

Analysis of Nonlinear Noisy Integrate&Fire Neuron Models: blow-up and steady states

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Abstract

Nonlinear Noisy Leaky Integrate and Fire (NNLIF) models for neurons networks can be written as Fokker-Planck-Kolmogorov equations on the probability density of neurons, the main parameters in the model being the connectivity of the network and the noise. We analyse several aspects of the NNLIF model: the number of steady states, a priori estimates, blow-up issues and convergence toward equilibrium in the linear case. In particular, for excitatory networks, blow-up always occurs for initial data concentrated close to the firing potential. These results show how critical is the balance between noise and excitatory/inhibitory interactions to the connectivity parameter.

Key-words: Leaky integrate and fire models, noise, blow-up, relaxation to steady state, neural networks.

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1 Introduction

The classical description of the dynamics of a large set of neurons is based on deterministic/stochastic differential systems for the excitatory-inhibitory neuron network [12, 23]. One of the most classical models is the so-called noisy leaky integrate and fire (NLIF) model. Here, the dynamical behavior of the ensemble of neurons is encoded in a stochastic differential equation for the evolution in time of the averaged action potential of the membrane $v(t)$ of a typical neuron representative of the network. The neurons relax towards their resting potential V_L in the absence of any interaction. All the interactions of the neuron with the network are modelled by an incoming synaptic current $I(t)$. More precisely, the evolution of the action potential follows, see [4, 1, 20, 7]

$$C_m \frac{dV}{dt} = -g_L(V - V_L) + I(t) \quad (1.1)$$

where C_m is the capacitance of the membrane and g_L is the leak conductance, normally taken to be constants with $\tau_m = g_L/C_m \approx 2ms$ being the typical relaxation time of the potential towards the leak

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reversal (resting) potential $V_L \approx -70mV$. Here, the synaptic current takes the form of a stochastic process given by:

$$I(t) = J_E \sum_{i=1}^{C_E} \sum_j \delta(t - t_{Ej}^i) - J_I \sum_{i=1}^{C_I} \sum_j \delta(t - t_{Ij}^i), \quad (1.2)$$

where δ is the Dirac Delta at 0. Here, J_E and J_I are the strength of the synapses, C_E and C_I are the total number of presynaptic neurons and t_{Ej}^i and t_{Ij}^i are the times of the j^{th} -spike coming from the i^{th} -presynaptic neuron for excitatory and inhibitory neurons respectively. The stochastic character is embedded in the distribution of the spike times of neurons. Actually, each neuron is assumed to spike according to a stationary Poisson process with constant probability of emitting a spike per unit time ν . Moreover, all these processes are assumed to be independent between neurons. With these assumptions the average value of the current and its variance are given by $\mu_C = b\nu$ with $b = C_E J_E - C_I J_I$ and $\sigma_C^2 = (C_E J_E^2 + C_I J_I^2)\nu$. We will say that the network is average-excitatory (average-inhibitory resp.) if $b > 0$ ($b < 0$ resp.).

Being the discrete Poisson processes still very difficult to analyze, many authors in the literature [1, 4, 20, 14] have adopted the diffusion approximation where the synaptic current is approximated by a continuous in time stochastic process of Ornstein-Uhlenbeck type with the same mean and variance as the Poissonian spike-train process. More precisely, we approximate $I(t)$ in (1.2) as

$$I(t) dt \approx \mu_c dt + \sigma_C dB_t$$

where B_t is the standard Brownian motion. We refer to the work [20] for a nice review and discussion of the diffusion approximation which becomes exact in the infinitely large network limit, if the synaptic efficacies J_E and J_I are scaled appropriately with the network sizes C_E and C_I .

Finally, another important ingredient in the modelling comes from the fact that neurons only fire when their voltage reaches certain threshold value called the threshold or firing voltage $V_F \approx -50mV$. Once this voltage is attained, they discharge themselves, sending a spike signal over the network. We assume that they instantaneously relax toward a reset value of the voltage $V_R \approx -60mV$. This is fundamental for the interactions with the network that may help increase their action potential up to the maximum level (excitatory synapses), or decrease it for inhibitory synapses. Choosing our voltage and time units in such a way that $C_m = g_L = 1$, we can summarize our approximation to the stochastic differential equation model (1.1) as the evolution given by

$$dV = (-V + V_L + \mu_c) dt + \sigma_C dB_t \quad (1.3)$$

for $V \leq V_F$ with the jump process: $V(t_0^+) = V_R$ whenever at t_0 the voltage achieves the threshold value $V(t_0^-) = V_F$; with $V_L < V_R < V_F$. Finally, we have to specify the probability of firing per unit time of the Poissonian spike train ν . This is the so-called firing rate and it should be self-consistently computed from a fully coupled network together with some external stimuli. Therefore, the firing rate is computed as $\nu = \nu_{ext} + N(t)$ where $N(t)$ is the mean firing rate of the network. The value of $N(t)$ is then computed as the flux of neurons across the threshold or firing voltage V_F . We finally refer to [11] for a nice brief introduction to this subject.

Coming back to the diffusion approximation in (1.3), we can write a partial differential equation for the evolution of the probability density $p(v, t) \geq 0$ of finding neurons at a voltage $v \in (-\infty, V_F]$ at a time $t \geq 0$. Standard Ito's rule gives the backward Kolmogorov or Fokker-Planck equation

$$\frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v} [h(v, N(t))p(v, t)] - a(N(t)) \frac{\partial^2 p}{\partial v^2}(v, t) = \delta(v - V_R)N(t), \quad v \leq V_F, \quad (1.4)$$

with $h(v, N(t)) = -v + V_L + \mu_c$ and $a(N) = \sigma_C^2/2$. We have the presence of a source term in the right-hand side due to all neurons that at time $t \geq 0$ fired, sent the signal on the network and then, their voltage was immediately reset to voltage V_R . Moreover, no neuron should have the firing voltage due to the instantaneous discharge of the neurons to reset value V_R , then we complement (1.4) with Dirichlet and initial boundary conditions

$$p(V_F, t) = 0, \quad p(-\infty, t) = 0, \quad p(v, 0) = p^0(v). \quad (1.5)$$

Equation (1.4) should be the evolution of a probability density, therefore

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

for all $t \geq 0$. Formally, this conservation should come from integrating (1.4) and using the boundary conditions (1.5). It is straightforward to check that this conservation for smooth solutions is equivalent to characterize the mean firing rate for the network $N(t)$ as the flux of neurons at the firing rate voltage. More precisely, the mean firing rate $N(t)$ is implicitly given by

$$N(t) := -a(N(t)) \frac{\partial p}{\partial v}(V_F, t) \geq 0. \quad (1.6)$$

Here, the right-hand side is nonnegative since $p \geq 0$ over the interval $[-\infty, V_F]$ and thus, $\frac{\partial p}{\partial v}(V_F, t) \leq 0$. In particular this imposes a limitation on the growth of the function $N \mapsto a(N)$ such that (1.6) has a unique solution N .

The above Fokker-Planck equation has been widely used in neurosciences. Often the authors prefer to write it in an equivalent but less singular form. To avoid the Dirac delta in the right hand side, one can also set the same equation on $(-\infty, V_R) \cup (V_R, V_F]$ and introduce the jump condition

$$p(V_R^-, t) = p(V_R^+, t), \quad \frac{\partial}{\partial v} p(V_R^-, t) - \frac{\partial}{\partial v} p(V_R^+, t) = N(t).$$

This is completely transparent in our analysis which relates on a weak form that applies to both settings.

Finally, let us choose a new voltage variable by translating it with the factor $V_L + b\nu_{ext}$ while, for the sake of clarity, keeping the notation for the rest of values of the potentials involved $V_R < V_F$. In these new variables, the drift and diffusion coefficients are of the form

$$h(v, N) = -v + bN, \quad a(N) = a_0 + a_1 N \quad (1.7)$$

where $b > 0$ for excitatory-average networks and $b < 0$ for inhibitory-average networks, $a_0 > 0$ and $a_1 \geq 0$. Some results in this work can be obtained for some more general drift and diffusion coefficients. The precise assumptions will be specified on each result. Periodic solutions have been numerically reported and analysed in the case of the Fokker-Planck equation for uncoupled neurons in [16, 17]. Also, they study the stationary solutions for fully coupled networks obtaining and solving numerically the implicit relation that the firing rate N has to satisfy, see Section 3 for more details.

There are several other routes towards modeling of spiking neurons that are related to ours and that have been used in neurosciences, see [9]. Among them are the deterministic I&F models with adaptation which are known for fitting well experimental data [3]. In this case it is known that in the quadratic (or merely superlinear) case, the model can blow-up [22]. One can also introduce

gating variables in neuron networks and this leads to a kinetic equation, see [6] and the references therein. Another method consists in coding the information in the distribution of time elapsed between discharges [19, 18], this leads to nonlinear models that exhibit naturally periodic activity, but blow-up has not been reported.

In this work we will analyse certain properties of the solutions to (1.4)–(1.5) with the nonlinear term due to the coupling of the mean firing rate given by (1.6). Next section is devoted to a finite time blow-up of weak solutions for (1.4)–(1.6). In short, we show that whenever the value of $b > 0$ is, we can find suitable initial data concentrated enough at the firing rate such that the defined weak solutions do not exist for all times. This implies that this model encodes complicated dynamics. As long as the solution exists in the sense specified in Section 2, we can get apriori estimates on the L^1_{loc} -norm of the firing rate. Section 3 deals with the stationary states of (1.4)–(1.6). We can show that there are unique stationary states for $b \leq 0$ and a constant but for $b > 0$ different cases may happen: one, two or no stationary states depending on how large b is. In Section 4, we discuss the linear problem $b = 0$ with a constant for which the general relative entropy principle applies implying the exponential convergence towards equilibrium. Finally, Section 5 is devoted to some numerical simulations of the model showing some of the results here and getting some conjectures about the nonlinear stability of the found stationary states.

