Double or nothing:

The Blinking Brain

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Fields Inst

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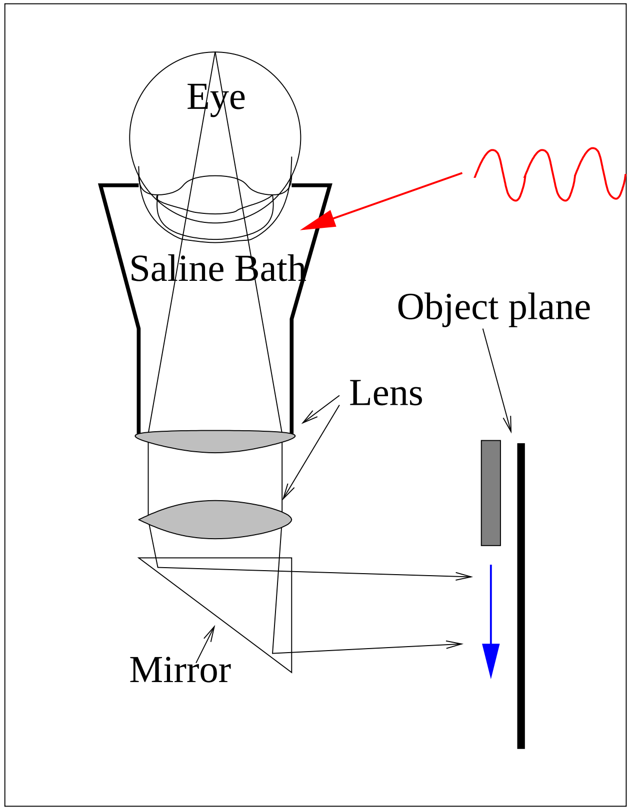
Introduction

- How does the brain respond to stimuli?
- This is one of the fundamental questions in neuroscience.
- Transient behavior to arbitrary stimuli is very difficult to study
- The nervous system tends to ignore constant (in time) inputs
- The simplest non-constant inputs are periodic
- Periodic stimuli can interact in complex ways with the intrinsic activity and rhythms in the nervous system

Periodic phenomena & Vision

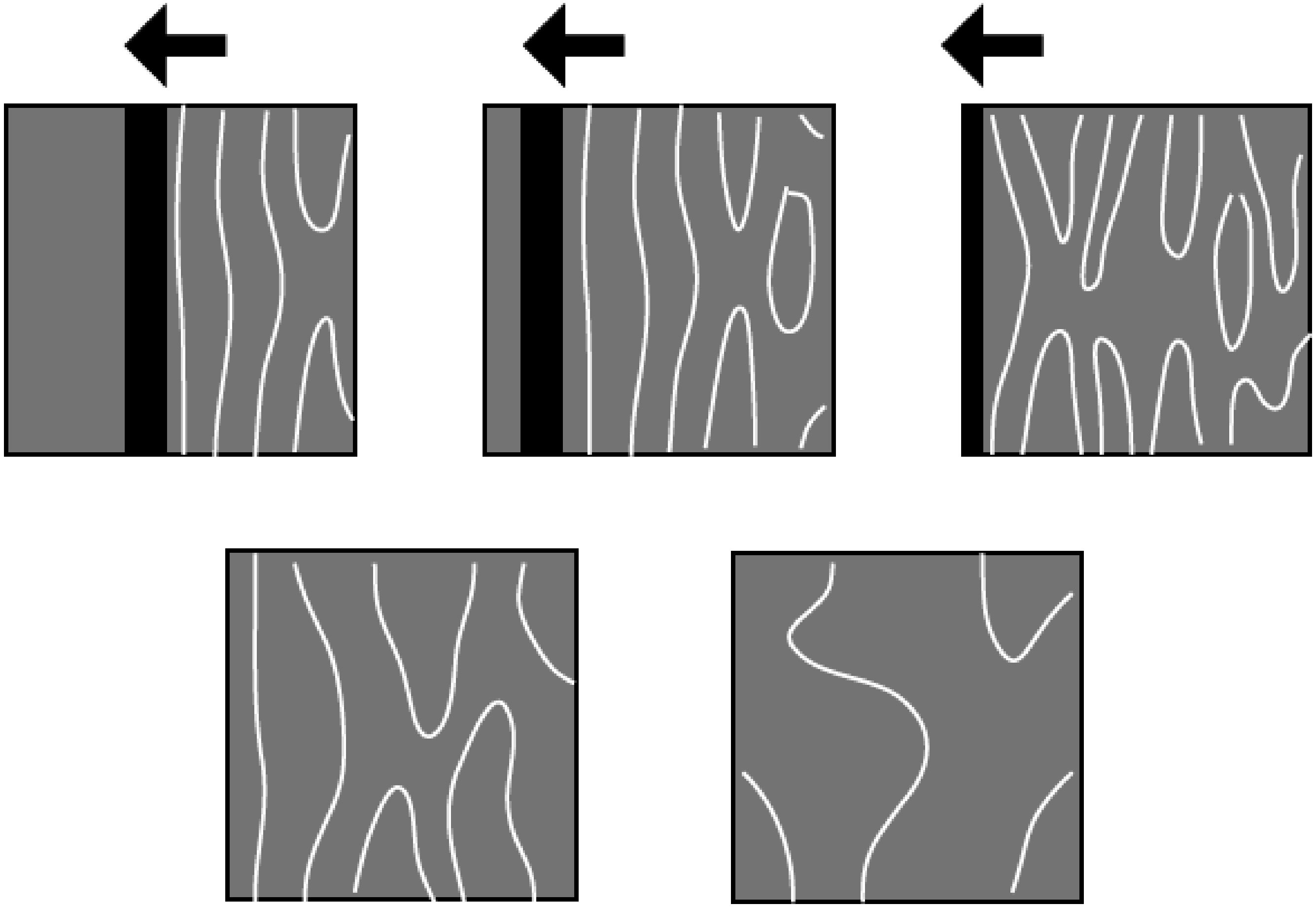
- Pathologies
  - Photic epilepsy Pokemon phenomenon
  - Migraines (remark: internal flcker of scotoma is 10-20 Hz)
- Visual illusions
  - Contour phosphenes
  - Flicker hallucinations

Contour Phosphenes



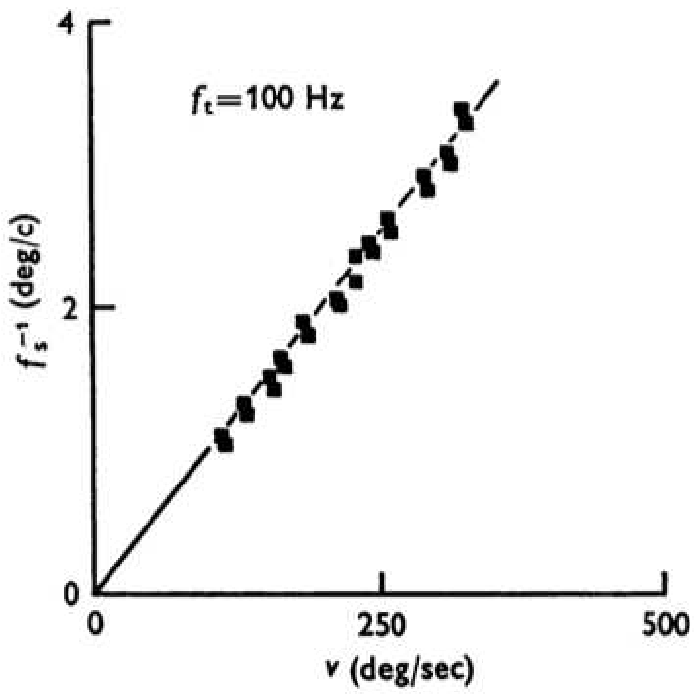
- Eye stimulated at 100 Hz
- Edge moved across visual field
- Vary velocity, frequency, shape etc
- R.H.S Carpenter (1973)

Slowly varying contours

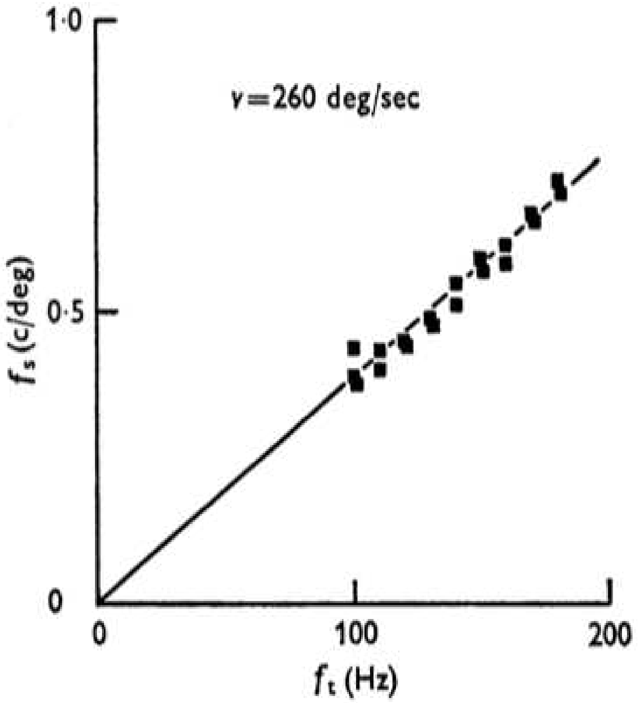


One line per cycle

Wavelength vs velocity

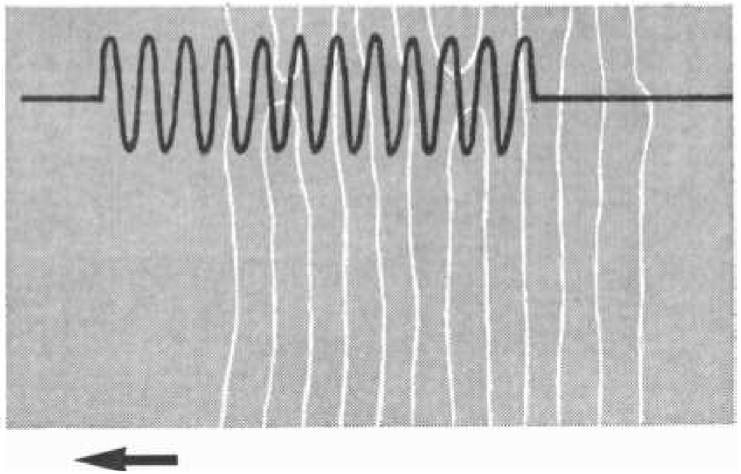


Spatial frequency vs temporal frequency

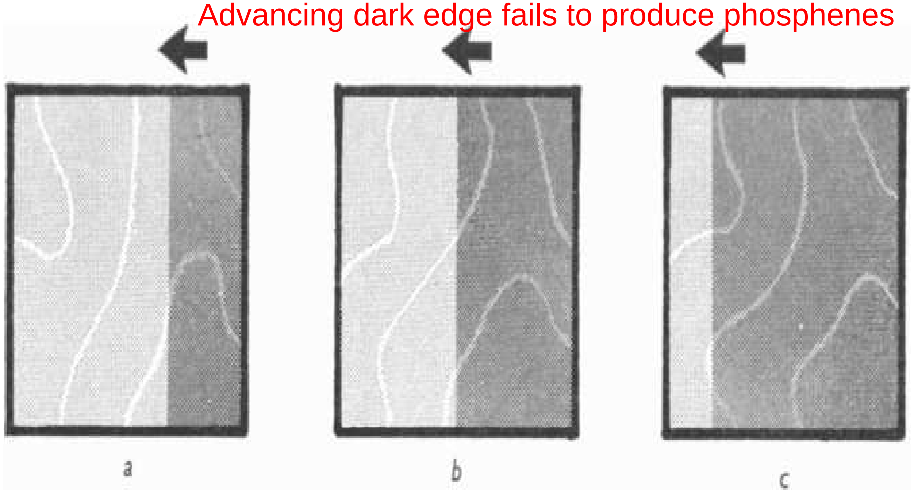


Additional properties

Limited sinusoidal stimulation results in limited extent



Advancing dark edge fails to produce phosphenes

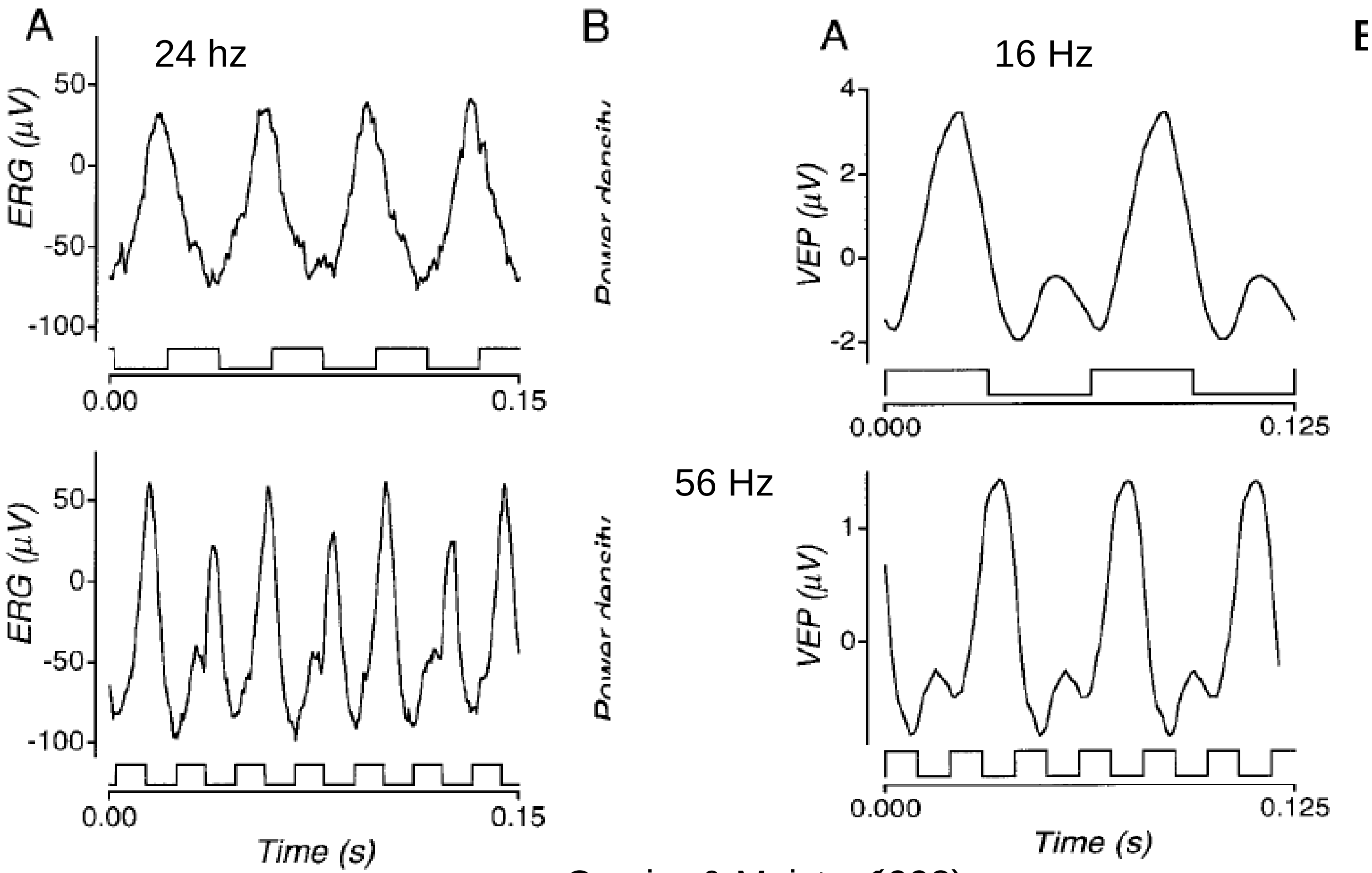


Mechanisms

- Carpenter suggests two possibilities
  - *The lines seen under electrical stimulation are interference fringes resulting from differences in conduction times in different parts of the retina as a result of differences in the degree of illumination they receive.*
  - *The lines represent nodes, separating areas of the retina that are responding in antiphase to each other. The effect of a sudden increase in illumination is to give an extra jolt to the system, sufficient to start a transient oscillation at the driving frequency.*
- J.B. Willis: Complex bistability model – does not give symmetric domains

