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TESI MAGISTRALE

**Analisi del modello differenziale NNLIF
di scarica random del potenziale
d'azione.**

**Random discharge potential NNLIF
model.**

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Riassunto. Oggetto della tesi sono i modelli NNLF (Nonlinear Noisy Leaky Integrate and Fire), basati su sistemi di PDE non lineari del tipo Fokker-Planck. Questi modelli descrivono l'attività del sistema neurale attraverso il potenziale di membrana, ovvero la differenza di potenziale tra l'interno e l'esterno del neurone. Quando il neurone riceve uno stimolo, il potenziale di membrana cresce e, raggiunta una certa soglia, genera un potenziale d'azione, ovvero un segnale elettrico che viene trasmesso agli altri neuroni tramite le sinapsi. Se il segnale ricevuto viene amplificato si parla di neurone eccitatorio, viceversa di neurone inibitorio.

Nel primo capitolo, che è una raccolta di risultati ottenuti in precedenza, approfondiremo in particolare il caso in cui il sistema neurale sia formato da neuroni solo eccitatori o solo inibitori e senza periodo refrattario. In particolare ci occuperemo di provare l'esistenza globale della soluzione nel caso di neuroni solo inibitori, mentre nel caso di neuroni solo eccitatori dimostreremo che le soluzioni esplodono a tempi finiti. Mostreremo poi come varia il numero di soluzioni stazionarie, al variare del parametro b che rappresenta la connettività tra i neuroni ($b > 0$ eccitatori, $b < 0$ inibitori).

Il secondo capitolo contiene i nuovi risultati e ha l'obiettivo di analizzare il caso in cui la scarica del potenziale d'azione sia random: questo significa che i segnali neuronali vengono trasmessi quando il potenziale di membrana raggiunge una soglia che non è fissa, ma casuale. Da un punto di vista matematico tale fenomeno si rappresenta aggiungendo un termine caratterizzato da una funzione ϕ_ϵ , chiamata tasso di scarico. Questa può essere scelta in vari modi, noi utilizzeremo prima una forma discontinua e poi una continua. Ci occuperemo in particolare di determinare le condizioni sui parametri affinché si abbiano 0, 1, o almeno 2 o 3 soluzioni stazionarie. Infine confronteremo i risultati dei due modelli mettendo in evidenza le differenze riscontrate.

Abstract. Subject of the thesis are the NNLIIF (Nonlinear Noisy Leaky Integrated and Fire) models, based on non-linear system of PDEs of Fokker-Planck type. These models describe the activity of the neural system through the membrane potential, that is the potential difference between the inside and outside of the neuron. When a neuron receives a stimulus, its membrane potential grows and, upon reaching a certain threshold, generates an action potential, or an electrical signal that is transmitted to the other neurons via the synapses. If the received signal is amplified it is called an excitatory neuron, vice versa an inhibitory neuron.

In the first chapter, which is a collection of previous results, we will investigate in particular the case in which the neural system is made up of average-excitatory or average-inhibitory neurons and without refractory period. In particular, we will prove global existence in the case of only inhibitory neurons, while in the case of only excitatory neurons we will demonstrate that the solutions blow up at finite times. Then we will show how the number of steady states varies in dependence of the parameter b which represents connectivity between neurons ($b > 0$ excitatory, $b < 0$ inhibitory).

The second chapter is the main part of this thesis as it contains the new results on the topic and has the aim of analyzing the case in which the discharge of the action potential is random: this means that the neuronal signals are transmitted when the membrane potential reaches a threshold which is not fixed, but random. From a mathematical point of view, this phenomenon is represented by adding a term characterized by a function ϕ_ϵ , called the discharge rate. This can be chosen in various ways, we will first use a discontinuous form and then a continuous one. We will deal in particular with the conditions on the parameters that allows us to have 0, 1, or at least 2 or 3 stationary solutions. Finally we will compare the results of the two models highlighting the differences found, and the differences with the fixed threshold model.

Introduction

The nervous system is a complex of specialized organs whose function can be briefly expressed as the ability to collect and recognize stimuli from the external and internal environment of the organism, elaborating voluntary and involuntary coordinated responses. The fundamental aspect of the physiology of the nervous system is that nerve functions depend on single units, called **neurons**, which have the same properties as those which make up other organs, but they are distinguished from the other cells for their marked ability to communicate: the combination of the functions of these cells results in the ability to integrate the functions of the other organs to allow optimal functioning.

In the last decades, mathematicians also began to study the functioning of the nervous system. There are a lot of types of mathematical models to describe the behaviour of neuronal network. The purpose of this thesis is to deepen one of the simplest self-contained mean-field models, the Nonlinear Noisy Leaky Integrate and Fire (NNLIF) model, which is based on nonlinear systems of PDEs of Fokker-Plank type.

Now let us firstly see how neurons work [11][12][15][23][22], and then we will describe the basic idea of NNLIF model [12][15][16][5][22].

Neurons

Neurons are highly specialized cells which are in charge of the reception of the nerve impulses. In each neuron we can find 4 parts: the cell body, the dendrites, the axon and the synaptic terminal (see Figure 1). The *cell body* is the genetic and metabolic center and is the portion of the neuron in which protein synthesis and processing take place. *Dendrites* are branched processes that emerge from the cell body; their plasma membrane is particularly rich in neurotransmitter receptors and they represent the main apparatus for receiving signals originating in other neurons. The *axon* also originates from the cell body but, unlike the dendrites that remain in the vicinity of the cell body, it can move away for considerable distances and has no ramifications. At the end of its course, the axon branches into numerous terminations, the *synaptic terminals*, which contain the synaptic vesicles and the complex molecular apparatus that regulates the release of neurotransmitters.

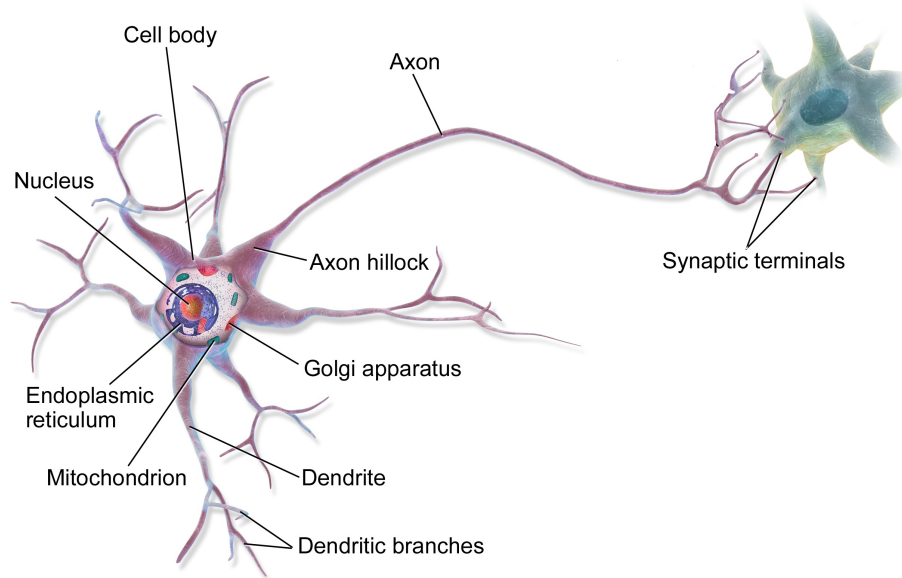


Figure 1: Structure of a neuron. Source: Wikipedia.

In order to send a nerve impulse, neurons generate action potentials (or spikes), which are electric impulses that appear as a reply to the stimuli they receive. These impulses arrive at the neuron by the dendrites, travel through the axon and pass from one to another by the synapses: it's important to know that the sending and reception of the nerve impulse is not an instantaneous process, because it passes a small period called *synaptic delay* since the signal leaves the presynaptic neuron until it reaches the postsynaptic one. On the other hand, the signal that they receive from other neurons can be **excitatory** or **inhibitory**, depending on whether they increase or decrease the probability of occurrence of an action potential.

Inside the neurons there are different ions, in particular sodium Na^+ and potassium K^+ . The neuron membrane is impermeable to these ions, but it has some ionic channels that allow the crossing of ions from inside to the outside or vice versa. This polarization generates a potential difference between the inside and outside of the cell, called **membrane potential** and defined as

$$V(t) := V_{int}(t) - V_{ext}(t).$$

Without signals, $V(t)$ relaxes towards an equilibrium or resting potential $V_{eq} \sim -70mV$. When a neuron receives current from a nerve impulse, the resting potential gets lost. First, as a reply to the stimulus, the sodium channels are opened, so that sodium enters the neuron due to the electrical attraction. As a consequence, the value of $V(t)$ increases. If it reaches a certain *threshold value*, V_F , an action potential is emitted. Moreover, while the sodium channels are

opened, the potassium channels are opened slower. Thus, potassium gets out of the cell due to the concentration difference, since usually there is a higher sodium concentration inside the neuron than outside. The exit of potassium makes the membrane potential negative again. Finally, the neuron remains some time in a *refractory period* and does not respond to stimuli, while the sodium-potassium pumps return every ion to its place and the membrane potential relaxes to a reset value V_R .

NNLIF model

By a mathematical point of view the time evolution of the membrane potential $V(t)$ can be modeled as an electrical circuit

$$C_m \frac{dV}{dt}(t) = I(t), \quad (1)$$

where $I(t)$ is the intensity of the applied current and C_m is the capacitance of the membrane. Nevertheless, as in a neuron there are several active ionic channels that influence directly the value of the membrane potential, we have to extend the equation (1) as follows:

$$C_m \frac{dV}{dt}(t) = -g_{Na}(V(t) - V_{Na}) - g_K(V(t) - V_K) - g_L(V(t) - V_L) + I(t), \quad (2)$$

where g_i is the conductance of the channel associated to the ion i , i.e. the ease with which the ions cross the channel, and V_i is the reversal potential of the channel i , i.e. the value of the potential that corresponds to an equilibrium between the inside and the outside fluxes. Moreover, in the term $I_L(t) := g_L(V(t) - V_L)$, which is called *leak current*, we join all the contributions of the other ions, distinct from sodium and potassium.

If we include the ionic currents of sodium and potassium also in the term that groups the leak currents $I_L(t)$, from (2) we find the **Integrate and Fire (IF) model**:

$$C_m \frac{dV}{dt}(t) = -g_L(V(t) - V_L) + I(t), \quad (3)$$

where g_L is the leak conductance and V_L is the leak reversal potential.

Now we can present the **Nonlinear Noisy Leaky Integrate and Fire (NNLIF) model**. We consider a neural network with n neurons (n_E excitatory and n_I inhibitory) described by the IF model, which depicts the activity of the membrane potential. The time evolution of the membrane potential $V(t)$ of an inhibitory neuron ($\alpha = I$) or an excitatory one ($\alpha = E$) is given by (see [3][4])

$$C_m \frac{dV^\alpha}{dt}(t) = -g_L(V^\alpha(t) - V_L) + I^\alpha(t) \quad (4)$$

where $I^\alpha(t)$ is the incoming synaptic current, which models all the interactions of the neuron with other neurons. The synaptic current takes the form of the following stochastic process:

$$I^\alpha(t) = J_E^\alpha \sum_{i=1}^{\bar{C}_E} \sum_i \delta(t - t_{E_j}^i - D_E^\alpha) - J_I^\alpha \sum_{i=1}^{C_I} \sum_i \delta(t - t_{I_j}^i - D_I^\alpha), \quad \alpha = E, I,$$

where:

- $\delta(t)$ is the Dirac delta;
- $D_E^\alpha \geq 0, D_I^\alpha \geq 0$ are the two synaptic delays;
- $t_{E_j}^i$ and $t_{I_j}^i$ are the times of the j^{th} -spike coming from the i^{th} -presynaptic neuron for excitatory and inhibitory neurons, respectively;
- C_E and C_I are the number of connections from excitatory and inhibitory neurons inside the network;
- $\bar{C}_E = C_E + C_{ext}$, where C_{ext} is the number of connections for each neuron in the network from excitatory neurons outside the network ;
- J_k^α are the strengths of the synapses.

The spike trains of all neurons in the network are supposed to be described by Poisson processes with a common instantaneous firing rate, $\nu_\alpha(t)$. These processes are supposed to be independent. By using these hypothesis, the mean value of the current, $\mu_C^\alpha(t)$, and its variance, $\sigma_C^{\alpha^2}(t)$, take the form

$$\mu_C^\alpha(t) = C_E J_E^\alpha \nu_E(t - D_E^\alpha) - C_I J_I^\alpha \nu_I(t - D_I^\alpha), \quad (5)$$

$$\sigma_C^{\alpha^2}(t) = C_E (J_E^\alpha)^2 \nu_E(t - D_E^\alpha) + C_I (J_I^\alpha)^2 \nu_I(t - D_I^\alpha), \quad (6)$$

Many authors [3][4][17][19] then approximate the incoming synaptic current by a continuous in time stochastic process

$$I^\alpha(t)dt \approx \mu_C^\alpha(t)dt + \sigma_C^\alpha(t)dB_t \quad (7)$$

where B_t is the standard Brownian motion. Summing up, the approximation to the differential equation model (4), with stochasticity given by the incoming synaptic current, taking the voltage and time units so that $C_m = g_L = 1$, finally yields

$$dV^\alpha(t) = (-V^\alpha(t) + V_L + \mu_C^\alpha(t))dt + \sigma_C^\alpha(t)dB_t, \quad V^\alpha \leq V_F, \quad \alpha = E, I, \quad (8)$$

with the jump process $V^\alpha(t_0^+) = V_R, V^\alpha(t_0^-) = V_F$, whenever at t_0 the voltage reaches the threshold value V_F . The firing rate of the Poisson spike train, $\nu_\alpha(t)$, is calculated in [20] as

$$\nu_\alpha(t) = \nu_{\alpha,ext} + N_\alpha(t), \quad \alpha = E, I,$$

where $\nu_{\alpha,ext}$ is the frequency of the external input and $N_\alpha(t)$ is the mean firing rate of the population α (in particular $\nu_{I,ext} = 0$ since the external connections are with excitatory neurons).

From (8) a system of coupled partial differential equations for the evolution of the **probability densities** $p_\alpha(v, t)$ can be written, where $p_\alpha(v, t)$ denotes the probability of finding a neuron in the population α , with a voltage $v \in (-\infty, V_F]$ at time $t \geq 0$. In [22][3][4][17][21], taking the limit $n \rightarrow +\infty$ and using Ito's rule the stochastic equations (4) and (7) lead to a system of coupled Fokker-Planck equations

$$\left\{ \begin{array}{l} \frac{\partial p_I}{\partial t}(v, t) + \frac{\partial}{\partial v} [h^I(v, N_E(t - D_E^I), N_I(t - D_I^I)) p_I(v, t)] + \\ -a_I(N_E(t - D_E^I), N_I(t - D_I^I)) \frac{\partial^2 p_I}{\partial v^2}(v, t) = M_I(t) \delta(v - V_R), \\ \\ \frac{\partial p_E}{\partial t}(v, t) + \frac{\partial}{\partial v} [h^E(v, N_E(t - D_E^E), N_I(t - D_I^E)) p_E(v, t)] + \\ -a_E(N_E(t - D_E^E), N_I(t - D_I^E)) \frac{\partial^2 p_E}{\partial v^2}(v, t) = M_E(t) \delta(v - V_R), \end{array} \right. \quad (9)$$

with $h^\alpha(v, N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) = -v + V_L + \mu_C^\alpha$ the *drift coefficient* and $a_\alpha(N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) = \frac{\sigma_C^{\alpha 2}}{2}$ the *diffusion coefficient* and N_α the **mean firing rates** which represents the flux of neurons across the threshold V_F and obey to

$$N_\alpha(t) = -a_\alpha(N_E(t), N_I(t)) \frac{\partial p_\alpha}{\partial v}(V_F, t) \geq 0 \quad \alpha = E, I. \quad (10)$$

Notice that (10) gives rise to the nonlinearity of the system (9) since firing rates are defined in terms of boundary conditions on distribution functions p_α . The right hand sides in (9) represents 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, denoted τ_α . Different choices of $M_\alpha(t)$ can be considered: $M_\alpha(t) = N_\alpha(t - \tau_\alpha)$ and $M_\alpha(t) = \frac{R_\alpha(t)}{\tau_\alpha}$. Thus, system (9) is completed with two ODEs for $R_\alpha(t)$, the probabilities to find a neuron from population α in the refractory state

$$\frac{dR_\alpha(t)}{dt} = N_\alpha(t) - M_\alpha(t), \quad \forall \alpha = E, I, \quad (11)$$

with Dirichlet boundary conditions and initial data

$$p_\alpha(-\infty, t) = p_\alpha(V_F, t) = 0, \quad p_\alpha(v, t) = p_\alpha^0(v) \geq 0, \quad R_\alpha(0) = R_\alpha^0 \geq 0 \quad \alpha = E, I. \quad (12)$$

In order to simplify the notation, we denote $b_k^\alpha = C_k J_k^\alpha \geq 0$, which represent the **connectivities of the network**, and $d_K^\alpha = C_k^\alpha (J_k^\alpha)^2 \geq 0$, for $k, \alpha = E, I$, and the variable v is translated with the factor $V_L + b_E^E \nu_{E,ext}$. So, using the expression (5) and (6), the drift and diffusion coefficients become

$$\begin{aligned} h^\alpha(v, N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) &= \\ &= -v - V_L - b_E^E \nu_{E,ext} + V_L + b_E^\alpha \nu_E(t - D_E^\alpha) - b_I^\alpha \nu_I(t - D_I^\alpha) = \\ &= -v + b_E^\alpha N_E(t - D_E^\alpha) - b_I^\alpha N_I(t - D_I^\alpha) + (b_E^\alpha - b_E^E) \mu_{E,ext}, \end{aligned} \quad (13)$$

$$a_\alpha(N_E(t - D_E^\alpha), N_I(t - D_I^\alpha)) = \frac{1}{2} (d_E^\alpha \nu_{E,ext} + d_E^\alpha N_E(t - D_E^\alpha) + d_I^\alpha N_I(t - D_I^\alpha)). \quad (14)$$

Since R_E and R_I represent probabilities and p_E and p_I are probability densities, the total mass is conserved:

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

The model (9)-(11) is quite complex and its mathematical analysis is difficult. This is the reason why it is necessary to start by studying some simplifications.

One simplification is to consider two population of neurons, excitatory and inhibitory, but without transmission delays between the neurons ($D_E = D_I = 0$) and without refractory state ($\tau_\alpha = 0$). In this case the model is reduced to a system of two PDEs:

$$\left\{ \begin{aligned} &\frac{\partial p_I}{\partial t}(v, t) + \frac{\partial}{\partial v} [h^I(v, N_E(t), N_I(t)) p_I(v, t)] - a_I(N_E(t), N_I(t)) \frac{\partial^2 p_I}{\partial v^2}(v, t) \\ &= N_I(t) \delta_{V_R}(v), \\ &\frac{\partial p_E}{\partial t}(v, t) + \frac{\partial}{\partial v} [h^E(v, N_E(t), N_I(t)) p_E(v, t)] - a_E(N_E(t), N_I(t)) \frac{\partial^2 p_E}{\partial v^2}(v, t) \\ &= N_E(t) \delta_{V_R}(v), \end{aligned} \right. \quad (15)$$

In this way, for $\alpha = E, I$, the drift and the diffusion terms in (15) are not delayed:

$$h^\alpha(v, N_E(t), N_I(t)) = -v + b_E^\alpha N_E(t) - b_I^\alpha N_I(t) + (b_E^\alpha - b_E^E) \nu_{E,ext}, \quad (16)$$

$$a_\alpha(N_E(t), N_I(t)) = \frac{1}{2} (d_E^\alpha \nu_{E,ext} + d_E^\alpha N_E(t) + d_I^\alpha N_I(t)), \quad (17)$$

and there are no refractory states, which 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:

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

Even so, the model (15) is still too complex and so we can consider a further simplification: only one population in average-excitatory or average-inhibitory, without transmission delays between the neurons, and without refractory state:

$$\frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v}[h(v, N(t))p(v, t)] - a(N(t)) \frac{\partial^2 p}{\partial v^2}(v, t) = N(t) \delta_{V_R}(v), \quad (18)$$

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:

- $b > 0$: means that the neurons of the network are average-excitatory;
- $b < 0$: means that the neurons of the network are average-inhibitory.

So in this sense we consider only one population on average-excitatory or average-inhibitory depending of the sign of the connectivity parameter b . This choice makes sense because if we consider the case of two populations (model (15)), if the population of inhibitory is empty ($N_I = 0$), then $b_\alpha^I = 0$, and so $h^E(v, N_E) = -v + b_E^E N_E$ ($b_E^E > 0$), and vice versa if the population of excitatory is empty ($N_E = 0$), then $b_\alpha^E = 0$, and so $h^I(v, N_I) = -v - b_I^I N_I$ ($b_I^I > 0$).

Again the model (18) is nonlinear because the mean firing rate is computed in terms of the derivative with respect to v of p at the border V_F :

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

Model (18) is studied in depth in [6].

In Chapter 1 we are going to summarize the main results regarding model (18). In particular in the first part we will study the existence of solutions and by proving Criterion 1.1.4 which correlates the maximum time of existence of solutions with the time of divergence of the firing rate $N(t)$, we will show in which cases there is a global existence: in particular we will prove that solutions blow-up if and only if the firing rate diverges at finite time. In the second part instead we will find the number of steady states depending on the value of parameters.

Second Chapter is the core of this thesis, and it contains some new results. We will consider a modification of model (18), presented in [7], which consists in assuming some randomness on the discharge potential. This makes sense

because neurons discharge when they reach a threshold, which is actually not a fixed value, but more or less close to V_F . So the new model is:

$$\frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v}[h(v, N(t))p(v, t)] - a(N(t))\frac{\partial^2 p}{\partial v^2}(v, t) + \phi_\epsilon(v)p = N(t)\delta_{V_R}(v), \quad (19)$$

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

$$N(t) = \int_{-\infty}^{+\infty} \phi_\epsilon(v)p(v, t)dv.$$

In particular we will study the number of steady states of this model and then in the chapter of conclusions we will compare it with the results of Chapter 1 about model (18).

Finally in Appendix A we will show Matlab codes used to generate some examples in Chapter 1 and in Appendix B we will develop some calculations of Chapter 2 in detail.

Relation with neurophysiological phenomena

From a biological point of view NNLIIF model could be interesting to describe phenomena well known in neurophysiology: synchronous and asynchronous states. As in [9][3] we will call asynchronous the states in which the firing rate tends to be constant in time and synchronous every other state. Experimental and computational results exhibiting such phenomena can be found in [3] and references therein.

Thus, on one hand, when the model does not have stable steady states, there are synchronous states. In this sense, the blow-up phenomenon could be understood as a synchronization of part of the network, because the firing rate diverges for a finite time. Possibly, this entails that a part of the network synchronizes, and thus fires at the same time. Synchronization between neurons is crucial for diseases of the nervous system such as Parkinson or epilepsy. For example, an epileptic attack is characterized by a very high level of neuronal synchronization.

On the other hand, the presence of asymptotically stable steady states implies asynchronous states, since the firing rate tends asymptotically to be constant in time. Moreover, the presence of several steady states could provide rich behaviours of the network, since multi-stability phenomena could appear. Multi-stable networks are related, for instance, to the decision making [2][14] and the visual perception. The last one involves several phenomena, including for example the perceptual bistability [18]. This is a particular phenomenon of visual perception that occurs when an ambiguous stimulus that has two distinct interpretations is presented to an observer, and so its perception alternates over time between the different possible percepts in an irregular manner, like happens by looking Figure 2.



Figure 2: the old and young women.

Chapter 1

One population without refractory states

In this Chapter we focus on the simplification (18) which we mentioned in the Introduction. All the results we are going to present here have already been dealt in previous articles [22][6][13]. We want to dedicate a chapter to this model because it is important to introduce to the study of NNLF models and will be essential to present and study the random discharge potential model which is the core of this thesis.

In the first section we deal with the existence of solutions of model (18). We show that the maximal time of existence of solutions T^* strictly depends on the time divergence of the firing rate $N(t)$. In particular, in the inhibitory case solutions are always defined on $t \in [0, +\infty)$, while in the excitatory case T^* can be a finite time.

In the second section we will consider the delayed model and we will prove the globally existence of solutions both in the inhibitory case and the excitatory case.

In the third section we are going to find the number of steady states of model (18). We will show that in the inhibitory case there is always only one steady state, while in the excitatory case, depending on the value of parameter b , there may be 0, 1 or at least 2.

