The Olfaction Way

Noise, synchrony, and rhythms

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SIAM 08

San Diego

Olfactory rhythms

- Local field potential oscillations (20-40 Hz) in olfactory bulb
- Mediated by inhibitory granule cells
- IPSPs last 300-500 msec - too long for 20 Hz
- Small random 10-20 msec IPSPs on top

Overall picture

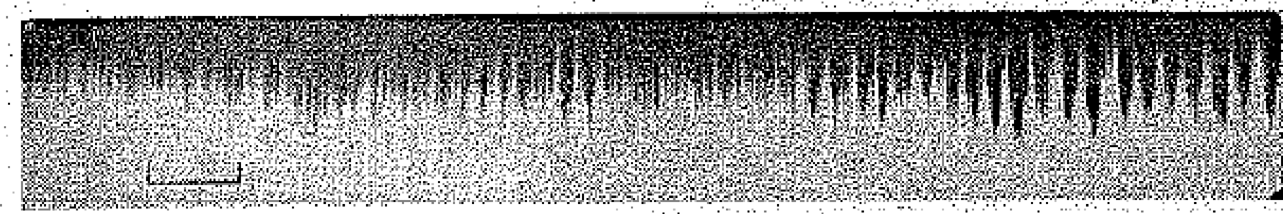
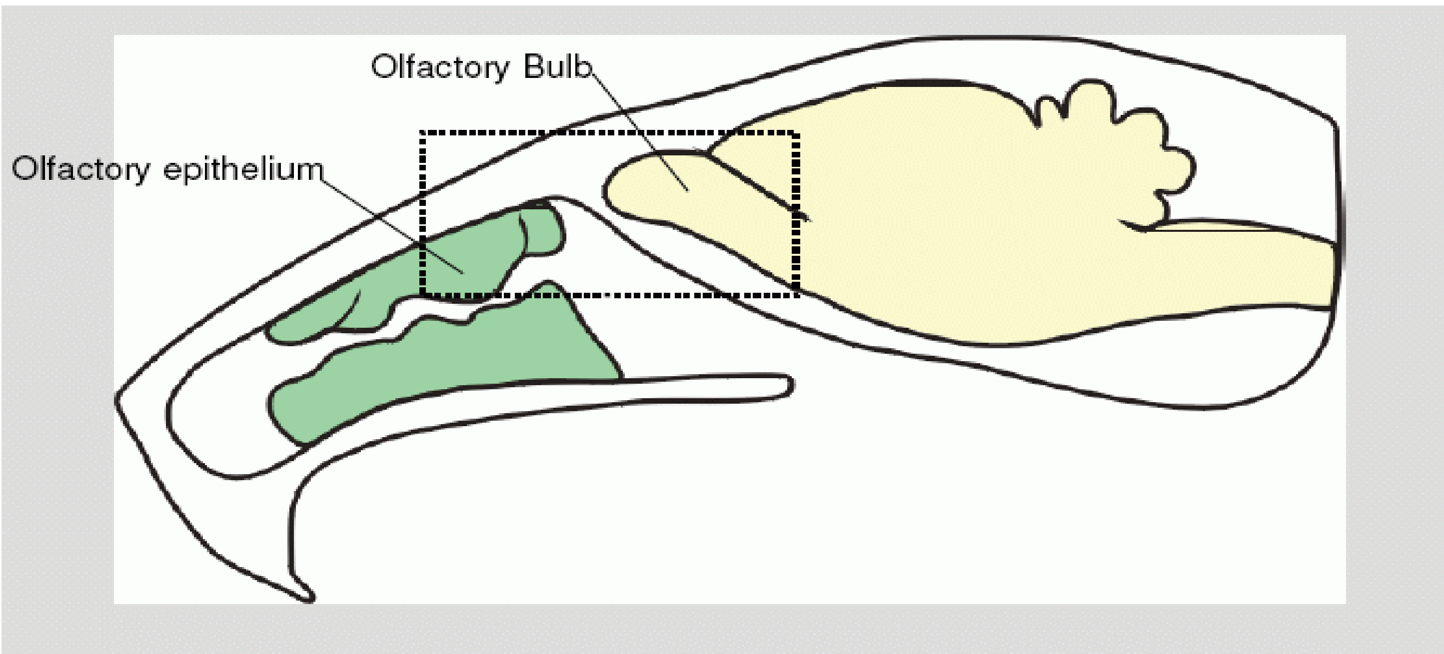
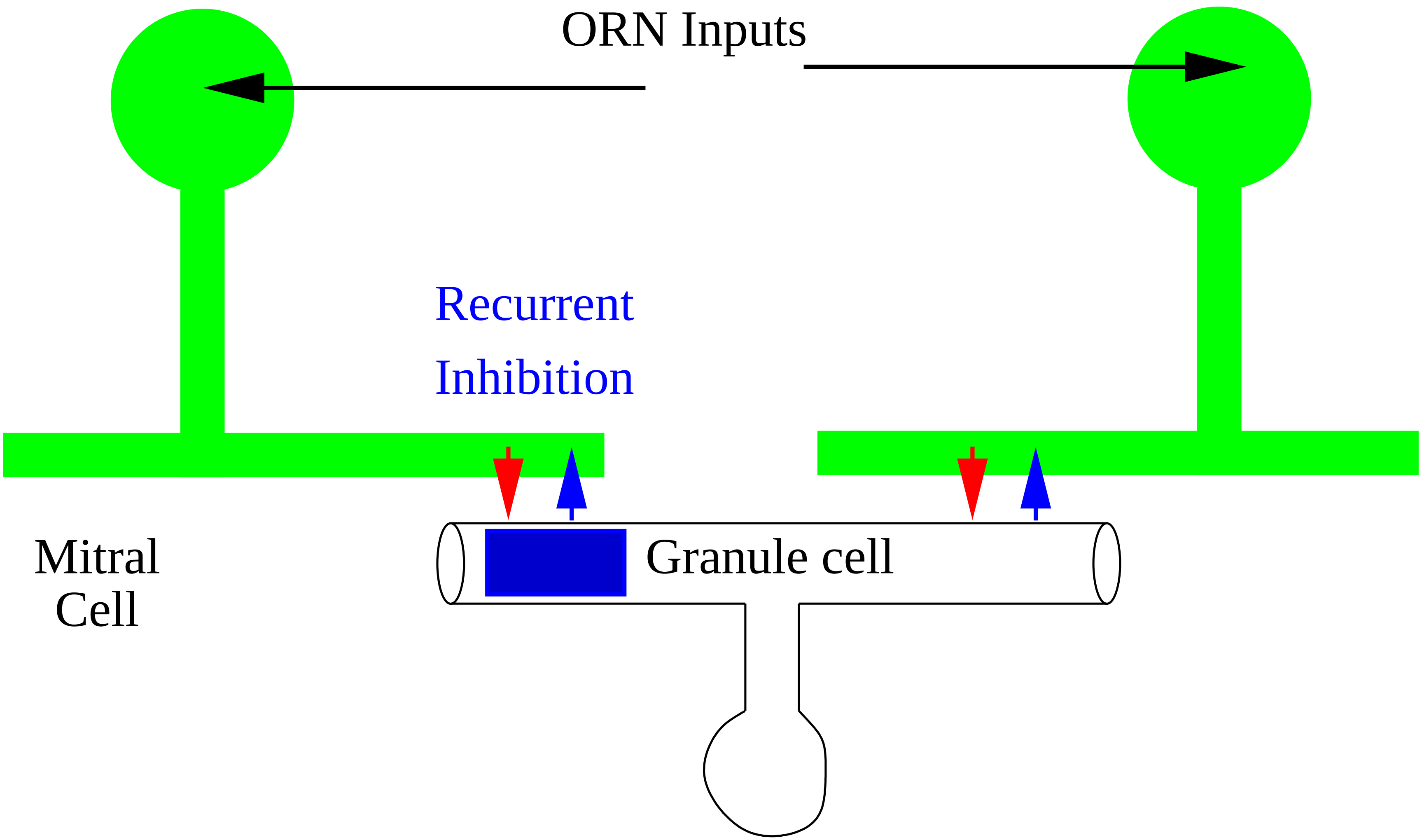


