THRESHOLDS FOR SOUND DISCRIMINATION

Amplitude discrimination

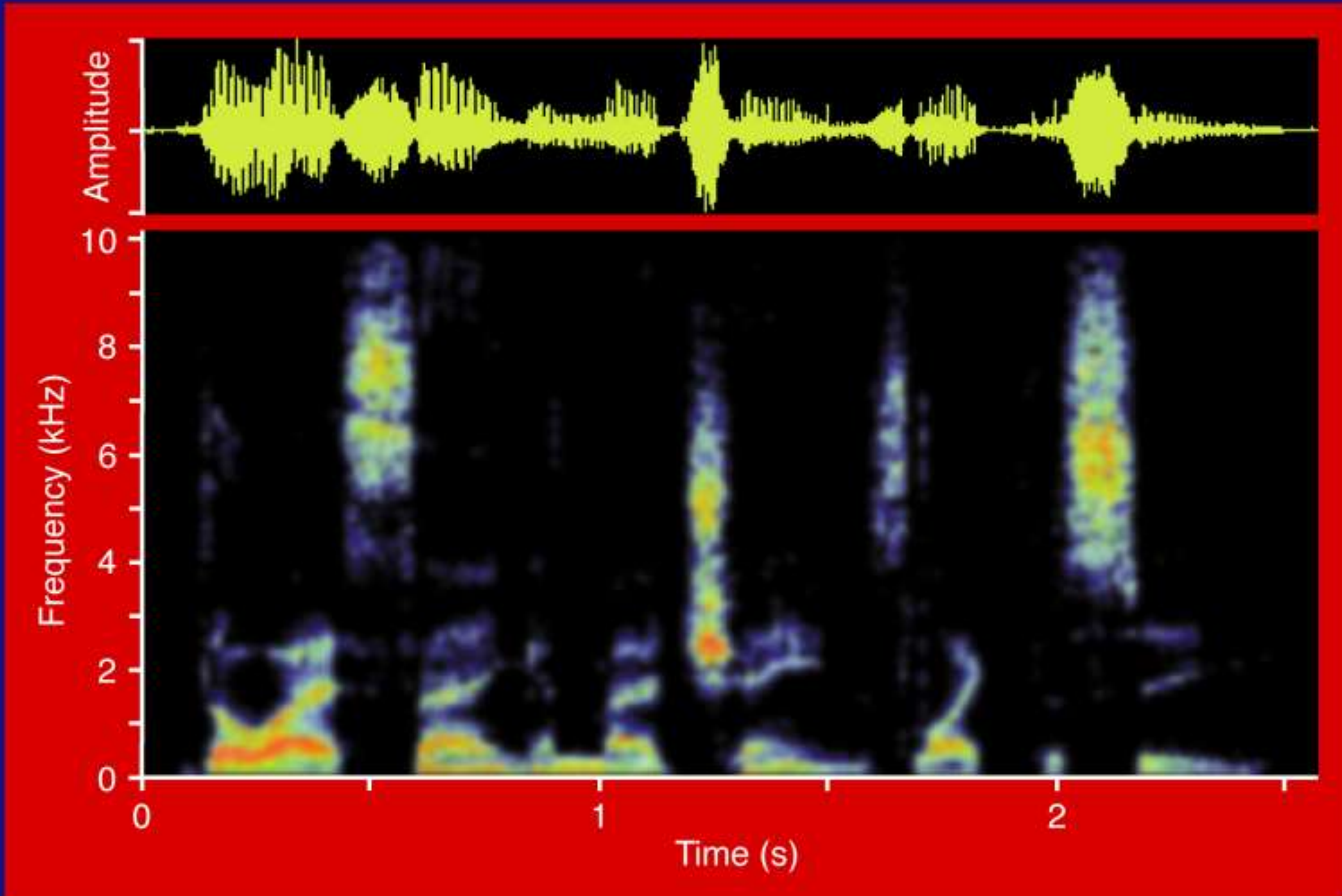
- 200% change in amplitude
- 100% change in amplitude
- 50% change in amplitude
- 20% change in amplitude
- 10% change in amplitude

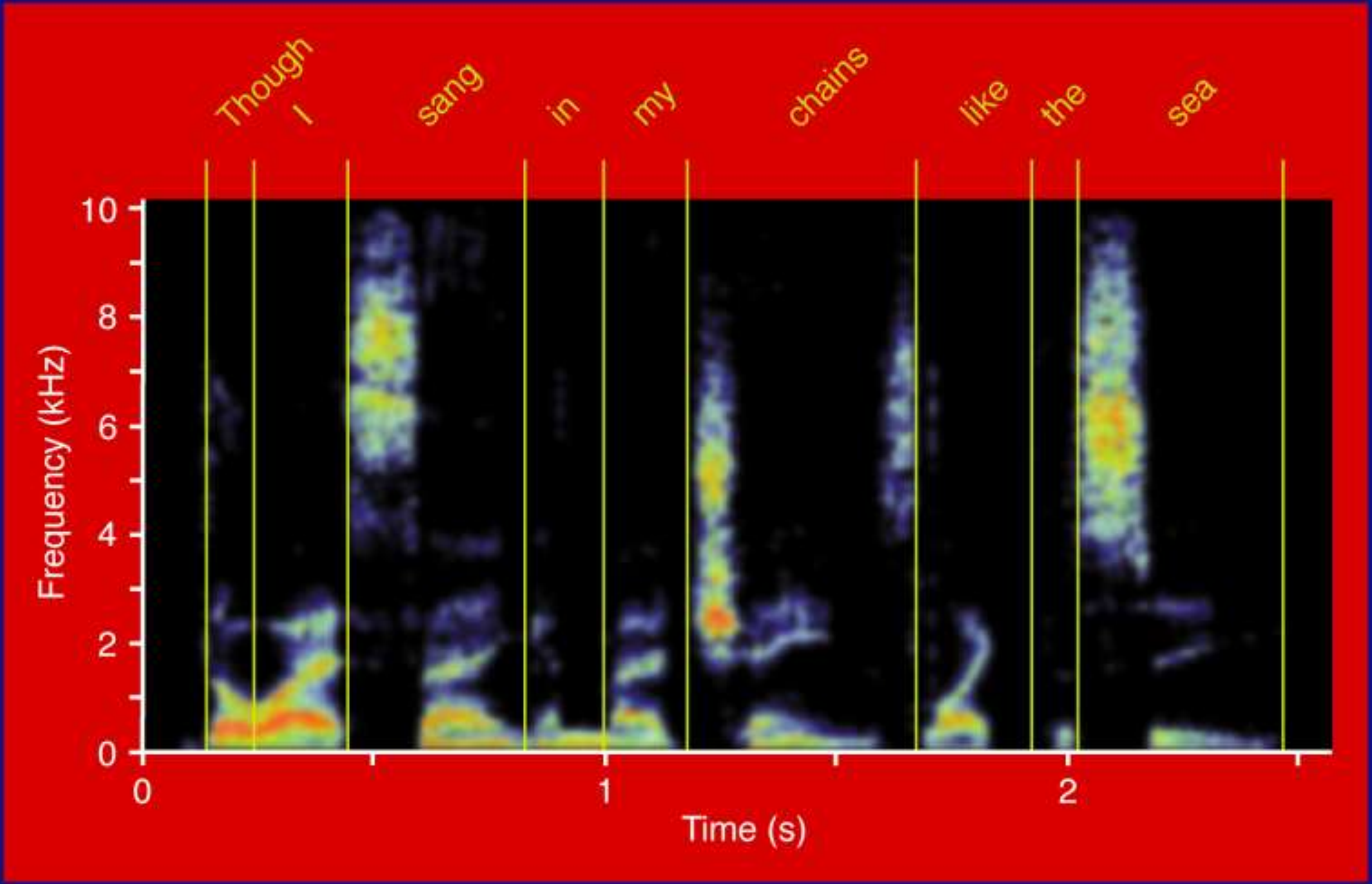
An increment of 20 decibels (20 dB), which represents a tenfold increase in amplitude (900% change), makes a sound about twice as loud.

Frequency discrimination

- 2% change in frequency
- 1% change in frequency
- 0.5% change in frequency
- 0.2% change in frequency
- 0.1% change in frequency

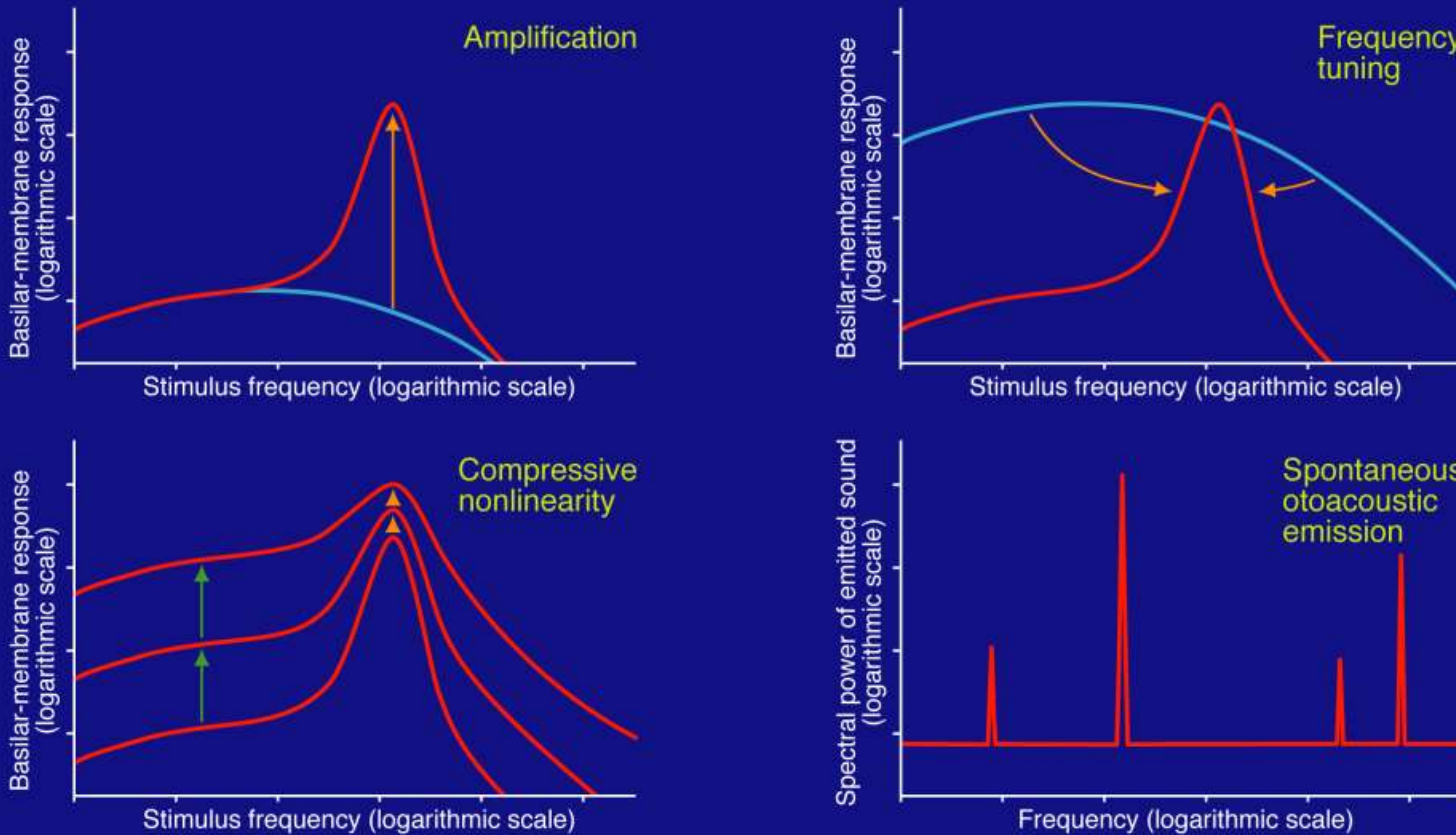
A semitone, or single note on the piano, represents a frequency change of about 6%.

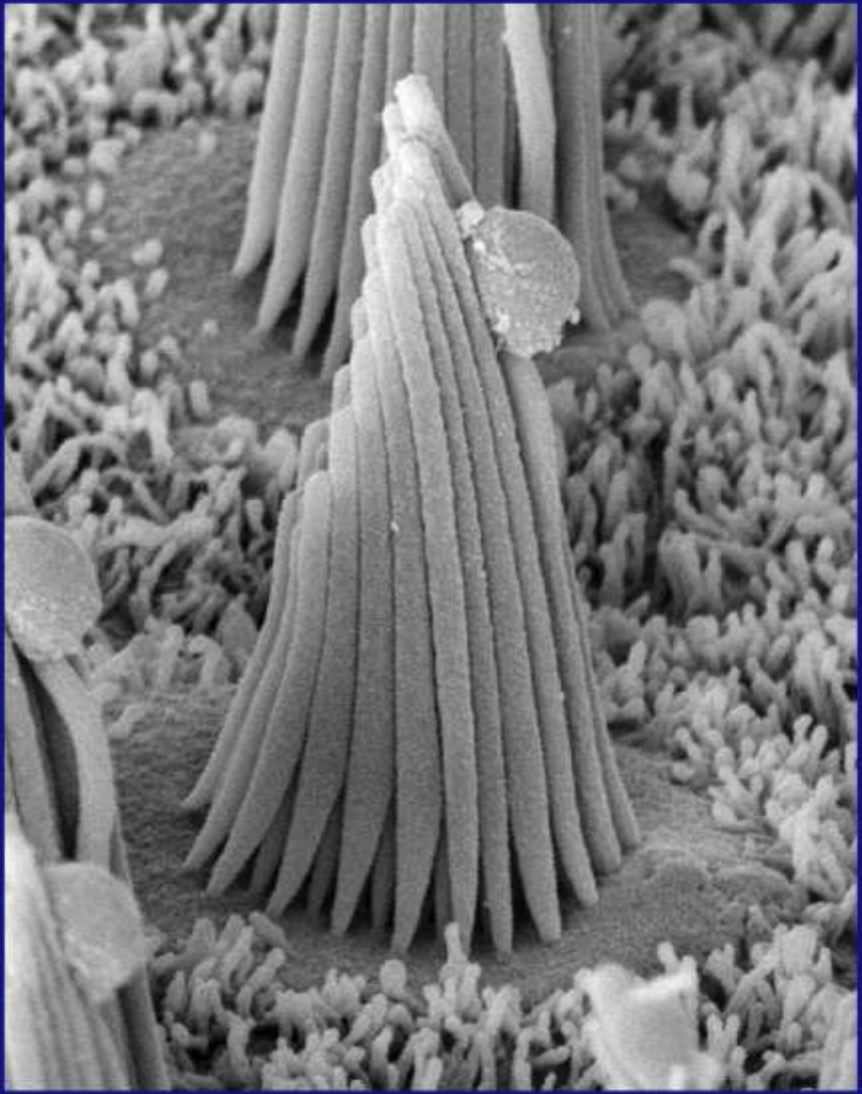

Amplitude
Frequency (kHz)
10
8
6
4
2
0
0
1
2
Time (s)

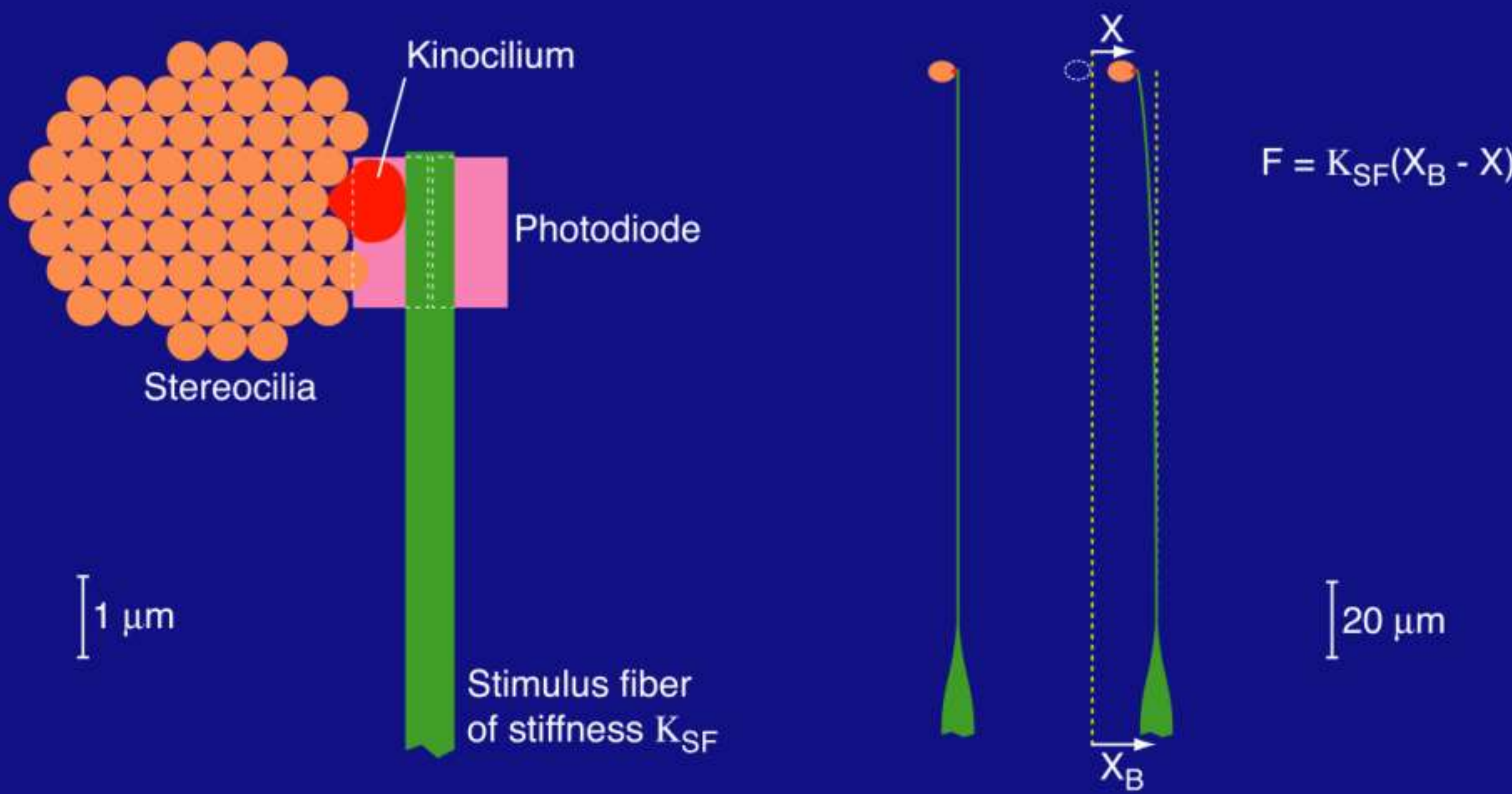


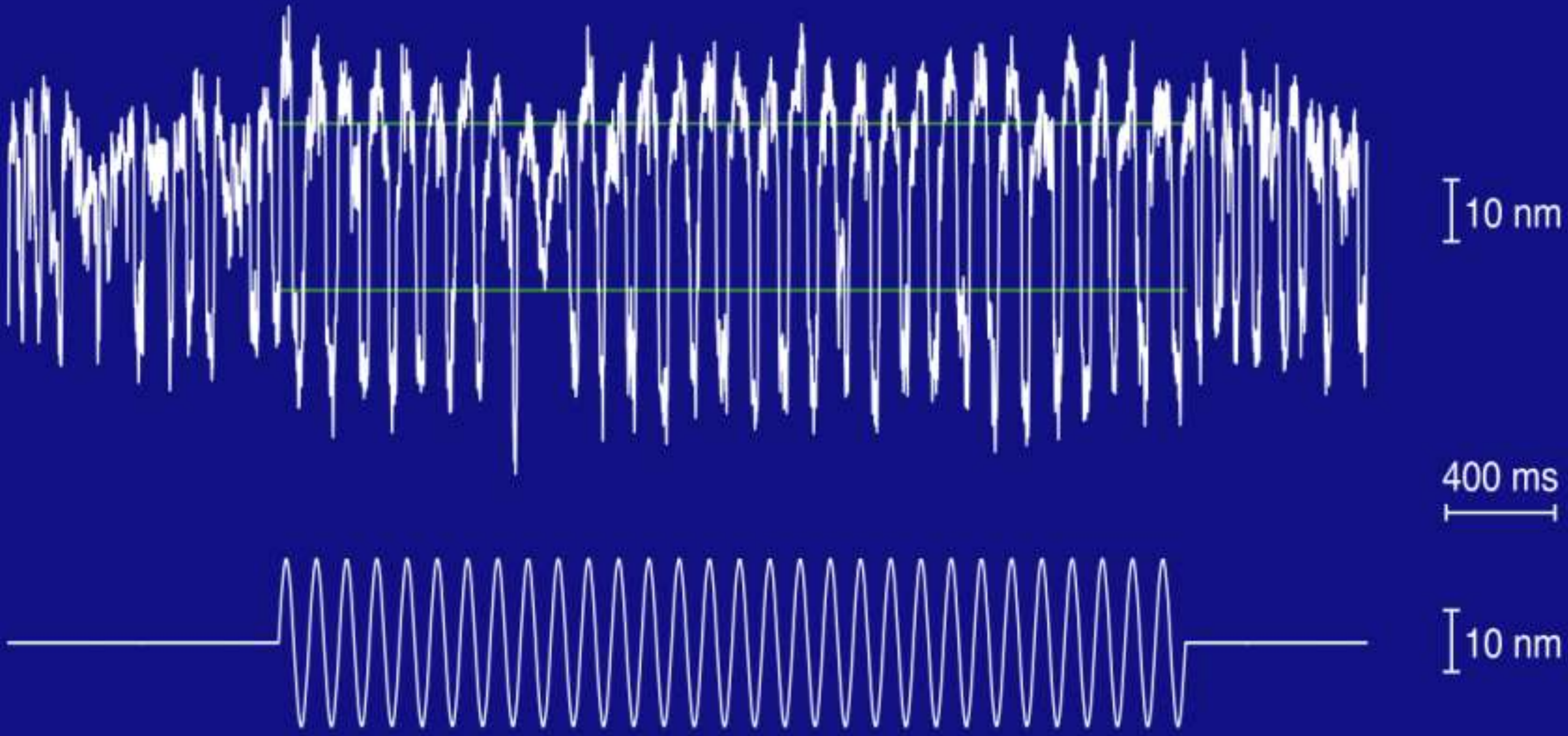
Though
I
sang
in
my
chains
like
the
sea
10
8
6
4
2
0
Frequency (kHz)
0
1
2
Time (s)

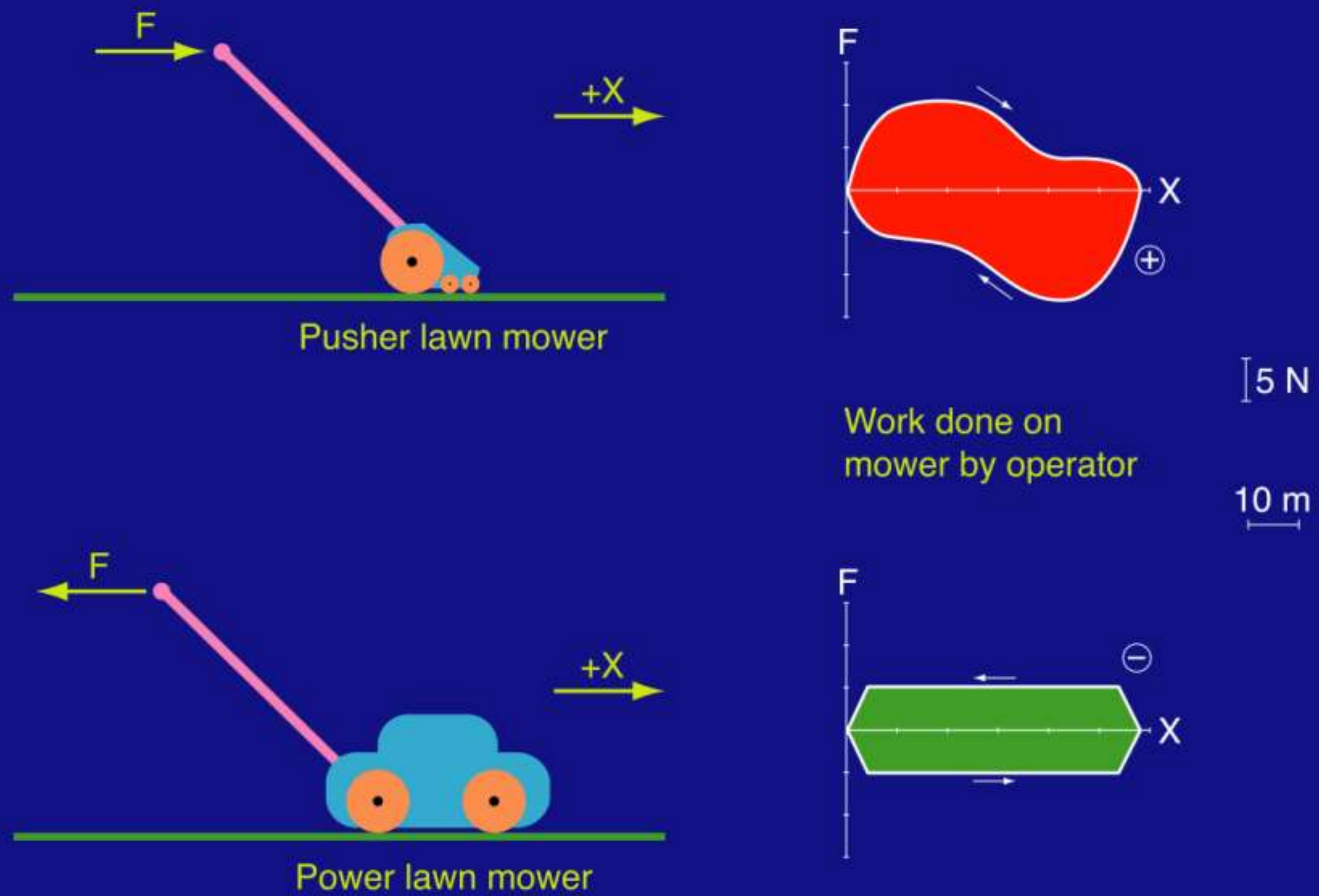
THE ACTIVE PROCESS OF HAIR CELLS






Kinocilium
Photodiode
Stereocilia
1 μm
Stimulus fiber
of stiffness K_{SF}
X
$F = K_{SF}(X_B - X)$
20 μm
X_B


