# Mechanics of hearing

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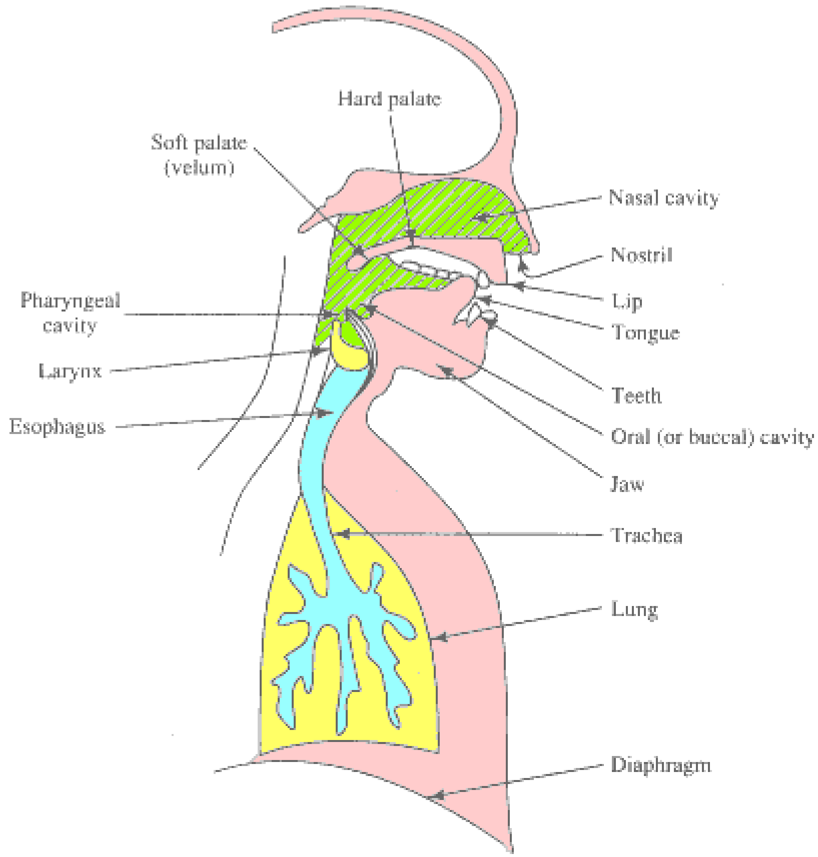
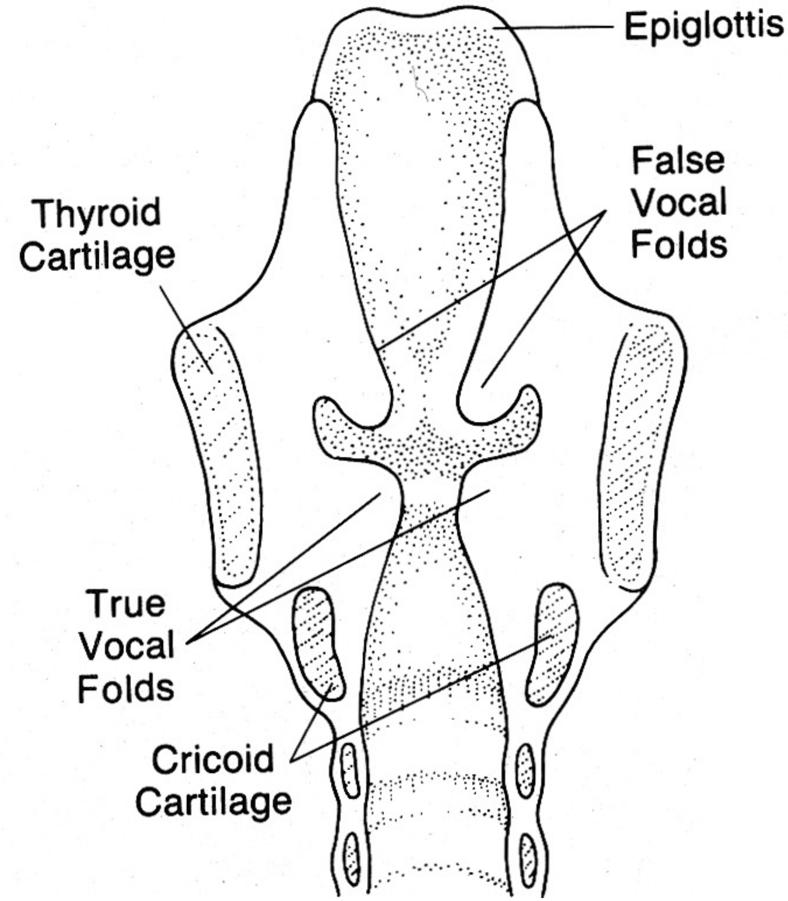
***Istituto Veneto di Medicina Molecolare (VIMM)***

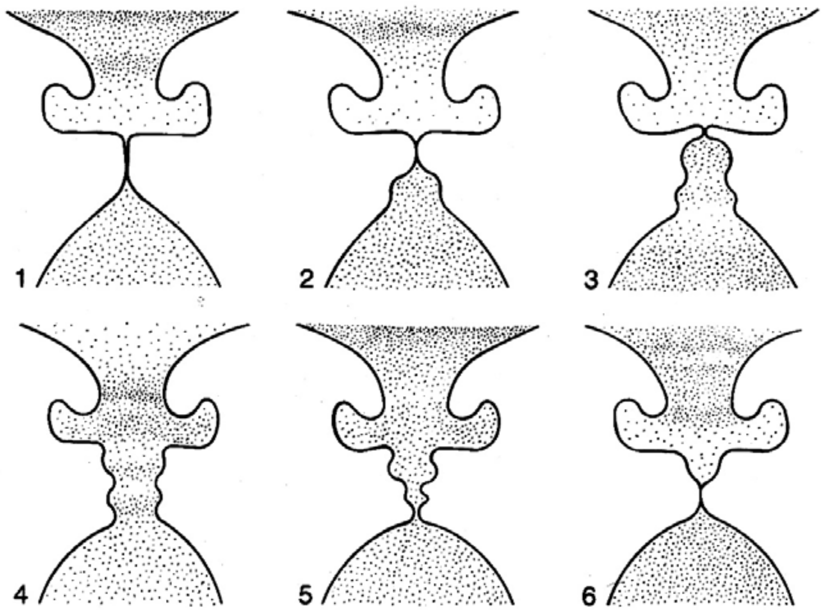
***UNIPD***

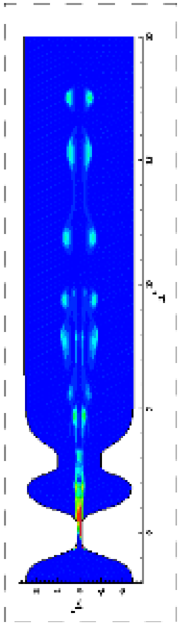
# Human communication: the organs of speech

