WEDNESDAY MORNING SESSION,

May 15, 1957.

PHYSIOLOGY OF HEARING

The International Conference on Audiology reconvened at 9:30 A.M., in the Auditorium of the Washington University School of Medicine, St. Louis, Missouri; Dr. Harvey Fletcher, Director of Research, Brigham Young University, Provo, Utah, presiding as Chairman.

DR. FLETCHER: We are to discuss today how the ear works, and the physiology of hearing. The transmission of sound to the ear, through the middle ear, and into the cochlea, has been divided into two parts: first, that part concerned with the process of sound conduction through the middle ear; second, transmission in the cochlea.

PROCESS OF SOUND CONDUCTION.*

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Many of us involved in the field of hearing do research out of curiosity. We would like to know how the ear works. The clinical otologist, on the other hand, is interested in how the ear works because he would like to know what to do when infection or trauma interfere with normal function. Specifically, he would like to know what certain steps that he might take would improve the performance of this disarranged mechanism; so the more basic knowledge revealed by the

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curious, the better off is the clinician, and there is no other area of auditory function that has so clearly shown this picture of basic knowledge contributing to successful clinical procedures than studies of the sound conduction process of the middle ear.

We see the successful beginning of middle-ear surgery back in 1890[6] with attempts at mobilizing ankylosed stapedes. Through many variations this procedure was replaced by the fenestration operation, first tried in one form or another around 1900,[7] and finally perfected to a single stage, and highly successful method, by Lempert some 15 years later.[5] Actually it was the success of this operation that inspired some concentrated research on the conductive processes of the ear, and as a result of the subsequent understanding of the middle-ear mechanics there has been developed a number of operative procedures for the reconstruction of chronic middle-ear conditions that up to now caused deafness that had to be lived with.

Our purpose here is to consider the way sound is transmitted through the middle ear and the principles of sound conduction that are involved. Because of time limitations the discussion is confined to two topics, the mechanical operation of the middle ear, and the fidelity with which the middle ear performs.

Of the peripheral structures the sensory cells of the organ of Corti are the most important. To have hearing these cells must be vibrated, and to survive they must be nourished. Because of their sensitivity to vibrations they cannot be nourished by any system that contains elements that might pulse or produce rapid movements through turbulent fluid flow, so we find these cells surviving without any direct blood supply but by being immersed in a fluid medium which moves imperceptibly, bringing nutrient material to the cells and carrying away waste products. Hearing results when the desired vibrations are introduced into this fluid medium and are effectively transmitted to the cells.

By placing a needle electrode in the vicinity of the cochlea, and recording the potentials that arise from vibrations of the sensory cells, it is possible to obtain a measure of the efficiency of vibrations introduced into the inner-ear fluids. Since there is no threshold or level of sound at which the potentials suddenly appear, it is necessary to use some constant voltage output in response to sounds of different frequencies as a measure of the ear's sensitivity. By recording the sound pressure necessary to produce this pre-established level of response at the various frequencies in the normal ear, and comparing this with the responses under experimentally altered conditions, it is possible to obtain a quantitative measure of the effects of the abnormal conditions.

For the purposes of simplifying the analysis of middle-ear function let us start with the condition in which there is no middle ear, the inner ear being bounded on the lateral side by the oval and round windows. Our first concern is whether one of these air-conduction routes is more efficient than the other.

Sound is first conducted by means of a small probe tube to the oval window and the sound pressure necessary to produce our pre-established response level measured by means of a calibrated probe-microphone system. The sound is then conducted to the round window and these measurements repeated. Fig. 1 shows the result of such an experiment. As is to be expected, considerably more sound pressure is needed to produce the required response when the middle ear is removed than when it is present, but it makes very little difference for effective vibration of the inner ear whether the sound is introduced into the oval window or the round window.

Because the two windows lie at opposite ends of a fluid system, it has long been suggested that a back and forth movement of this fluid column is essential for sensory-cell stimulation. This can be determined by carrying the above experiment a step farther. While the sound is being introduced into the oval window the round window can be blocked. This is a rather difficult thing to do effectively because the actual volume displacement of the fluids of the inner ear is so minute. It amounts to the volume of a sphere with the diameter of a red blood cell when the ear is stimulated by a sound of 1000 c.p.s. at 74 db above .0002 dynes/cm^2. An air

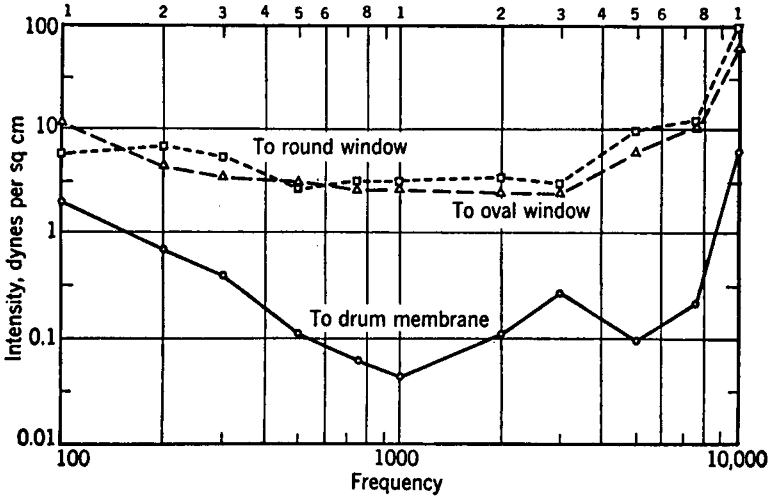

Fig. 1. A comparison of oval-window and round-window pathways after the middle ear has been removed. The ordinate shows the sound pressure necessary to produce 10 microvolts of response at the indicated frequencies; 1 dyne/cm^2 is equivalent to 74 db. above .0002 dyne/cm^2. From Reference 10.

