## INTRODUCTION TO MESOSCOPIC MODELS OF VISUAL CORTICAL STRUCTURES

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Neural Fields models

## OUTLINE

(9) Neural Fields models

Structure of primary visual cortex (V1)

- Anatomy
- Cortical lavers organization of V1
- Functional architecture of V1
(3) Applications of Neural field models
- The Ring Model of Orientation tun ing
- The Ermentrout-Cowan model
- Bressloff-Cowan-Golubitsky-Thomas-Wiener model
- A more realistic model of V1
- Grid cells
(4) Study of a $2 d$ neural field model of simple visual hallucinations


## NEURAL FIELDS

- Mesoscopic model of bounded cortical area $\Omega$


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

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- Population activity: vector $\mathrm{V}(\mathrm{x}, \mathrm{t})$ 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 $V(x, t)$ ?

## 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 $\nu_{i}(t)=S_{i}\left(V_{i}(t)\right)$, where $S_{i}$ is sigmoidal:

$$
S_{i}(x)=\frac{S_{i m}}{1+e^{-\sigma_{i}\left(x-\theta_{i}\right)}}
$$

$\sigma_{i}$ is the nonlinear gain and $\theta_{i}$ is the threshold

Recall the f-I curve from Lecture 2.

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(3) the number of spikes arriving between $t$ and $t+d t$ is $\nu_{j}(t) d t$, then the average membrane potential of population $i$ is:

$$
\begin{aligned}
& V_{i}(t)=\sum_{j} \int_{t_{0}}^{t} P S P_{i j}(t-s) S_{j}\left(V_{j}(s)\right) d s \\
& \nu_{i}(t)=S_{i}\left(\sum_{j} \int_{t_{0}}^{t} P S P_{i j}(t-s) \nu_{j}(s) d s\right)
\end{aligned}
$$

## THE VOLTAGE-BASED MODEL

It is based on the hypotheses:
(0) the post-synaptic potential has the same shape no matter what presynaptic population $j$ caused it, this leads to

$$
P S P_{i j}(t)=w_{i j} P S P_{i}(t)
$$

$w_{i j}$ is the average strength of the post-synaptic potential and if $w_{i j}>0$ (resp.
$w_{i j}<0$ ) population $j$ excites (resp. inhibits) population $i$
(2) if we assume that $P S P_{i}(t)=e^{-t / \tau_{i}} H(t)$ or equivalently

$$
\tau_{i} \frac{d P S P_{i}(t)}{d t}+P S P_{i}(t)=\delta(t)
$$

we end up with a system of ODEs:

$$
\tau_{i} \frac{d V_{i}(t)}{d t}+V_{i}(t)=\sum_{j} w_{i j} S_{j}\left(V_{j}(t)\right)+l_{e x t}^{i}(t)
$$

which we rewrite in vector form:

$$
\dot{\mathrm{V}}=-\mathrm{LV}+\mathrm{WS}(\mathrm{~V})+\mathrm{I}_{\text {ext }}
$$

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$$

which we rewrite in vector form:

$$
\dot{\mathrm{V}}=-\mathrm{LV}+\mathrm{WS}(\mathrm{~V})+\mathrm{I}_{\mathrm{ext}}
$$

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

It is based on the hypotheses:
(0) the same shape of a PSP depends only on the presynaptic cell, this leads to

$$
P S P_{i j}(t)=w_{i j} P S P_{j}(t)
$$

(2) we also suppose that $P S P_{j}(t)=e^{-t / \tau_{j}} H(t)$ and we end up with a system of ODE

$$
\tau_{i} \frac{d A_{i}(t)}{d t}+A_{i}(t)=S_{i}\left(\sum_{j} w_{i j} A_{j}(t)+l_{e x t}^{i}(t)\right)
$$

which we rewrite in vector form:

$$
\dot{A}=-L A+S\left(W A+I_{\text {ext }}\right)
$$

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$$

which we rewrite in vector form:

$$
\dot{\mathrm{A}}=-\mathrm{LA}+\mathrm{S}\left(\mathrm{WA}+\mathrm{I}_{\text {ext }}\right)
$$

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

## 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 $\mathrm{V}(r, t)$ (resp. $\mathrm{A}(\mathrm{r}, \mathrm{t})$ ) the state vector at point r in $\Omega$
(4) We introduce the $p \times p$ matrix $\mathrm{W}(r, \bar{r}, t)$

