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
- β-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

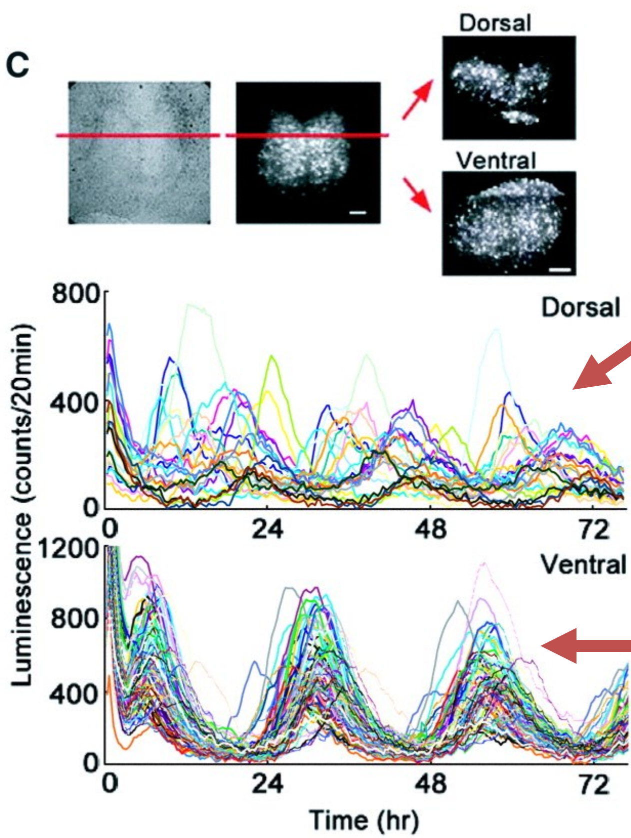
Male Fireflies flashing in unison

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)

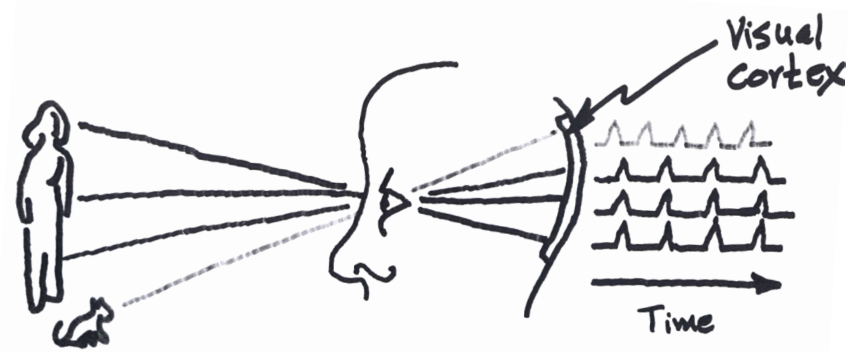


Incoherent

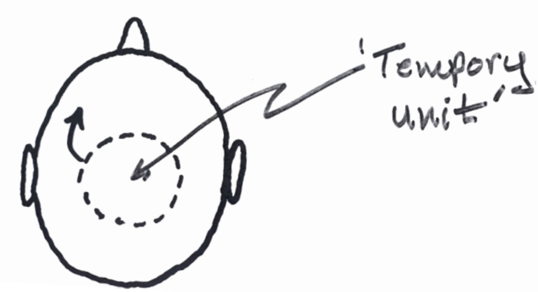
Coherent

Yamaguchi et al., Science, **302**,1408 (2003)

Synchrony in the Brain during perceptual "binding"

