Critical amplification in the cochlea

Frank Jülicher

Max Planck Institute
for the Physics of Complex Systems
Dresden

MAX-PLANCK-GESELLSCHAFT

mpipks

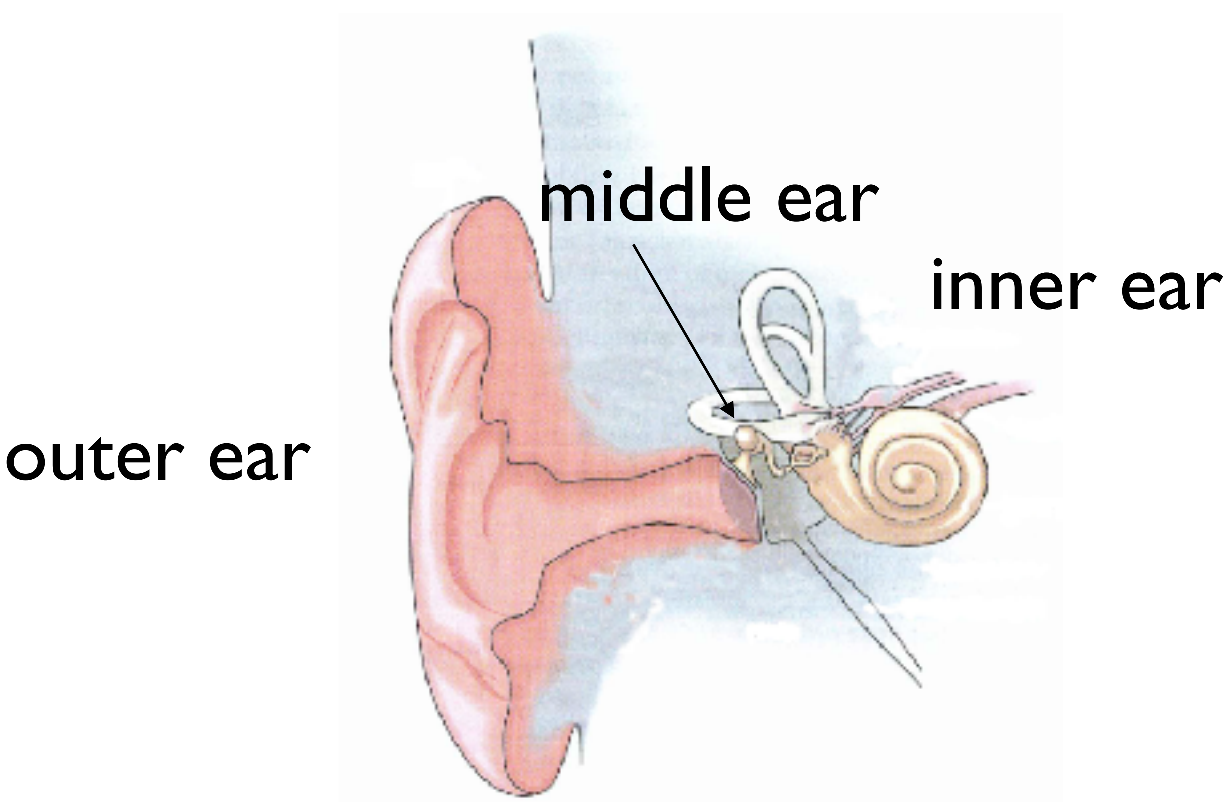
Acknowledgements

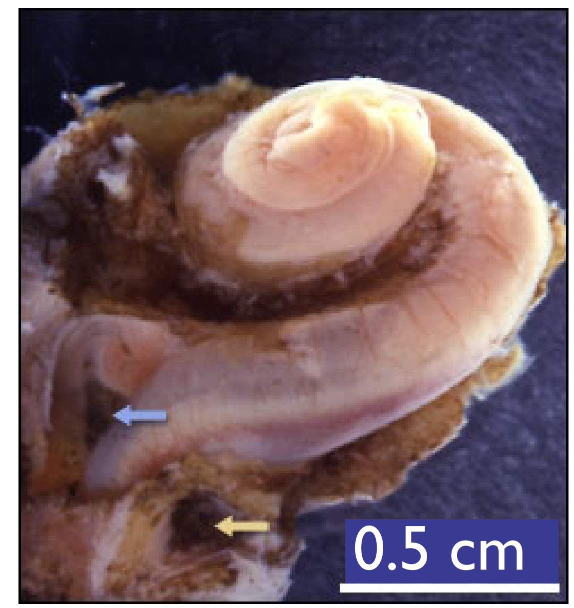
Thomas Duke
Pascal Martin
Jacques Prost
Jim Hudspeth

Daibhid. O Maoileidigh
Benjamin Lindner
Jean-Francois Joanny

Daniel Andor
Sebastian Camalet
Diana Clausnitzer
Kai Dierkes
Florian Fruth
Björn Nadrowski
Thomas Risler
Aditi Simha
Jean-Yves Tinevez

The cochlea





cochlea

Signal detector

sound waves → mechanical vibrations → electrical action potentials

Biophysics of hearing

physical basis of sound detection

19. century — resonant oscillators

von Helmholtz

1950 — wave mechanics

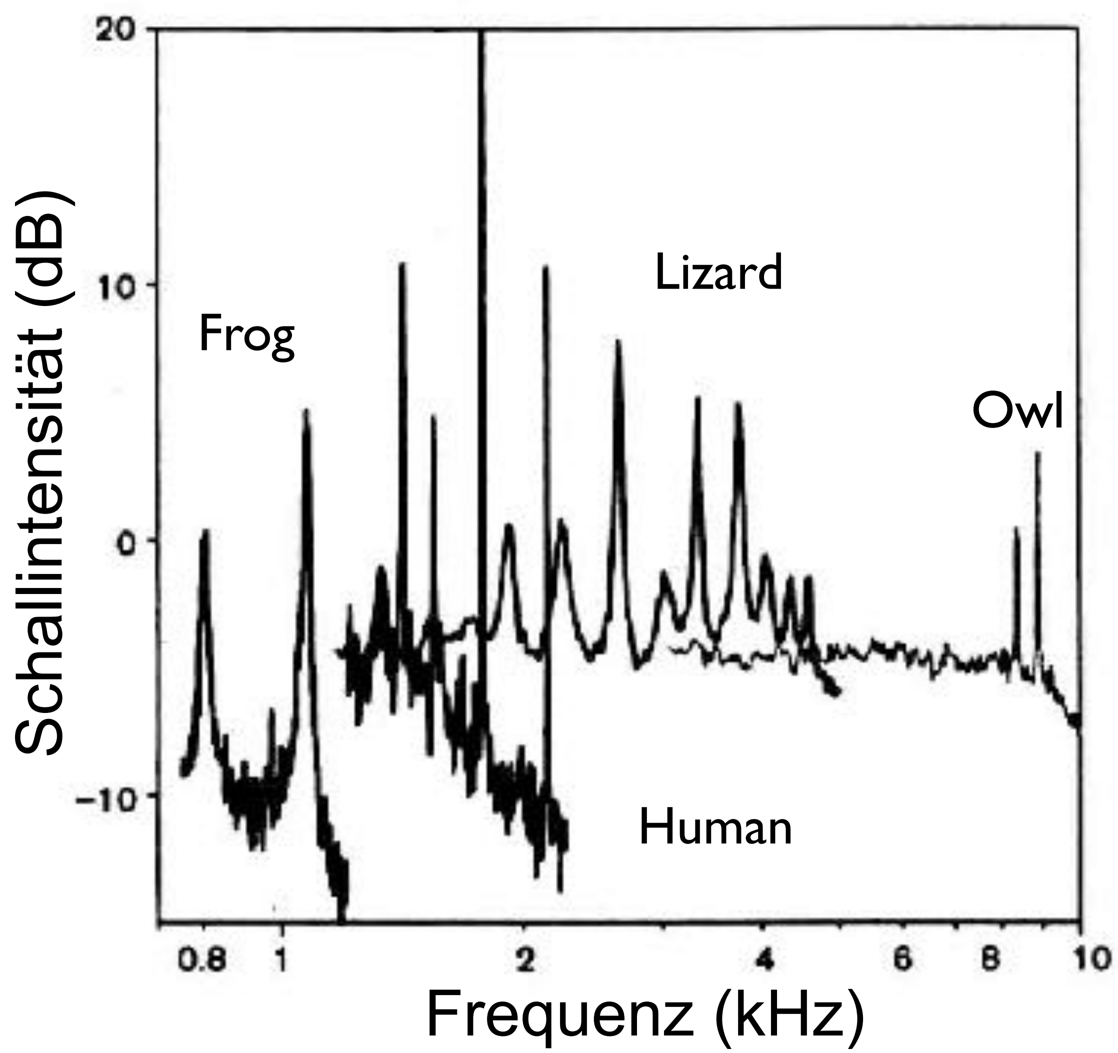
von Békésy

1980 — active amplification

Gold 1948

Otoacoustic emissions

Spontaneous oto-acoustic emissions (S.O.A.E)



G.A. Manley and C. Köppl, 1998

D. Kemp, 1979

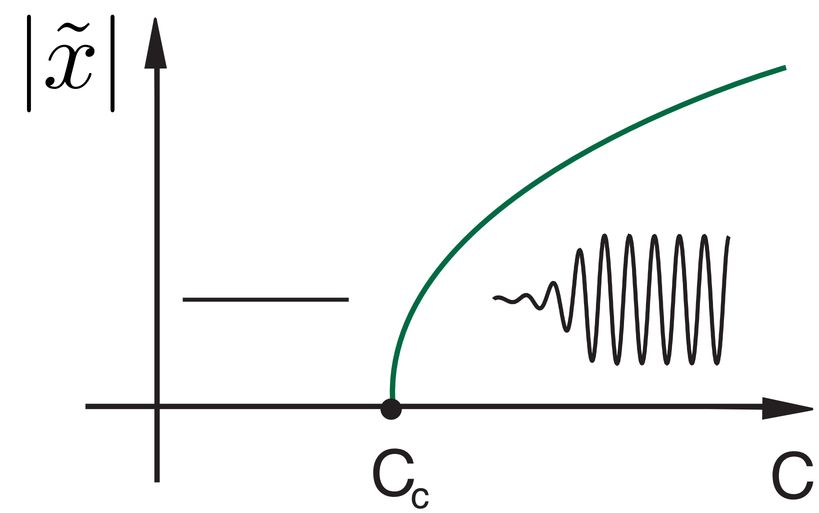
Signatures of active processes in the ear

compressive nonlinearity

nonlinear combination tones

oto-acoustic emissions

sharp frequency selectivity



evidence for nonlinear and active oscillators

These signatures require the intact life organ

Nonlinearity linked to the active process

A.J. Hudspeth, Neuron (2008)

Todays talk

compressive nonlinearity

nonlinear combination tones

oto-acoustic emissions

sharp frequency selectivity

How can these features
be implemented using
noisy dynamic cellular processes?

1.) Emergence of oscillations via a non-equilibrium phase transition

“Hopf bifurcation”

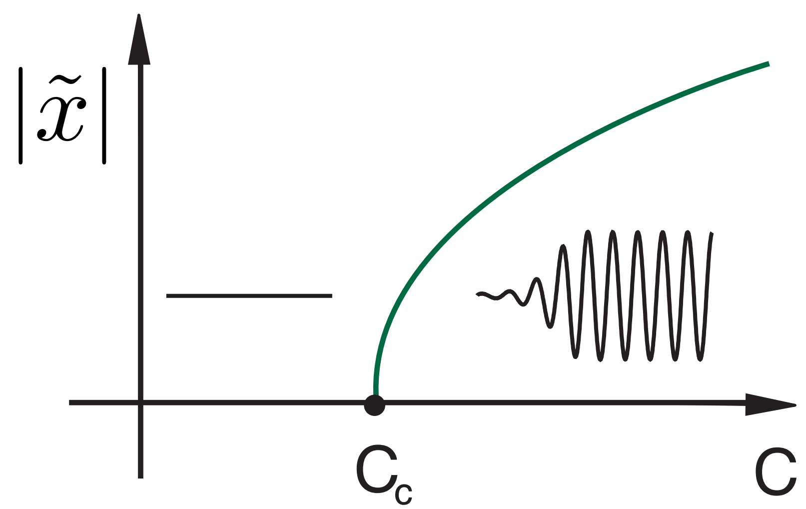
2.) Active and nonlinear wave phenomena in the cochlea

“Active traveling wave”

Nonlinear oscillators

Spontaneous oscillations via a non-equilibrium phase transition

Hopf bifurcation in nonlinear dynamics



Generic oscillator normal form

$$A(\omega)\tilde{x} + B|\tilde{x}|^2\tilde{x} \simeq \tilde{f}$$

$$\tilde{x} = \int x(t)e^{-i\omega t}dt \qquad f(t) = \tilde{f}e^{i\omega t} + \tilde{f}^* e^{-i\omega t}$$

T. Risler, J. Prost, F. Jülicher, PRL 93, 175702 (2004)

Nonlinear response

Single displacement variable (no noise)

$$x(t) = \sum_{n=-\infty}^{\infty} \tilde{x}_n e^{in\omega t}$$

$$\tilde{x}_n^* = \tilde{x}_{-n}$$

External force

$$f(t) = \sum_{n=-\infty}^{\infty} \tilde{f}_n e^{in\omega t}$$

$$\tilde{f}_n^* = \tilde{f}_{-n}$$

displacement-force relation

$$\tilde{x}_n = G_n^{(1)} \tilde{f}_n + \sum_k G_{nk}^{(2)} \tilde{f}_{n-k} \tilde{f}_k + \sum_{kl} G_{nkl}^{(3)} \tilde{f}_{n-k-l} \tilde{f}_k \tilde{f}_l + O(\tilde{f}^4)$$

Nonlinear response

Single displacement variable (no noise)

$$x(t) = \sum_{n=-\infty}^{\infty} \tilde{x}_n e^{in\omega t}$$

$$\tilde{x}_n^* = \tilde{x}_{-n}$$

External force

$$f(t) = \sum_{n=-\infty}^{\infty} \tilde{f}_n e^{in\omega t}$$

$$\tilde{f}_n^* = \tilde{f}_{-n}$$

displacement-force relation

$$\tilde{x}_n = G_n^{(1)} \tilde{f}_n + \sum_k G_{nk}^{(2)} \tilde{f}_{n-k} \tilde{f}_k + \sum_{kl} G_{nkl}^{(3)} \tilde{f}_{n-k-l} \tilde{f}_k \tilde{f}_l + O(\tilde{f}^4)$$

$$e^{in\omega t} \qquad e^{i(n-k)\omega t} e^{ik\omega t} \qquad e^{i(n-k-l)\omega t} e^{ik\omega t} e^{il\omega t}$$

Nonlinear response

Single displacement variable (no noise)

$$x(t) = \sum_{n=-\infty}^{\infty} \tilde{x}_n e^{in\omega t}$$

$$\tilde{x}_n^* = \tilde{x}_{-n}$$

External force

$$f(t) = \sum_{n=-\infty}^{\infty} \tilde{f}_n e^{in\omega t}$$

$$\tilde{f}_n^* = \tilde{f}_{-n}$$

displacement-force relation

$$\tilde{x}_n = G_n^{(1)} \tilde{f}_n + \sum_k G_{nk}^{(2)} \tilde{f}_{n-k} \tilde{f}_k + \sum_{kl} G_{nkl}^{(3)} \tilde{f}_{n-k-l} \tilde{f}_k \tilde{f}_l + O(\tilde{f}^4)$$

linear response

what happens when $G_n^{(1)}$ becomes large?

Inverse expansion

inverse exists in a vicinity of the region where $F_n^{(1)}$ is small

$$F_n^{(1)} = \frac{1}{G_n^{(1)}}$$

force-displacement relation

$$\tilde{f}_n = F_n^{(1)} \tilde{x}_n + \sum_k F_{nk}^{(2)} \tilde{x}_{n-k} \tilde{x}_k + \sum_{kl} F_{nkl}^{(3)} \tilde{x}_{n-k-l} \tilde{x}_k \tilde{x}_l + O(\tilde{x}^4)$$

displacement-force relation

$$\tilde{x}_n = G_n^{(1)} \tilde{f}_n + \sum_k G_{nk}^{(2)} \tilde{f}_{n-k} \tilde{f}_k + \sum_{kl} G_{nkl}^{(3)} \tilde{f}_{n-k-l} \tilde{f}_k \tilde{f}_l + O(\tilde{f}^4)$$

linear response

what happens when $G_n^{(1)}$ becomes large?

Critical point

When $F_n^{(1)}$ vanishes, a critical point occurs

$$F_n^{(1)} = \frac{1}{G_n^{(1)}}$$

$$F_1^{(1)}(\omega_c) = 0$$

$G_1^{(1)}(\omega_c)$ response function diverges

force-displacement relation

$$\tilde{f}_n = F_n^{(1)} \tilde{x}_n + \sum_k F_{nk}^{(2)} \tilde{x}_{n-k} \tilde{x}_k + \sum_{kl} F_{nkl}^{(3)} \tilde{x}_{n-k-l} \tilde{x}_k \tilde{x}_l + O(\tilde{x}^4)$$

displacement-force relation

$$\tilde{x}_n = G_n^{(1)} \tilde{f}_n + \sum_k G_{nk}^{(2)} \tilde{f}_{n-k} \tilde{f}_k + \sum_{kl} G_{nkl}^{(3)} \tilde{f}_{n-k-l} \tilde{f}_k \tilde{f}_l + O(\tilde{f}^4)$$

linear response

what happens when $G_n^{(1)}$ becomes large?

Critical point

When $F_n^{(1)}$ vanishes, a critical point occurs

$$F_n^{(1)} = \frac{1}{G_n^{(1)}}$$

$$F_1^{(1)}(\omega_c) = 0$$

force-displacement relation

$G_1^{(1)}(\omega_c)$ response function diverges

$$\tilde{f}_n = F_n^{(1)}\tilde{x}_n + \sum_k F_{nk}^{(2)}\tilde{x}_{n-k}\tilde{x}_k + \sum_{kl} F_{nkl}^{(3)}\tilde{x}_{n-k-l}\tilde{x}_k\tilde{x}_l + O(\tilde{x}^4)$$

small spontaneous motion in response to a resonant stimulus $f(t) = \tilde{f}_1 e^{i\omega t} + c.c.$

$$\tilde{f}_1 \simeq F_1^{(1)}\tilde{x}_1 + (F_{1,2}^{(2)} + F_{1,-1}^{(2)})\tilde{x}_{-1}\tilde{x}_2 + (F_{1,1,1}^{(3)} + 2F_{1,-1,1}^{(3)})\tilde{x}_1^2\tilde{x}_{-1}$$

$$0 \simeq F_2^{(1)}\tilde{x}_2 + F_{2,1}^{(2)}\tilde{x}_1^2$$

$$|\tilde{x}_n| \sim |\tilde{x}_1|^n$$

Critical point

When $F_n^{(1)}$ vanishes, a critical point occurs

$$F_n^{(1)} = \frac{1}{G_n^{(1)}}$$

$$F_1^{(1)}(\omega_c) = 0$$

$$G_1^{(1)}(\omega_c)$$ response function diverges

force-displacement relation

$$\tilde{f}_n = F_n^{(1)}\tilde{x}_n + \sum_k F_{nk}^{(2)}\tilde{x}_{n-k}\tilde{x}_k + \sum_{kl} F_{nkl}^{(3)}\tilde{x}_{n-k-l}\tilde{x}_k\tilde{x}_l + O(\tilde{x}^4)$$

small spontaneous motion in response to a resonant stimulus

$$\tilde{f}_1 \simeq F_1^{(1)}\tilde{x}_1 + (F_{1,2}^{(2)} + F_{1,-1}^{(2)})\tilde{x}_{-1}\tilde{x}_2 + (F_{1,1,1}^{(3)} + 2F_{1,-1,1}^{(3)})\tilde{x}_1^2\tilde{x}_{-1}$$

$$0 \simeq F_2^{(1)}\tilde{x}_2 + F_{2,1}^{(2)}\tilde{x}_1^2$$

$$\tilde{x}_2 \simeq -\frac{F_{2,1}^{(2)}}{F_2^{(1)}}\tilde{x}_1^2$$

Critical point

When $F_n^{(1)}$ vanishes, a critical point occurs

$$F_n^{(1)} = \frac{1}{G_n^{(1)}}$$

$$F_1^{(1)}(\omega_c) = 0$$

force-displacement relation

$G_1^{(1)}(\omega_c)$ response function diverges

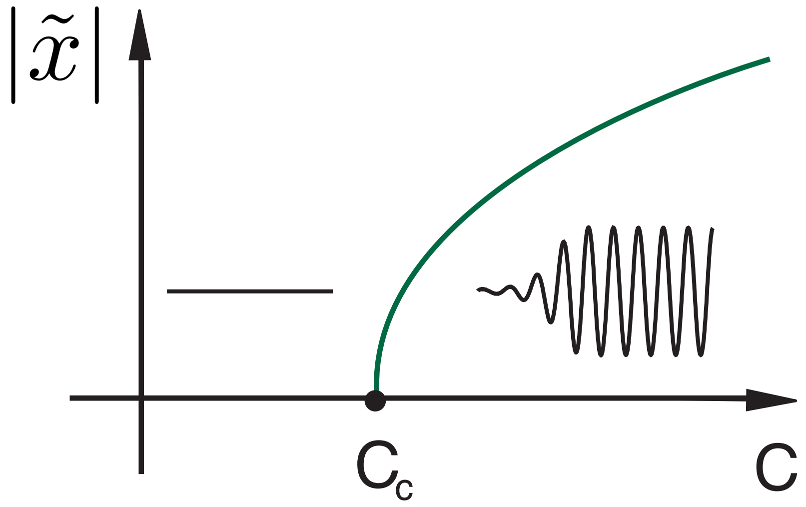
$$\tilde{f}_n = F_n^{(1)} \tilde{x}_n + \sum_k F_{nk}^{(2)} \tilde{x}_{n-k} \tilde{x}_k + \sum_{kl} F_{nkl}^{(3)} \tilde{x}_{n-k-l} \tilde{x}_k \tilde{x}_l + O(\tilde{x}^4)$$

small spontaneous motion in response to a resonant stimulus

$$\tilde{f}_1 \simeq A\tilde{x}_1 + B|\tilde{x}_1|^2 \tilde{x}_1 + ..$$

$$A = F_1^{(1)}$$
$$B = -(F_{2,1}^{(2)}/F_2^{(1)})(F_{1,2}^{(2)} + F_{1,-1}^{(2)}) + F_{1,1,1}^{(3)} + 2F_{1,-1,1}^{(3)}$$

