

# A Model for the Origin and Properties of Flicker-Induced Geometric Phosphenes

SIAM Life Sciences

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work performed under G. Bard Ermentrout,  
in collaboration with Matthew Stoffregen

August 8, 2012

# Motivations

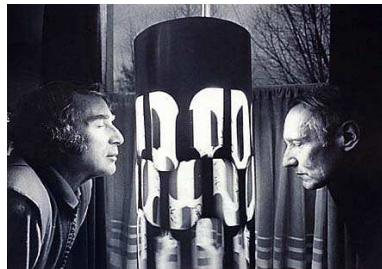
- Described by Jan Purkinje in 1819



Purkinje's Illustrations

# Motivations

- Described by Jan Purkinje in 1819
- Artistic and broader interest
  - Flicker hallucinations



William S. Burroughs & Biron Gysin  
with the "Dream Machine"

# Motivations

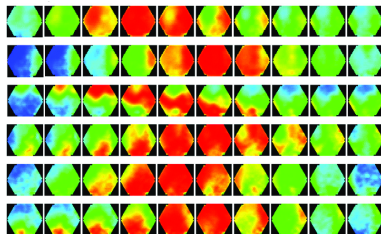
- Described by Jan Purkinje in 1819
- Artistic and broader interest
  - Flicker hallucinations
- Applications
  - Photosensitive epilepsy, migraines, vertigo



Pokemon television series

# Motivations

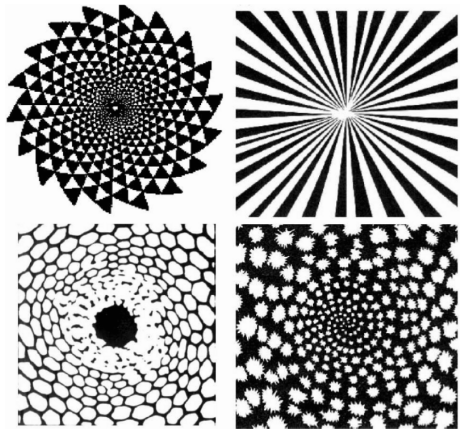
- Described by Jan Purkinje in 1819
- Artistic and broader interest
  - Flicker hallucinations
- Applications
  - Photosensitive epilepsy, migraines, vertigo
- Recurrent networks
  - Temporal encoding
  - Oscillations
  - Spatio-temporal coupling



Compression and Reflection of Visually Evoked Cortical Waves, Xu et al. 2007

## What are geometric phosphene hallucinations?

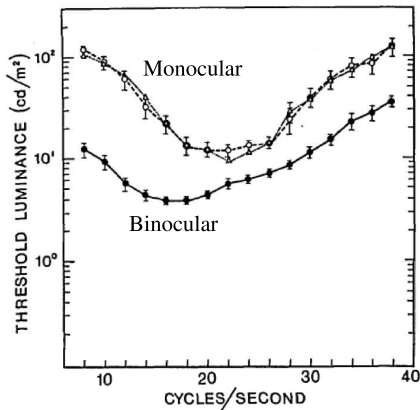
- Form constants (Kluver, 1960)
  - **reproducible** across subjects



Form constants, Bressloff et al. 2001

# What are geometric phosphene hallucinations?

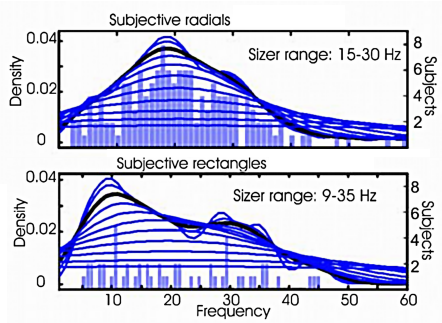
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  - **reproducible** across subjects
- 10-40 Hz (Remole, 1971)



Remole, 1973

# What are geometric phosphene hallucinations?

- Form constants (Kluver, 1960)
  - **reproducible** across subjects
- 10-40 Hz (Remole, 1971)
- Becker, Elliott (2006):
  - 10 Hz :  
honeycombs,  
rectangles, zigzags
  - 20-30 Hz:  
spirals, targets, lines,  
waves



