Population density models of integrate-and- fire neurons with jumps: Well-posedness

Grégory Dumont, Jacques Henry

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Well-posedness

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Abstract In this paper we study the well-posedness of different models of population of leaky integrate-and-fire neurons with a population density approach. The synaptic interaction between neurons is modeled by a potential jump at the reception of a spike. We study populations that are self excitatory or self inhibitory. We distinguish the cases where this interaction is instantaneous from the one where there is a repartition of conduction delays. In the case of a bounded density of delays both excitatory and inhibitory population models are shown to be well-posed. But without conduction delay the solution of the model of self excitatory neurons may blow up. We analyze the different behaviours of the model with jumps compared to its diffusion approximation.

Keywords Population density approach · Neural network · Coupled population · Integrate-and-fire · Nonlocal nonlinear partial differential equation · Well-posedness

1 Introduction

The time required by a computer to simulate a realistic model of networks of neurons taking into account each neuron seaparately and their connections is really important. The main reason is that even a simple model of a small part of the brain could contain tens of thousands of neurons and hundreds of thousands of synapses. To facilitate the simulation of large networks of neurons, a population density approach has been introduced in [13] and in [20] more than a decade ago. Starting from an ordinary differential equation modeling the dynamics of a single neuron, the leaky integrate-and-fire model, and under the main assumption that there is a large population of neurons all identical and with similar connections, the authors succeeded to derive a one dimensional partial differential equation (PDE) which describes the full population. More precisely, since the potential $v(t)$ is the state variable for a single neuron, they obtained a PDE giving the evolution in time of $\rho(t, v)$, the density of neuron at state v, at time t. Of course this is less informative than giving the state of each neuron in the population. Nevertheless interesting behaviours of the assembly of neurons as for example the synchronisation can be studied by this kind of model. Furthermore this modeling is completely insensitive to the number of neurons in the population.

Big efforts have been made, using finite difference or finite volume schemes as in [19] and [20], to reduce the compuational burden needed to solve numerically the PDE. It has also been proposed a more stable scheme using a discretization on the caracteristic curve in [12]. Therefore the formulation of the problem as a PDE has proved its interest for the simulation of a massive assembly of neurons. As it has been noticed in [19], [7], [10] and [20], the simulation of such a PDE is uncomparably faster than the use of a Monte Carlo simulation still privileged by biologists, (see [19] and [12] for a review of this subject).

G. Dumont
CNRS, IMB Bordeaux
E-mail: gregory.dumont@inria.fr

J. Henry
INRIA Bordeaux sud ouest, IMB Bordeaux
E-mail: jacques.henry@inria.fr

Today this approach has been enlarged: using more realistic models with two or three state variables describing the dynamics of a single neuron, one can derive a two or three dimensional PDE, see for instance [4], [15] and [9]. Such PDEs are obviously hard to simulate and hard to analyse. A lot of deep mathematical tools were used to moderate the computational time such as moment reduction [15], phase reduction [9] and [7]. In this paper we will study only one dimensional models, namely integrate-and-fire models where the only state variable is the potential of the neuron. In these models we consider that the reception of a spike at a synapse creates a potential jump. At the level of the population this leads to non local PDEs.

If the first goal of the population density approach was to reduce the computational time to simulate a huge population of neurons, the interest of the PDE approach seems today more related to understanding the behavior of a coupled population of neurons. As we know, see [10], [7], [8], [21], [22] and [9], coupled populations of neurons can exhibit various behaviours. For example oscillations of the activity of neuronal populations at various frequencies can be observed in different brain areas in vivo in normal as well as pathological condition. This can be interpreted as a kind of synchronisation. One can find in [8] and [21] and the references therein a deep investigation of occurence of synchronisation with a PDE approach. There are few results on a nonlinear analysis of the synchronisation [21], [26], [9], [23] and [10]. In this paper we will focus on the study of the well-posedness for various population density models of integrate-and-fire neurons. We give some mathematical results for the existence, the uniqueness and the positivity of the solution, but we also analyze situations were we fail to obtain the well-posedness.

The paper will be as follows. In the first part of the paper we consider a coupled population of self-excitatory integrate-and-fire neurons. We will show that the model is well-posed under some assumptions and we will take care of the special case when there is no conduction delay in the feedback: it can be ill-posed. The second part will deal with a coupled population of inhibitory integrate-and-fire neurons. As in the excitatory case, we will present the PDE of the model. We will then show an existence result for the model. In the last section we discuss the situations of blow up of the activity in relation with the synchronization. We also discuss the interest of the model with a diffusion approximation of potential jumps. Numerical simulations of the models are presented.

2 Populations of self-excitatory neurons

In this section, we will show the existence of a unique positive solution for the model of a large population of excitatory leaky integrate-and-fire (LIF) neurons.

2.1 The density of population model

Let us first recall the derivation of the partial differential equation used to model large populations of integrate-and-fire neurons structured by their potential as in [20].

First of all, we recall that the integrate-and-fire model is an ordinary differential equation describing the subthreshold dynamics of a single neuron. This ordinary differential equation, (see [11] for instance), represents the state of a (normalized) leaky capacitor receiving charge impulses and is given by

$$\begin{cases} \frac{d}{dt}v(t) = -v(t) + h\sum_{j=0}^{+\infty}\delta(t-t_j) \\ \text{If} \quad v > 1 \quad \text{then} \quad v = v_r, \end{cases} \tag{1}$$

where $v(t)$ represents the potential of the neuron at time t (normalized to the interval $[0,1]$). The t_j are the arrival times of external impulses. Here we model the effect of the reception of a spike at a synapse of the neuron by a jump of size h of the potential v. The jump is positive (resp. negative) when the spike is received from an excitatory (resp. inhibitory) neuron. Due to the incoming impulses, and consequently the potential jump process, v can cross the threshold potential normalized to 1. In this situation the neuron fires emitting a spike and is instantly reset to v_r, the reset potential with $0 < v_r < 1$. See [1] for a biological motivation and [2] for a large mathematical review of this model. See also [11] for other spiking models similar to (1).

Assuming that all the neurons of the population are identical, we can derive from (1) a partial differential equation which gives the evolution in time of the population density of neurons $\rho(t,v)$ at potential

v and at time t in the limit of an infinite number of neurons. In others words we have (normalizing the total population to 1)

$$\int_{v_1}^{v_2} \rho(t,v)\, dv = \{\text{Proportion of neurons with potential } v \in [v_1, v_2] \text{ at time } t\}\,.$$

The flux of spikes reaching the population is considered as deterministic and let $\sigma(t)$ be the reception rate by each neuron. The equation for the density is a conservation law (see [19], [10], [20] and [4] for instance) taking into account three fluxes: a drift term due to the continuous evolution in the LIF model, a flux due to the part of the population jumping when receiving excitatory impulses, a flux due to firing neurons that are reset to v_r.

$$\frac{\partial}{\partial t}\rho(t,v) - \overbrace{\frac{\partial}{\partial v}(v\rho(t,v))}^{\text{Integrate-and-fire}} + \sigma(t)\overbrace{(\rho(t,v) - \rho(t,v-h))}^{\text{Excitation}} = \delta(v-v_r)\,\sigma(t)\overbrace{\int_{1-h}^{1}\rho(t,w)\,dw}^{\text{Reset}}\,. \qquad (2)$$

Let us remark that the excitation term can be put under a divergence form for an excitation flux Φ_e

$$\Phi_e(t,v) = \sigma(t)\int_{v-h}^{v}\rho(t,w)dw.$$

For the well definition of (2) we extend ρ by 0 for $v < 0$. We impose the drift flux to be zero at the threshold

$$\rho(t,1) = 0.$$

Using the boundary condition, one can check easily the conservation property of the equation (2) by integrating it on the interval $(0,1)$,

$$\frac{d}{dt}\int_{0}^{1}\rho(t,w)\,dw = 0, \qquad (3)$$

so that if the initial condition satisfies

$$\int_{0}^{1}\rho_0(v)\,dv = 1, \qquad (4)$$

the solution of the nonlinear problem (10) satisfies the normalisation condition

$$\int_{0}^{1}\rho(t,w)\,dw = 1. \qquad (5)$$
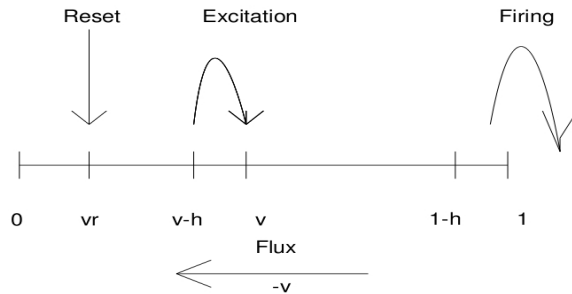
Fig. 1 The evolution of the density $\rho(t,v)$ at potential v is due to a drift term and to jumps from $v-h$. Due to the excitation the neuron can cross the threshold, here normalized to 1, and is reset to the potential v_r.

