

5 Networks of Phase Coupled Neuronal Oscillators

We consider small networks or simple networks in which cells are coupled only weakly, in the sense that then can effect each others timing but do not turn each other on or off or, more formally, do not effect the shape of each others limit cycle.

5.1 Basic formalism

Equation of motion for a general dynamical system

$$\frac{d\vec{X}}{dt} = F(\vec{X}; \mu) \quad (5.5)$$

where the $\vec{X}$ is a vector that contains all the dynamical variables and the μ are parameters. At steady state

$$\frac{d\vec{X}_0}{dt} = F(\vec{X}_0; \mu) \quad (5.6)$$

where a closed orbit satisfies

$$\vec{X}_0(t + T) = \vec{X}_0(t) \quad (5.7)$$

See attached figure from Kuromoto's book

We associate a value of ψ with each point along $\vec{X}(t)$. Thus the multidimensional trajectory is reduced to a single variable.

It is useful to extend the definition of ψ off of the limit cycle, or contour, C, to all points within a tube around C so that ψ is defined for all $\vec{X}$ in the tube. This will allow us to study perturbations to the original limit cycle.

Look on a surface, denoted G, normal to and in the neighborhood of C. Let P be a point on G and Q be the point on C, the limit cycle, that passes through the same surface. We posit that as the trajectories evolve, the point P will approach the closed orbit defined by C. There will be a phase difference between P and Q. This is equivalent to an initial phase difference among the points. The main idea is that the physical perturbation can be transformed into a phase shift along the original limit cycle, C, if the perturbed point collapses to or forever parallels the original limit cycle.

There are a set of points in the tube that will lead to the same phase shift. These define a surface of constant phase shifts, that is denoted $I(\psi)$. For all points $\vec{X}$ on $I(\psi)$ we have

$$\frac{d\psi(\vec{X})}{dt} = \omega \quad (5.8)$$

for the unperturbed system. But, by the chain rule,

$$\begin{aligned} \frac{d\psi}{dt} &= \sum_i \frac{\partial \psi}{\partial X_i} \frac{\partial X_i}{\partial t} \\ &= \vec{\nabla}_{\vec{X}} \psi \cdot \frac{d\vec{X}}{dt} \\ &= \vec{\nabla}_{\vec{X}} \psi \cdot \vec{F}(\vec{X}) \end{aligned} \quad (5.9)$$

Let's perturb the motion by

$$\vec{F}(\vec{X}) \rightarrow \vec{F}(\vec{X}) + \epsilon \vec{P}(\vec{X}, \vec{X}') \quad (5.10)$$

where ϵ is small in the sense that the shape of the original trajectory is unchanged as $\epsilon \rightarrow 0$ and $\vec{X}'$ contains all the variables that define the perturbation, e.g, the trajectory of a neighboring oscillator and the interaction between the two oscillating systems. Then

$$\begin{aligned} \frac{d\psi}{dt} &= \vec{\nabla}_{\vec{X}} \psi \cdot [F(\vec{X}) + \epsilon \vec{P}(\vec{X}, \vec{X}')] \\ &= \omega + \epsilon \vec{\nabla}_{\vec{X}} \psi \cdot \vec{P}(\vec{X}, \vec{X}') \end{aligned} \quad (5.11)$$

So far everything is exact, that is, all calculations are done with respect to the perturbed orbit. The difficulty is that the orbits are not necessarily closed. But if we can make ϵ small enough so that $|\vec{X}(t) - \vec{X}_0(t)| \rightarrow 0$ as $t \rightarrow \infty$, the perturbation will lead to a closed path. This results in periodic orbits, so that the independent variable can now be taken as the phase, ψ , rather than time, t , where the two are related by

$$\psi = 2\pi \frac{t}{T} \text{ modulo}(2\pi) \quad (5.12)$$

Using

$$\vec{X}(t) \rightarrow \vec{X}_0(\psi) \quad (5.13)$$

we have

$$\begin{aligned} \frac{d\psi}{dt} &= \omega + \epsilon \vec{\nabla}_{\vec{X}_0(\psi)} \psi \cdot \vec{P}[\vec{X}_0(\psi), \vec{X}'_0(\psi')] \\ &\equiv \omega + \epsilon \vec{Z}(\psi) \cdot \vec{P}(\psi, \psi') \end{aligned} \quad (5.14)$$

The term $\vec{Z}(\psi)$ depends only on the limit cycle of the oscillator and defines the sensitivity of the phase to perturbation. It clearly varies along the limit cycle and is

sometimes called a "phase-dependent sensitivity". It may be calculated directly by evaluating the trajectory of points inside a tube around the original limit cycle, or more expeditiously using a trick due to Bowtell, in which the perturbed system is rewritten in the form $\frac{d\vec{X}}{dt} = \mathbf{A}(t)\vec{X}$, with $\mathbf{A}(t) = \mathbf{A}(t + T)$, which can be shown to have only one periodic solution. A cute way to find the periodic solution is to solve the adjoint problem, $\frac{d\vec{Y}}{dt} = \mathbf{A}^T(t)\vec{Y}$, for which all of the solutions decay except for the periodic one. From this one backs out $\vec{Z}(\psi)$.

The cool thing is that the oscillator is seen to rotate freely (ω term) with phase-shifts and frequency shifts that are determined solely by the perturbations. The term $\vec{P}(\psi, \psi')$, which can be calculated from the perturbation, allows these perturbations to be interactions with neighbors.

Let's look at the nature of the perturbation term. The idea is that this is small, so that the shift in frequency on one cycle is small. We consider

$$\psi = \delta\psi + \omega t \quad (5.15)$$

Then the relative motion is given by

$$\begin{aligned} \frac{d\delta\psi}{dt} &= \epsilon \vec{Z}(\psi) \cdot \vec{P}(\psi, \psi') \\ &= \epsilon \vec{Z}(\delta\psi + \omega t) \cdot \vec{P}(\delta\psi + \omega t, \delta\psi' + \omega t) \end{aligned} \quad (5.16)$$

This can be further simplified. To the extent that the change in ψ is small over one cycle, i.e., $\frac{d\delta\psi}{dt} \ll \omega$, we can average the perturbation over a full cycle. We write

$$\frac{d\delta\psi}{dt} = \Gamma(\delta\psi, \delta\psi') \quad (5.17)$$

where

$$\Gamma(\delta\psi, \delta\psi') = \frac{\epsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\delta\psi + \theta) \cdot \vec{P}(\delta\psi + \theta, \delta\psi' + \theta) \quad (5.18)$$

The above result can be generalized to the case where the internal parameters, i.e., the $\vec{X}$'s are a bit different between oscillators, so that the underlying oscillations are slightly different frequency. We then have

$$\frac{d\delta\psi}{dt} = \Gamma(\delta\psi, \delta\psi') + \delta\omega \quad (5.19)$$

5.2 Simplified interaction among 2 oscillators.

We take the perturbation to be solely a function of the phase of the other oscillator. Thus

$$\Gamma(\delta\psi, \delta\psi') = \frac{\epsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\delta\psi + \theta) \cdot \vec{P}(\delta\psi' + \theta) \quad (5.20)$$

But this is just a correlation integral that is proportion to the differences in phase, i.e.,

$$\Gamma(\delta\psi' - \delta\psi) = \frac{\epsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\theta - (\delta\psi' - \delta\psi)) \cdot \vec{P}(\theta) \quad (5.21)$$

So that a system of two oscillators obeys

$$\begin{aligned} \frac{d\delta\psi}{dt} &= \Gamma(\delta\psi' - \delta\psi) \\ \frac{d\psi'}{dt} &= \Gamma(\delta\psi - \delta\psi') \end{aligned} \quad (5.22)$$

We subtract the two equations of motion for the phase to get

$$\begin{aligned} \frac{d(\delta\psi - \delta\psi')}{dt} &= [\Gamma(\delta\psi' - \delta\psi) - \Gamma(\delta\psi - \delta\psi')] \\ &\equiv \tilde{\Gamma}(\delta\psi' - \delta\psi) \\ &\equiv -\tilde{\Gamma}(\delta\psi - \delta\psi') \end{aligned} \quad (5.23)$$

The term $\tilde{\Gamma}(\delta\psi - \delta\psi')$ is an odd function with period T , with zeros at

$$x_0 \equiv \delta\psi - \delta\psi' = n\pi \quad n = 1, 2, 3, \dots \quad (5.24)$$

and possibly other places. By way of analysis,

- The zeros correspond to phase locking.
- The stability depends on the sign of $\left. \frac{d\tilde{\Gamma}(x)}{dx} \right|_{x_0}$
- $\left. \frac{d\tilde{\Gamma}}{dx} \right|_{x_0} < 0$ implies stability with even n ; attractive - phases converge.
- $\left. \frac{d\tilde{\Gamma}}{dx} \right|_{x_0} > 0$ implies stability with odd n ; repulsive - phases diverge.

5.3 Examples

5.3.1 Two oscillators with delayed coupling.

An interesting example due to Ermentrout is to consider two oscillators that interact by a synapse with a noninstantaneous rise time. Before we choose a realistic cell model, let's try some analytical methods and choose a form of $\vec{Z}(\delta\psi)$ that has variable sensitivity along the limit cycle. The simplest choice is $Z(t) = \sin \omega t$, or

$$Z(\delta\psi) = \sin(\delta\psi) \quad (5.25)$$

The interaction is given by an " α " function, i.e., $P(t \geq 0) = \frac{g_{synapse}}{c_m} \frac{t}{\tau} e^{-t/\tau}$. With the substitution $\psi = \omega t$, we have

$$\begin{aligned}
P(\delta\psi') &= 0 & \delta\psi' < 0 \\
&= \frac{g_{synapse}}{c_m} \frac{\delta\psi'}{\omega\tau} e^{-\delta\psi'/\omega\tau} & \delta\psi' \geq 0
\end{aligned} \tag{5.26}$$

The convolution for $\tilde{\Gamma}(\delta\psi' - \delta\psi)$ can be done by extending the range of integration over all time, so that

$$\begin{aligned}
\Gamma(\delta\psi' - \delta\psi) &= \frac{\epsilon}{2\pi} \int_0^\infty d\theta \vec{Z}(\theta - (\delta\psi' - \delta\psi)) \cdot \vec{P}(\theta) \\
&= \frac{g_{synapse}}{c_m} \frac{\epsilon}{2\pi} \omega\tau \int_0^\infty d\left(\frac{\theta}{\omega\tau}\right) \sin[\theta - (\delta\psi' - \delta\psi)] \left(\frac{\theta}{\omega\tau}\right) e^{-\theta/\omega\tau} \\
&= \frac{g_{synapse}}{c_m} \frac{\epsilon}{2\pi} \omega\tau \frac{1}{2i} \left(e^{-i(\delta\psi' - \delta\psi)} \int_0^\infty x dx e^{i\omega\tau x} e^{-x} - e^{i(\delta\psi' - \delta\psi)} \int_0^\infty x dx e^{-i\omega\tau x} e^{-x} \right) \\
&= \frac{g_{synapse}}{c_m} \frac{\epsilon}{2\pi} \omega\tau \frac{1}{2i} \left(\frac{e^{-i(\delta\psi' - \delta\psi)}}{(1 - i\omega\tau)^2} - \frac{e^{i(\delta\psi' - \delta\psi)}}{(1 + i\omega\tau)^2} \right) \int_0^\infty x dx e^{-x} \\
&= \frac{g_{synapse}}{c_m} \frac{\epsilon}{2\pi} \frac{\omega\tau}{[1 + (\omega\tau)^2]^2} \left([1 - (\omega\tau)^2] \sin(\delta\psi' - \delta\psi) + 2\omega\tau \cos(\delta\psi' - \delta\psi) \right)
\end{aligned} \tag{5.27}$$

and thus

$$\tilde{\Gamma}(\delta\psi' - \delta\psi) = \frac{g_{synapse}}{c_m} \frac{\epsilon}{\pi} \frac{\omega\tau [1 - (\omega\tau)^2]}{[1 + (\omega\tau)^2]^2} \sin(\delta\psi' - \delta\psi) \tag{5.28}$$

so that

$$\frac{d(\delta\psi - \delta\psi')}{dt} = \frac{g_{synapse}}{c_m} \frac{\epsilon}{\pi} \frac{\omega\tau [(\omega\tau)^2 - 1]}{[1 + (\omega\tau)^2]^2} \sin(\delta\psi - \delta\psi') \tag{5.29}$$

This says that, for excitatory connections ($g > 0$), the synchronized state, i.e., $\delta\psi' = \delta\psi$, is stable only for $\tau < \frac{1}{\omega}$. In contrast, for $\tau > \frac{1}{\omega}$ the antiphastic state with $\delta\psi' - \delta\psi = \pm\pi$ is stable.

