

Analysis of critical effects in a stochastic neural model

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Abstract

We investigate the dynamics of a finite fully connected network and analyse its large-time limit behaviour. We consider the mean interspike interval as a function of the coupling constants: in the case of inhibitory connections we estimate its rate of growth, and in the case of the excitatory connections we find its minimum.

1. Introduction

Recently a new stochastic network model was introduced in mathematical neurobiology [4]. There it is assumed that the electrical activity (the membrane potential) of a single independent neuron can be described by a Markov process. This model takes into account well-known facts from physiology: the spiking nature of the neuronal activity, the exponential decay of the membrane potential in the absence of afferent spikes, and the time dependence of the interactions between the neurons.

This model exhibits a number of interesting aspects. In fact, simulation studies [4] have shown its "closeness" to physiology. One can derive the stochastic models [1] or [2] from model [1]. Model [1] has also common features with known stochastic models [3].

The case of positive coupling constants (excitatory connections) is investigated in [6], where the exponentially fast synchronisation of the moments of firing is proved. Here we study the mean interval of the consecutive moments of firing (i.e. the interspike interval) in the case of excitatory connections by means of stochastic simulations. We find the critical connection constant which provides the minimum of the mean interspike interval.

Usually the state of the neuron is described by its "inhibition" [1]-[2]. The inhibition of a neuron represents the duration of time before the first moment of firing of this neuron if no interaction takes place meanwhile [2]. As is shown in [7], the description of our model in terms of the processes of the inhibitions is equivalent to one given in [1] and [2]. The main difference is that in our model, unlike the previous models, the interactions depend on the current state of the net, i.e. our model is not spatially homogeneous.

Inspired by [5], we find the underlying dynamics of the (stochastic) process of the inhibitions. We classify the vector-fields of the conditional mean jumps of

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Research supported by Project OT/89/12 of the Onderzoeksfonds K.U.Leuven, Belgium.

the Markov chain corresponding to the process of inhibitions. This classification together with results in [6] and [7] allows us to describe metastable states in the model and to estimate their life-times.

2. Model and results

We define a system of N right-continuous processes $S_i(t), t \geq 0, 1 \leq i \leq N$, with zero initial state, i.e. $S_i(0) = 0$ for $1 \leq i \leq N$. The process $S(t) := (S_1(t), \dots, S_N(t))$ has state space $[0, \infty)^N$ and is defined on some probability space (Ω, Σ, P) . In terms of our neural model, each coordinate $S_i(t)$ describes "an age" of an impulse (or the time elapsed since the last firing until the moment t) of the i -th neuron, $i \in \{1, \dots, N\}, t \geq 0$. We call any moment T such that $S_i(T) = 0$ for some $i \in \{1, \dots, N\}$ a moment of firing of the i -th neuron. Let $\eta_i(t), t \geq 0, 1 \leq i \leq N$, be Ornstein-Uhlenbeck processes satisfying the following system of Itô equations:

$$d\eta_i(t) = -\alpha_i \eta_i(t) dt + \sigma_i dW_i(t), \quad (1)$$

with initial conditions $\eta_i(0) = 0$, where $\alpha_i, \sigma_i > 0$, and $W_i(t), i \in \{1, \dots, N\}$ are standard Wiener processes on (Ω, Σ, P) , independent for different i . We define also the right-continuous processes

$$y_i(t) = y_i e^{-\alpha_i S_i(t)},$$

$$x_i(t) = \eta_i(S_i(t)) + [a_{ii} + a_i^0 \delta(t - S_i(t))] e^{-\alpha_i S_i(t)} + \sum_{j: S_j(t) < S_i(t)} a_{ij} e^{-\alpha_i S_j(t)} \quad (2)$$

to be the threshold function and the membrane potential of the i -th neuron, respectively. We assume, that at any moment T of firing of the i -th neuron, process $x_i(t), t \geq T$, restarts independently of its history. The parameters of any single neuron are assumed to be fixed and satisfy the following conditions: $y_i > 0, y_i > a_{ii}, a_i^0 < y_i - a_{ii}, i = 1, \dots, N$.

