

## Syracuse Scholar (1979-1991)

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Volume 3  
Issue 1 *Syracuse Scholar Spring 1982*

Article 9

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1982

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# Analysis of Sound in the Mammalian Ear:

*A History of Discoveries*

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Dr. Zwislocki's article is a slightly modified version of an article that originally appeared in *American Scientist* 69 (1981): 184-192. We are grateful to the publishers of *American Scientist* for permission to adapt their material.

In vision, when two wavelengths of visible light are combined, the sensation of a single color arises: A mixture of blue and yellow makes a green that is indistinguishable from the green resulting from one appropriate wavelength. In hearing, a mixture of two sound waves of different lengths never produces the same impression as one wave; when the difference between the wavelengths is sufficient, two distinct tones are heard. Rather than present to our consciousness the impression of a single sound, the ear decomposes complex sounds into their components. In fact, its analytic power is so great that we are able to pick single instruments out of a whole orchestra and to detect changes in tone frequency as small as 0.3%.

How is the ear capable of this feat? From centuries of arduous research we have gained some idea, but the answer is not yet complete. Current laboratory work is still in hot pursuit of certain crucial aspects of that answer. To the surprise of many, it appears that the main auditory analysis of sounds is performed almost entirely by mechanical rather than by electrical or neural means.

Our present knowledge of auditory sound analysis has emerged gradually, over centuries, but at an accelerating pace, from several scientific disciplines including physics, anatomy, physiology, and psychology. About 530 B.C. Pythagoras observed that musical pitch is uniquely related to the length of a vibrating string, and that halving the length produces an octave interval. History waited over a thousand years for a further insight by Galileo: The length of a string determines its natural vibration frequency, and the sensation of pitch depends on the frequency rather than directly on the string's length. The two parameters of length and frequency can be separated, since the natural frequency depends on a combination of length, mass, and tension.

Shortly after Galileo's insight, the phenomenon of resonance was discovered: A sound corresponding to the natural frequency of a string was seen to cause the string to vibrate; other frequencies did not have this capacity. A string, it was further found, has several natural

frequencies which are multiples of each other; these have come to be known as harmonics. When a string is made to vibrate with several harmonics simultaneously, its pattern of vibration depends on their number and relative amplitudes.

About 150 years later, Fourier discovered that any desired pattern of vibration can be obtained by an appropriate composition of harmonics; conversely, any single-valued function can be decomposed into a set of harmonics, described mathematically as sinusoids. In the same period, Ohm, whose name became attached to a well-known law of electrical circuits, observed that the ear performs a Fourier analysis of complex sounds—in other words, that we are able to hear their sinusoidal components.

It seemed plausible to conjecture that this analysis of sounds resulted from resonance within the ear. The ear would then have to contain a set of resonators, each tuned to a different frequency. The search for the resonators was on. However, the search required a level of knowledge of the ear's anatomy that was not reached until the middle of the nineteenth century.

## The search for resonators

It has been known as early as the seventeenth century that sound entering the *auditory canal* and striking the *tympanic membrane* was led through a set of small bones in the middle ear to a labyrinth of bony canals constituting the inner ear (see Fig. 1). One of these canals,

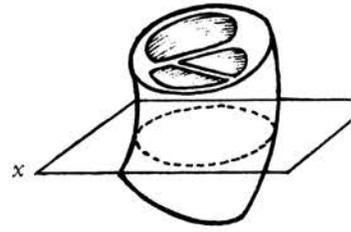


Figure 2. Schematic cross section of a single turn of the cochlea. Oval dotted lines indicate the area seen in more detail in Figure 3. Points *x* and *y* here correspond to *x* and *y* in Figure 3.

