The Lure of the Rings

Circle and Torus Flows in Biology

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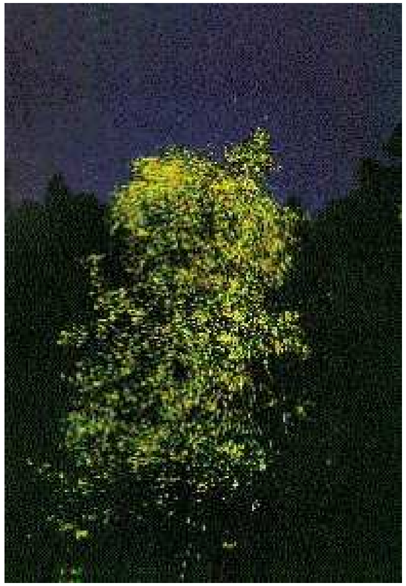
Introduction

- Many examples of patterns in Nature
- Here I am interested in the onset of spontaneous *temporal* order between individuals
- I will use simple differential equations to illustrate this
- As I go on, I will make this precise

Fireflies: A dramatic example



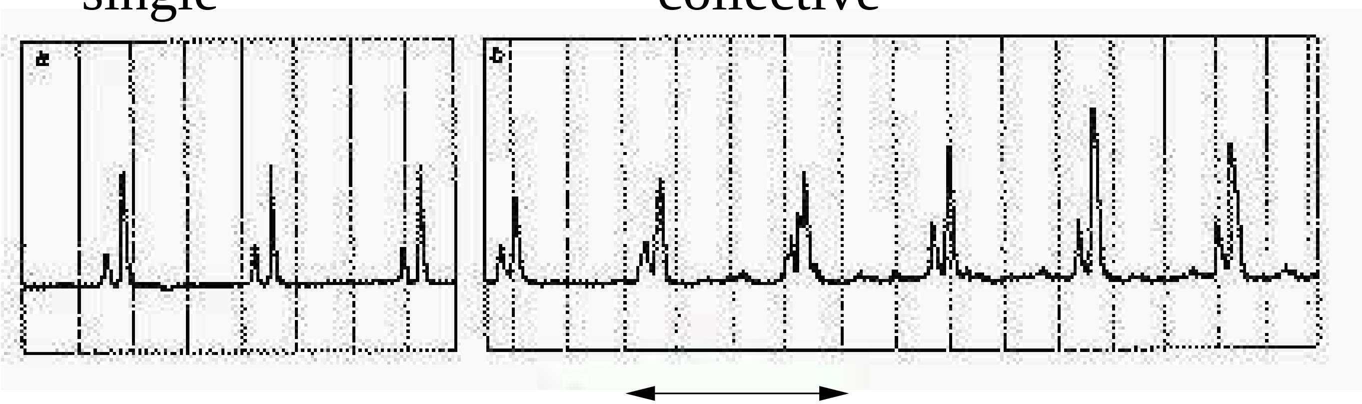
Properties

- Males congregate in large groups at dusk
- Within hours whole system synchronizes
- Global synch from local synch
- Why?
  - competition?
  - searchlight?
  - jamming?

How good is synchrony?

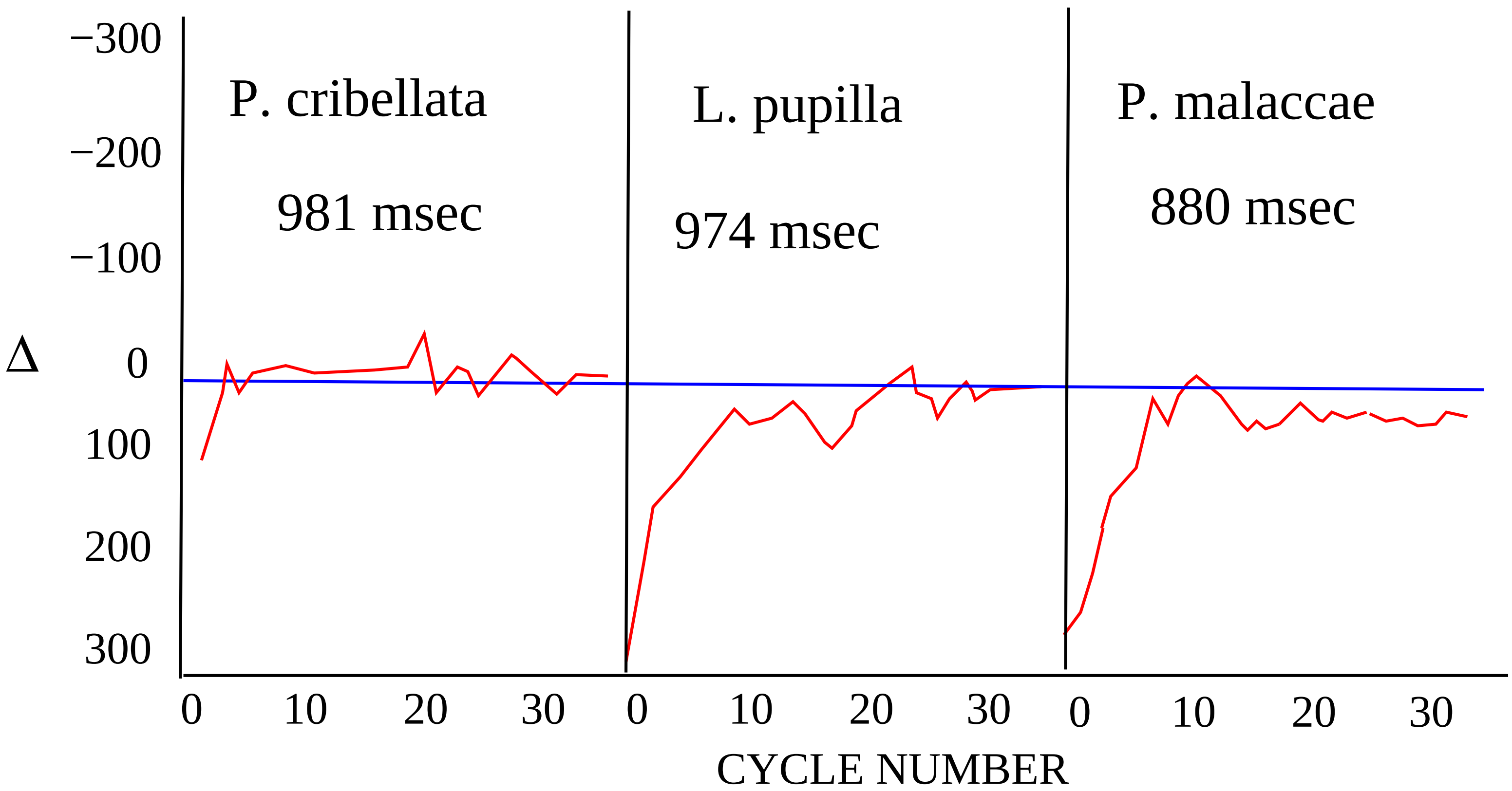
Pteroptyx malaccae isolated flash is almost indistinguishable from population rhythm

