Derivation of a voltage density equation from a voltage-conductance kinetic model for networks of integrate-and-fire neurons

Benoît Perthame, Delphine Salort

DERIVATION OF A VOLTAGE DENSITY EQUATION FROM A VOLTAGE-CONDUCTANCE KINETIC MODEL FOR NETWORKS OF INTEGRATE-AND-FIRE NEURONS*

BENOîT PERTHAME† AND DELPHINE SALORT‡

In memory of late David CAI, a pioneer in mathematical neuroscience

Abstract. In terms of mathematical structure, the voltage-conductance kinetic systems for neural networks can be compared to a kinetic equations with a macroscopic limit which turns out to be a voltage-based model for assemblies of Integrate-and-Fire (I&F) neurons. This article is devoted to the mathematical study of the slow-fast limit of the kinetic type equation towards the voltage-based population model. After proving the weak convergence of the voltage-conductance kinetic problem to the potential only equation, we study the main qualitative properties of the solution of the voltage model, with respect to the strength of interconnections of the network. In particular, we obtain long term convergence to a unique stationary state for weak connectivity regimes. For intermediate connectivities, we prove linear instability and numerically exhibit periodic solutions. These results about the voltage-based model for I&F neurons suggest that the solutions of the more complex kinetic equation shares several similar qualitative dynamical properties.

Keywords. Integrate-and-fire neurons; Voltage-conductance Vlasov equation; Neural networks; Slow-fast dynamics; Asymptotic analysis; Fokker-Planck kinetic equation;

AMS subject classifications. 35B65, 35Q84, 62M45, 82C32, 92B20.

1. Introduction

The voltage-conductance density systems for neural networks are nonlinear (2+1) dimensional kinetic Fokker-Plank equation which are established in [7, 25]. Based on neuro-physical concepts adapted in particular to the visual cortex, they describe the probability density $p_\varepsilon(v,g,t)$ to find neurons at time t with a membrane potential $v\in(V_R,V_E)$ and a conductance $g>0$. Here, V_E denotes the excitatory reversal potential and the reset potential satisfies $V_R\le V_L$ with V_L the leak potential. There are several variants of the equation depending on the physical interpretation of variable, see, e.g., [15, 17]. The mathematical structure of these systems is rather complex and has attracted the interest of mathematicians [2, 4, 23]. In particular difficulties related to boundary conditions and partial parabolicity make the system rather uneasy to handle and connect it to present interest about hypoellipticity in kinetic equations, see [13,18,27] and the references therein. A rather striking finding in [4] is the numerical observation of periodic solutions describing spontaneous activity of the network, a phenomena which is common to other neural assembly models (see [20–22, 24]).

Here, we deal with the probability density $p_\varepsilon(v,g,t)$ to find a neuron with potential v, conductance g at time t, which is assumed to be driven by the equation

$$\begin{aligned}\frac{\partial}{\partial t}p_\varepsilon+\frac{\partial}{\partial v}\ \left[\big(g_L(V_L-v)+g(V_E-v)\big)p_\varepsilon\right]+\frac{1}{\varepsilon}\frac{\partial}{\partial g}\left[(G_{eq}(v,b\mathcal{N}_\varepsilon(t))-g)p_\varepsilon\right]\\ -\frac{a}{\varepsilon}\frac{\partial^2}{\partial g^2}p_\varepsilon+\phi_F(v)p_\varepsilon=0,\qquad t\ge 0,\, V_R<v<V_E,\, g\ge 0,\end{aligned}\tag{1.1}$$

*Received date, and accepted date.

†Sorbonne Université, CNRS, Université de Paris, INRIA, Laboratoire Jacques-Louis Lions, F-75005 Paris, France. Email : Benoit.Perthame@sorbonne-universite.fr

‡Sorbonne Université, CNRS, Laboratoire de Biologie Computationnelle et Quantitative, UMR 7238, F-75005 Paris, France. Email : delphine.salort@sorbonne-universite.fr

with the no-flux boundary conditions

$$\begin{cases} (G_{eq}(v,b\mathcal{N}_\varepsilon(t))-g)p_\varepsilon(v,g,t)-a\frac{\partial}{\partial g}p_\varepsilon(v,g,t)=0 & \text{for } g=0, \\ [g_L(V_L-V_R)+g(V_E-V_R)]p_\varepsilon(V_R,g,t)=N_\varepsilon(g,t) & \text{and} \quad p_\varepsilon(V_E,g,t)=0, \end{cases} \tag{1.2}$$

and with an initial data that satisfies

$$p^0(v,g)\geq 0, \qquad \int_{V_R}^{V_E}\int_0^\infty p^0(v,g)dv\,dg=1. \tag{1.3}$$

A neuron spikes with a rate $\phi_F(v)$, typically very large for v larger than a firing potential, and we assume that its membrane potential is instantaneously set at the reset potential V_R. For the sake of analytical tractability, we have assumed that the firing potential is randomly distributed, with the firing rate $\phi_F(v)$, while it is often prescribed at a deterministic value V_F of the firing potential. Therefore, at each time, the firing rate (activity of the network) for neurons with conductance g and respectively the total firing rate of the network are defined as

$$N_\varepsilon(g,t):=\int_{V_R}^{V_E}\phi_F(v)p_\varepsilon(v,g,t)dv\geq 0, \qquad \mathcal{N}_\varepsilon(t):=\int_0^{+\infty}N_\varepsilon(g,t)dg. \tag{1.4}$$

Those definitions and boundary conditions, when integrating the equation (1.1), imply the conservation property

$$\int_{V_R}^{V_E}\int_0^\infty p_\varepsilon(v,g,t)dv\,dg=1, \tag{1.5}$$

which is in accordance with the interpretation that the solution is the probability density of neurons with potential v and conductance g at time t.

For the ease of use, we summarize the parameter interpretation, according to [7,25],

- V_E is the excitatory reversal potential,
- Firing occurs with a rate $\phi_F(v)\geq 0$, $\phi'_F(v)>0$,
- Reset is at V_R,
- V_L is the leak potential, $V_R<V_L<V_E$,
- $g_L>0$ denotes the leak conductance,
- $G_{eq}(v,\cdot)\geq 0$ is the conductance equilibrium (when ignoring noise),
- a represents the intensity of the synaptic noise,
- $\varepsilon>0$ denotes the time decay constant of the excitatory conductance,
- $b\geq 0$ denotes the synaptic strength of network excitatory coupling.

Concerning parameter range, in [8], see Eq. (3.2a), the authors choose $V_R=V_L$. Here we consider the more general case $V_R\leq V_L$. Also, to establish (1.1), [7, 25, 26] assume that the value ε is small enough. Following [7,8], this motivates to consider the limit $\varepsilon\to 0$ of Equation (1.1), which formally leads to a reduction of dimension with a (1+1) dimensional equation easier to tackle. More precisely, we are going to show that it can be described by the following voltage only neural network model for integrate&fire neurons (see [5, 10–12, 14] and references therein) for $t\geq 0$, $V_R<v<V_E$,

$$\begin{cases} \frac{\partial}{\partial t}n(v,t)+\frac{\partial}{\partial v}\left[\mathcal{G}(v,b\mathcal{N}(t))\big(V(b\mathcal{N}(t))-v\big)n(v,t)\right]+\phi_F(v)n(v,t)=0, \\ \mathcal{N}(t)=\displaystyle\int_{V_R}^{V_E}\phi_F(v)n(v,t)dv, \\ \mathcal{G}(V_R,b\mathcal{N}(t))\big(V(b\mathcal{N}(t))-V_R\big)n(V_R,t)=\mathcal{N}(t) \quad \text{and} \quad n(V_E,t)=0. \end{cases} \tag{1.6}$$

Our purpose is then, on the one hand, to derive this system in the slow-fast limit $\varepsilon \to 0$, to explain how noise comes in the expression of the drift, together with the property

$$V_L < V(b\mathcal{N}(t)) \leq V_E, \qquad \mathcal{G}(v, b\mathcal{N}(t)) > 0, \tag{1.7}$$

which explains the possibility to state the boundary conditions in (1.6). On the other hand, we aim at studying the qualitative properties of Equation (1.6), in order to formally obtain, with this more simplified equation, the main properties of Equation (1.1).

The situation at hand is similar to the derivation of macroscopic (fluid) models from kinetic (Boltzmann) equation in the phase space (position, velocity). This explains our terminology 'kinetic equation' for the voltage-conductance model.