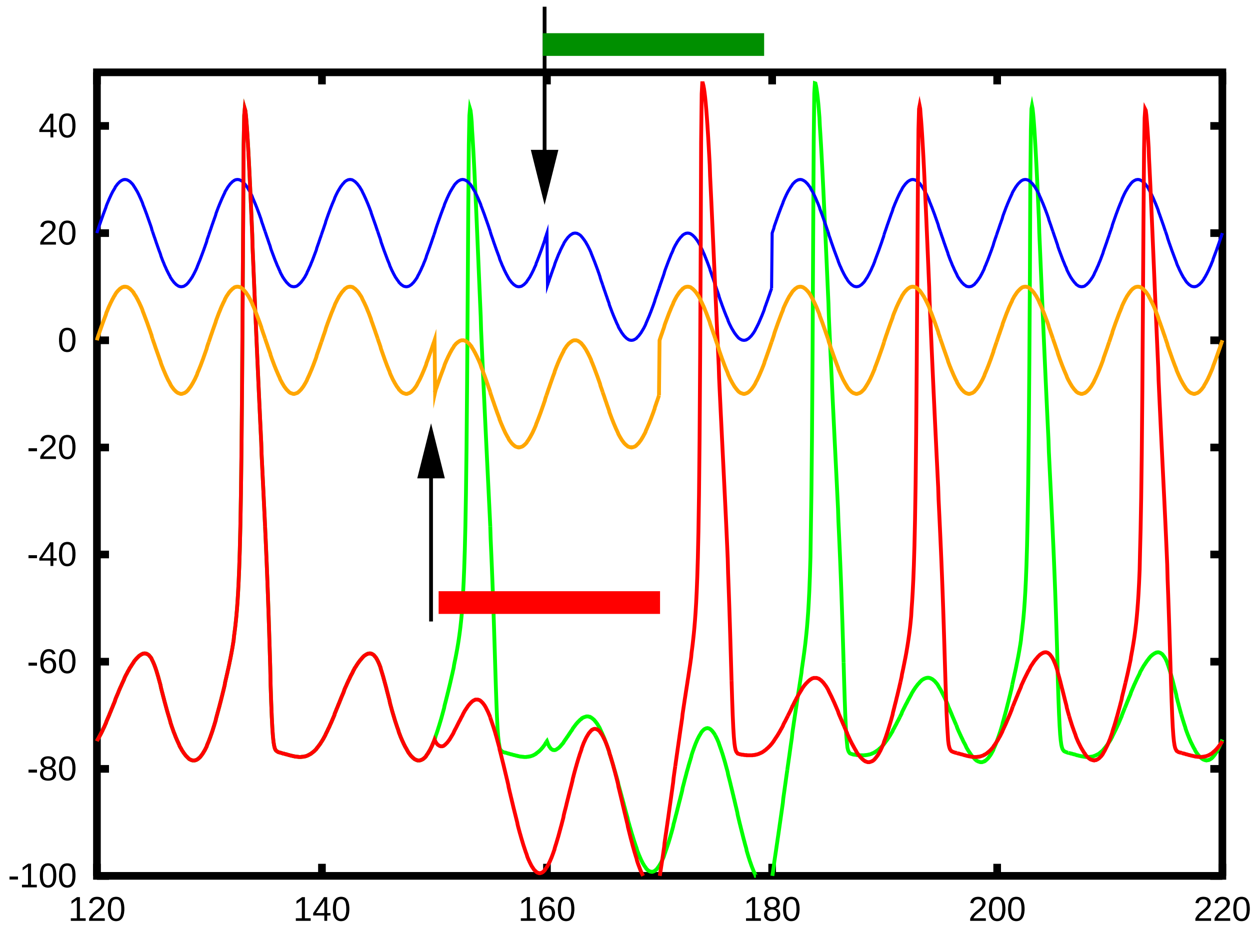
Period doubling in the forced retina

Response of human subjects to uniform flicker

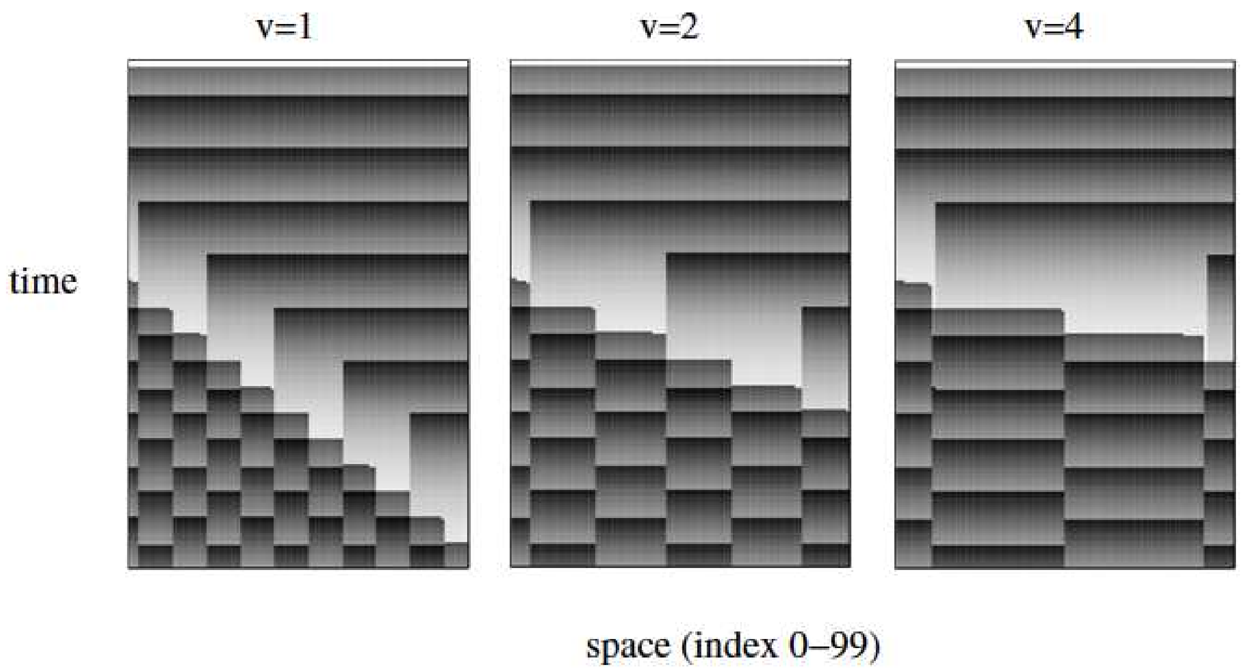


Crevier & Meister (1998)

Period doubling confers bistability

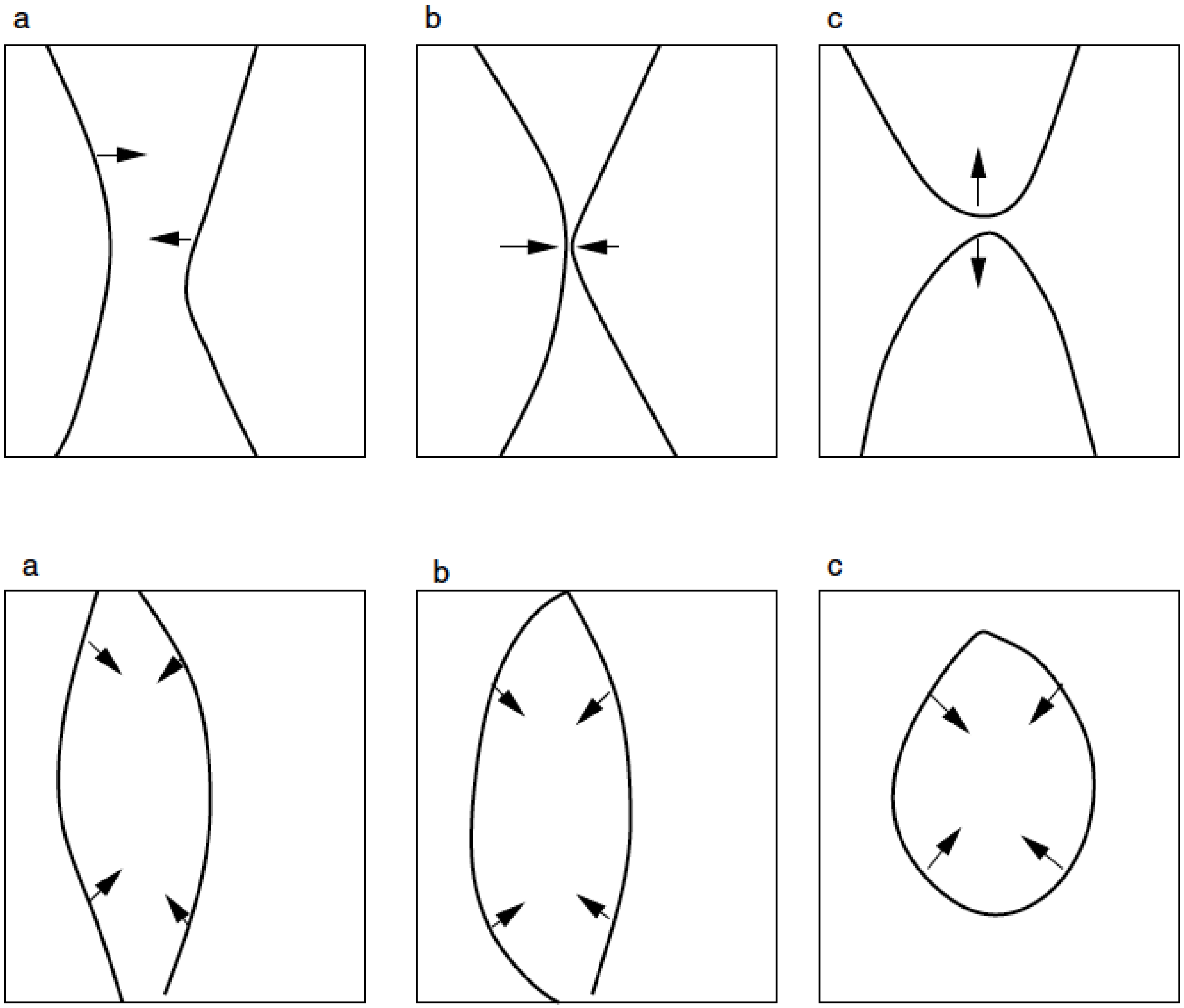


One-dim simulation

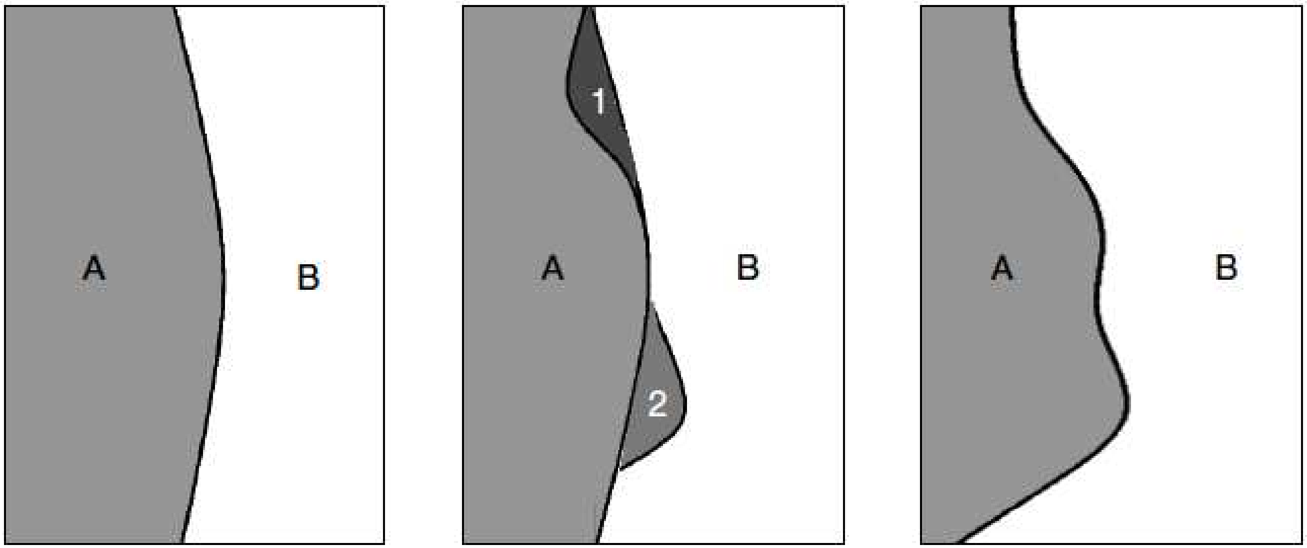


An array of HH neurons produces the desired division into domains and the number is dependent on the sweep velocity

Two-dimensions



Two-dimensions



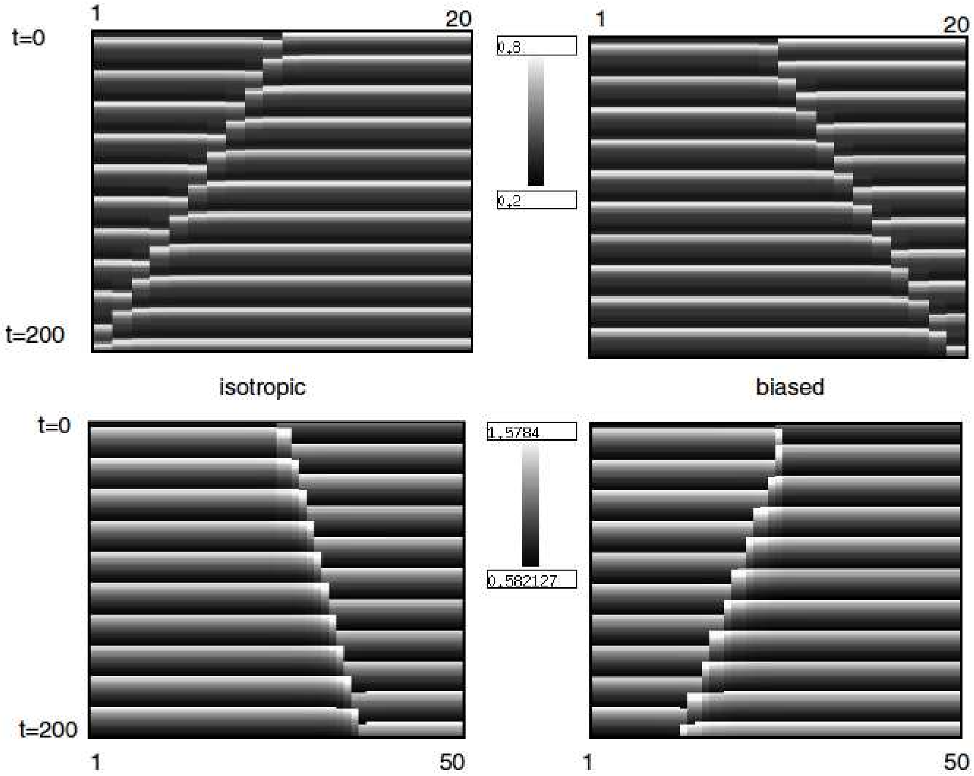
One domain overtakes another resulting in slow drift

Two-dimensions

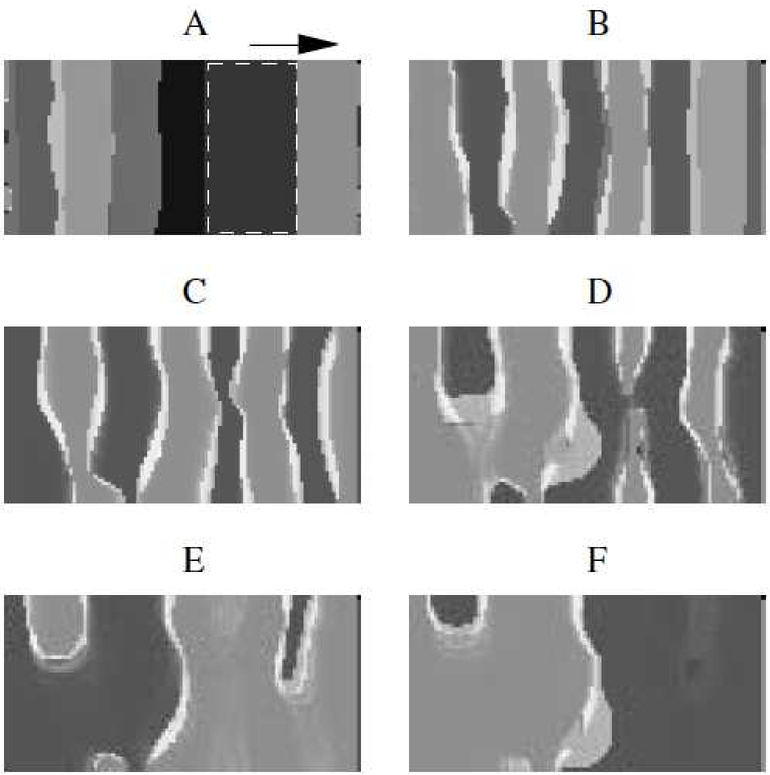
- Lines drift and merge
- Cannot be accounted for with just randomness
- Assume that there is local continuity but slowly varying heterogeneity

Movement requires interactions

Add gap junction coupling to get movement with or without bias



Simulations



Start external animation

An interesting phenomena

- Recall that in absence of isotropy, movement occurs
- The wave can go in either directions
- Bistable system is completely symmetric, so should be no tendency to move left or right
- What is going on?

