Towards a realistic NNLIF model: Analysis and numerical solver for excitatory-inhibitory networks with delay and refractory periods

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Abstract

The Network of Noisy Leaky Integrate and Fire (NNLIF) model describes the behavior of a neural network at mesoscopic level. It is one of the simplest self-contained mean-field models considered for that purpose. Even so, to study the mathematical properties of the model some simplifications were necessary [4, 5, 6], which disregard crucial phenomena. In this work we deal with the general NNLIF model without simplifications. It involves a network with two populations (excitatory and inhibitory), with transmission delays between the neurons and where the neurons remain in a refractory state for a certain time. We have studied the number of steady states in terms of the model parameters, the long time behaviour via the entropy method and Poincaré’s inequality, blow-up phenomena, and the importance of transmission delays between excitatory neurons to prevent blow-up and to give rise to synchronous solutions. Besides analytical results, we have presented a numerical resolutor for this model, based on high order flux-splitting WENO schemes and an explicit third order TVD Runge-Kutta method, in order to describe the wide range of phenomena exhibited by the network: blow-up, asynchronous/synchronous solutions and instability/stability of the steady states; the solver also allows us to observe the time evolution of the firing rates, refractory states and the probability distributions of the excitatory and inhibitory populations.

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1 Introduction

A wide variety of models have been usually considered in neuroscience, but their mathematical properties remain poorly understood. Mathematical studies on these models have advanced rapidly in the recent years, shedding light in this direction. In this line, we analyze in this paper the Network of Noisy Leaky Integrate and Fire (NNLIF) model, which describes the behavior of a neural network at mesoscopic level and is one of the simplest self-contained mean-field models used for that purpose. We refer to [3, 14, 18, 1, 15, 2, 17, 11, 12, 19, 13], and references therein, for a background on Integrate and Fire neuron models.

This mesoscopic model is based on a nonlinear system of two Partial Differential Equations (PDEs) of Fokker-Planck type and two Ordinary Differential Equations (ODEs), which are all nonlinearly coupled. Moreover, some terms include time delays. The system describes the behaviour of a network with excitatory and inhibitory neurons, which are considered as different populations. Thus, the unknowns of the system are the probability densities $\rho_\alpha(t, v)$ of finding a neuron of the excitatory population ($\alpha = E$) and the inhibitory one ($\alpha = I$), whose membrane potential is $v$ at time $t$; together with the refractory states $R_\alpha(t)$, one for each population, which represent the proportion of neurons that does not respond to stimuli.

As a starting point, crucial phenomena have been disregarded in order to deal with this model. For example, transmission delay of the neural spike, the existence of refractory states, or the fact that there are two populations, have been neglected in order to simplify it [4, 5, 6]. The simplest NNLIF model, widely studied in [4, 7, 8], corresponds to the case in which the neural network is assumed to be composed just by one population, which can be excitatory or inhibitory (in average), and where the neurons always respond to stimuli. In mathematical terms this is translated into a unique PDE, with a connectivity parameter $b$ whose sign determines whether the population is excitatory (positive $b$) or inhibitory (negative $b$). Many works have been developed in order to make the model more realistic: in [5], the authors analyzed a model for one population including the refractory state; in [6], a model for two populations was considered; and in [2], a quite complete model was studied that includes either one or two populations, refractory states and transmission delays.

In the current work we aim to study a more realistic NNLIF model consisting of two populations with refractory states and transmission delays, completing the results of [2]. We demonstrate that neural networks with part of their neurons in a refractory state always have steady states—which has been proved for the simpler case of only one population [5]. This shows that in the complete model with refractory states there is always at least one steady state, while in the absence of refractory states [6] there are some values of the parameters for which the model has no steady states. We are also able to give conditions for the values of the model parameters which ensure the uniqueness of the steady state. This result is completed with a proof of exponential convergence of the solution to the steady state for networks with small connectivity parameters and without transmission delay. The entropy method [7, 6] will be used to achieve this goal, with the additional difficulty that we deal with a complex system involving four equations, for which the entropy functional is composed of excitatory and inhibitory densities and their corresponding refractory probabilities. Moreover, we extend to this case the analysis of blow-up phenomena started in [5, 6]. We will observe that the network can blow-up in finite time if the transmission delay between excitatory neurons vanishes, even if there are transmission delays between inhibitory neurons or between inhibitory and excitatory neurons. Consequently, we show that the only way to avoid the blow-up is to consider a nonzero transmission delay between excitatory neurons. At the microscopic level, it is known that global-in-time solutions
exist if there is transmission delay in the case of only one average-excitatory population (see [10] and [9]).

On the other hand, in order to better understand some of the analytical open problems related to this model and show visually the behaviour of the network, we develop a numerical solver for the full model. Our solver is based on high order flux-splitting WENO schemes, TVD Runge-Kutta methods, and an efficient numerical strategy to deal with the saving and recovering of data needed to take the delays into account. This new numerical solver improves our previous ones [4, 5, 6] not only because it describes the complete NNLIF model, but also due to it being optimized. It allows us to describe the wide range of phenomena displayed by the network: blow-up, asynchronous/synchronous solutions, instability/stability of the steady states, as well as the time evolution of the firing rates, the proportion of refractory states, and the probability distributions of the excitatory and inhibitory populations. Besides, we explore numerically the importance of the transmission delay between excitatory neurons to avoid the blow-up phenomenon; situations which present blow-up without delay are prevented if a nonzero transmission delay is considered. Instead of blowing-up, solutions approach a stationary solution or synchronous state.

Our numerical scheme reproduces situations studied in [2] and completes them with the time evolution of the macroscopic (firing rates and refractory states) and the mesoscopic quantities (probability distributions). In this sense, our paper complements the work in [2] with the analysis of the number of steady states, their stability for small connectivity parameters, the study of the blow-up phenomenon and a numerical solver, which describes the evolution in time of the system.

To our knowledge, the numerical solver presented in this paper is the first deterministic solver to describe the behavior of the full NNLIF system including all the characteristic phenomena of real networks. Including all relevant phenomena is essential to explore some open problems, as for instance the stability in the case of large connectivity parameters, the importance of the transmission delay to avoid the blow-up of the solutions and to produce periodic solutions or the study of conditions for which synchronous solutions appear.

In the rest of this introduction we describe the model and the concept of solution considered. In Section 2 we analyze the number of steady states, prove exponential convergence to the unique stationary solution when the connectivity parameters are small enough, and present a criterion to obtain solutions that blow-up in finite time. All of these results are illustrated in Section 3 where we present our numerical scheme and explore the complex dynamics of the NNLIF model.

