Cochlear Hydrodynamics Demystified

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Abstract: Wave propagation in the mammalian cochlea (inner ear) is modeled as a unidirectional cascade of simple filters. The transfer functions of the low-order filter stages are completely determined by the wave-number *vs.* frequency solutions to the dispersion relations that describe the cochlea, which are in turn derived from two-dimensional approximations to the fluid mechanics. Active undamping effects of the outer hair cells are easily included in the analysis and modeling, so that the results can be directly applied in the design of active adaptive cochlear models.

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Introduction

Models of the cochlea, or inner ear, can be applied to a variety of problems in sound analysis or machine hearing. The popular notion of modeling the cochlea as a bandpass filterbank needs to be supported—and modified—by an improved treatment of cochlear hydrodynamics as an adaptive linear system. We present a simple way to understand cochlear hydrodynamics and implications for the design of cascade filterbank models of the cochlea.

We base our analysis on the classic work of Sir Horace Lamb, *Hydrodynamics* [Lamb 45], and of J. W. S. Rayleigh, *The Theory of Sound* [Rayleigh 45], which explain fluid flow problems and solutions very clearly. Lamb's chapters on two-dimensional flow and surface waves are particularly relevant, as is Rayleigh's section on capillarity. Our treatment of the hydrodynamics is rather lengthy, due to our attempt to make derivations understandable without resort to references. Our title reflects our observation that other publications in this field mystify the subject by omitting most of the relevant supporting detail, and are therefore hard to use for deriving or comparing new theories and models.

We treat the fluid-mechanics of the cochlea as a two-dimensional system, with waves propagating along the x dimension or length of the ducts, and with fluid motion depending on depth y. Variations across the third dimension (i. e., across the width of the cochlear partition and perhaps further if the ducts are wider than the flexible part of the partition) are also significant, but the characteristic lengths in that dimension tend to be larger than in the other dimensions, at least in the interesting best-frequency region. For the present analysis, we assume all fluid motions and pressures are independent of the third dimension.

The WKB approximation is used to relate local properties of the system to traveling waves on the cochlear partition; this approximation is equivalent to viewing the cochlea as a cascade of filters in which signals only propagate in the forward direction. The validity of this approach is based on the observation that the properties of the medium change only slowly and that wave energy is therefore not reflected to any significant degree [de Boer 80].

The effect of the outer hair cells is included as a variable negative damping term; the variable damping mechanism is shown to be effective as a wide-range automatic gain control (AGC) associated with a moderate change in sharpness of tuning with signal level. The system is not highly tuned, but rather achieves a high-gain *pseudoresonance* by combining the modest gains of many stages; nevertheless, sharp iso-output tuning curves result from the interaction of the adaptive gains and the filters, as has been observed experimentally in both neural frequency threshold curves and basilar membrane iso-velocity and iso-displacement curves.

In the final section we address a few of the active controversial concepts in cochlear mechanics and cochlear modeling: membrane mass, sharpness, second filter, filterbank structure, nonlinearity, etc.

Mathematical Approach

Sounds entering the cochlea initiate traveling waves of fluid pressure and cochlear partition motion that propagate from the base toward the apex. The fluid-mechanical system of ducts separated by a flexible partition is like a waveguide or transmission line, in which wavelength and propagation velocity depend on the frequency of a wave and on the physical properties of the waveguide. In the cochlea, the physical properties of the partition are not constant with distance, but instead change radically from base to apex. The changing parameters lead to the desirable behavior of sorting out sounds by their frequencies or time scales; unfortunately, the parameter variability makes the wave analysis a bit more complex. This section discusses the mathematics of waves in such varying media.

Mathematical Waves

The instantaneous value W of the pressure or displacement of a wave propagating in a one-dimensional medium often is described in terms of single frequencies as the real part of a complex exponential (see Appendix A for help with notation):

$$W(x,t) = A(x)\exp(i\theta) = A(x)\exp(i\{kx - \omega t\}) \tag{1}$$

in which θ is known in the field of geometric acoustics as the *eikonal*, and $A(x)$ is either constant or changing slowly in space compared to the wave oscillations. If frequency ω and wavenumber k (spatial frequency) are positive and real and $A(x)$ is constant, W is a wave propagating to the right (toward $+x$) at a phase velocity $c = \omega/k$ with no change in amplitude.

Differential equations involving W generally are derived from the physics of the system (or from an approximation, such as a 2D cochlear model). The differential equations are then converted to algebraic equations involving parameters of θ by noting that W can be factored out of its derivatives when $A(x)$ is constant (or if A is assumed constant when it is nearly so):

$$\frac{\partial W}{\partial x} = i\frac{\partial \theta}{\partial x}A\exp(i\theta) = ikW \tag{2}$$

$$\frac{\partial W}{\partial t} = i\frac{\partial \theta}{\partial t}A\exp(i\theta) = -i\omega W \tag{3}$$

and similarly for higher-order derivatives. The resulting algebraic equations are referred to as *eikonal equations* or *dispersion relations*. Pairs of ω and k that satisfy the dispersion relations represent waves compatible with the physical system.

From the dispersion relations, we can calculate the velocity of the wave. If c is independent of ω, all frequencies travel at the same speed and the medium is said to be *nondispersive*. Real media tend to be lossy and dispersive; in the cochlea, higher frequencies are known to propagate more slowly than lower frequencies. In dispersive media, the group velocity U, or the speed at which wave envelopes and energy propagate, is the derivative $d\omega/dk$, which differs from the phase velocity ω/k.

Dispersion relations generally have symmetric solutions, such that any wave traveling in one direction has a corresponding solution of the same frequency traveling with the same speed in the opposite direction. If, for a given real value of ω, the solution for k is complex, then the equations imply a wave amplitude that is growing or diminishing exponentially with distance x. If the imaginary part k_i of $k = k_r + ik_i$ is positive, the wave diminishes toward the right ($+x$); in a dissipative system, a wave diminishes in the direction that it travels. The wave may be written as

$$W(x,t) = A\exp(i\{k_r x - \omega t\})\exp(-k_i x) \tag{4}$$

which has a real part that is recognized as a traveling sinusoid damped in space:

$$\mathrm{Re}[W(x,t)] = A\cos(k_r x - \omega t)\exp(-k_i x) \tag{5}$$

An example of a damped traveling wave in one dimension is shown in Figure 1, with $k = 1.0 + 0.1\,i$. Two time snapshots separated by $1/\omega$ are shown, so the phase shift between them is 1 radian.

In the cochlea, working out the relations between ω and k is more complex than in a one-dimensional wave system, such as a vibrating string. The fluid-flow problem must be worked out first in two or three dimensions, but ultimately it is possible to represent displacement, velocity, and pressure waves on the cochlear partition in one spatial dimension as k varies with ω and x.

Nonuniform Media and Filter Cascades

As we will see, the dispersion relations that must be satisfied by pairs of ω and k involve the physical parameters of the cochlear partition and cochlear ducts, which are changing with the x dimension (conventionally referred to as the cochlear *place* dimension, or simply *place*). The differential equations that describe the nonuniform physical system are not solvable except under very specific restrictions of form. Nevertheless, excellent approximate solutions for wave propagation in such nonuniform media are well known, and correspond to a wave propagating locally according to local wavenumber solutions.

Any small section of the medium of length Δx over which the properties do not change much behaves just as would a small section in a uniform medium: It contributes a phase shift $k_r \Delta x$ and a log gain $-k_i \Delta x$. The amplitude $A(x)$ also may need to be adjusted to conserve energy as energy-storage parameters such as spring constants (membrane stiffness) change, even in a lossless medium. These observations are equivalent to the *WKB approximation* (named after the three physicists who applied it to quantum mechanics problems), which is often invoked to solve cochlear model differential equations. The WKB approximation simply states that

$$W(x,t) \approx A(x) \exp\left(i\{\textstyle\int k\, dx - \omega t\}\right) \tag{6}$$

If k is independent of x, $\int k\, dx$ is the same as kx, in which case the solution is exact; the approximation is good so long as k doesn't change by much in a wavelength (or in a distance $1/k$, which is less than a wavelength by a factor of 2π).

Steele [Steele 87] points out that the WKB method, named after Wentzel, Kramers, and Brillouin, might better be called the CLG method after the earlier workers Carlini, Liouville, and Green, or the Ranke method after the first application of such a technique to analysis of a 2D cochlear model [Ranke 50] (Ranke does not explain his method well enough that we can see the equivalence that Steele mentions; however, his paper is quite interesting for its historical perspective on the controversy of how to analyze the cochlea). All the references we have found for the WKB method (none of which are particularly enlightening except perhaps to a quantum mechanic) show a solution whose amplitude is $A(x) = k^{-1/2}$, with little or no explanation of how they arrived at that. A more careful consideration is needed in analyzing the cochlea to understand how wave amplitudes vary with wavenumber—see the subsection below on *Energy Flow and Wave Amplitudes*.

A wave-propagation medium can be approximated (for waves traveling in one direction) by a cascade of filters (single-input, single-output, linear, continuous-time or discrete-time systems) as illustrated in Figure 2. A filter is typically characterized by its transfer function $H(\omega)$, sometimes expressed as $H(s)$ or $H(Z)$, with $s = i\omega$ for continuous-time systems or $Z = \exp(i\omega\Delta t)$ for discrete-time systems. A nonuniform wave medium such as the cochlea can be spatially discretized by looking at the outputs of N short sections of length Δx; the section outputs, or *taps*, can be indexed by n, an integer place designator that corresponds to the x location $n\Delta x$. A cascade of filters $H_1, H_2, \ldots, H_n, \ldots, H_N$ can be designed to approximate the response of the wave medium at the output taps. In passing from tap $n-1$ to tap n, a propagating (complex) wave will be modified by a factor of $H_n(\omega)$, which should match the effect of the wave medium.

The equivalent transfer function $H_n(\omega)$, a function of place (tap number n) and frequency, is thus directly related to the complex wavenumber $k(\omega, x)$, a function of place and frequency. The relation between the filter cascade and the wave medium is

$$H_n(\omega) = \exp(ik\Delta x) \qquad \text{with } k \text{ evaluated at } x = n\Delta x \tag{7}$$

$$\text{or} \quad k(\omega, x) = \frac{\log(H_n(\omega))}{i\Delta x} \quad \text{for} \quad x = n\Delta x \tag{8}$$

If $A(x)$ is not constant, the transfer function magnitude should also include a DC-gain factor $A(n\Delta x)/A(\{n-1\}\Delta x)$, which is always near 1.

Because H and k may both be complex, the phase and loss terms may be separated using $\log(H) = \log(|H|) + i\arg(H)$:

$$\log(H) = ik\Delta x = ik_r\Delta x - k_i\Delta x \tag{9}$$

$$\log(|H|) = -k_i\Delta x \tag{10}$$

$$\arg(H) = k_r \Delta x \tag{11}$$

Therefore, if we want to model the action of the cochlea by a cascade of simple filters, each filter should be designed to have a phase shift or delay that matches k_r and a gain or loss that matches k_i, all as a function of frequency

$$\text{gain} = \exp\left(-k_i \Delta x\right) \tag{12}$$

$$\text{group delay} = \frac{d\text{phase}}{d\omega} = \frac{dk_r}{d\omega}\Delta x = \frac{\Delta x}{U} \tag{13}$$

(where U is the group velocity; the equation implies that the previous definition of group velocity, $d\omega/dk$, is correctly generalized to $d\omega/dk_r$). The overall transfer function of the cascade of filters, from input to tap m, which we call H^m, is

$$\begin{aligned}\mathrm{H}^m(\omega) &= \prod_{n=0}^{m} H_n(\omega) \\ &= \exp\left(\sum_{n=0}^{m} \log\left(H_n(\omega)\right)\right) \\ &= \exp\left(i\sum_{n=0}^{m} k(\omega, n\Delta x)\Delta x\right)\end{aligned} \tag{14}$$

The integral form of the sum in the last line in Equation 14 is the form usually used as the WKB approximation: $\int k\,dx$. This formulation implies that we will be more exact by using k values averaged over sections of x, rather than values at selected points.

These formulae provide a way to translate between a distributed-parameter wave view and a lumped-parameter filter view of the cochlea. The filter-cascade model can be implemented easily, with either analog or digital circuits, and will be realistic to the extent that waves do not reflect back toward the base and that the sections are small enough that the value of k does not change much within a section.

