# Pattern Formation and Symmetry in the Visual Cortex

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Date: August 8, 2002

> Klüver: We wish to stress merely one point, namely, that under diverse conditions **the visual system** responds in terms of a limited number of form constants.

# Outline

1. Visual Hallucinations

2. Structure of Visual Cortex

   (a) Hubel and Wiesel hypercolumns
   (b) local and lateral connections
   (c) isotropy versus anisotropy

3. Pattern Formation in Planar Systems

   (a) Symmetry
   (b) Four models

4. Interpretation of Patterns in Retinal Coordinates

   (a) threshold patterns
   (b) thin line contour patterns
   (c) time-periodic patterns

# Visual Hallucinations

- Drug **uniformly** forces activation of cortical cells
- Leads to spontaneous pattern formation on cortex
- Map from retina to primary visual cortex; translates pattern on cortex to visual image
- Patterns fall into four *form constants* (Klüver, 1928):
  - tunnels and funnels
  - spirals
  - lattices includes honeycombs and triangles
  - cobwebs

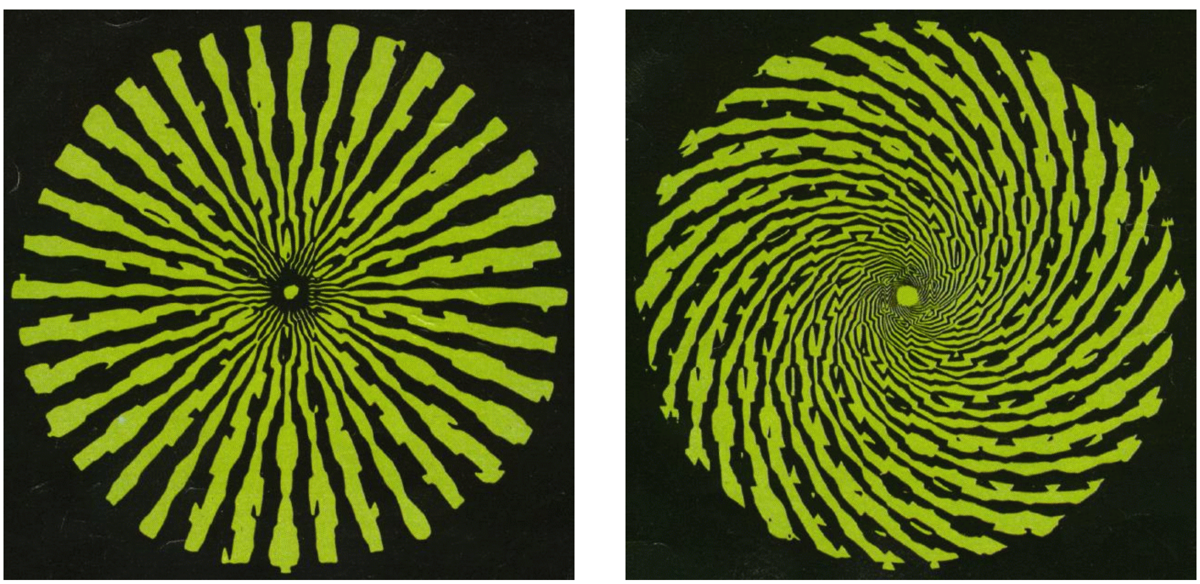


Figure 1: Funnels and spirals (G. Oster, *Scientific American*, 1970

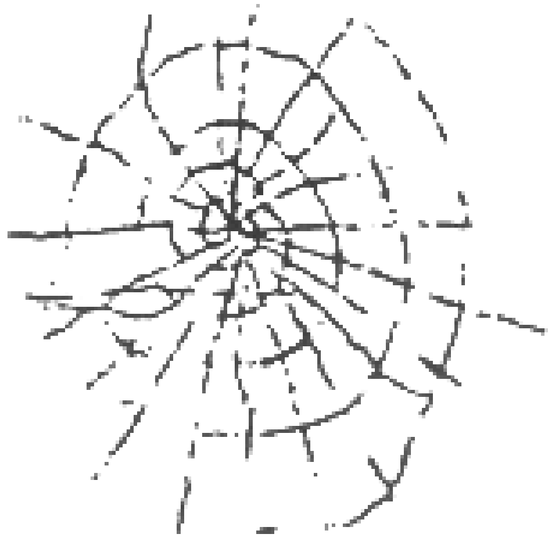


Figure 2: Cobweb (Patterson, 1992).

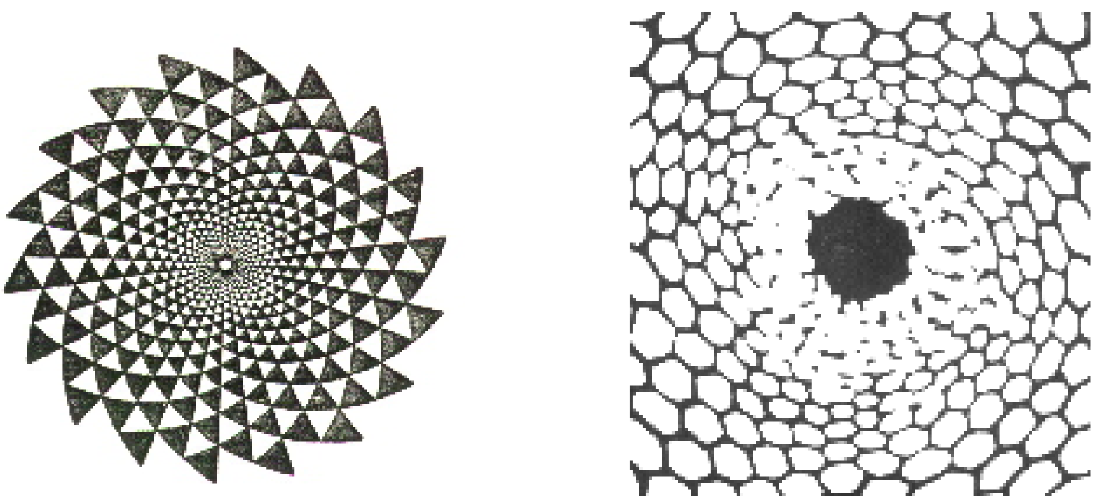


Figure 3: (Left) Phosphene produced by deep binocular pressure on eyeballs; (Right) Honeycomb generated by marihuana

