The statistics of spikes trains: a stochastic calculus approach

Jonathan Touboul, Olivier Faugeras

INRIA

INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

The statistics of spikes trains: a stochastic calculus approach

Jonathan Touboul and Olivier Faugeras

N° 6224

June 21, 2007

Thème BIO

ISSN 0249-6399 ISRN INRIA/RR--6224--FR+ENG

INRIA
SOPHIA ANTIPOLIS

The statistics of spikes trains: a stochastic calculus approach

Jonathan Touboul and Olivier Faugeras

Thème BIO — Systèmes biologiques
Projet Odyssée *

Rapport de recherche n° 6224 — June 21, 2007 — 46 pages

Abstract: We discuss the statistics of spikes trains for different types of integrate-and-fire neurons and different types of synaptic noise models. In contrast with the usual approaches in neuroscience, mainly based on statistical physics methods such as the Fokker-Planck equation or the mean-field theory, we chose the point of the view of the stochastic calculus theory to characterize neurons in noisy environments. We present four stochastic calculus techniques that can be used to find the probability distributions attached to the spikes trains. We illustrate the power of these techniques for four types of widely used neuron models. Despite the fact that these techniques are mathematically intricate we believe that they can be useful for answering questions in neuroscience that naturally arise from the variability of neuronal activity. For each technique we indicate its range of application and its limitations.

Key-words: neuron models, stochastic processes, spikes trains statistics, first hitting time

* Odyssée is a joint project between ENPC - ENS Ulm - INRIA

Unité de recherche INRIA Sophia Antipolis
2004, route des Lucioles, BP 93, 06902 Sophia Antipolis Cedex (France)
Téléphone : +33 4 92 38 77 77 — Télécopie : +33 4 92 38 77 65

Statistiques de trains de spikes: le point de vue du calcul stochastique

Résumé : Nous nous intéressons aux statistiques de trains de spikes pour différents types de neurons intègre-et-tire et différents types de modèles de bruit synaptique. A la différence des approches classiques en neurosciences, principalement basées sur des méthodes de physique statistique telles que l'équation de Fokker-Planck ou la théorie du champ moyen, nous choisissons le point de vue de la théorie du calcul stochastique pour charactériser les neurones dans des environnements bruités. Nous présentons quatre méthodes de calcul stochastique qui peuvent être utilisées pour charactériser la distribution de probabilité des trains de spikes. Nous illustrons la puissance de ces techniques pour quatre types de modèles de neurones couramment utilisés. Bien que ces techniques soient mathématiquement complexes, nous croyons qu'elles peuvent être utiles pour répondre aux questions de neuroscience qui se posent naturellement quand on s'intéresse à la variabilité de l'activité neuronale. Pour chacune des techniques proposées, nous indiquons son domaine d'application et ses limites.

Mots-clés : modèles de neurones, processus stochastiques, temps de spikes, premier temps d'atteinte

Introduction

During the past thirty years, modelling and understanding the effects of noise in cortical neurons has been a central and difficult endeavor in neuroscience. Many approaches have been used in order to characterize the spikes trains, most of them borrowed form statistical physics. At the level of the cell, the effects of noise have been studied first by Knight [33] who introduced and studied the first noisy integrate-and-fire neuron model. His work has been generalized by Gerstner [26]. Brunel used the Fokker-Planck equation to characterize the effect of noise at the level of the cell [12, 11] and of the network [10, 9]. Samuelides and his colleagues used the meanfield and large deviations framework to characterize large sets of randomly connected neurons driven by noise [56]. In the present paper we adopt the point of view of the theory of stochastic calculus in an attempt to characterize the stochastic properties of neuron models and the statistics of the spikes trains they generate. We illustrate these techniques with four types of widely used neuron models.

The techniques are mathematically quite intricate. Nevertheless, we believe that they can be useful for answering questions in neuroscience that naturally arise from the variability of neuronal activity. For instance, they can give access to the probability distribution of the spikes trains, while other methods only give partial informations on this distribution. Moreover, the use of stochastic calculus methods enables us to get rid of such technical hypotheses as the stationarity of the process, the sparsity of the networks or the time scales approximations, which are generally required. For each technique presented we indicate its range of applicability and its limitations.

In the first section, we discuss the origin of the variability in cortical neurons and their mathematical modelling, and justify the use of the Brownian motion. In the second section, we present different classical mathematical models, which differ in their intrinsic dynamics or in the noise models used. The third section is dedicated to the presentation of four important stochastic methods for computing spikes trains statistics, and to their application to the different types of neurons presented in the second section. A large appendix summarizes briefly the main mathematical notions that are needed in order for the paper to be self-consistent for readers whose stochastic calculus is a bit rusty.

1 Noise in neurons: sources and models

In vivo recordings of neuronal activity are characterized by their high variability. Different studies of the spikes trains of individual neurons indicate that the firing patterns seem to be random. The origin of the irregularity in the electrical activity of cortical neurons in vivo has been widely studied and has received no satisfactory answer so far. Nevertheless it is commonly admitted that a) part of this variability can be considered as noise [60, 58], and b) that a large part of the noise experienced by a cortical neuron is due to the intensive and random excitation of synaptic sites.

We describe some of the biological evidence that supports these statements and propose mathematical models of the synaptic noise.

1.1 Sources of variability

It is generally agreed that a large part of the noise experienced by a cortical neuron is due to the intensive and random excitation of synaptic sites.

It has been observed from *in vivo* recordings of cortical neurons, in awake [15] and anesthetized animals [18] that a spontaneous activity exists and that the related spike process can be considered as Poisson. This Poisson model of independent synaptic inputs, or rather its diffusion limit approximation, is the model we use here.

The origin of irregularities is still poorly known. Gerstner and Kistler in [26] discuss this question at length. They obtain an interesting classification, and show that we can distinguish between intrinsic noise sources that generates stochastic behavior at the level of the neuronal dynamics and extrinsic sources arising from network effects and synaptic transmission. We briefly summarize the main points:

- A permanent noise source is the thermal noise linked with discrete nature of electric charge carriers. Fluctuations linked with this phenomenon are however of minor importance compared to other noise sources in neurons.
- The finite number of ion channels is another noise source.Most of the ion channel have only two states: they are open or closed. The electrical conductivity of a patch of membrane is proportional to the number of open ion channels. The conductivity therefore fluctuates and so does the potential[1]
- Noise is also due to signal transmission and network effects (extrinsic noise): synaptic transmission failures, randomness of excitatory and inhibitory connections, for instance, and global networks effects (see for instance [10]) where random excitatory/inhibitory connectivity can produce highly irregular spikes trains even in the absence of noise.

In term of neuron models we concentrate on several classes of integrate-and-fire spiking neuron models because they bring together a relative mathematical simplicity and a great power of expression. In this field, Knight [33], pioneered the study of the effect of noise with a simplified model in which the threshold was drawn randomly after each spike. Gerstner [26] extended these results and studied both slow noise models, in which either the threshold or the reset is drawn randomly after each spike, and fast escape rate noise models. In the context of synchrony in neuronal networks, Abbott *et al* [1] studied a phase noise model. However, none of these models can represent in a realistic way the synaptic noise as experienced by cortical neurons.

We concentrate on the effect of synaptic currents. Synaptic currents can be described by a simple system of ordinary differential equations (see for instance [17]). We study the impact of noise originating from realistic synaptic models on the dynamics of the firing probability of a spiking neuron.

[1] There exists models taking into account the finite number of ion channel, and that they can reproduce the observed variability in some cases(see for instance [16])

Because of space constrains we only explore two levels of complexity for the synaptic currents, 1) instantaneous (described by delta function) synaptic currents, and 2) synaptic currents described by an instantaneous jump followed by an exponential decay. The dynamics of the firing probability of a neuron receiving a bombardment of spikes through such synaptic currents is studied in the framework of the diffusion approximation (in the neuronal context, see [66]). This approximation is justified when a large number of spikes arrive through synapses that are weak compared to the magnitude of the firing threshold, which is the relevant situation in the cortex. In the diffusion approximation, the random component in the synaptic currents can be treated as a Brownian motion in the case of instantaneous synapses. On the other hand, when synapses have a finite temporal response, as in the more realistic models, synaptic noise has a finite correlation time and thus becomes "colored" noise. Thanks to the diffusion approximation, the dynamics of the firing probability can be studied in the framework of the stochastic calculus theory (see for instance [31]).

