# Coupled Oscillations in Nervous Systems

## Theoretical Overview

## Experimental Evidence for Weak Coupling Between Oscillators

Direct Measurement of Phase-sensitivity Function, $Z(\psi)$

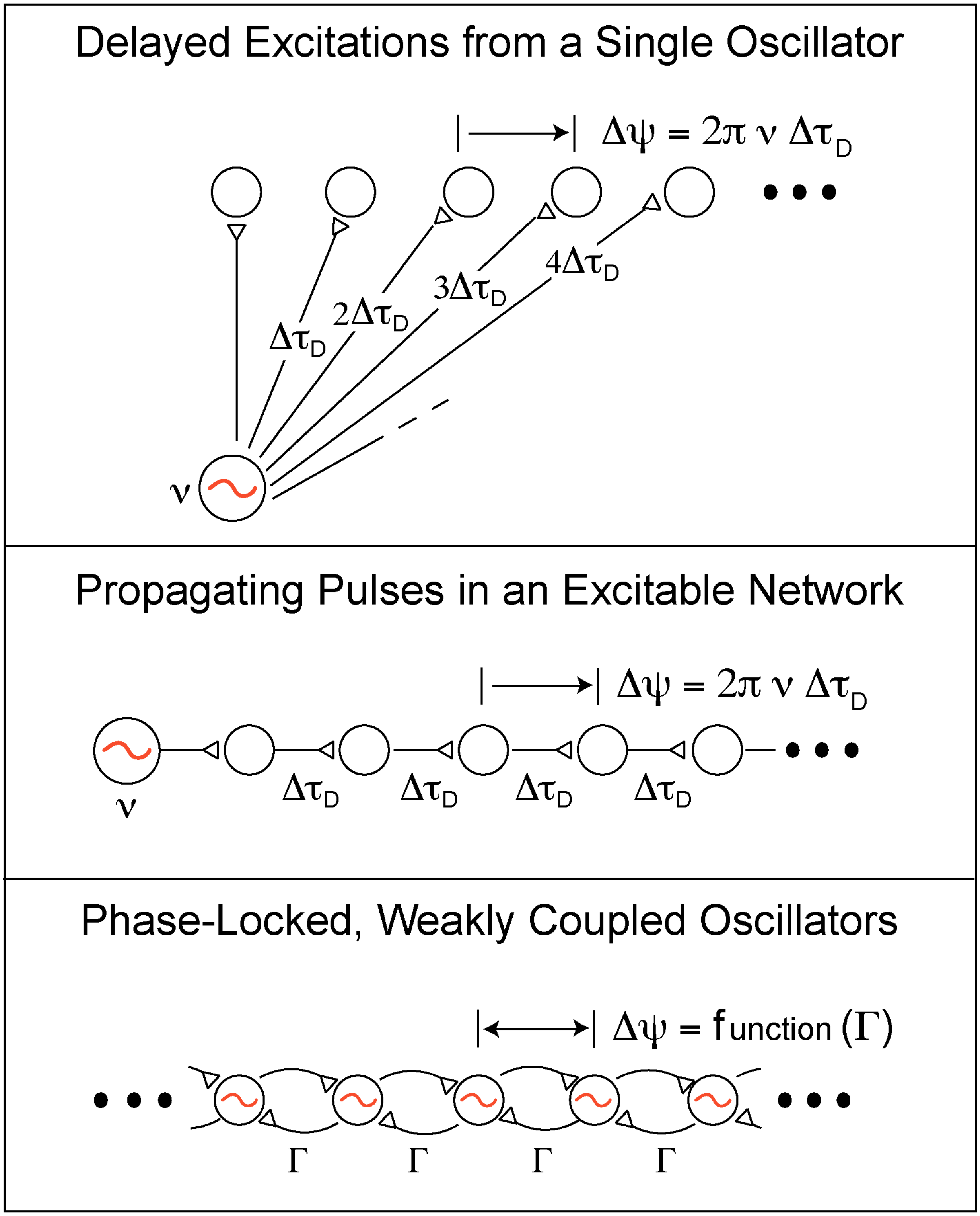
Behavior of Pairs and Networks of Inhibitory Neurons

## Electrical Waves During "Normal" Function

Linear Waves in an Invertebrate Central Olfactory Organ
(Consequence of an intrinsic frequency gradient)

Linear and Rotating Waves in Lower Vertebrate Visual System
(Linear part consistent with biased connectivity)

## Insights into Cortical Function from Nonlinear Spectral Mixing
(Problem of Combining Proprioceptive, or Reference Signals, with Contact Signals)



Delayed Excitations from a Single Oscillator
Δψ = 2π ν Δτ_D
Δτ_D
2Δτ_D
3Δτ_D
4Δτ_D
ν
Propagating Pulses in an Excitable Network
Δψ = 2π ν Δτ_D
ν
Δτ_D
Δτ_D
Δτ_D
Δτ_D
Phase-Locked, Weakly Coupled Oscillators
Δψ = function (Γ)
Γ
Γ
Γ
Γ

# Summary of Experimental Evidence for Traveling Waves in Cortex of Awake Animals

| System | Frequency (in Hz) | 'Band' | Interstimulus activity | Stimulus activity | Phase gradient across area (in radians) |
|---|---|---|---|---|---|
| **Molluscan olfactory procerebral lobe** (Delaney et al. 1994) | **1** | - | **Wave** | - | $\approx \pi$ |
| | | | - | **Synchrony** | - |
| **Turtle olfactory cortex** (Lam et al. 2000) | **12** | - | - | **Wave** | $\sim 3\pi/2$ |
| **Rabbit olfactory cortex** (Freeman 1978) | **50** | $\gamma$ | - | **Wave** | $\sim \pi/2$ |
| **Turtle visual cortex** (Prechtl et al. 1997) | **3** | - | **Wave** | **Wave** | $\approx \pi/2$ |
| | **20** | $\gamma$ | - | **Wave** | $\approx \pi$ (plane)<br>$2\pi$ (rotating) |
| **Cat visuomotor cortex** (Roelfsema et al. 1997) | **10** | $\alpha$ | **Wave** | - | $\approx \pi/2$ |
| | **20 - 40** | $\gamma$ | - | **Synchrony** | - |
| **Dog cortex** (Lopes da Silva & Storm van Leeuwen 1978) | **8 - 12** | $\alpha$ | **Wave** | - | $\approx \pi/2$ |
| **Human thalamus/cortex** (Ribary et al. 1991) | **40** | $\gamma$ | **Wave** | **Wave** | $\sim \pi$ |

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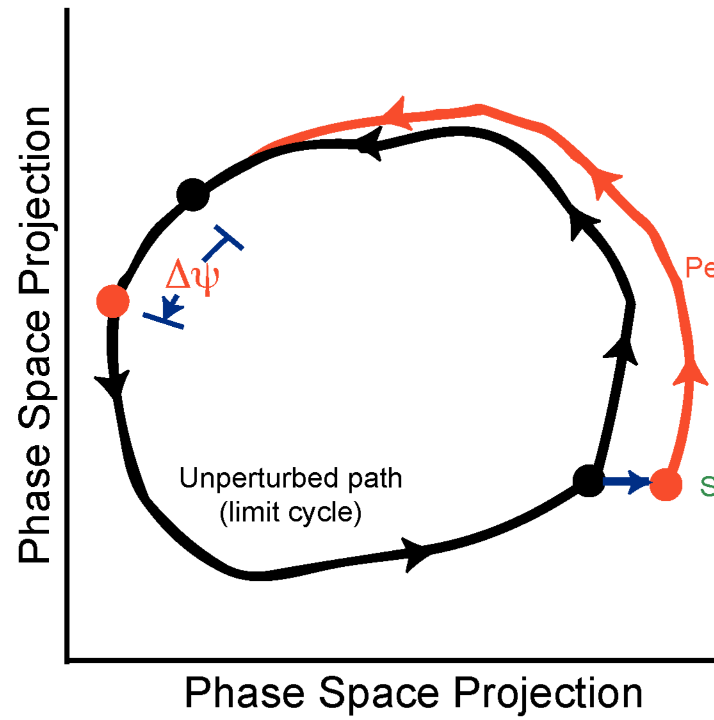
(Prospects for mapping spatial *as well as* temporal dynamics)

# Transformation of a Dynamic System (N-dim) into a "Phase" System (1-dim)

**Conditions (met only approximately in practice):**
- **Closed Orbits**
- **Weak Perturbations**
- **Infinite Relaxation Time**

**Perturbation → Phase Shift (Δψ)**




$$\frac{d\psi_i(t)}{dt} = \omega + \sum_{\text{neighbors, j}} \Gamma(\psi_i - \psi_j)$$

$$\Gamma(\psi_i - \psi_j) = \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{Z}(\psi_i + \theta) \bullet \underbrace{\mathbf{P}(\psi_i + \theta, \psi_j + \theta)}_{}$$

Perturbation

Sensitivity $\propto \left( \frac{\partial \psi_i}{\partial V}, \cdots \right)$

# The Phase Sensitivity Function

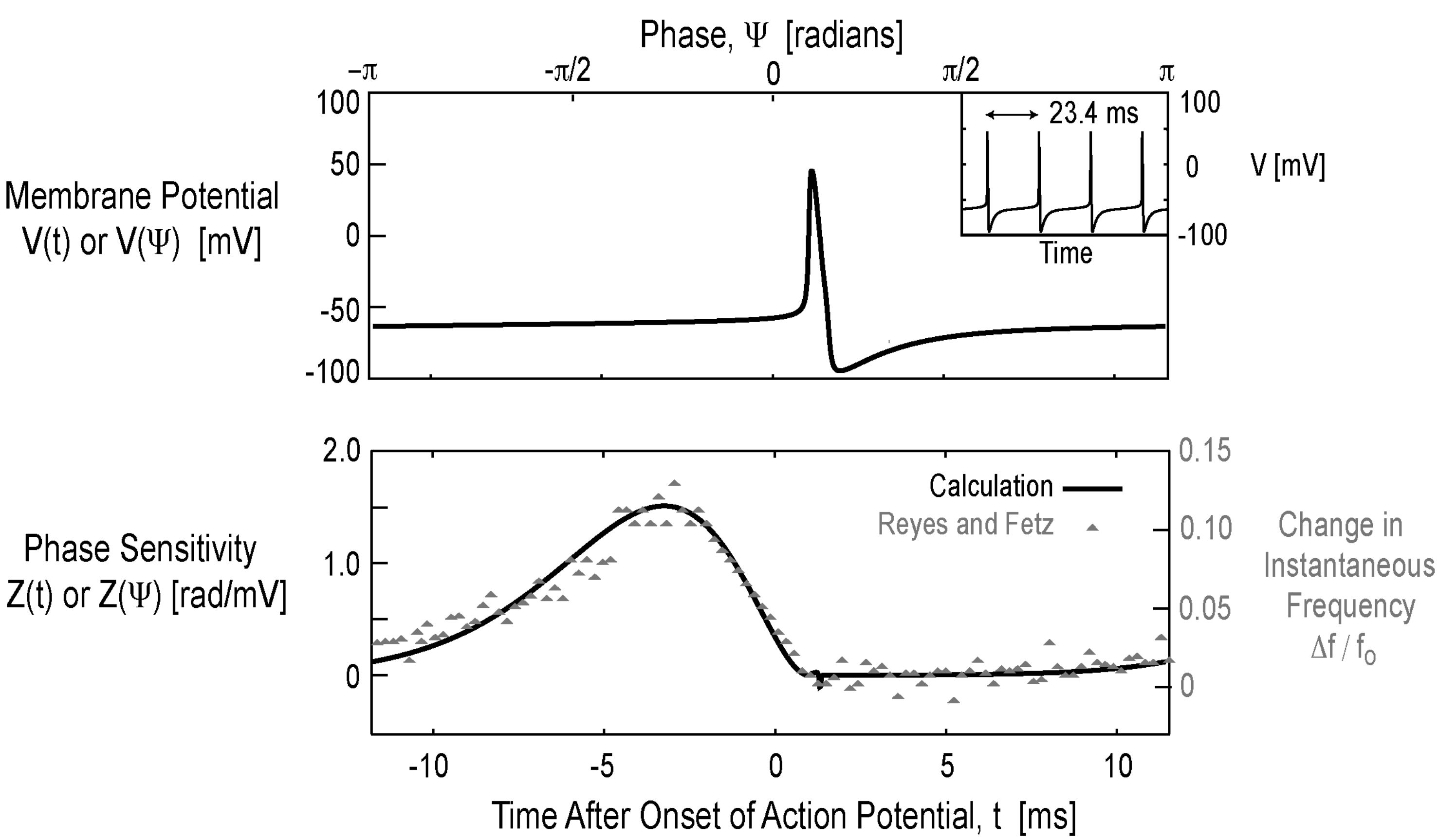
Calculation (Ermentrout & Kleinfeld 2000) vs. Experimental Data (Reyes & Fetz 1993)

Real system: $\frac{\partial V}{\partial t} = \bullet\bullet\bullet \; ; \; \frac{\partial n}{\partial t} = \bullet\bullet\bullet \; ;$ etcetera

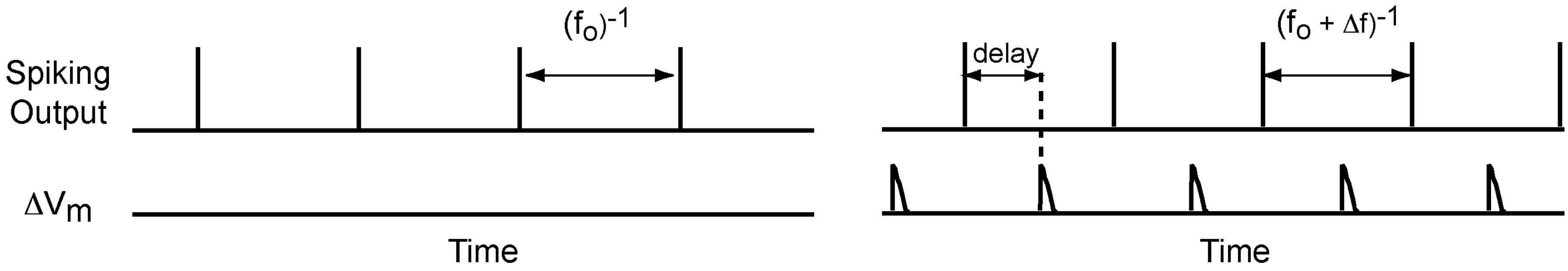
Phase reduction: $\frac{\partial \Psi_i}{\partial t} = \omega + \Gamma\left(\Psi_i - \Psi_j\right)$

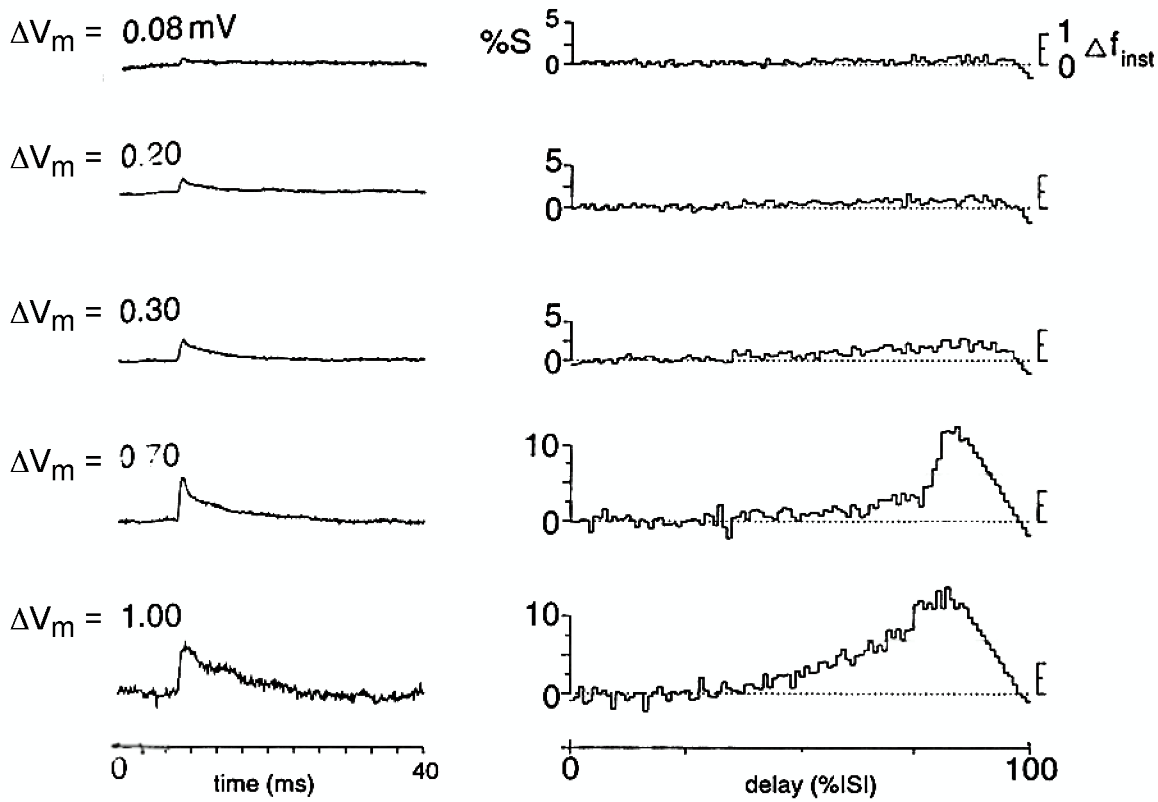
$$\frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \;\; \mathbf{Z}\left(\Psi_i - \theta\right) \bullet \mathbf{P}\left(\Psi_i - \theta;\; \Psi_j - \theta\right)$$

For perturbation solely in V: $\mathbf{Z}(\Psi) = \frac{\partial \Psi}{\partial V} \approx \frac{2\pi}{f_0}\frac{\Delta f}{\Delta V}$



# Experiment of Reyes and Fetz (J. Neurophysiol. 1993)



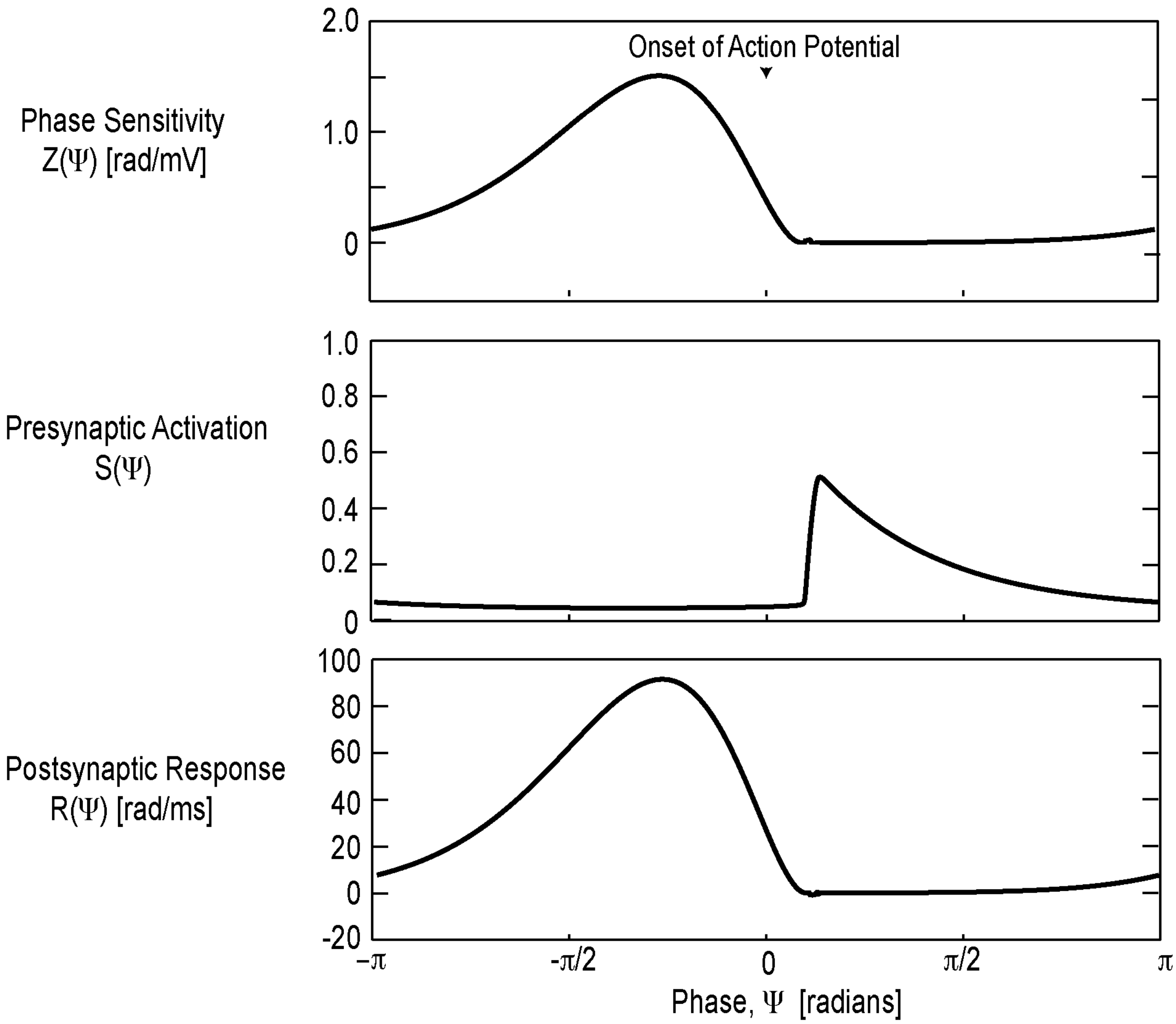
# Pairwise Interaction between Neuronal Oscillators, $\Gamma(\psi_i - \psi_j)$ is the Correlation of Presynaptic Activation with Postsynaptic Response

$$\Gamma\left(\Psi_i - \Psi_j\right) = \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{Z}\left(\Psi_i + \theta\right) \; \mathbf{P}\left(\Psi_i + \theta;\; \Psi_j + \theta\right)$$

$$\mathbf{P}\left(\Psi_i + \theta;\; \Psi_j + \theta\right) = \frac{g_{synapse}}{C_m} \; \mathbf{S}\left(\Psi_j + \theta\right)\left[E_{synapse} - \mathbf{V}\left(\Psi_i + \theta\right)\right]$$

$$= \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \frac{g_{synapse}}{C_m} \; \mathbf{Z}\left(\Psi_i + \theta\right)\left[E_{synapse} - \mathbf{V}\left(\Psi_i + \theta\right)\right] \mathbf{S}\left(\Psi_j + \theta\right)$$

$$\mathbf{R}\left(\Psi_i + \theta\right) = \frac{g_{synapse}}{C_m} \; \mathbf{Z}\left(\Psi_i + \theta\right)\left[E_{synapse} - \mathbf{V}\left(\Psi_i + \theta\right)\right]$$



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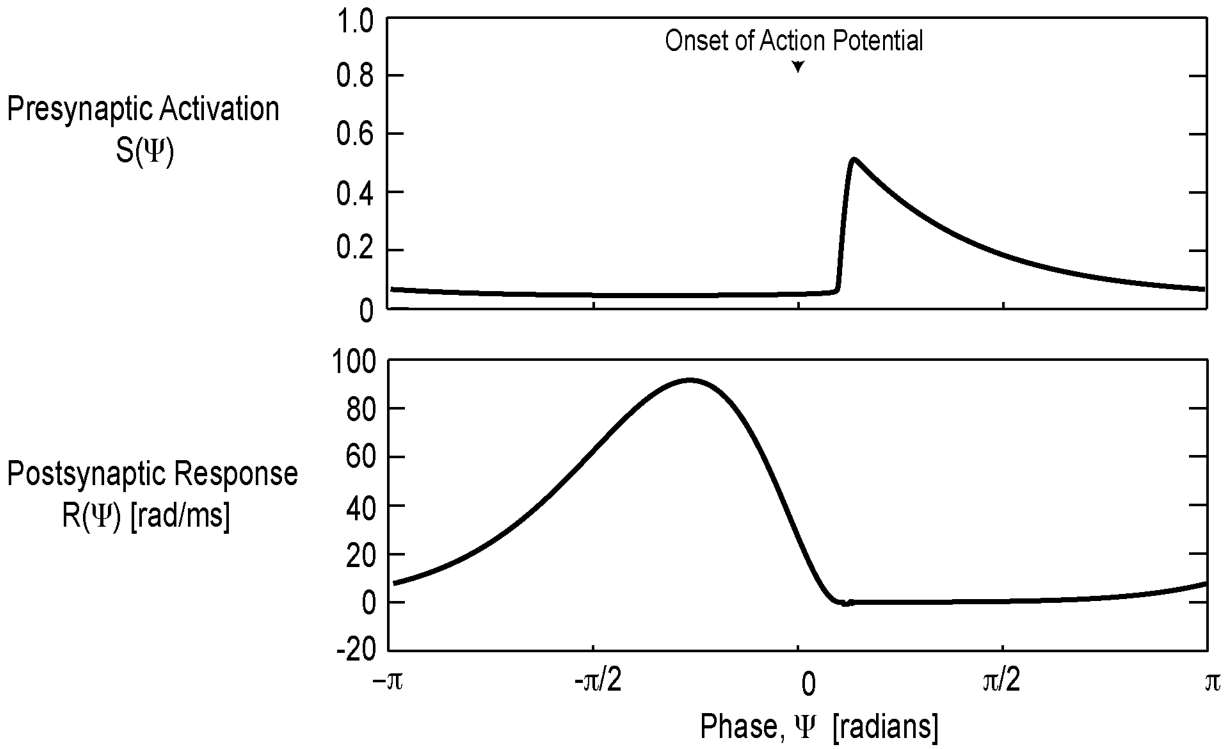
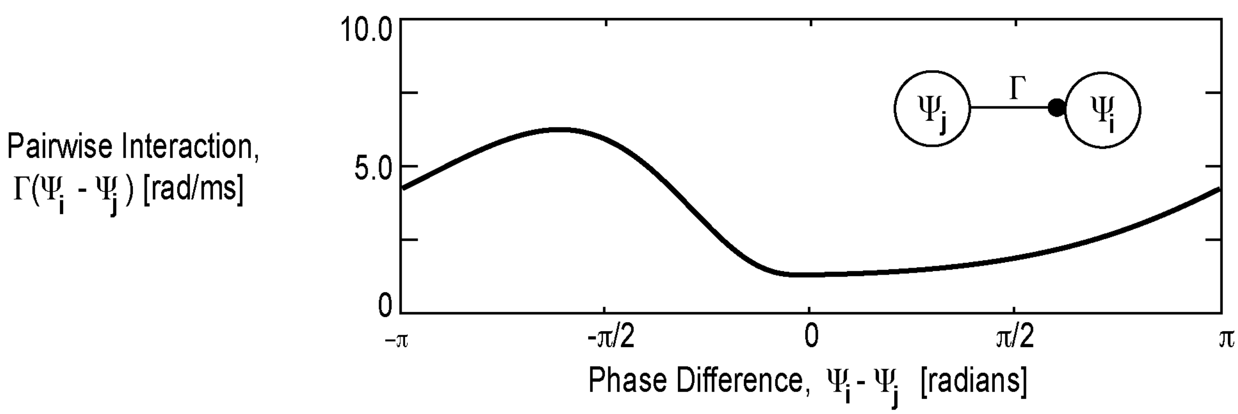


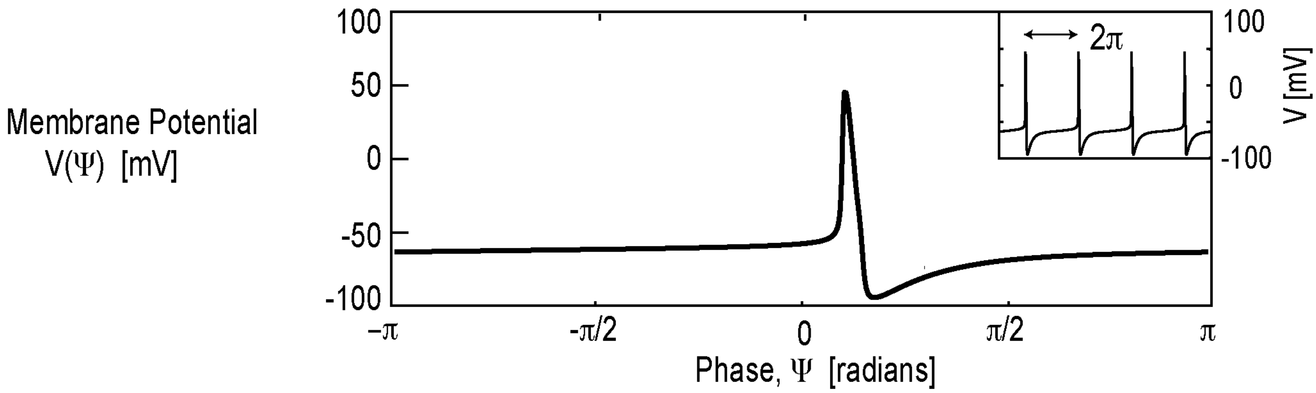

$$\Gamma(\Psi_i - \Psi_j) = \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{R}(\Psi_i + \theta) \; \mathbf{S}(\Psi_j + \theta)$$

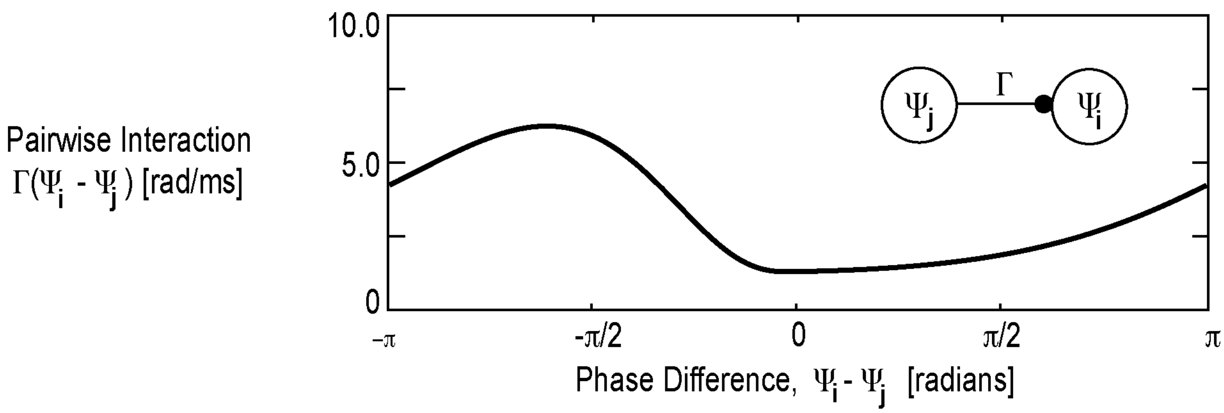
$$= \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{R}(\theta) \; \mathbf{S}\left[\theta - (\Psi_i - \Psi_j)\right]$$

Phase difference



# Nature of the Pairwise Interaction is Revealed by the Phase Shifts Between Two Reciprocally Connected Neuronal Oscillators

