INVARIANT MANIFOLDS IN MATHEMATICAL NEUROSCIENCES WINTER SCHOOL TOULOUSE 2017

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ABSTRACT. The goal of these lectures is to provide tools to study invariant manifold (*e.g.* center manifolds). As an application of the exposed results, we study a spatial neural network model of visual cortex with the aim to describe drug induced visual hallucinations. In effect, this boils down to the study of a static Turing bifurcation. We describe this application with minimal technicalities at the price of more computations and less efficient / abstract tools. We hope that this approach will reach a larger audience.

1. Neural fields models

We start here by presenting some basic facts of neurobiology and the derivation of the so-called **neural field equations** [Erm98]. We then present some elements of the neurobiology of visual and more particularly of the primary visual area V1.

Neurons have the particularity to be able to produce electrical impulses called action potential which are transmitted from neurons to neurons through connections called synapses. The action potential of a neuron influences the emission of action potentials in the contacted neurons.

We then consider neurons in population j are connected to neurons in population i. A single action potential from neurons in population j is seen as a post-synaptic potential $t \to PSP_{ij}(t-s)$ by the neurons in population i, where s is the time of the spike hitting the synapse and t the time after the spike.

Assuming that the spikes' contributions sum linearly, the average membrane potential of population i due to action potentials of population j is

$$V_i(t) = \sum_{t_k} PSP_{ij}(t - t_k - D_{ji}),$$

where the sum is taken over the arrival times t_k , at the synapse between the neurons j and i, of the spikes produced by the neurons in population j. The modeling delay D_{ji} is the time it takes for the signal to travel from one neuron to the next plus the time it takes to produce a significant effect on the neuron j's membrane potential. These spikes have been produced at time $t_k - d_{ji}$ by the neuron j. The number of spikes arriving between t and t + dt is $\nu_j(t - d_{ji})dt$ which is related to the membrane potential V_j by¹ $\nu_j(t) = S_j(V_j(t))$ with a sigmoidal function S_j . Therefore we have

(1)
$$V_i(t) = \sum_j \int_{t_0}^t PSP_{ij}(t-s-D_{ji})\nu_j(s-d_{ji}) ds$$

¹The mapping is called the f - I curve in neurosciences

or, equivalently

(2)
$$\nu_i(t) = S_i\left(\sum_j \int_{t_0}^t PSP_{ij}(t-s-D_{ji})\nu_j(s-d_{ji}) \, ds\right)$$

Note that the model as described above is not well defined since at $t = t_0$, all the potentials have all to be 0. The PSP_{ij} can depend on several variables in order to account for adaptation, learning...There are two main simplifying assumptions that appear in the literature [Erm98, PS96] and produce two different models that we describe below. Note that the previous equations are integral equations. It would simplify the analysis if we could write them as differential equations. This is possible if PSP_{ij} are sums of exponentials and powers as we assume below.

1.1. The voltage-based model. The simplifying assumption is that the post-synaptic potential has the same shape no matter which pre-synaptic population caused it, though its sign and amplitude may vary. This leads to the relation

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

If $w_{ij} > 0$ (resp. $w_{ij} < 0$) then population j excites (resp. inhibits) population i. The shape of synaptic response PSP_i is often approximated by a simple exponential decay $PSP_i(t) = k_i e^{-t/\tau_i} H(t)$ where H is the Heaviside function, or equivalently

(3)
$$\tau_i \frac{dPSP_i(t)}{dt} + PSP_i(t) = k_i \delta(t).$$

We end up with the following system of delay differential equations.

Lemma 1.1

Equation (1) implies that
(4)
$$\tau_i \frac{dV_i(t)}{dt} + V_i(t) = \sum_j w_{ij} S_j (V_j(t - \tau_{ji})) + I_{\text{ext}}^i(t).$$

Proof. Using (2), we compute

$$\tau_i \frac{d}{dt} V_i(t) = \sum_j \left[\tau_i PSP_{ij}(-D_{ji})\nu_j(t-d_{ji}) + w_{ij} \int_0^t \left(-PSP_i(t-s-D_{ji}) + k_j \delta_{t-s-D_{ji}} \right) \nu_j(s-d_{ji}) ds \right]$$

As $PSP_{ij}(t) = 0$ if t < 0, the first term vanishes and we find:

$$\tau_i \frac{d}{dt} V_i(t) = -V_i(t) + \sum_j w_{ij} k_j \nu_j (t - \tau_{ji})$$

which concludes the proof.

Equation (4) describes the dynamic behavior of a population. We have incorporated the constant k_i in the weights w_{ij} and added an external current $I_{\text{ext}}(t)$ to model non-local connections² of population *i*.

Since the decay is governed by the membrane properties of the post-synaptic cell, τ_i is legitimately called the membrane time constant.

We introduce the $p \times p$ matrices **J** such that $J_{ij} = w_{ij}/\tau_i$, and the function **S** : $\mathbb{R}^p \to \mathbb{R}^p$ such that **S**(**x**) is the vector of coordinates $S_i(x_i)$, if $x = (x_1, \dots, x_p)$. We rewrite (4) in vector form and obtain the following system of n delayed differential equations

(5)
$$\dot{\mathbf{V}}(t) + \mathbf{L}\mathbf{V}(t) = \mathbf{J}\,\mathbf{S}(\mathbf{V}_t) + \mathbf{I}_{\text{ext}}(t),$$

where **L** is the diagonal matrix $\mathbf{L} = \text{diag}(1/\tau_i)$ and \mathbf{V}_t is a compact notation for the delayed terms $V_j(t - \tau_{ji})$.

We now combine these local models to form a continuum of neural fields, *e.g.* in the case of a model of a significant part Ω of the cortex. We note $\mathbf{V}(\mathbf{x}, t)$ the *p*-dimensional state vector at the point \mathbf{x} of the continuum. We introduce the $p \times p$ matrix function $\mathbf{J}(\mathbf{x}, \mathbf{x}')$ which describes how the neural mass at point \mathbf{x}' influences that at point \mathbf{x} . We call \mathbf{J} the connectivity matrix function.

More precisely, $J_{ij}(\mathbf{x}, \mathbf{x}')$ describes how population j at point \mathbf{x}' influences population i at point \mathbf{x} .

Equation (5) can now be extended to

(6)
$$\frac{d}{dr}\mathbf{V}(\mathbf{x},t) = -\mathbf{L}\mathbf{V}(\mathbf{x},t) + \int_{\Omega} \mathbf{J}(\mathbf{x},\mathbf{x}')\mathbf{S}(\mathbf{V}(\mathbf{x}',t-\tau(\mathbf{x},\mathbf{x}')))\,d\mathbf{x}' + \mathbf{I}_{\text{ext}}(\mathbf{x},t),$$

The quantity $\tau(\mathbf{x}, \mathbf{x}')$ is the total delay for the processing of the information, from populations located at \mathbf{x}' to populations located at \mathbf{x} , it will be neglected in the rest of the document.

As before, we shall write the above equations in a condensed way:

(7)
$$\dot{\mathbf{V}}(t) = -\mathbf{L}\mathbf{V}(t) + \mathbf{J} \cdot \mathbf{S}(\mathbf{V}) + \mathbf{I}_{\text{ext}}(t).$$

A significant amount of work has been devoted to this or closely related problems, starting perhaps with the pioneering work of Wilson and Cowan [WC72]. A fairly recent review of this work, and much more, can be found in the paper by Coombes [Coo05].

1.2. Visual cortex. The primary visual (cortical) area V1 is a cortical area located at the back of the brain which processes basic properties of the visual scene such as local contour, ocular dominance... For the sake of the present lecture, we need the *retinotopy* property. The retinotopy in V1 is the fact that two adjacent points in the visual field are processed by V1 cells located next to one another in the same layer. Loosely speaking, the neighborhood in the visual field are conserved in V1. This is the reason why in Figure 1 Left, we draw a piece of the person's face located in the visual field. In the monkey, the map from visual field coordinates to cortical coordinates [TSSH88] is roughly a complex exponential far from the center of the visual field.

Several drug induced visual hallucinations have been reported [Sie77], some of which are shown in Figure 1 Right (b). When translated into cortical coordinates in Figure 1 Right (a), it shows regular patterns of activity of neural populations. One can see for example, stripe patterns or spot patterns very similar to Turing patterns.

²for example with the thalamus

1.3. **Goal of the lecture.** We can now describe the example of application of the theoretical tools that shall be presented. We assume that a neural field model can be used to (crudely) describe the neural activity of V1. We want to study this model to see if it can produce spontaneously regular patterns of activity which can be interpreted as visual hallucinations.



