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An analytical method for computing Hopf bifurcation curves in neural field networks with space-dependent delays

Une méthode analytique pour le calcul des courbes bifurcation de Hopf dans les champs neuronaux avec retards dépendant de l'espace

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ABSTRACT

We give an analytical parametrization of the curves of purely imaginary eigenvalues in the delay-parameter plane of the linearized neural field network equations with spacedependent delays. In order to determine if the rightmost eigenvalue is purely imaginary, we have to compute a finite number of such curves; the number of curves is bounded by a constant for which we give an expression. The Hopf bifurcation curve lies on these curves. © 2011 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

RÉSUMÉ

Dans ce compte-rendu, on donne une paramètrisation des courbes de valeurs propres imaginaires pures, dans le plan des paramètres décrivant le terme des retards, pour les équation linéarisées des champs neuronaux avec retards dépendant de l'espace. Afin de savoir si la valeur propre de plus grande partie réelle, est imaginaire pure, on doit calculer un nombre n de ces courbes, n étant borné par une constante que l'on fournit. La courbe de bifurcation de Hopf est incluse dans le graphe de ces courbes.

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1. Introduction

In this Note, we consider neural fields (see [9,1]), which are continuous assemblies of mesoscopic models of neural populations that are essential in the modeling of macroscopic parts of the cortex. They play an important role in the design of such models of the visual cortex as those proposed by Bressloff [2]. Neural fields describe the mean voltage potential $V_i(\mathbf{r})$ of a population $i \in [1, p]$ located at $\mathbf{r} \in \Omega$, an open bounded set of \mathbb{R}^d , by nonlinear integrodifferential equations. More specifically, the model features an exponential decay e^{-lt} , connections among populations (the integral term) and an external current $I_i^{ext}(\mathbf{r})$ representing the input from other cortical areas.

$$\begin{cases} \left(\frac{\mathrm{d}}{\mathrm{d}t}+l\right)V_{i}(t,\mathbf{r})=\sum_{j=1}^{p}\int_{\Omega}J_{ij}(\mathbf{r},\bar{\mathbf{r}})S\left[V_{j}\left(t-\tau(\mathbf{r},\bar{\mathbf{r}}),\bar{\mathbf{r}}\right)\right]\mathrm{d}\bar{\mathbf{r}}+I_{i}^{ext}(\mathbf{r},t), \quad t\ge0, \ 1\leqslant i\leqslant p\\ V_{i}(t,\mathbf{r})=\phi_{i}(t,\mathbf{r}), \quad t\in[-T,0], \ T=\max_{\mathbf{r},\bar{\mathbf{r}}\in\bar{\Omega}}\tau(\mathbf{r},\bar{\mathbf{r}}) \text{ (initial condition)} \end{cases}$$
(1)

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The connectivity function $J_{ij}(\mathbf{r}, \mathbf{\bar{r}})$ is in $\mathbf{L}^2(\Omega^2, \mathbb{R}^{p \times p})$ and the nonlinearity *S*, of sigmoidal shape, describe the relationship between firing rate and membrane potential. There are, at least, two types of delays that need to be taken into account. A constant delay *D* which corresponds to the synaptic integration time and the propagation delays due to the time taken to travel information along axons. The propagation delay function has recently been measured in feline cortical tissue (see [4]), leading to the following analytical form $\tau(\mathbf{r}, \mathbf{\bar{r}}) = D + c ||\mathbf{r} - \mathbf{\bar{r}}||_2$ where $c = v^{-1}$, *v* being the propagation speed. Propagation delays are an essential building block for modeling the visual cortex: indeed, because of long range connections, it is strongly believed that they shape the spatiotemporal dynamics of the cortical activity. The relative role of constant delays versus space-dependent delays is currently unknown. There are several papers (see, for example, [3,8]) which study the effects of propagation delays but the linear stability analysis is mainly numerical and somewhat long-winded. Numerical computations involving delay differential equations are very time consuming, therefore, it is difficult to experiment on how the connectivity shapes the dynamics in conjunction with the delays. This is why we believe that our explicit parametrization of the Hopf curve is a major step toward an understanding of the neural fields equations but also of delayed systems in general.

