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Concerning the pleasures of observing, and the mechanics of the inner ear

Nobel Lecture, December 11, 1961

Trying to do science in an unscientific way

For me, the most stimulating book on hearing was Helmholtz's *Die Lehre von den Tonempfindungen.* It was published in 1863. Although some of its details are not confirmed by measurements with today's instruments, the basic concepts still retain their value, and Helmholtz´s method of viewing physiology and psychology in physical terms is today just as fresh as the day it was written. Hehnholtz's magnificent start, however, was followed by stagnation in auditory research, and for almost 100 years the universities taught about the same thing. The whole field of acoustics made very little progress compared with the tremendous achievements in other areas of physics.

This may seem surprising, since acoustics and concepts of waves continued to influence the development of physics, particularly theoretical physics; and there are many instances in which acoustical concepts served to initiate new theories. For instance, the Mach wave was the model for the discoveries in the field of light radiation of Cerenkov, Frank, and Tamm[1], the Nobel Laureates of 1958.

Looking back, I think it is not too difficult to understand the slow progress in the physiology of hearing. Fig. 1 shows, along the ordinate, the vibration amplitudes of air particles and of the basilar membrane in the inner ear of man for sounds that were just audible at the frequencies noted on the abscissa. (The vibration amplitudes of the basilar membrane are plotted because the auditory nerves terminate in cells that are seated on that membrane; and as a result, its vibrations seem to be responsible for the stimulation of the auditory nerve.) As you can see, the vibration amplitudes are extremely small. At 3,000 cps (cycles per second), we can hear a vibration of the air particles that is 100 times smaller than the diameter of the orbit travelled by an electron around the nucleus of a hydrogen molecule. Even for sound pressures so high that they would produce unbearable pain in the ear, the vibra-
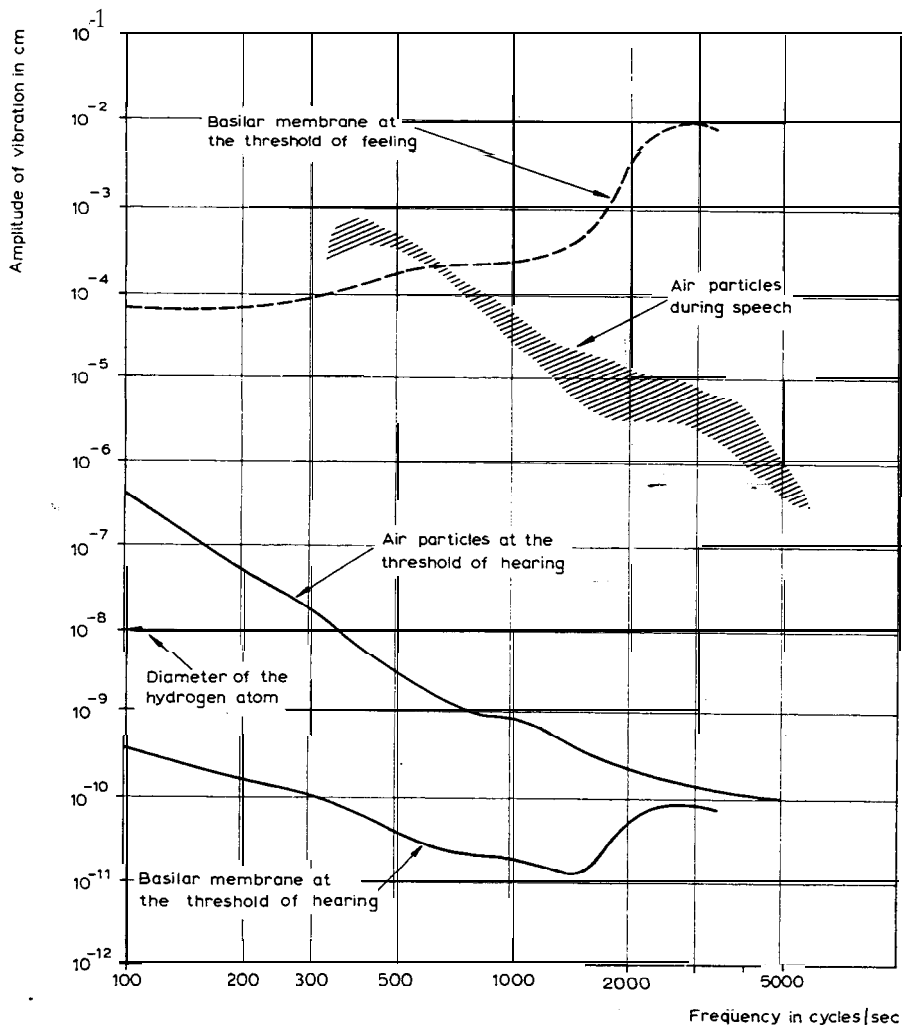
Fig. 1. Vibration amplitude of air particles, and of the basilar membrane of the inner ear at the threshold of hearing *(solid lines),* compared with the diameter of a hydrogen atom. Given for comparison are the vibration amplitudes of the basilar membrane for the maximum sound pressure that can be tolerated even for a few seconds *(dashed line).*

tion amplitudes for higher frequencies would be relatively small. There were until recent times no methods for measuring these small amplitudes, though these measurements constitute the most essential data on which to begin acoustic research. It was only with the invention of the amplifier that this difficulty was overcome.

Oddly enough, in my research on the mechanics of the inner ear, am-

Fig. 2. Baboon, Egypt, ca. 1,400 B.C.

plification has played only a minor role in the crucial experiments that were planned to decide between the different possible theories. But what was of importance to me was the kind of new concepts that were being developed in the field of communication engineering - concepts such as damping, transients, filter bandwidth, phase distortion, non-linearity, and so forth. These concepts originated with the mathematical treatment of transients by Heaviside[2], their exact formulation by K. W. Wagner[3], Carson[4], Küpfmüllers, Barkhausen[6], Laurent[7], and Feldtkeller[8], to mention only a few.