FIGURE 1. Left: Schematic representation of the visual pathway. Note the retinotopic representation and the magnification of the fovea. Each LGN has 6 layers which project to V1. For V1, we have represented the orientation and the retinotopy maps. Right: (b) Schematic representation of drug induced visual hallucinations. (a) Same hallucination in cortical coordinates (from [BCG⁺01]), where grayscale indicates the degree of activity of neural populations.

2. Basic bifurcations

Before we start looking at very general situations, we state two basic results concerning the creation of attractors. The first example describes the creation / annihilation of equilibria while the second example deals with the case of periodic orbits.

Theorem 2.1 (Saddle-Node bifurcation)

Assume f is a scalar $\mathcal{C}^k, k \geq 2$ map in a neighborhood of (0,0), and that it satisfies

$$f(0,0) = 0, \ \frac{\partial}{\partial u}f(0,0) = 0$$

and

$$\frac{\partial}{\partial \mu}f(0,0) := a \neq 0, \frac{\partial^2}{\partial^2 u}f(0,0) := 2b \neq 0$$

where μ is a parameter. Then, a saddle-node bifurcation occurs at $\mu = 0$. More precisely, the following properties hold in a neighborhood of 0 in \mathbb{R} for sufficiently small μ :

- if ab < 0 (resp. ab > 0) the differential equation has 2 equilibria $u_{\pm}(\epsilon), \epsilon = \sqrt{|\mu|}$ for $\mu > 0$ (resp., for $\mu < 0$), with opposite stabilities. Furthermore, the map $\epsilon \to u_{\pm}(\epsilon)$ is of class \mathcal{C}^{k-2} in a neighborhood of 0, and $u_{\pm}(\epsilon) = O(\epsilon)$.
- if ab < 0 (resp. ab > 0) the differential equation has no equilibria for $\mu < 0$ (resp., for $\mu > 0$).

We let the reader do the proof. One can note that $f(u, \mu) = a\mu u + bu^2 + \cdots$ and start studying the truncated vector field. Then, one can use the implicit functions theorem to deduce the results of the above theorem.

Theorem 2.2 (Hopf bifurcation)

Assume f is $C^k, k \geq 5$ in a neighborhood of $(0,0) \in \mathbb{R}^2 \times \mathbb{R}$, and that it satisfies

$$f(0,0) = 0, \ \mathbf{A} := \partial_u f(0,0) = 0.$$

Assume that the two eigenvalues of the linear operator **A** are $\pm i\omega$ for some $\omega > 0$. Finally, assume that the normal form can be written

$$\frac{d}{dt}A = (a\mu + i\omega)A + b|A|^2A + O((|\mu| + |A|^2)^2)$$

with $\Re a, \Re b \neq 0$. Then, **a Hopf bifurcation** occurs at $\mu = 0$. More precisely, the following properties hold in a neighborhood of 0 in \mathbb{R}^2 for sufficiently small μ :

- if $\Re a \Re b < 0$ (resp. ab > 0) the differential equation has precisely one equilibrium $u(\mu)$ for $\mu < 0$ (resp., for $\mu > 0$), with u(0) = 0. This equilibrium is stable when $\Re b < 0$ and unstable when $\Re b > 0$.
- if $\Re a \Re b < 0$ (resp. $\Re a \Re b > 0$) the differential equation possesses for $\mu > 0$ (resp., for $\mu < 0$) an equilibrium $u(\mu)$ and a unique periodic orbit $u(\mu) = O(\sqrt{|\mu|})$, which surrounds this equilibrium. The periodic orbit is stable when $\Re b < 0$ and unstable when $\Re b > 0$, whereas the equilibrium has opposite stability.

Again, we let the reader do the proof. One can start studying the case where the higher order terms are neglected using polar coordinates, and use the implicit functions theorem to deduce the results in the above theorem. Please note that the use of the implicit functions theorem is not completely trivial in this case.

3. NOTATIONS

• We write $\mathcal{V} \in \mathcal{V}_{\mathcal{Z}}(0)$ for the fact that \mathcal{V} is a neighborhood of 0 in \mathcal{Z} .

• We recall that a linear mapping $\mathbf{A} : \mathcal{Z} \to \mathcal{X}$ where \mathcal{Z}, \mathcal{X} are normed vectors spaces, is continuous if and only if $\|\mathbf{A}\|_{\mathcal{L}(\mathcal{Z},\mathcal{X})} \equiv \sup_{\|x\|_{\mathcal{Z}} \leq 1} \|\mathbf{A}x\|_{\mathcal{X}} < \infty$. We write $\mathcal{L}(\mathcal{Z}, \mathcal{X})$ the set of

continuous linear mappings between \mathcal{Z} and \mathcal{X} . If $\mathcal{Z} = \mathcal{X}$, we write $\mathcal{L}(\mathcal{X}) = \mathcal{L}(\mathcal{X}, \mathcal{X})$. We denote by $R(\mathbf{A})$ its range, $R(\mathbf{A}) = \{\mathbf{L}u \in \mathcal{X}; u \in \mathcal{Z}\} \subset \mathcal{X}$, and by ker(\mathbf{A}) its kernel, ker(\mathbf{A}) = $\{u \in \mathcal{Z}; \mathbf{A}u = 0\} \subset \mathbb{Z}$.

• We assume that $\mathcal{Z} \subset \mathcal{X}$ with continuous embedding, written $\mathcal{Z} \hookrightarrow \mathcal{X}$, and we define the resolvent set

 $\rho(\mathbf{A}) = \left\{ \lambda \in \mathbb{C} \mid (\lambda Id - \mathbf{A}) \text{ invertible and } (\lambda Id - \mathbf{A})^{-1} \in \mathcal{L}(\mathcal{X}) \right\}$

and the spectrum

$$\Sigma(\mathbf{A}) \stackrel{def}{=} \mathbb{C} \setminus \rho(\mathbf{A}).$$

Note that when the operator \mathbf{A} is real, the resolvent set and the spectrum of \mathbf{A} are both symmetric with respect to the real axis in the complex plane. The *point spectrum* or set of eigenvalues is the set $\Sigma_p(\mathbf{A}) \subset \Sigma(\mathbf{A})$ defined by $\lambda \in \Sigma(\mathbf{A})$ such that $\ker(\lambda Id - \mathbf{A}) \neq \{0\}$. In infinite dimensions, there are operators \mathbf{A} for which $\Sigma_p(\mathbf{A}) \subsetneq \Sigma(\mathbf{A})$.

We do not have the space here to define the notion of *closed operator*, for which the spectral theory is relatively "easy". Indeed, one can show that if $\rho(\mathbf{A}) \neq \emptyset$, then \mathbf{A} is necessarily closed. The interested reader can look at [Kat05]. We would like to mention that the Hypothesis 4.2 (see below) implies that \mathbf{A} is closed in \mathcal{X} .

• $\mathcal{C}^k(\mathcal{Z}, \mathcal{X})$ is the Banach space of k-times continuously differentiable functions $\mathbf{F} : \mathcal{Z} \to \mathcal{X}$ equipped with the sup norm on all derivatives up to order k,

$$\|\mathbf{F}\|_{\mathcal{C}^{k}} = \max_{j=1,\cdot,k} \sup_{y\in\mathcal{Z}} \left\| d^{j}\mathbf{F}(y) \right\|_{\mathcal{L}(\mathcal{Z}^{j},\mathcal{X})}$$

• For a positive constant $\eta > 0$, we define the space of **exponentially growing functions** $C_{\eta}(\mathbb{R}, \mathcal{X}) \equiv \{f \in C^{0}(\mathbb{R}, \mathcal{X}) \mid ||f||_{C_{\eta}(\mathbb{R}, \mathcal{X})} \equiv \sup_{t \in \mathbb{R}} e^{-\eta |t|} ||f(t)||_{\mathcal{X}} < \infty\}$, which is a Banach space when equipped with the norm $\|\cdot\|_{C_{\eta}}$. We note that we have a scale of Banach spaces with continuous embeddings $C_{\zeta}(\mathbb{R}, \mathcal{X}) \hookrightarrow C_{\eta}(\mathbb{R}, \mathcal{X})$ if $0 < \zeta < \eta$.

4. Center Manifolds

When studying dynamical systems, a fruitful approach consists in looking for sets that are invariant by the dynamics. Basic examples of those include *equilibria* or *periodic orbits*. Then comes the question of their stability. The importance of these sets lies in the fact that they allow to simplify the dynamics by studying the reduced dynamics on these invariant sets. In infinite dimensions, this is very useful as it may allow to reduce the initial dynamics to a regular ODE without further approximation.