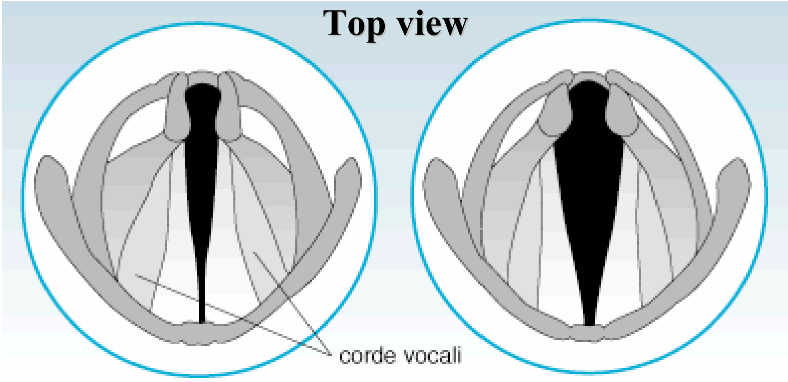


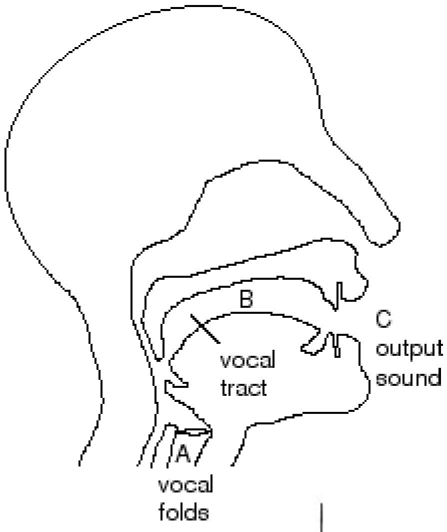
# Human larynx and vocal folds

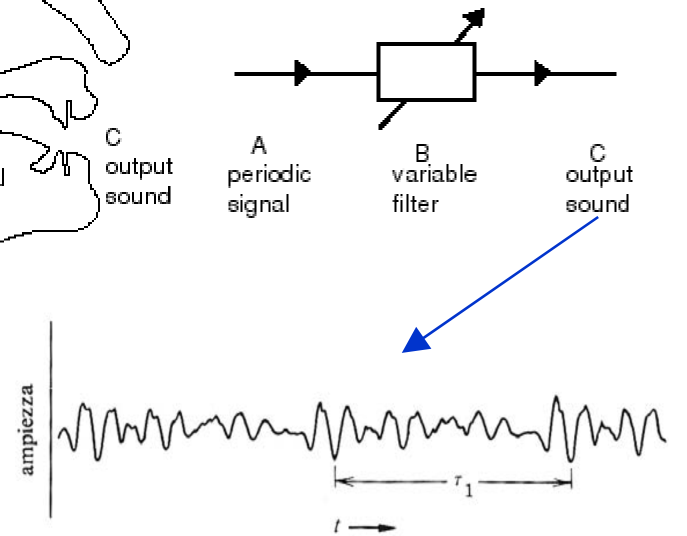


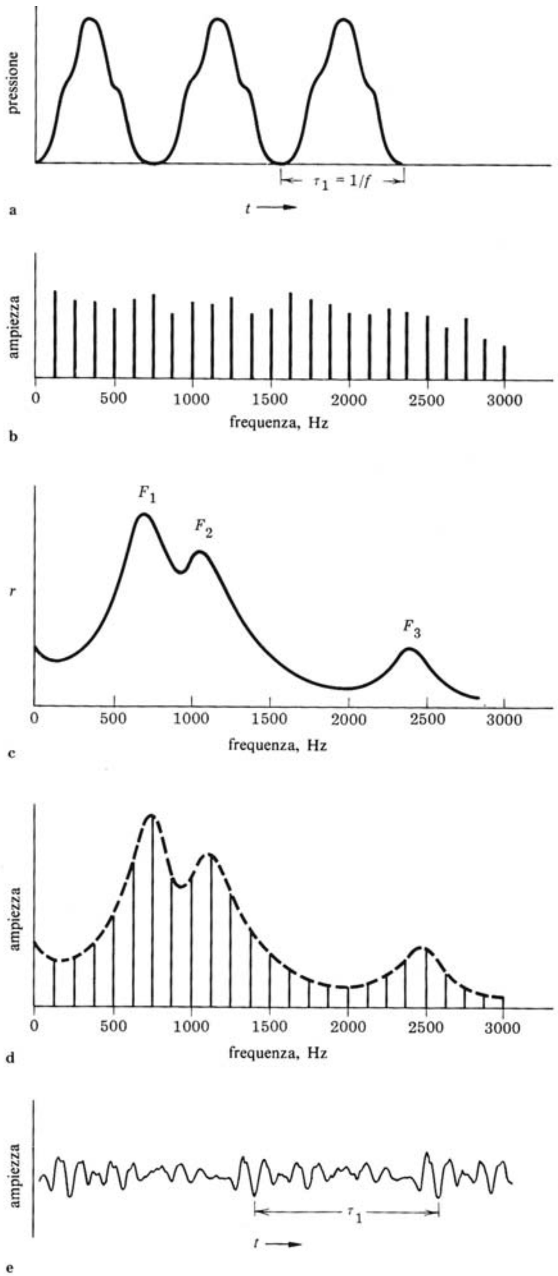



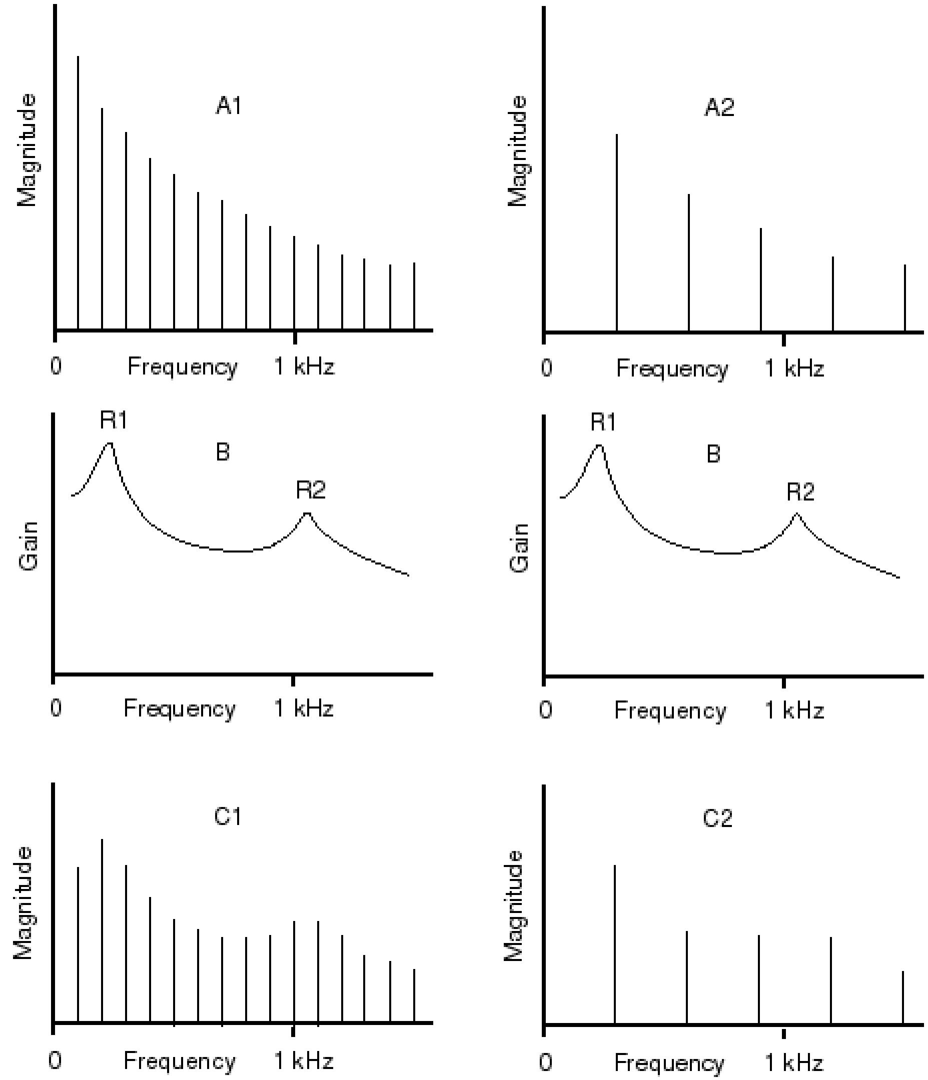


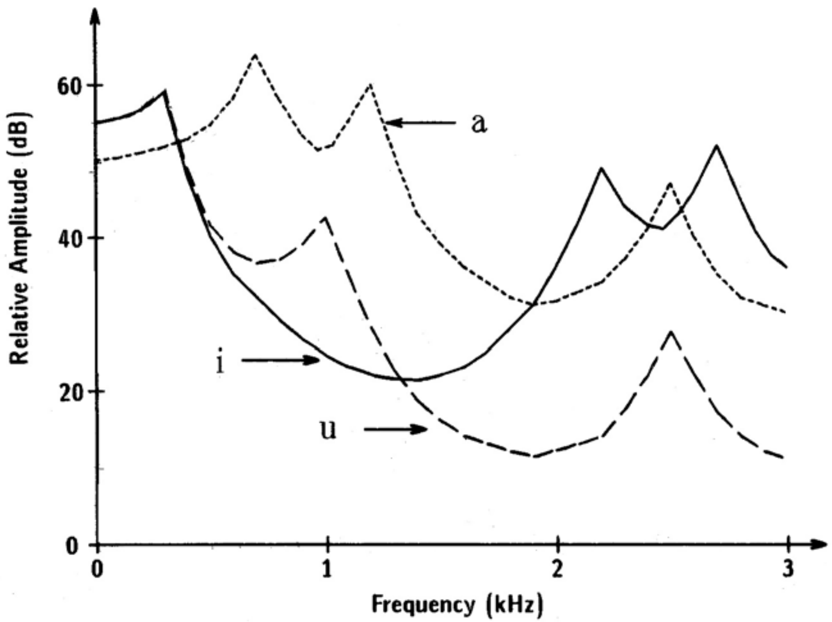



# Production of a voiced phoneme

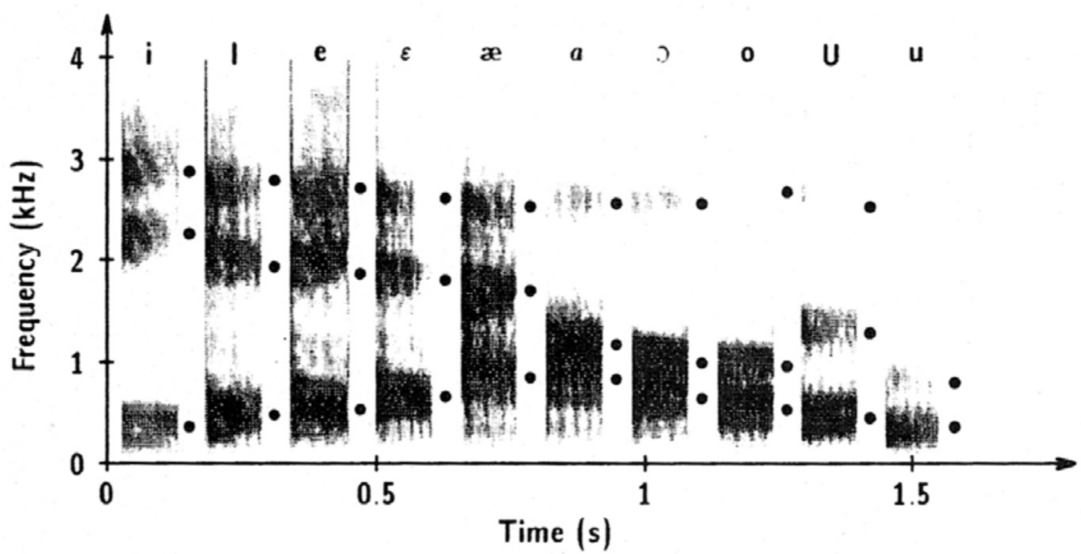


# Formant frequencies



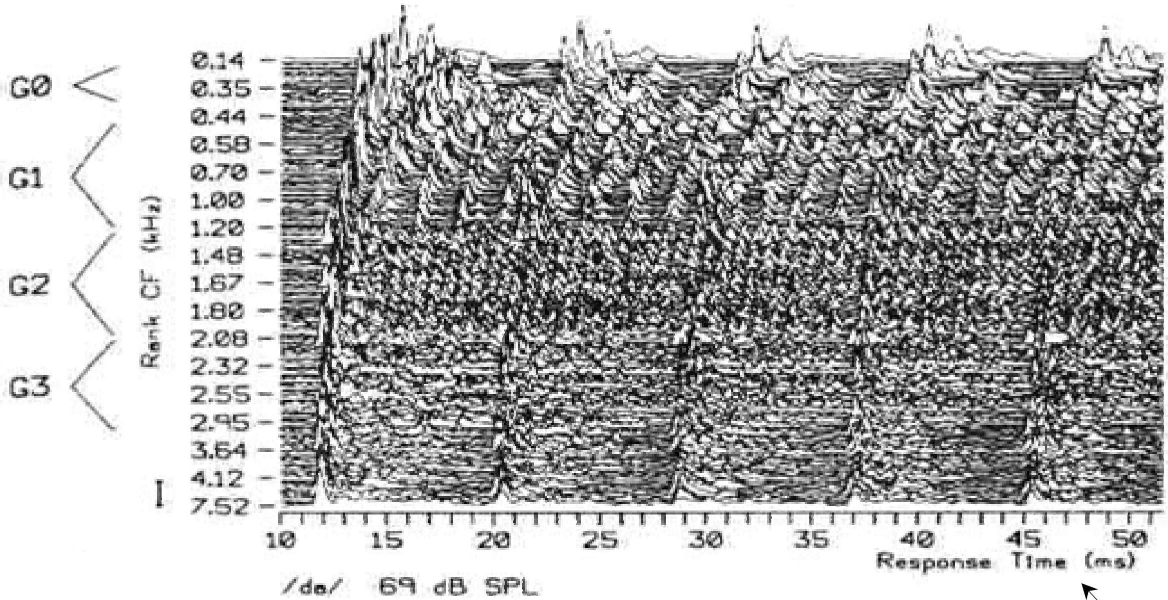

Cross sections of spectra from the middle of English vowels of a male speaker, showing formants as spectral peaks.

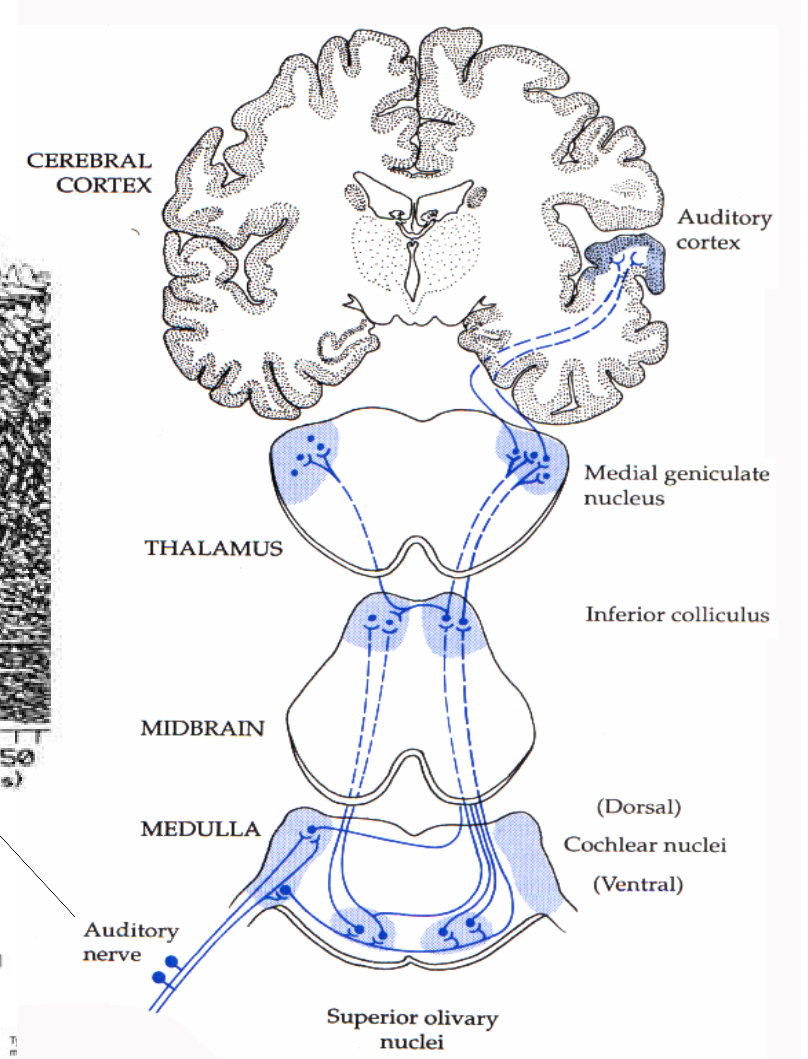


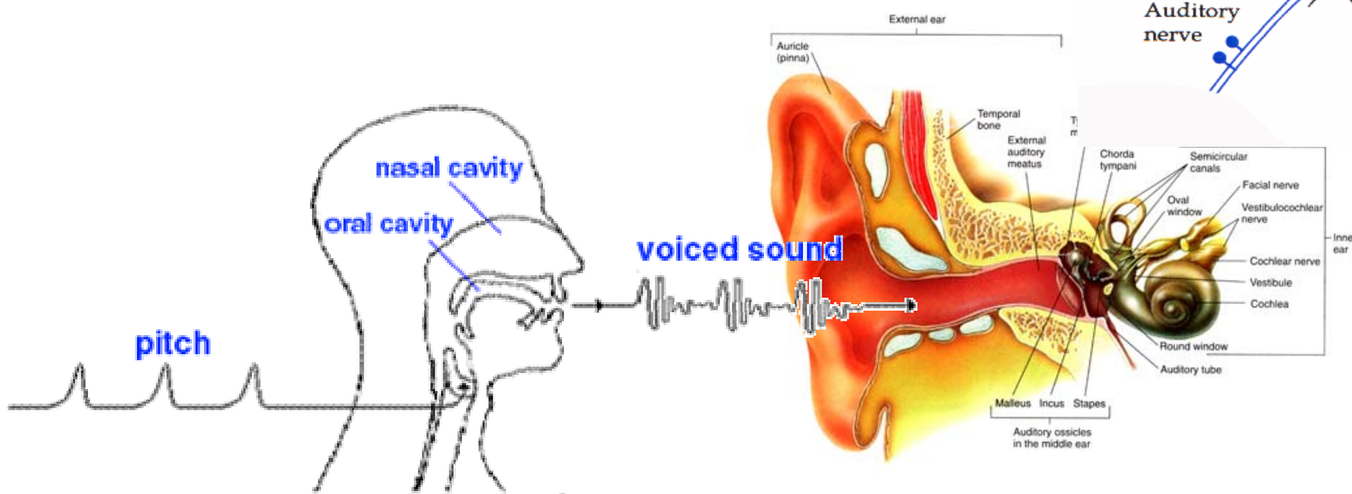

Spectrogram of short sections of English vowels from a male speaker. Formants for each vowel are noted by dots.

# Neural representation of speech-like sounds

Secker-Walker & Searle, JASA, 1990

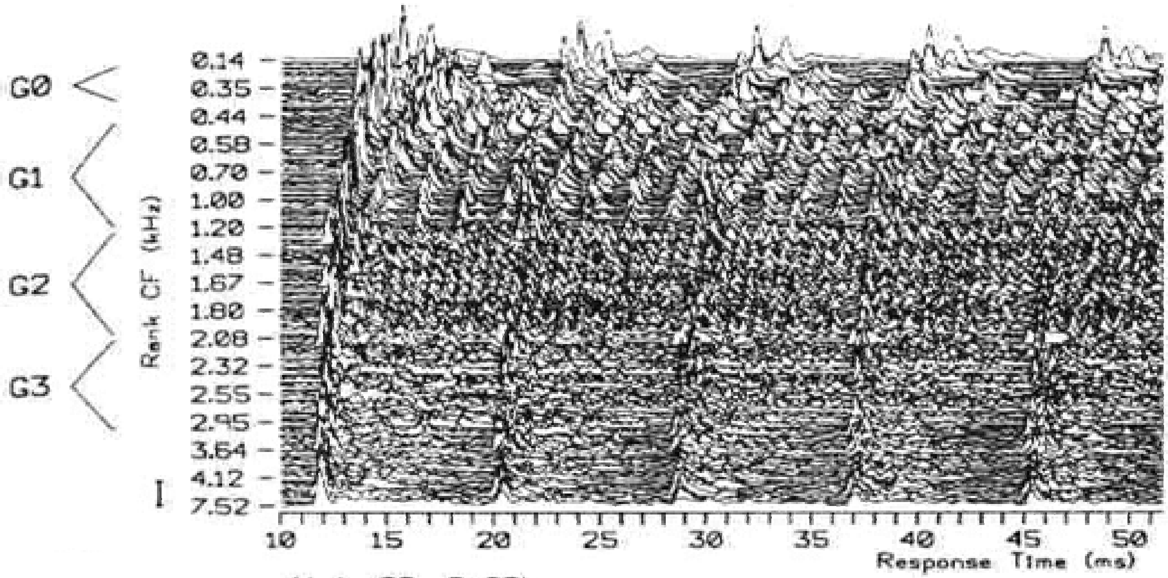


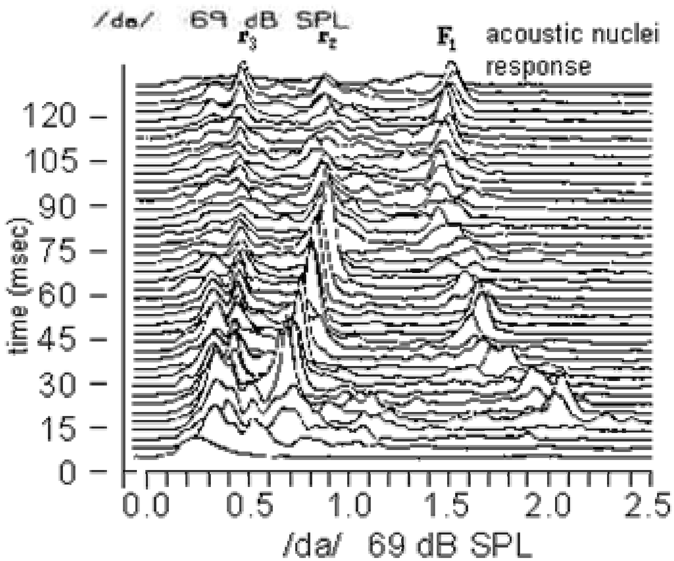



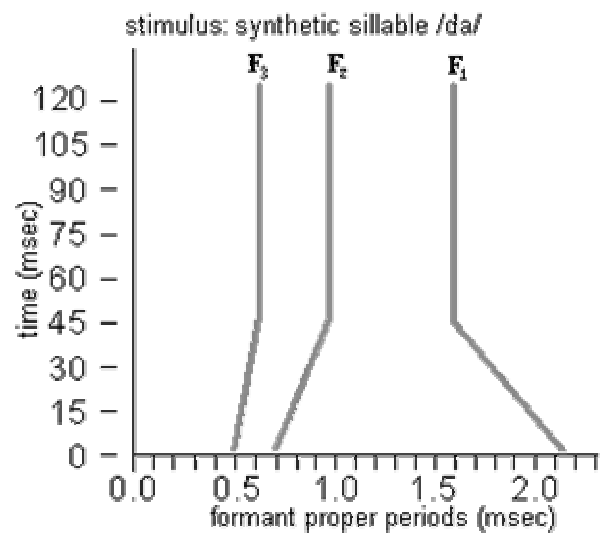
# Formant tracking by the peripheral auditory system

Secker-Walker & Searle, JASA, 1990




- pooled IPIs histograms are generated through smoothed root autocorrelation interval analysis and a final average over CF parameters.
- intervals between peaks in the instantaneous firing waveforms of auditory fibers directly encode the periods of acoustic resonances.