Spontaneous oscillations



$$|\tilde{x}_1|^2 = -\frac{A(\omega^*)}{B(\omega^*)}$$

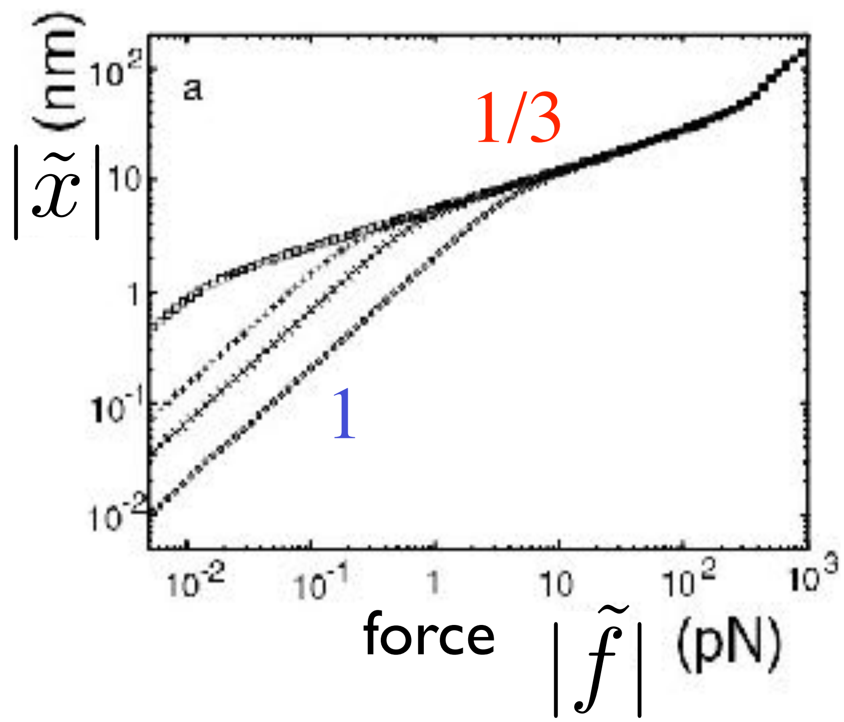
small spontaneous motion in response to a resonant stimulus

$$\tilde{f}_1 \simeq A\tilde{x}_1 + B|\tilde{x}_1|^2\tilde{x}_1 + ..$$

$$A(\omega, C) = \alpha(\omega - \omega_c) + \beta(C - C_c) + \dots$$

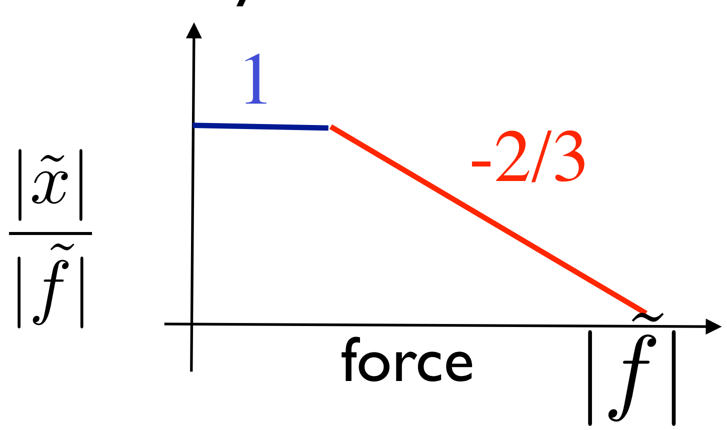
α, β complex

Signal amplification by nonlinear oscillators



$$\tilde{f}_1 \simeq A\tilde{x}_1 + B|\tilde{x}_1|^2\tilde{x}_1 + ..$$

Hopf bifurcation: $A(\omega_c) = 0$

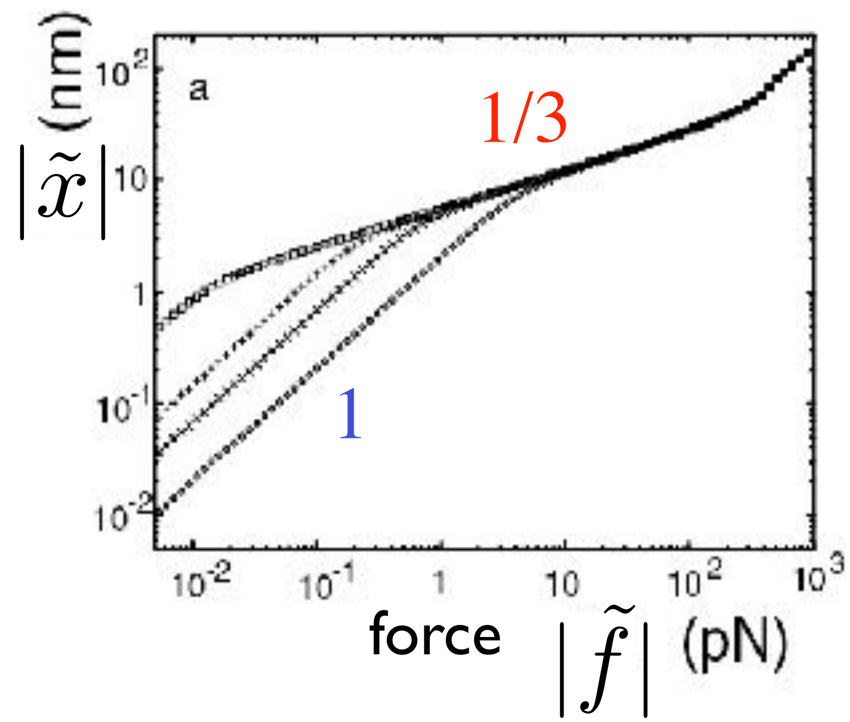


nonlinear response $|\tilde{x}_1| \sim |\tilde{f}_1|^{1/3}$

sensitivity $\frac{|\tilde{x}_1|}{|\tilde{f}_1|} \sim |\tilde{f}_1|^{-2/3}$

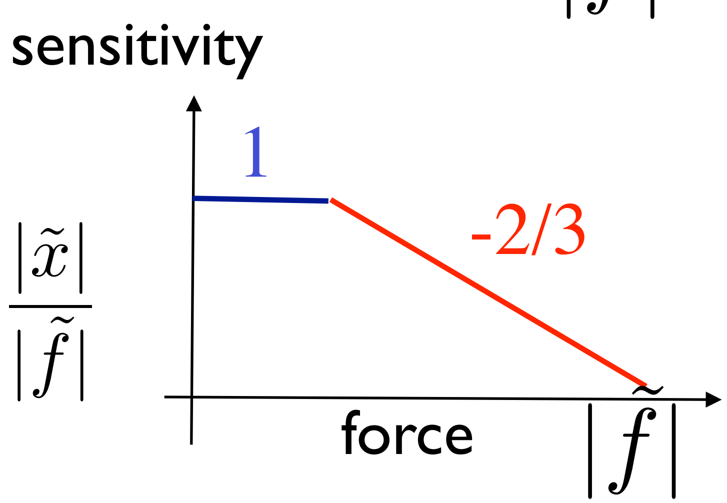
Camalet, Duke, Jülicher, Prost, PNAS 97, 3183 (2000)
Eguiluz, Ospek, Choe, Hudspeth, Magnasco, PRL 84, 5232 (2000)

Signal amplification by nonlinear oscillators



$$\tilde{f}_1 \simeq A\tilde{x}_1 + B|\tilde{x}_1|^2\tilde{x}_1 + ..$$

$$A(\omega, C) = \alpha(\omega - \omega_c) + \beta(C - C_c) + \ldots$$



nonlinear response $\quad |\tilde{x}_1| \sim |\tilde{f}_1|^{1/3}$

for $\quad |\tilde{f}_1| > \dfrac{|\alpha(C - C_c)|^{3/2}}{|B|^{1/2}}$

Camalet, Duke, Jülicher, Prost, PNAS 97, 3183 (2000)
Eguiluz, Ospek, Choe, Hudspeth, Magnasco, PRL 84, 5232 (2000)

Normal form

$$Z(t) \simeq \tilde{x}_1(t)e^{i\omega t}$$

$$r \sim (C - C_c)$$

$$\frac{dZ}{dt} = (i\omega_c - r)Z + B|Z|^2 Z + \frac{e^{i\theta}}{\Lambda} f(t)$$

forcing

$$\tilde{f}_1 \simeq A\tilde{x}_1 + B|\tilde{x}_1|^2\tilde{x}_1 + ..$$

$$A(\omega, C) = \alpha(\omega - \omega_c) + \beta(C - C_c) + \ldots$$

α, β complex

Coupled oscillators as a critical phenomenon

oscillators on a lattics

$$Z_n = \tilde{x}_n e^{i\omega t}$$

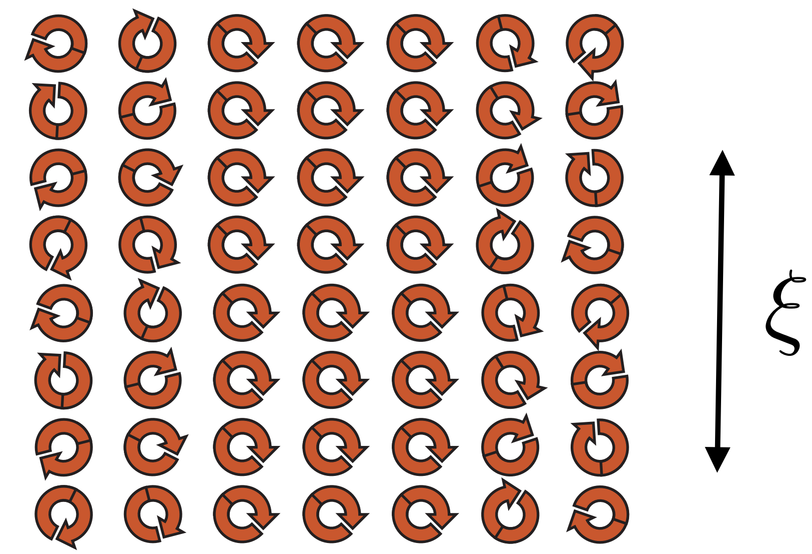
synchronization

Hopf Bifurkation

out of equilibrium

$$\xi \sim (C - C_c)^{-\nu}$$

$$\tilde{x} \sim \tilde{f}^{1/\delta}$$



Ising model

$$S_n = \pm 1$$

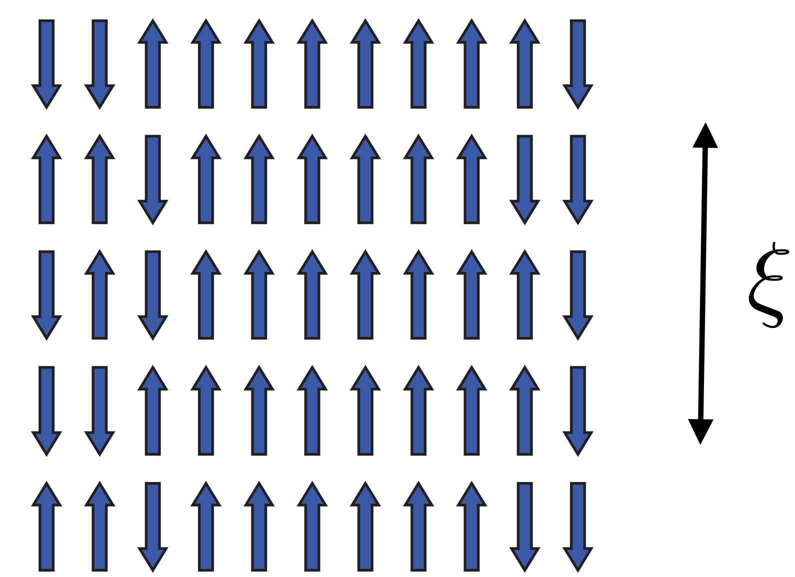
magnetization

critical point

equilibrium

$$\xi \sim (T - T_c)^{-\nu}$$

$$M \sim H^{1/\delta}$$

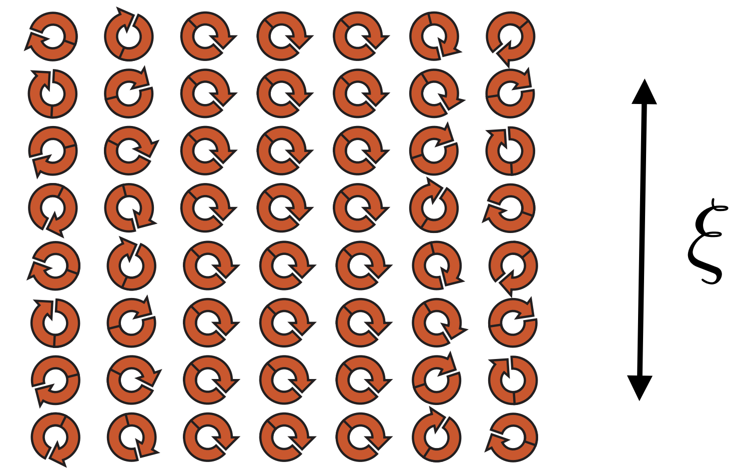


T. Risler, J. Prost, F. Jülicher, PRL 93, 175702 (2004)

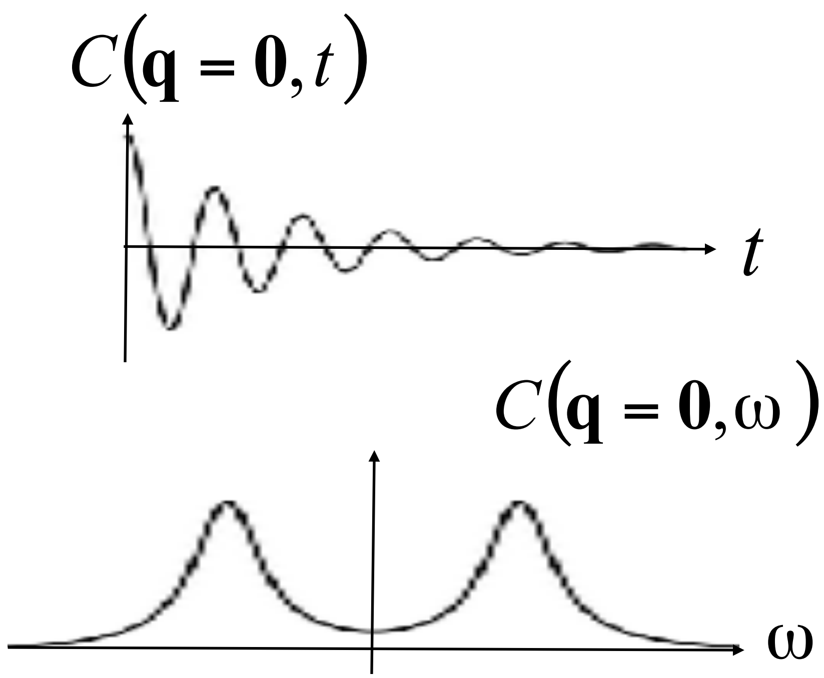
Critical oscillations as a Phase transition

Lattice of N coupled noisy oscillators $N \rightarrow \infty$

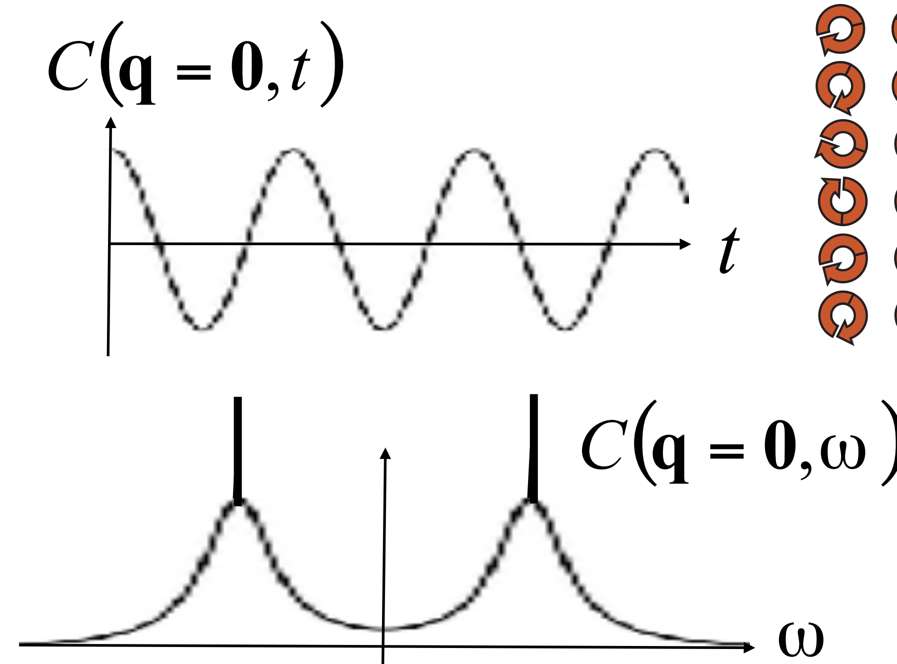
Synchronization transition



Stable state



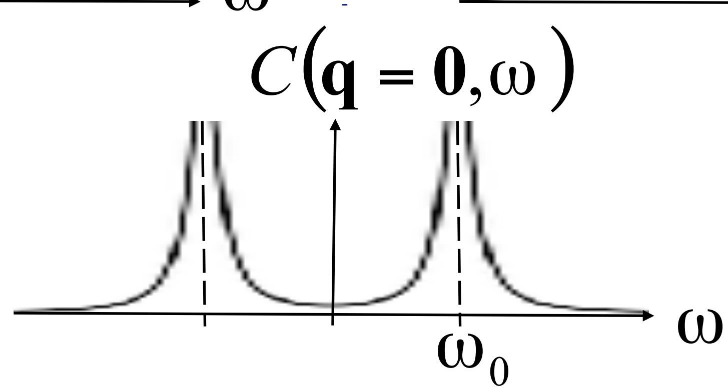
Oscillating state



Emergence of coherent oscillations

$$\tilde{x} \sim \tilde{f}^{1/\delta}$$

Critical point



$$C(\omega) \sim 1/|\omega - \omega_0|^{\sigma}$$

Signal-to-noise ratio peaks at resonance frequency

T. Risler, J. Prost, F. Jülicher, PRL 93, 175702 (2004)

Linear response functions

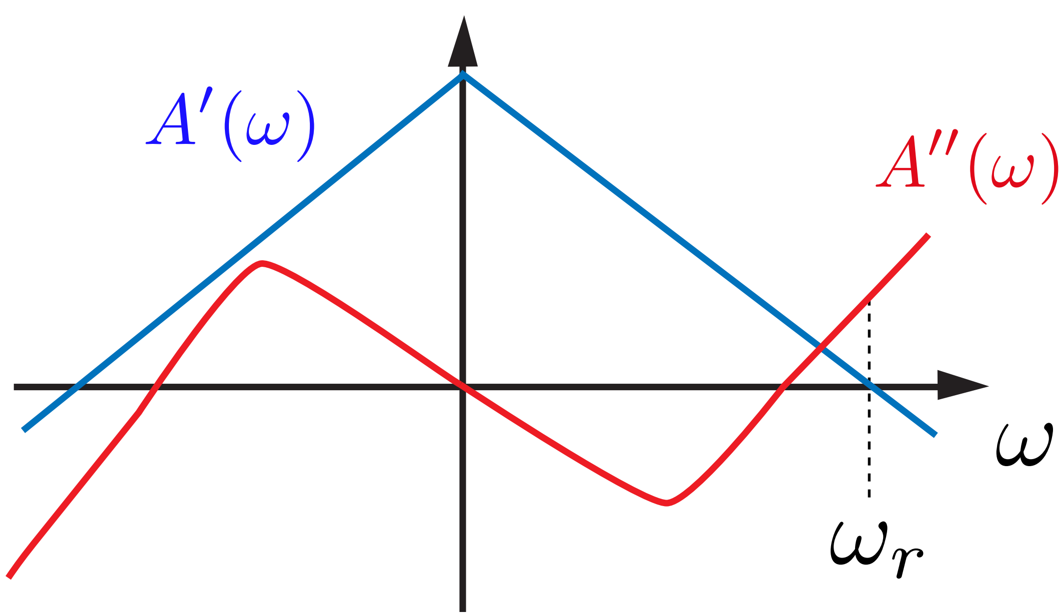
$A(\omega, C) = F_1^{(1)}(\omega, C)$ describes memory effects to linear order

stable region $C < C_c$

$$\tilde{f}_1 \simeq A(\omega, C)\tilde{x}_1 + B|\tilde{x}_1|^2\tilde{x}_1 + ..$$

$$|A(\omega)| > 0$$

$$A(\omega) = A'(\omega) + iA''(\omega)$$



$$A(-\omega) = A^*(\omega)$$

$A'(\omega)$ symmetric reversible

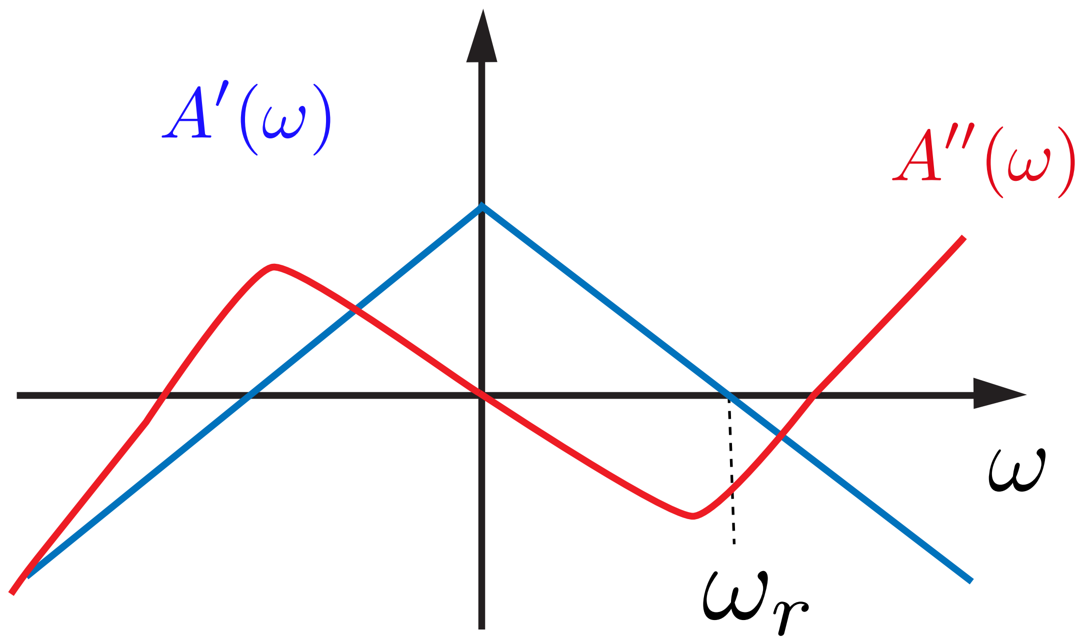
$iA''(\omega)$ antisymmetric dissipative

