# A critical network is what you hear

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# Hearing system properties:

- Ancestral to the nervous system
  (may explain aspects of the latter from the sensors' perspective)
- Verifiable (there is 'big' unexplained data)
- Simple fundamental model based on physical principles ('higher nonsense')
- Receives power when embedded into physiological context
- Explains a number of puzzling observations
- Model adaptable to more specific situations

# Overview:

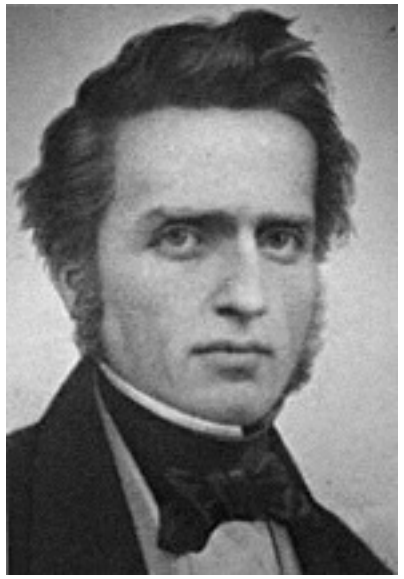
1998/9: Carver mead school cochleas
1999: Cochlea from scratch, based on fluid dynamics, energy-based approach
2000: Eguiluz, PRL: Hopf concept -> Hopf small signal amplifier, PRL 1995
2002: Kern’s thesis finished
2003: Kern’s thesis published
2003: Kern & Stoop, PRL
2003: Comment to Magnasco’s PRL
2004: Stoop & Kern, PRL, PNAS
2004: Efferent tuning, submitted to SNF
2005: Improved coupling, v.d.Vyver
2005: Hardware cochlea, v.d.Vyver
2006: v.d.Vyver’s thesis, ETHZ
2006: US Patent filed
2006: Insect hearing: Hopf in Drosophila antenna
2008: Cochlear re-mapping
2010: Local correlations of the perceived pitch, PRL
2011: Effect of Nuclei, NECO
2013: Pitch sensation involves stochastic resonance, Sci. Rep.
2014: Efferent tuning implements listening, Phys. Rev. Appl.
2014: Pitch sensation shaped by cochlear fluid, Nat. Phys.
2016: Signal-coupled subthreshold Hopf-type systems show sharpened collective response, PRL
2016: Auditory power-law activation avalanches exhibit a fundamental computational ground state, PRL

# I Q: What do we hear and why?

**CGLE describes isotropic extended systems near threshold of long-wavelength supercritical oscillatory instability (Andronov-Hopf bifurcation).**

## 1840: Berlin vs. Dresden

**Ohm**



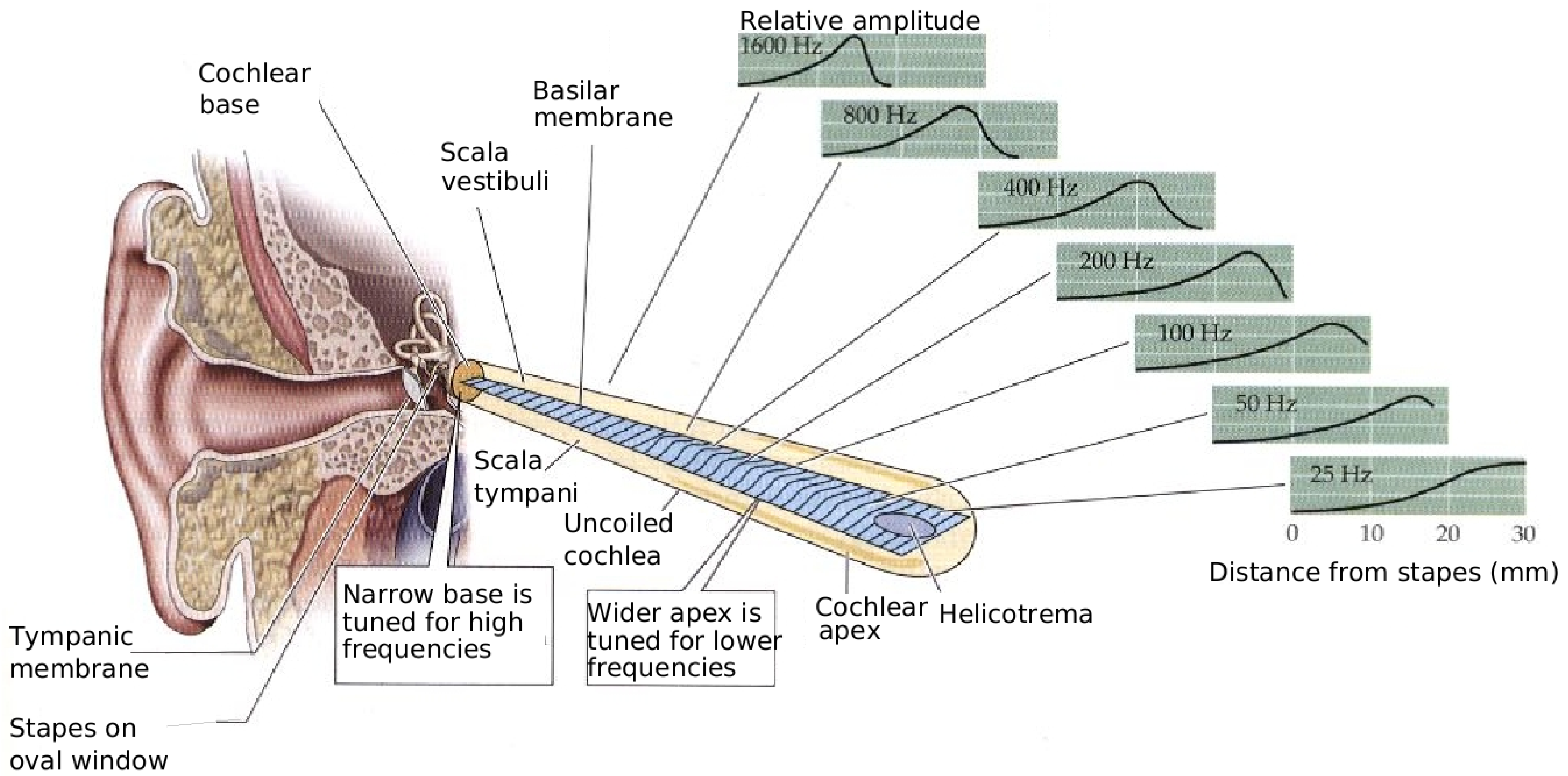
**Seebeck**

**What is the physical description of ‘pitch’ sensation?**

“Wodurch kann über die Frage, was zu einem Tone gehöre, entschieden werden, als eben durch das Ohr?”
(How else can the question as to what makes out a tone, be decided but by the ear?)

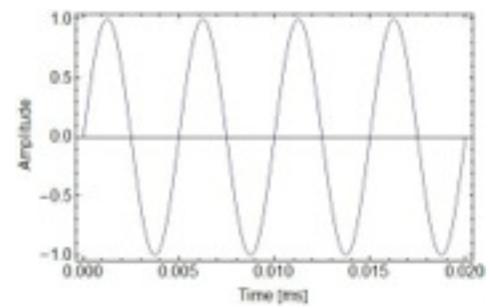
August Seebeck 1844

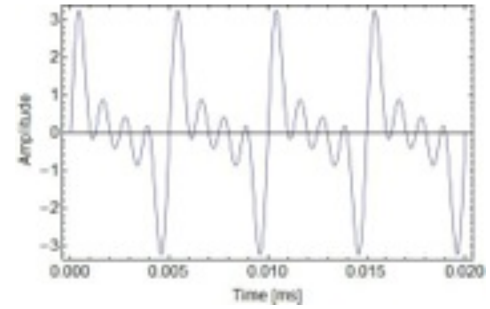
# Mammalian cochlea
## more that a frequency analyzer..



# Experiments

- simple tone: A*sin(2*π*f0*t)
- complex tone:
(frequency components
 f0, 2f0, 3f0, …)
- missing fundamental




**simple** **complex** **missing fundamental**

- Smoorenburg’s two-tone experiments:

1750/2000 ->1800/2000 Hz

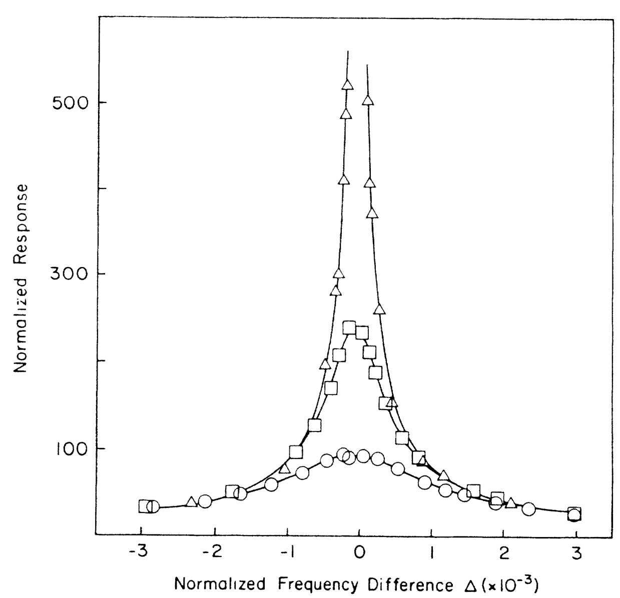
reversed

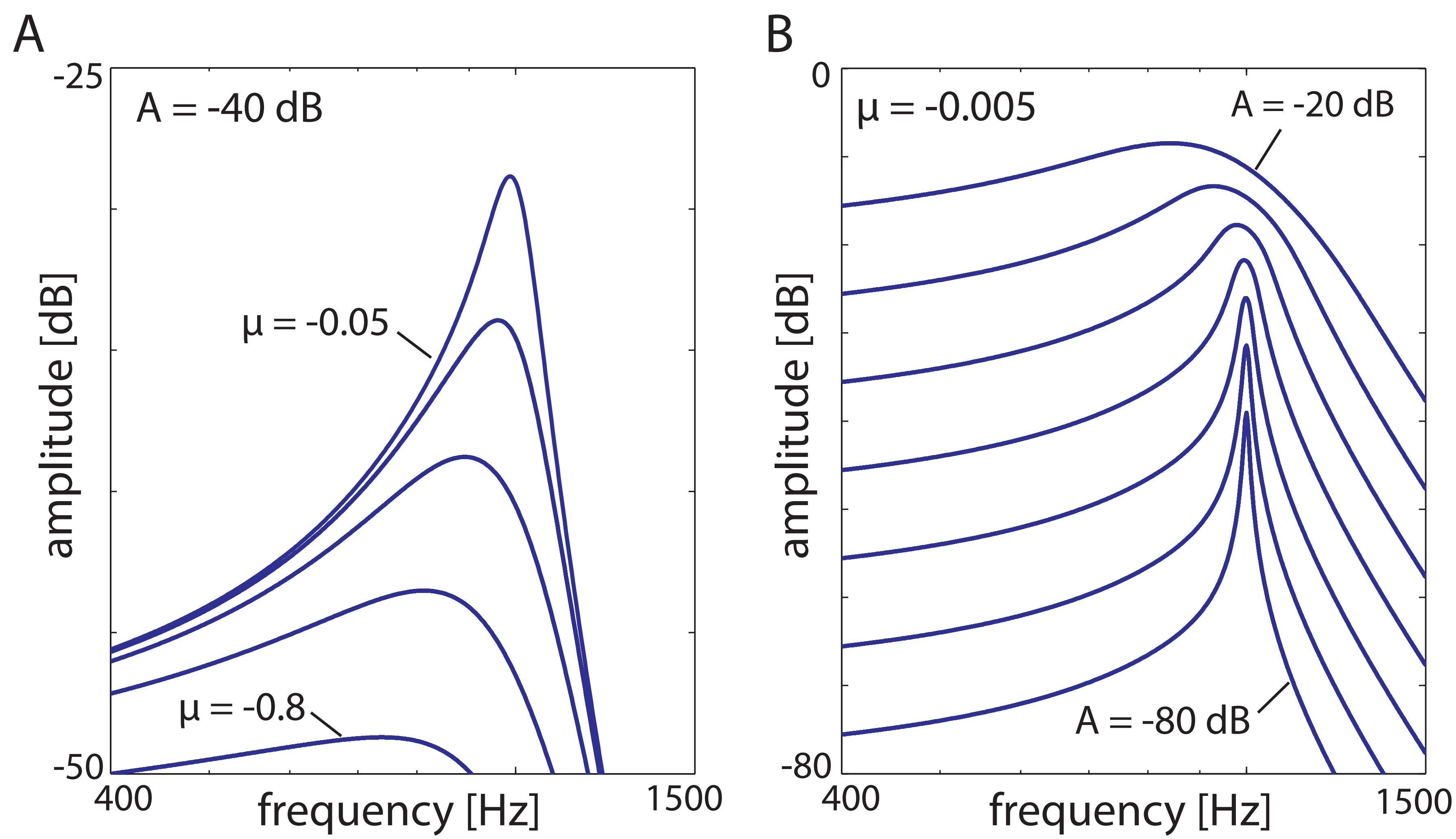
pitch down (250 -> 200 Hz, fundamental) or pitch up (partials) ?

# II Key for understanding hearing: nonlinearity
## ’small signal amplifier’

Wiesenfeld et al. PRL 1984/5/6:

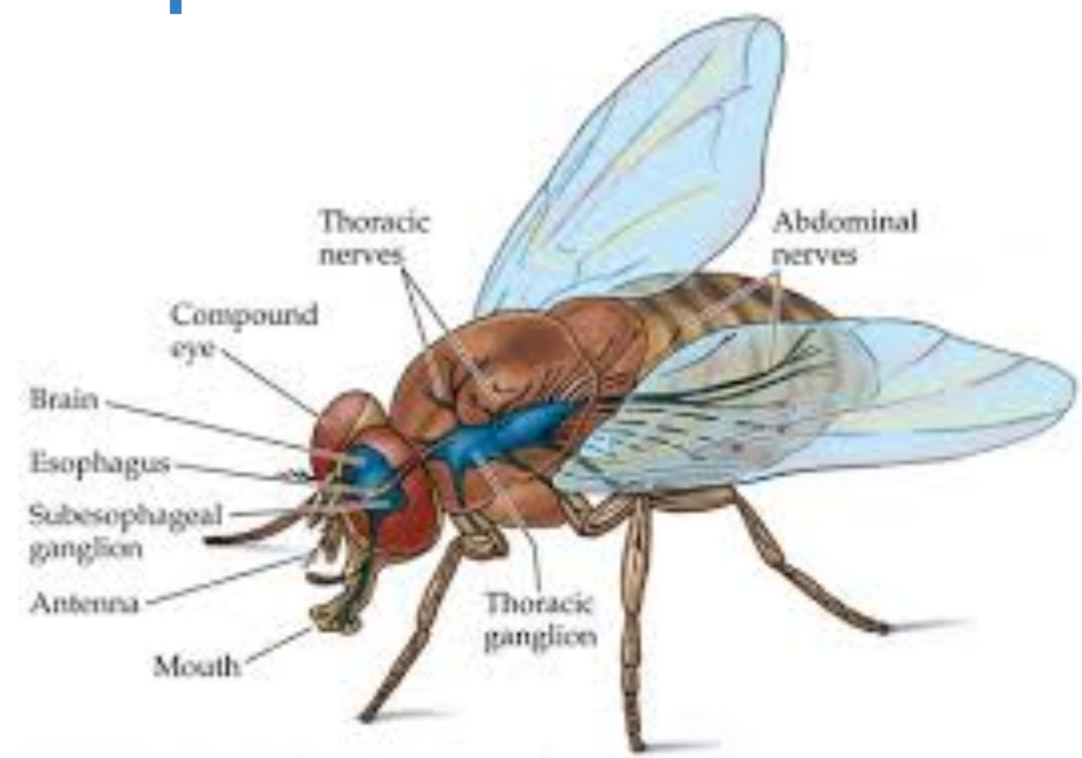
Systems close to a **period-doubling bifurcation** can be used as a small signal amplifier:
Signals with a certain ‘critical’ frequency are strongly amplified.

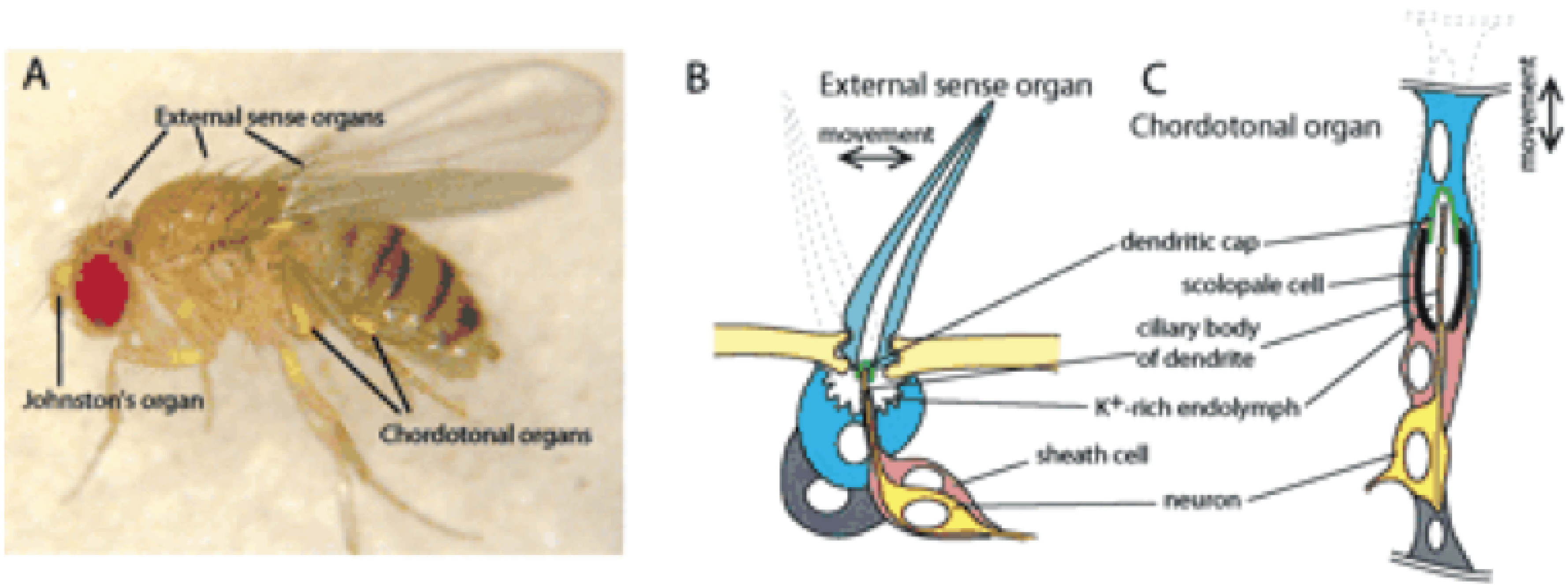


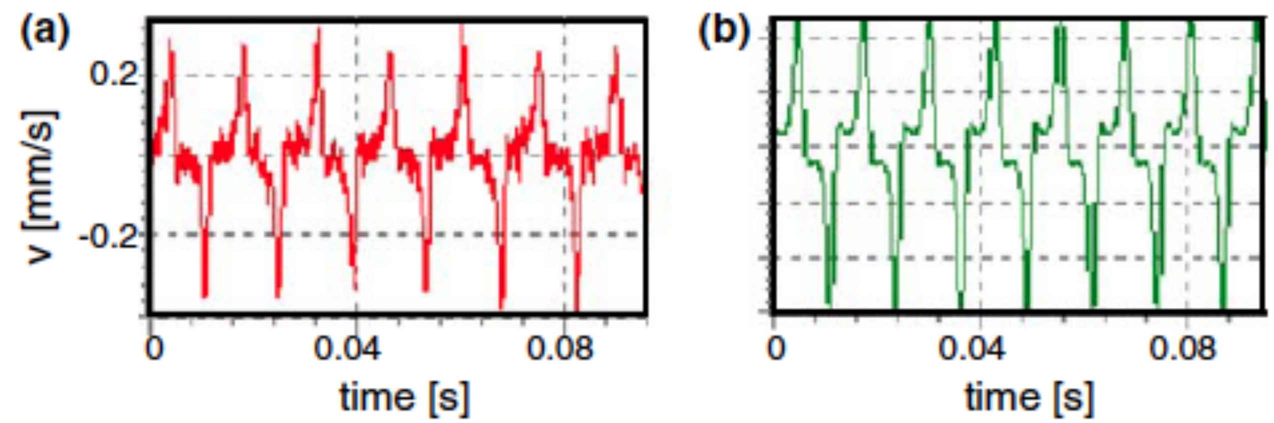

(Andronov-Hopf: Brun at al. PRL 1985)

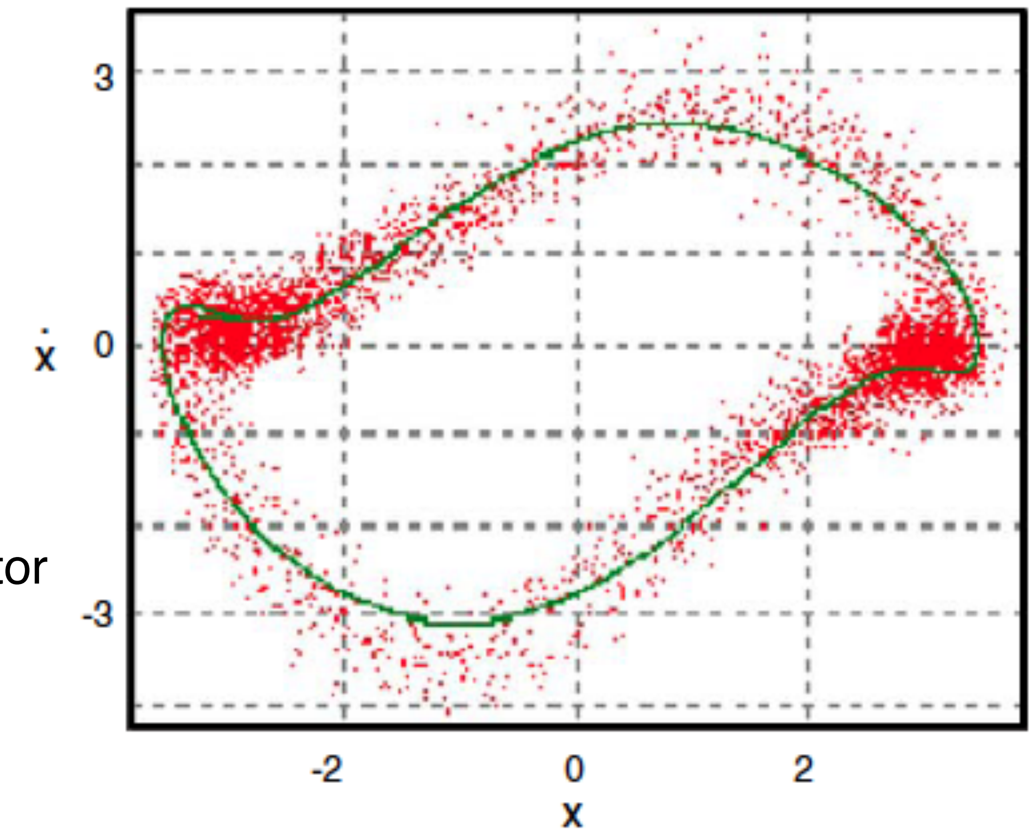
# Biological evidence of Hopf amplifiers



# Signals above bifurcation point demonstrate: Hopf !



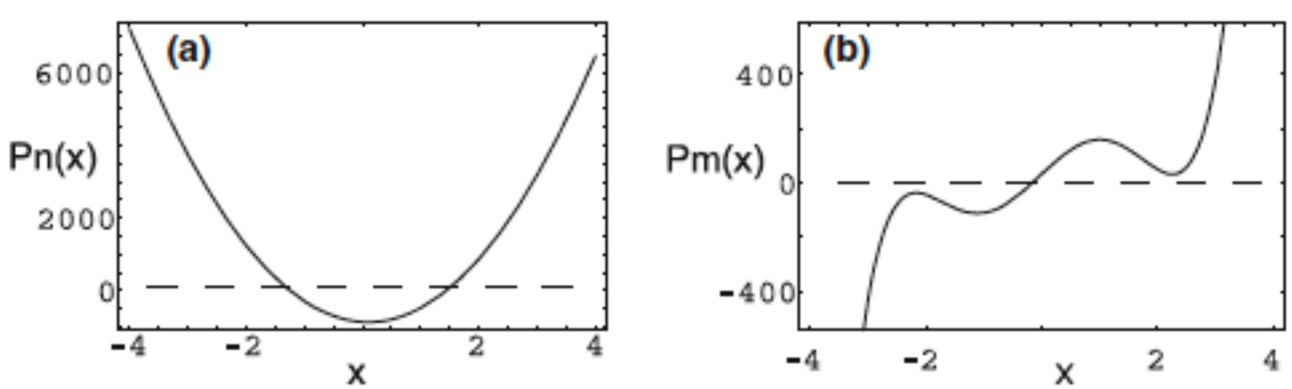




$$\ddot{x} - \mu(1 - x^2)\dot{x} + x = 0$$

$$\ddot{x} + P_n(x)\dot{x} + P_m(x) = 0$$

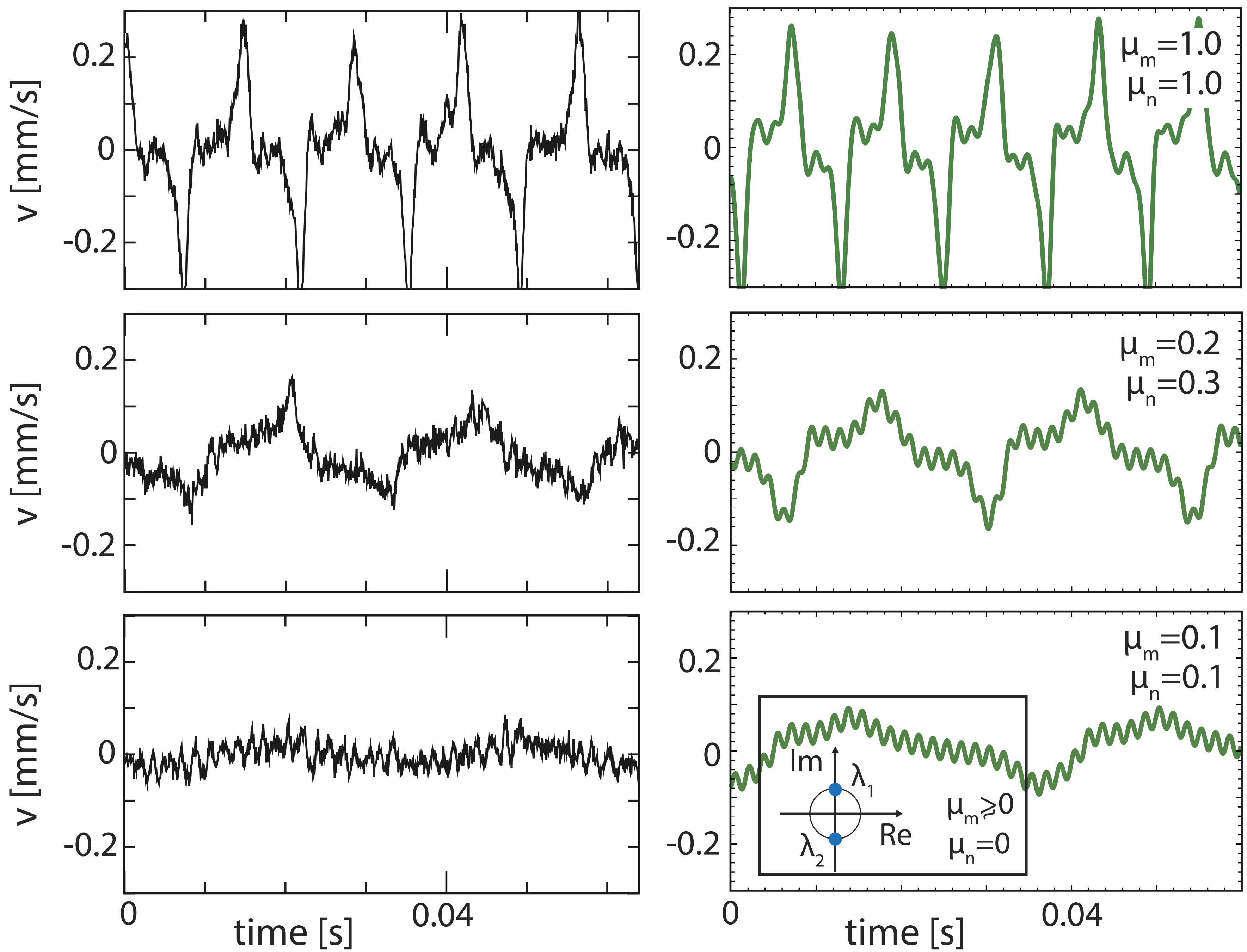
Generalized van der Pol oscillator

$\mu = 0$ : A.-Hopf bifurcation




P'm(x), restoring force, indicates areas of negative stiffness (P'm(x)<0): active amplification

**(R.S., Göpfert & Saratov friends Eur. Biophys. J. 2006)**




Polynomials were reduced by factors $\mu_m \simeq \mu_n$.

