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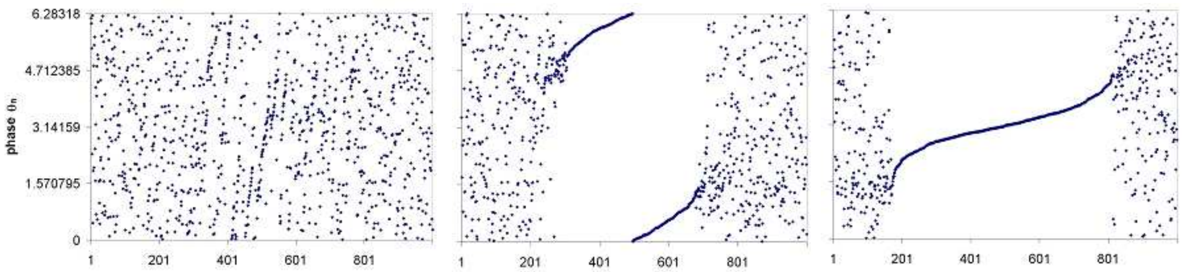
The Kuramoto Model: From Asynchrony to Synchrony



K = 0.7 K_C **K = 1.0 K_C** **K = 1.3 K_C**

Synchrony/phase locking increases with inhibition [Kuramoto 1984, Daniels 2005].

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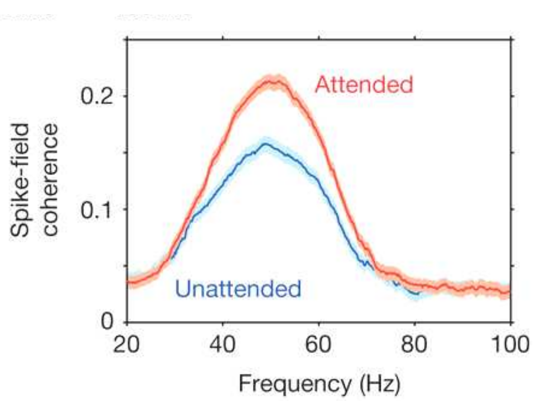
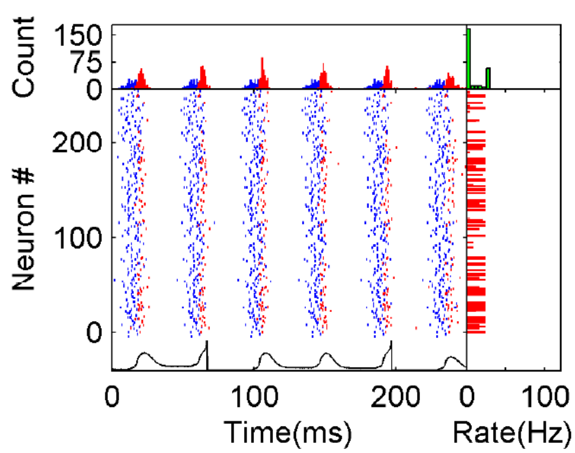
Attention--Synchrony Relation





Right: Synchrony enhances network coherence. Left: Inhibitory neuron (red) synchrony entrains excitatory neurons (blue).

Inhibitory neuron entrain excitatory ones.

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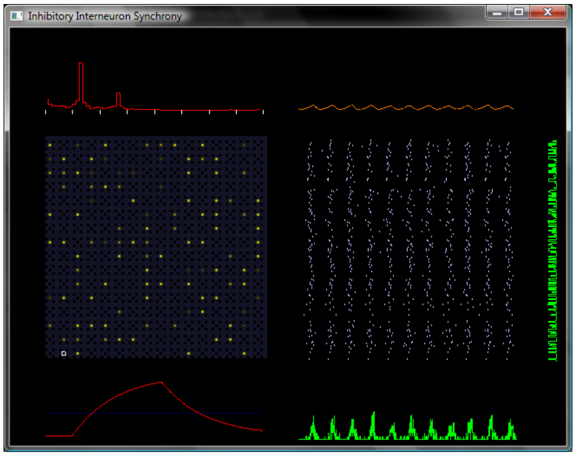
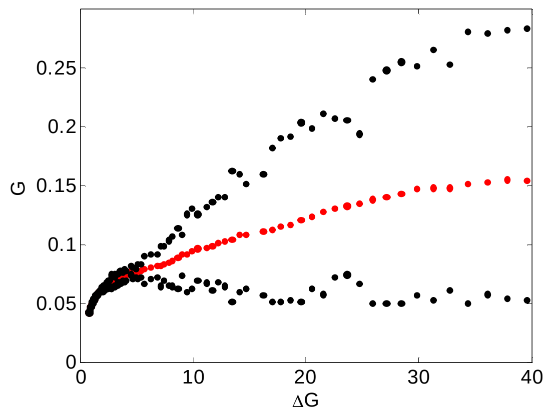
Transition to Synchrony