The Fokker-Plank equation which describes this model of one population without transmission delays or refractory states is

$$\frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v}[h(v, N(t))p(v, t)] - a(N(t))\frac{\partial^2 p}{\partial v^2}(v, t) = N(t)\delta_{V_R}(v), \quad (1.1)$$

with $v \in (-\infty, V_F]$ at a time $t \geq 0$, and

$$N(t) = -a(N(t))\frac{\partial p}{\partial v}(V_F, t) \geq 0, \quad (1.2)$$

where the right-hand side is nonnegative since $p \geq 0$ over the interval $(-\infty, V_F]$ and thus, $\frac{\partial p}{\partial v}(V_F, t) \leq 0$. The partial differential equation (1.1) is complemented with Dirichlet and initial boundary conditions

$$p(V_F, t) = p(-\infty, 0) = 0, \quad p(v, 0) \geq 0. \quad (1.3)$$

Furthermore, since there is no refractory state and $p(v, t)$ is a probability density, we have that

$$\int_{-\infty}^{V_F} p(v, t) dv = \int_{-\infty}^{V_F} p^0(v) dv = 1 \quad (1.4)$$

for all $t \geq 0$. Finally, we have already observed in the Introduction that the drift and diffusion coefficients are of the form

$$h(v, N) = -v + bN, \quad a(N) = a_0 + a_1N, \quad (1.5)$$

where $b > 0$ for excitatory-average networks, $b < 0$ for inhibitory-average networks, $a_0 > 0$ and $a_1 \geq 0$.

1.1 Blow up and global existence

Before showing the theorems regarding the existence of solutions, let us remember the definition of weak solution [6], which we will use for all our results.

Definition 1.1.1. *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 (1.1)-(1.5) if for any test function $\psi(v, t) \in C^\infty((-\infty, V_F] \times [0, T])$ such that $\frac{\partial^2 \psi}{\partial v^2}, v \frac{\partial \psi}{\partial v} \in L^\infty((-\infty, V_F] \times (0, T))$, we have*

$$\begin{aligned} & \int_0^T \int_{-\infty}^{V_F} p(v, t) \left[-\frac{\partial \psi}{\partial t} - \frac{\partial \psi}{\partial v} h(v, N) - a \frac{\partial^2 \psi}{\partial v^2} \right] dv dt = \quad (1.6) \\ & = \int_0^T N(t) [\psi(V_R, t) - \psi(V_F, t)] dt + \int_{-\infty}^{V_F} p^0(v) \psi(v, 0) dv - \int_{-\infty}^{V_F} p(v, T) \psi(v, T) dv. \end{aligned}$$

In particular, choosing test functions of the form $\zeta(t)\psi(v)$, for all $\psi \in C^\infty((-\infty, V_F])$ such that $v \frac{\partial \psi}{\partial v} \in C^\infty((-\infty, V_F])$, a weak solution of (1.1)-(1.5) satisfies

$$\begin{aligned} \frac{d}{dt} \int_{-\infty}^{V_F} \psi(v) p(v, t) dv &= \int_{-\infty}^{V_F} \left[\frac{\partial \psi}{\partial v} h(v, N) + a \frac{\partial^2 \psi}{\partial v^2} \right] p(v, t) dv \\ &+ N(t) [\psi(V_F, t) - \psi(V_R, t)], \quad (1.7) \end{aligned}$$

in the distributional sense. The first result we show [6] is that weak solutions of (1.1)-(1.3) can blow up at finite time in the case of an average-excitatory network (Theorem 1.1.3).

This result holds with less stringent hypotheses on the coefficients than in (1.5) with an analogous notion of weak solution as in Definition 1.1.1. Before presenting Theorem 1.1.3, we show the following lemma which will be useful in the proof.

Lemma 1.1.2. (*Gronwall's inequality*). *Let $[0, b]$ be an interval in \mathbb{R}_+ , $u \in C([0, b])$ and β, α nonnegative, summable functions on $[0, b]$ so that $u'(t) \leq \beta(t)u(t) + \alpha(t) \forall t \in (0, b)$ then*

$$u(t) \leq e^{\int_0^t \beta(s) ds} \left[u(0) + \int_0^t \alpha(s) e^{-\int_0^s \beta(s) ds} ds \right].$$

Theorem 1.1.3. *Assume that:*

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

Choosing $\mu > \max(\frac{V_F}{a_m}, \frac{1}{b})$, 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 close enough to $e^\mu V_F$, then there are no global-in-time weak solutions to (1.1)-(1.3).

Proof. We choose $\psi(v) = e^{\mu v}$. Observe that the i -derivative $\psi^{(i)}(v) = \mu^i \psi(v)$. For a weak solution according to (1.6), using the hypotheses on the diffusion and drift terms and the fact that $v \in (-\infty, V_F)$, we find from (1.7) that

$$\begin{aligned} \frac{d}{dt} \int_{-\infty}^{V_F} \psi(v) p(v, t) dv &\geq \mu \int_{-\infty}^{V_F} V_F (bN(t) - v) \psi(v) p(v, t) + \\ &+ \mu^2 a_m \int_{-\infty}^{V_F} \psi(v) p(v, t) dv + N(t) [\psi(V_R) - \psi(V_F)] \\ &\geq \mu [bN(t) + \mu a_m - V_F] \int_{-\infty}^{V_F} \psi(v) p(v, t) dv - N(t) \psi(V_F). \end{aligned} \quad (1.8)$$

Thus, denoting

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

we obtain, from (1.8),

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

and by Gronwall's inequality (Lemma 1.1.2):

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

After some more computations that include the fact that $\mu a_m - V_F > 0$, the right hand side of the previous inequality can be bounded by $-\frac{\psi(V_F)}{\mu b}$:

$$\begin{aligned}
& -\psi(V_F) \int_0^t N(s) e^{-\mu \int_0^s (bN(z) + \mu a_m - V_F) dz} ds \geq \\
& \geq -\frac{\psi(V_F)}{\mu b} \int_0^t \mu (bN(s) + \mu a_m - V_F) e^{-\mu \int_0^s (bN(z) + \mu a_m - V_F) dz} ds = \\
& = -\frac{\psi(V_F)}{\mu b} \int_0^t -\frac{d}{ds} e^{-\mu \int_0^s (bN(z) + \mu a_m - V_F) dz} ds = \\
& = -\frac{\psi(V_F)}{\mu b} [e^{-\mu \int_0^s (bN(z) + \mu a_m - V_F) dz}]_0^t = \\
& = -\frac{\psi(V_F)}{\mu b} [1 - e^{-\mu \int_0^t (bN(z) + \mu a_m - V_F) dz}] > -\frac{\psi(V_F)}{\mu b}.
\end{aligned}$$

Finally, the following inequality holds

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

This inequality produces a contradiction if $K := \left(M_\mu(0) - \frac{\psi(V_F)}{\mu b} \right) > 0$, because, remembering that $p(v, t)$ is a probability density:

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

which cannot be true for all $t \geq 0$. Therefore, to conclude the proof we only need to guarantee the nonnegativity of K . To verify this, we can approximate as much as we want by smooth initial probability densities an initial Dirac mass at V_F ($p^0(v) \approx \delta(v - V_F)$) which gives the condition

$$M_\mu(0) = \int_{-\infty}^{V_F} e^{\mu v} p^0(v) dv = e^{\mu V_F} > \frac{e^{\mu V_F}}{\mu b},$$

that is verified because $\mu > \frac{1}{b}$ from hypotheses. □

Now, more specifically, is possible to prove that, under suitable assumptions, solutions blow up if and only if the firing rates diverge at finite time. We are going to present a criterion [13] to determine the maximum time of existence for the solutions of problem (1.1)-(1.5).

Criterion 1.1.4. *Let $p^0(v)$ be a non-negative $C^1((-\infty, V_F]) \cap L^1(-\infty, V_F)$ function such that $p^0(V_F) = 0$ and*

$$\lim_{v \rightarrow -\infty} \frac{\partial p^0}{\partial v}(v) = 0.$$

There exists a unique classical solution to the problem (1.1)-(1.5) in the time interval $[0, T^*)$ with $T^* > 0$. The maximal existence time $T^* > 0$ can be characterized as

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

Furthermore:

- if $b < 0$ (average-inhibitory case) : $T^* = \infty$, therefore the solutions do not blow up;
- if $b > 0$ (average-excitatory case) : $T^* < \infty$, therefore the solutions blow up at finite time.

The steps of the proof of this Criterion are the following:

1. **Relation to the Stefan problem.**
2. **Local existence and uniqueness.**
3. **Maximal time of existence.**
4. **Global existence in the average-inhibitory case.**

In the following subsections we are going to go deeper into each step, proving the Criterion 1.1.4 for the problem (1.1)-(1.5) with $a(N) = 1$ and $V_F = 0$.

1.1.1 Relation to the Stefan problem

The main part of this subsection concerns the formulation of equation (1.1) as a free boundary Stefan problem with a nonstandard right hand side. For this we recall a well known change of variables [10], that transform Fokker-Plank type equations into a non-homogeneous heat equation. This change of variables is given by

$$y = e^t v, \quad \tau = \frac{e^{2t} - 1}{2},$$

that yields

$$p(v, t) = e^t w\left(e^t v, \frac{e^{2t} - 1}{2}\right) \iff w(y, \tau) = (2\tau + 1)^{-\frac{1}{2}} p\left(\frac{y}{\sqrt{2\tau + 1}}, \frac{1}{2} \log(2\tau + 1)\right).$$

In the sequel, to simplify the notation, we use $\alpha(\tau) = (2\tau + 1)^{-\frac{1}{2}} = e^{-t}$. Now, differentiating w with respect to τ , and using that p is solution of (1.1), yields

$$\begin{aligned} w_\tau(y, \tau) &= \alpha'(\tau) p(y\alpha(\tau), -\log(\alpha(\tau))) + \\ &+ y\alpha'(\tau)\alpha(\tau) p_v(y\alpha(\tau), -\log(\alpha(\tau))) - \alpha'(\tau) p_t(y\alpha(\tau), -\log(\alpha(\tau))) = \\ &- \alpha'(\tau) p_{vv}(y\alpha(\tau), -\log(\alpha(\tau))) + \\ &+ \alpha'(\tau) b N(-\log(\alpha(\tau))) p_v(y\alpha(\tau), -\log(\alpha(\tau))) - \alpha'(\tau) N(-\log(\alpha(\tau))) \delta(y\alpha(\tau) - V_R). \end{aligned}$$

Finally, taking into account that

$$-\alpha'(\tau) = \alpha^3,$$

$$w_y(y, \tau) = \alpha^2 p_v(y\alpha(\tau), -\log(\alpha(\tau))),$$

$$w_{yy}(y, \tau) = \alpha^3(\tau) p_{vv}(y\alpha(\tau), -\log(\alpha(\tau))),$$

we obtain

$$w_\tau(y, \tau) = w_{yy}(y, \tau) - \alpha(\tau) b N(t) w_y(y, \tau) + M(\tau) \delta \left(y - \frac{V_R}{\alpha(\tau)} \right), \quad (1.9)$$

where $M(\tau) = -w_y(0, \tau) = \alpha^2(\tau) N(t)$. Now, in order to remove the term with w_y in (1.9), we introduce a second change of variables

$$x = y - b \int_0^\tau N(s) \alpha(s) ds,$$

and define

$$u(x, \tau) = w \left(x + b \int_0^\tau N(s) \alpha(s) ds, \tau \right).$$

Differentiating u with respect to τ produces

$$u_\tau(x, \tau) = w_y \left(x + b \int_0^\tau N(s) \alpha(s) ds, \tau \right) b N(\tau) \alpha(\tau) + w_\tau \left(x + b \int_0^\tau N(s) \alpha(s) ds, \tau \right).$$

Using equation (1.9) to substitute w_τ yields

$$u_\tau(x, \tau) = w_{yy} \left(x + b \int_0^\tau N(s) \alpha(s) ds, \tau \right) + M(\tau) \delta \left(x + b \int_0^\tau N(s) \alpha(s) ds - \frac{V_R}{\alpha(\tau)} \right).$$

Taking into account that

$$u_x(x, \tau) = w_y \left(x + b \int_0^\tau N(s) \alpha(s) ds, \tau \right),$$

$$u_{xx}(x, \tau) = w_{yy} \left(x + b \int_0^\tau N(s) \alpha(s) ds, \tau \right),$$

defining

$$s(\tau) := -b \int_0^\tau N(s) \alpha(s) ds,$$

finally we obtain:

$$\left\{ \begin{array}{ll} u_\tau(x, \tau) = u_{xx}(x, \tau) + M(\tau)\delta(x - s_1(\tau)), & x < s(\tau), \tau > 0, \\ s_1(\tau) = s(\tau) + \frac{V_R}{\alpha(\tau)}, & \tau > 0, \\ s(\tau) = -b \int_0^\tau N(s)\alpha(s)ds, & \tau > 0, \\ M(\tau) = -u_x(s(\tau), \tau), & \tau > 0, \\ u(-\infty, \tau) = u(s(\tau), \tau) = 0, & \tau > 0, \\ u(x, 0) = u_I(x), & x < 0. \end{array} \right. \quad (1.10)$$

We now give a definition of classical solution for the Stefan-like free boundary problem (1.10). It is immediate to translate this to a notion of classical solution to the original problem (1.1)-(1.5) by substituting u by p , x by v , $M(t)$ by $N(t)$, $s_1(t)$ by V_R , and $s(t)$ by V_F .

Throughout the paper we will make the following assumption (H1) on the initial data u_I .

Assumption (H1):

- $u_I(x)$ is a non-negative $C^1((-\infty, V_F]) \cap L^1(-\infty, V_F)$ function,
- $u_I(V_F) = 0$,
- $\lim_{x \rightarrow -\infty} \frac{\partial u_I}{\partial x} = 0$.

Definition 1.1.5. *We say that $(u(x, t), s(t))$ is a classical solution to (1.10) in the time interval $J = [0, T)$ or $J = [0, T]$ for a given $0 < T \leq \infty$ and with initial data $u_I(x)$ satisfying (H1), if the following conditions are satisfied:*

1. $M(t)$ is a continuous function for all $t \in J$,
2. u is continuous in the region $\{(x, t) : -\infty < x < s(t), t \in J\}$,
3. u_{xx} and u_t are continuous in the region $\{(x, t) : -\infty < x < s_1(t), t \in J - \{0\}\} \cup \{(x, t) : s_1(t) < x < s(t), t \in J - \{0\}\}$,
4. $u_x(s_1(t)^-, t)$, $u_x(s_1(t)^+, t)$, $u_x(s(t)^-, t)$ are well defined,
5. $u_x(x, t) \rightarrow 0$ when $x \rightarrow -\infty$,
6. problem (1.10) is satisfied in the classical sense.

The next Lemma presents some of the a-priori properties of the solution to (1.10).

Lemma 1.1.6. *Let $u(x, t)$ be a solution to (1.10) in the sense of Definition 1.1.5. It holds:*

1. *the mass is conserved, i.e., for all $t > 0$*

$$\int_{-\infty}^{s(t)} u(x, t) dx = \int_{-\infty}^{s_I} u_I(x) dx,$$

2. *the flux across the free boundary s_1 is exactly the strength of the source term:*

$$M(t) := -u_x(s(t), t) = u_x(s_1(t)^-, t) - u_x(s_1(t)^+, t),$$

3. *for $b < 0$ (resp. $b > 0$) the free boundary $s(t)$ is a monotone increasing (resp. decreasing) function of time.*

1.1.2 Local existence and uniqueness

In this subsection we prove local existence of solutions to system (1.10). We first derive an integral formulation for the problem. Suitable differentiations yield an integral equation for the flux M , where a fixed point argument can be used to obtain short time existence. Once $M(t)$ is known, the function u is the solution of a linear problem.

Theorem 1.1.7. *Let $u_I(x)$ satisfy (H1). Problem (1.10) has a unique classical solution (u, s) in the sense of Definition 1.1.5 for any $t \in [0, T]$, $T > 0$. The existence time T is such that*

$$T < \left(\sup_{-\infty < x \leq 0} \left| \frac{\partial u_I}{\partial x} \right| \right)^{-1}.$$

The proof of this theorem will be divided in two steps:

1. Integral formulation of the solution.

The goal of this step is to find the integral form of the function M . To do this we need the concept of Green's function. Let us remember the definition and the main results.

Definition 1.1.8. *Let $L_{x,t}$ a second order linear differential operator, associated with a linear differential equation*

$$L_{x,t}[u] = f. \tag{1.11}$$

The Green's function, associated with the operator L is the solution of

$$L_{x,t}G(x, t, \zeta, \tau) = \delta_2(x - \zeta, t - \tau), \tag{1.12}$$

where δ_2 is the bidimensional Dirac delta function, defined as

$$\delta_2(a, b) := \begin{cases} 1 & \text{if } (a, b) = (0, 0), \\ 0 & \text{otherwise.} \end{cases}$$

Theorem 1.1.9. *If function $G(x, t, \zeta, \tau)$ is the solution of (1.12), then the function*

$$u(x, t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} G(x, t, \zeta, \tau) f(\zeta, \tau) d\tau \quad (1.13)$$

is the solution to (1.11). Furthermore the following Green's identity holds:

$$\frac{\partial}{\partial \zeta} \left(G \frac{\partial u}{\partial \zeta} - u \frac{\partial G}{\partial \zeta} \right) - \frac{\partial}{\partial \tau} (Gu) = 0. \quad (1.14)$$

Theorem 1.1.10. *Let $y = (x, t)$ and L_y a second order linear differential operator of the following form:*

$$L_y = \sum_{i=1}^2 a_i \frac{\partial}{\partial y_i} + \sum_{i=1}^2 b_i \frac{\partial^2}{\partial y_i^2}$$

then the Green's function associated with L is

$$G(y, \sigma) = \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \frac{P(k, y - \sigma)}{Q(k)} dk \quad (1.15)$$

where $\sigma = (\zeta, \tau)$ and

$$P(k, y - \sigma) := e^{i \sum_{j=1}^2 k_j (y_j - \sigma_j)},$$

$$Q(k) := \sum_{j=1}^2 a_j (ik_j) + \sum_{j=1}^2 b_j (ik_j)^2.$$

Proof. Remember that

$$\delta(y_j - \sigma_j) = \mathcal{F}^{-1}[1] = \frac{1}{2\pi} \int_{-\infty}^{+\infty} e^{ik_j(y_j - \sigma_j)} dk_j,$$

where \mathcal{F}^{-1} is the Fourier anti-transform, and so the bidimensional δ function can be represented as

$$\delta_2(y - \sigma) = \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} e^{i \sum_{j=1}^2 k_j (y_j - \sigma_j)} dk_1 dk_2.$$

Now, taking into account the expression (1.15) of G , we observe that

$$\begin{aligned} L_y G(y, \sigma) &= \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} L_y \left(\frac{P}{Q} \right) dk_1 dk_2 = \\ &= \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \left(\frac{L_y[P]}{Q} - \frac{PL_y[Q]}{Q^2} \right) dk_1 dk_2. \end{aligned}$$

On the other hand, it is immediate to calculate that

$$L_y[P(k, y - \sigma)] = Q(k)P(k, y - \sigma),$$

$$L_y[Q(k)] = 0,$$

and so

$$\begin{aligned} L_y G(y, \sigma) &= \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} P(k, y - \sigma) dk_1 dk_2 = \\ &= \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} e^{i \sum_{j=1}^2 k_j (y_j - \sigma_j)} dk_1 dk_2 = \delta_2(y - \sigma). \end{aligned}$$

□

In particular in our case $L = \partial_t - \partial_x^2$, then $a_1 = 1$, $a_2 = 0$, $b_1 = 0$, $b_2 = -1$ and so

$$\begin{aligned} G(x, t, \zeta, \tau) &= \frac{1}{(2\pi)^2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \frac{e^{i[k_1(x-\zeta) + k_2(t-\tau)]}}{ik_1 + k_2^2} dk_1 dk_2 = \\ &= \frac{1}{2\pi} H(t - \tau) \int_{-\infty}^{+\infty} e^{ik_2(x-\zeta) - k_2^2(t-\tau)} dk_2 = \frac{H(t - \tau)}{\sqrt{4\pi(t - \tau)}} e^{-\frac{(x-\zeta)^2}{4(t-\tau)}}, \end{aligned}$$

where H is the Heaviside function. To recover u we first integrate the identity (1.14) in the two regions

$$-\infty < \zeta < s_1(\tau), \quad 0 < \tau < t, \quad \text{and} \quad s_1(\tau) < \zeta < s(\tau), \quad 0 < \tau < t,$$

and then add up the results from the integration. We split the resulting expression into the following 4 terms:

$$I = \int_0^t \int_{-\infty}^{s_1(\tau)} \frac{\partial}{\partial \zeta} \left(G \frac{\partial u}{\partial \zeta} \right) d\zeta d\tau, \quad II = \int_0^t \int_{s_1(\tau)}^{s(\tau)} \frac{\partial}{\partial \zeta} \left(G \frac{\partial u}{\partial \zeta} \right) d\zeta d\tau,$$

$$III = \int_0^t \int_{-\infty}^{s(\tau)} \frac{\partial}{\partial \zeta} \left(u \frac{\partial G}{\partial \zeta} \right) d\zeta d\tau, \quad IV = \int_0^t \int_{-\infty}^{s(\tau)} \frac{\partial}{\partial \tau} (Gu) d\zeta d\tau.$$

Each term will be analyzed separately. Note that u and G have enough decay as $|\zeta| \rightarrow \infty$ to justify the following computations due to Definition 1.1.5. Since $G(x, t, -\infty, \tau) = 0$ it holds

$$I = \int_0^t \left[G \frac{\partial u}{\partial \zeta} \right]_{\zeta=-\infty}^{\zeta=s_1(\tau)} d\tau = \int_0^t G(x, t, s_1(\tau), \tau) \frac{\partial u}{\partial \zeta} \Big|_{s_1(\tau)^-} d\tau. \quad (1.16)$$

Next, we obtain

$$II = - \int_0^t \left(G|_{\zeta=s(\tau)} M(\tau) + G \frac{\partial u}{\partial \zeta} \Big|_{s_1(\tau)^-} \right) d\tau,$$

using the fact that $M(\tau) = -\frac{\partial u}{\partial \zeta} \Big|_{s(\tau)^-}$. For the third integral we have

$$III = - \int_0^t \left[\left(u \frac{\partial G}{\partial \zeta} \right) \Big|_{\zeta=s(\tau)} - \left(u \frac{\partial G}{\partial \zeta} \right) \Big|_{\zeta=-\infty} \right] d\tau = 0$$

because $u(s(\tau), \tau) = u(-\infty, \tau) = 0$. Finally, recalling $G(x, t, \zeta, t) = \delta_{x=\zeta}$, we get

$$\begin{aligned} IV &= \int_0^t \frac{\partial}{\partial \tau} \int_{-\infty}^{s(\tau)} G u d\zeta d\tau = \\ &= \int_{-\infty}^{s(0)} \delta_{eta=x} u(\zeta, t) d\zeta - \int_{-\infty}^{s(0)} G(x, t, \zeta, 0) u_I(\zeta) d\zeta. \end{aligned} \quad (1.17)$$

Combining (1.16)-(1.17), and part 2) of Lemma 1.1.6, we get that the solution u reads as

$$\begin{aligned} u(x, t) &= \int_{-\infty}^{s(0)} G(x, t, \zeta, 0) u_I(\zeta) d\zeta - \int_0^t M(\tau) G(x, t, s(\tau), \tau) d\tau + \\ &\quad + \int_0^t M(\tau) G(x, t, s_1(\tau), \tau) d\tau. \end{aligned} \quad (1.18)$$

Now, differentiating (1.18) respect to x and evaluating at $x = s(t)^-$, we obtain:

$$\begin{aligned} M(t) &= -2 \int_{-\infty}^{s(0)} G(s(t), t, \zeta, 0) U_I'(\zeta) d\zeta + \\ &+ 2 \int_0^t M(\tau) G_x(s(t), t, s(\tau), \tau) d\tau - 2 \int_0^t M(\tau) G_x(s(t), t, s_1(\tau), \tau) d\tau. \end{aligned} \quad (1.19)$$

2. Local existence and uniqueness for M and u .

Theorem 1.1.11. *Let $u_I(x)$ satisfy (H1). There exists a unique solution $M(t) \in [0, T]$ to (1.19) and the maximal existence time T is estimated as*

$$T \leq \left(\sup_{-\infty < x \leq s_I} \left| \frac{\partial u_I}{\partial x} \right| \right)^{-1}$$

This theorem, proved in [13], shows that we have short time existence of a mild solution for problem (1.10) (i.e., a solution in the integral sense). However, using the expression (1.18) of u , one can easily show that [13]:

Corollary 1.1.11.1. *There exists a unique solution of problem (1.10) in the sense of Definition 1.1.5 for $t \in [0, T]$.*

1.1.3 Maximal time of existence

The drawback for long time existence is the possible blow up of $\|u_x(\cdot, t)\|_\infty$ particularly at the free boundary, i.e. the blow up of $M(t)$. We now formalize this idea by showing that we can extend the solution as long as the firing rate $M(t)$ is bounded. The following Proposition is proved in [13].

Proposition 1.1.12. *Let (u, s) be a classical solution to (1.10) in the time interval $[0, T]$, as proven in Theorem 1.1.7. Assume, in addition, that*

$$U_0 := \sup_{x \in (-\infty, s(t_0 - \epsilon))} |u_x(x, t_0 - \epsilon)| < \infty \quad \text{and that} \quad M^* = \sup_{t \in (t_0 - \epsilon, t_0)} M(t) < \infty,$$

for some $0 < \epsilon \leq T$. Then

$$\sup\{|u_x(x, t)| \text{ with } x \in (-\infty, s(t)], t \in [t_0 - \epsilon, t_0]\} < \infty,$$

with a bound depending only on the quantities M^* , U_0 and t_0 .

