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THE TRANSFER OF ENERGY ACROSS THE COCHLEA

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THE TRANSFER OF ENERGY ACROSS THE COCHLEA

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THE TRANSFER OF ENERGY ACROSS THE COCHLEA

Two concepts concerning different aspects of cochlear function are in an apparent conflict: the pressure-wave concept (which maintains that the acoustic energy entering the cochlea by the oval window must leave *in toto* by the round window) and the traveling-wave concept of Bekesy. If the latter would really entail the progression and dissipation of energy in the direction of the helicotrema (according to the common definition of wave travel), this energy would have to be diverted from the pressure wave. The dilemma is solved by consideration of fluid motion in cochlear models.

Energy is transferred from the vestibular scala across the partition to the tympanic scala. In this process the partition responds to the velocity of the fluid motion. The latter fact accounts for the shape of the envelope over the traveling waves. The finding that the amplitude of fluid motion in both scalae decreases in a fenestro-apical direction is accounted for by the Reciprocity Theorem of Helmholtz.

It is the consensus of many writers in the field that the acoustic energy which enters the inner ear via the oval window passes through the cochlea and leaves *in toto* via the round window. Figure 1 shows this concept pictorially: a pressure wave which traverses the incompressible cochlear fluids thereby crossing the cochlear duct at the point of maximal stimulation. Consequently, the two cochlear windows are in exact phase opposition, a fact which has been confirmed experimentally by numerous investigators. This pressure-wave concept was further supported by measurements of Wever and Lawrence (12). These authors were able to cancel cochlear microphonics by simultaneous application of identical stimuli to both windows, provided the two were of equal amplitude and in phase opposition. This result coincides with the experience of the present author in studies on cochlear models (9, 10). As accurately as can be ascertained by microscopic observation, the displacement of the two cochlear windows is always equal in amplitude.

Figure 1, on purpose, was taken from an older publication by Wilkinson. It appeared in 1922 before Bekesy's experimental results (1) had become available. Since then the following questions have been raised: Can the simple concept of figure 1 be upheld in view of the

traveling-wave concept of cochlear stimulation? Or phrased differently: Does not the pressure-wave concept present a serious obstacle to the acceptance of the traveling-wave phenomenon? The apparent conflict between the two concepts may be stated briefly, as follows: In response to acoustic stimulation of the cochlea, a pattern of waves is established along the partition (fig. 2). These waves travel invariably toward the helicotrema. Their amplitude, after building up toward a maximum, decays rapidly with distance. By common definition, wave travel along a given path implies propagation of energy in the same direction. Furthermore, a decrement of amplitude along the same path is usually taken to indicate dissipation of the traveling energy with distance. If this be correct for the case of the cochlea, the dissipated portion of energy would be lost from the pressure wave. Consequently, less energy would be emitted from the round window than had entered the cochlea by the oval window. This of course is contrary to the pressure-wave concept.

Bekesy has never taken any position on this issue as he recently professed in a joint paper with Wever and Lawrence (13). Other writers have done so and have attempted to compromise between the two concepts which seemed to be mutually exclusive. Wever and Lawrence, in the joint article with Bekesy just mentioned,

have arrived at such a compromise. They assumed a dual mechanism of action: (1) a "primary zone" (up to and including the region of maximal membrane displacement) in which the transfer of energy was thought to be primarily through the fluid—that is, from window to window; and (2) a "secondary zone" (distal to the primary one) in which transfer of energy along the membrane was thought to attain more prominence. The present writer must confess that he had entertained an essentially similar notion until he was convinced otherwise by experimental evidence. It is the purpose of the present paper to show (1) that the pressure-wave concept of energy transfer through the cochlea is still valid, although its mode is somewhat more complex than it might appear from figure 1; and (2) that this mode of transfer is entirely compatible with the existence of traveling waves along the cochlear partition as first described by Bekesy (1).

In order to test the pressure-wave hypothesis once more, experiments were carried out on cochlear models such as the author had used before (9). Two models were employed which were identical except for their partitions which in one model was of the usual elastic variety. The other one possessed a solid partition

the helicotrema being the only communication between the two "perilymphatic scalae."¹ No traveling waves (in the sense of Bekesy) can develop in the second model, in contrast to the first one. A pressure wave traverses the scala vestibuli, crosses over at the helicotrema, and continues along the scala tympani, as if both scalae were one continuous channel.

If energy would actually be consumed in formation of the traveling waves, a difference should be noted between these two models as to the degree of energy transfer from window to window. It might first be noted in passing that the impedance of both models was not expected to be identical. Because of the total length of its channels, the model with the solid partition had a high degree of frictional resistance, which should affect transmission of *all* frequencies in an equal manner. However, this difference in frictional resistance was only of secondary interest with respect to the present problem. More important was the frequency characteristic of transmission between the two windows in the two different models. Three possibilities were visualized:

¹In the following, accepted anatomic terminology will be used in referring to the various structures of the models.