10 nm
400 ms
10 nm


F
+X
Pusher lawn mower
F
X
5 N
Work done on
mower by operator
10 m
F
+X
Power lawn mower
F
X

At any time,

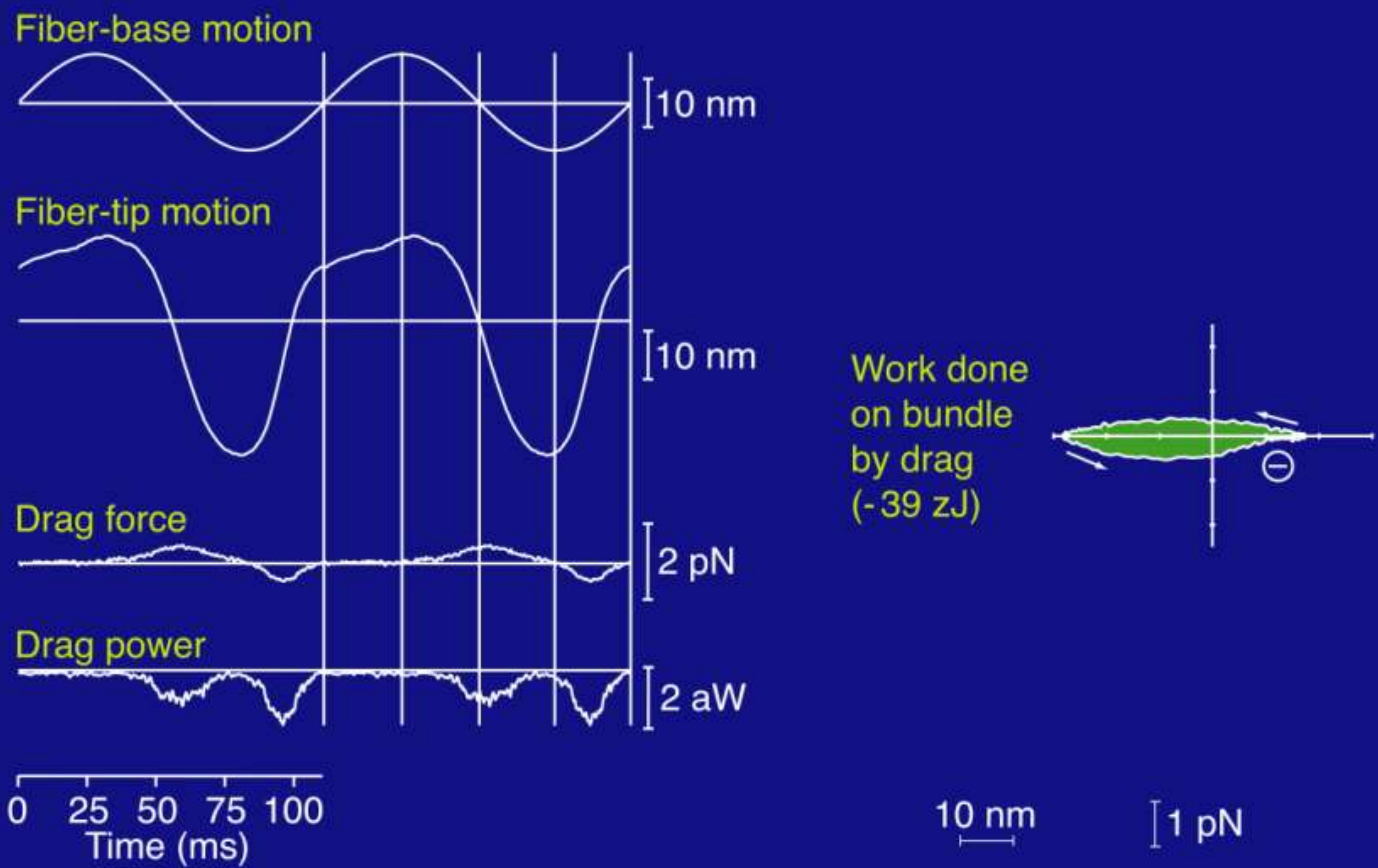
$$F_{EXTERNAL} + F_{INERTIAL} + F_{DRAG} + F_{ELASTIC} + F_{ACTIVE} = 0$$

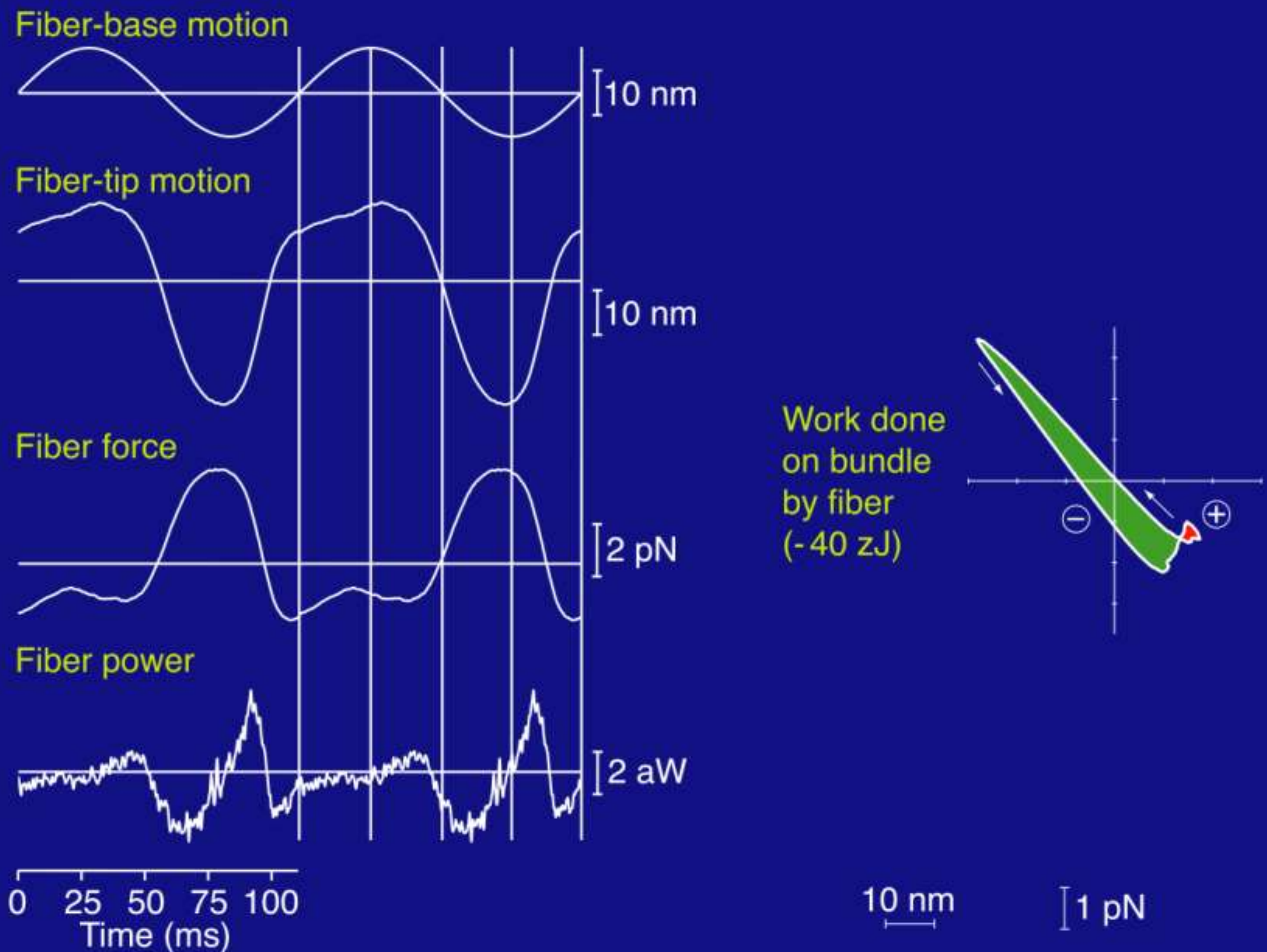
$$F_{ACTIVE} = - K_{SF}(X_B - X) - (m_{HB} + m_{SF})\cdot\frac{d^2X}{dt^2} - (\xi_{HB} + \xi_{SF})\cdot\frac{dX}{dt} - K_{HB}X$$

Over an average cycle,

$$\overline{W}_{EXTERNAL} + \cancel{\overline{W}_{INERTIAL}} + \overline{W}_{DRAG} + \cancel{\overline{W}_{ELASTIC}} + \overline{W}_{ACTIVE} = 0$$

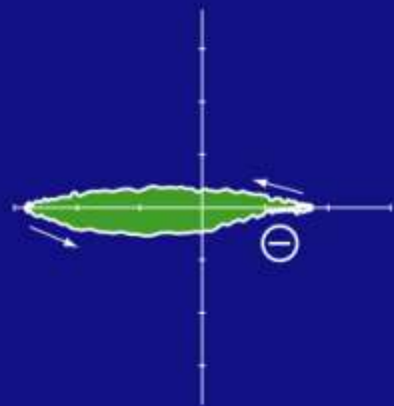
$$\overline{W}_{ACTIVE} = - K_{SF}\oint (X_B - X)\cdot dX - (\xi_{HB} + \xi_{SF})\oint \frac{dX}{dt}\cdot dX$$


Fiber-base motion
10 nm
Fiber-tip motion
10 nm
Drag force
2 pN
Drag power
2 aW
0 25 50 75 100
Time (ms)
Work done on bundle by drag (-39 zJ)
10 nm
1 pN

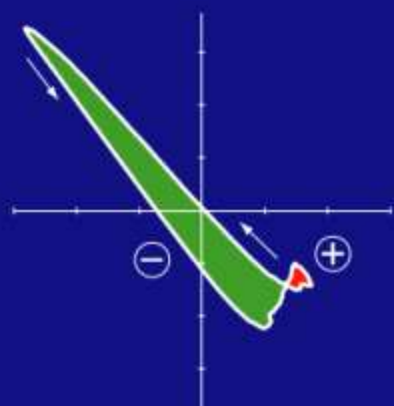


Fiber-base motion
10 nm
Fiber-tip motion
10 nm
Fiber force
2 pN
Fiber power
2 aW
0
25
50
75
100
Time (ms)
Work done
on bundle
by fiber
(-40 zJ)
10 nm
1 pN

Work done on bundle by drag (-39 zJ)



Work done on bundle by fiber (-40 zJ)



10 nm   1 pN

$$\overline{W}_{ACTIVE} = -\overline{W}_{DRAG} - \overline{W}_{FIBER}$$

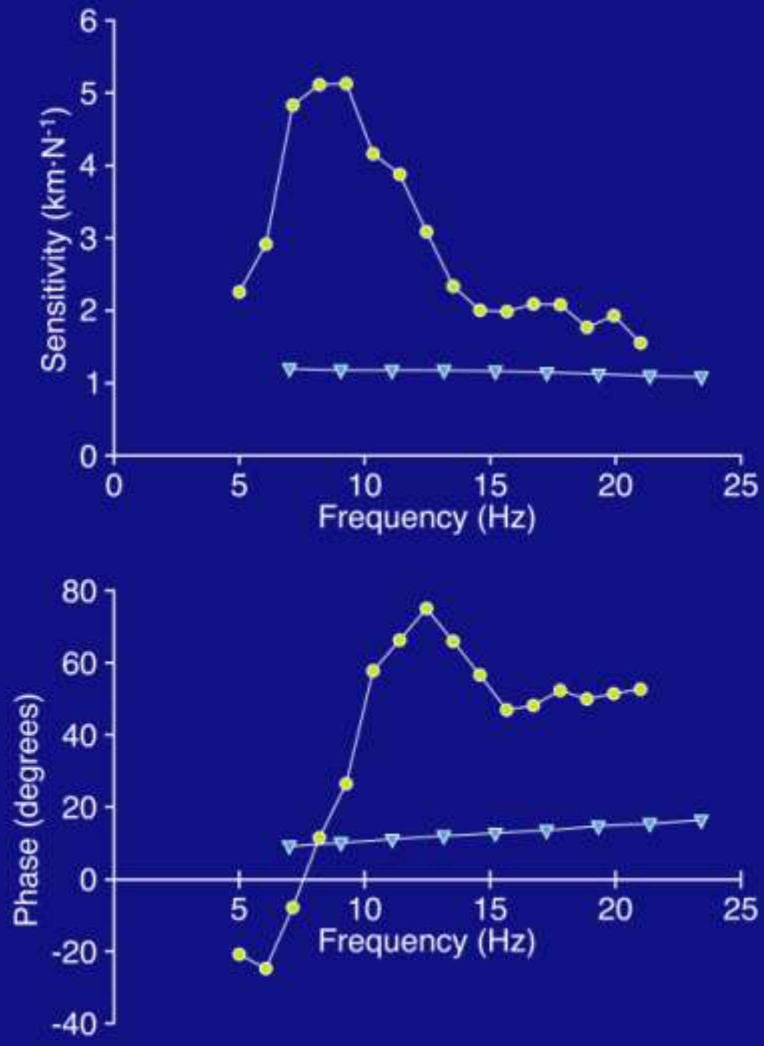
$$\overline{W}_{ACTIVE} = +79 \text{ zJ}$$

$\overline{W}_{ACTIVE} = -\overline{W}_{DRAG} - \overline{W}_{FIBER} = +48\ zJ$

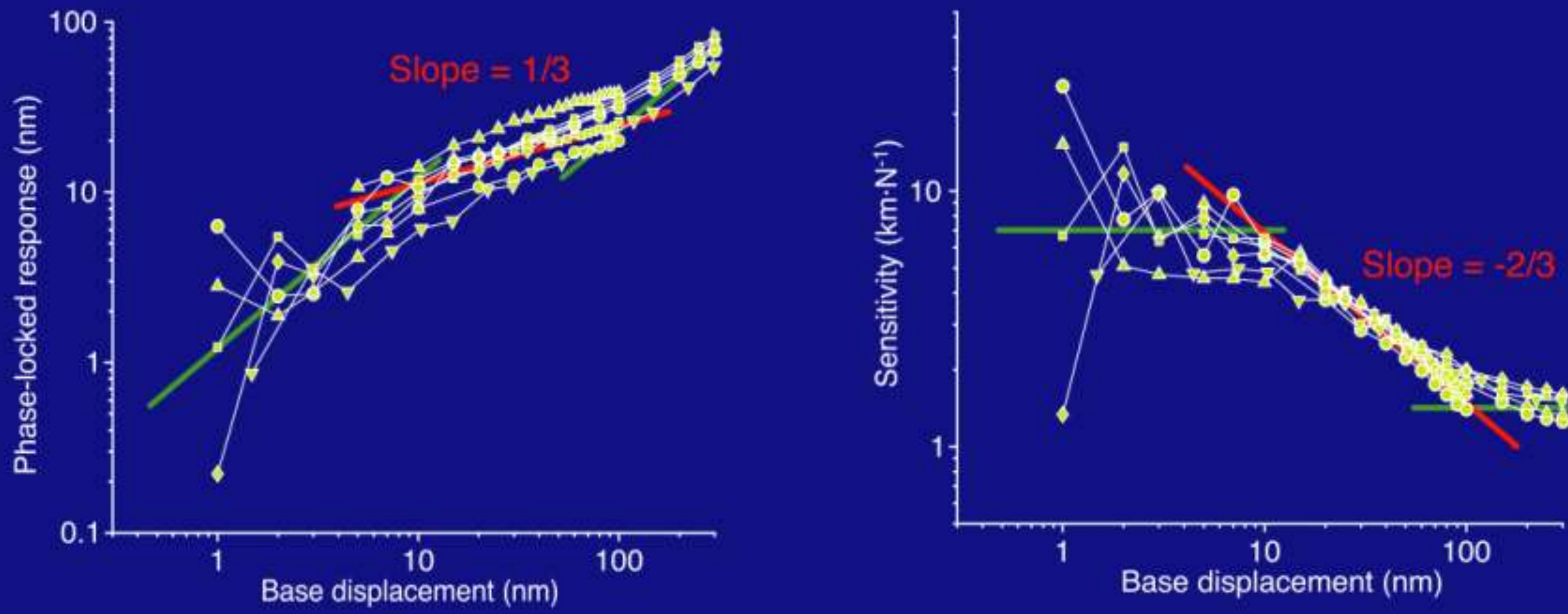
$\overline{W}_{ACTIVE} = -\overline{W}_{DRAG} - \overline{W}_{FIBER} = -1\ zJ$

10 nm

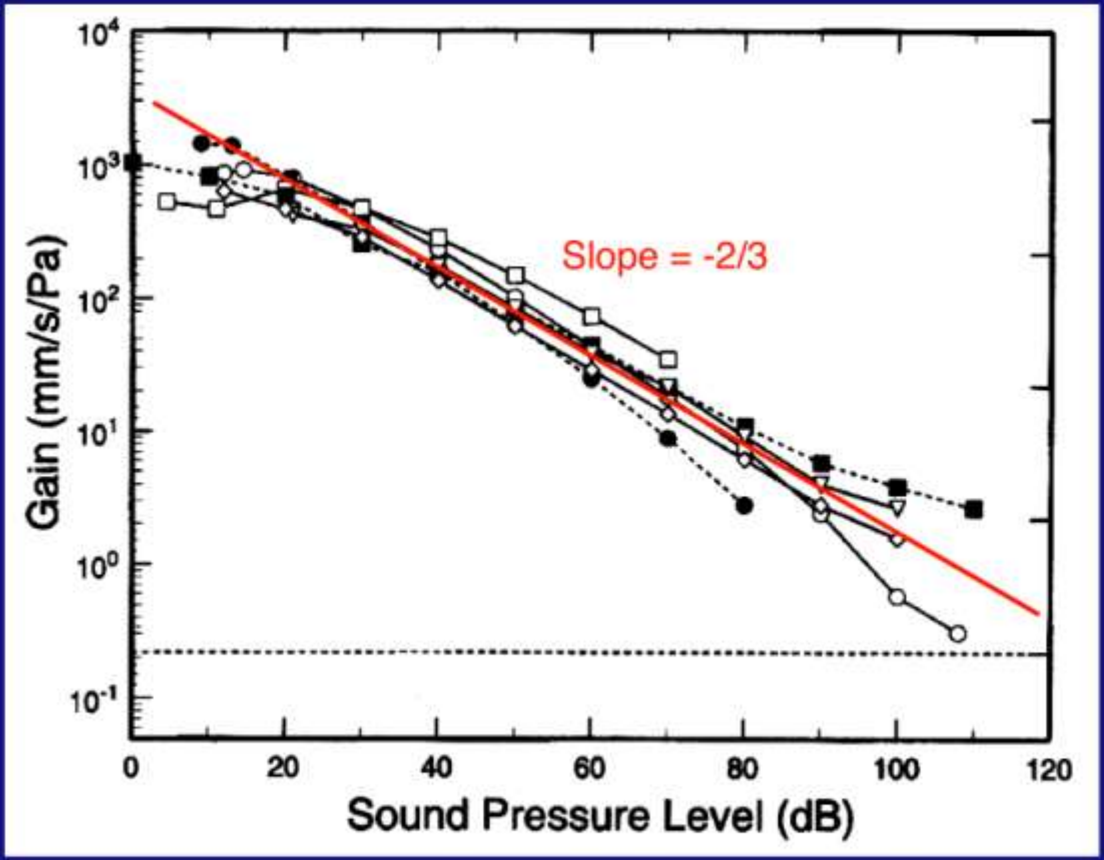
1 pN



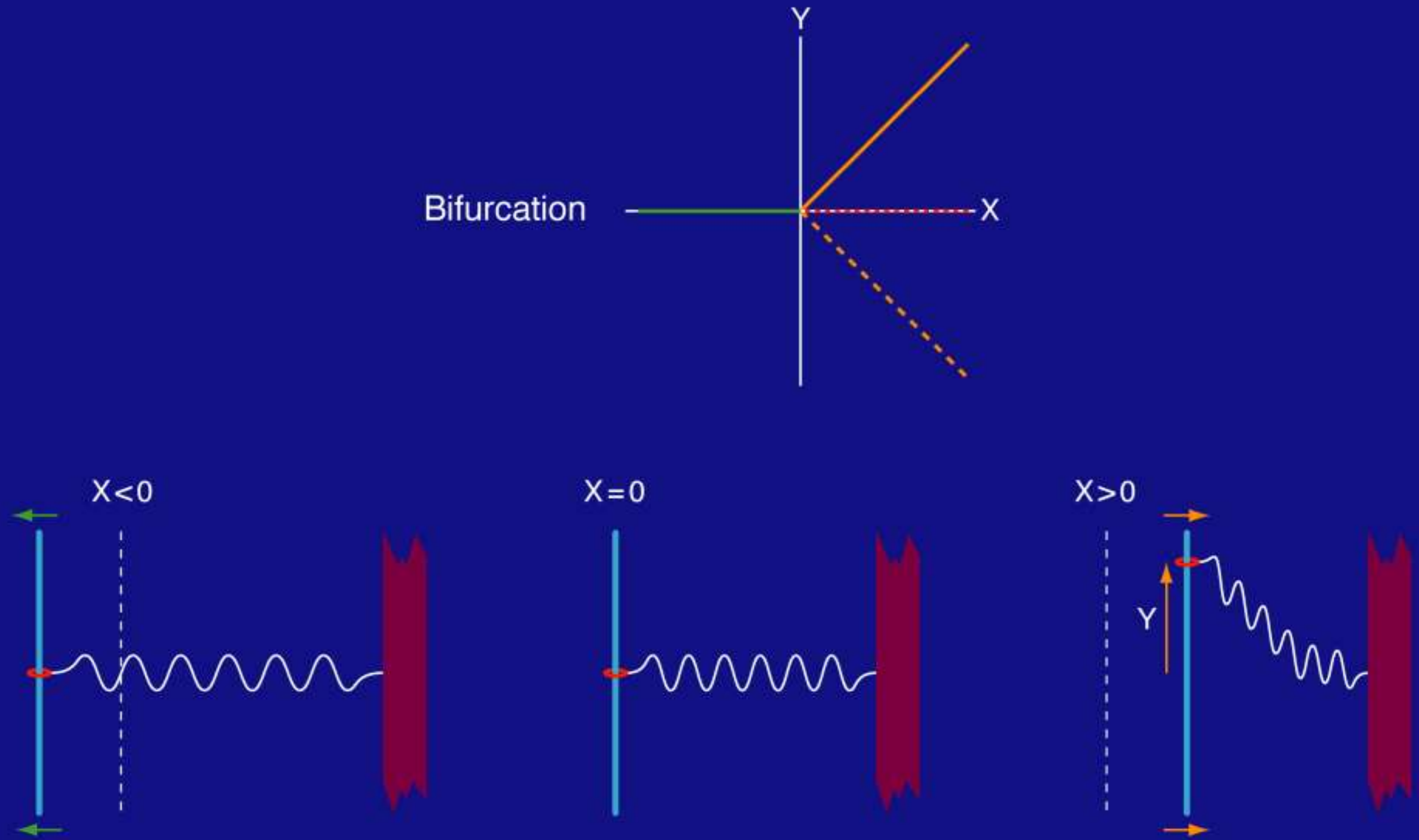
6
5
4
3
2
1
0
Sensitivity (km·N-1)
0
5
10
15
20
25
Frequency (Hz)
80
60
40
20
0
-20
-40
Phase (degrees)
5
10
15
20
25
Frequency (Hz)



Slope = 1/3
Phase-locked response (nm)
100
10
1
0.1
1
10
100
Base displacement (nm)
Sensitivity (km·N⁻¹)
Slope = -2/3
10
1
1
10
100
Base displacement (nm)



After Ruggero, Rich, Recio, Narayan, and Robles (1997)


Y
Bifurcation
X
X<0
X=0
X>0
Y

Equation for a generic Hopf bifurcation:

$$\frac{dz}{dt} = (\mu + i\omega_0)z - |z|^2 z$$

z, displacement (complex variable: $z = x + iy$)

