Pattern formation in the visual cortex

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EDP & Probabilités pour les sciences du vivant
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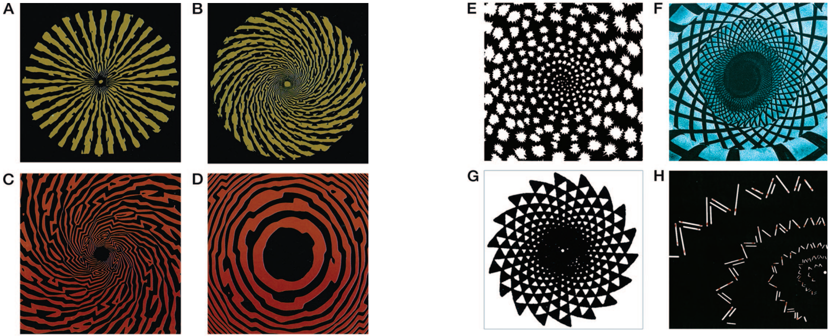
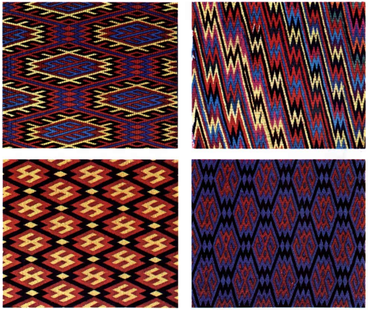
http://www.math.univ-toulouse.fr/∼gfaye/CoursM2/cirm16.pdf

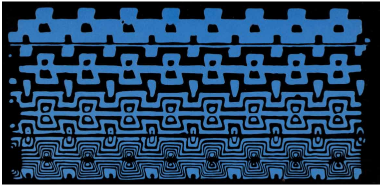
Geometric visual hallucinations



Redrawn from Oster 70, Siegel-Jarvik 75, Siegel 77 and Tyler 78.