1.1 The model

Let us consider a neural network composed of an excitatory population and an inhibitory population. We denote by $p_\alpha(v, t)$ the probability density of finding a neuron in the population $\alpha$, with a voltage $v \in (-\infty, V_F]$ at a time $t \geq 0$, where $\alpha = E$, if the population is excitatory, and $\alpha = I$, if it is inhibitory. We also consider the NNLIF model [2, 6] to describe the network, taking into account the transmission delay and the refractory state. We obtain a complicated system of two PDEs for the evolution of these probability densities $p_\alpha(v, t)$, coupled with another two ODEs for the refractory
studied in [2], and $M$ is defined in terms of the boundary conditions for $\rho_i$ and diffusion coefficients. Moreover, the system (1.1) is nonlinear because the firing rates, $\nu_{E,ext}$, both populations (excitatory and inhibitory) are coupled by means of the drift law:

$$
\frac{dR_\alpha(t)}{dt} = N_\alpha(t) - M_\alpha(t),
$$

$$
N_\alpha(t) = -a_\alpha(N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) \frac{\partial \rho_\alpha}{\partial v}(V_F, t) \geq 0,
$$

$$
\rho_\alpha(\infty, t) = 0, \quad \rho_\alpha(V_F, t) = 0, \quad \rho_\alpha(v, 0) = \rho_\alpha^0(v) \geq 0, \quad R_\alpha(0) = R_\alpha^0.
$$

For each population $\alpha$, $R_\alpha(t)$ denotes the probability to find a neuron in the refractory state and $D_i^\alpha$, for $i = E, I$, is the transmission delay of a spike arriving at a neuron of population $\alpha$, coming from a neuron of population $i$. The drift and diffusion coefficients are defined by

$$
h_\alpha(v, N_E(t), N_I(t)) = -v + b_E^\alpha N_E(t) - b_I^\alpha N_I(t) + (b_E^\alpha - b_I^\alpha)\nu_{E,ext},
$$

$$
a_\alpha(N_E(t), N_I(t)) = d_\alpha + d_E^\alpha N_E(t) + d_I^\alpha N_I(t), \quad \alpha = E, I,
$$

where, for $i, \alpha = E, I$, $b_i^\alpha > 0$, $d_\alpha > 0$ and $d_i^\alpha \geq 0$, and $b_i^\alpha$ are the connectivity parameters for a spike emitted by a neuron of population $i$ and arriving at a neuron of population $\alpha$, and $\nu_{E,ext} \geq 0$ describes the external synapses. Both populations (excitatory and inhibitory) are coupled by means of the drift and diffusion coefficients. Moreover, the system (1.1) is nonlinear because the firing rates, $N_\alpha$, are defined in terms of the boundary conditions for $\rho_\alpha$.

Denoting the refractory period $\tau_\alpha$, different choices of $M_\alpha(t)$ can be considered: $M_\alpha(t) = N_\alpha(t - \tau_\alpha)$ (studied in [2]), and $M_\alpha(t) = \frac{R_\alpha(t)}{\tau_\alpha}$ (analyzed in [5]). Depending on the refractory state used, slightly different behaviors of the solutions will appear.

On the other hand, since the number of neurons is assumed to be preserved, we have the conservation law:

$$
\int_{-\infty}^{V_F} \rho_\alpha(v, t) \, dv + R_\alpha(t) = \int_{-\infty}^{V_F} \rho_\alpha^0(v) \, dv + R_\alpha^0 = 1 \quad \forall \, t \geq 0, \quad \alpha = E, I.
$$

To finish the description of the model, we remark that system (1.1) also includes the case of only one population (in average excitatory or inhibitory), with refractory state and transmission delay. Specifically, we can remove $\alpha$ in (1.1) considering only one PDE for the probability density, $\rho(v, t)$,
which is coupled to an ODE for the probability that a neuron is in a refractory state, $R(t)$:

\[
\begin{aligned}
\frac{\partial \rho}{\partial t}(v, t) + \frac{\partial}{\partial v}[h(v, N(t-D))\rho(v, t)] - a(N(t-D))\frac{\partial^2 \rho}{\partial v^2}(v, t) &= M(t)\delta(v - V_R), \\
\frac{dR(t)}{dt} &= N(t) - M(t), \\
N(t) &= -a(N(t-D))\frac{\partial \rho}{\partial v}(V_F, t) \geq 0, \\
\rho(-\infty, t) &= 0, \quad \rho(V_F, t) = 0, \quad \rho(v, 0) = \rho^0(v) \geq 0, \quad R(0) = R^0,
\end{aligned}
\]  

(1.5)

with drift and diffusion terms

\[
\begin{aligned}
h(v, N(t)) &= -v + bN(t) + \nu_{\text{ext}}, \\
a(N(t)) &= d_0 + d_1 N_E(t),
\end{aligned}
\]  

(1.6)

(1.7)

where the connectivity parameter $b$ is positive for an average-excitatory population and negative for an average-inhibitory population, and where $d_0 > 0, d_1 \geq 0$, and $\nu_{\text{ext}}$ describes the external synapses (note that this parameter and $\nu_{E,\text{ext}}$ have different units, since $\nu_{\text{ext}}$ includes other model constants).

As in [4, 5, 6], the notion of solution that we consider is the following:

**Definition 1.1** Let $\rho_\alpha \in L^\infty(\mathbb{R}^+; L^1_{\text{loc}}((-\infty, V_F)))$, $N_\alpha \in L^1_{\text{loc,+}}(\mathbb{R}^+)$ and $R_\alpha \in L^\infty(\mathbb{R}^+)$ for $\alpha = E, I$. Then $(\rho_E, \rho_I, R_E, R_I, N_E, N_I)$ is a weak solution of (1.1)-(1.3) if for any test function $\phi(v, t) \in C^\infty((-\infty, V_F] \times [0, T])$ such that $\frac{\partial^2 \phi}{\partial v^2}, v\frac{\partial \phi}{\partial v} \in L^\infty((-\infty, V_F) \times (0, T))$ the following relation

\[
\begin{aligned}
\int_0^T \int_{-\infty}^{V_F} \rho_\alpha(v, t) \left[ -\frac{\partial \phi}{\partial t} - \frac{\partial \phi}{\partial v} h^\alpha(v, N_E(t-D_E^\alpha), N_I(t-D_I^\alpha)) - a_\alpha(N_E(t-D_E^\alpha), N_I(t-D_I^\alpha))\frac{\partial^2 \phi}{\partial v^2} \right] dv dt \\
= \int_0^T [M_\alpha(t)\phi(V_R, t) - N_\alpha(t)\phi(V_F, t)] dt + \int_{-\infty}^{V_F} \rho_0^\alpha(v)\phi(v, 0) dv - \int_{-\infty}^{V_F} \rho_\alpha(v, T)\phi(v, T) dv
\end{aligned}
\]  

(1.8)

is satisfied $\forall \alpha = E, I$, and $R_\alpha$, for $\alpha = E, I$, are solutions of the ODEs

\[
\begin{aligned}
\frac{dR_\alpha(t)}{dt} &= N_\alpha(t) - M_\alpha(t).
\end{aligned}
\]  

We recall some notations involved in Definition 1.1. For $1 \leq p < \infty$, $L^p(\Omega)$ is the space of functions such that $f^p$ is integrable in $\Omega$, $L^\infty(\Omega)$ is the space of essentially bounded functions in $\Omega$, $L^\infty_{\text{loc}}(\Omega)$ represents the space of non-negative essentially bounded functions in $\Omega$, $C^\infty(\Omega)$ is the set of infinitely differentiable functions in $\Omega$ and $L^1_{\text{loc,+}}(\Omega)$ denotes the set of non-negative functions that are locally integrable in $\Omega$.