Spontaneous oscillator: linear response

unstable region $C > C_c$

$$|A(\omega)| > 0$$

$$A(\omega) = A'(\omega) + iA''(\omega)$$



$$\tilde{f} \simeq A(\omega, C)\tilde{x} + B|\tilde{x}^2|\tilde{x}$$

$$A(-\omega) = A^*(\omega)$$

$A'(\omega)$ symmetric reversible

$iA''(\omega)$ antisymmetric dissipative

Critical oscillator: linear response

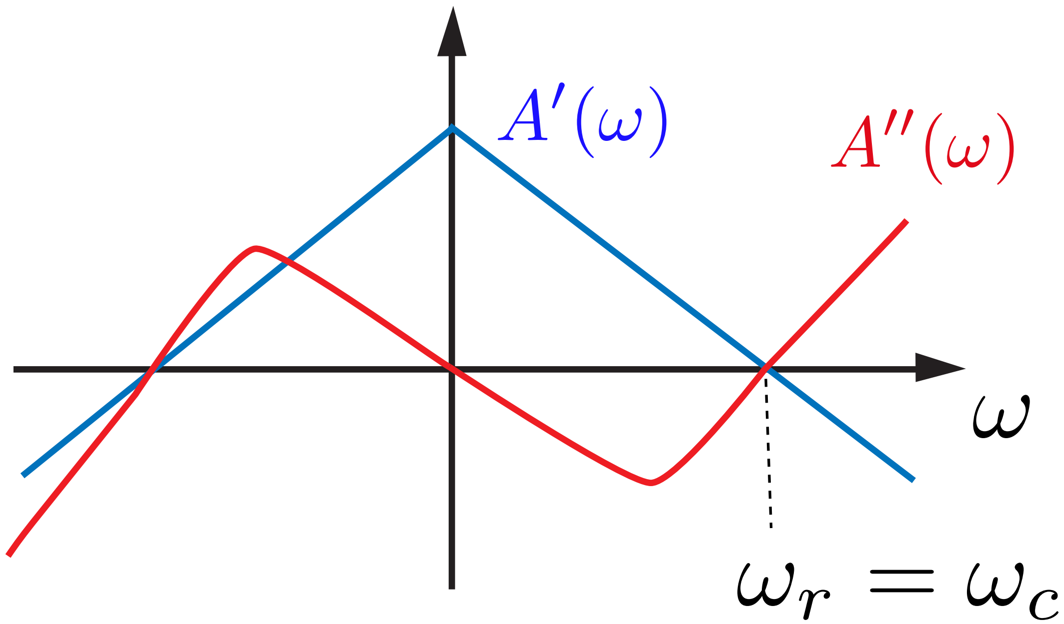
Critical point $C = C_c$

$$\tilde{f} \simeq A(\omega, C)\tilde{x} + B|\tilde{x}^2|\tilde{x}$$

$$A(\omega_r, C_c) = 0$$

$$A(\omega) = A'(\omega) + iA''(\omega)$$

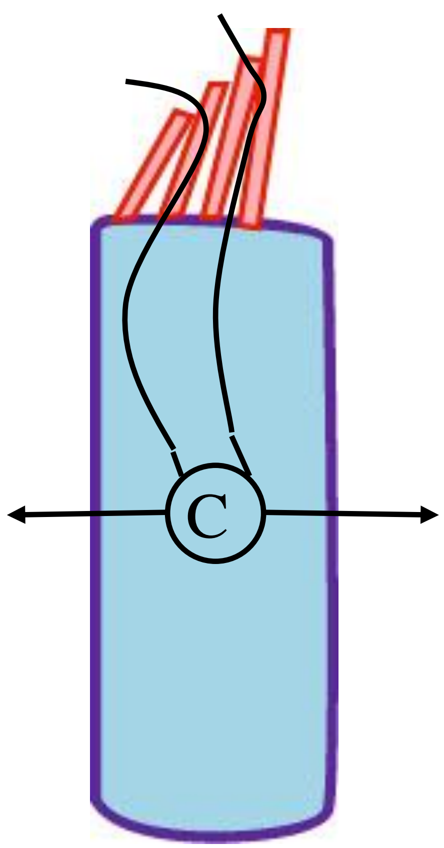
$$A(-\omega) = A^*(\omega)$$

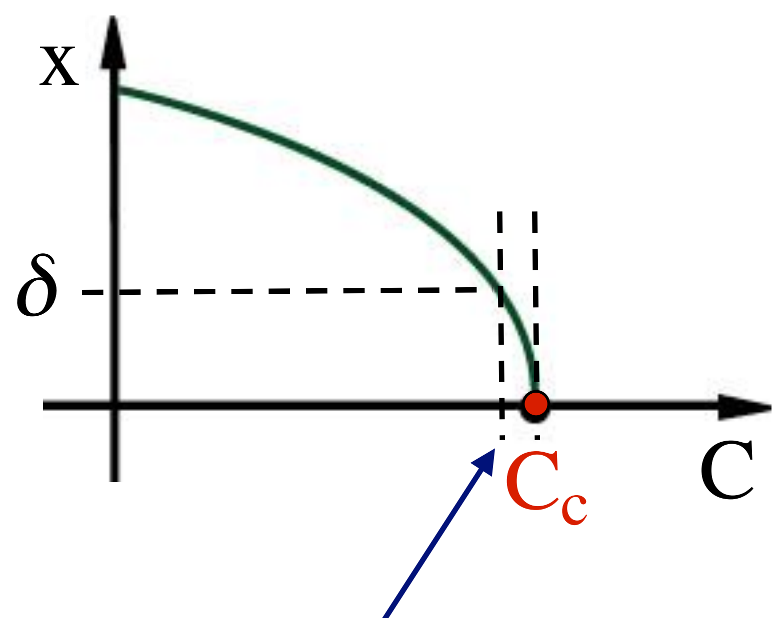


$A'(\omega)$ symmetric reversible

$iA''(\omega)$ antisymmetric dissipative

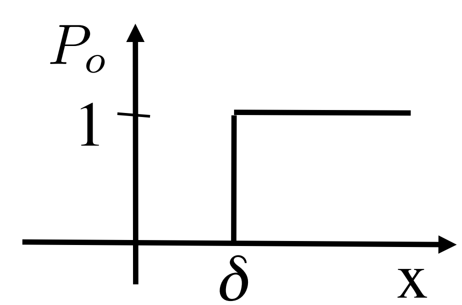
Self-regulation to the proximity of the critical point





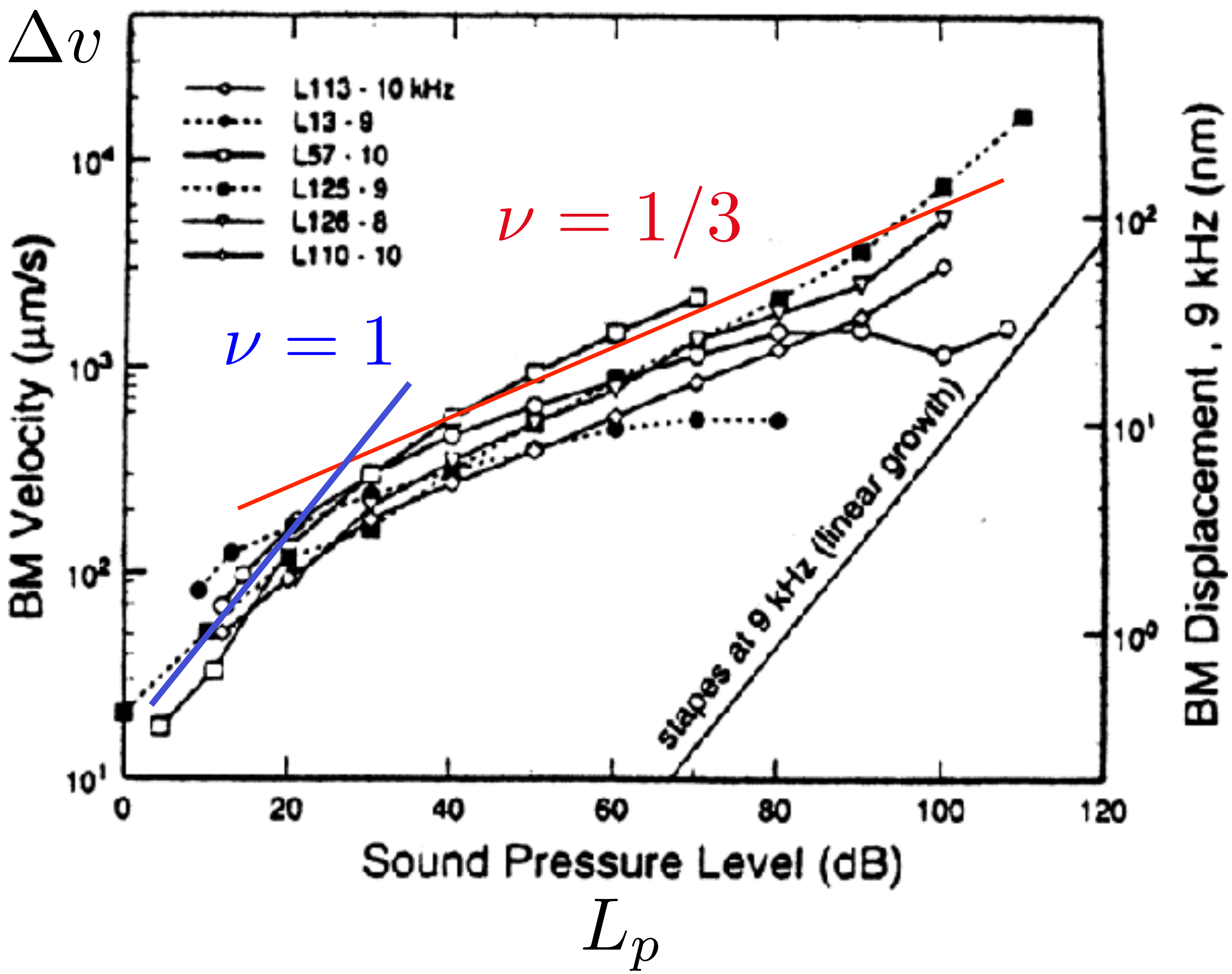
Operating point C_o $\quad \frac{C_o - C_c}{C_c} \simeq 10^{-5}$

$$\frac{dC}{dt} = -\frac{C}{\tau} + JP_o(x)$$



Camalet, Duke, Jülicher, Prost, PNAS 97, 3183 (2000)

Compressive nonlinearity



$h \sim P^{1/3}$

$v \sim P^{1/3}$

Sound Pressure Level:

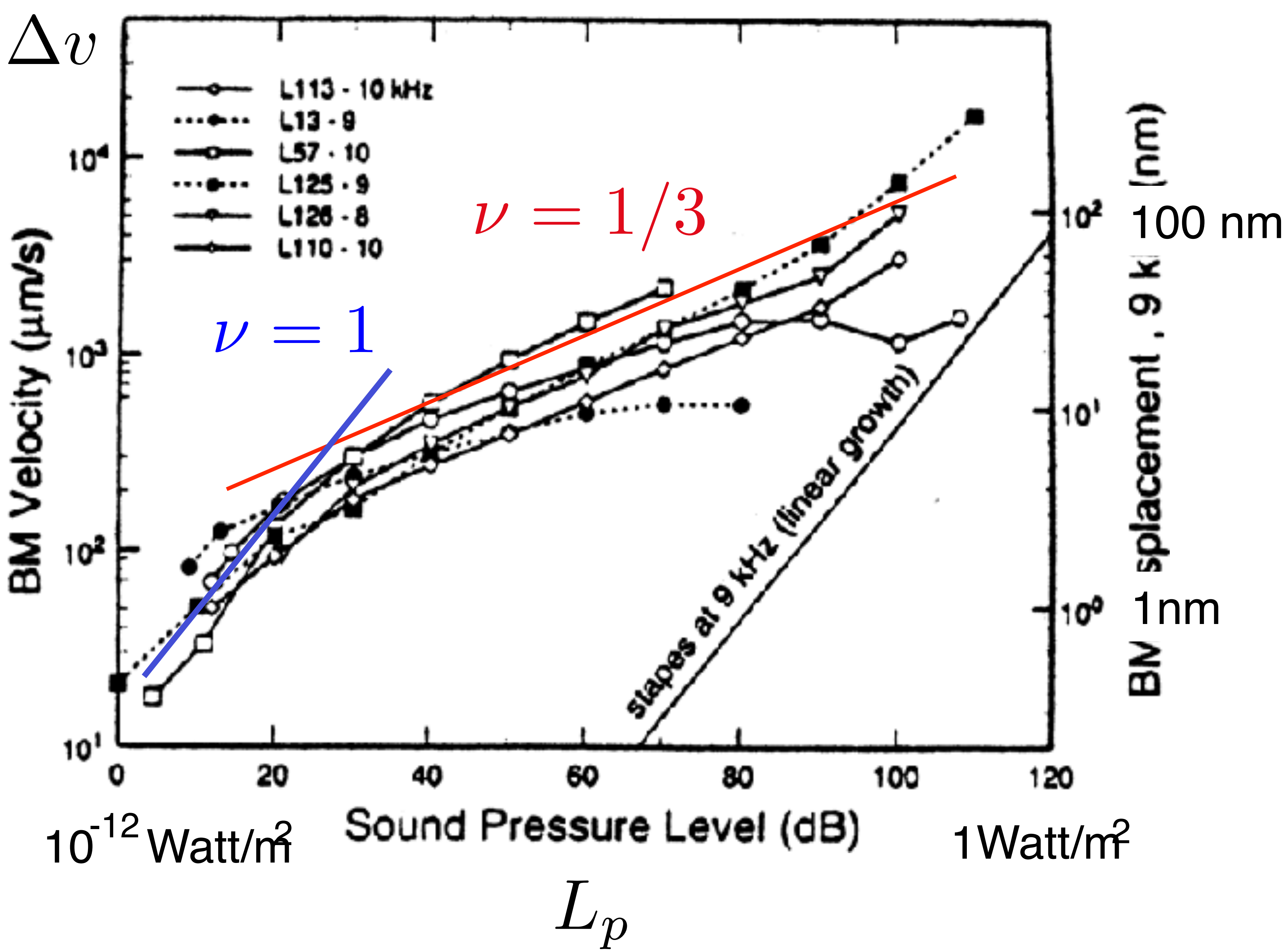
$$L_p = 20 \log \frac{\Delta P}{P_0}$$

$$P_0 = 20 \mu\text{Pa}$$

(Chinchilla)

M. Ruggero et al., J. Acoust. Soc. Am. 101, 2151 (1997)

Compressive nonlinearity



$h \sim P^{1/3}$

$v \sim P^{1/3}$

Sound Pressure Level:

$$L_p = 20 \log \frac{\Delta P}{P_0}$$

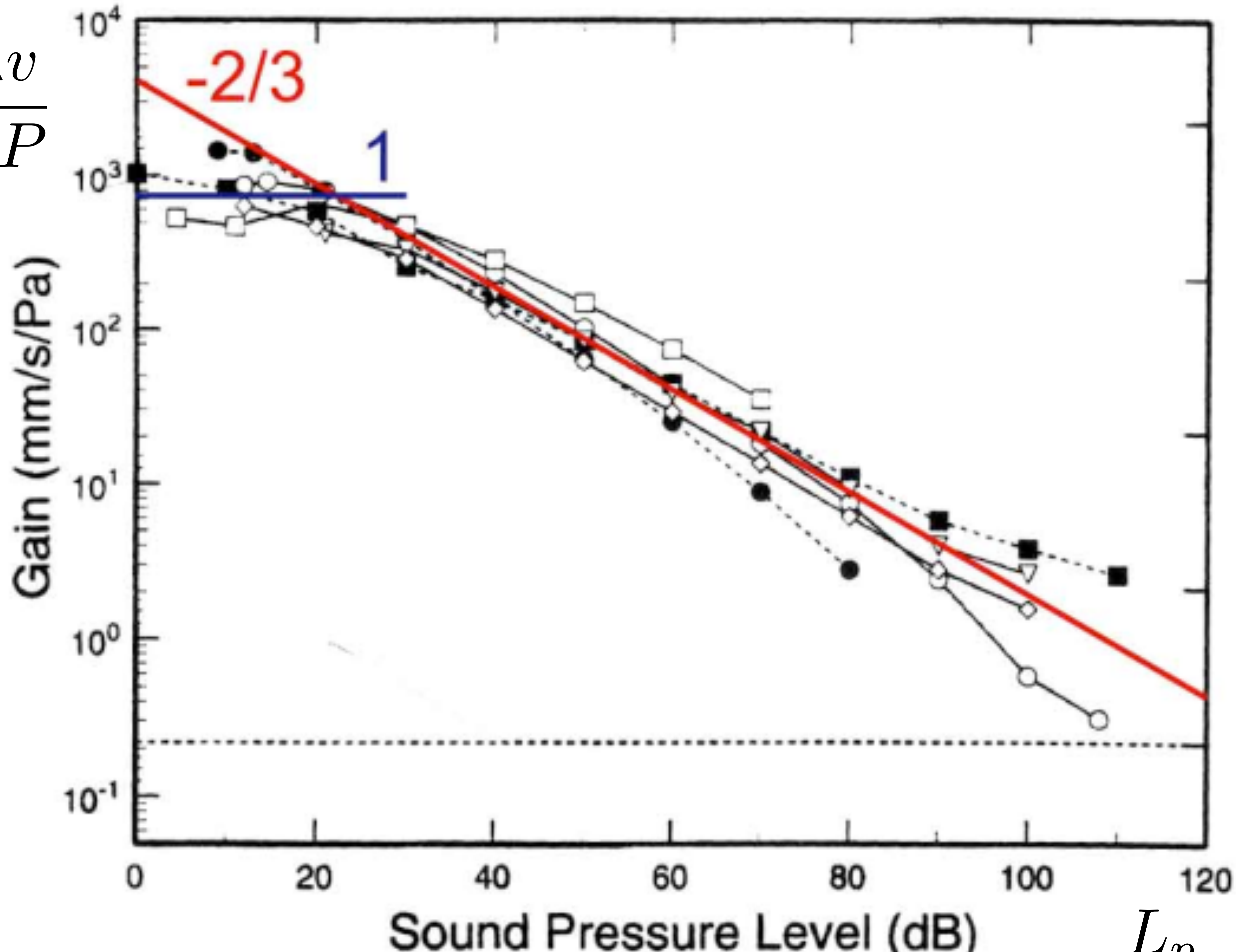
$$P_0 = 20 \mu\text{Pa}$$

(Chinchilla)

M. Ruggero et al., J. Acoust. Soc. Am. 101, 2151 (1997)

Nonlinear amplification

$$\frac{\Delta v}{\Delta P}$$



L_p

Sensitivity

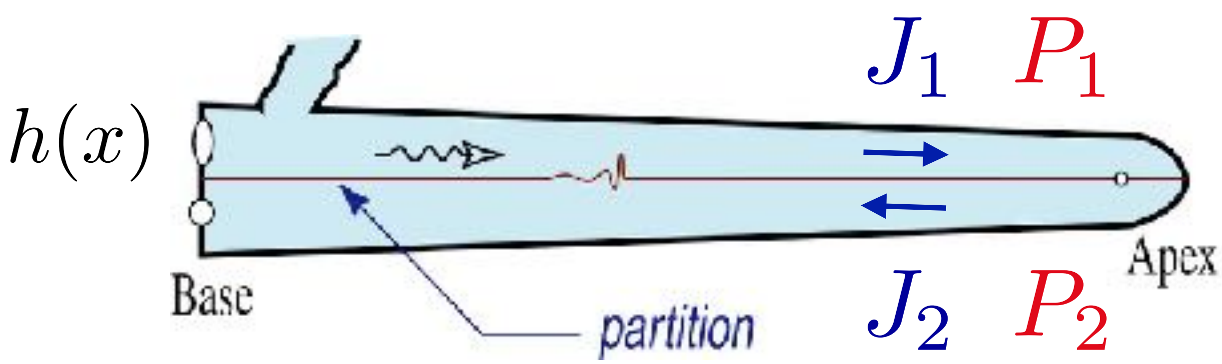
$$\frac{\Delta v}{\Delta P} \sim \Delta P^{-2/3}$$

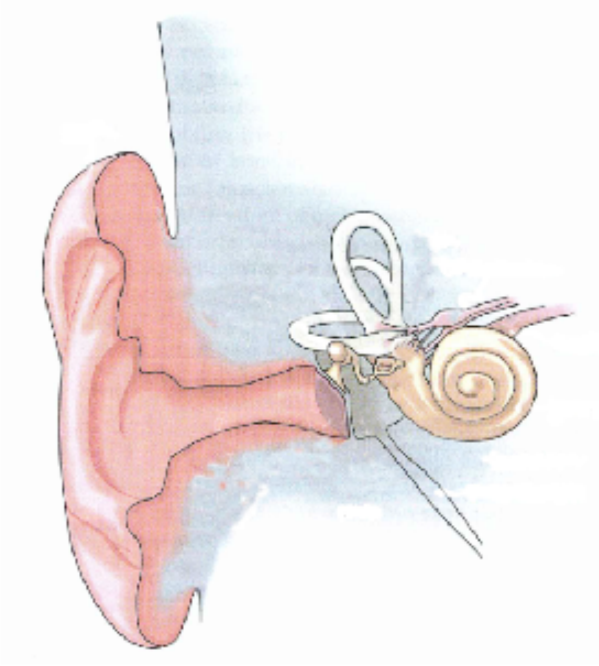
M. Ruggero et al., J. Acoust. Soc. Am. 101, 2151 (1997)

