Coupled Oscillations in Nervous Systems

Theoretical Overview Based on the Work of Prof. Kuromoto

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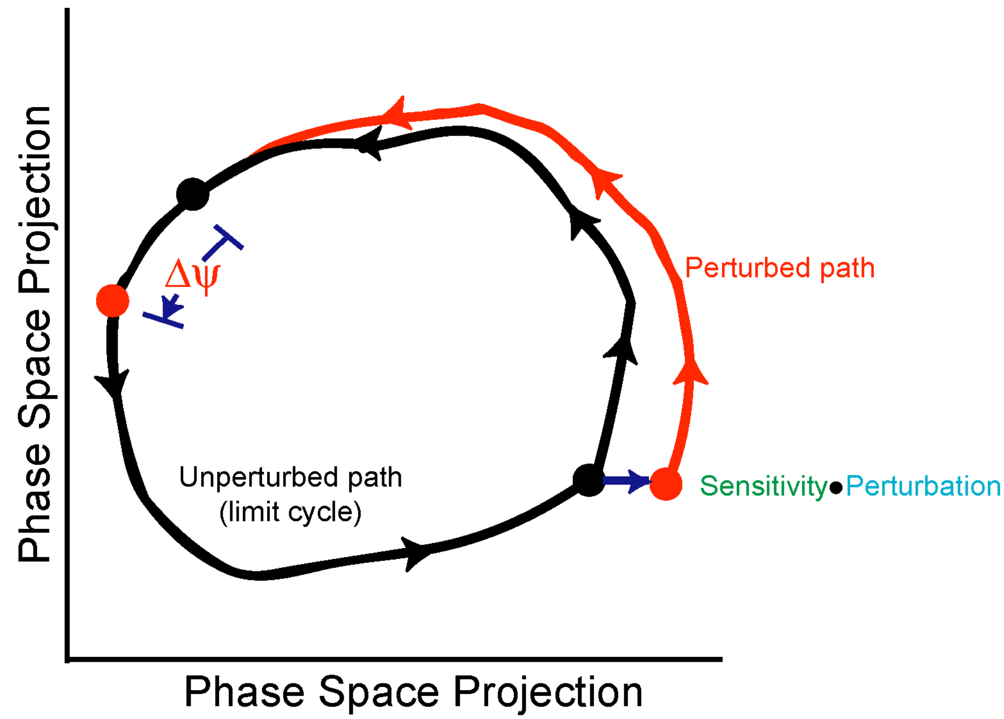
Conjecture on the Use of Oscillators for Arithmetic with Frequencies

Kuromoto's Insight: Transform a Dynamic System of N-Dimensional Oscillators into a "Phase" System of 1-Dimensional Oscillators

Perturbation → Phase Shift (Δψ)



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

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

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

The Kuromoto Phase Approach to Coupled Oscillators

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

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

Sensitivity Function — Perturbation

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

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

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

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

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

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

Phase difference: $(\Psi_i - \Psi_j)$

Lesson: Interation of Neuronal Oscillators is Given by Correlation of Presynaptic Activity with Postsynaptic Response

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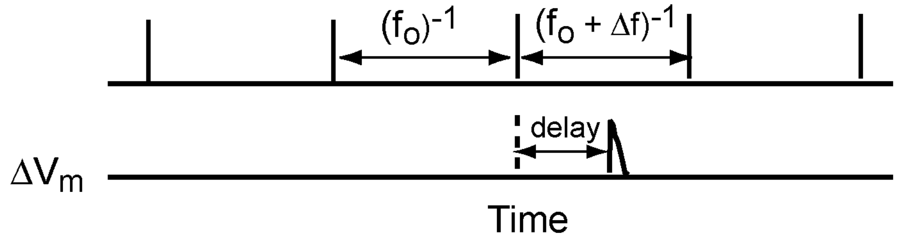
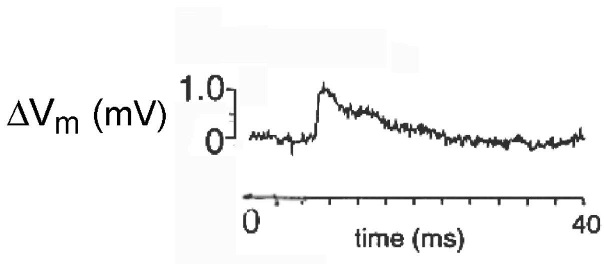
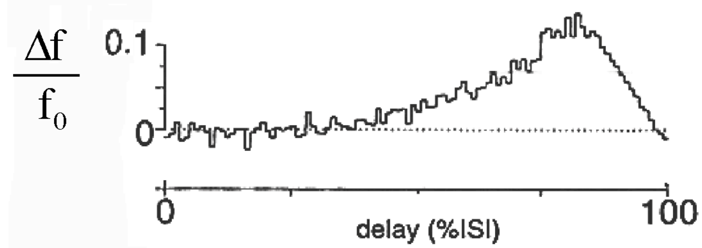
The Phase Sensitivity Function for Perturbation in Voltage

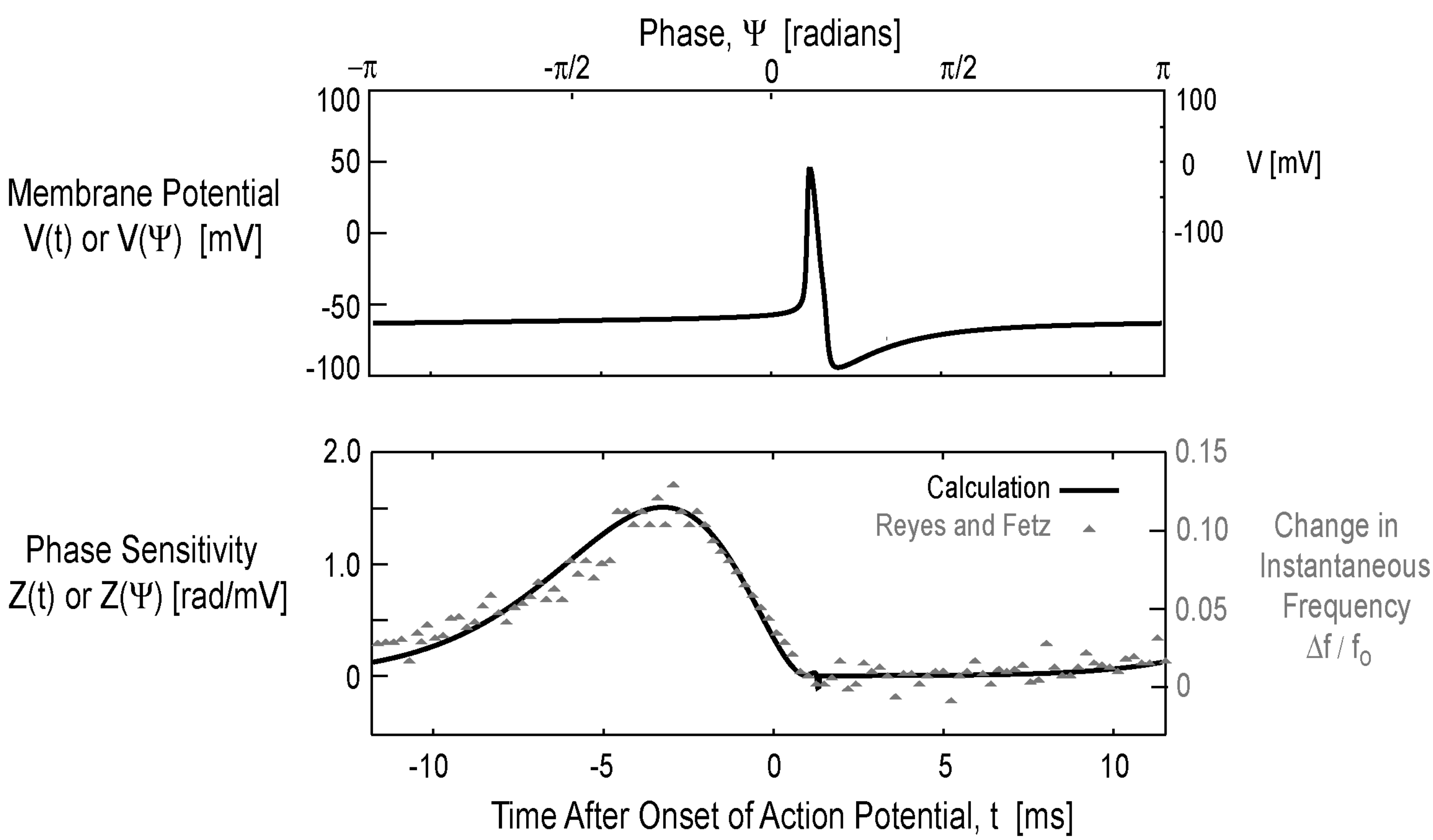
Data (Reyes & Fetz 1993) vs. Calculation (Ermentrout & Kleinfeld 2000)

$$\mathbf{Z}(\Psi) = \frac{\partial \Psi}{\partial V} \approx \frac{2\pi}{f_0} \frac{\Delta f}{\Delta V}$$



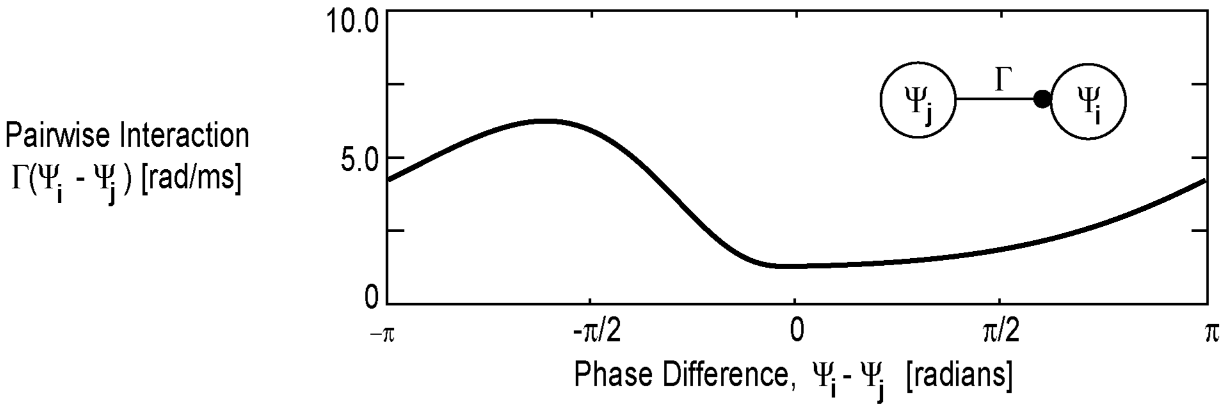






Lesson: Phase Sensitivity Concept Valid with Realistic PSPs

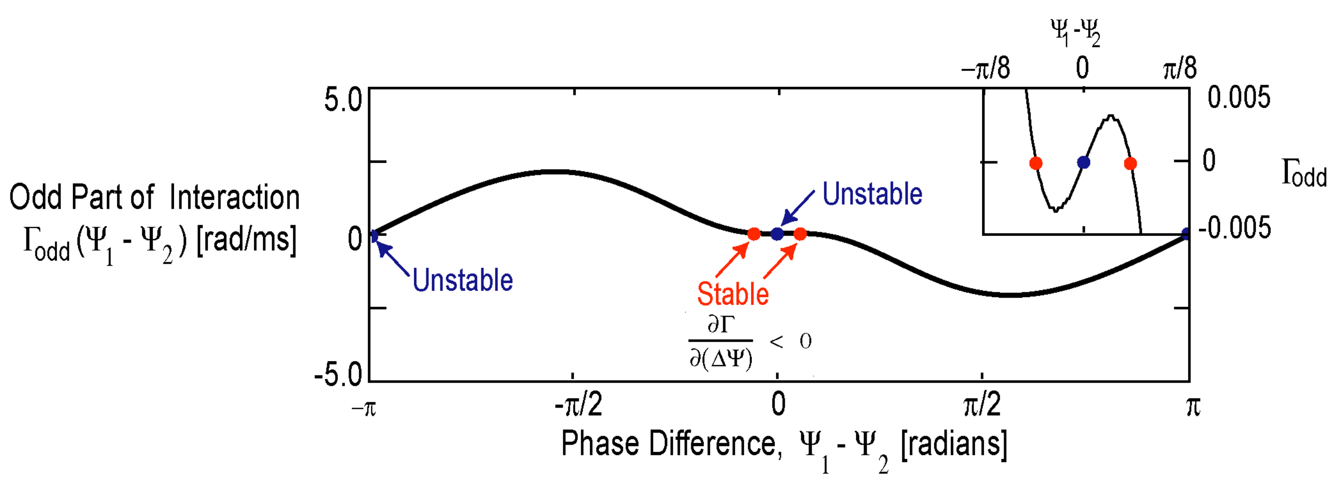
Nature of the Pairwise Interaction is Revealed by the Phase Shifts Between Two Reciprocally Connected Neurons