Assumptions on ϕ and G and initial data. In the rest of the paper, we make the following assumptions. We assume that the firing rate satisfies

$$\phi_F, \phi_F' \in L^\infty, \qquad \phi_F' \geq 0. \tag{1.8}$$

We also assume that $G(v,A) \geq 0$ and that there is a smooth increasing function $\bar{G} \geq 0$ such that,

$$\sup_{V_R \leq v \leq V_E} [G(v,A) + |\frac{\partial G(v,A)}{\partial v}|] \leq \bar{G}(A), \quad \forall A \geq 0. \tag{1.9}$$

For example, in [7, 25], we find the choice $G(v, b\mathcal{N}) = b\mathcal{N}$.

Finally, for the initial data, we assume, for $\varepsilon \leq 1$ and $k \geq 0$

$$\int_{V_R}^{V_E} \int_{g=0}^{+\infty} g^k p^0(v,g) dv dg \leq \mathcal{Q}^{(k),0} < \infty. \tag{1.10}$$

The microscopic model.

For the sake of completeness, we present the microscopic dynamics which generates the voltage-conductance kinetic equation in the limit of a large number of neurons. More on this model and its limit can be found in [2, 4, 26].

The following dynamical system governs the temporal evolution of the membrane potential $V_i(t)$ and the excitatory conductance $G_i(t) \geq 0$ of the i-th neuron in a pool of N excitatory neurons,

$$\tau \frac{dV_i}{dt} = -g_L(V_i - V_L) - G_i(V_i - V_E),$$

$$\sigma_E \frac{dG_I(t)}{dt} = -G_i(t) + \sum_\mu f_E \delta(t - t_i^\mu) + S_{EE} N_E \sum_{j=1}^N \sum_\mu p_j^{E\mu} \delta(t - t_j^\mu).$$

With the rate $\phi_F(V_i)$, the i-th neuron will fire at some random times t_i^μ and the potential is reset to V_R, then it spikes and sends instantaneously a current described by its strength f_E (self excitation) and S_{EE} the strength of excitatory coupling with N_E a normalizing constant. Noise (as a Wigner process) or random jumps can be added to also include the second derivative in g.

Outline.

The rest of the paper is organized as follows. Section 2 is devoted to the slow-fast limit study of Equation (1.1) to Equation (1.6). To this, we preliminary explain how to obtain the formal derivation. We then give uniforms estimates on the moments of the solution and of the firing rate with respect to ε, leading to prove rigorously the weak convergence of Equation (1.1) to Equation (1.6) when ε goes to 0. We finish this section by the construction of super-solutions leading to uniform L^∞ bounds for the solutions of (1.1) with respect to ε and for the solutions of Equation (1.6). In Section 3 we give the main qualitative properties of Equation (1.6) with a slightly simplified drift. To this, we first study the steady states of this equation as well as the asymptotic long time convergence to those steady states when the strength of connectivity parameter b is small enough. The method of proof is based on entropy methods. We finally consider the case with stronger interconnections where instabilities is proved for the linearized problem and we perform numerical simulations in order to illustrate the emergence of oscillatory solutions. We finish the paper with conclusions and perspectives.

2. From conductance-voltage to voltage only model

Departing with a formal derivation, we first explain, how, Equation (1.1) leads to Equation (1.6) when ε goes to 0. We then prove uniform estimates on the total firing rate and on the moments on the solution with respect to ε. This leads us to prove rigorously weak convergence of solutions of Equation (1.1) to Equation (1.6) (see Theorem 2.1). Finally, we prove uniform estimates in L^∞ when $V_R < V_L$ by the construction of super-solutions in Theorem 2.2.

2.1. Formal derivation

The relation between Equations (1.6) and (1.1) can be simply observed setting

$$n_\varepsilon(v,t) = \int_0^\infty p_\varepsilon(v,g,t)dg.$$

Then, integration in g of (1.1), using the no-flux boundary condition in g, gives

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon + \frac{\partial}{\partial v}\big[\mathcal{G}_\varepsilon(v,t)\big(V_\varepsilon(t)-v\big)n_\varepsilon\big] + \phi_F(v)n_\varepsilon = 0, \qquad t \geq 0,\, V_R < v < V_E, \\ \mathcal{N}_\varepsilon(t) = \displaystyle\int_{V_R}^{V_E} \phi_F(v) n_\varepsilon(v,t)dv, \\ \mathcal{G}_\varepsilon(V_R,t)\big(V_\varepsilon(t)-V_R\big)n_\varepsilon(V_R,t) = \mathcal{N}(t) \quad \text{ and } \quad n_\varepsilon(V_E,t)=0, \end{cases} \tag{2.1}$$

with the bulk conductance and voltage

$$\begin{cases} g_L \leq \mathcal{G}_\varepsilon(v,t) = \displaystyle\int_0^\infty (g_L+g)\frac{p_\varepsilon(v,g,t)}{n_\varepsilon(v,t)}dg, \\ V_L < V_\varepsilon(v,t) = \frac{1}{\mathcal{G}_\varepsilon(v,t)} \displaystyle\int_0^\infty (g_L V_L + g V_E)\frac{p_\varepsilon(v,g,t)}{n_\varepsilon(v,t)}dg \leq V_E. \end{cases} \tag{2.2}$$

In order to close this formula, we need to identify the first moment in g of the distribution $p_\varepsilon(v,g,t)$ in terms of n_ε.

To do so, we consider the limit p of p_ε and it formally solves

$$\frac{\partial}{\partial g}\left[(G_{eq}(v,b\mathcal{N}(t)) - g)p\right] - a\frac{\partial^2}{\partial g^2}p = 0,$$

With the no-flux boundary condition, we find

$$(G_{eq}(v,b\mathcal{N}(t))-g)p-a\frac{\partial p}{\partial g}=0, \qquad \text{thefore} \qquad p=n(v,t)\mathcal{P}(v,g,b\mathcal{N}(t)),$$

with n solution of Equation (1.6) and

$$\mathcal{P}(v,g,A)=\frac{1}{\mathcal{Z}(v,a,A)}\exp^{-\frac{(G_{eq}(v,A)-g)^2}{2a}}, \quad \mathcal{Z}(v,a,A)=\int_0^\infty \exp^{-\frac{(G_{eq}(v,A)-g)^2}{2a}}dg. \quad (2.3)$$

This expression allows us to compute the limiting flux in Equation (1.6) as stated Theorem 2.1 below.

Notice that $\mathcal{Z}(v,a,A)$ is controlled from above and below as

$$\frac{1}{2}\sqrt{2\pi a}=\int_{G_{eq}(v,A)}^\infty \exp-\frac{(G_{eq}(v,A)-g)^2}{2a}dg\le\mathcal{Z}(v,a,A)\le\sqrt{2\pi a}.$$

The effect of noise at the synaptic level is not a diffusion in v, as it is assumed in the standard voltage-based population model for Integrate and Fire neurons, see for instance [3]. Noise rises a change of the excitatory bulk conductance $\mathcal{G}_\varepsilon(v,t)$. It can be compared to the noiseless case $a\to 0$ which gives

$$\mathcal{G}_\varepsilon(v,0,b\mathcal{N}_\varepsilon(t))=G_{eq}(v,b\mathcal{N}_\varepsilon(t)).$$

In mathematical terms, the analysis of the limit $a\to 0$, i.e., the case without noise, yields difficulties similar to those of friction dominant particle flows, see [19] for instance.

2.2. Estimates on the firing rate/moments on the solution and rigorous limit

We now prove rigorously the above formal derivation. The result is stated in the following Theorem

THEOREM 2.1 (Slow-fast limit result). *We assume (1.8)–(1.10). Then, for all $k\ge 1$, there exists a constant $C(k)>0$ and a constant $C>0$ such that, for all $\varepsilon>0$ and $t\ge 0$, the following estimates hold*

$$\int_0^{+\infty} g^k p_\varepsilon(v,g,t)dvdg\le C(k) \qquad \text{and} \qquad \|\mathcal{N}_\varepsilon\|_{L^\infty(\mathbb{R}^+)}+\|\mathcal{N}_\varepsilon'\|_{L^\infty(\mathbb{R}^+)}\le C. \qquad (2.4)$$

Hence, in the weak topology of bounded measures,

$$p_\varepsilon\rightharpoonup n(v,t)\mathcal{P}(v,g,b\mathcal{N}(t))>0, \qquad \int_0^\infty \mathcal{P}(v,g,b\mathcal{N}(t))dg=1,$$

where the smooth function $\mathcal{P}(v,g,b\mathcal{N}(t))$ is determined by (2.3) and where $n(v,t)$ satisfies Equation (1.6) with the initial data $n^0(v)=\int_0^{+\infty}p^0(v,g)dg$ and

$$\mathcal{G}(v,A)=g_L+\int_0^{+\infty} g\mathcal{P}(v,g,A)dg>g_L,$$

$$V_L<V(v,A)=\frac{g_LV_L+V_E\int_0^{+\infty}g\mathcal{P}(v,g,A)dg}{\mathcal{G}(v,A)}<V_E.$$

This theorem states a general weak convergence result. It can be strengthen, with the expense on stronger assumptions as stated afterwards, see Theorem 2.2 in the next subsection.