Helmholtz, in a well-remembered talk, described the two roads to research: *(i)* the shaky ladder that every scientist has to climb, and *(ii)* the smooth royal path on which the results are presented to an audience. Since both Stevens and Davis[9], and Wever and Lawrence[10] reviewed my earlier

Fig. 3. Black-stone monkey from Bogas-Koi, ca. 3,000 B.C.

work, and Wever[II] edited all my earlier publications, I would like to talk not about the red carpet, but about some of the things that happened between the published lines.

I must admit that I have never liked to work hard. Preparing for college examinations was something I could do, but I hated to do it. Even today, I dislike deadlines. But there is one thing I am always ready to do, and that is to look at beautiful things. I can look for hours at an art object, and I am convinced that I owe a large part of my education to the museums of many countries. I mention this because curators of museums seldom receive prizes. It was in the museums that I first realized that there is something like a timeless beauty that persists in spite of all the endless wars and intrigues. A baboon from 1,400 B.C. (Fig. 2) gives us the same feeling of dignity now
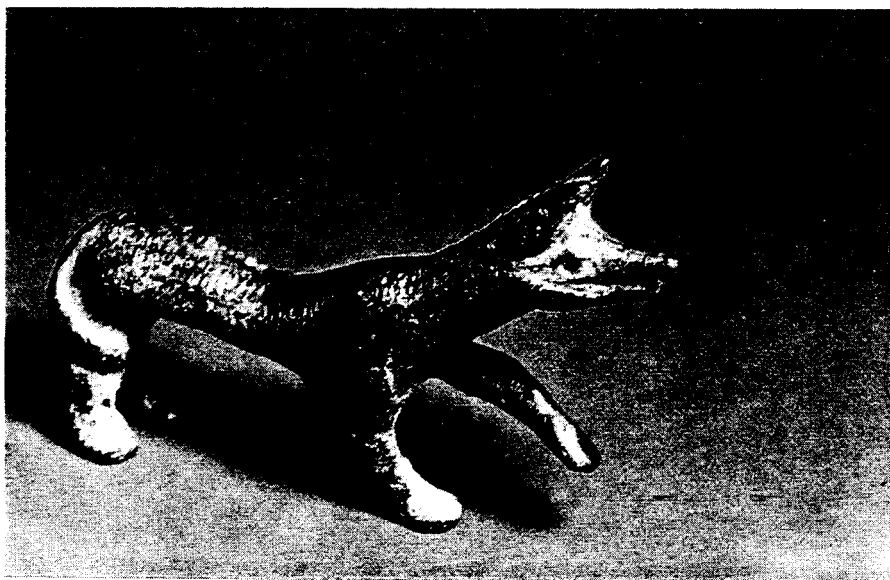
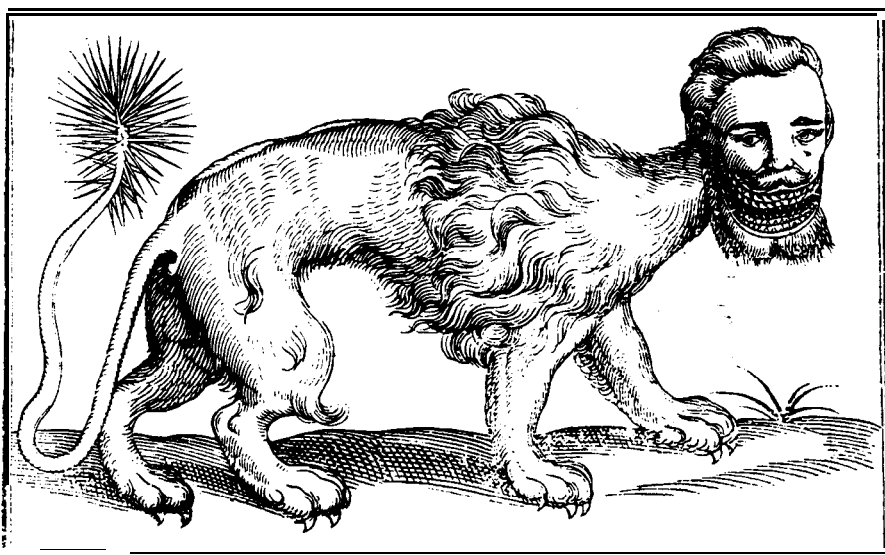Fig. 4. Bronze figure of a fox, Greece, 8th century B.C.

Fig. 5. Lion-man, 12th century. *(Reprinted with permission from T. H. White, "The Book of Beasts", G. P. Putnam, New York, 1954.)*
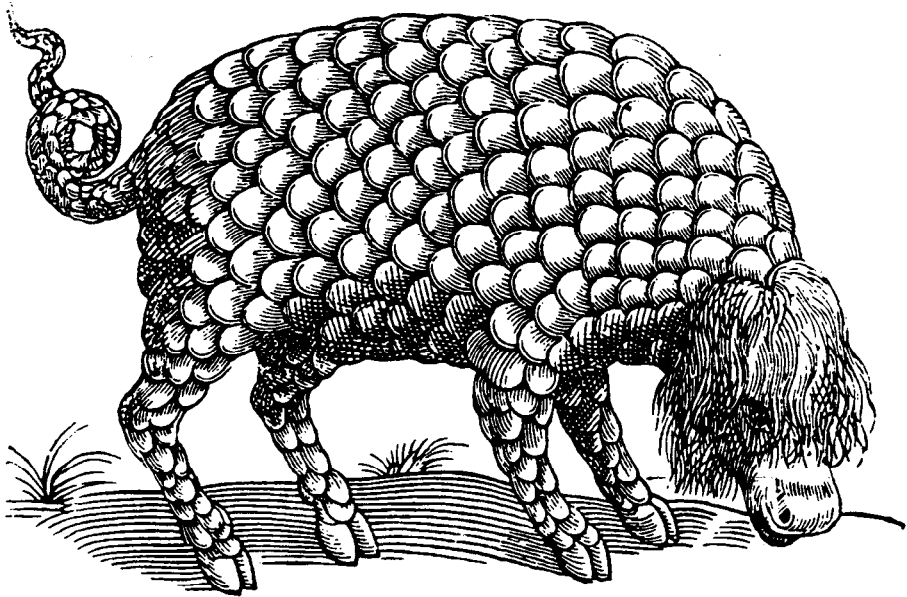
Fig. 6. Fantastic dog, 12th century. *(Reprinted with permission from T. H. White, "The Book of Beasts", G. P. Putnam, New York, 1954.)*

that he did in his day. A Hittite monkey (Fig. 3) looks just as helpless today as he did 5,000 years ago; and an early Greek fox (Fig. 4) behaves with all the shrewdness of a growing important nation.