Flicker-induced color & form: Interdependencies & relation to stimulation frequency & phase, Becker & Elliott, 2006

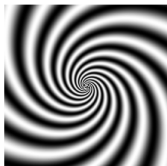


# Form Constants : Waves in Cortex

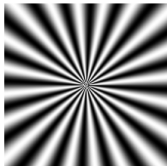
Retina

Cortex

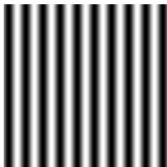
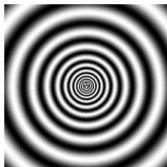
A



B



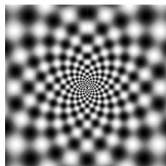
C



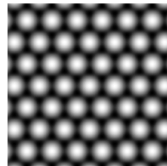
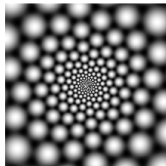
Retina

Cortex

D



E



# Geometric visual hallucinations : instabilities in V1

- Ermentrout, Cowan (1979) : inhibition, excitation **instability**
  - Migraine
  - Sensory deprivation
  - Hallucinogens
- Instability when driven with 'unnatural' stimuli
  - Geometric phosphenes from **uniform flickering light**
- Knoll (1963) : flicker phosphenes relate to resonance?
- Herrmann (2001): 10,20,40 Hz **resonance** in occipital EEG to flickering light

## Open problems addressed in this talk

- Can existing models of visual hallucination explain flicker-phosphenes?

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- Can existing models of visual hallucination explain flicker-phosphenes?
- How can spatially **uniform** stimuli lead to hallucinated **patterns**?
- Why do some stimuli induce hallucinations more readily than others?
- How do different **temporal** stimuli induce different **spatial** patterns?

# Wilson-Cowan equations: excitatory, inhibitory populations

$$\tau_e \dot{U}_e = -U_e + f(a_{ee}U_e - a_{ie}U_i - \theta_e + g_e S(t))$$

$$\tau_i \dot{U}_i = -U_i + f(a_{ei}U_e - a_{ii}U_i - \theta_i + g_i S(t))$$

$U_{e,i}$  : Population activation

$\tau_{e,i}$  : Time constants

$a_{ee,ei,ie,ii}$  : Population interaction

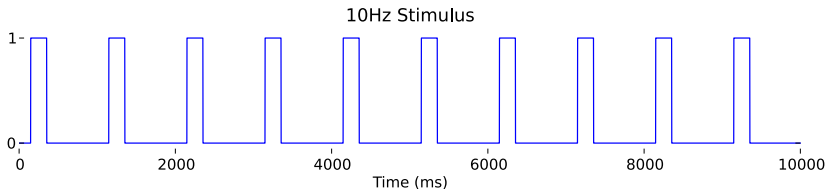
$\theta_{e,i}$  : Bias

$g_{e,i}$  : Stimulus coupling

Firing rate nonlinearity:

$$f(x) = \frac{1}{1+e^{-x}}$$

Periodic stimulus:  $S(t) = H(\sin(2\pi t/T) - 0.8)$



## Model: spatially extended Wilson-Cowan equations

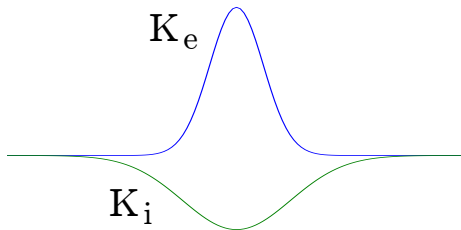
$$\tau_e \dot{U}_e(x, t) = -U_e(x, t) + f(a_{ee} K_e \star U_e(x, t) - a_{ie} K_i(x) \star U_i(x, t) - \theta_e + g_e S(t))$$

$$\tau_i \dot{U}_i(x, t) = -U_i(x, t) + f(a_{ei} K_e \star U_e(x, t) - a_{ii} K_i(x) \star U_i(x, t) - \theta_i + g_i S(t))$$

( based on Ermentrout and Cowan 1979 )