single collective



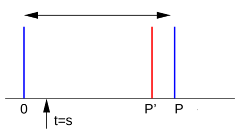
1 second

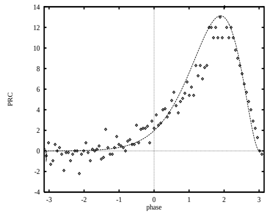
Easy to entrain



Aside # 1: PRCs

- Biological rhythms are governed by nonlinear oscillators



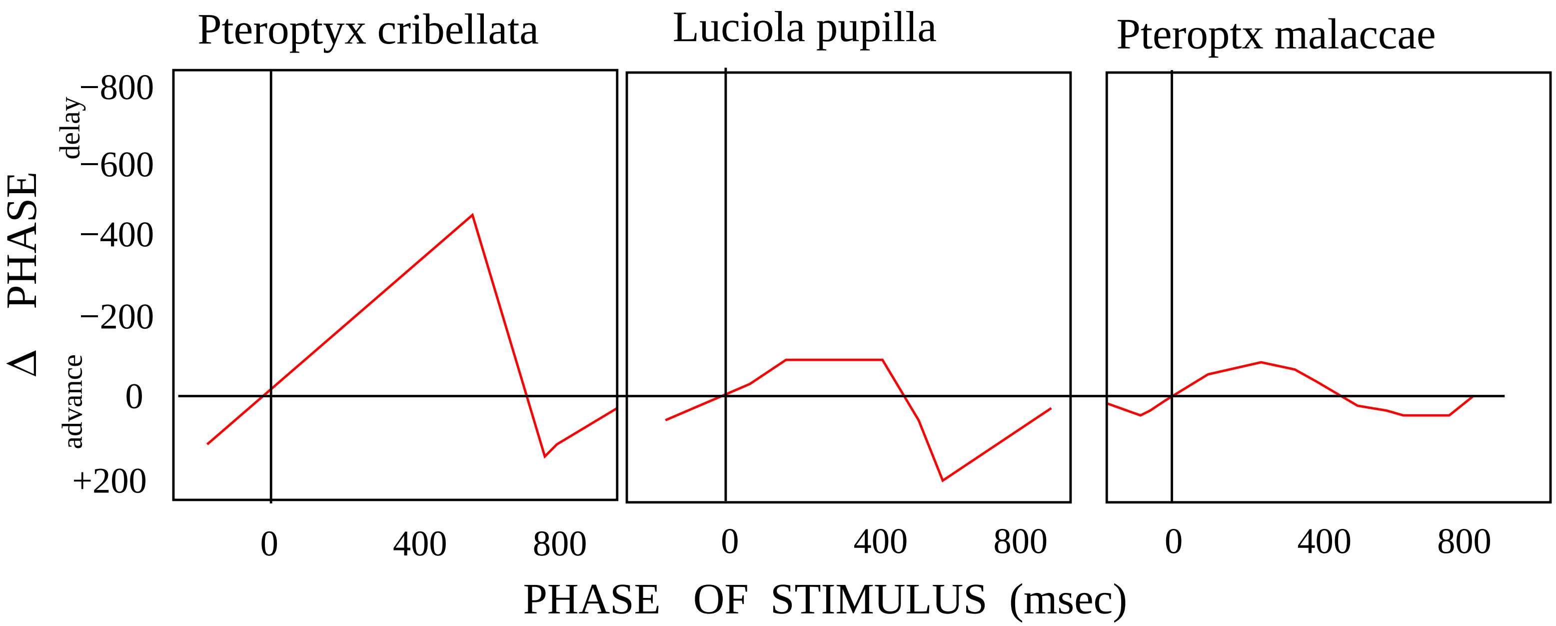


- The *Phase-resetting curve* (PRC) is defined as

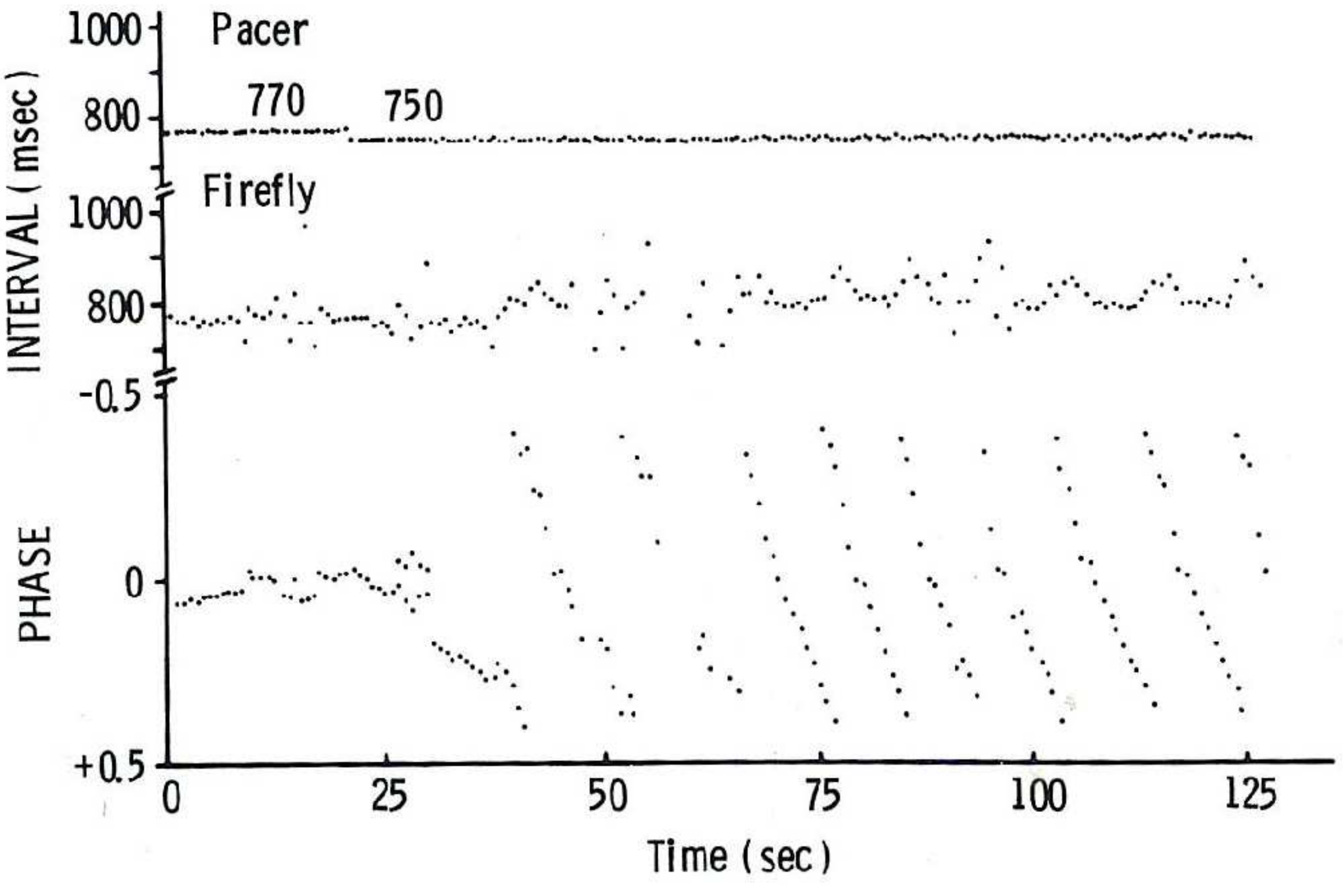
$$\Delta(\phi) = 1 - \frac{P'(\phi)}{P}, \quad \phi \equiv \frac{s}{P}$$

- tells us how an oscillator is changed due to the timing of inputs.

