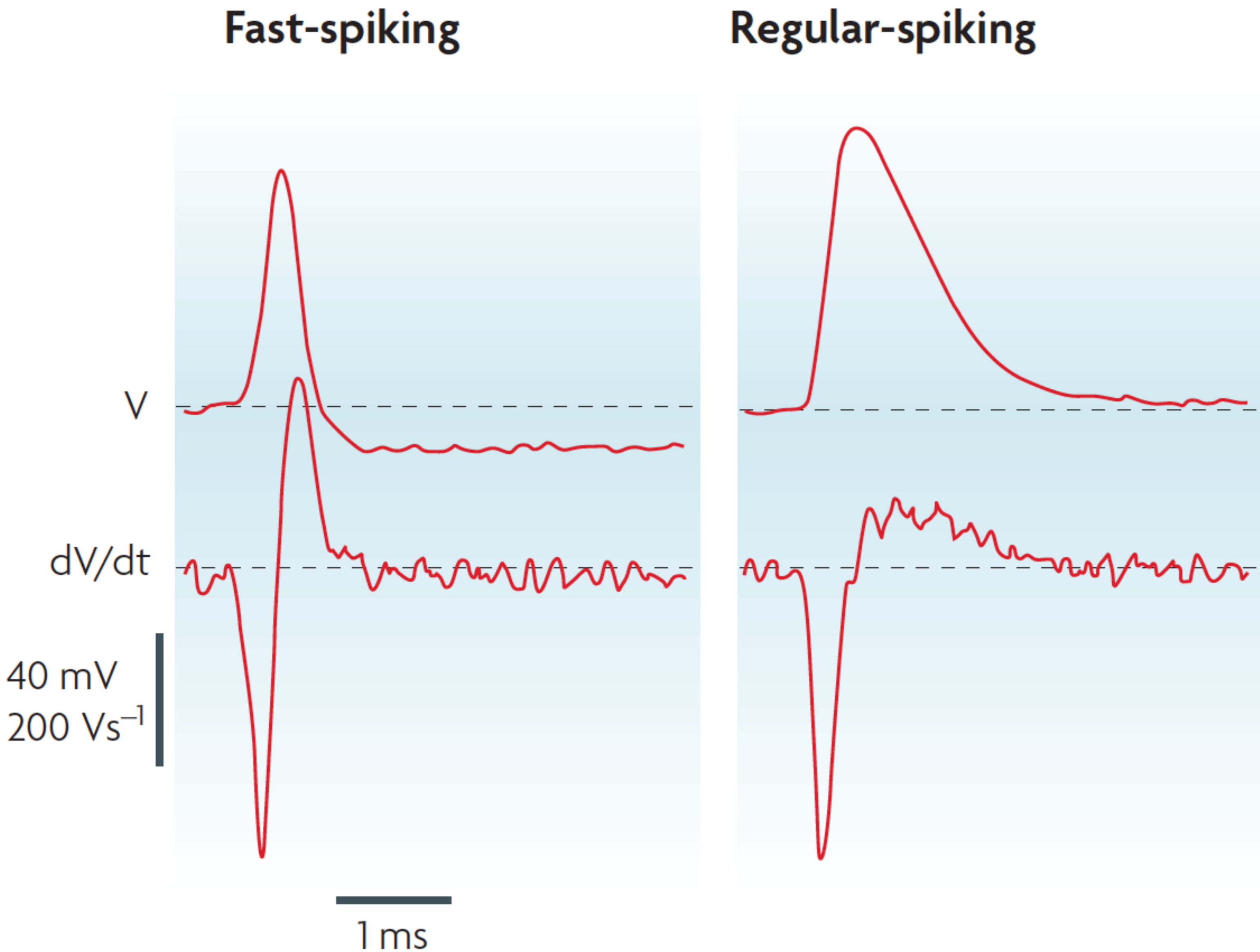
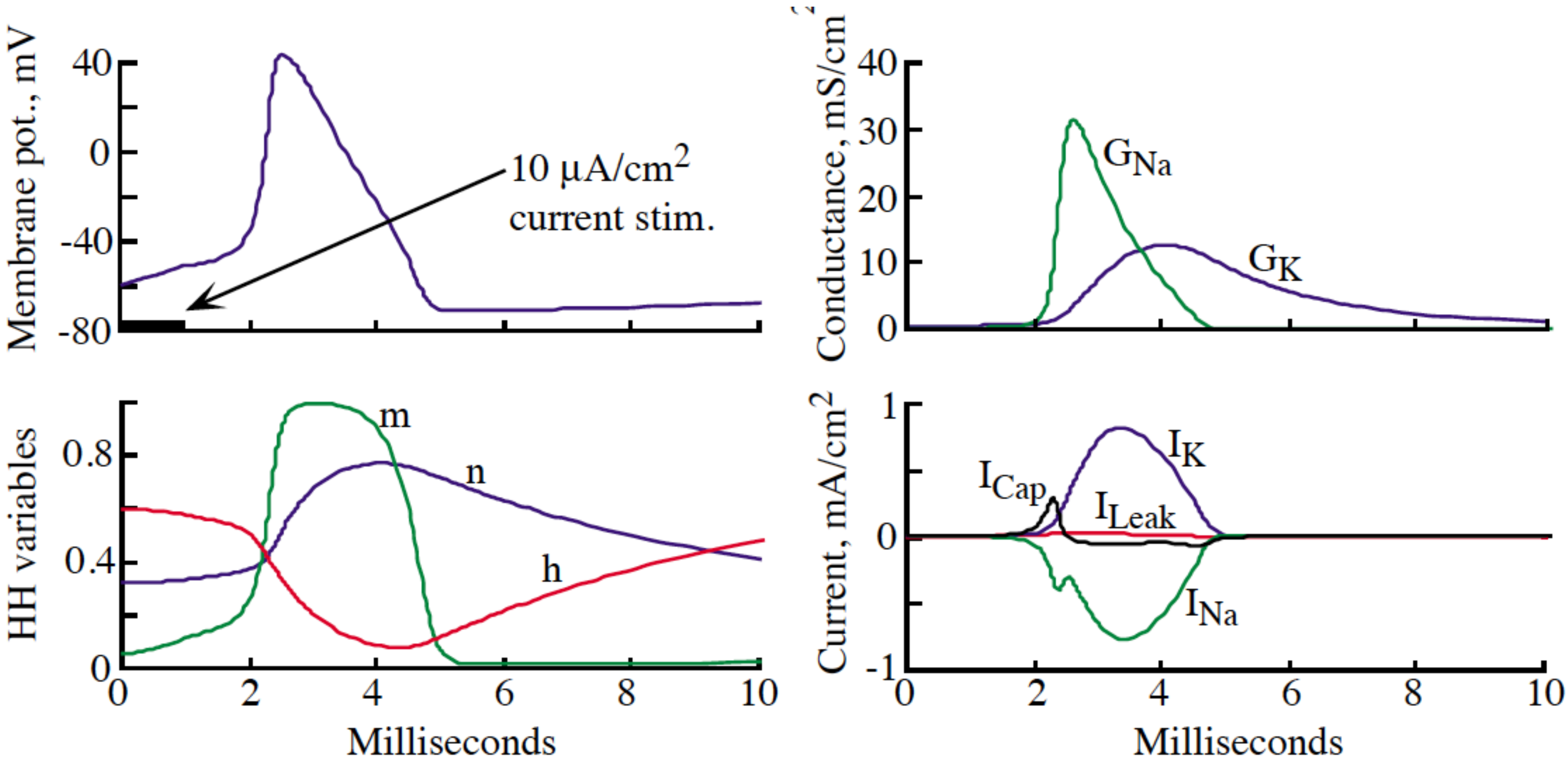
The Na^+ current leads to a similar rise across different classes of neurons