# Orientation Sensitivity of Cells in V1

- Most V1 cells sensitive to *orientation* of contrast edge

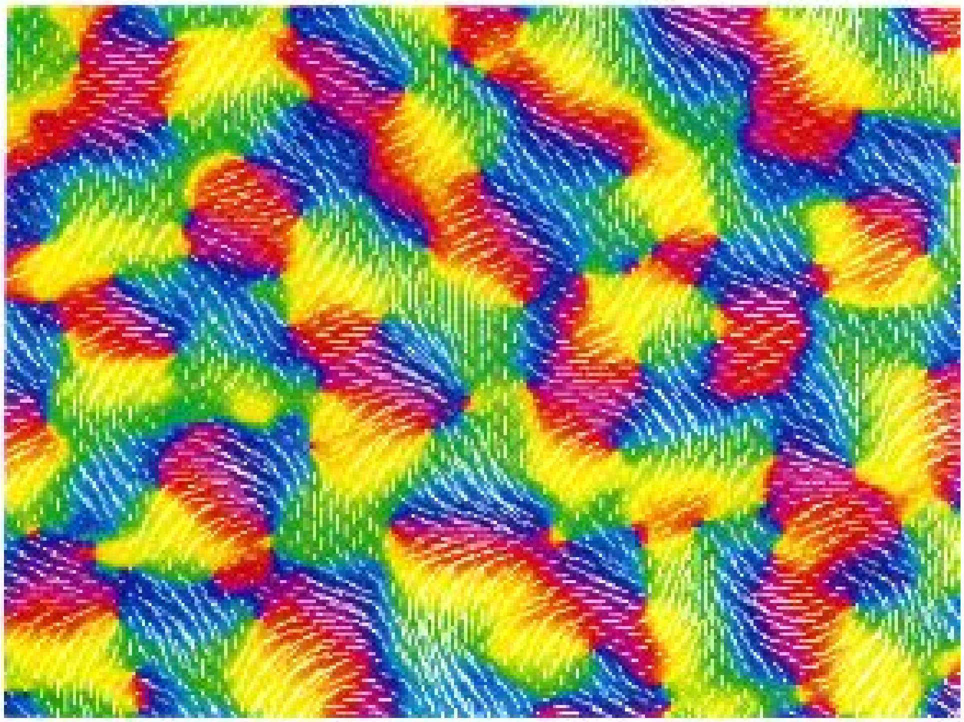


Figure 4: Distribution of orientation preferences in Macaque V1 (Blasdel)

- Hubel and Wiesel, 1974

  Each millimeter there is a *hypercolumn* consisting of orientation sensitive cells in every direction preference

## Structure of Primary Visual Cortex (V1)

- Optical imaging exhibits pattern of connection

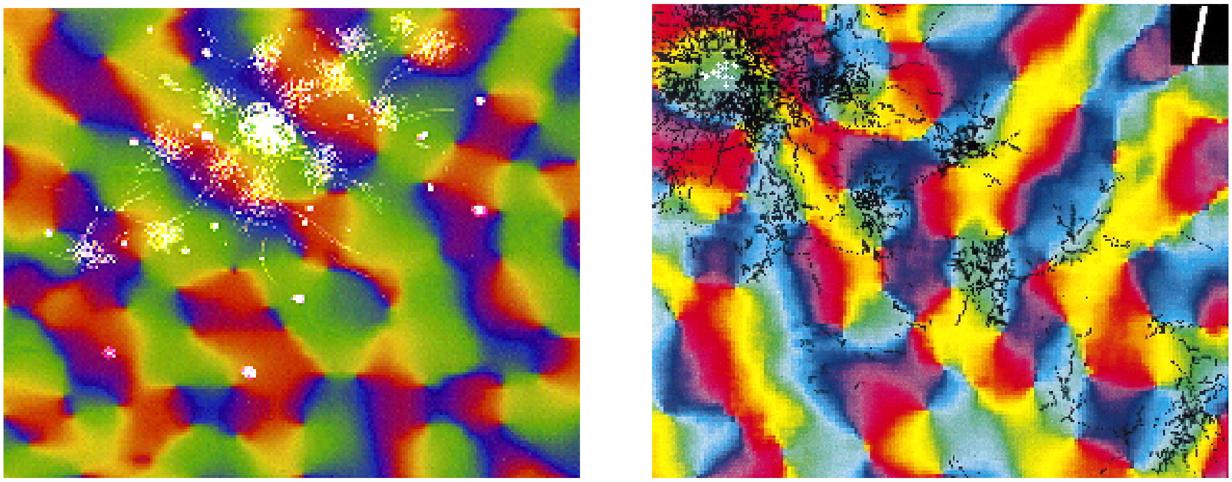


Figure 5: V1 lateral connections: Macaque (left, Blasdel) and Tree Shrew (right, Fitzpatrick)

- Two kinds of coupling: local and lateral

  (a) local: cells $< 1mm$ apart tend to connect equally with most neighbors

  (b) lateral: cells make contact each $mm$ along axons; connections in direction of cell's preference

