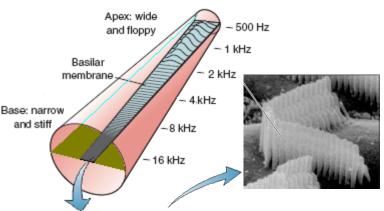
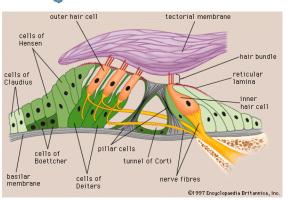
Viscous damping of acoustic resonance with a restricted zone of wall compliance





The Basilar Membrane (BM) and Organ of Corti still challenge our physiological understanding. The motility of Outer Hair Cells (OHC) is thought actively to cancel viscous energy dissipation, thereby allowing highly resonant frequency selectivity at the BM. But OHC motility could serve other functions as well, or instead, e.g.:

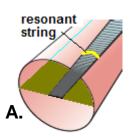
- Modulation rather than cancellation of viscous damping
- Reduction of resonant after-effects following brief transients
- Selection of optimal vibration modes
- Direction of energy flux to optimal sites
- Induction of flow in subtectorial space to stimulate IHCs*
- Circulation of fluid to clear the subtectorial space

This demonstration suggests that viscous damping may not in fact limit frequency selectivity as usually accepted following Gold (1948). If this is correct, then pursuit of other ideas about possible OHC functions become more interesting and challenging.

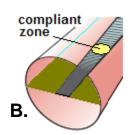
[[]top: after Bear & Paradiso: Neuroscience: Exploring the Brain (2006) bottom: (c) Encyclopedia Britannica 1997]

^{*} cf Novotny & Gummer (2006) PNAS 103, 2120-2125.

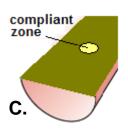
Gold's model for estimating viscous damping was like a piano string under water.



The model here is a compliant circular zone of membrane between two rigid chambers.



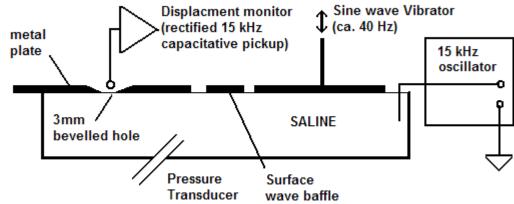
With symmetrical chambers, this is equivalent to a compliant zone between fluid and air.



Apparatus for studying resonance of a compliant circular fluid surface

(ca. cochlea x 10 scale)

A vibrator applies pressure fluctuations to the chamber. Movements of the fluid surface in a circular hole in a metal plate are measured by capacitative coupling to a ball electrode above the surface.



The compliance here is produced by surface tension at the interface. A stiffer surface membrane would produce a higher resonant frequency.

What is of interest is not the resonant frequency, but the time constant for dissipation of the energy of resonance.

This time constant is proportional to the area of such a zone and inversely to the fluid viscosity (from simple dimensional considerations). It depends on the spatial pattern of compliance and fluid flow, but not on the magnitude of the compliance, or resultant resonant frequency.

The flow pattern in the apparatus undoubtedly differs from that in the cochlea. But the time constants achievable with a 10x smaller cochlear zone must be able, with optimal profiling, to have at least as great a time constant as that inferred from scaling the results here (dividing the observed time constant by70, for the 100x reduction of area and 30% lower viscosity at 37degC).

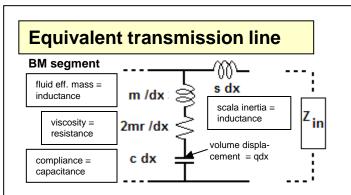
Scaling

The resonance characterisitcs depend on the radius R (m), viscosity η (kg.m⁻¹.s⁻¹), fluid density ρ (kg m⁻³), and surface tension T (kg s⁻²). Both the kinetic energy of fluid movement and the viscous energy dissipation for a given pattern of laminar flow vary in the same way with frequency and amplitude of the movement, so the ratio (the time constant τ for dissipation) is independent of these, inversely proportional to η (kg.m⁻¹.s⁻¹) and for dimensional consistency therefore proportional to η -1 ρ R².

