Wilson-Cowan Neuronal Interaction Models with Distributed Delays

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Abstract. A generalization of the well-known Wilson-Cowan model of excitatory and inhibitory interactions in localized neuronal populations is presented, by taking into consideration distributed time delays. A stability and bifurcation analysis is undertaken for the generalized model, with respect to two characteristic parameters of the system. The stability region in the characteristic parameter plane is determined and a comparison is given for several types of delay kernels. It is shown that if a weak Gamma delay kernel is considered, as in the original Wilson-Cowan model without time-coarse graining, the resulting stability domain is unbounded, while in the case of a discrete time-delay, the stability domain is bounded. This fact reveals an essential difference between the two scenarios, reflecting the importance of a careful choice of delay kernels in the mathematical model. Numerical simulations are presented to substantiate the theoretical results. Important differences are also highlighted by comparing the generalized model with the original Wilson-Cowan model without time delays.

Keywords: Wilson Cowan model, distributed delays, stability, bifurcations,chaos

1 Introduction

The original mathematical model describing excitatory and inhibitory interactions in localized neuronal populations has been derived in 1972 by Wilson and Cowan [10]. In this model, denoting by $E(t)$ and $I(t)$ the proportions of excitatory and inhibitory cells firing per unit of time, at the time instant t, it has been assumed that $E(t+\tau)$ and $I(t+\tau')$ are equal to the proportion of cells which are sensitive (i.e. not refractory) and which also receive at least threshold excitation at the moment of time t. Therefore, as a first step, the following system of integral equations has been obtained:

$$\begin{cases} E(t+\tau) = \left(1 - \int_{t-r}^{t} E(s)ds\right) \cdot \mathcal{S}_e \left[\int_{-\infty}^{t} h(t-s)\left(c_1 E(s) - c_2 I(s) + P_e(s)\right) ds\right] \\ I(t+\tau') = \left(1 - \int_{t-r'}^{t} I(s)ds\right) \cdot \mathcal{S}_i \left[\int_{-\infty}^{t} h(t-s)\left(c_3 E(s) - c_4 I(s) + P_i(s)\right) ds\right] \end{cases} \quad (1)$$

In this system, the first factors in the right hand side represent the proportion of sensitive excitatory / inhibitory cells, where r is the absolute refractory period (msc), the functions $\mathcal{S}_e$, $\mathcal{S}_i$ are sigmoid threshold functions, their arguments denoting the mean field level of excitation / inhibition generated in an excitatory /inhibitory cell at time t (assuming that individual cells sum their inputs and that the effect of the stimulation decays exponentially with a time course $h(t)$). Moreover, $c_i > 0$ are connectivity coefficients representing the average number of excitatory / inhibitory synapses per cell and P_e, P_i denote external inputs.

Applying time-coarse graining, the well-known Wilson-Cowan model [10] has been obtained and analyzed, consisting of a system of ordinary differential equations without time delays. Generalizations of this model including discrete time-delays have been investigated in several papers, often considering refractory periods r, r' being equal to zero. Based on the integral terms appearing in the original model (1) as arguments of the threshold functions, the following model with distributed delays will be analyzed in this paper:

$$\begin{cases} \dot{u}(t) = -u(t) + f\left[\theta_u + \displaystyle\int_{-\infty}^{t} h(t-s)\,(au(s) + bv(s))\,ds\right] \\ \dot{v}(t) = -v(t) + f\left[\theta_v + \displaystyle\int_{-\infty}^{t} h(t-s)\,(cu(s) + dv(s))\,ds\right] \end{cases} \tag{2}$$

where $u(t)$ and $v(t)$ represent the synaptic activities of the two neuronal populations, a, b, c, d are connection weights and θ_u, θ_v are background drives. The activation function f is considered to be increasing and of class C^1 on the real line.