1.2 Synaptic noise modeling

Many mathematical descriptions of the synaptic current I^{syn} have been proposed (see Destexhe *et al* [17] or [26]). We consider two types of increasingly complex synaptic current models:

(i). Instantaneous synapses: if we neglect the synaptic integration, considering that the synaptic time constants are small with respect to the membrane interaction, the post-synaptic input can be described by a Brownian motion, which is the diffusion approximation of a rescaled sum of Poisson processes. For this we assume that the synaptic inputs are spikes arriving at N synapses $i \in \{1, \ldots, N\}$, each with a synaptic efficiency ω_i, at the spikes times t_i^k. The input synaptic current can be written:

$$dI_t^{\text{syn}} = \sum_{i=1}^{N} \omega_i \sum_k \delta(t - t_i^k) \stackrel{\text{def}}{=} \sum_{i=1}^{N} \omega_i dS_i(t), \tag{1.1}$$

where the $S_i(t)$s are point processes representing the spikes trains arriving in each synapse.

Neurons are connected to thousand of neurons (in general, $N \approx 10^3 - 10^4$). If we assume that the synaptic input spikes times follow a probability law with mean μ_i and variance σ_i^2 (for instance Poisson processes, $\sigma_i^2 = \mu_i$) and are pairwise independent[2], I^{syn} is the sum of N independent Poisson processes, of mean $\omega_i \mu_i$ and of variance

[2]The independence hypothesis is a key hypothesis and is quite difficult to justify biologically. Nevertheless, the same result would hold under very technical and strong conditions on the decorrelation of the process. It is a very intricate theory and we will not deal with it here.

$\omega_i^2\mu_i$. We assume that the ω_is are such that there exist μ, σ in $(0,\infty)$ such that[3]:

$$\begin{cases} \sum_{i=1}^N \omega_i\mu_i \underset{N\to\infty}{\longrightarrow} \mu \\ \sum_{i=1}^N \omega_i^2\mu_i \underset{N\to\infty}{\longrightarrow} \sigma^2 \end{cases}$$

By Donsker's theorem [5]

$$\sum_{i=1}^N \omega_i\Big(S_i(t)-\mu_i t\Big) \xrightarrow{\mathcal{L}} \sigma W_t \tag{1.2}$$

where $(W_t)_{t\geq 0}$ is a standard Brownian motion (see Appendix A.1 for a definition), and the symbol $\xrightarrow{\mathcal{L}}$ indicates that the process on the lefthand side converges in law to the process on the righthand side when $N\to\infty$.

The diffusion approximation consists in approximating the synaptic jump process (1.1) by the continuous process:

$$I_t^{\text{syn}} = \mu t + \sigma W_t \tag{1.3}$$

(ii). Exponentially decaying synaptic current: because the postsynaptic interaction has a finite integration time, say τ_s, the following equation arises naturally

$$\tau_s dI_t^{\text{syn}} = -I_t^{\text{syn}}dt + \sum_{i=1}^N \omega_i \sum_k \delta(t-t_i^k) \tag{1.4}$$

Note that we have assumed that τ_s was the same for all synapses and neglected the rise time of the synaptic current. The second assumption is justified on the ground that the rise time of a synapse is typically very short compared to the relaxation time.

A diffusion approximation similar to the one in the previous paragraph yields the following diffusion approximation of the synaptic noise with exponential decay:

$$\tau_s dI_t^{\text{syn}} = \left(-I_t^{\text{syn}}+\mu\right)dt + \sigma dW_t \tag{1.5}$$

2 Neuron Models

In this paper, a *neuron model* is defined by (i) a membrane potential dynamics and (ii) a synaptic dynamics. The neuron emits a spike when its membrane potential reaches a, possibly time-varying, threshold function $\theta(t)$. We are interested in characterizing the sequence $\{t_i\}$, $i=1,\cdots$, $t_i>0$, $t_{i+1}>t_i$ when the neuron emits spikes. We present four

[3] In general this condition can be achieved by a rescaling and a change of time applied to the process

simple models of spiking neurons submitted to noisy synaptic input, discuss their biological relevance and perform a basic stochastic analysis of the spikes times. In detail, a neuron model is defined by an equation:

$$\tau_m dV_t = f(t, V_t)\, dt + I_e(t)\, dt + dI^{\text{syn}}(V_t, t) \tag{2.1}$$

where $f(t, v)$ governs the free membrane potential dynamics, $I_e(t)$ is the injected or external current and the deterministic term of synaptic integration, and I_t^{syn} represents the noisy synaptic inputs due to background synaptic activity.

In the following sections, we review different models of neuronal dynamics in which the synaptic current can be described by one of the models discussed in section 1.2.

2.1 Model I: The noisy leaky integrate-and-fire model with instantaneous synaptic current

The simplest model we consider is the integrate and fire where the membrane potential V follows the following stochastic differential equation:

$$\begin{cases} \tau_m dV_t = (V_{\text{rest}} - V_t + I_e(t))\, dt + \sigma dW_t \\ V_0 = 0 \end{cases} \tag{2.2}$$

where τ_m is the time constant of the membrane, V_{rest} the rest potential and W_t a Brownian process representing the synaptic input. This equation is the Ornstein-Uhlenbeck equation. The neuron emits a spike each time its membrane potential reaches a threshold θ or a threshold function $\theta(t)$. When a spike is emitted, the membrane potential is reinitialized to the initial value, e.g. 0.

This is the simplest continuous noisy spiking model. The leaky integrate-and-fire neuron was first introduced by Lapicque [37] in a discussion on membrane polarizability. It idealizes the neuron as a capacitor in parallel with a resistor and driven by a current I_e (see e.g. [26]).

The noisy integrate-and-fire neuron with instantaneous synaptic current (2.2) has recently received a lot of attention to investigate the nature of the neural code [42, 65, 13, 57]. As shown in section 1.2, equation (1.3), it can be seen as the diffusion approximation of Stein's model [25, 61] where the synaptic inputs are considered as Poisson processes.

It is one of the few neuronal models for which analytical calculations can be performed. Indeed, equation (2.2) can be solved in a closed form:

$$V_t = V_{\text{rest}}(1 - e^{-\frac{t}{\tau_m}}) + \tfrac{1}{\tau_m}\int_0^t e^{\frac{s-t}{\tau_m}} I_e(s)\, ds + \tfrac{\sigma}{\tau_m}\int_0^t e^{\frac{s-t}{\tau_m}} dW_s \tag{2.3}$$

The stochastic process V_t is Gauss-Markov. It is the sum of a deterministic part and the product of e^{-t/τ_m} with the random process $\int_0^t e^{s/\tau_m} dW_s$ defined by a stochastic integral (see appendix A.1). Thanks to a change of time scale through the Dubins-Schwarz' theorem A.6 it can be turned into a Brownian motion. It is easy to show that it is a centered Gauss-Markov process with covariance function $\rho(t) = \frac{\tau_m}{2}\left(e^{2\frac{t}{\tau_m}} - 1\right)$. This function is used in the

application of the Dubins-Schwarz' theorem to change the time scale to obtain a Brownian motion: $\int_0^t e^{s/\tau_m} dW_s \stackrel{\mathcal{L}}{=} W_{\rho(t)}$.

