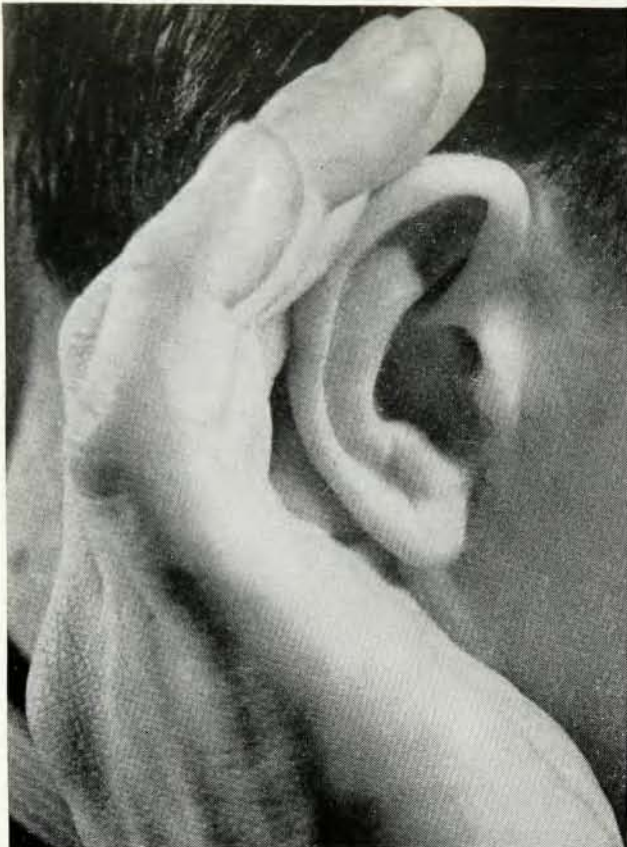




Ewing Galloway

HOW WE HEAR

Chipping away at the barrier between the senses and the physical world are those scientists whose research is in psychophysics. Here the author traces what happens to a sound wave in the ear until it reaches the auditory nerve endings.

by *Francis M. Wiener*

Ever since Einstein took his observers along on moving coordinate axes and left some behind to tell the tale of what happened within the stationary frame of reference, physics has changed in more than one respect. Physical science in general has begun to include research on these persistent observers and performers of experiments themselves. The workings of the human mechanism are currently under intense study by mathematicians and physicists, as well as by researchers in the life sciences.

Reaching across the borderline between the animate and the inanimate is the lively, many-faceted field of psycho-acoustics; and fundamental to this field is the question of how we hear. It is the physicist who can take a sound wave and follow it through the ear to a point where the physiologist steps in; finally, the psychologist takes over and measures the observer's responses.

Suppose we were to listen to a tone, not too high in frequency, and of moderate level. We would experience an auditory sensation with certain attributes such as loudness, pitch, and quality. Physically, the sound pressure activates certain parts of the auditory apparatus. Then the auditory nerve becomes affected, manifesting this by pulses of

electrochemical activity which move through complex neural linkages and cross connections towards the central nervous system. In a certain region of the brain, a complicated nervous stimulation pattern is set up—and, somehow, we hear the tone.

Too many of the processes taking place in the auditory system are still in the dark, but the mechanics of the ear can be examined in some detail to separate the mechanical action from neural phenomena. We shall trace the stimulus of a sound wave through the complex workings of the outer, middle, and inner ear to the train of pulses generated in the auditory nerve endings, and abandon it there so as not to encumber the discussion with excursions into incompletely mapped scientific territory of great complexity. Only recently has the study of the middle and inner ear been carried to a conclusive point. To be sure, many problems remain to be solved, but their number is steadily decreasing. Ours will be the reward of examining an intricate mechanical structure of fascinating detail, small in size, yet all important.

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The Ear in a Snailshell

The human ear is triply unique among the sense organs. First, it is an accomplished receptor organ in its own right; second, it is linked to the sound-producing organs in a state of mutual control which forms the basis for successful voice communication; and third, it is intimately associated with another sensory apparatus, namely the organs serving to insure equilibrium.