- Lateral coupling small compared to local coupling

  **Anisotropy in lateral coupling small**

Optical imaging suggests **spatial anisotropy**.
Tree shrew: anisotropy pronounced; major axis of connections parallel to visuotopic axis.
Macaque: most anisotropy is stretching in direction orthogonal to ocular dominance columns

# Action of Euclidean Group

- Euclidean group: rotations, reflections, translations
- Abstract Physical space of V1 is $\mathbf{R}^2 \times \mathbf{S}^1$ — not $\mathbf{R}^2$
  Hypercolumn becomes circle measuring orientation

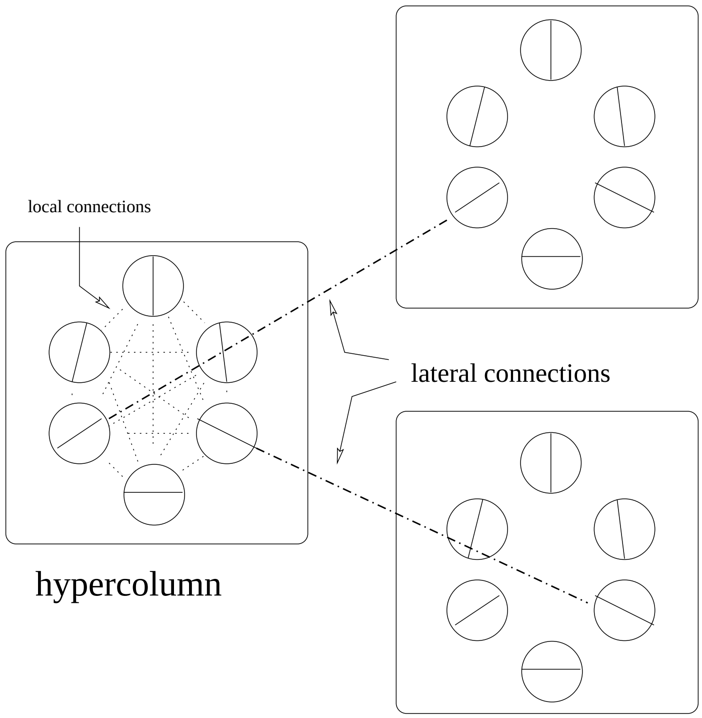



Figure 6: Abstraction of short and **anisotropic** long range connections in V1

- Euclidean groups acts on $\mathbf{R}^2 \times \mathbf{S}^1$ by

$$R_\theta(x, \varphi) = (R_\theta x, \varphi + \theta) \qquad \kappa(x, \varphi) = (\kappa x, -\varphi)$$

$$T_y(x, \varphi) = (T_y x, \varphi)$$

- Different action of $\mathbf{E}(2)$: expect new patterns

# Isotropic Lateral Connections

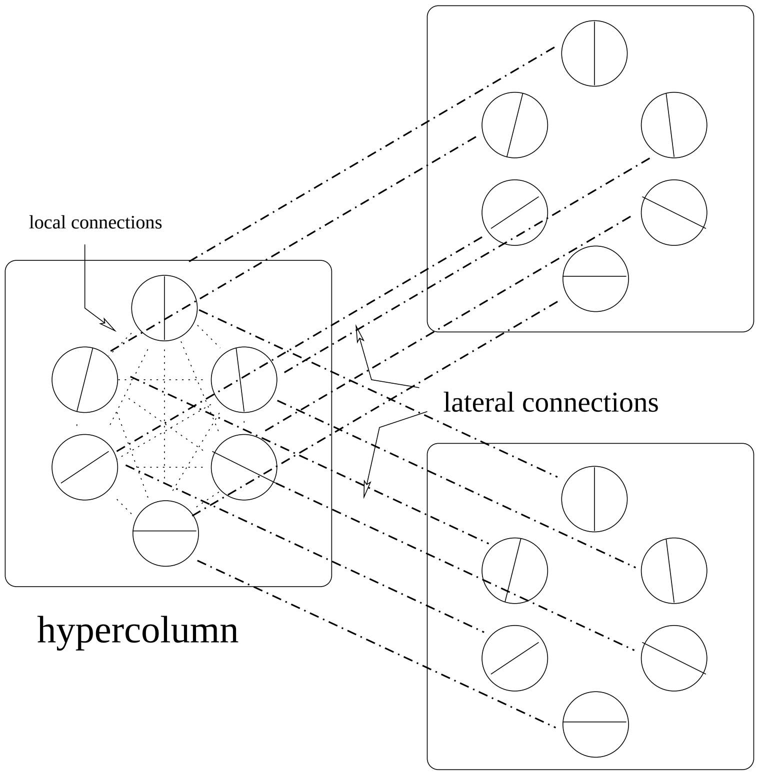



Figure 7: Abstraction of short and **isotropic** long range connections in V1

- Isotropic lateral connections imply **new** $\mathbf{S}^1$ symmetry

$$\hat{\phi}(x,\varphi) = (x, \varphi + \hat{\phi})$$

- Weak anisotropy is forced symmetry breaking of

$$\mathbf{E}(2)\dot{+}\mathbf{S}^1 \longrightarrow \mathbf{E}(2)$$

# Four Models

1. $\mathbf{E}(2)$ acting on $\mathbf{R}^2$ (Ermentrout-Cowan)
   neurons located at each point $x$
   **Funnels and spirals**

2. Shift-twist action of $\mathbf{E}(2)$ on $\mathbf{R}^2 \times \mathbf{S}^1$ (Bressloff-Cowan)
   hypercolumns located at $x$; neurons tuned to $\varphi$
   anisotropic lateral connections
   **Thin line hallucinations: cobwebs**