Right: Synchrony demo. Left: When inhibition surpasses a critical level, the network synchronizes.

For a good software demo, see:

http://tutorials.siam.org/dsweb/cotutorial/index.php?s=4&p=0

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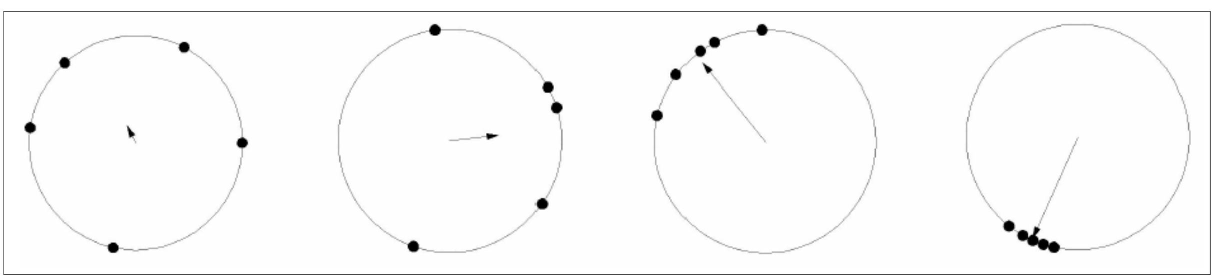
Kuramoto's Model (1984) was Inspired by Winfree



Synchrony/phase locking increases with inhibition [Kuramoto 1984, Daniels 2005].

Winfree's Assumptions:

- Neurons are globally and weakly coupled.
- Neurons express nearly identical frequencies and are identical in all other manners.

Winfree's Results:

- We can describe neurons only by their phases $[0,2\pi]$.
- We can describe the network of neurons from a mean field perspective.

Winfree's Simulations

- Synchrony emerges like a phase transition from a liquid to a solid.

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Kuramoto's Model (1984)

The evolution of phases is given by the sum of neurons interactions via their PRCs, proportional to a sinusoid:

$$\dot{\phi}_i = \omega_i + \frac{K}{N}\sum_{j=1}^{N}\sin[\phi_i-\phi_j], \qquad i = 1 \ldots N$$

The order parameter:

$$r e^{i\psi} = \frac{1}{N}\sum_{j=1}^{N} e^{i\phi_j}, \qquad i = 1 \ldots N$$

> *Question: Physically, what is* $\phi_i - \phi_j$*?*

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Mean Field Description

Consider the order parameter × $e^{-i\phi_i}$:

$$r e^{i(\psi-\phi_i)} = \frac{1}{N}\sum_{j=1}^{N} e^{i(\phi_j-\phi_i)}, \qquad i = 1 \ldots N$$

whose imaginary part equals:

$$r \sin[\psi-\phi_i] = \frac{1}{N}\sum_{j=1}^{N}\sin[\phi_j-\phi_i], \qquad i = 1 \ldots N$$

substitute into the phase equation:

