Pattern Formation and Symmetry in the Visual Cortex

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> 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

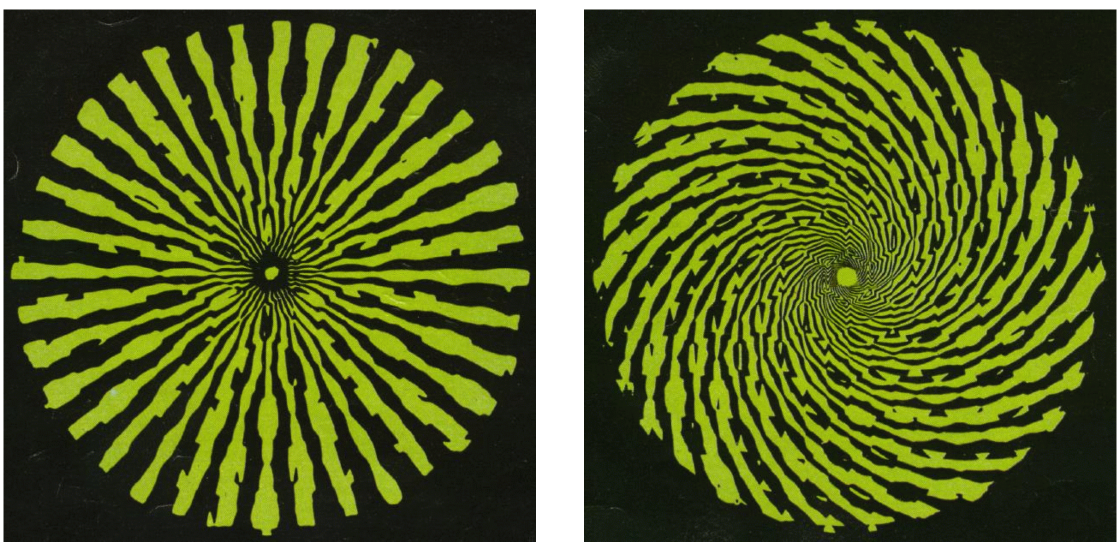


Figure 1: Funnels and spirals (G. Oster, *Scientific American*, 1970

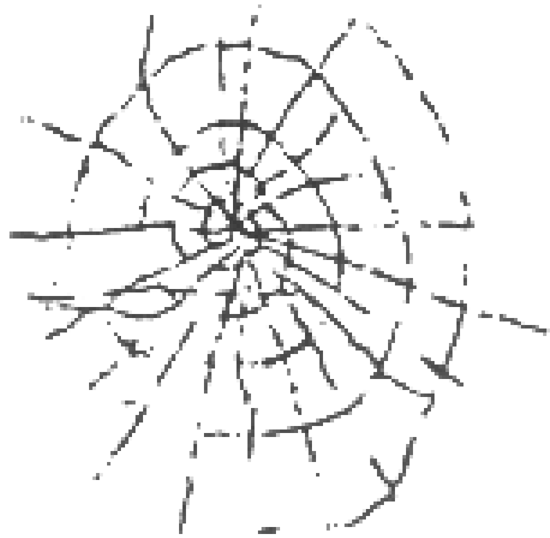


Figure 2: Cobweb (Patterson, 1992).

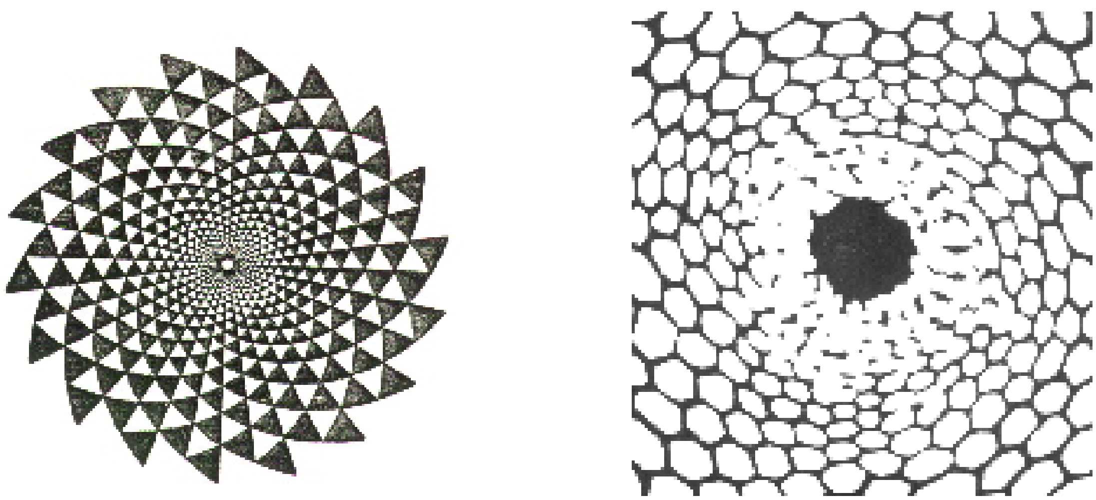


Figure 3: (Left) Phosphene produced by deep binocular pressure on eyeballs; (Right) Honeycomb generated by marihuana

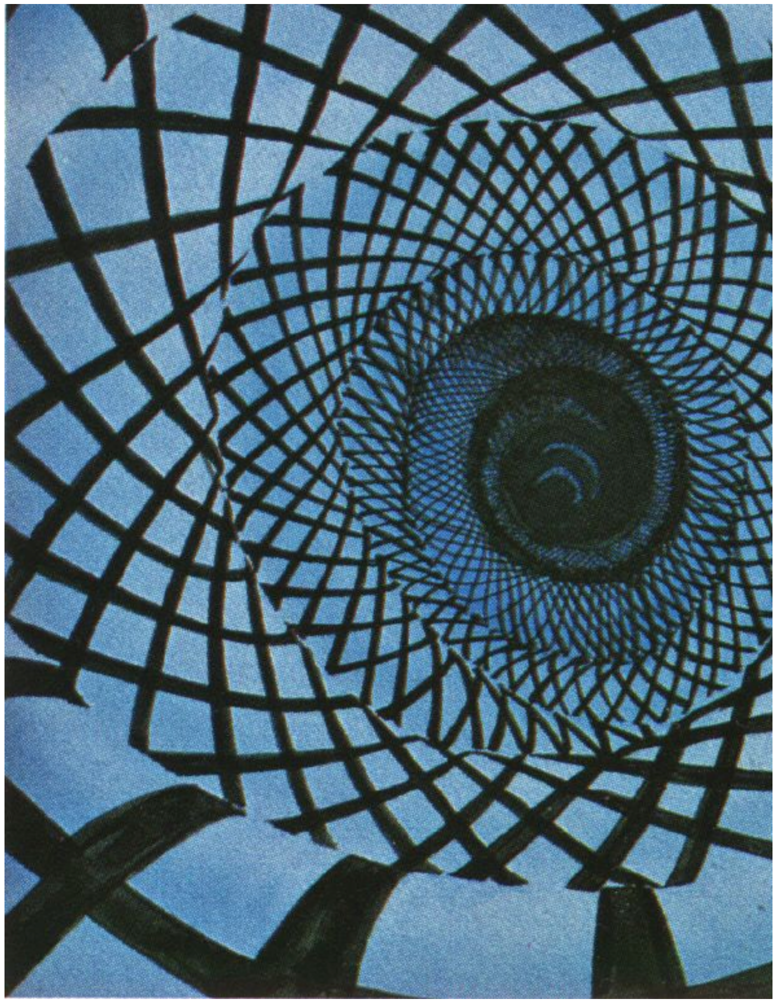


Figure 4: Lattice-tunnel generated by marihuana (Hall)

