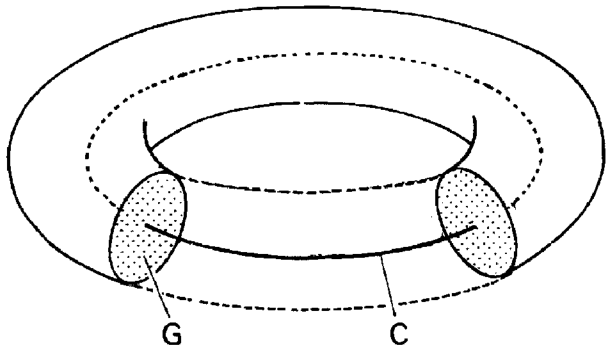
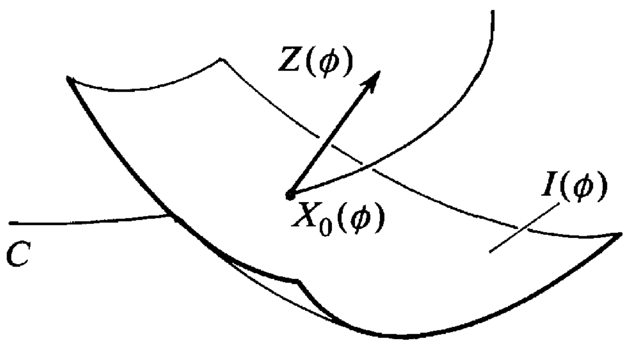
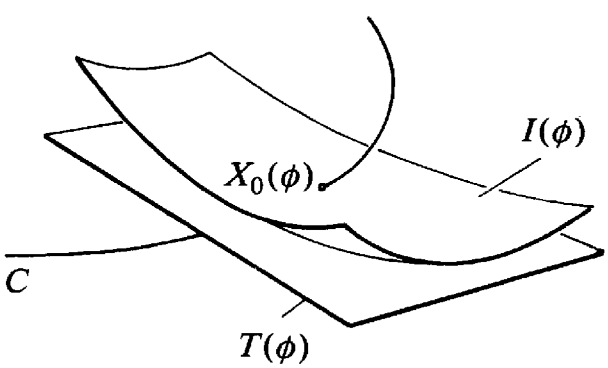


Limit cycle orbit enclosed in a thin tube



Geometrical meaning of $Z(\phi)$



$(n-1)$-dimensional hyperplane $T(\phi)$ tangent to the isochron $I(\phi)$ at point $X_0(\phi)$ lying on the limit cycle orbit C

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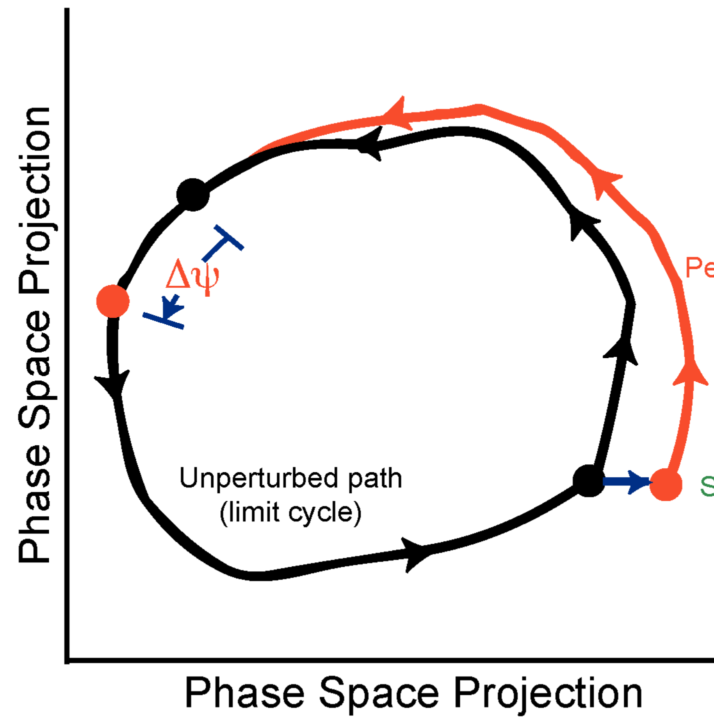
Transformation of a Dynamic System (N-dim) into a "Phase" System (1-dim)

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

Perturbation → Phase Shift ($\Delta\psi$)



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

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

Perturbation: $\mathbf{P}$

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

The Phase Sensitivity Function

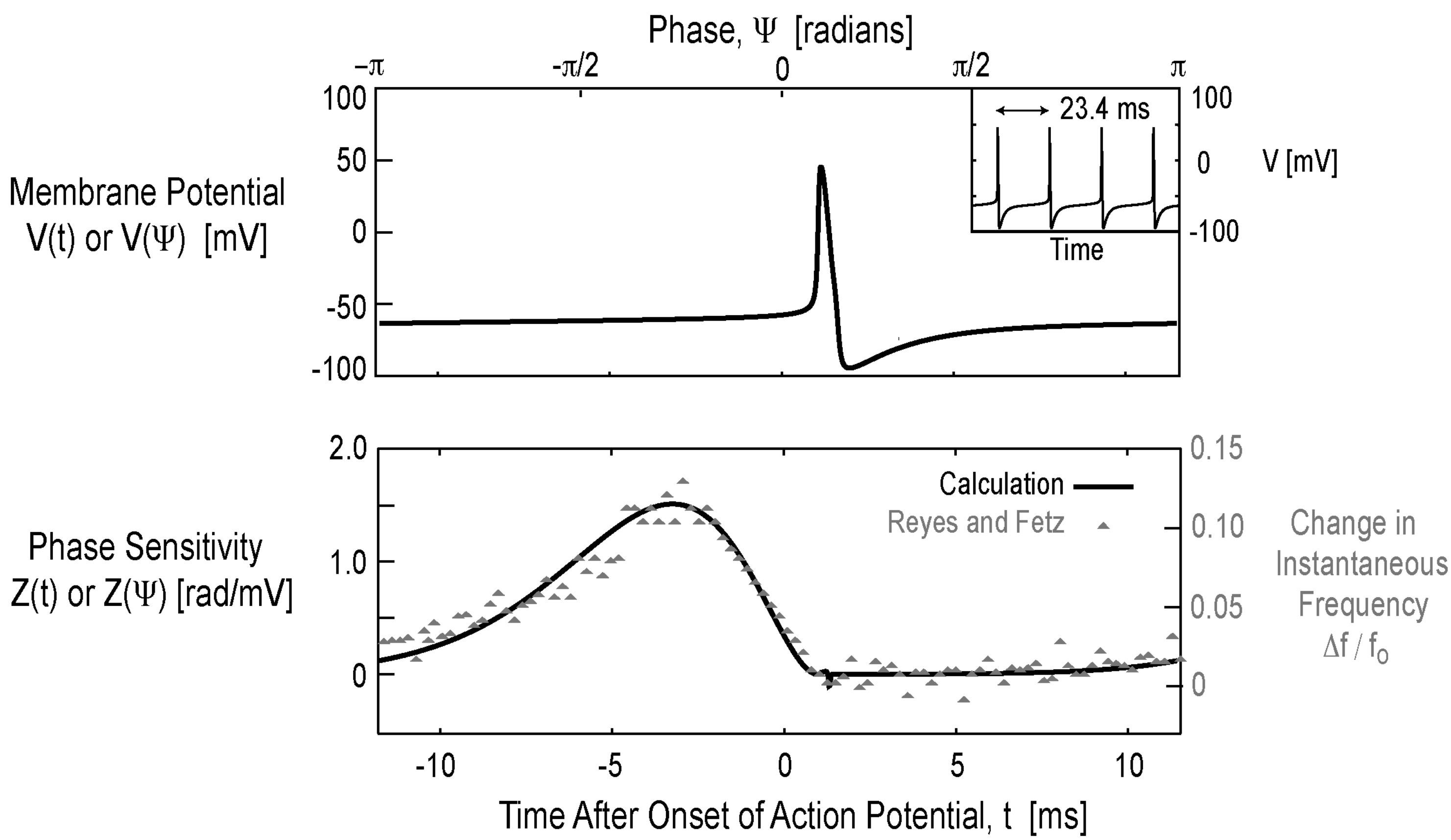
Calculation (Ermentrout & Kleinfeld 2000) vs. Experimental Data (Reyes & Fetz 1993)