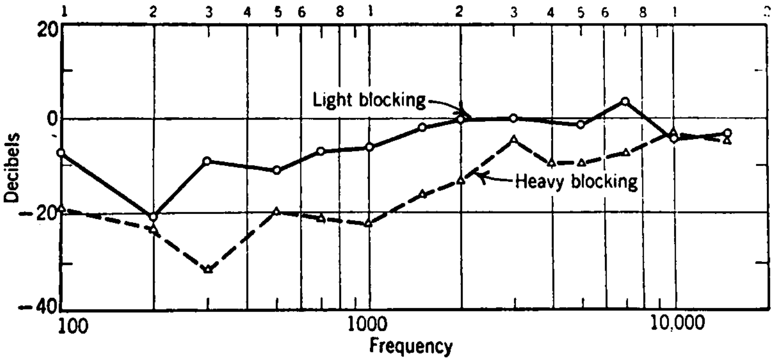

Fig. 2. The effect of blocking the round window upon the response to sound delivered via the oval window. From Reference 10.

bubble one million times this size, about one-third of a cubic millimeter, would allow almost complete freedom of the fluid movements.

Fig. 2 presents the result of such an experiment. The effects of two degrees of blocking are graphed to show something of the range of effects that can be obtained. The decrement is greatest for the low frequencies, and is in excess of 20 db for those below 1000 c.p.s. It is necessary to dry the surfaces and pack the niche completely with wax in order to produce the results shown. It is apparent that the oval window pathway is effective only as long as the round window is free at the other end of the system.

We find also that the oval window must be free to make the round window pathway effective. Because of the presence of the footplate of the stapes it is easier to block the oval window than the round window, and by embedding the stapes in wax the results of Fig. 3 are produced. Now the effects are most severe in the range immediately above 1000 c.p.s., indicating that the method of blocking the two windows has changed the frequency response properties in different ways, but the principle is still demonstrated that in order for vibrations entering by one window to be fully effective in stimulating the sensory elements, the other window must be free to act as a relief opening at the other end of the system. This was a theory first expressed by Edward Weber[8] more than a century ago.

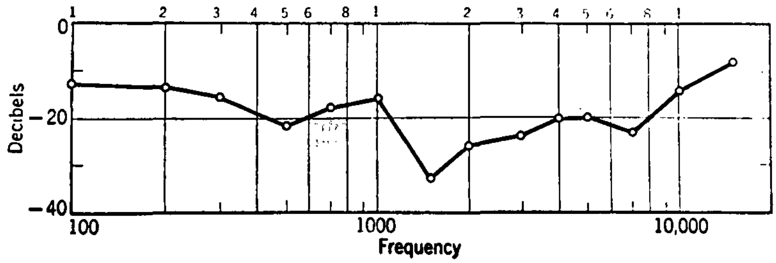

Fig. 3. The effect of blocking the oval window upon the response to sound delivered via the round window. From Reference 10.

This principle can be studied more quantitatively if we introduce sound into both windows at the same time. Such a situation would exist in an individual with no tympanic membrane or ossicles, so that both windows were exposed to the same sound field. Visualize the alternating positive and negative sound pressure of a sound wave reaching one of the windows as pushing the membrane in during the positive pressure phase and pulling it out during the negative pressure phase. If both windows are being pushed in at the same time the situation would be the same as blocking one of the windows, because no relief opening is available for either source of sound. This condition is portrayed schematically in Fig. 4. It can be seen that in such a phase relationship no movement of the basilar membrane with subsequent sensory-cell stimulation is possible. This is equally true of the phase relation when both windows are being pulled out at the same time; however, when one window is pushed in by a positive sound pressure and the other window is pulled out by a negative pressure brought about by delaying the sound by one-half a wave length, the effectiveness of the relief opening is enhanced. By such a situation the amplitude of vibration of the basilar membrane should be double that produced by sound in one window alone.

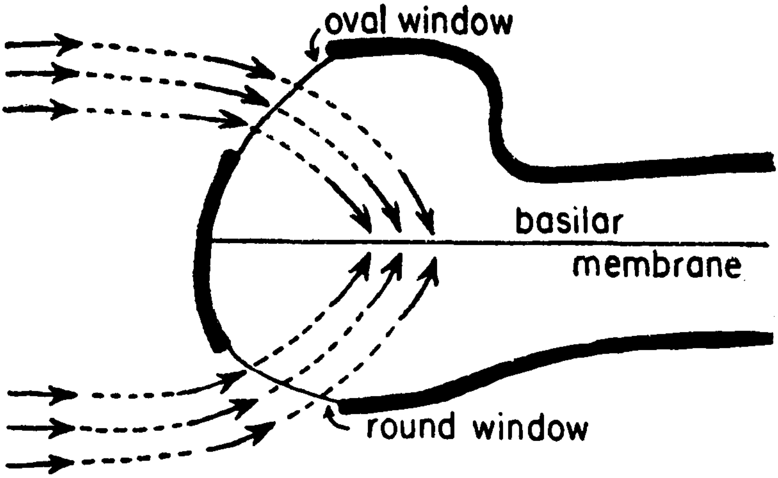

Fig. 4. Schematic representation of sound entering both oval and round windows at the same time. The phase condition represented here is such that there would be complete cancellation of response. The sounds are in phase at the two windows and of equal intensity. From Reference 11.

