TECHNICAL NOTES AND RESEARCH BRIEFS

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A demonstration apparatus of the cochlea
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The passive tonotopic traveling wave seen by von Békésy in his experiments on the cochlea is demonstrated with a hydrodynamic analog. The model apparatus consists of an 85-cm-long, 1.6-cm-i.d. horizontal tube representing the scala, closed at one end and driven by a diaphragm at the other. Projecting above this are about 120 closely spaced transparent vertical channels representing the cochlear partition, whose length varies exponentially from 21 cm near the diaphragm to 84 cm near the closed end. Water poured into the apparatus fills the horizontal tube and rises up the vertical channels to a height of 20 cm. The tops of the channels are then sealed, and the air trapped above the water surface acts like a place-dependent spring. By driving the diaphragm at various frequencies, a wave on the free surface can be seen traveling towards the channel that is resonantly excited, where most of the energy will be deposited. A derivation of the wave is presented. © 1997 Acoustical Society of America. [S0001-4966(97)04702-4]

INTRODUCTION

Part of the mystery of the mammalian cochlea is how it distinguishes different frequencies from one another so well. Even though it is small, filled with fluid, and made from tissue, its frequency selectivity corresponds to a quality factor Q which can be quite high—on the order of 100. The answer partially lies with an unusual traveling wave, first seen by von Békésy,[1] that passively deposits the energy of different frequencies at different positions along the basilar membrane. Starting with Zwislocki,[2] there have been numerous mathematical models of this wave throughout the years.[3] This paper describes a lecture demonstration, shown in Fig. 1, which pedagogically displays the essential physics of the wave and many of the properties of the models.

I. APPARATUS

Several theoretical models of the cochlea include a basilar membrane that has a uniform mass but has a stiffness that decreases exponentially with distance from the oval window. A membrane of this type is represented by a vertical 6.0-mm-thick LEXAN THERMOCLEAR sheet.[4] Usually used for architectural glazing, it is a hollow polycarbonate structure in the form of two thin sheets held apart by thin parallel ribs. In effect, it comprises many parallel rectangular channels, each of area 3.2×10^{-5} m^2 and spaced apart by 6.5 mm. The sheet is cut with the channels oriented vertically into a piece 76 cm across, with a height h that varies exponentially with the horizontal distance x given by the formula $h=h_0+H10^{x/D}$, where $h_0=20$ cm, $H=0.63$ cm, and $D=38$ cm. The overall size is limited by the desire for portability. The mass of the basilar membrane is represented by water which fills the channels up to a height of h_0. The channels of the vertical sheet are sealed at the top by a metal strip that has a small hole drilled in it above each channel. After filling, these holes are covered with vinyl electric tape to form a seal. The air trapped above the water columns, varying in length by a factor of 100, represents the stiffness of the basilar membrane.

The vertical sheet is glued into a slot cut along the length of a 85-cm-long horizontal plastic tube representing the scalas of the cochlea. Water flows freely between the horizontal tube and the vertical channels of the vertical sheet. The inside diameter of the tube is 16 mm, but smaller may be better (see below). A single vertical 0.95-cm-i.d. tube, about 40 cm long and open at the top, branches from the horizontal tube past the sheet to represent the helicotrema. A cap at the end of the horizontal scala tube allows for draining the fluid and cleaning. An aluminum frame supports the plastic pieces and protects the joint between the vertical sheet and the horizontal tube.

In the ear, the fluid in the scala is oscillated by the stapes pressing on the oval window. This function is represented by a 7-cm-diam 1.6-mm-thick rubber diaphragm driven in its center by a small plate. A connecting rod attached to the plate joins with an eccentric, flywheel, gearbox, and hand crank mechanism through a spring. The spring gives a little compliance to the coupling, so that approximately a frequency-independent reciprocating force, rather than displacement, is applied to the rubber diaphragm.[5] A small electromechanical shaker has been used to drive the diaphragm as well. It allows more control over the force, plus various waveforms can be applied, but with its electronics it is not nearly as portable.

Water mixed with food coloring and about 1/2 cc of Kodak Photo-Flo 200 solution[6] per liter is poured into the apparatus through the helicotrema tube while the seals at the top of the vertical sheet are open. Too much Photo-Flo and the water foams up; too little and the water does not slide freely and the Q is poor. After air is worked out of the drive mechanism, the level is topped off and the top of the vertical sheet is sealed with tape,

