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Local Bifurcations in Neural Field Equations

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Reference:

S.A. van Gils, S.G. Janssens, Yu.A. Kuznetsov, and S. Visser "On local bifurcations in neural field models with transmission delays",

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Neural activity dynamics $V(t, \mathbf{r})$ in an open connected brain domain $\Omega \subset \mathbb{R}^3$ is modeled by

$$\frac{\partial V}{\partial t}(t,\mathbf{r}) = -\alpha V(t,\mathbf{r}) + \int_{\Omega} J(\mathbf{r},\mathbf{r}') S(V(t-\tau(\mathbf{r},\mathbf{r}'),\mathbf{r}')) d\mathbf{r}'$$

[Wilson & Cowan, 1972; Amari, 1977]

- (H_J) The connectivity kernel $J \in C(\overline{\Omega} \times \overline{\Omega})$.
- (H_S) The synaptic activation function $S \in C^{\infty}(\mathbb{R})$ and its *k*th derivative is bounded for every $k \in \mathbb{N}_0$.
- (H_{τ}) The **delay function** $\tau \in C(\overline{\Omega} \times \overline{\Omega})$ is non-negative and not identically zero.

$$0 < h := \sup\{\tau(\mathbf{r}, \mathbf{r}') : \mathbf{r}, \mathbf{r}' \in \overline{\Omega}\} < \infty$$



Introduce

space	norm
$Y := C(\overline{\Omega})$	$\ y\ := \sup_{\mathbf{r}\in\Omega} y(\mathbf{r}) $
X := C([-h,0];Y)	$\ \phi\ := \sup_{t \in [-h,0]} \ \phi(t,\cdot)\ $

Define the nonlinear operator $G: X \to Y$ by

$$G(\phi)(\mathbf{r}) := \int_{\overline{\Omega}} J(\mathbf{r}, \mathbf{r}') S(\phi(-\tau(\mathbf{r}, \mathbf{r}'), \mathbf{r}')) d\mathbf{r}' \quad \forall \phi \in X, \forall \mathbf{r} \in \overline{\Omega}$$

The operator $G: X \to Y$ is Fréchet differentiable with derivative $DG(\phi) \in \mathscr{L}(X, Y)$ in the point $\phi \in X$ given by

$$(DG(\phi)\psi)(\mathbf{r}) = \int_{\overline{\Omega}} J(\mathbf{r},\mathbf{r}') S'(\phi(-\tau(\mathbf{r},\mathbf{r}'),\mathbf{r}'))\psi(-\tau(\mathbf{r},\mathbf{r}'),\mathbf{r}')) d\mathbf{r}'$$

for all $\psi \in X$ and all $\mathbf{r} \in \overline{\Omega}$.



The operator *G* is in $C^{\infty}(X, Y)$. For k = 1, 2, ... its *k*th Fréchet derivative $D^k G(\phi) \in \mathscr{L}_k(X, Y)$ in the point $\phi \in X$ is given by

$$egin{aligned} &(D^k G(\phi)(\psi_1,\ldots,\psi_k))(\mathbf{r}) = \ &\int_{\overline{\Omega}} J(\mathbf{r},\mathbf{r}') S^{(k)}(\phi(- au(\mathbf{r},\mathbf{r}'),\mathbf{r}')) \prod_{i=1}^k \psi_i(- au(\mathbf{r},\mathbf{r}'),\mathbf{r}') \, d\mathbf{r}' \end{aligned}$$

for $\psi_1, \ldots, \psi_k \in X$ and $\mathbf{r} \in \overline{\Omega}$.

These derivatives will be used in the computations of the normal form coefficients.



Define the **history** at time $t \ge 0$ by

$$V_t(oldsymbol{ heta}) \coloneqq V(t+oldsymbol{ heta}) \quad orall t \geq 0, \, oldsymbol{ heta} \in [-h,0]$$

Then studying of the neural field equation is equivalent to analyzing the following **Delay Differential Equation**:

$$\begin{cases} \dot{V}(t) = F(V_t) & t \ge 0\\ V(t) = \phi(t) & t \in [-h, 0] \end{cases}$$
(DDE)

where $V: [-h, \infty) \to Y$ and $\phi \in X$ is the initial condition, while $F: X \to Y$ is given by

$$F(\phi) := -lpha \phi(0) + G(\phi) \qquad orall \phi \in X$$

The operator F is globally Lipschitz continuous.

