introduction to mesoscopic models of visual cortical structures

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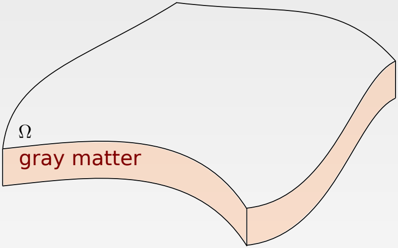
Neural Fields models

Outline

Neural fields

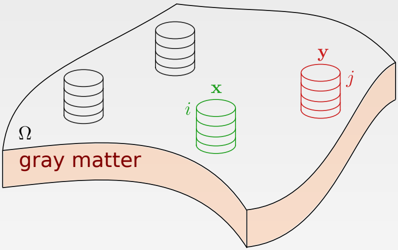
- Mesoscopic model of *bounded* cortical area Ω



See work of Bressloff, Coombes, Ermentrout, Atay, Hutt...

Neural fields

- Mesoscopic model of *bounded* cortical area Ω
- Continuum of populations



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Neural fields

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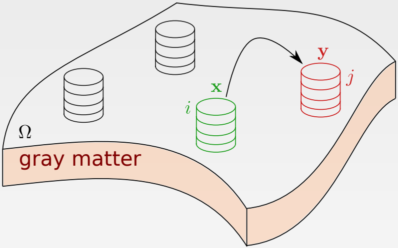
- Populations communicate via horizontal connections through gray matter with delays



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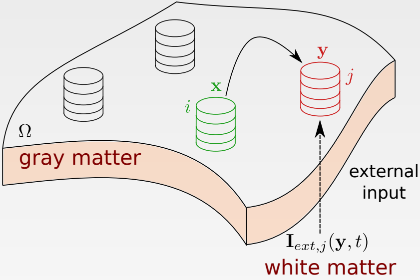
- Population activity: vector $\mathbf{V}(\mathbf{x}, t)$ of p components, one component per population



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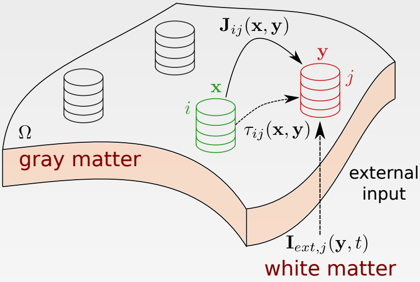

see **[Bressloff-Kilpatrick:09]**, **[Venkov-Coombes:07]**, **[Brunel et al. :05]**, work of Atay, Hutt see also the book **[Coombes-et al. 14]**. **Neural Fields**,

Local models for p interacting neural masses

1. each neural population i is described by its average membrane potential $V_i(t)$ or by its **average instantaneous firing rate** $\nu_i(t)$ with $\nu_i(t) = S_i(V_i(t))$, where S_i is sigmoidal:

$$S_i(x) = \frac{S_{im}}{1 + e^{-\sigma_i(x-\theta_i)}}$$

σ_i is the nonlinear gain and θ_i is the threshold

Recall the f-I curve from Lecture 2.

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3. the number of spikes arriving between t and $t+dt$ is $\nu_j(t)dt$, then the average membrane potential of population i is:

$$V_i(t) = \sum_j \int_{t_0}^{t} PSP_{ij}(t-s) S_j(V_j(s)) ds$$

$$\nu_i(t) = S_i \left(\sum_j \int_{t_0}^{t} PSP_{ij}(t-s) \nu_j(s) ds \right)$$

The voltage-based model

It is based on the hypotheses:

1. the post-synaptic potential has the same shape no matter what presynaptic population j caused it, this leads to

$$PSP_{ij}(t) = w_{ij} PSP_i(t)$$

   w_{ij} is the average strength of the post-synaptic potential and if $w_{ij} > 0$ (resp. $w_{ij} < 0$) population j excites (resp. inhibits) population i

2. if we assume that $PSP_i(t) = e^{-t/\tau_i} H(t)$ or equivalently

$$\tau_i \frac{PSP_i(t)}{dt} + PSP_i(t) = \delta(t)$$

   we end up with a system of ODEs:

$$\tau_i \frac{V_i(t)}{dt} + V_i(t) = \sum_j w_{ij} S_j(V_j(t)) + I_{ext}^i(t)$$

   which we rewrite in vector form:

$$\dot{\mathbf{V}} = -\mathbf{L}\mathbf{V} + \mathbf{W}\mathbf{S}(\mathbf{V}) + \mathbf{I}_{ext}$$

The activity-based model

It is based on the hypotheses:

1. the same shape of a PSP depends only on the presynaptic cell, this leads to

$$PSP_{ij}(t) = w_{ij} PSP_j(t)$$

2. we also suppose that $PSP_j(t) = e^{-t/\tau_j} H(t)$ and we end up with a system of ODE

$$\tau_i \frac{A_i(t)}{dt} + A_i(t) = S_i \left(\sum_j w_{ij} A_j(t) + I^i_{ext}(t) \right)$$

which we rewrite in vector form:

$$\dot{\mathbf{A}} = -\mathbf{L}\mathbf{A} + \mathbf{S}(\mathbf{W}\mathbf{A} + \mathbf{I}_{ext})$$

Neural fields models

1. idea: combine local models to form a continuum of neural fields
2. $\Omega \subset \mathbb{R}^d$, $d = 1, 2$ is a piece of cortex
3. We note $\mathbf{V}(\mathbf{r}, t)$ (resp. $\mathbf{A}(\mathbf{r}, t)$) the state vector at point $\mathbf{r}$ in Ω
4. We introduce the $p \times p$ matrix $\mathbf{W}(\mathbf{r}, \bar{\mathbf{r}}, t)$

Voltage-based neural fields equations

$$\frac{d\mathbf{V}(\mathbf{r}, t)}{dt} = -\mathbf{L}\mathbf{V}(\mathbf{r}, t) + \int_\Omega \mathbf{W}(\mathbf{r}, \bar{\mathbf{r}}, t)\mathbf{S}(\mathbf{V}(\bar{\mathbf{r}}, t))d\bar{\mathbf{r}} + \mathbf{I}_{ext}(\mathbf{r}, t)$$

Activity-based neural fields equations

$$\frac{d\mathbf{A}(\mathbf{r}, t)}{dt} = -\mathbf{L}\mathbf{A}(\mathbf{r}, t) + \mathbf{S}\left(\int_\Omega \mathbf{W}(\mathbf{r}, \bar{\mathbf{r}}, t)\mathbf{A}(\bar{\mathbf{r}}, t))d\bar{\mathbf{r}} + \mathbf{I}_{ext}(\mathbf{r}, t)\right)$$

Remarks

- when d $= 1$, most widely studied because of its relative mathematical simplicity but of limited biological interest
- when d $= 2$, more interesting from a biological point of view (the thickness is neglected), received less interest because of the computational difficulty
- unbounded domains: $\Omega = \mathbb{R}^d$ raises some mathematical questions and unrealistic
- number of populations: p $= 1$ or 2
- the sigmoid function can be approximated by a Heaviside function
- $\mathbf{W}(\mathbf{r}, \bar{\mathbf{r}}, t)$ is often chosen symmetric and translation invariant:

$$\mathbf{W}(\mathbf{r}, \bar{\mathbf{r}}, t) = \mathbf{W}(\mathbf{r} - \bar{\mathbf{r}}, t)$$