The impulse reception rate per neuron $\sigma(t)$ is the sum of the external impulses $\sigma_0(t)$ arriving from an other population of neurons, and the impulses caused by the population itself which is supposed to be self excitatory. We shall consider two cases: either we neglect the conduction delay within the population and the self excitation is instantaneous or we take into account a conduction delay with a density of

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Fig. 2 Scheme for the evolution of a population under an external influence with conduction delay. The population receives a known external influence $\sigma_0(t)$ from an excitatory population of neurons, and produces an activity $r(t)$, also called firing rate of the population. The expression of $r(t)$ is given in (8). If the population is coupled, $J \neq 0$, the own activity of the population $r(t)$ will participate to the excitation as a feedback which is expressed with a delay kernel α. The feedback is then given by $J \int_0^t \alpha(u) r(t-u)\, du$.

Fig. 3 Scheme for the evolution of a population under an external influence without conduction delay. The population receives a known external influence $\sigma_0(t)$, and produces an activity $r(t)$, also called firing rate of the population as in figure 2. We suppose now that there is no conduction delay: the feedback is instantaneous and given by $Jr(t)$.

delay function α. Let $r(t)$ be the firing rate of the population that is the flux through the threshold and J the average number of presynaptic neurons per neuron. With delay (see Figure 2), $\sigma(t)$ is given by

$$\sigma(t) = \sigma_0(t) + J \int_0^t \alpha(u) r(t-u)\, du, \tag{6}$$

$$\int_0^\infty \alpha(u)\, du = 1, \tag{7}$$

where the firing rate r is given by

$$r(t) = \sigma(t) \int_{1-h}^1 \rho(t,w)\, dw. \tag{8}$$

Without delay (see Figure 3), $\sigma(t)$ is given by

$$\sigma(t) = \sigma_0(t) + Jr(t). \tag{9}$$

The firing rate of the population (or activity) is an important output of the model for neuroscientists because it can be measured easily (see [8], [2] and [7] for more details about the firing rate of population of integrate-and-fire neurons and [8] for other models).

We finally give the model in its complete form

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) = \sigma(t)\left(\rho(t,v-h) - \rho(t,v)\right) \\
\qquad\qquad\qquad\qquad + \sigma(t)\delta(v-v_r)\displaystyle\int_{1-h}^1 \rho(t,w)\, dw \\
\sigma(t) = \sigma_0(t) + J\int_0^t \alpha(u) r(t-u)\, du \quad \text{with conduction delay, or} \\
\sigma(t) = \sigma_0(t) + Jr(t) \quad \text{without conduction delay} \\
r(t) = \sigma(t) \int_{1-h}^1 \rho(t,w)\, dw \\
\rho(t,1) = 0 \\
\rho(0,.) = \rho_0 \in L^1_+(0,1).
\end{cases} \tag{10}
$$

2.2 Well-posedness in the case with a conduction delay

We state now the main result for the model (10) with conduction delay.

Theorem 1 *Assuming that α belongs to $L^\infty(0, \infty)$ and satisfies (7), then for all $\sigma_0 \in C(\mathbb{R}_+, \mathbb{R}_+)$, for all $J \geq 0$ there exists a unique positive solution $\rho \in C\left(\mathbb{R}_+, L^1_+(0,1)\right)$ to Problem (10) with conduction delay. Furthermore the following estimate holds for the firing rate r given by (8): for $J \geq 0$*

$$r(t) \leq \|\sigma_0\|_\infty \exp(J\|\alpha\|_\infty t),$$

and for $J < 1$

$$r(t) \leq \frac{\|\sigma_0\|_\infty}{1 - J}.$$

In what follows, we will give a proof of Theorem 1 introducing a new problem with a truncation of the reception rate σ defined by the function D

$$D(x) = \min(M, \max(0, x)), \tag{11}$$

and M an arbitrary positive constant. It is clear that the function D satisfies the following properties

$$0 \leq D(x) \leq M, \quad |D(x_1) - D(x_2)| \leq |x_1 - x_2|.$$

This truncation done for mathematical purpose keeps a physical meaning to the reception rate which remains non negative and bounded. The new problem after truncation is

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) = D(\sigma(t))\left(\rho(t, v-h) - \rho(t,v)\right) \\
\qquad\qquad\qquad\qquad\qquad + D(\sigma(t))\delta(v - v_r)\displaystyle\int_{1-h}^{1} \rho(t,w)\,dw \\
\sigma(t) = \sigma_0(t) + J\int_0^t \alpha(u) r(t-u)\,du \\
r(t) = D(\sigma(t))\int_{1-h}^{1} \rho(t,w)\,dw \\
\rho(t,1) = 0 \\
\rho(0,.) = \rho_0 \in L^1_+(0,1).
\end{cases}
\tag{12}
$$

One can notice that if we suceed in proving the well-posedness of Problem (12) and if

$$0 \leq \sigma(t) \leq M,$$

then the solution ρ of (12) is indeed a solution of (10).

Proposition 1 *Let M be an arbitrary positive constant and let D be the function defined by (11), assuming that α belongs to $L^\infty(0, \infty)$ and satisfies (7), then for all $\sigma_0 \in C(\mathbb{R}_+, \mathbb{R}_+)$, for all $J \geq 0$ there exists a unique positive solution $\rho \in C\left(\mathbb{R}_+, L^1_+(0,1)\right)$ to Problem (12).*

We proceed in two steps: first we prove the result in the linear uncoupled case and then we will derive a proof for the coupled nonlinear model.

2.2.1 Linear case

The linear uncoupled case corresponds to $J = 0$. The function $\sigma(t) = \sigma_0(t) \geq 0$ is now given in $C([0,T])$. The problem then reduces to the following nonlocal linear PDE

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) = D(\sigma(t))\left(\rho(t, v-h) - \rho(t,v)\right) \\
\qquad\qquad\qquad\qquad\qquad + D(\sigma(t))\delta(v - v_r)\displaystyle\int_{1-h}^{1} \rho(t,w)\,dw \\
\rho(t,1) = 0 \\
\rho(0,v) = \rho_0(v).
\end{cases}
\tag{13}
$$

Let X be the Banach space endowed with the norm $\|\cdot\|_X$ given by

$$X = C\left([0,T], L^1(0,1)\right), \quad \|u\|_X = \sup_{0 \leq s \leq T} \|u(s)\|_{L^1(0,1)}.$$

Proposition 2 *For all function $\sigma \in C(0, +\infty), \sigma(t) \geq 0$ there exists an unique positive solution ρ in X to Problem (13).*

Proof In order to prove this result, we follow the idea presented in [23] for linear nonlocal partial differential equations. We define on the space $(X, \|\cdot\|_X)$ the mapping

$$\Lambda : \pi \longmapsto \rho,$$

where ρ satisfies the following equation

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t, v) - \dfrac{\partial}{\partial v}(v\rho(t, v)) + D(\sigma(t))\rho(t, v) = D(\sigma(t))\pi(t, v - h) \\
\qquad\qquad\qquad\qquad\qquad + D(\sigma(t))\delta(v - v_r) \displaystyle\int_{1-h}^{1} \pi(w)\,dw \\
\rho(t, 1) = 0 \\
\rho(0, .) = \rho_0 \in L^1_+(0; 1).
\end{cases}
\tag{14}
$$

Let $\rho_1, \rho_2, \pi_1, \pi_2$ be functions in X such that

$$\rho_1 = \Lambda(\pi_1), \quad \rho_2 = \Lambda(\pi_2).$$

Let ρ and π be defined by

$$\rho = \rho_1 - \rho_2, \quad \pi = \pi_1 - \pi_2.$$

The mapping Λ being affine, ρ is solution of the following partial differential equation

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t, v) - \dfrac{\partial}{\partial v}(v\rho(t, v)) + D(\sigma(t))\rho(t, v) = D(\sigma(t))\pi(t, v - h) \\
\qquad\qquad\qquad\qquad\qquad + D(\sigma(t))\delta(v - v_r) \displaystyle\int_{1-h}^{1} \pi(w)\,dw \\
\rho(t, 1) = 0 \\
\rho(0, .) = 0.
\end{cases}
\tag{15}
$$

