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A review about nonlinear noisy leaky integrate and fire models for neural networks

Abstract. In these notes we analyse a family of self-contained mean field systems, called nonlinear noisy leaky integrate and fire (NNLIF) models, which describe the activity of neural networks by means of the membrane potential. These models are based on nonlinear systems of PDEs of Fokker-Planck type. We study the wide range of phenomena that appear in this kind of models: blow-up/global existence, asynchronous/synchronous solutions, instability/stability of the steady states This review is intended to collect the main results of papers [8, 10, 11, 12, 13] in collaboration with José A. Carrillo, Benoît Perthame, Pierre Roux, Ricarda Schneider and Delphine Salort; as well as other results presented in [6, 7, 14, 15, 18, 19].

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1 - Introduction

Knowing the functioning of the human mind is one of the great challenges of today. In the 19th century Santiago Ramón y Cajal pointed the neuron as the primary functional unit of the nervous system. Much has been advanced ever since, from the point of view of different scientific disciplines, but not enough to discover how the brain works precisely. Over the last decades, this issue has been also tackled by mathematicians. There are a lot of types of mathematical models to describe the behaviour of neural networks. One of the simplest self-contained mean-field models considered to this purpose is the Nonlinear Noisy Leaky Integrate and Fire (NNLIF) model, which is based on nonlinear systems of PDEs of Fokker-Planck type. These models describe the neurons at the level of their membrane potential, and take into account the following neural phenomena:

- Neural networks are composed of excitatory and inhibitory neurons. Excitatory/inhibitory neurons increase/decrease the synaptic currents of other neurons, respectively.
- When the membrane potential reaches a *threshold value* V_F , the neurons emit an action potential, also called *spike*, as a result of depolarization of their membrane, and their voltage values return to a *reset value* V_R ($V_R < V_F$).
- Between the emission and reception of the spikes among neurons there are some transmission delays.

- The neurons remain in a refractory state; during a certain time they do not respond to stimuli. This period of time is called *refractory period*.

A complete derivation of the NNLIF models can be found in [5, 6, 7]. In the rest of this section we present the NNLIF models analyzed in this review.

1.1 - General model

For a membrane potential $v \in (-\infty, V_F]$, the general structure of this kind of models can be sketched as follows:

$$(1) \quad \frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v} [h(v, N(t-D))p(v, t)] - a(N(t-D)) \frac{\partial^2 p}{\partial v^2}(v, t) = M_\tau(t) \delta_{V_R}(v),$$

$$(2) \quad \frac{dR(t)}{dt} = N(t) - M_\tau(t),$$

$$(3) \quad N(t) := -a(N) \frac{\partial p}{\partial v}(V_F, t) \geq 0,$$

where $p(v, t)$ represents the limiting probability density of active neurons with a membrane potential v at time t , when the total number of neurons of the network, n , goes to infinity. The most general model splits the network in two populations: excitatory and inhibitory, and in that case $p(v, t) = (\rho_E, \rho_I)(v, t)$ with $\rho_E(v, t)$ the limiting probability density of active excitatory neurons with voltage v at time t , and $\rho_I(v, t)$ the limiting probability density of active inhibitory neurons.

At microscopic level the leaky integrate and fire model describes the behaviour of the neurons, in terms of Stochastic Differential Equations (SDEs) [6, 7, 37]. The randomness comes from the stochastic spike trains of all neurons in the network. Then, the Fokker-Planck equation (1) is obtained as a mean-field limit, assuming that these spike trains follow Poisson processes and a diffusion approximation for the synaptic current (generated by spike trains). It becomes exact in the infinitely large network limit if the synaptic strengths are scaled appropriately with the network sizes, see [37]. Therefore, the drift $\frac{\partial}{\partial v} [h(v, N(t-D))p(v, t)]$ and the diffusion terms $-a(N(t-D)) \frac{\partial^2 p}{\partial v^2}(v, t)$, produce a nonlinear system because take into account the firing rates of the neurons $N(t)$ defined by (3), at the delayed time $t-D$, where D is the transmission delay between the emission and reception of the spikes among neurons. The diffusion term represents the noisy of the model, caused by the diffusion approximation of the stochastic spike trains.

The right hand side of the equation (1) describes the neurons coming back to the reset value V_R when they arrive to the threshold value V_F . Equation (2)

models the evolution on time of the limiting proportion of neurons which do not respond to stimuli during a time τ , called refractory period. This proportion of neurons in a refractory state is denoted by $R(t)$ and it depends on $M_\tau(t)$. We will consider two different $M_\tau(t)$: $M_\tau(t) = N(t - \tau)$ and $M_\tau(t) = \frac{R(t)}{\tau}$. The proportion of neurons in a refractory state can also be split in two terms, $R = (R_E, R_I)$, if excitatory and inhibitory neurons are considered as different populations.

Given the initial data: $p^0(v) = p(0, v)$ and $R^0 = R(0)$, the system (1)-(2) satisfies the conservation law:

$$(4) \quad \int_{-\infty}^{V_F} p(t, v) dv + R(t) = \int_{-\infty}^{V_F} p^0(v) dv + R^0 = 1,$$

because the total number of neurons remains constant for all time t in the existence interval $[0, T)$.

In the following we present the exact expressions of all the terms in (1)-(2) for the different NNLIF models analysed in these notes. Let us start with the most general model, which takes into account all the phenomena previously mentioned. In that case Equation (1) is a system [6, 13]:

$$(5) \quad \begin{aligned} & \frac{\partial \rho_I}{\partial t}(v, t) + \frac{\partial}{\partial v} [h^I(v, N_E(t - D_E^I), N_I(t - D_I^I)) \rho_I(v, t)] \\ & \quad - a_I(N_E(t - D_E^I), N_I(t - D_I^I)) \frac{\partial^2 \rho_I}{\partial v^2}(v, t) = M_{\tau_I}(t) \delta_{V_R}(v), \\ & \frac{\partial \rho_E}{\partial t}(v, t) + \frac{\partial}{\partial v} [h^E(v, N_E(t - D_E^E), N_I(t - D_I^E)) \rho_E(v, t)] \\ & \quad - a_E(N_E(t - D_E^E), N_I(t - D_I^E)) \frac{\partial^2 \rho_E}{\partial v^2}(v, t) = M_{\tau_E}(t) \delta_{V_R}(v). \end{aligned}$$

There are two PDEs because the neural network are composed of excitatory and inhibitory neurons. Therefore, $p(v, t) = (\rho_E, \rho_I)(v, t)$ in (1) and the probability densities $\rho_\alpha(t, v)$ describe the limiting probability of a neuron of the excitatory population ($\alpha = E$) or of the inhibitory one ($\alpha = I$), with a membrane potential v at time t , when the total number of neurons of the network, n , goes to infinity. The drift and diffusion coefficients are given by

$$\begin{aligned} h^\alpha(v, N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) &:= -v + b_E^\alpha N_E(t - D_E^\alpha) - b_I^\alpha N_I(t - D_I^\alpha) \\ &\quad + (b_E^\alpha - b_E^E) v_{E,ext} \end{aligned}$$

and

$$a_\alpha(N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) := d_E^\alpha v_{E,ext} + d_E^\alpha N_E(t - D_E^\alpha) + d_I^\alpha N_I(t - D_I^\alpha),$$

respectively, and are delayed in terms of the synaptic delays D_E^α and D_I^α .

The model is nonlinear because the mean firing rates N_α obey to

$$N_\alpha(t) = -a_\alpha(N_E(t), N_I(t)) \frac{\partial \rho_\alpha}{\partial v}(V_F, t) \geq 0 \quad \alpha = E, I.$$

The rest of parameters of the model (d_E^α , d_I^α , $v_{E,ext}$, b_E^α and b_I^α) are non negative constants [6, 12, 13]. The main parameters are the connectivities of the network b_E^α and b_I^α and the synaptic delay between excitatory neurons D_E^E .

