

ACOUSTIC TRANSMISSION AND TRANSDUCTION IN THE PERIPHERAL HEARING APPARATUS

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I. INTRODUCTION

The review by Whitfield (1957) entitled *The Physiology of Hearing* covered the whole field from the mechanics of the cochlea to the electrical responses in the auditory cortex. The present article is limited in scope to the subject matter of the first sections of Whitfield's review, i.e. to transmission of the acoustic signal from air to the organ of Corti and to the problem of transduction of the energy of this signal from its acoustic form to an alternative mode of expression of energy. The main concern will be with low energy inputs and particularly with near-threshold values.

In addition to Whitfield's survey, other review articles and reports during the past decade which have been drawn upon for information and references include first of all von Békésy (1960), Davis (1957), Rasmussen and Windle (1960), and Wever (1966). A general introduction to the subject is presented by Groves (1965): more specifically related to the problems discussed here are the many quantitative assessments made by de Vries (1956).

A brief description of the peripheral structures involved in (mammalian) hearing will make it easier to visualize the accepted theories on the mechanics of the hearing apparatus.

One of the best illustrations of the ear is the composite drawing by Brodel (1946), Fig. 1, showing the external ear, the middle ear with the ossicles in an air space, and the bony labyrinth within the anterior portion of which—i.e. within the cochlea—lies the end-organ of hearing.

Figure 2 is an outline diagram of the route of acoustic transmission. This route goes through the air in the external auditory meatus, through the tympanic membrane and the bony ossicles to the perilymphatic fluid, and across the membranes bounding the cochlear duct.

Figure 3 shows the bony labyrinth with the membranous labyrinth outlined. Both windows have faces looking into the middle ear airspace.

Figure 4 is an actual dissection and staining of the cochlea: the outer layer of bone has been removed from the cochlea to reveal the spiral arrangement.

Figure 5 shows the cochlear duct in cross-section. Note the three fluid-filled scalae spiralling around the modiolus (central pencil of bone on left of diagram). The base of the scala media is the basilar membrane on which rests the organ of Corti—the receptor organ—with the sensory hair cells. Overlying the organ of Corti and in close association with the hair processes is the tectorial membrane.

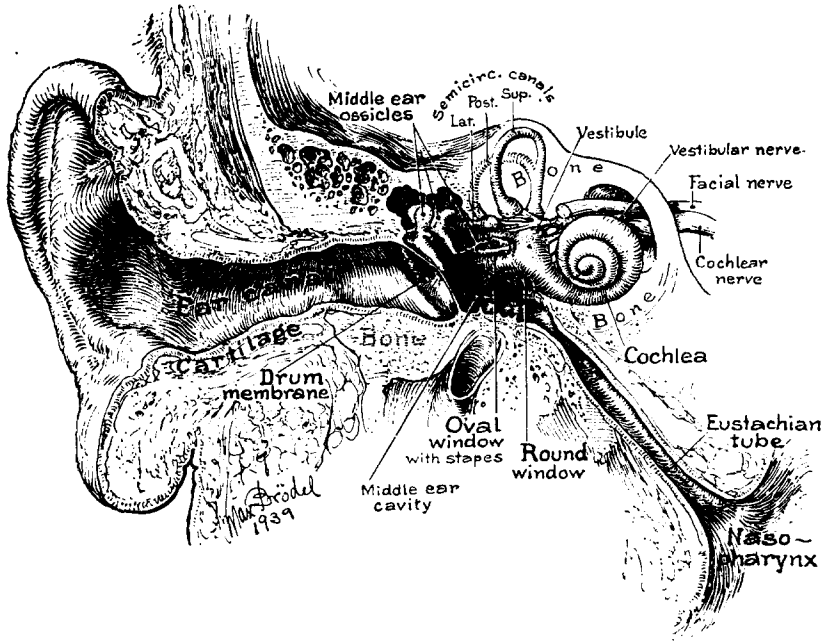


FIG. 1. A composite drawing of the ear. Brodel (1946).

II. CURRENT THEORY

The accepted theory of sound transmission and acoustic energy transduction is as follows:

Longitudinal waves, transmitted through air, enter the external auditory meatus and impress themselves on the tympanic membrane. The ear drum moves in response, and a high degree of impedance matching enables the sound energy to be transferred from a gas phase (air) to a liquid phase (inner ear fluids) without significant loss. This feat is accomplished by the drum membrane-ossicular chain system which amplifies pressures by means of a lever arrangement and a "hydraulic press" type of action. The movement of the stapes transmits the sound waves to the fluid of the scala vestibuli, i.e. the passage above the basilar membrane. The acoustic vibrations now continue through the fluids and are released, so to speak, at the round window which has one face towards the air space of the middle ear (Fig. 6).

The acoustic vibrations in the inner ear fluids set up a pattern of wave motion

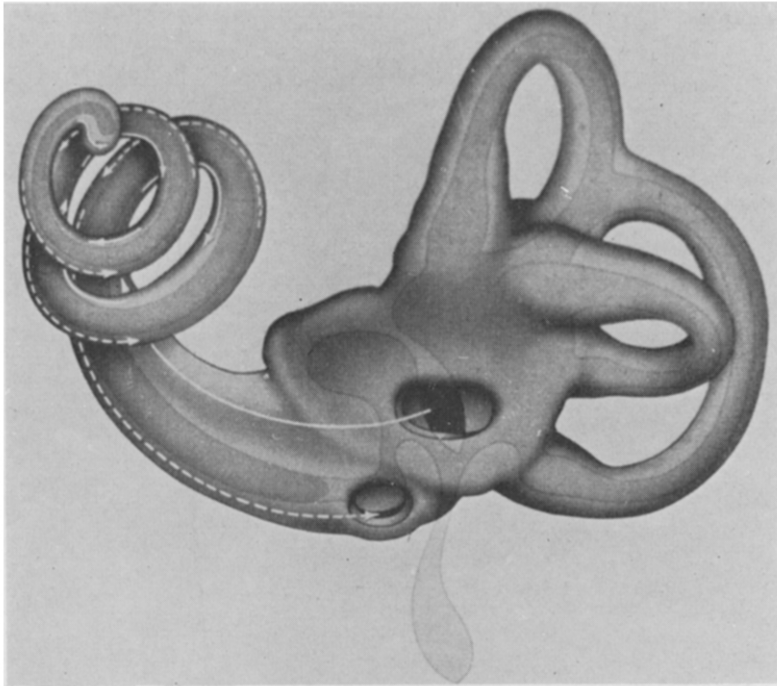
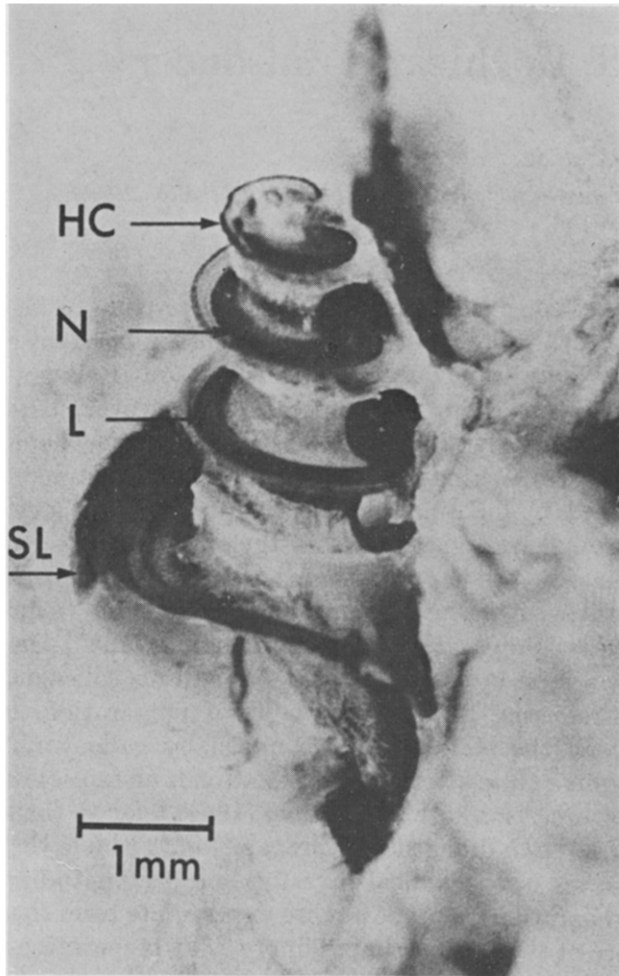