We can check that $|\rho(t, v)|$ satisfies the following inequality

$$
\frac{\partial}{\partial t}|\rho(t, v)| - \frac{\partial}{\partial v}(v|\rho(t, v)|) + D(\sigma(t))|\rho(t, v)| \leq D(\sigma(t))|\pi(t, v - h)|
$$
$$
+ D(\sigma(t))\delta(v - v_r) \int_{1-h}^{1} |\pi(w)|\,dw.
$$

Integrating on $[0, 1]$, we obtain

$$
\frac{d}{dt}\int_0^1 |\rho(t, w)|\,dw \leq D(\sigma(t)) \int_0^1 |\pi(t, w)|\,dw
$$
$$
\leq M \int_0^1 |\pi(t, w)|\,dw.
$$

Integrating in time on $[0, t]$, we obtain

$$
\int_0^1 |\rho(t, w)|\,dw \leq TM \sup_{0 \leq s \leq T} \int_0^1 |\pi(s, w)|\,dw,
$$

and taking the supremum, we have for T sufficiently small

$$\|\rho\|_X < \|\pi\|_X.$$

Because the same argument can be iterated on $[T, 2T], [2T, 3T]$ ..., we deduce the existence of an unique solution ρ to the Problem (13) by the use of the Banach-Picard fixed point theorem. As Λ given by (14) preserves the positivity, it is possible to construct a Picard iteration starting from a non negative function and thus ρ is non negative.

2.2.2 Nonlinear case

We define on the space $C([0,T])$ the mapping G

$$G(\sigma)(t) = D(\sigma(t)) \int_{1-h}^{1} \rho(t,w)\, dw,$$

where ρ is the solution of the linear problem (13) associated to σ.

Proposition 3 *The mapping G is locally Lipschitz continuous:*

$$\|G(\sigma_1) - G(\sigma_2)\|_{\infty} \leq (2MT + 1)\|\sigma_1 - \sigma_2\|_{\infty}.$$

Proof For $\sigma_1, \sigma_2 \in C([0,T])$ we denote $\rho_1, \rho_2 \in C([0,T], L^1(0,1))$ the associated solution of the linear problem (13). We denote

$$\rho = \rho_1 - \rho_2,$$

we can check that ρ satisfies the following PDE

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) = D(\sigma_1(t))\left(\rho(t,v-h) - \rho(t,v)\right) \\
\qquad\qquad\qquad + D(\sigma_1(t))\delta(v - v_r)\displaystyle\int_{1-h}^{1}\rho(t,w)\, dw \\
\qquad + \left(D(\sigma_1(t)) - D(\sigma_2(t))\right)\left(\rho_2(t,v-h) - \rho_2(t,v)\right) \\
\qquad + \left(D(\sigma_1(t)) - D(\sigma_2(t))\right)\delta(v - v_r)\displaystyle\int_{1-h}^{1}\rho_2(t,w)\, dw \\
\rho(t,1) = 0 \\
\rho(0,.) = 0.
\end{cases}
$$

Using the technique of Proposition 6.3 in [23] we derive an estimate on $|\rho(t,v)|$. We have

$$
\frac{\partial}{\partial t}|\rho(t,v)| - \frac{\partial}{\partial v}(v|\rho(t,v)|) + D(\sigma_1(t))|\rho(t,v)| \leq D(\sigma_1(t))|\rho(t,v-h)|
$$
$$
+ D(\sigma_1(t))\delta(v - v_r)\int_{1-h}^{1}|\rho(t,w)|\, dw
$$
$$
+ |D(\sigma_1(t)) - D(\sigma_2(t))||\rho_2(t,v-h) - \rho_2(t,v)|
$$
$$
+ |D(\sigma_1(t)) - D(\sigma_2(t))|\delta(v - v_r)\int_{1-h}^{1}|\rho_2(t,w)|\, dw.
$$

Integrating with respect to v on $[0,1]$ we get

$$\frac{d}{dt}\int_0^1|\rho(t,v)|\, dv \leq 2|D(\sigma_1(t)) - D(\sigma_2(t))|\int_0^1|\rho_2(t,v)|\, dv.$$

Integrating on $(0,t)$, we have

$$\int_0^1|\rho(t,v)|\, dv \leq 2T\|\sigma_1 - \sigma_2\|_{\infty}.$$

Now we can conclude

$$|G(\sigma_1)(t) - G(\sigma_2)(t)| = |D(\sigma_1(t))\int_{1-h}^{1}\rho_1(t,w)\, dw - D(\sigma_2(t))\int_{1-h}^{1}\rho_2(t,w)\, dw|$$

$$= |\frac{D(\sigma_1(t)) + D(\sigma_2(t))}{2}\int_{1-h}^{1}\rho(t,w)\, dw + (D(\sigma_1(t)) - D(\sigma_2(t)))\int_{1-h}^{1}\frac{\rho_1(t,w) + \rho_2(t,w)}{2}\, dw|$$

$$\leq \frac{|D(\sigma_1(t))| + |D(\sigma_2(t))|}{2}\int_0^1|\rho(t,w)|\, dw + |D(\sigma_1(t)) - D(\sigma_2(t))|$$

$$\leq (2MT + 1)\|\sigma_1 - \sigma_2\|_{\infty}.$$

Hence we have

$$\|G(\sigma_1) - G(\sigma_2)\|_\infty \leq (2MT + 1)\|\sigma_1 - \sigma_2\|_\infty.$$

We now prove Proposition 1.

Proof For some $T > 0$, we consider the solution of (13) on $[0, T]$. We define on $C([0, T])$ the mapping F

$$F(\sigma)(t) = \sigma_0(t) + J \int_0^t \alpha(u) r(t - u) \, du, \tag{16}$$

with

$$r(t) = D(\sigma(t)) \int_{1-h}^1 \rho(t, w) \, dw,$$

and ρ the solution to the linear problem (13) on $[0, T]$. From what we have done in the previous section, we know that, for a given σ, there exists a unique solution $\rho \in C([0, T], L_+^1(0, 1))$ to (13). Then F is a well defined mapping for which we are seeking a fixed point. Let σ_1, σ_2 be in $C([0, T])$ and ρ_1, ρ_2 the corresponding solution of the linear problem (13) with firing rates r_1, r_2, we have

$$|F(\sigma_1)(t) - F(\sigma_2)(t)| \leq J \int_0^t |\alpha(u)| |r_1 - r_2|(t - u) \, du$$

$$\leq J\|r_1 - r_2\|_\infty \int_0^t |\alpha(u)| \, du$$

$$\leq J\|r_1 - r_2\|_\infty \|\alpha\|_\infty T.$$

Then owing to Proposition 3 we obtain that

$$|F(\sigma_1)(t) - F(\sigma_2)(t)| \leq J\|\alpha\|_\infty T(2MT + 1).$$

We can find T such that F is a contraction. By the Banach-Picard theorem there is a fixed point of F. The same argument can be iterated on $[T, 2T]$: in fact in the new definition of F on this interval there is a part depending on r in the interval $[0, T]$ which is known and can be included in σ_0. The reasoning can be iterated which ends the proof of Proposition 1.

We now prove Theorem 1.

Proof Let $T > 0$, from Proposition 1 we know that there exists an unique solution to Problem (12). Let us show now that we can choose M such that the corresponding σ on $[0, T]$ given by Proposition 1 is less than M. Then the solution of Problem (12) is the unique solution of Problem (10) with conduction delay.

We fix the constant M of the truncation function D such that

$$M \geq \|\sigma_0\|_\infty \exp\left(J\|\alpha\|_\infty T\right).$$

From Proposition 1, we know that σ satisfies for $t \in [0, T]$

$$\sigma(t) = \sigma_0(t) + J \int_0^t |\alpha(t - u) D(\sigma(u)) \int_{1-h}^1 \rho(u, w) \, dw| \, du,$$

and thus, using the definition of D given by (11), we get

$$|\sigma(t)| \leq |\sigma_0(t)| + J \int_0^t |\alpha(t - u) \sigma(u) \int_{1-h}^1 \rho(u, w) \, dw| \, du$$

$$\leq \|\sigma_0\|_\infty + J\|\alpha\|_\infty \int_0^t |\sigma(u)| \, du.$$

Using Gronwall's inequality

$$|\sigma(t)| \leq \|\sigma_0\|_\infty \exp\left(J\|\alpha\|_\infty t\right) \leq \|\sigma_0\|_\infty \exp\left(J\|\alpha\|_\infty T\right) \leq M.$$

Consequently we have the first estimate of Theorem 1 and

$$D(\sigma(t)) = \sigma(t),$$

which shows that the solution of the problem (12) on $[0, T]$ is actually the solution of (10). Let us remark that the estimate on the firing rate that can be deduced from the previous inequality, depends exponentially on $\sup \alpha$ and becomes useless in the case with no conduction delay.