Orientation Sensitivity of Cells in V1

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

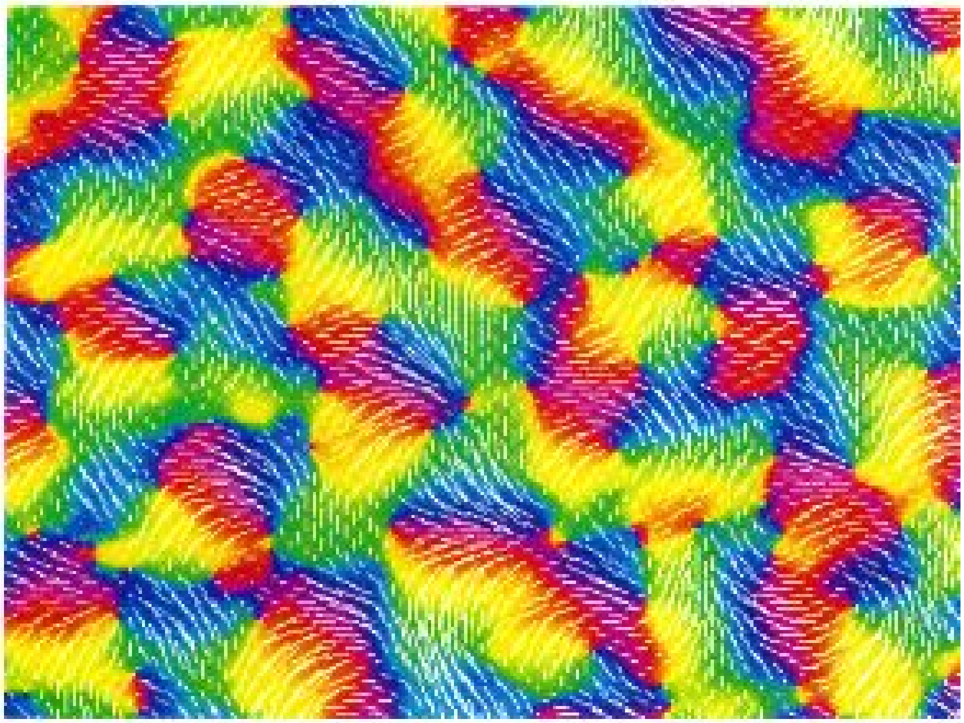


Figure 5: Distribution of orientation preferences in Macaque V1 (Blasdel)

- 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

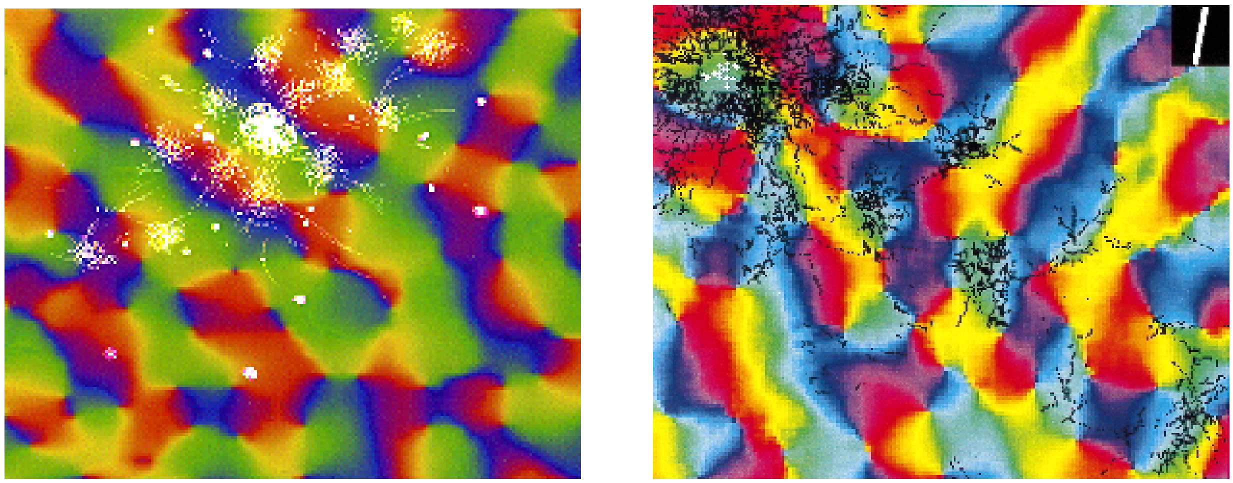


Figure 6: V1 lateral connections: Macaque (left, Blasdel) and Tree Shrew (right, Fitzpatrick)

- Two kinds of coupling: local and lateral

  (a) local: cells $< 1mm$ connect 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
Macaque: most anisotropy due to stretching in direction orthogonal to ocular dominance columns

Action of Euclidean Group

- Euclidean group: rotations, reflections, translations
- Many differential equations are Euclidean invariant
  Similarity of pattern formation due to symmetry
- Abstract physical space of V1 is $\mathbf{R}^2 \times \mathbf{S}^1$ — not $\mathbf{R}^2$
  Hypercolumn becomes circle measuring orientation