Lateral interaction  
kernel

$$K_{e,i} \propto e^{-x^2/\sigma_{e,i}^2}$$





# Notation

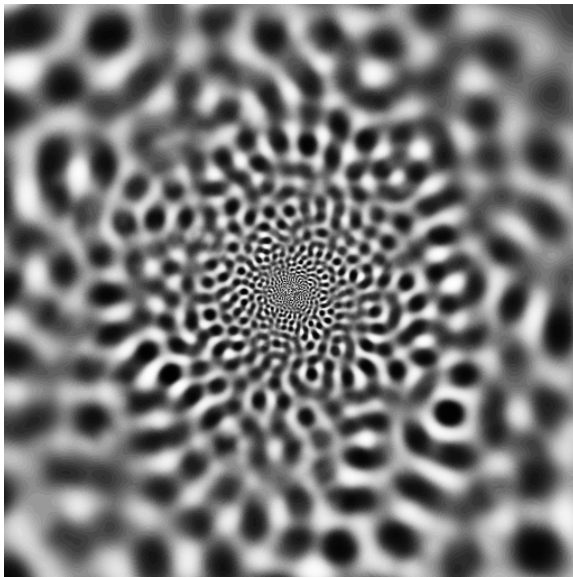
For succinctness, we sometimes denote this system as

$$\dot{U} = -DU + F(KU + GS(t))$$

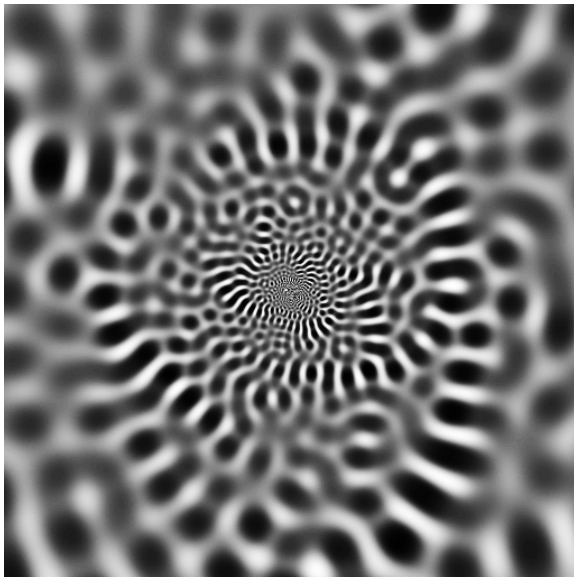
- $D$  : matrix of time constants
- $F$  : nonlinearity applied in each dimension
  - offsets  $\theta$  subsumed in to the nonlinearity,
- $K$  : matrix of interactions,
  - including lateral interactions and e-i interactions
- $GS(t)$  : stimulus drive to each dimension.

# Simulation

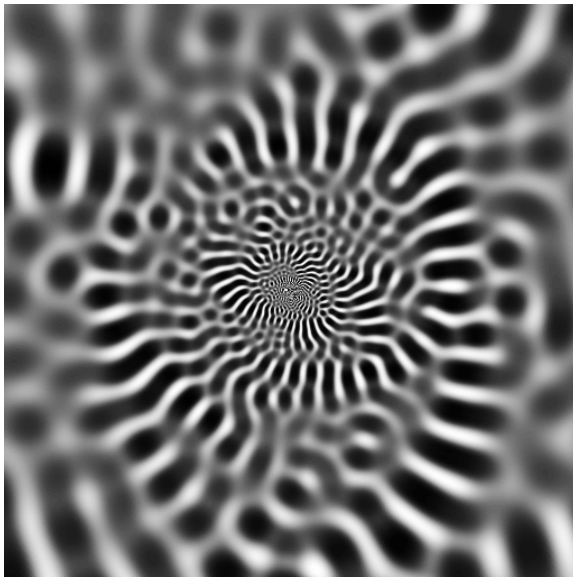
# Evolution of 2D patterns (subjective coordinates)