# The ear is a very sensitive transducer

**The largest acoustic pressure $\Delta p_m$ that the ear tolerates at the threshold of pain is about 28 Pa, whereas the faintest audible sound at 1 kHz is associated to a $\Delta p_m$ of about 28 μPa (threshold of hearing).**

| ↓ Sound level ↓ | **Pressure** $\Delta p$ | **Velocity** $u = \Delta p / Z$ | **Displacement** $s = u / 2\pi f$ |
|---|---|---|---|
| **Threshold of hearing** | **28 μPa** | **67 nm/s** | **11 pm** |
| **Threshold of pain** | 28 Pa | 67 mm/s | 11 μm |

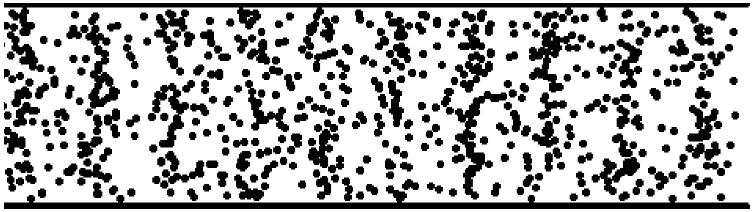
**Compare to:**

**HYDROGEN ATOM**
**Bohr's radius** $r_a = 52.9$ pm

**ATMOSPHERIC PRESSURE**
$p_o = 1.013 \times 10^5$ Pa = 0.1 MPa

- **The faintest sounds cause air molecule average displacements on the sub-atomic scale.**
- **Even for the loudest sounds, displacements are comparable to the thickness of a normal sheet of paper, divided by 7.**
- **At the threshold of pain, acoustic pressure is still less than the stationary atmospheric pressure, divided by 10000.**

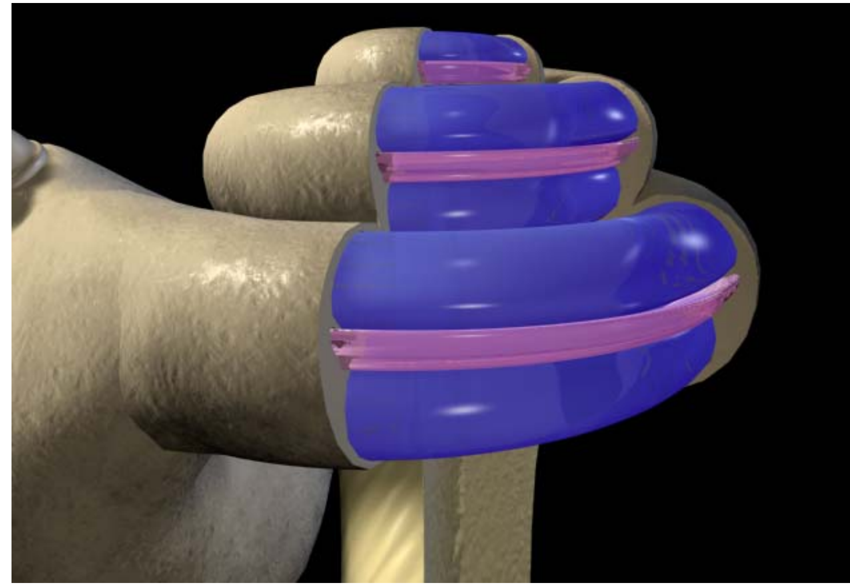
# Human Peripheral Auditory System

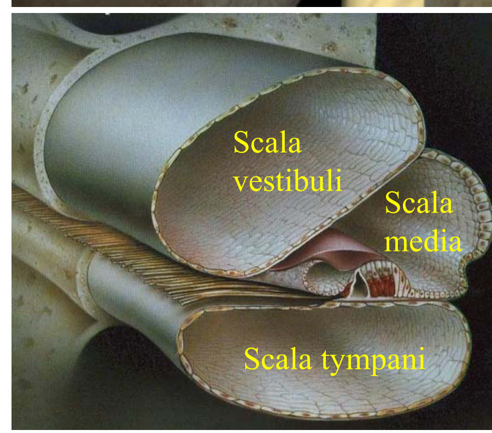



**External, middle and inner ear**

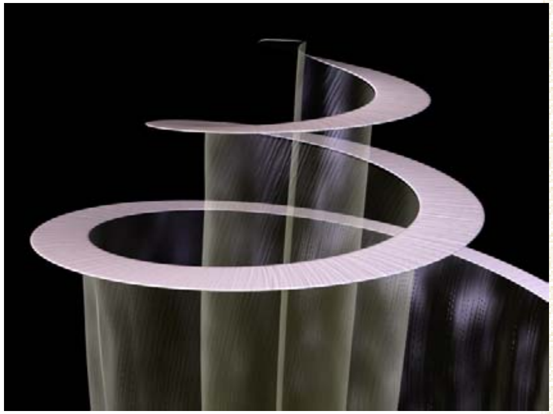
**The scala media is separated by from the scala vestibuli above by Reissner's membrane and from scala tympani below by the basilar membrane.**

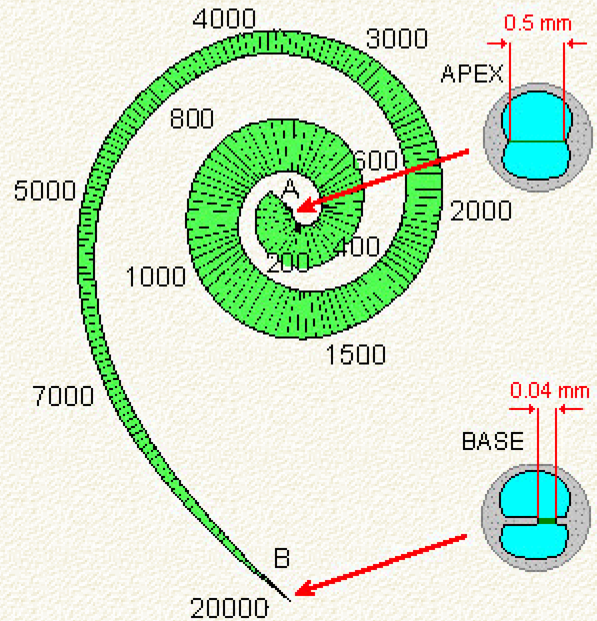
**The coclea is a fluid-filled coiled structure logitudinally divided in three sub-compatments, or scalae. The scale spiral together along the length of the cochlea.**





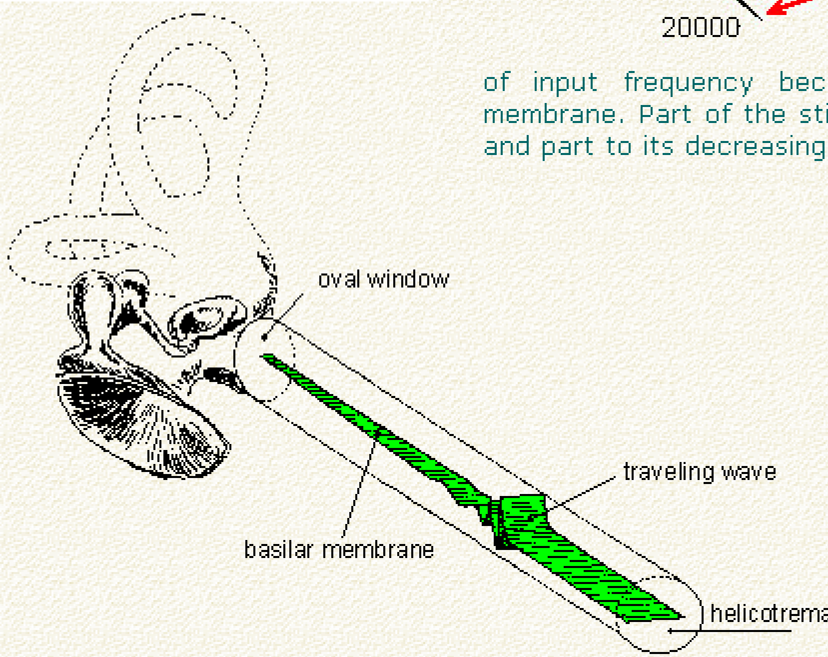

# Basilar membrane response to a pure tone

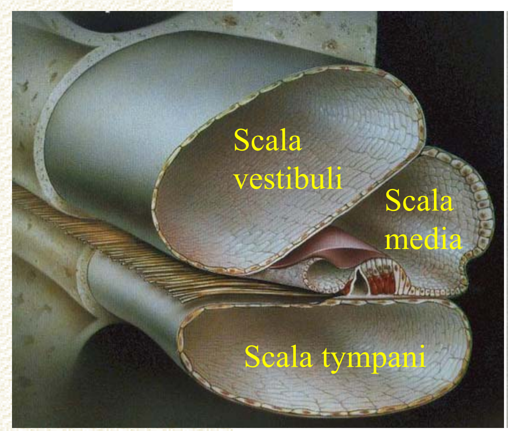





The basilar membrane is internally formed by thin elastic fibers tensed across the cochlear duct. The fibers are short and closely packed in the basal region, i.e. close to the stapes, and become longer and sparse proceeding towards the apex of the cochlea, where the basilar membrane ends in a foramen that joins the two partions of the spiral canal (see *Anatomy*). Being under tension, the fibers can vibrate like the strings of a musical instrument.

Traveling waves peak at frequency-dependent locations, higher frequencies peaking closer to more basal location. Peak position is an exponential function of input frequency because of the exponentially graded stiffness of the basilar membrane. Part of the stiffness change is due to the increasing width of the membrane and part to its decreasing thickness.

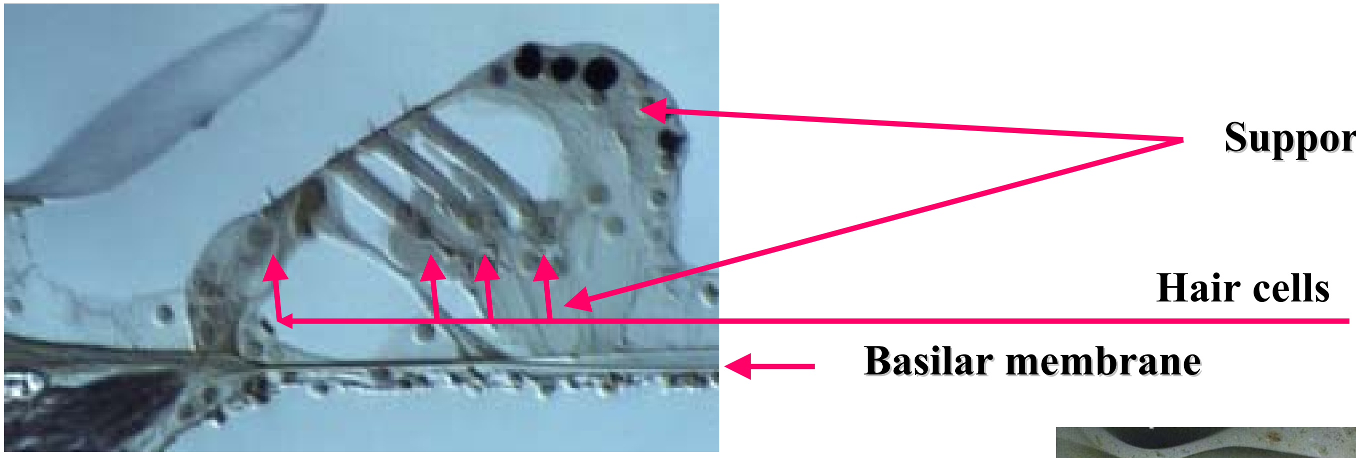


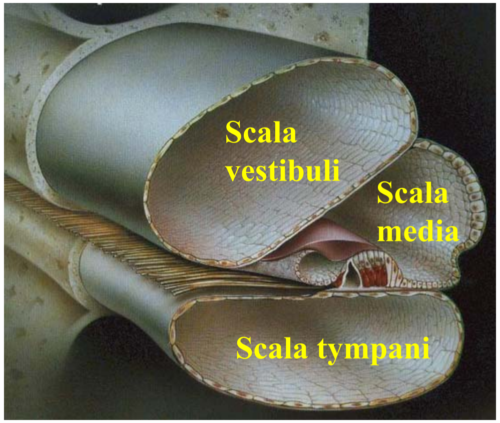


In response to sinusoidal pressure applied to the stapes (tones) the basilar membrane vibrates producing the phenomenon of traveling waves.

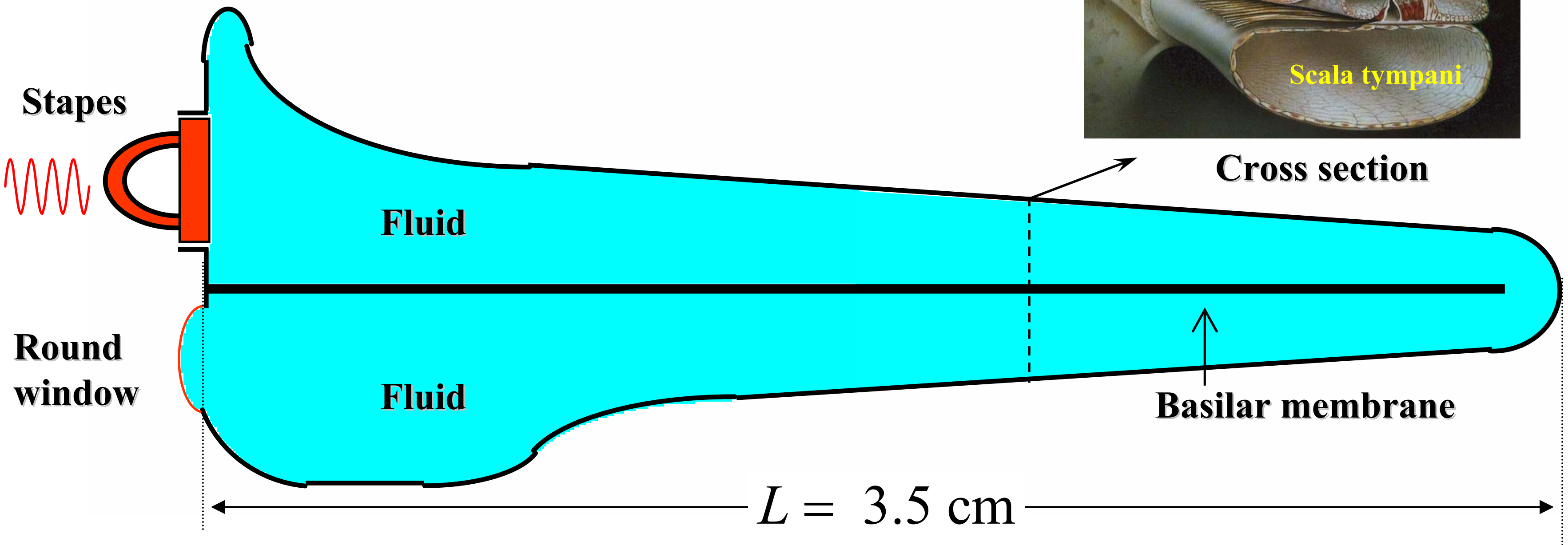
# The "uncoiled" cochlea



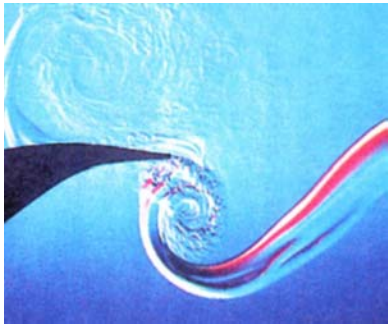

Organ of Corti



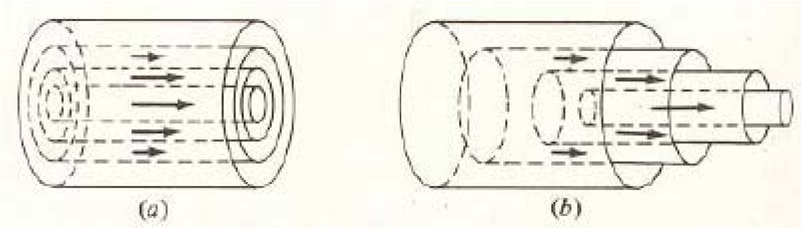

Cross section



# Cochlear fuid dynamics



**In a fluid-filled tube, transition from laminar to turbulent flow occurs at $N_R > 2000$**




**Laminar flow condition**

**Reynolds' number**

$$N_R = \frac{\rho\ \mathrm{v}\ D}{\eta} \approx \frac{(1000)\ (4.5\times10^{-3})\ (10^{-3})}{1.5\times10^{-3}} = 3 \ll 2000$$

v (max fluid speed) $\sim 4.5\times10^{-3}$ m s$^{-1}$ [T.Ren, at 90 dB SPL]

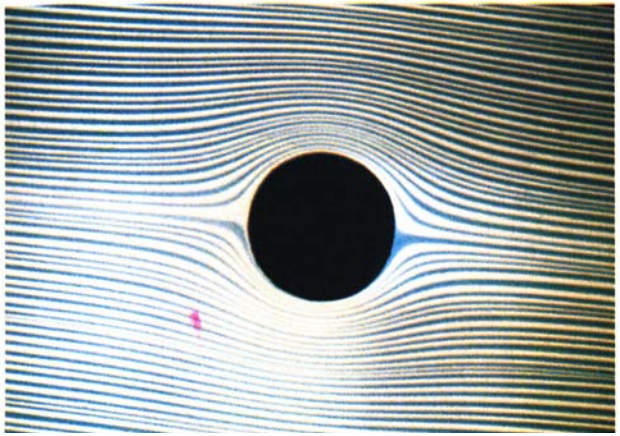
$\eta$ (viscosity) $\sim 1.5$ kg m$^{-1}$ s$^{-1}$ [von Békésy]