Interestingly, synchronous, all inhibitory ($g < 0$). networks are observed experimentally at high frequencies. This is consistent with

$$\frac{d(\delta\psi - \delta\psi')}{dt} = \frac{|g_{synapse}^{inhibitory}|}{c_m} \frac{\epsilon}{\pi} \frac{\omega\tau [(1 - \omega\tau)^2]}{[1 + (\omega\tau)^2]^2} \sin(\delta\psi - \delta\psi') \tag{5.30}$$

5.3.2 Two identical Hodgkin Huxley oscillators.

How well does the above analysis hold with more realistic cells.

Recall the Hodgkin Huxley equations for a point neuron, where $\vec{X} = (V, h, m, n)^T$, i.e.,

$$\begin{aligned}
\frac{\partial V(t)}{\partial t} &= \frac{-r_m}{2\pi a\tau} \left(\bar{g}_{Na} m^3 h (V - V_{Na}) + \bar{g}_K n^4 (V - V_K) + \bar{g}_{leak} (V - V_l) + I_{syn} \right) \\
\frac{dh(V, t)}{dt} &= \frac{h_\infty(V) - h(V, t)}{\tau_h(V)} \\
\frac{dm(V, t)}{dt} &= \frac{m_\infty(V) - m(V, t)}{\tau_m(V)} \\
\frac{dn(V, t)}{dt} &= \frac{n_\infty(V) - n(V, t)}{\tau_n(V)}
\end{aligned} \tag{5.31}$$

Hansel and later van Vreeswijk considered two Hodgkin Huxley cells with a synaptic current given by

$$I_{syn} = -G_{syn} [V(t) - V_{syn}] \sum_i^{spikes} f(t - t_i) \tag{5.32}$$

where he used an "alpha" function for $f(t)$. The form of $\vec{Z}(\psi + t)$ is found from directly evaluating perturbations to the limit cycle, which is found from the Hodgkin-Huxley equations with $I_{syn} = 0$. The perturbation is given by

$$P(\psi + t, \psi' + t) = -G_{syn} [V(\psi + \omega t) - V_{syn}] \sum_i^{spikes} f(\psi' + \omega t - \omega t_i) \tag{5.33}$$

The systematics as a function of α for fixed ω were explored by van Vreeswijk

The phase as a function of I_{ext} , really ω , for fixed α were explored by Hansel. He also examined where in the cycle the neuron is most sensitive to perturbations.

5.3.3 Two oscillators with different intrinsic frequency.

We take

$$\Gamma(\delta\psi - \delta\psi') \equiv -\Gamma_0 \sin(\delta\psi - \delta\psi') \tag{5.34}$$

Then

$$\begin{aligned}
\frac{d\delta\psi}{dt} &= \Gamma_0 \sin(\delta\psi' - \delta\psi) + \delta\omega \\
\frac{d\delta\psi'}{dt} &= \Gamma_0 \sin(\delta\psi - \delta\psi') + \delta\omega'
\end{aligned} \tag{5.35}$$

The system will phase lock, for which $\frac{d\delta\psi}{dt} = \frac{d\delta\psi'}{dt}$, so long as the interaction strength can satisfy

$$\tilde{\Gamma} = \Gamma_0 \sin(\delta\psi' - \delta\psi) - \Gamma_0 \sin(\delta\psi - \delta\psi') \quad (5.36)$$

$$= -2\Gamma_0 \sin(\delta\psi - \delta\psi') = \delta\omega - \delta\omega' \quad (5.37)$$

or

$$\frac{2\Gamma_0}{|\delta\omega' - \delta\omega|} > 1 \quad (5.38)$$

The phase shift is just

$$\delta\psi - \delta\psi' = \sin^{-1} \left(\frac{\delta\omega' - \delta\omega}{2\Gamma_0} \right) \quad (5.39)$$

and the frequency under phase lock is

$$\omega_{observed} = \omega + \frac{\delta\omega + \delta\omega'}{2} \quad (5.40)$$

The above are the two quantities are the ones measured in the lab!

Outside of the phase locked region, the system undergoes quasiperiodic motion with a time varying phase shift given by

$$\delta\psi - \delta\psi' = 2 \tan^{-1} \left[\frac{\sqrt{(\delta\omega - \delta\omega')^2 - 4\Gamma_0^2} \tan \left(\frac{\sqrt{(\delta\omega - \delta\omega')^2 - 4\Gamma_0^2} t}{2} \right) + 2\Gamma_0}{\delta\omega - \delta\omega'} \right] \quad (5.41)$$

5.3.4 Chain of oscillators with $\delta\omega \propto \Delta x$: The example of Limax.

$$\frac{d\delta\psi_x}{dt} = \delta\omega_x + \sum_{x \neq x'} \Gamma(\delta\psi_x - \delta\psi_{x'}) \quad (5.42)$$

with

$$\delta\omega_x \propto x + \text{constant} \quad (5.43)$$

When the system locks, there is a single frequency, but a gradient of phase shifts with $\frac{\Delta\psi_x}{dx}$ given by a monotonic function of x , like $\frac{\Delta\psi_x}{dx} \propto \text{constant}$, i.e., the phase shift appears as a traveling wave. The data from Limax shows traveling waves and a gradient of intrinsic frequencies. The article by Ermentrout and Kleinfeld summarizes this and other data.

5.3.5 Two oscillators with propagation delays.

We again take

$$\Gamma(\delta\psi - \delta\psi') \equiv -\Gamma_0 \sin(\delta\psi - \delta\psi') \quad (5.44)$$

Then

$$\begin{aligned}
\frac{d\delta\psi}{dt} &= \Gamma_0 \sin(\delta\psi'(t - \tau_D) - \delta\psi(t)) + \delta\omega_0 \\
\frac{d\delta\psi'}{dt} &= \Gamma_0 \sin(\delta\psi(t - \tau_D) - \delta\psi'(t)) + \delta\omega_0
\end{aligned} \tag{5.45}$$

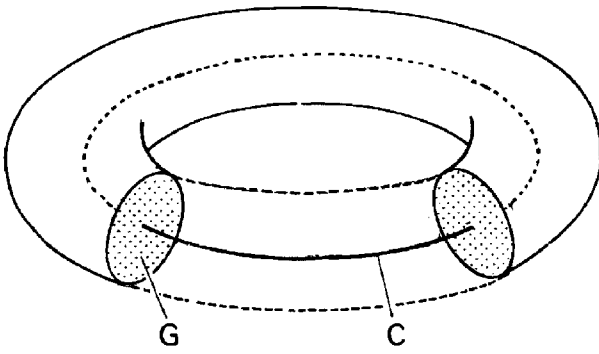
where the frequencies $\delta\omega_0$ are assumed to be equal. We assume a solution of the form

$$\delta\omega = \delta\omega_0 - \Gamma_0 \cos \alpha \sin \delta\omega\tau_D \tag{5.46}$$

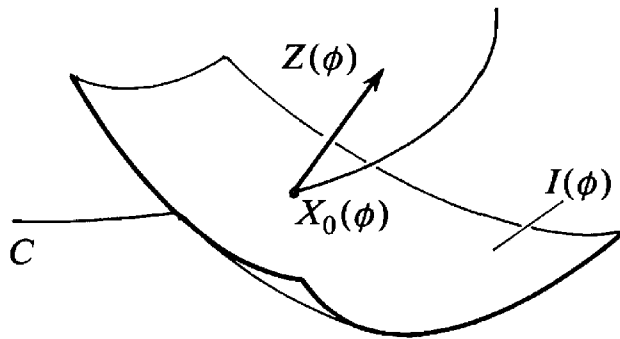
This is satisfied for

$$\alpha = \begin{cases} 0 & \text{if } \cos \omega\tau_D \geq 0 \\ \pi & \text{if } \cos \omega\tau_D < 0 \end{cases}$$

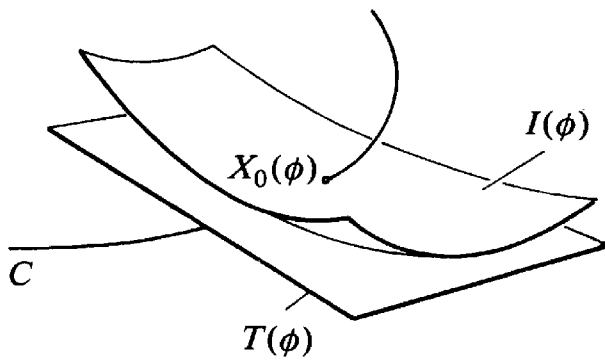
Thus we observe both frequency shifts and potential phase shifts. The synchronous state is stable only for $0 < \tau_D < \frac{\pi}{2\delta\omega}$. The details of this relation will change if the symmetry of the waveform changes, but the gist is correct.