$$\dot{\phi}_i = \omega_i - K\, r\, \sin[\psi - \phi_i], \qquad i = 1 \ldots N$$

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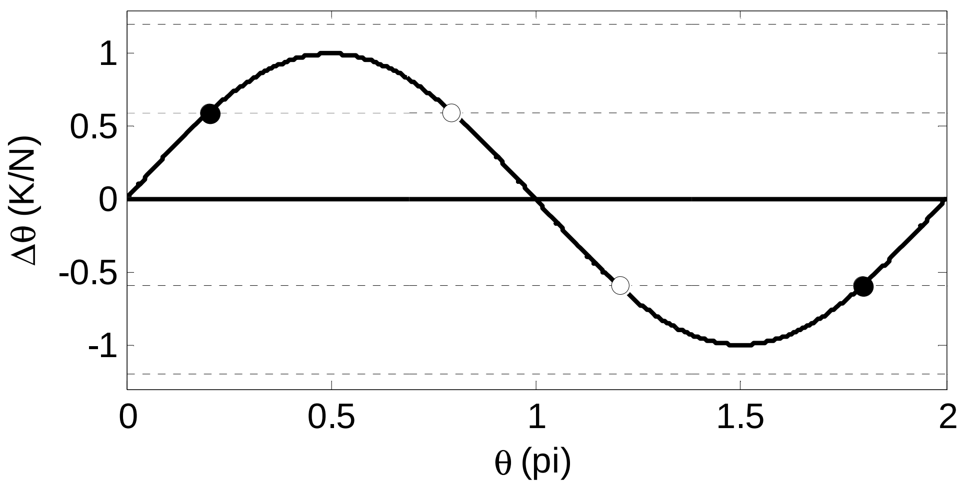
Phase Response Curve



Kuramoto uses a sinusoidal phase response curve.

For the i^{th} neuron to phase lock, $\dot{\phi}_i = 0$; therefore,

$$\omega_i = K\, r\, \sin[\psi - \phi_i]$$

since $-1 < \sin[\psi - \phi_i] < 1$, neurons can only lock if $|\omega_i| < K\, r$.

> *Question: What is the range of phases to which neurons can lock? At what phase do perfect neurons ($\omega_i = 0$) lock?*

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Steady-State Analysis I

The i^{th} oscillator is described by

$$\dot{\phi}_i = \omega_i + K\, r\, \mathrm{Sin}[\psi[t] - \phi_i] \text{ with } \psi[t] = \Omega\, t + \psi[0]$$

where Ω is the locked frequency. In this rotating reference frame, the oscillator's phase is

$$\theta_i = \phi_i - \psi[t] \Leftrightarrow \phi_i = \theta_i + \Omega\, t + \psi[0]$$

which leads to

$$\dot{\theta}_i = \omega_i - \Omega - K\, r\, \mathrm{Sin}[\theta_i]$$

Dropping the subcript and working in the continuum limit (N → ∞), we have

$$\omega = \Omega + K\, r\, \mathrm{Sin}[\theta] \Rightarrow \frac{d\omega}{d\theta} = K\, r\, \mathrm{Cos}[\theta]$$

in steady-state ($\dot{\theta} = 0$); the derivative will come in handy shortly.

Steady-State Analysis II

We obtain the coupling strength K required to synchronize oscillators with natural frequencies distributed with density $g(\omega)$ by calculating r, which, in the continuum limit, is given by

$$r = \frac{1}{N} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} e^{i\theta}\, N\, g[\theta]\, d\theta$$

where is $Ng(\theta)\, d\theta$ is the number of oscillators with phases between θ and $\theta + d\theta$. In terms of the frequencies' probability density, this number is given by $Ng(\omega)\, d\omega = Ng(\omega)\, (d\omega / d\theta)\, d\theta$. Thus, we have

$$r = \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} e^{i\theta}\, g[\omega]\, \frac{d\omega}{d\theta}\, d\theta$$

$$= K\, r \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} g[\omega]\, (\mathrm{Cos}[\theta] + i\, \mathrm{Sin}[\theta])\, \mathrm{Cos}[\theta]\, d\theta$$

As the $\sin(\theta)$ term is odd, it drops out, leaving

$$1 = K \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} g[\omega]\, \mathrm{Cos}^2[\theta]\, d\theta$$

after we divide by r—we can't factor $g(\omega)$ out because ω is a function of θ—an oscillator's natural frequency determines its phase.