Again, by recording the electrical responses of the cochlea it is possible to obtain a quantitative measure of the above. Sound from one electronic oscillator is used with the output

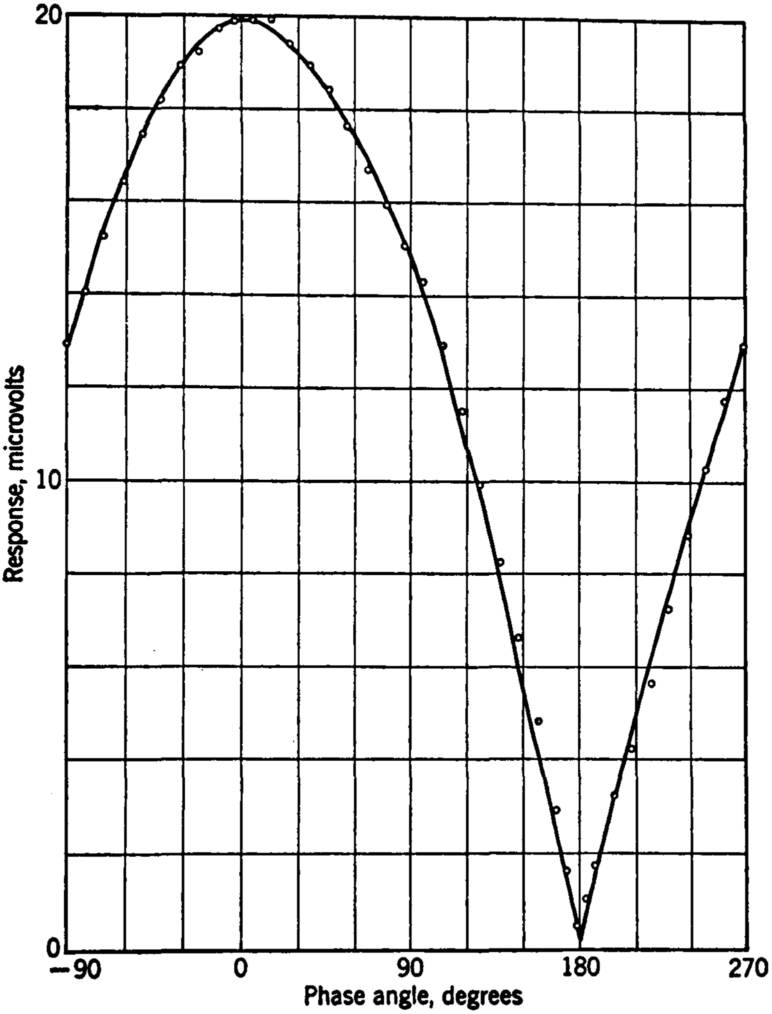

Fig. 5. Vectorial summation in the cochlear response to a tone introduced simultaneously by way of the oval and round windows. The phase relation of the two pathways was varied over a range of 360°, as shown on the abcissa. The points represent observations and the curve represents theoretical summation. From Reference 10.

passed through a dividing network. Into one channel a phase changer is introduced and the two sources separately led, by means of small tubes, to each window. The sound level is again recorded by a calibrated probe-microphone system, and the recorded electrical potentials serve as a measure of the effectiveness of the stimulus. Fig. 5 shows the magnitude of the cochlear response as the phase of the sound in one window is shifted with respect to the phase of the sound in the opposite window. The sound is first directed into one window alone and set at a sound pressure sufficient to give rise to a response of 10 microvolts. This tone is then shut off and that directed toward the opposite window set to give a 10 microvolt response. For the readings shown in the figure the tones are introduced into the two windows simultaneously. The response shows what is to be expected from the vectorial sum of two sine waves of equal intensity when one is varied in phase. As expected, in a phase relationship where one window is pushed in while the other is pulled out the response is double what sound in one window alone would give, and when they are 180 degrees from this condition, that is, both windows being pushed in or pulled out simultaneously, the response is completely cancelled. The interesting thing to note is that as the phase varies through the complete 360 degrees, the two-window response is as good or better than that from one window alone over a phase difference of 240 degrees, while the two-window response is worse over only 120 degrees. It is not likely that the sound, under conditions where both windows are exposed, hits them in the exact phase relation for cancellation. In the first place the windows are not in exactly the same plane, considered from the point of view of the sound-wave front, and secondly, one window contains a stapes or footplate and the other a membrane. These introduce phase differences, as will be shown shortly, and it does not take much of a phase shift to bring the response up to a level of that given by stimulation through one window alone. If the two windows were exactly alike they would have to be separated by a distance of about seven inches for a frequency of 1000 c.p.s. In the scheme behind our phylogenetic development this apparently was considered impractical.

Another factor influencing this two-window summation is the intensity of the tones introduced. Complete cancellation depends upon equal intensities, so this unwanted condition can also be avoided by the introduction of a more intense sound in one window than the other. To accomplish this, advantage has been taken of a fact which make a fluid-filled ear quite impractical in an air environment, as was the case some 250 million years ago, when the predecessors to the amphibians first found themselves on land.