In my student years I was very much concerned with the question, why it is so difficult to imagine something new? Where are the limits of fantasy, was my daily question. It is very difficult to recognize these borderlines in a chemistry or physics book. But it is easy to see them in the history of art. Between the 12th and 15th centuries it was the custom in Europe to use fantastic animals as decoration. If you compare the Figs. 5 through 9, it will surprise you to see how limited the fantasy really is, for most of the figures are nothing more than the combination of parts of other figures. They were much more original in the Near East in the first half of the first millennium B.C. But even so, my question remains, how is it possible to produce new discoveries in science when our imagination is so limited?

It was the study of the drawings of Leonardo da Vinci that gave me the answer. If you compare the drawing of the flower in Fig. 10 with the drawing of the storm in Fig. 11, you will have the impression that da Vinci was able to cover a velocity range that to my knowledge no other artist has been

Fig. 7. Luristan bronze handle, ca. 800 B.C.

able to equal. Why? I believe it is because da Vinci did not try to outdo Nature with his fantasy, but, quite the opposite, he tried to learn from Nature. It was this very simple finding that gave me, in my student years, the hope that perhaps in time I would be able to produce something of enduring interest.

Preliminary   experiments

After the First World War, the only place in Hungary that had some scientific instruments left and was willing to let me use them was the research laboratory of the Post Office. There were four floors and all of us there were
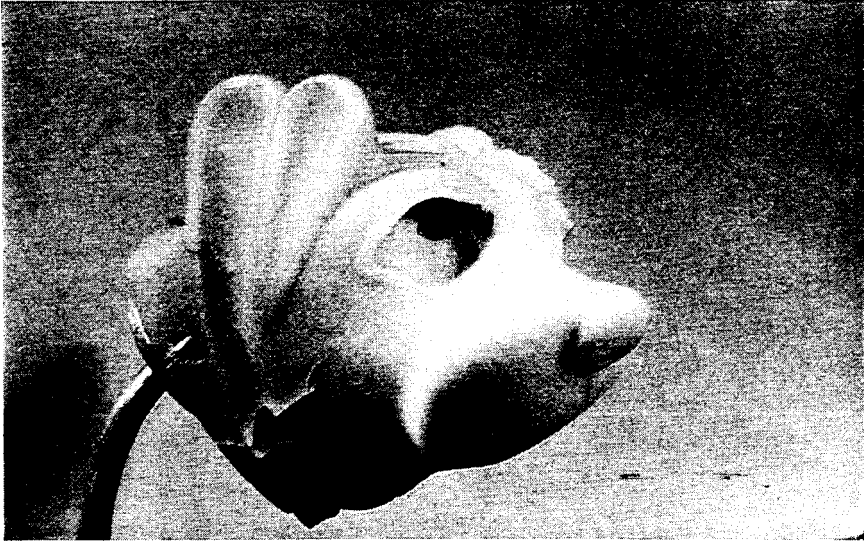
Fig. 8. Achameneid head (pink stone), ca. 500 B.C.

friends, forged together by the very hard facts of postwar life. At that time, many of the important telephone lines went through Hungary and there were constant complaints that Hungary did not keep its lines in order. The method used to test a telephone line was to put an A.C. voltage on a line, beginning in Budapest, let the current go to the different capitals, and then feed it back to Budapest and compare the input with the output voltage for different frequencies. A single measurement of the speech frequency range took more than 20 minutes. A few minutes after the measurement was completed, the lines were apt to be out of order again.

I wanted to find a method that could complete the test in a second. The idea was that, when a musician tests his violin by pluckinga string, he can tune it immediately. Theoretically, by plucking a telephone line it should be possible to obtain instantly all the data that are obtained by the cumbersome 20-minute test. Therefore, I transmitted a click through the line by switching in a small D.C. voltage and then listening and observing the returning signal. It turned out that the operator's switch always had some D.C. potential difference, and before long I was able to tell precisely in which city a disturbance of the lines had occurred just by listening to the clicks. After the clicks were localized, a private toll call stopped the complaint.

A little later the question came up, how could we improve the com-

Fig. 9. Terra cotta from North Syria, ca. 2,000 B.C.

munication? Should our attention go first to the earphone, the microphone, or the lines? To find an answer to this question, I simply applied a brief mechanical click to the eardrum and the microphone, and an electrical D.C. pulse to the earphone and the telephone lines. After a few days it was clear that our earphones were much inferior in quality to the eardrum. Fig. 12 shows the transient oscillations of the eardrum after it is subjected to a sharp click. From the form of these transients we can determine precisely the various resonant frequencies of the eardrum and the damping of the free oscillations. The higher the resonant frequencies are, the wider is the frequency range that is correctly transmitted; and the shorter the transient time, the flatter the frequency transmission. The upper photograph of Fig. 13 shows the response of the membrane of a telephone receiver to stimulation

with a sharp D.C. pulse; the lower drawing gives the response of a high-fidelity earphone to similar stimulation.