Let us consider a stationary point of (1) written V^f : we are interested in its linear stability. V^f is asymptotically stable iff the characteristic values $\lambda \in \mathbb{C}$, solutions of the characteristic equation (2), have a negative real part (see, for example, [6]):

$$(\lambda + l)U_{i}(\mathbf{r}) = \sum_{j=1}^{p} \int_{\Omega} J_{ij}(\mathbf{r}, \bar{\mathbf{r}}) e^{-\lambda \tau (\mathbf{r}, \bar{\mathbf{r}})} DS \left[V_{j}^{f}(\bar{\mathbf{r}}) \right] U_{j}(\bar{\mathbf{r}}) \, \mathrm{d}\bar{\mathbf{r}}, \quad 1 \leq i \leq p$$

$$\tag{2}$$

for some $U_i(\mathbf{r})$. We are interested in pairs (D, c) for which the rightmost characteristic value is purely imaginary. We suppose that V^f is asymptotically stable when there is no delay, *i.e.* when c = D = 0. If the propagation speed is infinite c = 0, an analytical formula for the characteristic values can be found. Indeed, in this case, Eq. (2) reduces to $\lambda + l = e^{-\lambda D} J_n$, where J_n is in the point spectrum of the integral operator with kernel $J_{ij}(\mathbf{r}, \mathbf{\bar{r}})DS[V_j^f(\mathbf{\bar{r}})]$. This equation is solved using the different branches W_k of the Lambert¹ function (see [5]) by:

$$\lambda_{k,n} = \frac{1}{D} W_k \left(D e^{lD} J_n \right) - l, \quad k \in \mathbb{Z}, \ n \in \mathbb{N}$$
(3)

2. Main result

We use the previous equation (3) to find the pairs (D, c) for which the rightmost characteristic value is purely imaginary $i\omega$, $\omega > 0$. The next theorem gives a parametrization of these pairs on a bounded set \mathcal{E} :

Theorem 2.1. Let us consider a stationary solution V^f and write J the integral operator of kernel $J_{qr}(\mathbf{r}, \bar{\mathbf{r}})DS[V_r^f(\bar{\mathbf{r}})]$. Suppose that the spectrum of $-l \cdot Id + J$ has negative real part. Consider the integral operator J(z) whose kernel is given by $J_{qr}(\mathbf{r}, \bar{\mathbf{r}})DS[V_r^f(\bar{\mathbf{r}})] \in \mathbb{Z}^{|\mathbf{r}-\bar{\mathbf{r}}|_2}$, $z \in \mathbb{C}$. J(iy), y > 0 is a Hilbert–Schmidt operator on $\mathbf{L}^2(\Omega, \mathbb{C}^p)$. We consider its spectrum $\Sigma[J(iy)]$ ordered by decreasing modulus: $|J_0(iy)| \ge |J_1(iy)| \cdots$. Then:

1. The solutions (i ω , D, c) of the characteristic equation i $\omega + l = e^{-i\omega D} J_n(ic\omega)$ are parametrized by the curve C_n :

$$\mathcal{C}_{n}: \left[il\sqrt{\left|J_{n}(iy)/l\right|^{2} - 1}, D_{n}(y), \frac{y}{l\sqrt{\left|J_{n}(iy)/l\right|^{2} - 1}} \right], \quad iy \in \mathcal{E}_{n}$$
where $D_{n}(y) = \frac{1}{\sqrt{\left|J_{n}(iy)/l\right|^{2} - 1}} \left(\left|\arg(J_{n}(iy))\right| - \arccos(\frac{l}{\left|J_{n}(iy)\right|})\right)$ and
 $iy \in \mathcal{E}_{n} = \left\{ iy \in i\mathbb{R}_{+} \mid \Im J_{n}(iy) > 0, \ l \leq \left|J_{n}(iy)\right| \text{ and } \arccos\left(\frac{l}{\left|J_{n}(iy)\right|}\right) \leq \left|\arg(J_{n}(iy))\right| \right\}$

2. If we look for solutions $(i\omega, D, c)$ with $c \leq c_{\infty}$, then the sets S_n are bounded by $y \leq c_{\infty} \|J(0)\|_2$.

3. The set \mathcal{E}_n is empty if $nl > ||J(0)||_2^2$. Hence, there are at most $\lfloor ||J(0)||_2^2/l \rfloor$ curves \mathcal{C}_n .

Proof. We first quote a result (see [7]): if we write $BC = \{z \in \mathbb{C}, \exists z \in \mathbb{C}, \exists z = 0\}$, then:

 $\begin{cases} \max_k \Re W_k(z) = \Re W_0(z), & z \notin BC \\ \max_k \Re W_k(z) = \Re W_0(z) = \Re W_{-1}(z), & z \in BC \end{cases}$

¹ It is the multivariate function *W* such that $W(z)e^{W(z)} = z$.



Fig. 1. Plot of the curves C_n for n = 0, 1, 2, 3, in the plane (c, D).