- in the case n $=$ d $= 1$, the connectivity function has a "Mexican-hat shape"
- features can be taken into account: $\mathbf{V}(\mathbf{r}, \theta, t)$ in the case of orientation

- NFE as mean limit of Hawkes process **[Chevallier et al. 17]** (Point process).
- **[Lucon et al. :18]** Limits of FitzHugh-Nagumo neurons $F(x,y) = \left(x - \frac{x^3}{3} - y, \frac{1}{\tau}(x + a - by)\right)$ with network:

$$\mathrm{d}X_{i,t} = \left(\delta F\left(X_{i,t}\right) - K\left(X_{i,t} - \frac{1}{N}\sum_{j=1}^{N} X_{j,t}\right)\right)\mathrm{d}t + \sqrt{2}\sigma \mathrm{d}B_{i,t}, i = 1, \ldots, N, t \geqslant 0$$

to

$$\mathrm{d}X_t = \left(\delta F\left(X_t\right) - K\left(X_t - \mathbb{E}\left[X_t\right]\right)\right)\mathrm{d}t + \sqrt{2}\sigma \mathrm{d}B_t, t \geqslant 0$$

- **[Crevat et al. 19]** similar with space but without noise. The limit is

$$\dot{V} = \frac{V^3}{3} - W + \mathcal{L}_{\rho_0}(V), \quad \dot{W} = V + a - bW$$

with $\mathcal{L}_\rho(V) := -(\Psi * \rho)V + \Psi * [\rho V]$

Cauchy problem for NFE

Ω is an open bounded set of $\mathbb{R}^d$. We define $\mathcal{F} = L^2(\Omega, \mathbb{R}^p)$ (Hilbert space). We can rewrite equation (1) in a compact form (function $\mathbf{V}(t)$ is thought of as mapping $\mathbf{V} : \mathbb{R}^+ \to \mathcal{F}$):

$$\begin{cases} \frac{d\mathbf{V}}{dt} = -\mathbf{L}\mathbf{V} + \mathbf{G}(t, \mathbf{V}), \quad t > 0 \\ \mathbf{V}(0) = \mathbf{V}_0 \in \mathcal{F} \end{cases} \tag{1}$$

The nonlinear operator $\mathbf{G}$ is defined by:

$$\mathbf{G}(t, \mathbf{V})(\mathbf{r}, t) = \int_\Omega \mathbf{W}(\mathbf{r}, \bar{\mathbf{r}}, t)\mathbf{S}(\mathbf{V}(\bar{\mathbf{r}}, t)) + \mathbf{I}_{ext}(\mathbf{r}, t), \ \forall \mathbf{r} \in \Omega$$

Theorem

If the following two hypotheses are satisfied:

- $\mathbf{W} \in \mathcal{C}(\mathbb{R}^+, L^\infty(\Omega^2, \mathbb{R}^p))$ and is uniformly bounded in time,
- the external input $\mathbf{I}_{ext} \in \mathcal{C}(\mathbb{R}^+, \mathcal{F})$

then for any function $V_0 \in \mathcal{F}$ there is a unique solution $\mathbf{V}$ defined on $\mathbb{R}^+$ and continuously differentiable of the initial value problem (1).

Element of the proof

- for all $t > 0, \mathbf{G}(t, \cdot) : \mathcal{F} \to \mathcal{F}$, (well-posedness of the problem)
- $\mathbf{G} : (t, \mathbf{V}) \to \mathbf{G}(t, \mathbf{V})$ is continuous in $(t, \mathbf{V})$
- $\|\mathbf{G}(t, \mathbf{V}_1) - \mathbf{G}(t, \mathbf{V}_2)\|_{\mathcal{F}} \leq KDS_m \sup_{t \in \mathbb{R}^+} \|\mathbf{W}(t)\|_{\mathrm{L}^\infty} \|\mathbf{V}_1 - \mathbf{V}_2\|_{\mathcal{F}}$ for all $t > 0$ and $\mathbf{V}_1, \mathbf{V}_2 \in \mathcal{F}$ where $DS_m = \sup_{i=1\cdots p} \|S_i'\|_\infty$ (Lipschitz continuity of R with respect to its second argument, uniformly with respect to the first)
- application of the Cauchy Lipschitz theorem in Banach spaces

Mean-field limits, McKean-Vlasov 2/2

Without space

- **[de Masi et al. 15]** spiking network

$$
\begin{aligned}
X_t^{N,i} = \quad & X_0^{N,i} - \lambda \int_0^t X_s^{N,i} ds - \int_0^t \int_0^\infty X_{s-}^{N,i} \mathbf{1}_{\left\{z \leq f\left(X_{s-}^{N,i}\right)\right\}} \mathbf{N}^i(ds, dz) \\
+ \quad & \tfrac{1}{N} \sum_{j \neq i} \int_0^t \int_0^\infty \mathbf{1}_{\left\{z \leq f\left(X_{s-}^{N,j}\right)\right\}} \mathbf{N}^j(ds, dz)
\end{aligned}
$$

  with limit $X_t = X_0 + \int_0^t \mathbb{E}(X_s) - \lambda X_s ds - \int_0^t \int_0^\infty X_{s-} \mathbf{1}_{\{z \leq f(X_{s-})\}} \mathbf{N}(ds, dz)$

- **[Cormier et al. 19]** spiking network

$$
X_t = X_0 + \int_0^t \mathbb{E}(X_s) + b(X_s) ds - \int_0^t \int_0^\infty X_{s-} \mathbf{1}_{\{z \leq f(X_{s-})\}} \mathbf{N}(ds, dz)
$$

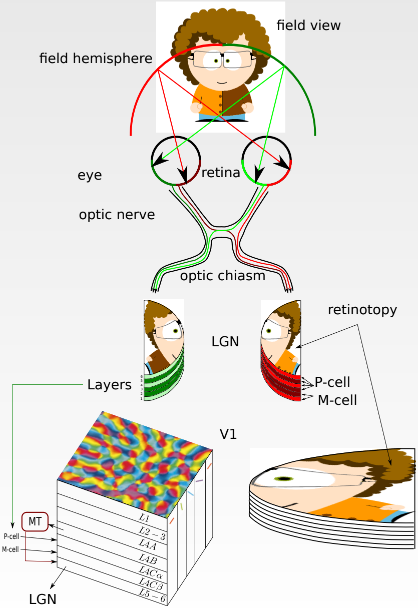
- Networks on random graphs, with adaptation, ...

What do you notice?