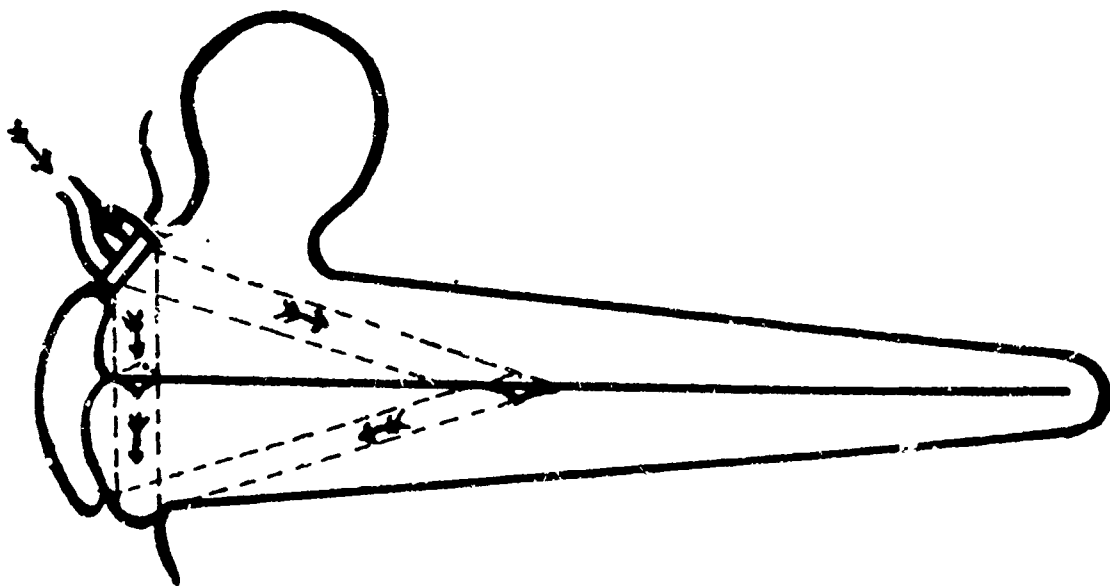
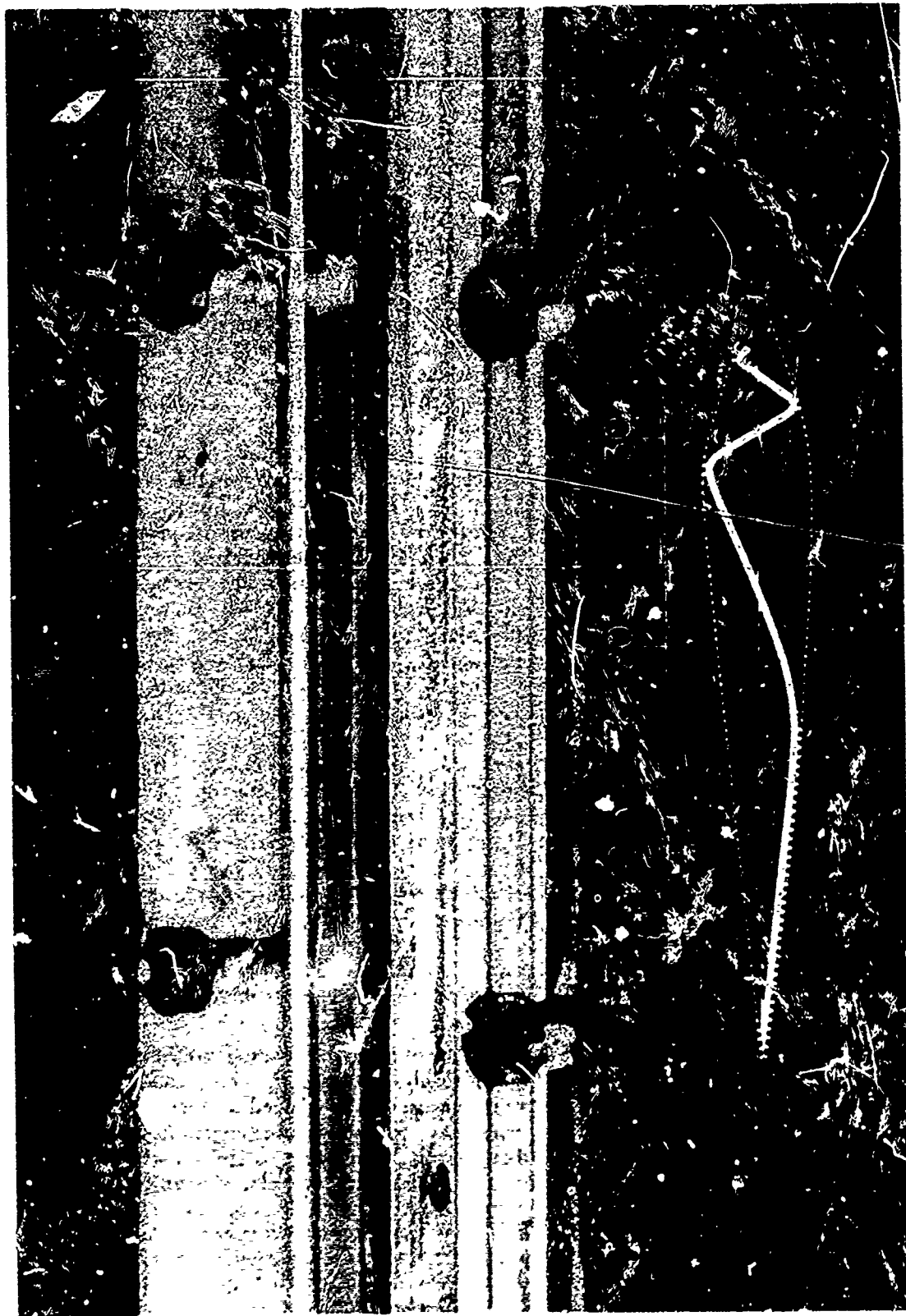