Evolutionarily speaking, these organs of equilibrium came first and are found in most vertebrates in essentially the form which they have in man: three semicircular canals, filled with liquid and embedded in the temporal bone. Although the mechanism is not yet completely understood, the evidence points to the fact that motion of the liquid in the vestibular apparatus, caused by moving the head, excites the endings of the vestibular nerve whose pulsed message is passed on to the higher nervous centers.

The auditory organ proper is thought to be a much later evolutionary development. Only in mammals is the cochlea fully developed, intricately coiled into a snailshell, and filled with liquid. It is divided along its length by a membranous partition on which the fibers of the cochlear nerve end. This

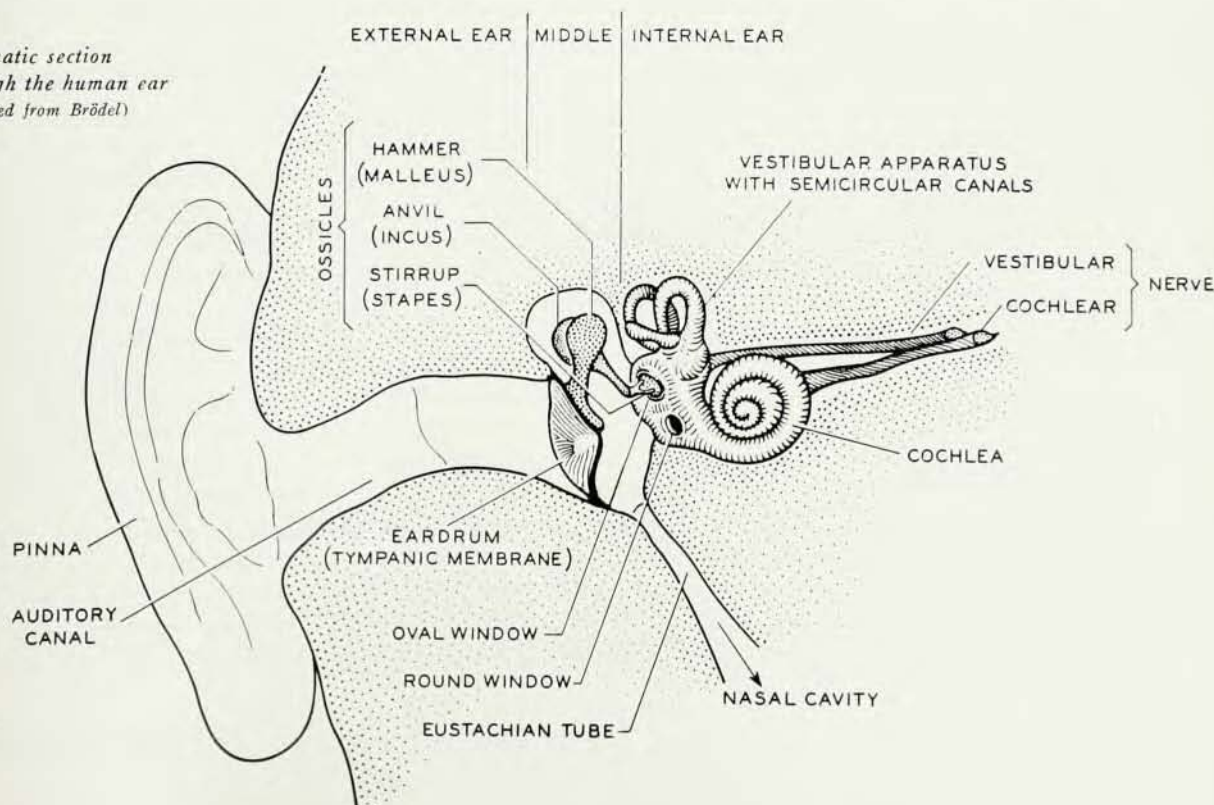
partition is set into vibrations driven through the liquid in the cochlea by the chain of the middle ear ossicles which are, in turn, linked to the eardrum which marks the end of the auditory canal. Excitation of the nerve fibers is thus accomplished.