As we said before, the right hand sides in (5) describe the fact that when neurons reach the threshold potential V_F , they emit a spike over the network, reset their membrane potential to the reset value V_R and remain some time in a refractory period τ_α . The limiting proportion of neurons that do not respond to stimuli is represented by $R_\alpha(t)$, for each $\alpha = E, I$. As it was indicated in (2) these proportions satisfy

$$(6) \quad \frac{dR_\alpha(t)}{dt} = N_\alpha(t) - M_{\tau_\alpha}(t), \quad \forall \alpha = E, I.$$

Two different $M_{\tau_\alpha}(t)$ can be considered: $M_{\tau_\alpha}(t) = N_\alpha(t - \tau_\alpha)$ [6] and $M_{\tau_\alpha}(t) = \frac{R_\alpha(t)}{\tau_\alpha}$ [10]. Therefore, the system (5) is completed with two ODEs for $R_\alpha(t)$, and with Dirichlet boundary conditions:

$$\rho_\alpha(-\infty, t) = 0 \quad \text{and} \quad \rho_\alpha(V_F, t) = 0,$$

and initial data: $R_\alpha(0) = R_\alpha^0 \geq 0$ and $\rho_\alpha(v, 0) = \rho_\alpha^0(v) \geq 0$, $\alpha = E, I$. We point out that the conservation law (4) for the system (5)-(6) is written as

$$(7) \quad \int_{-\infty}^{V_F} \rho_\alpha(t, v) dv + R_\alpha(t) = \int_{-\infty}^{V_F} \rho_\alpha^0(v) dv + R_\alpha^0,$$

for all time t in the existence interval $[0, T)$, and for each $\alpha = E, I$.

1.2 - Simplifications of the model

The model (5)-(6) is quite complex and its mathematical analysis is difficult. Therefore, firstly, it was necessary to study some simplifications.

1.2.1 - Two populations without transmission delays or refractory states

One simplification is to consider two populations: excitatory and inhibitory, but without transmission delays between the neurons and without refractory

state. In this case the model is reduced to a system of two PDEs:

$$(8) \quad \frac{\partial \rho_I}{\partial t}(v, t) + \frac{\partial}{\partial v}[h^I(v, N_E, N_I)\rho_I(v, t)] - a_I(N_E, N_I)\frac{\partial^2 \rho_I}{\partial v^2}(v, t) = N_I(t)\delta_{V_R}(v),$$

$$\frac{\partial \rho_E}{\partial t}(v, t) + \frac{\partial}{\partial v}[h^E(v, N_E, N_I)\rho_E(v, t)] - a_E(N_E, N_I)\frac{\partial^2 \rho_E}{\partial v^2}(v, t) = N_E(t)\delta_{V_R}(v).$$

In this way, for $\alpha = I, E$, the drift and the diffusion terms in (8) are not delayed:

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

$$a_\alpha(N_E(t), N_I(t)) = d_E^\alpha v_{E,ext} + d_E^\alpha N_E(t) + d_I^\alpha N_I(t),$$

and there are no refractory states, it means that all the neurons respond to stimuli just after they spike, and thus the right hand sides of the equations are written in terms of the mean firing rates:

$$N_\alpha(t) = -a_\alpha(N_E(t), N_I(t))\frac{\partial \rho_\alpha}{\partial v}(V_F, t).$$

1.2.2 - Only one population without transmission delays or refractory states

Even so the model (8) is complex and other reduction was considered [7, 8]; only one population in average-excitatory or average-inhibitory, without transmission delays between the neurons, and without refractory state:

$$(9) \quad \frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v}[h(v, N(t))p(v, t)] - a(N(t))\frac{\partial^2 p}{\partial v^2}(v, t) = \delta_{V_R}(v)N(t),$$

where $h(v, N) = -v + bN$ and $a(N) = a_0 + a_1N$ with $a_0 > 0$, $a_1 \geq 0$. In this model the connectivity parameter b describes the networks in terms of their nature;

- if on average the neurons of the network are excitatory b is positive, and
- if on average are inhibitory b is negative.

So in this sense we consider only one population on average-excitatory or average-inhibitory depending of the sign of the connectivity parameter b . Again the model (9) is nonlinear because the mean firing rate is computed in terms of the derivate with respect v of p at the border V_F :

$$N(t) := -a(N(t))\frac{\partial p}{\partial v}(V_F, t) \geq 0.$$

This simplest model can be completed considering refractory states as in (5) [10].

1.3 - Random discharge potential model

A modification of system (9) assuming some randomness on the discharge potential was proposed in [10]

$$(10) \quad \frac{\partial \rho}{\partial t} + \frac{\partial}{\partial v} [(-v + bN)\rho] - a(N) \frac{\partial^2 \rho}{\partial v^2} + \phi_\varepsilon(v)\rho = N(t)\delta_{V_R}(v),$$

where in this case the voltage v is considered in the whole $\mathbb{R}$ ($v \in \mathbb{R}$) and the mean firing rate is given by

$$N(t) = \int_{-\infty}^{+\infty} \phi_\varepsilon(v)\rho(v, t) dv,$$

in terms of the discharge rate at potential v , $\phi_\varepsilon(v)$. Several choices of ϕ_ε can be considered: $\phi_\varepsilon(v) = \frac{1}{\varepsilon}(v - V_F)_+$ or $\phi_\varepsilon(v) = \frac{1}{\varepsilon}\mathbf{1}_{\{v > V_F\}}$. Model (10) takes into account the refractory state adding a ODE for the refractory neurons as in Equation (5).

This family of NNLIF models was studied in [6, 7, 8, 10, 11, 12, 13, 14, 15] and references therein. In these notes we give a overview of the main results obtained in these works. To be more precise, in Section 2 we analyse the blow up phenomenon and the importance of the transmission delay between excitatory neurons to avoid it, which gives the key to prove global existence of the solutions. The shape and number of steady states and the long time behaviour for weak solutions of the models are described in Section 3. In Section 4 we show some numerical experiments which help to understand the models in the cases where the theoretical study do not get. Finally, the conclusions and open problems are included in Section 5.

Before explaining the main properties of the solutions of the NNLIF models in the following sections, let us mention that these properties can be related to neurophysiological phenomena. For instance, the blow-up can be interpreted as a synchronization of a part of the network, maybe associated with epilepsy. The presence of several steady states, with multi-stable phenomena, could be related, for example, to visual perception and decision making [2, 24]. And periodic or oscillatory states are also related to neurophysiological phenomena [38], for instance those observed during cortical processing [24, 26].

2 - Blow-up versus global existence

The blow up phenomenon for the simplest model (9) was proved in [8]. This result was very novel since this kind of models is thoroughly used by

neuroscientific but never observed its blow-up.

Before we present that theorem, we recall the notion of weak solution.

Definition 2.1 (Definition 2.1 in [8]). We say that a pair of nonnegative functions (p, N) with $p \in L^\infty(\mathbb{R}^+; L^1_+(-\infty, V_F))$, $N \in L^1_{\text{loc},+}(\mathbb{R}^+)$ is a weak solution of (9) if for any test function $\phi(v, t) \in C^\infty((-\infty, V_F] \times [0, T])$ such that $\frac{\partial^2 \phi}{\partial v^2}, v \frac{\partial \phi}{\partial v} \in L^\infty((-\infty, V_F) \times (0, T))$, we have

$$(11) \quad \int_0^T \int_{-\infty}^{V_F} p(v, t) \left[-\frac{\partial \phi}{\partial t} - \frac{\partial \phi}{\partial v} h(v, N) - a \frac{\partial^2 \phi}{\partial v^2} \right] dv dt = \int_0^T N(t) [\phi(V_F, t) - \phi(V_R, t)] dt \\ + \int_{-\infty}^{V_F} p^0(v) \phi(0, v) dv - \int_{-\infty}^{V_F} p(v, T) \phi(T, v) dv.$$

In particular, choosing test functions of the form $\psi(t)\phi(v)$, for all $\phi(v) \in C^\infty((-\infty, V_F])$ such that $v \frac{\partial \phi}{\partial v} \in L^\infty((-\infty, V_F))$, a weak solution of (9) satisfies

$$(12) \quad \frac{d}{dt} \int_{-\infty}^{V_F} \phi(v) p(v, t) dv = \int_{-\infty}^{V_F} \left[\frac{\partial \phi}{\partial v} h(v, N) + a \frac{\partial^2 \phi}{\partial v^2} \right] p(v, t) dv \\ + N(t) [\phi(V_F, t) - \phi(V_R, t)],$$

in the distributional sense.