In system (2), the delay kernel $h : [0, \infty) \to [0, \infty)$ is a probability density function representing the probability that a particular time delay occurs. It is assumed to be bounded, piecewise continuous and satisfy

$$\int_0^\infty h(s)ds = 1, \quad \text{with the average time delay} \quad \tau = \int_0^\infty sh(s)ds < \infty.$$

The particular case of discrete time delays (Dirac kernels) has been discussed in [4]. However, there are other important classes of delay kernels often used in the literature, such as Gamma kernels or uniform distribution kernels. It is worth mentioning that in the original Wilson-Cowan model [10], a weak Gamma kernel $h(t) = \tau^{-1}\exp(-t/\tau)$ has been used, so this case should be the original reference point. Analyzing mathematical models with particular classes of delay kernels (e.g. weak Gamma kernel or strong Gamma kernel $h(t) = 4\tau^{-2}t\exp(-2t/\tau)$) may shed a light on how distributed delays affect the dynamics differently from discrete delays. However, in the modeling of real world phenomena, one usually does not have access to the exact distribution, and approaches using general kernels may be more appropriate [1–3, 5–9, 11].

Initial conditions associated with system (2) are of the form:

$$u(s) = \varphi(s), \quad v(s) = \psi(s), \quad \forall\, s \in (-\infty, 0],$$

where φ, ψ are bounded real-valued continuous functions defined on $(-\infty, 0]$.

2 Main stability and bifurcation results

The equilibrium states of system (2) are the solutions of the following algebraic system:

$$\begin{cases} u = f(\theta_u + au + bv) \\ v = f(\theta_v + cu + dv) \end{cases} \tag{3}$$

The linearized system at an equilibrium state $(u^\star, v^\star)$ is

$$\begin{cases} \dot{u} = -u + \phi_1 \displaystyle\int_{-\infty}^{t} h(t-s)\,(au(s) + bv(s))\,ds \\ \dot{v} = -v + \phi_2 \displaystyle\int_{-\infty}^{t} h(t-s)\,(cu(s) + dv(s))\,ds \end{cases} \tag{4}$$

where $\phi_1 = \phi_1(u^\star, v^\star) = f'(\theta_u + au^\star + bv^\star) > 0$ and $\phi_2 = \phi_2(u^\star, v^\star) = f'(\theta_v + cu^\star + dv^\star) > 0$.

Applying the Laplace transform to the linearized system (4), we obtain:

$$\begin{cases} zU(z) - u(0) = -U(z) + \phi_1 H(z)\,(aU(z) + bV(z)) \\ zV(z) - v(0) = -V(z) + \phi_2 H(z)\,(cU(z) + dV(z)) \end{cases} \tag{5}$$

where $U(z)$ and $V(z)$ represent the Laplace transforms of the state variables u and v respectively, while $H(z)$ is the Laplace transform of the delay kernel h.

System (5) is equivalent to:

$$\begin{pmatrix} z + 1 - a\phi_1 H(z) & -b\phi_1 H(z) \\ -c\phi_2 H(z) & z + 1 - d\phi_2 H(z) \end{pmatrix} \begin{pmatrix} U(z) \\ V(z) \end{pmatrix} = \begin{pmatrix} u(0) \\ v(0) \end{pmatrix} \tag{6}$$

and hence, the characteristic equation associated to the equilibrium state $(u^\star, v^\star)$ is

$$\Delta(z) = (z+1)^2 - \alpha H(z)(z+1) + \beta H^2(z) = 0 \tag{7}$$

where

$$\alpha = a\phi_1(u^\star, v^\star) + d\phi_2(u^\star, v^\star) = af'(\theta_u + au^\star + bv^\star) + df'(\theta_v + cu^\star + dv^\star);$$
$$\beta = (ad - bc)\phi_1(u^\star, v^\star)\phi_2(u^\star, v^\star) = (ad - bc)f'(\theta_u + au^\star + bv^\star)f'(\theta_v + cu^\star + dv^\star).$$

The following delay-independent stability and instability results are easily obtained, based on the properties of the Laplace transform and the particularities of the characteristic equation (7):

Theorem 1 (Delay-independent stability and instability).

1. *In the non-delayed case, the equilibrium state $(u^\star, v^\star)$ of system (2) is locally asymptotically stable if and only if*

$$\alpha < \min\{2, \beta + 1\} \tag{8}$$

2. If the following inequality holds:

$$|\alpha| + |\beta| < 1 \tag{9}$$

then the equilibrium state $(u^\star, v^\star)$ of system (2) is locally asymptotically stable for any delay kernel $h(t)$.

3. If the following inequality holds:

$$\beta < \alpha - 1 \tag{10}$$

then the equilibrium state $(u^\star, v^\star)$ of system (2) is unstable for any delay kernel $h(t)$.