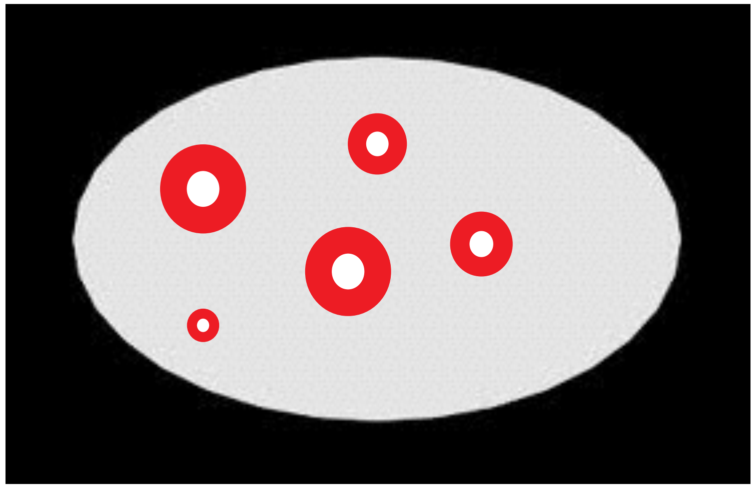
Close to bifurcation, $\mu_n$ precedes $\mu_m$, so that at bifurcation $\mu_m > 0$.

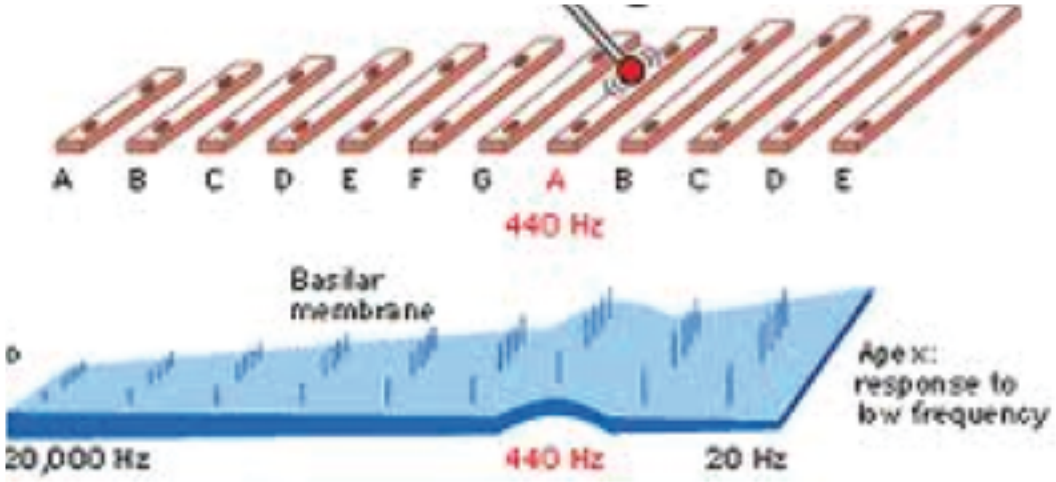
Inset: At crossing to quiescence, the linear analysis reveals an Andronov-Hopf bifurcation.

**(T.L., F.G. & R.S. Sci. Rep. 2015)**

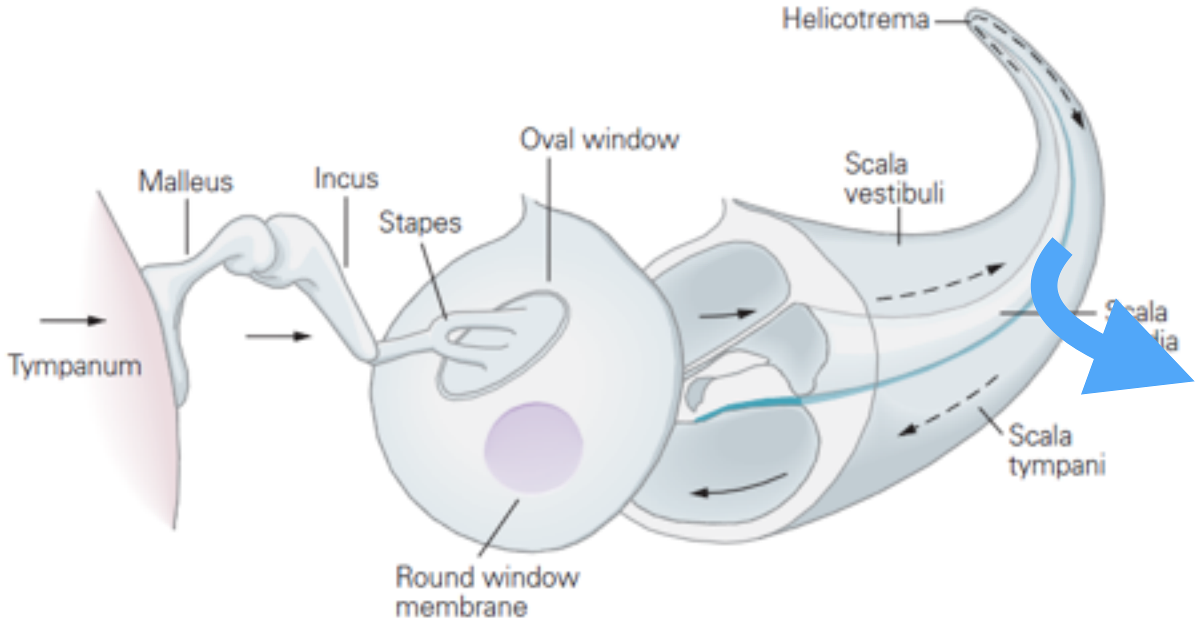
# III From many sensors to a cochlea:

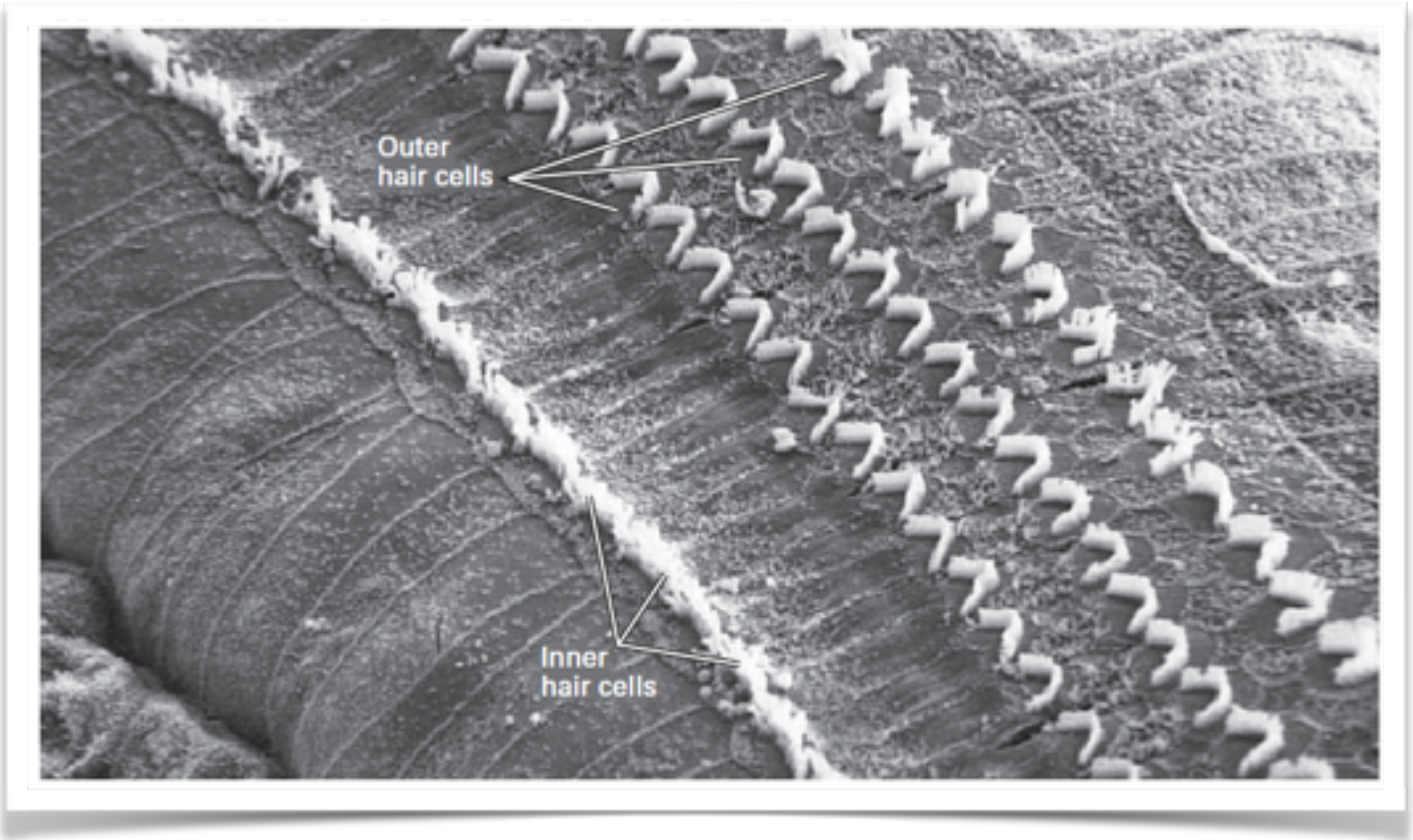
## the wiring problem






(Lorimer, Gomez, R.S., Sci. Rep. 2015)




Hudspeth 2013

# IV Mammalian cochlea from scratch

## energy-based cochlea modeling: A. Kern (2002) PhD

equilibrium:

$$\frac{\partial e}{\partial t} = -a(x, e, \omega) + d(x, \omega) e(x, \omega)$$

d: viscous damping rate, a: amplification, e: energy density

fundamental energy balance (Whitham):

$$\frac{\partial e}{\partial t} + \frac{\partial}{\partial x}(v_G e) = 0$$

$v_G$: group velocity

leads to:

$$\boxed{\frac{\partial e}{\partial x} = -\frac{1}{v_G(x,\omega)}\left(\frac{\partial v_G}{\partial x}(x, \omega) + d(x, \omega)\right) e(x, \omega) + \frac{a(e,x,\omega)}{v_G(x.\omega)}}$$

**cochlear ODE** passive active

(A.K. & R.S. PRL 2003)

# Equipartition theorem:

- wave amplitude $$A(x,\omega) = \sqrt{\frac{2e(x,\omega)}{\boxed{E(x)}}},$$

  (I)

  $E(x)$ BM-stiffness

- passive traveling wave:

$$A(x,\omega) = \frac{A_0(\omega)}{\sqrt{2}\sqrt{E(x)}}\sqrt{\frac{v_G(0,\omega)}{\boxed{v_G(x,\omega)}}}\exp\left[-\frac{1}{2}\int_0^x \frac{\boxed{d(x',\omega)}}{v_G(x',\omega)}dx'\right], \qquad \text{(III)}$$

(II)

- with $A_0(\omega)$ amplitude at stapes

(II) (III) : to be determined

# Dissipation rate:

- Lighthill:

$$\boxed{d(x,\omega) = \sqrt{\frac{\nu}{2\omega}\frac{\rho\omega^3}{E(x)}} + 4\nu k^2,} \qquad \text{(III)}$$

- dominant viscuous losses (inner friction $\nu$) compared to kinematic friction

# Group velocity:

- Patuzzi: Cochlea twodimensional surface wave

$$v_G = \frac{\partial \omega}{\partial k} = \frac{E(x)\rho(kh + \sinh(kh)\cosh(kh))}{2\omega(mk\sinh(kh) + \rho\cosh(kh))^2}, \qquad \text{(II)}$$

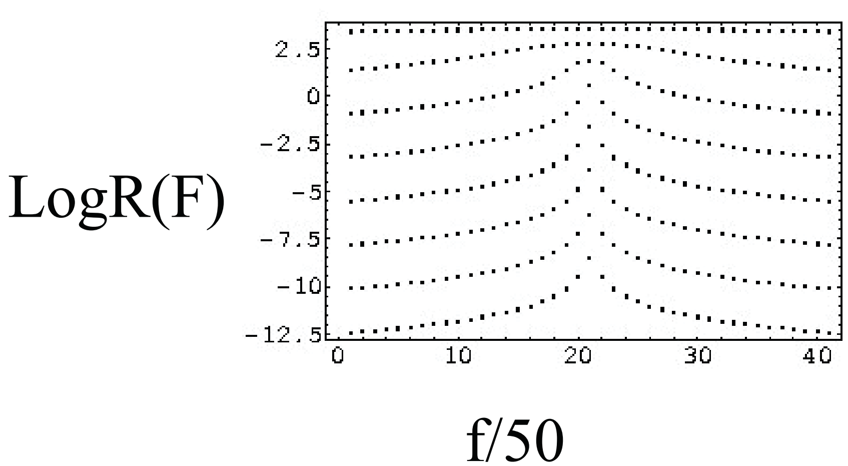
- ρ fluid density, m BM mass density, h depth of hearing canal

- dispersion relation:

$$k\tanh(kh) = \frac{\rho\omega^2}{E(x) - m\omega^2}$$

# Active response:
## generic Hopf equation

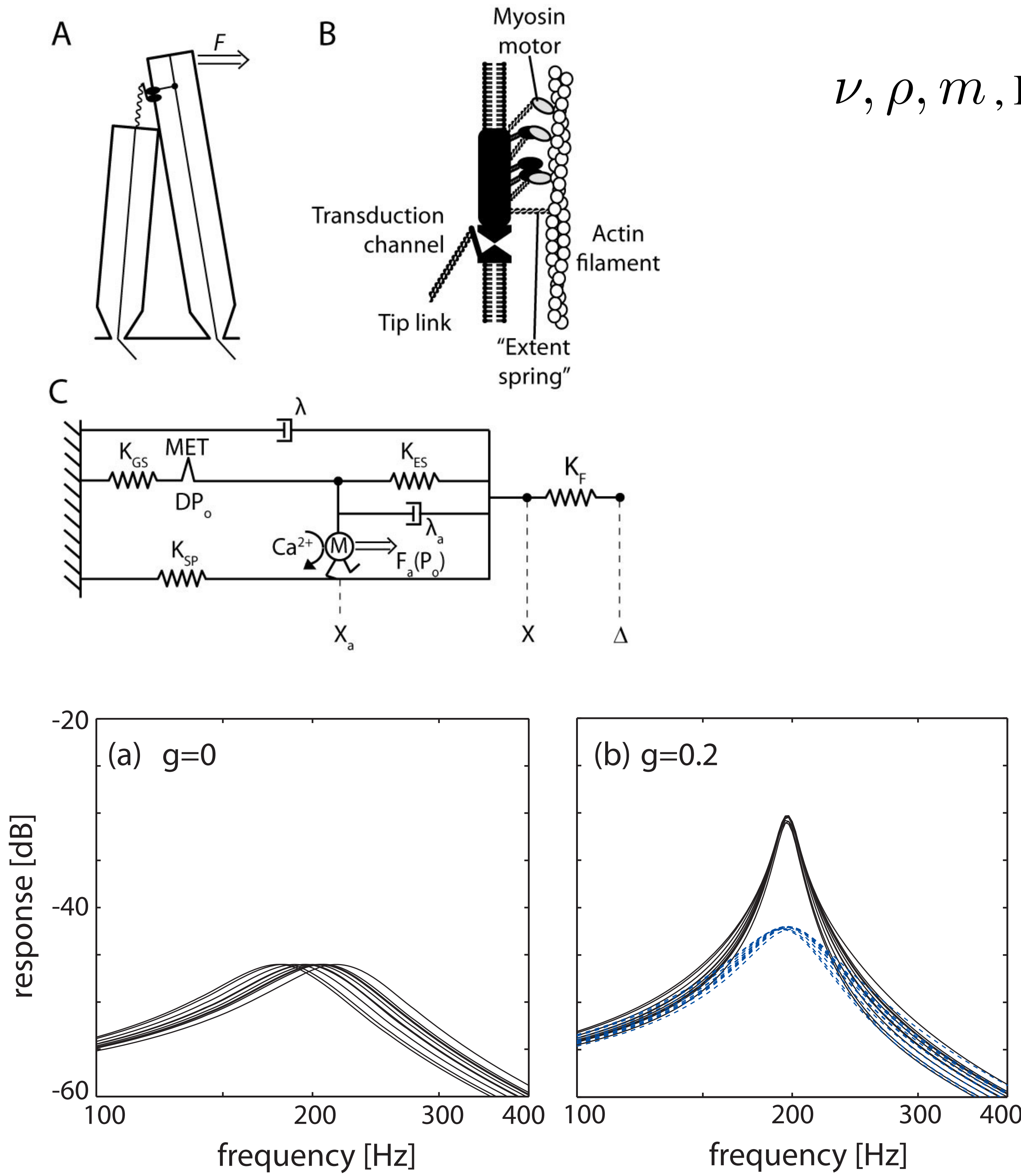
- Close to bifurcation point and resonance: $R = \boxed{F^{1/3}}$
- Before bifurcation point, small F: $R = -F/\mu$
- Charakteristic of Hopf-bifurcation




wc =1000 Hz, μ = -20, governs G
F = {0.004 $10^i$, i=0..7}

(Eguiluz et al. PRL 2000)