Analogous definitions for the rest of models described in the previous section can be found in [10, 12, 13].

Once we know the notion of weak solution, we can study the blow up phenomenon. More specifically, the theorem is as follows:

Theorem 2.1 (Theorem 2.2 of [8]). *Assuming:*

- $h(v, N) + v \geq bN$, $0 < a_m \leq a(N)$ for all $-\infty < v \leq V_F$ and all $N \geq 0$.
- $b > 0$ (this means an average-excitatory network),

if the initial data is concentrated enough around $v = V_F$, then there are no global-in-time weak solutions to (9).

In other words, this theorem shows that for an average-excitatory network the weak solutions can blow up for two different reasons:

- For b fixed: the initial condition is concentrated enough around V_F , in the sense that satisfies

$$(13) \quad \int_{-\infty}^{V_F} e^{\mu v} p^0(v) dv \geq \frac{e^{\mu V_F}}{b\mu} \quad \text{choosing} \quad \mu > \max\left(\frac{V_F}{a_m}, \frac{1}{b}\right).$$

- For p^0 fixed: the connectivity parameter b is large enough.

We note that the assumptions for the drift and the diffusion coefficients only indicate a more general drift term than in model (9), and a non vanish diffusion coefficient. The proof is given here since it is simple and useful to prove the blow up at microscopic level in similar models, see for instance [18, 25].

Proof. We choose $\phi(v) = e^{\mu v}$ with $\mu > \max\left(\frac{V_F}{a_m}, \frac{1}{b}\right)$, then a weak solution satisfies (see (12))

$$\begin{aligned} \frac{d}{dt} \int_{-\infty}^{V_F} \phi(v) p(v, t) dv &\geq \mu \int_{-\infty}^{V_F} (bN(t) - v) \phi(v) p(v, t) dv \\ &\quad + \mu^2 a_m \int_{-\infty}^{V_F} \phi(v) p(v, t) dv + N(t) (\phi(V_R) - \phi(V_F)) \\ &\geq \mu [bN(t) + \mu a_m - V_F] \int_{-\infty}^{V_F} \phi(v) p(v, t) dv - N(t) \phi(V_F). \end{aligned}$$

Thus, denoting $M_\mu(t) := \int_{-\infty}^{V_F} \phi(v) p(v, t) dv$, we obtain

$$\frac{d}{dt} M_\mu(t) \geq \mu [bN(t) + \mu a_m - V_F] M_\mu(t) - N(t) \phi(V_F)$$

and by Gronwall's lemma:

$$M_\mu(t) \geq e^{\mu \int_0^t (bN(s) + \mu a_m - V_F) ds} \left(M_\mu(0) - \phi(V_F) \int_0^t N(s) e^{-\mu \int_0^s (bN(z) + \mu a_m - V_F) dz} ds \right).$$

We can bound the right hand side of the previous inequality and obtain

$$M_\mu(t) \geq e^{\mu \int_0^t (bN(s) + \mu a_m - V_F) ds} \left(M_\mu(0) - \frac{\phi(V_F)}{\mu b} \right).$$

And this inequality produces a contradiction if $K := \left(M_\mu(0) - \frac{\phi(V_F)}{\mu b} \right) > 0$, because the exponential momentum $M_\mu(t)$ is bounded from below by $K e^{\mu(\mu a_m - V_F)t}$ with $\mu(\mu a_m - V_F) > 0$, since $bN(s) \geq 0$, but, in other hand, since $p(v, t)$ is a probability density, $\int_{-\infty}^{V_F} p(v, t) dv = \int_{-\infty}^{V_F} p^0(v) dv = 1$, and $\mu > 0$ then

$$M_\mu(t) = \int_{-\infty}^{V_F} \phi(v) p(v, t) dv \leq e^{\mu V_F},$$

leading to the contradiction. Therefore, to conclude the proof we only need to guarantee the non-negativity of K . And this holds, as it was sketched out before, if:

- For b fixed: the initial condition is concentrated enough around V_F , in the sense that satisfies

$$M_\mu(0) \geq \frac{e^{\mu V_F}}{b\mu},$$

which is true, for instance, if the initial datum is an approximation of a Dirac mass at V_F , because $b\mu > 1$.

- For p^0 fixed: the connectivity parameter b is large enough, such that:

$$b \geq \frac{e^{\mu V_F}}{M_\mu(0)\mu}. \quad \square$$

We also developed a numerical study of this phenomenon in [8], that it provided the key to understand the origin of the explosion. These numerical experiments showed that the solutions blow up if the firing rates diverge at finite time. Later this fact was proved in [15]. More specifically, the authors gave the following criterion to determine the maximum time of existence for the simplest model (9):

Criterion 2.1 (Theorem 1.1 of [15]). *The maximum time of existence of the solutions of (9) is*

$$T^* := \text{Sup}\{t \geq 0 : N(t) < \infty\}.$$

Moreover,

- For the average-inhibitory case ($b < 0$) $T^* = \infty$, therefore the solutions do not blow up.

- For the average-excitatory case ($b > 0$), since blow up was proved in [8], $T^* < \infty$.

After these two works [8, 15] the blow up phenomenon was also proved at the microscopic level in [18, 19] and presented well-posedness results. On the other hand, we proved that the explosion is avoided if a random discharge potential is considered [10]. To be more precise, we proved that the firing rate of model (10) is bounded and therefore, if the previous criterion holds, there is global existence. Moreover, we proved that the inclusion of the refractory period in the simplest model (9) does not prevent the blow-up [10].

Finally, we studied this phenomenon in the full NNLIF model (5) [12, 13]. And we proved that the system can blow-up in finite time if there is not transmission delay between excitatory neurons, $D_E^E = 0$ in two cases (see Theorem 3.5 in [13]):

- For initial data fixed and $b_E^E > 0$ large enough.
- For $b_E^E > 0$ fixed, when the initial datum is concentrated enough around V_F .