Let us show that in the particular case of J smaller than 1, we can derive an other estimate independent of the time t. We have

$$\sigma(t) = \sigma_0(t) + J \int_0^t |\alpha(u)\sigma(t-u) \int_{1-h}^1 \rho(t-u,w)\,dw|\,du,$$

and thus

$$|\sigma(t)| \leq \|\sigma_0\|_\infty + J\|\sigma\|_\infty \int_0^t \alpha(u)du$$

$$\leq \|\sigma_0\|_\infty + J\|\sigma\|_\infty.$$

This gives the desired estimate and ends the proof of Theorem 1.

2.2.3 Numerical simulations

We present in Figure 4 some simulations where all the mechanisms of the equation take place. They show the evolution in time of the potential distribution of the neuron population. In all the plots there are two curves: the black curve corresponding to a finite volume scheme discretisation of (10) and the red curve to a Monte Carlo simulation of the evolution of the assembly of neurons (see [20], [19] and [12] for the numerical schemes). The upper left plot of figure 4 represents the initial repartition ρ_0 which is a gaussian. Under the influence of external impulses with rate $\sigma_0(t)$, taken constant in the simulation, the density function ρ becomes positive near the threshold value, between $1 - h$ and 1. Then a positive quantity gets out of the domain and is reset to v_r the reset potential, see figure 3. This effect can be seen in the upper right plot of figure 4, where a bump is present at v_r. Due to the jump process, we can see in the middle plots of figure 4 that this bump propagates to $v_r + h$, $v_r + 2h$ and so on ... Finally the repartition tends to stabilize to a steady state which can be seen in the lower left plot of figure 4. In [26] one can find other behaviours of (10). We finally show, in the lower right plot of figure 4 the evolution in time of the activity of the population given by (8).

2.3 The case without conduction delay

In the current litterature related to this topic, (see for instance [9], [20], [26], [7] and [13] and the refences therein) the model (10) is frequently written without a conduction delay. The firing rate of the population $r(t)$ is supposed to excite instantly the population as a feedback. It was already noticed in [20] that a blow up may happen in finite time. In this section, we are going to show that without delay in the feedback the model is well-posed just for a weakly coupled population of neurons. Now model (10) reads

$$\begin{cases} \dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) = \sigma(t)\left(\rho(t,v-h) - \rho(t,v)\right) \\ \qquad\qquad\qquad\qquad + \sigma(t)\delta(v-v_r)\displaystyle\int_{1-h}^1 \rho(t,w)\,dw \\ \sigma(t) = \sigma_0(t) + Jr(t) \\ r(t) = \sigma(t)\int_{1-h}^1 \rho(t,w)\,dw \\ \rho(t,1) = 0 \\ \rho(0,.) = \rho_0 \in L_+^1(0;1). \end{cases} \tag{17}$$

The reception rate can be computed as

$$\sigma(t) = \frac{\sigma_0(t)}{1 - J\int_{1-h}^1 \rho(t,w)\,dw}. \tag{18}$$
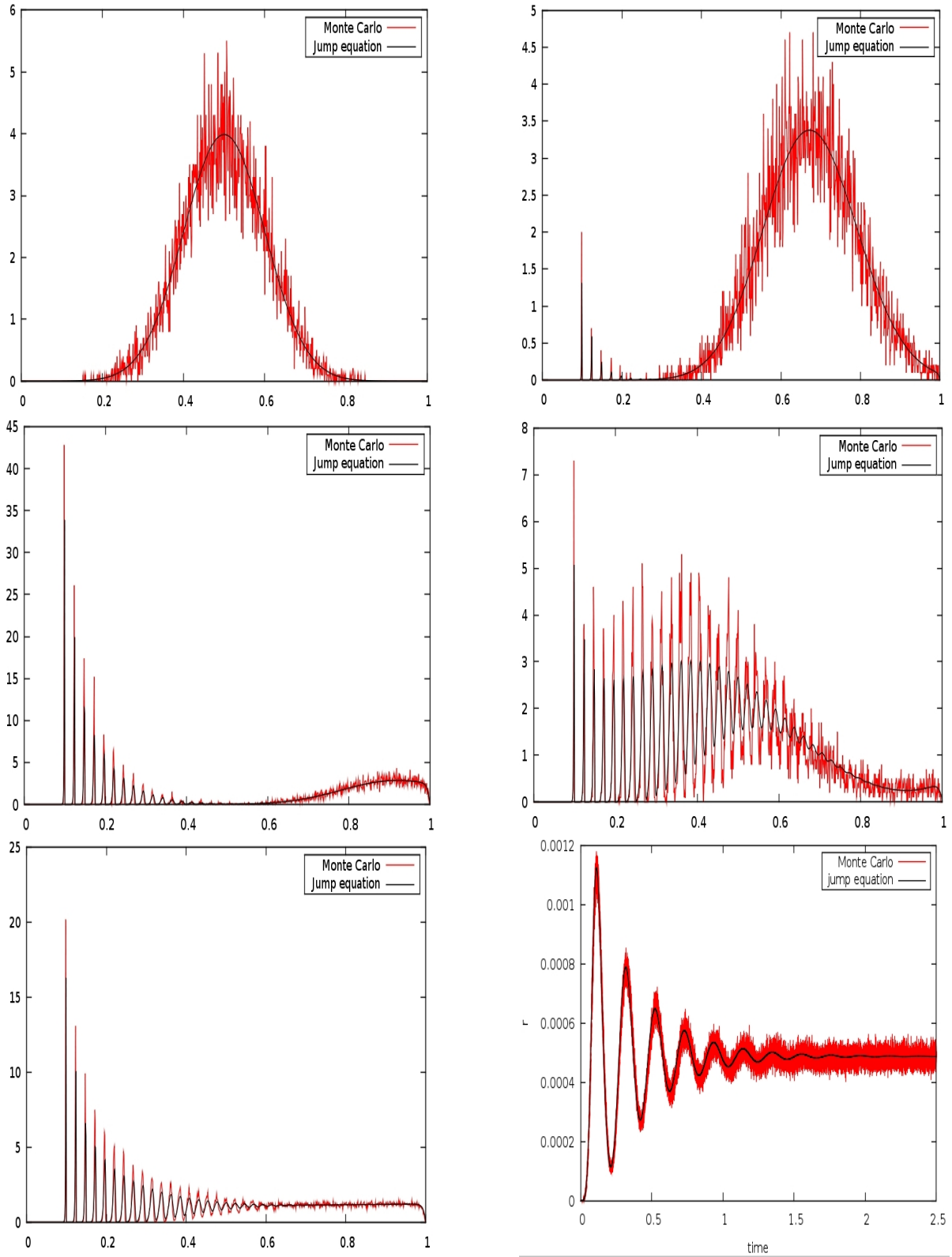
Fig. 4 Simulation of the nonlinear PDE (10), comparison between a Monte Carlo approach, red curve, and the PDE approach, black curve. A gaussian repartition was taken as initial repartition ρ_0, the external influence $\sigma_0(t)$ was taken constant $\sigma_0 = 50$, the potential jump size $h = 0.025$, the reset potential $v_r = 0.1$, the delay kernel $\alpha(u) = \delta(u - \Delta)$ with $\Delta = 5$, the coupling parameter $J = 0.5$.

This formula is singular if the denominator of the right hand side is zero. If J is larger than one which means that on average, each neuron receives impulse from more than one presynaptic neuron, one can find an initial condition ρ_0 such that the denominator is zero. This means an instantaneous blow up. We are now interested to show that the model is nevertheless well-posed for J strictly less than 1. We have the following theorem using some ideas that are presented in [24] and [22].

Theorem 2 *For all $\sigma_0 \in C(\mathbb{R}_+, \mathbb{R}_+)$ and for all $J < 1$, there exists a unique positive solution ρ belonging to $C\left(\mathbb{R}_+, L^1_+(0,1)\right)$ to the Problem (17). Furthermore the firing rate r given by (8) remains bounded on $\mathbb{R}_+$ and we have*

$$r(t) \le \frac{\|\sigma_0\|_\infty}{1 - J}.$$

To prove this result we introduce a truncation of the reception rate by D the funtion given by (11).