PRCs are different



P. malaccae entrainment



A simple model for entrainment

Let θ be the phase of the firefly and let $\omega = 1$ be his natural frequency. Let ω_z be the frequency at which he is forced. Assume he adjusts his speed proportionally to the phase difference (averaging) Since his response is roughly sinusoidal, we write:

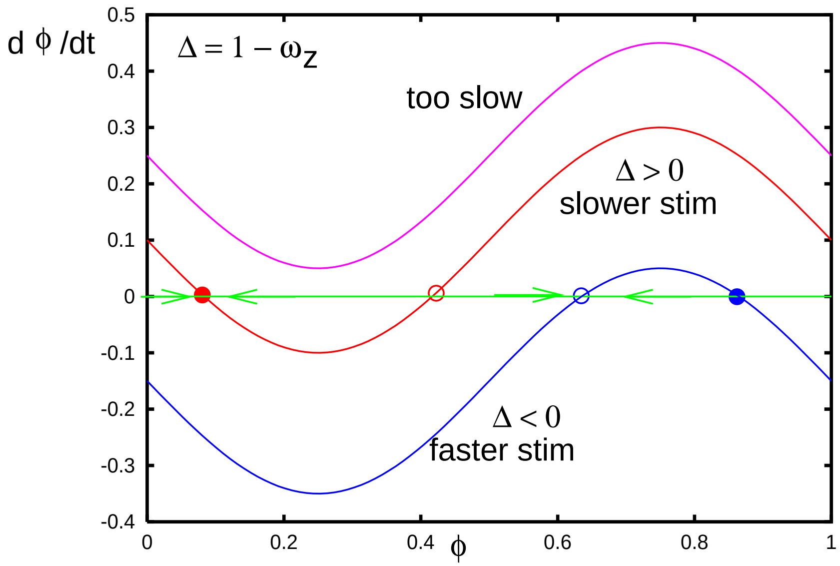
$$\frac{d\theta}{dt} = 1 + a\sin(2\pi(\omega_z t - \theta))$$

Note without a, he marches around the circle of circumference 1, once per second.

Analysis of entrainment

Let $\phi = \theta - \omega_z t$ be his relative phase with respect to the stimulus so that, eg $\phi = .25$ means he leads the stimulus by a quarter of a cycle.

$$\frac{d\phi}{dt} = 1 - \omega_z - a \sin 2\pi\phi$$



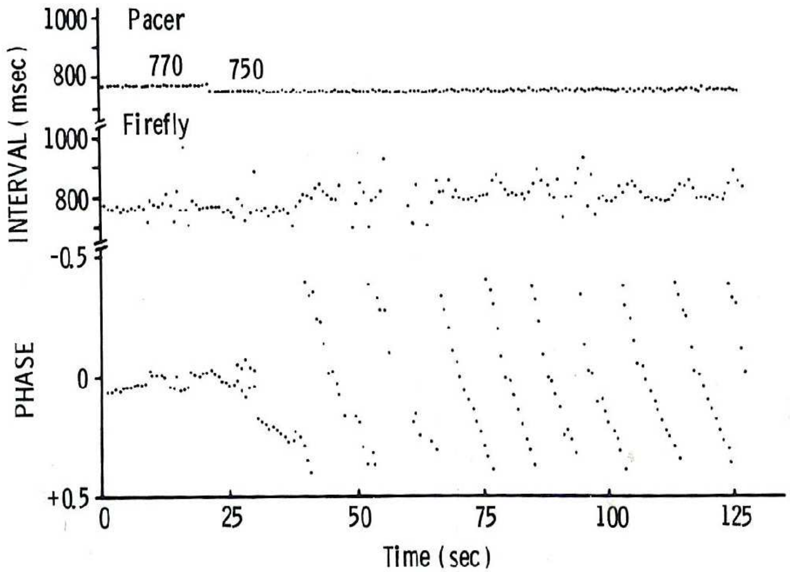
Analysis of walkthrough

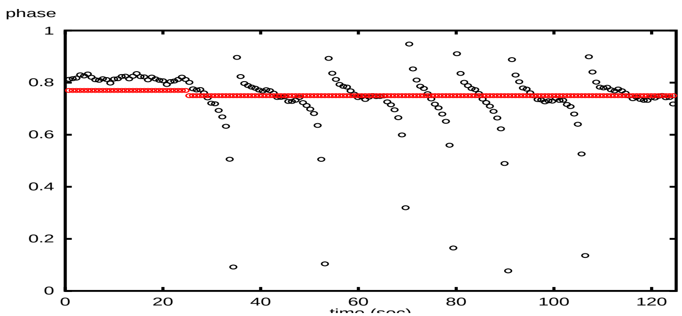
- What is the period of walk-through?
- Walk-through occurs when $|1-\omega_z| > a$, so, $\phi(t)$ moves continuously around the circle.
- T is the time to go from 0 to 1:

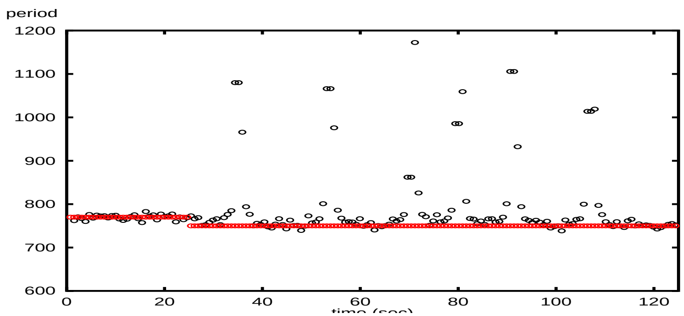
$$T = \int_0^1 \frac{d\phi}{1-\omega_z - a\sin 2\pi\phi} = \frac{1}{\sqrt{(1-\omega_f)^2 - a^2}}$$

- Period of walkthrough at 1.33 Hz is about 35 seconds, so $a \approx 0.328$ which implies that when $T_f = 800$ msec that $\phi \approx 0.18$. This is a little high. (PM actually alters ω.)

Simulation of walkthrough



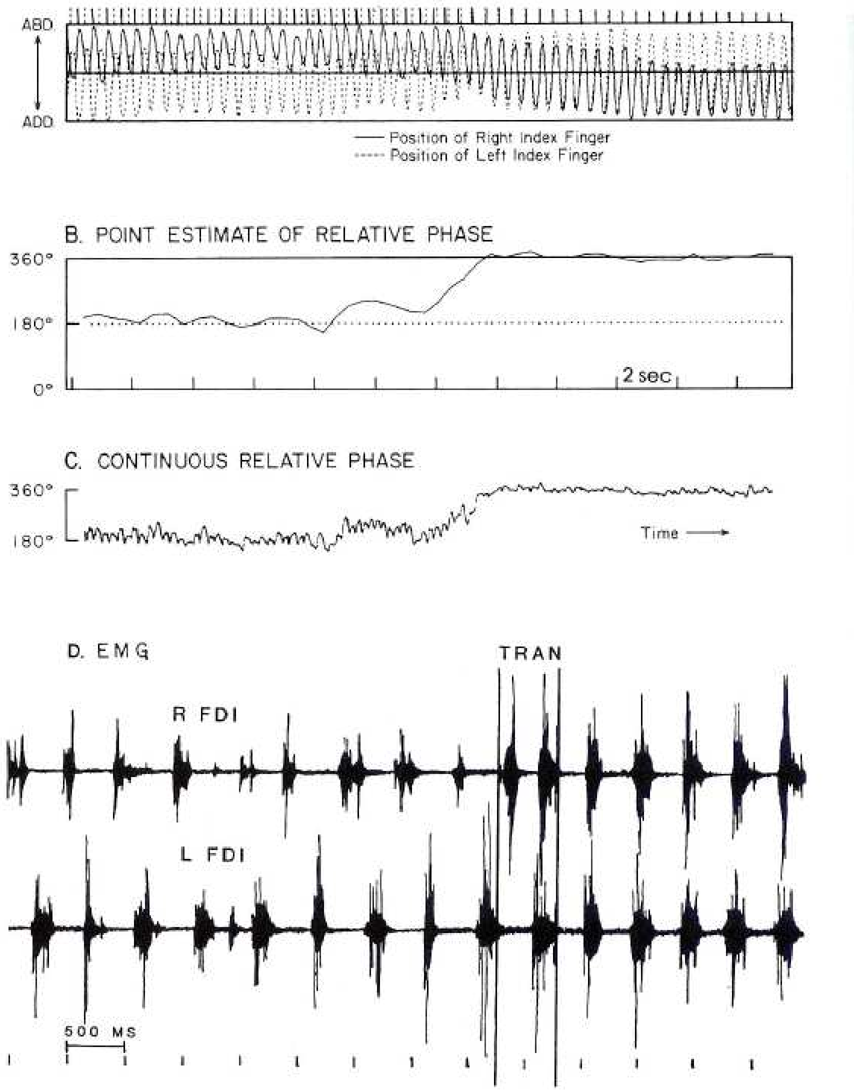




Finger tapping

- Task: tap two fingers in syncopation (alternately) while following a metronome
- As frequency goes up, it becomes impossible and subjects switch to synchrony
- Analogous to how a dog or horse switches gaits from a walk to a trot to a gallop as she attempts to run faster

