Imperial College London

Active mechanics and fluid dynamics of the inner ear

Tobias Reichenbach

Department of Bioengineering,
Imperial College London

Physics of Hearing:
From Neurobiology to Information Theory and Back

KITP, June 06 2017

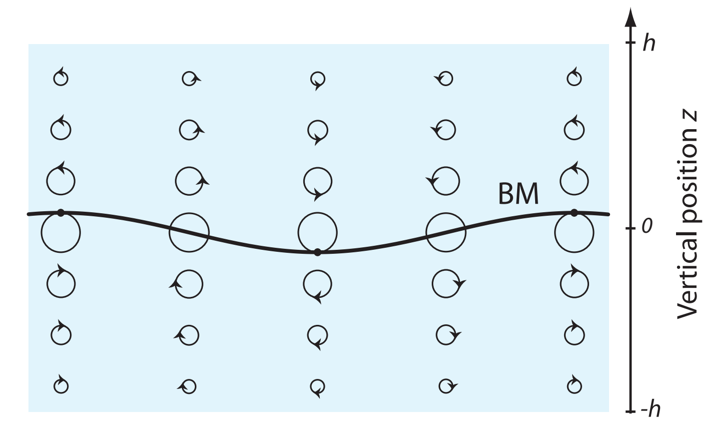
EPSRC
Pioneering research and skills

THE ROYAL SOCIETY

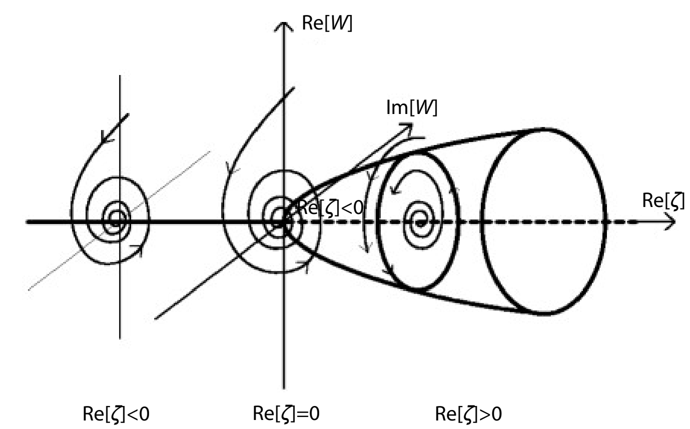
wellcome trust

Outline

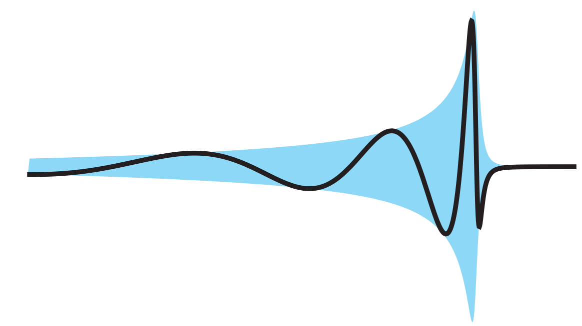
1. Waves on the basilar membrane and in the cochlear fluid



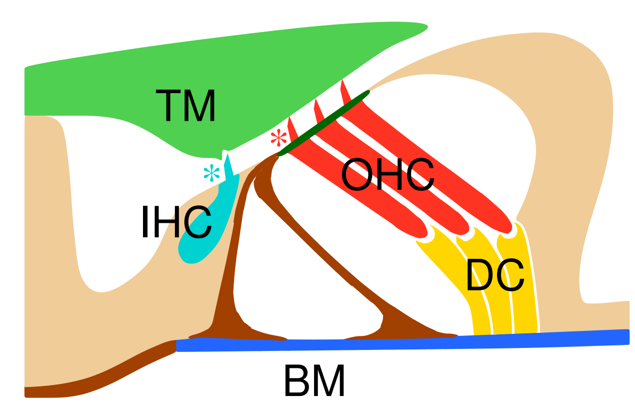
2. Passive and active resonance; Hopf bifurcation



3. Critical layer absorption and WKB approximation



4. Micromechanics of the organ of Corti at low frequencies



5. Otoacoustic emissions

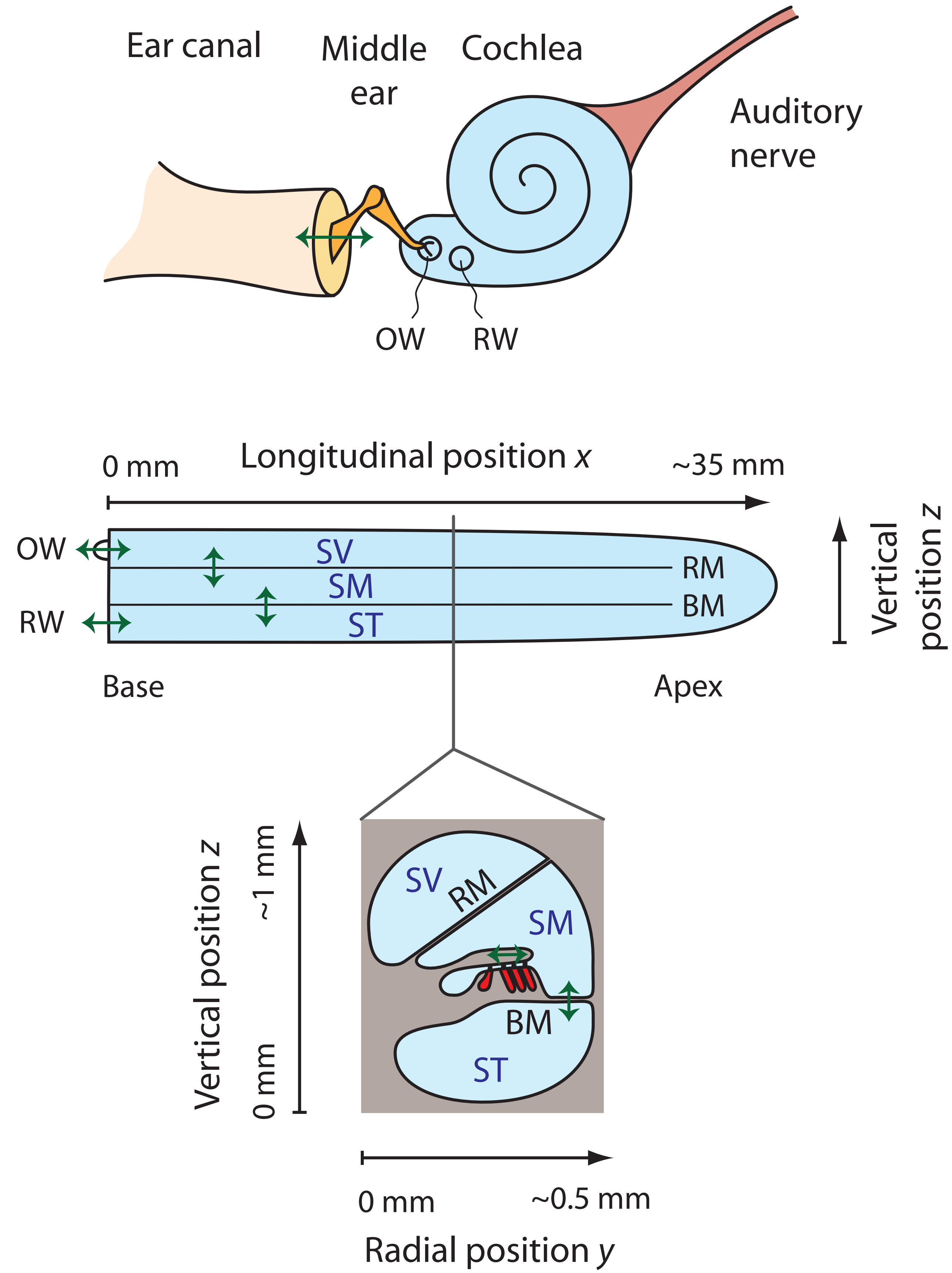
1. Waves on the basilar membrane and in the fluid

Geometry of the cochlea

<u>Three fluid-filled chambers:</u>
scala vestibuli
scala media
scala tympani

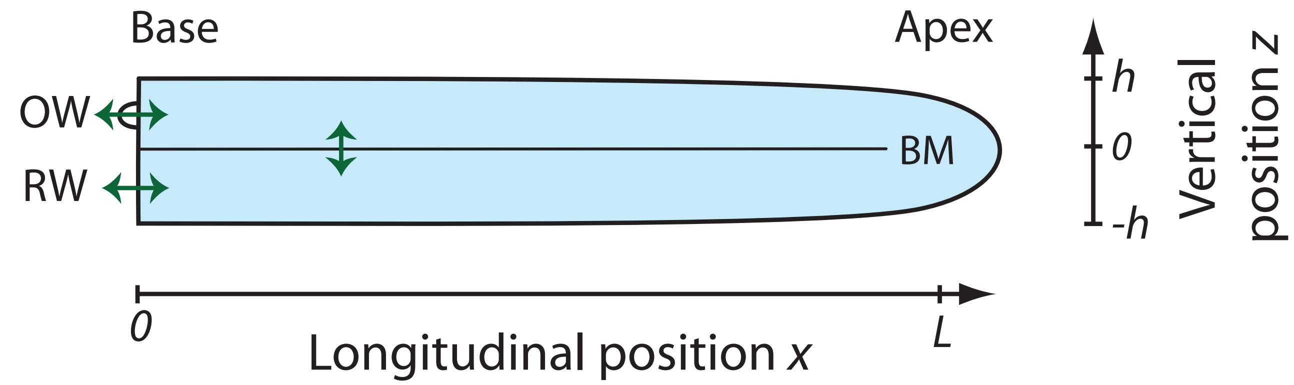
longitudinal section

transverse section

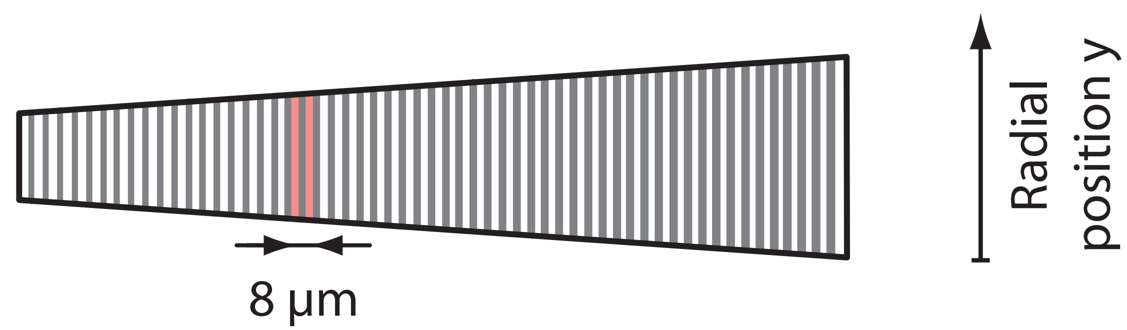


Waves in the cochlea

longitudinal section

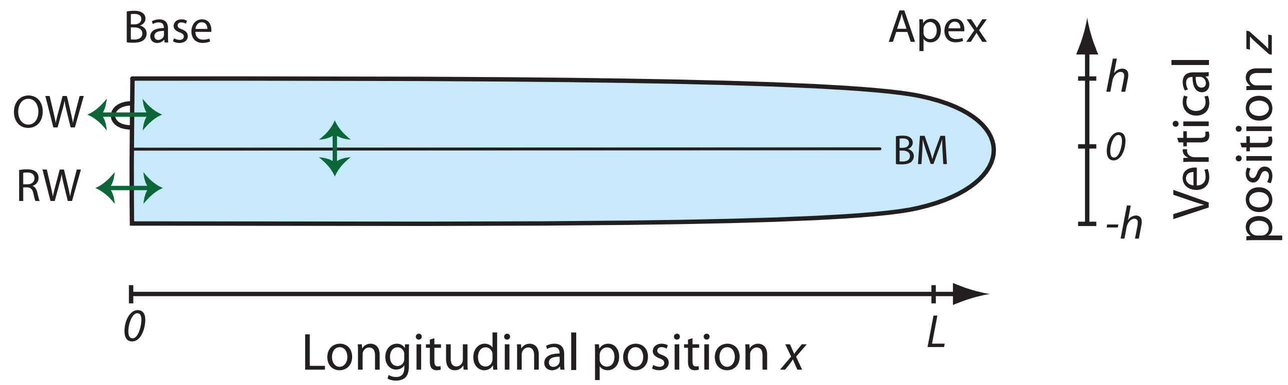


basilar membrane

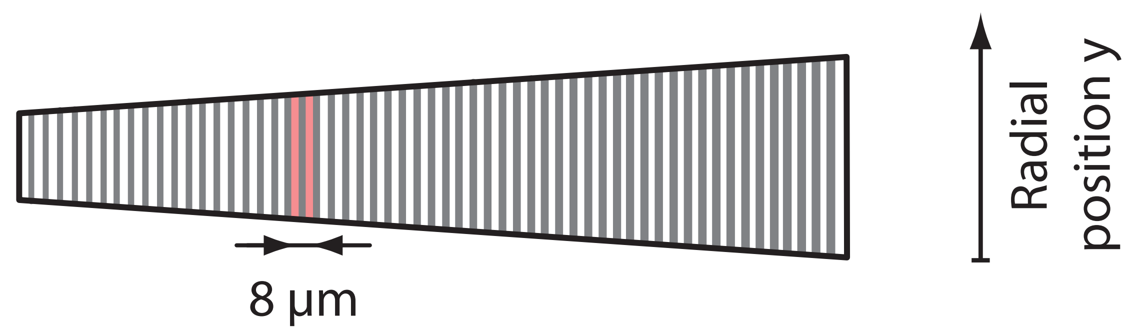


Waves in the cochlea

longitudinal section



basilar membrane



Consider oscillating pressures in chambers 1 and 2: $p^{(1,2)} = \tilde{p}^{(1,2)} e^{i\omega t} + c.c.$

single angular frequency ω

Waves in the cochlea

Wave equation: $$\Delta\tilde{p}^{(1,2)} = -\omega^2 \rho_0 \kappa \tilde{p}^{(1,2)}$$

fluid density

fluid compressibility

Boundary condition at the membrane: $$\tilde{V} = \frac{1}{Z}\left(\tilde{p}^{(2)} - \tilde{p}^{(1)}\right)\Big|_{z=0}$$

membrane velocity

membrane impedance

Waves in the cochlea

Wave equation: $\Delta\tilde{p}^{(1,2)} = -\omega^2\rho_0\kappa\tilde{p}^{(1,2)}$

fluid density

fluid compressibility

Boundary condition at the membrane: $\tilde{V} = \frac{1}{Z}\left(\tilde{p}^{(2)} - \tilde{p}^{(1)}\right)\Big|_{z=0}$

membrane velocity

membrane impedance

<u>Two solutions:</u>

1. Symmetric: $\tilde{p}^{(1)} = \tilde{p}^{(2)}$ => no membrane displacement, 'fast' sound wave

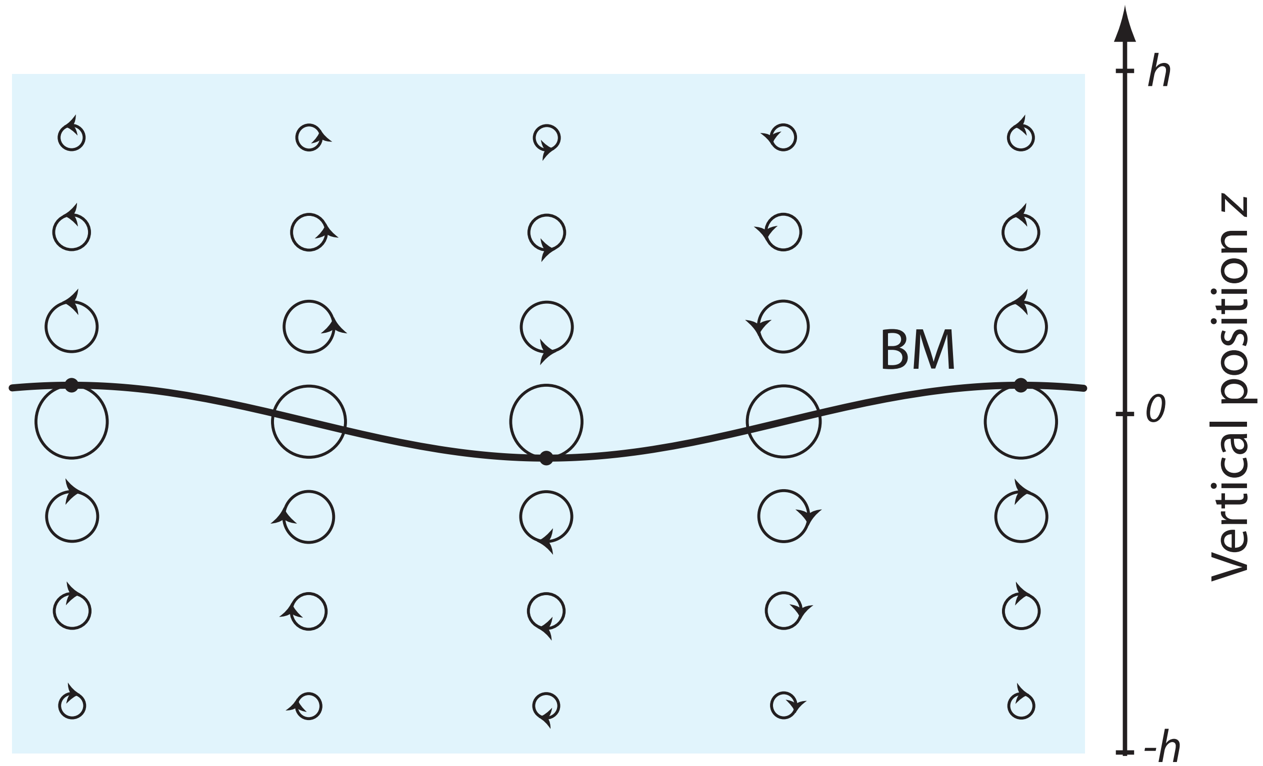
2. Antisymmetric: $\tilde{p}^{(1)} = -\tilde{p}^{(2)}$

$$\tilde{p}^{(1)} = \hat{p}\cosh[k(z-h)]e^{-ikx} + c.c.$$

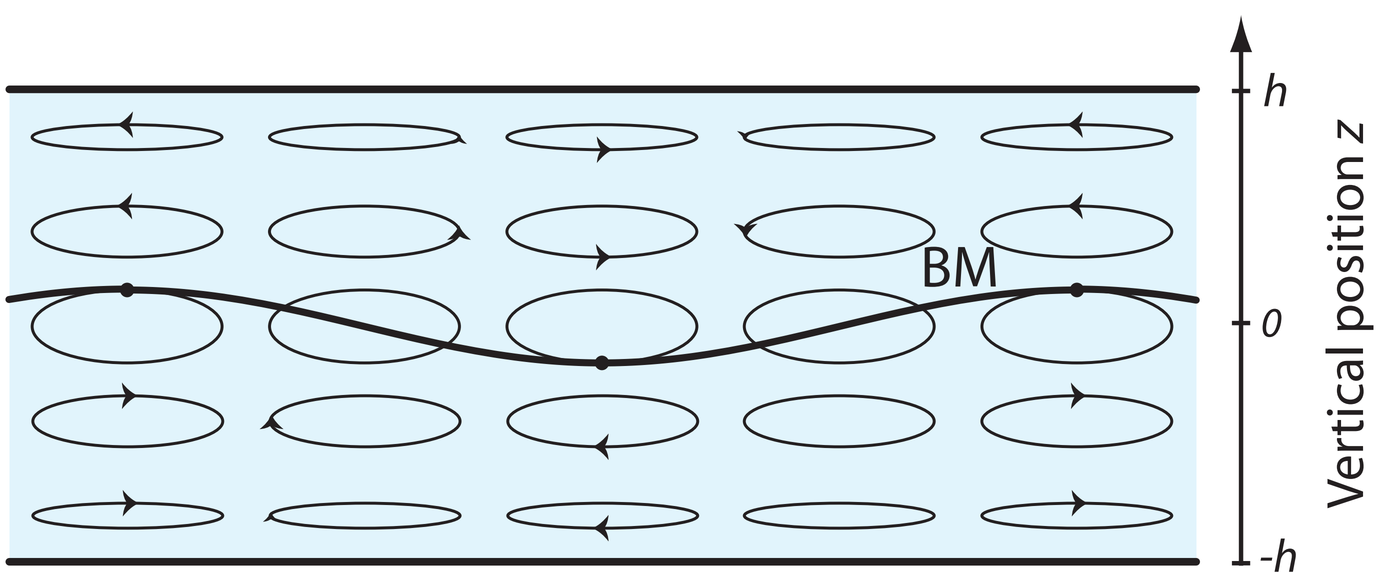
$$k\tanh[kh] = -2i\rho_0\omega / Z$$ => 'slow' wave

The ‘slow’ wave: particle motion

Deep chambers:



Shallow chambers:



Waves on a water surface

Digression: monster waves

ELSEVIER

23 October 2000

Physics Letters A 275 (2000) 386–393

PHYSICS LETTERS A

www.elsevier.nl/locate/pla

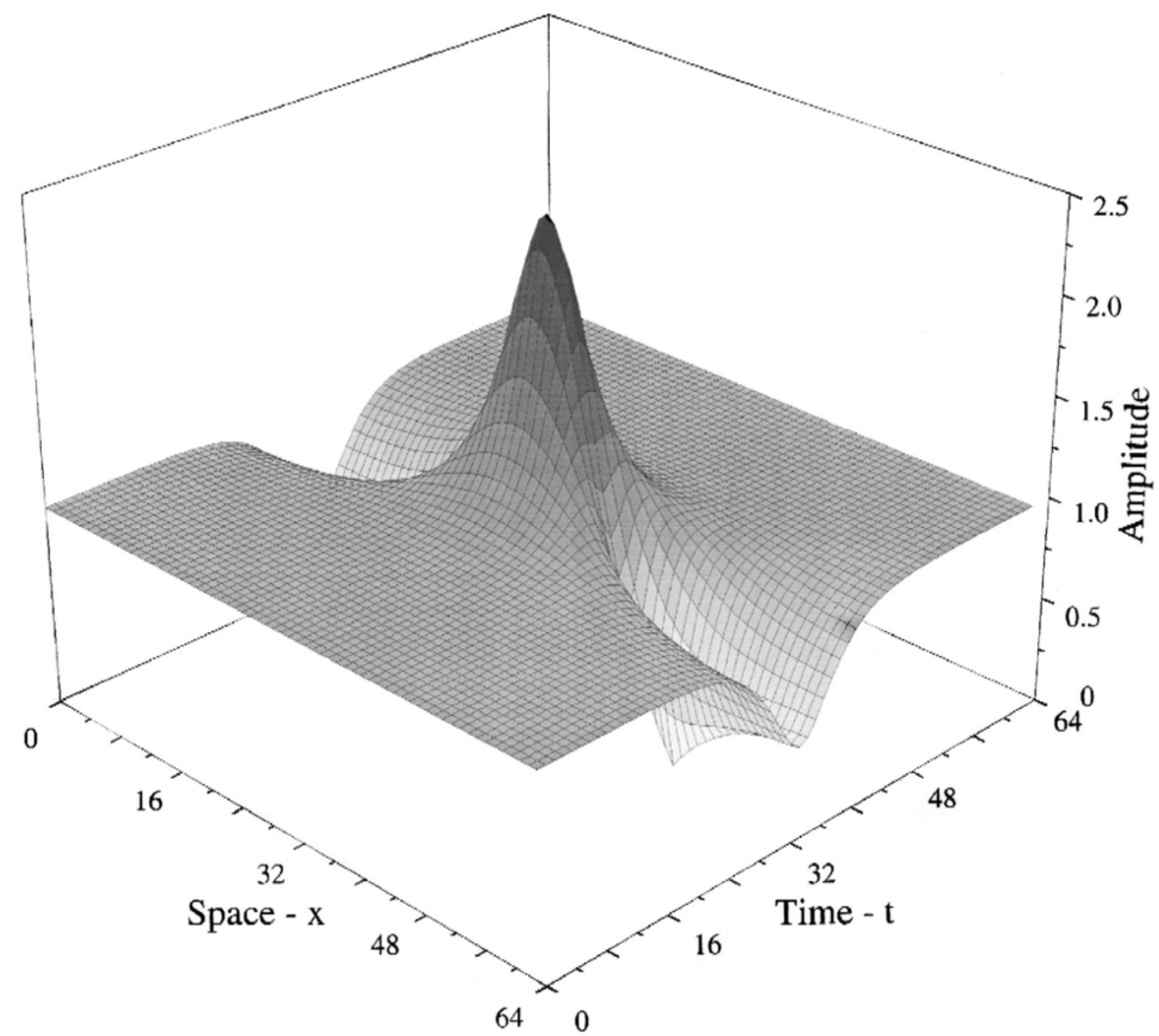
The nonlinear dynamics of rogue waves and holes in deep-water gravity wave trains

Alfred R. Osborne [a,2], Miguel Onorato [a,1,2], Marina Serio [a,2]

[a] *Dipartimento di Fisica Generale, Università di Torino, 10126 Torino, Italy*

Received 21 August 2000; accepted 28 August 2000

Communicated by A.R. Bishop



Digression: monster waves

ELSEVIER

23 October 2000

Physics Letters A 275 (2000) 386–393

PHYSICS LETTERS A

www.elsevier.nl/locate/pla

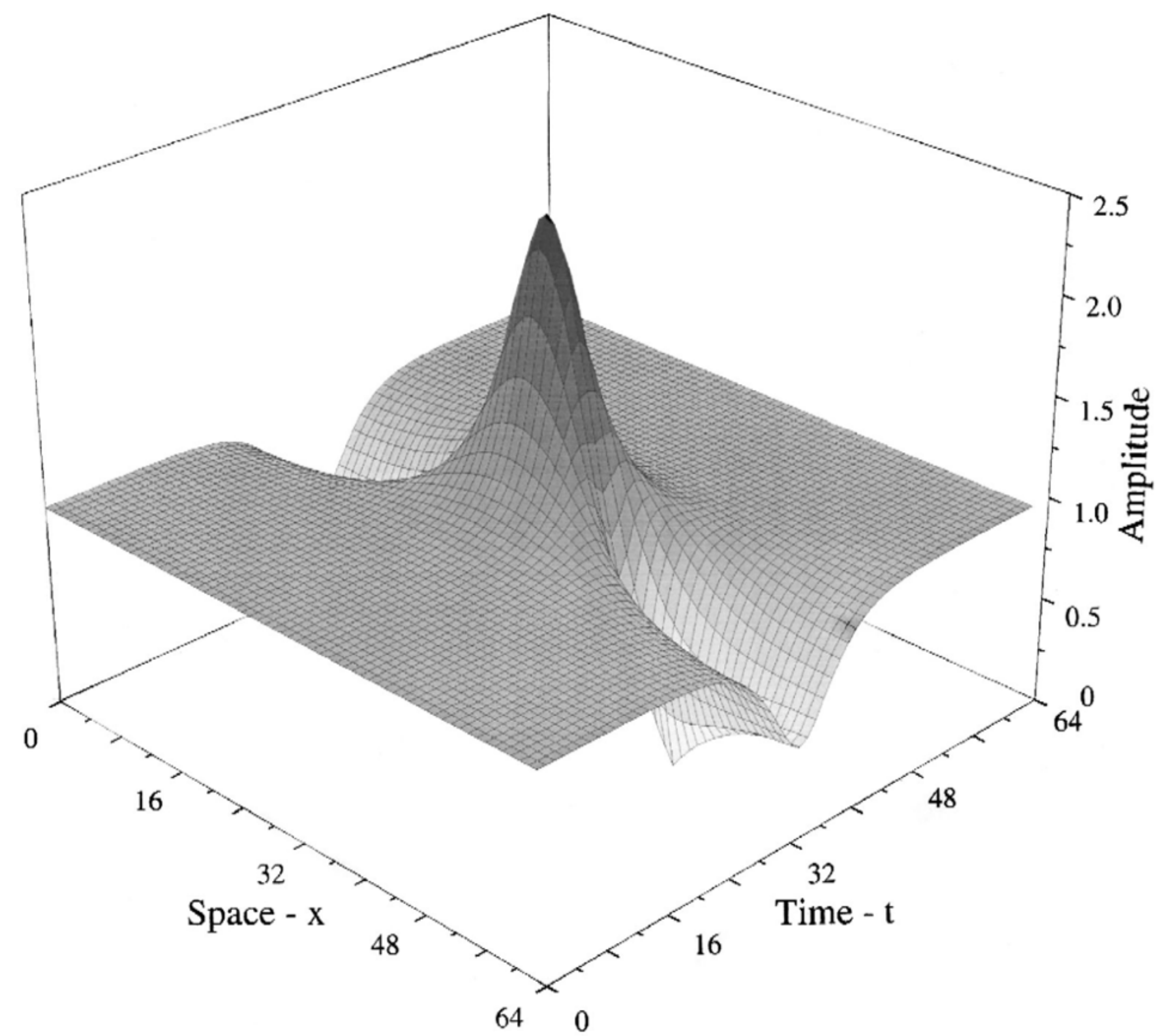
The nonlinear dynamics of rogue waves and holes in deep-water gravity wave trains

Alfred R. Osborne [a,2], Miguel Onorato [a,1,2], Marina Serio [a,2]

[a] *Dipartimento di Fisica Generale, Università di Torino, 10126 Torino, Italy*

Received 21 August 2000; accepted 28 August 2000

Communicated by A.R. Bishop



History: Bekesy and Lighthill

THE JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA VOLUME 19, NUMBER 3 MAY, 1947

The Variation of Phase Along the Basilar Membrane with Sinusoidal Vibrations*

GEORG V. BÉKÉSY
Budapest, Hungary

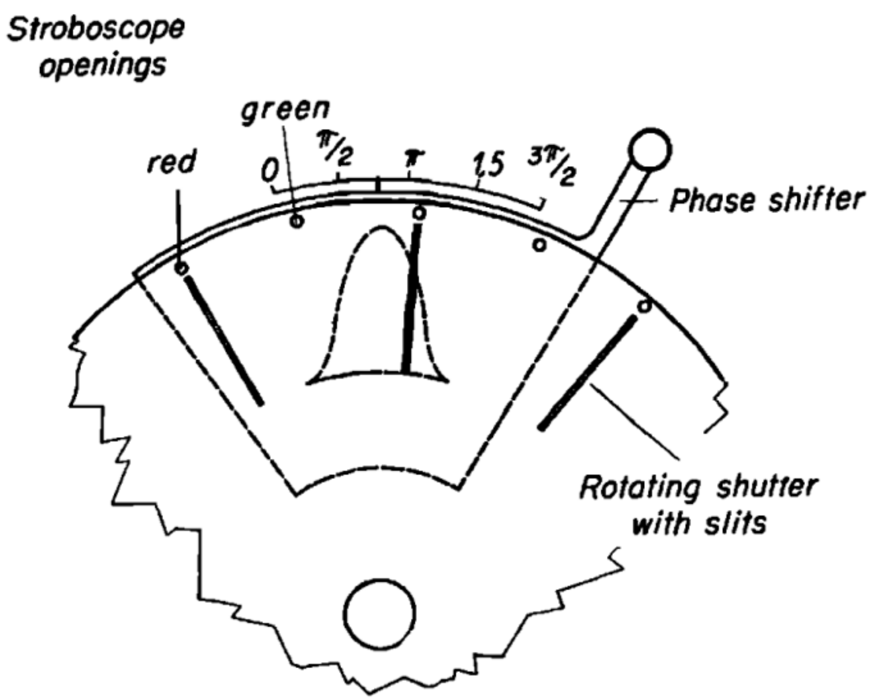


FIG. 3. Rotating shutter and diaphragm of the phase stroboscope. Slits in the rotating shutter pass over the sine-shaped opening. Phase angle can be adjusted by moving the phase shifter with the sine-shaped opening. For $3\pi/2$ read 2π; for 1.5 read $3\pi/2$.