Because of its simplicity, this click method has attained primary importance in research on the inner ear. In those days it was generally assumed by the medical profession that the mechanical properties of the tissues of the ear changed rapidly after death, and that there was virtually no possibility of determining the mechanical properties of the inner ear of man. Since it was clear to me from the beginning that if I started to make measurements of the inner ear it would take 2 or 3 years to collect the required data, I wanted to know, as precisely as possible, how fast the tissues disintegrate. With the click method, measurements can be made with such great precision that changes in elasticity or friction as small as 1 or 2 per cent can be detected. My studies of the tissues of the ear centered first on the eardrum, because the drum is so thin that a change in any part of the ear would result in drying or loosening there.

The first step in the test of the tissues was to record the vibrations of the handle of the hammer of the eardrum. When all the higher-order vibrations were filtered out, we obtained very regular damped oscillation, as is shown

Fig. 10.   Drawing by Leonardo da Vinci (no movement). *(Royal Collection, Windsor Castle; reproduced by gracious permission of H. M.* Queen *Elizabeth II.)*

Fig. 11. Drawing by Leonardo da Vinci (maximum movement). *(Royal Collection, Windsor Castle; reproduced by gracious permission of H. M. Queen Elizabeth II.)*

in Fig. 14. The amplitude of the oscillations, their decay, their resonant frequencies, and even the change in their decay and resonant frequency with amplitude can be measured with astounding precision under a microscope or a comparator. As a check on the method, vibrations were applied to a metallic membrane for days, but no change occurred.

In the investigation of the tissue, the tendons of the stapes and tympanic muscles of anesthetized animals were severed, and changes in the properties of the eardrum were observed during and following the animal's death. If the relative humidity was kept at 100 per cent, even at room temperature there was only an insignificant change, and that mostly in the friction. An even more sensitive method was developed specifically to test the changes in elastic property of the cochlear partition, and again with the same results. After these preliminary observations, the road was open to measure the mechanical properties of the cochlea in man and to compare it with the cochleas of different animals.

The travelling wave

It was very fortunate that even in Helmholtz's time the great anatomical discoveries by Corti[12], Kölliker[13], and Hasser[14] had already made it clear that the vibrating tissue most important for hearing is the basilar membrane of the inner ear, because the cells on which the nerve endings terminate are seated on this membrane. Later research by Retzius[15], Kolmer[16], and Held[17] described the anatomy of the inner ear with such perfection that the problem of how we hear was reduced largely to a mechanical question: how does the basilar membrane vibrate when the eardrum is exposed to a sinusoidal sound pressure? Since nobody could see these vibrations, a number of theories developed, which have been reported in a masterly way by Waetzmann[18]. And naturally, as time went on, all the possible mechanical vibrations were suggested. We had resonating systems, travelling waves, standing waves, and even no waves at all - just a bulged membrane.

Looking back now, I see that I had good luck with my first experiment.

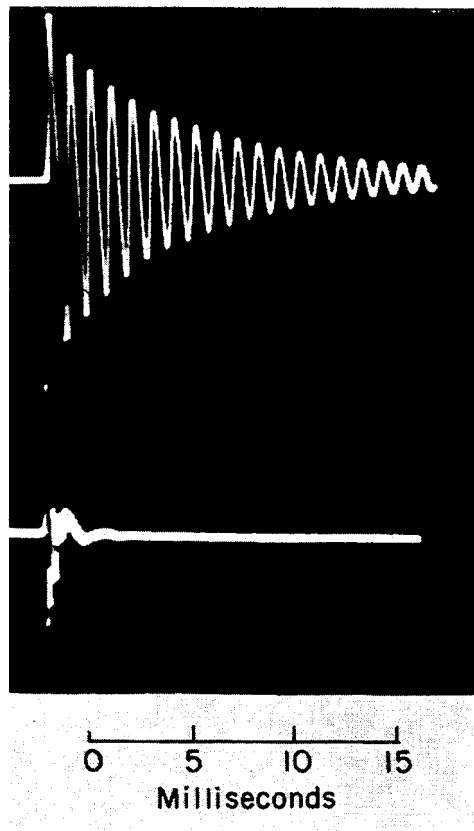Fig. 12. Vibration of the eardrum after exposure to a very short click.

Fig. 13. *(Upper curve)*: response of the membrane of a telephone receiver to direct cur-
rent applied suddenly. *(Lower curve)*: similar response of a high-fidelity earphone.

I took a tuning fork and touched its stem to any materials I could find -
threads, chains, springs, membranes, human skin, fluid surfaces - and with a
stroboscope observed the vibrations (Fig. 15). I think my most exciting dis-
covery was the observation that, if the frequency of the vibrations was high
enough, all objects that had internal elasticity showed traveling waves. The
waves travelled from the vibrator to the edge of the object, from which they
were more or less reflected back. Therefore, I could see no physical reason
whatsoever why the basilar membrane - a gelatinous mass imbedded in fluid
- should not also have travelling waves when one section of it was put in
motion by alternating pressure (Fig. 16). It would have been ridiculous for
me to submit these experiments for publication in a physics journal, for to a
physicist this was obvious. And I hesitated also to submit them to a phys-

iological journal, because in any handbook of physiology, one need only turn a few pages to see the connection between the movements of the basilar membrane and the pulse waves of the arteries.