Experimental data



Central pattern generators

- Groups of neurons in CNS responsible for rhythmicity.
- Left-right (or, front-back) are considered oscillators coupled together.
- Simple phase-models from neurons change shape with frequency

$$\begin{aligned}\frac{d\theta_L}{dt} &= \omega + H(\theta_R - \theta_L; \omega) \\ \frac{d\theta_R}{dt} &= \omega + H(\theta_L - \theta_R; \omega)\end{aligned}$$

Analysis

As with the FFs let $\phi = \theta_L - \theta_R$:

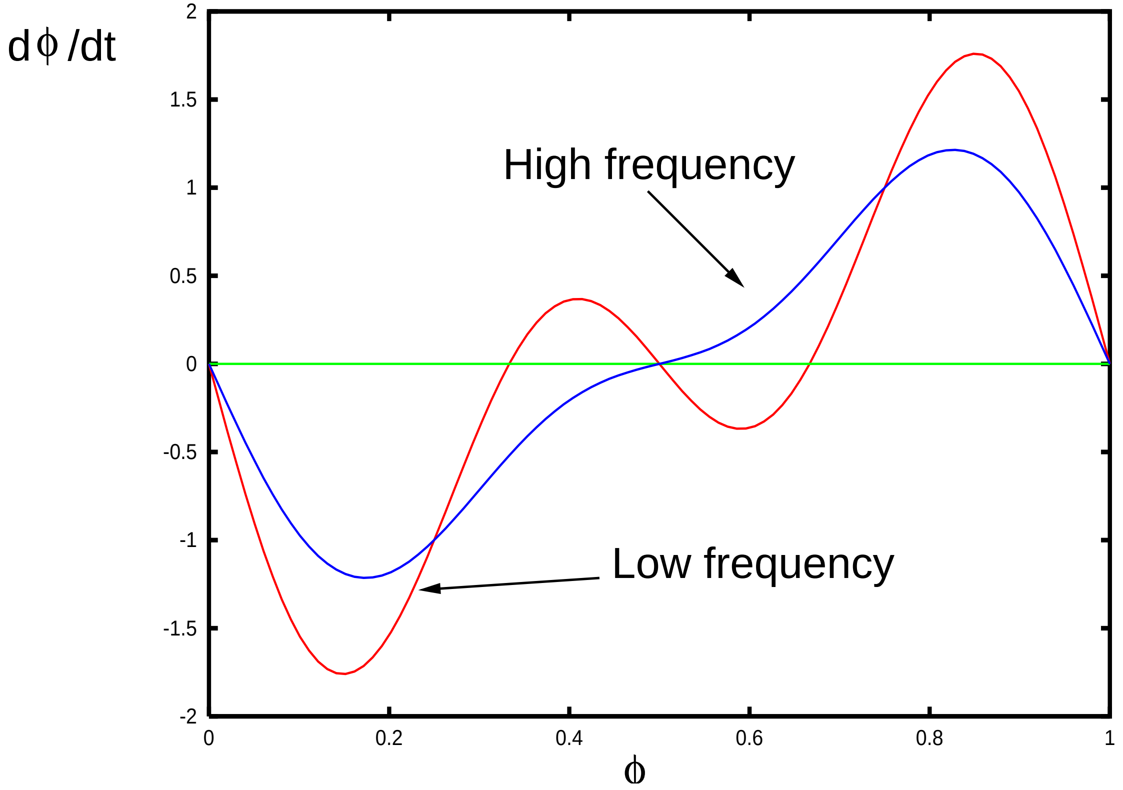
$$\frac{d\phi}{dt} = H(-\phi;\omega) - H(\phi;\omega) \equiv g(\phi;\omega)$$

For simplicity:

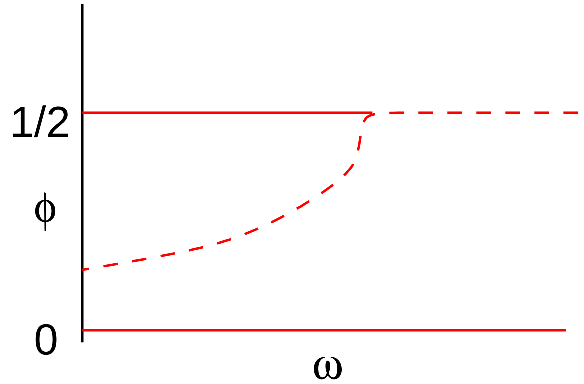
$$g(\phi) = -\sin 2\pi\phi - b(\omega)\sin 4\pi\phi$$

where $b(\omega)$ decreases as ω increases.

Phase-space



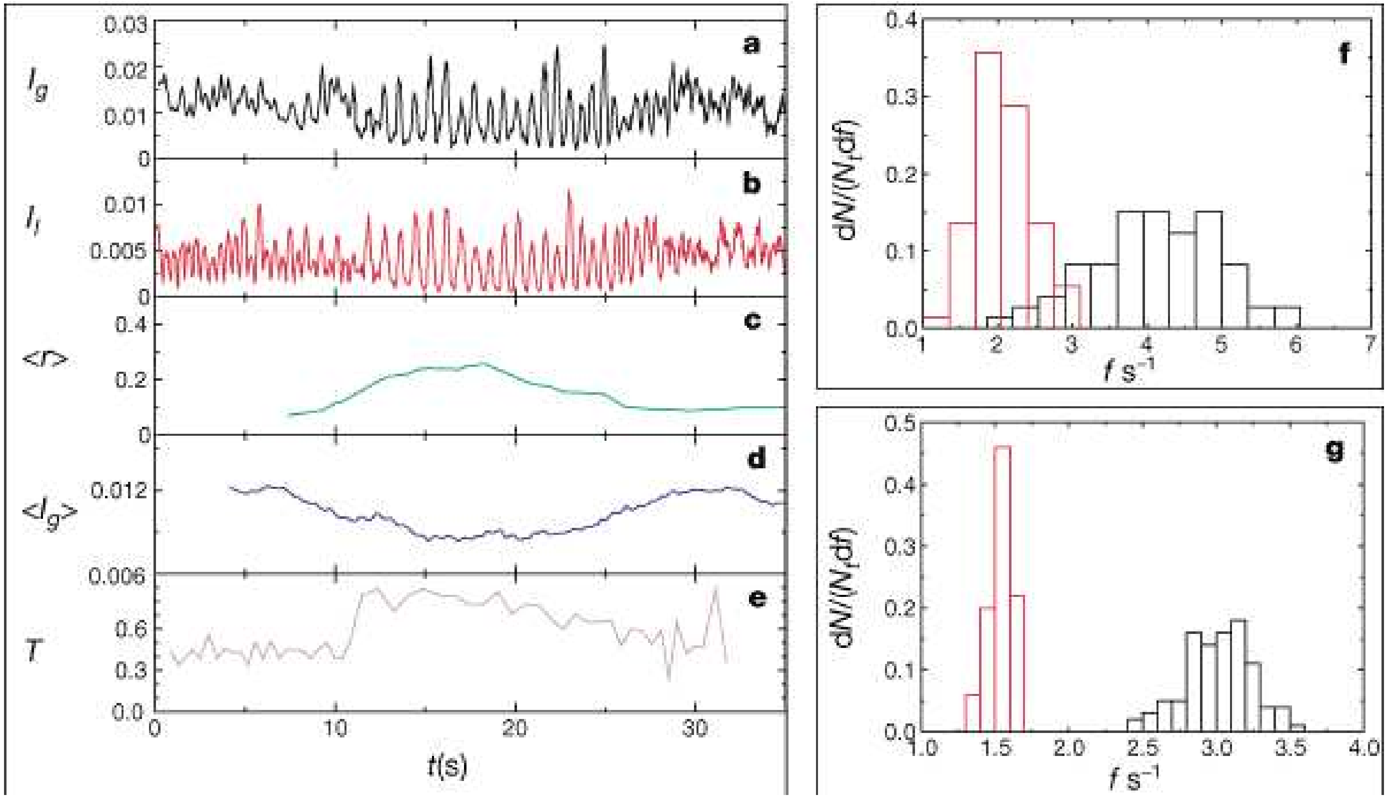
dφ /dt
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0
0.2
0.4
0.6
0.8
1
φ
High frequency
Low frequency