Wave propagation on the basilar membrane

$$p = P_1 - P_2$$

$$j = J_1 - J_2$$

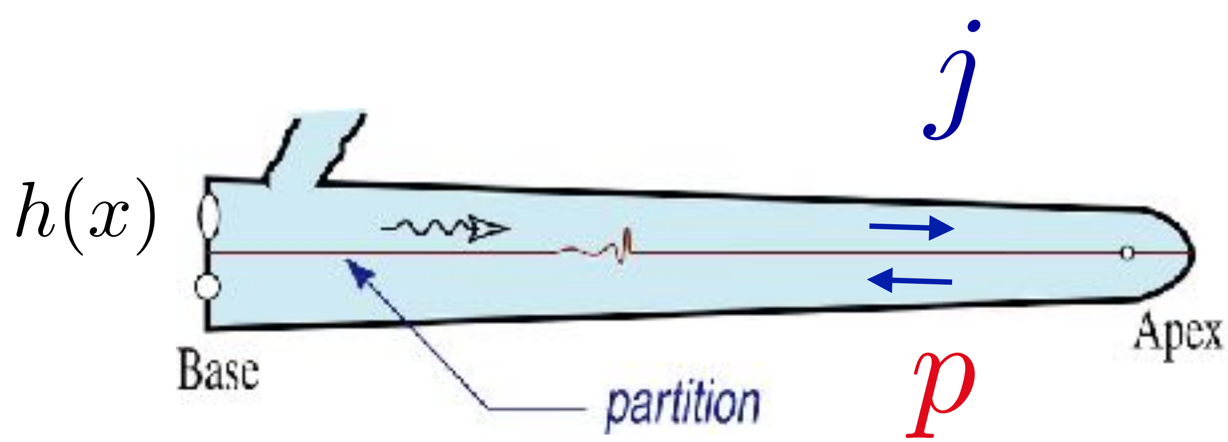


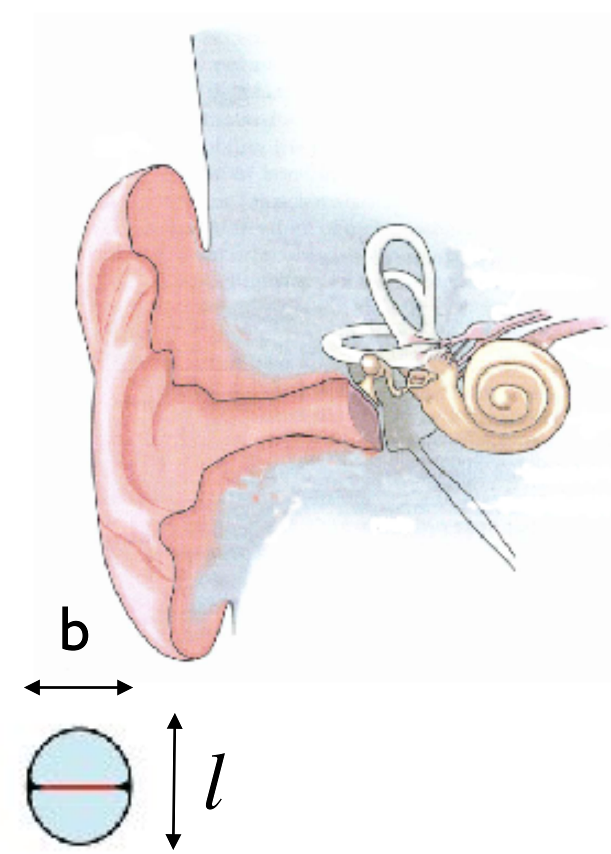


J. Zwislocki, G. Zweig, J. Lighthill, E. de Boer

Wave propagation on the basilar membrane

$$2\rho\partial_t^2 h = l\partial_x^2 p$$



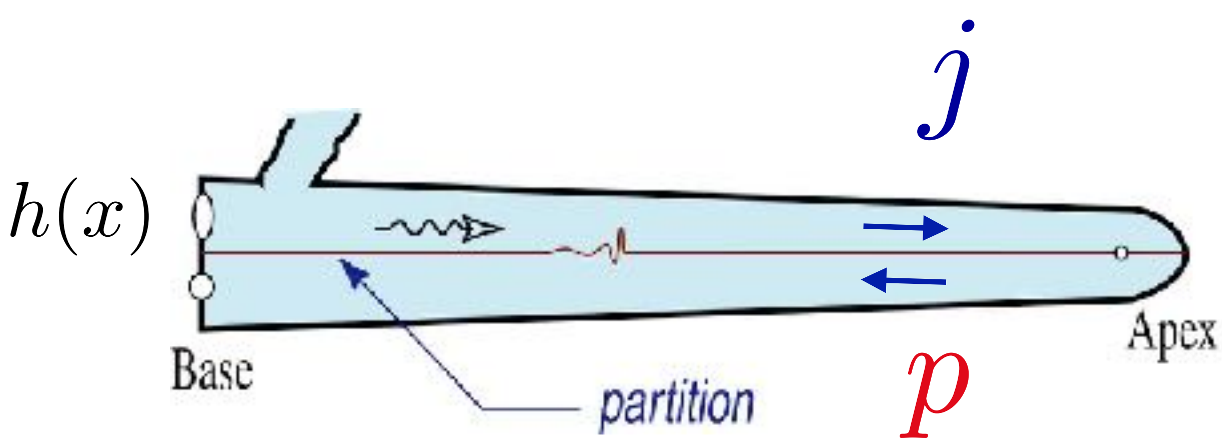


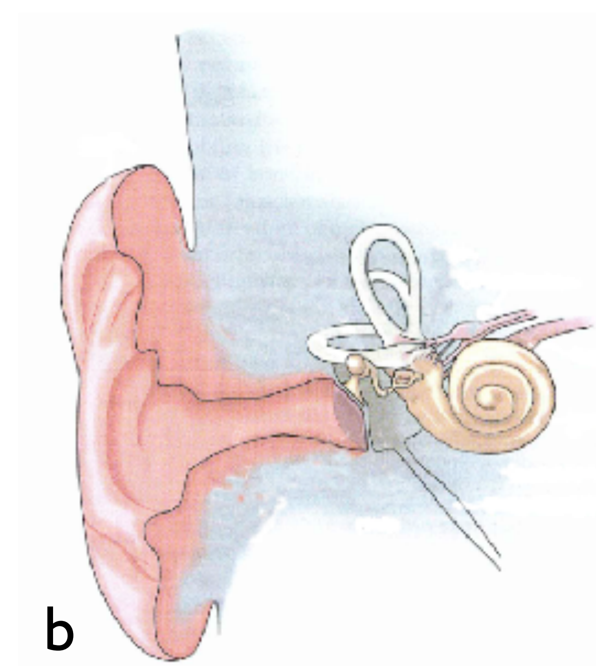
$$\tilde{p} = K^{-1}\tilde{h}$$

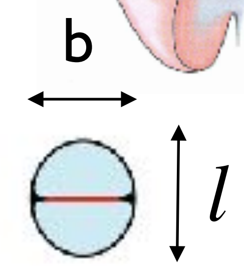
J. Zwislocki, G. Zweig, J. Lighthill, E. de Boer

Wave propagation on the basilar membrane

$$-2\rho\omega^2\tilde{h} = l\partial_x^2\tilde{p}$$





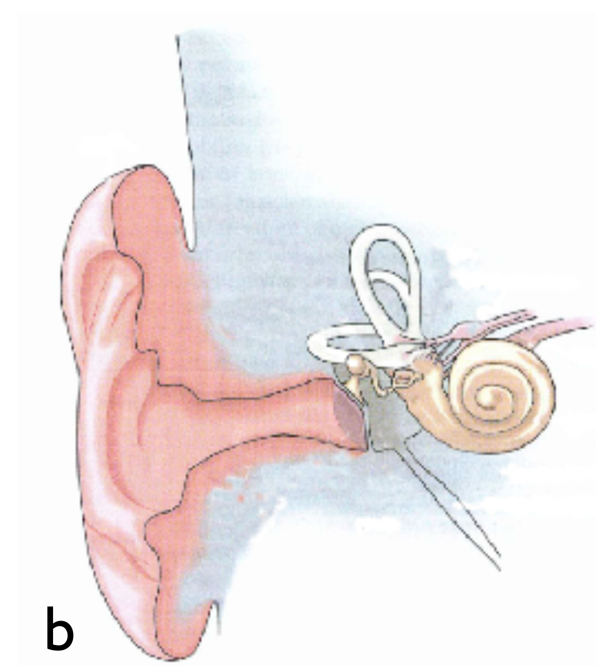


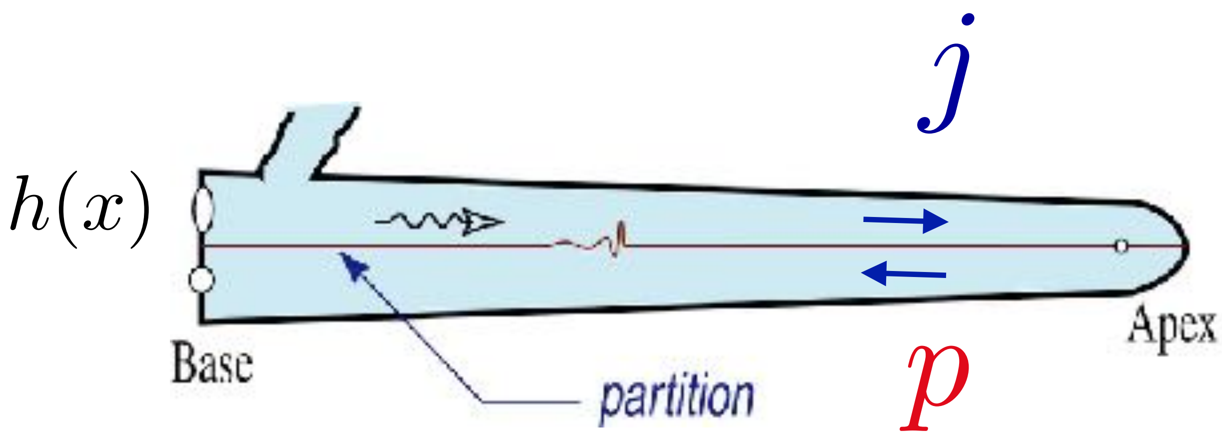
$$\tilde{p} = K^{-1}\tilde{h}$$

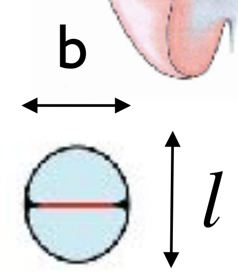
J. Zwislocki, G. Zweig, J. Lighthill, E. de Boer

Linear array of critical oscillators: nonlinear waves

$$-2\rho\omega^2\tilde{h} = l\partial_x^2\tilde{p}$$







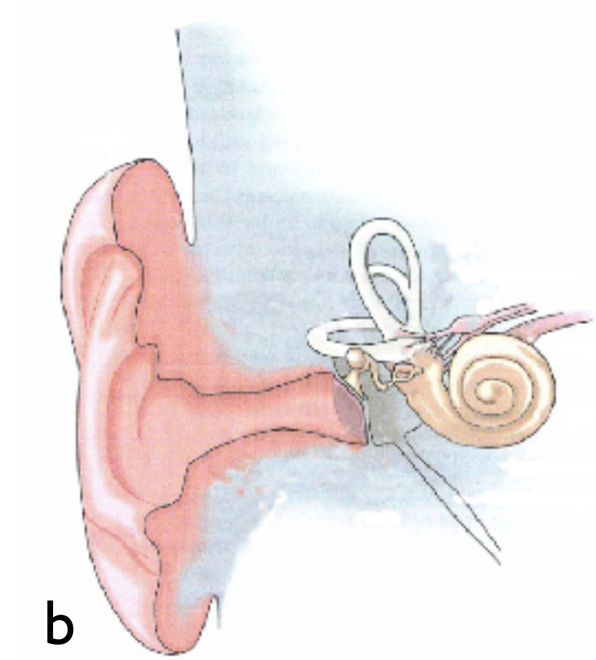
$$\tilde{p} = A(\omega, x)\tilde{h} + B|\tilde{h}|^2\tilde{h}$$

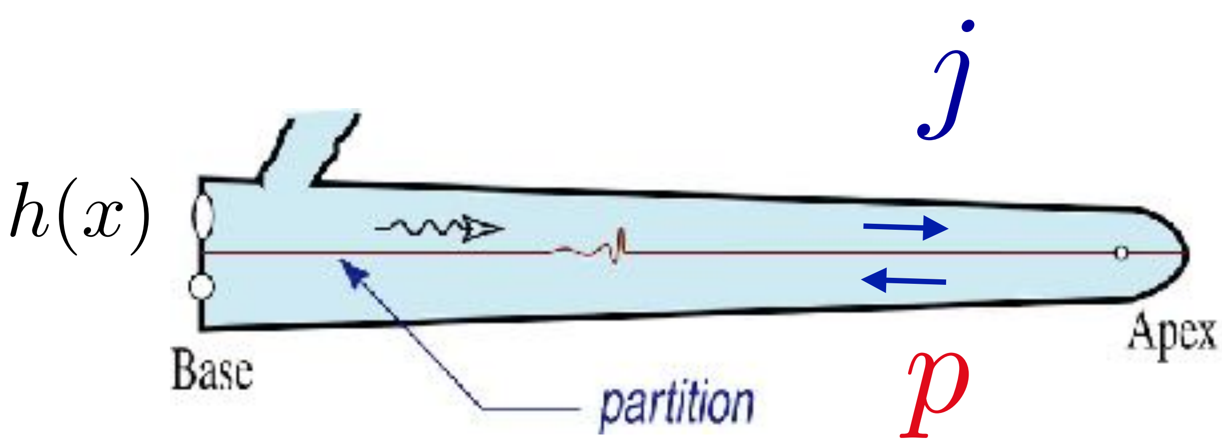
T. Duke and F. Jülicher, Phys. Rev. Lett. 90, 158101(2003)

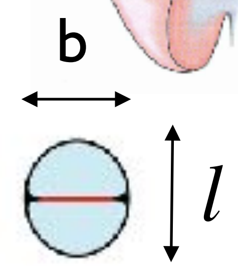
Linear array of critical oscillators: nonlinear waves

$$\omega_r(x) = \omega_0 e^{-x/d}$$

$$A(x,\omega) = \alpha(\omega_r(x) - \omega)$$







$$-2\rho\omega^2\tilde{h} = l\partial_x^2\left[A(x,\omega)\tilde{h} + B|\tilde{h}|^2\tilde{h}\right]$$

T. Duke and F. Jülicher, Phys. Rev. Lett. 90, 158101(2003)

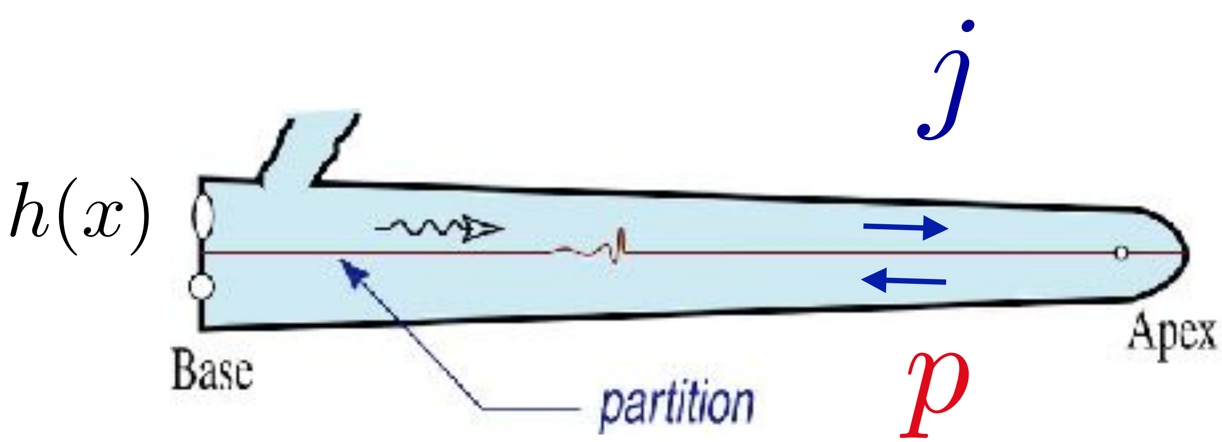
Linear array of critical oscillators: nonlinear waves

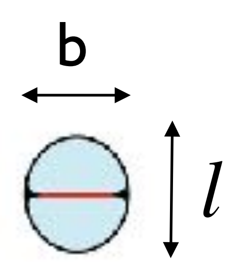
$$\omega_r(x) = \omega_0 e^{-x/d}$$

$$A(x,\omega) = \alpha(\omega_r(x) - \omega)$$

passive stiffness

$$K(x) \simeq \alpha\omega_r(x)$$

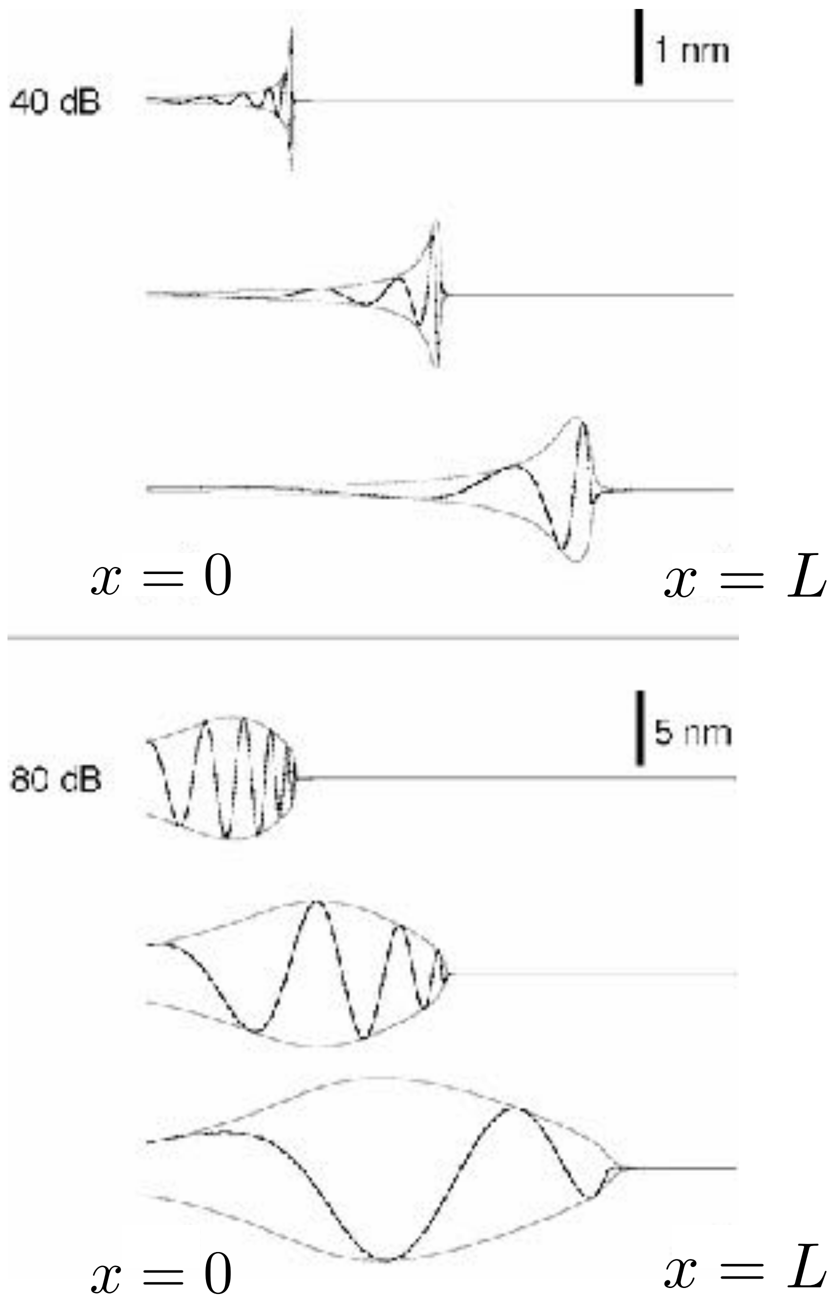


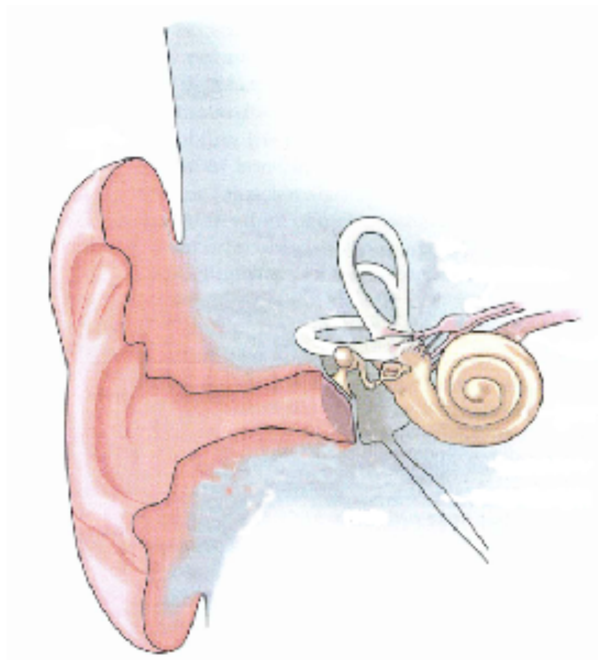


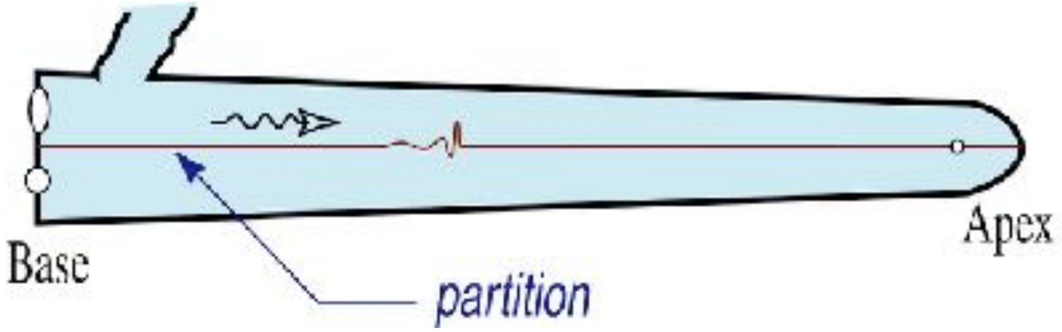
$$-2\rho\omega^2\tilde{h} = l\partial_x^2\left[A(x,\omega)\tilde{h} + B|\tilde{h}|^2\tilde{h}\right]$$