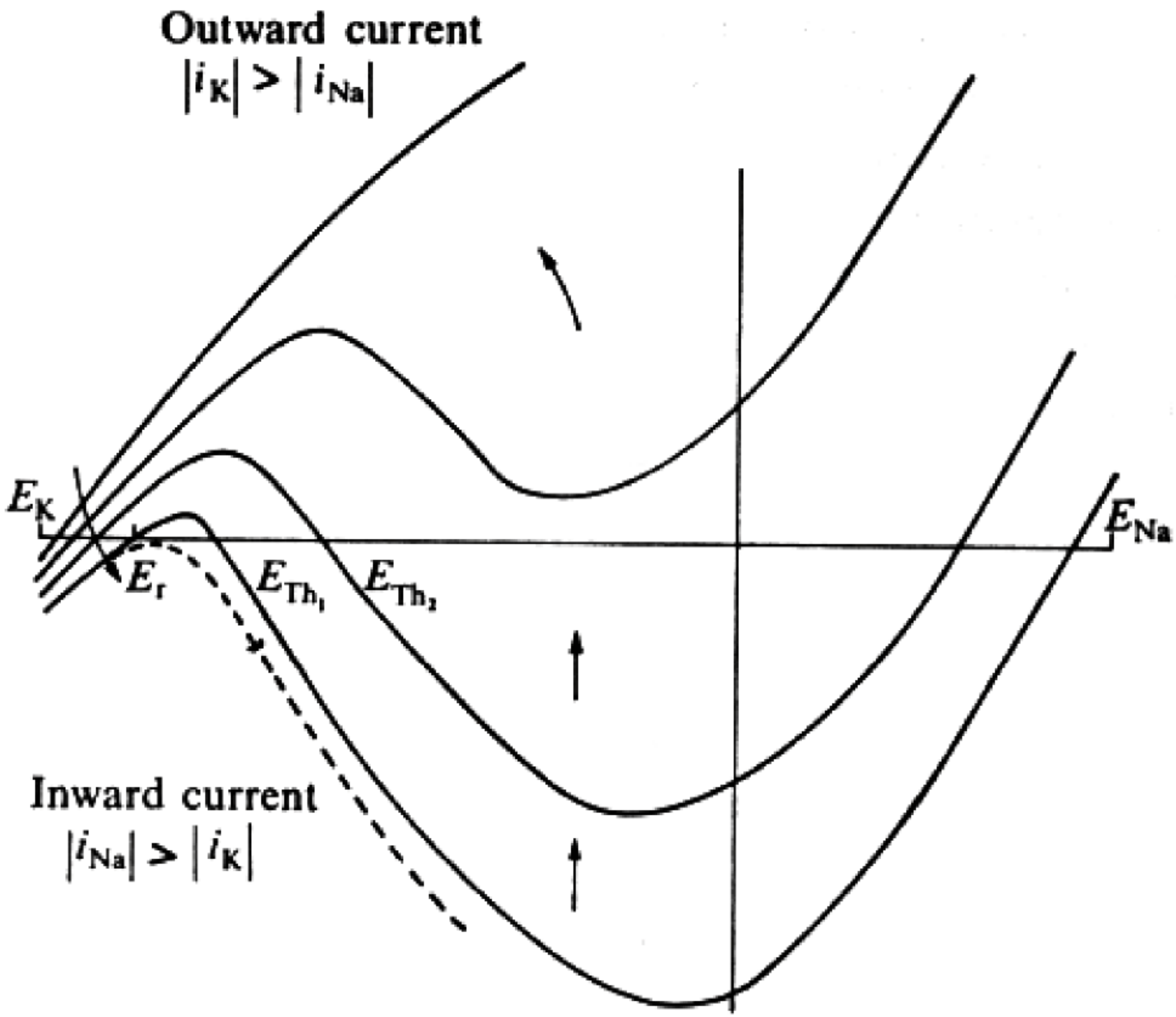


McCormick, Connors, Lighthall & Prince (J Neurophysiol 1985)