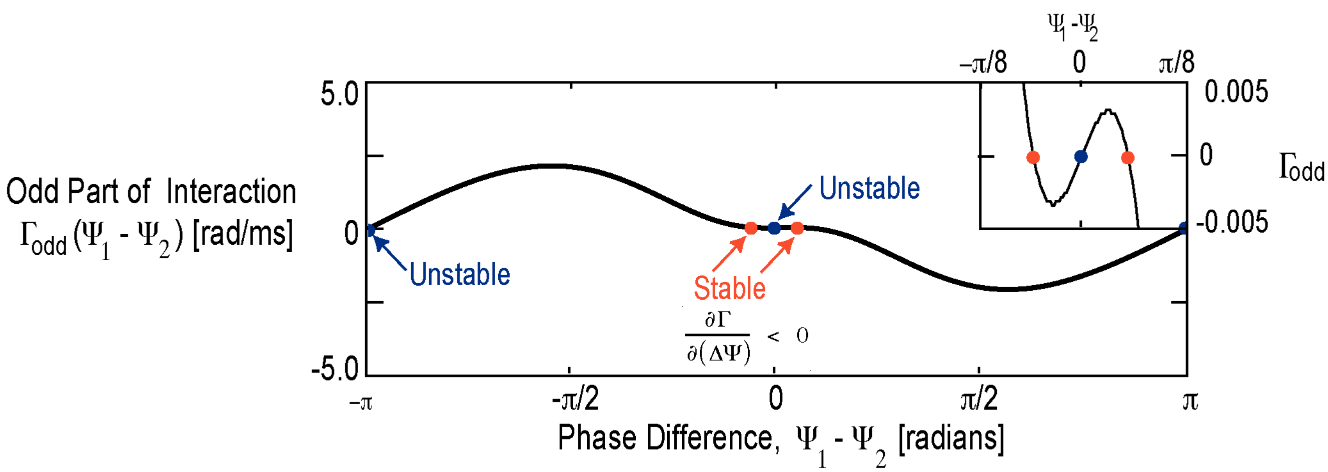



$$\frac{\partial \Psi_i}{\partial t} = \omega + \Gamma\left(\Psi_i - \Psi_j\right)$$

$$\frac{\partial \Psi_j}{\partial t} = \omega + \Gamma\left(\Psi_j - \Psi_i\right)$$

$$\frac{\partial\left(\Psi_i - \Psi_j\right)}{\partial t} = \Gamma\left(\Psi_i - \Psi_j\right) - \Gamma\left(\Psi_j - \Psi_i\right)$$



# Two Neuronal Oscillators with Synaptic Coupling

## Minimal Model for Insight into Network Behavior

(Hansel, Mato & Meunier 1993, 1995; von der Vreeswijk, Abbott & Ermentrout 1994)

Simpliest phase sensitivity function: $Z(\psi) = \sin(\psi)$ with $\psi = \omega t \;\; modulo(2\pi)$

Perturbation given by: $P(\psi\,) = \frac{g}{\tau}\frac{\psi}{\omega\tau}\, e^{-\psi/\omega\tau}$

Asymmetric part of the interaction controls $\Delta\psi \equiv \psi - \psi'$

$$\Gamma(\Delta\psi) - \Gamma(\text{-}\Delta\psi) \;= \frac{\epsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \vec{Z}(\psi+\theta)\cdot\vec{P}(\psi'+\theta) \;\propto\; g\,\frac{(\omega\tau)^2 - 1}{[1+(\omega\tau)^2]^2}\sin(\Delta\psi)$$

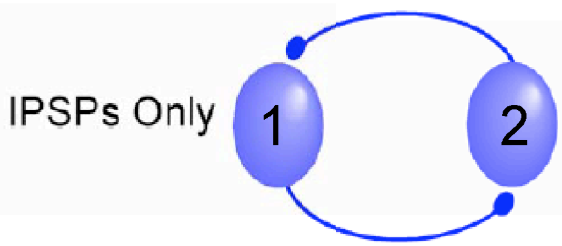
Stability (with our sign convention) requires $\frac{\partial\,[\Gamma(\Delta\psi) - \Gamma(\text{-}\Delta\psi)]}{\Delta\psi} < 0$

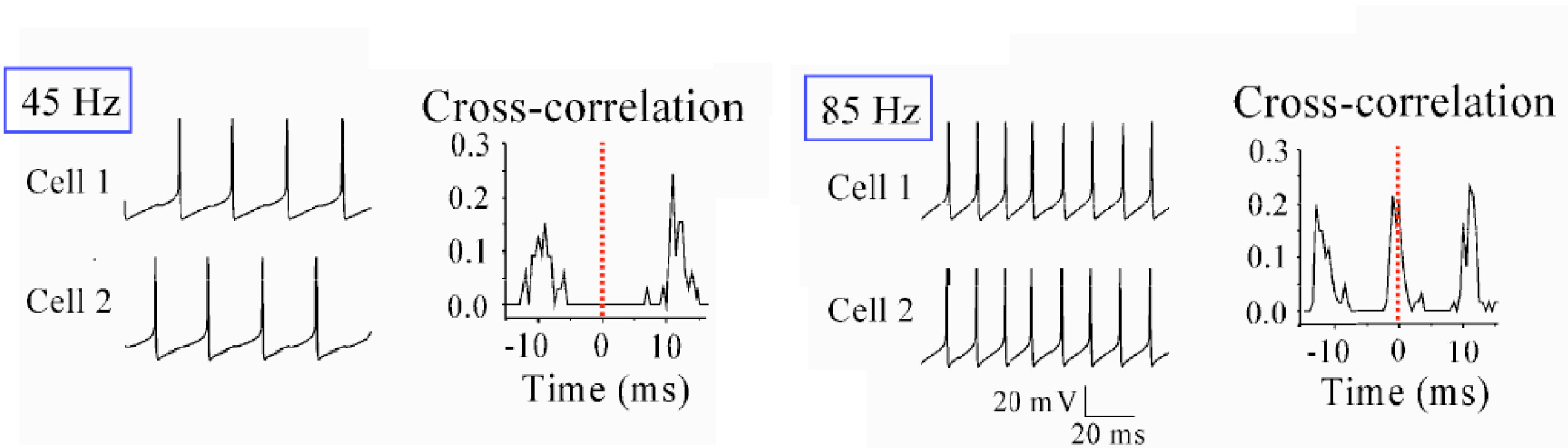
For inhibition (g < 0), synchrony ($\psi' = \psi$) is stable for $\tau > \frac{1}{\omega}$

Theory Meets Experiment

Pair-wise Reciprocal Inhibition among FS Interneurons in Neocortical Slice
Fireing Switches from Antisynchrony to Synchrony near 80 Hz
(data from Barry Connors Laboratory)

$$\Gamma(\Delta\psi) - \Gamma(-\Delta\psi) = g \frac{(\omega\tau)^2 - 1}{[1 + (\omega\tau)^2]^2} \sin(\Delta\psi)$$

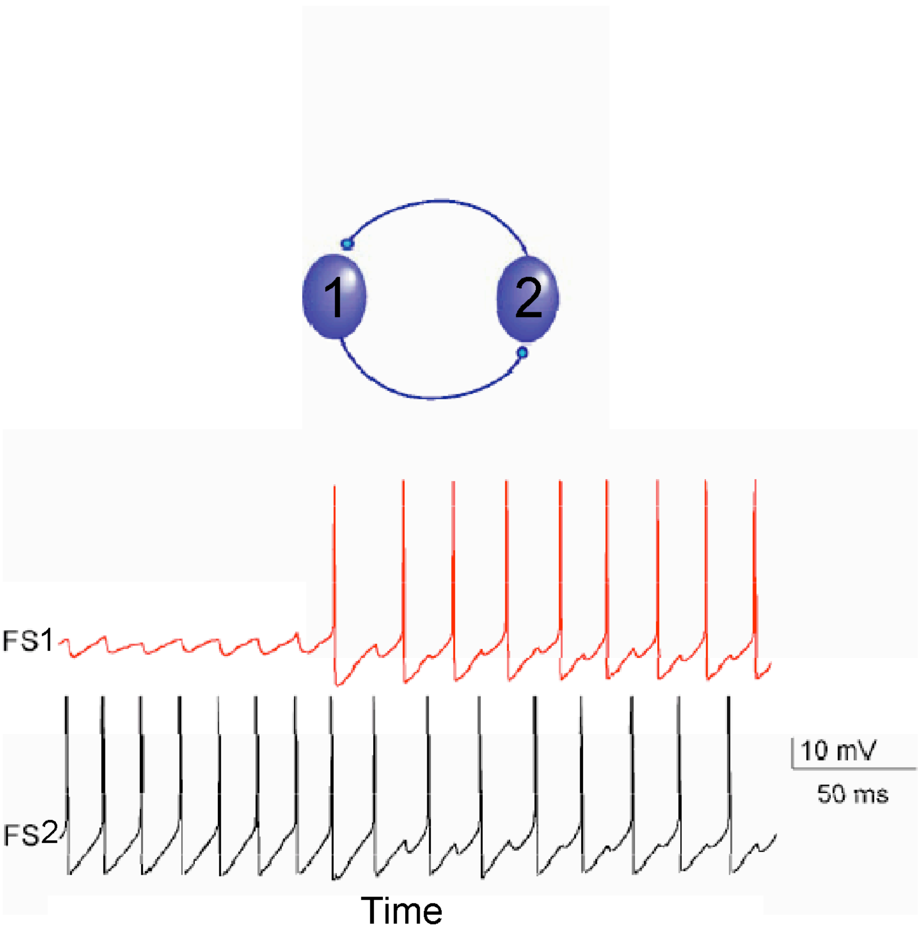


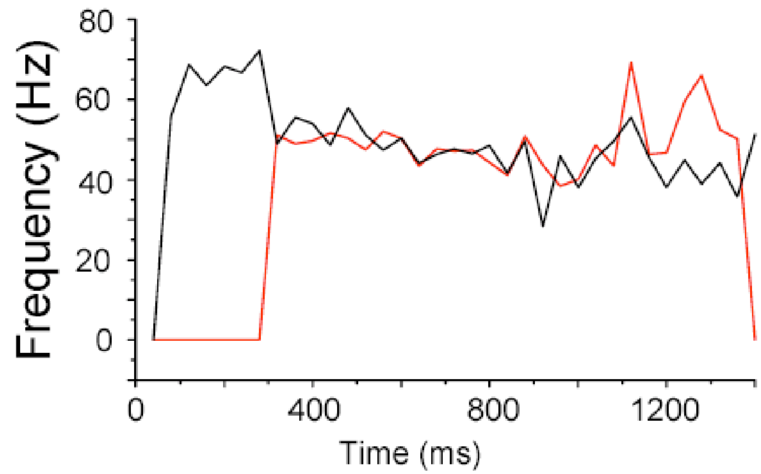



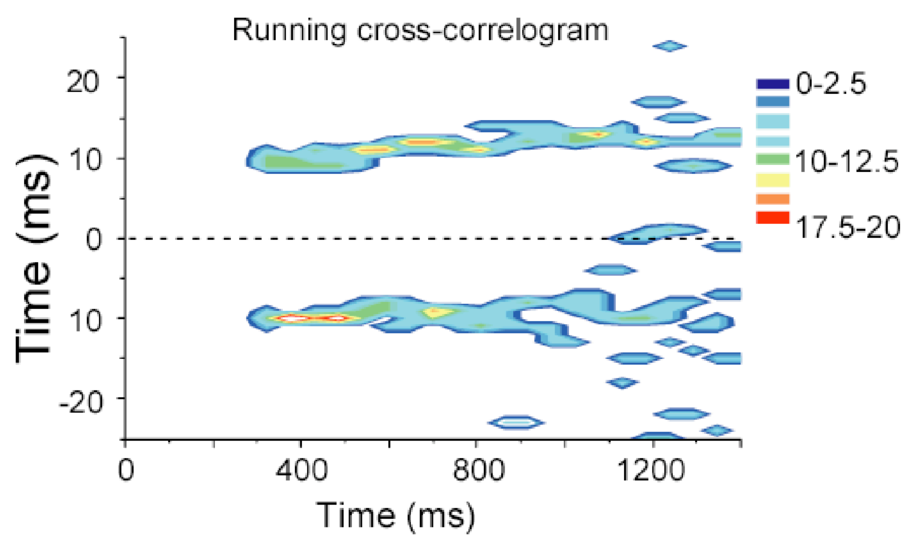
# Theory Meets Experiment

## Pair-wise Reciprocal Inhibition among FS Interneurons in Neocortical Slice Fire in Antisynchrony near 50 Hz ($\gamma$ band)

(data from Barry Connors Laboratory)

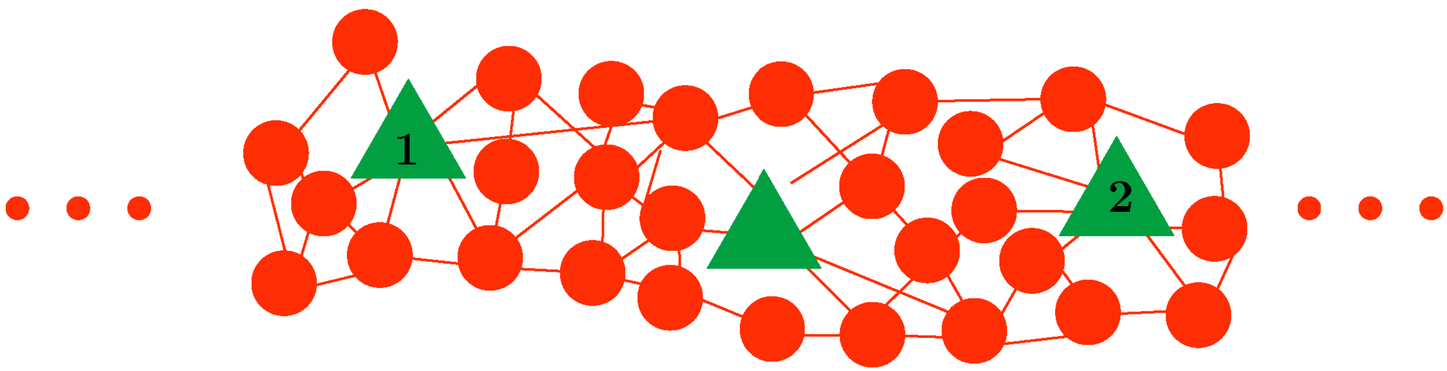


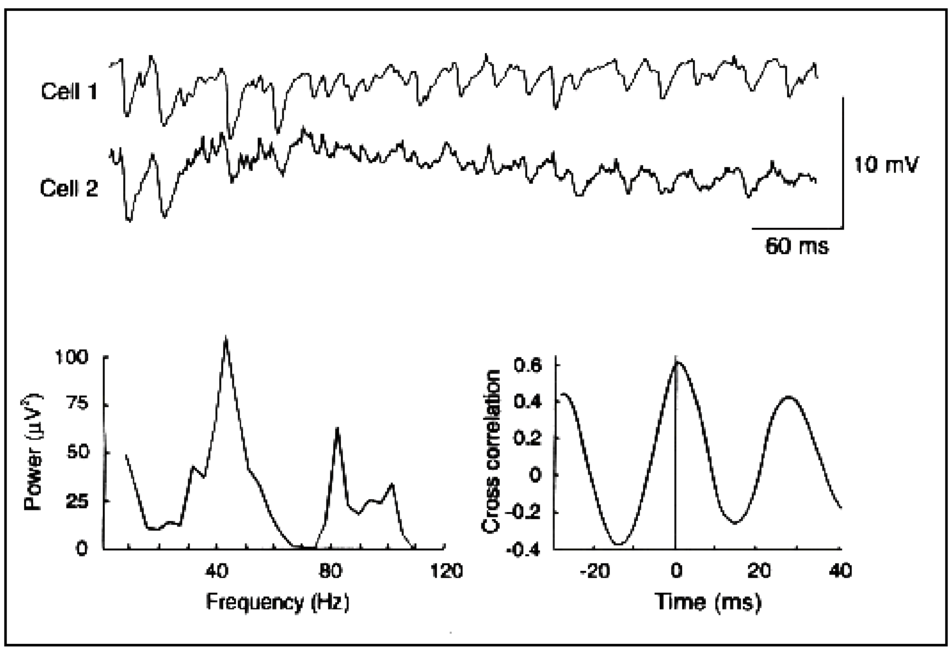



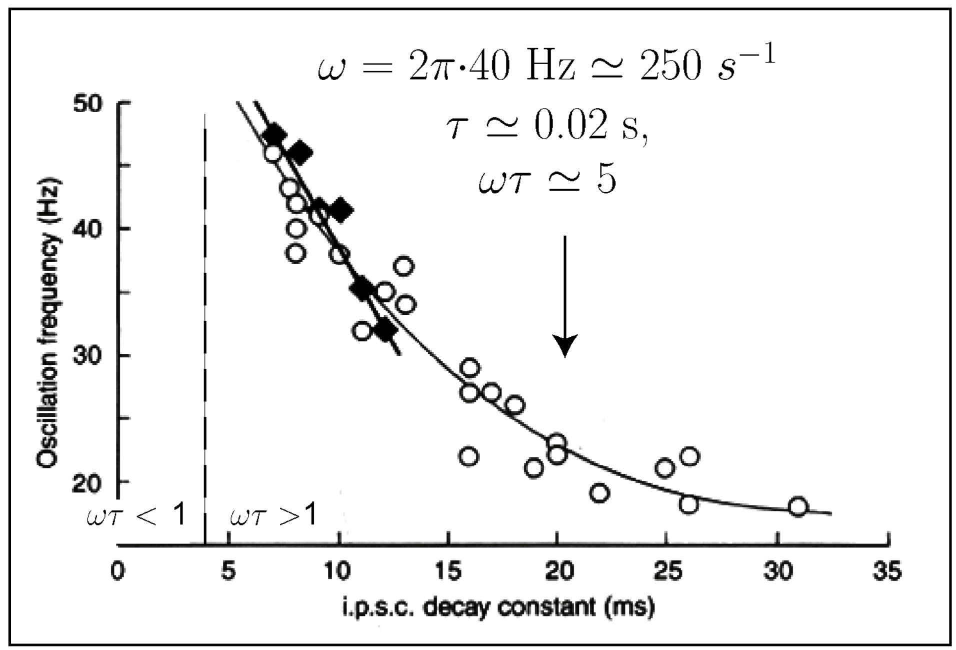



# Theory Meets Experiment
## Synchronized Oscillations in Interneuron (g < 0) Networks
(Whittington, Traub and Jeffreys 1995)

$$\Gamma(\Delta\psi) - \Gamma(-\Delta\psi) \;=\; g\,\frac{(\omega\tau)^2 - 1}{[1 + (\omega\tau)^2]^2}\,\sin(\Delta\psi)$$



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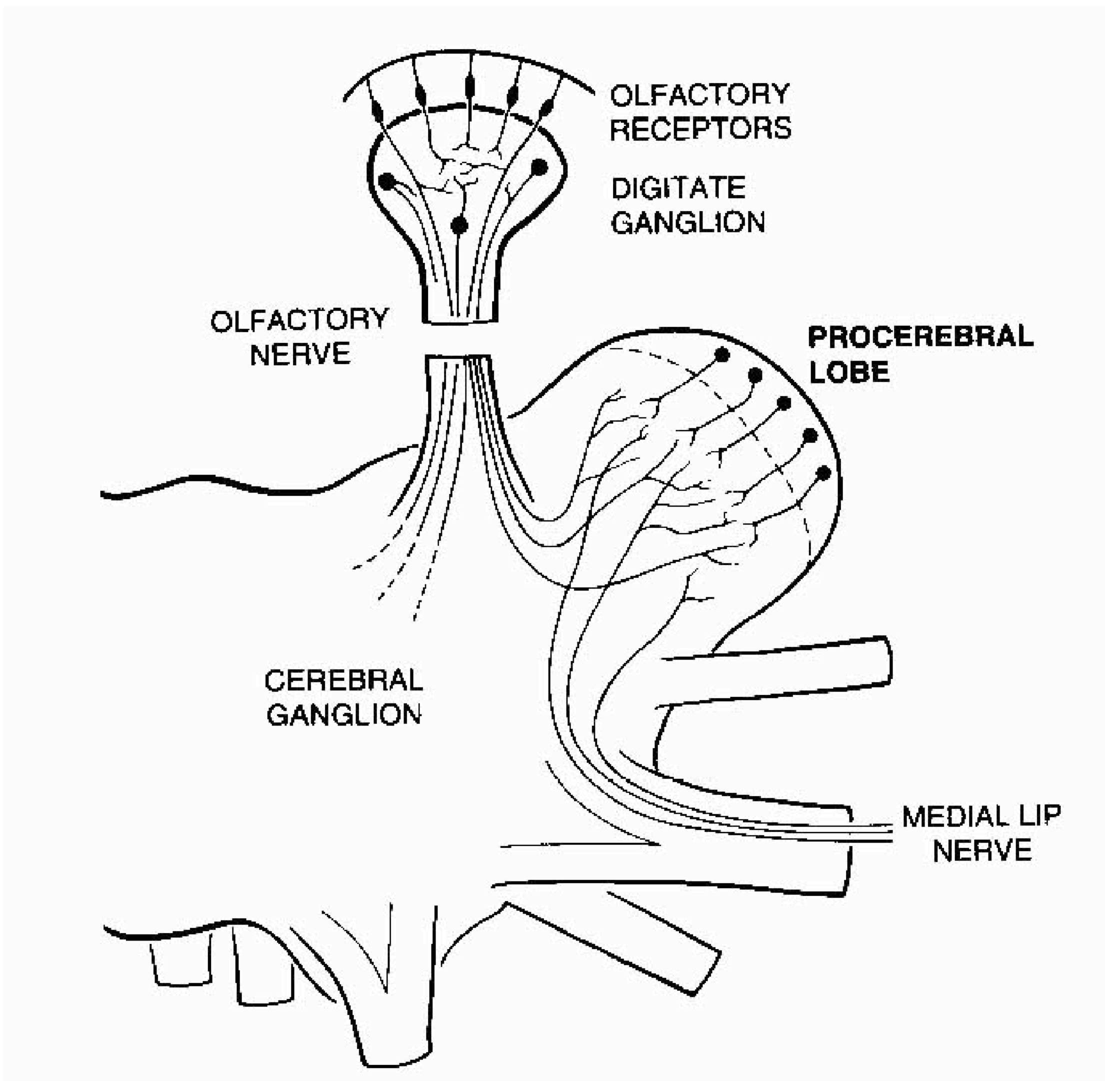
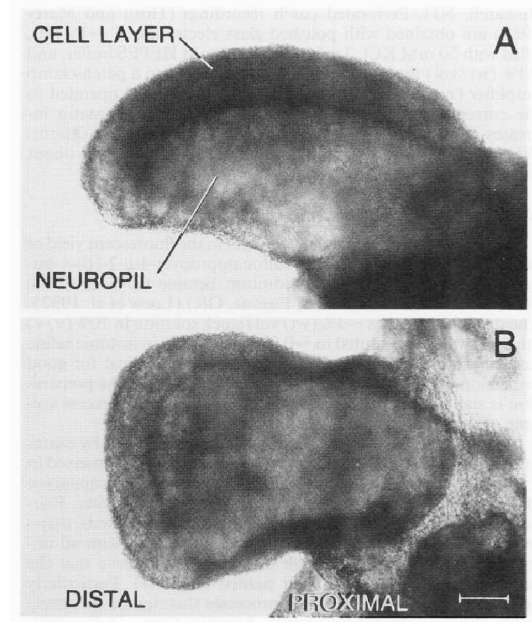
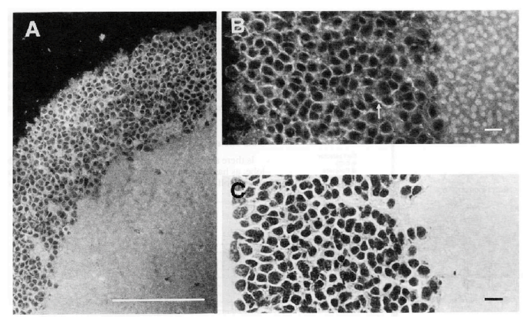
# Central Olfactory Organ in the Terrestrial Mollusk Limax

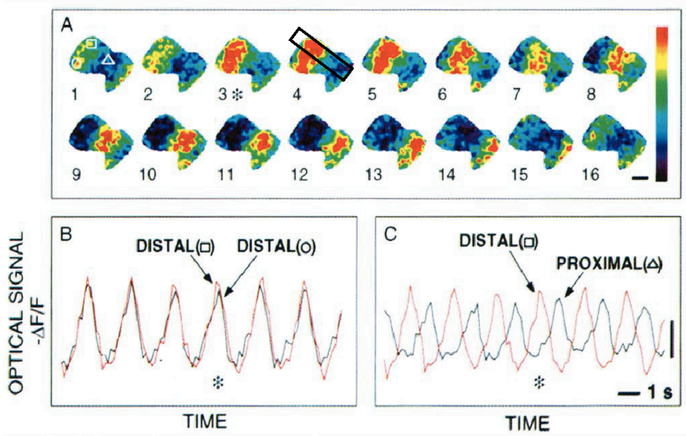


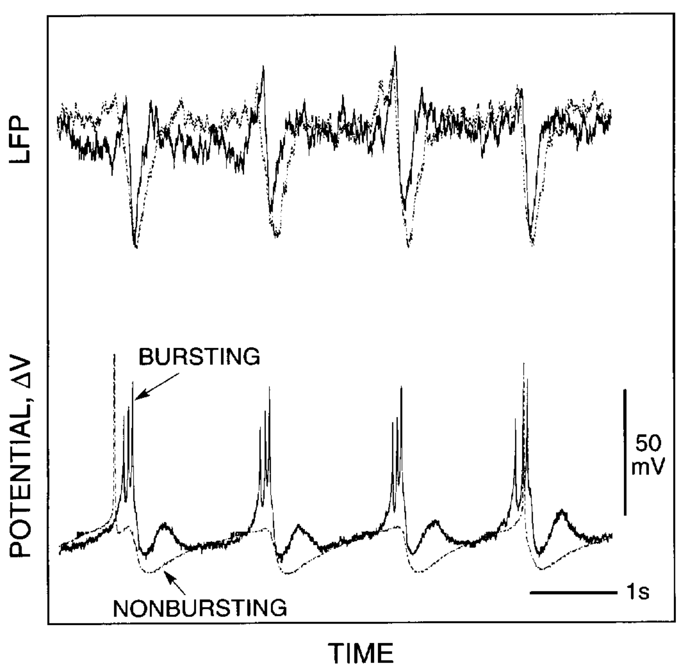



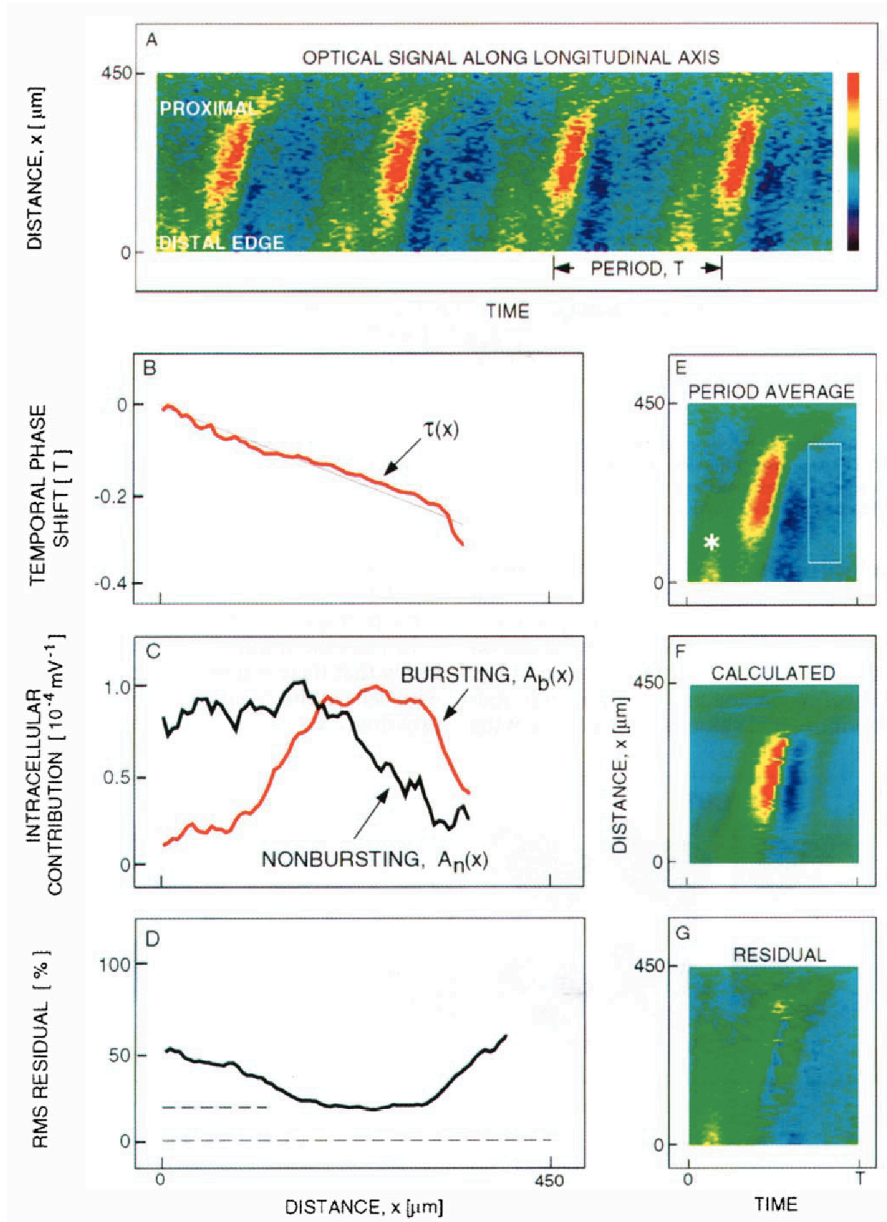



# Decomposition of Optical Signal into Underlying Intracellular Potentials

$$-\Delta F(x,t)/F(x) = A_B(x)\,V_B[t+\tau(x)] + A_{NB}(x)\,V_{NB}[t+\tau(x)]$$

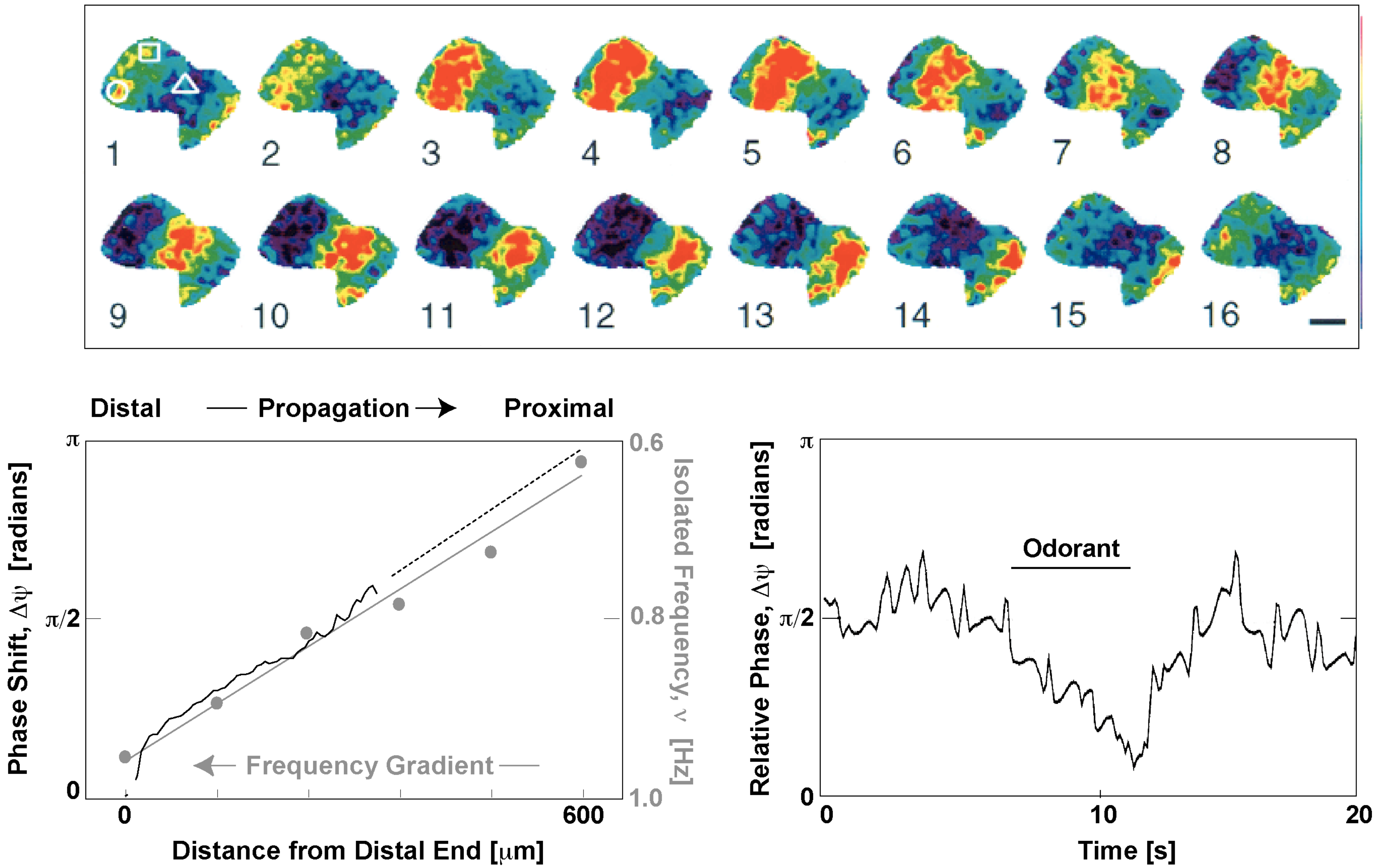


# Electrical Wave Propagation in the Central Olfactory Organ of Limax

(Delaney et al 1994; Kleinfeld et al 1994; Ermentrout et al 1996)



