Appendix B

Traveling Waves in the Mammalian Cochlea - A Simple Model

We outline here a simple model for mechanics of the mammalian cochlea. The main purpose is to show how simple considerations with regard to the anatomy and physics lead to the presence of traveling waves, which can propagate energy throughout the cochlea in a manner analogous to that of an electric transmission line.

B.0.9 Transmission Line

We briefly spend time here to discuss properties of an electric transmission line (TL), which will be apparent when used for analogy later. As shown in Fig.B-1, a coaxial transmission line can be formed by a long, straight wire surrounded by a conducting sheath. An infitesimal element of length Δz can be modeled by the circuit in Fig.B-2.

The space between the conductors will have a conductance G depending upon what the medium is. Both wires effectively act as *parallel-plate* capacitors and will have the resulting capacitance C between them. The resistance and inductance of the wires (per unit length) will be given by R and L respectively. In the loss-less condition, both G and R would identically be zero. Applying Kirchhoff's laws, we

have

$$v(z,t) - R \cdot \Delta z \cdot i(z,t) - L \cdot \Delta z \cdot \frac{\partial i(z,t)}{\partial t} - v(z + \Delta z, t) = 0 \qquad \text{(B.1)}$$

and

$$i(z,t) - G \cdot \Delta z \cdot v(z + \Delta z, t) - C \cdot \Delta z \cdot \frac{\partial v(z + \Delta z, t)}{\partial t} - i(z + \Delta z, t) = 0 \qquad \text{(B.2)}$$

Upon rearranging and taking the limit as $\Delta z \to 0$, we obtain the general TL equations

$$-\frac{\partial v}{\partial z} = R \cdot i(z,t) + L\frac{\partial i}{\partial t} \qquad \text{(B.3)}$$

$$-\frac{\partial i}{\partial z} = G \cdot v(z,t) + C\frac{\partial v}{\partial t} \qquad \text{(B.4)}$$

Solutions to these equations will be of the form $v(z,t) = \Re[V(z)e^{j\omega t}]$ and $i(z,t) = \Re[I(z)e^{j\omega t}]$. Note that we use j to represent $\sqrt{-1}$ to avoid confusion. This leads to

$$\frac{\partial^2 V}{\partial z^2} = \gamma^2 V(z) \qquad \text{(B.5)}$$

and
$$\frac{\partial^2 I}{\partial z^2} = \gamma^2 I(z) \qquad \text{(B.6)}$$

where $\gamma = \sqrt{(R + j\omega L)(G + j\omega C)}$, the propagation constant. The $(R + i\omega L)$ term is generally refered to as the series impedence Z while the $(G + i\omega C)$ term is the shunt admittance Y. Generally R is neglected and we have

$$\gamma \approx j\omega\sqrt{LC\left[1 + \frac{G}{j\omega C}\right]} \qquad \text{(B.7)}$$

A general solution to the equations will be the sum of a forward and backward trav-
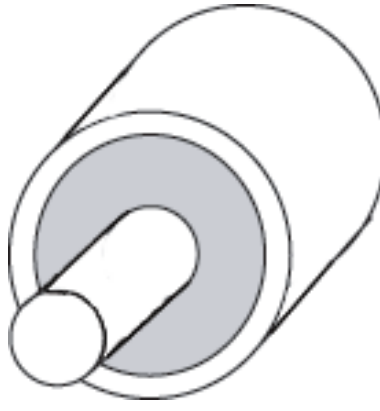
Figure B-1: Schematic showing a coaxial line, an inner conductor surrounded by an outer conductor with a dielectric medium inbetween.

eling wave. For the voltage $v(z, t)$, this will be given by

$$v(z, t) = e^{j\omega t}[V^+(z) + V^-(z)] = e^{j\omega t}[V_o^+ e^{-\gamma z} + V_o^- e^{\gamma z}] \tag{B.8}$$

which in turn solves the wave equation

$$\frac{\partial^2 v}{\partial z^2} - \frac{1}{\mu^2}\frac{\partial^2 v}{\partial t^2} = 0 \tag{B.9}$$

where $\mu = \omega/\gamma$ and describes the velocity of the traveling wave. It is insightful to stop here a moment and examine the result. Our analysis has shown that as the voltage changes across an infinitesimal cross-section of the coaxial line, this change will propagate outward with speed and attenuation defined by γ (it is the real part of γ which dictates how the wave amplitude changes). This derivation will provide insight by analogy as we develop the first stage of our cochlear model.

One other useful quantity to describe here is the characteristic *impedance* of the line, Z_o. This is defined as the ratio between the voltage and the current. For an infinitely long line with only a forward-traveling wave, we have

$$Z_o = \frac{V_0^+}{I_o^+} \approx \sqrt{\frac{j\omega L}{G + j\omega C}} \tag{B.10}$$

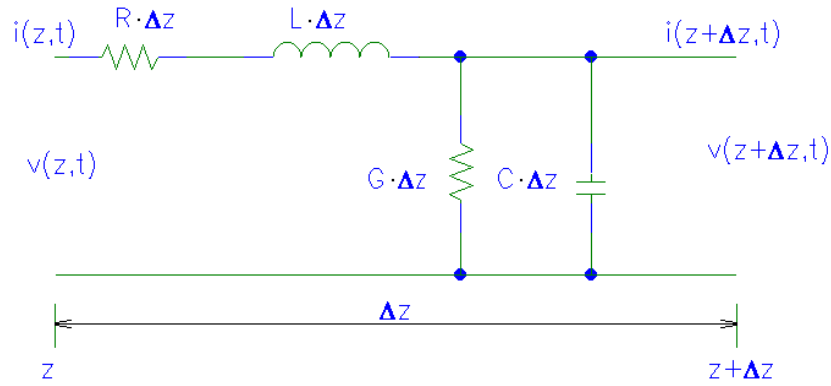**Figure B-2:** Circuit diagram for infitesimal transmission line element [Johansson].