Proof. **Proof of Theorem 2.1.**

Moments estimates.

Let us first prove the first inequality of (2.4). We set

$$\mathcal{Q}_\varepsilon^{(k)}(t) := \int_{V_R}^{V_E}\int_0^{+\infty} g^k p_\varepsilon(v,g,t)\,dvdg.$$

Multiplying Equation (1.1) by g^k and integrating, we compute for $k \geq 2$

$$\frac{1}{k}\frac{d}{dt}\mathcal{Q}_\varepsilon^{(k)}(t) = \frac{1}{\varepsilon}\int_{V_R}^{V_E}\int_0^{+\infty} g^{k-1}[G_{eq}(v,b\mathcal{N}_\varepsilon(t)) - g]p_\varepsilon dvdg - \frac{a}{\varepsilon}\int_{V_R}^{V_E}\int_0^{+\infty} g^{k-1}\frac{\partial p_\varepsilon}{\partial g}dvdg.$$

Therefore we find

$$\frac{d\mathcal{Q}_\varepsilon^{(k)}(t)}{dt} + \frac{k}{\varepsilon}\mathcal{Q}_\varepsilon^{(k)}(t) = \int_{V_R}^{V_E}\int_0^{+\infty}\left[\frac{k}{\varepsilon}g^{k-1}G_{eq}(v,b\mathcal{N}_\varepsilon(t)) + k(k-1)\frac{a}{\varepsilon}g^{k-2}\right]p_\varepsilon dvdg.$$

As p_ε is a density probability, then

$$\|\mathcal{N}_\varepsilon\|_{L^\infty(\mathbb{R}^+)} \leq \|\phi_F\|_{L^\infty}.$$

Using assumption (1.9), we deduce that there exists a constant C such that

$$\int_{V_R}^{V_E}\int_0^{+\infty} g^{k-1}G_{eq}(v,b\mathcal{N}_\varepsilon(t))p_\varepsilon dvdg \leq C\int_{V_R}^{V_E}\int_0^{+\infty} g^{k-1}p_\varepsilon dvdg.$$

Using again that p_ε is a density probability, and splitting the integral in g in two parts : from 0 to μ and from μ to $+\infty$, we deduce that for all $\mu > 0$ large enough, there exists a constant $C(\mu)$ such that

$$\int_{V_R}^{V_E}\int_0^{+\infty}(g^{k-1}+g^{k-2})p_\varepsilon dvdg \leq C(\mu) + \frac{1}{\mu}\mathcal{Q}_\varepsilon^{(k)}(t).$$

Consequently, we have for all $\mu > 0$ large enough

$$\frac{d}{dt}\mathcal{Q}_\varepsilon^{(k)}(t) + \frac{k}{\varepsilon}\mathcal{Q}_\varepsilon^{(k)}(t) \leq \frac{1}{\varepsilon}\left(C(k,\mu) + \frac{1}{\mu}\mathcal{Q}_\varepsilon^{(k)}(t)\right).$$

Taking μ large enough and using Gronwall inequality, we deduce the first part of estimate (2.4).

Uniform estimates on the firing rate.

The bound on $\mathcal{N}_\varepsilon(t)$ is easy to obtain. Because the total mass of p_ε is 1, we conclude from its definition that

$$\mathcal{N}_\varepsilon(t) \leq \|\phi_F\|_{L^\infty}.$$

Next, we prove the Lipschitz bound. We multiply equation (1.1) by ϕ_F and integrate in (v,g), we find

$$\begin{aligned}\left|\tfrac{d}{dt}\mathcal{N}_\varepsilon(t)\right| &\leq \left|\int \phi_F'(v)\big[g_L(V_L-v)+g(V_E-v)\big]p_\varepsilon(v,g,t)dgdv\right| \\ &\leq \|\phi_F'(v)\|_{L^\infty}V_E\int g p_\varepsilon(v,g,t)dgdv\end{aligned}$$

and we conclude using that the moments are uniformly bounded with respect to ε, thanks to (2.4).

Weak convergence.

Let us first deal with the term $G_{eq}(v, b\mathcal{N}_\varepsilon(t))$. With the second part of estimate (2.4), we deduce using the Ascoli theorem that, up to a subsequence, there exists a Lipschitz function $\mathcal{N}$ such that for all $T>0$,

$$\lim_{\varepsilon\to 0} \|\mathcal{N}_\varepsilon - \mathcal{N}\|_{L^\infty(0,T)} = 0.$$

As G is assumed to be regular, we deduce that, up to a subsequence, for all $T>0$,

$$\lim_{\varepsilon\to 0} \|G(v, b\mathcal{N}_\varepsilon) - G(v, b\mathcal{N})\|_{L^\infty((V_R,V_E)\times(0,T))} = 0.$$

Let us now study the convergence of p_ε. As p_ε is a density measure and as its moments is uniformly bounded with respect to ε, we deduce that up to a subsequence, there exists a bounded measure function p with total mass 1 and finite moments such that

$$p_\varepsilon \rightharpoonup p \qquad gp_\varepsilon \rightharpoonup gp.$$

Integrating Equation (2.1) with respect to the variable g, we find that

$$\widetilde{n}(v,t) := \int_0^{+\infty} p(v,g,t)dv$$

is solution of the equation

$$\partial_t \widetilde{n}(v,t) + \partial_v \left(g_L(V_L - v)\widetilde{n} + (V_E - v)\int_0^{+\infty} gpdg \right) + \phi(v)\widetilde{n}(v,t) = \delta_{v=V_R}\mathcal{N}(t).$$

Combining this with the equality

$$\frac{\partial}{\partial g}[(G_{eq}(v, b\mathcal{N}(t)) - g)p] - a\frac{\partial^2}{\partial g^2}p = 0,$$

and following the subsection 2.1, we conclude the proof of Theorem 2.1. □

2.3. L^∞ bound on p_ε and n

We now wish to prove uniform bounds on $p_\varepsilon(v,g,t)$ for the full problem (1.1). For this, we need a kind of non-characteristic condition between the transport in v and the boundary flux at V_R. Hence, to avoid technicalities, we assume that $V_R < V_L$ for Equation (1.1). For the limit Equation (1.6), the above condition can be relaxed with $V_R \le V_L$. The following theorem holds

Theorem 2.2 (L^∞ bound for p_ε and for n). *We assume (1.8)–(1.10), $V_R < V_L$, that $p_\varepsilon(t=0) \in L^\infty$ with sufficient (Gaussian) decay at $g=\infty$ uniformly in ε. Then, for all $T>0$, there exists a constant $C(T)$ independent of ε small enough such that the solution of (2.5) satisfies*

$$\sup_{0\le t\le T}\sup_{g\ge 0} N_\varepsilon(g,t) \le C(T),$$

$$\sup_{0\le t\le T}\sup_{V_R\le v\le V_E}\sup_{g\ge 0} p_\varepsilon(v,g,t) \le C(T).$$

Assume that $V_R \le V_L$ and (1.8)–(1.10). Then, there is a constant $C(T)$ such that, the solutions of (1.6) satisfy

$$\sup_{0\le t\le T}\sup_{V_R\le v\le V_E} n(v,t) \le C(T)\|n^0\|_{L^\infty}.$$

Proof. **Proof of Theorem 2.2**. We begin with the estimates on p_ε and then treat those for n.

Estimate for p_ε.

We consider $\mathcal{N}_\varepsilon(t)$ as a given data in the term G_{eq} and we build a super solution $\bar{p}_\varepsilon(v,g,t)$ of Equation (1.1) for $p_\varepsilon(v,g,t)$, that is a solution of the following Problem for $t \geq 0$, $g \geq 0$ and $V_R < v < V_E$,

$$\begin{cases} \frac{\partial}{\partial t}\bar{p}_\varepsilon + \frac{\partial}{\partial v}\left[\left(g_L(V_L-v)+g(V_E-v)\right)\bar{p}_\varepsilon\right] + \frac{1}{\varepsilon}\frac{\partial}{\partial g}\left[(G_{eq}(v,b\mathcal{N}_\varepsilon(t))-g)\bar{p}_\varepsilon\right] - \frac{a}{\varepsilon}\frac{\partial^2}{\partial g^2}\bar{p}_\varepsilon \geq 0, \\ a\frac{\partial}{\partial g}\bar{p}_\varepsilon - (G_{eq}(v,b\mathcal{N}_\varepsilon(t))-g)\bar{p}_\varepsilon = 0, \qquad \text{at } g=0,, \quad p_\varepsilon(V_E,g,t)=0, \\ [g_L(V_L-V_R)+g(V_E-V_R)]\bar{p}_\varepsilon(V_R,g,t) \geq N_\varepsilon(g,t) := \int \phi_F(v)p_\varepsilon(v,g,t)dv. \end{cases} \tag{2.5}$$

We construct it under the form

$$\bar{p}_\varepsilon(v,g,t) = Be^{\alpha(V_R-v)}M(v,g,t)e^{\varepsilon g^2}e^{\mu t}, \qquad \text{with } M(v,g,t) = \exp^{-\frac{(G_{eq}(v,b\mathcal{N}_\varepsilon(t))-g)^2}{2a}},$$

with B , α and μ three constants which are large enough.