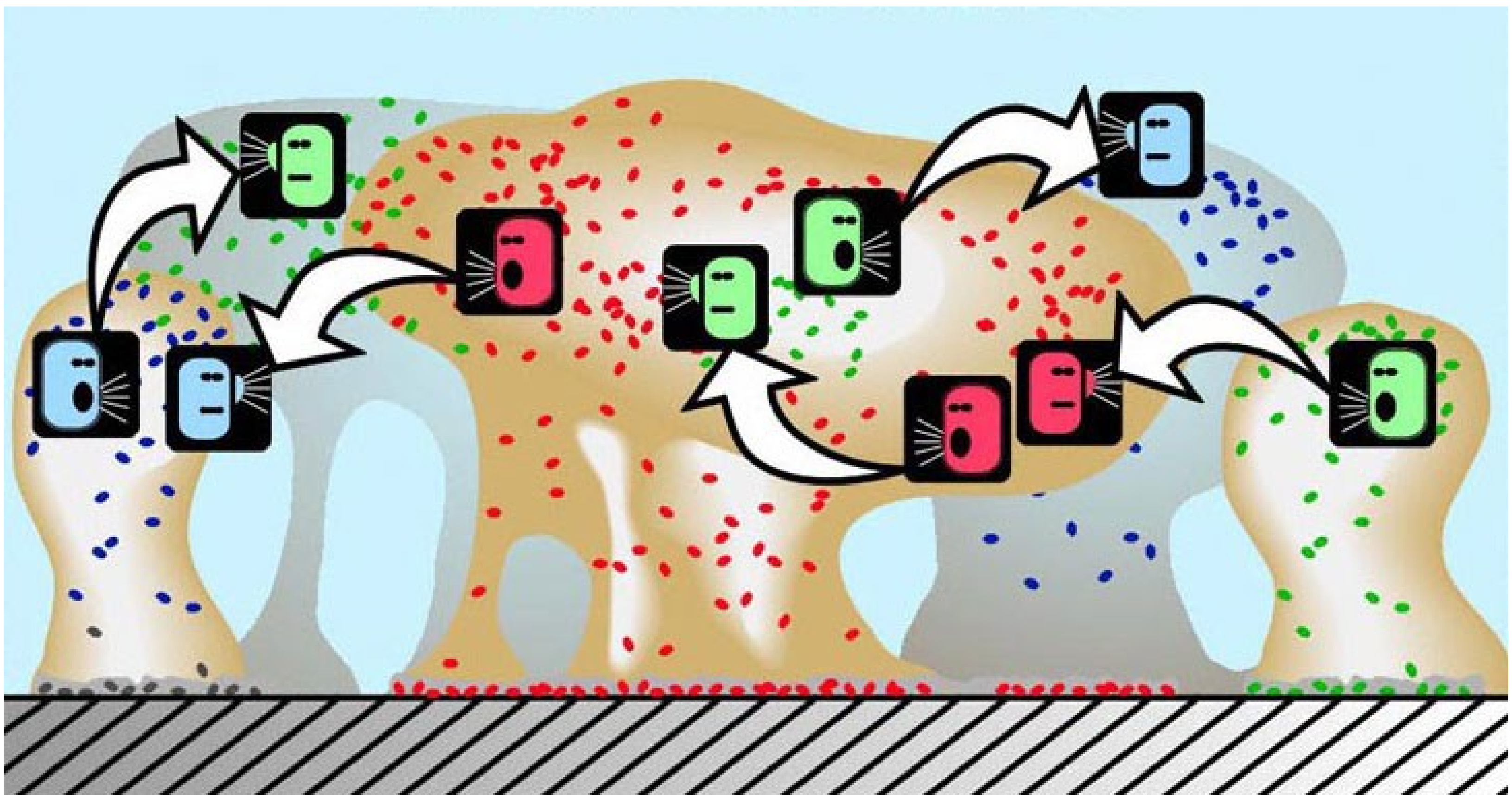


40 Hz oscillations



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

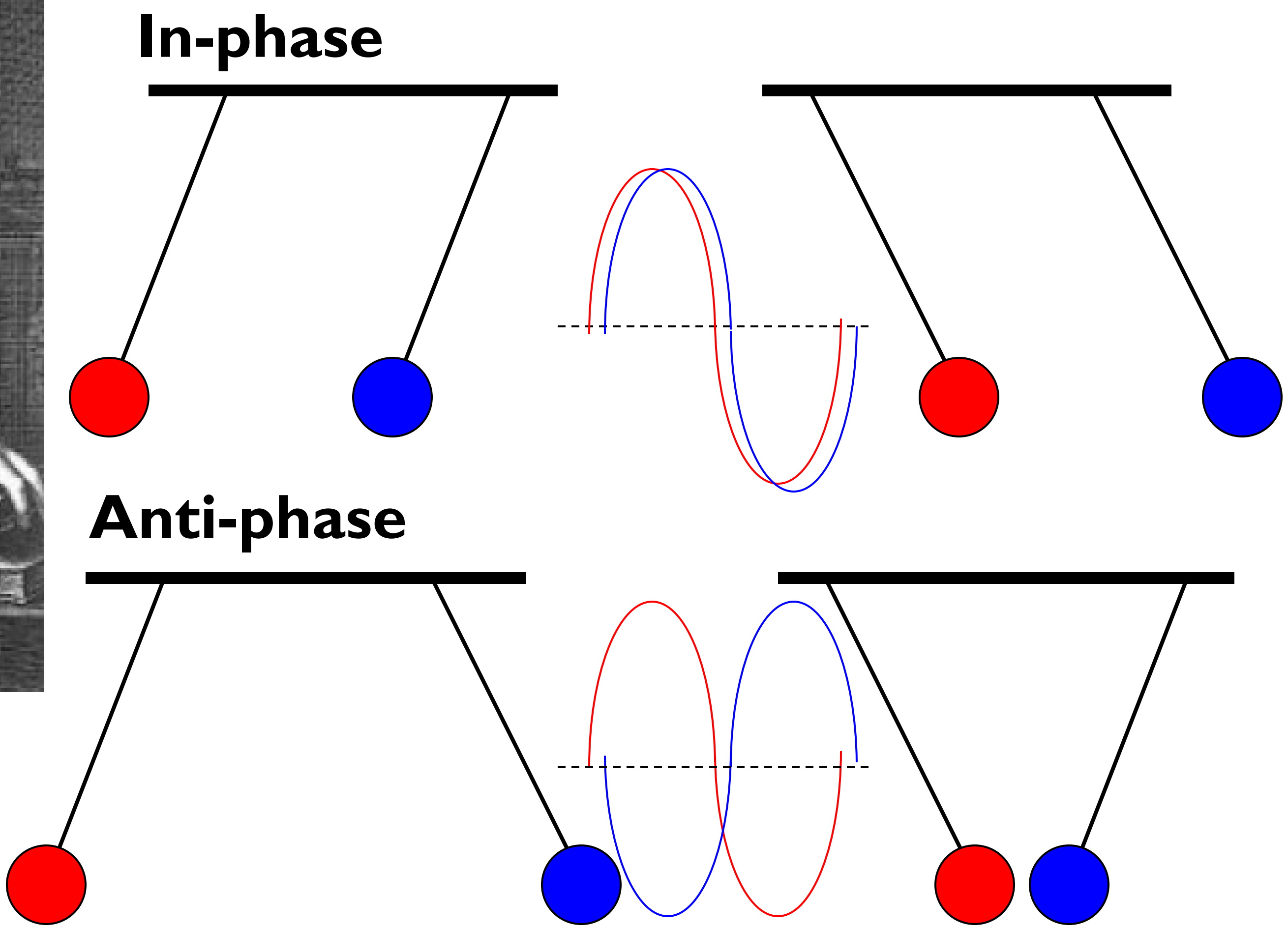
Transition to synchrony with increased coupling