The next problem was extremely difficult, and so I put aside my discovery in spite of all the enthusiasm of a young Ph.D. As you can see from Fig. 17, there are many types of wave, and not just one. There are: *(a)* compression waves, *(b)* shear waves, *(c)* dilation waves, *(d)* Rayleigh waves, *(e)* ordinary bending waves. My question was, which of these waves are present in the inner ear, and which one contributes to the stimulation of the auditory end organs? Clearly, if several of these waves were present simultaneously and in the same order of magnitude, my further investigations would have no chance for success. The difficulty is that, in a system as complex as the cochlear partition, if one type of wave lost its energy while traveling along the membrane, it would be able to get a new supply of energy from another type of wave that was not so damped during the travel. This interplay of energy would make any analysis or mathematical treatment very complicated. Therefore, it was essential to find out whether one of the waves
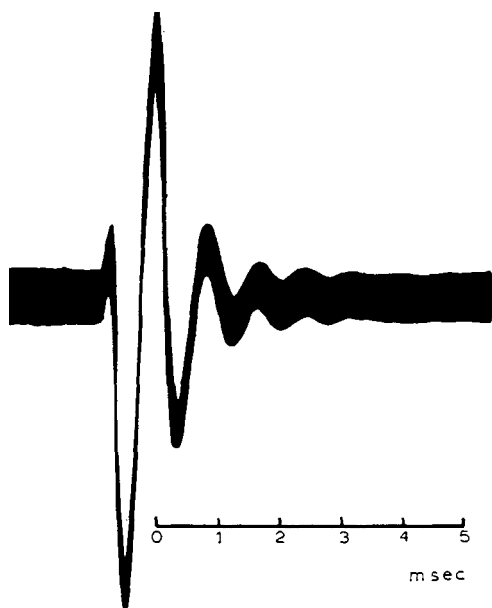

Fig. 14. Click response of the handle of the hammer of the eardrum after the higher resonances have been filtered out. This procedure permits precise measurements of changes in the pattern of oscillation over long periods of time.
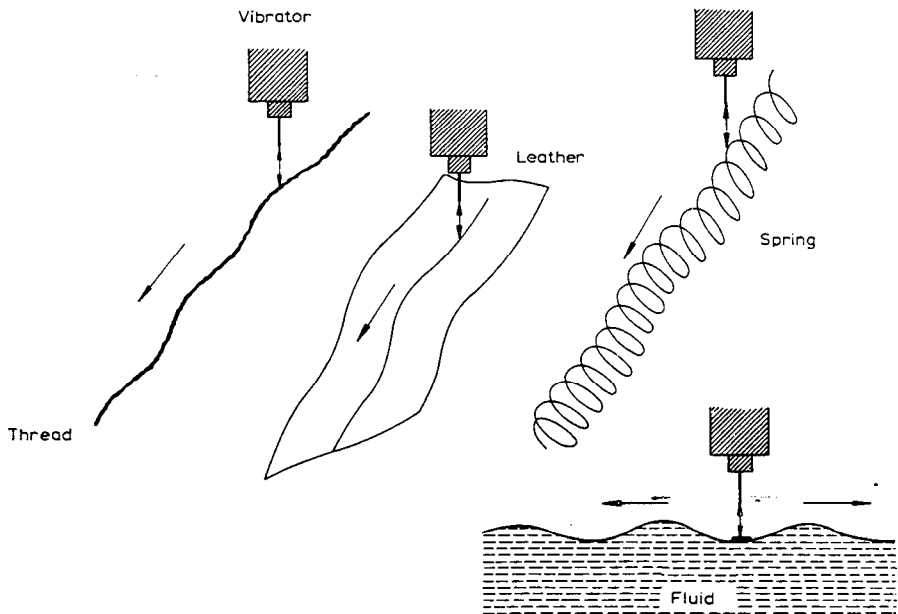
Fig. 15. Travelling waves observed on different objects brought in contact with a vibrator.

exceeded the others in magnitude to the extent that, at least for a first approach, the others could be neglected. I well remember the crucial night when I finally became convinced that, at least over the lower frequency range, the ordinary bending of the basilar membrane furnished an adequate description of the vibrations that stimulate the nerve endings. To appreciate that night, you have to remember that the whole inner ear of a guinea pig is about as large as a drop of water at the end of an eye dropper.

   This new possibility focused all my attention on the elasticity and friction of the basilar membrane, and I decided to measure these variables on fresh human temporal bones as well as on animals. I laid down a program of how I would proceed for the next 10 to 15 years. First I wanted to measure and map all the vibration amplitudes and phases for sinusoidal forces on the stapes footplate. After that, I wanted to determine the physical constants that are responsible for these vibration patterns. Even in a description that took account of the bending waves only, the number of constants involved would be so great that it would be impossible to measure them all. Consequently, the most important question was, which variables would suffice to produce a wave pattern that corresponded to the pattern observed in the inner ear?

With this knowledge a mechanical model could be constructed in which only the essential variables would be represented. If the wave pattern in the model should turn out to be identical with the pattern found in the inner ear, the road would then be open for a mathematical approach to the problem. No simple mathematical solution was likely, and plenty of pitfalls could be expected in the hydrodynamic part; for it is well known that hydrodynamics is a science in which there are more paradoxes than laws.