1/2
φ
0
ω

Hand clapping

Eastern European audiences drift between synchronous and asynchronized hand clapping:



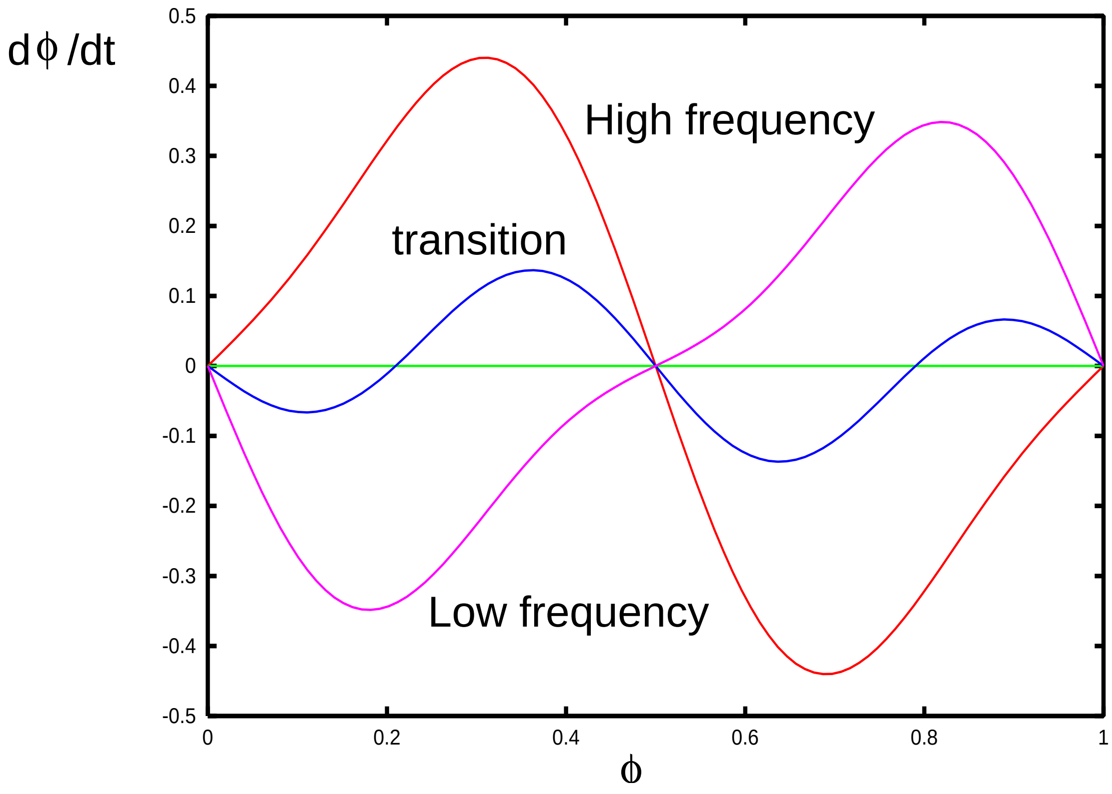
Mechanisms?

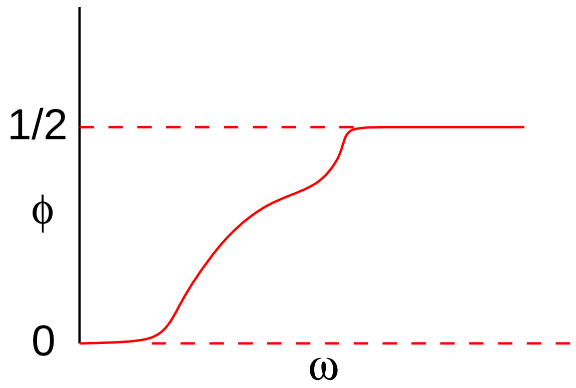
- At low frequencies, they synchronize – but the individual range is also much tighter
- At high frequencies, asynchronous – range of frequencies is broader
- Two possibilities
  - Broader range is harder to synchronize
  - Higher frequencies are harder to synchronize

Excitatory coupling

- Suppose clapping is generated by a CPG and the sound acts to couple different clappers.
- What kind of coupling leads to *destabilizing* synchrony as the frequency *increases*?
- Mutual excitation can do this.
- Let ϕ be the phase-difference between two clappers (as with the tapping)
$$\frac{d\phi}{dt} = a(\omega)\sin 2\pi\phi - b\sin 4\pi\phi$$
- As ω increases $a(\omega)$ changes from negative to positive.

Phase-space again!





Alternate mechanism

- Assume that interaction is insensitive to frequency
- Range of frequencies is broader when higher
- Simple model for $\phi = \theta_1 - \theta_2$:

$$\frac{d\phi}{dt} = k(\omega_1 - \omega_2) - a \sin \phi$$

- $k = 1$, entrain, but $k = 2$ (double frequency), don't entrain!

Aside 1:here’s the beef

- CPG’s consist of neural oscillators; assume they have PRC
- Assume coupling is “weak”
- Then averaging allows us to reduce to phase models:

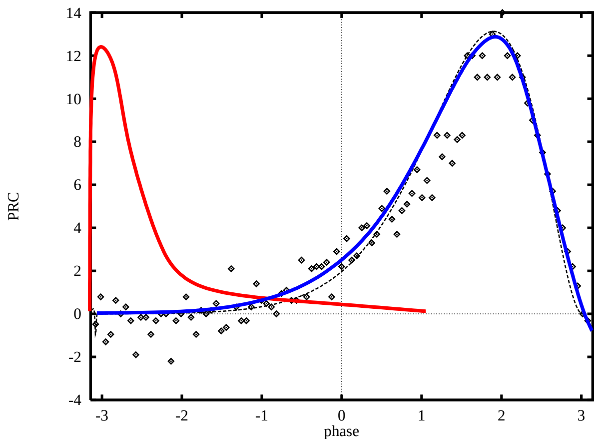
$$\theta_j' = \omega_j + \sum_k H_{jk}(\theta_k - \theta_j)$$

where (roughly)

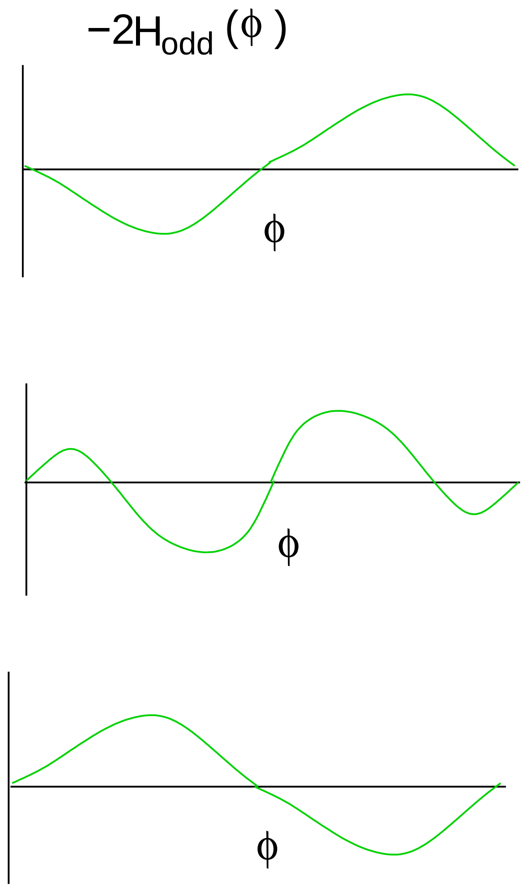
$$H(\phi) = \frac{1}{T}\int_0^T \Delta(t)S(t+\phi)\,dt$$