Kuramoto (1975) : Exactly solvable model of collective synchronization

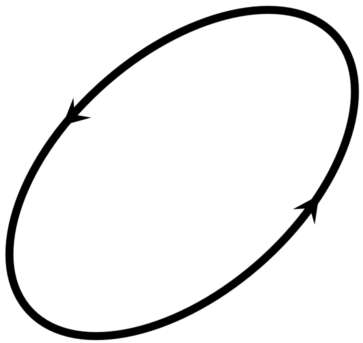
Synchronization of Coupled Oscillators

Christiaan Huygens

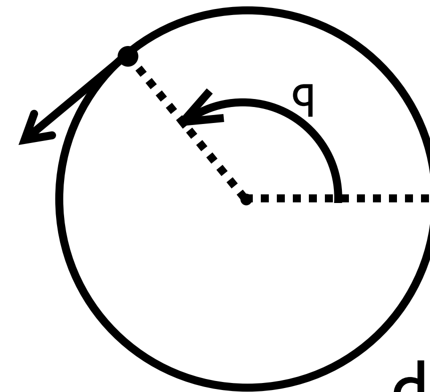
Feb 1665: Huygens observed phase-locking between two pendulum clocks hung side by side



Coupled Phase Oscillators



Changing variables



Limit cycle in phase space

$d\theta/dt = \omega$

Consider many 'phase oscillators' : $d\theta_i \,/\, dt = \omega_i \quad (i=1,2,\ldots,N >> 1)$

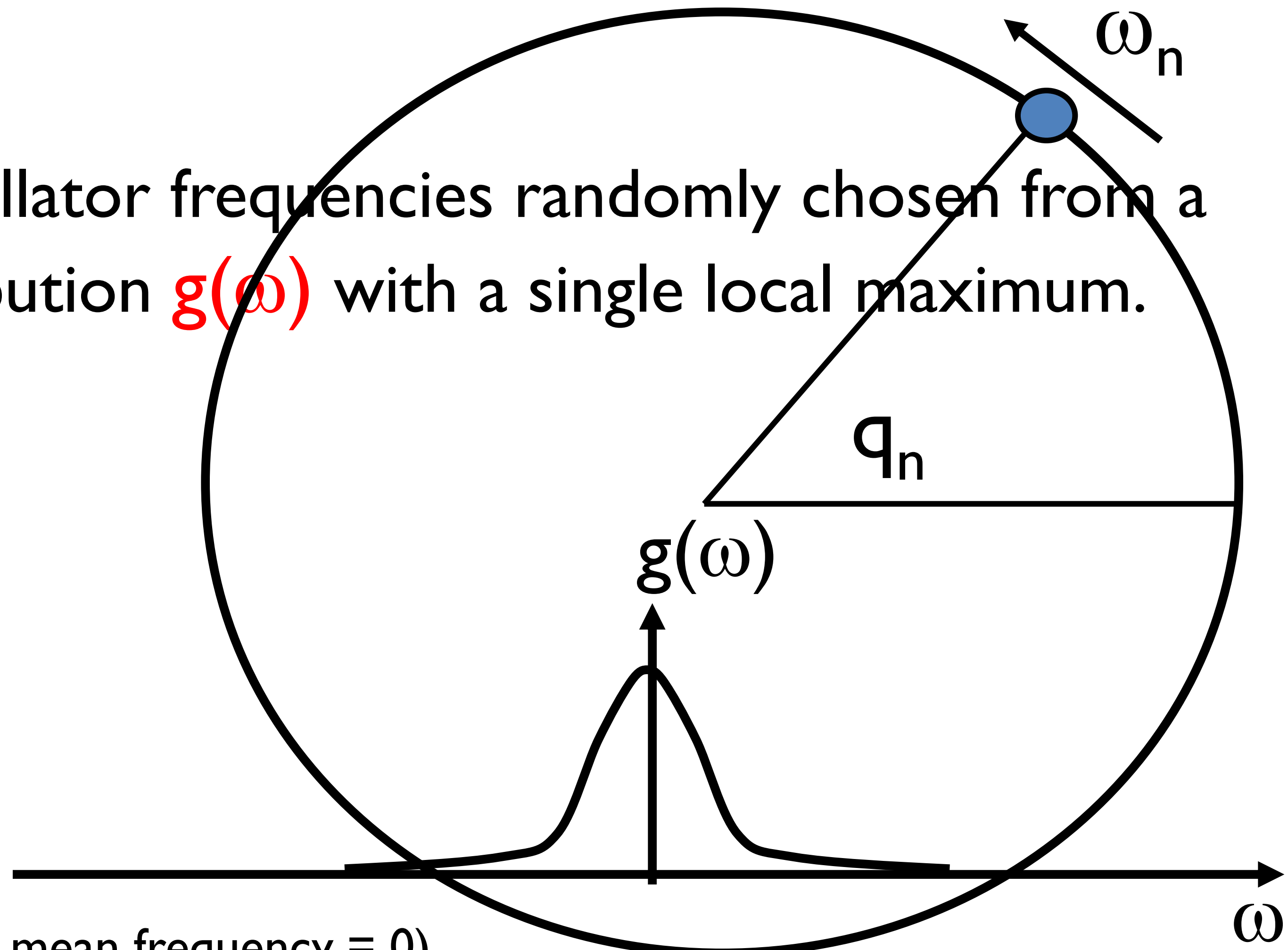
The coupled system: $d\theta_i \,/\, dt = \omega_i + \sum^{N}_{j=1} k_{ij} (\theta_j - \theta_i)$

$$k_{ii} (\phi) = 0, \; k_{ij} (\phi) = k_{ij} (\phi \pm 2\pi)$$

Assumption: Rapid convergence to limit cycle attractor

- N (>>1) oscillators described only by their phase θ

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



(Assume mean frequency = 0)