FIGURE 1

Schematic graph of an unrolled cochlea, after Wilkinson (14), showing his concept of the transfer of acoustic pressure waves across the cochlea. This concept is essentially based upon the assumption of localized resonance phenomena in the sense of Helmholtz.



Photograph of a traveling wave in a cochlear model along the partition. Travel from left to right. By comparison with the graph below, which shows the same phenomenon schematically, one notes two "troughs" and two "crests." Actually when in motion several more crests may be seen. Also shown is the lessening of wavelength from left to right which is a sign of the phase lag accumulating with distance. The broken outline in the graph represents the "envelope" over the traveling waves.

(1) if energy would actually be consumed in the wave travel along the (elastic) partition, it should be confined to the case of higher frequencies, for low frequencies, which do not form traveling waves, ought to transmit their energy through the helicotrema essentially in the same manner as it occurs in the model with the solid partition for all frequencies. In that case, therefore, the frequency characteristics of the two models should follow similar courses in the low-frequency region but become different at higher frequencies. More precisely, the two curves, although at different levels, should parallel each other in the low-frequency region, but should converge and possibly cross over at higher frequencies, provided the model with the solid partition had a higher frictional resistance. (2) if all sounds entering the oval window were to be transmitted to the round window in an equal manner in both models, the frequency characteristics should remain parallel to each other. (3) If the higher frequencies were to traverse the elastic partition at the point of maximal stimulation, their pathways would become relatively shorter with increasing frequency (cf. fig. 1). Consequently frictional resistance should be lessened and the rate of transmission be improved for these frequencies. In that case, the frequency characteristics of the two models might even diverge with frequency, provided again that the transmission through the model with solid partition be the lesser of the two because of its higher frictional resistance.

The actual experiments were conducted in the following manner. The oval window of the model was connected to a loud-speaker driver unit by means of a small, closed, and air-filled coupler. A probe-tube microphone was inserted into the coupler so as to obtain sound pressure in front of the window. In order to take measurements in a similar order of magnitude at the round window, an identical coupler was connected there, except that it was terminated by a thin membrane instead of the loud-speaker, and the probe-tube microphone was inserted into this coupler.

In all experiments sound pressure readings in front of the oval window were taken after first adjusting the pressure so as to produce a constant particle amplitude (i.e., 0.08 mm.)

within the cochlear fluids. (The latter phenomenon which can be observed under the microscope, must remain unexplained for the time being. Particle motion within the cochlear fluids will be fully discussed later on.) Since particle amplitude within the fluids of the model is inversely related approximately to the cube of frequency of the driving force produced in the coupler, the present method was limited to the use of frequencies lower than 60 cps. However, in terms of the present model, which is about $2\times$ larger than a human cochlea, 60 cps is a moderately high frequency, corresponding to approximately 360 cps in the human cochlea. It is well within the range of frequencies which form complete traveling waves along the elastic partition. Transfer of energy through the helicotrema becomes noticeable under the microscope at frequencies below 20 cps which for purposes of the present problems were considered low frequencies. In all experiments the range of frequencies used was 7.5 to 60 cps—that is, three octaves wide.

In figure 3, A shows the results obtained at the oval window and B shows those at the round window. The slope of the curves in these two parts of the figure is approximately 9 db/octave, although of opposite direction. The latter is simply due to the fact that the two measurements, both for constant particle amplitude within the cochlear fluids, were taken with the sound crossing the air-fluid boundary in opposite directions. This apparent effect of impedance mismatch can be eliminated by combining the curves of A and B. The result of this operation, C represents the transmission characteristics of the models from window to window. In all three parts of the figure, the curves pertaining to the two different models run nearly parallel to each other, those of A and B slightly diverging with frequency.

In line with the reasoning presented above, these results indicate that the model with the solid partition has indeed a higher frictional resistance than the other one. However, although traveling waves were clearly present in the model with the elastic partition, there is no measurable indication of energy consumption between the two windows due to their presence; viz., the frequency characteristics of the two models do not converge with frequency. On the contrary, they diverge slightly with

frequency—at least in A and B of figure 3. This fact had been taken to indicate that the pathway through the model with the elastic partition becomes shorter with increasing frequency in the sense of the schematic representation of figure 1.

