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Bifurcations in neural masses

Romain VELTZ⁺, Oliver FAUGERAS
⁺romain.veltz@sophia.inria.fr

Introduction

Neural continuum networks are an important aspect of the modeling of macroscopic parts of the cortex. They have been first studied by Amari[6]. These networks have then been the basis to model the visual cortex by Bresslov[4]. From a computational viewpoint, the neural masses could be used to perform image processing like segmentation, contour detection... Thus, there is a need to develop tools (theoretical and numerical) allowing the study of the dynamical and stationary properties of the neural masses equations.

In this paper, we look at the dependency of neural masses stationary solutions with respect to the stiffness of the nonlinearity. This choice is motivated by two reasons. First, it shows the differences with the case of an infinite stiffness (which corresponds formally to a heaviside nonlinear function) as used for example in Ermentrout[2]. Second, the study is generic and any other parameter could have been used with similar tools.

The study is done by using bifurcation theory in infinite dimensions. We provide a useful approximation of the connectivity matrix and give numerical examples of bifurcated branches which had not been yet fully computed in the literature. The analysis relies on the study of a simple model thought generic in the sense it has the properties that any neural mass system should possess generically.

1 General framework

We consider the following neural mass equation defined over a bounded piece of cortex $\Omega \subset \mathbb{R}^d$, $d = 1, 2, 3$ ¹ :

$$\mathbf{V}_t(\mathbf{r}, t) = -\mathbf{L}\mathbf{V}(\mathbf{r}, t) + [\mathbf{W} \cdot \mathbf{S}(\sigma\mathbf{V} - \theta)](\mathbf{r}, t) + \mathbf{I}_{ext}(\mathbf{r})$$

$\mathbf{V}(\cdot, t) \in L^2(\Omega, \mathbb{R}^p) = \mathcal{H}$, a real vector space, where p is the number of populations of neurons and we endow \mathcal{H} with the inner product

$$\langle \mathbf{V}_1, \mathbf{V}_2 \rangle_{\mathcal{H}} = \int_{\Omega} d\mathbf{r} \langle \mathbf{V}_1(\mathbf{r}), \mathbf{V}_2(\mathbf{r}) \rangle_{\mathbb{R}^p}$$

$\mathbf{S} : \mathbb{R}^p \rightarrow \mathbb{R}^p$ is defined by $\mathbf{S}(x) = [S(x_1), \dots, S(x_p)]^T$. $\sigma = \text{diag}(\sigma_1, \dots, \sigma_p)$ determines the slope of each of the p **sigmoid**² at the origin.

$\theta \in \mathbb{R}^p$ determines the threshold of each of the p sigmoids.

$\mathbf{W}(t)$ is a linear operator from \mathcal{H} to itself:

$$[\mathbf{W} \cdot \mathbf{V}](\mathbf{r}, t) = \int_{\Omega} \mathbf{W}(\bar{\mathbf{r}}, \mathbf{r}) \mathbf{V}(\bar{\mathbf{r}}) d\bar{\mathbf{r}},$$

where $\mathbf{W}(\mathbf{r}, \mathbf{r}', t)$ is a $p \times p$ matrix.

$\mathbf{L} = \text{diag}(\frac{1}{\tau_1}, \dots, \frac{1}{\tau_p})$ where the positive numbers τ_i , $i = 1, \dots, p$ determines the dynamics of each neural population. Par changing the variables, we can assume $\theta = 0$ and $\mathbf{L} = Id$.

In this article we focus on the influence of the slopes σ . We make the assumption that all slopes are equal to λ , $\sigma = \lambda Id_p$. We can therefore rename \mathbf{V} , \mathbf{W} and \mathbf{I}_{ext} to restrict our study to:

$$\mathbf{V}_t(\mathbf{r}, t) = -\mathbf{V}(\mathbf{r}, t) + [\mathbf{W} \cdot \mathbf{S}(\lambda\mathbf{V})](\mathbf{r}, t) + \mathbf{I}_{ext}(\mathbf{r}) \quad (1)$$

which we rewrite :

$$0 = -\mathbf{V}^f + \mathbf{W} \cdot \mathbf{S}(\lambda\mathbf{V}^f) + \mathbf{I}_{ext} \stackrel{\text{def}}{=} -F(\mathbf{V}^f, \lambda) \quad (2)$$