# Individual and coupled Hopf elements




$\nu, \rho, m$, BM-stiffness $\longrightarrow$ $\mu$

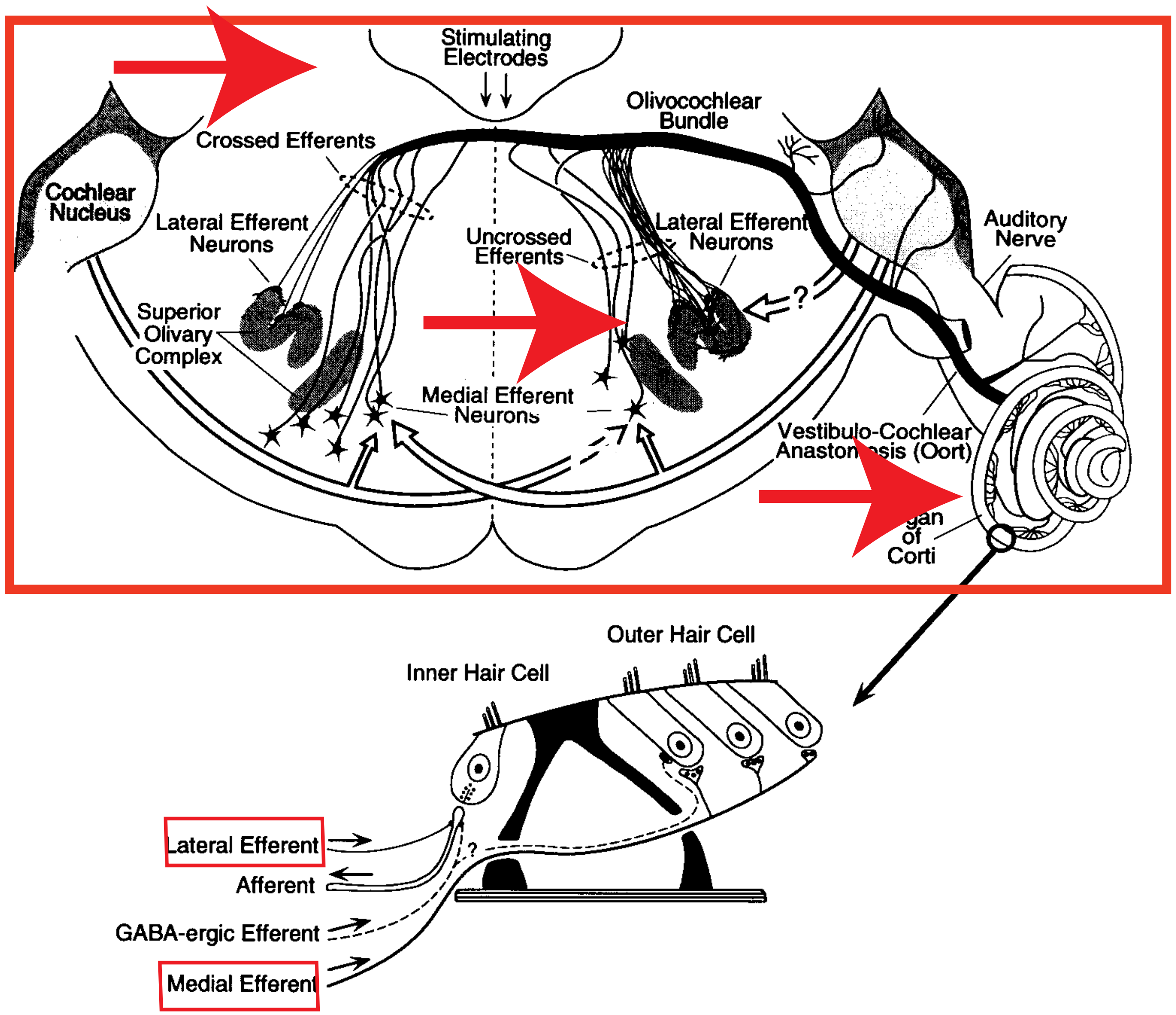
A.K. PhD thesis ETHZ 2003

F.G, T.L. & R.S. PRL 2016

no coupling

coupling

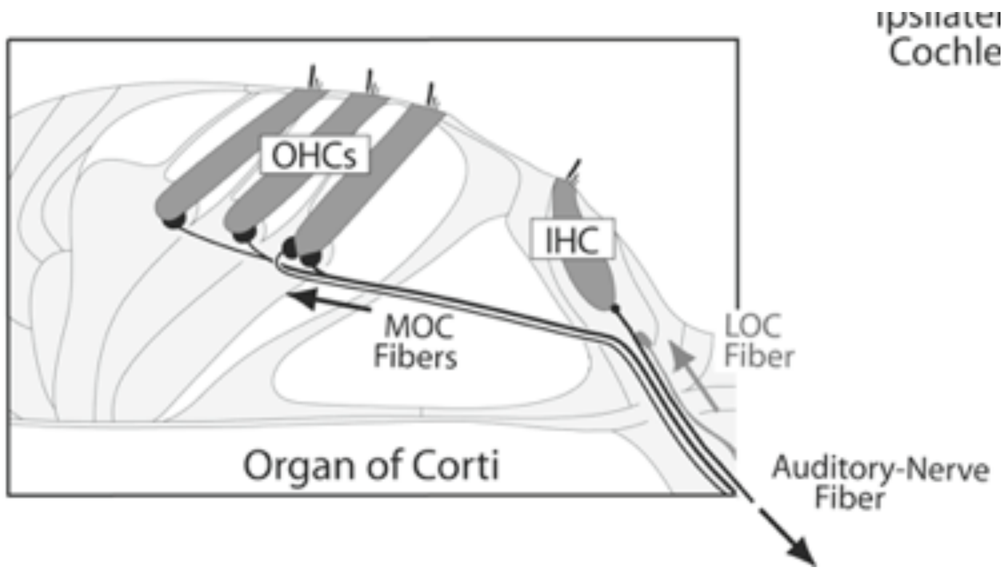
# Anatomical embedding

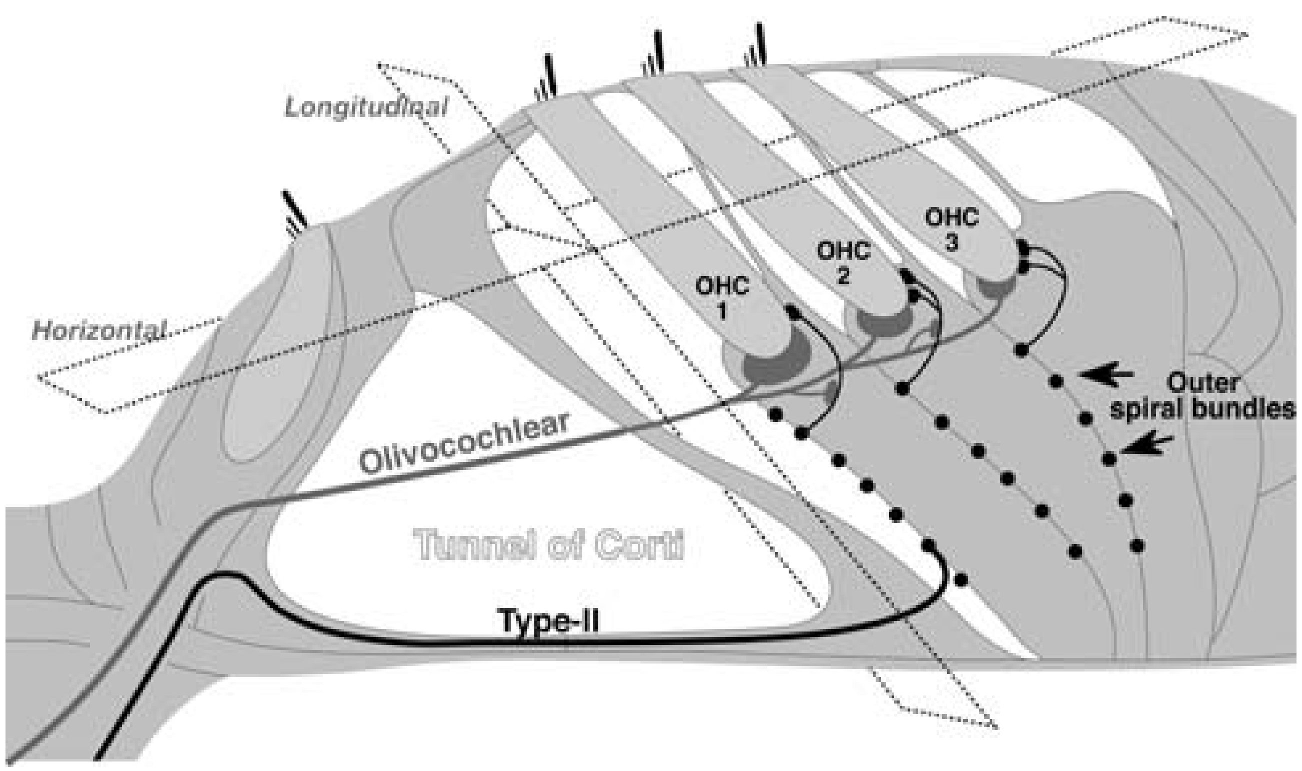



brain

cn (MOC)

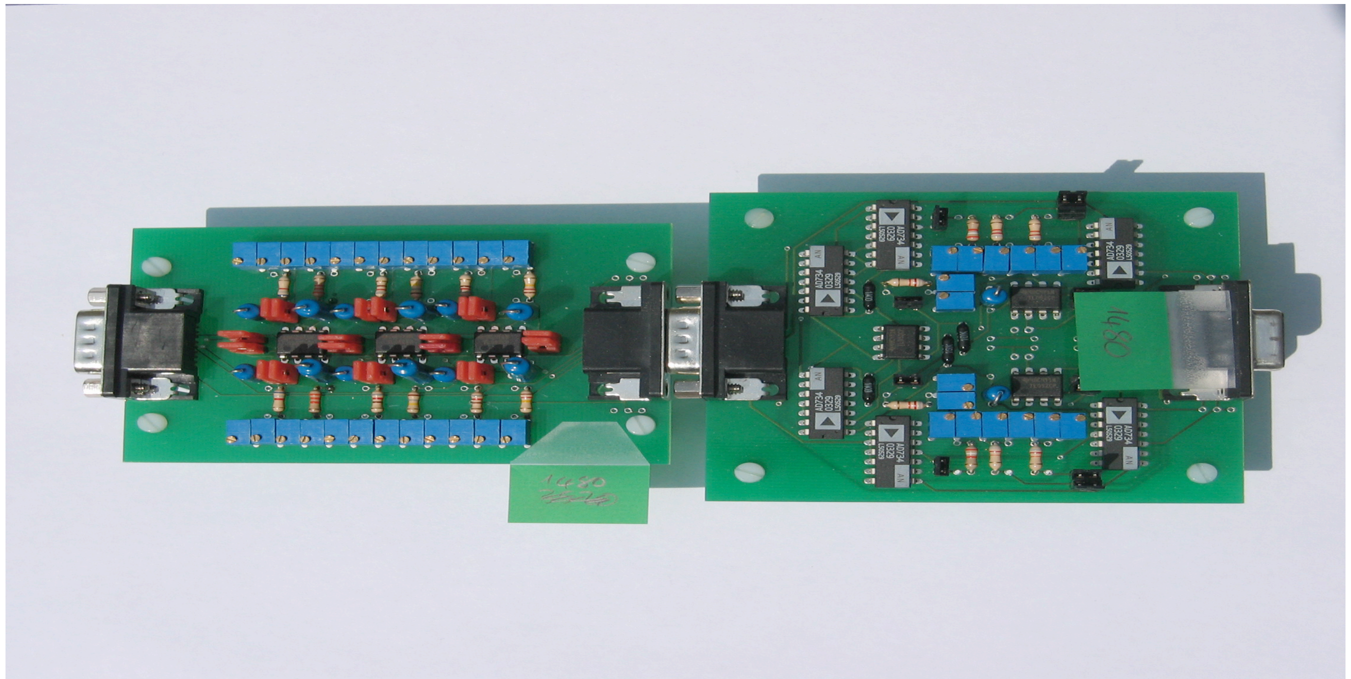
cochlea

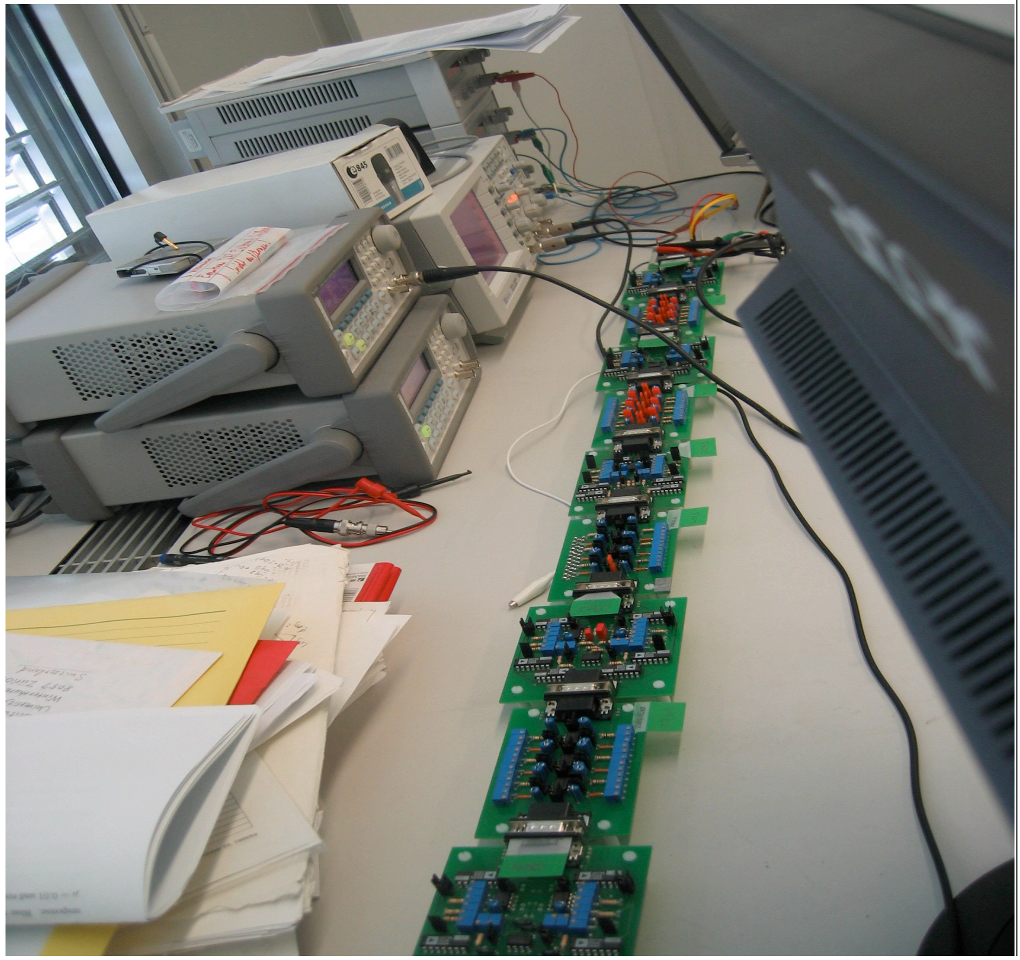


# V Active elements - fluid coupling

## Computational simplification



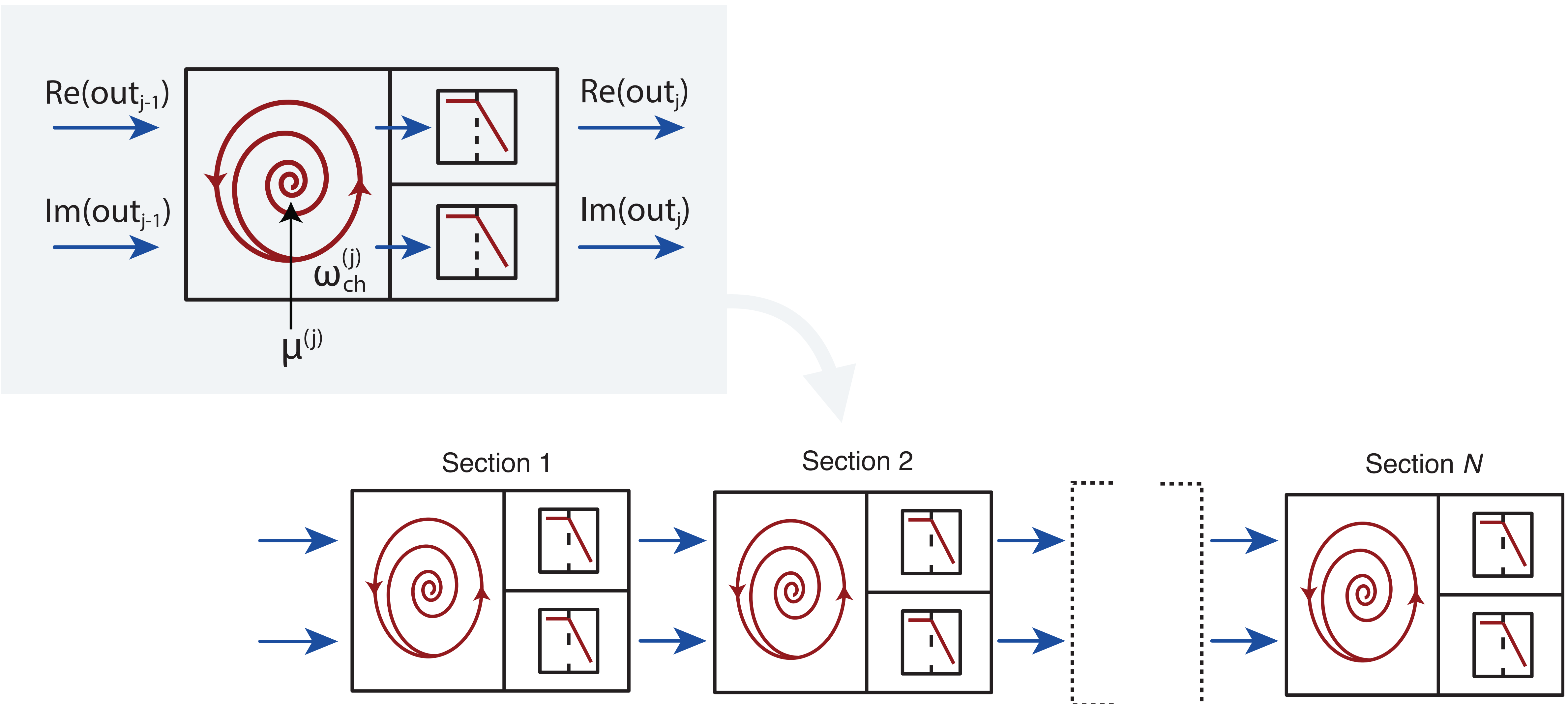


Vyver, Martignoli., R. S. Appl. Phys. Lett. 2008;

US-Patent 2007-2012

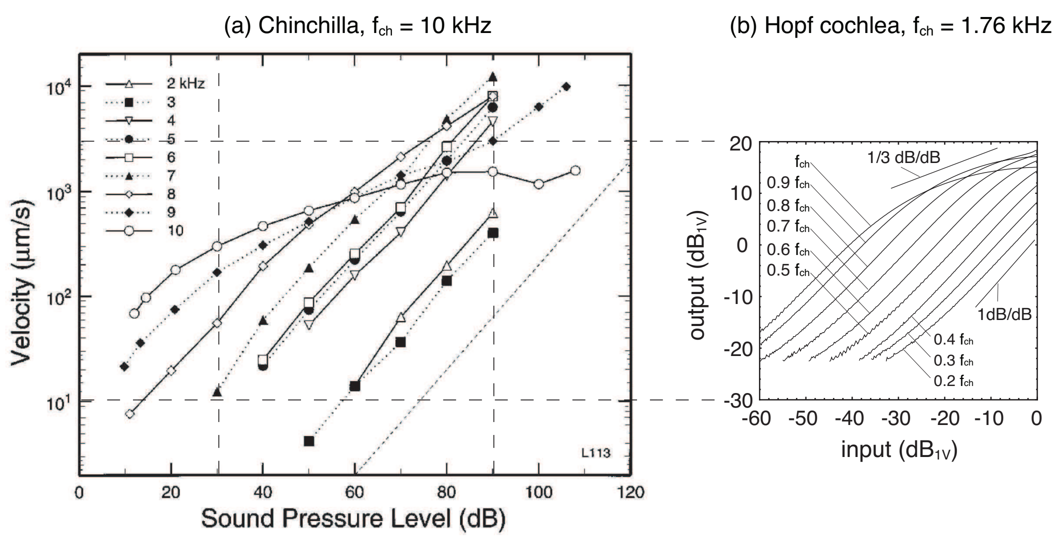
# 'Hopf cochlea'

$$\dot{z} = \omega_{ch}[(\mu + i)z - |z|^2 z + F(t)]; \quad z, F(t) \in \mathbb{C}$$

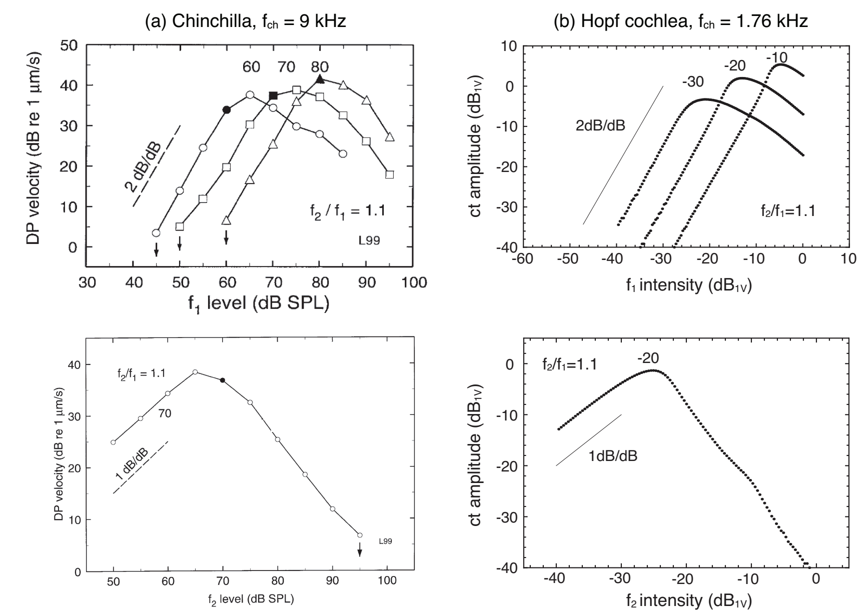



Martignoli, van der Vyver et al. *Appl Phys Lett*, 2007
Martignoli and Stoop *Phys Rev Lett*, 2010
Gomez and Stoop *Nat Phys*, 2014
Stoop and Gomez *Phys Rev Lett*, 2016

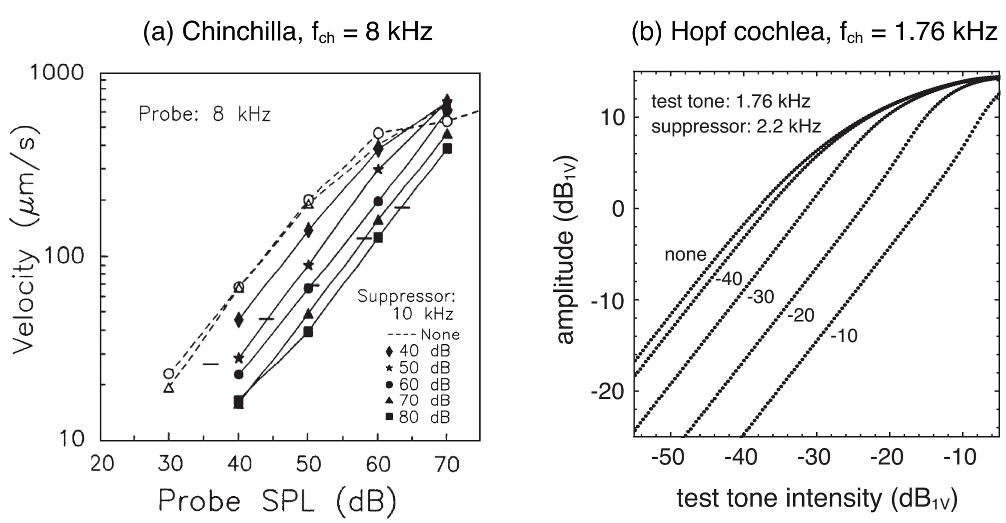
# Results

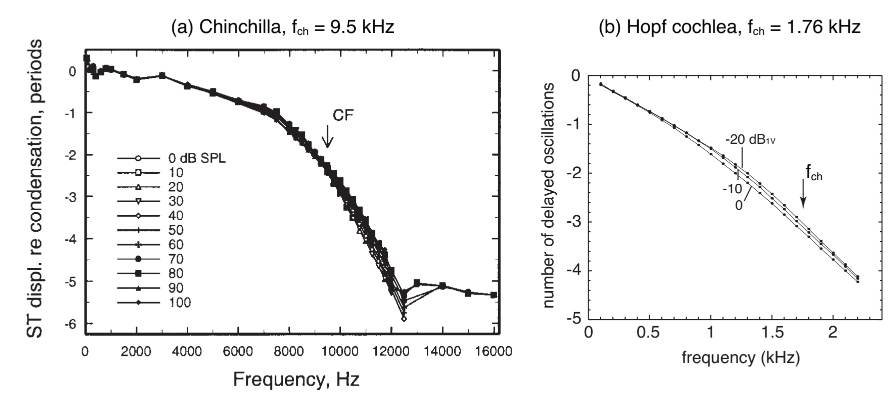



**Compression**: Iso-frequency input-output characteristics.




Amplitude of **combination tones** generated by simultaneous stimulation with two pure tones for (a) chinchilla (b) Hopf cochlea.
Top panels: dependence on $f_1$; bottom panels: dependence on $f_2$.



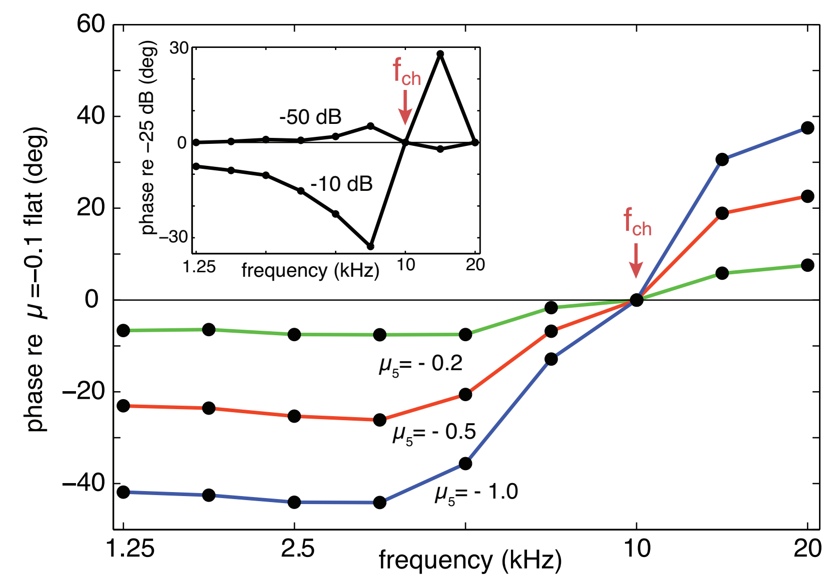




**Phase propagation along cochlea**: (a) chinchilla, (b) Hopf cochlea.

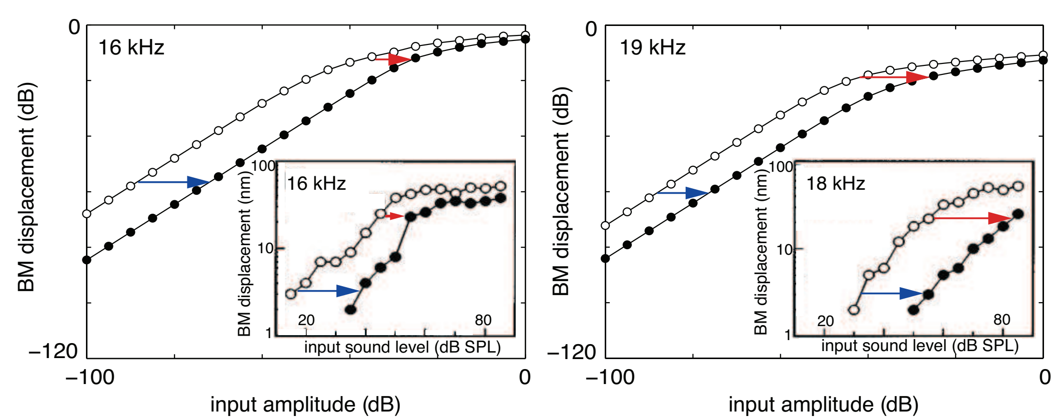
**Mutual suppression by two neighboring tones** ('test tone' and 'suppressor tone'), as a function of their intensity

mostly: Stoop and Kern *Phys Rev Lett*, 2004

# Results



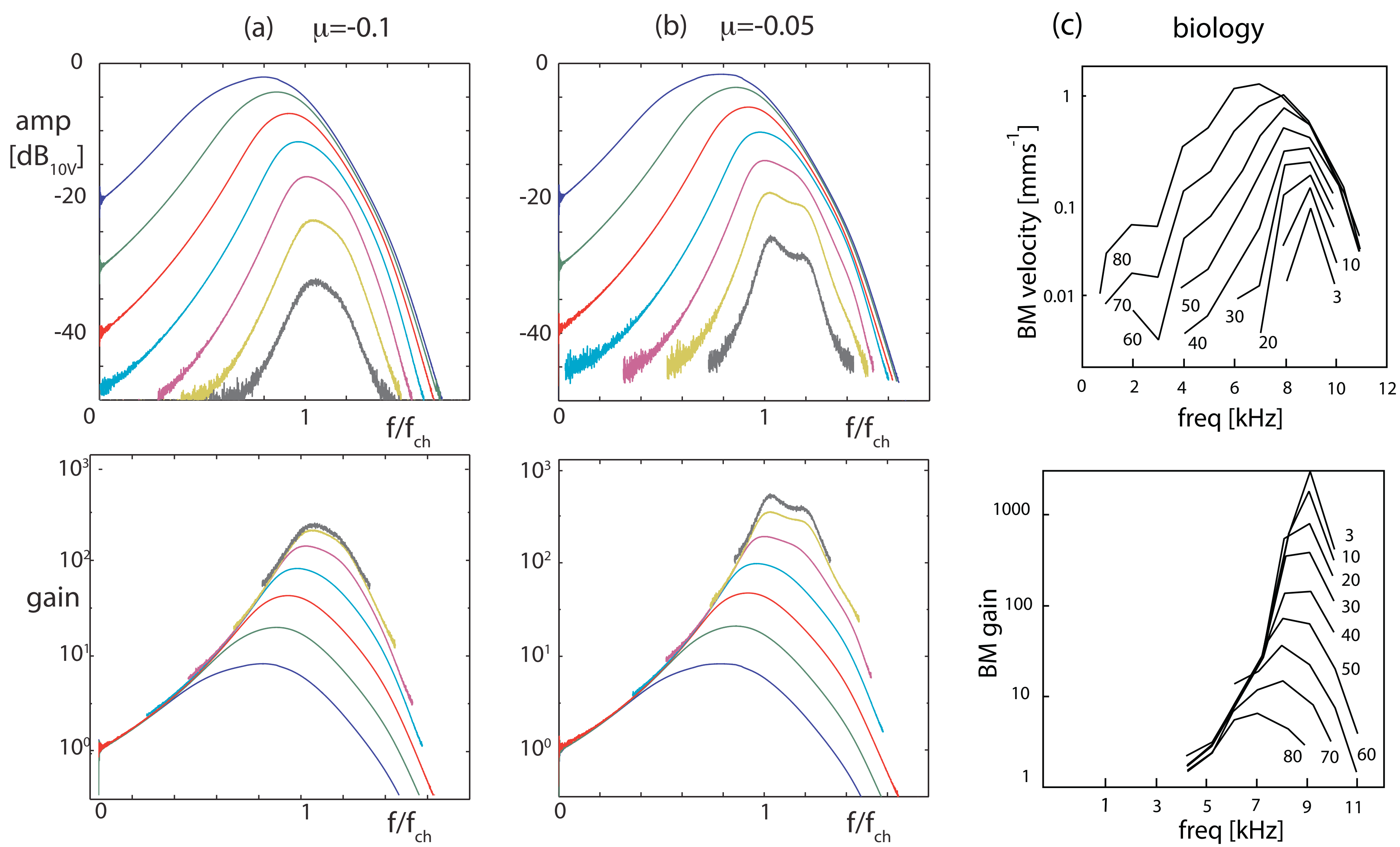

Effect on phase of **medial olivocochlear efferent stimulation**, modeled as detuning of $\mu$ [19]. Phase shift at 5th section ( $f_{ch}$ = 10.42 kHz), $\mu_5$ is tuned away from flat tuning $\mu = -0.1$ (stimulation at -25 dB).