B.0.10 Passive Linear Model

Cochlear Geometry

One of the first assumption we make is to unravel the snail-shaped cochlea into a straight tube. Previous calculations have shown that cochlear curvature can safely be neglected when considering the macromechanics because the radius of curvature is large compared to the spatial wavelength of the BM traveling waves [Steele and Zais, 1984]. Fig.B-3 shows a cross-section through the basal turn of a guinea pig. Separating the scala vestibuli (ScV) and scala media (DC) is a structure called Reissner's membrane. This avascular barrier serves to seperate the ionic constituents of the fluids on each side, but does not add any impedence and can thus be neglected. One important observation to note is the location of the basilar membrane (BM). As the bony projections juts out from the left (which encloses the nerves of the spiral ganglion), the BM stretches only a short distance across (from beneath the IHCs over to the right side wall). This is schematized in Fig.B-4, which shows the specific structures considered in our model. The wavelengths are large compared to the scalae height and thus pressure can be considered uniform across the cross-section (*long wavelength approximation*). It is important to note that the organ of cortii sits on top of the basilar membrane and surely plays an active role in the dynamics. We however here are going to focus solely on the macroscopic behavior and not the specifics of what is happening at the microscopic level.
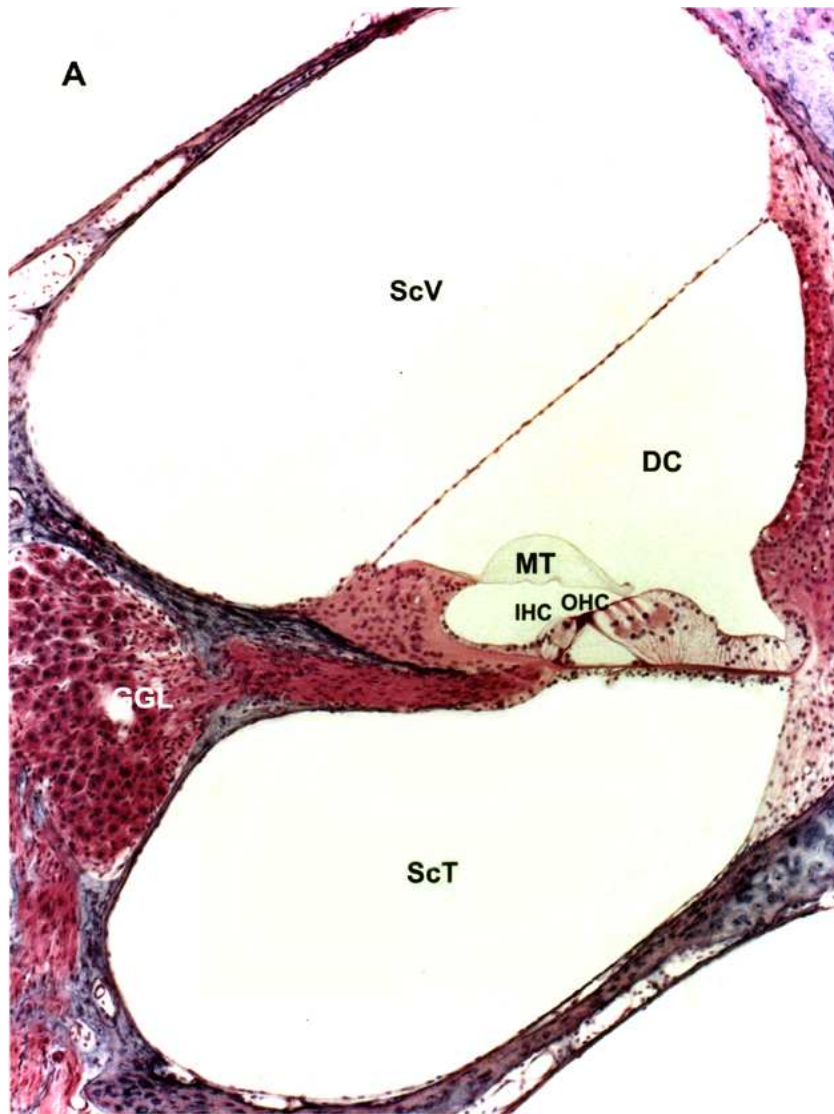
Figure B-3: Micrograph showing anatomy of a cochlear turn. [ScV - scala vestibuli, ScT - scala tympani, MT - tectorial membrane, IHC - inner hair cell, OHC - outer hair cell, DC - scala media]
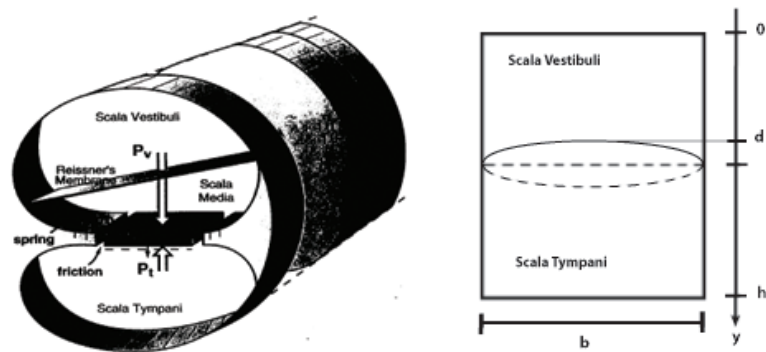

Figure B-4: Coordinate system for cross-section.