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

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

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



Lesson: Excitatory Coupling Among Cortical Neurons Can Lead to Cross-Correlations that Peak Away from Equal Time

Challenge for Experimentalists is to Distinguish this from Broadening

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Two Kuromoto-like Phase Oscillators with Synaptic Coupling

Minimal Model for Insight into All-Inhibitory Neuronal 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 $\frac{\partial\,[\Gamma(\Delta\psi)-\Gamma(\text{-}\Delta\psi)]}{\Delta\psi} < 0$

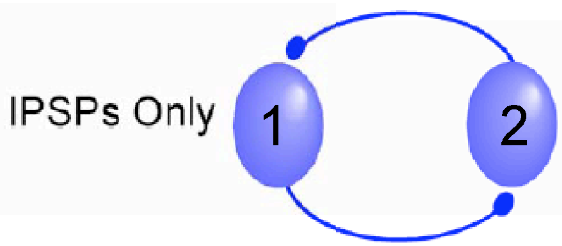
For inhibition (g < 0), synchrony ($\psi' = \psi$) is stable for $\tau > \frac{1}{\omega}$

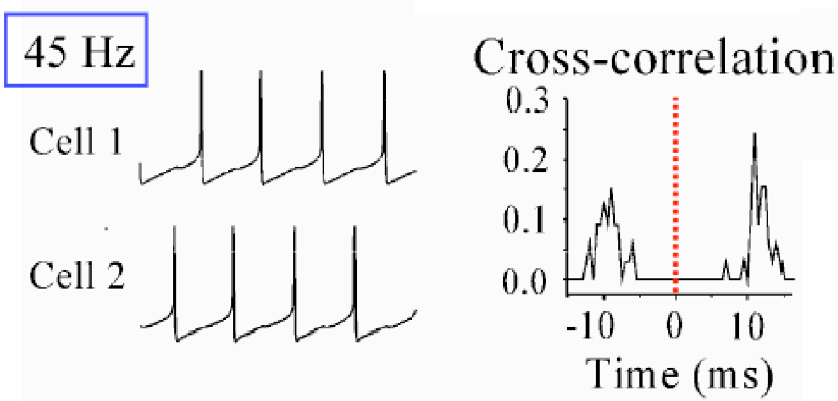
Reciprocal, Kuromoto-like Inhibitory Coupling Among Pairs of Neurons

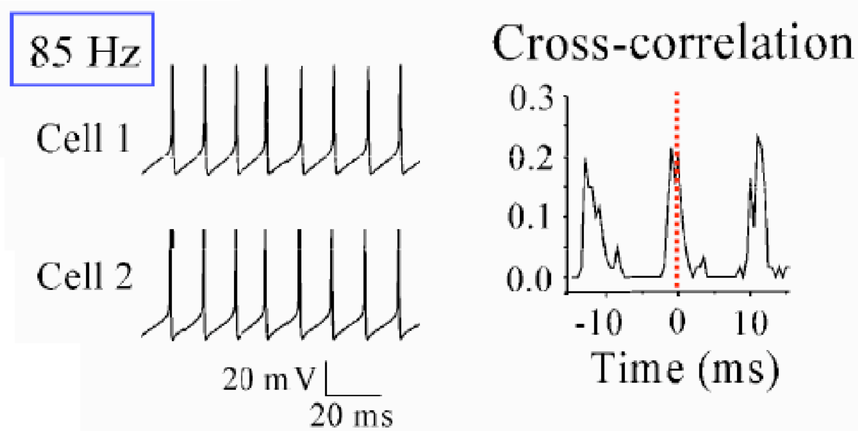
Firing Switches from Antisynchrony to Synchrony near 80 Hz

(data from Barry Connors Laboratory)

$$\Gamma(\Delta\psi) - \Gamma(-\Delta\psi) = g\,\frac{(\omega\tau)^2 - 1}{[1 + (\omega\tau)^2]^2}\sin(\Delta\psi) < 0 \text{ for } \omega > \tau^{-1}$$





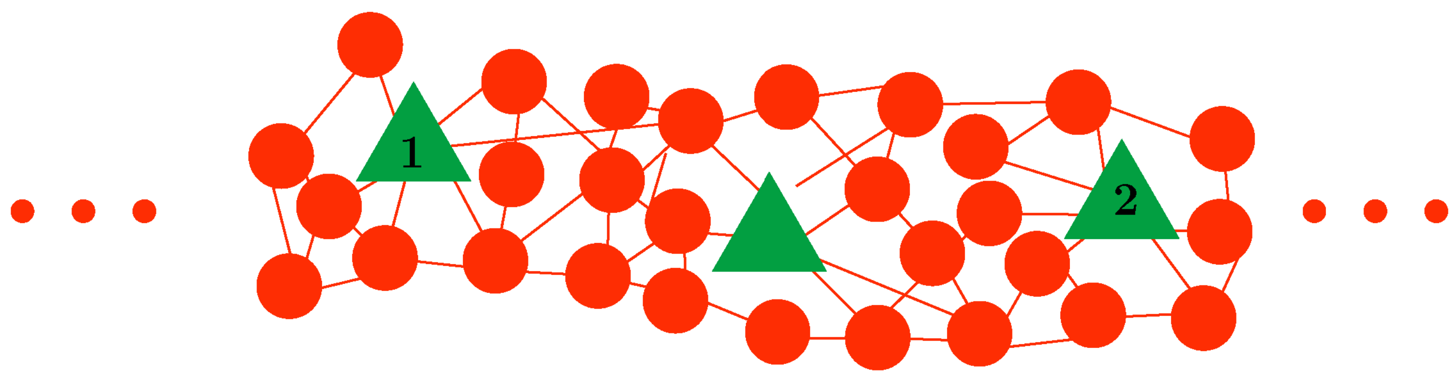


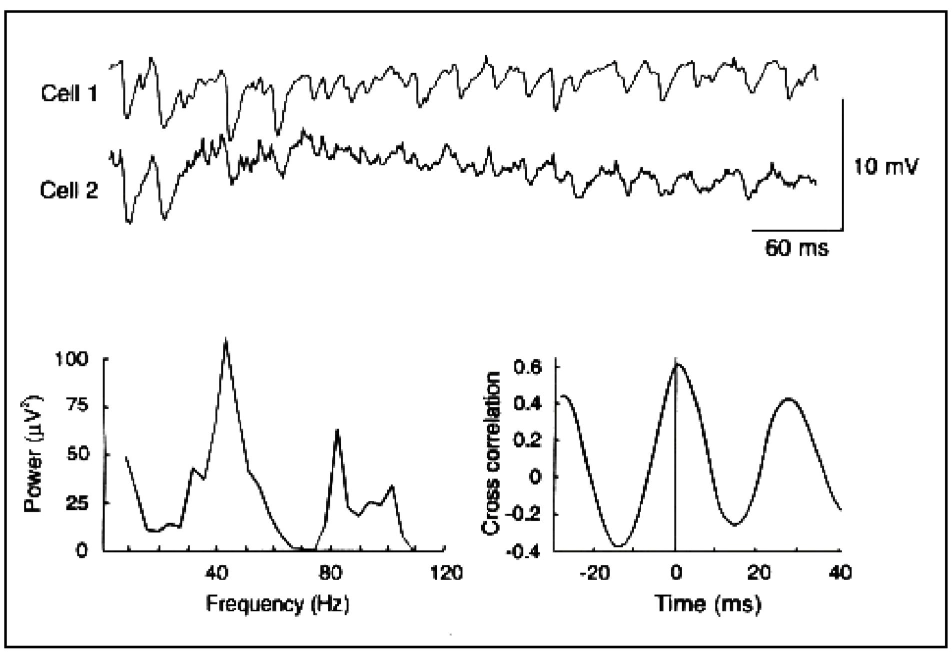
Reciprocal, Kuromoto-like Inhibitory Coupling in a Network of Neurons

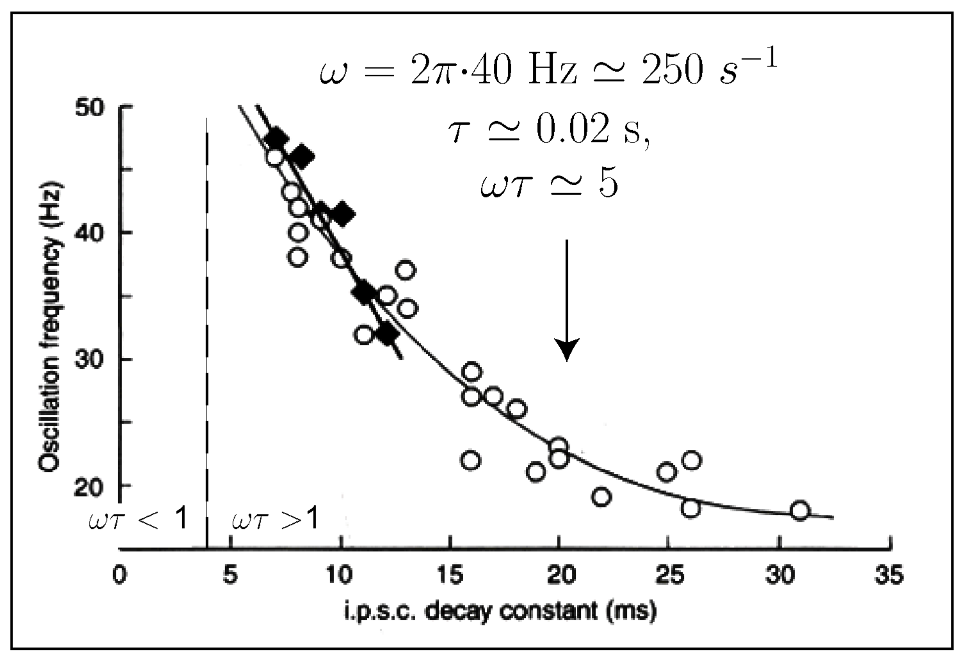
Synchronized Oscillations in an All Inhibitory (g < 0) Interneuron Network

(Whittington, Traub and Jeffreys 1995)

$$\Gamma(\Delta\psi) - \Gamma(-\Delta\psi) \;=\; g\,\frac{(\omega\tau)^2 - 1}{[1+(\omega\tau)^2]^2}\,\sin(\Delta\psi) < 0 \quad \text{for} \quad \omega\tau > 1$$