FIG. 3. Membranous labyrinth outlined within the bony labyrinth. Arrows start at oval window at the insertion of the stapes and end at the round window. *Gray's Anatomy* (1958).



in the basilar membrane, and this movement of the basilar membrane, in turn, lifts the hair cells in such a fashion that the hair processes undergo a shearing force because the tectorial membrane, in which the hair processes are embedded, does not move in concordance. This shearing effect is said to be the stimulus which triggers hair cell activity which, in turn, generates nerve impulses in the

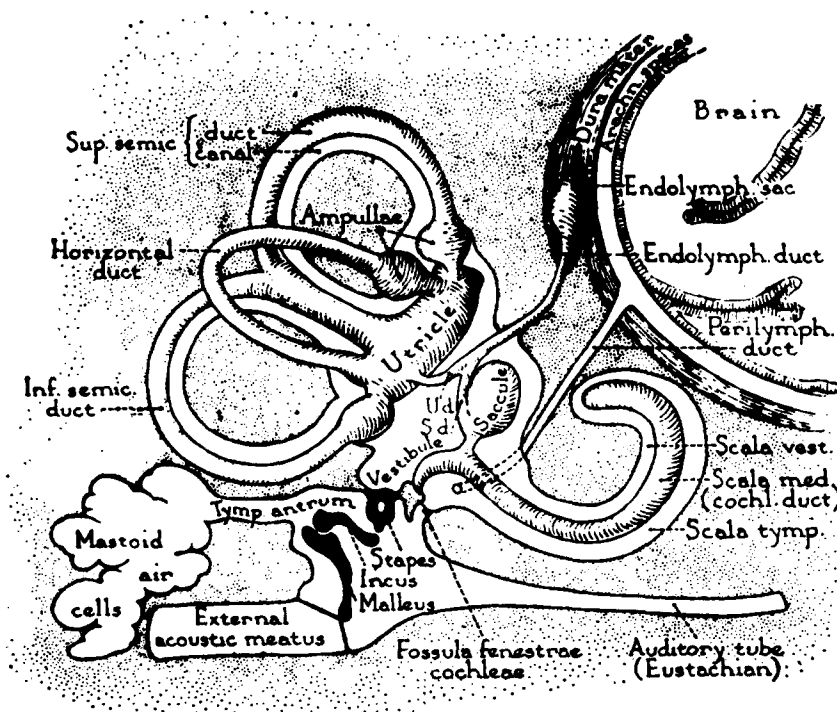


FIG. 2. General relationship of the various parts of the ear showing diagrammatically the route of acoustic transmission. U.d., utricular duct; S.d., saccular duct. Bast and Anson (1949).

8th nerve. Further elements of this theory are illustrated in Fig. 7 (Davis, 1961) showing the contribution of electrophysiological phenomena; but the essence of the current theory is that the basilar membrane undergoes a mechanical displacement in travelling wave fashion and as a result, a mechanical force is exerted on the hair processes (von Békésy, 1960). The travelling wave is generated by pressure variations in the scala vestibuli and has the property by virtue of the structure of the basilar membrane of causing, in the cochlear partition, a pattern of displacement amplitude which has a broad maximum, i.e. it is poorly tuned. This broad displacement cannot by itself account for the fine degree of audiofrequency discrimination subjectively experienced, but together with the phase changes in the vibration along the basilar membrane this peripheral system provides a pattern of mechanical stimuli to the nervous system, which then must sharpen the localization of signals—as produced in the cochlear

partition—to create the subjective appreciation of difference limens. There is thus a mode of frequency analysis by “place” or position of the maximum stimulation of the haircells and of the corresponding nerve supply.

III. SOME EVIDENCE NOT COVERED BY CURRENT THEORY

The current theory as outlined in the previous paragraphs is acceptable as a first approximation in most mammalian species for input energy values

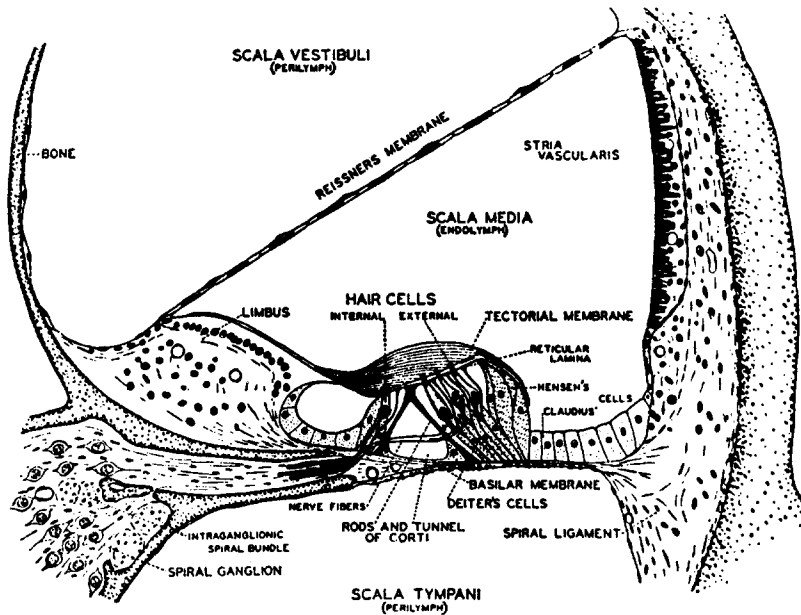


FIG. 5. Diagrammatic drawing of a cross section of the cochlear duct in the second turn of the guinea pig cochlea. Davis (1957).

from about 20 dB above threshold of hearing to near blast-wave energy. Closer examination, however, raises various problems in different fields from comparative biology to signal transduction, which are not readily encompassed by the travelling wave hypothesis, so that modifications or additional postulates become necessary for the theory of hearing to account for all the observed phenomena.

The travelling wave hypothesis was largely founded on observations resulting from the use of signals represented by continuous pure sine waves, and would provide a not unsatisfactory explanation of events if such signals, of sufficient energy, were the main acoustic problems to be taken into account. In addition to data derived from comparative biology and pathology what prompts a re-examination is the need to have an explanation of the simultaneous reception of the complex transients of speech and of the sustained signals of music,

both so received that their characteristics enable a fine degree of separate azimuth location of sources.

1. *Biological Evidence*

In Amphibia, particularly in toads and frogs, there is no basilar membrane but there seems good evidence that some species in this group can hear from 50 c/s to 5 or even 10 kc/s, discriminating frequencies at least in bands (Blair, 1963).

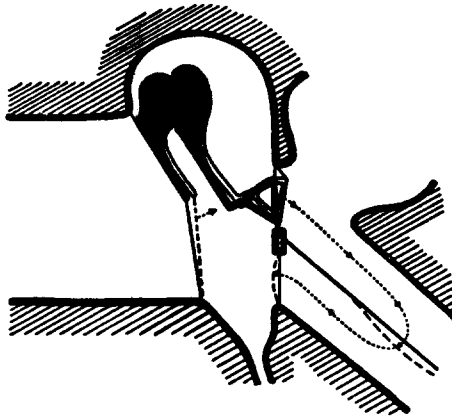


FIG. 6. Diagram of auditory portions of middle and inner ear showing position of ossicles and various membranes at rest and following inward displacement of tympanic membrane by a sound wave. Dotted line and arrows represent path of sound waves. Stevens and Davis (1938).

In the Cetacea, the whale and dolphin family, animals which have returned from land to water, the external auditory meatus is rudimentary, the ossicles are not only fused together but also are attached, not articulated, to the petromastoid bone which contains the cochlea. These mammals have unquestionably good hearing, but no lever or piston-like movement is possible from tympanic membrane to vestibule to initiate the fluid movements in the perilymph necessary to generate a travelling wave.

