Waves of electrical activity are a potential signature of coupled oscillators.

**Delayed Excitations from a Single Oscillator**

\[ \Delta \phi = 2\pi \Delta \tau_D f \]

**Propagating Pulses in an Excitable Network**

\[ \Delta \phi = 2\pi \frac{\Delta x}{V} f \]

**Phase Locked, Weakly Coupled Oscillators**

\[ \Delta \phi \]
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

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 (TPP) 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

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

\[ \Gamma(\psi_i - \psi_j) = \frac{\varepsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \mathcal{L}(\psi_i + \theta) \cdot \mathbf{P}(\psi_i + \theta, \psi_j + \theta) \]

Sensitivity \( \propto \left( \frac{\partial^2 \psi_i}{\partial V}, \ldots \right) \)
Relevance: Interaction of neuronal oscillators may be written in terms of the correlation of presynaptic spiking with the post synaptic response

Real system: \[
\frac{\partial V}{\partial t} = \cdots \; ; \; \frac{\partial n}{\partial t} = \cdots \; ; \text{etcetera}
\]

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

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

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

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

Phase difference

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

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

\[ \Delta V_m (\text{mV}) \]

\[ \text{time (ms)} \quad 0 \quad 40 \]

\[ \frac{\Delta f}{f_0} \]

\[ \text{delay (\%ISI)} \quad 0 \quad 100 \]

Membrane Potential \( V(t) \) or \( V(\Psi) \) [mV]

Phase Sensitivity \( Z(t) \) or \( Z(\Psi) \) [rad/mV]

Time After Onset of Action Potential, \( t \) [ms]

Lesson: Phase Sensitivity Concept Valid with Realistic PSPs
Nature of the Pairwise Interaction is Revealed by the Phase Shifts Between Two Reciprocally Connected Neurons

\[ \frac{\partial \Psi_i}{\partial t} = \omega + \Gamma(\Psi_i - \Psi_j) \]
\[ \frac{\partial \Psi_j}{\partial t} = \omega + \Gamma(\Psi_j - \Psi_i) \]

\[ \frac{\partial}{\partial t} (\Psi_i - \Psi_j) = \Gamma(\Psi_i - \Psi_j) - \Gamma(\Psi_j - \Psi_i) \]

Odd Part of Interaction
\[ \Gamma_{\text{odd}}(\Psi_1 - \Psi_2) \] [rad/ms]

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)

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

$$
\Gamma(\Delta \psi) - \Gamma(-\Delta \psi) = g \frac{(\omega \tau)^2 - 1}{[1 + (\omega \tau)^2]^2} \sin(\Delta \psi) < 0 \text{ for } \omega \tau > 1
$$
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 \( \Gamma(\psi - \psi') \equiv -\Gamma_0 \sin(\psi - \psi') \)

\[
\frac{d\psi}{dt} = \Gamma_0 \sin(\psi' - \psi) + \omega
\]

Then

\[
\frac{d\psi'}{dt} = \Gamma_0 \sin(\psi - \psi') + \omega'
\]

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 $\delta \omega \propto x$

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

$\delta \omega_x \propto x$

Single frequency

When the network locks:

Gradient of phase shifts with $\frac{\psi_x}{dx} \propto$ constant.
Phase-locking to link features across visual space
The binding hypothesis - still controversial!

Gray & Singer (PNAS 1989)
Phase-locking to link features across visual space
The binding hypothesis - still controversial!

Gray, König, Engel & Singer (Nature 1990)
Phase-locking to link features across visual space
Analysis: Phase interactions code features, i.e., relative orientation of bars

Grannan, Kleinfeld & Sompolinsky (Neural Computation 1993)