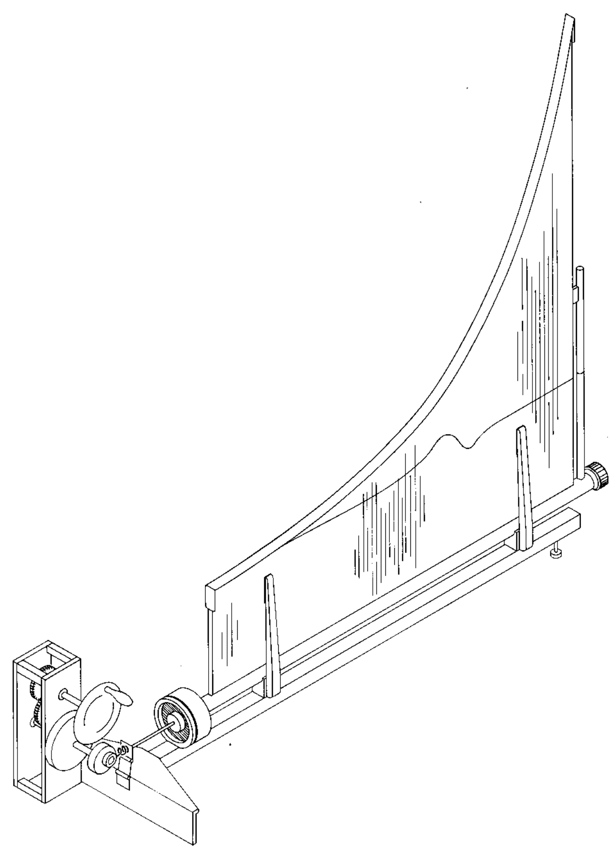

FIG. 1. The demonstration apparatus, driven by a hand crank, shows the cochlear wave on the surface of colored water contained within a hollow, ribbed plastic sheet.

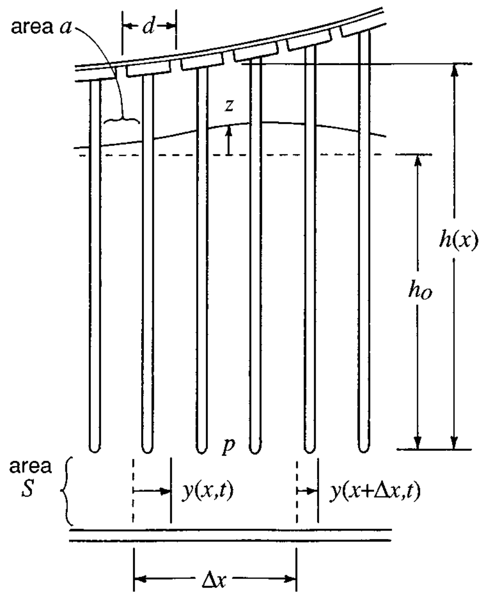

FIG. 2. Schematic detail of the vertical sheet and horizontal tube. Equilibrium positions of the liquid are shown with a dotted line; displaced positions with a solid line.

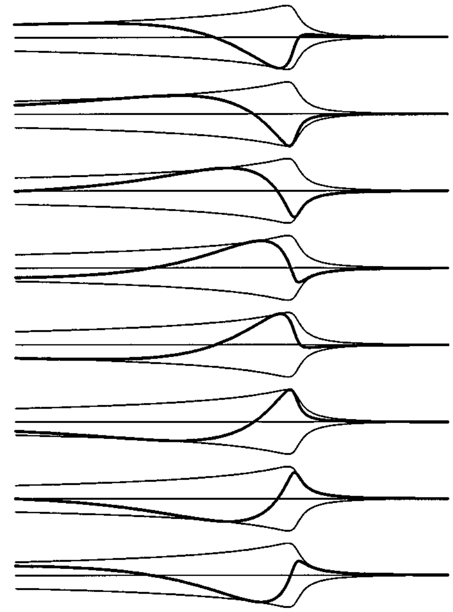

FIG. 3. Numerical results for the surface wave height z (heavy line) and its envelope (thin line) at progressive eighth cycles of the wave, from $x=0$ to 0.76 m, using, in mks units, $\omega=20\pi$, $S=1.98\times10^{-4}$, $a=3.16\times10^{-5}$, $d=6.45\times10^{-3}$, $h_0=0.203$, $H=6.35\times10^{-3}$, $D=0.381$, $R=0.0257$, $\rho=1000$, and $P_0=1.01\times10^5$.

trapping air in the vertical columns. With a turn of the crank a traveling wave appears on the water surface similar to the numerical results described below.

II. WAVE EQUATION WITH VARYING MODULUS

The derivation of the wave equation for the demonstration apparatus can proceed similarly to the derivation for sound in an ordinary fluid. Assuming harmonic time variations, let $y(x,t)=Y(x)e^{j\omega t}$ be the horizontal displacement of the fluid from equilibrium in the horizontal tube, $z(x,t)=Z(x)e^{j\omega t}$ be the vertical displacement of the fluid in the THERMOCLEAR sheet, and $p(x,t)=P(x)e^{j\omega t}$ be the excess oscillatory pressure at the base of the THERMOCLEAR sheet, as shown in Fig. 2. Neglecting dissipation in the horizontal tube,[7] Newton's force equation can be written

$$\frac{\partial p}{\partial x}+\rho\,\frac{\partial^2 y}{\partial t^2}=0, \tag{1}$$

where ρ is the density of water.

