

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Joint distribution of first exit times of a two dimensional Wiener process with jumps with application to a pair of coupled neurons

This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/137977> since 2015-12-31T10:59:49Z

Published version:

DOI:10.1016/j.mbs.2013.06.005

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)



UNIVERSITÀ DEGLI STUDI DI TORINO

This Accepted Author Manuscript (AAM) is copyrighted and published by Elsevier. It is posted here by agreement between Elsevier and the University of Turin. Changes resulting from the publishing process - such as editing, corrections, structural formatting, and other quality control mechanisms - may not be reflected in this version of the text. The definitive version of the text was subsequently published in

Mathematical Biosciences, Volume 245, Issue 1, September 2013, doi: 10.1016/j.mbs.2013.06.005

You may download, copy and otherwise use the AAM for non-commercial purposes provided that your license is limited by the following restrictions:

- (1) You may use this AAM for non-commercial purposes only under the terms of the CC-BY-NC-ND license.
- (2) The integrity of the work and identification of the author, copyright owner, and publisher must be preserved in any copy.
- (3) You must attribute this AAM in the following format: Creative Commons BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/deed.en>), [+ *Digital Object Identifier link to the published journal article on Elsevier's ScienceDirect® platform*]

Joint distribution of first exit times of a two dimensional Wiener process with jumps with application to a pair of coupled neurons

Laura Sacerdote, Cristina Zucca¹

Department of Mathematics “G. Peano”, University of Torino, Via Carlo Alberto 10, Turin, Italy

Abstract

Motivated by a neuronal modeling problem, a bivariate Wiener process with two independent components is considered. Each component evolves independently until one of them reaches a threshold value. If the first component crosses the threshold value, it is reset while the dynamics of the other component remains unchanged. But, if this happens to the second component, the first one has a jump of constant amplitude; the second component is then reset to its starting value and its evolution restarts. Both processes evolve once again until one of them reaches again its boundary. In this work, the coupling of the first exit times of the two connected processes is studied.

Keywords:

First passage time, Jump diffusion process, Wiener process, Integrate and fire neuronal model.

1. Introduction

Leaky integrate and Fire (LIF) models describe the membrane potential (MP) dynamics of single neurons through suitable diffusion processes constrained by a boundary. The process starts from the resting value of the membrane and evolves until it reaches, for the first time, a threshold value. These models assume that the MP of the neuron increases or decreases due to the arrival from the surrounding

Email addresses: laura.sacerdote@unito.it (Laura Sacerdote),
cristina.zucca@unito.it (Cristina Zucca)

¹Corresponding author: Cristina Zucca, Department of Mathematics “G. Peano”, University of Torino, Via Carlo Alberto 10, Turin, Italy, tel: +39-011-6702850, fax: +39-011-6702878.

network of excitatory or inhibitory postsynaptic potentials (PSPs). The neuron acts as an Integrator for the incoming inputs and the MP spontaneously decays in the absence of external inputs. When the inputs are of small amplitude and highly frequent, the discrete process describing the MP evolution is approximated by a diffusion process. The Ornstein-Uhlenbeck or the Feller (also known as Cox-Ingersoll-Ross) processes are the most popular diffusions used in LIF models (cf. [3, 4, 6, 14, 15, 16, 20]).

The analysis of these models requires the study of the First Exit Time (FET) problem of the diffusion through a boundary. Indeed the interspike intervals (ISIs) are identified with the FET of the stochastic process through the boundary. After each spike the membrane potential is reset to its resting value and successive ISIs are described by independent identically distributed (iid) random variables. The solution of the FET problem for diffusions is mathematically complex and considerable efforts have been put into its study. The only process for which a closed form expression of the FET distribution is available is the Wiener process. This process describes the membrane potential evolution disregarding its spontaneous decay toward the resting potential in the absence of external inputs. The model is known as the Integrate and Fire model (IF) and was proposed in a pioneering paper by Gerstein and Mandelbrot (cf. [8]). Despite its strong simplification, the IF model has played an important role in the study of single neurons dynamics. Numerical methods, reliable simulation techniques and approximate solutions are available for LIF models. However, no closed form solutions have been developed (cf. [20]). Hence, in order to develop suitable estimators for the parameters of the models and to get some insight on the qualitative behavior of LIF models, the Wiener process was used to test both numerical and simulation tools.

Simultaneous recordings of the spike activity of groups of neurons (the so called raster displays) are now available. Recent research disregards single neurons behaviors and focuses only on the features characterizing networks of neurons (cf. [2, 18, 24]). Observed dynamics include synchronism phenomena as well as delayed spikes and appearance of the specific spatio-temporal pattern in the raster displays (cf. [11]). Mathematical models have been an important tool for the study of the single neuron code and we expect that they will contribute to the understanding of neural networks. However, compared to single neuron models, neural networks present increased mathematical difficulties. Often researchers depend on simulations to study networks models. This fact may limit the interest of mathematical models. Hence the development of new mathematical tools for the study of neural networks is required. This paper is a first attempt in this direction.

Different classes of models describe neural networks. In some cases, the behavior of each neuron of the network is oversimplified and it is represented through a binary random variable. By contrast, Hodgkin and Huxley type models consider the most important biophysical features of the neuron but suffer from the drawback of using non linear systems of partial differential equations (cf. [9]). They are useful for simulation purpose [13] but their analytical study is discouraging. LIF models of single neurons are a good compromise between a reasonable realism and mathematical tractability. Hence they are good candidates for the mathematical study of neural networks as well as dependence properties of ISIs of groups of neurons. Some preliminary results in this frame can be found in [10, 25]. We propose the use of IF models as a first step toward the analytical study of a couple of neurons.

Mathematical difficulties of joint distributions of ISIs do not change when two or more neurons are considered. However, when dealing with many units networks, the notation become heavy. Hence, in this paper we limit ourselves to the study of two neurons. In Section 2 we consider the two neurons and following ([21, 22]) we model their MP evolution through diffusion processes with jumps. The dependence between the two neuron dynamics is determined by the jumps that occur in the MP of a neuron when the other neuron has a spike.

The description of the resulting coupled point processes requires the knowledge of the joint distribution of spike epochs of the two neurons. Unfortunately this study presents strong mathematical difficulties if the involved processes are the Ornstein Uhlenbeck or the Feller process. Previous research on this model used simulations but the development of suitable mathematical tools is desirable to achieve a better comprehension of the neural code. On the basis of the important role played by the IF models for the description of single neurons, in this paper we resort to the Wiener process with jumps to describe the MPs evolution. In Section 3 we introduce the necessary mathematical background and the notation required to deal with the processes involved in the model. In this frame we also introduce the forward times which characterize the spike time series. In Section 4, we present our results on the joint distribution of these times for the case of two neurons. Finally, in Section 5 some examples which illustrate the features of the considered network are discussed.

2. The model

We consider a couple of neurons. In absence of coupling, according to the IF paradigm, for $t > t_0$, we describe the subthreshold MP evolution of neuron 1

and 2 through two independent Wiener processes with drift $\mu_i \in \mathbb{R}$ and diffusion coefficient $\sigma_i > 0$,

$$dX_i(t) = \mu_i dt + \sigma_i dW_i(t). \quad (1)$$

with $X_i(t_0) = x_{0i}$, for $i = 1, 2$. Here $W_i(t), i = 1, 2$ are two independent standard Wiener processes.