Kuramoto model (1975): $k_{ij}(\phi) = k \sin \phi$

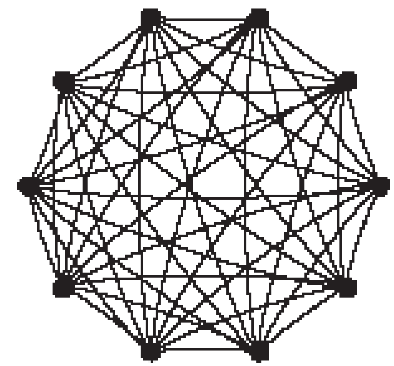
$$\frac{d\theta_n}{dt} = \omega_n + \frac{k}{N}\sum_{m=1}^{N}\sin(\theta_m - \theta_n)$$

n = 1, 2, …., N k = (coupling constant)

- Assumes sinusoidal all-to-all coupling.

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

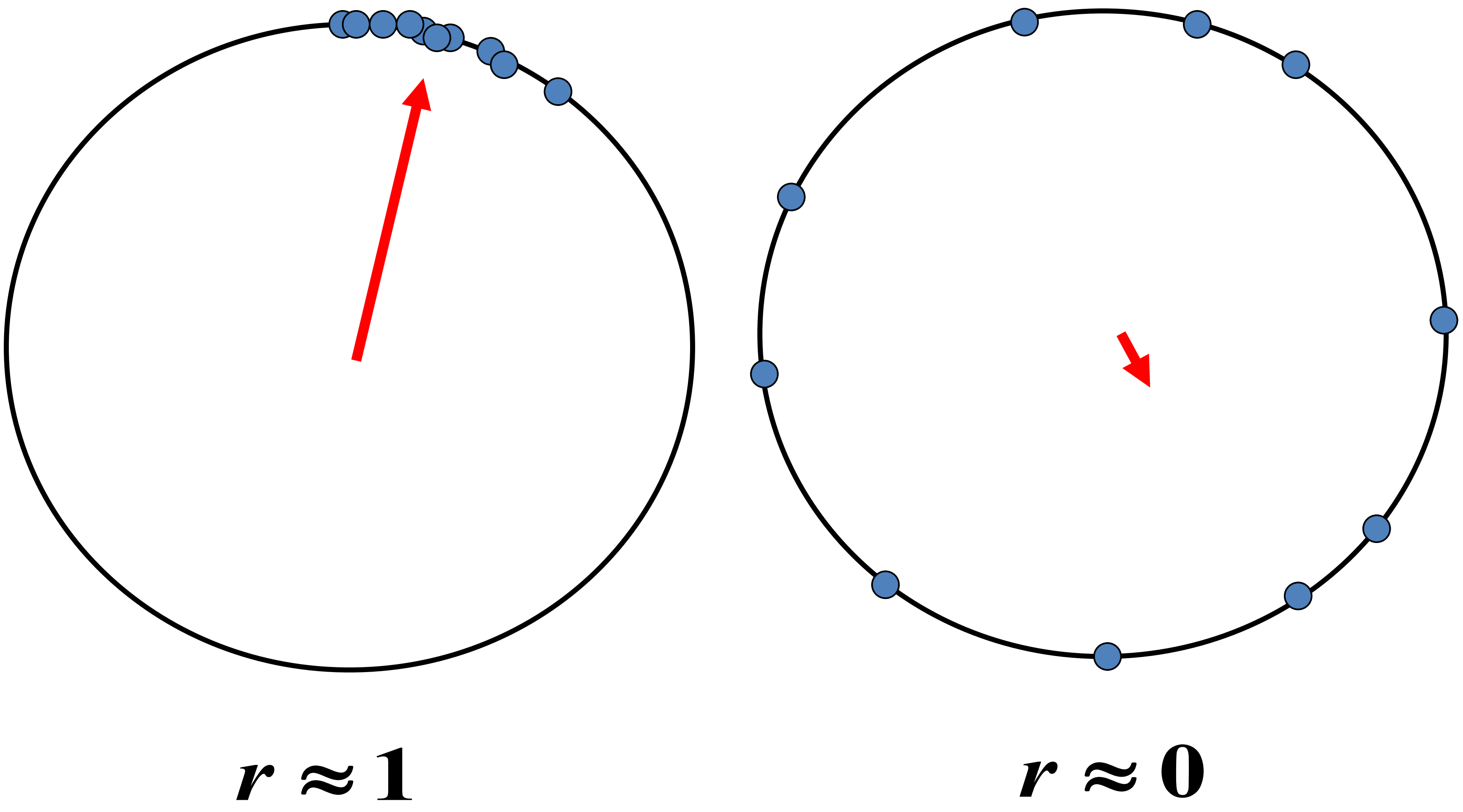
$$r = \left| \frac{1}{N}\sum_{m=1}^{N}\exp(i\theta_m) \right|$$