The equation of continuity would normally relate the divergence of the horizontal flow to a compression of the fluid. But here, as in the cochlea, the fluid is essentially incompressible and is allowed instead to move up the THERMOCLEAR sheet—the sheet acting as a yielding side wall to the horizontal tube. If we let Δx be a short length of horizontal tube such that $d\leqslant\Delta x\ll\lambda$, d being the distance between vertical channels in the THERMOCLEAR sheet (we are imagining that the channels in the sheet are close enough that they can be treated as a continuum) and λ being the local wavelength, then the volume of fluid entering the short section at x is $Sy(x,t)$, the volume leaving at $x+\Delta x$ is $Sy(x,t)+S\Delta x\ \partial y(x,t)/\partial x$, and volume leaving through the top is $z(x,t)\Delta x a/d$, where S is the area of the horizontal tube and a is the area of each vertical channel. The continuity equation then becomes a statement that the net volume change is zero, or

$$S\,\frac{\partial y}{\partial x}+\frac{za}{d}=0. \tag{2}$$

Third in the derivation for sound, an equation of state for the medium is used to relate the pressure fluctuations to the density fluctuations. Here, the mechanical properties of the vertical sheet performs this function, as does the basilar membrane in the cochlea. The pressure at the base of the vertical channels is given by the force per channel area needed to move the water column in the channel and compress the gas, given by

$$p=(K(x)+j\omega R-\omega^2 M)z/a, \tag{3}$$

where $K(x)$ is the position dependent spring constant of the gas spring, R is the mechanical resistance of the column, and $M=\rho a h_0$ is the water mass in the column. If isothermal compressions of the gas are assumed for simplicity, a little manipulation of the ideal gas law gives $K(x)=P_0 a/h(x)$, where P_0 is the ambient atmospheric pressure. The lengths $h(x)$ and h_0 are picked to make the local side wall resonant frequency $f=(2\pi)^{-1}(K(x)/M)^{1/2}$ reasonably low. With the lengths given above, f is calculated[8] to range from about 45 to 4.5 Hz. The damping term R can be estimated[9] by considering the effect of the dynamic viscosity η on the water oscillating in the vertical channels. Because the viscous penetration depth $\delta_\eta=(2\eta/\rho\omega)^{1/2}$ is small compared to the size of the channel—δ_η is 0.15 mm for $f=14$ Hz, the resonant frequency at the center of the apparatus—the resistive force per channel wall area is given[10] approximately by η/δ_η, so that $R=h_0\Pi(\eta\rho\omega/2)^{1/2}$, where Π is the inside perimeter of the channel cross section.

We now have three differential equations, Eqs. (1)–(3), for the three unknowns, y, z, and p. Taking the derivative of Eq. (3) with respect to x and substituting into Eq. (1), we obtain

$$\frac{1}{a}\,\frac{\partial z}{\partial x}\,(K(x)+j\omega R-\omega^2 M)+\frac{z}{a}\,\frac{\partial}{\partial x}\,(K(x)+j\omega R-\omega^2 M)+\rho\,\frac{\partial^2 y}{\partial t^2}=0. \tag{4}$$

For gradual enough variations in $K(x)$, the second term is negligible compared to the first and can be neglected. We do not want the variations to be too gradual, though, or the apparatus will be unnecessarily long. On the other hand, if the variations in K are too quick, a substantial amount of energy would be reflected back to the drive, which would not be so bad here, but in the ear it would mean that the cochlea was not absorbing all the energy that it could. So we will be guided by the "cochlear compromise" condition,[11] which is essentially the limit of validity of the WKB approximation, which states[12]

$$N\delta^{1/2}=D(4\ln_e 10)^{-1}(R/\omega h_0^2\rho S d)^{1/2}>1/4, \tag{5}$$

where N is approximately the total number of cycles of the wave, and $\delta=R/\omega M=1/Q$ is the damping function. This condition helps determine S in the design of the apparatus.

Continuing, by taking the derivative of Eq. (2) with respect to x and substituting into Eq. (4) with its second term dropped, we obtain

$$-(K(x)+j\omega R-\omega^2 M)S\ d\ a^{-2}\,\frac{\partial^2 y}{\partial x^2}+\rho\,\frac{\partial^2 y}{\partial t^2}=0, \tag{6}$$

or if rewritten in the form

$$\frac{\partial^2 \Upsilon}{\partial x^2} + \frac{\omega^2}{c^2(x)} \Upsilon = 0, \tag{7}$$

a position-dependent complex wave speed $c(x)$ and effective bulk modulus $B(x)$ can be identified, given by

$$c^2(x) = \rho^{-1} B(x) = \rho^{-1}[K(x) + j\omega R - \omega^2 M] S\ d\ a^{-2}. \tag{8}$$

Thus it can be seen that the essential difference between the passive classical cochlear wave in this model and ordinary sound is the varying wave speed, in this case due to the apparent bulk modulus given by the side wall. Other parameters such as the membrane mass or the scala area could be varied as well.

