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Current Status of Theories of Hearing

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By the middle of the 19th century a large number of theories of hearing had been proposed (*1*). At that time the main problem was to determine which part of the inner ear is set in vibration by sound waves. Since very little was known of the anatomy of the inner ear, the possibilities for theorizing were almost limitless, and the confusion became so great that, it is said, some lecturers in physiology simply did not treat the topic of hearing at all. After 1863, however, when Helmholtz proposed his resonance theory of hearing, the topic could no longer be ignored.

Helmholtz' theory was successful because it was based on anatomic and physical facts. When the cochlea was laid open in earlier times by cracking the temporal bone or chiseling away the bony wall, a half-dry gelatinous mass was found. It was not even clear whether the cochlea was filled with fluid or not. In my opinion, it was P. F. T. Meckel who performed the first basic experiment in the physiology of hearing when, in 1777, he opened the cochlea of a cat under water. He found no air bubbles coming out of the cochlea, thus proving that it is filled with fluid.

After histologists had found that a fixative acid would hold the gelatinous mass in its natural position, the anatomy of the inner ear could be worked out in detail by Corti, Hensen, and others. With this increased knowledge of the anatomy of the inner ear, Helmholtz and Hensen were able to conclude that the sensation of hearing is determined by the vibrations of the basilar membrane, a conclusion that is still generally accepted.

The next problem was, How does the basilar membrane vibrate? Helmholtz thought that the tension of the basilar membrane is greater transversely than longitudinally. Since it was known that the width of the membrane changes continuously from one end of the cochlea to the other, he concluded that it should behave like a set of resonators whose tuning changes continuously from one end to the other. The pitch discrimination of the ear could thus be accounted for since every frequency would bring a different resonator into vibration. Helmholtz' theory of pitch discrimination was not generally accepted, and the question of how the basilar membrane vibrates became and continues to be an issue. The various answers proposed have been presented as theories of hearing.

In my opinion, the words *theory of hearing* as commonly used are misleading. We know very little about the functioning of the auditory nerve and even less about the auditory cortex, and most of the theories of hearing do not make any statements about their functioning. Theories of hearing are usually concerned only with answering the question, How does the ear discriminate pitch? Since we must know how the vibrations produced by a sound are distributed along the length of the basilar membrane before we can understand how pitch is discriminated, theories of hearing are basically theories concerning the vibration pattern of the basilar membrane and the sensory organs attached to it.

The problem under discussion is a purely mechanical one, and it may well seem, at least to the layman, that it can easily be solved by looking at the vibration patterns in the cochlea. Unfortunately, this direct approach proves difficult, for without stroboscopic illumination and other special devices, we can observe almost no vibration in the nearly transparent gelatinous mass in the cochlea of a living organism.

Furthermore, the maximal physiological vibration amplitudes of the basilar membrane can be seen and measured only when they are magnified between 100 and 300 times. Although observations have been made with this magnification (*2*), it is important to find other methods of observing the vibration pattern of the basilar membrane. Since hearing is the common concern of many disciplines—physics, engineering, physiology, psychology, zoology, and even mathematics—it is understandable that a great variety of solutions have been proposed. Naturally, each investigator has thought primarily in terms of his own field, and it was forgotten, for example, that vibration patterns are really a physical problem and not a musical one.

Various Vibration Patterns of the Basilar Membrane

Reports of the various vibration patterns of the basilar membrane that have been proposed thus far are to be found in textbooks on the psychology of hearing (*3*). These reviews point up the differences between the various hypotheses, and some of them are very critical. Indeed, they are so critical that they give the impression that the psychology of hearing is nearing the end of its productive period and entering a phase of unconstructive criticism. I would like to show in this paper, therefore, how the various hearing theories are interrelated and how by manipulating two independent physical variables of the basilar membrane—absolute stiffness and coupling of adjacent parts—we can obtain a continuous series of vibration patterns, each group of which is in agreement with one of the four major theories of hearing. We may proceed continuously from curves predicted by the resonance theory to curves predicted by each of the other three theories in turn. It is thus shown that the various theories form one continuous series of vibration patterns.

