INTRODUCTION TO MESOSCOPIC MODELS OF VISUAL CORTICAL STRUCTURES

Romain Veltz / Etienne Tanré November 16th, 2023

NEURAL FIELDS MODELS

OUTLINE



Neural Fields models

- Structure of primary visual cortex (V1)
 - Anatomy
 - Cortical layers organization of V1
 - Functional architecture of V1
- 3 Applications of Neural field models
 - The Ring Model of Orientation tuning
 - The Ermentrout-Cowan mode
 - Bressloff-Cowan-Golubitsky-Thomas-Wiener model
 - A more realistic model of V1
 - Grid cells

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

- Mesoscopic model of bounded cortical area Ω



- Mesoscopic model of bounded cortical area $\boldsymbol{\Omega}$
- \cdot Continuum of populations



NEURAL FIELDS

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- Continuum of populations
- Populations communicate via horizontal connections through gray matter with delays



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- Population activity: vector V(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,

Can we write equations for $V(\mathbf{x}, t)$?

• 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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a single action potential from neurons in population j, is seen as a **post-synaptic potential** $PSP_{ij}(t - s)$ by neurons in population i (s is the time of the spike hitting the synapse and t the time after the spike)

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

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

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

we end up with a system of ODEs:

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

which we rewrite in vector form.

$$\dot{V} = -LV + WS(V) + I_{\text{ext}}$$

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

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which we rewrite in vector form:

$$\dot{V} = -LV + WS(V) + I_{\text{ext}}$$

 \Rightarrow the synapses are very short lasting, the dominant time constant is the membrane time constant

• 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

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

which we rewrite in vector form:

$$\dot{A} = -LA + S(WA + I_{ext})$$

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 \Rightarrow the synapses are long lasting, the dominant time constant is the membrane time constant

NEURAL FIELDS MODELS

- 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
- We note V(r, t) (resp. A(r, t)) the state vector at point r in Ω
- We introduce the $p \times p$ matrix $W(\mathbf{r}, \mathbf{\bar{r}}, t)$

Voltage-based neural fields equations

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

Activity-based neural fields equations

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

$$\left(\int_{\Omega} W(\mathbf{r}, \mathbf{\bar{r}}, t) \mathsf{A}(\mathbf{\bar{r}}, t) d\mathbf{\bar{r}}\right)_{i} := \sum_{j} \int_{\Omega} W_{ij}(\mathbf{r}, \mathbf{\bar{r}}, t) A_{j}(\mathbf{\bar{r}}, t) d\mathbf{\bar{r}}$$

- 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
- \cdot the sigmoid function can be approximated by a Heaviside function
- $W(r, \bar{r}, t)$ is often chosen symmetric and translation invariant:

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

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

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 V(t) is thought of as a mapping $V : \mathbb{R}^+ \to \mathcal{F}$):

The nonlinear operator **G** is defined by:

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

Theorem

If the following two hypotheses are satisfied:

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

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

- for all $t > 0, G(t, \cdot) : \mathcal{F} \to \mathcal{F}$, (well-posedness of the problem)
- $G: (t, V) \rightarrow G(t, V)$ is continuous in (t, V)
- $\|\mathbf{G}(t, \mathbf{V}_1) \mathbf{G}(t, \mathbf{V}_2)\|_{\mathcal{F}} \leq KDS_m \sup_{t \in \mathbb{R}^+} \|\mathbf{W}(t)\|_{L^{\infty}} \|\mathbf{V}_1 \mathbf{V}_2\|_{\mathcal{F}}$ 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

- 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:

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

to

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

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

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

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

Without space

• [de Masi et al. 15] spiking network

$$\begin{split} X_{t}^{N,i} &= X_{0}^{N,i} - \lambda \int_{0}^{t} X_{s}^{N,i} ds - \int_{0}^{t} \int_{0}^{\infty} X_{s-}^{N,i} \mathbf{1}_{\left\{z \leq f\left(X_{s-}^{N,i}\right)\right\}} \mathbf{N}^{i}(ds, dz) \\ &+ \frac{1}{N} \sum_{j \neq i} \int_{0}^{t} \int_{0}^{\infty} \mathbf{1}_{\left\{z \leq f\left(X_{s-}^{N,j}\right)\right\}} \mathbf{N}^{i}(ds, dz) \end{split}$$

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

• [Cormier et al. 19] spiking network

$$X_{t} = X_{0} + \int_{0}^{t} \mathbb{E}(X_{s}) + b(X_{s})ds - \int_{0}^{t} \int_{0}^{\infty} X_{s-1} \{z \le f(X_{s-1})\} \mathbf{N}(ds, dz)$$

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

What do you notice?

STRUCTURE OF PRIMARY VISUAL CORTEX (V1)

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

ANATOMY OF THE VISUAL PATHWAY



RETINOTOPY, FROM TOOTELL-1988 (MONKEY)

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



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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]



ORIENTATION COLUMNS

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

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



From [Dragoi et al. 2000] (Cat)



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?

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

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



Applications of Neural field models

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- 1 Neural Fields models
- 2) Structure of primary visual cortex (V1)
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RING MODEL OF ORIENTATION: EXPERIMENTAL FACTS




RING MODEL OF ORIENTATION: MECHANISM



Goal: reduce to one population.