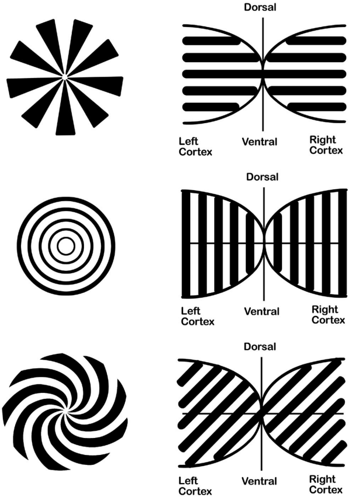
Other types of visual hallucinations

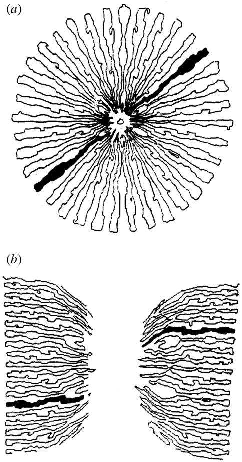




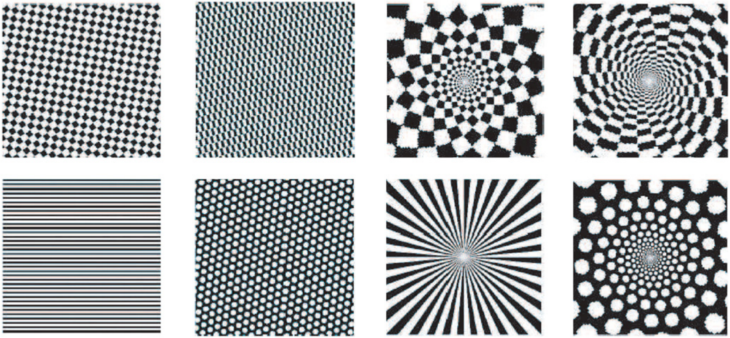
Oster 70 and Siegel 77

Retinotopy – Log-polar map



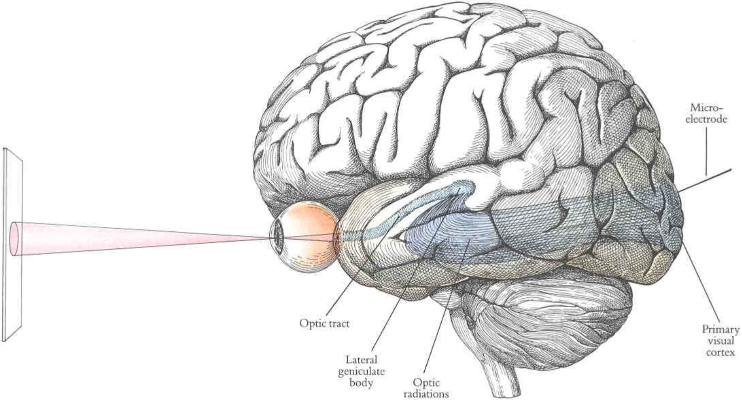


Visual hallucinations – Turing patterns in the visual cortex



Visual cortex Visual field

Primary visual cortex (V1)



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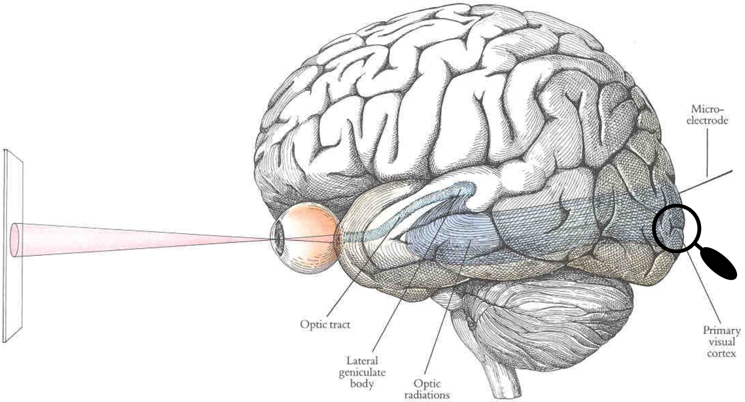
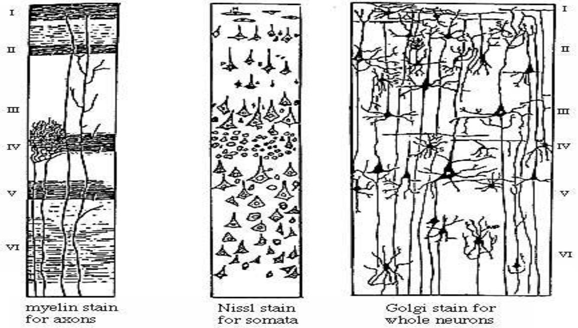


Laminar organization

Figure 1. Same area of cerebral cortex stained by three different methods to illustrate different neuronal elements. Refer also to DeArmond Fig. 84.



(Source: The Human Brain. J. Nolte. 2nd Ed. Mosby. 1988)

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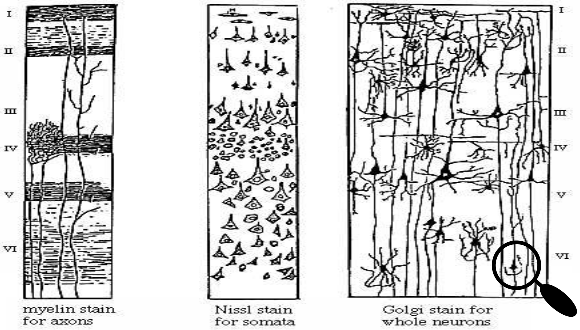
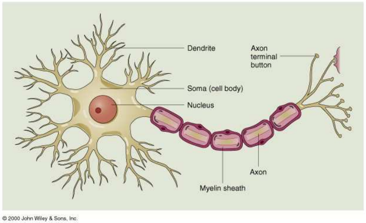
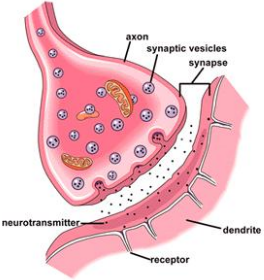