# Coupling of Two Oscillators with Different Intrinsic Frequencies

We take $\Gamma(\psi - \psi') \equiv -\Gamma_0 \sin(\psi - \psi')$

Then
$$\frac{d\psi}{dt} = \Gamma_0 \sin(\psi' - \psi) + \omega$$
$$\frac{d\psi'}{dt} = \Gamma_0 \sin(\psi - \psi') + \omega'$$

Lock, i.e., $\frac{d\psi}{dt} = \frac{d\psi'}{dt}$ so long as $\Gamma_0 \sin(\psi' - \psi) - \Gamma_0 \sin(\psi - \psi') = \omega - \omega'$

or

$$\frac{2\Gamma_0}{|\omega' - \omega|} > 1$$

The phase shift is $\Delta\psi \equiv \psi - \psi' = \sin^{-1}\left(\frac{\omega' - \omega}{2\Gamma_0}\right)$

# Wave Model for Limax

(Ermentrout, Flores & Gelperin 1998; Ermentrout, Wang, Flores & Gelperin 2001)

Chain of Oscillators with $\delta\omega \propto x$

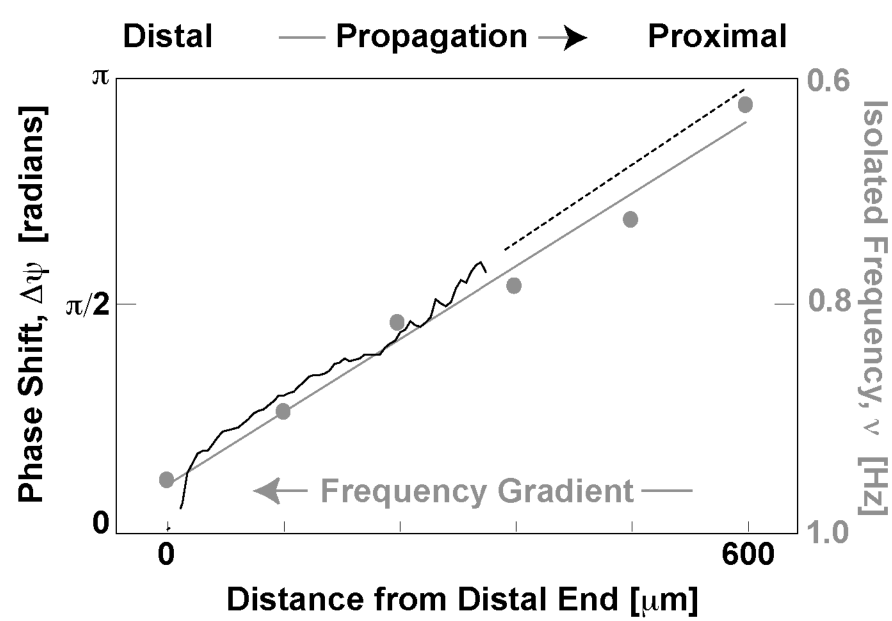
$$\frac{d\psi_x}{dt} = (\omega + \delta\omega_x) + \sum_{x \neq x'} \Gamma(\psi_x - \psi_{x'})$$

$$\delta\omega_x \propto x$$

When the network locks:

Single frequency

Gradient of phase shifts with $\frac{\psi_x}{dx} \propto \text{constant.}$



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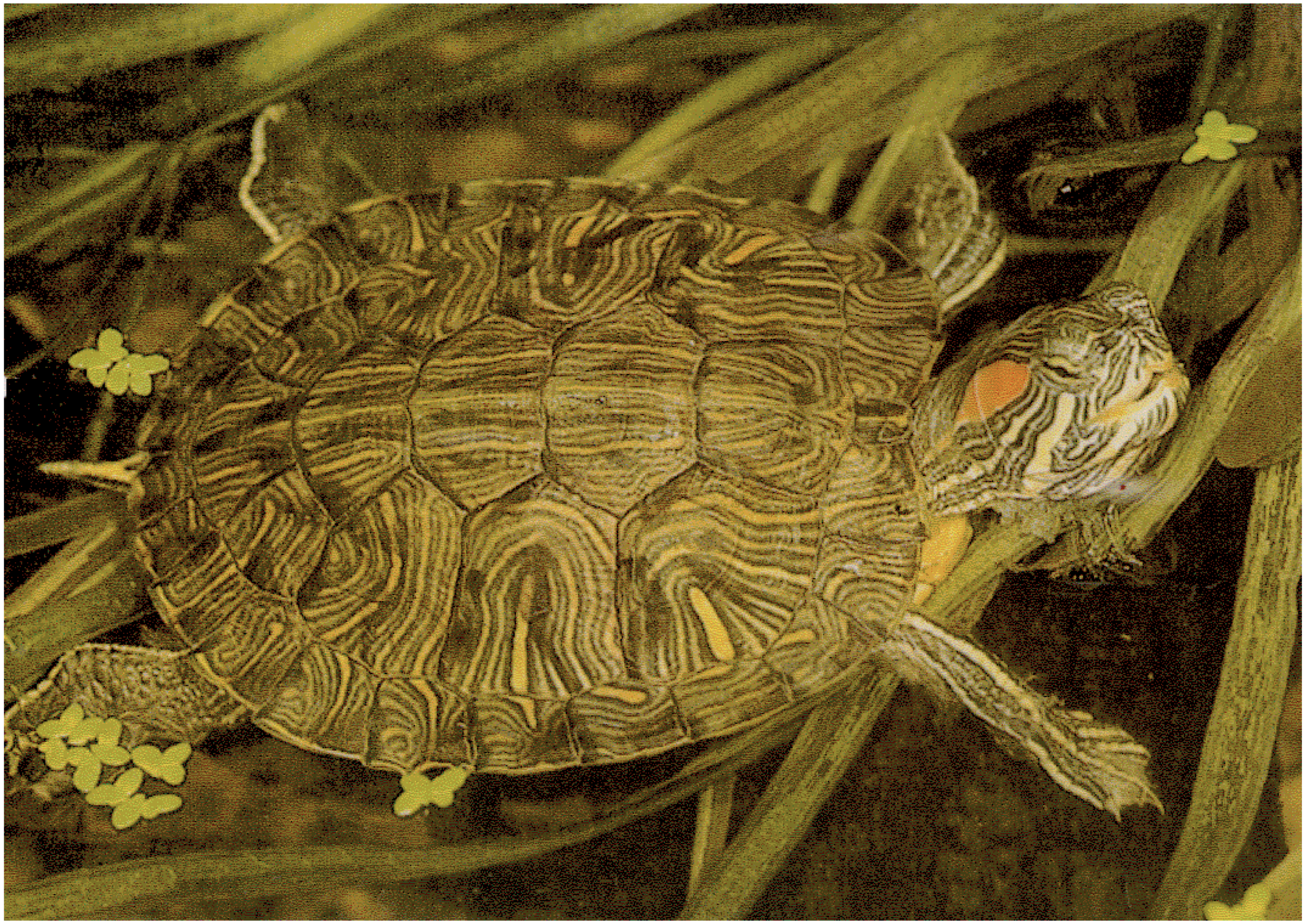
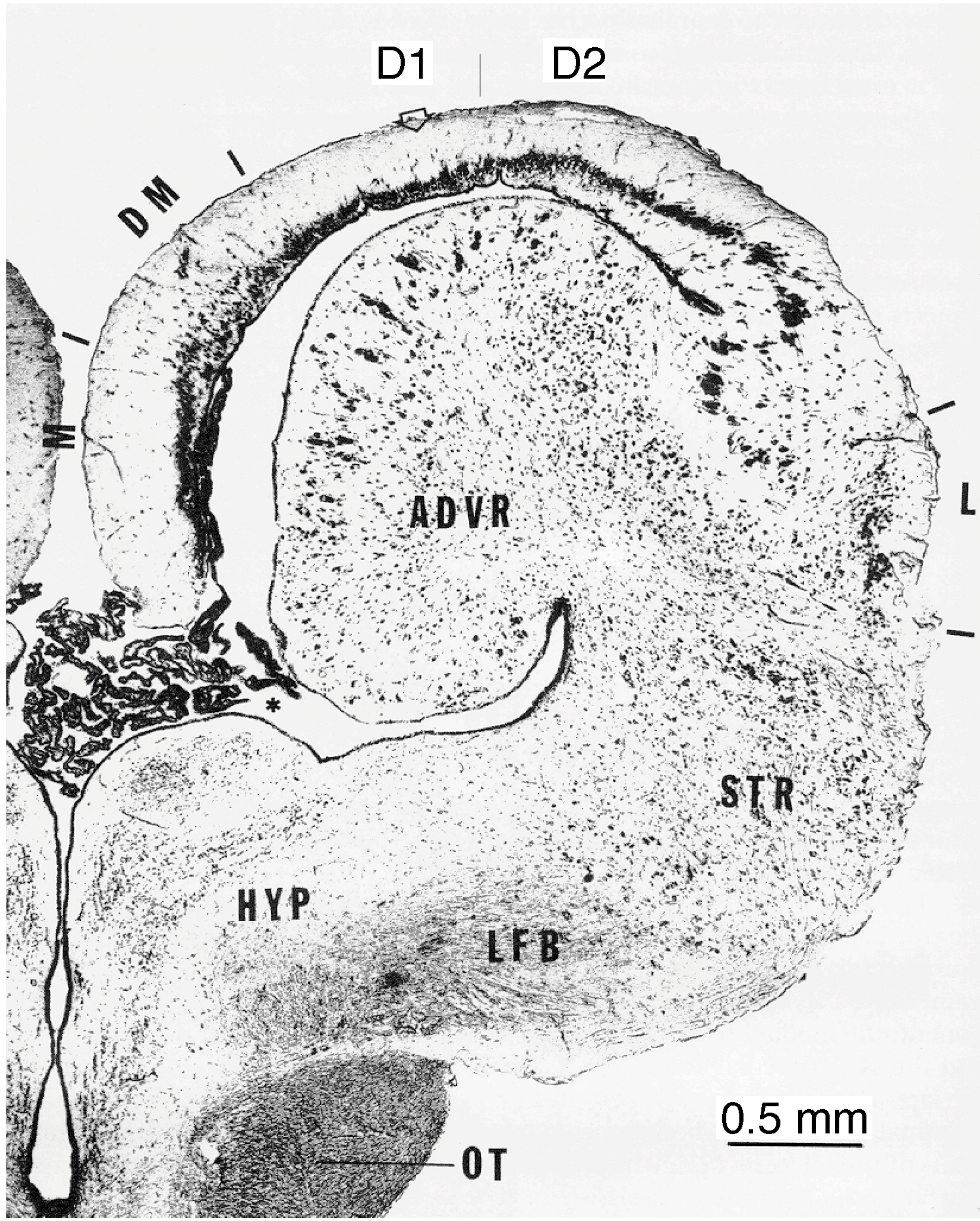
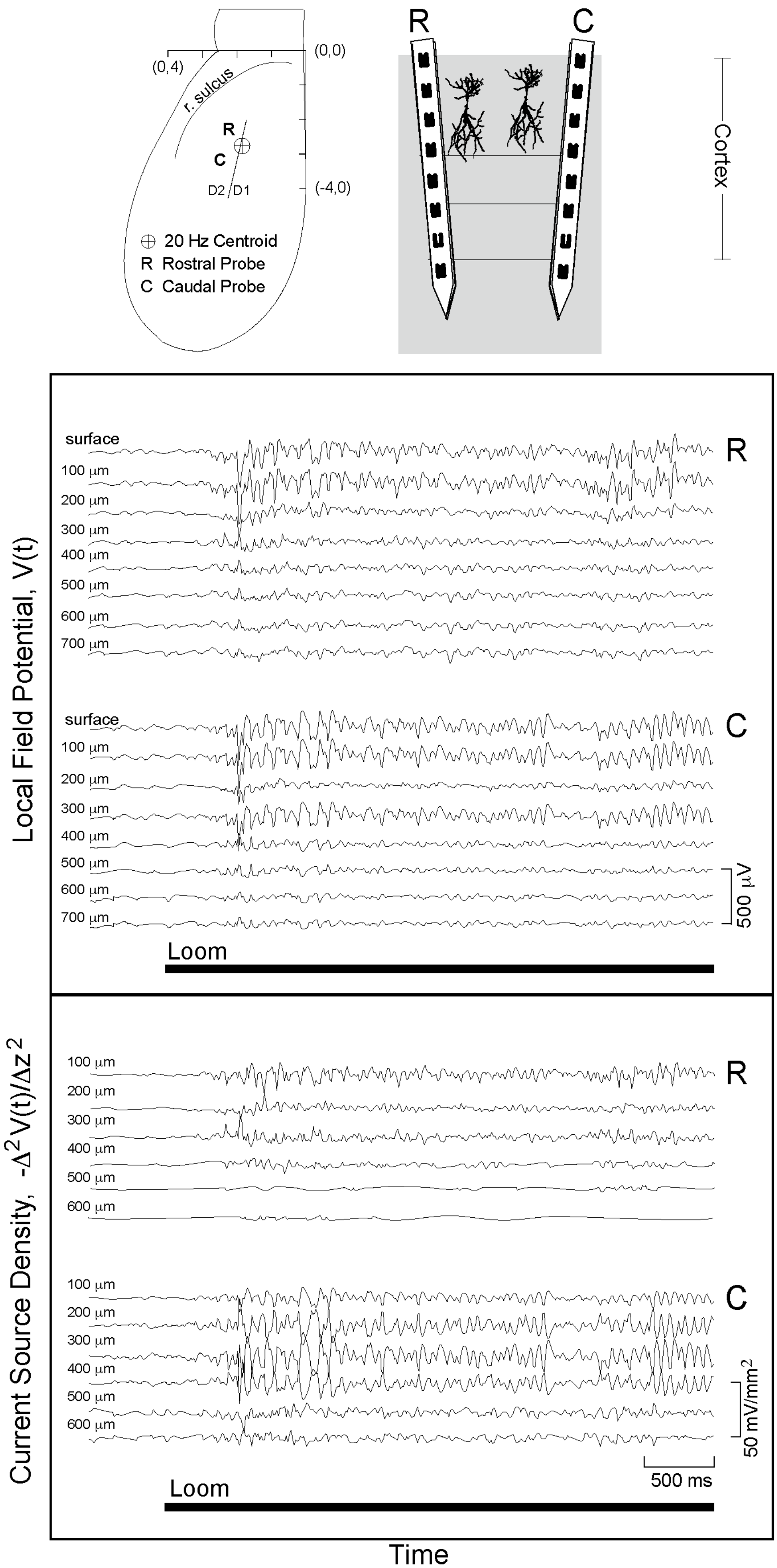


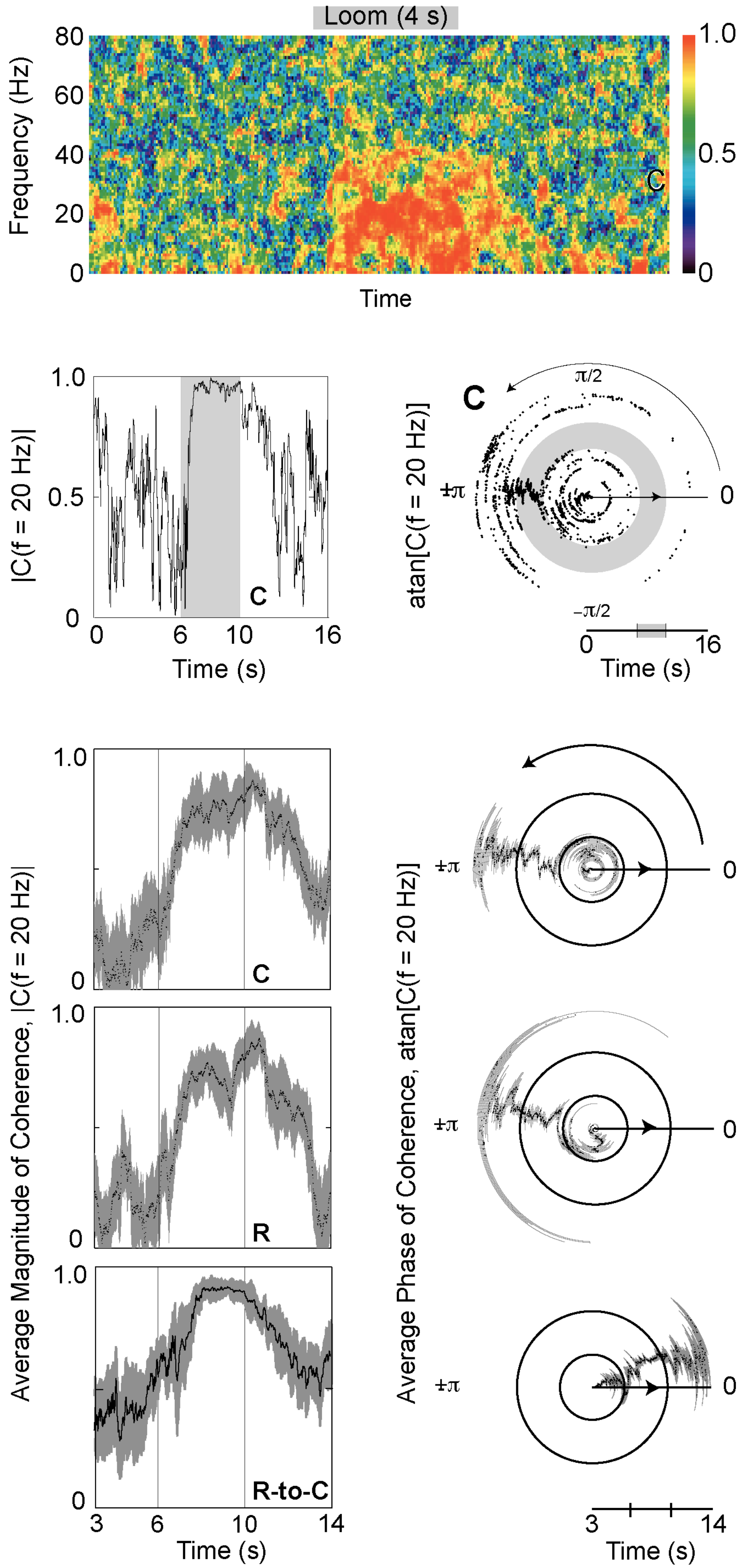
Transverse Nissl section through cerebral hemisphere of *Pseudemys scripta elegans*

- from P. S. Ulinski



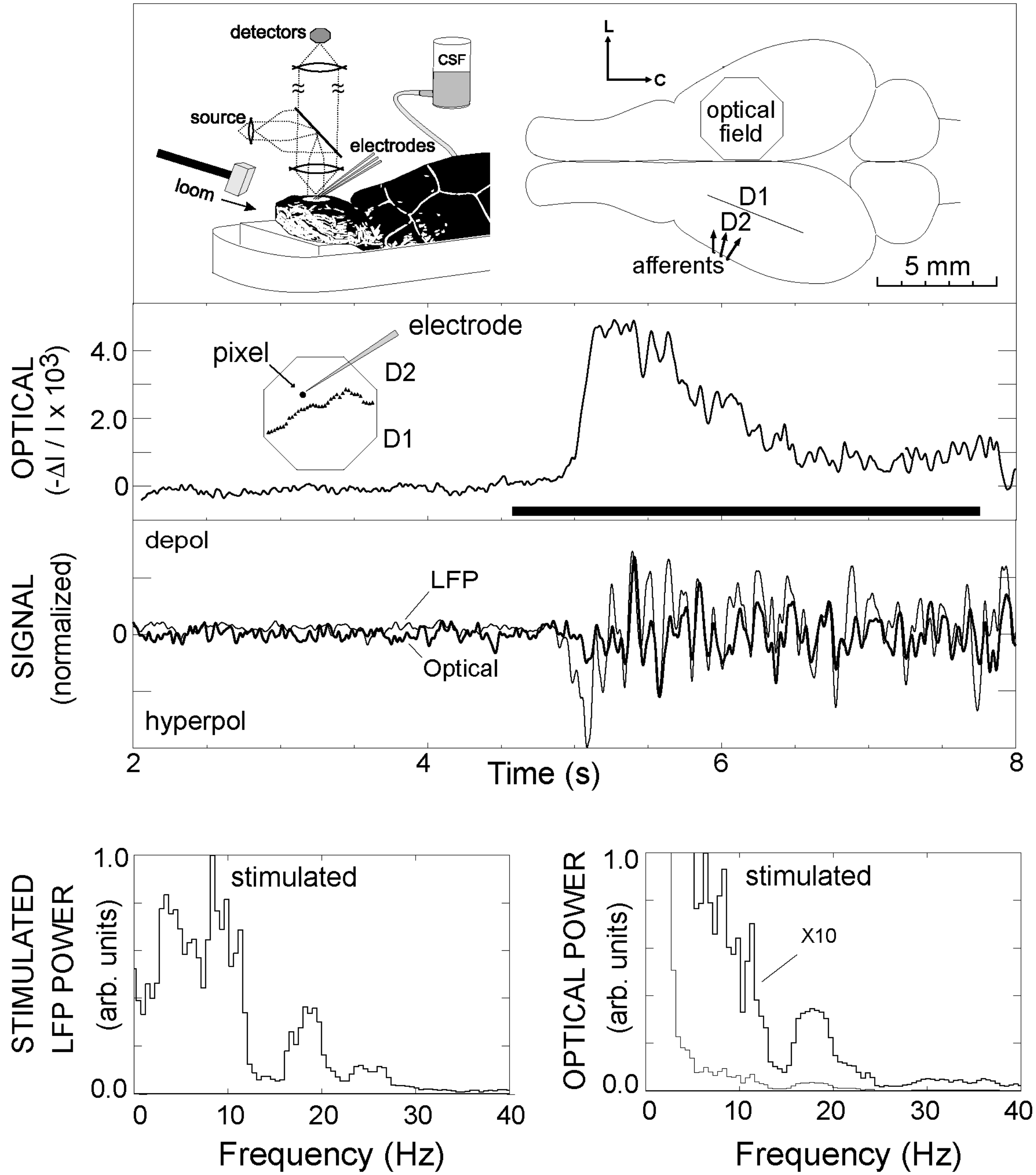


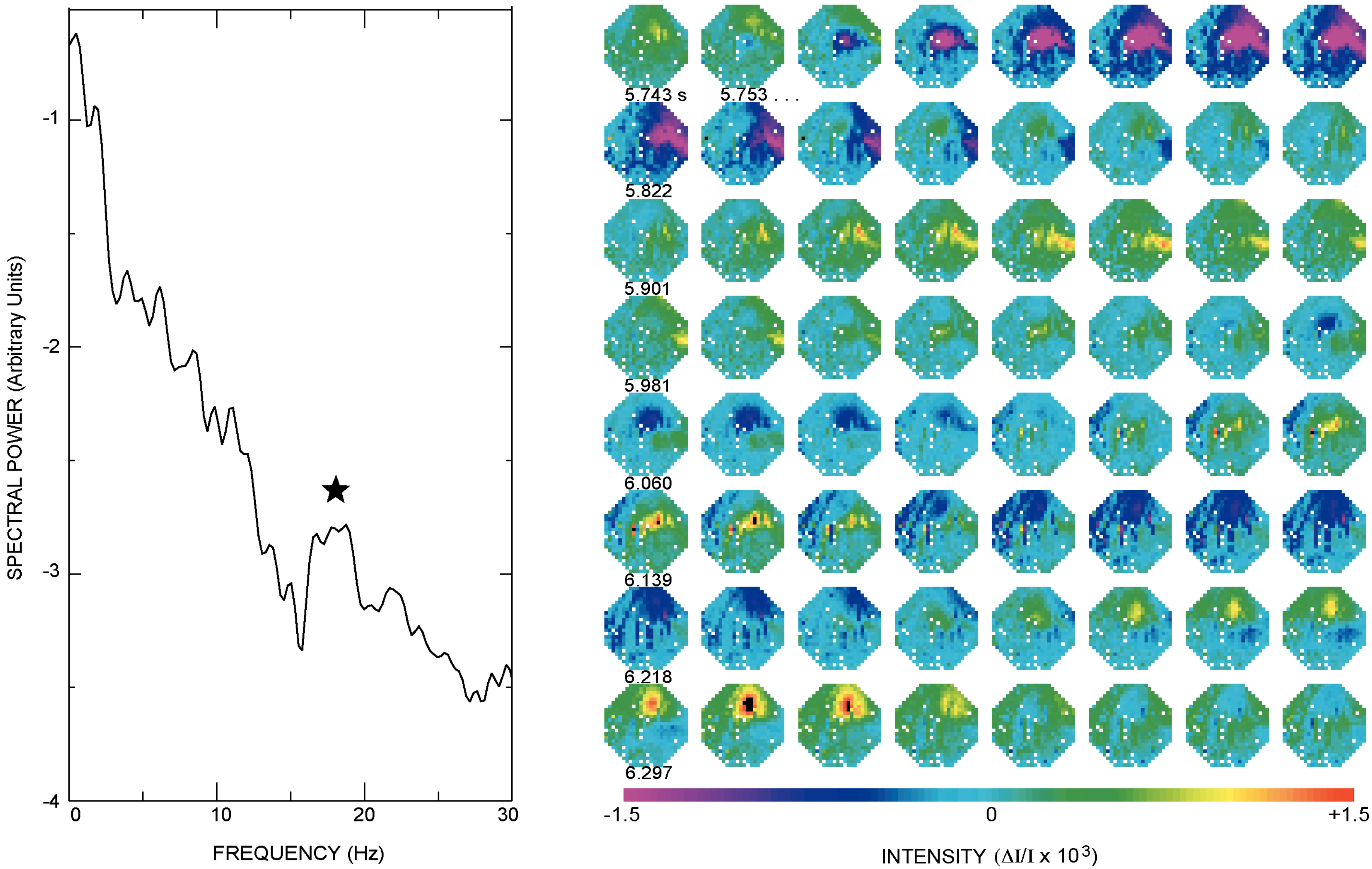

Prechtl, Bullock and Kleinfeld (2000)




Prechtl, Bullock and Kleinfeld (2000)

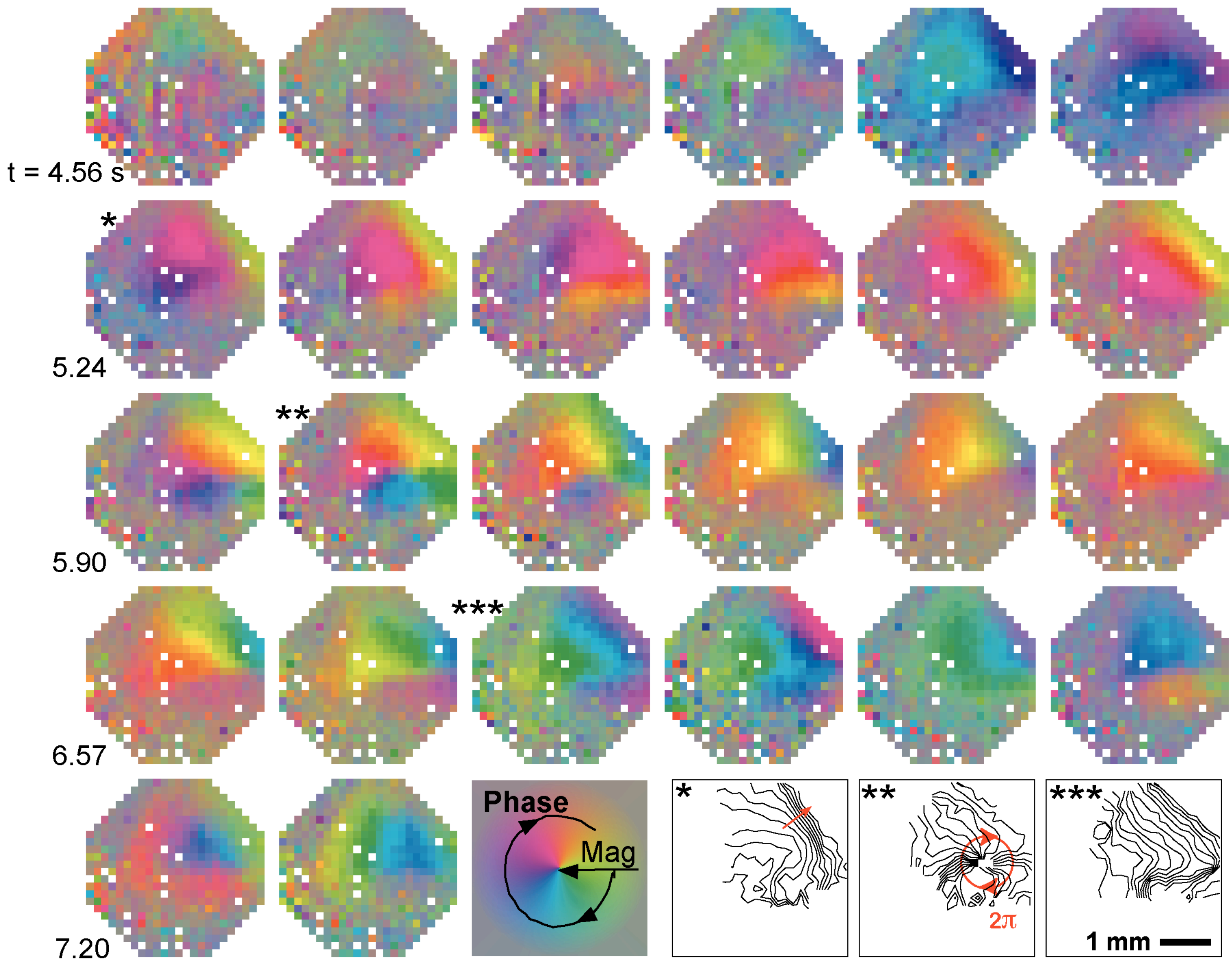
# Voltage Sensitive Dye Imaging of Turtle Visual Cortex