Oscillators are different: averaging

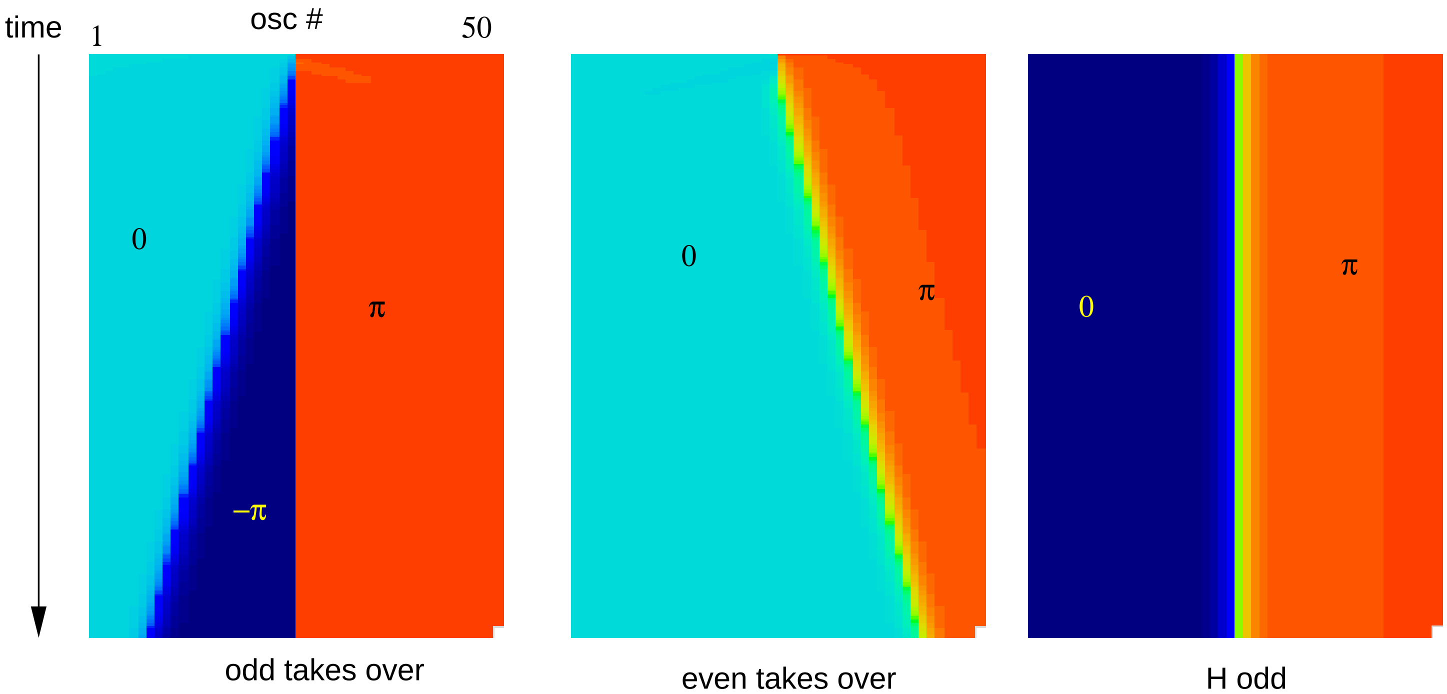
- Consider weakly forced weakly coupled pair of oscillators that can fire in 1:2 resonance with the driver. After averaging:

$$\theta_1' = f(\theta_j) + KH(\theta_k - \theta_j)$$

- $f(\theta + \pi) = f(\theta)$ $H(\theta + 2\pi) = H(\theta)$. $f(0) = f(\pi) = 0$ and $f'(0) = f'(\pi) < 0$ e.g $f(\phi) = -\sin 2\phi$.
- A priori, however, no such symmetry for $H(\theta)$. In particular H is not necessarily odd

Chain produces waves in eiother dir

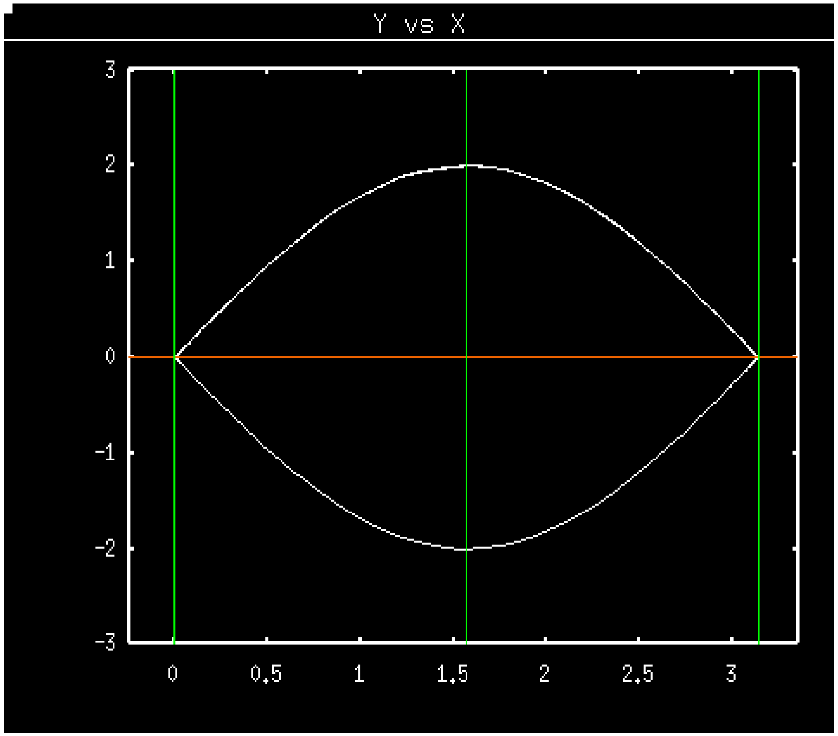
$$\theta_j' = -2\sin(2\theta_j) + K[H(\theta_{j+1} - \theta_j) + H(\theta_{j-1} - \theta_j)]$$



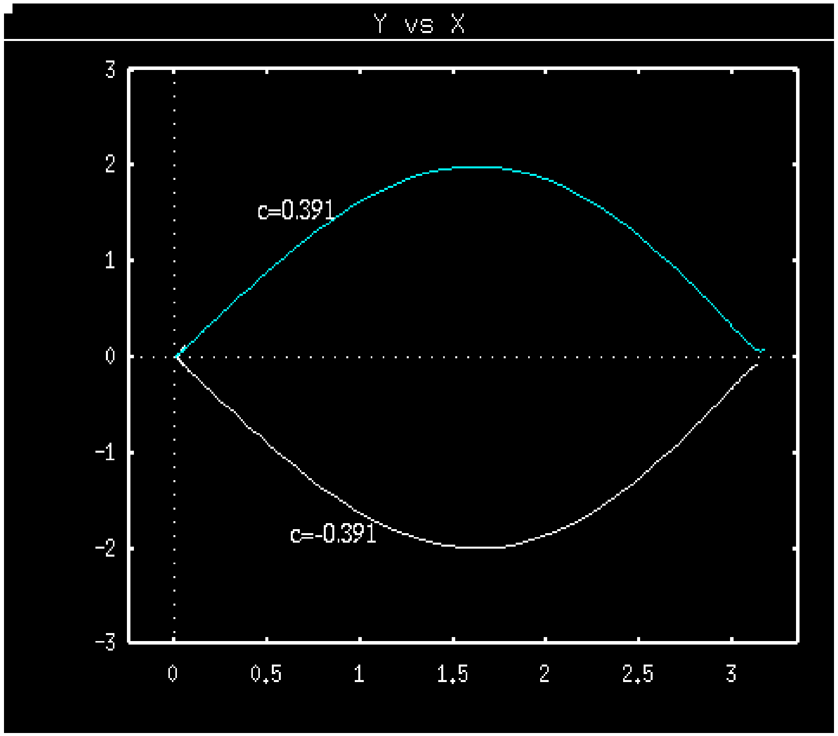
Continuum limit

$$\theta_t = -\sin(2\theta) + H'(0)\theta_{xx} + H''(0)\theta_x^2$$

H(x)=sin(x)



H(x) = sin(x+0.25) − sin(0.25)



Flicker hallucinations

- Visual cortex sits in a *balanced* state
- Small changes in the functional can induce spontaneous activity
  - Hallucinogens
  - Pre-epileptic/pre-migraine auras
  - Sensory deprivation (Charles Bonnet syndrome)
  - Flicker

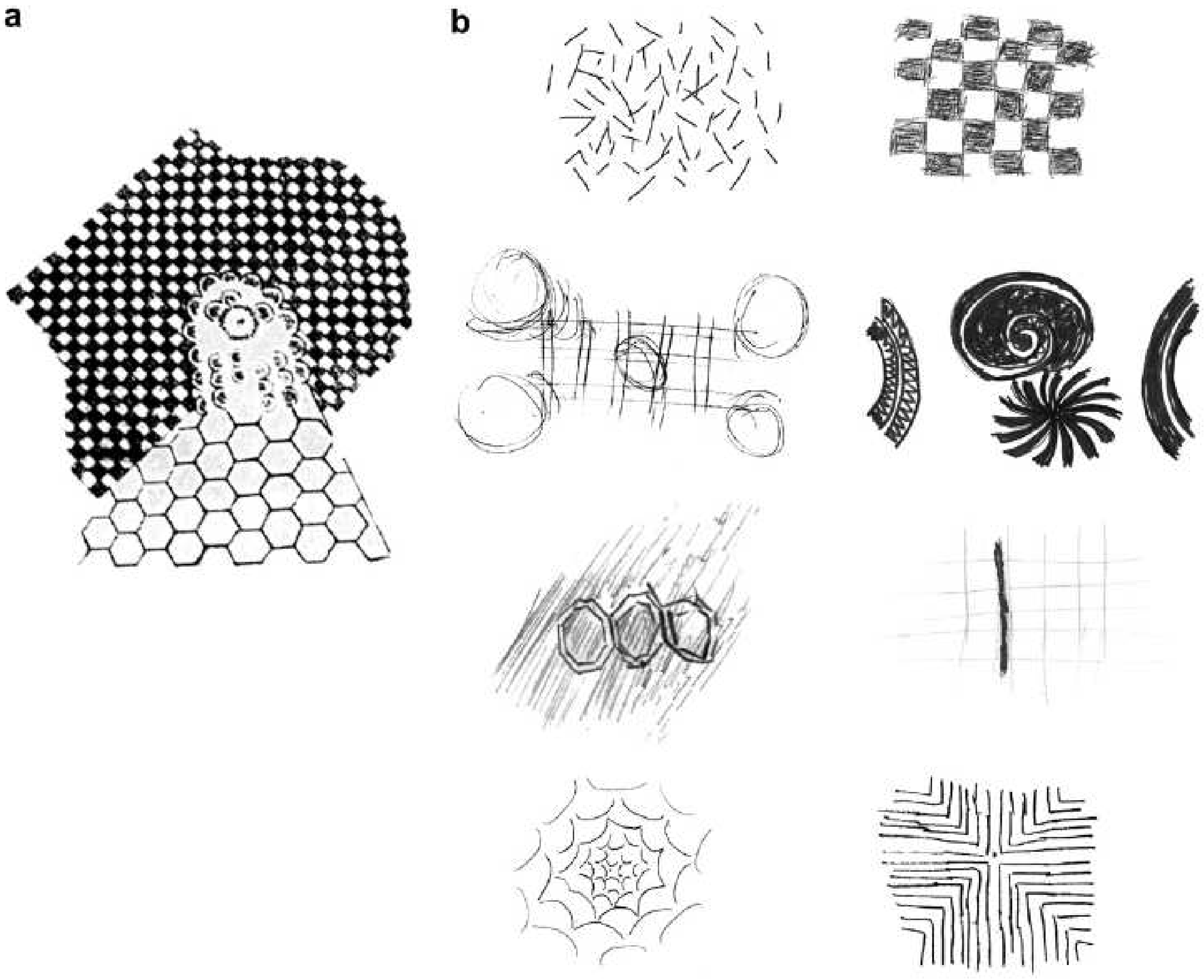
Flicker hallucinations

The lively mind of the child revels in the manifold stimuli of the external world. Who does not remember, if only dimly, such games from that beautiful time? One of them, which could keep us busy at a more serious age, is as follows: I stand in bright sunlight with closed eyes and face the sun. Then I move my outstretched, somewhat separated, fingers up and down in front of the eyes, so that they are alternately illuminated and shaded. In addition to the uniform yellow-red that one expects with closed eyes, there appear beautiful regular figures that are initially difficult to define but slowly become clearer. When we continue to move the fingers, the figure becomes more complex and fills the whole visual field (Jan Purkinje, 1819)

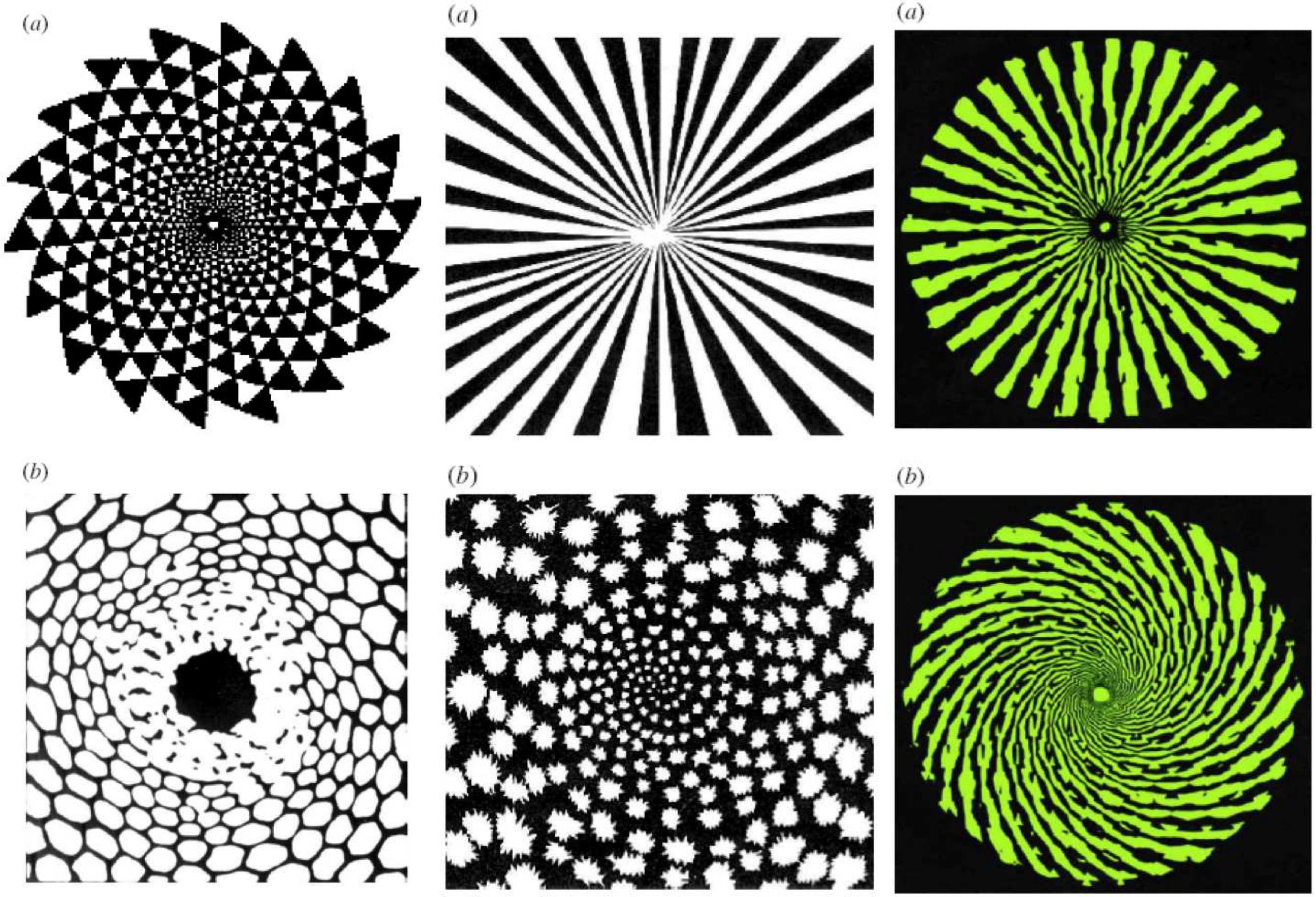
Flicker hallucinations

- Bright diffuse flickering light 16-20 Hz
- Long history
  - Helmholtz, Eldridge-Green (1920) “lattice-work”, “hexagons”
  - JR Smythies (1957,1958) Subjects reported a variety of geometric forms such as “mosaics, checker-boards, spirals”. One subject enjoyed it so much that he “expressed the conviction that they posessed the power of addiction” and “one developed an active desire to go on looking at them.”
  - Max Knoll (1963) $+$ Hallucinogens - strange model