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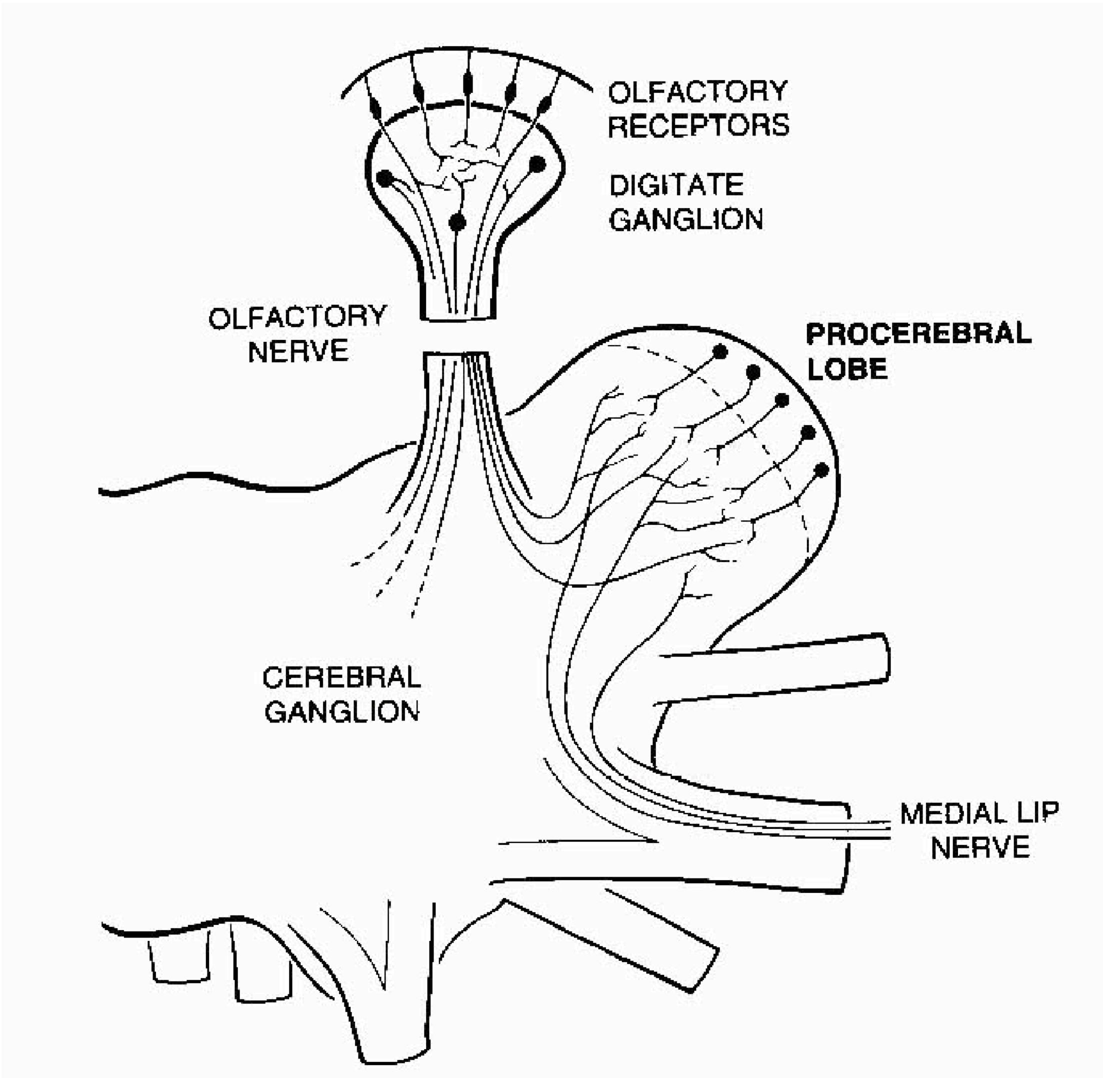
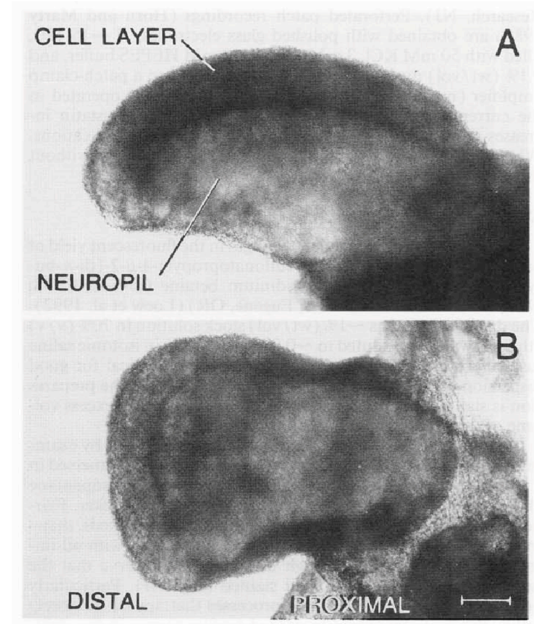
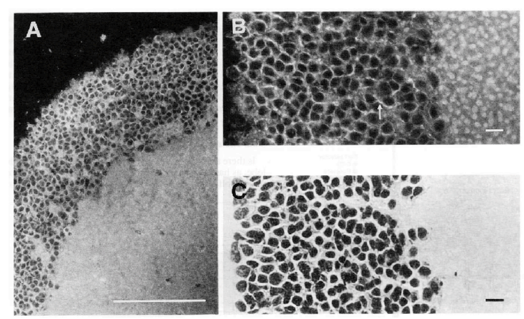
Central Olfactory Organ in the Terrestrial Mollusk Limax

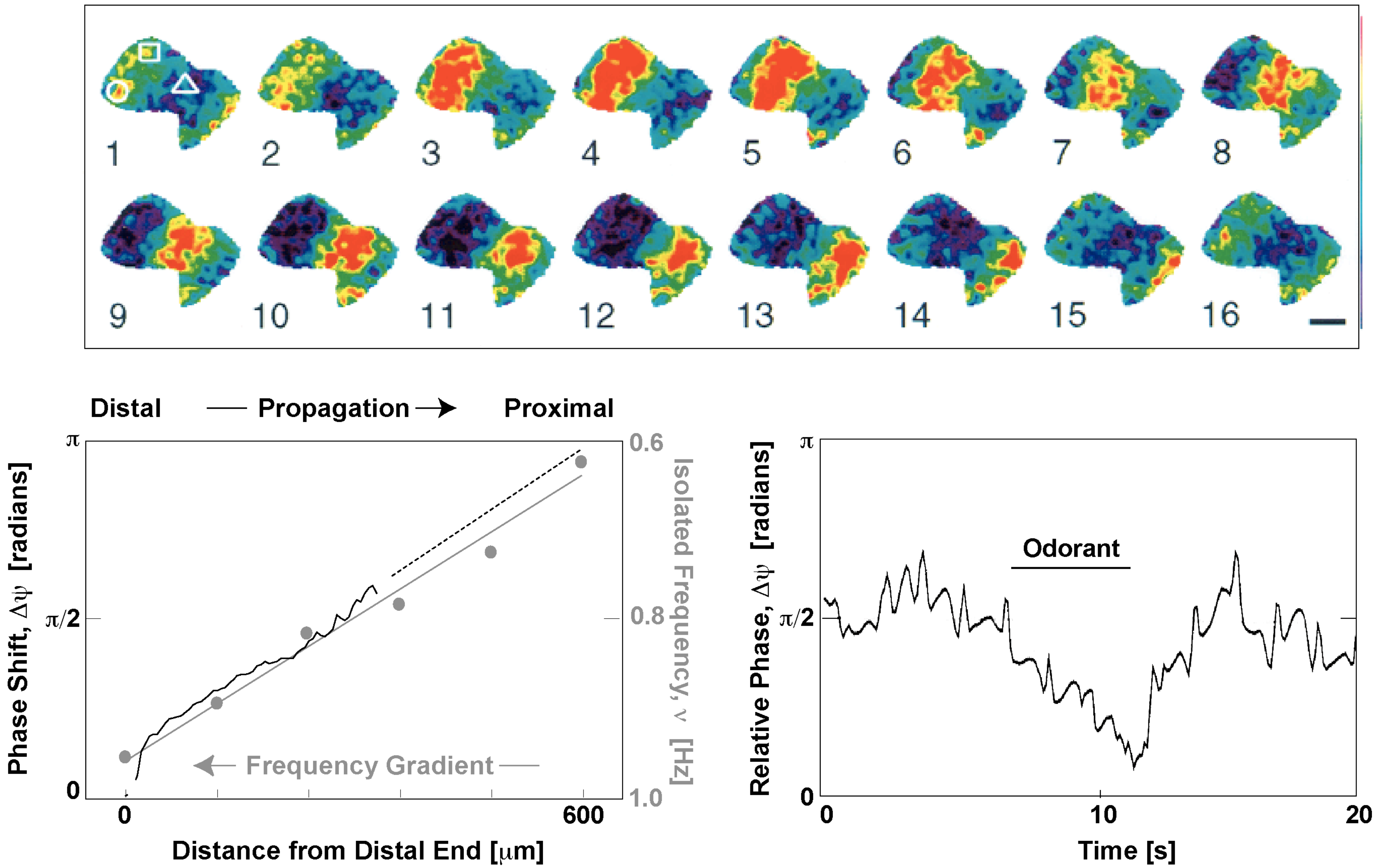






Electrical Wave Propagation in the Central Olfactory Organ of Limax

(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
$$\begin{aligned} \frac{d\psi}{dt} &= \Gamma_0 \sin(\psi' - \psi) + \omega \\ \frac{d\psi'}{dt} &= \Gamma_0 \sin(\psi - \psi') + \omega' \end{aligned}$$

Lock, i.e., $\dfrac{d\psi}{dt} = \dfrac{d\psi'}{dt}$ 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 $\Delta\psi \equiv \psi - \psi' = \sin^{-1}\left(\dfrac{\omega' - \omega}{2\Gamma_0}\right)$

Wave Model for Limax

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

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

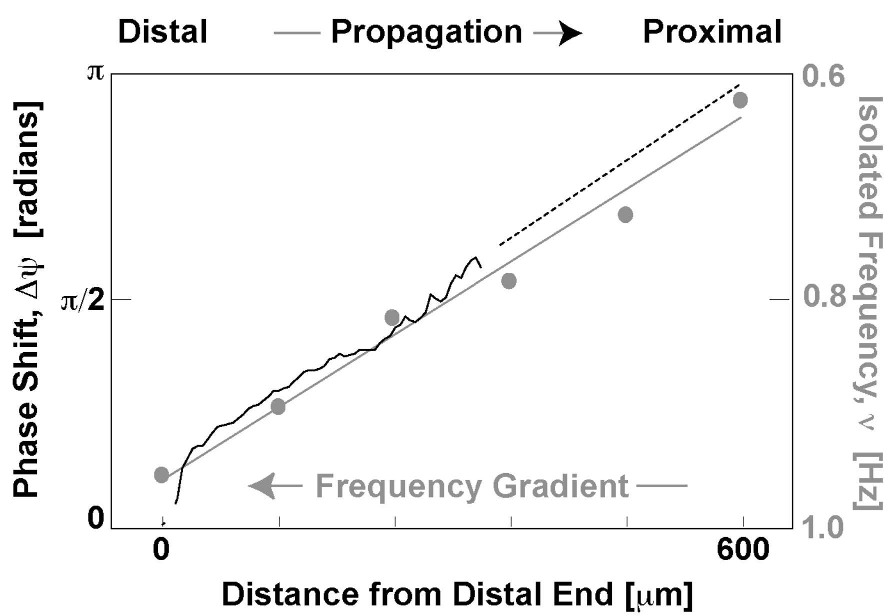
$$\frac{d\psi_x}{dt} = (\omega + \delta\omega_x) + \sum_{x \neq x'} \Gamma(\psi_x - \psi_{x'})$$

$$\delta\omega_x \propto x$$

When the network locks:

Single frequency

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



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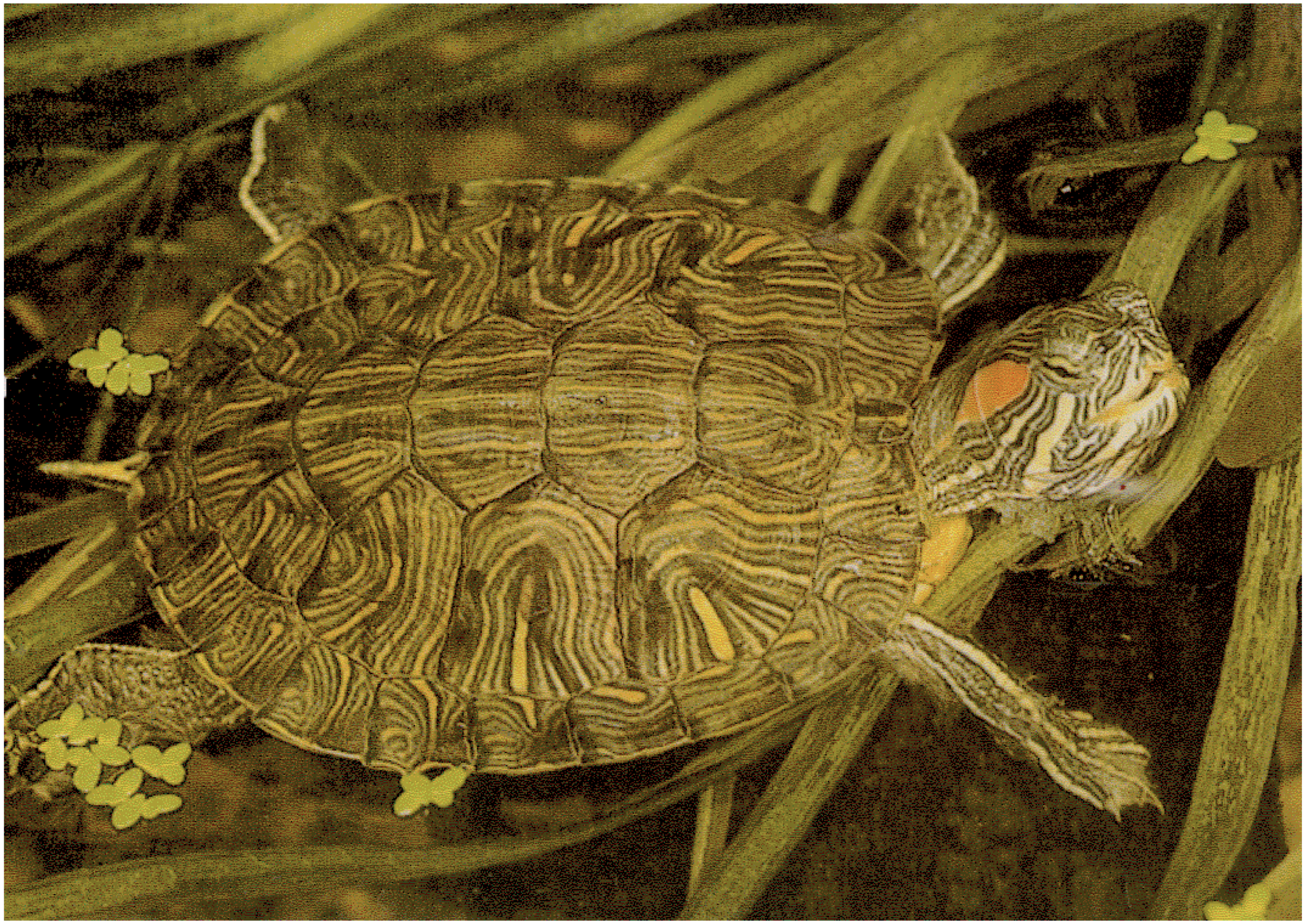
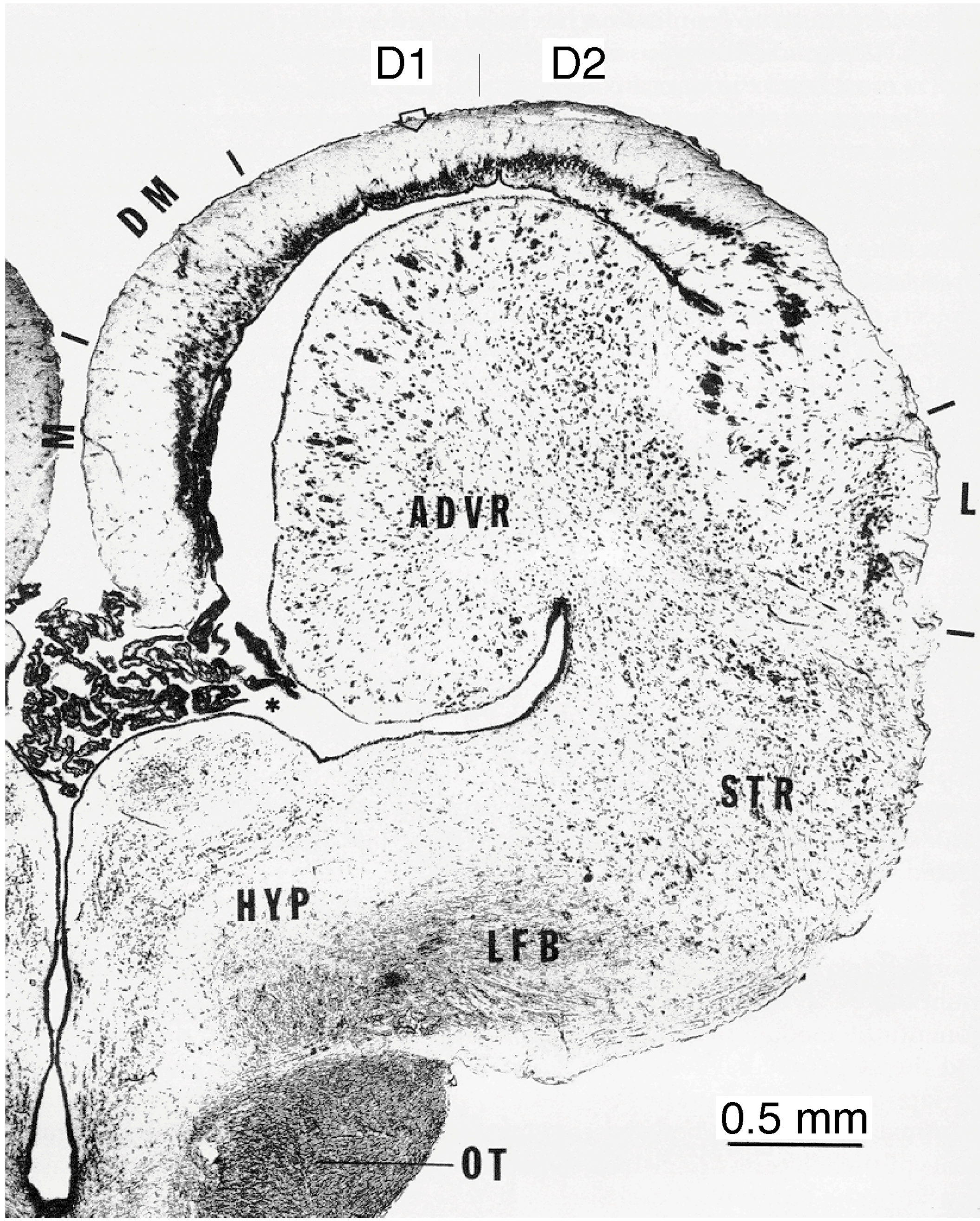
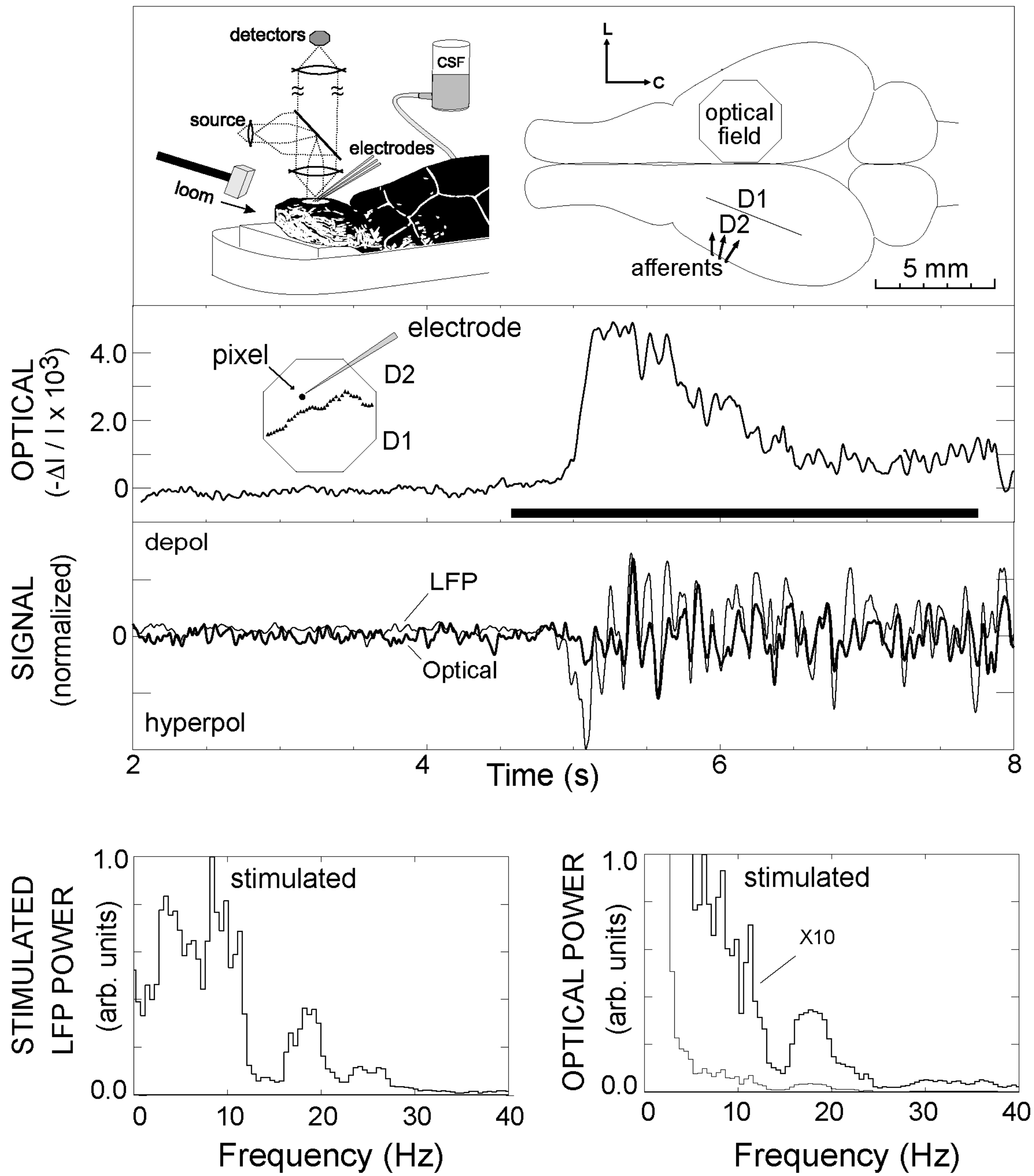


Transverse Nissl section through cerebral hemisphere of *Pseudemys scripta elegans*