With this result in hand, our solutions can be extended to a maximal time of existence. The maximal time can be characterized, as shown in the following theorem.

Theorem 1.1.13. *Let (u, s) be a solution to (1.10), as proven in Theorem 1.1.7. Then the solution u can be extended up to a maximal time $0 < T^* \leq \infty$ given by*

$$T^* = \sup\{t > 0 : M(t) < \infty\}.$$

Proof. By definition we have $T^* \leq \sup\{t > 0 : M(t) < \infty\}$. If $T^* = \infty$ there is nothing to show. Now, assume that $T^* < \infty$, let's show the equality by contradiction.

Let $T^* < \sup\{t > 0 : M(t) < \infty\}$. Then there exists $0 < \epsilon < T^*$ such that

$$M^* = \sup_{t \in (T^* - \epsilon, T^*)} M(t) < \infty.$$

Let U_0 be defined as in Proposition 1.1.12 with $t_0 = T^*$. Applying Proposition 1.1.12, we deduce that $u_x(x, t)$ is also uniformly bounded for $x \in (-\infty, s(t)]$ and $t \in [T^* - \epsilon, T^*)$ by a constant, denoted U^* . The same proposition tells us that U^* only depends on M^* and on U_0 . We may now use Theorem 1.1.7 to show that problem (1.10) has a classical solution in the time interval $[t_0, t_0 + \delta)$, with $t_0 \in [T^* - \epsilon, T^*)$ and δ depending only on U^* . Thus, we can extend the solution $(u(t), s(t))$ to (1.10) after T^* and find a continuous extension of $M(t)$ past T^* . We have then reached a contradiction and the conclusion of the Theorem follows. \square

1.1.4 Global existence in the average-inhibitory case

The following Proposition, proved in [13], shows that it is possible to extend the solution for a short (but uniform) time ϵ for $b < 0$.

Proposition 1.1.14. *For $b < 0$, let (u, s) , $t \in [0, t_0)$, be a classical solution to (1.10) as proven in Theorem 1.1.7. There exists $\epsilon > 0$ small enough such that, if*

$$M_0 = \sup_{x \in (-\infty, s(t_0 - \epsilon)]} |u_x(x, t_0 - \epsilon)| < \infty,$$

for $0 < \epsilon < t_0$ then

$$\sup_{t_0 - \epsilon < t < t_0} M(t) \leq C < \infty.$$

The constant ϵ does not depend on t_0 , and the constant C above only depends on M_0 .

The combination of Proposition 1.1.14 with Theorem 1.1.13 and Proposition 1.1.12 gives a unique global classical solution for $b < 0$.

1.2 Global existence of solutions for the delayed model

In this section we are going to consider the NNLIF model of one population without refractory state, but with transmission delay [8]. We want to show that in this case all solution are global both in the inhibitory and excitatory case. The model that we consider is:

$$\frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v} [(-v + bN(t-D))p(v, t)] - a(N(t-D)) \frac{\partial^2 p}{\partial v^2}(v, t) = N(t-D) \delta_{V_R}(v), \quad (1.20)$$

with $v \in (-\infty, V_F]$ at a time $t \geq 0$, $b > 0$, $D \geq 0$ and

$$N(t) = -a(N(t)) \frac{\partial p}{\partial v}(V_F, t) \geq 0. \quad (1.21)$$

The partial differential equation (1.20) is complemented with Dirichlet and initial boundary conditions

$$p(V_F, t) = p(-\infty, 0) = 0, \quad p(v, 0) \geq 0. \quad (1.22)$$

In [8] is shown that Criterion 1.1.4 holds also in this case. Then to prove the global existence of solutions we can show that the firing rate cannot diverge in finite time. This would allow us to conclude that the maximal time of existence T^* is not finite ($T^* = +\infty$). In order to do that, we introduce the notion of super-solution.

Definition 1.2.1. *Let $T \in \mathbb{R}_+$, $D \geq 0$, (\bar{p}, \bar{N}) is said to be a (strong) super-solution to (1.20)-(1.22) on $(-\infty, V_F] \times [0, T]$ if for all $t \in [0, T]$ we have $\bar{p}(V_F, t) = 0$ and*

$$\partial_t \bar{p} + \partial_v [(-v + b\bar{N}(t-D))\bar{p}] - a\partial_{vv} \bar{p} \geq \delta_{v=V_R} \bar{N}(t), \quad \bar{N}(t) = -a\partial_v \bar{p}(V_F, t), \quad (1.23)$$

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

We start proving the following comparison property between strong solutions and super solutions of (1.20)-(1.22).

Theorem 1.2.2. *Let $D > 0$, $0 < T < D$. Let (p, N) be a strong solution of (1.20)-(1.22) on $(-\infty, V_F] \times [0, T]$ for the initial condition (p^0, N^0) and let (\bar{p}, \bar{N}) be a strong super-solution of (1.20)-(1.22) on $(-\infty, V_F] \times [0, T]$. Assume that*

$$\forall v \in (-\infty, V_F], \bar{p}(v, 0) \geq p^0(v) \quad \text{and} \quad \forall t \in [-D, 0], \bar{N}(t) = N^0(t).$$

Then,

$$\forall (v, t) \in (-\infty, V_F] \times [0, T], \bar{p}(v, t) \geq p(v, t) \quad \text{and} \quad \forall t \in [0, T], \bar{N}(t) \geq N(t).$$

Proof. First, we prove that if $\bar{p}(v, t) \geq p(v, t)$ then $\bar{N}(t) \geq N(t)$. Due to the Dirichlet boundary condition for p and the definition of super-solution we have $p(V_F, t) = \bar{p}(V_F, t) = 0$ on $[0, T]$. Thus, as long as $\bar{p}(v, t) \geq p(v, t)$ holds, we have

$$-a \frac{\bar{p}(V_F, t) - \bar{p}(v, t)}{V_F - v} \geq -a \frac{p(V_F, t) - p(v, t)}{V_F - v}.$$

And taking the limit $v \rightarrow V_F$ we get $\bar{N}(t) \geq N(t)$.

Then, denoting $w = \bar{p} - p$, we have for all $(v, t) \in (-\infty, V_F] \times [0, T]$,

$$\partial_t w + \partial_v(-vw) + b\bar{N}(t-D)\partial_v \bar{p} - bN(t-D)_v p - a\partial_{vv} w \geq \delta_{v=V_R}(\bar{N}(t) - N(t)).$$

As we assume $T < D$ we have by hypothesis $\bar{N}(t-D) = N^0(t-D)$ for all $t \in [0, T]$. Thus, as long as $w \geq 0$ holds, since $\bar{N}(t) \geq N(t)$,

$$\partial_t w + \partial_v[(-v + bN^0(t))w] - a\partial_{vv} w \geq 0.$$

As $w(\cdot, 0) \geq 0$, by a standard maximum principle theorem, we have for all $t \in [0, T]$, $w(\cdot, t) \geq 0$, and we conclude the proof. \square

Now, fixed N^0 and chosen $\bar{N}(t) = N^0(t)$ in $[-D, 0]$, we look for a super-solution on $[0, D]$ of the form

$$\bar{p}(v, t) = e^{t\lambda} f(v), \tag{1.24}$$

where λ is large enough and f is a carefully selected function, such that \bar{p} satisfies (1.23), which means

$$(\lambda - 1)f + (-v + bN^0(t))f' - af'' \geq \delta_{v=V_R}(t)\hat{N}(t), \quad \hat{N}(t) = -af'(V_F). \tag{1.25}$$

We show that f defined as follow

$$f : (-\infty, V_F] \rightarrow \mathbb{R}_+$$

$$v \rightarrow \begin{cases} 1 & \text{on } (-\infty, V_R] \\ e^{V_R-v}\psi(v) + \frac{1}{\delta}(1-\psi(v))(1-e^{\delta(v-V_F)}) & \text{on } (V_R, V_F] \end{cases}$$

verifies (1.25). To complete the definition of f we explain which are ψ and δ :

1. For $\epsilon > 0$ small enough, such that $\frac{V_F+V_R}{2} + \epsilon < V_F$, we consider $\psi \in C_b^\infty(\mathbb{R})$ satisfying $0 \leq \psi \leq 1$ and

$$\psi = \begin{cases} 1 & \text{on } (-\infty, \frac{V_F+V_R}{2}) \\ 0 & \text{on } (\frac{V_F+V_R}{2} + \epsilon, +\infty). \end{cases}$$

2. For $B > 0$, such that $|-v + bN^0(t)| \leq B, \forall t \in [-D, 0), \forall v \in (V_R, V_F)$, we take $\delta > 0$ such that $a\delta - B \geq 0$.

Notice that f being the sum of two continuous non-negative functions that never vanish at the same point, we have

$$\inf_{v \in (V_R, \frac{V_F+V_R}{2} + \epsilon)} f(v) > 0.$$

With this choice, $\bar{p}(v, t)$ is a super-solution on $[0, D]$ for λ enough large, because:

- on $(-\infty, V_R)$ $f'(v) = f''(v) = 0$ and so if ≥ 1 (1.25) is verified;
- around the V_R point the inequality (1.25) has to hold in the sense of distribution, which means, integrating from $V_R - \epsilon$ and $V_R + \epsilon$,

$$\int_{V_R - \epsilon}^{V_R + \epsilon} (\lambda - 1)f + (-v + bN^0(t))f' dv - \int_{V_R - \epsilon}^{V_R + \epsilon} a f'' dv \geq \int_{V_R - \epsilon}^{V_R + \epsilon} \delta_{v=V_R}(t) \tilde{N}(t) dv.$$

For $\epsilon \rightarrow 0$ it becomes

$$-a[f']_{V_R^-}^{V_R^+} \geq -a f'(V_F),$$

or equivalently

$$f'(V_R^+) - f'(V_R^-) \leq f'(V_F)$$

which is satisfied because $f'(V_R^-) = 0, f'(V_R^+) = -1$ and $f'(V_F) = -1$;

- on $(V_R, \frac{V_F+V_R}{2} + \epsilon)$, we choose λ such that

$$(\lambda - 1) \inf_{v \in (V_R, \frac{V_F+V_R}{2} + \epsilon)} f(v) \geq \sup_{v \in (V_R, \frac{V_F+V_R}{2} + \epsilon)} (B|f'(v)| + a|f''(v)|),$$

which is possible because $\inf_{v \in (V_R, \frac{V_F+V_R}{2} + \epsilon)} f(v) > 0$. Then the super-solution inequality (1.25) holds;

- on $(\frac{V_F+V_R}{2} + \epsilon, V_F)$, the inequality (1.25) holds since

$$(-v + bN^0(t))f' - a f'' = e^{\delta(v-V_F)}[a\delta - (-v + bN^0(t))] \geq e^{\delta(v-V_F)}[a\delta - B] \geq 0.$$

Given this super-solution on $[0, D]$ for any fixed continuous $N^0(t)$, we can prove global existence for local solutions.

Theorem 1.2.3. (Global existence-excitatory and inhibitory case) *Let p^0 be a non-negative function in $C^0((-\infty, V_F]) \cup C^1((-\infty, V_R) \cap (V_R, V_F]) \cup L^1((-\infty, V_F))$, such that $p^0(V_F) = 0$ and $\frac{dp^0}{dv}$ decays at $-\infty$ and admits finite left and right limits at V_R ; let $N^0 \in C^0([-D, 0])$ with $D > 0$. Let (p, N) the corresponding strong solution of (1.20)-(1.22) on the maximal interval of existence $[0, T^*)$. Then $T^* = +\infty$.*

Proof. Assume that the maximal time of existence T^* is finite, this means, using Criterion 1.1.4, that firing rate N diverges when $t \rightarrow T^*$. We prove that this is a contradiction with the fact that \bar{p} given by (1.24) is a super-solution.

As the solution was showed previously to be unique, we assume without lost of generality that $T^* = \frac{D}{2} < D$ by using the new initial conditions

$$\tilde{p}^0(v) = p\left(v, T^* - \frac{D}{2}\right) \quad \forall v \in (-\infty, V_F]$$

and

$$\tilde{N}^0(\tilde{t}) = N\left(T^* - \frac{D}{2} + \tilde{t}\right), \quad \tilde{t} \in [-D, 0).$$

As \tilde{p}^0 is continuous and vanish at V_F and $-\infty$, it belongs to $L^\infty((-\infty, V_F])$ and therefore there exists $\alpha \in \mathbb{R}_+^*$ such that the super-solution \bar{p} we constructed satisfies

$$\alpha \bar{p}(v, 0) \geq \tilde{p}^0(v), \quad \forall v \in (-\infty, V_F],$$

where we use the fact that \bar{p} never vanish on $(-\infty, V_F)$. Then, by Theorem 1.2.2, we have

$$N\left(T^* - \frac{D}{2} + \tilde{t}\right) = \tilde{N}(\tilde{t}) \leq \bar{N}(\tilde{t}) = ae^{\lambda \tilde{t}} \quad \forall \tilde{t} \in \left[0, \frac{D}{2}\right).$$

Thus, $N(t) \leq ae^{\lambda(t - T^* + \frac{D}{2})}$ for all $t \in [T^* - \frac{D}{2}, T^*)$. Therefore, by continuity, there is no divergence of the firing rate N when $t \rightarrow T^*$, and thus by Criterion 1.1.4 we reach a contradiction. \square

1.3 Steady states

This section is devoted to find all smooth stationary solutions of the problem (1.1)-(1.5) (see [6]). Let us search for continuous stationary solutions of p of (1.1) such that p is C^1 regular except possibly at $V = V_R$ where it is Lipschitz.

The steady states of this NNLI model are solutions of

$$\frac{\partial}{\partial v} A(v) = 0$$

where

$$A(v) = (v - bN)p(v) + a(N)\frac{\partial p}{\partial v}(v) + NH(v - V_R),$$

with H being the Heaviside function. Therefore, we conclude that $A(v)$ is constant. Observe that, using the boundary condition $p(V_F) = 0$, we have that $A(V_F) = 0$, and so we can conclude that $A(v) = 0 \forall v \in (-\infty, V_F]$. Assuming that $a(N) = a$ is a constant, now the problem is to find the solutions of this equation:

$$\frac{\partial p}{\partial v} + \frac{(v - bN)}{a}p = -\frac{1}{a}NH(v - V_R).$$

With the variation of constants method we can find p :

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

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

$$p(v) = \frac{N}{a}e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw. \quad (1.26)$$

Now, remembering condition (1.4), and integrating (1.26) from $-\infty$ to V_F we obtain

$$1 = \frac{N}{a} \int_{-\infty}^{V_F} \left[e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw \right] dv. \quad (1.27)$$

We can rewrite the previous integral (and thus the condition for steady state) as

$$\begin{cases} \frac{1}{N} = I(N), \\ I(N) := \frac{1}{a} \int_{-\infty}^{V_F} \left[e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw \right] dv. \end{cases} \quad (1.28)$$

Remark 1.3.1. *To find the number of steady states we investigate how many times the two functions $I(N)$ and $\frac{1}{N}$ intersect. Now we are going to rewrite in some different useful ways $I(N)$ and to study its properties (Lemma 1.3.3).*

Using the following change of variables and notations

$$z = \frac{v - bN}{\sqrt{a}}, \quad u = \frac{w - bN}{\sqrt{a}}, \quad w_F = \frac{V_F - bN}{\sqrt{a}}, \quad w_R = \frac{V_R - bN}{\sqrt{a}},$$

the integral $I(N)$ can be rewritten as

$$I(N) = \int_{-\infty}^{w_F} \left[e^{-\frac{z^2}{2}} \int_{\max(z, w_R)}^{w_F} e^{\frac{u^2}{2}} du \right] dz. \quad (1.29)$$

Another alternative form of $I(N)$ follows from the change of variables

$$s = \frac{z - u}{2}, \quad \tilde{s} = \frac{z + u}{2},$$

to get

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

and consequently,

$$I(N) = \int_0^{+\infty} \frac{e^{-2s^2}}{s} (e^{sw_F} - e^{sw_R}) ds. \quad (1.30)$$

Remark 1.3.2. Let us rewrite (1.30) as

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

Taking the function $f(s) = e^{\frac{sV_F}{\sqrt{a}}} - e^{\frac{sV_R}{\sqrt{a}}}$ and a Taylor expansion up to second order at $s = 0$, we get $f(s) - f(0) - f'(0)s = f''(\theta)\frac{s^2}{2}$ with $f(0) = 0$, $f'(0) = \frac{V_F - V_R}{\sqrt{a}}$, and $\theta \in (0, s)$. It is easy to see that

$$|f''(\theta)| \leq \max \left(\frac{V_F^2}{a} e^{\frac{\theta V_F}{\sqrt{a}}}, \frac{V_R^2}{a} e^{\frac{\theta V_R}{\sqrt{a}}} \right),$$

for all $\theta \in (0, s)$. By distinguishing the cases based on the signs of V_F and V_R , this Taylor expansion implies that

$$\begin{aligned} \left| \frac{e^{\frac{sV_F}{\sqrt{a}}} - e^{\frac{sV_R}{\sqrt{a}}}}{s} - \frac{V_F - V_R}{\sqrt{a}} \right| &\leq \frac{\max(V_F^2, V_R^2)}{2a} s e^{\frac{s \max(|V_R|, |V_F|)}{\sqrt{a}}} \\ &=: C_0 s e^{\frac{s \max(|V_R|, |V_F|)}{\sqrt{a}}} \end{aligned} \quad (1.31)$$

for all $s \geq 0$.

Lemma 1.3.3. Let $I(N)$ the function defined in (1.28), then the following properties hold:

1. $I(N) > 0 \quad \forall N \geq 0$;
2. $I(0) < \infty$;

3. $I(N)$ is C^∞ and, for all integers $k \geq 1$,

$$I^k(N) = (-1)^k \left(\frac{b}{\sqrt{a}} \right)^k \int_0^\infty e^{-\frac{s^2}{2}} s^{k-1} (e^{sw_F} - e^{sw_R}) ds. \quad (1.32)$$

4. • if $b < 0$ (inhibitory case),

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

• if $b > 0$ (excitatory case),

$$\lim_{N \rightarrow +\infty} I(N) = 0 \quad \text{and} \quad \lim_{N \rightarrow +\infty} NI(N) = \frac{V_F - V_R}{b};$$

Proof. 1. Consider $I(N)$ in the form (1.30). Since $\frac{e^{-2s^2}}{s} (e^{sw_F} - e^{sw_R}) > 0$ $\forall s \in (0, \infty) \forall N \geq 0$, then $I(N) > 0 \forall N \geq 0$.

2. Consider $I(N)$ as in (1.29):

$$\begin{aligned} I(0) &= \int_{-\infty}^{w_F(0)} \left[e^{-\frac{z^2}{2}} \int_{\max(z, w_R(0))}^{w_F(0)} e^{\frac{u^2}{2}} du \right] dz \leq \\ &\leq (w_F(0) - w_R(0)) e^{\frac{\max(w_R^2(0), w_F^2(0))}{2}} \int_{-\infty}^{w_F(0)} e^{-\frac{z^2}{2}} dz \leq \\ &\leq \sqrt{2\pi} (w_F(0) - w_R(0)) e^{\frac{\max(w_R^2(0), w_F^2(0))}{2}} = \sqrt{2\pi} \frac{V_F - V_R}{\sqrt{a}} e^{\frac{\max(V_R^2, V_F^2)}{2a}} < \infty \end{aligned}$$

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

$$\dot{I}(N) = -\frac{b}{\sqrt{a}} \int_0^\infty e^{-\frac{s^2}{2}} (e^{sw_F} - e^{sw_R}) ds,$$

and for all integers $k \geq 1$,

$$I^k(N) = (-1)^k \left(\frac{b}{\sqrt{a}} \right)^k \int_0^\infty e^{-\frac{s^2}{2}} s^{k-1} (e^{sw_F} - e^{sw_R}) ds.$$

4. By (1.32) we deduce that:

- if $b < 0$, $I(N)$ is an increasing strictly convex function and thus

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

- if $b > 0$, $I(N)$ is a decreasing convex function, and furthermore, using the previous expansion (1.31) and the dominated convergence theorem, we conclude that

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

Moreover, using again (1.31), we deduce

$$\begin{aligned} & \left| NI(N) - N \frac{V_F - V_R}{\sqrt{a}} \int_0^\infty e^{-\frac{s^2}{2}} e^{-\frac{sbN}{\sqrt{a}}} ds \right| \leq \\ & \leq C_0 N \int_0^\infty s e^{-\frac{s^2}{2}} e^{-\frac{sbN}{\sqrt{a}}} e^{\frac{s \max(|V_R|, |V_F|)}{\sqrt{a}}} ds. \end{aligned} \quad (1.33)$$

A direct application of dominated convergence theorem shows that the right hand side converges to 0 as $N \rightarrow \infty$ since $sNe^{-\frac{sbN}{\sqrt{a}}}$ is a bounded function uniform in N and s . If we prove that

$$\lim_{N \rightarrow +\infty} N \int_0^\infty e^{-\frac{s^2}{2}} e^{-\frac{sbN}{\sqrt{a}}} ds = \frac{\sqrt{a}}{b}, \quad (1.34)$$

combining this result with the inequality (1.37), we can deduce that

$$\lim_{N \rightarrow +\infty} NI(N) = \frac{V_F - V_R}{b}.$$

So, let us prove (1.34). Remembering the definition of the complementary error function

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

we can rewrite

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

Finally, using L'Hopital's rule

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

□

Remark 1.3.4. Another way to write problem (1.28) is

$$\begin{cases} Q(N) = 1, \\ Q(N) := NI(N). \end{cases} \quad (1.35)$$

In this case the problem of finding the number of steady states is equivalent to find the number of intersections of $Q(N)$ and $h(N) = 1$.

A direct consequence of Lemma 1.3.3 and Remark 1.3.4 is the following Lemma, which lists the properties of $Q(N)$.

Lemma 1.3.5. Let $Q(N)$ the function defined in (1.35), then the following properties hold:

1. $Q(N) > 0 \forall N > 0$;
2. $Q(0) = 0$;
3. $Q(N)$ is $C^\infty(N)$ and $\dot{Q}(N) = I(N) + N\dot{I}(N)$;
4. • if $b < 0$,

$$\lim_{N \rightarrow +\infty} Q(N) = +\infty,$$

- if $b > 0$,

$$\lim_{N \rightarrow +\infty} Q(N) = \frac{V_F - V_R}{b}.$$

We can now prove the main result [6] on steady states:

Theorem 1.3.6. Considering the problem (1.1)-(1.5) with $a(N) = a$ a positive constant, we have:

1. If $b < 0$ (inhibitory case): there is a unique steady state to (1.1)-(1.5).
2. If $b > 0$ (excitatory case):
 - (a) if b is small enough there is a unique steady state;
 - (b) if $b < V_F - V_R$ or $b < \frac{(V_F - V_R)^2}{2a} V_R$, then there exists at least one steady state solution to (1.1)-(1.5);
 - (c) if $V_F - V_R < b < \frac{(V_F - V_R)^2}{2a} V_R$, then there are at least 2 steady states to (1.1)-(1.5);
 - (d) if $b > \beta_2 := \max(2(V_F - V_R), 2V_F I(0))$, then there is no steady states.

Proof. 1. Let $b < 0$. From Lemma 1.3.3 $I(N)$ is an increasing function, starting at $I(0) < \infty$ and such that

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

Therefore it crosses the function $\frac{1}{N}$ at a single point.

2. Let $b > 0$.

- (a) We first remark, by a direct application of the dominated convergence theorems and continuity theorems for integrals, that $I(N)$ and $\dot{I}(N)$ are continuous functions of b . Moreover these two functions are both C^∞ with respect to b since all their derivatives can be computed by differentiating under the integral sign by applying again dominated convergence theorems and differentiation theorems of integrals.

Furthermore, it is simple to realize that $I(N)$ is a decreasing function of the parameter b .

Now, choosing $b \leq b_* < \frac{V_F - V_R}{2}$, $I(N) \leq I_*(N)$ and $Q(N) \leq Q_*(N)$ for all $N \geq 0$ where $I_*(N)$, $Q_*(N)$ denote the functions associated to the parameter b_* , remembering that $\lim_{N \rightarrow \infty} Q_*(N) = \frac{V_F - V_R}{b_*}$, we can say that

$$\exists N_* = N_*(b_*) \text{ s.t. } Q_*(N) > \frac{V_F - V_R}{2b_*} > 1 \quad \forall N \geq N_*,$$

and so

$$Q(N) \geq Q_*(N) > 1 \quad \forall N \geq N_*.$$

Since $Q(0) = 0$ and $Q(N)$ is continuous, we conclude that there are solutions to $Q(N) = 1$ and all these solutions are on the interval $[0, N_*]$. We observe that

$$\lim_{b \rightarrow 0} I(N) = I(0) > 0, \quad \lim_{b \rightarrow 0} N\dot{I}(N) = 0$$

uniformly in the interval $[0, N_*]$. Therefore, for b small enough,

$$\dot{Q}(N) = I(N) + N\dot{I}(N) > 0, \quad N \in [0, N_*],$$

which means that $Q(N)$ is strictly increasing in this interval and so there is a unique solution to $Q(N) = 1$.