Equation (7) was solved numerically using parameters from the apparatus, and the surface height z was obtained from this solution with Eq. (2) and plotted at eight phases of the wave in Fig. 3. Near the driven end, the effective modulus B is spring-like, as in the case for ordinary sound, and a traveling wave is seen going from left to right. But as $K(x)$ gets softer the wave slows down and grows in amplitude because of the increased compliance and the compression of energy—much like ocean waves approaching a beach. At some point the mass inertia cancels the stiffness, leaving only the dissipative part, and the wave deposits its energy at this resonant position.[13] Further down, B is negative, c is imaginary, and the wave becomes evanescent, giving the cochlea an enhanced frequency selectivity because of the exponentially rapid falloff. The rapid falloff and the phase shifts from the traveling wave depend on the narrowness of the horizontal scala tube. The tube area chosen above for the apparatus is already somewhat large compared to the value $S = 4.2 \times 10^{-5}$ m^2 (a 7-mm-i.d. tube) given by the cochlear compromise condition, Eq. (5), at 10 Hz. Had the scala tube been much wider, all parts of the side wall would have been driven with the same pressure resulting in much larger displacements at the farther end. A smaller tube would give more cycles N of the traveling wave before reaching the resonant point, making for a better demonstration of the physics of the wave, although at the cost of increased dissipation in the horizontal tube.

III. CONCLUSIONS

The apparatus described here demonstrates von Békésy's classical passive wave, which still forms the foundation for understanding the mammalian cochlea. With additional machining of the horizontal tube, the apparatus could be modified to include the effects of variable basilar membrane mass or scala cross-sectional area. But the classical wave does not possess sufficient frequency selectivity to account for the tuning found in the healthy living ear. It remains a challenge to incorporate into the apparatus the active processes[14] included in more modern theories of the cochlea.

[1] G. v. Békésy, *Experiments in Hearing* (McGraw-Hill, New York, 1960; republished by the Acoustical Society of America, New York, 1989).
[2] J. Zwislocki, ''Theorie der Schneckenmechanik,'' Acta Otolaryngol. (Stockholm) Suppl. **72** (1948).
[3] For reviews, see: E. R. Lewis, E. L. Leverenz, and W. S. Bialek, *The Vertebrate Inner Ear* (CRC, Boca Raton, FL, 1985); or C. D. Geisler, ''Mathematical Models of the Mechanics of the Inner Ear,'' in *Handbook of Sensory Physiology*, Vol. V/3: Auditory System, edited by W. D. Keidel and W. D. Neff (Springer-Verlag, Berlin, 1976).
[4] General Electric Company, One Plastics Avenue, Pittsfield, MA 01201.
[5] At high enough frequencies, the accelerations of the vertical water columns are large enough that surface waves are parametrically excited at the water-air interface, foaming the water [M. Faraday, ''On the Forms and States assumed by Fluids in contact with vibrating elastic surfaces,'' Philos. Trans. R. Soc. London, 319–340 (1831)]. The spring helps with this problem.
[6] Eastman Kodak Company, Rochester, NY 14650, USA.
[7] Dissipation can be included with another term in Eq. (1), or by letting ρ here be complex.
[8] Slight deviations of f from these values occur because the gas compressions are actually somewhat in between being isothermal and adiabatic, which also adds some dissipation. Contributions due to gravity are negligible. A larger apparatus and lower frequencies would make a more impressive demonstration.
[9] This calculation neglects several other effects, such as turbulence generated by the sharp turn at the bottom and the slip-stick friction of the water–air interface which is being decreased by the Photo-Flo.
[10] L. D. Landau and E. M. Lifshitz, *Fluid Mechanics* (Pergamon, Oxford, 1959), p. 90, Eq. 24.6.
[11] G. Zweig, R. Lipes, and J. R. Pierce, ''The cochlear compromise,'' J. Acoust. Soc. Am. **59**, 975–982 (1976)
[12] To make connection to Zweig *et al.*'s Eq. (21), let their $\delta = R/2\omega M$, their $d = D/\ln_e 10$, their $L_1 = \rho/S$, and their $L = Md/a^2$.
[13] Numerical results with R about doubled give better agreement with the apparatus. The peak in the envelope is rounded a bit.
[14] T. Gold, ''Hearing II. The physical basis of the cochlea,'' Proc. Phys. Soc. London, Ser. B **135**, 492–498 (1948).