Limit cycle orbit enclosed in a thin tube



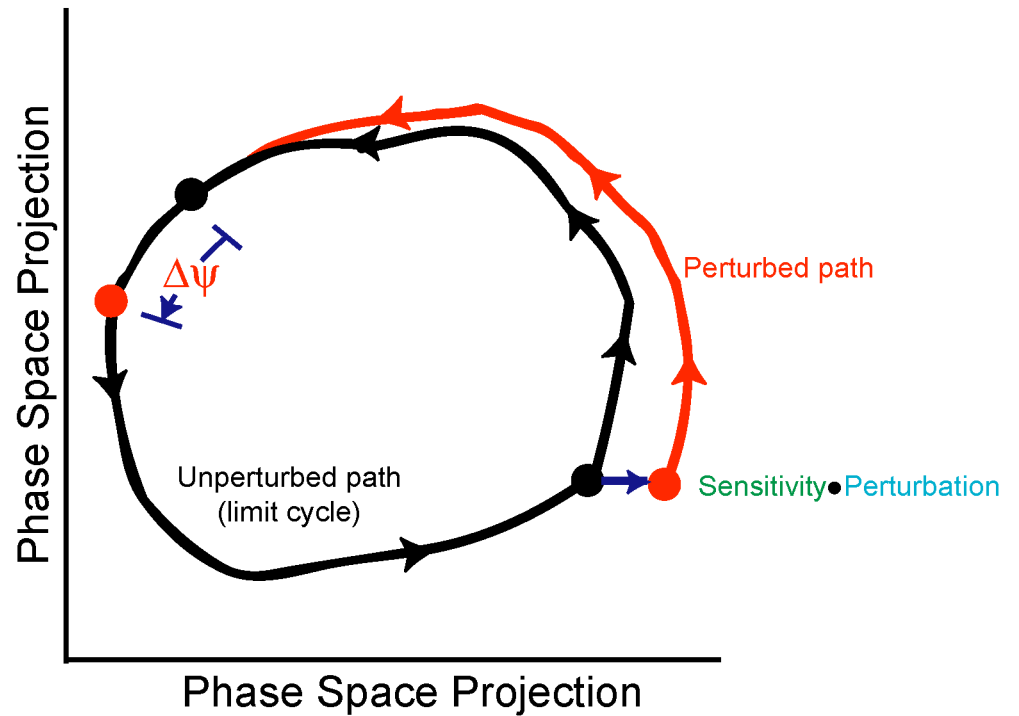
Geometrical meaning of $Z(\phi)$



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

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

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



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

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

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

The Kuromoto Phase Approach to Coupled Oscillators

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

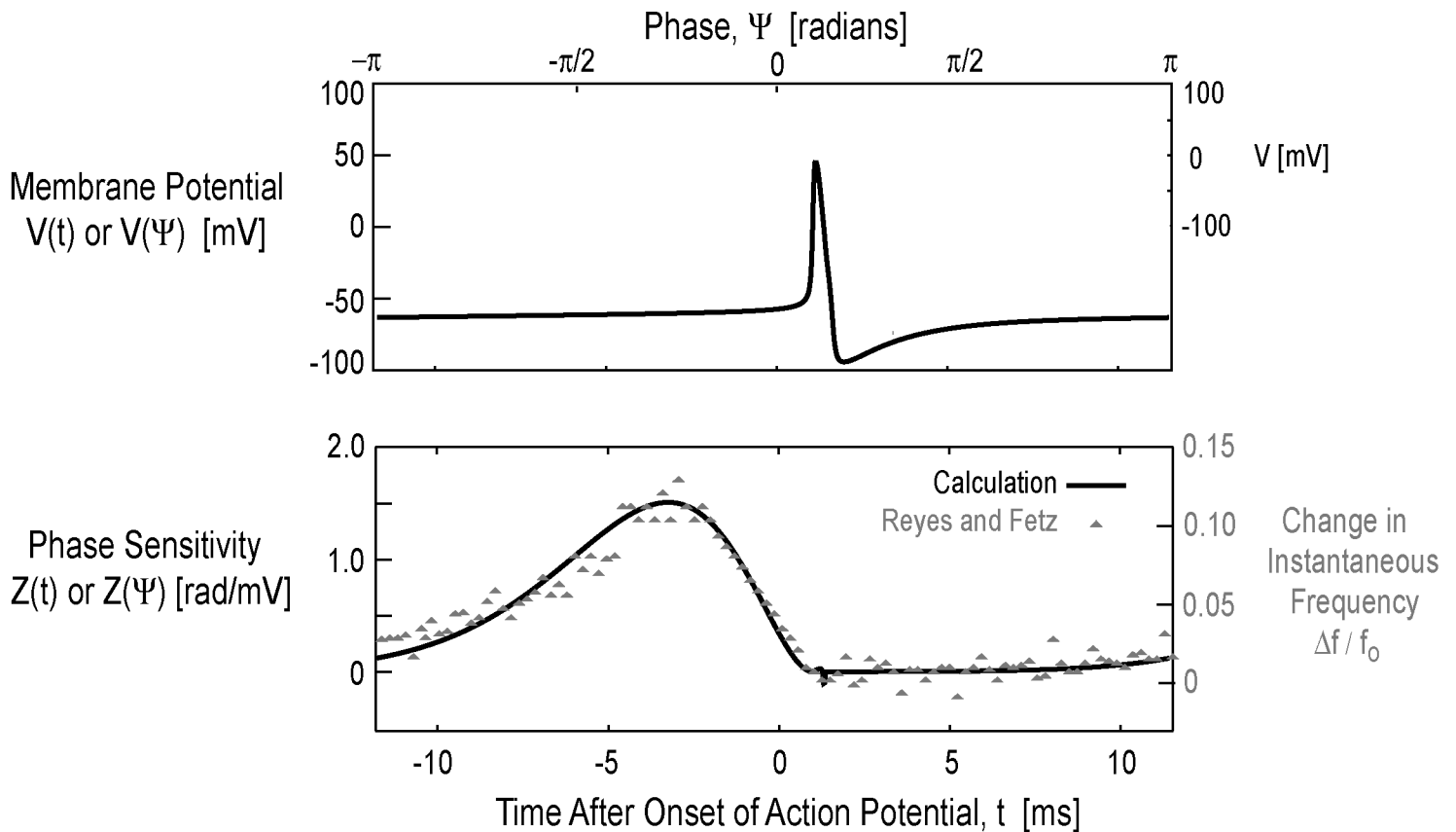
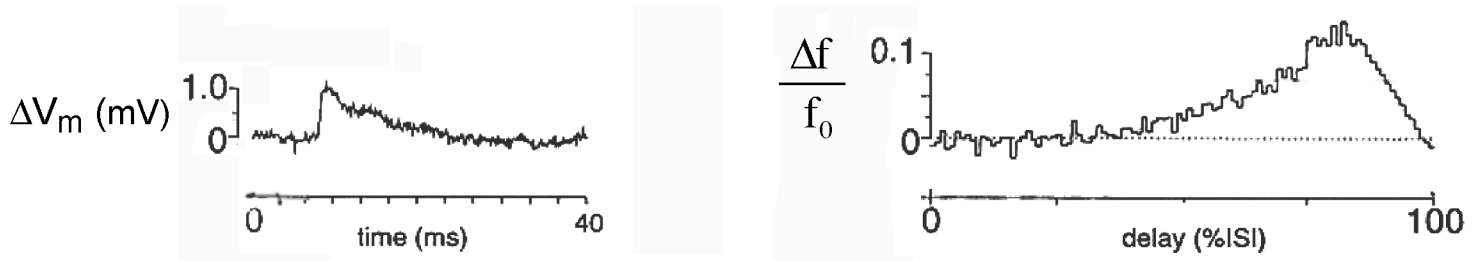
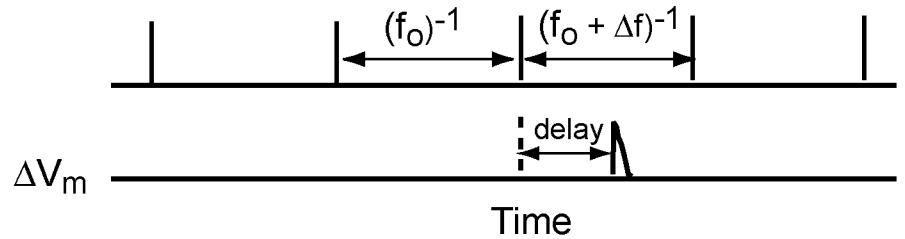
Phase reduction: $\frac{\partial \Psi_i}{\partial t} = \omega + \Gamma(\Psi_i - \Psi_j)$

$$\begin{aligned}
 \Gamma(\Psi_i - \Psi_j) &= \frac{\varepsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \quad \overset{\substack{\text{Sensitivity} \\ \text{Function}}}{\mathbf{Z}(\Psi_i + \theta)} \quad \overset{\text{Perturbation}}{\mathbf{P}(\Psi_i + \theta; \Psi_j + \theta)} \\
 &\quad \frac{g_{\text{synapse}}}{C_m} \mathbf{S}(\Psi_j + \theta) [E_{\text{synapse}} - \mathbf{V}(\Psi_i + \theta)] \\
 &= \frac{\varepsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \quad \frac{g_{\text{synapse}}}{C_m} \mathbf{Z}(\Psi_i + \theta) [E_{\text{synapse}} - \mathbf{V}(\Psi_i + \theta)] \mathbf{S}(\Psi_j + \theta) \\
 &\quad \mathbf{R}(\Psi_i + \theta) \\
 &= \frac{\varepsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \quad \mathbf{R}(\Psi_i + \theta) \mathbf{S}(\Psi_j + \theta) \\
 &= \frac{\varepsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \quad \mathbf{R}(\theta) \mathbf{S}[\theta - (\Psi_i - \Psi_j)] \\
 &\quad \text{Phase difference}
 \end{aligned}$$

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

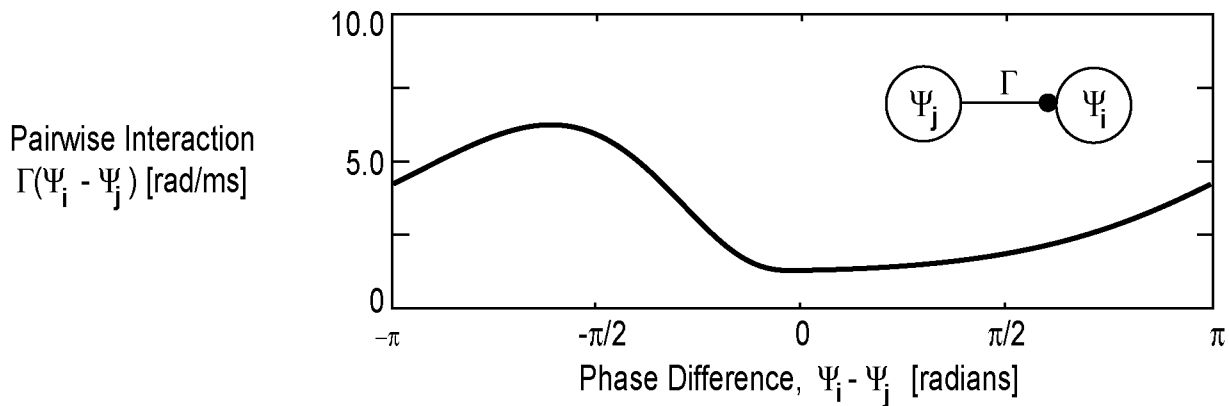
The Phase Sensitivity Function for Perturbation in Voltage Data (Reyes & Fetz 1993) vs. Calculation (Ermentrout & Kleinfeld 2000)

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

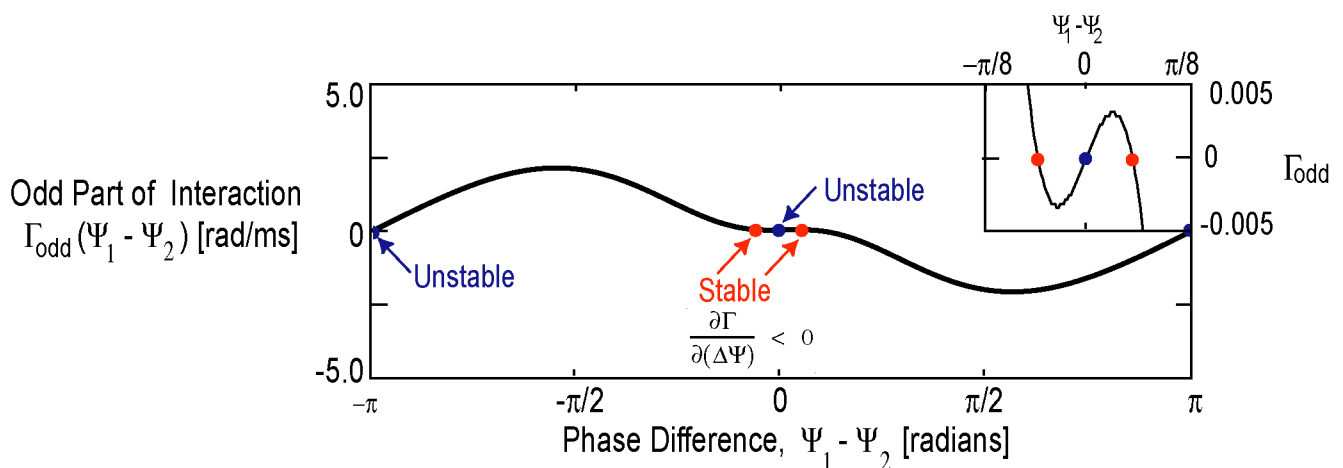


Lesson: Phase Sensitivity Concept Valid with Realistic PSPs

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



$$\begin{aligned} \frac{\partial \Psi_i}{\partial t} &= \omega + \Gamma(\Psi_i - \Psi_j) \\ \frac{\partial \Psi_j}{\partial t} &= \omega + \Gamma(\Psi_j - \Psi_i) \end{aligned} \quad \Rightarrow \quad \frac{\partial(\Psi_i - \Psi_j)}{\partial t} = \Gamma(\Psi_i - \Psi_j) - \Gamma(\Psi_j - \Psi_i)$$



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

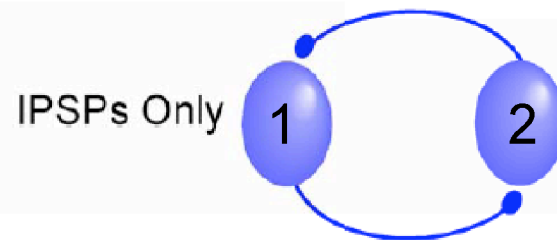
Challenge for Experimentalists is to Distinguish this from Broadening