Structure of primary visual cortex (V1)

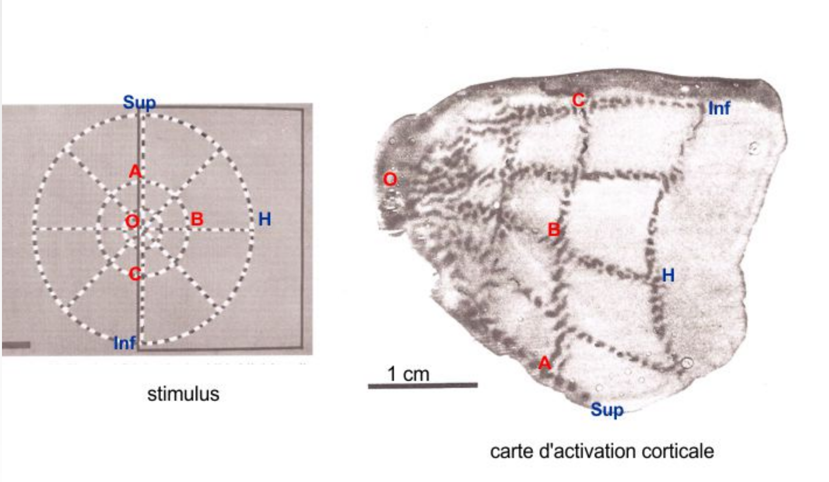
Outline

Anatomy of the visual pathway



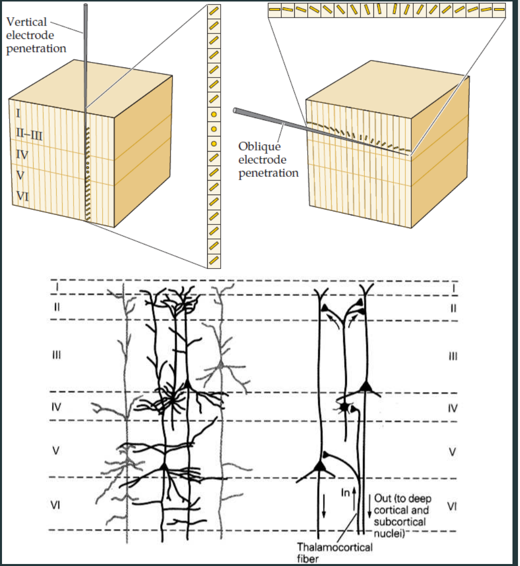
Retinotopy, From Tootell-1988 (Monkey)

$$z \to \log(z + 0.33) - \log(z + 6.66)$$

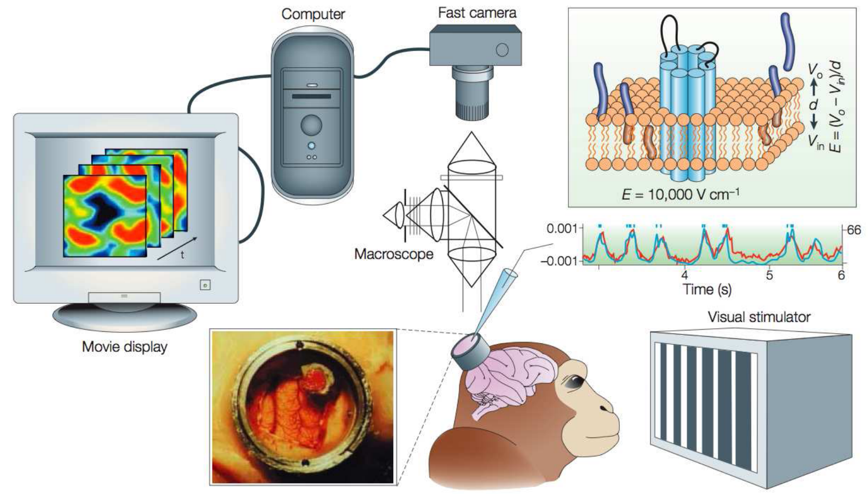


Cortical layers organization of V1 (Purves)

(David Hubel and Torsten Wiesel, Nobel 1981)

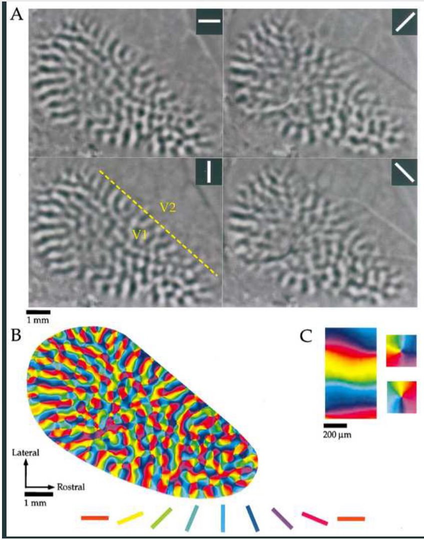


Optical imaging: methods



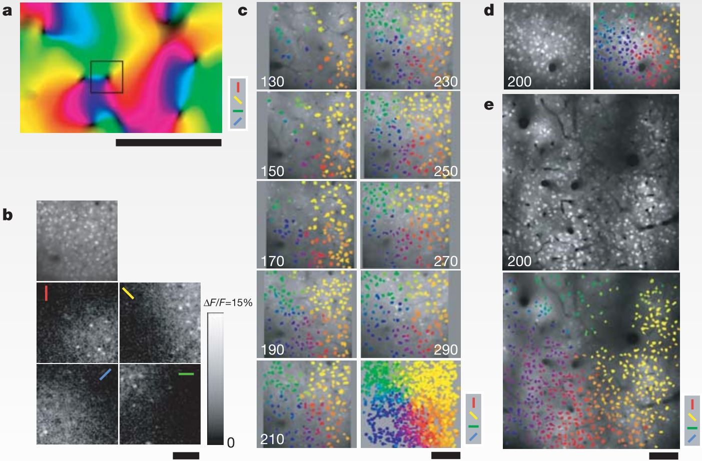
Optical imaging: methods

Orientation columns, **[Bosking et al. 97]**



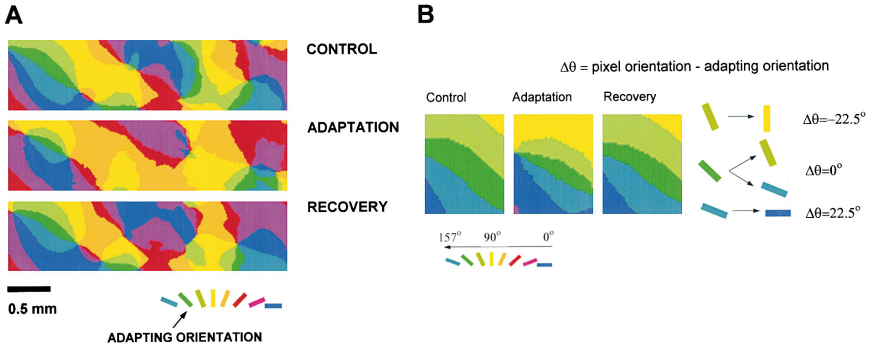
Closer look, **[Ohki et al. 06]** (cat)

Pinwheel points are not an averaging artifact. Selective cells (1,034 / 1,055).



Plasticity of representation

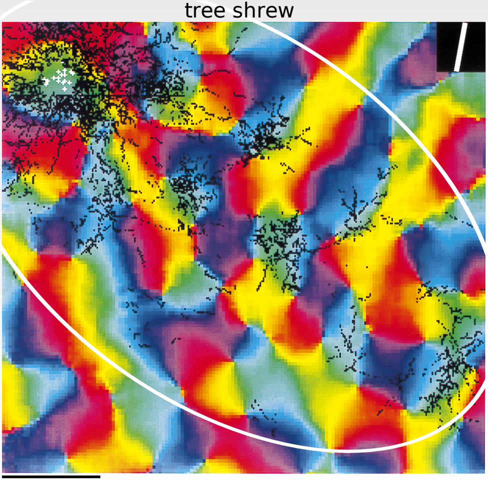
From **[Dragoi et al. 2000]** (Cat)