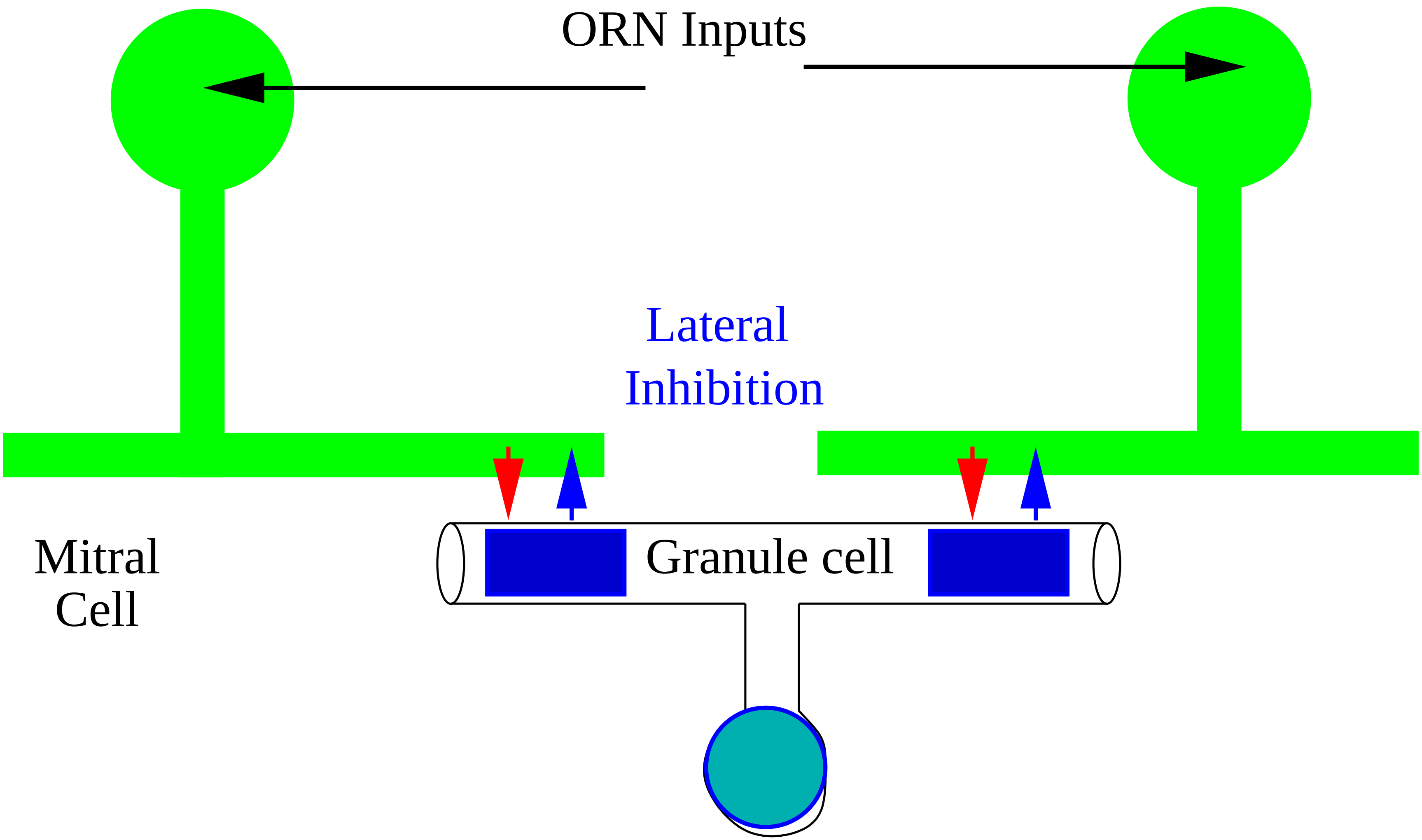
Fig. 12. Intense discharge produced by cigarette smoke. Hedgehog under chloralose with wire electrode in the olfactory bulb. Diffusion of smoke into the nose starts a series of volleys at 40 per sec. Adrian '42



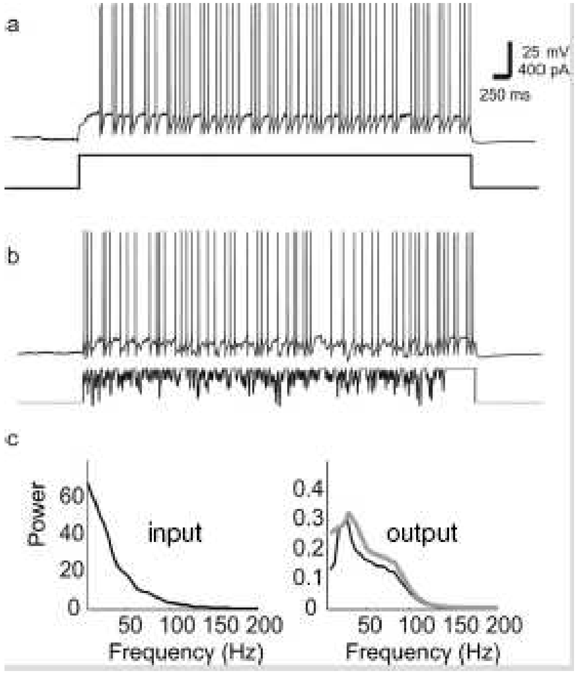
Diagram



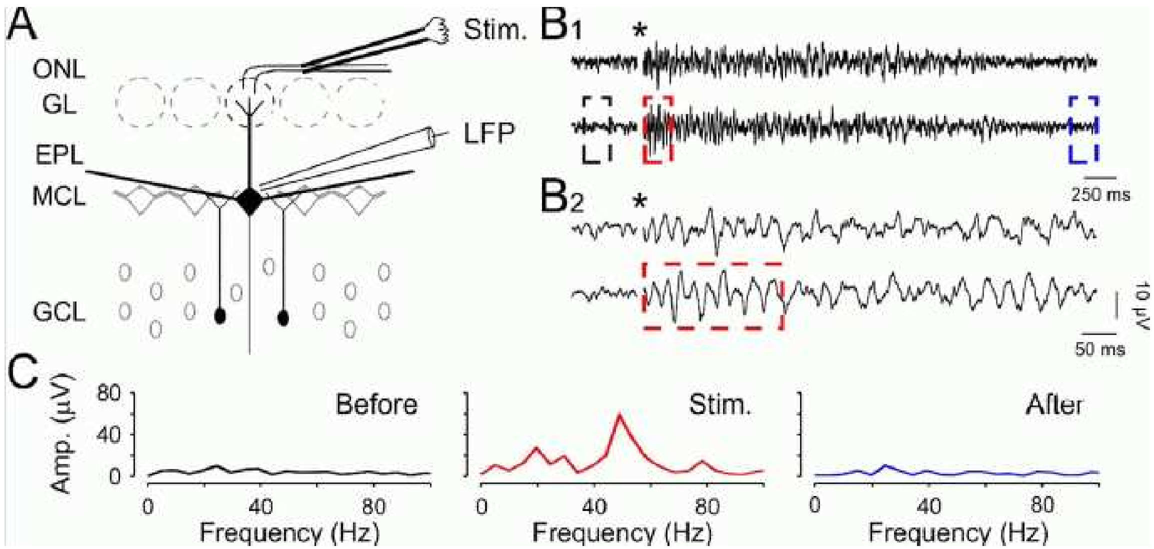
Diagram



Oscillations in the bulb



Galan et al 2006



Lagier et al 2004

Oscillations are good for

- Neocortical oscillations are altered as a function of behavioral state (e.g. attention, Desimone)
- Diminished neocortical oscillations seen in schizophrenic patients (McCarley)
- Electric fish – prey vs. nonprey recognition (Doiron, Longtin, Bastian)
- Odor discrimination in many species (Laurent, Kay)

Mechanisms

- PING/ING: fast short lasting feedback inhibition
- Entrainment to central pacemaker
- Noise induced synchrony (Stochastic synchrony)