Consider two populations E/I

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

Then

$$(\tau_E \frac{d}{dt} + 1) V_E = (J_{EE} - \alpha J_{EI} \cdot J_{IE}) \cdot S_E(V_E) + I_E - \alpha J_{EI} \cdot I_I$$

$$\equiv J \cdot S_E(V_E) + I$$

MEXICAN HAT CONNECTIVITY



Motivation for the Ring Model: single population on $\Omega=\mathsf{S}^1$



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

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

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:

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

where τ is a temporal synaptic constant ($\tau \approx 10ms$), $W(\mathbf{r}, \mathbf{\bar{r}}) = w(||\mathbf{r} - \mathbf{\bar{r}}||)$ 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:

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

GEOMETRIC VISUAL HALLUCINATIONS: REDRAWN



Figure 1. (a) 'Phosphene' produced by deep binocular





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



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

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

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

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

- $\cdot~$ 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



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]):

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

- $\cdot \, \, \Omega$ is a piece of visual cortex, open bounded.
- S is a sigmoid function, bounded, increasing
- I_{thal}(x), input from the thalamus, here = 0
- $\cdot \ J(x,y)$ is the connection strength between neurons at positions x and y
- Synaptic/Propagation delays neglected.
- \Rightarrow Note that we have lumped many populations in an equation for a single population!

See [Bressloff:03]

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

Local connections

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





Qualitative analysis of dynamics on \mathcal{T}_ϵ : Square lattice case







Some planforms in the square case









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
- $W(\mathbf{r}_j, \mathbf{r}_j) = G(\mathbf{r}_j \mathbf{r}_j le_{\theta_j})$, 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



$$S(t) = A \sin(2\pi t/T)$$

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

$$\tau \frac{d}{dt} V(\mathbf{x}, t) = -V(\mathbf{x}, t) + \int_{\mathbb{R}^2} J(\|\mathbf{x} - \mathbf{y}\|) S_0 \left[\sigma V(\mathbf{y}, t)\right] d\mathbf{y} \stackrel{def}{=} (-V + \mathbf{J} \cdot S_0(\mu V))(\mathbf{x})$$
(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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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 $S_0(0) = 0$. We note that V = 0 is an equilibrium and we rewrite (2) as $\frac{d}{dt}V = AV + R(V, \mu)$ with

$$\mathbf{A} = -Id + \sigma_c \mathsf{S}_1 \mathbf{J}, \quad \mathbf{R}(\mathsf{V}, \mu) = \mathbf{J} \cdot \mathsf{S}_0((\sigma_c + \mu)\mathsf{V}) - \sigma_c \mathsf{S}_1 \mathbf{J} \cdot \mathsf{V}.$$

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

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

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

This implies that $J \in L^{\infty}(\mathbb{R}^2)$ 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

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

of rotations

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

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?**

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

and of reflections

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

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*A, then its \mathbb{R}^2 -orbit $\mathbf{t} \to \mathcal{T}_t \cdot U$ 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 ${\cal L}$	Basis of \mathcal{L}^*
Square	D4	$\vec{l}_1 = (1,0), \vec{l}_2 = (0,1)$	$\vec{k}_1 = (0, 1), \vec{k}_2 = (1, 0)$
Rhombic	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	D ₆	$\vec{l}_1 = (\frac{1}{\sqrt{3}}, 1), \vec{l}_2 = (\frac{2}{\sqrt{3}}, 0)$	$\vec{k}_1 = (0, 1), \vec{k}_2 = (\frac{\sqrt{3}}{2}, -\frac{1}{2})$

 \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 $\mathbf{x} \in \mathbb{R}^2$.

⇒ 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 $\mathbf{x} \in \mathbb{R}^2$. It gives an equation on the **domain** $(0, 1)^2 \stackrel{def}{=} \mathcal{D}$ of the lattice:

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

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

Lemma

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

 \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:

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

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

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

where $\mathcal{D} = \left(-\frac{1}{2}, \frac{1}{2}\right)^2$. In order to have a differentiable reminder **R** and to be able to perform Taylor expansion, it is convenient that the domain of **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 $0 \in \Sigma(A)$. 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 $E_c = \ker A \neq \{0\}$. More precisely, we assume that

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

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 $1 = s_1 \sigma \hat{J}_k$ for some $\mathbf{k} \in \mathcal{L}^*$. We call these σ s **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.

Theorem (CMT)

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

$$TA = AT$$
, $TR(u) = R(Tu)$.

We further assume that the restriction T_0 of 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 T, *i.e.*, $T\Psi(u_0) = \Psi(T_0u_0)$ 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** $T \in \mathcal{L}(\mathbb{R}^n)$ which commutes with A and R, then the polynomials Φ , N commutes with 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 $\alpha, \beta, \gamma \in \mathbb{R}$.
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

$$V_{stripe}(x, y) \approx z_{st} e^{2i\pi k_1 x} c.c. = 2z_{st} \cos(2\pi x).$$

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 $z_{st}, z_{sp} \in \mathbb{R}$.

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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.





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:

$$\begin{split} \beta/\mu_c^3 \hat{\mathbf{j}}_{k_c} &= \mu_c S_2^2 \quad \left[\frac{\hat{j}_0}{1 - \hat{j}_0 / J_{k_c}} + \frac{\hat{j}_{2k_c}}{2(1 - \hat{j}_{2k_c} / \hat{j}_{k_c})} \right] &+ S_3/2 \\ \gamma/\mu_c^3 \hat{\mathbf{j}}_{k_c} &= \mu_c S_2^2 \quad \left[\frac{\hat{j}_0}{1 - \hat{j}_0 / J_{k_c}} + 2 \frac{\hat{j}_{(1,1)}}{1 - \hat{j}_{(1,1)} / \hat{j}_{k_c}} \right] &+ S_3. \end{split}$$