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

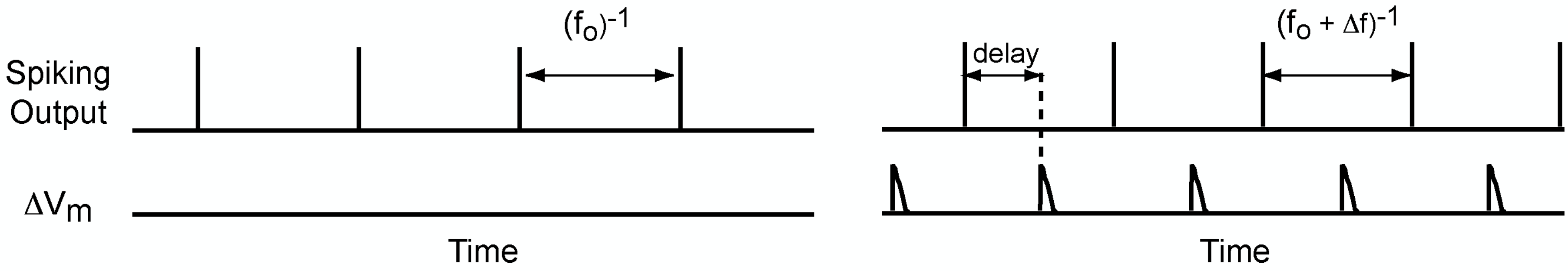
Phase reduction: $\frac{\partial \Psi_i}{\partial t} = \omega + \Gamma\left(\Psi_i - \Psi_j\right)$

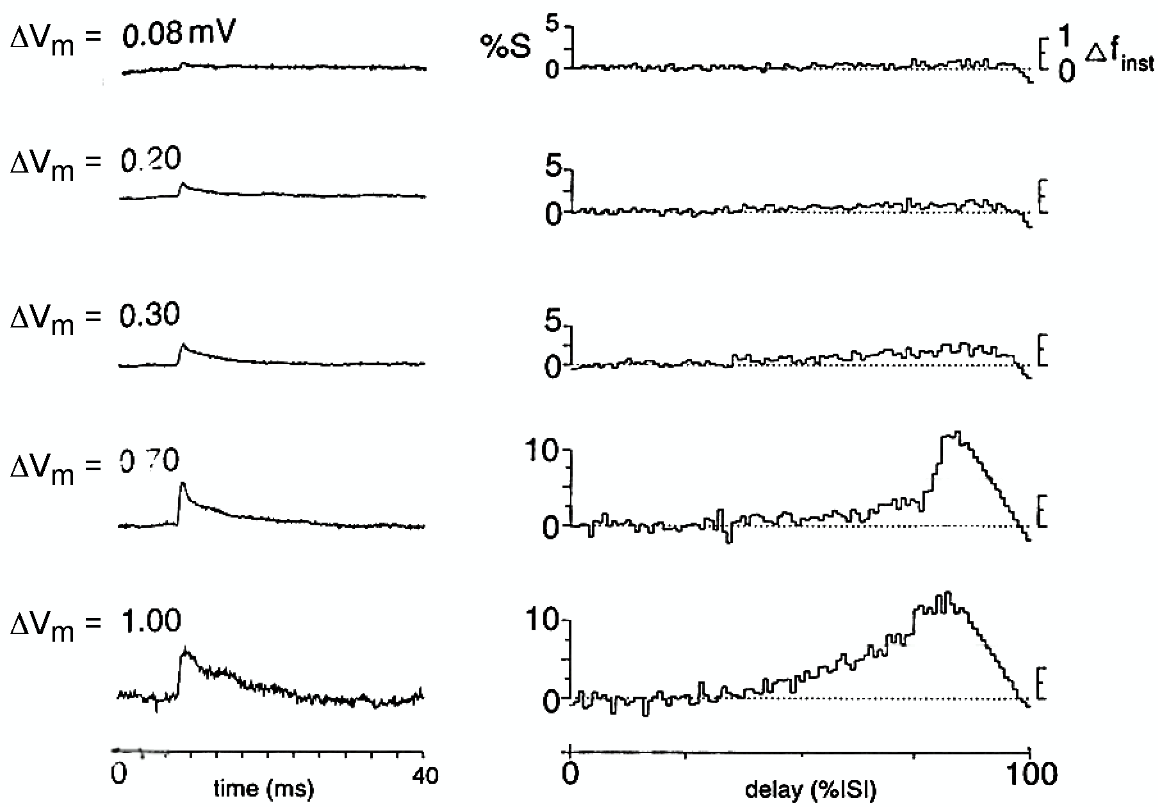
$$\frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta\ \mathbf{Z}\left(\Psi_i - \theta\right) \bullet \mathbf{P}\left(\Psi_i - \theta;\ \Psi_j - \theta\right)$$

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)





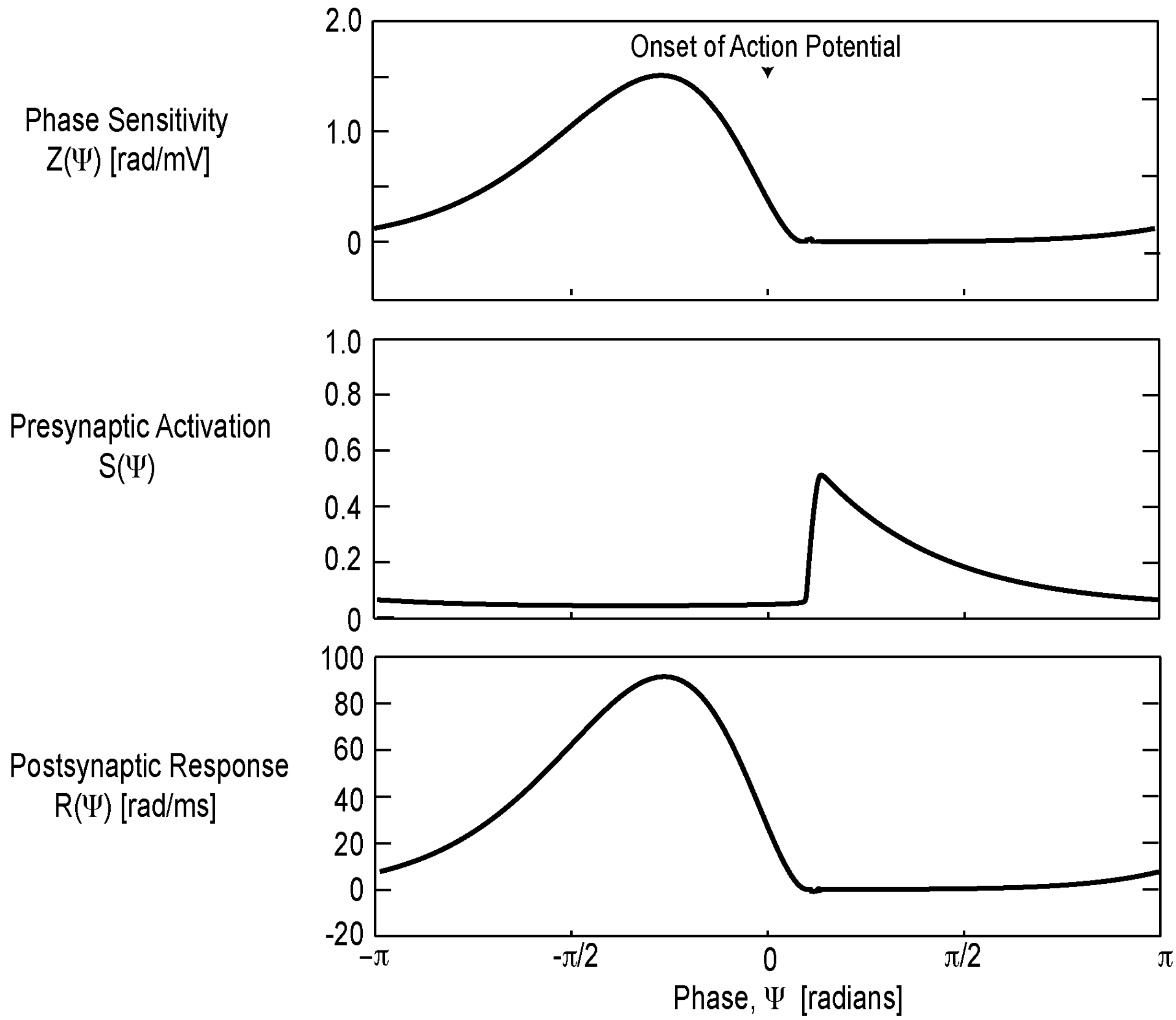
Pairwise Interaction between Neuronal Oscillators, $\Gamma(\psi_i - \psi_j)$ is the Correlation of Presynaptic Activation with Postsynaptic Response