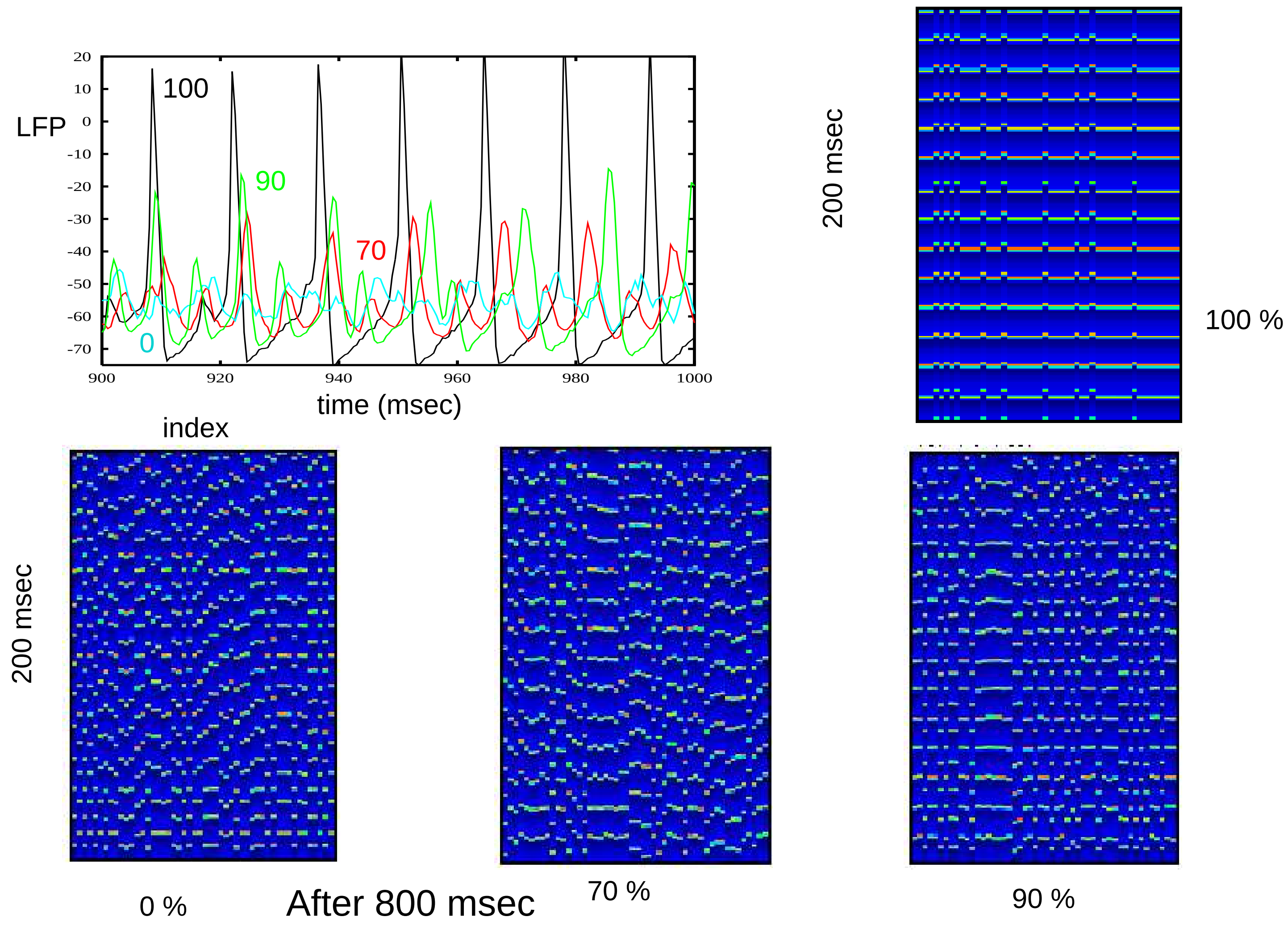
Stochastic synchrony

The basic idea is quite simple:

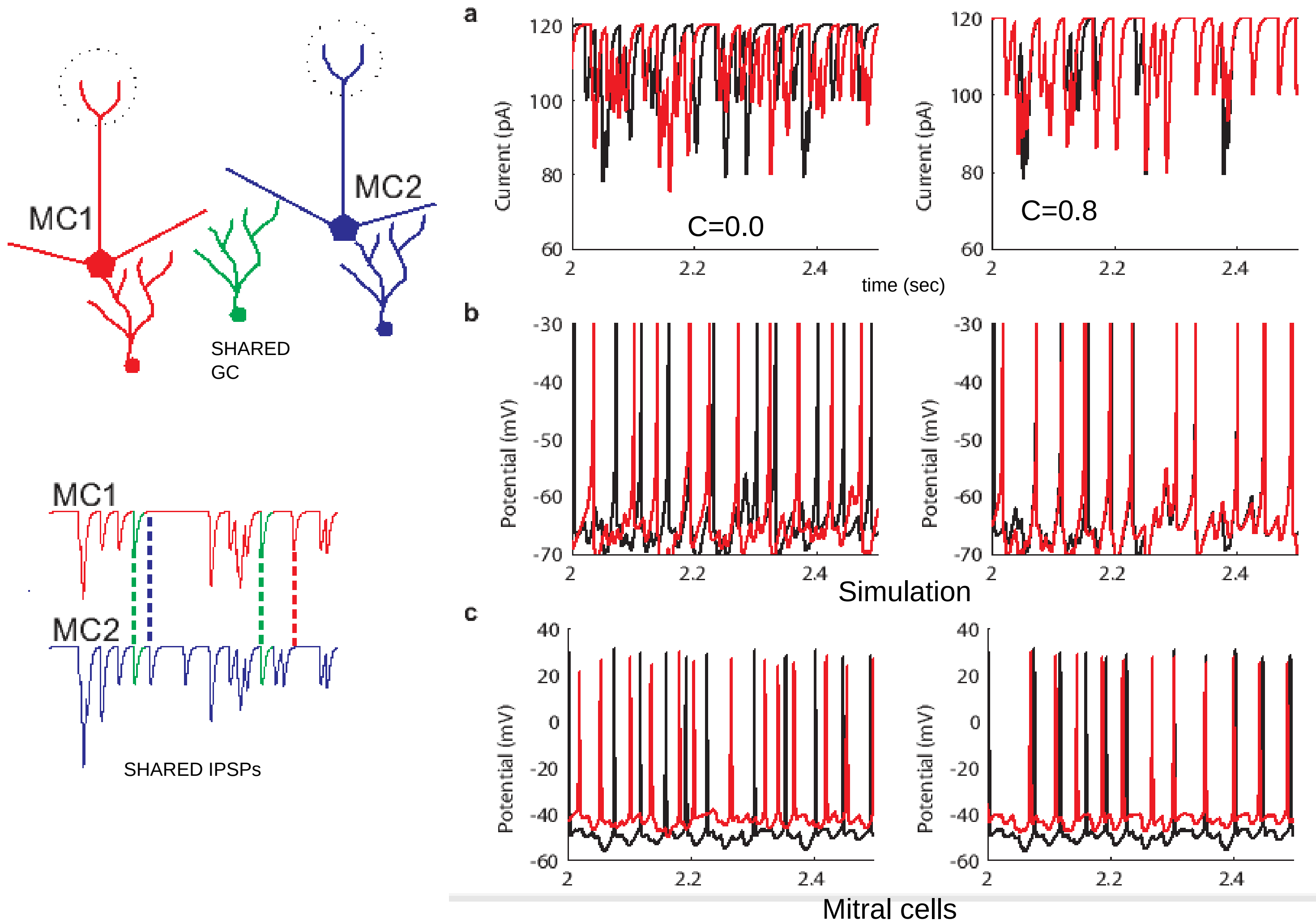
- Two oscillators share common noise
- Not enough to effect firing rate
- Push the phases together

$$X_j' = F(X_j) + q\ \underbrace{\Xi(t)}_{\text{Shared noise}} + \sqrt{1-q^2}\ \underbrace{\Xi_j(t)}_{\text{Independent noise}}$$