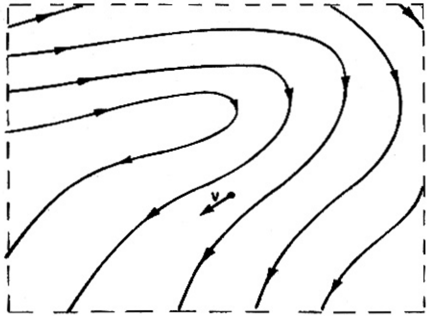
$\rho$ (density) $\sim 1000$ kg m$^{-3}$ [water]

$D$ (tube diameter) $\sim 1$ mm $= 10^{-3}$m [on average]

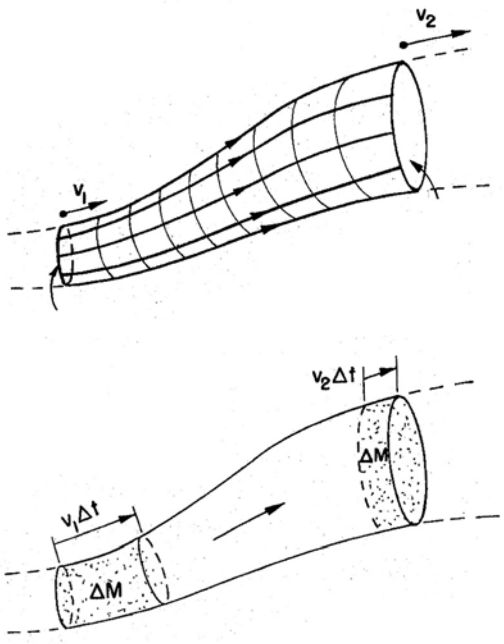
**Fluid flow in the cochlea is laminar.**

# Laminar fluid flow






Streamlines



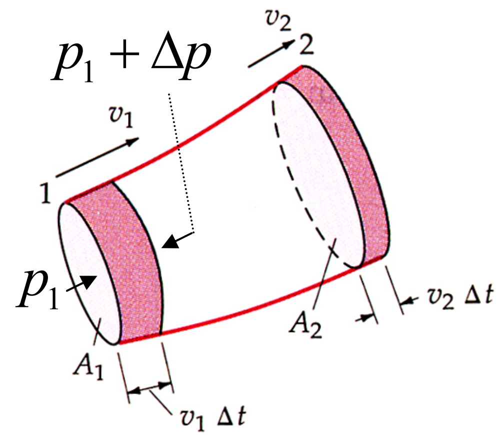

*Fluid motion in a flow tube*

$$v_1\ A_1 = v_2\ A_2$$

**Continuity equation** ($\rho$ = const.)

**— Mass conservation —**

# Euler's equation




**Newton's second law:** $\vec{F} = m\vec{a}$

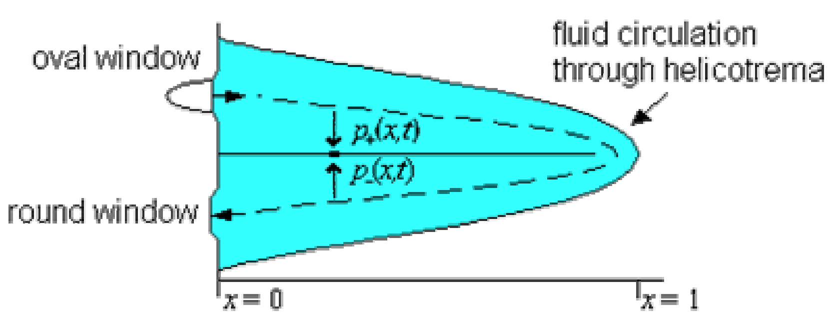
**Net force:** $F = p_1 A_1 - (p_1 + \Delta p) A_1$

**Mass:** $m = \rho\ \Delta V = \rho\ A_1\ \Delta x$

$$-\Delta p = \rho\ \Delta x\ a$$

**Euler's equation:** $-\vec{\nabla}\, p \;=\; \rho\ \vec{a}$

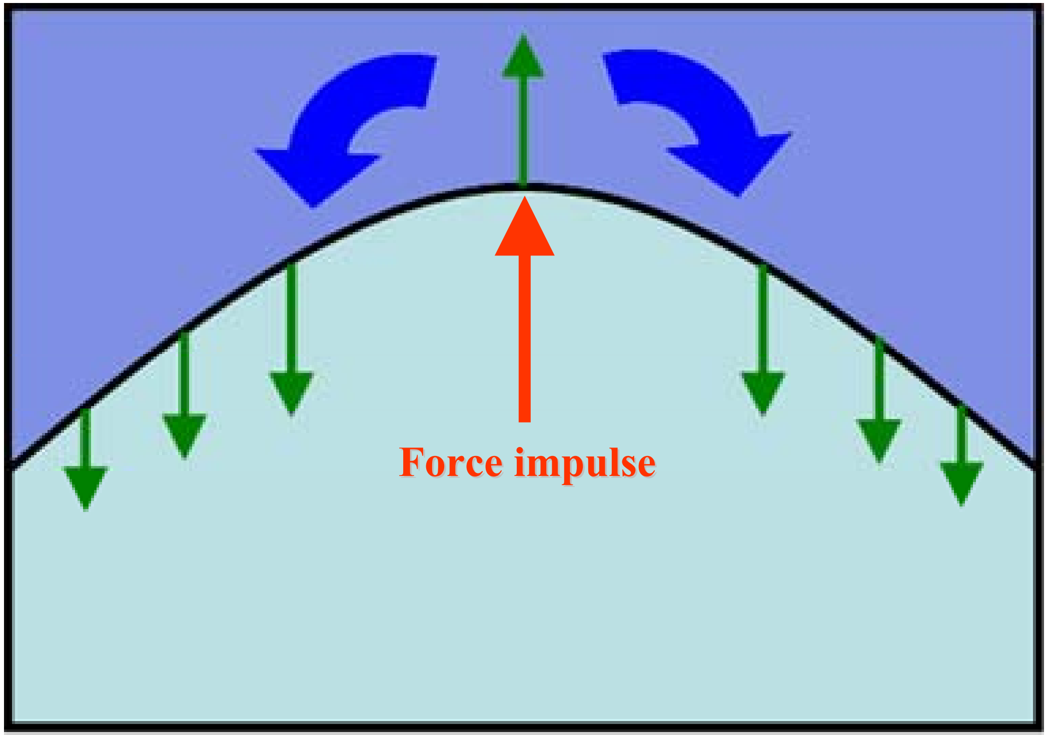
**<u>This equation is valid if the effects of fluid viscosity can be neglected</u>**




**<u>Kinetic presure field</u>**

**Local fluid accelerations are reciprocally related to the local pressure gradient through Eurler's equation**

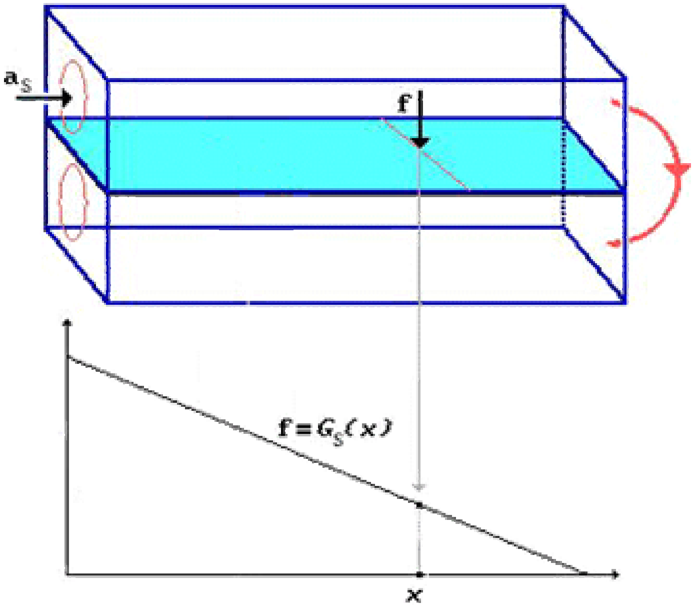
# Basilar membrane and instantaneous fluid coupling



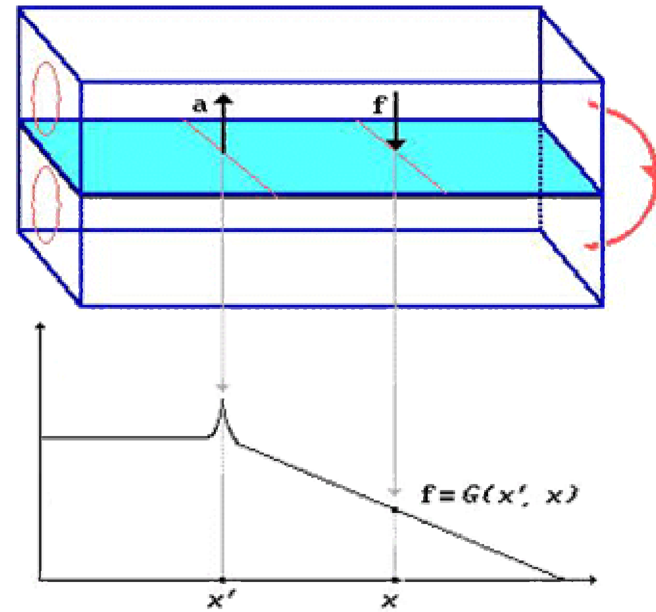

**Due to *fluid incompressibility* ($\rho$ = const.), pressure spreads instantaneously from the force application site and pushes adjacent membrane segments in the direction opposite to the force impulse (curved blue arrows).**

# Fluid coupling in the box model of the cochlea

*Magnitude of the hydrodynamic forces per unit input acceleration*




$f = G_S\,(x)$, force acting on the basilar membrane segment at $x$ caused by unit inward stapes acceleration $a_S$.

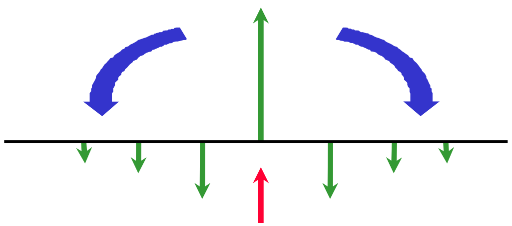


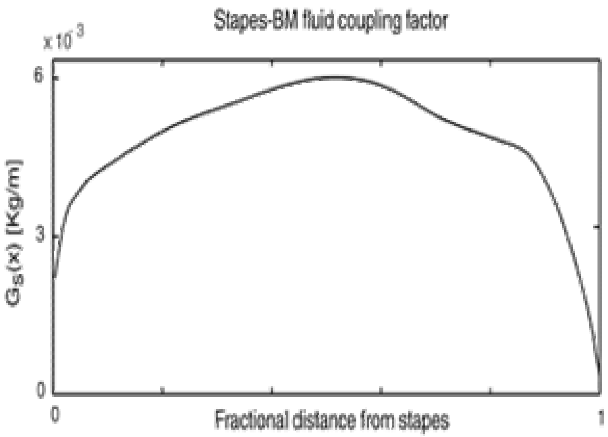

$f = G(x', x)$, force acting on the basilar membrane segment at $x$ caused by unit upward acceleration a of the basilar membrane at $x'$.

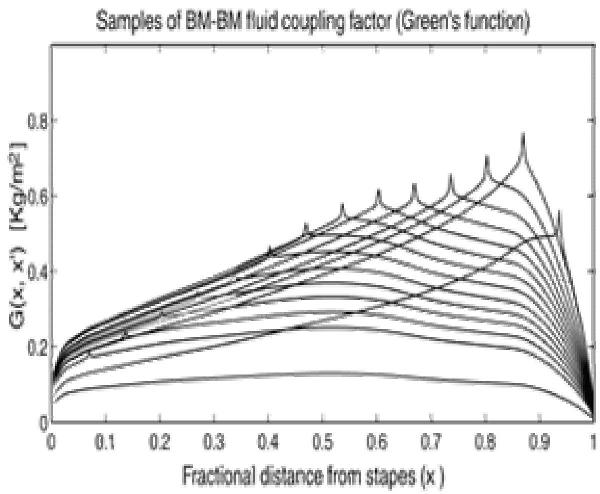
Allen J *JASA* 1977

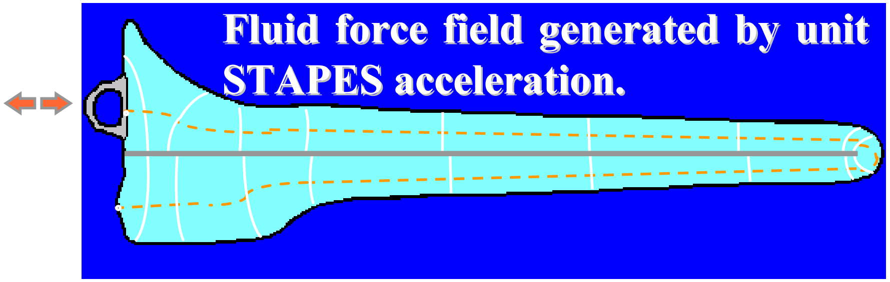
# Human cochlea

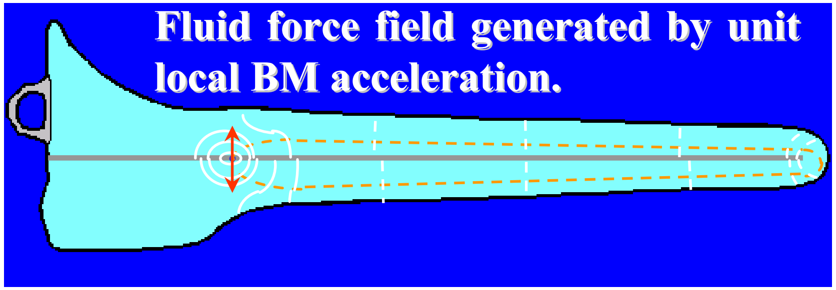
**Due to fluid incompressibility, pressure spreads instantaneously from the force application site and pushes adjacent membrane segments in the direction opposite to the force impulse (curved blue arrows).**



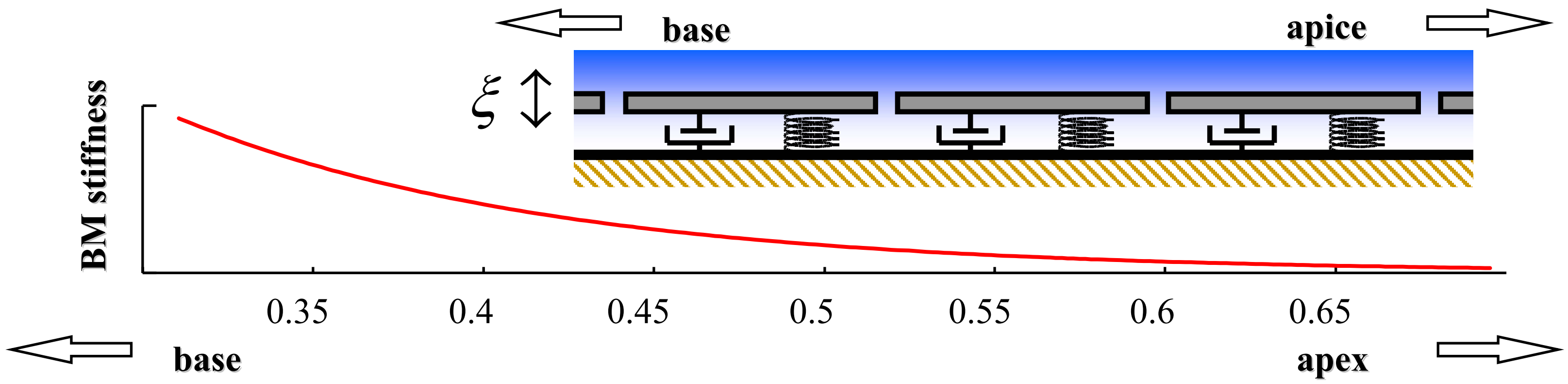



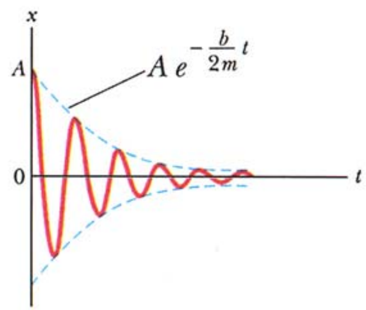

Nobili R, Vetešník A, Turicchia L, Mammano F, *JARO*, 2003

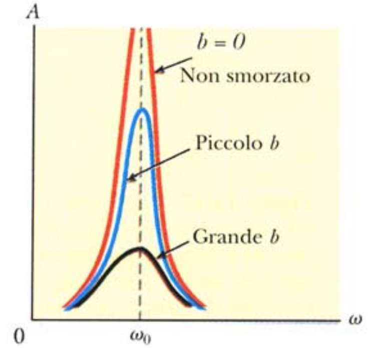
# Basilar membrane model



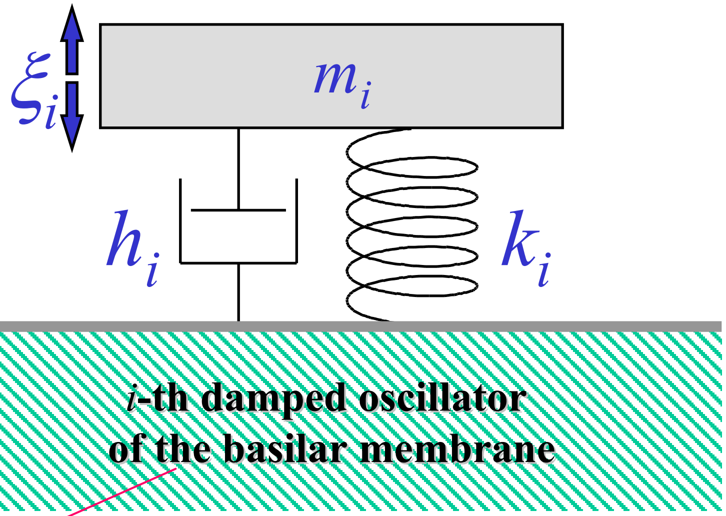

$$m(x)\frac{\partial^2 \xi}{\partial^2 t} + h(x)\frac{\partial\ \xi}{\partial\ t} + k(x)\ \xi = F\ (x)$$