Each neuron releases a spike when its MP reaches its threshold $b_i > x_{0i}$. After each spike their MP is reset to the resting value x_{0i} and the MP evolution restarts. ISIs of neurons are iid random variables. They are determined as FET of the Wiener process through their boundaries. Then we introduce the coupling between the two neurons dynamics as follows. The spike activity of neuron 2 determines an instantaneous jump, of amplitude h of the MP of neuron 1. When neuron 2 is excitatory the jump amplitude is positive while it is negative when neuron 2 is inhibitory. After the jump the MP of neuron 1 pursues its evolution as a Wiener process $X_1(t)$ until a new jump is determined by a spike of neuron 2 or until it attains its threshold b_1 (cf. Fig. 1). As soon as the MP value of neuron 1 becomes larger than the threshold value, neuron 1 releases a spike then its MP is instantaneously reset to its resting value. Then its evolution restarts with a new jump diffusion process. For neuron 1, the potential between spikes satisfies

$$d\tilde{X}_1(t) = \mu_1 dt + \sigma_1 dW_1(t) + h dN(t) \quad (2)$$

where $N(t)$ is a renewal process whose inter-event times have an inverse Gaussian distribution. Similar processes were studied in [12]. Neuron 1 and 2 spike simultaneously when the release of a spike from neuron 1 is determined by a jump of its MP. Note that in this model the spike activity of neuron 1 has no effect on neuron 2 but generalizations of this model could include a reciprocal effect of the spikes of the two neurons.

According to this model, the ISIs of neuron 1 are modeled as successions of FETs of the considered jump diffusion process from the interval $(-\infty, b_1)$ while the ISIs of neuron 2 are a sequence of FETs of the pure diffusion process through the threshold b_2 . ISIs of neuron 1 are independent random variables. However these random variables are dependent from the spikes epochs of neuron 2. In order to understand the properties of this dependence we have studied the joint distribution of specific times characterizing the two spike trains, specifically the joint distribution of forward times of the two spike trains (cf. [7]). In [22] simulations were used to study this distribution for the Ornstein Uhlenbeck process with jumps. Aiming to obtain analytical and numerical results, in this paper we limit our interest to the Wiener process with jumps. In the Section 4 we show

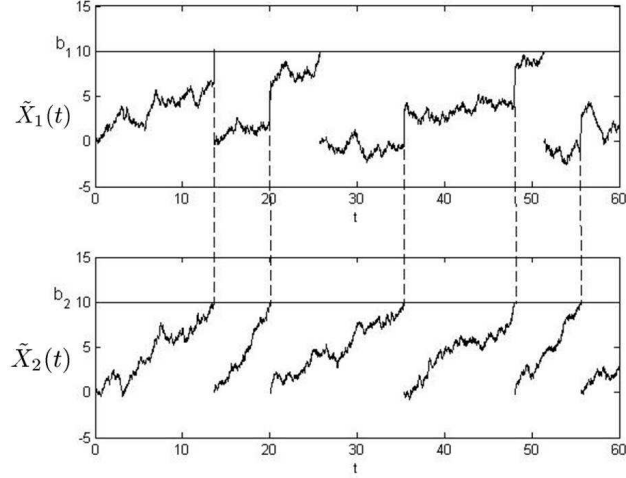


Figure 1: Trajectories of the evolution of the MP of the two neurons, with their spike times. The first spike time of \tilde{X}_1 and \tilde{X}_2 are synchronous due to the jump.

that this choice allows the determination of a closed form expression for this joint distribution, together with suitable bounds.

A particular instance of interest arises when the two neurons spike simultaneously. The proposed model allows the description of both this case and the case of ISIs which start at different epochs in the two spike trains. Extensions to more complex processes request further efforts that we will consider in future works.

3. Mathematical background

We consider the processes $\mathbf{X}(t) = \{(X_1, X_2)(t); t \geq t_0\}$, $\tilde{\mathbf{X}}(t) = \{(\tilde{X}_1, \tilde{X}_2)(t); t \geq t_0\}$ and $\mathbf{X}^a(t) = \{(X_1^a, X_2^a)(t); t \geq t_0\}$ and a two dimensional boundary $\mathbf{b} = (b_1, b_2) \in \mathbb{R}^2$. The first process is a two dimensional Wiener process whose components are independent and are described by (1). With $\tilde{\mathbf{X}}(t)$ we indicate the process obtained from $\mathbf{X}(t)$ by adding jumps to the first component any time the second component attains its boundary and characterized by instantaneous resetting of the spiking component, as explained in Section 2. Note that the realizations of the two processes are driven by the same Wiener process. Furthermore $\mathbf{X}^a(t)$ denotes the process $\mathbf{X}(t)$, with an absorbing boundary \mathbf{b} whose components are

$$X_i^a(t) = \begin{cases} X(t) & t < T_{b_i} \\ b_i & t \geq T_{b_i} \end{cases} \quad (3)$$

where $i = 1, 2$ and $b_1 > x_{01}$ and $b_2 > x_{02}$.

For a general process \mathbf{Y} we denote $F_{\mathbf{Y}}(\mathbf{y}, t | \mathbf{x}, s) = \mathbb{P}(\mathbf{Y}(t) < \mathbf{y} | \mathbf{Y}(s) = \mathbf{x})$ and

$$f_{\mathbf{Y}}(\mathbf{y}, t | \mathbf{x}, s) = \frac{\partial^2 \mathbb{P}(\mathbf{Y}(t) < \mathbf{y} | \mathbf{Y}(s) = \mathbf{x})}{\partial y_1 \partial y_2} \quad s < t \quad (4)$$

the transition probability distribution (pDf) and density function (pdf), respectively. Here we have $\mathbf{x} = (x_1, x_2) \in \mathbb{R}^2$ and $\mathbf{y} = (y_1, y_2) \in \mathbb{R}^2$. The transition pdf of $X_i^a(t)$, for $x, y \in (-\infty, b_i)$, $i = 1, 2$ is given by [5, 17]

$$f_{X_i^a}(x, t | y, s) = \frac{1}{\sigma_i \sqrt{2\pi(t-s)}} \left[\exp\left(-\frac{(x-y-\mu_i(t-s))^2}{2\sigma_i^2(t-s)}\right) - \exp\left(\frac{2\mu_i(b_i-y)}{\sigma_i^2} - \frac{(x-2b_i+y-\mu_i(t-s))^2}{2\sigma_i^2(t-s)}\right) \right]. \quad (5)$$

We denote the transition pDf as $F_{X_i^a}(x, t | y, s)$ (cf. [20]).

Each component of $\tilde{\mathbf{X}}$ attains its boundary b_i at times $\tilde{S}_{b_i}^{(k)}$, $k \in \mathbb{N}$ with $\tilde{S}_{b_i}^{(0)} = 0$. After each crossing the component is instantaneously reset to its initial value and restarts. Consider the k -th FET $\tilde{T}_{b_i}^{(k)}$ of the jump process \tilde{X}_i , that starts in x_{0i} at time $\tilde{S}_{b_i}^{(k-1)}$, through the boundary b_i for $k \in \mathbb{N}^+$. For $i = 1, 2$, $k \geq 2$, $\tilde{T}_{b_i}^{(k)}$ is a random variable whose distribution coincides with the conditional distribution of

$$\inf \left\{ t - \tilde{S}_{b_i}^{(k-1)} > 0 : \tilde{X}_i(t) > b_i \right\} \quad (6)$$

given $\tilde{S}_{b_i}^{(k-1)} = \rho$, where $\rho \geq 0$ and

$$\tilde{T}_{b_i}^{(1)} = \inf \{ t > 0 : \tilde{X}_i(t) > b_i \}. \quad (7)$$

Similarly, we denote as $T_{b_i}^{(k)}$ the k -th FET of the diffusion process X_i through the boundary b_i for $k \in \mathbb{N}$. Since $\tilde{X}_2(t)$ coincides with $X_2(t)$, we have $T_{b_2}^{(k)} = \tilde{T}_{b_2}^{(k)}$, where $\{T_{b_i}^{(k)}, k \geq 1\}$ are iid random variables with Inverse Gaussian (IG) distribution with mean $(b_i - x_{0i})/\mu_i$ and shape parameter $(b_i - x_{0i})^2/\sigma_i^2$, i.e., using the spatial homogeneity of the Wiener process, with pdf [5, 17]

$$f_{T_{b_i-x_{0i}}^{(k)}}(t) = \frac{b_i - x_{0i}}{\sqrt{2\pi\sigma_i^2 t^3}} \exp\left(-\frac{(b_i - x_{0i} - \mu_i t)^2}{2\sigma_i^2 t}\right). \quad (8)$$

We denote with $F_{T_{b_i-x_{0i}}^{(k)}}(t)$ its pDf (cf. [20]).