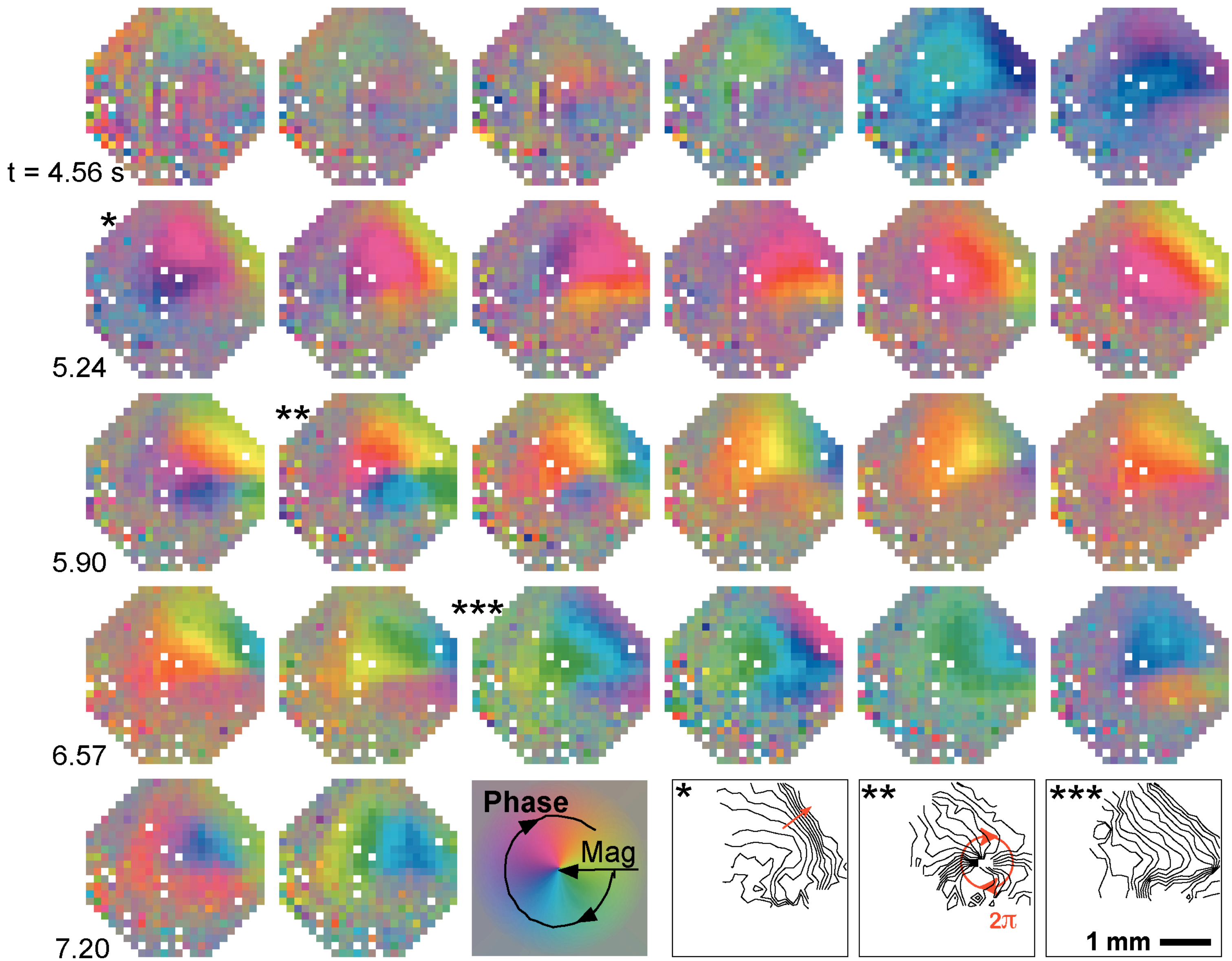
- from P. S. Ulinski



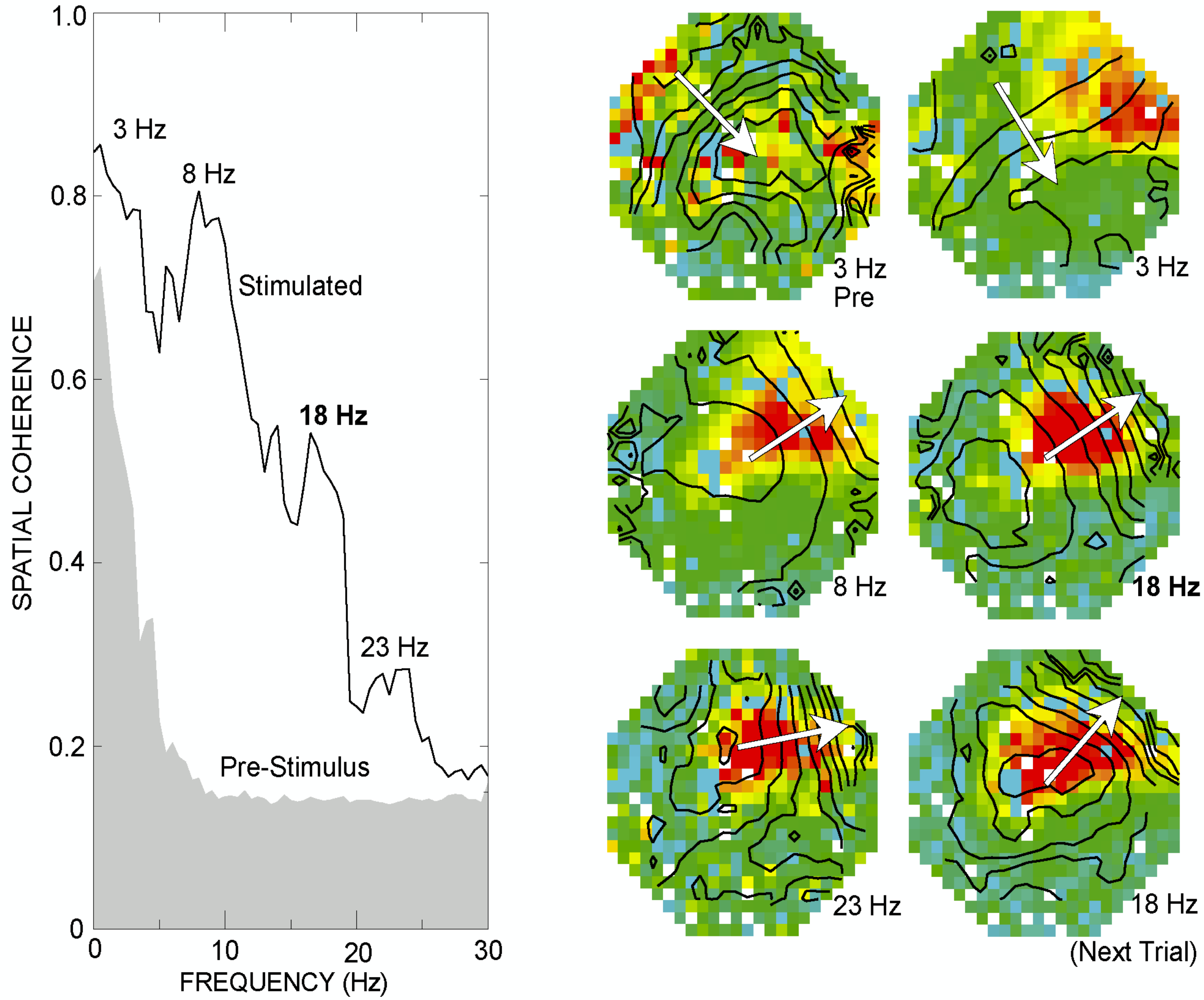
Voltage Sensitive Dye Imaging of Turtle Visual Cortex



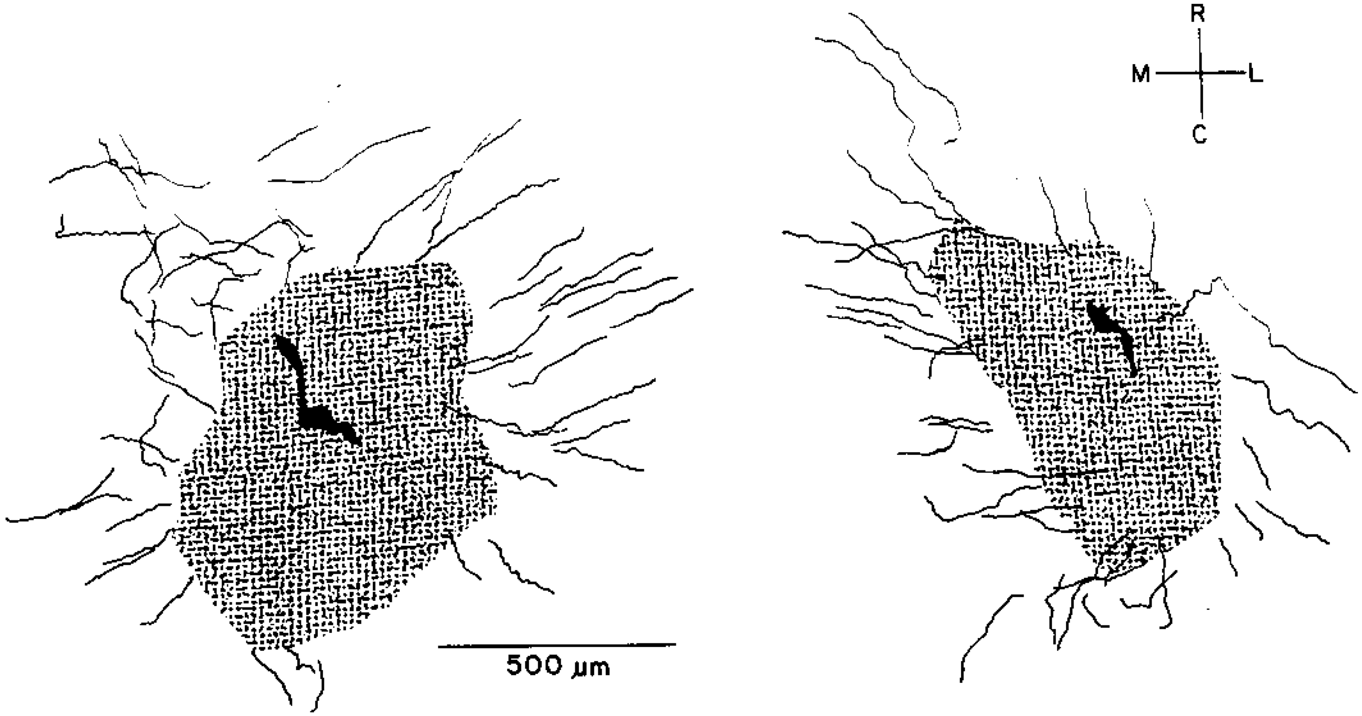
Demodulated Response at 18 Hz Versus Time
(Magnitude and Phase Plots)

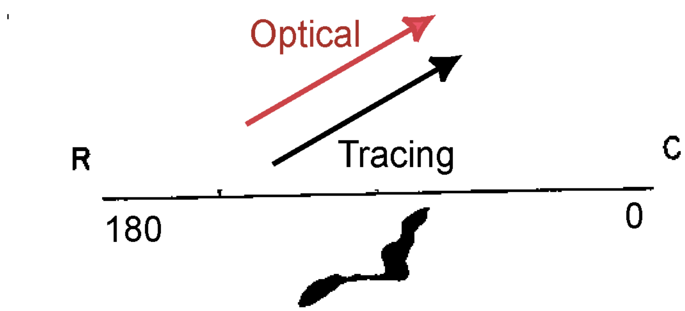


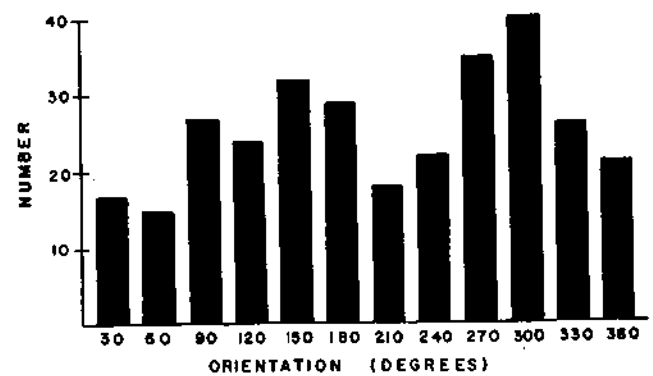
Dominant Spatial Modes are Revealed from a Spectral Decomposition (SVD) in Position (**x**) and Frequency (f)



Prechtl, Cohen, Pesaran, Mitra and Kleinfeld 1997


R
M
L
C
500 µm


Optical
Tracing
R
C
180
0


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

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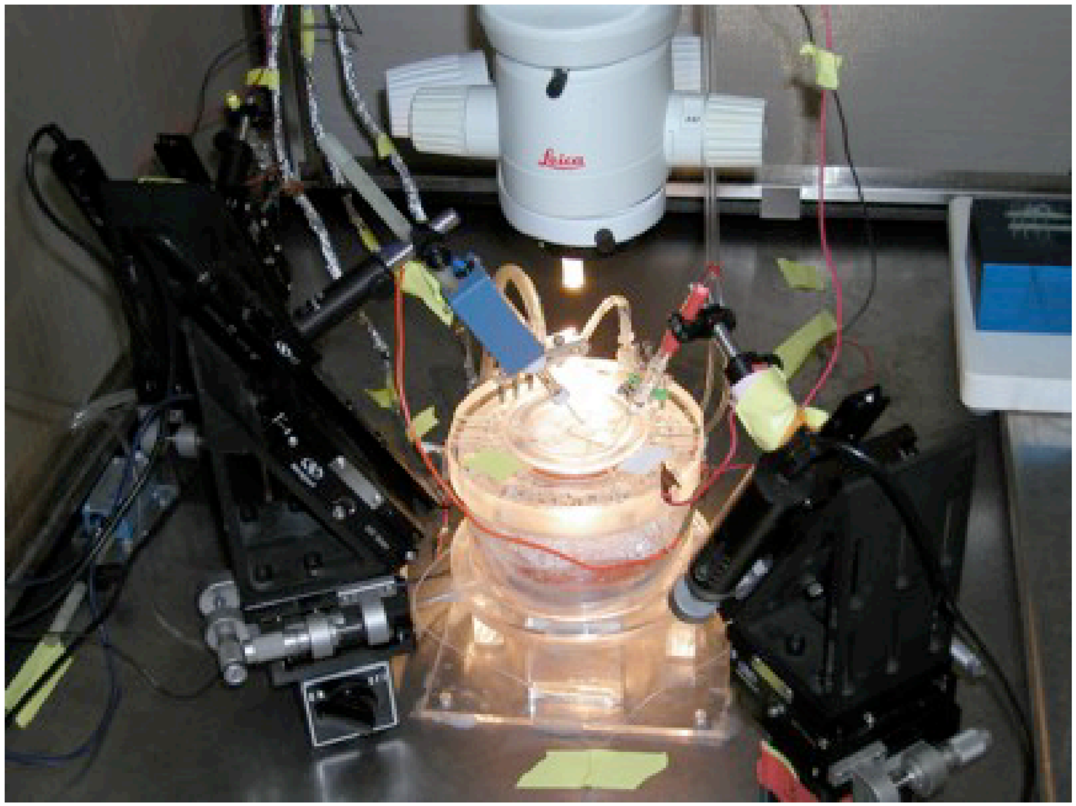
Upcoming Applications for Kuromoto-like Coupling

Spiral Waves in Disinhibited Mammalian Neocortex

(Huang, Troy, Yang, Ma, Laing, Schiff and Wu, 2004)



Electrical (local field potential) and optical (voltage sensitive dyes and brightfield illumination) recording of spatially averaged (~ 100 μm) activity across layer 2/3 tangential slice