The results of these experiments confirm the earlier findings of Wever and Lawrence (12). The following argument could have been made against their experiment. With the push-pull drive they had used, it would be conceivable that an equal amount of energy was drawn from either input to be consumed along the partition, and this would still have allowed for a balanced input at both windows. This doubt should be dispelled now; for in the present experiment, energy was supplied to only one side of the system.

However, the result of the present experiment still does not resolve the apparent dilemma between the pressure-wave concept of energy transmission through the cochlea and the simultaneous presence of traveling waves along the cochlear partition. In the following, an explanation will be offered derived from consideration of the mode of cochlear fluid motion

which accompanies the displacement of the cochlear partition. Cochlear fluid motion has been studied in cochlear models (9). In the present account, no mention is made of Bekezy's eddies, since they make their appearance only upon intense stimulation. Their inclusion would unnecessarily complicate matters at this stage. Also for the sake of simplification, stapedial displacement is assumed to be pistonlike. In reality, the stapes moves around a vertical axis through its posterior portion like a door on its hinges, according to Bekezy's description (2).

In response to stapedial vibrations, a vibratory fluid motion is set up in scala vestibuli. This fluid motion can be observed microscopically and is made visible by suspension of fine aluminum particles within the fluids. The use of glycerin-water solutions produces very stable solutions because of their high viscosity. For other experimental details reference must be made to the earlier publication (9). In the fenestral region, the fluid motion has the appearance of a simple pressure wave; that is, its direction is longitudinal (to and fro) and its amplitude is equal to that of the window membrane (fig. 4). However, as soon as the

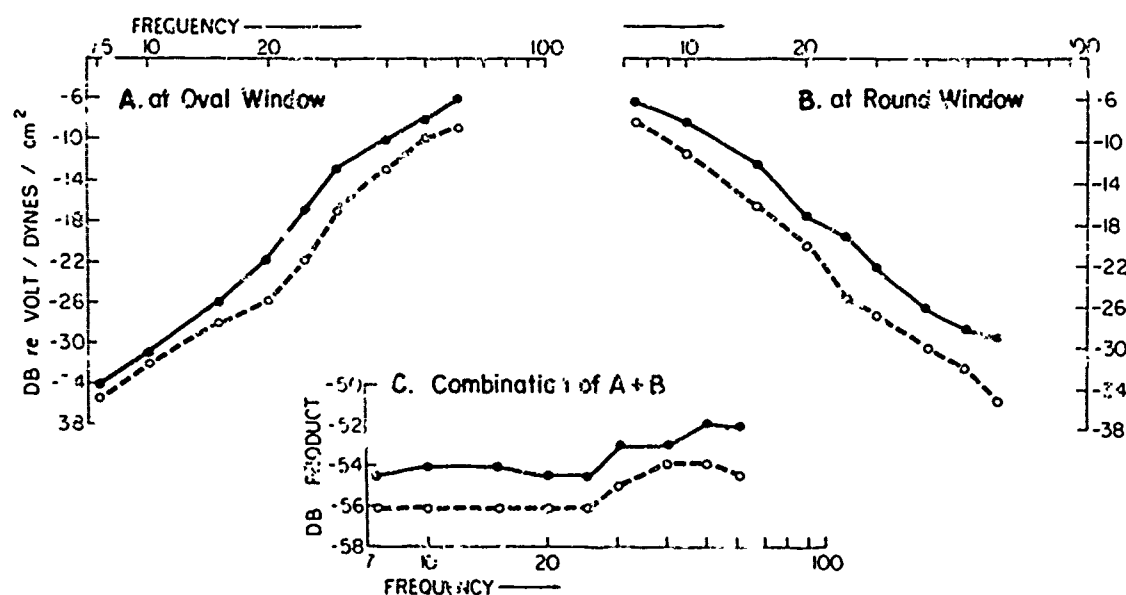


FIGURE 3

Frequency vs. sound pressure. A, At oval window. B, At round window. Both are measured for constant particle amplitude within the cochlear fluids (≈ 0.06 mm.). C, Combination of A and B. Solid lines and solid circles: solid cochlear partition. Broken lines and open circles: elastic cochlear partition.

region of the (yielding) basilar membrane is reached, a second (transversal) vector appears so that the mode of motion of individual particles is gradually converted from longitudinal pathways to elliptical orbits. The latter is known as a *trochoidal* mode of particle motion. In progressing farther along the cochlear partition one notices that the transversal orbital vector increases gradually at the expense of the longitudinal one. However, after passing through a definite maximum, the transversal vector loses amplitude very rapidly. In this region the longitudinal vector decreases too, although at a somewhat lesser rate with distance. Eventually, the total vectorial amplitude, transversal as well as longitudinal, is reduced to zero.