For λ given, let $\mathcal{B}_{\lambda} = \{\mathbf{V} / F(\mathbf{V}, \lambda) = 0\}$

In [1] we proved :

Proposition 1.1. $\forall \lambda \in \mathbb{R}, \mathcal{B}_{\lambda} \neq \emptyset$

In fact we can prove much better :

Proposition 1.2. *Given $a < b$ there exists a continuous curve $s \rightarrow (\mathbf{V}_s^f, \lambda(s))$ such that $\lambda([0, 1]) = [a, b]$ and $\forall s \mathbf{V}_s^f \in \mathcal{B}_{\lambda(s)}$*

2 Bifurcation theory

Once we have a solution \mathbf{V}_{λ}^f of $F(\mathbf{V}, \lambda) = 0$ over an interval $J = [a, b]$, we can study the steady states bifurcation i.e. find the solutions, if any, that are different from \mathbf{V}_{λ}^f . We start with a definition :

Definition 2.1. *We say that the equation $F(\mathbf{V}, \lambda) = 0$ bifurcates from $(\mathbf{V}_{\lambda_0}^f, \lambda_0)$ a solution $(\mathbf{U}_{\lambda}, \lambda)$ if there exists a sequence of solutions $(\mathbf{U}_n, \lambda_n)$ which satisfies*

$$\lim_{n \rightarrow \infty} \lambda_n = \lambda_0 \text{ and } \lim_{n \rightarrow \infty} \|\mathbf{U}_n - \mathbf{V}_{\lambda_0}^f\| = 0$$

¹We can formally have $\Omega \subset \mathbb{R}^d \times (0, 2\pi)^r$, see Bresslov

²ie the function $x \rightarrow (1 + e^{-x})^{-1}$

From $F(\mathbf{V}, \lambda) = \mathbf{V} - \mathbf{W} \cdot \mathbf{S}(\lambda \mathbf{V}) - \mathbf{I}_{\text{ext}}$

Writing $\mathbf{V} = \mathbf{V}_\lambda^f + \mathbf{U}$, we now consider (up to the identification $\tilde{F} = F$):

$$F(\mathbf{U}, \lambda) = L_\lambda \cdot \mathbf{U} + \tilde{G}(\mathbf{U}, \lambda),$$

where

$$\begin{cases} L_\lambda = \text{Id} - \mathbf{W} \cdot (\lambda DS(\mathbf{V}_\lambda^f)) \\ \tilde{G}(\mathbf{U}, \lambda) = \sum_{n \geq 2} D^{(n)} G(\mathbf{V}_\lambda^f, \lambda) \cdot \mathbf{U}^{(n)} \equiv \sum_{n \geq 2} G_n(\mathbf{U}, \lambda) \end{cases}$$

Then (Implicit functions theorem):

Proposition 2.2. *A necessary condition for λ_0 to be a bifurcation point is L_{λ_0} non invertible.*

These points λ_0 are possible bifurcation points (according to the previous definition). The bifurcation theory aims at telling what happens around such point λ_0 , if there are other branches of solutions and their number. This is interesting because it gives the stationary states of the neural masses equations.

3 PG-kernel approximation of the connectivity matrix

We focus on a class of connectivity functions which is very rich and can represent economically all kinds of biologically plausible cortical connectivity kernels. Moreover, such kernels allows to write the neural masses equations as finite dimensional ODEs. We therefore assume that \mathbf{W} is a PG-kernel.

Definition 3.1 (Pincherle-Goursat Kernels). *The connectivity $\mathbf{W}(\mathbf{r}, \mathbf{r}')$ is a PG-kernel if*

$$\mathbf{W}(\mathbf{r}, \mathbf{r}') = \sum_{k,l=0}^{N-1} a_{kl} X_k(\mathbf{r}) \otimes Y_l(\mathbf{r}')$$

where $(X^k, k = 1..N)$ are linearly independent functions of \mathcal{H} .