J. Fluid Mech. (1981), *vol.* 106, *pp.* 149–213
Printed in Great Britain

Energy flow in the cochlea

By JAMES LIGHTHILL
University College London

With moderate acoustic stimuli, measurements of basilar-membrane vi
cially, those using a Mössbauer source attached to the membrane) dem
(i) a high degree of *asymmetry*, in that the response to a pure tone fa
sharply above the characteristic frequency, although much more gradu
(ii) a substantial phase-lag in that response, and one which increases m
up to the characteristic frequency;
(iii) a response to a 'click' in the form of a delayed 'ringing' osci
characteristic frequency, which persists for around 20 cycles.
This paper uses energy-flow considerations to identify which features
matical model of cochlear mechanics are necessary if it is to reproduce
mental findings.
The response (iii) demands a travelling-wave model which incorpo
lightly damped resonance. Admittedly, waveguide systems including
described in classical applied physics. However, a classical wavegu
reflects a travelling wave, thus converting it into a standing wave devo

2. Passive and active resonance; Hopf bifurcation

Mechanical oscillator

response of a membrane segment (displacement X) to forcing (pressure p):

$$m\partial_t^2 X + \xi\partial_t X + KX = Ap$$

mass damping stiffness area

Resonance at

$$\omega_0 = \sqrt{K/m}$$

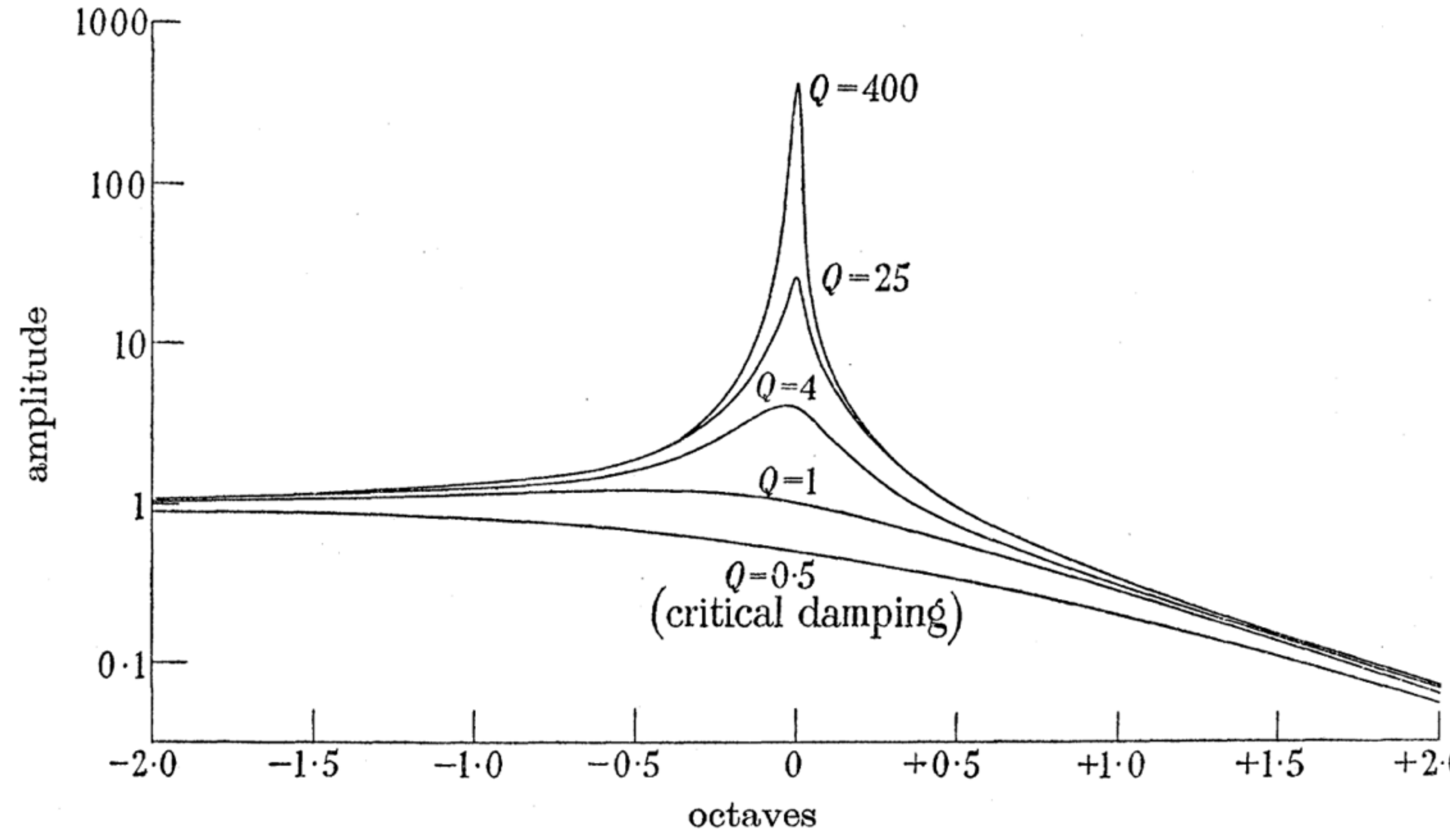
Thus, for example, it is known that the largest church-bells may be set in motion by a man, or even a boy, who pulls the ropes attached to them at proper and regular intervals, even when their weight of metal is so great that the strongest man could scarcely move them sensibly, if he did not apply his strength in determinate periodical intervals. When such a bell is once set in motion, it continues, like a struck pendulum, to oscillate for some time, until it gradually returns to rest, even if it is left quite by itself, and no force is employed to arrest its motion. The motion diminishes gradually, as we know, because the friction on the axis and the resistance of the air at every swing destroy a portion of the existing moving force.

Helmholtz (1954) On the Sensations of Tone

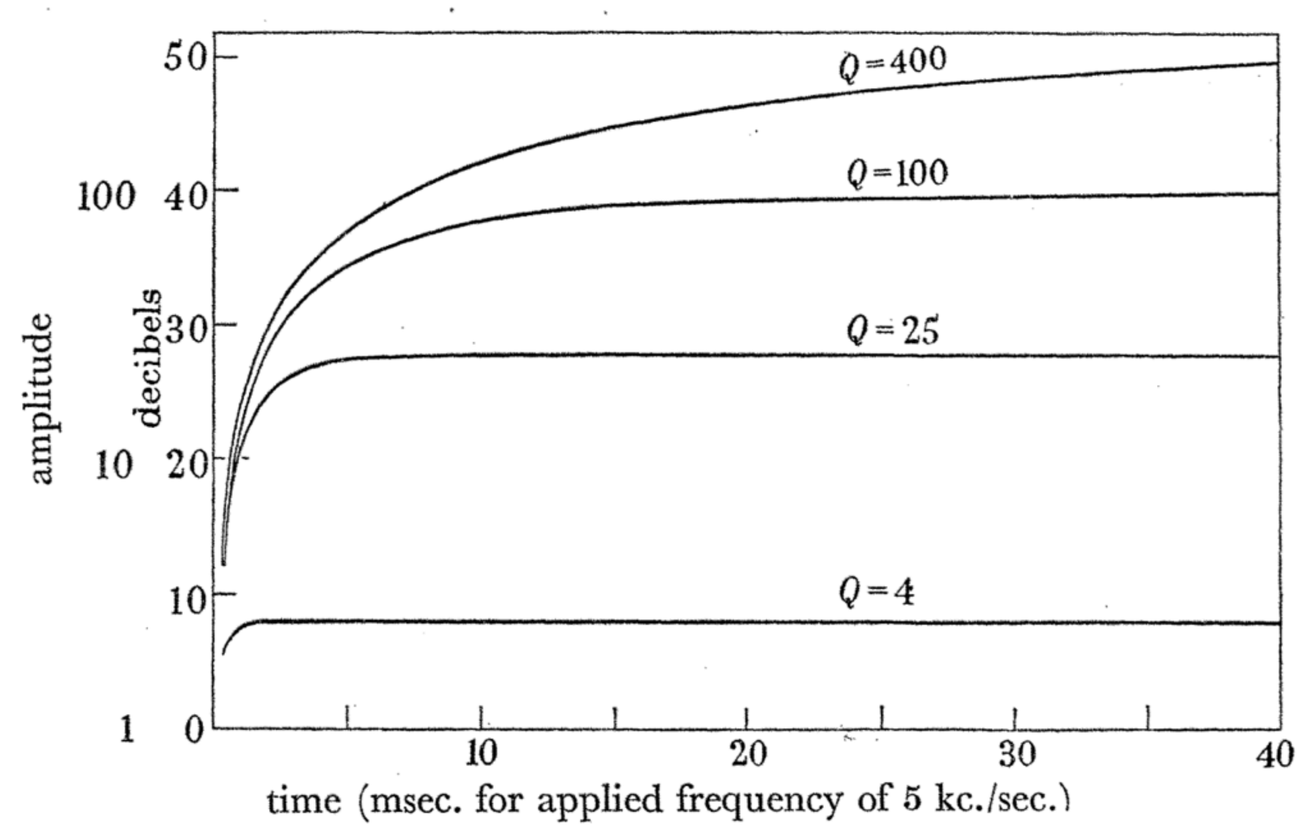
Damping, quality factor and temporal response

Sharpness of resonance measured by quality factor Q:

$$Q = \sqrt{Km}/\xi$$



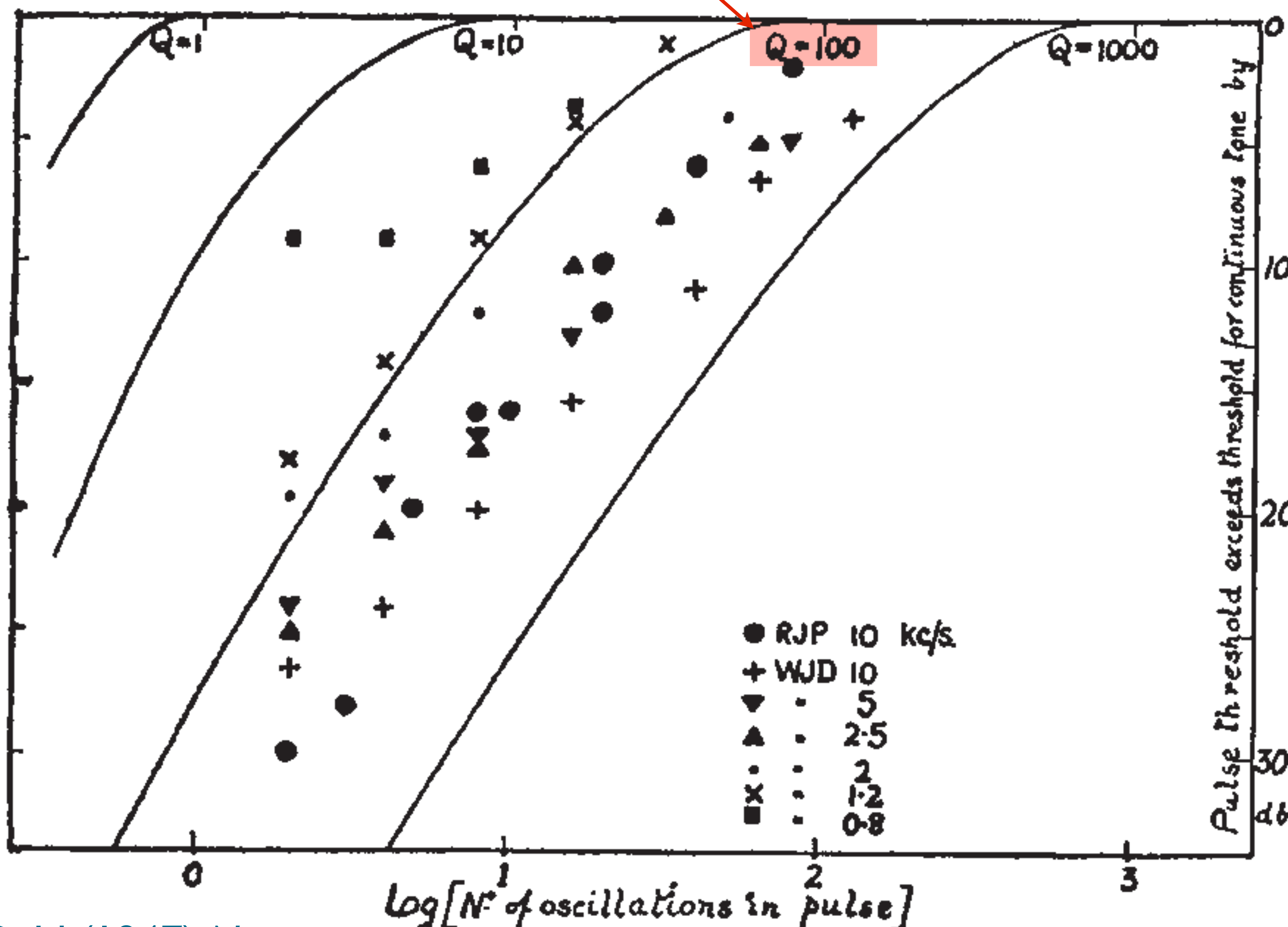
Oscillator responds slower to forcing for higher value of Q



Gold and Pumphrey (1948)
Proc. Roy. Soc. Lond. B

Active oscillator?

hard to get from a passive oscillator under water!



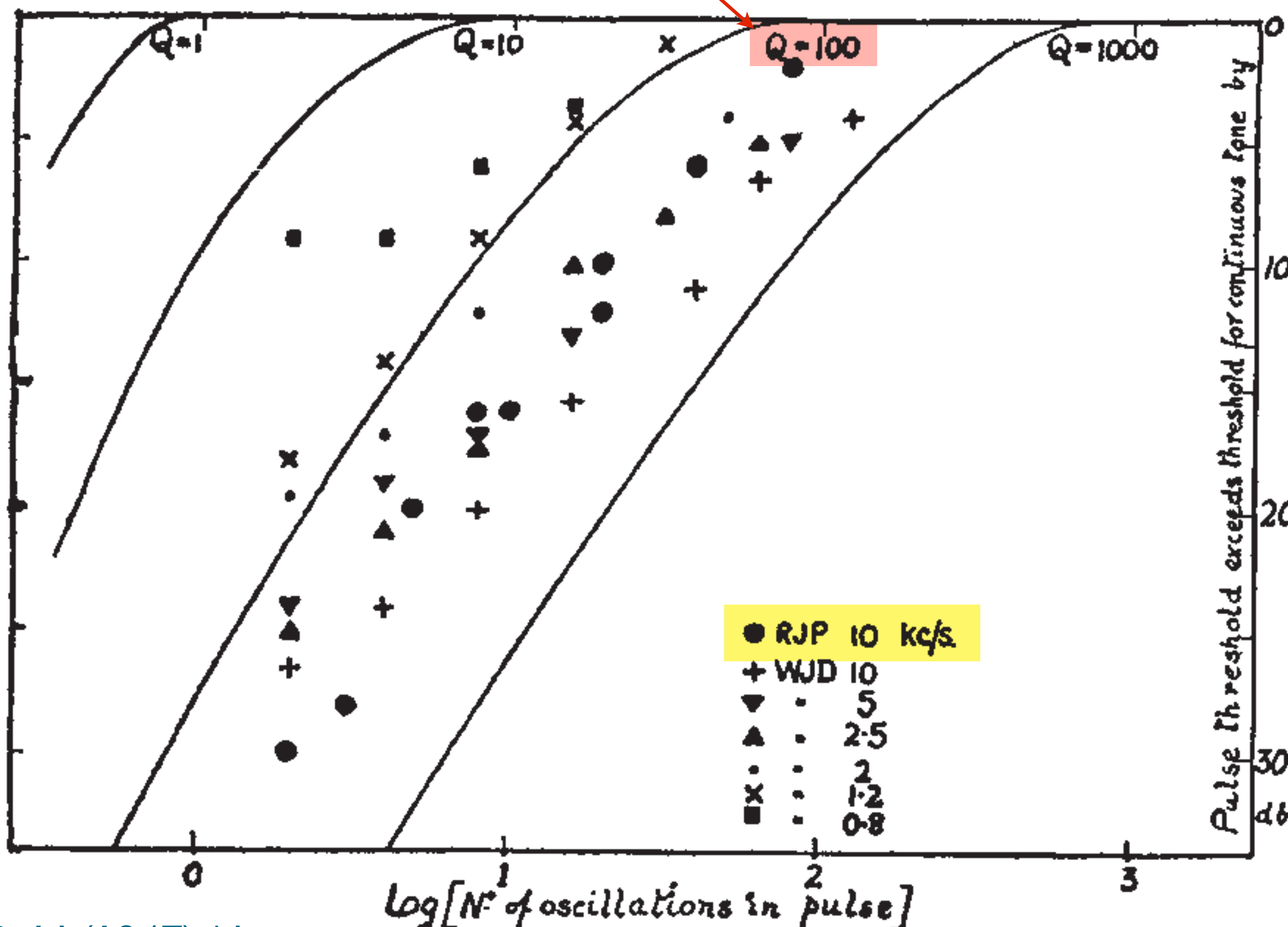
Psychacoustic experiment:

Theshold for detection of short tone pulses

R. J. Pumphrey and T. Gold (1947) *Nature*

Active oscillator?

hard to get from a passive oscillator under water!



Psychacoustic experiment:

Theshold for detection of short tone pulses

R. J. Pumphrey and T. Gold (1947) *Nature*

Hopf bifurcation

nonlinear response

mechanical oscillator: $$m\partial_t^2 X + \xi\partial_t X + KX + h_{nonlinear}(X,\partial_t X) = Ap$$

Wiggins (1990) Introduction to Applied Nonlinear Dynamical Systems and Chaos

Hopf bifurcation

nonlinear response

mechanical oscillator: $m\partial_t^2 X + \xi\partial_t X + KX + h_{nonlinear}(X,\partial_t X) = Ap$

can be written as $\partial_t \begin{pmatrix} X \\ V \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -K/m & -\xi/m \end{pmatrix} \begin{pmatrix} X \\ V \end{pmatrix} + g_{nonlinear}(X,V) + \begin{pmatrix} 0 \\ Ap/m \end{pmatrix}$

with velocity *V*: $V = \partial_t X$

Wiggins (1990) Introduction to Applied Nonlinear Dynamical Systems and Chaos

Hopf bifurcation

nonlinear response

mechanical oscillator: $m\partial_t^2 X + \xi\partial_t X + KX + h_{nonlinear}(X,\partial_t X) = Ap$

can be written as $\partial_t \begin{pmatrix} X \\ V \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -K/m & -\xi/m \end{pmatrix} \begin{pmatrix} X \\ V \end{pmatrix} + g_{nonlinear}(X,V) + \begin{pmatrix} 0 \\ Ap/m \end{pmatrix}$

with velocity *V*: $V = \partial_t X$

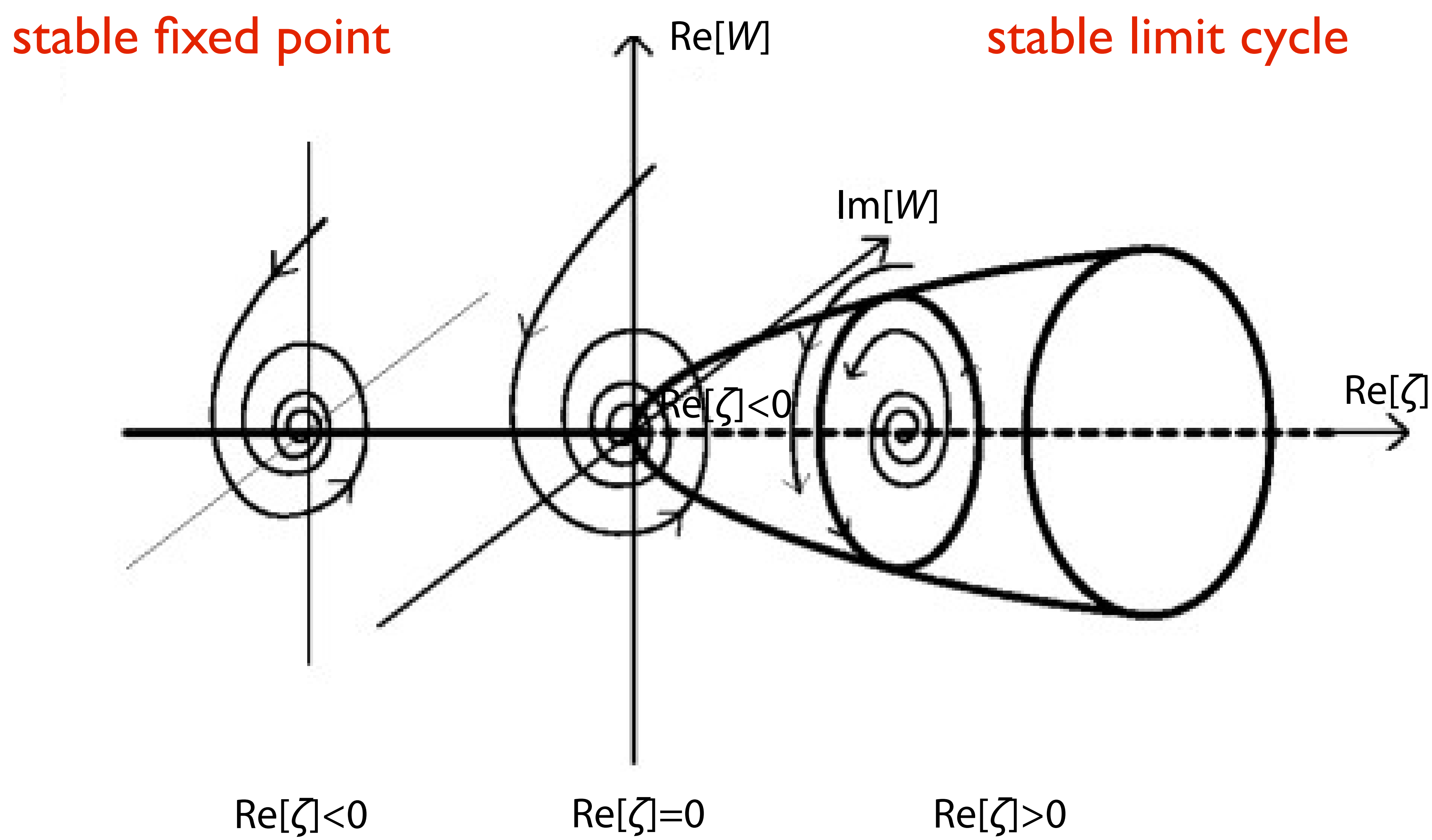
Theorem: can be transformed to $\partial_t W = (\zeta_r + i\omega_*)W - (\nu + i\sigma)|W|^2 W + P$

Normal form of the Hopf bifurcation!

Wiggins (1990) Introduction to Applied Nonlinear Dynamical Systems and Chaos

Hopf bifurcation

$$\partial_t W = (\zeta + i\omega_*)W - (\nu + i\sigma)|W|^2 W$$ normal form of the Hopf bifurcation

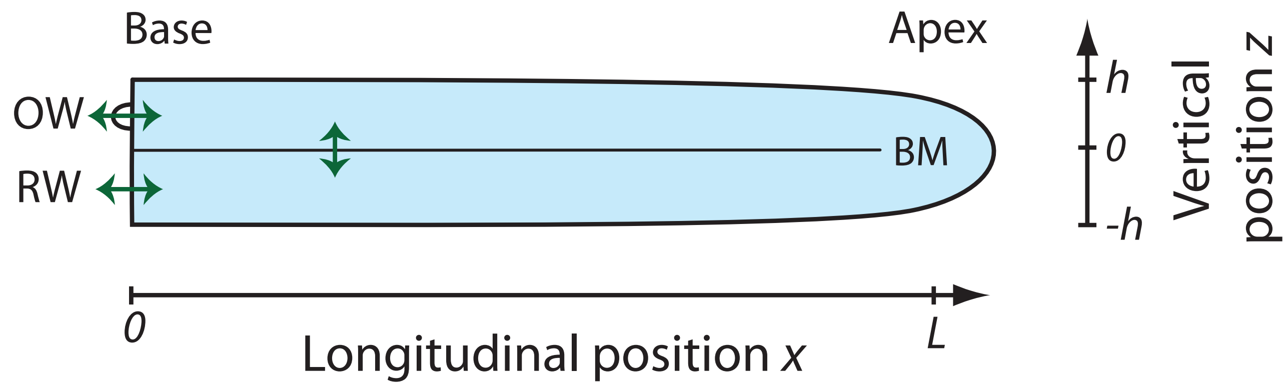


Choe, Magnasco, Hudspeth (1998) *Proc. Natl. Acad. Sci. USA*; Camalet, Duke, Jülicher Prost (2000) *Proc. Natl. Acad. Sci. USA*; Eguiluz, Ospeck, Choe Hudspeth, Magnasco (2000) *Phys. Rev. Lett.*; Duke and Jülicher (2003) *Phys. Rev. Lett.*; Kern, Stoop (2003) *Phys. Rev. Lett.*; Magnasco (2003) *Phys. Rev. Lett.*

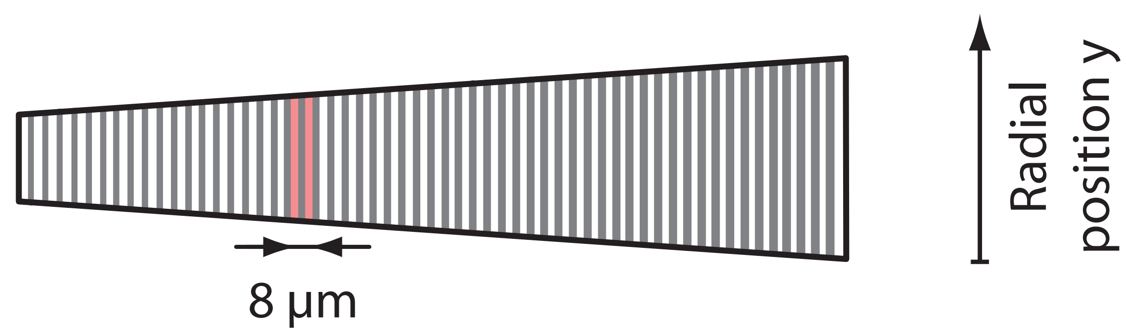
3. Critical layer absorption and WKB approximation

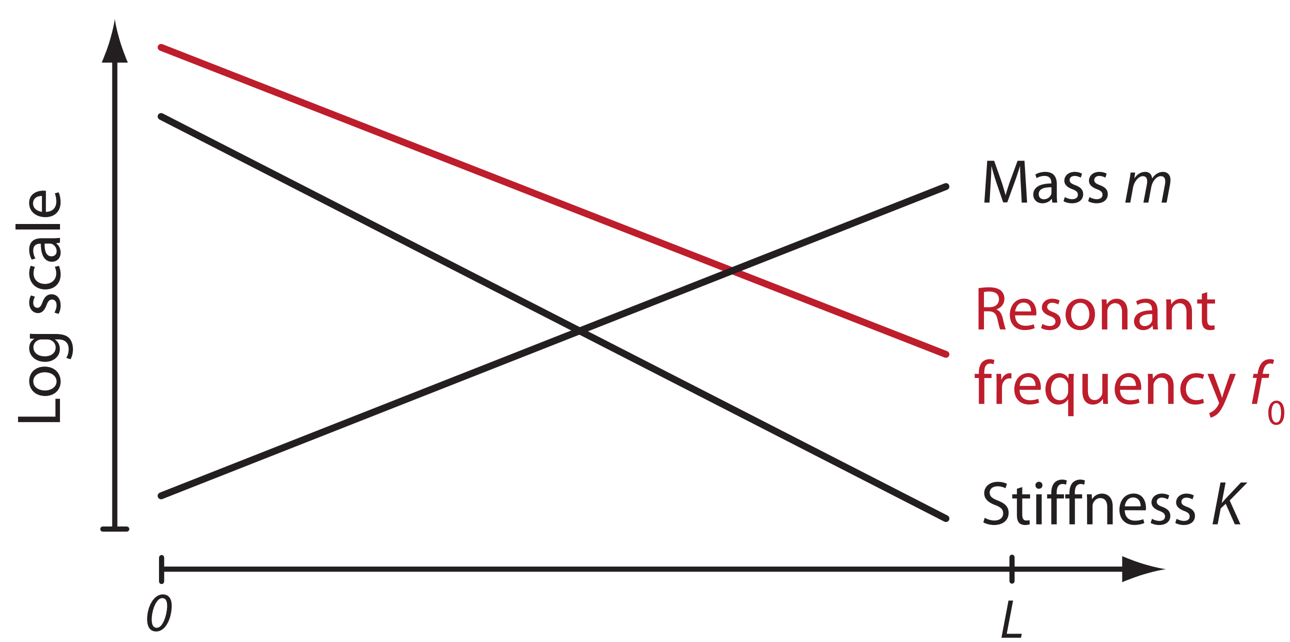
Local resonances in the cochlea

longitudinal section



basilar membrane





How do the local resonances shape the traveling wave?