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We will spend a moment here to describe the geometry of our problem such that we can make as many simplifying assumptions as possible for clarity and still retain the dynamical behavior as best we can. The distance x represents the distance along the length of the straightened cochlea from the stapes. At each point x, we consider the cross-section as shown in the right of Fig.B-4. We have chosen a rectangular shape for the cochlear aqueduct and neglected the bony projection, assuming that the BM simply stretches all the way across. This will be an adequate assumption since we are chiefly concerned with how BM motion effects the change of each scalae area in the cross-section. The cross-section has width $b(x)$ and a height $h(x)$ (with a reference of 0 at the bony top of the scala vestibuli). The quantity d describes the position of the BM. There are two points to be mentioned in regard to the figure. First, the magnitude of d has been greatly exaggerated for clarity. The height of a cochlear aqueduct in the guinea pig varies from 1.8 mm in the basal end to around 0.6 mm in the apical end. However, BM amplitude ranges only from 0.05 nm at the lowest levels up to 10-20 nm at the highest levels. We have also shown the lateral sides of the BM fixed. This will introduce a constant factor in how the area changes which can be safely neglected from our calculations below. One important initial assumption which we will make is that b and h are independent of x and thus the cross-sectional area of a volume element is constant (denoted by A_v or A_t). For example, this simplifies the expressions $\frac{\partial}{\partial t}[A_v(x) \cdot u_v(x,t)]$ to $A_v \cdot \partial u_v(x,t)/\partial t$ where $u_v(x,t)$ is the fluid velocity across the scala vestibuli. Since $A_v(x) = b(x) \cdot d(x,t)$, this is equivalent to assuming

$$\left|\frac{\partial u_v}{\partial x}\right| \gg \left|\frac{\partial d}{\partial x}, \frac{\partial b}{\partial x}\right| \tag{B.11}$$

We have already seen that $\partial d/\partial x$ will be quite small since the magnitude of the BM motion is relatively small.

Model

We assume that the fluid is incompressible. It is also assumed that cochlear fluids are not viscous, such that all energy entering the cochlea is dissipated by movement

of the cochlear partition. The fluid dynamics are also assumed to be linear, since the wavelengths are relatively large and the velocities small so we only need to worry about inertial forces, [deBoer, 1996]. As the pressure difference across the element $[p(x + \Delta x, t) - p(x, t)]$ is incremented, there will be a corresponding change in fluid flow through the element given by

$$\Delta t \cdot A_v \cdot [p_v(x, t) - p_v(x + \Delta x, t)] = \rho \cdot \Delta x \cdot A_v \cdot [u_v(x, t + \Delta t) - u_v(x, t)] \quad \text{(B.12)}$$

If we divide and take the limit, we obtain

$$\frac{\partial p_v}{\partial x} = -\rho \frac{\partial u_v}{\partial t} \tag{B.13}$$

The negative term arises because as $\partial p / \partial x$ increases, the pressure will grow larger on the right compared to the left and thus fluid is less likely to flow through. Because of our chosen coordinate system, we simiarly find for the scala tympani

$$\frac{\partial p_t}{\partial x} = -\rho \frac{\partial u_t}{\partial t} \tag{B.14}$$

Because the fluid is incompressible and the basilar membrane is flexible, we can derive an expression for fluid velocity to membrane displacement $[d(x, t)]$. Again considering a cross-sectional slice of thickness Δx, the change of mass inside the element will equal the product between the density and the change in volume

$$\Delta t \cdot A_v \cdot \rho \cdot [u(x, t) - u(x + \Delta x, t)] = \Delta x \cdot \rho \cdot b \cdot [d(x + \Delta x, t) - d(x, t)] \quad \text{(B.15)}$$

Which upon dividing and taking the limit, we obtain

$$A_v \frac{\partial u_v}{\partial x} = -b \frac{\partial d}{\partial t} \tag{B.16}$$

A consequence of our chosen coordinate system means that increasing d means a

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smaller scala tympani cross-sectional area, so we have

$$A_t \frac{\partial u_t}{\partial x} = b \frac{\partial d}{\partial t} \tag{B.17}$$