## 2 Steady states and long time behavior

The study of the number of steady states for excitatory and inhibitory NNLIF neural networks, with refractory periods and transmission delays of the spikes (1.1) (considering $R_\alpha$ either as defined in [5] or in [2]), can be done combining the ideas of [4, 5] and [6], with the additional difficulty that the
system to be dealt with is now more complicated. The steady states \((\rho_E, \rho_I, N_E, N_I, R_E, R_I)\) of (1.1) satisfy
\[
\frac{\partial}{\partial v} [h^\alpha(v)\rho_\alpha(v) - a_\alpha(N_E, N_I) \frac{\partial \rho_\alpha}{\partial v}(v) + \frac{R_\alpha}{\tau_\alpha} H(v - V_R)] = 0, \quad R_\alpha = \tau_\alpha N_\alpha, \quad \alpha = E, I,
\]
in the sense of distributions, with \(H\) denoting the Heaviside function and \(h^\alpha(v, N_E, N_I) = V_0^\alpha(N_E, N_I) - v\), where \(V_0^\alpha(N_E, N_I) = b_E^0 N_E - b_I^0 N_I + (b_E^0 - b_E^I) \nu_{E,ext}\). We remark that this equation is the same as the equation for stationary solutions in a network without transmission delays. Using the definition of \(N_\alpha\) and the Dirichlet boundary conditions of (1.1) we obtain an initial value problem for every \(\alpha = E, I,\) whose solutions are
\[
\rho_\alpha(v) = \frac{N_\alpha}{a_\alpha(N_E, N_I)} e^{-\frac{(v - V_0^\alpha(N_E, N_I))^2}{2a_\alpha(N_E, N_I)}} \int_{\max(v, V_F)}^{V_F} e^{-\frac{(w - V_0^\alpha(N_E, N_I))^2}{2a_\alpha(N_E, N_I)}} dw \quad \alpha = E, I. \tag{2.1}
\]

Moreover, the conservation of mass (1.4), which takes into account the refractory states, yields a system of implicit equations for \(N_\alpha\)
\[
1 - \tau_\alpha N_\alpha = \frac{N_\alpha}{a_\alpha(N_E, N_I)} \int_{-\infty}^{V_F} e^{-\frac{(v - V_0^\alpha(N_E, N_I))^2}{2a_\alpha(N_E, N_I)}} \int_{\max(v, V_R)}^{V_F} e^{-\frac{(w - V_0^\alpha(N_E, N_I))^2}{2a_\alpha(N_E, N_I)}} dw \, dv. \tag{2.2}
\]

If this system could be solved, the profile (2.1) would provide an exact expression for \(\rho_\alpha\). In order to handle the previous system more easily, we use two changes of variables as in [6]. First:
\[
\begin{align*}
 z &= \frac{v - V_0^E(N_E, N_I)}{\sqrt{a_E(N_E, N_I)}}, \quad u = \frac{w - V_0^E(N_E, N_I)}{\sqrt{a_E(N_E, N_I)}}, \quad w_F := \frac{V_F - V_0^E(N_E, N_I)}{\sqrt{a_E(N_E, N_I)}}, \quad w_R := \frac{V_R - V_0^E(N_E, N_I)}{\sqrt{a_E(N_E, N_I)}}, \\
 \tilde{z} &= \frac{v - V_0^I(N_E, N_I)}{\sqrt{a_I(N_E, N_I)}}, \quad \tilde{u} = \frac{w - V_0^I(N_E, N_I)}{\sqrt{a_I(N_E, N_I)}}, \quad \tilde{w}_F := \frac{V_F - V_0^I(N_E, N_I)}{\sqrt{a_I(N_E, N_I)}}, \quad \tilde{w}_R := \frac{V_R - V_0^I(N_E, N_I)}{\sqrt{a_I(N_E, N_I)}},
\end{align*}
\]
and (2.2) is then written as
\[
\frac{1}{N_E} - \tau_E = \frac{1}{a_E(N_E, N_I)} I_1(N_E, N_I), \quad \text{where } I_1(N_E, N_I) = \int_{-\infty}^{w_F} e^{-\frac{u^2}{2}} \int_{\max(z, w_R)}^{w_F} e^{\frac{w^2}{2}} du \, dz,
\]
\[
\frac{1}{N_I} - \tau_I = \frac{1}{a_I(N_E, N_I)} I_2(N_E, N_I), \quad \text{where } I_2(N_E, N_I) = \int_{-\infty}^{\tilde{w}_F} e^{-\frac{\tilde{u}^2}{2}} \int_{\max(\tilde{z}, \tilde{w}_R)}^{\tilde{w}_F} e^{\frac{\tilde{w}^2}{2}} du \, dz, \tag{2.3}
\]
with the additional restrictions
\[
N_\alpha < \frac{1}{\tau_\alpha} \quad \alpha = E, I, \tag{2.4}
\]

since \(R_\alpha = \tau_\alpha N_\alpha\) and \(R_\alpha < 1\) (we also observe these restrictions by the positivity of \(I_\alpha\), see [2.3]). Next, the change of variables \(s = \frac{z - \alpha}{\sqrt{2}}\) and \(\tilde{s} = \frac{\tilde{z} - \alpha}{\sqrt{2}}\) allows to formulate the functions \(I_1\) and \(I_2\) as
\[
I_1(N_E, N_I) = \int_0^{\infty} \frac{e^{-\frac{s^2}{2}}}{s} (e^{s w_F} - e^{s w_R}) \, ds, \tag{2.5}
\]
\[
I_2(N_E, N_I) = \int_0^{\infty} \frac{e^{-\frac{\tilde{s}^2}{2}}}{s} (e^{\tilde{s} \tilde{w}_F} - e^{\tilde{s} \tilde{w}_R}) \, ds. \tag{2.6}
\]
If \( b_I^E = b_E^I = 0 \) the equations are uncoupled and the number of steady states can be studied in terms of the values of \( b_I^E \), due to fact that for the inhibitory equation there is always a unique steady state [5]. The following theorem analyses the coupled case.

**Theorem 2.1** Assume that \( b_I^E > 0, b_E^I > 0, \tau_E > 0, \tau_I > 0, a_\alpha(N_E, N_I) = a_\alpha \) constant, and \( h^\alpha(v, N_E, N_I) = V_0^\alpha(N_E, N_I) - v \) with \( V_0^\alpha(N_E, N_I) = b_I^E N_E - b_I^I N_I + (b_E^E - b_E^I) v_{E,ext} \) for all \( \alpha = E, I \). Then there is always an odd number of steady states for (1.1).

Moreover, if \( b_I^E \) is small enough or \( \tau_E \) is large enough (in comparison with the rest of parameters), then there is a unique steady state for (1.1).

**Proof.** The proof is based on determining the number of solutions of the system

\[
1 = N_E (\tau_E + I_1(N_E, N_I)), \quad 0 < N_E < \frac{1}{\tau_E}, \tag{2.7}
\]

\[
1 = N_I (\tau_I + I_2(N_E, N_I)), \quad 0 < N_I < \frac{1}{\tau_I}. \tag{2.8}
\]

With this aim, we adapt some ideas of [5] and [6] to the system (2.7)-(2.8). We refer to [6] for details about the properties of the functions \( I_1 \) and \( I_2 \) (see (2.5) and (2.6)) and their proofs.

First, we observe that for every \( N_E > 0 \) fixed, there is a unique solution \( N_I(N_E) \) that solves (2.8), because for \( N_E > 0 \) fixed, the function \( f(N_I) = N_I (\tau_I + I_2(N_E, N_I)) \) satisfies: \( f(0) = 0, f(\frac{1}{\tau_I}) = 1 + \frac{I_2(N_N, \frac{1}{\tau_E})}{\tau_I} > 1 \) and is increasing, since \( I_2(N_E, N_I) \) is an increasing, strictly convex function on \( N_I \).

Then, taking into account that the function \( F(N_E) := N_E[I_1(N_E, N_I(N_E)) + \tau_E] \) satisfies that \( F(0) = 0 \) and \( F(\frac{1}{\tau_E}) = 1 + \frac{I_1(N_N, \frac{1}{\tau_E})}{\tau_E} > 1 \), it can be concluded that there is always an odd number of steady states.