In birds, a not insubstantial portion of the organ of Corti rests on solid bone (Sato, 1917) and a travelling wave of the kind observed in a membrane, given sufficient input energy to the membrane, is thus not possible. Other evidence derived from behavioural studies in birds will be more conveniently described in the next section. According to Shambaugh (1907) the basal end of the organ of Corti in the swine rests, as it does in birds, on fully ossified bone.

Since an important element in the travelling wave hypothesis is that a shearing force is produced on the hair cell processes by the tectorial membrane (von Békésy, 1953) it is of interest to examine the nature of the interacting components. Von Békésy (1947) describes the tectorial membrane as "together with its supporting structure it represents essentially a flat, delicate, thin-walled

tube filled with fluid . . .". Naftalin, Spencer Harrison and Stephens (1964) analysed the tectorial membrane and showed that it consisted of about 90% water structured by protein into a soft (i.e. delicate) gel. It should be emphasized, however, that this gel has no wall but has a watery surface in contact with the surrounding aqueous medium.

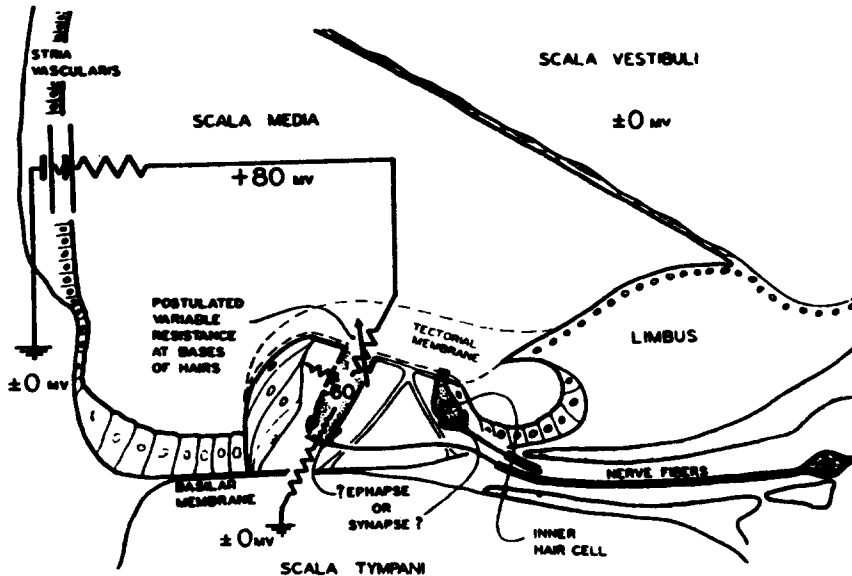


FIG. 7. Diagram of proposed receptor action of the organ of Corti. The interiors of the hair cells are negatively polarized, about 60 mV relative to their surroundings. Reissner's membrane separates scala media from scala vestibuli. The endolymph of scala media is about 80 mV positive relative to scala vestibuli and scala tympani. The source of the positive potential of scala media is in the stria vascularis. When the basilar membrane vibrates a shearing motion occurs between the tectorial membrane and the organ of Corti. The hairs of the hair cells, imbedded in the tectorial membrane, are therefore bent or subjected to a shearing force. If this bending or shearing causes a change in electrical resistance across the cell membrane at the base of the hairs (or along the hairs) the leakage current through the hair cell will increase or decrease. An increase in the leakage current presumably liberates chemical mediator at the base of the cell and the mediator stimulates the nerve endings (synaptic transmission), or else the current directly excites the nerve fibre or ending (ephaptic transmission). In the diagram the synaptic alternative is arbitrarily shown for the inner hair cells and the ephaptic alternative for the external hair cells. Actually both sets of cells presumably work the same way, but it is not known which alternative is correct. Davis (1961).

On the other hand, the hair processes (stereocilia) are described by Engström, Ades and Hawkins (1962) as standing upright like stiff bristles or fine rods, requiring pressure applied through a coverglass to make them bend. These authors also doubt whether more than the tips of the hair processes are in contact with the tectorial membrane. The question must then arise, can a delicate gel with a watery surface exert a shearing force, specifically and in localized fashion, on stiff rods, either to make them bend or to act as levers?

2. Pathological and Experimental Evidence

The next examples of hearing which appear to require some explanation additional to that given by the travelling wave theory come from human pathology of the inner ear and some animal experiments of a related nature. This evidence is summarized by Wever (1964) in this way: in earlier work Wever and Lawrence (1950) had shown that if a tone was applied simultaneously to the round and oval windows but so adjusted in phase that the two stimulations counteracted one another at the basilar membrane and there was thus no motion of the membrane, then the cochlear microphonics also fell to zero (Fig. 8).

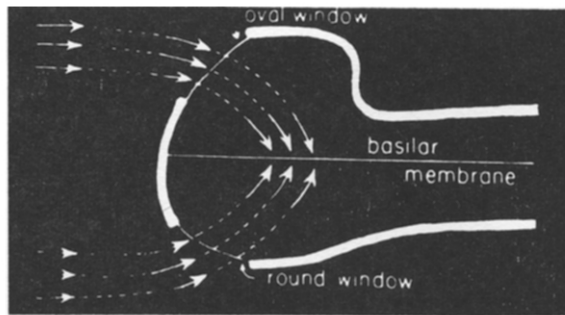


FIG. 8. Sounds applied simultaneously at oval and round windows have contrary effects on the basilar membrane, as indicated by the arrows. Wever (1964).

Yet this condition is one in which all the structures of the cochlear partition are exposed to a maximum sound pressure. It is clear that the hair cells do not respond to pressures as such.

This experiment by Wever and Lawrence may be compared with certain clinical findings concerning the effect of a round window baffle in middle ear disease. Total loss of the middle ear mechanism, leaving the two mobile windows equally exposed to sound waves results clinically in a hearing loss of some 40–60 dB. In an ear lacking drum-head, malleus and incus, remarkably good hearing is preserved if a membrane is placed in the middle ear cavity, across the lower part of the tympanum, so that a shield, but not a closely applied immobilizing shield, protects the round window from direct sound energy. In this way the 40–60 dB loss can be reduced to 25 dB, since there is a preferential sound conduction to the oval window and the pressures on the basilar membrane are unequal and out of phase.

On the basis of this type of evidence, Wever (1964) states that the form of the waves in the basilar membrane depends to a considerable extent on the coupling between the various parts of the membrane. The coupling is of two kinds, that afforded by continuity of the membrane itself and that produced by the surrounding fluid. The theories which suppose that the wave of displacement along the basilar membrane is determined solely by the membrane itself, or even by only the initial motion of the basal end of the membrane, are

over-simplifications and contrary to much evidence; for example, calcification may occur of the basal portion of the basilar membrane without any impairment of hearing from low and intermediate tones; or the presence in some post-mortem specimens of an aberrant artery crossing the basilar membrane which must have caused a damping effect on the membrane without any corresponding change in hearing being evident during life.

The conclusion Wever reaches from the evidence described above is that the propagation of the travelling wave up the cochlea represents an interaction between fluid and membrane, and that the energy driving the membrane at any point is derived jointly from the bordering regions of the membrane and from the surrounding fluid.

This conclusion contrasts with that of Tasaki, Davis and Legoux (1952) who explained the observations they made in experiments in which the effect of drilling holes in various parts of the (guinea-pig) cochlea was found to be negligible, by supporting the view that the vibrational wave travels along the cochlear partition and not along the fluid medium in the scala tympani and scala vestibuli.

3. *Clinical Evidence*

The data, in this field, which bear on the question of the travelling wave concern the problem of sound location. It is accepted that in binaural hearing, for frequencies below 1400 kcs, the time or phase differences are important in azimuth location (Nordlund, 1963). This involves the acceptance that the peripheral mechanism is transmitting and transducing in temporal order signal differences measured in microseconds (μsec), e.g. von Békésy (1930) found that human ears can discriminate interaural time differences in dichotic clicks of about 19 μsec . In the normal subject this may depend on a type of balancing system within a nervous network which has a bilateral input. In a subject who has lost one peripheral mechanism, after early bilateral hearing, the ability to locate is reduced but may still be remarkably good. Such a patient is making use of the nervous network by means of the crossed nervous pathways but the signals he uses are reflected pulses either from objects in his neighbourhood or, as Batteau (1964) has shown by the pulse forms produced by the pinna. In work to determine the role of the pinna, Batteau and his co-workers made a cast of a natural external ear and placed a microphone as the model's eardrum. Figures 9a and b illustrate the alteration in the oscilloscope trace introduced by placing a pinna on a bare microphone. The appearance of the oscillograms is more suggestive of sets of discrete delays than of a smooth continuum. In further work, Batteau was able to construct three-dimensional models on the assumption that the various paths of sound to the ear canal involved multiple delays due to path differences. These delays were found to be different for different aspects of the sound source to the pinna. The important point for the present discussion is that these differentiating delays enabling location to be carried out are of less, or much less, than millisecond (msec) duration.