Because of the extreme differences in the properties of elasticity and density between air and liquid, approximately 99.9 per cent of the acoustic energy is reflected back at an air-water interface. This means that there is a loss of 30 db in transmitting the vibratory energy from the air to the inner-ear fluids. By the use in one window only of a mechanism that matches these properties of air and water, it is possible to overcome both of the disadvantages of the two-window fluid system: *1.* the cancelling effect of equal-intensity, in-phase sound entering by the two windows is overcome by increasing the intensity in one window by 30 db over that in the other; *2.* the loss in transmitted energy due to the air-liquid interface is overcome by matching the properties of air to those of the denser liquid, and this apparently is just what the middle ear does.

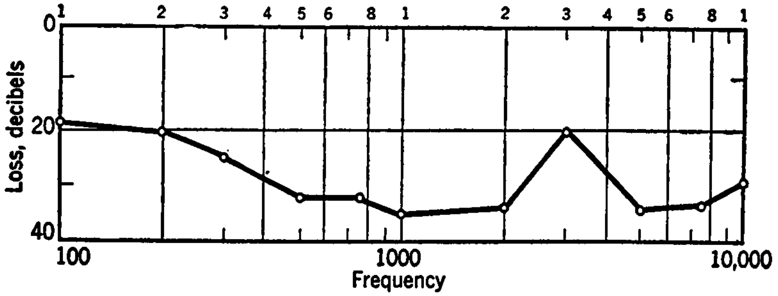

Fig. 6. The loss of sensitivity resulting from the removal of the middle ear mechanism in the cat. From Reference 10.

To see whether the middle ear is actually performing this function, and if so, how efficiently it is accomplishing the impedance match, we can again resort to an animal experiment, recording the electrical responses of the cochlea under conditions in which the ear is normal and those in which the middle ear is removed. Fig. 6 represents the loss, in the cat ear, resulting from removal of the middle ear structures up to the stapes. The loss is not the same for all frequencies, because of the resonant properties of the middle-ear structures, but the average is approximately 28 db, which is close to the theoretical loss of 30 db. It means that, considering the errors which can be attributed to the nature of the experiment, the middle ear of the cat is almost perfectly efficient.

Since the time of Helmholtz much research and thought have gone into the problem of how the middle-ear structures accomplish this match. Of the theories of action that have been proposed, two have been shown experimentally to contribute to the impedance matching process.

The first of these depends upon the *areal ratio* between the tympanic membrane and the footplate of the stapes. In man the average of the available data shows this ratio to be about 21 to 1. Considering the fact that the tympanic membrane is not like a piston, but rather like a stretched membrane attached around the edge, the effective area of the membrane must be reduced by about one-third, making the ratio 14 to 1.

The second characteristic of the middle ear that aids in the matching process is the *lever ratio* brought about by the peculiar arrangement of the ossicular chain. Measurements of this in the human are few and probably not very accurate. Dahmann[3] made what are probably the most reliable measures, by placing small mirrors on the drum membranes and then on the long process of the incus. The ratio so determined was found to be small: about 1.3 to 1.

The product of the areal ratio and the lever ratio give us the transformer ratio of the entire middle ear, which then amounts to approximately 18 to 1. This pressure increase at the footplate of the stapes is equivalent to 25 db, which is not enough to overcome completely the theoretical loss of 30 db., but these figures should not be taken too seriously because of the limitations in both the experimental data and theoretical calculations. In calculating the theoretical 30 db loss in the passage of sound from air to the fluids of the inner ear, data for boundless media were used, whereas the air of the middle-ear cavity or fluids of the inner-ear space are far from boundless. On the other hand, data used to determine the areal ratio are limited, and the data of the lever ratio may not be very accurate because of the difficulty of determining accurately from an optical lever the excursion of a vibration when the axis of rotation of the mirrors is not known; nevertheless, the figures are close enough to indicate that the principles described are the right ones.

Measurements of the transformer ratio, which have been made on human cadaver material, show that these figures are fairly accurate. Békésy[1] drained out the fluid of the inner ear, dissected away the cochlea, and then applied sound to the inner surface of the stapedial footplate. This he adjusted in intensity and phase so as to cancel the effects of another sound of the same frequency introduced at the drum membrane. A capacitative probe near the surface of the stapes showed when cancellation was complete. From these he obtained a transformer ratio of 10 at 100 c.p.s., rising to 18 at 2200 c.p.s. and then rapidly falling. This is shown in Fig. 7. Now the lever ratio and areal ratio of the middle ear will not change with frequency, so the variations in the transformer ratio can probably be attributed to the influence of the inherent response properties of the ossicular chain.

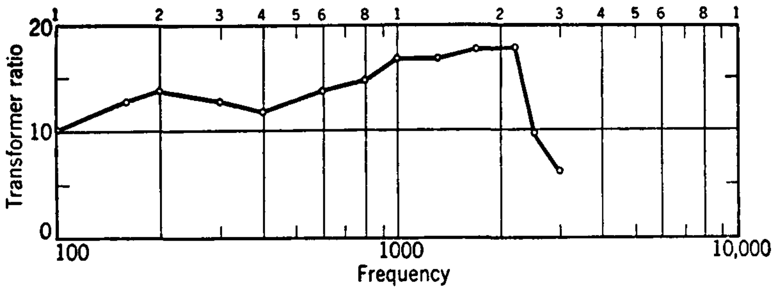

Fig. 7. The transformer ratio of the human (cadaver) ear according to Bekesy[1]. From Reference 10.