Firstly, the constant B is just used to satisfy the initial condition and we ignore it in the end of the proof.

Secondly, we fix α so that the boundary condition at V_L is fulfilled. That simply means (recall that we assume $V_R < V_L$)

$$[g_L(V_L-V_R)+g(V_E-V_R)]M(V_R,g,t) \geq \int \phi_F(v)e^{\alpha(V_R-v)}M(v,g,t)dv$$

which is possible, because large values of g are favorable, for α large enough.

Thirdly, because $M(v,g,t)$ satisfies

$$(G_{eq}-g)M - a\partial_g M = 0,$$

we deduce that

$$a\partial_g\bar{p}_\varepsilon - (G_{eq}-g)\bar{p}_\varepsilon = 2a\bar{p}_\varepsilon\varepsilon g \geq 0,$$

and hence, the zero flux boundary condition is satisfied at $g=0$.

Finally, building on the above calculation, we also find successively that

$$\partial_g((G_{eq}-g)\bar{p}_\varepsilon - a\partial_g\bar{p}_\varepsilon) = -2a\varepsilon Be^{\mu t}\partial_g(gM_\varepsilon e^{\varepsilon g^2}),$$

$$\partial_g((G_{eq}-g)\bar{p}_\varepsilon - a\partial_g\bar{p}_\varepsilon) = (-2a\varepsilon - a(2g\varepsilon)^2 + \varepsilon g(g-G_{eq}))\bar{p}_\varepsilon.$$

We deduce that there exists a constant C independent of ε small enough, such that for all $v \in (V_R,V_E)$ for all $g \geq 0$

$$\varepsilon^{-1}\partial_g((G_{eq}-g)\bar{p}_\varepsilon - a\partial_g\bar{p}_\varepsilon) \geq [\frac{g^2}{2} - C(1+g)]\bar{p}_\varepsilon. \tag{2.6}$$

On the other hand, we have

$$\partial_t\bar{p}_\varepsilon = (\mu + z_\varepsilon(v,g,t))\bar{p}_\varepsilon$$

with

$$z_\varepsilon(v,g,t) = \frac{b}{a}\frac{\partial G_{eq}}{\partial A}(g-G_{eq})\frac{d}{dt}\mathcal{N}_\varepsilon(t).$$

Using that $\mathcal{N}_\varepsilon$ is uniformly Lipschitz with respect to ε, see (2.4), we deduce that there exists a constant C independent of ε such that for all $v\in(V_R,V_E)$ for all $g\geq 0$

$$|z_\varepsilon| \leq C(1+g).$$

We then deduce that

$$\partial_t \bar{p}_\varepsilon \geq (\mu - C(1+g))\bar{p}_\varepsilon. \tag{2.7}$$

Simple computations show that there exists a constant C independent of ε such that for all $v\in(V_R,V_E)$ for all $g\geq 0$

$$\partial_v((g_L(V_L-v)+g(V_E-v))\bar{p}_\varepsilon) \geq -C(1+\alpha)(1+g)\bar{p}_\varepsilon. \tag{2.8}$$

Combining (2.6), (2.7), (2.8) and taking μ large enough, we deduce that

$$\partial_t \bar{p}_\varepsilon + \partial_v[(g_L(V_L-v)+g(V_E-v))\bar{p}_\varepsilon] + \frac{1}{\varepsilon}\partial_g[(G_{eq}-g)\bar{p}_\varepsilon - a\partial_g \bar{p}_\varepsilon] \geq 0.$$

This proves the first part of Theorem 2.2.

Estimate for n.

Due to (1.7), there exists a constant $\underline{b}>0$, such that

$$\mathcal{G}(V_R,A)\big(V(V_R,A)-V_R\big) \geq \underline{b} > 0. \tag{2.9}$$

Moreover, as n is a probability density, we have

$$\|\mathcal{N}\|_{L^\infty} \leq \|\phi_F\|_{L^\infty}.$$

To show that we can build a super-solution, we can reduced to construct $\bar{n}\geq 0$ such that

$$\partial_t \bar{n} + \partial_v\big[\mathcal{G}(v,b\mathcal{N}(t))\big(V(b\mathcal{N}(t))-v\big)\bar{n}\big] \geq 0$$

and

$$\big(\mathcal{G}(V_R,b\mathcal{N}(t))\big(V(b\mathcal{N}(t))-V_R\big)\bar{n}\big) \geq \|\phi_F\|_{L^\infty}.$$

Choosing

$$\bar{n}(v,t) := B\|n^0\|_{L^\infty} e^{At}$$

with A and B large enough and using assumption (2.9), we deduce that $\bar{n}$ is a super-solution which ends the proof of Theorem 2.2. $\square$

3. Qualitative study of the associatedpopulation model for I&F neurons

This section is devoted to the understanding of the qualitative and asymptotic behavior of Equation (1.6) with respect to the strength of interconnections of the network. To simplify the presentation, we consider a slightly simplified model of Equation (1.6) as follows.

$$\begin{cases} \frac{\partial n}{\partial t} + \frac{\partial}{\partial v}[(V_0(\mathcal{N})-v)n] + \phi_F(v)n = 0, & 0\leq v\leq V_E, \\ V_0(\mathcal{N}(t))n(v=0,t) = \mathcal{N}, \quad n(V_E,t)=0, & \mathcal{N}(t) = \int_0^{V_E}\phi_F(v)n(v,t)dv. \end{cases} \tag{3.1}$$

Here, firstly, following [7, 25], we choose $V_L = V_R = 0$. Secondly, we use a simpler drift V_0 independent of the variable v.

3.1. Steady states

The associated steady equation is given by

$$\begin{cases} \frac{\partial}{\partial v}[(V_0(\bar{\mathcal{N}})-v)\bar{n}]+\phi_F(v)\bar{n}=0, & 0\le v\le V_E, \\ V_0(\bar{\mathcal{N}})\bar{n}(v=0)=\bar{\mathcal{N}}, \quad p(V_E)=0, & \bar{\mathcal{N}}=\int_0^{V_E}\phi_F(v)\bar{n}(v)dv. \end{cases} \tag{3.2}$$

We assume that the smooth function $V_0(\cdot)$ satisfies

$$0<V_0(\mathcal{N})<V_E, \qquad \forall \mathcal{N}\ge 0. \tag{3.3}$$

One observes that, to avoid concentration as a Dirac mass at $v=V_0(\mathcal{N})$, it is useful to also assume

$$\phi_F(V_0(\mathcal{N}))>0 \qquad \forall \mathcal{N}\ge 0. \tag{3.4}$$

Indeed, we may write Equation (3.2) as

$$(V_0(\bar{\mathcal{N}})-v)\frac{\partial \bar{n}}{\partial v}+(\phi_F(v)-1)\bar{n}=0. \tag{3.5}$$

Therefore, near $v=V_0(\bar{\mathcal{N}})$, the solution behaves as $\frac{\partial \ln(\bar{n})}{\partial v}=-\frac{\phi_F(V_0(\bar{\mathcal{N}}))-1}{V_0(\bar{\mathcal{N}})-v}$ and thus, for some constant q_s

$$\bar{n}\approx q_s(V_0(\bar{\mathcal{N}})-v)^\alpha, \qquad \alpha=\phi_F(V_0(\bar{\mathcal{N}}))-1>-1,$$

which means that Condition (3.4) implies that $\bar{n}$ has an integrable singularity.