Basilar membrane **shifts** (arrows) at 2nd section, $f_{ch}$ = 16.99 kHz (18 sections, 20 – 1.25 kHz), stimulated by a 16 and 19 kHz (left and right) pure tone. Open circles: Flat tuning ($\mu = -0.05$). Filled circles: medial olivocochlear efferent stimulation; $\mu$ is shifted to $-0.5$.
Insets: Corresponding animal data [20].

**Mostly local properties**

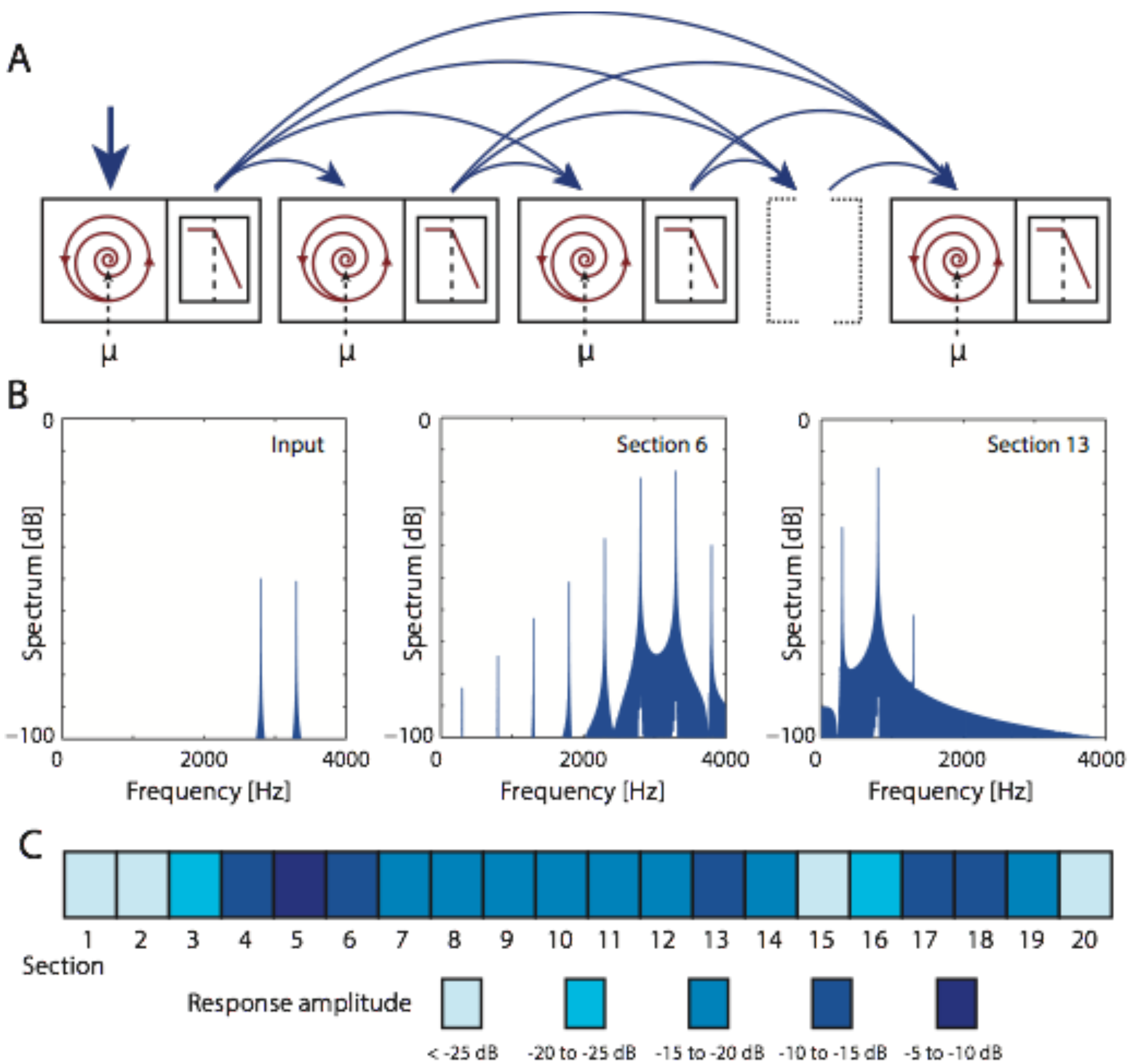
# Distance to bifurcation point / resolution



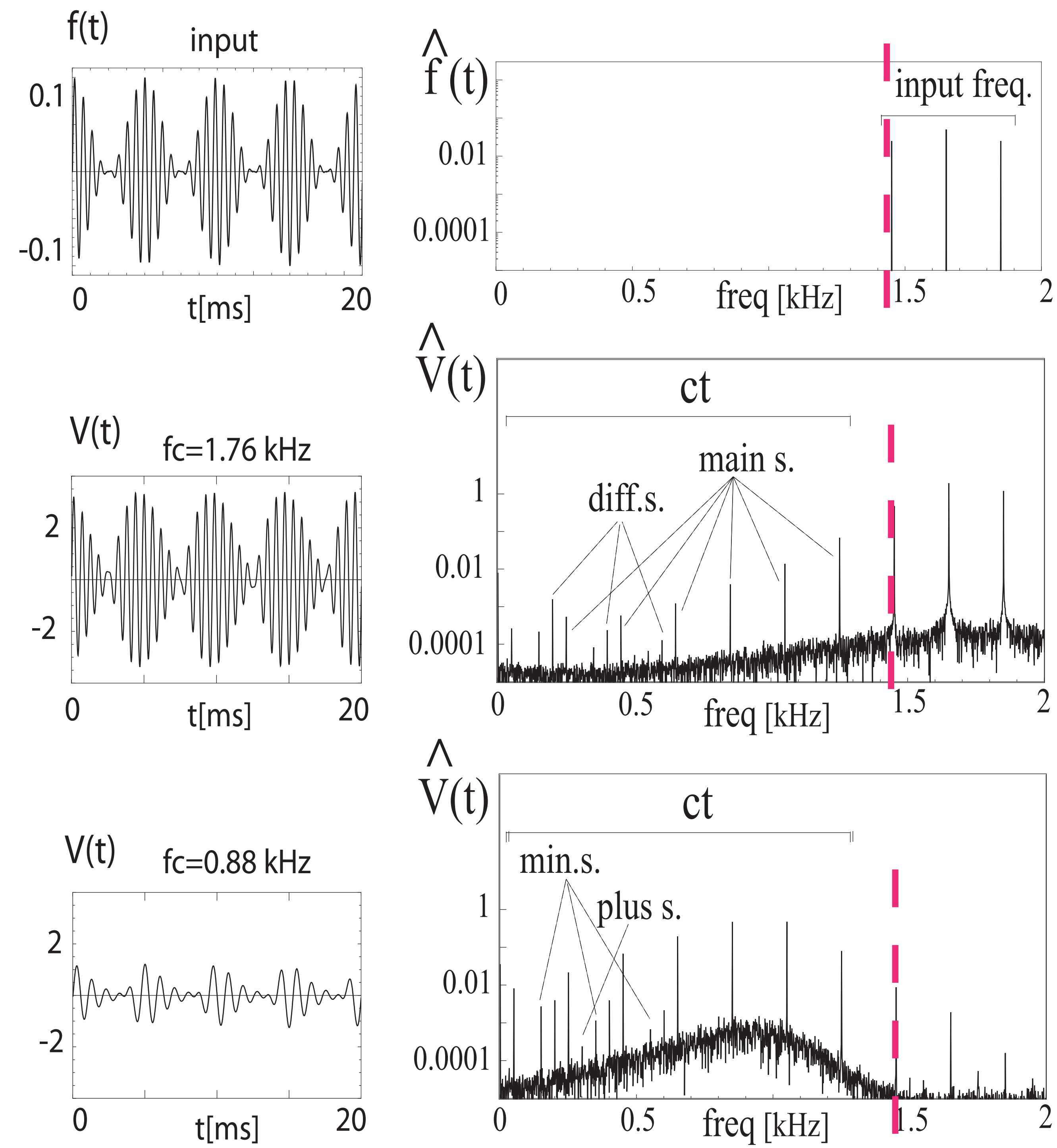

Ruggero, Curr. Opin. Neurobiol. 1992,

# VI Curse of nonlinearity

## simple signals: complex networks!




AM sound with fcar = 850 and fmod = 200 Hz inharmonic am tone f(t), A = 0.1, $f_{car}$ = 1.65 kHz, $f_{mod}$ = 0.2 kHz; waveforms f(t), V(t), Fourier transforms

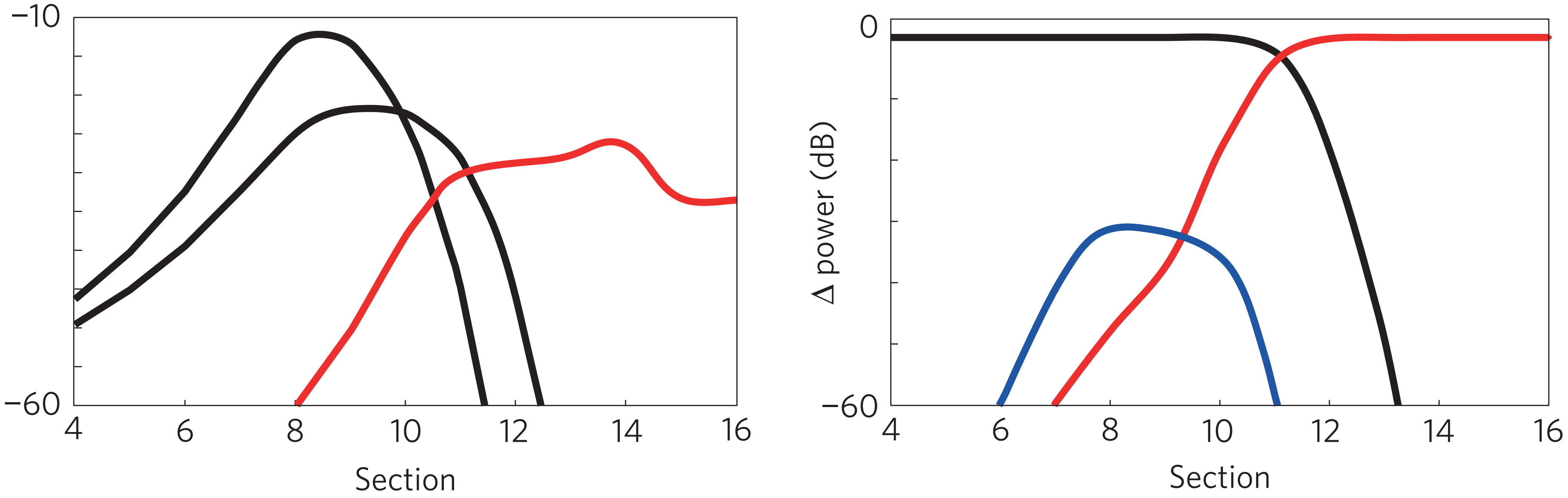



strong ct-generated signal at $f_c$ = 0.88 kHz that classically should be absent!

**(pitch is physical: S.M. & R.S. PRL 2010)**

# Combination tone saliency:

F.G. & R.S.,, Nat. Phys. 2014

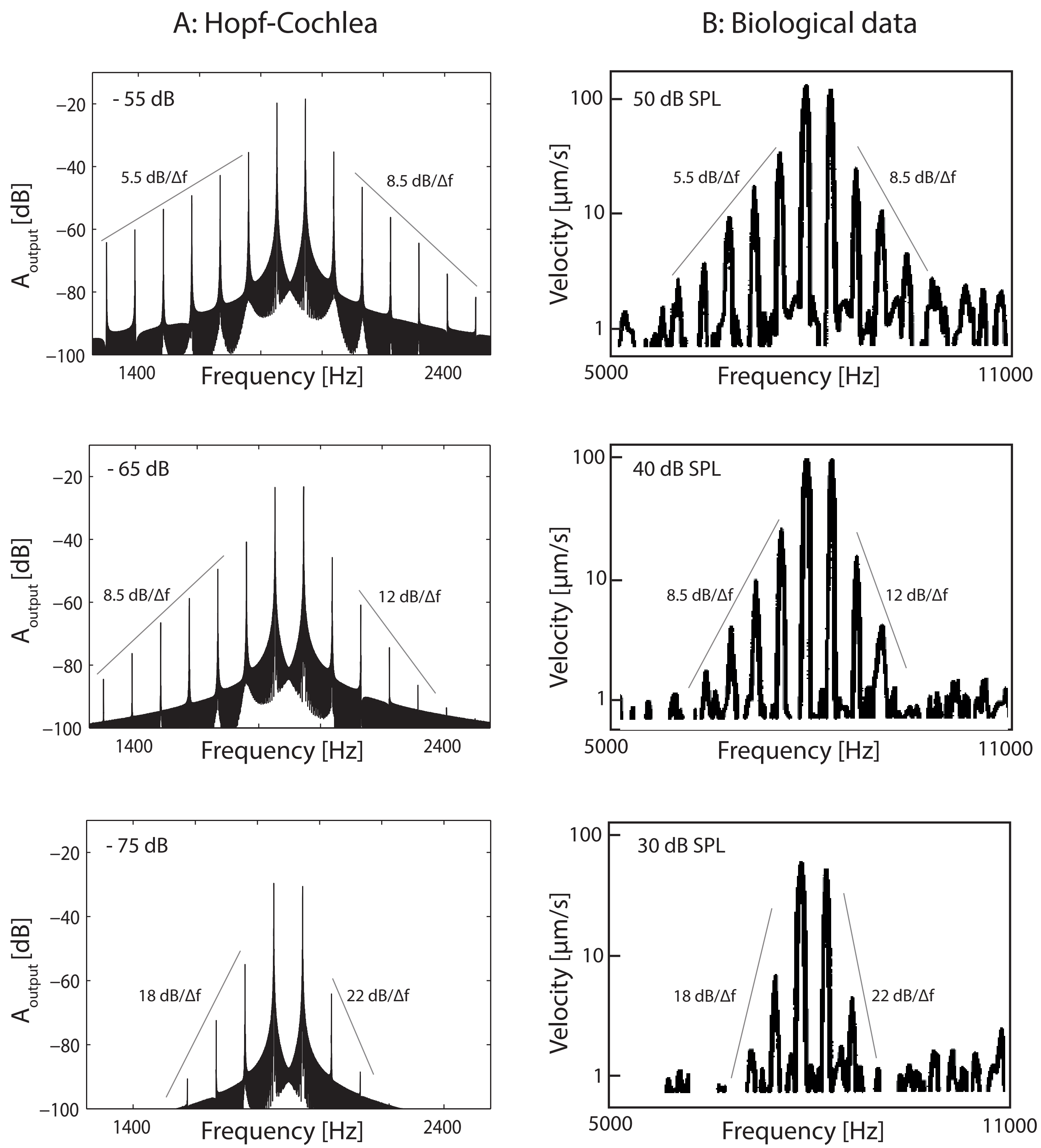



**Cochlear excitation for a complex two-tone stimulation (simulated) :**

**Left panel:** Black curves: signal power of frequencies $f_2$ and of $f_1$.
Red curve: sum of lower CT ($f < f_1$ ).

**Right panel:** Black curve: added signal power from frequencies $f_1$ and $f_2$ .
Red curve: signal power of lower CT.
Blue curve: signal power of higher CT ($f > f_2$ ) relative to the total signal power.

# Combination tones:



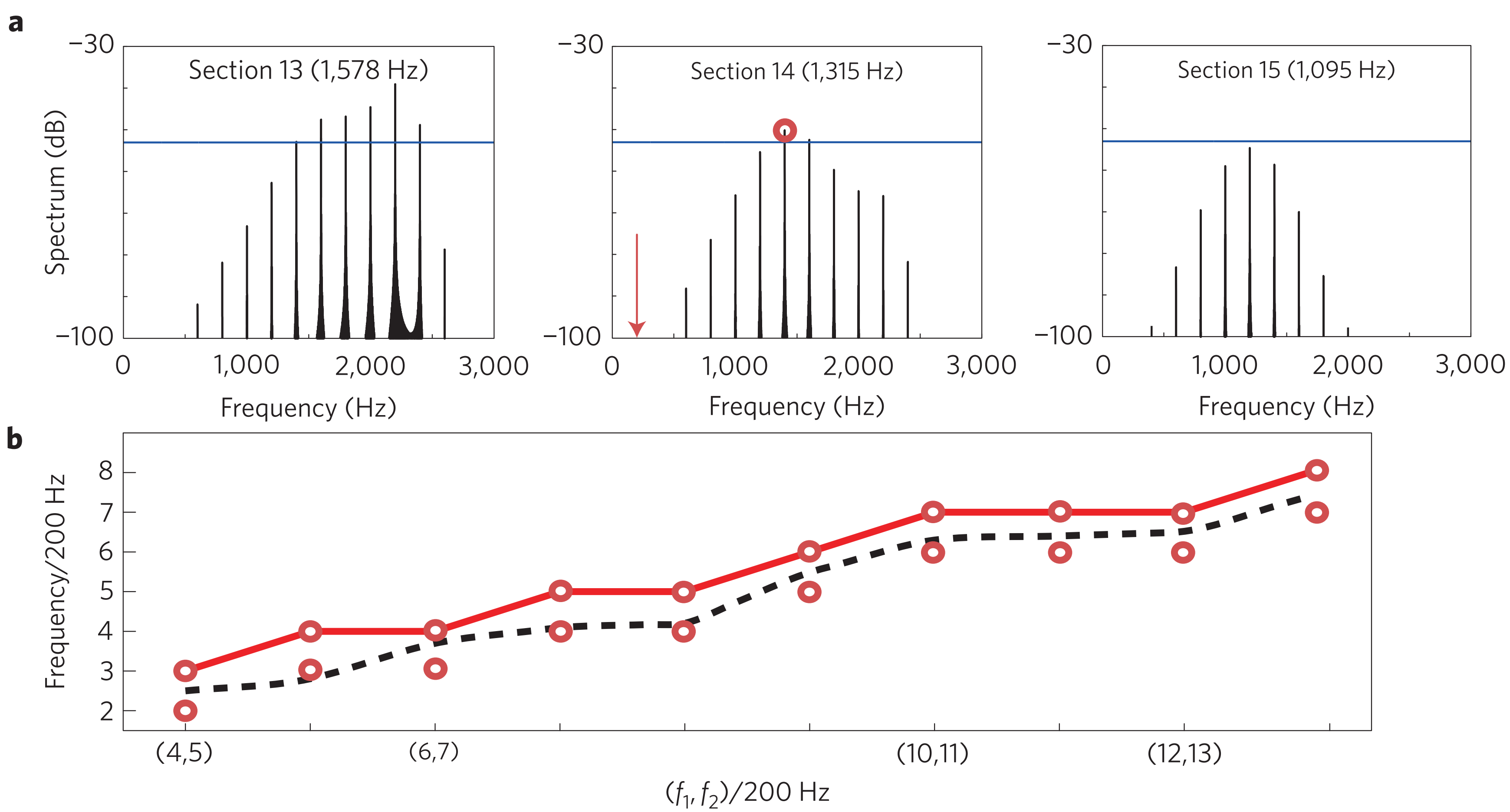

Spectrograms of basilar membrane responses to two-frequency stimulation of different amplitudes ($f_2/f_1$ = 1.05 and $2f_2–f_1$ = $f_{ch}$)

**Left:** Hopf-cochlea model, 17 sections, 3520 to 220Hz (output of 5th section, $f_{ch}$ = 1760 Hz).

**Right:** Biological data ($f_{ch}$ = 7500 Hz).

Place of measurement on the tonotopic map and choice of Hopf-cochlea section comparable (roughly one octave from cochlear base).

# Where is the pitch read off ? Smoorenburg:




a) Spectra for two-tone stimulation (−74 dB, $f1$ = 2200 Hz, $f2$ = 2400 Hz) at three cochlea sections. The lowest audible combination tone (CT) (hearing threshold: −53 dB, blue line) is the response at 1400 Hz (section 14, circled). The perceived pitch is the **residue pitch** (red arrow) associated with the spectrum at this location.

b) Psychoacoustical lower hearing frequency limit of CTs (dashed black line).
Simulation: Lowest CTs above the implemented amplitude threshold (solid red line) and highest CTs below the limit (unconnected red circles). The three characteristics differ by less than the section width.

