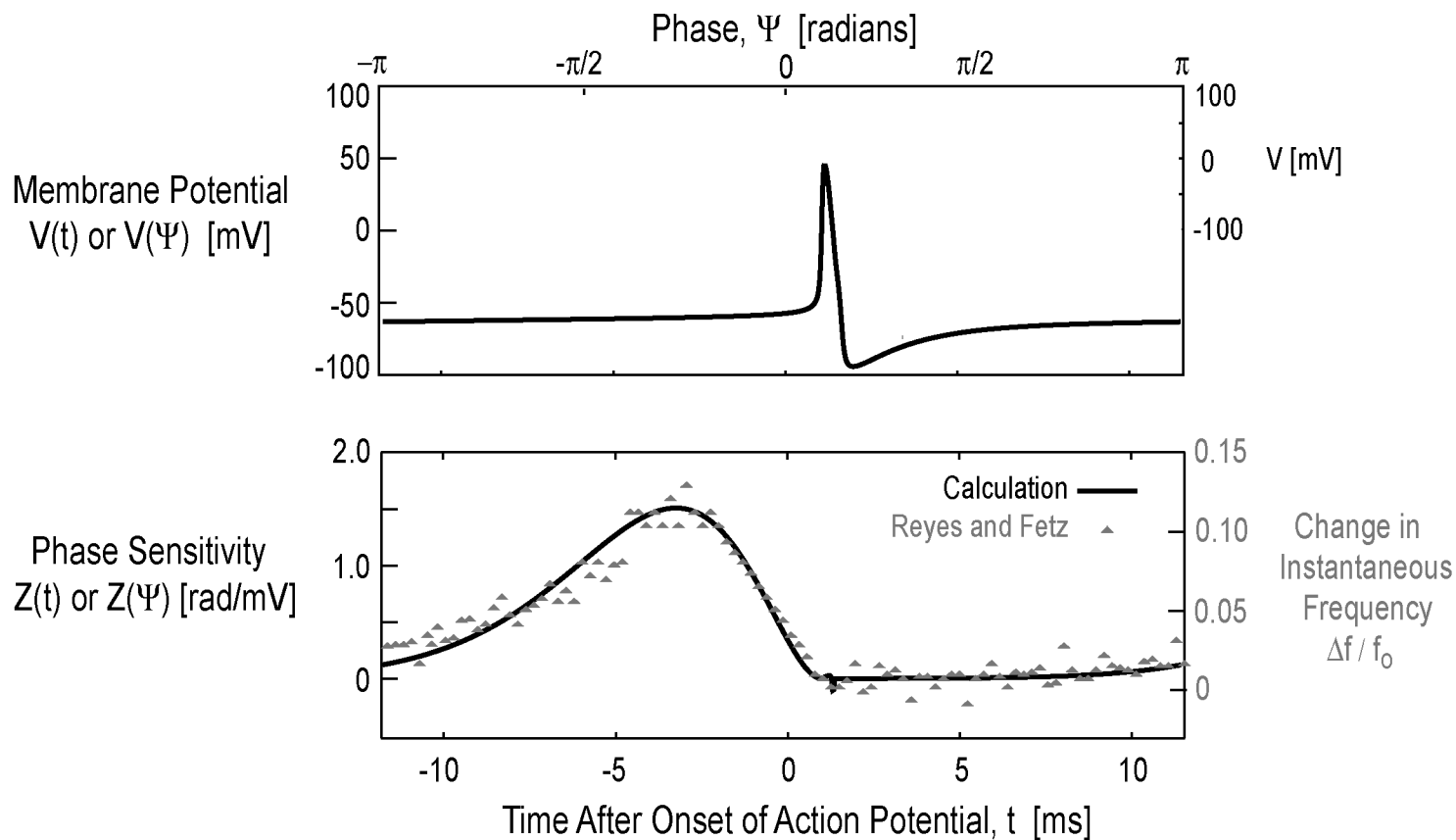
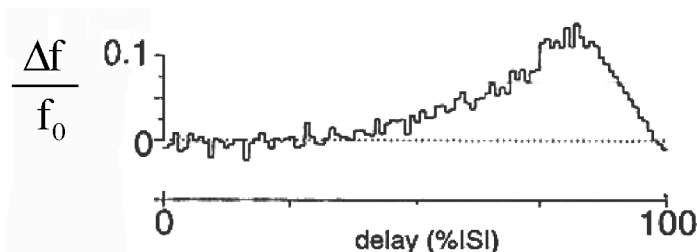
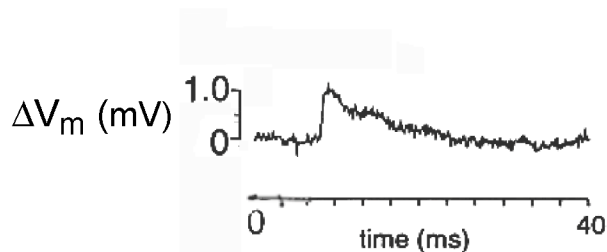
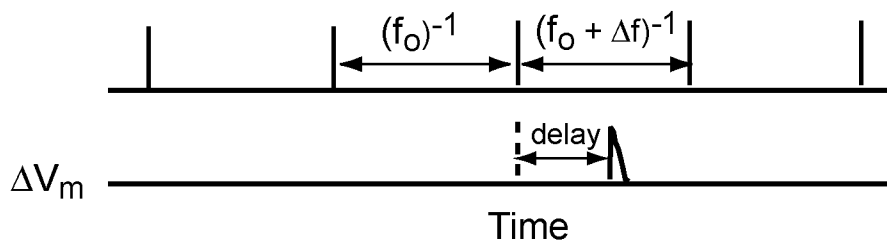