We now turn towards the forces acting upon the cochlear partition. There are three forces in addition to the inertial force which will have an effect:

$$F = F_{stiffness} + F_{drag} + F_{pressure} = \mu \cdot \Delta x \cdot \frac{\delta^2 d}{\delta t^2} \tag{B.18}$$

where $\mu \Delta x$ is the effective mass of section. The pressure force will be given by area $\cdot$ pressure difference $= \Delta x \cdot b \cdot [p_v(x,t) - p_t(x,t)]$. This is positive since $p_v > p_t$ means that d will increase. The drag force is the product of the velocity and the effective damping coefficient, $\alpha \cdot \Delta x$. This force will be negative since it works opposite the velocity when $\partial d / \partial t > 0$. Finally, the force due to stiffness will be the product of the displacement d and the effective stiffness $\kappa \cdot \Delta x$. Note that we assume that μ, α and κ are all independent of x. This yields the following equation of motion

$$\mathbf{b} \cdot [\mathbf{p_v(x,t)} - \mathbf{p_t(x,t)}] = \mu \cdot \frac{\delta^2 \mathbf{d(x,t)}}{\delta \mathbf{t^2}} + \alpha \cdot \frac{\delta \mathbf{d(x,t)}}{\delta \mathbf{t}} + \kappa \cdot \mathbf{d(x,t)} \tag{B.19}$$

We now wish to show that $A_{cs} \cdot (u_v(x,t) + u_t(x,t))$ is constant with respect to position and equal to zero (where $A_{cs} = A_v + A_t$). Consider the derivative

$$\frac{\partial}{\partial x} A_{cs} \cdot [u_v(x,t) + u_t(x,t)] \tag{B.20}$$

Which from our previous result, we can express this as

$$A_{cs} \cdot \left[-b \frac{\partial d}{\partial t} + b \frac{\partial d}{\partial t} \right] = 0 \tag{B.21}$$

Thus $u_v(x,t) + u_t(x,t)$ is constant at any place along the cochlea. At the base, any fluid change at the oval window (i.e. at the stapes footplate) must be equal and opposite in magnitude of the change at the round window. So we have $u_v(0,t) = -u_t(0,t)$ for

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all t. This then leads to

$$u_v(x, t) = -u_t(x, t) \tag{B.22}$$

This result can now be used to consider $\partial/\partial x[p_v(x, t) + p_t(x, t)]$, which will identically be 0. So we obtain

$$p_v(x, t) + p_t(x, t) = \alpha \tag{B.23}$$

where α is a constant.

We can now make some simplifications by introducing the variables $p \equiv p_v - p_t$ and $u \equiv A_{cs}(u_v - u_t)/2$. We assume that the time dependence of both p and u is sinusoidal and each can be expressed as $\mathbf{p(x, t)} = \Re[\mathbf{P}(x, \omega)\mathbf{e^{j\omega t}}]$ and $\mathbf{u(x, t)} = \Re[\mathbf{U}(x, \omega)\mathbf{e^{j\omega t}}]$ (ω is 2π times the frequency of stimulation). We can now write

$$\frac{\partial p}{\partial x} = \frac{\partial p_v}{\partial x} - \frac{\partial p_t}{\partial x} = -\rho \left(\frac{\partial u_v}{\partial t} - \frac{\partial u_t}{\partial t} \right) \tag{B.24}$$

which leads to

$$\frac{\partial p}{\partial x} = -\frac{2\rho}{A_{cs}} \frac{\partial u}{\partial t} \tag{B.25}$$

But since $\partial p/\partial x = e^{j\omega t}\partial P/\partial x$ and $\partial u/\partial t = i\omega e^{j\omega t}U$, we have

$$\Rightarrow \frac{\partial \mathbf{P}}{\partial \mathbf{x}} = -\frac{2\rho}{\mathbf{A_{cs}}}\mathbf{i}\omega\mathbf{U} = -\mathbf{ZU} \tag{B.26}$$

We can carry out a similar analysis for u to obtain an expression for $\partial U/\partial x$:

$$\frac{\partial p}{\partial x} = \frac{A_{cs}}{2} \left[-\frac{b}{A_{cs}} \left(\frac{\partial d}{\partial t} + \frac{\partial d}{\partial t} \right) \right] = -b\frac{\partial d}{\partial t} \tag{B.27}$$

Rearranging terms,

$$\frac{\partial d}{\partial t} = -b\frac{\partial u}{\partial x} = -\frac{e^{j\omega t}}{b} \frac{\partial U}{\partial x} \tag{B.28}$$

We can now integrate this to get an expression for $d(t)$.

$$d(t) = \int -\frac{e^{j\omega t}}{b} \frac{\partial U}{\partial x} dt = -\frac{e^{j\omega t}}{j\omega b} \frac{\partial U}{\partial x} \tag{B.29}$$

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This result can then be plugged back into the equation of motion (eqn.B.19) as follows

$$bp(x,t) = \frac{e^{j\omega t}}{j\omega b}\frac{\partial U}{\partial x}\left[-\mu^2 + \alpha i\omega + \kappa\right] = b \cdot Pe^{j\omega t} \qquad (\text{B.30})$$

Upon rearranging terms, we can write this as

$$\frac{\partial \mathbf{U}}{\partial \mathbf{x}} = -\frac{\mathbf{P}}{\mathbf{j}\omega\frac{\mu}{\mathbf{b^2}} + \frac{\alpha}{\mathbf{b^2}} + \frac{1}{\mathbf{j}\omega\frac{\mathbf{b^2}}{\kappa}}} = -\mathbf{YP} \qquad (\text{B.31})$$