- (b) Considering $Q(N)$ and using the results of Lemma 1.3.5 we know that:

- $Q(N)$ is continuous;
- $Q(0) = 0$;
- $\exists \tilde{N}$ such that $Q(\tilde{N}) > 1$, since:
 - if $b < V_F - V_R$:

$$\lim_{N \rightarrow +\infty} Q(N) = \frac{V_F - V_R}{b} > 1;$$

- if $b < \frac{(V_F - V_R)^2}{2a} V_R$, we can say that the interval $\left(\frac{2a}{(V_F - V_R)^2}, \frac{V_R}{b}\right)$ is not empty, and if we prove that $I(N) > \frac{1}{N}$ in this interval, then we can conclude that $Q(N) \geq 1$ for $N \in \left(\frac{2a}{(V_F - V_R)^2}, \frac{V_R}{b}\right)$.

Observe that condition $N < \frac{V_R}{b}$ is equivalent to $w_R > 0$, therefore, using the expression (1.29), we deduce

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

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

$$I(N) \geq \int_{w_R}^{w_F} \int_z^{w_F} du dz = \frac{(V_F - V_R)^2}{2a} > \frac{1}{N}$$

because $N > \frac{2a}{(V_F - V_R)^2}$.

So we can conclude that there exists at least one steady state.

- (c) We consider again $Q(N)$, and we observe again that $Q(N)$ is continuous, $Q(0) = 0$, and there exists an interval in which $Q(N) > 1$ because $b < \frac{(V_F - V_R)^2}{2a} V_R$. Moreover in this case the condition $b > V_F - V_R$ implies that

$$\lim_{N \rightarrow +\infty} Q(N) = \frac{V_F - V_R}{b} < 1.$$

Thus, we can conclude that there are at least 2 steady states.

- (d) Consider $b > \max(2(V_F - V_R), 2V_F I(0))$.

- For $N \leq \frac{2V_F}{b}$:

$$I(N) < I(0) < \frac{b}{2V_F} \leq \frac{1}{N};$$

- for $N > \frac{2V_F}{b}$, firstly observe that $N > \frac{V_F}{b}$ (i.e. $w_F < 0$), and moreover

$$\frac{V_F - V_R}{bN - V_F} < \frac{b}{2(bN - V_F)} < \frac{b}{bN} = \frac{1}{N}. \quad (1.36)$$

Now, consider $f(x) = e^{sx}$, for the mean-value theorem we have

$$\frac{f(w_F) - f(w_R)}{w_F - w_R} = f'(c), \quad c \in (w_R, w_F),$$

and so

$$\frac{e^{sw_F} - e^{sw_R}}{w_F - w_R} = se^{sc} < se^{sw_F},$$

or equivalently

$$\frac{e^{sw_F} - e^{sw_R}}{s} < (w_F - w_R)e^{sw_F}. \quad (1.37)$$

Finally, using $I(N)$ in the form (1.30) and the inequality (1.37), and remembering that $w_F < 0$, we have

$$\begin{aligned} I(N) &< (w_F - w_R) \int_0^\infty e^{-\frac{s^2}{2}} e^{sw_F} ds = \\ &= (w_F - w_R) e^{\frac{w_F^2}{2}} \int_0^\infty e^{-\frac{(s-w_F)^2}{2}} ds = (w_F - w_R) e^{\frac{w_F^2}{2}} \int_{-w_F}^\infty e^{-\frac{y^2}{2}} dy \leq \\ &\leq (w_F - w_R) e^{\frac{w_F^2}{2}} \int_{-w_F}^\infty \frac{y}{|w_F|} e^{-\frac{y^2}{2}} dy = \frac{V_F - V_R}{|w_F| \sqrt{a}} = \frac{V_F - V_R}{bN - V_F} < \frac{1}{N}, \end{aligned}$$

because of (1.36).

So, we can now conclude that $I(N) < \frac{1}{N} \forall N \geq 0$.

□

Denoting with β_1 a positive value such that there is a unique steady state $\forall 0 < b \leq \beta_1$ (it must exist, by Theorem 1.3.6) and supposing that

$$V_F - V_R < \frac{(V_F - V_R)V_R}{2a},$$

we can summarise the results of Theorem 1.3.6, with the following table.

inhibitory or excitatory	range for b	n. of steady states
$b < 0$	$b \in (-\infty, 0)$	1
$b > 0$	$b \in (0, \beta_1]$	1
	$b \in (\beta_1, V_F - V_R]$	at least 1
	$b \in \left(V_F - V_R, \frac{V_R(V_F - V_R)}{2a} \right]$	at least 2
	$b \in \left[\frac{V_R(V_F - V_R)}{2a}, \beta_2 \right]$?
	$b \in (\beta_2, +\infty)$	0

Chapter 2

Steady states of the random discharge potential model

This chapter is the core of the thesis, since it contains new results regarding NNLIF model. In particular we will focus on model (19), called **random discharge potential model**. The idea is, starting from model (18) described in Chapter 1, to assume some randomness on the discharge potential: this means that the neurons spike when their membrane potential exceed the value V_F with a certain discharge rate. From a mathematical point of view, this phenomenon is represented by adding a term characterized by a function $\phi_\epsilon(v)$, called the discharge rate.

Here we recall the model, already anticipated in the Introduction. In this chapter we assume in particular that $a(N) = a$ is a constant:

$$\left\{ \begin{array}{l} \frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v} [(-v + bN)p(v, t)] - a \frac{\partial^2 p}{\partial v^2}(v, t) + \phi_\epsilon(v)p(v, t) = \\ = N(t)\delta_{V_R}(v), \quad v \in \mathbb{R} \\ N(t) = \int_{-\infty}^{+\infty} \phi_\epsilon(v)p(v, t)dv. \end{array} \right. \quad (2.1)$$

Randomness on the discharge of the action potential implies that, while in the previous model $p(V_F) = 0$ because the neurons discharge when $v = V_F$, in this model $p(V_F)$ is a value different from 0 but that we do not know, because neurons discharge randomly when $v > V_F$.

The goal of this chapter is to study the number of steady states of model (2.1) and then find the differences compared to model with fixed threshold (1.1)-

(1.5) described in Chapter 1. To do that we will choose function $\phi_\epsilon(v)$ in two different ways:

$$\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}} \quad (2.2)$$

where $\mathbb{1}_{\{\cdot\}}$ denotes the characteristic function, and

$$\phi_\epsilon(v) = \frac{1}{\epsilon} (v - V_F)_+, \quad (2.3)$$

where $(\cdot)_+$ denotes the positive part.

In both choices we will distinguish, depending on the value of $p(V_F)$, two cases that we will call **case A** (if $p(V_F)$ is big enough) and **case B** (if $p(V_F)$ is small enough): we will show that case B, closer to model (1.1)-(1.5), is characterized by an odd number of steady states, while case A by an even number.

In the first section we consider the discharge rate like $\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}}$ and we show that if we consider a population in average-excitatory with ϵ large enough or a population in average-inhibitory, there are no steady states in case A and a unique steady state in case B, while if we consider a population in average-excitatory with ϵ in a small interval and the other parameters satisfying suitable conditions, there could be at least 2 or 3 steady states. We also show that the same results hold if we consider the transmission delay and the refractory period.

In the second section we consider the discharge rate as $\phi_\epsilon(v) = \frac{1}{\epsilon} (v - V_F)_+$ and we show that also here in the inhibitory case there are 0 or 1 steady states, while in the excitatory one we do not find sufficient conditions for the same result, but we show that if ϵ belongs to an interval and the other parameters satisfy suitable conditions, there could be at least 2 or 3 steady states.

To determine the steady states of the random discharge potential model we follow the same procedure used in Chapter 1. Also in this case, steady states are solution of

$$\frac{\partial}{\partial v} A(v) = 0$$

where

$$A(v) = (v - bN)p(v) + a \frac{\partial p}{\partial v}(v) + \int_{-\infty}^v \phi_\epsilon(w)p(w)dw + NH(v - V_R),$$

with H being the Heaviside function. Therefore, we conclude that $A(v)$ is constant. Observe that

$$\lim_{v \rightarrow -\infty} A(v) = 0,$$

so we can conclude that $A(v) = 0$. Now the problem is to find the solutions of this equation:

$$\frac{\partial p}{\partial v} + \frac{(v - bN)}{a} p = \frac{1}{a} g(v)$$

where

$$g(v) := \int_{-\infty}^v \phi_\epsilon(v)p(v)dv - NH(v - V_R) = \begin{cases} 0 & v < V_R \\ -N & V_R \leq v \leq V_F \\ \int_{-\infty}^v \phi_\epsilon p(w)dw - N & v > V_F. \end{cases} \quad (2.4)$$

With the variation of constants method we can find p :

$$p(v) = \frac{1}{a} e^{-\frac{(v-bN)^2}{2a}} \left[k + \int_{V_F}^v g(w) e^{\frac{(w-bN)^2}{2a}} dw \right].$$

As $p(V_F) = \frac{1}{a} e^{-\frac{(V_F-bN)^2}{2a}} k$ we conclude that $k = p(V_F) a e^{\frac{(V_F-bN)^2}{2a}}$. Unlike the original problem, in the random discharge potential model we do not know what is the value of p in $v = V_F$ and so p can be written as

$$p(v) = -\frac{1}{a} e^{-\frac{(v-bN)^2}{2a}} \int_v^{V_F} g(w) e^{\frac{(w-bN)^2}{2a}} dw + p(V_F) e^{\frac{(V_F-bN)^2}{2a}} e^{-\frac{(v-bN)^2}{2a}}. \quad (2.5)$$

Now, as in Chapter 1, the idea is to integrate (2.5) to find an equation which depends on N and whose solutions correspond to the steady states. We will do this in the two next sections of this Chapter, choosing ϕ_ϵ differently, as explained above.

2.1 Discharge rate $\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}}$

The aim of this section is to find the number of steady states of this model, choosing as discharge rate $\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}}$. We will firstly integrate (2.5) to find an equation which depends on N and whose solutions correspond to the steady states. Then, we will define exactly what is meant by case A and case B that we talked about at the beginning of the chapter, and we will show by Theorem 2.1.2 that the number of steady states in the two cases is different. Finally we will prove the main result of this section, Theorem 2.1.10, which shows the conditions on the parameters of the model clarifying the exact number of steady states.

Before starting is important to make the following remark:

Remark 2.1.1. *In this section we will consider*

$$N \in \left(0, \frac{1}{\epsilon} \right)$$

since,

$$N(t) = \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(v, t) dv < \frac{1}{\epsilon} \int_{-\infty}^{+\infty} p(v, t) dv = \frac{1}{\epsilon} \quad \forall t \geq 0.$$

Now we follow the same procedure as in Chapter 1 to find an equation which depends on N . Firstly we note that

$$\int_{-\infty}^{V_F} p(v) dv = \int_{-\infty}^{+\infty} p(v) dv - \int_{V_F}^{+\infty} p(v) dv = 1 - \epsilon N \quad (2.6)$$

and so, integrating (2.5) from $-\infty$ to V_F , we obtain:

$$\begin{aligned} 1 - \epsilon N &= -\frac{1}{a} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} g(w) e^{\frac{(w-bN)^2}{2a}} dw dv + \\ &\quad + p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} dv \end{aligned}$$

because $g(w) = 0$ if $w < V_R$. As $w \in (V_R, V_F)$, $g(w) = -N$ and so

$$\begin{aligned} 1 - \epsilon N &= \frac{N}{a} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw dv + \\ &\quad + p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} dv. \end{aligned}$$

We can rewrite the previous integral (and thus the condition for steady state) as

$$\begin{cases} \frac{1}{N} = J(N), \\ J(N) := \epsilon + I(N) + M(N), \end{cases} \quad (2.7)$$

where

$$I(N) := \frac{1}{a(N)} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw dv$$

is the function already defined in (1.28) and studied in Chapter 1, and

$$M(N) := \frac{K(N)}{N}$$

with

$$K(N) := p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} dv. \quad (2.8)$$

Using the change of variables $z = \frac{bN-v}{\sqrt{2a}}$, K can be rewritten as

$$\begin{aligned} K(N) &= \sqrt{2a} p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{\frac{bN-V_F}{\sqrt{2a}}}^{+\infty} e^{-z^2} dz = \\ &= \sqrt{\frac{\pi a}{2}} p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \operatorname{erfc}\left(\frac{bN - V_F}{\sqrt{2a}}\right) \end{aligned}$$

We notice that, unlike the previous chapter, the function we have to study is composed, in addition to $I(N)$, by the ϵ parameter and by a new function $M(N)$ which depends on $p(V_F)$. In particular $p(V_F) = 0$ if and only if $M(N) = 0$. However, for the reason explained at the beginning of Chapter 2, from now we assume that $p(V_F) \neq 0$, and so $M(N) \neq 0$ too.

Now we are going to define two different cases, according to the value of $p(V_F)$. To do that, we define the new parameter

$$c := K(0) = \sqrt{\frac{\pi a}{2}} p(V_F) e^{\frac{V_F^2}{2a}} \operatorname{erfc}\left(\frac{-V_F}{\sqrt{2a}}\right), \quad (2.9)$$

and the threshold

$$P := \frac{\sqrt{2}}{\sqrt{\pi a} e^{\frac{V_F^2}{2a}} \operatorname{erfc}\left(\frac{-V_F}{\sqrt{2a}}\right)}, \quad (2.10)$$

and we distinguish:

Case A : if $c > 1$, which is equivalent to

$$p(V_F) > P; \quad (2.11)$$

Case B : if $c < 1$, which is equivalent to

$$p(V_F) < P. \quad (2.12)$$

Observe that this classification does not depend on ϵ . Moreover, since in case B $p(V_F)$ is smaller than in case A, we note that case B is closer to model (1.1)-(1.3), in which $p(V_F) = 0$.

This classification is important because, as we prove in the following Theorem 2.1.2, the number of steady states in the two cases is different.

Theorem 2.1.2. *Considering the equation of random model (2.1) with $\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}}$ and $\epsilon > 0$ we have:*

- in case A (see (2.11)) there is an even number of steady states;

- in case B (see (2.12)) there is an odd number of steady states.

Note that this differentiation holds for both the inhibitory and the excitatory case, because does not depend on the value of b . Moreover, we observe that in case A there may not be steady states, while in case B there is always at least 1 steady state.

This theorem is a direct consequence of the properties of the function $J(N)$, shown in the following Lemma 2.1.3.

Lemma 2.1.3. *Let $J(N)$ the function defined in (2.7), then the following properties hold:*

1. $J(N) > \epsilon \quad \forall N > 0$;
2. $J(N) \rightarrow +\infty$ when $N \rightarrow 0$;
3. • if $b < 0$ (inhibitory case),

$$\lim_{N \rightarrow +\infty} J(N) = +\infty,$$

- if $b > 0$ (excitatory case),

$$\lim_{N \rightarrow +\infty} J(N) = \epsilon;$$

4. • in case A (see (2.11)), $J(N)$ intersects an even number of times $\frac{1}{N}$ on $\left(0, \frac{1}{\epsilon}\right)$,
 • in case B (see (2.12)), $J(N)$ intersects an odd number of times $\frac{1}{N}$ on $\left(0, \frac{1}{\epsilon}\right)$.

Proof. 1. The first property comes from the definition of $J(N)$ and the fact that $I(N)$ and $M(N) > 0$.

2. Since $I(0) < +\infty$ (see Lemma 1.3.3), when $N \rightarrow 0$, $J(N) \sim \frac{K(0)}{N} = \frac{c}{N} \rightarrow +\infty$.

3. Consider $b < 0$. From Lemma 1.3.3 we know that

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

Furthermore $M(N) \rightarrow \infty$ because $\frac{e^{N^2}}{N} \rightarrow \infty$ and $\operatorname{erfc}(-N) \rightarrow 2$ when $N \rightarrow +\infty$. So we conclude that $J(N) \rightarrow +\infty$ when $N \rightarrow +\infty$.

Now consider $b > 0$. From Lemma 1.3.3 we know that

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

Furthermore $M(N) \rightarrow 0$ because, using L'Hopital rule

$$\begin{aligned} \lim_{N \rightarrow +\infty} M(N) &= \sqrt{\frac{\pi a}{2}} p(V_F) \lim_{N \rightarrow +\infty} \frac{\operatorname{erfc}\left(\frac{bN - V_F}{\sqrt{2a}}\right)}{N e^{-\frac{(V_F - bN)^2}{2a}}} = \\ &= \sqrt{2a} p(V_F) \lim_{N \rightarrow +\infty} \frac{-e^{-\frac{(V_F - bN)^2}{2a}}}{\left(N \frac{b(V_F - bN)}{a} + 1\right) e^{-\frac{(V_F - bN)^2}{2a}}} = 0. \end{aligned}$$

So we conclude that $J(N) \rightarrow \epsilon$ when $N \rightarrow +\infty$.

4. When (2.11) holds (case A), then

- Since $c > 1$: when $N \rightarrow 0$, $J(N) \sim \frac{K(0)}{N} = \frac{c}{N} > \frac{1}{N}$;
- $J(N) > \frac{1}{N}$ when $N = \frac{1}{\epsilon}$ because of property 1;
- the two functions $J(N)$ and $\frac{1}{N}$ are both continuous on $\left(0, \frac{1}{\epsilon}\right)$.

So we can conclude that $J(N)$ intersects $\frac{1}{N}$ an even number of times on $\left(0, \frac{1}{\epsilon}\right)$.

When (2.12) holds (case B), then

- Since $c < 1$: when $N \rightarrow 0$, $J(N) \sim \frac{K(0)}{N} = \frac{c}{N} < \frac{1}{N}$;
- $J(N) > \frac{1}{N}$ when $N = \frac{1}{\epsilon}$ because of property 1;
- the two functions $J(N)$ and $\frac{1}{N}$ are both continuous on $\left(0, \frac{1}{\epsilon}\right)$.

So we can conclude that $J(N)$ intersects $\frac{1}{N}$ an odd number of times on $\left(0, \frac{1}{\epsilon}\right)$.

□

Now we are going to show an example of case A and an example of case B.

Example 2.1.4. Choosing $\epsilon = 0,5$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$ then $P = 0,0552$ and so:

- if $p(V_F) = 0,5 > P$ (Figure 2.1) we can observe that the number of intersections, and thus the number of steady states is 0 (which is an even number).
- if $p(V_F) = 0,01 < P$ (Figure 2.2) we can observe that there is 1 intersection, namely 1 steady state (which is an odd number).

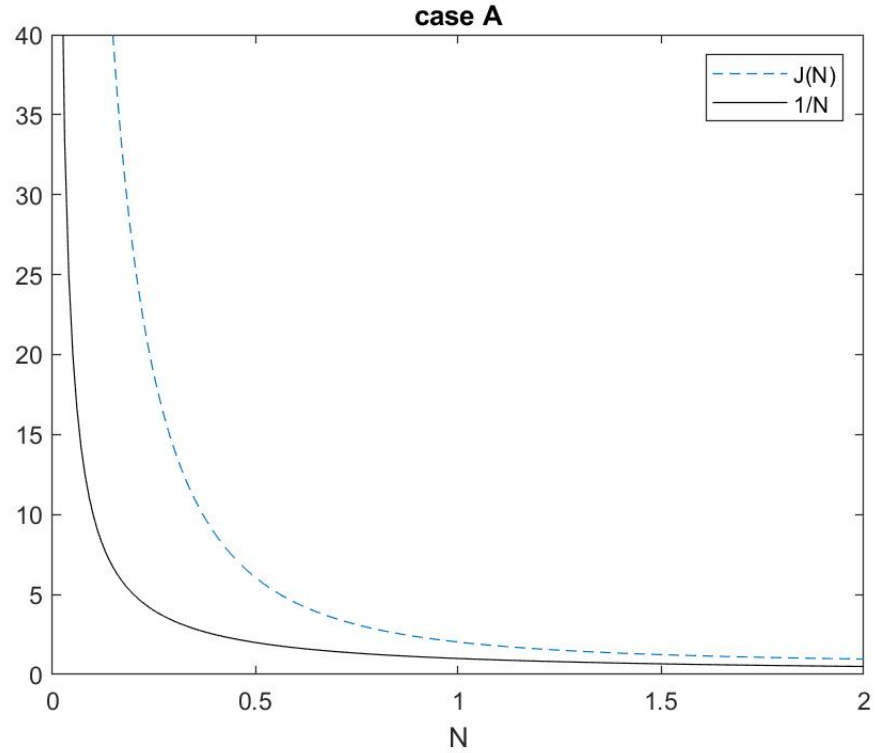


Figure 2.1: Graph of functions $J(N)$ and $\frac{1}{N}$ in case of $\epsilon = 0,5$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,5$

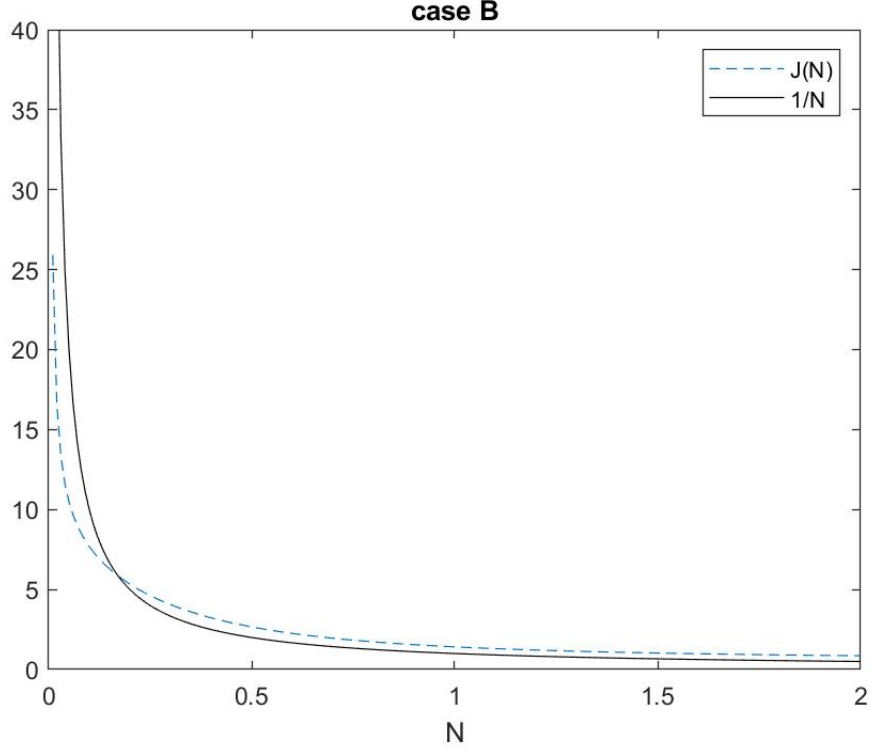


Figure 2.2: Graph of functions $J(N)$ and $\frac{1}{N}$ in case of $\epsilon = 0,5$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,01$

Up to now we have shown that the steady state number in case A is different from that in case B. Now we are going to find conditions on the parameters of the model clarifying the specific number of steady states. Before that, we illustrate some results that will be used in the proof of the final Theorem 2.1.10.