With profit, one might state the functional basis of the ear as follows: First, it transforms aerial vibrations into vibrations of the cochlear liquid, at the same time eliminating the disturbing effect of body noises and vibrations arising from vocalization or from muscle tremors. Second, the cochlea in the ear functions as an analyzer, providing a means for sorting out sounds of different pitch—the frequency dimension in auditory perception. Different frequencies have their greatest effect on different nerve endings along the cochlear spiral. Third, it originates the message in pulse code, to be transmitted toward the brain.

The External Ear

The openings of the two auditory canals, located as they are at the sides of one's head, are equivalent to a directional two-microphone array which can be oriented in space at will. Diffraction is responsible for the differences in sound pressure level and phase at the two ears when one listens to a sustained tone from a distant source of sound. By turning the

*Schematic section
through the human ear
(Adapted from Brödel)*



head, the stimuli at the two ears are changed in accordance with the angular dependence of this head diffraction phenomenon. Although much remains to be explained concerning our remarkable ability to sense the direction as well as the distance of a source of sound it is clear that those differences in the stimuli at the two ears must play an important role. Additional clues are probably furnished by small (involuntary) movements of the head when one tries to localize binaurally a source of sound. With transient sounds the important parameter appears to be the difference in time of arrival of the stimulus at the two ears.

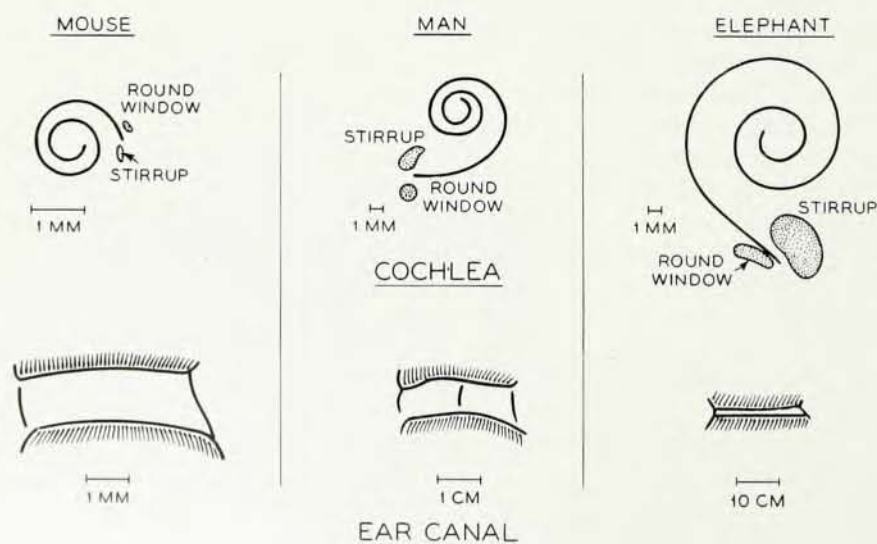
It is fortunate that, during speech, only a small fraction of the sound radiated for the listener's benefit reaches the ears of the talker through the air. Diffraction effects of a somewhat different sort account for this. For example, the average sound pressure level of vowels is reduced by about 20 decibels at the talker's ears as compared with the level at the mouth. Instead of being deafened by the sound of his own voice, the talker hears himself with the ears of his listener, more or less, to the benefit of intelligibility.

The vibrations of the vocal cords are also imparted, to some extent, directly to the middle and inner ear. It is remarkable that the auditory sensation caused by the airborne speech sounds diffracted around the head and entering the ear canal is of the same order of magnitude as that contributed through the alternate means of head vibrations (known as hearing by bone conduction).

Try as he may, man alive can never experience a state of absolute quiet, even though he may have retired to the padded cell. Breathing, the heart beat, muscle tremors, and the blood circulating through veins and arteries, they all contribute to the general noise level which determines the level of the faintest sound in the air which can just be heard. Contributions to this background noise arrive via the air path as well as the bone conduction path to the middle ear. To favor the airborne sounds over the disturbances heard through bone conduction, nature has provided an external ear structure with built-in "amplification."