It turns out that the study of non hyperbolic equilibria (may) provide the existence of a finite dimensional invariant manifold. More precisely, a **center manifold** for a Cauchy problem at equilibrium 0 is an invariant manifold containing 0 which is tangent to and of the same dimension as the generalized eigenspace of linearized vector field with spectrum elements of zero real part.

In the following section, we provide a very general setting, based on [VI92, HG11], for studying infinite dimensional Cauchy problems. One may be first overwhelmed by the amount of technical details necessary to the presentation of the main result (see Theorem 4.1). The reason for such generality is to provide enough freedom in the choice of spaces such that the assumption of Theorem 4.1 are satisfied. Actually, this is where the main difficulty lies. "Nothing is free": you may

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chose Hilbert spaces to simplify linear analysis by the use of the dot product but this may impair the nonlinear analysis for which Banach algebras are better suited (to do Taylor expansions for example).

4.1. Setting. Let us consider three Banach spaces $\mathcal{X}, \mathcal{Y}, \mathcal{Z}$ such that $\mathcal{Z} \hookrightarrow \mathcal{Y} \hookrightarrow \mathcal{X}$ with continuous embeddings³ and a differential equation in \mathcal{X} of the form

(8)
$$\frac{du}{dt} = \mathbf{F}(u) \stackrel{def}{=} \mathbf{A}u + \mathbf{R}(u) \in \mathcal{X}$$

We make some assumptions about this Cauchy problem ensuring that the jacobian of \mathbf{F} is continuous at $0 = \mathbf{F}(0)$ and that the reminder of \mathbf{F} is \mathbf{R} .

Hypothesis 4.1

- (1) $\mathbf{A} \in \mathcal{L}(\mathcal{Z}, \mathcal{X})$
- (2) for some $k \ge 2$, there exists a neighborhood $\mathcal{V} \subset \mathcal{Z}$ of 0 such that $\mathbf{R} \in \mathcal{C}^k(\mathcal{V}, \mathcal{Y})$ and $\mathbf{R}(0) = 0, d\mathbf{R}(0) = 0.$

The following graphics (Figure 4.1) may help to remember how the different spaces and operators are defined.



FIGURE 2. Different spaces and operators entering in the definition of the Cauchy problem. The mapping i is the inclusion mapping.

The reason why we chose such a general setting is to allow the study of more general situations than the case of ordinary differential equations (in a Banach space). Already in the linear case, it is not straightforward to define a solution in our setting (think about $\mathbf{A} = -\Delta^2 + Id$ for example) and one usually ends up with a semigroup of solutions instead of a group.

This being said, we need to define what is a solution of (8).

Definition 4.1

A solution of the differential equation (8) is a function $u: I \to \mathbb{Z} \subset \mathbb{X}$ defined on an interval $I \subset \mathbb{R}$, with the following properties:

• the map $u: I \to \mathcal{Z}$ is continuous;

³meaning the linear map $i: \mathcal{Y} \to \mathcal{X}$ (resp. $i: \mathcal{Z} \to \mathcal{Y}$) with i(x) = x is continuous or equivalently $||x||_{\mathcal{X}} \leq C ||x||_{\mathcal{Y}}$ (resp. $||x||_{\mathcal{Y}} \leq C' ||x||_{\mathcal{Z}}$)

- the map $u: I \to \mathcal{X}$ is continuously differentiable;
- the equality (8) holds in \mathcal{X} for all $t \in I$.

One can already see some difficulty appearing here as the solution needs to fight the loss of regularity imposed by $\mathbf{A}, \mathbf{R}, i.e.$ the fact that starting from \mathcal{Z} , one ends up at best in \mathcal{Y} .

Example : We give here an example of use of the previous formalism. We consider the Cauchy problem

$$\frac{\partial u}{\partial t} = \left(-1 + \frac{\partial^2 u}{\partial x^2}\right)^2 u + \mu u - u^3$$
$$u(0,t) = u(2\pi,t)$$

We define $\mathbf{A}u = \left(-1 + \frac{\partial^2 u}{\partial x^2}\right)^2 u + \mu u$ for $\mu \in \mathbb{R}$ and $\mathbf{R}(u) = u^3$. Here are some simple spaces for which Hypothesis 4.1 is satisfied. We use $\mathcal{X} = L^2_{per}([0,\pi])$ and the Sobolev space $\mathcal{Z} = \mathcal{Y} = H^4_{per}(0,2\pi)$ which is a Banach algebra.

4.2. Linear hypothesis. We now list the hypotheses related to the spectrum of the linear operator **A**. Basically, these hypothesis are giving conditions which ensure that the center manifold is finite dimensional. The center manifold being tangent to the linear subspace associated with spectrum elements of zero real part, this space must be finite dimensional.

Hypothesis 4.2 (Spectral hypothesis)

The spectrum of A is such that $\Sigma(\mathbf{A}) = \Sigma_{-} \cup \Sigma_{+} \cup \Sigma_{0}$ where $\Sigma_{-} = \{\lambda \in \Sigma(\mathbf{A}) \mid \Re \lambda < 0\}$, $\Sigma_{-} = \{\lambda \in \Sigma(\mathbf{A}) \mid \Re \lambda > 0\}$ and $\Sigma_{0} = \{\lambda \in \Sigma(\mathbf{A}) \mid \Re \lambda = 0\}$. Moreover the set Σ_{0} consists of a **finite** number of eigenvalues with finite algebraic multiplicities. Finally, we require the existence of a **spectral gap** *i.e.* that there is a positive constant $\gamma > 0$ satisfying $\inf_{\lambda \in \Sigma_{+}} (\Re \lambda) > \gamma$ and $\sup_{\lambda \in \Sigma_{-}} (\Re \lambda) < -\gamma$.

The sets $\Sigma_{-}, \Sigma_{+}, \Sigma_{0}$ bear the names of stable, unstable and central spectrum, respectively. We also note that this implies that $\rho(\mathbf{A}) \neq \emptyset$.

Under Hypothesis 4.2, there is a unique spectral projector [Kat05] $\mathbf{P}_0 \in \mathcal{L}(\mathcal{X}, \mathcal{Z}) \cap \mathcal{L}(\mathcal{X})$ corresponding to Σ_0 which commutes with \mathbf{A} on \mathcal{Z} ; it has a finite dimensional range. We also define a second projector (which we call the hyperbolic projector) $\mathbf{P}_h \stackrel{def}{=} Id - \mathbf{P}_0$ which belongs to $\mathcal{L}(\mathcal{X}) \cap \mathcal{L}(\mathcal{Y}) \cap \mathcal{L}(\mathcal{Z})$. We consider the spectral subspaces associated with these two projections:

$$\mathcal{E}_0 \stackrel{aej}{=} R(\mathbf{P}_0) = \ker(\mathbf{P}_h) \subset \mathcal{Z}, \ \mathcal{X}_h = R(\mathbf{P}_h) = \ker(\mathbf{P}_0) \subset \mathcal{X}$$

which provide the decomposition:

$$\mathcal{X} = \mathcal{E}_0 \oplus \mathcal{X}_h.$$

We also denote

$$\mathcal{Z}_h = \mathbf{P}_h \mathcal{Z} \subset \mathcal{Z}, \ \mathcal{Y}_h = \mathbf{P}_h \mathcal{Y} \subset \mathcal{Y}$$

and denote by $\mathbf{A}_0 \in \mathcal{L}(\mathcal{E}_0)$ and $\mathbf{A}_h \in \mathcal{L}(\mathcal{Z}_h, \mathcal{X}_h)$ the restrictions of \mathbf{A} to \mathcal{E}_0 and \mathcal{Z}_h . The spectrum of \mathbf{A}_0 is $\Sigma(\mathbf{A}_0) = \Sigma_0$ and the spectrum of $\Sigma(\mathbf{A}_h) = \Sigma_- \cup \Sigma_+$. We note that $\mathcal{E}_0 = \bigoplus_{\lambda \in \Sigma_0} E_{\lambda}$ where $E_{\lambda} = \bigcup_{k \geq 0} \ker(\lambda Id - \mathbf{A})^k$. Finally, we call \mathcal{E}_0 the **central** part and \mathcal{X}_h the **hyperbolic** part.

We need another hypothesis before we can state the theorem of the center manifold. This is arguably the most difficult requirement in applications.