At this point we must mention some other interpretations made on the basis of another experiment reported by Békésy in 1942.[2] In this instance he measured, also on cadaver specimens, the volume displacement of the round window for a number of conditions. In the first of these he cancelled out a tone applied to the inner ear through the intact middle-ear structures by a tone of the same frequency, but adjustable in intensity, applied through the round window. A determination of the current in the cancelling receiver gave a measure of the volume displacement. He then repeated the balancing process after removing all of the middle-ear structures, including the stapes and round window, by conducting the sound directly to the fluids of the inner ear through the oval and round window openings. These results showed considerably larger volume displacements at low frequencies than before, but their magnitude showed a progressive decrease as the frequency was raised until, at the higher frequencies, they became smaller than in the intact ear.

Fletcher[4] divided the first set of values by the corresponding ones in the second set, and regarded the quotient as representing the transformer ratio of the middle ear. The calculations, which he interpreted as demonstrating a middle-ear pressure reduction for frequencies below 650 c.p.s., are presented as curve *a* of Fig. 8. He saw advantages in this sort of action in that the system would discriminate against disturbing low frequencies, and on the basis of this it has been suggested that the middle ear does not at all act like an impedance-matching transformer; however, in this same series of experiments, Békésy made some other measurements that more accurately reflect the action of the middle ear. In this instance the second measurements were made with the drum membrane and outer ossicles removed but with the stapes left in the oval window and with the round window membrane intact.

When the values of volume displacement for the intact ear are divided by those for the above conditions we have a curve, *b* in Fig. 8, that is in better accord with the earlier results and testifies to a useful transformer action of the middle ear for all frequencies.

It is obvious from these determinations, and those showing the contribution of the middle ear to sensitivity, that the advantages are not the same for all frequencies. The middle ear is not a truly high-fidelity device, but it does remarkably well. Three forms of distortion, found in all forced-to-vibrate devices, that have been extensively studied in the middle-ear response to acoustic vibrations are frequency, phase and non-linear or amplitude distortion.

The first of these, frequency distortion, is illustrated in Fig. 6. This curve represents the frequency response for the middle ear of the cat. Like any other device, when forced to vibrate, it exerts its own resonance properties into the vibration and so alters the frequency characteristics. In the human ear this middle-ear frequency distortion is reflected, along with many other hearing phenomena, in the sensitivity curve.

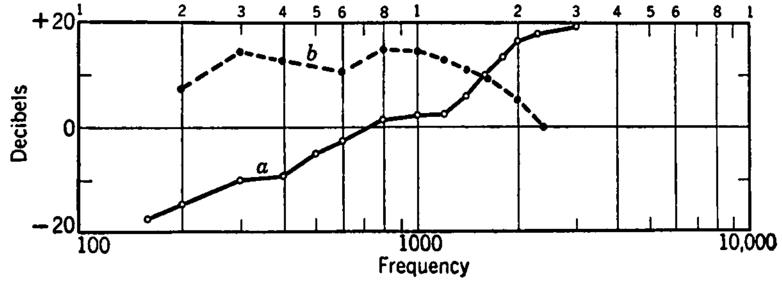

Fig. 8. The pressure amplification afforded by the middle-ear mechanism as derived from the observations of Bekesy.[2] Curve *a* shows the results of Fletcher's computations and curve *b* those of Wever and Lawrence[10]

Whenever there is frequency distortion due to the characteristic mass and stiffness properties of the driven structure, phase differences are also introduced into the vibratory response. This means that as the sound at the tympanic membrane reaches a positive-pressure peak or a negative-pressure peak the ossicular chain lags behind or, in fact, may appear to precede the movements of the air-borne vibration. Thus the chain of middle-ear bones introduces phase distortion, not only by shifting the phase but also by doing it differently and in varying amounts over the frequency range.

By employing a stimulating system similar to that described for studying the effects of different phase relations at the oval and round windows we can find out how much the middle ear shifts the phase for various stimulating tones.

Fig. 9 shows the phase shift introduced for frequencies from 100 to 10000 c.p.s. by the entire middle ear. Positive values indicate a phase lag introduced by the ossicular chain. The amount of phase variation is quite moderate for frequencies below 5000 c.p.s., and then grows greater and more variable for the higher frequencies. Actually these phase changes remain constant at the different frequencies and so, of course, make no noticeable difference to hearing. Since the sound being transmitted by this route to the oval window is more intense by about 30 db than that reaching the round window, any inner-ear effects due to the phase difference are negligible. When the middle ear is removed, however, so that this advantage is lost, any phase shift in one window relative to the other makes a great deal of difference, as was described earlier.

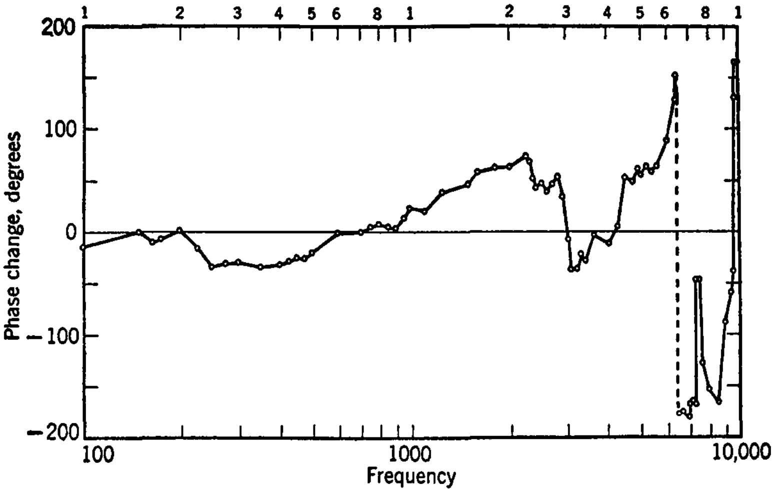

Fig. 9. Phase changes produced by the entire middle-ear apparatus. Positive degrees represent a retardation of phase. From Reference 10.