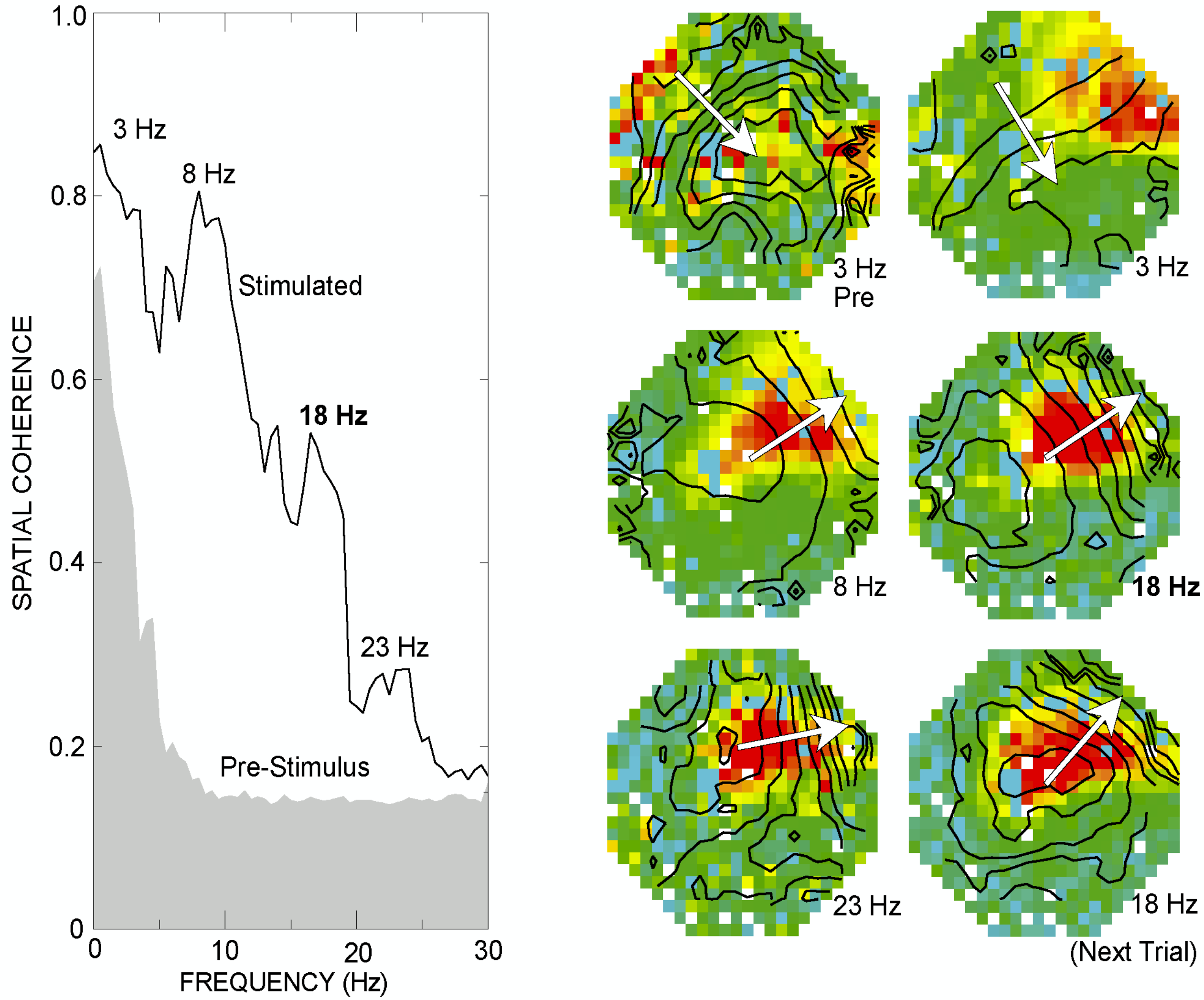


SPECTRAL POWER (Arbitrary Units)
-1
-2
-3
-4
0
10
20
30
FREQUENCY (Hz)
5.743 s
5.753 . . .
5.822
5.901
5.981
6.060
6.139
6.218
6.297
-1.5
0
+1.5
INTENSITY (ΔI/I x 10³)

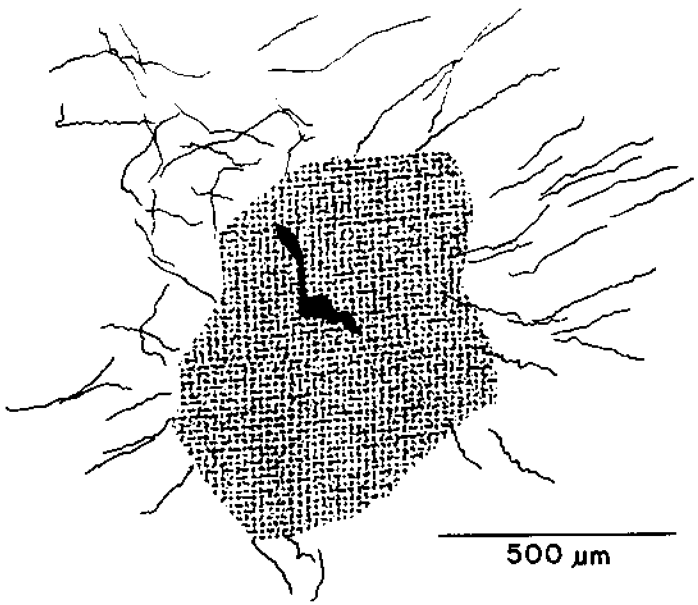
# Demodulated Response at 18 Hz Versus Time
# (Magnitude and Phase Plots)

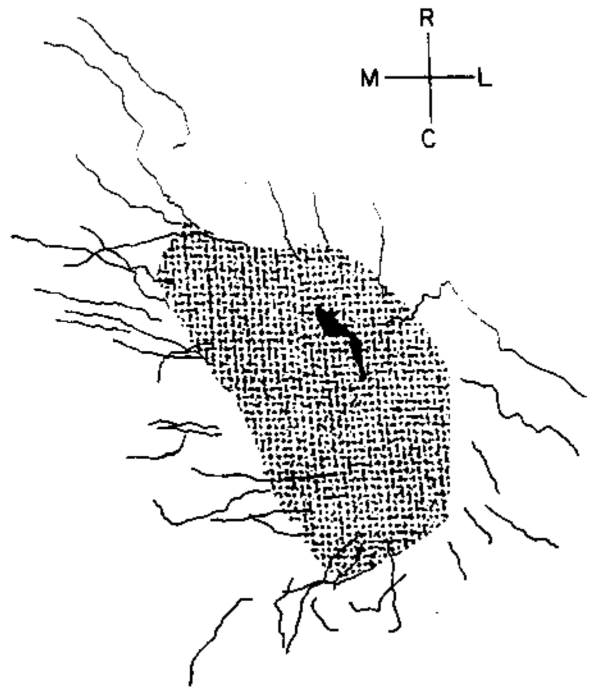


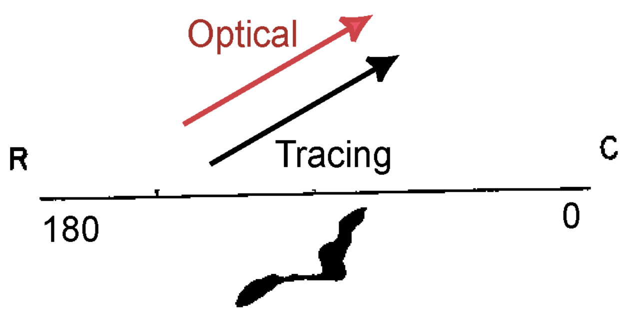
# Dominant Spatial Modes are Revealed from a Spectral Decomposition (SVD) in Position (**x**) and Frequency (f)

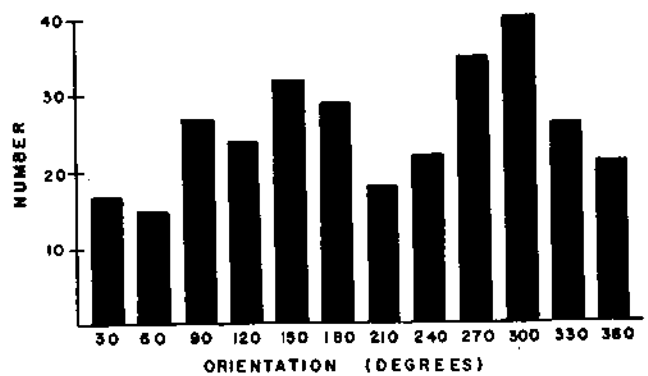


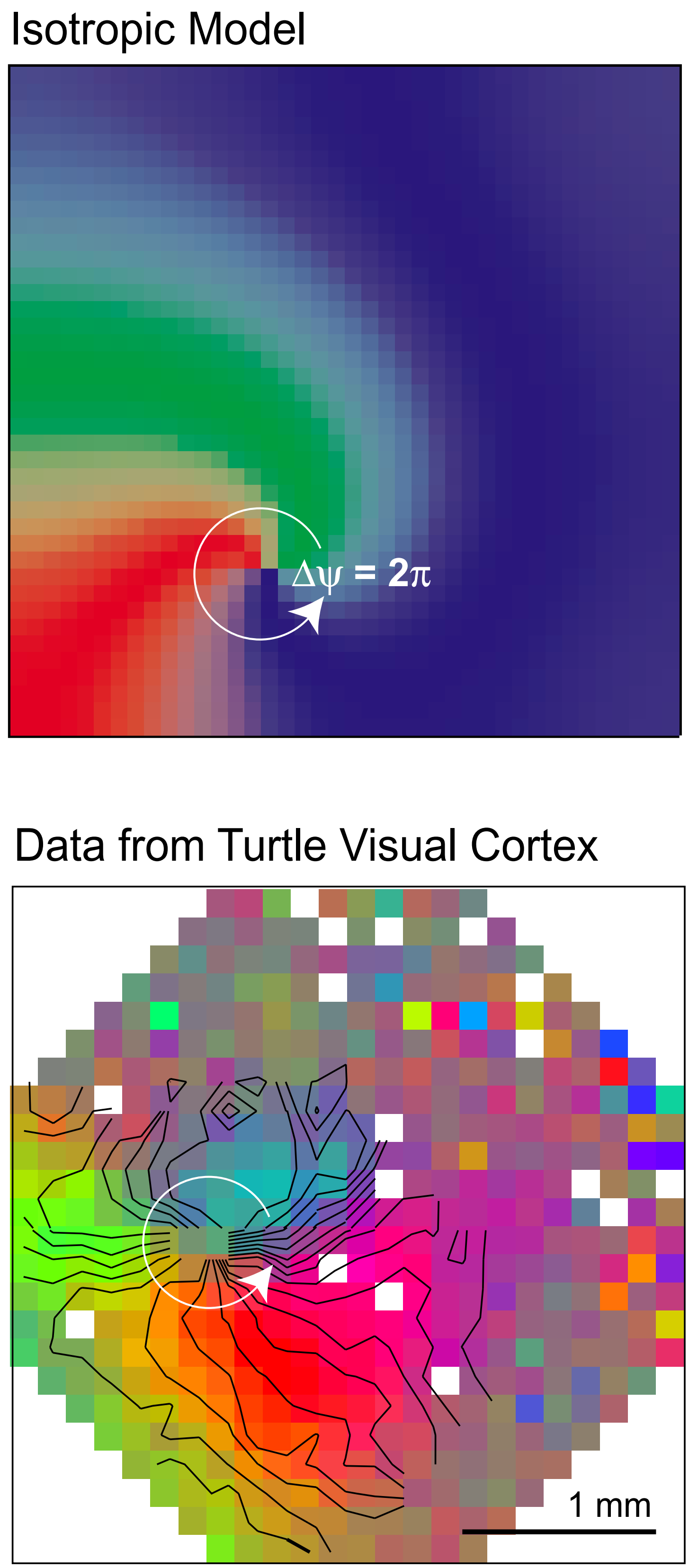

Prechtl, Cohen, Pesaran, Mitra and Kleinfeld 1997


500 µm


R
M
L
C


Optical
Tracing
R
C
180
0


NUMBER
40
30
20
10
30
60
90
120
150
180
210
240
270
300
330
360
ORIENTATION (DEGREES)


Isotropic Model
Δψ = 2π
Data from Turtle Visual Cortex
1 mm

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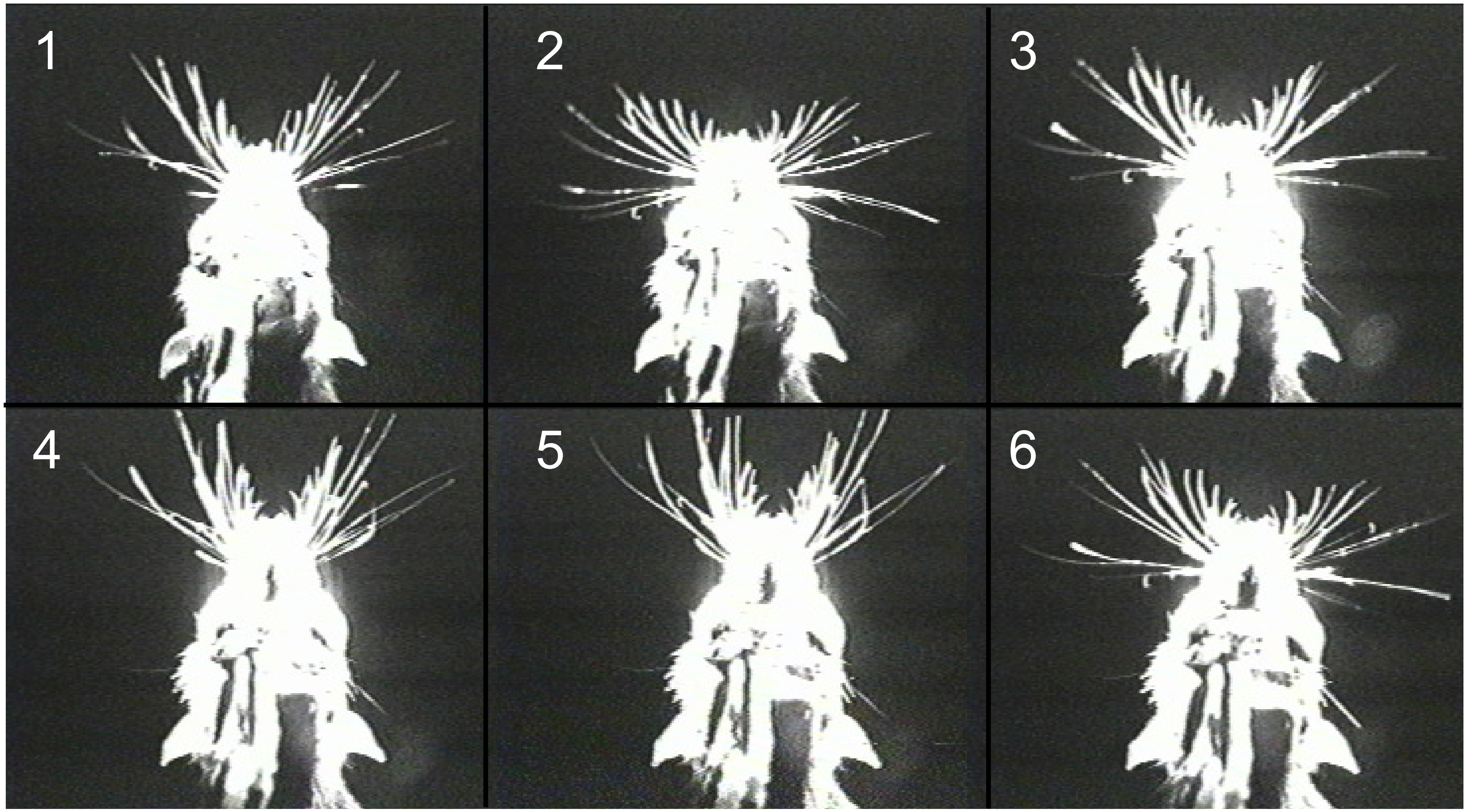
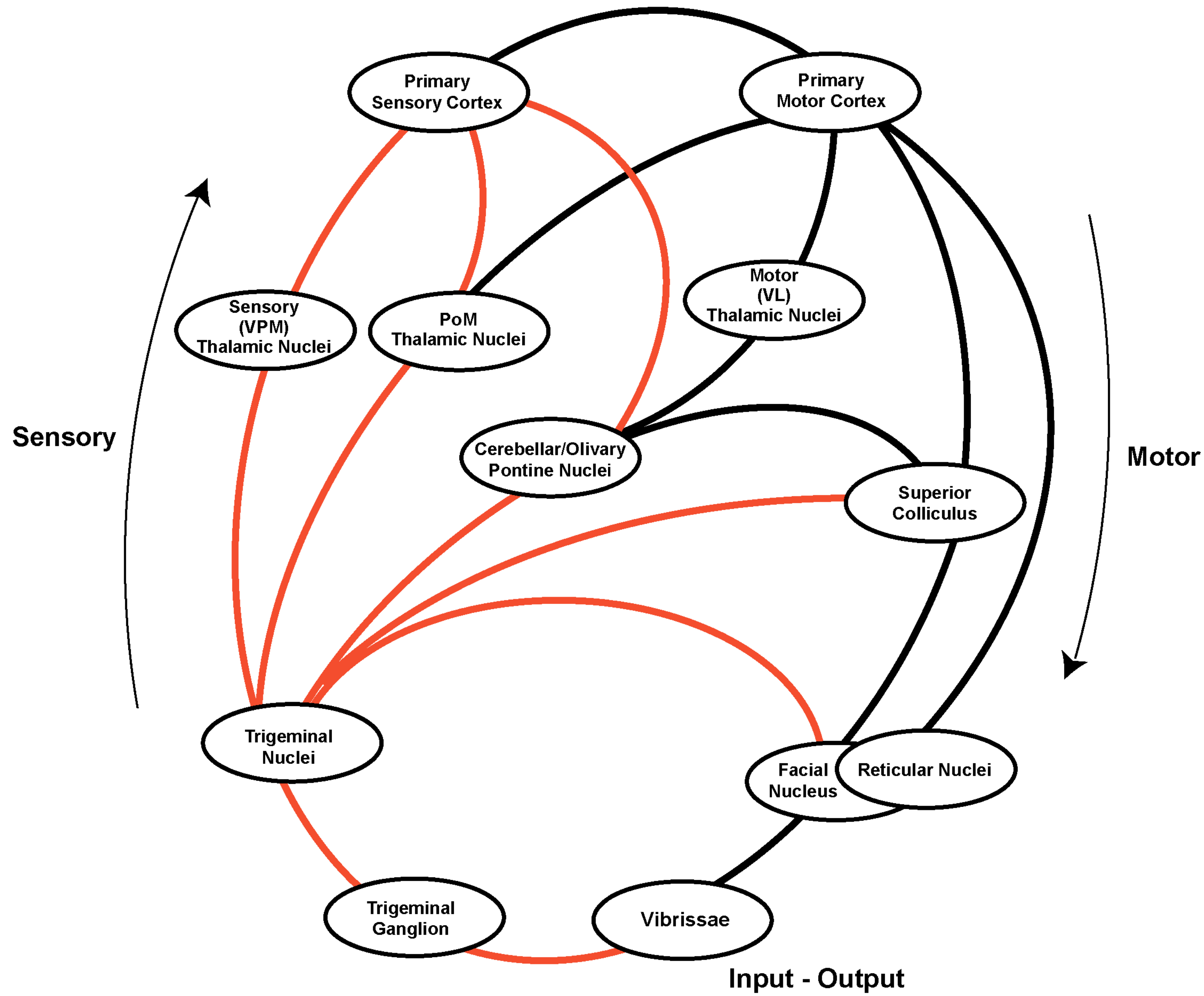
# Active Sensation by Rat:
# Loop Dynamics in Vibrissa Sensorimotor Control



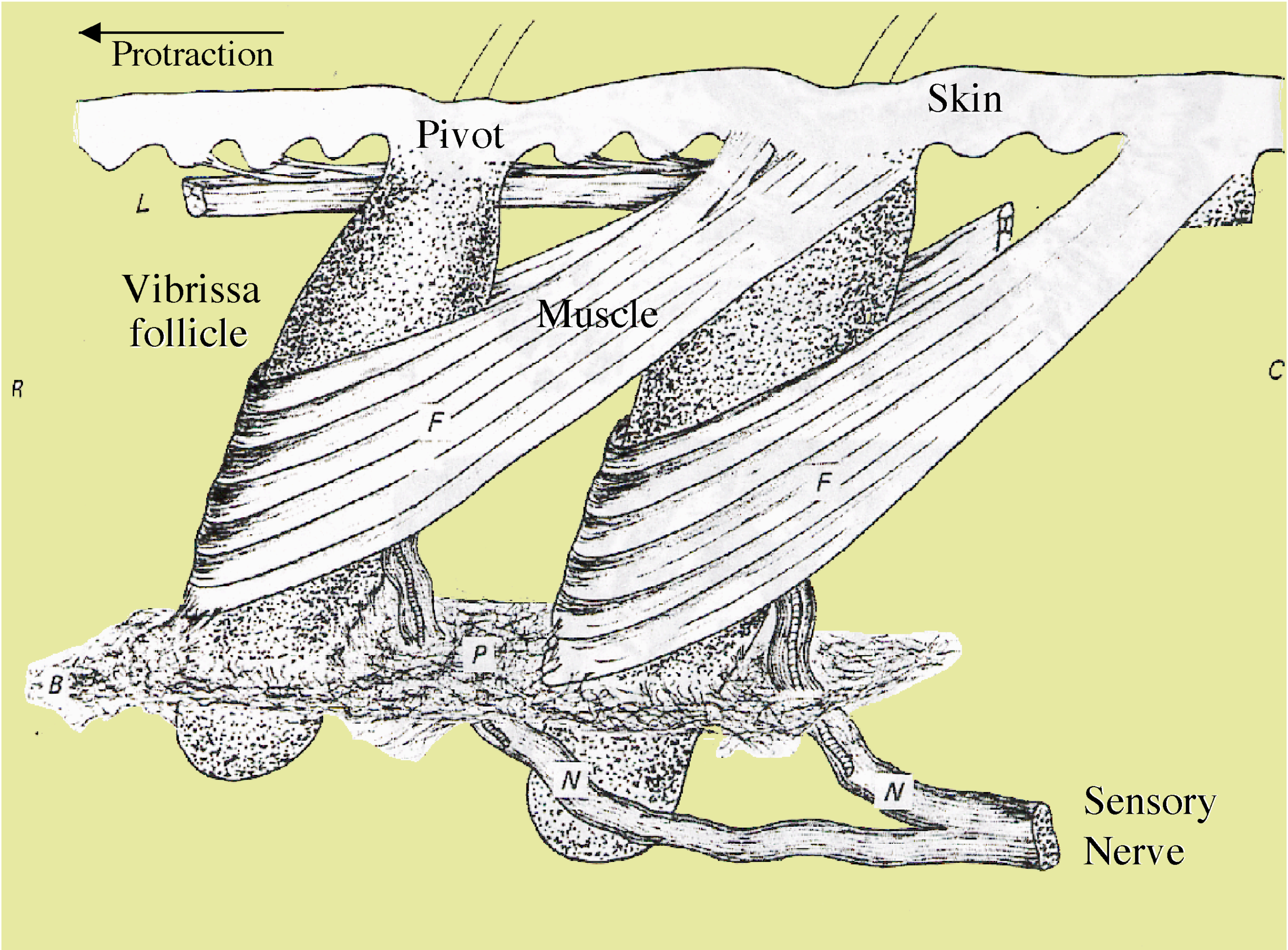

Free Ranging Rat (Blindfolded) that is Whisking in Air in Search of a Food Tube

Consecutive Video Rate Fields (60 Hz acquisition)

# The Vibrissa Sensorimotor System is Comprised of Nested Loops

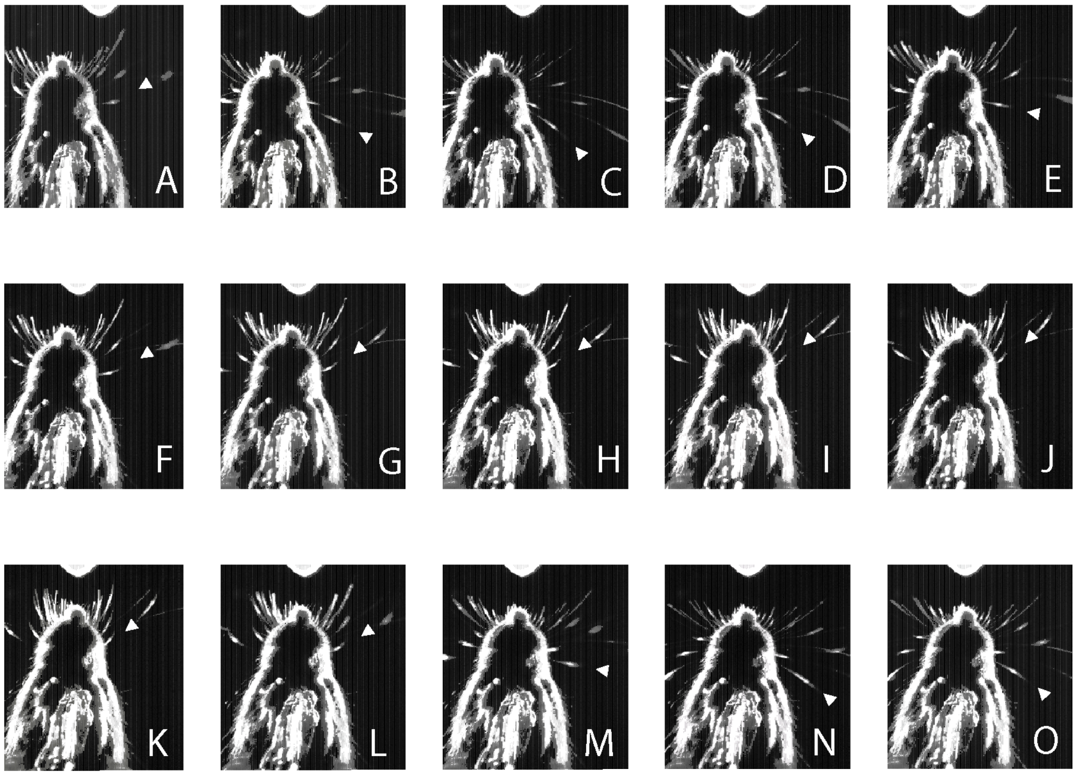


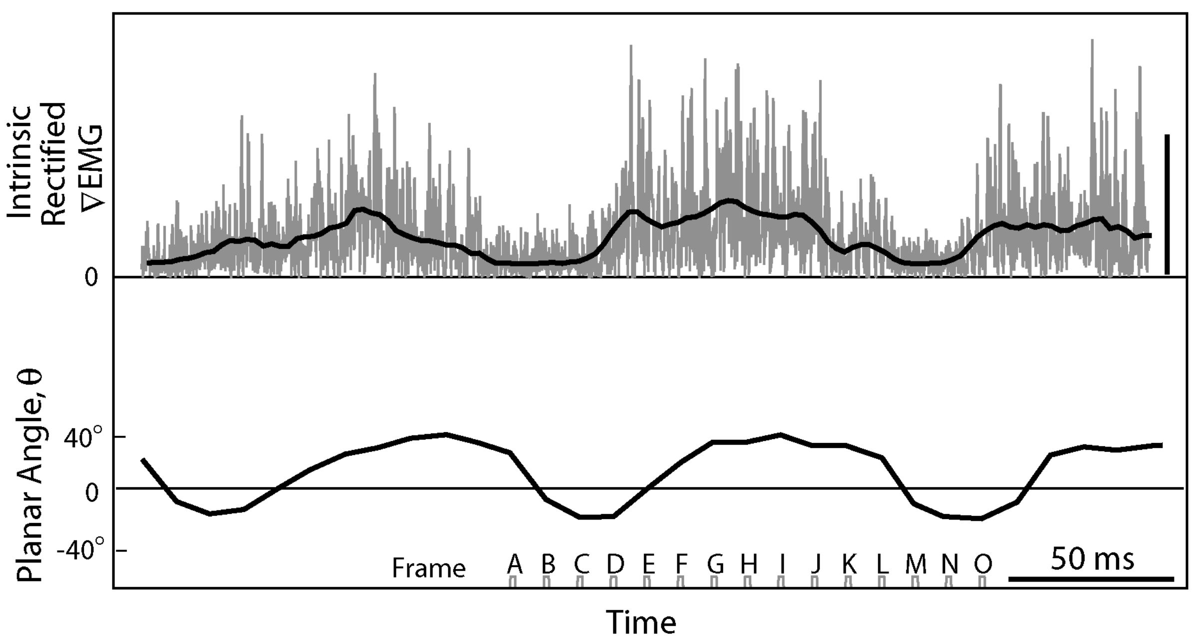
# Intrinsic Muscles Pull the Follicles Backward to Propel Vibrissae Forward




Dorfl (1982)

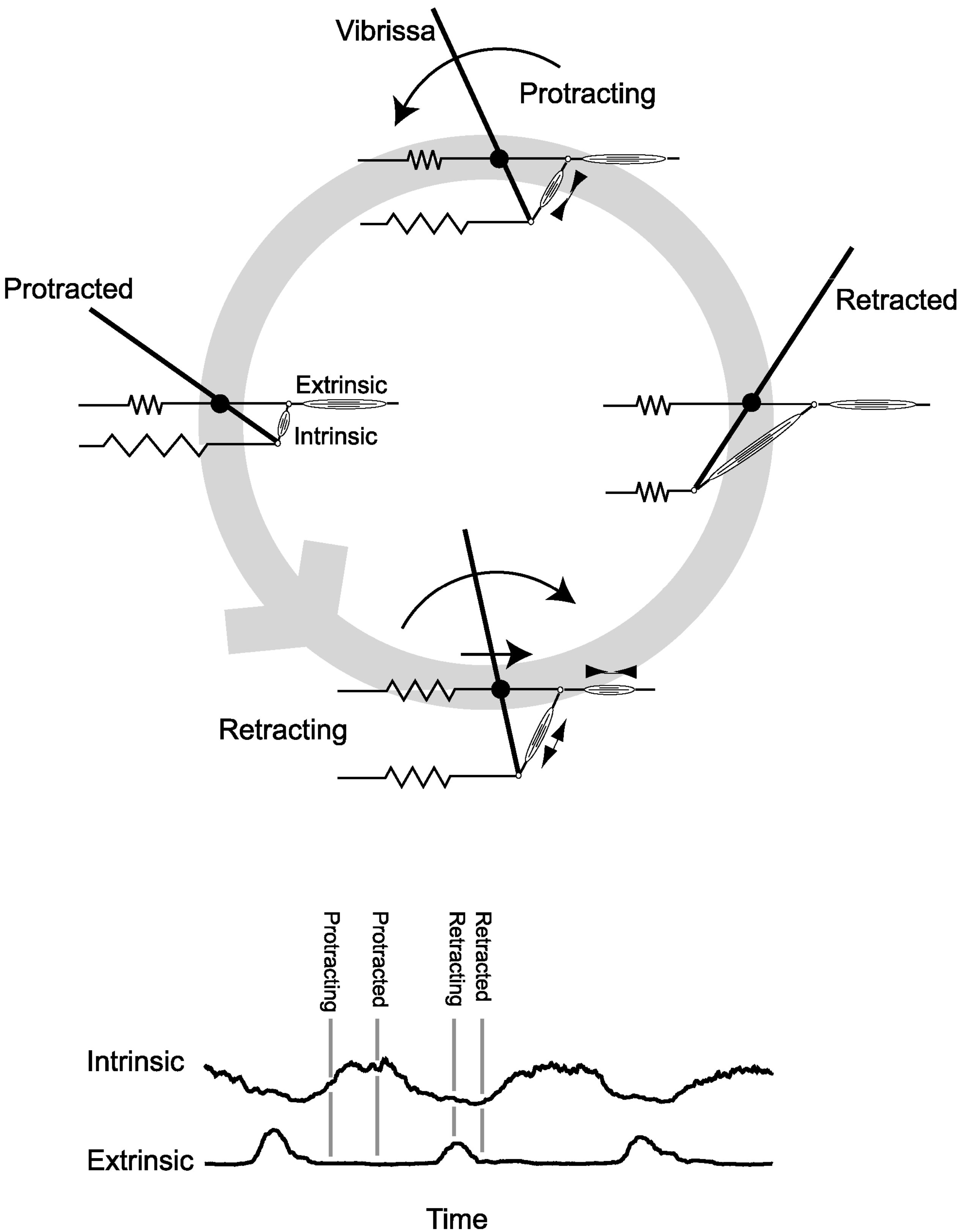
# 5 to 15 Hz Exploratory Whisking by Rat