2.1 - Transmission delays between excitatory neurons avoid the blow-up

The numerical experiments of [13] show that the transmission delay between excitatory neurons is the only ingredient to avoid the blow-up of this kind of models (with a fixed threshold potential). With this intuition we have proved the global existence of solutions of the delayed NNLIF model [11]:

$$(14) \quad \frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v} [h(v, N(t-D)) p(v, t)] - a(N(t-D)) \frac{\partial^2 p}{\partial v^2}(v, t) = \delta_{V_R}(v) N(t).$$

In general, there is global existence when a synaptic delay between excitatory neurons is taken into account. In other words, $D_E^E > 0$ avoids the blow-up. The main difficulty to prove the global existence arises in the average-excitatory case. For the inhibitory case, the criterion for the maximal time of existence (Criterion 2.1) extends the local existence to the global existence of solution, because the firing rate is proved to be uniformly bounded for every time. However, in the excitatory case, this procedure is not possible, since the firing rate sometimes is not uniformly bounded, as it was numerically shown in [13]. To overcome this obstacle we found a bound for the firing rate, at every time, by means of super solutions. The steps of the proof of the global existence of solution are the following:

1. *Rewriting as a Stefan like problem.* We adapt the changes of variables used in [15] to our model, and rewrite (14) as a free boundary Stefan-like problem with a nonstandard right hand side consisting of a Dirac Delta source

term. More specifically, for $\tau > 0$, $x < s(\tau) := -b \int_0^\tau N(s-D)\alpha(s) ds$,

where $D > 0$ and $\alpha(\tau) = \frac{1}{\sqrt{2\tau+1}}$, the equation (14) is rewritten as follows:

$$\begin{cases} u_t(x, \tau) = u_{xx}(x, \tau) + M(t)\delta_{s_1(\tau)}(x), \\ s_1(\tau) := s(\tau) + \frac{V_R}{\alpha(\tau)}, \\ M(\tau) = -u_x(s(\tau), \tau), \\ N(t) = N(0), & t \in (-D, 0], \\ u(-\infty, \tau) = u(s(\tau), \tau) = 0, \\ u(x, 0) = u_I(x), & x < 0. \end{cases}$$

We observe that the transmission delay between excitatory neurons becomes the system linear for t less than the delay D , and consequently the boundary of the Stefan-like problem fixed for short times.

2. *Local existence by means of an integral formulation.* The proof of local existence and uniqueness of classical solutions is obtained by means a fixed point argument for the integral formulation

$$\begin{aligned} M(t) = & -2 \int_{-\infty}^{V_R} G(s(t), t, \xi, 0) u'_I(\xi) d\xi - 2 \int_{V_R}^0 G(s(t), t, \xi, 0) u'_I(\xi) d\xi \\ & + 2 \int_0^t M(\tau) G_x(s(t), t, s(\tau), \tau) d\tau - 2 \int_0^t M(\tau) G_x(s(t), t, s_1(\tau), \tau) d\tau, \end{aligned}$$

where G is the Green's function for the heat equation on the real line

$$G(x, t, \xi, \tau) = \frac{1}{[4\pi(t-\tau)]^{\frac{1}{2}}} e^{-\frac{|x-\xi|^2}{4(t-\tau)}}.$$

We note that, in terms of the new variables, M is the equivalent of the firing rate N .

Finally, with the local existence and uniqueness of M we obtain the local existence and uniqueness of classical solutions of the Stefan-like problem,

using Duhamel's formula

$$\begin{aligned} u(x, t) &= \int_{-\infty}^{V_R} G(x, t, \xi, 0) u_I(\xi) d\xi + \int_{V_R}^0 G(x, t, \xi, 0) u_I(\xi) d\xi \\ &\quad - \int_0^t M(\tau) G(x, t, s(\tau), \tau) d\tau + \int_0^t M(\tau) G(x, t, s_1(\tau), \tau) d\tau, \end{aligned}$$

and consequently, the local existence and uniqueness for NNLIF model.

3. *Maximal time of existence.* The Criterion 2.1 is extended to the delayed NNLIF model (14).
4. *Super solutions and global existence result.* Using super-solutions, we show that for every maximal time of existence the firing rate of the solution is bounded. Therefore, the criterion proved in the previous step gives the global existence.

We recall that for $T \in \mathbb{R}_+$, $D \geq 0$ $(\bar{\rho}, \bar{N})$ is said to be a (classical) super solution to the delayed NNLIF model (14) on $(-\infty, V_F] \times [0, T]$ if for all $t \in [0, T]$ we have $\bar{\rho}(V_F, t) = 0$ and

$$\partial_t \bar{\rho} + \partial_v [(-v + b\bar{N}(t - D))\bar{\rho}] - a\partial_{vv}\bar{\rho} \geq \delta_{v=V_R}\bar{N}(t),$$

$$\bar{N}(t) = -a\partial_v \bar{\rho}(V_F, t),$$

on $(-\infty, V_F] \times [0, T]$ in the distributional sense and on $((-\infty, V_F] \setminus V_R) \times [0, T]$ in the classical sense, with arbitrary values for $\bar{N}$ on $[-D, 0)$.

We find a super solution $\bar{\rho}$ on $[0, D]$ of the form $\bar{\rho}(v, t) = e^{\xi t} f(v)$, where ξ is large enough and f is a carefully selected function [11], which provides a control over the firing rate. Due to the uniqueness of the solution, for every maximal time of existence T we can translated it to the interval $[0, D]$, and in this way, the previous super solution allows the control of the firing rate, and therefore provokes a contradiction with the criterion of maximal time of existence.

3 - Steady states and long time behaviour

The steady states of the NNLIF models $(p_\infty, N_\infty, R_\infty)$, in terms of their general structure given by (1)-(3), are solutions of

$$\begin{aligned} \frac{\partial}{\partial v} [h(v, N_\infty) p_\infty(v)] - a(N_\infty) \frac{\partial^2 p_\infty}{\partial v^2}(v) &= M_\tau(R_\infty) \delta_{V_R}(v), \\ M_\tau(R_\infty) &= N_\infty. \end{aligned}$$

Using the boundary conditions, previous system can be rewritten as

$$-h(v, N_\infty) p_\infty(v) + a(N_\infty) \frac{\partial p_\infty}{\partial v}(v) + N_\infty H(v - V_R) = 0,$$

in terms of the Heaviside function H . Therefore,

$$p_\infty(v) = \frac{N_\infty}{a(N_\infty)} e^{-\frac{h(v, N_\infty)^2}{2a(N_\infty)}} \int_v^{V_F} e^{\frac{h(v, N_\infty(w))^2}{2a(N_\infty(w))}} H(w - V_R) dw,$$

but this is not an explicit expression for the steady states because the model is nonlinear, and N_∞ depends on p_∞ . However, taking into account the conservation law (4), we obtain the following implicit equation for N_∞ , using that $R_\infty = \tau N_\infty$ ($\tau \geq 0$, where $\tau = 0$ means there is not refractory state),

$$\frac{N_\infty}{a(N_\infty)} \int_{-\infty}^{V_F} e^{-\frac{h(v, N_\infty)^2}{2a(N_\infty)}} \int_v^{V_F} e^{\frac{h(v, N_\infty(w))^2}{2a(N_\infty(w))}} H(w - V_R) dw dv + \tau N_\infty = 1,$$

or equivalently,

$$(15) \quad \frac{1}{a(N_\infty)} \int_{-\infty}^{V_F} e^{-\frac{h(v, N_\infty)^2}{2a(N_\infty)}} \int_v^{V_F} e^{\frac{h(v, N_\infty(w))^2}{2a(N_\infty(w))}} H(w - V_R) dw dv + \tau = \frac{1}{N_\infty}.$$

These equations are implicit because the right hand side of (15) depends on N_∞ . Then, if we denote by

$$I(N_\infty) := \frac{1}{a(N_\infty)} \int_{-\infty}^{V_F} e^{-\frac{h(v, N_\infty)^2}{2a(N_\infty)}} \int_v^{V_F} e^{\frac{h(v, N_\infty(w))^2}{2a(N_\infty(w))}} H(w - V_R) dw dv + \tau,$$

the equation (15) is rewritten as

$$I(N_\infty) = \frac{1}{N_\infty}.$$

In the linear case the function I is constant and consequently there is a unique steady states. However, the nonlinear case is more complicated and the number of steady states is determinated computing the number of crossings between the functions $I(N)$ and $\frac{1}{N}$. Even in the simplest model (9), with a only one population and without refractory states, this issue is arduous. And it requires studying the properties of I , which can be summed up in:

1. $I(0) < \infty$.
2. If $b < 0$ (average-inhibitory networks):
 - (a) I is an increasing strictly convex function,
 - (b) and $\lim_{N \rightarrow \infty} I(N) = \infty$.
3. If $b > 0$ (average-excitatory networks):
 - (a) I is a decreasing convex function,
 - (b) $\lim_{N \rightarrow \infty} I(N) = 0$,
 - (c) and $\lim_{N \rightarrow \infty} N I(N) = \frac{V_F - V_R}{b}$. So when $N \rightarrow \infty$:
 - i. $I(N) < \frac{1}{N}$ if $\frac{V_F - V_R}{b} < 1$.
 - ii. $I(N) > \frac{1}{N}$ if $\frac{V_F - V_R}{b} > 1$.