3. $\mathbf{E}(2) \dot{+} \mathbf{S}^1$ acting on $\mathbf{R}^2 \times \mathbf{S}^1$ (Wolf)
   isotropic lateral coupling
   **Time periodic hallucinations**
   **Rotating spirals and tunneling**

4. Symmetry breaking: $\mathbf{E}(2) \dot{+} \mathbf{S}^1 \to \mathbf{E}(2)$
   weakly anisotropic lateral coupling
   **Pulsations**

# Pattern Formation Outline

1. **Double-Periodicity and Planar Lattices**
   - Translations: **plane waves factors**
   - Reflections: **scalars** and **pseudoscalars**
   - Rotations: **infinite-dimensional** eigenspaces
   - Lattices: back to **finite** dimensions
2. **Bifurcation Theory with Symmetry**
   - Equivariant Branching Lemma
   - **Scalar** and **pseudoscalar** bifurcations
3. **Planforms**
   - Adaptation to **Visual Cortex**
     Line Fields, contours, and thresholding
   - Winner-take-all strategy
   - Cortex to Retina transformation

# Observations Using Symmetry

Bosch Vivancos, Chossat, Melbourne

- Assume differential equations on $\mathbf{R}^2 \times \mathbf{S}^1$ with Euclidean equivariant linearization $\mathsf{L}$

- **TRANSLATIONS** on $\mathbf{R}^2 \times \mathbf{S}^1$ imply

$$W_{\mathbf{k}} = \{u(\varphi)e^{i\mathbf{k}\cdot\mathbf{x}} + \text{c.c} : u : \mathbf{S}^1 \to \mathbf{C}\}$$

  is $\mathsf{L}$-invariant for every dual wave vector $\mathbf{k} \in \mathbf{R}^2$

  – Eigenfunctions have *plane wave* factors

- **REFLECTION** $\rho$ so that $\rho\mathbf{k} = \mathbf{k}$: $\rho : W_{\mathbf{k}} \to W_{\mathbf{k}}$

$$\rho\left(u(\varphi)e^{i\mathbf{k}\cdot\mathbf{x}}\right) = \rho(u(\varphi))e^{i\mathbf{k}\cdot\mathbf{x}}$$

  – $\rho^2 = 1$ implies $W_{\mathbf{k}} = W_{\mathbf{k}}^+ \oplus W_{\mathbf{k}}^-$ where $\rho$ acts as $+1$ on $W_{\mathbf{k}}^+$ and $-1$ on $W_{\mathbf{k}}^-$

  – Eigenfunctions are either **even** or **odd**

  **even** called **scalar** **odd** called **pseudoscalar**

- **ROTATIONS**: $R_\theta(W_{\mathbf{k}}) = W_{R_\theta(\mathbf{k})}$

$$R_\theta\left(u(\varphi)e^{i\mathbf{k}\cdot\mathbf{x}}\right) = R_\theta(u(\varphi))e^{iR_\theta(\mathbf{k})\cdot\mathbf{x}}$$

  – Rotation symmetry implies $\ker L$ is $\infty$-dimensional

# Planar Lattices

- **Double-periodicity**: Look for solns on lattice $\mathcal{L}$

$$\mathcal{F}_{\mathcal{L}} = \{f \in \mathcal{F} : f(\mathbf{x} + \boldsymbol{\ell}) = f(\mathbf{x}) \quad \forall \boldsymbol{\ell} \in \mathcal{L}\}$$

- Finite number of rotations: $\ker \mathsf{L}$ is finite-dimensional

- Choose lattice size so shortest dual vectors are critical

- Translations leave $\mathcal{F}_{\mathcal{L}}$ invariant
  $\mathbf{T}^2 = \mathbf{R}^2/\mathcal{L}$ is effective action of translations

- **Holohedry** $H_{\mathcal{L}} \subset \mathbf{O}(2)$ is group that preserves $\mathcal{L}$
  $H_{\mathcal{L}}$ leaves space $\mathcal{F}_{\mathcal{L}}$ invariant

- $\Gamma_{\mathcal{L}} = H_{\mathcal{L}} \dot{+} \mathbf{T}^2$ is group of symmetries

- **Two dispersion curves**: scalar and pseudoscalar

- The smallest $k^* = |\mathbf{k}|$ for which there is an eigenfunction is called the **critical wave number**
  Find $k^*$ using dispersion curves

# Equivariant Bifurcation Theory

- Symmetry group $\Gamma$: $\quad f(\gamma x) = \gamma f(x)$

- $\mathrm{Fix}(\Sigma) = \{x \in \mathbf{R}^n : \sigma x = x \quad \forall \sigma \in \Sigma\}$

- $\mathrm{Fix}(\Sigma)$ is flow invariant
  Proof: $f(x) = f(\sigma x) = \sigma f(x)$

## The Equivariant Branching Lemma

- Isotropy subgroup $\Sigma \subset \Gamma$ is *axial* if

$$\dim \mathrm{Fix}(\Sigma) = 1$$

  on critical eigenspace

- **Generically, there exists a branch of solutions with $\Sigma$ symmetry for every axial subgroup $\Sigma$**

# Planforms For Ermentrout-Cowan

**Square lattice**: Two axial subgroups of $\mathbf{T}^2\dot{+}\mathbf{D}_4$
$\mathbf{O}(2) \oplus \mathbf{Z}_2$ *stripes* and $\mathbf{D}_4$ *squares*

**Hexagonal lattice**: Two axial subgroups of $\mathbf{T}^2\dot{+}\mathbf{D}_6$
$\mathbf{O}(2) \oplus \mathbf{Z}_2$ *stripes* and $\mathbf{D}_6$ *hexagons*