ω_0, natural (characteristic) frequency

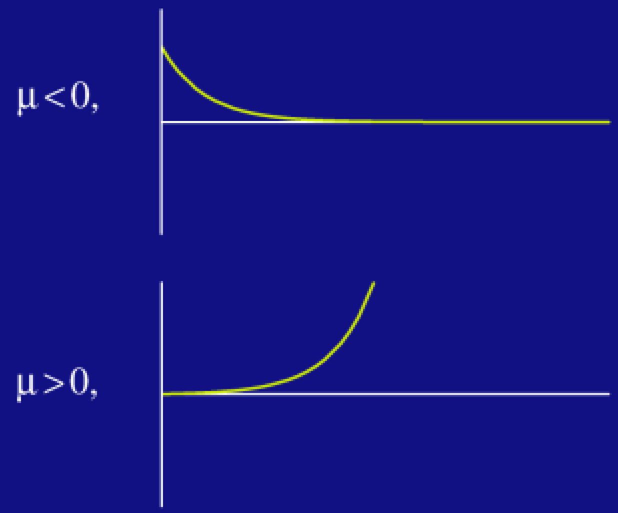
μ, control parameter

Equation for a generic Hopf bifurcation:

$$\frac{dz}{dt} = (\mu + i\omega_0)z - |z|^2 z$$

Simplified term:

$$\frac{dz}{dt} = \mu z \longrightarrow z = e^{\mu t}$$

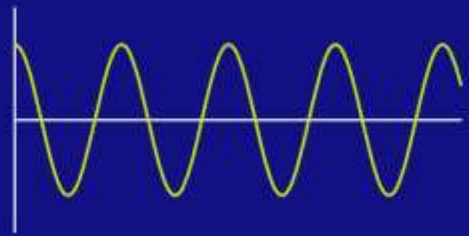


Equation for a generic Hopf bifurcation:

$$\frac{dz}{dt} = (\mu + i\omega_0)z - |z|^2 z$$

Simplified term:

$$\frac{dz}{dt} = i\omega_0 z \longrightarrow z = e^{i\omega_0 t}$$

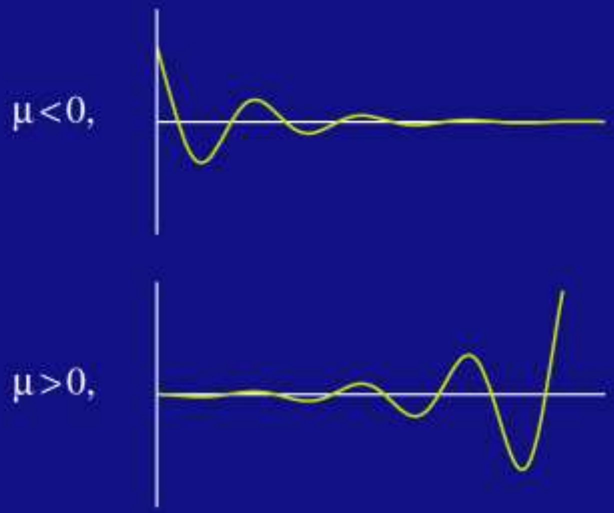


Equation for a generic Hopf bifurcation:

$$\frac{dz}{dt} = (\mu + i\omega_0)z - |z|^2 z$$

Simplified term:

$$\frac{dz}{dt} = (\mu + i\omega_0)z \longrightarrow z = e^{(\mu + i\omega_0)t}$$



During stimulation with a force $Fe^{i\omega t}$:

$$\frac{dz}{dt} = (\mu + i\omega_0)z - |z|^2 z + Fe^{i\omega t}$$

For a phase-locked response of the form $z = Re^{i(\omega t + \phi)}$,

$$F^2 = R^6 - (2\mu)R^4 + [\mu^2 + (\omega - \omega_0)^2]R^2$$

soluble cubic equation

yields F^2 in terms of R^2

At or near bifurcation, $\mu \approx 0$; at or near resonance, $\omega \approx \omega_0$:

$$F^2 \approx R^6$$

$$R \approx F^{1/3}$$

The system's mechanical sensitivity (S) is

$$S = \frac{R}{F} \approx F^{-2/3}$$

Equation for a generic Hopf bifurcation with stimulation by a force $Fe^{i\omega t}$:

$$\frac{dz}{dt} = (\mu + i\omega_0)z - |z|^2 z + Fe^{i\omega t}$$

z, displacement (complex variable: $z = x + iy$)

ω_0, natural (characteristic) frequency

μ, control parameter

In the absence of stimulation,

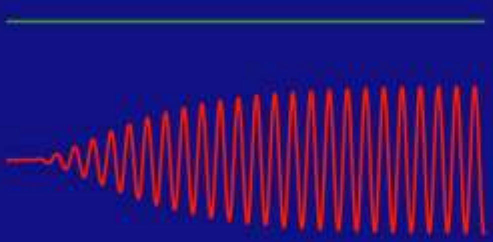
$\mu < 0$,

$z = 0$, a quiescent system

$\mu > 0$,

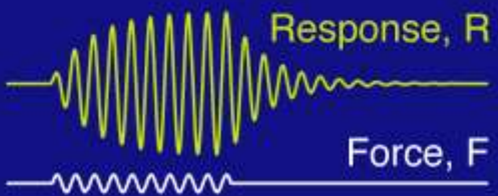
$z = 0$ is unstable

$z = \sqrt{\mu}\, e^{i\omega_0 t} = \sqrt{\mu}\, [\cos(\omega_0 t) + i \cdot \sin(\omega_0 t)]$, a stable limit cycle

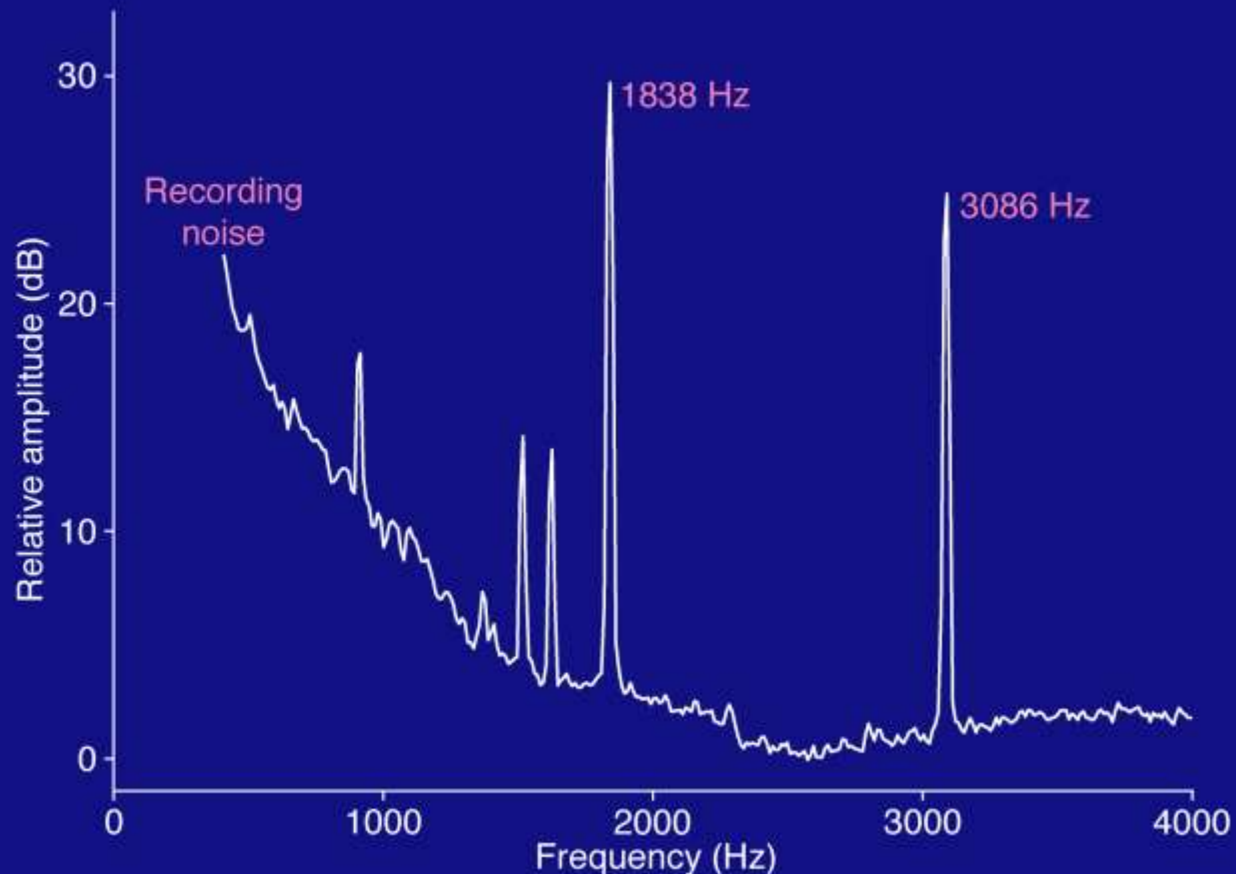


During stimulation near bifurcation ($\mu \approx 0$) and near resonance ($\omega \approx \omega_0$):

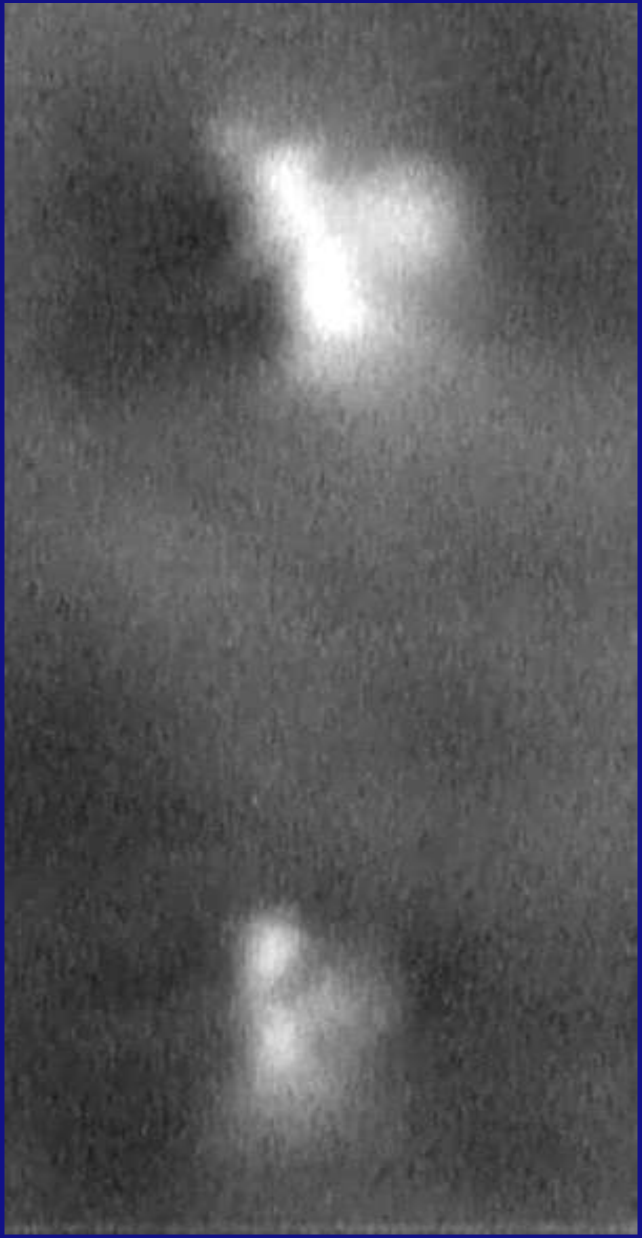
$R \approx F^{1/3}$, amplification with compressive nonlinearity

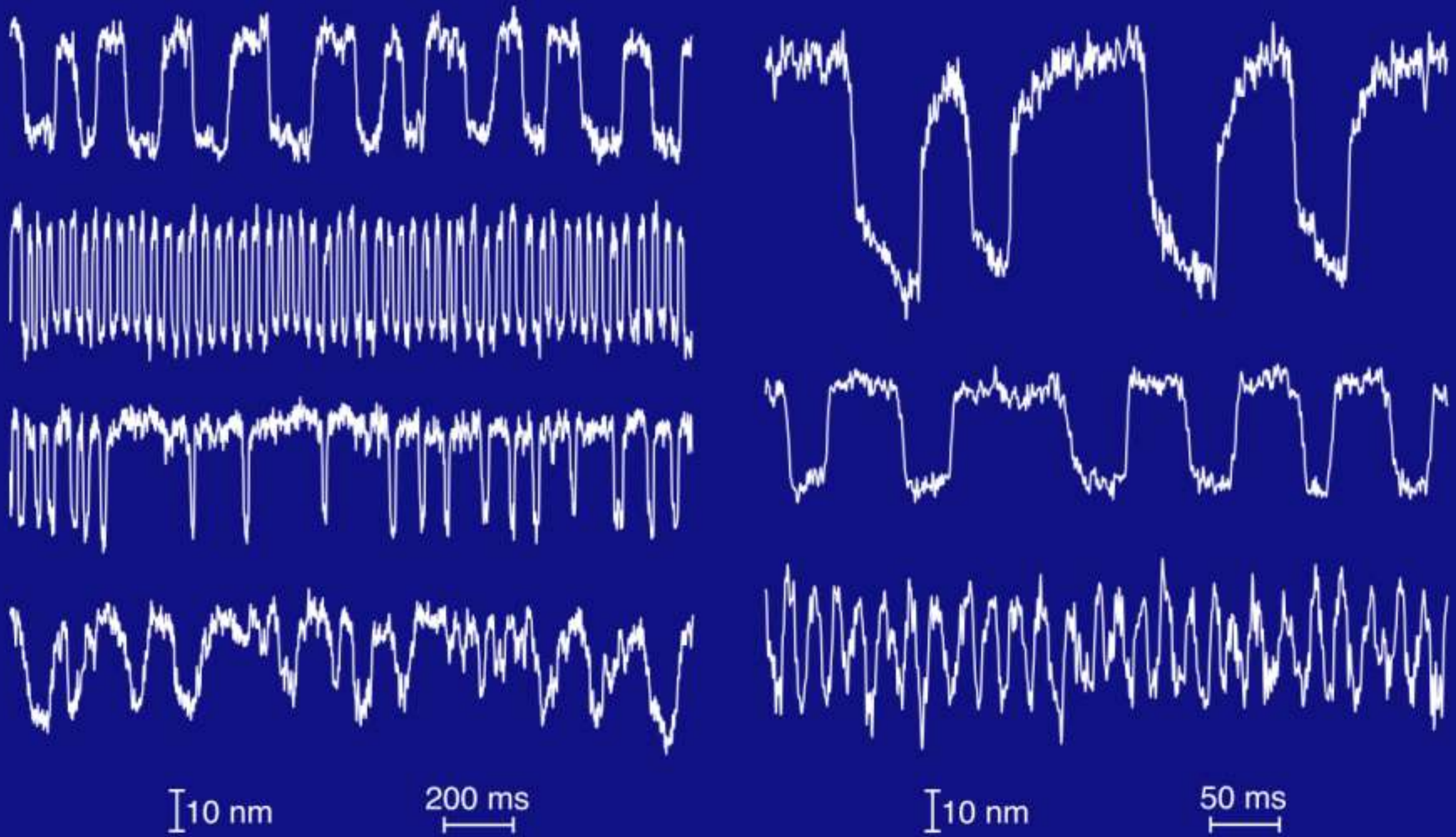


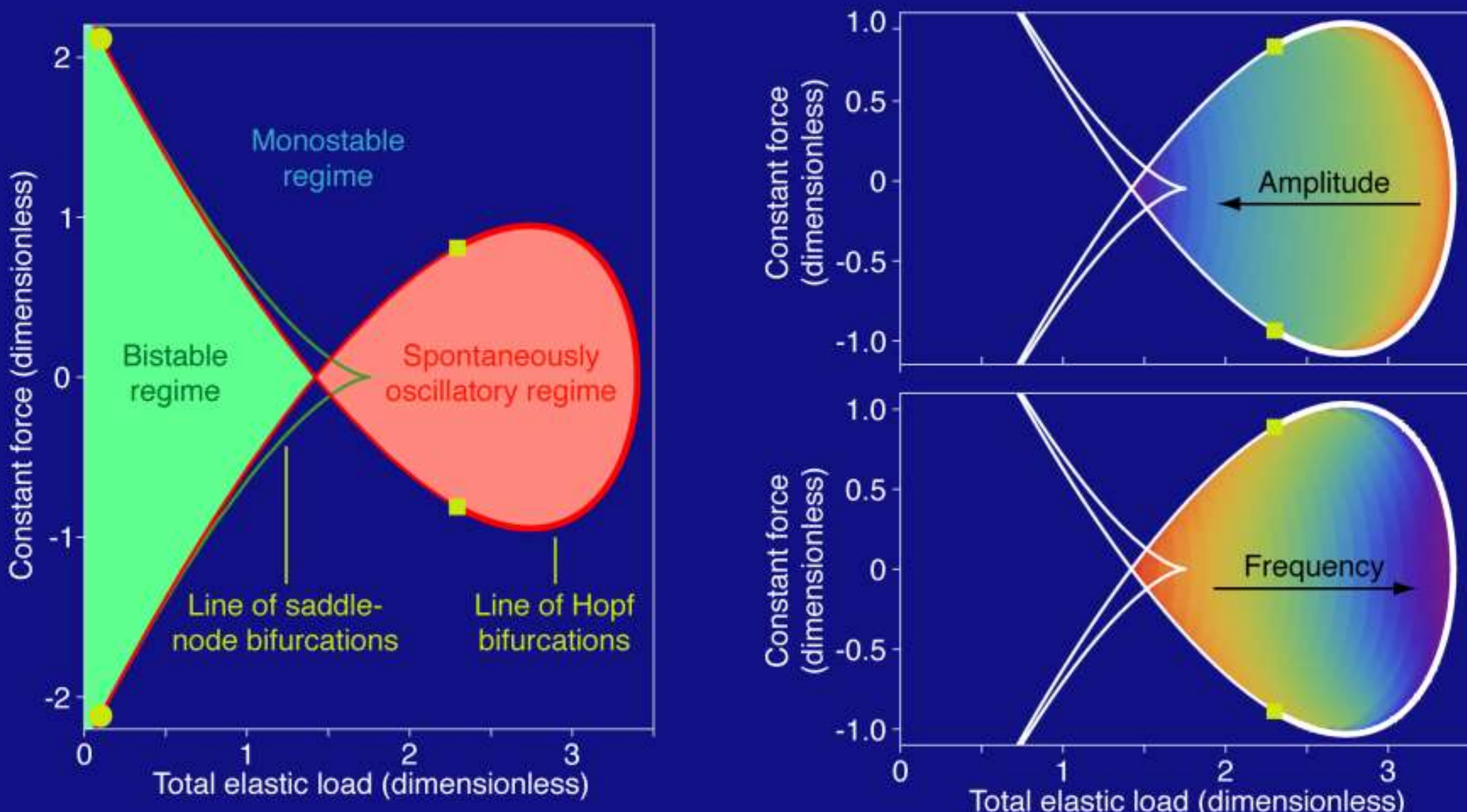
HUMAN SPONTANEOUS OTOACOUSTIC EMISSIONS (SOAEs)