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

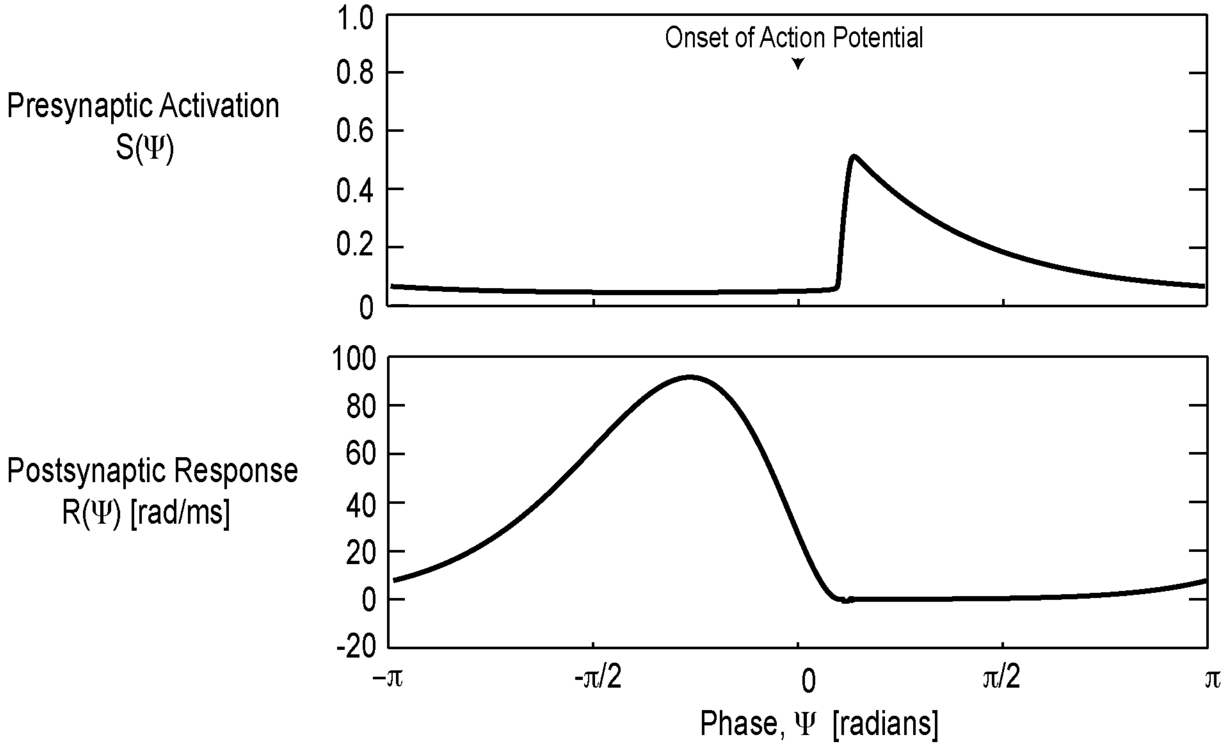
$$\mathbf{P}\left(\Psi_i + \theta;\; \Psi_j + \theta\right) = \frac{g_{\text{synapse}}}{C_m} \; \mathbf{S}\left(\Psi_j + \theta\right)\left[E_{synapse} - \mathbf{V}\left(\Psi_i + \theta\right)\right]$$

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

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



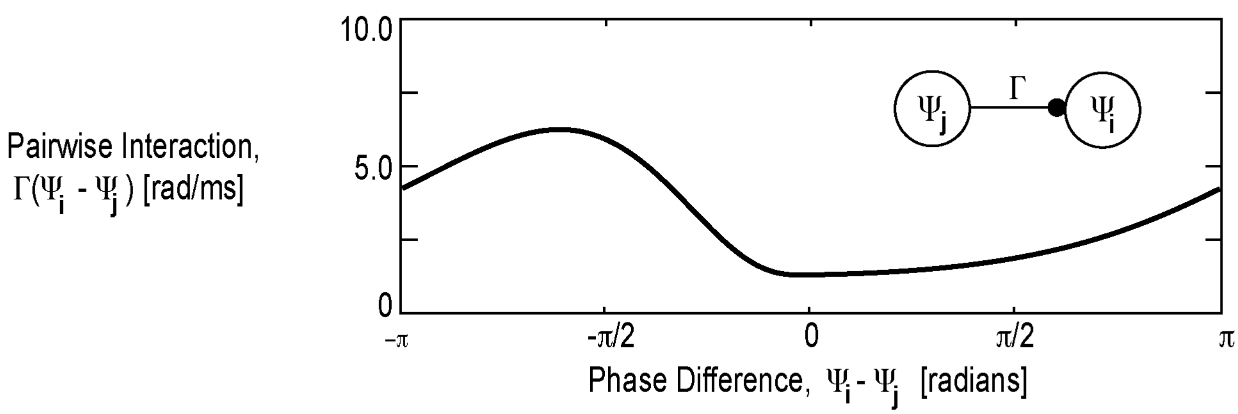
Pairwise Interaction between Neuronal Oscillators, $\Gamma(\psi_i - \psi_j)$ is the Correlation of Presynaptic Activation with Postsynaptic Response