The model allows one to estimate ion conductances over time

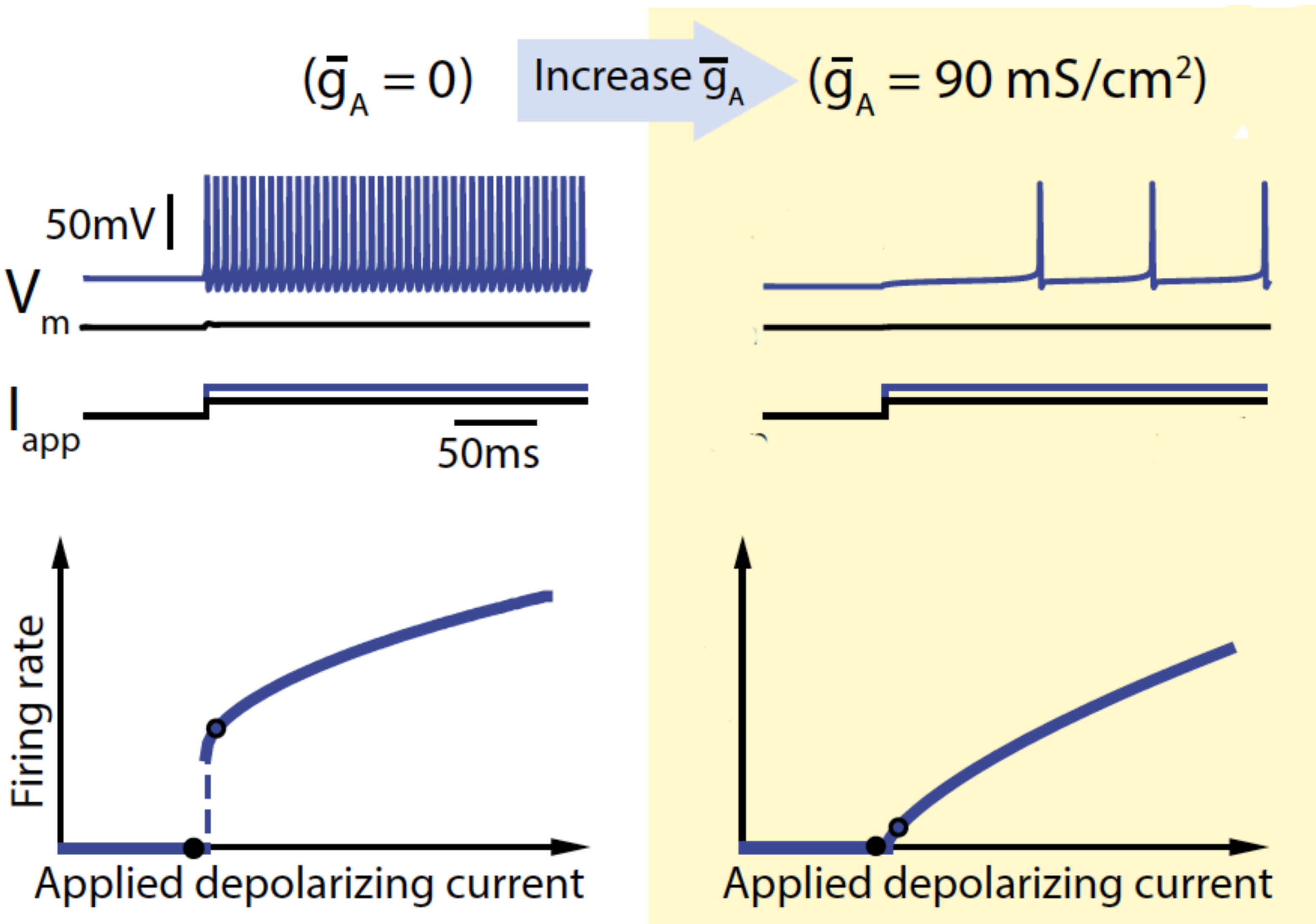


Modeling allows one to graph the I-V relation versus time

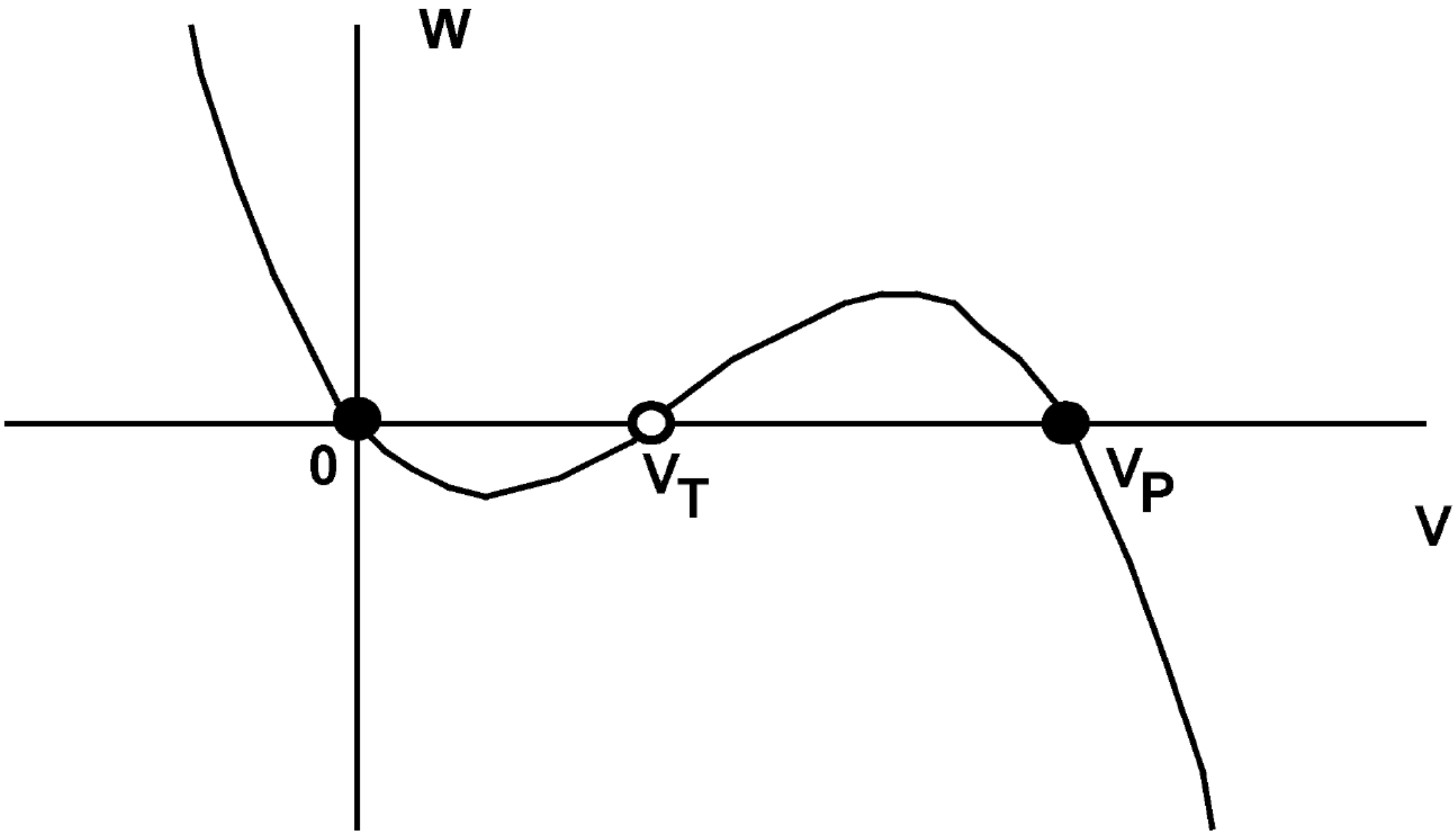


Lastly, the model predicts a discontinuous input (current) - output (spike rate) relation

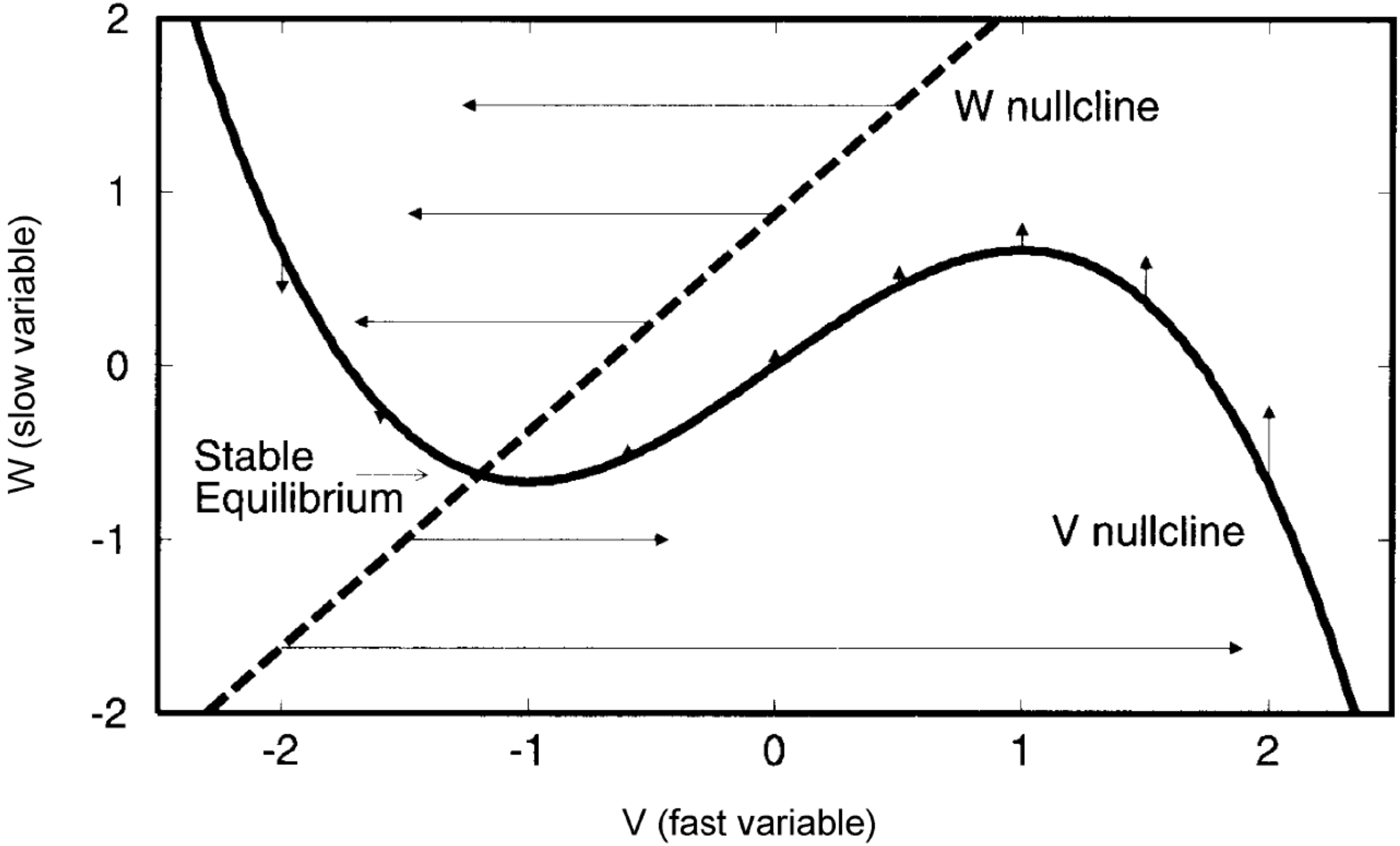
BTW, this is modified by the addition of inactivating K^+ channels



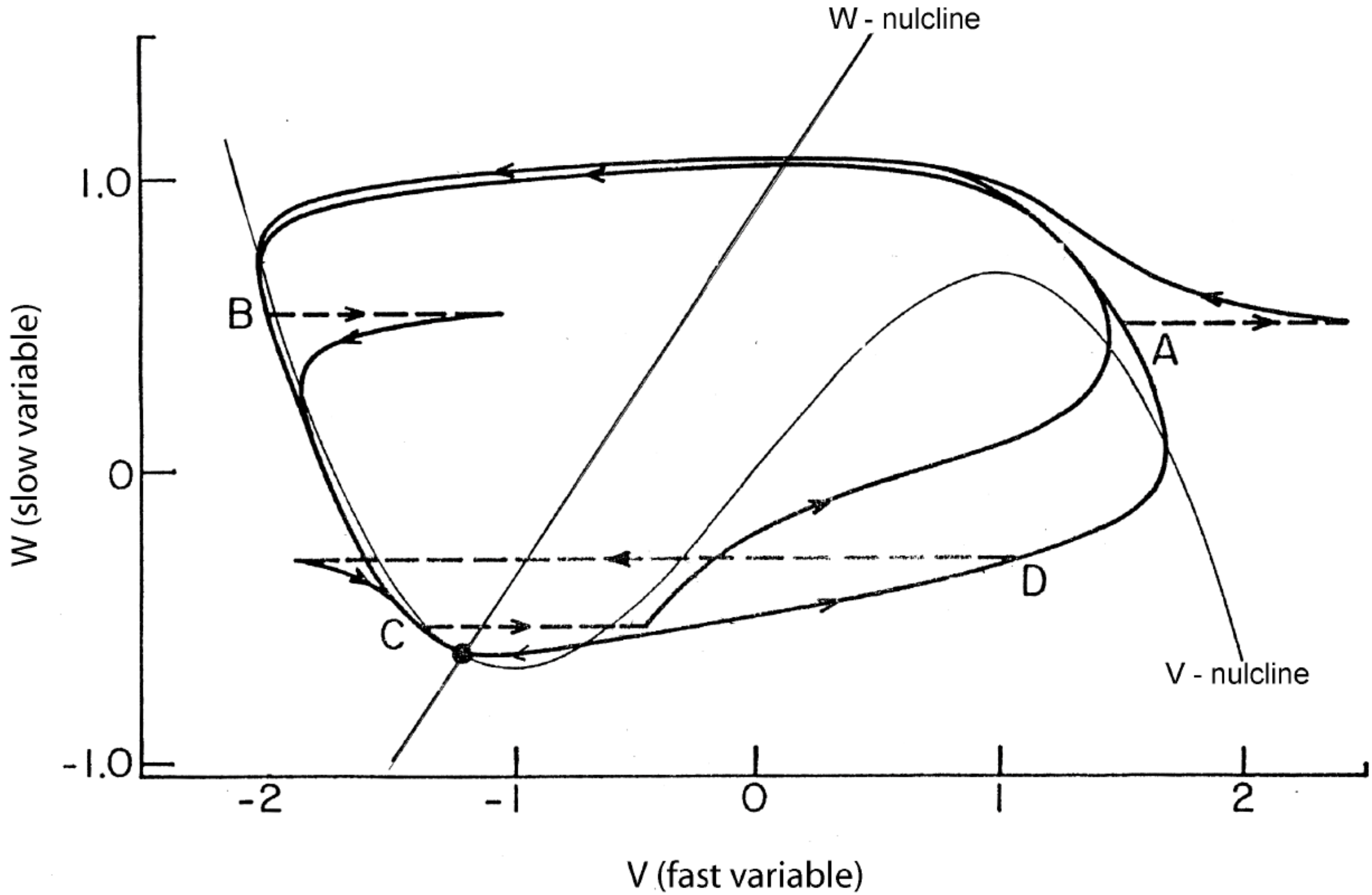
The initial, fast Na+ dynamics can be modeled by a cubic