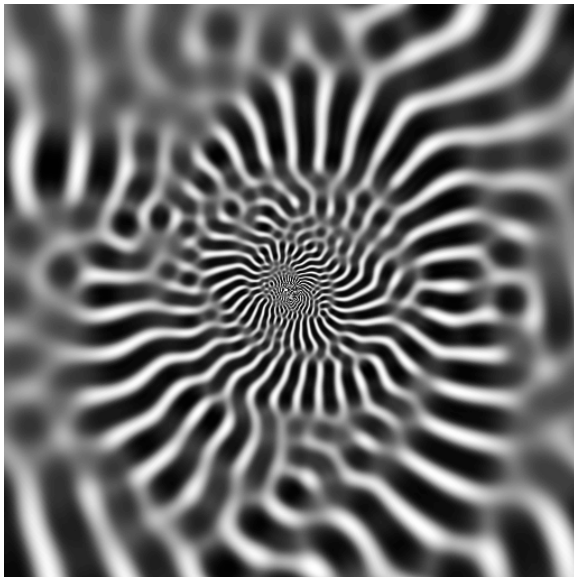
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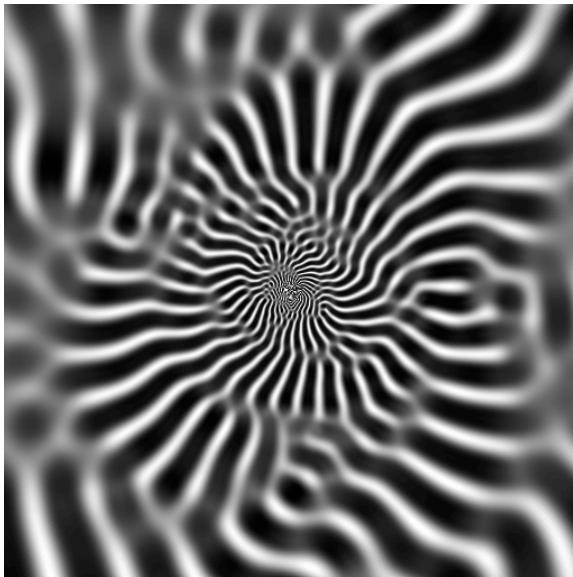
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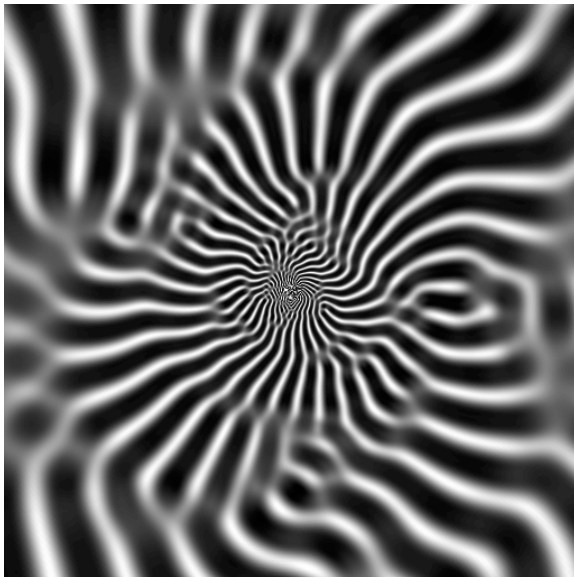
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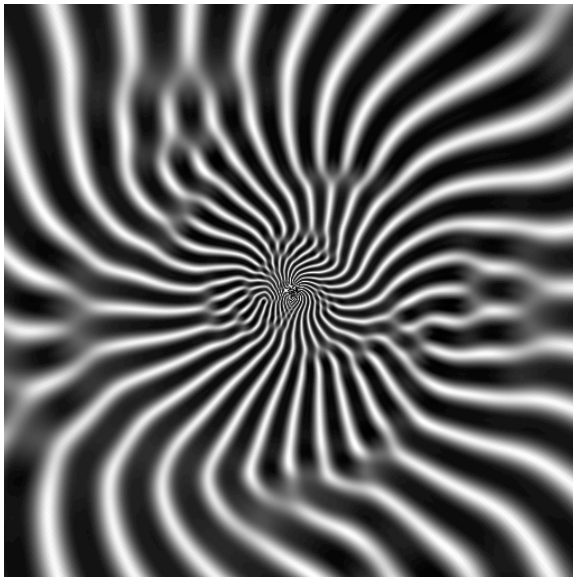