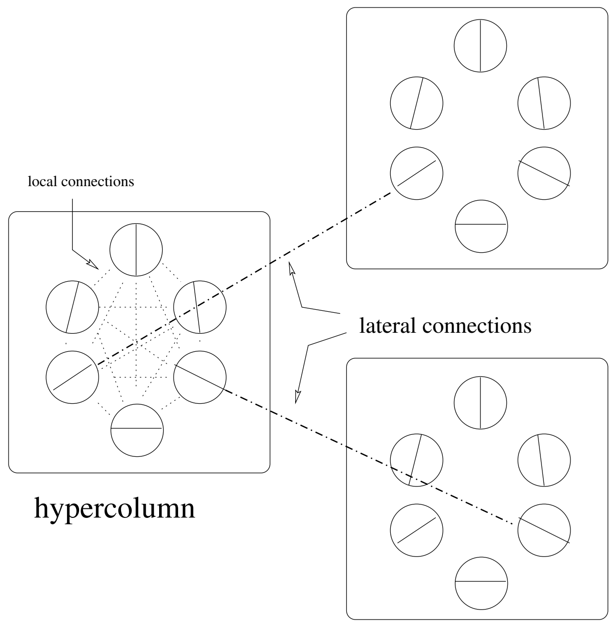


Figure 7: Abstraction of local and **anisotropic** lateral connections in V1

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

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

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

Isotropic Lateral Connections

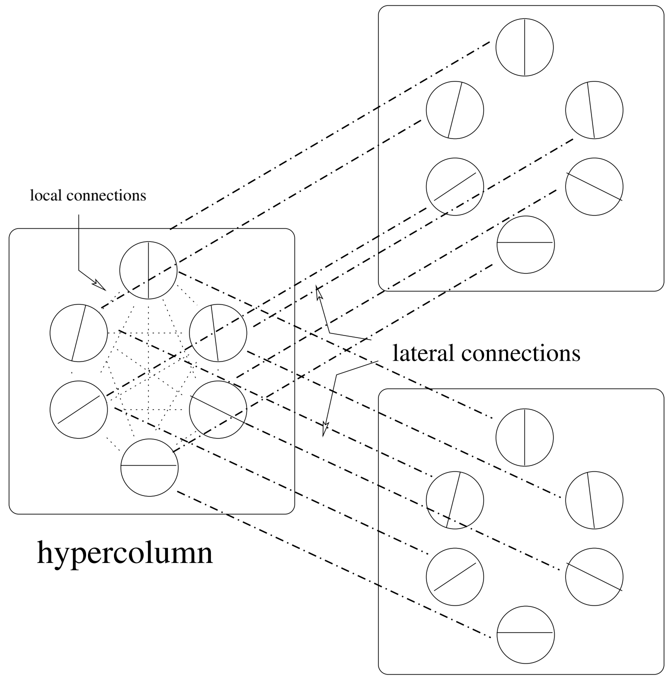


Figure 8: Abstraction of local and **isotropic** lateral connections in V1

- Isotropic lateral connections introduce **new O**(2) symmetry

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

- Weak anisotropy is forced symmetry breaking of

$$\mathbf{E}(2) \dot{+} \mathbf{O}(2) \rightarrow \mathbf{E}(2)$$

Four Models

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

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 φ
   anisotropic lateral connections

3. $\mathbf{E}(2)\dot{+}\mathbf{O}(2)$ acting on $\mathbf{R}^2 \times \mathbf{S}^1$ (Wolf)
   isotropic lateral coupling

4. Symmetry breaking: $\mathbf{E}(2)\dot{+}\mathbf{O}(2) \to \mathbf{E}(2)$
   weakly anisotropic lateral coupling

Pattern Formation Outline

1. **Double-Periodicity and Planar Lattices**
   - Translations: **plane waves**
   - Reflections: **even** and **odd** representations
   - 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 system of differential equations on $\mathbf{R}^2 \times \mathbf{S}^1$ with Euclidean equivariant linearization L

$$\mathsf{L}\gamma = \gamma\mathsf{L} \qquad \forall\gamma \in \mathbf{E}(2)$$

- Planforms are approximated by eigenfunctions of L
  Symmetry dictates eigenfunctions

- **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 L-invariant subspace for every dual wave vector

$$\mathbf{k} \in \mathbf{R}^2$$

- Eigenfunctions have *plane wave* factors

$$u(\varphi)e^{i\mathbf{k}\cdot\mathbf{x}} + \text{c.c.}$$

Action of Reflections

- Choose **REFLECTION** ρ so that $\rho\mathbf{k} = \mathbf{k}$

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

  So $\rho : W_{\mathbf{k}} \longrightarrow W_{\mathbf{k}}$

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

- Eigenfunctions are **even** or **odd**. When $\mathbf{k} = (1, 0)$

$$\begin{aligned} u(-\varphi) &= u(\varphi) & u \in W_{\mathbf{k}}^+ \\ u(-\varphi) &= -u(\varphi) & u \in W_{\mathbf{k}}^- \end{aligned}$$

- Both kinds of eigenfunctions occur in models

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

Action of Rotations

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

Therefore

$$R_\theta(W_{\mathbf{k}}) = W_{R_\theta(\mathbf{k})}$$

- Rotation symmetry implies $\ker L$ is ∞-dimensional

Planar Lattices

- **Double-periodicity**: Look for solns on lattice
- The space of *doubly periodic* functions w.r.t $\mathcal{L}$ is

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

- Finite number of rotations: $\ker \mathsf{L}$ is finite-dimensional
- Choose lattice size so shortest dual vectors are critical

Equivariant Bifurcation Theory

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

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

- Fix(Σ) 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 Σ symmetry for every axial subgroup Σ**

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*

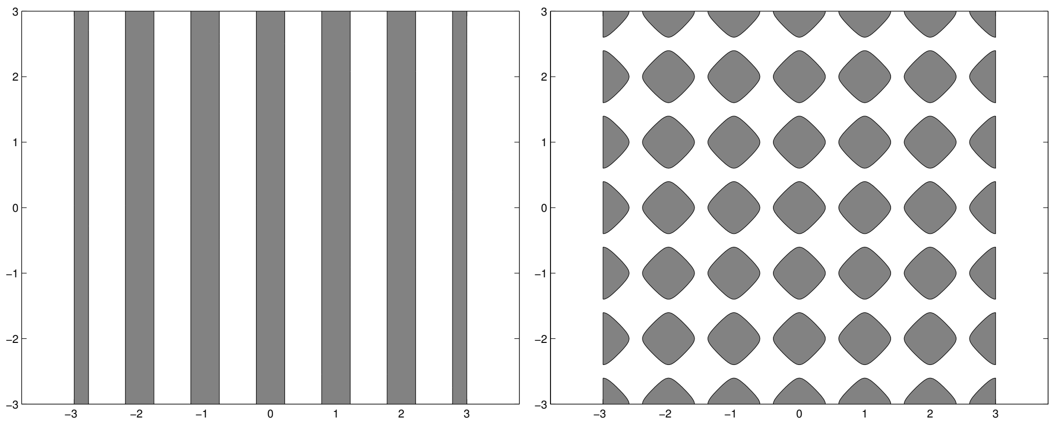


Figure 9: Thresholding of axial eigenfunctions: (left) *stripes*; (right) *squares*

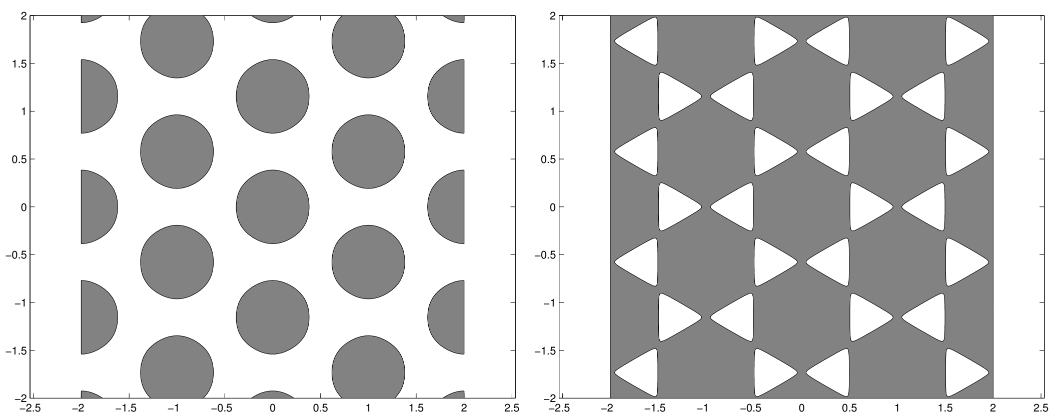


Figure 10: Thresholding of axial eigenfunction *hexagons*

Axial Subgroups in Orientation Tuned 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