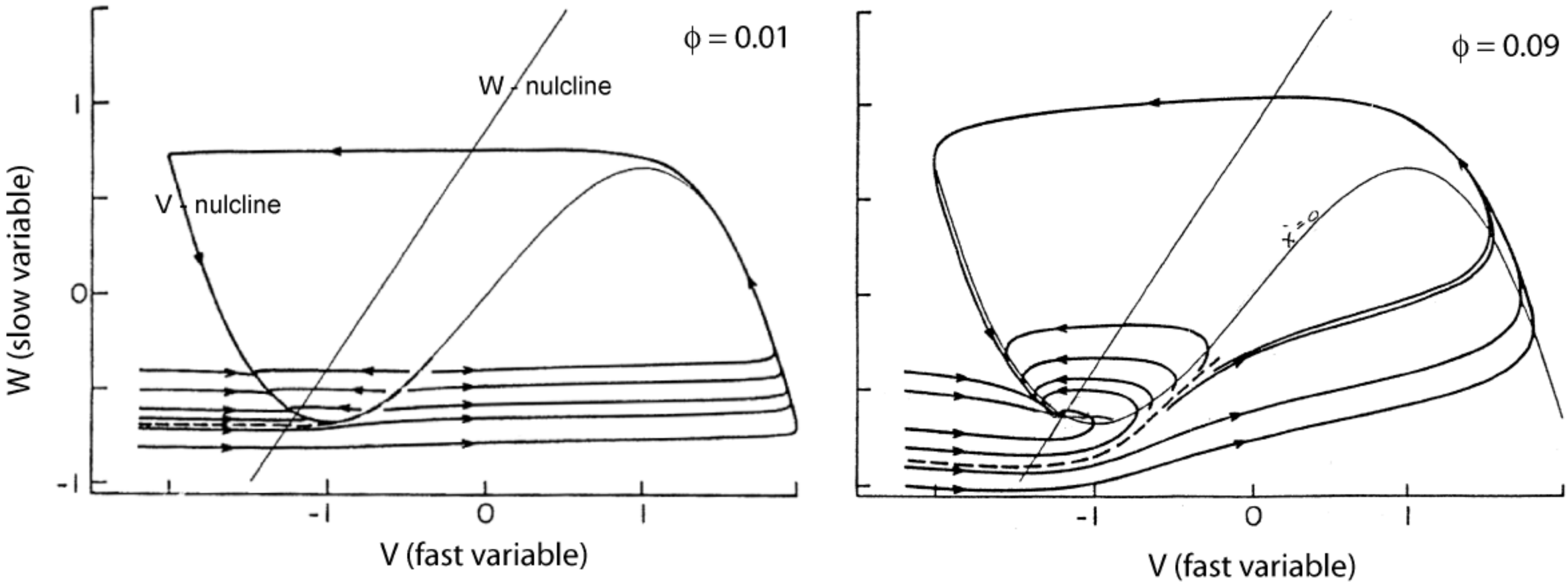
The equilibrium curves, or nullclines



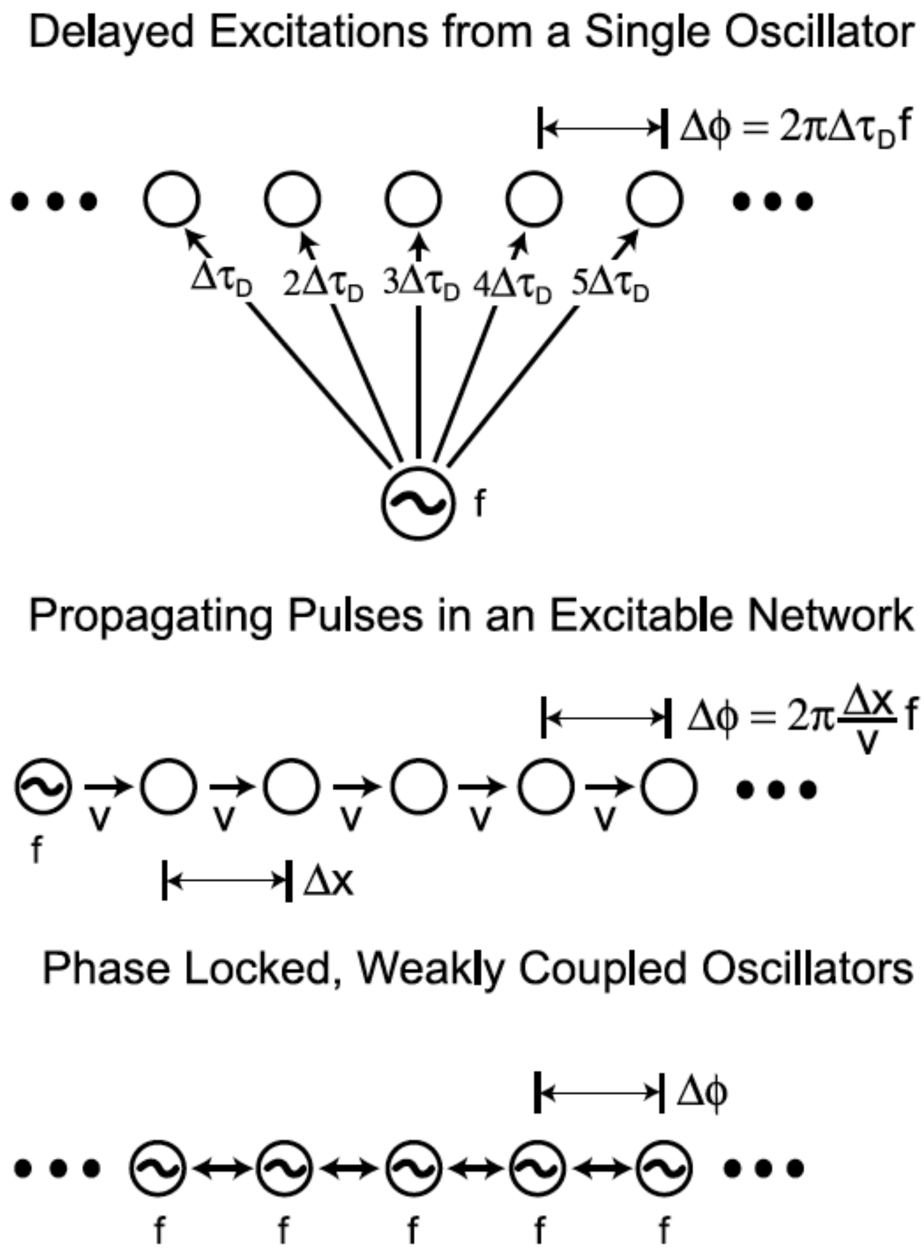
Examples (referenced to the notes)



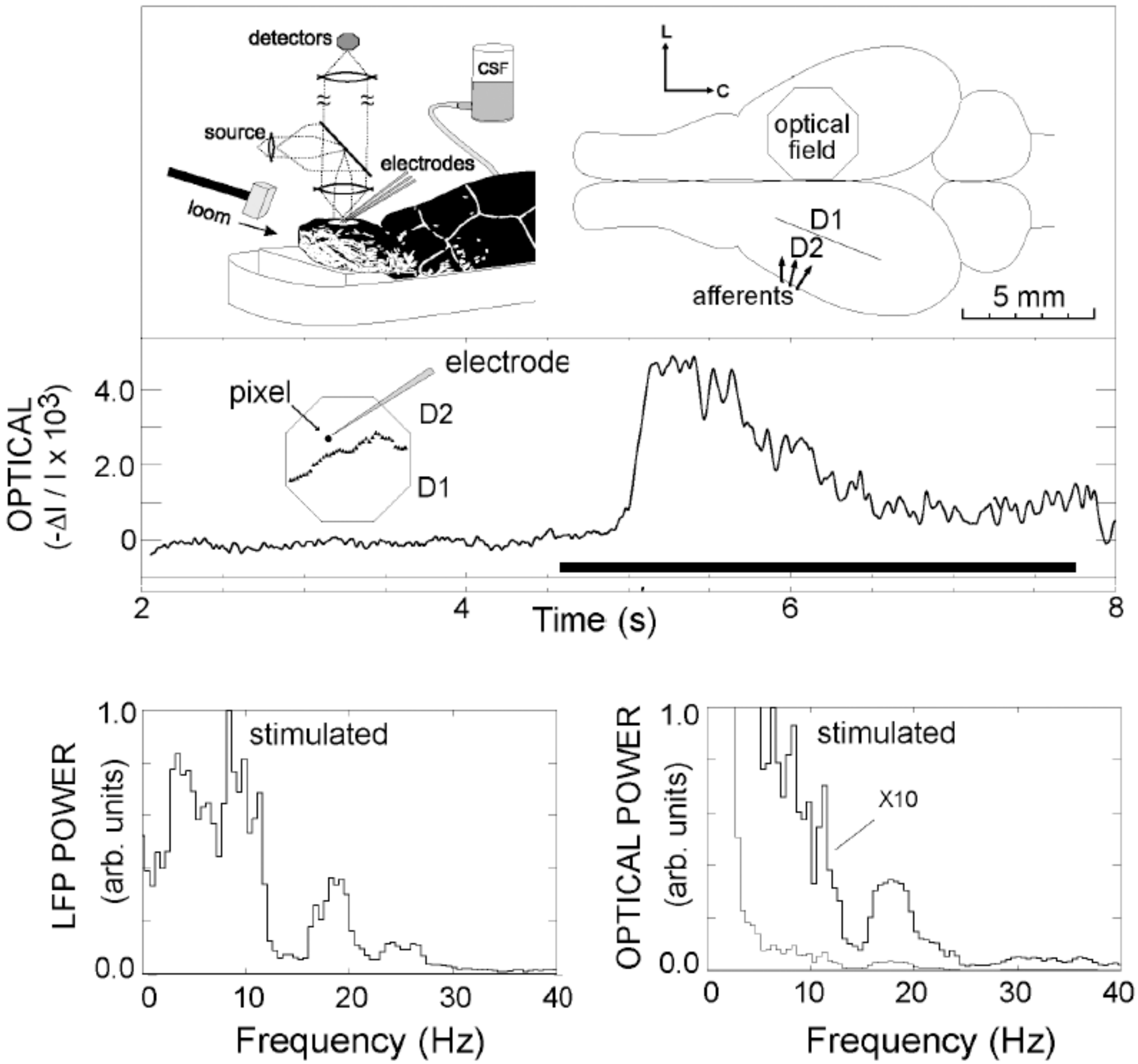
Comparison of trajectories at 100:1 versus 11:1 temporal differences in time-scale of the "Fast" to "Slow" variables