The ear canal affords an increase in stimulus level available to the middle ear, as measured by the ratio of the sound pressures at the drum and at the canal entrance. In man, the auditory canal is about $2\frac{1}{2}$ centimeters long and $\frac{3}{4}$ of a centimeter in diameter and slightly crooked. The pressure ratio reaches a shallow maximum at about 4000 cycles per second, where the length of the canal equals approximately one-quarter of the wavelength of the sound wave, resulting in resonance. This resonance effect can be predicted reasonably well from simple theory assuming rigid canal walls. It is to be superimposed on the head diffraction effect, mentioned earlier, when it comes to assessing the actual pressure increase at the drum relative to the incident free wave. This increase can amount to a factor of ten in the vicinity of the resonance of the auditory canal.

The variation in dimensions of the auditory canal



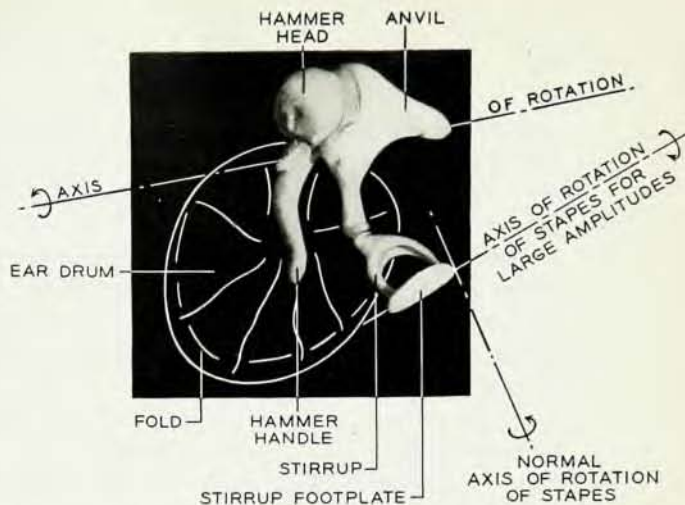
in mammals of different size is impressive compared with the variations in cochlear dimensions, as shown in the accompanying figure. For the elephantine ear canal, resonance would take place at a calculated frequency of about 500 cycles per second.

Much has been said about the connection between the size of the auricle or pinna—that part of the ear some people can wiggle—and auditory acuity. The example frequently cited is that of the bats, those winged insect hunters which are guided by their ultrasonic echo-location device. The pinnas of some species are perfectly enormous in relation to the size of the animal itself. On the other hand, other species, following the same habits, have auricles relatively only one-half or one-third as big. Be that as it may, it is certain that the pinna in man plays only a minor role. Comparatively small and immobile, its main effect appears to be one of high-frequency diffraction, an effect which is likely to aid in front-to-back discrimination of sources of sound. On the other hand, it should also be remembered that the simple device of cupping a hand around the ear is as effective today as it was before the advent of the electronic hearing aid.

The Three Little Bones

Known to science since the 16th century, the three little bones in the ear form a complicated mechanical structure. Even at very large sound pressures near the threshold of discomfort, the amplitude of vibration of the stirrup is only of the order of 10^{-5} centimeter. Indeed, at the absolute threshold of hearing for a normal observer, this amplitude is smaller still by six orders of magnitude for this frequency. At one glance these figures afford an insight into the minuteness of the vibrations on one hand and the enormity of the operating range on the other.

During even a casual examination of the photograph of hammer, anvil, and stirrup many questions come to mind: Why the complicated arrangement of the three ossicles? Why the rocking motion of the eardrum and stirrup about axes approximately tangent to their respective peripheries? Why the clumsy heads of hammer and anvil? Why are not the drum and stirrup coupled by that simple rigid bony rod found in lower vertebrates? It is impossible to answer these questions with certainty. Yet, it seems more than likely that the "explanations"



Showing how the ossicles vibrate (Adapted from Békésy)

skillfully devised by Bárány, Békésy, and others are substantially correct. These investigators maintain that the middle ear mechanism is designed so as to provide optimum transmission of the aerial vibrations in the ear canal to the cochlear fluid, and, at the same time, to reduce the effects of disturbances arriving via the bone conduction path.