Pseudoresonance

In the cochlea, the wavenumber increases roughly exponentially with place for a given frequency; that is, propagation velocity decreases exponentially, and hence wavelength decreases exponentially, as a wave travels from the base toward the apex. The energy in a wave "piles up" into smaller and smaller distances as the wave propagates.

From energy conservation considerations we find that wave amplitudes $A(x)$ for pressure or velocity potential (see section *Fluid Mechanical Preliminaries*) in a passive lossless cochlea are roughly constant (in the case of a 2D short-wave approximation, pressure and velocity-potential wave amplitudes are independent of k if the variation in k is caused by variation only of the stiffness parameter). Conversion to basilar-membrane displacement or velocity waves involves a spatial differentiation, so their amplitudes will increase roughly in proportion to k as the waves travel. Loss terms tend to be high order (i. e., roughly proportional to a high power of ω or k), so losses reduce the wave energy quickly near cutoff, more than canceling the slowly increasing $A(x)$. The resulting rise and fall has been termed a *pseudoresonance* [Holmes 83]; it does not involve a resonance between membrane mass and stiffness, as some models do, and it is not sharply tuned. Low-order passive-loss or active-gain terms mainly affect the height of the pseudoresonance, and have relatively less effect on its peak position and cutoff sharpness.

Scaling

A filter cascade or wave medium is said to *scale* (or be *scale-invariant*) if the response properties at any point are just like those at any other point with a change in time scale (or, equivalently, a change in frequency scale). It is particularly easy to build filter cascades that scale, because each stage is identical except that time constants change by a constant ratio from one stage to the next. In general, all numeric characteristics such as cutoff frequencies and component values in such a system will be geometric (exponential) functions of x, the place dimension, or of n, the stage index.

In a system that scales, the response for all places may be specified as a single transfer function $H(f)$, where f is a nondimensional normalized frequency:

$$f = \omega/\omega_N \tag{15}$$

and ω_N is any conveniently defined natural frequency that depends on the place (e. g., we choose $\omega_N = 1/\tau$ to characterize filters made with time constants of τ). Because of the assumed geometric variation of parameters, we can write ω_N as

$$\omega_N = \omega_0 \exp\left(\frac{-x}{d_\omega}\right) \tag{16}$$

where ω_0 is the natural frequency at $x = 0$ (at the base) and d_ω is the characteristic distance in which ω_N decreases by a factor of e.

Changing to a log-frequency scale in terms of $l_f = \log(f)$, we define the function $G(l_f) = H(f)$, which may be written as

$$G(l_f) = G(\log\left(\frac{\omega}{\omega_N}\right)) = G(\log\left(\frac{\omega}{\omega_0}\right) + \frac{x}{d_\omega}) \tag{17}$$

This equation shows that the transfer function G expressed as a function of log frequency l_f is identical to the transfer function for a particular frequency ω expressed as a function of place x, for an appropriate offset and place scaling. Thus, we can label the independent axes of transfer function plots interchangeably in either place or log frequency units, for a particular frequency or place respectively.

In the cochlea, the function G will be lowpass. Above a certain cutoff frequency, depending on the place, the magnitude of the response will quickly approach zero; equivalently, beyond a certain place, depending on frequency, the response will quickly approach zero.

The stiffness is the most important parameter of the cochlear partition that changes from base to apex, and has the effect of changing the characteristic frequency scale with place (ω_N varies as the square root of stiffness if other parameters such as duct size are constant). Over much of the x dimension of real cochleas, the stiffness varies approximately geometrically [Dallos 78]:

$$S \approx S_0 \exp\left(\frac{-2x}{d_\omega}\right) \tag{18}$$

in which the characteristic distance of stiffness variation is half the characteristic distance d_ω.

Geometric parameter variation is convenient, but not necessary to our analysis. Tension, mass, and loss parameters, if significant, should also vary as appropriate powers of $\exp(-x/d_\omega)$ in order to preserve simple scaling properties. In the real cochlea, responses scale only for frequencies above about 1 kHz (i. e., within the top four octaves of our hearing range—the lower octaves are more *compressed* onto the cochlear place dimension). The scaling assumption simply allows us the convenience of summarizing the response of an entire system by a single function G, and does not prevent us from adopting more realistic parameter variations later.

Fluid Mechanics of the Lossless Cochlea

Fluid Mechanical Preliminaries

Three approximations are needed to make the approach to the hydrodynamics problem simple. First, the cochlear fluids are assumed to have essentially zero viscosity, so that the sound energy is not dissipated in the bulk of the fluid, but is transferred into motion of the organ of Corti. Second, it is assumed that the fluid is incompressible, or equivalently that the velocity of sound in the fluid is large compared to the velocities of the waves on the cochlear partition (Lighthill discusses energy flow involving the fast and slow waves [Lighthill 81]). Third, fluid motions will be assumed to be small, so that second-order terms may be neglected; for sound levels below the threshold of pain, this is probably a good approximation.

Under the condition of no viscosity, the motion of a fluid that is initially at rest can be described in terms of a *velocity potential* ϕ. At any point (x, y) and at any time t, the velocity of a small volume element of the fluid will be given by a spatial derivative of $\phi(x, y, t)$. The x and y components of velocity are often called u and v, or are sometimes denoted by subscripts on a velocity vector $\mathbf{v}$. That is,

$$u = \mathbf{v}_x = -\frac{\partial \phi}{\partial x} \quad \text{and} \quad v = \mathbf{v}_y = -\frac{\partial \phi}{\partial y} \tag{19}$$

or, in terms of vector calculus notations,

$$\mathbf{v} = -\,\mathbf{grad}\,\phi = -\,\nabla\phi \tag{20}$$

This is Lamb's definition, which we adopt, but Rayleigh uses the opposite sign in defining velocity potential ($\mathbf{v} = \nabla\phi$).

If the fluid is incompressible, the flows into and out of a small region must balance (similar to Kirchhoff's current law). This means the velocity field must neither converge nor diverge, so that

$$\mathbf{div}\,\mathbf{v} = \nabla \cdot \mathbf{v} = \frac{\partial \mathbf{v}_x}{\partial x} + \frac{\partial \mathbf{v}_y}{\partial y} = 0 \tag{21}$$

or, in terms of velocity potential,

$$\mathbf{div}\ \mathbf{grad}\,\phi = \nabla^2\phi = \frac{\partial^2 \phi}{\partial x^2} + \frac{\partial^2 \phi}{\partial y^2} = 0 \tag{22}$$

Traveling Waves in Fluid-filled Ducts

Consider the idealized unrolled cochlea—a rectangular box with a flexible partition separating upper and lower ducts. One duct represents the scala tympani, and the other represents the combination of scala vestibuli and scala media (the thin Reissner's membrane is ignored). The separating partition represents the more substantial basilar membrane in combination with the tectorial membrane and the rest of the organ of Corti.

A duct is like a shallow pan of fluid of height h, with a hard wall at the bottom (at $y = 0$) and a springy partition at $y = h$. The velocity of the partition as it moves up and down will be the same as the y component of the fluid velocity at the surface, while the y component of the fluid velocity at the bottom will be always zero. The similar duct on the other side of the partition must satisfy all the same conditions, with a change of coordinates, as well as an anti-symmetry condition across the partitioin; for now, only one duct need be considered. The velocity potential ϕ will not be continuous across the partition, because the horizontal components of the fluid flows on opposite sides of the partition are in opposite directions, as shown in Figure 3.

We expect the fluid and partition combination to behave approximately as a linear time-invariant system, so it makes sense to characterize it in terms of its response to sinusoids or exponentials in time. The real solutions should be in terms of sinusoidal traveling waves. For now, we take the partition properties to be unchanging with x, so that we can understand the simple exact solutions for that case, which have constant wavelength and velocity. The equation that must be satisfied at all x, y, t is simply:

$$\nabla^2 \phi = 0 \tag{23}$$

under the boundary condition

$$\frac{\partial \phi}{\partial y} = 0 \quad \text{at} \quad y = 0 \tag{24}$$

and an as-yet unstated condition imposed by the partition at $y = h$. The time variation must be in terms of complex exponentials of frequency ω if we assume a sinusoidal source of that frequency.

We assume a solution of the form we want, namely a sinusoidal wave of amplitude P and frequency $f = \omega/2\pi$ Hz, traveling at a speed of $c = \omega/k$ cm s^{-1} in the $+x$ direction, with wavelength $\lambda = 2\pi/k$ cm:

$$\phi(x, y, t) = P\cos(kx - \omega t) = \frac{P}{2}[\exp(i\{kx - \omega t\}) + \exp(-i\{kx - \omega t\})] \tag{25}$$

Then we need to find out what P and k need to be (following Lamb). Hopefully, P will depend only on y, and k will not depend on y. Assuming P is independent of x, we find that

$$\nabla^2 \phi = -Pk^2 \cos(kx - \omega t) + \frac{\partial^2 P}{\partial y^2}\cos(kx - \omega t) \tag{26}$$

$$\frac{\nabla^2 \phi}{\phi} = -k^2 + \frac{1}{P}\frac{\partial^2 P}{\partial y^2} \tag{27}$$

$$\text{or} \quad \frac{\partial^2 P}{\partial y^2} = k^2 P \quad \text{to satisfy} \quad \nabla^2 \phi = 0 \tag{28}$$

The only solutions that satisfy this constraint are of the form

$$P(y) = A\exp(ky) + B\exp(-ky) \tag{29}$$

which is nice because it means the characteristic distance, or space constant, is the same in both the x and y dimensions. That is, the signal is damped by a factor $1/e$ in the y direction in the same distance $1/k$ as it takes to propagate through 1 radian of phase in the x direction.

The bottom boundary condition requires

$$\frac{\partial P}{\partial y} = kA\exp(ky) - kB\exp(-ky) = 0 \quad \text{at} \quad y = 0 \tag{30}$$

so we must choose $A = B$. Then P takes the form of a hyberbolic cosine:

$$P(y) = A\exp(ky) + A\exp(-ky) = 2A\cosh(ky) \tag{31}$$

To get a unit amplitude wave at the partition, we arbitrarily choose $2A = 1/\cosh(kh)$, so that

$$\phi = \frac{\cosh(ky)}{\cosh(kh)}\cos(kx - \omega t) \tag{32}$$

Thus, our desired solution works: The velocity potential is a simple lossless traveling wave in x, with an amplitude $P(y)$ that varies in a fairly simple way with position between the partition and the bottom wall.

Now, even though we haven't yet determined k, we are in a position to understand traveling waves in a layer of fluid. If the fluid is deep compared to a wavelength ($kh \gg 1$), then

$$\frac{\cosh(ky)}{\cosh(kh)} = \frac{\frac{1}{2}[\exp(ky) + \exp(-ky)]}{\frac{1}{2}[\exp(kh) + \exp(-kh)]} \approx \frac{\exp(ky)}{\exp(kh)} = \exp(k\{y - h\}) \tag{33}$$

so the fluid motion drops off exponentially with distance from the partition. On the other hand, if the fluid is shallow compared to a wavelength ($kh \ll 1$), then

$$\frac{\cosh(ky)}{\cosh(kh)} \approx \frac{1 + \frac{1}{2}(ky)^2}{1 + \frac{1}{2}(kh)^2} \approx 1 + \frac{(ky)^2 - (kh)^2}{2} \approx 1 \tag{34}$$

In that case, the velocity potential is relatively independent of y and the velocity is almost entirely horizontal.

Various authors invoke one or the other of the above *short-wave* or *long-wave* approximations in trying to get exact mathematical solutions to equations that only approximately represent the real wave mechanics of the cochlea. Rather than pick one of these regions, we will show how the behavior smoothly changes between them as parameters vary along the length of the cochlear partition. The intermediate condition of $kh = 1$ is illustrated in Figure 3, which shows streamlines (parallel to $\mathbf{v}$) at an instant of time. The deflection of the cochlear partition is assumed to be negligible, as mentioned above, so the region of fluid is bounded above and below by straight lines; nevertheless, we have exaggerated the deflection and displayed it along with the streamlines, to help in visualizing the traveling wave.

So far we have derived solutions for any real values of ω and k, independent of any constraints imposed by the partition. In the real system, pressures exerted on the fluid by the partition as it stretches and moves impose constraints that restrict the possible values of ω and k.