Waves of electrical activity are a potential signature of couples oscillators

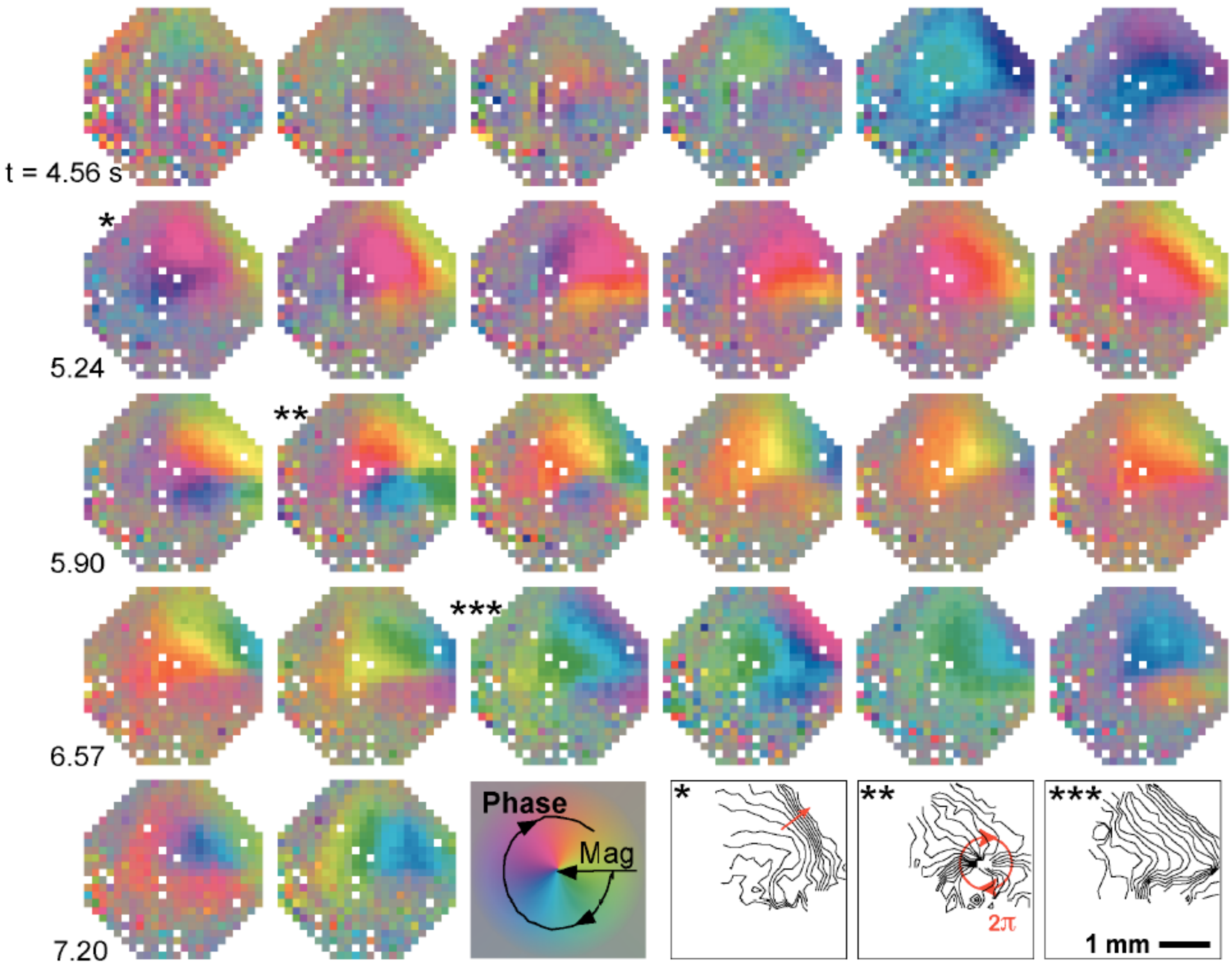


Linear and spiral waves in awake turtle visual cortex



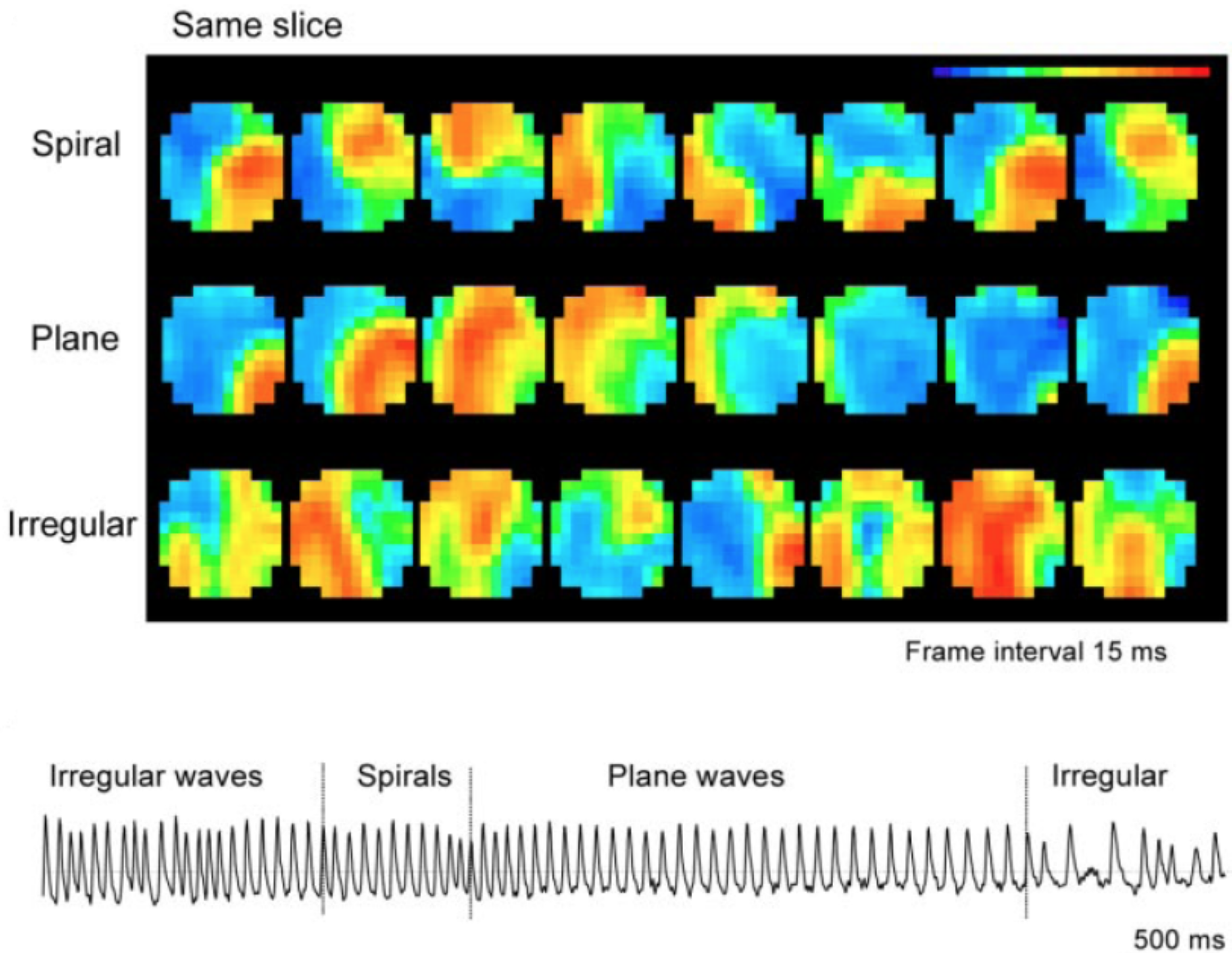
Prechtl, Cohen, Pesaran, Mitra & Kleinfeld (PNAS 1997)