To find the critical coupling, K_C, we need to pick the most favorable conditions for synchrony. This corresponds to $g(\omega)$'s peak, where the oscillators are spaced most closely in frequency. These oscillators will be the first to synchronize, locking at the frequency Ω where $g(\omega)$ peaks. As they span a small range, we can set $g(\omega) = g(\Omega)$, and obtain

$$1 = K_C\, g[\Omega] \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \mathrm{Cos}^2[\theta]\, d\theta \Rightarrow K_C = \frac{2}{\pi\, g[\Omega]}$$

We can obtain an approximate result for higher coupling strengths by expanding $g(\omega)$ to second-order. This yields a result that describes r's initial growth:

$$r = \sqrt{\frac{16}{\pi\, K_c^{3}\, \ddot{g}[\Omega]}\left(1 - \frac{K_c}{K}\right)}$$

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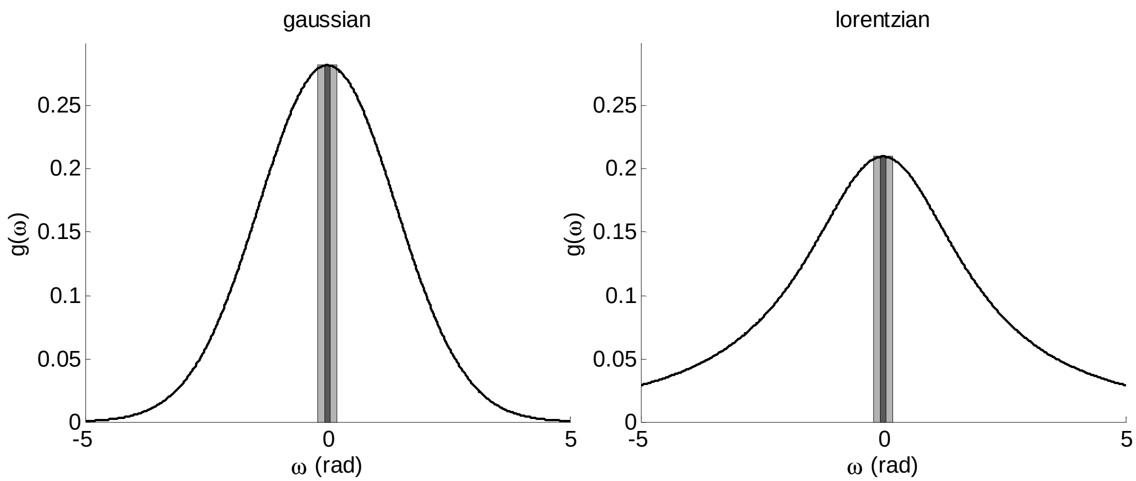
Kuramoto's Intuition



The first neurons to synchronize are those at the center of the distribution.

As K increases, more neurons are pulled into synchrony.

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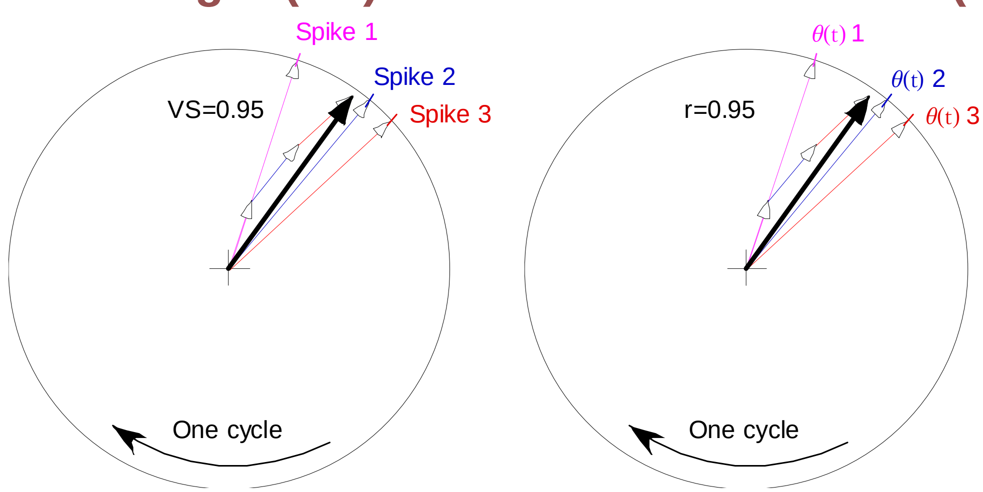
Vector Strength (VS) versus Order Parameter (r)