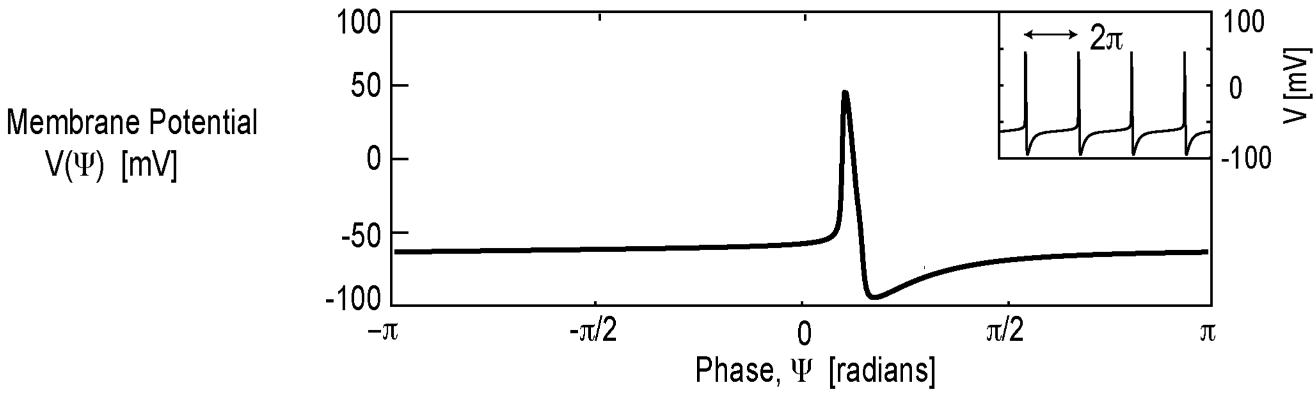
$$\Gamma\left(\Psi_i - \Psi_j\right) = \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{R}\left(\Psi_i + \theta\right) \; \mathbf{S}\left(\Psi_j + \theta\right)$$

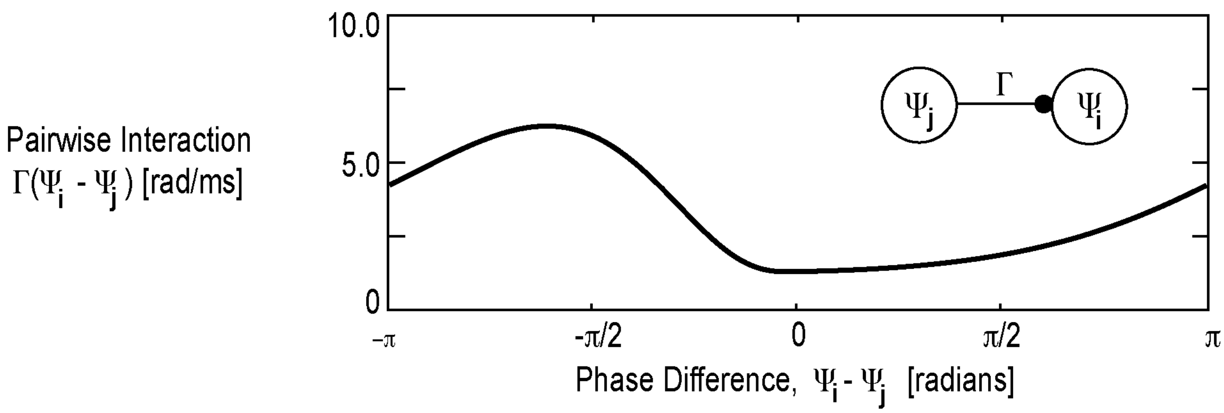
$$= \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{R}(\theta) \; \mathbf{S}\left[\theta - \left(\Psi_i - \Psi_j\right)\right]$$

Phase difference



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

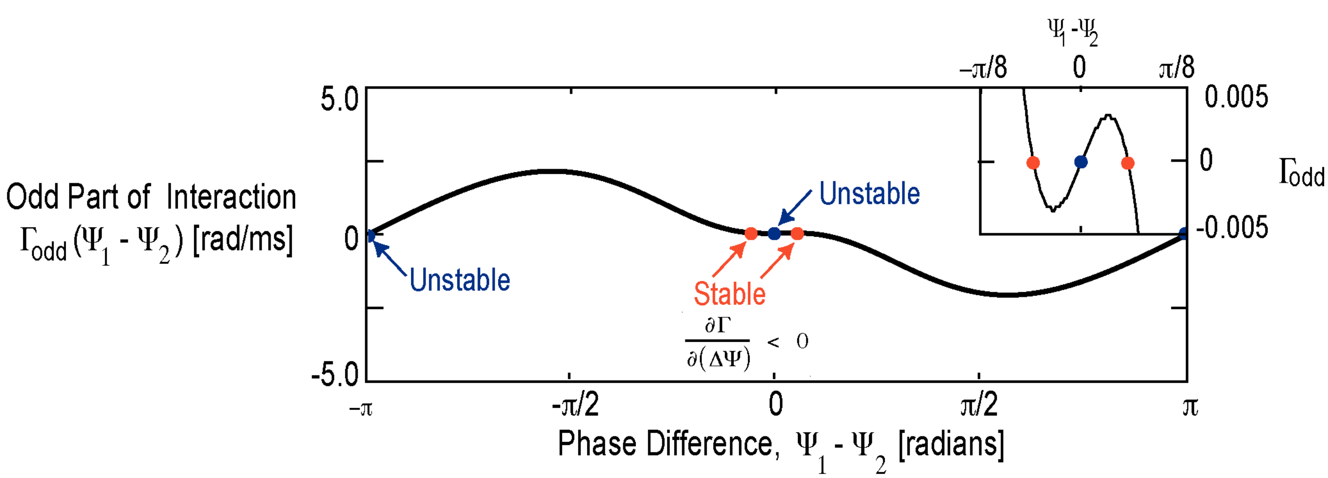




$$\frac{\partial \Psi_i}{\partial t} = \omega + \Gamma\left(\Psi_i - \Psi_j\right)$$

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

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



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 $\Delta\psi \equiv \psi - \psi'$

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

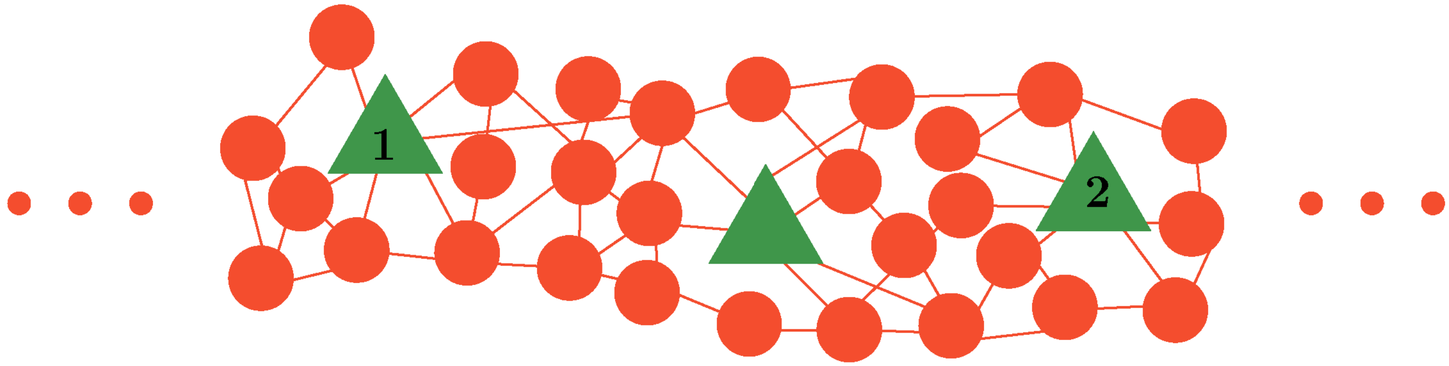
Stability (with our sign convention) requires $\frac{\partial\,[\Gamma(\Delta\psi) - \Gamma(\text{-}\Delta\psi)]}{\Delta\psi} < 0$