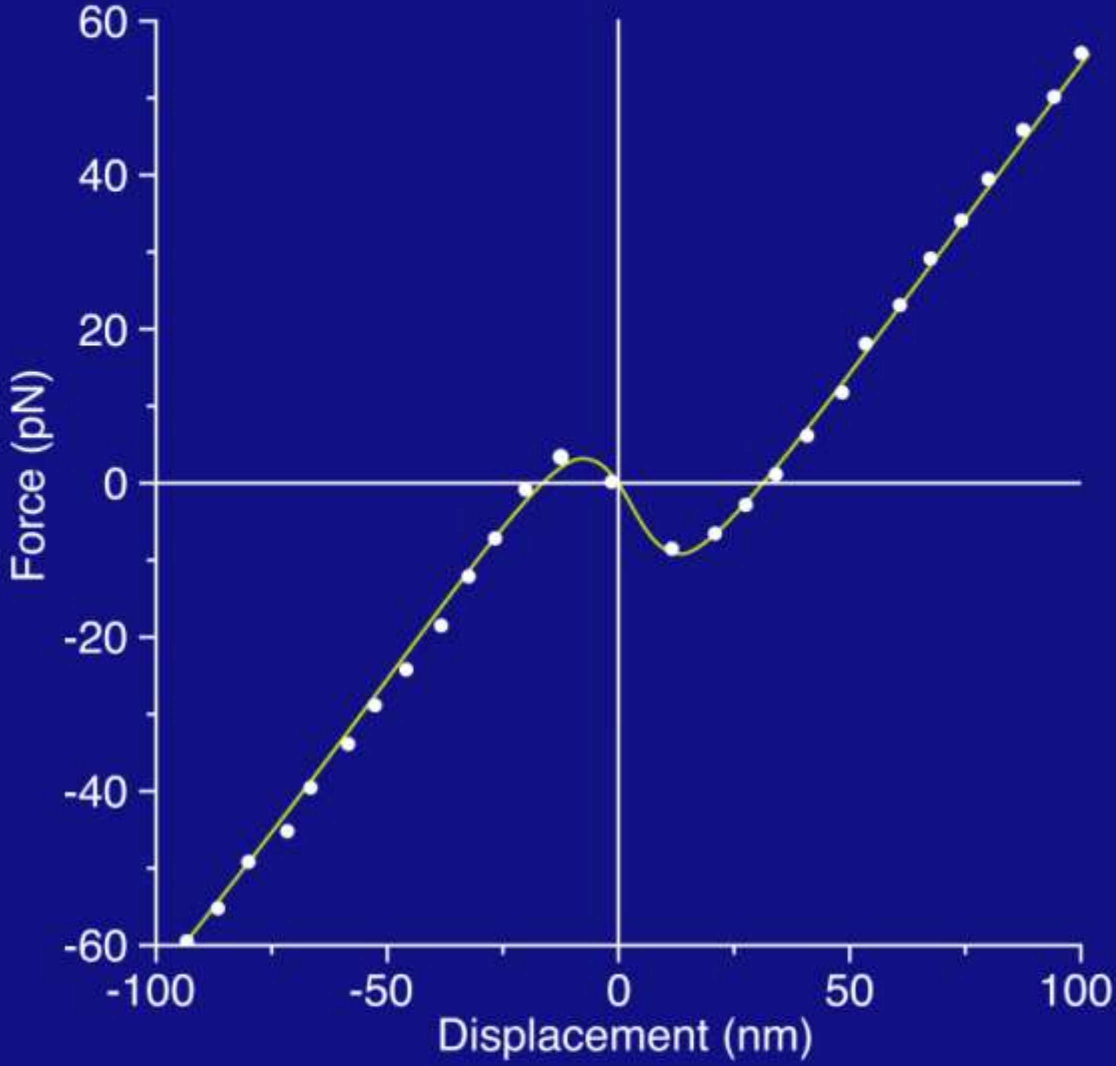
Data from P. van Dijk



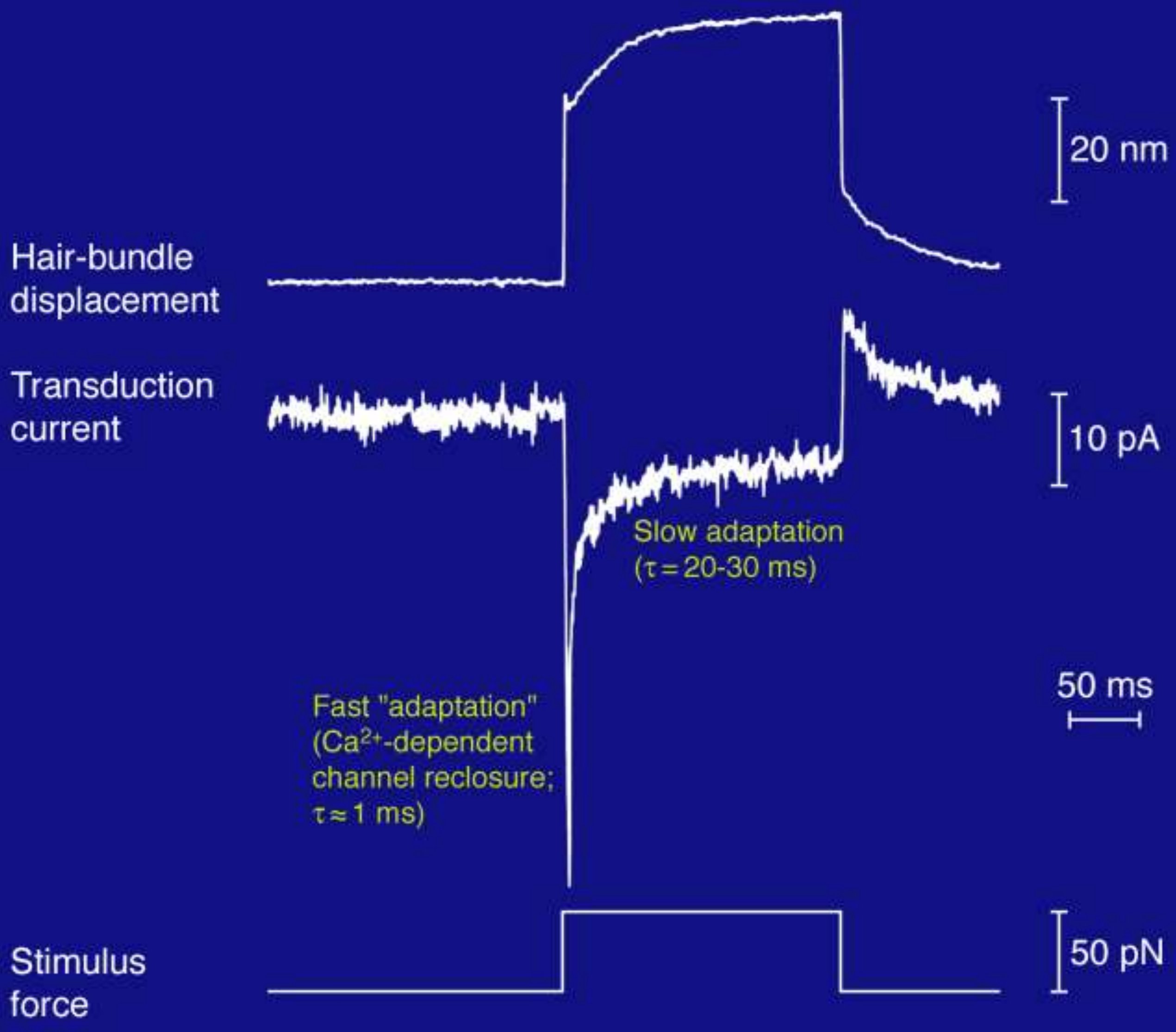

10 nm
200 ms
10 nm
50 ms

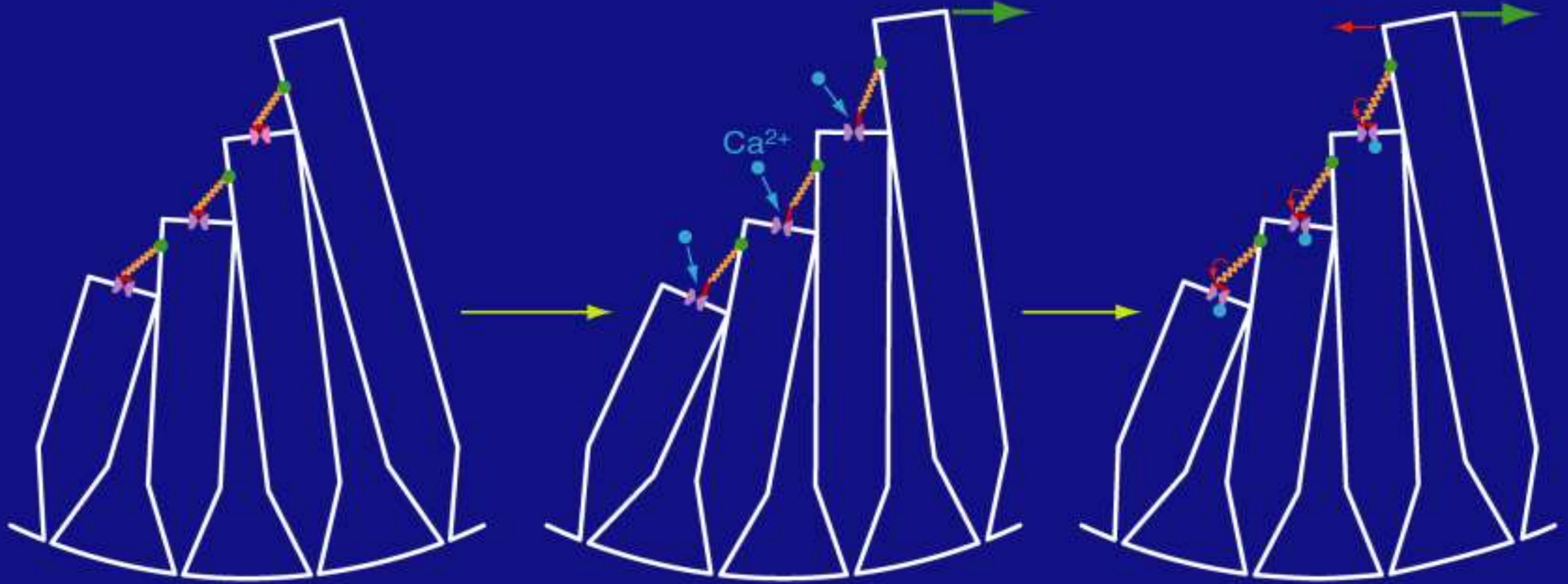


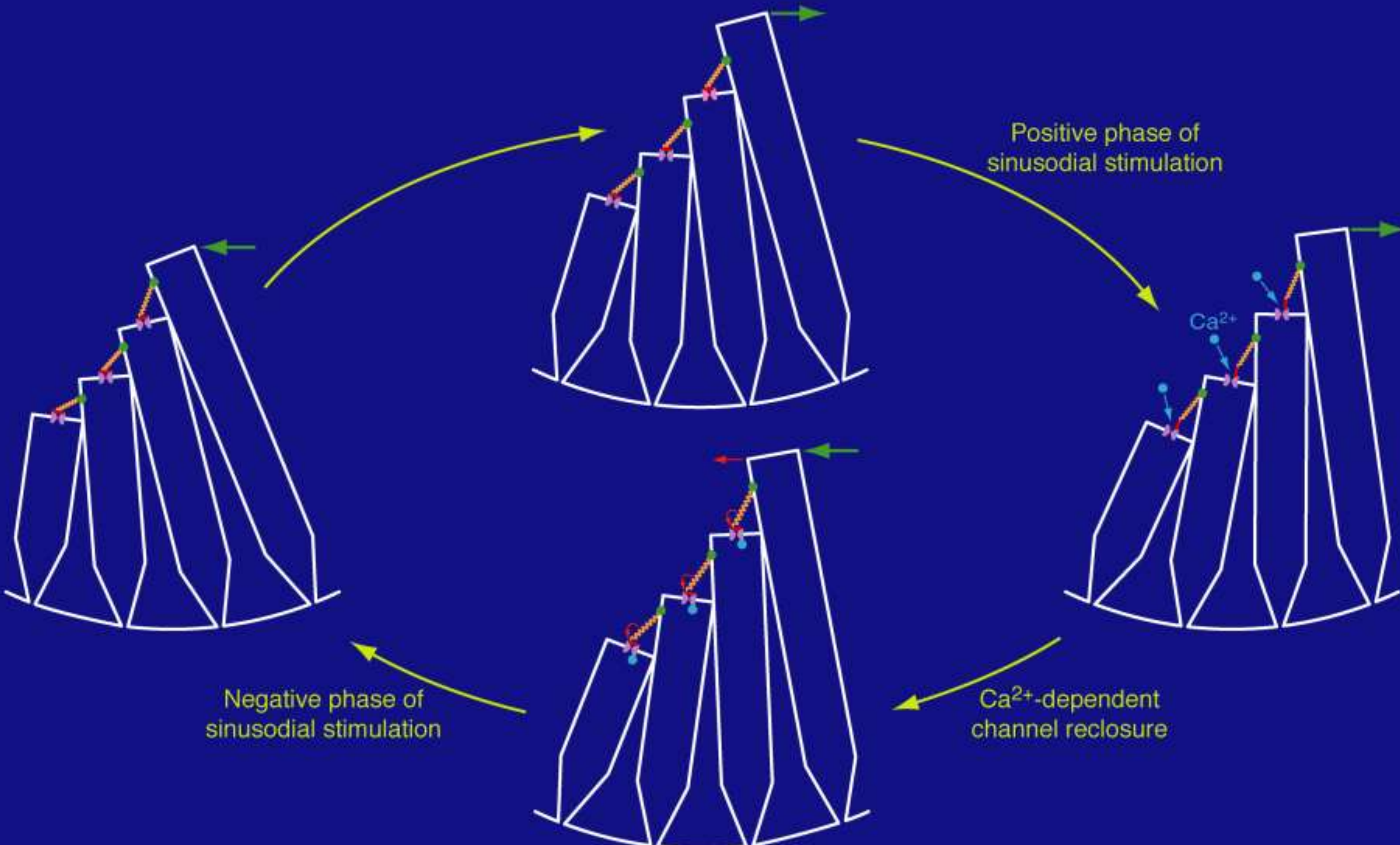
Monostable regime
Bistable regime
Spontaneously oscillatory regime
Line of saddle-node bifurcations
Line of Hopf bifurcations
Constant force (dimensionless)
Total elastic load (dimensionless)
2
1
0
-1
-2
0
1
2
3
Amplitude
Frequency
1.0
0.5
0
-0.5
-1.0



60
40
20
0
-20
-40
-60
Force (pN)
-100
-50
0
50
100
Displacement (nm)

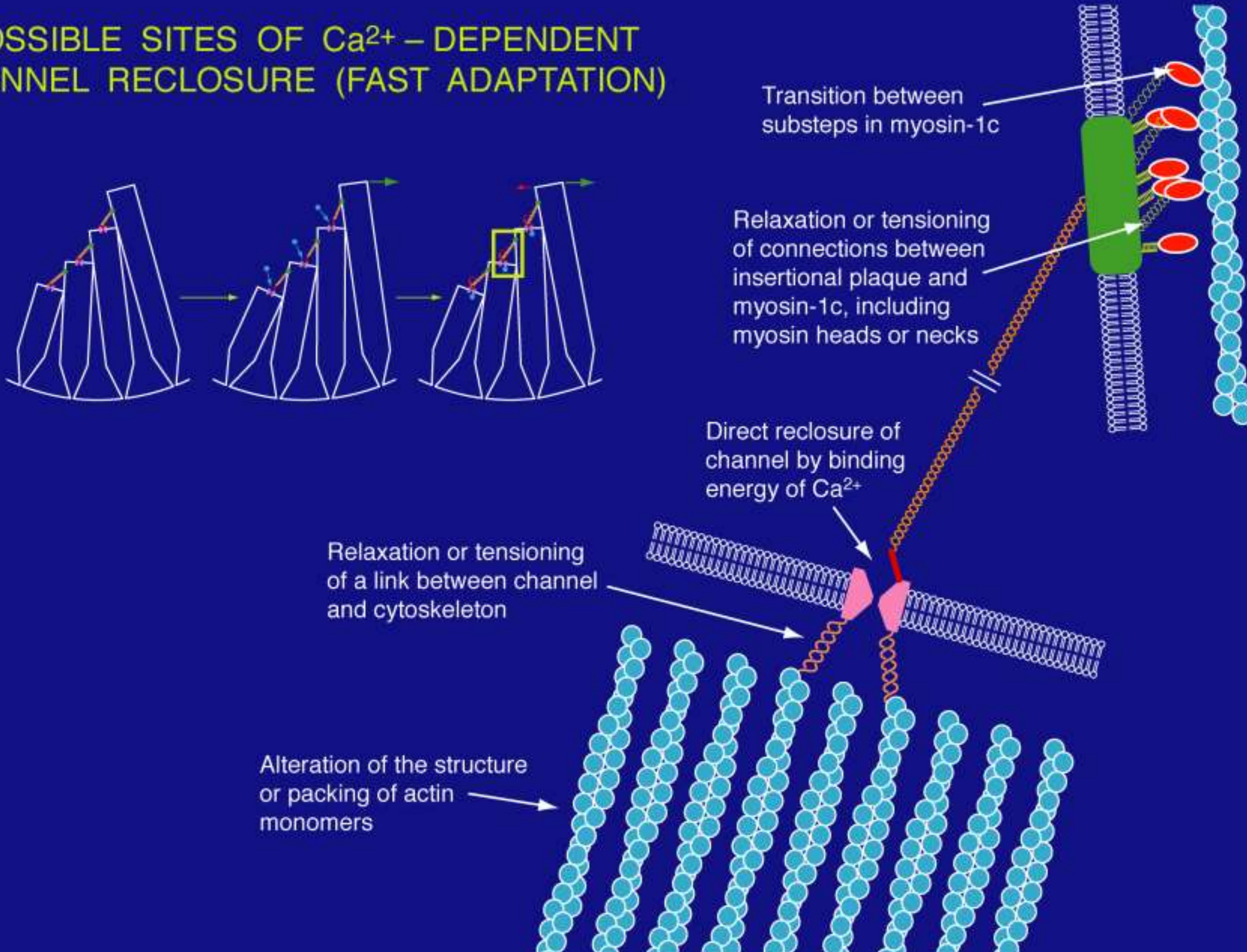

Hair-bundle displacement
Transduction current
Stimulus force
20 nm
10 pA
50 ms
50 pN
Slow adaptation
(τ = 20-30 ms)
Fast "adaptation"
(Ca2+-dependent
channel reclosure;
τ ≈ 1 ms)

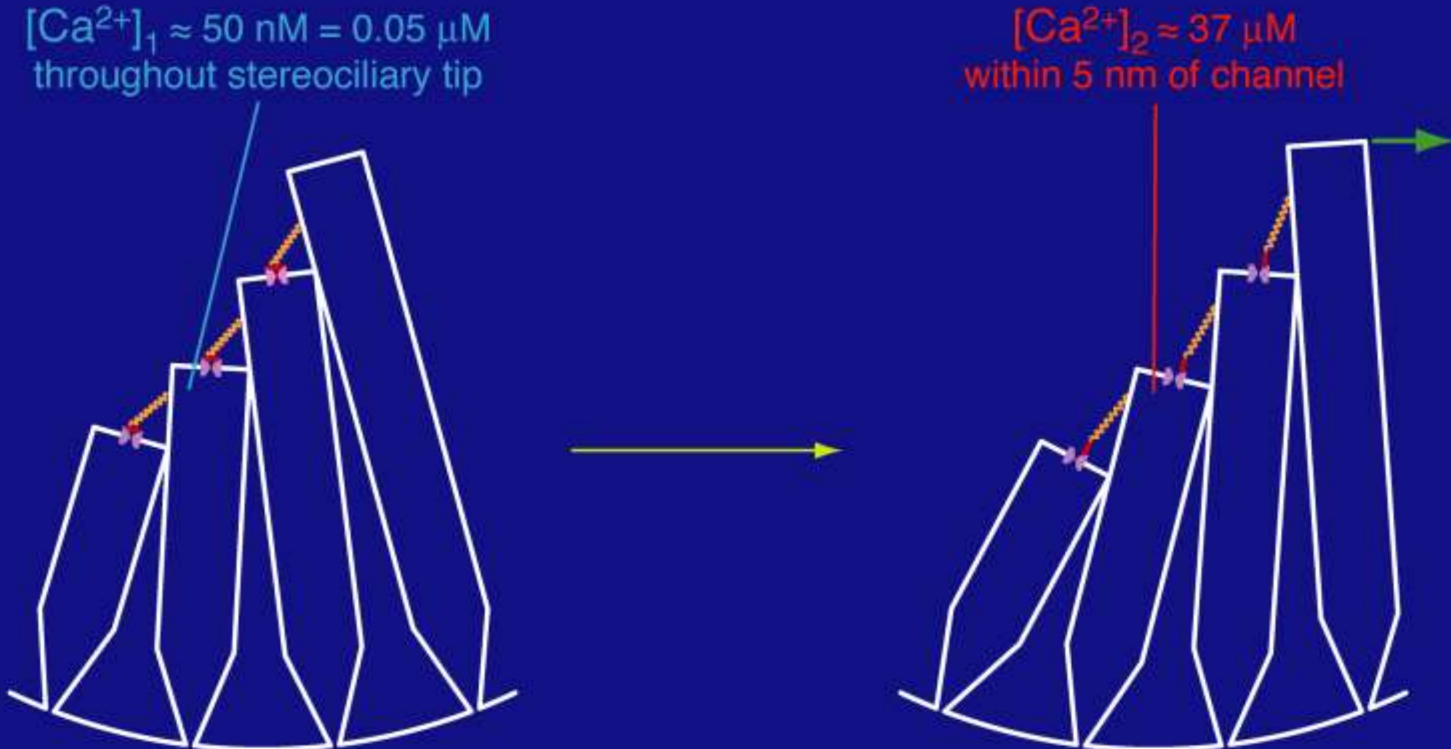

Ca2+



Positive phase of
sinusodial stimulation
Ca2+
Ca2+-dependent
channel reclosure
Negative phase of
sinusodial stimulation

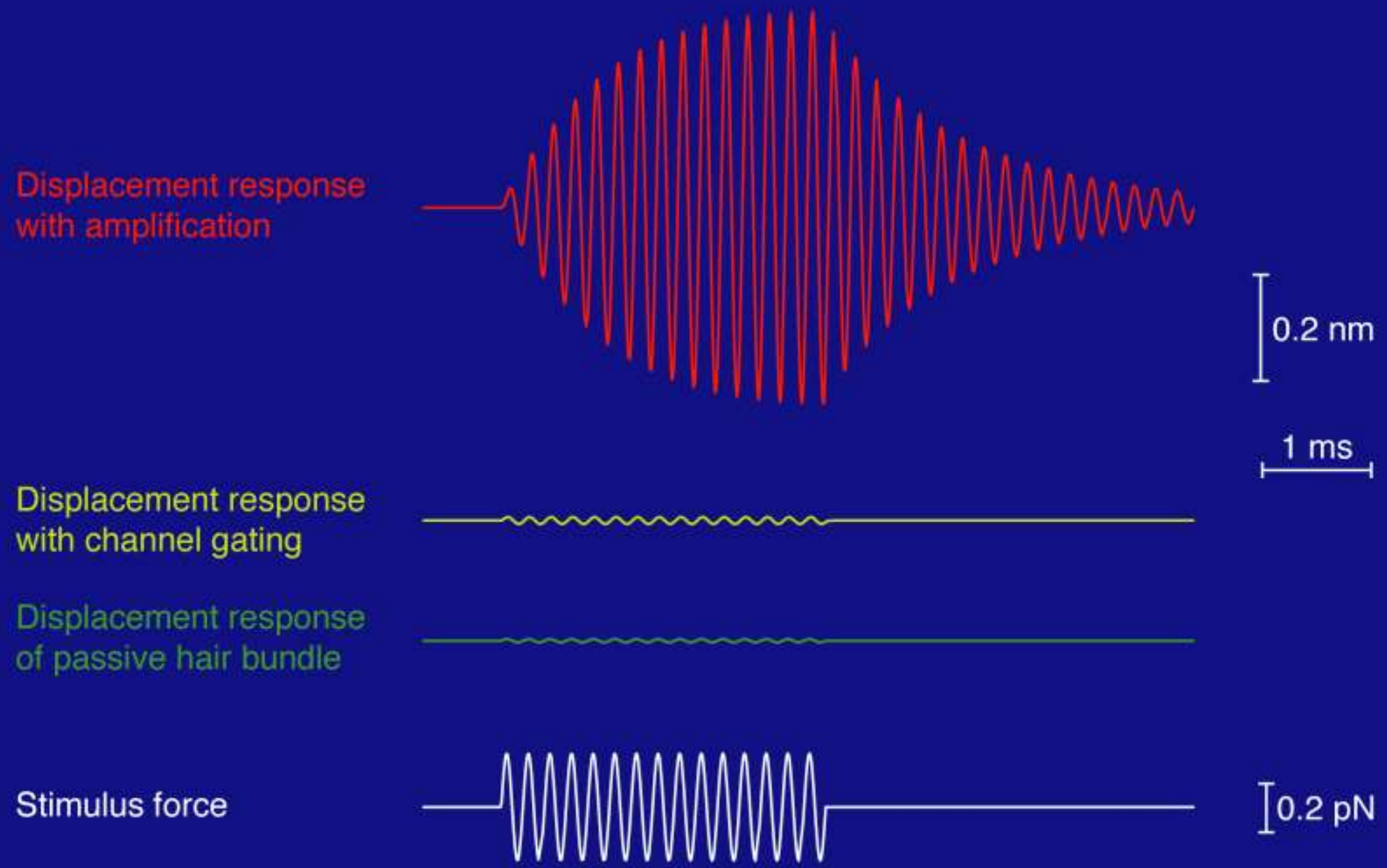
POSSIBLE SITES OF Ca^{2+} – DEPENDENT CHANNEL RECLOSURE (FAST ADAPTATION)

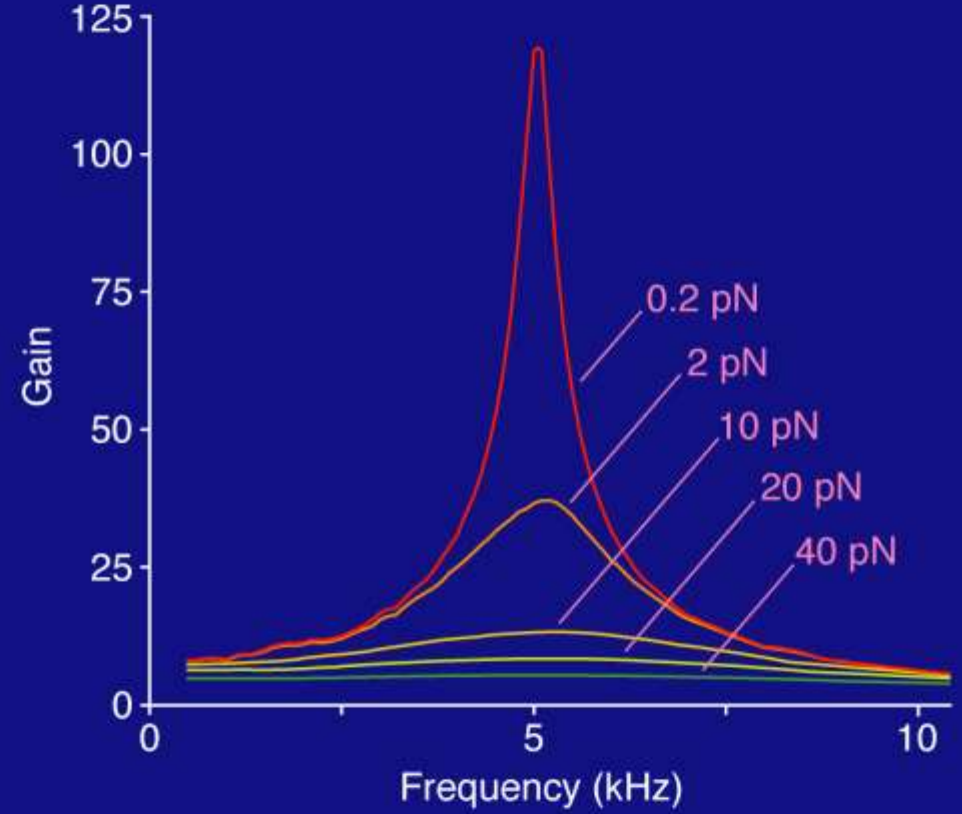


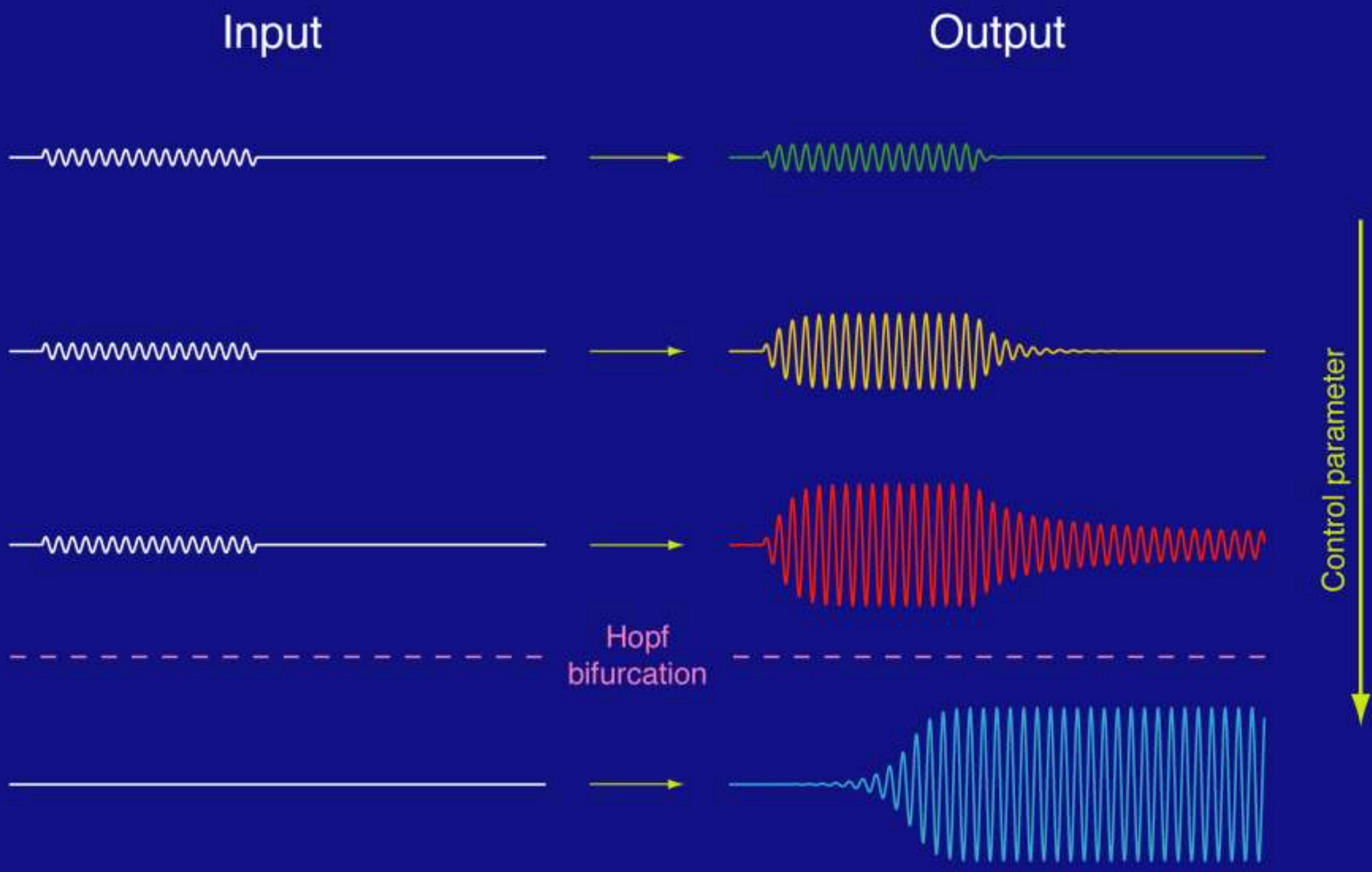


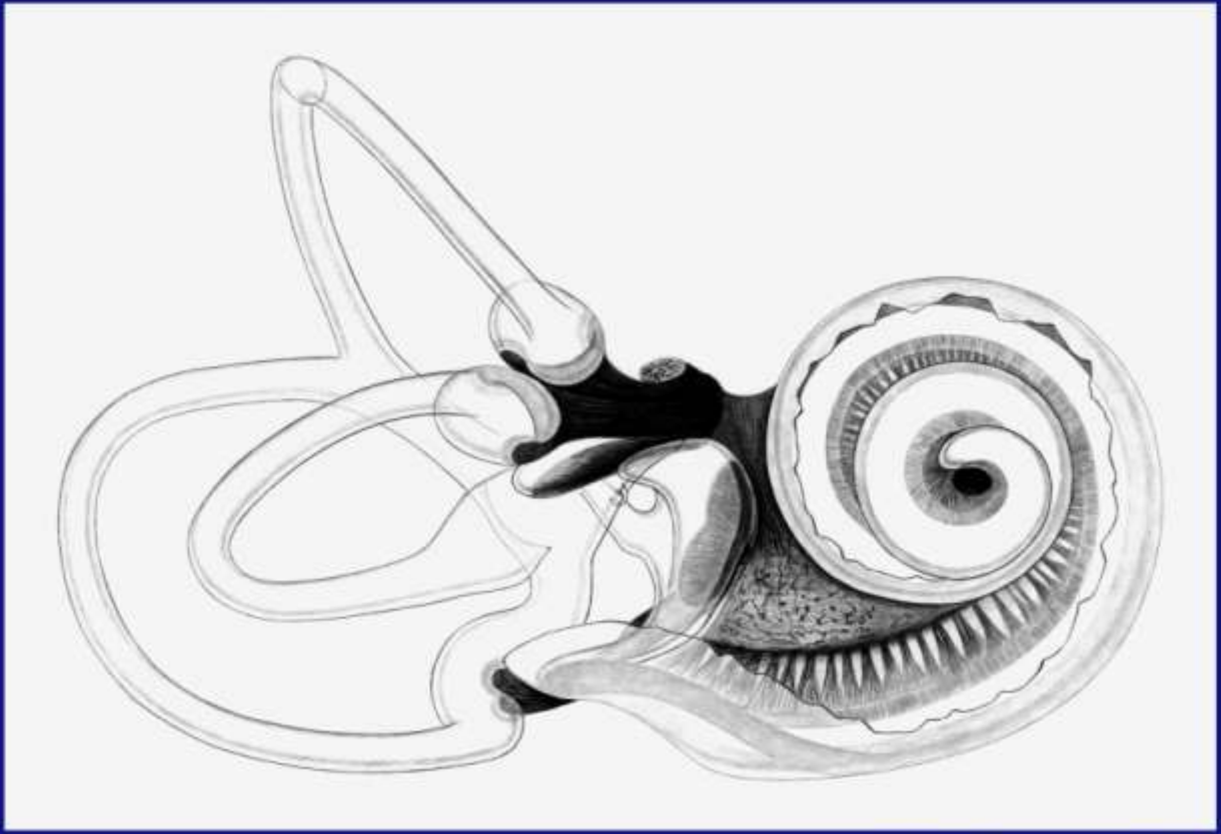
From the change in intracellular Ca^{2+} concentration,

$$\Delta G = kT \cdot \ln\left(\frac{[Ca^{2+}]_2}{[Ca^{2+}]_1}\right) = kT \cdot \ln\left(\frac{37\ \mu M}{0.05\ \mu M}\right) \approx 30\ zJ \approx 7 \cdot kT$$