How the middle ear mechanism has "solved" the problem of coupling the aerial vibrations to the cochlear liquid of the inner ear makes an interesting story many details of which are still not altogether clear. The idea of conceiving of the middle ear bones as a simple leverage device had to be abandoned very early. Indeed, the lever arm ratio of the motion of the stirrup in the oval window of the cochlea (see the illustration of the ear) to the motion of the hammer arm attached to the eardrum is not very much different from unity. On the other hand, the ratio of the pressure at the footplate of the stirrup to the sound pressure at the drum was found to be about twenty. This transformation is advantageous to the transfer of the vibrations of the air to the cochlear fluid.

The eardrum is a structure of conical shape which is endowed with a relatively soft fold extending over the lower half of its circumference. The handle of the hammer is fastened to the drum and lies approximately in a vertical plane. As a consequence of the presence of the fold and the conical shape, the eardrum is capable—at low frequencies at least—of executing a rocking motion about an approximately horizontal axis through the upper part of the hammer handle almost tangent to the rim of the drum. The bulky hammer head restores the dynamic balance and brings the center of gravity

close to the center of rotation. Because of this, head vibrations in the direction of the auditory canal are thus transmitted to the stapes only in very much reduced amount. It is easily verified that artificial "loading" of the hammer head by adding mass completely upsets this balance. The ligaments fastening the hammer and anvil to the walls of the middle ear cavity are several and terminate near the axis of rotation.

Let us examine now the stirrup (stapes). If the drum rocks about a horizontal axis, the stirrup executes a like motion about an axis, roughly tangent to the rear part of the oval window, the long axis of which is approximately horizontal, as can be seen from the figure. Adapted to the relatively high impedance level of the cochlear fluid, the annular membrane sealing the stirrup into the oval window is relatively stiff and very narrow. However, as shown by Stuhlman, its width in front is about ten times that in back—hence, the feasibility of the rocking motion as described.

We have already seen how the influence of horizontal head vibrations in the right-left direction is minimized. When the vocal cords are in action, relatively large vibrations are also transmitted to the head in a vertical direction which causes the ossicles to vibrate relative to it by virtue of their mass. The effect of this vertical motion, however, on the cochlear fluid is quite small since the stirrup is caused to rock only about its long axis in a nearly symmetrical fashion. Now to subject the ear mechanism to horizontal vibrations from front to back! Again it passes the test with flying colors, as the anvil-stirrup joint is very compliant in that direction and only sliding takes place, leaving the cochlear fluid virtually unaffected.

So much about the performance of the middle ear as an efficient transfer mechanism of minute vibrations over a wide frequency range, at the same time capable of reducing the disturbing influence of body vibrations.

But surely such a delicate mechanism needs protection from loud sounds and shocks to the fullest. It was observed by Békésy that for very large amplitudes the usual mode of oscillation of the ossicles is changed into another one in which the stirrup rocks about its long axis, thereby greatly reducing the effective volume displacement of the cochlear fluid. Second, there are the two middle ear muscles, acting on the drum and the stirrup in such a way as to

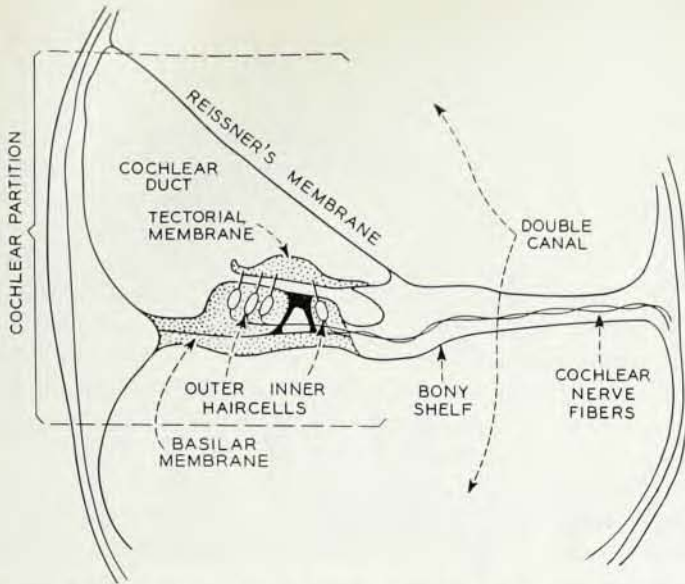
pull them both inward towards the middle ear cavity, when activated. The effect of these muscles on the transmission through the middle ear is not fully understood at present. It is known, however, that they are activated on a reflex basis in the presence of loud sounds and may thereby furnish additional protection to the auditory mechanism. The difficulties of gathering data on these muscles are readily appreciable if one reflects on the effect of the deep anesthesia, under which most animal experiments are conducted, in immobilizing those muscles.