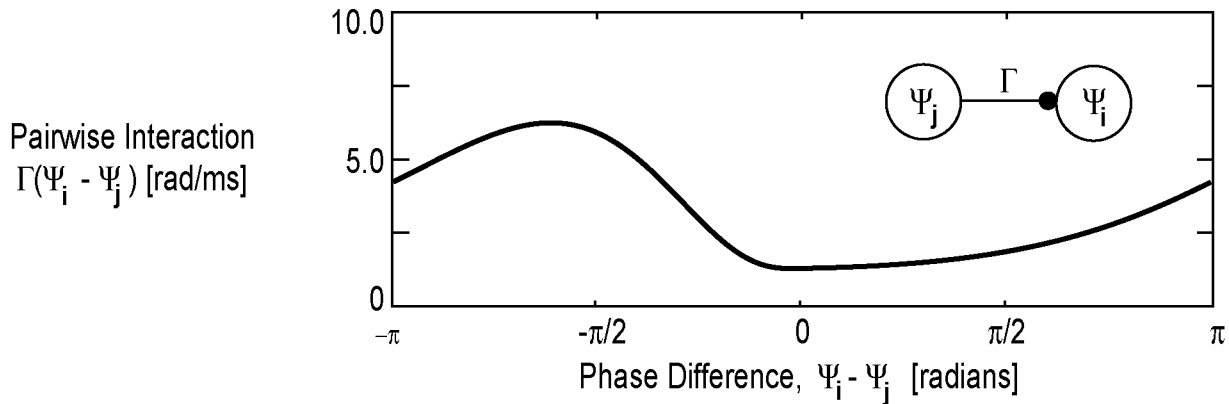
The Phase Sensitivity Function for Perturbation in Voltage Data (Reyes & Fetz 1993) vs. Calculation (Ermentrout & Kleinfeld 2000)

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



Lesson: Phase Sensitivity Concept Valid with Realistic PSPs

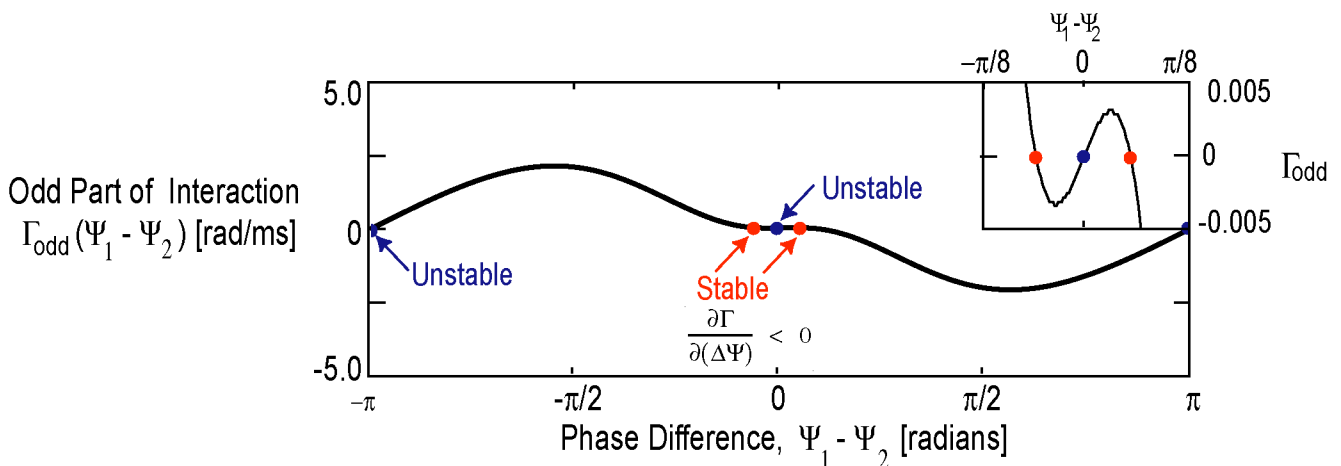
Nature of the Pairwise Interaction is Revealed by the Phase Shifts Between Two Reciprocally Connected Neurons