**Damped oscillator equation**

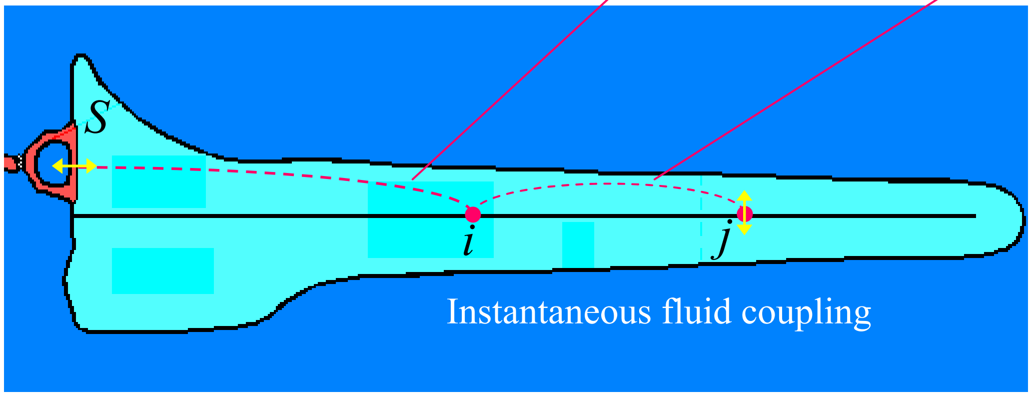


# Motion equation of the basilar membrane

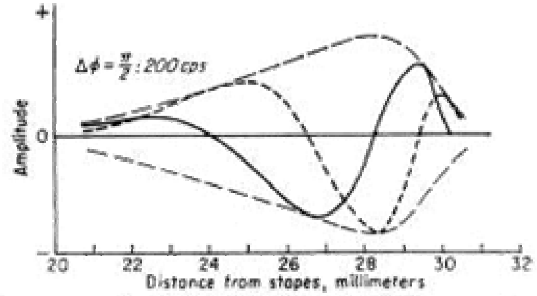


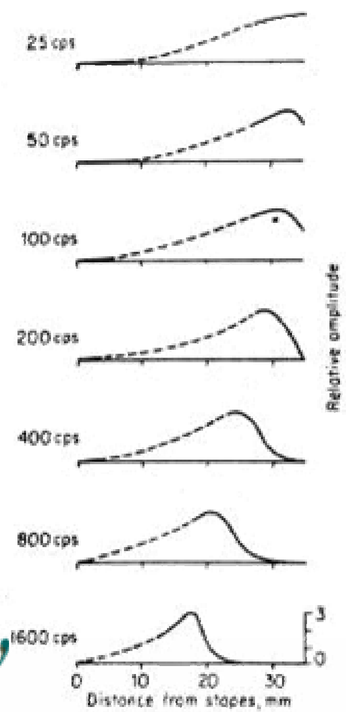

$$m_i \frac{\partial^2 \xi_i}{\partial^2 t} + h_i \frac{\partial \xi_i}{\partial t} + k_i \xi_i = -G_{i,S}\, a_S(t) - \sum_{j=1}^{N} G_i^j \frac{\partial^2 \xi_j}{\partial^2 t}$$




**Mammano F, Nobili R *JASA* 1993**

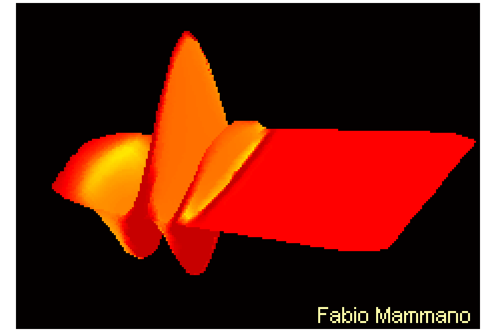
# Travelling waves



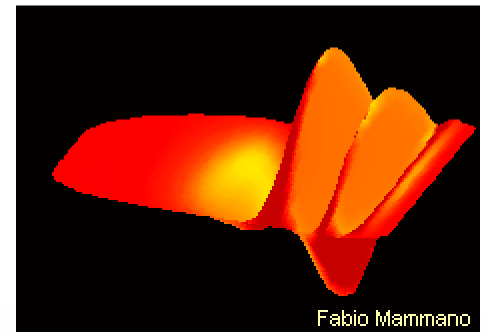




**Georg von Békésy**

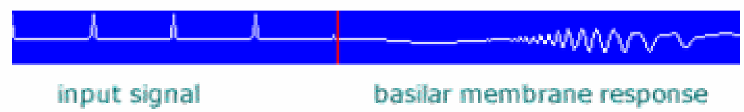
**High frequency**

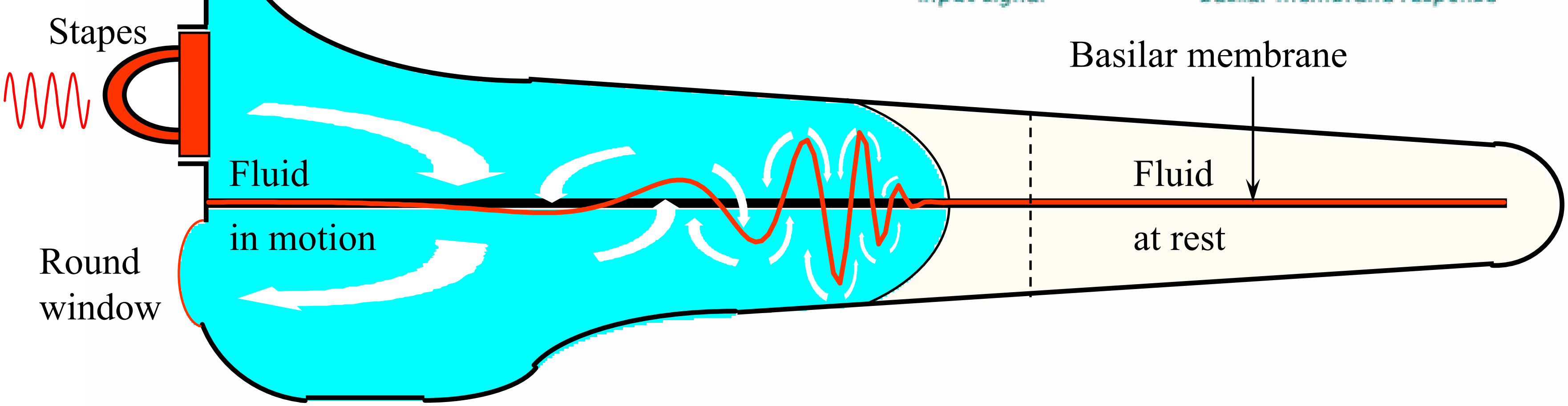



**Low frequency**




**Clicks**

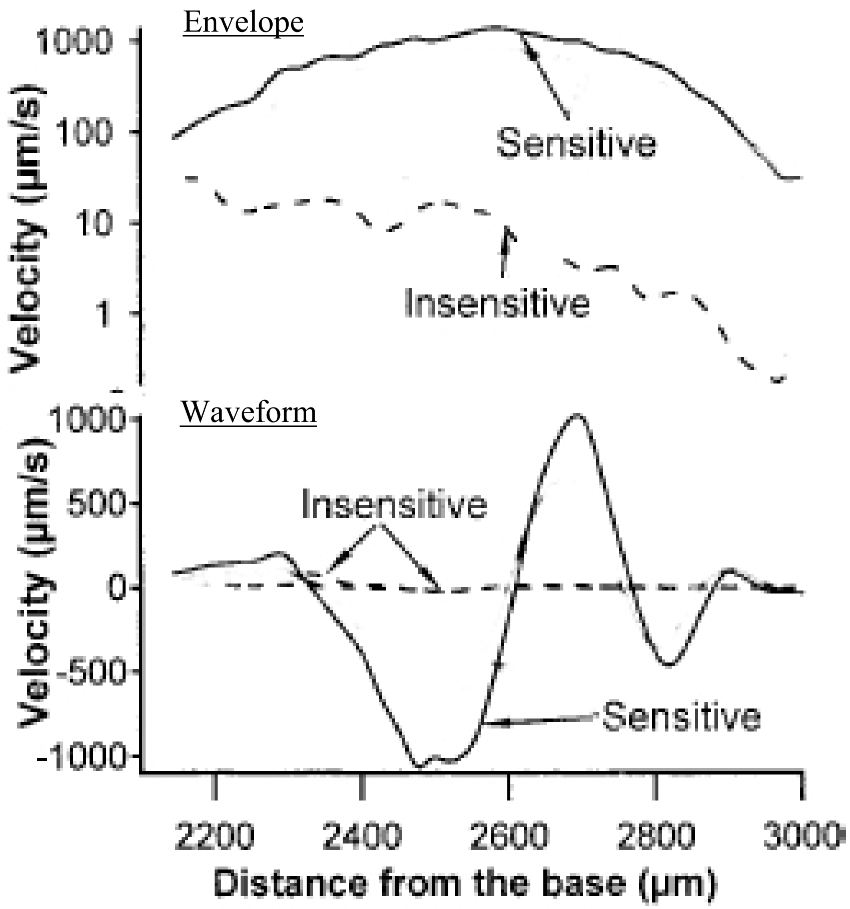


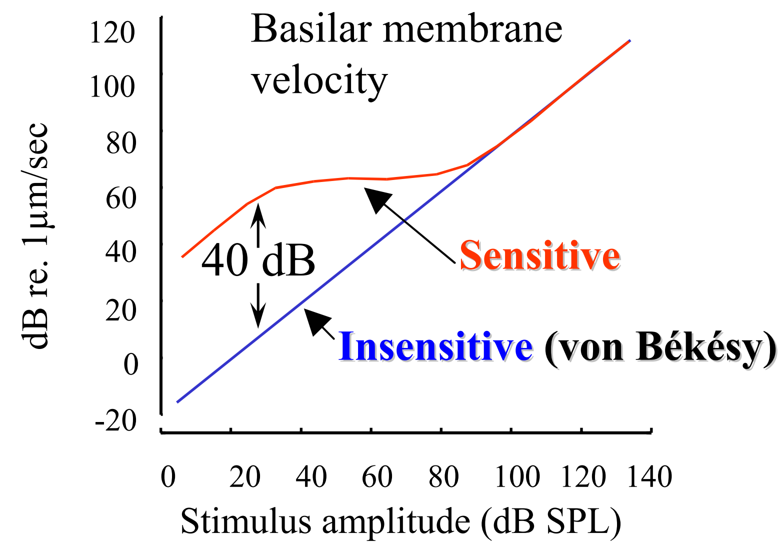



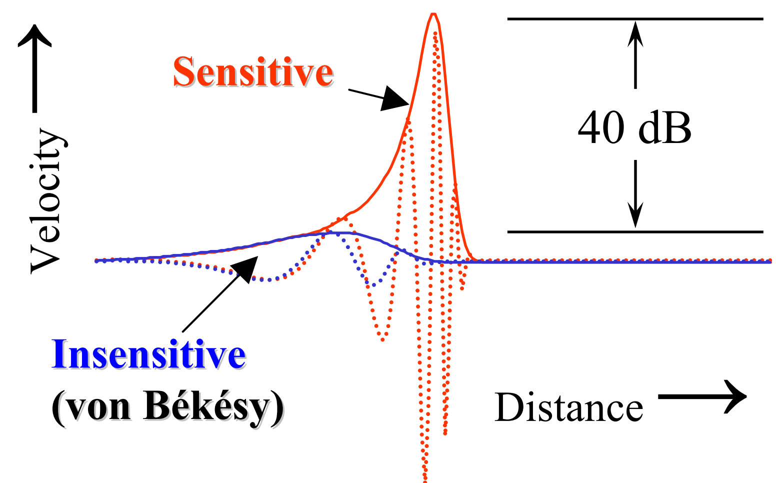

**Nobili R, Mammano F, Ashmore *TINS*, 1998**

# The cochlear amplifier

Longitudinal pattern of basilar membrane vibration in the sensitive cochlea



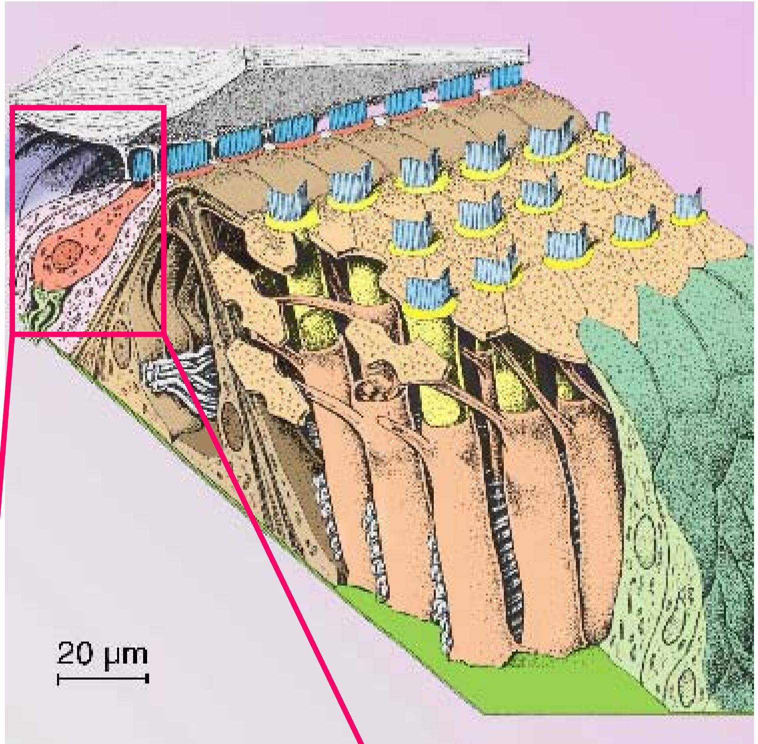



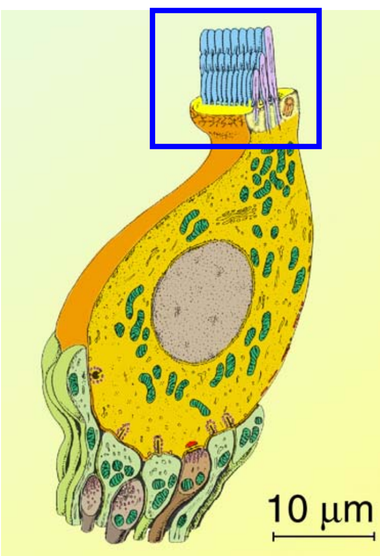




Ren T, 1998, *PNAS*, 2002

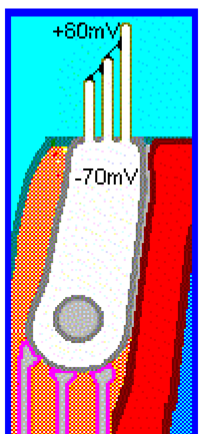
Nobili R , Mammano F, Ashmore 1998, *TINS*, 1998