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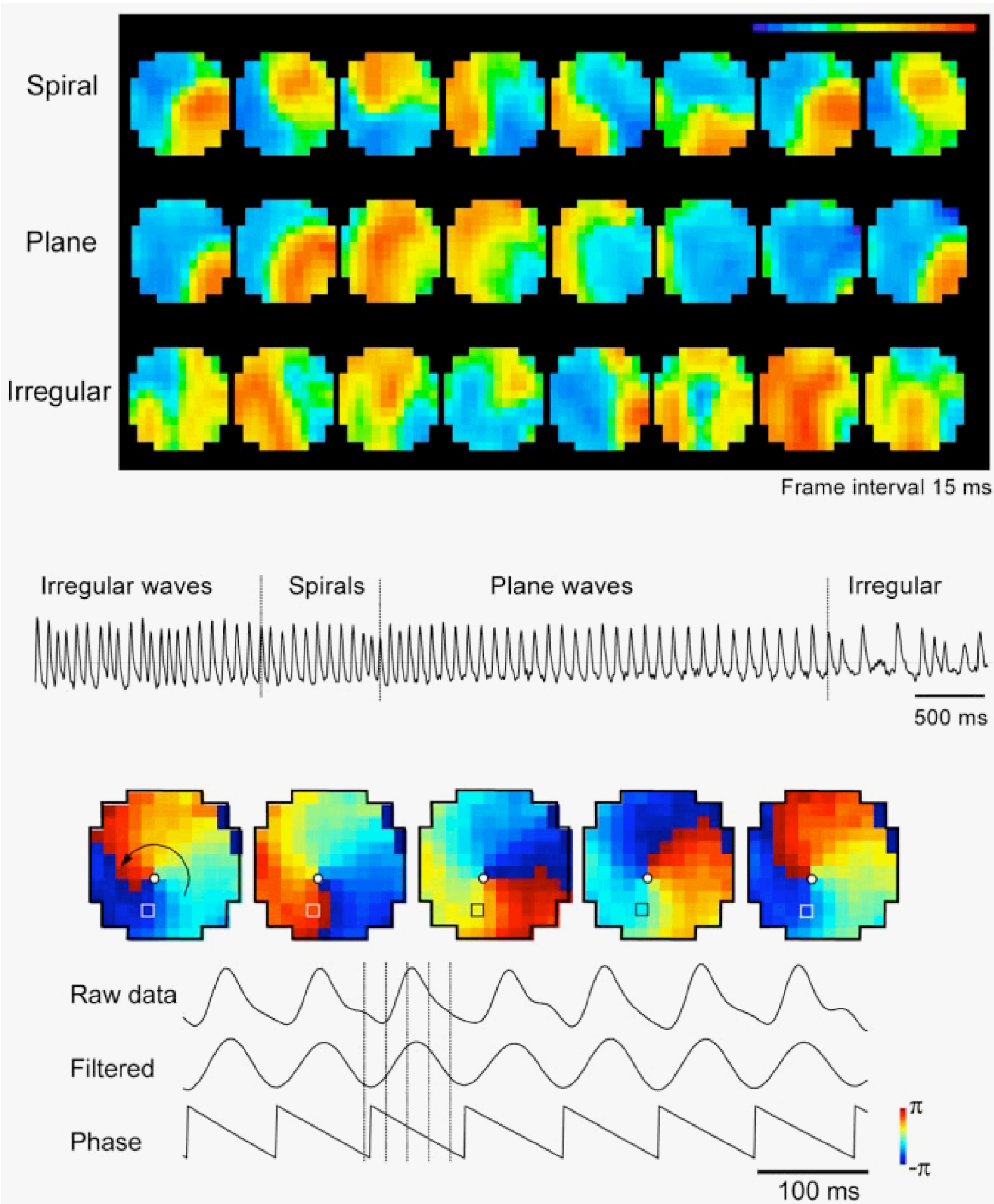
(Huang, Troy, Yang, Ma, Laing, Schiff and Wu, 2004)



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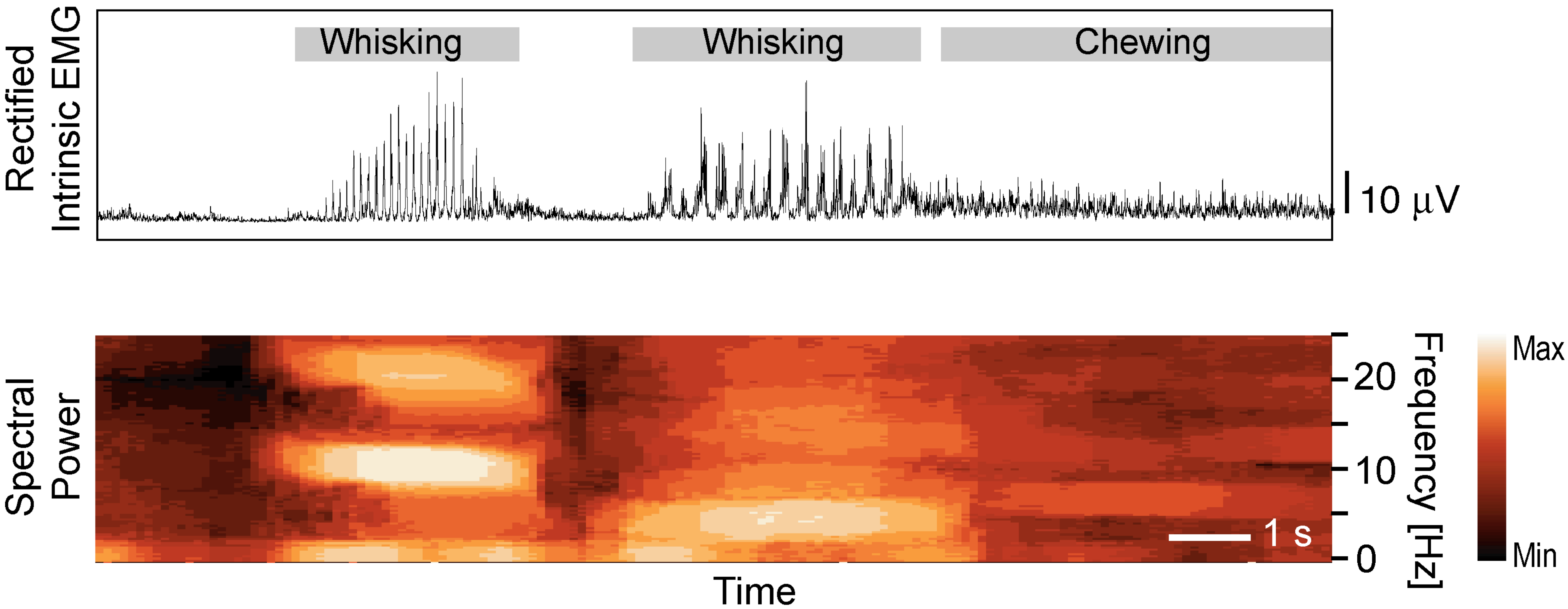
Exploratory Whisking by a Free Ranging Rat in Search of a Foodtube

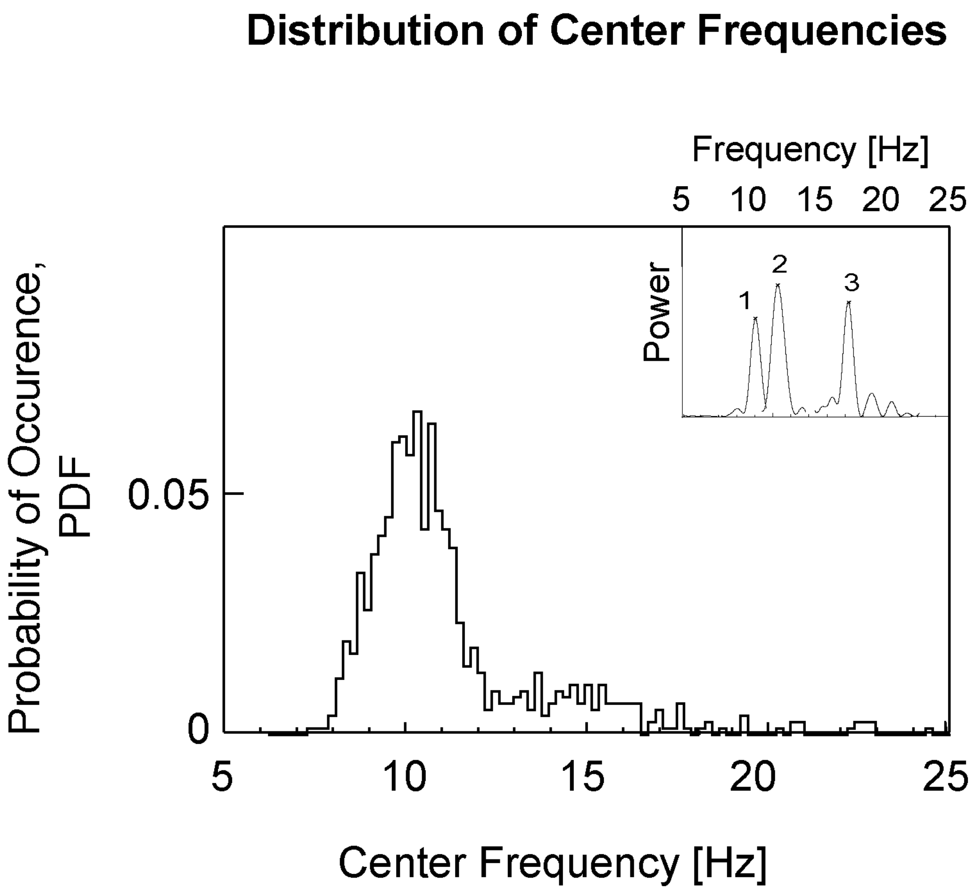
Consecutive Video Rate Fields (60 Hz acquisition)

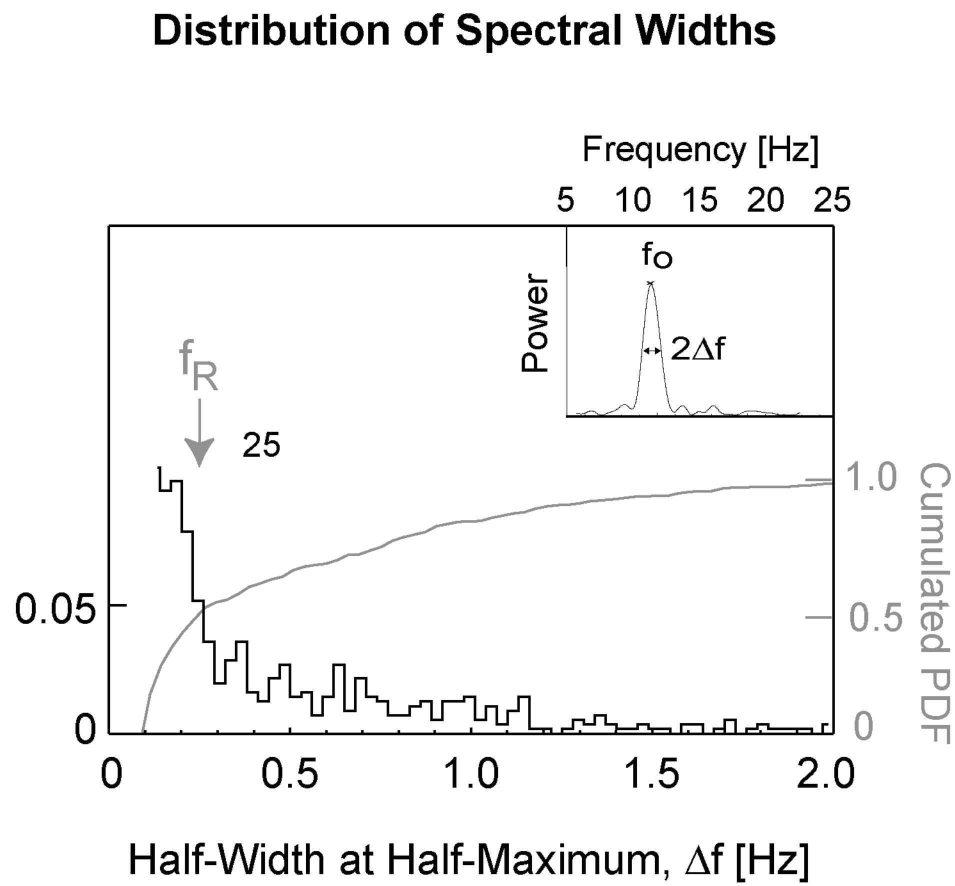
The Frequency of Whisking is Constant within an Epoch but Broadly Distributed from Epoch to Epoch



O'Connor, Berg and Kleinfeld 2001

The Distribution of Spectral Parameters for Free Whisking

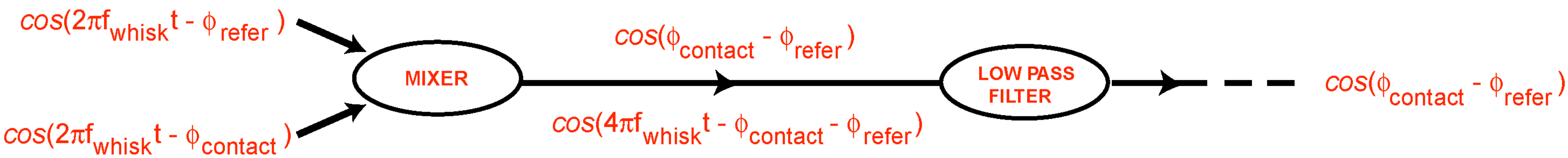




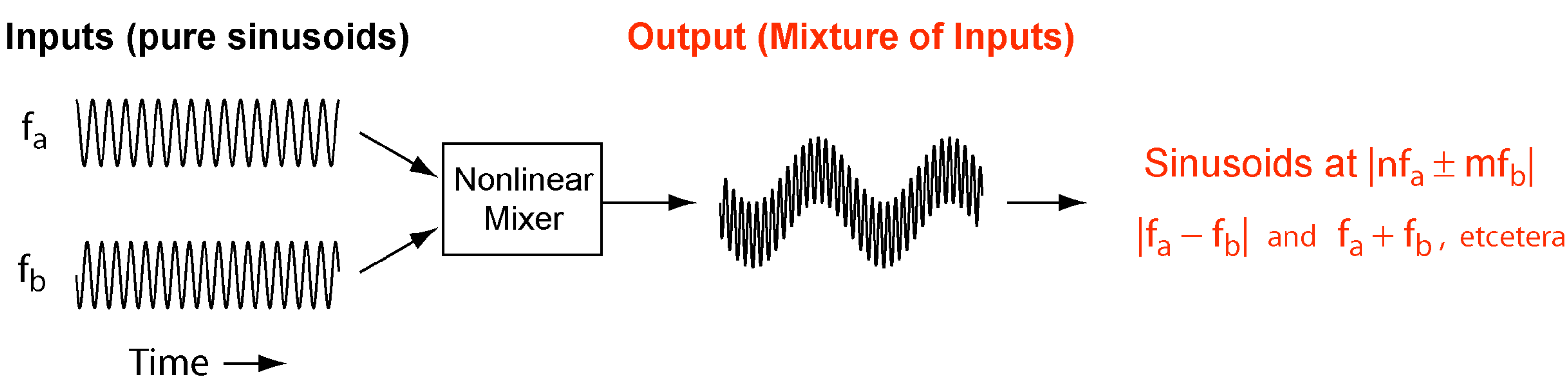
Berg and Kleinfeld (2003)