Reciprocal, Kuromoto-like Inhibitory Coupling Among Pairs of Neurons

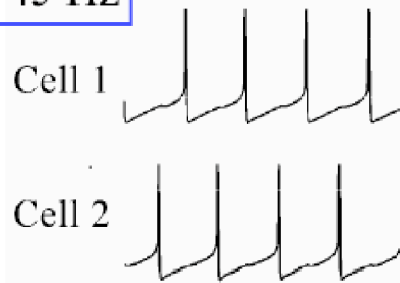
Firing Switches from Antisynchrony to Synchrony near 80 Hz

(data from Barry Connors Laboratory)

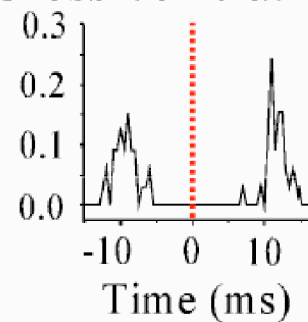
$$\Gamma(\Delta\psi) - \Gamma(-\Delta\psi) = g \frac{(\omega\tau)^2 - 1}{[1 + (\omega\tau)^2]^2} \sin(\Delta\psi) < 0 \text{ for } \omega > \tau^{-1}$$



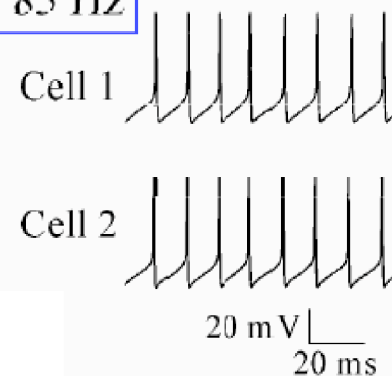
45 Hz



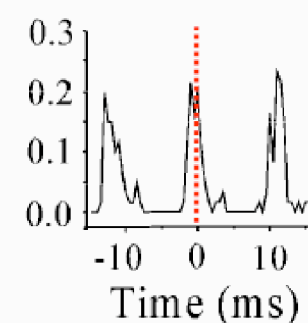
Cross-correlation



85 Hz



Cross-correlation

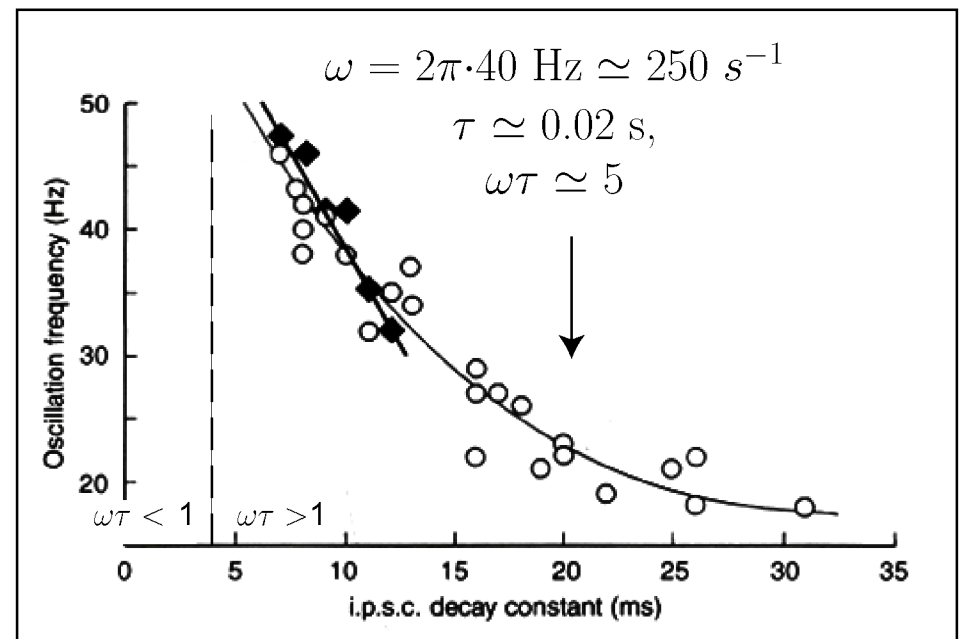
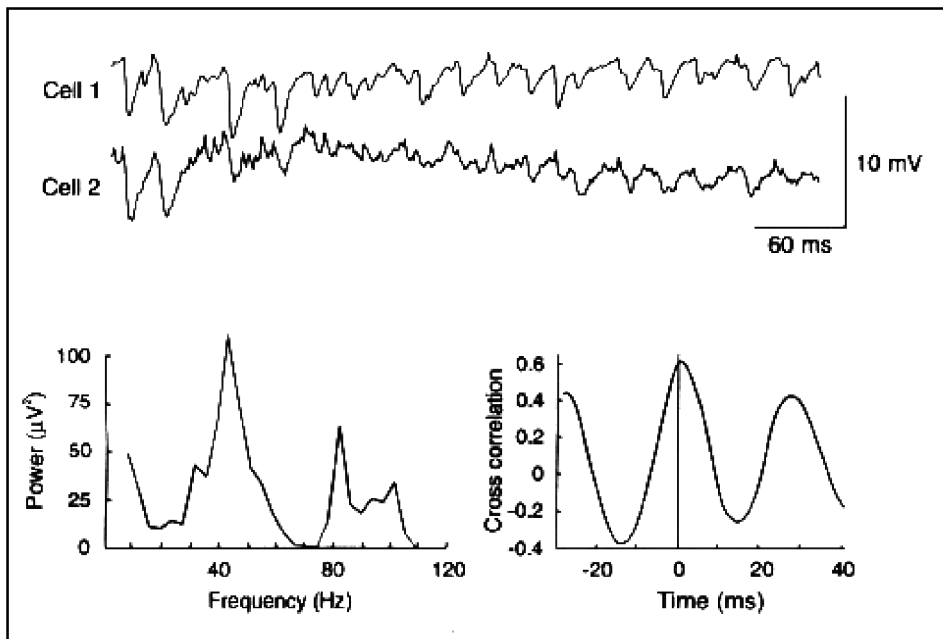
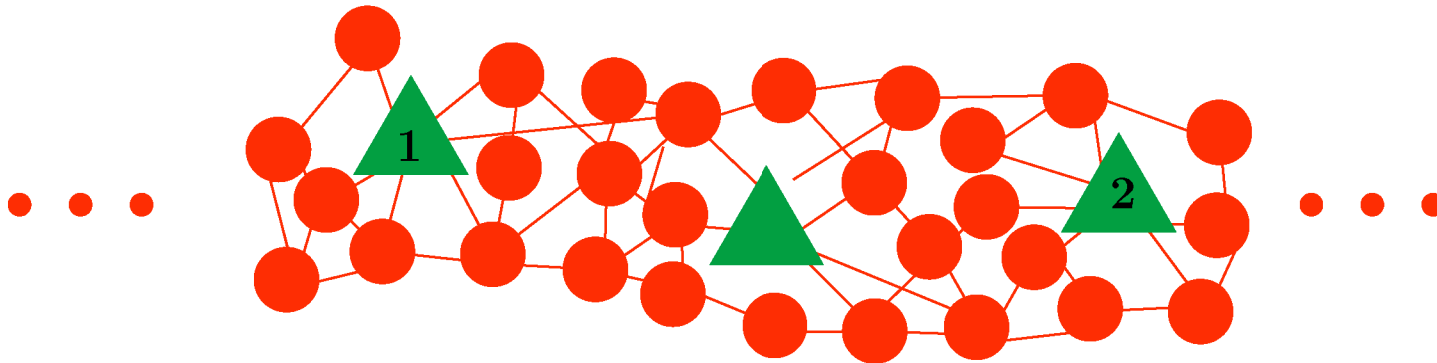


Reciprocal, Kuromoto-like Inhibitory Coupling in a Network of Neurons

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

(Whittington, Traub and Jeffreys 1995)

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



The Nature of the Coupling Between Segmental Oscillators of the Lamprey Spinal Generator for Locomotion: A Mathematical Model

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² Department of Theoretical and Applied Mechanics and Center for Applied Mathematics, Cornell University, Ithaca, NY 14853, USA

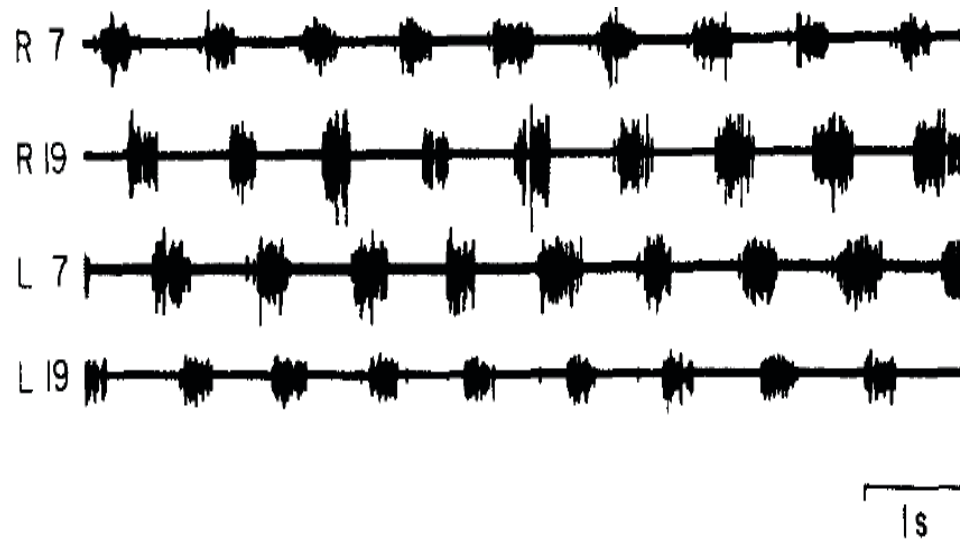
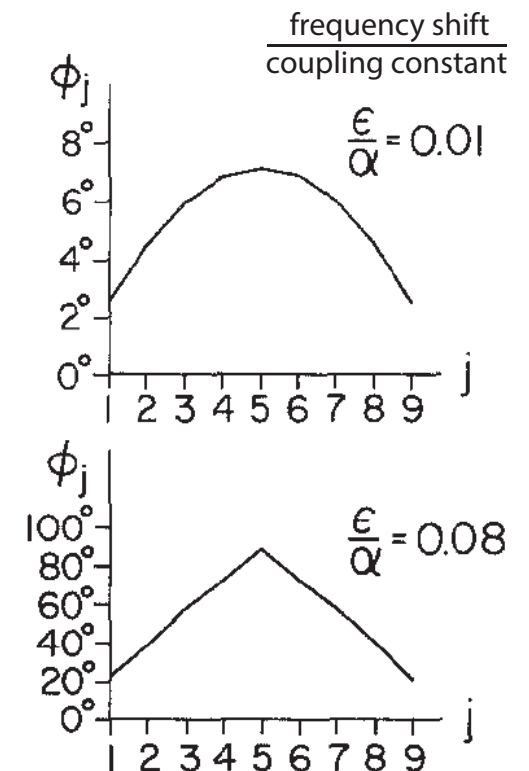
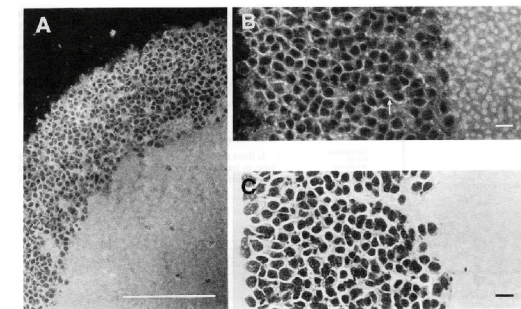
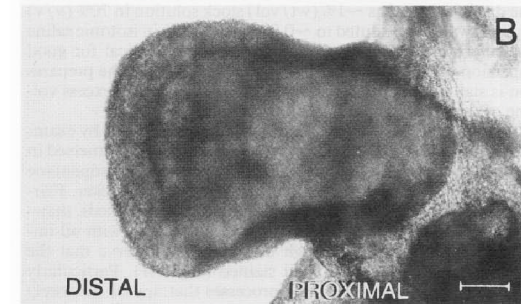
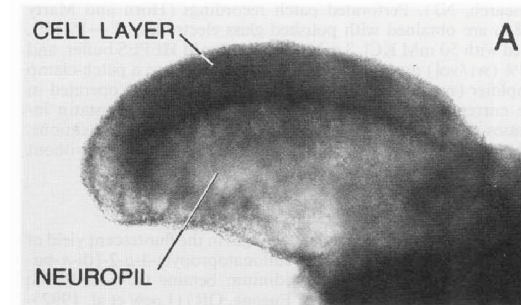
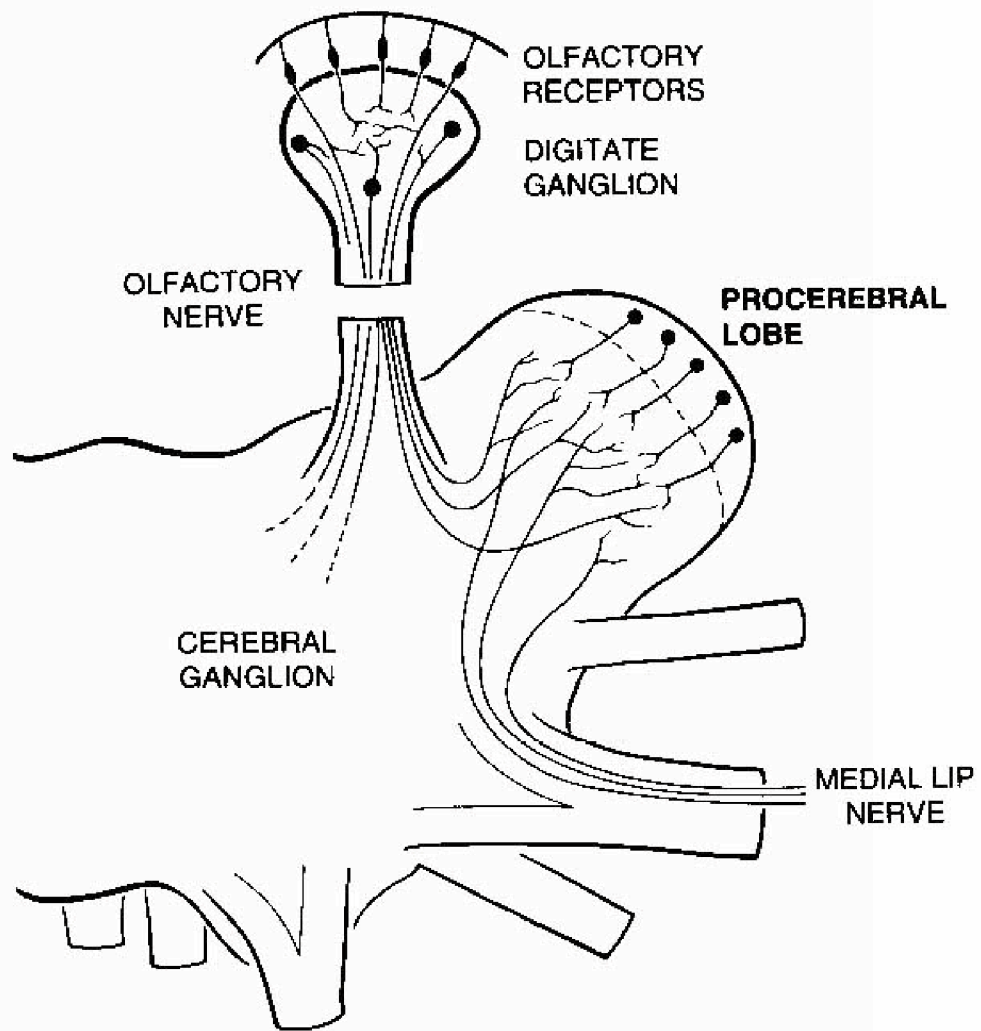