T. Duke and F. Jülicher, Phys. Rev. Lett. 90, 158101(2003)

Nonlinear waves patterns

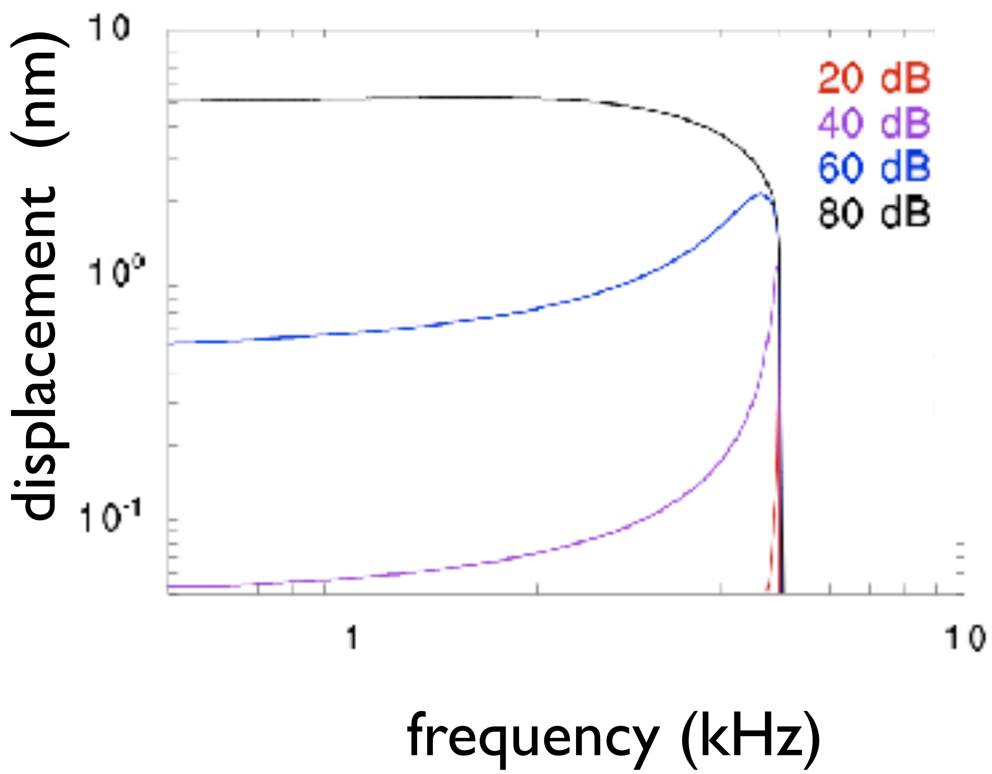


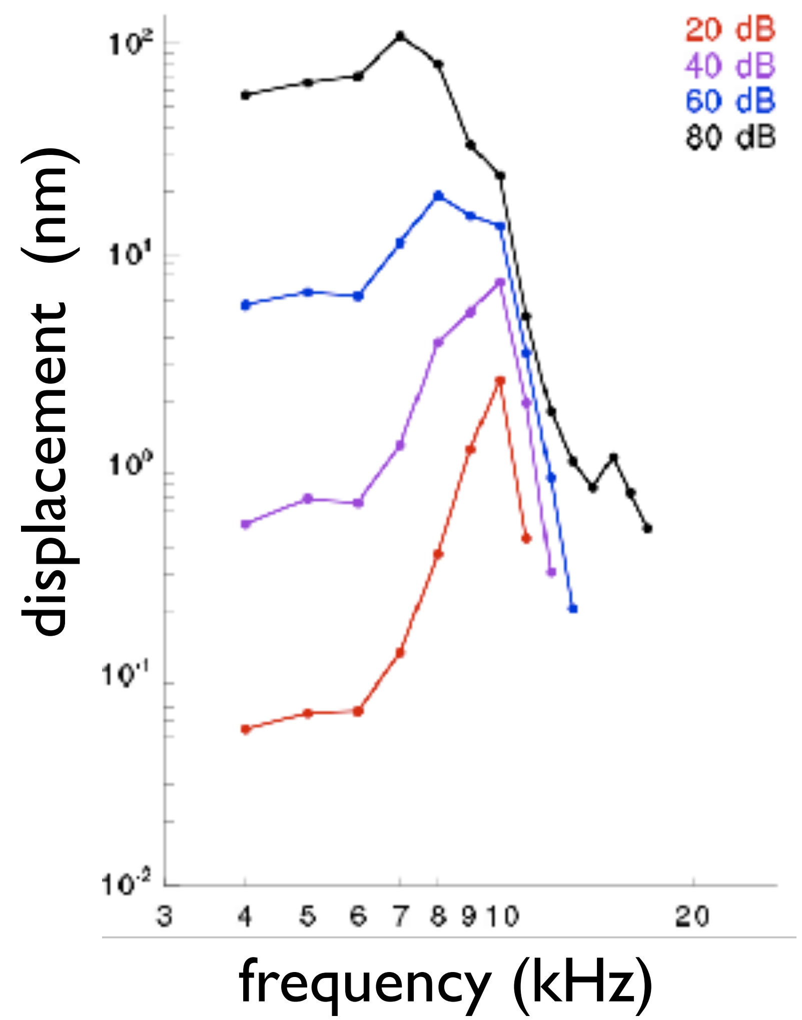




T. Duke and F. Jülicher, Phys. Rev. Lett. 90, 158101(2003)

Nonlinear traveling wave



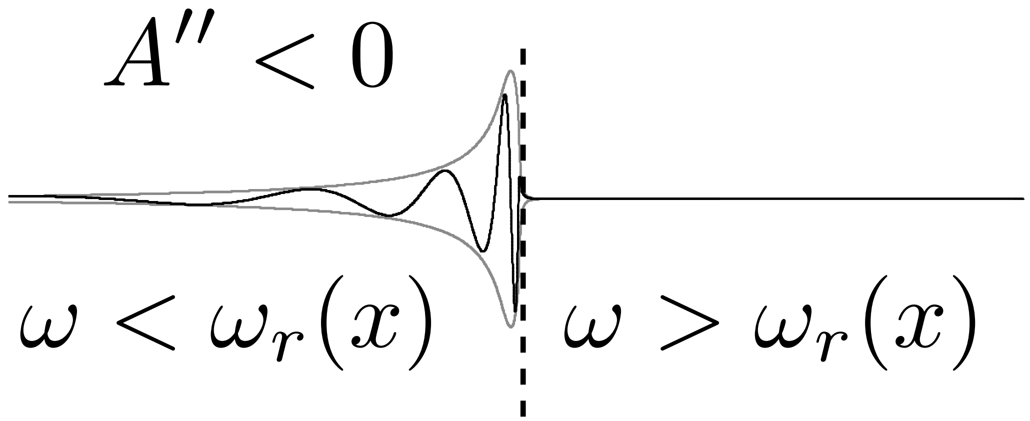


BM displacement as a function of frequency

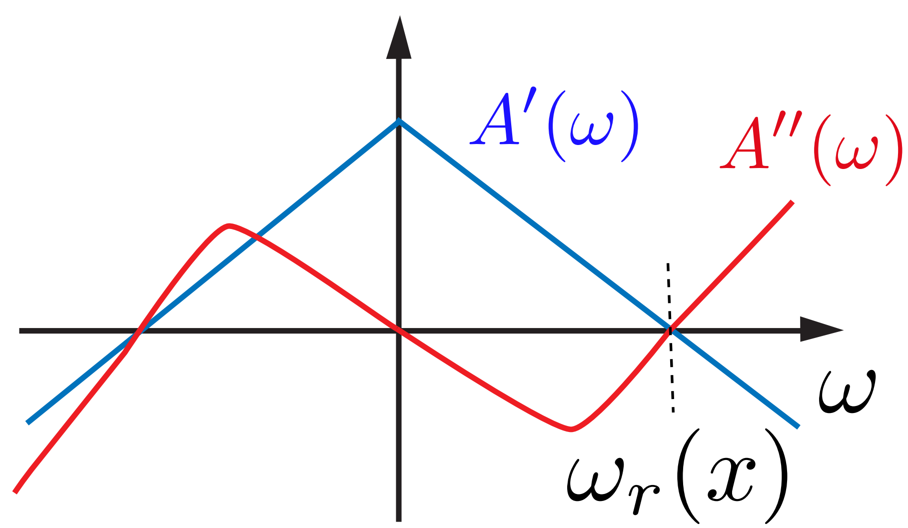
Ruggero et al, JASA 101 (1997)

T. Duke and F. Jülicher, Phys. Rev. Lett. 90, 158101(2003)

Pumping of the wave



Energy is supplied to the wave by the oscillators

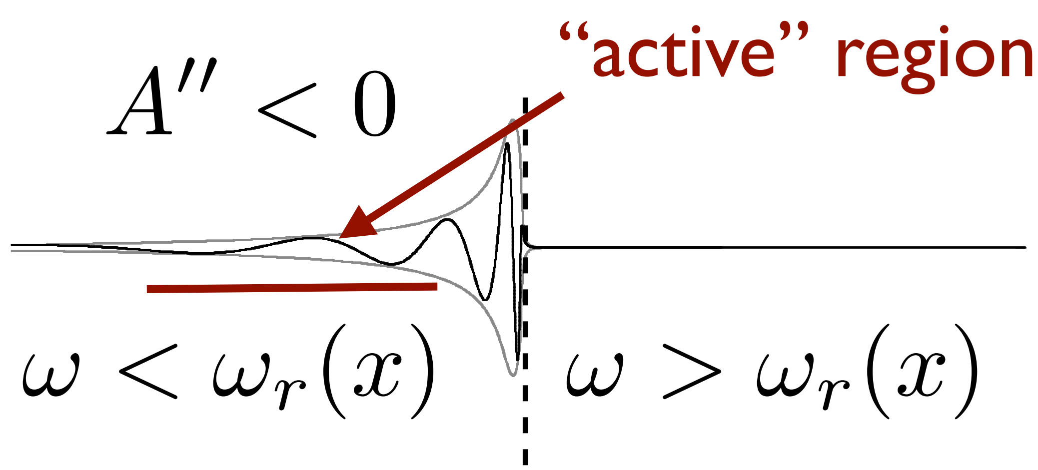


$$\omega_r(x) = \omega_0 e^{-x/d}$$

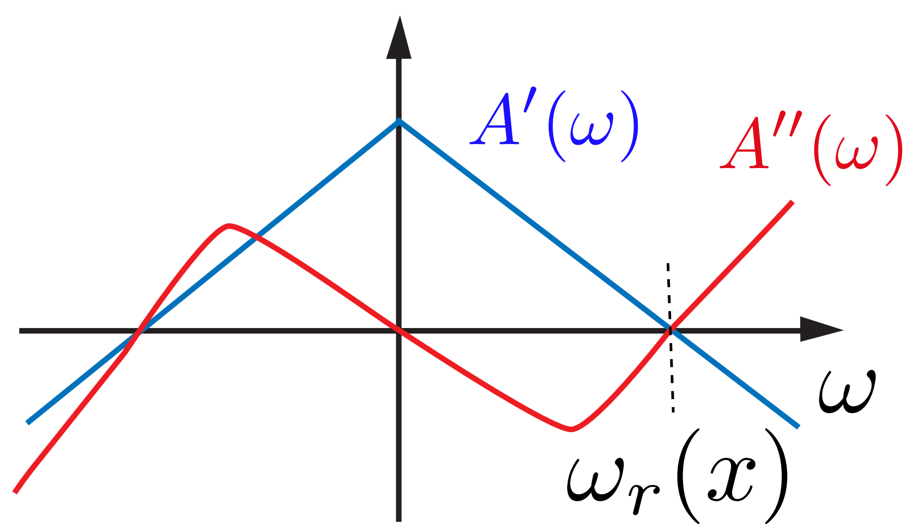
Wave equation for BM displacement

$$-2\rho\omega^2 \tilde{h} = l\partial_x^2 \left[A(x,\omega)\tilde{h} + B|\tilde{h}|^2 \tilde{h} \right]$$

Pumping of the wave



Energy is supplied to the wave by the oscillators



$$\omega_r(x) = \omega_0 e^{-x/d}$$

Wave equation for BM displacement

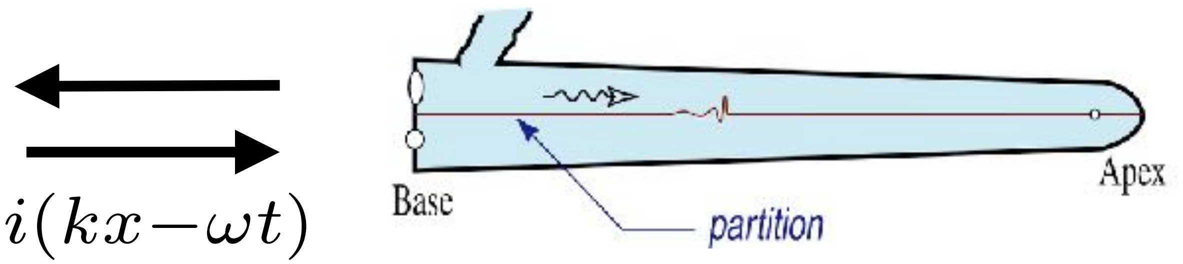
$$-2\rho\omega^2\tilde{h} = l\partial_x^2\left[A(x,\omega)\tilde{h} + B|\tilde{h}|^2\tilde{h}\right]$$

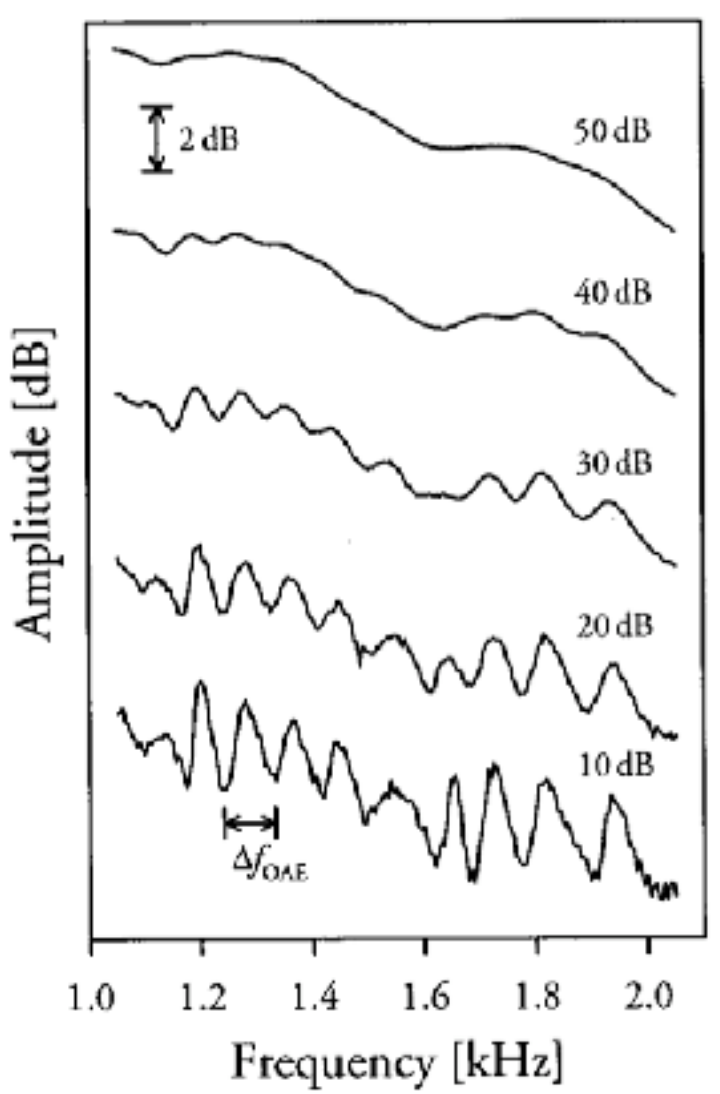
Localization of "active" region is automatically confined to the basal side of the characteristic place

Stimulus frequency otoacoustic emissions (SFOAE)

$$p_{\text{out}} e^{i(-kx-\omega t)}$$

$$p_{\text{in}} e^{i(kx-\omega t)}$$

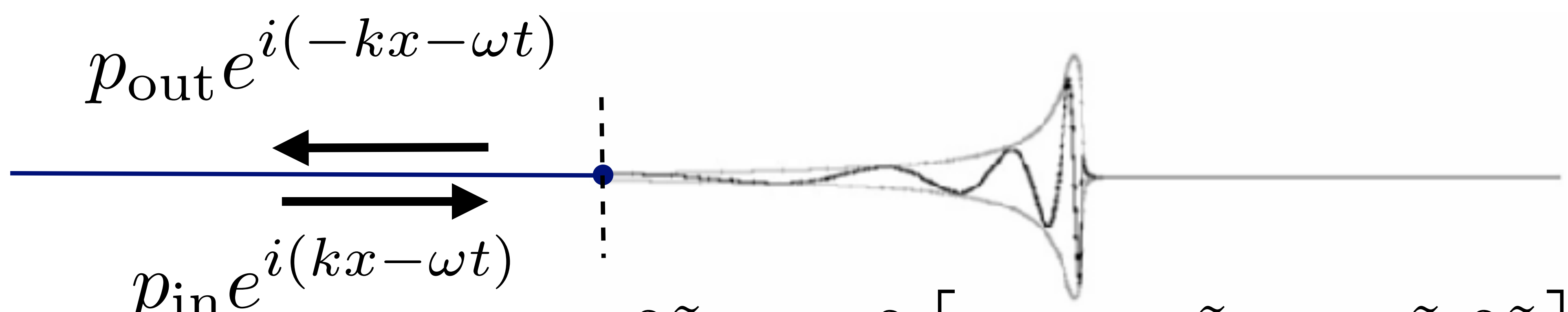




$$R_{\text{SFOAE}} = \frac{p_{\text{out}}}{p_{\text{in}}}$$

C. Shera, G. Zweig, JASA 98 (1995)
C. Shera, J. Guinan, JASA 105 (1999)

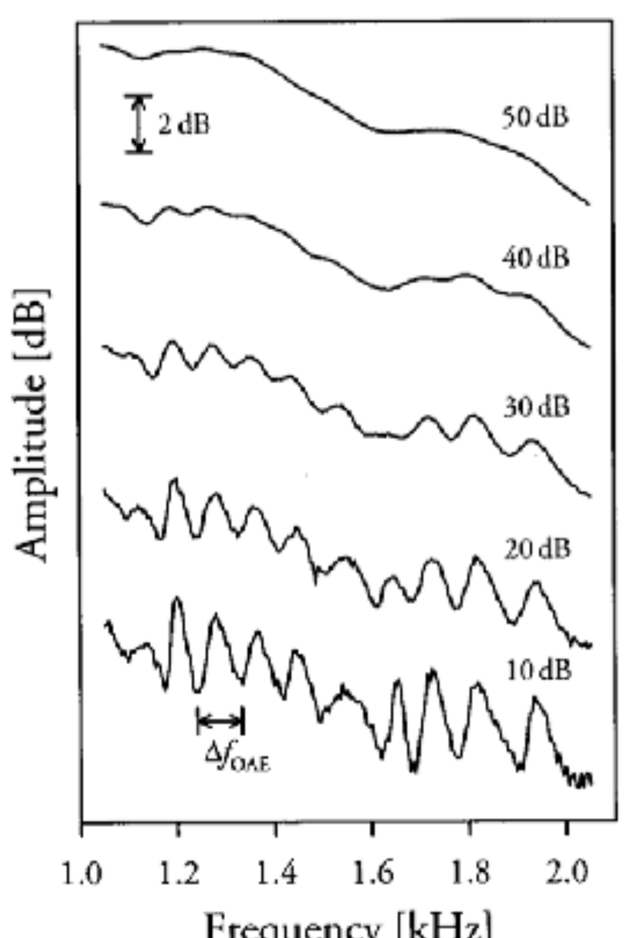
Nonlinear wave reflection



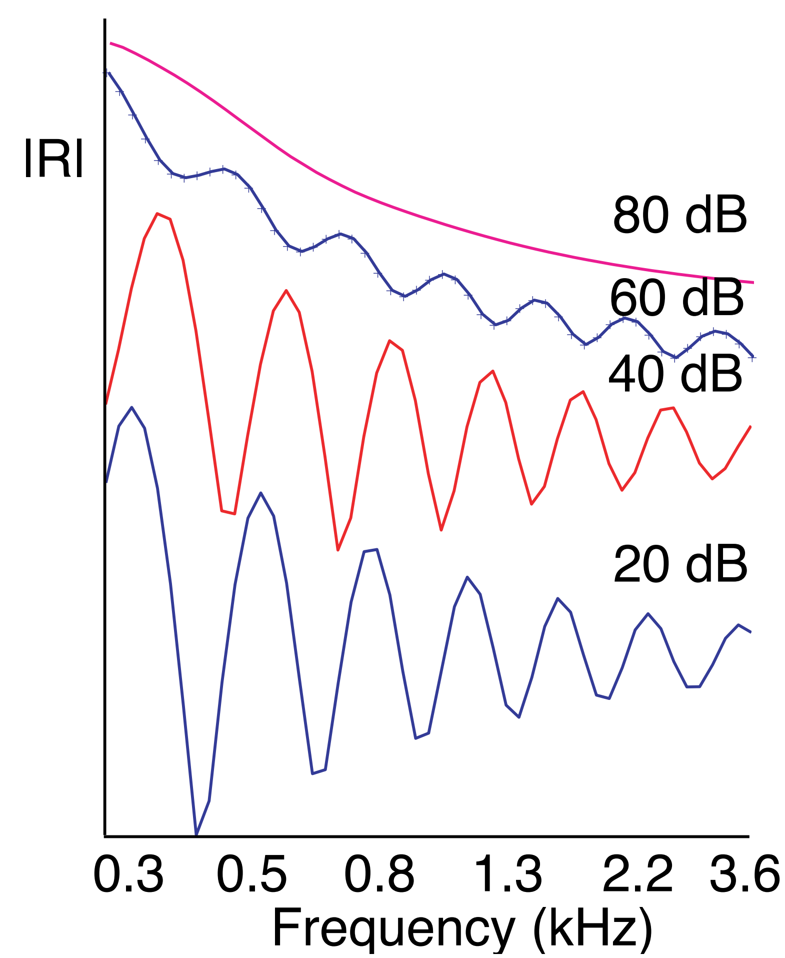
$$p_{\text{out}} e^{i(-kx-\omega t)}$$

$$p_{\text{in}} e^{i(kx-\omega t)}$$

$$-2\rho\omega^2 \tilde{h} = l\partial_x^2 \left[A(x,\omega)\tilde{h} + B|\tilde{h}|^2\tilde{h} \right]$$



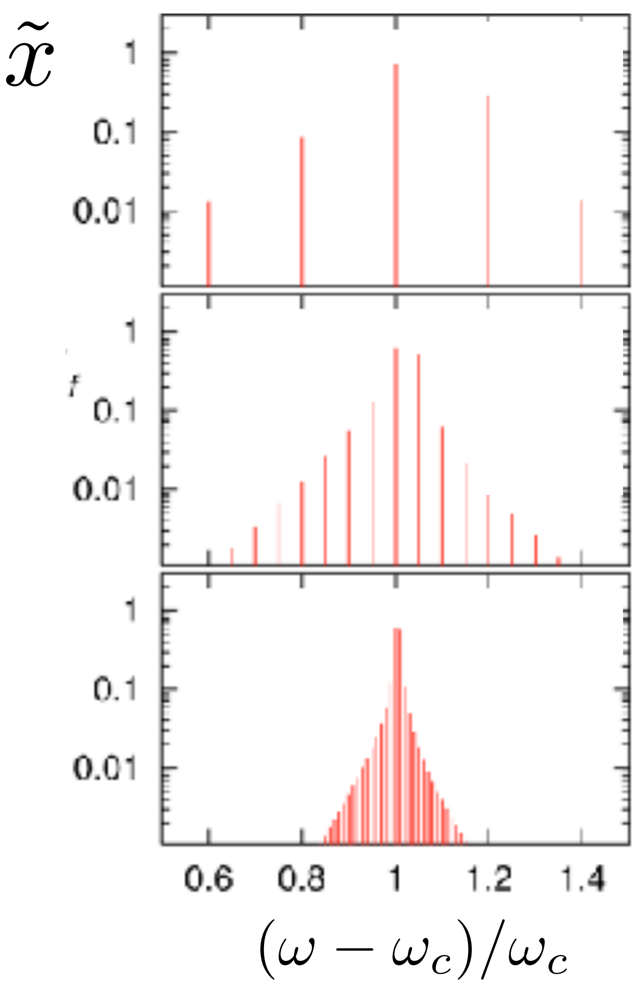
$$R_{\text{SFOAE}} = \frac{p_{\text{out}}}{p_{\text{in}}}$$

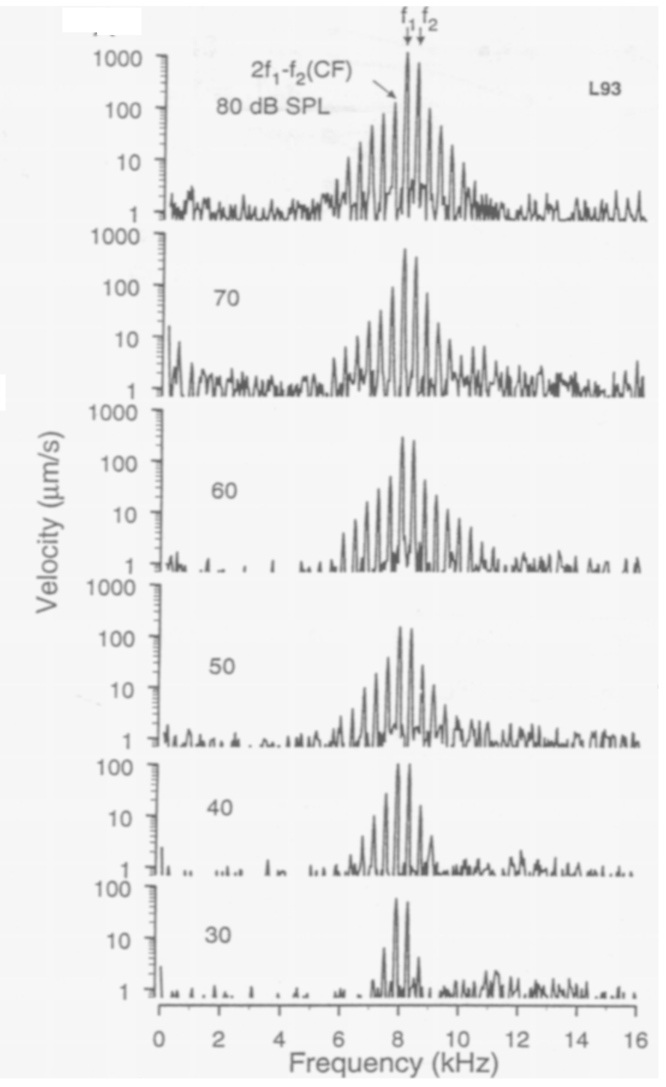


C. Shera, J. Guinan, JASA 105 (1999)

Aditi Simha, Daniel Andor

Combination tones





$$f(t) = \tilde{f}_1 e^{i\omega_1 t} + \tilde{f}_2 e^{i\omega_2 t}$$

$$x(t) \qquad n\omega_1 + m\omega_2$$

Coupling of frequency modes by nonlinearities

$$|X_k| \sim e^{-\lambda k}$$

Robles, Ruggero & Rich ‘97

Jülicher, Andor and Duke, PNAS 98, 9080 (2001)