We can now use these results to develop a single expression for each P and U. We first assume here that Z and Y have no x dependance. Plugging B.26 into B.31, we obtain

$$\frac{\partial^2 P}{\partial x^2} + \frac{1}{\ell^2}P = 0 \qquad (\text{B.32})$$

where $\ell = j\sqrt{1/ZY}$. This is just an expression for a traveling wave (the time dependance has already been effectively accounted for and this is the basic wave equation). So our result so far does allow for traveling waves (as we had hoped for). We get an analogous equation for U. Since we assumed $\ell = \ell(\omega)$ (and not $\ell(x,\omega)$), we can easily solve this to get $p(x,t)$. Allowing for both forward and backward traveling waves, we have

$$p(x,t) = P_1 e^{i(x/\ell+\omega t)} + P_2 e^{i(-x/\ell+\omega t)} \qquad (\text{B.33})$$

since $P(x,\omega) = P_1 e^{ix/\ell} + P_2 e^{-ix/\ell}$. The wavelength of the traveling wave will be given by $\lambda = 2\pi\ell$. When λ is purely real, this wave will travel decrement-free. However, imaginary parts of λ will cause a decay in the amplitude of the wave as it travels along (due to Z and Y, whose real and imaginary parts will always be positive for our system).

Comparison to Transmission Line Result

So we have developed a model based upon simple physical descriptions of our system which allows for traveling waves to propagate along the BM. Time was spent initially developing the dynamical equations for a transmission line and we see here that

our two results are analogous. Consider equations (B.5) and (B.6) in comparison to equations (B.26) and (B.31). Comparison of a simple case shows that these two pairs of equations are equivalent to each other. In the *loss-less* TL case, both R and G are identically 0. Thus γ is purely imaginary such that γ^2 is real and negative. Now consider the loss-less cochlea, where there is no damping or inertial terms (i.e. $\mu, \alpha = 0$). So we must have

$$\gamma^2 = -\frac{1}{\ell^2} \tag{B.34}$$

In comparing these two, we get

$$C \cdot L = \frac{b^2}{\kappa} \cdot \frac{2\rho}{A_{cs}} \tag{B.35}$$

So the capacitive term in the transmission line is analogous to the restorative spring term in the cochlea while the electrical inductance terms corresponds to a mass term. It is also easy to see that the resistive term R carries over to the damping term α.

It is interesting that our method for determining a model of the cochlea produced something which so closely quantitatively parallels the treatment of an electrical transmission line. A benefit gained is that results and insights into transmission line dynamics (which have been quite thoroughly developed) can potentially be used to provide insight back to the cochlear problem. For example, suppose we wanted to add a single pressure source at some point x_o along the cochlea (the reason will become more apparent later on when we discuss amplification). We can think of this being analogous to adding a single voltage source along the TL and being able to use a similar set of quantitative tools to describe the resulting behavior.

WKB Approximation

Unfortunately, some of the made assumptions were not too good for what happens in a real cochlea. For example, we know that BM stiffness and width changes along the length of the cochlea. So both α and b are functions of x and thus λ is as well. Since the wavelength changes along the cochlea, we will need to take a modified approach to obtain an expression for $p(x,t)$ [113].

In 1926, three authors (Wentzel, Kramers and Brillouin) independently published papers which approximated a wave function as an oscillatory wave depending upon a phase integral. This allowed for obtaining approximated solutions to the time-independent Schrodinger equation in one dimension [34]. If a particle with energy E is moving in a field of **constant** potential V where $E > V$, the wave function is given by

$$\psi(x) = Ae^{\pm jkx} \tag{B.36}$$

where $k \equiv \sqrt{2m(E - V)}/\hbar$. This is just a wave with constant amplitude A and wavelength $\lambda = 2\pi/k$. Now what if V was not constant, but varied slowly in comparison to λ (so that over a region containing many wavelengths, V is approximately constant)? The WKB approximation states that ψ will remain *practically* sinusoidal, but that the wavelength and amplitude will vary slowly with x. If we write k as $k(x) \equiv \sqrt{2m[E - V(x)]}/\hbar$, we get an approximate solution of the form [34]

$$\psi(x) \cong \frac{C}{\sqrt{k(x)}} e^{\frac{j}{\hbar} \int k(x)dx} \tag{B.37}$$

What is so useful about this result is that it can be applied to many other types of problems, such as describing light in a medium where the index of refraction is changing slowly or in our case, wave traveling along the cochlea.

If we assume that BM stiffness and scalae area changes rather *gradually*, then the cochlea could act as a uniform transmission line *locally*. Considering only forward traveling waves, our original solution had $P(x, \omega)$ in the form $P_o e^{\pm ix/\ell}$. So we can try a trial solution of the form

$$P(x, \omega) = A(x)e^{-j \int_0^x dx'/\ell(x', \omega)} \tag{B.38}$$

which is analogous to going from (B.36) to (B.37) in the quantum problem. We can substitute this back into the wave equation (B.32) to check its validity and determine the function $A(x)$. Since we assume that things vary gradually, we can assume that

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$\partial^2 A/\partial x^2$ is negligible and we have

$$\left[-\frac{2j}{\ell(x)} \frac{1}{A(x)} \frac{dA}{dx} - \frac{1}{\ell(x)^2} + \frac{j}{\ell(x)^2} \frac{d\ell}{dx} \right] + \frac{1}{\ell(x)^2} = 0 \tag{B.39}$$