It is important to note that the characteristic equation (7) has a root $z = 0$ if and only if $\beta = \alpha - 1$. To investigate for which combinations of parameters (α, β) the characteristic equation will have complex conjugated roots of the form $\pm i\omega$, we further assume that that $\hat{H}(z) = H(z/\tau)$ does not depend on the average time delay τ. In fact, for the most important classes of delay kernels we have:

a. Dirac kernel: $\hat{H}(z) = e^{-z}$;

b. p-Gamma kernel: $\hat{H}(z) = \left(\dfrac{p}{p+z}\right)^p$;

c. Uniform kernel: $\hat{H}(z) = e^{-z} \cdot \dfrac{\sinh(\rho z)}{\rho z}$.

We will further define $\hat{H}(i\omega) = \rho(\omega) e^{-i\theta(\omega)}$. The following equation will play an important role in the bifurcation analysis to follow:

$$\tau \sin\theta(\omega) + \omega \cos\theta(\omega) = 0. \tag{11}$$

A careful and lengthy theoretical investigation leads to the following theorems which characterize the stability region $S(\alpha, \beta)$ of the equilibrium $(u^\star, v^\star)$ from the (α, β)-plane (see Fig. 1).

Theorem 2. *Assuming that the equation (11) has at least one positive real root, let us denote:*

$$\omega_\tau = \min\{\omega > 0 \ : \ \tau \sin\theta(\omega) + \omega \cos\theta(\omega) = 0\} \quad \text{and} \quad \mu_\tau = \left(\rho(\omega_\tau)\cos\theta(\omega_\tau)\right)^{-1}.$$

The boundary of the stability region $S(\alpha, \beta)$ of the equilibrium state $(u^\star, v^\star)$ of system (2) is given by the union of the line segments and curve given below:

$$\begin{aligned}
&(l_0): \quad \beta = \alpha - 1 && , \ \alpha \in [1 + \mu_\tau, 2]; \\
&(l_\tau): \quad \beta = \mu_\tau(\alpha - \mu_\tau) && , \ \alpha \in [2\mu_\tau, 1 + \mu_\tau]; \\
&(\gamma_\tau): \quad \begin{cases} \alpha = \dfrac{2}{\rho(\omega)}\left[\cos\theta(\omega) - \dfrac{\omega}{\tau}\sin\theta(\omega)\right] \\ \beta = \dfrac{1}{\rho^2(\omega)}\left(1 + \dfrac{\omega^2}{\tau^2}\right) \end{cases} && , \ \omega \in (0, \omega_\tau).
\end{aligned}$$

At the boundary of the stability domain $S(\alpha, \beta)$, the following bifurcation phenomena take place in a neighborhood of the equilibrium $(u^\star, v^\star)$ of system (2):

a. *Saddle-node bifurcations take place along the open line segment* (l_0)*;*
b. *Hopf bifurcations take place along the open line segment* (l_τ) *and curve* (γ_τ)*;*
c. *Bogdanov-Takens bifurcation at* $(\alpha, \beta) = (2, 1)$*;*
d. *Double-Hopf bifurcation at* $(\alpha, \beta) = \left(2\mu_\tau, \mu_\tau^2\right)$*;*
e. *Zero-Hopf bifurcation* $(\alpha, \beta) = (1 + \mu_\tau, \mu_\tau)$.

Theorem 3. *If the equation (11) does not admit any positive real root, the boundary of the stability region* $S(\alpha, \beta)$ *of the equilibrium state* $(u^\star, v^\star)$ *of system* (2) *is given by the union of the half-line and curve given below:*

$$(l_0): \quad \beta = \alpha - 1 \qquad , \ \alpha \in (-\infty, 2];$$

$$(\gamma_\tau): \quad \begin{cases} \alpha = \dfrac{2}{\rho(\omega)} \left[\cos\theta(\omega) - \dfrac{\omega}{\tau} \sin\theta(\omega)\right] \\ \beta = \dfrac{1}{\rho^2(\omega)} \left(1 + \dfrac{\omega^2}{\tau^2}\right) \end{cases} \qquad , \ \omega > 0.$$

At the boundary of the stability domain $S(\alpha, \beta)$*, the following bifurcation phenomena take place in a neighborhood of the equilibrium* $(u^\star, v^\star)$ *of system* (2)*:*

a. *Saddle-node bifurcations take place along the open half-line* (l_0)*;*
b. *Hopf bifurcations take place along the curve* (γ_τ)*;*
c. *Bogdanov-Takens bifurcation at* $(\alpha, \beta) = (2, 1)$.