We make the following assumptions :

$$\Omega = [-1, 1]^2, \quad p = 2$$

and also :

$$\mathbf{S}(0) = 0, \quad \mathbf{I}_{\text{ext}} = 0$$

Thus, the persistent state $\mathbf{V}_\lambda^f = 0$ is a trivial solution of the equations 2.

We are interested in excitatory-inhibitory neural fields, thus the sign of the connectivity functions has to be like this :

$$\text{sign}(\mathbf{W}) = \begin{bmatrix} + & - \\ \pm & \pm \end{bmatrix}$$

3.1 Description of the connectivity matrix component

It is often seen in the literature that \mathbf{W}_{ij} is gaussian and the cortex is chosen infinite. For example one find in [2,5]

$$\begin{aligned} \mathbf{W}_{11}(\mathbf{r}, \mathbf{r}') &= \exp(-\|\mathbf{r} - \bar{\mathbf{r}}\|^2/2) = e^{-\|\mathbf{r}\|^2/2} e^{-\|\mathbf{r}'\|^2/2} e^{\langle \mathbf{r}, \mathbf{r}' \rangle} \\ &\approx e^{-\|\mathbf{r}\|^2/2} e^{-\|\mathbf{r}'\|^2/2} \left(1 + \langle \mathbf{r}, \mathbf{r}' \rangle + \frac{1}{2} \langle \mathbf{r}, \mathbf{r}' \rangle^2 + \dots \right) \end{aligned}$$

We notice two things :

- $1 + \langle \mathbf{r}, \mathbf{r}' \rangle + \frac{1}{2} \langle \mathbf{r}, \mathbf{r}' \rangle^2 + \dots$ is a polynomial
- $e^{-\|\mathbf{r}\|^2/2}$ is bell-shaped, we will approximate it with $\left(1 - \|\mathbf{r}\|^2\right)^a$ with $a > 0$. This choice is also motivated by the fact that $e^{-\|\mathbf{r}\|^2/2}$ tends to zero at the edges of the infinite cortex, so we choose to keep it ie $\left(1 - \|\mathbf{r}\|^2\right)^a = 0$ for $\mathbf{r} \in \partial[-1, 1]^2$.

Finally we will have the following simplified ($N = 2$) connectivity functions :

$$\mathbf{W}_{ij}(\mathbf{r}, \mathbf{r}') = \mathbf{C}_{ij} + \left(1 - \|\mathbf{r}\|^2\right)^a \left(1 - \|\mathbf{r}'\|^2\right)^a P_{ij}(\mathbf{r}, \mathbf{r}') \quad (3)$$

where P is a polynomial in \mathbf{r} and \mathbf{r}' and \mathbf{C} is a constant matrix.

From now, we will consider such an orthonormal family $(e_n)_{n \geq 0}$ of $L^2(\Omega, \mathbb{R})$ with e_0 being the constant function $1/2$, and $\forall (x, y) \in \Omega$ $e_n(x, y) = \left(1 - x^2 - y^2\right)^a P_n(x, y)$.

We deduce an orthonormal basis $(B_n)_{n \geq 0}$ of $L^2(\Omega, \mathbb{R}^2)$ which will be used in the next section :

$$B_{2n} = \begin{bmatrix} e_n \\ 0 \end{bmatrix}, \quad B_{2n+1} = \begin{bmatrix} 0 \\ e_n \end{bmatrix}$$

3.2 Toy model

We now choose the following connection matrix:

$$\mathbf{W}(\mathbf{r}, \mathbf{r}') = \begin{bmatrix} \alpha_1 + \alpha_2 e_n(\mathbf{r}) e_n(\mathbf{r}') & -\rho_1 + \rho_2 e_q(\mathbf{r}) e_r(\mathbf{r}') \\ \rho_1 + \rho_2 e_q(\mathbf{r}) e_r(\mathbf{r}') & \alpha_1 + \alpha_2 e_m(\mathbf{r}) e_m(\mathbf{r}') \end{bmatrix},$$

which can expressed as a PG-kernel. Adjusting the constants α_i, ρ_i allows to satisfy the condition on $\text{sign}(\mathbf{W})$. This connectivity matrix can be seen as the first order approximation of a given connectivity matrix \mathbf{W}_0 .