Measurements made of phase changes attributed to action of the stapes are shown in Fig. 10. These variations are small, never exceeding 15 degrees below 5000 c.p.s., but as shown in Fig. 5 it takes very little shift from the cancellation point to improve the situation. This demonstration of the phase characteristics of the stapes serves to emphasize the importance of establishing a favorable phase relationship between the two windows during any reconstructive surgery of the middle ear performed for the purpose of improving the hearing.

The third type of distortion concerns the ability of the structures to follow increases in amplitude of the driving vibration. A characteristic of the electrical response of the cochlea in response to a pure tone is that as the sound amplitude is increased the electrical output increases proportionally over a characteristic range, and then departs from this straight-line function until finally it reaches a maximum. The point at which the response becomes no longer proportional to the amplitude increases of the stimulating sound is called the "limit of linearity," and the point at which there are no increases in response to further increases of stimulus is called the "maximum," as shown in Fig. 11. The electrical response recorded in this instance reflects not only the transmission of sound through the middle ear and through the fluids of the inner ear, but also the process by which this

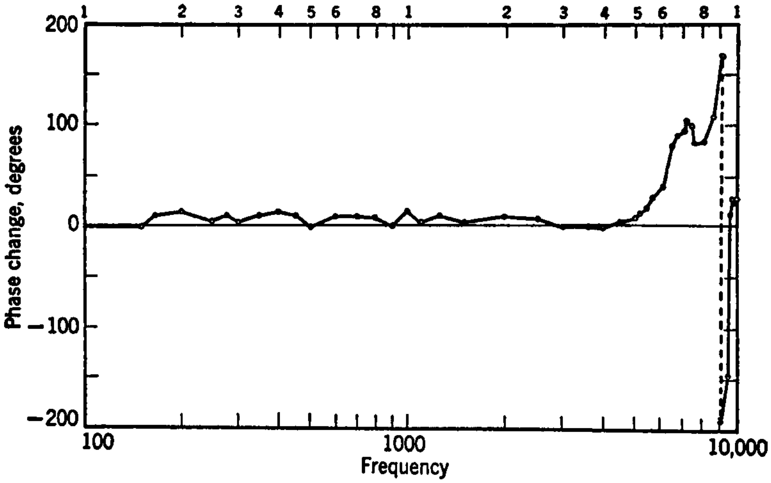

Fig. 10. Phase changes produced by the stapes. Positive degrees represent a phase lag in the oval-window pathway relative to the round-window pathway. From Reference 10.

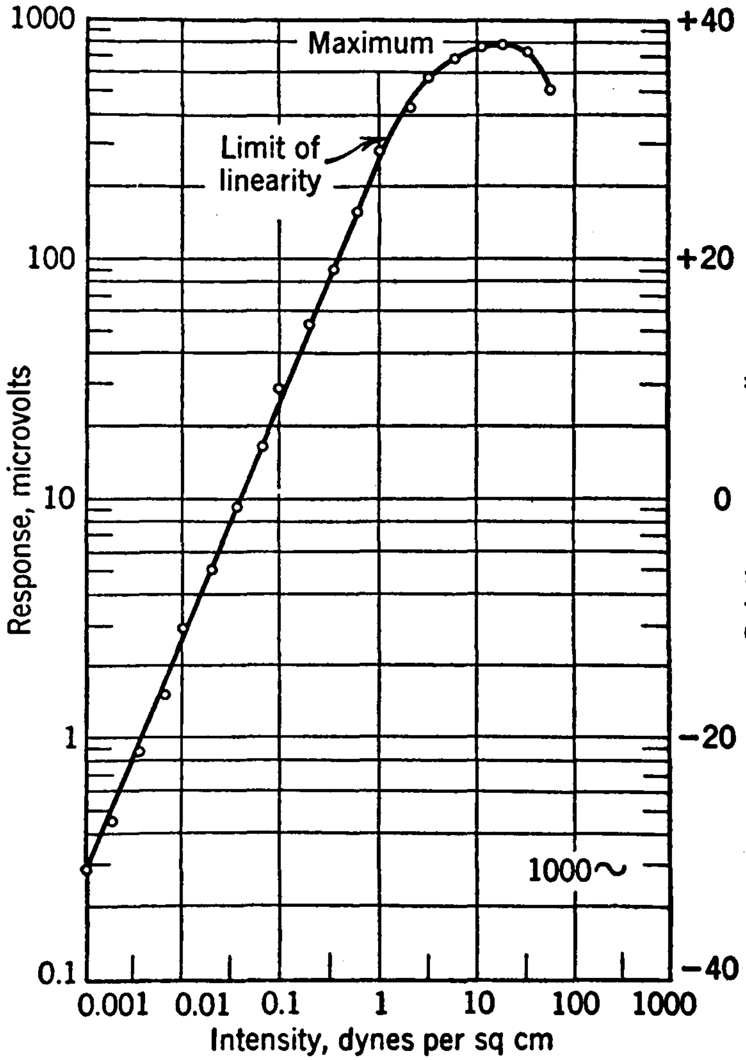

Fig. 11. The intensity function for the cochlear response recorded from the round window of the cat. The "limit of linearity" denotes the point in the response where it is no longer proportional to changes in the stimulus intensity. From Reference 10.

vibration is transformed into the recorded electrical response. We would like to know then, what structure or process brings on this departure from linearity and specifically, for our discussion here, we would like to know whether the conduction process in the middle ear is responsible for this.