It is a commonplace feature of the “cocktail party problem” that one can detect and locate a soprano and a bass voice simultaneously, and, again, this can be done, though less efficiently, with one (trained) ear. The signals used for this discrimination are those transients of speech which give the character of timbre. These simultaneous signals which may come from opposite directions are nevertheless interpreted, i.e. they are not confused as must happen if there is a millisecond delay for some components as compared with the microsecond transmission of others. The temporal order of all signals and their components must be maintained in the peripheral mechanism to permit their interpretation. This remains true even if subsequently several different nerve channels are used for different types of acoustic signal. This statement receives reinforcement from the experimental data reported by Boudreau (1965); in these experiments anaesthetized cats were equipped with implanted electrodes in the superior olivary complex and 15–20 msec tone bursts were fed to the contralateral ear. Using a technique involving a computer of average transients the frequency of the stimulating tone was reliably reproduced in the superior olivary complex up to 4.3 kc/s and a definite upper limit could not be established. Boudreau

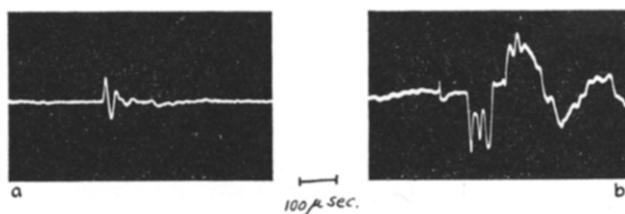


FIG. 9. Oscilloscope tracings comparing the signal as transduced by a bare microphone (a) and the effect of placing a model pinna over the microphone which was sited in the position of the ear drum (b). Batteau (1964).

concludes: “The surprising fact is that the introduction of a synapse at the cochlear nuclei and probably another at the accessory nucleus of the superior olivary complex . . . apparently does nothing to disturb the temporal relationship of interfibre volleying. This fact implies extremely accurate temporal resolution at the cochlear nuclei relay to maintain stable interfibre volleying relationships.” It may be added that the same accuracy of temporal resolution is implied also for all stages back to the original signal.

Nevertheless, serious evidence is presented (Tasaki, Davis and Legoux, 1952) that a 2 to 5 msec delay occurs for the lower tones. Tasaki *et al.* measured directly the time of travel of a given wave along the cochlear partition using as indicator the cochlear microphonics recorded from paired electrodes inserted into each turn of the guinea-pig cochlea. Both pure tones and tone pips were used as stimuli. Simultaneous timing pulses as reference markers were introduced into all channels. The experimenters found that there was, consistently, a long delay in the appearance of the cochlear microphonics in the apical turn—2 to 2.5 msec—as compared with the signal in the base. Davis (1957) quotes an observation by von Békésy which indicated a delay from base to helicotrema of

as much as 5 msec. This interpretation depends on the assumption that the wave-energy in the cochlear partition is propagated through the coupling of adjacent portions of the basilar membrane, and is again in contrast to the conclusion, mentioned earlier, reached by Wever that the energy must be contributed to at each point from the fluids to the cochlear partition.

The conflict of evidence and interpretation described above poses the problem that although temporal relationships of signals must be maintained throughout the peripheral mechanism, delay factors may be introduced which are compensated for by an appropriate integration time in the neural network. This possibility would seem to be excluded by evidence from sound localization experiments. Hall (1965) using click stimuli, which have both high and low frequency components, has shown that the probability that a cell, situated on one side of the medial olivary nucleus, will fire, depends on the relative time of arrival of the stimulus at the two ears. Thus if the stimulus to the ipsilateral ear precedes that to the contralateral ear by 500 μ sec, the probability of the neurone firing would be about twice that of the reverse situation, i.e. with the ipsilateral stimulus lagging. This time-scale is so very much shorter than the delay imposed by the travelling wave for low frequencies only, that azimuth localization of two sound sources, on either side of the head, simultaneously emitting signals containing both high and low frequency components, would be rendered impossible by the confusion introduced by the grossly differing time-scales for the separate components.

Interesting evidence on this point comes from studies on the auditory capabilities of the avian ear. Pumphrey (1961) discussing data obtained by the use of tape-recorders concerning the chaffinch song points out that for the human ear to resolve all the variations and appreciate all the detail, the chaffinch song would need to be slowed up some ten times. This speed of response of the avian ear is even more dramatically demonstrated by the oilbird (*Steatornis*), which uses sonar with a central frequency of the pulse signals about 7 kc/s, as compared with the 70 kc/s used by bats, to fly through darkened caves (Griffin, 1953). The pulse repetition rate of *Steatornis* is high, the silent interval being only 2–3 msec: in order to obtain a comparable discrimination of the delay of an echo, the receptive elements in an oilbird's ear would need to be about ten times as highly damped as in the bat's ear, and evidently the speed of response must be very much higher than that of which the human ear is capable.

It would seem that the peripheral mechanism in the avian cochlea is responding in microseconds—for the oilbird a delay approaching a millisecond for lower components only could prove fatal.

Pumphrey's conclusion that the receptor elements in the oilbird's ear would need to be about ten times as highly damped as in the bat's ear to achieve comparable discrimination is difficult to reconcile with the increased speed of the travelling wave in the avian cochlea necessary to permit the observed rate of auditory response, since the highly increased damping would slow, not increase, the rate of propagation of the travelling wave. The evidence is scanty regarding

this point of avian anatomy, but if Satoh's (1917) observation is generally valid, then there is the added difficulty that the more rapid response in the avian peripheral auditory mechanism is taking place in an organ based, at least in part, on bone.

IV. ENERGY CONSIDERATIONS

Further problems arise when, in addition to microsecond pulse signals, threshold energy values are taken into account.

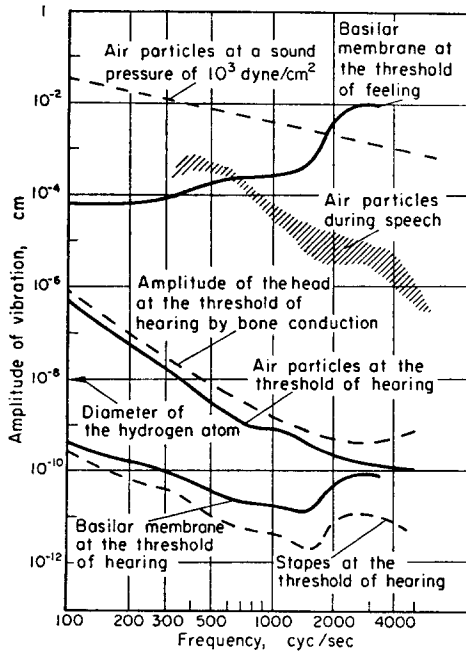


FIG. 10. The vibration amplitudes of different parts of the ear for the threshold of hearing and of air particles at different sound levels are compared with the diameter of a hydrogen atom. Taken from von Békésy (1962) Symposium of Soc. for Experimental Biology XVI. *Biological Receptor Mechanisms*, p. 269 (C.U.P.).

The threshold (of hearing) amplitude (for 1000 c/s) of the basilar membrane is given by the travelling wave theory as 1×10^{-11} cm—Fig. 10 (von Békésy, 1962).