# Forward transduction



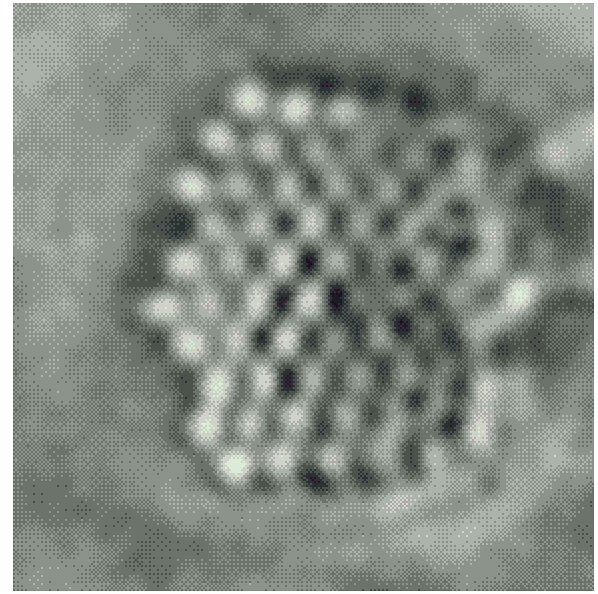




Inner hair cell



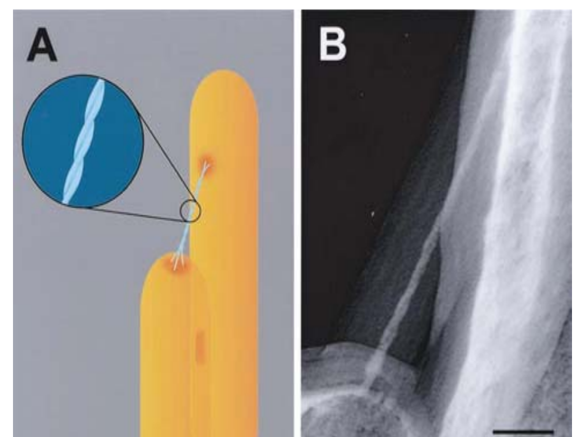

← Mechanically gated channels

Top view (lizard)