More precisely we have the

THEOREM 3.1. *With the assumptions (1.8), (3.3), (3.4), there is at least one steady state solution $\bar{n}$ which satisfies $\int_0^{V_E}\bar{n}=1$.*

Proof. It is possible to give an expression of the stationary solution $\bar{n}$. Using (3.5), we can write

$$\frac{\partial \ln(\bar{n})}{\partial v}=\begin{cases} \frac{1-\phi_F(v)}{V_0(\bar{\mathcal{N}})-v}, & \text{for } v<V_0(\bar{\mathcal{N}}), \\ 0, & \text{for } v>V_0(\bar{\mathcal{N}}). \end{cases}$$

Therefore we define

$$F(v,\bar{\mathcal{N}})=\int_0^v \frac{1-\phi_F(w)}{V_0(\bar{\mathcal{N}})-w}dw,$$

and we conclude that (and recall this $\bar{n}$ is integrable near $V_0(\bar{\mathcal{N}})$ as we saw it above)

$$\bar{n}(v)=\begin{cases} \frac{\bar{\mathcal{N}}}{V_0(\bar{\mathcal{N}})}e^{F(v,\bar{\mathcal{N}})}, & \text{for } v<V_0(\bar{\mathcal{N}}), \\ 0, & \text{for } v>V_0(\bar{\mathcal{N}}). \end{cases} \tag{3.6}$$

Indeed, from (3.5), we may also infer that $\bar{n}\equiv 0$ for $v>V_0(\bar{\mathcal{N}})$ and the sign of $\frac{\partial \bar{n}}{\partial v}$ is the sign of $1-\phi_F(v)$. Next, we choose the value $\bar{\mathcal{N}}$ so as to enforce the constraint $\int_0^{V_0(\bar{\mathcal{N}})}\bar{n}=1$. For $\bar{\mathcal{N}}=0$, the corresponding solution $\bar{n}$ vanishes, and for $\bar{\mathcal{N}}\to\infty$, we have $\bar{n}\to\infty$. By continuity, we may achieve the constraint. □

These considerations explain the numerical solutions depicted in the Figure 3.1. These are obtained with

$$V_R=0, \quad V_E=1, \quad \phi_F(v)=A\mathbf{1}_{\{v>.5\}}, \quad V_0(\mathcal{N})=.8+.2\frac{\mathcal{N}}{1+\mathcal{N}}, \tag{3.7}$$

and $A=.5$ for the figure on the left, $A=5.$ for the figure on the right. The value $V_0(\mathcal{N})$ can be identified because the solution vanishes for $v>V_0(\mathcal{N})$.

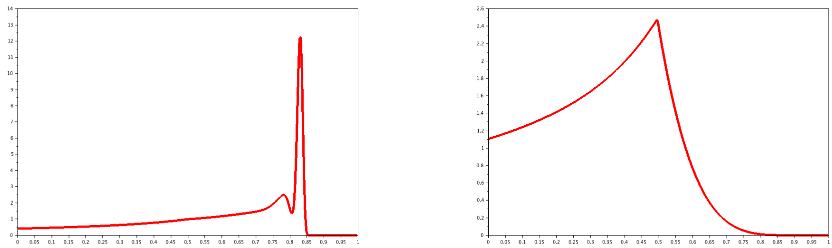

Fig. 3.1. Numerical solutions of the steady states in (3.2) with the date in (3.7) and two choices of the term $\phi_F(v)$. Abscissae are v. Left: firing rate $A=.5$; Right: Firing rate $A=5$.

Cases of uniqueness of the steady state.

We may complete the existence result in Theorem 3.1 with uniqueness cases

Theorem 3.2. *With the assumptions (3.3), (3.4), the steady state is unique in the two following cases.*

1. $\phi_F > 1$ *on* $[0, V_E]$ *and*

$$0 < \mathcal{N} V_0'(\mathcal{N}) < V_0(\mathcal{N}), \quad \forall \mathcal{N} > 0. \tag{3.8}$$

2. $\phi_F' \geq 0$ *and* $V_0' < 0$ Notice that Condition (3.8) is satisfied, for instance, by $V_0(\mathcal{N}) = \frac{a\mathcal{N}}{b+\mathcal{N}} + c$, with $a \geq 0$, $b > 0$ and $c \geq 0$, three constants.

Proof. **Proof of Theorem 3.2.**

Case 1. The condition providing the steady states in Theorem 3.1, that is $\int_0^{V_0(\bar{\mathcal{N}})} \bar{n} = 1$, is also written

$$\frac{V_0(\mathcal{N})}{\mathcal{N}} = \int_0^{V_0(\mathcal{N})} e^{F(v,\mathcal{N})} dv,$$

and we show that the two uniqueness cases correspond to left and right hand sides with opposite monotonicity.

The derivative of the left hand side is given by

$$\frac{\mathcal{N} V_0'(\mathcal{N}) - V_0(\mathcal{N})}{\mathcal{N}^2} < 0.$$

To treat the right hand side, we observe that, thanks to the assumption $\phi_F(v) > 1$, we have $e^{F(\mathcal{N}, V_R)} = 0$. Therefore its sign is given by that of $V_0'(\mathcal{N})$ because

$$\frac{\partial F(v,\mathcal{N})}{\partial \mathcal{N}} = -V_0'(\mathcal{N}) \int_0^v \frac{1-\phi_F(w)}{(V_0(\mathcal{N}) - w)^2} dw.$$

Because the latter expression has the sign opposite to $V_0'(\mathcal{N})$ we find the result.

Case 2. To consider also possible values $\phi_F < 1$ and to compute the derivative in $\mathcal{N}$ requires additional steps. We write, for $v < V_0(\mathcal{N})$,

$$F(v,\mathcal{N}) = \int_0^{v/V_0(\mathcal{N})} \frac{1-\phi_F(zV_0(\mathcal{N}))}{1-z} dz, \quad \text{and} \quad G(w,\mathcal{N}) = \int_0^w \frac{1-\phi_F(zV_0(\mathcal{N}))}{1-z} dz.$$

The formula (3.6) gives,

$$\int_0^{V_0(\bar{\mathcal{N}})} \bar{n}(v) = \bar{\mathcal{N}} \int_0^1 e^{G\left(w, V_0(\bar{\mathcal{N}})\right)} dw,$$

and $\bar{n}$ is a probability measure if

$$\frac{1}{\bar{\mathcal{N}}} = \int_0^1 e^{G\left(w, V_0(\bar{\mathcal{N}})\right)} dw.$$

Uniqueness follows under the condition that G is increasing in $\mathcal{N}$, which means

$$-\phi_F'\big(zV_0(\mathcal{N})\big) V_0'(\mathcal{N}) > 0,$$

and, since $\phi_F' \geq 0$, this gives the condition $V_0' < 0$. □

3.2. Asymptotic stability

Back to the evolution Equation (3.1), the next step is to determine if the solutions converge to a steady state in long time. We first consider the linear case and by a perturbation method conclude that the result still holds, assuming a weak nonlinearity. We use the Doeblin method which is very well adapted to the problem at hand, see [1, 9, 16] for recent presentations and results.

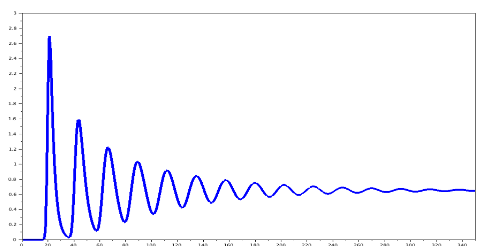

FIG. 3.2. NUMERICAL SOLUTIONS OF THE EVOLUTION EQUATION (3.1) $V_0(\mathcal{N}) = .95$, THAT IS THE LINEAR EQUATION. THIS SHOWS THAT THE SOLUTION RELAXES TO THE STEADY STATE DEPICTED IN FIG. 3.1 WITH DAMPED OSCILLATIONS.

Linear case. In the linear case (V_0 constant), we may apply the Theorem 2.3 in [9] to equation (3.1). We obtain the following criteria for exponential convergence to a unique stationary state. If, for a time $t_0 > 0$, we are able to construct non-negative sub-solution, uniformly with respect to all initial data in L^1, then the solution of our equation converges exponentially to a unique stationary state. More precisely, the following result holds

THEOREM 3.3 ([9]). *Assume that $V_0 > 0$ is constant and assume that there exist $t_0 > 0$ and a nonnegtive function $\nu \neq 0$ such that for all initial data $n^0 \in L^1_+(0, V_E)$ with $\int_0^{V_E} n^0(v)dv = 1$, the solution of (3.1) at time t_0 satisfies*

$$n(v, t_0) \geq \nu(v). \tag{3.9}$$

Then, there exists a unique stationary state $\bar{n}$ of Equation (3.1), there exist $\alpha > 0$, $C > 0$ such that for all $t \geq 0$ and for all density initial data $n^0 \in L^1$

$$\|n(t) - \bar{n}\|_{L^1} \leq Ce^{-\alpha t} \|n^0 - \bar{n}\|_{L^1}.$$

Notice that Doeblin's method is particular adapted to work with measures. However, in our context, we have control in L^1 and thus we restrict ourselves to this context. Once adapted to our case, we conclude that the following result holds

THEOREM 3.4. *Assume that V_0 is constant, $V_0>0$ and $\phi_F(V_0)>0$. Then, there exists $t_0>0$ and a non-negative function $\nu\neq 0$ such that for all initial data $n^0\in L^1_+(0,V_E)$ with $\int_0^{V_E} n^0(v)dv=1$, the solution of (3.1) at time t_0 satisfies estimate (3.9).*
As a consequence, there exist $\alpha>0$, $C>0$ such that for all $t\geq 0$

$$\|n(t)-\bar{n}\|_{L^1}\leq Ce^{-\alpha t}\|n^0-\bar{n}\|_{L^1},$$

where $\bar{n}$ is the stationary state of Equation (3.1).