Hypothesis 4.3 (Inhomogenous equation)

Assume that there exist positive constants $\omega_0 > 0, c > 0$ and $\alpha \in [0, 1)$ such that for all $\omega \in \mathbb{R}$, with $|\omega| \ge \omega_0$, we have that $i\omega$ belongs to the resolvent set $\rho(\mathbf{A})$ of \mathbf{A} , and

$$\|(i\omega - \mathbf{A})^{-1}\|_{\mathcal{L}(\mathcal{X})} \le \frac{c}{|\omega|}$$
$$\|(i\omega - \mathbf{A})^{-1}\|_{\mathcal{L}(\mathcal{Y},\mathcal{Z})} \le \frac{c}{|\omega|^{1-\alpha}}$$

This hypothesis can only be satisfied in the case where $\mathcal{Y} \neq \mathcal{X}$. The theorem below is true for a weaker assumption but we preferred to provide a "simple" characterization. There are cases (see for example [IK00]) where the above assumption is not satisfied whereas a center manifold exists.

In finite dimension, *i.e.* when $X = \mathbb{R}^n$, Hypothesis 4.3 is automatically satisfied. Also, note that if $\mathcal{X}, \mathcal{Y}, \mathcal{Z}$ are Hilbert spaces and $\mathcal{Y} \neq \mathcal{X}$, Hypothesis 4.3 is satisfied only if the first inequality is true. In addition, if the operator **A** is **sectorial**, then the Hypothesis 4.3 is satisfied.

We are now in position to give the Center Manifold Theorem.

Theorem 4.1 ([HG11])

Assume that Hypotheses 4.1, 4.2 and 4.3 hold. Then there exists a map $\Psi \in \mathcal{C}^k(\mathcal{E}_0, \mathcal{Z}_h)$ with

$$\Psi(0) = 0, \quad d\Psi(0) = 0$$

and a neighborhood \mathcal{O} of 0 in \mathcal{Z} such that the manifold:

$$\mathcal{M}_0 = \{ u_0 + \Psi(u_0), u_0 \in E_0 \}$$

has the following properties:

- \mathcal{M}_0 is **locally invariant**, *i.e.*, if u is a solution of (8) satisfying $u(0) \in \mathcal{O} \cap \mathcal{M}_0$ and $u(t) \in \mathcal{O}$ for all $t \in [0, T]$, then $u(t) \in \mathcal{M}_0$ for all $t \in [0, T]$.
- \mathcal{M}_0 contains the set of **bounded solutions** of (8) staying in \mathcal{O} for all $t \in \mathbb{R}$.

Proof. (Idea of proof in fact) In order to prove the existence of a stable (resp. unstable) manifold, one classically looks for solutions of (8) in the space $C_0(\mathbb{R}_+, \mathcal{X})$ (resp. $C_0(\mathbb{R}_-, \mathcal{X})$) which can then be embedded into a finite dimensional manifold. However, in the case where $\mathbf{A}_0 \neq 0$, the component on the center linear subspace \mathcal{E}_0 has at best a polynomial growth if $\mathbf{P}_0\mathbf{R}$ is bounded. In order to control this growth, one first note that for all $\delta > 0$, there is a constant k_{δ} such that $\|e^{t\mathbf{A}_0}\|_{\mathcal{X}} \leq k_{\delta}e^{\delta|t|}, t \in \mathbb{R}$. By analogy with the cases of the stable / unstable manifolds, this suggests to look for solutions of (8) in the spaces \mathcal{C}_{η} in order to find an invariant manifold tangent to \mathcal{E}_0 .

To adjust the **R** Lipschitz constant, we truncate it using a \mathcal{C}^{∞} cutoff function $\chi : E_0 \to \mathbb{R}$ which is nonzero in a neighborhood of zero. This also allows us to control the growth of the solutions such that they do not leave the domain \mathcal{V} of **R**. We then set $\mathbf{R}^{\epsilon}(u) \stackrel{def}{=} \chi\left(\frac{u_0}{\epsilon}\right) \mathbf{R}(u)$. We project

(8)

$$\dot{u}_0 = \mathbf{A}_0 u_0 + \mathbf{P}_0 \mathbf{R}^{\epsilon} (u_h + u_0), \quad \dot{u}_h = \mathbf{A}_h u_h + \mathbf{P}_h \mathbf{R}^{\epsilon} (u_h + u_0)$$

and look for solutions in $\mathcal{N}_{\eta,\epsilon} \stackrel{def}{=} \mathcal{C}_{\eta}(\mathbb{R}, \mathcal{E}_0) \times \mathcal{C}_0(\mathbb{R}, B_{\epsilon}(0, \mathcal{Z}_h)) \subset \mathcal{C}_{\eta}(\mathbb{R}, \mathcal{Z}).$

Hypothesis 4.2 allows to find $u_h \in C_\eta(\mathbb{R}, \mathcal{Z}_h)$ provided that $\mathbf{P}_h \mathbf{R}^{\epsilon}(u_h + u_0)$ belongs to $C_\eta(\mathbb{R}, \mathcal{Y}_h)$ with a linear continuous operator $\mathbf{K}_\eta \in \mathcal{L}(C_\eta(\mathbb{R}, \mathcal{Y}_h), C_\eta(\mathbb{R}, \mathcal{Z}_h))$ of norm bounded by a continuous map on $[0, \gamma]$: $C(\eta)$. Hence, we re-write our problem as a fixed point for the map

$$\mathbf{S}_{\epsilon}(\cdot; u_0(0)): u \to \left(e^{\mathbf{A}_0 \cdot} u_0(0) + \int_0^{\cdot} e^{\mathbf{A}_0(\cdot - s)} \mathbf{P}_0 \mathbf{R}^{\epsilon}(u(s)) ds, \quad \mathbf{K}_{\eta} \mathbf{P}_h \mathbf{R}^{\epsilon}(u)\right).$$

Using the polynomial growth of $e^{t\mathbf{A}_0}$, one finds

$$\mathbf{S}_{\epsilon}(\cdot; u_0(0)) : \mathcal{N}_{\eta,\epsilon} \to \mathcal{N}_{\eta,\epsilon}, \quad \|\mathbf{S}_{\epsilon}(u_1; u_0(0)) - \mathbf{S}_{\epsilon}(u_2; u_0(0))\|_{\mathcal{C}_{\eta}(\mathbb{R}, \mathcal{Z})} \le \frac{1}{2} \|u_1 - u_2\|_{\mathcal{C}_{\eta}(\mathbb{R}, \mathcal{Z})}$$

for ϵ small enough. Consequently, the map $\mathbf{S}_{\epsilon}(\cdot; u_0(0))$ is a contraction in the complete metric space $\mathcal{N}_{\eta,\epsilon}$ and has a unique fixed point $u \stackrel{def}{=} \Phi(u_0(0)) \in \mathcal{N}_{\eta,\epsilon}$ for any $u_0(0) \in \mathcal{E}_0$ and any $\eta \in (0, \gamma]$. We note that $\Phi(0) = 0$ by uniqueness of the fixed point. We now define the center manifold by taking the hyperbolic component of the fixed point evaluated at time t = 0:

$$\Psi(u_0(0)) \stackrel{def}{=} \mathbf{P}_h \Phi(u_0(0))(0).$$

One can show that $\mathcal{M}_{\eta,\epsilon} \stackrel{def}{=} \{u_0 + \Psi(u_0), u_0 \in E_0 \cap \mathcal{V}\}$ is flow invariant by using the fact that (8) is autonomous.

As for the regularity of Ψ , one first note that $\mathbf{R}^{\epsilon} : \mathcal{C}_{\eta}(\mathbb{R}, \mathcal{Z}) \to \mathcal{C}_{\zeta}(\mathbb{R}, \mathcal{Y})$ is of class \mathcal{C}^{k} if $0 \leq \eta < \frac{\zeta}{k}$ which prevents us from using the implicit functions theorem. This fact can nevertheless be used to prove that Ψ is of class \mathcal{C}^{k} using a technical lemma tailored for this situation (see [VVG87]).

We now wish to make some remarks concerning the center manifold.

- The center manifold is not unique because of the use of the cutoff.
- If $u_0(0) \in \mathcal{M}_0$, then there is a **reduced equation** for the flow on the invariant manifold

(9)

• The center manifold function satisfies

$$d\Psi(u_0) \cdot f(u_0) = \mathbf{P}_h \mathbf{A} \cdot \Psi(u_0) + \mathbf{P}_h \mathbf{R}(u_0 + \Psi(u_0))$$

 $\dot{u}_0 = \mathbf{A}_0 u_0 + \mathbf{P}_0 \mathbf{R}(u_0 + \Psi(u_0)) \equiv f(u_0).$

• The Taylor expansion of Ψ is uniquely determined.

There are two extensions which are particularly useful in applications. The first is when the vector field depends on a parameter and the second is when the vector field possesses some symmetry.