Pressure and Acceleration

Newton's law that relates force to acceleration via mass, $F = ma$, is well known to most of us. If we consider the mass of and force on a small element of fluid, we can derive the corresponding relations:

$$-\frac{\partial p}{\partial x} = \rho \frac{\partial \mathbf{v}_x}{\partial t} \quad \text{and} \quad -\frac{\partial p}{\partial y} = \rho \frac{\partial \mathbf{v}_y}{\partial t} \tag{35}$$

where p is the pressure in the fluid (a function of place and time), and ρ is the density, which is constant for an incompressible fluid. Extraneous internal forces, such as gravity acting on the fluid mass, are ignored.

Eliminating the spatial derivatives, and changing signs, these reduce to the simple relation:

$$p = \rho \frac{\partial \phi}{\partial t} \tag{36}$$

(assuming p now represents the deviation from the pressure at rest).

The pressure will assume the correct relation to ϕ throughout the bulk of the fluid for any of the solutions we have considered, but for a solution to be genuine, the pressure and displacement at the partition must match both the fluid solution and the physical properties of the partition.

The Cochlear Partition

The wave of cochlear-partition displacement (in the positive y direction) will be represented by $\delta(x, t)$ which must match the vertical fluid velocity according to:

$$\frac{\partial \delta}{\partial t} = \mathbf{v}_y = -\frac{\partial \phi}{\partial y} \tag{37}$$

The displacement is small enough that the fluid surface is still almost flat, or $h + \delta \approx h$.

The basilar membrane, which is the part of the partition usually emphasized in models, was once thought to be under tension, and to propagate waves and resonate much like a tensioned string. A membrane under tension prefers to be straight, rather than curved, and exerts a restoring pressure proportional to its curvature:

$$p_{\text{tension}} = -T\frac{\partial^2 \delta}{\partial x^2} \tag{38}$$

We'll keep the tension term for now, but the partition is actually more like stiff beams running across the width, with little tensional coupling between them. Because we don't consider the width dimension, in the 2D model the beams appear as a set of uncoupled springs, exerting a restoring pressure that only depends on the local displacement:

$$p_{\text{spring}} = S\delta \tag{39}$$

where S is the transverse stiffness of the partition (reciprocal of volume compliance or distensibility). The longitudinal stiffness is assumed to be zero, so that adjacent regions in x are not coupled to each other (the effect would be equivalent to tension, if included, but it is generally agreed that such effects are quite small, as required to get a sharp cutoff).

The mass of the partition (mostly in structures of the organ of Corti, rather than the basilar membrane itself) is a subject of considerable controversy. If it is significant, it leads to a much more resonant response than if it can be neglected, as we will see. The pressure due to acceleration of the mass is:

$$p_{\text{mass}} = M\frac{\partial^2 \delta}{\partial t^2} \tag{40}$$

The partition must also incorporate some loss mechanisms, such that sound energy will get deposited into a transducer (and into waste heat). But before we consider possible loss mechanisms, it is instructive to solve the lossless wave equation:

$$\begin{aligned} \rho\frac{\partial \phi}{\partial t} &= p_{\text{tension}} + p_{\text{spring}} + p_{\text{mass}} \\ &= -T\frac{\partial^2 \delta}{\partial x^2} + S\delta + M\frac{\partial^2 \delta}{\partial t^2} \quad \text{at} \quad y = h \end{aligned} \tag{41}$$

Differentiating both sides with respect to t, we can eliminate δ using the $\mathbf{v}_y$ relation of Equation 37, and get the partition boundary condition for ϕ:

$$\rho\frac{\partial^2 \phi}{\partial t^2} = T\frac{\partial^3 \phi}{\partial x^2 \partial y} - S\frac{\partial \phi}{\partial y} - M\frac{\partial^3 \phi}{\partial y \partial t^2} \quad \text{at} \quad y = h \tag{42}$$

The derivatives needed are easy in the lossless case with real k:

$$\begin{aligned} \phi &= 2A\cos(kx - \omega t)\cosh(ky) \\ \frac{\partial^2 \phi}{\partial t^2} &= -\omega^2 \phi \\ \frac{\partial \phi}{\partial y} &= k2A\cos(kx - \omega t)\sinh(ky) = k\tanh(ky)\phi \\ \frac{\partial^2 \phi}{\partial x^2} &= -k^2 \phi \\ \frac{\partial^3 \phi}{\partial x^2 \partial y} &= -k^3\tanh(ky)\phi \\ \frac{\partial^3 \phi}{\partial y \partial t^2} &= -\omega^2 k\tanh(ky)\phi \end{aligned} \tag{43}$$

Plugging in and eliminating ϕ and y yields the dispersion relation

$$-\omega^2 \rho = -Tk^3\tanh(kh) - Sk\tanh(kh) + M\omega^2 k\tanh(kh) \tag{44}$$

which may be simplified to

$$\omega^2 \rho = k \tanh(kh)[Tk^2 + S - M\omega^2] \tag{45}$$

If T is zero and M is positive, there is a resonant frequency $\omega_R = \sqrt{S/M}$ above which there is no real solution for k (because the bracketed quantity on the right-hand-side of Equation 45 becomes negative), even though the system is lossless. This result is discussed by Lighthill [Lighthill 81], who points out that the flattening out of the ω *vs.* k curve as ω approaches ω_R corresponds to a group velocity approaching zero, so that any small amount of damping will cause all the wave energy to be absorbed in a small boundary layer, resulting in a very sharp high-side cutoff. Lighthill contends that models that include tension or longitudinal stiffness (positive T) or that fail to include the partition mass M will not have a critical layer absorption phenomenon, and will therefore not do a good job of modeling the cochlea.

On the other hand, the importance of M depends on whether the losses are so low that the wave energy lasts to near the point of resonance, as opposed to being dissipated earlier, where the partition mass is negligible. The curve of ω *vs.* k will show a decreasing group velocity (though not to zero) even without the inclusion of mass, as we will see, and the resulting cochlear response has a well-defined best frequency and sharp cutoff even without partition resonance. Evidence on the transfer function sharpness from mechanical and neural measurements is still ambiguous at this time, due to the highly nonlinear behavior of real cochleas. We find that the sharp iso-output tuning curves that are often used to justify models with sharp transfer functions are better explained in terms of a nonlinear AGC involving rather broad filters, as will be discussed in the section on active undamping. Therefore, we will for now consider solutions with no mass and no tension.

In the long-wave region ($\tanh(kh) \approx kh$), the stiffness-only partition yields a nondispersive medium with $k = \omega\sqrt{\rho/hS}$ (constant phase velocity and group velocity $c = U = \omega/k = \sqrt{hS/\rho}$). In the short-wave region ($\tanh(kh) \approx 1$) the system is dispersive with $k = \omega^2\rho/S$; the group velocity is inversely proportional to frequency.

Because these solutions do not include any loss mechanism, the wavenumber k will continue to increase as frequency increases or stiffness decreases (there is no *cutoff*, or *critical frequency*, in the massless and lossless case). The partition displacement and velocity will also continue to increase without bound as k increases, because velocity is a spatial derivative of ϕ and the wavelength is getting arbitrarily short. These non-physical results are rectified in the next section, where loss mechanisms are considered.

Fluid Mechanics of the Lossy and Active Cochlea

Complex Variables and Lossy Waves

The extension to complex values of k requires a slightly different solution, because the solution from the previous section grows exponentially for either very large or very small x if k is complex, as shown below in Equation 48.

For the complex variable $z = x + iy$, defined to represent location in two dimensions, Lamb shows that ϕ is always the real part of an analytic function $\mathbf{w}(z)$. That is,

$$\phi + i\psi = \mathbf{w}(x + iy), \quad \text{for some differentiable} \quad \mathbf{w}(z) \tag{46}$$

That fact that $\mathbf{w}$ is analytic (has a definite differential with respect to z) implies that

$$\frac{\partial \phi}{\partial x} = \frac{\partial \psi}{\partial y} \quad \text{and} \quad \frac{\partial \phi}{\partial y} = -\frac{\partial \psi}{\partial x} \tag{47}$$

which implies that the contours of ψ align with the gradiants of ϕ and vice-versa. The function ψ, the imaginary part of $\mathbf{w}$, is therefore called the *stream function*, because its contours are streamlines of fluid flow.

Any analytic function $\mathbf{w}$ of either z or its complex conjugate $z^* = x - iy$ will have $\nabla^2\mathbf{w} = 0$, as will any linear combination of such functions. Therefore, any ϕ which is the real part of such a function will be a candidate velocity potential.

Having the solutions in the form of an analytic function is very convenient, because it is then easy to trace out contours of ψ to illustrate the fluid flow streamlines. It also makes some of the later differential equation solving easier, because complex exponentials often lead to simpler calculus and algebra than do real trigonometric functions.

Using $\mathrm{Re}[\cos(a + ib)] = \cosh(b)\cos(a)$, the solution from Equation 32 can be re-expressed as

$$\begin{aligned}\mathbf{w}(z) = \phi + i\psi &= 2A\cos(kz - \omega t) \\ &= A[\exp(i\{kz - \omega t\}) + \exp(-i\{kz - \omega t\})] \\ &= A[\exp(-k_i x - k_r y)\exp(i\{k_r x - k_i y - \omega t\}) \\ &\quad + \exp(k_i x + k_r y)\exp(-i\{k_r x - k_i y - \omega t\})]\end{aligned} \tag{48}$$

For complex values of k, the desired solutions are damped in x, but the solution as shown in the last line of Equation 48 may be seen to have its first component decaying with x (for positive k_i) while the second component grows with x. This can be fixed by going back to Equation 25, modifying one term to use the complex conjugate of k, so that it decays appropriately with x, and by making the P factor on one term be the complex conjugate of that on the other term, so that the result is still real:

$$\phi(x, y, t) = P\exp(i\{kx - \omega t\}) + P^*\exp(-i\{k^*x - \omega t\})) \tag{49}$$

Then, by repeating the analysis we find the solution must satisfy

$$P = \tfrac{A}{2}[\exp(ky) + \exp(-ky)] = A\cosh(ky) \tag{50}$$

$$P^* = \tfrac{A}{2}[\exp(k^*y) + \exp(-k^*y)] = A\cosh(k^*y) \tag{51}$$

With this solution for P, we have

$$\phi = A\cosh(ky)\exp(i\{kx - \omega t\}) + A\cosh(k^*y)\exp(-i\{k^*x - \omega t\}) \tag{52}$$

For the lossless case k and k^* are identical, so that with the same choice of A as before this formulation is the same as the solution in Equation 32.

The real function ϕ is not an analytic function of z, but is half the sum of an analytic function $\mathbf{w}$ and its complex conjugate:

$$\phi = \mathrm{Re}[\mathbf{w}] = \frac{\mathbf{w} + \mathbf{w}^*}{2} \tag{53}$$

Therefore, it is easy to find $\mathbf{w}$ by identifying the terms of ϕ that are analytic functions of z, and leaving out the terms that are functions of z^*. Expand and re-group ϕ thusly:

$$\begin{aligned}\phi &= \tfrac{A}{2}[\exp(ky)\exp(i\{kx - \omega t\}) + \exp(-ky)\exp(i\{kx - \omega t\}) \\ &\quad + \exp(k^*y)\exp(-i\{k^*x - \omega t\}) + \exp(-k^*y)\exp(-i\{k^*x - \omega t\})] \\ &= \tfrac{A}{2}[\exp(i\{kz^* - \omega t\}) + \exp(i\{kz - \omega t\}) \\ &\quad + \exp(-i\{k^*z - \omega t\}) + \exp(-i\{k^*z^* - \omega t\})]\end{aligned} \tag{54}$$

This version of ϕ leads to the analytic solution for $\mathbf{w}$, expressed here in several useful forms:

$$\begin{aligned}
\mathbf{w} &= A[\exp(i\{kz - \omega t\}) + \exp(-i\{k^* z - \omega t\})] \\
&= A[\exp(ik_r z - k_i z - i\omega t) + \exp(-ik_r z - k_i z + i\omega t)] \\
&= A\exp(-k_i x)\,[\exp(-k_r y)\exp(i\{-k_i y + k_r x - \omega t\}) \\
&\qquad + \exp(k_r y)\exp(-i\{k_i y + k_r x - \omega t\})] \\
&= A\exp(-k_i x - ik_i y)\,[\exp(-k_r y)\exp(i\{k_r x - \omega t\}) \\
&\qquad + \exp(k_r y)\exp(-i\{k_r x - \omega t\})] \\
&= 2A\exp(-k_i z)\cos(k_r z - \omega t)
\end{aligned} \tag{55}$$

Note that $\mathbf{w}^*(z) = \mathbf{w}(z^*) = A\exp(-k_i z^*)\cos(k_r z^* - \omega t)$ is an analytic function of z^*, but not of z.