Purkinje's patterns

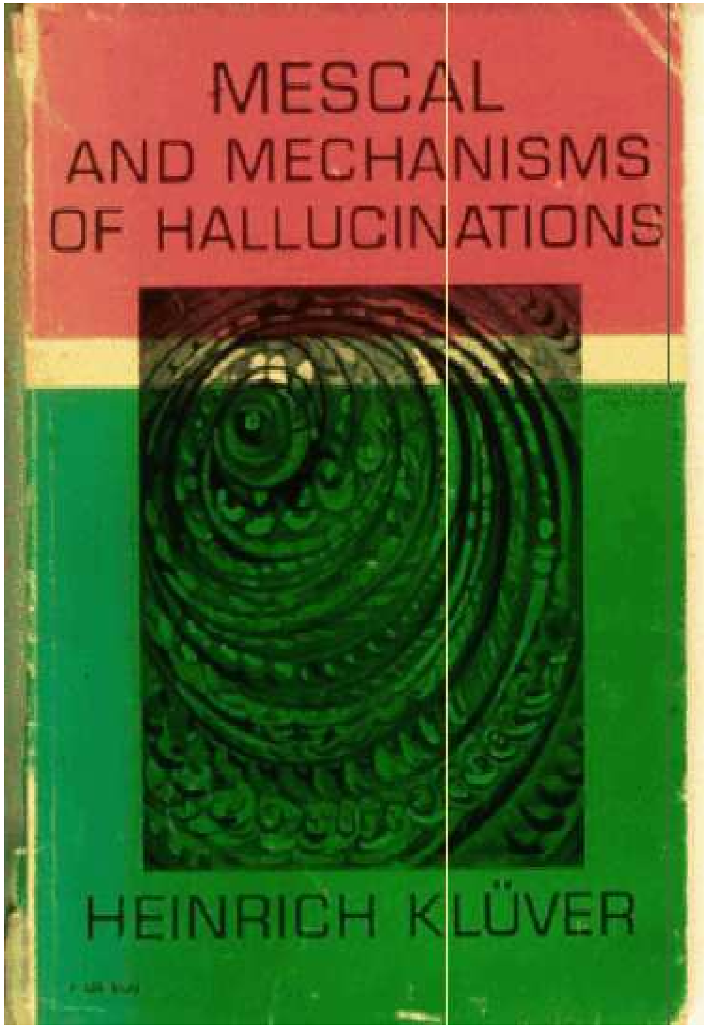


Classic patterns



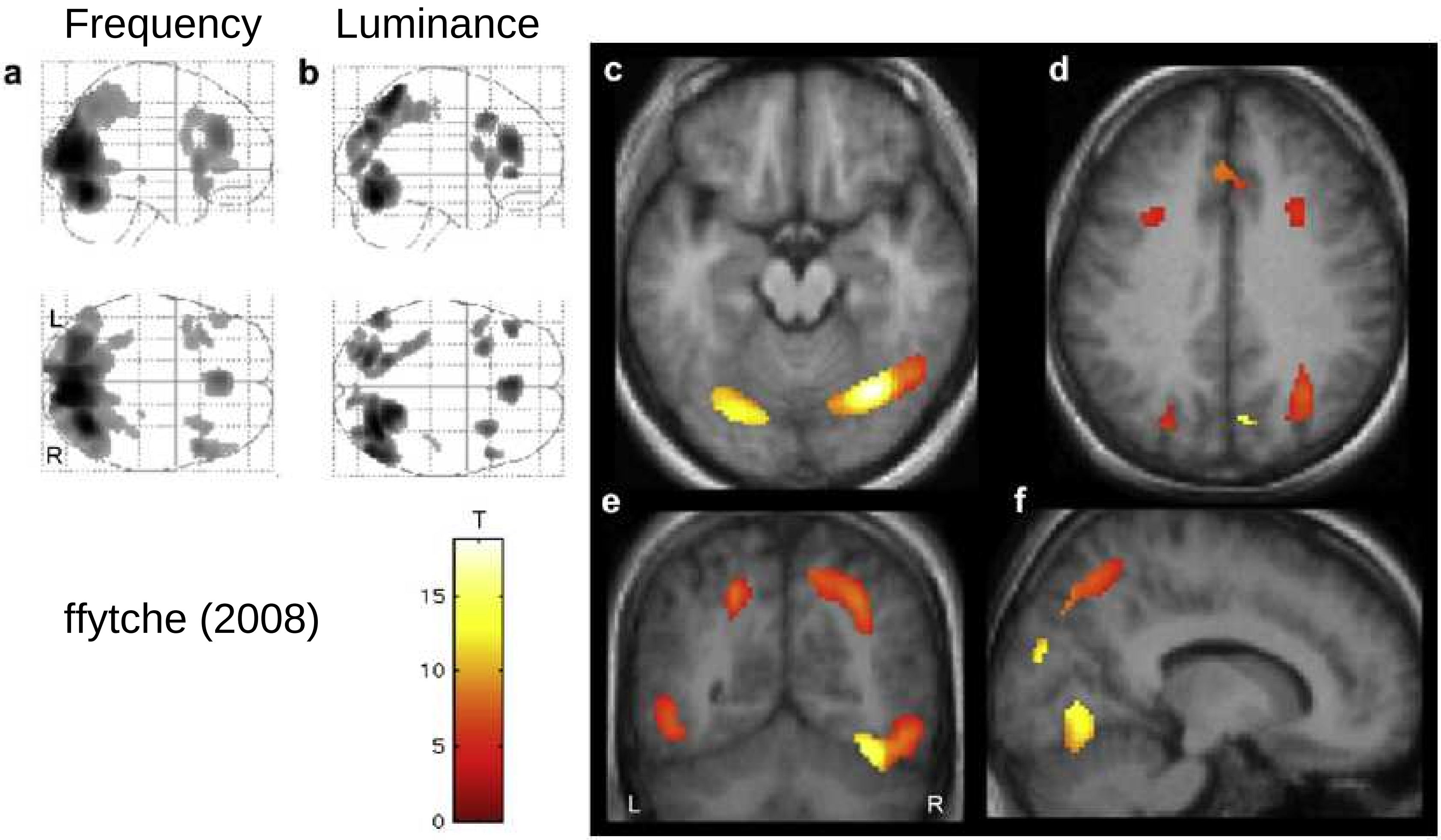
Bressloff et al

Form constants



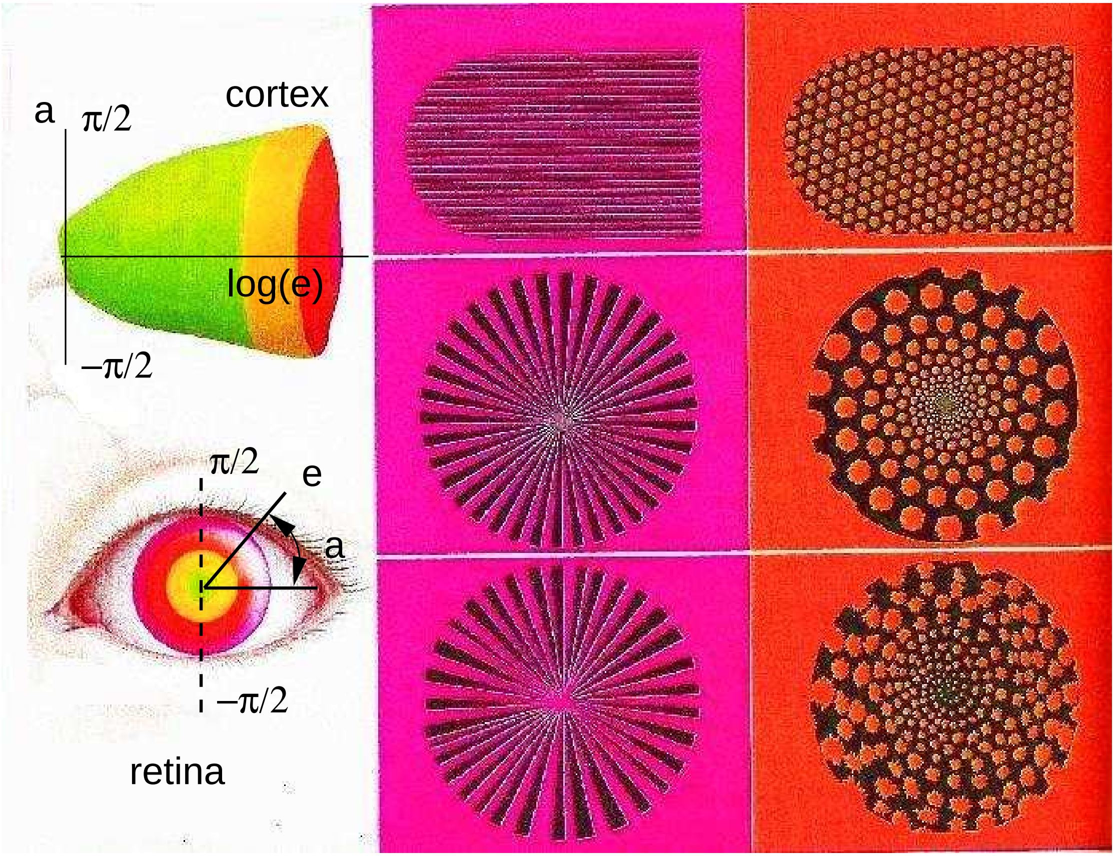
- Spiral/vortex
- Funnel/tunnel
- Cobwebs/filigrees
- Exploding light rays
- Mosaics

Cortical in origin



ffytche (2008)

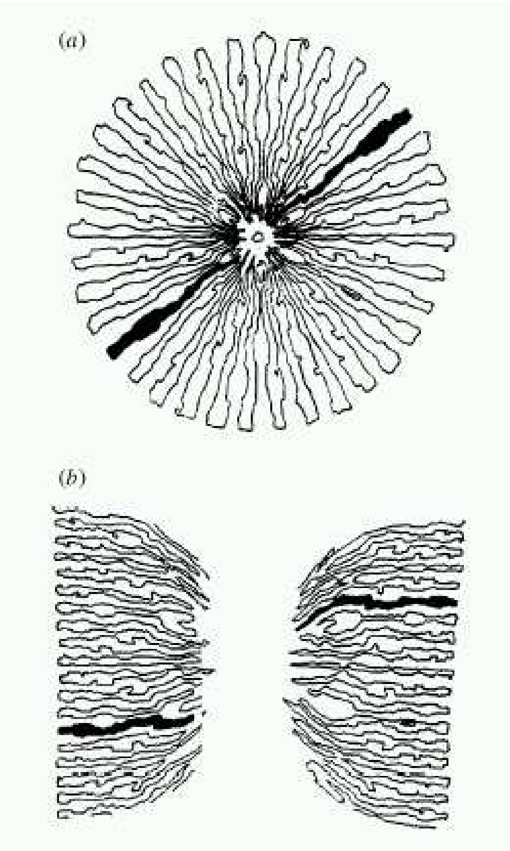
Retino-cortical transform

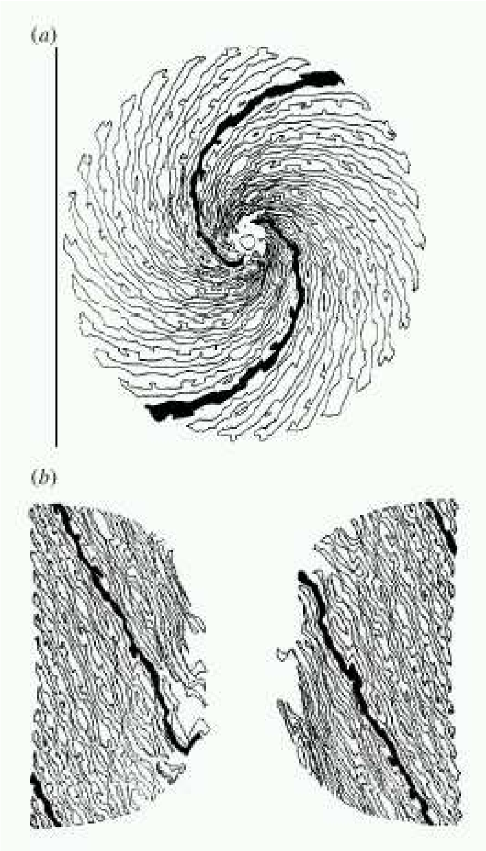


$$(e, a) \longrightarrow \left(\lambda \log(1 + e/e_0), -\lambda \frac{ea}{e_0 + e} \right)$$

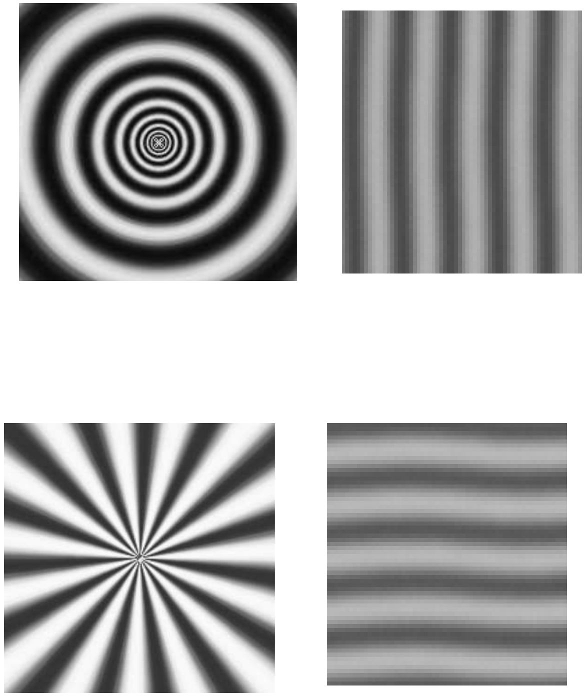
Like the complex logarithm

$$e\,\exp(ia) \to (\log e, a)$$





Psychophysics I



Most frequently reported patterns
(Tsou & Billock)