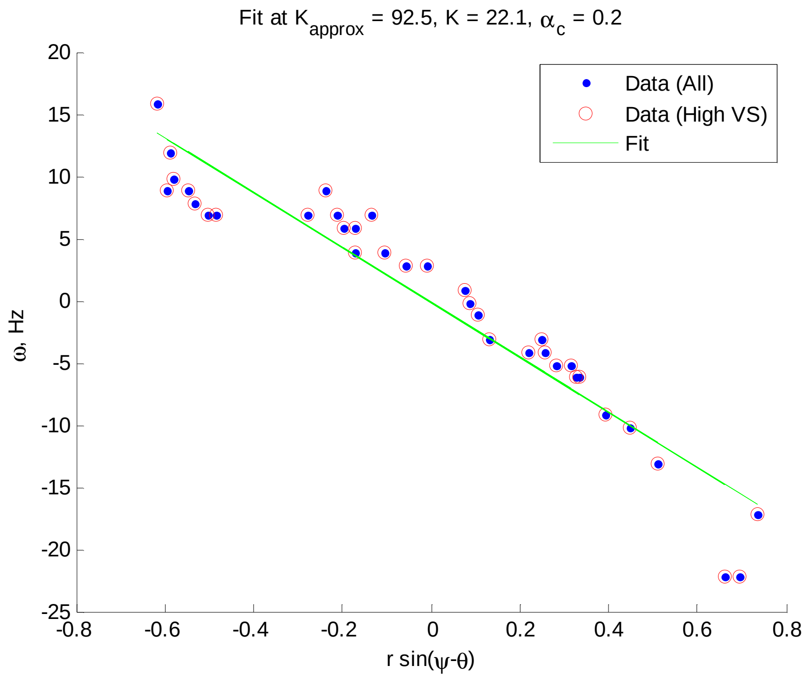
In many cases, VS and r are similar.

Both quantify synchrony in terms of vector sums of phase differences.

Vector strength sums spike phases across time, over at least on period.

The order parameter sums neuron phases at a point in time.

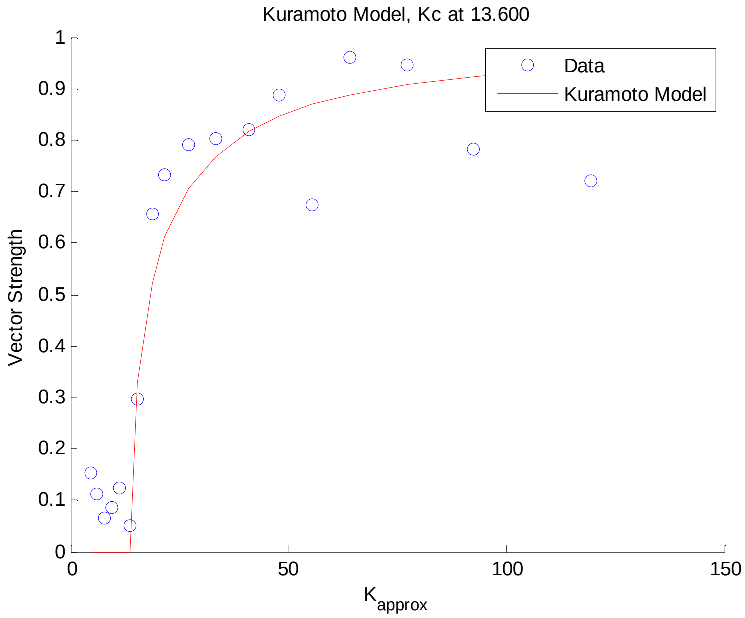
Does Kuramoto Apply?



$$\omega_i = 2\pi f_i = K\, r \sin(\psi - \theta_i)$$

Question: What assumptions of Kuramoto's model do we violate?

Does Kuramoto Apply? Yes, but ...



For the lorentzian distribution:

$$r = \sqrt{\left(1 - \frac{K_C}{K}\right)}$$

> *Question: Why does the model fit our data?*