Finally, to obtain values of the parameters such that there is a unique steady state, we analyze the derivative of \( F \):

\[
F'(N_E) = I_1(N_E, N_I(N_E)) + \tau_E + N_E \left[ -\frac{b_I^E}{\sqrt{a_E}} + \frac{b_E^I}{\sqrt{a_E}} N_I'(N_E) \right] \int_0^\infty e^{-s^2/2} (e^{s V_F}/\sqrt{a_I} - e^{s V_R}/\sqrt{a_I}) \, ds.
\]

It is non-negative for \( 0 < N_E < \frac{1}{\tau_E} \), for certain parameter values, and therefore there is a unique steady state in these cases. For \( b_I^E \) small, \( F'(N_E) \) is positive since all the terms are positive, because \( N'(N_E) \) is positive (see the proof of Theorem 4.1 in [6]). For \( \tau_E \) large, the proof of the positivity of \( F'(N_E) \) is more complicated. It is necessary to use

\[
N_I'(N_E) = \frac{b_I^E N_I^3(N_E) I(N_E)}{\sqrt{a_I} + b_I^I N_I^2(N_E) I(N_E)}, \tag{2.9}
\]

where

\[
I(N_E) = \int_0^\infty e^{-s^2/2} e^{-\frac{(b_I^E N_E - b_I^I N_I(N_E) + (b_E^E - b_E^I) v_{E,ext})}{\sqrt{a_I}}} \left( e^{s V_F}/\sqrt{a_I} - e^{s V_R}/\sqrt{a_I} \right) \, ds.
\]

The function \( N_I(N_E) \) is increasing and \( I(N_E) \) is decreasing, since \( 0 < N_I'(N_E) < \frac{b_I^E}{b_I^I} \) (see the proof of
Theorem 2.3. Consider system (1.5) and $M(t) = \frac{R(t)}{\tau}$. Assume that the connectivity parameter $b$ is small enough, $|b| \ll 1$, the diffusion term is constant, $a(N) = a$ for some $a > 0$, there is no transmission delay, $D = 0$, and that the initial datum is close enough to the unique steady state $(\rho_{\infty}, R_{\infty}, N_{\infty})$,

$$
\int_{-\infty}^{V_F} \rho_{\infty}(v) \left( \frac{\rho^0(v) - \rho_{\infty}(v)}{\rho_{\infty}(v)} \right)^2 dv + R_{\infty} \left( \frac{R(0)}{R_{\infty}} - 1 \right)^2 \leq \frac{1}{2|b|}.
$$

(2.10)

Then, for fast decaying solutions to (1.5) there is a constant $\mu > 0$ such that for all $t \geq 0$

$$
\int_{-\infty}^{V_F} \rho_{\infty}(v) \left( \frac{\rho(v) - \rho_{\infty}(v)}{\rho_{\infty}(v)} \right)^2 dv + \left( \frac{R(t) - R_{\infty}}{R_{\infty}} \right)^2 \leq e^{-\mu t} \left[ \int_{-\infty}^{V_F} \rho_{\infty} \left( \frac{\rho^0(v) - \rho_{\infty}(v)}{\rho_{\infty}(v)} \right)^2 dv + \left( \frac{R^0 - R_{\infty}}{R_{\infty}} \right)^2 \right].
$$
Proof. The proof combines a relative entropy argument with the Poincaré’s inequality that is presented in [5][Proposition 5.3]. Additionally, to deal with the nonlinearity (the connectivity parameter does not vanish) we follow some ideas of [7][Theorem 2.1]. Notice that along the proof we will use the simplified notation

\[ p(v, t) = \frac{\rho(v, t)}{\rho_\infty(v)}, \quad r(t) = \frac{R(t)}{R_\infty}, \quad \eta(t) = \frac{N(t)}{N_\infty}. \]

First, for any smooth convex function \( G : \mathbb{R}^+ \to \mathbb{R} \), we recall that a natural relative entropy for equation (1.5) is defined as

\[ E(t) := \int_{-\infty}^{V_F} \rho_\infty G(p(v, t)) \ dv + R_\infty G(r(t)). \] (2.11)

The time derivative of the relative entropy (2.11) can be written as

\[
\frac{d}{dt} E(t) = -a \int_{-\infty}^{V_F} \rho_\infty(v) G''(p(v, t)) \left[ \frac{\partial p}{\partial v} \right]^2 (v, t) \ dv \\
- N_\infty \left[ G(\eta(t)) - G(p(V_R, t)) - (r(t) - p(V_R, t)) G'(p(V_R, t)) - (\eta(t) - r(t)) G'(r(t)) \right] \\
+ b(N(t) - N_\infty) \int_{-\infty}^{V_F} \frac{\partial \rho_\infty}{\partial v} (v) \left[ G(p(v, t)) - p(v, t) G'(p(v, t)) \right] \ dv.
\] (2.12)

Expression (2.12) is achieved after some simple computations, taking into account that \((\rho, R, N)\) is a solution of equation (1.5) and that \((\rho_\infty, R_\infty, N_\infty)\) is the unique steady state of the same equation, thus given by

\[
\left\{ \begin{array}{l}
\frac{\partial}{\partial v}[h(v, N_\infty) \rho_\infty(v)] - a \frac{\partial^2 \rho_\infty}{\partial v^2} (v) = \frac{R_\infty}{\tau} \delta(v - V_R), \\
R_\infty = \tau N_\infty, \quad N_\infty = -a \frac{\partial \rho_\infty}{\partial v}(V_F) \geq 0, \\
\rho_\infty(-\infty) = 0, \quad \rho_\infty(V_F) = 0.
\end{array} \right.
\]

Specifically, we can obtain successively the following relations:

\[
\frac{\partial p}{\partial t} - \left( v - bN + \frac{2a \rho_\infty}{\rho_\infty} \frac{\partial p}{\partial v} \right) \frac{\partial p}{\partial v} - a \frac{\partial^2 p}{\partial v^2} = \frac{R_\infty}{\tau \rho_\infty} \delta(v - V_R) (r - p) - \frac{p}{\rho_\infty} b(N - N_\infty) \frac{\partial \rho_\infty}{\partial v}, \quad (2.13)
\]

\[
\frac{\partial G(p)}{\partial t} - \left( v - bN + \frac{2a \rho_\infty}{\rho_\infty} \frac{\partial p}{\partial v} \right) \frac{\partial G(p)}{\partial v} - a \frac{\partial^2 G(p)}{\partial v^2} = -G'(p) \frac{p}{\rho_\infty} b(N - N_\infty) \frac{\partial \rho_\infty}{\partial v} \\
- a G''(p) \left( \frac{\partial p}{\partial v} \right)^2 + G'(p) \frac{R_\infty}{\tau \rho_\infty} \delta(v - V_R) (r - p), \quad (2.14)
\]