Nonlinear Mixer: Essential Ingredient for Phase Sensitive Detection

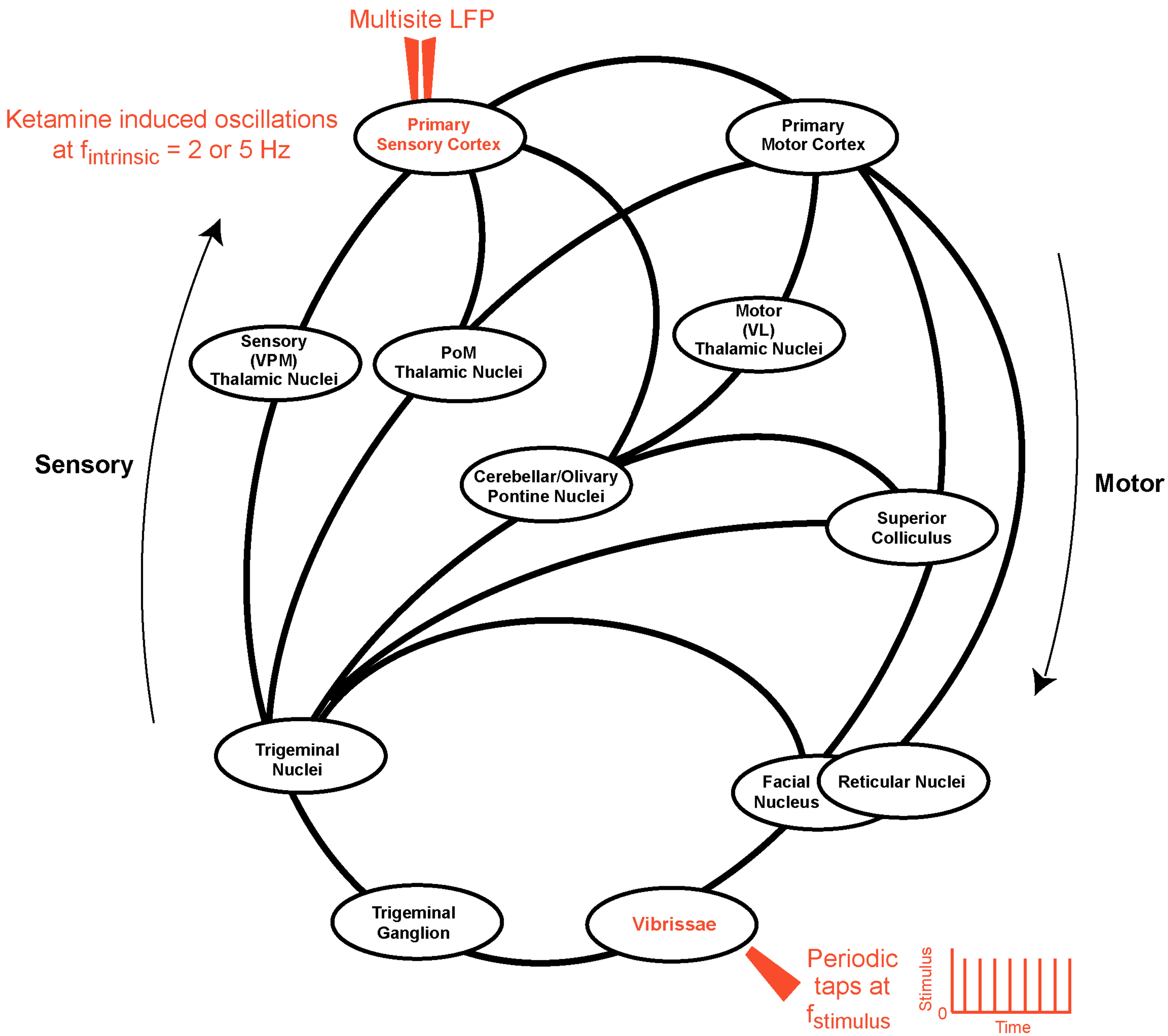
Motivation
Computation of Vibrissa Contact in Face-Centered Coordinates



Experimental Signature



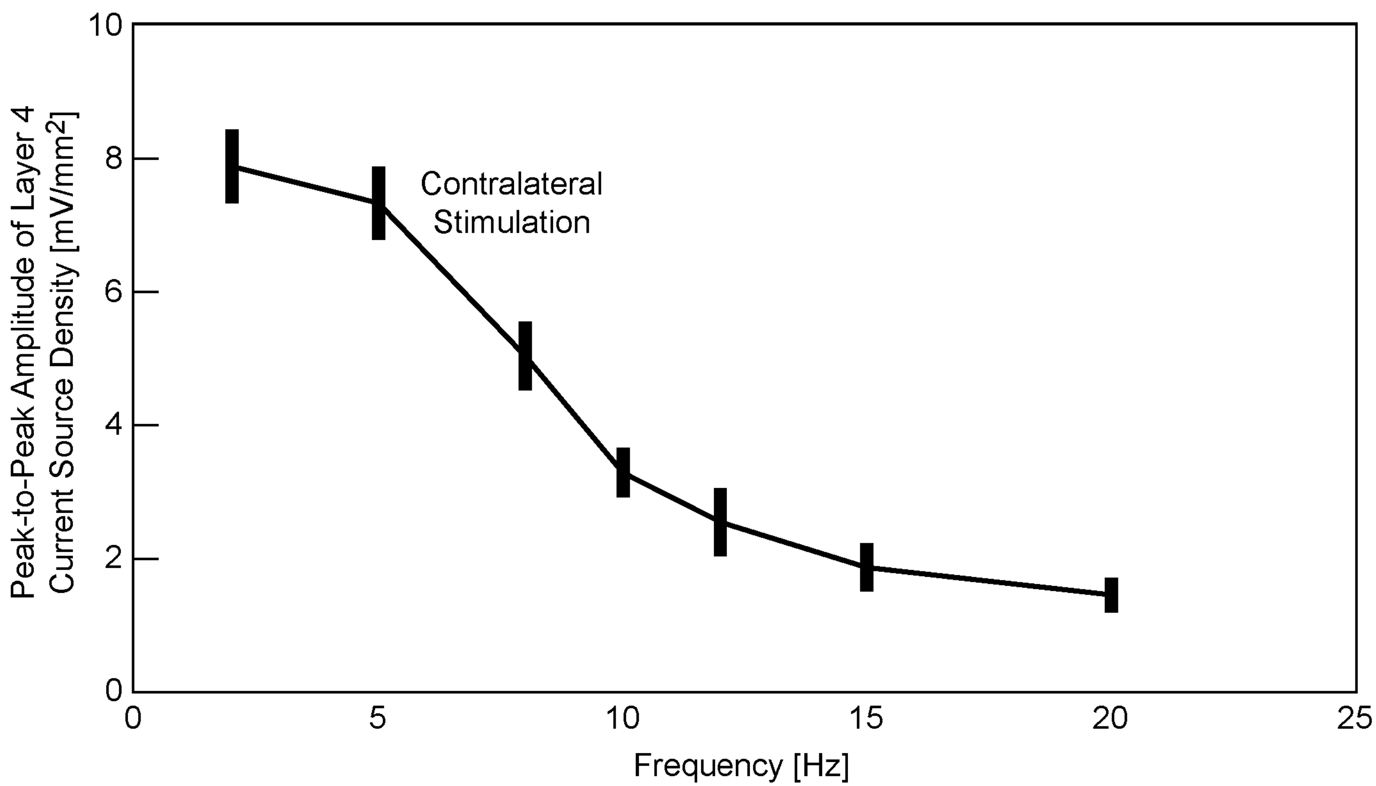
Stimulus Induced Current Flow in S1 Vibrissa Cortex in Anesthetized Rat



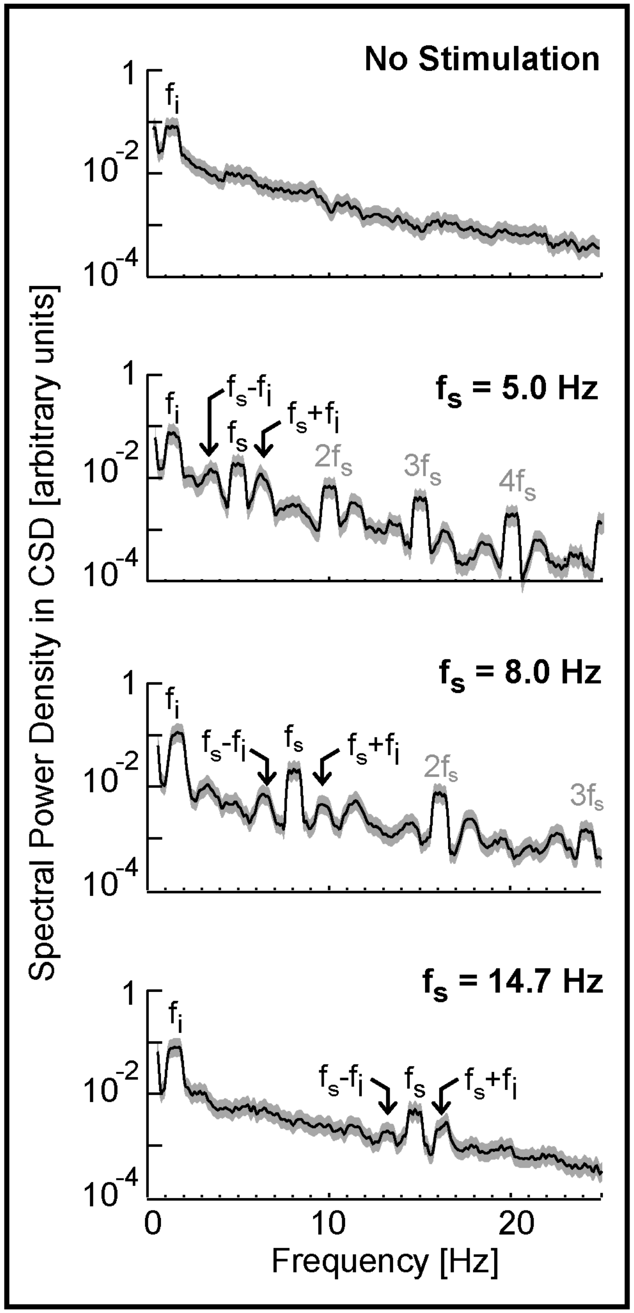
Paradigms to Detect Mixing of Two Oscillatory Signals in Cortex

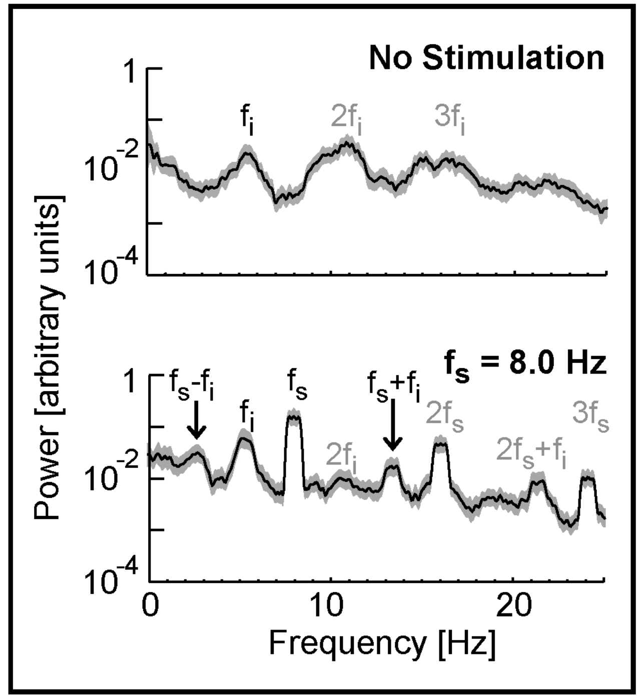
1 - Intrinsic (Ketamine Induced) Rhythm Plus Contralateral Stimulation

