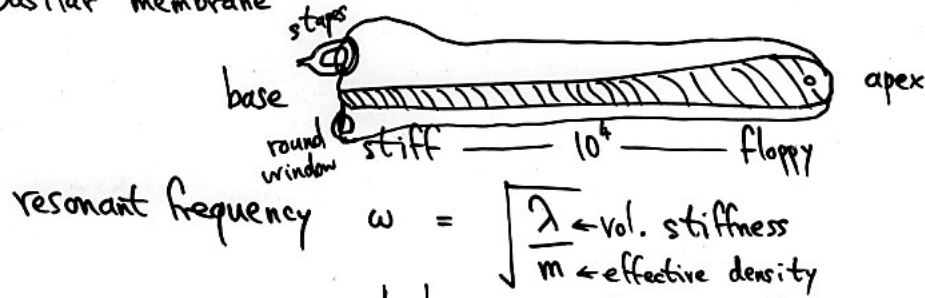


Mode conversion in the cochlea?

R. S. MacKay

• Anatomy of the ear : pictures

• Basilar membrane

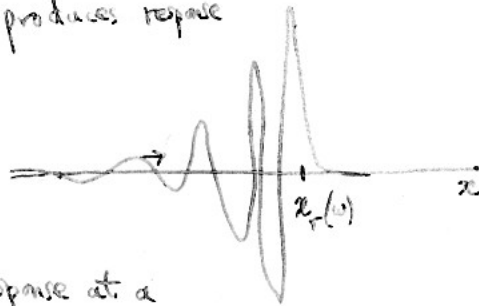


resonant frequency $\omega = \sqrt{\frac{\lambda \leftarrow \text{vol. stiffness}}{m \leftarrow \text{effective density}}}$

high 10³ low

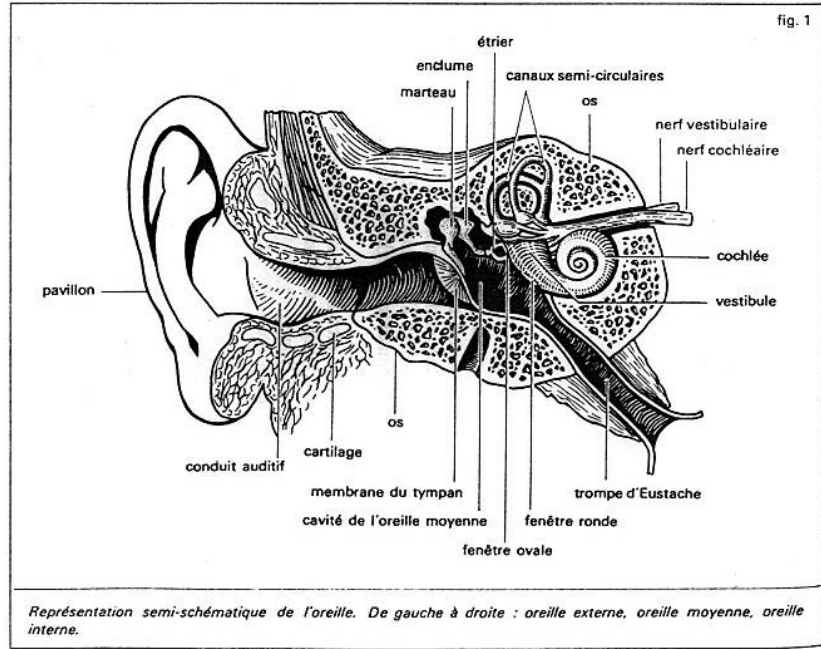
• inner hair cells transduce movement into neurd signals
 Travelling wave frequency $\omega \rightarrow$ place $x_r(\omega)$

Forcing at frequency ω produces response



Inferred by measuring response at a given x to forcing at a range of frequencies : picture