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

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

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



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

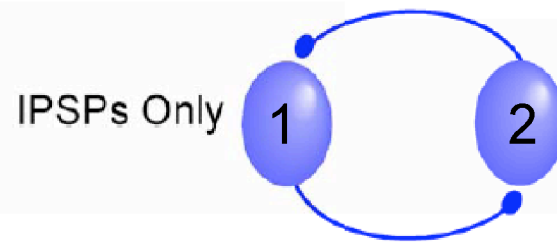
Challenge for Experimentalists is to Distinguish this from Broadening

Reciprocal, Kuromoto-like Inhibitory Coupling Among Pairs of Neurons

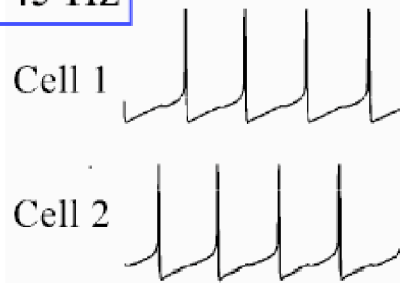
Firing Switches from Antisynchrony to Synchrony near 80 Hz

(data from Barry Connors Laboratory)

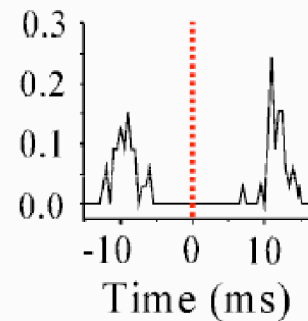
$$\Gamma(\Delta\psi) - \Gamma(-\Delta\psi) = g \frac{(\omega\tau)^2 - 1}{[1 + (\omega\tau)^2]^2} \sin(\Delta\psi) < 0 \text{ for } \omega > \tau^{-1}$$