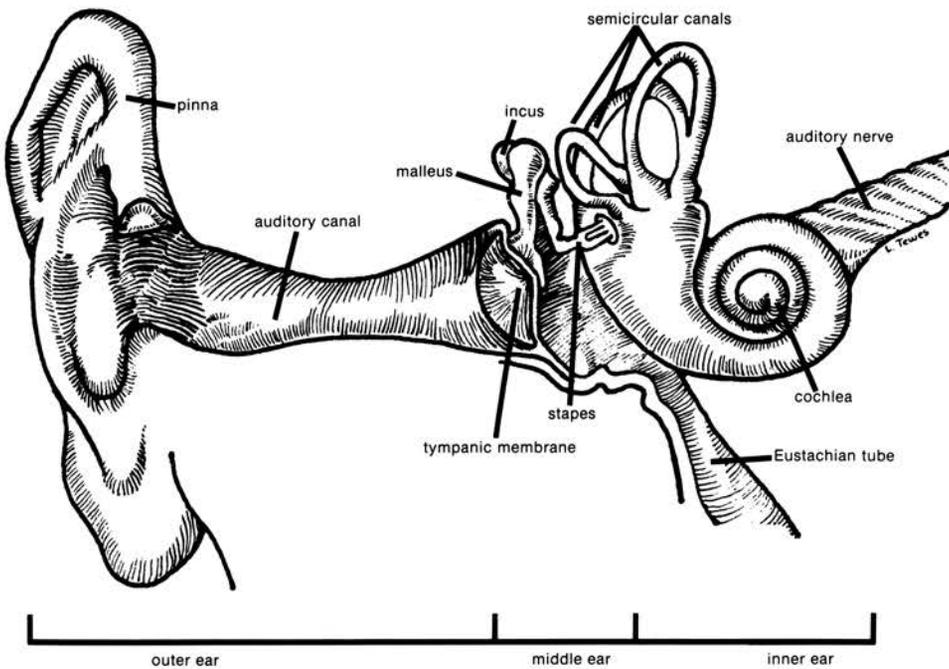
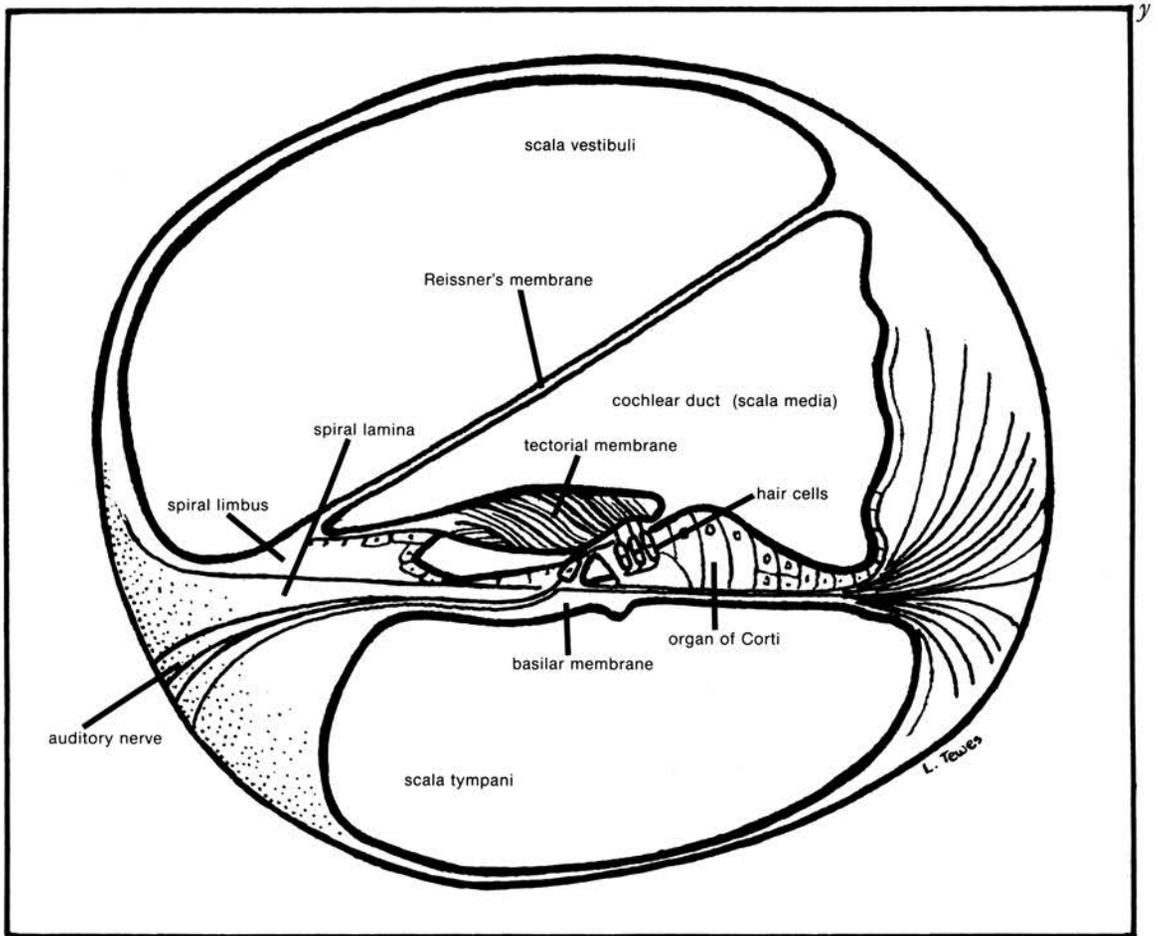