Since IG distribution is stable (cf. [19], p. 344), $S_{b_i}^{(k)}$ has again IG distribution with mean $(b_i - x_{0i})k/\mu_i$ and shape parameter $(b_i - x_{0i})^2 k^2 / \sigma_i^2$. We also note that the intertimes $\tilde{T}_{b_1}^{(k)}$, $k = 1, 2, \dots$ are not independent random variables, due to the absence of reset of the second component when the first component exits from its boundary.

In general, the boundary can be time dependent. We denote the FET of the Wiener process through the boundary $c(t)$ as $T_{c(t)}$.

For a given random variable Z we denote $F_Z(z) = \mathbb{P}(Z \leq z)$ and $f_Z(z)dz = \mathbb{P}(Z \in dz)$ the pDf and pdf, respectively. The pDf and pdf of the two dimensional random variable $\mathbf{T} = (T_{b_1}, T_{b_2})$, representing the FET of $\mathbf{X}(t)$ through \mathbf{b} , are $F_{\mathbf{T}}(\mathbf{t}) = \mathbb{P}(T_1 < t_1, T_2 < t_2)$ and $f_{\mathbf{T}}(\mathbf{t})$, respectively. Similar notation hold for the exit time $\tilde{\mathbf{T}}$.

We want to characterize the dependence between the two point processes determined by the sequence of crossings of the boundary. For this aim we introduce the forward time (cf. [7], p. 61). For $\tilde{S}_{b_1}^{(k)} = \rho$, with $\rho \geq 0$ we define the forward time $\Theta_{b_2}^{(\rho)}$ as the intertime between $\tilde{S}_{b_1}^{(k)}$ and the epoch, after $\tilde{S}_{b_1}^{(k)}$, when \tilde{X}_2 first crosses b_2 (cf. Fig. 2). The study of the joint distribution of $(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})$, given that $\tilde{S}_{b_1}^{(k)} = \rho$, characterizes the dependence between the two point processes and its study is the goal of this work.

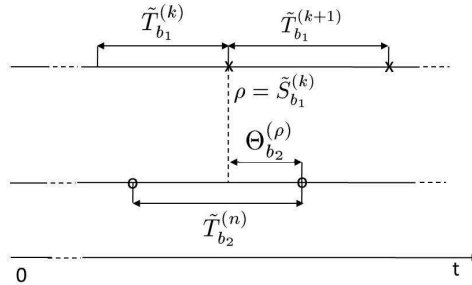


Figure 2: Scheme for the forward time $\Theta_{b_2}^{(\rho)}$.

4. Joint distribution of the forward times

The process $\tilde{X}_1(t)$ is not a Markov process due to the absence of resetting of the second component when the first crosses the boundary and due to the presence of jumps with intertimes characterized by IG distribution. However, both the bidimensional process $\tilde{\mathbf{X}}(t)$ and the second component $\tilde{X}_2(t)$ are Markov processes. Using this property we compute the joint pdf of the random variable $(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})$ conditioned on the event $\{\tilde{S}_{b_1}^{(k)} = \rho\}$.

This conditioning can then be removed by multiplying the conditioned density for the pdf $f_{\tilde{S}_{b_2}^{(k)}}(\rho)$, i.e. for the IG distribution, and integrating with respect to all admissible values of ρ . To simplify the notation, in the following we avoid to write explicitly the conditioning event, when not necessary.

Theorem 1. *Let us choose $k \in \mathbb{N}$, $S_{b_1}^{(k)} = \rho$. The joint pDf of $(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})$ is*

$$\begin{aligned}
F_{(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})}(u, v) &= \tag{9} \\
&= \int_0^{\min\{u, v\}} f_{T_{b_1}}(\tau) \int_{\tau}^v f_{\Theta_{b_2}^{(\rho)}}(\theta) d\theta d\tau + \\
&+ \int_0^{\min\{u, v\}} \int_{b_1-h}^{b_1} f_{X_1^a}(x, \rho + \theta | 0, \rho) f_{\Theta_{b_2}^{(\rho)}}(\theta) dx d\theta + \\
&+ \int_0^{\min\{u, v\}} f_{\Theta_{b_2}^{(\rho)}}(\theta) \int_{\theta}^u \underbrace{\sum_{n=0}^{\infty} \int_{\rho+\theta}^{\rho+\tau} \cdots \int_{\rho+\theta}^{\rho+\tau}}_{s_1 < s_2 < \dots < s_n} f_{(S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}, N_{[\rho+\theta, \rho+\tau]})}(s_1, \dots, s_n, n) \\
&\cdot \int_{-\infty}^{b_1} f_{T_{c_n(t)-\omega}}(\tau - \theta) f_{X_1^a}(\omega, \rho + \theta | 0, \rho) ds_1 \dots ds_n d\omega d\tau d\theta.
\end{aligned}$$

where

$$f_{\Theta_{b_2}^{(\rho)}}(v) = \int_{-\infty}^{b_2} f_{T_{b_2-z}}(v) \int_0^{\rho} f_{X_1^a}(z, \rho | 0, \xi) \sum_{k=0}^{\infty} f_{S_{b_2}^{(k)}}(\xi) d\xi dz, \tag{10}$$

$$\begin{aligned}
&f_{(S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}, N_{[\rho+\theta, \rho+\tau]})}(s_1, \dots, s_n, n) \tag{11} \\
&= f_{T_{b_2}^{(m)}}(s_1) f_{T_{b_2}^{(m+1)}}(s_2 - s_1) \dots f_{T_{b_2}^{(m+n)}}(s_n - s_{n-1}) (1 - F_{T_{b_2}^{(m+n+1)}}(\rho + \tau - s_k))
\end{aligned}$$

and

$$c_n(t) = \begin{cases} b_1 - h & t \in [0, s_1 - \rho - \theta] \\ b_1 - 2h & t \in (s_1 - \rho - \theta, s_2 - \rho - \theta] \\ \dots & \\ b_1 - nh & t \in (s_{n-1} - \rho - \theta, s_n - \rho - \theta] \\ b_1 - (n+1)h & t > s_n - \rho - \theta \end{cases} \quad (12)$$

Proof. To simplify the notation we set $k = 0$ and we write $\tilde{T}_{b_1}^{(1)} = \tilde{T}_{b_1}$. When $k \neq 0$ we have analogous formulae.