Lemma 2.1.5. *The function $y(x) := e^{x^2} \operatorname{erfc}(x)$ is decreasing.*

Proof. To prove this lemma we use the following upper and lower limitations from [1] for $y(x)$ when $x > 0$:

$$\frac{2}{\sqrt{\pi}(x + \sqrt{x^2 + 2})} < y(x) < \frac{2}{\sqrt{\pi}(x + \sqrt{x^2 + \frac{4}{\pi}})} \quad (2.13)$$

Now,

$$\dot{y}(x) = 2x e^{x^2} \operatorname{erfc}(x) - \frac{2}{\sqrt{\pi}} = 2xy(x) - \frac{2}{\sqrt{\pi}}$$

which is obviously negative if $x \leq 0$. If $x > 0$ we use the upper limitation:

$$\dot{y}(x) \leq 2x \left[\frac{2}{\sqrt{\pi}(x + \sqrt{x^2 + \frac{4}{\pi}})} \right] - \frac{2}{\sqrt{\pi}} = \frac{2x - 2\sqrt{x^2 + \frac{4}{\pi}}}{\sqrt{\pi}(x + \sqrt{x^2 + \frac{4}{\pi}})} < 0$$

And so y is a decreasing function. □

Lemma 2.1.6. *The function $\dot{y}(x) = 2x e^{x^2} \operatorname{erfc}(x) - \frac{2}{\sqrt{\pi}}$ is increasing.*

Proof. We have:

$$\ddot{y}(x) = (2 + 4x^2)e^{x^2} \operatorname{erfc}(x) - \frac{4x}{\sqrt{\pi}} = (2 + 4x^2)y(x) - \frac{4x}{\sqrt{\pi}},$$

which is obviously positive if $x \leq 0$. Now, using again (2.13), if $x > 0$ we have:

$$\ddot{y}(x) \geq \frac{4 + 8x^2}{\sqrt{\pi}(x + \sqrt{x^2 + 2})} - \frac{4x}{\sqrt{\pi}} = \frac{4x^2 + 4 - 4x\sqrt{x^2 + 2}}{\sqrt{\pi}(x + \sqrt{x^2 + 2})} > 0$$

And so \dot{y} is an increasing function. □

From Lemma 2.1.5 and Lemma 2.1.6 we can conclude that:

Corollary 2.1.6.1. *Considering $K(N)$ defined in (2.8) and $J(N)$ defined in (2.7), we have:*

- if $b > 0$: $\dot{K}(N) < 0$, $\ddot{K}(N) > 0$, $\dot{J}(N) < 0$;
- if $b < 0$: $\dot{K}(N) > 0$, $\ddot{K}(N) > 0$;

Proof. We have:

$$\begin{aligned} K(N) &= \sqrt{\frac{\pi a}{2}} p(V_F) y\left(\frac{bN - V_F}{\sqrt{2a}}\right) \\ \dot{K}(N) &= \sqrt{\frac{\pi a}{2}} p(V_F) \frac{b}{\sqrt{2a}} \dot{y}\left(\frac{bN - V_F}{\sqrt{2a}}\right) \\ \ddot{K}(N) &= \sqrt{\frac{\pi a}{2}} p(V_F) \frac{b^2}{2a} \ddot{y}\left(\frac{bN - V_F}{\sqrt{2a}}\right) \end{aligned}$$

Then if $b > 0$, $\dot{K}(N) < 0$ and $\ddot{K}(N) > 0$. Furthermore:

$$\dot{M} = \frac{\dot{K}}{N} - \frac{K}{N^2} < 0$$

and remembering that $\dot{I} < 0$ (see Lemma 1.3.3) we obtain that:

$$\dot{J} = \dot{I} + \dot{M} < 0$$

Instead if $b < 0$, $\dot{K}(N) > 0$ and $\ddot{K}(N) > 0$, but M is not a monotonic function and so we cannot conclude about the sign of the derivative of J . □

Remark 2.1.7. *It will be useful rewriting \dot{K} and \dot{I} in function of K :*

$$\begin{aligned} \bullet \dot{K}(N) &= \sqrt{\frac{\pi a}{2}} p(V_F) \frac{b}{\sqrt{2a}} \dot{y} \left(\frac{bN - V_F}{\sqrt{2a}} \right) = \\ &= \sqrt{\pi} p(V_F) b \left[\frac{bN - V_F}{\sqrt{2a}} e^{\frac{(V_F - bN)^2}{2a}} \operatorname{erfc} \left(\frac{bN - V_F}{\sqrt{2a}} \right) - \frac{1}{\sqrt{\pi}} \right] = \\ &= -b d_1(N), \end{aligned}$$

where

$$d_1(N) := - \left[\frac{bN - V_F}{a} K(N) - p(V_F) \right]; \quad (2.14)$$

$$\begin{aligned} \bullet \dot{I}(N) &= -\frac{b}{\sqrt{a}} \left[\int_0^{+\infty} e^{-\frac{s^2}{2} + s \frac{V_F - bN}{\sqrt{2a}}} ds - \int_0^{+\infty} e^{-\frac{s^2}{2} + s \frac{V_R - bN}{\sqrt{2a}}} ds \right] = \\ &= -\frac{b}{\sqrt{a}} \left[e^{\frac{(V_F - bN)^2}{2a}} \int_0^{+\infty} e^{-\left(\frac{s}{\sqrt{2}} - \frac{V_F - bN}{\sqrt{2a}}\right)^2} ds - e^{\frac{(V_R - bN)^2}{2a}} \int_0^{+\infty} e^{-\left(\frac{s}{\sqrt{2}} - \frac{V_R - bN}{\sqrt{2a}}\right)^2} ds \right]. \end{aligned}$$

Using the change of variables

$$y = \frac{s}{\sqrt{2}} - \frac{V_F - bN}{\sqrt{2a}} \quad z = \frac{s}{\sqrt{2}} - \frac{V_R - bN}{\sqrt{2a}},$$

we obtain:

$$\begin{aligned} \dot{I}(N) &= -b \sqrt{\frac{2}{a}} \left[e^{\frac{(V_F - bN)^2}{2a}} \int_{-\frac{V_F - bN}{\sqrt{2a}}}^{+\infty} e^{-y^2} dy - e^{\frac{(V_R - bN)^2}{2a}} \int_{-\frac{V_R - bN}{\sqrt{2a}}}^{+\infty} e^{-z^2} dz \right] = \\ &= -b \sqrt{\frac{2}{a}} \left[\frac{\sqrt{\pi}}{2} e^{\frac{(V_F - bN)^2}{2a}} \operatorname{erfc} \left(\frac{bN - V_F}{\sqrt{2a}} \right) - \frac{\sqrt{\pi}}{2} e^{\frac{(V_R - bN)^2}{2a}} \operatorname{erfc} \left(\frac{bN - V_R}{\sqrt{2a}} \right) \right] = \\ &= -b d_2(N), \end{aligned}$$

where

$$d_2(N) := \left[\frac{K(N)}{a p(V_F)} - \sqrt{\frac{\pi}{2a}} e^{\frac{(V_R - bN)^2}{2a}} \operatorname{erfc} \left(\frac{bN - V_R}{\sqrt{2a}} \right) \right]. \quad (2.15)$$

To determine more precisely the number of steady states it will be useful to reformulate the problem (2.7) in the following way:

$$\begin{cases} 1 = U(N), \\ U(N) := N J(N) = N(\epsilon + I(N)) + K(N), \end{cases} \quad (2.16)$$

Remark 2.1.8. (2.16) is the equivalent of (1.35) for problem with fixed threshold (1.28). So, like in Chapter 1, the idea to find the steady states is to find the intersections between $U(N)$ and the straight line $h(N) = 1$. Unlike $Q(N)$, we note that $U(N)$ is composed, in addition to the term $NI(N)$, by two new terms: $N\epsilon$ and $K(N)$. The positivity of $I(N)$ and $K(N)$ and the presence of the term $N\epsilon$ guarantee, as we see below, that $U(N)$ is greater than 1 in the extreme $N = \frac{1}{\epsilon}$ of the considered interval. We can now observe that the following properties hold:

- U is a continuous function;
- $U(0) = K(0) (= c)$;
- $U(\frac{1}{\epsilon}) = 1 + \frac{1}{\epsilon} I(\frac{1}{\epsilon}) + K(\frac{1}{\epsilon}) > 1$
- $U(N) \rightarrow +\infty$ when $N \rightarrow +\infty$ because:
 - if $b > 0$, $NI(N) \rightarrow \frac{V_F - V_R}{b}$, $K(N) \rightarrow 0$ when $N \rightarrow +\infty$;
 - if $b < 0$, $I(N) \rightarrow +\infty$, $K(N) \rightarrow +\infty$ when $N \rightarrow +\infty$.
- $\dot{U}(N) = \epsilon + I + N\dot{I}(N) + \dot{K}(N)$.

We can easily notice that the sign of $\dot{U}(N)$ is not constant for any choice of parameters. In the following Lemma 2.1.9 we find some conditions which guarantee the positivity of $\dot{U}(N)$ for all N in the considered interval.

Lemma 2.1.9. For $b > 0$, if

$$\epsilon > \bar{\epsilon} := \frac{-2\dot{I}(0)}{\dot{K}(0) + \sqrt{[\dot{K}(0)]^2 - 4\dot{I}(0)}} \quad (2.17)$$

then $\dot{U}(N) > 0 \quad \forall N \in (0, \frac{1}{\epsilon})$.

Proof. As \dot{I} and \dot{K} are increasing, and I is decreasing, $\forall N \in (0, \frac{1}{\epsilon})$ we have:

$$I\left(\frac{1}{\epsilon}\right) < I(N) < I(0) \quad (2.18)$$

$$N\dot{I}(0) < N\dot{I}(N) < N\dot{I}\left(\frac{1}{\epsilon}\right) \quad (2.19)$$

$$\dot{K}(0) < \dot{K}(N) < \dot{K}\left(\frac{1}{\epsilon}\right) \quad (2.20)$$

Therefore, $\dot{U}(N) > \epsilon + I(\frac{1}{\epsilon}) + N\dot{I}(0) + \dot{K}(0)$ and the right hand side in this inequality is positive, if $N < (\epsilon + I(\frac{1}{\epsilon}) + \dot{K}(0))/(-\dot{I}(0))$. So, if we prove that

$$\frac{1}{\epsilon} < \frac{\epsilon + I(\frac{1}{\epsilon}) + \dot{K}(0)}{-\dot{I}(0)} \quad (2.21)$$

then we can conclude the proof, since $N < \frac{1}{\epsilon}$.

We notice that the condition (2.21) is equivalent to

$$\epsilon^2 + \epsilon \left[I\left(\frac{1}{\epsilon}\right) + \dot{K}(0) \right] + \dot{I}(0) > 0$$

whose positive solutions are

$$\epsilon > \mu := \frac{-[I(\frac{1}{\epsilon}) + \dot{K}(0)] + \sqrt{[I(\frac{1}{\epsilon}) + \dot{K}(0)]^2 - 4\dot{I}(0)}}{2}$$

As

$$\begin{aligned} \mu &= \mu \cdot \frac{[I(\frac{1}{\epsilon}) + \dot{K}(0)] + \sqrt{[I(\frac{1}{\epsilon}) + \dot{K}(0)]^2 - 4\dot{I}(0)}}{[I(\frac{1}{\epsilon}) + \dot{K}(0)] + \sqrt{[I(\frac{1}{\epsilon}) + \dot{K}(0)]^2 - 4\dot{I}(0)}} = \\ &= \frac{-2\dot{I}(0)}{[I(\frac{1}{\epsilon}) + \dot{K}(0)] + \sqrt{[I(\frac{1}{\epsilon}) + \dot{K}(0)]^2 - 4\dot{I}(0)}} < \frac{-2\dot{I}(0)}{\dot{K}(0) + \sqrt{[\dot{K}(0)]^2 - 4\dot{I}(0)}} = \bar{\epsilon}, \end{aligned}$$

we conclude that if $\epsilon > \bar{\epsilon}$ then condition (2.21) applies and so $\dot{U}(N) > 0$ $\forall N \in (0, \frac{1}{\epsilon})$. □

Now we can prove the following theorem:

Theorem 2.1.10. *Considering the equation (2.1) with $\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > v_F\}}$ and $\epsilon > 0$ we have:*

1. *If $b < 0$ (inhibitory case):*
 - case A: *there is no steady state to (2.1);*
 - case B: *there is a unique steady state to (2.1).*
2. *If $b > 0$ (excitatory case): in case B there is always at least 1 steady state.*
Moreover, if $\epsilon > \bar{\epsilon} := \frac{-2\dot{I}(0)}{\dot{K}(0) + \sqrt{[\dot{K}(0)]^2 - 4\dot{I}(0)}}$
 - case A: *there is no steady state to (2.1);*
 - case B: *there is a unique steady state to (2.1).*

Proof. 1. If $b < 0$ we know that $\dot{I} > 0$ and from Corollary 2.1.6.1 $\dot{K} > 0$ and then:

$$\dot{U} = \epsilon + I + N\dot{I}(N) + \dot{K}(N) > 0,$$

i.e. U is an increasing function. Now,

- in case A from Remark 2.1.8 we deduce that $U(0) > 1$, and so $U(N) > 1 \forall N \in (0, \frac{1}{\epsilon})$, which means that there is no steady state;
 - in case B from Remark 2.1.8 we deduce that $U(0) < 1$, and so $\exists! N \in (0, \frac{1}{\epsilon})$ such that $U(N) = 1$, which means that there is a unique steady state.
2. If $b > 0$. In case B, since $U(0) < 1$, $U(\frac{1}{\epsilon}) > 1$ and U continuous, we can assert that $U(N)$ crosses $h(N) = 1$ at least 1 time, which means that there is always at least 1 steady state.
- Now, if $\epsilon > \bar{\epsilon}$, from Lemma 2.1.9 we have $\dot{U}(N) > 0 \forall N \in (0, \frac{1}{\epsilon})$ and so, as we explained in case $b < 0$ we can conclude that:

- case A: there is no steady state;

- case B: there is a unique steady state.

□

Remark 2.1.11. Notice that condition (2.17) is equivalent to

$$0 < b < \frac{\epsilon^2 d_2(0)}{\epsilon d_1(0)d_2(0) + d_2^2(0)} \quad (2.22)$$

where d_1 and d_2 are respectively defined in (2.14) and (2.15). This is true because

$$\bar{\epsilon} = \frac{-2\dot{I}(0)}{\dot{K}(0) + \sqrt{[\dot{K}(0)]^2 - 4\dot{I}(0)}} = \frac{2b d_2(0)}{-b d_1(0) + \sqrt{b^2 d_1^2(0) + 4b d_2(0)}},$$

and so $\epsilon > \bar{\epsilon}$ is equivalent to

$$\begin{aligned} \epsilon \sqrt{b^2 d_1^2(0) + 4b d_2(0)} &> \epsilon b d_1(0) + 2b d_2(0) \iff \\ \epsilon^2 b^2 d_1^2(0) + 4\epsilon^2 b d_2(0) &> (\epsilon b d_1(0))^2 + 4b^2 d_2^2(0) + 4\epsilon b^2 d_1(0)d_2(0) \iff \\ b^2 [4\epsilon d_1(0)d_2(0)] + 4d_2^2(0) - 4\epsilon^2 b d_2(0) &< 0 \iff \\ b[b(\epsilon d_1(0)d_2(0) + d_2^2(0)) - \epsilon^2 d_2(0)] &< 0, \end{aligned}$$

whose solution are given in (2.22).

Now, comparing the results of this Theorem with those of Theorem 1.3.6 about model with fixed threshold (1.1)-(1.5), we note that

- if (2.12) holds (case B), when $b < 0$ or $b > 0$ small enough, random model (2.1) has a unique steady state exactly as model with fixed threshold (1.1)-(1.5), and this makes sense because case B of the random discharge potential model is closer to model (1.1)-(1.5) since $p(V_F) \sim 0$;
- if (2.11) holds (case A), results are very different, because model (2.1) has no steady states both in case of $b < 0$ and $b > 0$ small enough.

Example 2.1.12. Choosing $\epsilon = 6$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,01$ (Figure 2.3).

We have:

$$P = 0,0552 > p(V_F) \Rightarrow \text{case B.}$$

Furthermore $b < \frac{\epsilon^2 d_2(0)}{\epsilon d_1(0)d_2(0) + d_2^2(0)} = 2,1358$ or equivalently $\bar{\epsilon} = 5,7928 < \epsilon \Rightarrow$ there is only 1 steady state.

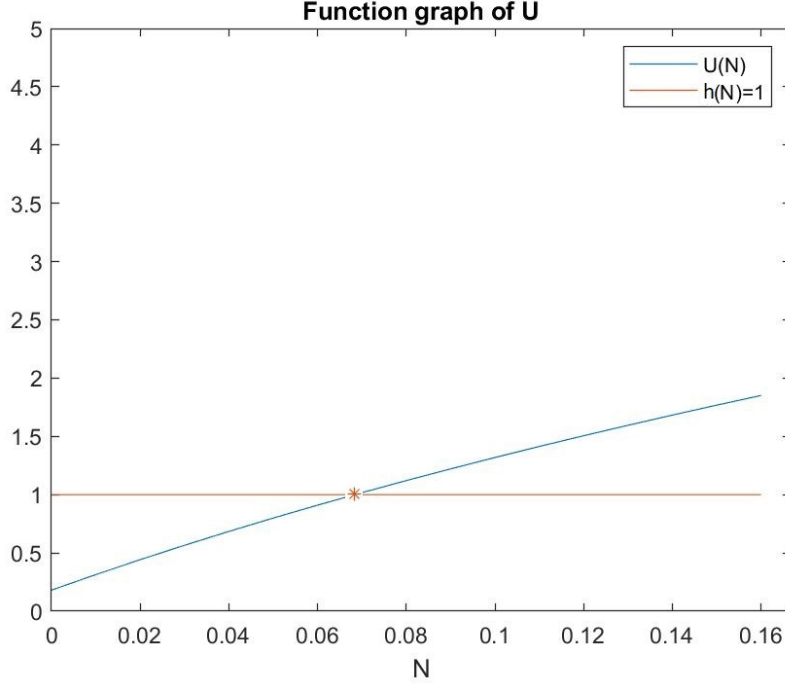
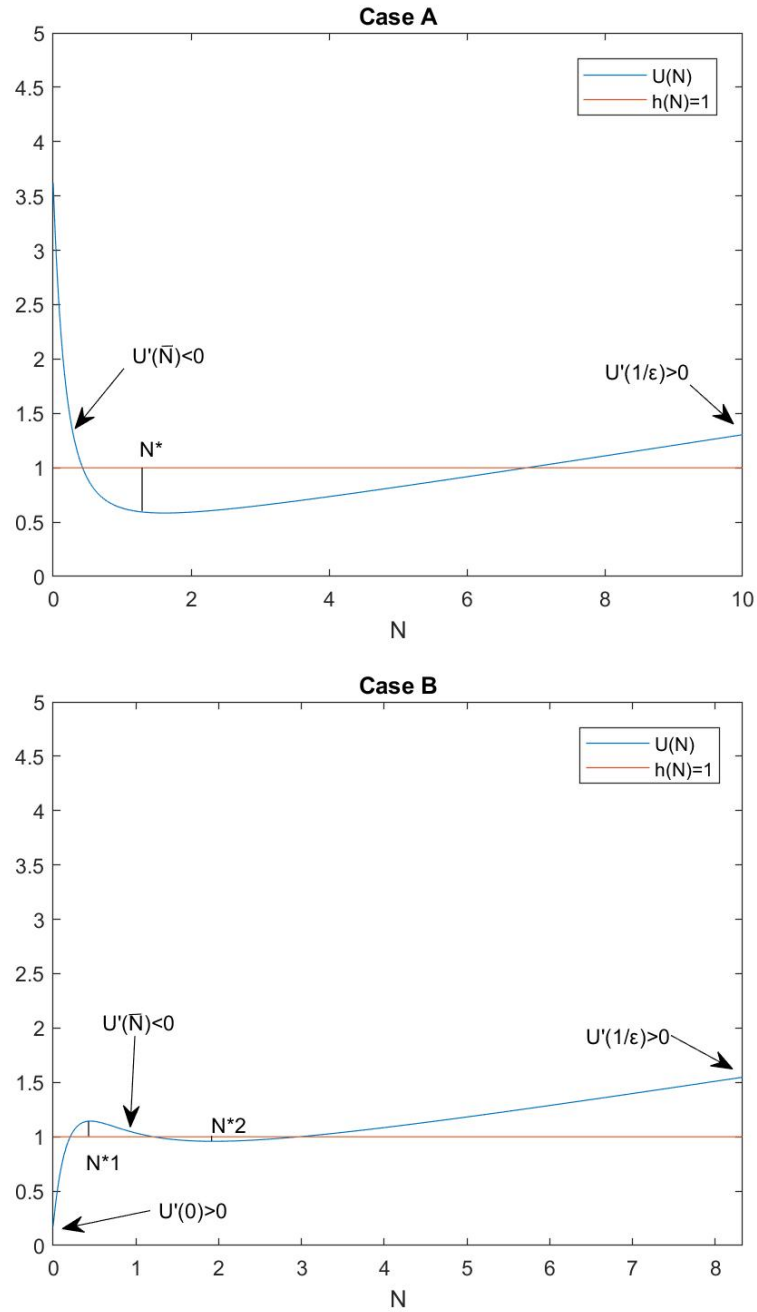


Figure 2.3: Steady states in the case of $\epsilon = 6$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0.01$ (case B)

Now, by studying function U in more detail and imposing conditions on it, we show that it is possible to find ϵ such that equation (2.1) admits more than one steady states. In particular:

- in case A the idea is that if we impose $\dot{U}(\frac{1}{\epsilon}) > 0$ and $\dot{U}(\bar{N}) < 0$ for a certain $\bar{N} < \frac{1}{\epsilon}$, then exists $N^* \in (\bar{N}, \frac{1}{\epsilon})$ a relative minimum of U and if we impose that $U(N^*) < 1$ then U intersects $h(N) = 1$ at least 2 times, since $U(0) > 1$, $U(\frac{1}{\epsilon}) > 1$ and U is continuous (see the top plot in Figure 2.4). Observe that a necessary condition to have $U(N^*) < 1$ is that $K(N^*) < 1$;
- in case B the idea is that if we impose $\dot{U}(\frac{1}{\epsilon}) > 0$, $\dot{U}(\bar{N}) < 0$ for a certain $\bar{N} < \frac{1}{\epsilon}$, and $\dot{U}(0) > 0$ then exist $N_2^* \in (\bar{N}, \frac{1}{\epsilon})$ a relative minimum of U and $N_1^* < \bar{N}$ a relative maximum of U and if we impose that $U(N_2^*) < 1$ and $U(N_1^*) > 1$ then U intersects $h(N) = 1$ at least 3 times, since $U(0) < 1$, $U(\frac{1}{\epsilon}) > 1$ and U is continuous (see the bottom plot in Figure 2.4).

Figure 2.4: Graphs of function $U(N)$

Now we are going to show two Lemmas that will be useful to understand which conditions the parameters must satisfy so that U has the characteristics we have just talked about.

In Lemma 2.1.14 and 2.1.15 we are going to use:

$$p_1 := \frac{1}{b} \left[\sqrt{\frac{\pi}{2a}} V_F \left[-1 + e^{\frac{(V_F - V_R)^2}{2a}} \operatorname{erfc} \left(\frac{V_F - V_R}{\sqrt{2a}} \right) \right] + I \left(\frac{V_F}{b} \right) \right],$$

$$p_2 := \frac{I(0)}{b} - \frac{V_F}{a}, \quad p_3 := \sqrt{\frac{2}{\pi a}},$$

$$b_1 := \sqrt{\frac{\pi a}{2}} e^{\frac{V_F^2}{2a}} \operatorname{erfc} \left(\frac{-V_F}{\sqrt{2a}} \right) \left[I \left(\frac{V_F}{b} \right) + \sqrt{\frac{\pi}{2a}} V_F \left(e^{\frac{(V_F - V_R)^2}{2a}} \operatorname{erfc} \left(\frac{V_F - V_R}{\sqrt{2a}} \right) - 1 \right) \right],$$

$$I_0 := b_1 \left(p_3 + \frac{V_F}{a} \right), \quad b_2 := \frac{I(0)}{p_3 + \frac{V_F}{a}}, \quad b_3 := \frac{I(0)}{\frac{V_F^2}{e^{\frac{V_F^2}{2a}} \operatorname{erfc} \left(\frac{-V_F}{\sqrt{2a}} \right)} + \frac{V_F}{a}}.$$

Remark 2.1.13. Notice that:

- $0 < b_2 < b_3$,
- $I(0) > I_0 \Rightarrow b_1 < b_2$,
- $b_1 < b \iff p_1 < P$,
- $b < b_3 \iff (0 <) P < p_2$,
- $b_2 < b \iff p_2 < p_3$.

Lemma 2.1.14. Let $I(0) > I_0$, $b \in (b_2, b_3)$, $p(V_F) \in (p_2, p_3)$ and

$$\tilde{\epsilon}_{1,12} < \epsilon < \tilde{\epsilon}_2, \tag{2.23}$$

where

$$\tilde{\epsilon}_{1,12} := \frac{-\dot{K} \left(\frac{12V_F}{b} \right) + \sqrt{I \left(\frac{12V_F}{b} \right)^2 + \dot{K} \left(\frac{12V_F}{b} \right)^2 - 4\dot{I} \left(\frac{12V_F}{b} \right)}}{2},$$

$$\tilde{\epsilon}_2 := \min \left(\frac{b}{7V_F}, \sqrt{\frac{\pi}{2a}} V_F \left[1 - e^{\frac{(V_F - V_R)^2}{2a}} \operatorname{erfc} \left(\frac{V_F - V_R}{\sqrt{2a}} \right) \right] + bp(V_F) - I \left(\frac{V_F}{b} \right) \right).$$

Then $\dot{U} \left(\frac{V_F}{b} \right) < 0$, $\dot{U} \left(\frac{1}{\epsilon} \right) > 0$ and $K \left(\frac{V_F}{b} \right) < 1$.

Proof. From Remark 2.1.13 we know that (b_2, b_3) and (p_2, p_3) are not empty, and also that (2.11) is satisfied, i.e. we are in case A.

Furthermore $p_1 < p(V_F)$ guarantees that $\tilde{\epsilon}_2 > 0$.

Now note that $\frac{V_F}{b} < \frac{1}{\epsilon}$ because

$$\epsilon < \tilde{\epsilon}_2 < \frac{b}{12V_F} < \frac{b}{V_F}$$

and

$$\begin{aligned} \dot{U}\left(\frac{V_F}{b}\right) < 0 &\iff \epsilon + I\left(\frac{V_F}{b}\right) + \frac{V_F}{b} \dot{I}\left(\frac{V_F}{b}\right) + \dot{K}\left(\frac{V_F}{b}\right) < 0 \\ \epsilon < \zeta &:= \sqrt{\frac{\pi}{2a}} V_F \left[1 - e^{\frac{(V_F - V_R)^2}{2a}} \operatorname{erfc}\left(\frac{V_F - V_R}{\sqrt{2a}}\right) \right] + bp(V_F) - I\left(\frac{V_F}{b}\right) \end{aligned} \quad (2.24)$$

where $\zeta > 0$ because $p(V_F) > p_1$. The inequality (2.24) is satisfied because $\epsilon < \tilde{\epsilon}_2$ and so $\dot{U}\left(\frac{V_F}{b}\right) < 0$.