Figure 1. Sound first passes through the outer ear, striking the tympanic membrane. The resulting vibration then enters the middle ear, a chamber containing three small ossicles, or bones. These ossicles (malleus, incus, and stapes) transmit sound to the inner ear, which consists of the cochlea and the semicircular canal system. Sound analysis occurs in the cochlea.



**Figure 3.** Schematic cross section of a single turn of the cochlea shows details of its structure. Note the relative positions of the three main canals within the cochlea: the scala vestibuli, scala tympani, and cochlear duct. Compare with Figure 2.

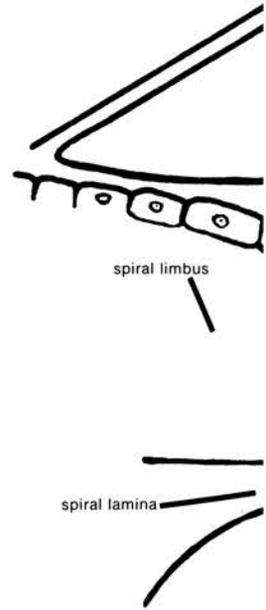
shaped like the spiral shell of a snail and called the *cochlea* (from the Greek word for snail), was regarded as the organ of hearing. The cochlear canal is divided longitudinally by a narrow partition that consists of two strips, one bony and one membranous. Only the bony part, the *spiral lamina*, was known in the seventeenth century. It is relatively wide near the cochlear base—the point where sound enters the cochlea—and becomes progressively narrower toward the cochlear apex.

Duverney, a famous French anatomist of the seventeenth century, suggested that the spiral lamina might act as a set of resonators, responding to low frequencies at the cochlear base and to high frequencies at the cochlear apex. However, improved anatomical techniques of the nineteenth century revealed that the membranous part of the cochlear partition, the *cochlear duct*, is the essential component, since it supports the sensory cells connected to the fibers of the auditory nerve. The duct is narrow at the cochlear base and wide at the apex. Accordingly, Duverney's idea was turned around; it was hypothesized that the resonators for high frequencies were located at the cochlear base, those for low frequencies at the apex.

Two schematic drawings of the cochlea based on modern anatomical knowledge show its structure in more detail (Figs. 3 and 4). The

cochlear duct divides the cochlea longitudinally into two parts—an upper portion, called the *scala vestibuli*, and a lower portion, the *scala tympani*, both filled with perilymph related to the cerebrospinal fluid. The cochlear duct, or *scala media*, itself is filled with endolymph, a fluid similar in ionic composition to intracellular fluid. Sound enters the cochlea through an opening in the bony wall of the basal part of the cochlea known as the *oval window* and leaves it through the *round window*, an opening in the basal wall of the scala tympani. A third opening, the *helicotrema*, equalizes static pressure between the scala vestibuli and the scala tympani. The fundamental configuration is clear from the simplified model of an uncoiled cochlea shown in Figure 3.

The scala media is separated from the scala vestibuli by a thin vestibular membrane known as *Reissner's membrane*, and from the scala tympani by the complex and much thicker *basilar membrane* and the spiral lamina. The *organ of Corti*, a cell mass resting on the basilar membrane, contains the stiff *arches of Corti* as well as the auditory sense cells, called *hair cells* because of the numerous cilia protruding from their apices. The hair cells are arranged in four rows running the length of the cochlea—three rows of outer hair cells on the outside of the arches of Corti, and a fourth row, containing the inner hair cells, on the inside (see Fig. 4). The two types of hair cells are quite different from each other and seem to perform different functions. All the hair cells are innervated by the afferent neurons of the auditory nerve, whose terminal fibers can be seen as a long striation through the spiral lamina. Interestingly, 90% to 95% of the fibers end on the less numerous inner hair cells; only 5% to 10% terminate on the outer hair cells, each innervating several of them.