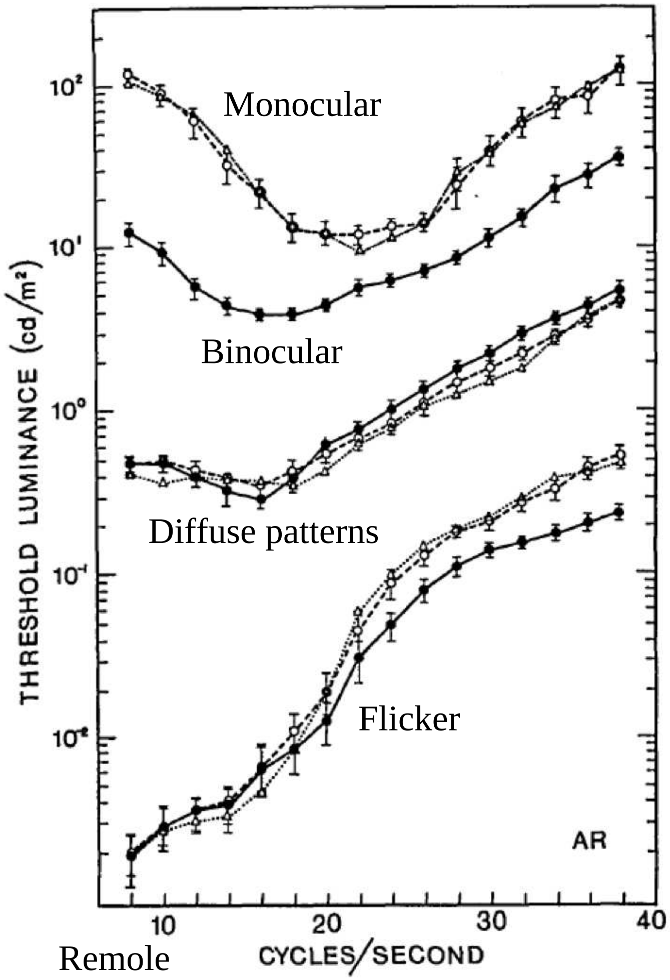
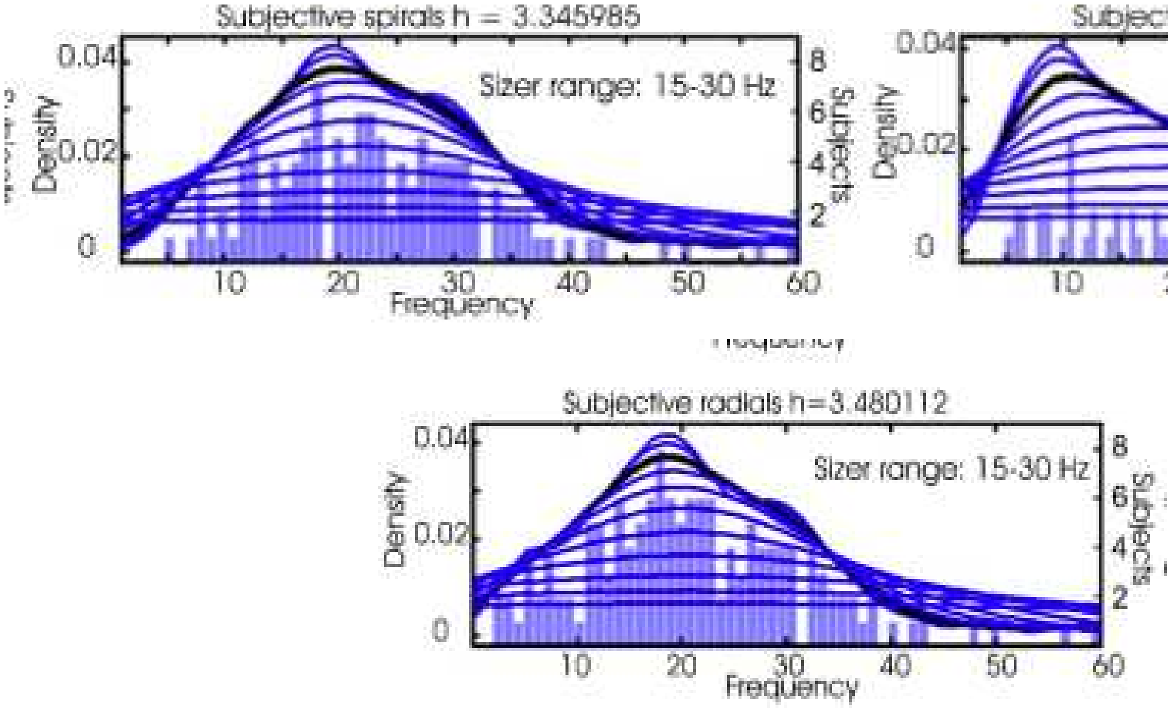


FIG. 1. Luminance thresholds for geometrical patterns (upper curves), diffuse patterns (intermediate curves), and flicker (lower curves). Right eye, ○– – –; left eye, △· · ·; both eyes together, ●——.

Psychophysics II



C. Becker, M.A. Elliott / Consciousness and Cognition 15 (2006) 175–196

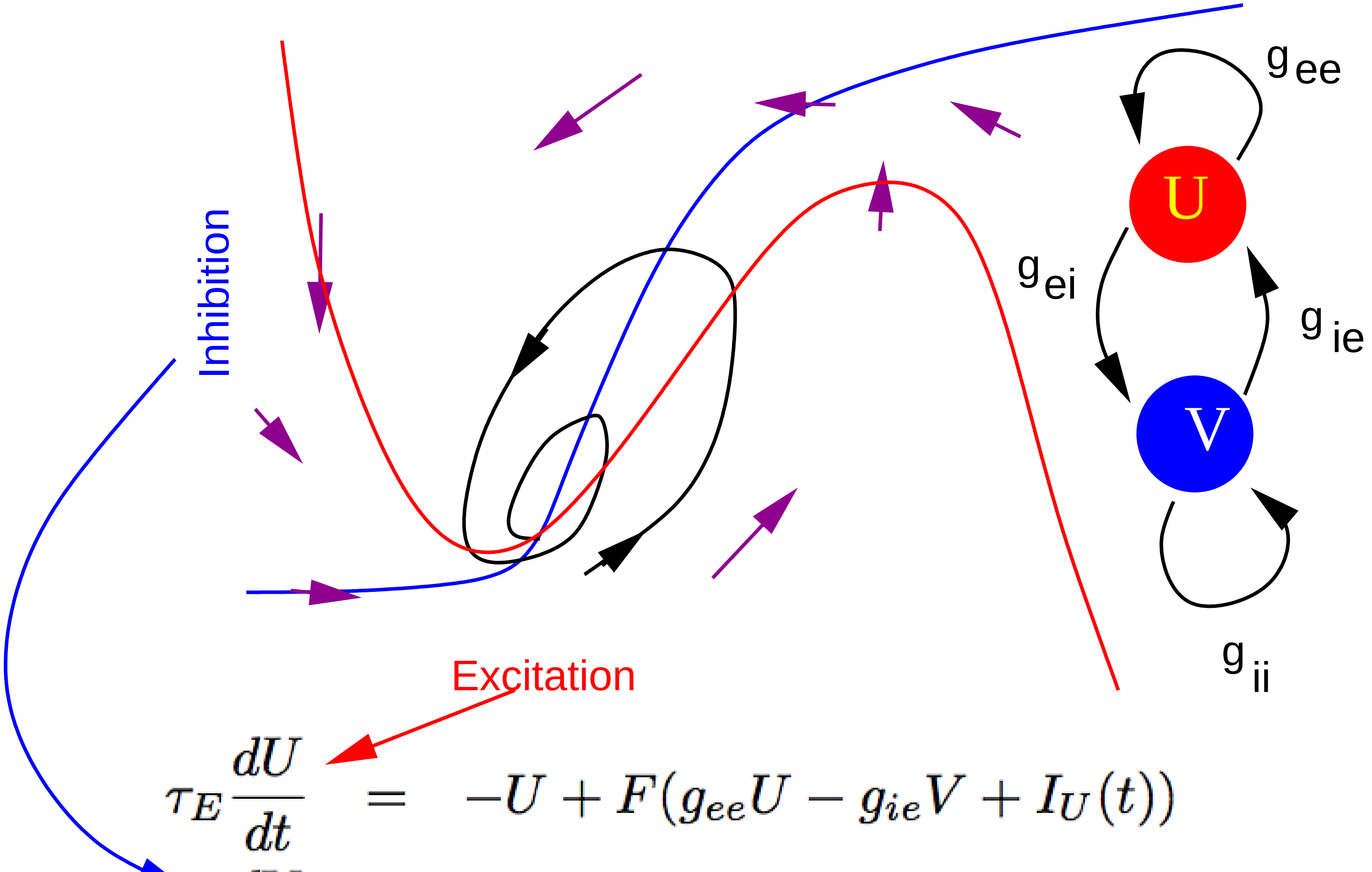
Summary

- Cortical in origin
- At high frequencies stripes
- At lower frequencies squares/hexagons

How could we model this?

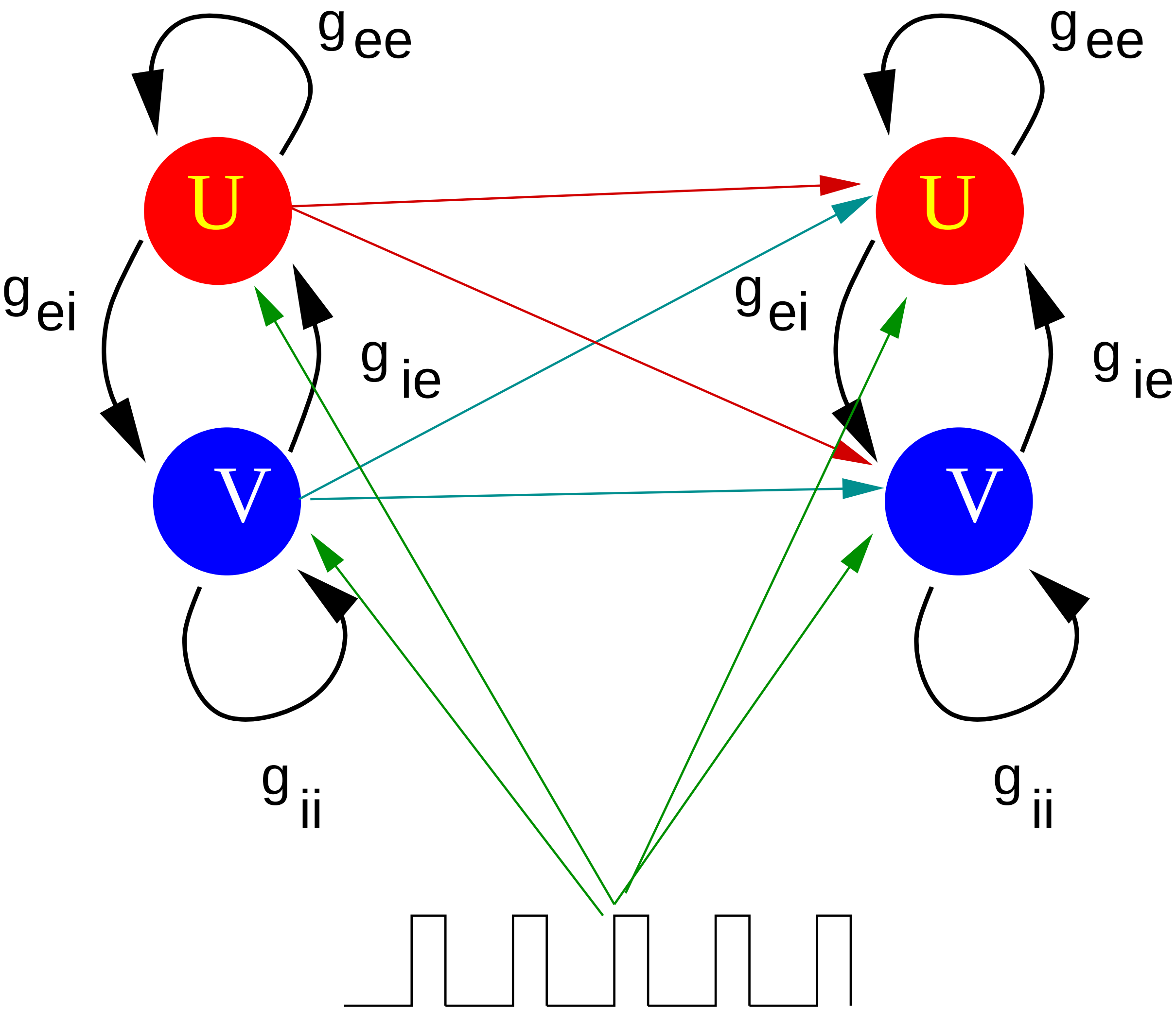
- Spontaneous pattern formation - spatial instability
- Coupled with resonance in the time domain
- Simple neural network with excitation and inhibition

The “simplest” model

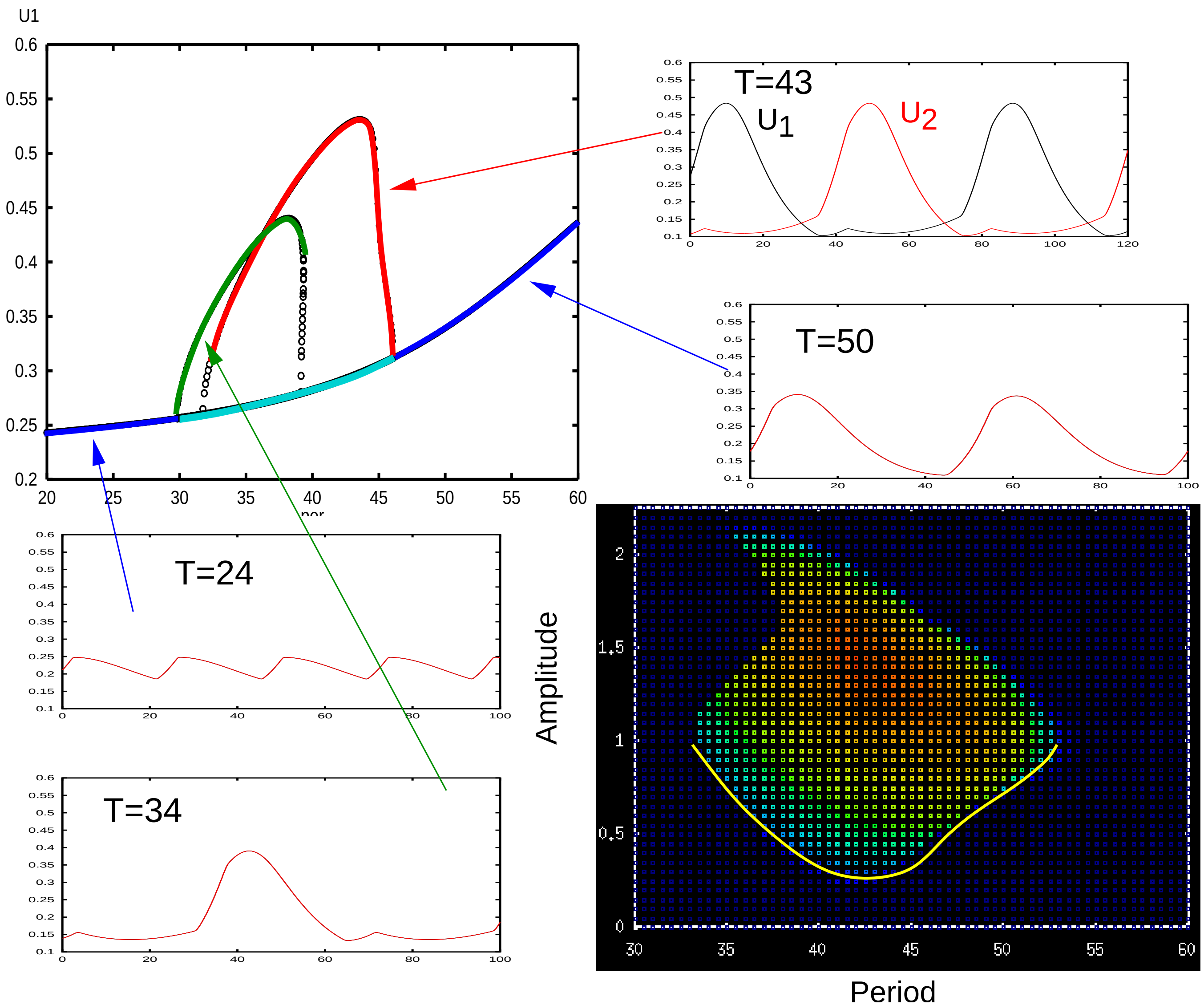


$$\tau_E \frac{dU}{dt} = -U + F(g_{ee}U - g_{ie}V + I_U(t))$$
$$\tau_I \frac{dV}{dt} = -V + F(g_{ei}U - g_{ii}V + I_V(t))$$