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

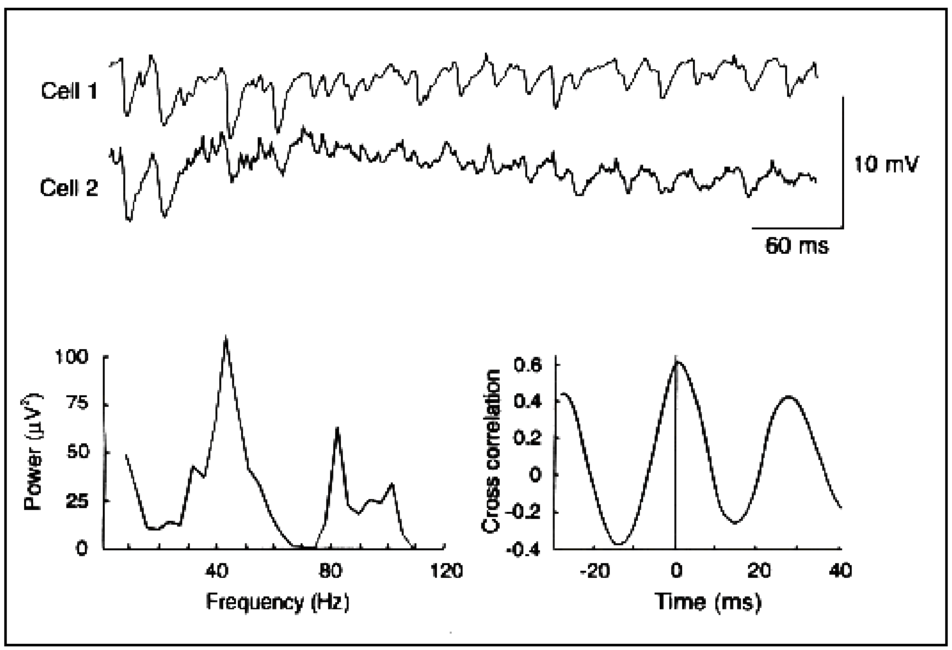
Synchronous, all inhibitory networks are observed!

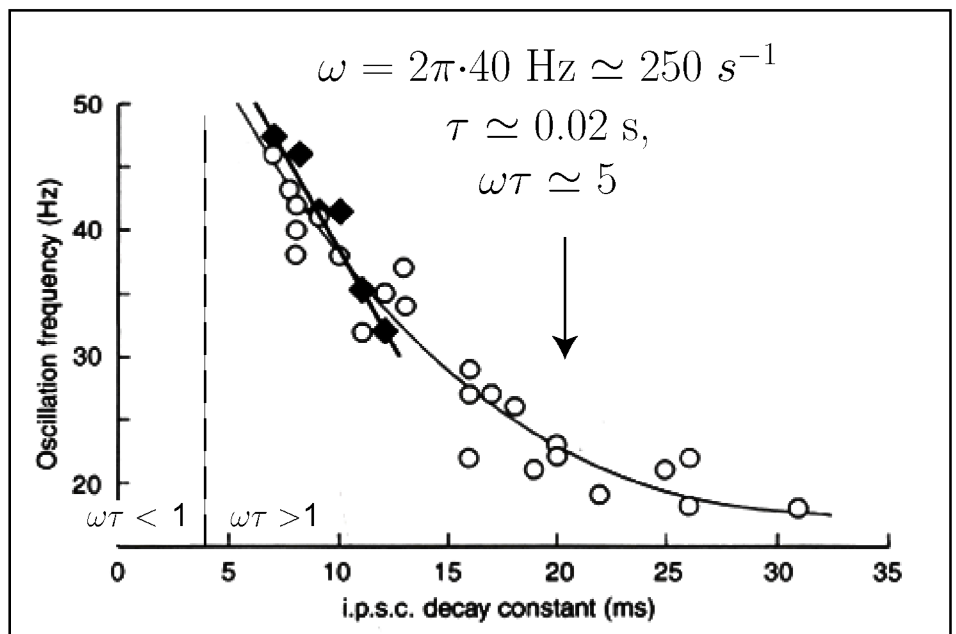
Synchronized Oscillations in Interneuron (all inhibitory) Networks

(Whittington, Traub and Jeffreys 1995)

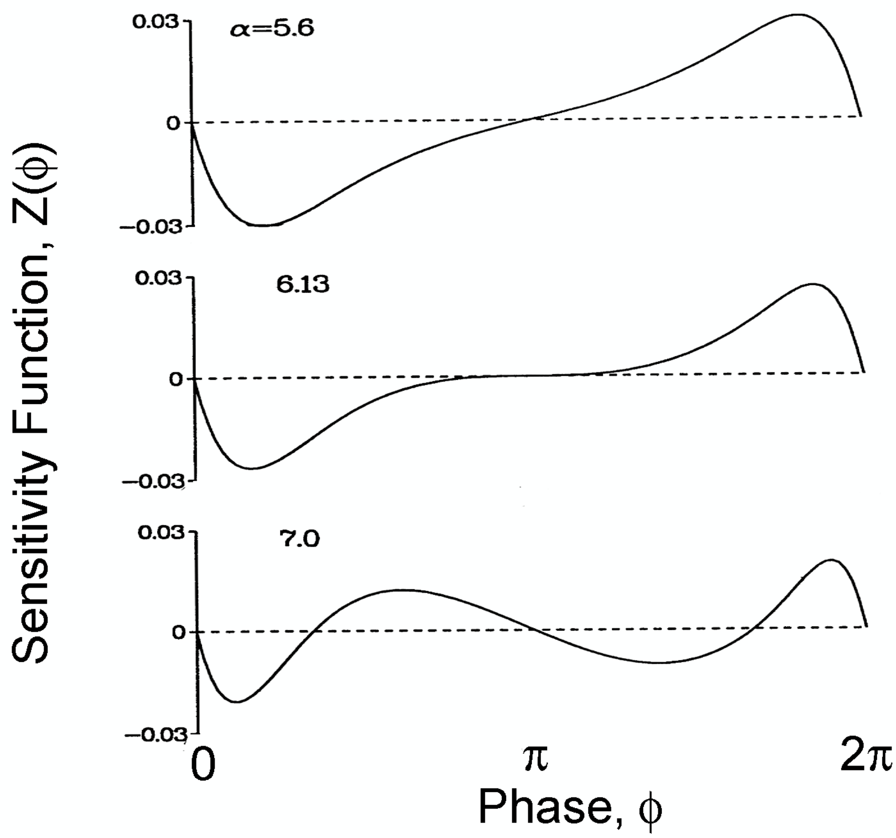


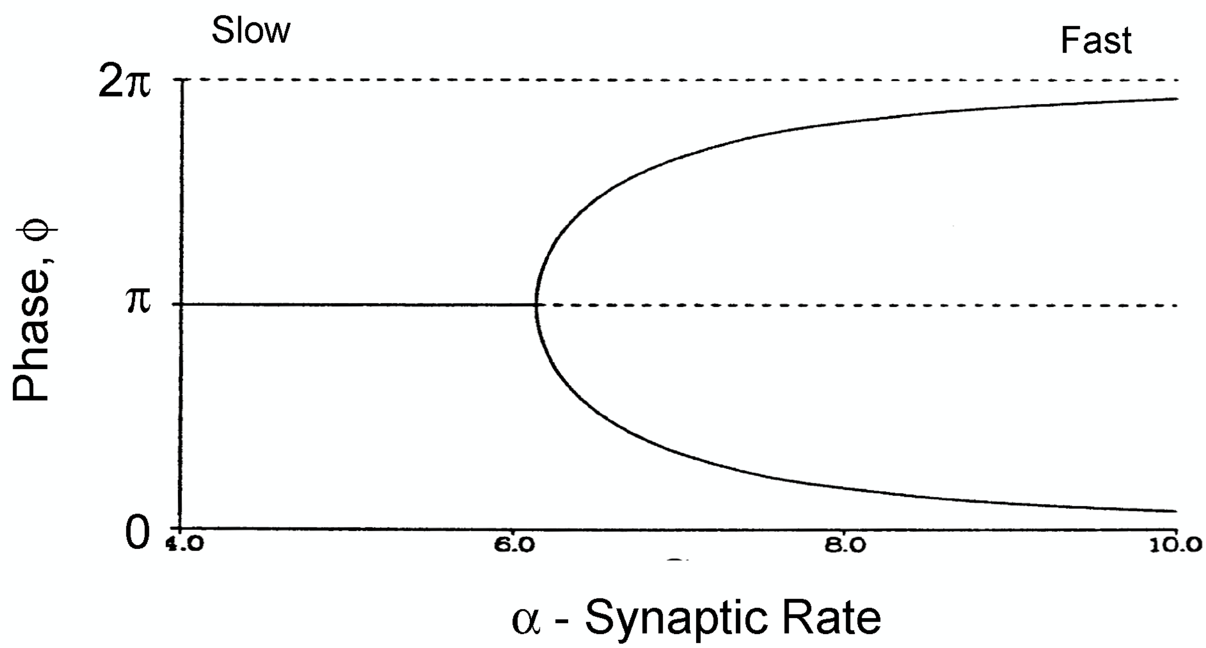
$$\Gamma(\Delta\psi) - \Gamma(\text{-}\Delta\psi) \;=\; g\,\frac{(\omega\tau)^2 - 1}{[1 + (\omega\tau)^2]^2}\,\sin(\Delta\psi)$$