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



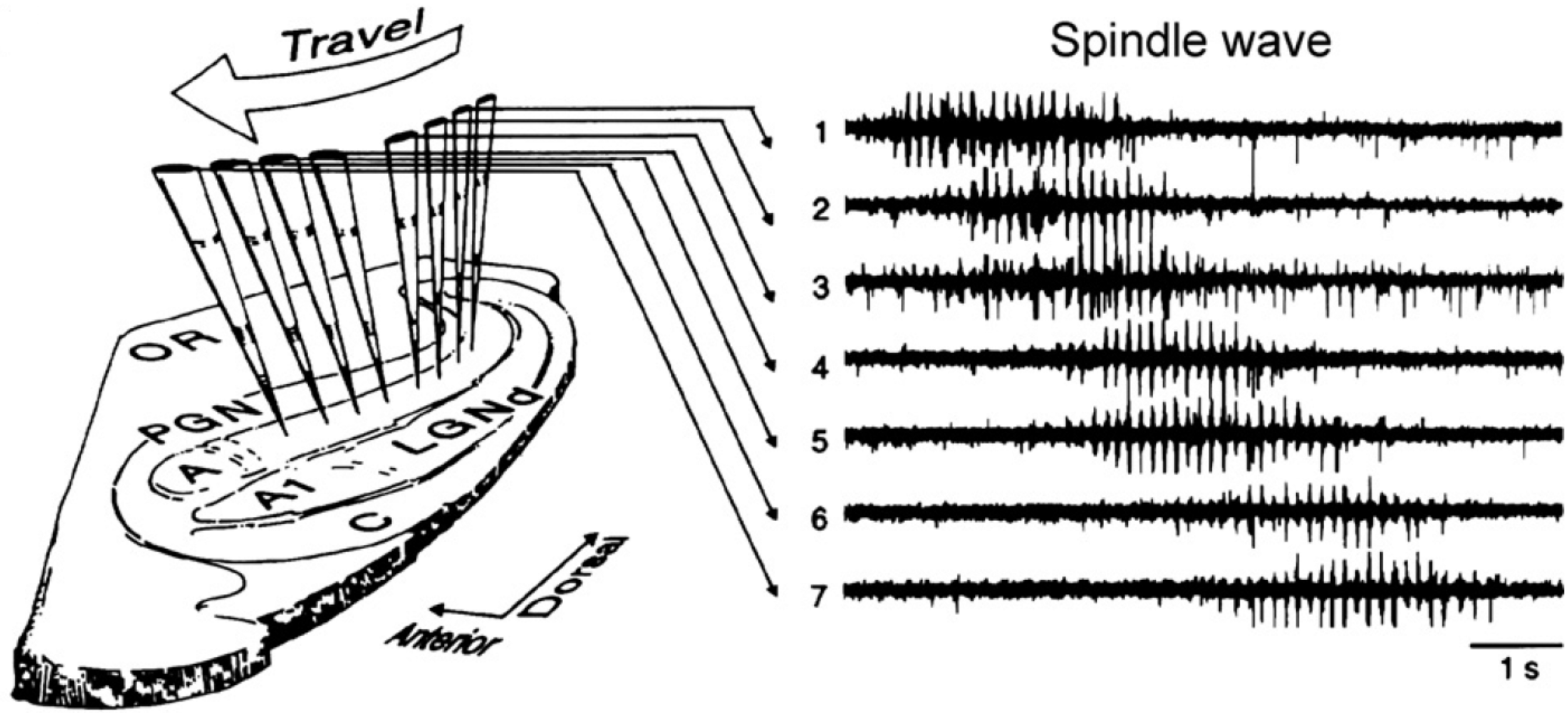
Prechtl, Cohen, Pesaran, Mitra & Kleinfeld (PNAS 1997)

Linear and spiral waves in disinhibited rat neocortex L4 brain slice



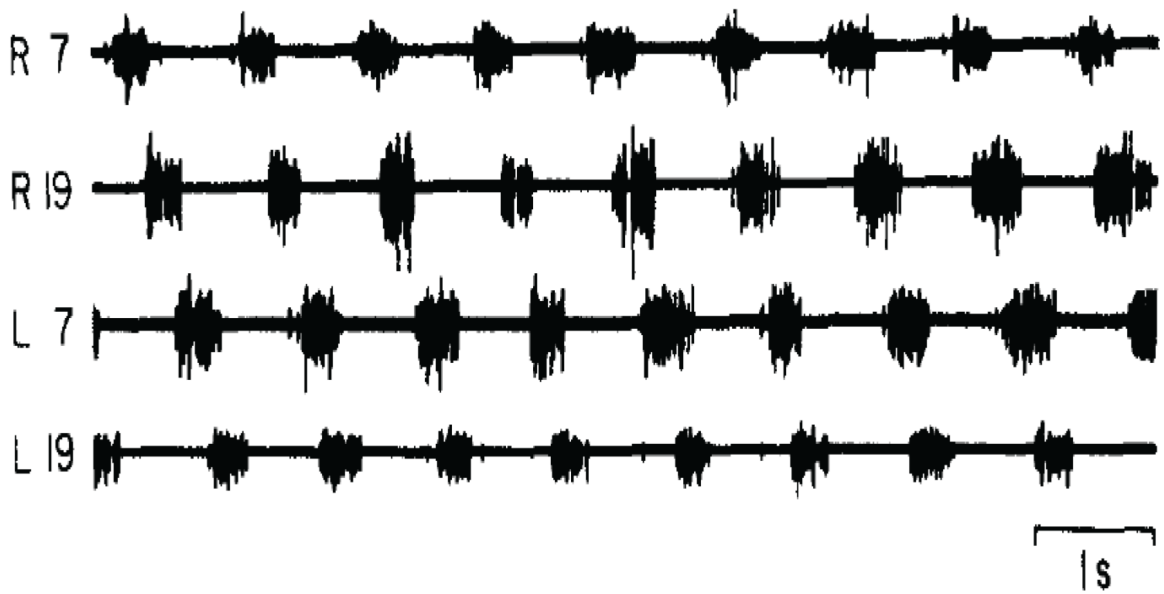
Huang, Troy, Yang, Ma, Laing, Schiff & Wu (Journal of Neuroscience 2004)

Traveling waves in ferret visual thalamus brain slice

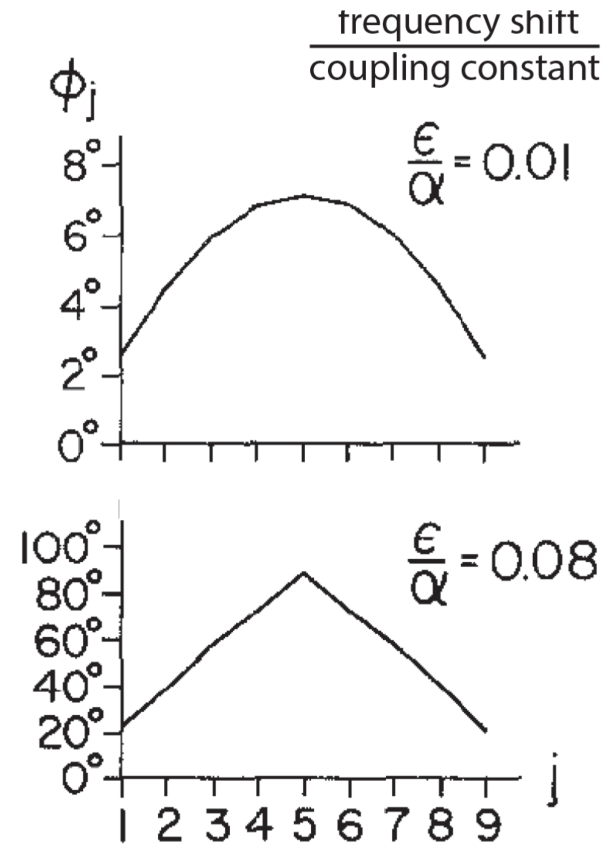


Kim, Bal & McCormick (Journal of Neurophysiology 1996)

Discretized waves that control swimming in lamprey



Ventral root recordings from an isolated piece of spinal cord.