It is easy to check that $\sigma(\mathbf{W}) = \{\alpha_1 \pm I\rho_1, \pm\rho_2, \alpha_2\}$ with $\alpha_2 \neq \rho_2$.

We write $\mathbf{V} = \sum_{i=1}^6 v_i X_i$ and obtain the following form for the neural masses equation by projecting on the family $(X_i)_i$ associated to $e_p, e_q \dots$:

$$\dot{v}_k = v_k + \left\langle \mathbf{W} \cdot \mathbf{S} \left(\sum_{i=1}^6 v_i X_i \right), X_k \right\rangle_{\mathcal{H}} / \|X_k\|_{\mathcal{H}}^2 \quad (4)$$

3.3 Bifurcation of the persistent states

We have prop.2.2 $\sigma(\mathbf{L}_\lambda) = -1 + \lambda s_1 \sigma_n$ where $\sigma_n \in \sigma(\mathbf{W})$. Thus the possible bifurcation points are

$$\lambda_n = \frac{1}{s_1 \sigma_n}$$

3.3.1 Case of the simple eigenvalues

Let's examine the case of the simple eigenvalues $\pm \rho_2$ associated with the eigenvectors $f^\pm = (\pm B_{2r+1} + B_{2q}) / \sqrt{2}$. We find for $\alpha^\pm \equiv \langle G_2(f^\pm, \lambda_1^\pm), f^\pm \rangle_{\mathcal{H}} \neq 0$ that λ_1^\pm is a **transcritical** bifurcation point and there is a **unique** bifurcated branch on each side of λ_1^\pm given (for example near λ_1^+) by

$$\begin{aligned} \mathbf{U}_\lambda^+ &\approx -2 \frac{-1 + \lambda s_1 \rho_2}{(\lambda_1^+)^2 \frac{s_2}{2} \rho_2 [\int_{\Omega} e_n^3 + e_q^3]} (B_{2r+1} + B_{2q}) \\ &\approx \rho_2 v_5^f(\lambda) \approx \rho_2 v_6^f(\lambda) \end{aligned}$$

Thus, for λ close to λ_1 , the bifurcated solution looks like the eigenvector $B_{2r+1} + B_{2q}$.

3.3.2 Case of the double eigenvalue

$\sigma_2 = \alpha_2$ is a double eigenvalue of \mathbf{W} with associated eigenvectors $f_1 = B_{2n}$, $f_2 = B_{2m+1}$.

The last possible steady state bifurcation parameter is

$$\lambda_2 = \frac{1}{s_1 \alpha_2}$$

Following [3], we find that (2) reduces (to the first order) to find $(x, y) \in \mathbb{R}^2$ such that

$$\begin{cases} (-1 + \lambda s_1 \alpha_2)x + \lambda^2 s_2 \alpha_2 x^2 \int_{\Omega} e_n^3 = 0 \\ (-1 + \lambda s_1 \alpha_2)y + \lambda^2 s_2 \alpha_2 y^2 \int_{\Omega} e_m^3 = 0 \end{cases}$$

which leads to

$$\begin{cases} x^f = \frac{1 - \lambda s_1 \alpha_2}{\lambda^2 s_2 \alpha_2 \int_{\Omega} e_n^3} \\ y^f = \frac{1 - \lambda s_1 \alpha_2}{\lambda^2 s_2 \alpha_2 \int_{\Omega} e_m^3} \end{cases}$$

Thus, from $(0, \lambda_2)$ bifurcates one branch of solution on each side of λ_2 .

3.3.3 Global bifurcation analysis of steady states

The bifurcation analysis gives us insight on the local vicinity of the bifurcation point, but what can we tell if we want information far away from a given bifurcation point. In that case, one has to use global bifurcation (Cf [3]). We first study the case of the bifurcation point $(0, \lambda_1^+)$.