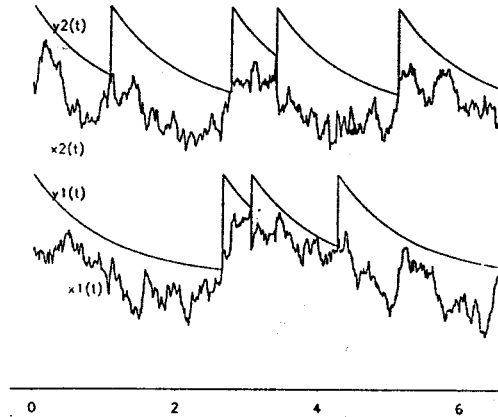


Fig. 1. The typical trajectories of the processes $x_i(t)$ and $y_i(t)$ for $N = 2, a_{ij} = -1, a_{ii} = 1, y_i = 4, \alpha_i = 1, \sigma_i = 2, i, j = 1, 2, i \neq j$.

2.1 Process of inhibitions. We define the right-continuous process $X(t) = (X_1(t), \dots, X_N(t))$, $t \geq 0$, with a state space $\mathbf{R}_+^N = (0, \infty)^N$ to be the process of inhibitions inductively in the following way.

i) The components $X_i(0)$, $i = 1, \dots, N$, are independent and

$$X_i(0) = \inf\{r > 0 : \eta_i(r) + (a_{ii} + a_i^0)e^{-\alpha_i r} = y_i e^{-\alpha_i r}\}. \quad (3)$$

ii) As long as all the components of $X(t)$ are strictly positive, they decrease in time with rate one until the first (random) time t_{i_1} that $X_{i_1}(t)$ reaches zero for some $i_1 \in \{1, \dots, N\}$. Let $T_1 = t_{i_1}$. Note that $t_{i_1} = \min_i X_i(0)$. Let, also

$$M_1 := \{1 \leq j \leq N : X_j = \min_i X_i(0)\}.$$

Then at time T_1 one has

$$X_i(T_1) = Y_i^{(1)}, \quad i \in M_1,$$

and

$$X_j(T_1) = X_j(0) - t_{i_1} + \theta_{jM_1}^{(1)}(X_j(T_1-)), \quad j \in \{1, \dots, N\} \setminus M_1, \quad (4)$$

where $Y_i^{(1)}$ for any i is an independent copy of the variable

$$Y_i = \inf\{\tau > 0 : \eta_i(\tau) + a_{ii}e^{-\alpha_i \tau} = y_i e^{-\alpha_i \tau}\}, \quad (5)$$

and for every $x > 0$, $1 \leq j \leq N$ and any subset $M \subseteq \{1, \dots, N\} \setminus \{j\}$, the random value $\theta_{jM}^{(1)}(x)$ is an independent copy of

$$\begin{aligned} \theta_{jM}(x) = \inf\{\tau > 0 : \eta_j(x + \tau) + a_{jj}e^{-\alpha_j(x+\tau)} + \\ + \sum_{i \in M} a_{ji}e^{-\alpha_j \tau} \geq y_j e^{-\alpha_j(x+\tau)} \mid \eta_j(x) + a_{jj}e^{-\alpha_j x} = y_j e^{-\alpha_j x}\}. \end{aligned} \quad (6)$$

iii) The process of the decreasing of all the components of the vector $X(t)$ starts all over again but now from the configuration $X(T_1)$.

Distributional equality of the sequence of firings in the net (2) and the sequence $\{T_n\}_{n=1}^\infty$ is proved in [7].

2.2 The vector-field of the conditioned mean jumps. Let, $a_{ij} \leq 0$ for all $i \neq j$, $i, j = 1, \dots, N$. Consider associated with the process of inhibitions $X(T_n)$, $n = 0, 1, \dots$, the Markov chain $\tilde{X}^n := X(T_n-)$, $n = 1, 2, \dots$, with state space

$$\mathbf{R}_{+,0}^N = \bigcup_{M \subseteq \{1, \dots, N\}} \mathbf{R}_{+,0}^{N,M},$$

where $\mathbf{R}_{+,0}^{N,M} := \{(x_1, \dots, x_N) : x_i = 0 \text{ if } i \in M, \text{ and } x_i > 0 \text{ if } i \notin M\}$. Note, that due to (3), (5) and (6), one has $\tilde{X}^n \in \bigcup_{i=1}^N \mathbf{R}_{+,0}^{N,i}$ with probability one, iff $a_{ij} \leq 0$ for all $i \neq j$, $i, j = 1, \dots, N$. If $\tilde{X}^n \in \mathbf{R}_{+,0}^{N,i}$ for some $1 \leq i \leq N$ and

$n \geq 1$, then it means in terms of our neural model, that the i -th neuron fires at time T_n .

