Pattern Formation:

Oscillatory Neuronal Networks

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Outline

- Classical ideas of pattern formation
- Networks with oscillatory dynamics
- Time delays $=$ effective inhibition
- Exploiting time delays

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  - Dendrites can flip parity
  - Axonal delays
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  - Dendrites can flip parity
  - Axonal delays
  - Heterogeneities
- One-species diffusion

The classical theory

Lateral Inhibition is the classic mechanism for pattern formation in biological systems: *Mexican hat*

What's wrong with this?

- Strictly positive "weights" $\longrightarrow$ dominant mode is same sign
- Thus assume that the extent of inhibition $>$ excitation
- Opposite holds in cortex!
- *Small world* is even "worse"

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- Thus assume that the extent of inhibition $>$ excitation
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- *Small world* is even "worse"
  - Encourages uniformity
  - Synchronize
  - Much "stronger" than local effects

Neurons have temporal structure

- Move beyond mean field theory
- Spikes have temporal structure which can have global consequences
  - Asynchrony needed for persistence (Laing, Golomb, others)
  - Work of Schiff on epilepsy
  - Sherman & Rinzel bursts

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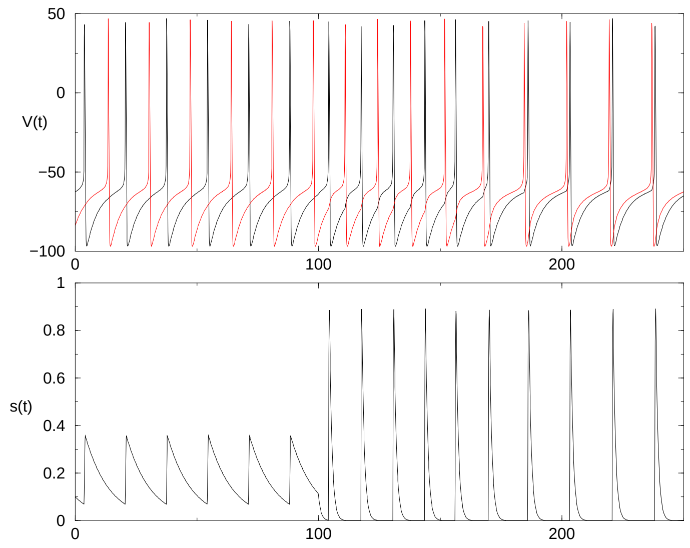
  - Sherman & Rinzel bursts
- Pattern formation in biological neural networks should take into account the temporal variability.
- Exploit this to generate complex patterns

A simple example

- Two identical mutually coupled excitatory neurons

$$C_m V_j' = -I_{ion}(V_j) - g s_k (V_j - V_{syn})$$

- Change timing of s(t)



It's just a matter of time

- Signal between neurons is "delayed" with longer τ
- Weak coupling limit; phase difference ϕ satisfies:

$$\begin{aligned} \phi' &= -2H_{odd}(\phi) \\ H(\phi) &= \frac{g}{T}\int_0^T s(t+\phi)R(t)dt \end{aligned}$$

- $R(t)$ proportional to PRC

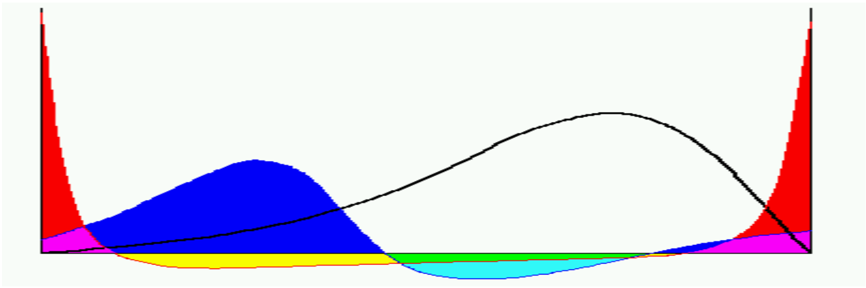
Weak coupling cont'd

- Recall:

$$\phi' = -2H_{odd}(\phi)$$

- Synchrony is stable iff $H'(0) > 0$ or

$$Z = \int_0^T R(t)s'(t)dt > 0$$



Implications for pattern formation?

