

Dynamics of a structured neuron population

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1 The neuron population model

We consider a population of neurons described by the probability density $n(s, t)$ of finding a neuron in 'state' s at time t where s represents the time elapsed since the last discharge. According to [12, 14] a simple model of the dynamics is given by the age-structured equation

$$\begin{cases} \frac{\partial n(s, t)}{\partial t} + \frac{\partial n(s, t)}{\partial s} + p(s, X(t)) n(s, t) = 0, \\ N(t) := n(s = 0, t) = \int_0^{+\infty} p(s, X(t)) n(s, t) ds, \end{cases} \quad (1)$$

completed with an initial probability density $n^0(s)$ that satisfies (the first inequality is motivated by the permanent regime, see Theorem 3.1)

$$0 \leq n^0(s) \leq 1, \quad \int_0^{\infty} n^0(s) ds = 1. \quad (2)$$

The coefficient $p(s, X)$ represents the firing rate of neurons in the 'state s ' and in an environment X resulting from the global neural activity. It is usually small (or even vanishes) during a rest phase that depends on X , and increases suddenly afterwards. The density of neurons undergoing a discharge at time t is denoted by $N(t)$ and the boundary condition at $s = 0$ means that the neuron re-enters the cycle at 'age $s = 0$ ' after firing.

The interactions between the neurons are taken into account through the global neural activity at time t , $X(t)$, that is given by

$$X(t) = J \int_0^t \alpha(u) N(t - u) du. \quad (3)$$

The parameter $J \geq 0$ represents the network connectivity (and thus the strength of the interactions), and the delay takes into account an averaged propagation time for the ionic pulse in this network. Here we assume that the neurons can discharge earlier when the neural activity is high.

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Notice that this nonlinear system has a remarkable conservation property

$$\int_0^\infty n(s, t) ds = \int_0^\infty n^0(s) ds = 1 \quad \forall t \geq 0, \quad (4)$$

which expresses the interpretation of $n(t, \cdot)$ as a probability density.

These modeling assumptions can be written on the (nonnegative) coefficients as

$$\int_0^\infty \alpha(u) du = 1, \quad \alpha(\cdot) \geq 0, \quad (5)$$

$$\frac{\partial}{\partial s} p(s, x) \geq 0, \quad p(s, x) = 0 \text{ for } s \in (0, s^*(x)) \quad p(s, x) > 0 \text{ for } s > s^*(x), \quad p(s, x) \xrightarrow{s \rightarrow \infty} R(x), \quad (6)$$

$$\frac{\partial}{\partial x} p(s, x) \geq 0, \quad p(s, x) \xrightarrow{x \rightarrow \infty} 1, \quad 0 < R(x) \xrightarrow{x \rightarrow \infty} 1. \quad (7)$$

Eqs. (3) expresses the hypotheses made about so-called postsynaptic potentials. These represent the impact of the firing in a pre-synaptic neuron on a post-synaptic one. The normalization condition (5) is for convenience since synaptic strength is represented in the parameter J . The main assumption here is that α is positive. This property ensures that firing in a presynaptic neuron increases the probability of firing in a postsynaptic neuron. In this sense, this hypothesis models excitatory connection between neurons. No further assumptions are made regarding the shape of α .

Equations (6) and (7) encompass the key biological properties incorporated into the model. The first is that following a discharge, a neuron loses its excitability, that is its propensity to discharge in response to a stimulation, and recovers it progressively in time. Furthermore, the mean firing rate of the neuron is a function of the stimulus level x , bounded by $R(x)$. The second is that the probability of neuronal firing increases with the intensity of excitatory inputs, until some saturation level is reached. Here again, no further assumptions are made regarding the shape of p .

The theorems and the proofs of the paper are written for a specific choice of the function p which is piecewise constant. This somewhat simplifies the presentation of the proofs but is not limiting. Indeed, the main stages of the proofs remain valid under less stringent hypotheses and the results are valid for a broader class of functions p as above. Namely we use

$$\begin{cases} p(s, x) = \mathbf{1}_{\{s > s^*(x)\}}, & \text{for some } s^* \in C_b^1, \quad \frac{d}{dx} s^*(x) \leq 0, \\ s^*(0) = s_+^*, & 0 < s^*(\infty) = s_-^* < s_+^* < 1. \end{cases} \quad (8)$$