(Source: The Human Brain. J. Nolte. 2nd Ed. Mosby. 1988)

Different spatial scales: neuronal level

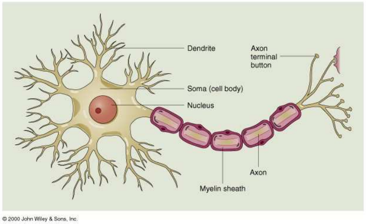


Neuron

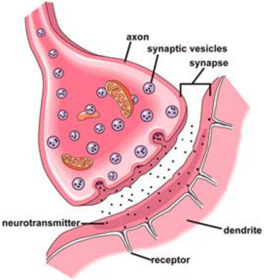


Synapse

Different spatial scales: neuronal level



Neuron

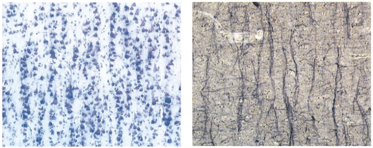


Synapse

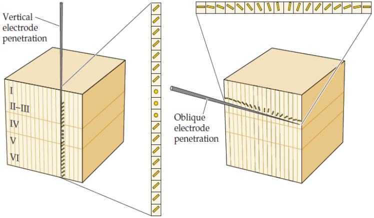
Question

Is it possible to gather neurons in order to form new elementary blocks on a larger scale?

Different spatial scales: cortical columns



Anatomical column. Buxhoeven 02.



Functional column. Kandel 00.

Different spatial scales

Type	Spatial scale	$\sharp$ neurons	Modeling scale
Neuron	μm	1	Microscopic
Anatomical column	40μm	80-100	Microscopic
Functional column	200-400μm	2.5e3-1e4	Micro/Meso-scopic
Hypercolumn	1mm	2e4-1e5	Mesoscopic
Primary visual cortex (V1)	2cm	4e6	Macroscopic

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Goal

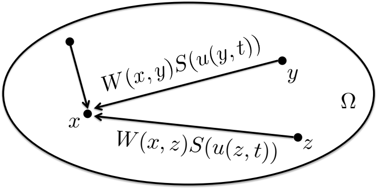
How to model at a mesoscopic or macroscopic scale?

Neural fields: key references

Neural Field Equation (NFE)

$$\partial_t V(x,t) = -V(x,t) + \int_\Omega W(x,x')S(V(x',t))\mathrm{d}x' + I_{\mathrm{ext}}(x,t)$$

- pioneer work: Wilson-Cowan 72, 73 and Amari 77,
- reviews: Ermentrout 98, Coombes 05 and Bressloff 12,
- rigorous derivation: Buice-Cowan 06-07, Bressloff 09, Touboul 12,



One population Ermentrout-Cowan model

We consider a 2D version of the neural field equation:

Neural field equation on the plane $\Omega = \mathbb{R}^2$

$$\partial_t V(\mathbf{r}, t) = -V(\mathbf{r}, t) + \int_{\mathbb{R}^2} W(\mathbf{r} \mid \mathbf{r}') S(\mu V(\mathbf{r}', t)) \mathrm{d}\mathbf{r}' \tag{1}$$

- S given by a sigmoidal function
- V_0 is a homogeneous solution,
- $W(\mathbf{r} \mid \mathbf{r}') = W(\|\mathbf{r} - \mathbf{r}'\|)$,
- W is invariant with respect to the Euclidean group $\mathcal{E}(2)$ (translation, rotation and reflection) $\Rightarrow$ equation (1) is $\underline{\mathcal{E}(2)\text{-equivariant}}$,
- μ is the bifurcation parameter of the problem (can be increased pharmacologically)