The spiking condition of this neuron, $V_t = \theta(t)$, can be written in term of this simpler stochastic process:

$$\int_0^t e^{\frac{s}{\tau_m}} dW_s = W_{\rho(t)} = \frac{\tau_m}{\sigma}\left[(\theta(t) - V_{\text{rest}})\, e^{\frac{t}{\tau_m}} + V_{\text{rest}} - \frac{1}{\tau_m}\int_0^t s e^{\frac{s}{\tau_m}} I_e(s)\, ds\right] \stackrel{\text{def}}{=} a(t) \quad (2.4)$$

In order to fulfill our program we are thus naturally led to study the first hitting time of the Brownian motion $W_{\rho(t)}$ to the curved boundary $a(t)$.

2.2 Model II: The noisy leaky integrate-and-fire model with exponentially decaying synaptic current

We modify the model of section 2.1 to include an exponentially decaying synaptic current as described in section 1.2, equation (1.5):

$$\begin{cases} \tau_m dV_t &= (V_{\text{rest}} - V_t)dt + I_e(t)dt + I_t^{\text{syn}} dt \\ \tau_s dI_t^{\text{syn}} &= -I_t^{\text{syn}} dt + \sigma dW_t \end{cases}$$

This model is a more precise description of the synaptic current and is still simple enough to be analyzed mathematically. Nevertheless, its analytical study is quite challenging and only a few results are available.

We integrate this system of two stochastic differential equations as follows. The first equation yields

$$V_t = V_{\text{rest}}(1 - e^{-\frac{t}{\tau_m}}) + \frac{1}{\tau_m}\int_0^t e^{\frac{s-t}{\tau_m}} I_e(s)\, ds + \frac{1}{\tau_m}\int_0^t e^{\frac{s-t}{\tau_m}} I_s^{\text{syn}}\, ds,$$

and the second equation can be integrated as

$$I_t^{\text{syn}} = I_0^{\text{syn}} e^{-\frac{t}{\tau_s}} + \frac{\sigma}{\tau_s}\int_0^t e^{\frac{s-t}{\tau_s}} dW_s,$$

where I_0^{syn} is a given random variable.

We define $\frac{1}{\alpha} = \frac{1}{\tau_m} - \frac{1}{\tau_s}$. Replacing in the first equation I_t^{syn} by its value in the second equation we obtain

$$V_t = V_{\text{rest}}(1 - e^{-\frac{t}{\tau_m}}) + \frac{1}{\tau_m}\int_0^t e^{\frac{s-t}{\tau_m}} I_e(s)\, ds + \frac{I_0^{\text{syn}}}{1 - \frac{\tau_m}{\tau_s}}(e^{-\frac{t}{\tau_s}} - e^{-\frac{t}{\tau_m}}) + \frac{\sigma}{\tau_m \tau_s} e^{-\frac{t}{\tau_m}} \int_0^t e^{\frac{s}{\alpha}} \left(\int_0^s e^{\frac{u}{\tau_s}} dW_u\right) ds$$

The membrane potential is the sum of a deterministic process and a function of the non-Markov Gaussian differentiable process[4] X_t defined by:

$$X_t = \int_0^t e^{s/\alpha} \left(\int_0^s e^{u/\tau_s} dW_u \right) ds \tag{2.5}$$

The spiking condition can be written:

$$X_t = -\frac{\alpha\tau_s}{\sigma} I_0^{\text{syn}} (e^{\frac{t}{\alpha}} - 1) + \frac{\tau_m \tau_s}{\sigma} \left[(\theta - V_{\text{rest}})\, e^{\frac{t}{\tau_m}} + V_{\text{rest}} - \frac{1}{\tau_m} \int_0^t e^{\frac{s}{\tau_m}} I_e(s)\, ds \right]. \tag{2.6}$$

Studying the spikes sequence of the LIF model with exponentially decaying synaptic currents amounts to studying the first hitting time of the process X_t defined by (2.5) to a continuous deterministic boundary.

With no significant analytical complexity we deal with a slightly more general process, which we call the *double integral process* (DIP), defined by:

$$X_t := \int_0^t g(s) M_s ds = \int_0^t g(s) \left(\int_0^s f(u) dW_u \right) ds \tag{2.7}$$

for some real measurable functions f and g.

We already noted that the process X_t was non Markovian. We show in appendix C that the two-dimensional process (X_t, M_t) is a Gaussian Markov process, and furthermore, conditionally to M_s, that the increments $(X_t - X_s, M_t - M_s)$ are independent of the σ-field $\mathcal{F}_s$ (see appendix A.1 for the definitions of these terms).

For a given t, the random variable $Y_t := (X_t, M_t)$ is a Gaussian two-dimensional variable of parameters:

$$\left\{ \begin{array}{ll} \mathbb{E}(Y_t) & = (0,0) \\ \mathbb{E}[Y_t^T \cdot Y_t] & = \begin{pmatrix} \rho_X(t) & C_{(X,M)}(t) \\ C_{(X,M)}(t) & \rho_M(t) \end{pmatrix} \end{array} \right. \tag{2.8}$$

where the functions $\rho_X(t)$, $C_{(X,M)}(t)$ and $\rho_M(t)$ are defined by:

$$\left\{ \begin{array}{ll} \rho_M(t) & := \int_0^t f(s)^2 ds \\ \rho_X(t) & := 2 \int_0^t g(s) \left(\int_0^s g(u) \rho_M(u) du \right) ds \\ C_{(X,M)}(t) & := \int_0^t g(s) \rho_M(s) ds \end{array} \right. \tag{2.9}$$

It can be checked that the Markov process $(Y_t)_t$ transition measure (see Appendix A.2 for a definition) has a Gaussian density w.r.t. Lebesgue's measure ds:

$$\mathcal{N}\left(\begin{pmatrix} x_s + m_s \int_s^t g(u) du \\ m_s \end{pmatrix}, \tilde{C}(s,t) \right) \tag{2.10}$$

[4] The proof that X_t is non-Markov is given in Appendix C.

where the correlation matrix $\tilde{C}(s,t)$ reads:

$$\tilde{C}(s,t) = \begin{pmatrix} 2\int_s^t g(u)\left(\int_s^u g(v)\int_s^v f(w)^2\, dw\, dv\right) du & \int_s^t g(u)\left(\int_s^u f(v)^2 dv\right) du \\ \int_s^t g(u)\left(\int_s^u f(v)^2 dv\right) du & \int_s^t f(u)^2 du \end{pmatrix} \tag{2.11}$$

We now define the simplest non trivial double integral process, which turns out to be of great interest for the study of the spike train statistics of the present model of neuron: the *Integrated Wiener Process* (IWP) where the functions f and g are identically equal to 1:

$$X_t \stackrel{\text{def}}{=} \int_0^t W_s\, ds \tag{2.12}$$

The transition measure of the process (X_t, W_t) can be written:

$$\mathbb{P}\Big[X_{t+s} \in du, W_{t+s} \in dv \Big| X_s = x, W_s = y\Big] \stackrel{\text{def}}{=} p_t(u\, v;\, x, y) du\, dv = \\ \frac{\sqrt{3}}{\pi t^2} \exp\Big[-\frac{6}{t^3}(u - x - ty)^2 + \frac{6}{t^2}(u - x - ty)(v - y) - \frac{2}{t}(v - y)^2\Big] du\, dv \tag{2.13}$$

2.3 Model III: The noisy nonlinear integrate-and-fire neuron with instantaneous synaptic current

The models studied so far are linear and cannot be used to model nonlinear behaviors of neurons. For instance, it is known that many neuron models such as the $I_{Na,P}$, I_K current models or the Hodgkin-Huxley model present an Andronov-Hopf bifurcation. To model the behavior of such neurons in the vicinity of these bifurcations, Izhikevich in [30] proposed the following one-dimensional model:

$$\begin{cases} dV_t = (V_t^2 + I_e(t))dt + \sigma dW_t \\ V_0 = V_{\text{reset}} \end{cases} \tag{2.14}$$

together with the spiking condition:

$$V(t^-) \geq \theta \Rightarrow V(t) = V_{\text{reset}} \text{ and a spike is emitted.}$$

Note that in the analytical model it can be useful to take $\theta = \infty$ and in this case, the problem is an explosion time problem and not a boundary crossing problem. Other types of nonlinearities can generate other possibly interesting bifurcations. This is an area of current research.