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) = D(\sigma(t))\left(\rho(t,v-h) - \rho(t,v)\right) \\
\qquad\qquad\qquad\qquad\qquad + D(\sigma(t))\delta(v-v_r)\displaystyle\int_{1-h}^1 \rho(t,w)\,dw \\
\sigma(t) = \sigma_0(t) + Jr(t) \\
r(t) = D(\sigma(t))\int_{1-h}^1 \rho(t,w)\,dw \\
\rho(t,1) = 0 \\
\rho(0,.) = \rho_0 \in L^1_+(0,1).
\end{cases}
\tag{19}
$$

Proof We introduce on the Banach space $C([0,T])$ the following mapping H

$$H(\sigma)(t) = \sigma_0(t) + Jr(t), \tag{20}$$

with

$$r(t) = D(\sigma(t))\int_{1-h}^1 \rho(t,w)\,dw,$$

where ρ is the solution to the linear problem (13) on $[0,T]$, given $\sigma(t)$ on $[0,T]$. As previously we are looking for a fixed point of H.

Let σ_1 and σ_2 be in $C([0,T])$. From Proposition 3 we have

$$\|H(\sigma_1) - H(\sigma_2)\|_\infty \le J(2MT+1)\|\sigma_1 - \sigma_2\|_\infty,$$

so that for all J strictly less than 1, one can always find T such that H is a contraction, and the argument can be iterated on $[T, 2T]$, $[2T, 3T]$ ... Let us show that for M sufficiently large the truncation D has no effect. We choose D as defined in (11) such that

$$M > \frac{\|\sigma_0\|_\infty}{1 - J},$$

then we have

$$
\begin{aligned}
\sigma(t) &= \sigma_0(t) + JD(\sigma(t))\int_{1-h}^1 \rho(t,w)\,dw \\
&\le \|\sigma_0\|_\infty + J\sigma(t).
\end{aligned}
$$

For $J < 1$ we get

$$\sigma(t) \le \frac{\|\sigma_0\|_\infty}{1 - J} < M,$$

which gives the desired estimate and ends the proof.

11

3 Population of self-inhibitory neurons

In this section, we consider a population of self-inhibitory neurons which means that each neuron when receiving an action potential emitted by a neuron of the population jumps from potential v to $v - h$ ($h > 0$). Furthermore we suppose that the population receives impulses from an external activating population at a given rate $\sigma(t)$. Due to this activation neurons may reach the threshold. The LIF model for one neuron now reads

$$\begin{cases} \frac{d}{dt} v(t) = -v(t) + h \sum_{j=1}^{+\infty} \delta(t - t_j) - h \sum_{k=1}^{+\infty} \delta(t - t_k) \\ \text{If} \quad v \geq 1 \quad \text{then} \quad v = v_r, \end{cases} \qquad (21)$$

where $v(t)$ is the potential of the neuron at time t, t_k are the spike times of the neurons of the population and t_j are those of the activating neurons of the external population. Let $I(t)$ be the reception rate by a neuron of the population of inhibitory impulses from the same population. The population density evolves under the mechanisms described in Figure 5. The conservation law yields

$$\frac{\partial}{\partial t} \rho(t, v) - \overbrace{\frac{\partial}{\partial v} (v \rho(t, v))}^{\text{integrate-and-fire}} + \sigma(t) \overbrace{(\rho(t, v) - \rho(t, v - h))}^{\text{Excitation}} = I(t) \overbrace{(\rho(t, v + h) - \rho(t, v))}^{\text{Inhibition}}$$

$$+ \delta(v - v_r) \, \sigma(t) \underbrace{\int_{1-h}^{1} \rho(t, w) \, dw}_{\text{Reset}}$$

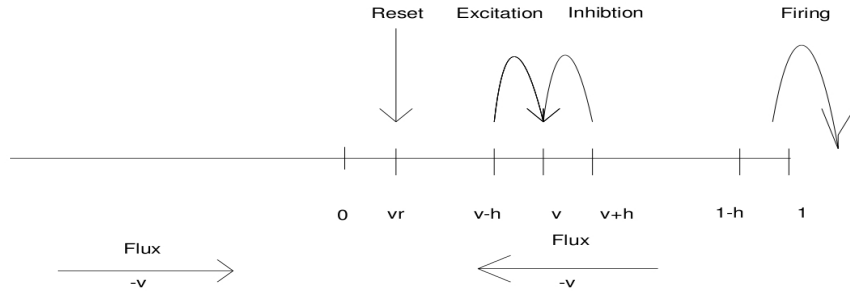Due to the negative jump of potential by inhibition, the population is distributed along the region

Fig. 5 The dynamics of the density $\rho(t, v)$ at potential v is due to a drift term, jumps from $v + h$ (inhibition), from $v - h$ (excitation) and the disappearing at the threshold with reset at v_r.

$(-\infty, 1)$. By the conservation of the total population we have

$$\int_{-\infty}^{1} \rho(t, w) \, dw = 1.$$

As previously we impose a zero incoming flux at the threshold, but we impose also the same at $v = -\infty$. We consider both cases of an instant propagation of the impulses within the population or of propagation
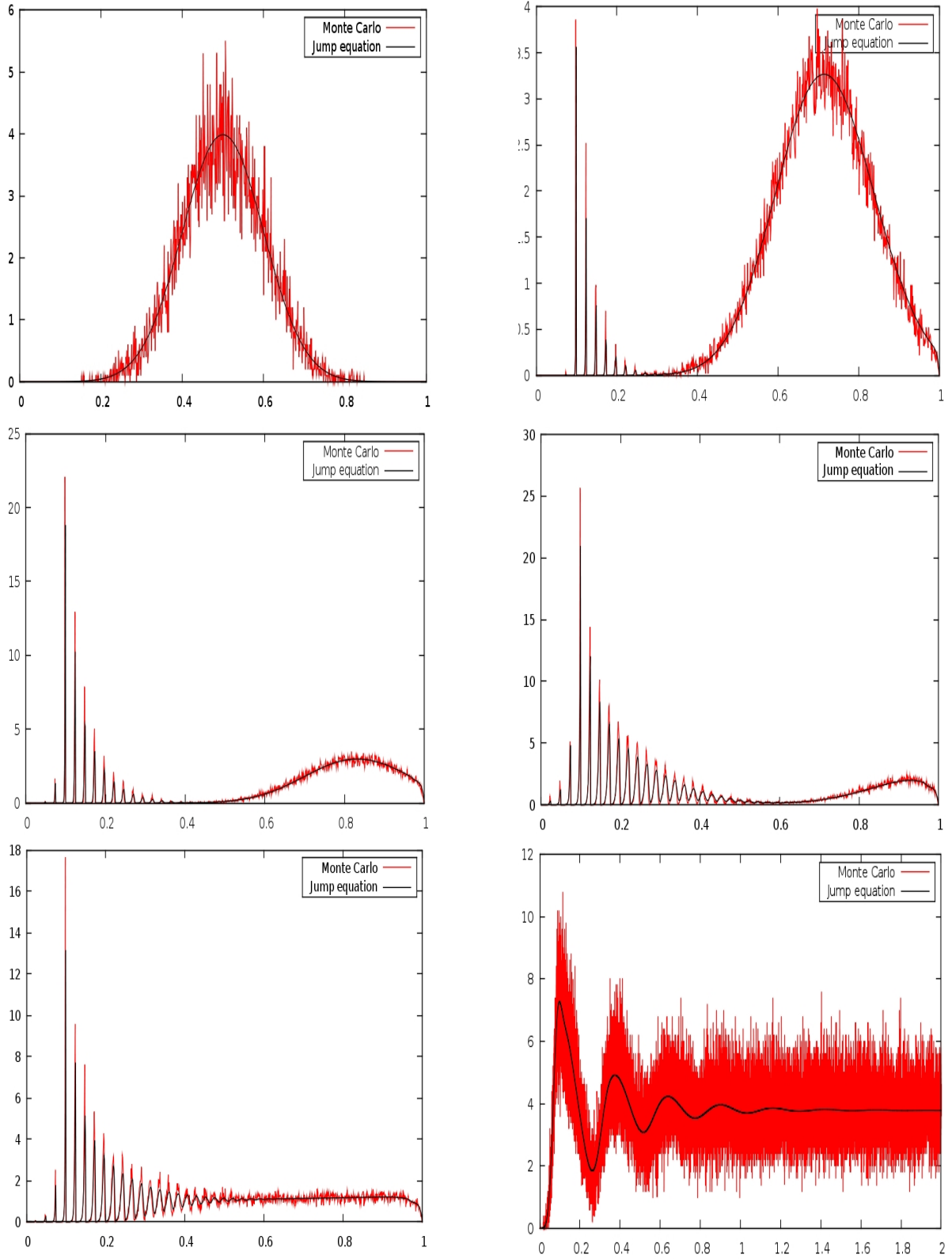
Fig. 6 Scheme for the evolution of a self inhibiting population with a conduction delay under an external influence. The population receives a known external excitatory influence $\sigma(t)$, and produces an activity $r(t)$. The own activity of the population $r(t)$ will inhibit it as a feedback. Due to the delay of conduction which is caracterised by a delay kernel α, the feedback is given by $J \int_0^t \alpha(u)r(t-u)\,du$.