Nonlinear coupling of frequencies

Two-tone interference

$$h(t) \simeq \tilde{h}_1 e^{i\omega_1 t} + \tilde{h}_2 e^{i\omega_2 t}$$

$$-2\rho\omega^2 \tilde{h}_1 = l\partial_x^2 \left[A\tilde{h}_1 + B|\tilde{h}_1|^2\tilde{h}_1 + \bar{B}|\tilde{h}_2|^2\tilde{h}_1 \right]$$

$$-2\rho\omega^2 \tilde{h}_2 = l\partial_x^2 \left[A\tilde{h}_2 + B|\tilde{h}_2|^2\tilde{h}_2 + \bar{B}|\tilde{h}_1|^2\tilde{h}_2 \right]$$

Nonlinear coupling of frequencies

Two-tone interference

Distortion product generation

$$h(t) \simeq \tilde{h}_1 e^{i\omega_1 t} + \tilde{h}_2 e^{i\omega_2 t} \qquad + \tilde{h}_{2,-1} e^{i(2\omega_2 - \omega_1)t}$$

$$-2\rho\omega^2 \tilde{h}_1 = l\partial_x^2 \left[A\tilde{h}_1 + B|\tilde{h}_1|^2 \tilde{h}_1 + \bar{B}|\tilde{h}_2|^2 \tilde{h}_1 \ + \hat{B}\tilde{h}^*_{2,-1} h_2^2 \right]$$

$$-2\rho\omega^2 \tilde{h}_2 = l\partial_x^2 \left[A\tilde{h}_2 + B|\tilde{h}_2|^2 \tilde{h}_2 + \bar{B}|\tilde{h}_1|^2 \tilde{h}_2 \ + \hat{B}\tilde{h}_{2,-1} h_2^* h_1 \right]$$

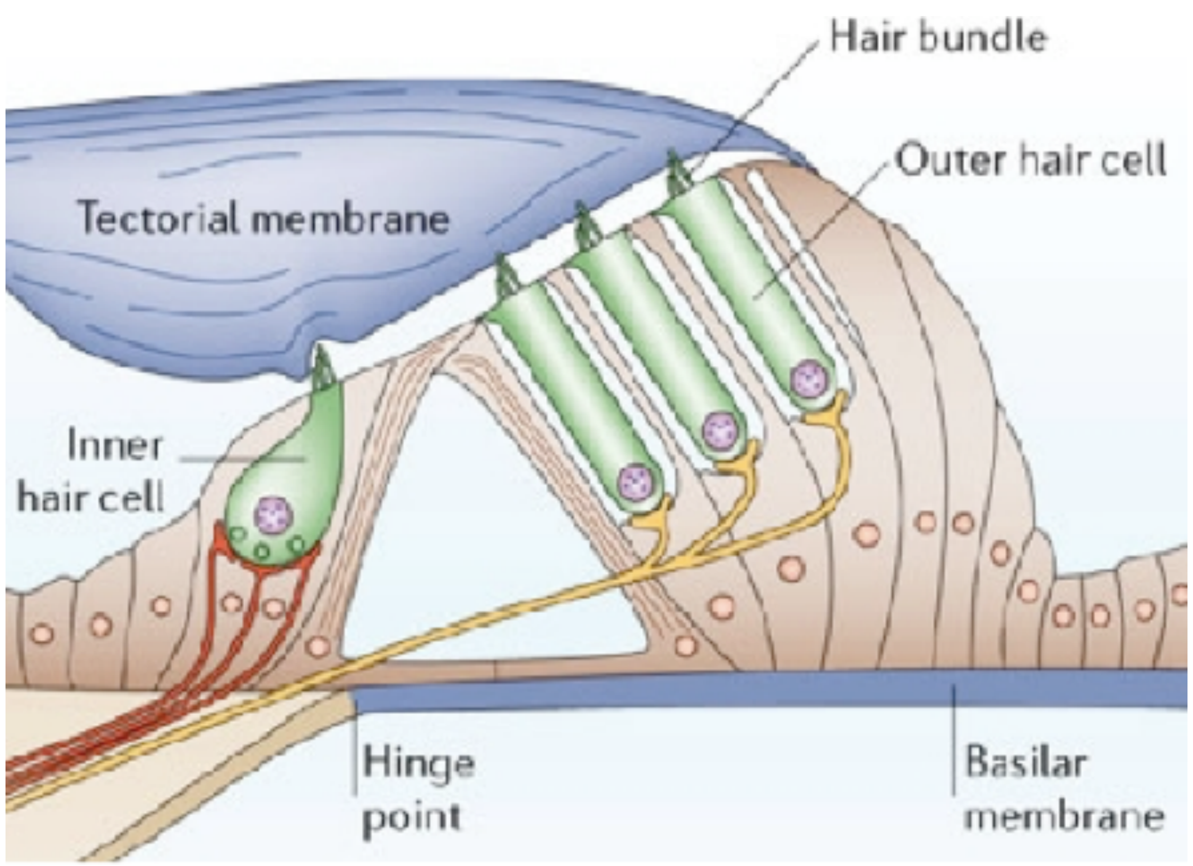
$$-2\rho\omega^2 \tilde{h}_{2,-1} = l\partial_x^2 [A\tilde{h}_{2,-1} + B|\tilde{h}_{2,-1}|^2 \tilde{h}_{2,-1} + \hat{B} h_2^2 h_1^*]$$

The cochlear amplifier

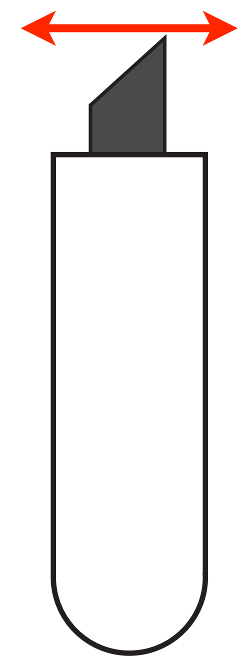
Amplification by coupled hair bundles

Interplay of hair bundle motility and electromotility in the cochlea

Hair cells in the organ of Corti



active hair bundle



hair bundle ocillations

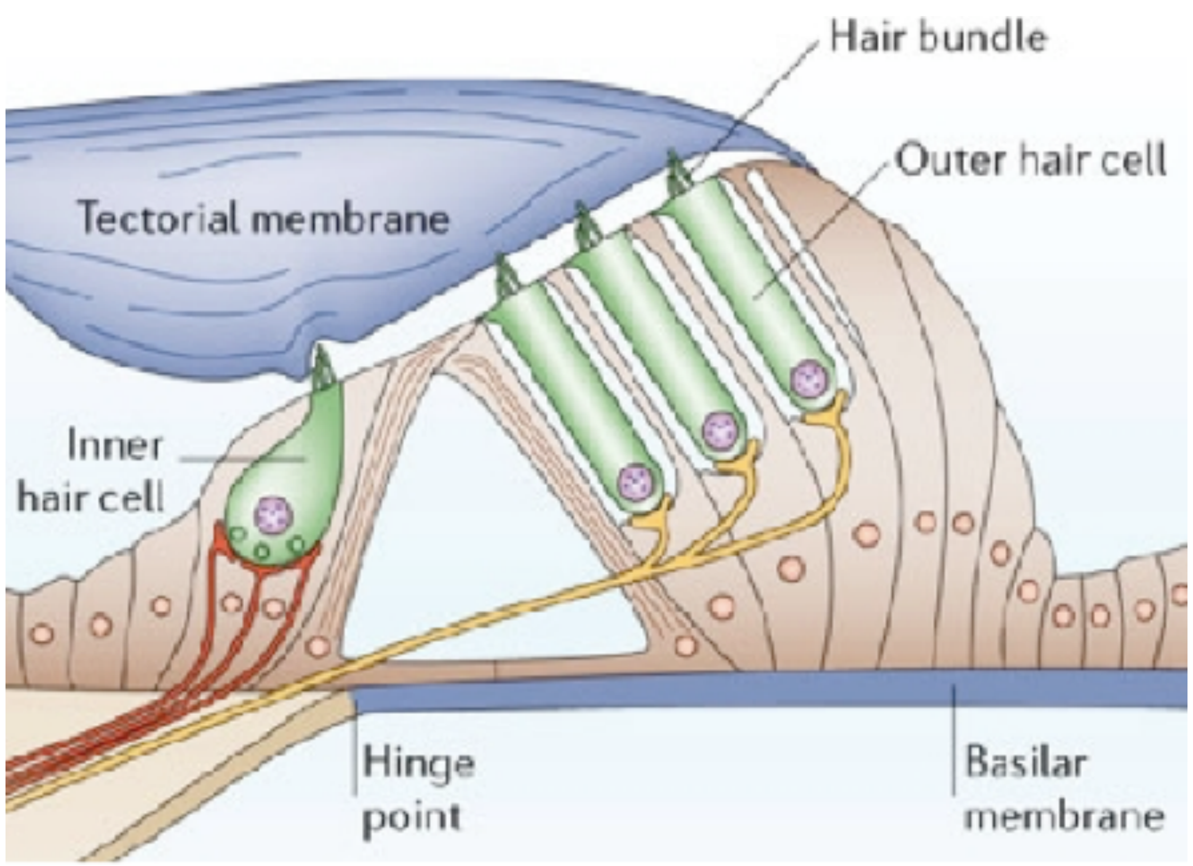
System of elastically coupled hair bundles

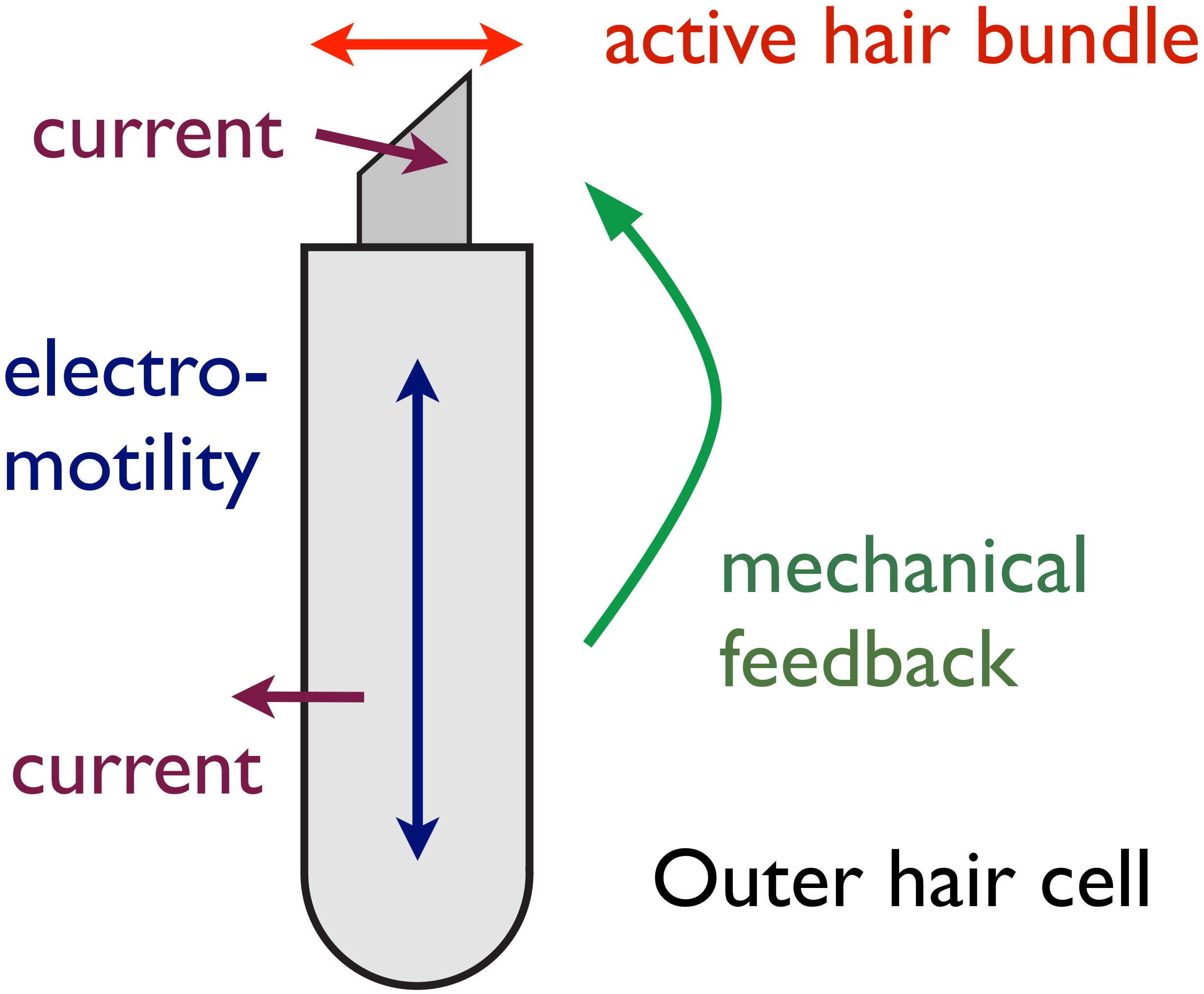
The cochlear amplifier

Amplification by coupled hair bundles

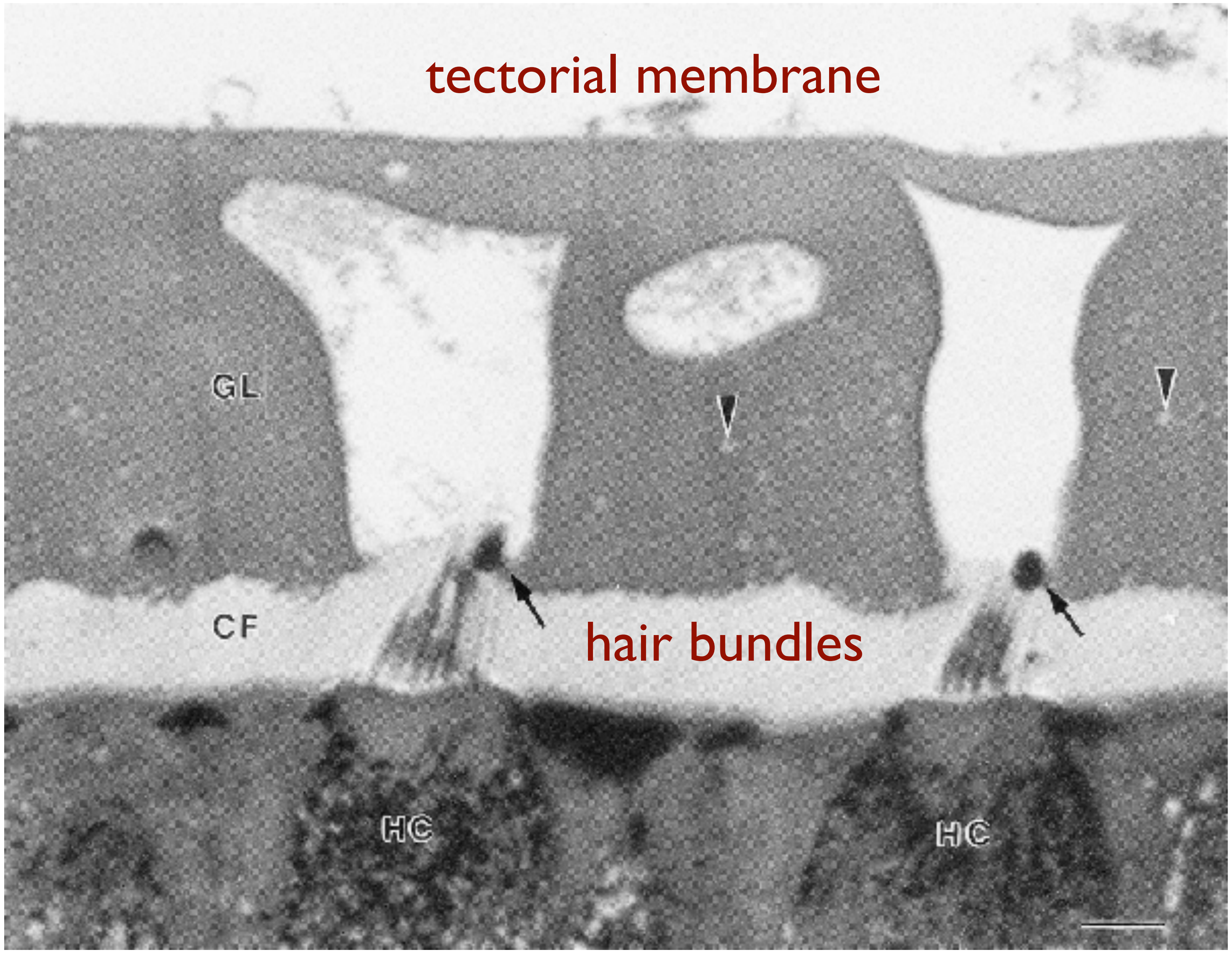
Interplay of hair bundle motility and electromotility in the cochlea