We write the joint pDf of $(\tilde{T}_{b_1}, \Theta_{b_2}^{(\rho)})$ as

$$\begin{aligned} F_{(\tilde{T}_{b_1}, \Theta_{b_2}^{(\rho)})}(u, v) &= \mathbb{P}(\tilde{T}_{b_1} < u, \Theta_{b_2}^{(\rho)} < v, \tilde{T}_{b_1} < \Theta_{b_2}^{(\rho)}) \\ &+ \mathbb{P}(\tilde{T}_{b_1} < u, \Theta_{b_2}^{(\rho)} < v, \tilde{T}_{b_1} > \Theta_{b_2}^{(\rho)}) \\ &+ \mathbb{P}(\tilde{T}_{b_1} < u, \Theta_{b_2}^{(\rho)} < v, \tilde{T}_{b_1} = \Theta_{b_2}^{(\rho)}). \end{aligned} \quad (13)$$

We start taking into account the first term in (13). When $\tilde{T}_{b_1} < \Theta_{b_2}^{(\rho)}$, the two components of $\tilde{\mathbf{X}}(t)$ evolve independently (cf. Figure 3 (b) and (d)). Hence we have $\tilde{T}_{b_1} = T_{b_1}$ and

$$\begin{aligned} \mathbb{P}(\tilde{T}_{b_1} < u, \Theta_{b_2}^{(\rho)} < v, \tilde{T}_{b_1} < \Theta_{b_2}^{(\rho)}) &= \int_0^{\min\{u, v\}} \mathbb{P}(\tau < \Theta_{b_2}^{(\rho)} < v | \tilde{T}_{b_1} = \tau) f_{T_{b_1}}(\tau) d\tau \\ &= \int_0^{\min\{u, v\}} f_{T_{b_1}}(\tau) \int_{\tau}^v f_{\Theta_{b_2}^{(\rho)}}(\theta) d\theta d\tau. \end{aligned} \quad (14)$$

To compute the distribution of $\Theta_{b_2}^{(\rho)}$ in (14), we first condition on the position of the second component $\tilde{X}_2(\rho)$ and then on the time ξ when \tilde{X}_2 crossed b_2 for the last time before ρ .

$$\begin{aligned} f_{\Theta_{b_2}^{(\rho)}}(\theta) d\theta &= \int_{-\infty}^{b_2} \mathbb{P}(\Theta_{b_2}^{(\rho)} \in d\theta | \tilde{X}_2(\rho) = z) \mathbb{P}(\tilde{X}_2(\rho) \in dz) \\ &= \int_{-\infty}^{b_2} f_{T_{b_2-z}}(\theta) \sum_{n=0}^{\infty} \int_0^{\rho} \mathbb{P}(\tilde{X}_2(\rho) \in dz | \tilde{S}_{b_2}^{(n)} = \xi) f_{\tilde{S}_{b_2}^{(n)}}(\xi) d\xi d\theta \\ &= \int_{-\infty}^{b_2} f_{T_{b_2-z}}(\theta) \sum_{n=0}^{\infty} \int_0^{\rho} f_{X_2^a}(z, \rho | 0, \xi) f_{\tilde{S}_{b_2}^{(n)}}(\xi) d\xi dz d\theta. \end{aligned} \quad (15)$$

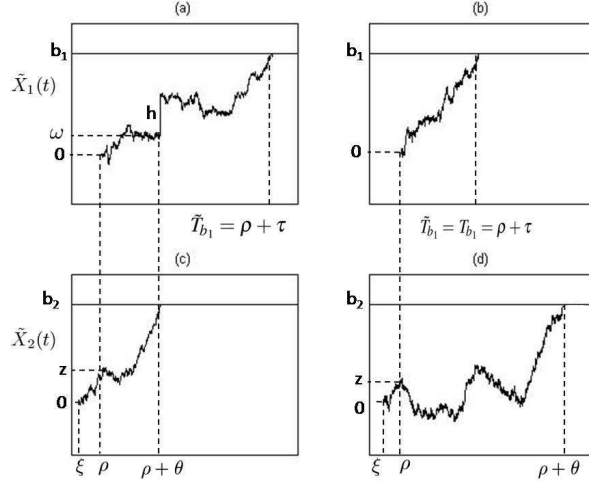


Figure 3: Trajectories of the two components in the case $\tilde{T}_{b_1} > \Theta_{b_2}^{(\rho)}$ ((a) and (c)) and in the case $\tilde{T}_{b_1} < \Theta_{b_2}^{(\rho)}$ where $\tilde{T}_{b_1} = T_{b_1}$ ((b) and (d)).

To write the second equality in (15) we used the Markov property and spatial homogeneity of the Wiener process.

Now we apply a similar procedure to compute the second term of (13). In this case the two components of $\tilde{\mathbf{X}}$ are not independent, due to the presence of one or more jumps. Since $\tilde{T}_{b_1} \neq T_{b_1}$

$$\mathbb{P}(\tilde{T}_{b_1} < u, \Theta_{b_2}^{(\rho)} < v, \tilde{T}_{b_1} > \Theta_{b_2}^{(\rho)}) = \int_0^{\min\{u,v\}} \int_{\theta}^u \mathbb{P}(\tilde{T}_{b_1} \in d\tau, \Theta_{b_2}^{(\rho)} \in d\theta) \quad (16)$$

Conditioning on the position of the process at the time of the first jump after $\tilde{S}_{b_1}^{(\rho)}$ we obtain (cf. Figure 3 (a) and (c))

$$\begin{aligned} & \mathbb{P}(\tilde{T}_{b_1} \in d\tau, \Theta_{b_2}^{(\rho)} \in d\theta) \\ &= \mathbb{P}(\tilde{T}_{b_1} \in d\tau | \Theta_{b_2}^{(\rho)} = \theta) \mathbb{P}(\Theta_{b_2}^{(\rho)} \in d\theta) \\ &= \int_{-\infty}^{b_1} \mathbb{P}(\tilde{T}_{b_1} \in d\tau | \Theta_{b_2}^{(\rho)} = \theta, \tilde{X}_1(\rho + \theta) = \omega) \\ & \quad \cdot \mathbb{P}(\tilde{X}_1(\rho + \theta) \in d\omega | \Theta_{b_2}^{(\rho)} = \theta) \mathbb{P}(\Theta_{b_2}^{(\rho)} \in d\theta). \end{aligned} \quad (17)$$

We have $\mathbb{P}(\tilde{X}_1(\rho + \theta) \in d\omega | \Theta_{b_2}^{(\rho)} = \theta) = f_{X_1^a}(\omega, \rho + \theta | 0, \rho) d\omega$ and $\mathbb{P}(\Theta_{b_2}^{(\rho)} \in$

$d\theta) = f_{\Theta_{b_2}^{(\rho)}}(\theta)d\theta$ is given in (15). Let m be the number of spikes of neuron 2 preceding $(\rho + \theta)$, $m \in \mathbb{N}$. The first term in the integral in (17) can be computed conditioning on the number and on the epochs of the jumps in $[\rho + \theta, \rho + \tau]$, that we denote with $N_{[\rho+\theta, \rho+\tau]}$ and $(S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)})$, respectively. We have

$$\begin{aligned} & \mathbb{P}(\tilde{T}_{b_1} \in d\tau | \Theta_{b_2}^{(\rho)} = \theta, \tilde{X}_1(\rho + \theta) = \omega) \\ &= \sum_{n=0}^{\infty} \underbrace{\int_{\rho+\theta}^{\rho+\tau} \dots \int_{\rho+\theta}^{\rho+\tau}}_{s_1 < s_2 < \dots < s_n} \\ & \quad \mathbb{P}((S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}) \in (ds_1, \dots, ds_n), N_{[\rho+\theta, \rho+\tau]} = n | \Theta_{b_2}^{(\rho)} = \theta, \tilde{X}_1(\rho + \theta) = \omega) \\ & \cdot \mathbb{P}(\tilde{T}_{b_1} \in d\tau | \Theta_{b_2}^{(\rho)} = \theta, \tilde{X}_1(\rho + \theta) = \omega, (S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}) = (s_1, \dots, s_n), N_{[\rho+\theta, \rho+\tau]} = n). \end{aligned} \quad (18)$$