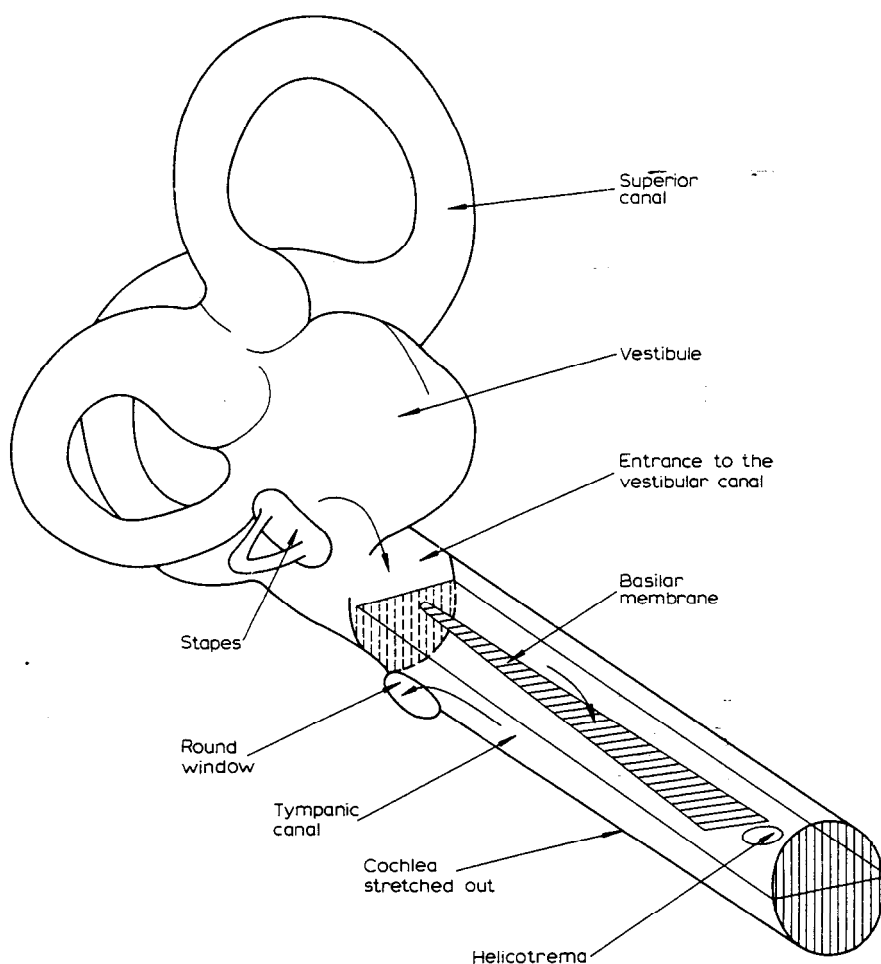The shape of the travelling wave in the human cochlea is shown in Fig. 18

Fig. 16. Schematic diagram of the inner ear showing the basilar membrane on which the sensitive nerve cells are located. The vibrations of the eardrum are transmitted through the stapes to the inner ear.

1 Compression wave

2 Shear wave

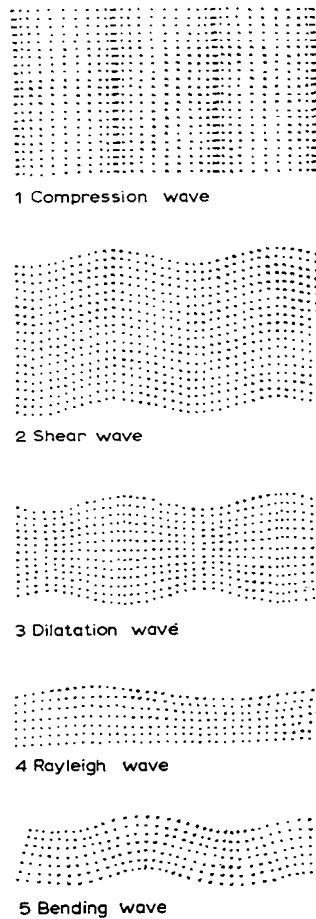3 Dilatation wave

4 Rayleigh wave

5 Bending wave

Fig. 17. The different types of waves (after Berger).

for stimulation by a tone of 200 cps. The envelope of the vibration amplitude has a maximum, but the maximum is relatively flat. This flatness indicates that very little mechanical frequency analysis is done by the inner ear. This conclusion is confirmed for the higher frequencies in Fig. 19 which shows the displacement of the maximum of the envelope for different frequencies. But although the maximum of the envelope is flat, it is clear that it shifts towards the left as the frequency of the stimulation is increased.

These measurements were not simple, since first it had to be established that the opening of the cochlear wall did not disturb the vibration pattern. I worked for 4 or 5 months to develop cements that would adhere to bone under water. (From a purely physical point of view, the problems of adhe-
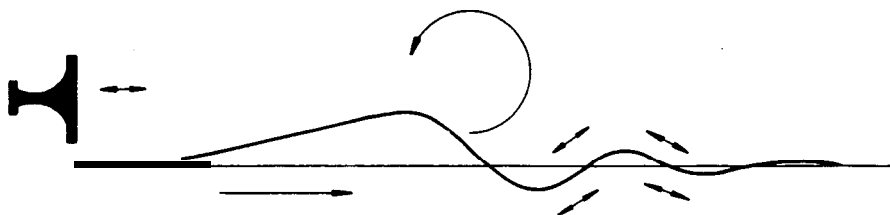
Fig. 18. Travelling wave along the human basilar membrane, showing the formation of eddies in the surrounding fluid.

sives are almost as interesting as the ear and very little has been written about them.) To my surprise, the vibration pattern turned out to be quite stable. It is hardly affected by an opening, it is independent of an increase in the dimensions of the space around it, and one can even change the mechanical properties of one section of the membrane without disturbing the vibration pattern of the remainder. Mathematically, we have, at present, no understanding of why the vibration pattern is so stable. Here again Nature is far ahead of us.

With these observations of vibration patterns, together with some quite specific measurements of variables of elasticity, such as the volume elasticity of the cochlear partition, it was possible to construct a model of the cochlea from a rubber membrane on a metal frame - a model that responded to stimulation with precisely the same vibratory behavior as the real cochlear partition. Thus with this model I was able to reduce the number of variables to the essential one. This mechanical model that I mention is not to be confused with the quite different models that have become popular in non-physical sciences, such as psychology, where they are now trying to develop mathematical models of human behavior. In my opinion, they should be called not models but rather analogies. In illustration of this point, the photograph in Fig. 20 shows a gold bracelet fashioned in Greece in about 1,000 B.C. It represents two snake heads facing each other. The fascinating feature is that each head has only one eye. The artist, 3,000 years ago, felt that this was a better representation of the situation than to give each of the heads two eyes. I do not know your judgment, but I would agree with him, even after so many years have passed, that it is a perfect artistic solution though it is not an anatomically correct representation. I feel the same way about some behavioral models.