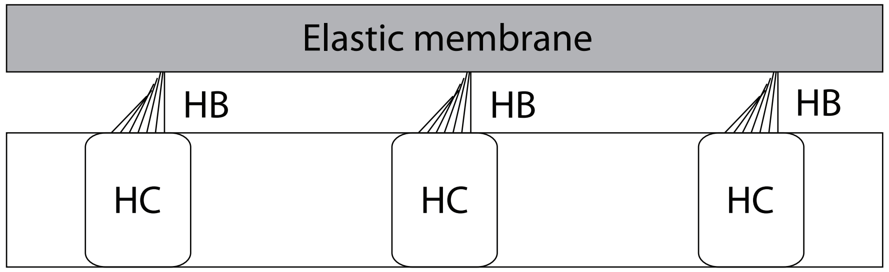
Hair cells in the organ of Corti



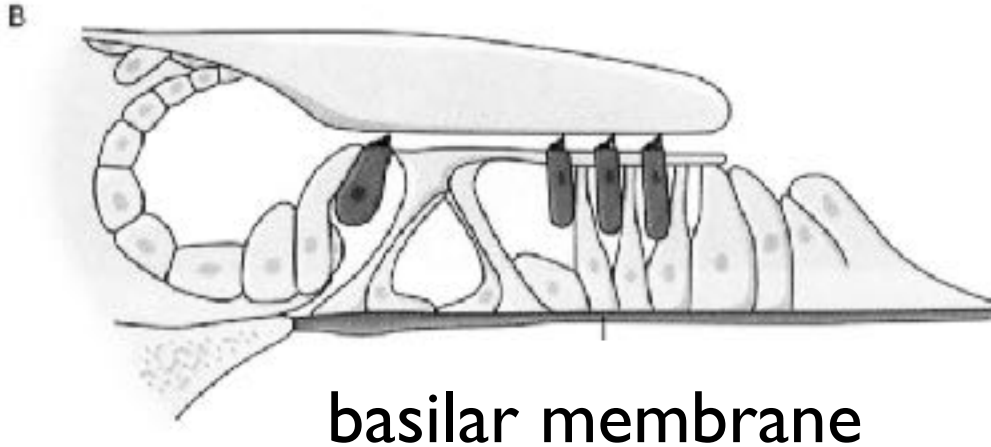


Mechanical coupling of hair cells





tectorial membrane



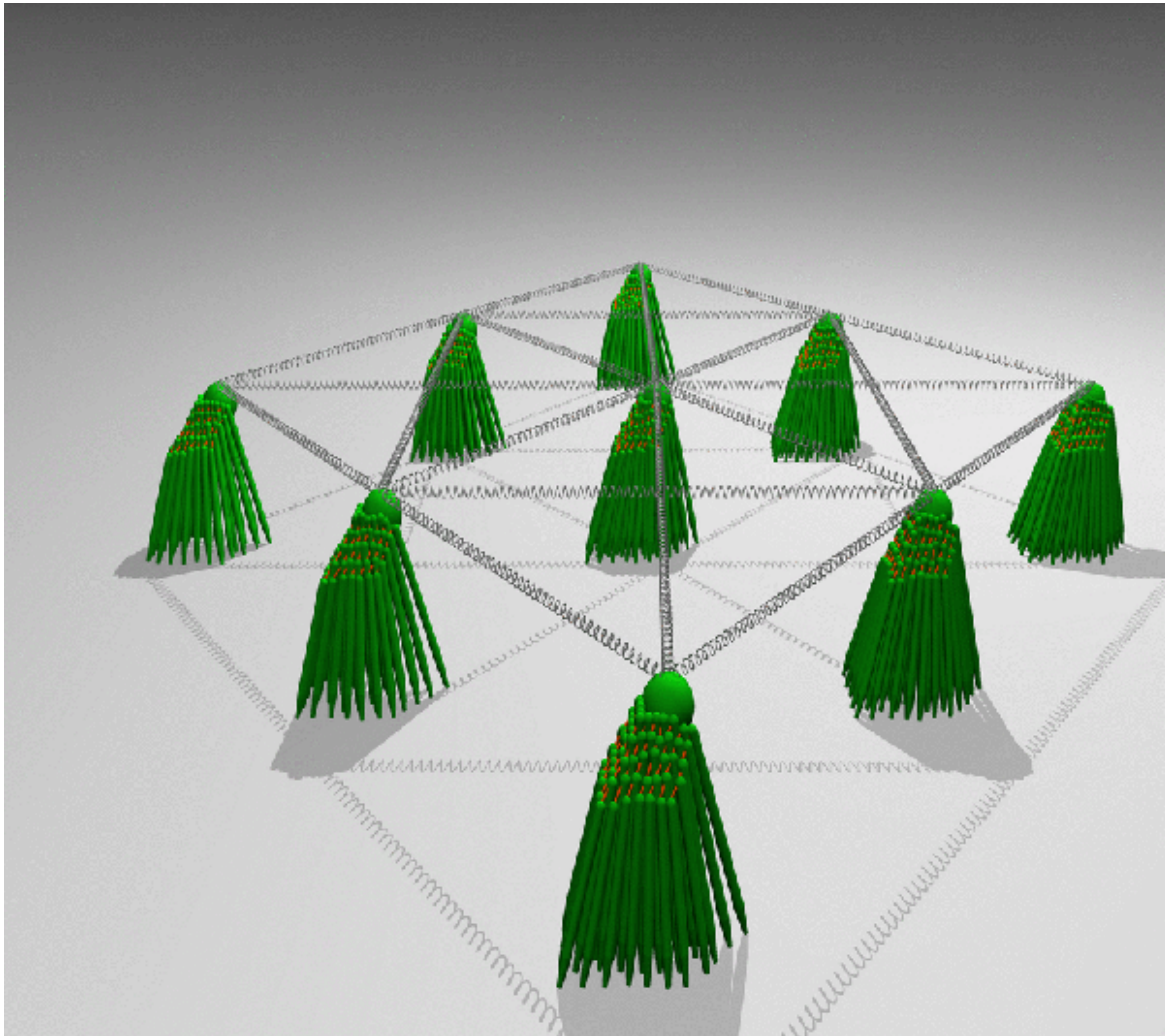
basilar membrane

B. Kachar et al., Hearing Research (1990)

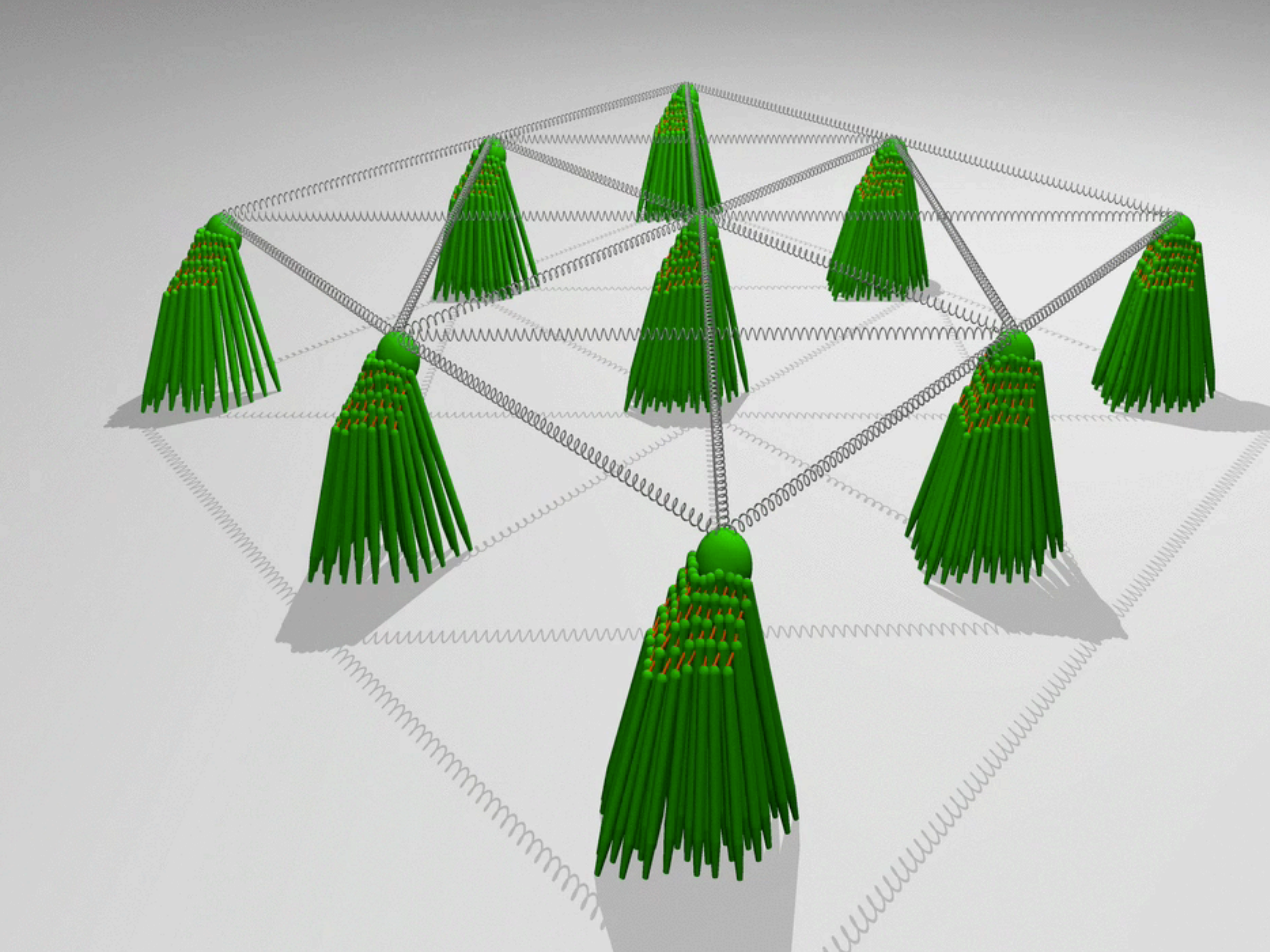
Mechanical coupling of hair cells

Mechanical coupling of
hair bundles by elastic springs

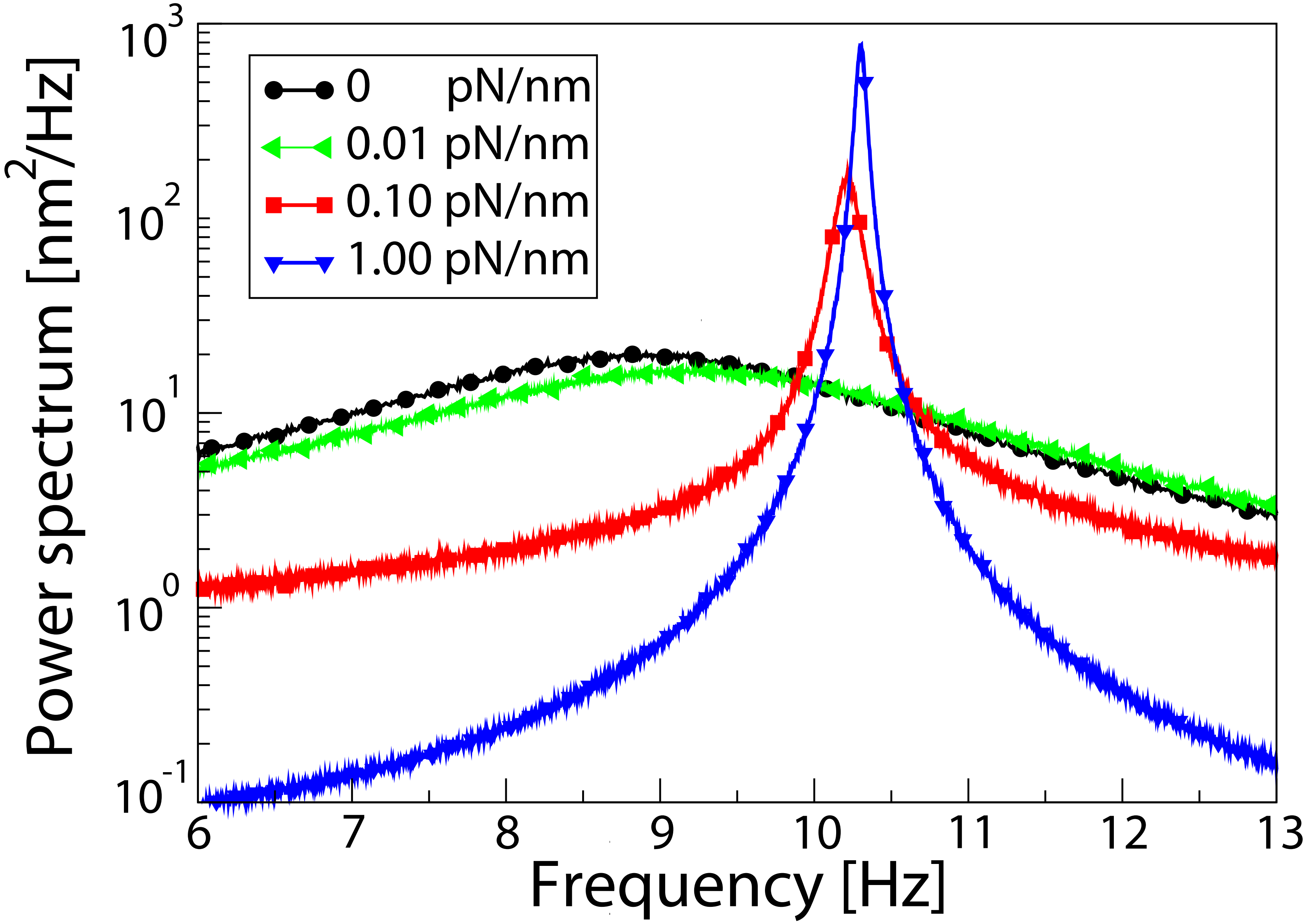
Spring stiffness K

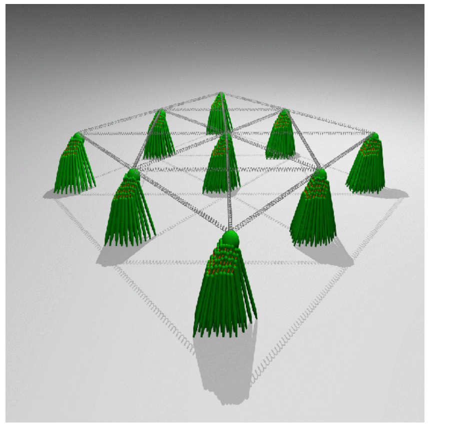


Dierkes, Lindner, Jülicher
PNAS 105, 18669 (2008)



Oscillation spectra

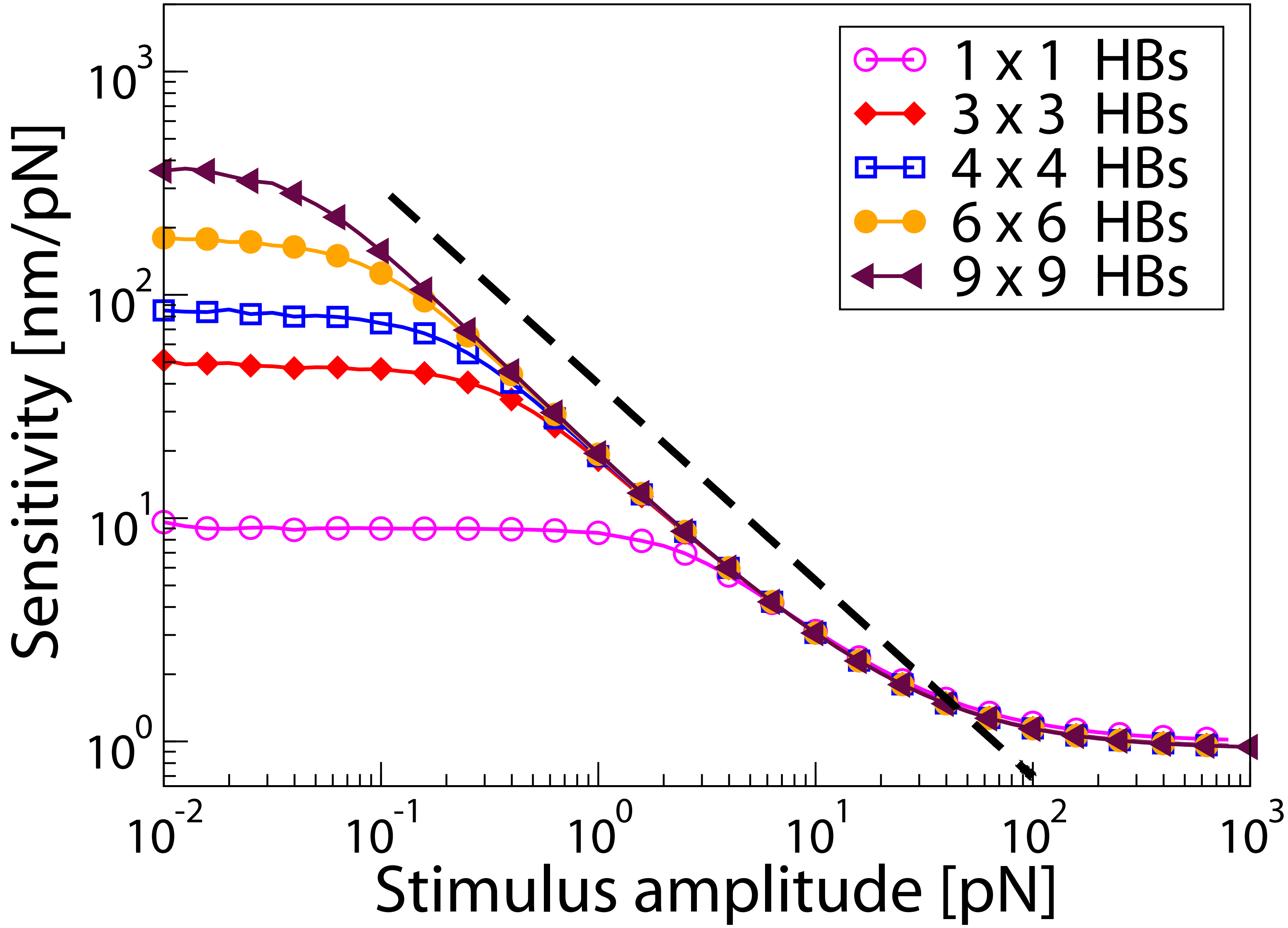


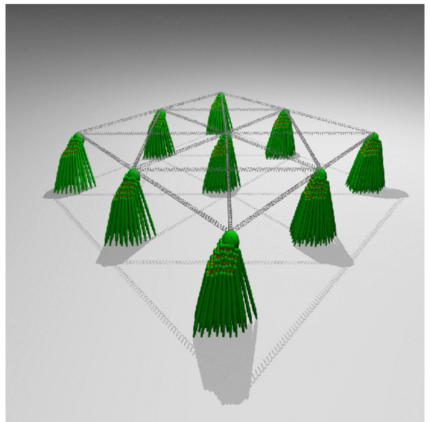


9x9 hair bundles

Dierkes, Lindner, Jülicher, PNAS (2008)

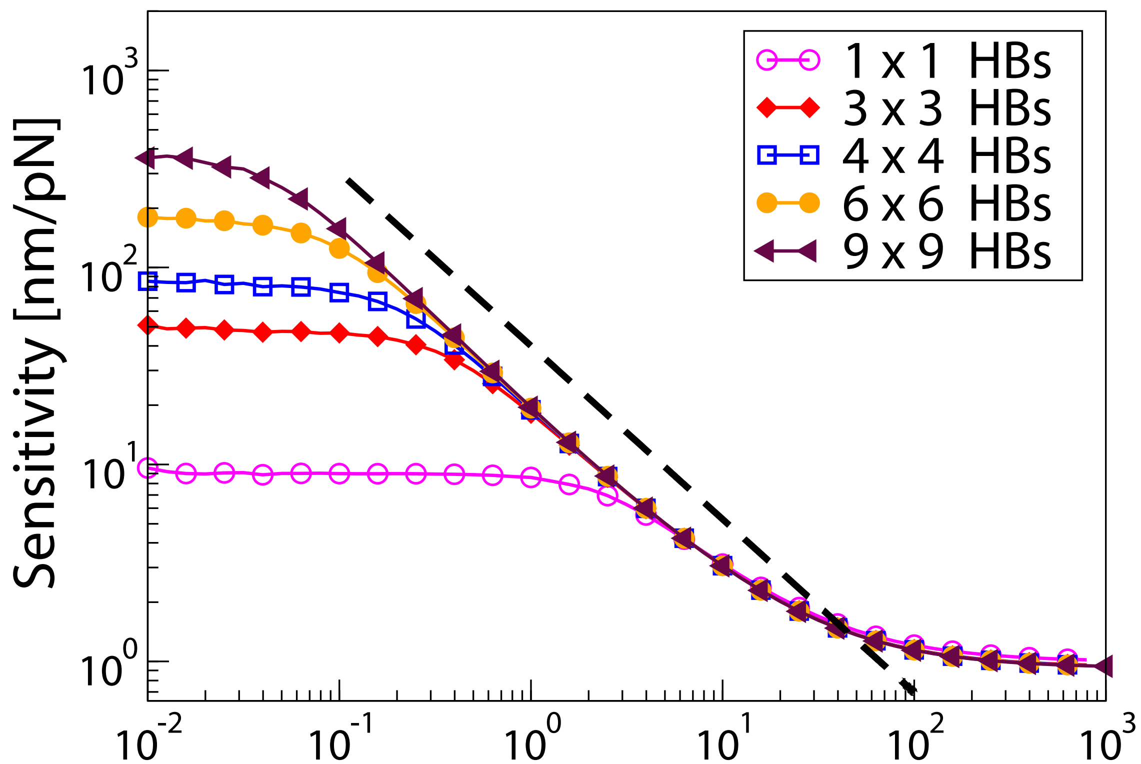
Compressive nonlinearity





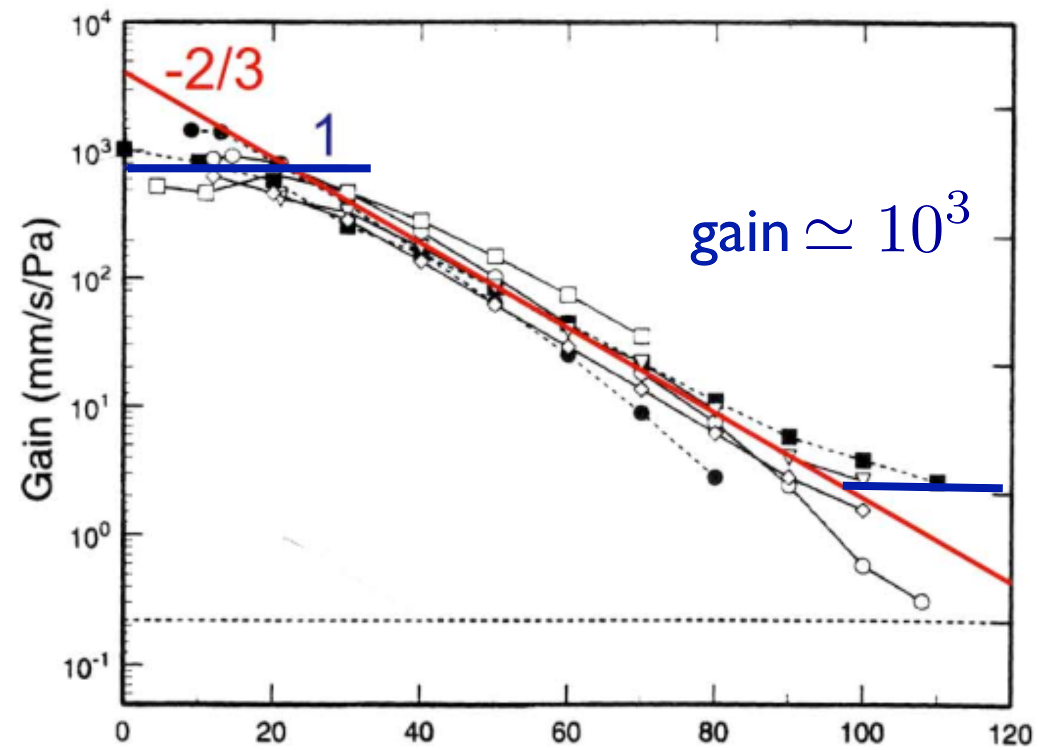
optimal coupling strength $K \simeq K_{\mathrm{sp}}$

Dynamic range of compressive nonlinearity



array of coupled hair bundles

Dierkes, Lindner, Jülicher
PNAS (2008)

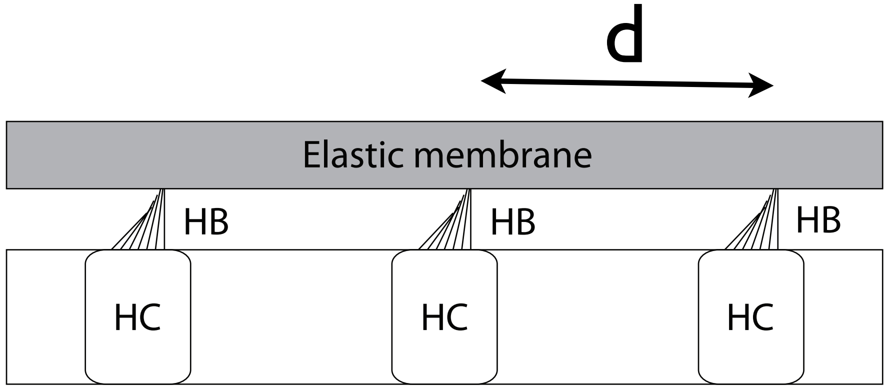


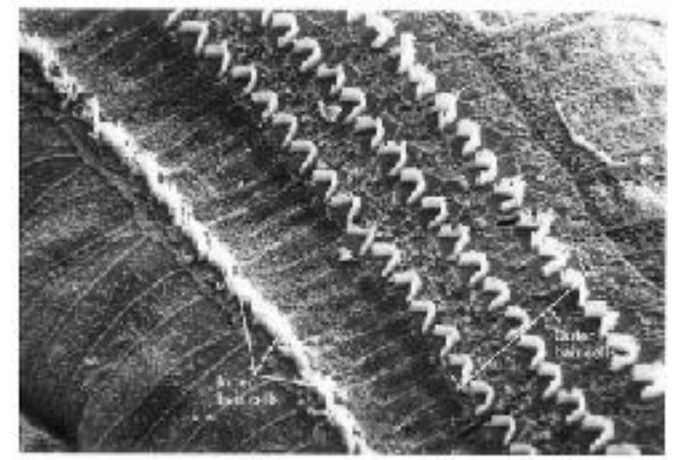
cochlea (Chinchilla)

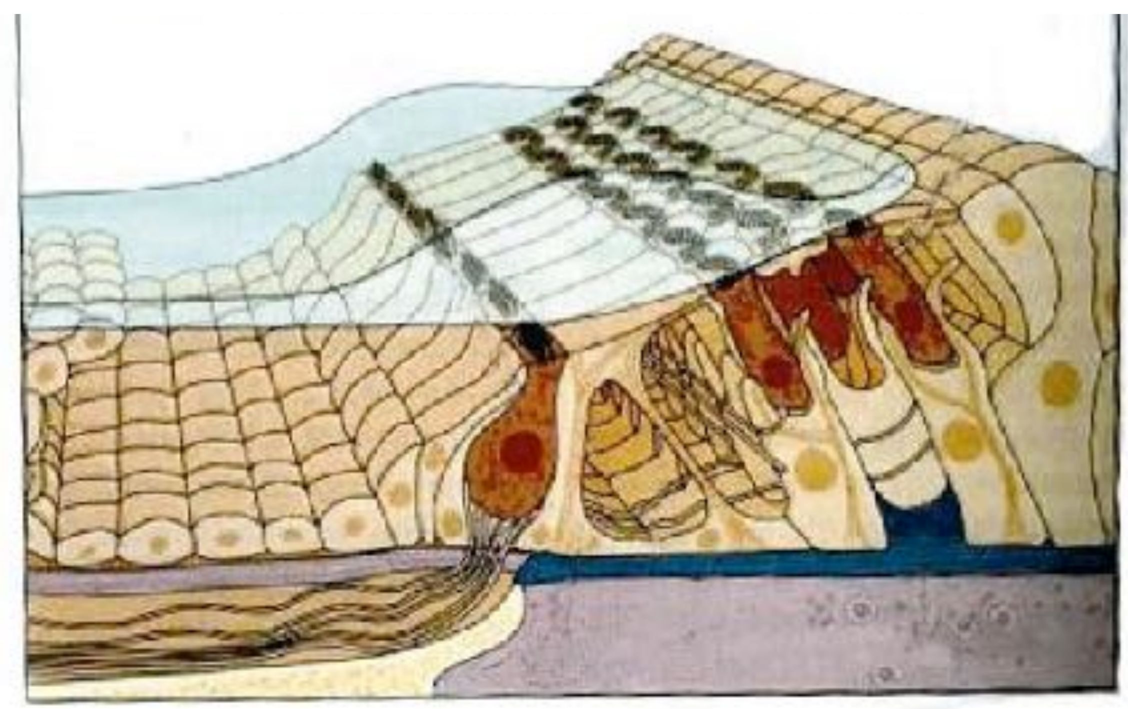
Robles and Ruggero
Physiol. Rev. 81, 1305 (2001)