This magnitude is, however, purely theoretical. The travelling wave was observed through a light microscope and the best resolution obtainable with visible light is about 0.1 to 0.2 μ . The microscope used by von Békésy (1949) had a magnification of about 100 times, i.e. the resolution obtained would be about 1.0 to 2.0 μ . Whatever means, e.g. a stroboscope, might be used to measure the rate of vibration of the basilar membrane under the conditions of the experiment, the resolution cannot have been greater than that made possible

by the optical system and the wavelength of visible light. These considerations yield a minimum value for the detected amplitude of about 1 to $2\ \mu$, i.e. 10^{-4} cm. Below an energy input sufficient to produce an amplitude of movement of the basilar membrane of about $1\ \mu$ it is not possible to state an observed value for a travelling wave, and extrapolation from 1×10^{-4} cm to 1×10^{-11} cm involves too great an assumption.

This point is considered by von Békésy (1952); in this paper he refers to his previous measurements (1936) that sound pressure at the pain threshold is of the order of 3×10^3 dynes/cm². "At this pressure the amplitude of vibration of the basilar membrane is about 3×10^{-3} mm for tones between 300 and 1500 c/s. With a microscope with a magnification of 140 times the amplitude of vibration becomes 0.4 mm. The sound pressure and amplitude as given are r.m.s. values, but in a microscope the extreme positive and negative positions of the movement are seen and so the visible vibration is larger by $2\sqrt{2}$. Hence the small silver crystals deposited on the cochlear partition (to make the movements visible—L.N.) are magnified to lines about 1 mm in length, which is sufficient for observation. In the frequency range from 2000 to 3000 c/s the maximal physiological amplitude is about five times larger. There was no need to raise the amplitude above a value that can be tolerated by a normal person, and the measurements were made at that level. The period of observation was always kept as short as possible. In general, one second was long enough for measurements of the amplitudes of the small silver crystals" (von Békésy, 1952).

The direct observations were made, then, at 134 dB above the threshold of hearing. In an earlier paper von Békésy (1947) draws attention to non-linearity in the vibration of the cochlear partition, and though he attributes the drop in pitch that occurs for a pure tone (of less than 800 c/s) mainly to neural mechanisms, he shows that the mechanical response of the cochlear partition becomes non-linear above the threshold of feeling. Lawrence, Wolsk and Schmidt (1962) showed that between 80 and 120 dB above threshold of hearing the electrical response is non-linear, i.e. it does not increase proportionally with the increasing vibration amplitudes, and the wave form of the response becomes distorted as harmonics of the driving frequency are generated in the transducing structures.

When, however, von Békésy, having admitted non-linearity occurs towards the upper end of the hearing decibel scale, writes that "there is no reason to suppose that in such a system (i.e. the cochlear partition) the pattern of vibration for very small amplitudes would be any different from that observed" (von Békésy, 1952) at 70–140 dB, he is, surely, begging the whole point of the discussion and makes no allowance for the increasing relative importance of internal frictional and viscous forces as the external driving force decreases. No direct observation has been made of the amplitude of vibration below 1×10^{-4} cm, and the extrapolation factor of 10^7 (or of 10^8 , if Wilska's, 1935, data are used as a basis) is too great to be accepted without further examination.

If we follow the argument on the basis of von Békésy's results and assumptions we arrive at the calculated amplitude value for the basilar membrane at

threshold of hearing of about 1% of the "diameter" of a hydrogen atom. This may be a convenient mathematical deduction but has no physical reality. Discussing this point, Naftalin (1965b) wrote, "Acceptance of subatomic movements by the basilar membrane involves also acceptance of subatomic movements of the ossicles and tympanic membrane. To one whose training makes him see chemical events in solution as collisional probabilities between atoms, i.e. suitable overlapping of electron orbitals, and events in the solid state as strains in a crystal lattice, such strains being changed relations of electron orbitals resulting from changes in atomic vibration distances—when intermolecular and interatomic structural relations are being considered against this background, the suggestion that whole large bodies can vibrate through a much smaller distance than the atomic thermal vibrations is unsatisfactory. It is not only that the whole body is said to be moving through less than its vibrating parts that is unsatisfactory, but that this movement, a small fraction of the random movement, is a specific, detectable and significant signal—this also is not satisfactory." This formulation was made with liquids and gels (the bulk constituents of living matter) in mind, and must be modified when the rigid lattice structure of metallic or refractory materials is taken into account. Even in such a condensed solid as a diamond the thermal vibrational amplitudes of the atoms in the lattice, at room temperature, is 0.02\AA . In the relatively large physical instruments—large when compared with hair cells and even more so with hair cell processes—such as the optical lever system described by Jones (1961), advantage is taken of the statistical cancelling-out of random atomic or molecular movements. This cancelling-out occurs when a macrostructure, such as the millimetre mirror of the optical lever, is used and mechanical movements of the wholly rigid structure is detectable down to $1 \times 10^{-12}\text{cm}$. This distance is the average value of a very large statistical system within the surface (to a depth much greater than $1 \times 10^{-12}\text{cm}$) of the rigid lattice of the mirror. This type of measurement is not possible in the liquid state or even in the gel state of living matter in which, in addition to thermal vibrations, metabolic turnover of the "front-line" of atoms and electrons has to be taken into account. The acoustic signal in the organ of Corti has, on any interpretation, to be made accessible to a transducer of molecular dimensions (see, e.g., Davis, 1960).

The crux of the matter would seem to lie here—does one conceive of small narrow columns of fluid, or of small solid rods, as moving in response to acoustic energy in one piece so that both ends are in phase irrespective of the (short) length of the column or rod and of the rate of movement, and movement is thus considered as a translational whole—and this is undoubtedly a convenient mathematical model yielding useful results in practice—or is this concept inherently wrong (however useful it may be for simplifying calculations) and the movement engendered by acoustic wave energy is not whole-body translational but is transmitted by intermolecular or group-molecular or even interatomic vibrational linkages.

This fundamental point is discussed in various ways in text books of acoustic and vibrational physics. Stephens and Bate (1966) in their chapter 3.2 discuss

the velocity of sound in a uniform rod as follows. Figure 11 represents a portion of a thin uniform rod, the section at A being distant x from some arbitrary origin in the rod.

Assume the section at A to suffer a displacement η , in the x direction at a particular instant when the rod is in a state of *longitudinal* vibration, and that the section at B , which is very near to A at $x + \delta x$, is displaced by an amount $\eta + \delta\eta$ at the same instant. The whole rod is strained and it is necessary to express this in terms of small lengths such as AB , because if A and B were taken to be an integral number of wavelengths apart, the displacement of the section A would be equal to that at section B , and no strain would be apparent. By taking small lengths this is eliminated.

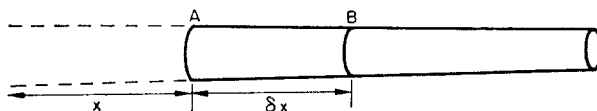


FIG. 11. Longitudinal propagation of sound in a thin uniform rod. Stephens and Bate (1966).

A somewhat different approach is used by the same authors for a different problem. In their appendix 22 (Stephens and Bate, 1966) the authors treat the question of the transmission of sound through walls as follows: "In practice this problem is a very complex one owing to the uncertainty of the boundary conditions and the following analysis merely 'pin-points' the essential physical features. The assumption is made that the wall thickness is small compared with the wavelength of the incident sound so that the elastic parameters of the wall may be neglected. Also the plane wave is incident in the normal direction upon the wall, which will be assumed to be vibrating at any instant with a velocity dependent on the frequency of the wave. Since the wall is thin compared with the wavelength up to quite high frequencies both faces can be assumed to be vibrating in phase."

The approach used in the last example is useful for problems concerned with absorption and transmission of sound but is not strictly valid since for both faces of a wall to be (absolutely) in phase within a fraction of a wavelength means that the velocity of sound through this portion of material is infinite and this, of course, is not proposed. Further, if the thickness of the wall is to be treated as a short rod being moved translationally, then "bugging" of the wall with a microphone would be impossible.

In another section, Stephens and Bate describe energy transfer during the passage of sound as not involving a bodily motion of the medium as a whole, but that as particles at points distant from the source are disturbed there must necessarily be a streaming of energy in the direction of wave propagation. This formulation applies to liquids as well as solids.