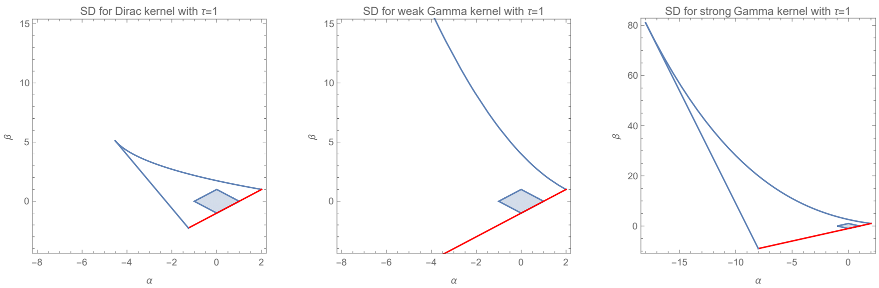

Fig. 1. Stability domain $S(\alpha, \beta)$ for different types of delay kernels, with a fixed average time delay $\tau = 1$. The stability domains are obtained based on Theorem 2 (left and right) and Theorem 3 (middle). The blue shaded region represents a delay-kernel-invariant subset of $S(\alpha, \beta)$. Along the blue curves and line segments Hopf bifurcations take place, while the red line corresponds to saddle-node bifurcations.

In Fig. 1, the stability domains given by the previous theorems are represented for four different delay kernels with the same average time delay $\tau = 1$. In each subfigure, the blue rhombus represents the delay-independent part of the stability domain given by Theorem 1. It is important to note that compared to discrete time-delays, the stability domains in the case of Gamma delay kernels are much larger. Moreover, in the case of a weak Gamma kernel (as it was the one included in the original Wilson-Cowan model [10], and therefore it produces the behavior of the model in its pure form, before the coarse-grain approximation), the stability region is unbounded, as in Theorem 3.

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3 Numerical simulations

The sigmoid activation function is chosen as in [4]: $f(x) = (1 + \exp(-\delta x))^{-1}$. For all numerical simulations, the following values of the system parameters are chosen: $\theta_u = 0.1$, $\theta_u = 0.2$, $a = d = -6$, $b = c = 3$ and $\delta = 40$. The following equilibrium is computed: $(u^\star, v^\star) = (0.0660694, 0.076733)$, with the characteristic parameters: $\alpha = -31.8118$ and $\beta = 188.846$. Based on Theorem 2, the critical value of the average time delay $\tau^\star$ responsible for the occurrence of a Hopf bifurcation which causes the loss of asymptotic stability of the equilibrium $(u^\star, v^\star)$ is determined in the case of a Dirac kernel $\tau_0^\star = 0.0674893$ and a strong Gamma kernel $\tau_2^\star = 0.202917$. The Hopf bifurcations are supercritical, causing the appearance of stable limit cycles, as it can be seen in Figs. 2.

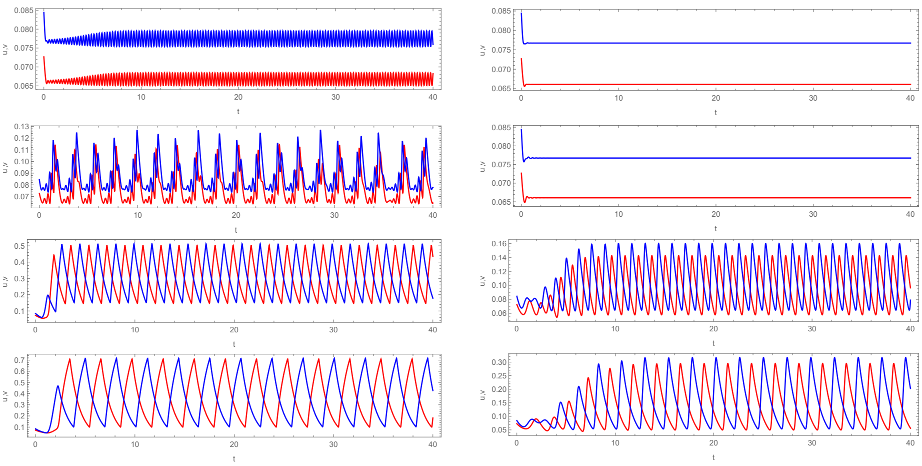

Fig. 2. Evolution of state variables $u(t)$ and $v(t)$ of system (2) with discrete time-delay (left) and strong Gamma kernel (right) for valued of the average time delay $\tau \in \{0.07, 0.1, 0.5, 1\}$ (top to bottom). The values of the parameters are fixed: $\theta_u = 0.1$, $\theta_u = 0.2$, $a = d = -6$, $b = c = 3$ and $\delta = 40$. The same initial condition has been chosen in a neighborhood of the equilibrium.