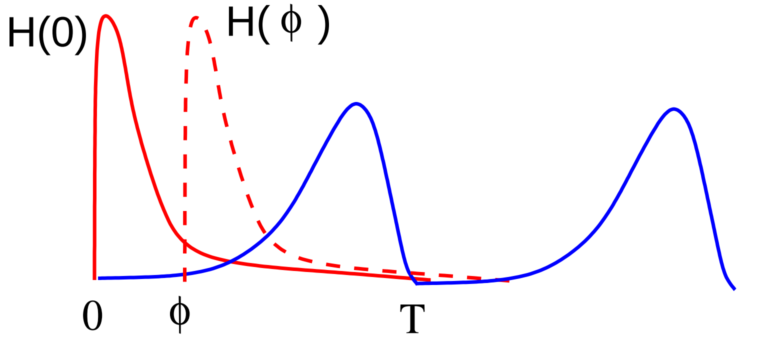
- $\Delta(t)$ is the PRC and $S(t)$ is signal from the other oscillator(s)
- **Odd part** of H determines pairwise synchrony

Aside 2: Details



Low frequency





High frequency

EXCITATORY

More than two???

- For $N = 2$, odd part of H is the whole show
- For “all-to-all”, odd part is most of the show
- For all other cases, “fugedaboutit”

One-dimensional arrays

Consider

$$\theta_i' = \omega_i + A^+ H(\theta_{i+1} - \theta_i) + A^- H(\theta_{i-1} - \theta_i), \qquad i = 1, \ldots, N$$

K & E proved that as $N \to \infty$

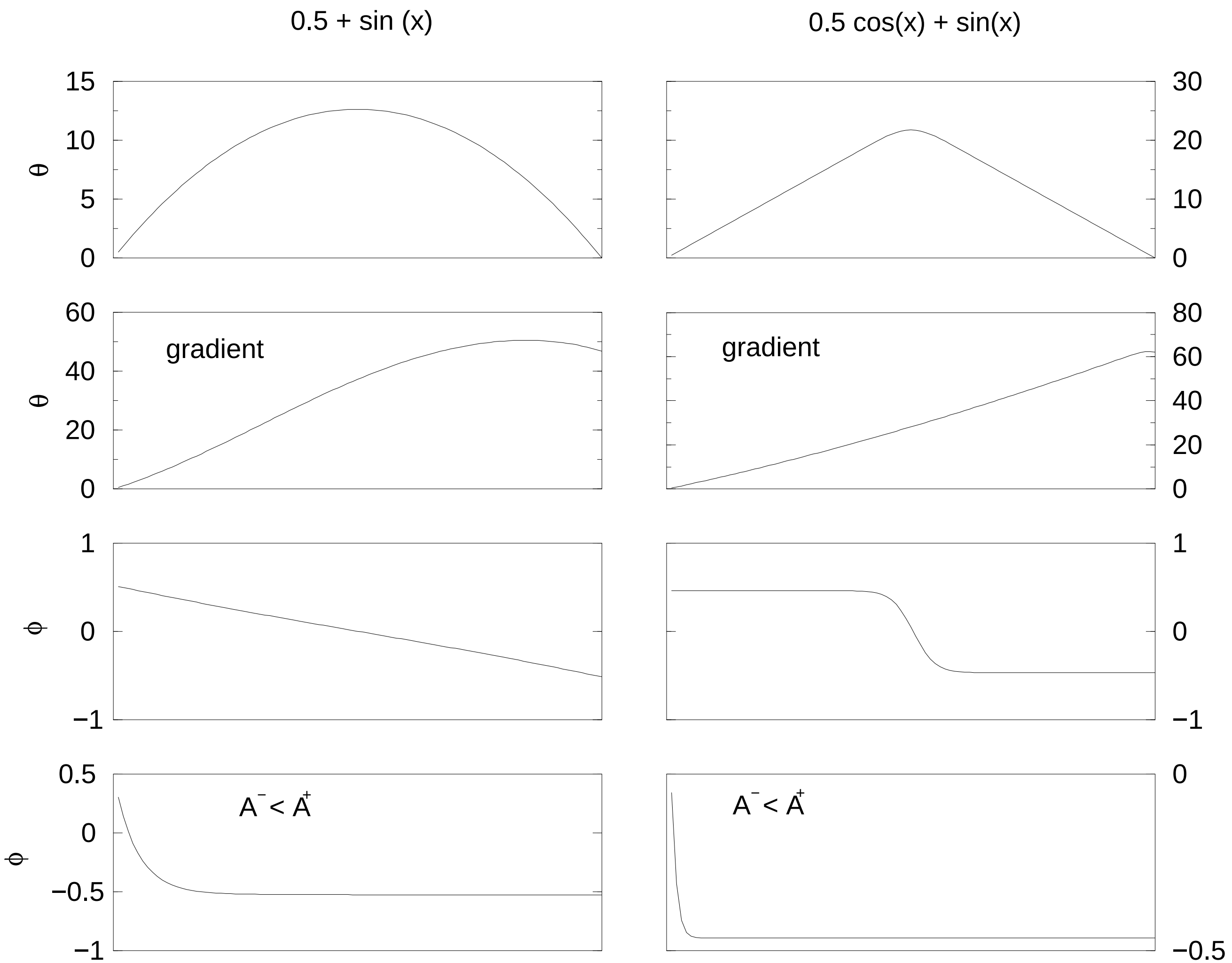
$$\begin{aligned} \Omega &= \omega(x) + f(\phi) + \frac{1}{N} g(\phi)_x \\ \Omega &= \omega(0) + A^+ H[\phi(0))] \\ \Omega &= \omega(1) + A^- H[-\phi(1)] \end{aligned}$$

Singularly perturbed two-point BVP

Boundary layers and asymmetry

- For purely “odd” coupling, trivial
- $a_0 + a_1 \cos(x) + \sin(x)$ behaves differently depending on relative sizes of a_0, a_1.
- For symmetric coupling, layer is in interior
- Asymmetries – layers at edges
- Gradients also break symmetry and produce bndry layers