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

- Isotropic connections imply EXTRA $\mathbf{O}(2)$ symmetry

- $\mathbf{O}(2)$ decomposes $W_{\mathbf{k}}$ into sum of irreducible subspaces

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

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

- $W^{+}_{\mathbf{k},p} = \{\cos(p\varphi) e^{i\mathbf{k}\cdot x}\}$ even case
  $W^{-}_{\mathbf{k},p} = \{\sin(p\varphi) e^{i\mathbf{k}\cdot x}\}$ odd case

- Wilson-Cowan models lead to
  $p = 0$ or $p = 1$ bifurcations in even case
  $p = 1$ bifurcations in odd case

- Compute pictures in $p = 1$ cases

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

Winner-Take-All Strategy
Creation of Line Fields

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

- 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 $\varphi_{\mathbf{x}}$

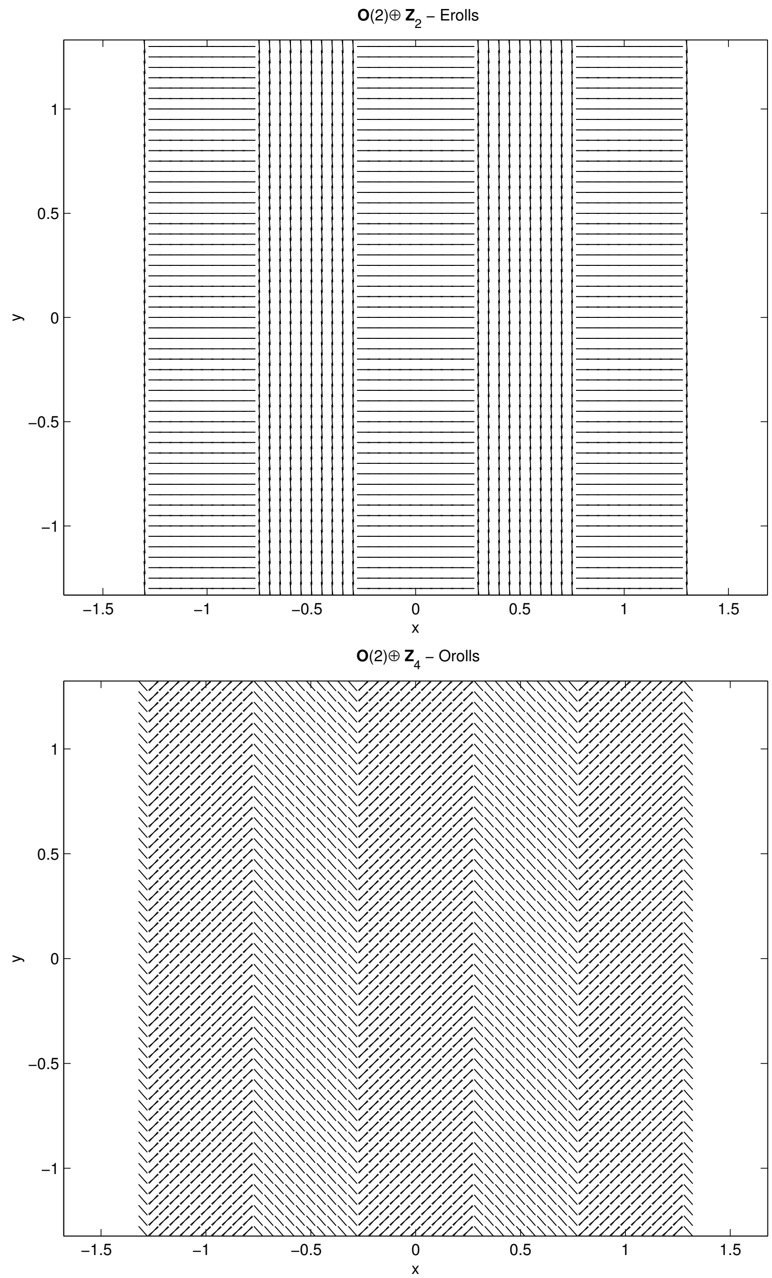


Figure 11: Even Stripes (upper); odd Stripes (lower)

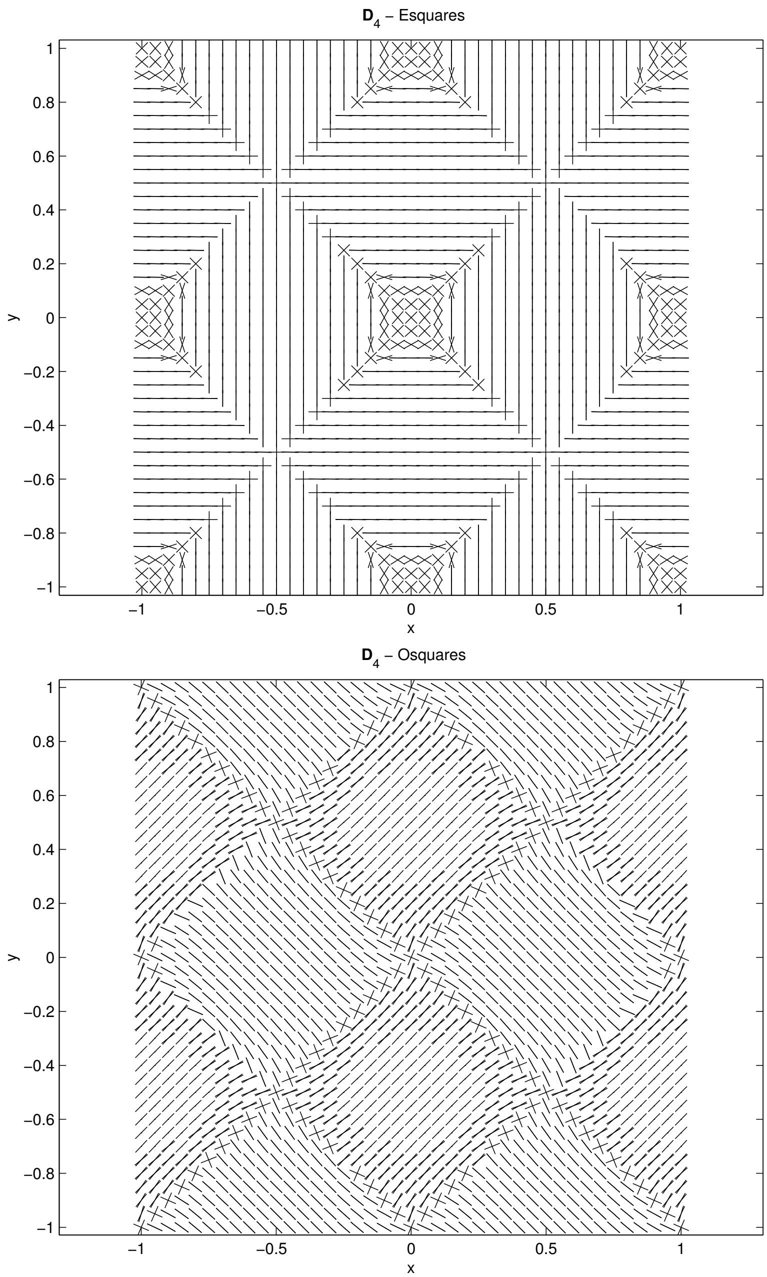


Figure 12: Even Squares (upper); odd Squares (lower)