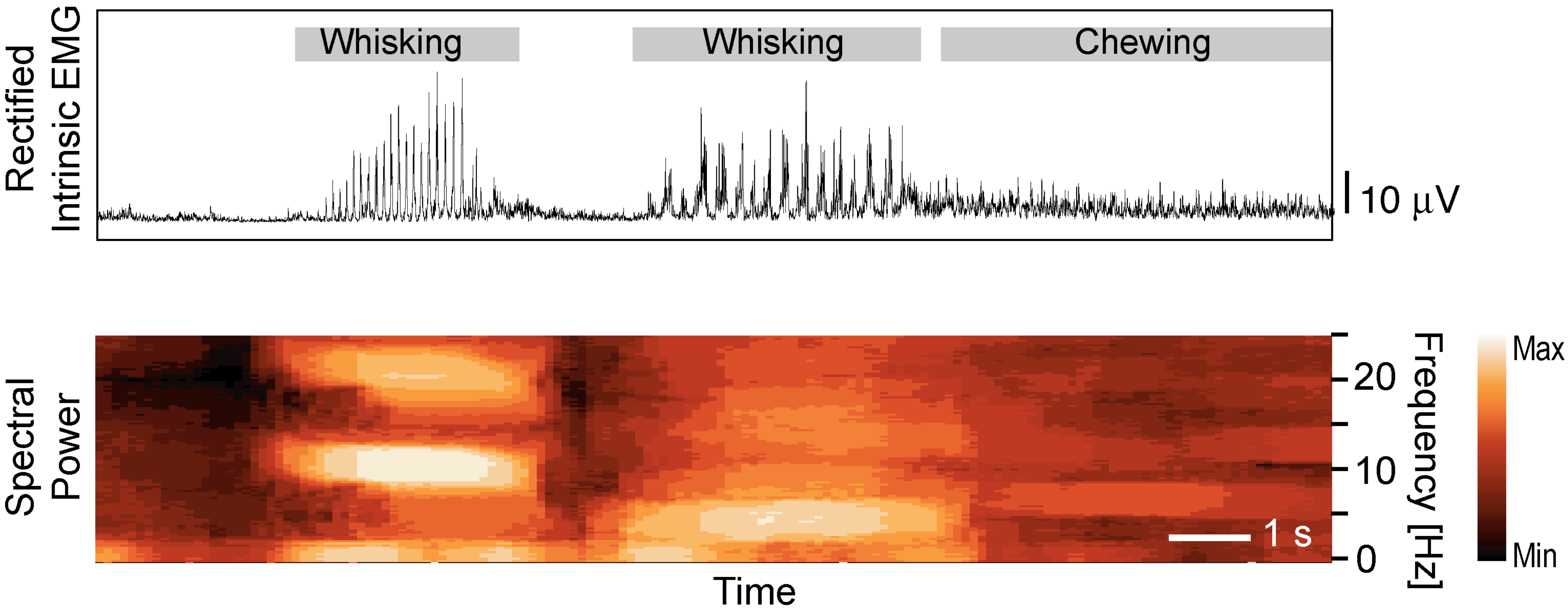

Berg and Kleinfeld, 2003

# The Rodent Whisk Cycle




Berg and Kleinfeld (2002)

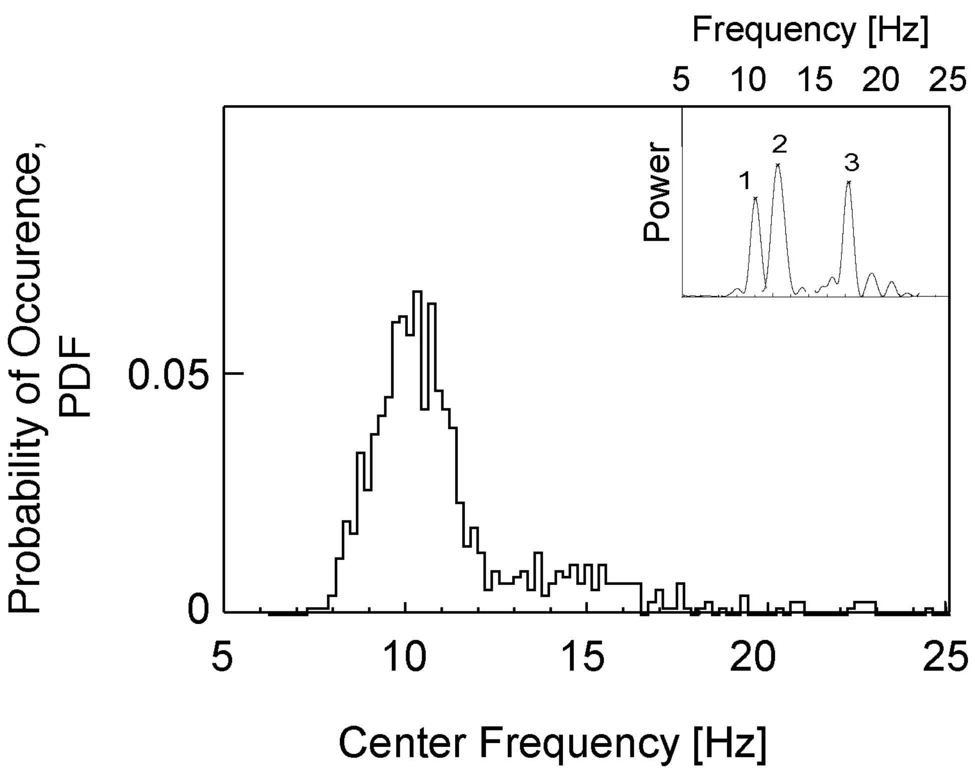
# The Frequency of Whisking is Constant within an Epoch but Broadly Distributed from Epoch to Epoch



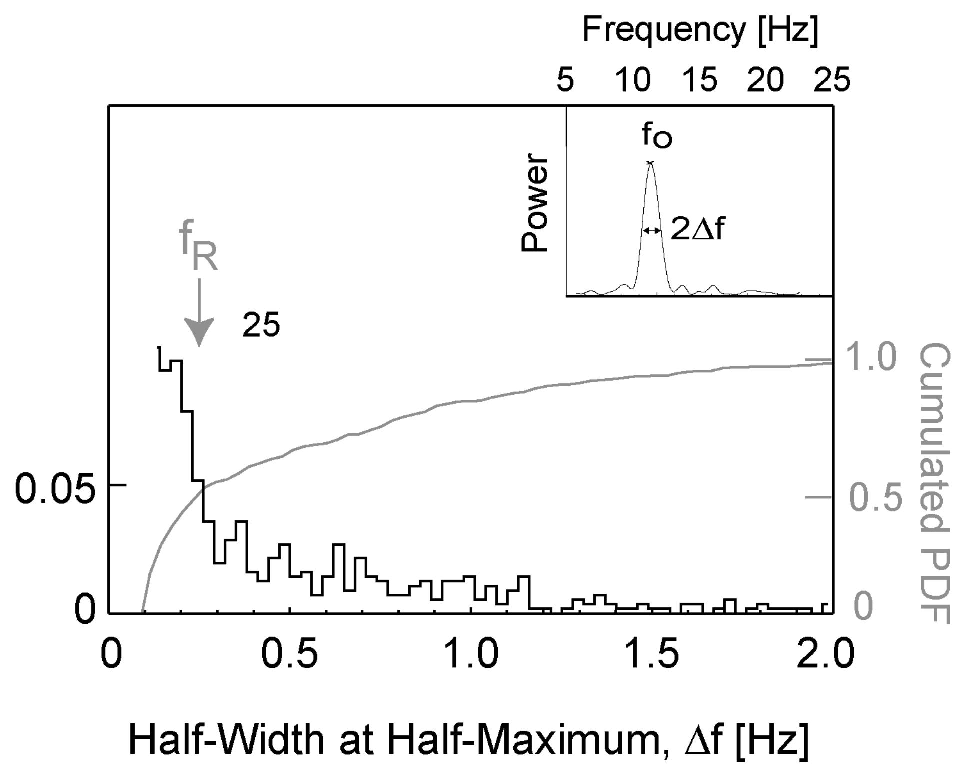

O'Connor, Berg and Kleinfeld 2001

# The Distribution of Spectral Parameters for Free Whisking

## Distribution of Center Frequencies

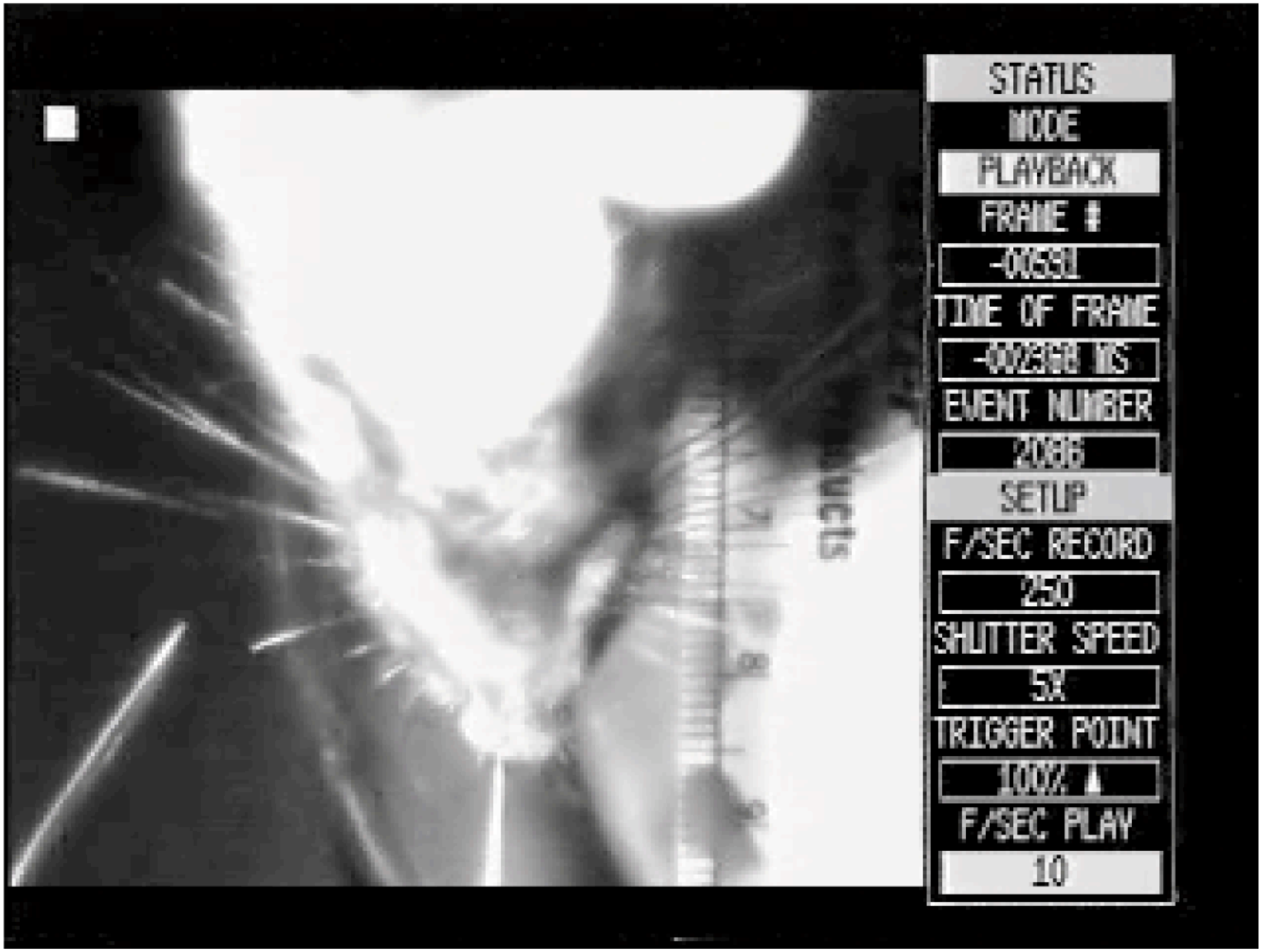



## Distribution of Spectral Widths



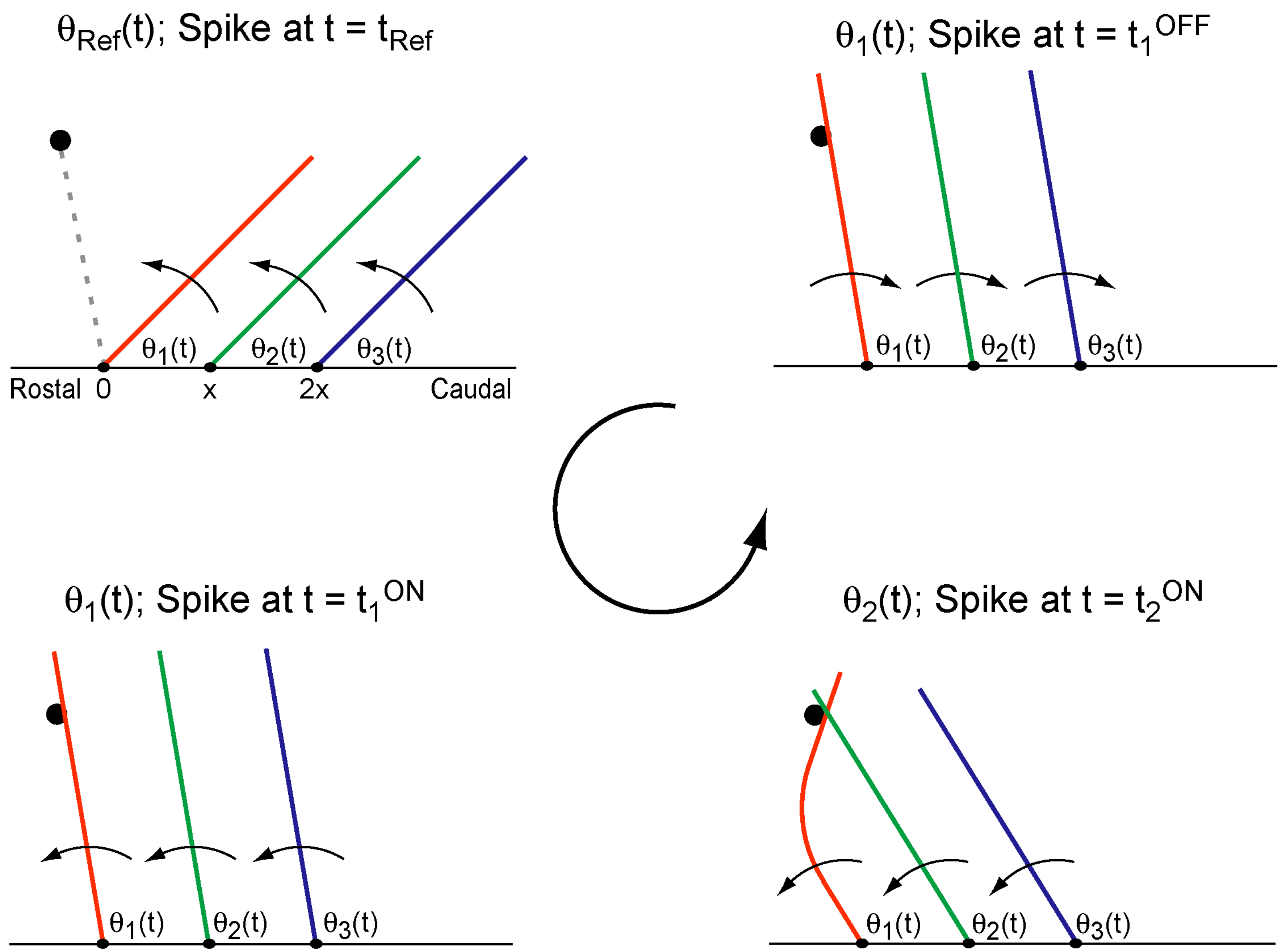

Berg and Kleinfeld (2003)

# Rats Can Detect Contact with a Single Vibrissa
(Hutson and Masterton, 1986)



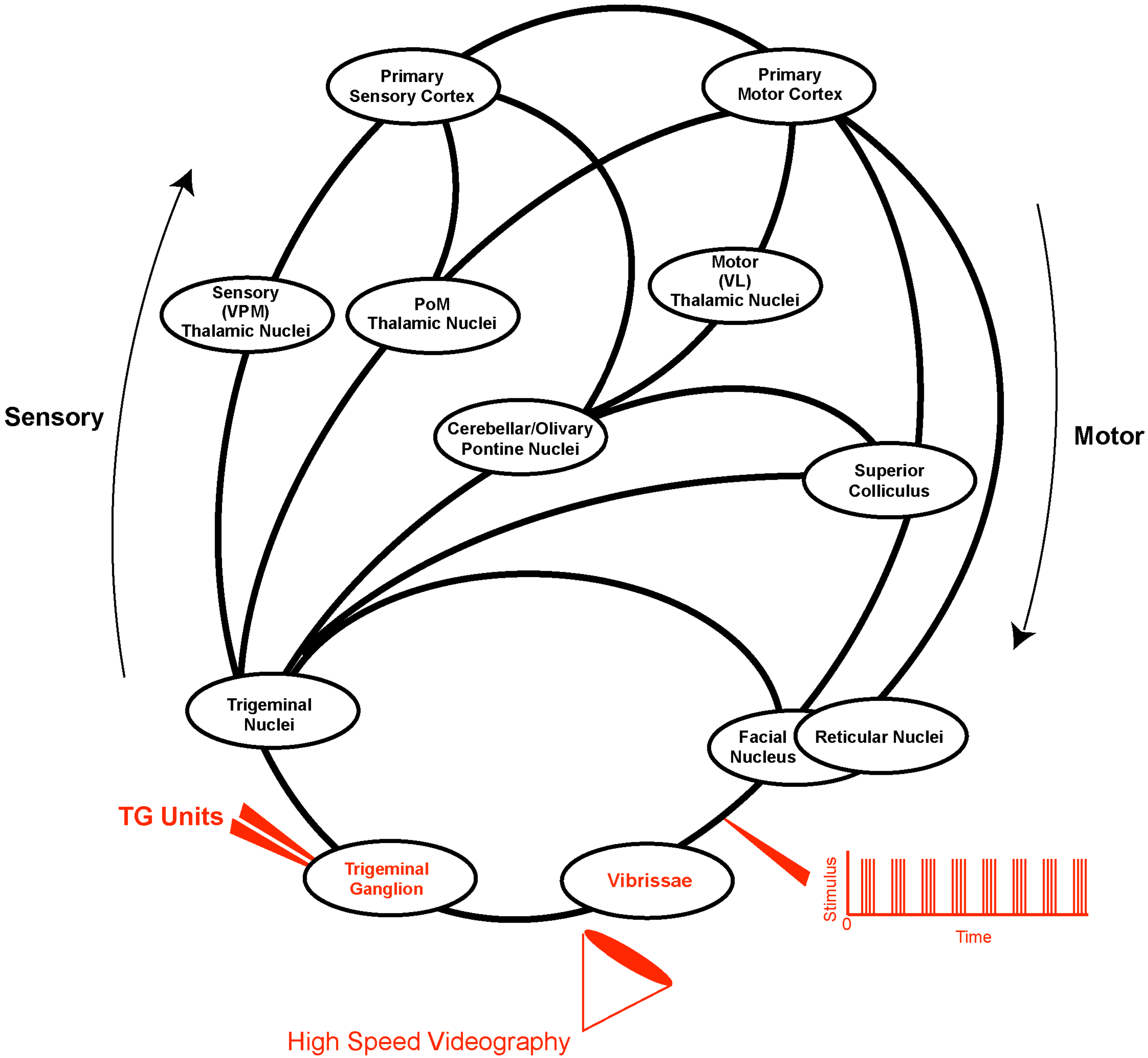

Sachdev, Berg, Champney, Kleinfeld, Ebner (2003)

# Hypothetical Reference and Contact (ON and OFF) Signals Associated with Vibrissa Movement and Object Contact

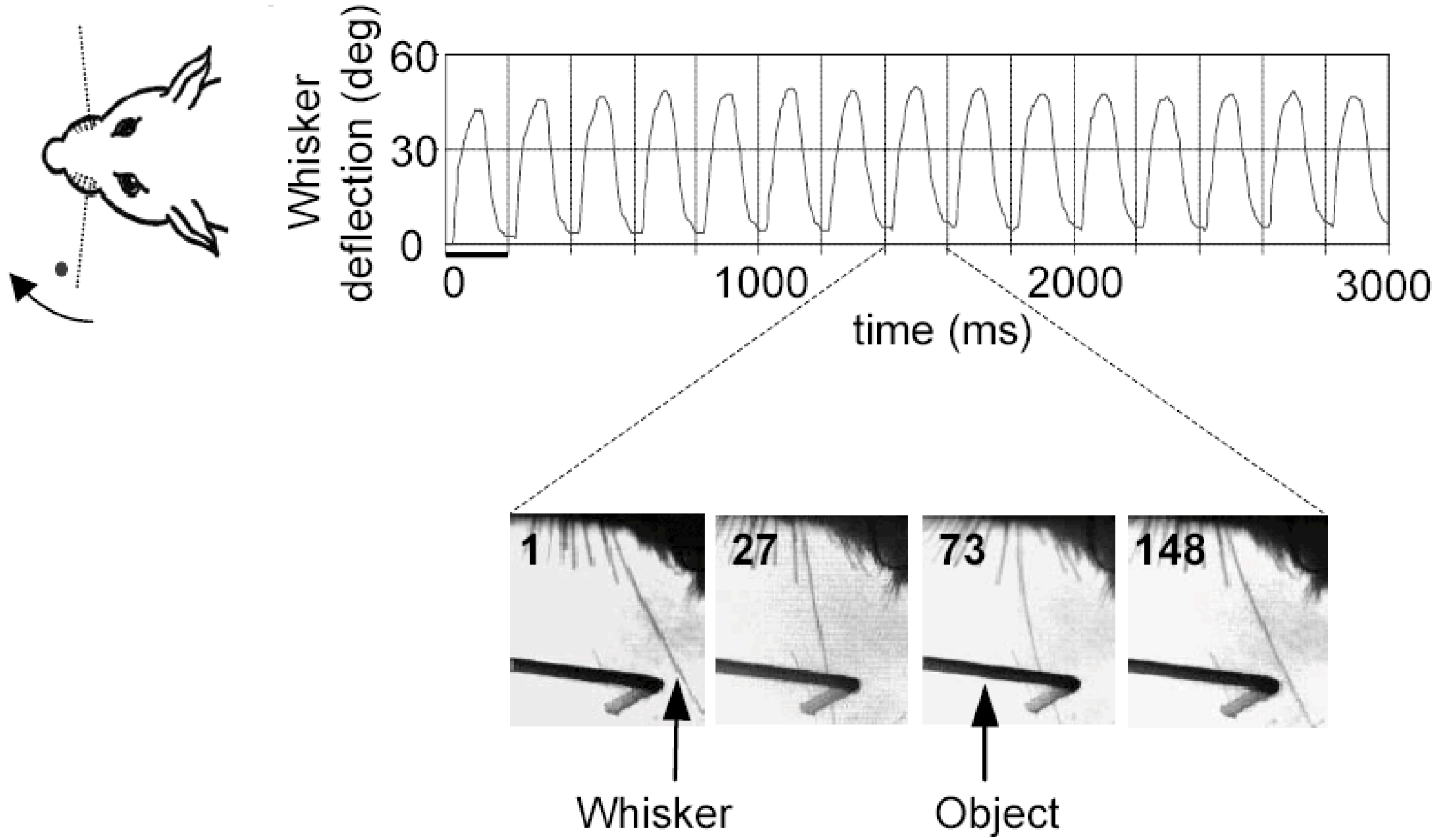



Object Localization Requires 1 + D Signals, e.g., Reference Plus ON for Angular (1-D) Localization

# Relation of Spiking in TG to Vibrissa Motion during Synthetic Whisking

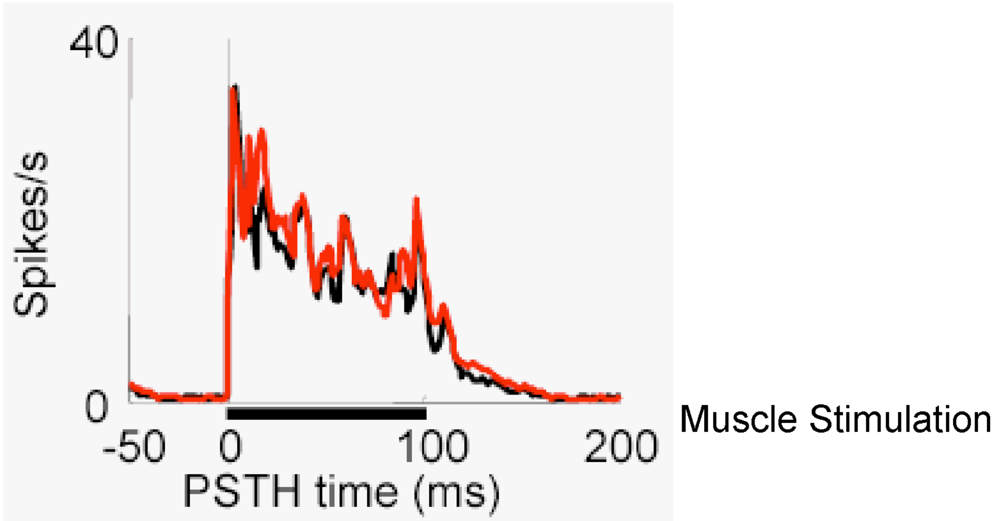


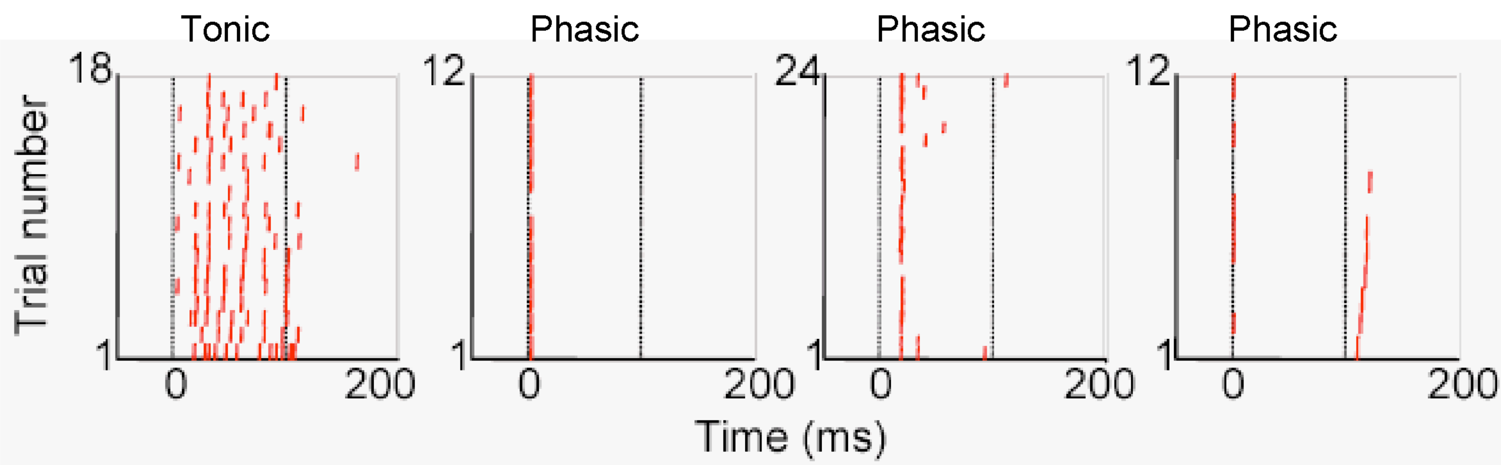
Synthetic Whisking in the Anesthetized Rat by Stimulating the Facial Motor Nerve
(after Zucker & Welker, 1969, Brown & Waite, 1974)