Using the independence and the identical distribution of the intertimes $T_{b_2}^{(k)}$ we get

$$\begin{aligned} & \mathbb{P}((S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}) \in (ds_1, \dots, ds_n), N_{[\rho+\theta, \rho+\tau]} = n | \Theta_{b_2}^{(\rho)} = \theta, \tilde{X}_1(\rho + \theta) = \omega) \\ &= \mathbb{P}(T_{b_2}^{(m)} = ds_1, T_{b_2}^{(m+1)} = d(s_2 - s_1), \dots, T_{b_2}^{(m+n)} = d(s_n - s_{n-1}), T_{b_2}^{(m+n+1)} > \rho + \tau - s_n). \\ &= f_{T_{b_2}^{(m)}}(s_1) f_{T_{b_2}^{(m+1)}}(s_2 - s_1), \dots, f_{T_{b_2}^{(m+n)}}(s_n - s_{n-1}) (1 - F_{T_{b_2}^{(m+n+1)}}(\rho + \tau - s_n)) ds_1 \dots ds_n. \end{aligned} \quad (19)$$

The spatial and temporal homogeneity of the Wiener process allows to rewrite the last term in (18) as $f_{T_{c_n(t)-\omega}}(\tau - \theta)$, the FET pdf of a Wiener process through the time dependent boundary $c_n(t)$ (12) (cf. Figure 4 (a)).

The synchronism $\tilde{T}_{b_1} = \Theta_{b_2}^{(\rho)}$ is considered in the last term of (13). It arises when the first component crosses its boundary at a jump epoch, hence

$$\begin{aligned} & \mathbb{P}(\tilde{T}_{b_1} < u, \Theta_{b_2}^{(\rho)} < v, \tilde{T}_{b_1} = \Theta_{b_2}^{(\rho)}) \\ &= \int_0^{\min\{u, v\}} \mathbb{P}(\tilde{T}_{b_1} = \Theta_{b_2}^{(\rho)} | \Theta_{b_2}^{(\rho)} = \theta) \mathbb{P}(\Theta_{b_2}^{(\rho)} \in d\theta) \\ &= \int_0^{\min\{u, v\}} \mathbb{P}(\tilde{X}_1(\theta) \in [b_1 - h, b_1] | \Theta_{b_2}^{(\rho)} = \theta) \mathbb{P}(\Theta_{b_2}^{(\rho)} \in d\theta) \\ &= \int_0^{\min\{u, v\}} \int_{b_1 - h}^{b_1} f_{X_1^a}(x, \rho + \theta | 0, \rho) f_{\Theta_{b_2}^{(\rho)}}(\theta) dx d\theta. \end{aligned} \quad (20)$$

and we get the result. \square

Remark 1. Theorem 1 requests the knowledge of the density $f_{T_{c_n(t)-\omega}(\tau-\theta)}$ in (9). Note that the boundary $c_n(t)$ is a step function with jumps at times s_i , $i = 1, \dots, n$ (cf. Figure 4 (a)).

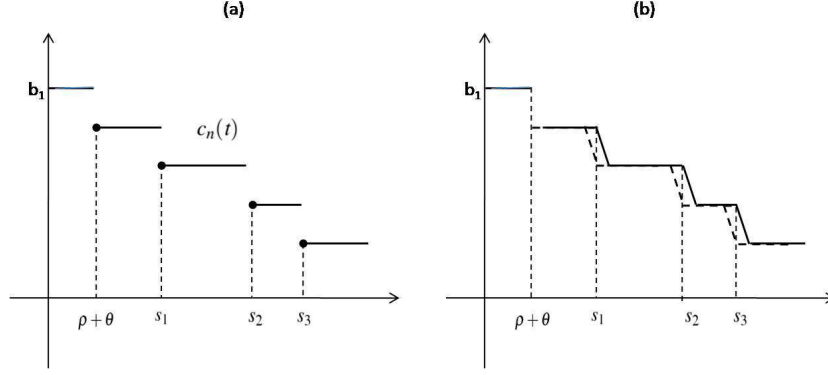


Figure 4: Scheme of: (a) the step boundary $c_n(t)$, (b) the two stepwise linear boundary: the lower bound $c_n^\alpha(t)$ (dotted line) and the upper bound $c_n^\beta(t)$ (solid line).

This density can be approximated using a result in [26] for a Wiener process with a stepwise linear boundary. We propose two stepwise linear boundaries $c_n^\alpha(t)$ and $c_n^\beta(t)$ to bound the step function $c_n(t)$ (cf. Figure 4 (b)).

$$c_n^\alpha(t) = \begin{cases} b_1 - h & t \in [0, s_1 - \rho - \theta - \varepsilon] \\ \frac{h}{\varepsilon}(s_1 - \rho - \theta - x) + (b_1 - 2h) & t \in (s_1 - \rho - \theta - \varepsilon, s_1 - \rho - \theta] \\ b_1 - 2h & t \in (s_1 - \rho - \theta, s_2 - \rho - \theta - \varepsilon] \\ \dots & \\ b_1 - nh & t \in (s_{n-1} - \rho - \theta, s_n - \rho - \theta - \varepsilon] \\ \frac{h}{\varepsilon}(s_n - \rho - \theta - x) + (b_1 - (n+1)h) & t \in (s_n - \rho - \theta - \varepsilon, s_n - \rho - \theta] \\ b_1 - (n+1)h & t > s_n - \rho - \theta \end{cases}$$

$$c_n^\beta(t) = \begin{cases} b_1 - h & t \in [0, s_1 - \rho - \theta] \\ \frac{h}{\varepsilon}(s_1 - \rho - \theta - x) + (b_1 - h) & t \in (s_1 - \rho - \theta, s_1 - \rho - \theta + \varepsilon] \\ b_1 - 2h & t \in (s_1 - \rho - \theta + \varepsilon, s_2 - \rho - \theta] \\ \dots & \\ b_1 - nh & t \in (s_{n-1} - \rho - \theta + \varepsilon, s_n - \rho - \theta] \\ \frac{h}{\varepsilon}(s_n - \rho - \theta - x) + (b_1 - nh) & t \in (s_n - \rho - \theta, s_n - \rho - \theta + \varepsilon] \\ b_1 - (n+1)h & t > s_n - \rho - \theta + \varepsilon \end{cases}$$

Clearly $c_n^\alpha(t) < c_n(t) < c_n^\beta(t)$, for each $t > 0$. Moreover, if ε is small, the probability of crossing of $c_n^\alpha(t)$, $c_n^\beta(t)$ or $c_n(t)$ are close.