Proof. **Proof of Theorem 3.4.** Equation (3.1) can be written as

$$\frac{\partial n}{\partial t}+(V_0-v)\frac{\partial n}{\partial v}+(\phi_F(v)-1)n=0.$$

With the method of characteristics, we obtain that

$$n(v,t)=0 \quad \text{ for } \quad v\geq [V_E-V_0]e^{-t}+V_0.$$

In the interval

$$V_0(1-e^{-t})\leq v\leq [V_E-V_0]e^{-t}+V_0,$$

we have

$$n(v,t)=e^{t-\int_0^t \phi_F(v+V_0(e^{-t}-1)+V_0(1-e^{-s}))ds}n(0,ve^t+V_0(1-e^t)), \tag{3.10}$$

and finally, in the interval

$$0\leq v\leq V_0(1-e^{-t}),$$

we have

$$n(v,t)=\frac{1}{V_0}\mathcal{N}(t+\ln(V_0-v)-\ln(V_0))e^{-\ln(V_0-v)+\ln(V_0)-\int_0^{-\ln(V_0-v)+\ln(V_0)}\phi_F(V_0(1-e^{-s}))ds}. \tag{3.11}$$

Using formula (3.10), we deduce that

$$\mathcal{N}(t)\geq e^{t(1-\|\phi_F\|_{L^\infty})}\int_{V_0(1-e^{-t})}^{[V_E-V_0]e^{-t}+V_0}\phi_F(v)n^0\big(ve^t+V_0(1-e^t)\big)dv.$$

Now, we use that $\phi_F(V_0)>0$ and that ϕ_F is regular. This implies that there exist a constant $C>0$ and $t_1>0$ such that for

$$V_0(1-e^{-t_1})\leq v\leq [V_E-V_0]e^{-t_1}+V_0, \qquad \text{we have } \phi_F(v)\geq C>0.$$

Hence, for $t\geq t_1$, we have

$$\mathcal{N}(t)\geq Ce^{t(1-\|\phi_F\|_{L^\infty})}\int_{V_0(1-e^{-t})}^{[V_E-V_0]e^{-t}+V_0}n^0\big(ve^t+V_0(1-e^t)\big)dv.$$

Now, using that $\int_0^{V_E} n^0(v)dv=1$, we obtain the following estimate, independent of the initial data, that is

$$\mathcal{N}(t)\geq Ce^{-\|\phi_F\|_{L^\infty}t} \quad \forall t\geq t_1. \tag{3.12}$$

Using now formula (3.11), we deduce that for $t_0 = 2t_1$, and for

$$v \in [0, V_0(1 - e^{-\frac{t_0}{2}})] \text{ with } 0 \leq -\ln(V_0 - v) + \ln(V_0) \leq \frac{t_0}{2},$$

we have

$$n(v, t_0) \geq C e^{-\|\phi_F\|_{L^\infty} t_0}.$$

This implies, that there exists a time $t_0 := 2t_1$ and a nonnegative function ν with $\int \nu > 0$, such that, for all initial data in L^1, (3.9) condition is satisfied. This ends the proof of Theorem 3.4. ∎

Nonlinear case.

We now consider the nonlinear Equation (3.1), which means that V_0 is not necessary a constant. The following theorem holds

THEOREM 3.5. *Assume (3.3), (3.4) and that there is a constant $D > 0$, small enough, such that*

$$\left(\left\| \left(\frac{N}{V_0(N)} \right)' \right\|_{L^\infty} + \|V_0'\|_{L^\infty} \right) \|\phi_F\|_{L^\infty} \leq D.$$

Then, there exists a unique stationary state n^* of Equation (3.1) and there exists constants $\alpha > 0$ and $C > 0$ such that for all initial data $n^0 \in L^1(0, V_E)$, $\int_0^{V_E} n^0(v)dv = 1$, the solution of Equation (3.1) satisfies

$$\|n(t) - n^*\|_{L^1} \leq C e^{-\alpha t} \|n0 - n^*\|_{L^1}.$$

Proof. **Proof of Theorem 3.5.** As the assumptions of Theorem 3.1 hold, there exists a stationary state of Equation (3.1), we denote it by $(n^*, \mathcal{N}^*)$.For a density n^0 as above, we call $S_t(n^0)$ the solution of the linear equation

$$\begin{cases} \frac{\partial n}{\partial t} + \frac{\partial}{\partial v}[(V_0(\mathcal{N}^*) - v)n] + \phi_F(v)n = 0, & 0 \leq v \leq V_E, \\ V_0(\mathcal{N}^*)n(v=0,t) = \mathcal{N}^*, \quad n(V_E, t) = 0, & n(v,0) = n^0. \end{cases} \tag{3.13}$$

Then, using Duhamel's principle, the solution of Equation (3.1) with initial data n^0 can be written as

$$n(v,t) = S_t(n^0) + \int_0^t S_{t-\tau}(V_0(\mathcal{N}^*) - V_0(\mathcal{N}(\tau))\; n(\tau, v)d\tau + \\ \delta_{v=0} \int_0^t S_{t-\tau} \left(\frac{\mathcal{N}(\tau)}{V_0(\mathcal{N}(\tau))} - \frac{\mathcal{N}^*}{V_0(\mathcal{N}^*)} \right) d\tau.$$

From this, inserting absolute values, integrating in v and using that the total mass of n is 1, we obtain

$$\|n(t) - n^*\|_{L^1} \leq \|S_t(n^0) - n^*\|_{L^1} + \int_0^t \left| S_{t-\tau}(V_0(\mathcal{N}^*) - V_0(\mathcal{N}(\tau)) + \frac{\mathcal{N}(\tau)}{V_0(\mathcal{N}(\tau))} - \frac{\mathcal{N}^*}{V_0(\mathcal{N}^*)}) \right| d\tau$$

and we now use Theorem 3.4 to obtain two constants $C > 0$ and $\beta > 0$ such that

$$\|n(t) - n^*\|_{L^1} \leq e^{-\beta t} \|n^0 - n^*\|_{L^1} \\ + \int_0^t e^{-\beta(t-\tau)} \left| \left(V_0(\mathcal{N}^*) - V_0(\mathcal{N}(\tau)) + \frac{\mathcal{N}(\tau)}{V_0(\mathcal{N}(\tau))} - \frac{\mathcal{N}^*}{V_0(\mathcal{N}^*)} \right) \right| d\tau.$$

To conclude, it remains to estimate

$$\left|\left(V_0(\mathcal{N}^*)-V_0(\mathcal{N}(\tau))+\frac{V_0(\mathcal{N}(\tau))}{\mathcal{N}(\tau)}-\frac{V_0(\mathcal{N}^*)}{\mathcal{N}^*}\right)\right|.$$

To do so, we notice that

$$|V_0(\mathcal{N}^*)-V_0(\mathcal{N}(\tau)|\leq \|V_0'\|_{L^\infty}|\mathcal{N}^*-\mathcal{N}(\tau)|\leq \|V_0'\|_{L^\infty}\|\phi_F\|_{L^\infty}\|n(\tau)-n^*\|_{L^1}.$$

and

$$\left|\frac{\mathcal{N}(\tau)}{V_0(\mathcal{N}(\tau))}-\frac{\mathcal{N}^*}{V_0(\mathcal{N}^*)}\right|\leq \left\|\left(\frac{N}{V_0(N)}\right)'\right\|_{L^\infty}\|\phi_F\|_{L^\infty}\|n(\tau)-n^*\|_{L^1}.$$

With the weak nonlinearity assumption

$$|V_0'\|_{L^\infty}\|\phi_F\|_{L^\infty}+\left\|\left(\frac{N}{V_0(N)}\right)'\right\|_{L^\infty}\|\phi_F\|_{L^\infty}<\beta,$$

we conclude Theorem 3.5 using the Gronwall lemma and choosing

$$\alpha=\beta-\|V_0'\|_{L^\infty}\|\phi_F\|_{L^\infty}+\left\|\left(\frac{N}{V_0(N)}\right)'\right\|_{L^\infty}\|\phi_F\|_{L^\infty}.$$

□

3.3. Oscillatory states

As observed in [4], the voltage-conductance model (1.1) can produce periodic solutions which represent the spontaneous activity of the network. This desirable property also holds for other neural network models; see [6] for the Leaky Integrate&Fire population model and [21,22] for the time elapsed model.