• Nonlinearity e.g. compressive maximum response : picture



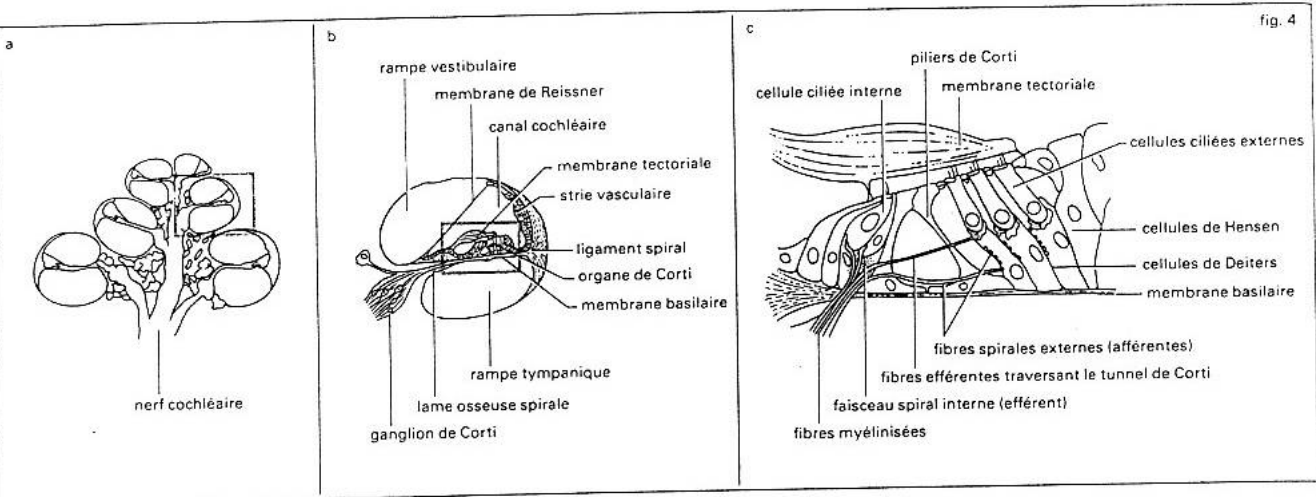


fig. 4

La cochlée : en a, coupe de la cochlée suivant l'axe (modiolus); en b, coupe transversale du tube cochléaire; en c, détail de l'organe de Corti.

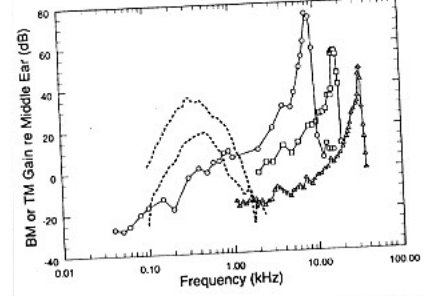


fig. 6. Maximum gains of BM or TM responses, relative to middle-ear vibration, from basal and apical cochlear sites. Basal BM responses to low-level tones have been normalized to responses of the incus (guinea pig and cat) or the stapes (chinchilla). The TM data for the chinchilla apex, normalized to the vibrations of the umbo of the tympanic membrane, were selected to indicate the range of sensitivities. Chinchilla base (circles): CF = 8.4 kHz, data from Ruggero et al. (328); Chinchilla apex (dashed lines): CF = 0.25–0.5 kHz, data from Rhode and Cooper (299); guinea pig (squares): CF = 17 kHz, data from Selick et al. (360); cat (triangles): CF = 30 kHz, data from Cooper and Rhode (47).

frequency well below CF grow linearly with stimulus intensity and, appropriately, response phases at those frequencies are invariant with respect to stimulus intensity. At near-CF stimulus frequencies, response magnitudes grow nonlinearly, and phases vary systematically

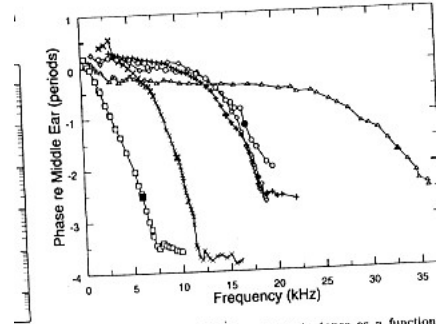


fig. 7. The phases of BM responses to tones as a function of frequency. The phases of BM displacement toward scala tympani expressed relative to inward ossicular displacement. The data were obtained at basal sites of the cochlea of squirrel monkey, chinchilla, guinea pig, and cat. CFs are indicated by closed symbols. Guinea (diamonds): data from Sattali and Dolan (259); guinea pig (circles): data from Selick et al. (360); chinchilla (X): CF = 0.7 kHz, data from Narayan et al. (320); chinchilla (crosses): CF = 15 kHz, data from Rhode (293); squirrel monkey (squares): data from Rhode (293); cat (triangles): data from Cooper and Rhode (47).