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If $F \equiv 0$, then the solution semigroup corresponding to (DDE) is the **shift semigroup** T_0 , defined as

$$(T_0(t)\phi)(heta) = egin{cases} \phi(t+ heta) & -h \leq t+ heta \leq 0 \ \phi(0) & 0 \leq t+ heta \end{cases}$$

for all $\phi \in X$, $t \ge 0$, $\theta \in [-h, 0]$.

Let $X^{\odot} \subset X^*$ be the maximal subspace of strong continuity of T_0^* :

$$X^{\odot} = \overline{D(A_0^*)},$$

where A_0 is the infinitesimal generator of T_0 . It holds

$$X^{\odot} = Y^* \times L^1([0,h];Y^*),$$

where the second factor is the space of Bochner integrable Y^* -valued functions on [0, h] [Greiner & Van Neerven, 1992]



Let T_0^{\odot} be the strongly continuous semigroup on X^{\odot} obtained by restriction of T_0^* to X^{\odot} .

Its infinitesimal generator A_0^{\odot} is

$$D(A_0^{\odot})=\{\phi^{\odot}\in D(A_0^*):A_0^*\phi^{\odot}\in X^{\odot}\}, \qquad A_0^{\odot}\phi^{\odot}=A_0^*\phi^{\odot}$$

Performing this construction once more, but now starting from the strongly continuous semigroup $T_0^{\odot}(t)$ on the Banach space X^{\odot} , we obtain the adjoint semigroup $T_0^{\odot*}$ on the dual space $X^{\odot*}$.

Inspired by Diekmann et al.[1995], we study the relationship between DDEs and Abstract Integral Equations.



The original space X is canonically embedded into $X^{\odot*}$ via $j: X \to X^{\odot*}$ given by

$$\langle \phi^{\odot}, j \phi \rangle \mathrel{\mathop:}= \langle \phi, \phi^{\odot} \rangle \quad \forall \, \phi \in X, \, \forall \, \phi^{\odot} \in X^{\odot}$$

Define $E: X \to X^{\odot \star}$ by

$$E(\phi) := (F(\phi), 0)$$

for all $\phi \in X$. Hence *E* maps into $Y \times \{0\}$ which is a closed subspace of $X^{\odot \star}$.



Consider the Abstract Integral Equation

$$u(t) = T_0(t)\phi + j^{-1}\left(\int_0^t T_0^{\odot \star}(t-s)E(u(s))\,ds\right) \quad \forall t \ge 0 \qquad \text{(AIE)}$$

where $\phi \in X$ is an initial condition, $u \in C([0,\infty);X)$ is the unknown and the convolution integral is of weak^{*} Riemann type. Then

- (i) Suppose that u ∈ C([0,∞);X) satisfies (AIE). Define
 x : [-h,∞) → Y by x₀ = φ and x(t) = u(t)(0) for t ≥ 0. Then
 x is a global solution of (DDE).
- (ii) Conversely, suppose that x is a global solution of (DDE). Define $u : [0, \infty) \to X$ by $u(t) = x_t$. Then $u \in C([0, \infty); X)$ and u satisfies (AIE).

This implies that for any $\phi \in X$ problem (DDE) has a unique global solution.