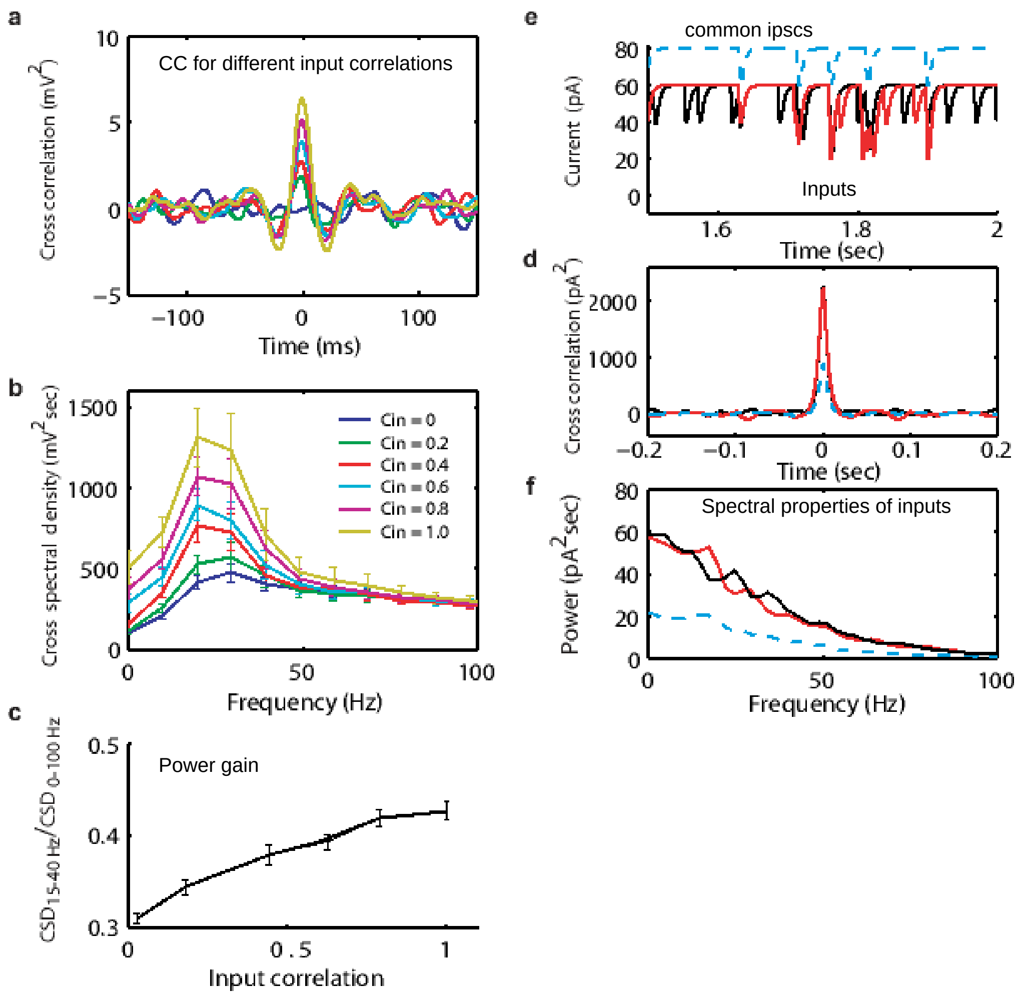
Hodgkin Huxley Example



Mitral cell example

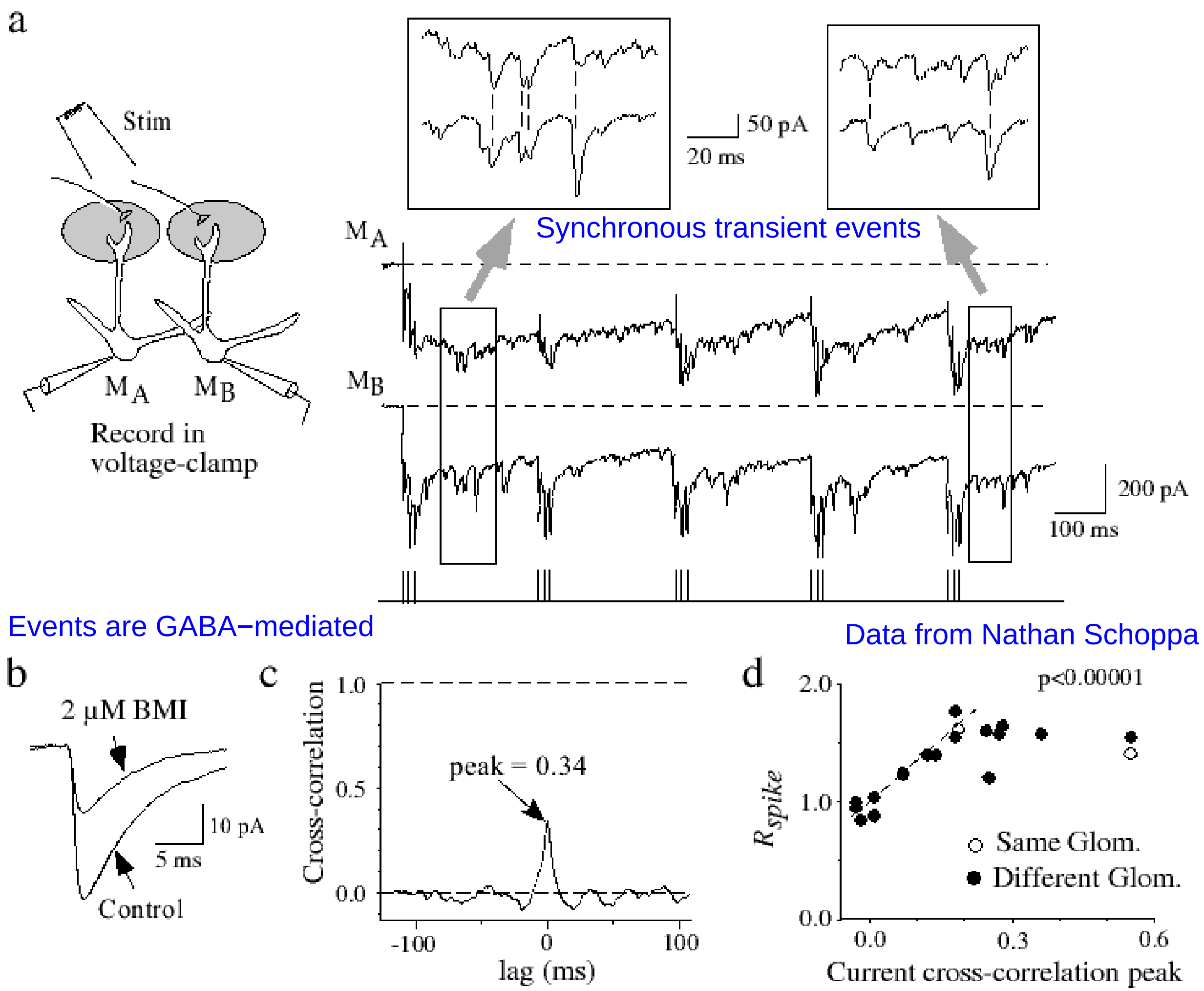


Power boost

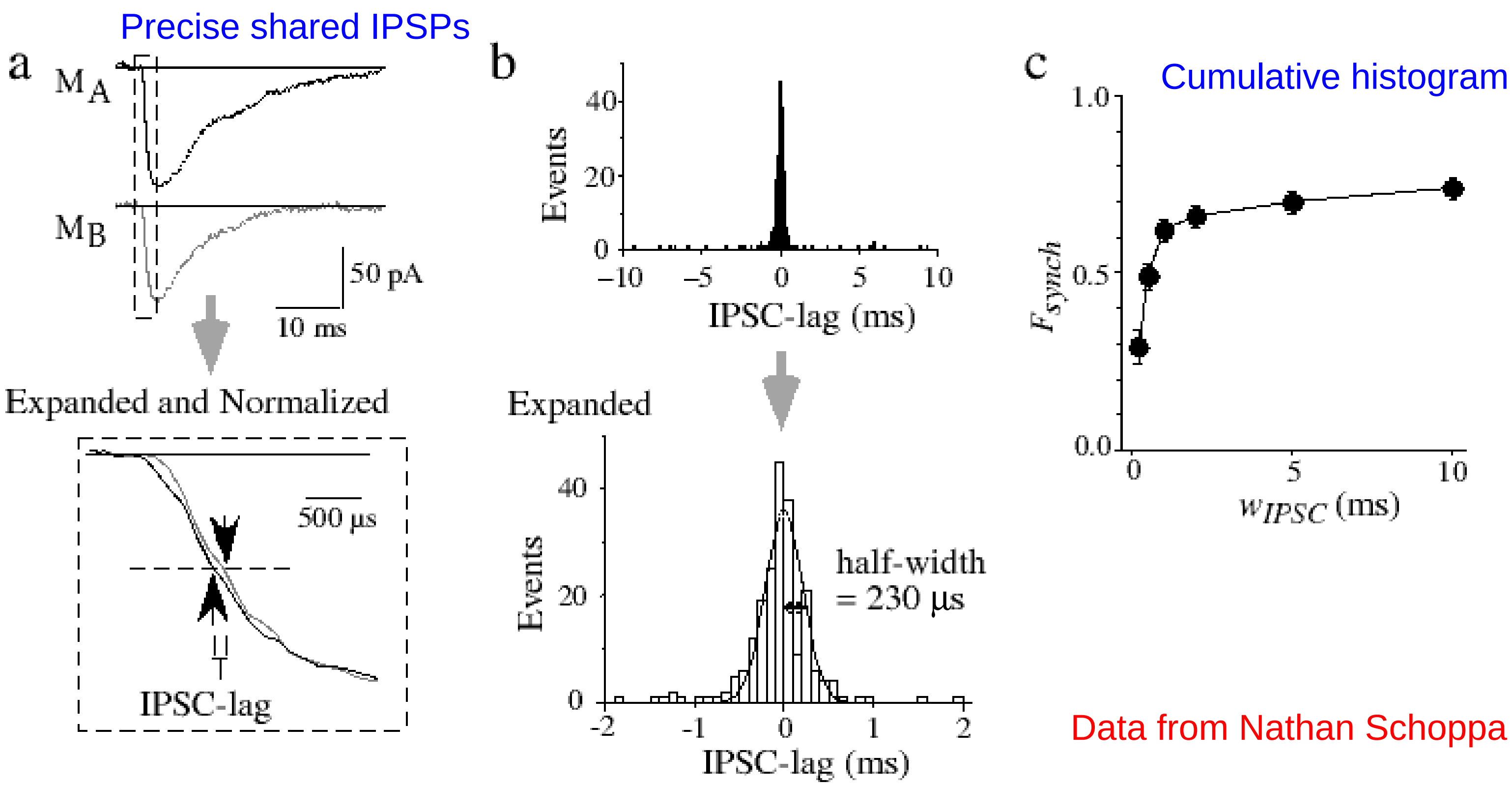


a
CC for different input correlations
Cross correlation (mV^2)
Time (ms)
b
Cross spectral density (mV^2 sec)
Cin = 0
Cin = 0.2
Cin = 0.4
Cin = 0.6
Cin = 0.8
Cin = 1.0
Frequency (Hz)
c
Power gain
CSD 15-40 Hz/CSD 0-100 Hz
Input correlation
e
common ipscs
Inputs
Current (pA)
Time (sec)
d
Cross correlation (pA^2)
Time (sec)
f
Spectral properties of inputs
Power (pA^2sec)
Frequency (Hz)

Could it happen naturally?