Critical layer resonance e.g. Peterson & Bogert, 1950

Suppose fluid motion is 1D



Mass conservation: $\frac{\partial a}{\partial t} = \frac{\partial j}{\partial x}$

Horizontal momentum: $\sigma \frac{\partial j}{\partial t} = -\frac{\partial p}{\partial x}$

$\sigma = \frac{\rho_1 + \rho_2}{A_1 A_2}$

So $\frac{\partial^2 a}{\partial t^2} = -\frac{\partial}{\partial x} \frac{1}{\sigma} \frac{\partial p}{\partial x}$

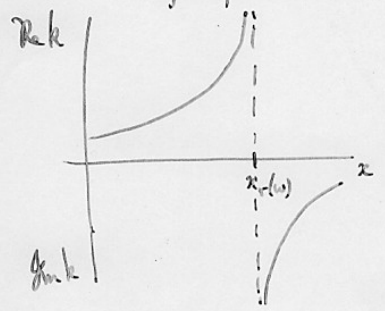
Vertical momentum: $m \frac{\partial^2 a}{\partial t^2} = -p - \lambda a$

So $(\lambda + m \frac{\partial^2}{\partial t^2}) \frac{\partial}{\partial x} \frac{1}{\sigma} \frac{\partial p}{\partial x} = \frac{\partial^2 p}{\partial t^2}$

If λ, m, σ constant, get dispersion relation $k^2 = \frac{\sigma \omega^2}{\lambda - m\omega^2}$

But $\lambda(x)$ decreases, m, σ roughly constant, so for given ω
 $k(x) \rightarrow \infty$ at $x_c(\omega)$ and is imaginary afterward.

A place x where $k^2(x)$ goes through 0 is called a "critical layer resonance"



Booker & Bretherton 1967
 Budden 1955

Equation is singular at x_c , but addition of infinitesimal damping regularises it and shows that incident wave energy is totally absorbed there.

e.g. group velocity $c_g = \frac{(\lambda - m\omega^2)^{3/2}}{\lambda \sigma^{1/2}} \rightarrow 0$ as $x \rightarrow x_c$

and travel time $t = \int \frac{dx}{c_g} \propto \frac{1}{\sqrt{x_c - x}} \rightarrow \infty$

Actually WKB fails near the critical layer, but conclusion is correct

Show pictures for affine impedance
 exponential impedance

Actually 1D fluid motion fails when $kh \approx 1$, so have to replace $\omega^2 a = -\frac{k^2}{\sigma} p$ by $p = -\frac{\sigma \omega^2 h}{|k|}$, so

$|k| = \frac{\sigma \omega^2 h}{\lambda - m\omega^2}$ and then WKB is uniformly

good for $\beta \ll h$, $\beta = \frac{\lambda'}{\sigma \omega^2}$

but amplitude and phase profiles change a bit.

Also, there are damping processes and active processes (outer hair cells), so amplitude profiles can change more and phase profiles somewhat.

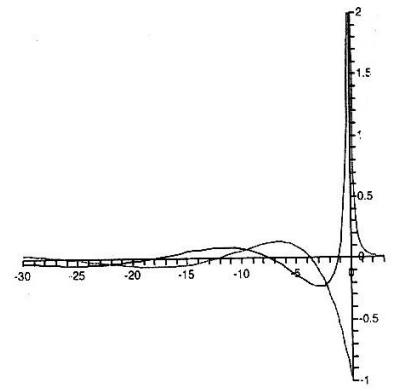


Figure 1: Graph of $a(x)$ for some solutions of (6), plotted against $X = \frac{x - x_c(\omega)}{\beta}$.