Linear stability of the homogeneous state

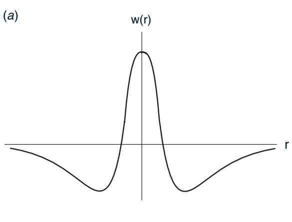
Linearizing equation (1) about V_0 by writing $V(\mathbf{r}, t) = V_0 + U(\mathbf{r})e^{\lambda t}$ leads to

$$\lambda U(\mathbf{r}) = -U(\mathbf{r}) + \mu S'(V_0) \int_{\mathbb{R}^2} W(\|\mathbf{r} - \mathbf{r}'\|)U(\mathbf{r}')\mathbf{r}' = \mathbf{L}_\mu U(\mathbf{r})$$

The continuous spectrum is generated by $U(\mathbf{r}) = e^{i\mathbf{k}\cdot\mathbf{r}}$ with dispersion relation

$$\lambda = \lambda(k) = -1 + \mu S'(V_0)\widehat{W}(k), \quad k = \|\mathbf{k}\|.$$

Critical value for μ is at $\mu_c = \left(S'(V_0)\widehat{W}(k_c)\right)^{-1}$.



Restriction to doubly-periodic functions

Problem: at the bifurcation $\mu = \mu_c$, there is a full circle $\|\mathbf{k}\| = k_c$ of neutrally stable modes

$$\Rightarrow \text{infinite-dimensional center manifold}$$

Solution: restrict the problem to doubly-periodic functions.
If ℓ_1, ℓ_2 are two linearly independent vectors of $\mathbb{R}^2$ and $\ell_i \cdot \mathbf{k}_j = \delta_{i,j}$ then

$$\begin{aligned} \mathcal{L} &= \{m_1\ell_1 + m_2\ell_2 \mid (m_1, m_2) \in \mathbb{Z}^2\} \text{ (lattice)} \\ \mathcal{L}^* &= \{m_1\mathbf{k}_1 + m_2\mathbf{k}_2 \mid (m_1, m_2) \in \mathbb{Z}^2\} \text{ (dual lattice)} \end{aligned}$$

Let $\mathcal{D}$ be the fundamental domain of the lattice, then on the following Banach space $\mathcal{X} = \{f \in \mathrm{L}^2(\mathcal{D}) \mid f(\mathbf{r} + \ell) = f(\mathbf{r}), \forall \ell \in \mathcal{L}\} \subset \mathrm{L}^2(\mathcal{D})$, the spectrum is now discrete.

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Name	Holohedry	Basis of $\mathcal{L}$	Basis of $\mathcal{L}^*$
Hexagonal	$\mathbf{D}_6$	$\ell_1 = (\frac{1}{\sqrt{3}}, 1)$, $\ell_2 = (\frac{2}{\sqrt{3}}, 0)$	$\mathbf{k}_1 = (0, 1)$, $\mathbf{k}_2 = (\frac{\sqrt{3}}{2}, -\frac{1}{2})$
Square	$\mathbf{D}_4$	$\ell_1 = (1, 0)$, $\ell_2 = (0, 1)$	$\mathbf{k}_1 = (1, 0)$, $\mathbf{k}_2 = (0, 1)$
Rhombic	$\mathbf{D}_2$	$\ell_1 = (1, -\cot\theta)$, $\ell_2 = (0, \cot\theta)$	$\mathbf{k}_1 = (1, 0)$, $\mathbf{k}_2 = (\cos\theta, \sin\theta)$

Case studied: square lattice

General setting: the center manifold is now 4-dimensional and can be written

$$\mathcal{E}_0 = \left\{ U(\mathbf{r}) = \sum_{j=1}^{2} z_j e^{2i\pi \mathbf{k}_j \cdot \mathbf{r}} + \text{c.c} \mid z_j \in \mathbb{C}, \|\mathbf{k}_j\| = 1 \right\} \cong \mathbb{C}^2$$