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

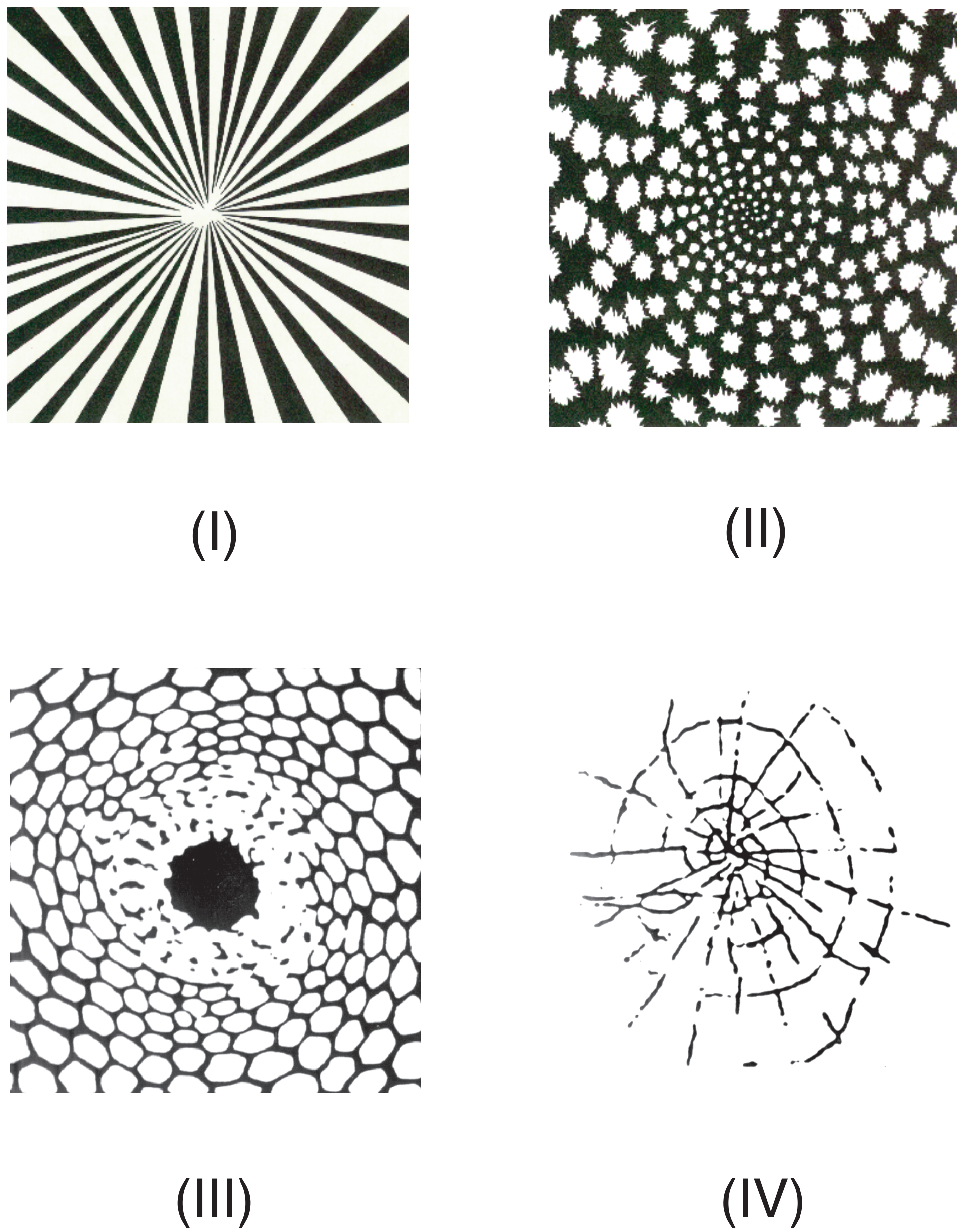
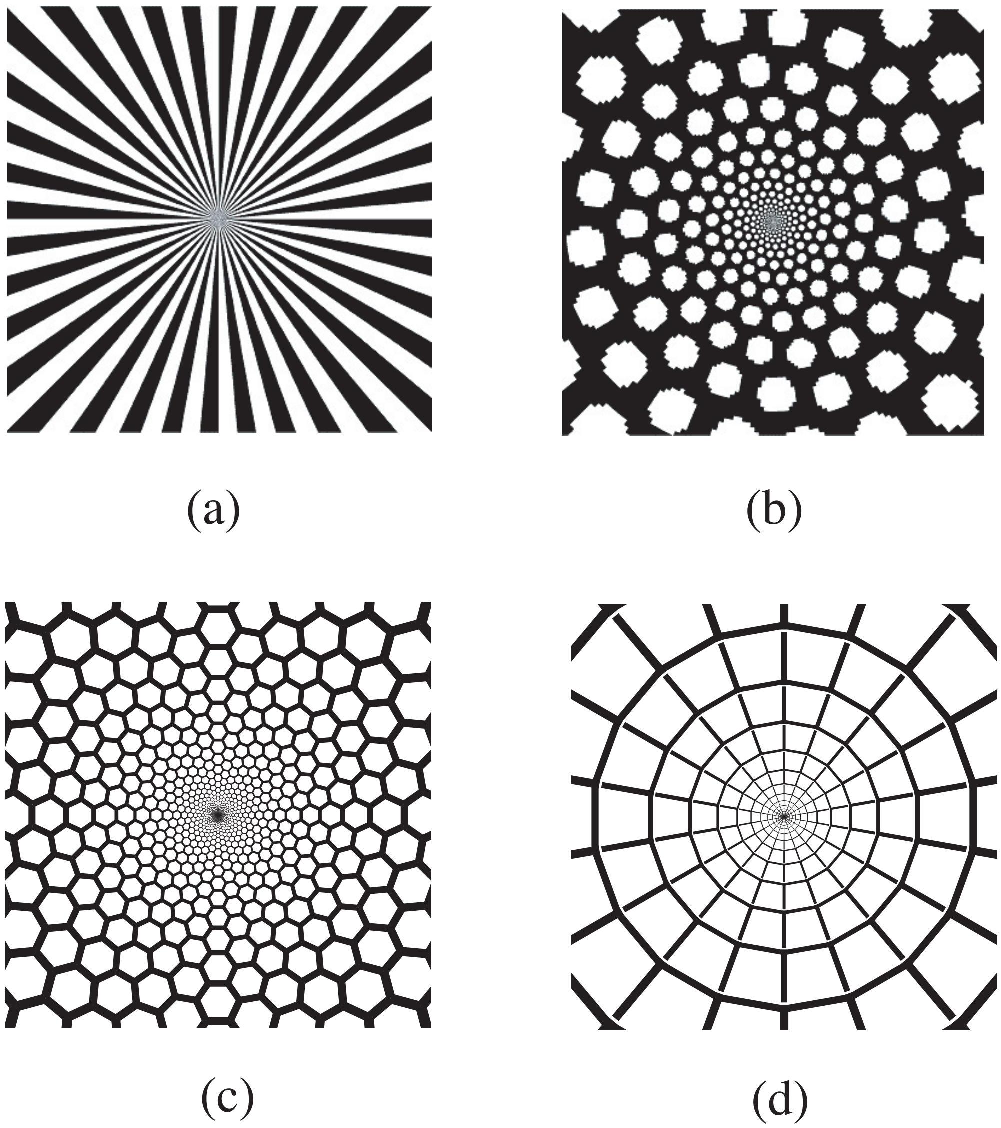