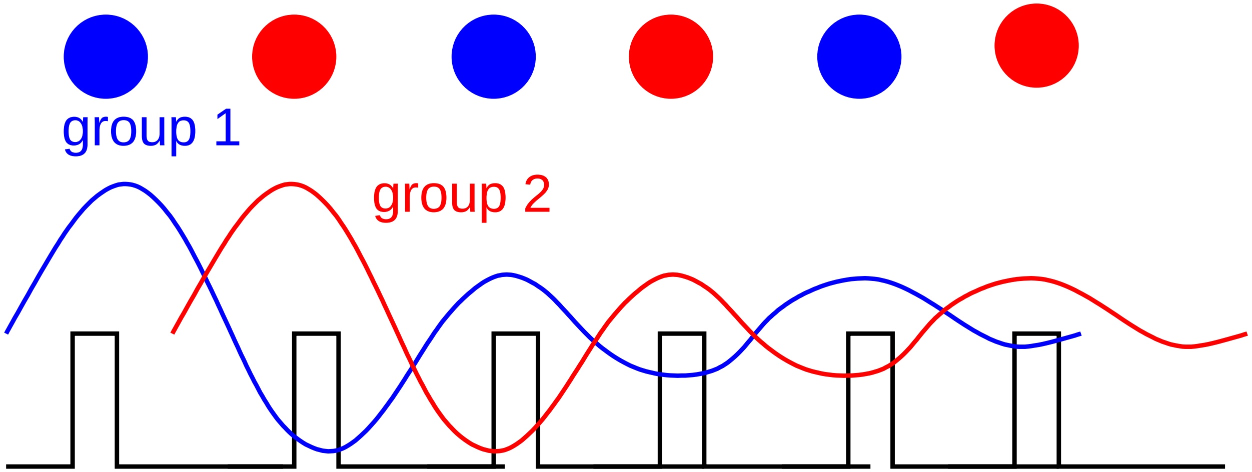
Coupling a pair



Pair simulations



2:1 resonance

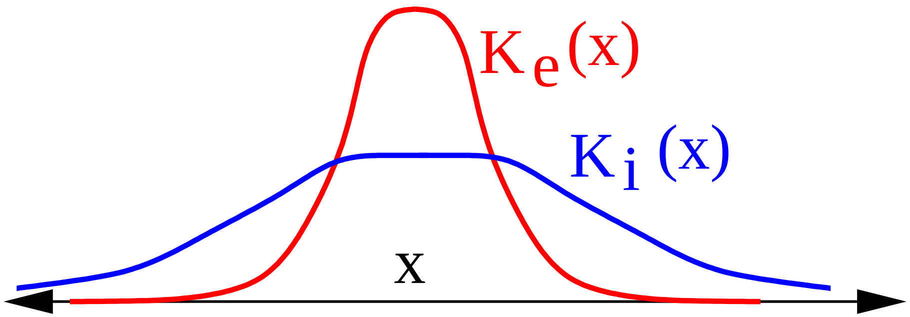


- Damped return to rest
- Mutual (lateral) inhibition encourages anti-phase
- Resonances at twice the frequency and at the frequency
- theta/alpha (8-12 Hz) rhythm

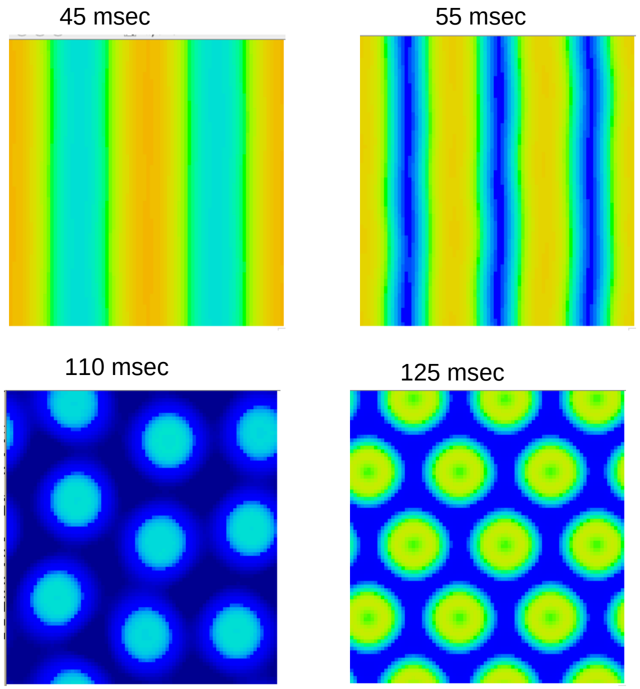
What about two dimensions?

- Pair shows plausibility, but spatial frequency and patterns are undetermined.
- Coupled E and I cells with spatially decaying coupling on a two-dimensional grid

$$
\begin{aligned}
U_t &= -U + F(g_{ee}K_e(\mathbf{x}) * U - g_{ie}K_i(\mathbf{x}) * V + \beta_e S(t)) \\
V_t &= -V + F(g_{ei}K_e(\mathbf{x}) * U - g_{ii}K_i(\mathbf{x}) * V + \beta_i S(t)) \\
K(\mathbf{x}) * U &= \int\int_\Omega K(\mathbf{x} - \mathbf{y})U(\mathbf{y}, t)\, d\mathbf{y}
\end{aligned}
$$

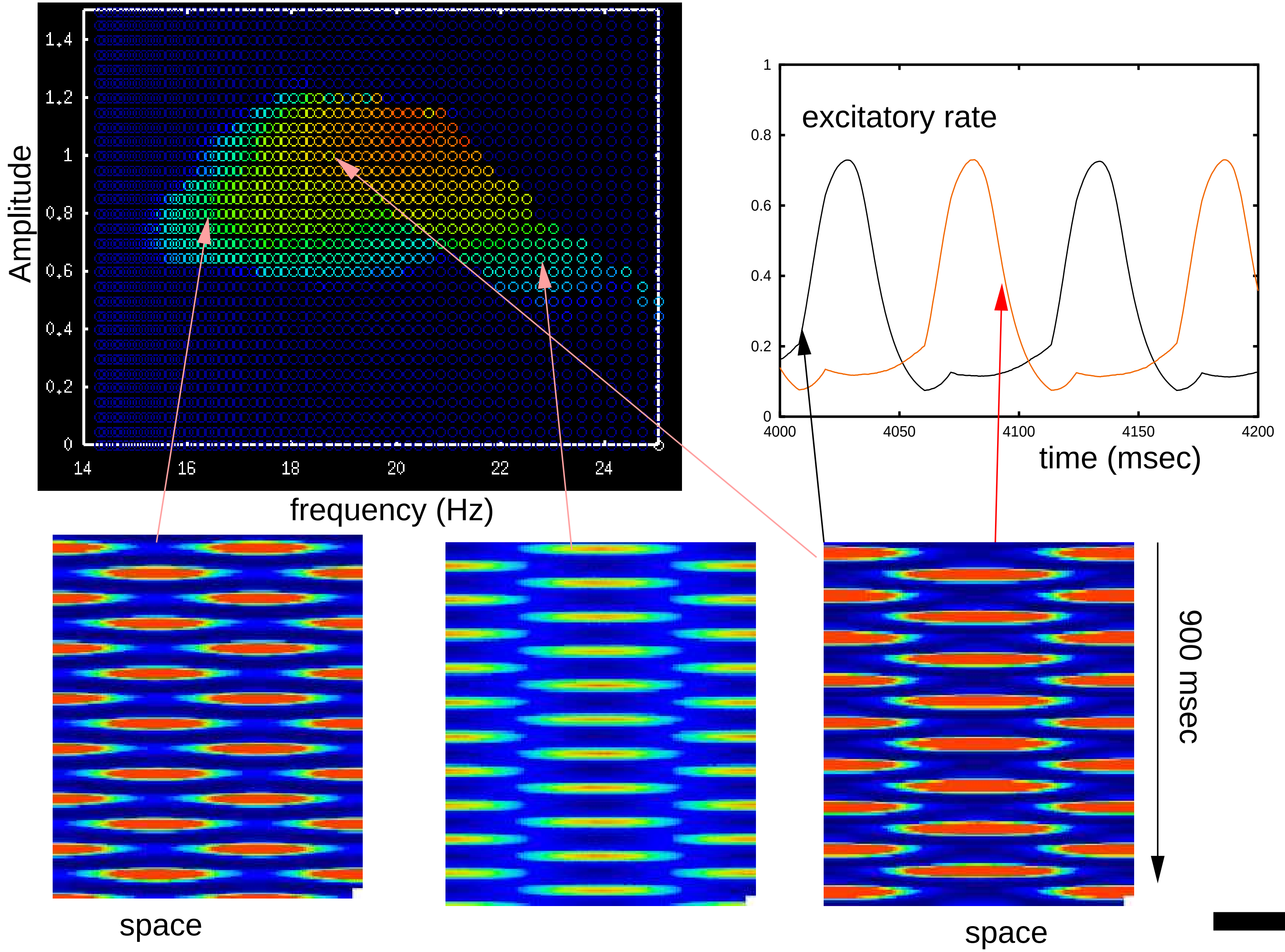


Low vs high frequency

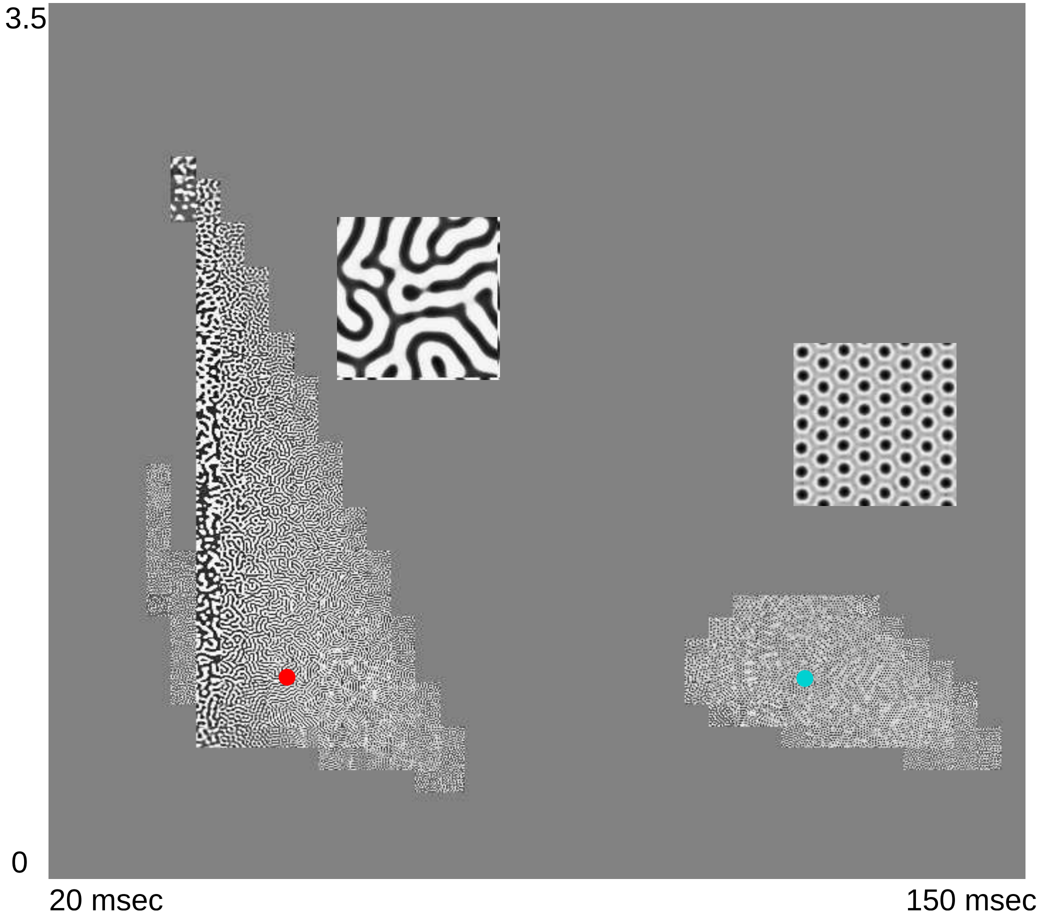


Note that in the 15-25 Hz regime, stripes emerge while in the 8-10 Hz regime, hexagonal patterns.

One-dimensional domain



Big picture



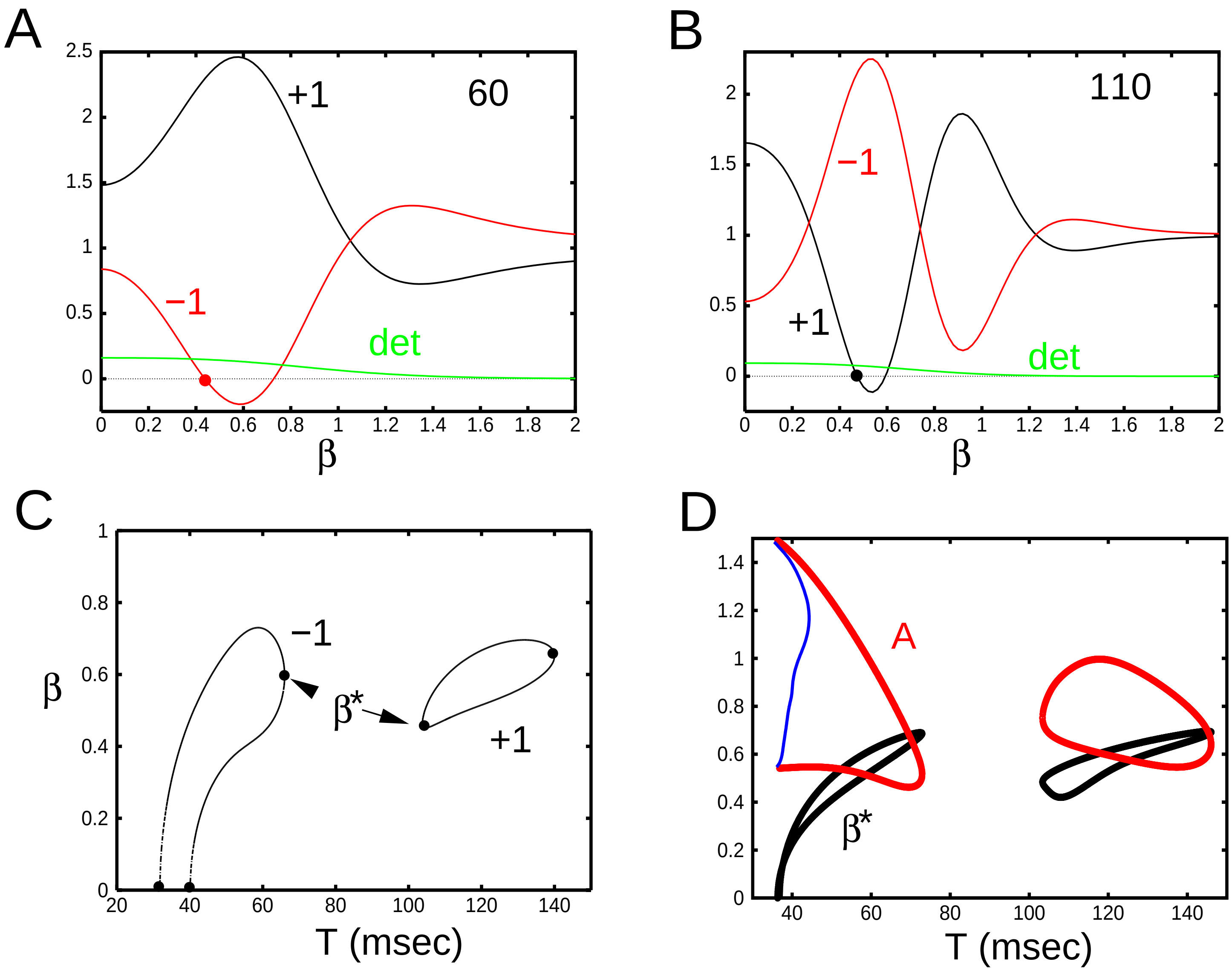
Summary of sims

- Hexagons at low frequencies
- Stripes at high frequencies
- Frequency in space increases with frequency in time
- Can this be understood?