This yields

$$\frac{1}{\ell(x)} \frac{d\ell}{dx} = 2 \frac{1}{A(x)} \frac{dA}{dx} \tag{B.40}$$

This is easily solved and shows that the amplitude will be proportional to the square root of the wavelength. Also note that propagation velocity is now going to vary as well. We can now derive a specific expression for $\ell(x,\omega)$, expanding out Z and Y. This yields

$$\ell(x,\omega) = j \left[\frac{j\omega L + R + 1/j\omega C}{j\omega M} \right]^{1/2} \tag{B.41}$$

Now we introduce some new variables. Let $\omega_r(x) \equiv 1/\sqrt{LC}$, $\beta(x,\omega) \equiv \omega/\omega_r(x)$, $\delta \equiv \omega_r(x)RC$ and $N \equiv (l/4)\sqrt{M/L}$. Here, $\omega_r(x)$ is just the local resonant frequency of a given spot along the length of the BM. In a human ear, this ranges from about 20 kHz at $x = 0$ to 20 Hz at $x = 35$ mm in a logarithmic fashion. The variable l is a constant which will be further described in the following section. With these variables, we can rewrite the wavelength as

$$\ell(x,\omega) = \frac{l}{4N} \frac{(1 - \beta^2 + j\delta\beta)^{1/2}}{\beta} \tag{B.42}$$

So we are thus able to now write the wavelength as a function of $\ell(\omega/\omega_r(x))$. The pressure variation at a given spot x_o depends upon the relationship between the stimulation frequency ω and the local resonant frequency $\omega_r(x_o)$. We can now use this expression for the wavelength to derive the BM transfer function.

Transfer Function

Making measurements of BM motion is difficult due to the cochlea being encased in a bony structure. Removing the bone to expose the cochlear aqueduct runs the risk of greatly degrading the viability of a living cochlea. However, careful measurements

have been made and take the form of comparing BM motion at different points along the cochlear length to that of the stapes. Thus we will develop an expression for the complex *transfer function*, given by

$$T(x, \omega) = \frac{\text{BM velocity}}{\text{stapes velocity}} \tag{B.43}$$

We can now use the WKB approximation (B.38) and our expression for the wavelength (B.42) to find $T(x, \omega)$. BM velocity is just given by $\partial d/\partial t$, which we can use equations (B.29), (B.31), (B.38) and (B.42) to obtain. Stapes velocity will be the scala vestibuli volume velocity at $x = 0$ divided by the area of the stapes (which we assume to just be A_v). Expanding this out, we have

$$\text{BM velocity} = \frac{e^{j\omega t}}{b} \ell^2(x, \omega) Y e^{-j \int_0^x dx'/\ell(x', \omega)} \tag{B.44}$$

We will get something similar for the stapes velocity, except that this will be evaluated solely at $x = 0$ and thus no integral will appear in the denominator. Thus it becomes apparent that we are going to need to solve for a specific expression of equation (B.38) using (B.42). For convenience, we will assume that N and l are constant with respect to x. We need to expand out our definition for ω_r since this is a function of position. Remember that this represents the local resonant frequency at a given point along the BM. Experimental evidence has shown that the tonotopic organization of the cochlea is logarithmic with higher frequencies at the basal end. Thus we can characterize this by

$$\omega_r(x) = \omega_{max} e^{-x/l} \tag{B.45}$$

where ω_{max} is the highest frequency which can be heard (at $x = 0$) and l is the distance along the BM which this characteristic resonant frequency changes by a factor of e (and is independent of x). Since we have $\beta = \omega/\omega_r$, we have

$$dx = \ell \frac{d\beta}{\beta} \tag{B.46}$$

Using this substitution, the integral to be evaluated can be written as

$$4N \int_0^x \frac{d\beta}{[1 - \beta^2 + j\delta\beta]^{1/2}} \tag{B.47}$$

This can be simplified even further by the substitution $u(x,\omega) = \beta(x,\omega) - j\delta/2$. If we assume that δ^2 term is negligible (the validity of which is physiologically reasonable), the expression reduces to

$$\int_0^x \frac{du}{\sqrt{1-u^2}} = \sin^{-1} u(x) - \sin^{-1} u(0) \tag{B.48}$$

Putting everything together, we can write a closed expression for the transfer function, given by [114]

$$\mathbf{T}(\mathbf{x}, \omega) \approx \mathbf{T_0 j}\beta(\mathbf{x}, \omega) \left[\frac{\omega_{\mathbf{max}}}{\omega_{\mathbf{r}}(\mathbf{x})} \right] \frac{\mathbf{e^{j4N\{sin^{-1}[\beta(x,\omega) - j\delta/2] - sin^{-1}[\beta(0,\omega) - j\delta/2]\}}}}{[\mathbf{1} - \beta^2(\mathbf{x}, \omega) + \mathbf{j}\delta\beta(\mathbf{x}, \omega)]^{3/4}} \tag{B.49}$$

Here, T_0 is a constant real coefficient. This equation now gives us a means to directly test the model, as we will show in the following section.