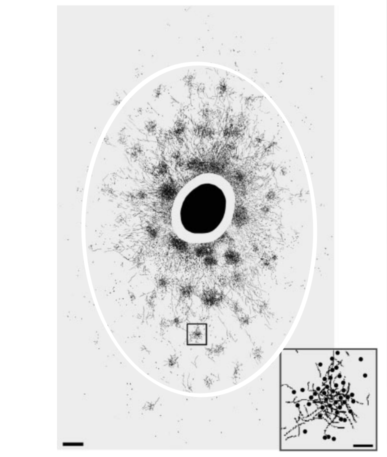
Link function - anatomy

Long range connections **[Bosking:1997]**,**[Angelucci:2002]**

tree shrew

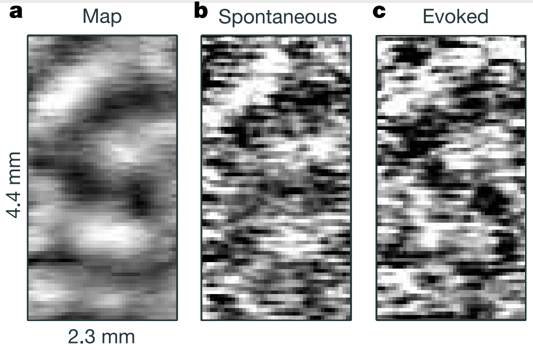


macaque



Anesthetised Cat, spontaneous activity

A bit controversial, **[Kenet et al. 03]**

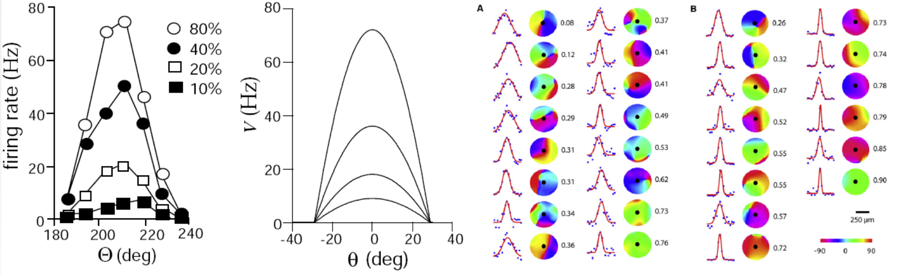


Very important question: is the response **modulated** by the cortex or strongly **generated** by the cortex?

$$Res = F(I_{thal}) \quad v.s \quad Res = F(Res, \epsilon I_{thal}).$$

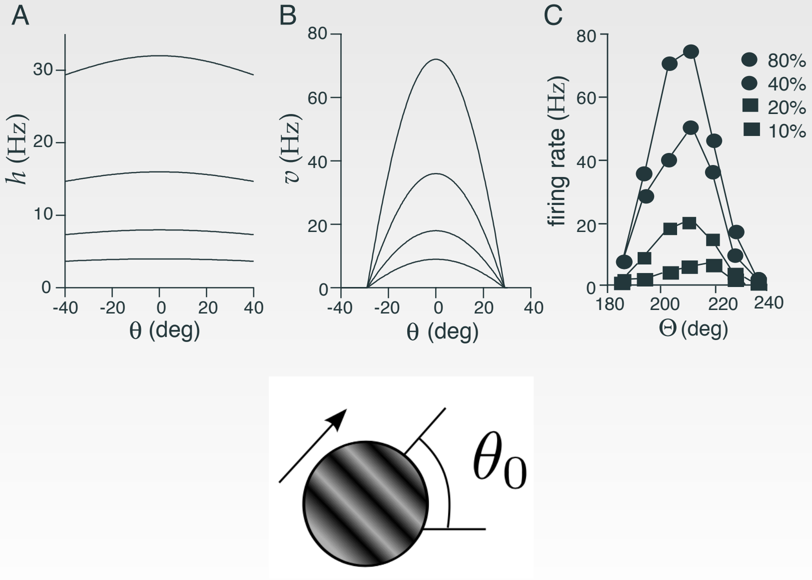
A closer look at orientation selectivity

From **[Sclar et al. 82]** and **[Nauhaus et al. 08]**

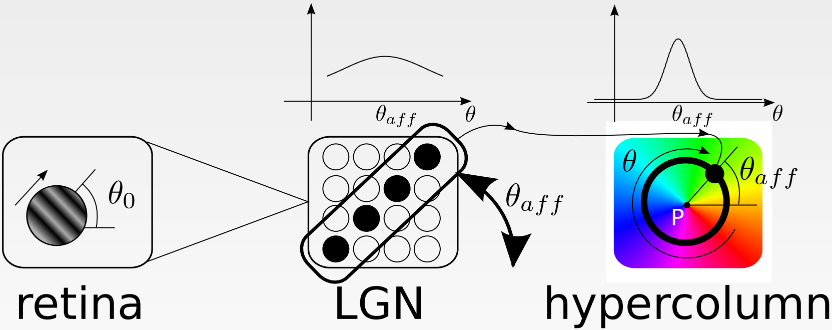


Applications of Neural field models

Outline


A
B
C
h (Hz)
30
20
10
0
-40
-20
0
20
40
θ (deg)
v (Hz)
80
60
40
20
0
-40
-20
0
20
40
θ (deg)
firing rate (Hz)
80
60
40
20
0
180
200
220
240
Θ (deg)
80%
40%
20%
10%
θ_0

Ring Model of orientation: mechanism



Mexican hat connectivity

Goal: reduce to one population.

Consider two populations E/I

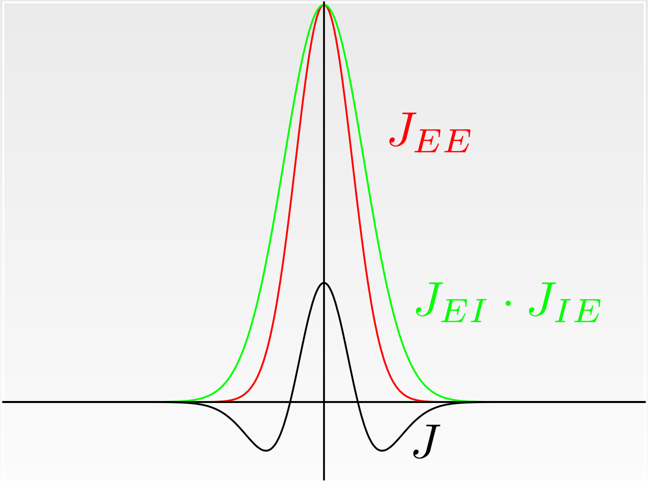
$$\begin{aligned}\left(\tau_E \frac{d}{dt}+1\right) V_E &= J_{EE}\cdot S_E(V_E) - J_{EI}\cdot S_I(V_I) + I_E\\ \left(\tau_I \frac{d}{dt}+1\right) V_I &= J_{IE}\cdot S_E(V_E) + I_I\end{aligned}$$

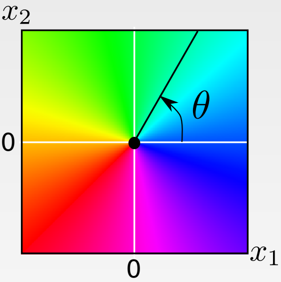
- Neglect J_{II}
- Gaussian kernels
- Inhibition is recruited $S_I(V_I) \approx \alpha V_I$

Then

$$\begin{aligned}\left(\tau_E \frac{d}{dt}+1\right) V_E &= \Big(J_{EE} - \alpha J_{EI}\cdot J_{IE}\Big)\cdot S_E(V_E) + I_E - \alpha J_{EI}\cdot I_I\\ &\equiv J\cdot S_E(V_E) + I\end{aligned}.$$

Mexican hat connectivity





- One population with Mexican hat connectivity
- $\overline{V}(\theta, t) \equiv \int_0^1 rV(r, \theta, t)dr$

Then we can find a Ring Model approximation for $\overline{V}$.