2 Finite time blow-up and apriori estimates for weak solutions

Since we study a nonlinear version of the backward Kolmogorov or Fokker-Planck equation (1.4), we start with the notion of solution:

Definition 2.1 *We say that a pair of nonnegative functions (p, N) with $p \in L^\infty(\mathbb{R}^+; L^1_+(-\infty, V_F))$, $N \in L^1_{loc,+}(\mathbb{R}^+)$ is a weak solution of (1.4)–(1.7) 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*

$$\int_0^T \int_{-\infty}^{V_F} p(v, t) \left[-\frac{\partial \phi}{\partial t} - \frac{\partial \phi}{\partial v} h(v, N) - a \frac{\partial^2 \phi}{\partial v^2} \right] dv dt = \int_0^T N(t) [\phi(V_R, t) - \phi(V_F, t)] dt \quad (2.1)$$

$$+ \int_{-\infty}^{V_F} p^0(v) \phi(0, v) dv - \int_{-\infty}^{V_F} p(v, T) \phi(T, v) dv.$$

Let us remark that the growth condition on the test function together with the assumption (1.7) imply that the term involving $h(v, N)$ makes sense. By choosing test functions of the form $\psi(t)\phi(v)$, this formulation is equivalent to say that for all $\phi(v) \in C^\infty((-\infty, V_F])$ such that $v \frac{\partial \phi}{\partial v} \in L^\infty((-\infty, V_F))$, we have that

$$\frac{d}{dt} \int_{-\infty}^{V_F} \phi(v) p(v, t) dv = \int_{-\infty}^{V_F} \left[\frac{\partial \phi}{\partial v} h(v, N) + a \frac{\partial^2 \phi}{\partial v^2} \right] p(v, t) dv + N(t) [\phi(V_R, t) - \phi(V_F, t)] \quad (2.2)$$

holds in the distributional sense. It is trivial to check that weak solutions conserve the mass of the initial data by choosing $\phi = 1$ in (2.2), and thus,

$$\int_{-\infty}^{V_F} p(v, t) dv = \int_{-\infty}^{V_F} p^0(v) dv = 1. \quad (2.3)$$

The first result we show is that global-in-time weak solutions of (1.4)–(1.6) do not exist for all initial data in the case of an average-excitatory network. This result holds with less stringent hypotheses on the coefficients than in (1.7) with an analogous notion of weak solution as in Definition 2.1.

Theorem 2.2 (Blow-up) *Assume that the drift and diffusion coefficients satisfy*

$$h(v, N) + v \geq bN \quad \text{and} \quad a(N) \geq a_m > 0, \quad (2.4)$$

for all $-\infty < v \leq V_F$ and all $N \geq 0$, and let us consider the average-excitatory network where $b > 0$. If the initial data is concentrated enough around $v = V_F$, in the sense that

$$\int_{-\infty}^{V_F} e^{\mu v} p^0(v) dv$$

is large enough with $\mu > \max(\frac{V_F}{a_m}, \frac{1}{b})$, then there are no global-in-time weak solutions to (1.4)–(1.6).

Proof. We choose a multiplier $\phi(v) = e^{\mu v}$ with $\mu > 0$ and define the number

$$\lambda = \frac{\phi(V_F) - \phi(V_R)}{b\mu} > 0$$

by hypotheses. For a weak solution according to (2.1), we find from (2.2) that

$$\begin{aligned} \frac{d}{dt} \int_{-\infty}^{V_F} \phi(v) p(v, t) dv &\geq \mu \int_{-\infty}^{V_F} (bN(t) - v) \phi(v) p(v, t) dv + \mu^2 a_m \int_{-\infty}^{V_F} \phi(v) p(v, t) dv - \lambda b \mu N(t) \\ &\geq \mu \int_{-\infty}^{V_F} \phi(v) p(v, t) dv [bN(t) + \mu a_m - V_F] - \lambda b \mu N(t) \end{aligned} \quad (2.5)$$

where (2.4) and the fact that $v \in (-\infty, V_F)$ was used. Let us now choose μ large enough such that $\mu a_m - V_F > 0$ according to our hypotheses and denote

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

which satisfies

$$\frac{d}{dt} M_\mu(t) \geq b \mu N(t) [M_\mu(t) - \lambda].$$

If initially $M_\mu(0) \geq \lambda$ and using Gronwall's Lemma since $N(t) \geq 0$, we have that $M_\mu(t) \geq \lambda$, for all $t \geq 0$, and back to (2.5) we find

$$\frac{d}{dt} \int_{-\infty}^{V_F} \phi(v) p(v, t) dv \geq \mu(\mu a_m - V_F) \int_{-\infty}^{V_F} \phi(v) p(v, t) dv$$

which in turn implies,

$$\int_{-\infty}^{V_F} \phi(v) p(v, t) dv \geq e^{\mu(\mu a_m - V_F)t} \int_{-\infty}^{V_F} \phi(v) p^0(v) dv.$$

On the other hand, since $p(v, t)$ preserves the mass, see (2.3), and $\mu > 0$ then

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

leading to a contradiction.

It remains to show that the set of initial data satisfying the size condition in the statement is not empty. To verify this, we can approximate as much as we want by smooth initial probability densities an initial Dirac mass at V_F which gives the condition

$$e^{\mu V_F} \geq \lambda = \frac{e^{\mu V_F} - e^{\mu V_R}}{b\mu} \quad \text{together with } \mu a_m > V_F.$$

This can be equivalently written as

$$\mu \geq \frac{1 - e^{-\mu(V_F - V_R)}}{b} \quad \text{and } \mu > \frac{V_F}{a_m}.$$

Choosing μ large enough, these conditions are obviously fulfilled. \square

As usual for this type of blow-up result similar in spirit to the classical Keller-Segel model for chemotaxis [2, 8], the proof only ensures that solutions for those initial data do not exist beyond a finite maximal time of existence. It does not characterize the nature of the first singularity which occurs. It implies that either the decay at infinity is false, although not probable, implying that the time evolution of probability densities ceases to be tight, or the function $N(t)$ may become a singular measure in finite time instead of being an $L^1_{loc}(\mathbb{R}^+)$ function. Actually, in the numerical computations shown in Section 4, we observe a blow-up in the value of the mean firing rate in finite time. This will need a modification of the notion of solution introduced in Definition 2.1.

Nevertheless, it is possible to obtain some a priori bounds with the help of appropriate choices of the test function ϕ in (2.1). Some of these choices are not allowed due to the growth at $-\infty$ of the test functions. We will say that a weak solution is fast-decaying at $-\infty$ if they are weak solutions in the sense of Definition 2.1 and the weak formulation in (2.2) holds for all test functions growing algebraically in v .

Lemma 2.3 (A priori estimates) *Assume (1.7) on the drift and diffusion coefficients and that (p, N) is a global-in-time solution of (1.4)–(1.6) in the sense of Definition 2.1 fast decaying at $-\infty$, then the following apriori estimates hold:*

(i) *If $b \geq V_F - V_R$, then*

$$\begin{aligned} \int_{-\infty}^{V_F} (V_F - v)p(v, t)dv &\leq \max \left(V_F, \int_{-\infty}^{V_F} (V_F - v)p^0(v)dv \right), \\ (b - V_F + V_R) \int_0^T N(t)dt &\leq V_F T + \int_{-\infty}^{V_F} (V_F - v)p^0(v)dv, \end{aligned}$$

(ii) *If $b < V_F - V_R$ then*

$$\int_{-\infty}^{V_F} (V_F - v)p(v, t)dv \geq \min \left(V_F, \int_{-\infty}^{V_F} (V_F - v)p^0(v)dv \right).$$

Moreover, if in addition a is constant then

$$\int_0^T N(t)dt \leq (1 + T)C(b, V_F - V_R, a).$$

Proof. With our decay assumption at $-\infty$, we may use the test function $\phi(v) = V_F - v \geq 0$. Then (2.2) gives

$$\frac{d}{dt} \int_{-\infty}^{V_F} \phi(v)p(v,t)dv = \int_{-\infty}^{V_F} [v - bN(t)]p(v,t)dv + N(t)(V_F - V_R).$$

This is also written as

$$\frac{d}{dt} \int_{-\infty}^{V_F} \phi(v)p(v,t)dv + \int_{-\infty}^{V_F} \phi(v)p(v,t)dv = V_F - N(t) [b - (V_F - V_R)]. \quad (2.6)$$

To prove (i), with our condition on b the term in $N(t)$ is nonpositive and both results follow after integration in time.

To prove (ii), we first use again (2.6) and, because the term in $N(t)$ is nonnegative, we find the first result. Then, we use a truncation function $\phi(v) \in C^2$ such that

$$\phi(V_F) = 1, \quad \phi(v) = 0 \text{ for } v \leq V_R, \quad \phi'(v) \geq 0.$$

Equation (2.2) gives

$$\frac{d}{dt} \int_{V_R}^{V_F} \phi(v)p(v,t)dv + N(t) = \int_{V_R}^{V_F} \phi'(v)(-v + bN(t))p(v,t)dv + a \int_{V_R}^{V_F} \phi''(v)p(v,t)dv.$$

Except regularity at $v = V_R$, we can have in mind $\phi'(v) = 1/(V_F - V_R)$ for $v > V_R$, and we can be as close as we want of this choice by paying a large second derivative of ϕ . So with the parameter

$$\delta = \frac{1}{2} \left[1 - \frac{b}{V_F - V_R} \right]$$

we may achieve with $C(\delta)$ large

$$\frac{d}{dt} \int_{V_R}^{V_F} \phi(v)p(v,t)dv + \delta N(t) \leq a \int_{V_R}^{V_F} \phi''(v)p(v,t)dv \leq C(\delta).$$

And this leads directly to the result after integration in time. \square

Corollary 2.4 *Under the assumptions of Lemma 2.3 and assuming $v^2 p^0(v) \in L^1(-\infty, V_F)$ and $0 < b < V_F - V_R$, then the following apriori estimates hold:*

(i) *If additionally a is constant, for all $t \geq 0$ we have*

$$\int_{-\infty}^{V_F} v^2 p(v,t)dv \leq C(1+t)$$

(ii) *If additionally $-b \min \left(V_F, \int_{-\infty}^{V_F} (V_F - v)p^0(v)dv \right) + a_1 + bV_F + \frac{V_R^2 - V_F^2}{2} \leq 0$, then*

$$\int_{-\infty}^{V_F} v^2 p(v,t)dv \leq \max \left(a_0, \int_{-\infty}^{V_F} v^2 p^0(v,t)dv \right).$$

Proof. We use $\phi(v) = v^2/2$ as test function to get

$$\begin{aligned} \frac{d}{dt} \int_{-\infty}^{V_F} \frac{v^2}{2} p(v, t) dv + \int_{-\infty}^{V_F} v^2 p(v, t) dv &= bN(t) \int_{-\infty}^{V_F} vp(v, t) dv + a(N(t)) + N(t) \frac{V_R^2 - V_F^2}{2} \\ &= bN(t) \int_{-\infty}^{V_F} (v - V_F) p(v, t) dv + a(N(t)) + N(t) \left[bV_F + \frac{V_R^2 - V_F^2}{2} \right] \\ &\leq a_0 + N(t) \left[-b \min \left(V_F, \int_{-\infty}^{V_F} (V_F - v) p^0(v) dv \right) \right] + a_1 + bV_F + \frac{V_R^2 - V_F^2}{2} \end{aligned}$$

thanks to the first statement of Lemma 2.3 (ii).