The entire build-up and decay of the transversal vector parallels exactly the shape of the envelope over the traveling waves along the partition as first described by Bekesy (1). (Cf. fig. 2) Bekesy had also described a phase lag of the membrane displacement which accumulates gradually with distance along the

partition; it is this phase lag which is one of the foremost characteristics of the traveling waves as he had described them. Essentially the same phase lag occurs in the motion of fluid particles along their individual orbits (i.e., particles in the apical region lag in phase with respect to those in the fenestral region). The extent and the gradual accumulation to this phase lag with distance is identical to that of the membrane displacement.

In scala tympani (i.e., on the other side of the cochlear partition) the mode of particle motion within the fluid is an exact replica of that within scala vestibuli. This likeness includes: (1) the exchange between longitudinal and transversal vectors with distance along the partition; (2) the phase lag of particles along their respective orbits (which gradually accumulates with distance and is paralleled by the phase lag in the displacement pattern of the partition); and (3) the rapid decrement of the transversal vector after passing the point of maximal displacement. The only, although important, difference between the two

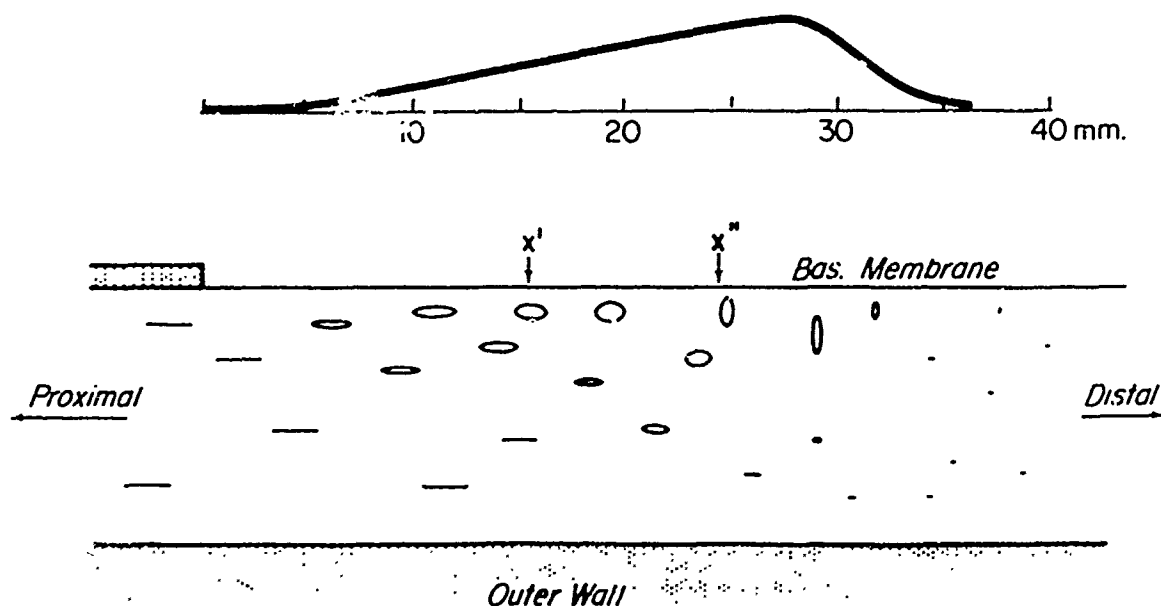


FIGURE 4

Particle motion in elliptical orbits within scala vestibuli of a cochlear model (schematic) in response to a 50 cps signal. Orbits at $x' = 15$ mm. and at $x'' = 24$ mm. measured 0.08 mm. along their major axes, but 0.04 mm. and 0.03 mm., respectively, along their minor axes. The envelope over the traveling wave in the same event along the partition is indicated in the upper portion. The scale of distance is common to both portions. Motion in scala tympani is an exact mirror image of the events shown here.

scalae is that the phase of particle motion in scala tympani lags by exactly 180° behind that of scala vestibuli at all corresponding points across the partition. (The restriction to "corresponding points" must be made because of the cumulative phase lag referred to above which occurs in either scala with distance.) The phase opposition of particles along their respective orbits in the two scalae is schematically given in figure 5. Shown are four instances spaced at intervals of $\frac{1}{4}$ cycle. Particles invariably revolve along their orbits as indicated.

Knowing the direction of particle motion along their individual orbits permits one to determine the phase of the displacement of the cochlear partition with respect to the bilateral fluid motion. The direction of the arrows in figure 5 indicates that the transversal vector (associated with the displacement of the partition) leads the longitudinal vector (associated with the window movement) by

a phase angle of 90° . Consequently, the membrane displacement corresponds to the *velocity* of the original pressure wave entering scala vestibuli. The situation is analogous to the phase relationship between an alternating current and voltage at a capacitor through which the current (velocity) leads the voltage (amplitude of wave displacement) by 90° in phase.

In order to understand the exact phase relationship across the partition it must be recalled that the cochlear partition is bounded bilaterally by incompressible fluids. Therefore, the phase relations of figure 5 is identical for *all* frequencies and also along the *entire* partition as far as particle motion may be observed. That is, it is independent of the alteration of membrane stiffness as well as of the cumulative phase lag with distance in either scala.