Excitatory $t\,e^{-\alpha t}$ Coupling btwn Integrate & Fire Neurons





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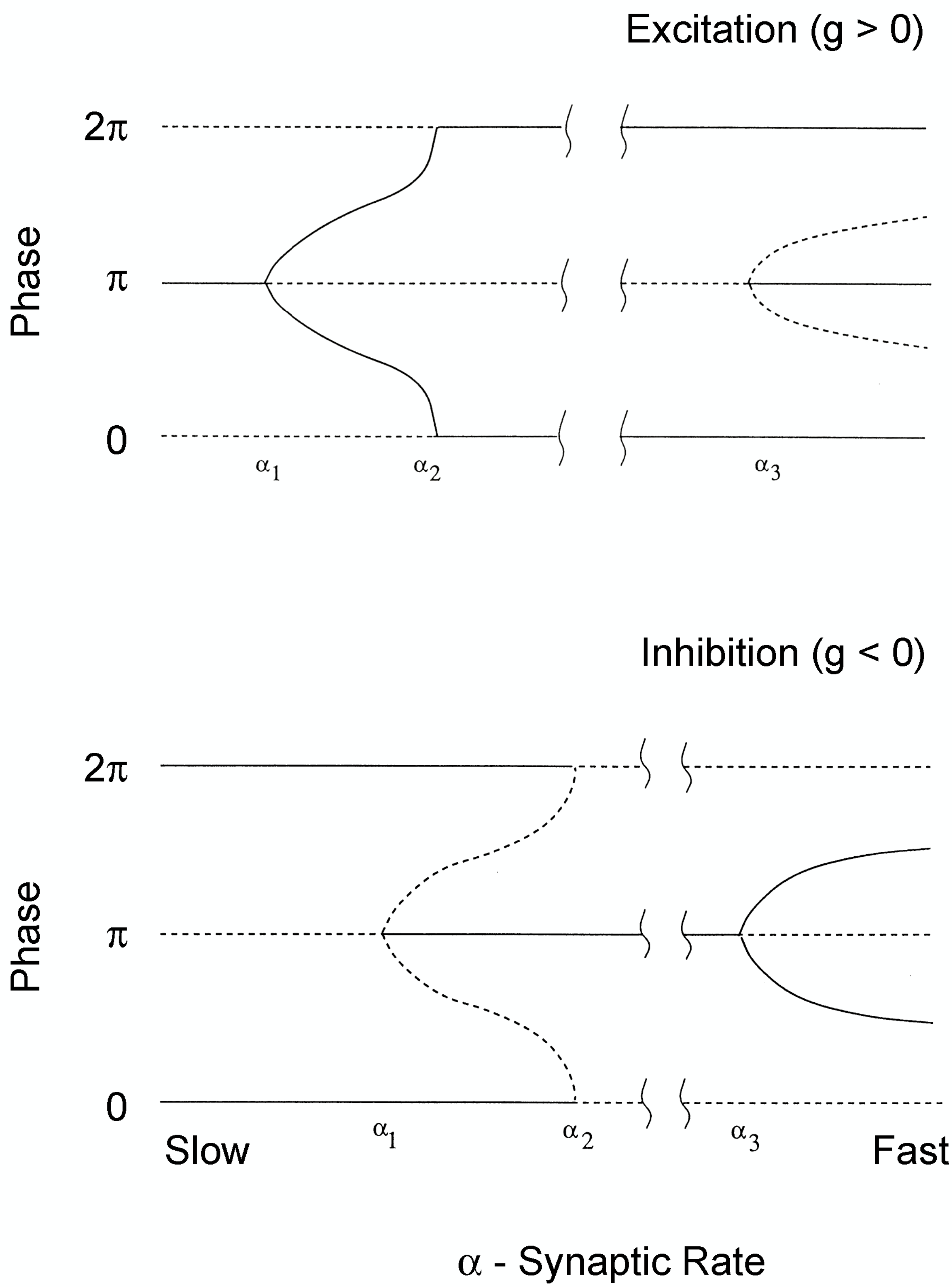
$t\,e^{-\alpha t}$ Coupling between Hodgken-Huxley Neurons



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Coupling of Two Oscillators with Different Intrinsic Frequencies

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

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

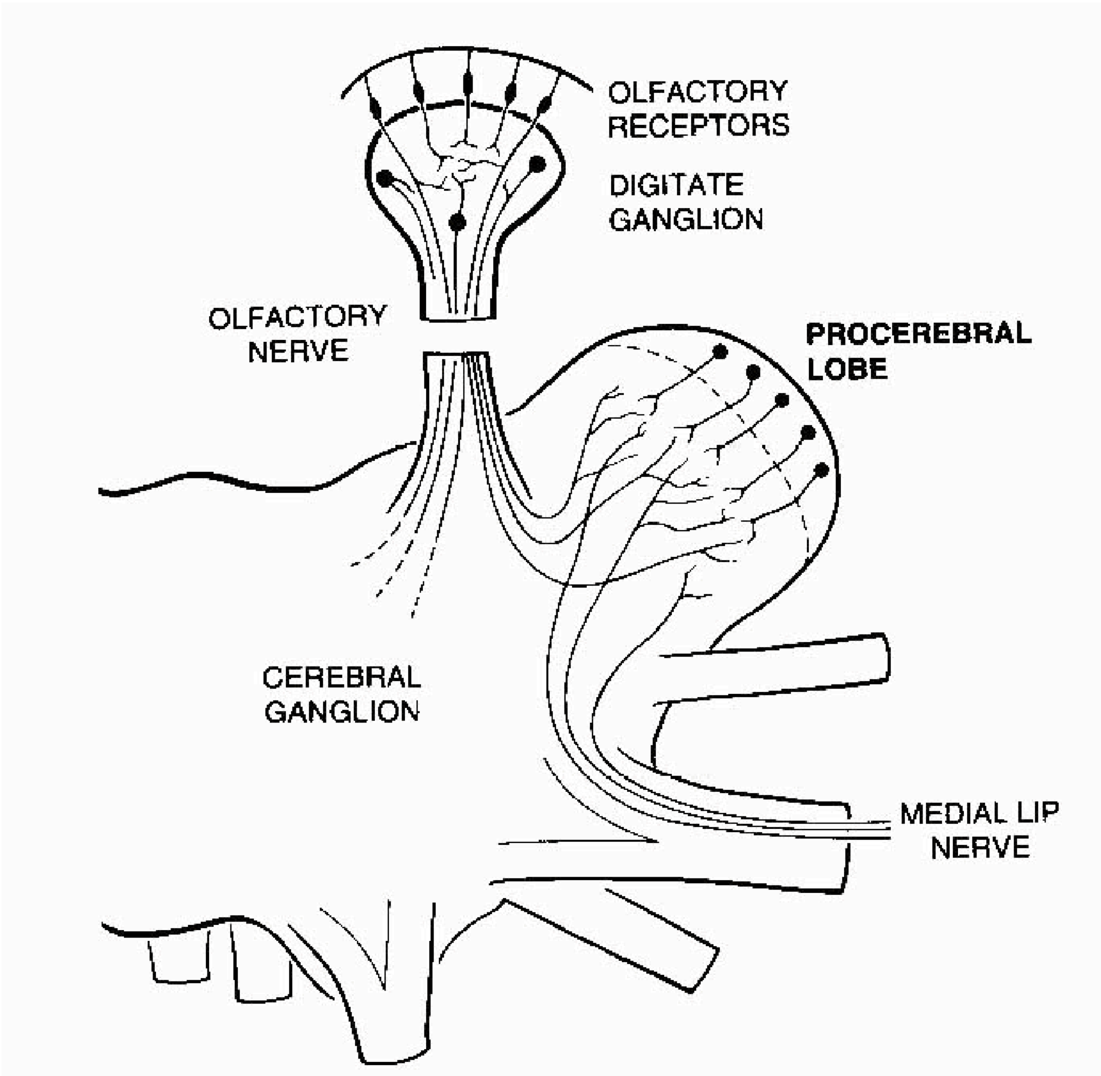
Lock, i.e., $\frac{d\psi}{dt} = \frac{d\psi'}{dt}$ so long as $\Gamma_0 \sin(\psi' - \psi) - \Gamma_0 \sin(\psi - \psi') = \omega - \omega'$