The real part of this simple analytic function may also be expressed in various ways, using k_r and k_i instead of k and k^* as used above:

$$\begin{aligned}
\phi = \mathrm{Re}[\mathbf{w}] &= \frac{\mathbf{w} + \mathbf{w}^*}{2} \\
&= A[\exp(-k_i z)\cos(k_r z - \omega t) + \exp(-k_i z^*)\cos(k_r z^* - \omega t)] \\
&= \tfrac{A}{2}[\exp(-k_i x - ik_i y + ik_r x - k_r y - \omega t) \\
&\qquad + \exp(-k_i x - ik_i y - ik_r x + k_r y + \omega t) \\
&\qquad + \exp(-k_i x + ik_i y + ik_r x + k_r y - \omega t) \\
&\qquad + \exp(-k_i x + ik_i y - ik_r x - k_r y + \omega t)] \\
&= A[\exp(-k_i x + k_r y)\cos(k_i y + k_r x - \omega t) \\
&\qquad + \exp(-k_i x - k_r y)\cos(-k_i y + k_r x - \omega t)] \\
&= A\exp(-k_i x)\,[\exp(+k_r y)\cos(k_i y + k_r x - \omega t) \\
&\qquad + \exp(-k_r y)\cos(-k_i y + k_r x - \omega t)]
\end{aligned} \tag{56}$$

The last two lines of Equation 56 can be interpreted as representing a pair of waves traveling in directions not quite aligned with x—one traveling slightly upward, with large amplitude near the partition, and depositing energy into the partition (for positive loss k_i), and other one smaller, traveling away from the partition. For both waves, the direction of amplitude change is orthogonal to the direction of propagation—that is, there is no change in amplitude along the direction that the waves are propagating, though there is a reduction in amplitude along the x dimension.

The above expressions for $\mathbf{w}(z)$ or $\phi(x, y)$ are still slightly too complicated to allow us to easily solve the wave equations. It will be useful to consider two more approximate solutions based on the observation that the wave enters the short-wave regime before it damps significantly. For any region we will assume that either (a) the solution for k is real, as considered earlier ($k_i = 0$), or (b) the wavelength is short compared to the depth ($kh \gg 1$), in which case the term that decreases exponentially as $\exp(-k_r y)$ may be discarded. Then the solutions for $\mathbf{w}$ and ϕ are, (a) for the undamped region:

$$\mathbf{w} = A\cos(k_r z - \omega t) \tag{57}$$

$$\phi = 2A\cos(k_r x - \omega t)\cosh(k_r y) \tag{58}$$

and, (b) for the short-wave region:

$$\phi = A\exp(-k_i x + k_r y)\cos(k_i y + k_r x - \omega t) \quad \text{for} \quad k_r y \gg 1 \tag{59}$$

$$\begin{aligned}
\mathbf{w} &= A\exp(k_r y - k_i x)\exp(-i\{k_r x + k_i y - \omega t\}) \\
&= A\exp(-i\{k_r z - \omega t\})\exp(-k_i z) \\
&= A\exp(-i\{k^* z - \omega t\})
\end{aligned} \tag{60}$$

If neither of these region approximations holds, i. e., if the wavelength is long enough while the system is lossy enough, then our presumed solution does not seem to actually lead to a consistent solution—factoring out **w** from its derivatives doesn't work, so we don't get an algebraic dispersion relation to solve. We're still not sure how to resolve this problem—it may be an indication that the WKB approximation does not hold in this case, possibly because the combination of loss and long wavelength leads to significant reflection even in a uniform medium.

Loss Mechanisms

The mechanisms that take energy from the traveling wave are not exactly known, but it seems reasonable to consider two possible forms for such loss. First, a pressure proportional to partition velocity can be included, perhaps representing a viscous loss in the small spaces of the organ of Corti as fluid streams through and drags over the hair cells. The corresponding pressure term, with loss coefficient β, is

$$p_{\text{velocity}} = \beta \mathbf{v}_y = \beta \frac{\partial \delta}{\partial t} \tag{61}$$

Second, the rate of local longitudinal bending of the partition may contribute a pressure representing energy lost to friction in the partition itself. The pressure term, with coefficient γ, is

$$p_{\text{bending}} = -\gamma \frac{\partial^3 \delta}{\partial x^2 \partial t} \tag{62}$$

Now we can write the complete lossy wave equation:

$$\begin{aligned} \rho \frac{\partial \phi}{\partial t} &= p_{\text{tension}} + p_{\text{spring}} + p_{\text{mass}} + p_{\text{velocity}} + p_{\text{bending}} \\ &= -T \frac{\partial^2 \delta}{\partial x^2} + S\delta + M \frac{\partial^2 \delta}{\partial t^2} + \beta \frac{\partial \delta}{\partial t} - \gamma \frac{\partial^3 \delta}{\partial x^2 \partial t} \quad \text{at} \quad y = h \end{aligned} \tag{63}$$

As before, eliminating δ using Equation 37 we have the equation in terms of ϕ only:

$$\rho \frac{\partial^2 \phi}{\partial t^2} = T \frac{\partial^3 \phi}{\partial x^2 \partial y} - S \frac{\partial \phi}{\partial y} - M \frac{\partial^3 \phi}{\partial y \partial t^2} - \beta \frac{\partial^2 \phi}{\partial y \partial t} + \gamma \frac{\partial^4 \phi}{\partial x^2 \partial y \partial t} \quad \text{at} \quad y = h \tag{64}$$

Because the loss only becomes significant in the short-wave region (at least for the values of parameters that we think are reasonable), the following short-wave solutions with complex k will be used:

$$
\begin{aligned}
\phi &= A\cos(k_r x + k_i y - \omega t)\exp(k_r y - k_i x) \quad \text{for} \quad k_r y \gg 1 \\
\text{instead of } \phi \text{ use} \quad w &= \phi + i\psi \\
&= A\exp(-i\{k_r x + k_i y - \omega t\})\exp(k_r y - k_i x) \\
&= A\exp(i\omega t)\exp(-ik^* x)\exp(k^* y) \\
\frac{\partial \mathbf{w}}{\partial t} &= i\omega \mathbf{w} \\
\frac{\partial^2 \mathbf{w}}{\partial t^2} &= -\omega^2 \mathbf{w} \\
\frac{\partial \mathbf{w}}{\partial y} &= k^* \mathbf{w} \\
\frac{\partial^3 \phi}{\partial y \partial t^2} &= -\omega^2 k^* \mathbf{w} \\
\frac{\partial^2 \mathbf{w}}{\partial y \partial t} &= i\omega k^* \mathbf{w} \\
\frac{\partial^2 \mathbf{w}}{\partial x^2} &= -k^{*2} \mathbf{w} \\
\frac{\partial^3 \mathbf{w}}{\partial x^2 \partial y} &= -k^{*3} \mathbf{w} \\
\frac{\partial^4 \mathbf{w}}{\partial x^2 \partial y \partial t} &= -i\omega k^{*3} \mathbf{w}
\end{aligned} \tag{65}
$$

The dispersion relation for the short-wave region with complex k is then

$$
-\omega^2 \rho = k^*[-Tk^{*2} - S + M\omega^2 - i\beta\omega - i\gamma\omega k^{*2}] \tag{66}
$$

which is equivalent, by sign change and conjugation, to

$$
\omega^2 \rho = k[Tk^2 + S - M\omega^2 - i\beta\omega - i\gamma\omega k^2] \tag{67}
$$

Approximate Wavenumber Solutions

The dispersion relation Equation 67 can be separated into real and imaginary parts such that the two unknowns k_r and k_i can both be solved for approximately in the short-wave region:

$$
\begin{aligned}
\omega^2 \rho = k_r[T\{k_r^2 - k_i^2\} + S - M\omega^2 + 2\gamma\omega k_r k_i] \\
+ k_i[\beta\omega + \gamma\omega\{k_r^2 - k_i^2\} - 2Tk_r k_i] \\
+ i\{k_r[\beta\omega + \gamma\omega\{k_r^2 - k_i^2\} - 2Tk_r k_i] \\
- k_i[T\{k_r^2 - k_i^2\} + S - M\omega^2 + 2\gamma\omega k_r k_i]\}
\end{aligned} \tag{68}
$$

As before, we may choose T and M to be zero for a simpler model, which leads to the simpler separated dispersion relation

$$
\begin{aligned}
\omega^2 \rho = k_r[S + 2\gamma\omega k_r k_i] + k_i\omega[\beta + \gamma\{k_r^2 - k_i^2\}] \\
+ i\{k_r\omega[\beta + \gamma\{k_r^2 - k_i^2\}] - k_i[S + 2\gamma\omega k_r k_i]\}
\end{aligned} \tag{69}
$$

At this point, it is appropriate to notice that the two dispersion relations for the two regions (Equation 45 and Equation 67) may be combined into one equation that is accurate in both regions and probably also between regions:

$$
\omega^2 \rho = k\tanh(kh)[Tk^2 + S - M\omega^2 - i\beta\omega - i\gamma\omega k^2] \tag{70}
$$

Some authors simply start from the lossless analysis and add imaginary terms into the dispersion relation to model loss, without concern for the physical mechanisms or for the corresponding wave solutions; they arrive at an equation similar to this one but without the separate orders of loss. We have agonized over the derivations more, so that the mechanisms of loss can be understood and modified into mechanisms of gain and loss appropriate to model the active effects of the outer hair cells.

It is instructive to look at approximations that make clear the dependence of k on the parameters. In practice, the solutions for k are achieved by Newton's method, starting from simple approximations, and using the combined dispersion relation Equation 70. Note that Newton's method works for a complex function of a complex variable only if the function is analytic, since the derivative is needed to compute an improved approximation.

In the lossless region, ignoring tension and mass, the long-wave approximation is a good start:

$$k \approx \omega\sqrt{\rho/hS} \tag{71}$$

In the short-wave region, starting with real k and ignoring tension, a good approximation from Equation 69 is:

$$k_r \approx \omega^2\rho/S \tag{72}$$

Given an approximate solution for k_r, a first approximation for k_i may be obtained by solving the imaginary part of the dispersion relation in Equation 69, assuming $k_i \ll k_r$ and ignoring terms with k_i^2 and k_i^3. Assuming only bending loss ($\beta = 0$), we find $k_i \approx k_r^3\gamma\omega/S$. Substituting in the short-wave approximation for k_r, we find that the bending loss comes in as a rather high power of frequency and stiffness: $k_i \approx \gamma\omega^7\rho^3/S^4$ (which is proportional to $S^{-7/2}$ if the response scales, because γ^2 is proportional to S).

Considering only velocity loss instead (still with no tension), the corresponding approximation is $k_i \approx k_r\beta\omega/S \approx \beta\omega^3\rho/S^2$. The loss still increases with frequency and decreases with stiffness, but much more slowly for this simpler loss mechanism.

The *relative* loss, or damping, may be defined as

$$\xi = \arg(k) \approx \frac{k_i}{k_r} \tag{73}$$

When both loss mechanisms are included, the approximate solutions above simply add, so the complete loss and damping approximations become

$$k_i \approx \frac{\gamma\omega^7\rho^3}{S^4} + \frac{\beta\omega^3\rho}{S^2} \tag{74}$$

and

$$\xi \approx \frac{k_i}{k_r} \approx \frac{\gamma\omega^5\rho^2}{S^3} + \frac{\beta\omega}{S} \tag{75}$$

The approximations for wavenumber k_r and damping ξ may be interpreted either as frequency dependent at a constant place (constant S, β, and γ), or as place dependent at a constant frequency (constant ω). Thus a wave of frequency ω will propagate until the damping gets large; the damping grows ultimately as $\exp(5x/d_\omega)$ (assuming the geometric dependence of S discussed earlier, and with geometric γ proportional to ω_N or $\exp(-x/d_\omega)$). Therefore, the damping is near zero for low x and then comes up very fast at a *critical place* x_C. Similarly, at a given place, low frequencies are propagated with little loss, but as ω grows, the damping grows ultimately as ω^5 and kills waves above a *critical frequency* ω_C.