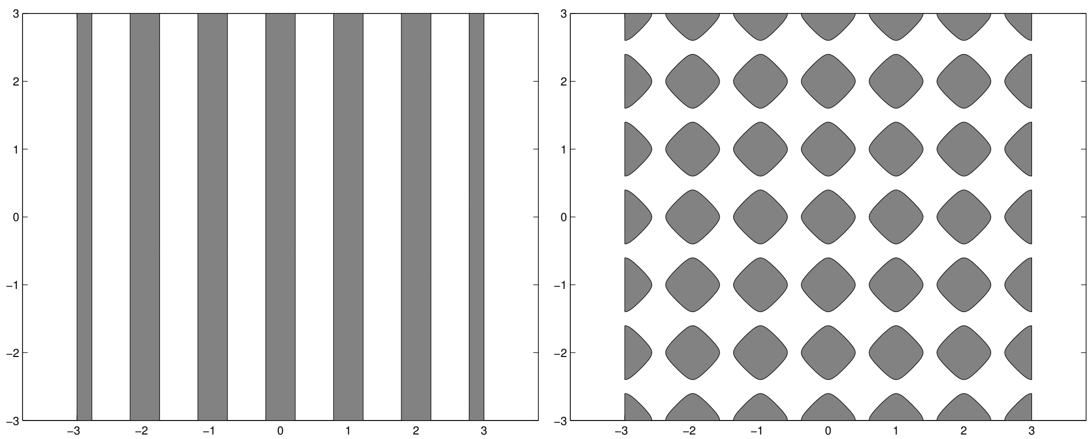


Figure 8: Thresholding of axial eigenfunctions: (left) *stripes*; (right) *squares*

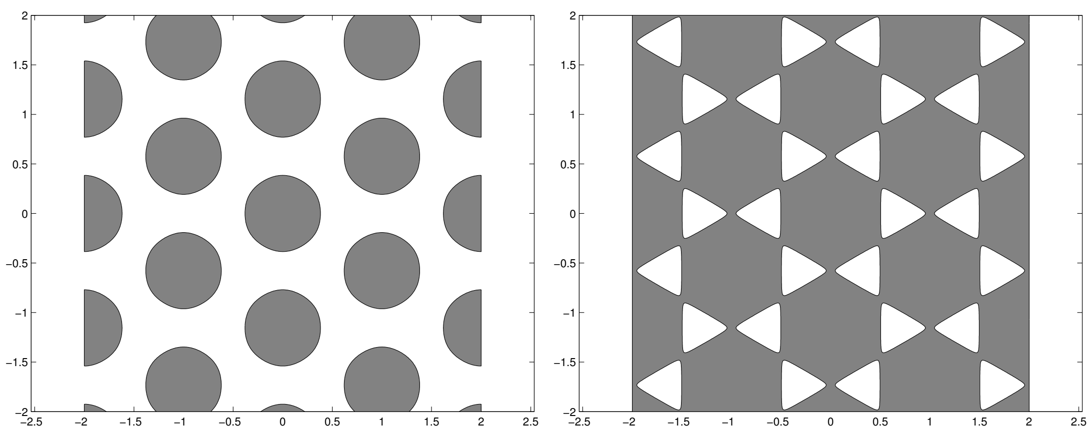


Figure 9: Thresholding of axial eigenfunction *hexagons*

# Adaptations for Orientation Tuned Cortex

- Study nonoriented directions: $u(\mathbf{x}, \varphi + \pi) = u(\mathbf{x}, \varphi)$

- Two dispersion curves: one for even and one for odd

$\boxed{\text{even} = \text{scalar action} \qquad \text{odd} = \text{pseudoscalar action}}$

Both representations occur in reasonable models

| Name | Axial | Planform Eigenfunction |
|---|---|---|
| squares | $\mathbf{D}_4$ | $u(\varphi)\cos x + u\left(\varphi - \frac{\pi}{2}\right)\cos y$ |
| stripes | $\mathbf{O}(2) \oplus \mathbf{D}_1$ | $u(\varphi)\cos x$ |
| hexagons | $\mathbf{D}_6$ | $\sum_{j=0}^{2} u\left(\varphi - j\pi/3\right)\cos(\mathbf{k}_j \cdot \mathbf{x})$ |
| stripes | $\mathbf{O}(2) \oplus \mathbf{D}_1$ | $u(\varphi)\cos(\mathbf{k}_1 \cdot \mathbf{x})$ |

Table 1: Axial planforms when $u(\varphi) = u(-\varphi)$ is even.

| Name | Axial | Planform Eigenfunction |
|---|---|---|
| square | $\mathbf{D}_4^*$ | $u(\varphi)\cos x - u\left(\varphi - \frac{\pi}{2}\right)\cos y$ |
| stripes | $\mathbf{O}(2) \oplus \mathbf{D}_1^*$ | $u(\varphi)\cos x$ |
| hexagons | $\mathbf{Z}_6$ | $\sum_{j=0}^{2} u\left(\varphi - j\pi/3\right)\cos(\mathbf{k}_j \cdot \mathbf{x})$ |
| triangles | $\mathbf{D}_3$ | $\sum_{j=0}^{2} u\left(\varphi - j\pi/3\right)\sin(\mathbf{k}_j \cdot \mathbf{x})$ |
| rectangles | $\mathbf{D}_2$ | $u\left(\varphi - \frac{\pi}{3}\right)\cos(\mathbf{k}_2 \cdot \mathbf{x}) - u\left(\varphi + \frac{\pi}{3}\right)\cos(\mathbf{k}_3 \cdot \mathbf{x})$ |
| stripes | $\mathbf{O}(2) \oplus \mathbf{D}_1^*$ | $u(\varphi)\cos(\mathbf{k}_1 \cdot \mathbf{x})$ |

Table 2: Axial planforms when $u(\varphi) = -u(-\varphi)$ is odd. $^*$ = glide reflection