Ring Model of orientation tuning: equation

We consider the following equation:

$$\tau \frac{dV(\theta,t)}{dt} = -V(\theta,t) + \int_{-\pi/2}^{\pi/2} J(\theta-\theta')S(V(\theta',t))\frac{d\theta'}{\pi} + \epsilon I(\theta)$$

where τ is a temporal synaptic constant ($\tau \approx 10ms$), $J(\theta-\theta')$ is a connectivity function (excitatory/inhibitory) and S is the sigmoidal function:

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

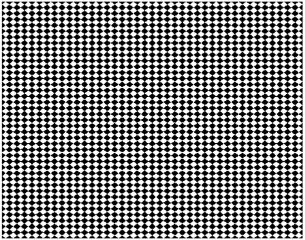
$I(\theta)$ is an input coming from the LGN given by:

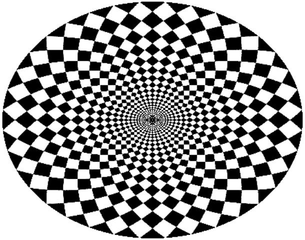
$$I(\theta) = 1-\beta+\beta\cos\left(2\left(\theta-\theta_{aff}\right)\right)$$

Moreover, we take the simplest possible connectivity function:

$$J(\theta) = -1 + J_1\cos(2\theta)$$

Patterns of the Ermentrout-Cowan model of visual hallucinations





We consider the following equation:

$$\tau \frac{dV(\mathbf{r},t)}{dt} = -V(\mathbf{r},t) + \int_{\mathbb{R}^2} W(\mathbf{r},\bar{\mathbf{r}}) S(V(\bar{\mathbf{r}},t)) d\bar{\mathbf{r}}$$

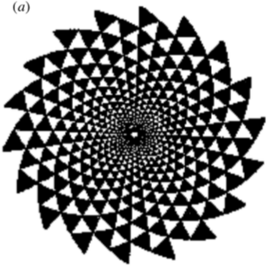
where τ is a temporal synaptic constant ($\tau \approx 10ms$), $W(\mathbf{r},\bar{\mathbf{r}}) = w\left(\|\mathbf{r}-\bar{\mathbf{r}}\|\right)$ is a connectivity function (excitatory/inhibitory) and S is the sigmoidal function:

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

We choose a "Mexican-hat" connectivity function:

$$w(r) = \frac{A_1}{\sigma_1} e^{-\frac{r^2}{\sigma_1^2}} - \frac{A_2}{\sigma_2} e^{-\frac{r^2}{\sigma_2^2}}$$

(a)



(b)

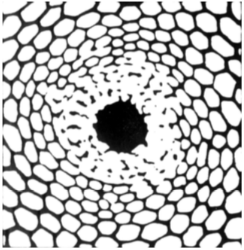
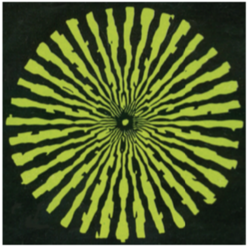


Figure 1. (a) ‘Phosphene’ produced by deep binocular

(a)



(b)

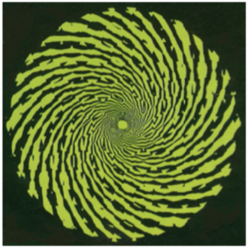
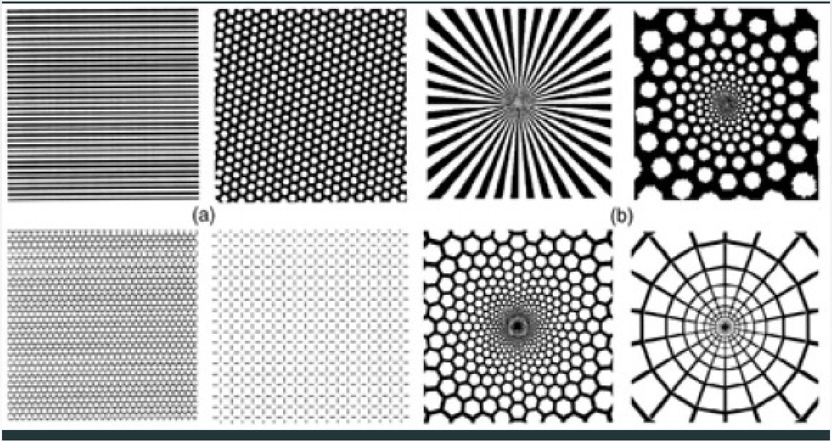


Figure 2. (a) Funnel and (b) spiral hallucinations generated by LSD. Redrawn from Oster (1970).

Geometric visual hallucinations: theory



Bressloff-Cowan-Golubitsky-Thomas-Wiener model

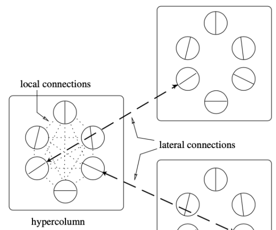
We consider the following equation **[Bressloff-etal.:01]**:

$$\tau \frac{dV(\mathbf{r},\theta,t)}{dt} = -V(\mathbf{r},\theta,t) + \int_{\mathbb{R}^2} \int_{-\pi/2}^{\pi/2} W(\mathbf{r},\theta|\bar{\mathbf{r}},\theta') S(V(\bar{\mathbf{r}},\theta',t)) d\bar{\mathbf{r}} \frac{d\theta'}{\pi}$$

where τ is a temporal synaptic constant ($\tau \approx 10ms$), S is the sigmoidal function: $S(x) = \frac{1}{1+e^{-x+k}} - \frac{1}{1+e^{k}}$ and

$$W(\mathbf{r},\theta|\bar{\mathbf{r}},\theta') = J(\theta-\theta')\delta_{\mathbf{r},\bar{\mathbf{r}}} + \beta\,(1-\delta_{\mathbf{r},\bar{\mathbf{r}}})\, w_{lat}(\mathbf{r}-\bar{\mathbf{r}},\theta)$$

- for $\beta = 0$, we recover the Ring Model of orientation tuning
- if $V(\mathbf{r},\theta,t)$ is independent of θ we recover the Ermentrout-Cowan model
- we will try to infer some properties from the case $\beta = 0$ to the case $0 < \beta \ll 1$ and in the same time we will use similar method as for the Ermentrout-Cowan model



Another network model of the visual cortex area V1

We write the equations for the average membrane potential $V(\mathbf{x})$ of neurons at position $\mathbf{x} \in \Omega \subset V1$ (see **[Veltz-etal:15]**):

$$\tau \frac{dV(\mathbf{x})}{dt} = -V(\mathbf{x}) + \int_{\Omega} J(\mathbf{x},\mathbf{y}) S\left(V(\mathbf{y})\right) d\mathbf{y} + I_{thal}(\mathbf{x})$$

- Ω is a piece of visual **cortex**, open bounded.
- S is a sigmoid function, bounded, increasing
- $I_{thal}(\mathbf{x})$, input from the **thalamus**, **here $= 0$**
- $J(\mathbf{x},\mathbf{y})$ is the **connection strength** between neurons at positions $\mathbf{x}$ and $\mathbf{y}$
- Synaptic/Propagation delays neglected.