As I mentioned before, a great number of hearing theories were proposed in the years before it was possible to observe directly the vibration pattern of

the waves on the cochlear partition. These theories fall into four major classes: (1) the resonance theory of Helmholtz; (2) the telephone theory, which assumes that the cochlear partition moves as a whole up and down, (3) the travelling-wave theory, and (4) the standing-wave theory of Ewald[19]. For many decades, there was rivalry among these hypotheses, with little productive result.
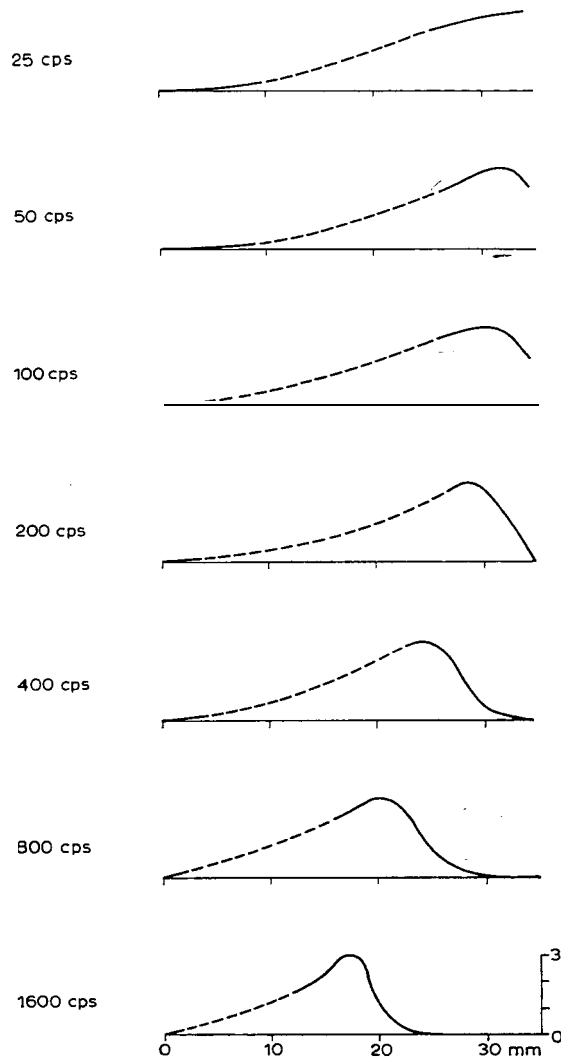
Fig. 19. Showing the shift in the place of maximum vibration amplitude along the basilar membrane for stimulation with different frequencies. (Abscissa: distance from stirrup.)
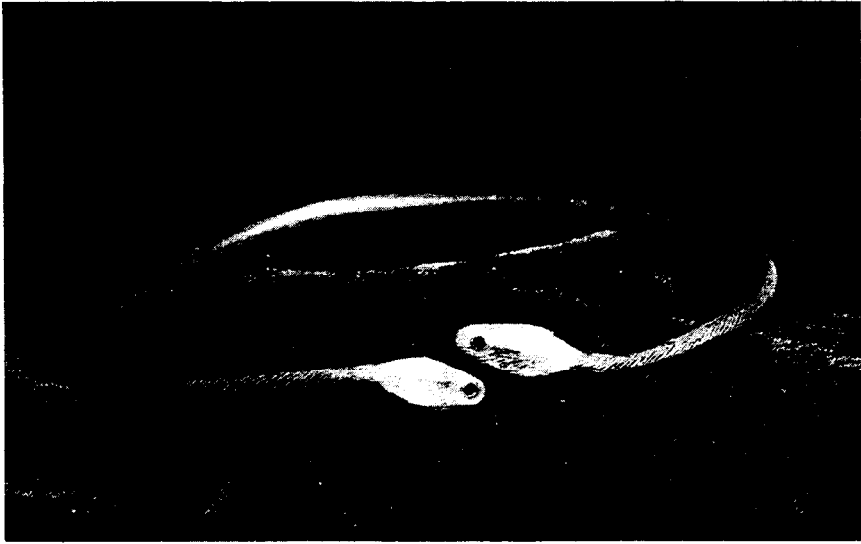
Fig. 20. Golden bracelet from the Mediterranean (with snake heads, each of which has a single eye), ca. 1,000 B.C.

Although the handbooks especially were much occupied with pointing out the differences among the four theories, I reversed the question and tried to find their common features. The result was surprising: it turned out that it was possible to go continuously from one theory to the other merely by changing the numerical value of one parameter, namely, the volume elasticity. Thus, all these apparently contradictory theories belonged to one large family. Their close relatedness can be demonstrated easily on the metal model with a rubber membrane. As is shown in Fig. 21, we can make a rubber membrane whose lateral tension is such that a point pressed into the membrane produces an elliptical bulge; this membrane behaves in exactly the way described by the resonance theory. If we make the rubber membrane quite thick, deformations on it are almost round, as in the second drawing, and the whole membrane moves up and down as a unit, at the same time, in the manner predicted by the telephone theory. If the membrane is made thinner, travelling waves appear; and if the membrane is still thinner, the waves change into standing waves. Fig. 22 shows the different vibration patterns that result from changes in the volume elasticity of the membrane. Thus it became clear that the way to decide which of the four theories was representative of the inner ear was simply to measure the volume elasticity, since
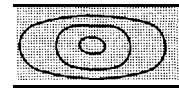
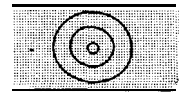Theories   Lateral   view   Top   view

Resonance
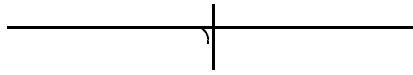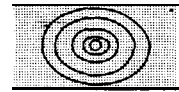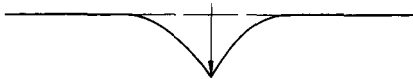
Telephone

Travelling
waves

Standing
waves

Fig. 21. Different types of deformation produced in a rubber membrane, depending
on the thickness and the lateral stress of the membrane.
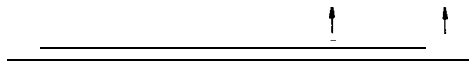
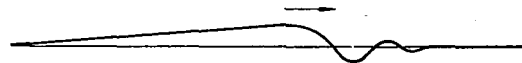Theories: Steady tone
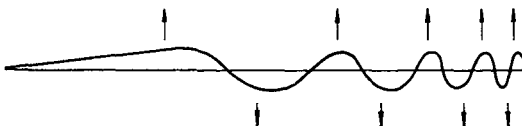
Resonance

Telephone

Travelling
waves

Standing
waves

Fig. 22. All the different hearing theories form one family of vibration patterns, dif-
fering only in the stiffness of the membrane.

it is the magnitude of this variable that determines the pattern. These measurements, which are not difficult to make, confirm the existence of travelling waves along the basilar membrane. A simple mechanical model can be used successfully to demonstrate, not only these basic question, but some very detailed problems also, as Tonndorf[20] has shown.