This model has been studied analytically for constant inputs. The nonlinear stochastic differential equation is quite intricate to analyze in general. We review some of its main properties. First, without spiking mechanism, the process blows up almost surely in finite

time, hence the neuron will fire almost surely in finite time. Secondly, there exists a weak solution up to the explosion time but the law of the process is unknown apart from the fact that is not Gaussian. Its transition density is unknown so far. Usual approaches like the Fokker-Planck equation (see appendix A.2) fail in finding this law as we show next.

If the external current is constant, the infinitesimal generator of the process (2.14) is defined by $\mathcal{L} := \frac{1}{2}\sigma^2\partial_x^2 + (x^2 + I_e)\partial_x$ (see appendix A.2). Its transition probability density $p(t,x,y)$ is formally solution of the Fokker-Planck equation:

$$\frac{\partial p}{\partial t}(t,x,y) = \mathcal{L}^* p(t,x,y) \tag{2.15}$$

$$= \frac{1}{2}\sigma^2\partial_y^2 p(t,x,y) - \partial_y\left[(y^2 + I_e)p(t,x,y)\right]. \tag{2.16}$$

A formal solution is provided by Heun's triconfluent function h_t (see [54] and Maple10®documentation). The solution can be written $p(t,x,y) = f_1(x)f_2(t)$ where:

$$\begin{cases} f_1(x) & = \alpha_1\, h_t\left(-\left(\frac{3}{2}\right)^{2/3} \frac{c_1}{\sigma^{2/3}}, -3, \frac{Ie\sqrt[3]{12}}{\sigma^{4/3}}, -\sqrt[3]{\frac{2}{3\sigma^2}}x\right) \\ & \quad +\beta_1\, e^{-\frac{2x(3\,Ie+x^2)}{3\sigma^2}} h_t\left(-\left(\frac{3}{2}\right)^{2/3} \frac{c_1}{\sigma^{2/3}}, 3, \frac{Ie\sqrt[3]{12}}{\sigma^{4/3}}, 1/3\,\sqrt[3]{\frac{2}{3\sigma^2}}\right) \\ f_2(t) & = \alpha_2\, e^{\frac{c_1}{2\tau}t} \end{cases}$$

α_1, β_1, β_2 and c_1 are real constants. Unfortunately Heun's triconfluent function is a very fast-diverging function which is not integrable on $\mathbb{R}$. Hence the function $p(t,x,y) = f_1(x)f_2(t)$ is not a transition probability density: there is no solution of the Fokker-Planck equation for this process.

2.4 Model IV: Nonlinear integrate-and-fire models with decaying synaptic current

The previous model is a special case in a larger class of nonlinear models defined by the two equations

$$\begin{cases} \tau_m dV_t = (f(V_t) + I_e(t))dt + I_{\text{syn}}(t)dt \\ dI_{\text{syn}}(t) = -I_{\text{syn}}(t)dt + \sigma dW_t \end{cases} \tag{2.17}$$

together with the spiking condition:

$$V(t^-) \geq \theta \Rightarrow V(t) = V_{\text{reset}} \text{ and a spike is emitted.}$$

f is a non-linear function, for instance a quadratic function $f(v) = v^2$ ([30], contains an exponential function $f(v) = e^v - v$ ([8]), or a quartic function $f(v) = v^4$ ([63]).

As expected from the previous discussion very little can be obtained analytically, since the model combines the difficulties of the last two models: as in the LIF model with exponentially decaying synaptic current of section 2.2, the membrane potential is non Markovian and, as in the quadratic IF model, it blows up in finite time almost surely.

3 Stochastic approach for the statistic of spike trains

In this section we characterize the spikes trains statistics of the four types of neurons defined in the first part of this paper.

We have seen that the problem was equivalent to the first hitting time problem, also called the first passage time, for stochastic processes (see equations (2.4) and (2.6)). The information we would like to obtain is the probability density function of the spikes times, which contain all the information on the statistics of the spikes trains (mean, variance, higher order moments, when they exist).

First passage time problems for one-dimensional diffusion processes through time-dependent boundary have received a lot of attention over the last three decades. Unfortunately, the evaluation of the first passage time pdf through a constant or time dependent boundary is in general an arduous task which has still not received a satisfactory solution. Analytic results are scarce and fragmentary, even if closed form solutions exist for some very particular cases. One is led either to the study of the asymptotic behavior of this function and of its moments (see e.g. [46, 47]), or to setting up of *ad-hoc* numerical procedures yielding approximate evaluations of first passage time distributions. Such procedures can be classified as follows: (i) those that are based on probabilistic approaches (see e.g. [51, 20, 14, 52, 21, 44]), and (ii) purely numerical methods, such as the widely used Monte-Carlo method which applies without any restriction, but whose results are generally too coarse (for numerical methods, see e.g. [32, 27, 3, 23]).

In two or higher dimensions, the problem is even more complex and results can hardly be found. For the *simplest* two dimensional process, the Integrated Wiener Process (IWP) defined in (2.12), people like McKean [43] Goldman [28], Lachal [34, 35, 36] solved the problem for a constant boundary with stochastic calculus methods. Lefebvre used the Kolmogorov (Fokker-Planck) equation to find in some special cases closed-form solutions [40]. Generalizations of these formulas to other boundaries and other kinds of processes are simply not available. We have recently proposed a formula for approximating these hitting times for general Double Integral Processes (DIP) and general boundaries [64].

We focus on analytical or partially analytical methods. The main goal is to compute the probability distribution of the spikes times. When this is not possible one can be satisfied to obtain some statistics of the spikes trains, such as the mean firing rate [12, 24, 11]. This can be achieved in some cases by approximating the Kolmogorov equation.

Table 1 shows in its left column the four methods we emphasize in this paper together with their possible use for solving the problem for the neuron models presented in section 2. The letter "Y" indicates that the method can be applied to solve the problem, the letter "N" that it cannot. Question marks "?" are used for open problems that have no known solution, the main issue being that we do not have a closed form of the transition probability of the stochastic process representing the membrane potential. The bold face indicates the problems we provide solutions for in this paper, including negative results. The star, "*", is used if the result is new, to our knowledge.

	I	II	III	IV
Volterra	**Y** section 3.1.2	$\mathbf{N}^*$ section 3.1.3	?	?
Feynman-Kac	**Y** section 3.2.1	?	$\mathbf{N}^*$ section 3.2.2	?
Durbin	$\mathbf{Y}^*$ section 3.3	N	N	N
Touboul-Faugeras	Y^*	$\mathbf{Y}^*$ section 3.4	?	?

Table 1: Analytical and semi-analytical methods which can be applied to find spike statistics for different models. The symbols used in the table are explained in the text.

3.1 The Volterra Method

This method consists in finding a Volterra integral equation satisfied by the probability density function p of the first hitting time τ of a stochastic process $(X_t)_{t\geq 0}$ to a curved boundary. It has been applied by Plesser to the leaky integrate-and-fire neuron in [49] to find the pdf of the first hitting time of a leaky IF neuron driven by a general input current.

In this section we first describe the method and generalize Plesser's result to the problem of an IF neuron modeled as a continuous one dimensional Gauss-Markov process $(X_t)_{t\geq 0}$ where the spiking condition is given by a smooth curved boundary denoted by $a(t)$. We then apply this to the models I and II.