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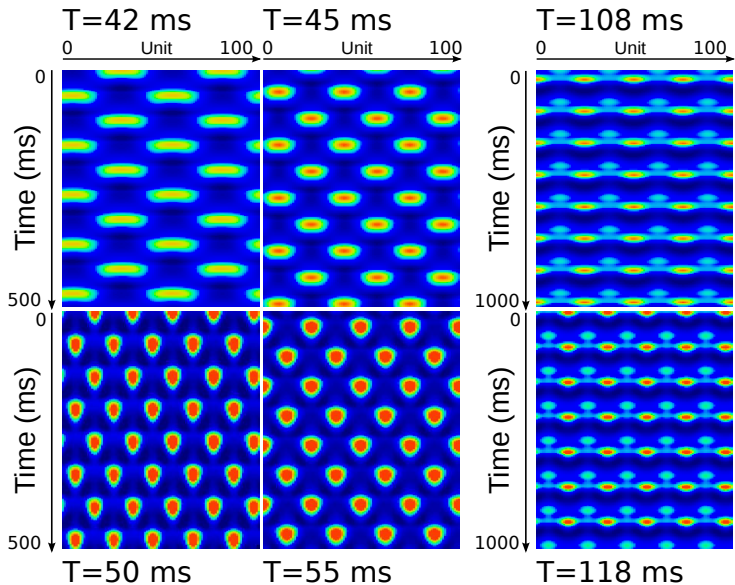




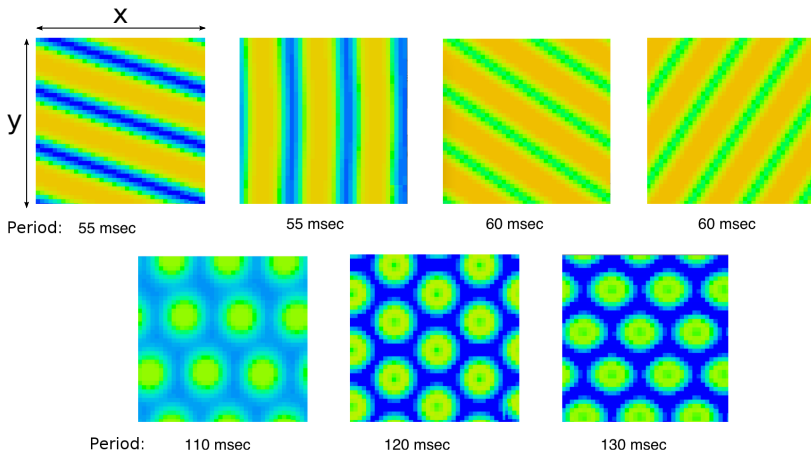
# Evolution of 2D patterns (subjective coordinates)