Symmetry: $\Gamma = \mathbf{D}_4 \ltimes \mathbb{T}^2$ is the new symmetry group for (1)

Group action:

Action of Γ on the plane: $\begin{cases} \xi \cdot \mathbf{r} = \mathcal{R}_\xi \mathbf{r} & \text{rotation centered at 0 of angle } \pi/2 \\ \kappa \cdot \mathbf{r} = \kappa \mathbf{r} & \text{reflection of axis } Ox \\ \ell \cdot \mathbf{r} = \mathbf{r} + \ell & \text{translation} \end{cases}$

For all $\gamma \in \Gamma$, the action on $U \in \mathcal{X}$ is $\gamma \cdot U(\mathbf{r}) = U(\gamma^{-1} \cdot \mathbf{r})$.

Action of Γ on $\mathcal{E}_0$: $\begin{cases} \xi(\mathbf{z}) = (\bar{z}_2, z_1) \\ \kappa(\mathbf{z}) = (z_1, \bar{z}_2) \\ \ell(\mathbf{z}) = (e^{-2i\pi m_1} z_1, e^{-2i\pi m_2} z_2) & \ell = m_1 \ell_1 + m_2 \ell_2 \end{cases}$

Symmetry-breaking bifurcation

Suppose that we have a differential system on a Banach space $\mathcal{X}$ of the form

$$\frac{dV}{dt} = \mathbf{L}V + \mathbf{R}(V, \mu) = \mathcal{F}(V, \mu) \text{ on } \mathcal{X}$$

Assume that

- Γ is a compact group that acts linearly and $\mathcal{F}$ is Γ-equivariant,
- Γ acts absolutely irreducibly on $\mathcal{E}_0 \Rightarrow D_V\mathcal{F}(V_0, \mu) = c(\mu)Id$,
- $\mathbf{L}$ has 0 as an isolated eigenvalue with finite multiplicity at $\mu = \mu_c$.

Theorem (Equivariant Branching Lemma)

If H is an isotropy subgroup of Γ with $\dim Fix(H) = 1$ and if $c'(\mu_c) \neq 0$, then it exists a unique branch of solutions with symmetry H bifurcating off the branch $V = V_0$ at $\mu = \mu_c$.

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- when $H < \Gamma$, the bifurcating solutions in $\mathrm{Fix}(H)$ have lower symmetry than the basic solution V_0. This effect is called spontaneous symmetry breaking,
- references: Golubitsky-Schaeffer 85, Chossat-Lauterbach 00.

Application to the square lattice

Checking the hypotheses:

- $\Gamma = \mathbf{D}_4 \ltimes \mathbb{T}^2$ is compact and acts linearly
- Γ acts absolutely irreducibly on $\mathcal{E}_0$ and $c(\mu) = \frac{\mu - \mu_c}{\mu_c}$
- $\mathbf{L}$ has 0 as an isolated eigenvalue of multiplicity 4.

Isotropy subgroups:

H	Generators H	$\mathrm{Fix}(H)$	$\dim \mathrm{Fix}(\Sigma)$	Name
$\mathbf{D}_4$	ξ, κ	$(1,1)$	1	Squares/Spots
$\mathbf{O}(2) \times \mathbf{Z}_2$	$\xi^2, \kappa, [0, m_2]$	$(1,0)$	1	Rolls/Stripes

Structure of the solutions: $V(\mathbf{r}) \simeq z_1 e^{2i\pi \mathbf{k}_1 \cdot \mathbf{r}} + z_2 e^{2i\pi \mathbf{k}_2 \cdot \mathbf{r}} + \text{c.c}$

$$
\begin{array}{rclll}
H = \mathbf{D}_4 & V(\mathbf{r}) & \simeq & 2z(\cos(2\pi x) + \cos(2\pi y)) & z_1 = z_2 = z \\
H = \mathbf{O}(2) \times \mathbf{Z}_2 & V(\mathbf{r}) & \simeq & 2z\cos(2\pi x) & z_1 = z, z_2 = 0
\end{array}
$$

Stripes or spots?