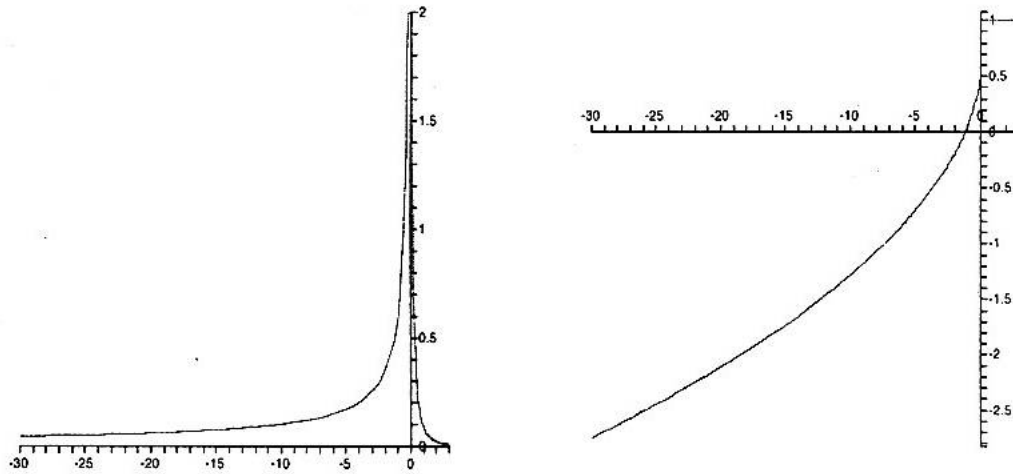


Figure 2: Amplitude $A(X)$ and scaled phase $\phi(X)/\pi$ for the affine impedance critical layer model.

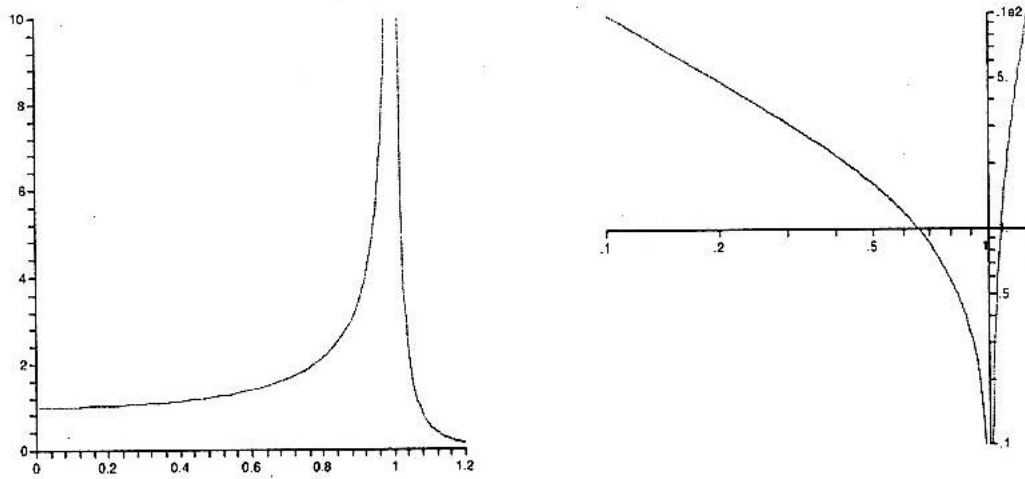
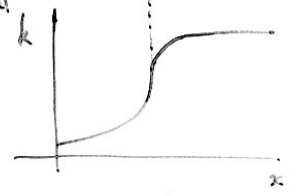


Figure 3: Exponential model with $\frac{\alpha^2 m}{\sigma} = 1/4$ (REDO for $1/40!$): (a) Amplitude $|a|$ of response at a given place x to forcing of a given energy flux, as a function of scaled frequency $\frac{\omega_w}{\omega(x)}$, with $\omega(x)$ being the resonant frequency at x ; (b) a tuning curve.