# Winner-Take-All Strategy
## Creation of Line Fields

- Given: Activity of neuron in hypercolumn at $\mathbf{x}$ sensitive to direction $\varphi$

- Assumption: Most active neuron in hypercolumn suppresses other neurons in hypercolumn

- Consequence: For all $\mathbf{x}$ find $\varphi_{\mathbf{x}} \in \mathbf{S}^1$ where activity is maximum

- Planform: Draw small line segment at $\mathbf{x}$ oriented at angle $\varphi_{\mathbf{x}}$

# How to Find Amplitude Function $u(\varphi)$

- Isotropic connections imply EXTRA $\mathbf{S}^1$ symmetry
- $\mathbf{S}^1$ decomposes $W_{\mathbf{k}}$ into sum of irreducible subspaces

$$W_{\mathbf{k},p} = \{ z e^{p\varphi i} e^{2\pi i \mathbf{k}\cdot x} + \text{c.c.} : z \in \mathbf{C} \} \cong \mathbf{R}^2$$

  Generically, eigenfunctions of $\mathsf{L}$ lie in $W_{\mathbf{k},p}$ for some $p$

- $W^+_{\mathbf{k},p} = \{ \cos(p\varphi) e^{2\pi i \mathbf{k}\cdot x} \}$ scalar case
  $W^-_{\mathbf{k},p} = \{ \sin(p\varphi) e^{2\pi i \mathbf{k}\cdot x} \}$ pseudoscalar case
- Wilson-Cowan models lead to
  $p = 0$ or $p = 1$ bifurcations in scalar case
  $p = 1$ bifurcations in pseudoscalar case
- Compute pictures in $p = 1$ cases

$$u(\varphi) \approx \cos(\varphi) \text{ and } u(\varphi) \approx \sin(\varphi)$$

# Cortex to Retina

- Neurons on cortex are uniformly distributed
- Neurons in retina fall off by $1/r^2$ from fovea
- Unique conformal map takes uniform density square to $1/r^2$ density disk: complex exponential
- Cortex to retinal map is

$$\begin{aligned} r &= \omega \exp(\epsilon x) \\ \theta &= \epsilon y \end{aligned}$$

  In retinal images we take

$$\omega = 30/e^{2\pi} \quad \text{and} \quad \epsilon = 2\pi/n_h$$

  where $n_h = 36 = \#$ hypercolumn widths in cortex

- Straight lines on cortex $\mapsto$ circles, logarithmic spirals, and rays in retina