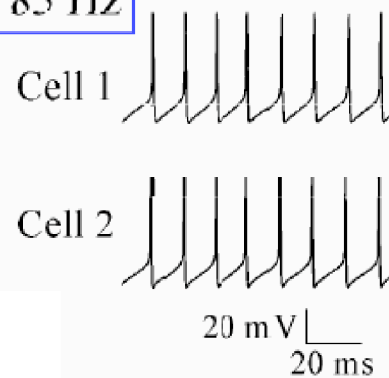
45 Hz



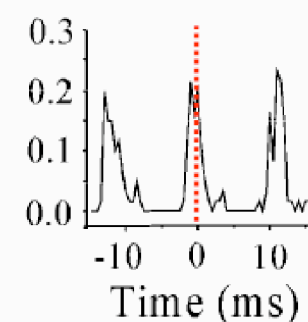
Cross-correlation



85 Hz



Cross-correlation

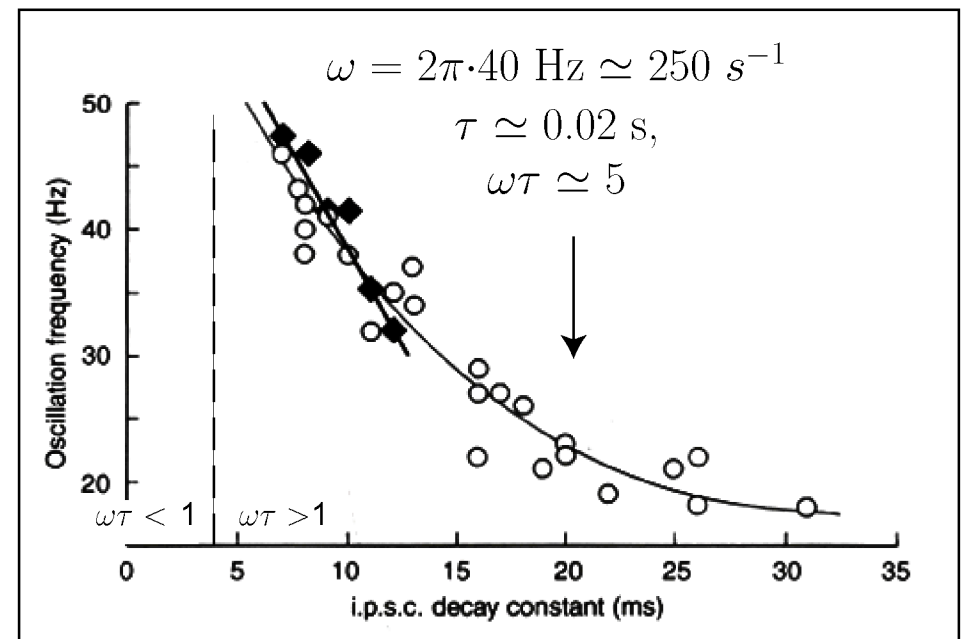
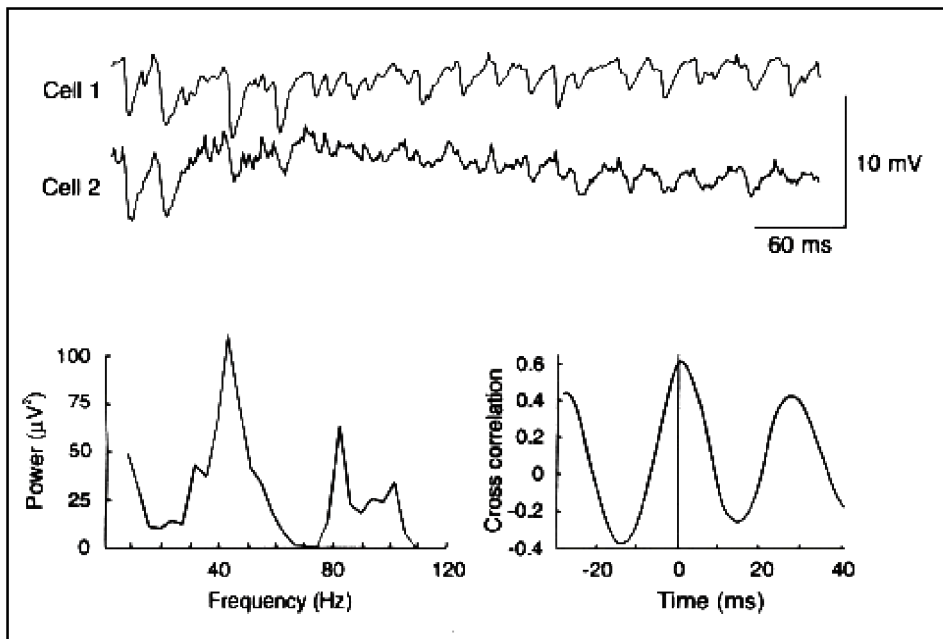
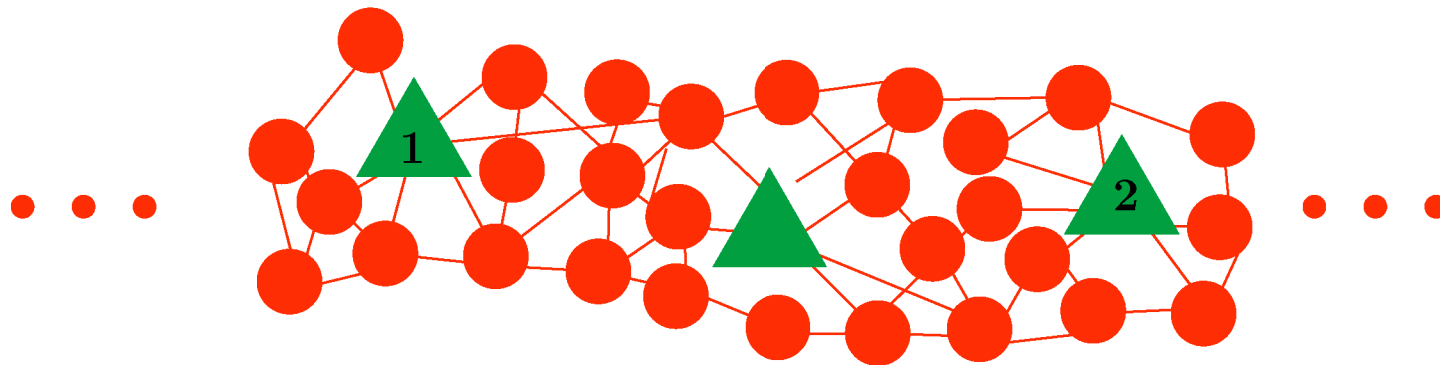