WKB approximation and energy flow

ansatz for pressure at the membrane: $\tilde{p} = \hat{p}(x)\exp\left[-i\int_0^x dx'k(x')\right]$

<u>WKB approximation:</u>
assume length scale at which impedance changes is long compared to wavelength
=> wave vector follows from local impedance:

$$k^2(x) = -2i\omega\rho_0 / [Z(x)h]$$

=> wavelength: $\lambda \sim \sqrt{Z}$ speed: $c \sim \sqrt{Z}$

amplitude: $\hat{p} \sim \sqrt[4]{Z}$

WKB approximation and energy flow

ansatz for pressure at the membrane: $\tilde{p} = \hat{p}(x)\exp\left[-i\int_0^x dx' k(x')\right]$

<u>WKB approximation:</u>

assume length scale at which impedance changes is long compared to wavelength

=> wave vector follows from local impedance:

$$k^2(x) = -2i\omega\rho_0 / [Z(x)h]$$

=> wavelength: $\lambda \sim \sqrt{Z}$ speed: $c \sim \sqrt{Z}$

amplitude: $\hat{p} \sim \sqrt[4]{Z}$

=> energy flow is conserved:

energy flow ~ pVc with $V = p/Z$

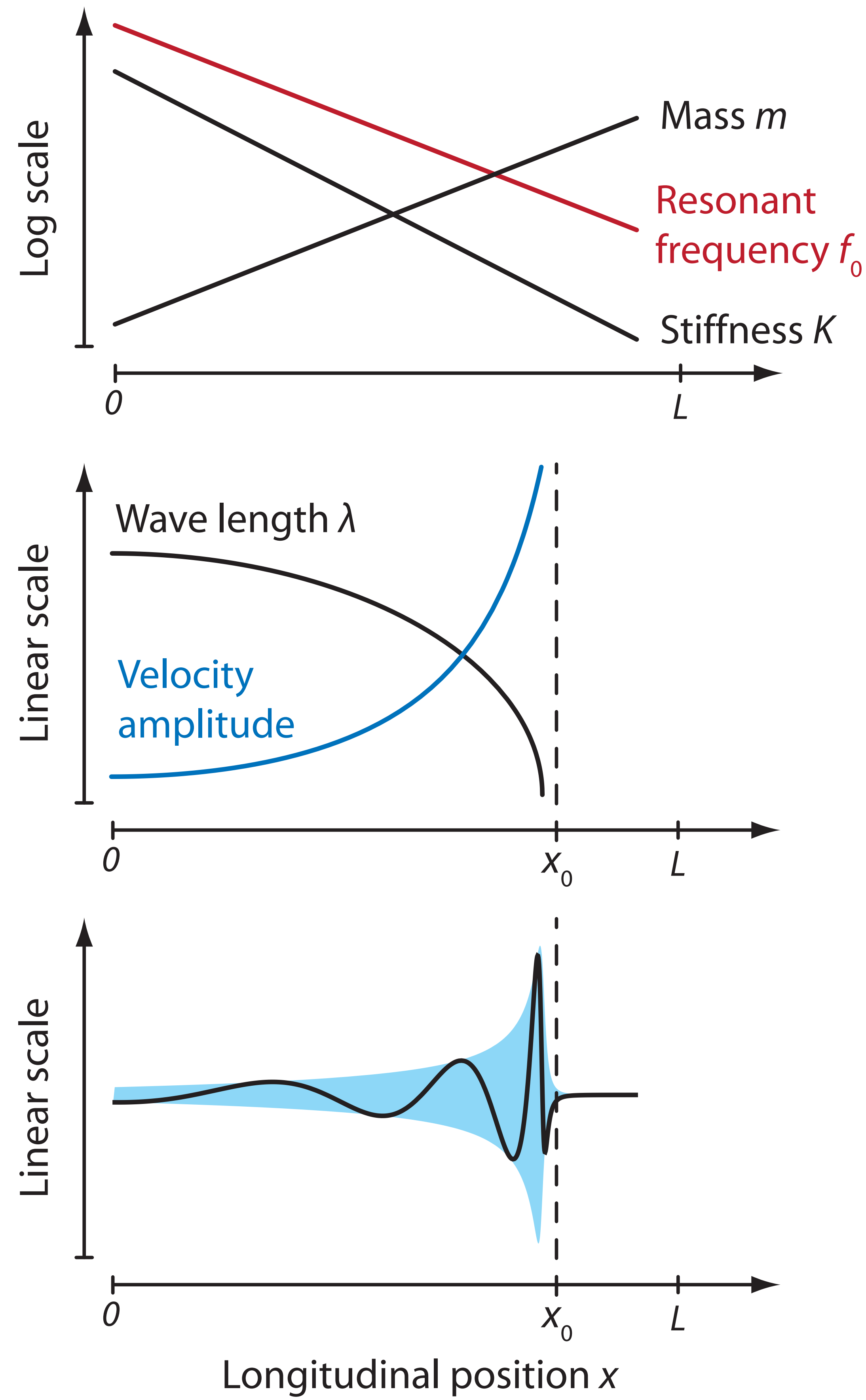
=> energy flow ~ $p^2 c \sim \sqrt{Z}\sqrt{Z}/Z \sim 1$

Critical-layer absorption

Basilar-membrane vibration slows upon approaching resonant position and peaks near it

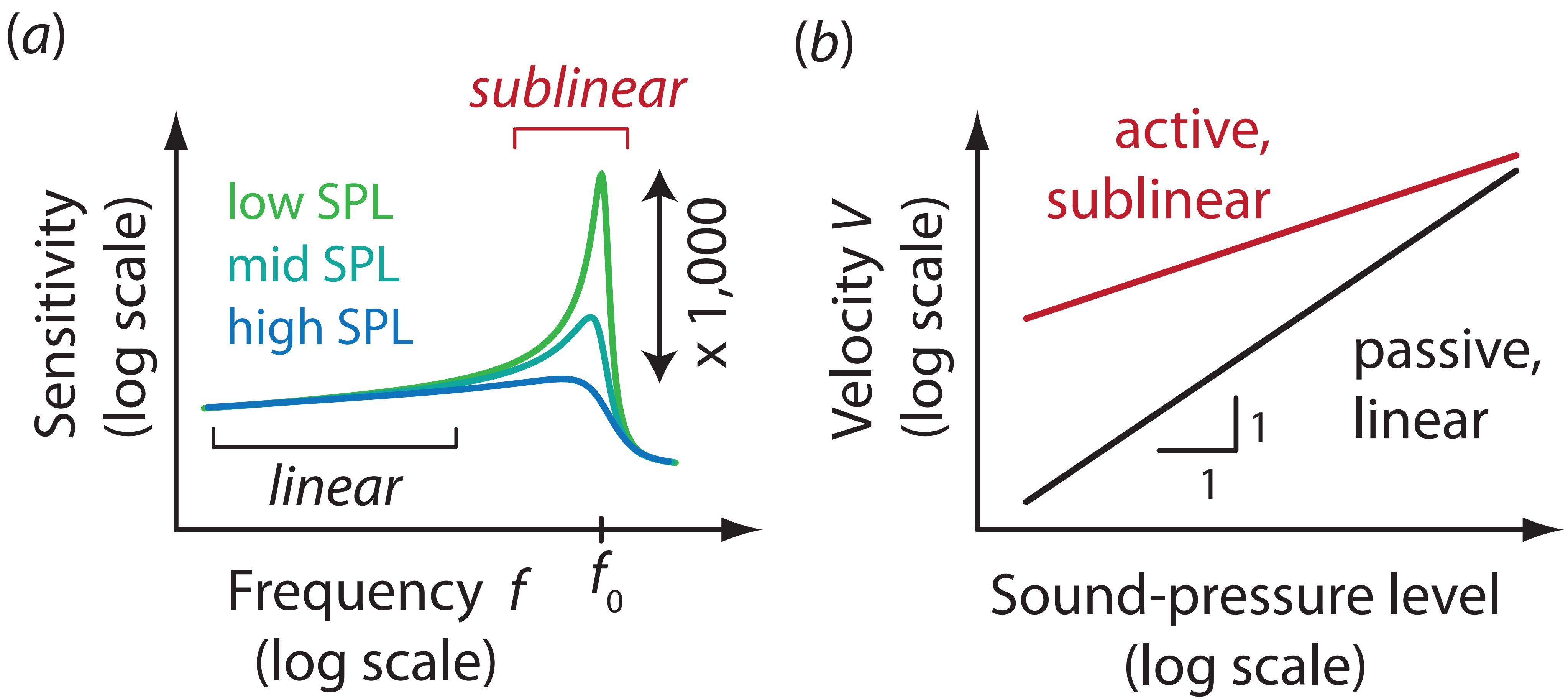
Energy dissipation mostly in this 'critical layer'

traveling wave (displacement/velocity)



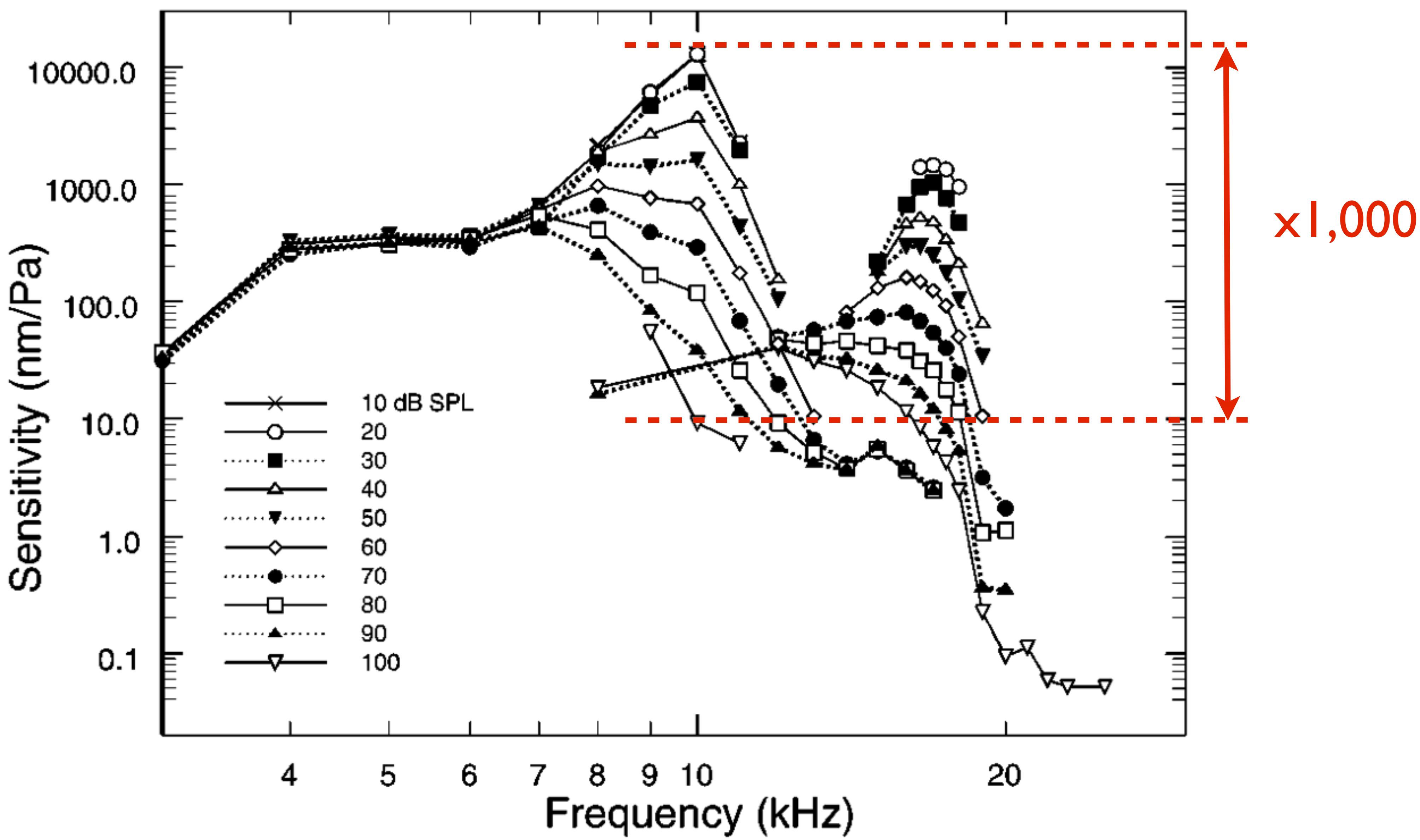
Active wave

Combine traveling wave with nonlinear response of the membrane near the resonance



Duke and Jülicher (2003) *Phys. Rev. Lett.*
Kern, Stoop (2003) *Phys. Rev. Lett.*
Magnasco (2003) *Phys. Rev. Lett.*

Amplification in the cochlea



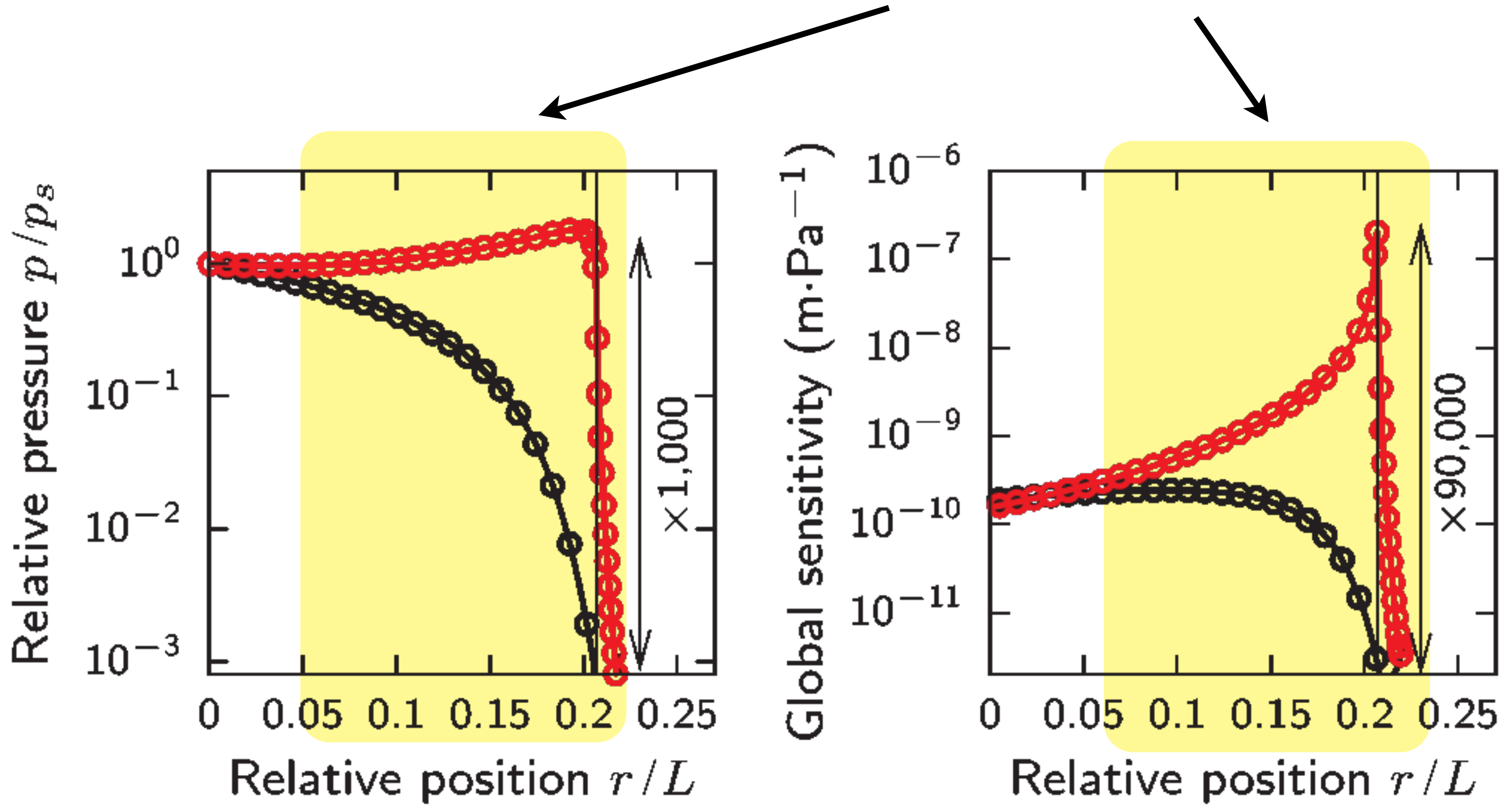
How can such a large gain results from *local* amplification?

Robles and Ruggero (2001) *Physiol. Rev.*

Accumulation of amplification

red: active
black: passive

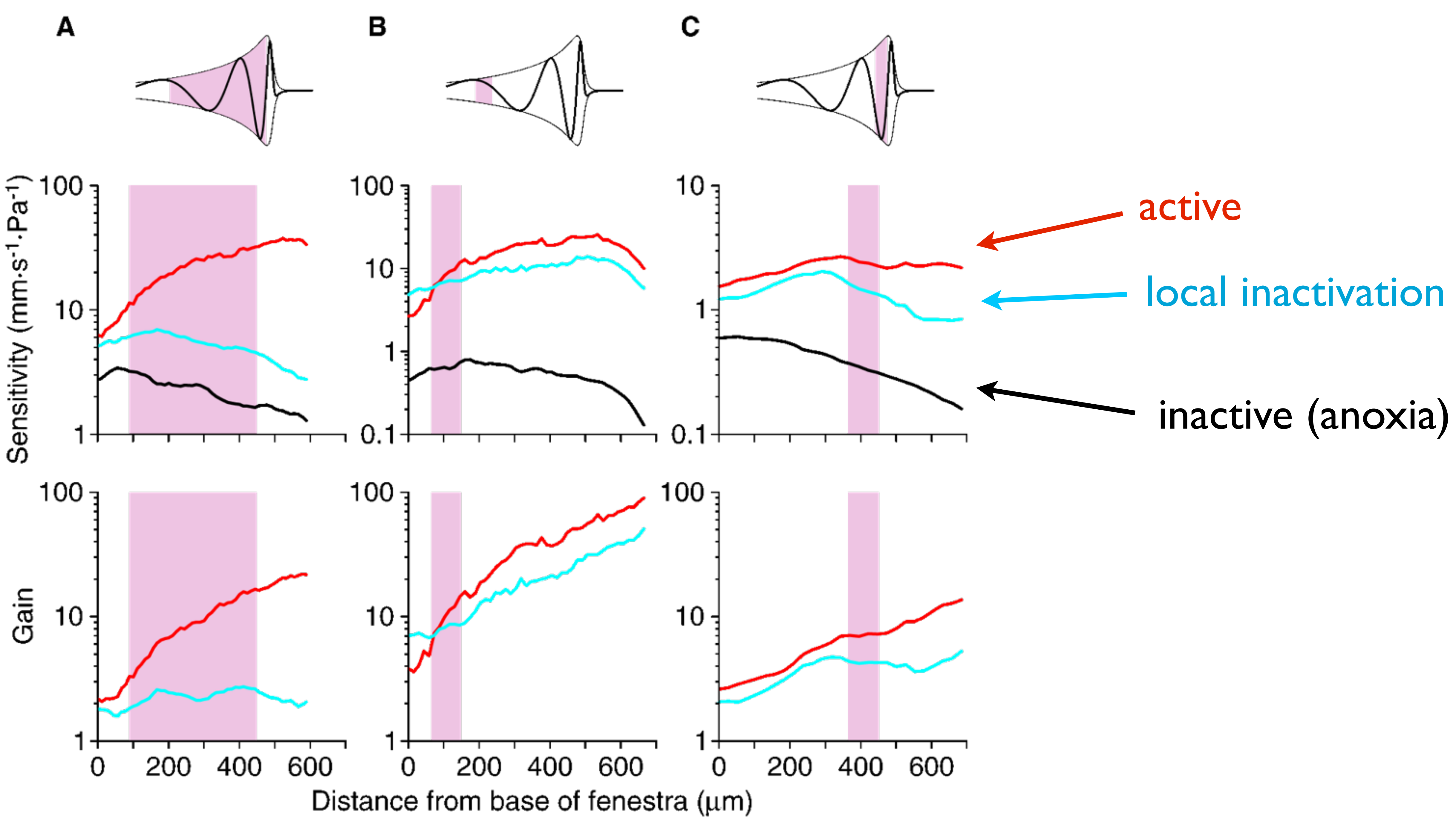
Amplification *accumulates* along the wave!



Reichenbach and Hudspeth (2010) *Phys. Rev. Lett.*

Experimental test of gain accumulation

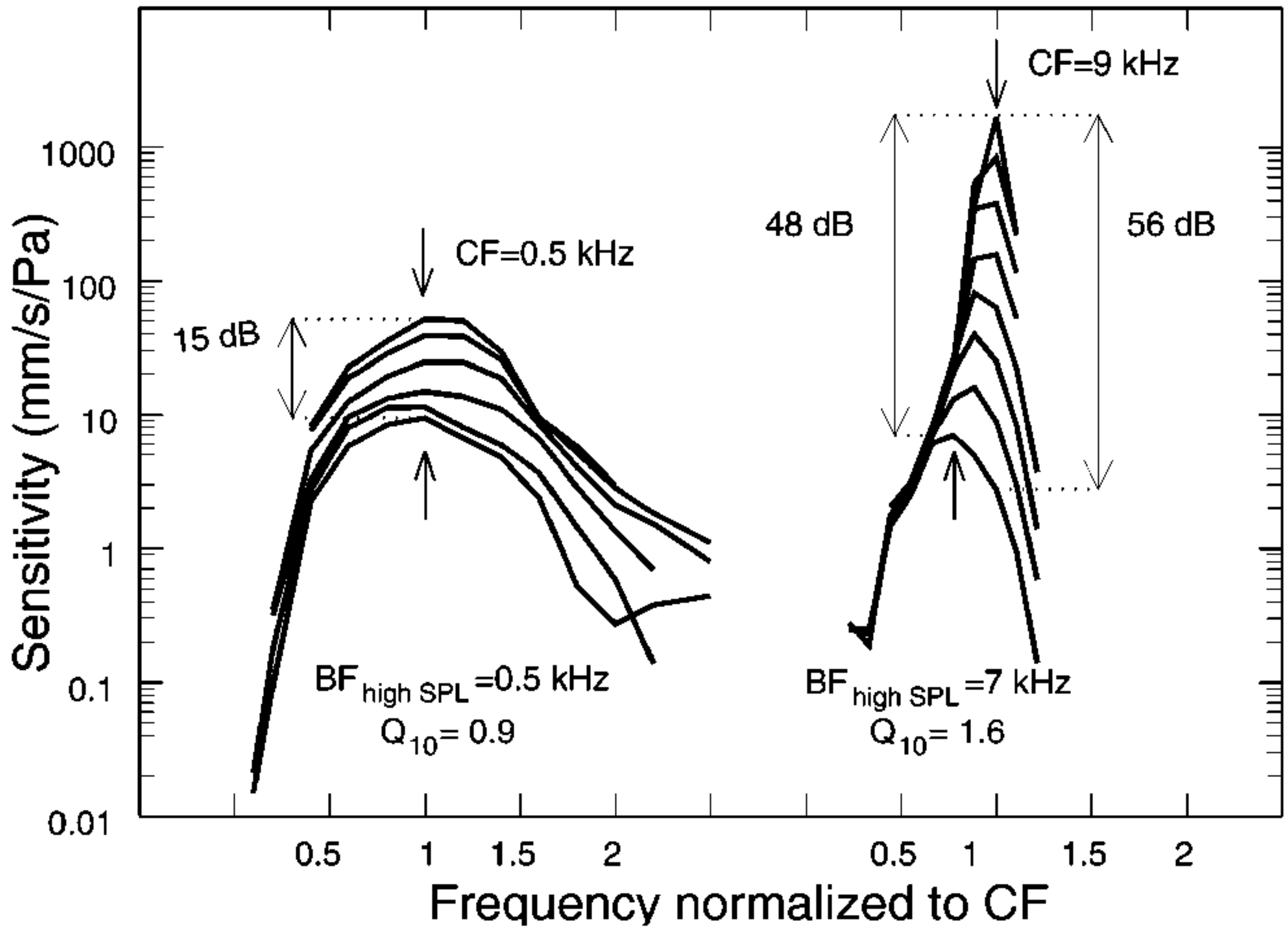
Photo-Inactivation of the active process in specific cochlear regions in a chinchilla through 4-acidosalicylate



Fisher, Nin, Reichenbach, Uthaiah and Hudspeth (2012) *Neuron*

4. Micromechanics of the organ of Corti at low frequencies

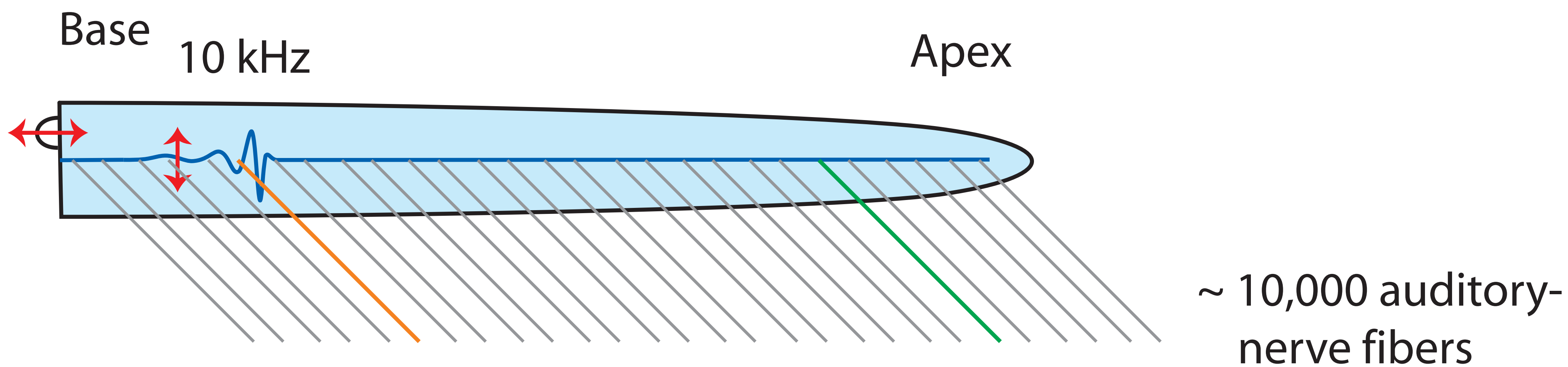
Cochlear mechanics at high and at low frequencies

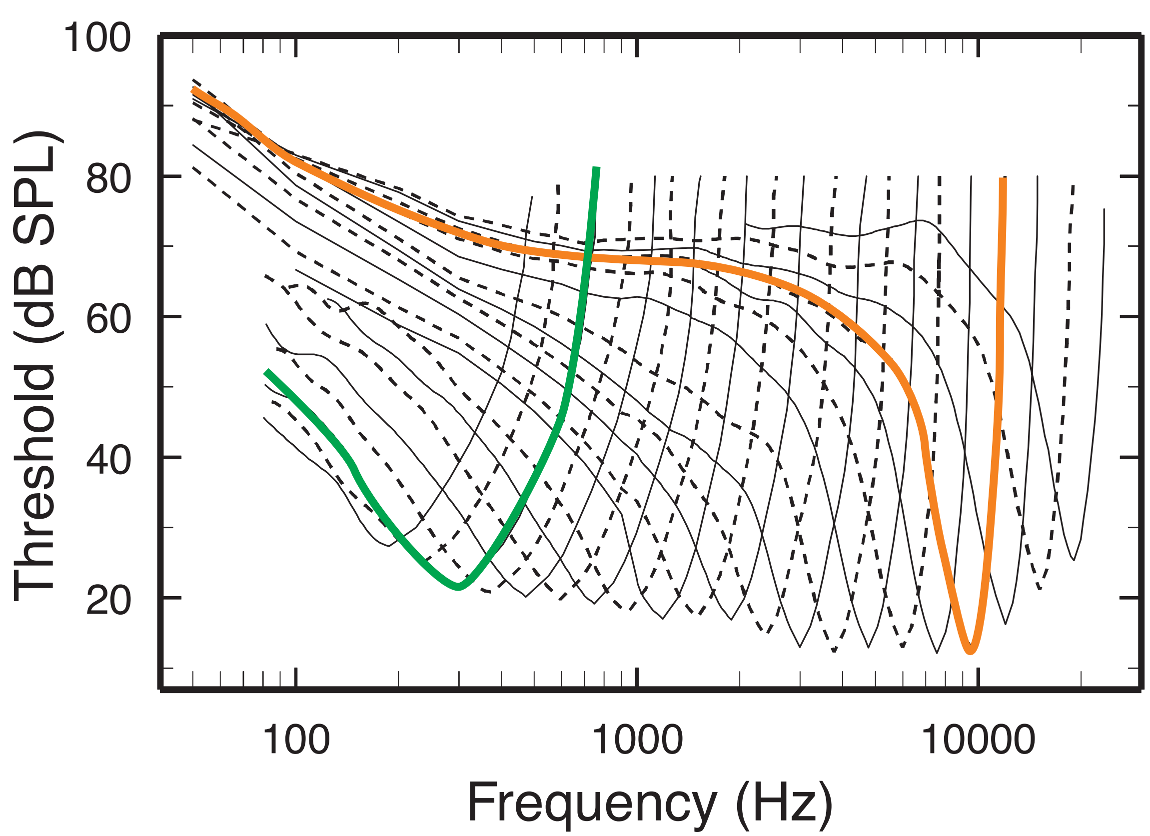


Much less gain and broader resonance at low frequencies!