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Transmission on an array of resonators, coupled by pressure & inertia in the scalae



 $\mathbf{q} = \text{vol displaced / unit length} : m^2 [\equiv C/m]$

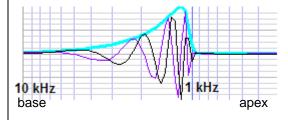
 $\mathbf{c} = \text{compliance} = \mathbf{q} / \text{pressure} : m^2 / \text{Pa} [\equiv F / \text{m}]$

m = generalised mass for transverse flow

= 2 energy / $(dq/dt)^2$: kg m⁻³ [\equiv Hm]

 \mathbf{s} = series mass = 2 energy / flow² : kg m⁻⁵ [\equiv H/m]

 \mathbf{r} = rate constant for resonance decay : s^{-1} [$\equiv \Omega/H$]



Travelling waves on a resonant line:

Here the cochlea was simulated as a passive resonant transmission line with 100 elements (resonant frequencies 10-0.1 kHz), stimulated at 1 kHz. The time constant for resonant amplitude decay was set uniformly at 2 ms (r=0.5 ms⁻¹).

Resonant (ang) frequency $\Theta = 1/\sqrt{(mc)}$ Velocity for ang freq $\varpi = \sqrt{((1-\varpi^2/\Theta^2)/sc)}$ Wavelength = $2\pi \sqrt{((1/\varpi^2 - 1/\Theta^2)/sc)}$ Note how both wavelength and velocity of the wave, travelling from the base, decrease near the resonant point. Nearly all energy is lost beyond this point. 76% was actually absorbed before it reached the point of maximum response, and 99% before the point of maximum resonant sensitivity.

These travelling wave effects are due largely to the combined effect of the series inertia (s) and BM compliance (c) rather than viscosity.

If OHCs were to act to stiffen the BM at frequencies below its local resonance, much of this energy loss could be eliminated.

Three ways of assessing viscous energy dissipation

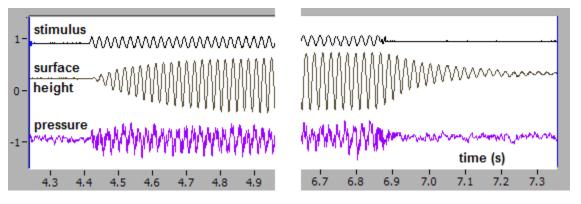


Fig. 1. Time course of build up and decay of the resonant response. The sinusoidal displacement of the fluid surface at the resonant frequency (43.4 Hz) takes about 150 ms to build up and to decay to 1/e (37%). This corresponds to a time constant ca. 2ms for a zone 10x smaller (radius 0.15 mm) at 37 degC. Note that the measured pressure changes build up and decay almost immediately. Note that the time constant for energy disspation is half that for amplitude decay.

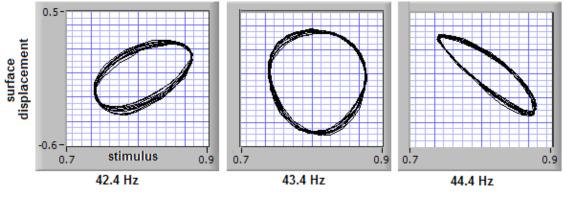


Fig. 2. Response (surface displacement) plotted against stimulus (volts applied to vibrator) at the resonant frequency and \pm 1 Hz. This range corresponds approximately to the 3dB 'bandwidth', as evidenced by \pm 45° phase shifts and amplitude reduced to $1/\sqrt{2}$ (energy one half, -3dB). **2Hz bandwidth** corresponds to **Q=22**, time constant for amplitude decay = **160 ms**.

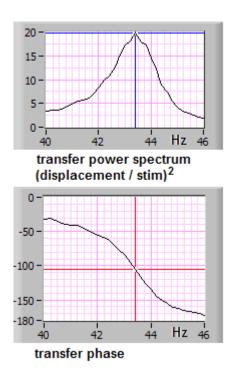


Fig. 3. The full frequency spectrum of the resonance is shown here, derived from a slow scan changing frequency from 35 to 50 Hz over 10s. The 3dB (half energy) points are 42.3 Hz and 44.4 Hz, corresponding to a bandwidth of 2.1 Hz, Q = 21, time constant for amplitude decay = 152 ms. The equivalent time constant at the cochlea, scaled down 10x to 0.3mm diameterand at 37°C, is 2.2 ms.