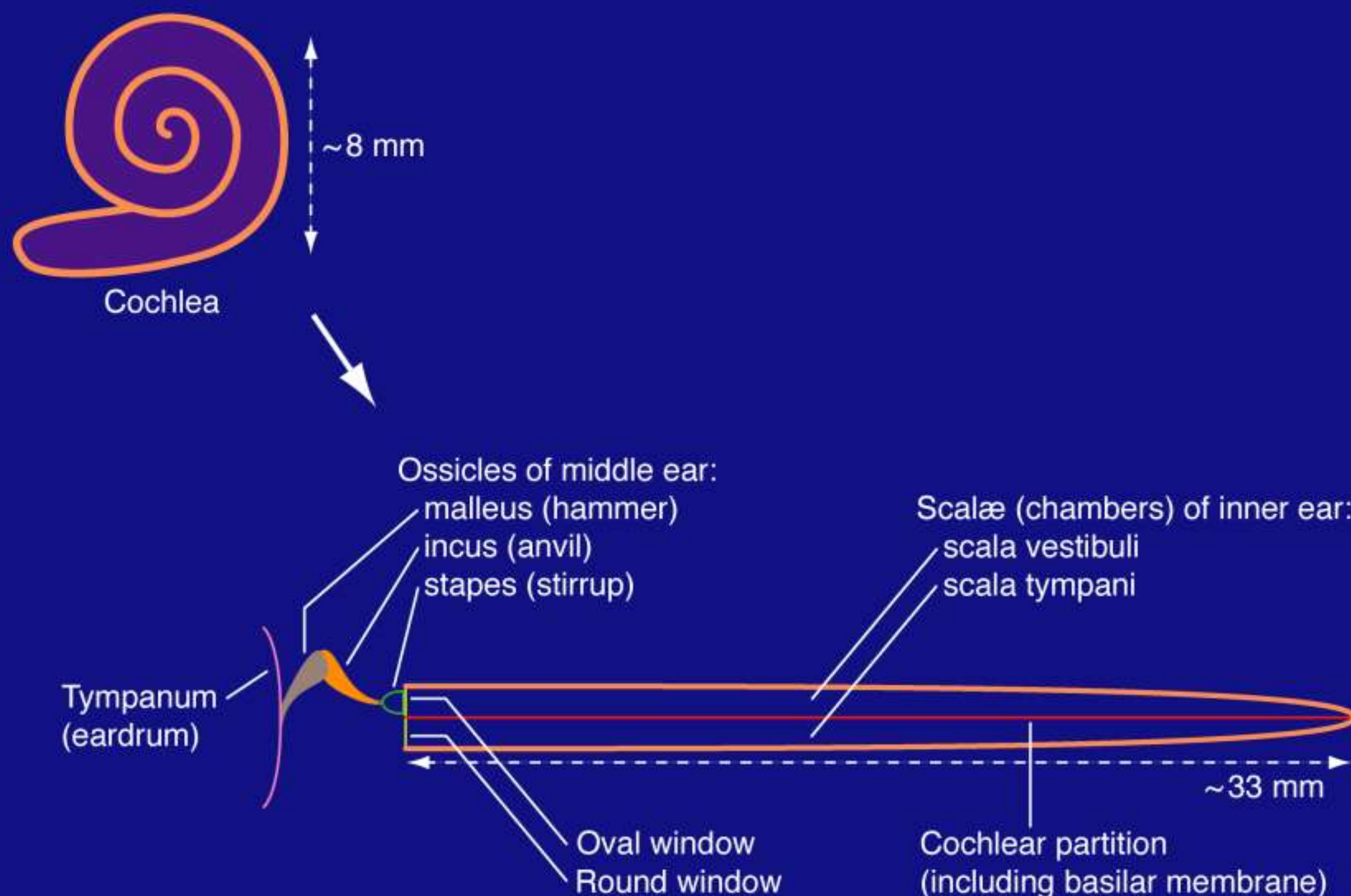

Displacement response
with amplification
0.2 nm
1 ms
Displacement response
with channel gating
Displacement response
of passive hair bundle
Stimulus force
0.2 pN

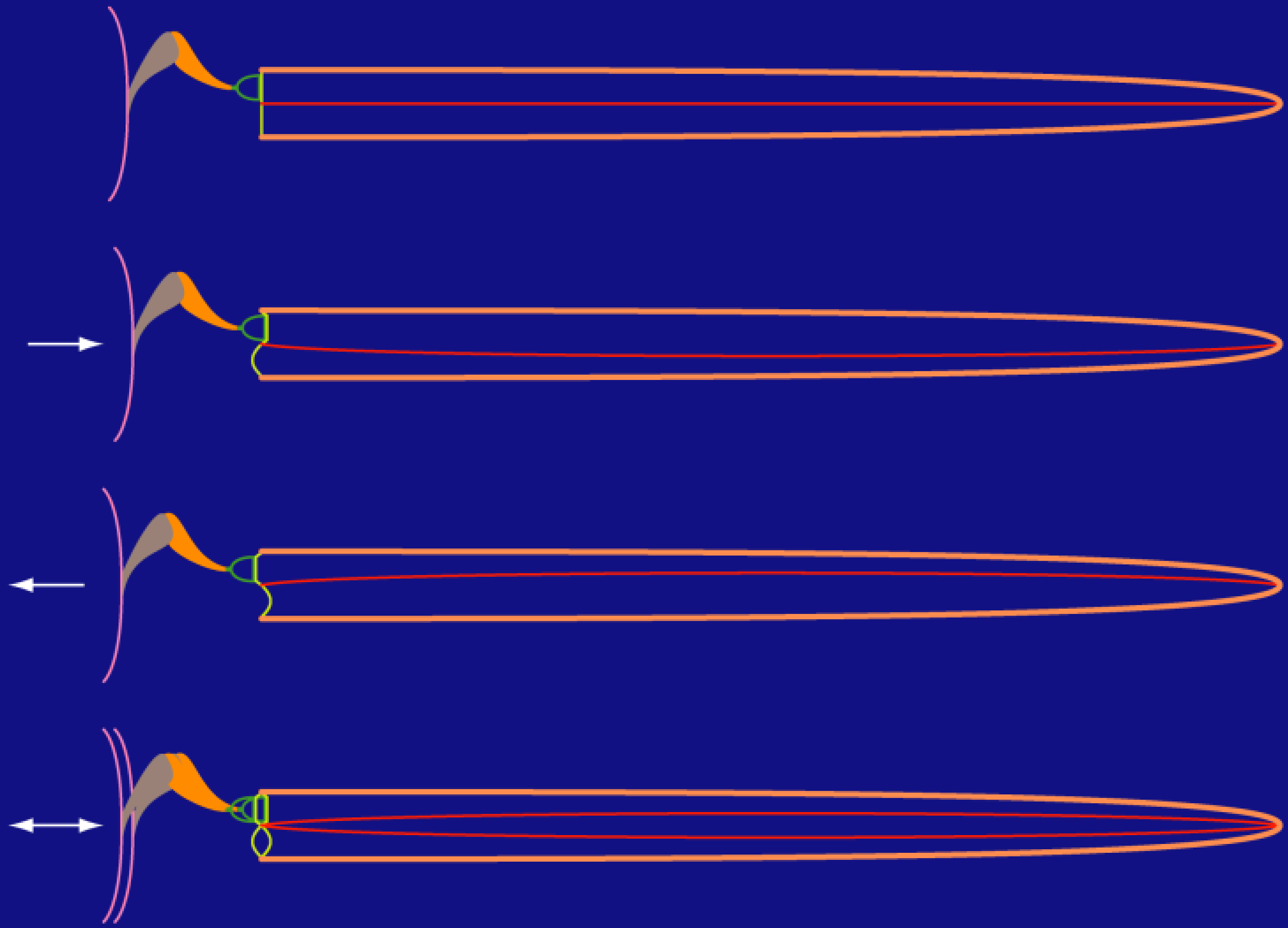

125
100
75
50
25
0
Gain
0
5
10
Frequency (kHz)
0.2 pN
2 pN
10 pN
20 pN
40 pN

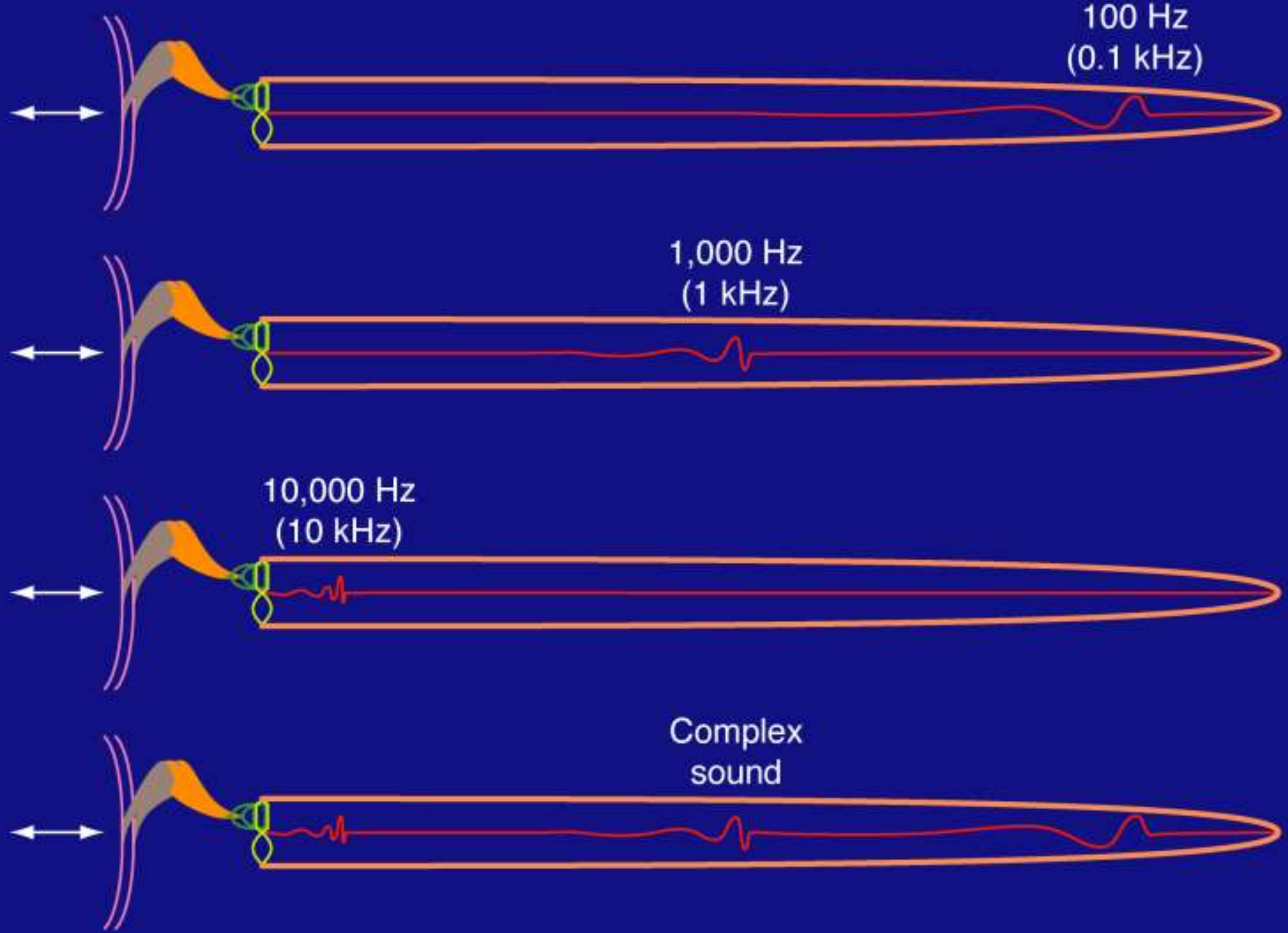

Input
Output
Hopf
bifurcation
Control parameter

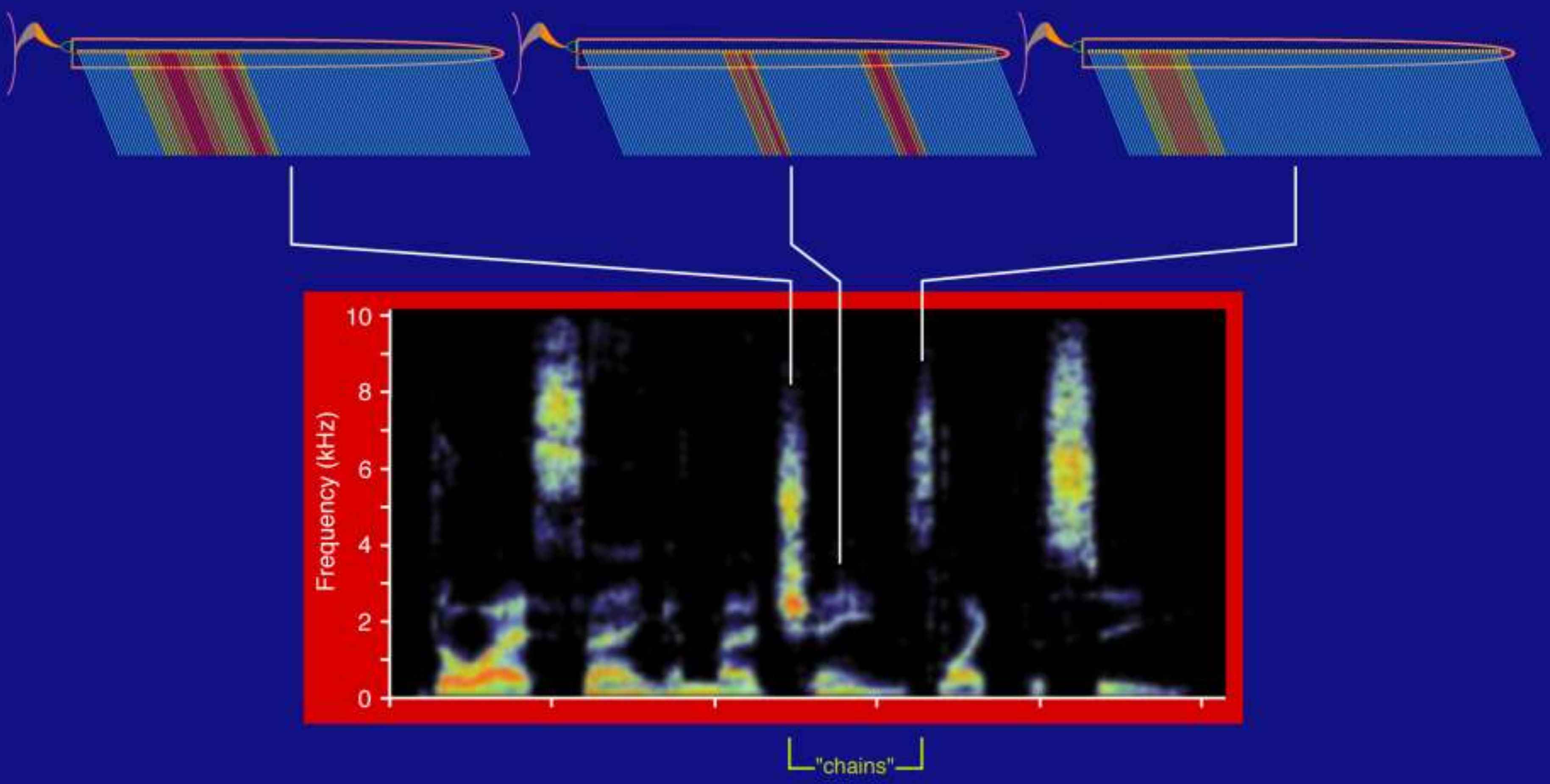


After Retzius, 1884

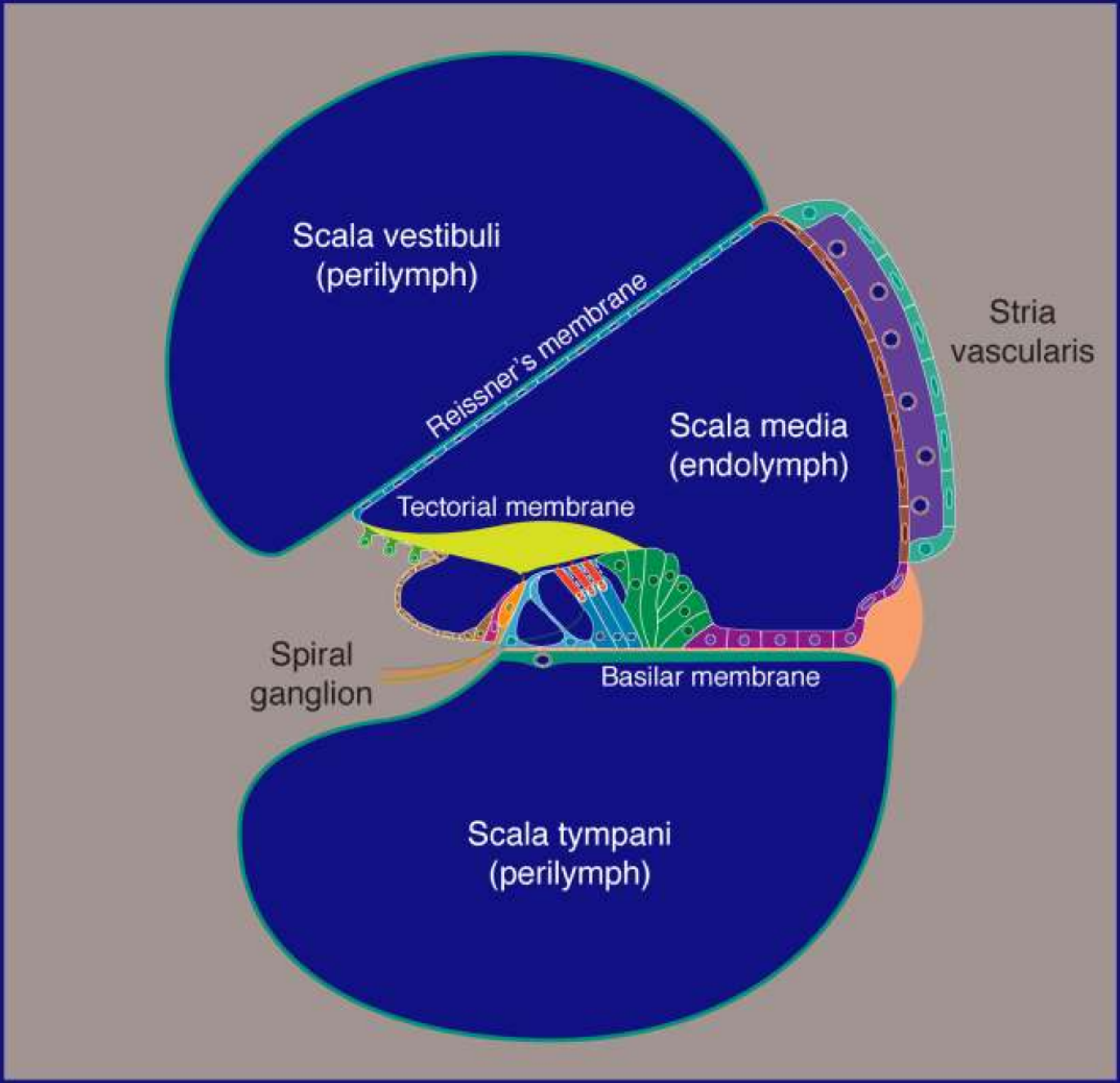

~8 mm
Cochlea
Ossicles of middle ear:
malleus (hammer)
incus (anvil)
stapes (stirrup)
Scalæ (chambers) of inner ear:
scala vestibuli
scala tympani
Tympanum
(eardrum)
~33 mm
Oval window
Round window
Cochlear partition
(including basilar membrane)