Robles and Ruggero (2001) *Physiol. Rev.*

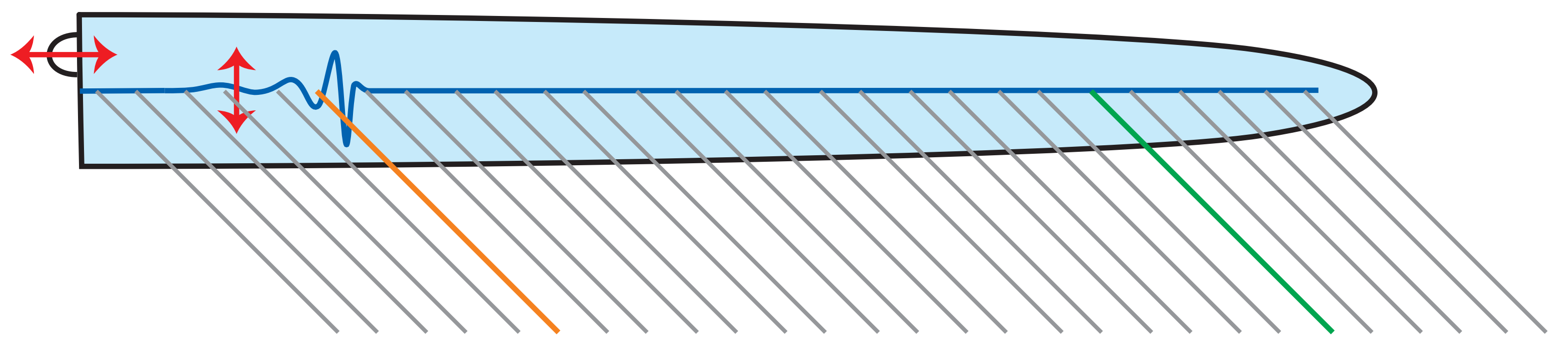
Tuning curves of auditory nerve fibers

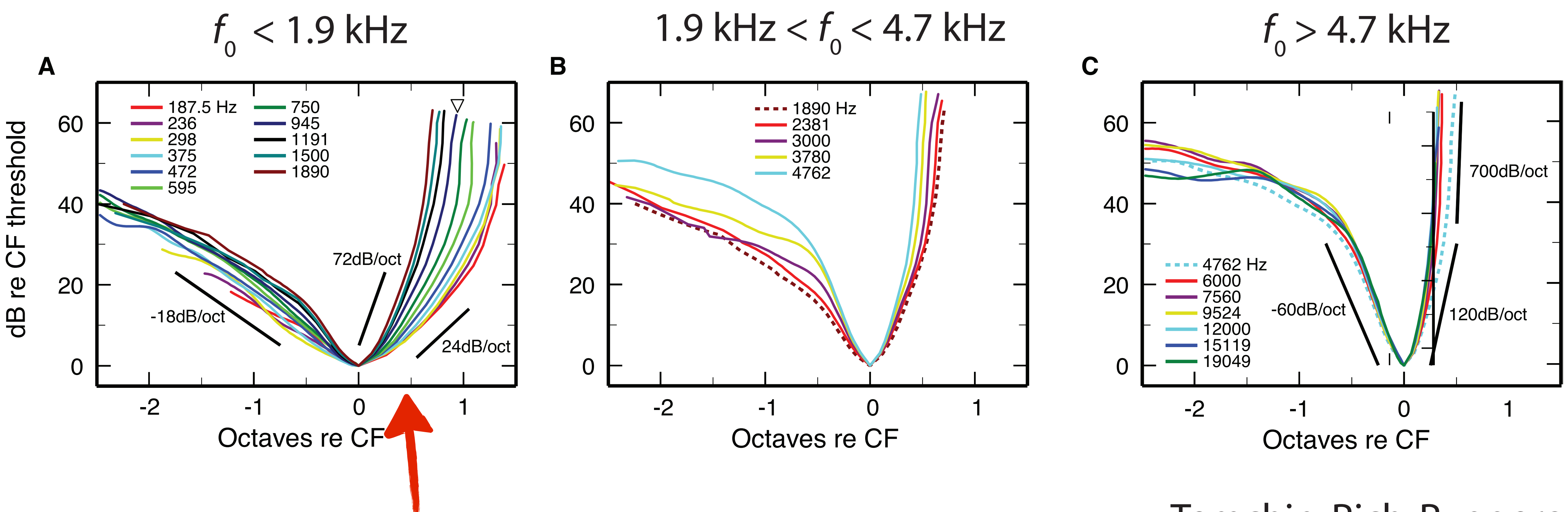




Temchin, Rich, Ruggero, *J. Neurophysiol.* (2008)

Tuning curves of auditory nerve fibers





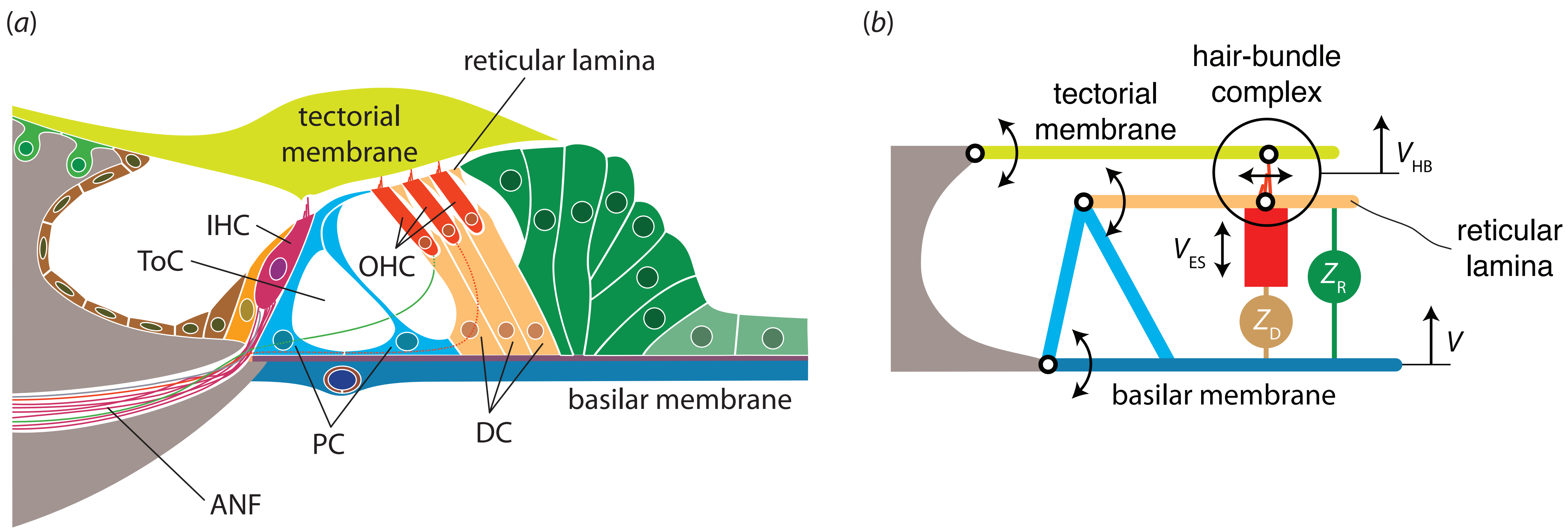
Critical-layer absorption violated!

Temchin, Rich, Ruggero, *J. Neurophysiol.* (2008)

Micromechanics of the Organ of Corti

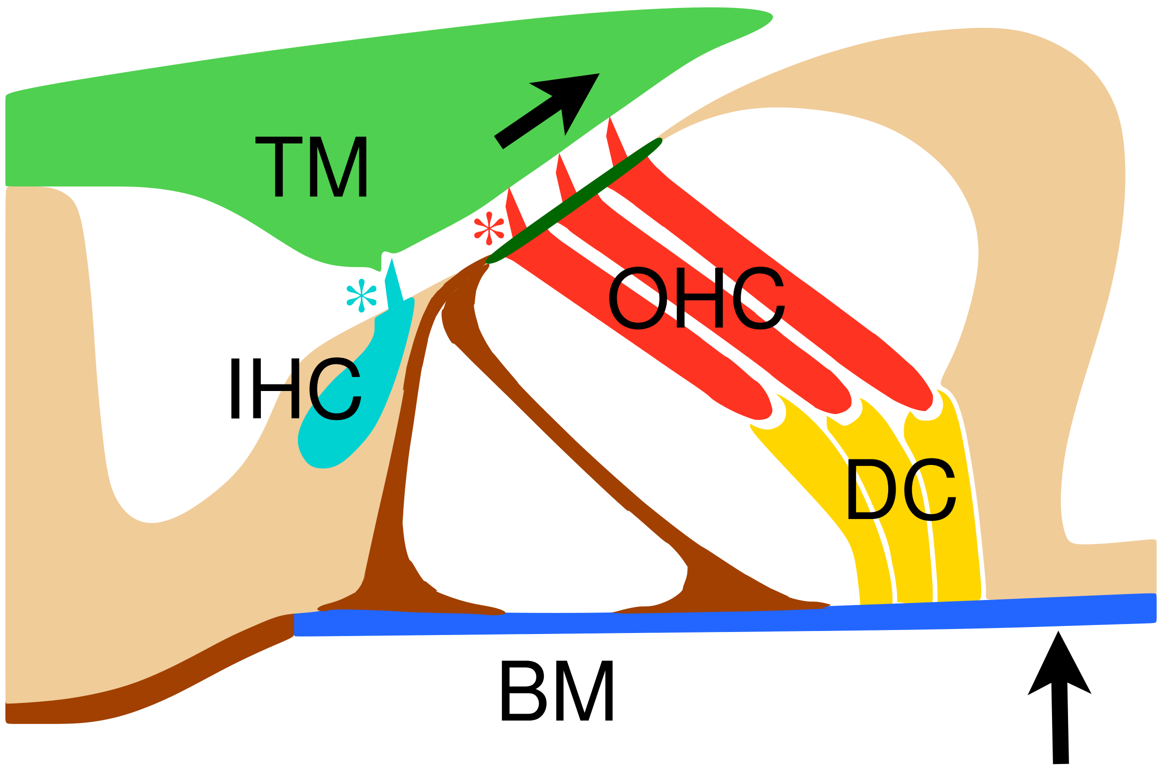
Cross-section of the organ of Corti

Micromechanical model



Reichenbach & Hudspeth, Rep. Prog. Phys. (2014)