3.1.1 Gauss-Markov processes

By Doob's theorem [19], we know that there exist a Brownian motion W, a non-zero real function g and a non-decreasing real function h such that :

$$\forall t \geq 0 \qquad X_t = g(t)\, W_{h(t)},$$

and hence the transition probability density function $q(t, x|s, y)$ of this process can be written using that of the standard Brownian motion (see appendix A.1):

$$q(t,x|s,y) = \frac{1}{\sqrt{2\pi(h(t)-h(s))}} \exp\left(-\frac{\left(\frac{x}{g(t)} - \frac{y}{g(s)}\right)^2}{2(h(t)-h(s))} \right) \tag{3.1}$$

The smoothness of the functions h and g determines that of the covariance function of the process. Indeed we have, for $s \leq t$:

$$\mathbb{E}\Big[X_t X_s\Big] = g(t)g(s)h(s)$$

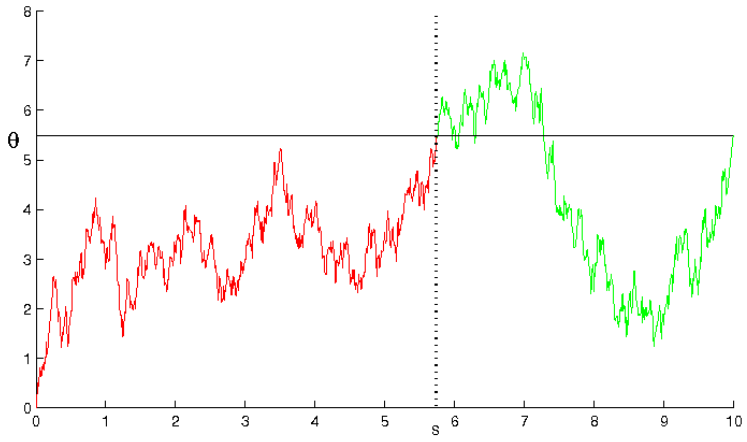


Figure 1: Principle of the Volterra's method: conditioning the transition probability density by the location of the first hitting time s of the curve θ.

We assume that this autocorrelation function is continuously differentiable with respect to s and t, which is the case for most of the processes encountered in practice. Let $x_0 < a(0)$ the starting point at $t = 0$ of the process (X_t). By the strong Markov property (see Appendix A.1 for the definition) of X_t, conditioning on the first hitting time s of the process to a (see figure 1), we can write:

$$\begin{aligned} q(t, a(t)|0, x_0) &= \int_0^t \mathbb{P}(t, a(t), \tau \in ds|0, x_0) \\ &= \int_0^t q(t, a(t)|s, a(s))p(s)ds \\ &= \int_0^t \frac{1}{\sqrt{2\pi(h(t) - h(s))}} \exp\left(-\frac{\left(\frac{a(t)}{g(t)} - \frac{a(s)}{g(s)}\right)^2}{2(h(t)-h(s))} \right) p(s)\, ds \end{aligned} \tag{3.2}$$

This equation is a weakly singular Volterra equation of the first kind. Indeed, it has a square root singularity at $s = t$ since we have:

$$\begin{cases} h(t) - h(s) \underset{s\to t}{\sim} h'(t)(t-s) \\ \dfrac{\left(\frac{a(t)}{g(t)} - \frac{a(s)}{g(s)}\right)^2}{2(h(t) - h(s))} \underset{s\to t}{\sim} \dfrac{\left[\frac{a}{g}\right]'(t)}{h'(t)}(t-s) \end{cases}$$

Hence the Volterra equation can be solved: we have existence and uniqueness of a solution (see e.g. [41]) which is necessarily the pdf we are looking for.

Different algorithms can be used to numerically solve this problem. They are reviewed for instance in Linz' book [41]. We have used in our for simulations a two points block-by-block method which amounts to solving a linear system. This method appears to be computationally very efficient and rather robust.

Other Volterra equations have been proposed, for instance in [14] or [44]. The equation proposed in [44] is a second-kind Volterra equation which can be deduced straightforwardly from (3.2). The formula proposed by Buonocore in [14] is slightly different, and has the advantage of removing the singularity of the kernel in the Volterra equation. The author proposes a simple algorithm to solve this equation.

Note that this approach can be applied to any other kind of neuron model which has a Markovian membrane potential dynamics. Nevertheless the main difficulty is to find the transition probability density of the underlying process and to check if the singularity of its transition kernel is integrable or not. For instance the transition probability density of the quadratic integrate-and-fire neuron is not known and the Fokker-Planck's theorem A.12 cannot be applied (see section 2.3).

3.1.2 LIF neuron with instantaneous synaptic currents

The previous method applies directly to the LIF neuron with instantaneous synaptic conductances (model I) since we have seen in section 2.1 that the membrane potential of such a neuron is governed by a Gauss-Markov process (an Ornstein-Uhlenbeck process). Consider the Gauss-Markov process

$$U_t := \int_0^t e^{\frac{s-t}{\tau_m}} dW_s.$$

it has the covariance function:

$$\mathbb{E}(U_t U_s) = \frac{\tau_m}{2} e^{-(t+s)} \left(e^{\frac{2s}{\tau_m}} - 1 \right) \quad 0 \leq s \leq t$$

With the notations of the last section, we have:

$$\begin{cases} g(t) = e^{-t} \\ h(t) = \frac{\tau_m}{2} \left(e^{\frac{2t}{\tau_m}} - 1 \right) \end{cases}$$

The associated Volterra kernel is weakly singular, hence the method described in the last section applies directly.

Indeed, according to equation (2.3), the membrane potential of such a neuron can be written:

$$V_t = V_{\text{rest}}(1 - e^{-\frac{t}{\tau_m}}) + \frac{1}{\tau_m} \int_0^t e^{\frac{s-t}{\tau_m}} I_e(s)\, ds + \frac{\sigma}{\tau_m} U_t$$

and hence the spiking condition reads:

$$U_t = a(t) \stackrel{\text{def}}{=} \frac{\tau_m}{\sigma} \Big\{ \theta(t) - V_{\text{rest}}(1 - e^{-\frac{t}{\tau_m}}) - \frac{1}{\tau_m} \int_0^t e^{\frac{s-t}{\tau_m}} I_e(s)\, ds \Big\},$$

where $\theta(t)$ is a time varying threshold.

The block-by-block algorithm of [41] for computing the solution of a weakly singular Volterra equation can be applied to compute the probability distribution of the spikes for any input current and any (autonomous) threshold function. This method is very general and converges very fast towards the expected solution. The mid-point approximation can also be used, and its precision is $\mathcal{O}(\sqrt{k})$ where k is the mesh step used for the integral approximation. Nevertheless the observed convergence order is higher. For the block-by-block method, the precision of the algorithm cannot be computed easily since the kernel is neither Lipschitz nor differentiable. Nevertheless, it is commonly accepted that it has a higher precision than the mid-point method. Those two quadrature methods amounts solving a linear system, which can be implemented in a very efficient way. On a an Intel®Core 2 CPU 6700 2.66GHz, it takes less than 0.02 seconds for around for a time step of 0.01 on the interval $[0, 5]$.

Figure 2 shows some examples of the pdfs associated to various inputs. When the variance is high the law of the first hitting time of the LIF neuron converges to that of the standard Brownian motion. In the small variance case, the behavior of the first hitting time depends on the existence of a spike in the deterministic case ($\sigma = 0$). When there is no deterministic spike, a interesting phenomenon appears: the probability distribution of the spike is very diffuse over $\mathbb{R}$ and vanishes slowly, see figure 3.

3.1.3 Exponentially decaying synaptic currents

The problem becomes more difficult for two-dimensional processes such as the ones arising with the linear or nonlinear neuron models with exponentially decaying synaptic currents. In this section we derive the equation satisfied by the probability density of the first hitting time for the LIF model with exponentially decaying synaptic currents, model II, show that this equation is not well-posed and that classical methods for solving integral equations fail.