To prove (i), we just use the second statement of Lemma 2.3 (ii) valid for a constant which tells us that the time integration of the right-hand side grows at most linearly in time and so does $\int_{-\infty}^{V_F} v^2 p(v, t) dv$.

To prove (ii), we just use that the bracket is nonpositive and the results follows. \square

3 Steady states

3.1 Generalities

This section is devoted to find all smooth stationary solutions of the problem (1.4)-(1.6) in the particular relevant case of a drift of the form $h(v) = V_0(N) - v$. Let us search for continuous stationary solutions p of (1.4) such that p is C^1 regular except possibly at $V = V_R$ where it is *Lipschitz*. Using the definition in (2.2), we are then allowed by a direct integration by parts in the second derivative term of p to deduce that p satisfies

$$\frac{\partial}{\partial v} \left[(v - V_0(N))p + a(N) \frac{\partial p}{\partial v} + NH(v - V_R) \right] = 0 \quad (3.1)$$

in the sense of distributions, with H being the Heaviside function, i.e., $H(u) = 1$ for $u \geq 0$ and $H(u) = 0$ for $u < 0$. Therefore, we conclude that

$$(v - V_0(N))p + a(N) \frac{\partial p}{\partial v} + NH(v - V_R) = C.$$

The definition of N in (1.6) and the Dirichlet boundary condition (1.5) imply $C = 0$ by evaluating this expression at $v = V_F$. Using again the boundary condition (1.5), $p(V_F) = 0$, we may finally integrate again and find that

$$p(v) = \frac{N}{a(N)} e^{-\frac{(v-V_0(N))^2}{2a}} \int_v^{V_F} e^{\frac{(w-V_0(N))^2}{2a}} H[w - V_R] dw$$

which can be rewritten, using the expression of the Heaviside function, as

$$p(v) = \frac{N}{a(N)} e^{-\frac{(v-V_0(N))^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-V_0(N))^2}{2a}} dw. \quad (3.2)$$

Moreover, the firing rate in the stationary state N is determined by the normalization condition (2.3), or equivalently,

$$\frac{a(N)}{N} = \int_{-\infty}^{V_F} \left[e^{-\frac{(v-V_0(N))^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-V_0(N))^2}{2a}} dw \right] dv. \quad (3.3)$$

Summarizing all solutions with the above referred regularity of the stationary problem (3.1) are of the form in (3.2) with N being any positive solution to (3.3).

Let us first comment that in the linear case $V_0(N) = 0$ and $a(N) = a > 0$, we then get a unique stationary state p_∞ given by the expression

$$p_\infty(v) = \frac{N_\infty}{a} e^{-\frac{v^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{w^2}{2a}} dw. \quad (3.4)$$

with N_∞ the normalizing constant to unit mass over the interval $(-\infty, V_F]$, as obtained in [4].

The rest of this section is devoted to find conditions on the parameters of the model clarifying the number of solutions to (3.3). With this aim, it is convenient to perform a change of variables, and use new notations

$$z = \frac{v - V_0}{\sqrt{a}}, \quad u = \frac{w - V_0}{\sqrt{a}}, \quad w_F = \frac{V_F - V_0}{\sqrt{a}}, \quad w_R = \frac{V_R - V_0}{\sqrt{a}}, \quad (3.5)$$

where the N dependency has been avoided to simplify notation. Then, we can rewrite the previous integral (and thus the condition for a steady state) as

$$\begin{cases} \frac{1}{N} = I(N), \\ I(N) := \int_{-\infty}^{w_F} \left[e^{-\frac{z^2}{2}} \int_{\max(z, w_R)}^{w_F} e^{\frac{u^2}{2}} du \right] dz. \end{cases} \quad (3.6)$$

Another alternative form of $I(N)$ follows from the change of variables $s = (z - u)/2$ and $\tilde{s} = (z + u)/2$ to get

$$I(N) = 2 \int_{-\infty}^0 \int_{w_R+s}^{w_F+s} e^{-2s\tilde{s}} d\tilde{s} ds = - \int_{-\infty}^0 \frac{e^{-2s^2}}{s} (e^{-2s w_F} - e^{-2s w_R}) ds,$$

and consequently,

$$I(N) = \int_0^\infty \frac{e^{-s^2/2}}{s} (e^{s w_F} - e^{s w_R}) ds. \quad (3.7)$$

3.2 Case of $a(N) = a_0$.

We are now ready to state our main result on steady states.

Theorem 3.1 *Assume $h(v, N) = bN - v$, $a(N) = a_0$ is constant and $V_0 = bN$.*

i) For $b < 0$ and $b > 0$ small enough there is a unique steady state to (1.4)-(1.6).

ii) Under either the condition

$$0 < b < V_F - V_R, \quad (3.8)$$

or the condition

$$0 < 2a_0b < (V_F - V_R)^2 V_R, \quad (3.9)$$

then there exists at least one steady state solution to (1.4)-(1.6).

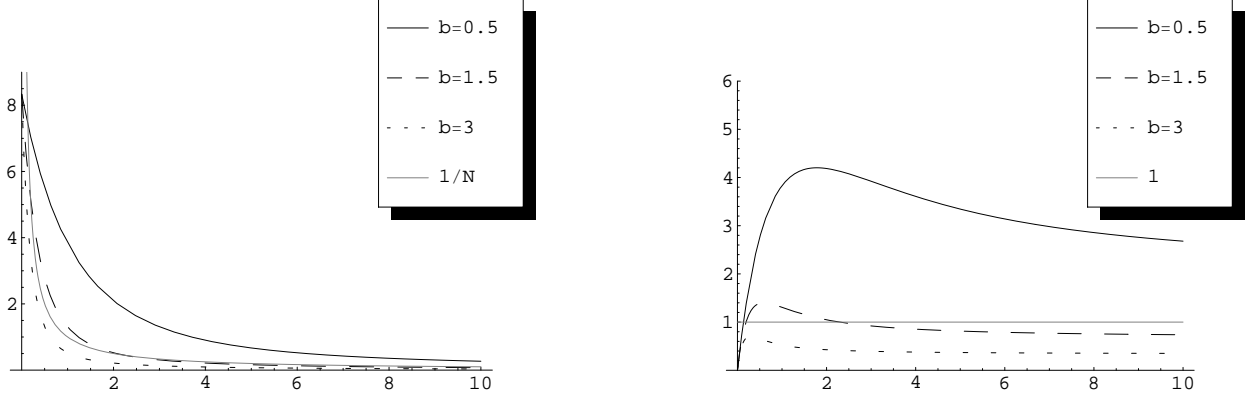


Figure 1: For several values of b , the function $I(N)$ in (3.6) is plotted against the function $1/N$ (Left Figure) and the function $NI(N)$ against the constant function 1 (Right Figure). Here $a \equiv 1$, $V_R = 1$, $V_F = 2$.

- iii) If both (3.9) and $b > V_F - V_R$ hold, then there are at least two steady states to (1.4)-(1.6).
- iv) There is no steady state to (1.4)-(1.6) under the high connectivity condition

$$b > \max(2(V_F - V_R), 2V_F I(0)). \quad (3.10)$$

Remark 3.2 It is natural to relate the absence of steady state for b large with blow-up of solutions. However, Theorem 2.2 in Section 2 shows this is not the only possible cause since the blow-up can happen for initial data concentrated enough around V_F independently of the value of $b > 0$. See also Section 5 for related numerical results.

Proof. Let us first study properties of the function $I(N)$. We first rewrite (3.7) as

$$I(N) = \int_0^\infty e^{-s^2/2} e^{-\frac{sbN}{\sqrt{a_0}}} \frac{e^{\frac{sV_F}{\sqrt{a_0}}} - e^{\frac{sV_R}{\sqrt{a_0}}}}{s} ds.$$

A direct Taylor expansion implies that

$$\left| \frac{e^{\frac{sV_F}{\sqrt{a_0}}} - e^{\frac{sV_R}{\sqrt{a_0}}}}{s} - \frac{V_F - V_R}{\sqrt{a_0}} \right| \leq C_0 s e^{\frac{sV_F}{\sqrt{a_0}}} \quad (3.11)$$

for all $s \geq 0$. Then, a direct application of the dominated convergence theorem and continuity theorems of integrals with respect to parameters show that the function $I(N)$ is continuous on N on $[0, \infty)$. Moreover, the function $I(N)$ is C^∞ on N since all their derivatives can be computed by differentiating under the integral sign by direct application of dominated convergence theorems and differentiation theorems of integrals with respect to parameters. In particular,

$$I'(N) = -\frac{b}{\sqrt{a_0}} \int_0^\infty e^{-s^2/2} (e^{sV_F} - e^{sV_R}) ds,$$

and for all integers $k \geq 1$,

$$I^{(k)}(N) = (-1)^k \left(\frac{b}{\sqrt{a_0}} \right)^k \int_0^\infty e^{-s^2/2} s^{k-1} (e^{s w_F} - e^{s w_R}) ds.$$

As a consequence, we deduce:

1. Case $b < 0$: $I(N)$ is an increasing strictly convex function and thus

$$\lim_{N \rightarrow \infty} I(N) = \infty.$$

2. Case $b > 0$: $I(N)$ is a decreasing convex function. Also, it is obvious from the previous expansion (3.11) and dominated convergence theorem that

$$\lim_{N \rightarrow \infty} I(N) = 0.$$

It is also useful to keep in mind that, thanks to the form of $I(N)$ in (3.6),

$$I(0) \leq \sqrt{2\pi} [w_F(0) - w_R(0)] e^{\max(w_R^2(0), w_F^2(0))/2} = \sqrt{2\pi} \frac{(V_F - V_R)}{a_0} \exp \left\{ \frac{\max(V_R^2, V_F^2)}{2a_0} \right\} < \infty. \quad (3.12)$$

Now, let us show that for $b > 0$, we have

$$\lim_{N \rightarrow \infty} N I(N) = \frac{V_F - V_R}{b}. \quad (3.13)$$

Using (3.11), we deduce

$$\left| N I(N) - N \frac{V_F - V_R}{\sqrt{a_0}} \int_0^\infty e^{-s^2/2} e^{-\frac{sbN}{\sqrt{a_0}}} ds \right| \leq C_0 N \int_0^\infty s e^{-s^2/2} e^{-\frac{sbN}{\sqrt{a_0}}} e^{\frac{s V_F}{\sqrt{a_0}}} ds.$$