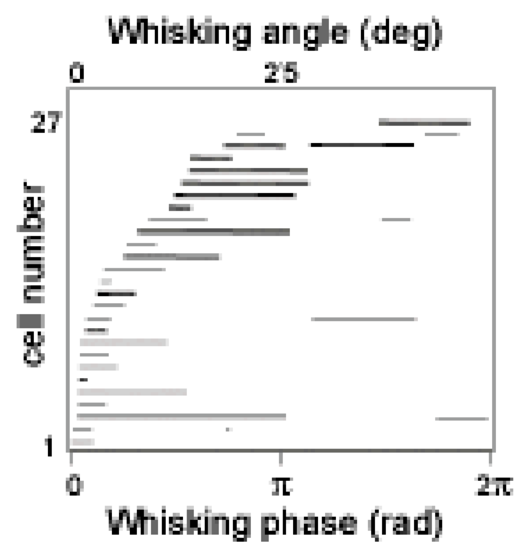



**Szwed, Bagdasarian and Ahissar (submitted)**

# Sensory Neurons in the Trigeminal Ganglion that Respond to Vibrissa Position (Reference Cells)

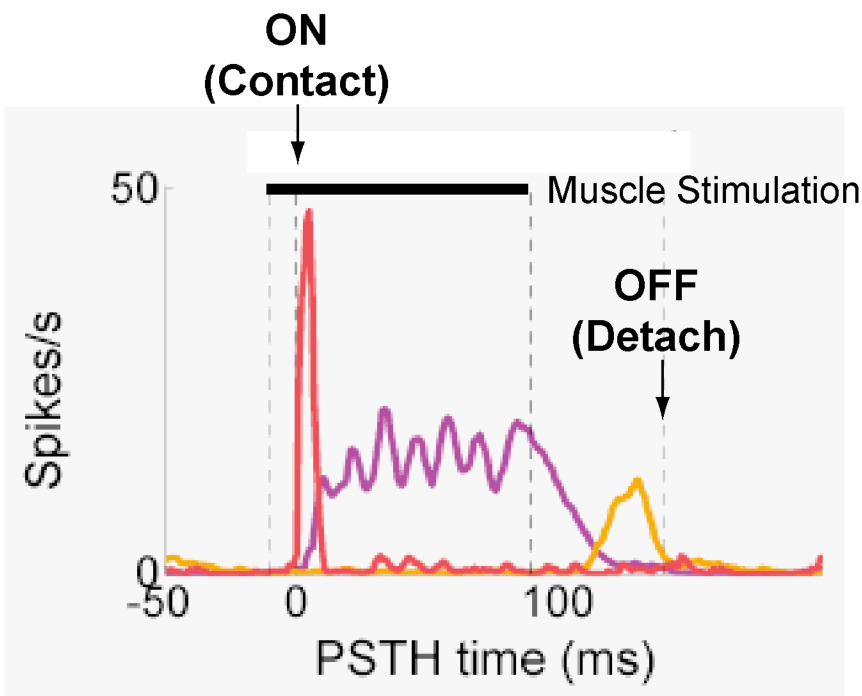


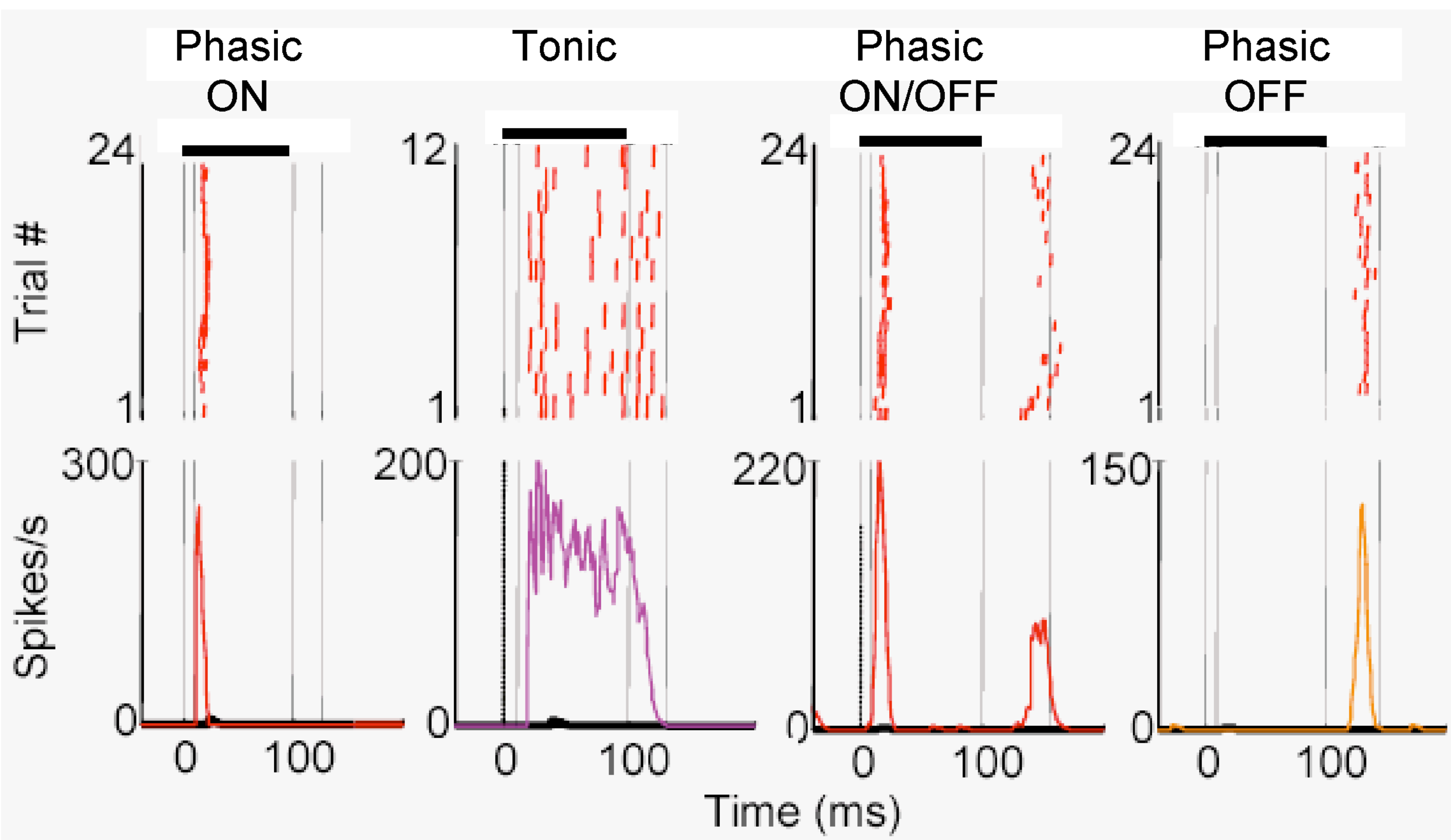




**Szwed, Bagdasarian and Ahissar (submitted)**

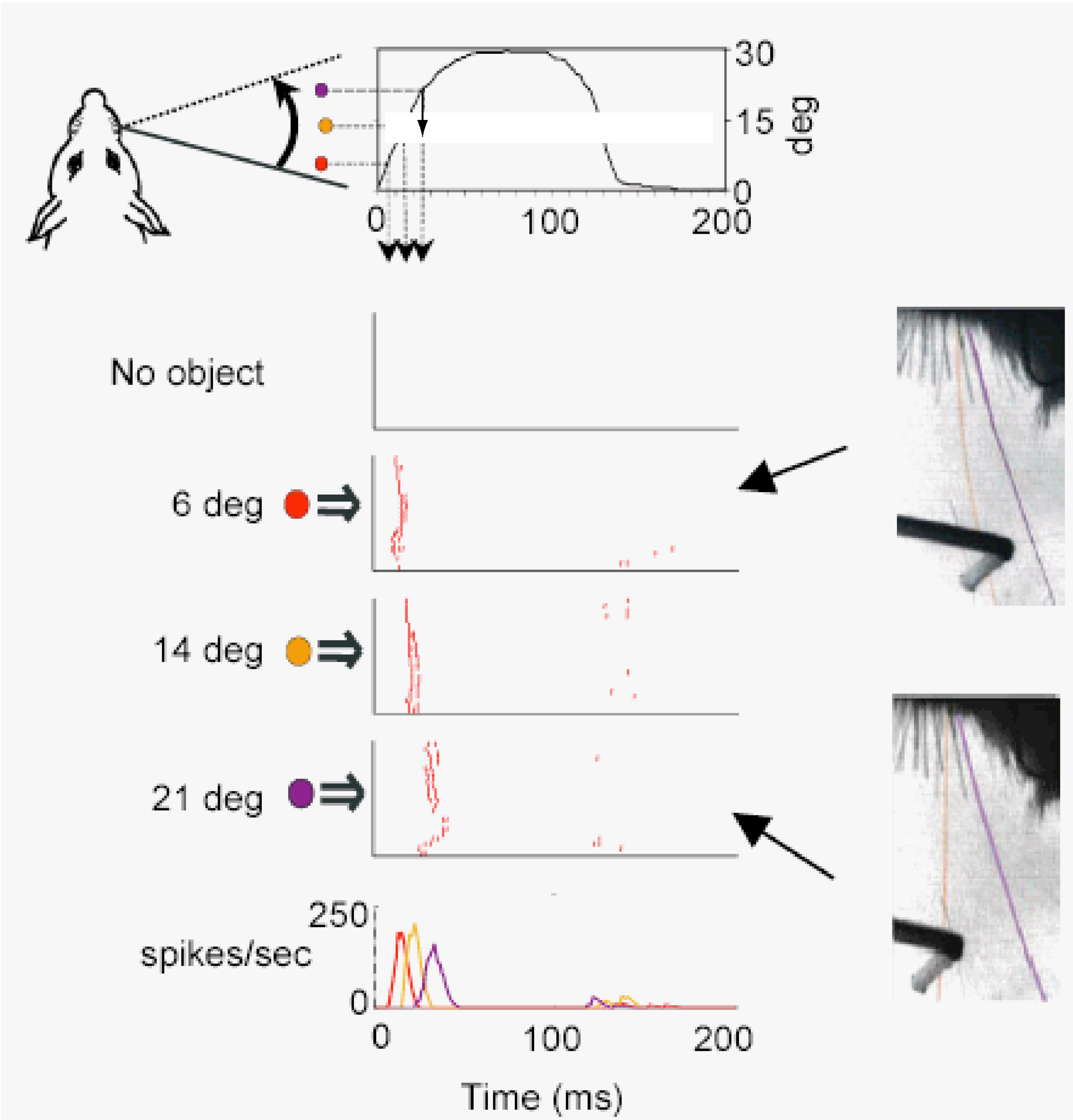
# Sensory Neurons in the Trigeminal Ganglion that Respond to Vibrissa Contact




**Szwed, Bagdasarian and Ahissar (submitted)**

# Phasic-ON Neuron in the Trigeminal Ganglion




**Szwed, Bagdasarian and Ahissar (submitted)**

# Neocortical Parcellation in Rat

Flattened hemisphere with cytochrome *c* oxidase stain

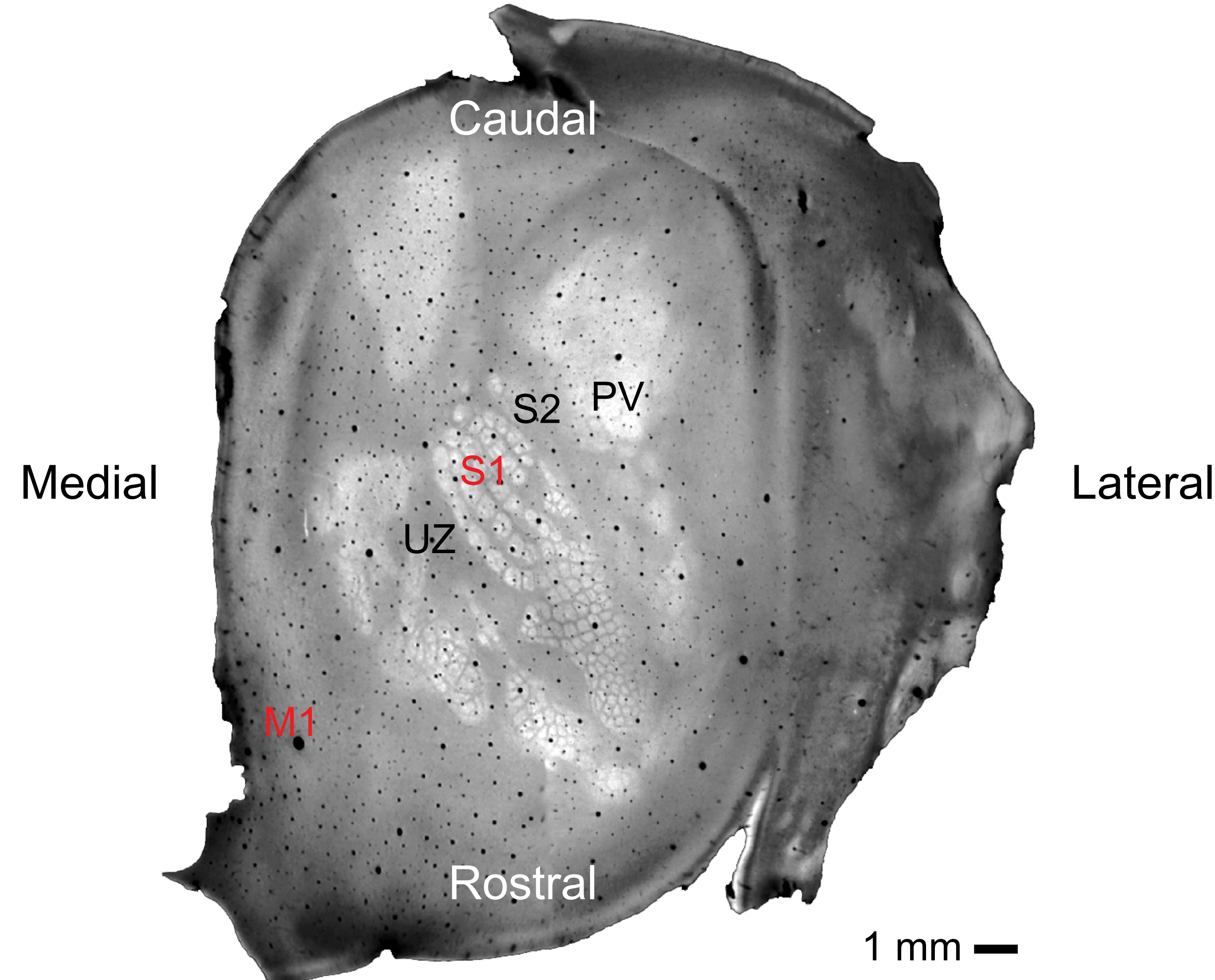
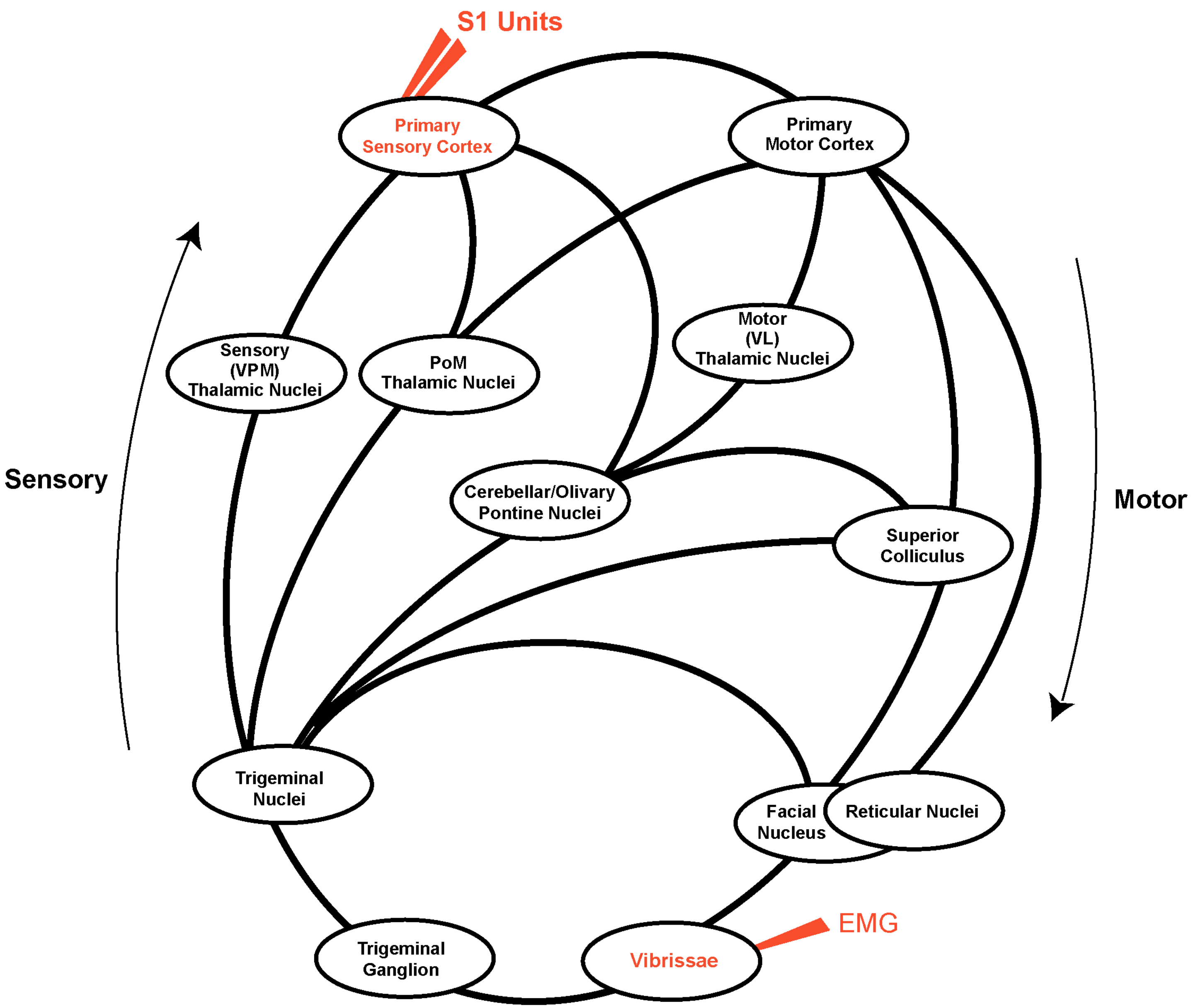
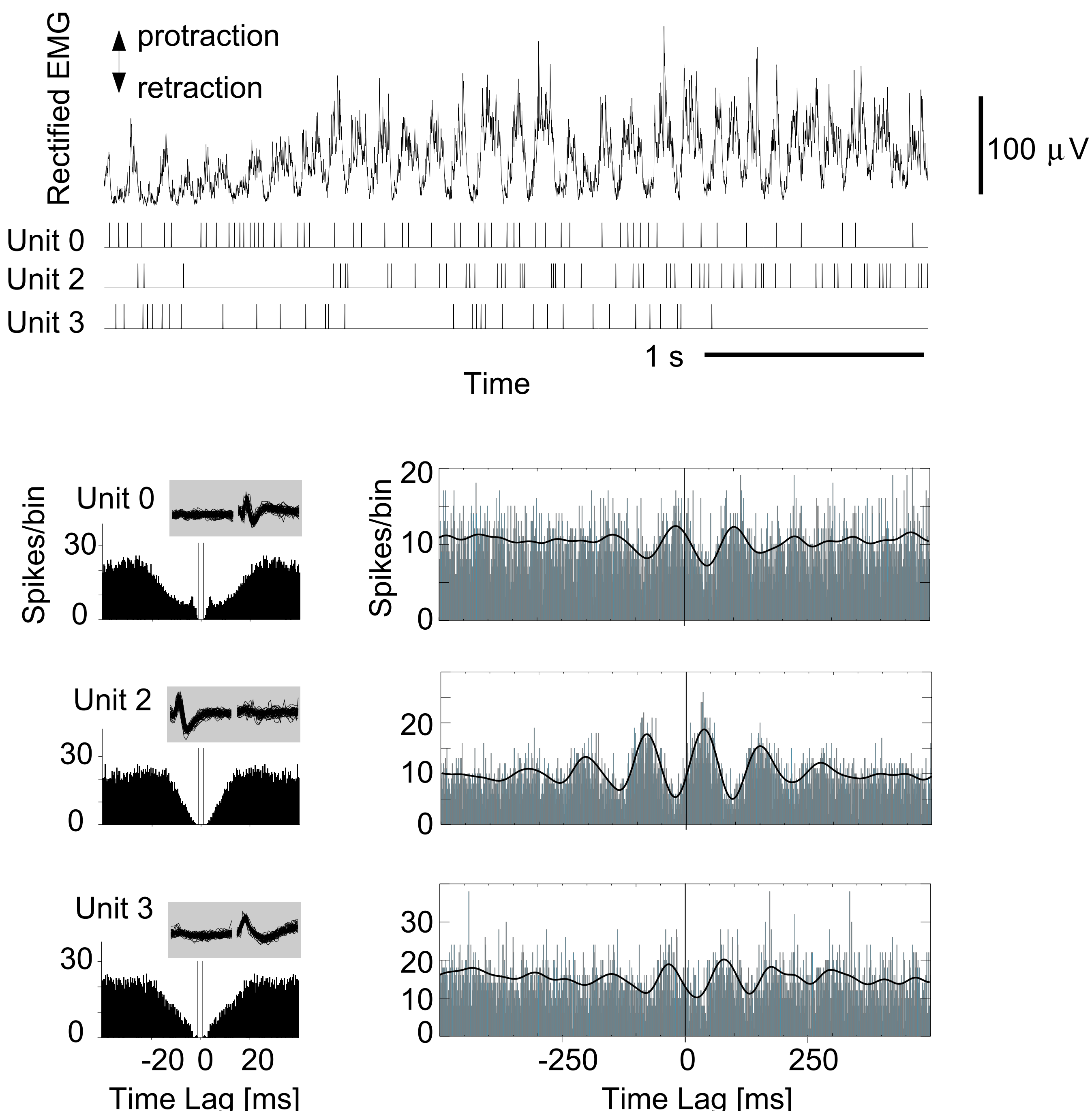



Figure courtesy of Ford Ebner Laboratory
(Assignments after Fabri and Burton 1991)

# Relation of Spiking in S1 Cortex to EMG Activity during Free Whisking in Air

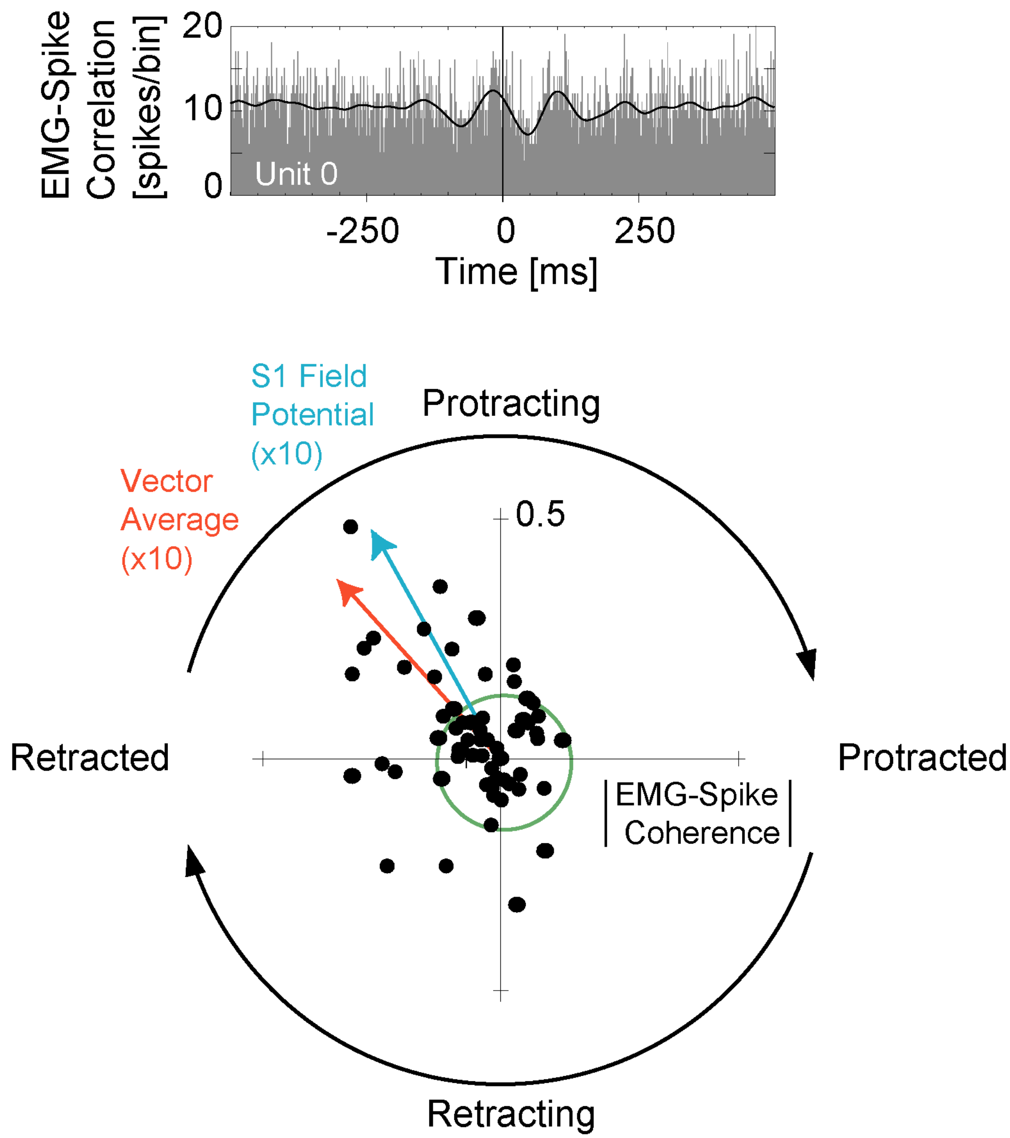


# Simultaneous Recording of EMG and Single Units in S1 Cortex




Fee, Mitra and Kleinfeld 1997

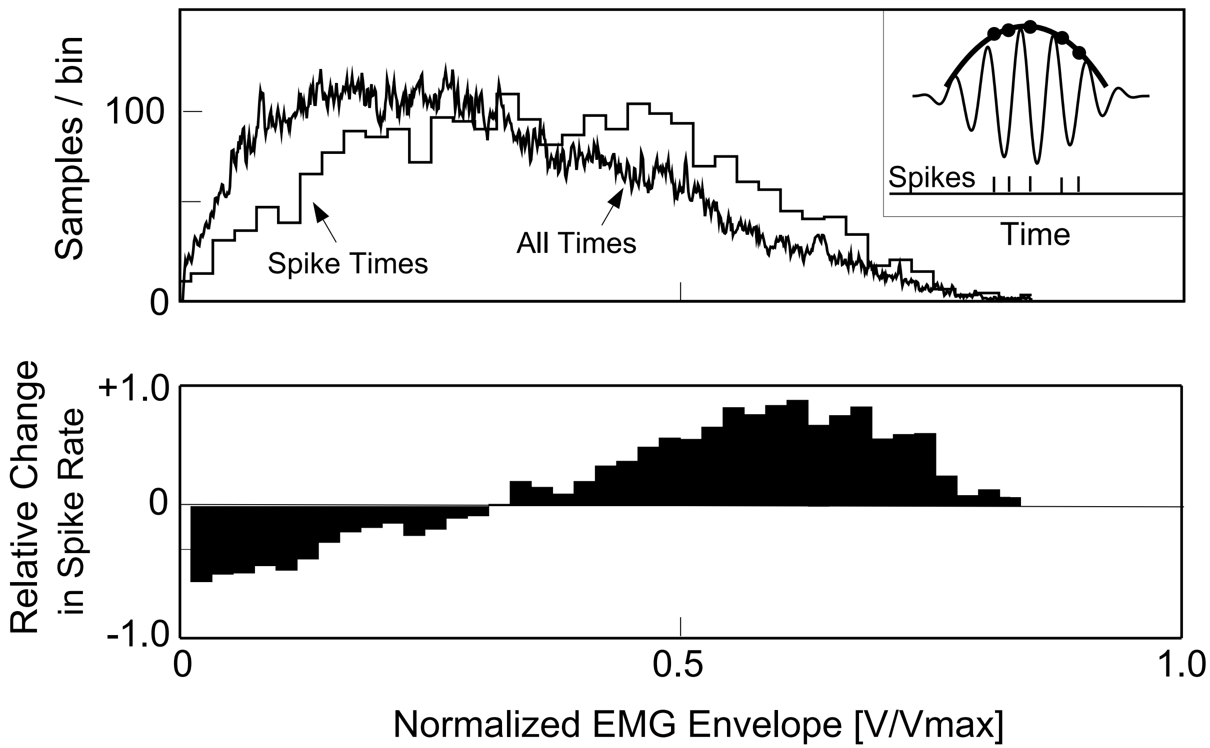
# Single Unit as well as Field Potential Activity in Vibrissa S1 Cortex Codes the Phase of Vibrissa Position During Free Whisking




"Unbiased" Population Average: 0.05 Spikes per Whisk (Modulation Level is 0.1 Spikes per Whisk)

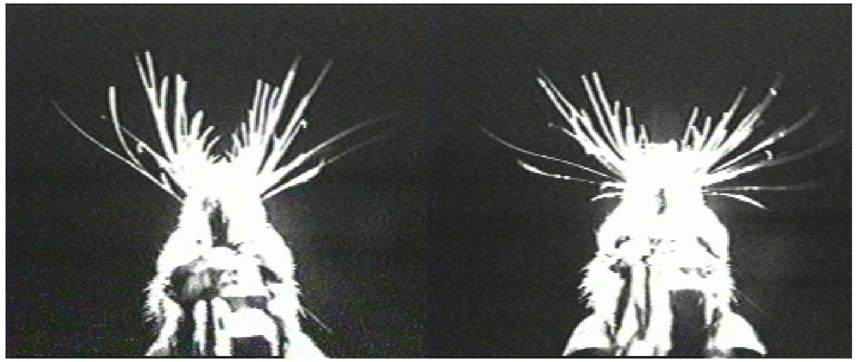
Fee, Mitra and Kleinfeld 1997; O'Connor, Berg and Kleinfeld 2001

# Single Unit Activity in Vibrissa S1 Cortex Codes the Amplitude of Vibrissa Position During Free Whisking

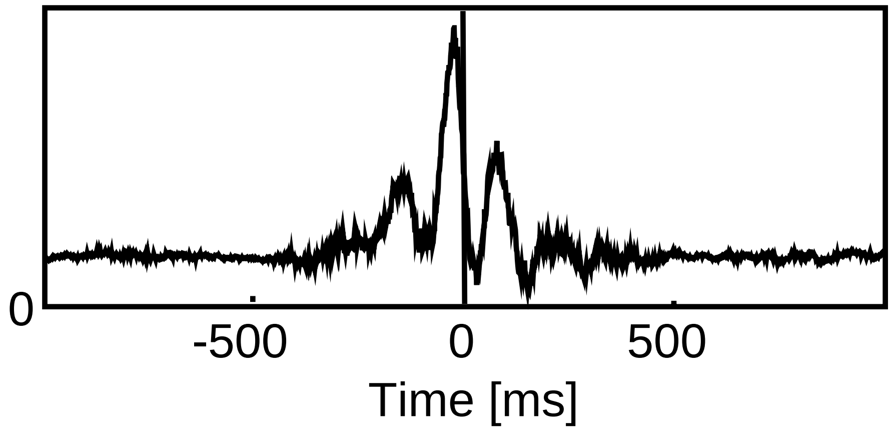



Fee, Mitra and Kleinfeld 1997; O'Connor, Berg and Kleinfeld 2001

# The Output of Units in S1 Cortex Can Be Used to Predict the Position of the Vibrissae (Mystatial EMG) on a Single-Trial Basis

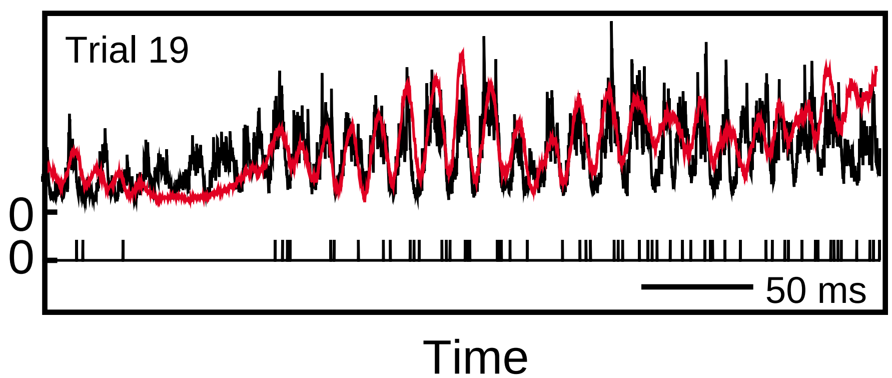


Trial Averaged Transfer Function, K(t)