Figure 13: Hallucinatory form constants. (I) funnel and (II) spiral images seen following ingestion of LSD [Siegel & Jarvik, 1975], (III) honeycomb generated by marihuana [Clottes & Lewis-Williams (1998)], (IV) cobweb petroglyph [Patterson, 1992].

Planforms in the Visual Field



Visual field planforms

Isotropic Coupling: Extra $\mathbf{O}(2)$ 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

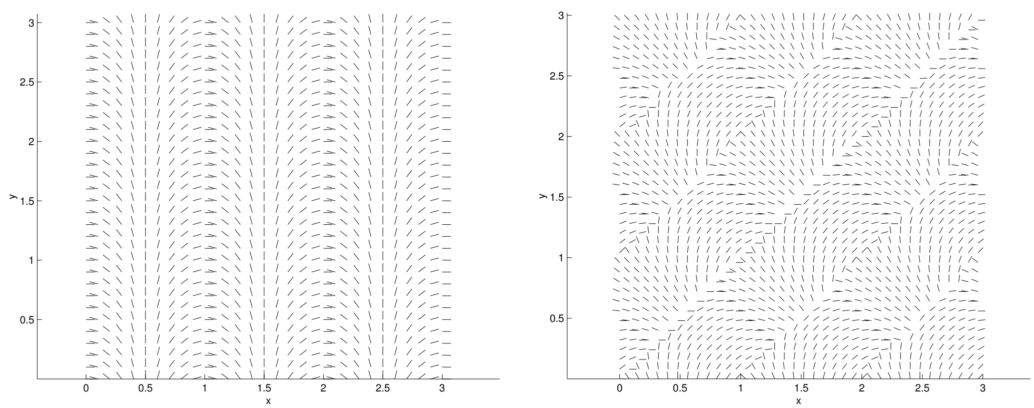
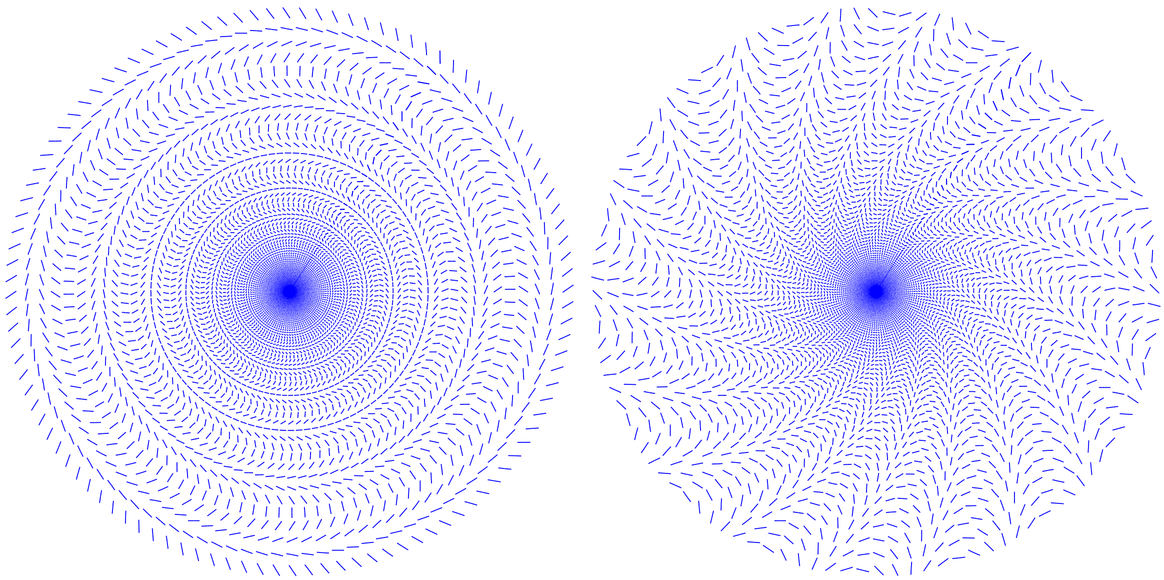


Figure 14: Direction fields of new planforms in isotropic model.

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



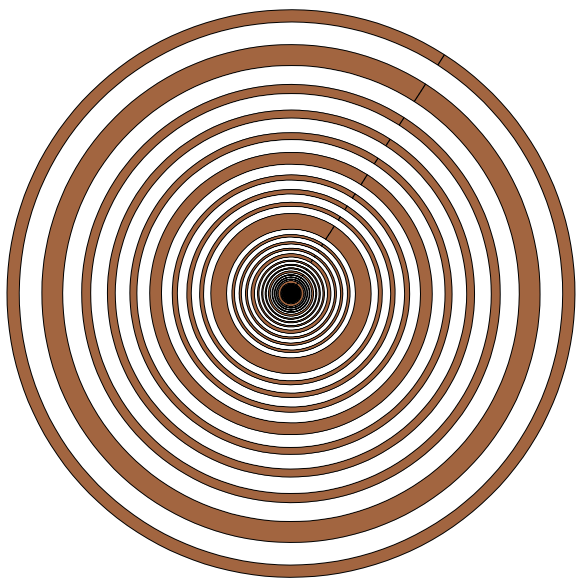


Figure 15: (Top) Conjugate solutions (7); (bottom) threshold.