Consider one of the two bounds, for example $c_n^\alpha(t)$. Consider the time sequence $\{t_i, i = 1, \dots, 2n\}$ where $t_{2j} = s_j - (\rho + \theta)$ and $t_{2j-1} = s_j - (\rho + \theta) - \varepsilon$, for $j = 1, \dots, n$ and denotes with $c = \{c_i, i = 1, \dots, 2n\}$ the sequence of knots of the stepwise linear boundary, where $c_{2j} = b_1 - (j+1)h - \omega$ and $c_{2j-1} = b_1 - jh - \omega$, for $j = 1, \dots, n$. Note that, conditioning on the position of the process \tilde{X}_1 at the time of the $2n$ jumps $t_i, i = 1, \dots, n$ and using Markov property and the result in [26], we get

$$\begin{aligned} & f_{T_{c_n^\alpha(t)-\omega}}(\tau - \theta) \\ &= \int_{-\infty}^{b_1 - (n+1)h} \left[f_{T_{b_1 - (n+1)h - x}}(\rho + \tau - s_n) \mathbb{E}[g(X_1(t_1), \dots, X_1(t_{2n}); c)] \right] dx \end{aligned} \quad (21)$$

where

$$g(x_1, \dots, x_{2n}; c) = \prod_{j=1}^{2n} I(x_j < c_j) \left(1 - \exp \left[-\frac{2(c_{j-1} - x_{j-1})(c_j - x_j)}{t_j - t_{j-1}} \right] \right). \quad (22)$$

Remark 2. If the jumps h are downward, the random variable $(\tilde{T}_{b_1}, \Theta_{b_2}^{(\rho)})$ admits pdf

$$\begin{aligned} & f_{(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})}(u, v) \\ &= \begin{cases} f_{T_{b_1}}(u) f_{\Theta_{b_2}^{(\rho)}}(v) & u \leq v \\ f_{\Theta_{b_2}^{(\rho)}}(v) \sum_{n=0}^{\infty} \underbrace{\int_{\rho+v}^{\rho+u} \cdots \int_{\rho+v}^{\rho+u}}_{s_1 < s_2 < \dots < s_n} f_{(S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}, N_{[\rho+v, \rho+u]})}(s_1, \dots, s_n, n) \\ \quad \cdot \int_{-\infty}^{b_1} f_{T_{c_n(t)-\omega}}(u-v) f_{X_1^a}(\omega, \rho+v | 0, \rho) ds_1 \dots ds_k d\omega & u > v \end{cases}, \end{aligned} \quad (23)$$

where $f_{\Theta_{b_2}^{(\rho)}}(v)$ is given by (10). On the contrary, for positive jumps, the pdf is singular.

Remark 3. Note that if $\tilde{T}_{b_1}^{(k+1)} < \Theta_{b_2}^{(\rho)}$ the component \tilde{X}_1 reaches its boundary before the component \tilde{X}_2 . It means that there are no jumps and therefore the two components are independent.

A special instance arises after a pair of synchronous crossings of the two components. In this case the forward time coincides with the intertime between two crossings of X_2 through b_2 . The following corollary holds

Corollary 2. *If $X_1(0) = X_2(0) = 0$, the joint pDf of $(\tilde{T}_{b_1}^{(1)}, \Theta_{b_2}^{(0)})$ is*

$$\begin{aligned}
F_{(\tilde{T}_{b_1}^{(1)}, \Theta_{b_2}^{(0)})}(u, v) &= \tag{24} \\
&= \int_0^{\min\{u, v\}} f_{T_{b_1}}(\tau) \int_{\tau}^v f_{T_{b_2}}(\theta) d\theta d\tau + \\
&+ \int_0^{\min\{u, v\}} \int_{b_1-h}^{b_1} f_{X_1^a}(x, \theta | 0, 0) f_{T_{b_2}}(\theta) dx d\theta + \\
&+ \int_0^{\min\{u, v\}} f_{T_{b_2}}(\theta) \int_{\theta}^u \sum_{n=0}^{\infty} \underbrace{\int_{\theta}^{\tau} \cdots \int_{\theta}^{\tau}}_{s_1 < s_2 < \dots < s_n} f_{(S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}, N_{[\theta, \tau]})}(s_1, \dots, s_n, n) \\
&\quad \int_{-\infty}^{b_1} f_{T_{c_n(t)-\omega}}(\tau - \theta) f_{X_1^a}(\omega, \theta | 0, 0) ds_1 \dots ds_k d\omega d\tau d\theta.
\end{aligned}$$

where $f_{(S_{b_2}^{(m)}, \dots, S_{b_2}^{(m+n)}, N_{[\rho+\theta, \rho+\tau]})}(s_1, \dots, s_n, n)$ is given by (11).

Proof. It is analogous to the proof of Theorem 1. \square

Since the density $f_{T_{c_n(t)-\omega}}(\tau - \theta)$ requests a strong computational effort, it is useful to determine alternative bounds for the joint pDf of $(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})$.

Theorem 3. *Let us choose $k \in \mathbb{N}$, $S_{b_1}^{(k)} = \rho$, the joint pDf of $(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})$ satisfies*

$$F_{(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})}^{\alpha}(u, v) \leq F_{(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})}(u, v) \leq F_{(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})}^{\beta}(u, v) \tag{25}$$

where

$$\begin{aligned}
F_{(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})}^{\alpha}(u, v) &= \tag{26} \\
&= \int_0^{\min\{u, v\}} f_{T_{b_1}}(\tau) \int_{\tau}^v f_{\Theta_{b_2}^{(\rho)}}(\theta) d\theta d\tau + \\
&+ \int_0^{\min\{u, v\}} \int_{b_1-h}^{b_1} f_{X_1^a}(x, \rho + \theta | 0, \rho) f_{\Theta_{b_2}^{(\rho)}}(\theta) dx d\theta +
\end{aligned}$$

$$\begin{aligned}
& + \int_0^{\min\{u,v\}} f_{\Theta_{b_2}^{(\rho)}}(\theta) \int_{\theta}^u \sum_{n=0}^{\infty} \left[F_{S_{b_2}^{(n)}}(\tau - \theta) - F_{S_{b_2}^{(n+1)}}(\tau - \theta) \right] \\
& \cdot \int_{-\infty}^{b_1} f_{T_{b_1-h-\omega}}(\tau - \theta) f_{X_1^a}(\omega, \rho + \theta | 0, \rho) d\omega d\tau d\theta.
\end{aligned}$$

and

$$\begin{aligned}
F_{\left(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)}\right)}(u, v) & = \tag{27} \\
& = \int_0^{\min\{u,v\}} f_{T_{b_1}}(\tau) \int_{\tau}^v f_{\Theta_{b_2}^{(\rho)}}(\theta) d\theta d\tau + \\
& + \int_0^{\min\{u,v\}} \int_{b_1-h}^{b_1} f_{X_1^a}(x, \rho + \theta | 0, \rho) f_{\Theta_{b_2}^{(\rho)}}(\theta) dx d\theta + \\
& + \int_0^{\min\{u,v\}} f_{\Theta_{b_2}^{(\rho)}}(\theta) \int_{\theta}^u \sum_{n=0}^{\infty} \left[F_{S_{b_2}^{(n)}}(\tau - \theta) - F_{S_{b_2}^{(n+1)}}(\tau - \theta) \right] \\
& \cdot \int_{-\infty}^{b_1} f_{T_{b_1-h(n+1)-\omega}}(\tau - \theta) f_{X_1^a}(\omega, \rho + \theta | 0, \rho) d\omega d\tau d\theta.
\end{aligned}$$

where $f_{\Theta_{b_2}^{(\rho)}}(v)$ is given by (10).