In the case $N = 2$ the investigation of the process \tilde{X}^n can be simply reduced to the investigation of the Markov chain $\xi_n, n = 0, \dots$, on a line, where

$$\xi_n := \xi(\tilde{X}^{n+1}) := \begin{cases} \tilde{X}_1^{n+1}, & \text{if } \tilde{X}_1^{n+1} > 0, \\ -\tilde{X}_2^{n+1}, & \text{if } \tilde{X}_2^{n+1} > 0, \\ 0, & \text{otherwise.} \end{cases} \quad (7)$$

Let us define the conditioned mean jump function $V(u), u \in \mathbf{R}$:

$$V_i(u) := \mathbf{E}\{\xi_{n+1} - \xi_n \mid \xi_n = u\},$$

which is clearly time-homogeneous. In the case $M = \{j\}$ for $i \neq j$ we will write $\theta_{ij}(u) := \theta_{iM}(u)$. Consider now $\mathbf{E}\theta_{ij}(u)$ as a function of u and a_{ij} . We will use the notation $\theta_{ij}(u, a_{ij}) := \theta_{ij}(u)$. It is not difficult to derive the following bounds:

$$\mathbf{E}\theta_{ij}(u, a_{ij}) \leq C_1 e^{-\alpha_i u} |a_{ij}| \quad (8)$$

for all $|a_{ij}| \geq 0, u \geq 0$, and

$$C_1(\log |a_{ij}| - \alpha_i u) + B_1 \leq \mathbf{E}\theta_{ij}(u, a_{ij}) \leq C_2(\log |a_{ij}| - \alpha_i u) + B_2 \quad (9)$$

for all $|a_{ij}| > e^{\alpha_i u}, u \geq 0$, where $B_k, C_k, k = 1, 2$, are some positive constants independent of a_{ij} .

In the case $\alpha_i = \alpha > 0$ and $\sigma_i = \sigma > 0$ for all $i = 1, 2$, one can obtain an explicit classification of the vector field $V(u)$ on the line in terms of the parameters of the model. Namely, let for $i \neq j, i, j = 1, 2$

$$Q_i(|a_{ij}|) = \frac{1}{\alpha} \log \frac{|a_{ij}|}{y_j - a_{jj}} := \frac{\log \rho_{ij}}{\alpha}. \quad (10)$$

Then $V(Q_i) = 0$, if $\rho_{ij} > 1, i \neq j, i, j = 1, 2$, and

$$\begin{aligned} V(u) &> 0, & \text{if } u \in (-\infty, -\max\{Q_2, 0\}) \cup (0, \max\{Q_1, 0\}), \\ V(u) &< 0, & \text{if } u \in (-\max\{Q_2, 0\}, 0) \cup (\max\{Q_1, 0\}, \infty). \end{aligned} \quad (11)$$

Furthermore, from (8) we obtain:

$$\lim_{u \rightarrow +\infty} V(u) = -\mathbf{E}Y_2 < 0, \quad \lim_{u \rightarrow -\infty} V(u) = \mathbf{E}Y_1 > 0. \quad (12)$$

By analogy with dynamical systems, if $V(u) = 0$, we shall call the point u an attracting point of the chain $\{\xi_n\}$. In general, if $\rho_{ij} > 1$ for all $i \neq j$, then there are N attracting points q_i , lying on the hyperplanes $\mathbf{R}_{+,0}^{N,i}, i = 1 \dots, N$: $q_i := (Q_{1i}, \dots, Q_{Ni})$, with Q_{ji} defined by (10) for all $i \neq j$ and $Q_{ii} = 0$ for any $1 \leq i \leq N$.

It was proved in [7] that the process of inhibitions in the case $N = 2$ converges to a certain limit distribution, so that each neuron fires infinitely often with

probability one. Nevertheless, in the case when Q_1 or Q_2 is sufficiently large, one can expect according to (10)-(12), that only one neuron can keep firing for a "long" period of time.

In fact, simulation results (see Fig. 2) show clearly a linear growth of the mean time interval during which a neuron does not fire as a function of $|a|$ ($a < 0$), where $a = a_{ij}$ for all $i, j = 1, \dots, 10, i \neq j$, in the simulated net (2) with 10 neurons. We emphasize that the linear growth implies rather long time intervals of silence for one neuron. This should be compared to the bounds (8)-(9) for $E\theta_{ij}(x)$. The last fact confirms an idea in [4] concerning metastable effects in the stochastic neural network (2).