Fig. 7 Scheme for the evolution of a self inhibiting population without conduction delay. The situation is similar to figure 6 but we suppose that the effect of the feedback is intantaneous and it is given by $Jr(t)$.

delays with a distribution α.

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) + \sigma(t)\left(\rho(t,v) - \rho(t,v-h)\right) = I(t)\left(\rho(t,v+h) - \rho(t,v)\right) \\
\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad + \sigma(t)\delta(v-v_r)\displaystyle\int_{1-h}^{1}\rho(t,w)\,dw \\
I(t) = J\int_0^t \alpha(s)r(t-s)\,ds \quad \text{with conduction delay, or} \\
\quad I(t) = Jr(t) \quad \text{without conduction delay} \\
r(t) = \sigma(t)\int_{1-h}^{1}\rho(t,w)\,dw \\
\rho(t,1) = 0 \\
\lim_{v\to-\infty} v\rho(t,v) = 0 \\
\rho(0,.) = \rho_0 \in L_+^1(-\infty,1),
\end{cases}
\tag{22}
$$

with a given normalized initial data $\rho_0(v)$,

$$
\int_{-\infty}^{1}\rho_0(v)dv = 1.
$$

3.1 The case with conduction delay

Theorem 3 *Assuming that α belongs to $L^\infty(0,\infty)$ and satisfies (7), then for all $\sigma \in C\left(\mathbb{R}_+,\mathbb{R}_+\right)$ and for all $J \geq 0$, there exists a unique positive solution $\rho \in C\left(\mathbb{R}_+, L_+^1(-\infty,1)\right)$ to Problem (22) with conduction delay.*

We will not reproduce the proof here since it can be done in the same way as for Theorem 1.

We present in Figure 8 some simulations similar to the ones of figure 4 but in the case of a self-inhibiting population. The presence of inhibtion can be seen by an accumulation present at $v_r - h$, and then at $v_r - 2h$, and so on... Finally the distribution tends to stabilise to a steady state which can be seen in the lower left plot of Figure 8. We finally show in the lower right plot of Figure 8 the activity of the population as a function of time as we have shown it in Figure 4.

3.2 The case without conduction delay

We state now the existence result for the model (22) without conduction delay.

Theorem 4 *For all $\sigma \in C\left(\mathbb{R}_+,\mathbb{R}_+\right)$ and for all $J \geq 0$, there exists a unique positive solution $\rho \in C\left(\mathbb{R}_+, L_+^1(-\infty,1)\right)$ to Problem (22) without conduction delay.*

Fig. 8 Simulation of the nonlinear PDE (22), comparison between a Monte Carlo approach (red curve) and the PDE simulation (black curve). A gaussian distribution is taken as initial condition ρ_0; the excitatory external influence $\sigma(t)$ is taken constant $\sigma = 50$; potential jump size $h = 0.025$, reset potential $v_r = 0.1$, delay kernel $\alpha(u) = \delta(u - \Delta)$ with $\Delta = 0.5$, coupling parameter $J = 5$.

Proof To prove Theorem 4, we introduce the following mapping

$$F : \pi \longmapsto \rho; \qquad C((0,T), L^1(-\infty, 1)) \longmapsto C((0,T), L^1(-\infty, 1)), \tag{23}$$

where ρ satisfies the following problem

$$\begin{cases} \dfrac{\partial}{\partial t} \rho(t, v) - \dfrac{\partial}{\partial v} (v\rho(t, v)) + \sigma(t) \left(\rho(t, v) - \pi(t, v - h) \right) = S(I(t)) \left(\pi(t, v + h) - \rho(t, v) \right) \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad + \sigma(t)\delta(v - v_r) \displaystyle\int_{1-h}^1 \pi(t, w)\, dw \\ I(t) = J\sigma(t) \int_{1-h}^1 \pi(t, w)\, dw \\ \rho(t, 1) = 0 \\ \lim\limits_{v \to -\infty} v\rho(t, v) = 0 \\ \rho(0, .) = \rho_0 \in L^1_+(-\infty, 1), \end{cases} \tag{24}$$

where S is the positive part function, given by

$$S(I) = \max(0, I).$$

It is clear that F is a well defined mapping. As we have done it before we show that the mapping F is a contraction for T sufficiently small.

Let π be an element of the ball $B(0, M)$ of $C((0,T), L^1(-\infty, 1))$, where M is supposed to be strictly larger than 1. We will show that for T sufficiently small, the image ρ of π by F is still in $B(0, M)$. We have

$$\frac{\partial}{\partial t} \rho(t, v) - \frac{\partial}{\partial v}(v\rho(t, v)) + \sigma(t)\rho(t, v) + S(I(t))\rho(t, v) = \sigma(t)\pi(t, v - h) + S(I(t))\pi(t, v + h)$$
$$+ \sigma(t)\delta(v - v_r) \int_{1-h}^1 \pi(t, w)\, dw.$$

As we have done it before, we deduce an estimate of $|\rho(t, v)|$: we have

$$\frac{\partial}{\partial t} |\rho(t, v)| - \frac{\partial}{\partial v}(v|\rho(t, v)|) + \sigma(t)|\rho(t, v)| + S(I(t))|\rho(t, v)| \leq \sigma(t)|\pi(t, v - h)| + S(I(t))|\pi(t, v + h)|$$
$$+ \sigma(t)\delta(v - v_r) \int_{1-h}^1 |\pi(t, w)|\, dw.$$

Integrating the last inequation with respect to v, we get

$$\frac{d}{dt} \int_{-\infty}^1 |\rho(t, v)\, dv| \leq \sigma(t) \int_{-\infty}^1 |\pi(t, v)| dv + S(I(t)) \int_{-\infty}^1 |\pi(t, v)| dv.$$

As π is in the ball $B(0, M)$,

$$\sup_{0 < t < T} \int_{-\infty}^1 |\pi(t, v)|\, dv \leq M, \quad S(I(t)) \leq J\|\sigma\|_\infty M.$$

Integrating in time

$$\int_{-\infty}^1 |\rho(t, v)\, dv| \leq \underbrace{\int_{-\infty}^1 |\rho_0(w)|\, dw}_{=1} + T(J\|\sigma\|_\infty M^2 + \|\sigma\|_\infty M).$$

We can deduce from the previous computations that for M strictly larger than 1, it is always possible to find T such that the image ρ is still in the ball $B(0, M)$ if π was in it. We are going to show now that F is a contraction for T sufficiently small. Let $\rho_1, \rho_2, \pi_1, \pi_2$ be in $B(0, M)$ such that

$$\rho_1 = F(\pi_1), \quad \rho_2 = F(\pi_2).$$

We denote

$$\rho = \rho_1 - \rho_2, \quad \pi = \pi_1 - \pi_2, \quad I_1(t) = J\sigma(t)\int_{1-h}^{1}\pi_1(t,w)\,dw, \quad I_2(t) = J\sigma(t)\int_{1-h}^{1}\pi_2(t,w)\,dw.$$

We then get that ρ satisfies the following problem

$$
\begin{cases}
\dfrac{\partial}{\partial t}\rho(t,v) - \dfrac{\partial}{\partial v}(v\rho(t,v)) + \sigma(t)\rho(t,v) + S(I_1(t))\rho(t,v) + (S(I_1(t)) - S(I_2(t)))\rho_2(t,v) \\
\qquad = \sigma(t)\pi(t,v-h) + S(I_1(t))\pi(t,v+h) + (S(I_1(t)) - S(I_2(t)))\pi_2(t,v+h) \\
\hspace{9cm} + \sigma(t)\delta(v - v_r)\displaystyle\int_{1-h}^{1}\pi(t,w)\,dw \\
\rho(t,1) = 0 \\
\lim_{v \to -\infty} v\rho(t,v) = 0 \\
\rho(0,.) = 0.
\end{cases}
\tag{25}
$$