## Helmholtz's theory

The current concept of how the cochlea analyzes sound has its roots in the resonance theory proposed by Helmholtz in the middle of the nineteenth century. His work coincided with rapid progress in cochlear anatomy, and he modified his theory as new knowledge became available. At first Helmholtz thought that the arches of Corti acted as

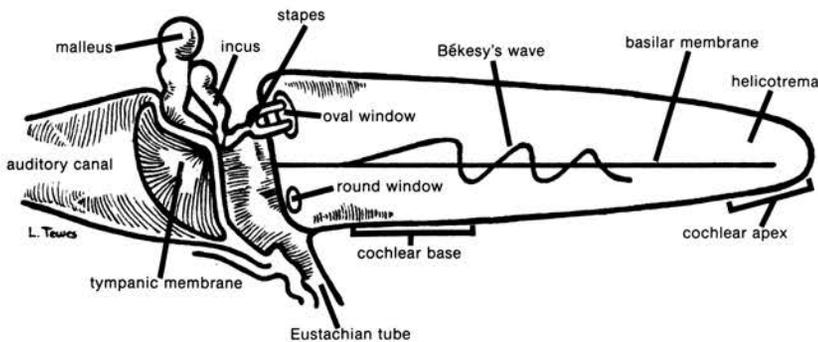
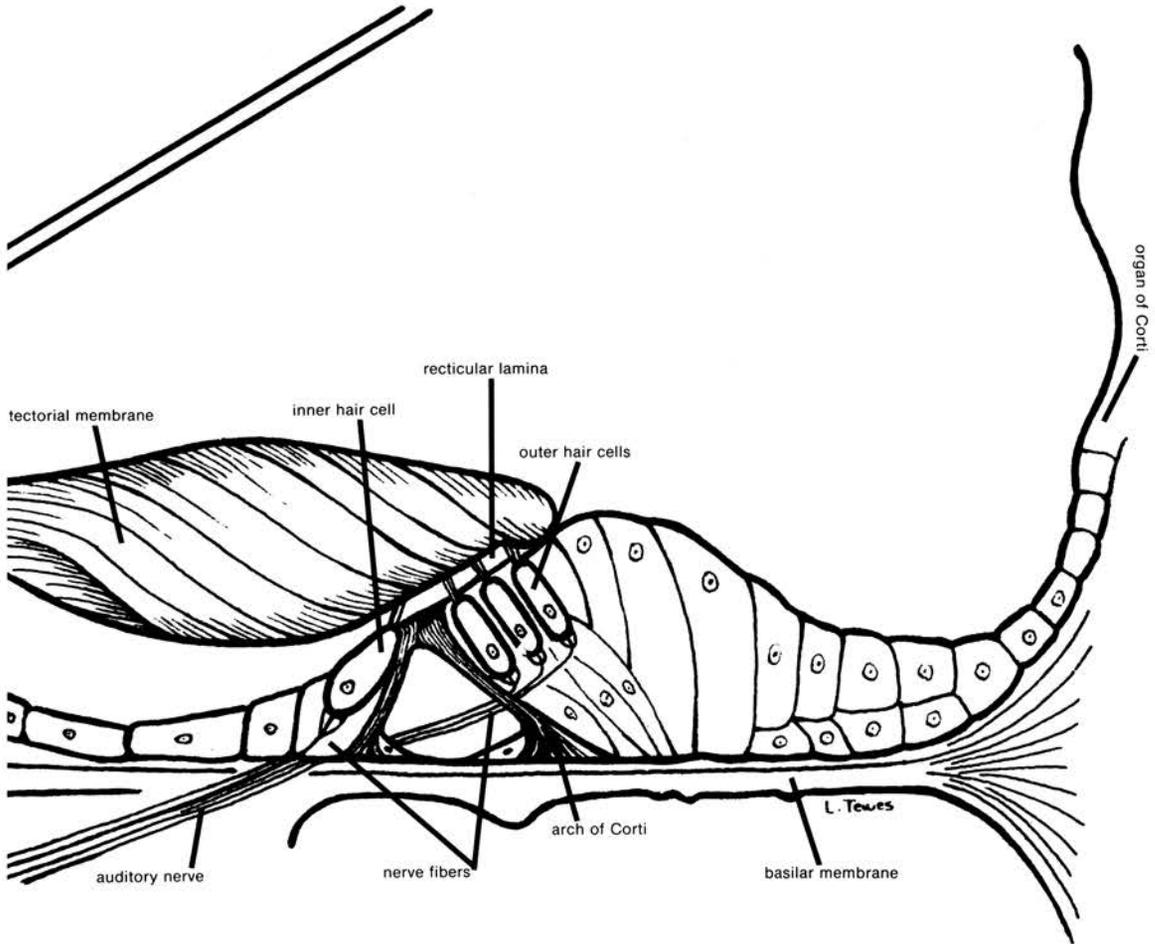


Figure 4. Longitudinal section of uncoiled cochlea (simplified version) shows the two "windows" (oval and round) by which sound enters and leaves the organ. Note the wave pattern drawn according to Békesy's observations.