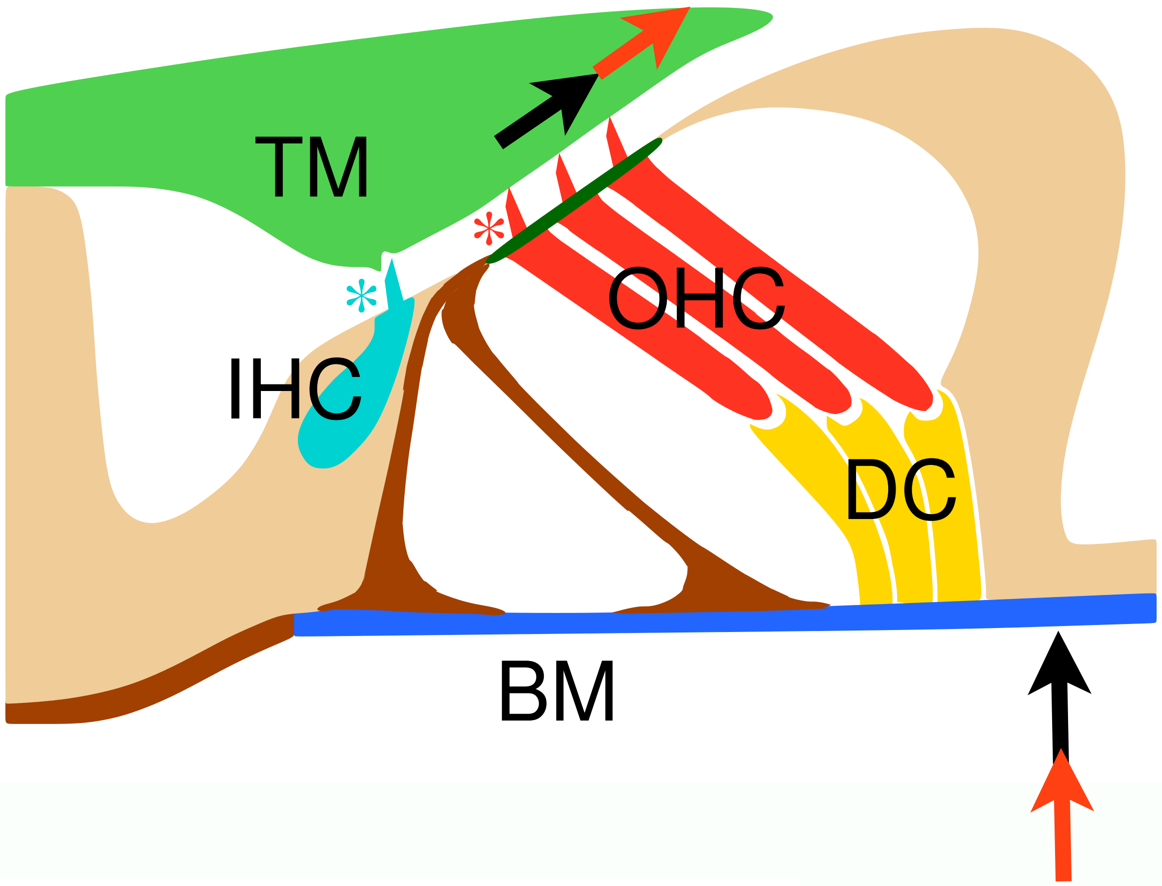
Amplification mechanisms

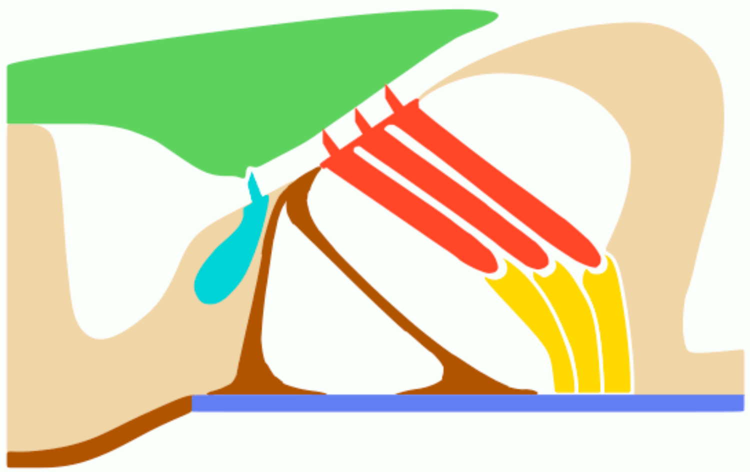


passive

Amplification mechanisms

Active hair-bundle motility

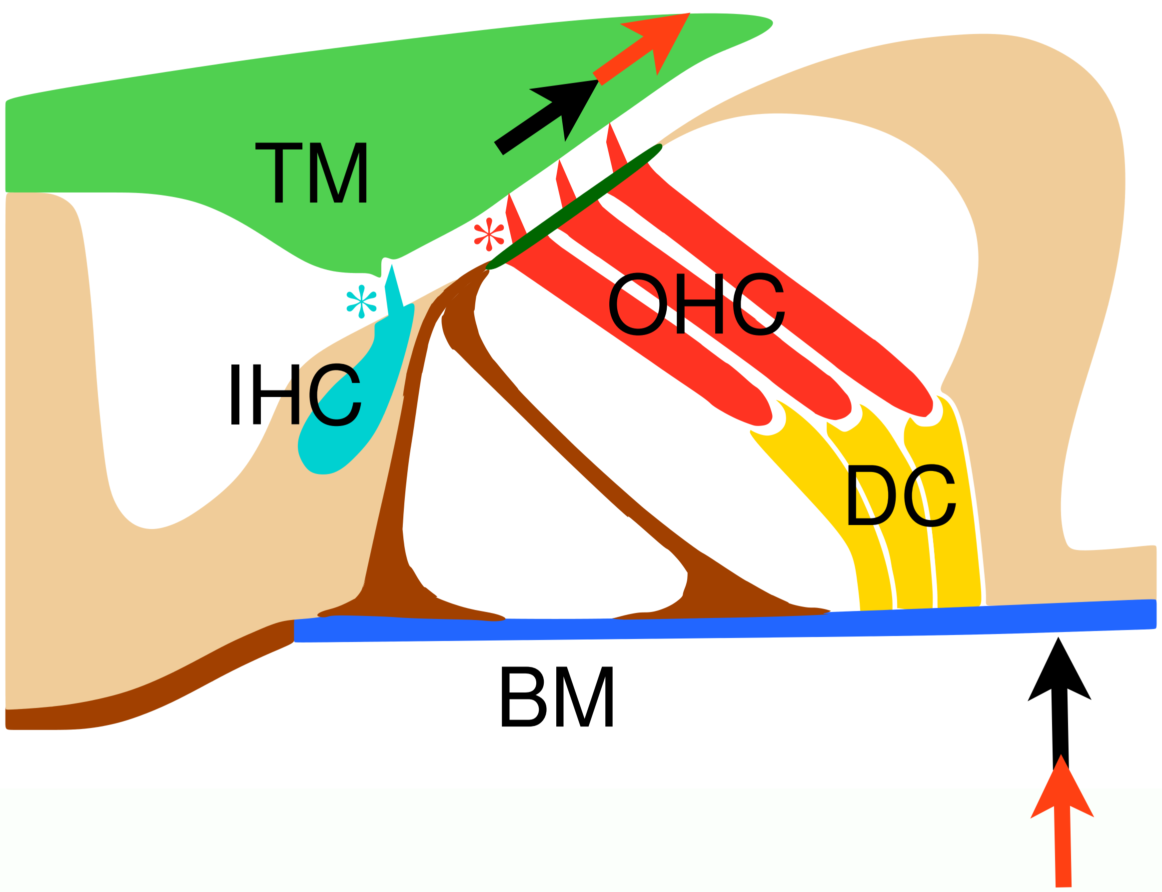


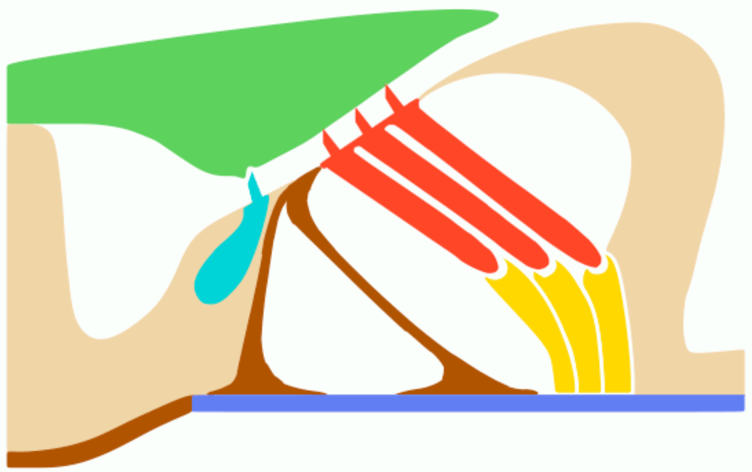


passive

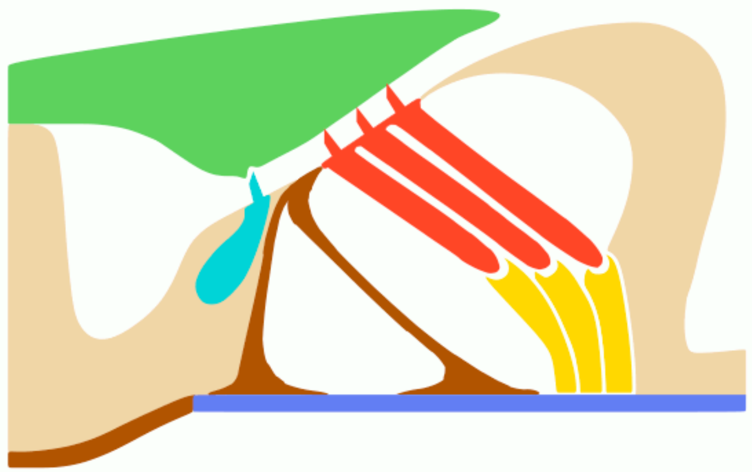
Amplification mechanisms

Active hair-bundle motility





passive

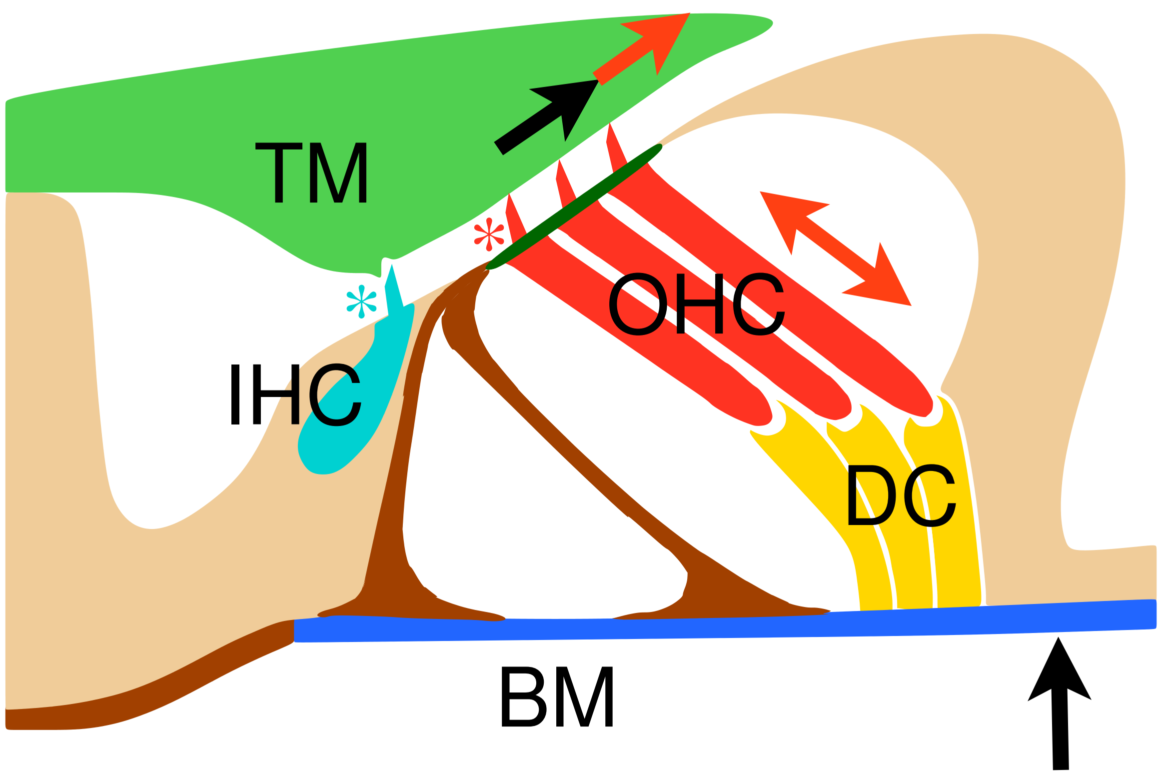


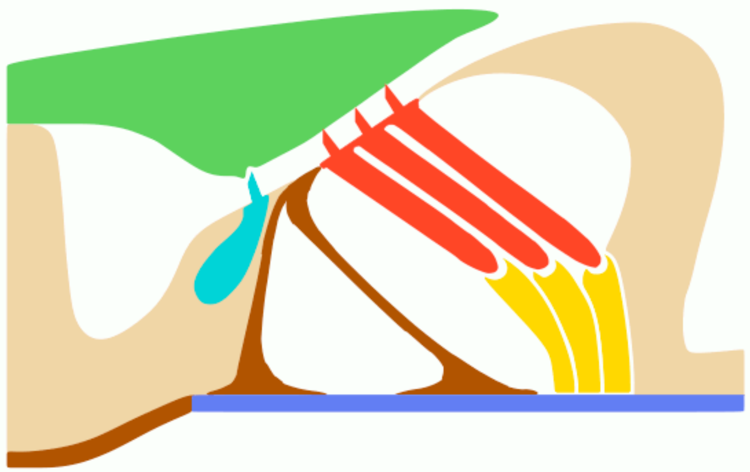
active hair-bundle motility

Amplification mechanisms

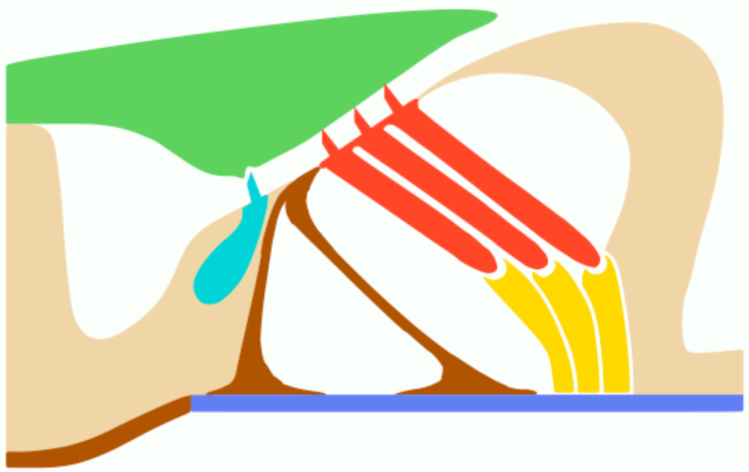
Active hair-bundle motility

Electromotility





passive

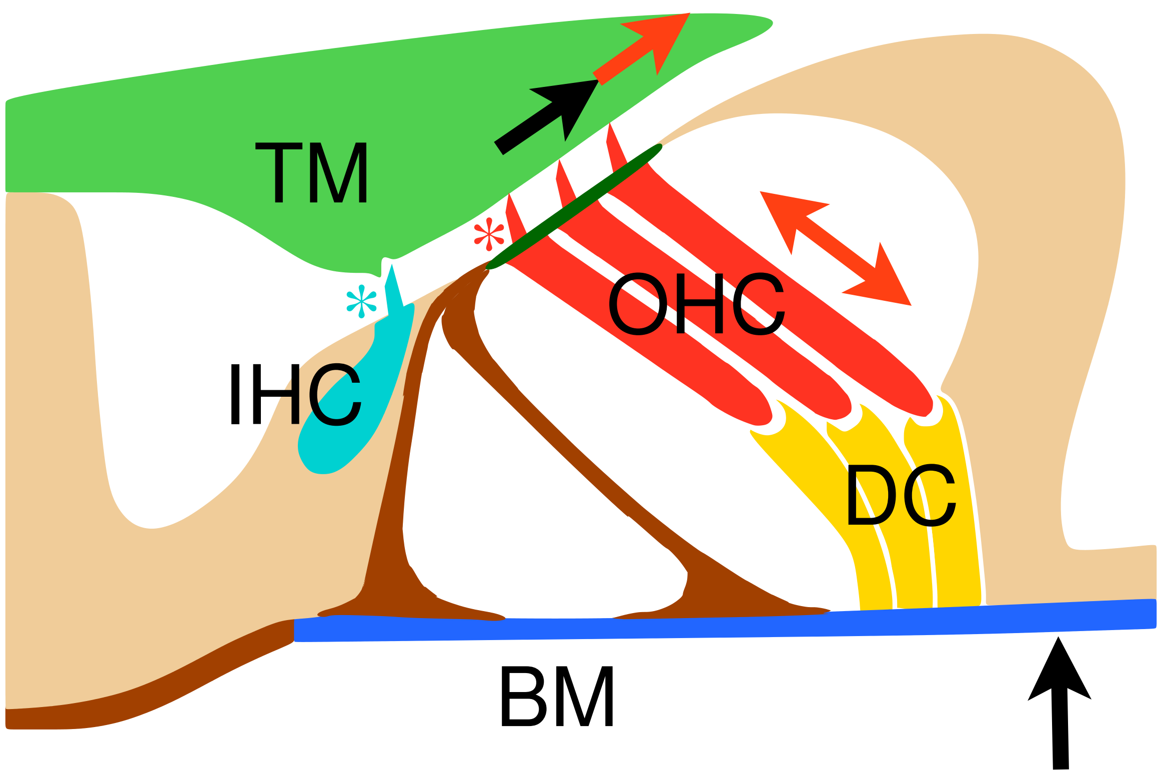


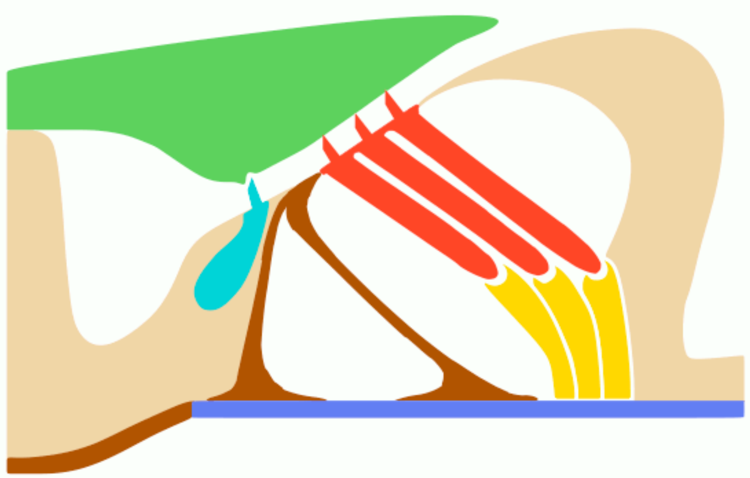
active hair-bundle motility

Amplification mechanisms

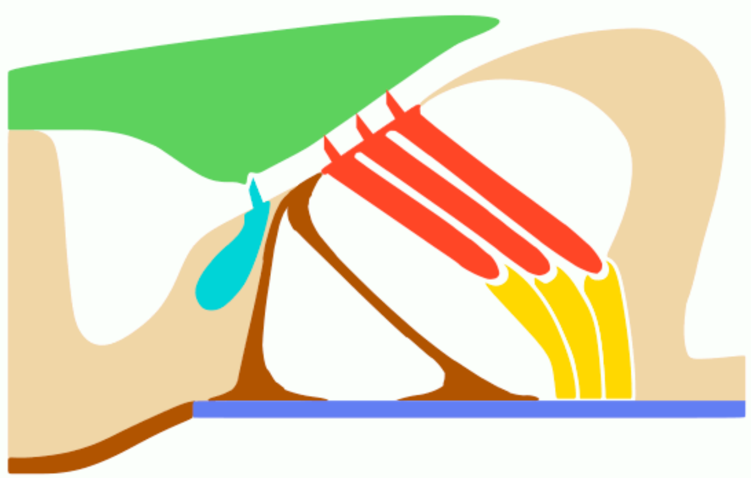
Active hair-bundle motility

Electromotility

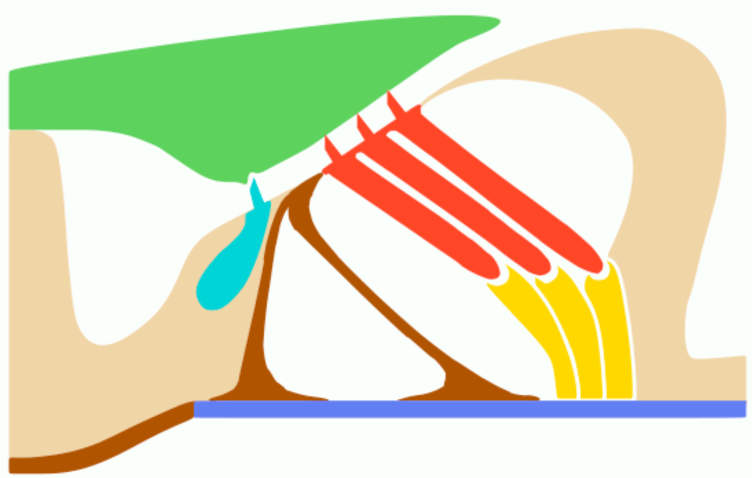




passive

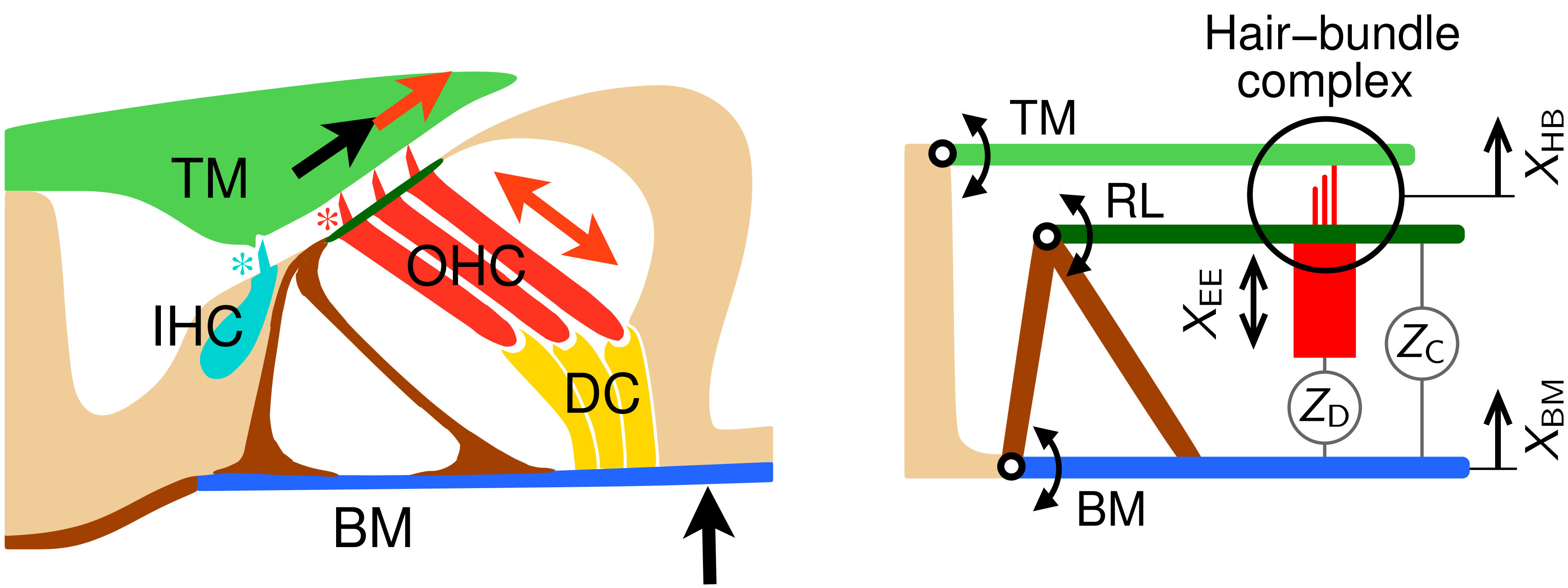


active hair-bundle motility

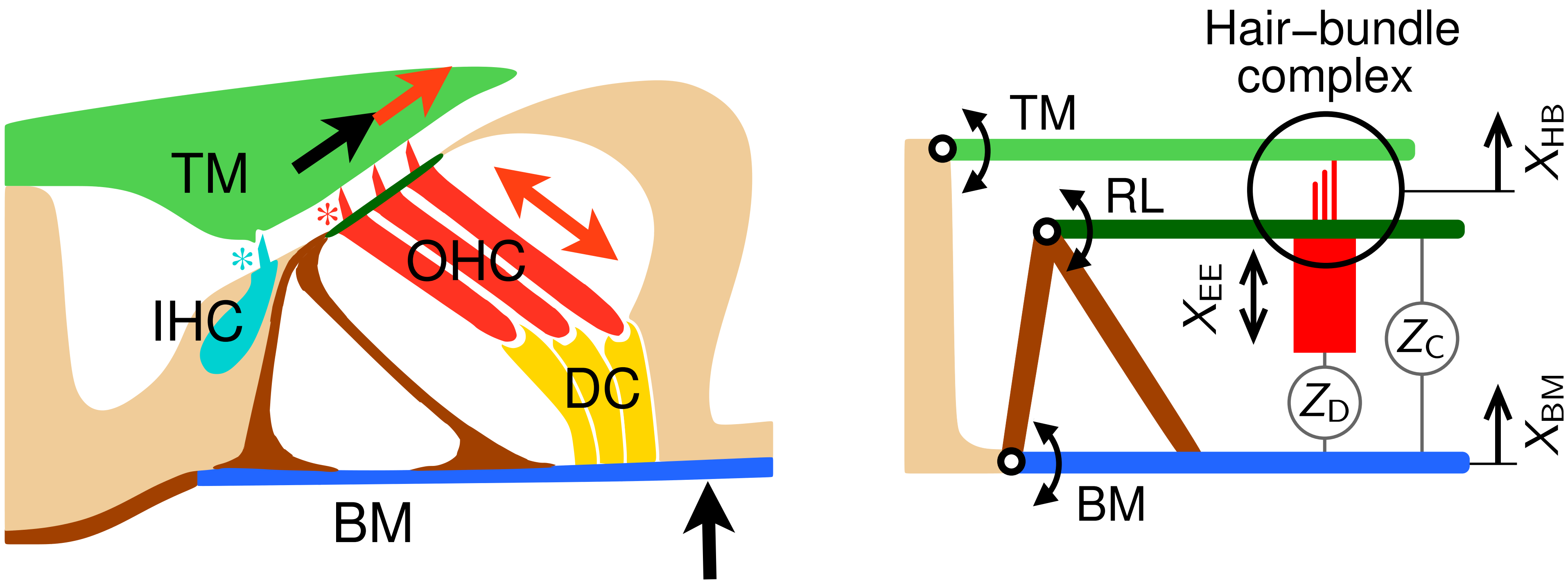


unidirectional amplification

Model for unidirectional amplification

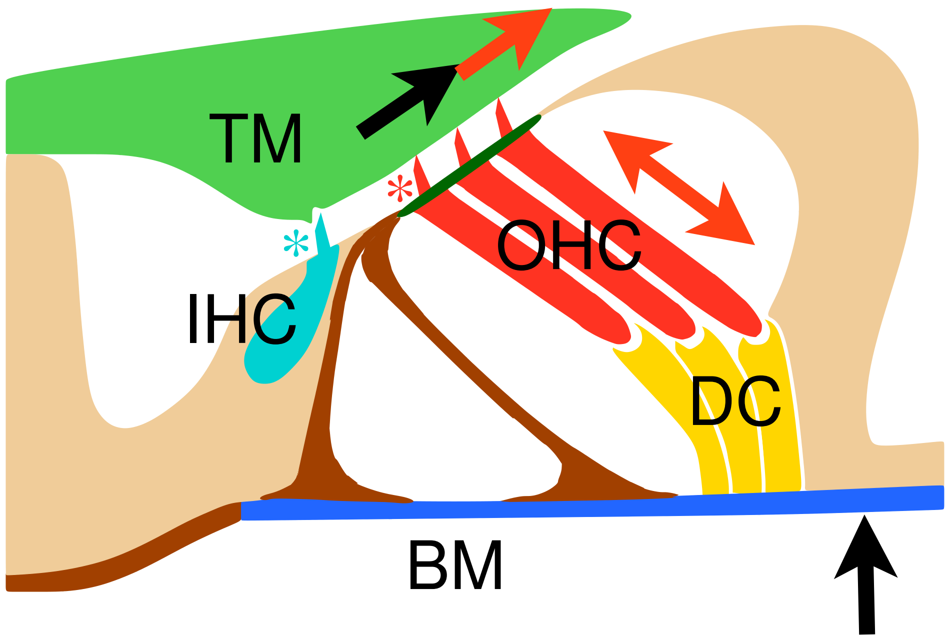


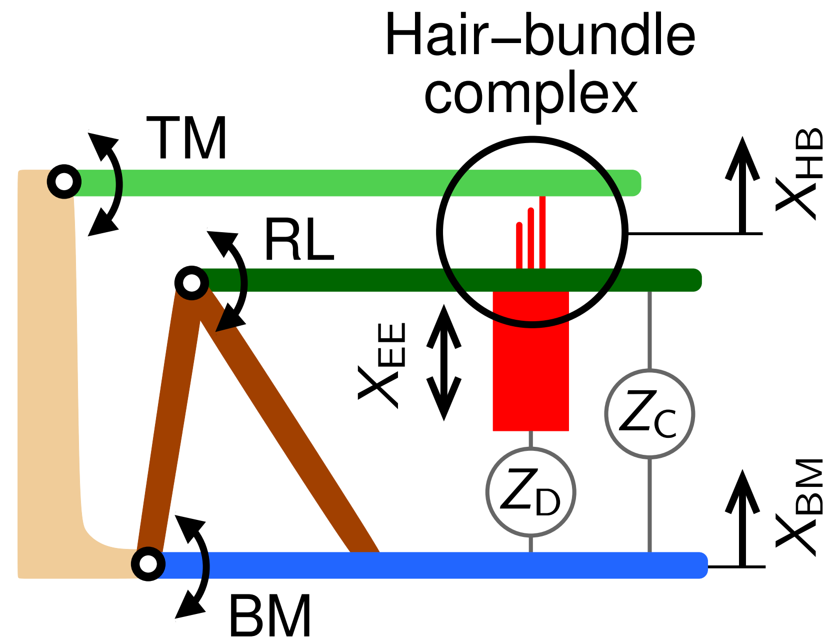
Model for unidirectional amplification



$$\tilde{X}_{\mathrm{EE}} = -\alpha \tilde{X}_{\mathrm{HB}}$$

Model for unidirectional amplification

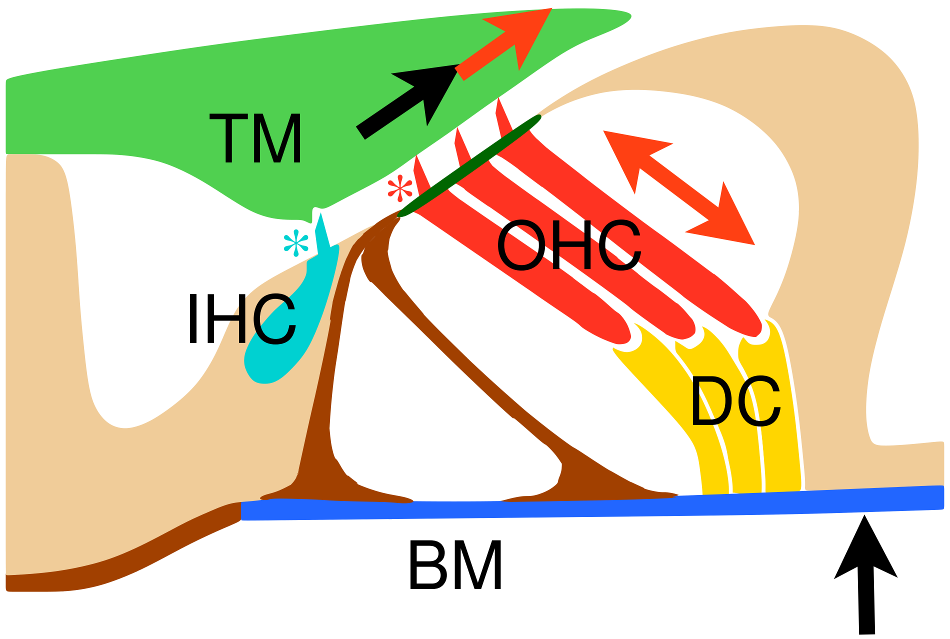


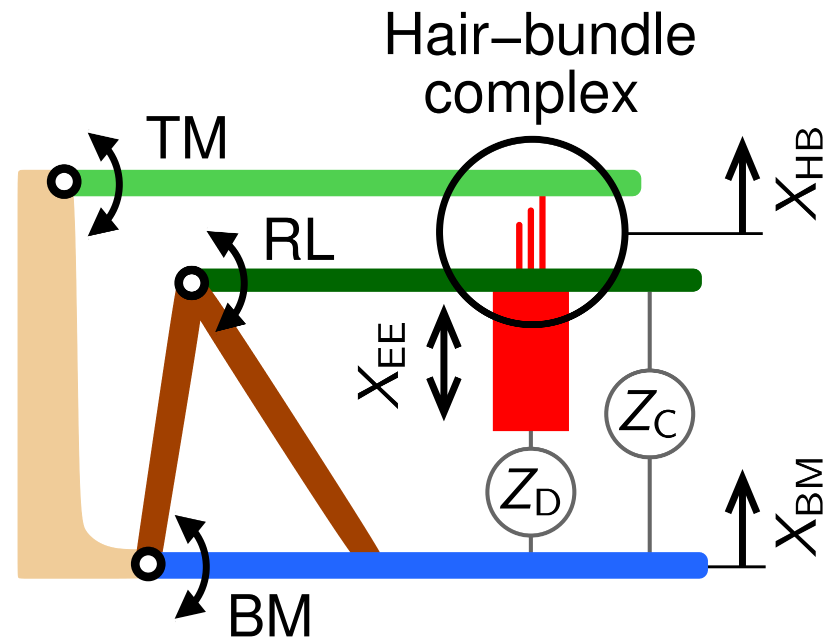


$$\tilde{X}_{\mathrm{EE}} = -\alpha \tilde{X}_{\mathrm{HB}} \qquad A \begin{pmatrix} \tilde{X}_{\mathrm{HB}} \\ \tilde{X}_{\mathrm{BM}} \end{pmatrix} = \frac{1}{2\pi i f} \begin{pmatrix} \tilde{F}_{\mathrm{int}} \\ \tilde{F}_{\mathrm{ext}} \end{pmatrix}$$

$$A = \begin{pmatrix} Z_{\mathrm{HB}} + (1+\alpha) Z_{\mathrm{D}} + Z_{\mathrm{C}} & -Z_{\mathrm{D}} - Z_{\mathrm{C}} \\ -(1+\alpha) Z_{\mathrm{D}} - Z_{\mathrm{C}} & Z_{\mathrm{BM}} + Z_{\mathrm{D}} + Z_{\mathrm{C}} \end{pmatrix}$$

Model for unidirectional amplification



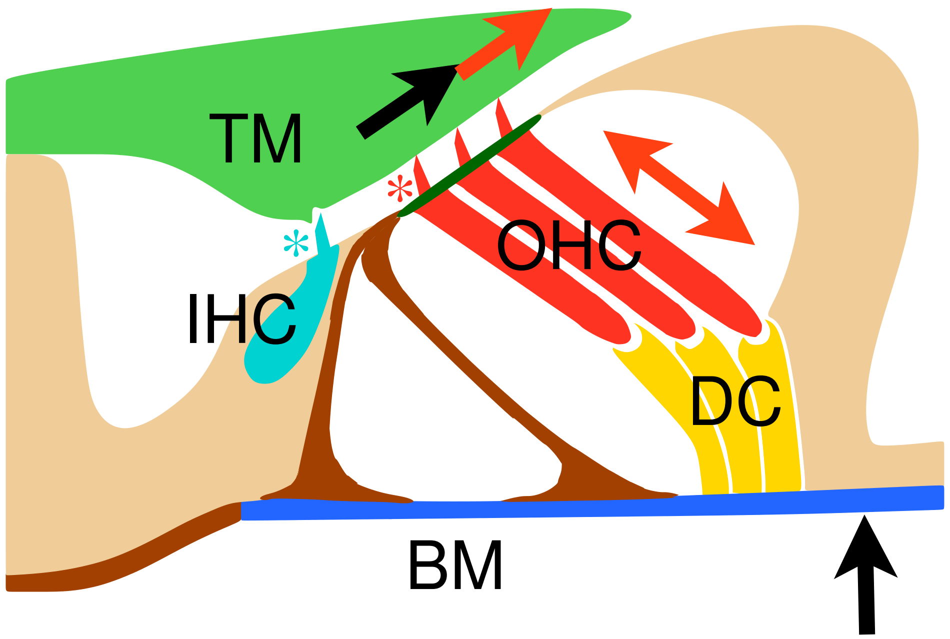


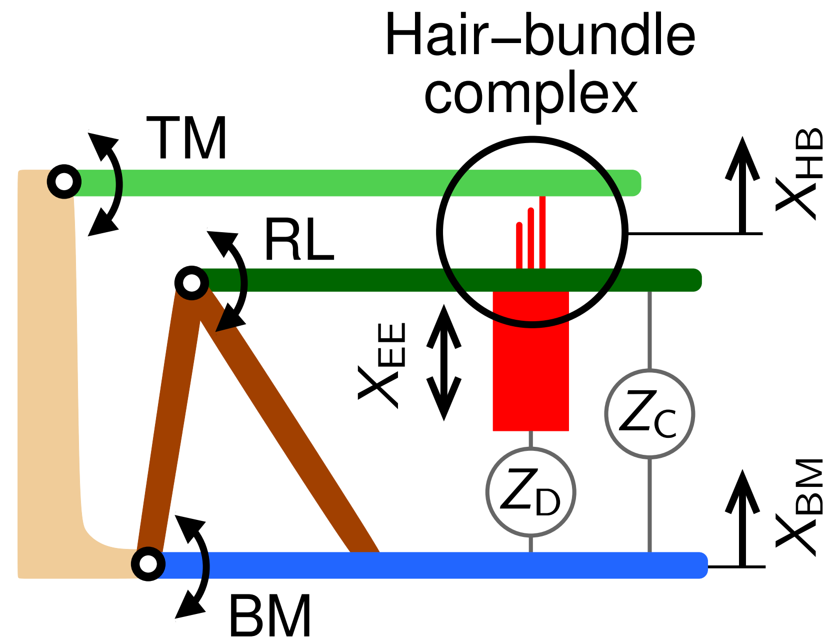
$$\tilde{X}_{\mathrm{EE}} = -\alpha \tilde{X}_{\mathrm{HB}} \qquad A \begin{pmatrix} \tilde{X}_{\mathrm{HB}} \\ \tilde{X}_{\mathrm{BM}} \end{pmatrix} = \frac{1}{2\pi i f} \begin{pmatrix} \tilde{F}_{\mathrm{int}} \\ \tilde{F}_{\mathrm{ext}} \end{pmatrix}$$

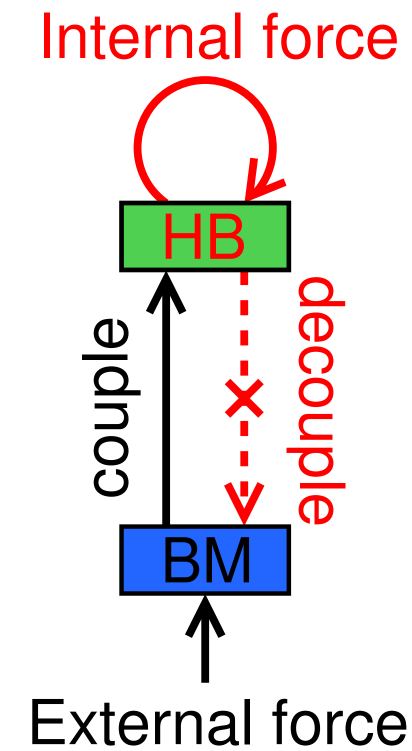
$$A = \begin{pmatrix} Z_{\mathrm{HB}} + (1+\alpha) Z_{\mathrm{D}} + Z_{\mathrm{C}} & -Z_{\mathrm{D}} - Z_{\mathrm{C}} \\ -(1+\alpha) Z_{\mathrm{D}} - Z_{\mathrm{C}} & Z_{\mathrm{BM}} + Z_{\mathrm{D}} + Z_{\mathrm{C}} \end{pmatrix}$$

$= 0 \quad \text{at} \quad \alpha_* = -1 - Z_C / Z_D$

Model for unidirectional amplification





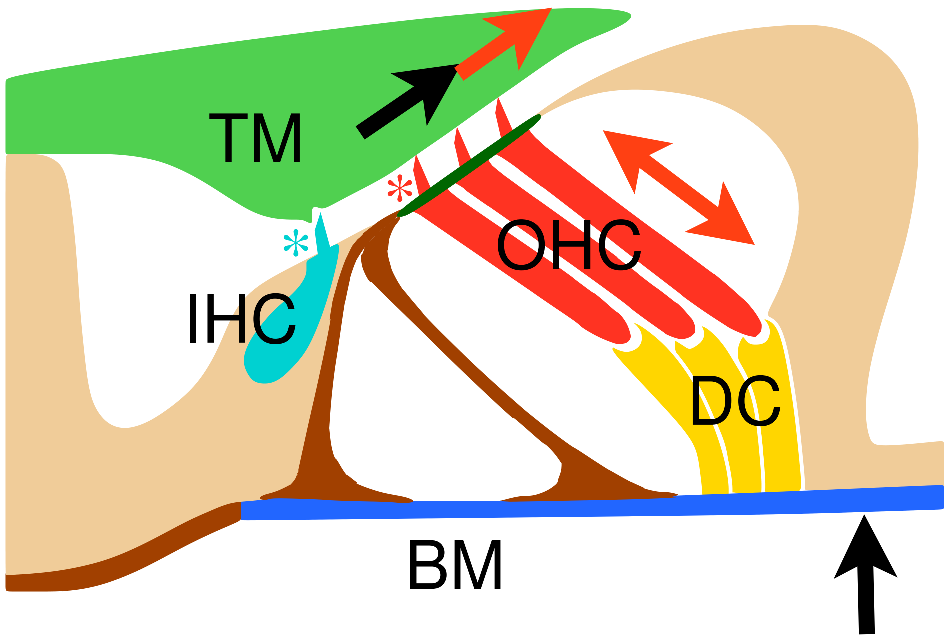


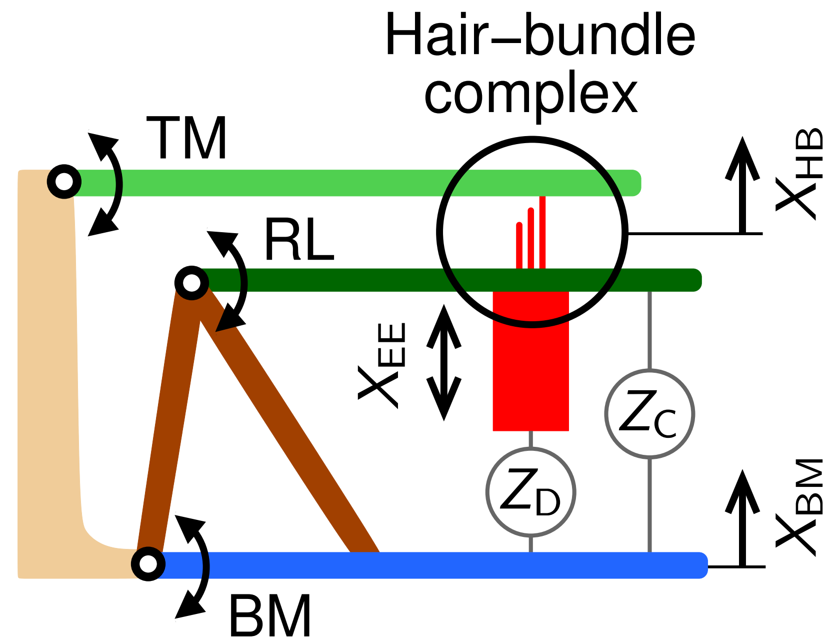
$$\tilde{X}_{\rm EE} = -\alpha \tilde{X}_{\rm HB} \qquad A\begin{pmatrix}\tilde{X}_{\rm HB}\\ \tilde{X}_{\rm BM}\end{pmatrix} = \frac{1}{2\pi i f}\begin{pmatrix}\tilde{F}_{\rm int}\\ \tilde{F}_{\rm ext}\end{pmatrix}$$