What about the important question of nonlinear distortion? Much has been written on this subject and all is not in agreement. Both the eardrum and the ossicles are potential sources of nonlinear distortion at high sound levels. Experiments with model ossicles indeed show this to be true. Evidence, on the other hand, obtained on human ear preparations supports the conclusion that the system is essentially linear in the normal hearing range. Nature "achieved" this by the simple process of linearization. The drum impedance as seen from the auditory canal is controlled at low and medium frequencies by the stiffness of the air enclosed in the middle ear cavity. This impedance, linear in character, overrides any nonlinearity the drum might have introduced.

The Cochlea as a Frequency Analyzer

In the preceding sections, we were able to trace the auditory stimulus through the outer and middle ear mechanisms to the stirrup, rocking as it does in the oval window and imparting its oscillations to the fluid of the cochlea. The story of the three ossicles has been an interesting one; the happenings in the snailshell are perhaps even more remarkable.

The human cochlea is embedded in the thick wall of the temporal bone and, therefore, well protected against injury and compression, like the vestibular apparatus with whose canals it is directly in communication. In man, the length of the spiral is about 35 millimeters with a cross section of about 4 square millimeters at the stirrup end, which decreases to about one-fourth that size at the far end. Structures like the cochlea are an anatomist's delight; others, perhaps, find difficulty in describing it adequately (see the cross sectional sketch). A bony ledge stretches more than halfway across its central part dividing it into two canals, of roughly



Schematic cross section through the human cochlea

(Adapted from Stevens and Davis)

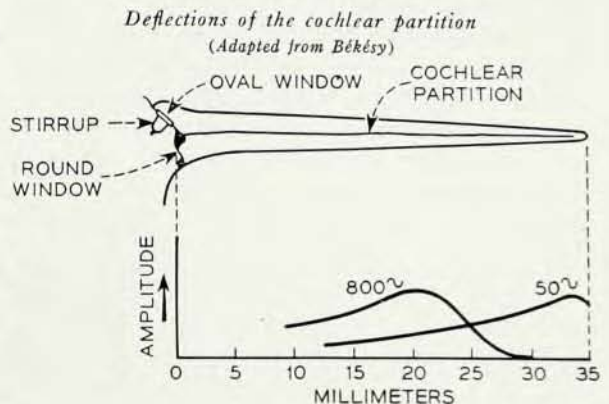
equal cross section. At the very end of the last of the two and three-quarter turns the two halves of the double canal are connected through a small opening. At its base, one canal connects with the vestibular apparatus and the stirrup is inserted there. The round window, covered with a thin membrane, terminates the basal end of the other.

There is a membranous tube, the cochlear partition, suspended between the end of the bony ledge and the opposite wall of the cochlea. It spirals faithfully along the cochlea and ends in a blind sac near the apex of the snailshell. Filled with a viscous liquid, this cochlear duct is of V-shaped cross section and is capable of crosswise movement. The leg of the V in line with the bony ledge is formed by a gelatinous plate, the so-called basilar membrane. This membrane, in turn, supports a structure containing the important haircells—many thousands of them. To these cells the nerve endings of the cochlear nerve are attached. The bundle of these fibers, twisted in rope fashion and forming the cochlear nerve, finally emerges near the axis of the cochlea at its largest turn.