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Let $L := DG(\hat{\phi}) \in \mathscr{L}(X, Y)$ be the Fréchet derivative of *G* at the **equilibrium** $\hat{\phi} \in X$, i.e. $\hat{\phi}$ is independent of time (but possibly dependent on space) and

$$-lpha\hat{\phi}+G(\hat{\phi})=0$$

The solution of the linearized problem

$$\begin{cases} \dot{x}(t) = -\alpha x(t) + Lx_t & t \ge 0\\ x(t) = \phi(t) & t \in [-h, 0] \end{cases}$$

defines a strongly continuous semigroup T on X generated by $A: D(A) \subset X \to X$ where

$$D(A) = \{\phi \in X : \phi' \in X \text{ and } \phi'(0) = -\alpha \phi(0) + L\phi\}, \ A\phi = \phi'$$



Since

$$D(A^*)=D(A_0^*),$$

the sun-duals of *X* with respect to T_0 and *T* are identical and may both be denoted by X^{\odot} . Moreover,

$$D(A^{\odot}) = \{\phi^{\odot} \in D(A^*) : A^*\phi^{\odot} \in X^{\odot}\}, \ A^{\odot} = A^*$$

It also follows that if $\phi \in C^1([-h, 0]; Y)$ then $j\phi \in D(A^{\odot \star})$ and

$$A^{\odot\star}j\phi = (0,\phi') + (DF(\hat{\phi})\phi,0).$$

Finally, all **spectra** coincide:

$$\sigma(A) = \sigma(A^*) = \sigma(A^{\odot}) = \sigma(A^{\odot\star})$$



For
$$f \in Y$$
 and $z \in \mathbb{C}$, let $(\varepsilon_z \otimes f) \in X$ be such that

$$(\boldsymbol{\varepsilon}_{z}\otimes f)(\boldsymbol{\theta})=e^{\boldsymbol{\theta}z}f$$

for $\theta \in [-h, 0]$. Define

 $egin{aligned} & L_z \in \mathscr{L}(Y), & L_z f \mathrel{\mathop:}= L(arepsilon_z \otimes f) \ & H_z \in \mathscr{L}(X), & (H_z \phi)(heta) \mathrel{\mathop:}= \int_{ heta}^0 e^{z(heta - s)} \phi(s) \, ds \ & S_z \in \mathscr{L}(X,Y), & S_z \phi \mathrel{\mathop:}= \phi(0) + L H_z \phi \end{aligned}$

for all $f \in Y$, $\phi \in X$ and $\theta \in [-h, 0]$.

Introduce the characteristic operator

$$\Delta(z) := z + \alpha - L_z \in \mathscr{L}(Y)$$



Then $\phi \in \mathscr{R}(z-A)$ if and only if

$$\Delta(z)f=S_z\phi$$

has a solution $f \in Y$ and, moreover, $z \in \rho(A)$ if and only if f is also unique. If such is the case, then

$$R(z,A)\phi = (\varepsilon_z \otimes \Delta(z)^{-1}S_z\phi) + H_z\phi$$

Furthermore, $\lambda \in \sigma(A)$ if and only if $0 \in \sigma(\Delta(\lambda))$ and $\psi \in D(A)$ is an eigenvector corresponding to λ if and only if $\psi = \varepsilon_{\lambda} \otimes q$ where $q \in Y$ satisfies $\Delta(\lambda)q = 0$ [Engel & Nagel, 2000].

The set $\sigma(A) \setminus \{-\alpha\}$ consists of isolated eigenvalues of finite type.



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Normalization on Center Manifold

Assume $\hat{\phi} \equiv 0$. Suppose that *A* has $n_c \ge 1$ critical eigenvalues with Re $\lambda = 0$. This implies the existence of an invariant **center manifold** \mathcal{W}_{loc}^c on which

$$\dot{u}(t) = j^{-1} \left(A^{\odot \star} j u(t) + R(u(t)) \right) \qquad \forall t \in \mathbb{R}$$

where

$$R(\phi) = E(\phi) - DE(0)\phi = \frac{1}{2}B(\phi, \phi) + \frac{1}{3!}C(\phi, \phi, \phi) + O(||\phi||^4)$$

The projection of u(t) onto $X_0 = T_{\hat{\phi}} \mathcal{W}_{loc}^c$ satisfies the **normal form** in some coordinates $z \in \mathbb{R}^{n_c}$ on X_0 ,

$$\dot{z}(t) = \sum_{1 \le |\mathbf{v}| \le 3} g_{\mathbf{v}} z^{\mathbf{v}}(t) + O(|z(t)|^4) \qquad \forall t \in \mathbb{R}$$