# Smoorenburg's pitch-shift experiments (1970)

## First pitch-shift effect

AM-sound at fixed $f_{car} = 800 + df$,
$f_{mod} = 200$ Hz, noise level = 0.07

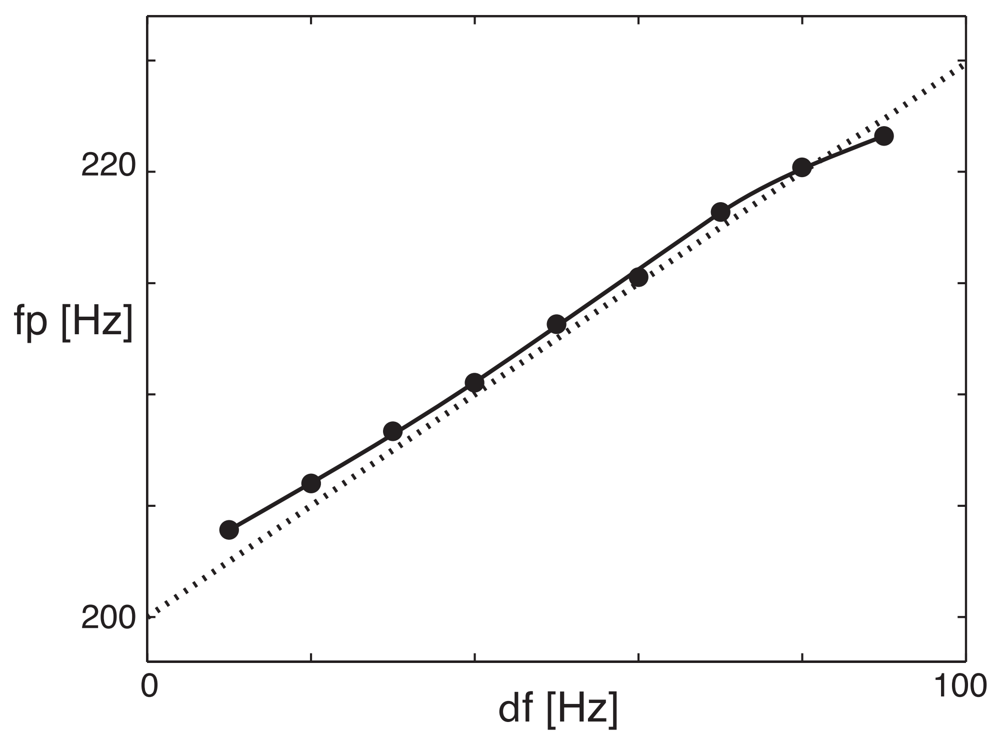
dotted line $f_p = 200 + df/4$ Hz: first pitch shift formula
bullets: measurement at one cochlea section,
match human perception

$$\boxed{\begin{array}{l} f1 = k\ fo + df, \\ f2 = (k+1)\ fo + df \end{array}}$$

leads to

$$\boxed{fp = fo + df / (k+1/2)}$$

first pitch shift formula,
basend on simple physics

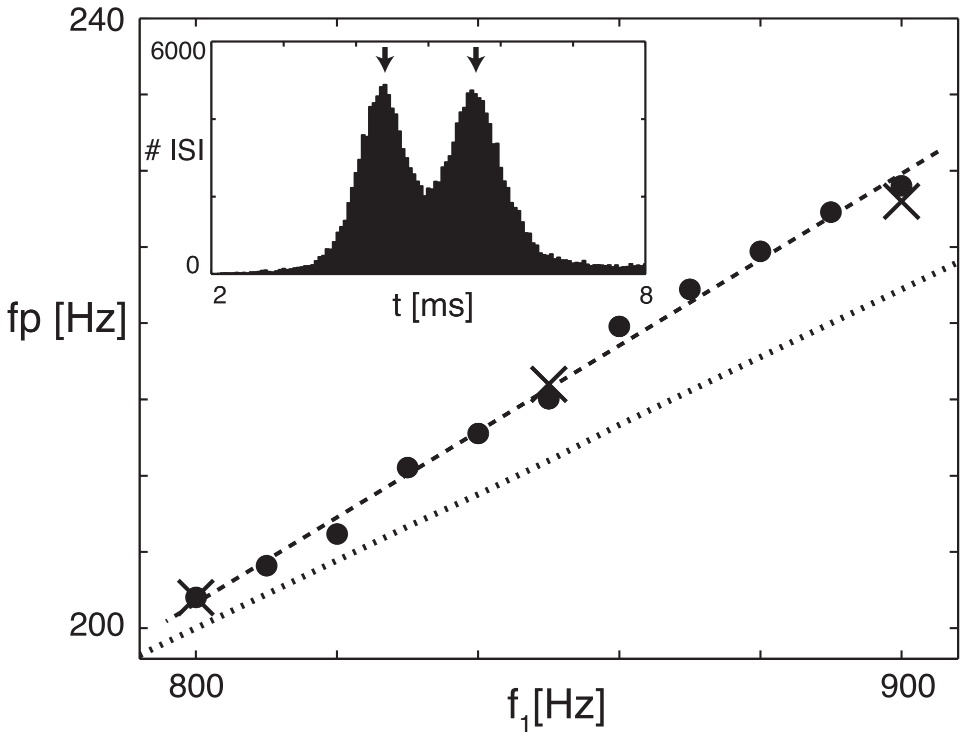



correct variation with df

# Second pitch shift effect

Two-frequency stimulation $f_1$ and $f_2 = f_1 + 200$ Hz, cochlea output at $f_c = 622$ Hz (second pitch shift effect): psychoacoustic data (crosses), measured data (full dots)

Inset: ISI-histogram for $f_1 = 900$ Hz, showing $f_p$ for $k = 4$ (left peak, for the rightmost cross) and for $k = 5$ (right peak, cross at $f_p < 178$ Hz)



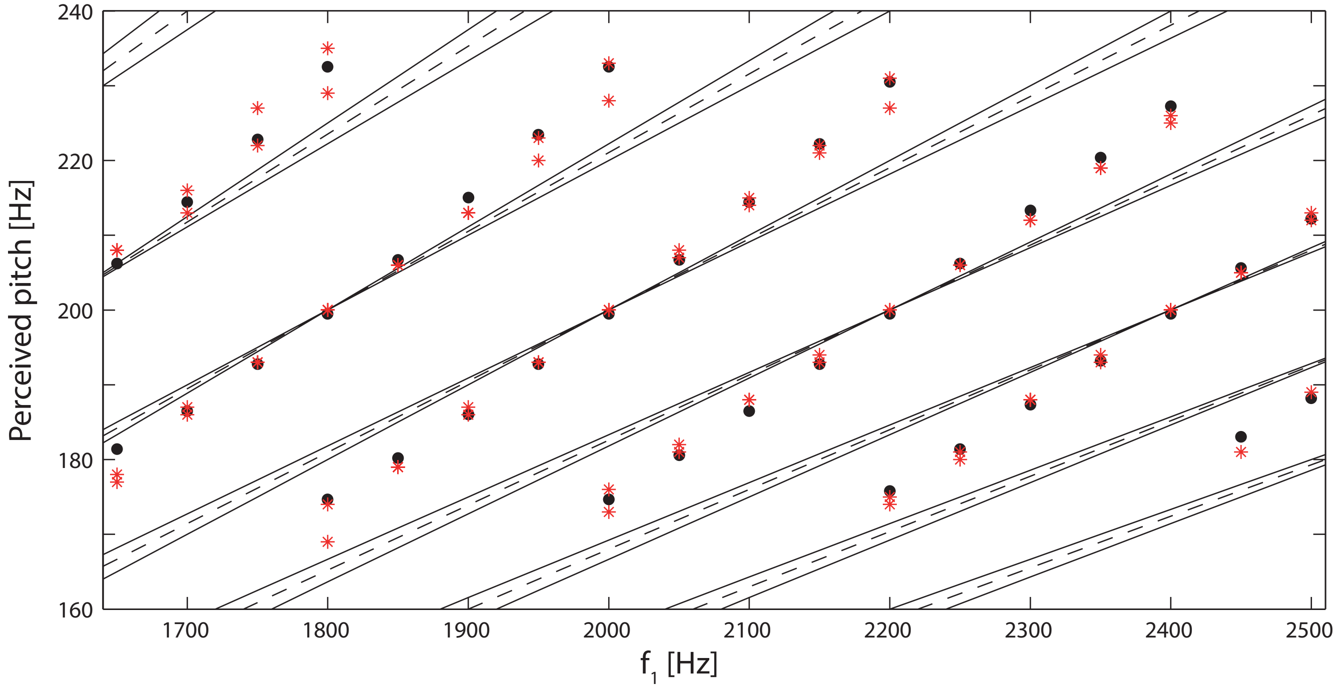

**second pitch shift**

**first pitch shift law $f_p = (f1 + f2)/(2k + 1)$, $k = 4$, coherently violated**

**Inset: ISI-histogram end of auditory nerve (S.M., F.G. & R.S. Sci. Rep. 2015)**

# Second pitch shift:

## red: psychophysical experiments; black: model




Two-frequency stimuli with $f_2 = f_1 + 200$ Hz.

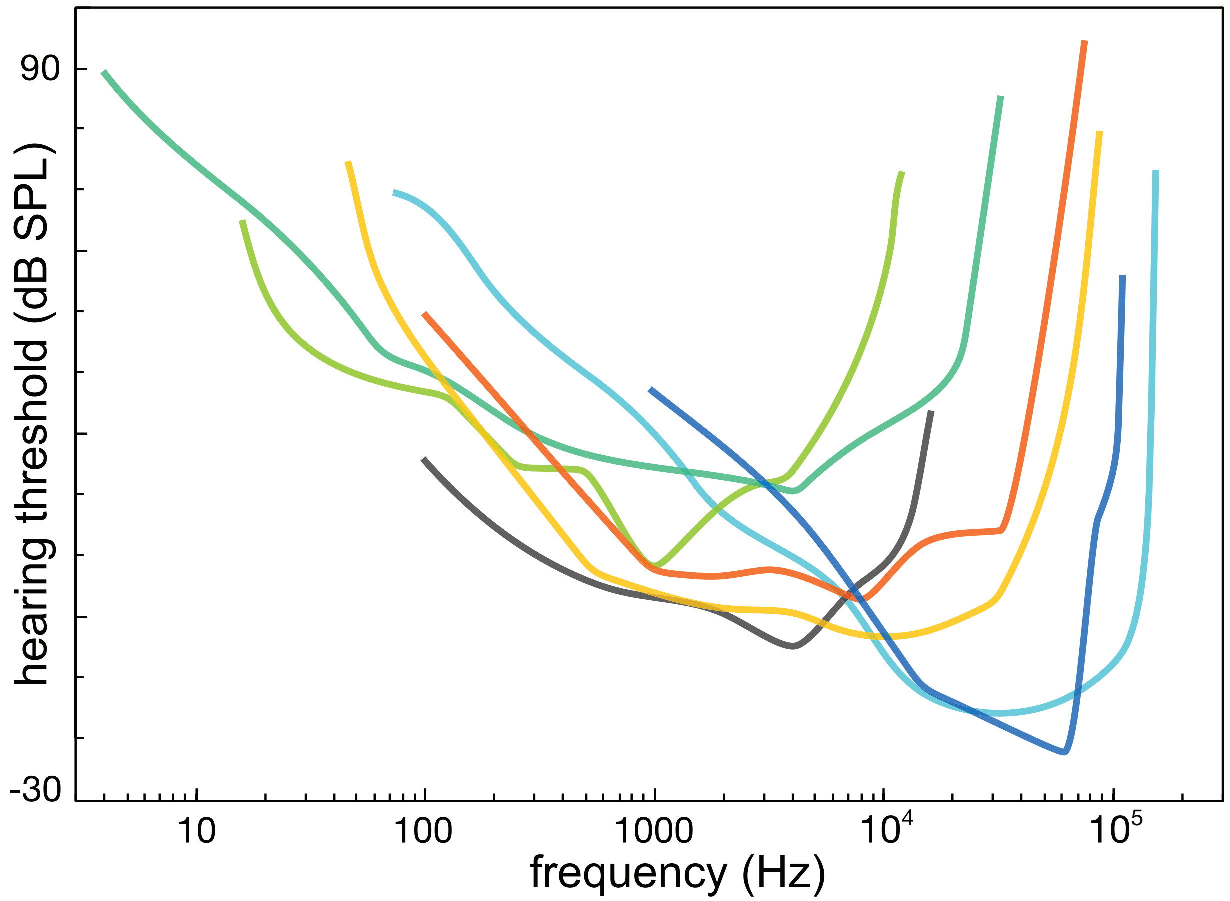
**Red**: Psychoacoustic data (partial amplitudes 40 dB SPL)
**Black**: Hopf cochlea simulation (7th section with $f_{ch}$ = 1245 Hz, partial amplitudes -63 dB).
**Solid lines**: classical predictions of the perceived pitch.

: solves Ohm-Seebeck dispute !

**second pitch shift due to cochlear fluid: F.G. & R.S. Nat. Phys. 2014,**
**requested slight 'tuning' of the Hopf amplifiers (no-flat tuning of Hopf parameters)**

# VII Hearing threshold

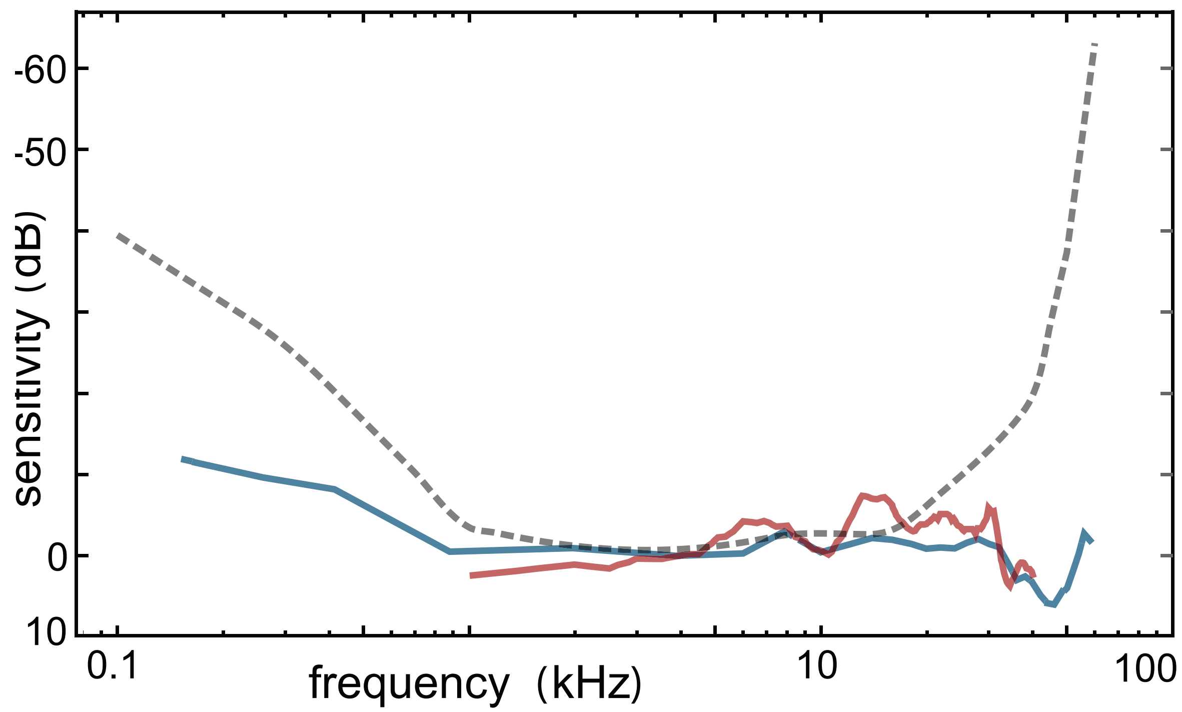
## Animal evidence (nonspecialists)




**Dogma : Frequency dependence of the hearing threshold is exclusively determined by outer and middle ear**

Behavioral audiograms: prairie dog [23], elephant [24], lemur [25], domestic cat [26], human psychoacoustial hearing threshold [4], white-beaked dolphin [27] (smoothened data), false killer whale [28], from top to bottom, sorted by the curves' minima.
Full extension of the audiogram not accessed in all cases.

# Animal evidence

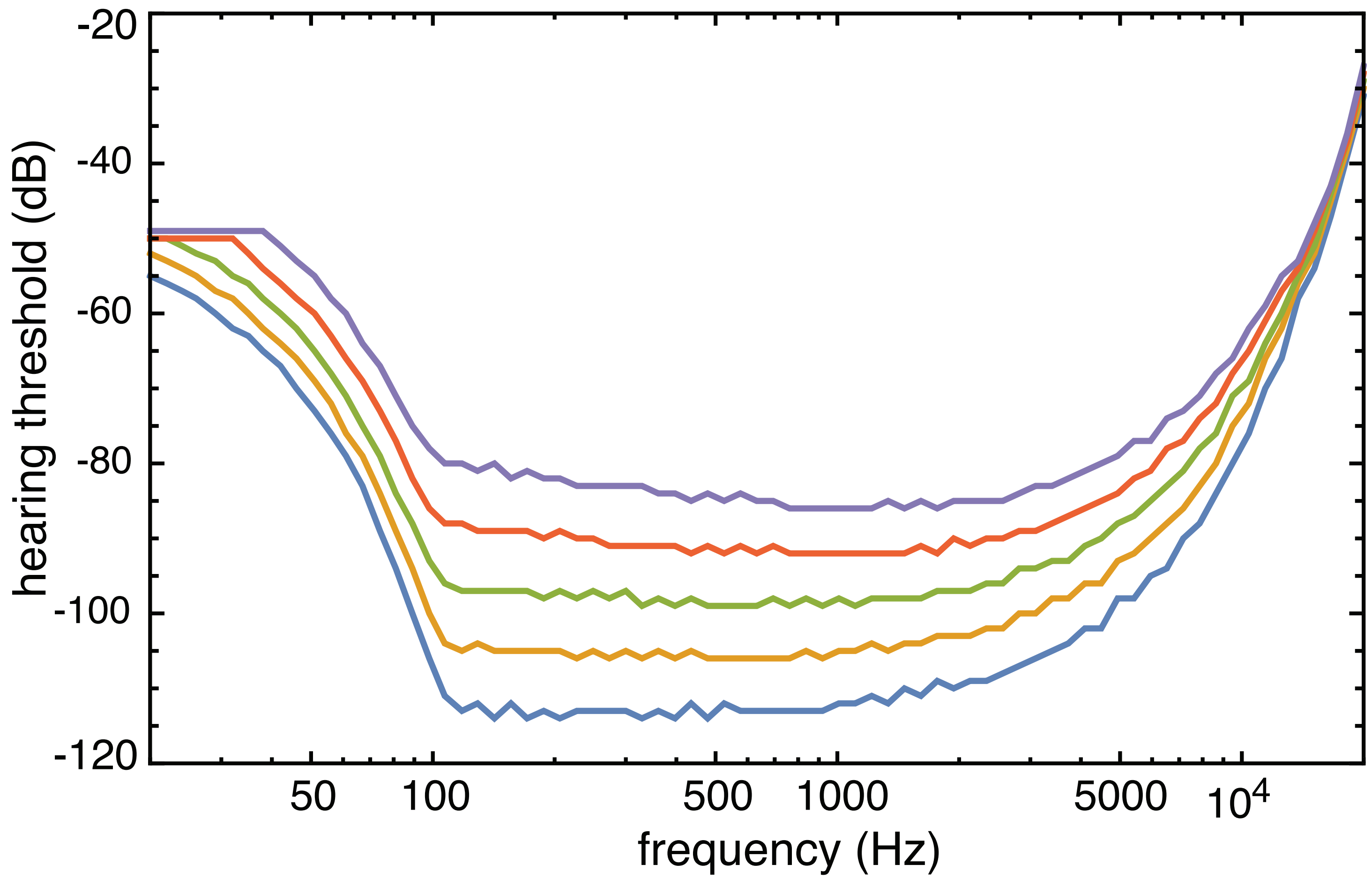



Ruggero and Temchin 2002

Outer-middle ear transfer functions, Mongolian gerbil.
Dashed: Behavioral hearing threshold.
Blue: Pressure in scala vestibuli near stapes footplate.
Red: Stapes velocity.

# What could the inner ear contribute?

## flat-tuned cochlea:



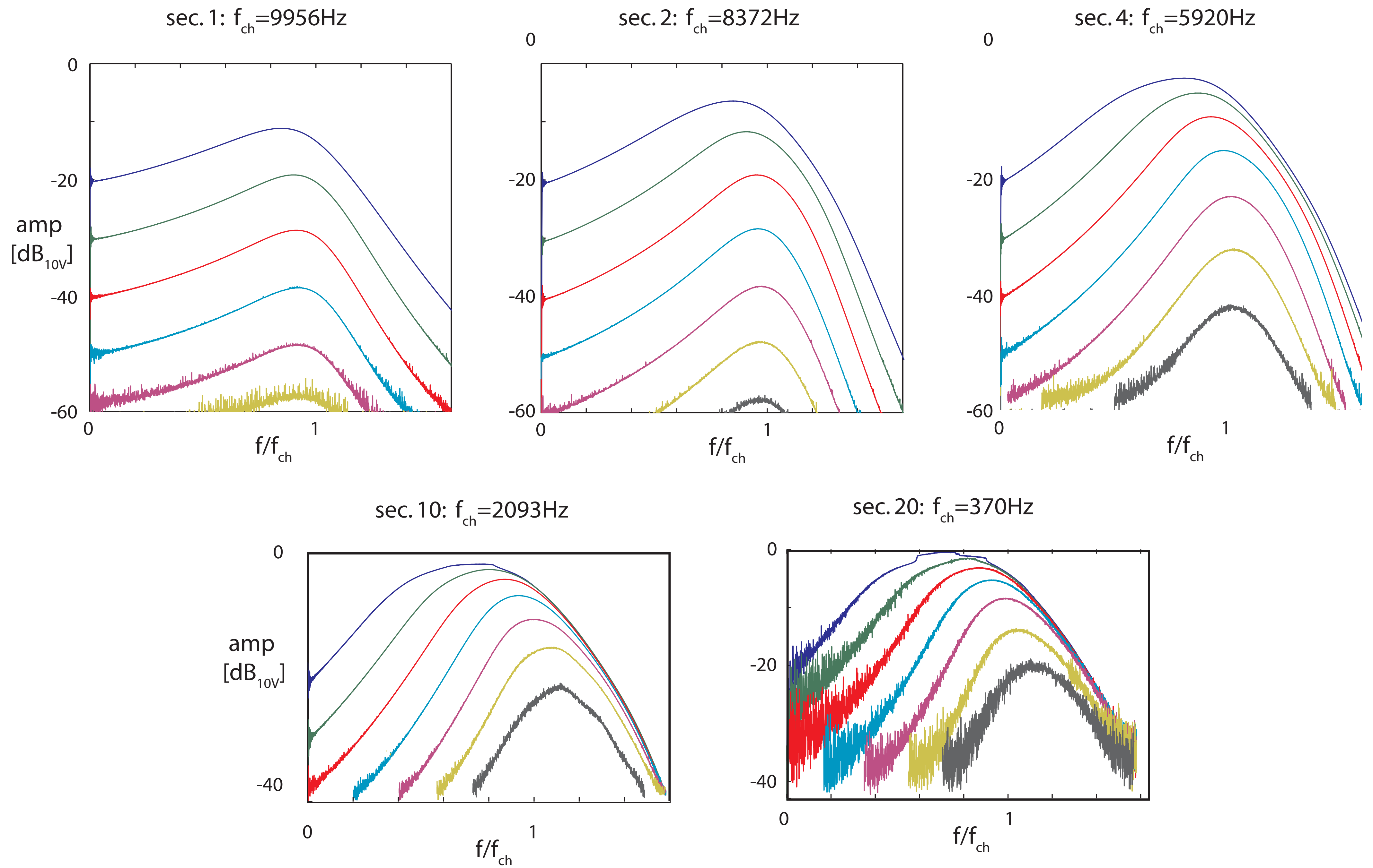

**flat tunings: $\mu^{(j)}$ = constant**

Hopf cochlea with N=29
$f_{ch}$ = 110…14080 Hz
$\mu^{(j)}$ is the same for all sections:
$\mu^{(j)} = -0.40$
$\mu^{(j)} = -0.35$
$\mu^{(j)} = -0.30$
$\mu^{(j)} = -0.25$
$\mu^{(j)} = -0.20$

**F.G., K.K., T.L. & R.S. submitted**

1. Response of section j is defined as $R_j = 20\log_{10}[(\max(\mathrm{Re}(out_j))]$
2. The maximal response of Hopf cochlea is $R_{max} = \max(\{R_j : j = 1,2,\ldots,N\})$
3. *Hearing threshold* of a pure tone stimulus $F(t) = A\exp(-i2\pi ft)$ : defined as the input level $L = 20\log_{10}[A]$ that gives rise to $R_{max} \simeq -50$ dB
4. 0 dB SPL input in experiments corresponds to -114 dB input to Hopf cochlea

# Change of profile as in nature ?



## Kern 2003: *Detune* Hopf parameters towards apex !

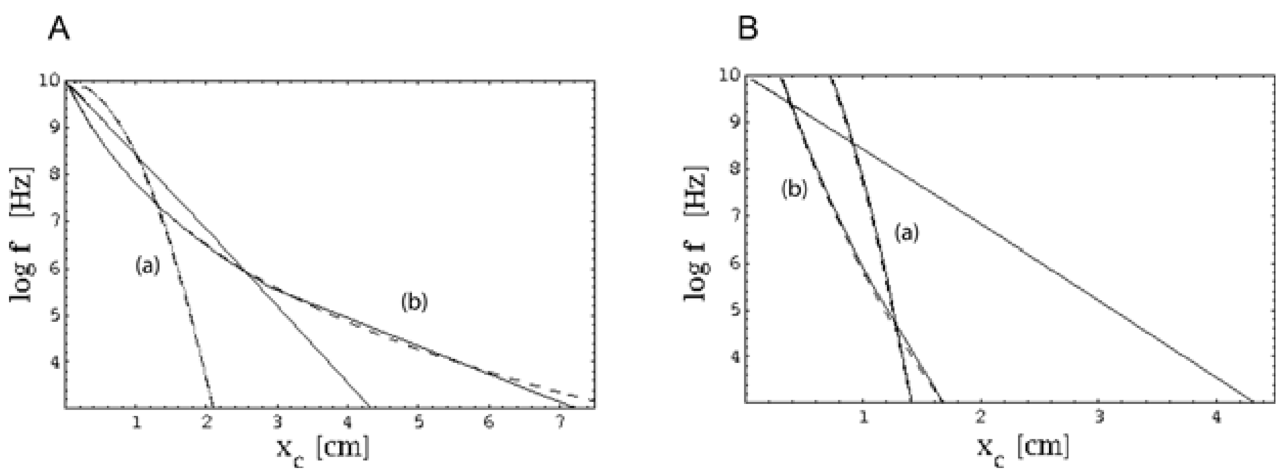
### Theorem

(I) Space-dependent or -independent increase/decrease of $\rho$, $\nu$, and $m$ result in left-/right-shifts of the TM.