By an ingenious series of experiments on cadavers, Békésy has shown that excitation of the cochlear fluid with a sinusoidal force results in deflections of the basilar membrane (and indeed of the whole of the cochlear partition) which show a local maximum at a certain point along the length of the cochlea. As the frequency is increased the point of maximum deflection shifts towards the stirrup and vice versa. Furthermore, the relative phase of the oscillations changes through an angle of over five hundred degrees, as observed at a fixed point, as the frequency is varied and the "resonance" curve traced out. Last but not least, all this was

found to take place in a linear fashion even for amplitudes far exceeding the levels of threshold of discomfort.

Although the difficulties of these experiments are enormous and although they had to be restricted to low and medium frequencies, the evidence can be interpreted to mean that waves travel along the basilar membrane whose velocity of propagation decreases considerably as the apical end is approached. The relatively broad local maxima are the envelopes of these traveling waves. In a search for the cause of this behavior it was found that the basilar membrane changes its properties significantly along the length of the cochlea. Its stiffness near the stirrup is two orders of magnitudes larger than near the apex of the cochlea. This finding was of the greatest importance since it led to a series of model experiments with water waves in a trough where the basilar membrane was imitated by a suitably shaped rubber membrane. This membrane behaved in a manner entirely analogous to the organic structure it was designed to represent. It could be shown that the double canal feature, the canal cross section, the



spiral shape and the place of excitation of the liquid could all be classed as second-order items, as far as the oscillations of the cochlear partition are concerned.

This important work paved the way for a theoretical treatment of the cochlear hydrodynamics undertaken by several investigators, most successfully perhaps by Zwislocki, Peterson, and Bogert who showed theoretically that cochlear localization of the sort to fit the experimental evidence can be accounted for by considering a membrane of the same varying elasticity as exhibited by the basilar membrane, embedded in a canal of uniform cross section filled with a fluid of proper density. Zwislocki has taken into account also dissipation, most likely contributed in the actual cochlea by the basilar membrane and the fluid in the cochlear duct. He also made calculations concerning the vortices in the fluid observed in the models near the point of maximum deflection and presumably present also in the actual cochlear mechanism.

The high degree of damping built into the cochlea which results in very good transient response characteristics can be appreciated by the fact that the rate of decay of the deflections of the cochlear partition was measured at roughly 10 decibels per cycle, essentially independent of frequency.

Electrical Activity in the Cochlea

We have now a picture of the analyzing mechanism of the cochlea, not very frequency-selective, to be sure, but capable of performing the task of supplying the frequency dimension of the stimulus over a wide range of frequencies; ample damping is present.

The pattern of mechanical excitation of the cochlear partition is transmitted to the brain by pulses of electrochemical activity originating in the multitude of nerve endings along the basilar membrane. Position along the cochlear spiral is indicated by

the particular set of fibers involved; intensity of stimulation is measured by the number of nerve pulses in unit time. Here we are in the realm of pulse transmission circuits of a nonlinear character interacting with each other and possessing great complexity. The exact operation and form of the transducers in the inner ear which are mechanically excited and respond electrically is as yet a matter of conjecture. Available evidence points towards the haircells.

Early investigators of potentials in the auditory nerve endings were confounded by electrical activity of a different sort. Wever and Bray discovered that there exists a potential difference of the cochlea as a whole with respect to other parts of the ear when acoustic stimulation is present. These cochlear potentials are radically different from the nerve impulses in that their wave form often is a faithful replica of the acoustic stimulus. Neither the function nor the exact origin of these cochlear microphonics, as they are called by some, is known at present.

We are now in a position to see briefly whether the mechanical action of the ear can account for some of the properties of hearing as revealed by psycho-acoustic measurements. Such phenomena as auditory fatigue, masking, the different decay rates of sensation and mechanical activity of the inner ear, variation of pitch with level of the stimulus, and others—they all have no compelling explanation in terms of the mechanics of the ear as we know them. Work on neural phenomena has been pursued for some time, loudness and pitch functions have been devised, and the remarkable discriminatory powers of the auditory system are a matter of record. But we still are far from an even moderately comprehensive picture. Indeed, the answer to the question posed at the outset is yet to be found in that vast field for potentially fruitful and exciting effort—the exploration of the circuits of our nervous system in all their complexity and ramifications.