## Voltage-based neural fields equations

$$
\frac{d V(r, t)}{d t}=-\operatorname{LV}(r, t)+\int_{\Omega} W(r, \bar{r}, t) S(V(\bar{r}, t)) d \bar{r}+I_{\text {ext }}(r, t)
$$

## Activity-based neural fields equations

$$
\begin{aligned}
& \frac{d A(r, t)}{d t}=-L A(r, t)+S\left(\int_{\Omega} W(r, \bar{r}, t) A(\bar{r}, t) d \bar{r}+I_{\text {ext }}(r, t)\right) \\
& \left(\int_{\Omega} W(r, \bar{r}, t) A(\bar{r}, t) d \bar{r}\right)_{i}:=\sum_{j} \int_{\Omega} W_{i j}(r, \bar{r}, t) A_{j}(\bar{r}, t) d \bar{r}
\end{aligned}
$$

## REMARKS

- when $d=1$, most widely studied because of its relative mathematical simplicity but of limited biological interest
- when $\mathrm{d}=2$, 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
- $\mathbf{W}(r, \bar{r}, t)$ is often chosen symmetric and translation invariant:

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

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


## CAUCHY PROBLEM FOR NFE

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

$$
\left\{\begin{array}{l}
\frac{d \mathrm{~V}}{d t}=-\mathrm{LV}+\mathrm{G}(t, \mathrm{~V}), \quad t>0  \tag{1}\\
\mathrm{~V}(0)=\mathrm{V}_{0} \in \mathcal{F}
\end{array}\right.
$$

The nonlinear operator G is defined by:

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

## Theorem

If the following two hypotheses are satisfied:

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


## ELEMENT OF THE PROOF

- for all $t>0, \mathrm{G}(t, \cdot): \mathcal{F} \rightarrow \mathcal{F}$, (well-posedness of the problem)
- $\mathrm{G}:(t, \mathrm{~V}) \rightarrow \mathrm{G}(t, \mathrm{~V})$ is continuous in $(t, \mathrm{~V})$
- $\left\|\mathrm{G}\left(t, \mathrm{~V}_{1}\right)-\mathrm{G}\left(t, \mathrm{~V}_{2}\right)\right\|_{\mathcal{F}} \leq K D S_{m} \sup _{t \in \mathbb{R}^{+}}\|\mathrm{W}(t)\|_{\mathrm{L}^{\infty}}\left\|\mathrm{V}_{1}-\mathrm{V}_{2}\right\|_{\mathcal{F}}$ for all $t>0$ and $\mathrm{V}_{1}, \mathrm{~V}_{2} \in \mathcal{F}$ where $D S_{m}=\sup _{i=1 \cdots p}\left\|S_{i}^{\prime}\right\|_{\infty}$ (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 1/2

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

$$
\dot{V}=V-\frac{V^{3}}{3}-W+\mathcal{L}_{\rho_{0}}(V), \quad \dot{W}=V+a-b W
$$

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

## Mean-Field limits, McKean-VLASOV 2/2

## Without space

- [de Masi et al. 15] spiking network

$$
\begin{array}{ll}
x_{t}^{N, i}= & x_{0}^{N, i}-\lambda \int_{0}^{t} x_{s}^{N, i} d s-\int_{0}^{t} \int_{0}^{\infty} x_{s-}^{N, i} 1_{\left\{z \leq f\left(x_{s-}^{N, i}\right)\right\}^{N^{i}}(d s, d z)}^{+} \quad \frac{1}{N} \sum_{j \neq i} \int_{0}^{t} \int_{0}^{\infty} 1_{\left\{z \leq f\left(x_{s-}^{N, j}\right)\right\}^{N^{j}(d s, d z)}}
\end{array}
$$

with limit $X_{t}=X_{0}+\int_{0}^{t} \mathbb{E}\left(X_{s}\right)-\lambda X_{s} d s-\int_{0}^{t} \int_{0}^{\infty} X_{s-1} 1_{\left\{z \leq f\left(X_{s-}\right)\right\}} N(d s, d z)$

- [Cormier et al. 19] spiking network

$$
x_{t}=X_{0}+\int_{0}^{t} \mathbb{E}\left(X_{s}\right)+b\left(X_{s}\right) d s-\int_{0}^{t} \int_{0}^{\infty} X_{s-1} 1_{\left\{z \leq f\left(x_{s-}\right)\right\}} N(d s, d z)
$$

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

What do you notice?