Measured EMG, $E_{meas}(t)$

Measured Spike Train, $S_{meas}(t)$

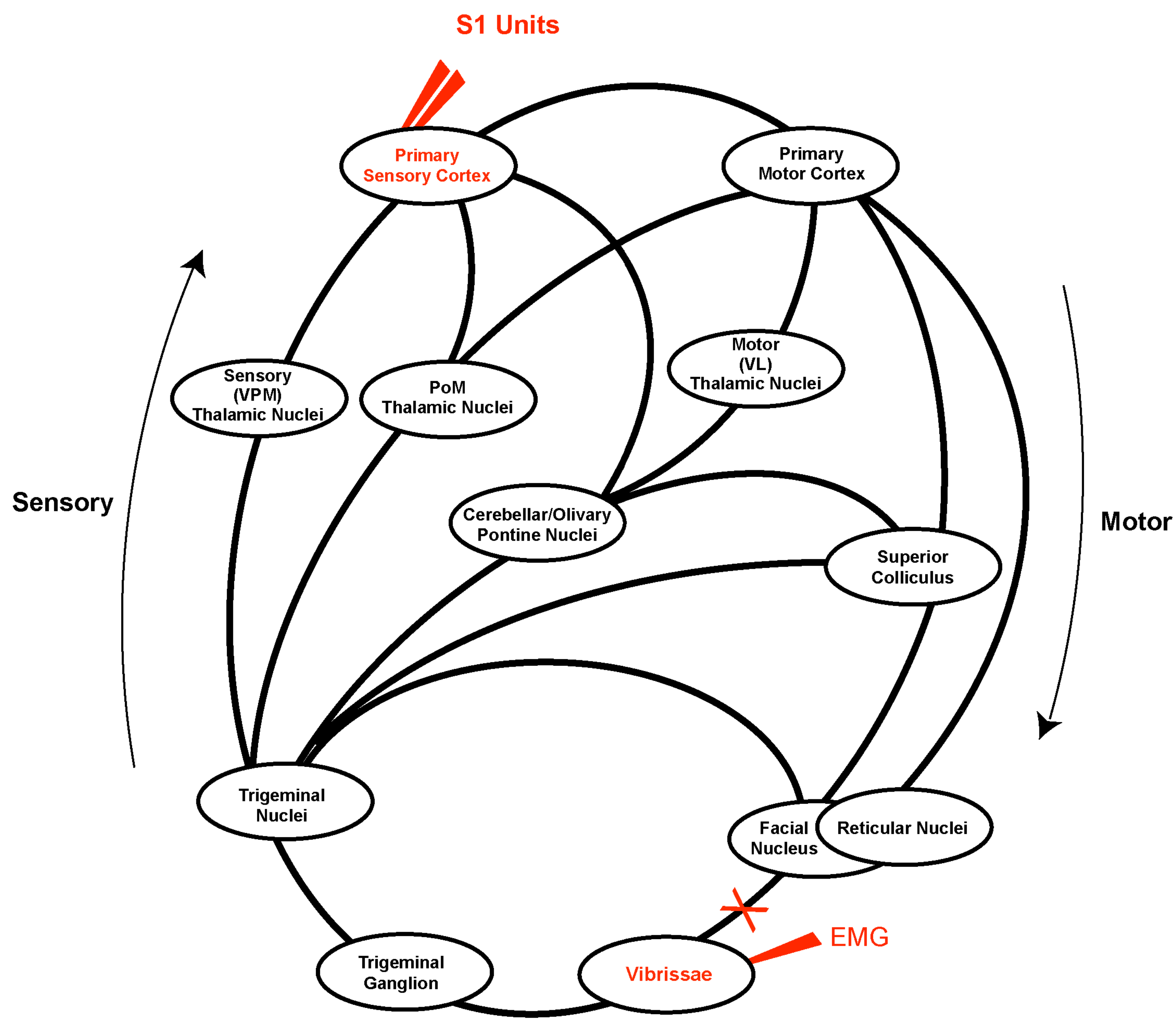



Predicted EMG, $E_{pre}(t)$

$$= \int_{-\infty}^{t} dt' \, K(t - t') \, S_{meas}(t')$$

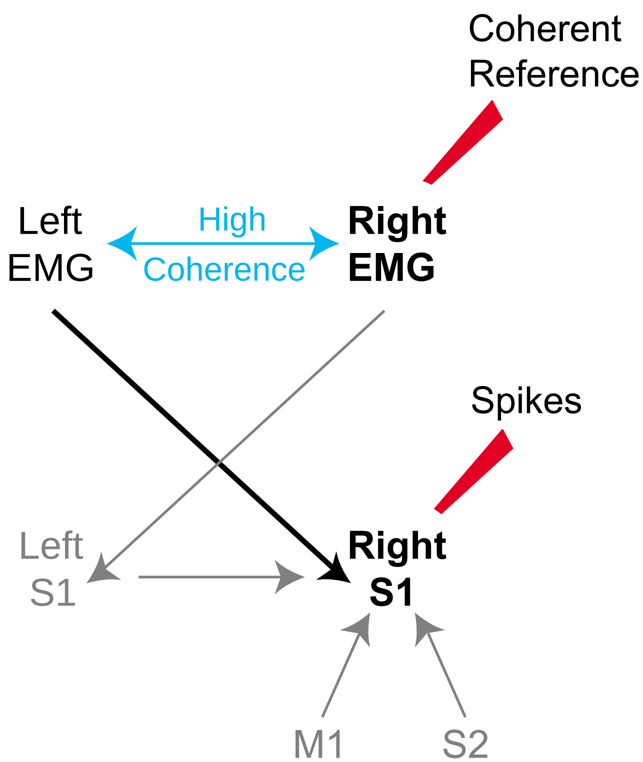
Fee, Mitra and Kleinfeld 1997

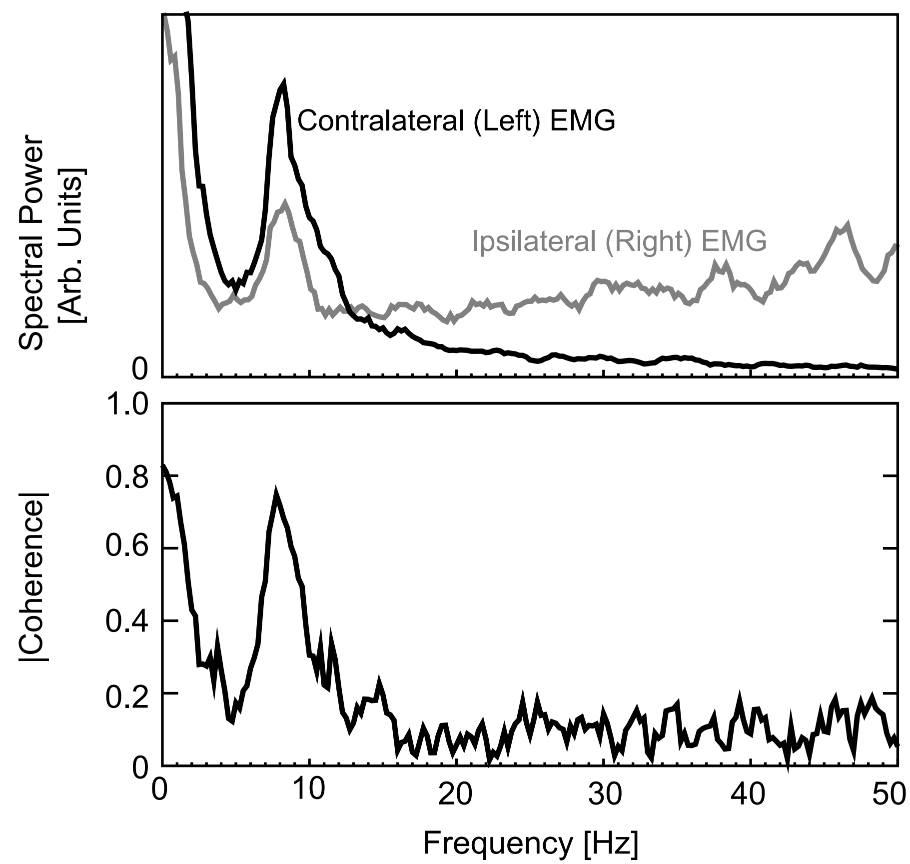
# Is the Origin of the Reference Signals in S1 Cortex Peripheral (Reafference) or Central (Efferent Copies)?



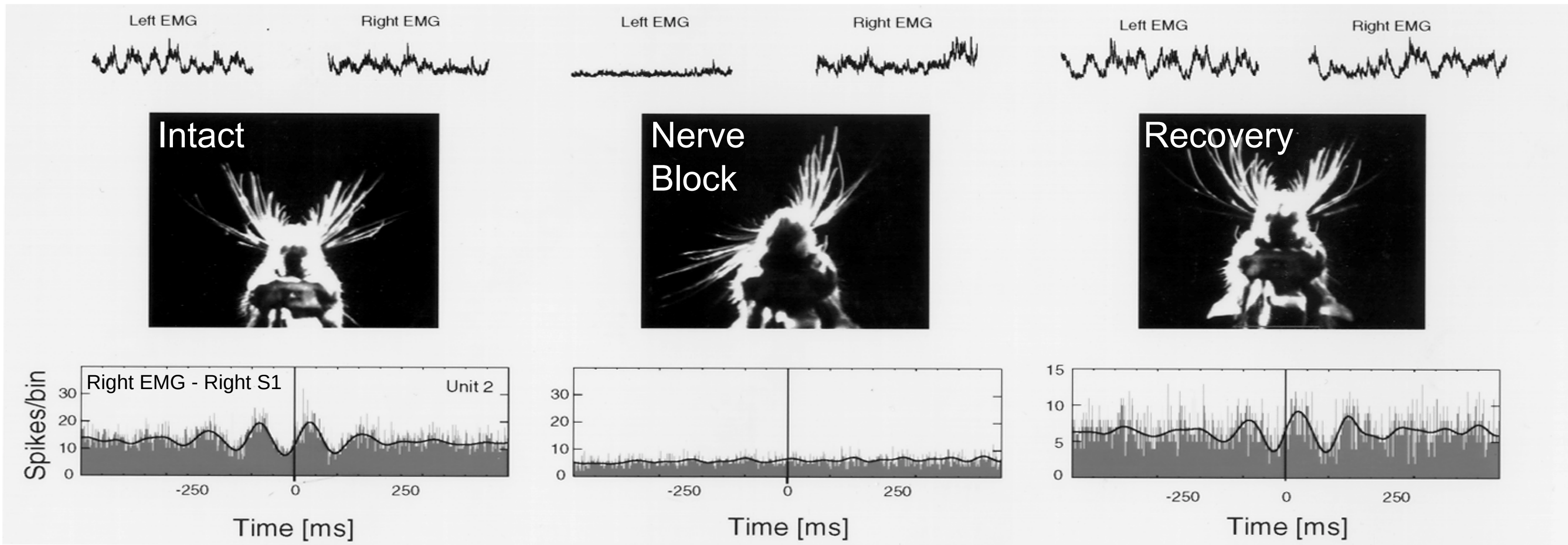
# Facial Nerve Block to Determine if the Free Whisking Response in S1 Cortex Results Peripheral Reafference versus Efferents Copy

## Key: The Ipsilateral EMG Provides a Coherent Reference

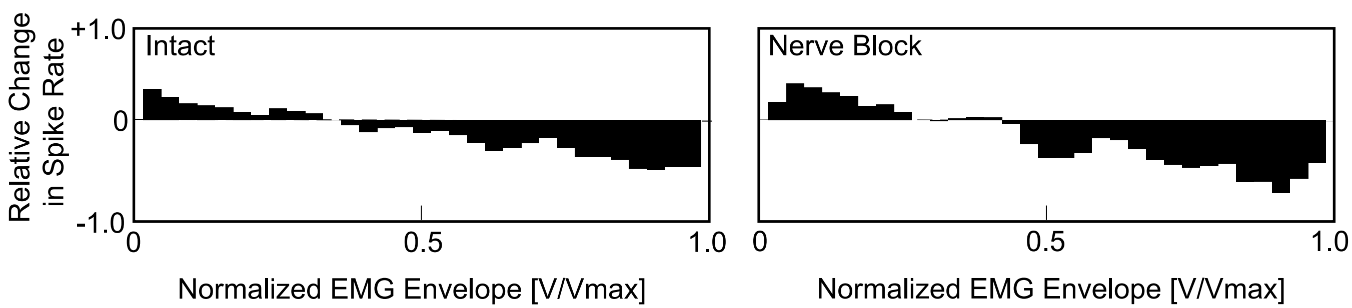


# Phasic Coherence between Vibrissa Position and Spiking in S1 Cortex Depends on Peripheral Reafference - Not an Efferents (Central) Copy

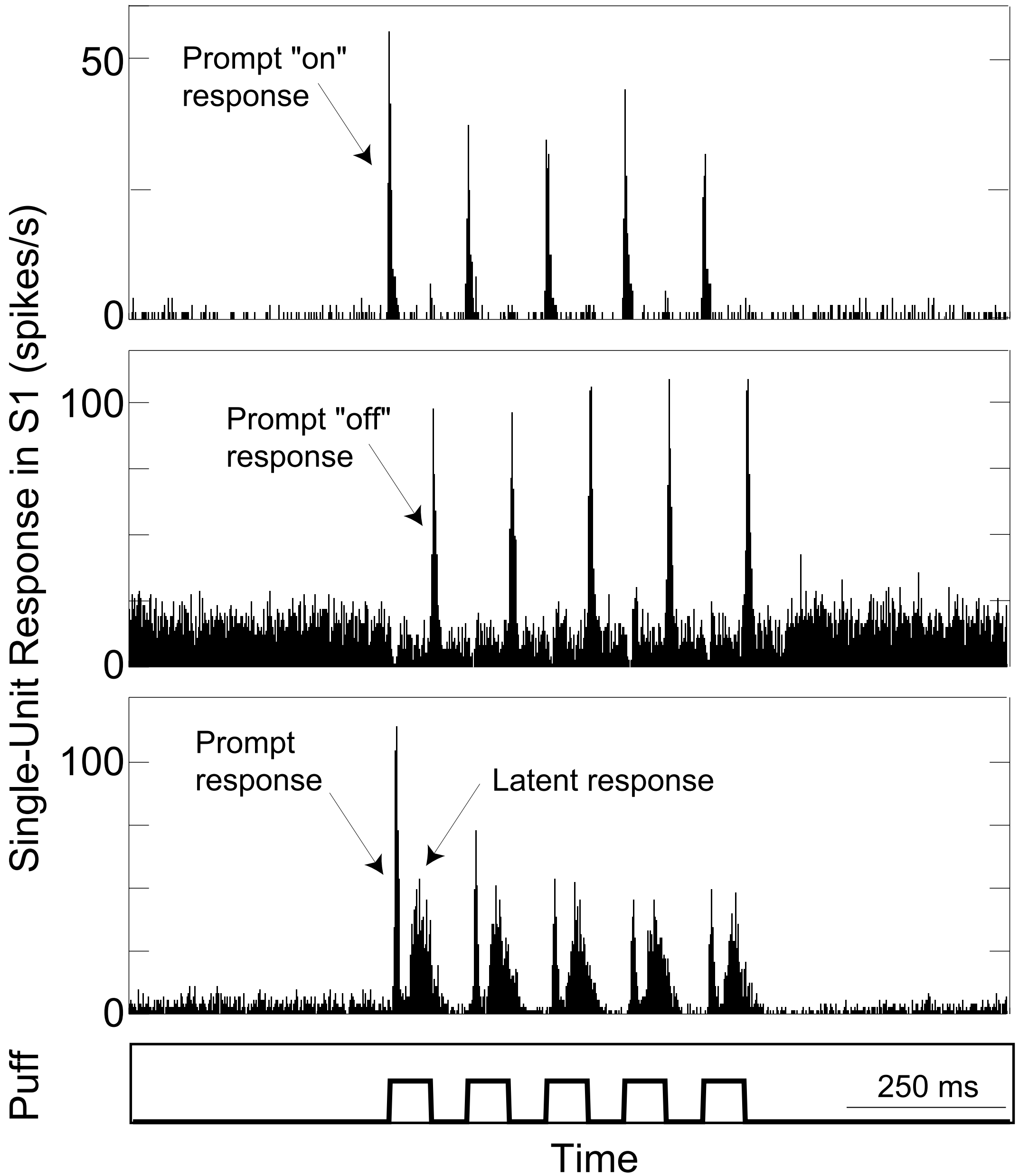



In Contrast, Coherence between the Slowly Varying Envelope of Vibrissa Position and Spiking in S1 Cortex Depends on an Efferents (Central) Copy



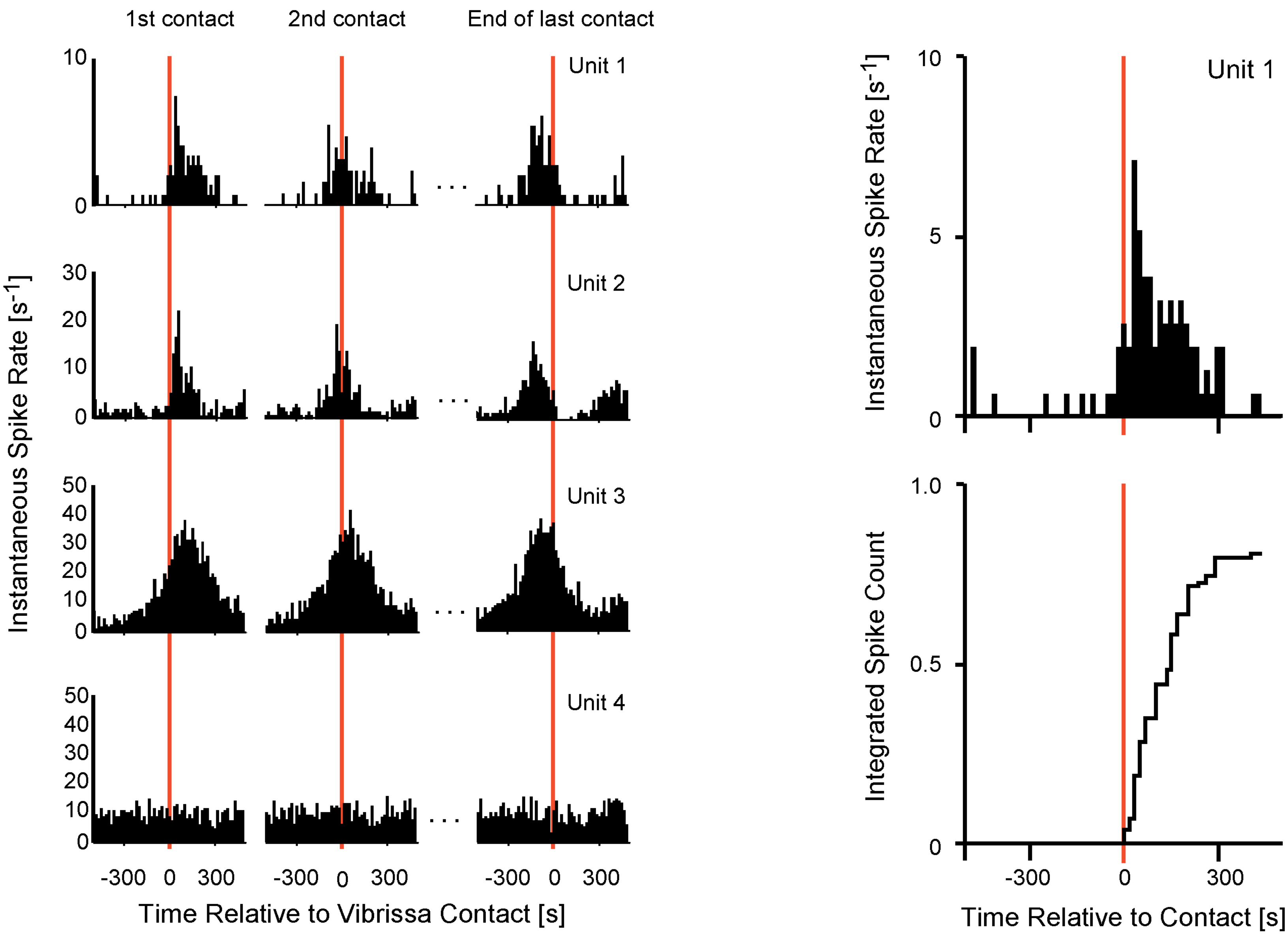

Fee, Mitra and Kleinfeld 1997

# Stimulation of Vibrissae with the Facial Nerve Blocked Does Not Inpede the Sensory Response in S1 Cortex



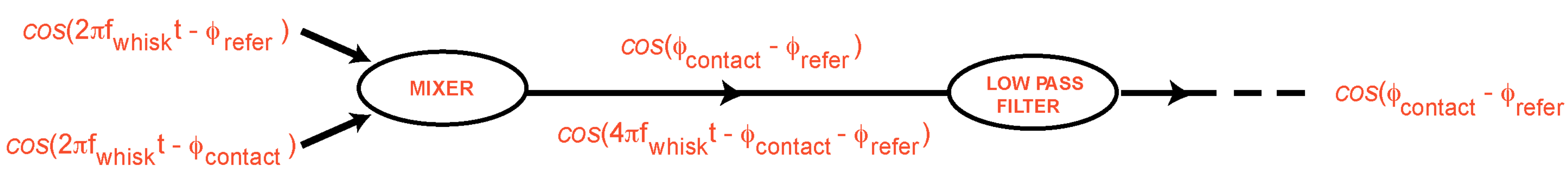

Fee, Mitra and Kleinfeld 1997

# Single Unit Response in S1 Cortex during Discrimination Task

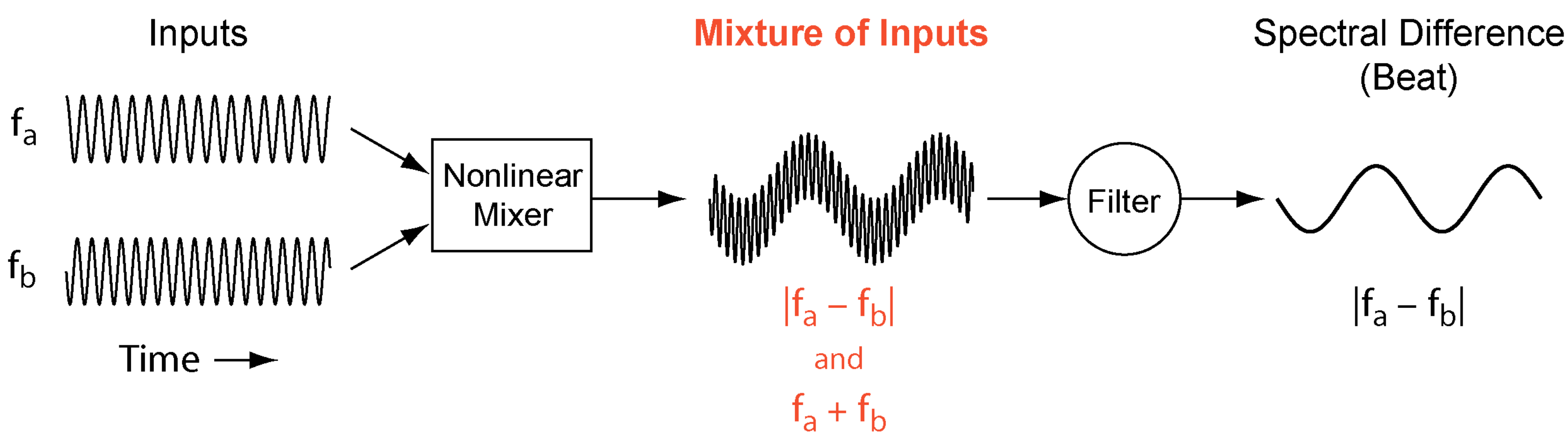



Fee and Kleinfeld, in "Spikes" (Rieke et al.) 1996

# Nonlinear Mixer - Essential Ingredient for Phase Sensitive Detection

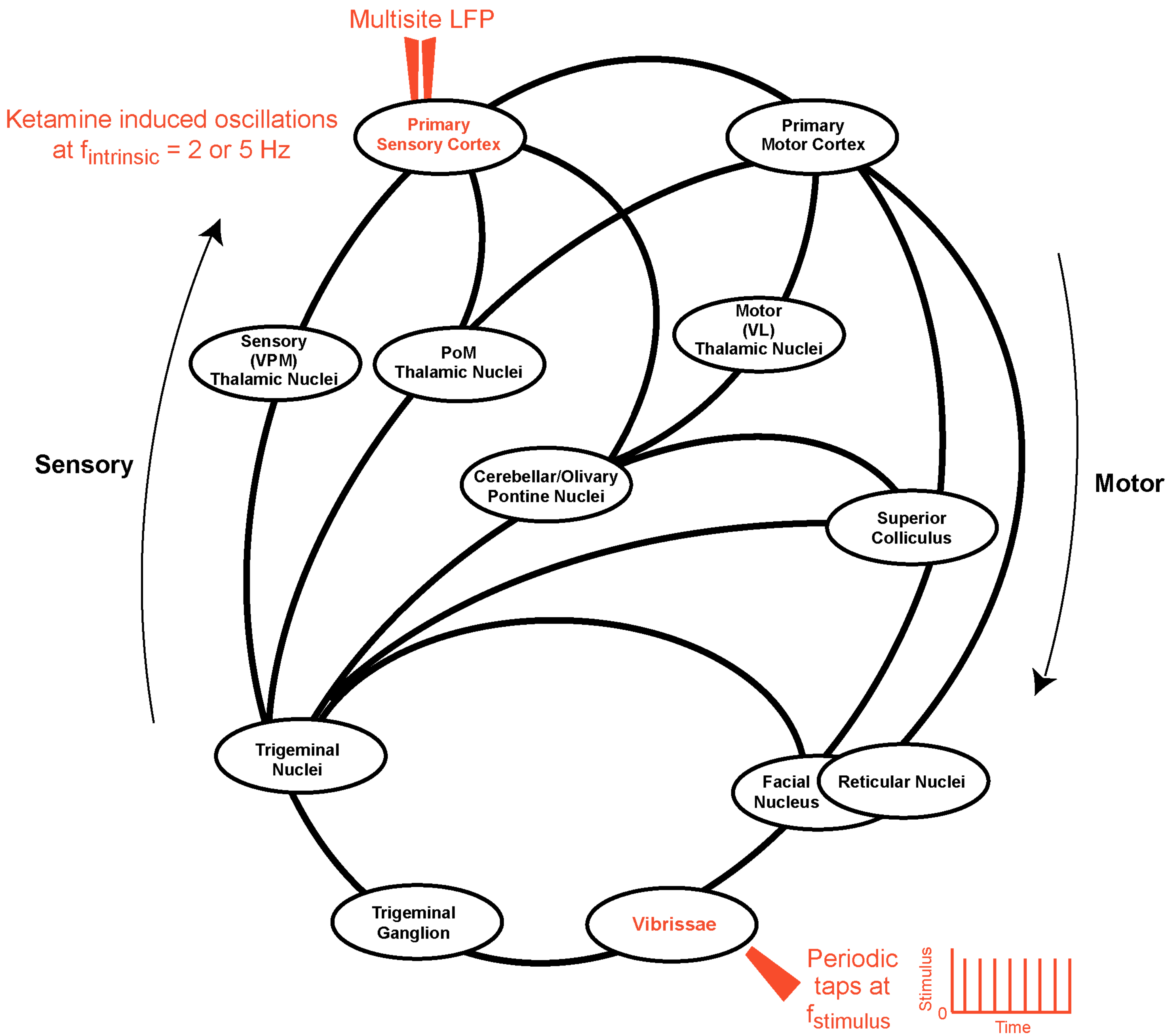



# Nonlinear Mixer - Experimental Signature

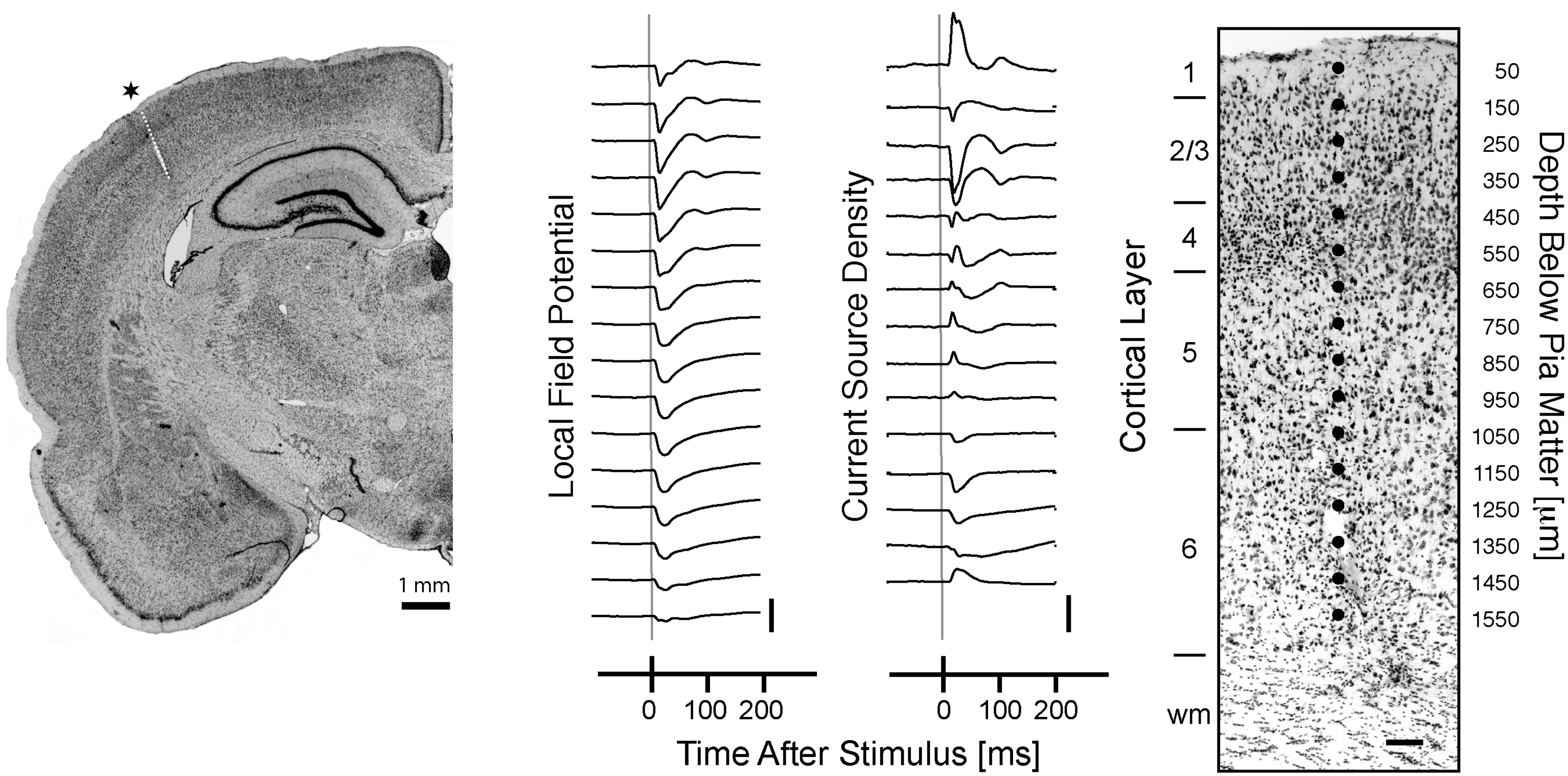



In general, input pure sinusoids with $f_a$ and $f_b$ and get output with sinusoids at $|nf_a \pm mf_b|$