A schematic cross-section of the ear is presented in Fig. 1. Sound enters the external meatus and sets the tympanic membrane in motion, and the vibrations

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are conducted through the ossicles to the fluid in the cochlea. The basilar membrane, which acts as a partition between the two channels, is set in motion by any movement of the ossicles. Since the fluid is incompressible, the fluid displacement produced by the stapes is equal to the deformation of the round window. The question is, then, How is the basilar membrane displaced and how does it move during a sinusoidal vibration of the ossicles?

Although the movement of a membrane depends on other factors as well, we shall turn our attention first to the elastic properties of membranes. Three elastic properties of the membrane in a cochlear model can be varied: the absolute value of stiffness; the slope of stiffness along the length; and the coupling between adjacent parts.

1) The absolute value of the stiffness of the membrane can be changed. If the membrane is stiff, a pressure difference across the membrane causes only a small displacement or deformation.

2) The stiffness of the membrane can be constant, or it can vary along the whole length. The basilar membrane is stiffer near the stapes than it is near the helicotrema; for man and most other vertebrates, the stiffness near the stapes is about 100 times greater than it is at the other end.

3) The coupling between the adjacent parts of the membrane can be varied. In a membrane made of thin elastic fibers stretched across a frame, when there is no coupling between one strand and its adjacent strands, each strand can vibrate freely. The strands can be coupled by a thin sheet of rubber placed along the whole set. The coupling becomes larger as the thickness of the rubber sheet is increased. A membrane can also be made of a smooth sheet of rubber alone, without individual strands.

These three possibilities may be expressed mathematically by saying that we have three independent variables for the elasticity of the membrane.

There are two methods for investigating the effect of manipulating these variables on the vibration pattern of a membrane. First, we can calculate the vibrations. Unfortunately this is a time-consuming job. Or second, we can construct a model of the cochlear membrane and vary its elastic properties. I have made models the size of the human cochlea and models that were larger. The enlarged models were constructed in the same way that full-scale ships are constructed from small-scale models. As is well known, this kind of dimensional enlargement has proved quite successful.

Figures 2 and 3 show some of the effects that are obtained by varying the elastic properties of the membrane. Figure 2a shows a small section of the membrane model consisting of coupled strands acted on by a point force (needle tip). The absolute value of the elasticity of the different strands varies continuously from 100 to 1 from left to right along the membrane. Seen from the top, the deformation pattern is a group of elongated ellipses, the deformation spreading neither to the left nor to the right. The side view shows this limited lateral spread even better. This model simulates the system of almost freely vibrating elastic resonators that is postulated by the resonance theory of hearing. If we immerse this membrane in fluid, the vibration pattern seen in Fig. 3a is obtained for a steady tone.

With the same slope of elasticity and the same driving frequency, but with an increase in the absolute value of the membrane stiffness, a steady tone causes the whole membrane to vibrate in phase (all parts of the membrane reaching their maximal elongation simultaneously), in the manner of a telephone diaphragm, as shown in Fig. 3b. This is the pattern of vibration assumed by the telephone theory of hearing. The vibration pattern for the steady tone is independent of the coupling between adjacent parts of the membrane because the whole membrane vibrates in phase, with no force acting laterally. Because of the increase in stiffness, the same point force that was used before now produces a smaller deformation (Fig. 2b); if the rubber strands are replaced by a flat plastic sheet that is stretched and clamped along the two long sides to the frame of the model, the point force produces the same lateral spread.

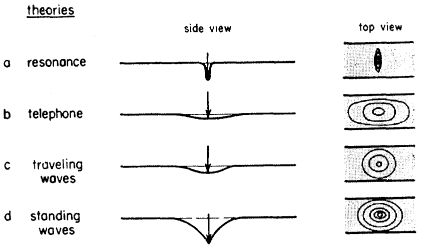

Fig. 2. Deformation patterns in membranes acted upon by a point force.

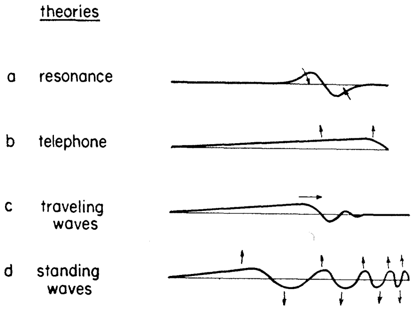

Fig. 3. Vibration patterns in membranes for a continuous tone (with normal damping). The arrows indicate the direction of movement at a given instant.