A direct application of dominated convergence theorem shows that the right hand side converges to 0 as $N \rightarrow \infty$ since $sN \exp(-\frac{sbN}{\sqrt{a_0}})$ is a bounded function uniform in N and s . Thus, the computation of the limit is reduced to show

$$\lim_{N \rightarrow \infty} N \int_0^\infty e^{-s^2/2 - \frac{sbN}{\sqrt{a_0}}} ds = \frac{\sqrt{a_0}}{b}. \quad (3.14)$$

With this aim, we rewrite the integral in terms of the complementary error function defined as

$$\operatorname{erfc}(x) := \frac{2}{\sqrt{\pi}} \int_x^\infty e^{-t^2} dt,$$

and then

$$\int_0^\infty e^{-s^2/2 - \frac{sbN}{\sqrt{a_0}}} ds = e^{\frac{b^2 N^2}{2a_0}} \int_0^\infty e^{-\left(\frac{s}{\sqrt{2}} + \frac{bN}{\sqrt{2a_0}}\right)^2} ds = \frac{\sqrt{\pi}}{\sqrt{2}} e^{\frac{b^2 N^2}{2a_0}} \operatorname{erfc} \left(\frac{bN}{\sqrt{2a_0}} \right).$$

Finally, we can obtain the limit (3.14) using L'Hôpital's rule

$$\lim_{N \rightarrow \infty} N \int_0^\infty e^{-s^2/2 - \frac{sbN}{\sqrt{a_0}}} ds = \frac{\sqrt{\pi}}{\sqrt{2}} \lim_{N \rightarrow \infty} \frac{\operatorname{erfc} \left(\frac{bN}{\sqrt{2a_0}} \right)}{\frac{e^{-\frac{b^2 N^2}{2a_0}}}{N}} = \sqrt{2} \lim_{N \rightarrow \infty} \frac{-\frac{b}{\sqrt{2a_0}} e^{-\frac{b^2 N^2}{2a_0}}}{-\frac{b^2}{a_0} e^{-\frac{b^2 N^2}{2a_0}} - \frac{1}{N^2} e^{-\frac{b^2 N^2}{2a_0}}} = \frac{\sqrt{a_0}}{b}.$$

With this analysis of the function $I(N)$ we can now proof each of the statements of Theorem 3.1:

Proof of i). Let us start with the case $b < 0$. Here, the function $I(N)$ is increasing, starting at $I(0) < \infty$ due to (3.12) and such that

$$\lim_{N \rightarrow \infty} I(N) = \infty.$$

Therefore, it crosses to the function $1/N$ at a single point.

Now, for the case $b > 0$ small, we first remark that similar dominated convergence arguments as above show that both $I(N)$ and $I'(N)$ are smooth functions of b . Moreover, it is simple to realize that $I(N)$ is a decreasing function of the parameter b . Now, choosing $0 < b \leq b_* < (V_F - V_R)/2$, then $I(N) \geq I_*(N)$ for all $N \geq 0$ where $I_*(N)$ denotes the function associated to the parameter b_* . Using the limit (3.13), we can now infer the existence of $N_* > 0$ depending only on b_* such that

$$NI(N) \geq NI_*(N) > \frac{V_F - V_R}{2b_*} > 1$$

for all $N \geq N_*$. Therefore, by continuity of $NI(N)$ there are solutions to $NI(N) = 1$ and all possible crossings of $I(N)$ and $1/N$ are on the interval $[0, N_*]$. We observe that both $I(N)$ and $I'(N)$ converge towards the constant function $I(0) > 0$ and to 0 respectively, uniformly in the interval $[0, N_*]$ as $b \rightarrow 0$. Therefore, for b small N $I(N)$ is strictly increasing on the interval $[0, N_*]$ and there is a unique solution to $NI(N) = 1$.

Proof of ii). Case of (3.8). The claim that there are solutions to $NI(N) = 1$ for $0 < b < V_F - V_R$ is a direct consequence of the continuity of $I(N)$, (3.12) and (3.13).

Case of (3.9). We are going to prove that $I(N) \geq 1/N$ for $\frac{2a_0}{(V_R - V_F)^2} < N < \frac{V_R}{b}$, which concludes the existence of a steady state since $I(0) < \infty$ due to (3.12) implies that $I(N) < 1/N$ for small N . Condition (3.9) only asserts that this interval for N is not empty. To do so, we show that

$$I(N) \geq \frac{(V_R - V_F)^2}{2a} \quad \text{for } N \in \left[0, \frac{V_R}{b}\right]$$

which obviously concludes the desired inequality $I(N) \geq 1/N$ for the interval of N under consideration.

The condition $\frac{V_R}{b} > N$ is equivalent to $w_R > 0$, therefore, using (3.5) and the expression for $I(N)$ in (3.6), we deduce

$$I(N) \geq \int_{w_R}^{w_F} \left[e^{-\frac{z^2}{2}} \int_{\max(z, w_R)}^{w_F} e^{\frac{u^2}{2}} du \right] dz \geq \int_{w_R}^{w_F} \left[e^{-\frac{z^2}{2}} \int_z^{w_F} e^{\frac{u^2}{2}} du \right] dz.$$

Since $z > 0$ and $e^{\frac{u^2}{2}}$ is an increasing function for $u > 0$, then $e^{\frac{u^2}{2}} \geq e^{\frac{z^2}{2}}$ on $[z, w_F]$, and we conclude

$$I(N) \geq \int_{w_R}^{w_F} \int_z^{w_F} du dz = \frac{(V_R - V_F)^2}{2a_0}.$$

Proof of iii). Under the condition (3.9), we have shown in the previous point the existence of an interval where $I(N) > 1/N$. On one hand, $I(0) < \infty$ in (3.12) implies that $I(N) < 1/N$ for N

small and the condition $b > V_F - V_R$ implies that $I(N) < I/N$ for N large enough due to the limit (3.13), thus there are at least two crossings between $I(N)$ and $1/N$.

Proof of iv). Under assumption (3.10) for b , it is easy to check that the following inequalities hold

$$I(0) < 1/N \quad \text{for } N \leq 2V_F/b \quad (3.15)$$

and

$$\frac{V_F - V_R}{bN - V_F} < \frac{1}{N} \quad \text{for } N > 2V_F/b. \quad (3.16)$$

We consider N such that $N > V_F/b$, this means that $w_F < 0$. We use the formula (3.7) for $I(N)$ and write the inequalities

$$\begin{aligned} I(N) &< (w_F - w_R) \int_0^\infty e^{-s^2/2} e^{sw_F} = (w_F - w_R) e^{w_F^2/2} \int_0^\infty e^{-(s-w_F)^2/2} \\ &= (w_F - w_R) e^{w_F^2/2} \int_{-w_F}^\infty e^{-s^2/2} \leq (w_F - w_R) e^{w_F^2/2} \int_{-w_F}^\infty \frac{s}{|w_F|} e^{-s^2/2} = \frac{V_F - V_R}{\sqrt{a}|w_F|} \end{aligned}$$

where the mean-value theorem and $w_F < 0$ were used. Then, we conclude that

$$I(N) < \frac{V_F - V_R}{\sqrt{a}|w_F|} = \frac{V_F - V_R}{bN - V_F}, \quad \text{for } N > V_F/b.$$

Therefore, using Inequality (3.16):

$$I(N) < \frac{1}{N}, \quad \text{for } N > 2V_F/b$$

and due to the fact that I is decreasing and Inequality (3.15), we have $I(N) < I(0) < 1/N$, for $N \leq 2V_F/b$. In this way, we have shown that for all N , $I(N) < 1/N$ and consequently there is no steady state. \square

Remark 3.3 *The functions $I(N)$ and $1/N$ are depicted in Figure 1 for the case $V_0(N) = bN$ and $a(N) = a_0$ illustrating the main result: steady states exist for small b and do not exist for large b while there is an intermediate range of existence of two stationary states. The numerical plots of the function $NI(N)$ might indicate that there are only three possibilities: one stationary state, two stationary states and no stationary state. However, we are not able to prove or disprove the uniqueness of a maximum for the function $NI(N)$ eventually giving this sharp result.*

Remark 3.4 *The condition (3.9) can be improved by using one more term in the series expansion of the exponentials inside the integral of the expression of $I(N)$ in (3.7). More precisely, if $w_F > w_R > 0$, we use*

$$e^{sw_F} - e^{sw_R} = \sum_{n=0}^{\infty} \frac{s^n}{n!} (w_F^n - w_R^n) \geq \sum_{n=0}^2 \frac{s^n}{n!} (w_F^n - w_R^n).$$

In this way, we get

$$I(N) \geq \int_0^\infty e^{-s^2/2} \left(\frac{V_F - V_R}{\sqrt{a}} + \frac{1}{2} (w_F^2 - w_R^2) s \right) ds \geq \frac{(V_F - V_R) (\sqrt{2\pi a} + (V_F - V_R))}{2a},$$

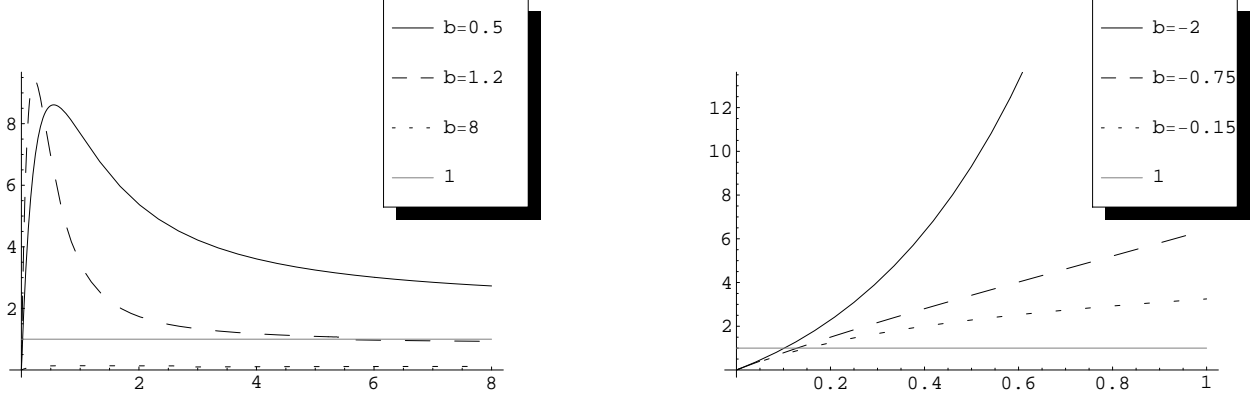


Figure 2: Left Figure: the function $NI(N)$ against the constant 1 when $a(N)$ is linear. For $b = 0.5$ we have considered $a(N) = 0.5 + N/8$, for $b = 1.2$: $a(N) = 0.4 + N/100$ and for $b = 8$: $a(N) = 6 + N/100$. Right Figure: the function $NI(N)$ against the constant 1 with $b < 0$ and $a(N) = 1 + N$. Here $V_R = 1$; $V_F = 2$.