Implications for the Cochlea

The time constant of amplitude decay (ca. **152 ms** for a 3mm diameter zone at 20°C), would correspond at the cochlea (37°C), for a circular zone equal in diameter to a BM width = **W mm**, to a time constant of **24 ms x W**². This yields a resonance bandwidth (3dB below maximum energy) of **0.013 W**⁻² **kHz**.

This bandwidth, calculated for the two ends of the guinea-pig cochlea (basal **W=0.1-0.12 mm**, apical **W=0.24-0.34mm**: Greenwood, 1952), is here superimposed on a Figure from Moore (2003) and Evans (1989) showing Equivalent Rectangular Bandwidths (ERB) inferred from both behavioural and neural data for the guinea-pig. The limit on frequency selectivity inferred from viscous damping in the observed model, not even optimised for frequency selectivity, is consistent with most of the data: few measurements have a narrower bandwidth.

Though the Organ of Corti may increase or decrease damping compared with this crude model, it is hard to maintain that frequency selectivity is fundamentally inconsisent with passive viscous damping.

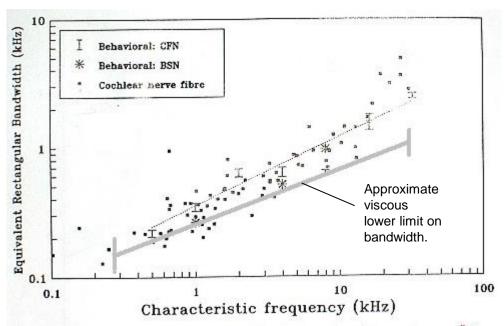


FIGURE 3.13 A comparison of ERBs estimated from behavioral masking experiments and from neurophysiological measurements of the tuning curves of single neurons in the auditory nerve. All data were obtained from guinea pigs.

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ABSTRACT:

Viscous damping of acoustic resonance with a restricted zone of wall compliance

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The basis of cochlear frequency analysis lies in the compliance of the basilar membrane, separating two fluid chambers that are subjected to acoustic pressure differences. Modelling of the viscous damping associated with resonances in this structure (Gold, 1948) has led to the widely accepted conclusion that passive resonance could not be sharp enough to be consistent with psychophysical and physiological measurements. Active mechanisms (capable of generating force) associated with outer hair cells may therefore be critical in the establishment of sharp resonance. Though this account may be correct, it is not the only way in which active mechanisms could be relevant to acoustic function of the cochlea. For example, they could modulate rather than cancel the viscous damping, they might limit the resonant after-effects of brief transients, or they might somehow act to restrict and concentrate the energy absorption of the Organ of Corti in zones where it will have greatest effect.

Gold's model was based on calculations treating a zone of the basilar membrane as analogous to a piano string immersed in water. An alternative is to consider a portion of the basilar membrane (responsive to a particular frequency), as a small compliant zone of the wall separating two chambers with otherwise relatively rigid walls. This begs the question of in what sense, or perhaps by what active mechanism, the rest of the basilar membrane could be considered rigid for the purposes of analysing the dynamics of a single zone, but it provides an alternative model for analysing the ultimate constraint that viscosity places on the sharpness of resonance in a cochlear structure.

The model adopted here considers a circular compliant zone of membrane of radius R and zero mass, with a relatively large chamber on each side subjected to distant pressure variation. Resonance involves alternating transfer between potential energy associated with extension of the compliant membrane and kinetic energy (KE) of fluid movement towards and away from the membrane. The KE and viscous dissipation are both mainly in fluid within a radius of the membrane, where velocities are highest. Measurements with ×10 scale models and calculations with simplified flow patterns suggest that the time constant (T) for energy loss with a compliant zone of radius R=0.1mm can exceed 2ms (yielding for example a 3 dB resonance bandwidth equal to 4% of a center frequency f = 2 kHz, Q3dB = 2pfT = 25). The value of T due to viscosity scales with R2/K (where K=kinematic viscosity, ca. 0.7×10^{-6} m2/s at 37oC). With plausible dimensions this would appear to be able to account passively for frequency selectivity substantially greater than is inferred at any frequency from physiological and psychophysical data (Moore, 2003). A key issue would be how energy could be directed to optimal vibration modes for maximum sensitivity and selectivity.

Gold T (1948). *Proc R Soc Lond B Biol Sci* 135, 492-8 Moore BCJ (2003). *An Introduction to the Psychology of Hearing, 5th ed.*, Elsevier (USA)