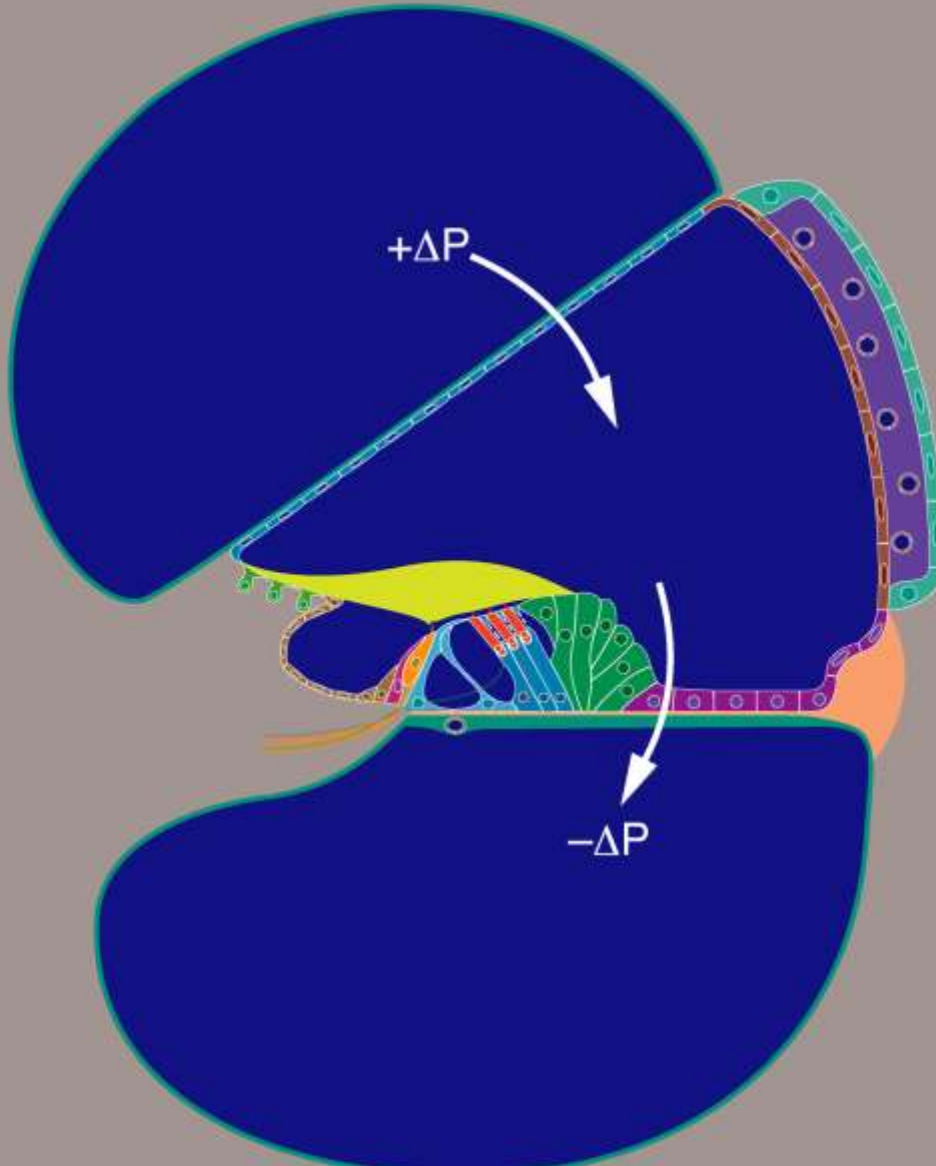



100 Hz
(0.1 kHz)
1,000 Hz
(1 kHz)
10,000 Hz
(10 kHz)
Complex
sound

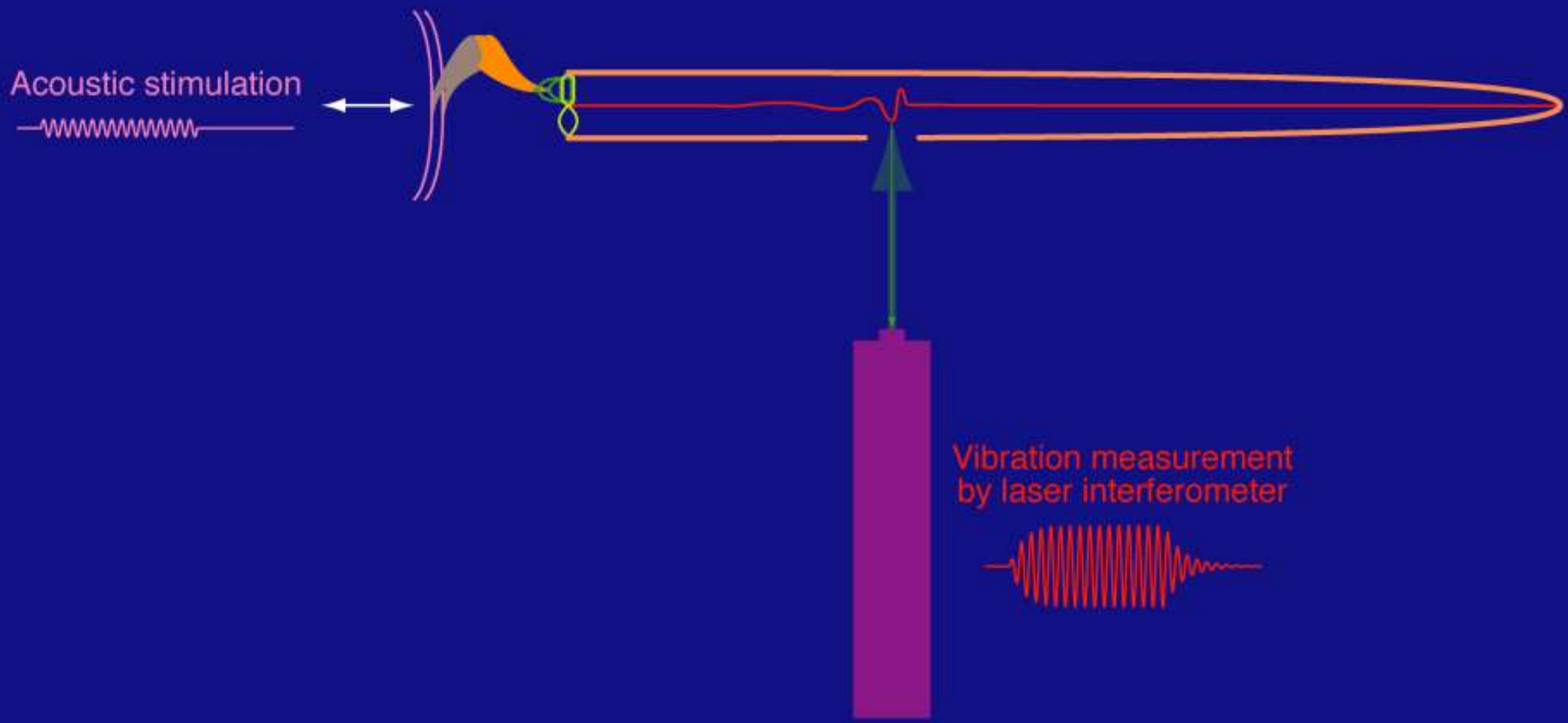


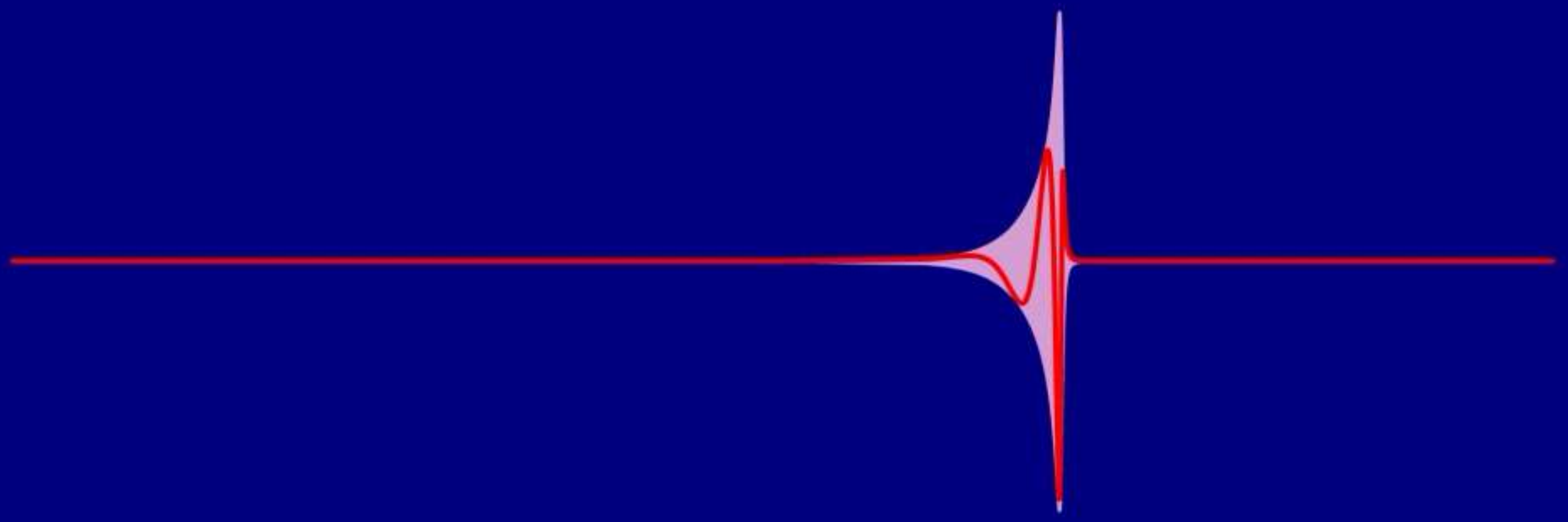
10
8
6
4
2
0
Frequency (kHz)
"chains"


Scala vestibuli
(perilymph)
Reissner's membrane
Stria
vascularis
Scala media
(endolymph)
Tectorial membrane
Spiral
ganglion
Basilar membrane
Scala tympani
(perilymph)

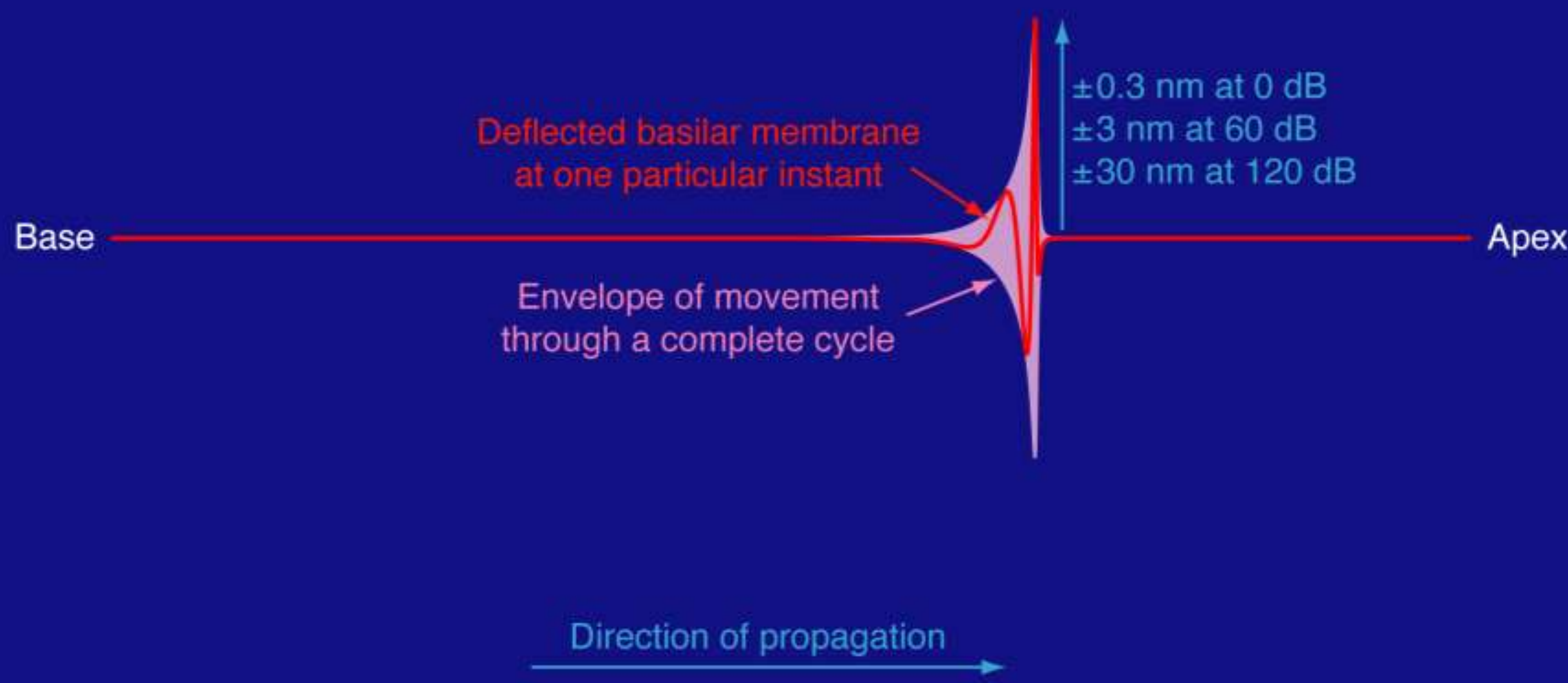


+ΔP
−ΔP


Acoustic stimulation
Vibration measurement
by laser interferometer

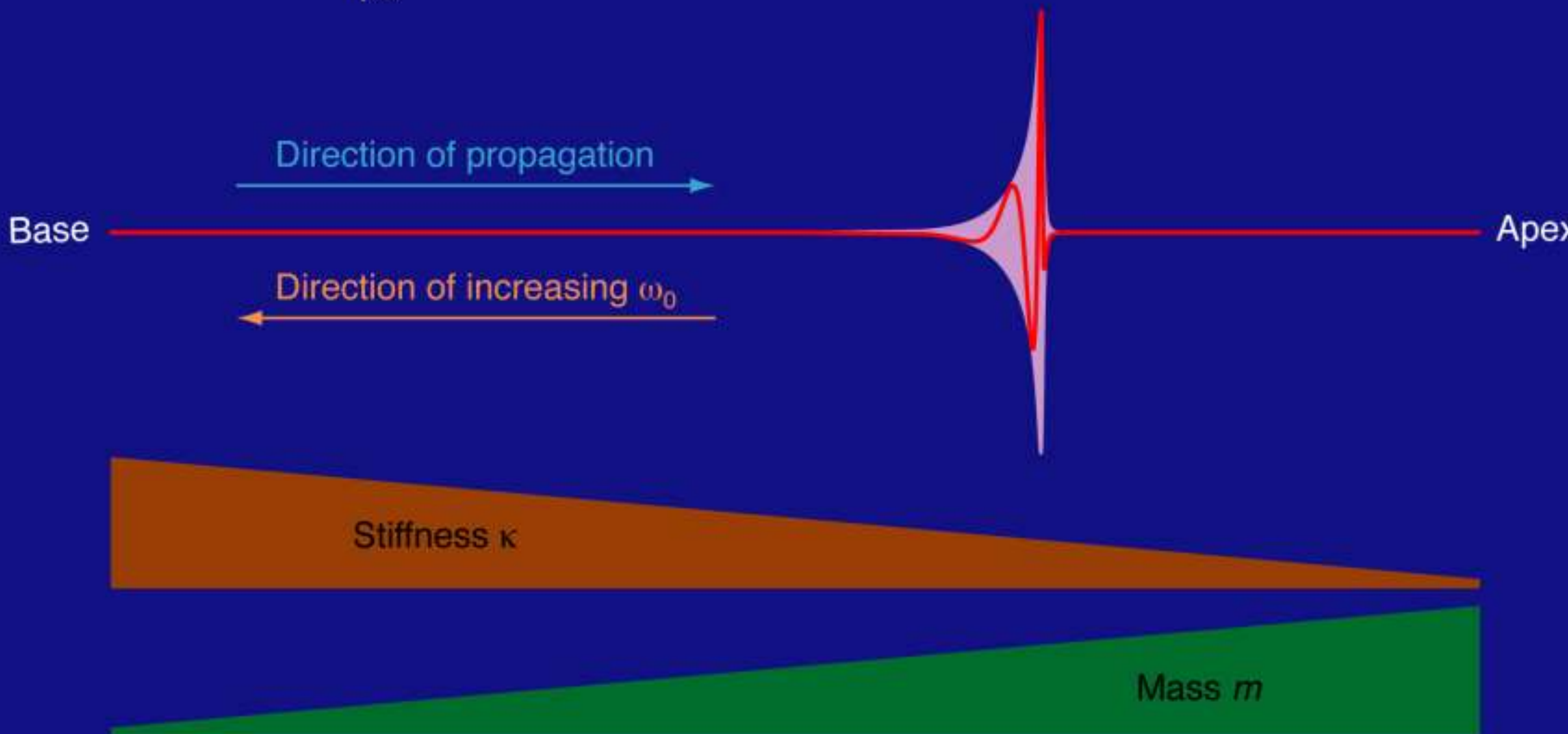


THE COCHLEAR TRAVELING WAVE

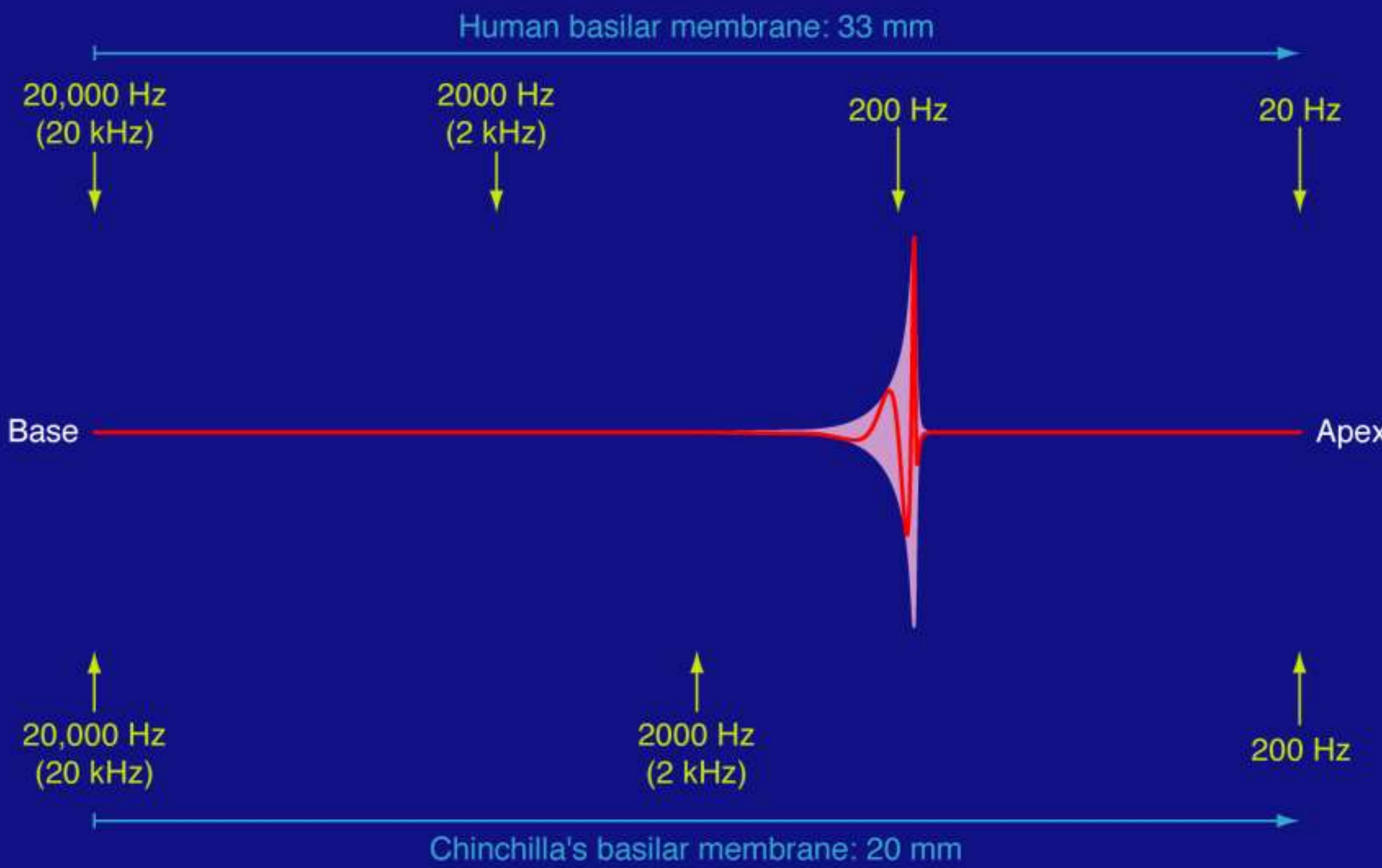


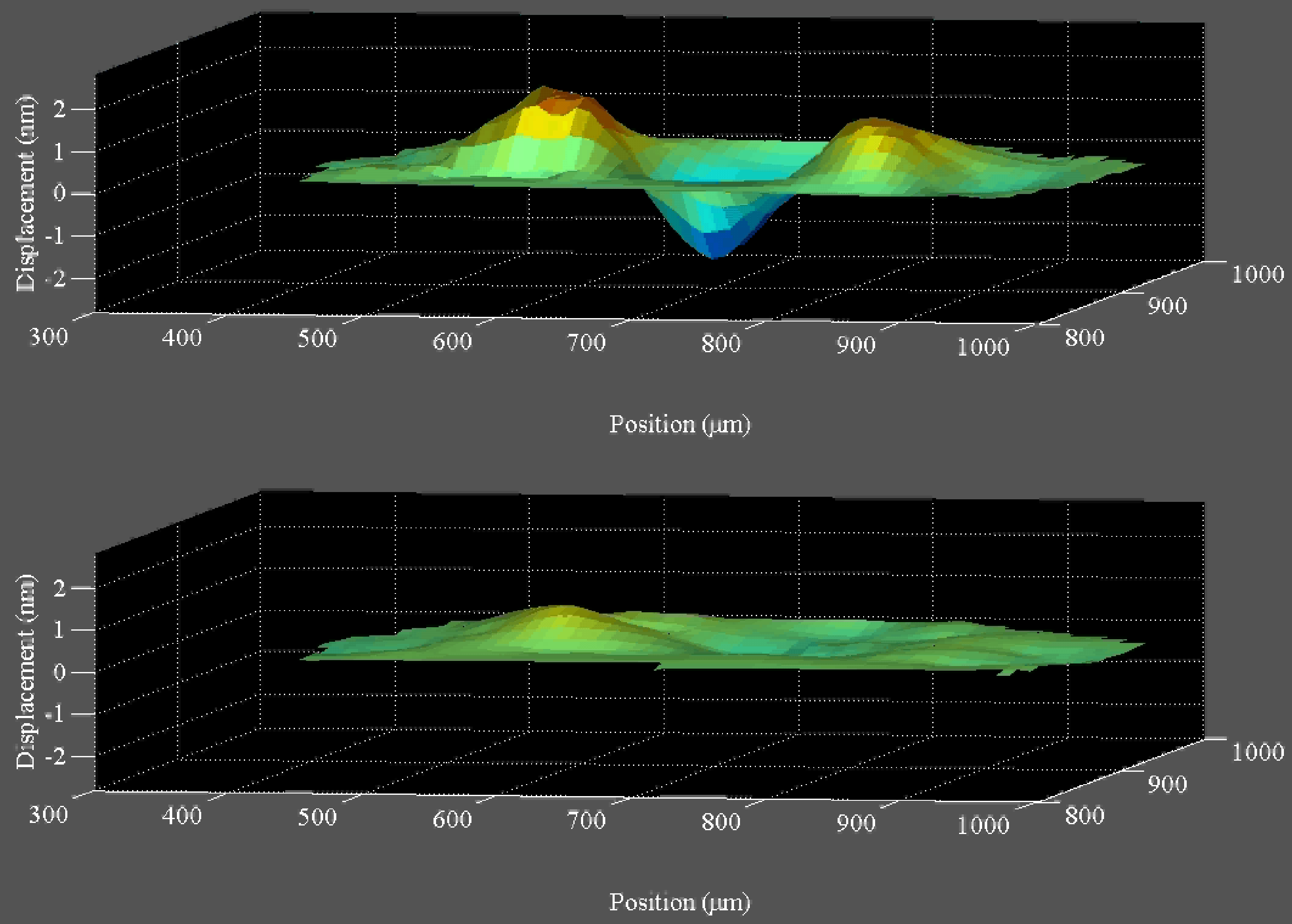
THE COCHLEAR TRAVELING WAVE

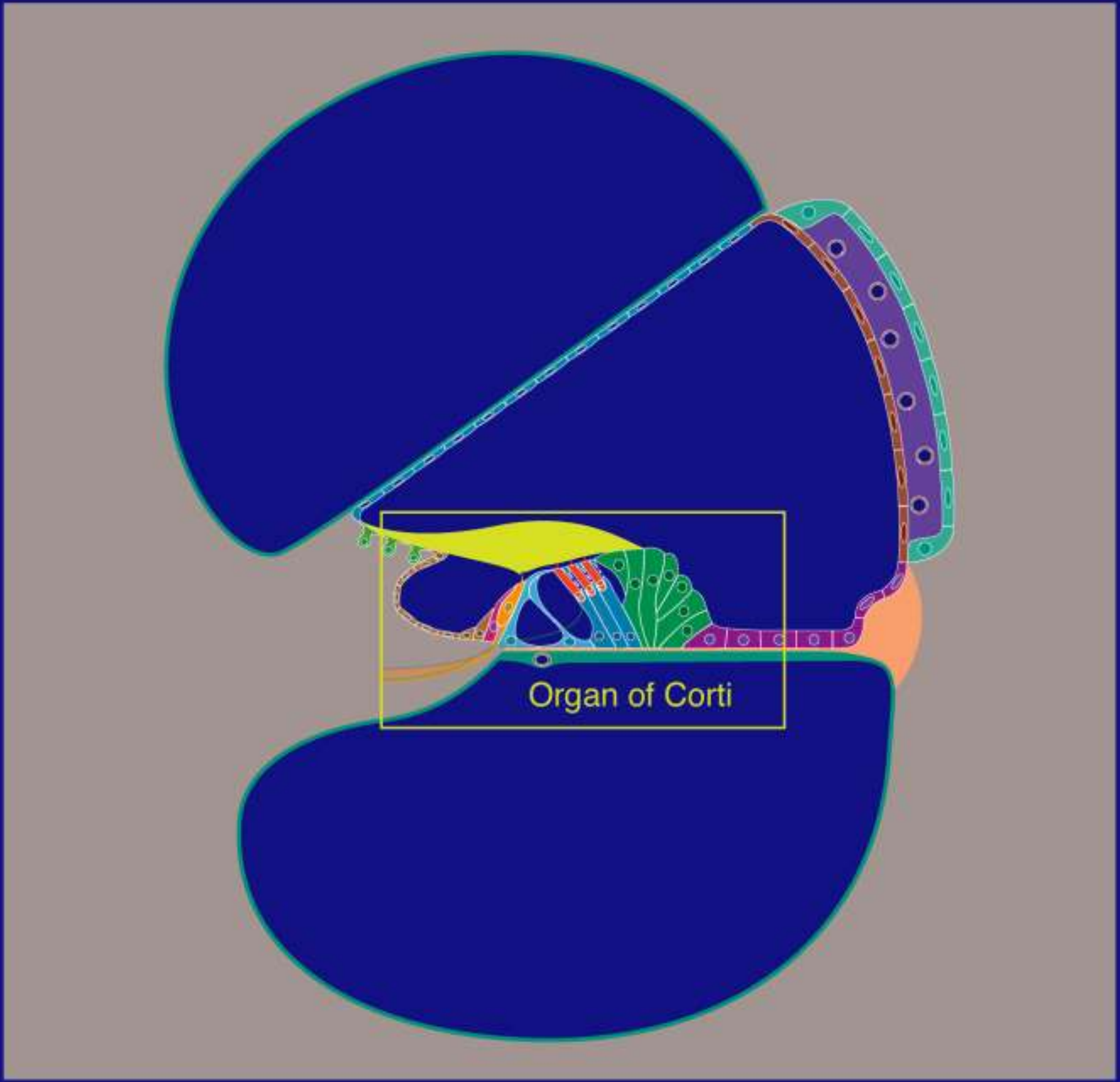
$$k = \sqrt{\frac{2\rho}{Am}} \frac{\omega}{\sqrt{\frac{\kappa}{m} - \omega^2}} = \sqrt{\frac{2\rho}{Am}} \frac{\omega}{\sqrt{\omega_0^2 - \omega^2}}$$