(II) A change of the transversal stiffness exponent from $\alpha x$ into $\alpha' g(x')$, with $g(x)$ invertible but otherwise arbitrary, affects the TM as follows (with $\eta$ as in Equation 10):

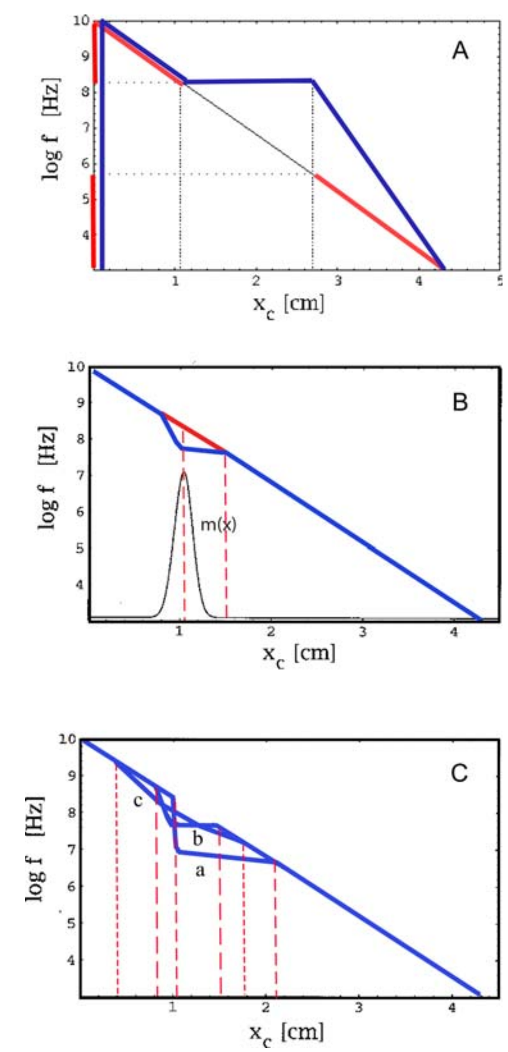
$$x'_c(\omega) = g^{-1}\left(\frac{\alpha}{\alpha'}\frac{\ln(f)-\eta}{\mu} - \frac{1}{\alpha'}\ln\left(\frac{E_0}{E'_0}\right)\right). \qquad (12)$$

$\nu, \rho, m$ : fluid kinematic viscosity,
cochlear fluid density,
BM mass density




Analytical prediction (dashed) and corresponding numerical evaluation (solid).

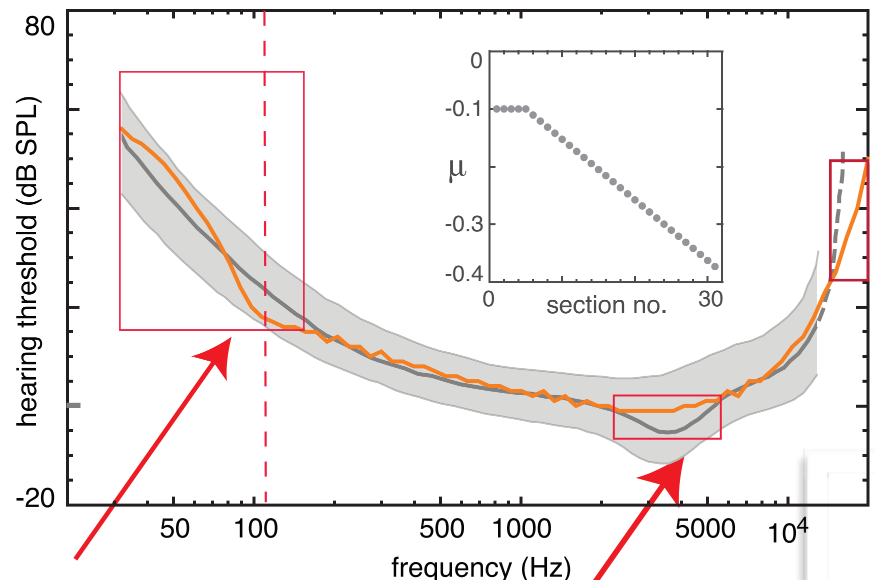
R.S. & al. PLOS Comp. Biol. 2008




'Remapping' the tonotopic map

# Tuning of amplifiers

$\mu^{(j)}$ detuning as in Smoorenburg

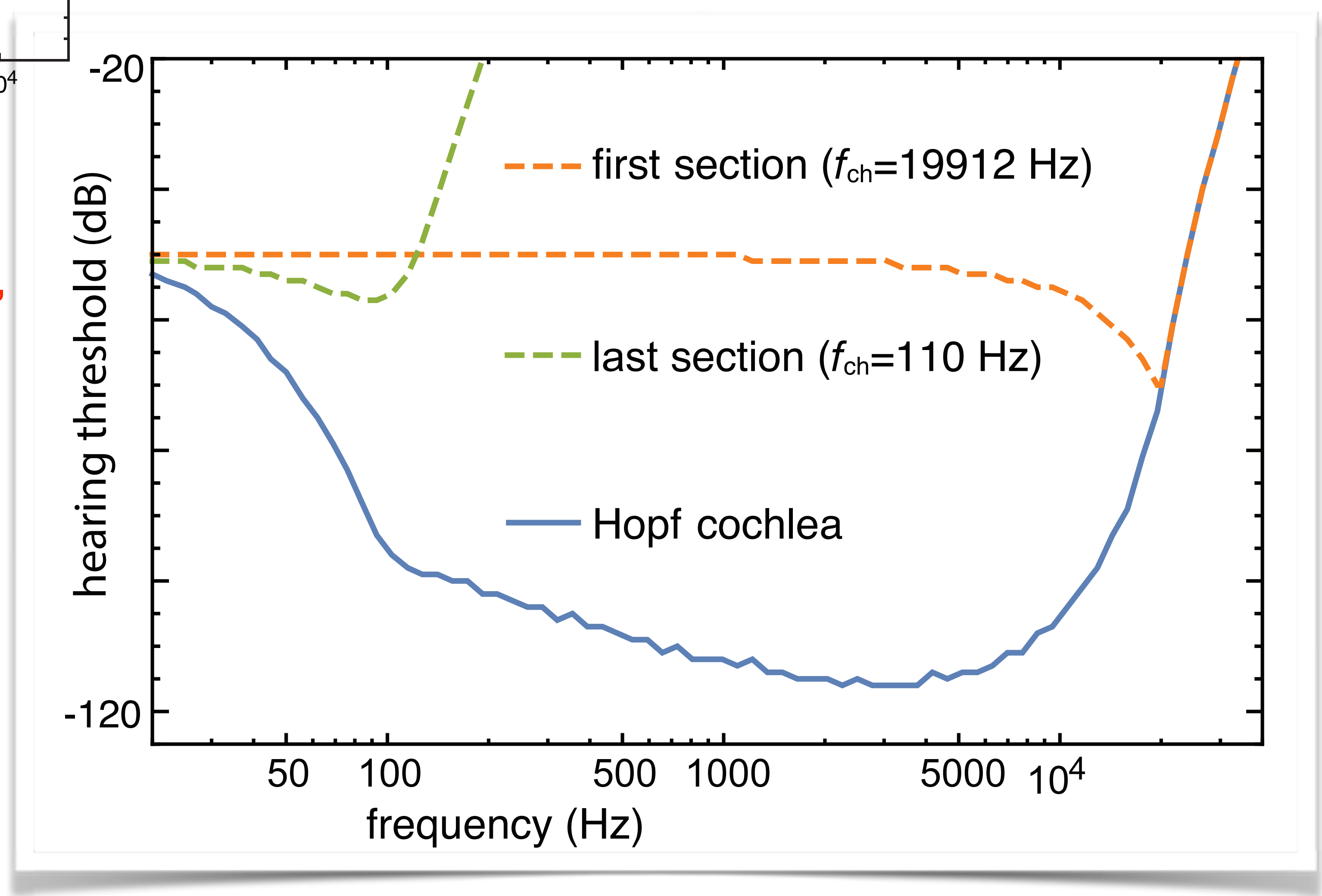



**no data available**

**gray: human variability (Fastl / Zwicker 2007)**

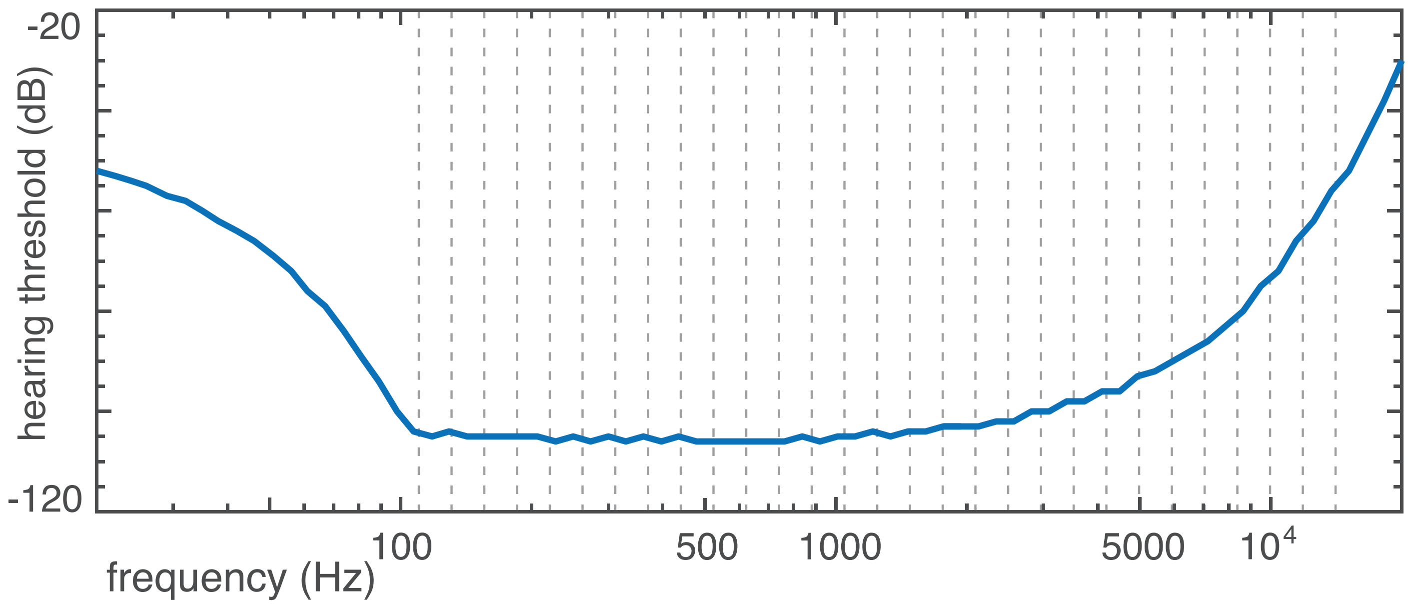
**discretization effect**

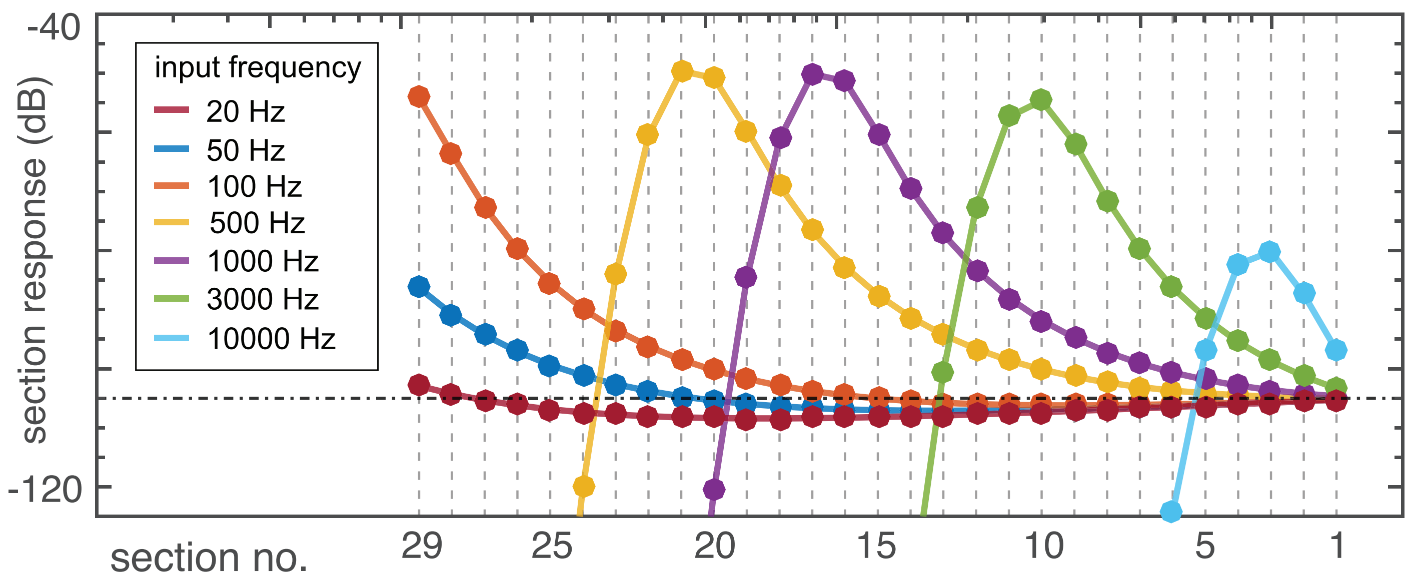
**resonance middle/outer ear: <10 dB, around 4000 Hz (Shaw 1974): Perfect agreement**




contradiction to schoolbook wisdom ..

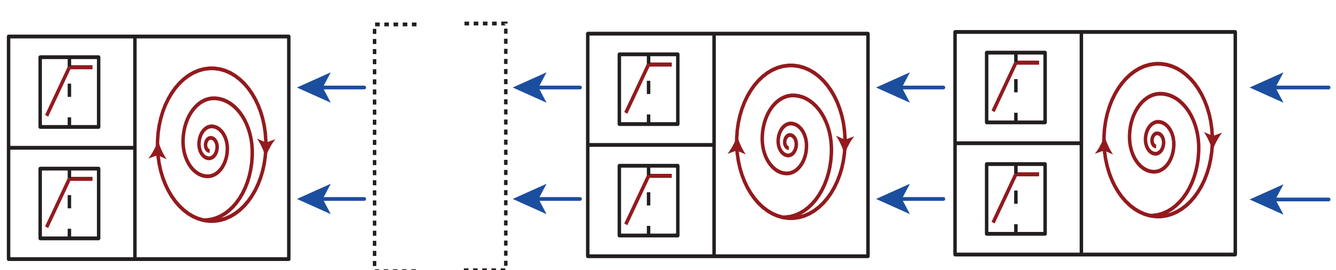
# Collective amplification (untuned)



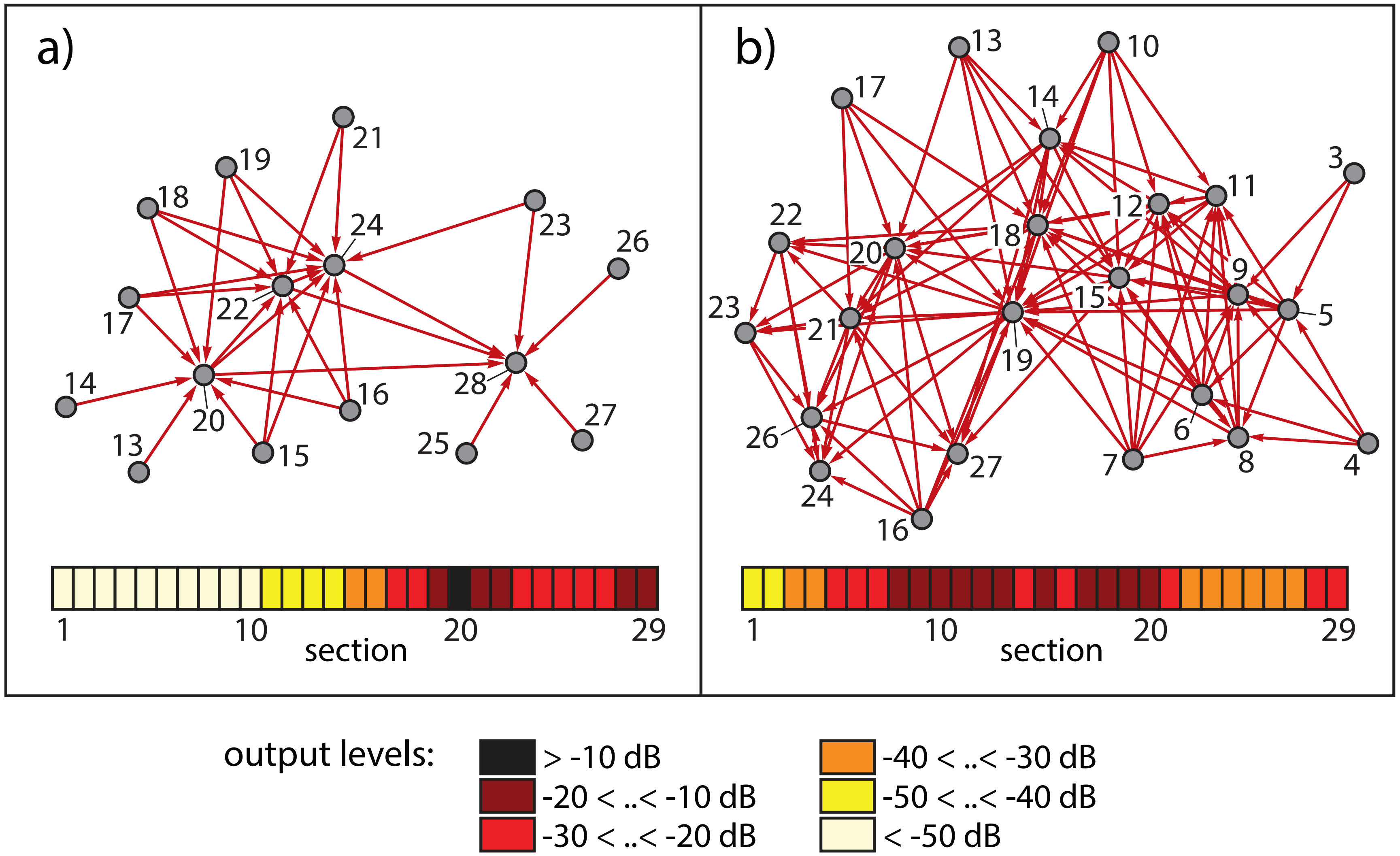




Hopf cochlea with N=29
$f_{ch}$ = 110…14080 Hz

**blue:** Hopf cochlea
$\mu^{(j)}$ = -0.25 for all sections



# VIII Activation networks are the signal..




a) two pure tones input (3/8, 1/2 kHz)

b) two complex tones (2, 3.35 kHz, with 5 harmonics each)

Cochlea: 29 sections, covering (0.11, 14.08) kHz on a logarithmical scale; $\mu$=-0.25 at all sections; input: -60 dB each tone.
Upper: Activated networks (='above hearing threshold'), lower: corresponding activations on the unrolled cochlea.

**(R.S. & F.G. PRL 2016)**

## Build-up of a cochlear network:

# Hearing @ criticality?

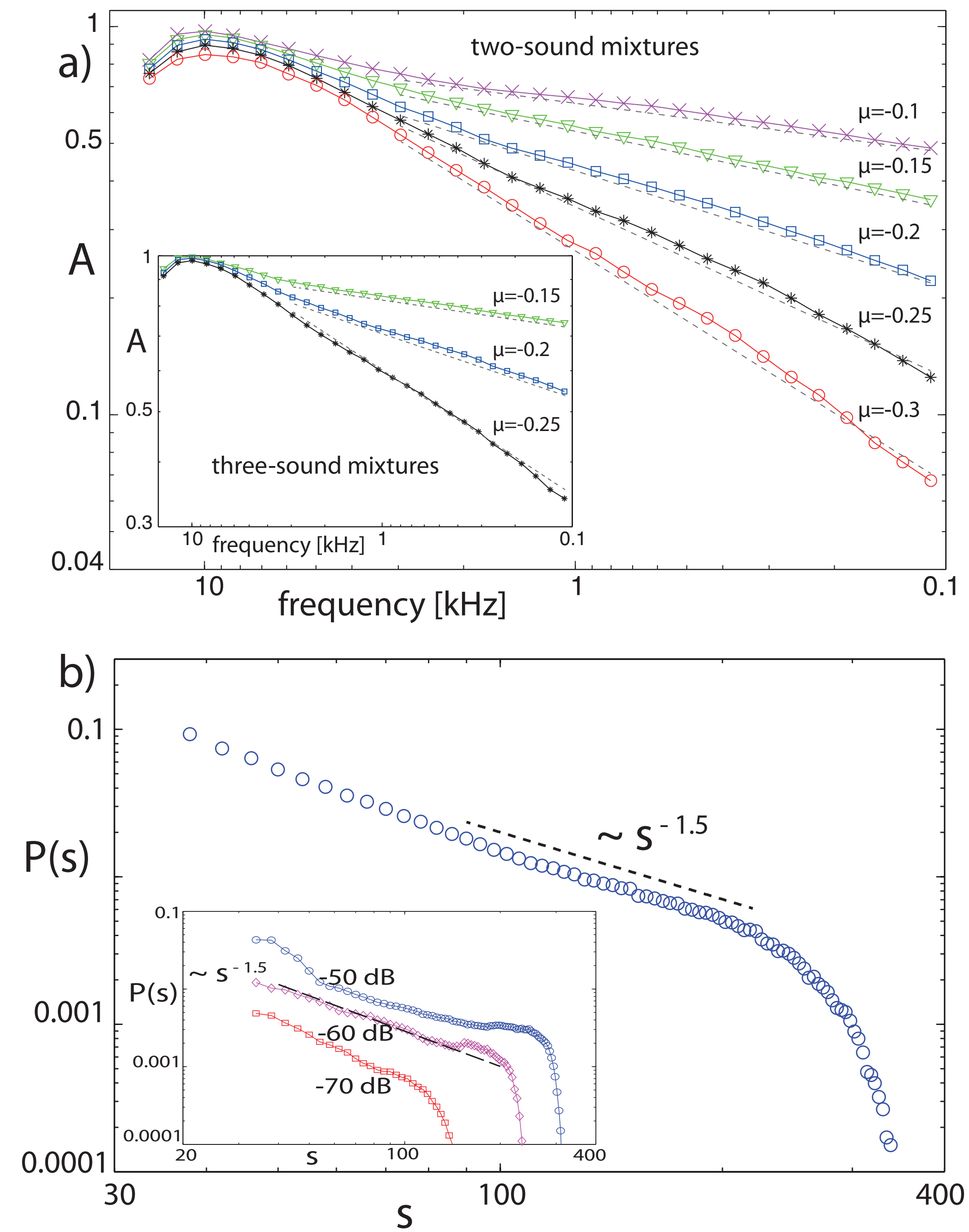
**A: number of activations i.e. above hearing threshold**

Random sound levels (-80,-40) dB (rms) complex tones

**s: size of activation network by number of links**

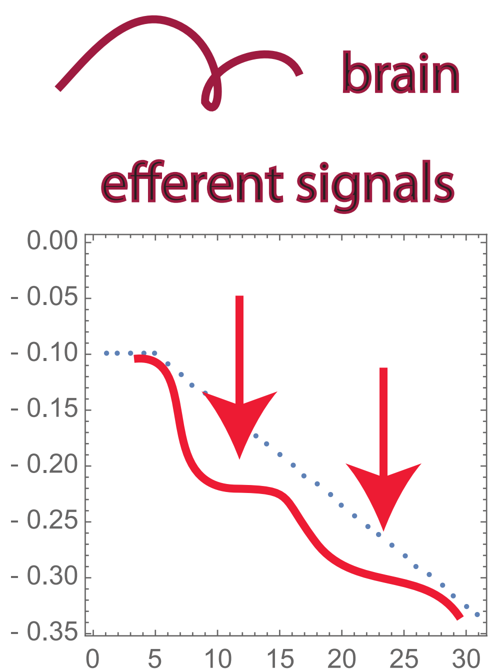
Two complex tones (random amplitude and frequency):
power-law activation networks!
branching percolation universality class?