Reciprocal, Kuromoto-like Inhibitory Coupling in a Network of Neurons

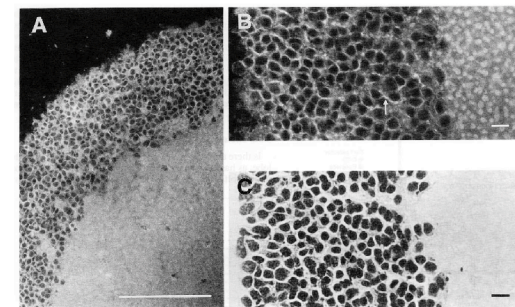
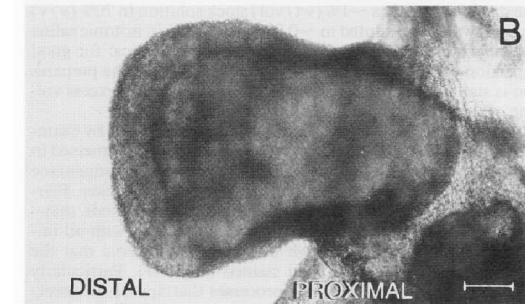
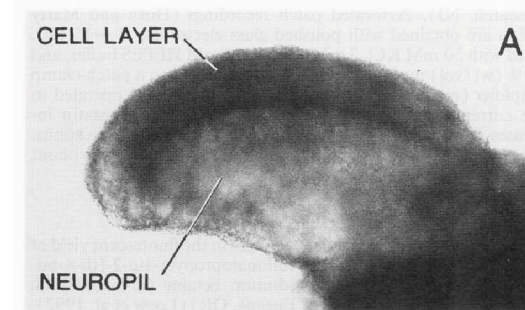
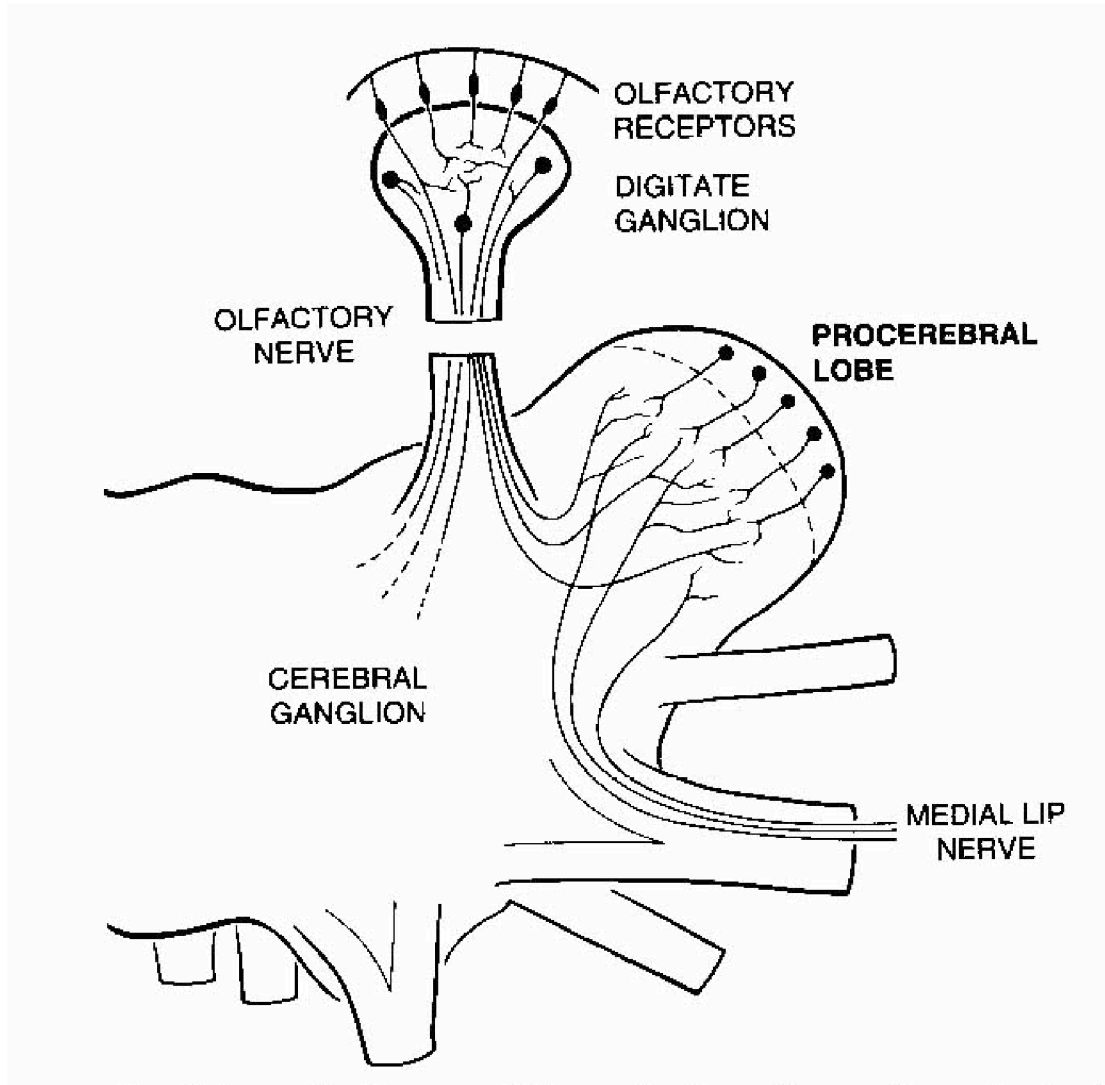
Synchronized Oscillations in an All Inhibitory ($g < 0$) Interneuron Network

(Whittington, Traub and Jeffreys 1995)