Theorem 3.2 (Global Bifurcation). *Under some verified assumptions, any bifurcated branch can be either*

- *unbounded in $\mathcal{F} \times \mathbb{R}$*
- *contains an odd number of points $(0, \lambda_i) \neq (0, \lambda_0)$ such that λ_i^{-1} are eigenvalues of \mathbf{L}_λ with odd algebraic multiplicities.*

Using Cauchy Schwarz inequality one find that :

$$\left\| \mathbf{V}_\lambda^f \right\|_{\mathcal{F}} \leq C \lambda, \text{ with } C \in \mathbb{R} \text{ (recall that } p = 2 \text{)}$$

Case of the bifurcation point $(0, \lambda_1^+)$:

Using these results, one find the following diagram for the persistent states on fig.1.

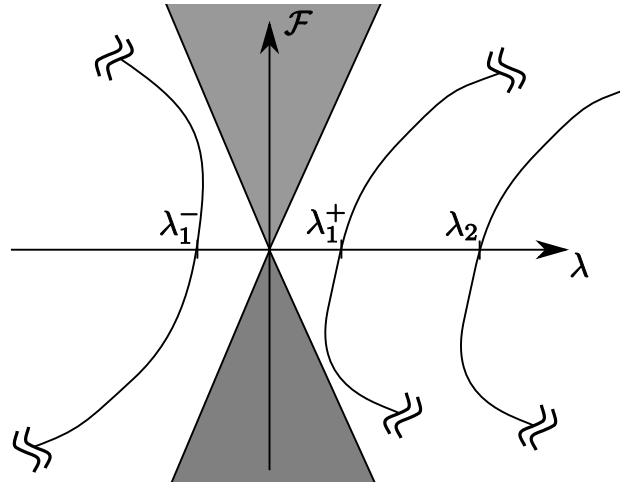


Figure 1: Predicted shape of the bifurcated branches. The cone represents the domain where the steady states cannot be.

3.3.4 Case of the complex eigenvalue

Recall that $-1 + \lambda s_1 (\alpha_1 \pm I \rho_1)$ are complex eigenvalues of \mathbf{L}_λ . The singular value

$$\lambda_H = \frac{1}{s_1 \alpha_1}$$

and the eigenvalue is

$$\beta(\lambda_H) = I \frac{\rho_1}{\alpha_1}$$

Recall that the neural masses equation is $\frac{d\mathbf{V}}{dt} = -F(\mathbf{V}, \lambda)$. To have an Hopf bifurcation, we need to check if $Re\beta'(\lambda_H) \neq 0$. Here, we find

$$Re \frac{d\beta}{d\lambda}(\lambda_H) = 2s_1\alpha_1 > 0$$

In order to know if we are in the supercritical or the subcritical case, we compute the Floquet exponent :

$$\ddot{\mu}_2(0) = 2 \frac{(\alpha_1^2 + \rho_1^2)^2 (s_2^2 - s_1 s_3)}{\alpha_1^2 s_1^4}, \quad s_1 = S'(0), \quad s_2 = S^{(2)}(0)/$$

The Floquet exponent tells if the bifurcated periodic solution is attractive ($\mu_2 > 0$) or repulsive ($\mu_2 < 0$).

\Rightarrow We have an Hopf bifurcation and the appearance of a periodic solution to equation (1), it is called **Breathers** in [5].

3.4 Numerical example

In this section, we do a simulation of the evolution equation (??). A simple way to ensure the assumptions on the non linearity is to choose :

$$S(z) = Sig(z - 2) - Sig(-2)$$

where Sig is the sigmoid function define on page 1. Note that any sigmoidal function would work.

We use the Gegenbauer polynomials G_q (Cf. eq.3) as a basis of $L^2((-1, 1), \mathbb{R})$. They are associated to the dot product :

$$\langle f, g \rangle = \int_{-1}^1 (1-x^2)^{a-1/2} f(x)g(x)dx, \quad a > 0 \text{ or } \frac{-1}{2} < a < 0$$

For a the polynomials, we use the functions $P_n(x, y) = G_{n_1}(x)G_{n_2}(y)$. For the numerical applications, we take the following parameters :

$$n = [4, 2], \quad m = [6, 6], \quad q = [2, 2], \quad r = [4, 4], \quad a = 4$$

$$\alpha_1 = 6, \quad \alpha_2 = 3, \quad \rho_1 = 6, \quad \rho_2 = 4$$

From this family added with the constant $e_0 = 1/2$, we build an orthonormal family $(e_i)_{i=0..4}$.