Proof. The ordering of the boundaries $b_1 - h(n+1) - \omega \leq c_n(t) \leq b_1 - h - \omega$, where $c_n(t)$ is given by (12), implies the stochastic ordering of the corresponding FETs [23]

$$T_{b_1-h-\omega} \leq_{st} T_{c_n(t)-\omega} \leq_{st} T_{b_1-h(n+1)-\omega} \tag{28}$$

that, for each $t > 0$, implies

$$F_{T_{b_1-h(n+1)-\omega}}(t) \leq F_{T_{c_n(t)}}(t) \leq F_{T_{b_1-h-\omega}}(t) \tag{29}$$

Applying these inequalities to (9) we get the result. \square

Remark 4. Similar results can be obtained considering backward times instead of forward times (cf. [7]).

5. Examples

We apply the results proved in Section 4 to some special cases of the couples of neurons in order to enlighten the dependency between their spiking activity in

terms of the parameters values. For simplicity we look for the joint distribution function of $(\tilde{T}_{b_1}^{(k+1)}, \Theta_{b_2}^{(\rho)})$ under the hypothesis of Corollary 2, i.e. in the case $\rho = 0$ and $k = 0$. We implement the bounds (26) and (27) and the pdf (23) for negative jumps, noting that all the functions involved are known in closed form for a Wiener process. The integrals are treated by means of quadrature methods and the series is truncated.

To interpret the figures of the following examples it is useful to recall that for $u < v$, the joint distribution describes the behavior of the MP of two independent neurons, while for $u > v$ it describes the effect of jumps.

5.1. One jump

Here we hypothesize that only one jump is admissible and that the two components start simultaneously. When process \tilde{X}_2 reaches its boundary it is absorbed; meanwhile, \tilde{X}_1 has a jump of amplitude h and then it pursues its evolution independently until it reaches its boundary. Under these hypothesis the result (24) is easily computable in closed form and becomes

$$\begin{aligned}
F_{(\tilde{T}_{b_1}^{(1)}, \Theta_{b_2}^{(0)})}(u, v) &= & (30) \\
&= \int_0^{\min\{u, v\}} f_{T_{b_1}}(\tau) \int_{\tau}^v f_{T_{b_2}}(\theta) d\theta d\tau + \\
&+ \int_0^{\min\{u, v\}} \int_{b_1-h}^{b_1} f_{X_1^a}(x, \theta|0, 0) f_{T_{b_2}}(\theta) dx d\theta + \\
&+ \int_0^{\min\{u, v\}} f_{T_{b_2}}(\theta) \int_{\theta}^u \int_{-\infty}^{b_1} f_{T_{b_1-h-\omega}}(\tau - \theta) f_{X_1^a}(\omega, \theta|0, 0) d\omega d\tau d\theta.
\end{aligned}$$

In Figure 5 the joint pdf and the corresponding contour plot of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ is shown. The parameters of the process are $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 10 \text{ mV}$ and the jump $h = 0.5 \text{ mV}$ is positive. Even if the parameters of the two components are the same, the joint pdf is not symmetric. This is explained by the one-way jumps that break the symmetry of the problem. Positive jumps, i.e. excitatory neuron 2, increase the probability that $\tilde{T}_{b_1} \approx \tilde{T}_{b_2}$. Indeed positive jumps create a discontinuity in the cDf along the synchronicity line $u = v$.

In Figure 6 the joint pdf of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ is shown with parameters $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = 10 \text{ mV}$, $b_2 = 8 \text{ mV}$ and positive jump $h = 0.5 \text{ mV}$. The difference between the boundaries determines a shift in the location of the probability mass, with respect to the case of Figure 5. Note that $b_1 > b_2$ implies

faster activity for neuron 2 with respect to neuron 1. However, the excitatory input from neuron 2 increases the frequency of neuron 1.

In Figure 7 the case of negative jump is described. The parameters of the process are $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 10 \text{ mV}$, and the jump $h = -2 \text{ mV}$ is negative. We note that there is no synchronous activity, due to the presence of negative jumps. Negative jumps, i.e. inhibitory activity of neuron 2, determine an increase of the mean of the spike intertimes of neuron 1. Furthermore, the probability mass is divided into two regions. The distance between these regions is related to the effect of the negative jumps and it increases as the jump $h < 0$ decreases (not shown in the figure).

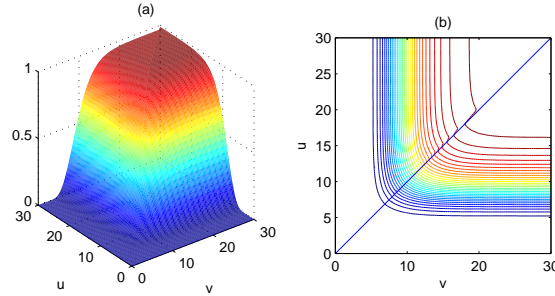


Figure 5: 1 jump: Joint pDf of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ with parameters $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 10 \text{ mV}$, $h = 0.5 \text{ mV}$: (a) pDf, (b) contour plot

5.2. n jumps

Here we extend the study performed in the previous subsection to the case of n jumps.

In Figure 8 the bounds of the joint pDf $F_{(\tilde{T}_{b_1}, \tilde{T}_{b_2})}(u, v)$ is shown for different value of u . The parameters of the process are $\mu_1 = \mu_2 = 0.7 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 5 \text{ mV}$, and the jump $h = 1 \text{ mV}$ is positive. Like in the one jump case, the presence of an excitatory neuron increases the probability that

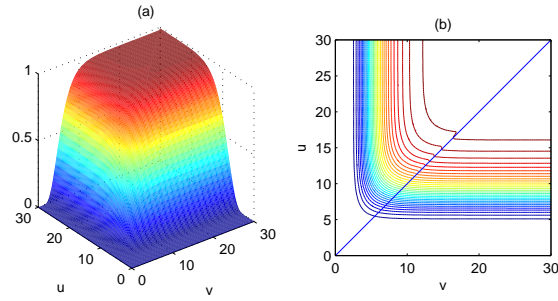


Figure 6: 1 jump: Joint pDf of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ with parameters $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = 10 \text{ mV}$, $b_2 = 6 \text{ mV}$, $h = 0.5 \text{ mV}$: (a) pDf, (b) contour plot

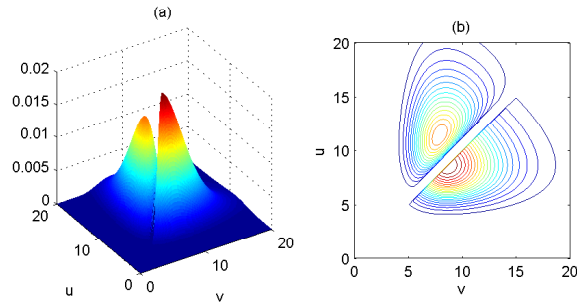


Figure 7: 1 jump: Joint pdf of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ with parameters $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 10 \text{ mV}$, $h = -2 \text{ mV}$: (a) pdf, (b) contour plot

$\tilde{T}_{b_1} \approx \tilde{T}_{b_2}$ as shown by the jump in the distribution. The two bounds are close and indicate a good approximation.

In Figure 9 the case of negative jump is described. The parameters of the process are $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 5 \text{ mV}$, and the jump $h = -0.5 \text{ mV}$ is negative. In this case we do not observe synchronous spikes.