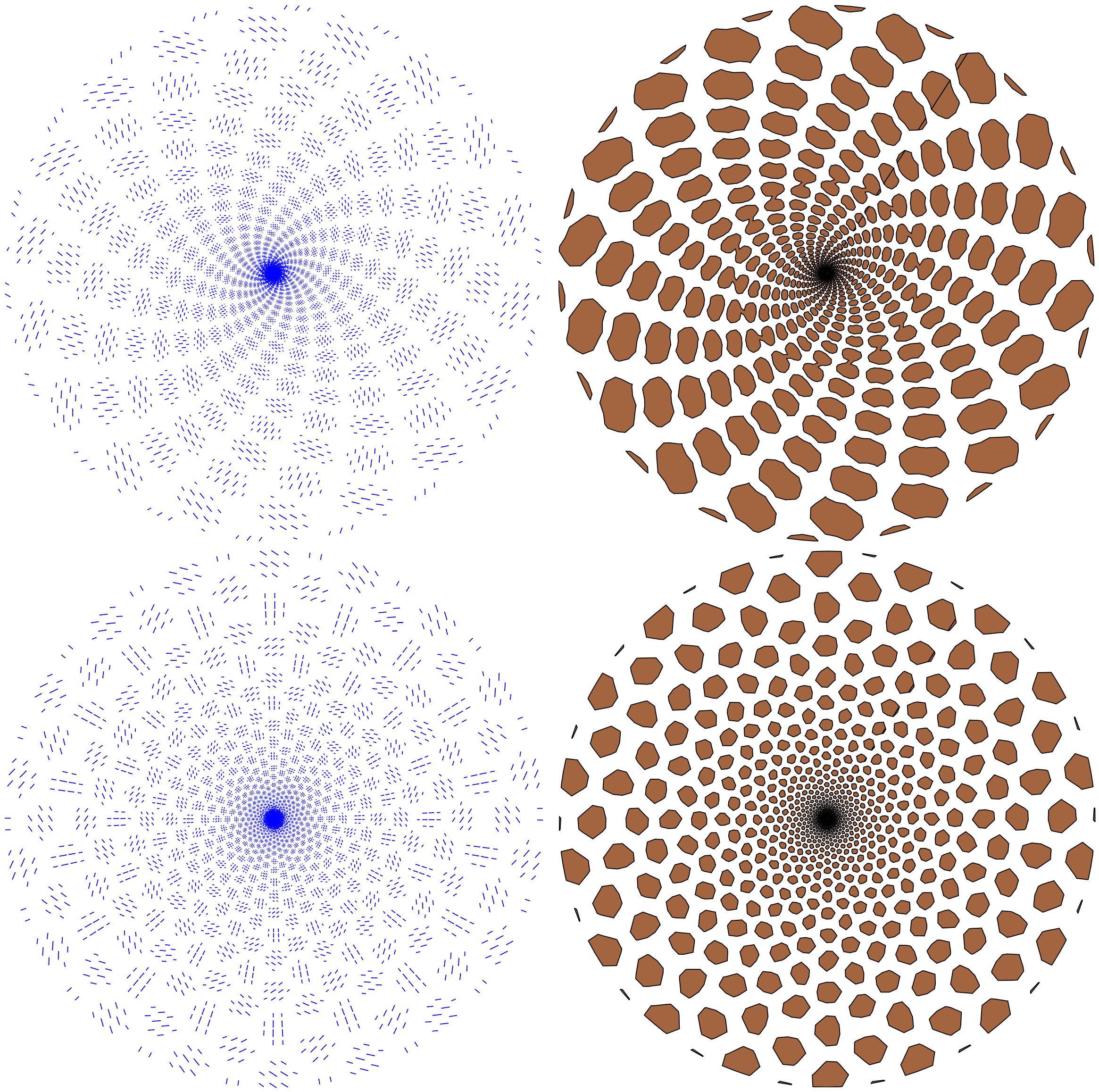


Figure 16: Phosphene-like planforms: (top) planform (12); (bottom) planform (9)

Weakly Anisotropic Coupling

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

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

Landau Theory of Phase Transitions for a Liquid Crystal

- nematic phase

  preferred direction along which molecules align

- Alignment of molecules represented by

  3×3 symmetric trace zero matrices $Q(x)$

- Molecule at x aligns along eigendirection of $Q(x)$ corresponding to largest eigenvalue

- Q is second moment of probability distribution for alignment of rod-like molecule

- Action of $\mathbf{E}(3)$: Let $\gamma \in \mathbf{O}(3)$ and $y \in \mathbf{R}^3$

$$
\begin{aligned}
(T_y Q)(x) &= Q(x - y) \\
(\gamma \cdot Q)(x) &= \gamma Q(\gamma^{-1} x) \gamma^{-1}
\end{aligned}
$$

Scalar and Pseudoscalar Eigenspaces

Chillingworth and Golubitsky

- Spatially uniform liquid crystal: Q independent of x
  homeotropic — all molecules aligned in one direction
  isotropic — equally likely to align in any direction

- Bifurcation from Euclidean invariant Q_0
  Translation invariance implies Q_0 is constant
  Rotation invariance implies: $Q_0 = \alpha \begin{bmatrix} -1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 2 \end{bmatrix}$

- $\alpha > 0$: homeotropic — directors point vertically

- $\alpha < 0$: isotropic — directors equally likely to point in any horizontal direction

- Q_0 is invariant under up-down reflection: $\tau = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & -1 \end{bmatrix}$

- Symmetry group is $\Gamma = \mathbf{E}(2) \oplus \mathbf{Z}_2(\tau)$
  Just like Bénard convection with midplane reflection

Linear Theory

- Translations: eigenfunctions have form $e^{2\pi i\mathbf{k}\cdot x}Q + \text{c.c.}$

$$W_{\mathbf{k}} = \{e^{2\pi i\mathbf{k}\cdot x}Q + \text{c.c.} : Q \text{ is complex-valued}\}$$

  where $\dim W_{\mathbf{k}} = 10$

- Four possible bifurcations

scalar/pseudoscalar

τ acts trivially/nontrivially

- Since L commutes with τ, we can subdivide

$$W_{\mathbf{k}} = W_{\mathbf{k}}^{++} \oplus W_{\mathbf{k}}^{+-} \oplus W_{\mathbf{k}}^{-+} \oplus W_{\mathbf{k}}^{--}$$