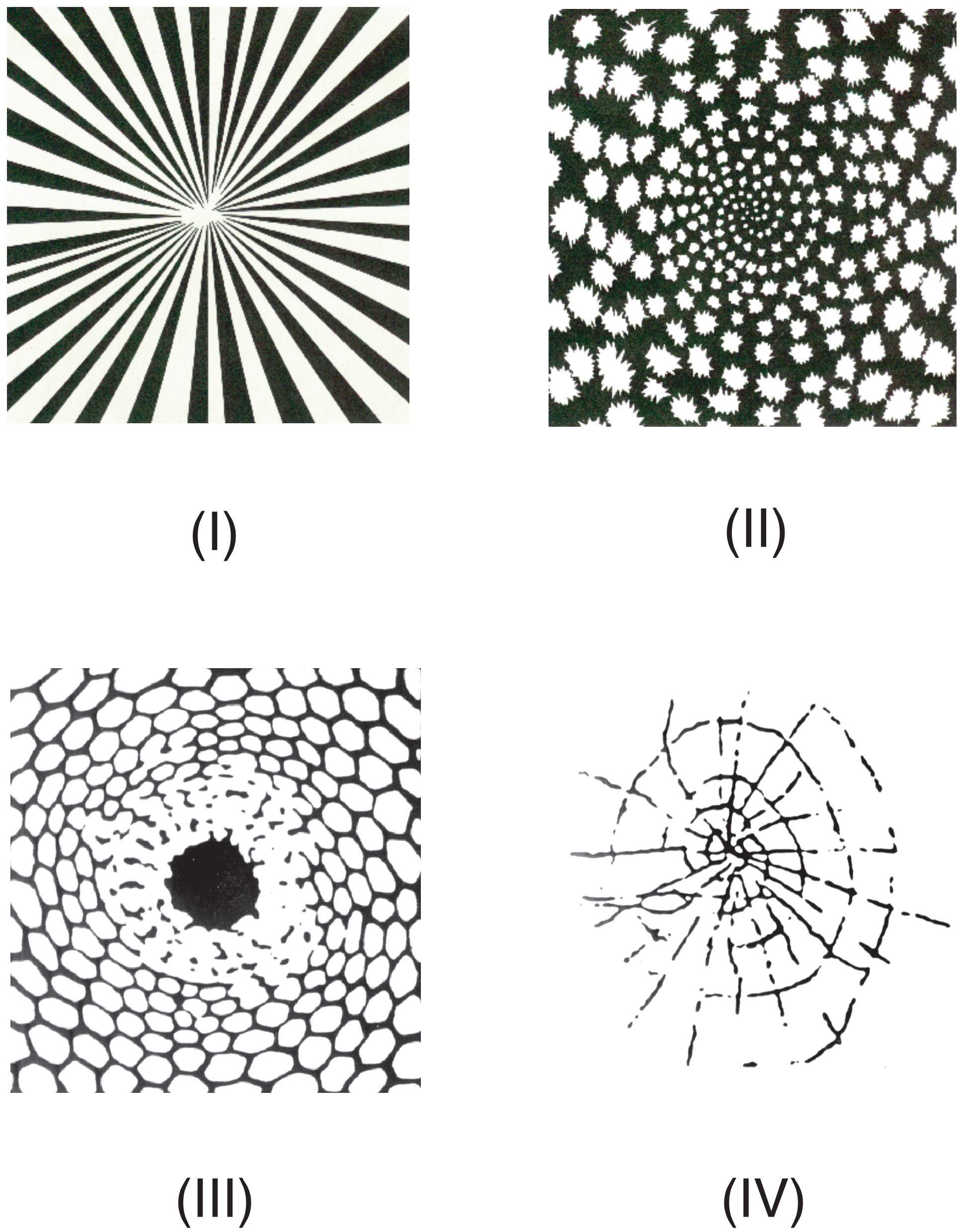
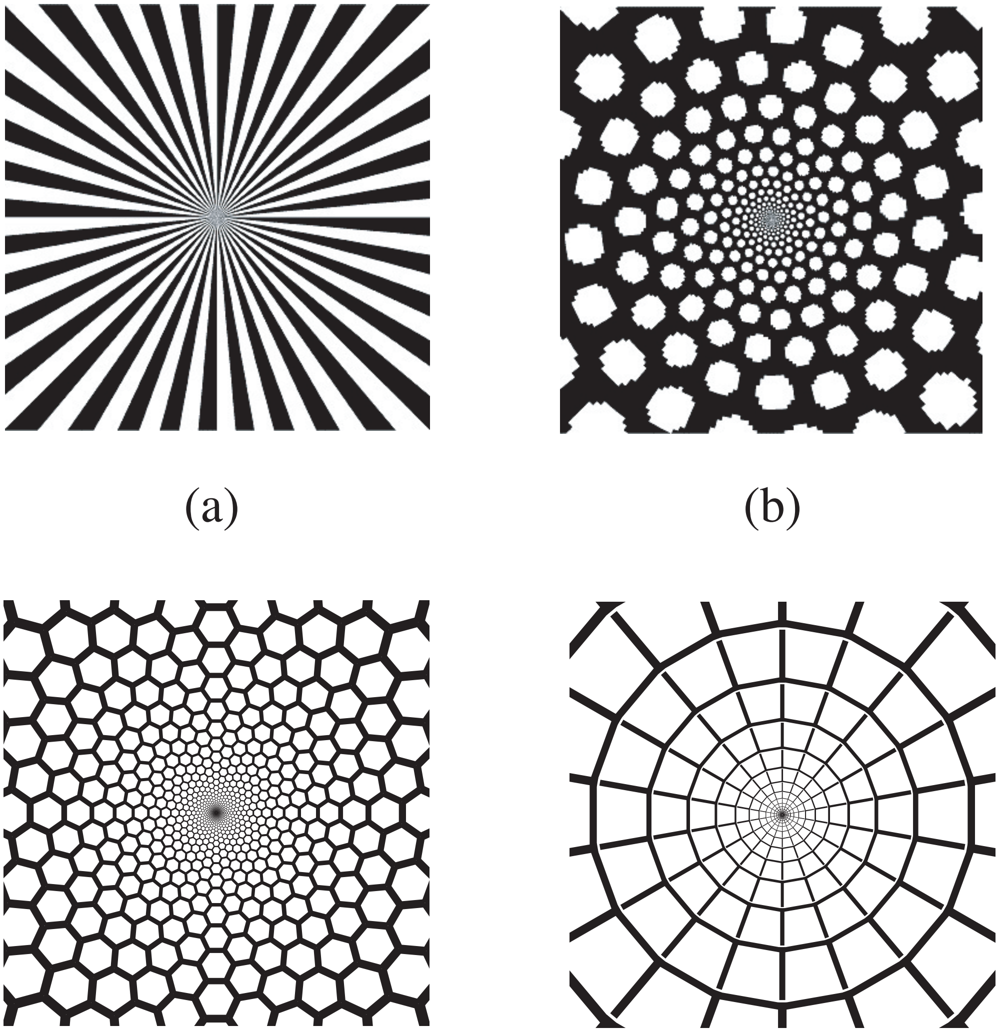



Figure 10: Hallucinatory form constants. (I) funnel and (II) spiral images seen following ingestion of LSD [Siegel & Jarvik, 1975], (III) honeycomb generated by marihuana [Clottes & Lewis-Williams (1998)], (IV) cobweb petroglyph [Patterson, 1992].

# Planforms in the Visual Field




Visual field planforms

## Isotropic Coupling: Additional $\mathbf{S}^1$ symmetry

- $\widehat{\varphi}(\mathbf{x}, \varphi) = (\mathbf{x}, \varphi + \widehat{\varphi})$

- Eigenspaces: sum of even and odd

- Square lattice:
  four axials
  one maximal subgroup with 2D fixed-point subspace

- Hexagonal lattice:
  Nine axials
  three maximal subgroups with 2D fixed-pt subspaces