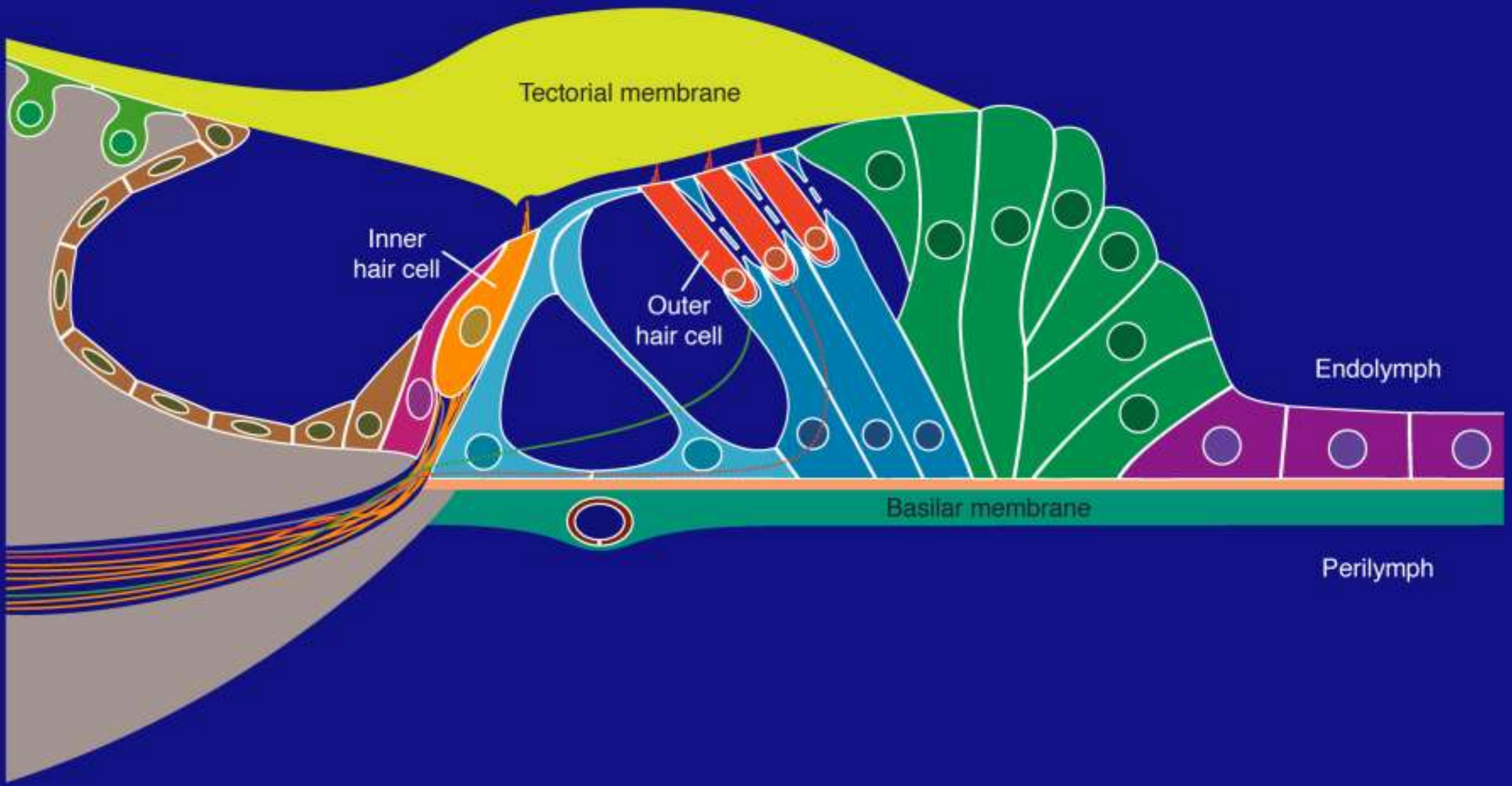
COCHLEAR TONOTOPIC MAPS

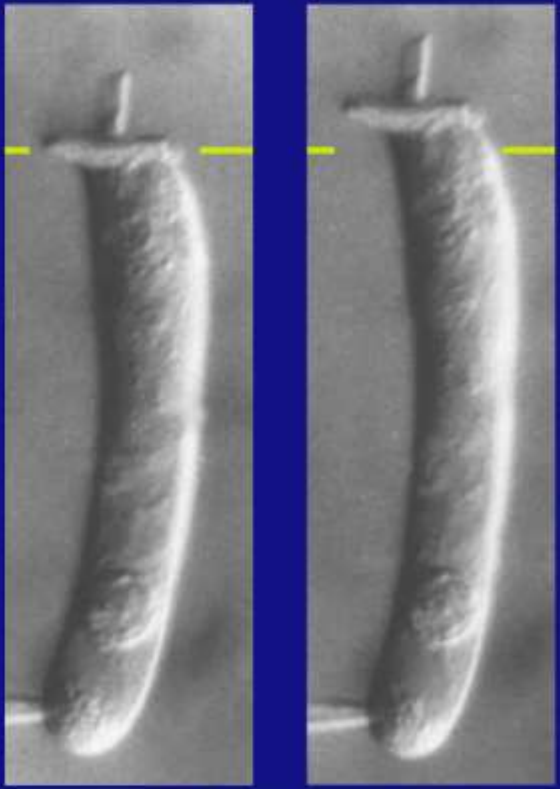



Displacement (nm)
2
1
0
-1
-2
300
400
500
600
700
800
900
1000
800
900
1000
Position (µm)
Displacement (nm)
2
1
0
-1
-2
300
400
500
600
700
800
900
1000
800
900
1000
Position (µm)

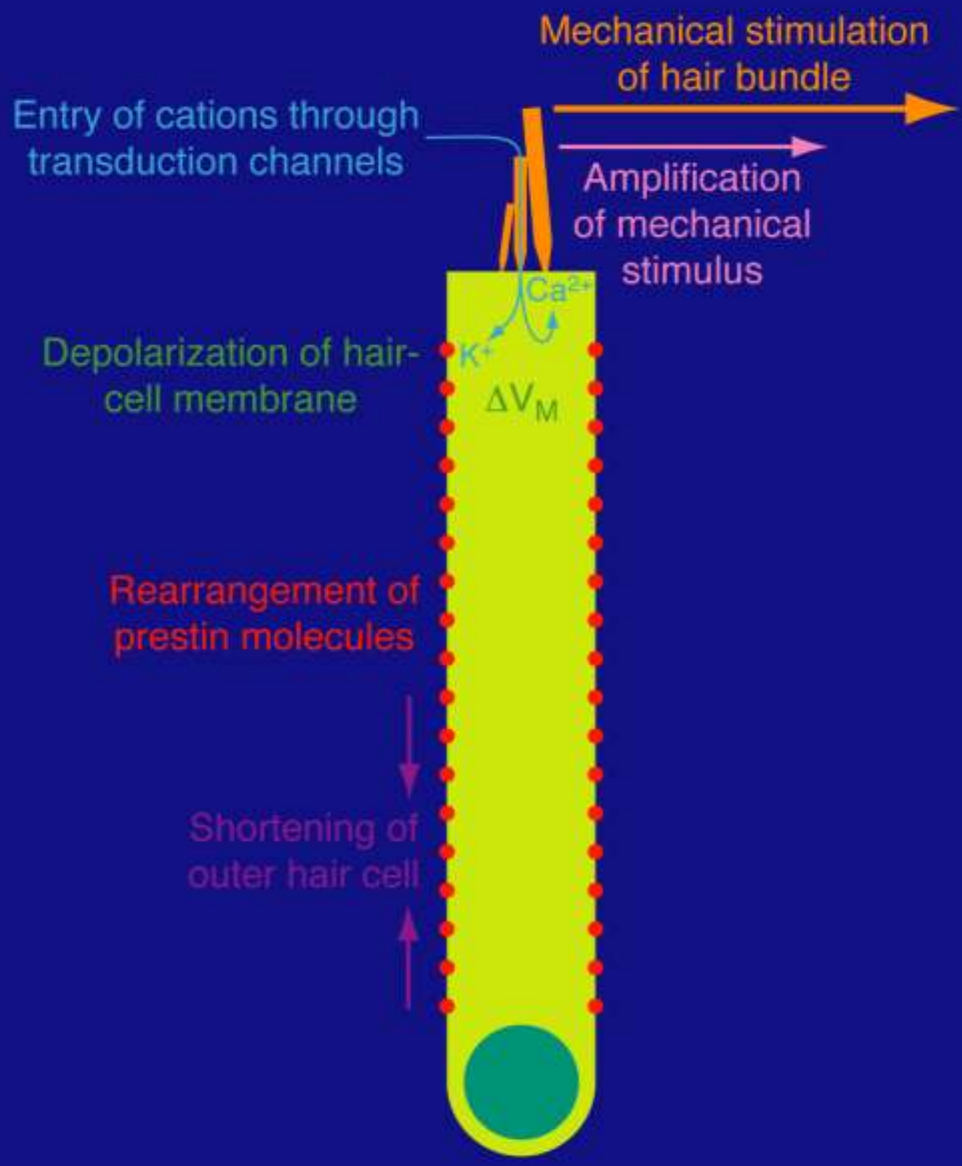


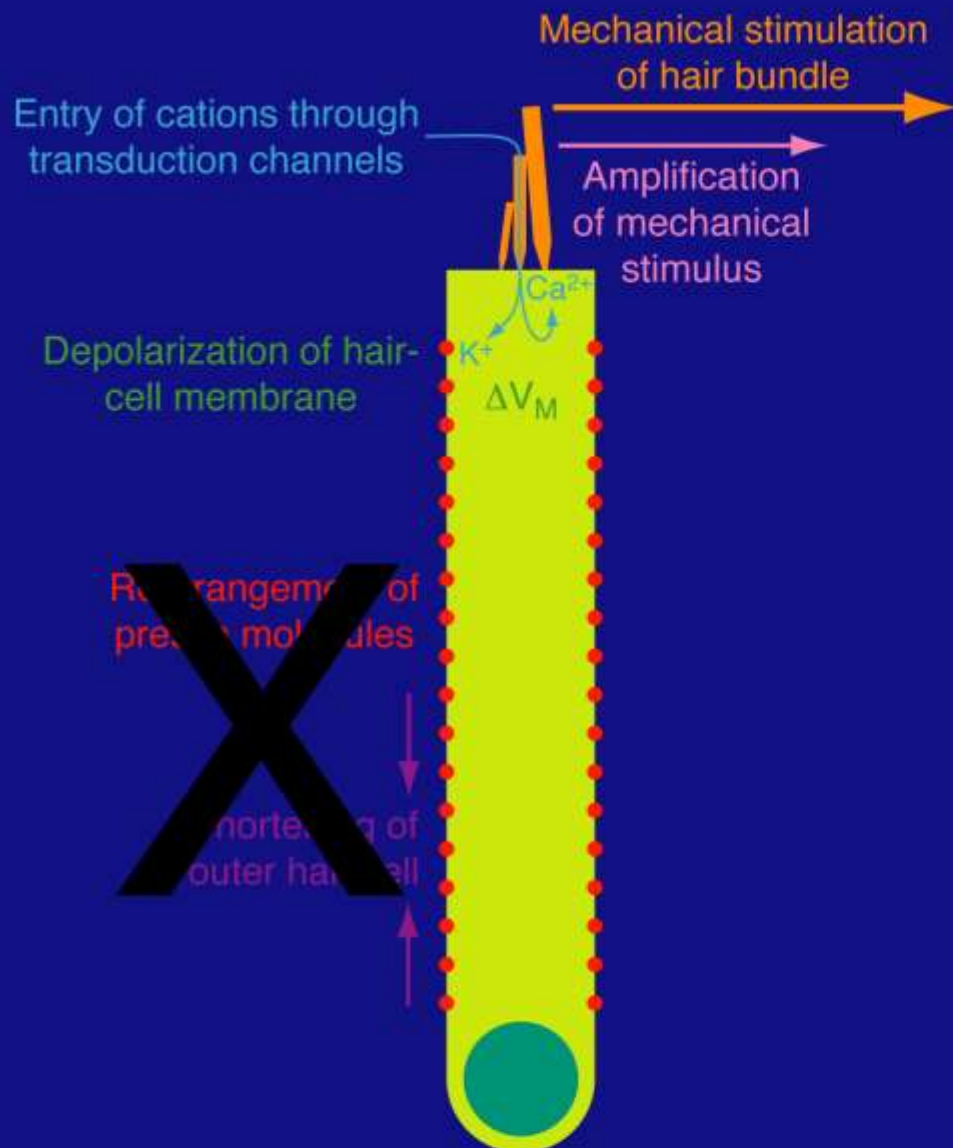
Organ of Corti

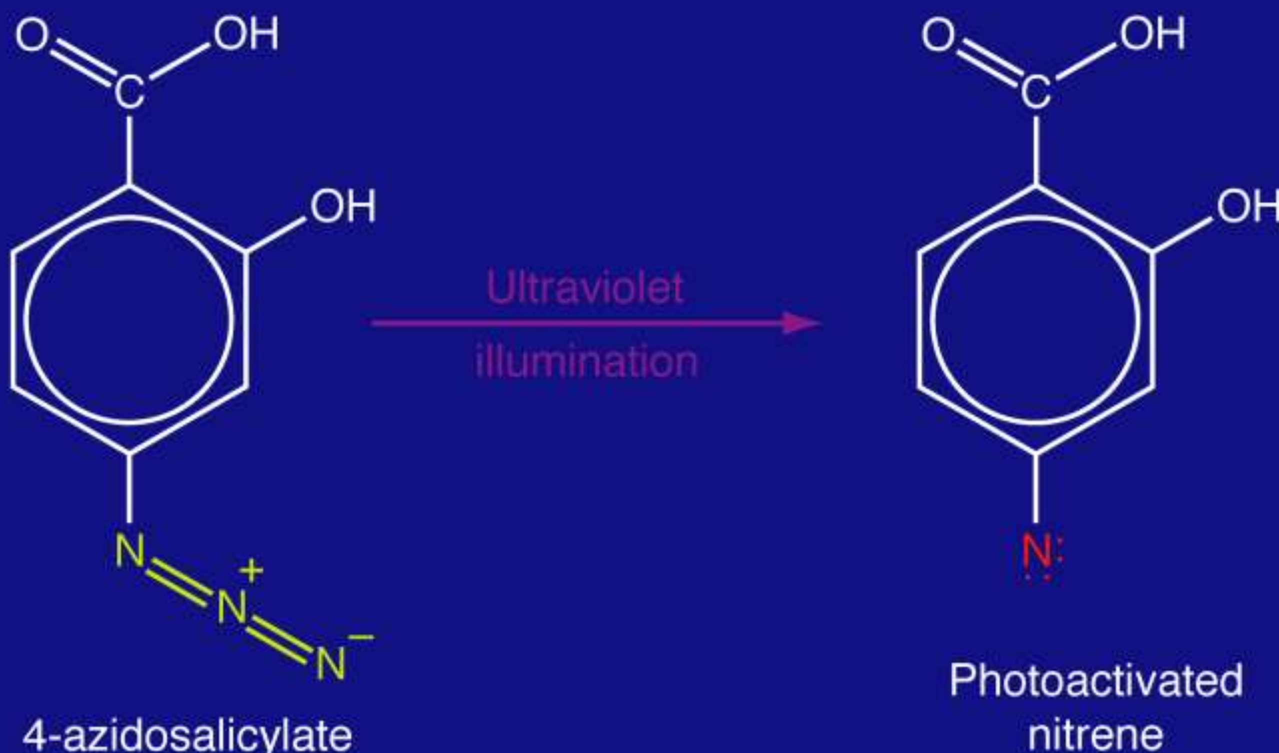

Tectorial membrane
Inner
hair cell
Outer
hair cell
Endolymph
Basilar membrane
Perilymph

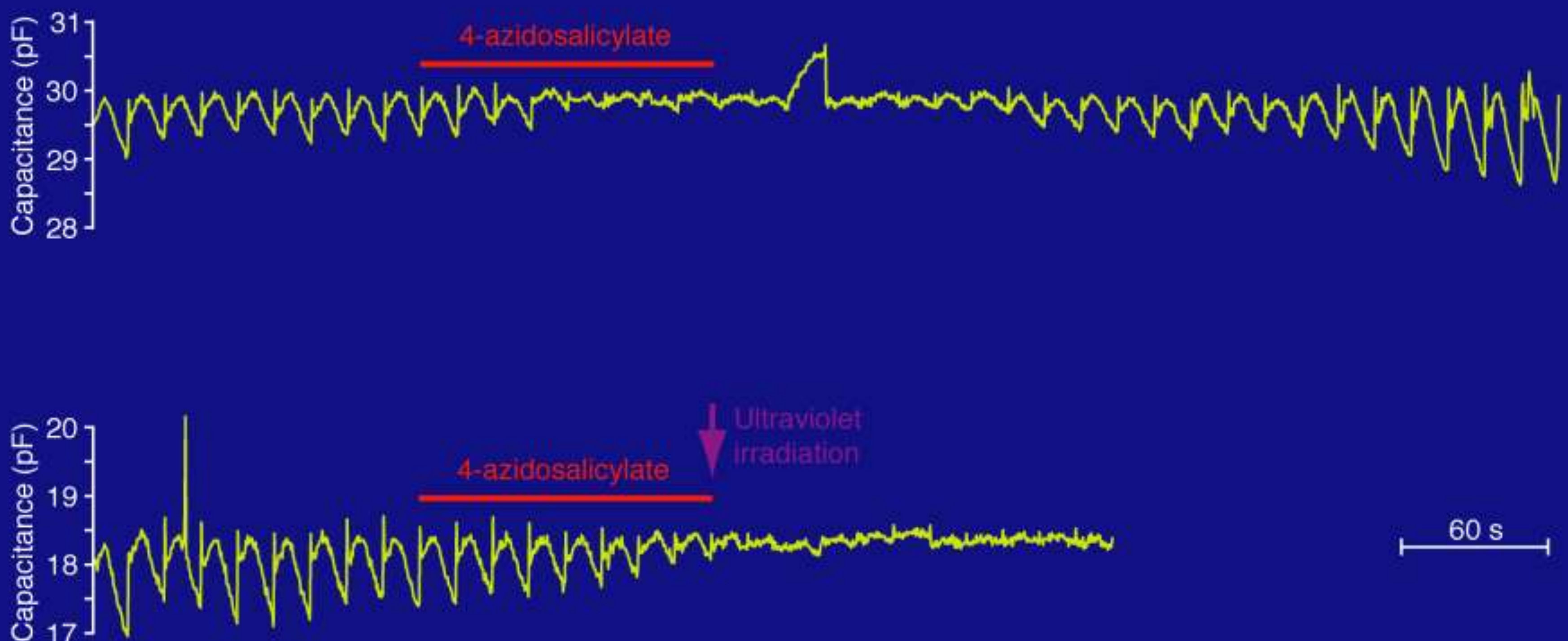


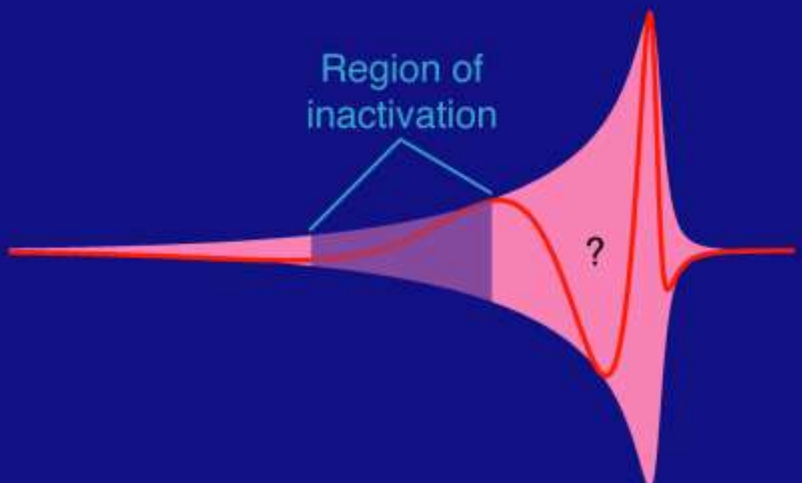
From J. Ashmore and M. Holley

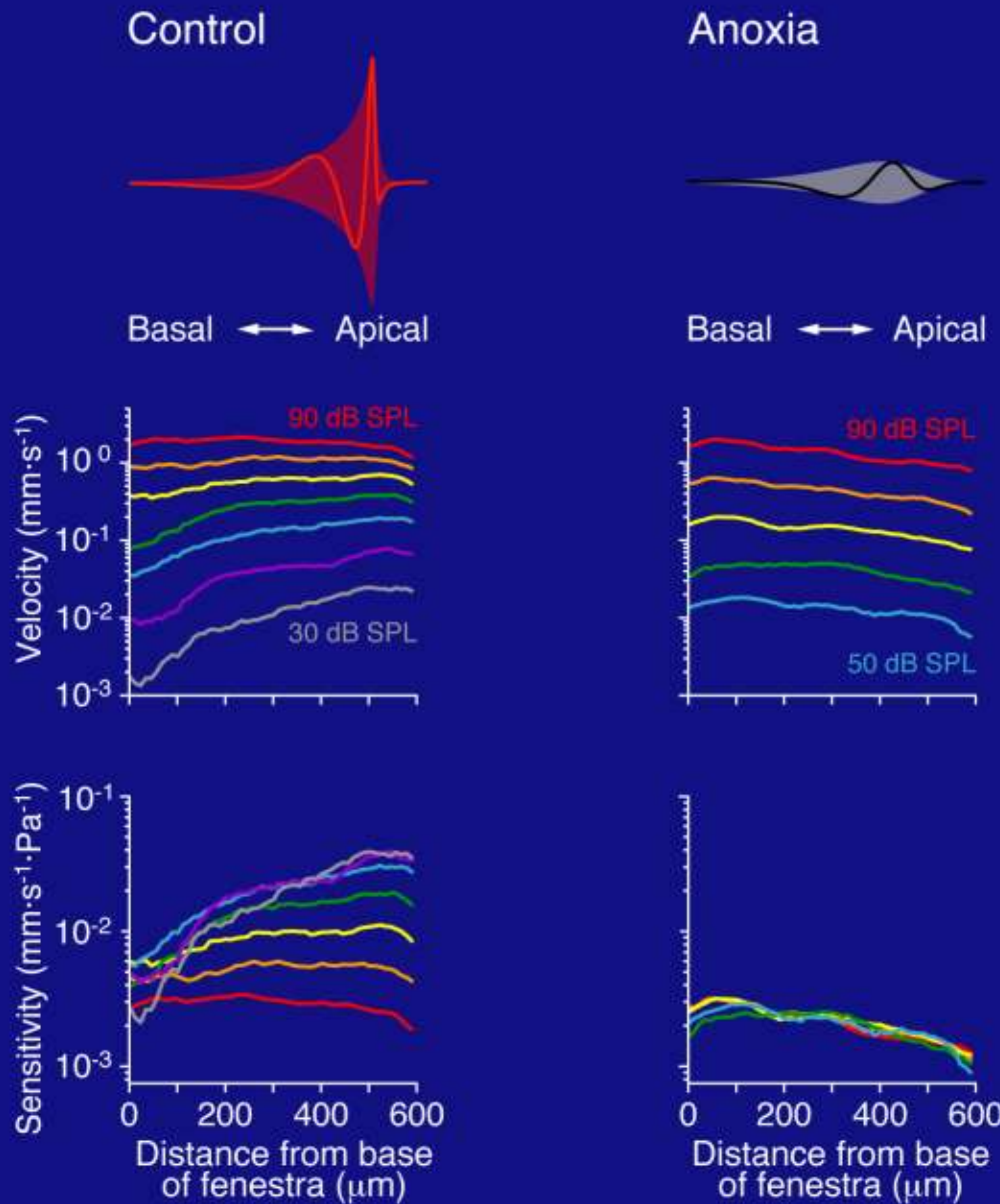

Mechanical stimulation of hair bundle
Entry of cations through transduction channels
Amplification of mechanical stimulus
Ca2+
K+
Depolarization of hair-cell membrane
ΔVM
Rearrangement of prestin molecules
Shortening of outer hair cell