  where each $W_{\mathbf{k}}^{\pm\pm}$ is L-invariant

-

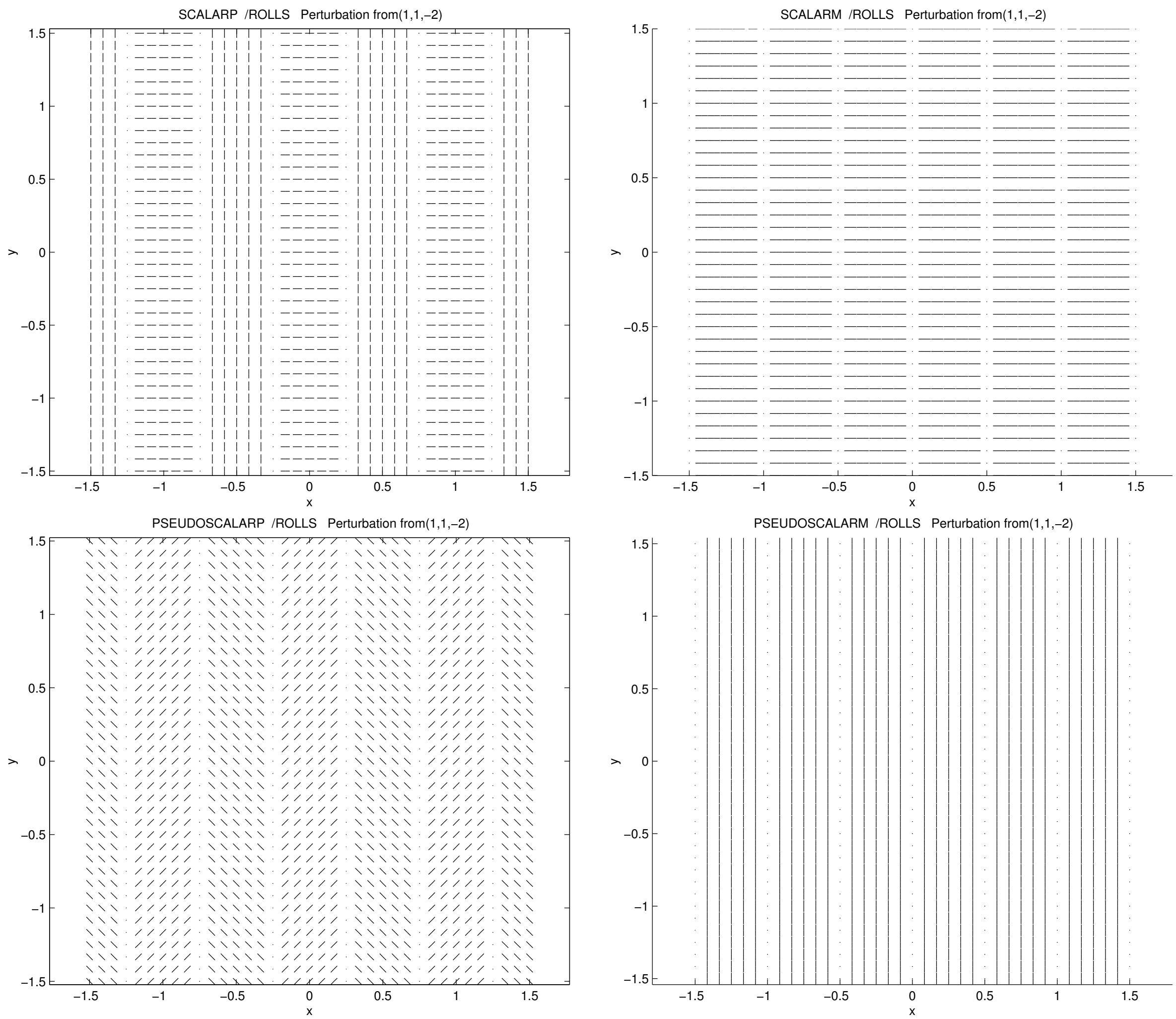
$$Q^{++} = \begin{bmatrix} a & 0 & 0 \\ 0 & b & 0 \\ 0 & 0 & -a-b \end{bmatrix} \qquad Q^{+-} = \begin{bmatrix} 0 & 0 & i \\ 0 & 0 & 0 \\ i & 0 & 0 \end{bmatrix}$$

  and

$$Q^{-+} = \begin{bmatrix} 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \qquad Q^{--} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & i \\ 0 & i & 0 \end{bmatrix}$$

Pattern Formation from the Isotropic State

Rolls solutions on bifurcation from αQ_0 when $\alpha < 0$

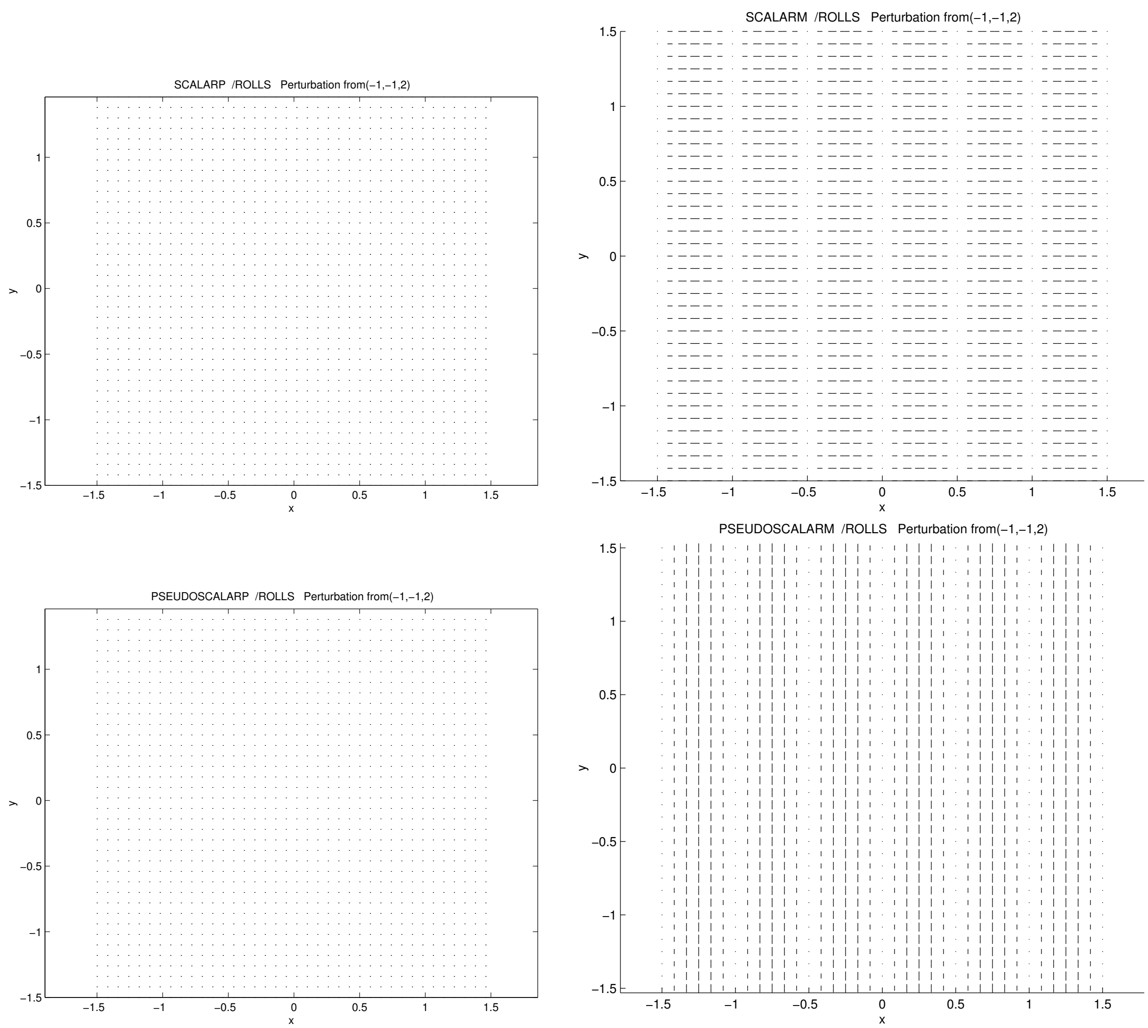


$\tau = +1$ $\tau = -1$

Figure 17: Rolls perturbation from $-Q_0$: (upper) scalar; (lower) pseudoscalar $\tau = +1$.

Pattern Formation from the Homeotropic State

Rolls solutions on bifurcation from αQ_0 when $\alpha > 0$



$\tau = +1$ $\tau = -1$

Figure 18: Rolls perturbation from Q_0: (upper) scalar; (lower) pseudoscalar $\tau = +1$.