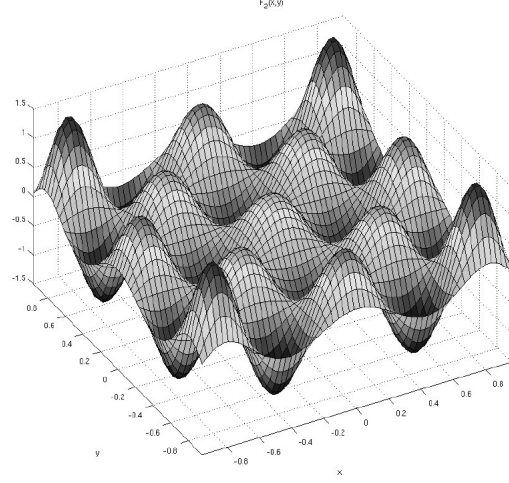


Figure 2: Representation of e_2 used for the orthonormal family.

We use the ODE representation of the neural masses equation to compute the evolution of a given initial state $\mathbf{V}(0)$. This reduces to a 6-dimensional ODE system, easily solved using MATLAB or SCILAB.

For example, the following picture shows the periodic orbit arising at the Hopf bifurcation point, the plot shows the coordinates used in the definition of eq.4.

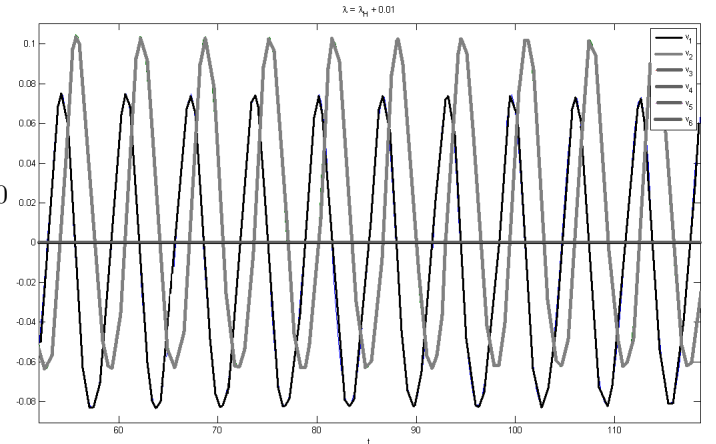


Figure 3: The periodic orbit

As we know the bifurcation type around λ_1^+ , we can use the pseudo - arc length continuation method in order to follow the steady states numerically when the slope varies. **We find for the first bifurcation point, the predicted turning point by the global analysis.** This is shown on fig.4.

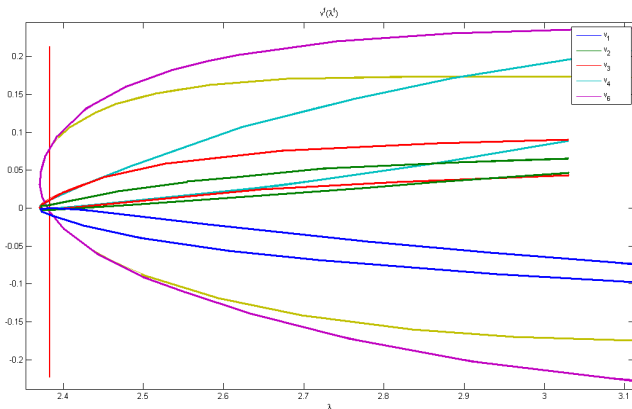


Figure 4: Representation of the different branch of solutions (λ, \vec{v}) near the bifurcation point λ_1^+ . The red line represent the bifurcation point λ_1^+ .

Conclusion

We provided theoretical tool to study the dynamics of the neural masses. Once we have a global understanding of the dynamics, we can perform numerical simulation. To this hand, a convenient method of approximation have been presented allowing to follow the bifurcated branches even if there are dynamically unstable. We think that this will prove to be useful when considering computational applications of the neural masses.

There still lack a study of the asymptotic behavior when the nonlinearity stiffness goes to infinity.

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