The cochlea is known to have very sharp cutoff behavior, so it is reasonable to suppose that the γ loss term is most significant in determining the critical points. The critical points may be estimated to be near $\xi = 1$, ignoring β, as:

$$\omega_C \approx \left[S^3/\gamma\rho^2\right]^{1/5} \tag{76}$$

If the system scales, critical frequencies and critical places are related geometrically:

$$\omega_C \approx \left[S_0^3/\gamma_0\rho^2\right]^{1/5} \exp\left(\frac{-x}{d_\omega}\right) \tag{77}$$

$$x_C \approx d_\omega[-\log(\omega) + .2\log(S_0^3/\gamma_0\rho^2)] \tag{78}$$

If the damping and stiffness coefficients do not scale geometrically, there is still a critical place as a function of frequency, but it is not a simple function of $\log(\omega)$.

For the two-region (lossless and short-wave) approach to be accurate, it is important that the damping be small (say less than 0.1, corresponding to less than a factor of two amplitude change in a wavelength, as in Figure 1) near the transition from lossless to short-wave regions (say at $kh \approx 1$). That is,

$$\xi < 0.1 \quad \text{at} \quad k_r h = 1$$

The point $k_r h = 1$ may be estimated using the short-wave approximation as $k_r = 1/h \approx \omega^2\rho/S$, which can be used to define a *characteristic frequency* or *characteristic place* related to h and independent of loss coefficients:

$$\begin{aligned} \omega_h &= \sqrt{S/\rho h} = \sqrt{S_0/\rho h}\, \exp\left(\frac{-x}{d_\omega}\right) \\ x_h &= d_\omega[-\log(\omega) + .5\log(S_0/\rho h)] \end{aligned} \tag{79}$$

Then a nearly equivalent requirement is

$$\xi < 0.1 \quad \text{at} \quad \omega = \omega_h \quad \text{or} \quad x = x_h \tag{80}$$

The *best frequency* for a place (where the partition velocity or displacement is maximized) depends on both β and γ, and will be significantly higher than the characteristic frequency and somewhat lower than the critical frequency.

The definition of ω_h can be plugged in for ω in the approximation for damping ξ in Equation 75, to show that β and γ must be small enough to satisfy

$$\beta + \gamma/h^2 < 0.1\sqrt{S\rho h} \tag{81}$$

If the losses are low and the partition mass is significant, the cutoff will be associated with the resonant frequency, rather than with the place where damping gets large. If we take M constant to be consistent with the scaling of the other parameters, the resonant frequency and place are given by:

$$\begin{aligned} \omega_R &= \sqrt{S/M} = \sqrt{S_0/M}\, \exp\left(\frac{-x}{d_\omega}\right) \\ x_R &= d_\omega[-\log(\omega) + .5\log(S_0/M)] \end{aligned} \tag{82}$$

Whether the mass is significant then depends on whether the critical frequency or the resonant frequency is lower. The mass may be neglected if

$$\begin{aligned} \omega_C &\ll \omega_R \\ \left[S^3/\gamma\rho^2\right]^{1/5} &\ll [S/M]^{1/2} \end{aligned} \tag{83}$$

or equivalently, in terms of a critical mass M_C, if

$$M \ll M_C = S\left[\gamma\rho^2/S^3\right]^{2/5} = S^{-1/5}\gamma^{2/5}\rho^{4/5} \tag{84}$$

In the real cochlea, which does not quite scale geometrically, it is likely that the mass is significant only for the basal (high-frequency) regions, where the extra stiffness needed comes from an increasing thickness and hence mass of the membrane. The changing significance of mass may explain why the cochlear tuning is observed to be sharper at high frequencies than at low frequencies.

In the far cutoff region, where $\omega \gg \omega_C$ or $x \gg x_C$, we can see from Equation 67 that the high-order loss dominates to give

$$k^3 \approx \frac{j\omega\rho}{\gamma} \tag{85}$$

Therefore the model wavenumber approaches an angle of $\pi/6$ in the complex plane, with a magnitude growing only as $\omega^{1/3}$. The actual behavior in this region will of course be strongly dependent on what high-order loss mechanisms are operating in the cochlea.

Numerical Wavenumber Solutions

Figure 4 shows numerical solutions of k *vs.* x for two conditions: (1) high-order γ loss only, an ideal passive condition; (2) γ loss and β gain, an active condition. The real and imaginary parts of k are separately plotted on a log scale. For the region where k_i is negative due to active gain, the log of its absolute value is plotted; a cusp in the k_i curve indicates the transition between gain and loss for the active condition. The place scale has arbitrary units with 1500 units spanning three decades of characteristic frequency ($d_\omega = 217.15$); the horizontal axis may also be interpreted as log frequency (with a fixed place) instead of as place (with a fixed frequency).

Energy Flow and Wave Amplitudes

Energy in a wave flows at a rate equal to the group velocity $U = d\omega/dk$. In order to understand how wave amplitudes vary with position x and wavenumber k in nonuniform media, consider the power, or rate of flow of energy: the power should be constant as x varies in a lossless medium. Because the energy moves a distance U in unit time, this problem is equivalent to conserving the energy stored in a distance proportional to U as x varies, ignoring the imaginary part of k. We should be able to separately work the problem in terms of kinetic energy (energy of fluid motion alone, for the massless membrane case) or of potential energy (energy in deformation of the membrane), and get the same answer.

For the short-wave region, we found that $k = \omega^2\rho/S$, which gives the group velocity

$$U = \frac{d\omega}{dk} = \frac{\sqrt{S}}{2\sqrt{k\rho}} \tag{86}$$

Because S is spatially varying and ω is a constant, we substitute in

$$\frac{\sqrt{S}}{\sqrt{\rho}} = \frac{\omega}{\sqrt{k}} \tag{87}$$

to obtain a relation between U and k that turns out to be proportional to the phase velocity (but only within the short-wave region):

$$U = \frac{\omega}{2k} \propto c = \frac{\omega}{k} \tag{88}$$

The kinetic energy of fluid is $E_{\text{kinetic}} = \frac{1}{2}mv^2$ where m is the effective mass of moving fluid in a distance proportional to U and v is the rms velocity in that mass of fluid. The effective mass is proprotional to the 2D area with a width proportional to U and a height $1/k$ (because $1/k$ is the space constant or effective depth in the short-wave region). The rms velocity is proportional to the membrane velocity, so we can treat v as the amplitude of the membrane velocity wave, yielding the kinetic energy relation

$$E_{\text{kinetic}} = \tfrac{1}{2}mv^2 \propto \frac{U}{k}v^2 \propto k^{-2}v^2 \tag{89}$$

$$\text{or} \quad v \propto k \propto S^{-1} \quad \text{for } E_{\text{kinetic}} \text{ constant} \tag{90}$$

The potential energy in the membrane deformation with rms displacement δ is

$$E_{\text{potential}} = \tfrac{1}{2}US\delta^2 \propto k^{-2}\delta^2 \tag{91}$$

$$\text{or} \quad \delta \propto k \propto S^{-1} \quad \text{for } E_{\text{potential}} \text{ constant} \tag{92}$$

The amplitudes of the displacement and velocity waves must remain in a fixed proportion determined by ω, so the above results are self-consistent: membrane displacement and velocity increase in proportion with k as a wave of a fixed frequency travels through the cochlea.

The velocity wave amplitude is related to the velocity-potential wave amplitude via the defining relation $\mathbf{v} = -\nabla\phi$; the spatial derivative contributes a factor of k to the velocity amplitude, so ϕ has a constant amplitude.

The pressure wave p also is spatially differentiated to arrive at a membrane accelerating force; the space constant $1/k$ in depth implies an acceleration (and hence velocity and displacement) proportional to kp, so the pressure wave amplitude must be constant also.

These amplitude solutions for the short-wave case illustrate the reasoning and technique—we assume the system is lossless and constrain the solution to conserve energy. The corresponding solution for the more general case follows.

In the lossless region with $T = 0$ and $M = 0$, Equation 45 gives a closed-form solution for ω that can be differentiated to find U:

$$\omega = \sqrt{S/\rho}\sqrt{k\tanh(kh)} \tag{93}$$

$$U = \frac{\sqrt{S/\rho}}{2\sqrt{k\tanh(kh)}}[\tanh(kh) + kh\,\text{sech}^2(kh)] \tag{94}$$

To conserve power of the propagating wave, we require $E_{\text{potential}}$ in a distance U to be constant, as above

$$E_{\text{potential}} = \tfrac{1}{2}US\delta^2 \propto \frac{\sqrt{S/\rho}}{\sqrt{k\tanh(kh)}}[\tanh(kh) + kh\,\text{sech}^2(kh)]S\delta^2 \tag{95}$$

Substituting in for $S = \omega^2\rho/k\tanh(kh)$ we get the relation between k and δ:

$$\delta \propto \frac{k\tanh(kh)}{\sqrt{\tanh(kh) + kh\,\text{sech}^2(kh)}} \tag{96}$$

To find the amplitudes of the velocity-potential wave and the pressure wave, we need to divide out the magnitude of a spatial derivative in the y dimension, so the factor is not k as before, but $k\tanh(kh)$. Hence

$$\phi \propto p \propto \frac{1}{\sqrt{\tanh(kh) + kh\,\text{sech}^2(kh)}} \tag{97}$$

In the long-wave region, Equation 96 simplifies to

$$v \propto \delta \propto k^{3/2} \propto S^{-3/4} \tag{98}$$

and Equation 97 simplifies to

$$\phi \propto p \propto k^{-1/2} \propto S^{1/4} \tag{99}$$

Thus, in the long-wave region, the displacement wave amplitude grows more rapidly than k, but does not grow as quickly with x (with decreasing stiffness) as it does in the short-wave region. That is, the *log-displacement vs. place* function has two different slopes on the basal side of the response peak: It is flatter near the base, where the long-wave result applies, and steeper nearer to the response peak. Finally, the form of the velocity-potential and pressure wave amplitudes in the long-wave region corresponds to the solution $k^{-1/2}$ usually associated with the WKB approximation for one-dimensional problems.

Gain Control and Tuning Curves

The outer hair cells have been accepted as a source of active energetics in the cochlea. We model their effect as a negative viscosity, causing waves to be amplified rather than attentuated. But the function of the outer-hair-cell arrangement is not just to provide gain, but rather to provide control of the gain, which it does by a factor of about 100 in amplitude (10,000 in energy).

When the sound signal is small, the outer hair cells are not inhibited and they feed back energy. They reduce the damping until the signal reaching the higher brain centers is large enough. The AGC system works for sound power levels within a few decades of the bottom end of our hearing range by making the structure slightly more resonant and thereby much higher gain—by reducing the damping until it is sufficiently negative in some regions.

Figure 5 shows the sound pressure level required to produce a fixed membrane displacement amplitude or velocity, compared with the level required to produce a certain increase in the rate of firing of a single auditory nerve fiber. The data were obtained by Robles and his associates [Robles 85], using the Mössbauer effect in chinchilla cochlea. Curves such as these are termed *iso-output* or *iso-response* curves, because the input level is adjusted to produce the same output level (response) at each frequency; the region above an iso-output curve is known as the *response area*.

The curves show reasonable agreement between neural and mechanical data, implying that the response area is already determined at the mechanical level. Without the outer hair cells, the sensitivity is at least 30 dB less, and the curve tips are much broader [Kim 84]. The sharpness of such tuning curves (i. e., response area widths of only about one-fourth to one-tenth of the center frequency) often misleads model developers into thinking that the system is narrowly tuned, when in fact the curves are quite different from transfer functions. As frequency changes, the input level and AGC gains change enormously, in opposite directions, to keep the output at a constant level. The filter-gain shapes are difficult to infer from this kind of measurement, but they must be broader than are the iso-output tuning-curve shapes.