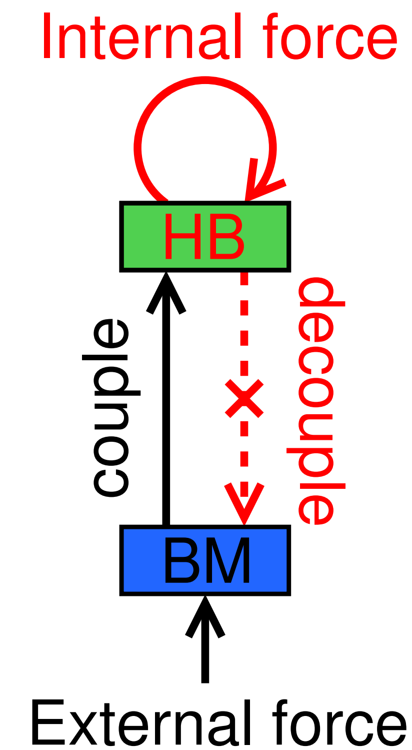
$$A = \begin{pmatrix} Z_{\rm HB} + (1+\alpha)Z_{\rm D} + Z_{\rm C} & -Z_{\rm D} - Z_{\rm C} \\ -(1+\alpha)Z_{\rm D} - Z_{\rm C} & Z_{\rm BM} + Z_{\rm D} + Z_{\rm C} \end{pmatrix}$$

$$= 0 \quad \text{at} \quad \alpha_* = -1 - Z_C/Z_D$$

Model for unidirectional amplification







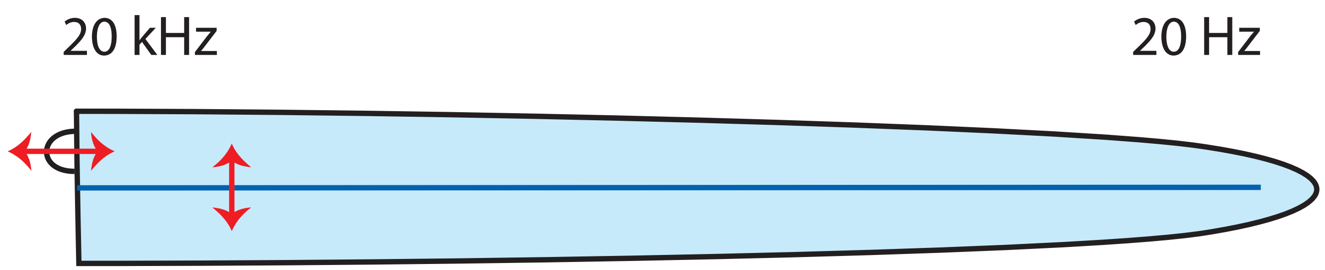
$$\tilde{X}_{\mathrm{EE}} = -\alpha \tilde{X}_{\mathrm{HB}} \qquad A\begin{pmatrix}\tilde{X}_{\mathrm{HB}}\\ \tilde{X}_{\mathrm{BM}}\end{pmatrix} = \frac{1}{2\pi i f}\begin{pmatrix}\tilde{F}_{\mathrm{int}}\\ \tilde{F}_{\mathrm{ext}}\end{pmatrix}$$

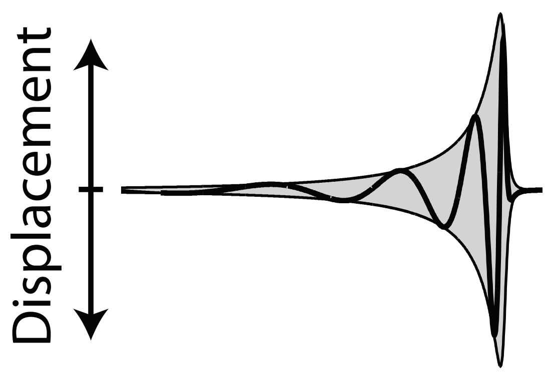
depends nonlinearly on X_{HB}!

$$A = \begin{pmatrix} Z_{\mathrm{HB}} + (1+\alpha)Z_{\mathrm{D}} + Z_{\mathrm{C}} & -Z_{\mathrm{D}} - Z_{\mathrm{C}} \\ -(1+\alpha)Z_{\mathrm{D}} - Z_{\mathrm{C}} & Z_{\mathrm{BM}} + Z_{\mathrm{D}} + Z_{\mathrm{C}} \end{pmatrix}$$

$= 0 \quad \text{at} \quad \alpha_* = -1 - Z_C/Z_D$

Cochlear mechanics

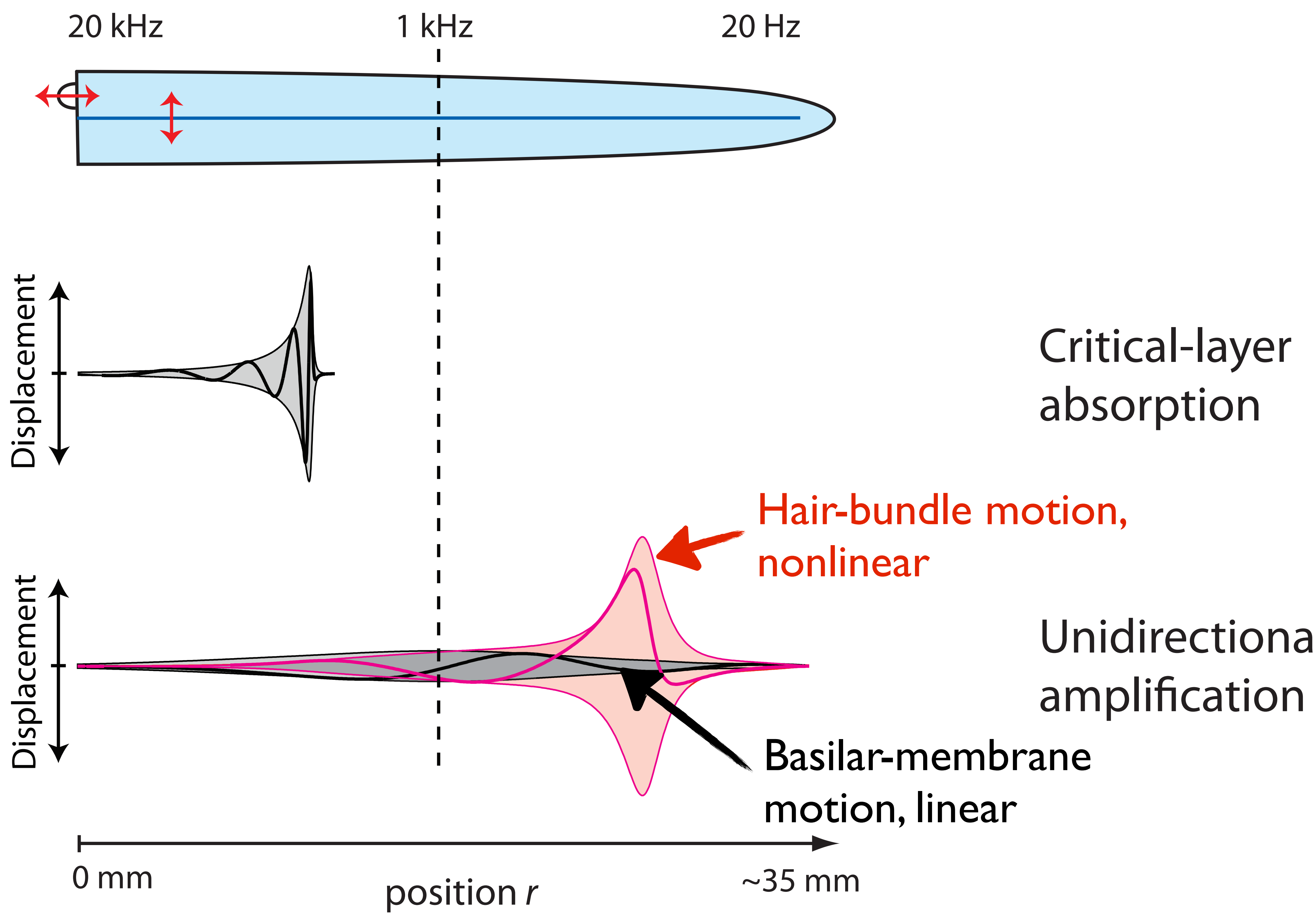




Critical-layer absorption

T. Reichenbach & A. J. Hudspeth, ***PNAS*** (2010), ***Phys. Rev. Lett.*** (2010)

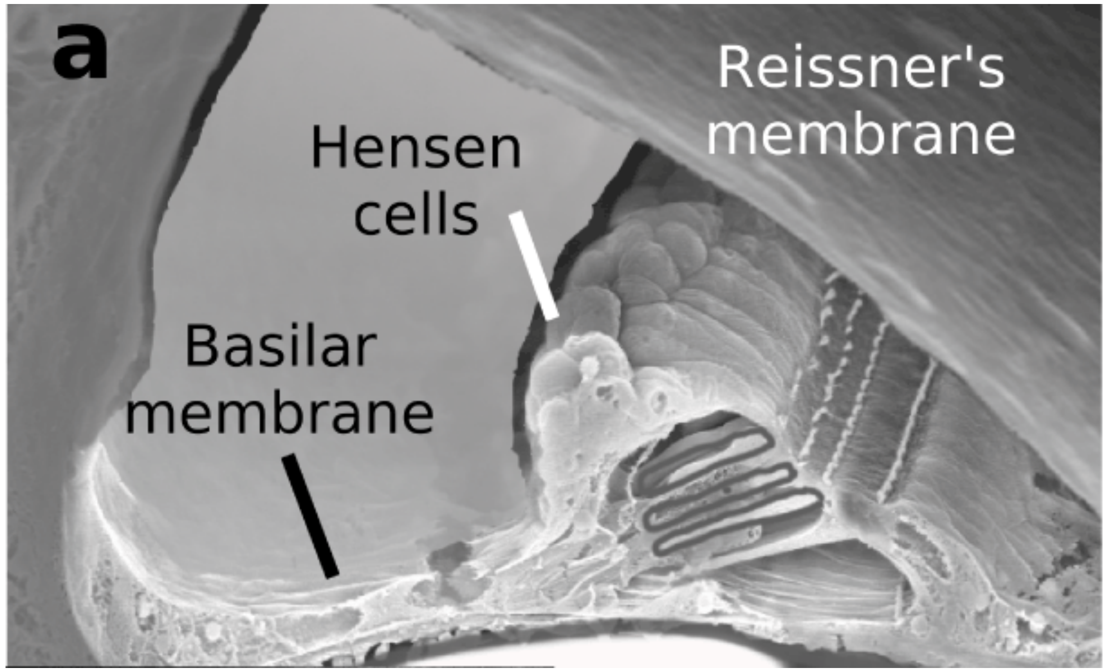
Cochlear mechanics

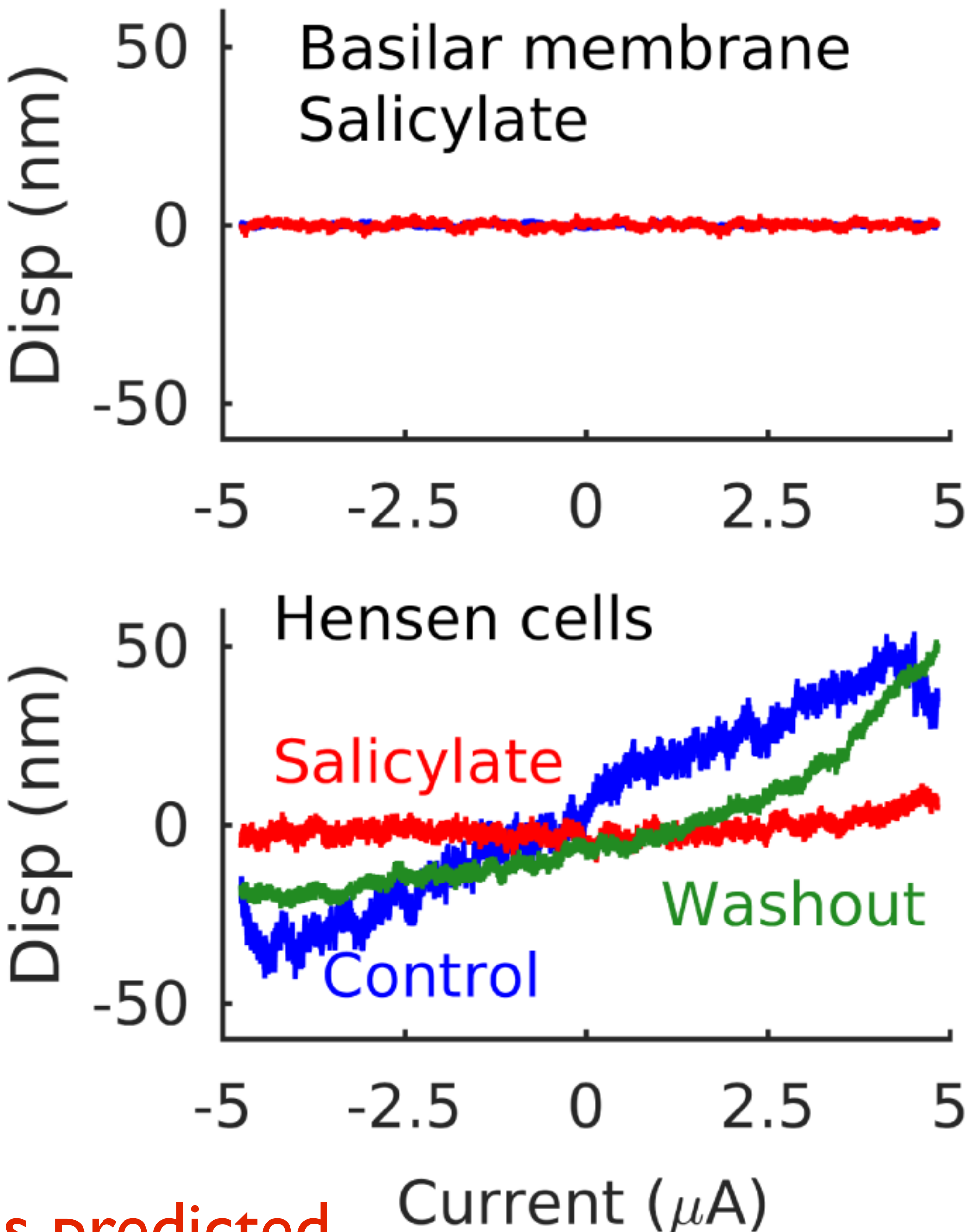


T. Reichenbach & A. J. Hudspeth, ***PNAS*** (2010), ***Phys. Rev. Lett.*** (2010)

Experimental results from the cochlear apex

Laser interferometry during electrical stimulation:

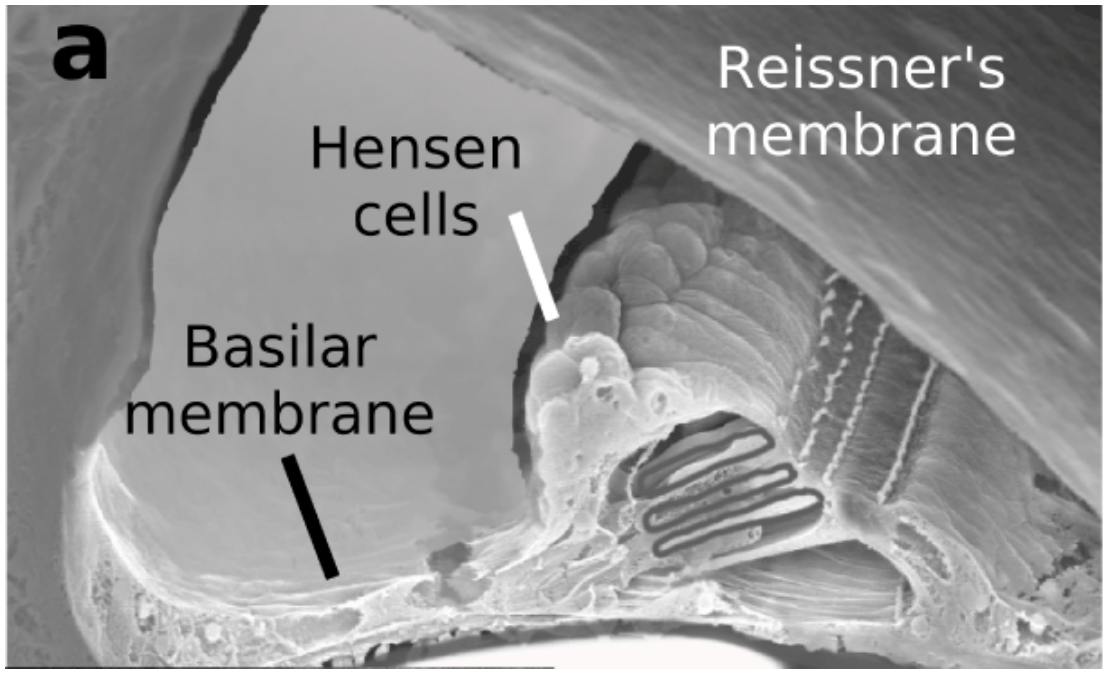


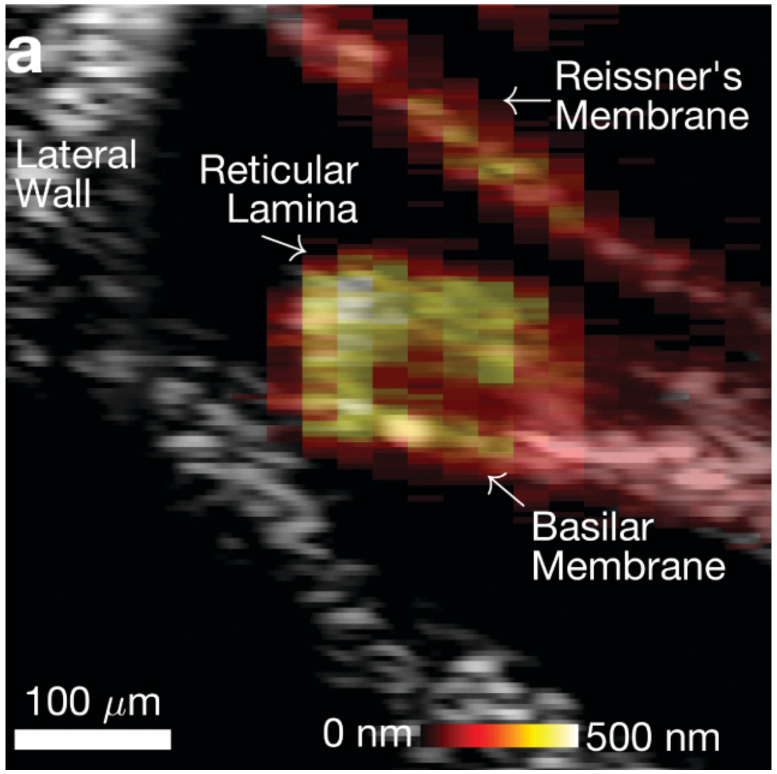


Much larger motion at the Hensen cells as predicted by unidirectional amplification!

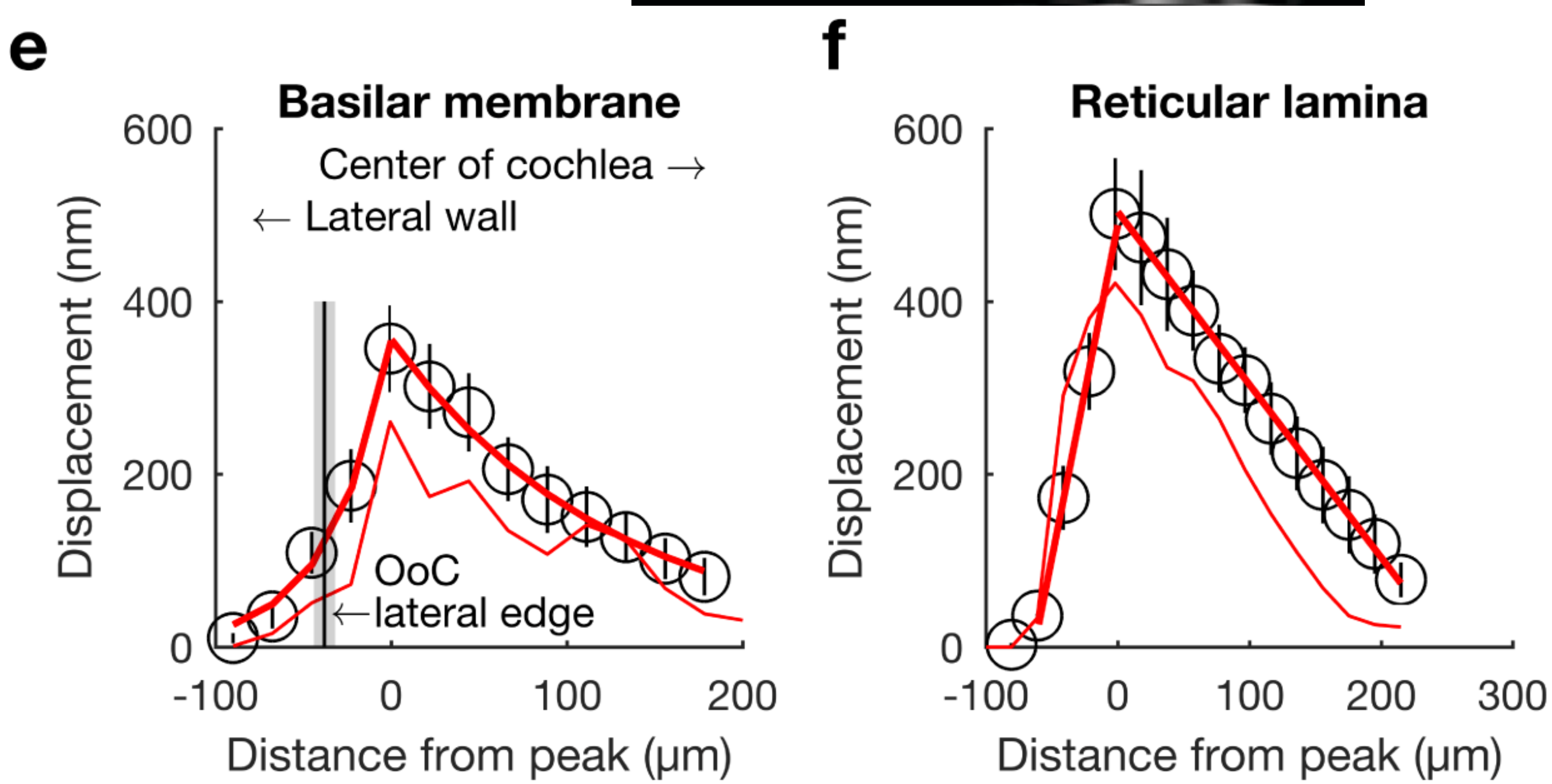
Warren, Ramamoorthy, Ciganovic, Zhang, Wilson, Reichenbach, Nuttall, Fridberger, PNAS (2016)

Experimental results from the cochlear apex





Optical coherence tomography:



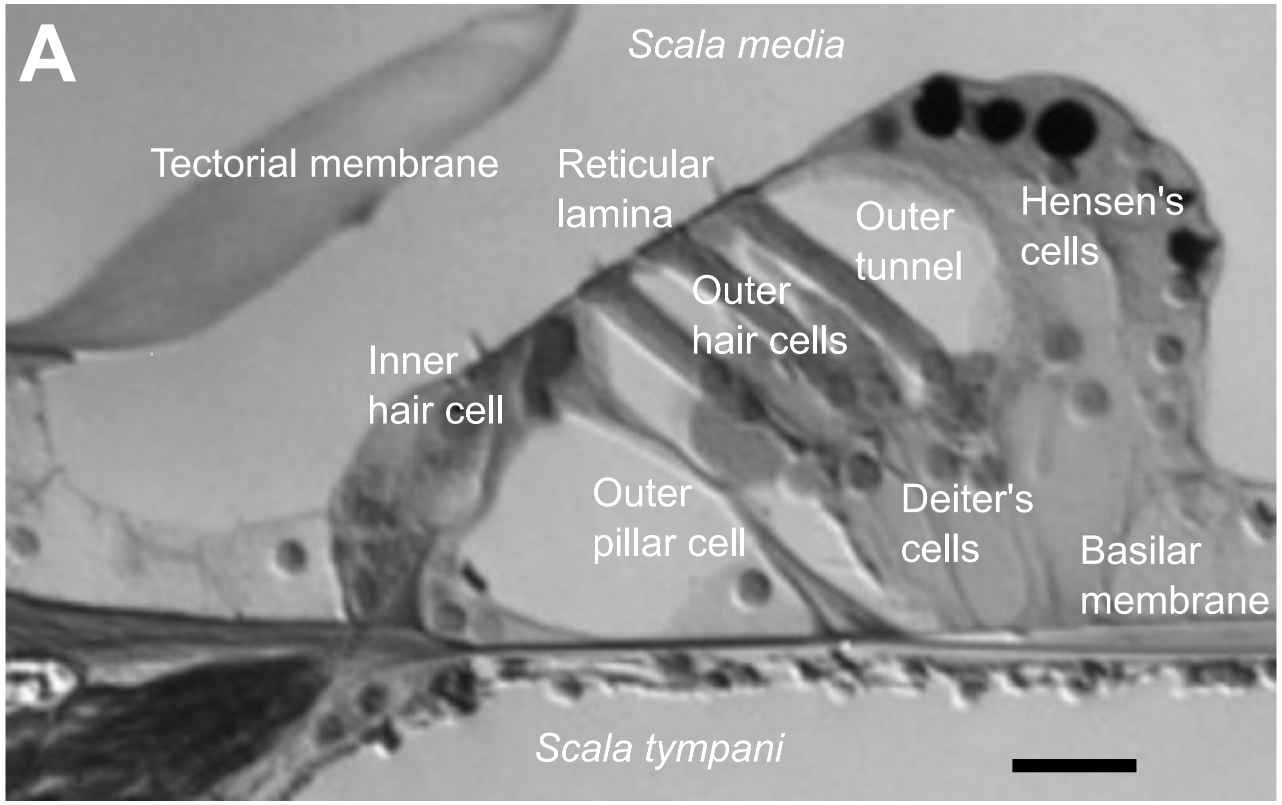
Warren, Ramamoorthy, Ciganovic, Zhang, Wilson, Reichenbach, Nuttall, Fridberger, PNAS (2016)

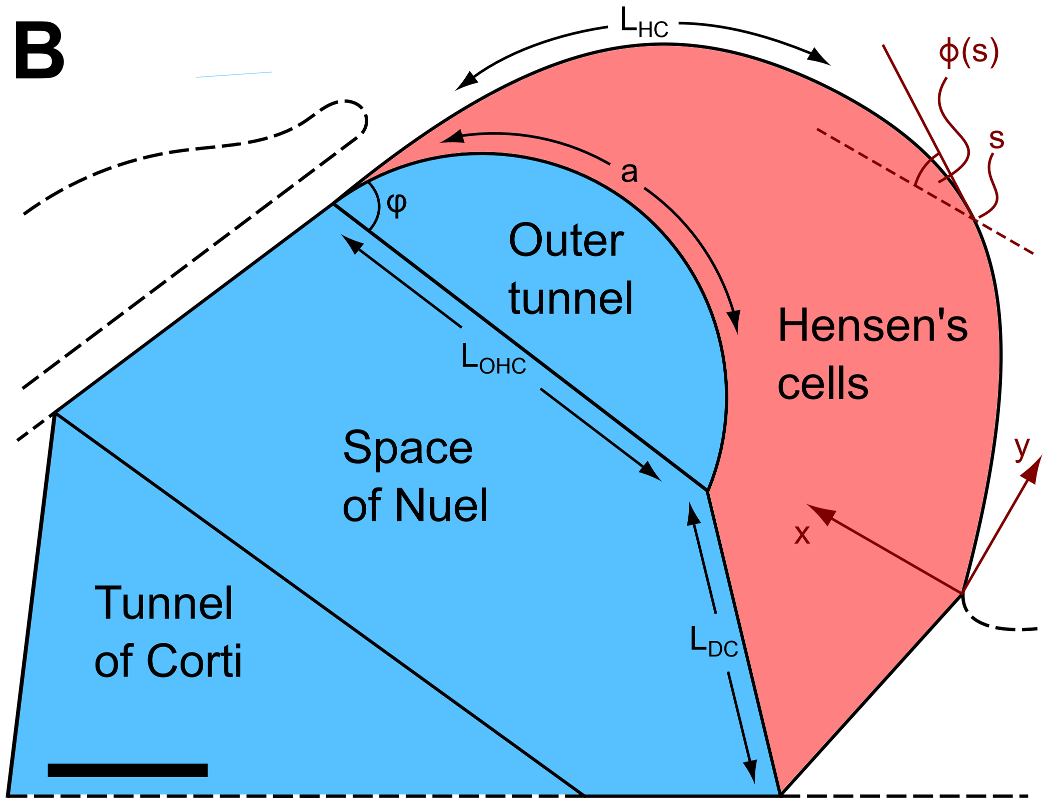
Nonlinear deformation of the organ of Corti at the apex