Secondly notice that $\dot{U}\left(\frac{1}{\epsilon}\right) > 0$ if and only if

$$\epsilon^2 + \epsilon \left(I\left(\frac{1}{\epsilon}\right) + \dot{K}\left(\frac{1}{\epsilon}\right) \right) + \dot{I}\left(\frac{1}{\epsilon}\right) > 0, \quad (2.25)$$

whose positive solutions are

$$\epsilon > \eta(\epsilon) := \frac{-(I(\frac{1}{\epsilon}) + \dot{K}(\frac{1}{\epsilon})) + \sqrt{(I(\frac{1}{\epsilon}) - \dot{K}(\frac{1}{\epsilon}))^2 - 4\dot{I}(\frac{1}{\epsilon})}}{2}.$$

Since $\epsilon < \tilde{\epsilon}_2 < \frac{b}{12V_F}$, then $\frac{12V_F}{b} < \frac{1}{\epsilon}$ and so

$$\begin{aligned} \eta(\epsilon) &< \frac{-(\dot{K}(\frac{1}{\epsilon})) + \sqrt{I(\frac{1}{\epsilon})^2 + \dot{K}(\frac{1}{\epsilon})^2 - 4\dot{I}(\frac{1}{\epsilon})}}{2} \\ &< \frac{-(\dot{K}(\frac{12V_F}{b})) + \sqrt{I(\frac{12V_F}{b})^2 + \dot{K}(\frac{12V_F}{b})^2 - 4\dot{I}(\frac{12V_F}{b})}}{2} \end{aligned}$$

which is less than ϵ because $\epsilon > \tilde{\epsilon}_{1,12}$. So the inequality (2.25) is satisfied and we can conclude that $\dot{U}\left(\frac{1}{\epsilon}\right) > 0$.

Finally, since $p(V_F) < p_3$ then

$$K\left(\frac{V_F}{b}\right) = \sqrt{\frac{\pi a}{2}} p(V_F) < 1.$$

□

Lemma 2.1.15. *Let $I(0) > I_0$, $b \in (\max(0, b_1), b_3)$, $p(V_F) \in (p_1, p_2)$ and*

$$\tilde{\epsilon}_{1,7} < \epsilon < \tilde{\epsilon}_2, \quad (2.26)$$

where

$$\tilde{\epsilon}_{1,7} := \frac{-\dot{K}(\frac{7V_F}{b}) + \sqrt{I(\frac{7V_F}{b})^2 + \dot{K}(\frac{7V_F}{b})^2 - 4I(\frac{7V_F}{b})}}{2}.$$

Then $\dot{U}(0) > 0$, $\dot{U}(\frac{V_F}{b}) < 0$ and $\dot{U}(\frac{1}{\epsilon}) > 0$.

Proof. From Remark 2.1.13 we know that $(\max(0, b_1), b_3)$ and (p_1, p_2) are not empty. Furthermore, since $p_2 > P$, we cannot conclude if we are in case A or B.

Now we are going to prove the thesis. Observe that

$$\begin{aligned} \dot{U}(0) > 0 &\iff \epsilon + I(0) + \dot{K}(0) > 0 \iff \\ \epsilon > -I(0) - \dot{K}(0) &= -I(0) + b \left[\frac{V_F}{a} K(0) + p(V_F) \right]. \end{aligned}$$

Since $p(V_F) < p_2$ and $K(0) < 1$ (as $p(V_F) < P$), then

$$-I(0) - \dot{K}(0) < -I(0) + b \left[\frac{V_F}{a} + p(V_F) \right] < 0$$

and so we conclude that $\dot{U}(0) > 0 \forall \epsilon > 0$.

Now notice that

$$\begin{aligned} \dot{U}\left(\frac{V_F}{b}\right) < 0 &\iff \epsilon + I\left(\frac{V_F}{b}\right) + \frac{V_F}{b} \dot{I}\left(\frac{V_F}{b}\right) + \dot{K}\left(\frac{V_F}{b}\right) < 0 \\ \epsilon < \zeta &:= \sqrt{\frac{\pi}{2a}} V_F \left[1 - e^{\frac{(V_F - V_R)^2}{2a}} \operatorname{erfc}\left(\frac{V_F - V_R}{\sqrt{2a}}\right) \right] + bp(V_F) - I\left(\frac{V_F}{b}\right) \end{aligned} \quad (2.27)$$

where $\zeta > 0$ because $p(V_F) > p_1$. The inequality (2.27) is satisfied because $\epsilon < \tilde{\epsilon}_2$ and so $\dot{U}(\frac{V_F}{b}) < 0$. Finally, since $\epsilon > \tilde{\epsilon}_{1,7}$ and $\epsilon < \frac{b}{7V_F}$ we conclude that $\dot{U}(\frac{1}{\epsilon}) > 0$ like in Lemma 2.1.14 \square

From Lemma 2.1.14 and 2.1.15 we can say that:

Corollary 2.1.15.1. *Let $I(0) > I_0$:*

- *Case A: if $b \in (b_2, b_3)$ and $p(V_F) \in (p_2, p_3)$, then it could exist a range of ϵ such that there are at least 2 steady states.*
- *Case B: if $b \in (\max(0, b_1), b_3)$ and $p(V_F) \in (p_1, P)$, then it could exist a range of ϵ such that there are at least 3 steady states.*

Proof. Let $I(0) > I_0$.

- Case A.

From Lemma 2.1.14, if $\tilde{\epsilon}_{1,12} < \epsilon < \tilde{\epsilon}_2$, then $\dot{U}(0) < 0$, $\dot{U}(\frac{1}{\epsilon}) > 0$ and $K(\frac{V_F}{b}) < 1$. Since U is continuous, then exists $N^* \in (\frac{V_F}{b}, \frac{1}{\epsilon})$ a relative minimum of U in $(0, \frac{1}{\epsilon})$. Furthermore, since $K(\frac{V_F}{b}) < 1$ and K is decreasing, then $K(N^*) < 1$.

Now we are going to prove that could exist an interval such that there are at least 2 steady states. This is true if and only if

$$U(N^*) < 1 \quad (2.28)$$

Observe that

$$\dot{U}(N^*) = 0 \iff N^* = \frac{\epsilon + I(N^*) + \dot{K}(N^*)}{-\dot{I}(N^*)}$$

and so (2.28) can be rewritten as

$$\epsilon^2 + [2I(N^*) + \dot{K}(N^*)]\epsilon + I(N^*)\dot{K}(N^*) + I^2(N^*) - \dot{I}(N^*)(1 - K(N^*)) < 0 \quad (2.29)$$

which has real solutions because

$$\begin{aligned} \Delta &:= [2I(N^*) + \dot{K}(N^*)]^2 - 4[I(N^*)\dot{K}(N^*) + I^2(N^*) - \dot{I}(N^*)(1 - K(N^*))] = \\ &= \dot{K}^2(N^*) - 4\dot{I}(N^*)(1 - K(N^*)) > 0 \end{aligned}$$

since $K(N^*) < 1$.

So the solution of (2.29) are

$$\epsilon_a(N^*) < \epsilon < \epsilon_b(N^*),$$

where

$$\epsilon_a(N) := \frac{-2I(N) - \dot{K}(N) - \sqrt{\dot{K}^2(N) - 4\dot{I}(N)(1 - K(N))}}{2}, \quad (2.30)$$

$$\epsilon_b(N) := \frac{-2I(N) - \dot{K}(N) + \sqrt{\dot{K}^2(N) - 4\dot{I}(N)(1 - K(N))}}{2}. \quad (2.31)$$

Finally if $\epsilon \in (\max(\tilde{\epsilon}_1, \epsilon_a(N^*)), \min(\epsilon_b(N^*), \tilde{\epsilon}_2))$, then (2.29) is satisfied and so $U(N^*) < 1$ which means that U intersects the straight line $h(N) = 1$ at least 2 times in the interval $(0, \frac{1}{\epsilon})$, i.e. there are at least 2 steady

states.

We cannot prove that the interval $(\max(\tilde{\epsilon}_1, \epsilon_a(N^*)), \min(\epsilon_b(N^*), \tilde{\epsilon}_2))$ is always not empty, but we can find values of parameters such that it is (see Example 2.1.17).

- Case B.

Since $b < b_3$, then $P < p_2$ and so if $\tilde{\epsilon}_{1,7} < \epsilon < \tilde{\epsilon}_2$, by Lemma 2.1.15, we have that $\dot{U}(0) < 0$, $\dot{U}(\frac{V_F}{b}) < 0$ and $\dot{U}(\frac{1}{\epsilon}) > 0$. So, since U is continuous, then exist $N_1^* < \frac{V_F}{b} < N_2^*$ a relative maximum and a relative minimum of U in $(0, \frac{1}{\epsilon})$.

Finally if we prove that $U(N_1^*) > 1$ and $U(N_2^*) < 1$ we can conclude that there are at least 3 steady states.

Defining $\epsilon_{a,i} := \epsilon_a(N_i^*)$, $\epsilon_{b,i} := \epsilon_b(N_i^*)$ (see (2.30) and (2.31)) and using the same reasonings of case A we know that

$$\epsilon_a(N_2^*) < \epsilon < \epsilon_b(N_2^*) \Rightarrow U(N_2^*) < 1 \tag{2.32}$$

and

$$\epsilon < \epsilon_a(N_1^*) \text{ or } \epsilon > \epsilon_b(N_1^*) \Rightarrow U(N_1^*) > 1 \tag{2.33}$$

So, if ϵ satisfying (2.41), (2.32) and (2.33) exists, then U intersects the straight line $h(N) = 1$ at least 3 times, i.e. there are at least 3 steady states.

We cannot prove that it is always possible to find an ϵ of this type, but we can find values of parameters such that ϵ satisfies (2.41), (2.32) and (2.33) (see Example 2.1.16).

□

We can summarize and better visualize the results of the Corollary 2.1.15.1 in the following table.

If $I(0) > I_0$ and $b \in (b_2, b_3)$ then, depending on the value of $p(V_F)$:

$p(V_F) \in$	$(0, p_1)$	(p_1, P)	(P, p_2)	(p_2, p_3)	$(p_3, +\infty)$
case	B	B	A	A	A
n. of steady state	odd	3	even	2	even

Example 2.1.16. Choosing $\epsilon = 0,12$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,01$, $k = 7$ (Figure 2.5).

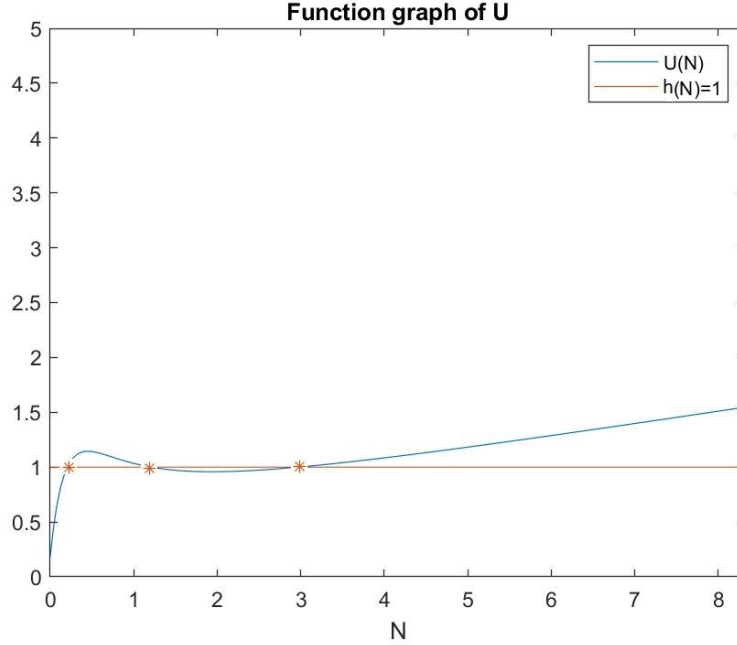


Figure 2.5: Steady states in the case of $\epsilon = 0,12$, $a = 1$, $b = 2$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,01$ (case B)

We have:

$$P = 0,0552 > p(V_F) \Rightarrow \text{case B.}$$

Conditions of Lemma 2.1.15 are satisfied because

I_0	b_1	b_3	p_1	$\tilde{\epsilon}_{1,7}$	$\tilde{\epsilon}_2$
-14,8565	-5,3099	4,0555	-0,1467	0,1191	0,1429

\Rightarrow exist $N_1^* < \frac{V_F}{b} = 1 < N_2^*$ relative maximum and minimum of U .

$\epsilon_{a,1}$	$\epsilon_{a,2}$	$\epsilon_{b,1}$	$\epsilon_{b,2}$
-4,5422	-0,8711	-0,660	0,1297

$\Rightarrow \max(\tilde{\epsilon}_{1,7}, \epsilon_{a,2}) = 0,1191 < \epsilon < \min(\tilde{\epsilon}_2, \epsilon_{b,2}) = 0,1297 \Rightarrow$ at least 3 steady states.

Example 2.1.17. Choosing $\epsilon = 0,1$, $a = 1$, $b = 3,5$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,7$ (Figure 2.6).

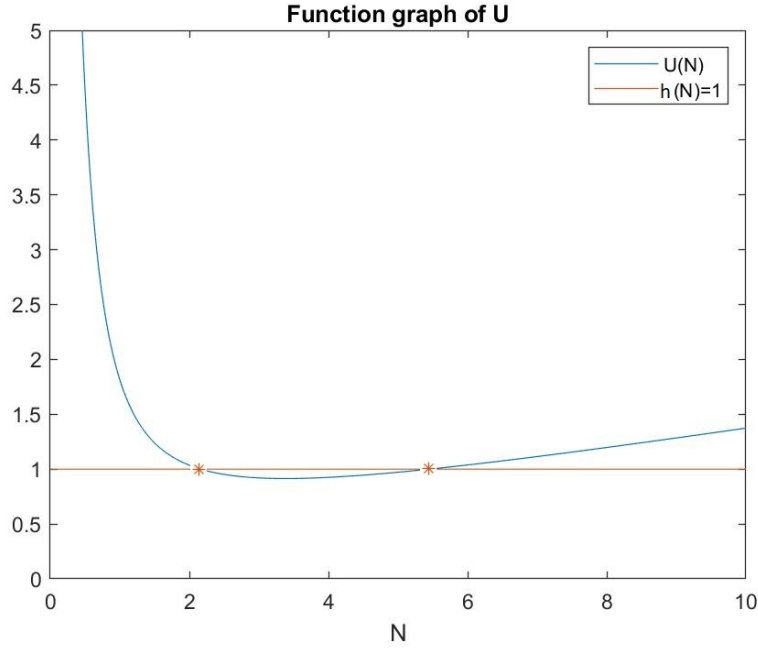


Figure 2.6: Steady states in the case of $\epsilon = 0,1$, $a = 1$, $b = 3,5$, $V_R = 1$, $V_F = 2$, $p(V_F) = 0,7$ (case A)

We have:

$$P = 0,0552 < p(V_F) \Rightarrow \text{case A.}$$

Conditions of Lemma 2.1.14 are satisfied because

I_0	b_2	b_3	p_2	p_3	$\tilde{\epsilon}_{1,12}$	$\tilde{\epsilon}_2$
-14,8565	2,979	4,0555	0,3814	0,7979	0,0884	0,1458

\Rightarrow exist $N^* > \frac{V_F}{b} = 0,5714$ relative minimum of U .

$\epsilon_a(N^*)$	$\epsilon_b(N^*)$
-0,4010	0,1540

$\Rightarrow \max(\tilde{\epsilon}_{1,12}, \epsilon_a(N^*)) = 0,0884 < \epsilon < \min(\tilde{\epsilon}_2, \epsilon_b(N^*)) = 0,1458 \Rightarrow$ at least 2 steady states.

2.1.1 Case with transmission delays and refractory states

In this subsection we consider the random discharge potential model with refractory state and transmission delay. In this case the model (2.1) becomes, considering

$$M_\tau(t) = \frac{R(t)}{\tau}:$$

$$\left\{ \begin{array}{l} \frac{\partial p}{\partial t}(v, t) + \frac{\partial}{\partial v} [(-v + bN(t - D))p(v, t)] - a \frac{\partial^2 p}{\partial^2 v}(v, t) + \phi_\epsilon(v)p(v, t) \\ = M(t)\delta_{V_R}(v), \\ N(t) = \int_{-\infty}^{+\infty} \phi_\epsilon(v)p(v, t)dv, \\ \frac{dR(t)}{dt} = N(t) - M_\tau(t). \end{array} \right. \quad (2.34)$$

And so, the search for steady states consists in finding the solutions of

$$\left\{ \begin{array}{l} \frac{\partial}{\partial v} [(-v + bN)p(v)] - a \frac{\partial^2 p}{\partial^2 v}(v) + \phi_\epsilon(v)p(v) = N(t)\delta_{V_R}(v), \\ N = \int_{-\infty}^{+\infty} \phi_\epsilon(v)p(v)dv, \\ R = N\tau. \end{array} \right. \quad (2.35)$$

We can immediately observe that the presence of the delay does not produce any change.

Instead, let's see how the presence of the refractory period influences the search for steady states. With the same calculations previously made we obtain

$$p(v) = -\frac{1}{a} e^{-\frac{(v-bN)^2}{2a}} \int_v^{V_F} g(w) e^{\frac{(w-bN)^2}{2a}} dw + p(V_F) e^{\frac{(V_F-bN)^2}{2a}} e^{-\frac{(v-bN)^2}{2a}}, \quad (2.36)$$

with $g(v)$ defined in (2.4). In this case, because of the refractory period, the following identity holds:

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

from which we deduce that

$$\int_{-\infty}^{V_F} p(v)dv = \int_{-\infty}^{+\infty} p(v)dv - \int_{V_F}^{+\infty} p(v)dv = 1 - R - \epsilon N. \quad (2.37)$$

Therefore, integrating (2.36) from $-\infty$ to V_F , we obtain:

$$1 - R - \epsilon N = -\frac{1}{a} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} g(w) e^{\frac{(w-bN)^2}{2a}} dw dv +$$

$$+ p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} dv$$

because $g(w) = 0$ if $w < V_R$. As $w \in (V_R, V_F)$, $g(w) = -N$ and so

$$1 - (\tau + \epsilon)N = \frac{N}{a} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw dv +$$

$$+ p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} dv.$$

We can rewrite the previous integral (and thus the condition for steady state) as

$$\begin{cases} \bar{J}(N) = \frac{1}{N}, \\ \bar{J}(N) := (\tau + \epsilon) + I(N) + M(N), \end{cases} \quad (2.38)$$

or equivalently as

$$\begin{cases} \bar{U}(N) = 1. \\ \bar{U}(N) := N(\tau + \epsilon) + NI(N) + K(N), \end{cases} \quad (2.39)$$

Notice that in this case, since $I(N)$ and $M(N)$ are both positive, for the problem to have solutions it is necessary that

$$N < \frac{1}{\tau + \epsilon}.$$

Now we can easily verify that the following properties of $\bar{J}(N)$ are valid. The proof of the following Lemma is the same as Lemma 2.1.3.

Lemma 2.1.18. *Let $\bar{J}(N)$ the function defined in (2.38), then the following properties hold:*

1. $\bar{J}(N) > \tau + \epsilon \quad \forall N > 0$;
2. $\bar{J}(N) \rightarrow +\infty$ when $N \rightarrow 0$;
3. • if $b < 0$ (inhibitory case),

$$\lim_{N \rightarrow +\infty} \bar{J}(N) = +\infty,$$

- if $b > 0$ (excitatory case),

$$\lim_{N \rightarrow +\infty} \bar{J}(N) = \tau + \epsilon;$$

4. • if (2.11) holds, $\bar{J}(N)$ intersects an even number of times $\frac{1}{N}$ on $\left(0, \frac{1}{\tau + \epsilon}\right)$,
- if (2.12) holds, $\bar{J}(N)$ intersects an odd number of times $\frac{1}{N}$ on $\left(0, \frac{1}{\tau + \epsilon}\right)$.

Now, simply by replacing ϵ with $(\tau + \epsilon)$ is possible to find the main result on steady states:

Theorem 2.1.19. *Considering the equation (2.34) with $a(N) = a$ a positive constant and $\epsilon > 0$ we have:*

1. If $b < 0$:

- case A: there is no steady state to (2.34);
- case B: there is a unique steady state to (2.34).

2. If $b > 0$: if $\epsilon + \tau > \bar{\epsilon} := \frac{-2\dot{I}(0)}{\dot{K}(0) + \sqrt{[\dot{K}(0)]^2 - 4\dot{I}(0)}}$

- case A: there is no steady state to (2.34);
- case B: there is a unique steady state to (2.34).

At the same way it is easy to prove the following two Lemma, from which we deduce the same result of the case without delays or refractory periods, which illustrates the conditions that must hold to have at least 2 or 3 steady states (Corollary 2.1.15.1).

Lemma 2.1.20. *If $I(0) > I_0$, $b \in (b_2, b_3)$, $p(V_F) \in (p_2, p_3)$ and*

$$\tilde{\epsilon}_{1,12} < \tau + \epsilon < \tilde{\epsilon}_2, \quad (2.40)$$

where $\tilde{\epsilon}_{1,12}$ and $\tilde{\epsilon}_2$ are defined in Lemma 2.1.14.

Then $\dot{U}(\frac{V_F}{b}) < 0$, $\dot{U}(\frac{1}{\tau + \epsilon}) > 0$ and $K(\frac{V_F}{b}) < 1$.

Lemma 2.1.21. *If $I(0) > I_0$, $b \in (\max(0, b_1), b_3)$, $p(V_F) \in (p_1, p_2)$ and*

$$\tilde{\epsilon}_{1,7} < \tau + \epsilon < \tilde{\epsilon}_2, \quad (2.41)$$

where $\tilde{\epsilon}_{1,7}$ is defined in Lemma 2.1.15

Then $\dot{U}(0) > 0$, $\dot{U}(\frac{V_F}{b}) < 0$ and $\dot{U}(\frac{1}{\tau + \epsilon}) > 0$.

2.2 Discharge rate $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$

The aim of this section is to study the steady states of system (2.1) choosing $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$. Since in this case the calculations are more involved, we report here the main results and refer to Appendix B for details and explicit computations.

In this case finding the steady states is equivalent to solving the following equation:

$$\begin{cases} \tilde{U}(N) = 1, \\ \tilde{U}(N) := NI(N) + L(N) - O(N), \end{cases} \quad (2.42)$$

where

$$L(N) := \sqrt{2\pi a} p(V_F) e^{\frac{(V_F - bN)^2}{2a}},$$

$$O(N) = \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F) \tilde{I}(N, l) dl,$$

with

$$\tilde{I}(N, l) := \int_0^{+\infty} \frac{e^{-\frac{s^2}{2}}}{s} (e^{-sw_F} - e^{-sw_l}) ds.$$

Now, as in Section 2.1, defining the parameter

$$\tilde{c} := \tilde{U}(0) = L(0) - O(0) = \sqrt{2\pi a} p(V_F) e^{\frac{V_F^2}{2a}} - O(0)$$

and the threshold

$$\tilde{P} := \frac{1 + O(0)}{\sqrt{2\pi a} e^{\frac{V_F^2}{2a}}} \quad (2.43)$$

we can distinguish two different cases according to the value of $p(V_F)$ again:

Case A : if $\tilde{c} > 1$, which is equivalent to

$$p(V_F) > \tilde{P}; \quad (2.44)$$

Case B : if $\tilde{c} < 1$, which is equivalent to

$$p(V_F) < \tilde{P}. \quad (2.45)$$

Notice that \tilde{P} depends on ϵ because $O(0) = \frac{1}{\epsilon}E(0)$. This implies that when $\epsilon \gg 1$ then

$$\tilde{P} \sim \frac{1}{\sqrt{2\pi a} e^{\frac{V_F^2}{2a}}}$$

Instead when $\epsilon \ll 1$ then \tilde{P} is much bigger, which means that case B is more likely.

In the following Lemma 2.2.1 we show some property of $\tilde{U}(N)$, useful to solve the the problem (2.42).

Lemma 2.2.1. *The following properties on $\tilde{U}(N)$ hold:*

1. *If $b < 0$ or if $b > 0$ and ϵ is big enough, then*

$$\lim_{N \rightarrow \infty} \tilde{U}(N) = +\infty;$$

2.
 - *if (2.44) holds, i.e. we are in case A, then $\tilde{U}(N)$ intersects $h(N) = 1$ an even number of times.*
 - *if (2.45) holds, i.e. we are in case B, then $\tilde{U}(N)$ intersects $h(N) = 1$ an odd number of times.*

Now we can present the main result of this section, Theorem 2.2.2, which is a direct consequence of Lemma 2.2.1.