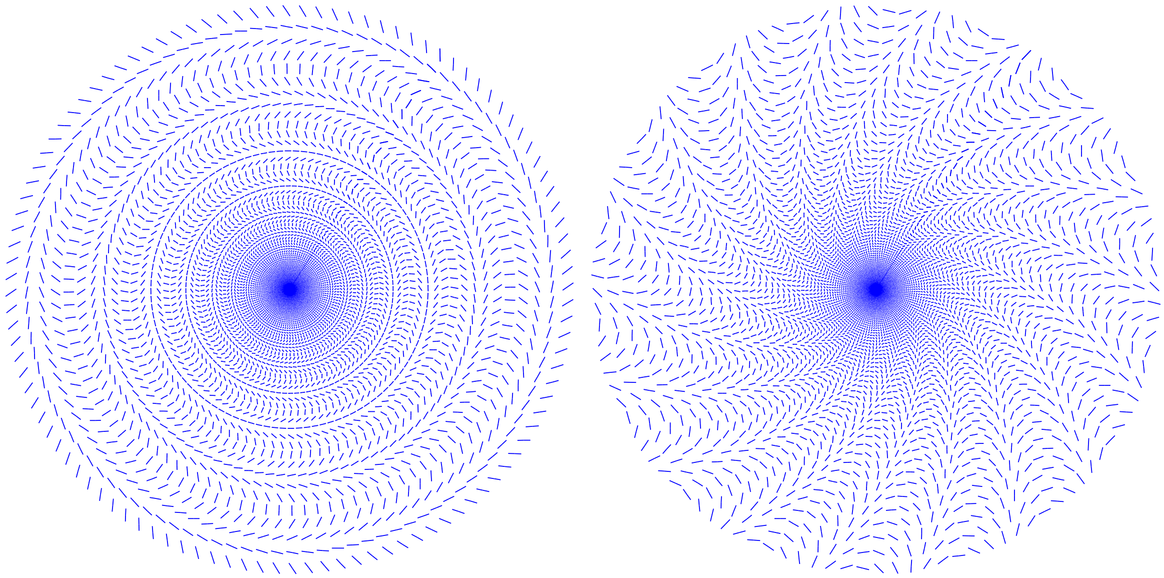


Figure 11: (Top) Conjugate solutions (7)

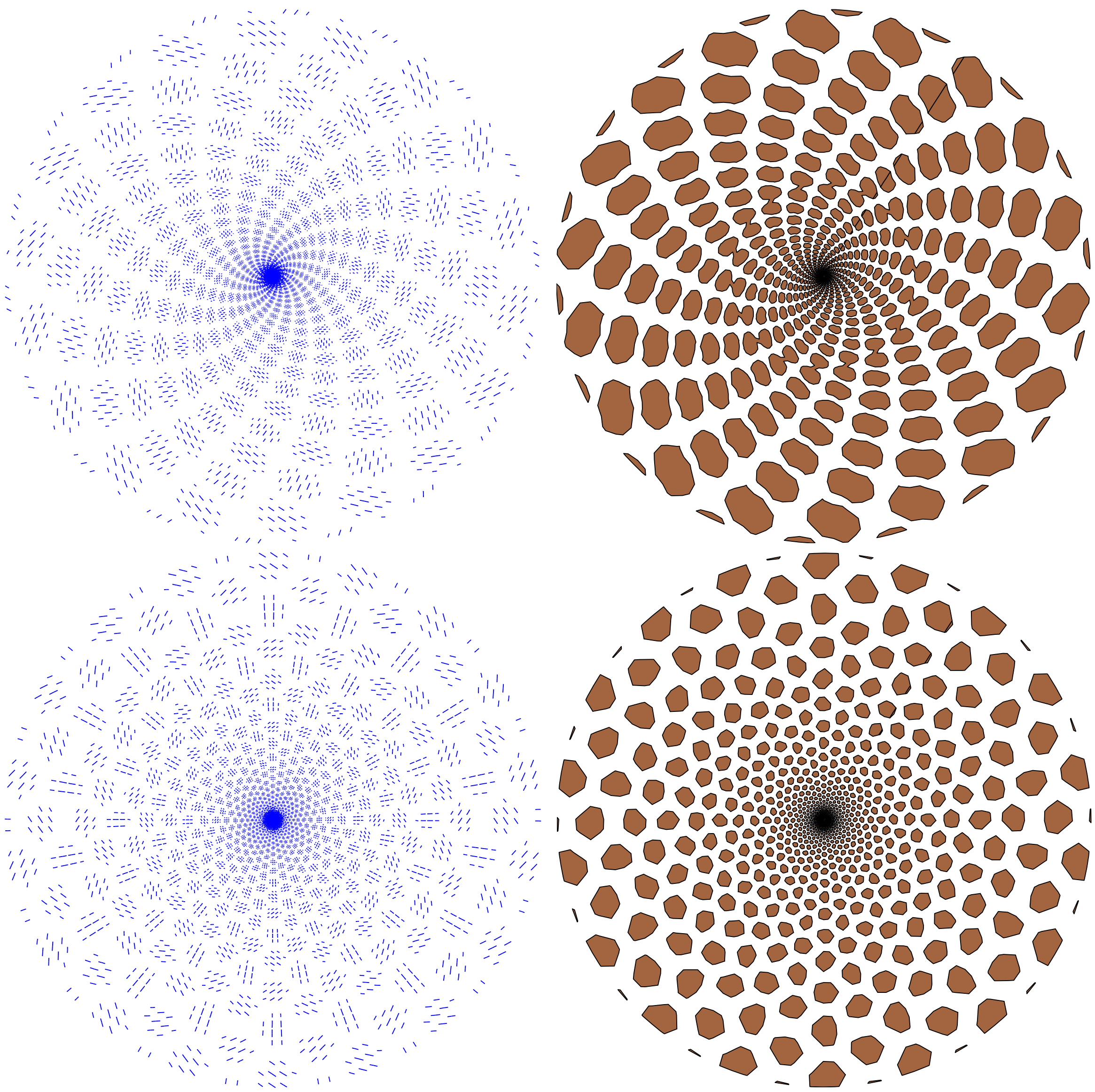


Figure 12: Phosphene-like planforms: (top) planform (12); (bottom) planform (9)

# Weakly Anisotropic Coupling

- Square lattice: Forced symmetry-breaking to
  1. scalar and pseudoscalar stripes
  2. scalar and pseudoscalar squares
  3. two new equilibrium planforms
  4. a time-periodic rotating wave

- Hexagonal lattice: Forced symmetry-breaking to
  1. seven types of equilibia
  2. two contracting or expanding periodic states
  3. two rotating waves
  4. state that is an equilibrium or time-periodic