## Structure of primary visual cortex (V1)

## OUTLINE

(1) Neural Fields models
(2) Structure of primary visual cortex (V1)

- Anatomy
- Cortical layers organization of V1
- Functional architecture of V1
(3) Annlications of Neural field models
- The Ring Model of Orientation tuning
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## ANATOMY OF THE VISUAL PATHWAY



## Retinotopy, From Tootell-1988 (Monkey)

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



## 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]


## ORIENTATION COLUMNS

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]


## 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?

$$
\text { Res }=F\left(I_{\text {thal }}\right) \quad \text { V.s } \quad \text { Res }=F\left(\text { Res, }\left.\epsilon\right|_{\text {thal }}\right) .
$$

## A CLOSER LOOK AT ORIENTATION SELECTIVITY

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





## Applications of Neural field models

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## RING MODEL OF ORIENTATION: EXPERIMENTAL FACTS



C




## MEXICAN HAT CONNECTIVITY

Goal: reduce to one population.

Consider two populations E/I

$$
\begin{aligned}
\left(\tau_{E} \frac{d}{d t}+1\right) V_{E} & =J_{E E} \cdot S_{E}\left(V_{E}\right)-J_{E I} \cdot S_{I}\left(V_{I}\right)+I_{E} \\
\left(\tau_{I} \frac{d}{d t}+1\right) V_{I} & =J_{I E} \cdot S_{E}\left(V_{E}\right)+I_{I}
\end{aligned}
$$

- Neglect /I
- Gaussian kernels
- Inhibition is recruited $S_{l}\left(V_{l}\right) \approx \alpha V_{1}$

Then

$$
\begin{aligned}
\left(\tau_{E} \frac{d}{d t}+1\right) V_{E} & =\left(J_{E E}-\alpha J_{E I} \cdot \jmath_{I E}\right) \cdot S_{E}\left(V_{E}\right)+\jmath_{E}-\alpha J_{E I} \cdot \jmath_{।} \\
& \equiv \jmath \cdot S_{E}\left(V_{E}\right)+।
\end{aligned}
$$



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



- One population with Mexican hat connectivity
- $\bar{V}(\theta, t) \equiv \int_{0}^{1} r V(r, \theta, t) d r$

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

## Ring Model of orientation tuning: EQuation

We consider the following equation:

$$
\tau \frac{d V(\theta, t)}{d t}=-V(\theta, t)+\int_{-\pi / 2}^{\pi / 2} J\left(\theta-\theta^{\prime}\right) S\left(V\left(\theta^{\prime}, t\right)\right) \frac{d \theta^{\prime}}{\pi}+\epsilon I(\theta)
$$

where $\tau$ is a temporal synaptic constant ( $\tau \approx 10 \mathrm{~ms}$ ), $J\left(\theta-\theta^{\prime}\right)$ 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:

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

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



## ERMENTROUT-COWAN MODEL

We consider the following equation:

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

where $\tau$ is a temporal synaptic constant ( $\tau \approx 10 \mathrm{~ms}$ ), $W(r, \bar{r})=W(\|r-\bar{r}\|)$ 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




## BRESSLOFF-COWAN-GOLUBITSKY-THOMAS-WIENER MODEL

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

$$
\tau \frac{d V(\mathbf{r}, \theta, t)}{d t}=-V(\mathbf{r}, \theta, t)+\int_{\mathbb{R}^{2}} \int_{-\pi / 2}^{\pi / 2} W\left(\mathbf{r}, \theta \mid \overline{\mathbf{r}}, \theta^{\prime}\right) S\left(V\left(\overline{\mathrm{r}}, \theta^{\prime}, t\right)\right) d \overline{\mathbf{r}} \frac{d \theta^{\prime}}{\pi}
$$

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

$$
W\left(\mathbf{r}, \theta \mid \overline{\mathbf{r}}, \theta^{\prime}\right)=J\left(\theta-\theta^{\prime}\right) \delta_{\mathrm{r}, \overline{\mathbf{r}}}+\beta\left(1-\delta_{\mathrm{r}, \overline{\mathbf{r}}}\right) W_{l a t}(\mathbf{r}-\overline{\mathbf{r}}, \theta)
$$

- for $\beta=0$, we recover the Ring Model of orientation tuning
- if $V(r, \theta, t)$ is independent of $\theta$ 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 $V(x)$ of neurons at position $x \in \Omega \subset$ V1 (see [Veltz-etal:15]):

$$
\tau \frac{d V(\mathrm{x})}{d t}=-V(\mathrm{x})+\int_{\Omega} J(\mathrm{x}, \mathrm{y}) S(V(\mathrm{y})) d \mathrm{y}+I_{\text {thal }}(\mathrm{x})
$$

- $\Omega$ is a piece of visual cortex, open bounded.
- $S$ is a sigmoid function, bounded, increasing
- $I_{\text {thal }}(x)$, input from the thalamus, here $=0$
- $J(x, y)$ 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!