since

$$\int_0^\infty e^{-s^2/2} ds = \sqrt{\frac{\pi}{2}}, \quad \int_0^\infty e^{-s^2/2} s ds = 1 \quad \text{and} \quad V_0 < V_R.$$

Then, condition (3.9) can be improved to

$$2ab < V_R (V_F - V_R) \left(\sqrt{2\pi a} + (V_F - V_R) \right).$$

3.3 Case of $a(N) = a_0 + a_1 N$

We now treat the case of $a(N) = a_0 + a_1 N$, with $a_0, a_1 > 0$ with $b > 0$. Proceeding as above we can obtain from (3.7) the expression of its derivative

$$I'(N) = -\frac{d}{dN} \left[\frac{V_0(N)}{\sqrt{a(N)}} \right] (I_1(N) - I_2(N)) + \frac{d}{dN} \left(\frac{1}{\sqrt{a(N)}} \right) (V_F I_1(N) - V_R I_2(N)), \quad (3.17)$$

where

$$I_1(N) = \int_0^\infty e^{-s^2/2} e^{s w_F} ds \quad \text{and} \quad I_2(N) = \int_0^\infty e^{-s^2/2} e^{s w_R} ds.$$

Therefore $I(N)$ is decreasing since

$$\frac{d}{dN} \left[\frac{V_0(N)}{\sqrt{a(N)}} \right] = \frac{2ba_0 + ba_1 N}{2(a_0 + a_1 N)^{3/2}} > 0 \quad \text{and} \quad \frac{d}{dN} \left(\frac{1}{\sqrt{a(N)}} \right) = -\frac{a_1}{(a_0 + a_1 N)^{3/2}} < 0.$$

Moreover, we can check that the computation of the limit (3.13) still holds. Actually, we have

$$\begin{aligned} \lim_{N \rightarrow \infty} \frac{NI(N)}{V_F - V_R} &= \lim_{N \rightarrow \infty} \frac{N}{\sqrt{a}} \int_0^\infty e^{-s^2/2} e^{-sbN/\sqrt{a}} ds = \lim_{N \rightarrow \infty} \sqrt{\pi} \frac{\operatorname{erfc}\left(\frac{bN}{\sqrt{2a}}\right)}{\frac{e^{-\frac{b^2 N^2}{2a}}}{\frac{N}{\sqrt{2a}}}} \\ &= \lim_{\alpha \rightarrow \infty} \sqrt{\pi} \frac{\operatorname{erfc}(b\alpha)}{\frac{e^{-b^2 \alpha^2}}{\alpha}} = \lim_{\alpha \rightarrow \infty} \sqrt{\pi} \frac{-\frac{2}{\sqrt{\pi}} b e^{-b^2 \alpha^2}}{\frac{-2b^2 \alpha^2 e^{-b^2 \alpha^2} - e^{-b^2 \alpha^2}}{\alpha^2}} = \frac{1}{b}, \end{aligned}$$

where we have used the change $\alpha = \frac{N}{\sqrt{2a}}$ and L'Hôpital's rule. In the case $b < 0$, we can observe again by the same proof as before that $I(N) \rightarrow \infty$ when $N \rightarrow \infty$, and thus, by continuity there is at least one solution to $NI(N) = 1$. Nevertheless, it seems difficult to clarify perfectly the number of solutions due to the competing monotone functions in (3.17).

The generalization of part of Theorem 3.1 is contained in the following result. We will skip its proof since it essentially follows the same steps as before with the new ingredients just mentioned.

Corollary 3.5 *Assume $h(v, N) = bN - v$, $a(N) = a_0 + a_1 N$ with $a_0, a_1 > 0$.*

- i) Under either the condition $b < V_F - V_R$, or the conditions $b > 0$ and $2a_0 b + 2a_1 V_R < (V_F - V_R)^2 V_R$, then there exists at least one steady state solution to (1.4)-(1.6).*
- ii) If both $2a_0 b + 2a_1 V_R < (V_F - V_R)^2 V_R$ and $b > V_F - V_R$ hold, then there are at least two steady states to (1.4)-(1.6).*
- iii) There is no steady state to (1.4)-(1.6) for $b > \max(2(V_F - V_R), 2V_F I(0))$.*

These behaviours are depicted in Figure 2. Let us point out that if a is linear and $b < 0$, $I(N)$ may have a minimum for $N > 0$.

4 Linear case and relaxation

We study specifically the linear case, $b = 0$ and $a(N) = a$, i.e.,

$$\begin{cases} \frac{\partial p(v, t)}{\partial t} - \frac{\partial}{\partial v} [vp(v, t)] - a_0 \frac{\partial^2}{\partial v^2} p(v, t) = \delta(v - V_R)N(t), & v \leq V_F, \\ p(V_F, t) = 0, & N(t) := -a_0 \frac{\partial}{\partial v} p(V_F, t) \geq 0, \quad a_0 > 0, \\ p(v, 0) = p^0(v) \geq 0, & \int_{-\infty}^{V_F} p^0(v) dv = 1. \end{cases} \quad (4.1)$$

For later purposes, we remind that the steady state $p_\infty(v)$ given in (3.4) satisfies

$$\begin{cases} -\frac{\partial}{\partial v} [vp_\infty(v)] - a_0 \frac{\partial^2}{\partial v^2} p_\infty(v) = \delta(v - V_R)N_\infty, & v \leq V_F, \\ p_\infty(V_F) = 0, & N_\infty := -a_0 \frac{\partial}{\partial v} p_\infty(V_F) \geq 0, \\ \int_{-\infty}^{V_F} p_\infty(v) dv = 1. \end{cases} \quad (4.2)$$

We will assume in this section that solutions of the linear problem exist with the regularity needed in each result below and such that for all $T > 0$ there exists $C_T > 0$ such that $p(v, t) \leq C_T p_\infty(v)$ for all $0 \leq t \leq T$. These solutions might be obtained by the method developed in [10] and will be analysed elsewhere.

We prove that the solutions converge in large times to the unique steady state $p_\infty(v)$. Two relaxation processes are involved in this effect: dissipation by the diffusion term and dissipation by the firing term. This is stated in the following result about relative entropies for this problem.

Theorem 4.1 *Fast-decaying solutions to equation (4.1) satisfy, for any smooth convex function $G : \mathbb{R}^+ \rightarrow \mathbb{R}$, the inequality*

$$\begin{aligned} \frac{d}{dt} \int_{-\infty}^{V_F} p_\infty(v) G\left(\frac{p(v, t)}{p_\infty(v)}\right) &= -N_\infty \left[G\left(\frac{N(t)}{N_\infty}\right) - G\left(\frac{p(v, t)}{p_\infty(v)}\right) - \left(\frac{N(t)}{N_\infty} - \frac{p(v, t)}{p_\infty(v)}\right) G'\left(\frac{p(v, t)}{p_\infty(v)}\right) \right] \Big|_{V_F} \\ &\quad - a_0 \int_{-\infty}^{V_F} p_\infty(v) G''\left(\frac{p(v, t)}{p_\infty(v)}\right) \left[\frac{\partial}{\partial v} \left(\frac{p(v, t)}{p_\infty(v)}\right) \right]^2 dv \leq 0. \end{aligned} \quad (4.3)$$

The following result is in fact standard on Poincaré inequalities on \mathbb{R} once q and p_∞ have been extended to the full line by odd symmetry with respect to V_F because p_∞ has a Gaussian behaviour at infinity thanks to (3.4), see [13].

Proposition 4.2 *There exists $\nu > 0$ such that*

$$\nu \int_{-\infty}^{V_F} p_\infty(v) \left(\frac{q(v)}{p_\infty(v)}\right)^2 \leq \int_{-\infty}^{V_F} p_\infty(v) \left[\frac{\partial}{\partial v} \left(\frac{q(v)}{p_\infty(v)}\right)\right]^2$$

for all functions q such $\frac{q}{p_\infty} \in H^1(p_\infty(v)dv)$.

Note that performing the even symmetry of q with respect to V_F ensures that the extended function \tilde{q} satisfies

$$\int_{\mathbb{R}} \tilde{q}(v) dv = 0.$$

These two theorems have direct consequences as in [15].

Corollary 4.3 (Exponential decay) *Fast-decaying solutions to the equation (4.1) satisfy*

$$\int_{-\infty}^{V_F} p_\infty(v) \left(\frac{p(v, t) - p_\infty(v)}{p_\infty(v)}\right)^2 \leq e^{-2a_0 \nu t} \int_{-\infty}^{V_F} p_\infty(v) \left(\frac{p^0(v) - p_\infty(v)}{p_\infty(v)}\right)^2.$$

Proof. Taking $q = p(v, t) - p_\infty(v)$ and $G(x) = (x - 1)^2$ in the relative entropy inequality (4.3), we obtain

$$\frac{d}{dt} \int_{-\infty}^{V_F} p_\infty(v) \left(\frac{p(v, t)}{p_\infty(v)} - 1\right)^2 \leq -2a_0 \int_{-\infty}^{V_F} p_\infty(v) \left[\frac{\partial}{\partial v} \left(\frac{p(v, t)}{p_\infty(v)} - 1\right)\right]^2.$$

Poincaré's inequality in Proposition 4.2 bounds the right hand side on the previous inequality

$$\frac{d}{dt} \int_{-\infty}^{V_F} p_\infty(v) \left(\frac{p(v, t)}{p_\infty(v)} - 1\right)^2 \leq -2a_0 \mu \int_{-\infty}^{V_F} p_\infty(v) \left(\frac{p(v, t)}{p_\infty(v)} - 1\right)^2.$$

Finally, the Gronwall lemma directly gives the result. \square

The proof of Theorem 4.1 is based on the following computations.