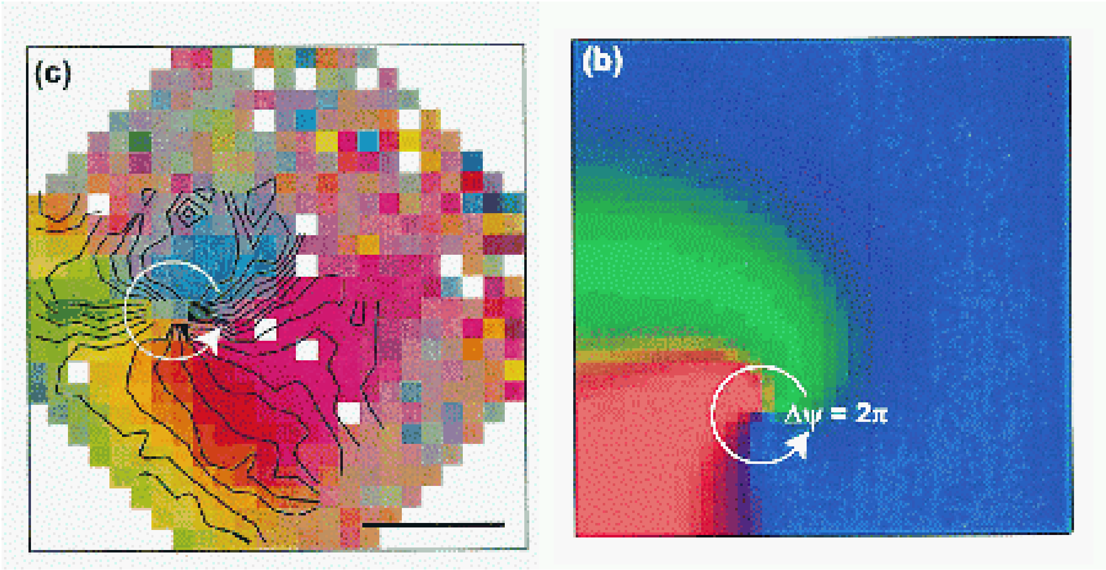
- Altering the timing leads to pairwise shift between synchrony and antisynchrony
- “Inhibition” and “Excitation” lose meaning
- “Sign” of coupling is not the whole story!
- The remainder of this talk will discuss examples.

Multistability due to phase gradient

- Scalar, two-D diffusion, noflux, $f(u)$ has single stable FP. Then tend to homogeneous state.
- Not so with oscillators – even if synchrony is stable!
- Key is extra degree of freedom due to phase shifts
- Stable phase gradients can emerge, eg waves in a ring

Two-dimensional arrays

- Classic work of Petsche - rabbit ctx has rotating waves
- Recent work of Kleinfeld et al in turtle visual area



Existence proof!

- Simple NN array of sine models:

$$\theta'_{ij} = \omega + \sum_{i',j'} \sin(\theta_{i'j'} - \theta_{ij})$$

- Even N and for $N = 4$ get single scalar equation for ξ which is AS!

0	ξ	π/2−ξ	π/2
−ξ	0	π/2	π/2+ξ
3π/2+ξ	3π/2	π	π−ξ
3π/2	3π/2−ξ	π+ξ	π

Continuous vs lurching waves

- Many types of waves in ctx and thal
- In disinhibited cortex, wave propagation is smooth and fast. Propagation is mediated by excitation.
- In thalamic slices, models exhibit “lurching” waves which are an order of magnitude slower than cortical waves. Propagation is mediated by inhibition.
- The release from inhibition causes neurons to fire (PIR)
- Acts like a delay between connections