On the other hand, in the case of a weak Gamma kernel, from Theorem 3 it follows by numerical computations that for the specific values of α and β given above, the equilibrium $(u^\star, v^\star)$ is asymptotically stable, for any $\tau > 0$. Therefore, no oscillations or bursting behavior is expected to occur in a neighborhood of the equilibrium if a weak Gamma kernel is considered in the mathematical model. This reflects an important difference between the different types of behavior that can be observed for different types of delay kernels. The weak Gamma kernel has a particular importance as it has been included in the original Wilson-Cowan model before applying time-coarse graining.

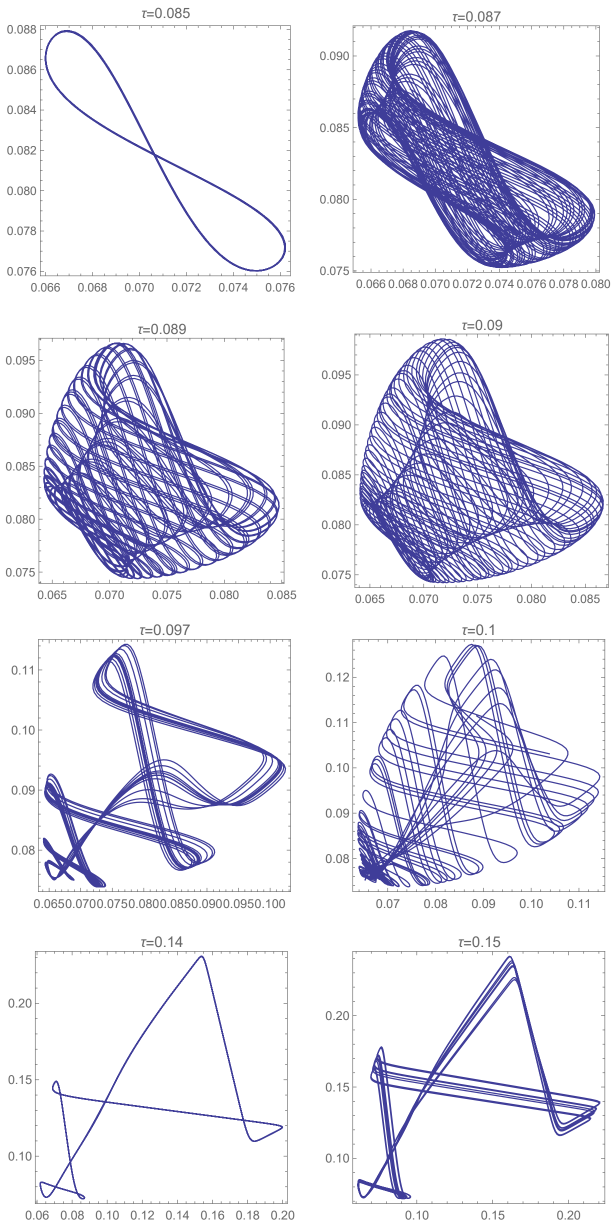

Fig. 3. Periodic, quasi-periodic and chaotic orbits shown in the (u, v)-phase-plane for the Wilson-Cowan model with discrete time-delay, obtained for different values of τ.

Numerical simulations also reveal complex bursting and quasi-periodic behavior in the Wilson-Cowan model with a discrete time delay (see Fig. 3), suggesting a series of bifurcations involving limit cycles. Interestingly, these phenomena could not be observed in the case of strong Gamma kernels with the same system parameters.

4 Conclusions

A local stability and bifurcation analysis has been presented for a generalization of the Wilson-Cowan model of excitatory and inhibitory interactions in localized neuronal populations, incorporating general distributed delays. Essential differences have been pointed out for different scenarios involving diverse delay kernels, emphasizing the importance of a careful choice of delay kernels in the mathematical model.

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