Stereocilia

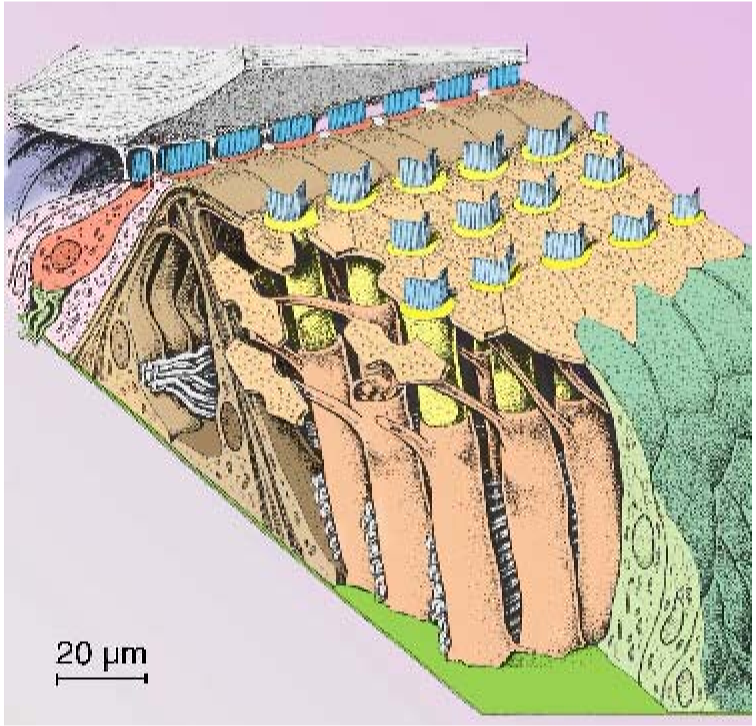
Davis Q || Freeman D, *ARO*, 1995

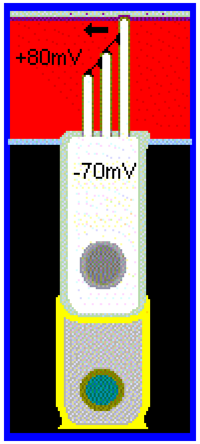


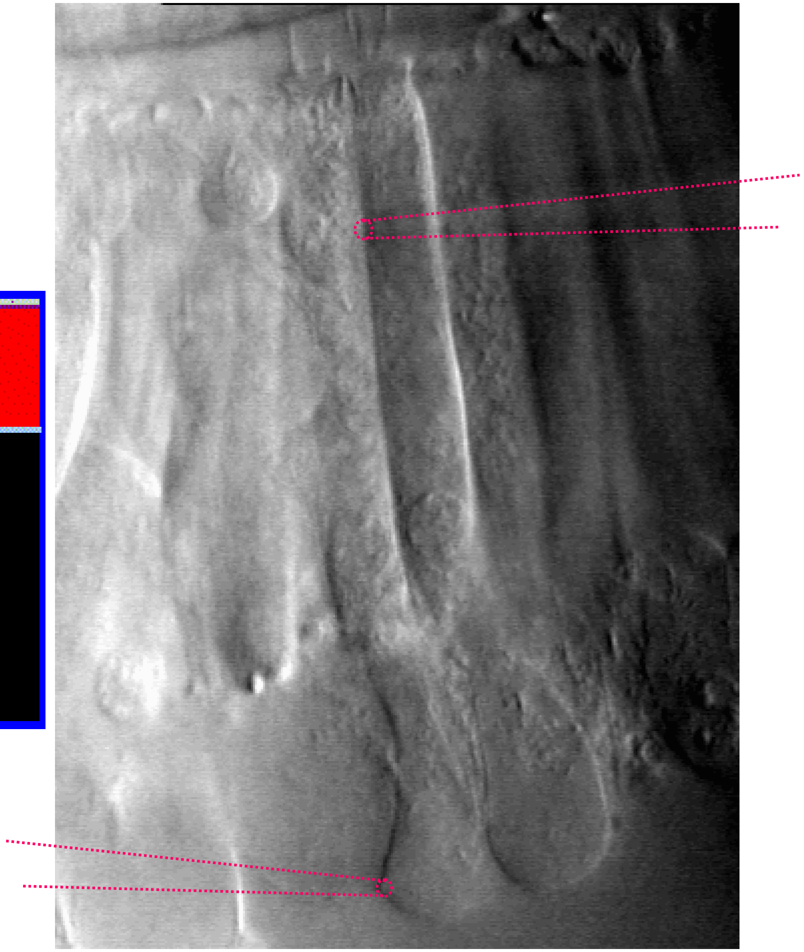

Tip links

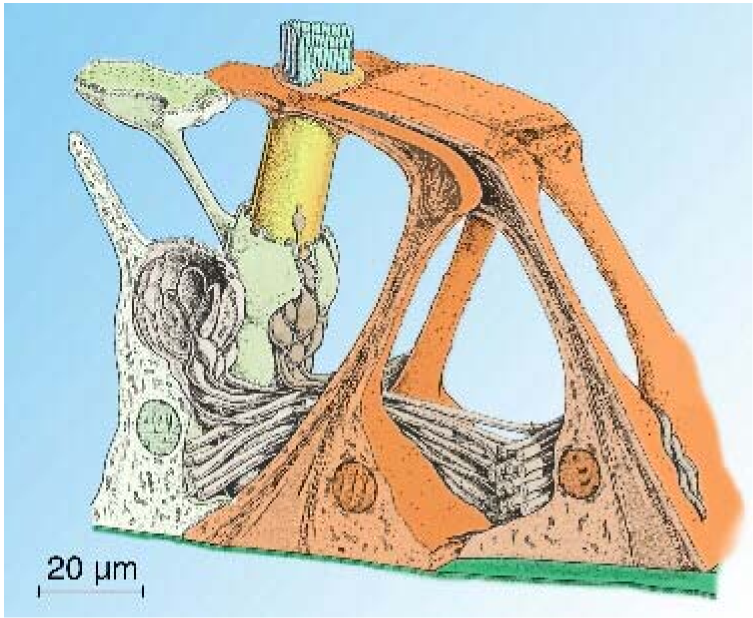
Kachar B || Gillespie PG, *PNAS*, 2000

# Outer hair cells and supporting cells

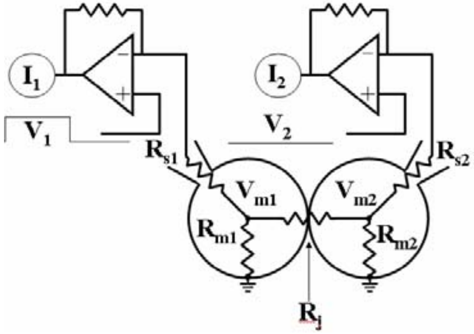


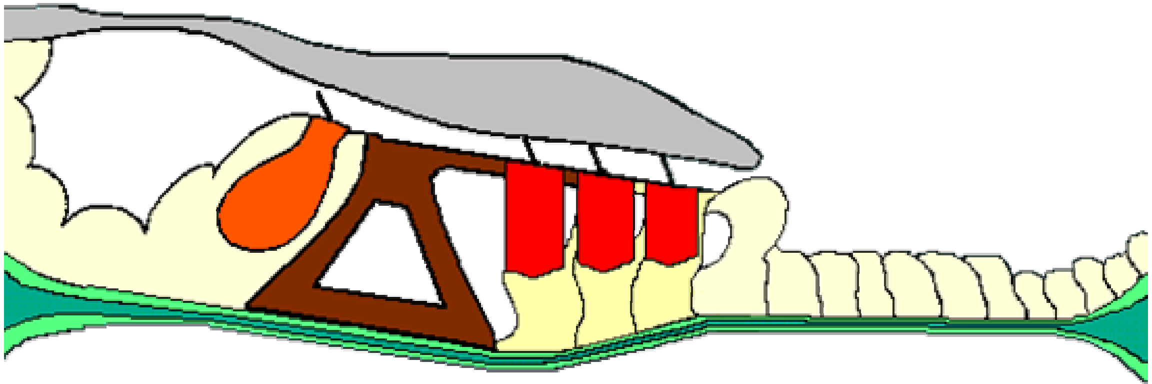






Lagostena L || Mammano F, *Cell Comm Adhes*, 2001

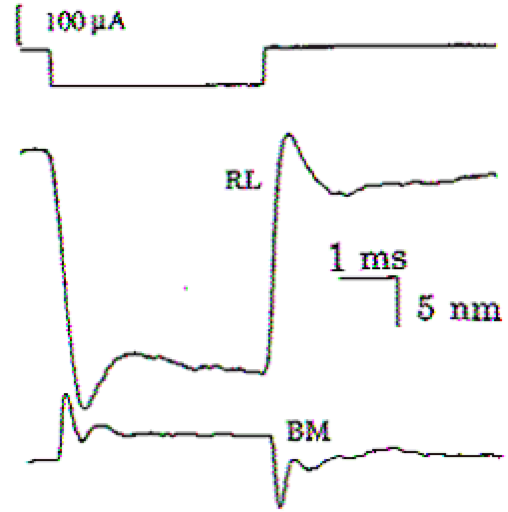


# Reverse transduction

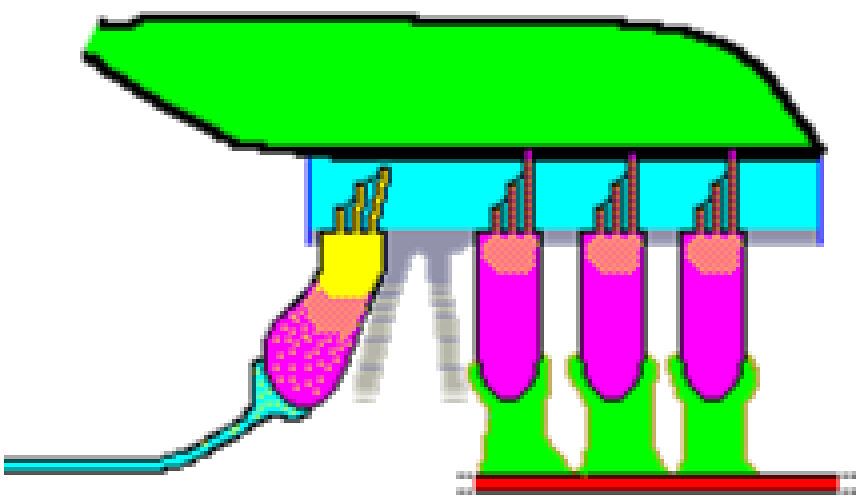


Sound OFF, only outer hair cells

Mammano F, Nobili R , *JASA*, 1993



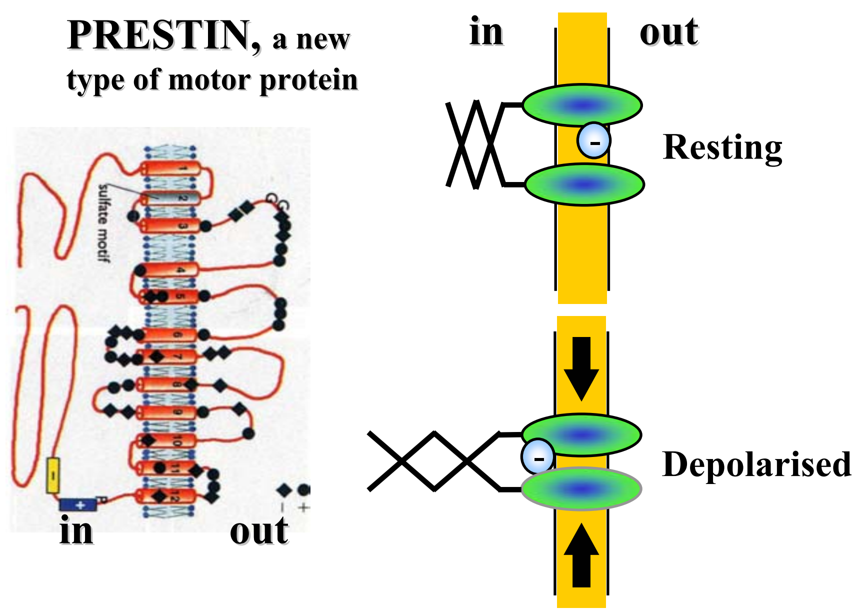

Mammano F, Ashmore JF, *Nature*, 1993



Sound ON, in the RL reference system

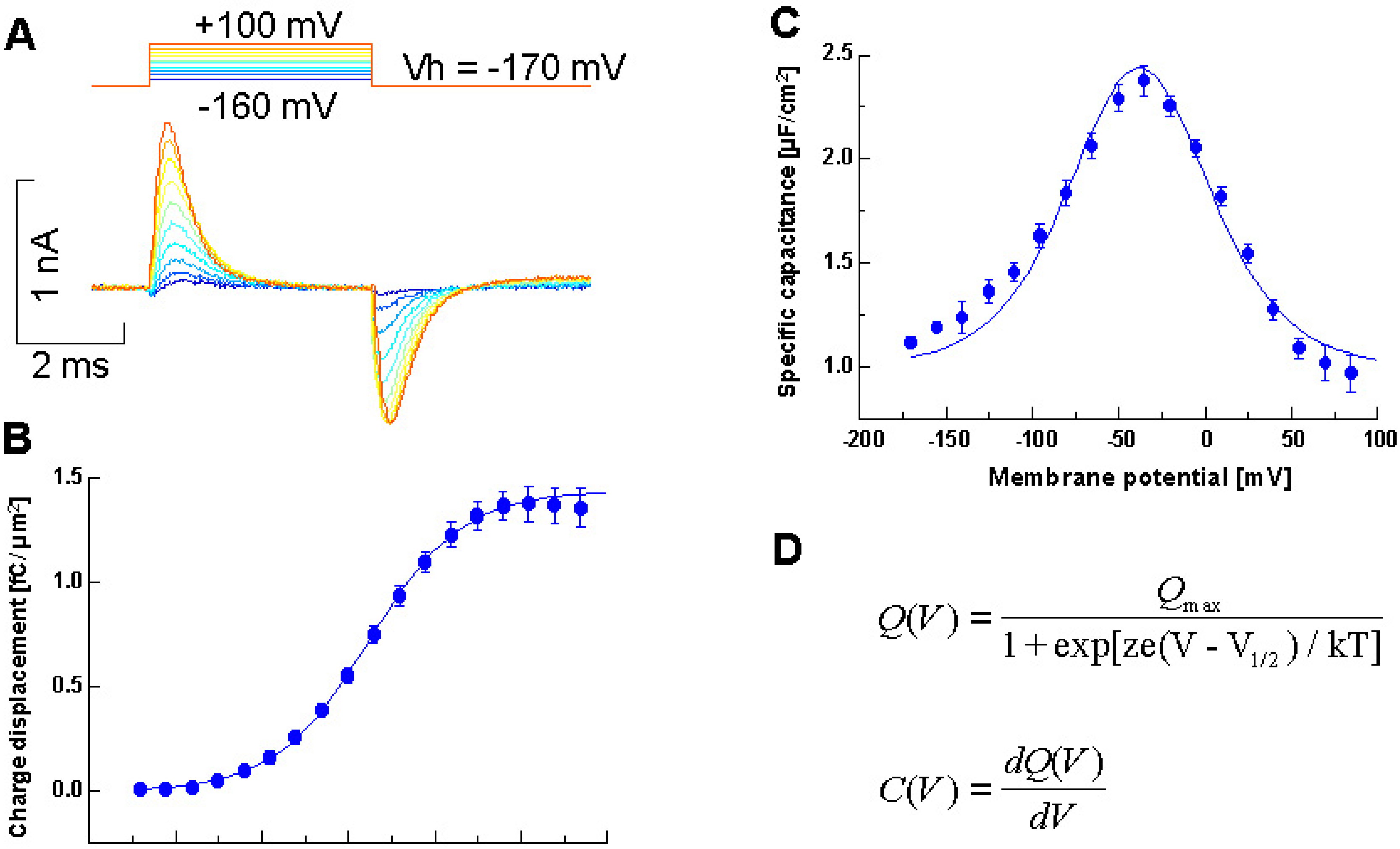
Nobili F, Mammano F, *JASA*, 1996

**PRESTIN,** a new type of motor protein




Dallos P, Fakler B, *Nature*, 2002

# Prestin's electrical signature: OHC "gating" currents



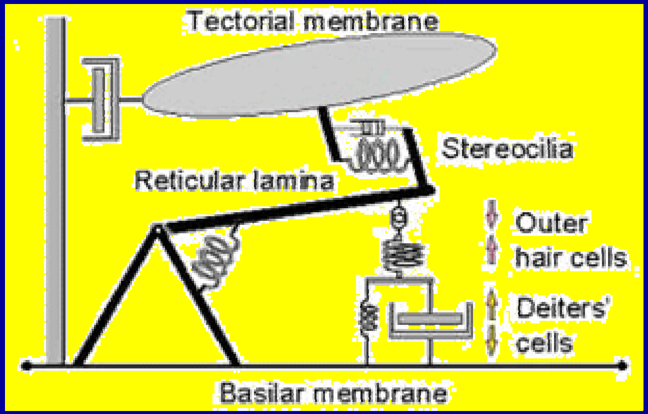

D

$$Q(V) = \frac{Q_{max}}{1 + \exp[ze(V - V_{1/2}) / kT]}$$

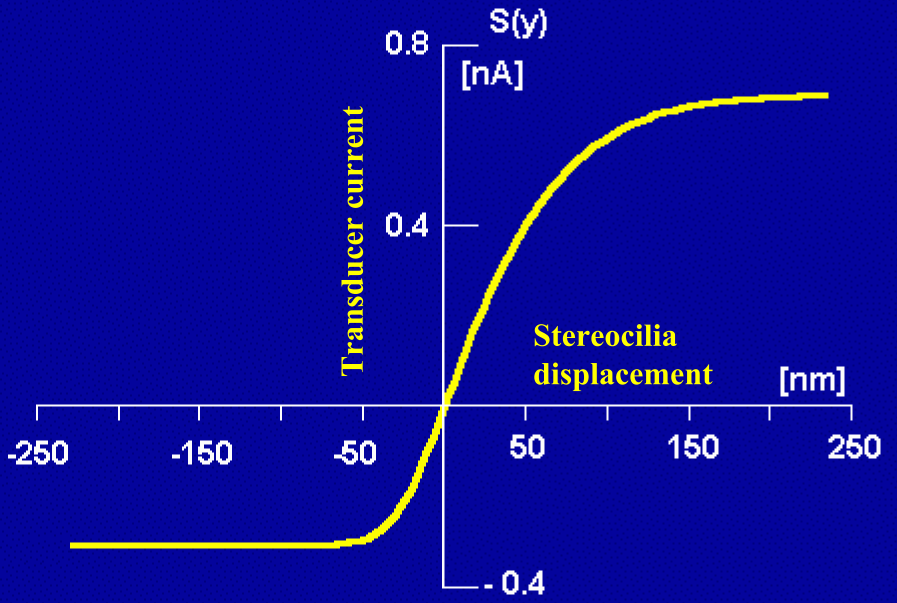
$$C(V) = \frac{dQ(V)}{dV}$$

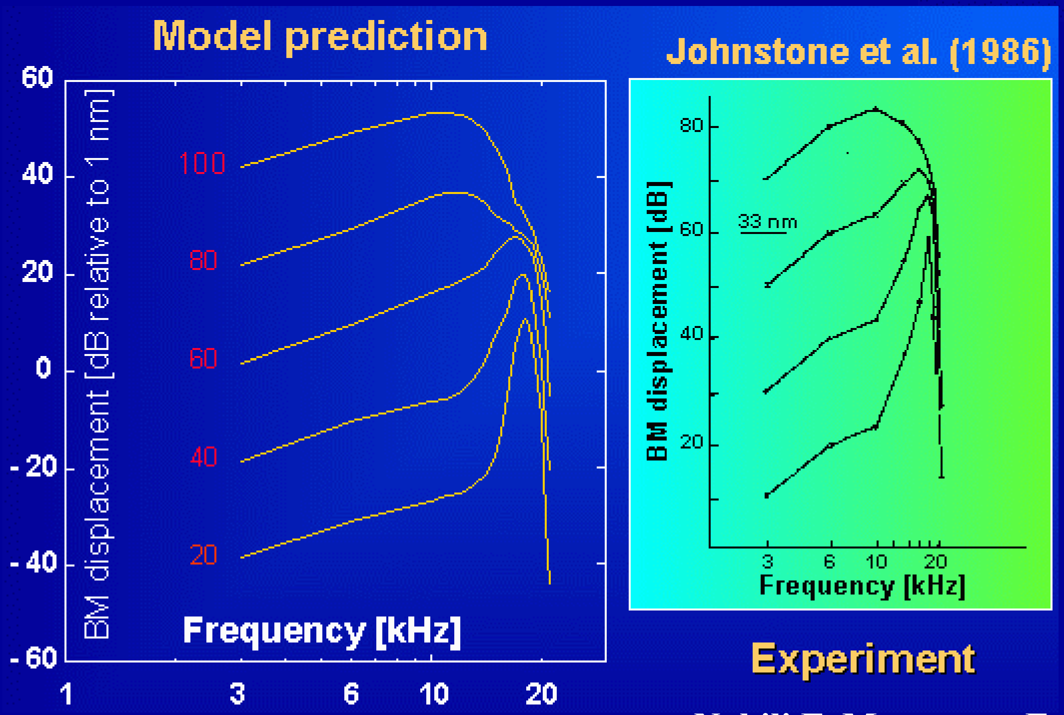
Mammano F || Kachar B, *J. Neurosci.*, 1999