As previously, we get an estimate on $|\rho(t,v)|$. We have

$$
\frac{\partial}{\partial t}|\rho(t,v)| - \frac{\partial}{\partial v}(v|\rho(t,v)|) + \sigma(t)|\rho(t,v)| + S(I_1(t))|\rho(t,v)|
$$
$$
\leq |(S(I_1(t)) - S(I_2(t)))||\rho_2(t,v)| + \sigma(t)|\pi(t,v-h)| + S(I_1(t))|\pi(t,v+h)|
$$
$$
+ |(S(I_1(t)) - S(I_2(t)))||\pi_2(t,v+h)| + \sigma(t)\delta(v-v_r)\int_{1-h}^{1}|\pi(t,w)|\,dw.
$$

Integrating this equation on the domain and using the fact that

$$
S(I_i(t)) \leq J\|\sigma\|_\infty \int_{-\infty}^{1}|\pi_i(t,w)|\,dw \leq J\|\sigma\|_\infty M, \quad \forall i = 1,2,
$$
$$
|S(I_1(t)) - S(I_2(t))| \leq J\|\sigma\|_\infty \int_{-\infty}^{1}|\pi(t,w)|\,dw,
$$

we get

$$
\frac{d}{dt}\int_{-\infty}^{1}|\rho(t,w)|\,dw \leq |(S(I_1(t)) - S(I_2(t)))|M +
$$
$$
\|\sigma\|_\infty \int_{-\infty}^{1}|\pi(t,w-h)|\,dw + J\|\sigma\|_\infty M \int_{-\infty}^{1}|\pi(t,w+h)|\,dw
$$
$$
+ |(S(I_1(t)) - S(I_2(t)))|M + \|\sigma\|_\infty \int_{1-h}^{1}|\pi(t,w)|\,dw
$$
$$
\leq (3MJ\|\sigma\|_\infty + \|\sigma\|_\infty)\int_{-\infty}^{1}|\pi(t,w)|\,dw.
$$

Integrating in time we deduce that for T sufficiently small, the mapping F is a contraction.

We can see that the fixed point ρ is actually a solution of the problem (22) without conduction delay on $[0,T]$. Then ρ is non negative and

$$
\int_{-\infty}^{1}|\rho(T,w)|\,dw = \int_{-\infty}^{1}\rho(T,w)\,dw = 1.
$$

The previous reasoning can then be iterated in time on $\mathbb{R}_+$.

4 Discussion on the modeling

In this paper we have proved the mathematical well-posedness of a nonlinear non local deterministic model for large populations of leaky integrate-and-fire neurons. This model is based on the paper [20] where neurons respond by a finite potential jump to receiving a spike. In this section we will discuss the situations where there is no well-posedness result and we will compare these results with those obtained with the model with a diffusion approximation for small jumps h. The idea under such approximation is to remove the nonlocal jump term $\rho(t, v - h)$ and $\rho(t, v + h)$ present in (10) and in (22). This kind of nonlocal term makes hard the computation of the stationary state, and the nonlinear analysis of the model. Let μ be defined by

$$\mu(t) = h\sigma(t).$$

Assuming that h is small we have

$$\sigma(t)(\rho(t, v - h) - \rho(t, v)) \simeq \mu(t)\frac{\partial}{\partial v}\rho(t, v) - \frac{h}{2}\mu(t)\frac{\partial^2}{\partial v^2}\rho(t, v),$$

and

$$\sigma(t)\int_{1-h}^{1}\rho(t, w)\, dw \simeq \mu(t)\rho(t, 1) - \frac{h}{2}\mu(t)\frac{\partial}{\partial v}\rho(t, 1).$$

Plugging these two last expresssions in (10), one obtains the diffusion approximation for the integrate-and-fire model of self-excitatory neurons given by

$$\begin{cases} \dfrac{\partial}{\partial t}\rho(t, v) + \dfrac{\partial}{\partial v}((\mu(t) - v)\rho(t, v)) - \dfrac{h}{2}\mu(t)\dfrac{\partial^2}{\partial v^2}\rho(t, v) = \delta(v - v_r)r(t) \\ \mu(t) = h\sigma_0(t) + Jh\int_0^t \alpha(u)r(t - u)\, du \quad \text{with conduction delay, or} \\ \mu(t) = h\sigma_0(t) + Jhr(t) \quad \text{without conduction delay} \\ r(t) = -\dfrac{h}{2}\mu(t)\dfrac{\partial}{\partial v}\rho(t, 1) \\ \rho(t, 1) = 0 \\ \lim_{v \to -\infty}(\mu(t) - v)\rho(t, v) - \dfrac{h}{2}\mu(t)\dfrac{\partial}{\partial v}\rho(t, v) = 0 \\ \rho(0, .) = \rho_0 \in L_+^1(-\infty, 1). \end{cases} \quad (26)$$

Let us remark that this equation has the same structure than the Fokker Planck equation for the noisy integrate-and-fire neuron model. We will not discuss here the well-posedness of the model (26) in the case of conduction delay. We present in Figure 9 a numerical simulation for a comparison between the model for a self excitatory population with potential jumps and its diffusion approximation. The diffusion approximation smoothes out the oscillations due to the jump effect at low potentials but nevertheless it allows a good simulation of the activity of the population. This model without conduction delay was studied in [3].

Let us now discuss the situations where the mathematical well-posedness of the model was not proved as in section 2.3 for $J \geq 1$.

There are at least three explanations for the absence of well-posedness result:

– the solution does exist but the mathematical tools of the proof are not powerful enough (or not well used) to prove this existence;
– some events may occur that are not taken into account in the model; under these events the mathematical model may have no solution and more elaborate model may be necessary;
– when proving results of well-posedness the solution is sought in some functional space; the a priori choice for this space may not be well adapted and the solution may exists in a larger space.

First we rule out the first hypothesis: we have shown in section 2.3 that for the model (10) without conduction delay there exist initial data such that the reception rate given by (18) is singular at the initial instant.

The same holds true for the diffusion approximation (26) without conduction delay even for any value of $J > 0$ (i.e. also for $0 < J < 1$ unlike our result for the model with jumps). Here $\mu(t)$ is given by
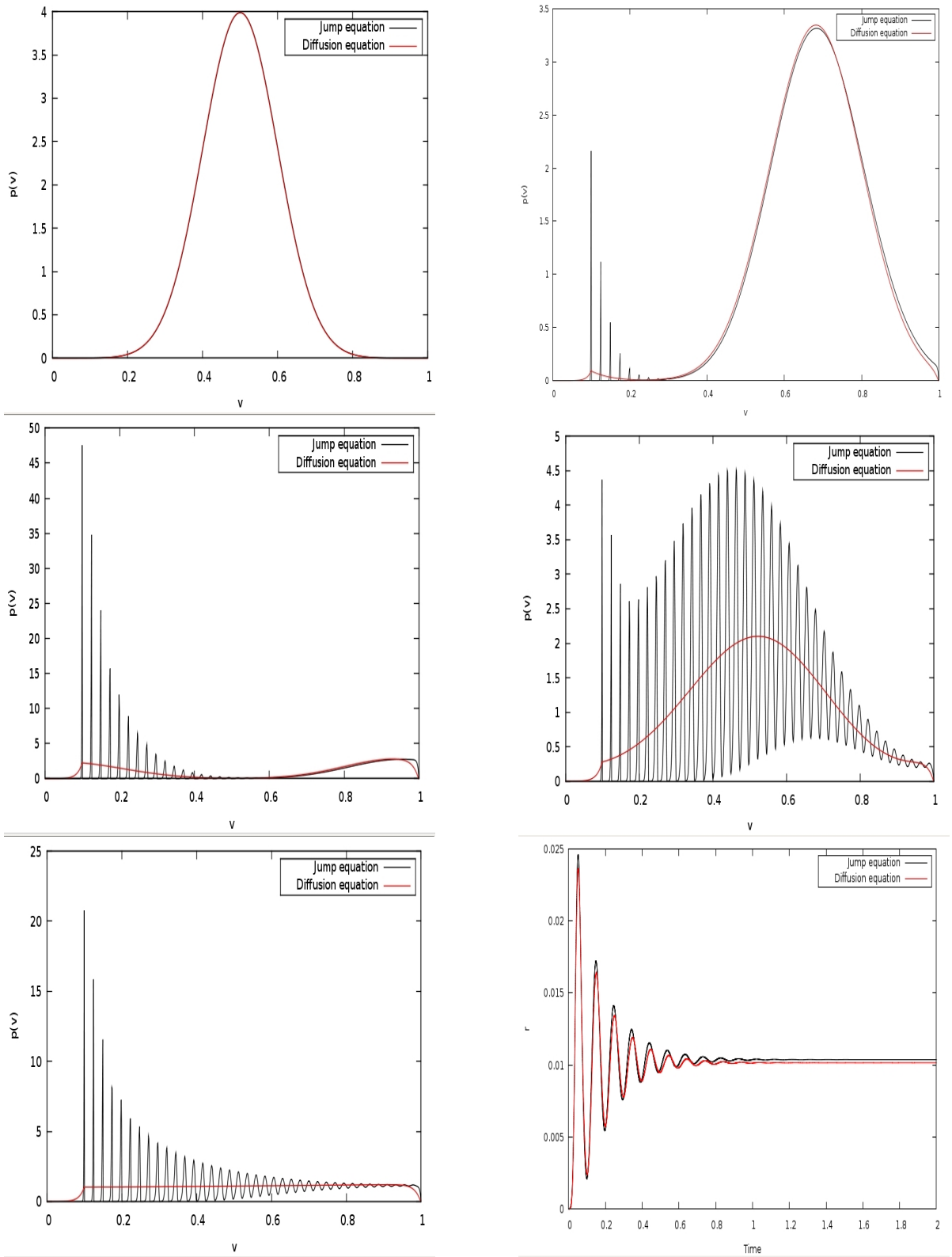
Fig. 9 Comparison between the nonlinear PDE (10) with potential jumps (black curve) and its diffusion approximation PDE (26) (red curve). All parameters are the same as in Figure 4