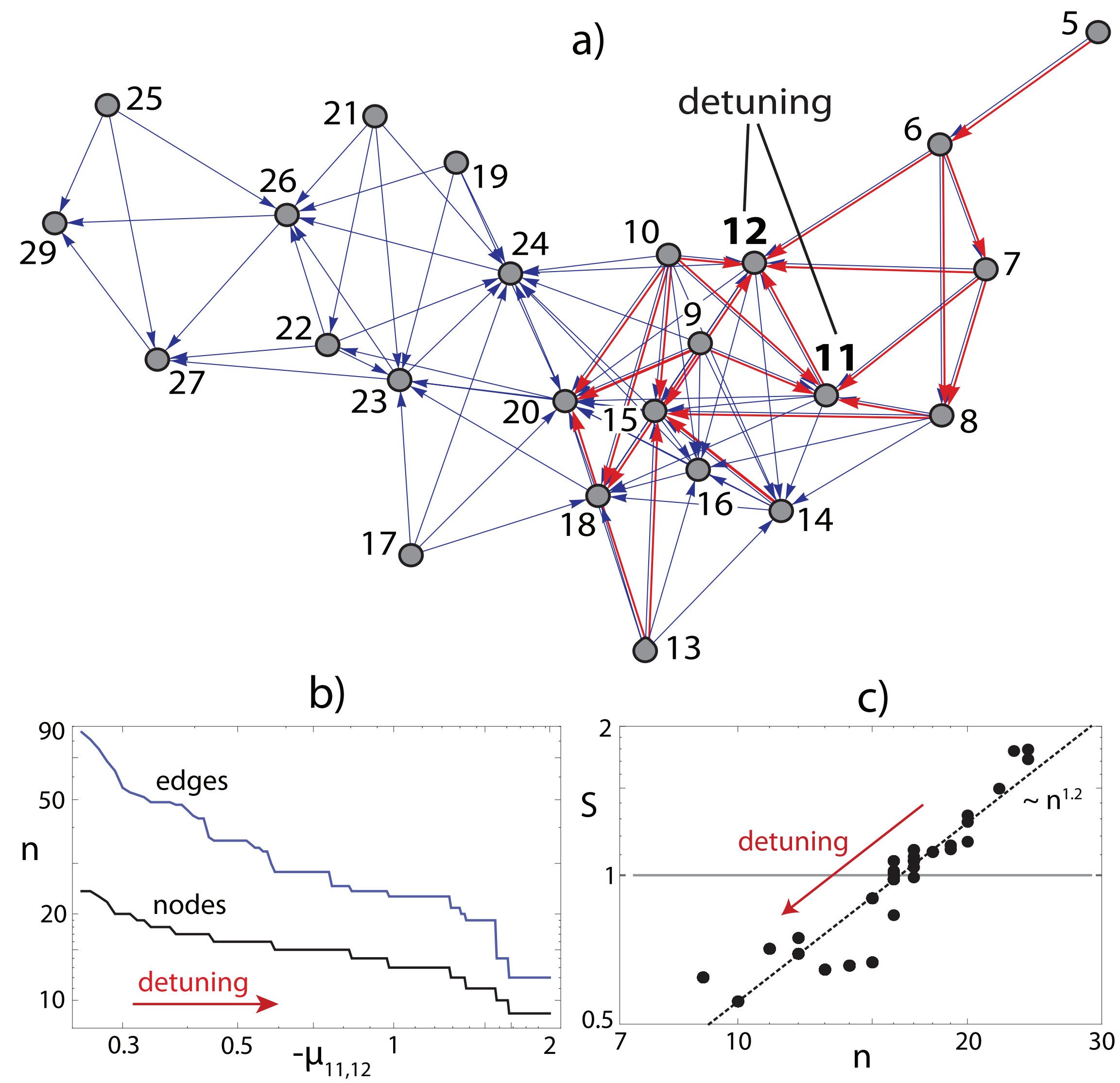
Inset: fixed amplitudes:
subcritical, critical, supercritical




**(R.S. & F.G. PRL 2016)**

# Listening means tuning

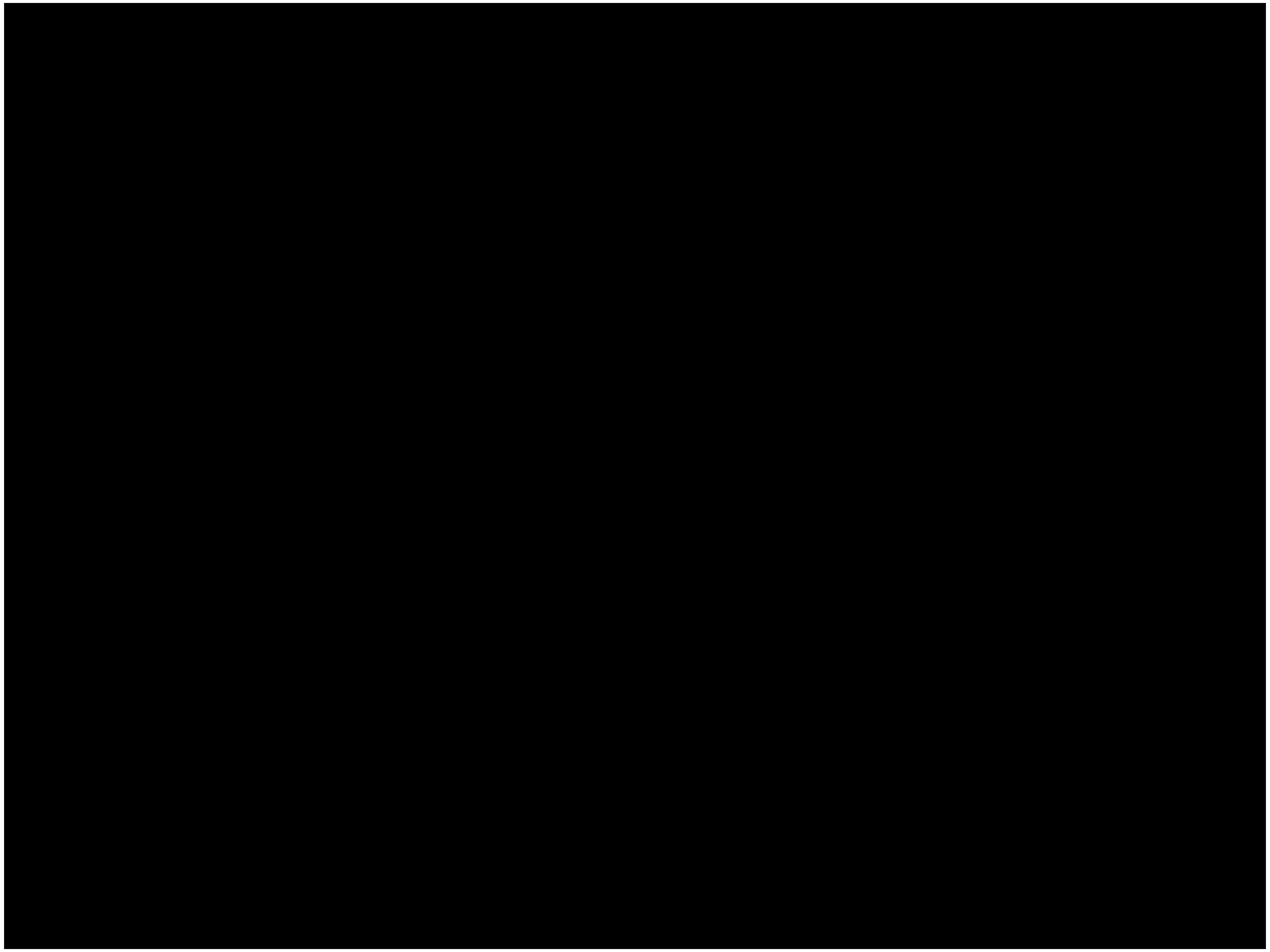


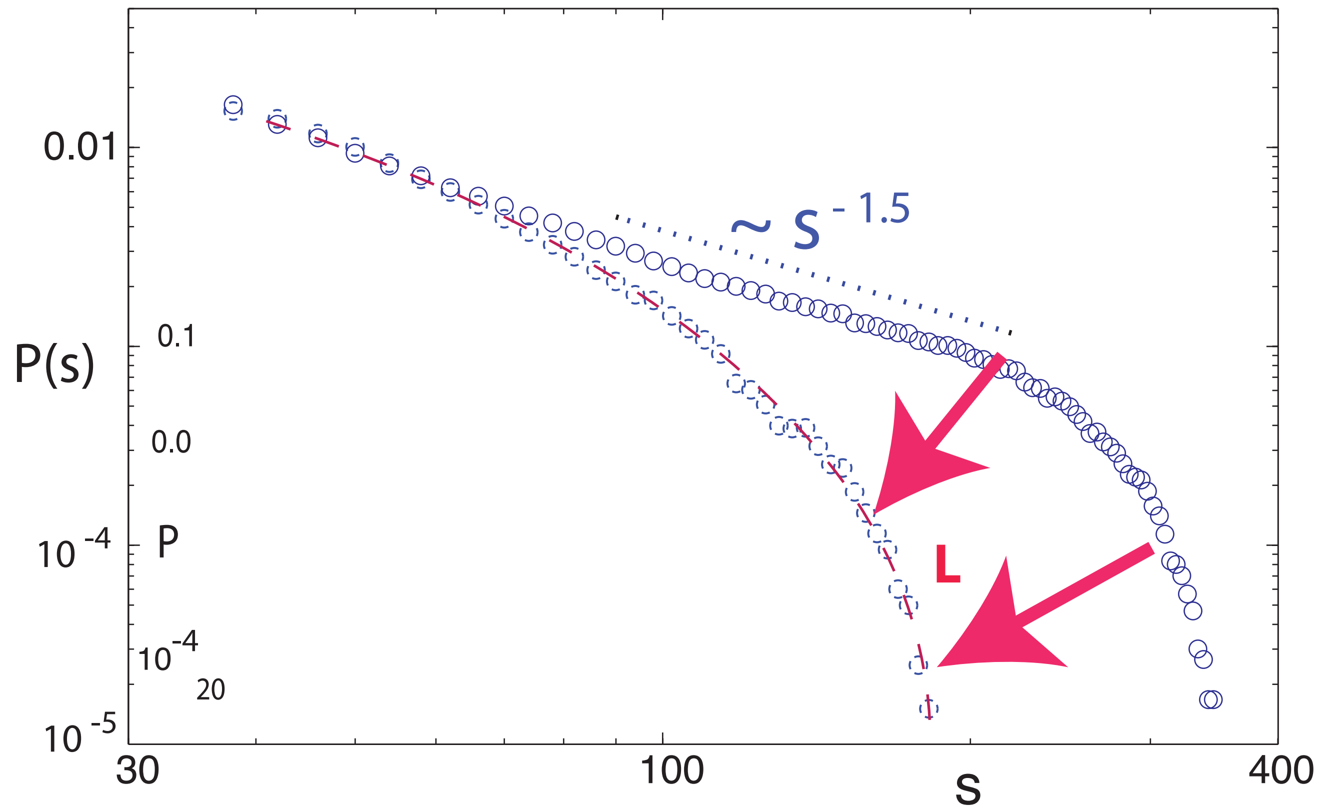

Effect of tuning on activation networks.
a) Activation networks, unbiased (blue), tuned (red) cochlea. The red graph is a subgraph of the blue graph.
b) Activity network characteristics, as a function of the de-tuning of $\mu${11,12}.
c) Small worldness S as a function of activity network size.

F.G., R.S. & al. PRAppl 2014

# Tuning away from criticality

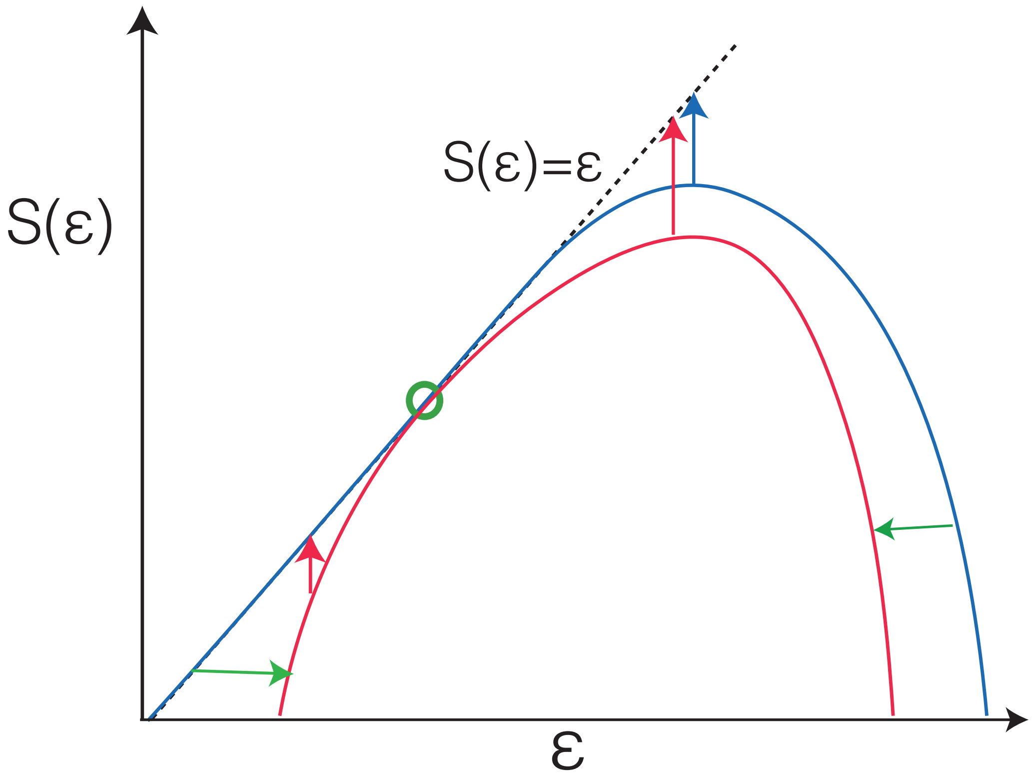


# Statistical meaning of learning




Detuning of two frequency bands (nodes 15,16 and nodes 19,20,21) from $\mu = -0.25$ to $\mu = -2.0$:
The initial power-law distribution $s^{-1.5}$ changes into a strictly convex distribution shape (line L)!

# Thermodynamic formalism




Power law=Ground-state of network-distributed computation

**Effect of learning: Loss of power-law**

**Observability O** of an invariant measure ε decays with time t as **$O(\varepsilon, t) \sim e^{-t\,(\varepsilon - S(\varepsilon))}$**
**Diagonal points $\varepsilon = S(\varepsilon)$** : measures that do not suffer exponential temporal decay

**Blue**: Entropy function S(λ) of intermittent systems, associated with power-law characteristics
**Red**: Entropy function associated with non-power-law behavior, from focusing on a particular measure

→ **Listening (learning) drives system away from criticality!!!**

# Thanks for listening..

## .. and for having me here !

# Measuring listening efficacy

(F.G, V.S., N.B., R.S., Phys. Rev. Appl. 2014)

models of pitch perception suggest comparison:

- SACF: sum of normalized autocorrelations of each section's output
  vs.
- NACF: normalized autocorrelation of the target signal
  desired signal x / unwanted signal y / $f_i$ output of i-th section

$$\boxed{TE\,(x,y) := \frac{\|\mathrm{NACF}(x) - \sum_i \mathrm{NACF}(f_i(x+y))/N\|_2}{\|\mathrm{NACF}(y) - \sum_i \mathrm{NACF}(f_i(x+y))/N\|_2}}$$

TE in [0,infinity]:
high (>>1) TE: bad tuning, low (<1): (very) good tuning

:TE-optimization problem in multidimensional μ-space

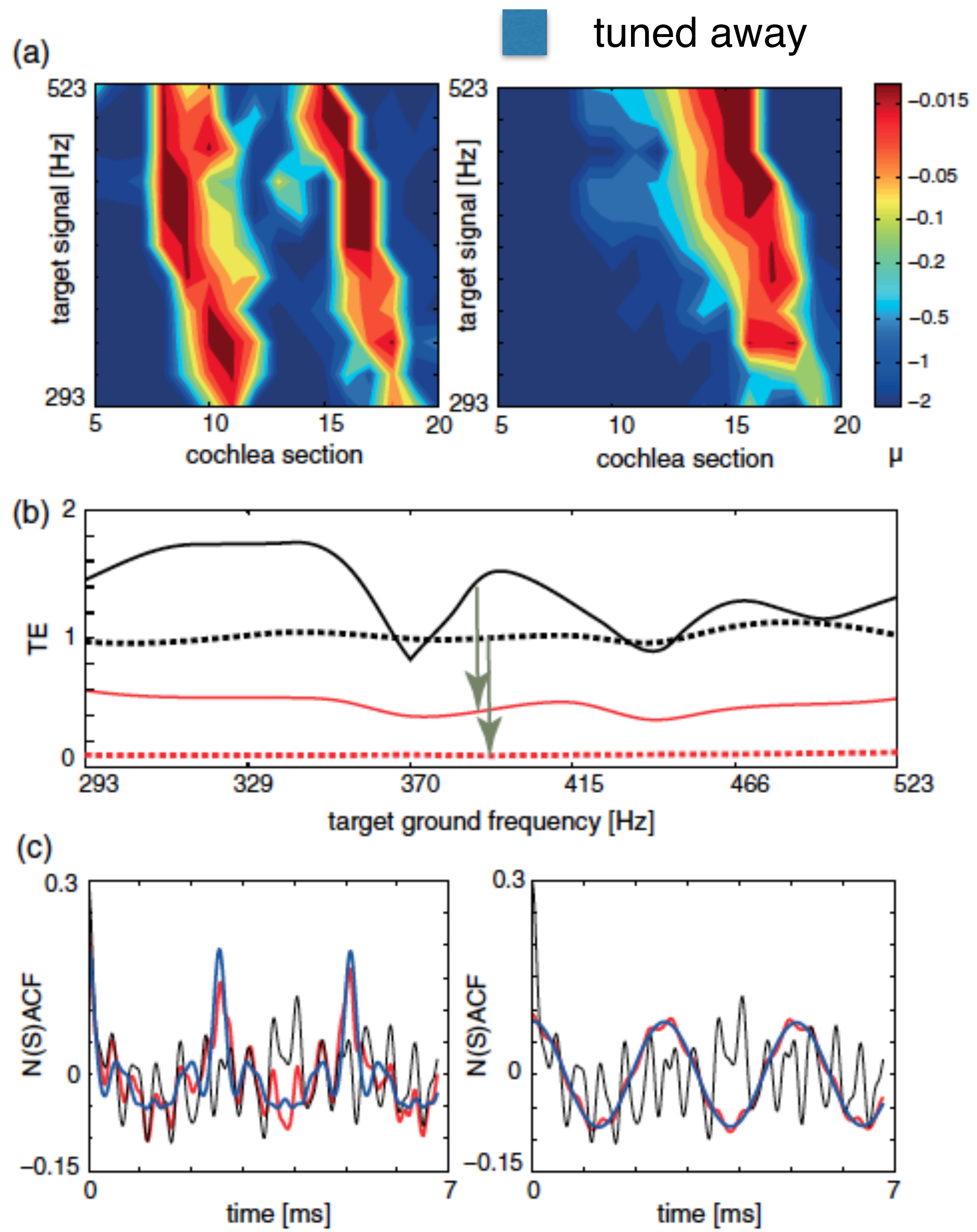
# Results :

two complex instruments:
'Flute' vs.'Zinke'(both parts of church organs)

Tuning patterns: red: close to bifurcation,
blue: away from bifurcation.
red: close to bifurcation,

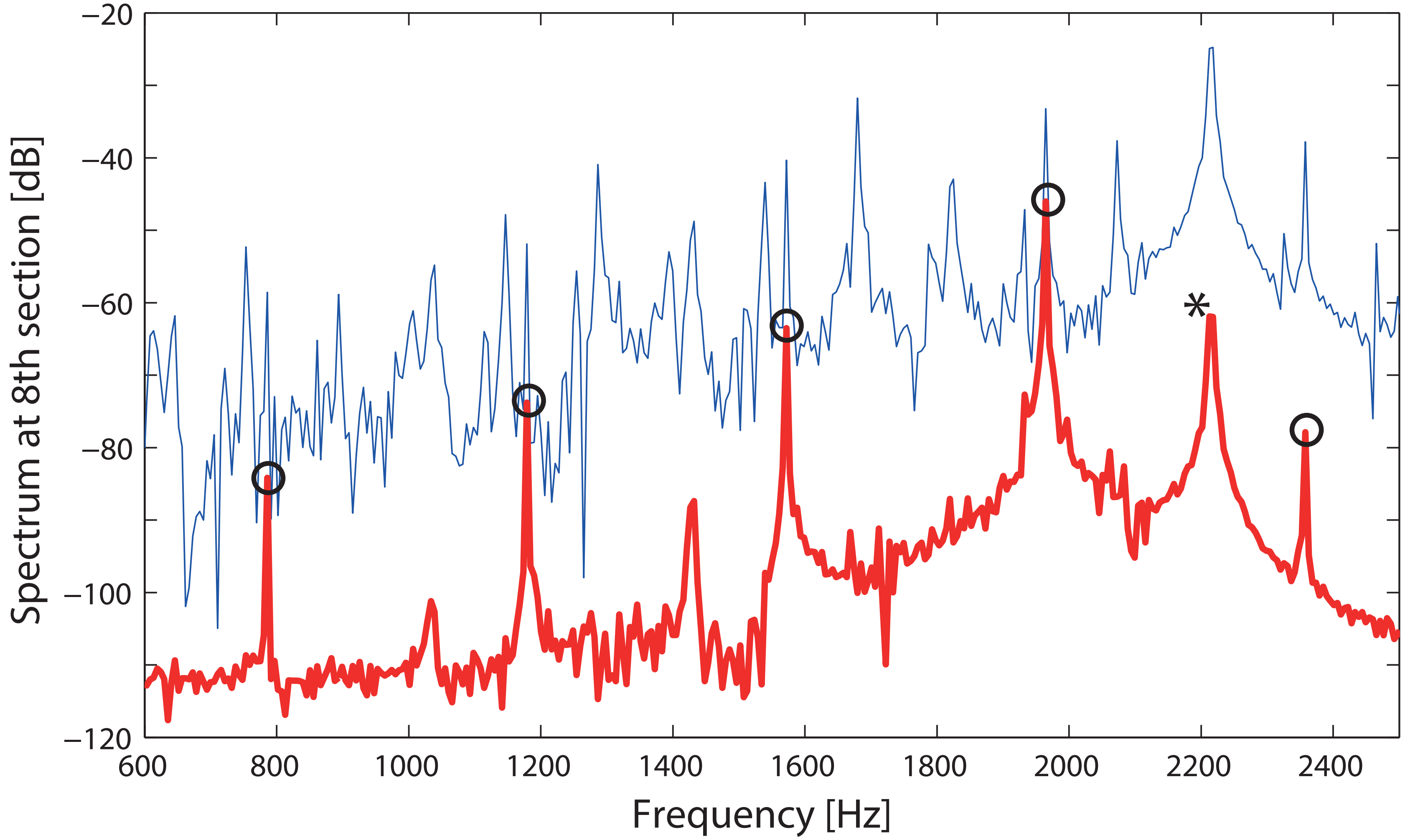
a) left: sweeping "Reel" target
right: sweeping "Flute" target
(tuning towards "Reel" requests
enhancement of the 3rd and 5th harmonics
(two parallel reddish stripes)

TE consistently < 1:
strong target enhancement
Black: flat tuning; red: TE-tuning




**(F.G, V.S., N.B., R.S., Phys. Rev. Appl. 2014)**

# Using pitch as guiding control feature:




original: flute and reel

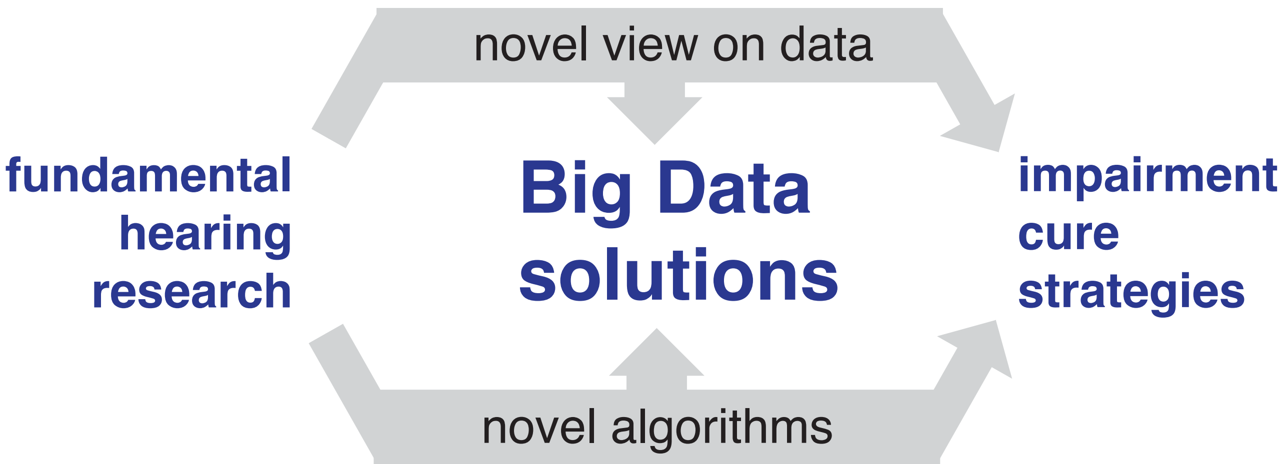
disturber (flute) and crossproducts removed; harmonic series restored

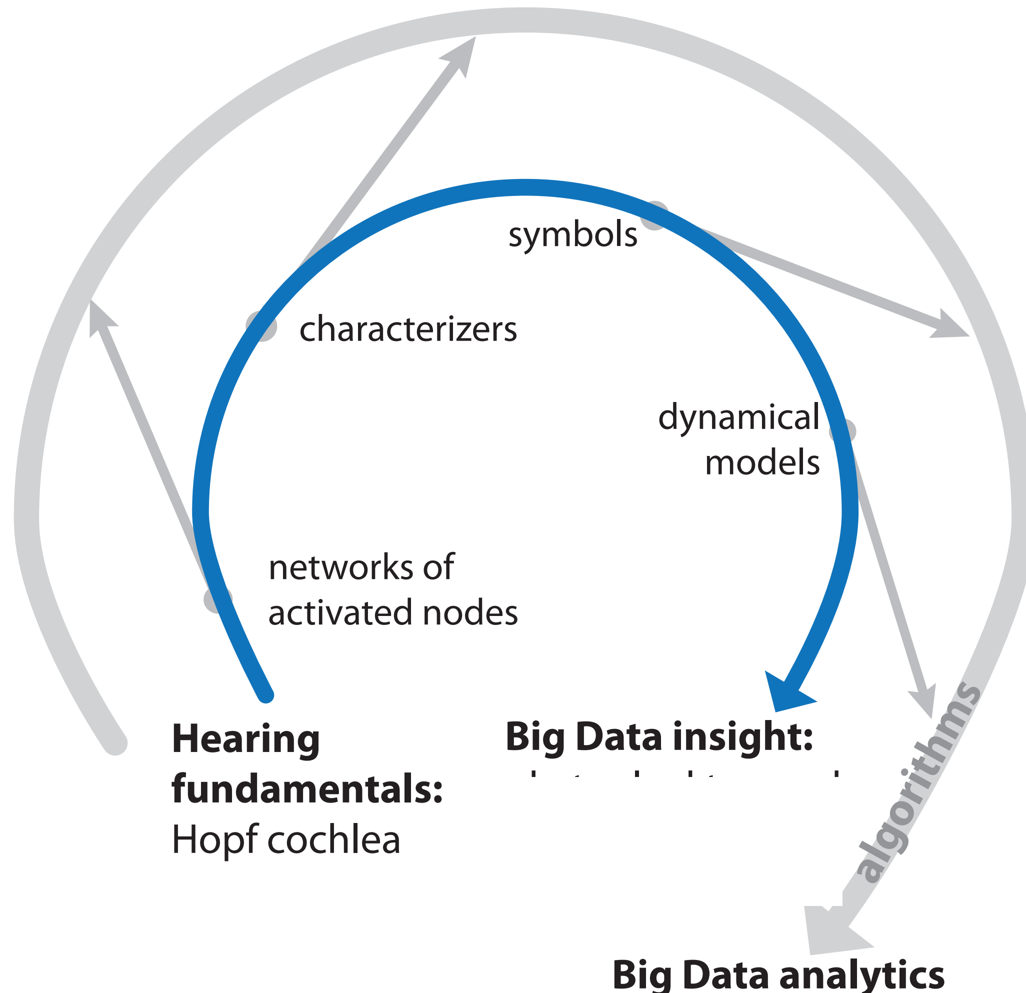
: efficient biomorphic tool for source separation!