Correlated GC IPSPs



Data from Nathan Schoppa

Questions

- What is the mechanism?
- How does the rate of synchrony depend on the oscillator?
- What is the output vs input correlation?
- Do the properties of the noise matter?

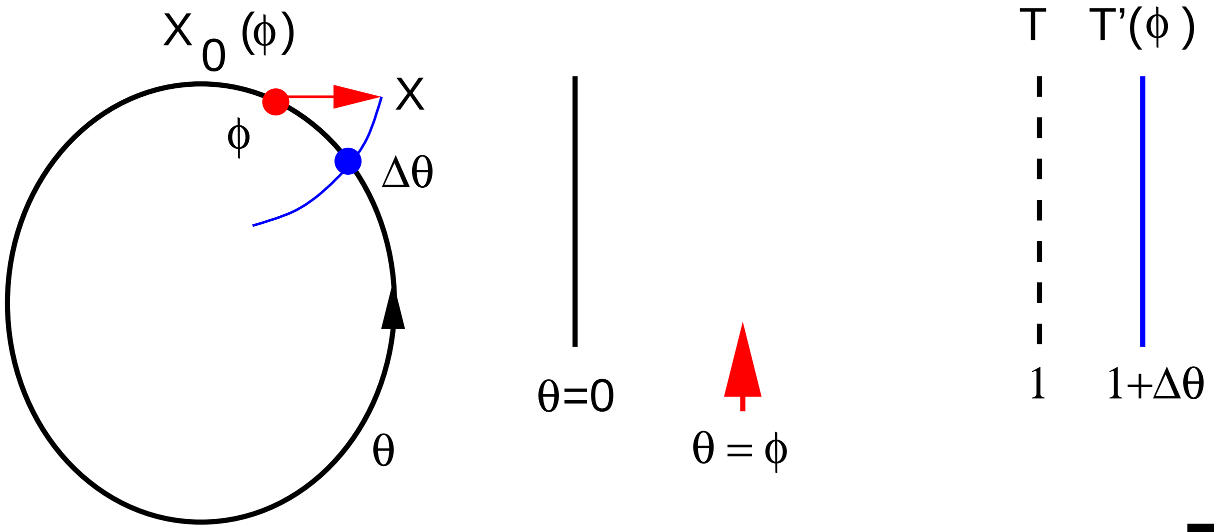
Oscillator theory

$$\frac{dX}{dt} = F(X) + \Xi(t)$$

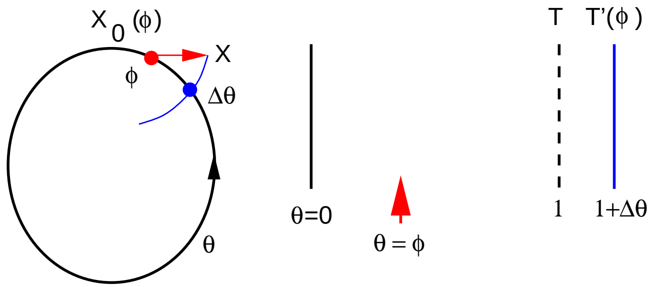
Change to phase coordinates; $X(t) = X_0(\theta(t))$:

$$\frac{d\theta}{dt} = 1 + \nabla_X \Theta(X_0(\theta)) \cdot \Xi(t)$$

where $\Theta(X)$ maps a neighborhood of $X_0(t)$ to the asymptotic phase.



Phase resetting curve



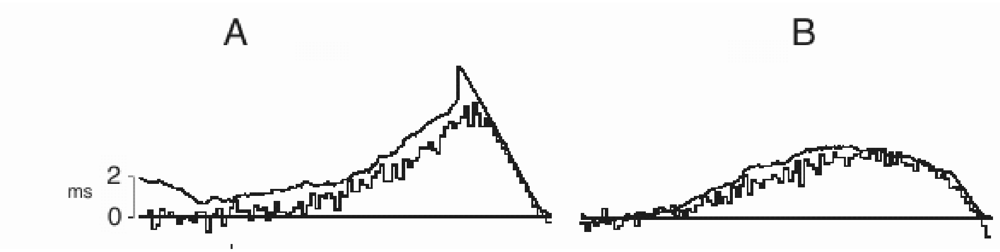
$$\Delta(\phi) \equiv 1 - \frac{T'(\phi)}{T}.$$

If the input $\Xi(t)$ is only injected current, then:

$$\frac{d\theta}{dt} = 1 + \Delta(\theta)\xi(t)$$

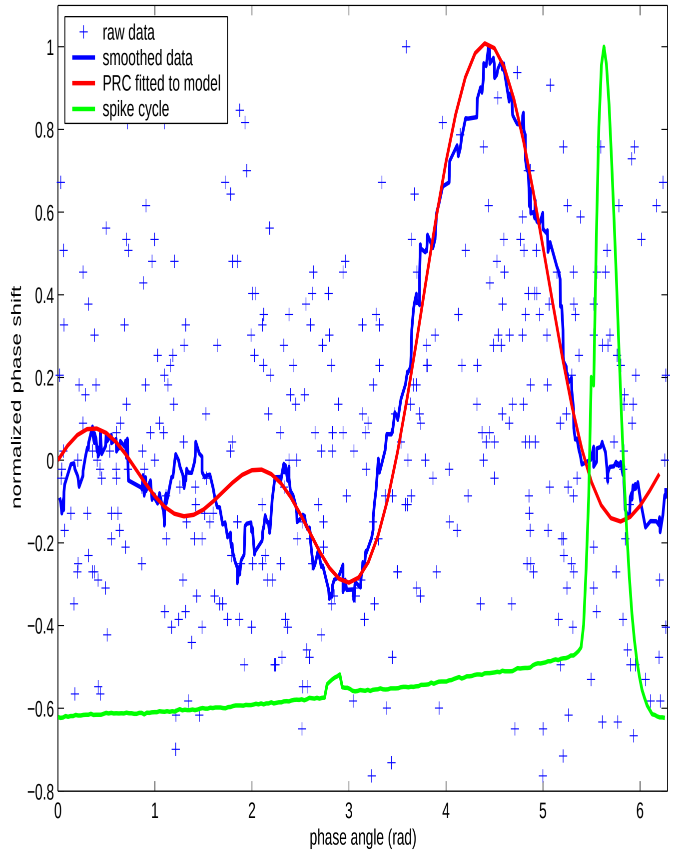
where $\xi(t)$ is the "voltage-component" of $\Xi(t)$.

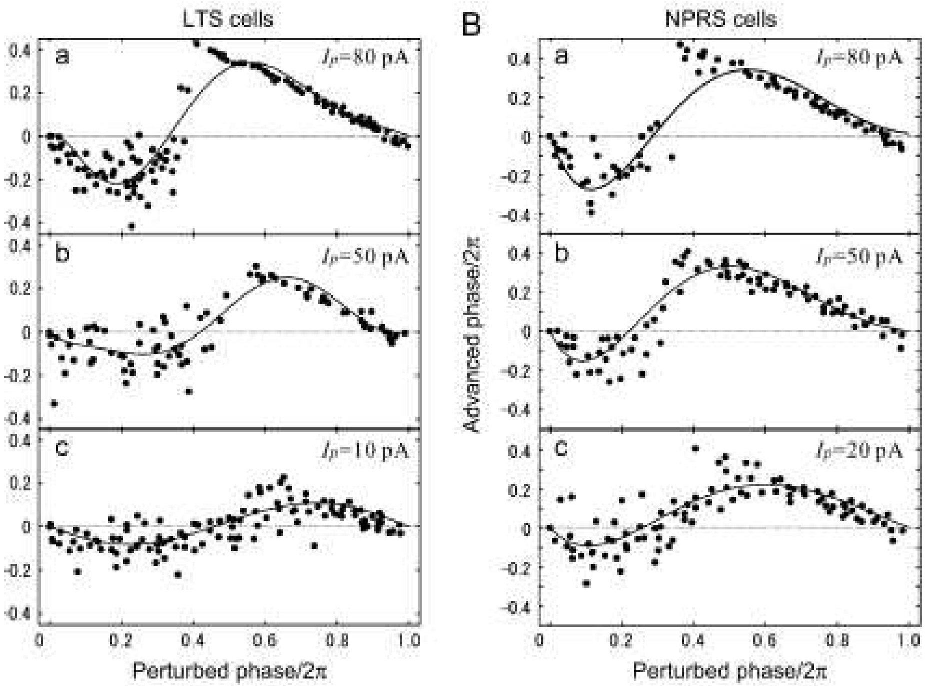
Experimental PRCs



Reyes (2005)