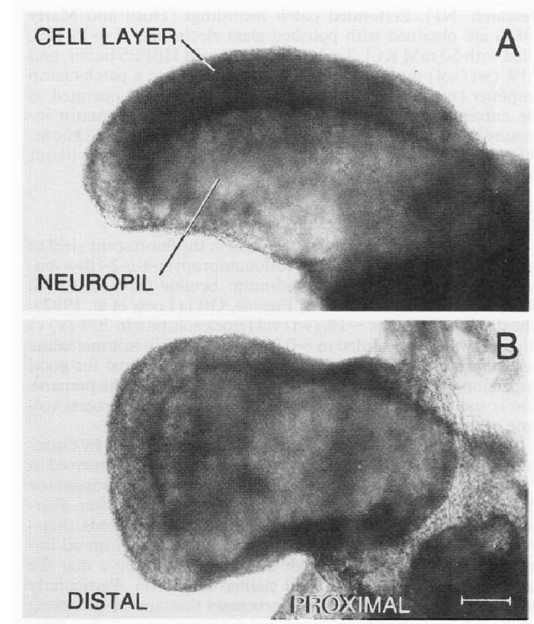
or

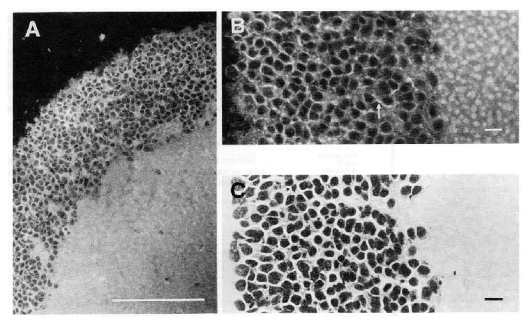
$$\frac{2\Gamma_0}{|\omega' - \omega|} > 1$$