## 1D patterns in time

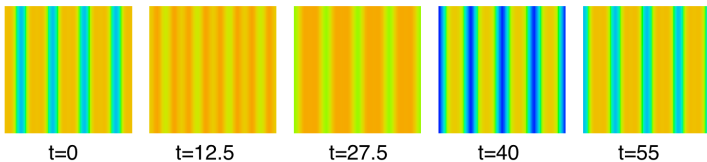


# 2D patterns: stripes and hexagons

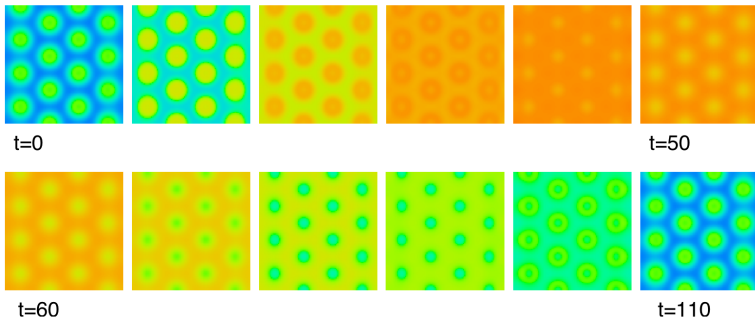


## 2D patterns: synchronous and period doubling

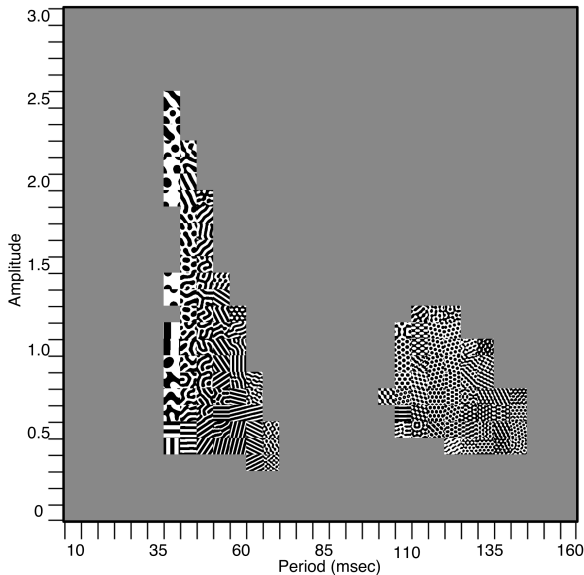
18 Hz : Symmetric, alternating stripes



9 Hz : Hexagons



# Frequency-dependent pattern formation



# Stability

# Stability analysis

- **Nonlinear**
  - Linearize at **spatially homogeneous** solution and examine stability
- Coefficients vary in time
  - When stimulated, there are no fixed points, perhaps fixed **orbits**?
  - Exploit periodicity and use Floquet theory to understand evolution
    - Numerically compute monodromy matrix, examine eigenvalues

## Solving spatially homogeneous case

$$\dot{U}(x) = -DU(x) + F(KU(x) + GS(t))$$

If the system is spatially homogeneous, lateral interactions can be replaced with constants. This is a simpler 2D nonlinear system. Call this solution  $V$ .

$$\dot{V} = -DV + F(KV + S(t))$$



## Linearizing around homogeneous solution

Once you have the spatially homogeneous solution  $V$ ,

$$\dot{V} = -DV + F(KV + S(t))$$

decompose  $U$  into  $V$ , and a perturbation around  $V$ , which we will call  $Z$ .

$$\dot{Z} = -DZ + F'(K_oV(t) + S(t))(KZ)$$

Let  $B(t) = -D + F'(K_oV(t) + S(t)) * K$ , such that  $\dot{Z} = B(t)Z$

## Assessing stability of periodic orbits

The spatially homogeneous solution  $V$  is periodic

$$V(t) = V(t + T)$$

At critical points (orbits),  $Z$  is an  $\epsilon$  departure from the spatially homogeneous solution.

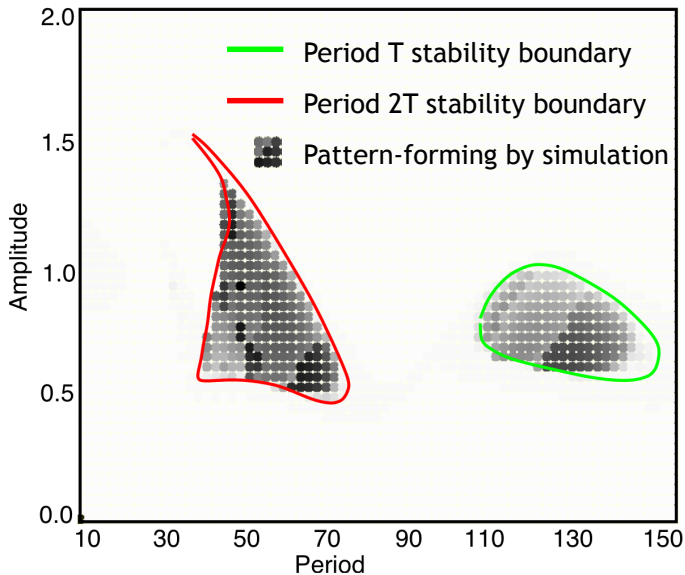
- Treat spatial eigenfunctions independently
- Examine how each eigenfunction evolves over one period

For a particular eigenfunction  $\beta$ , eigenvalues of the monodromy matrix will tell us whether  $\beta$  is growing.