Cohen & Wallen (Experimental Brain Research 1980)
Cohen, Holmes & Rand (Journal of Mathematical Biology 1982)

Macroscopic spiral waves in the human brain

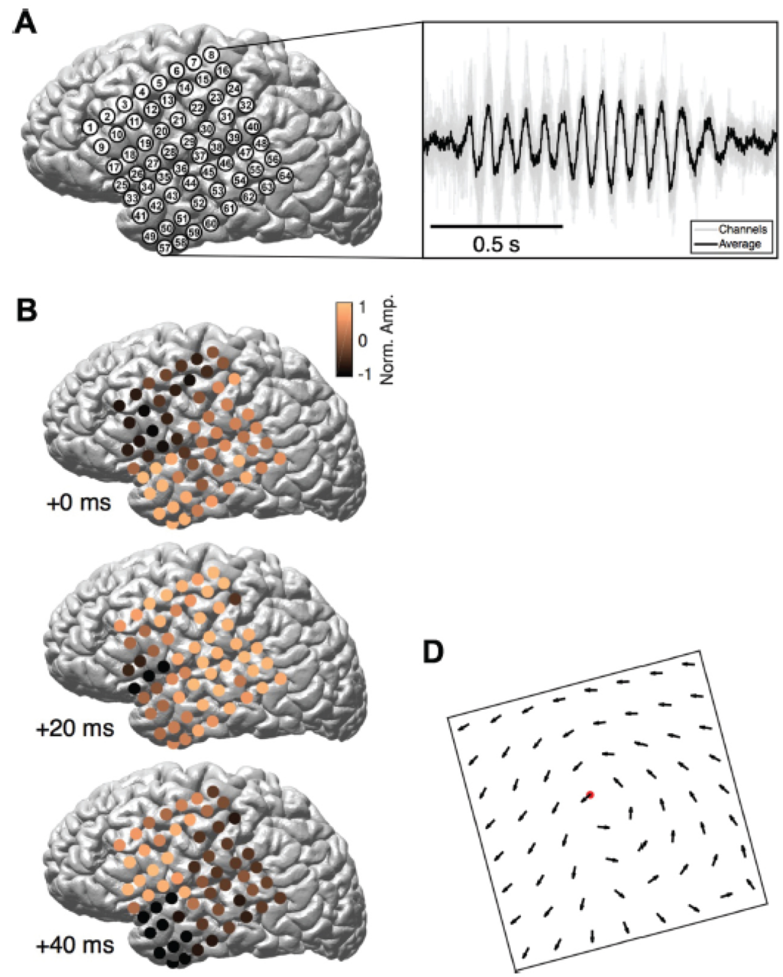


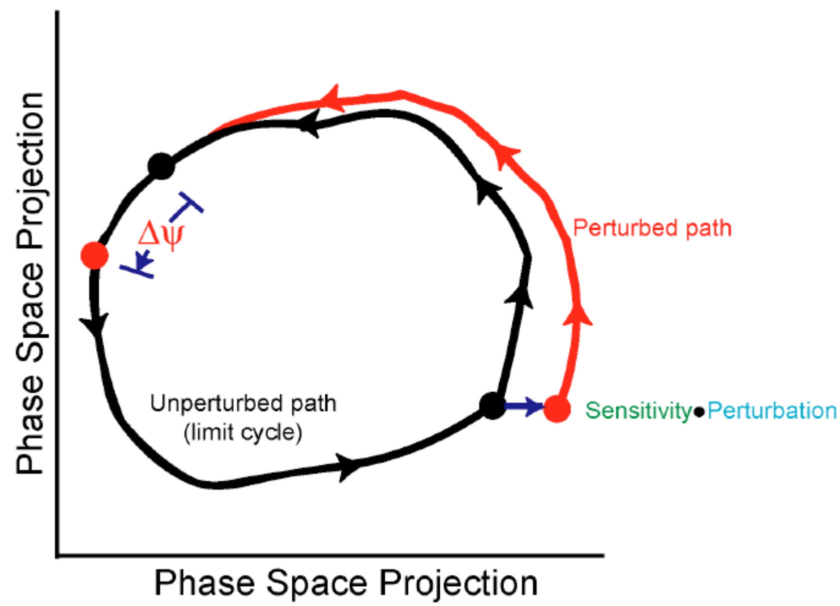
Figure 1. Rotating waves during spindles. (A) Electrode placement for subject 1 (left), with a stereotypical spindling epoch observed on the array (right). The right panel depicts the average over channels (black) together with the individual channels (gray). (B) When visualized on the cortex, individual spindle cycles are often organized as rotating waves traveling from temporal (+0 ms, top) to parietal (+20 ms, middle) to frontal (+40 ms, bottom) lobes. (D) The field of propagation directions, aligned on the putative rotation center and averaged across oscillation cycles and across subjects, shows a consistent flow in the temporal → parietal → frontal (TPF) direction. The center point is marked in red.

Muller, Piantoni, Cash, Koller, Halgren & Sejnowski (Elife 2016)

Kuromoto's insight:

- **Transform high-dimensional dynamic systems into one-dimensional (1-d) oscillators**
- **Assume interaction between pairs of 1-d oscillators is weak so that they are only advanced or retarded along their limit cycle**
- **Write the interaction between pairs of 1-d oscillators in terms of their relative phase**

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



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

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

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

Relevance: Interaction of neuronal oscillators may be written in terms of the correlation of presynaptic spiking with the post synaptic response

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

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

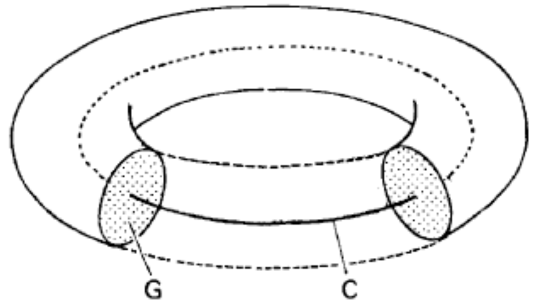
$$\Gamma\left(\Psi_i - \Psi_j\right) = \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \underbrace{\mathbf{Z}\left(\Psi_i + \theta\right)}_{\text{Sensitivity Function}} \; \underbrace{\mathbf{P}\left(\Psi_i + \theta;\; \Psi_j + \theta\right)}_{\text{Perturbation}}$$

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

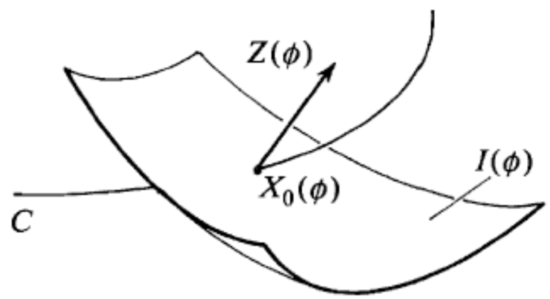
$$= \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \underbrace{\frac{g_{\text{synapse}}}{C_m}\, \mathbf{Z}\left(\Psi_i + \theta\right)\left[E_{synapse} - \mathbf{V}\left(\Psi_i + \theta\right)\right]}_{\mathbf{R}\left(\Psi_i + \theta\right)} \; \mathbf{S}\left(\Psi_j + \theta\right)$$

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

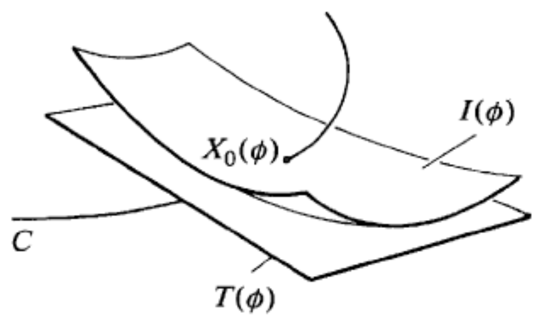
$$= \frac{\varepsilon}{2\pi}\int_{-\pi}^{\pi} d\theta \; \mathbf{R}(\theta)\, \mathbf{S}\Big[\theta - \underbrace{\left(\Psi_i - \Psi_j\right)}_{\text{Phase difference}}\Big]$$