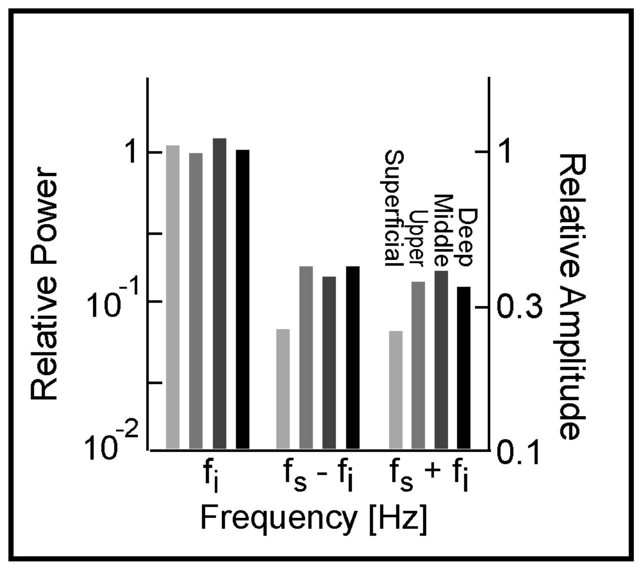
2- Simultaneous Contralateral and Ipsilateral Stimulation



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



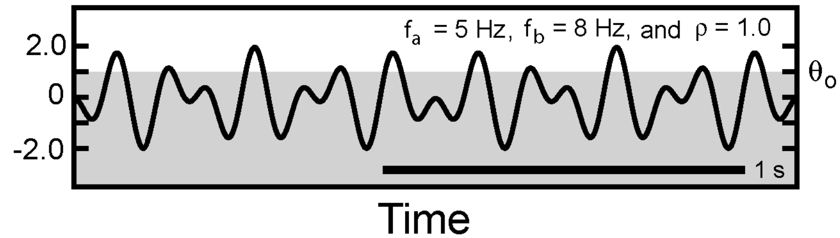




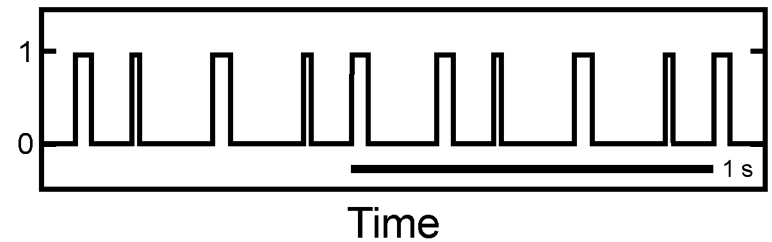
Ahrens, Levine, Suhl and Kleinfeld (2002) in press

Threshold Nonlinearity as a Model for Spectral Mixing of Sinusoidal Inputs

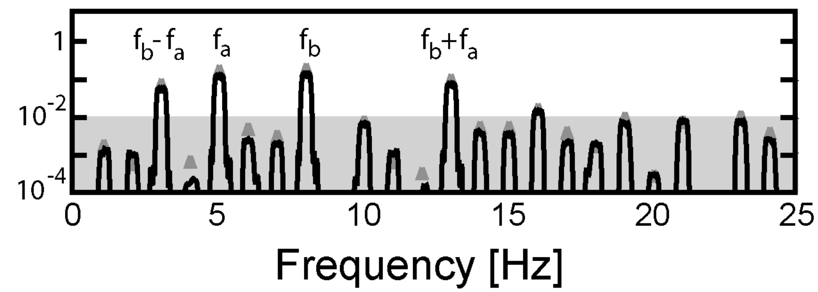
Input = $\cos(2\pi f_a t) + \rho \cos(2\pi f_b t)$



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



Spectral Power Density [Hz^{-1}]



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

Phase Term

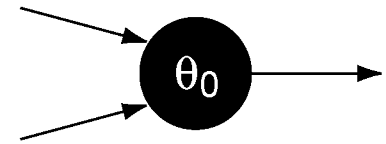
Amplitude Term

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

Ahrens, Levine, Suhl and Kleinfeld (2002)

Neural Hardware for Arithmetic with Frequencies

Mixing ← Threshold Units



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

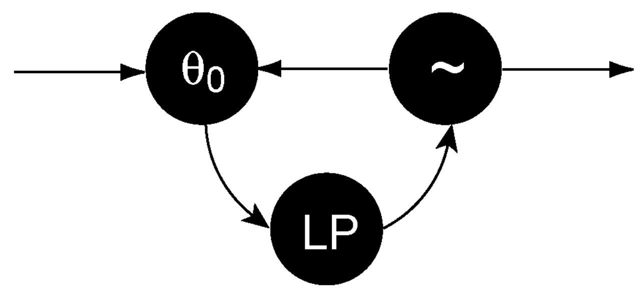
Output $= H\{\text{Input} - \Theta_o\} \propto \sum_{n=-\infty}^{\infty} \sum_{m=-\infty}^{\infty} e^{i[n(\psi_a + \pi/2) + m(\psi_b + \pi/2)]} \bullet e^{i 2\pi(nf_a + mf_b)t} \bullet I_{nm}(\theta_0)$

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

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

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

Phase Shifting ← Phase-Locked Loops



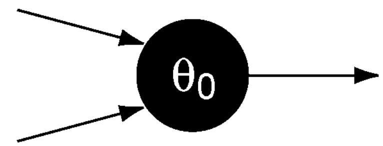
Input $= \cos(2\pi f_a t)$

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

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

Neural Hardware for Arithmetic with Frequencies

Mixing ← Threshold Units



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

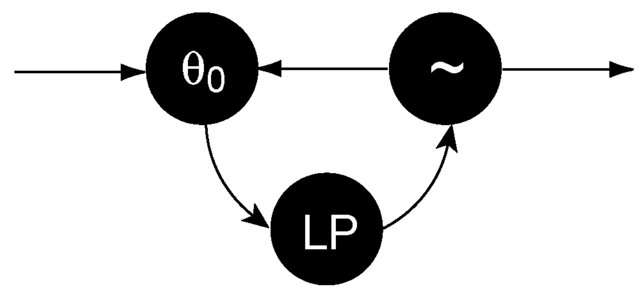
Output $= H\{\text{Input} - \Theta_0\} \propto \sum_{n=-\infty}^{\infty} \sum_{m=-\infty}^{\infty} e^{i[n(\psi_a + \pi/2) + m(\psi_b + \pi/2)]} \bullet e^{i 2\pi(n f_a + m f_b)t} \bullet I_{nm}(\theta_0)$

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

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

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

Phase Shifting ← Phase-Locked Loops



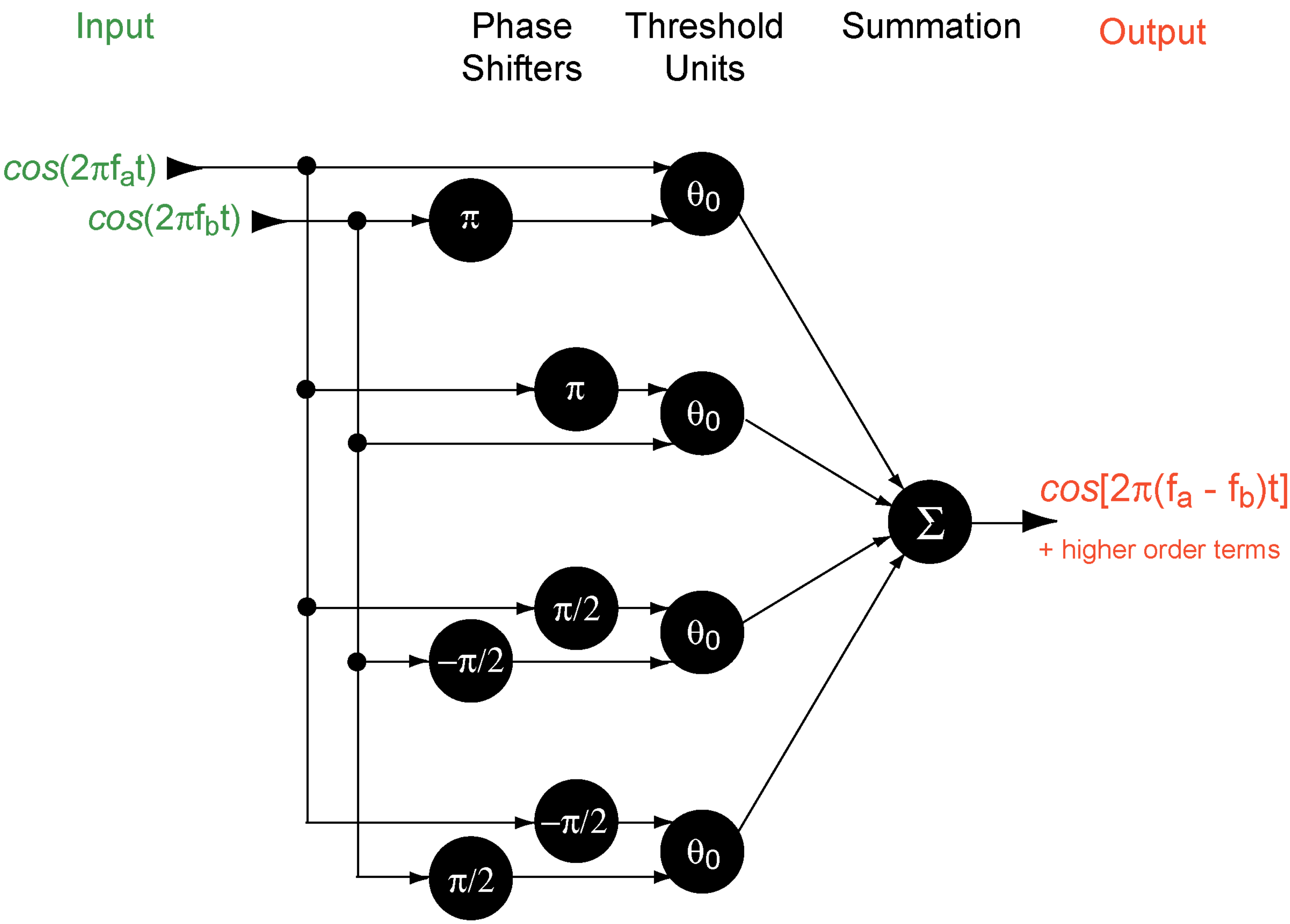
Input $= \cos(2\pi f_a t)$

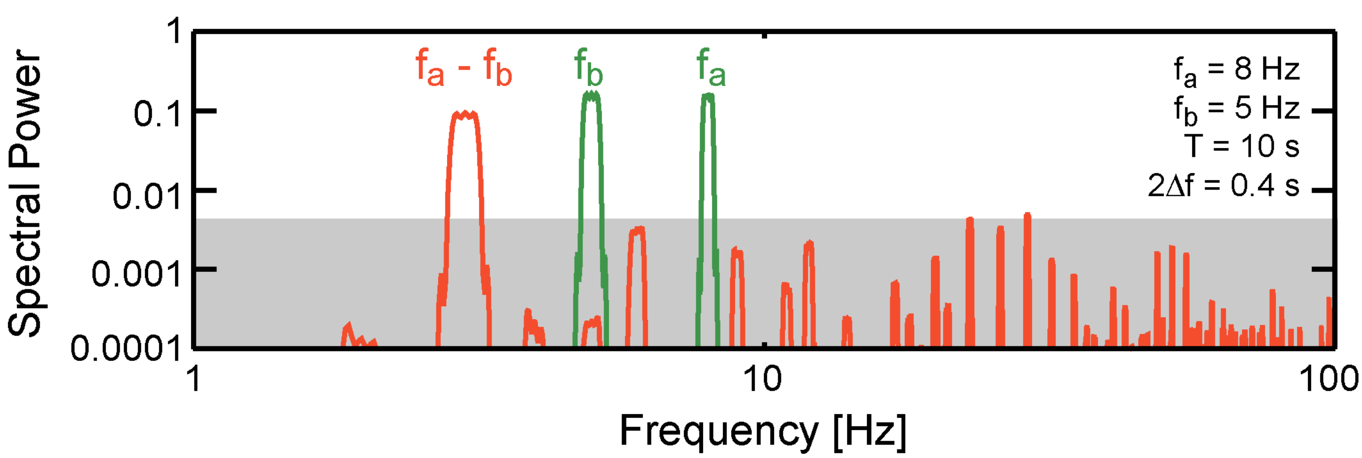
Output $= \cos(2\pi f_a t + \pi/2)$

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

Neural Hardware for Subtraction of Two Frequencies

(15 neurons, 23 synapses)





Coupled Oscillations in Nervous Systems

Theoretical Overview Based on the Work of Prof. Kuromoto

Experimental Evidence for Weak Coupling Between Neuronal Oscillators

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

Behavior of Pairs and Networks of Inhibitory Neurons
(Phase shifts consistent with minimalist models)

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

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

Linear and Rotating Waves in Epileptic Mammalian Cortical Slice
(Rotating part consistent with random connectivity)

Experimental Evidence for Spectral Mixing of Neuronal Oscillations

Conjecture on the Use of Oscillators for Arithmetic with Frequencies

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