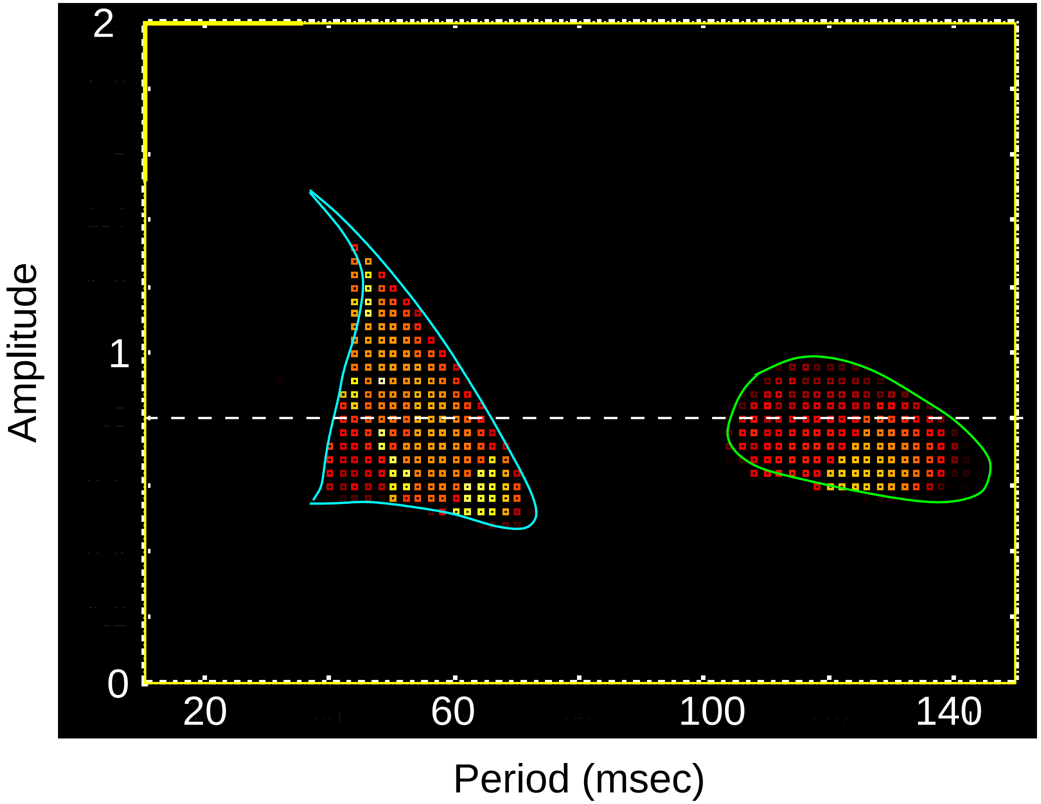
A little bit of theory

- Compute spatially homogeneous periodic solution and linearize
- Use the translation invariance of the convolution kernels to compute the monodromy matrix as a function of $\beta := |k|^2$.
- Find critical values of β for ± 1 Floquet multipliers
- Track as a function of, say, amplitude and period

An example


A
2.5
2
1.5
1
0.5
0
+1
60
−1
det
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8 2
β
B
2
1.5
1
0.5
0
110
−1
+1
det
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8 2
β
C
1
0.8
0.6
0.4
0.2
0
β
−1
β*
+1
20 40 60 80 100 120 140
T (msec)
D
1.4
1.2
1
0.8
0.6
0.4
0.2
0
A
β*
40 60 80 100 120 140
T (msec)

Compare to simulations

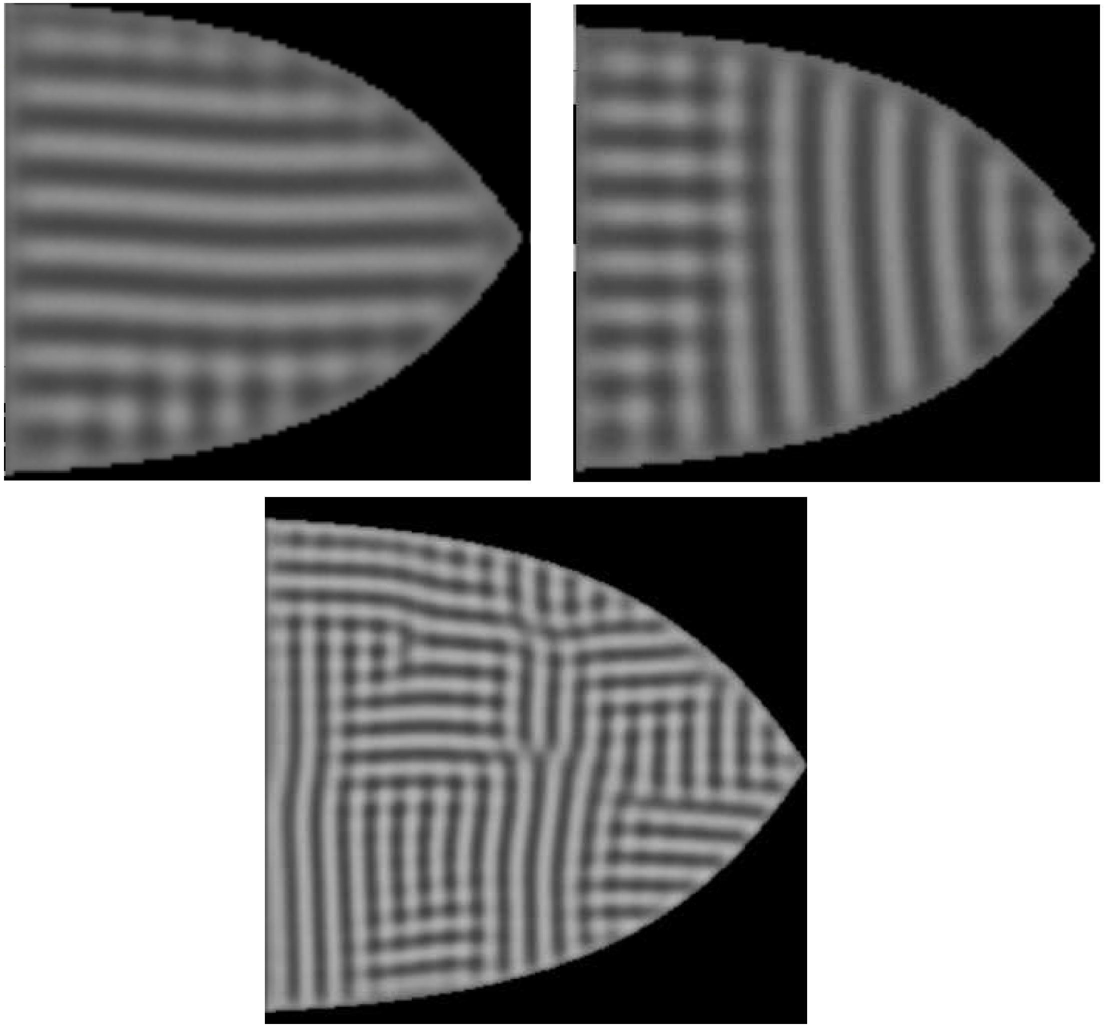


Stripes vs Hexagons

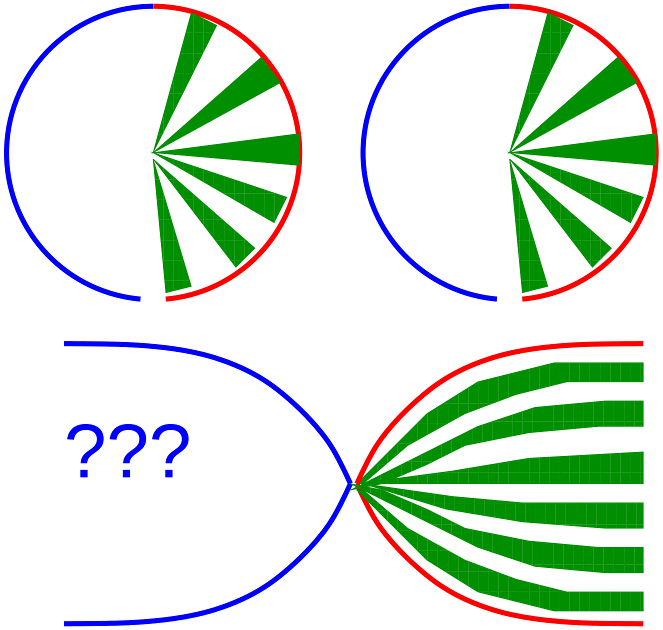
Why do you see stripes at high frequencies and hexagons at low?

- At high frequencies, -1 Floquet multiplier implies certain symmetries in the normal form: in particular, there are no quadratic terms. Stripes will be selected
- At low frequencies, +1 Floquet multiplier implies quadratic terms in the normal form so that hexagons bifurcate first and you expect them to be selected

Domain shape doesn't matter

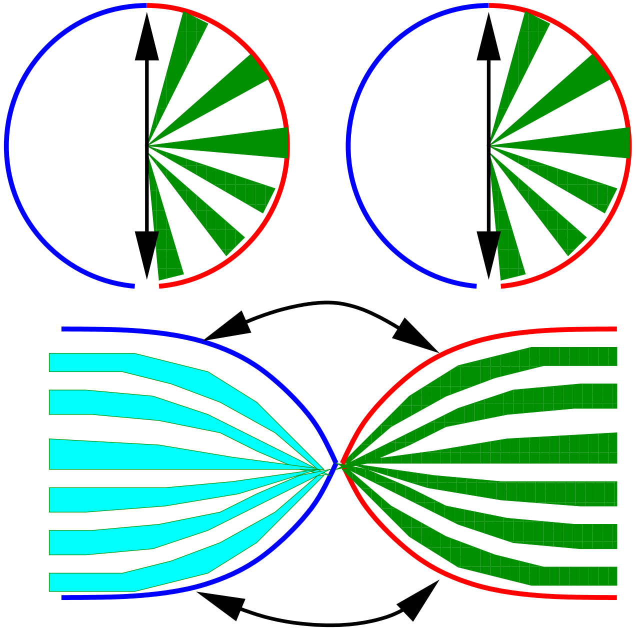


Left and right hemifields



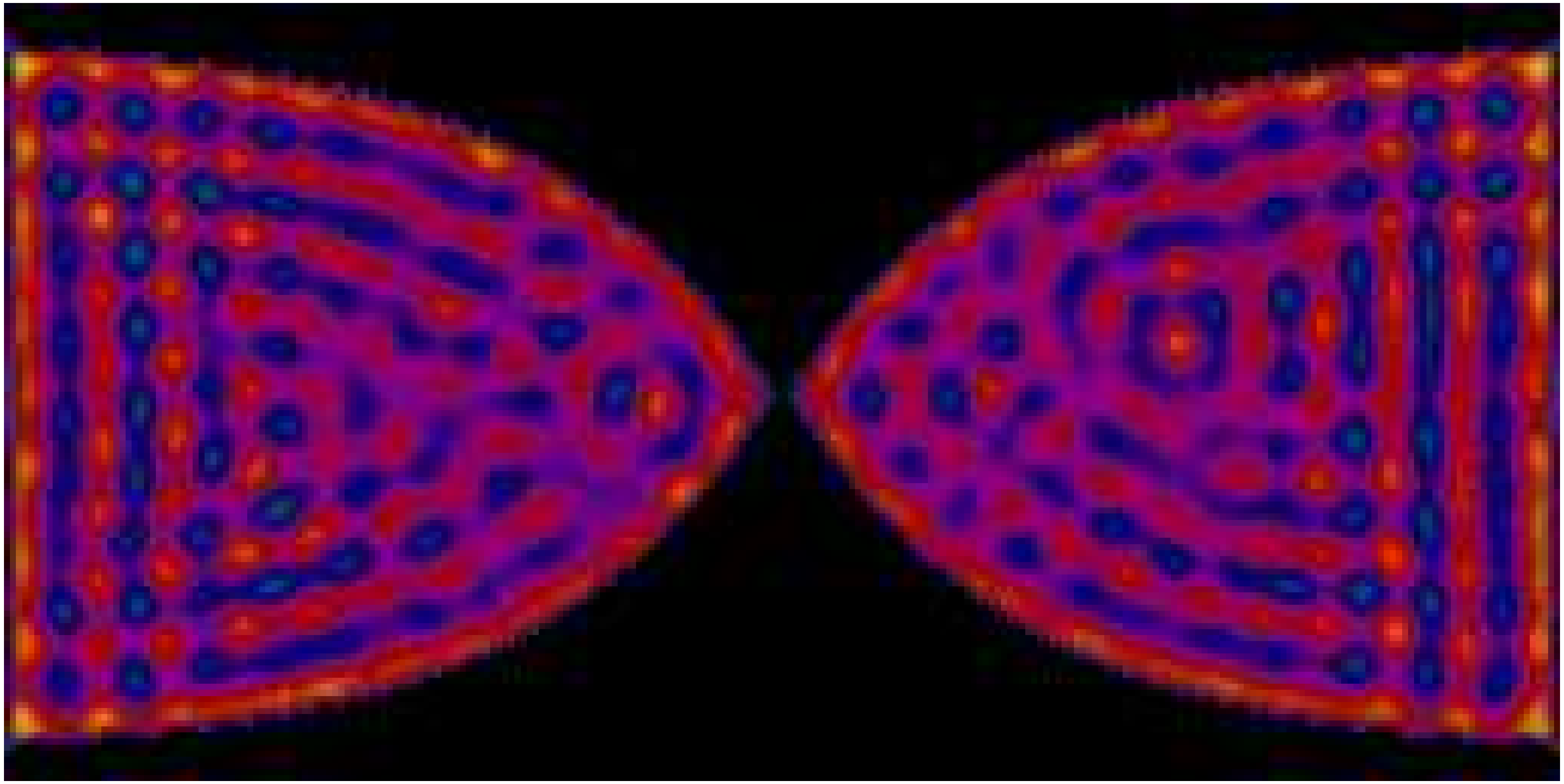
Since stripes of either orientation emerge, how are they consistent? How do they maintain phase continuity?

Left and right hemifields



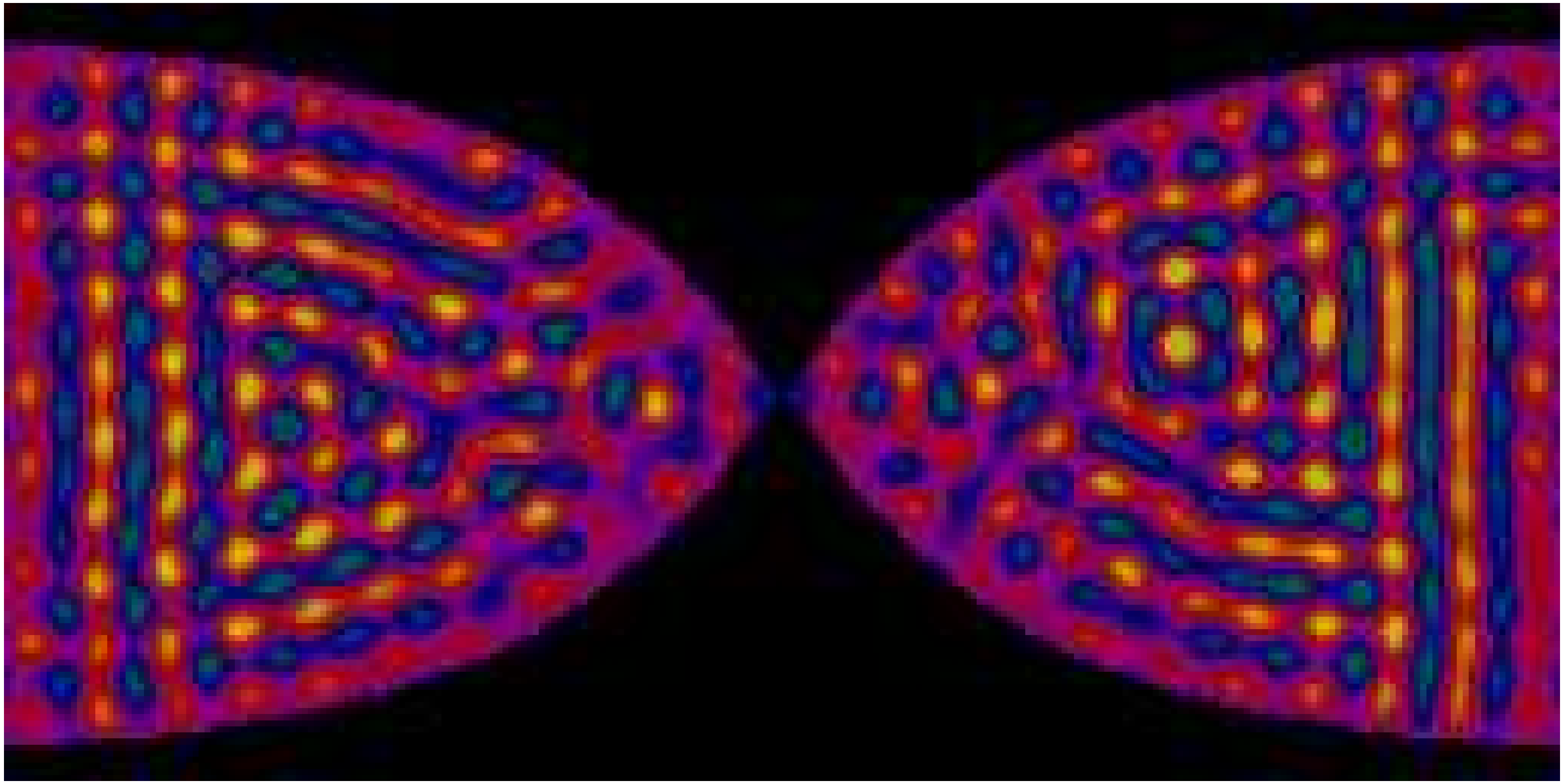
Coupling along the midline (borders of V1) could do it.