The invariance of \mathscr{W}_{loc}^{c} , which is given by the graph of

$$\mathscr{H}(z) = \sum_{1 \le |\nu| \le 3} \frac{1}{\nu!} h_{\nu} z^{\nu} + O(|z|^4),$$

implies the **homological equation** [Iooss & Adelmeyer, 1992]

 $A^{\odot\star}j\mathscr{H}(z) + R(\mathscr{H}(z)) = j(D\mathscr{H}(z)\dot{z})$

Collecing the z^{v} -terms leads to a linear equation

$$(\lambda - A^{\odot \star})\phi^{\odot \star} = \psi^{\odot \star}$$

Let $\lambda \in \mathbb{C} \setminus \{-\alpha\}$. Then this equation is solvable for $\phi^{\odot \star} \in D(A^{\odot \star})$ given $\psi^{\odot \star} \in X^{\odot \star}$ if and only if $\langle \phi^{\odot}, \psi^{\odot \star} \rangle = 0$ for all $\phi^{\odot} \in \mathcal{N}(\lambda - A^*)$ (Fredholm Solvability)



Let ϕ and ϕ^{\odot} be complex eigenvectors of *A* and *A*^{*} corresponding to $\lambda_1 = i\omega_0$,

$$A\phi = i\omega_0\phi, \ A^*\phi^\odot = i\omega_0\phi^\odot,$$

and satisfying $\langle \phi, \phi^{\odot} \rangle = 1$.

• Poincaré normal form [Arnold, 1972]:

$$\dot{z} = i\omega_0 z + g_{21} z |z|^2 + O(|z|^4), \ z \in \mathbb{C}$$

where $l_1 = \frac{1}{2\omega_0} \text{Re } g_{21}$ is the **first Lyapunov coefficient**. • Center manifold expansion:

$$\mathscr{H}(z,\overline{z})=z\phi+\overline{z}\overline{\phi}+\displaystyle{\sum_{2\leq j+k\leq 3}}\displaystyle{rac{1}{j!k!}}h_{jk}z^{j}\overline{z}^{k}+O(|z|^{4})$$



The homological equation

$$A^{\odot\star}j\mathscr{H}(z,\overline{z}) + R(\mathscr{H}(z,\overline{z})) = j\left(D_z\mathscr{H}(z,\overline{z})\dot{z} + D_{\overline{z}}\mathscr{H}(z,\overline{z})\dot{\overline{z}}\right)$$

gives

$$egin{aligned} &jh_{20}=-(A^{\odot\star})^{-1}B(\phi,\overline{\phi})\ &jh_{11}=(2i\omega_0-A^{\odot\star})^{-1}B(\phi,\phi) \end{aligned}$$

as well as

$$(i\omega_0 I - A^{\odot \star})jh_{21} = C(\phi, \phi, \overline{\phi}) + B(\overline{\phi}, h_{20}) + 2B(\phi, h_{11}) - 2g_{21}j\phi$$

so that

$$g_{21} = \frac{1}{2} \langle \phi^{\odot}, C(\phi, \phi, \overline{\phi}) + B(\overline{\phi}, h_{20}) + 2B(\phi, h_{11}) \rangle$$



Evaluation of normal form coefficients

To compute $\psi^{\odot \star} = R(z, A^{\odot \star})(y, 0)$, we need to solve

$$(z - A^{\odot \star})\psi^{\odot \star} = (y, 0)$$

where $z \in \rho(A)$, $y \in Y$ and $\psi^{\odot \star} \in D(A^{\odot \star})$.

For each $y \in Y$ the function $\psi = \varepsilon_z \otimes \Delta(z)^{-1}y$ is the unique solution in $C^1([-h, 0]; Y)$ of the system

$$\begin{cases} z\psi(0) - DF(0)\psi = y \\ z\psi - \psi' = 0 \end{cases}$$

Then $\psi^{\odot\star} = j\psi$.

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Let P^{\odot} and $P^{\odot \star}$ be the spectral projections on X^{\odot} and $X^{\odot \star}$ corresponding to a simple $\lambda \in \sigma(A)$. We want to evaluate $\langle \phi^{\odot}, \phi^{\odot \star} \rangle$ where $\phi^{\odot \star} = (y, 0) \in Y \times \{0\} \subset X^{\odot \star}$.