and

\[
\frac{\partial}{\partial t} \rho_\infty G(p) - \frac{\partial}{\partial v} [(v - bN) \rho_\infty G(p)] - \frac{\partial^2}{\partial v^2} [\rho_\infty G(p)] = b(N - N_\infty) \frac{\partial \rho_\infty}{\partial v} [G(p) - p G'(p)] \\
- a \rho_\infty G''(p) \left( \frac{\partial p}{\partial v} \right)^2 + \frac{R_\infty}{\tau} \delta(v - V_R) [(r - p) G'(p) + G(p)], \quad (2.15)
\]
Finally, (2.12) is obtained after integrating (2.16) with respect to \( v \), between \(-\infty\) and \( V_F \), taking into account that
\[
a \frac{\partial}{\partial v} [\rho_\infty G(p)]_{v=V_F} = -N_\infty G(\eta),
\]
due to the boundary condition at \( V_F \) and the l'Hopital rule, and adding
\[
\frac{d}{dt} R_\infty G(r) = \frac{R_\infty}{\tau} R_\infty G'(r)(\eta - r). \tag{2.16}
\]
To obtain the exponential rate of convergence stated in the theorem, we consider \( G(x) = (x-1)^2 \) in (2.12). Its first term is negative and will provide the strongest control when combined with the Poincaré's inequality. After some algebraical computations, the second term can be written as
\[
-N_\infty[G(\eta(t)) - G(p(V_R,t)) - (r(t) - p(V_R,t))G'(p(V_R,t)) - (\eta(t) - r(t))G'(r(t))]
\]
\[
= -N_\infty[(r(t) - \eta(t))^2 + (r(t) - p(V_R,t))^2].
\]
Applying the inequality \((a + b)^2 \geq \epsilon(a^2 - 2b^2)\), for \( a, b \in \mathbb{R} \) and \( 0 < \epsilon < \frac{1}{2} \), we obtain
\[
-N_\infty(r(t) - \eta(t))^2 \leq -\epsilon N_\infty(\eta(t) - 1)^2 + 2\epsilon N_\infty(r(t) - 1)^2. \tag{2.17}
\]
Recalling the Poincaré’s inequality of [5][Proposition 5.3], and in a similar way as in [7], for small connectivity parameters, there exists \( \gamma > 0 \) such that:
\[
\int_{-\infty}^{V_F} \left( \frac{\rho - \rho_\infty}{\rho_\infty} \right)^2 dv + \frac{(R - R_\infty)^2}{R_\infty} \leq \frac{1}{\gamma} \left[ \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv + N_\infty(r(t) - p(V_R,t))^2 \right], \tag{2.18}
\]
thus
\[
(r(t) - 1)^2 \leq \frac{1}{\gamma R_\infty} \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv + \frac{N_\infty}{\gamma R_\infty}(r(t) - p(V_R,t))^2, \tag{2.19}
\]
and therefore
\[
2\epsilon N_\infty(r(t) - 1)^2 \leq \frac{2\epsilon N_\infty}{\gamma R_\infty} \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv + \frac{2\epsilon N_\infty}{\gamma R_\infty} N_\infty(r(t) - p(V_R,t))^2. \tag{2.20}
\]
Joining now estimates (2.17) and (2.20), choosing \( 0 < \epsilon < \frac{1}{2} \) such that \( \frac{2\epsilon N_\infty}{\gamma R_\infty} < \min(\frac{\epsilon}{2}, \frac{1}{2}) \) and denoting \( C_0 := \epsilon N_\infty \) yields
\[
-N_\infty[G(\eta(t)) - G(p(V_R,t)) - (r(t) - p(V_R,t))G'(p(V_R,t)) - (\eta(t) - r(t))G'(r(t))]
\]
\[
\leq -C_0 G(\eta(t)) + \frac{a}{2} \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv - \frac{1}{2} N_\infty(r(t) - p(V_R,t))^2. \tag{2.21}
\]
The third term can be bounded in the same way as in [7]. Thus, for some $C > 0$ we have

\[
\begin{align*}
& b(N(t) - N_\infty) \int_{-\infty}^{V_F} \frac{\partial \rho_\infty(v)}{\partial v} [G(p(v, t)) - p(v, t) G'(p(v, t))] \, dv \\
& \leq C(2b^2 + |b|)(\eta(t) - 1)^2 + a \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv \left( \frac{1}{2} + |b| \int_{-\infty}^{V_F} \rho_\infty(v)(p(v, t) - 1)^2 \, dv \right).
\end{align*}
\]  

(2.22)

Combining estimates (2.21) and (2.22) gives the bound

\[
\frac{d}{dt} E(t) \leq - C_0(\eta(t) - 1)^2 + C(2b^2 + |b|)(\eta(t) - 1)^2 - \frac{1}{2} N_\infty(r(t) - p(V_R, t))^2
\]

\[- a \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv \left( 1 - |b| \int_{-\infty}^{V_F} \rho_\infty(v)(p(v, t) - 1)^2 \, dv \right) .
\]

Taking now $b$ small enough such that $C(2b^2 + |b|) \leq C_0$ we obtain

\[
\frac{d}{dt} E(t) \leq - \tilde{C} \left[ \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv + N_\infty(r(t) - p(V_R, t))^2 \right]
\]

\[- a \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv \left( 1 - 2|b| \int_{-\infty}^{V_F} \rho_\infty(v)(p(v, t) - 1)^2 \, dv \right) \]

\[\leq - \mu E(t) - \frac{a}{2} \left( 1 - 2|b| \right) E(t) \int_{-\infty}^{V_F} \rho_\infty(v) \left( \frac{\partial p}{\partial v} \right)^2 (v, t) \, dv,
\]

where Poincaré’s inequality (2.13) was used, with $\tilde{C} = \min \left( \frac{2}{\gamma}, \frac{1}{\gamma} \right)$, $\mu = \tilde{C} \gamma$. Finally, thanks to the choice of the initial datum (2.10) and Gronwall’s inequality, the relative entropy decreases for all times so that, $E(t) \leq \frac{1}{2|b|}$, \( \forall t \geq 0 \), and the result is proved:

\[
E(t) \leq e^{-\mu t} E(0) \leq e^{-\mu t} \frac{1}{2|b|}.
\]

\[\square\]

For two populations with refractory states (as given in model [5]), this exponential rate of convergence to the unique steady can also be proved. The proof is achieved by considering the full entropy for both populations:

\[
\mathcal{E}[t] := \int_{-\infty}^{V_F} \rho_\infty^E(v) \left( \frac{\rho_E(v) - \rho_\infty^E(v)}{\rho_\infty^E(v)} \right)^2 \, dv + \int_{-\infty}^{V_F} \rho_\infty^I(v) \left( \frac{\rho_I(v) - \rho_\infty^I(v)}{\rho_\infty^I(v)} \right)^2 \, dv
\]

\[
+ \frac{(R_E(t) - R_\infty^E)^2}{R_E^\infty} + \frac{(R_I(t) - R_\infty^I)^2}{R_I^\infty},
\]

and proceeding in the same way as in [6][Theorem 4.2], taking into account that now there are some terms with refractory states which have to be handled, as in Theorem 2.3.

**Theorem 2.4** Consider system (1.1) for two populations, with $M_\alpha(t) = \frac{R_\alpha(t)}{r_\alpha}$, $\alpha = I, E$. Assume that the connectivity parameters $b_i^\alpha$ are small enough, the diffusion terms $a_\alpha > 0$ are constant, the transmission delays $D_i^\alpha$ vanish ($\alpha = I, E, i = I, E$), and that the initial data $(\rho_0^E, \rho_0^I)$ are close enough...
to the unique steady state \((\rho_\infty^E,\rho_\infty^I)\):

\[ \mathcal{E}[0] < \frac{1}{2 \max \left( b_E^E + b_I^E, b_E^I + b_I^I \right) \max(v)} \]

Then, for fast decaying solutions to (1.1), there is a constant \(\mu > 0\) such that for all \(t \geq 0\)

\[ \mathcal{E}[t] \leq e^{-\mu t} \mathcal{E}[0] \]

Consequently, for \(\alpha = E, I\)

\[ \int_{-\infty}^{V_F} \rho_\alpha^\infty(v) \left( \frac{\rho_\alpha(v) - \rho_\infty^\alpha(v)}{\rho_\infty^\alpha(v)} \right)^2 dv + \frac{(R_\alpha(t) - R_\infty^\alpha)^2}{R_\infty^\alpha} \leq e^{-\mu t} \mathcal{E}[0] \]

To conclude the study about the long time behavior we have to remember that solutions to (1.1) may blow-up in finite time if there are no delays. Specifically, following similar steps as those developed in [5][Theorem 3.1] and [6][Theorem 3.1], we can prove an analogous result for the general system (1.1) without delay between excitatory neurons, this is \(D_E^E = 0\):