**Figure 5.** Cross section through the organ of Corti and the tectorial membrane near the cochlear apex illustrates the anatomical relationship of these two bodies, nearly equal in area. Note the three rows of outer hair cells, attached to the tectorial membrane by their stereocilia, and one row of inner hair cells.

resonators. Because the size of the arches increases with the distance from the cochlear base, he concluded that the base of the cochlea responded to high frequencies, the apex to low frequencies—just the opposite of what Duverney had assumed. When it became known that the basilar membrane is narrow at the base, gradually widening toward the apex, and that it contains fibers that span its width like the strings of a musical instrument, he abandoned the arches of Corti as possible resonators in favor of the fibers.

According to Helmholtz's theory, sound is transmitted to the basilar membrane through the perilymph of the scala vestibuli and the endolymph of the cochlear duct, producing maximum vibration at the place where the basilar membrane is tuned to the particular frequency of the sound. When the sound contains several frequencies, each produces a separate vibration maximum at a different location of the basilar membrane. In this way the frequency spectrum is resolved spatially along the cochlea. Extending Johannes Müller's doctrine of specific nerve energies, Helmholtz proposed that the cochlear nerve fibers ending at the location of maximum vibration were maximally excited and determined the pitch sensation. Thus excitation of the fibers in the

cochlear base by high frequencies produced a sensation of high pitch, and excitation of the fibers near the apex by low frequencies gave rise to a sensation of low pitch. Because of this relation between pitch and cochlear location, Helmholtz's theory is now often called the *place theory*.

Helmholtz's resonance theory did not answer all the relevant questions. It stirred up a prolonged controversy leading to numerous counterproposals and experiments with mechanical models that more or less reproduced the mechanical features of the cochlea. Finally, Georg von Békésy, a Hungarian physicist, laid most of the controversy to rest in the first half of this century with the help of ingenious experiments making use of cochlear models and postmortem preparations. His results indicated that the place theory was correct but that the local vibration maximum of the basilar membrane was *not* due to ordinary resonance, as Helmholtz had imagined.

## Békésy's experiments

In a series of experiments Békésy constructed enlarged models of the human cochlea, attempting to preserve the proportions among the various cochlear dimensions as closely as possible. To simplify both the construction of the model and the observation of vibration, he did not attempt to duplicate the cochlear spiral but straightened it out, obtaining the configuration shown in Figure 4.

Békésy replaced the cochlear duct with a rubber membrane. The model was then filled with water, whose viscosity could be varied by means of glycerin and whose motion was made visible by the addition of carbon dust. Like the basilar membrane, the rubber membrane increased in width between the basal end of the model and its apex. Sound entered the model through vibration of a miniature piston suspended in a small opening that simulated the cochlear oval window. The resulting volume displacements of water were equalized through another opening placed on the opposite side of the partition, the equivalent of the round window.

Békésy observed that sound produced transversal waves on the partition, and that the location at which these waves reached an amplitude maximum depended on the frequency of the sound. At high frequencies the amplitude maximum occurred near the windows, gradually moving toward the other end of the model as the frequency was decreased—just as Helmholtz had predicted. However, in their movement toward the apex, the waves traveled right through the amplitude maximum without any apparent reflection—a pattern that seemed to Békésy to be incompatible with Helmholtz's resonance theory. The mechanism that accounted for the amplitude maximum appeared unclear to him and remained so for many years, although several theoreticians attempted to explain it.

Empirical confirmation of Békésy's model experiments did not become possible until almost twenty years later. During the intervening period he succeeded in improving dissection and microscopic techniques to the point where he was able to observe the waves in post-mortem preparations of human cochleas—work that eventually earned him the 1961 Nobel Prize. Using amplitude and phase measurements, he reconstructed the cochlear wave pattern, an example of which

appears in Figure 4. The systematic measurements had to be limited to apex of the cochlea, however, where the low frequencies have their amplitude maxima. Another twenty years passed before the fundamental features of Békesy's findings could be confirmed for the cochlear base.