Fig. 1.2. Ventral root recordings from an isolated piece of spinal cord. Recordings are from the right and left roots of segments 7 and 19 (from Cohen and Wallén, 1980)



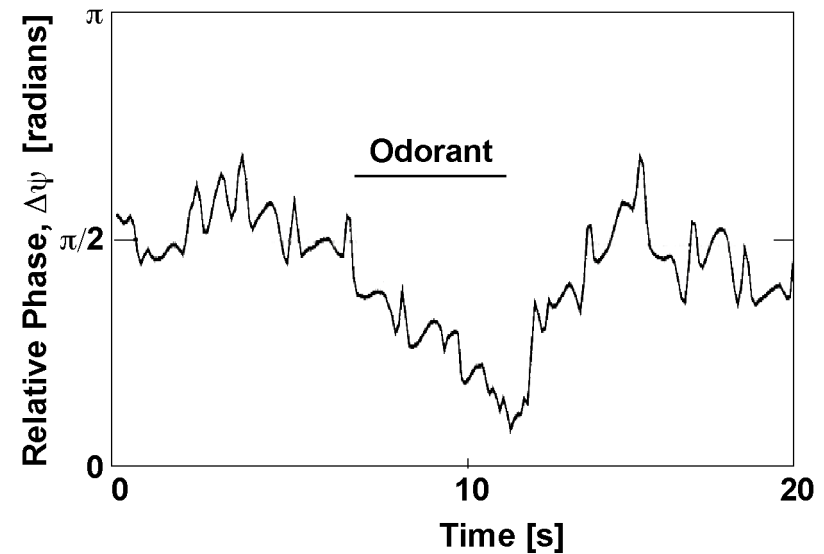
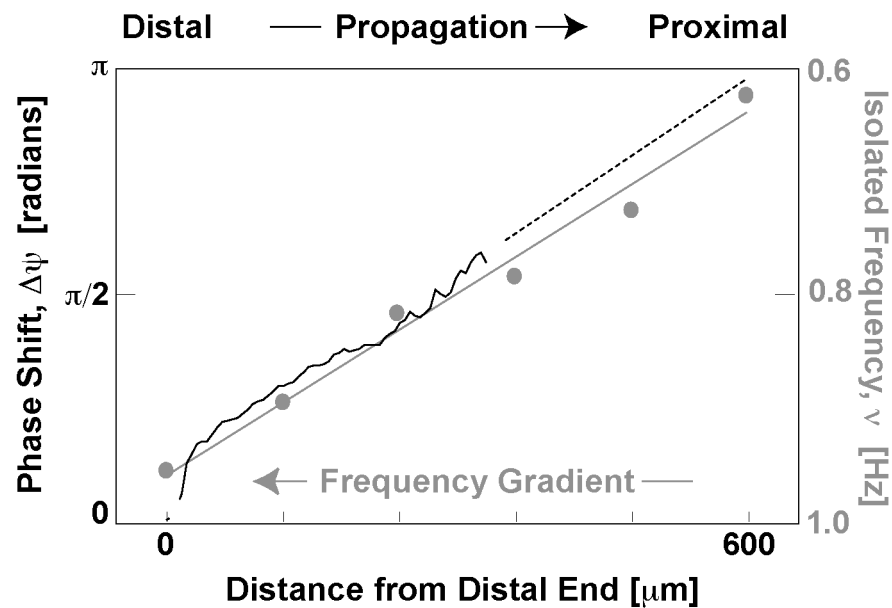
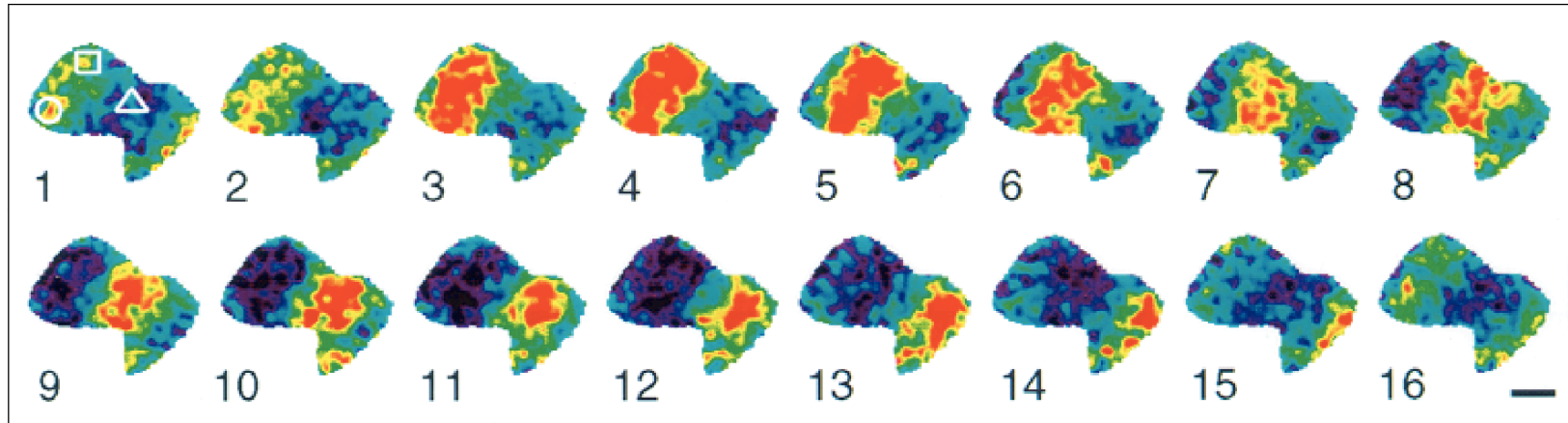


Central Olfactory Organ in the Terrestrial Mollusk *Limax*



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., $\frac{d\psi}{dt} = \frac{d\psi'}{dt}$ 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)

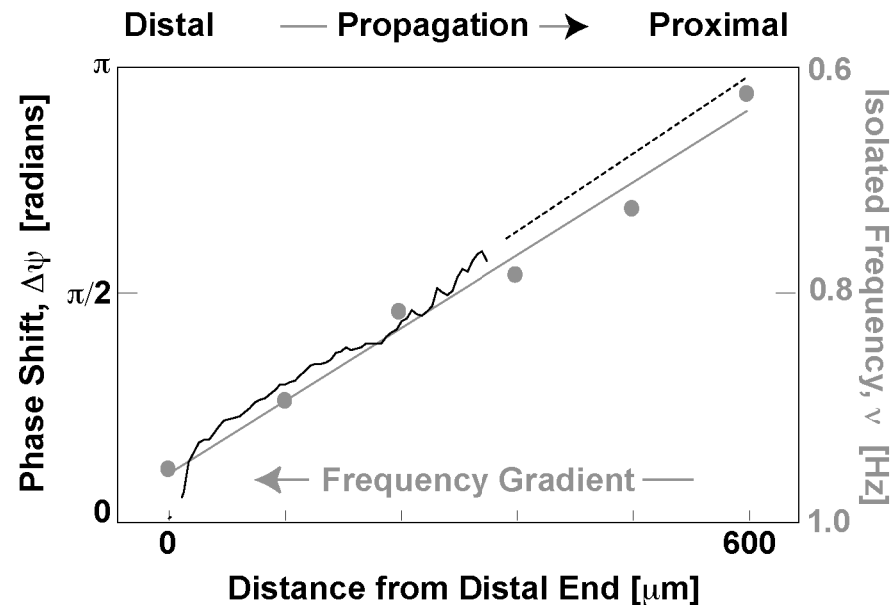
Chain of Oscillators with $\delta\omega \propto x$