4.3. Parameter dependent case. We consider a parameter-dependent Cauchy problem in \mathcal{X} of the form:

(10)
$$\frac{du}{dt} = \mathbf{F}(u,\mu) \stackrel{def}{=} \mathbf{A}u + \mathbf{R}(u,\mu) \in \mathcal{X}.$$

We replace Hypothesis 4.1 with the following one:

(

Hypothesis 4.4

- (1) $\mathbf{A} \in \mathcal{L}(\mathcal{Z}, \mathcal{X})$
- (2) for some $k \geq 2$, there exists a neighborhood $\mathcal{V}_u \subset \mathcal{Z}$ of 0 and \mathcal{V}_μ of 0 in \mathbb{R}^m such that $\mathbf{R} \in \mathcal{C}^k(\mathcal{V}_u \times \mathcal{V}_\mu, \mathcal{Y})$ and $\mathbf{R}(0, 0) = 0$, $d_u \mathbf{R}(0, 0) = 0$.

The analogue of center manifold Theorem 4.1 for the parameter-dependent equation is the following result.

Theorem 4.2 (Parameter-dependent center manifolds)

Assume that Hypotheses 4.4, 4.2 and 4.3 hold. Then there exists a map $\Psi \in \mathcal{C}^k(\mathcal{E}_0 \times \mathbb{R}^m, \mathcal{Z}_h)$ with

$$\Psi(0,0) = 0, \quad d_u \Psi(0,0) = 0$$

and a neighborhood $\mathcal{O}_u \times \mathcal{O}_\mu$ of 0 in $\mathcal{Z} \times \mathbb{R}^m$ such that for all $\mu \in \mathcal{O}_\mu$ the manifold:

 $\mathcal{M}_0(\mu) = \{ u_0 + \Psi(u_0, \mu), u_0 \in E_0 \}$

has the following properties:

- $\mathcal{M}_0(\mu)$ is **locally invariant**, *i.e.*, if u is a solution of (10) satisfying $u(0) \in \mathcal{O}_u \cap \mathcal{M}_0(\mu)$ and $u(t) \in \mathcal{O}_u$ for all $t \in [0, T]$, then $u(t) \in \mathcal{M}_0(\mu)$ for all $t \in [0, T]$.
- $\mathcal{M}_0(\mu)$ contains the set of **bounded solutions** of (10) staying in \mathcal{O}_u for all $t \in \mathbb{R}$ *i.e.* if u is a solution of (10) staying in \mathcal{O}_u for all $t \in \mathbb{R}$, then $u_0(0) \in \mathcal{M}_0(\mu)$.

Proof. The idea is to apply Theorem 4.1 to the extended system $\tilde{u} = (u, \mu)$ with the additional equation $\frac{d\mu}{dt} = 0$. Hence $\frac{d}{dt}\tilde{u} = \tilde{\mathbf{A}}\tilde{u} + \tilde{\mathbf{R}}(\tilde{u})$ with $\tilde{\mathbf{A}}\tilde{u} = (\mathbf{A}u + d_{\mu}\mathbf{R}(0,0)\mu, 0)$ and $\tilde{\mathbf{R}}(\tilde{u}) = (R(u,\mu) - d_{\mu}\mathbf{R}(0,0)\mu, 0)$. It remains to show that the Hypotheses 4.1, 4.2 and 4.3 hold for $\tilde{\mathbf{A}}$ and $\tilde{\mathbf{R}}$.

The next extension of Theorem 4.1 allows to deal with situations where the vector field (10) has some symmetry.

Theorem 4.3 (Center manifold theorem for equivariant equations)

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 subspace \mathcal{E}_0 is an isometry. Under the assumptions in Theorem 4.1, then 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 (9) commutes with T_0 .

The isometry condition is required to find a cutoff function which is invariant by \mathbf{T}_0 thereby giving an equivariant vector field \mathbf{R}^{ϵ} (see proof of Theorem 4.1). Taking the Euclidean norm in E_0 , which is finite-dimensional, for any isometry \mathbf{T}_0 on E_0 we can choose the cutoff to be a smooth function of $||u_0||^2$. The rest of the proof is very similar.

Note that we can combine the two previous theorems for parameter dependent equivariant Cauchy problems.

5. Normal form

The previous section allows us, in infinite dimensions, to reduce the study of the original system (10) to a *finite* dimensional invariant manifold. Usually, one ends up studying the reduced equation (9) using a Taylor expansion of the reduced vector field. There is however a way which allows, by a polynomial change of variables, to simplify this polynomial vector field into a normal form. The study of these normal forms allows then to tackle the different reduced equations swiftly. In short, close to a bifurcation, the "details" of the Cauchy problem (or of the model in theoretical biology) do not matter.

The idea of the normal form theory is to find a polynomial change of variables which *simplifies* locally a **finite dimensional** Cauchy problem of the form

(11)
$$\dot{u} = \mathbf{A}u + \mathbf{R}(u, \mu).$$

We make the following hypothesis

Hypothesis 5.1

- (1) **A** is a linear map in \mathbb{R}^n ,
- (2) for some $k \geq 2$, there exist neighborhoods $\mathcal{V}_u \in \mathbb{R}^n$ and $\mathcal{V}_\mu \in \mathbb{R}^m$ of 0 such that $\mathbf{R} \in \mathcal{C}^k(\mathcal{V}_u \times \mathcal{V}_\mu, \mathbb{R}^n)$ and

$$\mathbf{R}(0,0) = 0, \ d_u \mathbf{R}(0,0) = 0$$

Theorem 5.1

Assume that hypothesis 5.1 holds. Then for any positive integer $p, 2 \le p \le k$, there exist neighborhoods \mathcal{V}_1 and \mathcal{V}_2 of 0 in \mathbb{R}^n and \mathbb{R}^m , respectively, such that for any $\mu \in \mathcal{V}_2$, there is a polynomial $\Phi_{\mu} : \mathbb{R}^n \to \mathbb{R}^n$ of degree p with the following properties:

• The coefficients of the monomials of degree q in Φ_{μ} are functions of μ of class \mathcal{C}^{k-q} , and

$$\Phi_0(0) = 0, \ d\Phi_0(0) = 0$$

• For any $u \in \mathcal{V}_1$, the polynomial change of variable $u = v + \Phi_u(v)$ transforms (11) into the normal form

$$\dot{v} = \mathbf{A}v + \mathbf{N}_{\mu}(v) + \rho(v,\mu)$$

and the following properties hold:

(1) For any $\mu \in \mathcal{V}_2$, \mathbf{N}_{μ} is a polynomial $\mathbb{R}^n \to \mathbb{R}^n$ of degree p, with coefficients depending upon μ , such that the coefficients of the monomials of degree q are of class \mathcal{C}^{k-q} , and

$$N_0(0) = 0, \ d_v N_0(0) = 0$$

(2) the equality $\mathbf{N}_{\mu}(e^{t\mathbf{A}^*}v) = e^{t\mathbf{A}^*}\mathbf{N}_{\mu}(v)$ holds for all $(t,v) \in \mathbb{R} \times \mathbb{R}^n$ and $\mu \in \mathcal{V}_2$ (3) the maps ρ belongs to $\mathcal{C}^{k}(\mathcal{V}_{1} \times \mathcal{V}_{2}, \mathbb{R}^{n})$ and

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$$\forall \mu \in \mathcal{V}_2, \ \rho(v,\mu) = o(\|v\|^p).$$

We note that \mathbf{N}_{μ} is only polynomial in v. We can of course Taylor expand the monomials in μ to find their expression. It can be useful to use an expression which is equivalent⁴ to the above equality:

$$d_y \mathbf{N}_{\mu}(v) \mathbf{A}^* y = \mathbf{A}^* \mathbf{N}_{\mu}(v), \ \forall v \in \mathbb{R}^n, \ \mu \in \mathcal{V}_2.$$

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 Φ, \mathbf{N} commutes with \mathbf{T} .