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

Central Olfactory Organ in the Terrestrial Mollusk Limax

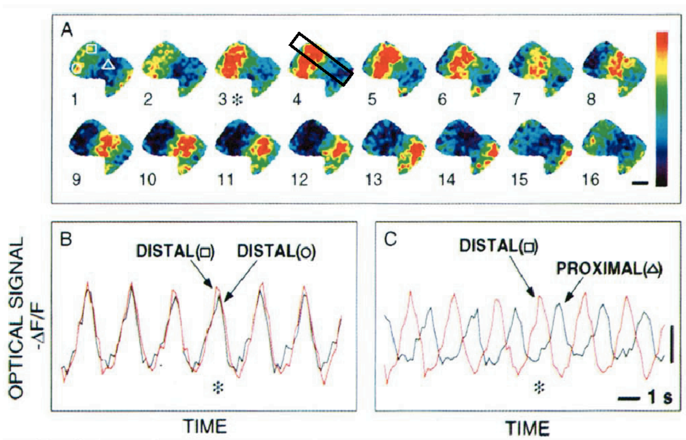


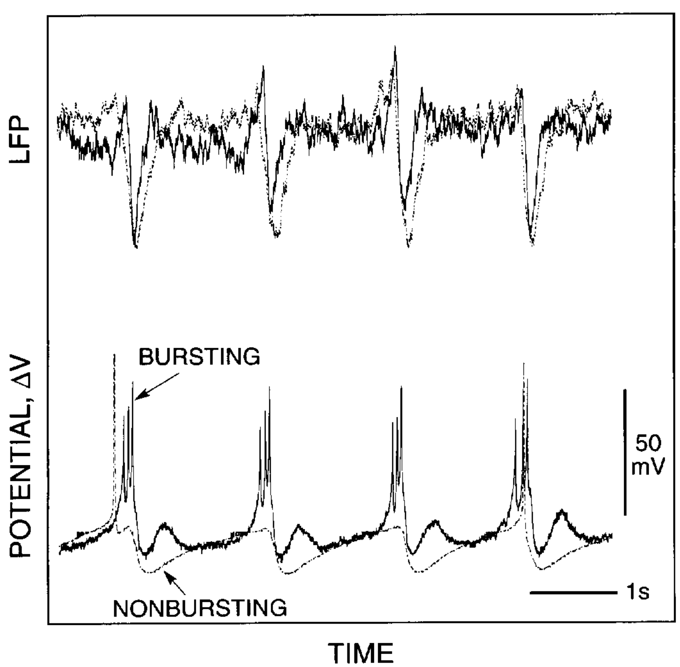


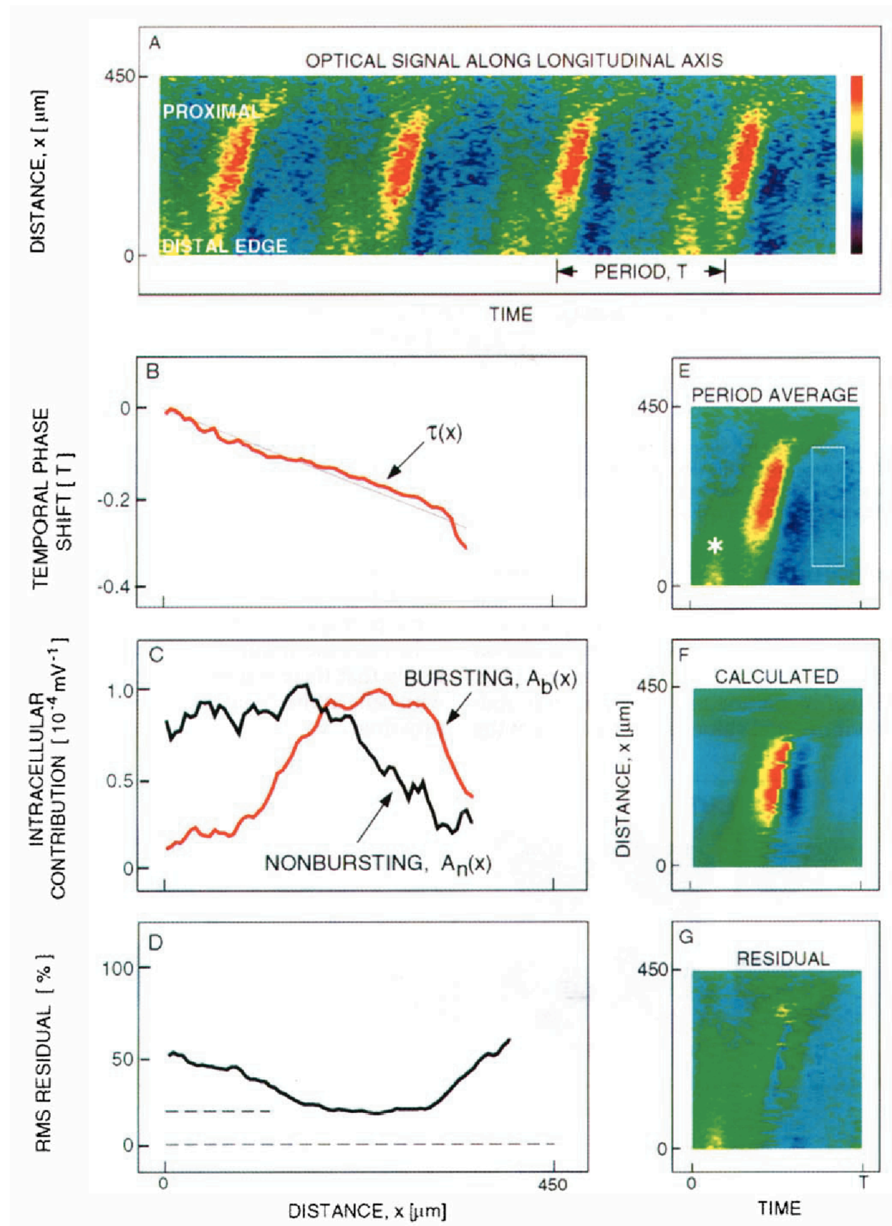


Decomposition of Optical Signal into Underlying Intracellular Potentials

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

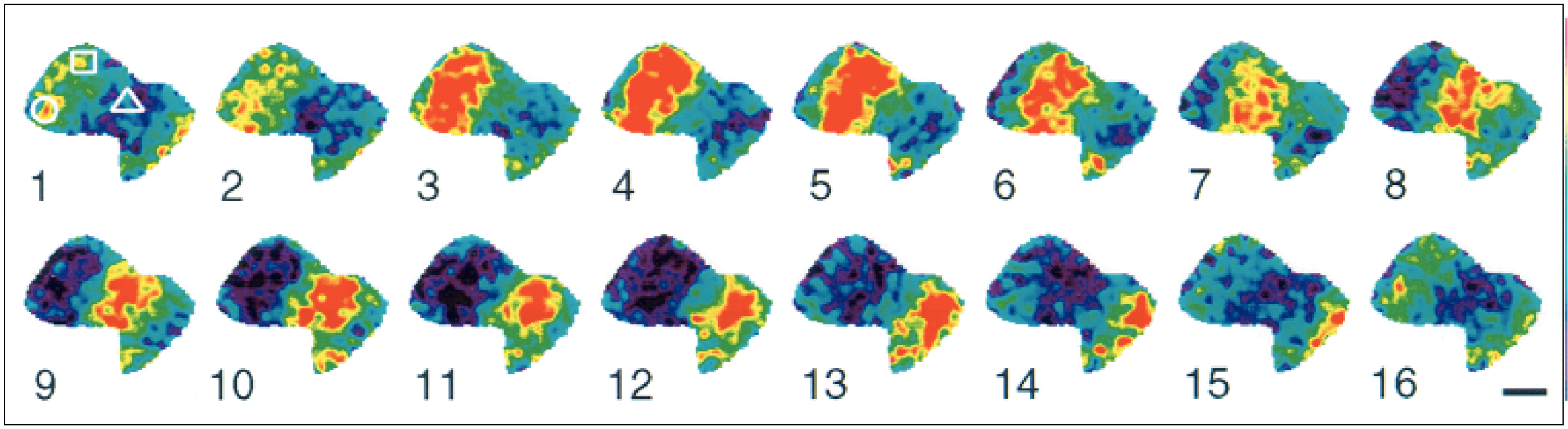


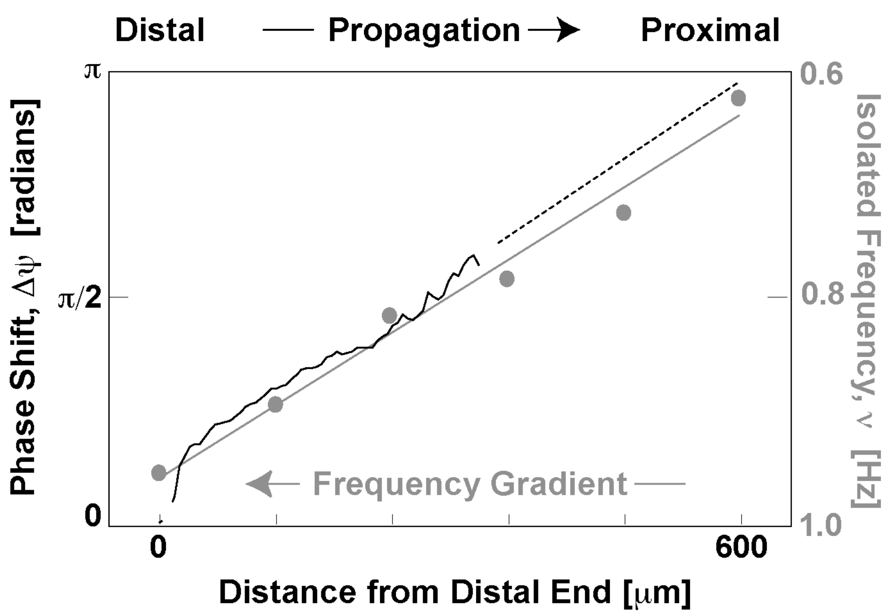


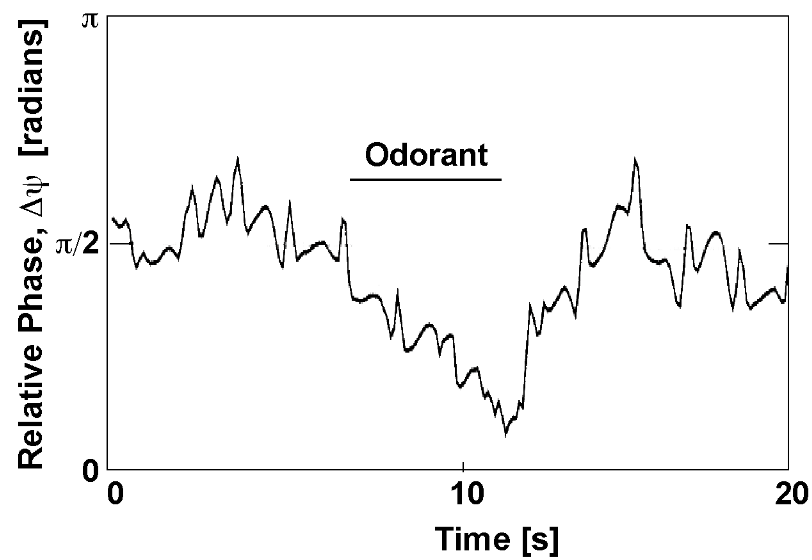


Electrical Wave Propagation in the Central Olfactory Organ of Limax

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







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 $\frac{\psi_x}{dx} \propto \text{constant.}$