Linear instability.

While in Subsection 3.2 we have studied the nonlinear asymptotic stability of the steady state, one can also find conditions for its instability.

The linearization of Equation (3.2) around a steady state $\bar{n}(v)$ is to find $(r(v),\mu)$ satisfying

$$\begin{cases}\frac{\partial r}{\partial t}+\frac{\partial}{\partial v}[(\bar{V}_0-v)r]+\bar{V}_0'\mu\frac{\partial \bar{n}(v)}{\partial v}+\phi_F r=0, & 0\leq v\leq V_E,\\ \mu:=\int_0^{V_E}\phi_F r dv, \qquad \int_0^{V_E} r dv=0, & \bar{V}_0 r(0)=\mu[1-\bar{V}_0'\bar{n}(0)],\end{cases}$$

with $\bar{V}_0=V_0(\bar{\mathcal{N}})$.

We look for a solution with exponential behavior in time $r(v)e^{\lambda t}$ which gives

$$\begin{cases}\lambda r+\frac{\partial}{\partial v}[(\bar{V}_0-v)r]+\bar{V}_0'\mu\frac{\partial \bar{n}(v)}{\partial v}+\phi_F r=0, & 0\leq v\leq V_E,\\ \mu:=\int_0^{V_E}\phi_F r dv, \qquad \bar{V}_0 r(0)=\mu[1-\bar{V}_0'\bar{n}(0)]. & \end{cases} \tag{3.14}$$

Because $\bar{n}(v)=0$ for $v>\bar{V}_0$, we also have $r(v)=0$ for $v>\bar{V}_0$ and it remains to solve the problem for $v\in(0,\bar{V}_0)$. Notice that the condition $\int_0^{V_E} r dv=0$ follows by integration when $\lambda\neq 0$.

Proposition 3.1. *We assume that $\phi_F(v)=\phi_1\mathbf{I}_{\{v>v1\}}$ and $\phi_1>1$. We also assume that*

$$\frac{V_0}{\bar{\mathcal{N}}_0}-\phi_1\bar{V}_0'+\bar{V}_0'\frac{\bar{\mathcal{N}}}{\bar{V}_0}(\bar{V}_0-v_1)^{\phi_1-2}<0.$$

Then there is a solution of the problem (3.14) *with* $\lambda > 0$. *In other words the steady state* $\bar{n}$ *is unstable.*

Proof. To solve this problem, we notice that $q = \frac{r}{\bar{n}}$ satisfies

$$\lambda q + (\bar{V}_0 - v)\frac{\partial q}{\partial v} + \frac{\bar{V}_0' \mu}{\bar{n}} \frac{\partial \bar{n}(v)}{\partial v} = 0,$$

and thus, using (3.2),

$$\frac{\partial (\bar{V}_0 - v)^\lambda q}{\partial v} = -(\bar{V}_0 - v)^{\lambda - 1} \frac{\bar{V}_0' \mu}{\bar{n}} \frac{\partial \bar{n}(v)}{\partial v} = \bar{V}_0' \mu (\bar{V}_0 - v)^{\lambda - 2} (\phi_F - 1),$$

$$(\bar{V}_0 - v)^\lambda q = (\bar{V}_0)^\lambda q(0) + \bar{V}_0' \mu \frac{\bar{V}_0^{\lambda - 1} - (\bar{V}_0 - v)^{\lambda - 1}}{\lambda - 1} (\langle \phi_F(v) \rangle - 1)$$

where $\langle \phi_F(v) \rangle$ ranges for some average of ϕ_F on $(0, v)$.

At this stage we recall the singularity of $\bar{n}(v) \approx q_s (V_0(\bar{\mathcal{N}}) - v)^\alpha$, $\alpha = \phi_F(\bar{V}_0) - 1 > -1$. This means that $r = q\,\bar{n}$ is integrable for $\lambda < \phi_F(\bar{V}_0)$, $1 < \phi_F(\bar{V}_0)$.

Then, eliminating μ, the parameter λ is chosen so as to satisfy

$$1 = (\bar{V}_0)^{\lambda - 1} [\frac{V_0}{\bar{\mathcal{N}}_0} - \bar{V}_0'] \int \frac{\bar{n}(v)}{(\bar{V}_0 - v)^\lambda} dv + \bar{V}_0' \int \frac{\bar{n}(v)}{(\bar{V}_0 - v)^\lambda} \frac{\bar{V}_0^{\lambda - 1} - (\bar{V}_0 - v)^{\lambda - 1}}{\lambda - 1} (\langle \phi_F(v) \rangle - 1) dv,$$

a relation that we write, with obvious notations, as

$$I(\lambda) = 1.$$

Now we assume that $\phi_F > 1$ is constant on its support. On the one hand, as $\lambda \to \phi_F$, the term $\int \frac{\bar{n}(v)}{(\bar{V}_0 - v)^\lambda} dv$ tends to $+\infty$ and $\lambda - 1 \to \phi_F - 1$ for $v \approx \bar{V}_0$. Therefore,

$$I(\lambda) \approx (\bar{V}_0)^{\lambda - 1} \frac{V_0}{\bar{\mathcal{N}}_0} \int \frac{\bar{n}(v)}{(\bar{V}_0 - v)^\lambda} dv \to +\infty \quad as \quad \lambda \to \phi_F.$$

On the other hand, as $\lambda \to 0$,

$$\bar{V}_0 I(\lambda) \approx \frac{V_0}{\bar{\mathcal{N}}_0} - \phi_F \bar{V}_0' + \bar{V}_0' (\phi_F - 1) \int \frac{\bar{n}(v)}{\bar{V}_0 - v} dv.$$

Since $\bar{n} = \frac{\bar{\mathcal{N}}}{\bar{V}_0(\bar{V}_0 - v_1)} (\bar{V}_0 - v)$, Proposition 3.1 follows by the mean value theorem. $\square$

Numerical illustration.

Numerical evidence, indicates that periodic solutions occur for the simple limiting model (1.6). We use the range of parameters produced in the previous subsection, when the firing rate ϕ_F is large enough and the nonlinear voltage $V_0(\mathcal{N})$ is stiff enough. The computed solution is depicted in the Figure 3.3 for the evolution equation (3.1). Here the choice of parameters and nonlinearities (which are far form the regimes where uniqueness of a steady state has been established) is given by the expressions

$$\phi_F(v) = 5\,\mathbf{I}_{\{v > .7\}}, \qquad V_0 = .75 + .22 \min(\mathcal{N}, 1). \tag{3.15}$$

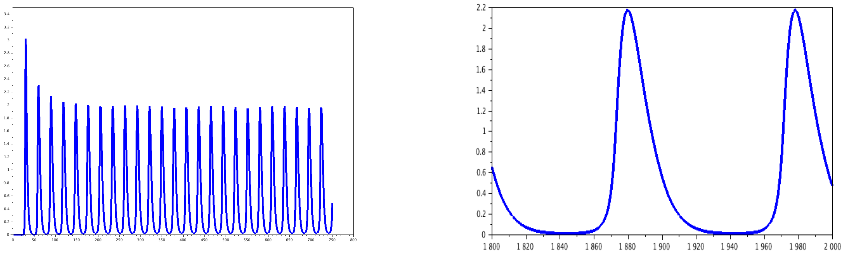

Fig. 3.3. Numerical solutions of the evolution equation (3.1) with data in (3.15). Abscissae are v. Left: firing rate $V_0(\mathcal{N})=.75+.15\frac{\mathcal{N}}{.1+\mathcal{N}}$; Right: Zoom on two oscillations.

4. Conclusion and perspectives

Neural networks are by nature highly complex systems and mean field models are a way to circumvent the modeling. In [7, 25], the authors propose a kinetic mean field equation of neural assemblies to make a fine description of the dynamic of neural networks with respect to the membrane potential and the conductance of the neurons. The patterns that emerge from those models are very rich, and exhibit oscillations, bifurcations... However, this model is very difficult to tackle both from a numerical viewpoint [4], where efficient numerical schemes are complex to implement and from a theoretical viewpoint [23], where classical methods failed due to the particular boundary conditions and the degenerate diffusion involved in the equation. To overcome those difficulties, in [7, 25], the authors propose a reduction of dimension of this equation by closure moments. In this article, we give an alternative with a new kinetic model where the singular boundary condition is replaced by an integral absorption in order to obtain more precise theoretical results and to simulate the different types of dynamics that can emerge with a relatively simple algorithm on the limiting voltage-based population equation for I&F neurons.