Since the range of $P^{\odot \star}$ is spanned by $j\phi$ we have

$$P^{\odot\star}\phi^{\odot\star}=\kappa j\phi$$

for a certain $\kappa \in \mathbb{C}$. Furthermore,

$$\langle \phi^{\odot}, \phi^{\odot \star}
angle = \langle P^{\odot} \phi^{\odot}, \phi^{\odot \star}
angle = \langle \phi^{\odot}, P^{\odot \star} \phi^{\odot \star}
angle = \kappa \langle \phi^{\odot}, j \phi
angle = \kappa$$

Thus [Dunford & Schwartz, 1958]

$$P^{\odot\star}\phi^{\odot\star} = rac{1}{2\pi i} \oint_{\partial C_{\lambda}} R(z, A^{\odot\star})\phi^{\odot\star} dz = \kappa j\phi$$

and the first component shows that κ can be found from

$$\frac{1}{2\pi i}\oint_{\partial C_{\lambda}}\Delta(z)^{-1}y\,dz=\kappa\phi(0)$$



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Explicit example

Consider a homogeneous neural field with transmission delays due to a finite propagation speed of action potentials as well as a finite, fixed delay $\tau_0 \ge 0$ caused by synaptic processes. Space and time are each rescaled such that $\overline{\Omega} = [-1, 1]$ and the propagation speed is 1. This yields

$$au(r,r') = au_0 + |r-r'| \qquad orall r, r' \in \overline{\Omega}$$

For the connectivity function we take a linear combination of $N \ge 1$ exponentials,

$$J(r,r') = \sum_{i=1}^{N} c_i e^{-\mu_i |r-r'|} \qquad \forall r,r' \in \overline{\Omega}$$

where

$$c_i \in \mathbb{C}$$
 with $c_i \neq 0$, $\mu_i \in \mathbb{C}$ with $\mu_i \neq \mu_j$ for $i \neq j$



We study the stability of a spatially homogeneous steady state $\hat{\phi} \equiv 0$, requiring that S(0) = 0 and S'(0) = 1. Let

$$k_i(\lambda) := \lambda + \mu_i \qquad \forall i = 1, \dots, N$$

and

$$\mathscr{S} := \{ \lambda \in \mathbb{C} : \exists i, j \in \{1, \dots, N\}, i \neq j, \text{ s.t. } k_i^2(\lambda) = k_j^2(\lambda) \}.$$

Define for $\lambda \notin \mathscr{S}$ the characteristic polynomial

$$\mathscr{P}(\rho) \coloneqq rac{e^{\lambda au_0}(\lambda+lpha)}{2} \prod_{j=1}^N (
ho^2 - k_j(\lambda)^2) + \sum_{i=1}^N c_i k_i(\lambda) \prod_{\substack{j=1 \ j \neq i}}^N (
ho^2 - k_j(\lambda)^2)$$

and assume that it has 2*N* distinct roots, denoted by $\pm \rho_i(\lambda)$ for i = 1, 2, ..., N, and such that

$$k_j(\lambda) \neq \pm
ho_i(\lambda) \qquad \forall i, j = 1, 2, \dots, N$$



....hama

Under above conditions, introduce

$$S(\lambda) := egin{bmatrix} S_\lambda^- & S_\lambda^+ \ S_\lambda^+ & S_\lambda^- \end{bmatrix}$$

where

$$[S_{\lambda}^{-}]_{j,i} := \frac{e^{\rho_{i}(\lambda)}}{\lambda + \mu_{j} - \rho_{i}(\lambda)}, \qquad [S_{\lambda}^{+}]_{j,i} := \frac{e^{-\rho_{i}(\lambda)}}{\lambda + \mu_{j} + \rho_{i}(\lambda)}$$
Then λ is an eigenvalue of A if and only if det $S(\lambda) = 0$. The corresponding eigenfunction is $\varepsilon_{\lambda} \otimes q_{\lambda}$ with

$$q_{\lambda}(x) = \sum_{i=1}^{N} \left[\gamma_{i} e^{\rho_{i}(\lambda)x} + \gamma_{-i} e^{-\rho_{i}(\lambda)x} \right] \qquad \forall x \in [-1, 1]$$

where $\Gamma = [\gamma_1, \gamma_2, \dots, \gamma_N, \gamma_{-1}, \gamma_{-2}, \dots, \gamma_{-N}]$ is a solution to $S(\lambda)\Gamma = 0$.