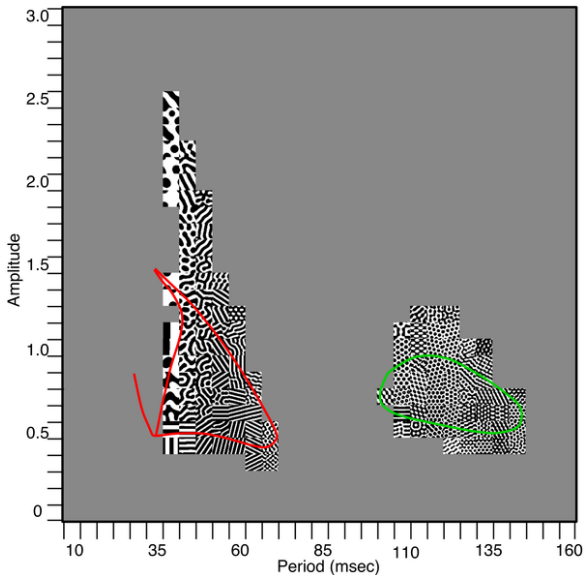
- Since the interactions are a convolution, the eigenfunctions are Fourier space.

$$Z_\beta(t + T) = M_\beta Z_\beta(t)$$

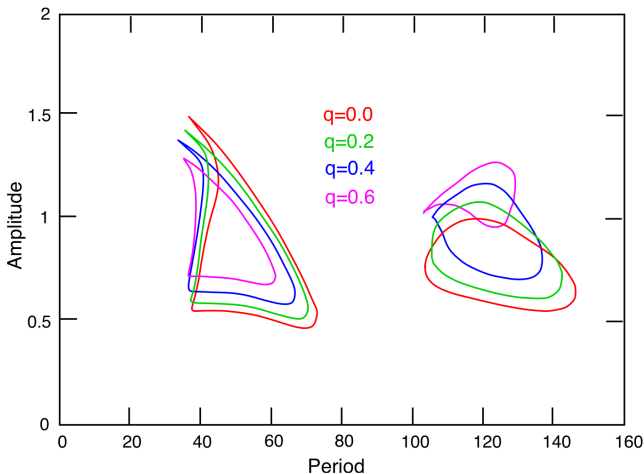
## Stability analysis agrees with 1D simulation



## 2D simulation?



## Parameter exploration: Feedforward Inhibition



$q = \frac{g_i}{g_e}$ : ratio of feed-forward inhibition and excitation

## Open problems addressed in this talk

- Simple models of visual hallucination **can** simulate flicker-phosphenes.

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- Simple models of visual hallucination **can** simulate flicker-phosphenes.
- Spatially uniform periodic stimuli may cause pattern formation by forcing the neural field into a pattern-forming periodic orbit.
- Resonant visual stimuli more readily induce patterns, but period-doubling pattern forming regimes are also favored.



# Open questions

## Modeling

- Better approximations of V1 network
  - Orientation: Bressloff et al?
  - Color: red-green effect in flicker, epilepsy
- Migraine?
- Epilepsy?

## Experimental

- Psychophysics?
- Electrophysiology?

# Acknowledgments

## Coauthors

- **G. Bard Ermentrout**
- Matthew Stoffregen

Program in Neural Computation  
at CMU-Pitt CNBC



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- NIH funded Program in Neural Computation summer REU program
- NSF EMSW21-RTG0739261
- NSF DMS0817131

(this is the end of the talk)