Figure 6 shows iso-output curves for a cochlear model composed of a cascade of second-order variable-Q filters, under two linear conditions (a passive low-gain condition, as in a cochlea with dead or damaged outer hair cells, and an active high-gain condition, as in a hypothetical cochlea with active outer hairs of constant gain and unlimited energy), and under the condition of an AGC that acts to adapt the gain between the two linear conditions in response to the average output level. The curves show that a simple gain-control loop can cause a broadly-tuned filter to appear to have a much narrower response when observed with an iso-output criterion; further examples of this effect have been shown by Lyon and Dyer [Lyon 86].

This neural/mechanical AGC is an intelligently designed gain-control system. It takes effect before the signal is translated into nerve pulses, just as does the visual gain-control system in the retina [Werblin 73]. Nerve pulses are by their very nature a horrible medium into which to translate sound. They are noisy and erratic, and can work over only a limited dynamic range of firing rates. It makes sense to have a first level of AGC *before* the signal is turned into nerve pulses, because this approach reduces the noise associated with the quantization of the signal.

Filter Cascades

A cascade of linear filters to model the uni-directional wave propagation in the cochlea can be constructed using very simple stages, each having only a few s-plane poles (or using digital filters with a few Z-plane poles and perhaps one or more zeroes at $Z = -1$ as well). By cascading stages with time-constants increasing geometrically, a filter structure that scales is the result—a more realistic model would space the stage time constants disproportionately further apart at the far end of the cascade, modeling the transition from log to linear frequency mapping toward the apical end of the cochlea.

A cascade of first-order (one-pole lowpass) filters is not a very good model even of a lossy passive cochlea, since the gain drops too rapidly (quadratically) at low frequencies ($1/|H_i|^2 = 1 + f^2$, with $f = \omega\tau_1$).

A cascade of second-order (two-pole lowpass) filters, with a Q value of about 0.7 to 0.9, makes a fair model of wave propagation in the cochlea, since such filters provide gain slightly greater than unity for frequencies over a moderate band before rolling off. The response magnitude is given by $1/|H_{ii}|^2 = 1 - (2 - 1/Q^2)f^2 + f^4$, with $f = \omega\tau_2$. The quadratic term needs a positive coefficient ($Q^2 > 0.5$) to get a gain bump.

The resulting pseudoresonance peak is a bit too broad (too low-order)—according to the hydrodynamic analysis, a response that is flat to second power at low frequencies is needed. A cascade of third-order filters, made by alternating the first- and second-order stages just discussed, provides the possibility of tuning up the pseudoresonant peak to be a little sharper, by cancelling the second-power terms of the first- and second-order stage responses.

The third order stage frequency response, using a ratio of first- and second-order stage time constants of $\rho = \tau_2/\tau_1$ and with $f = \omega\tau_2$, is $1/|H_{iii}|^2 = 1+[(1/\rho^2)-(2-1/Q^2)]f^2+[1-(1/\rho^2)(2-1/Q^2)]f^4+(1/\rho^2)f^6$. The quadratic term may be made to vanish by adjusting the time constants so that $\rho = 1/\sqrt{2-1/Q^2}$, in which case the transfer function simplifies to $1/|H_{iii}|^2 = 1+[1-(1/\rho^4)]f^4+(1/\rho^2)f^6$. To get a gain bump requires a negative coefficient on the fourth-power term, so we need $Q > 1$ or $\rho < 1$ (first-order stage time constant longer than second-order state time constant) to model an active cochlea. For example, with $Q = 1.2$ and $\rho = 0.875$, the response is flat at low frequencies and provides a gain bump of about 0.13 dB. The width of the gain bump, measured at half height on a log-gain scale, is slighly less than an octave, or about 0.6 times as wide as the second-order filter gain bump.

Plots of typical gain bumps for the hydrodynamic model, the second-order stage, and the third-order stage are shown in Figure 7. Apparently the third-order filter provides a very good match to the transfer functions implied by our hydrodynamic analysis for a cochlea with a massless partition. The second-order model is the simplest way to get an adjustable gain bump and thereby make a qualitative cochlear model—it is the basis of the chip we built, and is described in detail elsewhere [Lyon&Mead 88 and Mead 89].

A geometric cascade of filters of any order will model also the delay of the cochlea. The free parameters of our model that affect the gain also affect the delay. Perhaps the best way to match models, once the structure is appropriate, is to match the observed delay of about five cycles for a sinusoid on the cochlear partition. In the case of third-order stages, the ratio of time constants from one stage to the next needs to be about 0.99 (i.e., about 70 stages per octave) to get this much delay (somewhat dependent on the Q and on how the delay is measured). It seems likely that a filter cascade with only half as many stages and half as much delay would still be a useful model of the cochlea.

Three-dimensional Effects

A three-dimensional analysis of cochlear hydrodynamics is somewhat more complicated, but has been tackled by various researchers using a variety of approaches. We have a simple way of thinking about the main 3D effects.

In the long-wave region, wavelengths are long compared to the duct height and width (both about h) and compared to the width of the flexible partition (b, which is significantly less than h, especially near the base). In the short-wave region, wavelengths are short compared to these two quantities. In either of these regions, an equivalent stiffness (and other parameters) for a 2D model may be easily calculated. However, when the length $1/k$ is smaller than h but larger than b, things are more interesting.

In the long-wave region, the wave motion is constrained in depth and in width by the duct walls. In the short-wave region, waves are constrained in width only, since the influence can only reach a distance $1/k$ beyond the edges of the partition. In between however, the wave is not constrained in either depth or width—the influence of the wave spreads out in a circle from the thin ribbon-like partition into the wide open space of the duct. The result is that the dispersion relation of k versus ω is even steeper than in the short-wave region ($k \propto \omega^3$ instead of $k \propto \omega^2$), rather than being an intermediate steepness as the 2D analysis would suggest. See Steele 87 for more on 3D solutions.

We interpret the extra width h relative to b near the base of the cochlea as a mechanism for preventing long-wave behavior. As a result of the 3D structure of the cochlea, the rather clean short-wave region solution may actually be a better model overall than the more complete 2D solution (except for the low-frequency asymtotic behavior, where the short-wave solution implies zero delay).

Summary and Conclusions

We hope to convert this rather mysterious demystification into something that could actually be published, and to expand on our interpretations of cochlear function. Suggestions and criticism toward that end are welcome.

There are a number of controversies in the field of cochlear function that our models and interpretations have some bearing on, and we hope to contribute to settling some of them. In particular, let us summarize a few main points that we would like to expand on in future publications:

1. The cochlea operates mainly in the short-wave region, rather than in the long-wave region.
2. The mass of the cochlear partition is negligible, except perhaps near the base, and the tension of the cochlear partition is also negligible.
3. The hydrodynamic system of the cochlea is not highly tuned (in the sense of being highly frequency selective), and the best frequency for a place is quite level dependent.
4. Sharp iso-response tuning curves are the result of an AGC operating in conjunction with a broadly tuned hydrodynamic system—no "second filter" or other tuned sharpening mechanism is needed to model cochlear tuning.
5. A bandpass filterbank to model cochlear response ought to be designed as a cascade, rather than as a parallel bank of independent filters.
6. Nonlinearity in the cochlea is important mainly as an adaptive mechanism—the short-time response is nearly linear (distortion products in the hydrodynamic system are barely audible under special conditions).
7. A model of the active adaptive cochlea must be extremely nonlinear over a wide range of signal level, mainly to effect gain control.
8. In the normally-functioning cochlea, energy travels in one direction—standing waves, acoustic emissions, and reflections may be neglected except in pathologies.

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Figure Captions

Figure 1. Two snapshots of a traveling one-dimensional wave with damping. Between the two snapshots separated by a time $1/\omega$, the wave has changed phase by 1 radian, or moved to right a distance $1/k_r$, and has diminshed in amplitude by a factor $\exp(-k_i)$. For this illustration, k is $1 + i0.1$.

Figure 2. A cascade of filters modeling uni-directional wave propagation along one dimension.

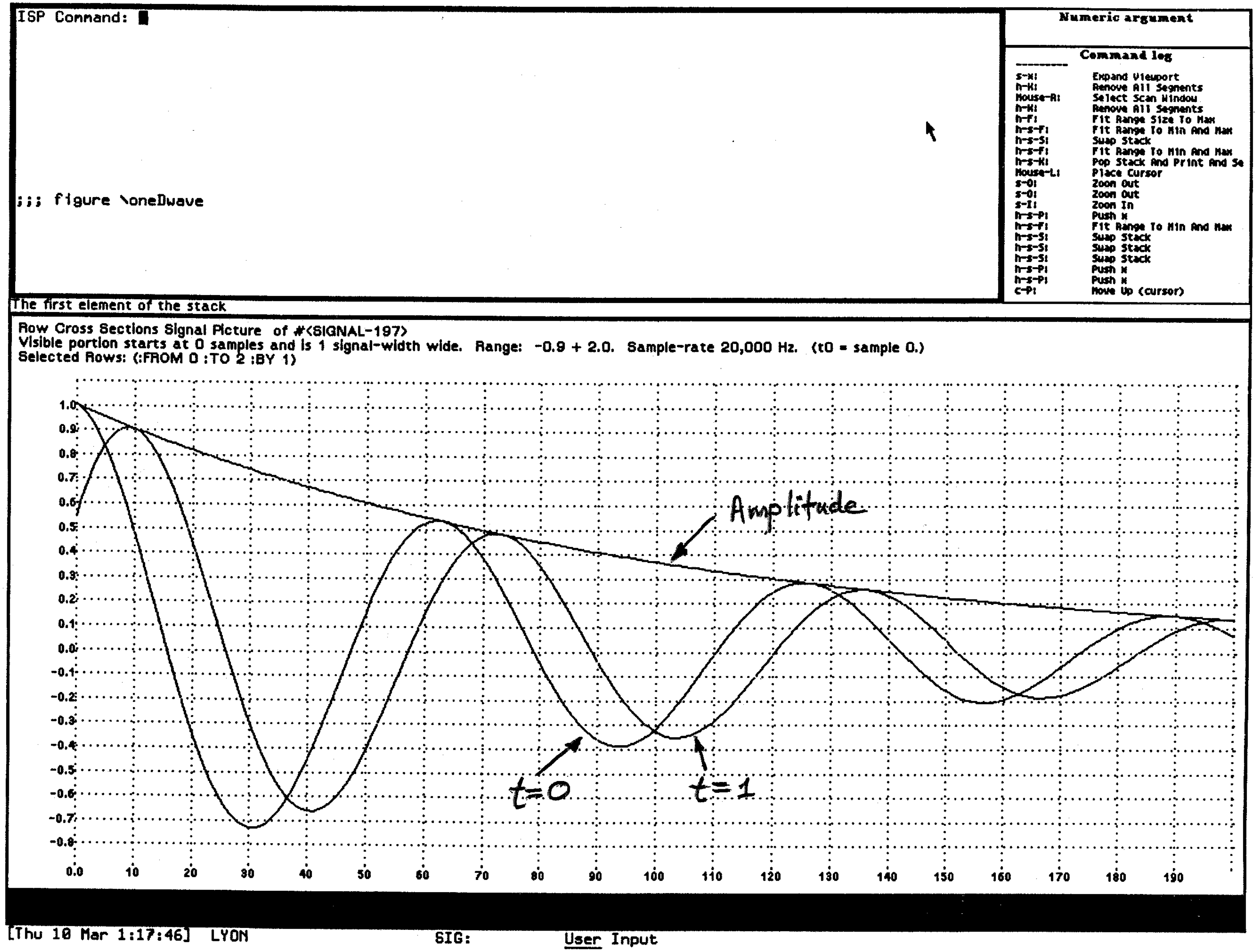
Figure 3. Fluid flow streamlines and velocity potential in a pair of ducts separated by a flexible membrane, for the case $kh = 1$. Between the long-wave and short-wave regions, the bottom wall of the duct has a significant but not overwhelming effect on the streamlines of fluid flow. The deflection of the top surface, corresponding to the displacement wave on the cochlear partition is exaggerated for clarity.

Figure 4. Numerical solutions of k *vs.* x for two conditions: (1) high-order γ loss only, an ideal passive condition; (2) γ loss and β gain, an active condition. The real and imaginary parts of k are separately plotted on a log scale. For the region where k_i is negative due to active gain, the log of its absolute value is plotted; a cusp in the k_i curve indicates the transition between gain and loss for the active condition. The place scale has arbitrary units with 1500 units spanning three decades of characteristic frequency ($d_\omega = 217.15$); the horizontal axis may also be interpreted as log frequency (with a fixed place) instead of as place (with a fixed frequency).