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

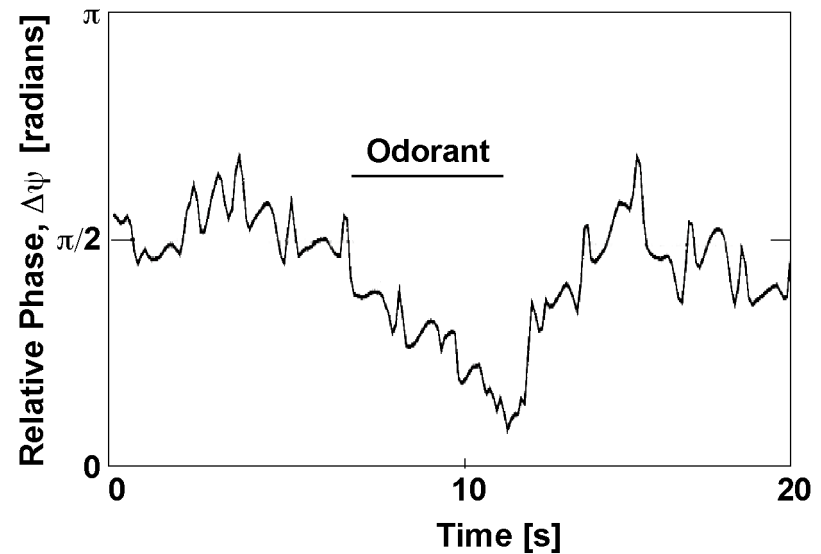
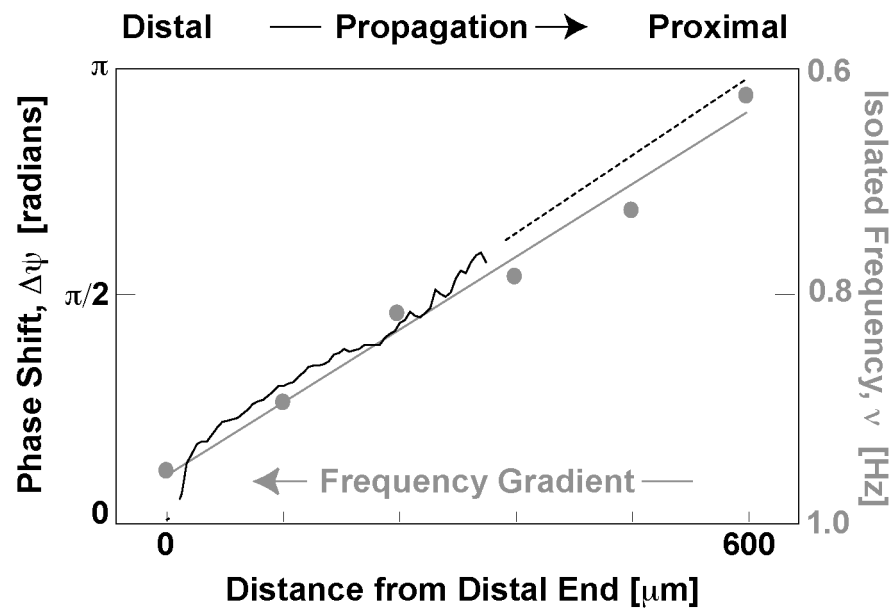
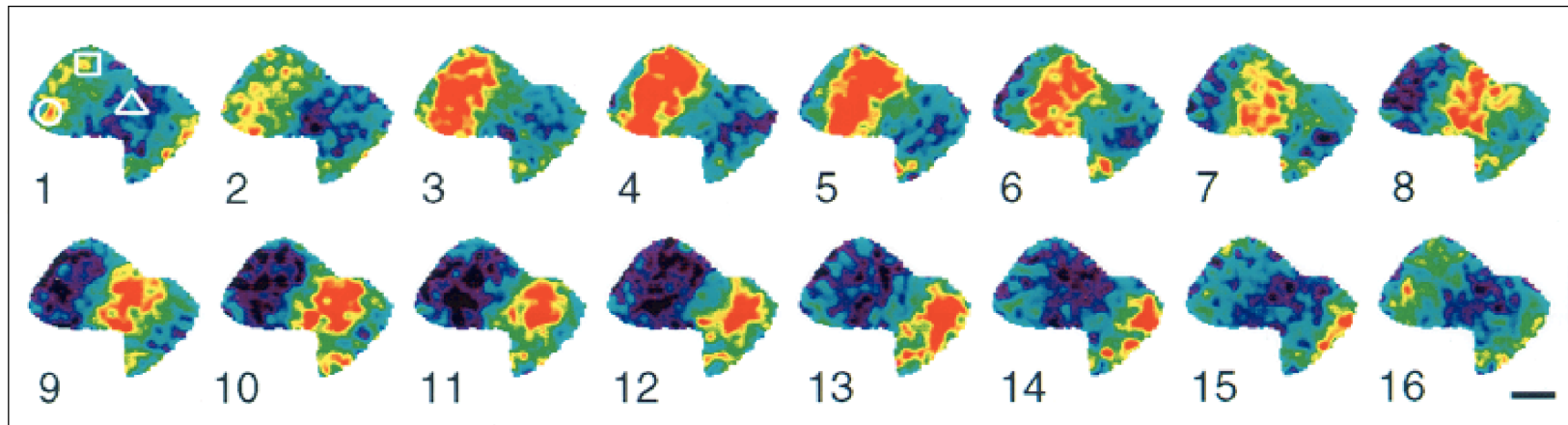