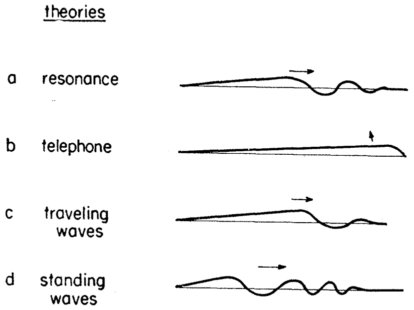

Fig. 4. Vibration patterns in membranes for the transient state (with normal damping).

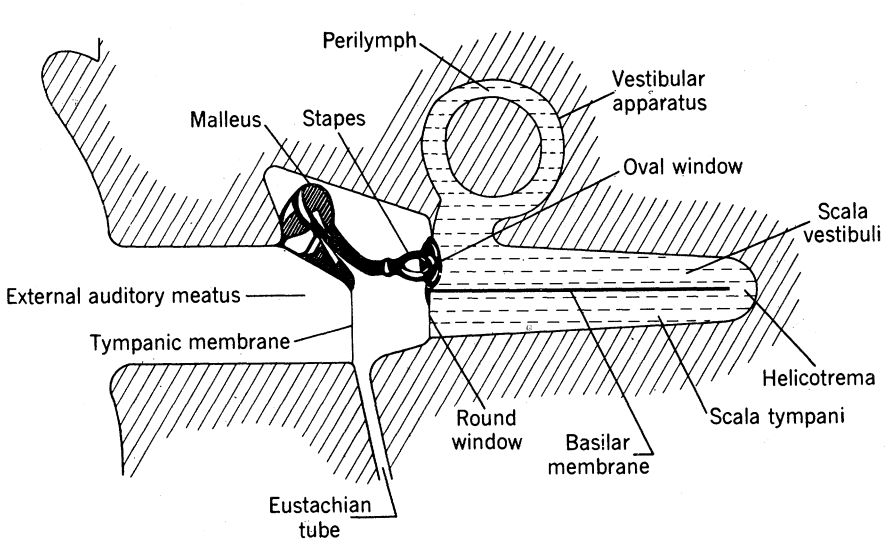

Fig. 1. Schematic cross-section of the human ear.

We obtain substantiation of two other types of hearing theories simply by decreasing the thickness of the plastic sheet. As the thickness decreases, the maximal amplitude of the displacement becomes greater. When the thickness of the sheet is decreased slightly, the same steady tone produces a traveling wave moving away from the source (Figs. 2c and 3c). When a thinner sheet is used, the same point force pushes the partition out still farther; and the same steady tone produces traveling waves that get shorter and travel farther until some are reflected from the end of the membrane and standing waves result (Fig. 3d). The standing-wave theory was proposed by Ewald.

A change in the frequency of a steady tone moves the maximum of the vibrations along the basilar membrane, as the resonance theory assumes. An increase in the frequency moves the maximum of the vibrations toward the stapes. The resonance theory of hearing is a place theory in which pitch discrimination depends on locating the place along the membrane that is set in maximal vibration. According to the telephone theory, a change in frequency need not affect the displacement of the membrane, and pitch discrimination depends on some unknown function of the brain. The traveling-wave theory is also a place theory, since an increase in the frequency moves the maximum of the vibrations toward the stapes, and a decrease moves it toward the helicotrema. According to the standing-wave theory, an increase in frequency increases the number of nodes and decreases the distance between them. The brain uses this information to determine pitch.

As we can see from Fig. 3, four basically different vibration patterns can be obtained for a steady sinusoidal tone simply by manipulating two variables, the absolute stiffness of the membrane and the coupling between its adjacent parts. Since it is possible to go continuously from one pattern to another, an infinite number of intermediate patterns can be obtained; but all these belong to a single family of curves. Additional vibration patterns have been proposed, some of which I have tried to verify on models, but I have come to the conclusion that they are only drawings and have no physical existence. I believe that Fig. 3 shows all the principal patterns there are.