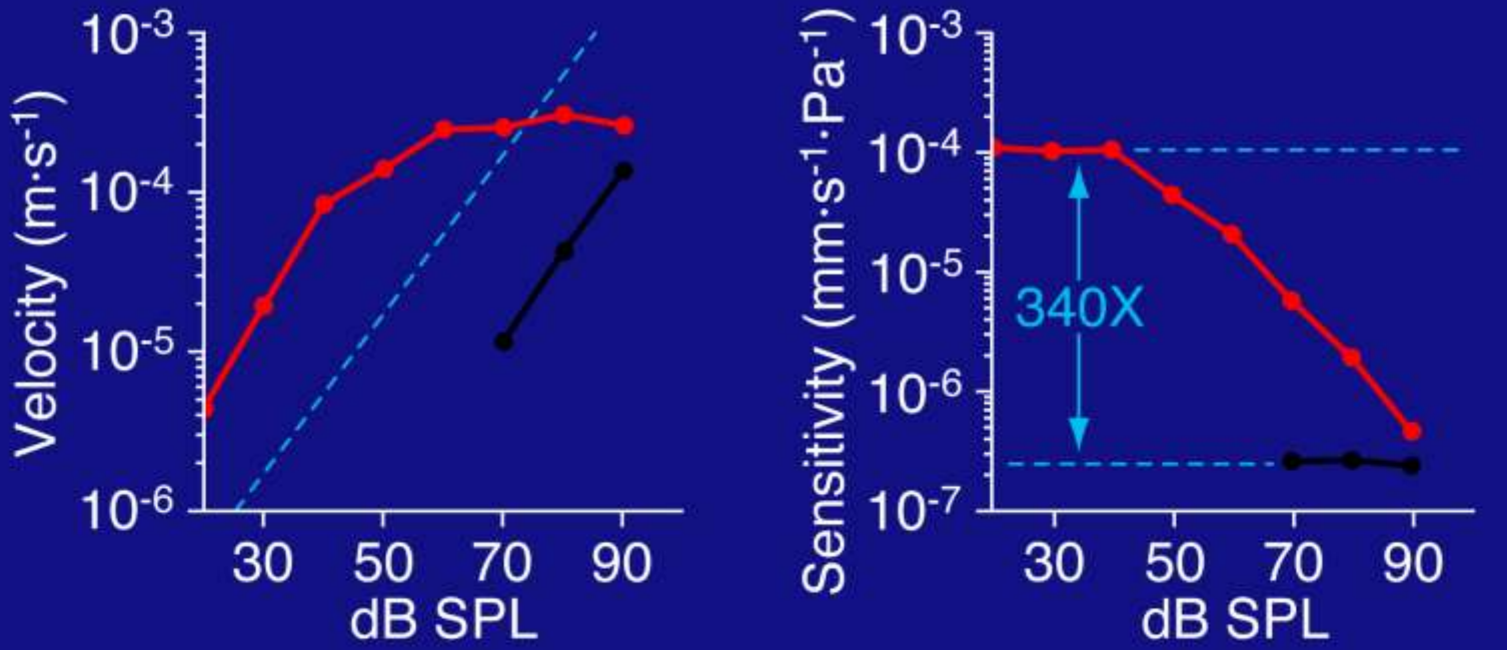

Mechanical stimulation of hair bundle
Entry of cations through transduction channels
Amplification of mechanical stimulus
Ca^{2+}
K^{+}
Depolarization of hair-cell membrane
ΔV_M


O
OH
C
OH
N
N
N
4-azidosalicylate
Ultraviolet
illumination
O
OH
C
OH
N
Photoactivated
nitrene

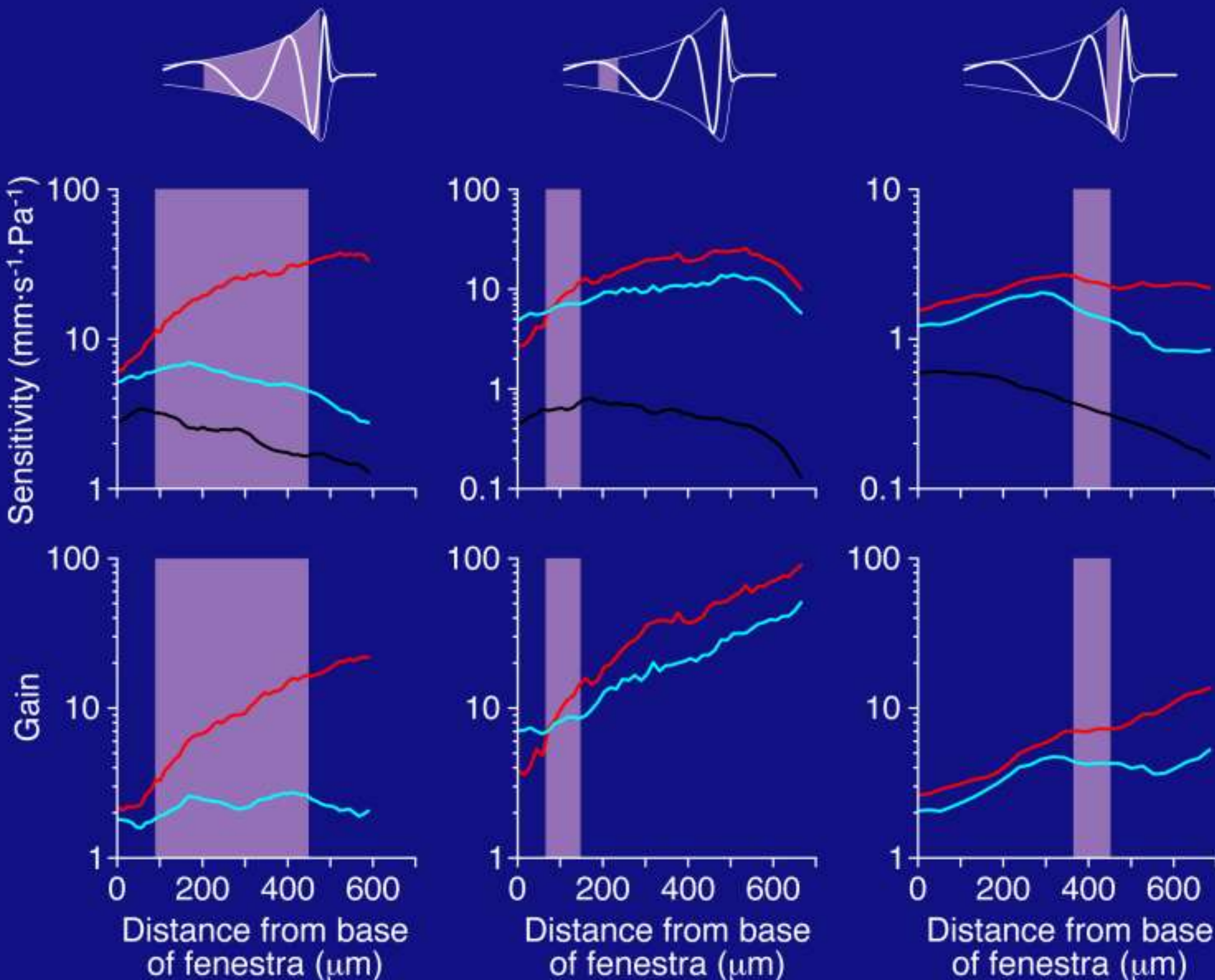

Capacitance (pF)
31
30
29
28
4-azidosalicylate
Capacitance (pF)
20
19
18
17
4-azidosalicylate
Ultraviolet
irradiation
60 s


Region of
inactivation
?

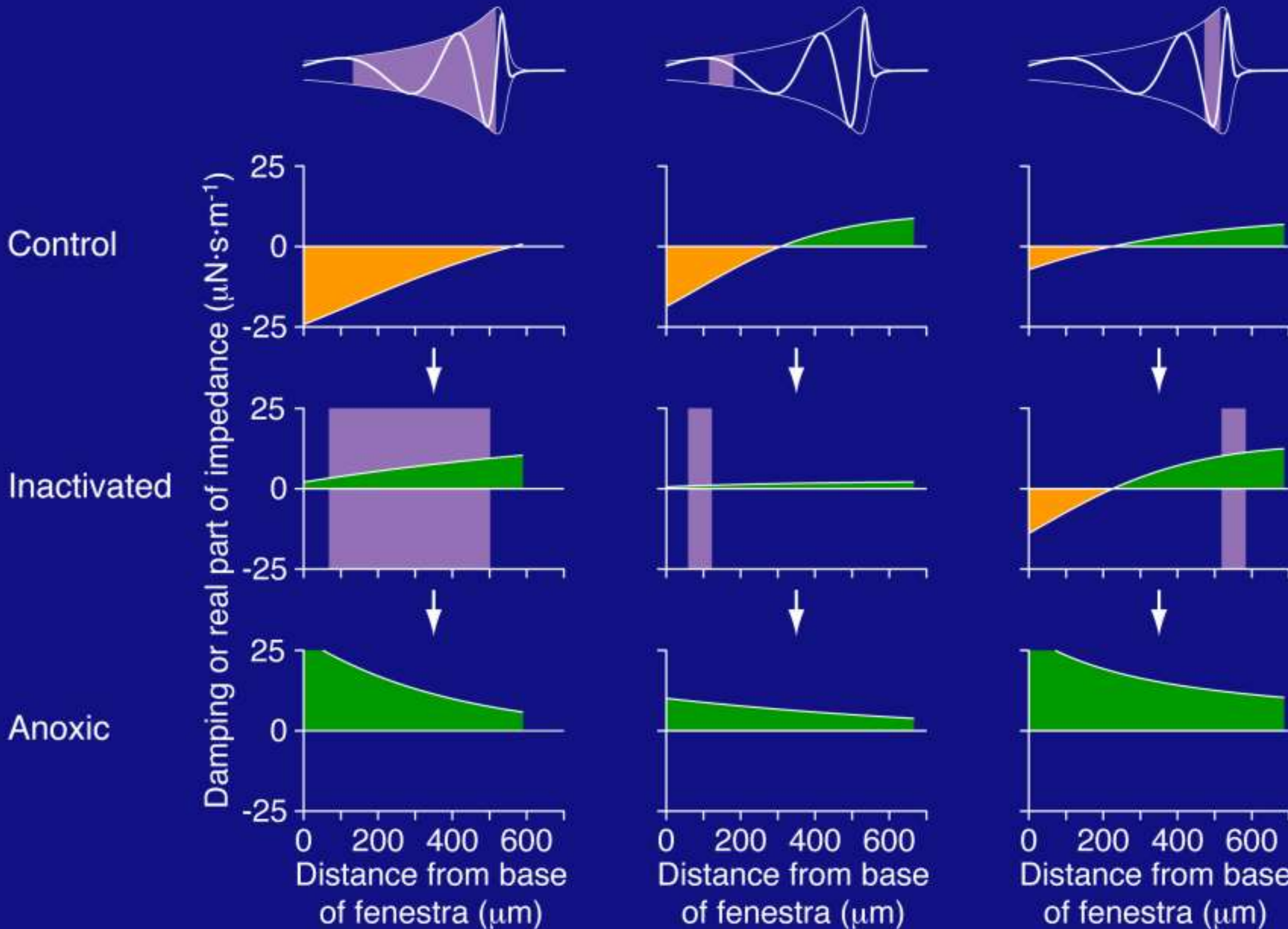

Control
Anoxia
Basal
Apical
Basal
Apical
90 dB SPL
30 dB SPL
90 dB SPL
50 dB SPL
Velocity (mm·s⁻¹)
10⁰
10⁻¹
10⁻²
10⁻³
Sensitivity (mm·s⁻¹·Pa⁻¹)
10⁻¹
10⁻²
10⁻³
0
200
400
600
Distance from base of fenestra (μm)
0
200
400
600
Distance from base of fenestra (μm)



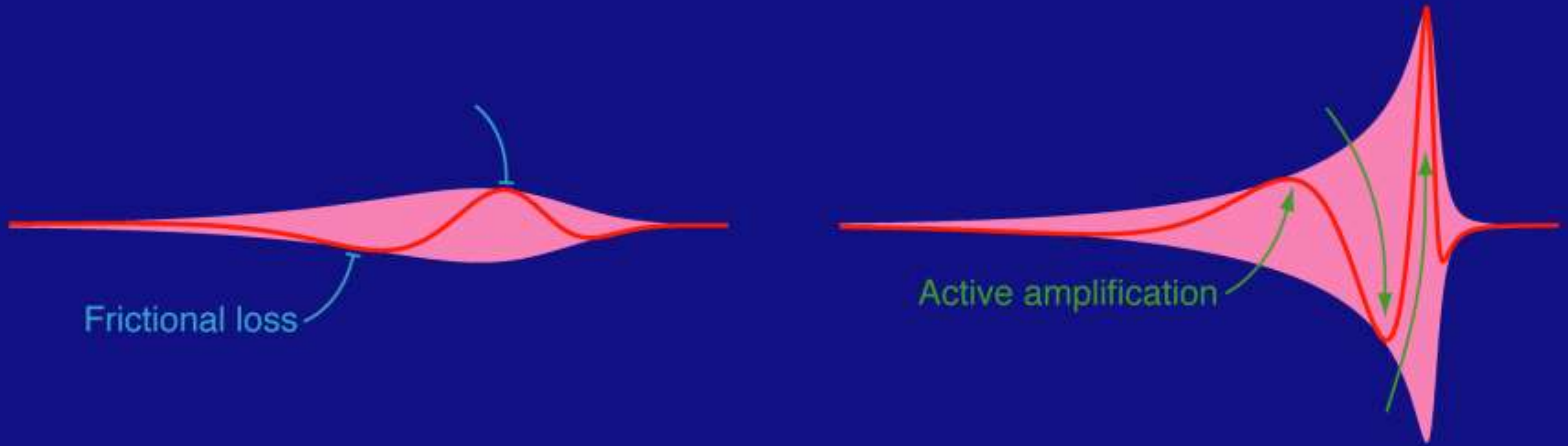
Velocity (m·s-1)
10-3
10-4
10-5
10-6
30
50
70
90
dB SPL
Sensitivity (mm·s-1·Pa-1)
10-3
10-4
10-5
10-6
10-7
340X
30
50
70
90
dB SPL



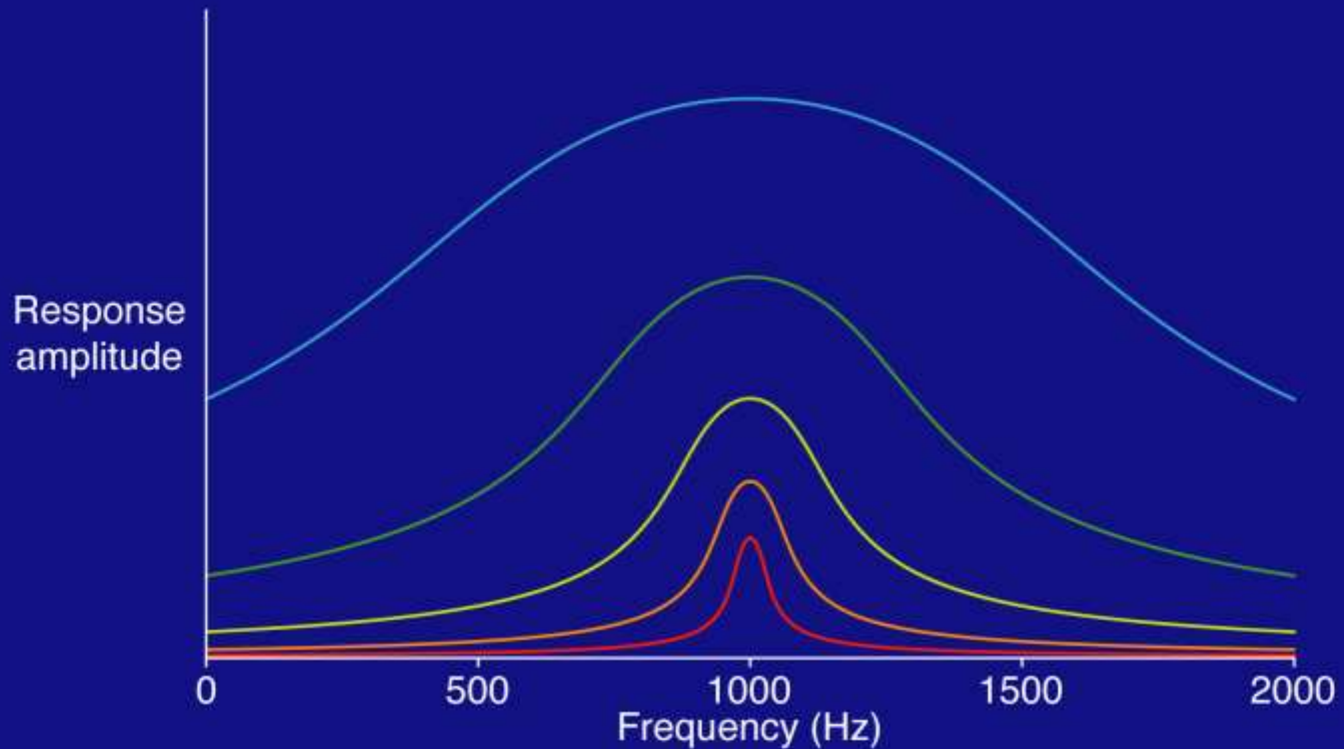
Sensitivity (mm·s⁻¹·Pa⁻¹)
100
10
1
0.1
Gain
0
200
400
600
Distance from base of fenestra (μm)

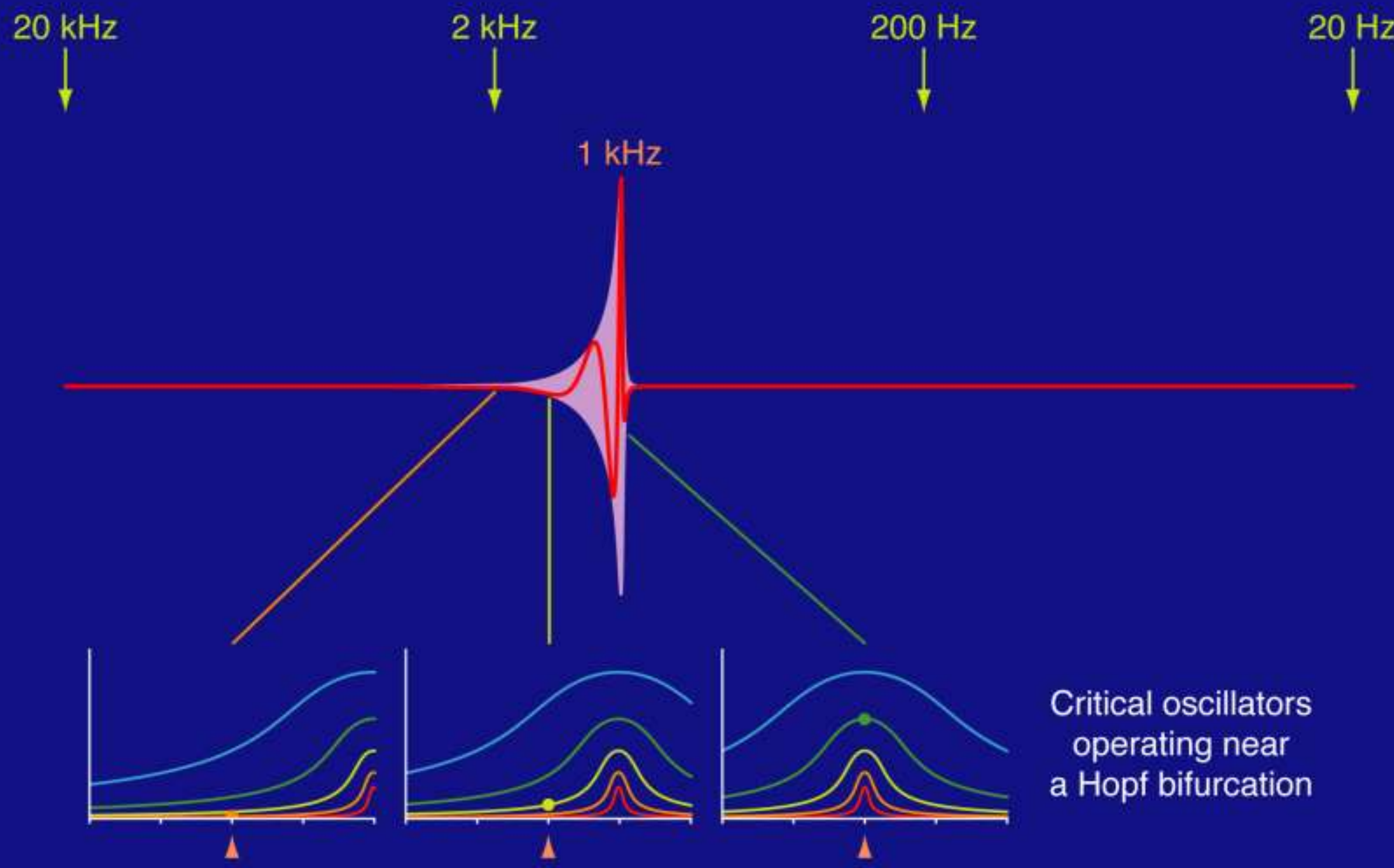


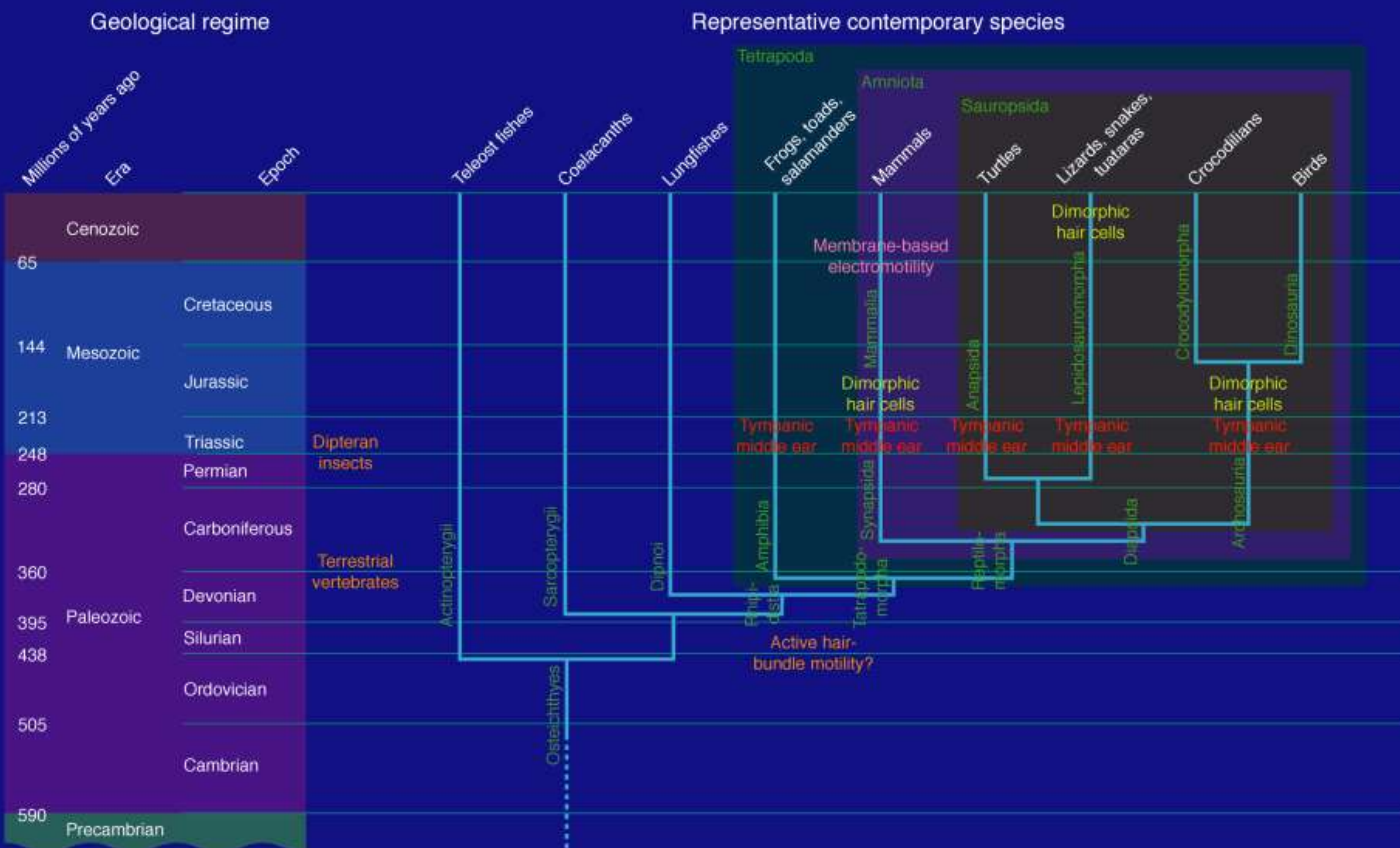
Control
Inactivated
Anoxic
Damping or real part of impedance (μN·s·m⁻¹)
25
0
-25
0
200
400
600
Distance from base of fenestra (μm)


Frictional loss
Active amplification

TUNING OF A CRITICAL OSCILLATOR




20 kHz
2 kHz
200 Hz
20 Hz
1 kHz
Critical oscillators
operating near
a Hopf bifurcation



Geological regime
Representative contemporary species
Millions of years ago
Era
Epoch
Teleost fishes
Coelacanths
Lungfishes
Frogs, toads, salamanders
Mammals
Turtles
Lizards, snakes, tuataras
Crocodilians
Birds
Tetrapoda
Amniota
Sauropsida
Cenozoic
65
Cretaceous
144
Mesozoic
Jurassic
213
Triassic
248
Permian
280
Carboniferous
360
Devonian
395
Paleozoic
Silurian
438
Ordovician
505
Cambrian
590
Precambrian
Dipteran insects
Terrestrial vertebrates
Membrane-based electromotility
Dimorphic hair cells
Dimorphic hair cells
Dimorphic hair cells
Tympanic middle ear
Tympanic middle ear
Tympanic middle ear
Tympanic middle ear
Tympanic middle ear
Active hair-bundle motility?
Actinopterygii
Sarcopterygii
Dipnoi
Osteichthyes
Rhipidistia
Amphibia
Tetrapodomorpha
Synapsida
Mammalia
Anapsida
Lepidosauromorpha
Diapsida
Reptiliomorpha
Crocodylomorpha
Dinosauria
Archosauria