Roughly speaking, these properties provide:

- Average-inhibitory networks have a unique steady state.
- Average-excitatory networks
 - with high connectivity have not steady state.
 - with small connectivity have a unique steady state.
 - with intermediate connectivity have at least one or at least two steady states.

The precise formulation of this result was presented in [8] as follows:

Theorem 3.1 (Theorem 3.1 in [8]). *Assume $h(v, N) = bN - v$ and $a(N) = a_0$ is constant.*

- i) *For $b < 0$ and $b > 0$ small enough there is a unique steady state to (9).*

ii) *Under either the condition*

$$(16) \quad 0 < b < V_F - V_R,$$

or the condition

$$(17) \quad 0 < 2a_0b < (V_F - V_R)^2 V_R,$$

then there exists at least one steady state solution to (9).

iii) *If both (17) and $b > V_F - V_R$ hold, then there are at least two steady states to (9).*

iv) *There is no steady state to (9) under the high connectivity condition*

$$(18) \quad b > \max(2(V_F - V_R), 2V_F I(0)).$$

If the simplest model (9) takes into account the refractory period, thus there is always an odd number of steady states [10]. In particular, this means that the fact that the neurons remain some period of time inactive guarantees the existence of at least one steady state. In other words, if during some time the neurons do not respond to stimuli, the system always has steady states.

The analysis of the general system (5) follows a similar strategy, but it is more complicated since the equation (15) becomes a system (see [12, 13] for details)

$$\begin{cases} \frac{1}{N_E} = I_E(N_E, N_I), \\ \frac{1}{N_I} = I_I(N_E, N_I). \end{cases}$$

In this case the idea to obtain the number of steady states lies in the fact that for every fixed N_E there is a unique solution $N_I(N_E)$, such that

$$\frac{1}{N_I(N_E)} = I_I(N_E, N_I(N_E)),$$

and equivalently

$$N_I(N_E) I_I(N_E, N_I(N_E)) = 1.$$

Thus, the analysis of steady state is reduced to determine the number of solutions to

$$F(N_E) = 1,$$

where $F(N_E) := N_E I_E(N_E, N_I(N_E))$.

In a few words we can say that there is always an odd number of steady states, if the model takes into account the refractory states, while without refractory states for some values of the parameters the model has an even number of steady states, and in other cases there is an odd number of them [12, 13]. Some interesting situations are:

- If b_E^E is small enough then there is a unique stationary solution.
- If b_E^E is large enough and there are not refractory states, then there are no steady states.

The precise results for the general model were proved in [12, 13]:

Theorem 3.2 (Theorem 4.1 in [12] and Theorem 3.1 in [13]). *Assume that the connectivity parameters b_I^E and b_E^I do not vanish ($b_I^E, b_E^I > 0$) and a_α is independent of N_E and N_I , $a_\alpha(N_E, N_I) = a_\alpha$, for all $\alpha = E, I$. Then:*

1. *For the system (8) without refractory states:*

(a) *There is an even number of steady states or there are no steady states for (8) if*

$$(19) \quad (V_F - V_R)^2 < (V_F - V_R)(b_E^E - b_I^I) + b_E^E b_I^I - b_I^E b_E^I.$$

If b_E^E is large enough in comparison with the rest of connectivity parameters, there are no steady states. Specifically, there are no steady states if both (19) and

$$(20) \quad \max \left\{ I_1(0)2(V_F + b_I^E N_I(\bar{N}_E)), \frac{b_E^I b_I^E}{b_I^I}, 2(V_F - V_R) \right\} < b_E^E$$

are fulfilled, where

$$(21) \quad \bar{N}_E = \max \left\{ N_E^* \geq 0 : N_E^* = \frac{2(b_E^I N_I(N_E^*) + V_F)}{b_E^E} \right\}.$$

(b) *There is an odd number of steady states for (8) if*

$$(22) \quad (V_F - V_R)(b_E^E - b_I^I) + b_E^E b_I^I - b_I^E b_E^I < (V_F - V_R)^2.$$

If b_E^E is small enough in comparison with the rest of connectivity parameters, there is a unique steady state.

2. *For the system (5) with refractory states (6) there is always an odd number of steady states.*

Moreover, if b_E^E is small enough or τ_E is large enough (in comparison with the rest of parameters), then there is a unique steady state.

3.1 - Long time behaviour

In [8] we studied the long time behaviour of the simplest NNLIF model in the linear case ($b = 0$) and proved the exponential convergence to the unique steady state, by means of the entropy method. Then, in [14] this results was extended for the non linear case but with $|b|$ small (there is a unique steady state). Recently, in [11, 12, 13] we have proved the exponential convergence of the solutions to the unique steady states of the more general NNLIF models.

The idea of the entropy dissipation method [3, 4, 39] lies on the use of an entropy functional $E[t]$, which is decreasing and whose entropy production $\frac{dE[t]}{dt} (\leq 0)$ can be controlled by itself

$$(23) \quad \frac{dE[t]}{dt} \leq -\mu E[t], \quad \mu > 0.$$

Finally, using Gronwall's inequality in (23) provides the exponential convergence:

$$E[t] \leq e^{-\mu t} E(0), \quad \mu > 0.$$

Often Poincaré's inequality

$$\gamma \int_{-\infty}^{V_F} p_{\infty}(v) \left(\frac{p(v, t)}{p_{\infty}(v)} - 1 \right)^2 dv \leq \int_{-\infty}^{V_F} p_{\infty}(v) \left(\frac{\partial}{\partial v} \frac{p(v, t)}{p_{\infty}(v)} \right)^2 dv$$

helps to obtain the inequality (23).

For the simplest model (9) we considered the following entropy functional:

$$E[t] := \int_{-\infty}^{V_F} p_{\infty}(v) G \left(\frac{p(v, t)}{p_{\infty}(v)} \right) dv,$$

where G is a convex function, that in this case was chosen $G(x) = (x - 1)^2$, and p_{∞} is the unique steady state. If the refractory states are considered the entropy functional includes them:

$$E[t] := \int_{-\infty}^{V_F} \frac{(p(v, t) - p_{\infty}(v))^2}{p_{\infty}(v)} dv + \frac{(R(t) - R_{\infty})^2}{R_{\infty}}.$$

And for the general model (5) the entropy is the sum of the entropies for the

excitatory and the inhibitory populations:

$$E[t] := \int_{-\infty}^{V_F} \frac{(\rho_E(v, t) - \rho_E^\infty(v))^2}{\rho_E^\infty(v)} dv + \frac{(R_E(t) - R_E^\infty)^2}{R_E^\infty} \\ + \int_{-\infty}^{V_F} \frac{(\rho_I(v, t) - \rho_I^\infty(v))^2}{\rho_I^\infty(v)} dv + \frac{(R_I(t) - R_I^\infty)^2}{R_I^\infty}.$$

Using this entropy functional, we proved the exponential converge to the unique steady state, which is formulated as follows:

Theorem 3.3 (Theorem 3.4 in [13]). *Assume that the connectivity parameters b_i^α are small enough, the diffusion terms $a_\alpha > 0$ are constant, the transmission delays D_i^α vanish, and that the initial data (ρ_E^0, ρ_I^0) are close enough to the unique steady state $(\rho_E^\infty, \rho_I^\infty)$ to the system (5) with $M_\alpha(t) = \frac{R_\alpha(t)}{\tau_\alpha}$, ($\alpha = I, E$, $i = I, E$):*

$$E[0] < \frac{1}{2 \max(b_E^E + b_I^E, b_E^I + b_I^I)}.$$

Then, for fast decaying solutions to (5), there is a constant $\mu > 0$ such that for all $t \geq 0$