Implication for the cochlea

Matching gradient of tectorial membrane elasticity enhances sensitivity of small goups of HB's







gradient of K_{sp}

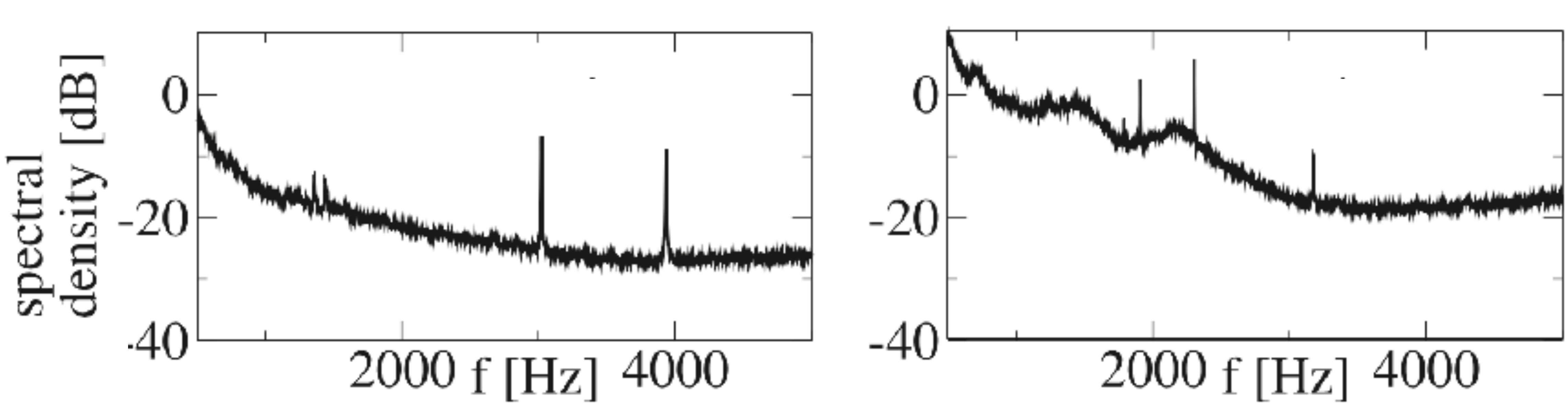
$$K \simeq Ed$$

Youngs modulus E

Dierkes, Lindner, Jülicher PNAS 105, 18669 (2008)

Statistics of spontaneous oto-acoustic emissions

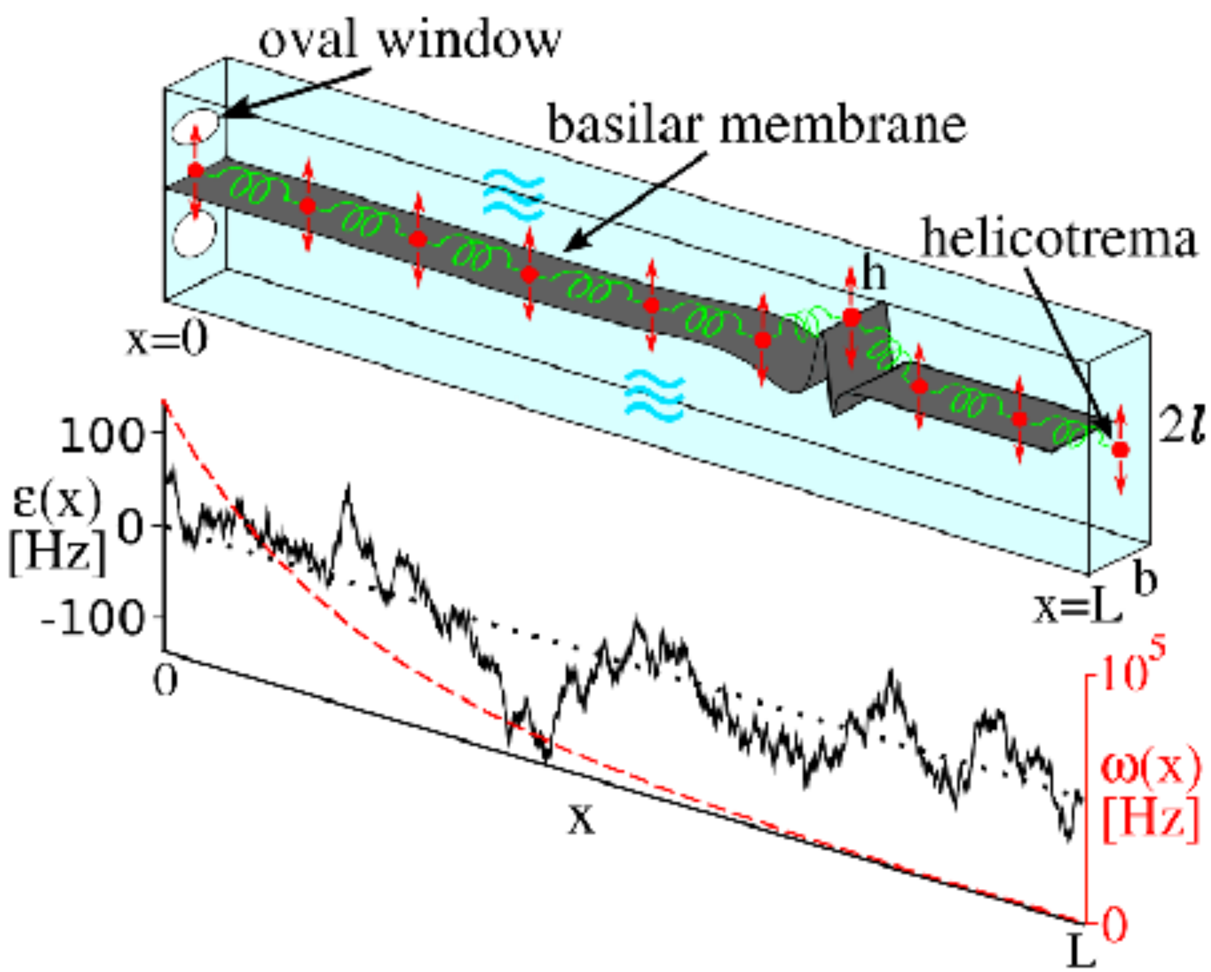
examples of emission spectra of two individuals



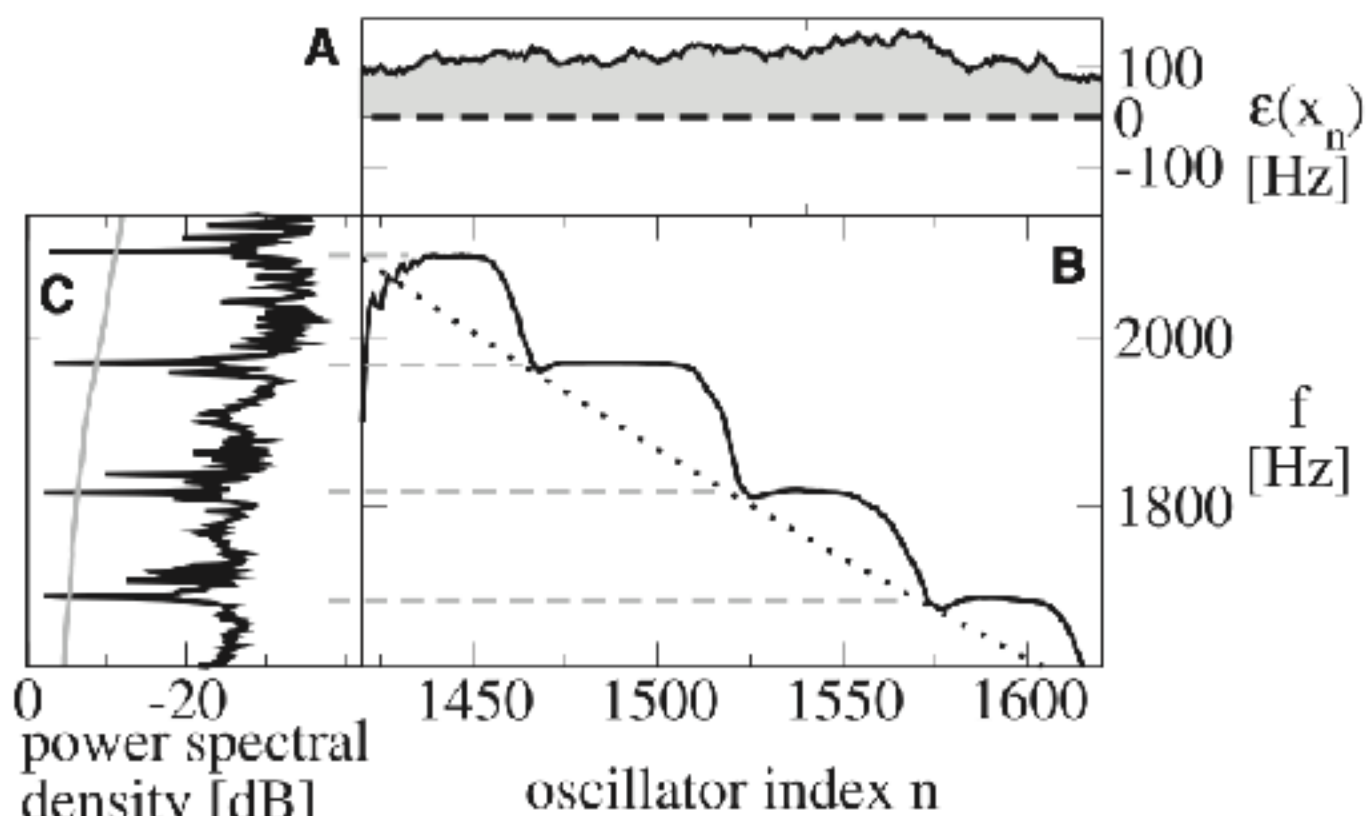
origin of variability?

Talmadge et al , Hearing Research 1993

Cochlear model with disorder



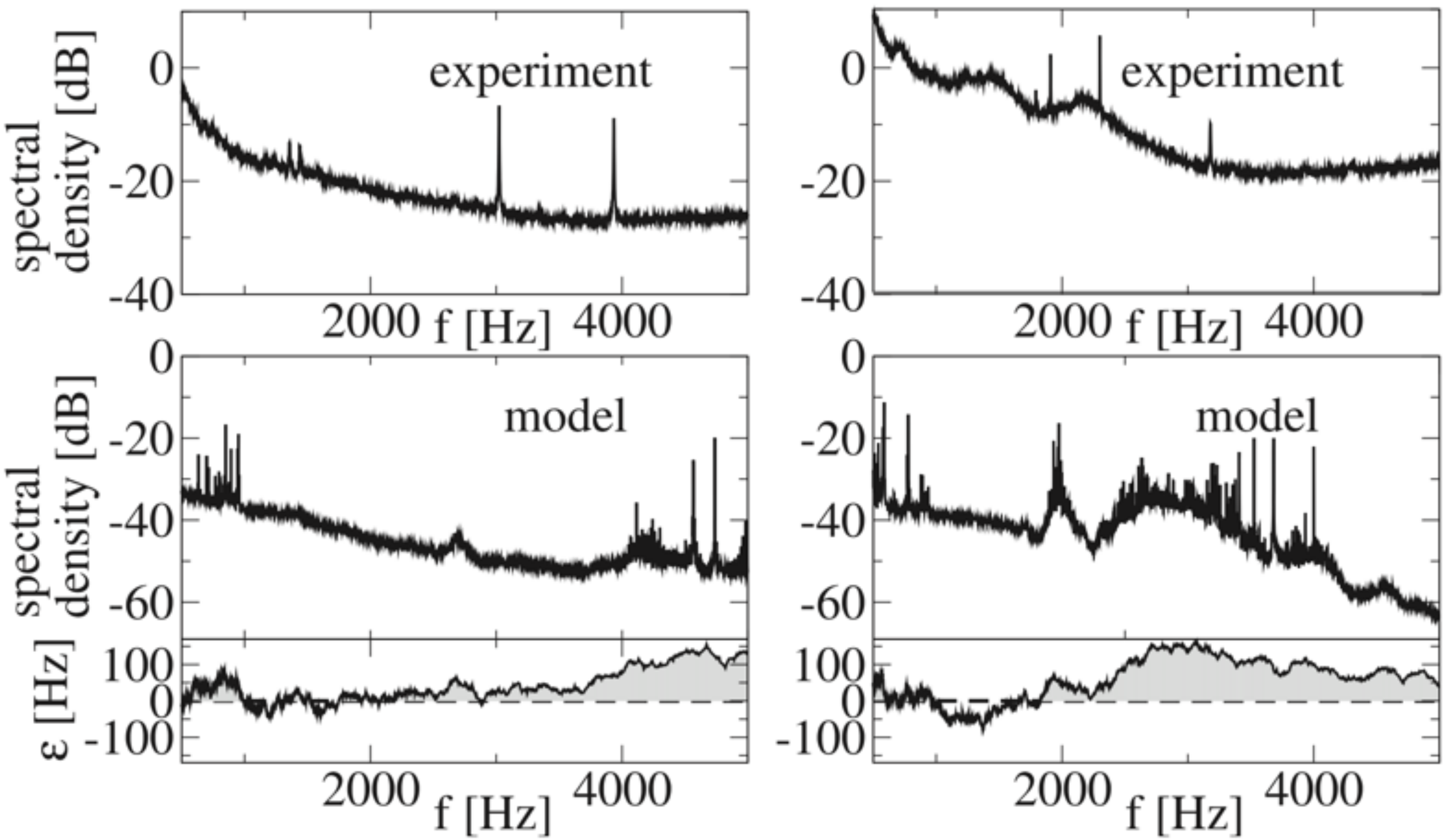
- Cochlear model
- linear array of active oscillators
- elastic coupling of hair bundles



- Frozen disorder:
  detuning from criticality
- noise

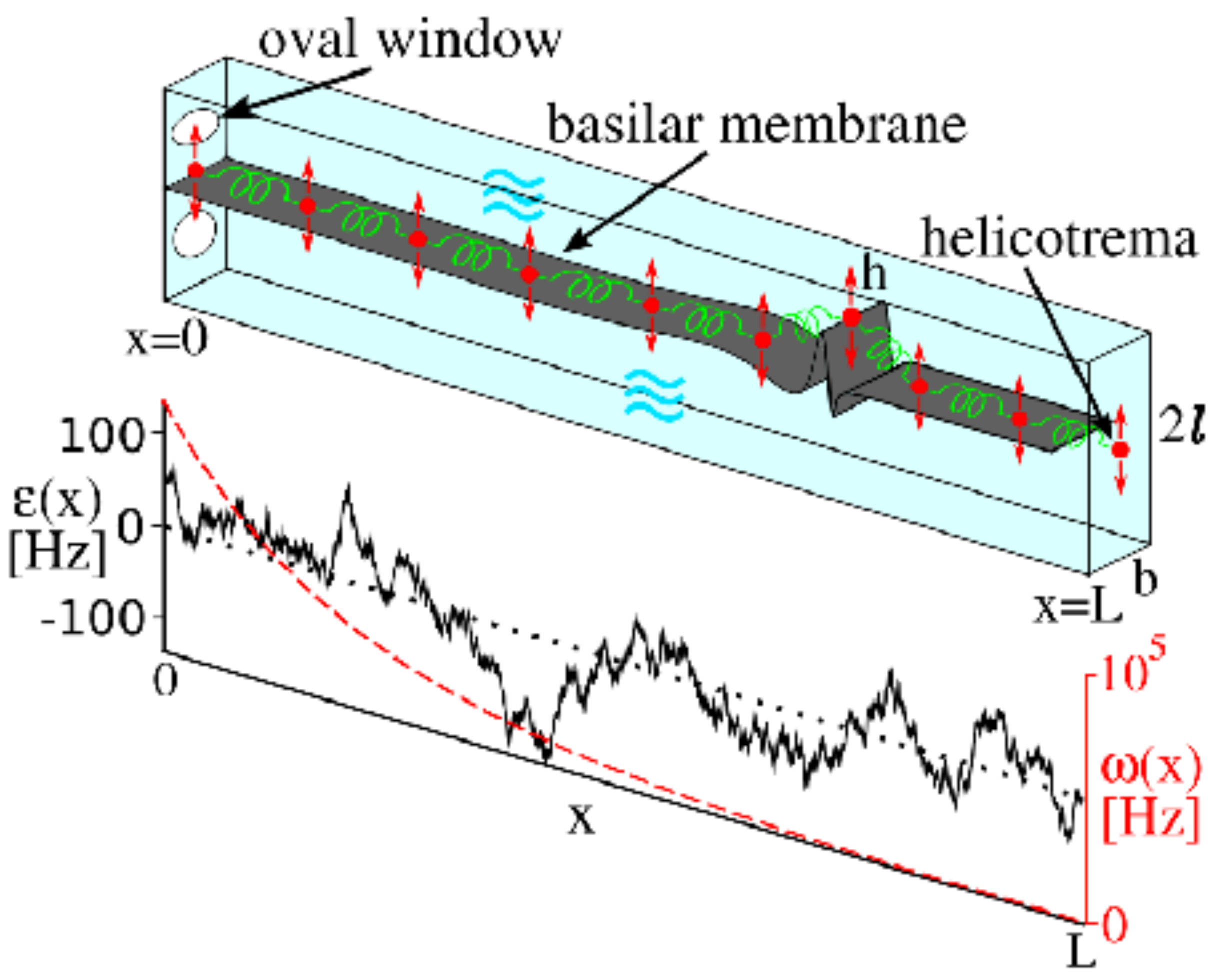
Fruth, Jülicher, Lindner Biophys. J. (2014)

Otoacoustic emissions

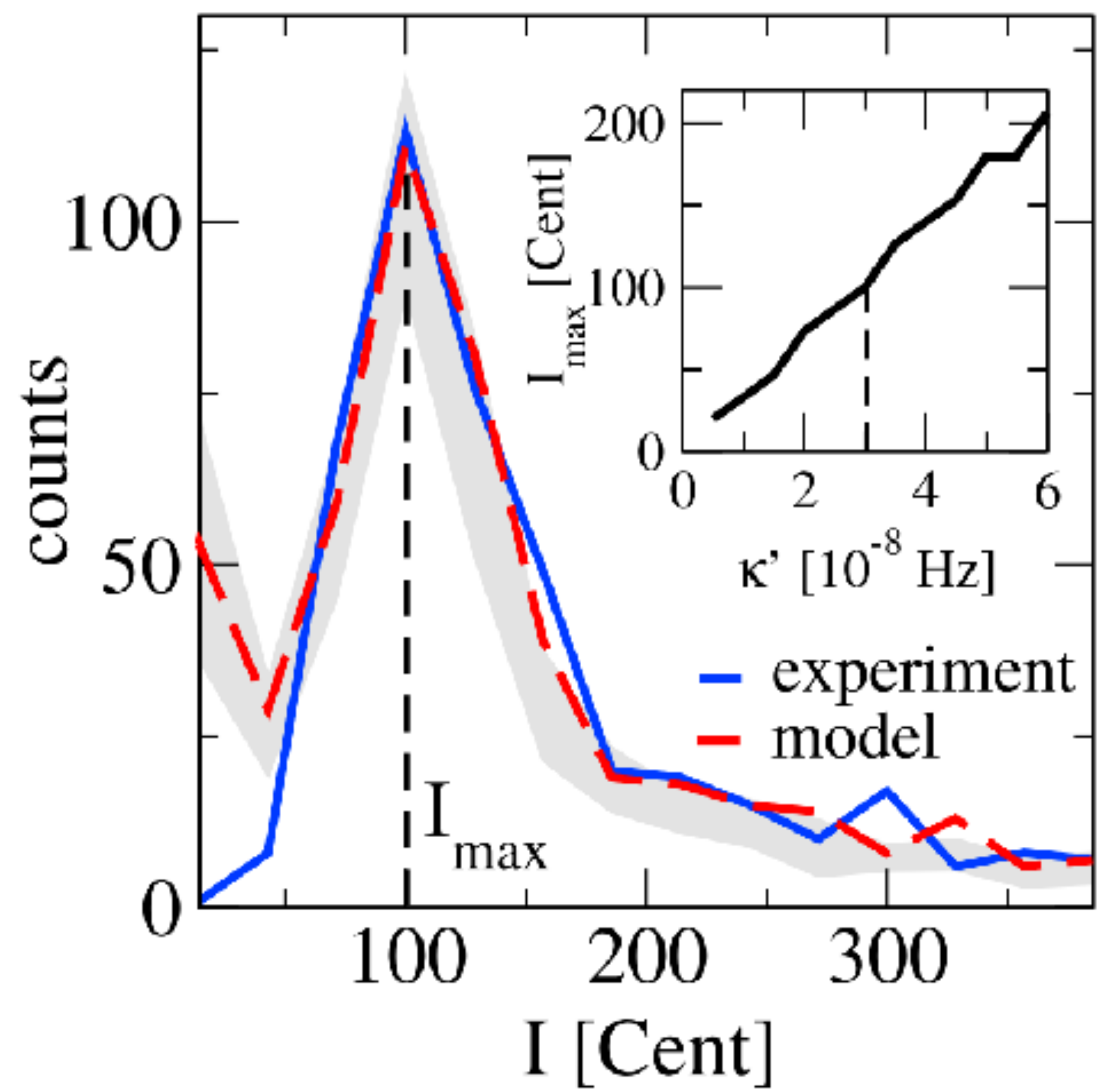


Fruth, Jülicher, Lindner Biophys. J. (2014)

Otoacoustic emissions



Statistics of emission frequency intervals

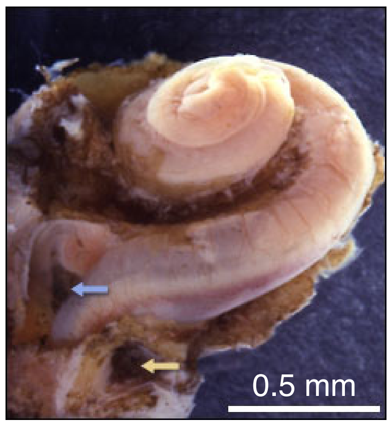


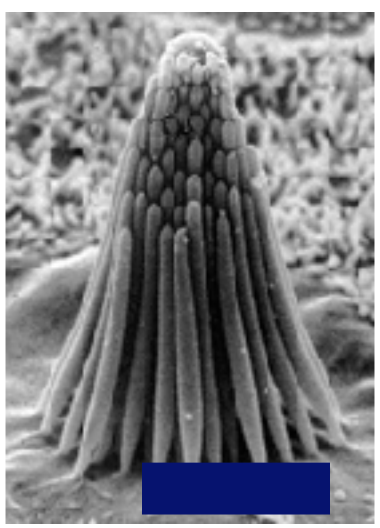
$$I = 1200 \log_2(f_2/f_1)$$

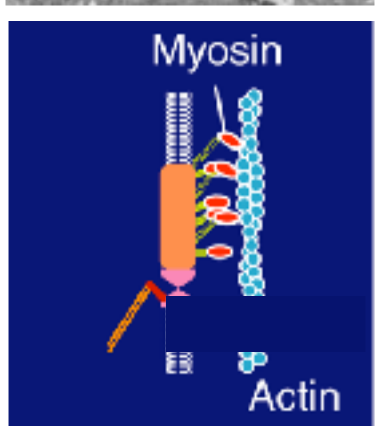
one semitone = 100 cent

Fruth, Jülicher, Lindner Biophys. J. (2014)

Signal amplification by nonlinear oscillators







General principle for frequency selective nonlinear signal detection

- large dynamic range
- compressive nonlinearity
- highest sensitivity and frequency discrimination for weak stimuli

Combination tones and frequency coupling

Applications to other sensory systems?

Acknowledgements

Thomas Duke
Pascal Martin
Jacques Prost
Jim Hudspeth

Daibhid. O Maoileidigh
Benjamin Lindner
Jean-Francois Joanny

Daniel Andor
Björn Nadrowski
Kai Dierkes
Diana Clausnitzer
Thiomas Risler
Aditi Simha
Florian Fruth
Jean-Yves Tinevez

Acknowledgements

K. Dierkes
D. Clausnitzer
D. O Maoileidigh
B. Lindner
F. Fruth

B. Nadrowski
T. Risler
A. Simha

P. Martin
J-Y. Tinevez
J. Barras
V. Bormuth

J. Prost
J.-F. Joanny

T. Duke
D. Andor