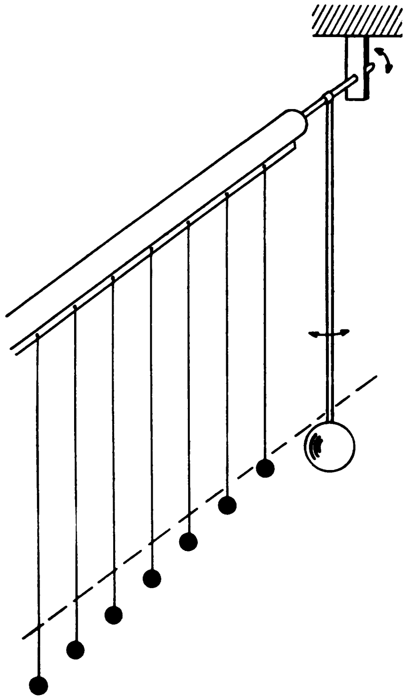

Fig. 5. Pendulum system set up to demonstrate occurrence of traveling waves in a system of free resonators.

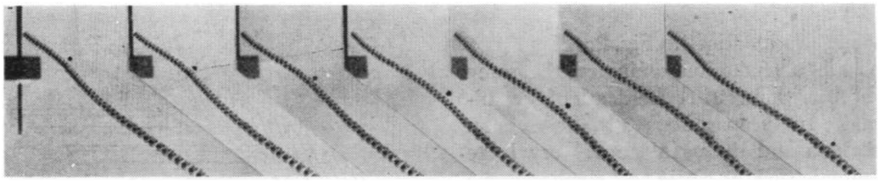

Fig. 6. Film strip showing a system of free resonators with wave traveling toward the longer pendulums (from right to left) during the onset of a continuous tone. The black dots indicate the positions of the maximal lateral displacement.

We have seen how, for a continuous tone, it is easy to substantiate each theory in turn simply by manipulating the elastic properties of the membrane. The differences among the theories depend wholly on the sizes of these variables. It is even more surprising, however, to find that for transients—for example, the onset of a steady tone—the differences between the resonance, traveling-wave, and standing-wave theories disappear completely, despite the emphasis that these differences have received. Traveling waves develop during the onset of vibrations in membranes whose vibration patterns are described by these three theories, as shown in Fig. 4. (The driving frequency is the same as it is in Fig. 3.) Only the telephone theory assumes that all parts of the membrane vibrate in phase, in complete conformity with the movements of the driving stapes.

It is especially difficult to understand how in a system of free resonators the onset of a continuous tone produces traveling waves. A simple experiment was set up to demonstrate the occurrence of traveling waves in a system of free resonators (Fig. 5). A pendulum with a large mass was clamped to a long, horizontal driving rod from which a series of small pendulums was suspended. The lengths of the pendulums increased continuously from one end of the system to the other, from right to left in the figure. One pendulum in the middle of the series was of the same length as the heavy driving pendulum. During continuous oscillation of the driving pendulum, the resonant pendulum was set in motion by small movements that were transmitted through the oscillating supporting rod. A change in the period of the driving pendulum made a different pendulum resonate—that is, the whole series was a system of free resonators, each of which resonated at a different frequency. The onset of the oscillations of the driving pendulum set in motion a large section of the system, and a traveling wave was observed moving toward the longer pendulums, as can be seen in the sequence of film shown in Fig. 6.

To complete this survey of the various hearing theories, I should mention that at very low frequencies the movement of a vibrating system is independent of its mass; the displacement of the various parts of the membrane is determined solely by their elasticity. Since the slope of elasticity along the membrane is the same in all four models, the vibration patterns for low frequencies are similar, as shown schematically in Fig. 7. The largest excursions appear in the standing-wave model, which has the most yielding membrane.

Another factor that affects the movement of the basilar membrane is the damping provided by the fluid in the cochlea. In our models, when the viscosity is high, the differences between the various theories tend to disappear. When the fluid friction is extremely high, the movements of the membrane are determined solely by the frictional forces in the fluid, independent of the elasticity values of the membrane. Here again the vibration patterns are identical for all the theories, and even the displacements are equal (Fig. 8).