**Theorem 2.5** Assume that

\[ h^E(v, N_E, N_I) + v \geq b_E^E N_E - b_I^E N_I, \quad (2.23) \]

\[ a_E(N_E, N_I) \geq a_m > 0, \quad (2.24) \]

\(\forall v \in (-\infty, V_F]\), and \(\forall N_I, N_E \geq 0\). Assume also that \(D_E^E = 0\) and that there exists some \(C > 0\) such that

\[ \int_0^t N_I(s - D_I^E) \, ds \leq C t, \quad \forall t \geq 0. \quad (2.25) \]

Then, a weak solution to the system (1.1) cannot be global in time because one of the following reasons:

- \(b_E^E > 0\) is large enough, for \(\rho_\infty^E\) fixed.
- \(\rho_\infty^E\) is ‘concentrated enough’ around \(V_F\):

\[ \int_{-\infty}^{V_F} e^{\mu v} \rho_\infty^E(v) \, dv \geq \frac{e^{\mu V_F}}{b_E^E \mu}, \quad \text{for a certain } \mu > 0 \quad (2.26) \]

and for \(b_E^E > 0\) fixed.

Therefore, thanks to Theorem [2.4] and Theorem [2.5] we may conclude that, even with a unique steady state, if system (1.1) has immediate spike transmissions between excitatory neurons, (that is \(D_E^E = 0\)) then solutions can blow-up, whether initially they are close enough to the threshold potential or whether the excitatory neurons are highly connected (that is \(b_E^E\) is large enough). In the following numerical experiments we will show that the transmission delay between excitatory neurons prevent the blow-up phenomenon, but the remaining transmission delays cannot avoid it.
3 Numerical experiments

3.1 Numerical Scheme

The numerical scheme used to simulate equation (1.5) approximates the advection term by a fifth order finite difference flux-splitting Weighted Essentially Non-Oscillatory (WENO) scheme. The flux-splitting considered is the Lax-Friedrich splitting \[16\]

\[ f^\pm(\rho) = \frac{1}{2}(f(\rho) \pm \alpha \rho) \quad \text{where} \quad \alpha = \max_\rho |f'(\rho)|. \]

In our case \( f(\rho) = h(v, N)\rho \), and thus \( \alpha = \max_{v \in (-\infty, V_F)} |h(v, N)| \). The diffusion term is estimated by standard second order finite differences and the time evolution is calculated by an explicit third order Total Variation Diminishing (TVD) Runge-Kutta method.

Due to the delay, during the time evolution of the solution we have to recover the value of \( N \) at time \( t - D \), for every time \( t \). To implement this, we fix a time step \( dt \) and define an array of \( M = \frac{D}{dt} \) positions. Therefore, this array will save only \( M \) values of \( N(t) \) for a time interval \([kD, (k+1)D]\), \( k = 0, 1, 2, \ldots \) In the time interval \([(k+1)D, (k+2)D]\) these values of the array will be used to obtain the delayed values \( N(t - D) \) by linear interpolation between the corresponding positions of the array. We assume that \( N(t) = 0 \) \( \forall t < 0 \), so initially all the values of the array are zero, and the recovered values for the first time interval \( (k = 0) \) are all zero. Notice that we use linear interpolation since the time step \( dt \) for the time evolution is taken according to the Courant-Friedrich-Levy (CFL) condition.

Furthermore, once a position of the array is no longer necessary for the interpolation, it is overwritten.

The refractory state used in \([2]\) is based on considering a delayed firing rate, \( N(t - \tau) \), on the right hand side of the PDE for \( \rho \). This value is recovered in the same manner as the delayed \( N \) that appears due to the transmission delay. The refractory period \( \tau \) and the delay \( D \) do not usually coincide, and thus the firing rates have to be saved in two different arrays. The refractory state for which \( M(t) = \frac{R(t)}{t} \) was implemented using a finite difference approximation of its ODE.

The numerical approximation of the solution for the two-populations model was implemented using the same numerical scheme as that described above for one population. The main difference here is that the code runs over two cores using parallel computational techniques, following the ideas in \([6]\). Each core handles the equations of one of the populations. At the end of every time step the cores communicate via Message Passing Interface (MPI) to exchange the values of the firing rates. Also the transmission delays were handled as for one population, taking into account that now each processor has to save two arrays of firing rates, one for each population, since there are four different delays. The approximation of the different refractory states was done as for one population.

3.2 Numerical results

For the following simulations we will consider a uniform mesh for \( v \in [-V_{eft}, V_F] \), where \(-V_{eft} \) is chosen so that \( \rho_0(-V_{eft}, t) \sim 0 \). Moreover, unless otherwise specified, \( V_F = 2, V_R = 1, \nu_{E, ext} = 0 \) and \( a_\alpha(N_E, N_I) = 1 \). We will consider two different types of initial condition:

\[ \rho^0_\alpha(v) = \frac{k}{\sqrt{2\pi}} e^{-\frac{(v-v_0)^2}{2\sigma_0^2}}, \]

(3.1)
where $k$ is a constant such that $\int_{-V_{sfr}}^{V_{p}} \rho^{0}_\alpha(v) \, dv \approx 1$ numerically, and

$$
\rho^{0}_\alpha(v) = \frac{N_\alpha}{a_\alpha(N_E, N_I)} e^{\frac{(v-V^\alpha_0(N_E, N_I))^2}{2a^2_\alpha(N_E, N_I)}} \int_{\max(v, V_R)}^{V_p} e^{\frac{(w-V^\alpha_0(N_E, N_I))^2}{2a^2_\alpha(N_E, N_I)}} \, dw, \quad \alpha = E, I,
$$

(3.2)

with $V^\alpha_0(N_E, N_I) = b^\alpha_E N_E - b^\alpha_I N_I + (b^\alpha_E - b^\alpha_E) \nu_{E,ext}$ and where $N_\alpha$ is an approximated value of the stationary firing rate. The second kind of initial data is an approximation of the steady states of the system and allows us to study their local stability.

Notice that we will also refer to (3.1) as the initial condition for the one-population model by just considering $\rho_\alpha = \rho$, $v^\alpha_0 = v_0$ and $\sigma^2_\alpha = \sigma^2_0$.

### 3.2.1 Analysis of the number of steady states

As a first step in our numerical analysis we illustrate numerically some of the results of Theorem 2.1. Fig. 1 shows the behaviour of $F(N_E) := N_E \left[ I_1(N_E, N_I(N_E)) + \tau_E \right]$ for different parameter values, which produces bifurcation diagrams. In the figure on the left we observe the influence of the excitatory refractory period $\tau_E$, considering fixed the rest of parameters; a large $\tau_E$ gives rise to the uniqueness of the steady state. In figure on the right one, the impact of the connectivity parameter $b^E_E$ is described. In this case, a small $b^E_E$ guarantees a unique stationary solution. Moreover, as noted in Remark 2.2, we observe the uniqueness of the steady state if the system is highly connected between excitatory and inhibitory neurons, or if the excitatory neurons have enough refractory period.

As happens in the case of only one population [5], for two populations (excitatory and inhibitory), neurons in a refractory state guarantee the existence of stationary states. (However, the refractory state itself does not prevent the blow-up phenomenon, as we will show later).