# Stimulus Induced Current Flow in S1 Vibrissa Cortex in Anesthetized Rat



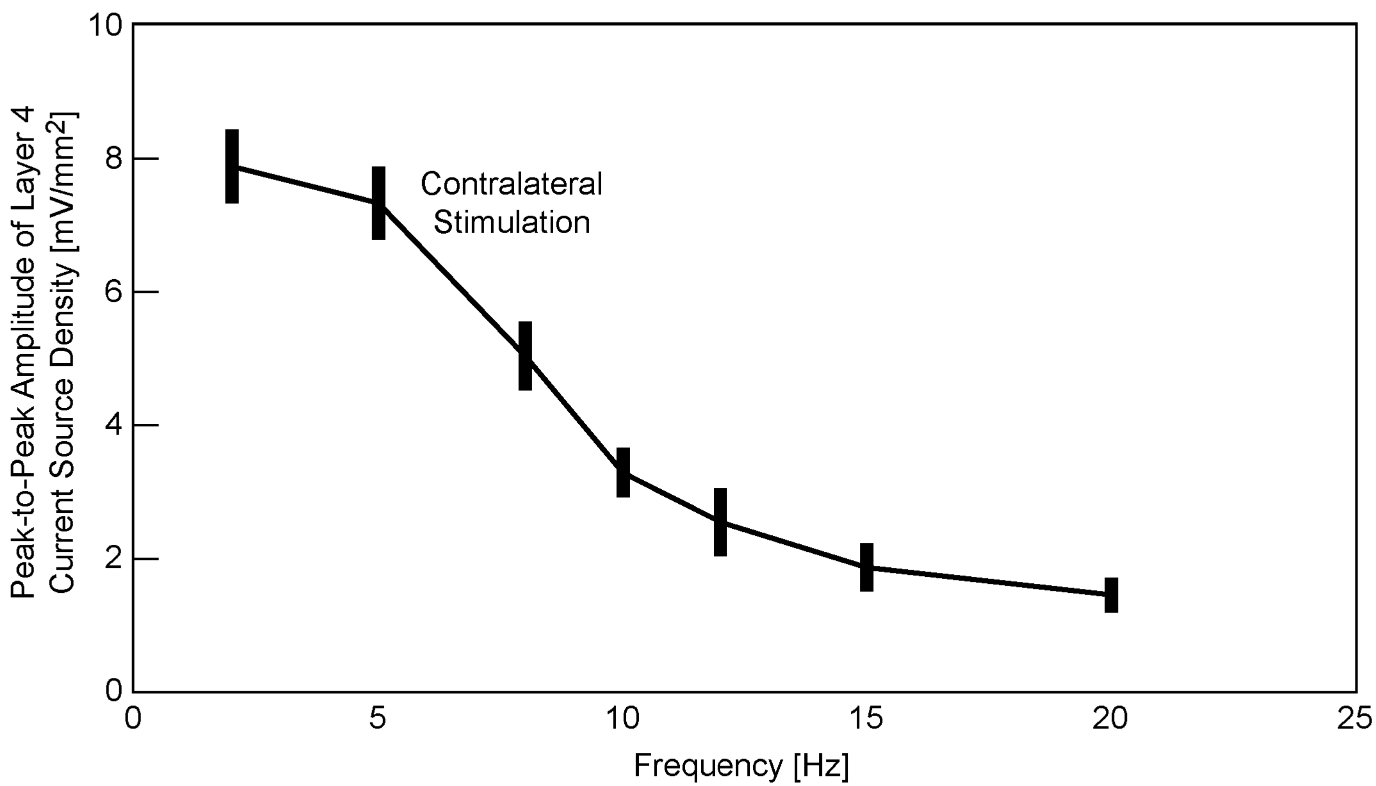
# Simultaneous Multisite Measurements of Radial Current Flow (Current Source Density) in Primary Vibrissa Sensory Cortex



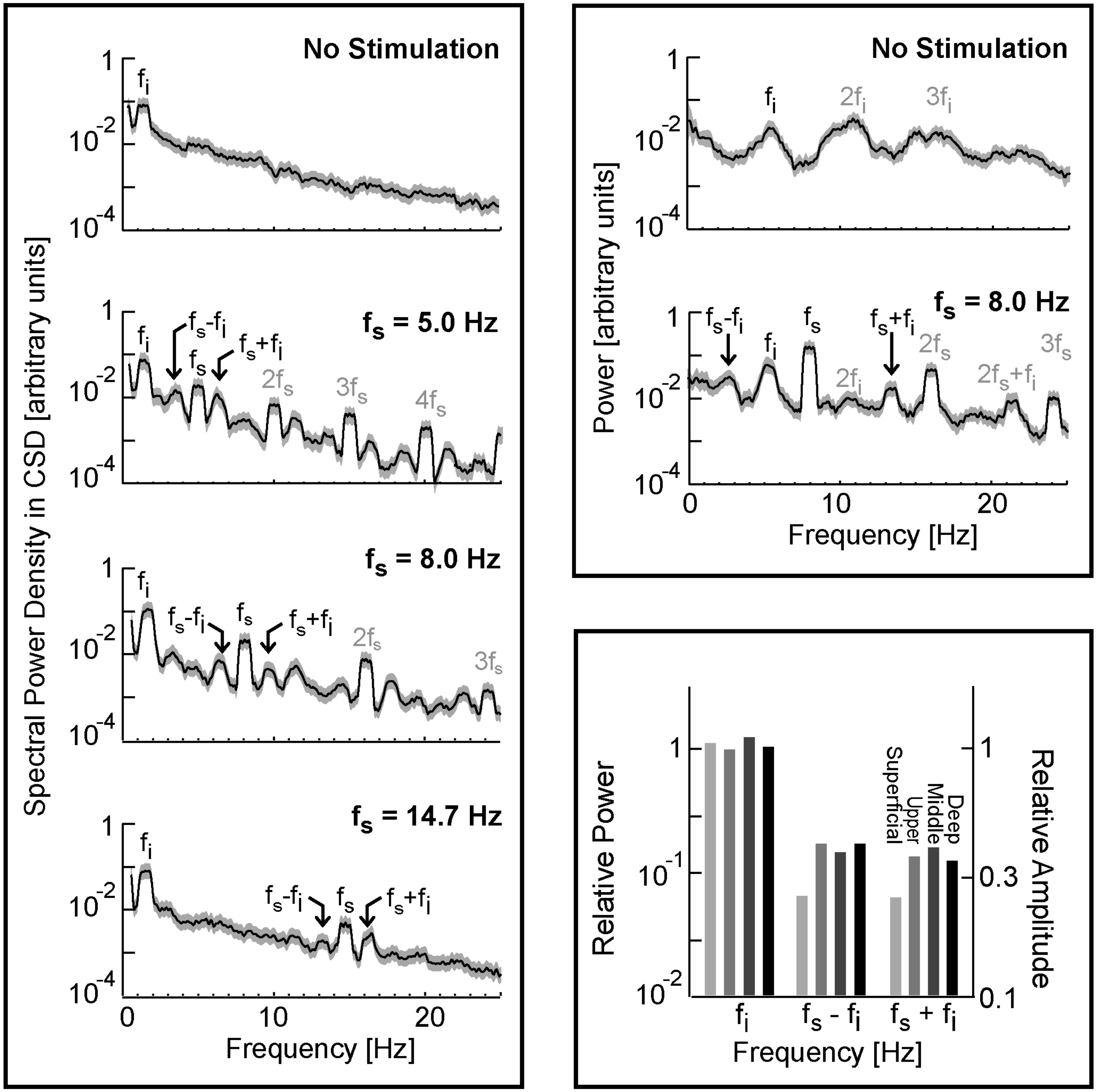
# Paradigms to Detect Mixing of Two Oscillatory Signals in Cortex

1 - Intrinsic (Ketamine Induced) Rhythm Plus Contralateral Stimulation

2- Simultaneous Contralateral and Ipsilateral Stimulation



# Spectral Mixing in Radial Current Flow (CSD) in S1 Vibrissa Cortex




Ahrens, Levine, Suhl and Kleinfeld (2002) in press

# Paradigms to Detect Mixing of Two Oscillatory Signals in Cortex

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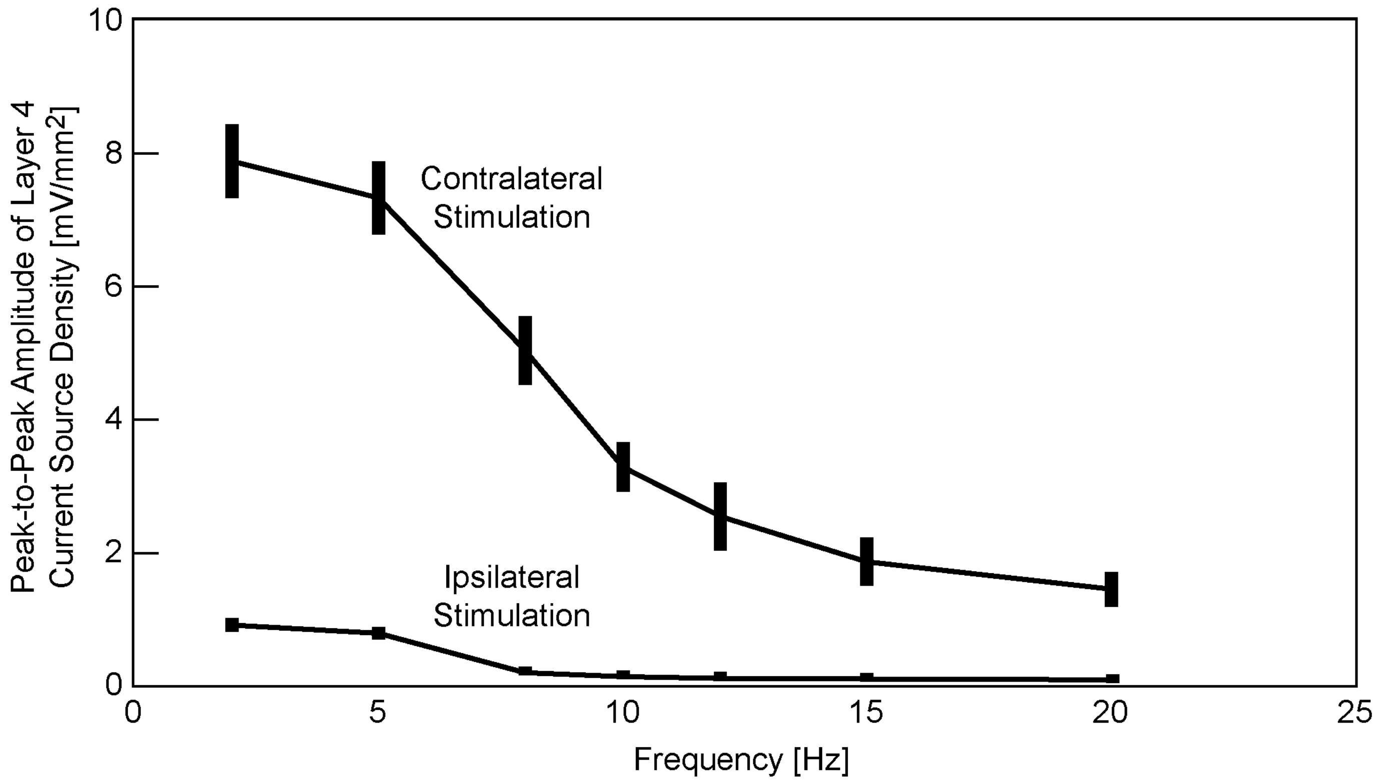
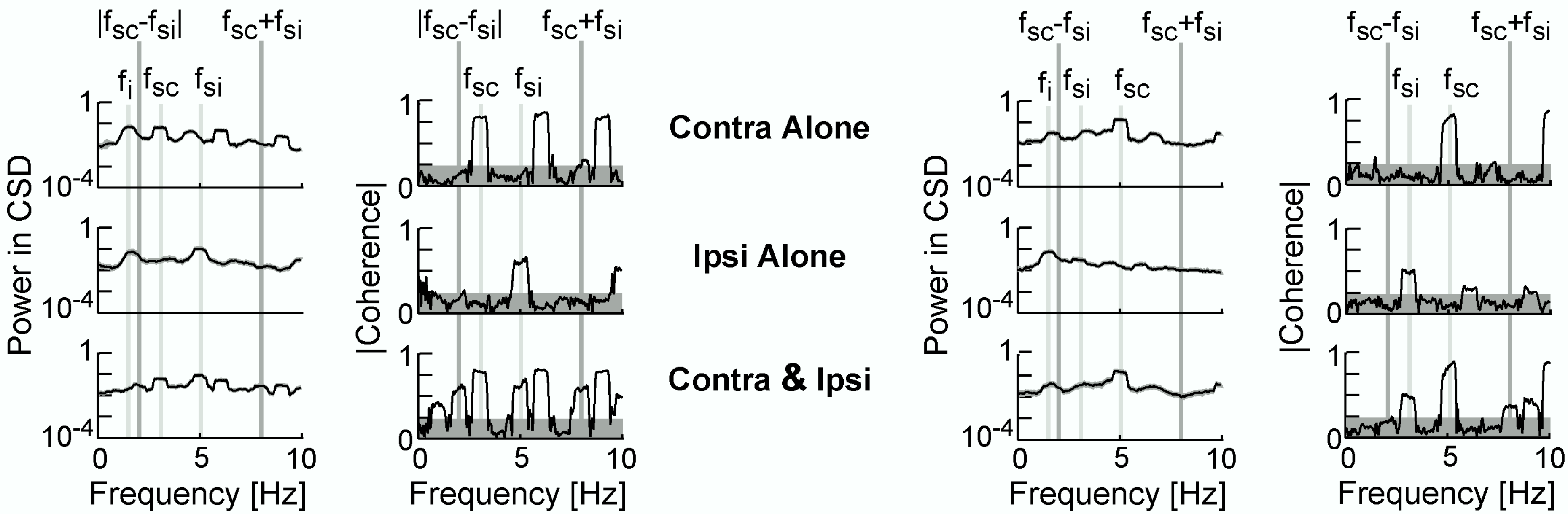
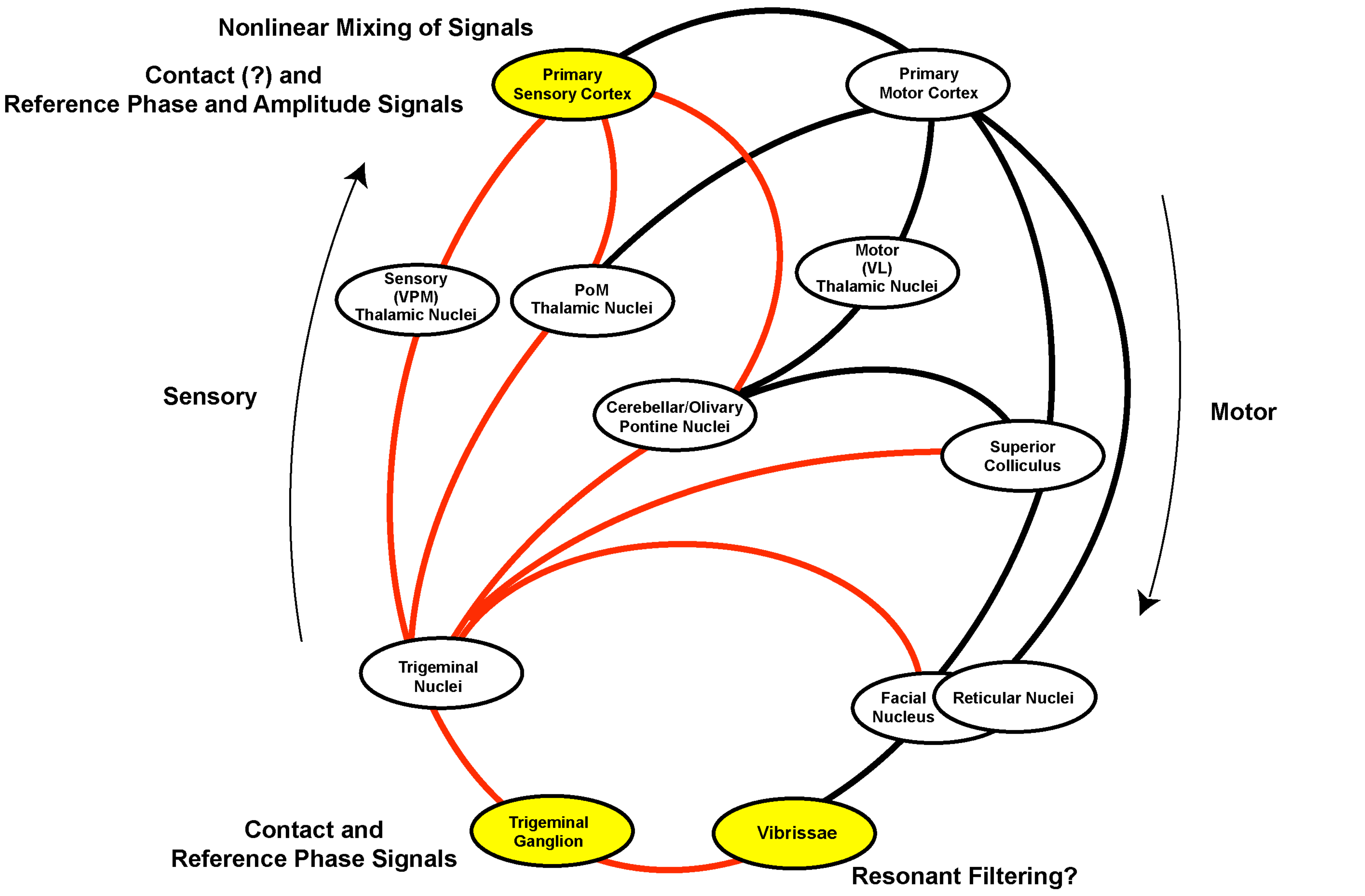


# Spectral Mixing in Radial Current Flow (CSD) in S1 Vibrissa Cortex
# (contralateral plus ipsilateral stimulus-induced rhythm)



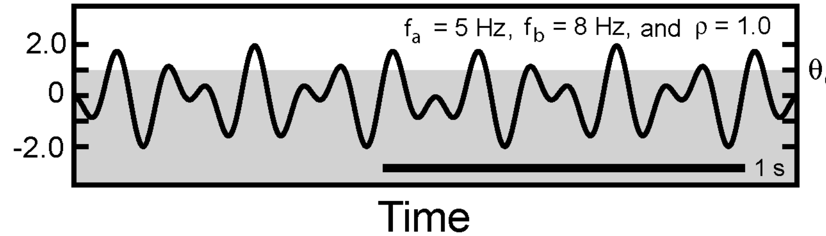

Ahrens, Levine, Suhl and Kleinfeld (2002) in press

# Synopsis on Closed Loop Computation in the Vibrissa Sensorimotor System

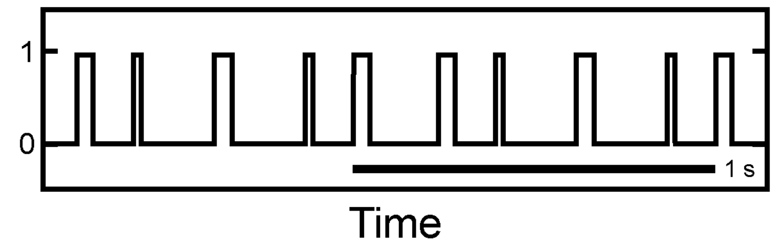


# Threshold Nonlinearity as a Model for Spectral Mixing of Sinusoidal Inputs

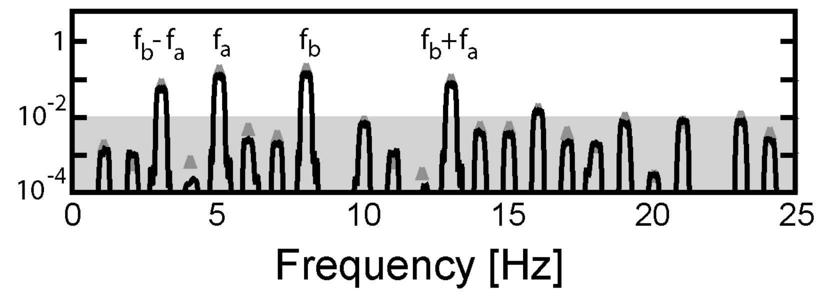
Input = $\cos(2\pi f_a t) + \rho\cos(2\pi f_b t)$




Output = $H\{\text{input} - \Theta_o\}$




Spectral Power Density [$Hz^{-1}$]




$$\text{Output} = \frac{i}{2\pi}\sum_{n=-\infty}^{\infty}\sum_{m=-\infty}^{\infty} e^{i\frac{\pi}{2}(n+m)} \bullet \int_{-\infty}^{+\infty} d\Omega\, \frac{e^{-i\Omega\theta_0}}{\Omega} J_n(\Omega) J_m(\rho\Omega) \bullet e^{i2\pi(nf_a + mf_b)t}$$

Phase Term

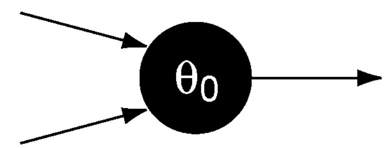
Amplitude Term

Sinusoids at $f = |\pm nf_a \pm mf_b|$

Ahrens, Levine, Suhl and Kleinfeld (2002)

# Neural Hardware for Arithmetic with Frequencies

## Mixing ← Threshold Units




$$\text{Input} = \cos(2\pi f_a t + \psi_a) + \cos(2\pi f_b t + \psi_b)$$

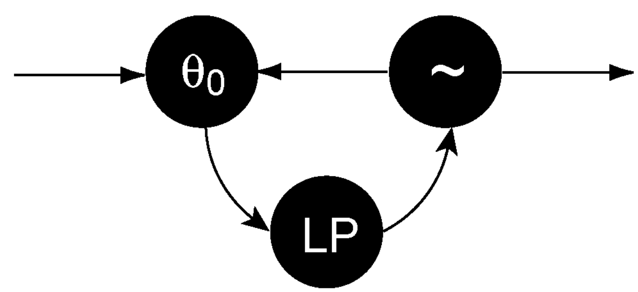
$$\text{Output} = H\{\text{Input} - \Theta_o\} \propto \sum_{n=-\infty}^{\infty}\sum_{m=-\infty}^{\infty} e^{i[n(\psi_a + \pi/2) + m(\psi_b + \pi/2)]} \bullet e^{i2\pi(nf_a + mf_b)t} \bullet I_{nm}(\theta_0)$$

$$\text{"} \quad \propto 2 \bullet I_{00}(\theta_0) + \cos[2\pi f_a t + \psi_a] \bullet I_{10}(\theta_0) + \cos[2\pi f_b t + \psi_b] \bullet I_{01}(\theta_0)$$

$$- \cos[2\pi(f_a - f_b)t + \psi_a - \psi_b] \bullet I_{11}(\theta_0) - \cos[2\pi(f_a + f_b)t + \psi_a + \psi_b] \bullet I_{11}(\theta_0)$$

$$- \cos[4\pi f_a t + 2\psi_a] \bullet I_{20}(\theta_0) - \cos[2\pi f_b t + 2\psi_b] \bullet I_{02}(\theta_0) + \bullet\bullet\bullet$$

## Phase Shifting ← Phase-Locked Loops



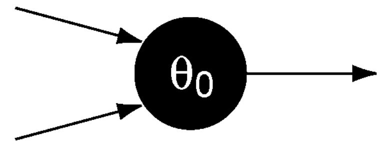

$$\text{Input} = \cos(2\pi f_a t)$$

$$\text{Output} = \cos(2\pi f_a t + \pi/2)$$

$$\text{"} \quad = \sin(2\pi f_a t)$$

# Neural Hardware for Arithmetic with Frequencies

## Mixing ← Threshold Units




Input $= \cos(2\pi f_a t + \psi_a) + \cos(2\pi f_b t + \psi_b)$

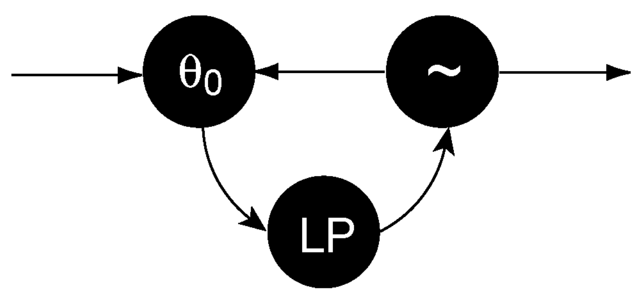
Output $= H\{\text{Input} - \Theta_0\} \propto \sum_{n=-\infty}^{\infty} \sum_{m=-\infty}^{\infty} e^{i[n(\psi_a + \pi/2) + m(\psi_b + \pi/2)]} \bullet e^{i 2\pi(nf_a + mf_b)t} \bullet I_{nm}(\theta_0)$

" $\propto 2 \bullet I_{00}(\theta_0) + \cos[2\pi f_a t + \psi_a] \bullet I_{10}(\theta_0) + \cos[2\pi f_b t + \psi_b] \bullet I_{01}(\theta_0)$

$- \cos[2\pi(f_a - f_b)t + \psi_a - \psi_b] \bullet I_{11}(\theta_0) - \cos[2\pi(f_a + f_b)t + \psi_a + \psi_b] \bullet I_{11}(\theta_0)$

$- \cos[4\pi f_a t + 2\psi_a] \bullet I_{20}(\theta_0) - \cos[2\pi f_b t + 2\psi_b] \bullet I_{02}(\theta_0) + \bullet\bullet\bullet$

## Phase Shifting ← Phase-Locked Loops



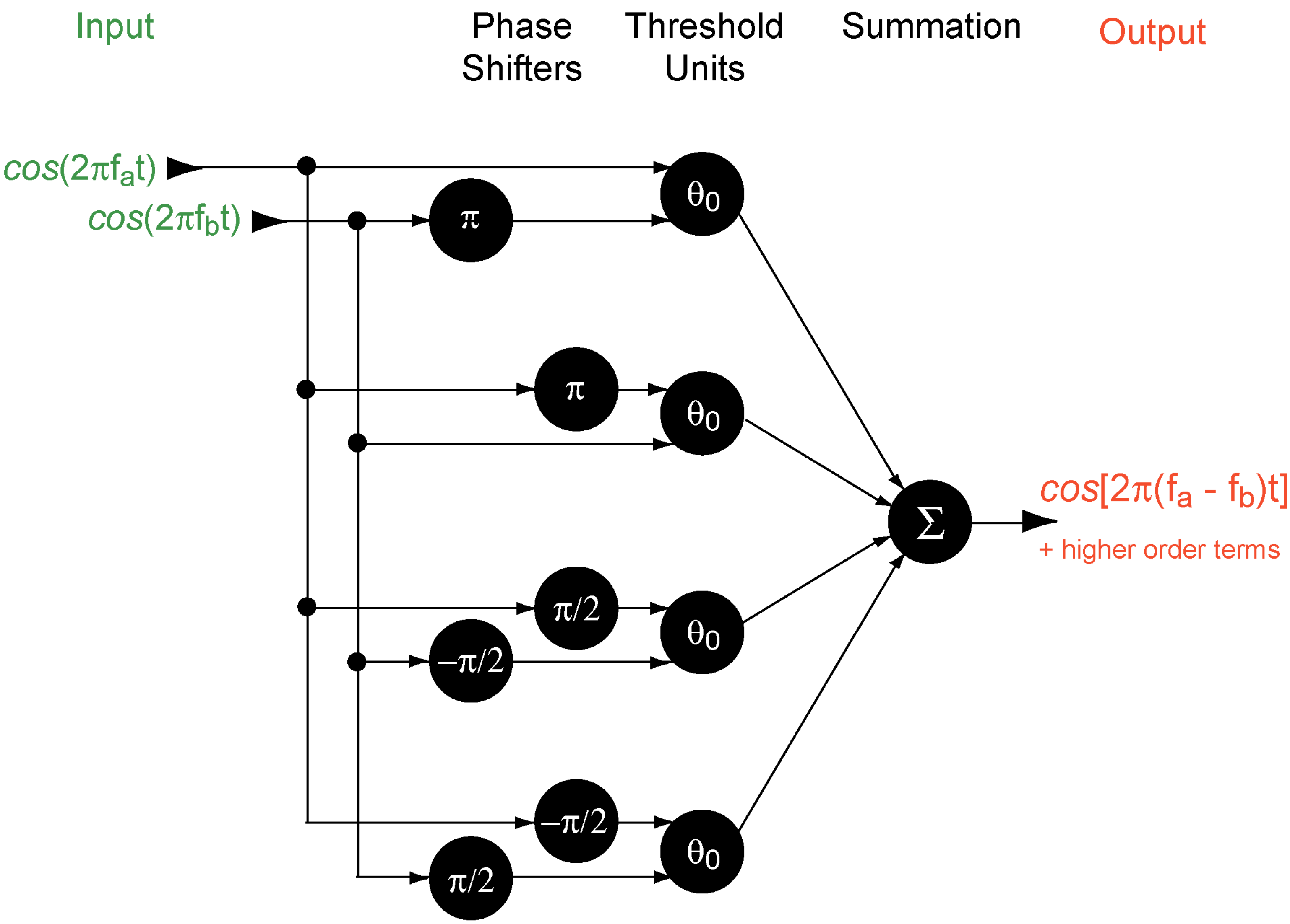

Input $= \cos(2\pi f_a t)$

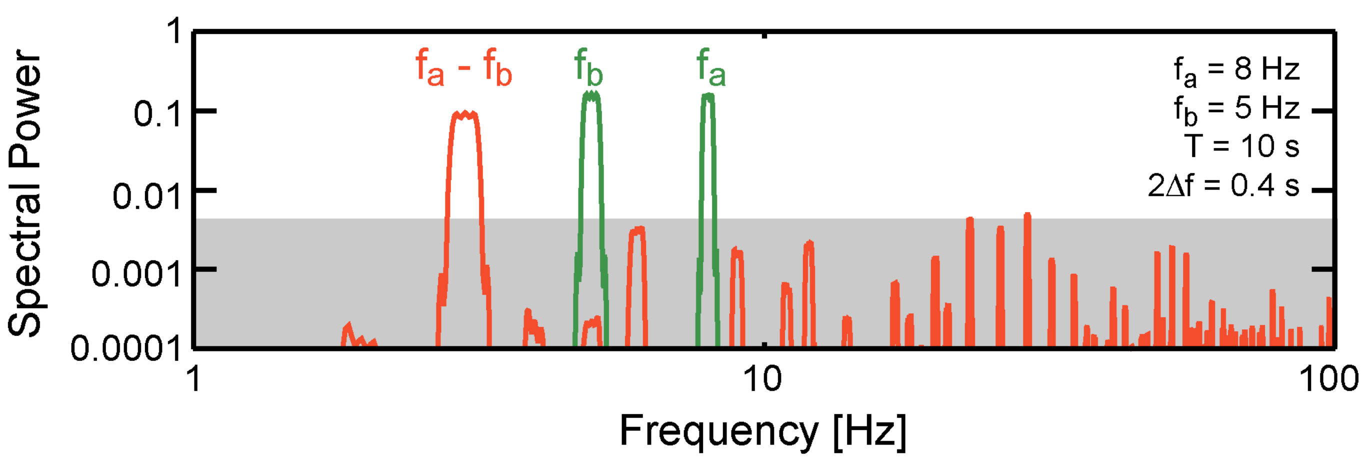
Output $= \cos(2\pi f_a t + \pi/2)$

" $= \sin(2\pi f_a t)$

# Neural Hardware for Subtraction of Two Frequencies

(15 neurons, 23 synapses)



# Coupled Oscillations in Nervous Systems

## Theoretical Overview

## Experimental Evidence for Weak Coupling Between Oscillators

### Direct Measurement of Phase-sensitivity Function, $Z(\psi)$

### Behavior of Pairs and Networks of Inhibitory Neurons

## Electrical Waves During "Normal" Function

### Linear Waves in an Invertebrate Central Olfactory Organ
(Consequence of an intrinsic frequency gradient)

### Linear and Rotating Waves in Lower Vertebrate Visual System
(Linear part consistent with biased connectivity)

## Insights into Cortical Function from Nonlinear Spectral Mixing
(Problem of Combining Proprioceptive, or Reference Signals, with Contact Signals)

# Program in Active Sensation
# Kleinfeld Neurophysics Laboratory

Kurt Ahrens
Rune Berg
John Curtis
Michale Fee
Karunesh Ganguly
Samar Mehta
Lynne Merchant
Quoc Nguyen
Sean O'Connor
Suri Venkatachalam
Ralf Wessel
Diane Whitmer


Ehud Ahissar
Mathew Diamond
Ford Ebner
Beth Friedman
David Golomb
Murray Jarvis
Herbert Levine
Partha Mitra
Robert Sachdev
Harry Suhl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