Figure 5. Mechanical and neural iso-output tuning curves, based on data from Robles and his associates [Robles 85]. The mechanical measurements (amount of input needed to get 1 mm/sec basilar membrane displacement velocity or 19 Å basilar membrane displacement amplitude) were made by measuring doppler-shifted gamma rays (Mössbauer effect) from a small radioactive source mounted on the cochlear partition. The neural tuning curve was measured by looking for a specified increase in firing rate of a single fiber in the cochlear nerve.

Figure 6. Model iso-output tuning curves for linear models (dashed curves) and for a particular nonlinear AGC scheme (solid curve) that varies the model gain by varying the Q of the cascaded filter stages. The similarity in the response area shape and width between the active adaptive model and the biological system (Figure 5) is striking. For this simulation, all filter stage Q values are equal, and are computed from a feedback gain β that is a maximum value minus a constant times the total output of 100 channels. The relation of Q values to overall gains and overall transfer functions is discussed in the text.

Figure 7. Plots of log-magnitude gain of (a) a length of active cochlea, according to the hydrodynamic model, (b) a second-order filter, and (c) a third-order filter adjusted to be flat at low frequency. The horizontal log-frequency scales are arbitrarily shifted, and the gains are not adjusted to be identical.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Numeric argument
Command log
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h-K: Remove All Segments
Mouse-R: Select Scan Window
h-K: Remove All Segments
h-F: Fit Range Size To Max
h-s-F: Fit Range To Min And Max
h-s-S: Swap Stack
h-s-F: Fit Range To Min And Max
h-s-K: Pop Stack And Print And Se
Mouse-L: Place Cursor
s-O: Zoom Out
s-O: Zoom Out
s-I: Zoom In
h-s-P: Push x
h-s-F: Fit Range To Min And Max
h-s-S: Swap Stack
h-s-S: Swap Stack
h-s-S: Swap Stack
h-s-P: Push x
h-s-P: Push x
c-P: Move Up (cursor)
The first element of the stack
Row Cross Sections Signal Picture of #<SIGNAL-197>
Visible portion starts at 0 samples and is 1 signal-width wide. Range: -0.9 + 2.0. Sample-rate 20,000 Hz. (t0 = sample 0.)
Selected Rows: (:FROM 0 :TO 2 :BY 1)
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0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
0.0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190
Amplitude
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t=1
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SIG:
User Input

Figure 1

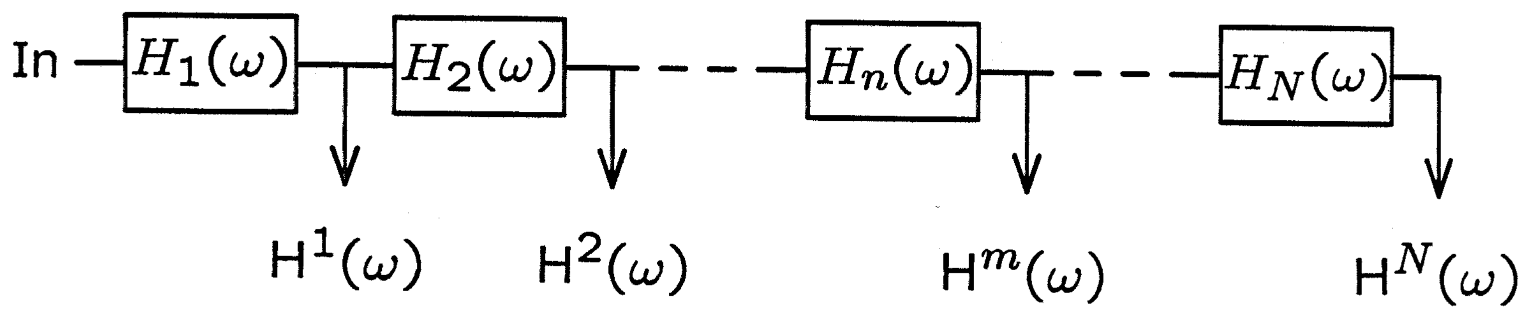
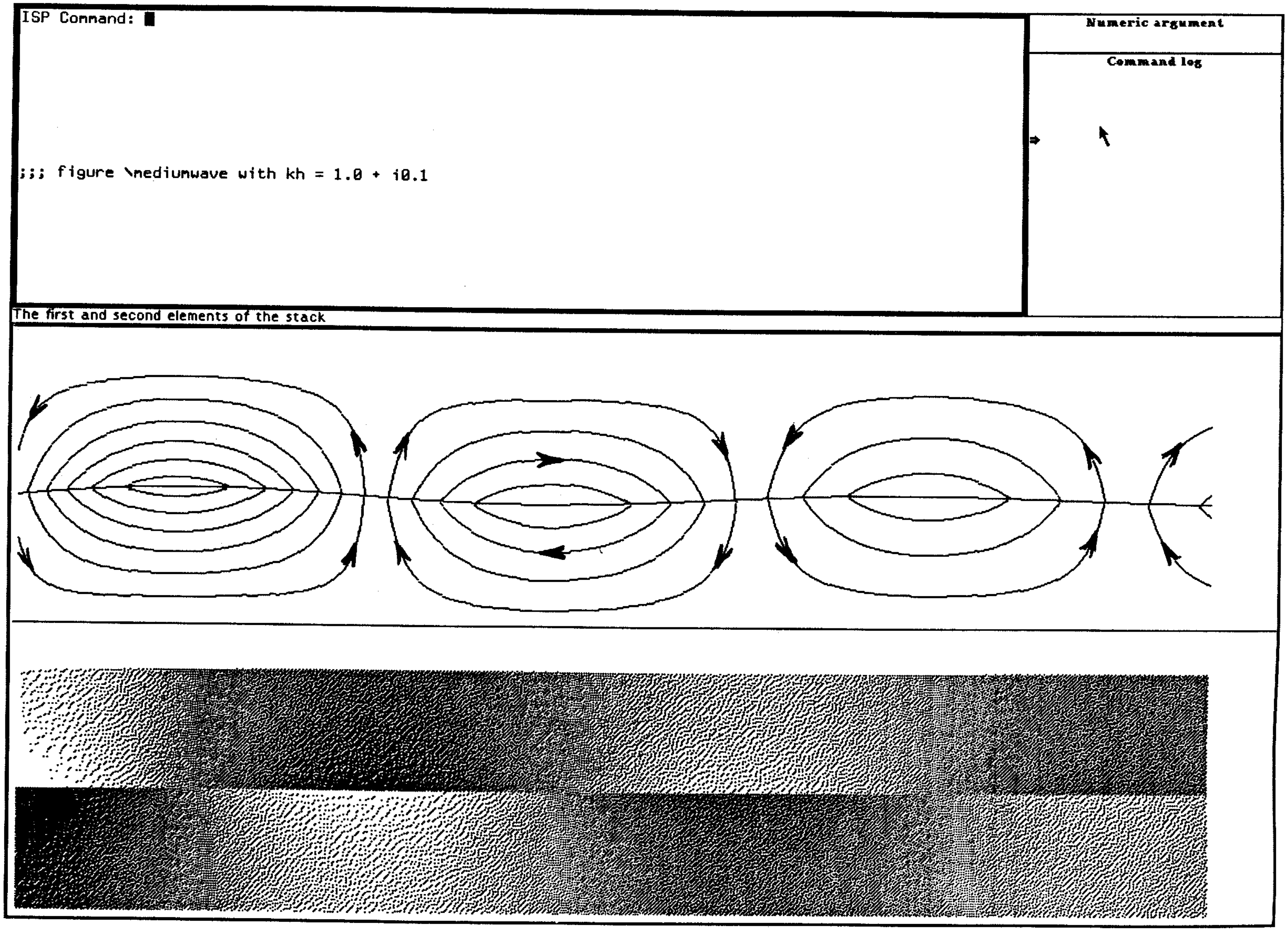

In
$H_1(\omega)$
$H_2(\omega)$
$H_n(\omega)$
$H_N(\omega)$
$H^1(\omega)$
$H^2(\omega)$
$H^m(\omega)$
$H^N(\omega)$

Figure 2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Numeric argument
Command log
The first and second elements of the stack