## CONNECTIONS MODEL FOR VISUAL CORTEX

See [Bressloff:03]

$$
J(x, y)=J_{\text {loc }}(\|x-y\|)+\epsilon \operatorname{l}_{\text {lat }}(x, y)
$$

## Local connections

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

Long-range connections, symmetry-breaking term
$J_{L R}(\mathrm{x}, \mathrm{y})=G_{\sigma_{\theta}}(\theta(\mathrm{x})-\theta(\mathrm{y})) J_{0}\left(\chi, R_{-2 \theta(\mathrm{x})}(\mathrm{x}-\mathrm{y})\right)$

- Anisotropy function $J_{0}(x)=\exp -\left((1-\chi) x_{1}^{2}+x_{2}^{2}\right) / 2 \sigma_{\text {lat }}^{2}, \chi \in[0,1]$
(1) $\chi>0$ Tree Shew
(2) $\chi=0$ Macaque


## EXAMPLES OF PO MAPS, TILINGS OF $\Omega 2 / 2$

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


## BIFURCATION DIAGRAM, SQUARE CASE, $\epsilon=0$



## QUALITATIVE ANALYSIS OF DYNAMICS ON $\mathcal{T}_{\epsilon}$ : SQUARE LATTICE CASE




$$
\begin{array}{|l|l|l|}
\hline- & - & - \\
\hline-: & - \\
\hline-: & - \\
\hline-: & - \\
\hline- & - & - \\
\hline \text { PO } \operatorname{ma\rho } \rho^{2}
\end{array}
$$

## GRID CELLS MODEL 1/2

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

$$
\tau \frac{d A\left(\mathbf{r}_{i}, t\right)}{d t}=-A\left(\mathbf{r}_{i}, t\right)+S\left(\sum_{j} W\left(\mathbf{r}_{j}, \mathbf{r}_{j}\right) A\left(\mathbf{r}_{j}, t\right)+I_{\text {ext }}\left(\mathbf{r}_{i}, t\right)\right)
$$

- Inverted mexican hat function $G$
- $W\left(r_{j}, r_{j}\right)=G\left(r_{j}-r_{j}-l e_{\theta_{j}}\right)$, all inhibitory
- $l_{\text {ext }}\left(r_{i}\right)=A\left(x_{i}\right)\left(1+\alpha e_{\theta_{j}} \cdot v\right)$



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

$$
\begin{equation*}
\tau \frac{d}{d t} V(\mathbf{x}, t)=-V(\mathbf{x}, t)+\int_{\mathbb{R}^{2}} J(\|\mathbf{x}-\mathbf{y}\|) S_{0}[\sigma V(\mathbf{y}, t)] d \mathbf{y} \stackrel{\text { def }}{=}\left(-V+\mathrm{J} \cdot \mathrm{~S}_{0}(\mu V)\right)(\mathbf{x}) \tag{2}
\end{equation*}
$$

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 $S_{0}(0)=0$.
$\Rightarrow$ Mathematical analysis of the model of Ermentrout-Cowan of visual hallucinations. The membrane potential $V(x, t)$ of the population at location $x \in \mathbb{R}^{2}$ satisfies the equation

$$
\begin{equation*}
\tau \frac{d}{d t} V(x, t)=-V(x, t)+\int_{\mathbb{R}^{2}} J(\|x-y\|) S_{0}[\sigma V(\mathbf{y}, t)] d \mathbf{y} \stackrel{\text { def }}{=}\left(-V+J \cdot S_{0}(\mu V)\right)(x) \tag{2}
\end{equation*}
$$

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 $\frac{d}{d t} V=A V+R(V, \mu)$ with

$$
\mathrm{A}=-I d+\sigma_{c} S_{1} J, \quad \mathrm{R}(V, \mu)=J \cdot S_{0}\left(\left(\sigma_{c}+\mu\right) V\right)-\sigma_{c} S_{1} J \cdot V
$$