### 3.2.2 Blow-up

In [5], the blow-up phenomenon for one population of neurons with refractory states was shown. Theorem 2.5 extends this result to two populations of neurons, one excitatory and the other one inhibitory. The refractory period is not enough to deter the blow-up of the network; if the membrane potentials of the excitatory population are close to the threshold potential, or if the connectivity parameter $b^E_E$ is large enough, then the network blows-up in finite time. To achieve the global-in-time existence, it seems necessary some transmission delay between excitatory neurons, as we observe in our simulations and as it was proved at the microscopic level for one population [9].

We start the analysis of the blow-up phenomenon by considering only one average-excitatory population (we recall that there is global existence for one average-inhibitory population, see [8]). In [4], it was proved that some solutions blow-up. In Fig. 2 we show how the transmission delay of the spikes between neurons prevents the network from blowing-up in finite time. Have the networks refractory states or not, we observe that the blow-up phenomenon appears in absence of a transmission delay.

In [6], the excitatory-inhibitory system without refractory states was studied. In the current paper, we extend this analysis to the presence of refractory states. Figs. 3 and 4 illustrate the results of Theorem 2.5, if there is no transmission delay between excitatory neurons, the solution blows-up because most of the excitatory neurons have a membrane potential close to the threshold potential, or because excitatory neurons are highly connected, that is, $b^E_E$ is large enough. We observe in Fig. 5 that the remaining delays do not avoid the blow-up phenomenon, since in this figure all the delays
are 0.1, except $D_E^E = 0$. The importance of $D_E^E$ is discerned in Fig. 6. We show the evolution in time of the solution of (1.1), with the same initial data as considered in Fig. 4 and with $D_E^E = 0.1$; in this case, the solution exists for every time, thus avoiding the blow-up.

### 3.2.3 Steady states and periodic solutions

In Fig. 1 we examined several choices of the model parameters, for which the system (1.1) presents three steady states. For one of these cases, the analysis of their stability is numerically investigated in Fig. 7. For $\alpha = E, I$, the initial conditions $\rho_0^\alpha - 1, 2, 3$ are given by the profiles (3.2), where $N_\alpha$ are approximations of the stationary firing rates. The evolution in time of the probability densities, the firing rates and the refractory states show that the lower steady state seems to be stable, while the two others are unstable. Moreover, considering as initial data (3.2) with $N_\alpha$ approximations of the higher stationary firing rates the solution blows-up in finite time, while with the intermediate firing rate the solution tends to the lower steady state. Fig. 8 also describes the stability when there are three steady states. In this case the intermediate state is very close to the highest one. Here, the lower steady state also appears to be stable. The two others are unstable, but the higher one does not blow-up in finite time.

The transmission delay not only prevents the blow-up phenomenon, but also should produce periodic solutions. In Fig. 9 we analyze the influence of the transmission delay for one average-excitatory population; if the initial datum is concentrated around $V_F$, periodic solutions appear; on the contrary, if it is far from $V_F$, the solution reaches a steady state. In Figs. 10 and 11 for one average-inhibitory population with transmission delay, we show that periodic solutions emerge if the initial condition is concentrated around the threshold potential, and even if the initial datum is far from the threshold and $v_{ext}$ is large. A comparison between $R(t)$ and $N(t)$ for $M(t) = \frac{R(t)}{\tau}$ and $M(t) = N(t) - \tau$ is presented in Fig. 12. In both cases the steady state is the same and the solutions tend to it. If the system tends to a synchronous state, these states are also almost the same for both possible choices of $M$.

Synchronous states appear also in the case of two populations (excitatory and inhibitory), as it is described in Fig. 13. In this particular case, they seem to appear due to the inhibitory population, which tends to a periodic solution. What is more, the excitatory population presents a solution that oscillates close around the equilibrium.

---

**Figure 1:** Number of steady states for system (1.1) described by Theorem 2.1. Left: For fixed $b_I^F = 7$, $b_I^I = 2$, $b_I^E = 0.01$, $b_E^E = 3$ and $\tau_I = 0.2$, we observe the influence of the excitatory refractory period $\tau_E$. Right: For fixed $b_I^F = 7$, $b_I^I = 2$, $b_I^E = 0.01$ and $\tau_E = \tau_I = 0.2$, we observe the influence of the connectivity parameter $b_E^E$.  

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Figure 2: System (1.5) (only one population) presents blow-up, if there is no transmission delay. We consider the initial data (3.1) with \( v_0 = 1.83 \), and \( \sigma_0 = 0.0003 \), and the connectivity parameter \( b = 0.5 \). Top: Without refractory state; Left: \( N \) blows-up in finite time, if there is no delay, \( D = 0 \). Right: \( N \) does not blow-up if there is delay, \( D = 0.1 \). Middle: With refractory state (\( M(t) = \frac{R(t)}{\tau} \)), \( R(0) = 0.2, \tau = 0.025 \) and \( D = 0 \), since there is no transmission delay \( N \) and \( R \) blow-up in finite time. Bottom: With refractory state (\( M(t) = \frac{R(t)}{\tau} \)), \( R(0) = 0.2, \tau = 0.025 \) and \( D = 0.07 \), the solution tends to the steady state, due to the transmission delay.
Figure 3: System (1.1) (two populations: excitatory and inhibitory) presents blow-up, if there are no transmission delays. We consider initial data (3.1) with $v_0^E = v_0^I = 1.25$, $\sigma_0^E = \sigma_0^I = 0.0003$, the connectivity parameters $b_{EE}^E = 6$, $b_{EI}^E = 0.75$, $b_{II}^I = 0.25$, $b_{IE}^I = 0.5$, and with refractory states ($M_{\alpha}(t) = N_{\alpha}(t - \tau_{\alpha})$) where $\tau_{\alpha} = 0.025$. We observe that the initial data are not concentrated around the threshold potential but the solution blows-up because $b_{EE}^E = 6$ is large enough and there are no transmission delays (see Theorem 2.5).

Figure 4: System (1.1) (two populations: excitatory and inhibitory) presents blow-up, if there are no transmission delays. We consider initial data (3.1) with $v_0^E = 1.89$, $v_0^I = 1.25$, $\sigma_0^E = \sigma_0^I = 0.0003$, the connectivity parameters $b_{EE}^E = 0.5$, $b_{EI}^E = 0.75$, $b_{II}^I = 0.25$, $b_{IE}^I = 0.5$, and with refractory states ($M_{\alpha}(t) = N_{\alpha}(t - \tau_{\alpha})$) where $\tau_{\alpha} = 0.025$. We observe that $b_{EE}^E = 0.5$ is not large enough, but the solution blows-up because the initial condition for the excitatory population is concentrated around the threshold potential and there are no transmission delay (see Theorem 2.5).
System (1.1) (two populations: excitatory and inhibitory) presents blow-up, if there is no excitatory transmission delay. We consider initial data (3.1) with $v^E_0 = 1.89$, $v^I_0 = 1.25$ and $\sigma^E_0 = \sigma^I_0 = 0.0003$, the connectivity parameters $b^E_E = 0.5$, $b^E_I = 0.75$, $b^I_I = 0.25$, $b^I_E = 0.5$, and with refractory states ($M_\alpha(t) = N_\alpha(t - \tau_\alpha)$) where $\tau_\alpha = 0.025$. All the delays are 0.1, except $D^E_E = 0$. We observe that the other delays do not avoid the blow-up due to a concentrated initial condition for the excitatory population.
Figure 6: System (two populations: excitatory and inhibitory) avoids blow-up, if there is a transmission delay between excitatory neurons. We consider initial data with $v_0^E = 1.89$, $v_0^I = 1.25$, and $\sigma_0^E = \sigma_0^I = 0.0003$, the connectivity parameters $b_E^E = 0.5$, $b_I^E = 0.75$, $b_I^I = 0.25$, $b_I^I = 0.5$, $D_I^E = D_I^I = D_I^I = 0$, and with refractory states ($M_\alpha(t) = N_\alpha(t - \tau_\alpha)$) where $\tau = 0.025$. We observe that if there is a transmission delay between excitatory neurons $D_E^E = 0.1$, the blow-up phenomenon is avoided. Top: Firing rates. Middle: Refractory states. Bottom: Probability densities.
Figure 7: Numerical analysis of the stability in the case of three steady states for the system (1.1). If $b_I^E = 7$, $b_I^I = 2$, $b_E^I = 0.01$, $\tau_E = \tau_I = 0.2$ and $b_I^E = 3$, there are three steady states (see Fig. 1). Top: Initial conditions $\rho_0^\alpha - 1, 2, 3$ given by the profile (3.2), where $N_\alpha$ are approximations of the stationary firing rates, and evolution of densities 2 and 3 after some time. Middle: Evolution of the excitatory firing rates and the refractory states. Bottom: Evolution of the inhibitory firing rates and the refractory states.