Lemma 4.4 Given p a fast-decaying solution of (4.1), p_∞ given by (3.4) and $G(\cdot)$ a convex function, then the following relations hold:

$$\frac{\partial}{\partial t} \frac{p}{p_\infty} - \left(v + \frac{2a_0}{p_\infty} \frac{\partial}{\partial v} p_\infty \right) \frac{\partial}{\partial v} \frac{p}{p_\infty} - a_0 \frac{\partial^2}{\partial v^2} \frac{p}{p_\infty} = \frac{N_\infty}{p_\infty} \delta(v - V_R) \left(\frac{N}{N_\infty} - \frac{p}{p_\infty} \right), \quad (4.4)$$

$$\begin{aligned} \frac{\partial}{\partial t} G \left(\frac{p}{p_\infty} \right) - \left(v + \frac{2a_0}{p_\infty} \frac{\partial}{\partial v} p_\infty \right) \frac{\partial}{\partial v} G \left(\frac{p}{p_\infty} \right) - a_0 \frac{\partial^2}{\partial v^2} G \left(\frac{p}{p_\infty} \right) \\ = -a_0 G'' \left(\frac{p}{p_\infty} \right) \left(\frac{\partial}{\partial v} \frac{p}{p_\infty} \right)^2 + \frac{N_\infty}{p_\infty} \delta(v - V_R) \left(\frac{N}{N_\infty} - \frac{p}{p_\infty} \right) G' \left(\frac{p}{p_\infty} \right), \end{aligned} \quad (4.5)$$

$$\begin{aligned} \frac{\partial}{\partial t} p_\infty G \left(\frac{p}{p_\infty} \right) - \frac{\partial}{\partial v} \left[v p_\infty G \left(\frac{p}{p_\infty} \right) \right] - a_0 \frac{\partial^2}{\partial v^2} \left[p_\infty G \left(\frac{p}{p_\infty} \right) \right] \\ = -a_0 p_\infty G'' \left(\frac{p}{p_\infty} \right) \left(\frac{\partial}{\partial v} \frac{p}{p_\infty} \right)^2 + N_\infty \delta(v - V_R) \left[\left(\frac{N}{N_\infty} - \frac{p}{p_\infty} \right) G' \left(\frac{p}{p_\infty} \right) + G \left(\frac{p}{p_\infty} \right) \right]. \end{aligned} \quad (4.6)$$

Proof. Since $\frac{\partial}{\partial v} \left(\frac{p}{p_\infty} \right) = \frac{1}{p_\infty} \frac{\partial p}{\partial v} - \frac{p}{p_\infty^2} \frac{\partial p_\infty}{\partial v}$ we obtain

$$\frac{\partial p}{\partial v} = p_\infty \frac{\partial}{\partial v} \left(\frac{p}{p_\infty} \right) + \frac{p}{p_\infty} \frac{\partial p_\infty}{\partial v}.$$

and

$$\frac{\partial^2 p}{\partial v^2} = p_\infty \frac{\partial^2}{\partial v^2} \left(\frac{p}{p_\infty} \right) + 2 \frac{\partial}{\partial v} \left(\frac{p}{p_\infty} \right) \frac{\partial p_\infty}{\partial v} + \frac{p}{p_\infty} \frac{\partial^2 p_\infty}{\partial v^2}.$$

Using these two expressions in

$$\frac{\partial}{\partial t} \left(\frac{p}{p_\infty} \right) = \frac{1}{p_\infty} \frac{\partial p}{\partial t} = \frac{1}{p_\infty} \left\{ \delta(v - V_R) N(t) + \frac{\partial}{\partial v} [v p(v, t)] + a_0 \frac{\partial^2}{\partial v^2} p(v, t) \right\}$$

we obtain (4.4).

Equation (4.5) is a consequence of Equation (4.4) and the following expressions for the partial derivatives of $G \left(\frac{p}{p_\infty} \right)$:

$$\frac{\partial}{\partial t} G \left(\frac{p}{p_\infty} \right) = G' \left(\frac{p}{p_\infty} \right) \frac{\partial}{\partial t} \left(\frac{p}{p_\infty} \right), \quad \frac{\partial}{\partial v} G \left(\frac{p}{p_\infty} \right) = G' \left(\frac{p}{p_\infty} \right) \frac{\partial}{\partial v} \left(\frac{p}{p_\infty} \right)$$

and

$$\frac{\partial^2}{\partial v^2} G \left(\frac{p}{p_\infty} \right) = G'' \left(\frac{p}{p_\infty} \right) \left(\frac{\partial}{\partial v} \left(\frac{p}{p_\infty} \right) \right)^2 + G' \left(\frac{p}{p_\infty} \right) \frac{\partial^2}{\partial v^2} \left(\frac{p}{p_\infty} \right).$$

Finally, Equation (4.6) is obtained using Equation (4.5) and the fact that p_∞ is solution of (4.2). \square

Proof Theorem 4.1. We integrate from $-\infty$ to $V_F - \alpha$ in (4.6) and let α tend to 0^+ and use L'Hôpital's rule

$$\lim_{v \rightarrow V_F} \frac{p(v, t)}{p_\infty(v)} = \lim_{v \rightarrow V_F} \frac{\frac{\partial p}{\partial v}(v, t)}{\frac{\partial p_\infty}{\partial v}(v)} = \frac{N(t)}{N_\infty}. \quad (4.7)$$

Since $p(v, t) \leq C_T p_\infty$ with $0 \leq t \leq T$, then

$$\begin{aligned} & \frac{d}{dt} \int_{-\infty}^{V_F} p_\infty G\left(\frac{p}{p_\infty}\right) dv - a_0 \frac{\partial}{\partial v} \left[p_\infty G\left(\frac{p}{p_\infty}\right) \right] \Big|_{V_F} \\ &= -a_0 \int_{-\infty}^{V_F} p_\infty G''\left(\frac{p}{p_\infty}\right) \left(\frac{\partial p}{\partial v}\right)^2 dv + N_\infty \left[\left(\frac{N}{N_\infty} - \frac{p}{p_\infty}\right) G'\left(\frac{p}{p_\infty}\right) + G\left(\frac{p}{p_\infty}\right) \right] \Big|_{V_R}. \end{aligned}$$

The Dirichlet boundary condition (1.5) implies that

$$-a_0 \frac{\partial}{\partial v} \left[p_\infty G\left(\frac{p}{p_\infty}\right) \right] \Big|_{V_F} = -a_0 \frac{\partial p_\infty}{\partial v} G\left(\frac{p}{p_\infty}\right) \Big|_{V_F} = N_\infty G\left(\frac{N(t)}{N_\infty}\right),$$

where we used that

$$p_\infty \frac{\partial}{\partial v} G\left(\frac{p}{p_\infty}\right) \Big|_{V_F} = p_\infty G'\left(\frac{p}{p_\infty}\right) \frac{-N p_\infty + N_\infty p}{p_\infty^2 a_0} \Big|_{V_F} = G'\left(\frac{q}{p_\infty}\right) \left(\frac{-N}{a_0} + \frac{N_\infty p}{a_0 p_\infty}\right) \Big|_{V_F} = 0,$$

due to (4.7). Collecting all terms leads to the desired inequality. \square

5 Numerical results

We consider an explicit method to simulate the numerical approximation for the>NNLIF (1.4). We base our algorithm on standard shock-capturing methods for the advection term and second-order finite differences for the second-order term. More precisely, the first order term is approximated by finite difference WENO-schemes [21].

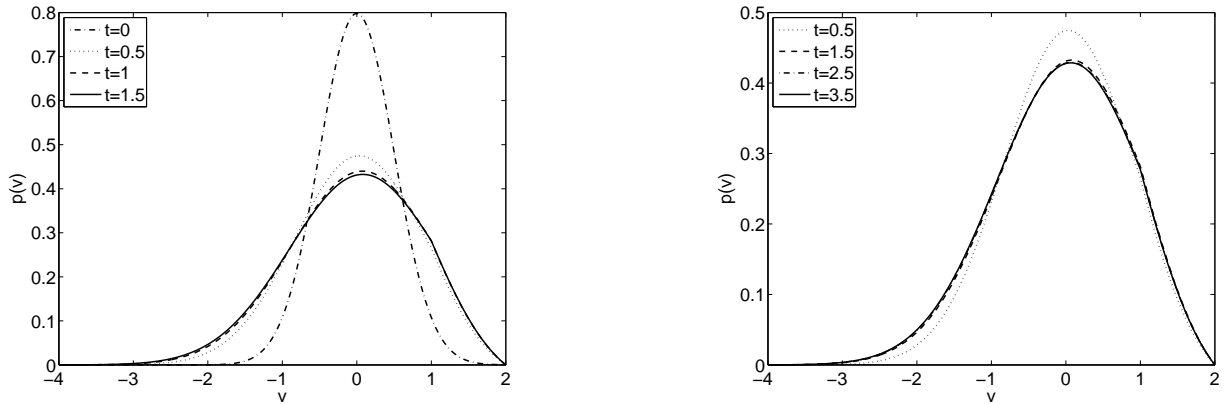


Figure 3: Distribution functions $p(v, t)$ for $b = 0.5$ and $a = 1$ at different times.

The time evolution is performed with a TVD Runge-Kutta scheme. Other finite difference scheme for the Fokker-Planck equation has been used such as the Chang-Cooper method [5] similarly to the approximation studied in [6] for a model with variable voltage and conductance. The Chang-Cooper method presents difficulties when the firing rate becomes large and the diffusion coefficient $a(N)$ is constant. To discuss this, we have just to remind the reader that the Chang-Cooper method performs a kind of θ -finite difference approximation of p/M where M is a Maxwellian in the kernel of the linear Fokker-Planck operator. Whenever $a(N)$ is constant, $b > 0$ and N is large, the drift of the

Maxwellian, in terms of which is rewritten the Fokker-Planck equation, practically vanishes on the interval $(-\infty, V_F]$ and this particular Chang-Cooper method is not suitable.

In our simulations we consider a uniform mesh in v , for $v \in [V_{min}, V_F]$. The value V_{min} (less than V_R) is adjusted in the numerical experiments to fulfill that $p(V_{min}, t) \approx 0$, while V_F is fixed to 2 and $V_R = 1$. Most of our initial data are Maxwellians:

$$p_0(v) = \frac{1}{\sigma_0\sqrt{2\pi}} e^{-\frac{(v-v_0)^2}{2\sigma_0^2}},$$

where the mean v_0 and the variance σ_0^2 are chosen according to the analyzed phenomenon. When the system has two steady states, we also take as initial data the profiles given by (3.2) with N an approximate value of the stationary firing rate, in order to start close to the stationary state with larger firing rate.