Before his direct observation of the wave pattern, Békesy measured some essential physical parameters of the cochlea, especially the compliances of the membranous parts of the cochlear duct. Finding the stiffness of the basilar membrane to be the greatest, and that of Reissner's membrane negligible, he suggested that the basilar membrane effectively determined the elastic properties of the duct, which he often called (after Helmholtz) the *cochlear partition*. According to his measurements, the compliance of the basilar membrane increased from the base to the apex by between two and three orders of magnitude, apparently as a result of the membrane's increasing width and decreasing thickness.

## Fundamental mathematical analysis

Békesy's measurements of the cochlear constants, together with the known cochlear anatomy, made it possible for me to derive the cochlear waves mathematically and so to explain their nature. According to classical hydrodynamic theory, cochlear waves belong to the class of surface waves that can be observed on the free surface of water. In the case of the cochlea, the waves arise through the interaction between the stiffness of the basilar membrane and the inertia of the cochlear fluids; this interaction provides the longitudinal coupling necessary for wave propagation.

The elastic longitudinal coupling within the basilar membrane was found to be negligible because of the narrowness of the basilar membrane relative to the wavelength. It should be mentioned at this point that the name *basilar membrane* is quite misleading. The membrane behaves mechanically like a plate, as Békesy has demonstrated and as its morphological structure suggests; but the name was given before these things became known, and biologists tend to call thin partitions *membranes*.

According to my theory, the increasing compliance of the basilar membrane from the cochlear base to the apex should cause the length of the cochlear waves to decrease and their amplitude to increase with the distance from the base, in agreement with Békesy's observations. If the membrane and the cochlear fluids were inviscid and no friction intervened, the amplitude would increase all the way to the cochlear apex, where a wave reflection would take place, leading to standing waves.

However, Békesy had found a strong damping of transient oscillations of the basilar membrane, indicating substantial friction. The theory says that friction should gradually convert the mechanical energy of the waves to heat, as the waves are propagated toward the cochlear apex. The process is accelerated as the compliance increases, and the effect of friction gains in relative importance. Ultimately, the energy loss causes the wave amplitude to decrease. The location at which this begins to occur depends on sound frequency, since the effect of stiffness is inversely proportional to the frequency. As a consequence, the higher the frequency, the closer the point of vibration maximum to

the cochlear base. The theory shows that, in the presence of strong friction, the vibration maximum has to occur before the waves reach the location of basilar-membrane resonance for a given frequency. At the resonance location the wave amplitude is already so small that it cannot be measured.

The theoretical picture sketched above provided a sufficient explanation of the wave pattern seen by Békesy and also accounted for the fact that he could not detect any resonance phenomena. Most importantly, it defined the relation between sound frequency and the location of maximum vibration in the cochlea. This relationship was confirmed by a series of measurements.

Békesy's measurements, together with my theory, appeared to account satisfactorily for the fundamental mechanical process responsible both for sound analysis in the cochlea and for the pitch scale. In the 1950s, measurements of cochlear potentials with pairs of electrodes, one placed in the scala vestibuli and one in the scala tympani, seemed to fit the same picture, in that the distribution of the potentials along the cochlea approximated the distribution of mechanical amplitudes found by Békesy. It was believed that these potentials were generated by the hair cells and that they represented the state of excitation of these cells. The picture appeared satisfactorily cohesive, even though recordings from single nerve units of the auditory system, which became possible for the first time in the 1940s, indicated a much sharper frequency analysis. This was not disturbing, however, since Békesy had advocated the possibility of a neural refinement of the coarse mechanical sound analysis in the cochlea as early as the 1920s, envisioning a mechanism similar to that which produces contrast effects and the well-known Mach bands in vision.

## New insights into cochlear mechanics

By the late 1960s, however, the picture began to show deep cracks. Applying the Mössbauer technique, based on absorption of gamma rays, Johnstone and Boyle succeeded in measuring the vibration of the basilar membrane in live guinea pigs. They discovered that the amplitude maximum was considerably sharper than what Békesy had seen in post-mortem preparations. At first their discovery was received with disbelief, both because of Békesy's stature and because such a sharp maximum seemed incompatible with biological tissues, which usually exhibit high damping. Nevertheless, the findings were soon confirmed by Rhode on squirrel monkeys. Rhode also compared the amplitude maximum in live monkeys with that obtained postmortem and found striking discrepancies.