Nevertheless, in the application of physical principles to acoustic problems in the inner ear, it can be held that because the cross-sectional area of the canals

of the cochlea is so very small (averaging less than 1 mm^2) the velocity of sound is greatly reduced and viscous forces predominate. In the case of a circular tube, the governing factor in the behaviour of fluid motion is the relationship between the radius of cross-section ρ and the wavelength, λ . If $\frac{2\pi\rho}{\lambda}$ is less than 1, the tube is said to be narrow and frictional resistance predominates over inertia. For the cochlear channels this factor is probably less than 0.05, so that normal wave motion in the fluid can be discounted and movement of the fluid as a whole-body takes place.

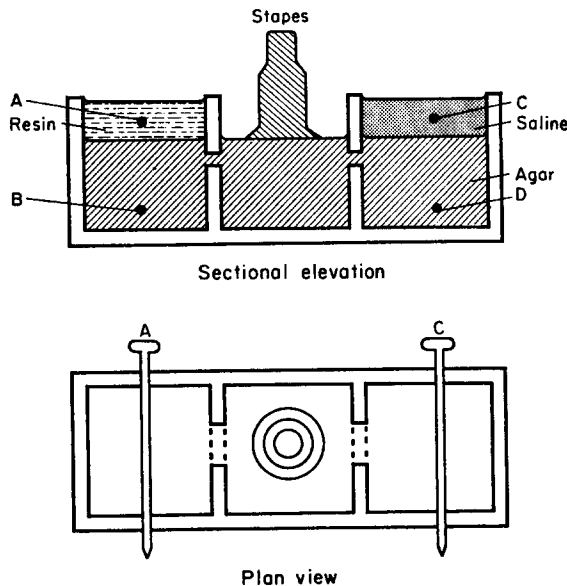


FIG. 12. Diagrams illustrating the construction of the ionic microphone. The casing was made from polythene or from "Perspex". Agar-gel filled the base to beyond the gaps connecting the three chambers. A, B, C, and D were stainless steel pins rigidly fixed through the walls of the casing: these pins acted as electrodes. One chamber was filled with saline, the other with the resin-mix described in the text. No signal was obtainable from the saline side. The acoustic signal was transmitted to the "stapes" (made from brass or wood) by the diaphragm of the earpiece from a hearing-aid.

This concept of whole-body translational movement is difficult to reconcile with direct evidence from the operations of stapes mobilization or of stapedectomy for the relief of otosclerosis. Surgeons have repeatedly noted that when the operation is conducted under local anaesthesia the patient will immediately announce better hearing as the stapes is released from the oval window and some perilymph escapes. In earlier forms of the operation the footplate of the stapes was replaced by a pad of soft fat and hearing was substantially restored. In these circumstances it is not easy to attribute the transmission of the acoustic signal to the whole-body movement of fluid as in a capillary tube.

A further obstacle to the concept of whole-body movement as the mode

of acoustic transmission in a capillary fluid column is to be found in the experiment briefly reported by Naftalin and Stephens (1963) on an ionic microphone. In this experiment a liquid system consisting of two immiscible phases, having no material membrane between them, was so arranged as to act as a microphone capable of the high degree of fidelity necessary for recognition of timbre and inflexion of voice. The system was made originally by saturating butanol with a saturated solution of salt in water, and adding this saline saturated butanol to the liquid anion exchange resin, "Amberlite" LA-1, † drop by drop until by trial and error a maximum electrical signal was obtained from an acoustic input in the apparatus illustrated in Fig. 12. The resin is not miscible with water, and butanol was used to bring the saline phase into contact with the resin. In later experiments, it was realized that the original bulk of resin-mix was unnecessary and that the thinnest film permitting contact between the fixed electrodes and the transmitting agar-gel (Fig. 12) was all that was required. This system worked by the fixation of one ion to the resin with the counter-ion held in the surrounding medium and separated from, or brought closer to, the fixed ion by the acoustic wave. Although the film could be made smaller than the critical dimensions (mentioned earlier for the limitation of wave motion), the mode of action of this system can only have been by transmission of acoustic wave energy through molecular linkages, and not by whole-body movement.

Hueter and Bolt, in their treatise on *Sonics* (1955), consider this conflict of approach by regarding the physical properties of any medium as capable of being described either from a macroscopic or microscopic point of view. On the macroscopic scale bulk properties are measured and no knowledge of internal structure is assumed. The microscopic viewpoint, on the other hand, requires a detailed knowledge of internal structure and composition of matter, and this involves, for example, the forces between atoms and molecules, their distribution in space and the energies they possess. Sound absorption in fluids (i.e. both liquids and gases) is determined mainly by viscosity, heat conduction and molecular effects. The kinetic mechanisms of viscosity and heat conduction are related to the mean free path in the case of a gas, or the average intermolecular spacing and the binding energies in the case of a liquid.

At the low level of energy involved at the threshold of hearing it would seem necessary to adopt what Hueter and Bolt call the microscopic point of view.

The input energy used by von Békésy to observe the travelling wave was above the threshold of feeling. At the threshold of hearing the total energy available is much less, only about 10^{-16} watt/cm² (Stevens and Davis, 1938,) for 1000 c/s. Threshold pressure is 0.0002 dyne/cm² and in order to determine how this force may perform work we have to describe how this pressure is set up and maintained. "Macroscopic" treatment discusses "particle displacement" to evaluate the amplitude of the wave. But in the "microscopic" method we begin by saying there is no bodily movement of the medium—i.e. the mathematical "particle" is replaced by the random movements of the molecules of the air; at lower † "Amberlite" LA-1 was obtained from British Drug Houses, Poole, England.

amplitudes some molecules will even be going in the reverse direction to that of the sound wave propagation. The acoustic pressure in air is set up by a change in a vectorial component of the air molecules so that the "particle" is formed by the temporary alignment of a greater or lesser number of air molecules (Naftalin, 1963 and 1965b).

From macroscopic (bulk) parameters the actual energy of a sound wave in air is given by

$$2\pi^2\rho a^2n^2$$

where ρ is the density of air,
 a is the amplitude of the "particle",
 and n is the frequency of the wave,
 so that for a sound of average intensity of 1000 c/s, i.e.

$a \simeq 10^{-4}$ cm (Fig. 10), the energy = 2.6×10^{-4} erg/cm³,
 and where $a = 10^{-9}$ cm ($n = 1000$), the energy = 2.6×10^{-14} erg/cm³.

The maximum energy available as acoustic signal impinging on the tympanic membrane during 1 cycle 1 msec, is that contained in a column 33 cm long and 1 cm² in cross-section, i.e. approximately 85×10^{-4} erg ($a = 10^{-4}$) and 85×10^{-14} erg ($a = 10^{-9}$); in round figures, about 10^{-2} erg and 10^{-12} erg for average and threshold intensities.

De Vries (1956) from different assumptions and parameters arrived at a threshold power value of 20×10^{-12} erg/sec and since threshold value rises for transients, a value of 20×10^{-14} or 10^{-13} erg/msec.

Let us now make an estimate of the energy required to move a portion of the basilar membrane.

The dimensions of the basilar membrane are given (Stevens and Davis, 1938) as:

Length 30 mm.

Average width 0.33 mm.

The depth of the organ of Corti together with the basilar membrane does not exceed 100 μ .

The volume of the basilar membrane is thus of the order of 1 mm³.

Since these living structures have a high proportion of water in them, the mass of the cochlear partition may be taken as approximately 1 mg. However, only that part of the basilar membrane exhibiting a natural resonance to the input frequency (or other suitable characteristic responsive to the travelling wave) will have a maximum amplitude; there will be smaller displacements on either side of the maximum and the mass of the cochlear partition being displaced for a pure tone may be assumed to be about 1×10^{-4} g.

Any short portion of the basilar membrane being moved as part of the travelling wave will be moved initially in simple harmonic motion, in which the force F for a mass m is given by

$$F = \frac{4\pi^2 mx}{T^2}$$

where F is in dynes; m in grammes; x , the displacement, in centimetres; and T , the period, in seconds. If $m = 1 \times 10^{-4}$ and $T = 1 \times 10^{-3}$ (1000 c/s),

$$\begin{aligned} F &= 4 \times 10^3 \text{ dynes/cm } (x = 1) \\ &= 4 \times 10^{-1} \text{ dynes}/\mu. \end{aligned}$$

This force acts once per cycle; this statement rests on the fact that the travelling wave is a forced oscillation operating in a system of very high damping. Von Békésy does not mention the travelling wave as continuing after the input ceases.