The transfer of energy through the helicotrema in the case of very low frequencies may merit a brief description of its own. In such a case,

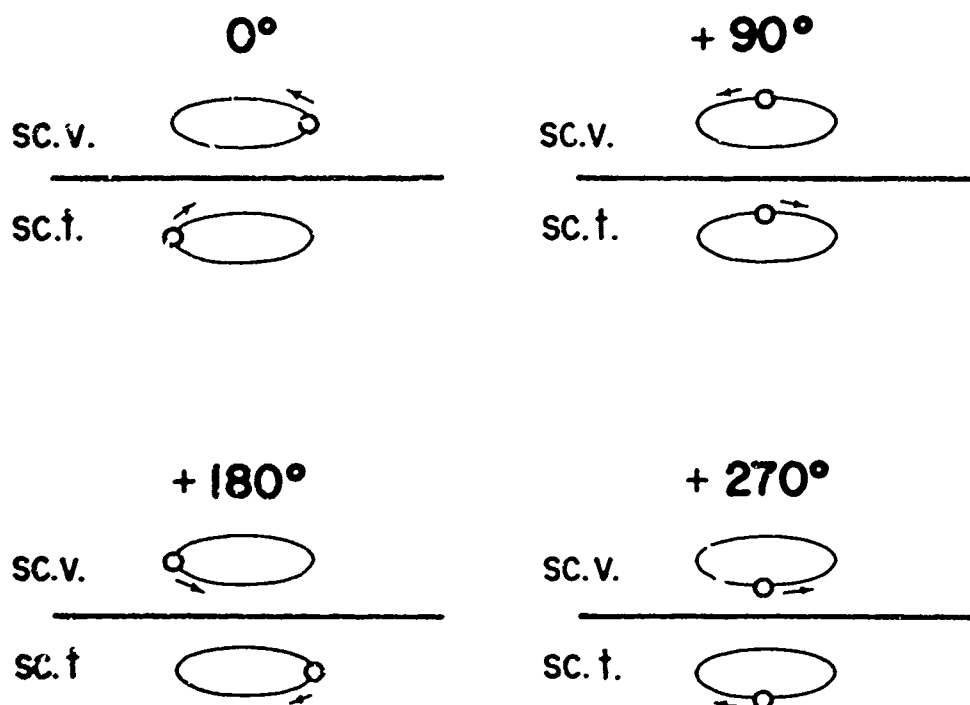


FIGURE 5

Relative positions of particles (small circles) along their respective orbits across the partition (schematic). Given are four instances, $\frac{1}{4}$ cycle apart. Note the direction in which particles are revolving (small arrows on each orbit). Not indicated is the displacement of the partition: toward scala vestibuli (sc.v.) in position $+90^\circ$ and toward scala tympani (sc.t.) in position $+270^\circ$.

particle motion remains predominantly longitudinal, since the transversal vector develops in direct proportion to the degree of membrane displacement which, of course, is small in this instance. This "front" of longitudinal fluid motion gradually bends over as it approaches the helicotrema and continues right through the opening (fig. 6). A similar bend, back in the fenestral direction, is observed in scala tympani. The effect as far as the required phase difference between both scalae is concerned is exactly the same as that in the exchange through the membrane where motion is trochoidal on either side (cf. figs. 4 and 5). Consequently, there is a smooth transition for intermediate frequencies and "clashes" in phase between energy transferred partly through the membrane and partly through the helicotrema are avoided. The event shown in figure 6 is essentially similar to that described previously for the case of a "frictional" partition (9).

The statement was made above that "the transversal vector increases gradually at the expense of the longitudinal one" within the region proximal to the locus of maximal membrane displacement. This statement must be qualified to some extent. It stands to reason that in such an exchange between vectors the circumferential length of the elliptical orbits must be kept constant, if total amplitude is to remain unaltered. The relationship between the circumference of an ellipse and the length of its two axes (the vectors of the present

case) is fairly complex. However, a simple comparison can be made between two orbits in which the major axes appear equal but are exactly reversed in position. Such orbits are indicated in positions x' and x'' of figure 4. If the minor axes of these two orbits would also be equal, the vectorial exchange would indeed be straightforward. To cite a typical example: for a frequency of 50 cps, which had formed its maximal displacement at 28 mm. along a membranous partition of a total length of 50 mm., orbits with identical major axes (0.08 mm.) but in reversed positions were found at x' to be 15 mm. and at x'' to be 24 mm. The size of the minor axes was measured as 0.04 mm. and 0.03 mm., respectively. This result indicates that from point x' to point x'' along the partition total amplitude had been reduced, regardless of the fact that over the same distance the amplitude of the transversal vector had been doubled.

