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Beyond blow-up in excitatory integrate and fire neuronal networks: Refractory period and spontaneous activity

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HIGHLIGHTS

- We complete the analysis of the excitatory integrate and fire neuronal networks.
- We have increased the knowledge about NNLIF model, including the refractory state.
- We have extended the blow-up results for a deterministic value firing potential.
- Neurons in refractory state can produce more stationary states than without it.
- For a random discharge potential spontaneous activity arises.

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ABSTRACT

The Network Noisy Leaky Integrate and Fire equation is among the simplest model allowing for a self-consistent description of neural networks and gives a rule to determine the probability to find a neuron at the potential v. However, its mathematical structure is still poorly understood and, concerning its solutions, very few results are available. In the midst of them, a recent result shows blow-up in finite time for fully excitatory networks. The intuitive explanation is that each firing neuron induces a discharge of the others; thus increases the activity and consequently the discharge rate of the full network.

In order to better understand the details of the phenomena and show that the equation is more complex and fruitful than expected, we analyze further the model. We extend the finite time blow-up result to the case when neurons, after firing, enter a refractory state for a given period of time. We also show that spontaneous activity may occur when, additionally, randomness is included on the firing potential V_F in regimes where blow-up occurs for a fixed value of V_F.

1. Introduction

The Network Noisy Leaky Integrate and Fire (NNLIF in short) model is certainly one of the simplest self-contained mean field equation for neural networks. It describes, at time t, the probability $p(v,t)$ to find a neuron at a voltage v, assuming each individual neuron follows a simple integrate and fire dynamics and the coupling changes the current. Integrate and Fire models, for a single neuron or a population of neurons, with or without noise, have been used very widely (Abbott and Vreeswijk, 1993; Brunel and Hakim, 1999; Renart et al., 2004; Touboul, 2009; Newhall et al., 2010a, 2010b), compared to experimental data (Brette and Gerstner, 2005; Rossant et al., 2011) and qualitative properties have been studied (Brunel, 2000; Brunel and Hakim, 1999; Touboul, 2008; Dumont and Henry, 2013b). Many references can be found in surveys and books, see Gerstner and Kistler (2002), Tuckwell (1988), Guillamon (2004) among others. However its mathematical structure is still poorly understood and very few results are available concerning its solutions. For instance, very recent results are large time existence for the inhibitory case (Carrillo et al., 2013), short time existence of smooth solutions for the excitatory case (Delarue et al., 2012) and global existence for the model when firing neurons induce finite jumps (Dumont and Henry, 2013a). Another striking mathematical property is that for fully excitatory networks, the system blows-up in finite time; this holds for any initial data for a large enough network connectivity and for any connectivity if the initial data is concentrated enough near the firing potential denoted by V_F in the sequel, see Cáceres et al. (2011a).

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This also remains true when the discrete nature of interactions is kept (Dumont and Henry, 2013b). The intuitive explanation is that each firing neuron induces a discharge of the others; thus increases the activity and consequently the discharge rate of the full network. Finally, synchronous states, where the firing rate does not tend asymptotically to constant in time but network produces spontaneous activity, have also been observed in several neuronal networks models: systems of coupled nonlinear oscillators (Abbott and Vreeswijk, 1993), inhibitory NNLIF with synaptic integration (Brunel and Hakim, 1999), excitatory–inhibitory coupled NNLIF (Brunel, 2000), Fokker–Planck equations for uncoupled neurons (Newhall et al., 2010a, 2010b), kinetic models (Rangan et al., 2008; Cáceres et al., 2011b) and elapsed time models (Pakdaman et al., 2013).

In order to better understand the details of the phenomena observed in NNLIF, we analyze a model with a refractory state. The refractory state takes into account the fact that neurons during the refractory period do not respond on stimuli. We describe the influence of that period coupling the NNLIF equation, considered in Cáceres et al. (2011a), with a ODE for the refractory state:

$$\begin{cases} \frac{\partial p}{\partial t}(v,t)+\frac{\partial}{\partial v}[h(v,N(t))p(v,t)]-a(N(t))\frac{\partial^2 p}{\partial v^2}(v,t)=\frac{R(t)}{\tau}\delta(v-V_R), \quad v\le V_F, \\ \frac{dR(t)}{dt}=N(t)-\frac{R(t)}{\tau}, \\ N(t):=-a(N(t))\frac{\partial p}{\partial v}(V_F,t)\ge 0, \\ p(V_F,t)=0, \quad p(-\infty,t)=0, \quad p(v,0)=p^0(v)\ge 0, \quad R(0)=R^0>0. \end{cases} \tag{1}$$

In this system, $p(v,t)$ represents the density of active neurons (those which respond on stimuli) in the network at voltage $v\in(-\infty,V_F)$, $R(t)$ denotes the probability density to find a neuron in the refractory state and $N(t)$ is the flux of firing neurons. The presentation of the model ends up with the description of the parameters:

- V_R and V_F are the reset and the firing potentials, respectively. As in Cáceres et al. (2011a) voltage variable is translated in terms of the resting potential and the external stimuli. In this sense, we can choose $v=0$ for the relaxation potential (see $h(v,N)$ below).
- τ measures the mean duration of the refractory period.
- $h(v,N)$ is the drift coefficient and usually will be $h(v,N)=-v+bN$.
- b represents the connectivity of the network: $b>0$ for excitatory networks and $b<0$ for inhibitory.
- $a(N)$ denotes the activity dependant noise; it is usual to take the form $a(N)=a_0+a_1N$ and here we just assume

$$a(N)\ge a_m>0. \tag{2}$$

An important and deep literature has been devoted to the derivation of mean field equations as (1) for large systems of coupled neurons, see Tuckwell (1988), Guillamon (2004), Rangan et al. (2008), Delarue et al. (2012), and Pakdaman et al. (2010), for instance.

The first property of the system (1) that one readily checks is the conservation of the total number of neurons, that is

$$R(t)+\int_{-\infty}^{V_F}p(v,t)\,dv=R^0+\int_{-\infty}^{V_F}p^0(v)\,dv=1. \tag{3}$$

Brunel (2000) presents a different model to depict the presence of refractory state, he considers

$$R(t)=\int_{t-\tau}^{t}N(s)\,ds$$

and couple it with the equation for the active neurons in the network written as

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

The conservation property (3) still holds since we have

$$\frac{d}{dt}\left[\int p(v,t)\,dv+R(t)\right]=0,$$

at least if N is properly extended for times $t\in(-\tau,0)$. This latter model considered in Brunel (2000) and the system (1) are particular cases of a general version

$$\begin{cases} \frac{\partial p}{\partial t}(v,t)+\frac{\partial}{\partial v}[h(v,N(t))p(v,t)]-a(N(t))\frac{\partial^2 p}{\partial v^2}(v,t)=M(t)\delta(v-V_R) \\ \frac{dR(t)}{dt}=N(t)-M(t). \end{cases} \tag{4}$$

We recover the model in Brunel (2000) with the choice $M(t)=N(t-\tau)$ and the model (1) with $M(t)=R(t)/\tau$. Our results and proofs below also hold within the more general setting (4) and therefore remain true for the Brunel's model.

We consider throughout this paper weak solutions which definition is recalled in Section 2. Our main result is that weak solutions to (1) with $b>0$ blow-up in the same condition than when the refractory state is ignored; this result is proved in Section 3. Then we study the existence and multiplicity of steady states in Section 4, both with a general result and some numerical illustrations (see Section 7). For $b\le 0$ there is a unique steady state and we can show that the linear equation, that is $b=0$, comes with a natural energy which explains the long time relaxation to the unique steady state (Section 5).

Self-sustained oscillations can also be obtained for the excitatory NNLIF when the deterministic value V_F is changed to a random discharge potential. We study two examples of discharge laws and prove in Section 6 that solutions are a priori globally bounded. Numerical illustrations are finally given in Section 7. Section 8 summarizes the paper and gives conclusions on our results about the NNLIF with refractory state; it also presents several open questions.

2. Notation and definitions

In this section we present the notations that are used throughout this paper and the definition of weak solutions of (1). We recall some usual notations: $L^p(\Omega)$ with $1\le p<\infty$ is the space of functions such that f^p is integrable in Ω, L^∞ represents the space of bounded functions in Ω and $C^\infty(\Omega)$ denotes the space of infinitely differentiable functions in Ω.

Definition 2.1. Let $p\in L^\infty(\mathbb{R}^+;L^1_+(-\infty,V_F))$, $N\in L^1_{loc,+}(\mathbb{R}^+)$ and $R\in L^\infty_+(\mathbb{R}^+)$. We say that (p,N,R) is a weak solution of (1) if for any test function $\phi(v,t)\in C^\infty((-\infty,V_F]\times\mathbb{R}^+)$ such that $\partial^2\phi/\partial v^2$, $v\partial\phi/\partial v\in L^\infty((-\infty,V_F)\times\mathbb{R}^+)$ we have

$$\int_0^T\int_{-\infty}^{V_F}p(v,t)\left[-\frac{\partial\phi}{\partial t}-h(v,N(t))\frac{\partial\phi}{\partial v}-a(N(t))\frac{\partial^2\phi}{\partial v^2}\right]dv\,dt$$
$$=\int_0^T\left[\frac{R(t)}{\tau}\phi(V_R,t)-N(t)\phi(V_F,t)\right]dt$$
$$+\int_{-\infty}^{V_F}p^0(v)\phi(v,0)\,dv-\int_{-\infty}^{V_F}p(v,T)\phi(v,T)\,dv \tag{5}$$

and R is a solution of the ODE

$$\frac{dR(t)}{dt}=N(t)-\frac{R(t)}{\tau}.$$