Unfortunately, the mathematical approach is much more difficult than the experimental one. The pioneer work in this field was done by Fletcher[21]. I am deeply grateful to Ranke[22] who quite early applied the theory of the pulse waves to the vibrations of the basilar membrane and brought out several new findings that have been important for the experiments. Recently, Zwislocki[23] and Zwicker[24], as well as scientists at the Bell Telephone Laboratories, have contributed valuable new information. It is easy to understand why the mathematical approach is so difficult. The cochlear partition-consists of a membrane whose elastic properties change continuously from very stiff to very soft. At the present time, mathematical tools have not been developed that can handle wave motions along such continuously varying media, and the propagation of the waves is sometimes strange and paradoxical. It is the same in optics, where light travels in circles if it is propagated through a medium of continuously changing optical properties, in total contradiction to our concept of the straight path of a light beam.

Synthesis

Since the essential variables and their magnitudes were now in hand, it was now possible to think about building an enlarged model of the cochlea. It is common practice to start with small models of airplanes and boats in order to test their performance, and if they are satisfactory to enlarge them, according to well-known rules, to their final size; all modern airplanes are constructed in this way. For the cochlea it was necessary to develop a special set of rules, and this was done by Diestel[25] in the widely known laboratory of Erwin Meyer in Göttingen. After some modification, the final version of the model consists of a plastic tube filled with water, and a membrane 30 cm in length; when it is stimulated with a vibration it shows travelling waves of the same type as those seen in the normal human ear. The usable frequency range is two octaves.

Since this development went along so easily, I decided to go one step further and make a model of the inner ear with a nerve supply. An attempt
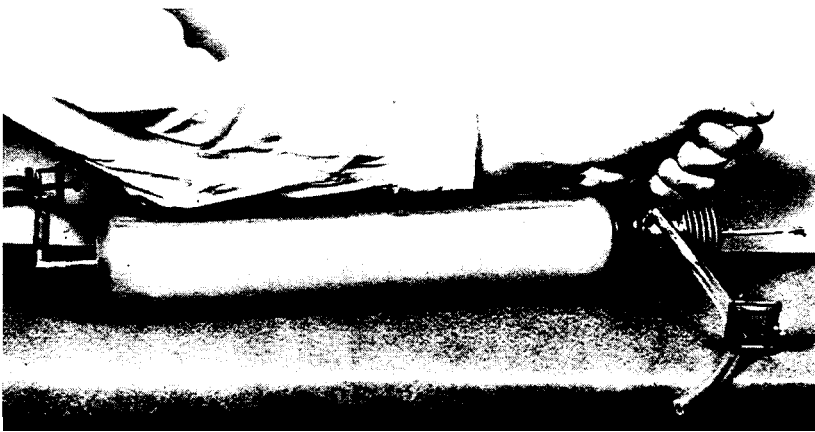
Fig. 23. Enlarged model of the human cochlea with nerve supply showing a very close analogy to the phenomena observed during hearing.

to use a frog skin as a nerve supply had at an earlier time proved to be impractical, and so I simply placed my arm against the model (Fig. 23). To my surprise, although the travelling waves ran along the whole length of the membrane with almost the same amplitude, and only a quite flat maximum at one spot, the sensations along my arm were completely different. I had the impression that only a section of the membrane, 2 to 3 cm long, was vibrating. When the frequency of the vibratory stimulus was increased, the section of sensed vibrations travelled toward the piston (at the right of the figure), which represents the stapes footplate of the ear; and when the frequency was lowered, the area of sensation moved in the opposite direction. The model had all the properties of a neuromechanical frequency-analyzing system, in support of our earlier view of the frequency analysis of the ear. My surprise was even greater when it turned out that two cycles of sinusoidal vibration are enough to produce a sharply localized sensation on the skin, just as sharp as for continuous stimulation. This was in complete agreement with the observations of Savart[26], who found that two cycles of a tone provide enough cue to determine the pitch of the tone. Thus the century-old problem of how the ear performs a frequency analysis - whether mechanically or neurally - could be solved; from these experiments it was evident that the ear contains a neuromechanical frequency analyzer, which combines a preliminary mechanical frequency analysis with a subsequent sharpening of the sensation area.

I think the happiest period of my research was when I started to repeat all

the great experiments that have been done on the ear in the past - but now on the model ear with nerve supply. All the small details could be duplicated on the skin. Nothing has been more rewarding than to concentrate on the little discrepancies that I love to investigate and see them slowly disappear. This always gives me the feeling of being on the right track, a new track.

The simple fact that on the model the whole arm vibrates (as can be seen under stroboscopic illumination), but only a very small section is recognized as vibrating, proves that nervous inhibition must play an important role. Further investigation has shown that every local stimulus applied on the skin produces strong inhibition around the place of stimulation. This seems to be true, not only for the skin, but also for the ear and the retina. Involuntarily, this had led me to begin an investigation of the analogies between the ear and the skin and the eye. Maybe the time is not too far-off when these three sense organs - ear, skin, and eye - so sharply separated in the textbooks of physiology, will have some chapters in common. This would lead toward a simplification of our descriptions of the sense organs.

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