From the above finding the conclusion is warranted that the deficit of total amplitude was caused by the fact that energy had been transferred through the cochlear partition. Consequently, the transfer begins already *before* the region of maximal membrane displacement is reached—that is, before the rapid decrement of the transversal vector is noted. It is reasonable to suppose that this transfer occurs over the entire area in which a transversal vector is present. (This area is identical to the extent of the envelope of the traveling waves.) Furthermore, the rate of this transmission at any

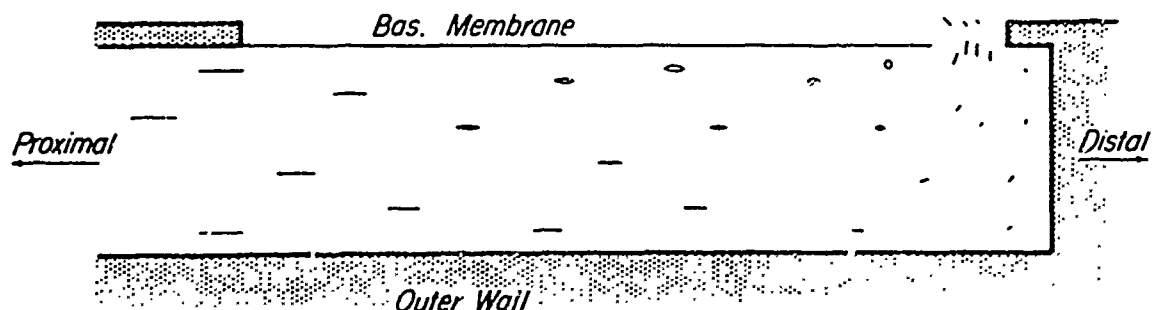


FIGURE 6

Particle motion within scala vestibuli in response to a low-frequency signal of 7.5 cps. Note the bending of the longitudinal axes of particle orbits toward the helicotrema where most of the energy is transferred into scala tympani. Motion in scala tympani is an exact mirror image of the events shown here.

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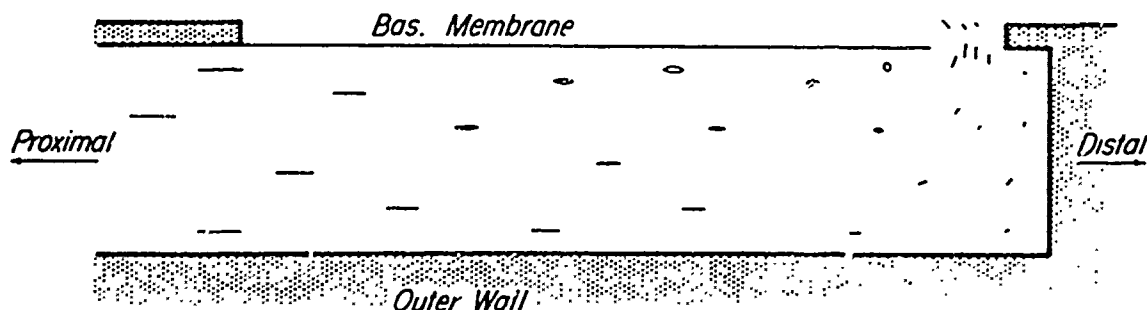


FIGURE 6

Particle motion within scala vestibuli in response to a low-frequency signal of 7.5 cps. Note the bending of the longitudinal axes of particle orbits toward the helicotrema where most of the energy is transferred into scala tympani. Motion in scala tympani is an exact mirror image of the events shown here.

where particle motion is purely longitudinal, amplitude decreases gradually in a fenestropical direction. Figure 7 (curve A) shows this latter decrement plotted against distance for a frequency of 20 cps. The result is an S-shaped curve. The transversal vector was said to correspond to the velocity of the longitudinal vector. The velocity of a given function is its first derivative. For reason of the velocity leading the pressure wave in phase (cf. fig. 5), the derivative must be formed of curve B in figure 7, which is the inverse of curve A. It turns out that the first derivative of curve B is a curve which coincides with the envelope over the traveling waves. The latter curve is given as curve C. It was measured by a method described elsewhere (9). The agreement is quite satisfactory. Both curves are asymmetric. The point of reversal of curve B occurs at an amplitude of 0.88 and at a distance of 42 mm., at which point the maximal displacement of curve C is located.

This result is interesting for the following reason: several investigators have pointed out the difficulty in reconciling the broadness of the envelope over the traveling waves of Bekesy with the ability of frequency discrimination of the human ear. Some sensory "sharpening" process has therefore been postulated. Huggins and Licklider (5) have shown that theoretically such sharpening can be achieved by forming consecutive derivatives of the envelope curve. It turns out now that in the process of energy transfer from the cochlear fluids to the basilar membrane a first derivative is formed. Therefore, the envelope over the traveling wave, broad as it may be, must be considered the necessary first step in the postulated sharpening process.