Introduction  
○○○○○

Model  
○○○

Simulation  
○○○○○

Stability  
○○○○○○○

Conclusions  
○○○○●

# Appendix

# Retinotopic mapping of primary visual cortex

# Retinotopic mapping of primary visual cortex



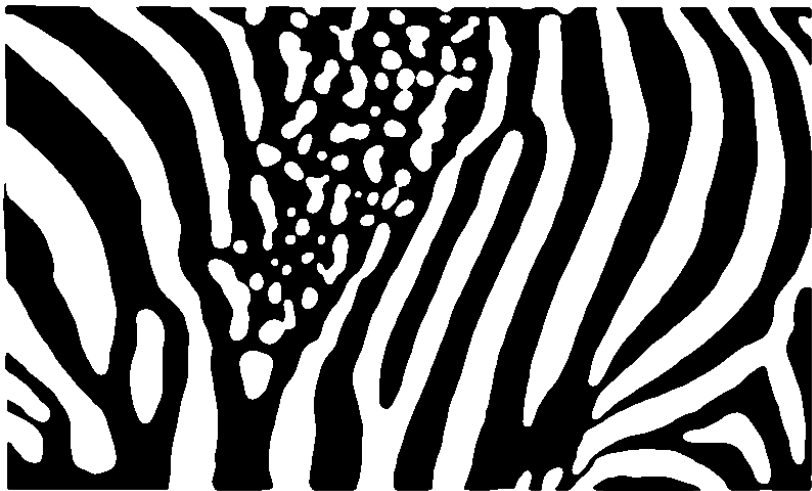




# Stability in a simplified model

Stripes or spots?

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Stripes or spots?

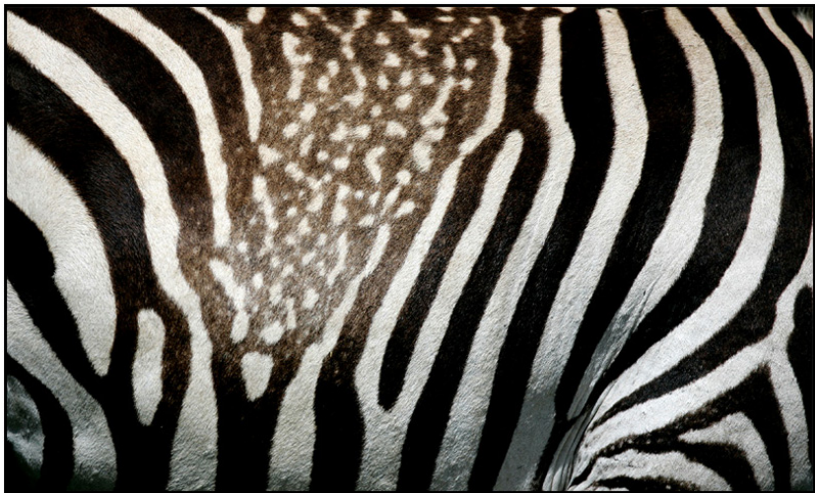


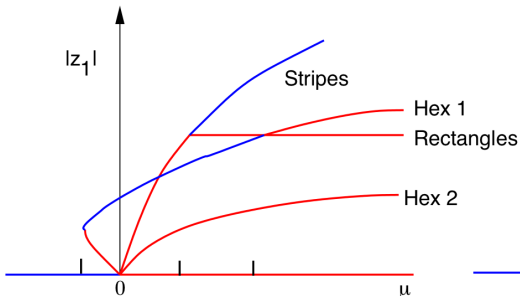
Image credit: Farid Radjouh

## Sums of plane waves

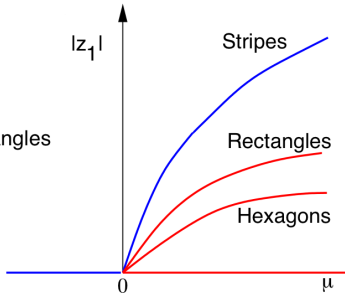


## Stripes or spots?

Low Frequency (7-10Hz)



High Frequency (15-30 Hz)



Bifurcation parameter  $\mu$  is a function of model parameters  $g_e, g_i, a_{ee}, a_{ie}, a_{ei}, \theta_e, \theta_i, \frac{T}{\tau_e}, \frac{\tau_i}{\tau_e}, \frac{\sigma_i}{\sigma_e}$ . There is no closed form solution for  $\mu$ .  $\mu$  can also be expressed as a function of the eigenvalues of the monodromy matrix. When  $\mu < 0$  the homogeneous solution is stable. As  $\mu$  departs from 0 in the positive direction, we move in to pattern-forming regimes. Blue curves indicate stable patterns.

# Big picture

- Spatially coupled, nonlinear systems exhibit complex resonance phenomena
  - Resonance associated with instability in e-i dynamics
- Nonlinearity and spatial coupling create multiple resonance peaks
  - Spatial patterns depend on frequency

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