$\Rightarrow$ Mathematical analysis of the model of Ermentrout-Cowan of visual hallucinations.
The membrane potential $V(x, t)$ of the population at location $x \in \mathbb{R}^{2}$ satisfies the equation

$$
\begin{equation*}
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$$
\mathbf{A}=-I d+\sigma_{c} S_{1} J, \quad R(V, \mu)=J \cdot S_{0}\left(\left(\sigma_{c}+\mu\right) V\right)-\sigma_{c} S_{1} J \cdot V
$$

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

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

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

of rotations

$$
\mathcal{R}_{\theta} \cdot V(x)=V\left(R_{-\theta} x\right), \quad R_{\theta}=\left(\begin{array}{cc}
\cos \theta & \sin \theta \\
-\sin \theta & \cos \theta
\end{array}\right)
$$

and of reflections

$$
\mathcal{S} \cdot V(x)=V\left(S^{-1} x\right), \quad S=\left(\begin{array}{cc}
1 & 0 \\
0 & -1
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$$

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$$

These transformations raise an issue in view of the application of the center manifold Theorem. Why?
$\Rightarrow$ if $U(\mathrm{x})$ is in the kernel kerA, then its $\mathbb{R}^{2}$-orbit $\mathrm{t} \rightarrow \mathcal{T}_{\mathrm{t}} \cdot U$ gives an infinite center part $\Sigma_{0}(\mathrm{~A})$. 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}=\left\{m \vec{l}_{1}+n \vec{l}_{2}, m, n \in \mathbb{Z}\right\}
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It forms a discrete subgroup of $\mathbb{R}^{2}$.

## EUCLIDEAN GROUP AND LATTICE

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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 $\vec{k}_{i} \cdot \vec{l}_{j}=\delta_{i j}$

$$
\mathcal{L}^{*}=\left\{n \vec{k}_{1}+m \vec{k}_{2}, m, n \in \mathbb{Z}\right\}
$$

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 | $\mathrm{D}_{4}$ | $\vec{l}_{1}=(1,0), \vec{l}_{2}=(0,1)$ | $\vec{k}_{1}=(0,1), \vec{k}_{2}=(1,0)$ |
| Rhombic | $\mathrm{D}_{2}$ | $\vec{l}_{1}=(1,-\cot \theta), \vec{l}_{2}=(0, \cot \theta)$ | $\vec{k}_{1}=(1,0), \vec{k}_{2}=(\cos \theta, \sin \theta)$ |
| Hexagonal | $\mathrm{D}_{6}$ | $\vec{l}_{1}=\left(\frac{1}{\sqrt{3}}, 1\right), \vec{l}_{2}=\left(\frac{2}{\sqrt{3}}, 0\right)$ | $\vec{k}_{1}=(0,1), \vec{k}_{2}=\left(\frac{\sqrt{3}}{2},-\frac{1}{2}\right)$ |

## 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 $V(x+\mathrm{l})=V(\mathrm{x})$ for all $\mathrm{I} \in \mathcal{L}_{\text {square }}$ and $\mathbf{x} \in \mathbb{R}^{2}$.

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

$$
\dot{V}=-V+\tilde{\jmath} \cdot \mathrm{S}_{0}(\mu V)=\mathrm{A} V+\mathrm{R}(V, \mu)
$$

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

## Lemma

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


## 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 $\mathrm{D}_{4}=\left\langle\mathcal{R}_{\pi / 4}, \mathcal{S}\right\rangle$ generated by $\mathcal{R} \stackrel{\text { def }}{=} \mathcal{R}_{\pi / 4}$ 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:

$$
G_{s q}=D_{4} \times \mathbb{T}^{2} .
$$

## 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

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

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

$$
\mathcal{Z}=H_{p e r}^{1}(\mathcal{D})
$$

The Cauchy problems is formulated with $\mathrm{A}=-i d+\mu_{c} S_{1} \tilde{J} \in \mathcal{L}(\mathcal{Z}, \mathcal{X})$ and $\mathrm{R}(V, \mu)=\tilde{\jmath} \cdot S_{0}(\mu V)-\mu_{c} S_{1} \tilde{\jmath} \cdot u \in C^{\infty}(\mathcal{Z} \times \mathbb{R}, \mathcal{X})$.