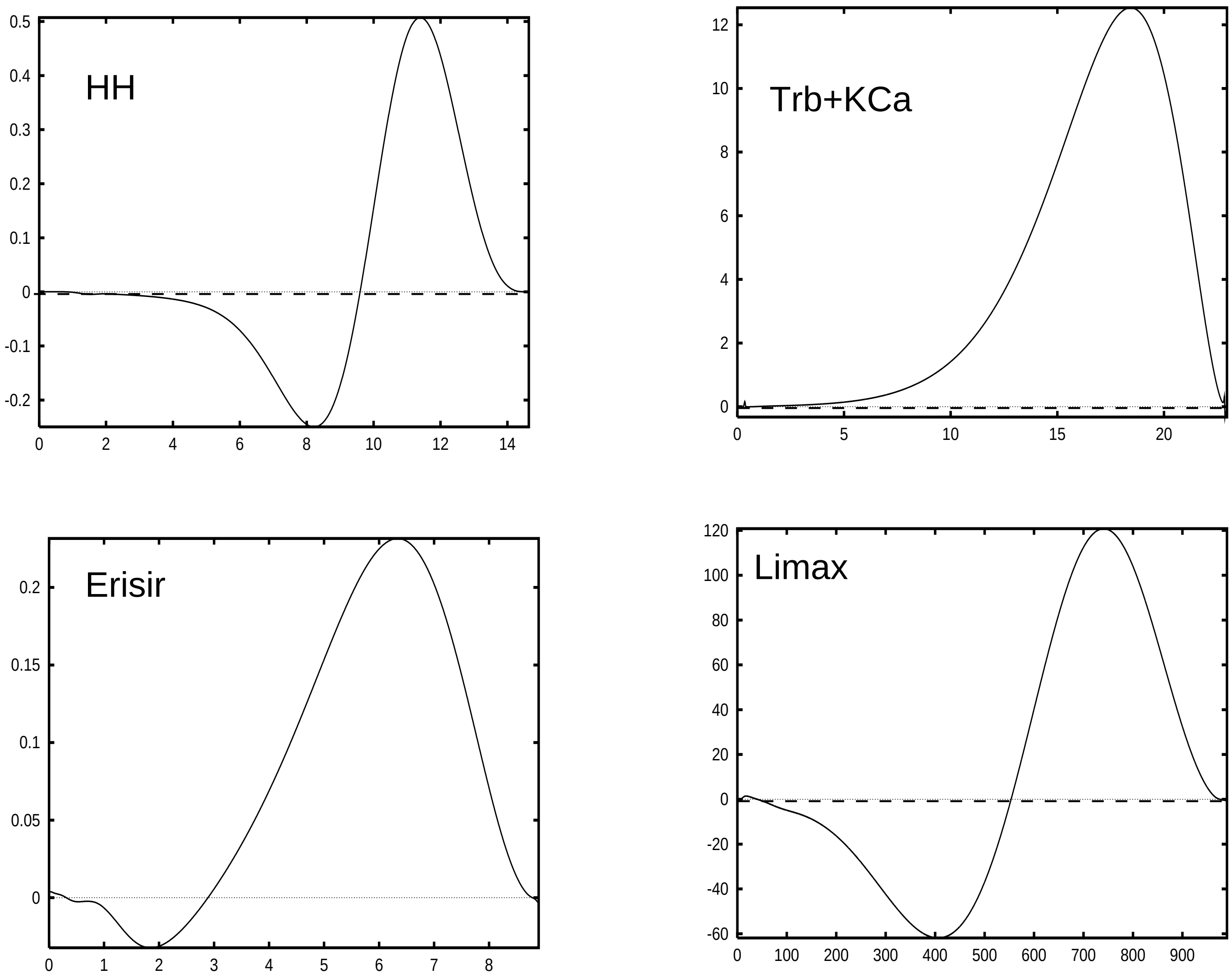
Galan et al (2005)





Tateno eta al (2007)

Model PRCs



Stochastic synchrony I. White noise

Consider two oscillators:

$$\begin{aligned}\theta_1' &= 1 + \Delta(\theta_1)\xi(t) \\ \theta_2' &= 1 + \Delta(\theta_2)\xi(t)\end{aligned}$$

The phase difference, ϕ satisfies:

$$\phi' = [\Delta(\theta_1 + \phi) - \Delta(\theta_1)]\xi(t) \approx \Delta'(\theta_1)\phi\xi.$$

How does ϕ vary over time?

Ito to the rescue

Let $y = \log \phi$. Then:

$$y' = -\Delta'(\theta_1)^2 \frac{\sigma^2}{2} + \Delta'(\theta_1)\xi(t)$$

On average:

$$\lambda = -\frac{\sigma^2}{2} \int_0^1 \Delta'(\theta)^2 P(\theta)\, d\theta.$$

where $P(\theta)$ is the invariant density for θ_1.

This is the **Liapunov exponent.**

$$0 = -\frac{dP}{d\theta} + \frac{\sigma^2}{2} \frac{d^2 \Delta(\theta)^2 P}{d\theta^2}$$

Poisson inputs

$$\begin{aligned}\theta_{n+1} &= \theta_n + T_n + \Delta(\theta_n)\\ \phi_{n+1} &\approx [1+\Delta'(\theta_n)]\phi_n\end{aligned}$$

For this model, we can compute:

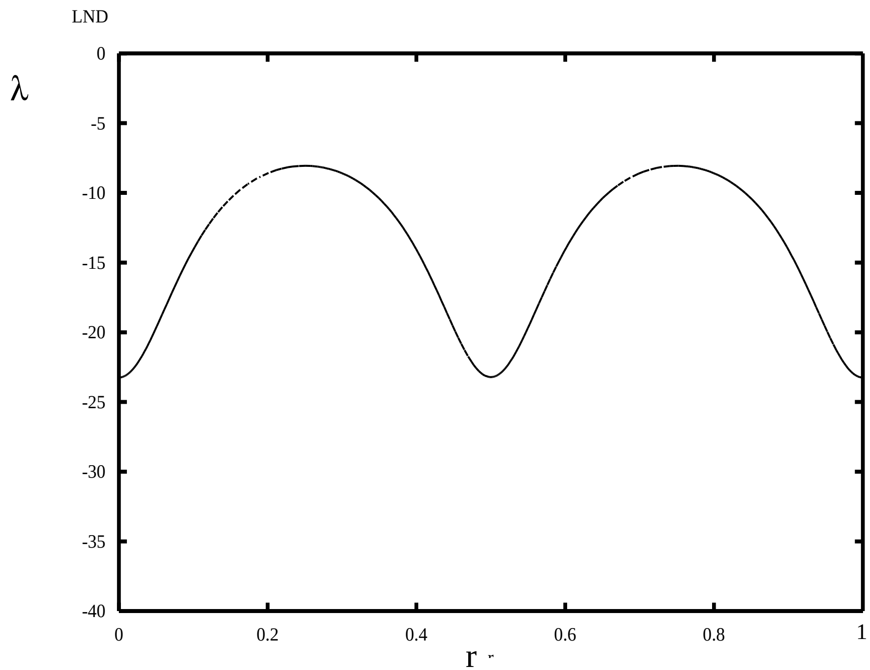
$$\begin{aligned}\lambda &= \int_0^1 \log[1+\Delta'(\theta)]P(\theta)\ d\theta\\ P(\theta) &= \int_0^1 Q(\theta-\phi-\Delta(\phi))P(\phi)\ d\phi.\end{aligned}$$

Thus, $P(\theta)$ satisfies a linear integral equation.