The input force therefore acts once per cycle and if this force moves 10^{-4} g of material a distance of, say, 10^{-4} cm before elastic forces bring it to rest and a return to base line, then *work done per cycle* to sustain the travelling wave at a given point in the basilar membrane will be of the order of

$$4 \times 10^{-1} \times 10^{-4} = 4 \times 10^{-5} \text{erg.}$$

10^{-4} cm, as previously considered, is the smallest experimentally determined amplitude. Even if one accepts extrapolation down to 1\AA (10^{-8} cm) as a distance through which a whole-body's "front" can still be said to move, this nevertheless requires 4×10^{-9} erg. This leaves a discrepancy with threshold energy of about 10^4 or 10^6 .

1\AA is the lower limit below which the "front" of a macromolecular, or larger body in biological systems cannot be said to move coherently; to observe below 1\AA is experimentally impossible and to extrapolate theoretically impermissible, but even so to extend the calculation by a further three orders of magnitude still would not meet the discrepancy.

If there is insufficient energy to move a section of the basilar membrane, there is clearly insufficient at and near threshold to move the tympanic membrane and ossicles. (The optical demonstration of the vibration of the tympanic membrane when subjected to sufficient acoustic energy to make this experiment possible is a different proposition.) The three ossicles together have a mass of about 10 mg (Bast and Anson, 1949). To move the ossicles 1u would require work done per cycle of 10^{-3} erg (and for 1\AA , 10^{-7} erg) in addition to the work done on the section of basilar membrane, increasing the discrepancy with the known input threshold energy. This discrepancy still does not take into account frictional losses but assumes 100% efficiency of transmission.

The eardrum normally transmits the incoming acoustic signal as such and does not convert it in a manner that it generates sound. An interesting demonstration by nature of the truth of this statement has been recently noted in the following case history,† the details of which will be reported elsewhere.

A young child has been observed from several months old to, at the time of writing, $2\frac{1}{2}$ years of age, to be suffering from "objective tinnitus". Tinnitus is the name given to "ringing" in the ear, or ears, and since nearly everyone has their own experience of this, even if only transitorily and very occasionally,

† I am indebted to Mr. Spencer Harrison, Consultant Otolaryngologist, at the National Hospital for Nervous Diseases, Queen Square, London, for information on the observations made. The responsibility for the interpretation offered is, however, the author's only.—L.N.

the phenomenon is accepted as a clinical reality though no-one has ever heard another person's tinnitus.† The child in question is the exception. A note, which has been recorded on magnetic tape under fully controlled conditions by expert sound engineers, is emitted from both eardrums, the frequency being about 7500 c/s. More detailed investigation is required but must await the development of the infant to a co-operative age.

The essential point in the interpretation of this observation is that whatever is emitting this signal is doing so into an air-space or the outside observer could not hear it, i.e. it is unlikely to be an inner ear derangement. This is borne out by the fact that the emission of the sound ceased during an attack of otitis media, and by the cessation of the sound also, by placing water in the external meatus. The sound the observer hears from the child's ears is coming via the tympanic membrane, i.e. the eardrum is, in this case, acting as a drum.

An explanation of this phenomenon may lie in postulating a localized derangement of the central nervous system—since the condition is bilateral—whereby an imbalance of the middle ear muscles is so set up that while continuing to work at their physiological rates, they “hunt” (cf. electronic oscillating circuit) a balance with one another, similarly to the tremor of Parkinson's disease, and in so doing trigger the equivalent of an alarm clock mechanism, this secondary vibrator having a natural frequency of 7500 c/s. Since considerable work is being done it is reasonable to look to muscle action for this, and the arrangement of the middle ear muscles, the stapedius and tensor tympani (*Gray's Anatomy*, 1958; Hallpike, 1935), is the necessary arrangement both with regard to the insertion and action of their tendons and to their innervation. It may be worth mentioning, in parenthesis, that the interpretation offered is open to experimental confirmation in a suitable animal.

None the less, it is important to remember the prediction made by Gold (1948), on the basis of the work of Gold and Pumphrey (1948), that a case of objective tinnitus would be conclusive proof of their hypothesis that the basilar membrane consisted of a series of resonating elements. The prediction suggested that by means of a positive feedback a signal from the basilar membrane would be amplified so that it could be registered by an external observer.

The problem Gold and Pumphrey were essentially dealing with was also that there was insufficient energy at low acoustic inputs to move the basilar membrane unless there was resonance. The damping of the basilar membrane by the labyrinthine fluids could be shown by their theory to be offset by a positive feedback mechanism involving the electrophysiological phenomena of the cochlea. In this way, a low energy input signal could still actuate a resonant element. However, a difficulty in accepting the prediction of objective tinnitus from the theory of Gold and Pumphrey is that if sufficient energy were generated in the inner ear to be fed back along the route to the tympanic membrane and perform the necessary work there for sound emission, the energy would have to be of such intensity that the structures of the inner ear might well be damaged.

† Unilateral objective tinnitus due to oberrant arterial pulsation, or to non-aural muscle disturbance, is not being considered in this context.

V. SIGNAL LOCATION

Both the resonance and travelling wave hypotheses provided a means of locating the acoustic signal, and if neither of these theories could be considered wholly satisfactory it became necessary to find some other mechanism which not only did not dissipate the very small amount of signal energy available at threshold but actually concentrated this energy in a locality of the transducing mechanism on the cochlear partition. This need led to the suggestion (Naftalin, 1965 a and b) that the internal geometrical design of the cochlea was the primary frequency analyser.

As pointed out elsewhere (Naftalin, 1967), biological observations provide strong supporting evidence—in particular the fact that in the human species the cochlea reaches adult size and geometrical configuration at 6 months' gestation, which implies that the nervous system does not need to relearn a new distribution of acoustic signal energy with each period of growth. In the chick, the otic capsule is complete by the 10th day of incubation (Friedmann, 1959). In those animals, e.g. mice, where the cochlea is not mature at birth, the nervous connections are also not complete and cochlear microphonics are not obtainable until a final stabilized system in terms of growth has been formed (Alford and Ruben, 1963; Kikuchi and Hilding, 1965).

From the above data it was thought that useful information might be obtained by making a series of models imitating, by increasingly complex steps, the interior geometry of the cochlea. This has been briefly reported (Naftalin, 1966) and in greater detail (Naftalin, 1967). It was found, using a new vibration sensor, that the pattern of acoustic energy distribution in a liquid medium depended substantially on the geometry of the container. A repeat three-dimensional interference pattern was obtained in a uniform rectangular tank, whereas a selection of signals was found when the walls of the container were sloped to approximate to the geometry of the mammalian cochlea.† This selection consisted of a linear distribution of maximal signals, as registered from the probe connected to the oscilloscope, the lower frequencies appearing at the shallow "apical" end and the higher frequencies towards the deep "basal" end. Depending on the individual construction of a given model, some lower frequencies showed a sharp maximum without a second placement; other frequencies showed a definite maximum with lesser maxima towards the base. The higher frequencies had no representation towards the apex. No basilar membrane was required for this demonstration, but when a wedge-shaped "tectorial membrane" made from agar-gel was placed across the basilar gap the placement of the signal maxima was sharpened, a maximum being "placed" within 2 mm. A further experiment of cutting the "tectorial membrane" into four pieces demonstrated that continuity lengthwise of the gel was not essential for its function. This

† The avian "cochlea" is not only shorter and straight but does not appear to show the same degree of convergence of the walls from base to apex. Nevertheless, from such limited data as are available on this point of avian anatomy, it is permissible to conclude, provisionally, that there is sufficient convergence of the walls to provide frequency distribution to a first approximation.

finding is in conformity with the conclusion of Wever mentioned earlier (p. 10), that, in terms of the cochlear partition, energy was contributed to it at each point from the surrounding labyrinthine media as well as from its own internal coupling.

It is worth noting that the distribution of acoustic energy within the cochlea by virtue of its internal geometry contributes the type of peripheral analysis which is suitable for the "edge-detection" mode of neural coding described by Whitfield (1967).