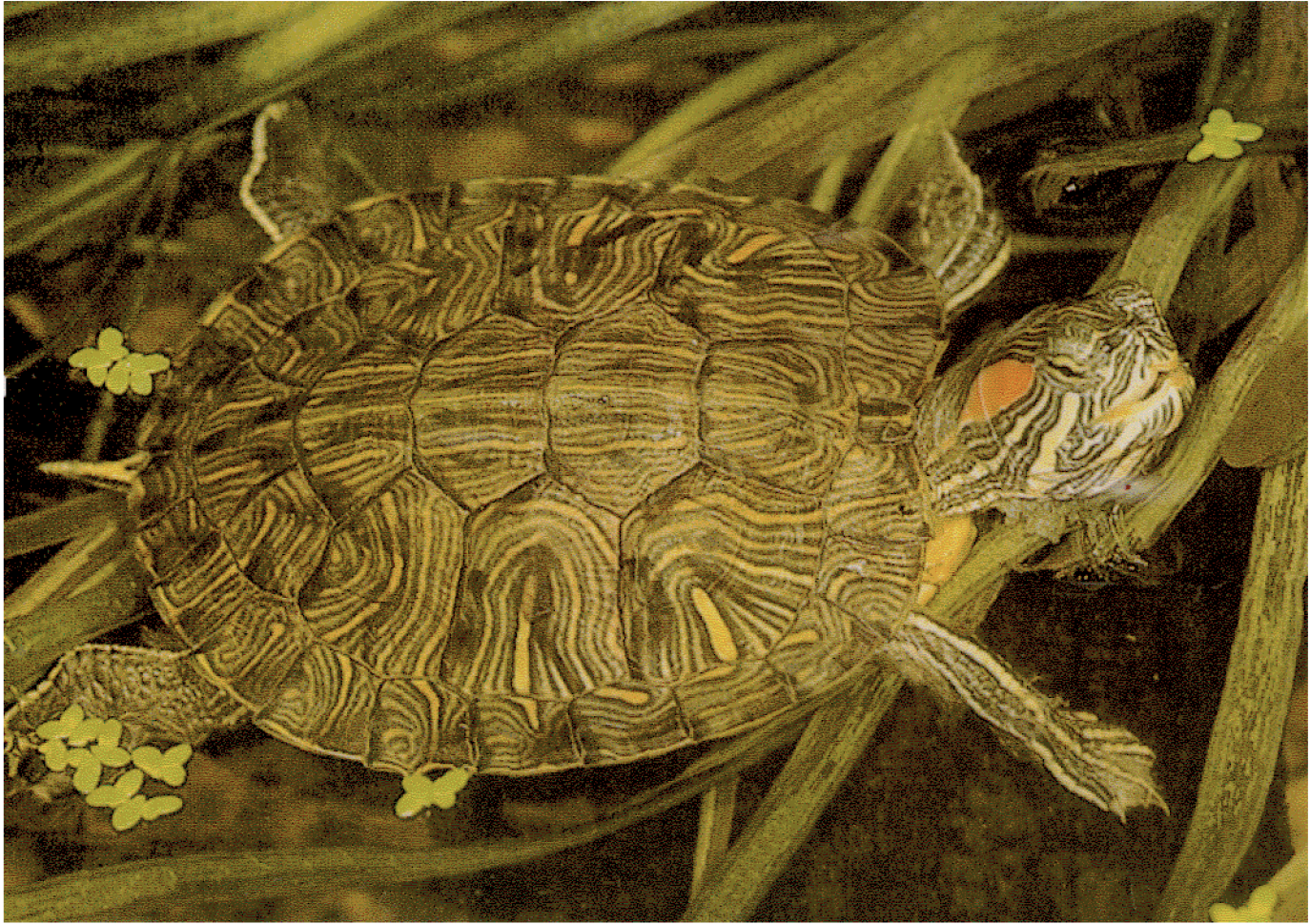
$$\frac{d\psi_x}{dt} = (\underbrace{\omega + \delta\omega_x}_{\delta\omega_x \propto x}) + \sum_{x \neq x'} \Gamma(\psi_x - \psi_{x'})$$

Single frequency

When the network locks:

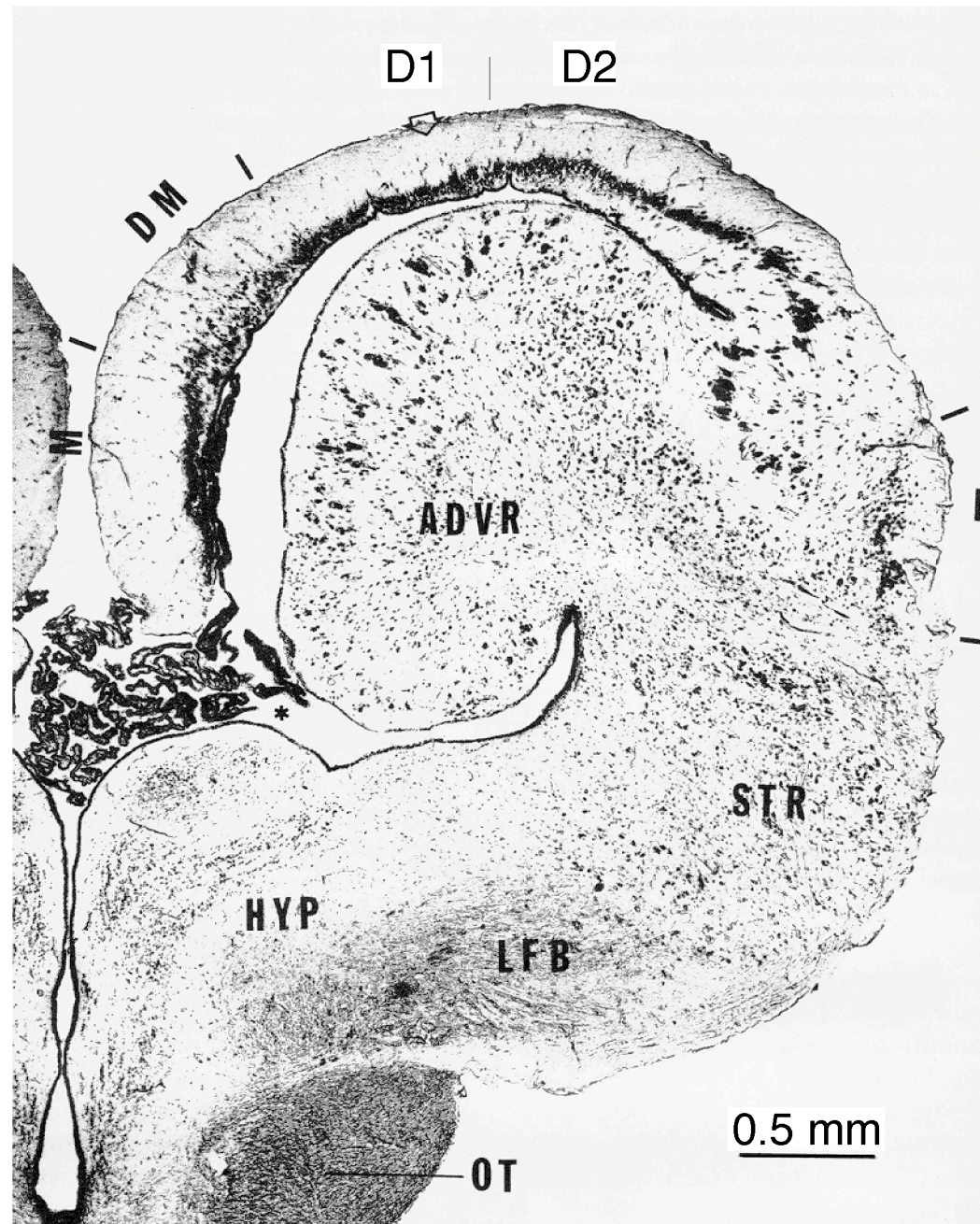
Gradient of phase shifts with $\frac{\psi_x}{dx} \propto \text{constant}$.



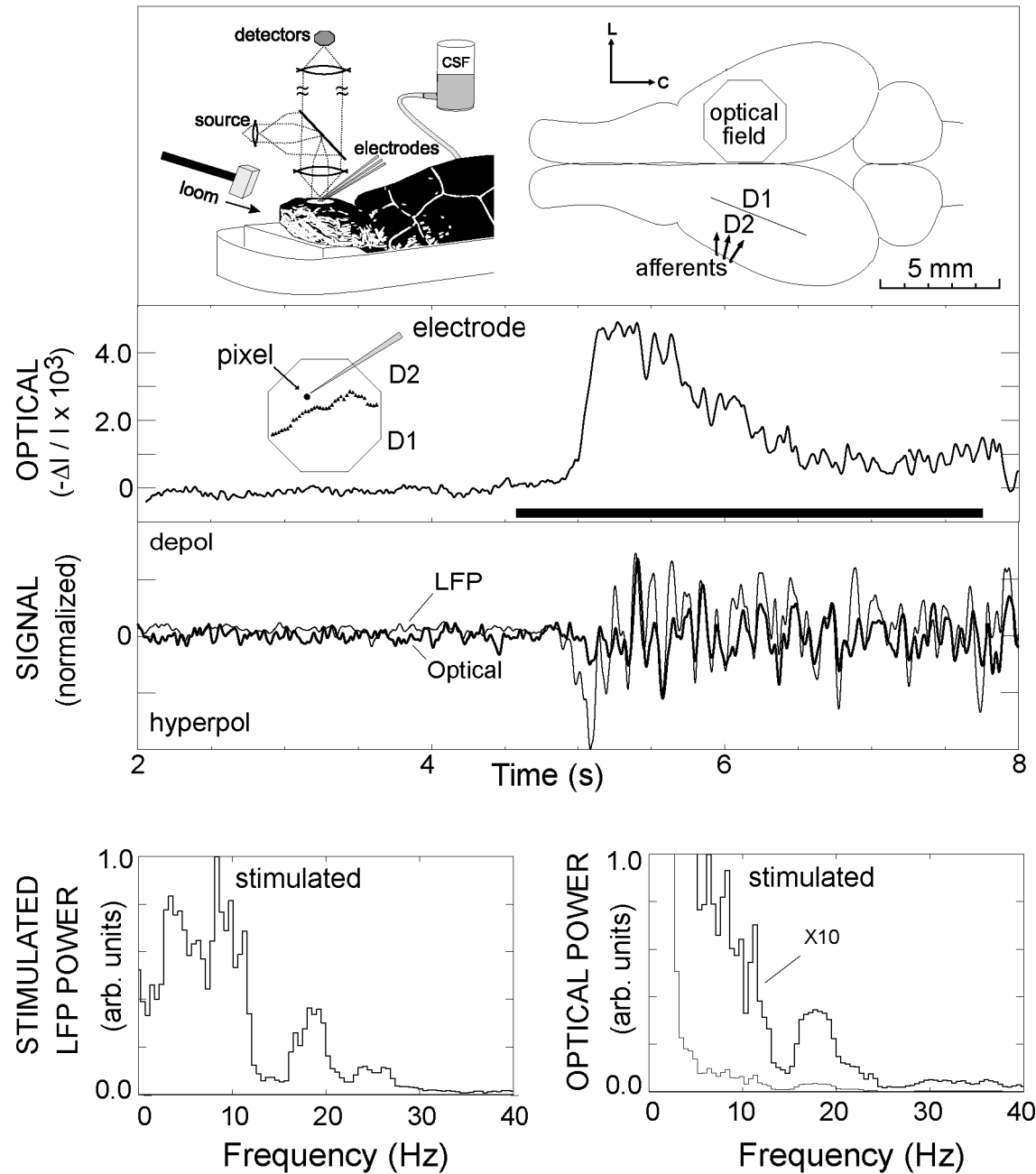


Transverse Nissl section through cerebral hemisphere of *Pseudemys scripta elegans*