18

$$\mu(t) = \frac{h\sigma_0(t)}{1 + \dfrac{h^2}{2} J \dfrac{\partial}{\partial v} \rho(t,1)}.$$

The expression of $\mu(t)$ is singular if the denominator of the right hand side is zero. Here one can always find an initial repartition ρ_0 such that μ is singular at the initial instant. Furthermore for this model the authors of [3] give an upper bound of the time when a weighted L^1 norm of the solution blows up for initial data sufficiently concentrated near the threshold. For $J < 1$ there is no amplification factor and the occurrence of a blow up seems unrealistic.

The second hypothesis is quite interesting from the biological viewpoint as it may be related to the synchronization of the firing of the population. It is a well established observation that some populations of neurons exhibit periods of totally or partially synchronized firing as well as periods of desynchronized firing. Some neuroscientists find this synchronization mechanism quite meaningful to understand neural coding. Many mathematical studies have been devoted to this problem, a pioneering work being [16].

An inadequacy of our model seems to be due to the fact that it includes the artificial feature of excitatory networks of integrate-and-fire neurons with instantaneous synapses. With this integrate-and-fire model, a neuron will respond to an input by firing at exactly the same time as any superthreshold excitatory input. If, when a neuron fires, any other neurons are close to threshold, they will also fire at the exact same moment. These firings in turn will imply new potential jumps and new firings. Eventually, all neurons may fire at the same time. Such phenomena, called *cascade firing event*, have been pointed out recently in [17] and [18] for population of excitatory integrate-and-fire neurons. If the cascade is not complete, in the sense that not all neurons of the population, but just a part of them fire, the authors of [5] and [6] called such event *big burst*. They add to their model a second step of evolution with time being fixed during the burst. In our model for large population a neuron can experience only one potential jump at each instant. Adding burst mechanisms similar to the one of [5] may be the subject of a new research.

We may also discuss our results with respect to the third explanation considered above: we were seeking the solution as being in L^1 in potential and continuous in time. But at instants of partial or full synchrony the firing rate becomes a Dirac mass in time. So is the reception rate σ and the population density ρ becomes discontinuous in time and will include Dirac masses in potential after the reset. We are clearly outside the spaces used in this paper. But if one wants to extend the model (10) to these spaces, he is faced to the difficulty of defining the product of σ with a Dirac mass by ρ being discontinuous at the same time. This is also a subject for a new research.

Let us go back to the comparison between the model with jumps and its diffusion approximation for small jumps. For self-activating populations without conduction delay we have seen that the result on the existence of a singularity in the diffusion approximation differs from the model with jumps in the case $0 < J < 1$. We now turn to self-inhibitory populations following the same ideas. Let μ and ν be defined by

$$\mu(t) = h\sigma(t), \quad \nu(t) = hI(t).$$

Plugging the same kind of second order approximation in (22), we get the diffusion approximation for the integrate-and-fire model of a self-inhibitory population. We have

$$\begin{cases} \dfrac{\partial}{\partial t}\rho(t,v) + \dfrac{\partial}{\partial v}((\mu(t) - \nu(t) - v)\rho(t,v)) - \dfrac{h}{2}(\mu(t) + \nu(t))\dfrac{\partial^2}{\partial v^2}\rho(t,v) = \delta(v - v_r)r(t) \\ \nu(t) = Jh \int_0^t \alpha(u)r(t-u)\,du \quad \text{with conduction delay, or} \\ \nu(t) = Jhr(t) \quad \text{without conduction delay} \\ r(t) = -\dfrac{h}{2}(\mu(t) + \nu(t))\dfrac{\partial}{\partial v}\rho(t,1) \\ \rho(t,1) = 0 \\ \lim_{v \to -\infty}(\mu(t) - \nu(t) - v)\rho(t,v) - \dfrac{h}{2}(\mu(t) + \nu(t))\dfrac{\partial}{\partial v}\rho(t,v) = 0 \\ \rho(0,.) = \rho_0 \in L^1_+(-\infty,1). \end{cases} \quad (27)$$

In the case without conduction delay, we get

$$\nu(t) = -\frac{J\dfrac{h^2}{2}\mu(t)\dfrac{\partial}{\partial v}\rho(t,1)}{1 + J\dfrac{h^2}{2}\dfrac{\partial}{\partial v}\rho(t,1)}.$$

This expression for $\nu(t)$ is singular if the denominator of the right hand side is zero. In section 3.2 the model (22) without conduction delay was shown to be well-posed for every $J \geq 0$. Here, for any $J \geq 0$, one can always find an initial repartition ρ_0 such that there is a singularity at $t = 0$. Even one can use a similar argument to the one used in [3] to derive an upper bound for the time of bursting of the solution for an initial condition sufficiently concentrated near the threshold. Once again this behaviour of the diffusion approximation does not seem realistic as it is not plausible that the firing rate of a self-inhibitory population could blow up.

One can relate this unsatisfactory feature of the diffusion approximation to the fact that, due to the boundary condition at $v = 1$, only the diffusive effect appear in the expression of the firing rate: it has a symmetry (the expression is unchanged when changing h to $-h$) which is not true for the model with jumps. In the diffusion term activation and inhibition act in the same way.

5 Conclusion

In this paper we have proved the existence, uniqueness and positivity of the solution of the model for a large population of self-excitory (10), as well as self-inhibitory (22) integrate-and-fire neurons with conduction delay that was introduced in [20]. To our knowledge, this result was not known. The delay, as long as its repartition remains bounded smoothes the solution. We also took a special care to the case when there is no delay in the feedback for both the excitatory (17) and inhibitory (22) populations. It turned out that the model of inhibiting integrate-and-fire neurons (22) without delay in the feedback is well-posed. Nevertheless in the case of an excitatory population without propagation delay (17), the model can burst in finite time. It is well-posed just for a weakly coupled ($J < 1$) population of neurons. Interpreting J as the average number of connections received per neuron, the case $J < 1$ corresponds to a population of neurons where one neuron is connected on average to less than one upstream neuron. In other word, the network would be likely to have large numbers of isolated neurons. Such neuron can receive action potentials from other populations but not from the considered one.

The ill-posedness of the model (10) seems to be due to the well-known artificial feature of excitatory networks of integrate-and-fire neurons with instantaneous synapses. This feature may produce events called cascade firing events or big burst where all the population or a part of it fires at the same time. Our model does not include a description of these events as it is done in [5] and so it cannot be valid over such a period. Including such events in the model will be the object of a future research.

With respect to the properties of well-posedness we also discussed the diffusion approximation and we have shown some drawbacks of this approach.

In the future, it seems to us be really interesting to show that for a constant external stimulation with parameter $\sigma_0(t) = \sigma_0$ there exists an unique stationary state, both in the linear case and nonlinear case. In the simulation (cf. Figure 4 and see also [25] and [14]), the density function converges asymptotically to an equilibrium. To our knowledge the existence of an unique equilibrium solution to the model (10) is not known.

Probably the most important goal to reach, in order to predict the convergence to an asynchronisation state or the occurence of synchronisation as it has been proposed in [8] and [26], is to manage a nonlinear analysis of the equation (10). More precisely, it is desirable to find under which condition the stability or instability of the steady state occurs, which could give us a guess for the existence of a periodic solution.

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