Global coupling

Measuring coherence of oscillations in the system

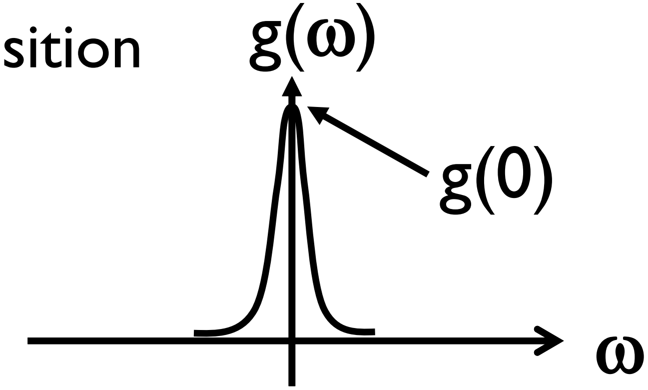
$$r = \left| \frac{1}{N} \sum_{m=1}^{N} \exp(i\theta_m) \right|$$

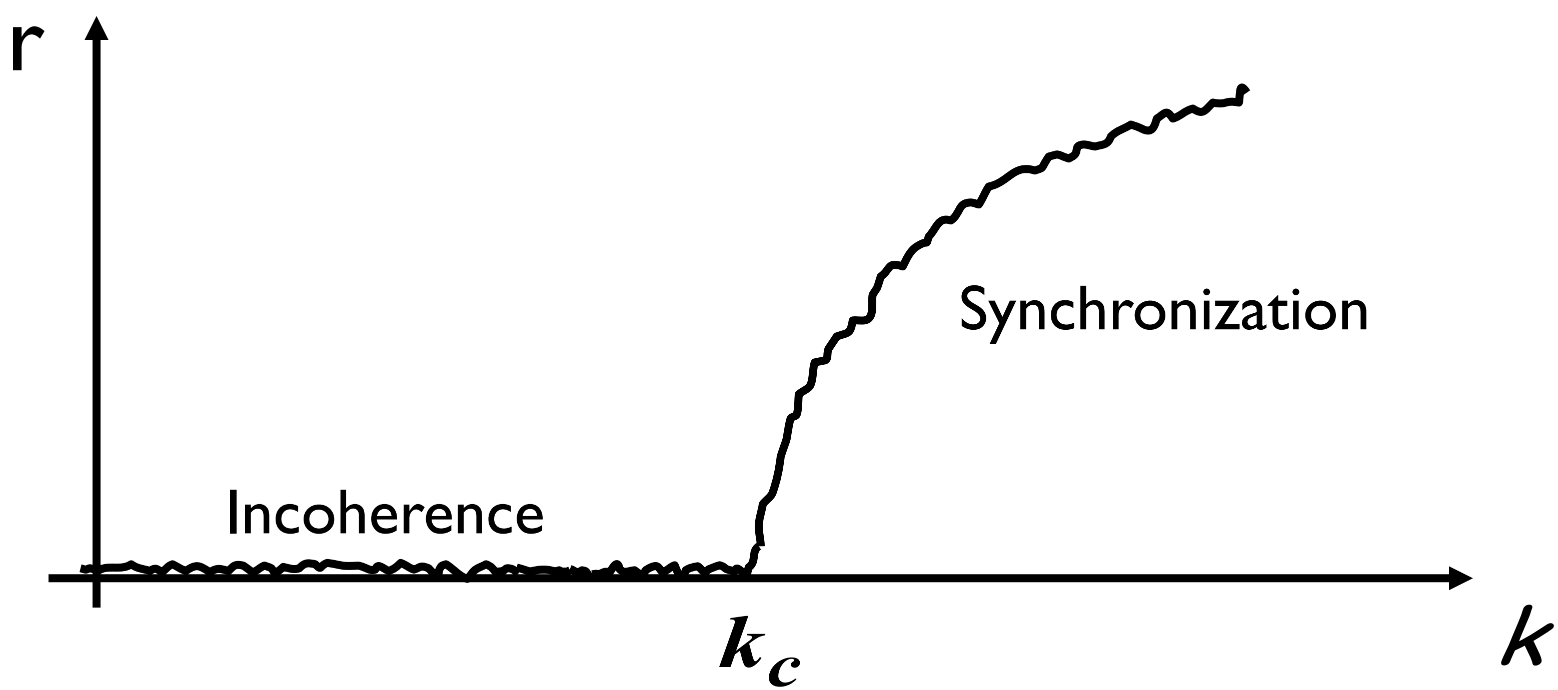


Synchronization-desynchronization transition in Kuramoto model

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

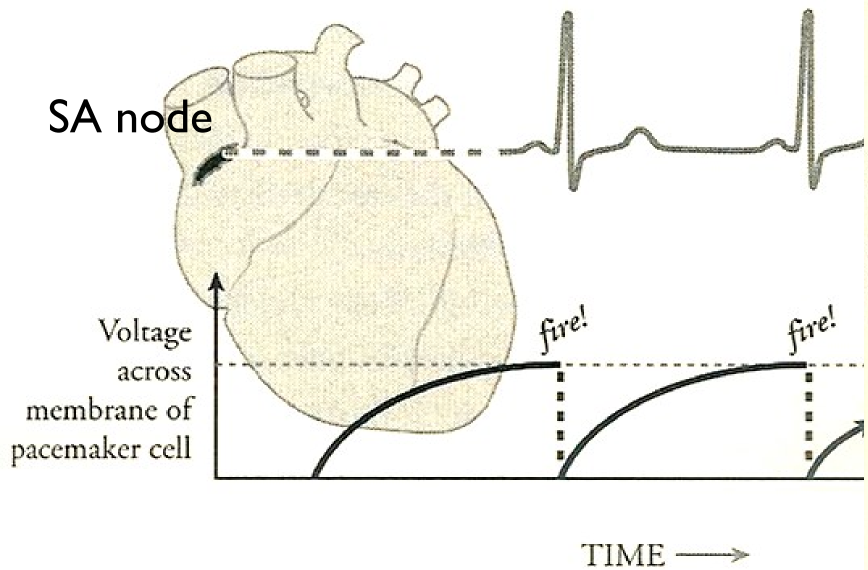