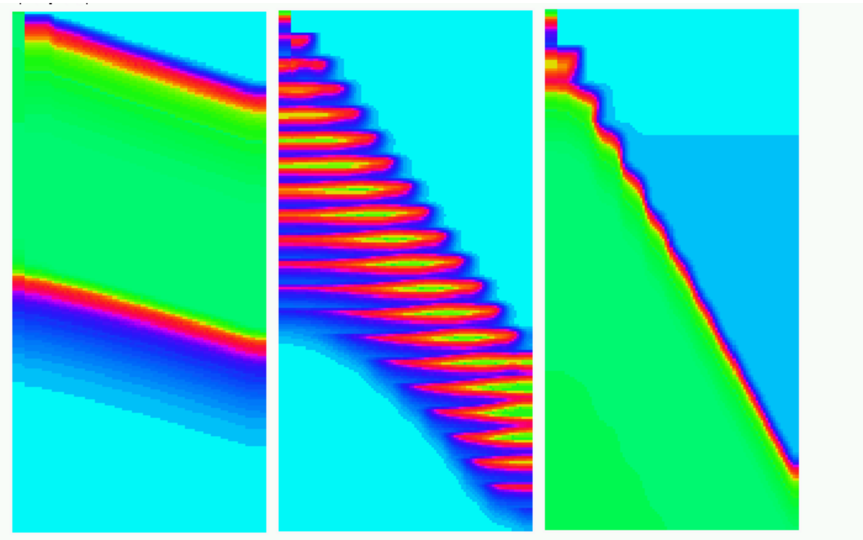
Simple example

A simple neural net model can generate a smoothly propagating wave.

Can the presence of a delay alter the form of the wave?

- No amount of delay can destabilize fronts destabilize the wave.
- Pulses are destabilized via delays
- Need to “complete the circle” reset the wave.

Numerical example

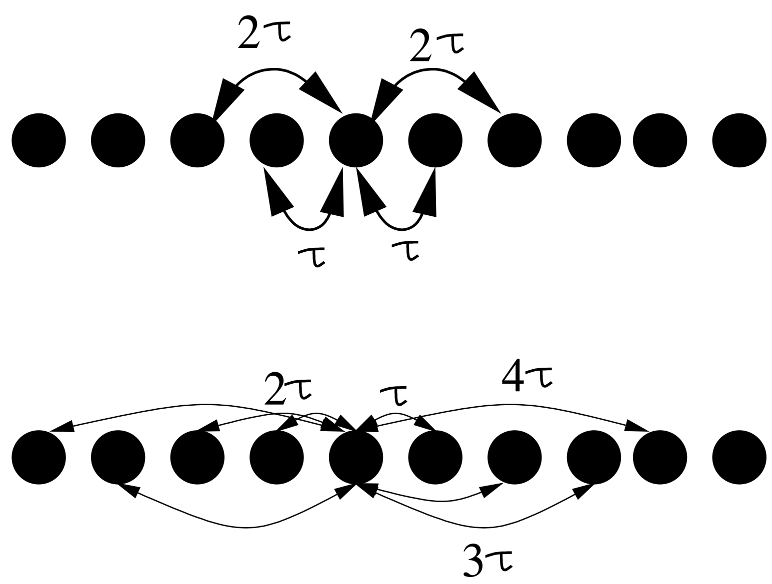


Waves & synchrony in 1D

- Synchronous oscillation in visual ctx
- Waves in olfactory bulb
- Intuition:
  - Local cnxs yield waves
  - Long range promotes synchrony (Small world)

Distance-dependent delay

- A chain of oscillators
- Decaying connectivity
- Finite conduction time – delay