$\Rightarrow$ Note that we have lumped many populations in an equation for a single population!

Connections model for visual cortex

See **[Bressloff:03]**

$$J(\mathbf{x},\mathbf{y}) = J_{loc}(\|\mathbf{x}-\mathbf{y}\|) + \epsilon J_{lat}(\mathbf{x},\mathbf{y})$$

Local connections

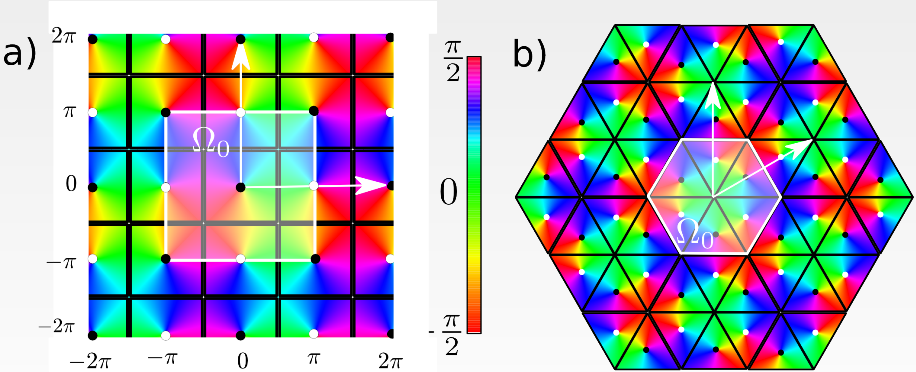
- J_{loc} is a difference of Gaussians
- Translation invariance on cortical plane (see next)
- Gradient system if $\epsilon = 0$

Long-range connections, symmetry-breaking term

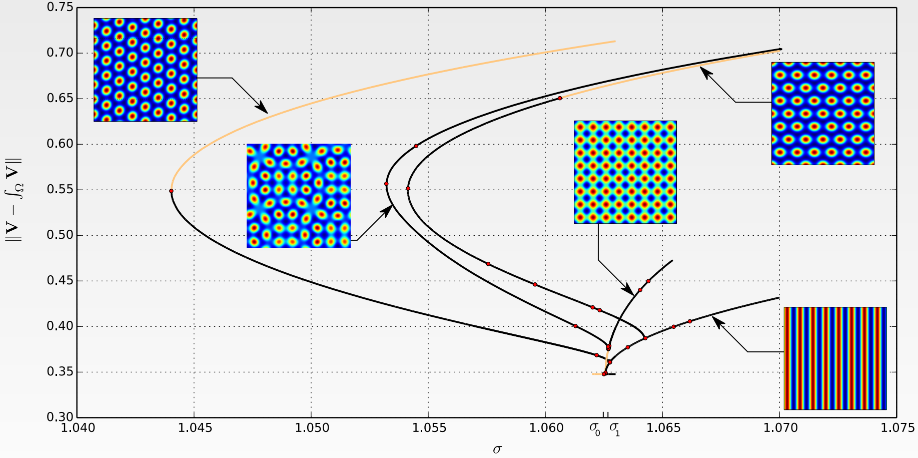
$J_{LR}(\mathbf{x},\mathbf{y}) = G_{\sigma_\theta}(\theta(\mathbf{x}) - \theta(\mathbf{y}))J_0(\chi, R_{-2\theta(\mathbf{x})}(\mathbf{x}-\mathbf{y}))$

- Anisotropy function $J_0(\mathbf{x}) = \exp - \left((1-\chi)x_1^2 + x_2^2\right)/2\sigma_{lat}^2,\ \chi \in [0,1]$
  1. $\chi > 0$ Tree Shew
  2. $\chi = 0$ Macaque

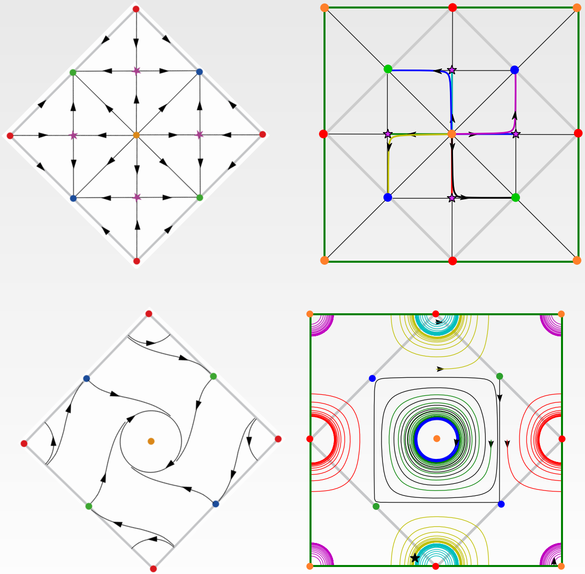
The PO map θ defines a tiling of Ω (or $\mathbb{R}^2$), characterized by its wallpaper group (invariance group of θ).



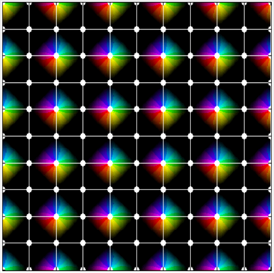
Bifurcation diagram, square case, $\epsilon = 0$

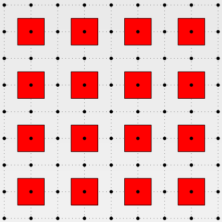


Qualitative analysis of dynamics on $\mathcal{T}_\epsilon$: Square lattice case

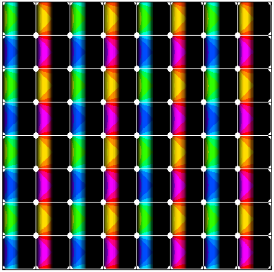


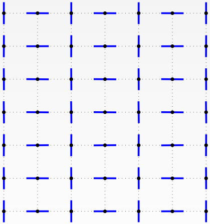
Some planforms in the square case





PO map θ^{1}





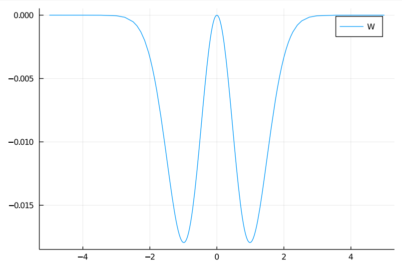
PO map θ^{2}

Grid cells model 1/2

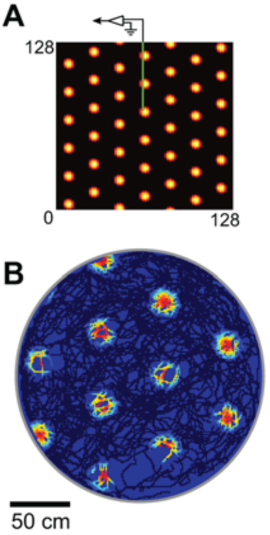
[Burak-Fiete 2009] We consider the following equation:

$$\tau \frac{dA(\mathbf{r}_i, t)}{dt} = -A(\mathbf{r}_i, t) + S\left(\sum_j W(\mathbf{r}_j, \mathbf{r}_j) A(\mathbf{r}_j, t) + I_{ext}(\mathbf{r}_i, t)\right)$$

- Inverted mexican hat function G
- $W(\mathbf{r}_j, \mathbf{r}_j) = G(\mathbf{r}_j - \mathbf{r}_j - l e_{\theta_j})$, all inhibitory
- $I_{ext}(\mathbf{r}_i) = A(x_i)\left(1 + \alpha e_{\theta_j} \cdot \mathbf{v}\right)$



Grid cells model 2/2



Flickering stimulus and hallucinations

See Rule - Ermentrout 2011.