Theorem 2.2.2. *Considering the equation (2.1) with $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$ and $\epsilon > 0$ we have:*

1. *If $b < 0$ (inhibitory case):*

- *case A: there is no steady state to (2.1);*
- *case B: there is a unique steady state to (2.1).*

2. *If $b > 0$ (excitatory case) and ϵ big enough:*

- *case A: there is an even number of steady state to (2.1);*
- *case B: there is an odd number of steady state to (2.1).*

Finally, like in the case of $\phi_\epsilon(v) = \frac{1}{\epsilon}\mathbb{1}_{\{v > V_F\}}$, by studying function \tilde{U} in more detail and imposing conditions on it, we show that it is possible to find ϵ such that equation (2.1) admits more than one steady state. Before showing Corollary 2.2.2.1 we introduce some notations:

$$\tilde{b} := \frac{I^2\left(\frac{V_F}{b}\right)}{\sqrt{\frac{2\pi}{a}\left(2e^{\frac{V_F^2}{2a}} - e^{\frac{V_R^2}{2a}}\right)}}, \quad \tilde{p}_1 := \frac{I\left(\frac{V_F}{b}\right)}{bV_F \sqrt{\frac{2\pi}{a} e^{\frac{V_F^2}{2a}}}},$$

$$\tilde{p}_2 := \frac{I^2\left(\frac{V_F}{b}\right) - b\sqrt{\frac{2\pi}{a}}\left(2e^{\frac{V_F^2}{2a}} - e^{\frac{V_R^2}{2a}}\right)}{I\left(\frac{V_F}{b}\right)b\sqrt{\frac{2\pi}{a}}V_F e^{\frac{V_F^2}{2a}}}, \quad \tilde{p}_3 := \frac{I(0)}{bV_F\sqrt{\frac{2\pi}{a}}e^{\frac{V_F^2}{2a}}}.$$

Corollary 2.2.2.1. *If $b > 0$:*

- *case A: if $p(V_F) > \tilde{p}_3$ it could exist an interval of ϵ such that there are at least 2 steady states.*
- *case B: if $b < \tilde{b}$ and $p(V_F) < \min(\tilde{p}_1, \tilde{p}_2)$ then it could exist an interval of ϵ such that there are at least 3 steady states.*

2.3 Comparison between case $\phi_\epsilon(v) = \frac{1}{\epsilon}\mathbb{1}_{\{v > V_F\}}$ and case $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$

First of all we notice that for both choices of discharge rate (2.2) and (2.3) we distinguish in two cases, depending on the value of $p(V_F)$. When $p(V_F)$ is small, close to zero, we are in case B, characterized by an odd number of steady states; when $p(V_F)$ is bigger than a certain threshold we are in case A, characterized instead by an even number of steady states. We note that only in the case of $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$ it is necessary that ϵ be large enough to guarantee this result when we consider a population of neurons in average-excitatory ($b > 0$).

It is easy to see that when we consider a population in average-inhibitory ($b < 0$) the number of steady states in (2.2) and (2.3) is the same: in case A there is no steady states, in case B there is 1 steady state.

Let us analyze the case of a population in average-excitatory ($b > 0$).

Unfortunately in the case of $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$, which is much more difficult to study, we cannot find conditions such that there are no more than one steady state. In the case of $\phi_\epsilon(v) = \frac{1}{\epsilon}\mathbb{1}_{\{v > V_F\}}$ instead, if ϵ is big enough (or equivalently, b is small enough), it is shown that in case A there are no steady states, while in case B there is only one steady state.

For both choices of $\phi_\epsilon(v)$ (2.2) and (2.3) we observe that by studying function U (see (2.16)) and \tilde{U} (see (2.42)) in more detail and imposing more stringent conditions on the parameters, is possible to find an interval for ϵ such that model (2.1) has more than one steady state (at least 2 in case A, and 3 in case B). The problem is that we are not able to prove that this interval is always not empty. To prove that this interval is not always empty, in case $\phi_\epsilon = \frac{1}{\epsilon}\mathbb{1}_{\{v > V_F\}}$ we have shown some examples in which there are 2 or 3 steady states.

Conclusion

In this thesis we have investigated some NNLIF models for the neural activity. In the first Chapter we focused on the simplest model, the one that describes the case of a population of neurons, inhibitory or excitatory, without refractory period. Referring to previous articles [22][6][13], we dealt with the existence of the solutions and subsequently with the number of steady states. Remember, as explained in the Introduction, that steady states are related to the synchronous or asynchronous functioning of neurons in the network and the possibility of multi-stable phenomena, such as for example visual perception [18] and decision making [2][14]. The study of the model with fixed threshold in Chapter 1 was important to introduce the new problem we wanted to tackle in this thesis and which is treated in Chapter 2: the random discharge potential model. This is already presented in [7], but it had not yet been studied in depth. In particular in this thesis we focus on studying the number of steady states of this model, choosing two types of discharge rate $\phi_\epsilon(v)$:

$$\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}}$$

that is not continuous but is simpler to study, and

$$\phi_\epsilon(v) = \frac{1}{\epsilon} (v - V_F)_+$$

that is continuous, but is more difficult to study. We have seen that the number of steady states with the two choices is not very different.

What is interesting to see is the difference about the steady states between the model with fixed threshold (1.1)-(1.5) and the random model (2.1). To do this comparison, for the random discharge potential model we refer in particular to the case with $\phi_\epsilon(v) = \frac{1}{\epsilon} \mathbb{1}_{\{v > V_F\}}$, which is more detailed.

Let us start considering a population of neurons in average-inhibitory ($b < 0$). In this case we have shown that in model (2.1), when $p(V_F)$ is small enough (this is what we called *case B*), there is a unique steady state exactly as in model (1.1)-(1.5). Instead, when $p(V_F)$ is big enough (that we called *case A*), there are no steady states: this result is really different from the model with fixed threshold.

Instead, consider now a population of neurons in average-excitatory ($b > 0$). An important difference is that in model (1.1)-(1.5) for b big enough there are

no steady states, while in case B of model (2.1) there is always at least one steady state. Going into more detail, in the random discharge potential model, in case B we have shown that when ϵ is big enough, or equivalently b is small enough, there is a unique steady state exactly as in model (1.1)-(1.5), while in case A with the same condition on ϵ there are no steady state. Moreover we know that in model (2.1) there is an interval for b such that there are at least 2 steady states, while in the random discharge potential model we found intervals for ϵ and conditions for the other parameters such that in case A there are at least 2 and in case B there are at least 3, which is an absolute novelty. As we have already mentioned above the problem is that we are not able to prove that conditions to have at least 2 or 3 steady states can always be satisfied. This is because the range to which ϵ should belong may also be empty. However, we have found examples in which this interval is not empty, to demonstrate that there are cases in which there can actually be 2 or 3 steady states in the random discharge potential model.

What this thesis did not deal with, but which it would be interesting to address, would be the existence of the solutions of the discharge potential model. If we proved that Criterion 1.1.4, presented in Chapter 1 for the model (1.1)-(1.5), also holds for model (2.1), we could say that the maximal time of existence is given by

$$T^* = \sup\{t \geq 0 : N(t) < \infty\},$$

and since in the discharge potential model the firing rate N is bounded, we could conclude that $T^* = +\infty$, which means that solution are globally defined.

It would then be interesting to study the discharge potential model from a numerical point of view, to try to understand what value $p(v, t)$ assumes in $v = V_F$, and for what value of the potential v , p is very close to zero.

Furthermore, [7] shows through numerical simulations the presence of periodic solutions for the random discharge potential model: it would be interesting to try to prove their existence in a rigorous way.

Appendix A

Matlab Codes

A.1 Code to establish the existence of a maximum and a minimum of U

```
function [minmax] = esistenza_minmax_B(eps,VR,VF,a,b,pVf)

n=1/eps;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR) .* (exp(s.*(wF-wR))-1) ./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
Ieps=INT;
Keps= sqrt(pi*a/2)*pVf*exp((b/eps-VF)^2/2)*erfc((b/eps-VF)/sqrt(2*a));
dotKeps=b*((b*n-VF)*Keps/a-pVf);
dotIeps=b*(-Keps/(a*pVf)+sqrt(pi/(2*a))*exp((VR-b/eps)^2/(2*a))*
erfc((b/eps-VR)/sqrt(2*a)));
n=0;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR) .* (exp(s.*(wF-wR))-1) ./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
I0=INT;
K0= sqrt(pi*a/2)*pVf*exp((-VF)^2/2)*erfc((-VF)/sqrt(2*a));
dotI0=b*(-K0/(a*pVf)+sqrt(pi/(2*a))*exp((VR)^2/(2*a))*
erfc((-VR)/sqrt(2*a)));
dotK0=b*((-VF)*K0/a-pVf);

h=VF/b;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR) .* (exp(s.*(wF-wR))-1) ./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
Ivfb=INT;
Kvfb= sqrt(pi*a/2)*pVf*exp((VF-VF)^2/2)*erfc((VF-VF)/sqrt(2*a));
dotKvfb=b*(-pVf);
dotIvfb=b*(-Kvfb/(a*pVf)+sqrt(pi/(2*a))*exp((VR-VF)^2/(2*a))*
erfc((VF-VR)/sqrt(2*a)));
dotUvfb=eps+Ivfb+VF*dotIvfb/b+dotKvfb;
```

A.1. Code to establish the existence of a maximum and a minimum of U

```

n=7*VF/b;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR).*(exp(s.*(wF-wR))-1)./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
I7vfb=INT;
K7vfb= sqrt(pi*a/2)*pVf*exp((6*VF)^2/2)*erfc((6*VF)/sqrt(2*a));
dotK7vfb=b*(-pVf+6*VF*K7vfb/a);
dotI7vfb=b*(-K7vfb/(a*pVf)+sqrt(pi/(2*a))*exp((VR-7*VF)^2/(2*a))*
erfc((7*VF-VR)/sqrt(2*a)));

%Parametri:
B1=sqrt(pi*a/2)*exp(VF^2/(2*a))*erfc(-VF/sqrt(2*a))*(Ivfb+sqrt(pi/(2*a))*
VF*(exp((VR-VF)^2/(2*a))*erfc((VF-VR)/sqrt(2*a))-1));
PVF3=sqrt(2/(a*pi));
B3=I0/(PVF3/(exp(VF^2/(2*a))*erfc(-VF/sqrt(2*a))+VF/a);
EPS1=(-dotK7vfb+sqrt(I7vfb^2+dotK7vfb^2-4*dotI7vfb))/2;
EPS2_1=b/(7*VF);
EPS2_2=sqrt(pi/(2*a))*VF*(1-exp((VF-VR)^2/(2*a))*erfc((VF-VR)/sqrt(2*a))
+b*pVf-Ivfb);
PVF2=I0/b-VF/a;
PVF1=(sqrt(pi/(2*a))*VF*(exp((VF-VR)^2/(2*a))*erfc((VF-VR)/sqrt(2*a))-1)
+Ivfb)/(b)
EPSBAR=-2*dotI0/(dotK0+sqrt(dotK0^2-4*dotI0));
I_0=B1*(PVF3+VF/a);

if( I0>I_0 & eps>EPS1 & eps<EPS2_1 & eps<EPS2_2 & b>B1 & b<B3 & pVf>PVF1)
    disp("esistono un minimo e un massimo di U");minmax=true;
    elseif eps>EPSBAR disp("U è crescente, cè solo 1 steady state");
        minmax=false;
else disp("non sappiamo se esistono un minimo e un massimo di U");
    minmax=false;
end
end

```


A.2 Code to find a minimum and a maximum N_2^* and N_1^* and determine if there are at least 3 steady states

```

function [MIN] = trova_minmax(eps,VR,VF,a,b,pVf)
n=[0:0.01:1/eps];MIN=0;MAX=0;
for i=1:length(n)
wF(i)=(VF-b*n(i))/sqrt(a);wR(i)=(VR-b*n(i))/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR(i)).*(exp(s.*(wF(i)-wR(i)))-1)./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
I(i)=INT;
K(i)= sqrt(pi*a/2)*pVf*exp(wF(i)^2/2)*erfc(-wF(i)/sqrt(2));
dotK(i)=b*(b*n(i)-VF)*K(i)/a-pVf/sqrt(pi);
dotI(i)=b*(-K(i)/(a*pVf)+sqrt(pi/(2*a))*exp((VR-b*n(i))^2/(2*a))
*erfc((b*n(i)-VR)/sqrt(2*a)));
M(i)=K(i)/n(i);
U(i)=n(i)*(eps+I(i))+K(i);
dotU(i)=eps+I(i)+n(i)*dotI(i)+dotK(i);
if (i>2 & U(i)>U(i-1) & U(i-1)<U(i-2)) MIN=i-1;
end
if (i>2 & U(i)<U(i-1) & U(i-1)>U(i-2)) MAX=i-1;
end
end

epsAMIN=(-2*I(MIN)-dotK(MIN)-sqrt(dotK(MIN)^2-4*(dotI(MIN)*(1-K(MIN)))))/2
epsAMAX=(-2*I(MAX)-dotK(MAX)-sqrt(dotK(MAX)^2-4*(dotI(MAX)*(1-K(MAX)))))/2
epsBMIN=(-2*I(MIN)-dotK(MIN)+sqrt(dotK(MIN)^2-4*(dotI(MIN)*(1-K(MIN)))))/2
epsBMAX=(-2*I(MAX)-dotK(MAX)+sqrt(dotK(MAX)^2-4*(dotI(MAX)*(1-K(MAX)))))/2
if (eps>epsAMIN & eps<epsBMIN & (eps<epsAMAX || eps>epsBMAX))
disp("ci sono 3 steady states");
else disp("ci sono 1 steady states");
end

```

A.3 Code to establish the existence of a minimum of U

```

function [min] = esistenza_minimo_A(eps,VR,VF,a,b,pVf)

n=0;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR).*(exp(s.*(wF-wR))-1)./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
I0=INT
K0= sqrt(pi*a/2)*pVf*exp(wF^2/2)*erfc(-wF/sqrt(2));
dotK0=b*(b*n-VF)*K0/a-pVf);

n=12*VF/b;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR).*(exp(s.*(wF-wR))-1)./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
I7vfb=INT;
K7vfb= sqrt(pi*a/2)*pVf*exp((11*VF)^2/2)*erfc((11*VF)/sqrt(2*a));
dotK7vfb=b*(-pVf+11*VF*K7vfb/a);
dotI7vfb=b*(-K7vfb/(a*pVf)+sqrt(pi/(2*a))*exp((VR-12*VF)^2/(2*a))*
erfc((12*VF-VR)/sqrt(2*a)));

n=VF/b;
wF=(VF-b*n)/sqrt(a);wR=(VR-b*n)/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR).*(exp(s.*(wF-wR))-1)./s;
INT=integral(fun,0,300,'AbsTol',1e-12);
Ivfb=INT;
Kvfb= sqrt(pi*a/2)*pVf*exp((VF-VF)^2/2)*erfc((VF-VF)/sqrt(2*a));
dotKvfb=b*(-pVf);
dotIvfb=b*(-Kvfb/(a*pVf)+sqrt(pi/(2*a))*exp((VR-VF)^2/(2*a))*
erfc((VF-VR)/sqrt(2*a)));
dotUvfb=eps+Ivfb+VF*dotIvfb/b+dotKvfb;

%Parametri
B1=sqrt(pi*a/2)*exp(VF^2/(2*a))*erfc(-VF/sqrt(2*a))*(Ivfb+sqrt(pi/(2*a))*
VF*(exp((VR-VF)^2/(2*a))*erfc((VF-VR)/sqrt(2*a))-1))
PVF3=sqrt(2/(a*pi));
EPS1=(-dotK7vfb+sqrt(I7vfb^2+dotK7vfb^2-4*dotI7vfb))/2
EPS2_1=b/(12*VF)
EPS2_2=sqrt(pi/(2*a))*VF*(1-exp((VF-VR)^2/(2*a))*erfc((VF-VR)/sqrt(2*a)))
+b*pVf-Ivfb
PVF2=I0/b-VF/a
B3=I0/(PVF3/(exp(VF^2/(2*a))*erfc(-VF/sqrt(2*a)))+VF/a)
B2=I0/(PVF3+VF/a)
PVF3=sqrt(2/(a*pi))
I0A=B1*(PVF3+VF/a)

if (I0>I0A & B2<b & b<B3 & eps<EPS2_1 & eps<EPS2_2 & eps>EPS1 & pVf>PVF2
& pVf<PVF3)
disp("esiste un minimo di U"); min=true;
else disp("non sappiamo se esiste un minimo di U"); min=false
end

```

A.4 Code to find the minimum N^* and determine if there are at least 2 steady states

```

function [MIN] = trova_min(eps,VR,VF,a,b,pVf)
n=[0:0.01:1/eps];MIN=1;
for i=1:length(n)%trovare il minimo
wF(i)=(VF-b*n(i))/sqrt(a);wR(i)=(VR-b*n(i))/sqrt(a);
fun=@(s) exp(-(s.^2)./2 + s.*wR(i)).*(exp(s.*(wF(i)-wR(i)))-1)./s;
INT=integral(fun,0,350,'AbsTol',1e-12);
I(i)=INT;
K(i)= sqrt(pi*a/2)*pVf*exp(wF(i)^2/(2))*erfc(-wF(i)/sqrt(2));
dotK(i)=b*((b*n(i)-VF)*K(i)/a-pVf);
dotI(i)=b*(-K(i)/(a*pVf)+sqrt(pi/(2*a))*exp((VR-b*n(i))^2/(2*a))*
erfc((b*n(i)-VR)/sqrt(2*a)));
M(i)=K(i)/n(i);
U(i)=n(i)*(eps+I(i))+K(i);
dotU(i)=eps+I(i)+n(i)*dotI(i)+dotK(i);
if (i>2 & U(i)>U(i-1) & U(i-1)<U(i-2)) MIN=i-1;
end end
epsAMIN=(-2*I(MIN)-dotK(MIN)-sqrt(dotK(MIN)^2-4*(dotI(MIN)*(1-K(MIN)))))/2;
epsBMIN=(-2*I(MIN)-dotK(MIN)+sqrt(dotK(MIN)^2-4*(dotI(MIN)*(1-K(MIN)))))/2;

if ( eps>epsAMIN & eps<epsBMIN ) disp("ci sono 2 steady states");
else disp("ci sono 0 steady states");
end

```

A.4. Code to find the minimum N^* and determine if there are at
76 least 2 steady states

Appendix B

Random discharge potential model with $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$

The aim of this appendix is to study in depth the problem of finding the number of steady states of system (2.1) choosing $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$. The main results have been already presented in Section 2.2.

As in Section 2.1, we will firstly integrate (2.5) to find an equation which depends on N and whose solutions correspond to the steady states. Then, we will define again what is meant by case A and case B, and we will show by Theorem B.0.6 and Corollary B.0.8.1 the conditions on the parameters of the model clarifying the exact number of steady states.

Firstly we recall an important result from [7].

Theorem B.0.1. *Assume $a(N) \leq a_0 + a_2 N^2$, $\int_{-\infty}^{+\infty} (1 + |v|^3) p^0(v) dv < \infty$ and the discharge rate $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$, then the solution of (2.1) satisfy the a-priory bounds*

$$N(t) \leq \max \left(C, \int_{V_F}^{\infty} (v - V_F)^3 p^0(v) dv \right) e^{\frac{ct}{\epsilon^2}}.$$

This allows us to say that N is bounded, and since in this case N is given by

$$N = \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(v)(v - V_F) dv,$$

we can suppose bounded also other quantities as

$$\int_{V_F}^{+\infty} p(v)(v - V_F)^2 dv, \quad \int_{V_F}^{+\infty} p(v)(v - V_F)^2 e^{\frac{v^2}{2\alpha}} dv.$$

Now we proceed by looking for a function that depends on N . Remembering the definition of function g in (2.4), in this case we have

$$g(v) = \begin{cases} 0 & v < V_R \\ -N & V_R \leq v \leq V_F \\ \frac{1}{\epsilon} \int_{V_F}^v (w - V_F)p(w)dw & v > V_F \end{cases},$$

and integrating (2.5) from $-\infty$ to $+\infty$ we obtain

$$1 = \frac{1}{a} \int_{-\infty}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} \int_{V_F}^{\max(v, V_R)} g(w) e^{\frac{(w-bN)^2}{2a}} dw dv + \\ + p(V_F) e^{\frac{(V_F-bN)^2}{2a}} \int_{-\infty}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} dv$$

because $g(w) = 0$ if $w < V_R$. Splitting the first integral and remembering that $g(w) = -N$ when $w \in (V_R, V_F)$ and $g(w) = \frac{1}{\epsilon} \int_{V_F}^v (w - V_F)p(w)dw$ when $v > V_F$,

$$1 = \frac{N}{a} \int_{-\infty}^{V_F} e^{-\frac{(v-bN)^2}{2a}} \int_{\max(v, V_R)}^{V_F} e^{\frac{(w-bN)^2}{2a}} dw dv + \\ - \frac{1}{a} \int_{V_F}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} \int_{V_F}^v e^{\frac{(w-bN)^2}{2a}} \int_w^{\infty} \frac{1}{\epsilon} p(l)(l - V_F) dl dw dv + \sqrt{2\pi a} p(V_F) e^{\frac{(V_F-bN)^2}{2a}}.$$

We can rewrite the previous integral (and thus the condition for steady state) as

$$\begin{cases} \tilde{U}(N) = 1, \\ \tilde{U}(N) := NI(N) + L(N) - O(N), \end{cases} \quad (\text{B.1})$$

where

$$L(N) := \sqrt{2\pi a} p(V_F) e^{\frac{(V_F-bN)^2}{2a}},$$

$$O(N) := \frac{1}{\epsilon} E(N)$$

where

$$E(N) := \frac{1}{a} \int_{V_F}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} \int_{V_F}^v e^{\frac{(w-bN)^2}{2a}} \int_w^{\infty} p(l)(l - V_F) dl dw dv.$$

and $I(N)$ is the function already defined in (1.28). Notice that L , O and I are all positive functions.

Remark B.0.2. $O(N)$ can be rewritten in a more useful way.

$$\begin{aligned} O(N) &= \frac{1}{a} \int_{V_F}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} \int_{V_F}^{+\infty} \frac{1}{\epsilon} p(l)(l - V_F) \int_{V_F}^{\min(l,v)} e^{\frac{(w-bN)^2}{2a}} dw dl dv = \\ &= \frac{1}{a} \int_{V_F}^{+\infty} \frac{1}{\epsilon} p(l)(l - V_F) \int_{V_F}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} \int_{V_F}^{\min(l,v)} e^{\frac{(w-bN)^2}{2a}} dw dv dl = \\ &= \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F) \tilde{I}(N, l) dl, \end{aligned}$$

where

$$\begin{aligned} \tilde{I}(N, l) &= \frac{1}{a} \int_{V_F}^{+\infty} e^{-\frac{(v-bN)^2}{2a}} \int_{V_F}^{\min(l,v)} e^{\frac{(w-bN)^2}{2a}} dw dv = \quad (\text{B.2}) \\ &= \frac{1}{a} \int_{V_F}^l \int_w^{+\infty} e^{-\frac{(v-bN)^2}{2a}} e^{\frac{(w-bN)^2}{2a}} dv dw, \end{aligned}$$

which became, with the change of variables $z = \frac{v-bN}{\sqrt{a}}$, $u = \frac{w-bN}{\sqrt{a}}$,

$$\tilde{I}(N, l) = \int_{\frac{V_F-bN}{\sqrt{a}}}^{\frac{l-bN}{\sqrt{a}}} \int_u^{+\infty} e^{\frac{u^2-z^2}{2}} dz du. \quad (\text{B.3})$$

With an other change of variables $s = \frac{z-u}{2}$, $\tilde{s} = \frac{z+u}{2}$, \tilde{I} can also be rewritten as

$$\tilde{I}(N, l) = 2 \int_0^{+\infty} \int_{s+w_F}^{s+w_l} e^{-2s\tilde{s}} d\tilde{s} ds = \int_0^{+\infty} \frac{e^{-\frac{s^2}{2}}}{s} (e^{-sw_F} - e^{-sw_l}) ds$$

where $w_F = \frac{V_F-bN}{\sqrt{a}}$ and $w_l = \frac{l-bN}{\sqrt{a}}$. Finally we have

$$\begin{aligned} O(N) &= \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F) \int_0^{+\infty} \frac{e^{-\frac{s^2}{2}}}{s} (e^{-sw_F} - e^{-sw_l}) ds dl = \\ &= \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F) \int_0^{+\infty} e^{-\frac{s^2}{2}} \cdot e^{\frac{sbN}{\sqrt{a}}} \frac{(e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}})}{s} ds dl. \end{aligned}$$

Using the form of $\tilde{I}(N, l)$ in (B.2) we observe that

$$\begin{aligned} |\tilde{I}(0, l)| &= \left| \frac{1}{a} \int_{V_F}^{+\infty} \int_{V_F}^{\min(l,v)} e^{-\frac{v^2}{2a}} e^{\frac{w^2}{2a}} dw dv \right| < \left| \frac{1}{a} \int_{V_F}^{+\infty} (l - V_F) e^{-\frac{v^2}{2a}} e^{\frac{\max(l^2, V_F^2)}{2a}} dv \right| < \\ &< \frac{1}{a} (l - V_F) e^{\frac{l^2}{2a}} \left| \int_{-\infty}^{+\infty} e^{-\frac{v^2}{2a}} dv \right| = \sqrt{\frac{2\pi}{a}} e^{\frac{l^2}{2a}} (l - V_F), \end{aligned}$$

and so

$$O(0) < \sqrt{\frac{2\pi}{a}} \cdot \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F)^2 e^{\frac{l^2}{2a}} dl, \quad (\text{B.4})$$

which is a bounded quantity because $\int_{V_F}^{+\infty} p(l)(l - V_F)^2 e^{\frac{l^2}{2a}} dl$ is supposed to be bounded. Now, as in Section 2.1, defining the parameter

$$\tilde{c} := \tilde{U}(0) = L(0) - O(0) = \sqrt{2\pi a} p(V_F) e^{\frac{V_F^2}{2a}} - O(0)$$

and the threshold

$$\tilde{P} := \frac{1 + O(0)}{\sqrt{2\pi a} e^{\frac{V_F^2}{2a}}}$$

we can distinguish two different cases according to the value of $p(V_F)$ again:

Case A : if $\tilde{c} > 1$, which is equivalent to

$$p(V_F) > \tilde{P}; \quad (\text{B.5})$$

Case B : if $\tilde{c} < 1$, which is equivalent to

$$p(V_F) < \tilde{P}. \quad (\text{B.6})$$

Note that \tilde{P} depends on ϵ because $O(0) = \frac{1}{\epsilon} E(0)$. This implies that when $\epsilon \gg 1$ then

$$\tilde{P} \sim \frac{1}{\sqrt{2\pi a} e^{\frac{V_F^2}{2a}}}$$

Instead when $\epsilon \ll 1$ then \tilde{P} is much bigger, which means that case B is more likely.