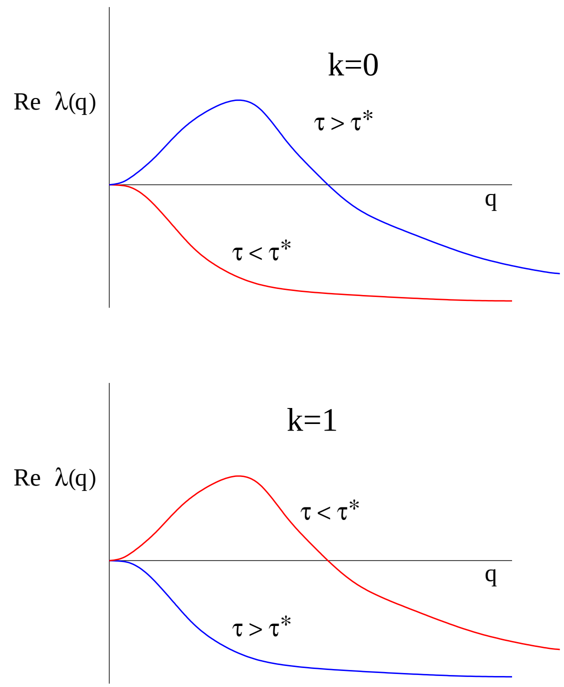


Continuum phase model

$$\theta_t = \omega + \frac{1}{\sigma}\int_{-\infty}^{\infty} w(\frac{y}{\sigma})H(\theta(x+y) - \theta(x) - |y|/c)\,dy$$

- c, σ conduction velocity & space constant
- $\theta(x,t) = \Omega(k)t - kx$ are traveling waves
- Stability depends on $k, \tau = \sigma/c$.

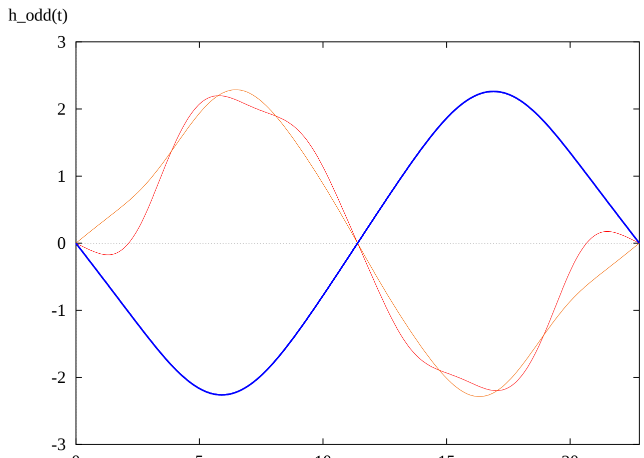
Stability



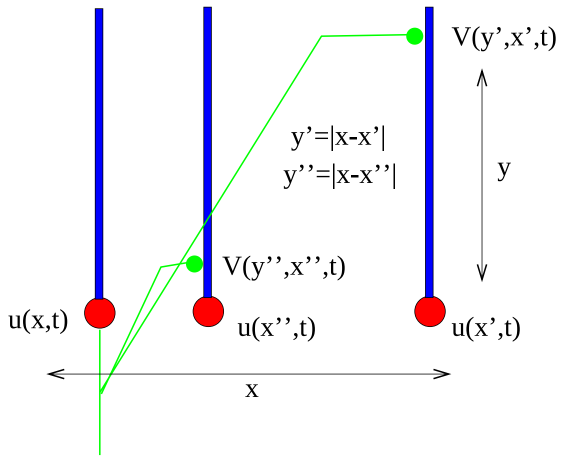
Long range recurrent excitatory connectivity makes the synchronous solution lose stability!

Dendrites and oscillations

- Filtering properties of dendrites can induce an effective delay.
- Thus, the position of a synapse on a dendrite can sculpt the relative phase lags in coupled arrays of oscillators.
- Weakly coupled oscillators:



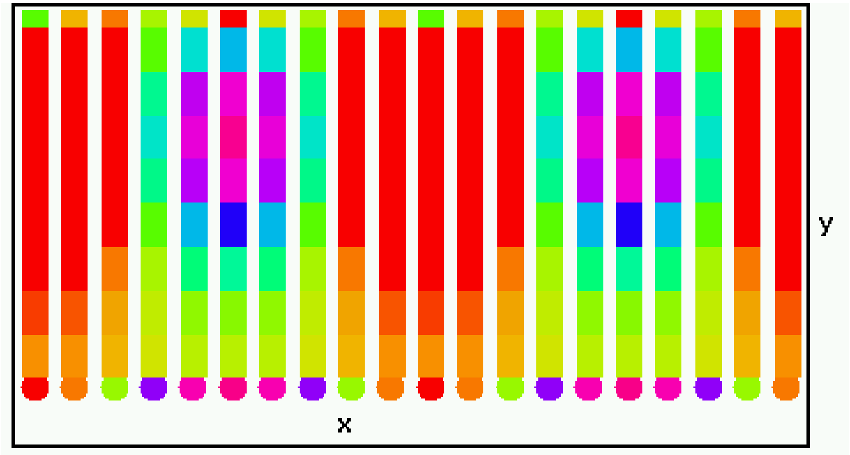
An example due to P. Bressloff



Connections between neurons are made on apical dendrites a distance from the soma proportional to the distance between the neurons.

Equations

$$
\begin{aligned}
u_t(x,t) &= -u(x,t) + g[v(0,x,t) - u(x,t)] \\
\tau v_t(y,x,t) &= -y(x,y,t) + D v_{yy}(x,y,t) \\
&+ w[f(u(x-y,t)) + f(u(x+y,t))]
\end{aligned}
$$