Rhode discovered other interesting features of cochlear mechanics—in particular, a small notch in the amplitude pattern above the frequency of the vibration maximum, as well as an infinite wavelength beginning in the same frequency region. The infinite wavelength indicates, according to mathematical theory, that the resonance frequency of the basilar membrane has been exceeded. Rhode also found that the amplitude maximum became flatter as the sound input to the cochlea increased. This suggests that the damping of the basilar membrane increases with amplitude.

Since Rhode could not measure the vibration of the basilar membrane at very low amplitudes compatible with the threshold of audibility and measurements of neural sensitivity, speculation arose that the basilar membrane may be as sharply tuned as the auditory neurons at very low vibration amplitudes. If this were true, the neural sharpening suggested by Békesy would be unnecessary. The speculation was strengthened by direct recording of receptor potentials of the inner hair cells pioneered by Russell and Sellick in 1977. They not only have shown that the hair cells are as sharply tuned as the neurons but also have concluded, on the basis of resistance measurements of the cells, that the sharp tuning is produced by mechanical means. This discovery eliminated several hypotheses of neural or electrophysiological sharpening of cochlear frequency analysis.

The question remains, nevertheless, whether the basilar membrane is indeed as sharply tuned as the hair cells, or whether some mechanical process taking place between the membrane and the hair cells provides the additional sharpening. A series of experiments performed on alligator lizards by scientists at the Massachusetts Institute of Technology suggests that such additional sharpening may take place. The lizard's basilar membrane does not provide any frequency analysis, yet its hair cells and the neurons that innervate them do, achieving a tuning only moderately less sharp than that found in mammals.

## The search continues

Suspicion that some mechanical process in the cochlea had been overlooked also arose from mathematical considerations. Even the most refined theories of cochlear mechanics were not able to match the wave patterns found empirically by Rhode. The solution to the dilemma may be hiding in the structure of the organ of Corti and its micromechanics (Fig. 5). The tectorial membrane—which is not a membrane at all but rather a viscoelastic plate of varying thickness consisting mainly of protein protofibrils—is suspended over the cell mass of the organ of Corti. It is attached to the outer hair cells through their hairs, or *stereocilia*. (Whether the tectorial membrane is also attached in this fashion to the inner hair cells is not yet clear.)

Since the beginning of this century it has been assumed that the hair cells are stimulated through a shearing motion that occurs between the tectorial membrane and the upper surface of the organ of Corti, a motion that must lead directly—or indirectly, through entrainment of adjacent fluid—to a bending of the stereocilia. The deformation of the hair cells themselves during this movement is probably small, since they are held rigidly in the *reticular lamina*, a stiff, netlike structure covering the top surface of the organ of Corti.

It has been shown repeatedly that the bending of stereocilia in an appropriate plane produces excitation of similar hair cells in organs related to the cochlea. Anatomically, the appropriate plane for the cochlea is the cross-sectional plane shown in Figure 5. Ter Kuile in 1900 suggested that the motions of the part of the basilar membrane supporting the organ of Corti and of the tectorial membrane could be viewed in cross section as rotations of stiff beams around their respective axes—the edge of the spiral lamina for the basilar membrane and

the edge of the *spiral limbus* for the tectorial membrane. If the two membranes rotated around parallel but different axes, a shearing motion would have to result between them, as is easy to demonstrate by a simple geometrical construction.

Whereas Ter Kuile's suggestion still appears acceptable for the basilar membrane, various studies of the tectorial membrane are more consistent with the assumption that it bends over its whole free section between the spiral limbus and the inner hair cells. If this is true, the shearing motion of the tectorial membrane relative to the organ of Corti must depend on its stiffness and on the stiffness of its attachments to the upper surface of the organ. It is possible to show by reasonably simple mathematics that the shearing motion almost disappears when the former stiffness is much smaller than the latter, when the length of the cochlear waves is sufficiently large, and when the mass of the tectorial membrane can be disregarded. Such conditions are likely to prevail at low frequencies; but at sufficiently high frequencies, the mass of the tectorial membrane, which is of the same order of magnitude as the entire cell mass of the organ of Corti, must make itself felt.