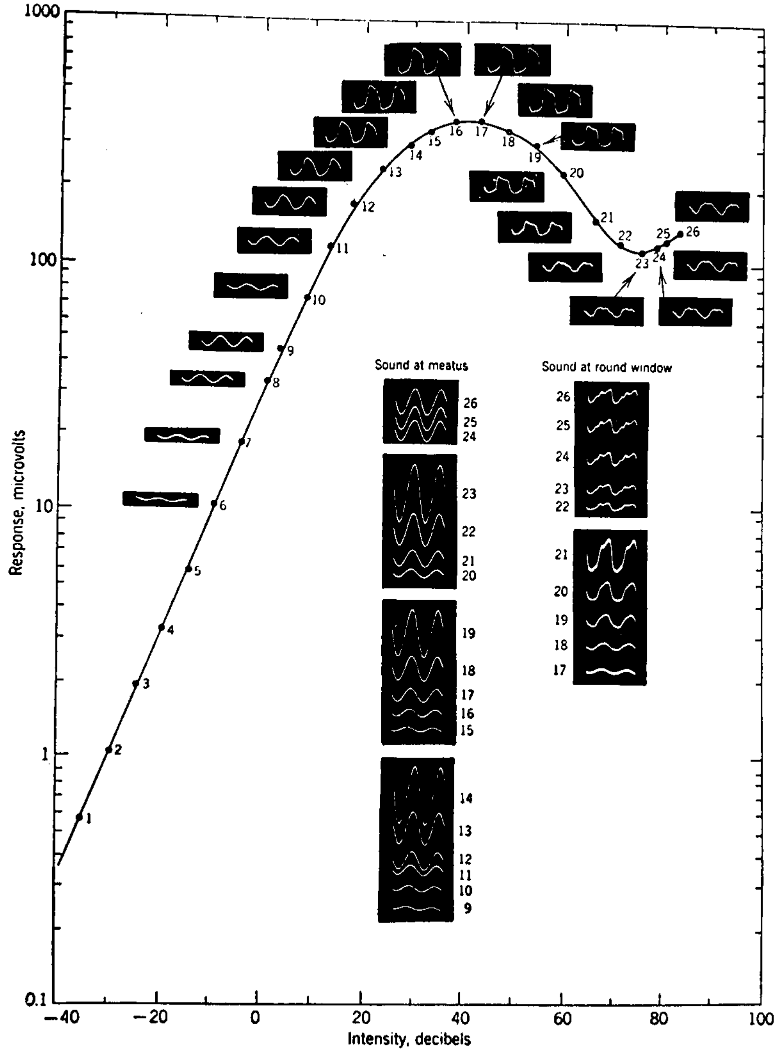

Fig. 12. The intensity function for the cochlear responses of the cat's ear, with a display of wave forms of this response at different levels. The intensity scale is in decibels relative to 1 dyne/cm^2 (74 db above .0002 dyne/cm^2). The points of measurement along the curve are numbered, and from 6 on, each has adjacent to it an oscillogram of the cochlear response obtained. For these waves the amplification of the oscillograph was constant up to point 9, and then was reduced and held constant thereafter for points 10 to 26. In two columns below are oscillograms for some of the sounds entering the ear at the meatus and also for sounds picked up from the round window. In recording these sounds the amplification of the oscillograph was constant for each block of pictures but was varied between blocks. From Reference 10.

The evidence gathered over the last few years has shown conclusively that the inner ear is responisble for this early departure from a linear response. One way to study this is to record the magnitude of the electrical response as well as its wave shape, and compare this to the wave shape of the stimulating sound and that of the sound after it has been relayed by the ossicular chain to the fluids of the inner ear and escapes from the round window. A comparison is made in Fig. 12. The wave shape of the sound coming from the round window is still undistorted to a level of stimulating sound that has brought about severe wave form distortion in the electrical response. If distortion had occurred in the middle ear this would have been transmitted through the fluids to the round window.

Another test for the locus of this amplitude distortion has been made by applying a vibrator, first to the umbo of the malleus then to the head of the stapes, and recording the cochlear response in both instances. If the middle ear is responsible for this type of distortion, departure from linearity should occur at a lower response level when the middle ear is present than when it is removed. Results are shown in Fig. 13. The limit of linearity occurs at the same response level for both methods of stimulation, indicating that the middle ear is not responsible. Since the middle-ear lever, which reduces stapes amplitude while increasing pressure is removed in one instance, the response through the stapes alone is greater for equal sound pressures than the response after traversing the ossicular chain.

It is true that if the middle ear is driven hard enough it, too, will become non-linear but not until a level of sound has been reached that would have destroyed the inner ear, and nothing seems to affect this ability of the middle ear to respond linearly over a conisderable range of sound intensities. The middle ear can be filled with fluid or the stapes ankylosed and, although sensitivity is lost, the middle-ear dynamic range is very little affected.