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

Consequently, for $\alpha = E, I$

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

Note that this theorem does not include the general model (5) since the delays were assumed to vanish. To deal with the transmission delay, D , is necessary to compare the firing rate at $t - D$ and t ($N(t - D)$ and $N(t)$), using a L^2 control over the firing rate. And this provides the following result:

Theorem 3.4 (Theorem 5.3 in [11]). *Let b_1 such that there exists a steady state $(\rho_\infty^{b_1}, N_\infty^{b_1})$ for (9) with delay D (see (14)). Let $V_M \in (V_R, V_F)$, (ρ^0, N^0) an initial condition and $S(b_1, V_M) := \int_{V_M}^{V_F} \frac{\rho^0(v)^2}{\rho_\infty^{b_1}(v)} dv$. If there exists C_0 such that $\rho^0(\cdot) \leq C_0 \rho_\infty^{b_1}(\cdot)$ (consequently $S(b_1, V_M) < +\infty$), then:*

- If $b > 0$, there exists $\eta \in \mathbb{R}_+^*$ depending only on $\rho^0, N^0, S(b_1, V_M), D$ and V_M such that if $0 < b < \eta$, then there exist $A_0, \mu, \gamma \in \mathbb{R}_+^*$ depending only on (ρ^0, N^0) such that

$$\begin{aligned} \int_{-\infty}^{V_F} \rho_\infty \left(\frac{\rho - \rho_\infty}{\rho_\infty} \right)^2 (v, t) dv &\leq A_0 e^{-\mu t} \left[\int_{-\infty}^{V_F} \rho_\infty \left(\frac{\rho^0 - \rho_\infty}{\rho_\infty} \right)^2 (v) dv \right. \\ &\quad \left. + \frac{8b^2}{a} \int_{-D}^0 (N^0(s) - N_\infty)^2 e^{\gamma(s+D) - \int_{-D}^0 (N^0(u) - N_\infty)^2 du} ds \right]. \end{aligned}$$

- If $b < 0$, there exists $\eta \in \mathbb{R}_+^*$, independent of $S(b_1, V_M)$ such that if $-\eta < b < 0$, there exist $T, \mu, \gamma \in \mathbb{R}_+^*$ depending only on the initial condition, and $A_0 \in \mathbb{R}_+^*$ depending only on the values of N on $[0, T]$, such that for all $t \in (T, +\infty)$,

$$\begin{aligned} \int_{-\infty}^{V_F} \rho_\infty \left(\frac{\rho - \rho_\infty}{\rho_\infty} \right)^2 (v, t) dv &\leq A_0 e^{-\mu t} \left[\int_{-\infty}^{V_F} \rho_\infty \left(\frac{\rho^0 - \rho_\infty}{\rho_\infty} \right)^2 (v) dv \right. \\ &\quad \left. + \frac{8b^2}{a} \int_{-D}^0 (N^0(s) - N_\infty)^2 e^{\gamma(s+D) - \int_{-D}^0 (N(u) - N_\infty)^2 du} ds \right]. \end{aligned}$$

Theorem 3.4 can be extended to the general model (5) and gives the exponential convergence of the solutions to the unique steady state.

Until now, we have studied the steady states of the models, their stability, and the blow up phenomenon. To conclude this section we tackle other natural question: have the NNLIF models periodic solutions? In [11] we gave a partial answer: the simple model (14) has not periodic solutions if b is large enough and $V_F \leq 0$:

Theorem 3.5 (Theorem 5.4 in [11]). *If $b > V_F - V_R$, and $V_F \leq 0$, then for any $D \geq 0$ there are no classical periodic solutions to equation (9) with delay D (see (14)), such that $\int_{-\infty}^{V_F} |v| \rho^0(v) dv < +\infty$.*

And consequently there are non steady states.

In the following section we try to widen the study of periodic solutions from a numerical point of view (see Section 4.3).

4 - Numerical experiments

Numerical experiments help to obtain a better understanding of the model, because shed light on issues where we are not able to give analytical proofs. Within this context, we have observed numerically properties of the solutions of the models, which were not proved analytically: bistability of the steady states, the influence of the transmission delay and the refractory period, and the existence of periodic solutions. We note that in the jargon of Neuroscience (see [6]) *synchronous states* have firing rates that do not tend to be constant, unlike the firing rates of *asynchronous states* converge to a stationary value.

For the numerical experiments, unless otherwise specified, the parameters are $V_F = 2$, $V_R = 1$, $\nu_{E,ext} = 0$, $a_\alpha(N_E, N_I) = 1$ and two different types of initial condition are considered, for $\alpha = E, I$:

$$(24) \quad \rho_\alpha^0(v) = \frac{k}{\sqrt{2\pi}} e^{-\frac{(v-v_0^\alpha)^2}{2\sigma_0^{\alpha 2}}},$$

where k is a constant such that $\int_{-\infty}^{V_F} \rho_\alpha^0(v) dv \approx 1$ numerically, and

$$(25) \quad \rho_\alpha^0(v) = \frac{N_\alpha}{a_\alpha(N_E, N_I)} e^{-\frac{(v-V_0^\alpha(N_E, N_I))^2}{2a_\alpha(N_E, N_I)}} \int_{\max(v, V_R)}^{V_F} e^{-\frac{(w-V_0^\alpha(N_E, N_I))^2}{2a_\alpha(N_E, N_I)}} dw,$$

with $V_0^\alpha(N_E, N_I) = b_E^\alpha N_E - b_I^\alpha N_I + (b_E^\alpha - b_E^E) \nu_{E,ext}$ and where N_α is an approximated value of the stationary firing rate. For the models of only one population we consider $\rho_\alpha = \rho$, $v_0^\alpha = v_0$, $\sigma_0^{\alpha 2} = \sigma_0^2$ and $V_0^\alpha(N_E, N_I) = V_0(N) = bN$.

4.1 - Bistability

In Theorem 3.1 was shown that for the simplest model (9) there are values of the parameters for which the model has several steady state. This situation was extended to the model with two populations (8) in Theorem 3.2. Thus, a natural question arises: does the bistability phenomenon happen? The numerical analysis developed in [10] shows that this phenomenon does not happen (see Figure 4 in [10]) and the same situation is observed for the more general system (8), which is illustrated in the top of Figure 1 (see [13]). In both models the simulations indicate that, in general, the solutions tend to the lowest steady state (in terms of the value of their stationary firing rates), while the