Limit cycle orbit enclosed in a thin tube



Geometrical meaning of $Z(\phi)$

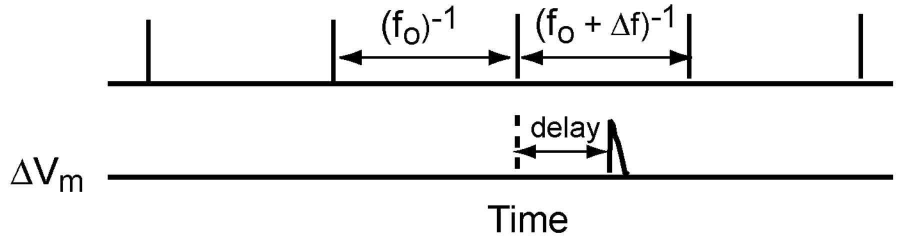


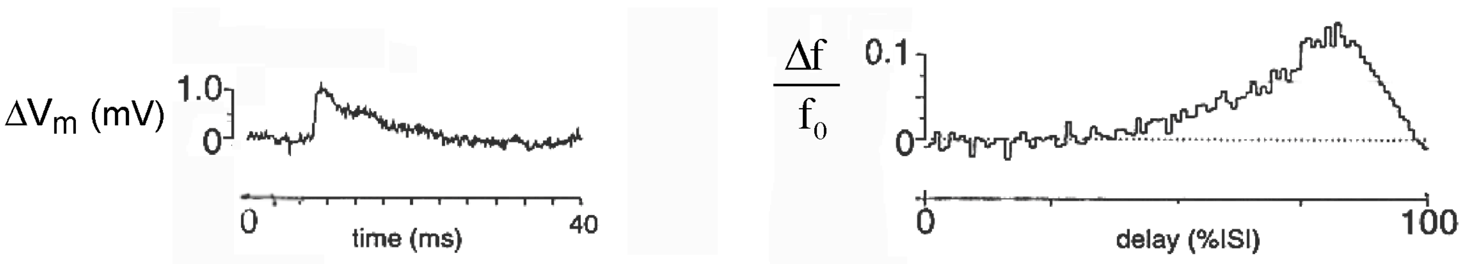
$(n-1)$-dimensional hyperplane $T(\phi)$ tangent to the isochron $I(\phi)$ at point $X_0(\phi)$ lying on the limit cycle orbit C

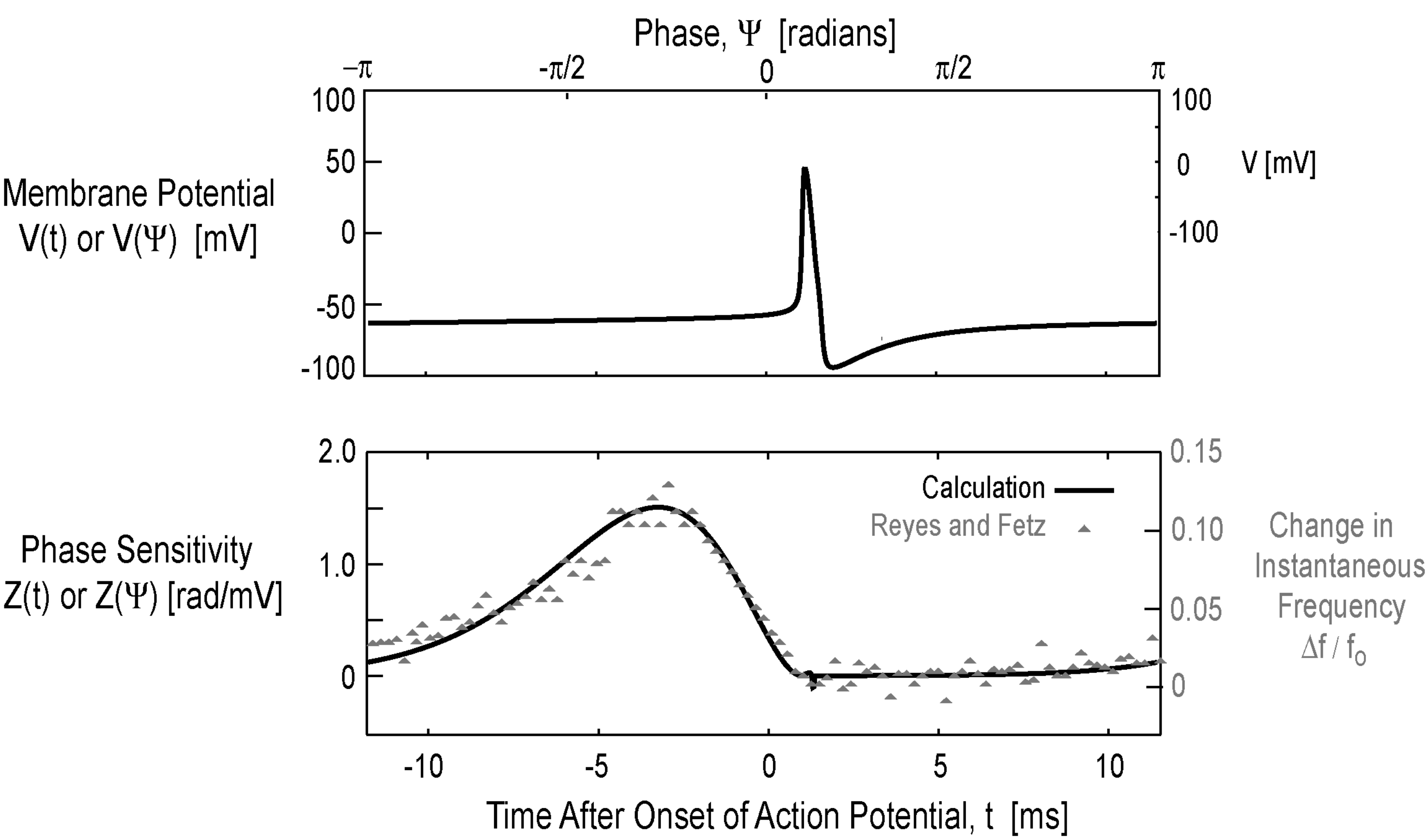
The Phase Sensitivity Function for Perturbation in Voltage

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

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

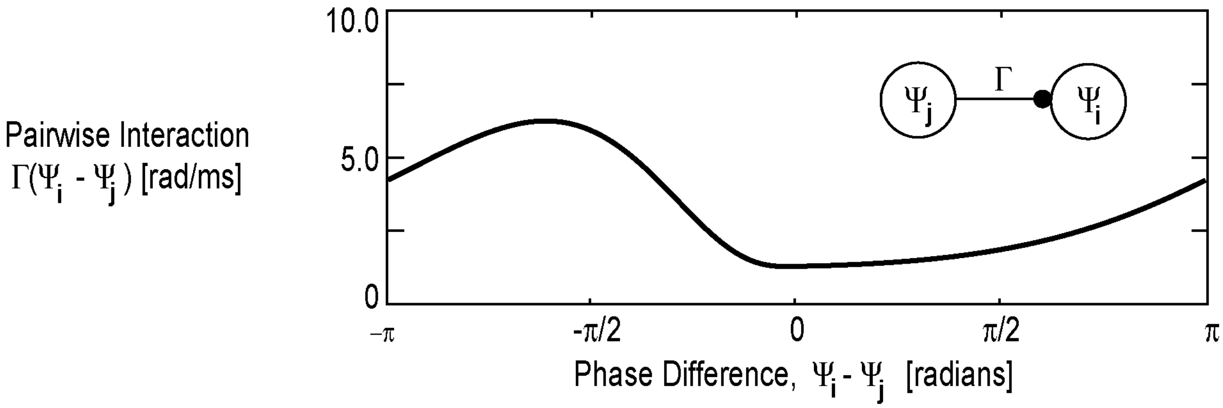






Lesson: Phase Sensitivity Concept Valid with Realistic PSPs

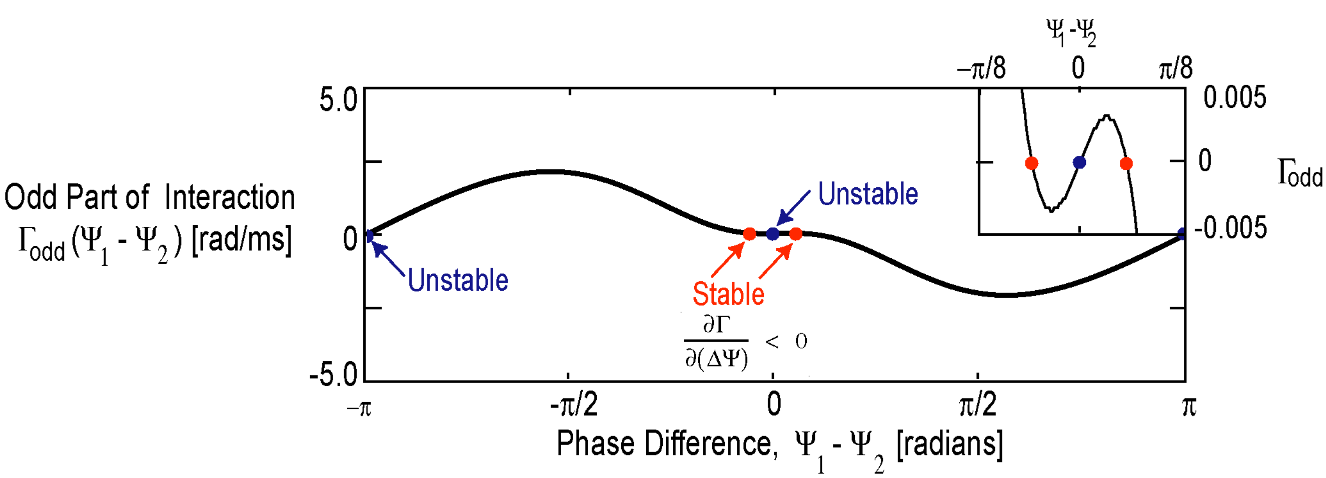
Nature of the Pairwise Interaction is Revealed by the Phase Shifts Between Two Reciprocally Connected Neurons



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

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

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



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