B.0.11 Model Comparison to Experimental Data

In the 1930's, Georg von Bekesy made important measurements in human cadaver temporal bones that showed the existence of traveling waves along the BM (for his extensive work in hearing, he was subsequently awarded the Nobel prize for Physiology or Medicine in 1961). It was however not until 1971 when measurements made by Bill Rhode in a living squirrel monkey using the Mossbauer technique showed strongly non-linear behavior such as compressive growth [Rhode, 1971]. This indicates some source of nonlinearity inside living ears (haven taken into account the nonlinear nature of the Mossbauer technique). This data from Rhode was used as the basis for an *inverse* model proposed by the physicist George Zweig that argues that the cochlear impedance exhibits a region where the real part becomes negative (*i.e. amplification*) [Zweig, 1991]. It is these results from Rhode which we will use to compare the model
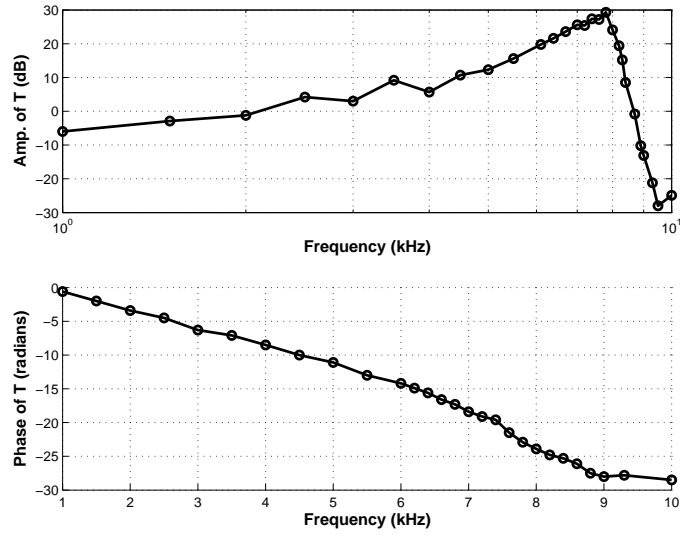
Figure B-5: Data obtained by Rhode from a single squirrel monkey. The transfer function T here is shown as BM motion relative to the stapes. Imaging was done at one specific place while frequency was swept. [Rhode, 1971]

to. Data from a single monkey is shown in Fig.B-5.

The transfer function of the model has the following free parameters which we will have to adjust to get the best possible fit (as well as constrain to stay within physiological bounds if the model is to work!): T_0, N and δ. It appears that the resonant frequency ω_r (or center frequency, CF) at the place the measurements were made is approximately 7.8 kHz. Using the mapping given by equation (B.45) where $\omega_{max}/2\pi \approx 50$ kHz and $l \approx 5$ mm for the squirrel monkey, we have $x \cong 9$ mm. Reasonable physiological values for N and T_0 have an order of magnitude of 10^0 and δ is around 10^{-1}. Optimizing these values within that range, we obtain a fit to the data as shown in Fig.B-6. The fit is quite reasonable considering the number of simplifying assumption which were made. However, higher frequencies are not well covered as the amplitude falls off much more quickly. Additionally, there is a dip in the phase not seen in the actual data. We can also make a plot of the wavelength λ (B.42). Figure B-7 has two parts: one at $x = 9.25$ mm and frequency varied (top) and the other with frequency fixed at $\omega = 7.8$ Hz. The real part of λ gives the physical wavelength while the imaginary part give the inverse of the damping constant. Below the CF, λ is purely real and the result is a traveling wave propagating unperturbed.
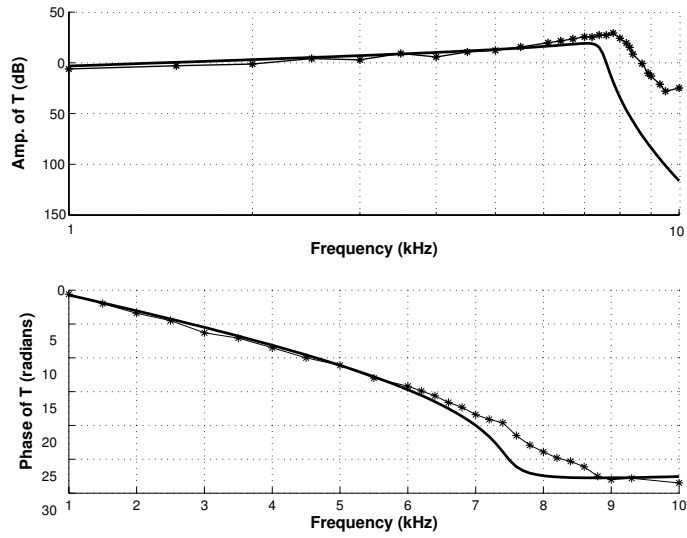
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Figure B-6: Fit to Rhode's data using the transfer function given in equation (B.49). The model fit is the bold solid line. The fitting parameters used are $\delta = 1/40$, $T_0 = 2$, $N = 5$ and $x = 9.25$ mm.
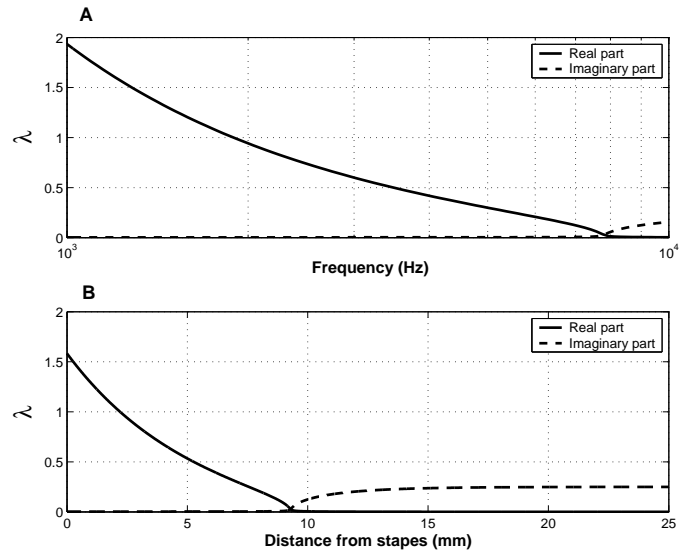