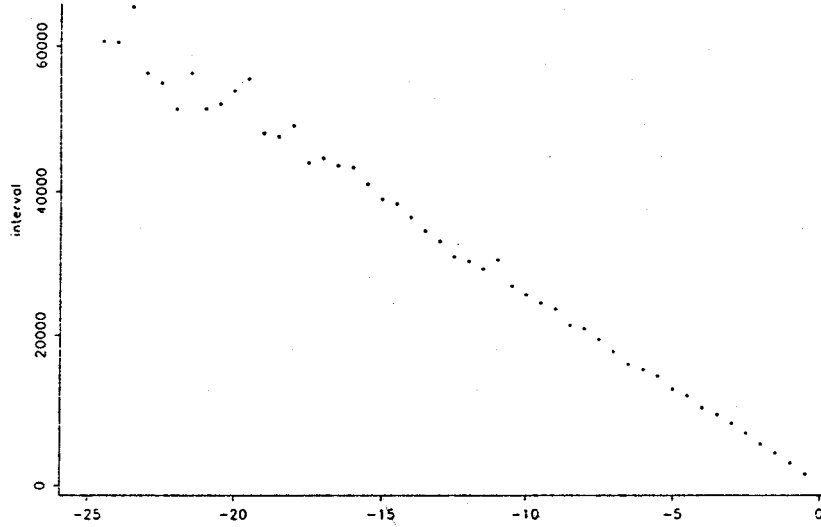


Fig. 2. The mean interspike interval as a function of $a < 0$
 for $N = 10$, $a_{ij} = a$, $a_{ii} = 1$, $y_i = 4$, $\alpha_i = 1$, $\sigma_i = 2$, $i, j = 1, \dots, 10, i \neq j$.

2.3 Minimum of the mean firing spacing in the model with excitatory connections. In Fig. 3 we depict the simulations of the mean interspike intervals as a function $a < 0$ in the simulated net (2) with 10 neurons, where $a_{ij} = a$ for all $i, j = 1, \dots, 10, i \neq j$. Note that the mean spacing characterizes the number of moments of firing per time unit. The importance of this is discussed in [3]. One can derive explicit formulas for the distributions of the random value $I_i(a)$ of the interspike intervals of the i -th neuron, $1 \leq i \leq N$, for two marginal cases $a = 0$ and $a = \infty$:

$$p_{i0}(u) := \frac{d}{du} \Pr\{I_i(0) < u\} = \frac{2\alpha_i e^{2\alpha_i u} \sqrt{\alpha_i} (y_i - a_{ii})}{\sigma_i \sqrt{\pi} (e^{2\alpha_i u} - 1)^3} \exp\left(-\frac{\alpha_i (y_i - a_{ii})^2}{(\sigma_i^2 e^{2\alpha_i u} - 1)}\right),$$

$$p_i(u) := \frac{d}{du} \Pr\{I_i(\infty) < u\} = p(u) := \frac{d}{du} \left(\prod_{j=0}^N \int_0^u p_{j0}(v) dv \right). \quad (13)$$

Although the case $a = \infty$ is unsuitable for neuronal modelling, formula (13) allows us to derive an upper bound for the minimum mean interspike interval, which minimum corresponds to the critical (finite!) value a_{cr} . This value exhibits the highest stable (in time) collective neuronal activity. Notice also that for any $E I_i(a_{cr}) < U < E I_i(\infty)$ there are two values of a , such that $E I_i(a) = U$.

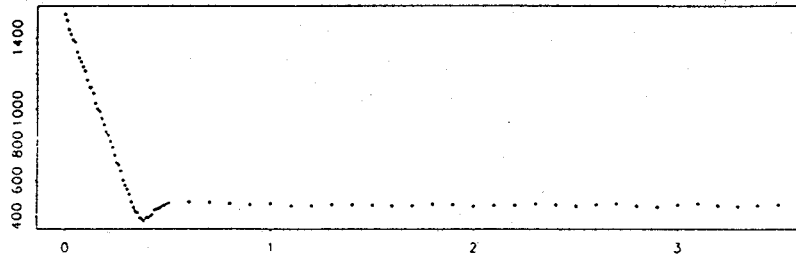


Fig. 3. The mean interspike interval as a function of $a > 0$ for $N = 10$, $a_{ij} = a$, $a_{ii} = 1$, $y_i = 4$, $\alpha_i = 1$, $\sigma_i = 2$, $i, j = 1, \dots, 10$, $i \neq j$.

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