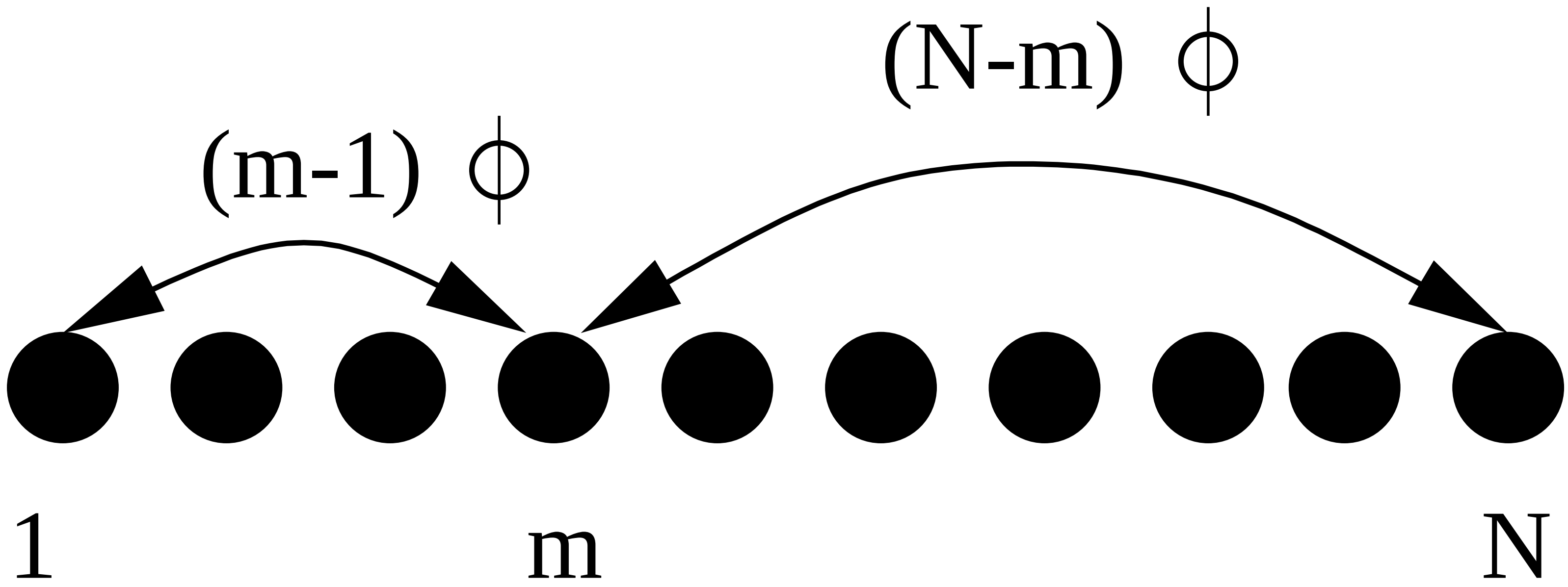


Heterogeneous coupling

- Can small heterogeneities propagate global patterns?
- Koch & Leisman: long-distant excitatory connections with delays lead to “Turing-Hopf” with synaptic strengthening
- Jirsa and Kelso: Similar numerical simulations; connections across hemispheres – global patterns

A tractable example

- Similar ideas used by Kopell & GBE for waves in lamprey CPG
- Locally connected chain with middle-to-end connections