Figure B-7: **A**. The real and imaginary parts of the wavelength $\lambda(x, \omega)$. Here, x is held constant at 9.25 mm. **B** Similar to above, but ω is held constant at the CF $2\pi \cdot 7.8$ kHz.
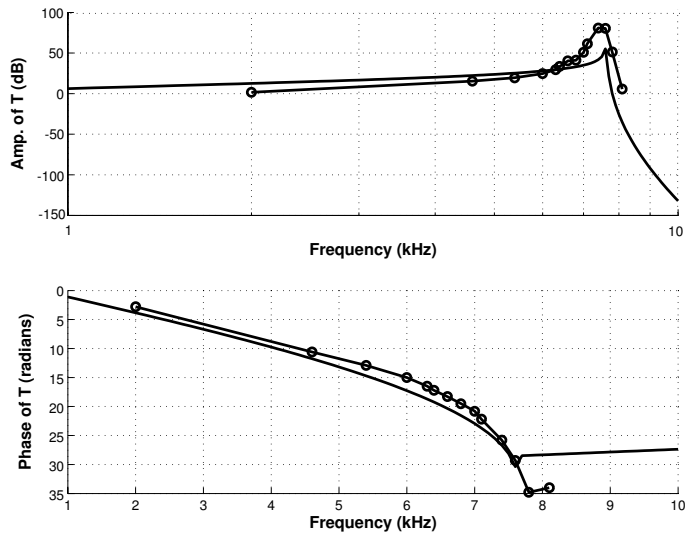
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Figure B-8: Fit to Rhode's data extrapolated to lower sound levels ([114]). The fitting parameters used are $\delta = 1/5000$, $T_0 = 6$, $N = 6$ and $x = 9.4$ mm.

However, as you come closer to the CF, the imaginary part starts to increase from zero, causing the wave to damp out. Above the CF, λ is purely imaginary and there is only damping and no wave propagation.

Presumably, cochlear amplification is most prevalent at low sound intensities. At higher levels, this amplifier is effectively turned down (or washed out), thereby causing compressive (*i.e.* nonlinear) growth observed in a number of different measurements. Rhode's data presented in Fig.B-5 were likely taken at higher intensities (70-90 dB SPL). The data has subsequently been extrapolated to lower levels near threshold [Zweig, 1991], which we can further use to test our model. This fit to the new data is shown in Fig.B-8.

The fit is decent, though we had to push δ beyond the physiological range. Since this term relates to damping combined with the model's peak being much smaller at CF, this implies that there is some active mechanism which is adding energy into the system. It should also be noted that the peak in the model is much narrower than the experimental data. This may stem from the fact that when using the WKB approximation, we assume that the wavelength and amplitude vary slowly compared to x. This is probably not true in the region around the CF where amplification is likely to occur.

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B.0.12   Conclusions

While we have seen that this simple model model works reasonably well in comparison to experimental data, the model is insufficient to capture all the features observed in the ear. Most notably (albeit not shown here), the model is entirely linear, which we know the ear not to be. And while the model can account for responses in a *dead* ear, it does not exhibit the features seen in a living, healthy ear (such as sharp tuning and large phase delays).

A logical next step in the model would be to include features which would account for *active amplification* mechanisms that have been proposed to exist in the ear. These could take the form of pressure sources distributed along the length of the cochlea. This effectively could describe *feedback* mechanisms which could arise from possible generators such as OHC motility or stereociliary bundle/transduction channel dynamics. A good starting point would be to model these with delta functions and work out the transfer function with these additional terms to see if the model predictions better match the data. A further step would be to try to model these active elements more as physiological entities rather than lumped elements. This would allow for the model to make better predictions about what the possible amplification mechanisms are and the significance of their roles.

Differences between data and model aside, this simple view has given us considerable insight into the function of the inner ear. In responses to sound pressure (propagated through the external and middle ears to the cochlea), traveling waves are set up that propagate energy thru the cochlea to its characteristic place (analogous to an electric transmission line). This conclusion stems from a few simple physical laws as well as basic knowledge about mammalian cochlear anatomy (*i.e.* a flexible membrane with graded mass/stiffness, *etc.*). It is interesting to ask whether this simple physical description is valid in the non-mammalian ear, where inner ear anatomy differs greatly.

One final point to emphasize here: the model described here, while fairly simple, borrowed from a number of different flavors of science such as electro-dynamics,

quantum mechanics and physiology. It is in this regard that the study of hearing (or most of biology for that matter) is truly a multi-disciplinary science, making it so engaging and challenging.