Example : We give here an example of application to the **Hopf bifurcation** in dimension 2. Hence, we consider the case where $\mathbf{A} \in \mathcal{L}(\mathbb{R}^2)$ has a pair of simple complex eigenvalues $\pm i\omega$ with eigenvectors ζ and its complex conjugate $\overline{\zeta}$. **A** is a diagonal matrix in the basis $(\zeta, \overline{\zeta})$: $\mathbf{A} = diag(i\omega, -i\omega)$. We may write a vector $u \in \mathbb{R}^2$ as $u = z\zeta + \overline{z}\overline{\zeta}$. We shall show that the normal form $\mathbf{N}(u)$ is such that $\mathbf{N}(u) = (zQ(|z|^2), \overline{zQ}(|z|^2))$ in the basis $(\zeta, \overline{\zeta})$ where $Q \in \mathbb{C}[X]$ and Q(0) = 0. In this basis, one finds that the exponential of the adjoint reads $e^{t\mathbf{A}^*} = diag(e^{-i\omega t}, e^{i\omega t})$. We write

In this basis, one finds that the exponential of the adjoint reads $e^{t\mathbf{A}^*} = diag\left(e^{-i\omega t}, e^{i\omega t}\right)$. We write $\mathbf{N} = \left(P(z, \bar{z}), \bar{P}(z, \bar{z})\right)_{(\zeta, \bar{\zeta})}$ and look for $P \in \mathbb{C}[X]$. One finds $P(e^{-i\omega t}z, e^{i\omega t}\bar{z}) = e^{-i\omega t}P(z, \bar{z})$ using the commutation relation in Theorem 5.1. Looking for monomials $z^a \bar{z}^b$, one obtains the equation a = b + 1 which provides the result $P(z, \bar{z}) = zQ(|z|^2)$. Q(0) = 0 comes from $d\mathbf{N}(0) = 0$. The hopf normal form at lowest order is

$$\dot{z} = z(a\mu + i\omega - b|z|^2) +
ho(z, ar{z})$$

Note that the truncated vector field commutes with $\mathbf{T} : z \to e^{i\theta} z$ for $\theta \in \mathbb{R}$ but not the reminder $\rho(z, \bar{z})$. This symmetry of the **truncated** vector field allows us to use polar coordinates to study the Hopf normal form.

6. Combination of center manifold and normal form results

Recall that $u = u_0 + \Psi(u_0, \mu)$ where $u_0 \in E_0$ and $\Psi(u_0, \mu) \in \mathbb{Z}_h$. Hence, performing the normal form change of variables on the reduced equation (9) leads to

$$\frac{d}{dt}v_0 = A_0v_0 + \mathbf{N}_0\mu(v_0) + \rho(v_0,\mu).$$

Consequently, we can write $u = v_0 + \tilde{\Psi}(v_0, \mu)$ with $\tilde{\Psi}(v_0, \mu) = \Phi_{\mu}(v_0) + \Psi(v_0 + \Phi_{\mu}(v_0), \mu) \in \mathbb{Z}$. Note that $\tilde{\Psi}$ does not belong to the hyperbolic projection of \mathbb{Z} .

Upon differentiating the expression $u = v_0 + \tilde{\Psi}(v_0, \mu)$, one obtains:

$$\dot{u} = \mathbf{A}u + \mathbf{R}(\mu) = \left[Id + d\tilde{\Psi}(v_0) \right] (\mathbf{A}_0 v_0 + \mathbf{N}_0 \mu(v_0) + \rho(v_0, \mu))$$

= $\mathbf{A}(v_0 + \tilde{\Psi}(v_0, \mu)) + \mathbf{R}(v_0 + \tilde{\Psi}(v_0, \mu))$

which gives

(12)
$$d\tilde{\Psi}(v_0)\mathbf{A}_0v_0 - \mathbf{A}\tilde{\Psi}(v_0,\mu) + \mathbf{N}_{\mu}(v_0) = \Pi_p \left(\mathbf{R}(v_0 + \tilde{\Psi}(v_0,\mu) - d\tilde{\psi}(v_0,\mu)\mathbf{N}_0\mu(v_0)\right)$$

where $\Pi_p(f)$ is the truncated Taylor expansion at order p. The previous equation gives an equation for the change of variables effectively linking the original Cauchy problem to its normal form. Any example of use will be shown in the next section

⁴It is easily proved by taking the differential in t at t = 0

7. Application to a neural field model

We consider of model of visual cortex described by a single population of neurons. More precisely, the membrane potential $V(\mathbf{x}, t)$ of the population at location $\mathbf{x} \in \mathbb{R}^2$ satisfies the equation

(13)
$$\tau \frac{d}{dt} V(\mathbf{x}, t) = -V(\mathbf{x}, t) + \int_{\mathbb{R}^2} J(\|\mathbf{x} - \mathbf{y}\|) S_0 \left[\mu V(\mathbf{y}, t)\right] d\mathbf{y} \stackrel{def}{=} (-V + \mathbf{J} \cdot S_0(\mu V))(\mathbf{x})$$

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

This equation can be posed on various Banach spaces depending on the regularity of connectivity kernel J. Our aim is not to be as general as possible but to show how the previous tools can be applied in a simple setting.

We note that V = 0 is an equilibrium and we rewrite (13) as $\frac{d}{dt}u = \mathbf{A}u + \mathbf{R}(u, \mu)$ with

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

Hence, we perform a perturbation of V = 0 around the parameter value $\sigma = \sigma_c$ that we shall precise later. We now make the following assumptions concerning our problem (13).

Hypothesis 7.1

- we assume that $J \in \mathrm{H}^2(\mathbb{R}^2)$
- 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 (13) consist in their symmetries. Indeed, the following linear representations of the symmetries commute with the vector field (13), we have the symmetries of translations

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

of rotations

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

and of reflexions

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

These transformations raise an issue in view of the application of the center manifold Theorem 4.1. Indeed, if $U(\mathbf{x})$ is an element of 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.

7.1. Euclidean group and lattice. To circumvent this issue, we further assume that the membrane potential V has some periodicity. More precisely, we define a planar lattice \mathcal{L} as a set of integer linear combinations of two independent vectors l_1 and l_2

$$\mathcal{L} = \{ ml_1 + nl_2, \ m, n \in \mathbb{Z} \}.$$

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 k_1 and k_2 that satisfy $k_i \cdot l_j = \delta_{ij}$

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

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	$l_1 = (1,0), l_2 = (0,1)$	$\mathbf{k}_1 = (0,1), \mathbf{k}_2 = (1,0)$
Rhombic	\mathbf{D}_2	$l_1 = (1, -\cot\theta), l_2 = (0, \cot\theta)$	$\mathbf{k}_1 = (1,0), \mathbf{k}_2 = (\cos\theta, \sin\theta)$
Hexagonal	\mathbf{D}_6	$l_1 = (\frac{1}{\sqrt{3}}, 1), \ l_2 = (\frac{2}{\sqrt{3}}, 0)$	$\mathbf{k}_1 = (0,1), \mathbf{k}_2 = (\frac{\sqrt{3}}{2}, -\frac{1}{2})$

7.2. Reduction of symmetries. We now look for solutions V of (13) which are doubly periodic on the square lattice with basis $l_1 = \mathbf{k}_1 = (1,0)$ and $l_2 = \mathbf{k}_2 = (0,1)$. More precisely, we require that $V(\mathbf{x} + \mathbf{l}) = V(\mathbf{x})$ for all $\mathbf{l} \in \mathcal{L}_{square}$ and $\mathbf{x} \in \mathbb{R}^2$. Hence, it gives the following 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 $\tilde{J} \stackrel{def}{=} \sum_{l \in \mathcal{L}} J(\cdot + l)$. It follows that \tilde{J} is doubly periodic. Also, $\tilde{J} \in L^2(\mathcal{D})$ since $J \in L^1(\mathbb{R}^2)$.

The previous symmetries have been reduced to

The restriction to the square lattice periodicity have reduced the symmetry group of the equations. Because of our assumptions, 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. These transformations form the 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:

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

7.3. Functional setting. We wish to apply Theorem 4.1 in a Hilbert spaces setting for simplicity. It is also more convenient for the linear analysis to have Hilbert spaces as it provides projectors. 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 **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

$$\mathcal{Z} = H^2_{per}(\mathcal{D}).$$

The Cauchy problems is formulated with $\mathbf{A} = -id + \mu_c s_1 \tilde{\mathbf{J}}$ and $\mathbf{R}(u, \mu) = \tilde{\mathbf{J}} \cdot S_0(\mu u) - \mu_c s_1 \tilde{\mathbf{J}} \cdot u$.

Lemma 7.1

Assume that $0 \in \Sigma(\mathbf{A})$. Then, the neural fields equations (13) have a parameter dependent center manifold $\mathcal{M}(\mu)$.

Proof.

Hyp 4.4 We leave to the reader to prove that $\mathbf{R} \in C^3(\mathcal{Z} \times \mathbb{R}, \mathcal{Z})$. The linearized operator $\mathbf{A} = -Id + s_1 \mu_c \tilde{\mathbf{J}}$ is continuous from \mathcal{X} to \mathcal{X} using the Cauchy-Schwartz inequality.