We observe that the lowest steady state is stable and the other two are unstable.
Figure 8: Numerical analysis of the stability in the case of three steady states for the system (1.1). If $b_f^E = 7$, $b_f^I = 2$, $b_f^E = 0.01$, $\tau_E = 0.3$, $\tau_I = 0.2$ and $b_f^E = 3$, there are three steady states (see Fig. 1). Top: Initial conditions $\rho_0^\alpha - 1, 2, 3$ given by the profile (3.2), where $N_\alpha$ are approximations of the stationary firing rates, and evolution of densities 2 and 3 after some time. Middle: Evolution of the excitatory firing rates and the refractory states. Bottom: Evolution of the inhibitory firing rates and the refractory states. We observe that the lowest steady state is stable and the other two are unstable.
Figure 9: System (1.5) (only one average-excitatory population) presents periodic solutions, if there is a transmission delay. We consider initial data (3.1) with $\sigma_0 = 0.0003$, the connectivity parameter $b = 1.5$, the transmission delay $D = 0.1$, $v_{ext} = 0$ and with refractory states ($M(t) = \frac{R(t)}{\tau}$), where $\tau = 0.025$ and $R(0) = 0.2$. Periodic solutions appear if the initial condition is concentrated enough around the threshold potential Top: $v_0 = 1.83$. Botton: $v_0 = 1.5$. 
Figure 10: System (1.5) (only one average-inhibitory population) presents periodic solutions, if there is a transmission delay. We consider initial data (3.1) with $\sigma_0 = 0.0003$, the connectivity parameter $b = -4$, the transmission delay $D = 0.1$, and with refractory states ($M(t) = \frac{R(t)}{\tau}$), where $\tau = 0.025$ and $R(0) = 0.2$.

Periodic solutions appear if the initial condition is concentrated enough around the threshold potential, but even if the initial datum is far from the threshold and the $v_{ext}$ is large. Top: $v_0 = 1.83$, $v_{ext} = 20$. Middle: $v_0 = 1.5$, $v_{ext} = 20$. Bottom: $v_0 = 1.5$, $v_{ext} = 0$. 


Figure 11: System (1.5) (only one average-inhibitory population) presents periodic solutions, if there is a transmission delay. We consider initial data (3.2) with $N = 3.669$, the connectivity parameter $b = -4$, the transmission delay $D = 0.1$, $v_{ext} = 20$ and with refractory states $(M(t) = R(t)\tau)$, where $\tau = 0.025$ and $R(0) = 0.091725$.

Periodic solutions also appear if the initial condition (top right) is very close to the unique equilibrium when $v_{ext}$ is large. Indeed, for this parameter space, solutions always converge to the same periodic solution. Top: Description of the unique steady state. Left: $F(N) = N(I(N) + \tau)$ crosses with the constant function 1 giving the unique $N_\infty$. Right: Unique steady state given by the profile (3.2) with firing rate $N = 3.669$. Middle: Evolution of the firing rate and the refractory state for the solution with initial data given by (3.2) with firing rate $N = 3.669$. Bottom: Influence of $v_{ext}$ in the behaviour of the system.
Figure 12: Comparison between $R(t)$ and $N(t)$ for $M(t) = \frac{R(t)}{\tau}$ and $M(t) = N(t - \tau)$. Top: initial data (3.1) with $v_0 = 1.83$ and $\sigma_0 = 0.0003$, the connectivity parameter $b = -4$, the transmission delay $D = 0.1$, $\tau = 0.025$, $R(0) = 0.2$ and $v_{\text{ext}} = 20$. Middle: parameter space of Fig. 2, bottom. The qualitative behavior is the same for both models, even the solutions seem to be hardly the same.
We consider initial data \( v_0^E = v_0^I = 1.25 \) and \( \sigma_0^E = \sigma_0^I = 0.0003 \), \( v_{ext} = 20 \) and the connectivity parameters \( b_{E}^E = 0.5 \), \( b_{E}^I = 0.75 \), \( b_{I}^I = 4 \), \( b_{I}^E = 1 \) and with refractory states \( (M_\alpha(t) = N_\alpha(t - \tau_\alpha)) \) where \( \tau_\alpha = 0.025 \). Top: Time evolution of the excitatory and inhibitory firing rates. Bottom: Time evolution of the excitatory and inhibitory refractory states.

4 Conclusions and open problems

In this work, we have extended the results presented in [4, 5, 6] to a general network with two populations (excitatory and inhibitory) with transmission delays between the neurons, and where the neurons remain in a refractory state for a certain time. From an analytical point of view we have explored the number of steady states in terms of the model parameters (Theorem 2.1), the long time behaviour for small connectivity parameters (Theorem 2.3), and blow-up phenomena if there is not a transmission delay between excitatory neurons (Theorem 2.5).

Besides analytical results, we have presented a numerical resolutor for this model (1.1), based on high order flux-splitting WENO schemes and an explicit third order TVD Runge-Kutta method, in order to describe the wide range of phenomena displayed by the network: blow-up, asynchronous/synchronous solutions and instability/stability of the steady states. The solver also allows to observe the time evolution of not only the firing rates and refractory states, but also of the probability distributions of the excitatory and inhibitory populations.

The resolutor was used to illustrate the result of Theorem 2.5 as long as the transmission delay of the excitatory to excitatory synapses is zero \( (D_{E}^E = 0) \), blow-up phenomena appear in the full NNLIF model, even if there are nonzero transmission delays in the rest of the synapses.

We remark that the numerical results suggest that blow-up phenomena disappear when the excitatory to excitatory transmission delay is nonzero, and the solutions may tend to a steady state or to a synchronous state. In the case of only one average-inhibitory population the behavior of the solutions
after preventing a blow-up phenomenon seems to depend on the strength of the external synapses $v_{\text{ext}}$. Furthermore, we have also observed periodic solutions for small values of the excitatory connectivity parameter combined with an initial data far from the threshold potential. Thus, synchronous solutions are not a direct consequence of having avoided the blow-up phenomenon.

Our numerical study is completed with the stability analysis of the steady states, when the network presents three of them. In our simulations, we do not observe bistability phenomena since the two upper stationary firing rates are unstable, while the lowest one is stable.

Finally, to our knowledge, the numerical solver presented in this paper is the first deterministic solver to describe the behavior of the full NNLIF system involving all the characteristic phenomena of real networks. Including all relevant phenomena is essential to explore some open problems, as for instance, the analytical proof of the global existence of solution when there is a nonzero excitatory to excitatory transmission delay, the reasons why solutions sometimes tend to a steady state and sometimes to a synchronous state, and an analytical study of the stability of the steady states when the connectivity parameters are not small.

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