$$k_c = 2 / \pi\, g(0)\, N$$

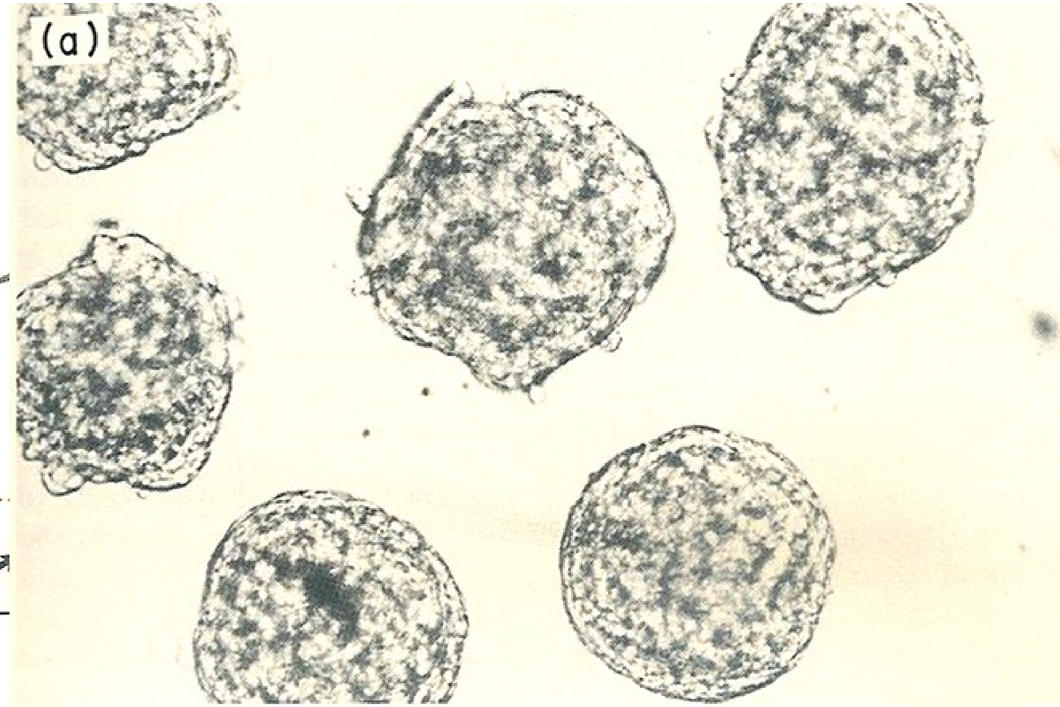




Rhythmic activity in the heart is driven by pacemaker cells

Shrier Lab

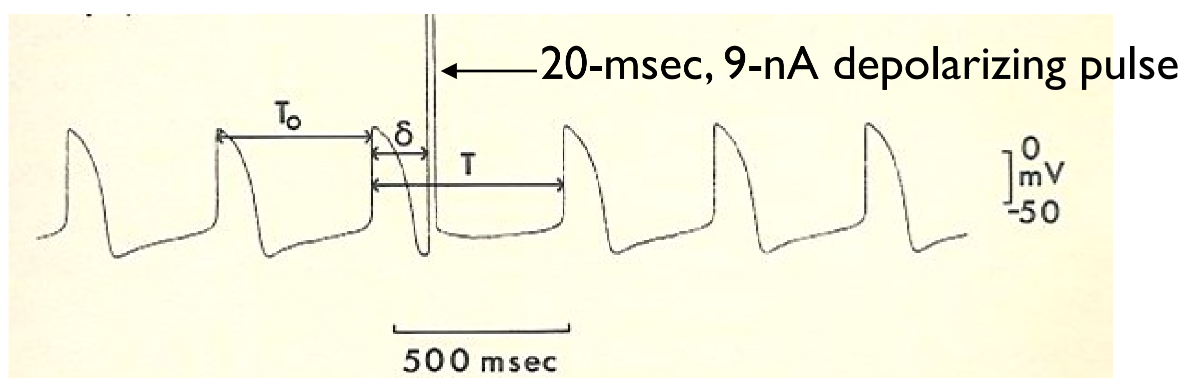




Spontaneously beating aggregates of 7-day chick embryo ventricular cells

Oscillations of all cells in an aggregate are synchronized by gap junction coupling