- Experimental data from Prof. A Fridberger, University of Linköping

- Development of a geometric model for the deformation of the organ

- Central assumption: cross-section remains constant



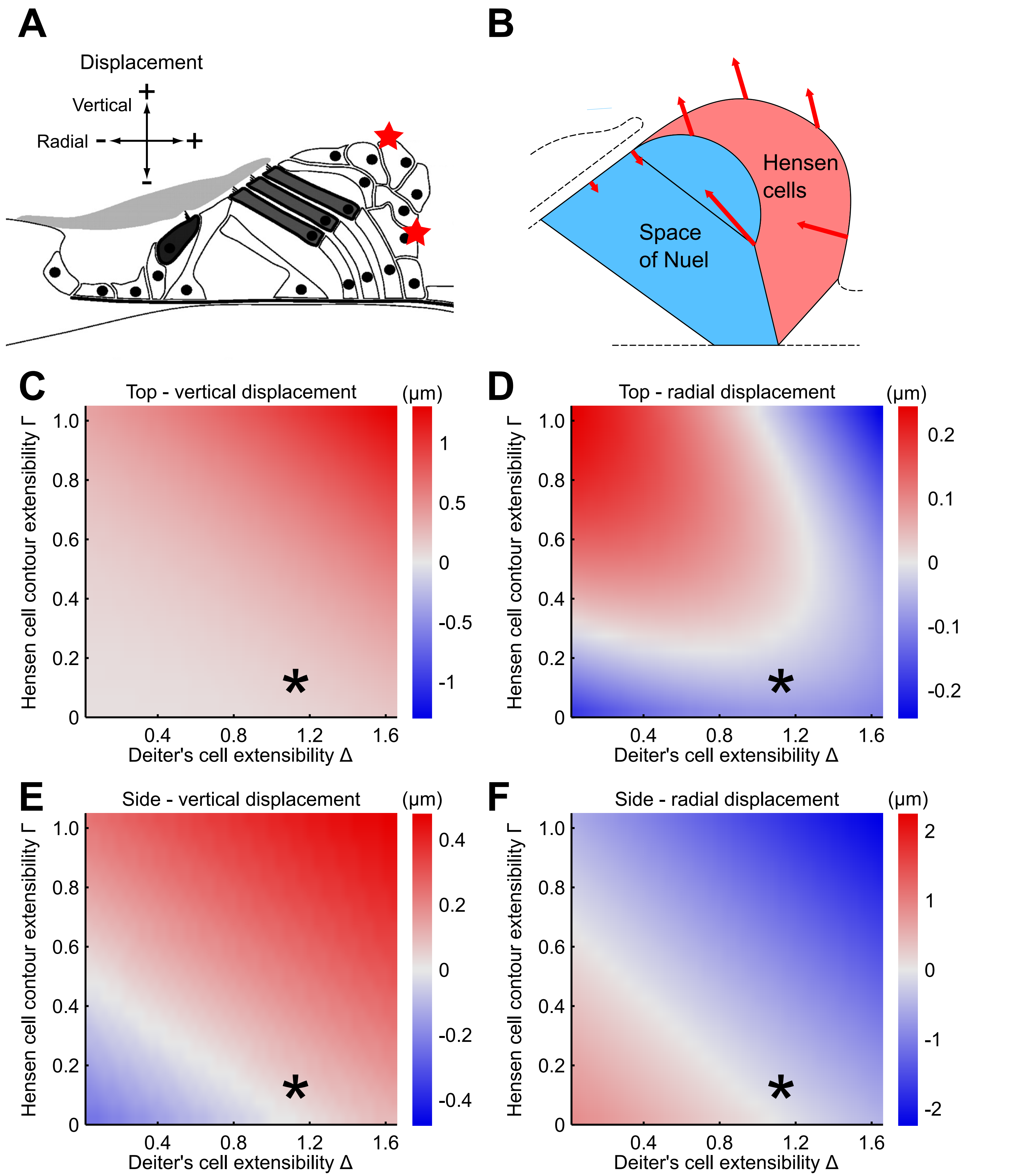


Determining model parameters

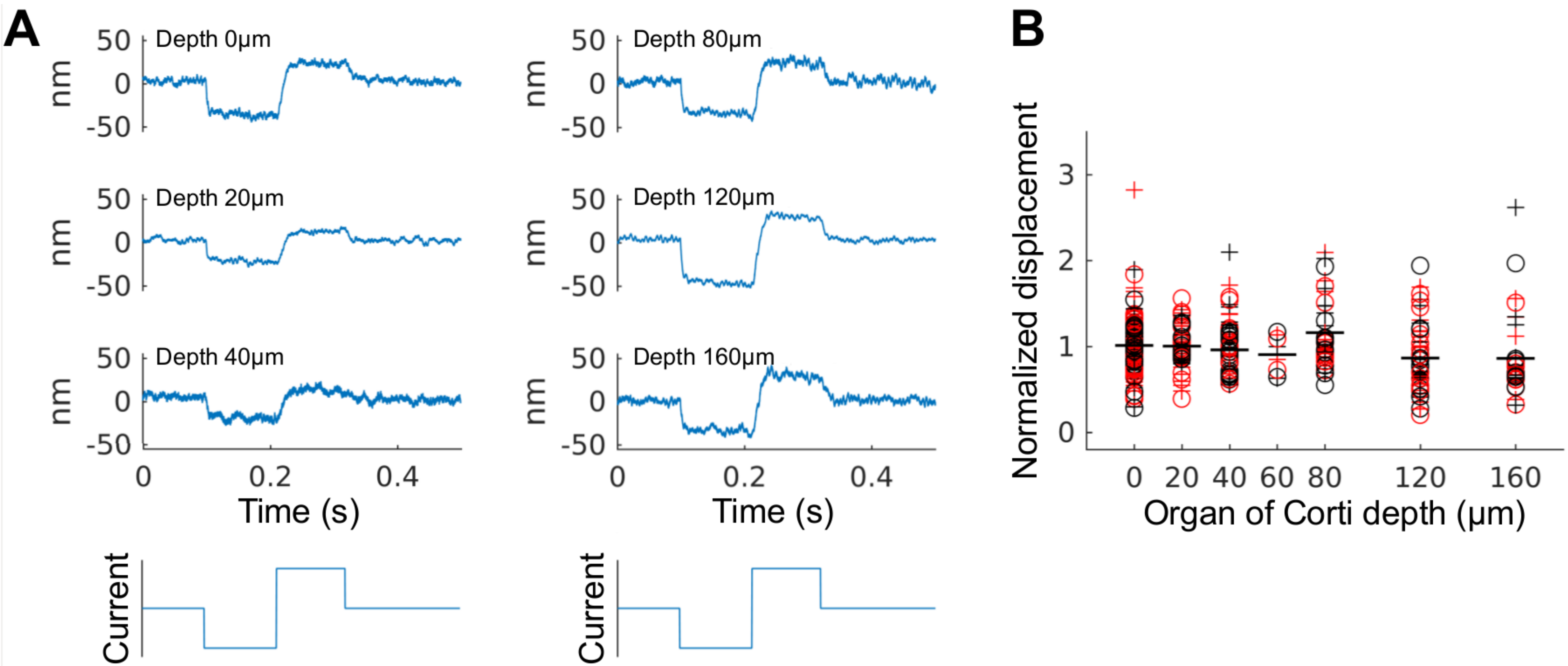
- Model contains only two parameters

- Model parameters can be fixed through comparison with experimental results

- Hensen cells move upward when the outer hair cells contract!



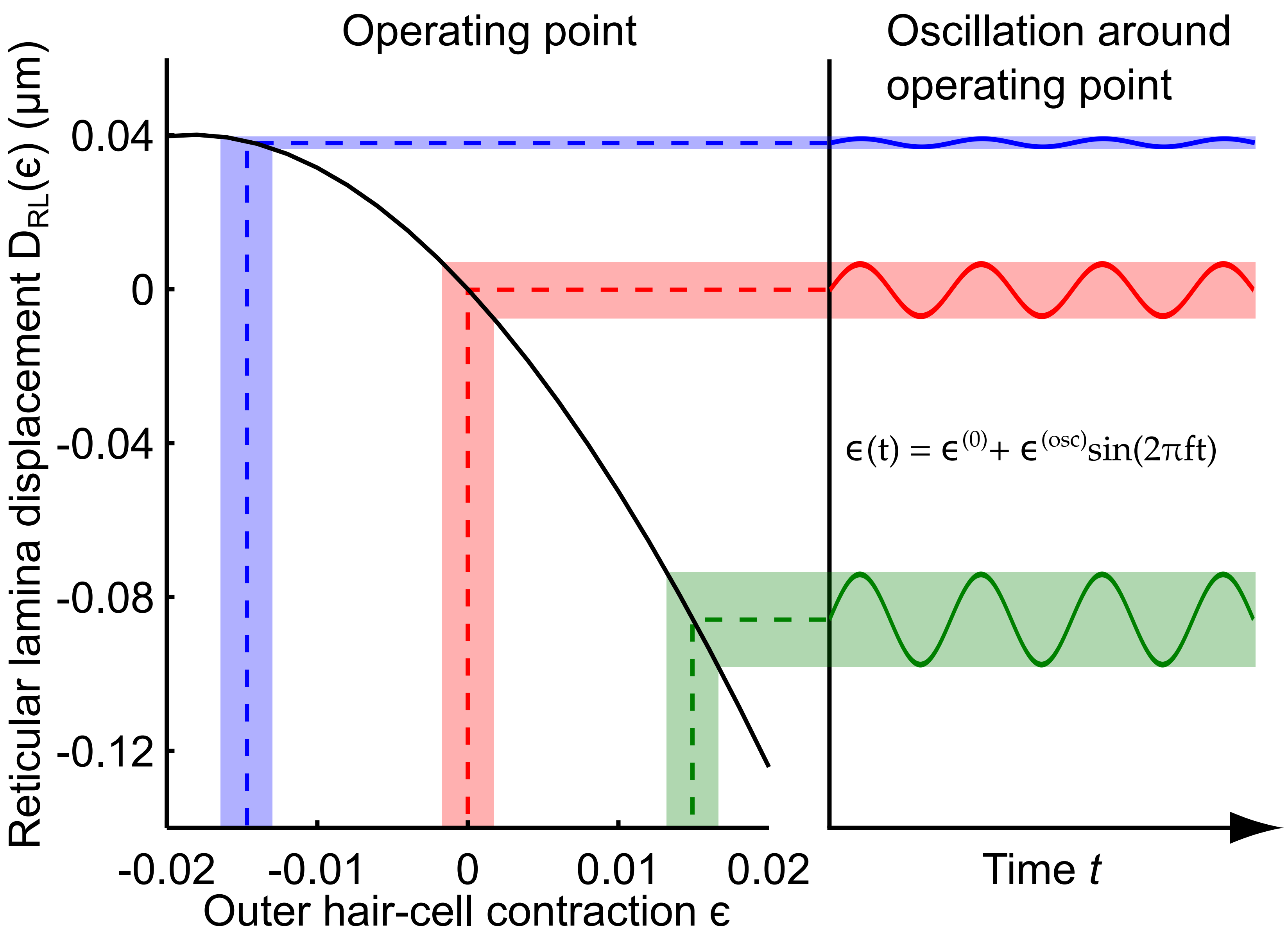
Correct model predictions of deformation behavior



Displacements keep similar amplitude and polarity ‘under’ the arc of Hensen cells

Ciganovic, Warren, Fridberger and Reichenbach (2017) *submitted*

Nonlinearity in the hair-bundle's amplitude

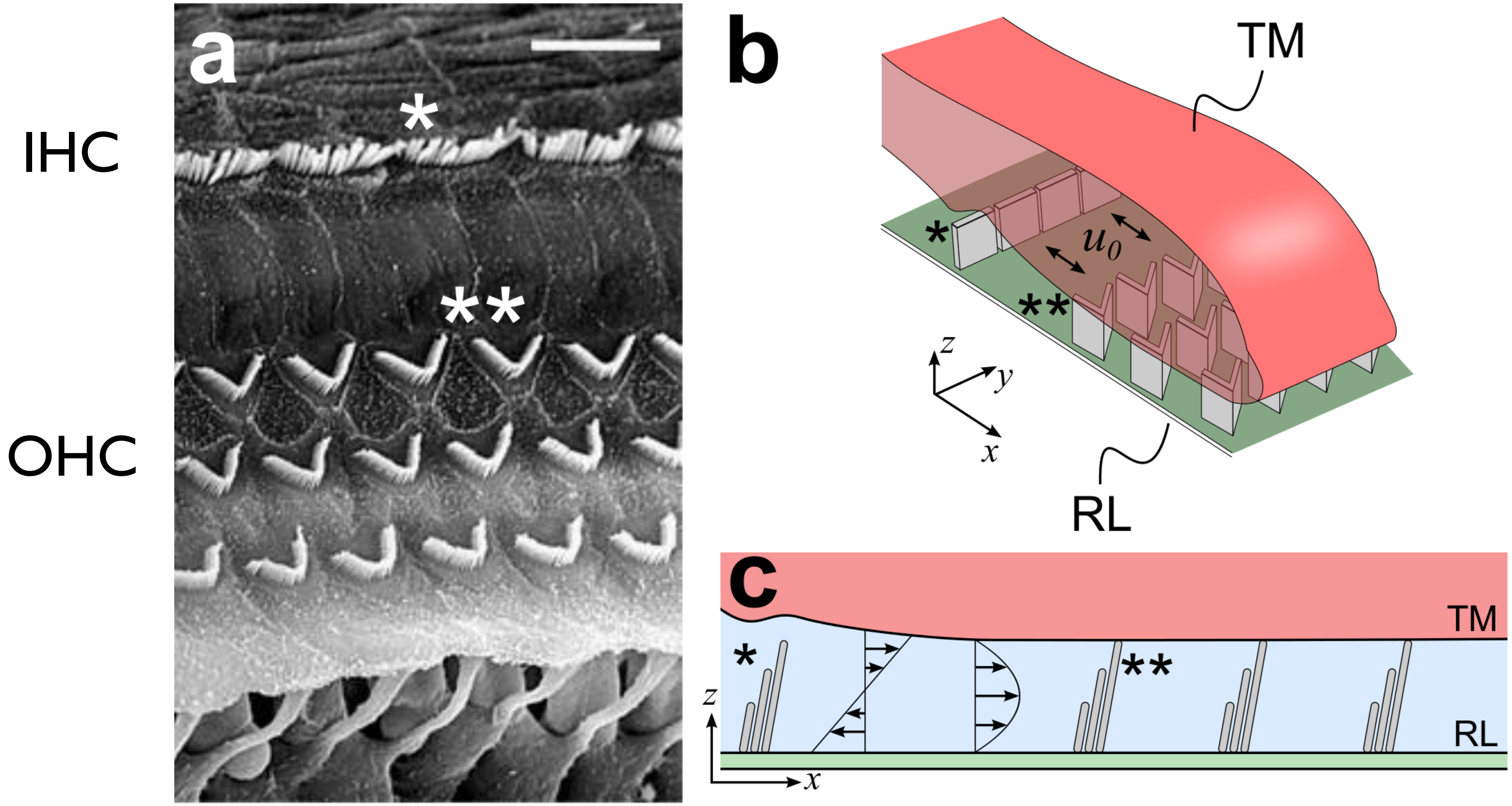


=> organ of Corti acts as an electromechanical transistor!

=> opens route for efferent nerve fibers to influence sound transmission by regulating the length of the outer hair cells!

Ciganovic, Warren, Fridberger and Reichenbach (2017) *submitted*

Fluid flow in the subtectorial space

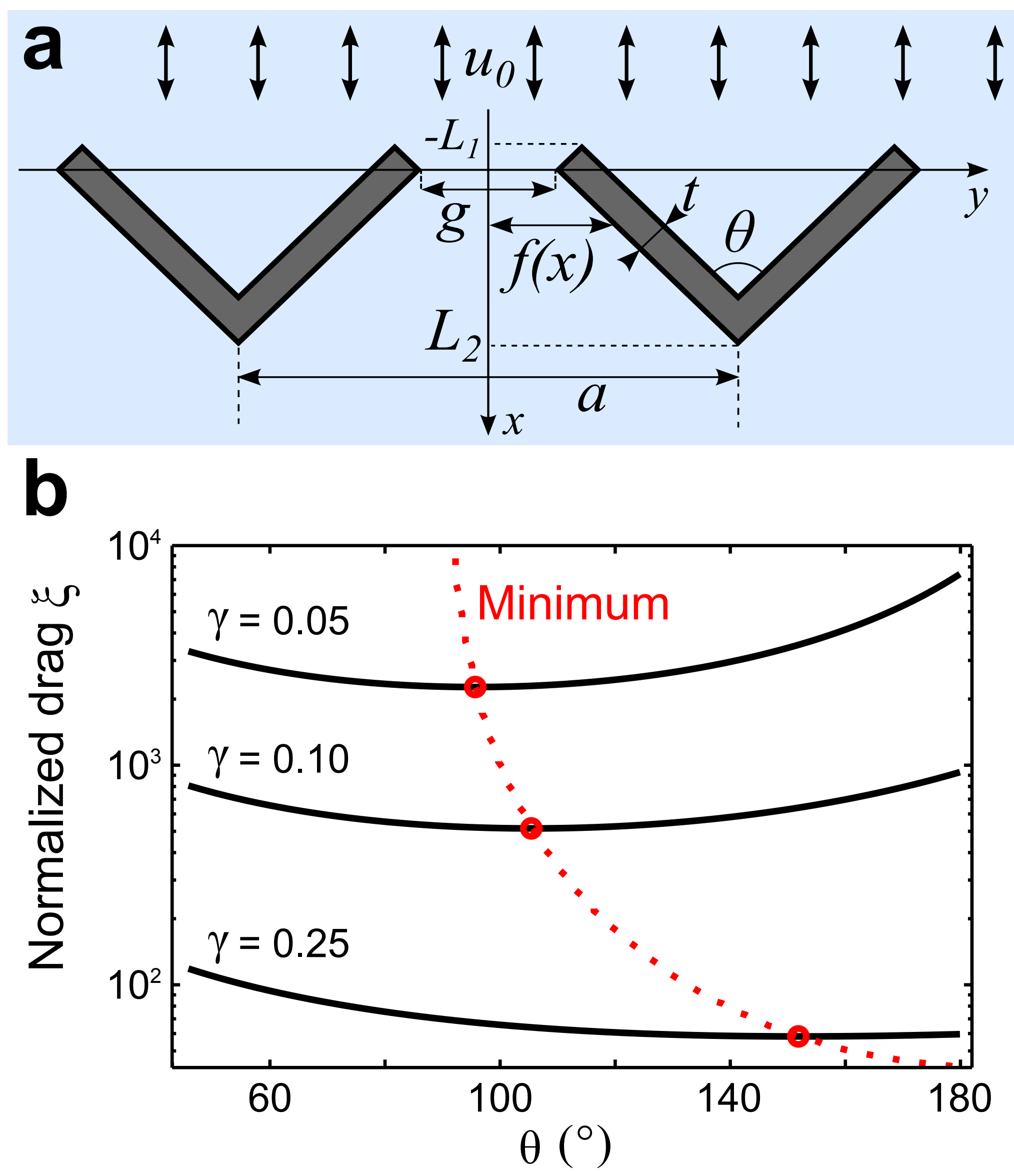


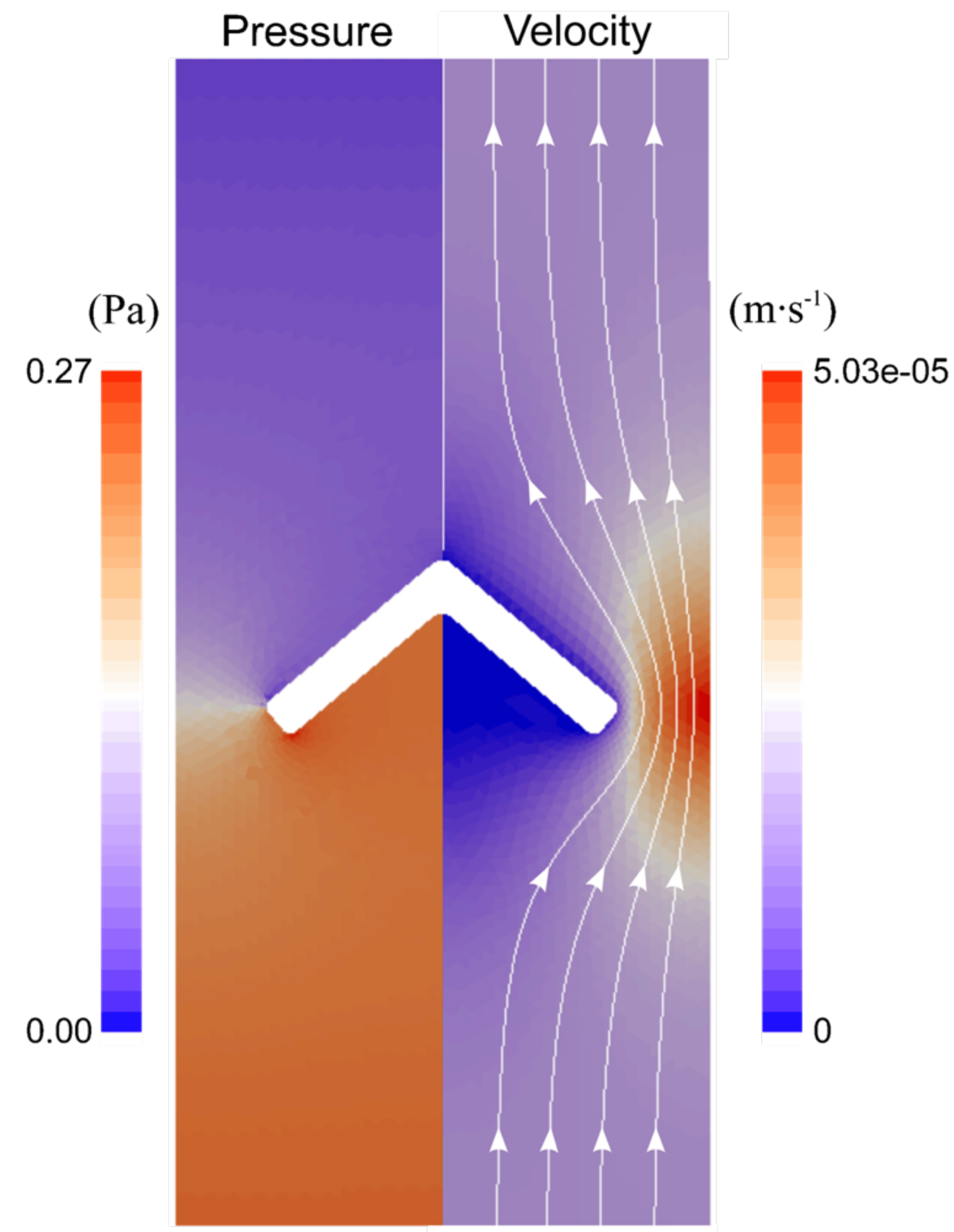
Evidence for net fluid flow between tectorial membrane and reticular lamina

Ciganovic, Wolde-Kidan and Reichenbach (2017) *Sci. Rep.*

Specialization in hair-bundle shape

Lubrication theory and computational fluid dynamics for flow across a lattice of hair bundles



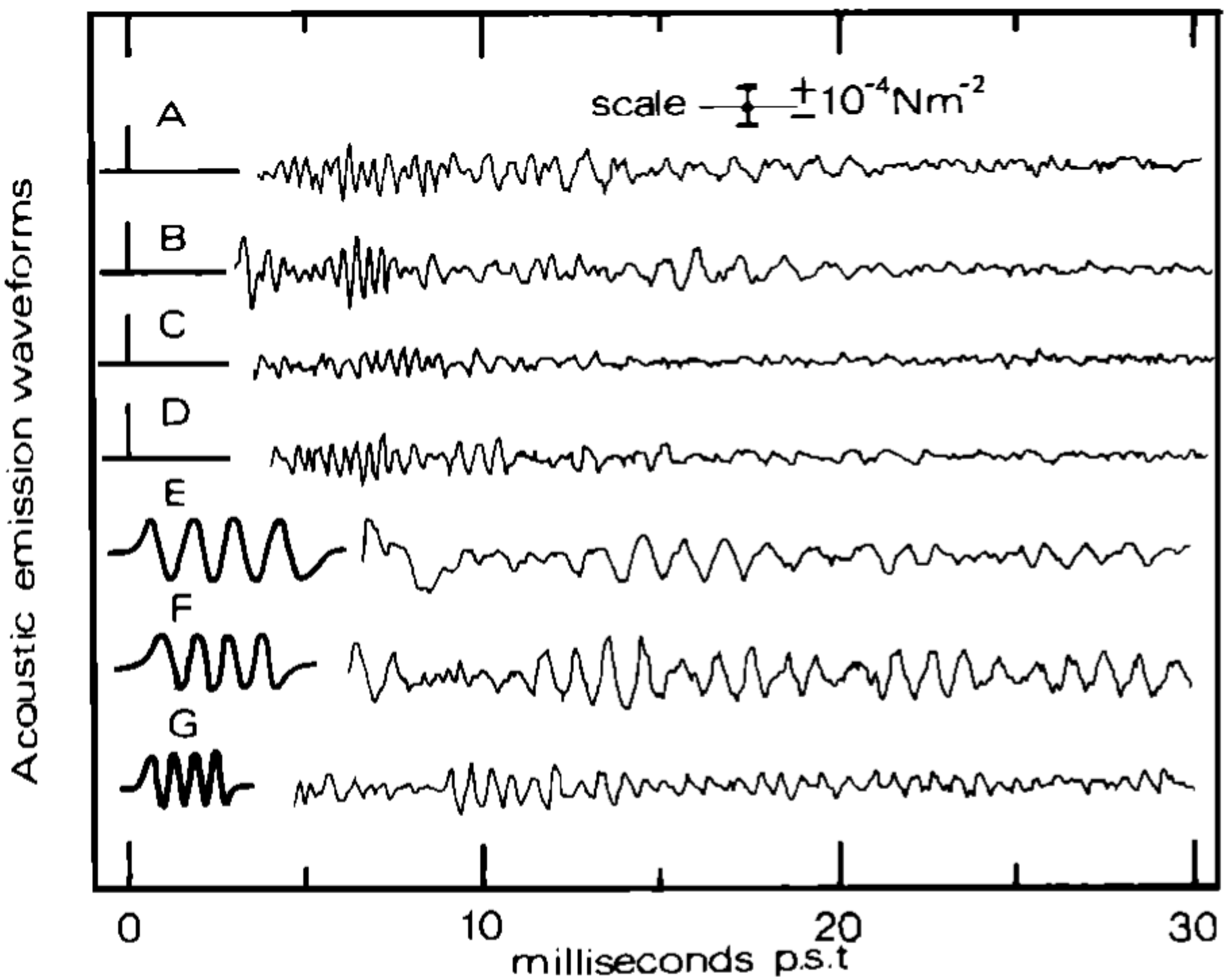


<u>Resistance minimal for opening angle of ca. 100°!</u>

Ciganovic, Wolde-Kidan and Reichenbach (2017) *Sci. Rep.*

5. Otoacoustic emissions

Echoes from the ear



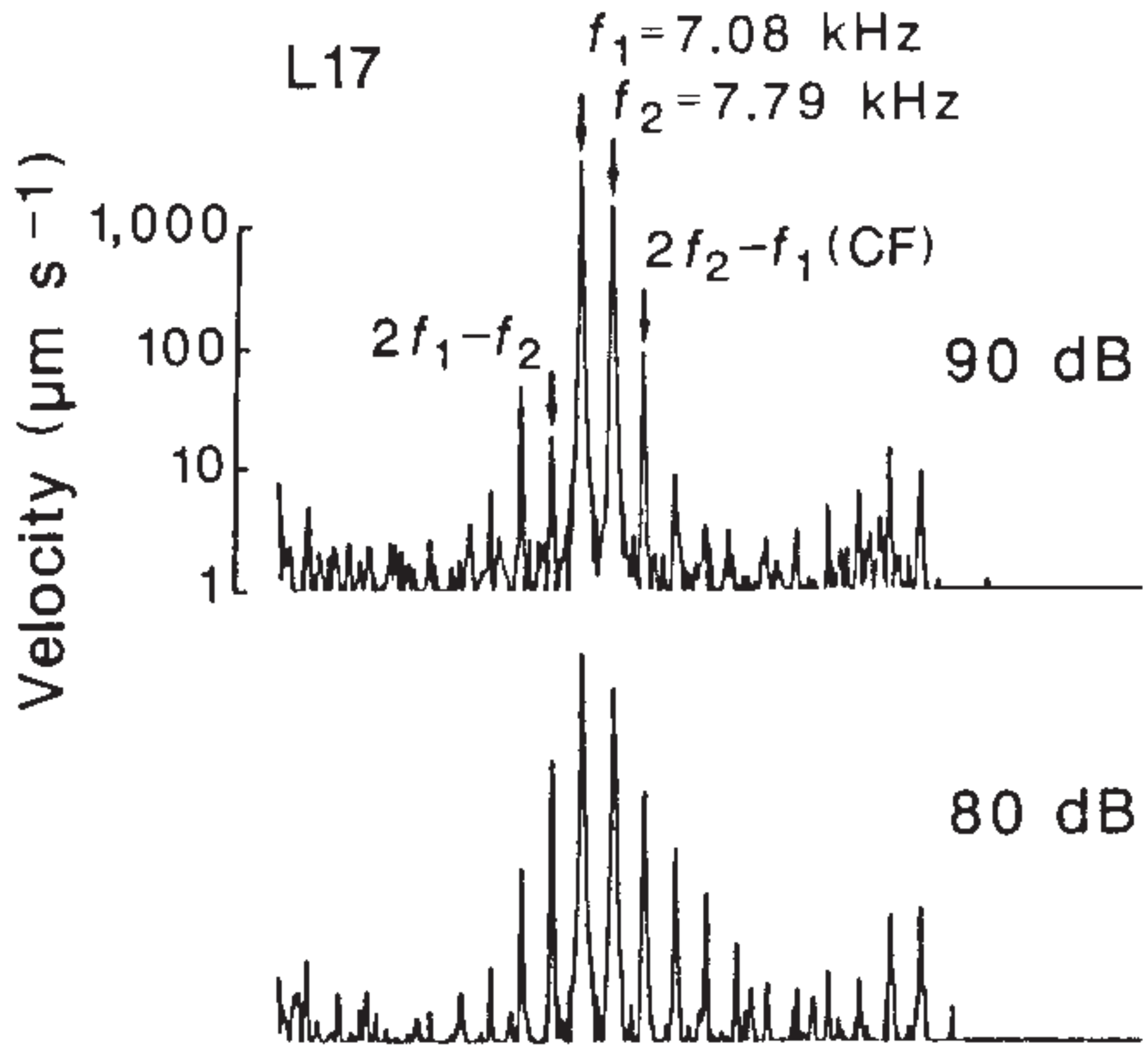
Kemp (1978) *J. Acoust. Soc. Am.*

Distortion-Product Otoacoustic Emissions (DPOAEs)