If the damping of a mechanical system consisting of a mass attached to a vibrating support by a stiffness (spring) is small, the system will resonate when excited at its natural frequency. At resonance, the amplitude of the mass can far exceed that of the support. Since the amplitude decreases sharply as the frequency changes either upward or downward from the resonance frequency, a sharp filter effect, or tuning, results. If the tectorial membrane with its elastic attachments to the organ of Corti can resonate, a sharply tuned shearing motion between it and the reticular lamina must result, leading to a sharply tuned excitation of the inner hair cells.

The idea of such a resonance is supported by a great deal of indirect evidence. For instance, the stereocilia of hair cells have been found to be quite stiff and to consist of elastic fibers of actin, the same material that constitutes muscle fibers. The length of the stereocilia of the outer hair cells increases from 1  $\mu\text{m}$  in the cochlear base to 5  $\mu\text{m}$  or 6  $\mu\text{m}$  in the apex. If the mass of the tectorial membrane remained constant, this factor alone would account for a change in resonance frequency by a factor of about 25, since the resonance frequency of an elastic beam is inversely proportional to the square of its length. But the mass of the tectorial membrane increases considerably toward the apex, further lowering the resonance frequency. These two factors together could easily account for the frequency range of over 50 to 1 in the mammalian cochlea.

Some possible effects of a resonance of the tectorial membrane have been demonstrated through construction of a simple mechanical model: A steel reed was clamped rigidly onto the vibrating tip of an electrodynamic vibrator at a small angle to the direction of vibration. The vibrating tip represented a short section of the basilar membrane; the reed, a stereocilium. A small brass weight was placed on the tip of the reed to simulate the mass of the tectorial membrane. Of course, there are a great many stereocilia in a short section of the organ of Corti; but this does not affect the essential mechanical relations we are considering, except for increasing the stiffness of the attachment of the tectorial membrane.

When the vibrator without the reed was excited by an electric current

of slowly increasing frequency, its amplitude remained constant up to a cutoff frequency and gradually decreased above that frequency. No amplitude maximum occurred, because the damping was too high. When the reed was secured in place, it moved up and down with the vibrator tip without any amplitude or phase difference until the frequency approached its transversal-mode resonance. It then began a strong transversal vibration that reached its maximum at the resonance frequency. Since the reed's amplitude decreased rapidly on both sides of the resonance frequency, a sharp tuning resulted. In addition to the sharp tuning, another, not unexpected, phenomenon was observed. Near its resonance frequency, the reed appreciably affected the vibration amplitude of the vibrator tip. Just below the resonance frequency, this amplitude increased sharply, went through a maximum, and decreased to a minimum at the resonance frequency. Above the resonance frequency it showed a small secondary peak before beginning to decrease in nearly the same manner as it had without the reed. The amplitude perturbation near the reed's resonance is due to the strong force the reed exerts on the vibrator during its maximum oscillation. Depending on the timing of this force, the vibrator amplitude is increased or decreased.

If the tectorial membrane undergoes a resonance, a similar amplitude perturbation may be expected in the vibration of the basilar membrane. Rhode seems to have observed this.

The vibrator model revealed still another effect that has been repeatedly noted in the cochlea. Near the resonance of the reed a strong nonlinearity showed up in the wave form of the vibrator. The reason for this is obvious. It must occur in every coupled system where one part vibrates at right angles to the vibration of another part. Whether the reed moves to the right or to the left in the model, it always exerts a downward force on the vibrator tip. If the reed stood perfectly vertically on the vibrator tip, the force would be symmetrical and would follow the second harmonic of the vibrator motion, producing a purely quadratic distortion. Because the reed stands at a small angle from the vertical, higher harmonics, especially the third harmonic, arise in addition to the second.

A similar situation must prevail in the ear if the tectorial membrane can vibrate nearly orthogonally to the vibration of the basilar membrane, as appears likely. In any event, wave distortions of the type seen in the vibrator model have been observed in the vibration of the basilar membrane, in the output of auditory nerve fibers, and in the subjective responses of listeners.

Although calculations and experiments with models strongly suggest that resonance of the tectorial membrane system, as outlined above, is within the realm of possibility, and although a large number of phenomena observed by physical as well as physiological and psychological methods are consistent with such a resonance, only a direct experiment can demonstrate this beyond reasonable doubt. Too many parameters still remain unknown to make any theoretical calculations, or modeling, conclusive. Neither the internal viscosity of the tectorial membrane, nor its stiffness, nor the stiffness of its attachments to the organ of Corti is precisely known. As a consequence, much remains to be explored, and we are expecting some exciting years of research on cochlear mechanics.