The main difficulty is that the stochastic term X_t defined in (2.5) of the membrane potential V_t of the neuron is non-Markovian, but the pair $(X_t, I_t^{\text{syn}})_{t\geq 0}$ is. As usual we denote by τ the first hitting time of the process X_t to a curved boundary $a(t)$. We prove in [64] that the pair $(\tau, I_\tau^{\text{syn}})$ has a density p with respect to Lebesgue's measure:

$$p(t, x; 0, x_0, y_0)\, dt\, dx = \mathbb{P}\Big(\tau \in dt,\, I_\tau^{\text{syn}} \in dx \Big| V_0 = x_0, I_0^{\text{syn}} = y_0\Big)$$

We use an adapted version of the Markov argument of section 3.1.1 to obtain the following integral equation:

$$\mathbb{P}\Big(X_t \geq a(t) \big| X_0 = x_0, I_0^{\text{syn}} = I_0\Big) = \int_0^t \int_{\mathbb{R}} \mathbb{P}\Big(X_t \geq a(t) \big| X_s = a(s), I_s^{\text{syn}} = y\Big) p(s, y; 0, x_0, I_0) ds\, dy \quad (3.3)$$

This equation is a Fredholm integral equation with respect to y and a Volterra equation of type I with respect to s. The kernel, noted $K(t, z; s, y)$, is equal to $\mathbb{P}\left(X_t \geq a(t) \big| X_s = a(s), I_s^{\text{syn}} = y\right)$.

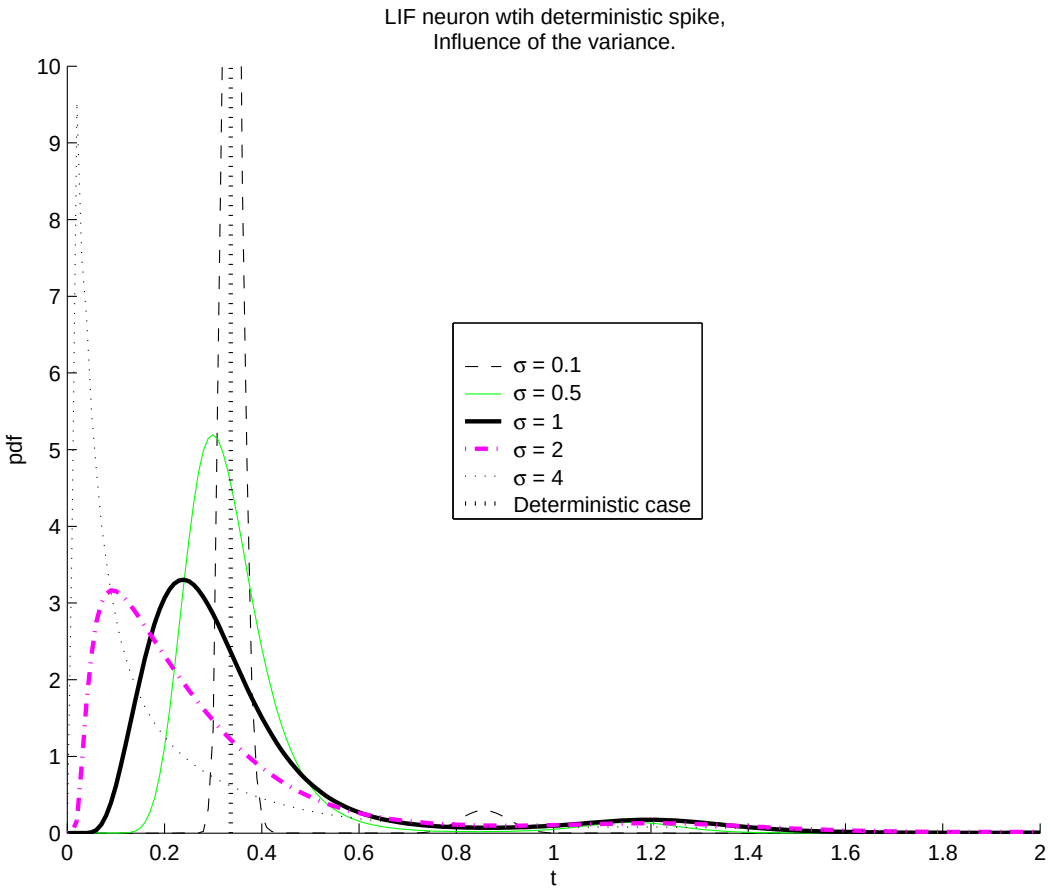
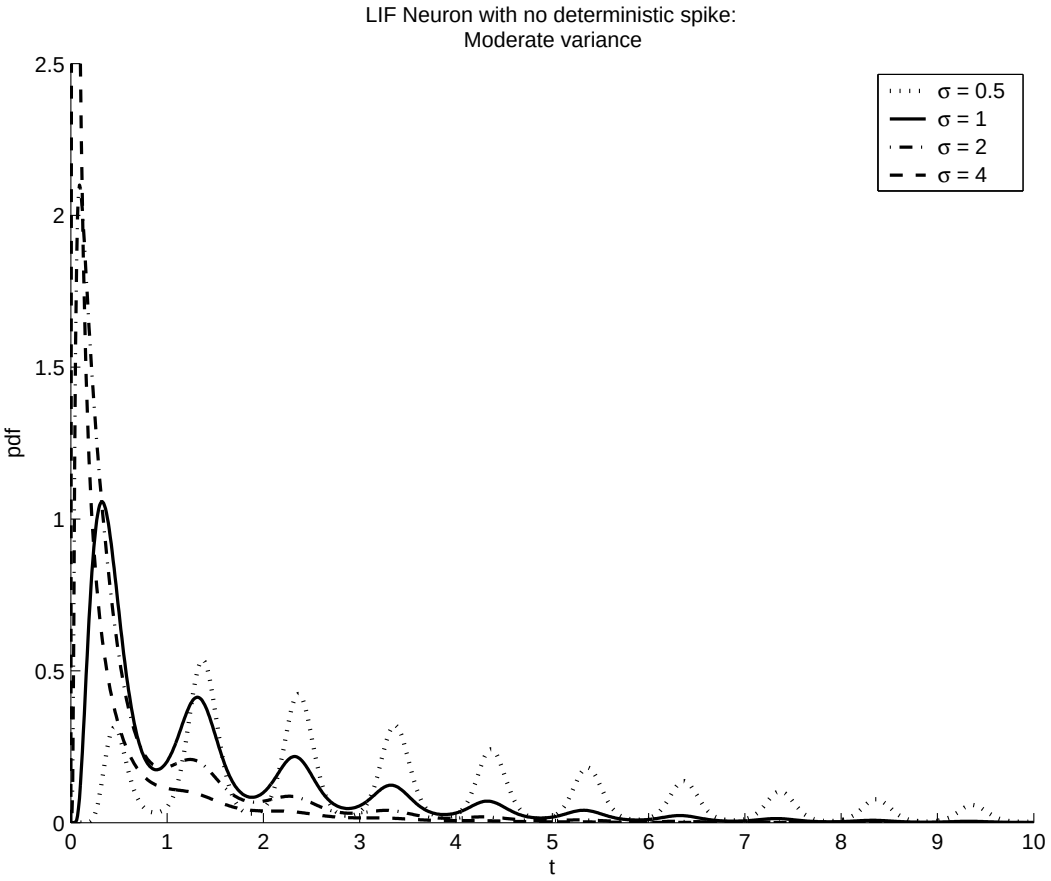
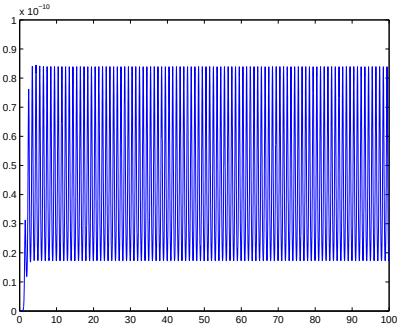


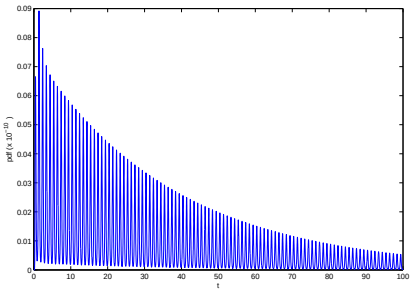
Figure 2: Influence of the variance of the noise on the statistics of spike train when a spike is emitted in the deterministic case: the pdf of the first hitting time ranges from a Dirac distribution located at the deterministic spike time in the small variance case, to the distribution of the Brownian motion first hitting time in the large variance case.