Inadequacies of critical layer models

① Even with 3D fluid flow, damping, active processes, it seems impossible to simultaneously make amplitude and phase profiles match experiment.
 In particular, phase $\phi \rightarrow \infty$ and $k = \frac{2\phi}{2x} \rightarrow \infty$.

② Longitudinal stiffness is ignored. Even if small, it would make $\lambda - m\omega^2 = \left(\frac{\sigma\omega^2}{k^2} - \frac{\sigma\omega^2 h}{|h|}\right) \rightarrow \propto k^4$
 so:



If damping removes most energy before wave discovers plateau then maybe irrelevant, but damping is observed to be very small (at low amplitude) — effect of active processes

③ If the active processes make net damping negative, then critical layers turn into emitters rather than absorbers
 2 & 3 are symptoms of the "structural instability" of critical layer models — not robust to small changes in the model

④ Kemp's echo: a sound coming out of ear at a well-defined frequency in response to a click: picture

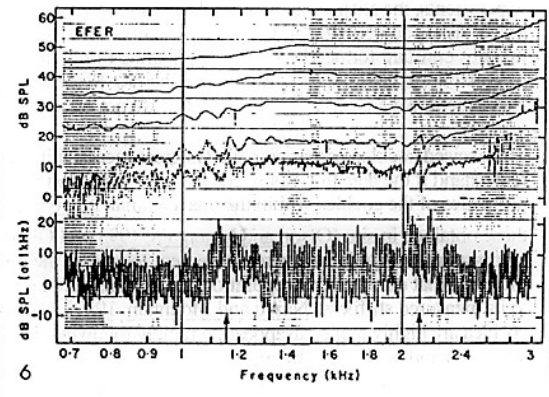
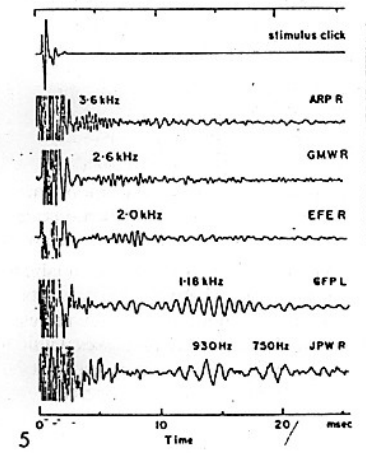
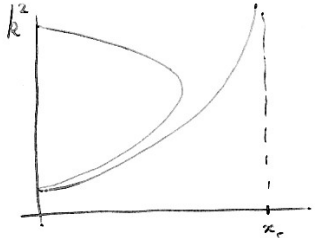


Fig. 5. Cochlear echoes in five ears in response to click stimulation. Note the differing frequencies of re-emission and their differing latencies to peak response. (From Wilson, 1980b).

• Mode conversion

Instead of a zero in $k^2(x)$, suppose a turning point ($\neq 0, \infty$)



Note: zero in $k^2(x)$ is well known "cutoff"

Then the group velocity has opposite sign on the 2 branches, and a wave coming in on lower branch turns round and comes out on the other branch: "mode conversion"

Stix 1965: $\eta p^{(4)} - X p'' + p = 0 \quad \eta > 0$

dispersion curve $X = -(\eta k^2 + \frac{1}{k^2})$

fold at $X = -2\eta^{1/2}, k = \eta^{-1/4}$

Plot $a \propto p''$

Amplitude and phase plots

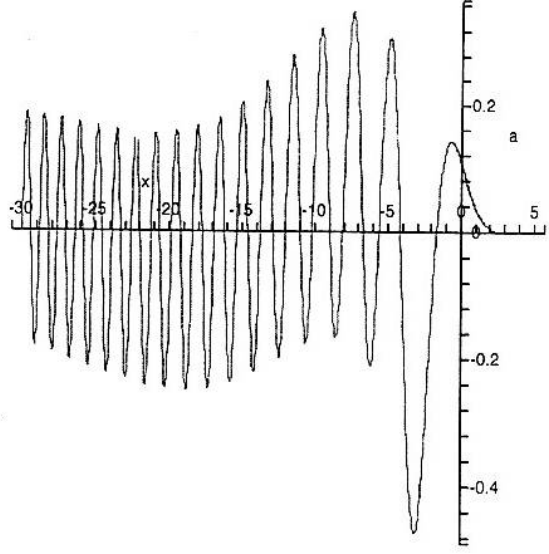


Figure 5: $a(X) \propto p''(X)$ for a solution of (12) for $\mu = 1$.