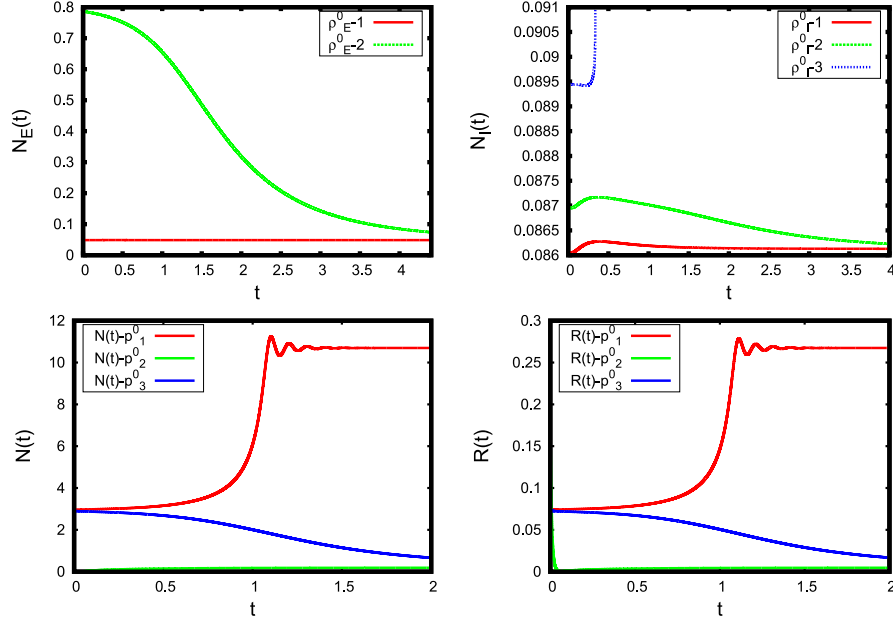


Fig. 1. **Asynchronous solutions** (Pictures of Figure 8 in [13] and Figure 3 in [10]). TOP: *Non bistability phenomenon for System (5) with three steady states* .- $b_I^E = 7$, $b_I^I = 2$, $b_E^I = 0.01$, $\tau_E = \tau_I = 0.2$ and $b_E^E = 3$. The initial conditions $\rho_\alpha^0 - 1, 2, 3$ are given by the profile (25), where N_α are approximations of the stationary firing rates. BOTTOM: *Bistability phenomenon for System (9) with refractory states (only one average-excitatory population) with three steady states* .- $V_F = 2$, $V_R = 1$, $a = 1$, $b = 1.5$ and $\tau = 0.025$. Evolution of $N(t)$ and $R(t)$ for different initial data: p_1^0 is the profile (25) with $N = 3$ and $R(0) = N\tau$, p_2^0 is the profile (25) with $N = 2.929$ and $R(0) = N\tau$ and $p_3^0(v) = ce^{-\frac{v^2}{0.5}}$ and $R(0) = 0.2$, where c is a constant such that the conservation of the total number of neurons is satisfied.

other steady states seem to be unstable. This means that these models describe an asynchronous behaviour for global solutions.

However, the presence of refractory states (which guarantee the existence of at least one steady states) seems to cause the bistability phenomenon, as it is observed in the bottom of Figure 1 (see [10]). These pictures show the evolution of the firing rates and the refractory states for different solutions of the model with only one average-excitatory population and refractory states (see System (9)). In this case the model has three steady states. As initial conditions were considered data of the shape (25) to start with solutions very close to the three steady states. The numerical experiments show that the lowest and the upper steady states are stable, while the middle one is unstable.

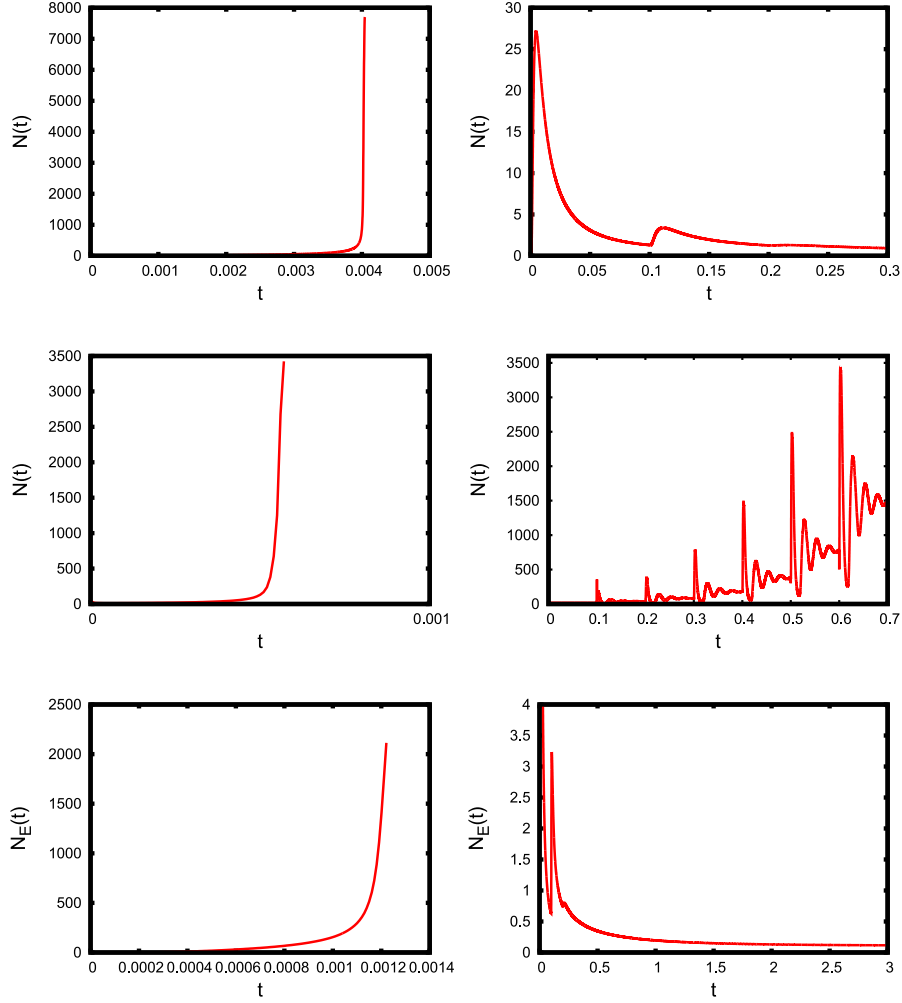


Fig. 2. **The transmission delay between excitatory neurons avoids the blow-up phenomena** (Pictures of Figures 2, 6 and 7 in [13]).

We consider the initial data (24).

TOP: *System (9) (only one population without refractory states)* with $v_0 = 1.83$, $\sigma_0 = 0.0003$ and the connectivity parameter $b = 0.5$. Left: N blows-up in finite time, if there is no delay, $D = 0$. Right: N tends to a steady state, if there is delay, $D = 0.1$.

MIDDLE: *System (9) (only one population without refractory states)* with $v_0 = 1.83$, $\sigma_0 = 0.003$ and the connectivity parameter $b = 2.2$. Left: N blows-up in finite time, if there is no delay, $D = 0$. Right: N does not blow-up if there is delay, $D = 0.1$.

BOTTOM: *System (5) (two populations: excitatory and inhibitory)* with $v_0^E = 1.89$, $v_0^I = 1.25$ and $\sigma_0^E = \sigma_0^I = 0.0003$, the connectivity parameters $b_E^E = 0.5$, $b_I^E = 0.75$, $b_I^I = 0.25$, $b_E^I = 0.5$, and with refractory states ($M_\alpha(t) = N_\alpha(t - \tau_\alpha)$) where $\tau_\alpha = 0.025$. Left: All the delays are 0.1, except $D_E^E = 0$. Right: All the delays are 0, except $D_E^E = 0.1$.

4.2 - *The transmission delay avoids the blow-up*

The blow-up phenomenon and how the transmission delay between excitatory neurons avoids it was described in Section 2. These facts are shown in Figure 2. In these pictures we can observe that the transmission delay prevents the solutions blowing-up: they tend to a steady state in the case that there exists, while, if there is not stationary solution, their firing rates increase in the time, but do not diverge in finite time. We point out that this later situation shows that it is not easy to find a uniform bound for the firing rate at every time of its local existence interval. And this is the reason why the existence proof presented in [15] can not be extended to the average-excitatory model with transmission delay (see Section 2).

On the other hand, the plots of the bottom of Figure 2 show the importance of the transmission delay between excitatory neurons in the general NNLIIF model (5), which includes all the phenomena of the network. More specifically, we observe that the transmission delay between excitatory neurons D_E^E avoids the blow-up, while the rest of delays are not able to prevent it.