In the latter case, there are two rightmost roots corresponding to W_0 and W_1 , one of which serves as the critical root for stability. We solve the characteristic equation $\lambda + l = e^{-\lambda D} J_n(c\lambda)$ with the help of the Lambert function: $\lambda_{k,n} = \frac{1}{D} W_k [De^{lD} J_n(c\lambda_{k,n})] - l = l(\frac{W_k [De^{lD} J_n(c\lambda_{k,n})]}{lD} - 1).$

- 1. According to (2), the rightmost characteristic corresponds to k = 0. We look for conditions such that $\lambda_{0,n}$ is purely imaginary. Write X = lD, then $\lambda_{0,n} = l(\frac{W_0[XJ_n(c\lambda_{k,n})/l]}{W_0(X)} 1)$. For a given $iy \in \mathcal{E}_n = \{iy \in i\mathbb{R}_+ \mid \Im J_n(iy) > 0, l \leq |J_n(iy)| \text{ and } \arccos(\frac{l}{|J_n(iy)|}) \leq |\arg(J_n(iy))|\}$, there is a unique $X_0(y) = W_0(lD(y))$ such that $W_0(X_0(y)) = \Re W_0(X_0(y)J_n(y))$ (see Appendix A). Then $\frac{1}{D(y)}W_0(lD(y)e^{lD(y)}J_n(y)) l = iz \in i\mathbb{R}_+$ where $z = l\sqrt{|J_n(iy)/l|^2 1}$. Then choose c = y/z > 0: it gives a solution (y, D(y), y/z) to the characteristic equation parametrized by y, $iy \in \mathcal{E}_n$.
- choose c = y/z > 0: it gives a solution (y, D(y), y/z) to the characteristic equation parametrized by y, $iy \in \mathcal{E}_n$. 2. If $iy \in \mathcal{E}_n$, we can find a solution $(i\omega, D, c)$ of the characteristic equation and $y = c\omega$. It remains to show that $|\omega| \leq ||J(0)||_2$. We have $i\omega + l = e^{-i\omega D} J_n(ic\omega)$, hence: $|\omega| = |\Im(e^{-i\omega D} J_n(ic\omega))| \leq |e^{-i\omega D} J_n(ic\omega)| = |J_n(ic\omega)| \leq ||J(ic\omega)||_2 \leq ||J(0)||_2$.
- 3. As J(z) is a Hilbert–Schmidt operator, we have $\sum_{q=0}^{\infty} |J_q(z)|^2 \leq ||J(z)||_2^2$. It gives $q|J_q(z)|^2 \leq ||J(z)||_2^2 \leq ||J(\Re z)||_2^2$. If $||J(0)||_2^2 < n$, then $\frac{||J(0)||_2^2}{n} < 1$ and $|J_n(iy)|^2 \leq \frac{||J(0)||_2^2}{n} < 1$ for all $y \in \mathbb{R}$ which implies that $\mathcal{E}_n = \emptyset$. \Box

3. Numerical analysis

From this theorem, if we want to compute the curves for $c \leq c_{\infty}$, we need to compute the eigenvalues $J_n(y)$ for $y \leq c_{\infty} ||J(0)||_2$ and $n \leq ||J(0)||_2$. Notice that the computation of the Hopf bifurcation curve requires to find the eigenvalues of a matrix of size $(N_t N_{\Omega})^2$, $(N_t$ points in [-T, 0], N_{Ω} points in Ω) and we have to look for the bifurcation curve in the parameter plane. The computation of the eigenvalues of J(iy) for a given y requires to find the eigenvalues of a matrix of size $(N_{\Omega})^2$ and, with our formulas, we directly have the bifurcation curve. We give a numerical example when $S(x) = \frac{1}{1+e^{-x}} - \frac{1}{2}$, $\Omega = (-\frac{\pi}{2}, \frac{\pi}{2})$, $J(x, x') = -(0.5 + 2.1 \cos(2x - 2x')]\frac{2}{\pi}$ and l = 1. Fig. 1 is a plot of the curves C_n for n = 0, ..., 3. Notice that C_0 and C_1 have an intersection point (D_{FH}, c_{FH}) , there are two rightmost characteristic values which are purely imaginary, leading to a Hopf–Hopf bifurcation if certain non-degeneracy conditions are satisfied.