- Hyp 4.4 We write $\hat{J}_{\mathbf{k}} = \int_{\mathcal{D}} \tilde{J}(\mathbf{y}) e^{2i\pi \mathbf{k} \cdot \mathbf{y}} d\mathbf{y}$. Then, the spectrum of \mathbf{A} is the set $\Sigma(\mathbf{A}) = \{-1 + \mu_c s_1 \hat{J}_{\mathbf{k}}\} \cup \{0\}$ which is composed of eigenvalues with finite multiplicities. Indeed, to find the spectrum, one needs to find $\lambda \in \mathbb{C}$ such that for all $V \in \mathcal{X}$ there is a unique $U \in \mathcal{X}$ such that $\lambda U \mathbf{A}U = V$. Taking Fourier transforms, one finds $(\lambda + 1 s_1\sigma_c s_1 \hat{J}_{\mathbf{k}})\hat{V}_{\mathbf{k}} = \hat{U}_{\mathbf{k}}$ for all $\mathbf{k} \in \mathcal{L}_{sq}^*$ which implies $\lambda \notin \{-1\} \cup \{-1 + s_1\sigma_c \hat{J}_{\mathbf{k}}, \mathbf{k} \in \mathcal{L}^*\}$. Reciprocally, if $\lambda \notin \{-1\} \cup \{-1 + s_1\sigma_c \hat{J}_{\mathbf{k}}, \mathbf{k} \in \mathcal{L}^*\}$ is summable because $\{-1\} \cup \{-1 + s_1\sigma_c \hat{J}_{\mathbf{k}}, \mathbf{k} \in \mathcal{L}^*\}$ is compact, hence yielding to a solution of $\lambda U \mathbf{A}U = V$. The kernel ker \mathbf{A} is finite dimensional from the Parseval's equality.
- Hyp 4.3 From $\mathbf{A} \in \mathcal{L}(\mathcal{X})$, we find: $\|i\omega \mathbf{A}\|_{\mathcal{L}(\mathcal{X})} \geq |\omega| \|\mathbf{A}\|_{\mathcal{L}(\mathcal{X})}$. Hence, for ω large enough (above $\|\mathbf{A}\|$), one finds $\|i\omega \mathbf{A}\|_{\mathcal{L}(\mathcal{X})} \geq |\omega|/2$ and $i\omega \mathbf{A}$ is invertible. This gives $\|(i\omega \mathbf{A})^{-1}\|_{\mathcal{L}(\mathcal{X})} \leq \frac{2}{|\omega|}$.

We could avoid the above computations by noting that $\tilde{\mathbf{J}}$ is a compact operator. Hence, it has a discrete spectrum and so does \mathbf{A} . For the resolvent estimate, we note that \mathbf{A} is a sectorial operator because it is a bounded operator.

We now assume that (13) features a static bifurcation, meaning that $E_0 = \ker \mathbf{A} \neq \{0\}$. 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 7.1

In practice, we can apply the Theorem 4.1 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.

Lemma 7.2

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

(14)
$$\begin{cases} \dot{z}_1 = z_1 \left(\alpha + \beta |z_1|^2 + \gamma |z_2|^2 \right) \\ \dot{z}_2 = z_2 \left(\alpha + \beta |z_2|^2 + \gamma |z_1|^2 \right) \end{cases}$$

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

Proof. The restriction of G_{sq} on E_0 gives:

$$\begin{aligned} \mathcal{R} \cdot (z_1, z_2) &= (\bar{z}_2, z_1) \\ \mathcal{S} \cdot (z_1, z_2) &= (z_1, \bar{z}_2) \\ \mathcal{T}_{\mathbf{t}} \cdot (z_1, z_2) &= (e^{-2i\pi t_1} z_1, e^{-2i\pi t_1} z_2), \ \mathbf{t} = t_1 l_1 + t_2 l_2, \ t_i \in [0, 1). \end{aligned}$$

We look for the normal form $\mathbf{N} = N_1 e^{2i\pi x} + N_2 e^{2i\pi y} + c.c.$ The structure of $\mathbf{A}_0 = 0$ gives no information when using the normal form commutation equation. We are left taking advantage of the symmetries. The fact that \mathbf{N} commutes with \mathcal{T}_t gives

$$e^{-2i\pi t_j}N_j(z_1,\bar{z}_1,z_2,\bar{z}_2) = N_j(e^{-2i\pi t_1}z_1,e^{2i\pi t_1}\bar{z}_1,e^{-2i\pi t_1}z_2,e^{2i\pi t_2}\bar{z}_2).$$

Looking for monomials, the shows that $N_j(z_1, \bar{z}_1, z_2, \bar{z}_2) = z_j P_j(|z_1|^2, |z_2|^2)$ for some polynomials $P_j \in \mathbb{C}[X, Y]$. The rotation R^2 symmetry gives

$$(N_1(\bar{z}_1, \bar{z}_2), N_2(\bar{z}_1, \bar{z}_2)) = (\overline{N_1(z_1, z_2)}, \overline{N_2(z_1, z_2)})$$

which yields $P_j \in \mathbb{R}[X, Y]$. The reflexion symmetry implies that $P_1 = P_2$. This completes the proof of the lemma.

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 (14) 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

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

Hence, depending on the stability of the equilibria of (14), one finds that the solutions of (13) close to the equilibrium V = 0 for $\sigma \approx \sigma_c$ converge to V = 0 or to stripe / spot patterns.

7.4. Computation of the normal form coefficients. 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 in (13). We perform these computations in the following lemma.

Lemma 7.3

The normal form (14) has the following coefficients:

(15)
$$\beta/\mu_c^3 \hat{\mathbf{J}}_{\mathbf{k}_c} = \mu_c s_2^2 \quad \left[\frac{\hat{\mathbf{J}}_0}{1 - \hat{\mathbf{J}}_0 / \mathbf{J}_{\mathbf{k}_c}} + \frac{\hat{\mathbf{J}}_{2\mathbf{k}_c}}{2(1 - \hat{\mathbf{J}}_{2\mathbf{k}_c} / \hat{\mathbf{J}}_{\mathbf{k}_c})} \right] \quad + \quad s_3/2$$
$$\gamma/\mu_c^3 \hat{\mathbf{J}}_{\mathbf{k}_c} = \mu_c s_2^2 \quad \left[\frac{\hat{\mathbf{J}}_0}{1 - \hat{\mathbf{J}}_0 / \mathbf{J}_{\mathbf{k}_c}} + 2 \frac{\hat{\mathbf{J}}_{(1,1)}}{1 - \hat{\mathbf{J}}_{(1,1)} / \hat{\mathbf{J}}_{\mathbf{k}_c}} \right] \quad + \quad s_3.$$

Proof. Let us write the nonlinear change of variable $\tilde{\Psi}$ to bring the neural field equations to the normal form (14). We Taylor expand $\tilde{\Psi}$:

$$\tilde{\Psi}(v_0,\mu) = \sum_{l_1+l_2+p_1+p_2+r>1} z_1^{l_1} \bar{z}_1^{l_2} z_2^{p_1} \bar{z}_2^{p_2} \mu^r \tilde{\Psi}_{l_1,l_2,p_1,p_2,r}, \ \tilde{\Psi}_{l_1,l_2,p_1,p_2,r} \in \mathcal{Z},$$

where $\tilde{\Psi}$ satisfies $\tilde{\Psi}(0,0) = 0$, $D_{v_0}\tilde{\Psi}(0,0) = 0$. Using the equation (12) satisfied by $\tilde{\Psi}$, we find the following equations with $\zeta_1 = e^{2i\pi x}$, $\zeta_2 = e^{2i\pi y}$, $\zeta_1^* = e^{-2i\pi x}$, $\zeta_2^* = e^{-2i\pi y}$:

$$\begin{array}{lll} 0 &=& -2L\Psi_{2,1,0,0,0} + 2\beta\zeta_1 - 4\mathbf{R}_2(\Psi_{1,1,0,0,0},\zeta_1) - 4\mathbf{R}_2(\bar{\zeta}_1,\Psi_{2,0,0,0,0}) - 6\mathbf{R}_3(\zeta_1,\zeta_1,\bar{\zeta}_1) \\ 0 &=& -L\Psi_{1,1,1,0,0} + \gamma\zeta_2 - 2\mathbf{R}_2(\Psi_{0,1,1,0,0},\zeta_1) - 2\mathbf{R}_2(\bar{\zeta}_1,\Psi_{1,0,1,0,0}) - 2\mathbf{R}_2(\zeta_2,\Psi_{1,1,0,0,0}) \\ && -6\mathbf{R}_3(\zeta_2,\zeta_1,\bar{\zeta}_1) \end{array}$$

where \mathbf{R}_p is the differential $\mathbf{R}_p \equiv \frac{1}{p!} D^p \mathbf{R}(0, \mu_c)$ and $L = -Id + \mu_c s_1 \tilde{\mathbf{J}}$. From the Fredholm alternative, we find:

$$\beta = \langle \zeta_1^*, 2\mathbf{R}_2(\Psi_{1,1,0,0,0}, \zeta_1) + 2\mathbf{R}_2(\zeta_1, \Psi_{2,0,0,0,0}) + 3\mathbf{R}_3(\zeta_1, \zeta_1, \zeta_1) \rangle_2 \gamma = \langle \zeta_2^*, 2\mathbf{R}_2(\Psi_{0,1,1,0,0}, \zeta_1) + 2\mathbf{R}_2(\bar{\zeta}_1, \Psi_{1,0,1,0,0}) + 2\mathbf{R}_2(\zeta_2, \Psi_{1,1,0,0,0}) + 6\mathbf{R}_3(\zeta_2, \zeta_1, \bar{\zeta}_1) \rangle_2$$

