors L_0 and L_d , and the actual masses and rotational axes of various middle-ear structures (Section 6.4.2). Also, recent data concerning the function of the tympanic membrane (Tonndorf and Khanna, 1970) should be studied with regard to their application to the model.

Ultimately it would be desirable if the model could be used to study ultrasonic hearing (Brown, 1970, 1971). This is not yet possible because the lumped-parameter circuit model cannot be used at such high frequencies.

7.2.4 Parameter-calculation techniques. The technique described in Section 6.2.2, for calculating model-parameter values from the measured no-drum impedance, is reasonably straightforward and easy. It would be even more so if the effect of R_{b2} on f_1 and f_2 could be expressed analytically, that is, if one could obtain exact equations for the parameters without having first to assume that $R_{b2}=0$. I have tried to obtain these equations by simply expressing the magnitude of the impedance as a function of (C_e+C_{b1}) , C_{b2} , R_{b2} , L_{b2} and ω , and then differentiating this expression with respect to ω to locate the minima and maxima, using the symbolic-algebra language PL/I-FORMAC (Tobey et al., 1967) on the McGill University IBM 360/75. To obtain expressions for the resonance and anti-

resonance frequencies one would then have to factor an eighth-order polynomial in ω^2 , the coefficients being functions of the model parameters. To attempt this task as it stands would be impractical. It may be possible to find suitable approximations which will reduce the problem to a more manageable level.

Modelling the normal impedance is even more difficult than modelling the no-drum impedance. The increased difficulty is due both to the lack of constant features in the normal data, and to the greater number of parameters in the model: there are four parameters to adjust in the no-drum model, and the data present several reliable landmarks such as resonances and antiresonances, while the normal model includes seven additional parameters and the data present no useful features that are recognizable in all or even most animals.

The above considerations dictate that, at least for the moment, parameter values for the normal model must be arrived at by trial and error. I have conducted these trials manually, rather than implementing some automatic optimization procedure. The main reason for this was that the process of varying the parameters and looking for a good fit served to familiarize me with the model, and in particular served as a search for properties of the model which could be used to simplify the modelling task. Two examples of this sort of property are: (1) the low-frequency difference between the normal and the no-drum impedance is determined mainly by C_0 ; and (2) the form of the impedance curve around 9 or 10 kHz is strongly affected by all of the parameters except C_0 . (These properties hold if the parameter values are on the same order of magnitude as those chosen by Zwislocki, 1963).

Even armed with such properties, it is extremely difficult to determine the "best" set of parameters for a given set of data. The large number of degrees of freedom makes a purely manual approach impractical. On the other hand, it is difficult to incorporate known properties of the model into an automatic curve-fitting procedure. In order easily to obtain the best possible fit to the data, consistent with certain constraints on the parameter values, and taking advantage of known

properties of the model, will require an interactive man-machine system, with fast computation. The human operator, watching a visual display, could pick out significant features of a particular animal's frequency characteristic; the computer would then try to match these particular features rather than just looking for a least-squares fit to the entire frequency response. At any time the operator could constrain the values of particular variables if this seemed desirable; for example, he could estimate C_0 based on the low-frequency impedance, and then force the programme to use that value.

7.3 Conclusions

The work described in this thesis has been the beginning of a study of the function of the middle-ear muscles in the guinea pig. The accomplishments so far have been to

- (1) develop a simple means of continuously measuring both the amplitude and phase of the acoustical impedance, taking advantage of a general-purpose laboratory computer;
- (2) extend the work of Mundie (1962) on the guinea-pig ear, by further measurements of both impedance and volume;
- (3) discover a relationship between body weight and middle-ear volume, both in my data and in previously unpublished data of Mundie (1971);
- (4) study the time courses of the magnitude and phase changes due to spontaneous middle-ear-muscle contractions in the guinea pig;
- (5) revise the topology of the middle-ear model of Zwislocki (1963), to better fit the arrangement of the actual mechanoacoustical system; and
- (6) show that the model can, at least qualitatively, explain the effects of the middle-ear muscles on the frequency characteristics of the ear's impedance.

Appendix

ANALYSIS OF NO-DRUM IMPEDANCE

In this appendix I shall derive the equations presented in Section 6.2.2, which relate parameters of the middle-ear model to certain features of the no-drum impedance curves.

The electrical analogue of the middle ear with the tympanic membrane destroyed is shown in Fig. 29. If $R_{b2}=0$, then this circuit has a resonance, that is, an impedance minimum, when the reactances of C_{b2} and L_{b2} cancel; that is,

$$\frac{1}{C_{b2}} = \omega_1^2 L_{b2},$$

where ω_1 is the resonance frequency (in units of sec^{-1}). The antiresonance, that is, the impedance maximum, occurs when the reactance of L_{b2} cancels the reactance of the series combination of C_{b2} with the parallel combination of C_e and C_{b1} ; that is,

$$\frac{1}{C_e + C_{b1}} + \frac{1}{C_{b2}} = \omega_2^2 L_{b2},$$

where ω_2 is the antiresonance frequency. A third equation is obtained by noting that at low frequencies the circuit reduces, approximately, to a parallel combination of C_e , C_{b1} and C_{b2} ; thus,

$$C_e + C_{b1} + C_{b2} = C_1,$$

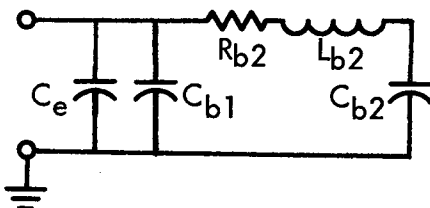


Fig. 29. Analogue of the middle ear with the tympanic membrane destroyed.

where C_1 is defined as the low-frequency compliance of the middle ear. These three equations may now easily be combined to yield expressions for the model parameters in terms of ω_1 , ω_2 and C_1 . Substituting $2\pi f$ for ω then gives the equations of Section 6.2.2. Note that this derivation assumes R_{b2} to be zero.

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