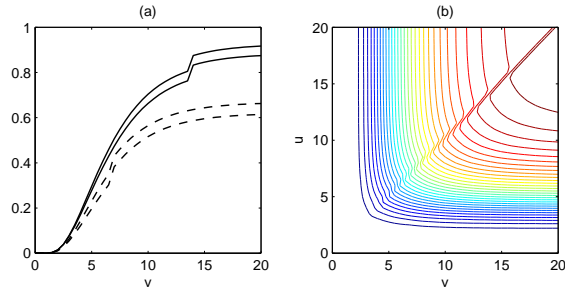


Figure 8: n jumps: Bounds for the joint pDf of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ with parameters $\mu_1 = \mu_2 = 0.7 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 5 \text{ mV}$, $h = 1 \text{ mV}$:(a) $u = 7$ (dotted line), $u = 15$ (solid line), (b) contour plot of the upper bound

6. Conclusions

The analysis of the dependence properties of the point processes is of interest for their application to neuronal networks. This study requests the knowledge of the joint distribution of the inter- and forward-times. Simulations are the typical methods for the study of these times. The use of the Wiener process to model the underlying behavior of the considered network allows an analytical and numerical approach. The proposed model considers a bivariate Wiener process whose components are linked via jumps and are constrained by boundaries. We derive a closed form expression of the joint distribution of FET and forward times and we implement it, performing a numerical study of the involved integrals. This suggests to pursue in this direction with the analysis of successive intertimes, i.e.

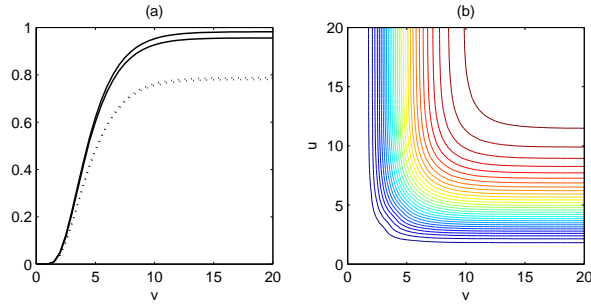


Figure 9: n jumps: Bounds for the joint pDf of of $(\tilde{T}_{b_1}, \tilde{T}_{b_2})$ with parameters $\mu_1 = \mu_2 = 1 \text{ mV ms}^{-1}$, $\sigma_1 = \sigma_2 = 1 \text{ mV ms}^{-1/2}$, $b_1 = b_2 = 5 \text{ mV}$, $h = -0.5 \text{ mV}$:(a) $u = 7$ (dotted line), $u = 15$ (solid line), (b) contour plot of the upper bound

$(\sum_{n=0}^{m_1} \tilde{T}_{b_1}^{(n)}, \Theta_{b_2}^{(\rho)} + \sum_{n=k+1}^{m_2} \tilde{T}_{b_2}^{(n)})$ for each choice of $k \in \mathbb{N}$, $m_1 \in \mathbb{N}$ and $m_2 \in \mathbb{N}$, $m_2 > k$. Other extensions could concern a model with more than two components. In this case the procedure is similar but numerics becomes computationally expensive. Unfortunately, a direct extension of the methodologies to other processes is not possible since the method is based on the Markov property and on the spatio-temporal homogeneity of the Wiener process.

The analytical results obtained in this work can be used to improve the statistical results obtained in [22].

Acknowledgments

Work supported in part by MIUR Project PRIN-Cofin 2008 and by project AMALFI - Advanced Methodologies for the AnaLysis and management of the Future Internet (Università di Torino/Compagnia di San Paolo).

References

- [1] Abramowitz M. and Stegun I. A. Handbook of Mathematical Functions With Formulas, Graphs, and Mathematical Tables. Dover, New York (1964)

- [2] Brunel N. and Hansel D. How noise affects the synchronization properties of recurrent networks of inhibitory neurons. *Neural Comput.* **18**, 1066–110 (2006)
- [3] Burkitt A.N. A review on Integrate-and-Fire neuron model: I . The Homogeneous synaptic input. *Biol Cybern* **95**, 1–19, (2006)
- [4] Burkitt A.N. A review on Integrate-and-Fire neuron model: I . The Inhomogeneous synaptic input and network properties. *Biol Cybern.* **95**, 97-112, (2006)
- [5] Cox H.D. and Miller D.R. *The Theory of Stochastic Processes.* Chapman & Hall (1965)
- [6] Capocelli R.M. and Ricciardi L.M. Diffusion approximation and the first passage time for a model neuron. *Kybernetik* **8**: 214-223 (1971)
- [7] Cox D.R. and Lewis P.A.W. *The Statistical Analysis of Series of Events.* Chapman and Hall, (1966)
- [8] Gerstein G.L. and Mandelbrot B. Random walk models for the spike activity of a single neuron. *Biophys. J.* **4**, 4168 (1964)
- [9] Gerstner W. and Kistler W.M. *Spiking Neuron Models Single Neurons, Populations, Plasticity.* Cambridge University Press, Cambridge (2002)
- [10] Giraudo M.T., Sacerdote L. and Sirovich R. Effects of random jumps on a very simple neuronal diffusion model. *BioSystems* **67**, 75–83 (2002)
- [11] Grün S. and Rotter P. *Analysis of Parallel Spike Trains.* Springer, New York (2010)
- [12] Hespanha J.P. and Teel A.R. Stochastic impulsive systems driven by renewal processes, in 17th International Symposium on Mathematical Theory of Networks and Systems (MTNS06), Kyoto, Japan, (2006)
- [13] Lago-Fernandez L.F., Huerta R., Corbacho F. and Siguenza J.A. Fast Response and Temporal Coding on Coherent Oscillations in Small-World Networks, *Phys. Rev. Lett.* **84**, 2758 (2000)

- [14] Lánský P. and Ditlevsen S. A review of the methods for signal estimation in stochastic diffusion leaky integrate-and-fire neuronal models. *Biol. Cybernetics*, **99**, 253–262, (2008)
- [15] Lánský P. and Lanska V. Diffusion approximations of the neuronal model with synaptic reversal potentials. *Biol. Cybern.* **56**, 19-26 (1987)
- [16] Lindner B., Schimansky-Geier L. and Longtin A. Maximizing spike train coherence or incoherence in the Leaky Integrate-and-Fire Model. *Physical Review E*, **66**, 031916, (2002)
- [17] Mehr C.B. and McFadden J.A. Certain properties of Gaussian processes and their first passage times. *J. Roy. Statist. Soc. Ser. B* **27** 505–22 (1965)
- [18] Paninski L., Lau B. and Reyes A. Noise-driven adaptation: in vitro and mathematical analysis. *Neurocomputing* **5254** 877-883 (2003)
- [19] Shiryaev A.N. *Probability*. Springer. (1996)
- [20] Sacerdote L. and Giraudo M.T. Stochastic integrate and fire models: a review on mathematical methods and their applications. To appear in *Lecture Notes in Mathematics, Series Mathematical biosciences* (2010)
- [21] Sacerdote L. and Sirovich R. Multimodality of the interspike interval distribution in a simple jump-diffusion model *Scientiae Mathematicae Japonicae*. **58** 2, 307–321 (2003)
- [22] Sacerdote L., Tamborrino M. and Zucca C. Detecting dependencies between spike trains of pairs of neurons through copulas, *Brain Res.* **1434**, 243–256 (2012)
- [23] Shaked M. and Shanthikumar J.G. *Stochastic Orders*. Springer (2007)
- [24] Tuckwell H.C. and Jost J. Moment analysis of the Hodgkin-Huxley system with additive noise. *Physica A* **388** 4115–4125 (2009)
- [25] Turova T.S. Analysis of a biologically plausible neural network via an hour-glass model. *Markov Process. Rel. Fields* **2**, 487–510 (1996)
- [26] Wang L. and Pötzelberger K. Boundary crossing probability for Brownian motion and general boundaries. *J. Appl. Probab.* **34**, 54–65 (1997)