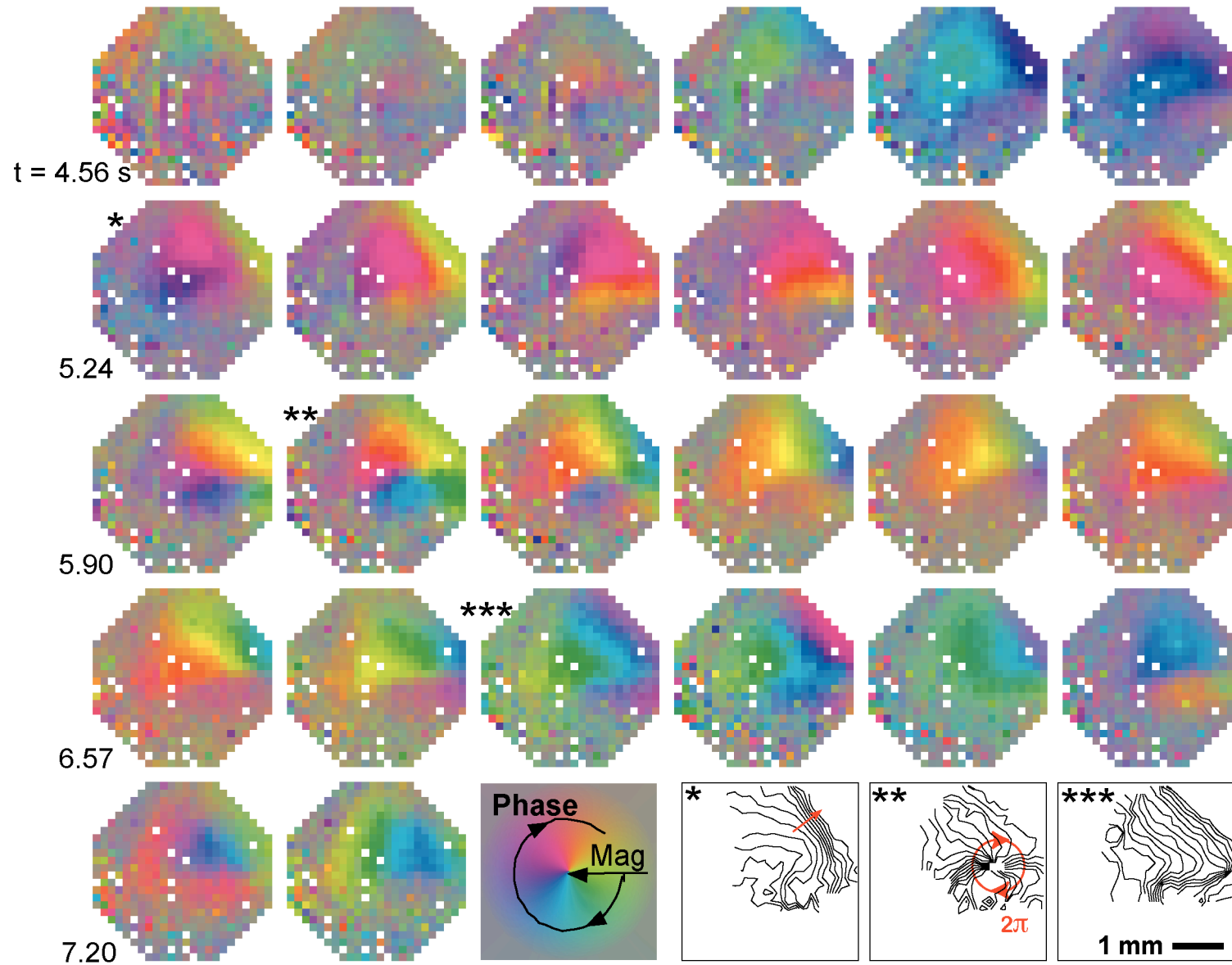
- from P. S. Ulinski



Voltage Sensitive Dye Imaging of Turtle Visual Cortex

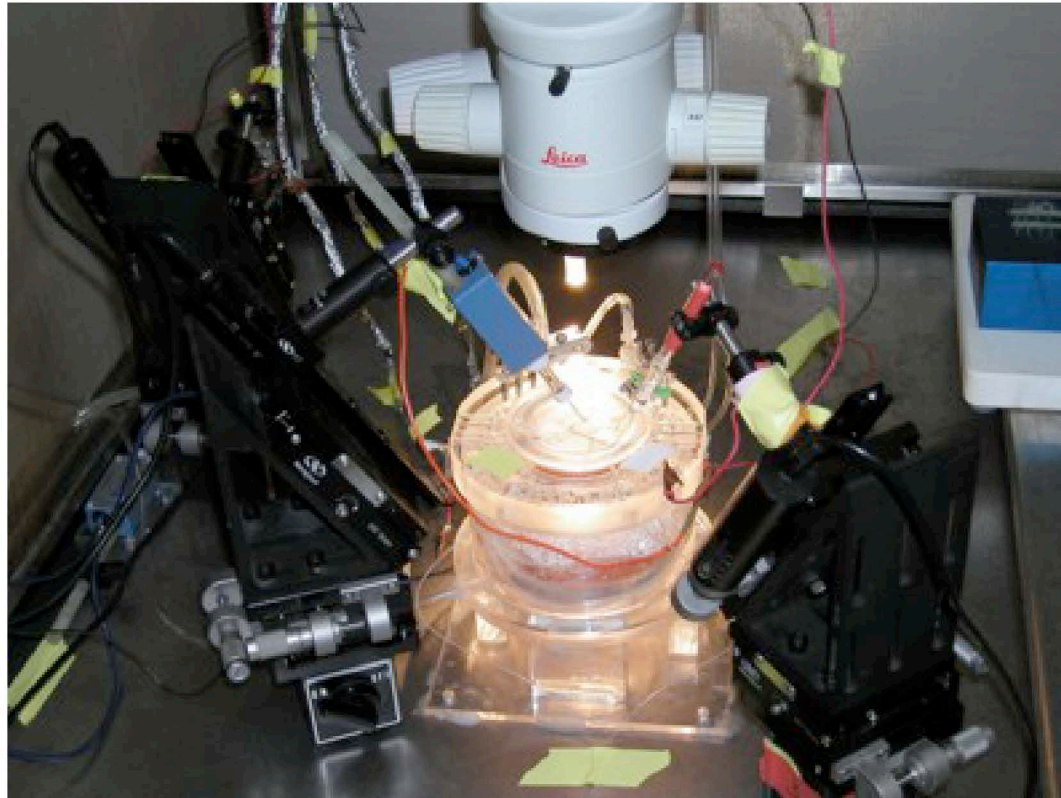


Demodulated Response at 18 Hz Versus Time (Magnitude and Phase Plots)



Upcoming Applications for Kuromoto-like Coupling

Spiral Waves in Disinhibited Mammalian Neocortex (Huang, Troy, Yang, Ma, Laing, Schiff and Wu, 2004)

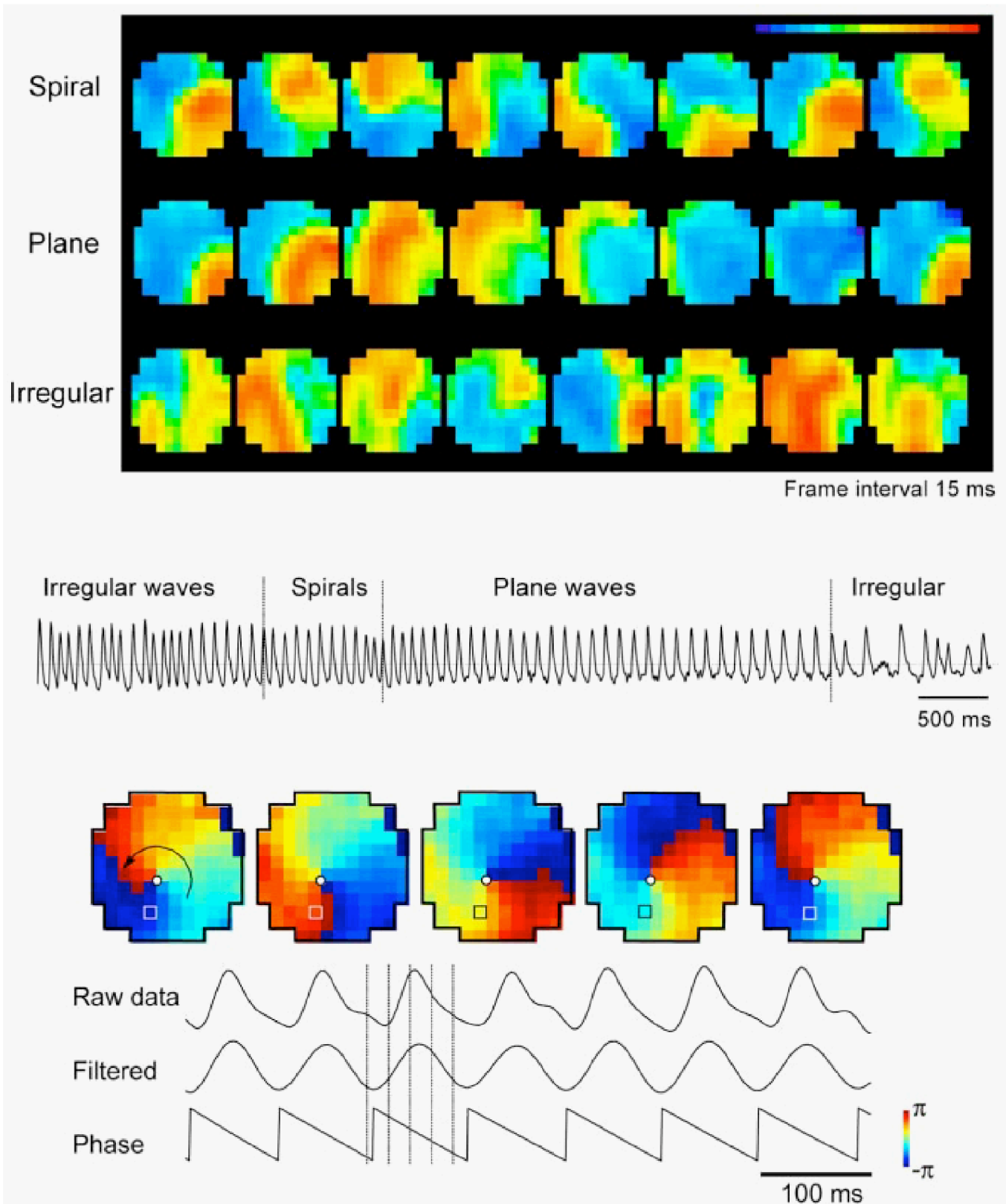


Electrical (local field potential) and optical (voltage sensitive dyes and brightfield illumination) recording of spatially averaged ($\sim 100 \mu\text{m}$) activity across layer 2/3 tangential slice

Upcoming Applications for Kuromoto-like Coupling

Spiral Waves in Disinhibited Mammalian Neocortex

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





Rotating waves during human sleep spindles organize global patterns of activity that repeat precisely through the night

Lyle Muller¹, Giovanni Piantoni², Dominik Koller¹, Sydney S Cash², Eric Halgren^{3,4}, Terrence J Sejnowski^{1*}

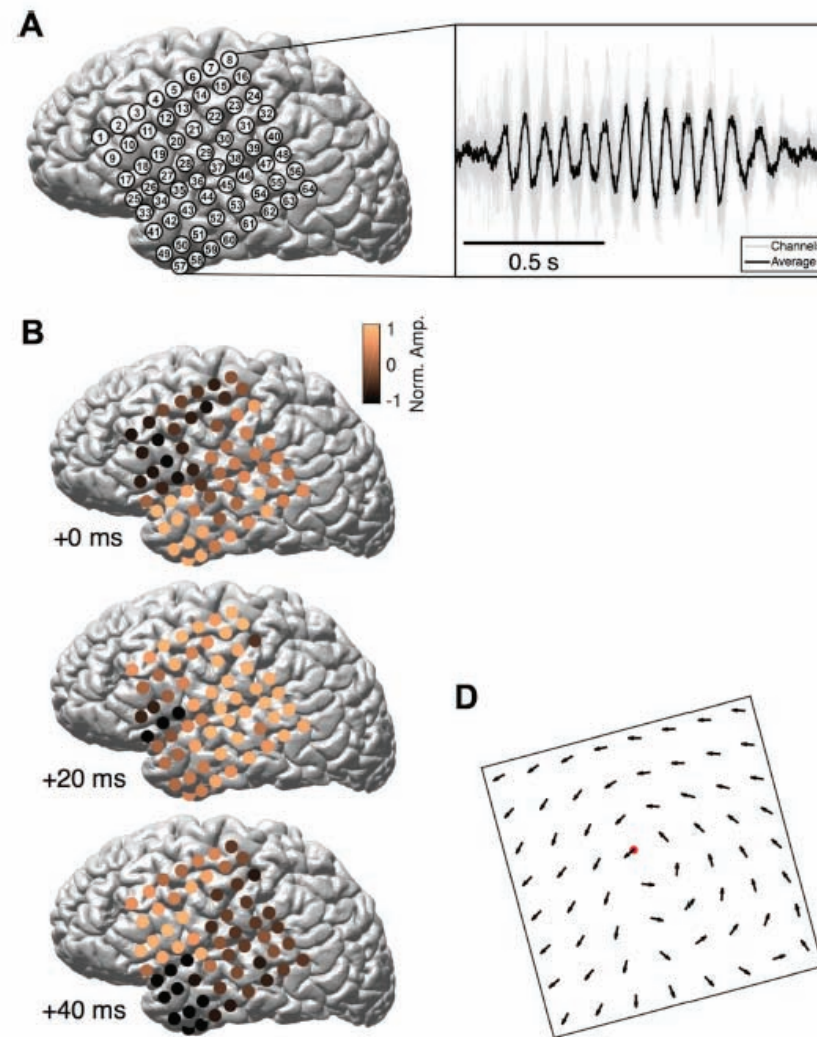
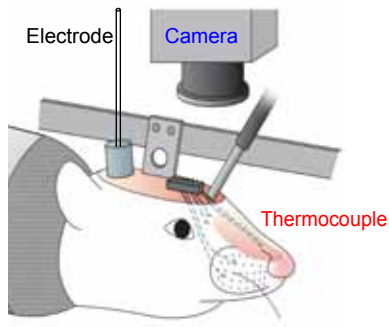


Figure 1. Rotating waves during spindles. (A) Electrode placement for subject 1 (left), with a stereotypical spindling epoch observed on the array (right). The right panel depicts the average over channels (black) together with the individual channels (gray). (B) When visualized on the cortex, individual 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.