Demo!!

Study of a 2d neural field model of simple visual hallucinations

$\Rightarrow$ **Mathematical analysis of the model of Ermentrout-Cowan of visual hallucinations.**

The membrane potential $V(\mathbf{x}, t)$ of the population at location $\mathbf{x} \in \mathbb{R}^2$ satisfies the equation

$$\tau \frac{d}{dt} V(\mathbf{x}, t) = -V(\mathbf{x}, t) + \int_{\mathbb{R}^2} J(\|\mathbf{x} - \mathbf{y}\|) S_0 \left[\sigma V(\mathbf{y}, t)\right] d\mathbf{y} \stackrel{def}{=} (-V + \mathbf{J} \cdot S_0(\mu V))(\mathbf{x}) \quad (2)$$

where $S_0(x) = s_1 x + \frac{s_2}{2} x^2 + \frac{s_3}{6} x^3 + \cdots$ is C^3 bounded and such that $S_0(0) = 0$.

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We note that $V = 0$ is an equilibrium and we rewrite (2) as $\frac{d}{dt} V = \mathbf{A} V + \mathbf{R}(V, \mu)$ with

$$\mathbf{A} = -Id + \sigma_c s_1 \mathbf{J}, \quad \mathbf{R}(V, \mu) = \mathbf{J} \cdot S_0((\sigma_c + \mu) V) - \sigma_c s_1 \mathbf{J} \cdot V.$$

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Hence, we perform a perturbation of $V = 0$ around the parameter value $\sigma = \sigma_c$ that we shall precise later.

Assumptions regarding the connectivity

We make the following assumptions concerning our problem (2).

- we assume that $J \in \mathrm{H}^1(\mathbb{R}^2)$ for regularity of the nonlinearity
- we assume that $J \in \mathrm{L}^1(\mathbb{R}^2)$ to be able to perform Fourier transforms.

This implies that $J \in \mathrm{L}^\infty(\mathbb{R}^2)$ by Sobolev embedding theorems.

A fundamental feature of the equations (2) lies in their symmetries. Indeed, the following linear representations of the symmetries commute with the vector field (2), we have the symmetries of translations

$$\mathcal{T}_{\mathbf{t}} \cdot V(\mathbf{x}) = V(\mathbf{x} - \mathbf{t}),$$

of rotations

$$\mathcal{R}_\theta \cdot V(\mathbf{x}) = V(\mathbf{R}_{-\theta}\mathbf{x}), \quad \mathrm{R}_\theta = \begin{pmatrix} \cos\theta & \sin\theta \\ -\sin\theta & \cos\theta \end{pmatrix},$$

and of reflections

$$\mathcal{S} \cdot V(\mathbf{x}) = V(\mathbf{S}^{-1}\mathbf{x}), \quad \mathbf{S} = \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix}.$$

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These transformations raise an issue in view of the application of the center manifold Theorem. **Why?**

$\Rightarrow$ if $U(\mathbf{x})$ is in the kernel $ker\mathbf{A}$, then its $\mathbb{R}^2$-orbit $\mathbf{t} \to \mathcal{T}_{\mathbf{t}} \cdot U$ gives an infinite center part $\Sigma_0(\mathbf{A})$. Hence, we need to reduce the symmetry group in order to bypass this difficulty.

To circumvent this issue, we further assume that V has some **periodicity**. More precisely, we define a **planar lattice** $\mathcal{L}$ as a set of integer linear combinations of two independent vectors $\vec{l}_1$ and $\vec{l}_2$

$$\mathcal{L} = \{m\vec{l}_1 + n\vec{l}_2,\ m, n \in \mathbb{Z}\}.$$

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It forms a discrete subgroup of $\mathbb{R}^2$. To each lattice, we associate a dual lattice $\mathcal{L}^*$ generated by two linearly independent vectors $\vec{k}_1$ and $\vec{k}_2$ that satisfy $\vec{k}_i \cdot \vec{l}_j = \delta_{ij}$

$$\mathcal{L}^* = \{n\vec{k}_1 + m\vec{k}_2,\ \ m, n \in \mathbb{Z}\}.$$

The largest subgroup of $O(2)$ which keeps the lattice invariant is called the **holohedry** of the lattice. There are 3 lattices in the plane as summarized in the next table.

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

Reduction of symmetries 1/2

$\Rightarrow$ We look for solutions V of (2) which are doubly periodic on the **square lattice** with basis $\vec{l}_1 = \vec{k}_1 = (1,0)$ and $\vec{l}_2 = \vec{k}_2 = (0,1)$.

We require that $V(\mathbf{x}+\mathbf{l}) = V(\mathbf{x})$ for all $\mathbf{l} \in \mathcal{L}_{square}$ and $\mathbf{x} \in \mathbb{R}^2$.

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We require that $V(\mathbf{x}+\mathbf{l}) = V(\mathbf{x})$ for all $\mathbf{l} \in \mathcal{L}_{square}$ and $\mathbf{x} \in \mathbb{R}^2$. It gives an equation on the **domain** $(0,1)^2 \stackrel{def}{=} \mathcal{D}$ of the lattice:

$$\dot{V} = -V + \tilde{\mathbf{J}} \cdot S_0(\mu V) = \mathbf{A}V + \mathbf{R}(V,\mu)$$

where $\tilde{\mathbf{J}} \cdot U = \int_{\mathcal{D}} \tilde{J}(\cdot - \mathbf{y})U(\mathbf{y})d\mathbf{y}$ and $\tilde{J} \stackrel{def}{=} \sum_{l \in \mathcal{L}} J(\cdot + l)$.

Lemma

- $\tilde{J}$ is doubly periodic.
- $\tilde{J} \in \mathrm{L}^2(\mathcal{D})$ since $J \in \mathrm{L}^1(\mathbb{R}^2)$.

Reduction of symmetries 2/2

$\Rightarrow$ Reduction of the symmetry group of the equations.

- The group of spatial translations is now isomorphic to the torus $\mathbb{T}^2 \equiv \mathbb{R}^2/\mathbb{Z}^2$.
- The model is also symmetric with respect to the transformations that leave the basic structure invariant i.e. *dihedral* group $\mathbf{D}_4 = \langle \mathcal{R}_{\pi/4}, \mathcal{S} \rangle$ generated by $\mathcal{R} \stackrel{def}{=} \mathcal{R}_{\pi/4}$ and $\mathcal{S}$ which act on the membrane potential as: $\mathcal{R} \cdot V(x, y) = V(y, x)$ and $S \cdot V(x, y) = V(x, -y)$.