Several open questions about the present voltage only I&F model remain open. The first one concerns a more precise theoretical study on the mechanisms beyond the oscillations in the Integrate and Fire model presented in this equation. Indeed, to our knowledge, there do not exists theoretical results of existence of periodic solutions for this kind of PDE. However, Equation (3.1) shares, in its structure, some similarity with the time elapsed model, where we can built explicit periodic solutions (see [22]). Indeed, as for the time elapsed model, in some regimes, the total firing rate satisfy a delay type equation, which may be tractable. As an example, considering for $k\in\mathbb{N}$ big enough (let us assume to simplify $V_R=0$, $V_E=1$) and the particular function

$$\phi_F(v)=k\mathbb{I}_{v\geq\alpha},\alpha>0,\quad 0<\alpha<1,$$

using the method of characteristics, we obtain the following formula on the total firing rate of Equation (3.1)

$$\mathcal{N}(t)=k\left(1-\int_{\varphi(t)}^{t}\mathcal{N}(s)ds\right)$$

with $\varphi(t) \leq t$ such that

$$\alpha = e^{-(t-\varphi(t))} \int_0^{t-\varphi(t)} V_0(\mathcal{N}(s+\varphi(t)))e^s ds.$$

This system is however more complex than the one obtained in [22], due to its specific coupling, but may be exploitable.

Coming back to the conductance and voltage-conductance kinetic model developed in [7, 25], a second important question, concerns the theoretical study of this equation which was initiated in [23]. Indeed, beside the question of well-posedness which is rather difficult, typical questions as the asymptotic convergence to a stationary state for very weak interconnections, is not yet understood.

The standard I&F model for networks is closely related to (1.6) with two main differences. On the one hand firing is taken pointwise, rather than the nonlocal definition of firing in (1.6), which is our choice of a simplification. On the other hand noise is taken into account differently, directly by a diffusion term in the standard I&F model, rather than by dispersion of the drift terms. It is written

$$\begin{cases} \frac{\partial}{\partial t} n + \frac{\partial}{\partial v}\left[h(b\mathcal{N}(t), v)n\right] - a\frac{\partial^2 n}{\partial v^2} = \mathcal{N}(t)\delta(v - V_R), \qquad t \geq 0, v < V_E, \\ n(V_E, t) = 0, \qquad \mathcal{N}(t) = -a\frac{\partial n}{\partial v}|_{v=V_E}. \end{cases}$$

Another question is to derive this model from the voltage-conductance equation in a diffusive limit rather than an hyperbolic limit.

Acknowledgments BP has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 740623).

B.P. and D.S. acknowledge partial funding from the ANR blanche project Kibord ANR-13-BS01-0004 funded by the French Ministry of Research.

REFERENCES

[1] Vincent Bansaye, Bertrand Cloez, and Pierre Gabriel. Ergodic behavior of non-conservative semi-groups via generalized Doeblin's conditions. working paper or preprint, September 2018. 3.2

[2] Mireille Bossy, Olivier Faugeras, and Denis Talay. Clarification and complement to "Mean-field description and propagation of chaos in networks of Hodgkin-Huxley and FitzHugh-Nagumo neurons". *J. Math. Neurosci.*, 5:Art. 19, 23, 2015. 1, 1

[3] N. Brunel and V. Hakim. Fast global oscillations in networks of integrate-and-fire neurons with long firing rates. *Neural Computation*, 11:1621–1671, 1999. 2.1

[4] M. J. Cáceres, J. A. Carrillo, and L. Tao. A numerical solver for a nonlinear fokker-planck equation representation of neuronal network dynamics. *J. Comp. Phys.*, 230:1084–1099, 2011. 1, 1, 3.3, 4

[5] María J. Cáceres, José A. Carrillo, and Benoît Perthame. Analysis of nonlinear noisy integrate & fire neuron models: blow-up and steady states. *J. Math. Neurosci.*, 1:Art. 7, 33, 2011. 1

[6] María J. Cáceres and Benoît Perthame. Beyond blow-up in excitatory integrate and fire neuronal networks: refractory period and spontaneous activity. *J. Theoret. Biol.*, 350:81–89, 2014. 3.3

[7] D. Cai, L. Tao, M. Shelley, and McLaughlin D. W. An effective kinetic representation of fluctuation-driven neuronal networks with application to simple and complex cells in visual cortex. *PNAS*, 101:7757–7762, 2004. 1, 1, 1, 3, 4

[8] David Cai, Louis Tao, Aaditya V. Rangan, and David W. McLaughlin. Kinetic theory for neuronal network dynamics. *Commun. Math. Sci.*, 4(1):97–127, 2006. 1

[9] Jose Canizo and Havva Yaldas. Asymptotic behaviour of neuron population models structured by elapsed-time. *Nonlinearity*, In press. 3.2, 3.2, 3.3

[10] J. A. Carrillo, M. d. M. González, M. P. Gualdani, and M. E. Schonbek. Classical solutions for a nonlinear fokker-planck equation arising in computational neuroscience. *Comm. in Partial Differential Equations*, 38(3):385–409, 2013. 1

[11] José Antonio Carrillo, Benoît Perthame, Delphine Salort, and Didier Smets. Qualitative properties of solutions for the noisy integrate and fire model in computational neuroscience. *Nonlinearity*, 28(9):3365–3388, 2015. 1

[12] François Delarue, James Inglis, Sylvain Rubenthaler, Etienne Tanré, et al. Global solvability of a networked integrate-and-fire model of mckean–vlasov type. *The Annals of Applied Probability*, 25(4):2096–2133, 2015. 1

[13] Jean Dolbeault, Clément Mouhot, and Christian Schmeiser. Hypocoercivity for linear kinetic equations conserving mass. *Trans. Amer. Math. Soc.*, 367(6):3807–3828, 2015. 1

[14] G. Dumont and P. Gabriel. The mean-field equation of a leaky integrate-and-fire neural network: measure solutions and steady states. *ArXiv e-prints*, October 2017. 1

[15] N. Fourcaud and N. Brunel. Dynamics of the firing probability of noisy integrate-and-fire neurons,. *Neural Comp.*, 14:2057–2110, 2002. 1

[16] Pierre Gabriel. Measure solutions to the conservative renewal equation. In *CIMPA School on Mathematical Models in Biology and Medicine*, volume 62 of *ESAIM Proc. Surveys*, pages 68–78. EDP Sci., Les Ulis, 2018. 3.2

[17] Wulfram Gerstner and Werner M. Kistler. *Spiking neuron models: Single neurons, populations, plasticity*. Cambridge university press, 2002. 1

[18] Maxime Herda and L. Miguel Rodrigues. Large-Time Behavior of Solutions to Vlasov-Poisson-Fokker-Planck Equations: From Evanescent Collisions to Diffusive Limit. *J. Stat. Phys.*, 170(5):895–931, 2018. 1

[19] Pierre-Emmanuel Jabin. Macroscopic limit of Vlasov type equations with friction. *Ann. Inst. H. Poincaré Anal. Non Linéaire*, 17(5):651–672, 2000. 2.1

[20] Stéphane Mischler and Qilong Weng. Relaxation in time elapsed neuron network models in the weak connectivity regime. *ACAP*, 2018. 1

[21] Khashayar Pakdaman, Benoît Perthame, and Delphine Salort. Dynamics of a structured neuron population. *Nonlinearity*, 23(1):55–75, 2010. 1, 3.3

[22] Khashayar Pakdaman, Benoît Perthame, and Delphine Salort. Relaxation and self-sustained foscillations in the time elapsed neuron network model. *SIAM J. Appl. Math.*, 73(3):1260–1279, 2013. 1, 3.3, 4

[23] Benoît Perthame and Delphine Salort. On a voltage-conductance kinetic system for integrate & fire neural networks. *Kinet. Relat. Models*, 6(4):841–864, 2013. 1, 4

[24] J. Pham, K. Pakdaman, J. Champagnat, and J.-F. Vivert. Activity in sparsely connected excitatory neural networks: effect of connectivity. *Neural Networks*, 11:415–434, 1998. 1

[25] Aaditya V. Rangan, David Cai, and Louis Tao. Numerical methods for solving moment equations in kinetic theory of neuronal network dynamics. *J. Comput. Phys.*, 221(2):781–798, 2007. 1, 1, 1, 3, 4

[26] Aaditya V. Rangan, Gregor Kova ˇ cič, and David Cai. Kinetic theory for neuronal networks with fast and slow excitatory conductances driven by the same spike train. *Phys. Rev. E (3)*, 77(4):041915, 13, 2008. 1, 1

[27] Cédric Villani. Hypocoercivity. *Mem. Amer. Math. Soc.*, 202(950):iv+141, 2009. 1