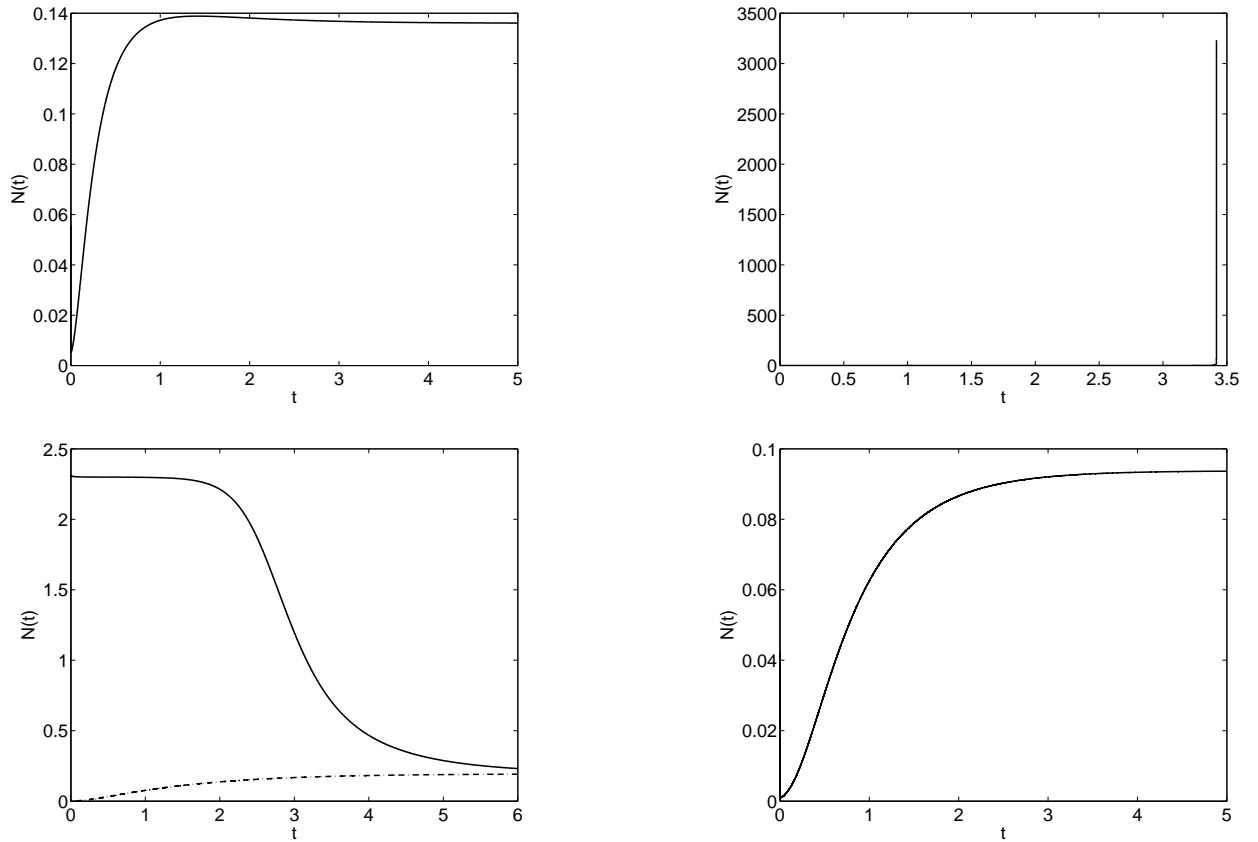


Figure 4: Firing rates $N(t)$ for $a = 1$. Top left: $b = 0.5$ with initial data a Maxwellian with: $v_0 = 0$ and $\sigma_o^2 = 0.25$. Top right: $b = 3$ with initial data a Maxwellian with: $v_0 = -1$ and $\sigma_o^2 = 0.5$. Bottom left: $b = 1.5$ considering two different initial data: a Maxwellian with: $v_0 = -1$ and $\sigma_o^2 = 0.5$ and a profile given by the expression (3.2) with $N = 2.31901$. Bottom right: $b = -1.5$ with initial data a Maxwellian with: $v_0 = -1$ and $\sigma_o^2 = 0.5$. The top right case seems to depict a blow-up phenomena demonstrated in Theorem 2.2.

Steady states.- As we show in Section 3, for b positive there is a range of values for which there are either one or two or no steady states. With our simulations we can observe all the cases represented in Figures 1 and 2.

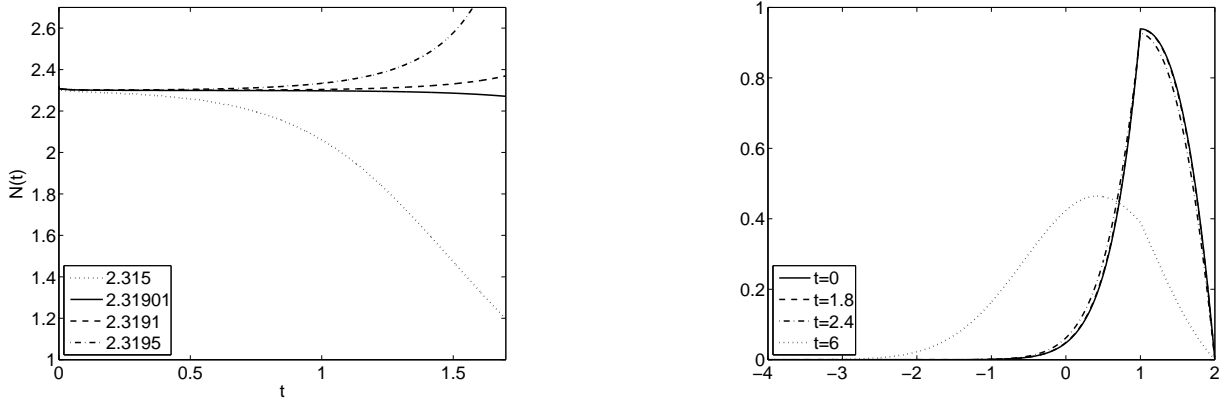


Figure 5: For $b = 1.5$ and $a(N) = 1$ figures show unstability of the steady state with higher firing rate. Left: Evolution on time of the firing rate considering different initial firing rate. Right: Evolution on time of the distribution function with initial firing rate 2.31901. In both figures we have considered $V_R = 1$; $V_F = 2$.

In Figure 3 we show the time evolution of the distribution function $p(v, t)$, in the case of $a = 1$ and $b = 0.5$, considering as initial data a Maxwellian with $v_0 = 0$ and $\sigma_0^2 = 0.25$. We observe that the solution after 3.5 time units numerically achieves the steady state with the imposed tolerance. The top left subplot in Figure 4 describes the time evolution of the firing rate, which becomes constant after some time. This clearly corresponds to the case of a unique locally asymptotically stable stationary state. Let us remark that in the right subplot of Figure 3, we can observe the Lipschitz behavior of the function at V_R as it should be from the jump in the flux and thus on the derivative of the solutions and the stationary states, see Section 3.

For $b = 1.5$, we proved in Section 3 that there are two steady states. With our simulations we can conjecture that the steady state with larger firing rate is unstable. However the stationary solution with low firing rate is locally asymptotically stable. We illustrate this situation in the bottom left subplot in Figure 4. Starting with a firing rate close to the high stationary firing value, the solution tends to the low firing stationary value.

In Figure 5 we analyze in more details the behavior of the steady state with larger firing rate. The left subplot presents the evolution on time of the firing rate for different distribution function starting with profiles given by the expression (3.2) with N an approximate value of the stationary firing rate. We show that, depending of the initial firing rate considered, its behavior is different: tends to the lower steady state or goes to infinity. The firing rate for the solution with initial $N_0 = 2.31901$ remains almost constant for a period of time. Observe in Figure 5 that the difference between the initial data and the distribution function at time $t = 1.8$ is almost negligible. However, the system evolves slowly and at $t = 6$ the distribution is very close to the the lower steady state, see the bottom left subplot in Figure 4.

In the bottom right subplot of Figure 4 we observe the evolution for a negative value of b , where we know that there is always a unique steady state, and its local asymptotic stability seems clear from the numerical experiments.

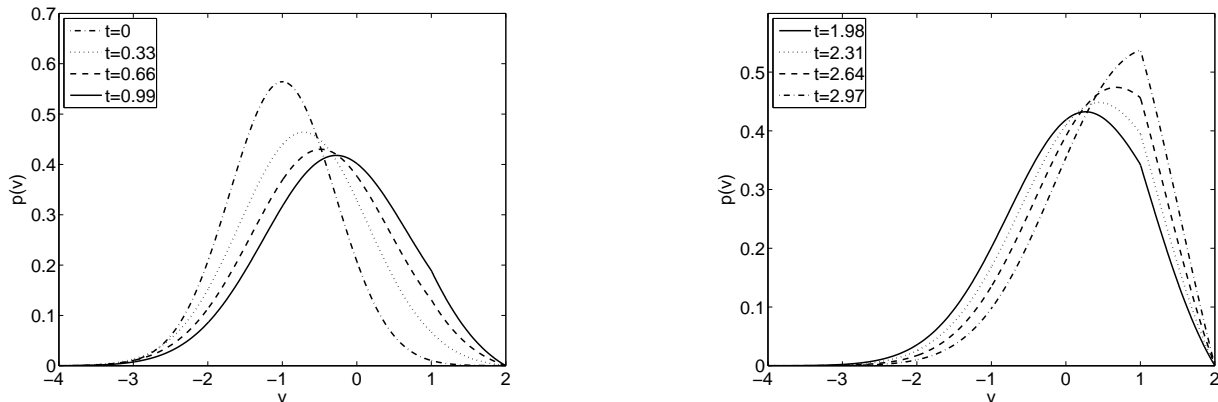


Figure 6: Distribution functions $p(v, t)$ for $a = 1$ and $b = 3$ at different times. See Figure 4 for the corresponding plots of $N(t)$.

No steady states.- Our results in Section 3 indicate that there are no steady states for $b = 3$. In Figure 6 we observe the evolution on time of the distribution function p . In Figure 4 (right top) we show the time evolution of the firing rate, which seems to blow up in finite time. We observe how the distribution function becomes more and more peaked at V_R and V_F producing an increasing value of the firing rate.

Blow up.- According to our blow-up Theorem 2.2, the blow-up in finite time of the solution happens for any value of $b > 0$ if the initial data is concentrated enough on the firing rate. In Figures 7 and 8, we show the evolution on time of the firing rate with an initial data with mass concentrated close to V_F for values of b in which there are either a unique or two stationary states. The firing rate increases without bound up to the computing time. It seems that the blow-up condition in Theorem 2.2 is not as restrictive as to say that the initial data is close to a Dirac Delta at V_F . Let us finally mention that blow-up appears numerically also in case of $a(N) = a_0 + a_1 N$, but here the blow-up scenario is characterized by a break-up of the condition under which (1.6) has a unique solution N , i.e.,

$$a_1 \left| \frac{\partial p}{\partial v}(V_F, t) \right| < 1.$$

Therefore, the blow-up in the value of the firing rate appears even if the derivative of p at the firing voltage does not diverge.