The full symmetry group is then:

$$G_{sq} = \mathbf{D}_4 \times \mathbb{T}^2.$$

Functional setting

We wish to apply the CMT in a Hilbert spaces setting for simplicity. Hence, we consider the space of periodic square integrable functions

$$\mathcal{X} = \mathrm{L}^2_{per}(\mathcal{D})$$

where $\mathcal{D} = \left(-\frac{1}{2}, \frac{1}{2}\right)^2$. In order to have a differentiable reminder $\mathbf{R}$ and to be able to perform Taylor expansion, it is convenient that the domain of $\mathbf{R}$ is a Banach algebra. This is the case for example when we consider the Sobolev space of periodic functions

$$\mathcal{Z} = H^1_{per}(\mathcal{D}).$$

The Cauchy problems is formulated with $\mathbf{A} = -id + \mu_c s_1 \tilde{\mathbf{J}} \in \mathcal{L}(\mathcal{Z}, \mathcal{X})$ and $\mathbf{R}(V, \mu) = \tilde{\mathbf{J}} \cdot S_0(\mu V) - \mu_c s_1 \tilde{\mathbf{J}} \cdot u \in C^\infty(\mathcal{Z} \times \mathbb{R}, \mathcal{X})$.

Lemma

Assume that $0 \in \Sigma(\mathbf{A})$. Then, the neural fields equations (2) have a parameter dependent center manifold $\mathcal{M}(\mu)$.

Static bifurcation

We now assume that (2) features a static bifurcation, meaning that $E_c = \ker \mathbf{A} \neq \{0\}$. More precisely, we assume that

$$\ker \mathbf{A} = \left\{ z = \sum_{j=1}^{2} z_j e^{2i\pi \mathbf{k}_j \cdot \mathbf{x}} + c.c.,\ z_i \in \mathbb{C} \right\} \subset \mathcal{Z}$$

which is a 4-dimensional space. Note that it is possible to have an 8-dimensional space by carefully choosing the eigenvectors. This condition sets the value σ_c of the stiffness parameter, namely, we set

$$\sigma_c = \inf_{\sigma \in \mathbb{R}_+} \{\exists \mathbf{k} \in \mathcal{L}^*,\ 1 = s_1 \sigma \hat{J}_{\mathbf{k}}\}.$$

Remark

In practice, we can apply the CMT to every σ such that $1 = s_1 \sigma \hat{J}_{\mathbf{k}}$ for some $\mathbf{k} \in \mathcal{L}^*$. We call these σs **bifurcation points** of the Cauchy problem. However, the bifurcation points larger than σ_c will generally lead to unstable trajectories which is why we focus on σ_c here.

Equivariant version of CMT and NFT

Theorem (CMT)

We assume that there is there is a linear operator $\mathbf{T} \in \mathcal{L}(\mathcal{X}) \cap \mathcal{L}(\mathcal{Z})$ which commutes with the vector field:

$$\mathbf{TA} = \mathbf{AT}, \quad \mathbf{TR}(u) = \mathbf{R}(\mathbf{T}u).$$

We further assume that the restriction $\mathbf{T}_0$ of $\mathbf{T}$ to the center subspace $\mathcal{E}_0$ is an isometry. Under the assumptions CMT, one can find a reduction function Ψ which commutes with $\mathbf{T}$, *i.e.*, $\mathbf{T}\Psi(u_0) = \Psi(\mathbf{T}_0 u_0)$ for all $u_0 \in \mathcal{E}_0$, and such that the vector field in the reduced equation commutes with T_0.

Theorem (Normal form)

If we further assume that there is an **isometry** $\mathbf{T} \in \mathcal{L}(\mathbb{R}^n)$ which commutes with $\mathbf{A}$ and $\mathbf{R}$, then the polynomials $\Phi, \mathbf{N}$ commutes with $\mathbf{T}$.

Lemma

The normal form at order three associated with the 4-dimensional space of the G_{sq}-equivariant problem satisfies:

$$\begin{cases} \dot{z}_1 = z_1 \left(\alpha + \beta|z_1|^2 + \gamma|z_2|^2\right) \\ \dot{z}_2 = z_2 \left(\alpha + \beta|z_2|^2 + \gamma|z_1|^2\right) \end{cases}$$

where $\alpha, \beta, \gamma \in \mathbb{R}$.

Stripes or spots?

Close to the bifurcation point $\sigma = \sigma_c$, we have $V(x,t) = v_0(x,t) + \tilde{\Psi}(v_0(x,t),\mu)$. The above normal form has equilibria $(0,0), (z_{st}, z_{st}), (z_{sp}, 0), (0, z_{sp})$ with opposite stability where $z_{st}, z_{sp} \in \mathbb{R}$.

The ODE - NF is easy to study with polar coordinates for example. One then finds

$$V_{spot}(x,y) \approx z_{sp} e^{2i\pi k_1 x} + z_{sp} e^{2i\pi k_1 y} + c.c. = 2z_{sp} \left(\cos(2\pi x) + \cos(2\pi y)\right)$$

or

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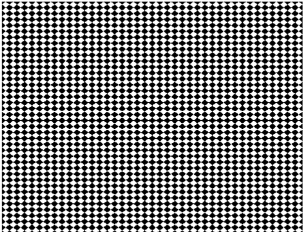
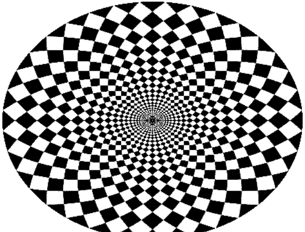
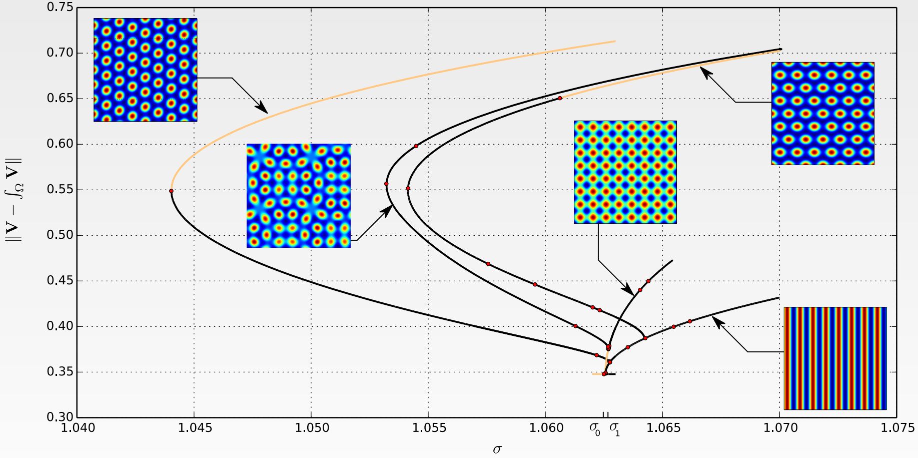
Hence, depending on the stability of the equilibria of (58), one finds that the solutions of (2) close to the equilibrium $V = 0$ for $\sigma \approx \sigma_c$ converge to $V = 0$ or to stripe / spot patterns.





Recall the bifurcation diagram...



Bonus

In order to be able to tell whether the stripe or spot patterns are stable, we need to be able to compute the coefficients α, β, γ of the normal form as function of the different parameters of the model.

Lemma

The normal form has the following coefficients:

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

$$\gamma/\mu_c^3\hat{\mathbf{J}}_{\mathbf{k}_c} = \mu_c s_2^2 \quad \left[\frac{\hat{\mathbf{J}}_0}{1-\hat{\mathbf{J}}_0/\mathbf{J}_{\mathbf{k}_c}} + 2\frac{\hat{\mathbf{J}}_{(1,1)}}{1-\hat{\mathbf{J}}_{(1,1)}/\hat{\mathbf{J}}_{\mathbf{k}_c}}\right] \quad + \quad s_3.$$

Internships

Have a look at
http://romainveltz.pythonanywhere.com/internships/