In order to find the coefficients of the normal form, we are led to compute some of the coefficients of $\tilde{\Psi}$. By looking at the second order monomials, we find:

$$\begin{array}{rclrr} 0 & = & 2L\Psi_{2,0,0,0,0} + 2\mathbf{R}_2(\zeta_1,\zeta_1) \\ 0 & = & L\Psi_{1,1,0,0,0} + 2\mathbf{R}_2(\zeta_1,\bar{\zeta}_1) \\ 0 & = & L\Psi_{0,1,1,0,0} + 2\mathbf{R}_2(\zeta_2,\bar{\zeta}_1) \\ 0 & = & L\Psi_{1,0,1,0,0} + 2\mathbf{R}_2(\zeta_1,\zeta_2) \end{array}$$

which are solved by

$$\begin{split} \Psi_{2,0,0,0,0} &= Span(\zeta_1,\zeta_2,\bar{\zeta}_1,\bar{\zeta}_2) + \frac{\mu_c^2 s_2}{2} \frac{\mathbf{J}_{2\mathbf{k}_c}}{1-s_1\mu_c \hat{\mathbf{J}}_{2\mathbf{k}_c}} \zeta_1^2 \\ \Psi_{1,1,0,0,0} &= Span(\zeta_1,\zeta_2,\bar{\zeta}_1,\bar{\zeta}_2) + 2\frac{\mu_c^2 s_2}{2} \frac{\hat{\mathbf{J}}_0}{1-s_1\mu_c \hat{\mathbf{J}}_0} \\ \Psi_{0,1,1,0,0} &= Span(\zeta_1,\zeta_2,\bar{\zeta}_1,\bar{\zeta}_2) + 2\frac{\mu_c^2 s_2}{2} \frac{\hat{\mathbf{J}}_{(1,1)}}{1-s_1\mu_c \hat{\mathbf{J}}_{(1,1)}} \zeta_2 \bar{\zeta}_1 \\ \Psi_{1,0,1,0,0} &= Span(\zeta_1,\zeta_2,\bar{\zeta}_1,\bar{\zeta}_2) + 2\frac{\mu_c^2 s_2}{2} \frac{\hat{\mathbf{J}}_{(1,1)}}{1-s_1\mu_c \hat{\mathbf{J}}_{(1,1)}} \zeta_1 \zeta_2 \end{split}$$

Let us indicate how to solve the first equation for example. Note that $\mathbf{R}_2(\zeta_1,\zeta_1) = \frac{\mu_c^2 s_2}{2} \mathbf{\tilde{J}} \cdot \zeta_1^2 = \frac{\mu_c^2 s_2}{2} \mathbf{\hat{J}}_{2\mathbf{k}_c} \zeta_1^2$. A particular solution is given by $A\zeta_1^2$ where A satisfies $(1 - s_1 \mu_c \mathbf{\hat{J}}_{2\mathbf{k}_c})A = \frac{\mu_c^2 s_2}{2} \mathbf{\hat{J}}_{2\mathbf{k}_c}$ to which we must add any null vector of L. This gives the coefficient $\Psi_{2,0,0,0,0}$. It is then straightforward to obtain β and γ .

8. CONCLUSION

The tools presented in this lecture are applicable to many models of mathematical neurosciences and more generally to models of mathematical biology. Roughly speaking, their use is relatively straightforward for parabolic PDEs for which the estimates of Hypothesis 4.3 can be checked easily. However, the case of transport equations [Per07] or delay differential equations is much more involved and require a specific analysis (see for example [IK00, DG91]).

We have presented the very simple application of the case of the theory of visual hallucinations $[BCG^+01]$ based on the neural field equations. Of course, this is a particular model and other "mean field" models of neural networks could be used at the price of a higher technical cost.

The center manifold theory is helpful because it gives a finite dimensional representation of the flow. To this end, the hypotheses are quite strong and may be very difficult to check. In INVARIANT MANIFOLDS IN MATHEMATICAL NEUROSCIENCES WINTER SCHOOL TOULOUSE 2017 19

this case, one can look only at the existence of particular solutions like periodic orbits using the Liapunov-Schmidt method [CH82] which relies on weaker assumptions.

The center manifold theory gives results concerning the local behavior of the flow around an equilibrium for parameters close to the bifurcation point. Hence, the largest neighborhood in the parameter space for which the reduced equation is valid has diameter bounded by the distance to the next bifurcation point. However, the diameter can be very small and the reduced equation may only capture a tiny region of the state space (see for example [VCF15]).

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References

- [BCG⁺01] Paul C. Bressloff, Jack D. Cowan, Martin Golubitsky, Peter J. Thomas, and Matthew C. Wiener. Geometric visual hallucinations, Euclidean symmetry and the functional architecture of striate cortex. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 356(1407):299-330, March 2001. [CH82] Shui-Nee Chow and Jack K. Hale. Methods of Bifurcation Theory, volume 251 of Grundlehren der mathematischen Wissenschaften. Springer New York, New York, NY, 1982. [Coo05] S. Coombes. Waves, bumps, and patterns in neural field theories. 2005. [DG91] Odo Diekmann and Stephan A. van Gils. The center manifold for delay equations in the light of suns and stars. In Mark Roberts and Ian Stewart, editors, Singularity Theory and its Applications, number 1463 in Lecture Notes in Mathematics, pages 122–141. Springer Berlin Heidelberg, 1991. [Erm98] Bard Ermentrout. Neural networks as spatio-temporal pattern-forming systems. Rep. Prog. Phys, 1998. [HG11] Mariana Haragus and Gerard Iooss. Local Bifurcations, Center Manifolds, and Normal Forms in Infinite-Dimensional Dynamical Systems. Springer London, London, 2011. [IK00] Grard Iooss and Klaus Kirchgssner. Travelling Waves in a Chain of Coupled Nonlinear Oscillators. Communications in Mathematical Physics, 211(2):439-464, April 2000. [Kat05] Tosio Kato. Perturbation theory for linear operators. Springer, Berlin, 2005. OCLC: 823680095. Benot Perthame. Transport equations in biology. Frontiers in mathematics. Birkhuser, Basel, 2007. [Per07] [PS96] Brumberg Pinto and Ermentrout Simons. A Quantitative Population Model of Whisker Barrels: Re-Examining the Wilson-Cowan Equations. Journal of Computational Neuroscience, 1996. [Sie77] Ronald K. Siegel. Hallucinations. Scientific American, 237(4):132-141, 1977. [TSSH88] R. B. Tootell, E. Switkes, M. S. Silverman, and S. L. Hamilton. Functional anatomy of macaque striate cortex. II. Retinotopic organization. The Journal of Neuroscience, 8(5):1531-1568, May 1988.
- [VCF15] Romain Veltz, Pascal Chossat, and Olivier Faugeras. On the Effects on Cortical Spontaneous Activity of the Symmetries of the Network of Pinwheels in Visual Area V1. The Journal of Mathematical Neuroscience (JMN), 5(1):1–28, May 2015.

[VI92] Andr Vanderbauwhede and G. Iooss. Center manifold theory in infinite dimensions. In Dynamics reported, pages 125–163. Springer, 1992.

[VVG87] A. Vanderbauwhede and S. A. Van Gils. Center manifolds and contractions on a scale of Banach spaces. Journal of Functional Analysis, 72(2):209–224, 1987.

[WC72] Hugh R. Wilson and Jack D. Cowan. Excitatory and inhibitory interactions in localized populations of model neurons. *Biophysical journal*, 12(1):1, 1972.

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