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 \textit{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.
Easy to entrain

- **P. cribellata**
  - 981 msec

- **L. pupilla**
  - 974 msec

- **P. malaccae**
  - 880 msec

The graph shows the entrainment of three species of cricket, with cycle numbers on the x-axis and Δ (a measure of phase shift) on the y-axis.
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

![Graph showing the phase response curves (PRCs) of different species.](image)

- **Pteroptyx cribellata**
- **Luciola pupilla**
- **Pteroptx malaccae**

The plots illustrate the phase shifts in response to different stimuli. The x-axis represents the phase of the stimulus in milliseconds (msec), while the y-axis shows the phase difference (ΔPHASE) in milliseconds. The curves demonstrate how each species responds to stimuli, with different patterns indicating distinct phase response characteristics.
P. malaccae entrainment
A simple model for entrainment

Let $\theta$ be the phase of the firefly and let $\omega = 1$ be his natural frequency. Let $\omega_z$ 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 $\omega$.)
Simulation of walkthrough

![Graphs showing simulation results.](image)
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.
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

\[
\frac{d\theta_L}{dt} = \omega + H(\theta_R - \theta_L; \omega)
\]

\[
\frac{d\theta_R}{dt} = \omega + H(\theta_L - \theta_R; \omega)
\]
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 $\omega$ increases.
Phase-space

\[ \frac{d\phi}{dt} \]

High frequency

Low frequency

The Lure of the Rings – p.18/
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
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 $\phi$ 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 $\omega$ increases $a(\omega)$ changes from negative to positive.
Phase-space again!

The Lure of the Rings – p.22
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

**High frequency**

\[ H(0) \]

\[ H(\phi) \]

**Low frequency**

\[ -2H_{\text{odd}}(\phi) \]

**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”
Consider

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

K & E proved that as \( N \to \infty \)

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

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

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

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 $4 \times 4$ 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!
THEOREM (Paulett & GBE, 1992)

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

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

The Lure of the Rings – p.39/??
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 gradients
  - 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 $\alpha = 0.3$