We use normal form theory to compute the reduced equations on $\mathcal{E}_0$

$$\left\{\begin{array}{rcl} \dot{z}_1 & = & z_1\left[\frac{\mu-\mu_c}{\mu_c}+\beta|z_1|^2+\gamma|z_2|^2\right] + \text{ h.o.t} \\ \dot{z}_2 & = & z_2\left[\frac{\mu-\mu_c}{\mu_c}+\beta|z_2|^2+\gamma|z_1|^2\right] + \text{ h.o.t} \end{array}\right.$$

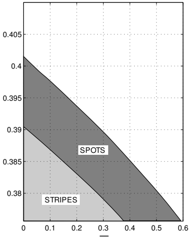
Lemma

- *Spot solution* $(1,1)$ *is stable if and only if* $\beta < -|\gamma| < 0$.
- *Stripe solution* $(1,0)$ *is stable if and only if* $\gamma < \beta < 0$.

If $s_2 = S''(V_0)$ and $s_3 = S'''(V_0)$ then

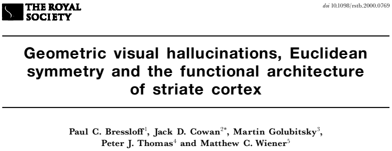
$$\beta/\mu_c^3\widehat{W}_{\mathbf{k}_c} = \mu_c s_2^2\left[\frac{\widehat{W}_0}{1-\widehat{W}_0/\widehat{W}_{\mathbf{k}_c}}+\frac{\widehat{W}_{2\mathbf{k}_c}}{2(1-\widehat{W}_{2\mathbf{k}_c}/\widehat{W}_{\mathbf{k}_c})}\right]+\frac{s_3}{2}$$

$$\gamma/\mu_c^3\widehat{W}_{\mathbf{k}_c} = \mu_c s_2^2\left[\frac{\widehat{w}_0}{1-\widehat{W}_0/\widehat{W}_{\mathbf{k}_c}}+2\frac{\widehat{W}_{\mathbf{k}_1,\mathbf{k}_2}}{1-\widehat{W}_{\mathbf{k}_1,\mathbf{k}_2}/\widehat{W}_{\mathbf{k}_c}}\right]+s_3$$



Concluding remarks

- geometric visual hallucinations can be explained simply by symmetry-breaking bifurcation (like Turing patterns) on the visual cortex abstracted by $\mathbb{R}^2$,
- can be extended to incorporate the functional architecture of the visual cortex ($\mathbb{R}^2 \times \mathbf{S}^1$), Bressloff et al 01, Bressloff-Cowan 02.



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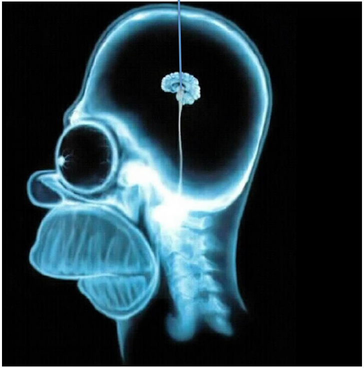
doi 10.1098/rstb.2000.0769

Geometric visual hallucinations, Euclidean symmetry and the functional architecture of striate cortex

Paul C. Bressloff[1], Jack D. Cowan[2*], Martin Golubitsky[3], Peter J. Thomas[4] and Matthew C. Wiener[5]

- can be extended to non-Euclidean geometry for texture perception (Subject of my PhD Thesis).

$$\partial_t u(x,t) = -u(x,t) + \int_{\mathbb{R}} W(x-y)S(u(y,t))dy$$



THANK YOU !