Transmembrane potential time series from an aggregate

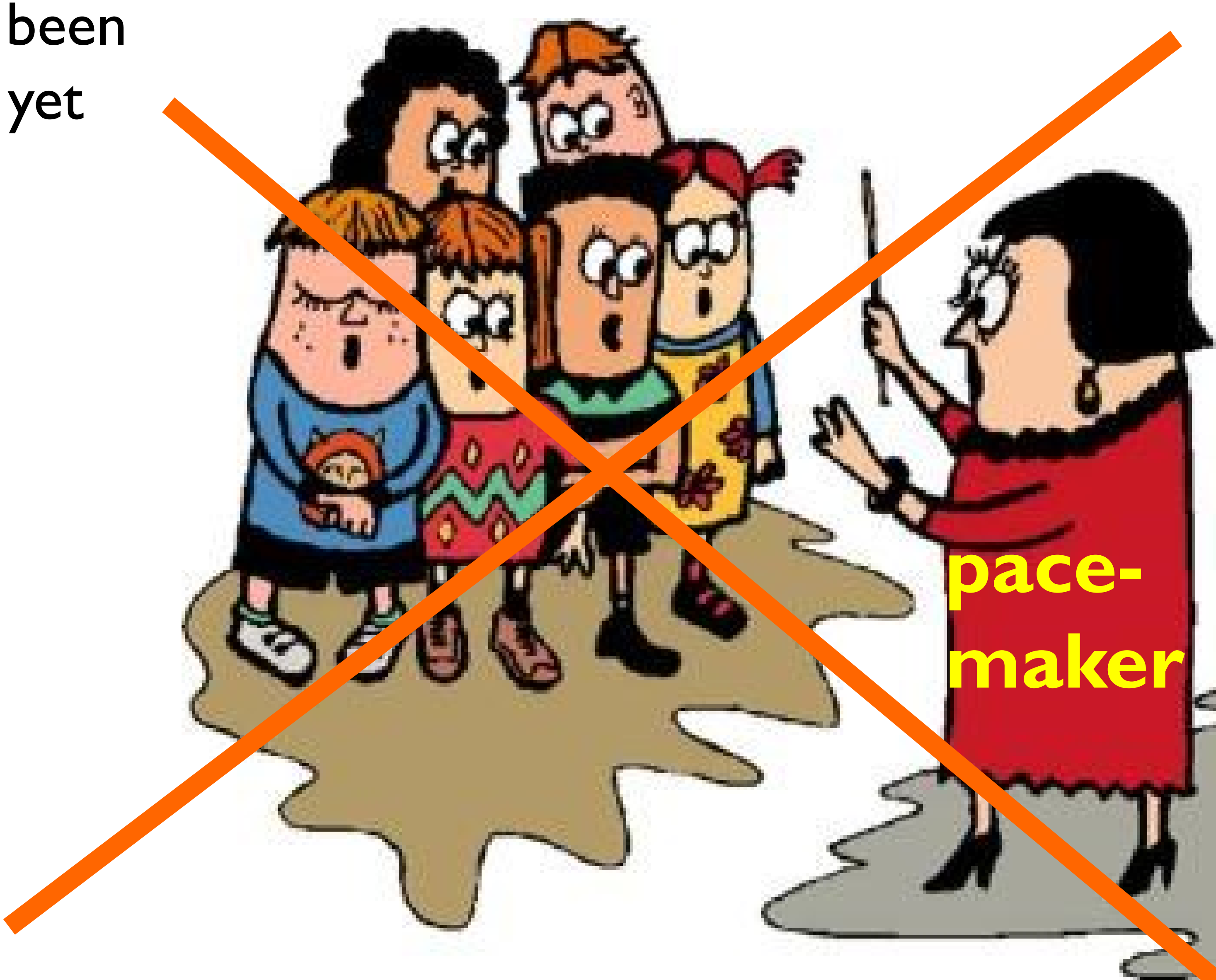


The synchrony is mediated by centralized coordination

For many biological processes

No centralized coordination

agency have been identified as yet



Ordering without centralized coordination

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

Wikipedia

Wikipedia

Examples:
flocking and swarming

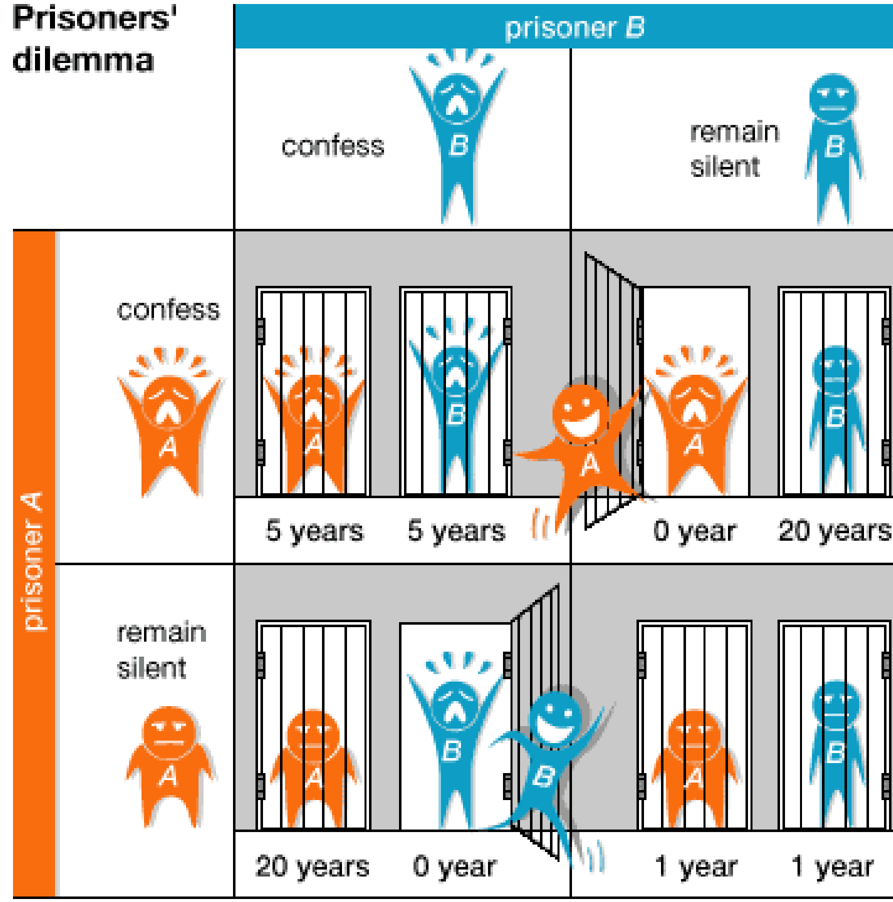
Co-ordination among organisms

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

	Cooperate	Defect
Cooperate	R,R	S,T
Defect	T,S	P,P