According to the foregoing discussion, the question of which hearing theory is valid reduces to the more easily answered question, What are the numerical values of the elasticity and coupling along the basilar membrane? In these experiments, when the tip of a needle was pressed perpendicularly on the surface of the basilar membrane of some lightly anesthetized vertebrates (guinea pig, mouse, cat, and pigeon), the resulting deformation was almost circular; both the top and side

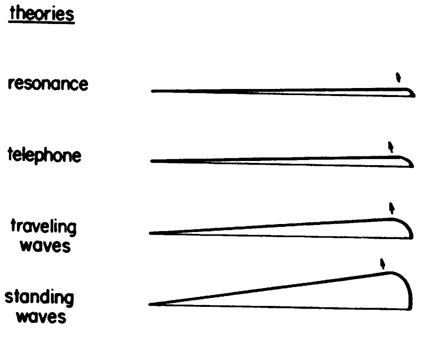

Fig. 7. Vibration patterns in membranes for continuous tones of very low frequency.

views are identical to Fig. 2c. The shape of the deformation remained the same for many hours after the death of the animal. In preparations of the human cochlea and the cochleae of very large animals such as cattle and elephants, the same circular deformation is found. The shape of the deformation proves that the coupling between the adjacent parts of the basilar membrane is so large that it invalidates the resonance theory of hearing.

The side view of the deformation makes it clear that the stiffness of the basilar membrane is too great for standing waves to occur. The formation of standing waves along the basilar membrane is improbable also because standing waves with large amplitudes occur only at certain frequencies; if standing waves were to occur, the sensitivity of the ear would undergo large fluctuations during a continuous change in frequency. Figure 9 shows the type of audiogram we would obtain under these conditions.

It is clear, therefore, that the vibration of the basilar membrane cannot be accounted for by either the resonance theory or the standing-wave theory.

Observation of the basilar membrane in mammals substantiates the traveling-wave theory. Under stroboscopic illumination, a steady tone of 1000 cycles per second produces traveling waves similar to those pictured in Fig. 3c. When the frequency is lowered, the maximal amplitude moves toward the helicotrema (toward the right side of Fig. 3c), and the length of the membrane that is vibrating practically in phase is increased. The place of the maximum reaches that end of the membrane in the different animals at the following frequencies: mouse at 400 cycles per second, pigeon at 80, rat at 180, guinea pig at 200, man at 30, and elephant at 30. Below these frequencies the basilar membrane vibrates in phase, as postulated by the telephone theory (Fig. 3b).

Below the critical frequency, pitch discrimination depends entirely on the temporal sequence of the stimulation of the nerves. Above the critical frequency, there is a second factor, the shifting of the place of maximal stimulation along the basilar membrane. We must now ask, Is pitch discrimination improved by this shifting of the place of maximal stimulation as compared with the conditions under which it depends wholly on the temporal sequence of the vibrations? The problem is no longer mechanical, but one of how the nerves react to different vibration patterns on the basilar membrane.

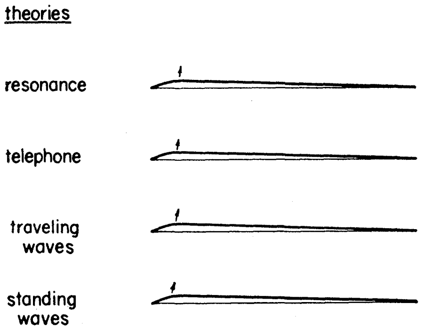

Fig. 8. Vibration patterns in membranes immersed in fluid with very high viscosity (for continuous tones).

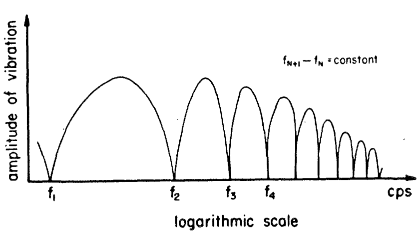

Fig. 9. Hypothetical audiogram for standing-wave theory showing large fluctuations which would occur during a continuous change in frequency.

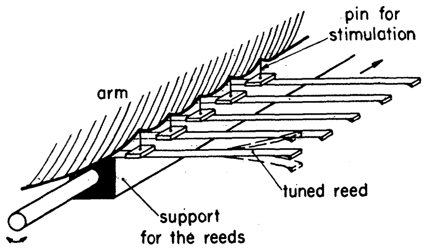

Fig. 10. Mechanical model for the resonance theory, with the skin of the arm substituted for the nerve supply of the basilar membrane. The reed system transforms any change in frequency into an easily observable displacement of the stimulated area on the skin.