A discontinuity in this coefficient is not realistic but does not change the behavior of solutions that we describe below; it has the advantage of allowing for simpler explicit expressions and thus it simplifies the proofs. In the range $x \approx 0$, the value s_+^* represents the spontaneous activity due to noise. In the range $x \gg 1$ we will use the decay rates D and \tilde{D} defined by

$$\limsup_{J \rightarrow \infty} \sup_{x \geq \frac{J}{(1+s_+^*)}} \frac{J |s^{*'}(x)|}{(1+s^*(x))^2} := D, \quad (9)$$

$$\limsup_{J \rightarrow \infty} \sup_{x \in \mathcal{C}_J} J |s^{*'}(x)| := \tilde{D}, \quad (10)$$

where

$$\mathcal{C}(J) = [J(1-s_+^*), J]. \quad (11)$$

Later on, we will use the condition that the constants D and \tilde{D} are small enough, this means that $s^*(x) \rightarrow s_-^*$ fast enough as $x \rightarrow \infty$. This holds for example if $s^*(x) = s_-^*$ for x large enough or more generally if $|s^{*'}(x)| \leq 1/x^2$ (then $D = 0$ and $\tilde{D} = 0$). The condition $D < 1$ or $\tilde{D} < 1$ corresponds to $|s^{*'}(x)| \leq A/x$ with A small enough.

The equation (1) is an original nonlinear version of a standard linear equation, the renewal equation. It arises in various biological applications as epidemic spread, cell division cycle or even ecology (see [?, 11, ?]).

Our goal is to study the existence of solutions to (1) and their long time behavior. Before we consider the steady states and the linear equation corresponding to $X \equiv 0$.

2 Steady states

Let $J \geq 0$ and assume the simple situation (8). A function $A_J(s)$ associated with the neural activity X_J^* , is a unit mass stationary solution to (1), (3) if and only if

$$\begin{cases} \frac{\partial A_J}{\partial s} + p(s, X_J^*) A_J = 0, \\ A_J(0) = (1 + s^*(X_J^*))^{-1}, \\ X_J^* = J (1 + s^*(X_J^*))^{-1}. \end{cases} \quad (12)$$

Indeed we have

$$A_J(s) = A_J(0) e^{-\int_0^s p(\sigma, X_J^*) d\sigma}, \quad A_J(0) = \left(\int_0^\infty e^{-\int_0^s p(\sigma, X_J^*) d\sigma} ds \right)^{-1} = (1 + s^*(X_J^*))^{-1}.$$

It is noticeable that the steady states do not depend on the delay kernel $\alpha(\cdot)$.

Consequently, the third equation of (12) defines steady states and, from our assumptions on $s^*(x)$, for all J there is at least one steady state. It is easy to see that there can be several steady states when $s^*(x)$ has large enough derivative.

Uniqueness is equivalent to find a unique X_J^* such that

$$X_J^* = J (1 + s^*(X_J^*))^{-1}.$$

Therefore uniqueness always holds true for J small enough. Uniqueness of the steady state also holds true, for all $J \geq 0$, under the condition

$$\frac{J |s^{*'}(x)|}{(1 + s^*(x))^2} < 1, \quad \forall x > 0,$$

but such a regime is very restrictive. We can relax it and notice that

Lemma 2.1 *With the assumptions (8), the steady state is unique for J large enough under the condition $D < 1$ in (9).*

3 Existence and behaviour

Before we study its stability, we first establish a general existence theorem for the nonlinear problem under consideration.

Theorem 3.1 *Assume (2), (8). Assume furthermore that there exists $q > 1$ such that $\alpha \in L^q(\mathbb{R}^+)$. Then, there exists a unique solution to (1), (3), $n \in C(\mathbb{R}^+; L^1(\mathbb{R}^+))$ and*

$$0 \leq n(s, t) \leq 1, \quad \forall t, s \geq 0, \quad (13)$$

$$0 \leq N(t) \leq 1, \quad X(t) \in \mathcal{C}(J), \quad \forall t \geq 0 \quad (14)$$

where $\mathcal{C}(J)$ is defined by (11).

The assumption $\alpha \in L^q(\mathbb{R}^+)$ with $q > 1$ is crucial in our proof. However the case with no delay and more generally undistributed delay, $\alpha(s) = \delta(s - \tau)$, can be handled by the same ideas when the firing rate p is Lipschitz continuous in s in place of (8).