Optimal shape

The Liapunov exponent describes how rapidly two identical cells will synchronize when forced with common noise. How does the shape of the PRC contibute to the magnitude of λ. E.g

$$\Delta(x) = (\sin(2\pi(x+r) - \sin(2\pi r) - 0.25\sin(4\pi x))/N$$



Theory

Minimize:

$$\lambda = -\int_0^1 \Delta'(x)^2 P(x)\, dx$$

subject to

$$\int_0^1 \Delta^2(x)\, dx = 1$$

and

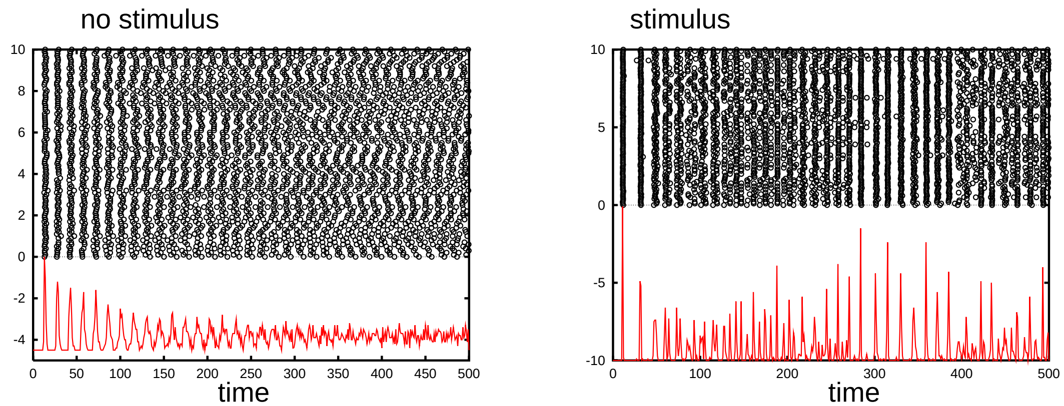
$$\frac{\sigma^2}{2}\frac{d(\Delta^2(x)P)}{dx} - P + 1 = 0$$

For $0 < \sigma \ll 1$ can solve resulting variational problem and find

$$\Delta(x) \approx \sin 2\pi x$$

Optimal time scales & reliability

Given the same stimulus over and over, are the spike-times of a neuron reliably timed? This is equivalent to stochastic synchrony, since each neuron is regarded as an independent oscillator. Does the dynamical system approach a **spike time attractor**?



“Conventional wisdom” has it that white noise is optimal for reliability.

Colored noise 1

Fix the PRC and drive with filtered noise scaled to keep the variance constant, e.g., Ornstein-Uhlenbeck:

$$d\xi = -\beta\xi dt + \sqrt{\beta} dW$$

The Liapunov exponent satisfies:

$$\begin{aligned}\theta' &= 1 + \Delta(\theta)\xi(t) \\ \lambda &= \lim_{T\to\infty} \frac{1}{T}\int_0^T \Delta'(\theta(t))\xi(t)\; dt.\end{aligned}$$

Colored noise 2

For small noise:

$$\theta(t) \approx t + \int_0^t \Delta(s)\xi(s)\, ds$$

So that

$$\lambda \approx \lim_{T\to\infty} \frac{1}{T} \int_0^T \Delta''(t) \int_0^t \Delta(s) C(t-s)\, ds$$

where

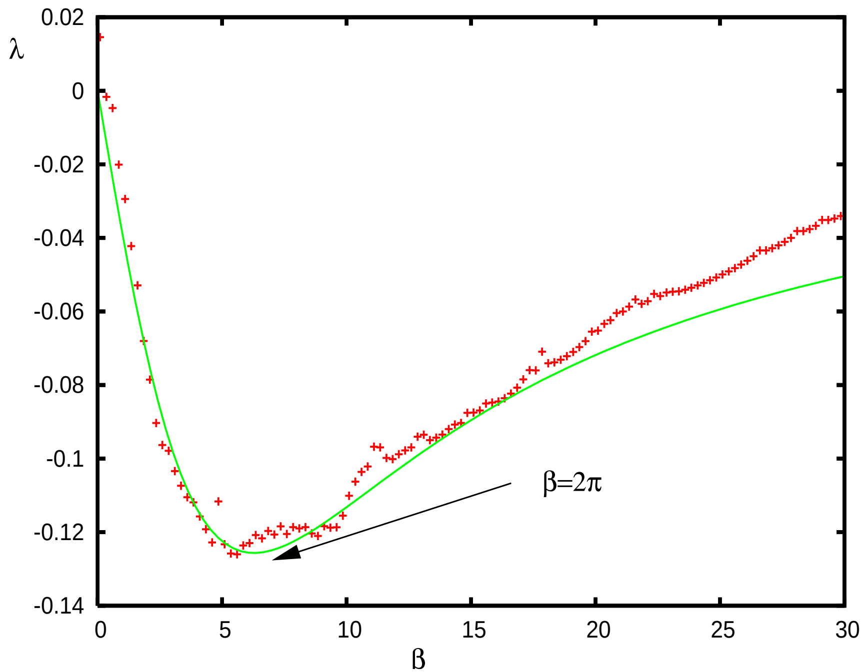
$$C(t) = < \xi(t)\xi(0) > .$$

Example

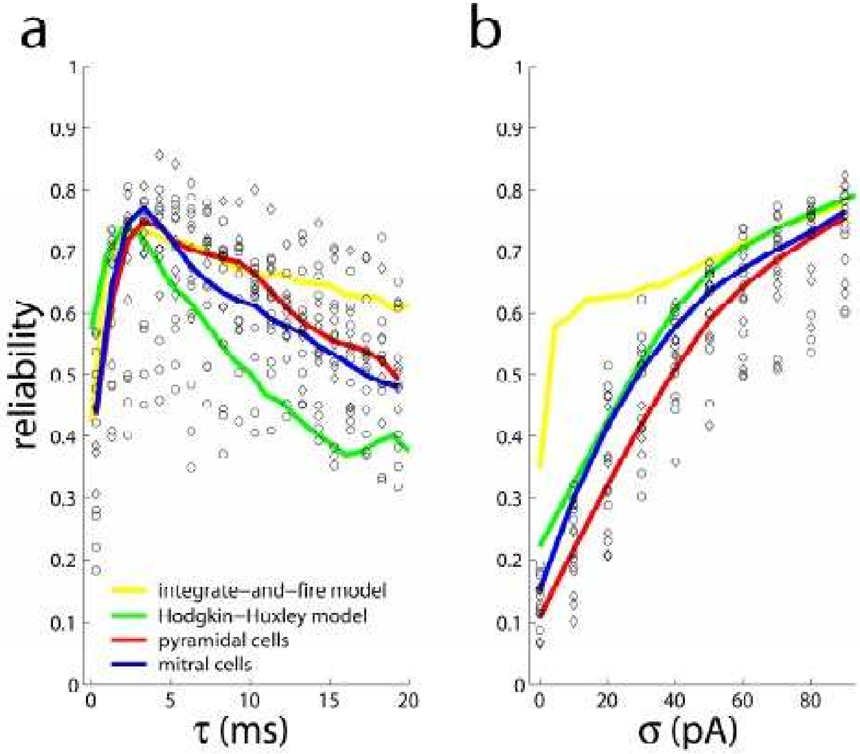
$$\Delta(x) = a\sin 2\pi x, \qquad C(t) = \frac{1}{2}e^{-\beta|t|}$$

$$\lambda = -(2\pi a)^2 \frac{b}{b^2 + 4\pi^2}$$

In general $\tau_{opt} \approx T/2\pi$



Experiments



(color)

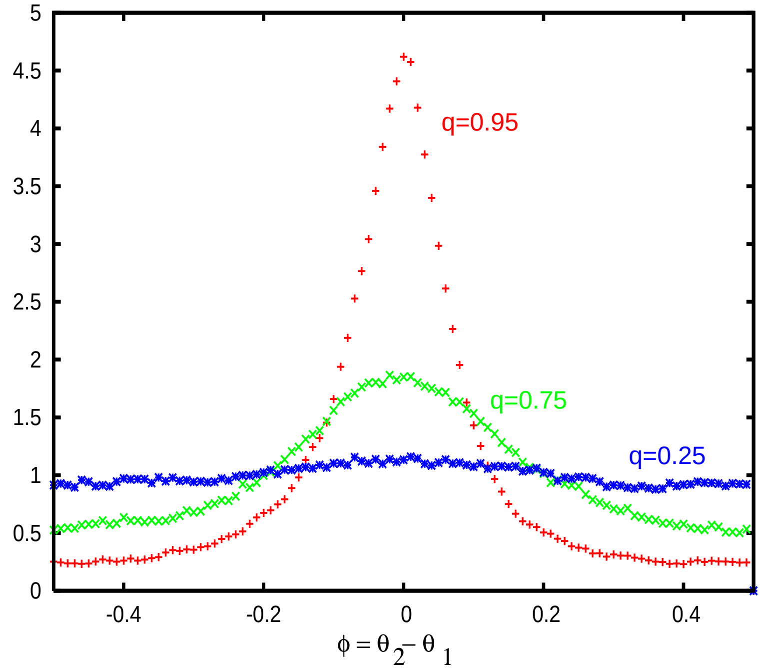
(amplitude)

Input/output correlations

Suppose that only some of the noise is shared:

$$\begin{aligned}\theta_1' &= 1 + (q\xi(t) + \sqrt{1-q^2}\xi_1(t))\Delta(\theta_1) \\ \theta_2' &= 1 + (q\xi(t) + \sqrt{1-q^2}\xi_2(t))\Delta(\theta_2)\end{aligned}$$

Here $\xi(t)$ is the common signal and ξ_j is the independent noise.