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Appendix A. Technical lemma

Lemma A.1. If $J = |J|e^{i\psi}$, $\psi \in (-\pi, \pi]$, there is a (unique) solution $X_0 > 0$ to $\Re W_0(JX) = W_0(X)$ iff $1 \le |J|$ and $\operatorname{arccos}(\frac{1}{|J|}) \le |\psi|$. This solution is given by $X_0 = \xi_0 e^{\xi_0}$ with $\xi_0 = \frac{1}{\sqrt{|J|^2 - 1}} (|\psi| - \operatorname{arccos}(\frac{1}{|J|}))$. Then $\frac{\Im W_0(JX_0)}{W_0(X)} = \frac{\operatorname{sign}(\psi)}{\sqrt{|J|^2 - 1}}$. **Proof.** Let us define $H(z) = ze^z$, by definition $H(W_0(z)) = z$, hence the equation becomes $H(\Re W_0(JX)) = X > 0$. We write $W_0(JX) = \xi + i\eta$ with $\eta \in (-\pi, \pi]$ (by definition of the principal branch) and $JX = |J|Xe^{i\psi}$, $\psi \in (-\pi, \pi]$. As $sign(\Im(W_0(z))) = sign(arg z)$ (see [5]), we find that $sign(\psi) = sign(\eta)$. From the symmetry $W_0(z) = W_0(\bar{z})$, we conclude that $\eta(\psi)$ can be written $sign(\psi)\eta(|\psi|)$: we can suppose that $\psi \ge 0$ and thus that $\eta \ge 0$. By definition of W_0 , $JX = H(\xi + i\eta)$, it gives:

$$\begin{cases} |J|X\cos(\psi) = e^{\xi} (\xi \cos(\eta) - \eta \sin(\eta)) \\ |J|X\sin(\psi) = e^{\xi} (\xi \sin(\eta) + \eta \cos(\eta)) \end{cases}$$

Using $\xi e^{\xi} = X$, we find $(\frac{\eta}{\xi})^2 = |J|^2 - 1 \Rightarrow \frac{\eta}{\xi} = \sqrt{|J|^2 - 1}$ and the two equations reduce to

$$e^{i(\psi-\eta)} = \frac{1}{|J|} \left[1 + i\sqrt{|J|^2 - 1} \right] = e^{i\phi}, \quad \phi = \arccos\left(\frac{1}{|J|}\right) \in \left[0, \frac{\pi}{2}\right]$$

This gives $\eta = \psi - \phi$ [2π]. If $\psi - \phi \ge 0$, then we have a solution $\eta = \psi - \phi$. However, if $\psi - \phi < 0$, the only potential solution is $\eta = \psi - \phi + 2\pi$, but $\psi - \phi + 2\pi \ge -\frac{\pi}{2} + 2\pi > \pi$ but $\eta \le \pi$. Hence there is a (unique) solution iff $\psi - \phi \ge 0$ which is $\eta = \psi - \phi$. In this case $\xi = \frac{\psi - \operatorname{arccos}(\frac{1}{|J|})}{\sqrt{|J|^2 - 1}}$. \Box

References

- [1] S.-I. Amari, Dynamics of pattern formation in lateral-inhibition type neural fields, Biological Cybernetics 27 (2) (June 1977) 77-87.
- [2] P.C. Bressloff, J.D. Cowan, M. Golubitsky, P.J. Thomas, M.C. Wiener, Geometric visual hallucinations, Euclidean symmetry and the functional architecture of striate cortex, Philos. Trans. R. Soc. Lond. B 306 (1407) (March 2001) 299–330.
- [3] P.C. Bressloff, Z.P. Kilpatrick, Nonlocal Ginzburg-Landau equation for cortical pattern formation, Physical Review E 78 (4) (2008) 41916.
- [4] J.M.L. Budd, K. Kovács, A.S. Ferecskó, P. Buzás, U.T. Eysel, et al., Neocortical axon arbors trade-off material and conduction delay conservation, PLoS Comput. Biol. 6 (3) (2010) e1000711.
- [5] R.M. Corless, G.H. Gonnet, D.E.G. Hare, D.J. Jeffrey, D.E. Knut, On the Lambert W function, Advances in Computational Mathematics 5 (1996) 329-359.
- [6] J.K. Hale, S.M.V. Lunel, Introduction to Functional Differential Equations, Springer-Verlag, 1993.
- [7] H. Shinozaki, Lambert W Function Approach to Stability and Stabilization Problems for Linear Time-Delay Systems, Kyoto Institute of Technology, 2007.
- [8] N.A. Venkov, S. Coombes, P.C. Matthews, Dynamic instabilities in scalar neural field equations with space-dependent delays, Physica D: Nonlinear Phenomena 232 (2007) 1–15.
- [9] H.R. Wilson, J.D. Cowan, A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue, Biological Cybernetics 13 (2) (September 1973) 55–80.