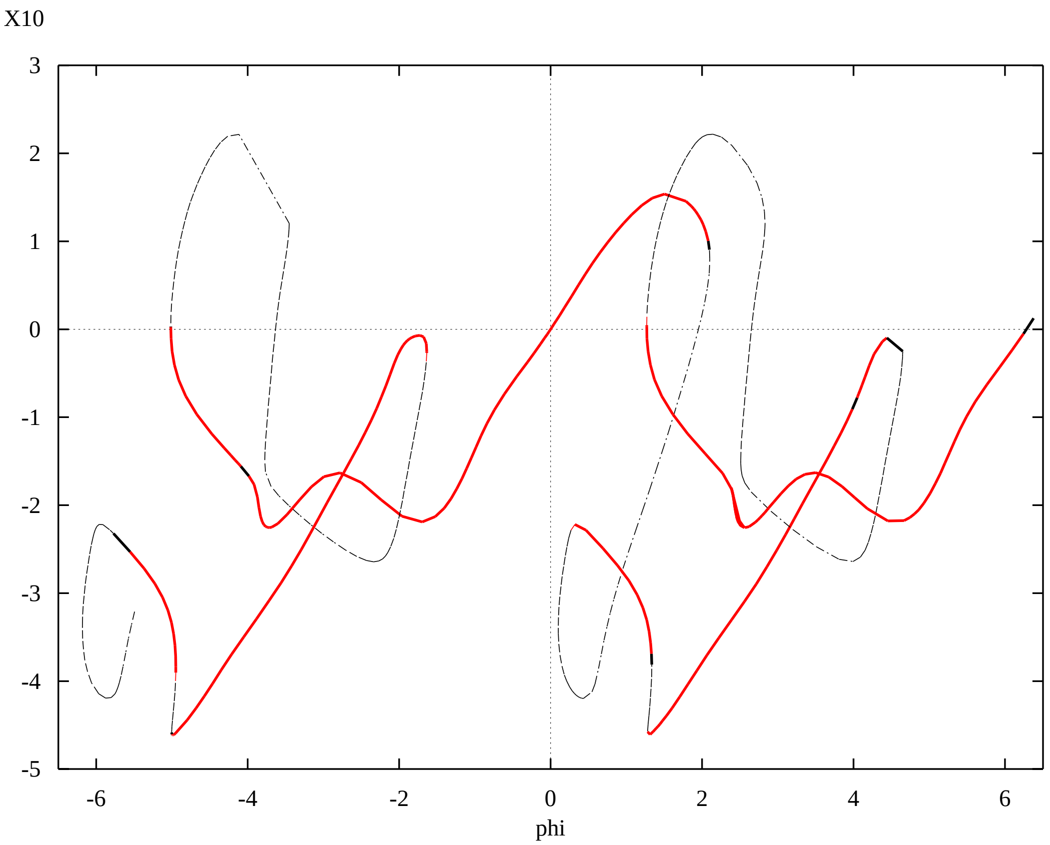


Phase model

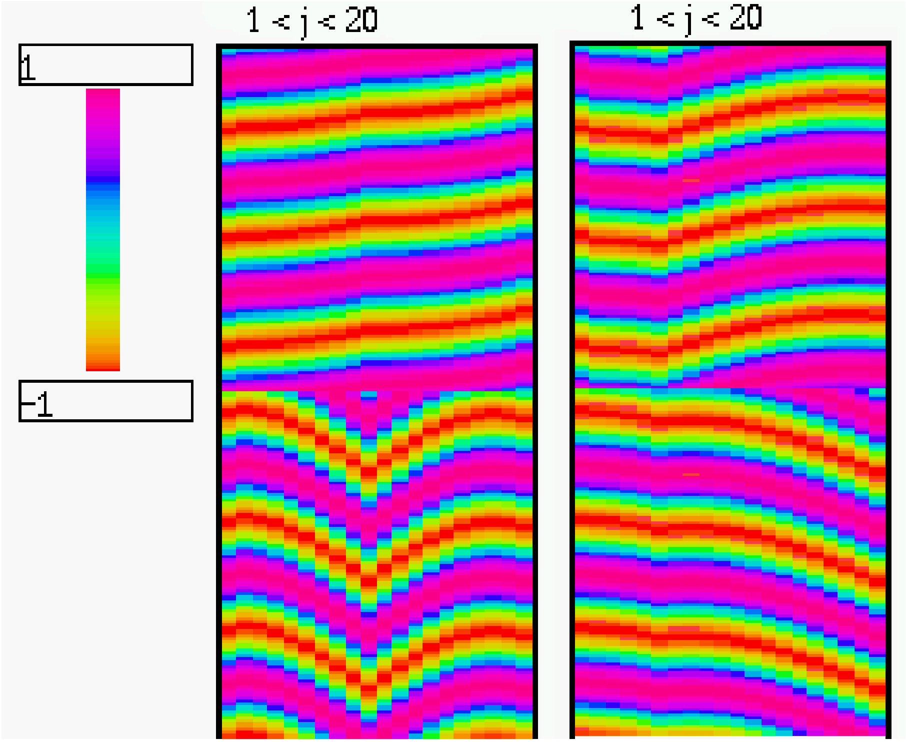
$$
\begin{aligned}
\theta'_{1,N} &= \omega + (2-c)H(\theta_{2,N-1} - \theta_{1,N}) + cH(\theta_m - \theta_{1,N} + \phi) \\
\theta'_j &= \omega + H(\theta_{j-1} - \theta_j) + H(\theta_{j+1} - \theta_j) \\
\theta'_m &= \omega + (H(\theta_{m-1} - \theta_m) + H(\theta_{m+1} - \theta_m)) \\
&+ c[H(\theta_1 - \theta_m + \phi) + H(\theta_N - \theta_m + \phi)]
\end{aligned}
$$

- ϕ characterizes the end-middle delay
- Synchrony is a stable solution when there is no delay.
- Small delays resulting in a smoothly dependent deviation. But abruptly, the branch of solutions is lost and a jump to new behavior is observed.

Bifurcation diagram



Space-time behavior



Left:end – middle(#10)   Right: end – #6

One-variable coupling

- Sompolinsky & Lowenstein : gap-junction coupling between the dendrites of two resting neurons can lead to oscillatory activity in the somata.
- Illustration of a general result suggested by GBE & Mark Lewis
- Mechanism is a Turing-Hopf bifurcation.
- May be relevant in Limax - blocking gap junctions destroys oscillatory LFP

Theory

Linearization about fixed point leads to an eigenvalue equation:

$$\lambda^3 + a_2(k^2)\lambda^2 + a_1(k^2)\lambda + a_0(k^2) = 0$$

a_j depend monotonically on wave number k^2 .

- No purely spatial patterns formation
- $a_1(k^2)a_2(k^2) - a_0(k^2)$ can become negative at non-zero k^2 leading to spatio-temporal patterns

Conclusions

- Pattern formation goes beyond the **Mexican Hat**
- Exploiting temporal dynamics leads to richer behavior
- Oscillatory activity is exquisitely sensitive to timing
- Ideal means to sculpt spatio-temporal patterns

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