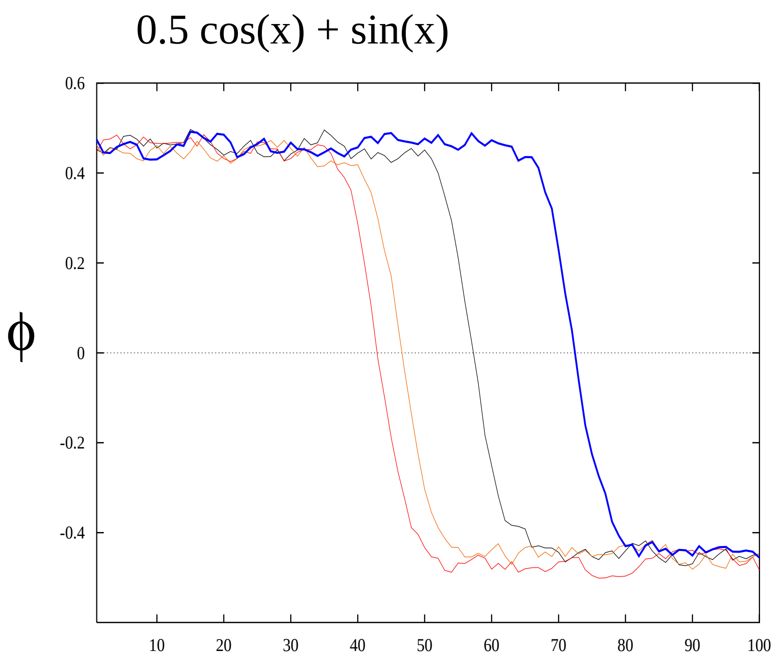
Example

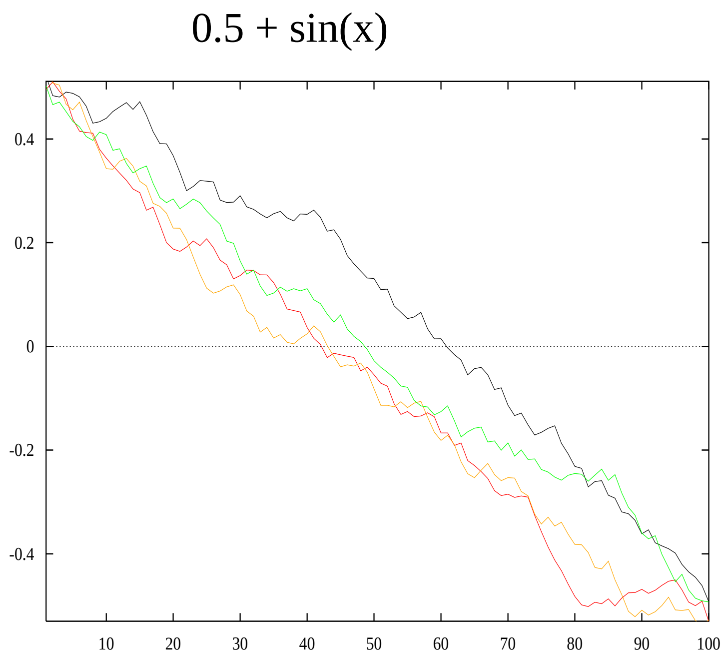


0.5 + sin (x)
0.5 cos(x) + sin(x)
15
10
5
0
θ
30
20
10
0
60
40
20
0
gradient
80
60
40
20
0
gradient
1
0
−1
ϕ
1
0
−1
0.5
0
−0.5
−1
ϕ
A⁻ < A⁺
0
−0.5
A⁻ < A⁺

Remarks etc

- For $H(u) = c + g(u)$, $g(\phi_j) = c(N - 2j)/N$ (parabolic)
- For $H(u) = f(u) + g(u)$, $\phi_j \approx K\text{sign}(j - N/2)$ (linear)
- Layer is sloppy – heterogeneities move it





Stability

THEOREM (Ermentrout '94) Let $\{\phi_1, \ldots, \phi_N\}$ be a phaselocked solution to

$$\theta_i' = \omega_i + H_i(\theta_1 - \theta_i, \ldots, \theta_N - \theta_i)$$

and $c_{ij} = \partial H_i / \partial u_j$ evaluated at the soln. If $c_{ij} \geq 0$ and the matrix $C = (c_{ij})$ is irreducible, then the soln is orbitally asymptotically stable.

Two- and higher dimensional lattices

THEOREM (Ren & Ermentrout, '97). Suppose we have a nearest neighbor coupled system in $m > 1$ dimensions and fix all but one of the coordinates. Then the phase-differences along that one-dimensional system are the same as that of the corresponding one-dimensional chain. That is, if

$$\theta'_{ij} = \omega + H^{X,+}(\theta_{i+1,j} - \theta_{i,j}) + \dots$$

then

$$\theta_{ij} = \Omega t + \Phi_i + \Psi_j$$

Consequences of the theorem

- **Bullseyes:** If $H(u) = g(u) + C$

$$\theta_x \approx 2K(x - 1/2) \quad \theta_y \approx 2K(y - 1/2)$$

and

$$\theta \approx \Omega t + K[(x - 1/2)^2 + (y - 1/2)^2]$$

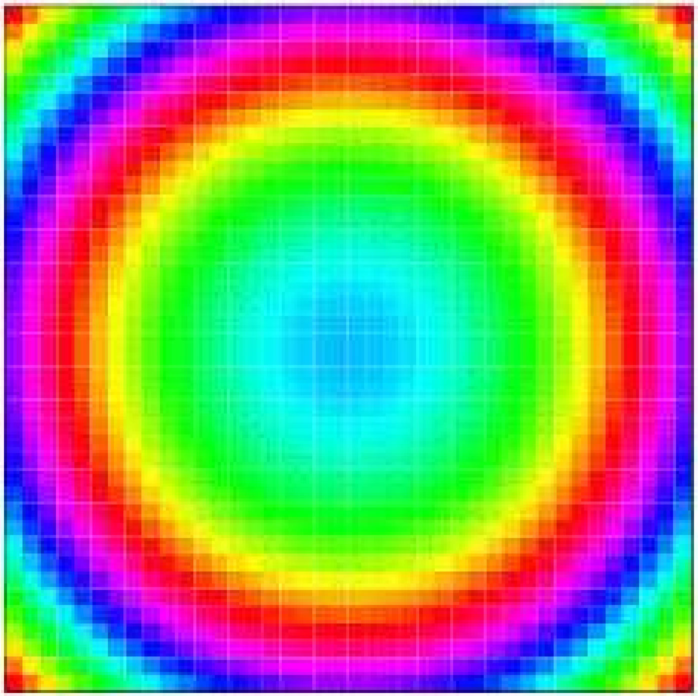
- **Squares:** If $H(u) = f(u) + g(u)$

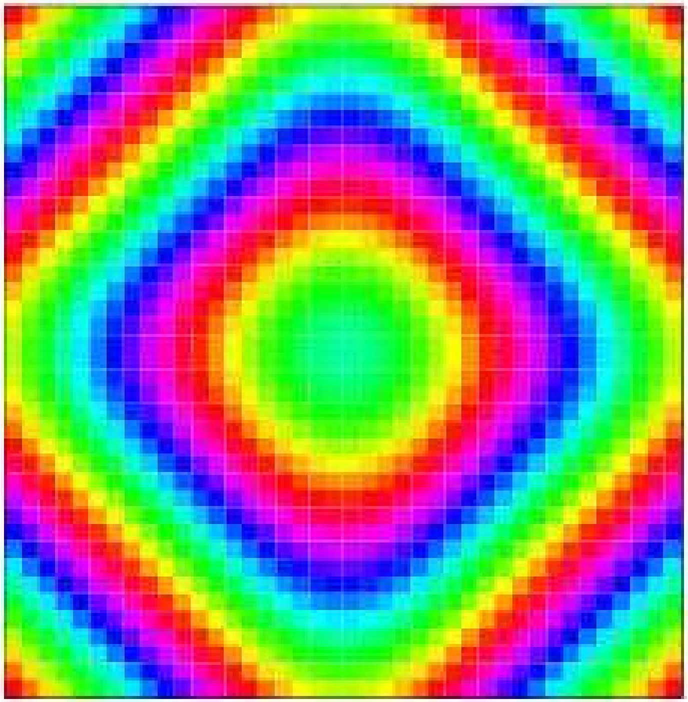
$$\theta_x \approx K\text{sign}(x - \frac{1}{2}) \quad \theta_y \approx K\text{sign}(y - \frac{1}{2})$$