Coupled domains



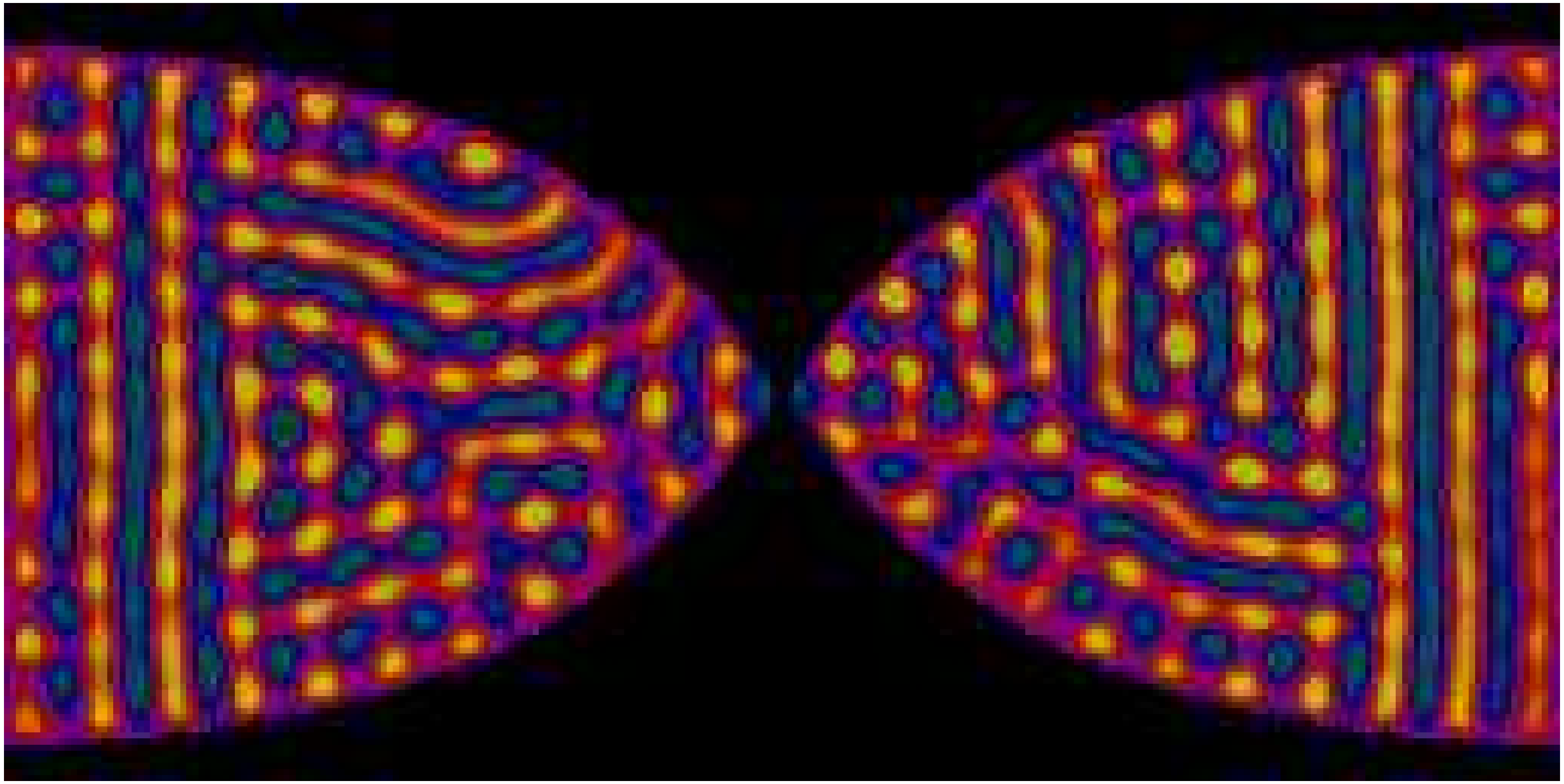
Start external animation

Coupled domains



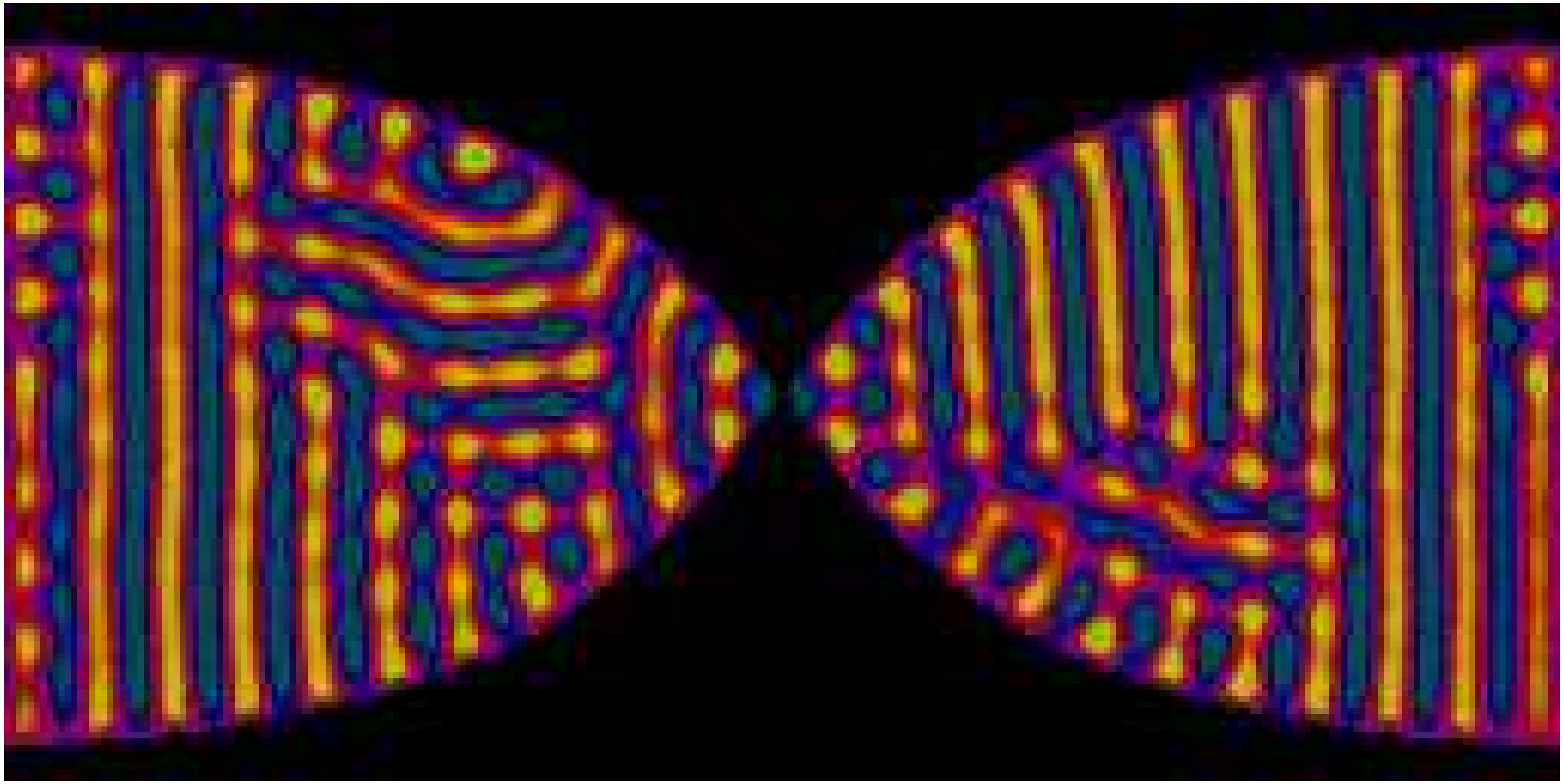
Start external animation

Coupled domains



Start external animation

Coupled domains



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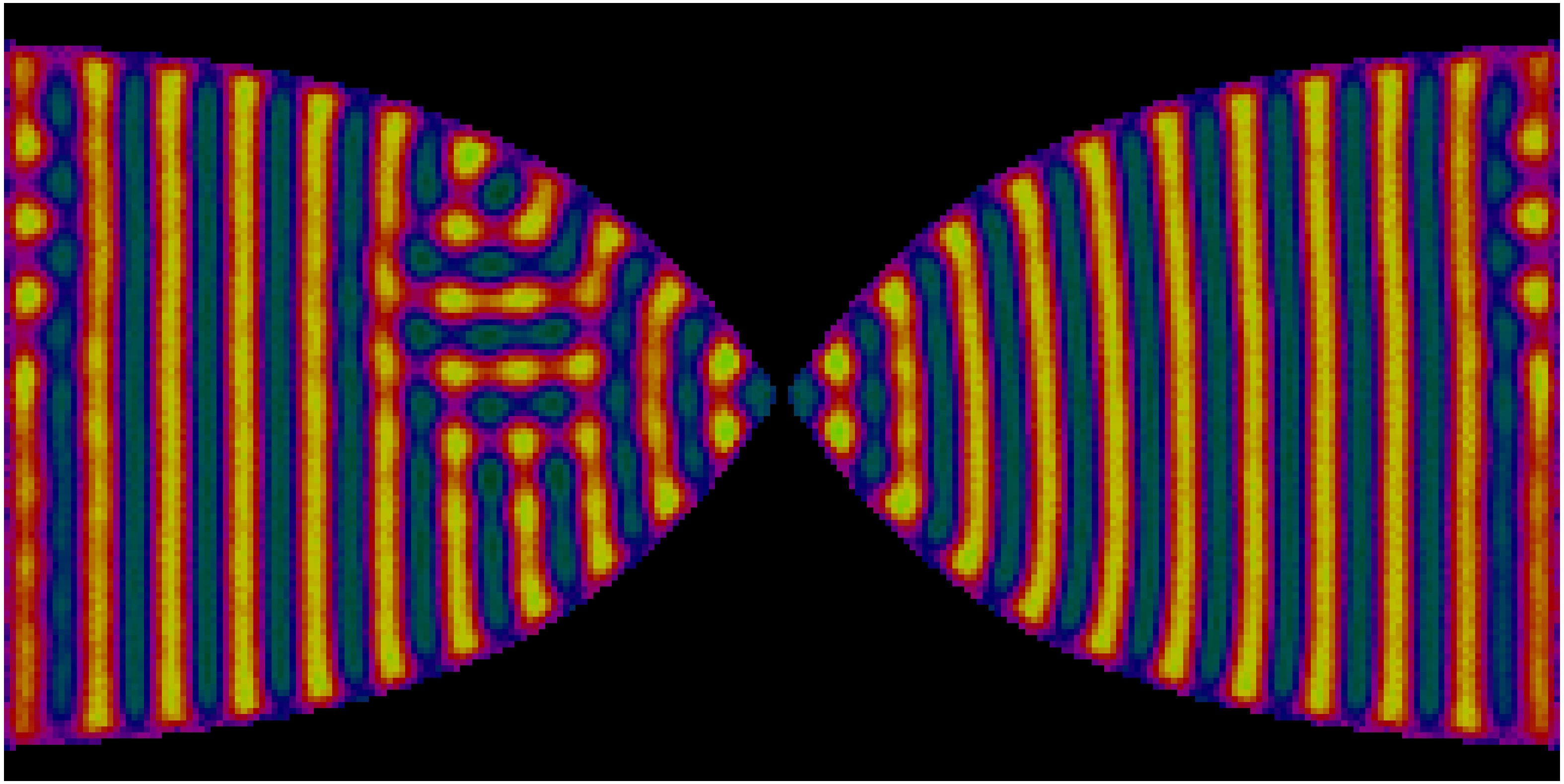
Coupled domains



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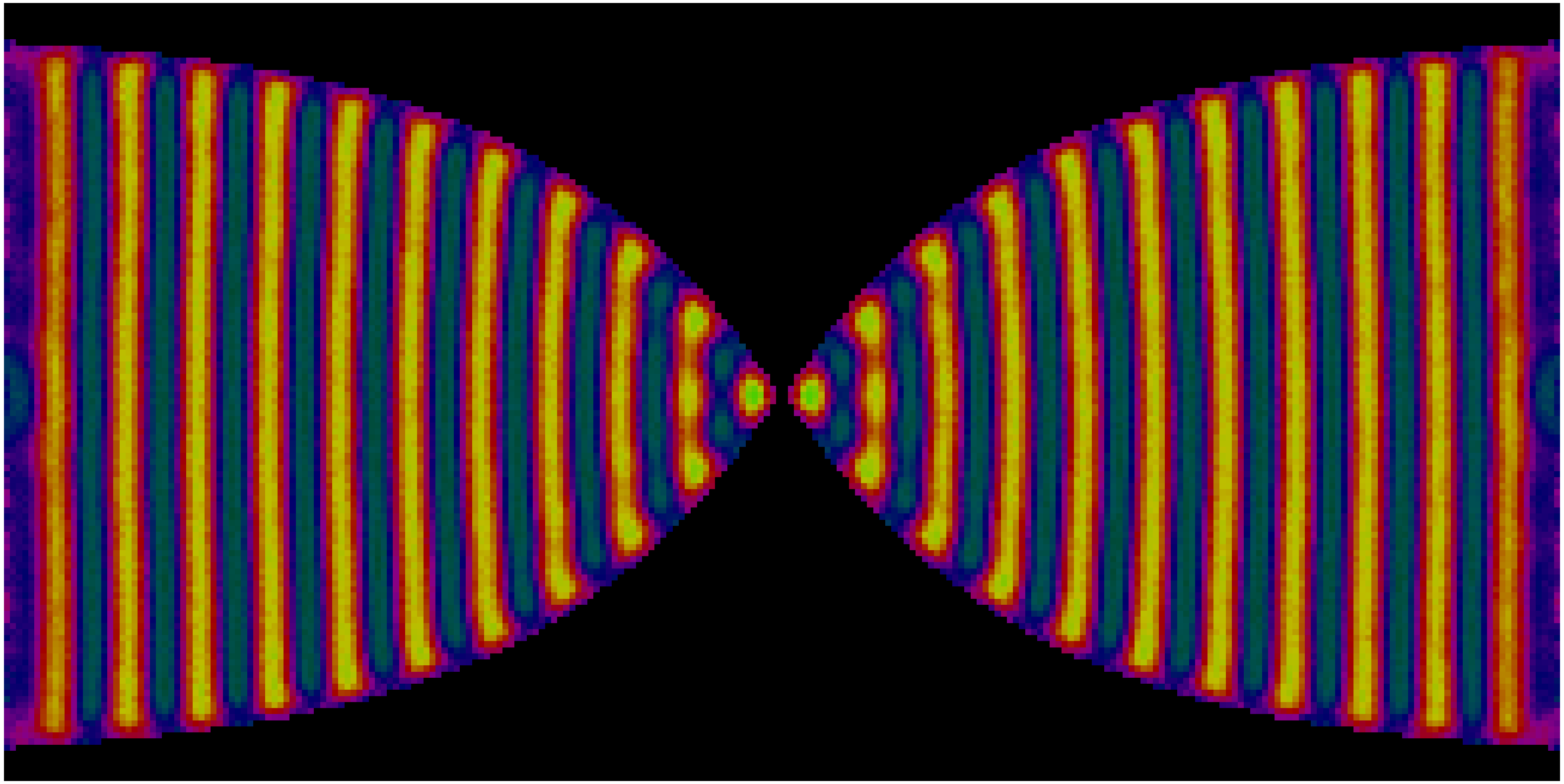
Coupled domains



Start external animation

Questions remain

Questions remain

- What do different patterns of light do?
- What about color effects?
- Billock & Tsou stabilize the patterns

Acknowledgments

- Jon Drover (Cornell), Helen Parker (RTG), Jon Rubin
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