4.3 - *Periodic solutions*

The synchronization of the networks is a well-known phenomenon in Neuroscience. It happens when the firing rates do not tend to be constant. In this sense, the blow-up phenomenon provides a synchronization of part of the network, since the firing rate diverges at finite time. Other possible situations of synchronization are given by periodic solutions.

We have found periodic solutions in the general NNLIIF system, where all the phenomena of the network are included in the model (two populations of neurons: excitatory and inhibitory, synaptic delays and refractory periods) [13]. We do not observe periodic solutions if the synaptic delays and the refractory periods are not taken into account, in other words, if there are not steady states and the solutions can blow-up. On the other hand, for the random discharge potential model (10) we find periodic solutions [10]. In this case the model does not present blow-up and there are strong controls on the firing rate $N(t)$.

In the top of Figure 3 we observe periodic solutions for the system (9) with refractory states and a transmission delay. On the left, the synchronization is a consequence of consider one average-excitatory population with an initial condition concentrated enough around the threshold potential, for which without transmission delay the solution blows-up. On the right, the synchronization is not a consequence of avoiding the blow-up, since blow-up phenomenon does not happen for one average-inhibitory population. In this picture we can analyse

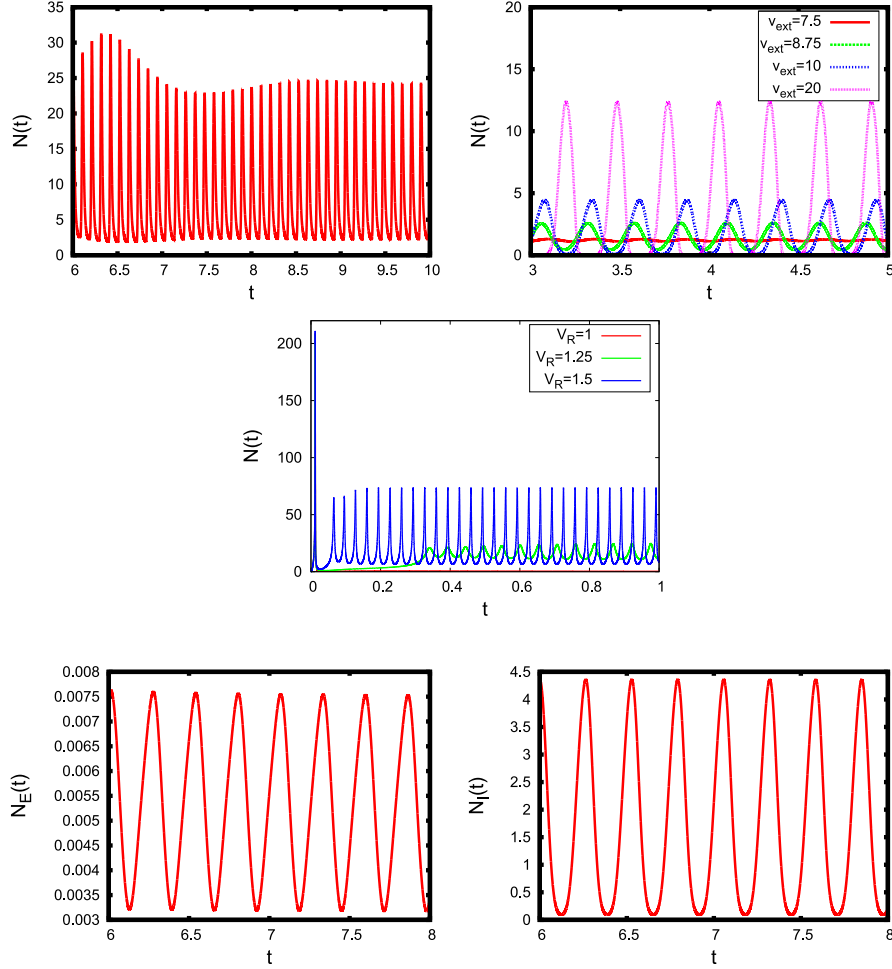


Fig. 3. **Synchronous solutions** (Pictures of the Figures 10, 12 and 14 in [13] and Figure 5 in [10]).

TOP: Left: *Periodic solutions of the model with only one average-excitatory population with refractory states and a transmission delay (System (14)).*- Initial datum (24), $v_0 = 1.83$, $\sigma_0 = 0.0003$, $b = 1.5$, $D = 0.1$, $v_{ext} = 0$ and $M(t) = \frac{R(t)}{\tau}$, where $\tau = 0.025$ and $R(0) = 0.2$.

Right: *Periodic solutions of the model with only one average-inhibitory population with refractory states and a transmission delay (System (14)).*- Initial datum (25) with $N = 3.669$, $b = -4$, $D = 0.1$, $M(t) = \frac{R(t)}{\tau}$, where $\tau = 0.025$ and $R(0) = 0.091725$.

MIDDLE: *Spontaneous activity for the model with randomness on the firing threshold V_F (System (10)).*- Initial datum (24), $\phi_\varepsilon(v) = \frac{1}{\varepsilon}(v - V_F)_+$, $V_F = 2$, $a = 1$, $b = 1.5$, $\tau = 0.025$ and $\epsilon = 1/14000$.

BOTTOM: *Periodic solutions of the model with two populations: excitatory and inhibitory with refractory states and a transmission delay (System (5)).*- Initial data (24), $v_0^E = v_0^I = 1.25$, $\sigma_0^E = \sigma_0^I = 0.0003$, $v_{ext} = 20$, $b_E^E = 0.5$, $b_I^E = 0.75$, $b_I^I = 4$, $b_E^I = 1$ and $M_\alpha(t) = N_\alpha(t - \tau_\alpha)$ where $\tau_\alpha = 0.025$.

the influence of the external stimuli received by the neurons of the network, described by the parameter v_{ext} , in the production of periodic solutions.

The middle plot of Figure 3 shows that the randomness on the firing threshold produces spontaneous activity.

Finally, the plots on the bottom of Figure 3 illustrate the presence of periodic solutions in the general model (5). We observe the periodicity of the excitatory firing rate N_E , although it seems almost constant. However, the periodicity of the inhibitory firing rate N_I is the cause of the periodicity of the solution.

5 - Conclusions and open problems

We have summarized the main properties of the solutions of Nonlinear Noisy Leaky Integrate and Fire (NNLIF) models studied in [6, 7, 8, 10, 11, 12, 13, 14, 15, 18, 19]. These models describe the activity of neural networks in terms of the membrane potential and are based on nonlinear PDEs of Fokker-Planck type.

In this kind of models, a wide range of properties of their solutions appear: blow-up/global existence, asynchronous/synchronous solutions, instability/stability of the steady states . . . These properties, which were proved analytically or showed numerically, can be related to neurophysiological phenomena. For instance, the blow-up can be interpreted as a synchronization of a part of the network, maybe associated with epilepsy. The presence of several steady states, with multi-stable phenomena, could be related, for example, to visual perception and decision making [2, 24]. And periodic or oscillatory states are also related to neurophysiological phenomena, for instance those observed during cortical processing [24, 26].

Although in the last years the mathematical knowledge about NNLIF models has improved a lot, from the analytical point of view there are still several open problems: the stability of the models when there is more than one stationary solution; criteria to have oscillatory states; a more general notion of solution that allows to continue after blow-up and studying relations with other PDE models which describe the activity of the networks at the level of the membrane potential, for instance: Population density models of Integrate and Fire neurons with jumps [20, 21, 22, 30], Fokker-Planck equations for uncoupled neurons [28, 29]; Fokker-Planck equations including conductance variables, [9, 34, 35, 36], time elapsed models [31, 32, 33] which have been recently derived as mean-field limits of Hawkes processes [16, 17], McKean-Vlasov equations [1, 27], which are the mean-field equations related to the behaviour of Fitzhugh-Nagumo neurons [23], etc.

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