and

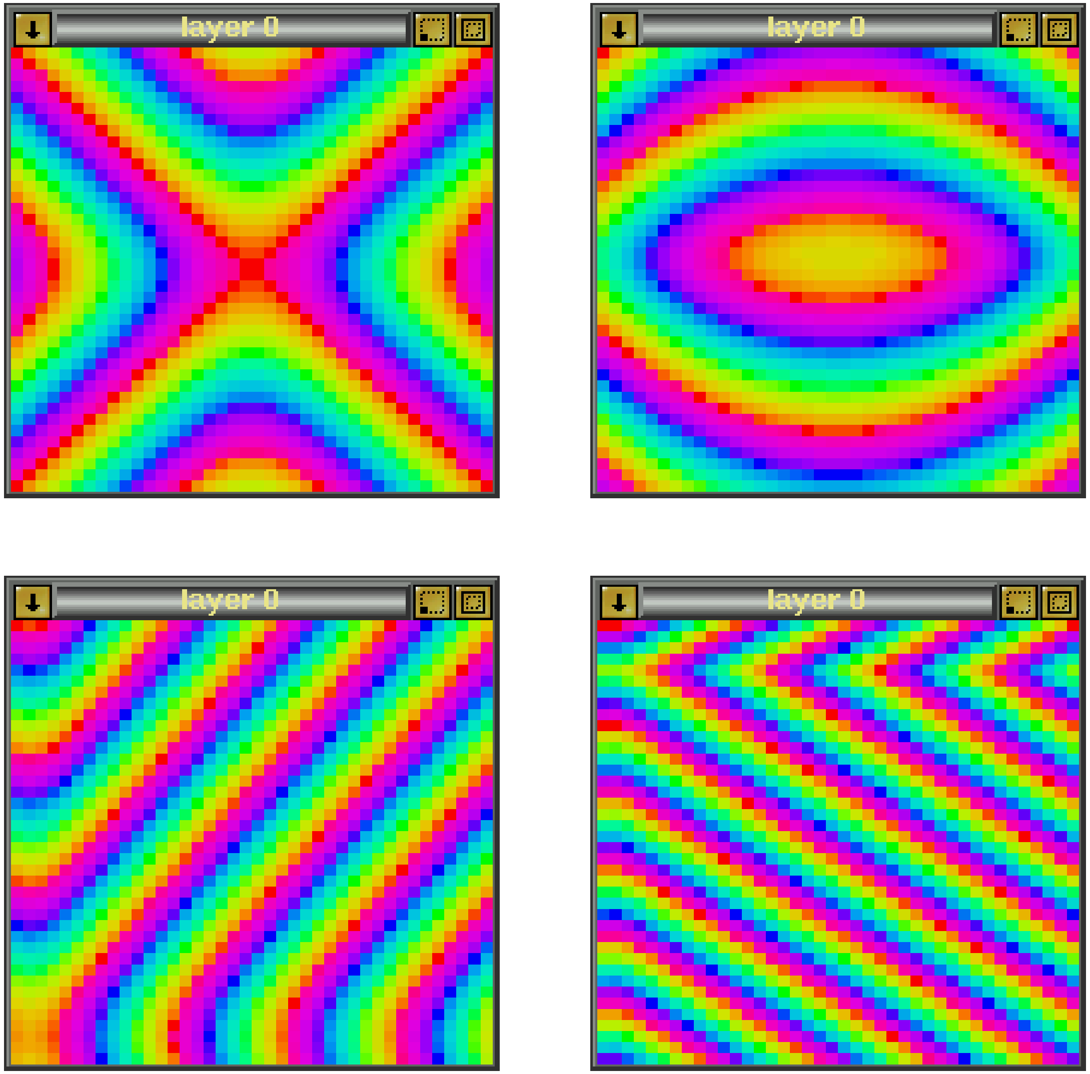
$$\theta \approx \Omega t + K(|(x - 1/2)| + |y - 1/2|)$$

Example I. Isotropy





Example II. Various anisotropies



Is that all there is?

- These patterns are homotopic to synchrony
- Driven by boundary effects
- Are there non-trivial patterns?

Is that all there is?

- These patterns are homotopic to synchrony
- Driven by boundary effects
- Are there non-trivial patterns?
- Simplest nontrivial pattern on 4×4 lattice with sine coupling:

$$\begin{array}{cccc} 0 & \xi & \pi/2-\xi & \pi/2 \\ -\xi & 0 & \pi/2 & \pi/2+\xi \\ 3\pi/2+\xi & 3\pi/2 & \pi & \pi-\xi \\ 3\pi/2 & 3\pi/2-\xi & \pi+\xi & pi \end{array}$$

where $\cos 2\xi = 2\sin\xi$.

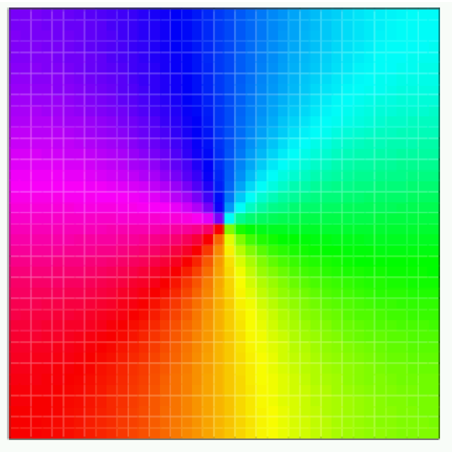
An asymptotically stable rotating wave!

Then what?

THEOREM (Paulett & GBE, 1992)

- $H(u)$ is an odd periodic and $H'(u) > 0$ for $u \in (-\pi/2, \pi/2)$
- $$\theta'_{ij} = \omega + \sum_{\{i'j'\}\in \text{NN}} H(\theta_{i'j'} - \theta_{ij}), \quad i,j = 1,\ldots,2m$$

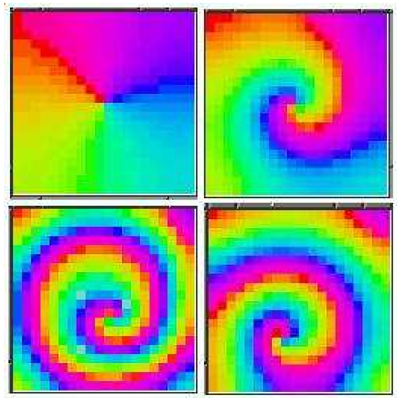
Then, there exists an asymptotically stable rotating wave.

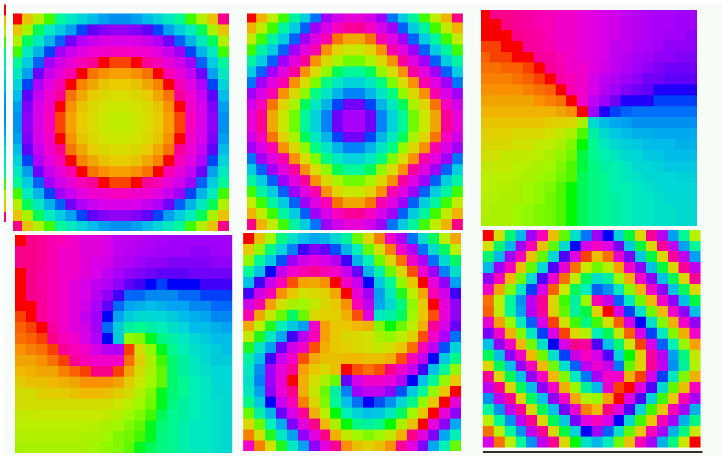


Non-odd terms matter

- Add even terms which vanish at 0 so there are no boundary effects
- Leads to a twisting of the isophase lines
- Spiral waves rather than rotors
- As relative power of even terms increases, “core” lose stability
  - Hopf bifurcation leads to “wobble”
  - Zero eigenvalue leads to drift
  - Eventually chaotic motion

Examples





What about 3D?

- Stack the 2D spirals together to form a scroll wave.
- Can *nontrivial* 3D patterns occur?
- Problems
  - In discrete models, twisted scrools etc can develop large phase gradiuents
  - Must increase range over which $H'(\phi) > 0$.
  - E.g. $H(\phi) = \sin\phi - a\sin 2\phi$ with $0 < a < 1/2$.

Tilted scrolls with $a = 0.3$