Mechanical Models of the Cochlea

In order to investigate this aspect of the problem, I built cochlear models in which the skin of the forearm was substituted for the nerve supply of the basilar membrane. Three mechanical models were made that stimulated the skin of the arm in accordance with the three vibration patterns in Fig. 3a, b, and c. No model with standing waves was built because change in frequency would produce a large change in amplitude, and consequently it would be very difficult to distinguish amplitude changes from frequency changes (which is not the case in the ear).

The mechanical model for the resonance theory is shown in Fig. 10, for the telephone theory in Fig. 11, and for the traveling-wave theory in Fig. 12.

The resonating model consisted of a series of tuned steel reeds attached to a metal support that oscillated slightly around its longitudinal axis. The length of the support was equal to the length of the forearm. Thirty-six reeds, tuned in equal intervals over a range of two octaves, were distributed along the whole length. A small pin on each reed, fastened close to the support, touched the surface of the skin of the arm. The pins had rather small points, so that the skin would not pick up too much energy from the vibrating reeds; otherwise it would not have been possible to obtain a sharp resonance of the reeds. When the arm is placed carefully along the pins, so that the points just touch the skin, the reed system transforms any change in frequency into an easily observable displacement of the stimulated area on the skin.

The model for the telephone theory is a triangular metal frame made of tubes (Fig. 11). The frame vibrates perpendicularly to the axis of the edge in contact with the forearm. The rigidity of the frame insured that all the stimulating parts touching the skin would vibrate in phase. From time to time, phase constancy along the frame was verified by stroboscopic illumination.

The model for the traveling waves was a section of a model of the human cochlea, enlarged by dimensional analysis. The frequency range was two octaves. The model was a plastic tube cast around a brass tube with a slit. The tube was filled with fluid. Figure 12 shows the position of the arm on the vibrating membrane. A vibrating piston sets the fluid inside the tube in motion, and forces in the fluid produce waves that travel from the hand to the elbow. The traveling waves thus produced are similar to those observed in preparations of human cochlea. The maximum amplitude of vibration is rather broad, and when it is observed under stroboscopic illumination, it moves along the membrane as the frequency is changed. Although the maximum is quite flat as it moves along the arm, the sensation of vibration is concentrated on a relatively short length (about 2 to 4 centimeters); hence, any frequency change is easily

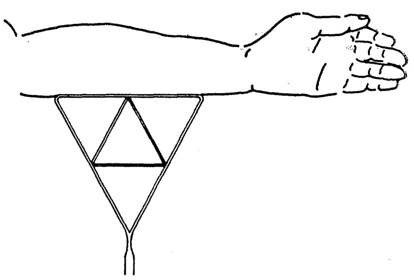

Fig. 11. Mechanical model for the telephone theory, with the skin of the arm substituted for the nerve supply of the basilar membrane. All parts of the triangular frame in contact with the arm vibrate in phase.

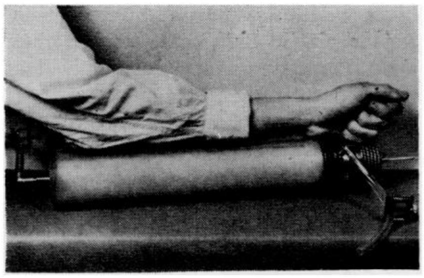

Fig. 12. Mechanical model for the traveling-wave theory, with the skin of the arm substituted for the nerve supply of the basilar membrane. A vibrating piston sets the fluid in the tube in motion, producing waves traveling from the hand to the elbow.

recognized by a shift in the stimulated area. Seemingly the nerve network in the skin inhibits all the sensation to either side of the maximum of the vibration amplitude, thereby producing a sharpening of the stimulated area.

If we compare the three models, we find that the difference limen for "pitch" discrimination below 40 cycles per second is the same because the skin is able to discriminate the roughness of the vibrations as such. But for higher frequencies, displacements of the sensation along the arm, produced either by the resonating model or the traveling-wave model, permit much more accurate frequency discrimination than the telephone-theory model does.