Figure 3

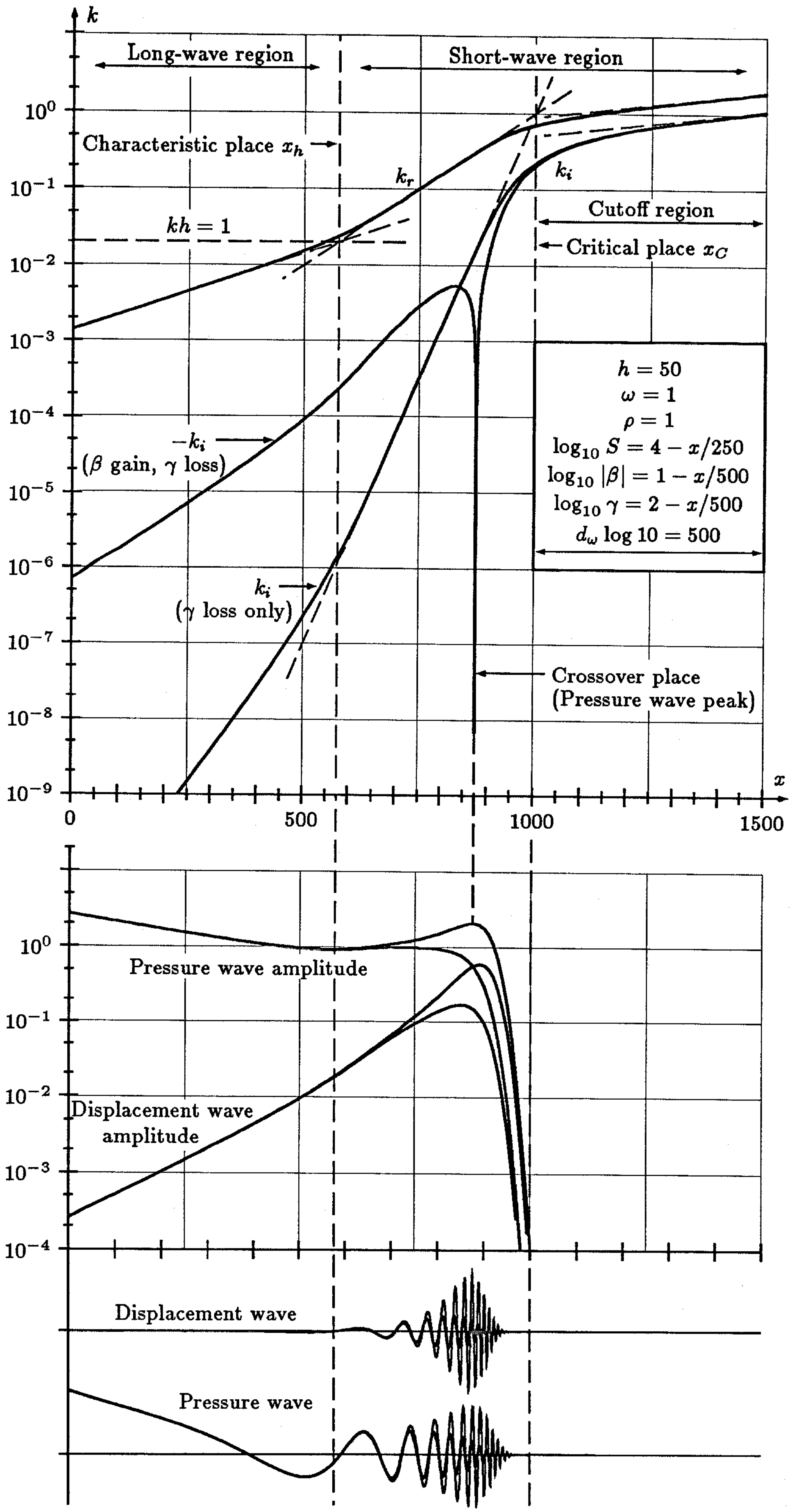


Figure 4
& more

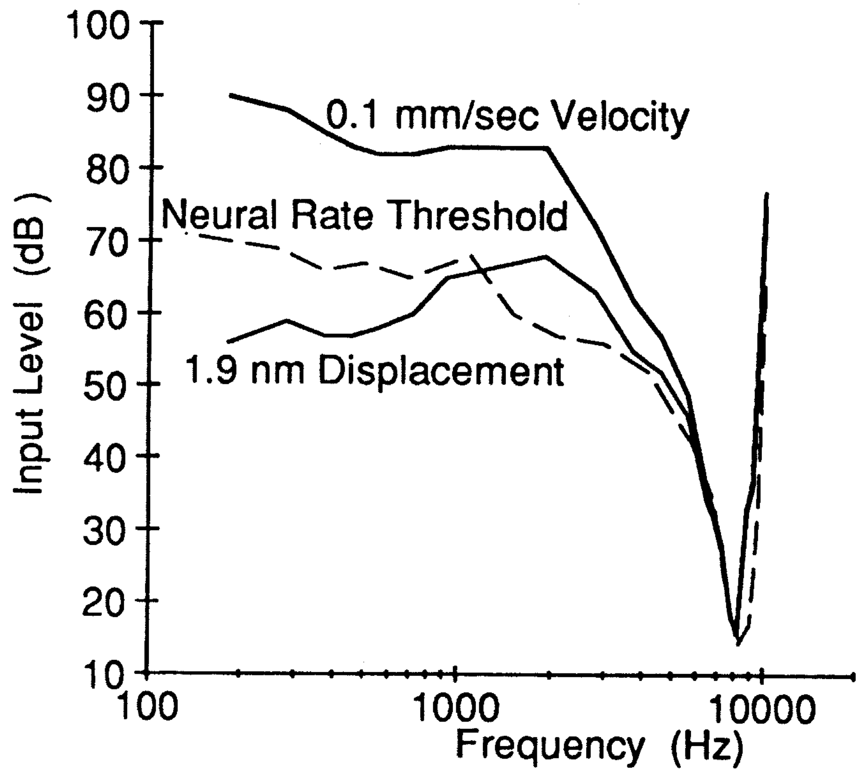


Figure 5

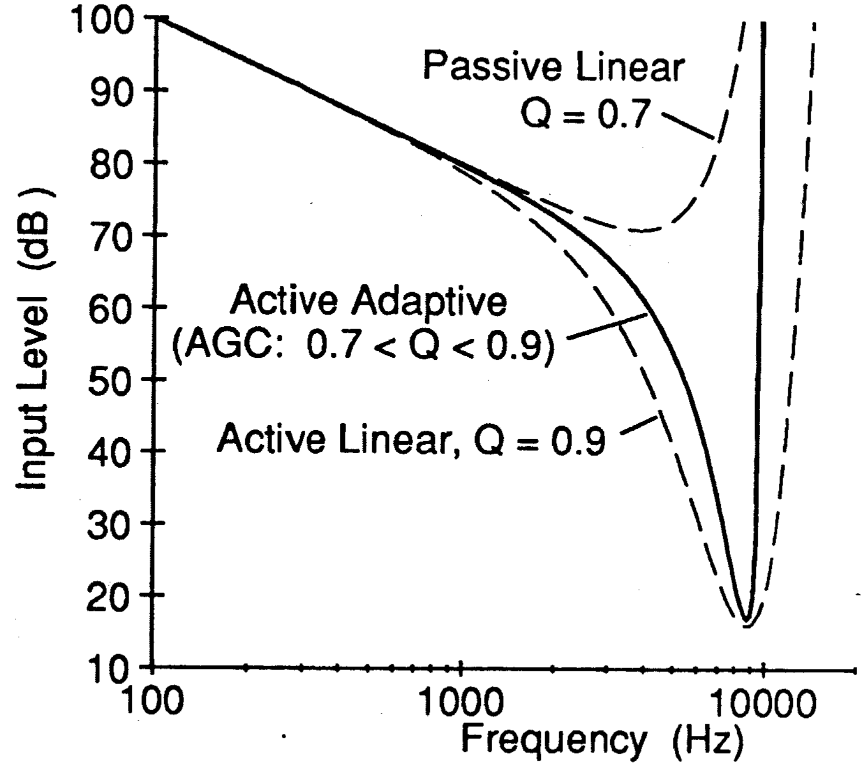
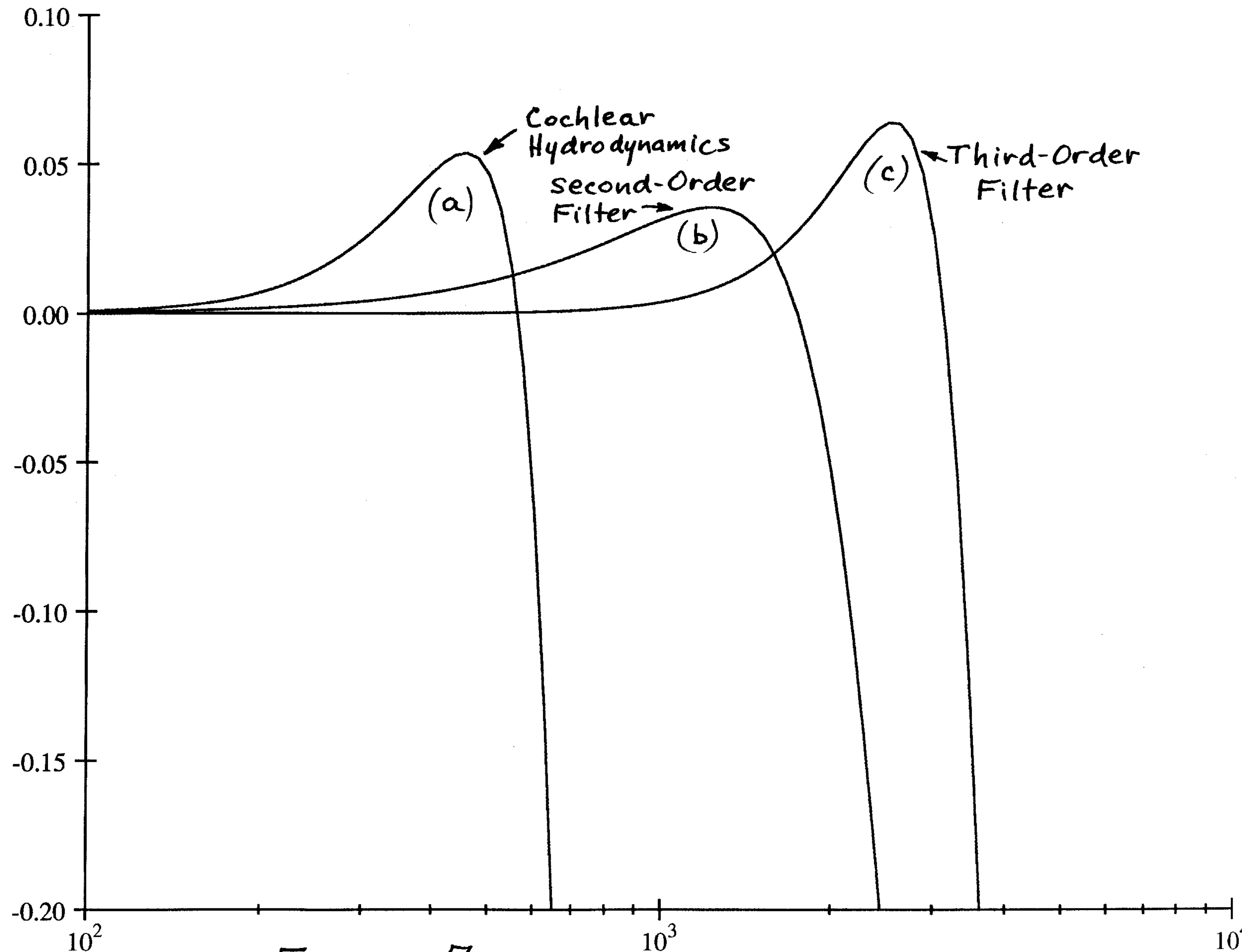


Figure 6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0.00
-0.05
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-0.20
10^2
10^3
10^4
Cochlear Hydrodynamics
Second-Order Filter
Third-Order Filter
(a)
(b)
(c)

Figure 7

Appendix A — Notation

The following symbols are used more or less consistently in the text:

t = time in seconds (cgs units are used where relevant).
x = the cochlear *place* dimension (in centimeters), measured from the base.
y = the *vertical* dimension in a cochlear duct (perpendicular to the partition).
z = the complex variable $x + iy$ that represent place in two dimensions.
h = the height of a cochlear duct, such that $y = h$ at the cochlear partition.
W = a wave, a function of place and time.
A, B = arbitrary constants in solutions to differential equations.
P = a function of y used in solutions to differential equations.
$\mathbf{v} = (\mathbf{v}_x, \mathbf{v}_y) = (u, v)$ the velocity vector of the fluid.
ϕ = the velocity potential of the fluid in a duct.
ψ = the stream function of the fluid in a duct.
$\mathbf{w}$ = the complex function $\phi + i\psi$.
$\mathrm{Re}[\cdot]$ = the *real-part* operator.
$\mathrm{Im}[\cdot]$ = the *imaginary-part* operator.
ω = frequency in radians s^{-1}.
f = frequency in cycles s^{-1}, or normalized frequency.
λ = wavelength in cm (per cycle).
k = wavenumber in radians cm^{-1}.
k_r, k_i = real and imaginary parts of k.
$k^* = (k_r - ik_i)$, the complex conjugate of k.
c = the phase velocity ω/k of a traveling wave.
U = the group velocity $d\omega/dk$ of a traveling wave.
ω_N = any conveniently defined measure of natural frequency.
d_ω = the characteristic distance for geometrically changing ω_N.
$l_f = \log(f)$ is the log of the normalized frequency ω/ω_N.
F = force.
m = mass.
a = acceleration.
p = pressure in the fluid (dynes cm^{-2}).
ρ = density of the fluid (grams cm^{-3}).
δ = partition displacement, a one-dimensional traveling wave.
T = partition tension (dyne cm^{-1}).
M = partition mass (gram cm^{-1}).
S = partition stiffness (dyne cm^{-3}, reciprocal of volume compliance).
S_0 = partition stiffness at the basal end of the cochlea.
β = partition velocity loss coefficient (units?).
γ = partition bending loss coefficient (units?).
ξ = damping coefficient k_i/k_r.
ω_C = a critical frequency, depending on place, such that damping is large.
x_C = a critical place, depending on frequency, such that damping is large.
M_C = a critical mass, such that resonance occurs near the critical frequency.
ω_h = a characteristic frequency, depending on place, such that $kh \approx 1$.
x_h = a characteristic place, depending on frequency, such that $kh \approx 1$.
s = the laplace transform variable, $i\omega$.
Z = the Z-transform variable, $\exp(i\omega\Delta t)$.
Δt = the sampling period of a discrete-time system.
Δx = the spatial sampling period along the x dimension.

E_{kinetic} = the energy of fluid motion in a distance U.
$E_{\text{potential}}$ = the energy of membrane distortion in a distance U.

These standard definitions are included for reference:
e = base of natural logarithms (2.71828...).
i = principal complex square root of -1.
$\exp(x)$ = the exponential function e^x.
$\log(x)$ = the natural logarithm, the inverse function of exp.
$\cos(x)$ = the cosine function $\frac{1}{2}[\exp(ix) + \exp(-ix)]$.
$\sin(x)$ = the sine function $\frac{1}{2i}[\exp(ix) - \exp(-ix)]$.
$\cosh(x)$ = the hyperbolic cosine function $\frac{1}{2}[\exp(x) + \exp(-x)]$.
$\sinh(x)$ = the hyperbolic sine function $\frac{1}{2}[\exp(x) - \exp(-x)]$.
$\tanh(x)$ = the hyperbolic tangent function $\sinh(x)/\cosh(x)$.
$\mathrm{sech}(x)$ = the hyperbolic secant function $1/\cosh(x)$.
$|x|$ = the absolute magnitude of the complex number x.
$\arg(x)$ = the phase angle of the complex number x.
d, ∂ are names for the operators of differential calculus.
∇, **div**, **grad** are names for the vector operator $(\frac{\partial}{\partial x}, \frac{\partial}{\partial y})$.