(a) Influence of the variance of the noise on the statistics of the spike train when no spike is emitted in the deterministic case. Case of a moderate variance.



(b) No deterministic spike emitted and small variance: The distribution is almost uniform, hence the spike time contains very little information



(c) idem with a higher variance: note the slow decay

Figure 3: Different simulations with Volterra's method of the pdf of the hitting time of the LIF neuron with instantaneous synaptic currents,when no spike is emitted in the deterministic case (see text).

The term on the lefthand side of the equation, noted $g(t,z)$, is equal to $\mathbb{P}\left(X_t \geq a(t) \middle| X_0 = x_0, I_0^{\text{syn}} = I_0\right)$. With these notations, equation (3.3) can be rewritten as

$$g(t,z) = \int_0^t \int_{\mathbb{R}} K(t,z;s,y) p(s,y;0,x_0,I_0) dy\, ds \tag{3.4}$$

Expressions for g and K can be deduced from the law of the underlying two-dimensional process and the results of section 2.2. The process X_t is a Gaussian process of mean $x_0 + I_0 \int_0^t g(u)du$ of variance $\rho_X(t)$ given by (2.9).

Since g can be written:

$$g(t,z) = \mathbb{P}\Big(X_t \geq a(t) \Big| X_0 = x_0, I_{\text{syn}}(0) = I_0\Big) = \frac{1}{2}\left(\text{erf}\Big(\frac{a(t) - x_0 - I_0\tau_s(e^{t/\tau_s}-1)}{\sqrt{2\pi\rho_X(t)}}\Big) - 1\right)$$

it is regular for all values of (t,z).
The kernel K can be written:

$$\begin{aligned} K(t,z;s,y) &:= \mathbb{P}\Big(X_t \geq a(t) \Big| X_s = a(s), I_{\text{syn}}(s) = y\Big) \\ &= \frac{1}{2\pi\sqrt{D(s,t)}} \exp\left(-\frac{1}{2}(X(t,y) - \mu(s,t,z))^T C(s,t)^{-1}(X(t,y) - \mu(s,t,z))\right), \end{aligned}$$

where

$$\begin{cases} D(s,t) = \det(C(s,t)) \\ \mu(s,t,z) = \begin{pmatrix} a(s) + z\int_s^t g(u)\,du \\ z \end{pmatrix} \\ X(t,y) = \begin{pmatrix} a(t) \\ y \end{pmatrix} \end{cases},$$

and $C(s,t)$ is the cross-correlation matrix (2.8).

The general theory for finding solutions to such an integral equation relies on the regularity and integrability of g and K and on the reduction to an integral equation of the second type. The reduction to the second type can be achieved formally by taking the partial derivative of both sides of (3.4) with respect to the variable t. Reordering the terms this yields

$$g_t(t,z) - \int_{\mathbb{R}} K(t,z;t,y) p(t,y;0,x_0,I_0) dy = \int_0^t \int_{\mathbb{R}} K_t(t,z;s,y) p(s,y;0,x_0,I_0) dy\, ds$$

Because $K(t,z;t,y) = \delta(y-z)$ (δ is the Dirac delta function), this can be rewritten as

$$g_t(t,z) - p(t,z;0,x_0,I_0) = \int_0^t \int_{\mathbb{R}} K_t(t,z;s,y)p(s,y;0,x_0,I_0)dy\,ds$$

A Taylor expansion at $s=t$ shows that K_t is singular of order $(t-s)^{-3}$ and hence does not satisfy the integrability conditions that are necessary for this equation to be well-posed.

3.2 The Feynman-Kac's Method

We apply this technique to models I and III.

3.2.1 Leaky Integrate-and-fire neuron with constant external current and instantaneous synaptic currents

We consider a leaky integrate-and-fire neuron with constant current input I_e and instantaneous synaptic white noise current. Let $W := (W_t)_{t\geq 0}$ be a standard Brownian motion. Thanks to a change of origin of V_t in equation (2.2), the associated membrane potential process is an Ornstein-Ulhenbeck (OU) process $V := (V_t)_{t\geq 0}$ with parameter $\lambda \in \mathbb{R}$, solution of the linear SDE:

$$\begin{cases} dV_t = -\lambda V_t dt + dW_t \\ V_0 = x \in \mathbb{R} \end{cases} \tag{3.5}$$

The process V_t is a diffusion process with infinitesimal generator denoted by $\mathcal{L}$, given by (see appendix A):

$$\mathcal{L}f(x) = \frac{1}{2}\frac{\partial^2 f}{\partial x^2}(x) - \lambda x \frac{\partial f}{\partial x}(x), \quad x \in \mathbb{R} \tag{3.6}$$

This equation is central to the theory of Hermite's functions, see appendix B. The properties of the first hitting time of the OU process have been widely studied. For instance, in [2], the authors give three representations of the probability density of these processes, and in [52] we find an explicit expression of the moments of those hitting times.

Let $a \in \mathbb{R}$ be a given fixed real number and denote by τ_a the first passage time of the process V_t to the constant a.

The Laplace transform of τ_a can be computed as follows [59, 7].

Proposition 3.1. For $x < a$ the Laplace transform of τ_a is given by

$$\mathbb{E}_x\left[e^{-\alpha\tau_a}\right] = \frac{\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})}{\mathcal{H}_{-\alpha/\lambda}(-a\sqrt{\lambda})} = \frac{e^{\lambda x^2/2}\mathcal{D}_{-\alpha/\lambda}(-x\sqrt{2\lambda})}{e^{\lambda a^2/2}\mathcal{D}_{-\alpha/\lambda}(-a\sqrt{\lambda})} \tag{3.7}$$

where $\mathcal{H}_\nu$ stands for the Hermite function and $\mathcal{D}_{-\alpha/\lambda}$ for the parabolic cylinder functions respectively (see Lebedev [39, chapter 10] for a detailed study of these functions).

Proof. We use the hitting time characterization given by the Feynman-Kac equations, obtained in section 2.4. The Laplace transform of the first passage time is given by theorem A.9 as the unique solution of the boundary value problem:

$$\begin{cases} \mathcal{L}u(x) & = \alpha u(x), \text{ for } x < a \\ u(a) & = 1 \\ \lim\limits_{x\to-\infty} u(x) & = 0 \end{cases} \tag{3.8}$$

The theory of parabolic equations applies since the coefficients of the diffusion operator $\mathcal{L}$ are $\mathcal{C}^\infty$. This is a singular value problem since the interval is not bounded. Nevertheless one can prove that the solution can be written (see theorem A.10):

$$\mathbb{E}_x\left[e^{-\alpha\tau_a}\right] = \frac{\psi_\alpha(x)}{\psi_\alpha(a)}$$

where $\psi_\alpha(\cdot)$ is, up to some multiplicative constant, the unique increasing positive solution of the equation $\mathcal{L}u = \alpha u$ which is, up to a change of variable, the equation for the Hermite's functions, see appendix B. The two fundamental solutions of this linear differential equations are $\mathcal{H}_{-\alpha/\lambda}(x\sqrt{\lambda})$ and $\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})$. The function ψ_α is up to a positive constant the one that is increasing. With the series expansion of the Hermite's functions, see equation (B.2), it is clear that $\psi_\alpha(x) = \mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})$. This proves the first equality in (3.7). The second equality relies on the relation between $\mathcal{H}_\nu$ and $\mathcal{D}_\nu$.