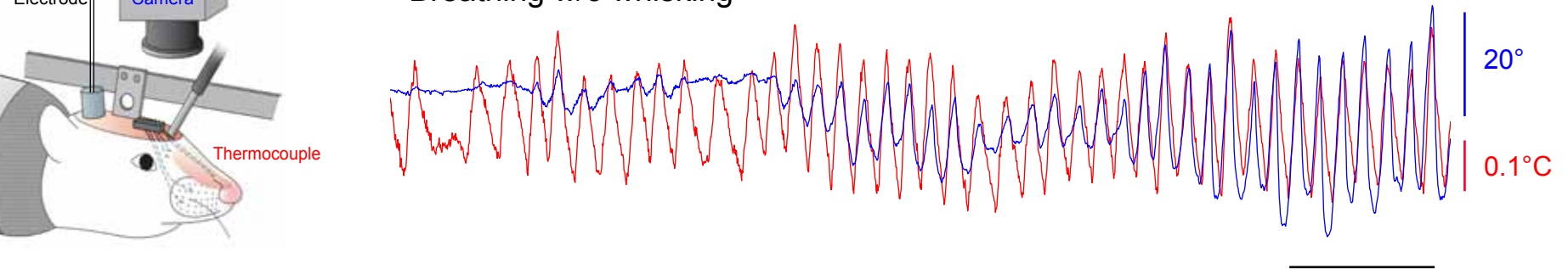
2012-02-05 13:23:26 7952 -78639,6[ms] 416x362, 80 Hz, 100
μs, *1, HiSpec 1 #00194, V1.11.9

Phase resetting of **whisking** by **breathing** (sniffing & basal respiration)

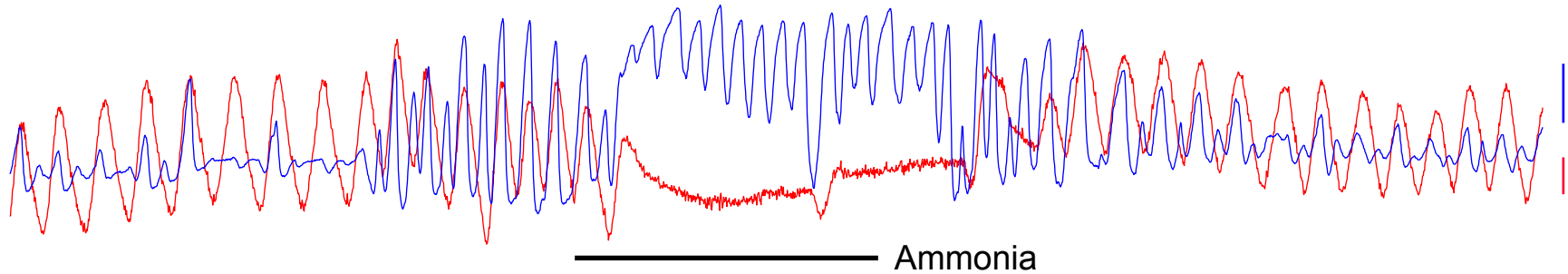


Breathing w/o whisking

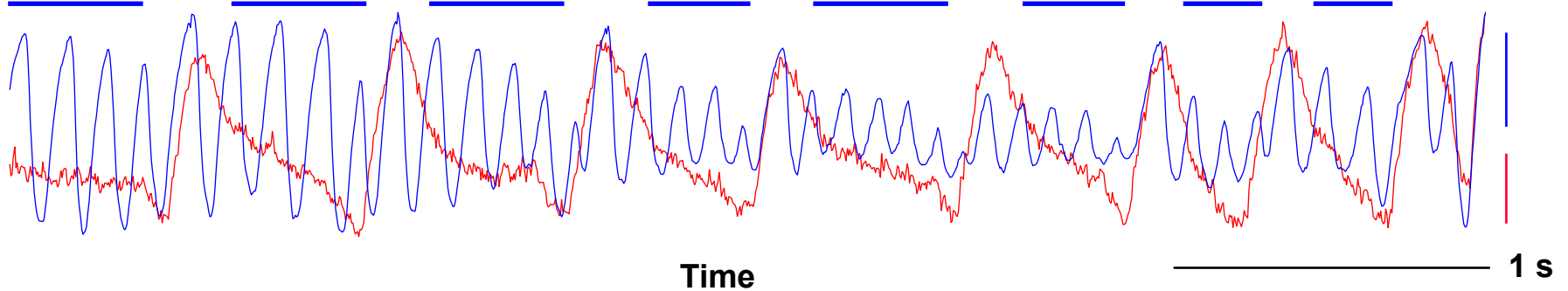
Sniffing and whisking



Whisking w/o breathing



Intervening
whisks



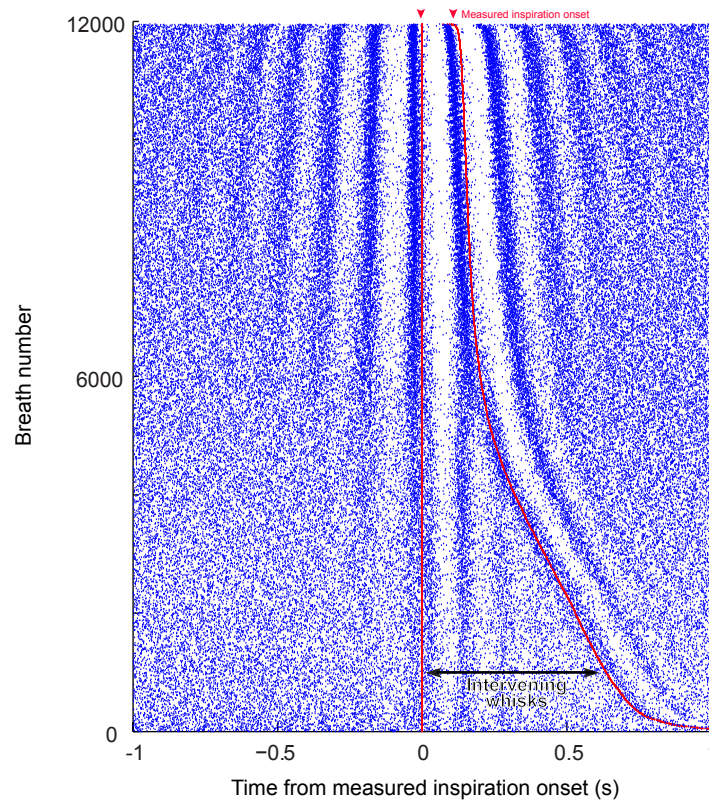


Figure S2. Coordination of whisking and breathing in one rat.

Temporal relationship between whisking and breathing events. Raster plots of inspiration and protraction onset times relative to each breath are sorted by the duration of the breath. In an individual animal, the intrinsic whisking oscillation frequency is stable and locked to the measured breathing onset time at both basal respiratory frequencies as well as sniffing frequencies. During basal respiration, the first, second, and third whisks following inspiratory drive occur at stereotypic times relative to breathing.

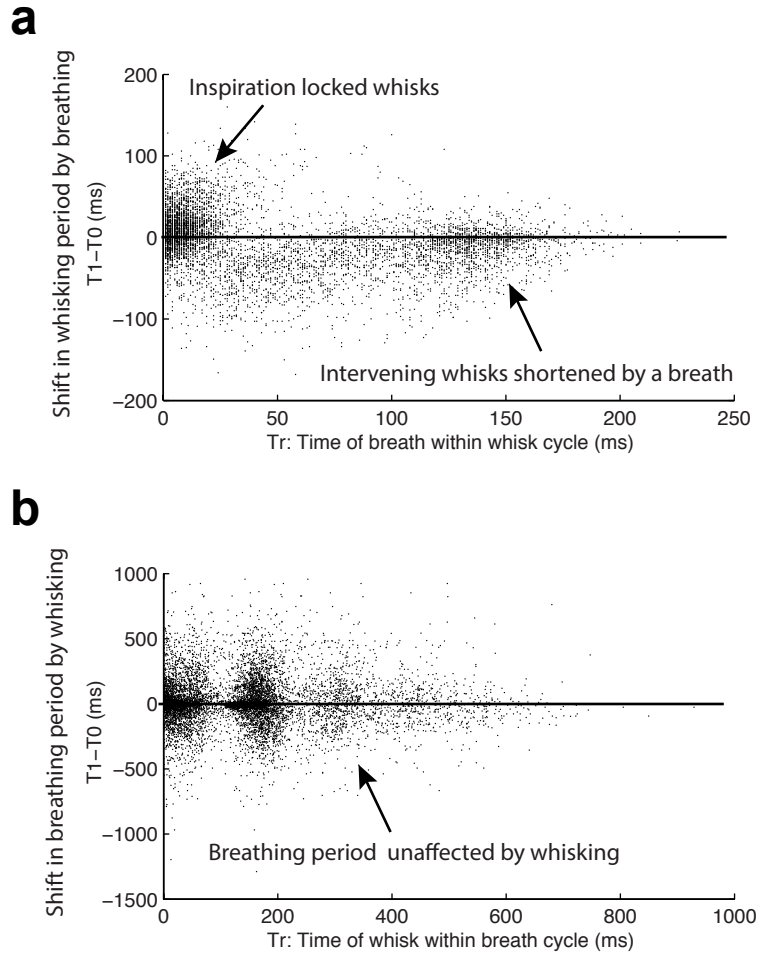


Figure S5. Response of the whisking rhythm to breathing versus the breathing rhythm to whisking

To emphasize the asymmetric interaction between whisking and breathing, we plot the shift in period ($T_1 - T_0$) of each behavior as a function of the time within the cycle when the other behavior occurs (treset). As in **Figure S4**, T_0 represents the expected period of the perturbed behavior, taken as the period of the cycle prior to that which contains an interrupting event, and T_1 represents the interrupted period. Unlike **Figure S4**, both sniffing and basal respiratory frequencies are included in the analysis to permit a symmetric comparison between the response of whisking to breathing and the response of breathing to whisking.

(a) Shift in whisking period ($T_1 - T_0$) relative to the reset by an inspiration (at times treset). As in Figure S4, there is a bias for the intervening whisks to be shortened by the onset of breathing during basal respiration. The inhalation locked whisks during sniffing are not in steady state and not so constrained.

(b) Shift in respiratory period ($T_1 - T_0$) relative to the reset by a vibrissa protraction (at times treset). There is a no apparent bias for the period of breathing to be shifted by the presence of a whisk during either sniffing or basal respiration.