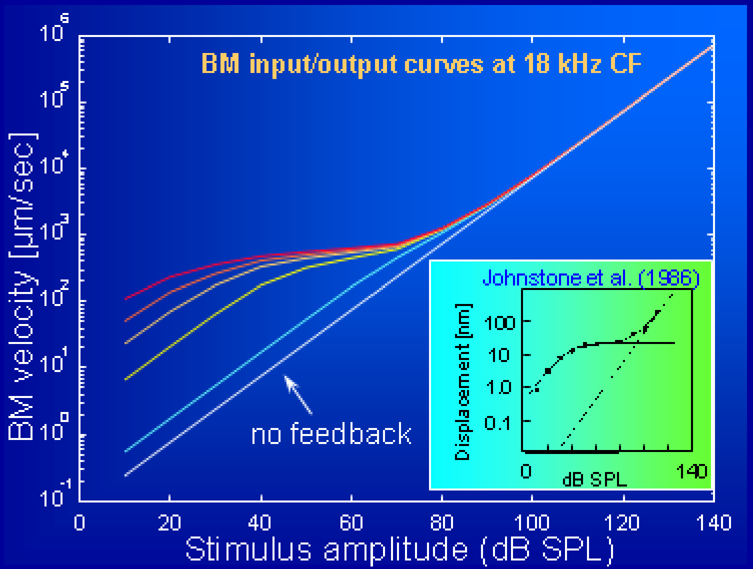
# Nonlinear amplification




The role of the tectorial membrane

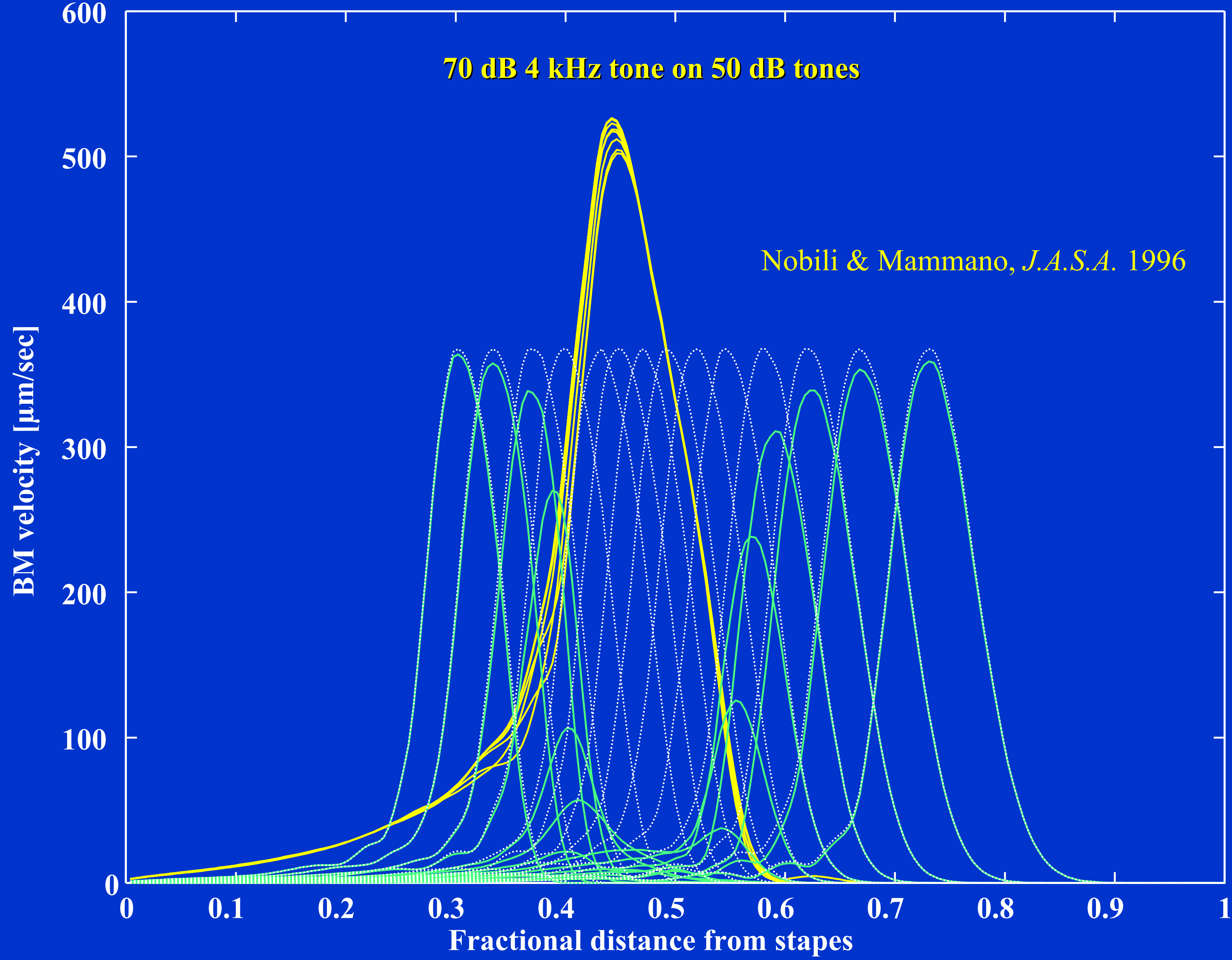


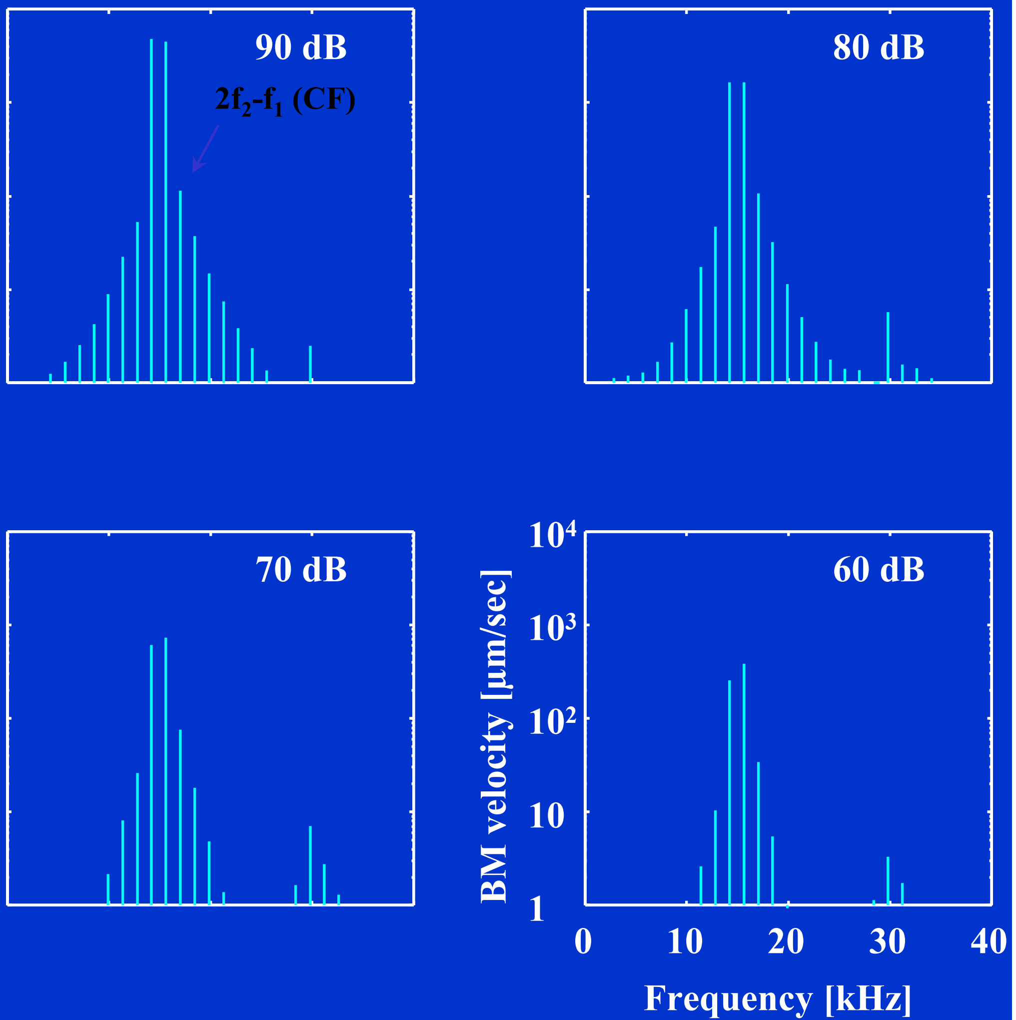



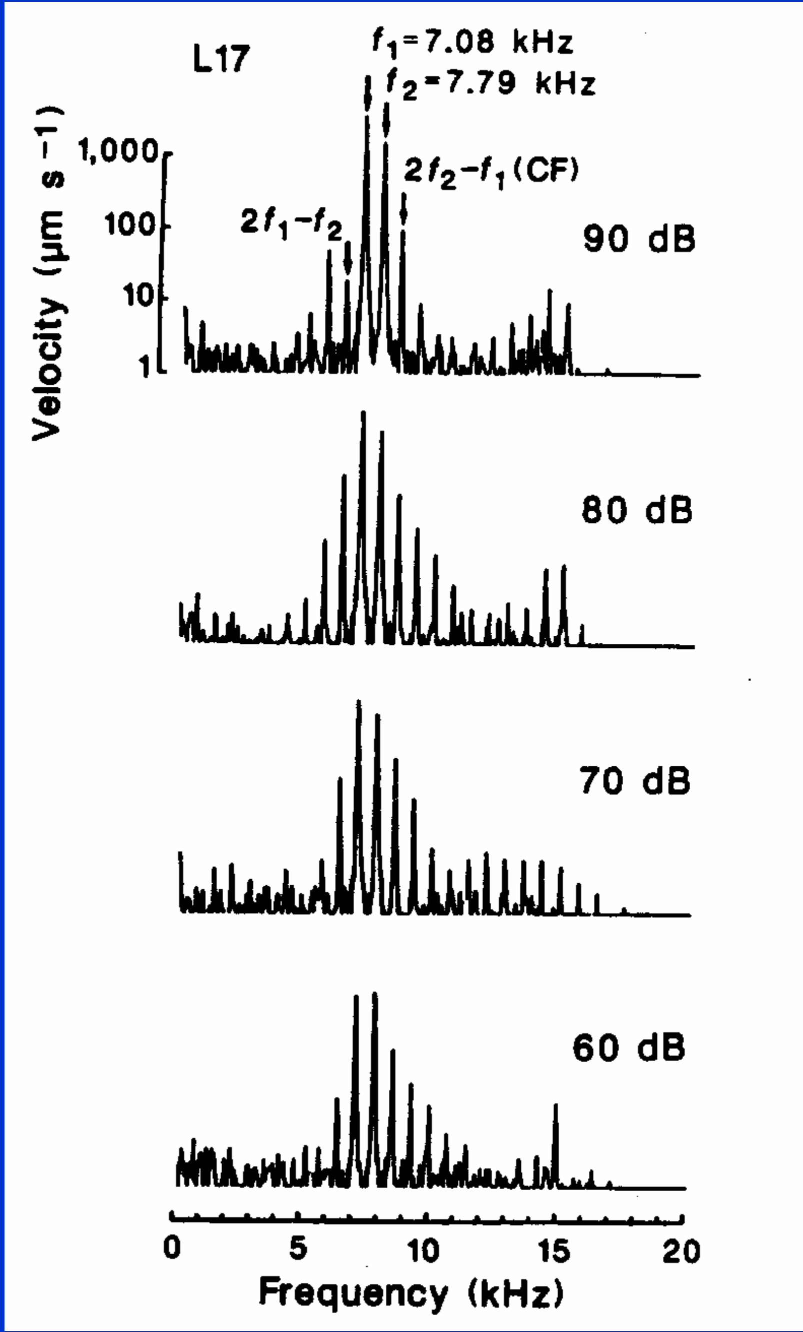

Nobili F, Mammano F, *JASA*, 1996

# Two-tone suppression



# Distortion products

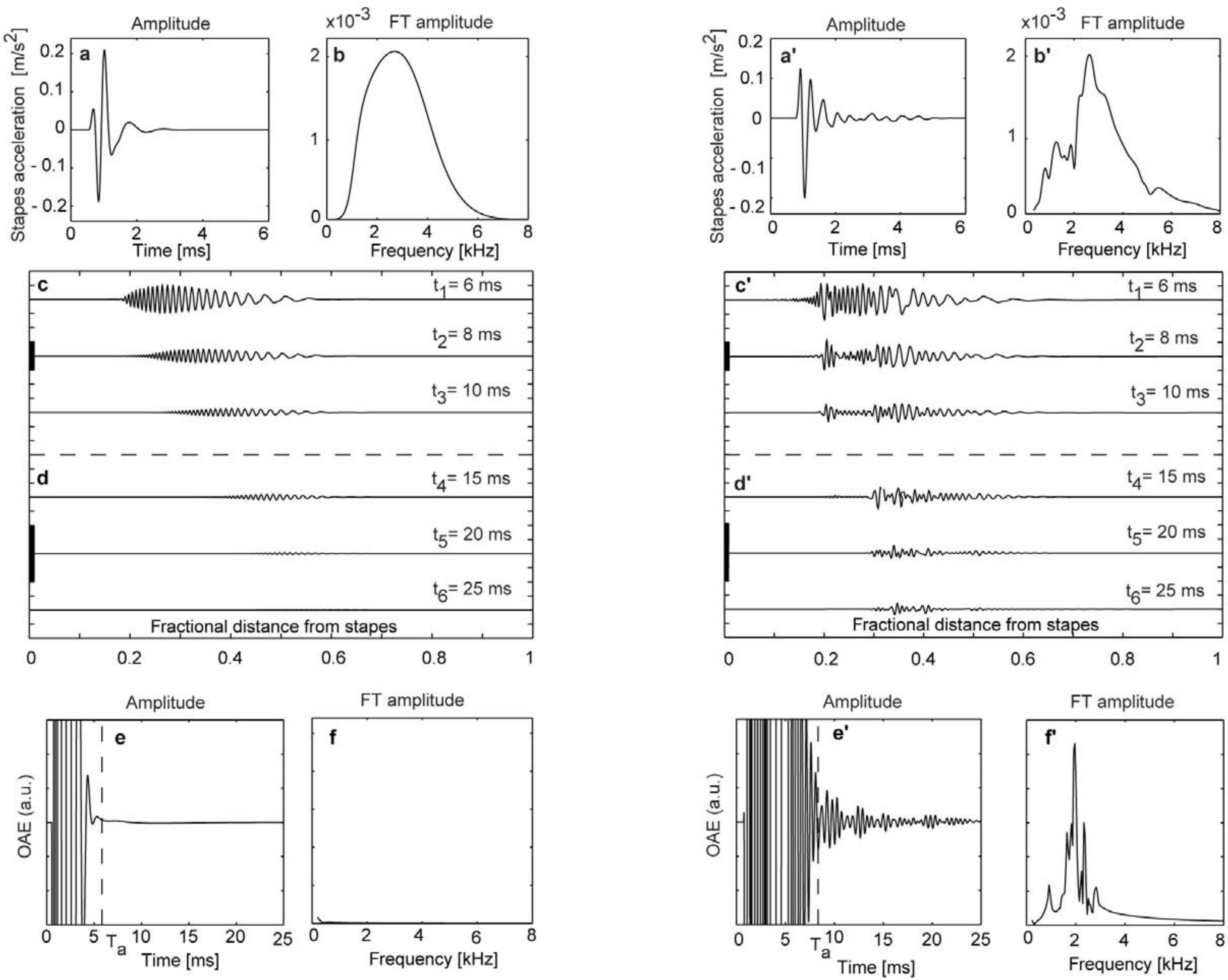



Nobili & Mammano, *J.A.S.A.* 1996

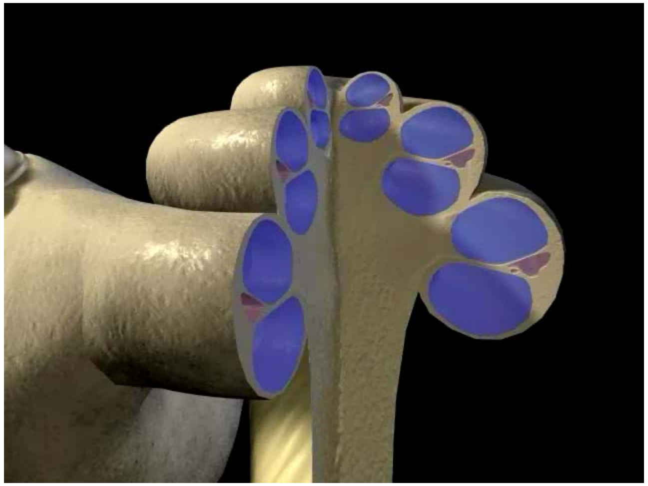
Robles, Ruggero and Rich, 1991

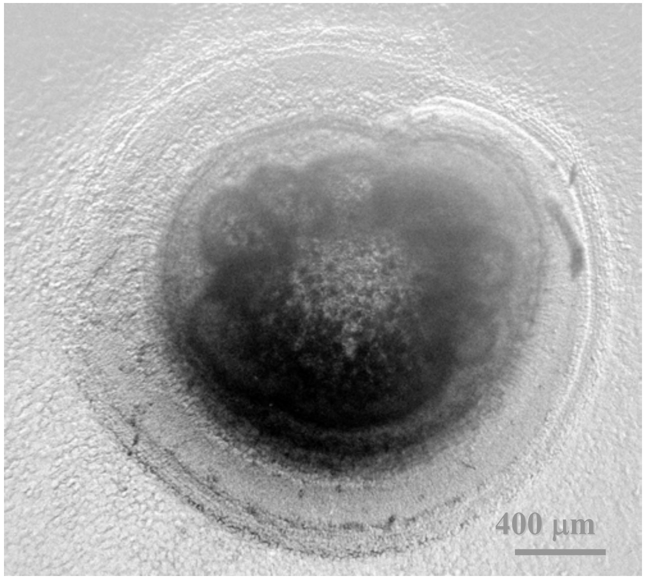
# Otoacoustic emissions from residual oscillations of the basilar membrane



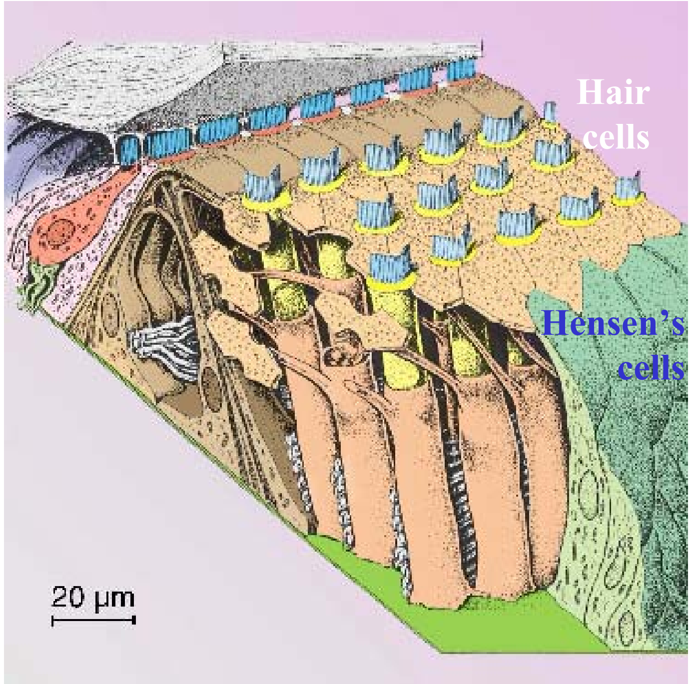

Nobili R, Vetešník A, Turicchia L, Mammano F, *JARO*, 2003

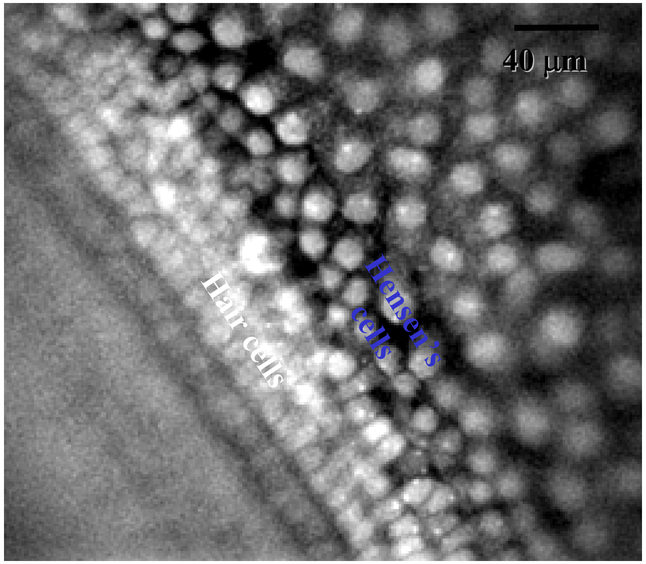
# Cochlear cultures





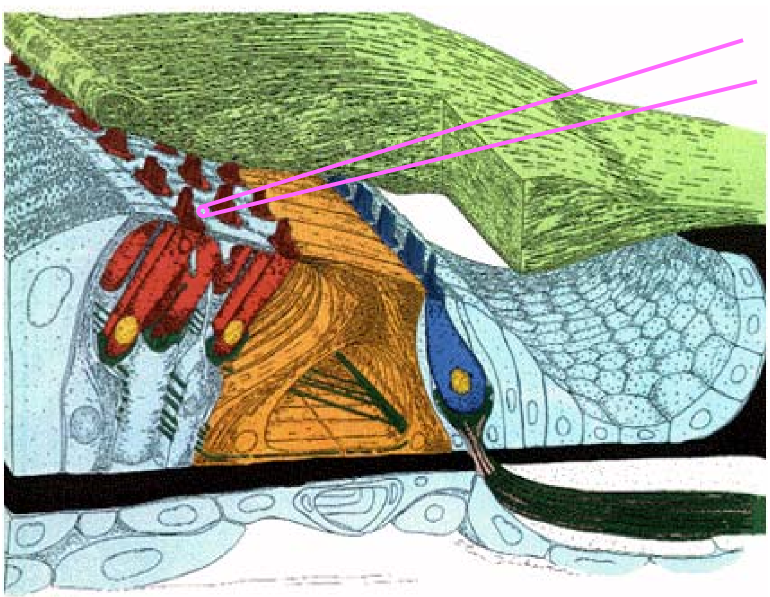

Organotypic culture (rat) P0-P2



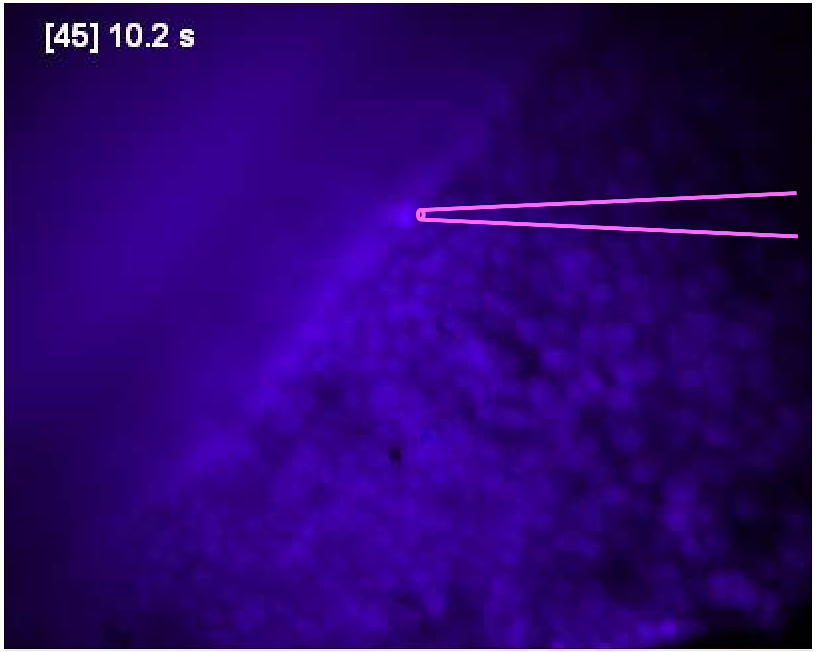




Fura-2 AM, 380 nm

# $Ca^{2+}$ waves elicited by mechanically stimulating a single hair cell in culture



Changes in $[Ca^{2+}]_i$ were monitored while pressing a glass micropipette against a single hair cell.




Mechanical manipulation elicited an intercellular $Ca^{2+}$ wave that spread to the surrounding support cells in the organ of Corti.

1.0 $\Delta R$ 0

Fura-2: R=340nm / 380nm

# http://vimm.it/cochlea