Suppose that $z \in \rho(A)$ and the above conditions hold. Then the solution to the resolvent equation

$$(z-A)\psi = \phi, \ \phi \in X,$$

is given by $\psi_z = \varepsilon_z \otimes q_z + H_z \phi$ with

$$q_{z}(x) = \frac{h_{z}(x)}{z + \alpha} + \sum_{i=1}^{N} \left[\gamma_{i,z}(x) e^{\rho_{i}(z)x} + \gamma_{-i,z}(x) e^{-\rho_{i}(z)x} \right] \qquad \forall x \in [-1, 1]$$

where

$$h_{z}(x) := \phi(0,x) + \int_{-1}^{1} \int_{-\tau_{0}-|x-r|}^{0} J(x,r) e^{-z(\tau_{0}+s)-z|x-r|} \phi(s,r) \, ds \, dr$$

and

$$\mathsf{F}_{z} = [\gamma_{1,z}, \gamma_{2,z}, \dots, \gamma_{N,z}, \gamma_{-1,z}, \gamma_{-2,z}, \dots, \gamma_{-N,z}]$$

can be found by matrix inversion and integration.

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Numerical Example

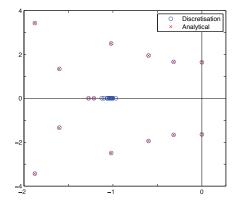
Take

$$J(r,r') = \hat{c}_1 e^{-\mu_1 |r-r'|} + \hat{c}_2 e^{-\mu_2 |r-r'|} \quad \forall r,r' \in [-1,1]$$
and

$$S(V) = \frac{1}{1+e^{-rV}} - \frac{1}{2} \quad \forall V \in \mathbb{R}$$
Here $S'(0) = \frac{r}{4}$ and hence $c_i = \frac{r}{4} \hat{c}_i$ for $i = 1, 2$.
Let
 $\alpha = 1, \ \tau_0 = 1, \ \hat{c}_1 = 3, \ \hat{c}_2 = -5.5, \ \mu_1 = 0.5, \ \mu_2 = 1.$



Hopf bifurcation at r = 4.220215



The approximate eigenvalues were computed with DDE-BIFTOOL [Engelborghs et al., 2002].

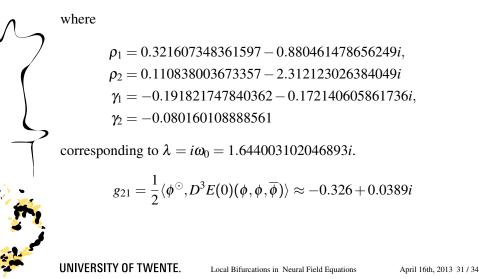
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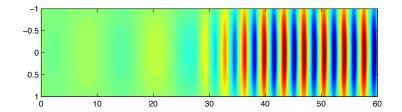
$$\phi(t,x) = e^{\lambda t} \left[\gamma_1 (e^{\rho_1 x} + e^{-\rho_1 x}) + \gamma_2 (e^{\rho_2 x} + e^{-\rho_2 x}) \right] \qquad \forall t \in [-h,0]$$





Thus, the first Lyapunov coefficient is $l_1 \approx -0.198 < 0$ indicating a **supercritical** Hopf bifurcation.

A transient to periodic inhomogeneous oscillations at r = 6:



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• The **double Hopf** case has been treated as well. We have observed multiple stable periodic inhomogeneous oscillations.

• The theory covers bifurcations from inhomogeneous equilibria, although we do not have relevant numerical examples yet.

- Unbounded domains ???
- Arbitrary Banach space Y [Thursday's talk by S. Janssens].