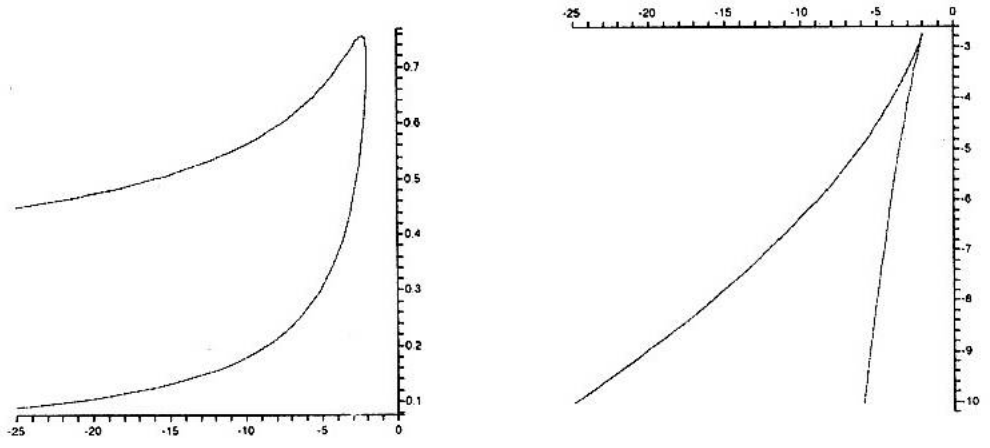


Figure 6: Amplitude $|a|$ and scaled phase $\phi/\eta^{1/4}$ of oscillation as functions of $X/\eta^{1/2}$ for the WKB approximation of (12). The long-wave mode has the lower amplitude and shallower phase curve.

Remarks: • No singularity at fold

• Conserved wave energy flux

$$\Phi = \int_{\text{in}} (\eta p^4 \bar{p}^{(2)} - p \bar{p}^i)$$

associated to Hamiltonian formulation

$$H = \frac{1}{2} (\eta |p^{(2)}|^2 - \chi |p|^2 + 2 \operatorname{Re}(p \bar{p}^i) - |p|^4)$$

$$\omega(p, q) = \int_{\text{in}} (\eta p^4 \bar{q}^{(2)} - p \bar{q}^i)$$

and phase rotation symmetry

If suppose short wave mode is damped or averaged away by measurements then this could fit observed behaviour, especially phase, since get a minimum wavelength $2\pi \eta^{1/4} > 0$.

Need to incorporate 3D fluid flow effects, and to propose physiological origin for $\eta p^{(4)}$.

Actually, Hurley proposed mode conversion in 1969, without the theory, and suggested two physiological origins. I propose outer hair cell active feedback

force
$$-\frac{\partial^2}{\partial t^2} \frac{\partial}{\partial x} \nu \frac{\partial a}{\partial x}$$

(in addition to cancelling damping on lower branch)

This gives dispersion relation (in 1D flow approx.)

$$\nu \omega^2 k^4 - (\lambda - m\omega^2) k^2 + \sigma \omega^2 = 0$$

so a fold where $\lambda(\omega) = (m + 2\sqrt{\nu\sigma}) \omega^2$

wavenumber
$$k = \left(\frac{\sigma}{\nu}\right)^{1/4} \omega$$

2nd derivative in x , because net force and longitudinal torque by OHCs must be zero

2nd derivative int, because Mammano & Nobili claim "inertial reaction of tectorial membrane makes the triggering mechanism of the OHCs increase as the square of the frequency" (1993)

Also because would get instability otherwise:

$$\frac{\partial^2 a}{\partial t^2} = -\frac{\partial}{\partial x} \frac{1}{\sigma} \frac{\partial p}{\partial x} \Rightarrow \omega^2 = \frac{\lambda k^2 - K k^4}{\sigma + m k^2}$$

$$m \frac{\partial^2 a}{\partial t^2} = -K \frac{\partial^2 a}{\partial x^2} - \lambda a - p \quad < 0 \text{ for large } k$$