In the process of conducting sound from the external meatus to the fluids of the inner ear the tympanic membrane and ossicular chain do not only an amazingly efficient job of

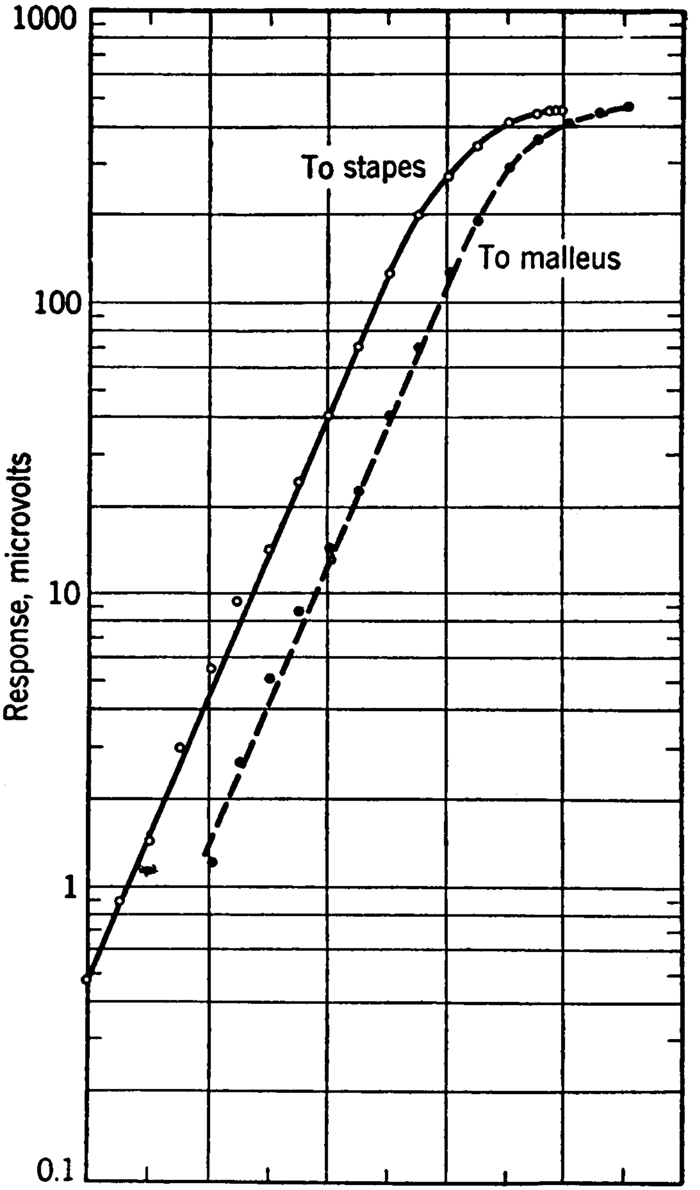

Fig. 13. The cochlear response recorded from the round window in response to mechanical vibration at a frequency of 1000 c.p.s. of the stapes and the malleus. The "limit of linearity" occurs at the same response level in both instances. From Reference 10.

matching the properties of air to those of the dense perilymph so as to introduce sound with a minimum of loss, but do so over a wide range of frequencies with no amplitude distortion within the range of inner-ear response and with tolerable frequency and phase distortion.

REFERENCES.

1. BÉKÉSY, G. VON: Über die Messung der Schwingungsamplitude der Gehörknochelchen mittels einer kapazitiven Sonde. *Akust. Zeits.*, 6:1-16, 1941.

2. BÉKÉSY, G. VON: Über die Schwingungen der Schneckentrennwand beim Präparat und Ohrenmodell. *Akust. Zeits.*, 7:173-186, 1942; trans., The Vibration of the Cochlear Partition in Anatomical Preparation and in Models of the Inner Ear. *Jour. Acoust. Soc. Amer.*, 21:233-245, 1949.

3. DAHMANN, H.: Zur Physiologie des Hörens; Experimentelle Untersuchungen über die Mechanik der Gehörknöchelchenkette, sowie über deren Verhalten auf Ton und Luftdruck. *Zeits. f. Hals-Nasen-Ohrenheilk.*, 24:462-497, 1929; and 27:329-368, 1930.

4. FLETCHER, H. The Dynamics of the Middle Ear and Its Relation to the Acuity of Hearing. *Jour. Acoust. Soc. Amer.*, 24:129-131, 1952.

5. LEMPERT, J.: Improvement of Hearing in Cases of Otosclerosis: a New One-Stage Surgical Technique. *Arch. Otolaryngol.*, 28:42-97, 1938.

6. MIOT, C.: De la Mobilisation de l'Etrier. *Rev. de Laryngol. Otol., Rhinol.*, 10:49-64, 83-99, 113-130, 145-162, 200-216, 1890.

7. SIEBENMANN, F.: Traitement Chirurgical de la Sclérose Otique. XIII Internat. Cong. Med., Sec. d'Otol., Paris, 1900, 170-177; and Ann. des mal. Oreille, 26, ii:467-474, 1900.

8. WEBER, E. F.: Über den Zweck der Fenestra Rotunda und die Vorrichtung der Schnecke im Gehörorgane der Menschen und der Säugethiere. Amtlicher Bericht Versamml. Deutsch. Naturf. Aerzte, 19te Versamml. Gesellsch. Deutsch. Naturf. Aerzte, 1841; Braunschweig, 83-84, 1842.

9. WEVER, E. G., and LAWRENCE, M.: "Physiological Acoustics," Princeton University Press, Princeton, N. J., 1954.

10. WEVER, E. G., and LAWRENCE, M.: The Acoustic Pathways to the Cochlea. *Jour. Acoust. Soc. Amer.*, 22:460-467, 1950.

DISCUSSION OF DR. LAWRENCE'S PAPER ON "PROCESS OF SOUND CONDUCTION."

HENNING E. VON GIERKE.*

The starting point for any serious discussion is a point of disagreement, of doubt, or a question mark. It would be very hard to pick out such a point from Dr. Lawrence's excellent presentation. I think it became quite clear from his

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