Stimulation of the inner ear at two frequencies f_1 and f_2

=> Nonlinear response yields combination tones (distortion)

in particular at
$2f_1 - f_2$ and $2f_2 - f_1$



Robles, Ruggero and Rich (1991) *Nature*

Generation and propagation of OAEs in the cochlea

nonlinear wave equation: $\partial_x^2 \tilde{V} - \frac{2i\omega\rho_0}{Zh}\tilde{V} = -\alpha \tilde{V} * \tilde{V} * \tilde{V}$ cubic nonlinearity

Compute Green's function $\tilde{V}^{(G,x_0)}$ that satisfies $\partial_x^2 \tilde{V}^{(G,x_0)} - \frac{2i\omega\rho_0}{Zh}\tilde{V}^{(G,x_0)} = \delta(x - x_0)$

Generation and propagation of OAEs in the cochlea

nonlinear wave equation: $\partial_x^2 \tilde{V} - \frac{2i\omega\rho_0}{Zh}\tilde{V} = -\alpha \tilde{V} * \tilde{V} * \tilde{V}$ cubic nonlinearity

Compute Green's function $\tilde{V}^{(G,x_0)}$ that satisfies $\partial_x^2 \tilde{V}^{(G,x_0)} - \frac{2i\omega\rho_0}{Zh}\tilde{V}^{(G,x_0)} = \delta(x - x_0)$

Ansatz $\tilde{V}^{(G,x_0)} = \int_{-\infty}^{\infty} dk g(k) e^{-ik(x-x_0)}$ yields $g(k) = \frac{1}{2\pi L(k)}$ with

$L(k) = [k^2 + 2i\omega\rho_0 / (Zh)]$; $L(k) = 0$ is the dispersion relation

Generation and propagation of OAEs in the cochlea

nonlinear wave equation: $\partial_x^2 \tilde{V} - \frac{2i\omega\rho_0}{Zh} \tilde{V} = -\alpha \tilde{V} * \tilde{V} * \tilde{V}$ cubic nonlinearity

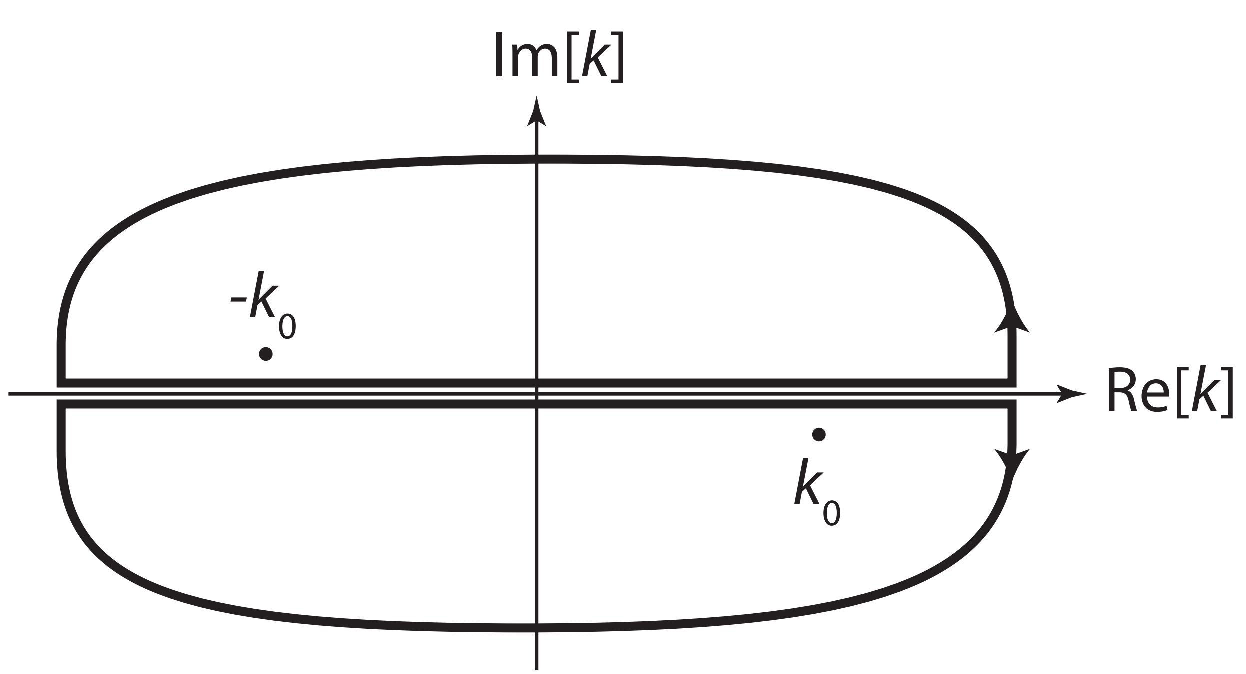
Compute Green's function $\tilde{V}^{(G,x_0)}$ that satisfies $\partial_x^2 \tilde{V}^{(G,x_0)} - \frac{2i\omega\rho_0}{Zh} \tilde{V}^{(G,x_0)} = \delta(x - x_0)$

Ansatz $\tilde{V}^{(G,x_0)} = \int_{-\infty}^{\infty} dk g(k) e^{-ik(x-x_0)}$ yields $g(k) = \frac{1}{2\pi L(k)}$ with

$L(k) = [k^2 + 2i\omega\rho_0 / (Zh)]$; $L(k) = 0$ is the dispersion relation

Integral can be solved by shifting the poles away from the real axis (damping!) and complex integration

=> 'Feynman propagator'



Generation and propagation of OAEs in the cochlea

Solution to the nonlinear wave equation:

$$\tilde{V}(x) = -\alpha \int dx_0 \tilde{V}^{(G,x_0)}(x)(\tilde{V} * \tilde{V} * \tilde{V})(x_0)$$

Green's function cubic nonlinearity

Generation and propagation of OAEs in the cochlea

Solution to the nonlinear wave equation:

$$\tilde{V}(x) = -\alpha \int dx_0 \tilde{V}^{(G,x_0)}(x)(\tilde{V} * \tilde{V} * \tilde{V})(x_0)$$

Green's function cubic nonlinearity

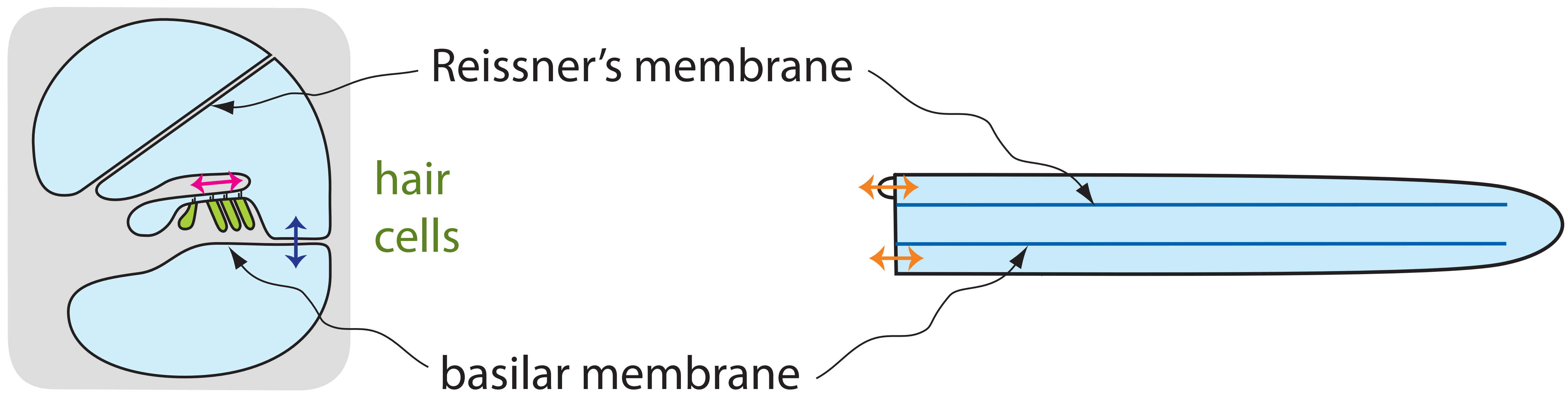
Problem: implicit equation for the velocity!

Born approximation: $\tilde{V}_1(x) = -\alpha \int dx_0 \tilde{V}^{(G,x_0)}(x)(\tilde{V}_0 * \tilde{V}_0 * \tilde{V}_0)(x_0)$

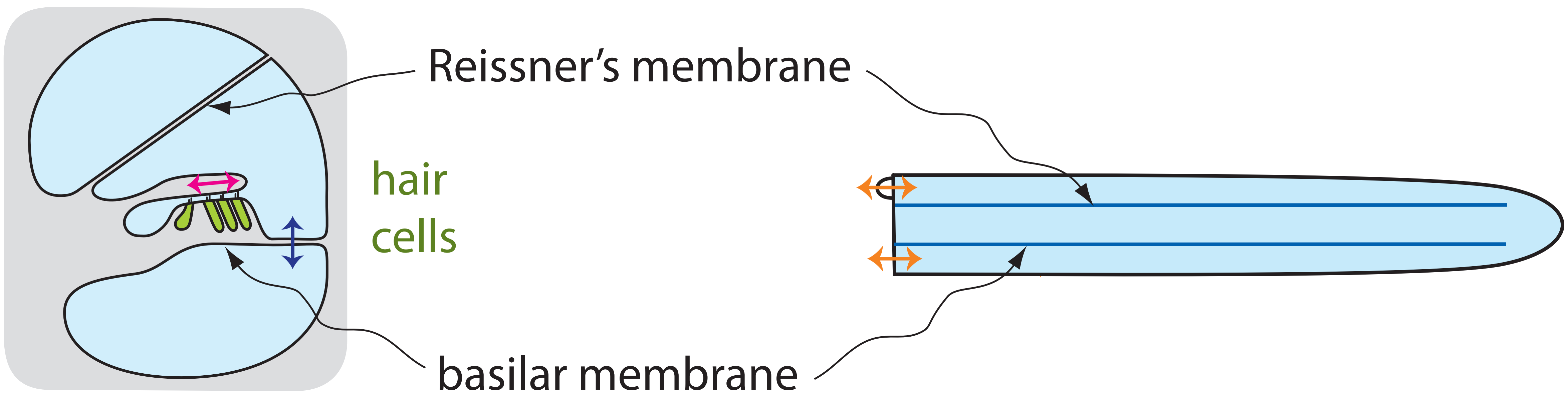
with V_0 solution to linear (passive) wave equation

Full solution: $\tilde{V} = \tilde{V}_0 + \tilde{V}_1$

Waves on Reissner's membrane



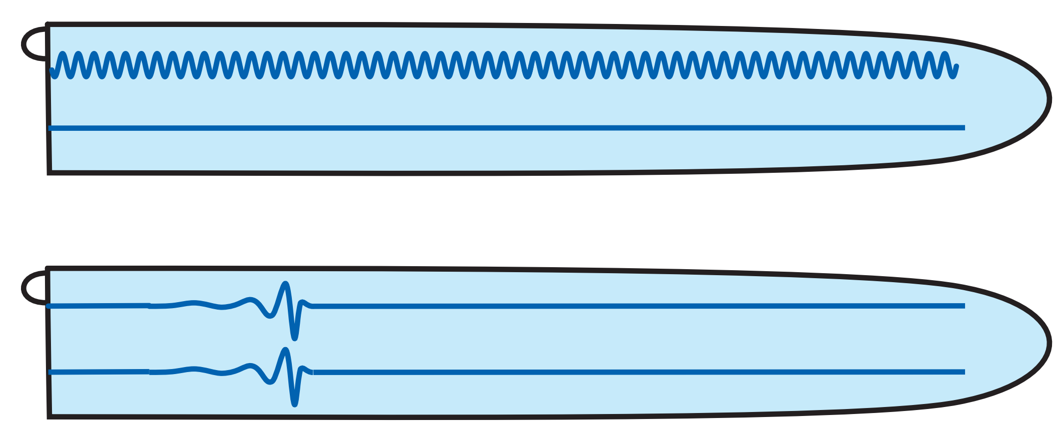
Waves on Reissner's membrane



Theory:

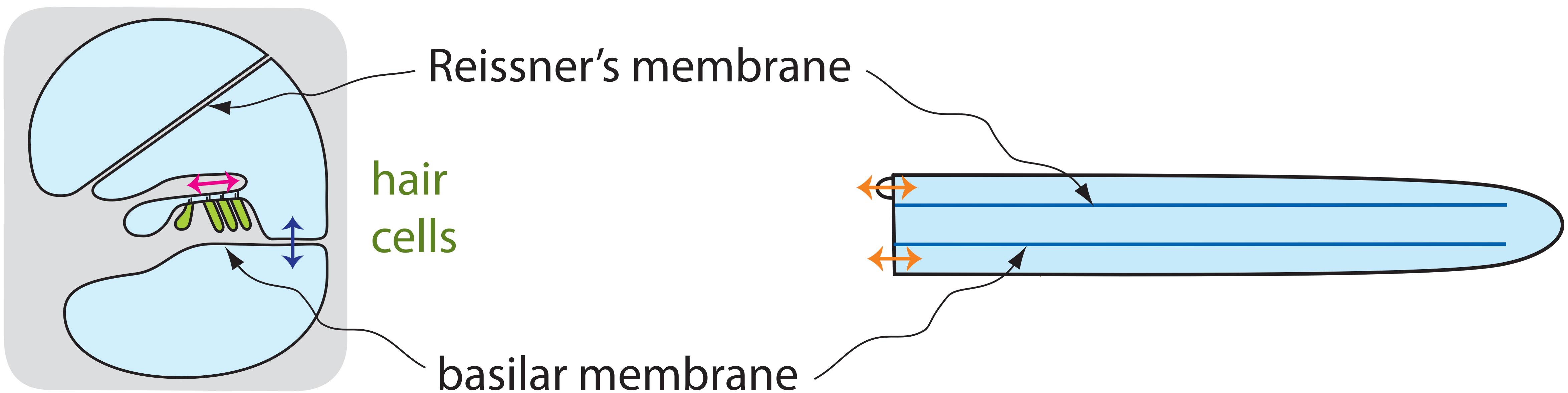
two wave modes on the two parallel membranes

play a role in ***otoacoustic emission***



T. Reichenbach, A. Stefanovic, F. Nin & A. J. Hudspeth, ***Cell Reports*** (2012)

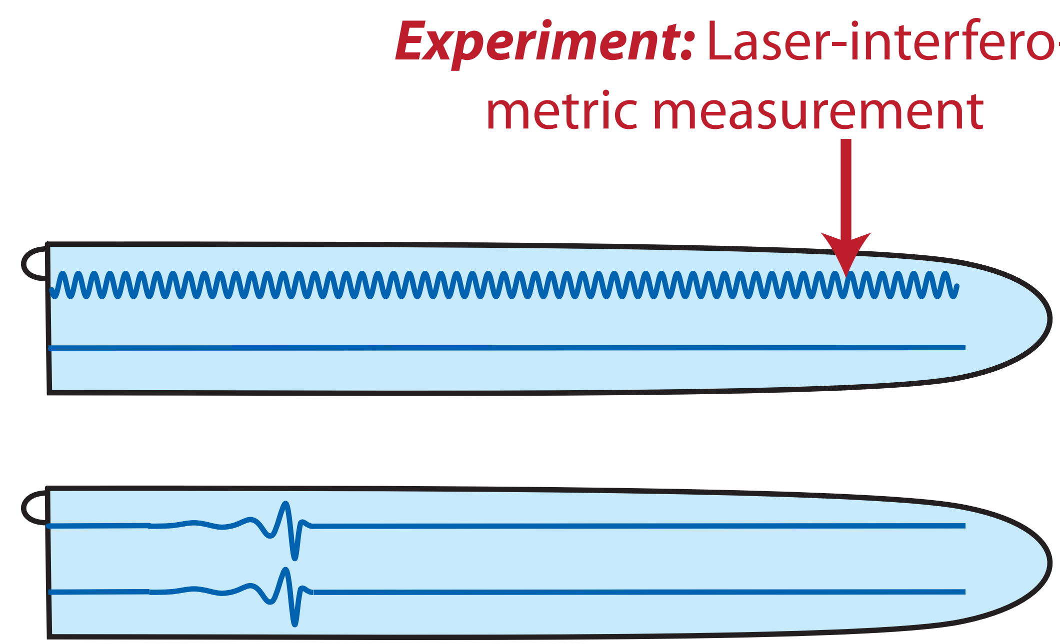
Waves on Reissner's membrane



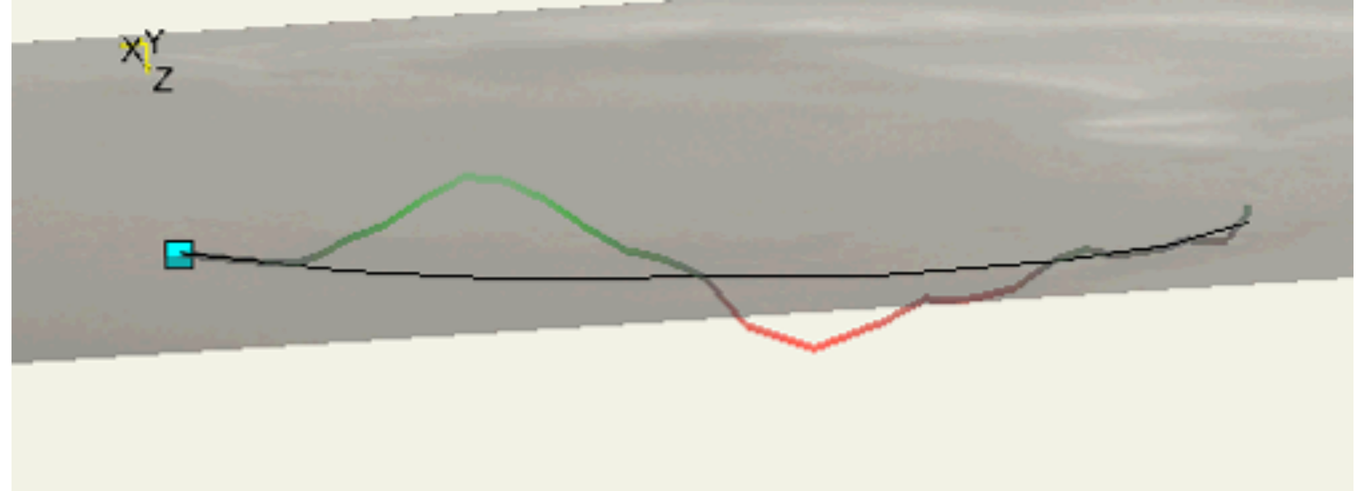
Theory:

two wave modes on the two parallel membranes

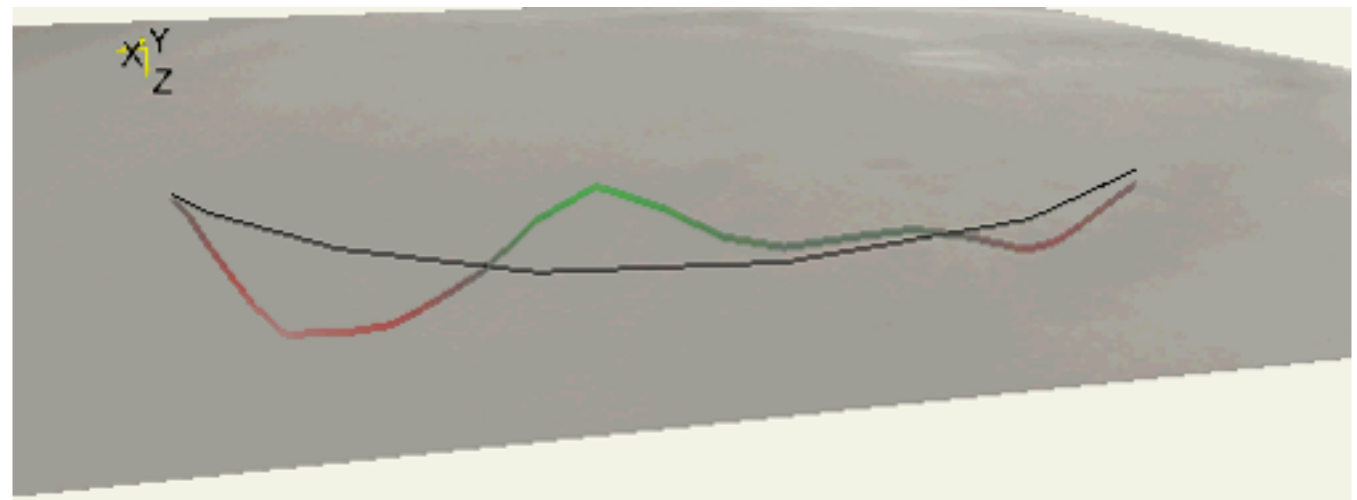
play a role in ***otoacoustic emission***



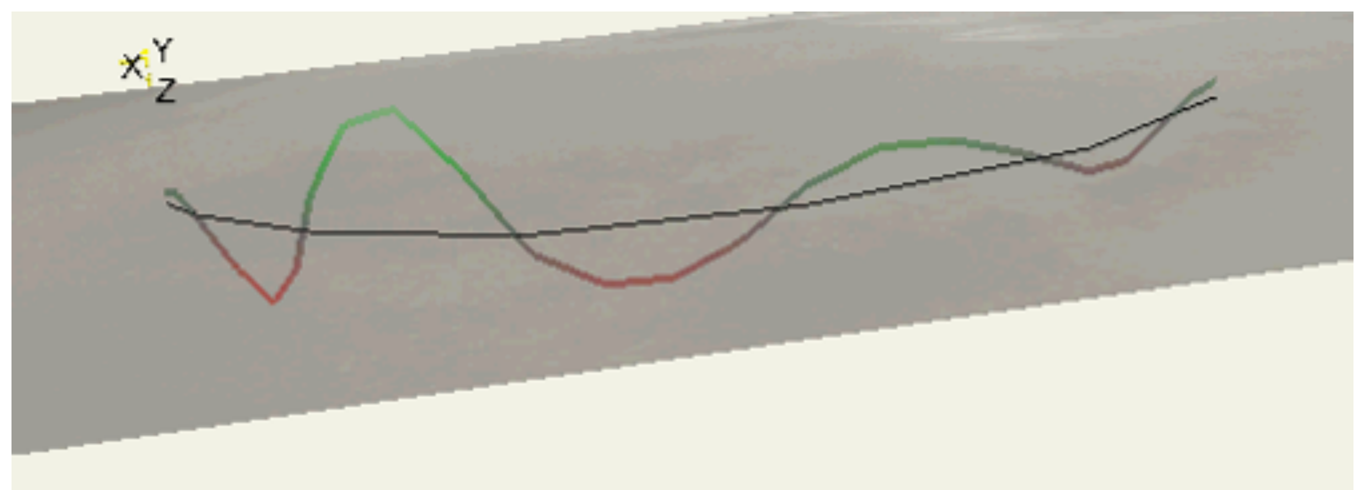
T. Reichenbach, A. Stefanovic, F. Nin & A. J. Hudspeth, ***Cell Reports*** (2012) *f*=1 kHz:



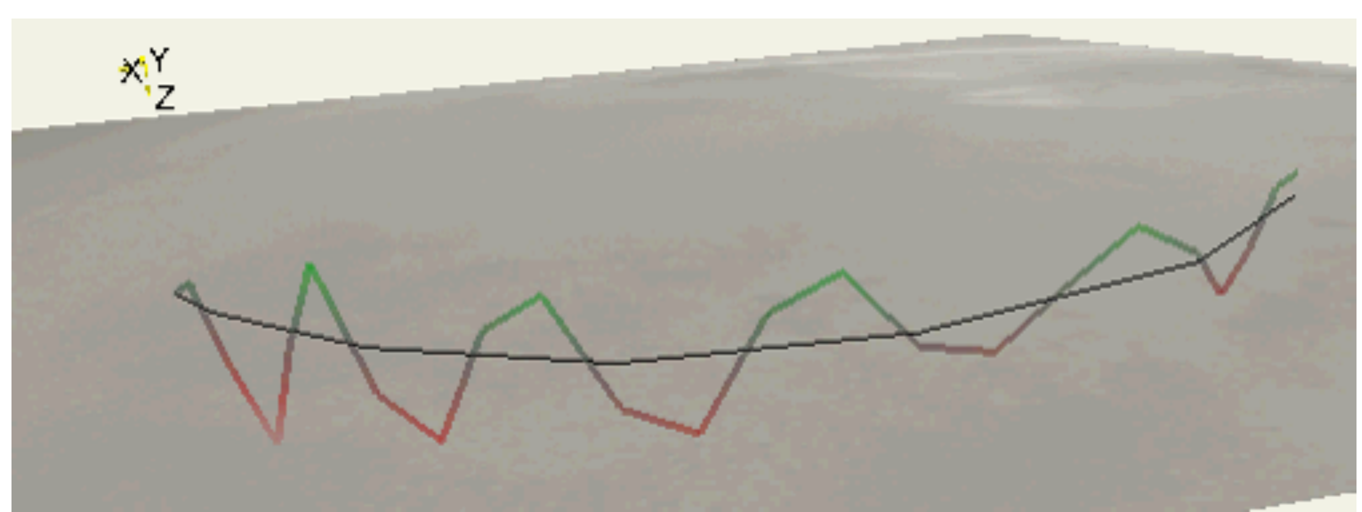
f=2 kHz:



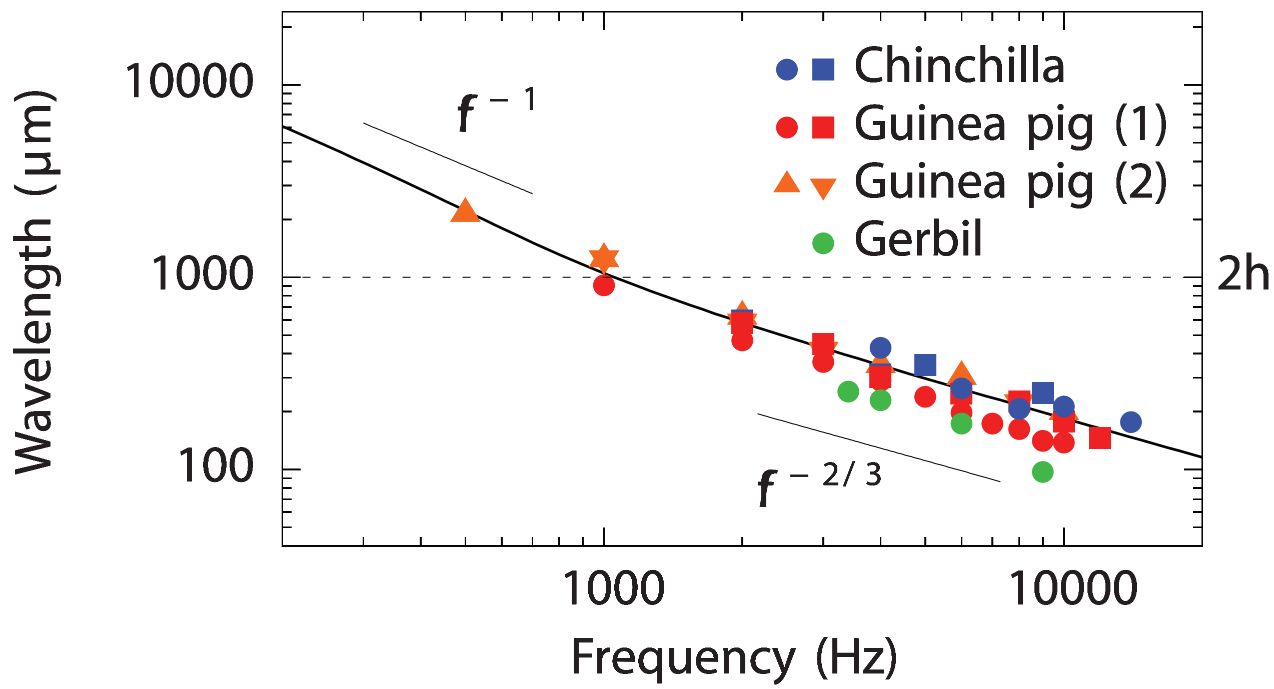
f=4 kHz:



f=8 kHz:



Dispersion relation



Chinchilla

constitute a mechanism for otoacoustic emissions:
T. Reichenbach, A. Stefanovic, F. Nin & A. J. Hudspeth, ***Cell Reports*** (2012)

another mechanism: waves on the cochlear bone:
T. Tchumatchenko & T. Reichenbach, ***Nat. Commun.*** (2014)

Conclusions

- Critical-layer absorption and nonlinear response can explain high-frequency cochlear mechanics
- Traveling waves can accumulate gain
- Unidirectional amplification may occur at low frequencies
- Shape of hair bundles of outer hair cells may be specialized for reducing resistance to cross-flow
- Generation and propagation of otoacoustic emissions can be described by 'classicized' methods developed in quantum field theory
- Reissner's membrane may play a role in back-propoagation of otoacoustic emissions