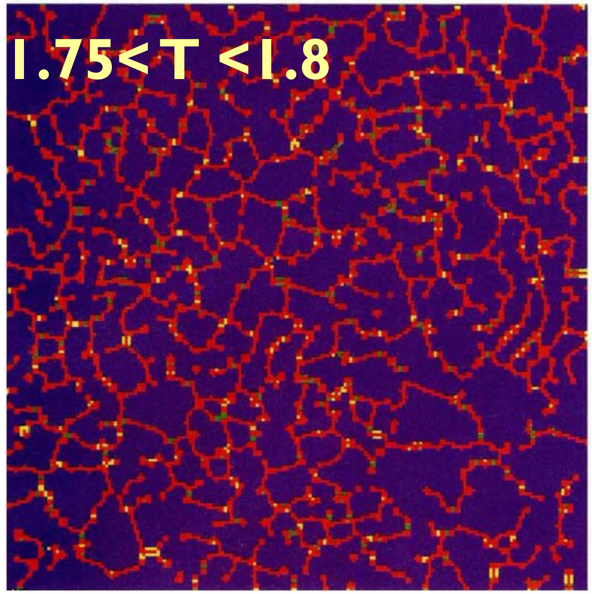
T: Temptation to defect
R: Reward for cooperation
P: Punishment for mutual defection
S: Sucker's payoff
In general, T > R > P > S
Usually, R=1, P=0, S=0 and 1<T<2

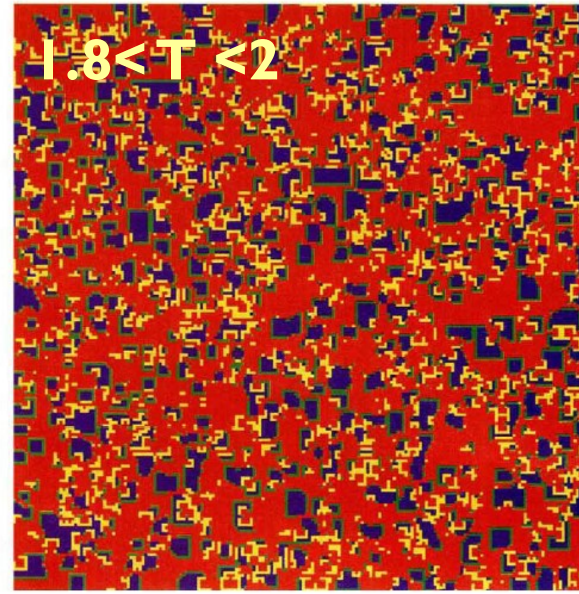
Spatial Prisoners Dilemma

Nowak & May, Nature 1992

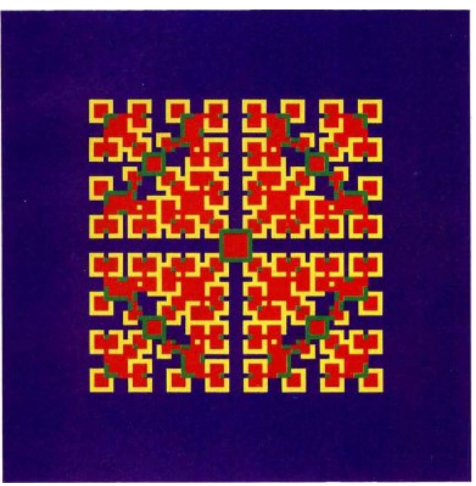
Agents play with neighbors on a lattice, adopting strategy of neighbor with highest payoff

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

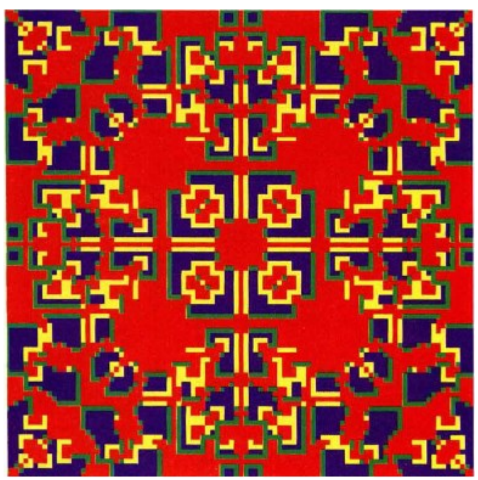




t = 30



t = 217



t = 219

t = 221