## 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 $E_{c}=\operatorname{ker} A \neq\{0\}$. More precisely, we assume that

$$
\operatorname{ker} \mathrm{A}=\left\{z=\sum_{j=1}^{2} z_{j} e^{2 i \pi \mathrm{k}_{j} \cdot x}+\text { c.c., } z_{i} \in \mathbb{C}\right\} \subset \mathcal{Z}
$$

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 $\sigma_{c}$ of the stiffness parameter, namely, we set

$$
\sigma_{c}=\inf _{\sigma \in \mathbb{R}_{+}}\left\{\exists \mathrm{k} \in \mathcal{L}^{*}, 1=s_{1} \sigma \hat{\jmath}_{\mathrm{k}}\right\}
$$

## Remark

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

## EQUIVARIANT VERSION OF CMT AND NFT

## Theorem (CMT)

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

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

We further assume that the restriction $\mathrm{T}_{0}$ of T to the center subspace $\mathcal{E}_{0}$ is an isometry. Under the assumptions CMT, one can find a reduction function $\Psi$ which commutes with T , i.e., $\mathrm{T} \Psi\left(u_{0}\right)=\Psi\left(\mathrm{T}_{0} u_{0}\right)$ 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 $T \in \mathcal{L}\left(\mathbb{R}^{n}\right)$ which commutes with A and R , then the polynomials $\Phi, \mathrm{N}$ commutes with T .

## Lemma

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

$$
\left\{\begin{array}{l}
\dot{z}_{1}=z_{1}\left(\alpha+\beta\left|z_{1}\right|^{2}+\gamma\left|z_{2}\right|^{2}\right) \\
\dot{z}_{2}=z_{2}\left(\alpha+\beta\left|z_{2}\right|^{2}+\gamma\left|z_{1}\right|^{2}\right)
\end{array}\right.
$$

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

Close to the bifurcation point $\sigma=\sigma_{c}$, we have $V(x, t)=v_{0}(x, t)+\tilde{\Psi}\left(v_{0}(x, t), \mu\right)$. The above normal form has equilibria $(0,0),\left(z_{s t}, z_{s t}\right),\left(z_{s p}, 0\right),\left(0, z_{s p}\right)$ with opposite stability where $z_{s t}, z_{\text {sp }} \in \mathbb{R}$.
The ODE - NF is easy to study with polar coordinates for example. One then finds

$$
V_{\text {spot }}(x, y) \approx z_{s p} e^{2 i \pi k_{1} x}+z_{s p} e^{2 i \pi k_{1} y}+c . c .=2 z_{s p}(\cos (2 \pi x)+\cos (2 \pi y))
$$

or

$$
V_{\text {stripe }}(x, y) \approx z_{\text {st }} e^{2 i \pi k_{1} x} \text { c.c. }=2 z_{\text {st }} \cos (2 \pi x)
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## STRIPES OR SPOTS?

Close to the bifurcation point $\sigma=\sigma_{c}$, we have $V(x, t)=v_{0}(x, t)+\tilde{\Psi}\left(v_{0}(x, t), \mu\right)$. The above normal form has equilibria $(0,0),\left(z_{s t}, z_{s t}\right),\left(z_{s p}, 0\right),\left(0, z_{s p}\right)$ with opposite stability where $z_{s t}, z_{s p} \in \mathbb{R}$.

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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.


## 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 $\alpha, \beta, \gamma$ of the normal form as function of the different parameters of the model.

## Lemma

The normal form has the following coefficients:

$$
\begin{aligned}
& \beta / \mu_{c}^{3} \hat{\jmath}_{\mathbf{k}_{c}}=\mu_{c} S_{2}^{2} \quad\left[\frac{\hat{\jmath}_{0}}{1-\hat{\jmath}_{0} / J_{k_{c}}}+\frac{\hat{\jmath}_{2 k_{c}}}{2\left(1-\hat{\jmath}_{2 k_{c}} / \hat{\jmath}_{k_{c}}\right)}\right]+s_{3} / 2 \\
& \gamma / \mu_{c}^{3} \hat{\jmath}_{\mathbf{k}_{c}}=\mu_{c} S_{2}^{2} \quad\left[\frac{\hat{\jmath}_{0}}{1-\hat{\jmath}_{0} / J_{\mathbf{k}_{c}}}+2 \frac{\hat{\jmath}_{(1,1)}}{1-\hat{\jmath}_{(1,1)} / \hat{\jmath}_{k_{c}}}\right]+s_{3} .
\end{aligned}
$$