↑ (negative to get fold in dispersion curve)

whereas
$$m \frac{\partial^2 a}{\partial t^2} = -\nu \frac{\partial^2}{\partial t^2} \frac{\partial}{\partial x} \nu \frac{\partial}{\partial x} - \lambda a - p \Rightarrow \omega^2 = \frac{\lambda k^2}{\sigma + m k^2 + \nu k^4}$$

• Time-domain (8)

To treat stability properly, address impulse response and nonlinearity, it is best to switch from frequency to time-domain

Pictures of impulse response (+ recall Kemp echo)
 more Kemp echo
 tinnitus

Formulation as time-evolution: e.g. 1D flow, no OHC force

Given profile a of basilar membrane and deflection v of oval window (stapes) (measured as volume displaced),

solve:

$$\begin{cases} m \frac{\partial}{\partial x} \frac{1}{\sigma} \frac{\partial p}{\partial x} - p = \lambda a, & \text{subject to} \\ p + \frac{\rho}{\sigma_0} p' = 0 & \text{at } x = x_h \text{ (apex) (helicotrema)} \\ A p - \frac{M}{\sigma_0} p' = -\mu v + F & \text{at } x = 0 \text{ (base) (stapes)} \end{cases}$$

Then evolve a and v by

$$\begin{cases} \frac{\partial^2 a}{\partial t^2} = -\frac{\partial}{\partial x} \frac{1}{\sigma} \frac{\partial p}{\partial x} \\ \frac{\partial^2 v}{\partial t^2} = -\frac{1}{\sigma_0} p'(0) \end{cases}$$

cf. water waves

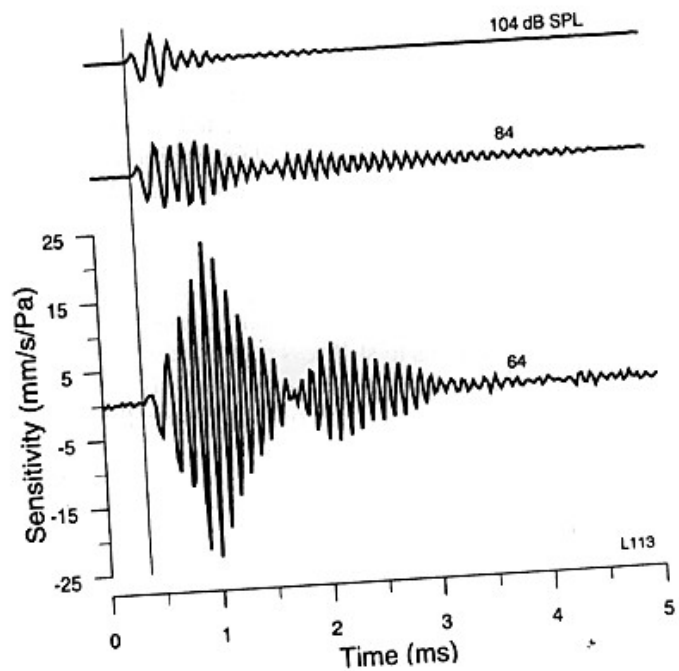


FIG. 9. BM responses to rarefaction clicks. The response waveforms, recorded at a basal site of the chinchilla cochlea, are displayed with a uniform scale of sensitivity (velocity per unit pressure). The thin vertical line indicates the onset of vibration of the middle-ear ossicles. Positive values indicate velocity toward scala vestibuli. Peak stimulus pressures (in dB/20 μ Pa) are indicated above each trace. [Data from Recio et al. (290).]

