Systems Biology: A Personal View
XXIX. Synchronization in Biology

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Collective ordering of spatially distributed oscillators is ubiquitous in nature …

- Pacemaker cells in the heart
- $\beta$-cells in the pancreas
- Long-range synch across brain during perception
- Contractions in the pregnant uterus
- Rhythmic applause
- Pedestrians on a bridge falling in step with the swinging motion of bridge

Male Fireflies flashing in unison
Each insect has its own rhythm – but the phase alters based on seeing its neighbors lights, bringing harmony
... and vital for the proper functioning of many biological systems

Examples:

Cellular clocks (day-night cycle)

Synchrony in the Brain during perceptual “binding”

Quorum Sensing
Synchrony triggered by cell density via exchange of signaling molecules through a homogeneous extracellular medium

http://mpkb.org/
Peskin (1975) : Model for sino-atrial node
Collection of N identical integrate-and-fire oscillators

Results for the simple case of all-to-all coupling

- For arbitrary initial conditions, the system approaches a state in which all oscillators are synchronously active.
- Proved for N=2, later for arbitrary N
- Also true when oscillators are not quite identical (No proof!).
- Hopfield (1994): local coupling \(\equiv\) slider-block model of earthquakes \(\Rightarrow\) Self-organized criticality (SOC)

Winfree (1967) : Populations of biological oscillators
Mean-field model of weakly coupled limit-cycle oscillators
Transition to synchrony with increased coupling

Kuramoto (1975) : Exactly solvable model of collective synchronization
Synchronization of Coupled Oscillators

Feb 1665: Huygens observed phase-locking between two pendulum clocks hung side by side

In-phase

Anti-phase

Christiaan Huygens
Coupled Phase Oscillators

Consider many ‘phase oscillators’: \( \frac{d\theta_i}{dt} = \omega_i \quad (i=1,2,\ldots,N \gg 1) \)

The coupled system: \( \frac{d\theta_i}{dt} = \omega_i + \sum_{j=1}^{N} k_{ij} (\theta_j - \theta_i) \)

\[ k_{ii} (\phi) = 0, \quad k_{ij} (\phi) = k_{ij} (\phi \pm 2\pi) \]

Assumption: Rapid convergence to limit cycle attractor
• \( N (\gg 1) \) oscillators described only by their phase \( \theta \)

• Oscillator frequencies randomly chosen from a distribution \( g(\omega) \) with a single local maximum.

(Assume mean frequency = 0)
Kuramoto model (1975): \( k_{ij}(\phi) = k \sin \phi \)

\[
\frac{d\theta_n}{dt} = \omega_n + \frac{k}{N} \sum_{m=1}^{N} \sin(\theta_m - \theta_n)
\]

\( n = 1, 2, \ldots, N \quad k = \text{(coupling constant)} \)

- Assumes sinusoidal all-to-all coupling.

- Macroscopic coherence in the system is characterized by the order parameter:

\[
r = \left| \frac{1}{N} \sum_{m=1}^{N} \exp(i \theta_m) \right|
\]
Measuring coherence of oscillations in the system

\[ r = \frac{1}{N} \sum_{m=1}^{N} \exp(i \theta_m) \]

\( r \approx 1 \) and \( r \approx 0 \)
Synchronization-desynchronization transition in Kuramoto model

With increasing strength of coupling \(k\), a transition to coherence \((r > 0)\) at a critical value of \(k\)

\[ k_c = \frac{2}{\pi} g(0) N \]
Rhythmic activity in the heart is driven by pacemaker cells

Spontaneously beating aggregates of 7-day chick embryo ventricular cells
Oscillations of all cells in an aggregate are synchronized by gap junction coupling

Transmembrane potential time series from an aggregate
The synchrony is mediated by centralized coordination.
For many biological processes,
no centralized coordination agency has been identified as yet.
Ordering without centralized coordination

Local interactions can lead to order without an organizing center in complex systems.

Examples: flocking and swarming
Co-ordination among organisms

For example, How can cooperation emerge at the level of collective behavior through interactions between individuals looking to maximize their individual benefit?
Prisoners Dilemma

originally framed by Merrill Flood and Melvin Dresher at RAND (1950)

In the iterative setting, an ideal model for analyzing the conditions for the emergence of cooperation

Payoff Matrix

<table>
<thead>
<tr>
<th></th>
<th>Cooperate</th>
<th>Defect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperate</td>
<td>R,R</td>
<td>S,T</td>
</tr>
<tr>
<td>Defect</td>
<td>T,S</td>
<td>P,P</td>
</tr>
</tbody>
</table>

T: Temptation to defect
R: Reward for cooperation
P: Punishment for mutual defection
S: Sucker’s payoff
In general, T > R > P > S
Usually, R=1, P=0, S=0 and 1 < T < 2
Spatial Prisoners Dilemma

Agents play with neighbors on a lattice, adopting strategy of neighbor with highest payoff.

Waves of cooperation and defection are observed to propagate along the lattice.

\[ 1.75 < T < 1.8 \]

\[ 1.8 < T < 2 \]

\[ t = 30 \quad t = 217 \quad t = 219 \quad t = 221 \]