Although the natural tectorial membrane is known to be a non-collagenous protein (Naftalin, Spencer Harrison and Stephens, 1964; Bairati, Iurato and Pernis, 1960), agar-gel was chosen as the material for making a synthetic "tectorial membrane" because of its ease of workability, its cross-linking, and most importantly, a character it shares with the natural tectorial membrane, agar-gel having a solid-type lattice structure, has a water-structured surface which is not separated by any boundary from the liquid water of the surrounding medium. This property may be the essential one which makes the transducing mechanism so efficient, in that no loss of energy will occur as is usually the case in the transference of the acoustic signal from the liquid phase to the solid phase.

The frequency distribution demonstrated indicates a possible mechanism for acoustic signal placement of more than the minimum of 2 cycles necessary for a cue to frequency determination. It seems not unreasonable to extend the suggestion by postulating that pulses less than 2 cycles are also "placed" in the lattice of the tectorial membrane by a matching of energy characteristics of the pulse to the lattice structure. Such a concept accommodates the observations that loud sounds have a greater frequency spread than sounds of weak intensity.

The demonstration that the geometry of the container influences the distribution of acoustic energy in a liquid medium and the suggestion that energy migration of a transient pulse may take place to a matching position in the lattice structure of the gel, have recently received additional interest from the analogous discovery, in solid state semiconductor work, that so-called "domain originated functional integrated circuits" have the property of controlling the current through the device by virtue of its geometry (Sandbank, 1967). Thus, if an electromagnetic field property can be controlled by the geometry of its "container" it should not be unexpected that an acoustic field should be similarly influenced.

VI. TRANSDUCTION

The travelling wave theory requires that a shearing force be exerted on the hair processes and that this mechanically deforming stimulus should then trigger the electrochemical events in the hair cell. Presumably the transmission and conversion of this mechanical force is by a depolarization of a membrane, or change in configuration of some macromolecule, but this involves a degree of speculation and is not specifically stated. If, instead of the travelling wave mode we accept that the distribution of acoustic energy may occur as outlined above governed initially by the internal geometry of the cochlea, then we are not

concerned with the "macroscopic" viewpoint, i.e. conventional mechanics cannot solve the problem; we have to adopt the "microscopic" mode of analysis and interpret the transduction as occurring through molecular interactions.

Amongst the various methods of transduction at molecular level which have been proposed there are the ionic microphone (Naftalin and Stephens, 1963) mentioned previously; the protein electret model (Naftalin and Stephens, 1966) which is capable of responding microphonically to extremely low—close to threshold—levels of airborne acoustic energy, and the (probably) related phenomena of displacement potentials of hyaluronate molecules described by Vilstrup and Jensen (1960). In Vilstrup's experiments, developed by Christiansen (1963), preparations of hyaluronic acid in a capillary tube showed a definite electrical signal when moved lengthwise within the capillary tube, and the polarity of the signal was reversed when the direction of movement was reversed. These experimental demonstrations that protein and complex carbohydrate molecules can, either by a form of resonance or by a conformational change, exhibit an electrical signal corresponding to a weak, or very weak, applied acoustic signal, remind one of the possibility that the biochemical responses obtained by Vinnikov and Titova (1964) could be the expression of "tuning" of the hair cells (or processes), or matching of a macromolecular constituent, to the energy characteristics of the acoustic signal.

The results of the analysis of the tectorial membrane (Naftalin *et al.*, 1964) indicated that the tectorial membrane had an ionic structure different from both endolymph and perilymph, and the possibility therefore existed that the d.c. potential within the tectorial membrane might be different from that found in the surrounding fluids. Recently, Lawrence (1965, 1967) has explored this point and has discovered that the tectorial membrane lies at zero potential between the positive d.c. endolymphatic potential (of about 80 mV) and the negative d.c. potential in the region of the intercellular spaces below the reticular lamina. Thus any fluctuation of the tectorial membrane would give rise to (cochlear) microphonics and indeed any change in surface polarity engendered by ionic shifts—as in the ionic microphone (Naftalin and Stephens, 1963)—would lead to an amplified electrical signal. It is worth noting that a characteristic of such a system would be the absence of threshold and this would correspond to the *in vivo* findings for cochlear microphonics, and also the response could be expected to be linear up to high intensities. The energy for the amplification originates in the metabolic activity of the cells maintaining the d.c. potentials.

The examples given above do not exhaust the possibilities of molecular mechanisms for transduction. For example, although a piezo-electric property has been often postulated for some structure in the inner ear, Wever (1966) could write: "A passive process (in energy transfer) is one in which the mechanical energy of the stimulus is transformed into electrical energy; an active process is one in which the stimulus is a trigger that liberates energy from a local source. The passive type of process has the advantage of simplicity but a disadvantage in that it is difficult (though not impossible) to conceive of mechano-electrical conversion of energy in tissues. The piezo-electrical effect is such a conversion

that occurs in crystals with a peculiar arrangement of changes in their structure. Such an effect in the ear, or anything closely analogous, has not been demonstrated and does not seem likely."

Recently, however, it has been demonstrated by several groups of workers that bone possesses piezo-electric properties, e.g. Fukada and Yasuda (1957), and Shamos and Lavine (1967) suggest that other tissues may also exhibit this characteristic. Another approach to the electrical properties, arising from structure, of living tissues, is given by Friedenbergl, Danielli and co-workers (1966 a, b and c); in these papers it is shown that lipoprotein macromolecules when organized in a membrane, as in a cell surface membrane, produce an electric field which can have influence on macromolecules in solution up to 100 Å distance from the surface. Such a property must modify profoundly the description of intercellular relations and the mode of action of electrophysiological phenomena.

There is thus, clearly, a sufficiency of molecular mechanisms capable of performing localized transduction of low intensity acoustic signals. In an earlier discussion (Naftalin, 1965b) a further possibility was offered—that of a phonon-electron interaction, and while this is more speculative than the experimental models described above, the suggestion should not be ignored that an electron transfer or orbital matching (equivalent to radiationless transfer of energy) may be worth examining, since, in biological material, enzyme configuration, determined by electron shifts, is the characteristic mode of energy transfer and thus possibly also of signal transduction.†

If we look again at the power value of the signal at threshold, viz. 10^{-12} erg/msec, approximately, and, remembering that transduction of transients is occurring within the millisecond interval, we see, by translating into electron volts (eV), that the question of enzyme participation is less speculative than at first sight. 10^{-12} erg = 1 eV (approx.), and if this small amount of energy were to be distributed throughout a large volume—and in this connection a "large volume" would be anything greater than one hair cell process—the signal-to-noise ratio would be such as to swamp completely the signal despite the proposal made, e.g. by de Vries (1956), that several signals in phase could enable a computer mechanism to pick out the signal and allow the random noise to cancel out. A single impulse requires a 30 : 1 signal-to-noise ratio to have a probability of error of 0.01 (Raisbeck, 1964); the hearing mechanism for bats using sonar to locate moving insects against background noise must have this degree of accuracy. The signal-to-noise ratio would be less for signals in phase. However, the noise we are concerned with here is the thermal noise in the hair processes, and as Brownian movement has been shown to be greater than the threshold

† Two papers by Niauxsat (1967) and Niauxsat and Legouix (1967) present experimental evidence that the cochlear microphonics are not in the direct line of transduction from acoustic energy to 8th nerve action potential. Should these authors prove to be correct, the position would then be that the cochlear microphonics should be regarded as by-products of the structure, position and relations of the tectorial membrane, and the possibility of a phonon-electron interaction (Noftalin, 1965b) being the mode of transduction would require to be given more serious consideration.

signal (de Vries, 1956) the dissipation of the acoustic signal to form several stimuli in phase would simultaneously reduce the energy content per stimulus to a yet poorer signal-to-noise ratio. What the system seems to require is a concentration (localization) of energy as a wave-packet and the threshold value just about meets the energy-needs to raise a molecule into a semiconducting state. The demonstration of electrode activity of quinone-tanned protein by Digby (1965) is relevant here in that such a complex has the character of a free radical, the unpaired electron of which can be readily brought to a semiconducting level. It may not be a difficult transition within a cell-membrane structure for an energy transfer to occur from a semiconducting protein to an enzymic molecule.

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