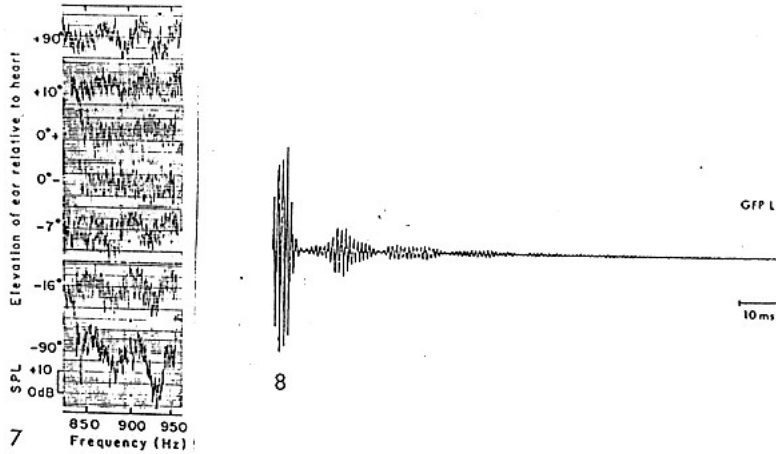


Fig. 7. Békésy audiograms showing fine-structure, with body tilt as parameter. This changes the hydrostatic pressure on the stapes and thereby its acoustic impedance. Near the horizontal position the ripples disappear indicating absence of internal reflection and near-perfect impedance matching. (From Wilson, 1980b).

Fig. 8. Using a short (4 waves at left) tone burst tuned to the ear's optimal frequency of re-emission, the echo is comparable with the stimulus amplitude and multiple reflections can be seen. Tinnitus and spontaneous emission commenced shortly after this record was taken. (From Wilson & Sutton, 1981)

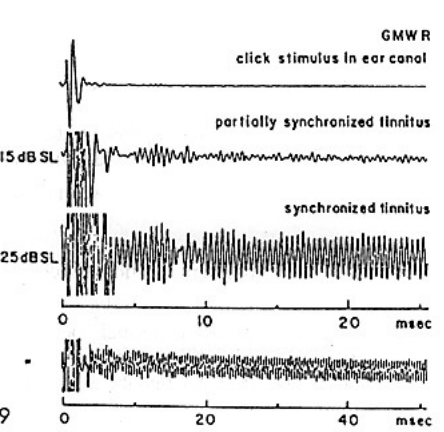
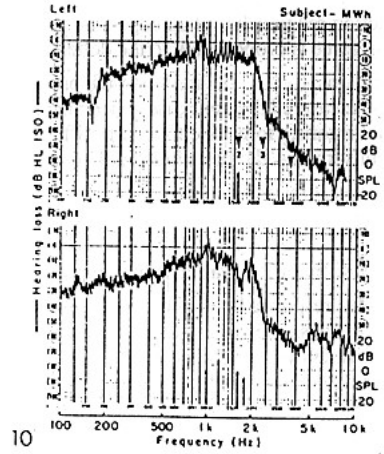


Fig. 9. A stimulus click 15 dB above subjective threshold partially synchronizes a spontaneous emission as indicated on an averaged response: at 25 dB above threshold the emission is fully synchronised (i.e. phase-locked) to the click. (From Wilson, 1980b).

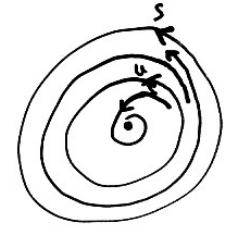


10

So expect a continuous spectrum (because critical layer allows any frequency to fit best) plus an eigenvalue.

Eigenvalue could be the frequency of impulse response, Kemp echo and tinnitus!

Also of spontaneous otoacoustic emissions (picture)
 Idea is that OHCs cancel damping, ~~so~~ so thermal noise gets a resonant response at eigen mode, and if OHCs overdo cancellation, can get a Hopf bifurcation to oscillation at this mode. Wilson's pictures suggest actually subcritical, requiring a threshold stimulus



Lots more to do:

(16)

- Inclusion of mode conversion term makes spectrum discrete, but closely spaced (need 2 more bcs)
- Predict impulse response, esp. 2-lobed waveform
- Explain impedance oscillations with frequency (picture)
- Formulate nonlinear WKB for prediction of effects of nonlinearity e.g. compressive peak
 - 2-tone suppression & variants
 - combination tones
 - nonlinearity of otoacoustic emissions