The main theorem on long time asymptotics is the following

Theorem 3.2 *Assume (2), (8) and*

$$\int_0^\infty \psi(s) |n^0(s) - A_J(s)| ds < +\infty$$

where A_J is given by equation (12) and consider the solution n to (1), (3).

Then, for J small enough, the following estimate holds

$$\lim_{t \rightarrow +\infty} \int_0^\infty \psi(s) |n(s, t) - A_J(s)| ds = 0.$$

For J large enough, and assuming that estimate (10) holds with \tilde{D} small enough, the following estimate holds

$$\lim_{t \rightarrow +\infty} \int_0^\infty \psi(s) |n(s, t) - A_J(s)| ds = 0.$$

The figures show however that periodic regimes may exist for middle range values of J

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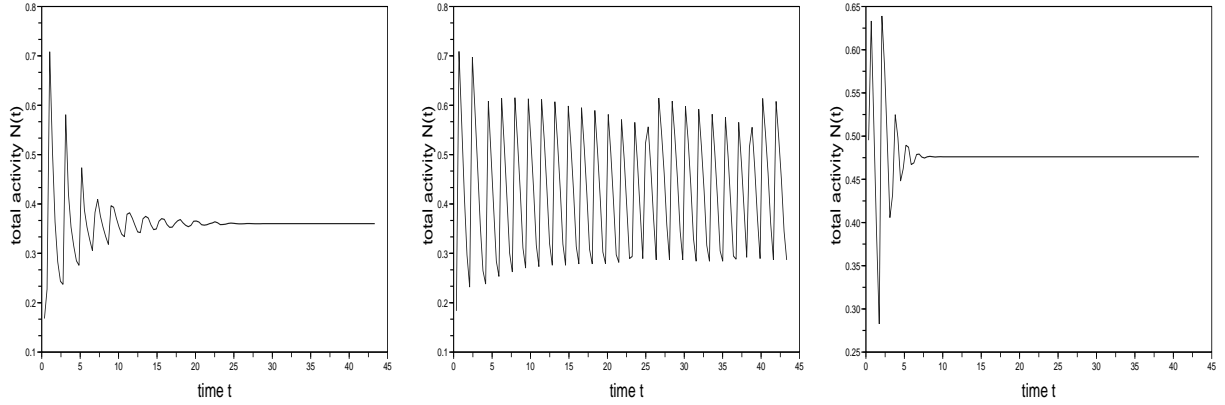


Figure 1: Total neural activity $N(t)$ in the case with no delay. Three different values of the network connectivity have been used, left: $J = 2$, center $J = 3$, right $J = 3.5$.

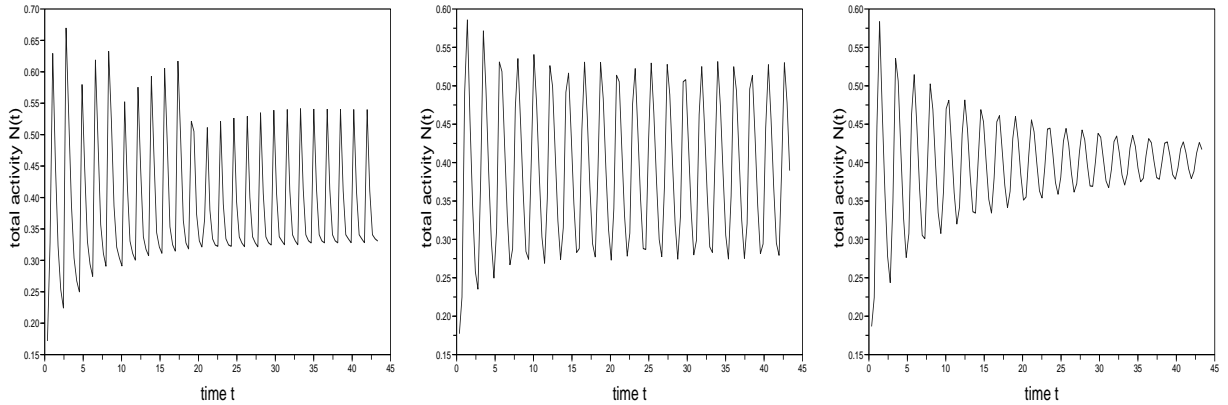


Figure 2: Total neural activity $N(t)$ in the case with delay. We used the network connectivity $J = 2.5$. Left: no delay, center $a = 5$, right $a = 4$.

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