Central Olfactory Organ in the Terrestrial Mollusk *Limax*



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

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

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 $\delta\omega \propto x$

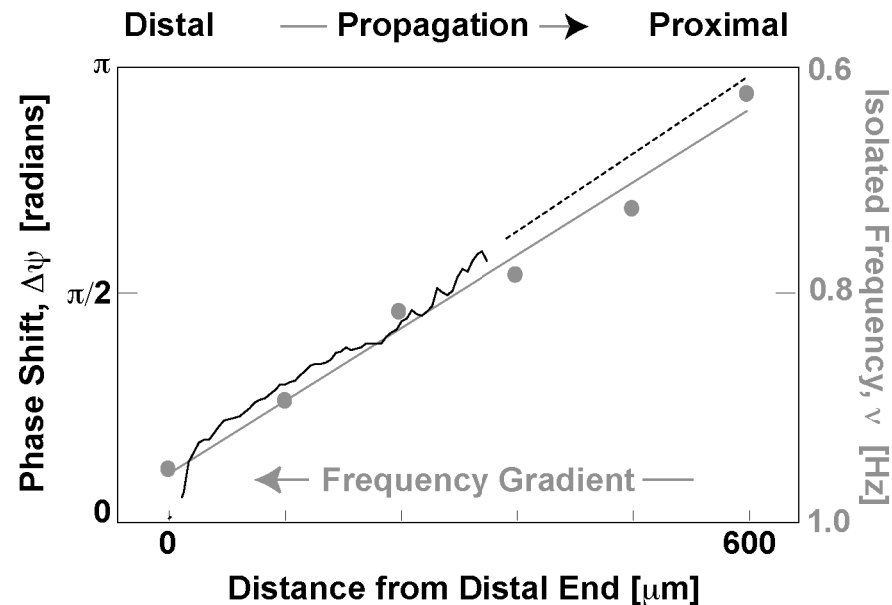
$$\frac{d\psi_x}{dt} = (\omega + \delta\omega_x) + \sum_{x \neq x'} \Gamma(\psi_x - \psi_{x'})$$

$\delta\omega_x \propto x$

Single frequency

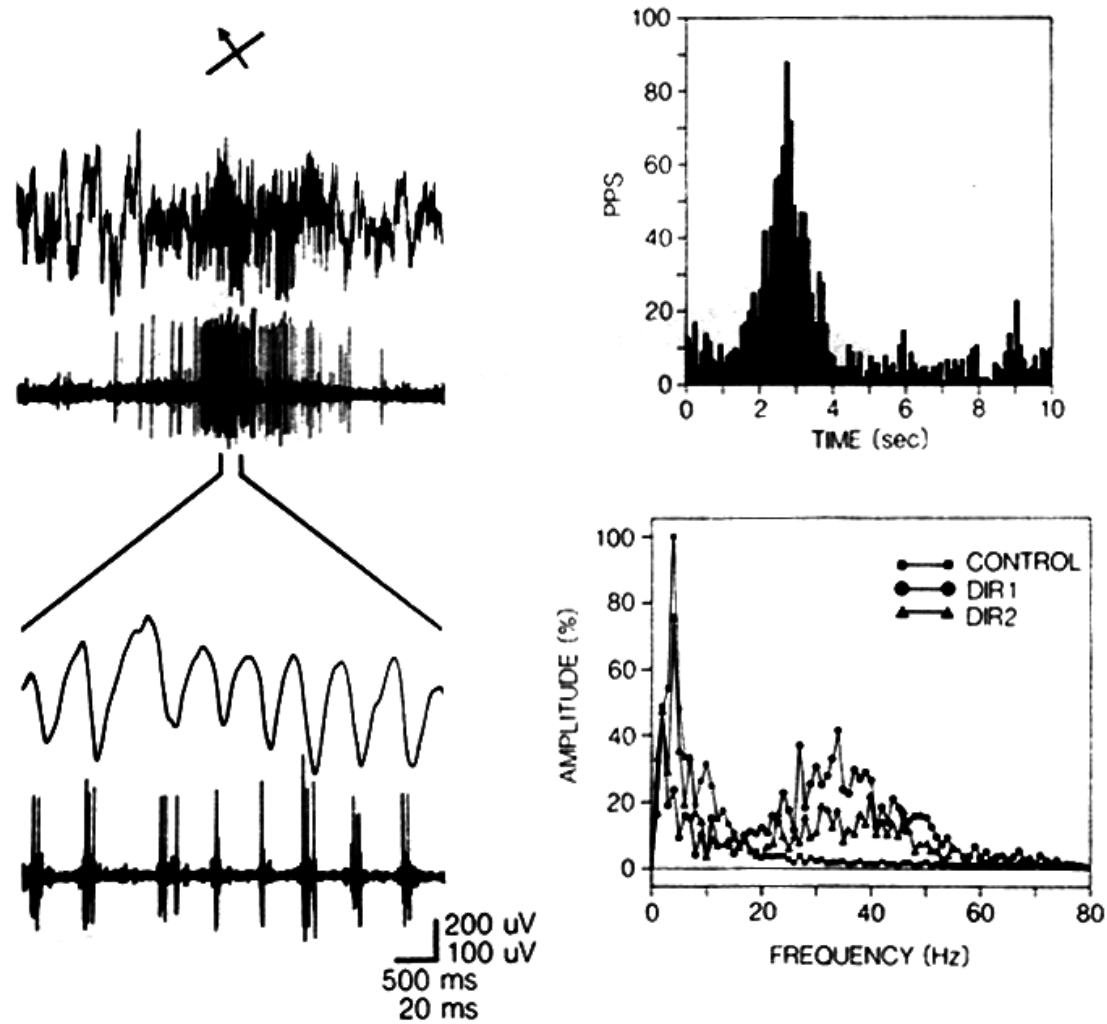
When the network locks:

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



Phase-locking to link features across visual space

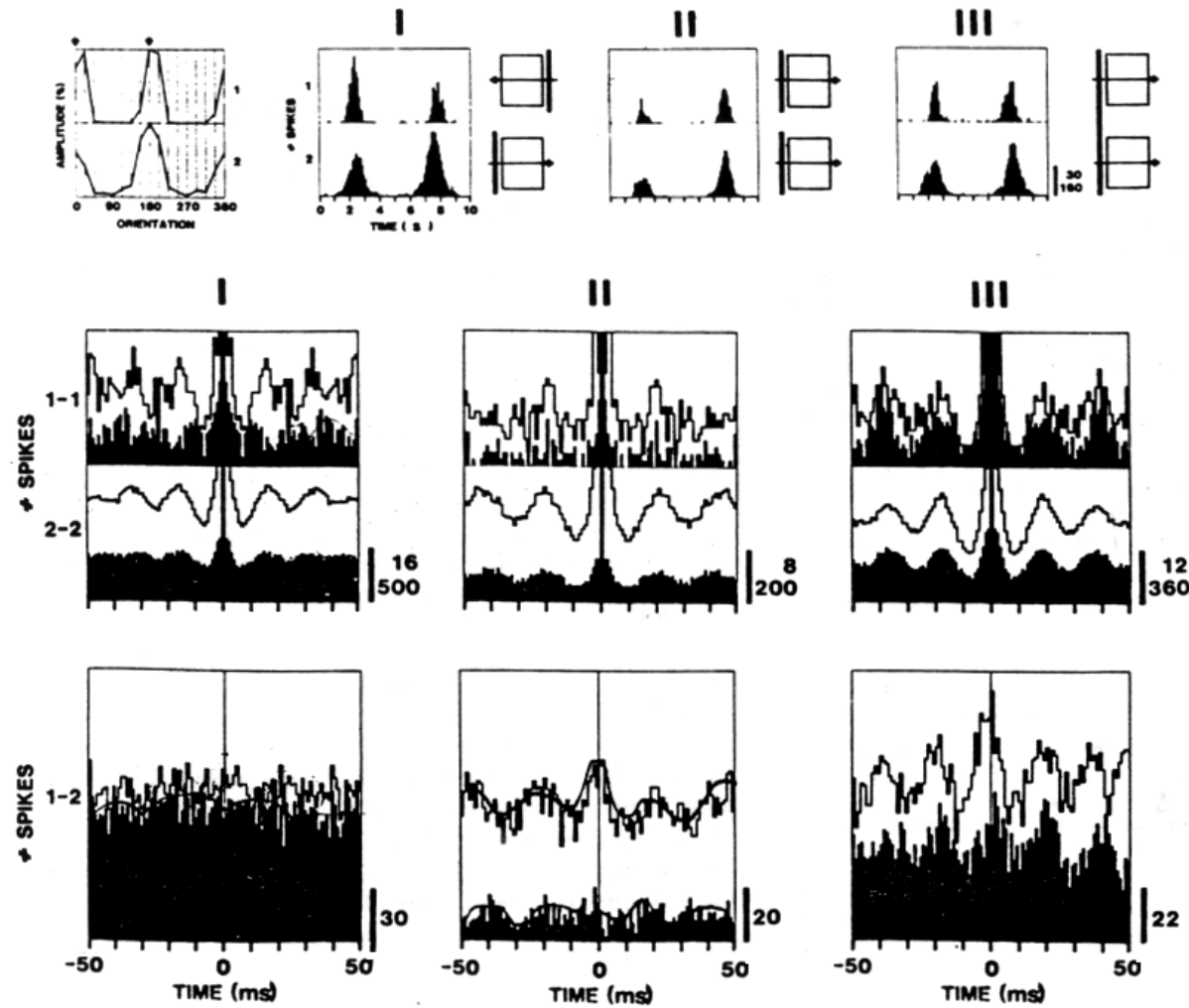
The binding hypothesis - still controversial!



Gray & Singer (PNAS 1989)

Phase-locking to link features across visual space

The binding hypothesis - still controversial!



Gray, König, Engel & Singer (Nature 1990)

Phase-locking to link features across visual space

Analysis: Phase interactions code features, i.e., relative orientation of bars