Theory

The phase-difference, $\phi = \theta_2 - \theta_1$ satisfies:

$$\begin{aligned} \phi' &= q[\Delta(\theta_1 + \phi) - \Delta(\theta_1)]\xi(t) \\ &+ \sqrt{1-q^2}[\Delta(\theta_1 + \phi)\xi_2(t) + \Delta(\theta_1)\xi_1(t)] \end{aligned}$$

For small noise, θ_1 is nearly uniform. So we get a scalar diffusion equation, which has a closed form solution:

$$P(\phi) = \frac{N}{1 - q^2 h(\phi)/h(0)}$$

where

$$h(\phi) = \int_0^1 \Delta(\theta + \phi)\Delta(\theta)\, d\theta.$$

Thy & example

Circular statistics quantify the width of the distribution:

$$C = \int_0^1 \cos 2\pi x P(x)\, dx.$$

For $P(x)$ uniform, $C = 0$ and for $P(x)$ a Dirac delta function $C = 1$.
For $\Delta(x) = a \sin 2\pi x$,

$$\begin{aligned} P(x, q) &= \frac{\sqrt{1 - q^4}}{1 - q^2 \cos 2\pi x} \\ C(q) &= \frac{1 - \sqrt{1 - q^4}}{q^2} \end{aligned}$$

Coupling and correlation

- Intrinsic activity of neurons is governed by their interactions (coupling)
- What happens when there is coupling in addition to correlated inputs?

$$\begin{aligned} d\theta_1 &= [\omega + Kg(\theta_2, \theta_1)]dt + \sigma\Delta(\theta_1)dW_1 \\ d\theta_2 &= [\omega + Kg(\theta_1, \theta_2)]dt + \sigma\Delta(\theta_2)dW_1 \end{aligned}$$

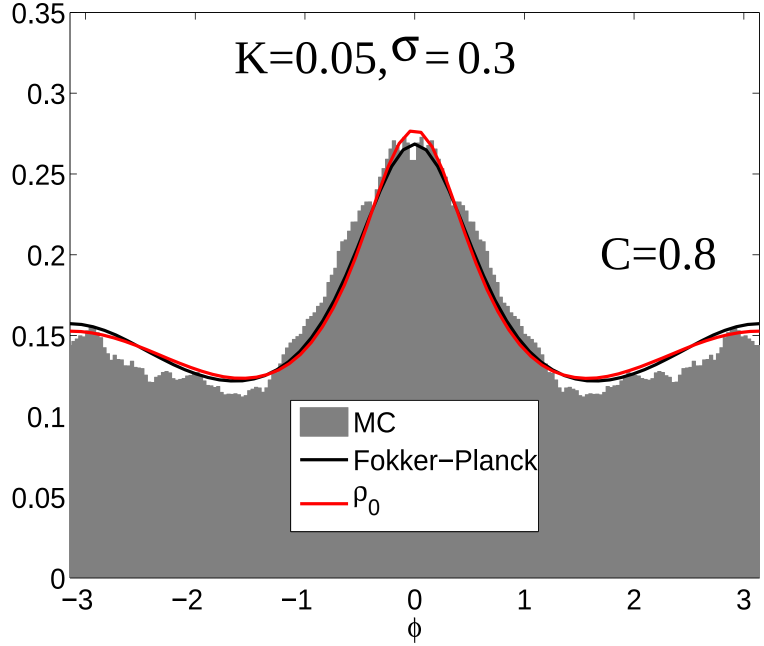
- If coupling encourages synchrony, then like noisy synchronization (peak around 0 phase difference)
- **Coupling antiphase** + correlations - most interesting case

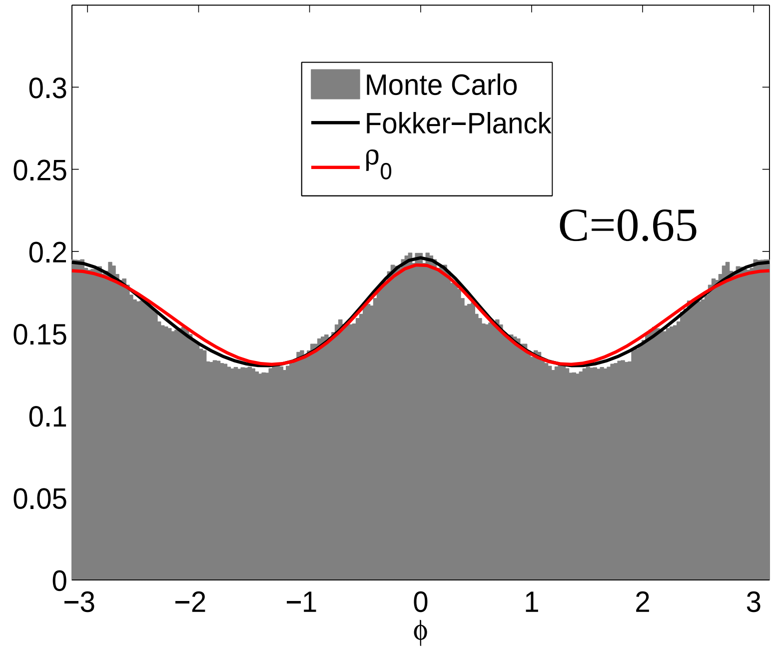
Theory

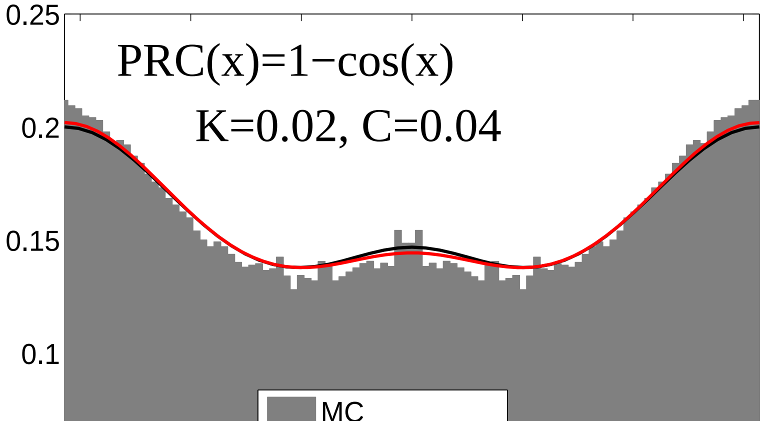
- Write FP equations - not the diffusion terms is complicated due to phase-dependence and correlations
- $0 < K \approx \sigma^2 \ll 1$ we can obtain $\rho(\theta_1, \theta_2)$, the invariant density (using Fredholm alternative, of course)
- Stochastic bifurcations and “bistability”

Example

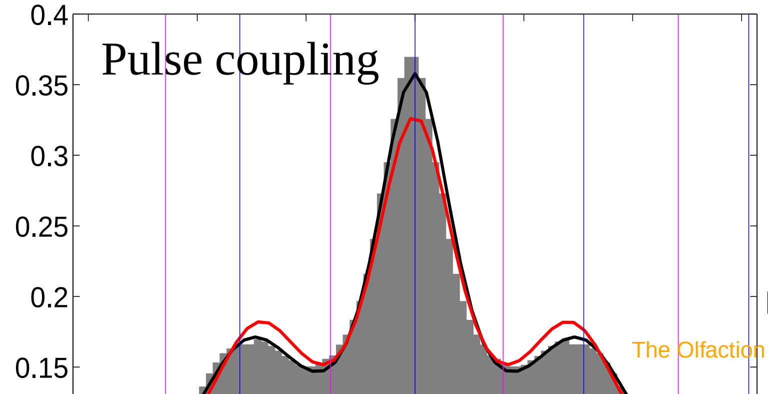
PRC(x)=−sin(x),   g(y,x)=−sin(x−y)+0.4 sin(2(x−y))





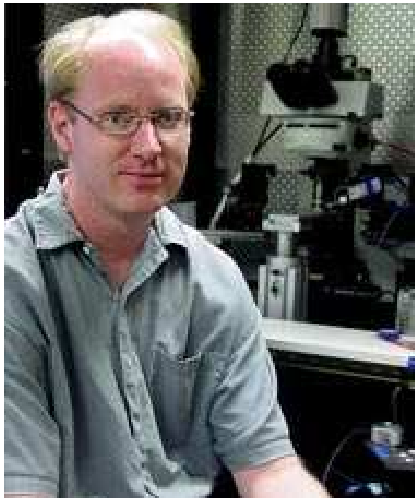


g(y,x)=P(y) PRC(x)



Collaborators

Sashi Marella



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WHERE DISCOVERIES BEGIN