The most surprising outcome of these experiments with models was that pitch discrimination did not deteriorate when the presentation time of the tone was very short. Even when the stimulus was only two cycles, the pitch discrimination for both the resonance model and the traveling-wave model was just as good as it was for a continuous tone of longer duration. Closer examination showed that in both models the place of maximal amplitude was determined during the first two cycles of the onset of a tone. Figure 4 shows that for transients there is very little difference between the vibration patterns of the resonance and traveling-wave theories. In both, waves travel over quite a long section of the vibrating system. The surprising fact is the inhibitory action of the nerve supply, which suppresses all sensation except on a small spot near the maximal amplitude of vibration. In the ear the situation seems to be the same because, there too, two cycles of a tone are enough to enable us to discriminate the pitch of the tone.

Summary

In summing up the current status of the hearing theories, it may be said that each of the vibration patterns of the basilar membrane postulated by the four major theories of hearing can be obtained by varying two elastic properties of the membrane—namely, the coupling between adjacent parts and the absolute value of the elasticity. If these two variables are adjusted to their numerical values in the cochlea of a living animal or a fresh preparation of the human ear, traveling waves are observed along the membrane. These traveling waves have a flat maximum that shifts its location along the membrane with a change of frequency—the place of the maximum determining the pitch. An enlarged dimensional model of the cochlea in which the nerve supply of the sensory organs on the basilar membrane was replaced by the skin of the arm indicates that the inhibitory action in the nervous system can produce quite sharp local sensations, which shift their place with changes in the frequency of the vibrations.

References and Notes

1. This article is based on a lecture given at the meeting of the American Otological Society in Chicago on 10 October 1955. The enlarged model of the cochlea was demonstrated at that meeting. Those present were able to try out the model for themselves and to observe the change in location of the stimulated area on the skin when the driving frequency of the model was changed. This article was prepared under contract N5ori-76 between Harvard University and the Office of Naval Research (project NR142-201, report PNR-179).
2. Articles of mine that are concerned with measurement of the vibration pattern of the human cochlea have appeared in the main in *J. Acoust. Soc. Amer.* from 1947 to the present.
3. S. S. Stevens and H. Davis, *Hearing: Its Psychology and Physiology* (Wiley, New York, 1938); E. G. Wever, *Theory of Hearing* (Wiley, New York, 1949); O. F. Ranke, *Physiologie des Gehörs* (Springer, Berlin, 1953); E. G. Wever and M. Lawrence, *Physiological Acoustics* (Princeton Univ. Press, Princeton, N.J., 1954); and T. C. Ruch, "Audition and the auditory pathways," in Howell's *Textbook of Physiology*, J. F. Fulton, Ed. (Saunders, Philadelphia, ed. 17, 1955), pp. 399–423. For additional titles see S. S. Stevens, J. C. G. Loring, D. Cohen, *Bibliography on Hearing* (Harvard Univ. Press, Cambridge, Mass., 1955).

Secrecy and Scientific Progress

Lloyd V. Berkner

Serious technological secrecy is relatively recent, having emerged sharply as a product of the upsurgence of our technological revolution. There are, of course, a few earlier examples extending throughout history, but they were almost insignificant. But as society generally has become deeply dependent on technological development, so too have the military organizations increased their dependence on science and technology. Initially, at least, it appeared reasonable that the military should restrict the exchange of ideas having military implications on the ground that to permit the free flow of information would hand the enemy our developmental achievements "on a platter."

In the modern world, however, all the important areas of science have military implications and, under our present policies, must therefore fall inevitably under the cloak of military secrecy. Not long ago, for instance, a responsible scientist mentioned to me that he had endeavored to arrange a scientific conference on fundamental high-temperature physics. He found that this was impossible, however, because all the important recent advances were "classified information." At the same time, Marguerite Higgins has reported in the New York *Herald Tribune* for 6 February 1956, "An Indian engineer told me, for example, that Soviet development of heat-resistant materials was far more advanced than anything he had seen in the West." A great many such examples can be cited. Since more and more of our scientific activity is coming within the purview of secrecy, the need for appraisal of the effects of secrecy on our scientific stature and progress, and therefore on our national security, becomes of increasing importance. It

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Dr. Berkner is president of Associated Universities, Inc. This article is based on his statement to the Government Information Subcommittee of the Committee on Government Operations, House of Representatives, on 7 Mar. 1956.