The concept of transmission of energy across the cochlea presented here may serve to explain two phenomena which had puzzled earlier investigators. As part of the classical temporal bone study by Crowe, Guild, and Polvogt,

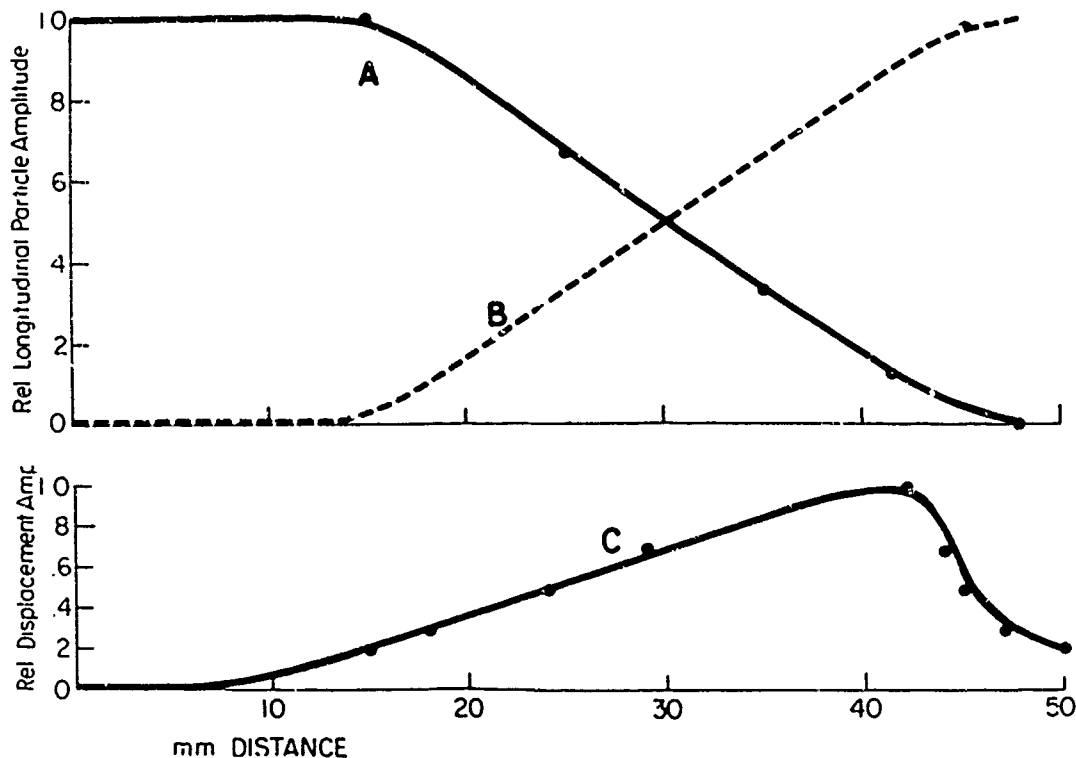


FIGURE 7

Curve A (upper portion): decrement of longitudinal particle amplitude within scala vestibuli with distance; frequency: 20 cps. Curve B (upper portion): inverse of curve A. Curve C (lower portion): envelope over the traveling wave along the cochlear partition for the same frequency. The scale of distance is common to both portions.

the latter author (6) compared the results of their histologic studies in a large series of human temporal bones with audiograms which had been obtained prior to death. Among others, two forms of malformations were found in some cases: (1) localized portions of the basilar membrane completely ossified; and (2) open communications between scala vestibuli of the first turn and scala tympani of the second turn. The curious fact was that in both cases the hearing for frequencies, which were lower than would correspond to the locus of the lesion, was normal. Similarly, Tasaki et al. (8) produced open communications between adjacent scalae of two turns in the ears of guinea pigs and reported cochlear microphonics to be unaffected when picked up from turns distal to the locus of injury.

Both of these lesions can be simulated to a degree in cochlear models. If part of the basilar membrane is covered by a small piece of modeling clay, traveling waves are formed normally in the portion proximal to the obstacle—that is, in response to higher frequencies. However, in the case of lower frequencies, fluid motion in the region of the obstacle is purely longitudinal, even when a small transversal vector had already appeared proximally. Thus energy is transmitted beyond the obstacle, and traveling waves commence normally as soon as the region of

a yielding membrane is reached. Depending upon the transversal diameter of such obstacles small eddies may be formed proximally to them (9).

It is not possible to duplicate an open communication between adjacent turns in an uncoiled cochlear model. However, energy transfer through such an opening cannot be very large because of the fact that particle motion which is purely longitudinal along the outer wall is only a small fraction of total particle amplitude in a given location (cf. fig. 4). Furthermore, when one scala of the model was connected to another small fluid-filled chamber which contained an air bubble (for an elastic boundary), the longitudinal fluid motion continued straight over the opening as long as the latter was small and stimulus intensity was moderate. A transversal vector which appears to be necessary for the transfer of energy into the second chamber was not formed. It was only at higher intensities when small eddies were formed around the opening that some transfer seemed to occur, although its degree was too small to be measured.

Whether or not other communications of the cochlea, the cochlear aqueduct or the inner meatus (via the tractus foraminosus spiralis), may act as pressure outlets in case of closure of the windows (otosclerosis), cannot be decided on the basis of the present study.

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