As we did in Section 2.1 for the problem (2.7), the idea to find solution of (B.1) is to study the graph of function $\tilde{U}(N)$, to understand how many times and under what conditions it intersects the straight line $h(N) = 1$. Like in case $\phi_\epsilon(v) = \frac{1}{\epsilon} 1_{\{v > V_F\}}$ each intersection represents a steady state.

In order to do that, firstly we have to show some properties of $O(N)$ with Lemma B.0.4, but before we need to do the following remark.

Remark B.0.3. Taking the function $f(s) = e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}}$ and Taylor expanding up to second order at $s = 0$, we get $f(s) - f(0) - f'(0)s = f''(\theta)s^2/2$ with $f(0) = 0$, $f'(0) = (l - V_F)/\sqrt{a}$, and $\theta \in (0, s)$. It is easy to see that for all $\theta \in (0, s)$

$$|f''(\theta)| \leq \max\left(\frac{l^2}{a} e^{-\frac{\theta l}{\sqrt{a}}}, \frac{V_F^2}{a} e^{-\frac{\theta V_F}{\sqrt{a}}}\right) \leq \max\left(\frac{l^2}{a}, \frac{V_F^2}{a}\right) = \frac{l^2}{a}.$$

This Taylor expansion implies that

$$\left| \frac{(e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}})}{s} - \frac{l - V_F}{\sqrt{a}} \right| \leq \frac{sl^2}{2a}. \quad (\text{B.7})$$

Lemma B.0.4. *The following properties of $O(N)$ hold:*

1. $O(N)$ is C^∞ on N and, for all integers $k \geq 1$,

$$O^k(N) = \frac{b^k}{\epsilon a^{\frac{k}{2}}} \int_{V_F}^{+\infty} p(l)(l - V_F) \int_0^{+\infty} s^{k-1} e^{-\frac{s^2}{2} + \frac{sbN}{\sqrt{a}}} (e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}}) ds dl. \quad (\text{B.8})$$

2. A limitation for $\dot{O}(N)$ can be:

$$|\dot{O}(N)| < \left| b \sqrt{\frac{\pi}{2a}} N e^{\frac{(V_F - bN)^2}{2a}} \operatorname{erfc} \left(\frac{V_F - bN}{\sqrt{2a}} \right) \right|. \quad (\text{B.9})$$

3. $\dot{O}(N) = 0$.

4. • If $b < 0$ (inhibitory case):

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

• If $b > 0$ (excitatory case):

$$\lim_{N \rightarrow \infty} O(N) = \infty$$

Proof. 1. A direct application of the dominated convergence theorem and continuity theorems of integrals with respect to parameters show that $\tilde{I}(N, l)$ and $O(N)$ are continuous on N on $[0, +\infty)$. Moreover, $\tilde{I}(N, l)$ and $O(N)$ are C^∞ 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,

$$\frac{\partial \tilde{I}}{\partial N}(N, l) = \frac{b}{\sqrt{a}} \int_0^{+\infty} e^{-\frac{s^2}{2}} \cdot e^{\frac{sbN}{\sqrt{a}}} (e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}}) ds,$$

$$\dot{O}(N) = \frac{1}{\epsilon} S(N)$$

where

$$S(N) := \frac{b}{\sqrt{a}} \cdot \int_{V_F}^{+\infty} p(l)(l - V_F) \int_0^{+\infty} e^{-\frac{s^2}{2}} \cdot e^{\frac{sbN}{\sqrt{a}}} (e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}}) ds dl.$$

$$\ddot{O}(N) = \frac{b^2}{a} \cdot \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F) \int_0^{+\infty} s \cdot e^{-\frac{s^2}{2}} \cdot e^{\frac{sbN}{\sqrt{a}}} (e^{-s\frac{V_F}{\sqrt{a}}} - e^{-s\frac{l}{\sqrt{a}}}) ds dl.$$

2.

$$\begin{aligned}
|\dot{O}(N)| &< \left| \frac{b}{\sqrt{a}} \cdot \frac{1}{\epsilon} \int_{V_F}^{+\infty} p(l)(l - V_F) dl \cdot \int_0^{+\infty} e^{-\frac{s^2}{2}} \cdot e^{\frac{sbN}{\sqrt{a}}} \cdot e^{-s\frac{V_F}{\sqrt{a}}} ds \right| = \\
&= \left| \frac{b}{\sqrt{a}} N e^{\frac{(V_F - bN)^2}{2a}} \int_0^{+\infty} e^{-\left(\frac{s}{\sqrt{2}} + \frac{(V_F - bN)}{\sqrt{2a}}\right)^2} ds \right| = \\
&= \left| b\sqrt{\frac{\pi}{2a}} N e^{\frac{(V_F - bN)^2}{2a}} \operatorname{erfc}\left(\frac{V_F - bN}{\sqrt{2a}}\right) \right|.
\end{aligned}$$

3. Follows directly by point 2) of this Lemma.

4. • If $b < 0$: $O(N)$ is a decreasing convex function. Also, from the previous expansion (B.7) and dominated convergence theorem we have that

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

• If $b > 0$: $O(N)$ is an increasing convex function and thus

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

□

Taking into account the properties of $O(N)$, we can now prove some properties of $\tilde{U}(N)$.

Lemma B.0.5. *The following properties on $\tilde{U}(N)$ hold:*

1. If $b < 0$ or if $b > 0$ and ϵ big enough, then

$$\lim_{N \rightarrow \infty} \tilde{U}(N) = +\infty;$$

2. • if (B.5) holds, i.e. we are in case A, then $\tilde{U}(N)$ intersects $h(N) = 1$ an even number of times.

• if (B.6) holds, i.e. we are in case B, then $\tilde{U}(N)$ intersects $h(N) = 1$ an odd number of times.

Proof. 1. Observe that

$$\dot{L}(N) = -b\sqrt{\frac{2\pi}{a}} p(V_F)(V_F - bN) e^{\frac{(V_F - bN)^2}{2a}}, \quad (\text{B.10})$$

then:

• If $b < 0$: $I(N) \rightarrow +\infty$, $L(N) \rightarrow +\infty$ and $O(N) \rightarrow 0$ when $N \rightarrow +\infty$, then

$$\lim_{N \rightarrow \infty} \tilde{U}(N) = \lim_{N \rightarrow \infty} (NI(N) + L(N) - O(N)) = \infty.$$

- If $b > 0$: using the form of $\tilde{I}(N, l)$ in (B.3) we observe that

$$\begin{aligned} \tilde{I}(N, l) &< \int_{\frac{V_F - bN}{\sqrt{a}}}^{\frac{l - bN}{\sqrt{a}}} e^{\frac{u^2}{2}} \int_{-\infty}^{+\infty} e^{-\frac{z^2}{2}} dz du = \sqrt{2\pi} \int_{\frac{V_F - bN}{\sqrt{a}}}^{\frac{l - bN}{\sqrt{a}}} e^{\frac{u^2}{2}} du < \\ &< \sqrt{2\pi} \frac{l - V_F}{\sqrt{a}} e^{\frac{m}{2a}} \end{aligned}$$

where $m := \max((V_F - bN)^2, (l - bN)^2)$. Observe that if $l < 2bN - V_F$ then $m = (V_F - bN)^2$, if $l > 2bN - V_F$ then $m = (l - bN)^2$. Now, considering $N > \frac{V_F}{b}$ then

$$O(N) < \frac{1}{\epsilon} \sqrt{\frac{2\pi}{a}} \left[e^{\frac{(V_F - bN)^2}{2a}} T(N) + Z(N) \right]$$

where

$$\begin{aligned} T(N) &:= \int_{V_F}^{2bN - V_F} p(l)(l - V_F)^2 dl, \\ Z(N) &:= \int_{2bN - V_F}^{+\infty} p(l)(l - V_F)^2 e^{\frac{(l - bN)^2}{2a}} dl \end{aligned}$$

Note that

$$\lim_{N \rightarrow \infty} Z(N) = 0,$$

$$\lim_{N \rightarrow \infty} T(N) = \int_{V_F}^{+\infty} p(l)(l - V_F)^2 dl$$

So we have that

$$\begin{aligned} \tilde{U}(N) &= NI(N) + L(N) - O(N) > \\ &> NI(N) + \left[\sqrt{2\pi} ap(V_F) - \frac{1}{\epsilon} \sqrt{\frac{2\pi}{a}} T(N) \right] e^{\frac{(V_F - bN)^2}{2a}} - \frac{1}{\epsilon} \sqrt{\frac{2\pi}{a}} Z(N) \end{aligned}$$

which tends to $+\infty$ because $NI(N) \rightarrow \frac{V_F - V_R}{b}$ (see Lemma 1.3.3), $Z(N) \rightarrow 0$ and

$$\left[\sqrt{2\pi} ap(V_F) - \frac{1}{\epsilon} \sqrt{\frac{2\pi}{a}} \int_{V_F}^{+\infty} p(l)(l - V_F)^2 dl \right] > 0$$

when ϵ is big enough, since $\int_{V_F}^{+\infty} p(l)(l - V_F)^2 dl$ is bounded.

2. $\tilde{U}(N) \rightarrow +\infty$ when $N \rightarrow \infty$ from point 1) and $\tilde{U}(N)$ is continuous, moreover:

- in case A we have $\tilde{U}(0) > 1$ and so we conclude that $\tilde{U}(N)$ intersects $h(N) = 1$ an even number of times;
- in case B we have $\tilde{U}(0) < 1$ and so we conclude that $\tilde{U}(N)$ intersects $h(N) = 1$ an odd number of times.

□

Now we are going to show the main result for the number of steady states of (2.1), Theorem B.0.6, which is a direct consequence of the previous Lemma B.0.5.

Theorem B.0.6. *Considering the equation (2.1) with $\phi_\epsilon(v) = \frac{1}{\epsilon}(v - V_F)_+$ and $\epsilon > 0$ we have:*

1. *If $b < 0$ (inhibitory case):*
 - *case A: there is no steady state to (2.1);*
 - *case B: there is a unique steady state to (2.1).*
2. *If $b > 0$ (excitatory case) and ϵ big enough:*
 - *case A: there is an even number steady state to (2.1);*
 - *case B: there is an odd number of steady state to (2.1).*

Proof.

1. *If $b < 0$: from Lemma B.0.5 we know that*

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

Moreover $\dot{I}(N) > 0$ and $\dot{O}(N) < 0$, so

$$\dot{\tilde{U}}(N) = N\dot{I}(N) + I(N) + \dot{L}(N) - \dot{O}(N) > 0 \quad \forall N \geq 0.$$

So we can conclude that

- case A: $\tilde{U}(0) > 1$, $\tilde{U}(N)$ is an increasing function and then does not cross the straight line $h(N) = 1$, which means that there is not steady state.
- case B: $\tilde{U}(0) < 1$, $\tilde{U}(N)$ is an increasing function which tends to ∞ and then has to cross the straight line $h(N) = 1$ one time, which means that there is 1 steady state.

2. *If $b > 0$. The proof follows directly by Lemma B.0.5.*

□

Now, like in the case of $\phi_\epsilon(v) = \frac{1}{\epsilon}\mathbb{1}_{\{v > V_F\}}$, by studying function \tilde{U} in more detail and imposing conditions on it, we show that it is possible to find ϵ such that equation (2.1) admits more than one steady state. In particular:

- in case A the idea is again that if we impose $\dot{\tilde{U}}(0) < 0$, since $\tilde{U}(N) \rightarrow +\infty$ for $\epsilon > \tilde{\epsilon}$, then exists N^* a minimum of \tilde{U} and if we impose that $\tilde{U}(N^*) < 1$ then \tilde{U} intersects $h(N) = 1$ at least 2 times;
- in case B the idea is that if we impose $\dot{\tilde{U}}(0) > 0$ and $\dot{U}(\bar{N}) < 0$ for a certain $\bar{N} > 0$ then exist $N_2^* > \bar{N}$ a relative minimum of \tilde{U} and $N_1^* < \bar{N}$ a relative maximum of \tilde{U} and if we impose that $\tilde{U}(N_2^*) < 1$ and $\tilde{U}(N_1^*) > 1$ then \tilde{U} intersects $h(N) = 1$ at least 3 times.

Lemma B.0.7 and Lemma B.0.8 tell us which conditions the parameters have to satisfy for $\tilde{U}(N)$ to have the characteristics just described.

Before showing the two Lemmas, we introduce some notations:

$$\bar{\epsilon} := \frac{bS\left(\frac{V_F}{b}\right)}{\sqrt{a}I\left(\frac{V_F}{b}\right)}, \quad \tilde{b} := \frac{I^2\left(\frac{V_F}{b}\right)}{\sqrt{\frac{2\pi}{a}}\left(2e^{\frac{V_F^2}{2a}} - e^{\frac{V_R^2}{2a}}\right)},$$

$$\tilde{p}_1 := \frac{I\left(\frac{V_F}{b}\right)}{bV_F\sqrt{\frac{2\pi}{a}}e^{\frac{V_F^2}{2a}}}, \quad \tilde{p}_2 := \frac{I^2\left(\frac{V_F}{b}\right) - b\sqrt{\frac{2\pi}{a}}\left(2e^{\frac{V_F^2}{2a}} - e^{\frac{V_R^2}{2a}}\right)}{I\left(\frac{V_F}{b}\right)b\sqrt{\frac{2\pi}{a}}V_Fe^{\frac{V_F^2}{2a}}}, \quad \tilde{p}_3 := \frac{I(0)}{bV_F\sqrt{\frac{2\pi}{a}}e^{\frac{V_F^2}{2a}}}.$$

Lemma B.0.7. *If $b > 0$ and $p(V_F) > \tilde{p}_3$ then $\dot{\tilde{U}}(0) < 0$.*

Proof. By Lemma B.0.4 we know that $\dot{O}(0) = 0$ and so

$$\dot{\tilde{U}}(0) = I(0) + \dot{L}(0) - \dot{O}(0) = I(0) + \dot{L}(0) = I(0) - bV_F\sqrt{\frac{2\pi}{a}}p(V_F)e^{\frac{V_F^2}{2a}},$$

which is negative because $p(V_F) > \tilde{p}_3$. □

Lemma B.0.8. *If $b > 0$, $p(V_F) < \tilde{p}_1$ and $\epsilon < \bar{\epsilon}$ then $\dot{\tilde{U}}(0) > 0$ and $\dot{\tilde{U}}\left(\frac{V_F}{b}\right) < 0$*

Proof. By Lemma B.0.4 we know that $\dot{O}(0) = 0$ and so

$$\begin{aligned} \dot{\tilde{U}}(0) &= I(0) + \dot{L}(0) - \dot{O}(0) = I(0) + \dot{L}(0) = \\ &= I(0) - bV_F\sqrt{\frac{2\pi}{a}}p(V_F)e^{\frac{V_F^2}{2a}} > I\left(\frac{V_F}{b}\right) - bV_F\sqrt{\frac{2\pi}{a}}p(V_F)e^{\frac{V_F^2}{2a}}, \end{aligned}$$

which is positive because $p(V_F) < \tilde{p}_1$. As $\epsilon < \bar{\epsilon}$,

$$I\left(\frac{V_F}{b}\right) < \frac{b}{\sqrt{a}}\frac{1}{\epsilon}S\left(\frac{V_F}{b}\right) = \frac{b}{\sqrt{a}}\dot{O}\left(\frac{V_F}{b}\right)$$

and so, since \dot{I} is negative and $\dot{L}\left(\frac{V_F}{b}\right) = 0$,

$$\dot{\tilde{U}}\left(\frac{V_F}{b}\right) = I\left(\frac{V_F}{b}\right) + \dot{L}\left(\frac{V_F}{b}\right) + \frac{V_F}{b}\dot{I}\left(\frac{V_F}{b}\right) - \dot{O}\left(\frac{V_F}{b}\right) < 0.$$

□

Corollary B.0.8.1. *If $b > 0$ (excitatory case):*

- *case A: if $p(V_F) > \tilde{p}_3$ it could exist an interval of ϵ such that there are at least 2 steady states.*
- *case B: if $b < \tilde{b}$ and $p(V_F) < \min(\tilde{p}_1, \tilde{p}_2)$ then it could exist an interval of ϵ such that there are at least 3 steady states.*

Proof. Let $b > 0$.

- From Lemma B.0.7 we know that $\dot{\tilde{U}}(0) < 0$. If ϵ big enough, $\tilde{U}(N) \rightarrow +\infty$ when $N \rightarrow +\infty$, then exists N^* a minimum of $\tilde{U}(N)$.

If $\tilde{U}(N^*) < 1$ holds, then we can conclude that $\tilde{U}(N)$ intersects at least 2 times the straight line $h(N) = 1$ and so there are at least 2 steady states.

Notice that

$$\dot{\tilde{U}}(N^*) = 0 \iff N^* = \frac{I(N^*) + \dot{L}(N^*) - \dot{O}(N^*)}{-\dot{I}(N^*)},$$

and so

$$\begin{aligned} \tilde{U}(N^*) < 1 &\iff \frac{I(N^*) + \dot{L}(N^*) - \dot{O}(N^*)}{-\dot{I}(N^*)} I(N^*) + L(N^*) - O(N^*) < 1 \\ &\iff I(N^*)^2 + I(N^*)\dot{L}(N^*) - I'(N^*)(L(N^*) - 1) < \dot{O}(N^*)I(N^*) - O(N^*)\dot{I}(N^*) = \\ &= \frac{1}{\epsilon} [I(N^*)S(N^*) - R(N^*)\dot{I}(N^*)]. \end{aligned}$$

Notice that the right hand side is always positive. So, if the left hand side is negative the inequality is always satisfied; if the left hand side is positive the inequality is however satisfied if

$$\epsilon < \epsilon_a(N^*) := \frac{I(N^*)S(N^*) - R(N^*)\dot{I}(N^*)}{|I(N^*)(I(N^*) + \dot{L}(N^*)) - \dot{I}(N^*)(L(N^*) - 1)|}$$

- From Lemma B.0.8 we know that $\dot{\tilde{U}}(0) > 0$ and $\dot{\tilde{U}}(\frac{V_F}{b}) < 0$. If ϵ big enough, $\tilde{U}(N) \rightarrow +\infty$ when $N \rightarrow +\infty$, then exist $N_1^* < \frac{V_F}{b} < N_2^*$ maximum and minimum of $\tilde{U}(N)$.

If $\tilde{U}(N_1^*) > 1$ and $\tilde{U}(N_2^*) < 1$ hold, then we can conclude that $\tilde{U}(N)$ intersects at least 3 times the straight line $h(N) = 1$ and so there are at least 3 steady states.

As in case A

$$\dot{\tilde{U}}(N_i^*) = 0 \iff N_i^* = \frac{I(N_i^*) + \dot{L}(N_i^*) - \dot{O}(N_i^*)}{-\dot{I}(N_i^*)} \quad i = 1, 2.$$

And so

$$\begin{aligned} \tilde{U}(N_2^*) < 1 &\iff \frac{I(N_2^*) + \dot{L}(N_2^*) - \dot{O}(N_2^*)}{-\dot{I}(N_2^*)} I(N_2^*) + L(N_2^*) - O(N_2^*) < 1 \\ &\iff I(N_2^*)^2 + I(N_2^*)\dot{L}(N_2^*) - \dot{I}(N_2^*)(L(N_2^*) - 1) < \dot{O}(N_2^*)I(N_2^*) - O(N_2^*)\dot{I}(N_2^*) = \\ &= \frac{1}{\epsilon} [I(N_2^*)S(N_2^*) - R(N_2^*)\dot{I}(N_2^*)]. \end{aligned}$$

Note that the right hand side is always positive. So, if the left hand side is negative the inequality is always satisfied; if the left hand side is positive the inequality is however satisfied if

$$\epsilon < \epsilon_a(N_2^*) := \frac{I(N_2^*)S(N_2^*) - R(N_2^*)\dot{I}(N_2^*)}{|I(N_2^*)(I(N_2^*) + \dot{L}(N_2^*)) - \dot{I}(N_2^*)(L(N_2^*) - 1)|}.$$

Furthermore,

$$\begin{aligned} \tilde{U}(N_1^*) > 1 &\iff \frac{I(N_1^*) + \dot{L}(N_1^*) - \dot{O}(N_1^*)}{-\dot{I}(N_1^*)} I(N_1^*) + L(N_1^*) - O(N_1^*) > 1 \\ &\iff \\ I(N_1^*)(I(N_1^*) + \dot{L}(N_1^*)) - \dot{I}(N_1^*)(L(N_1^*) - 1) &> \frac{1}{\epsilon} [I(N_1^*)S(N_1^*) - R(N_1^*)\dot{I}(N_1^*)]. \end{aligned} \tag{B.11}$$

Note that the right hand side is always positive.

Moreover, since $p(V_F) < \tilde{p}_2$ (which is positive because $b < \tilde{b}$), then

$$\begin{aligned} I^2 \left(\frac{V_F}{b} \right) - b \sqrt{\frac{2\pi}{a}} (2e^{\frac{v_E^2}{2a}} - e^{\frac{v_R^2}{2a}}) &> I \left(\frac{V_F}{b} \right) b \sqrt{\frac{2\pi}{a}} V_F e^{\frac{v_E^2}{2a}} p(V_F) = \\ &= -I \left(\frac{V_F}{b} \right) \dot{L}(0). \end{aligned} \tag{B.12}$$

And so, using (B.12) we have $I^2(\frac{V_F}{b}) + \dot{I}(0) > -I(\frac{V_F}{b})\dot{L}(0)$ because:

$$\begin{aligned} &I^2 \left(\frac{V_F}{b} \right) + \dot{I}(0) = \\ &= I^2 \left(\frac{V_F}{b} \right) - b \sqrt{\frac{2\pi}{a}} \left(e^{\frac{v_E^2}{2a}} \operatorname{erfc} \left(\frac{-V_F}{\sqrt{2a}} \right) - e^{\frac{v_R^2}{2a}} \operatorname{erfc} \left(\frac{-V_R}{\sqrt{2a}} \right) \right) > \\ &> I^2 \left(\frac{V_F}{b} \right) - b \sqrt{\frac{2\pi}{a}} \left(2e^{\frac{v_E^2}{2a}} - e^{\frac{v_R^2}{2a}} \right) > -I \left(\frac{V_F}{b} \right) \dot{L}(0). \end{aligned}$$

Now, since \dot{I} and \dot{L} are increasing functions and I is a decreasing function, and remembering that $0 < N_1^* < \frac{V_F}{b}$,

$$I^2(N_1^*) + \dot{I}(N_1^*) > I^2 \left(\frac{V_F}{b} \right) + \dot{I}(0) > -I \left(\frac{V_F}{b} \right) \dot{L}(0) > -I(N_1^*)\dot{L}(N_1^*),$$

or equivalently

$$I(N_1^*)(I(N_1^*) + \dot{L}(N_1^*)) + \dot{I}(N_1^*) > 0$$

from which we deduce that the left hand side of the inequality (B.11) is positive too.

We can finally conclude that if

$$\epsilon > \tilde{\epsilon}_a(N_1^*) = \frac{I(N_1^*)S(N_1^*) - R(N_1^*)\dot{I}(N_1^*)}{|I(N_1^*)(I(N_1^*) + \dot{L}(N_1^*)) - \dot{I}(N_1^*)(L(N_1^*) - 1)|}$$

then (B.11) is verified and so $\tilde{U}(N_1^*) > 1$.

□

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