(F.G.,V.S.,N.B., R.S.. Phys. Rev. Appl. 2014)

# Solution:

**Big Data :** Information promoted by information hubs that actively amplify it, and generate and promote




- **Complex networks characteristics (betweenness, etc.) to be tested as simple Big Data characterizers**
- **Final aim is to select, for a specific data application, the most appropriate characterizers and to understand their information-theoretic meaning. All of this can be done in real-time**
- **For all data applications the Big Data model is identical (a network of active nodes), this will result in novel algorithmic approaches tailored for general Big Data, reaching beyond the hearing domain**
- **Partition sets of Big Data systems into similar behavior. At the level of symbols, a more refined approach: language analysis (Drosophila pre-copulatory language) This will provide additional insight into the nature of exemplary Big Data, and potentially beyond**

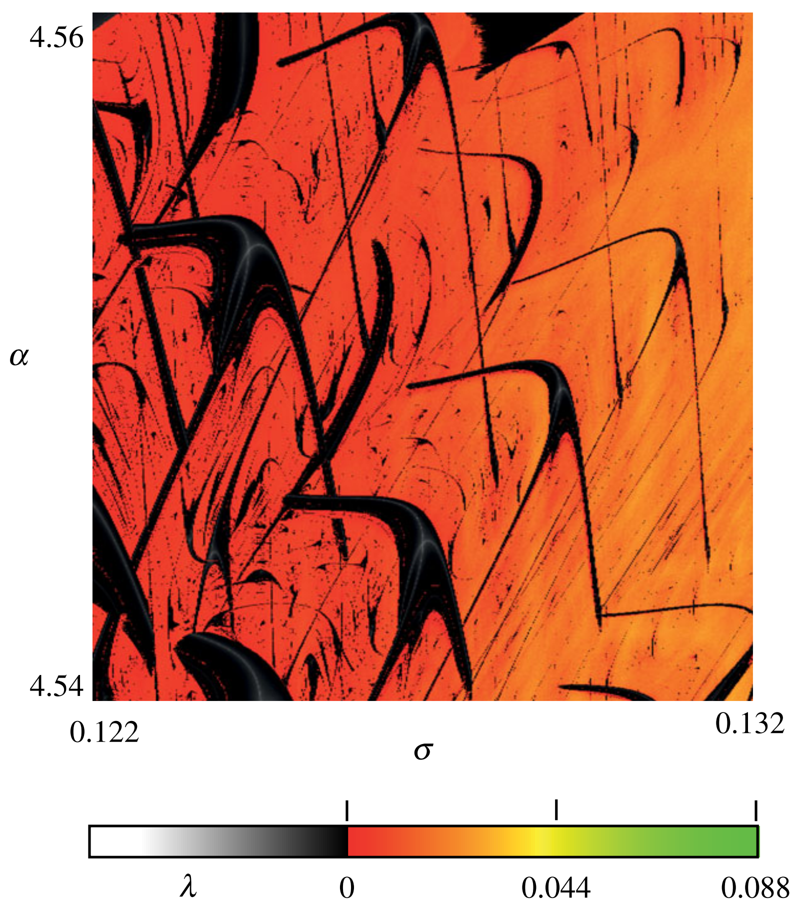
# X Big Data connection

**Big Data**: information 'too big, too complex and too quickly varying' to be analyzed conventionally.

Evolution: mammalian hearing has effortlessly ramped up hearing with ever increasing demand in information processing.

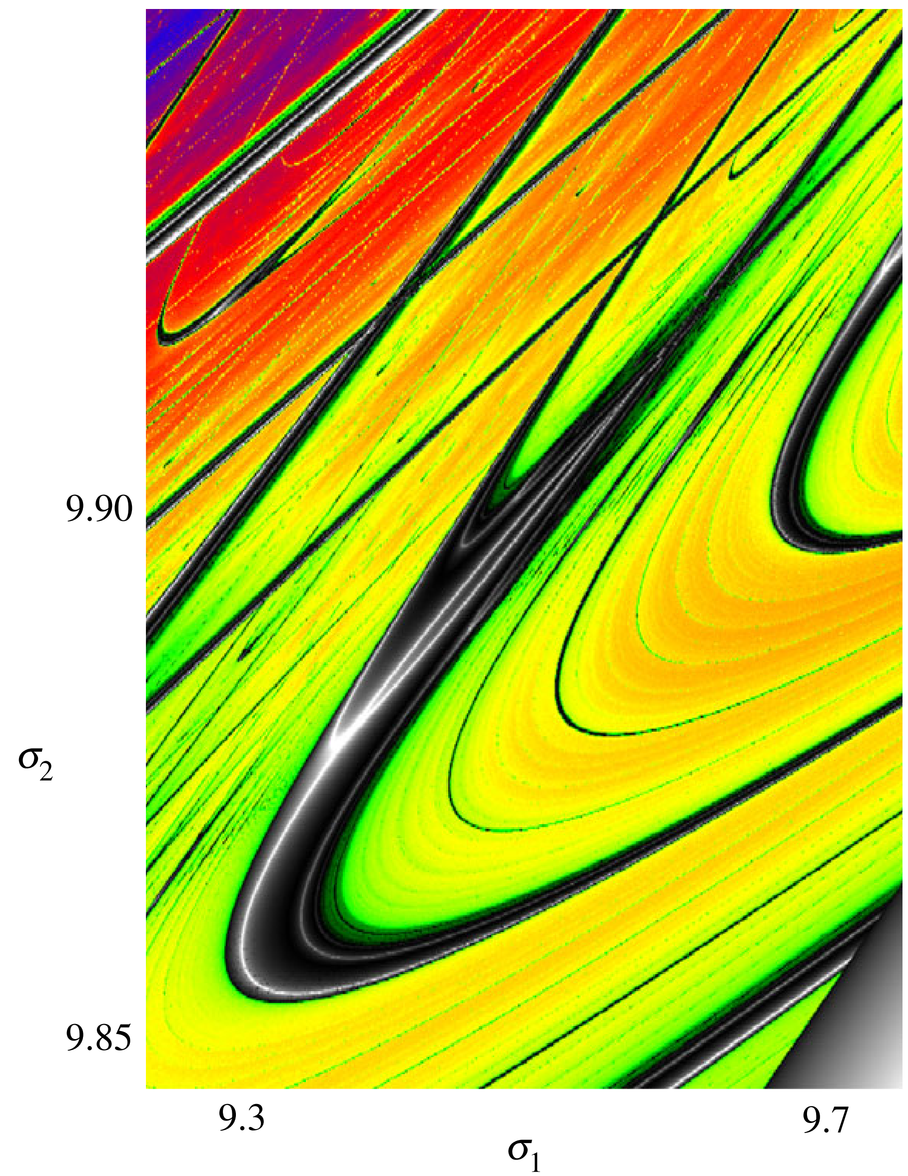
**Hypothesis**: mammalian auditory processing hosts still undiscovered novel approach to information processing.

What does this **not** mean?

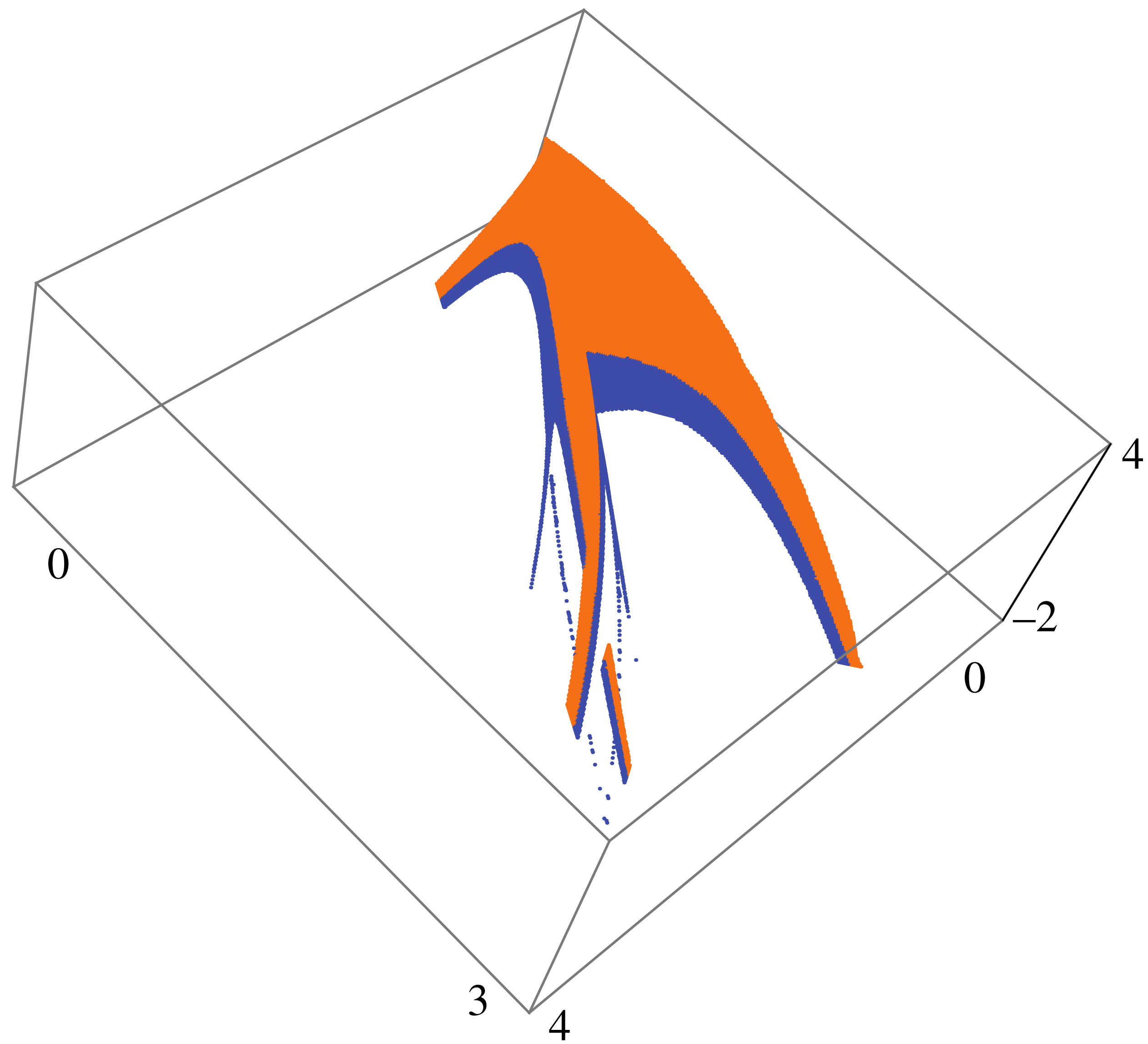



Shrimp-domains of Rulkov's model of neuronal firing.
Black: domains of stable firing;
red: domains of unstable response, expressed in terms of largest Lyapunov exponent λ

Biochemical model by Decroly & Goldbeter:

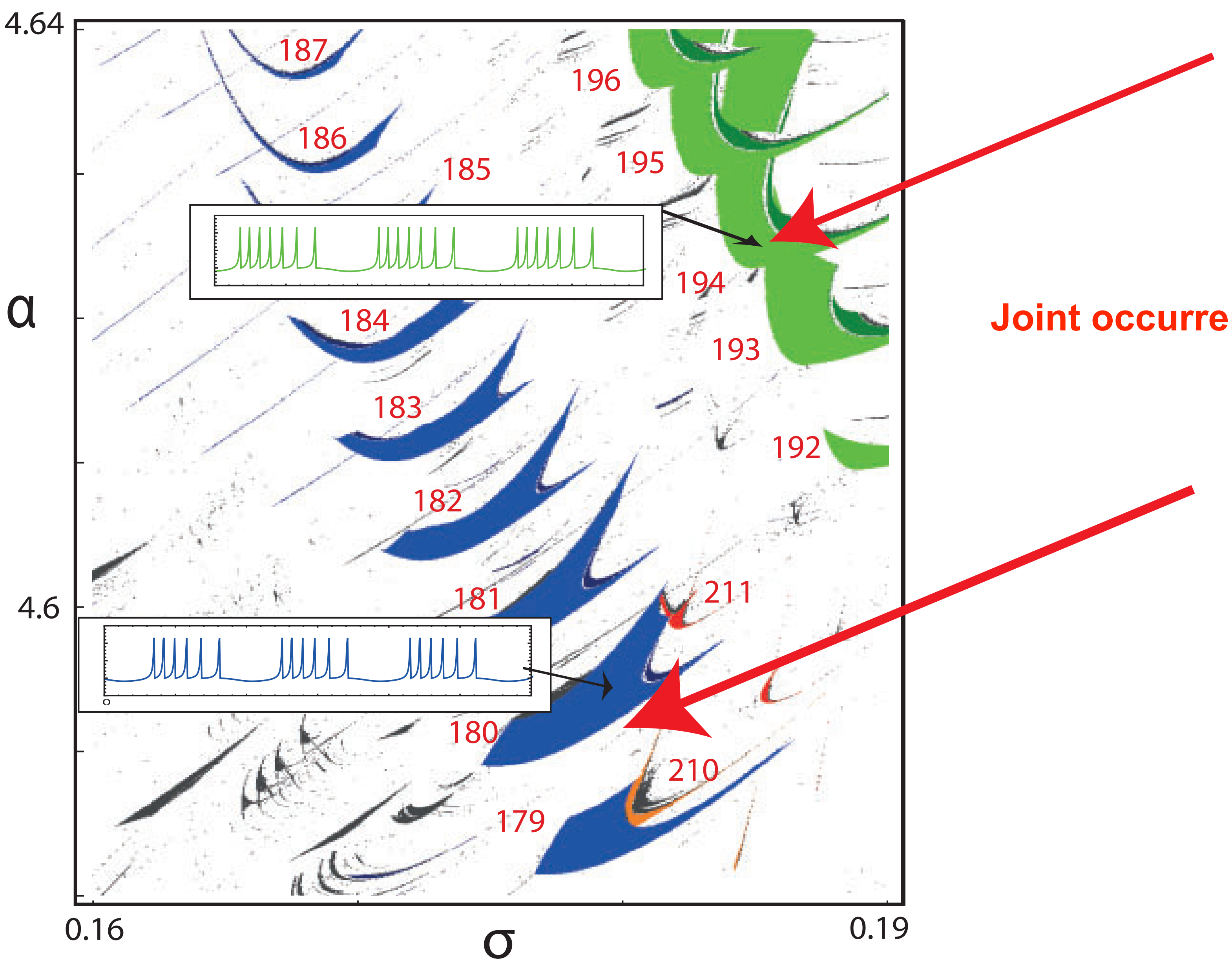



Feature space: $(x, y) \rightarrow (x + y, x + \ln(1+|y|), xy)$



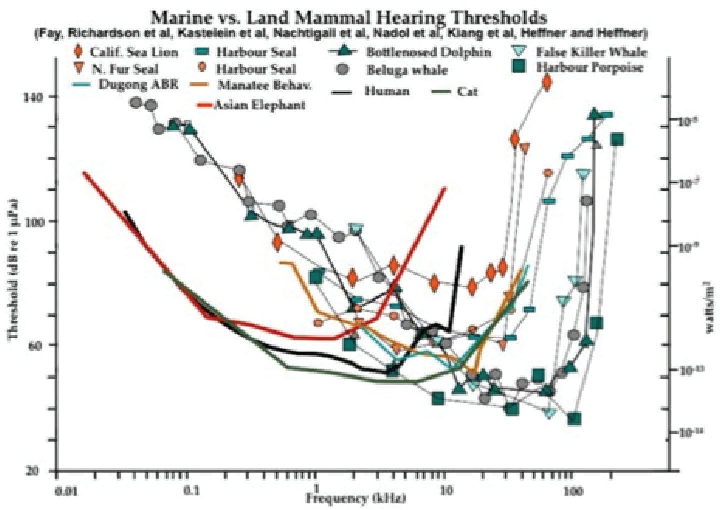

**(F.G.) T.L. J.H. & R.S., Phil. Trans. Roy.Soc. 2017**

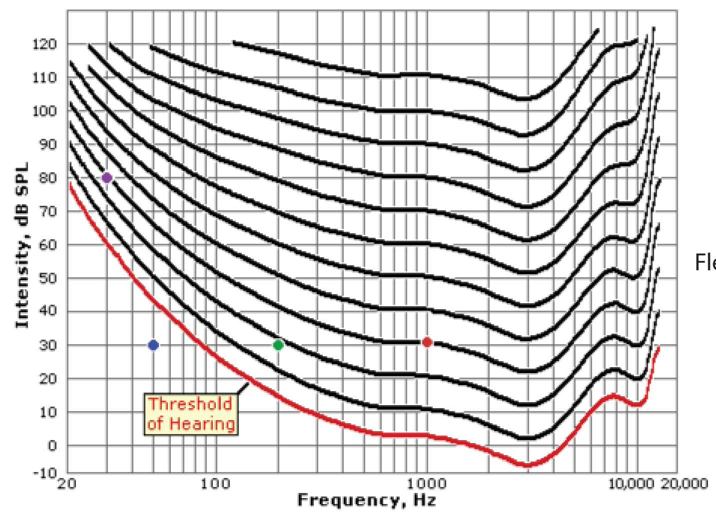
# Problem:



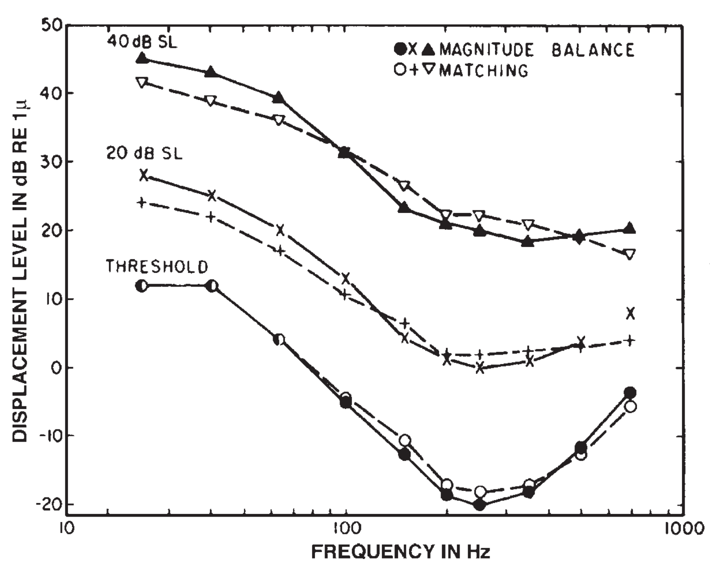

**Joint occurrence across different time-scales**

# Hearing threshold

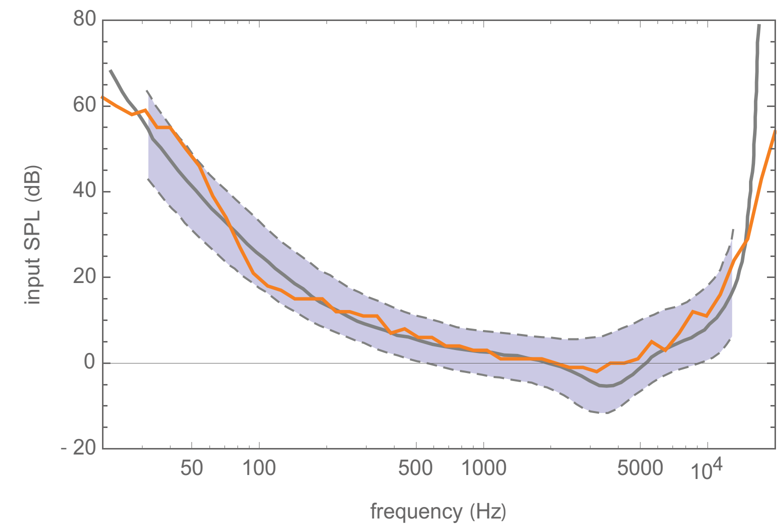


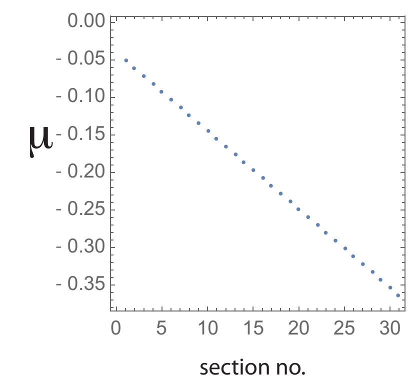



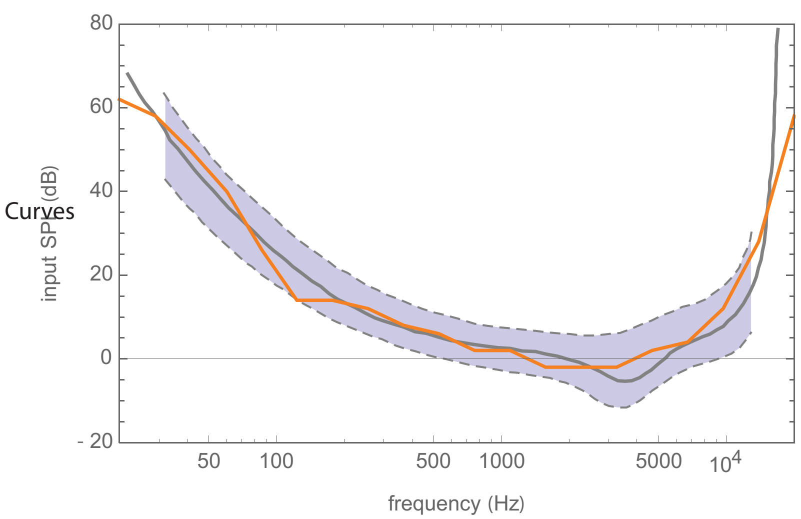

Fletcher-Munson Curves

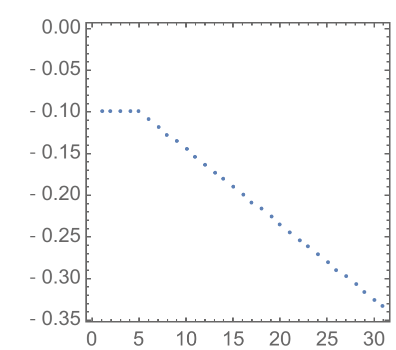


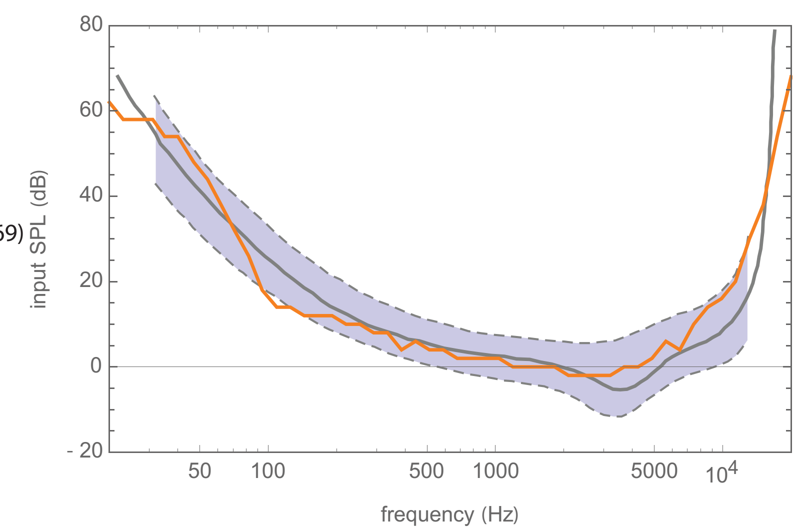

Verrillo et al. (1969)

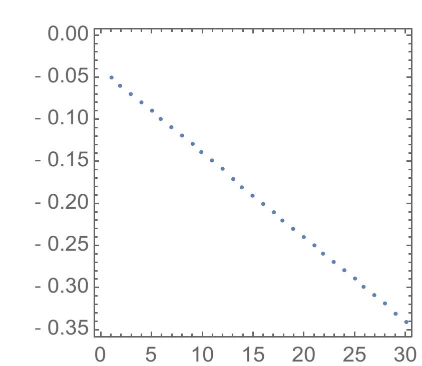




Verrillo, R.T., Fraioli, A., and Smith, R.L. Sensory magnitude of vibrotactile stimuli. Percept. Psychophys. 6: 366–372, 1969..

# Measuring listening efficacy

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vs.
- NACF: normalized autocorrelation of the target signal

desired signal x / unwanted signal y / $f_i$ output of i-th section

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