6 Conclusion

The nonlinear noisy leaky integrate and fire (NNLIF) model is a standard Fokker-Planck equation describing spiking events in neuron networks. It was observed numerically in various places, but never stated as such, that a blow-up phenomena can occur in finite time. We have described a class of situations where we can prove that this happens. Remarkably, the system can blow-up for all connectivity parameter $b > 0$, whatever is the (stabilizing) noise.

The nature of this blow-up is not mathematically proved. Nevertheless, our estimates in Lemma 2.3 indicate that it should not come from a vanishing behaviour for $v \approx -\infty$, or a lack of fast decay rate because the second moment in v is controlled uniformly in blow-up situations. Additionally,

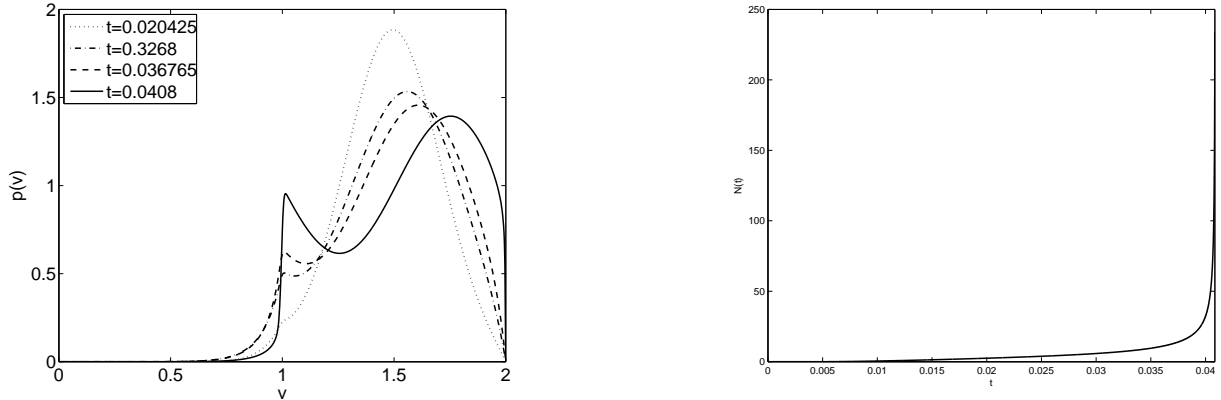


Figure 7: Parameter values are $a = 1$ and $b = 1.5$ and this corresponds to two steady states. Left: Evolution of the distribution function $p(v, t)$ in time of an initial Maxwellian centered at $v = 1.5$ and with variance 0.005. Right: Time evolution of the firing rate; again we observe numerically a blow-up behaviour for an initial data enough concentrated near V_F .

numerical evidence is that the firing rate $N(t)$ blows-up in finite time whenever a singularity in the system occurs. This scenario is compatible with all our theoretical knowledge on the NNLIF and in particular with L^1 estimates on the total network activity (firing rate $N(t)$).

Blow-up has also been proved to occur in the deterministic quadratic adaptive Integrate-and-Fire model in [22]. The blow-up scenario here is quite different from ours in many aspects; the model is a linear model (in our terminology) for a single neuron not a network. Remarkably, the blow-up scenario arises on the adaptation variable that we do not have in the NNLIF. These are interesting questions to know if blow-up could occur in a noisy 'linear' adaptive situation.

We have established that the set of steady states can be empty, a single state or two states depending on the network connectivity. These are all compatible with blow-up profile, and when they exist, numerics can exhibit convergence. Several questions are left open; is it possible to have triple or more steady states? Which of them are stable? Can a bifurcation analysis help to understand and compute the set of steady states?

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References

- [1] N. Brunel, Dynamics of sparsely connected networks of excitatory and inhibitory spiking networks, *J. Comp. Neurosci.* 8, (2000) 183–208.
- [2] A. Blanchet, J. Dolbeault, and B. Perthame, Two-dimensional Keller-Segel model: optimal critical mass and qualitative properties of the solutions, *Electron. J. Differential Equations* 44, (2006) 32 pp. (electronic).
- [3] R. Brette and W. Gerstner, Adaptive exponential integrate-and-fire model as an effective description of neural activity. *Journal of neurophysiology*, 94, (2005) 3637–3642.
- [4] N. Brunel and V. Hakim, Fast global oscillations in networks of integrate-and-fire neurons with long firing rates, *Neural Computation* 11, (1999) 1621–1671.
- [5] C. Buet, S. Cordier, and V. Dos Santos, A conservative and entropy scheme for a simplified model of granular media, *Transp. Theory Statist. Phys.* 33, (2004), 125–155.

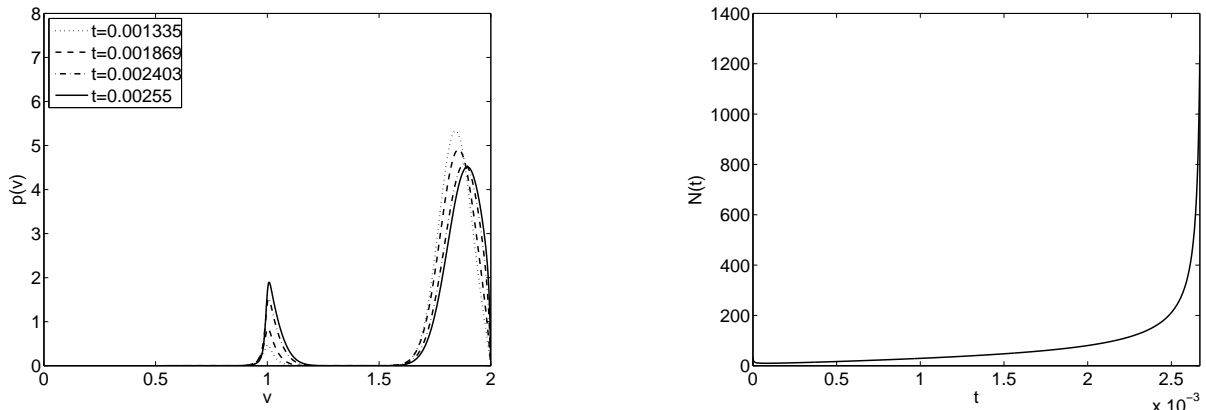


Figure 8: Parameter values are $a = 1$ and $b = 0.5$ and this corresponds to a single steady state. Left: Evolution of the distribution function $p(v, t)$ in time of an initial Maxwellian centered at $v = 1.83$ and with variance 0.003. Right: Time evolution of the firing rate; again this seems to be a typical blow-up behaviour.

- [6] M. J. Cáceres, J. A. Carrillo, and L. Tao, A numerical solver for a nonlinear Fokker-Planck equation representation of neuronal network dynamics, to appear in *J. Comp. Phys.*
- [7] A. Compte, N. Brunel, P. S. Goldman-Rakic, and X.-J. Wang, Synaptic mechanisms and network dynamics underlying spatial working memory in a cortical network model, *Cerebral Cortex* 10, (2000) 910–923.
- [8] L. Corrias, B. Perthame, and H. Zaag, Global solutions of some chemotaxis and angiogenesis systems in high space dimensions, *Milan J. Math.* 72, (2004) 1–28.
- [9] W. Gerstner and W. Kistler. *Spiking neuron models*. Cambridge Univ. Press (2002).
- [10] M. d. M. González and M. P. Gualdani, Asymptotics for a symmetric equation in price formation, *App. Math. Optim.* 59, (2009) 233–246.
- [11] T. Guillamon, An introduction to the mathematics of neural activity, *Butl. Soc. Catalana Mat.* 19 (2004), 25–45.
- [12] L. Lapicque, Recherches quantitatives sur l’excitation électrique des nerfs traitée comme une polarisation, *J. Physiol. Pathol. Gen.* 9, (1907) 620–635.
- [13] M. Ledoux, *The concentration of measure phenomenon*. AMS math. surveys and monographs 89. Providence 2001.
- [14] M. Mattia and P. Del Giudice, Population dynamics of interacting spiking neurons, *Phys. Rev. E* 66, (2002) 051917.
- [15] P. Michel, S. Mischler, and B. Perthame, General relative entropy inequality: an illustration on growth models, *J.Math.Pures Appl.* 84, (2005) 1235–1260.
- [16] K. Newhall, G. Kovačič, P. Kramer, A.V. Rangan, and D. Cai, Cascade-Induced Synchrony in Stochastically-Driven Neuronal Networks, preprint 2010.
- [17] K. Newhall, G. Kovačič, P. Kramer, D. Zhou, A.V. Rangan, and D. Cai, Dynamics of Current-Based, Poisson Driven, Integrate-and-Fire Neuronal Networks, *Comm. in Math. Sci.* 8 (2010) 541–600.
- [18] K. Pakdaman, B. Perthame, D. Salort, Dynamics of a structured neuron population, *Nonlinearity* 23 (2010) 55–75.
- [19] J. Pham, K. Pakdaman, J. Champagnat and J.-F. Vivert, Activity in sparsely connected excitatory neural networks: effect of connectivity. *Neural Networks* 11 (1998) 415–434.
- [20] A. Renart, N. Brunel, and X.-J. Wang, Mean-Field Theory of Irregularly Spiking Neuronal Populations and Working Memory in Recurrent Cortical Networks, Chapter 15 in *Computational Neuroscience: A comprehensive approach*, edited by Jianfeng Feng, Chapman & Hall/CRC Mathematical Biology and Medicine Series, 2004.
- [21] C.-W. Shu, Essentially Non-Oscillatory and Weighted Essentially Non-Oscillatory schemes for hyperbolic conservation laws, *Advanced Numerical Approximation of Nonlinear Hyperbolic Equations*, B. Cockburn, C. Johnson, C.-W. Shu and E. Tadmor (Editor: A. Quarteroni), *Lecture Notes in Mathematics*, volume 1697, Springer, 1998, pp. 325–432.

- [22] J. Touboul, Importance of the cutoff value in the quadratic adaptive integrate-and-fire model. *Neural Computation* 21, 2114-2122 (2009).
- [23] H.C. Tuckwell, *Introduction to Theoretical Neurobiology*, Cambridge, Cambridge University Press, 1988.