□

From this characterization, we can compute all the moments of the law of τ_a by differentiating the Laplace transform at 0. This provides the first three moments which are used later to validate some of our numerical techniques, see [52] for a proof of this:

Theorem 3.2. *Let us define* $\alpha := \frac{\mu}{\sigma}$ *and* $\beta := \frac{\sigma}{\theta\sqrt{\tau}}$ *and the three following functions:*

$$\Phi_1(z) := \frac{1}{2}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})(z-\alpha)^n$$

$$\Phi_2(z) := \frac{1}{2}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})\left(\Psi(\frac{n}{2}) - \Psi(1)\right)(z-\alpha)^n$$

$$\Phi_1(z) := \frac{3}{8}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})(z-\alpha)^n\rho_n^{(3)}$$

where Γ *is the gamma function,* $\Psi(z) = \frac{\Gamma'(z)}{\Gamma(z)}$ *is the digamma function, and*

$$\rho_n^{(3)} = \left(\Psi(\frac{n}{2}) - \Psi(1)\right)2 + \left(\Psi'(\frac{n}{2}) - \Psi'(1)\right)$$

If τ_θ is the hitting time of an OU process starting at 0 to the barrier θ, we have:

$$\begin{aligned}
\mathbb{E}[\tau_\theta] &= \tau(\Phi_1(1) - \Phi_1(0)) \\
\mathbb{E}[\tau_\theta^2] &= \tau^2(2\Phi_1(1)^2 - \Phi_2(1) - 2\Phi_1(1)\Phi_1(0) + \Phi_2(0)) \\
\mathbb{E}[\tau_\theta^3] &= \tau^3 \left\{6\Phi_1(1)^3 - 6\Phi_1(1)\Phi_2(1) + \Phi_3(1)\right. \\
&\quad \left. -6(\Phi_1(1)^2 - 3\Phi_2(1))\Phi_1(0) + 3\Phi_1(1)\Phi_2(0) - \Phi_3(0)\right\}
\end{aligned}$$

3.2.2 Quadratic Integrate-and-fire neuron

The Feynman-Kac method relies heavily on the very strong assumption that there exists a solution satisfying the limit condition $\lim_{x\to-\infty} u(x) = 0$. This assumption is in effect satisfied only in very few cases. Furthermore, this method can only be applied to autonomous systems, and hence cannot be applied to neuron models with deterministic time-dependent synaptic inputs. For instance we show here that it cannot be applied to the one-dimensional quadratic integrate-and-fire neuron defined in section 2.3, even in the simple case of a constant external current.

Assume that the membrane potential of the neuron satisfies the stochastic differential equation:

$$dX_t = f(X_t)dt + \sigma dW_t$$

The infinitesimal operator of the associated semigroup $\mathcal{L}$ is givenby:

$$\mathcal{L}h(x) = \frac{1}{2}\sigma^2 \frac{d^2h}{dx^2}(x) + f(x)\frac{\mathrm{d}h}{\mathrm{d}x}(x), \quad x \in \mathbb{R} \tag{3.9}$$

Let u_λ be the Laplace transform of the first hitting time τ_a to a constant a:

$$u_\lambda(x) = \mathbb{E}\Big(e^{-\lambda\tau_a}\Big|X_0 = x\Big)$$

u_λ is a solution, when it exists, of the Feynman-Kac differential equation (A.11), which in the case of the quadratic integrate-and-fire neuron can be written:

$$\begin{cases} \frac{1}{2}\sigma^2 \frac{d^2\, u_\lambda(x)}{dx^2} + (x^2 + I_e)\frac{\mathrm{d}u_\lambda(x)}{\mathrm{d}x} - \lambda u_\lambda(x) = 0 \\ u_\lambda(a) = 1 \\ u_\lambda(x) \underset{x\to-\infty}{\longrightarrow} 0 \end{cases} \tag{3.10}$$

This ordinary differential equation is a triconfluent Heun equation with boundary conditions (see e.g. [54, Prop.1.3.6] and Maple ®documentation). As in section 2.3 we denote by h_t the triconfluent Heun function. We have

$$u_\lambda(x) = \alpha h_t\left(-\frac{3^{2/3}\lambda}{\sqrt[3]{a}}, 3, \frac{b\sqrt[3]{3}}{a^{2/3}}, -1/3\,\frac{3^{2/3}x}{\sqrt[3]{a}}\right) + \beta h_t\left(-\frac{3^{2/3}\lambda}{\sqrt[3]{a}}, -3, \frac{b\sqrt[3]{3}}{a^{2/3}}, 1/3\,\frac{3^{2/3}x}{\sqrt[3]{a}}\right) e^{-1/3\,\frac{x\left(3\,b+x^2\right)}{a}} \quad (3.11)$$

It can be verified again that the triconfluent Heun function $h_t(\alpha, 3, \beta, x)$ diverges very fast when $|x| \to \infty$. Hence there is no solution to the boundary problem (3.10).

3.3 Durbin's Method

The problem of the first hitting time of the Brownian motion to a (convex or concave) boundary has also been studied by Durbin [20, 21] who uses an integral equation like the one arising in Volterra's method. This equation characterizes the probability density function of the first hitting time of the process. He uses this integral equation to deduce a series approximation of the pdf and proves convergence when the curve is concave or convex.

This result is summarized in the

Theorem 3.3 (Durbin)**.** *Let $(W_t)_{t\geq 0}$ be a standard Brownian motion and $a(\cdot)$ be a continuously differentiable boundary function such that $a(0) > 0$. The first-passage density $p(t)$ of W_t to $a(t)$ is solution of the following integral equation*

$$q_0(t) = p(t) + \int_0^t p(r)\left(\frac{a(t)-a(s)}{t-s} - a'(t)\right) f(t|s)\, ds,$$

which can be written as

$$p(t) = \sum_{j=1}^{k} (-1)^{j-1} q_j(t) + r_k(t),$$

where

$$q_j(t) = \int_0^t q_{j-1}(s)\left(\frac{a(t)-a(s)}{t-s} - a'(t)\right) f(t|s)\, ds \quad j \geq 1.$$

$a'(t)$ is the derivative of $a(t)$ and q_0 is given by

$$q_0(t) = \left(\frac{a(t)}{t} - a'(t)\right) f_0(t),$$

where $f_0(t)$ is the density of W_t on the boundary, i.e.

$$f_0(t) = \frac{1}{\sqrt{2\pi t}} e^{-\frac{a(t)^2}{2t}},$$

and $f(t|s)$ is the joint density of W_s and $W_t - W_s$ on the boundary, i.e.

$$f(t|s) = f_0(s)\frac{1}{\sqrt{2\pi(t-s)}}e^{-\frac{(a(t)-a(s))^2}{2(t-s)}}$$

The remainder $r_k(t)$ goes to 0 if $a(t)$ is convex or concave.

This theorem is quite restrictive: the process must be a Brownian motion, the boundary must be convex or concave, and there is no estimation of the convergence of the approximation. Nevertheless we have been able in our simulations to compare the results of Durbin's method applied to non-convex or non-concave boundaries and the expansion seems to converge, see figure 5. Unfortunately these findings are only experimental.

3.3.1 LIF neuron with instantaneous synaptic currents and constant external input current

In the case of the LIF neuron with instantaneous synaptic currents and a constant deterministic external input current, the membrane potential is the realization of an Ornstein-Uhlenbeck (OU) process, and the threshold function $a(t)$ is convex. Hence the hypotheses of Durbin's theorem are satisfied, and Durbin's expansion converges to the law of the first hitting time. A comparison of the values of the first three moments computed from the pdf of the hitting time obtained from Durbin's theorem, Volterra's equation and by Monte-Carlo simulation with the analytical values of theorem 3.2 (obtained by truncating the series Φ_i) is shown in table 2. This table shows that the theoretical values can be closely approximated

method	$\mathbb{E}[T]$	$\mathbb{E}[T^2]$	$\mathbb{E}[T^3]$
theoretical values	1.9319289	7.1356162	40.0830265
Durbin, 30 terms, $T_{max} = 10^{36}$, step $= 10^{-2}$	1.9292822	7.1269290	39.8541918
Monte-Carlo, 10^6 realizations, step $= 10^{-4}$	1.932180	7.139402	40.079556
Volterra, step $= 0.02$	1.9319291	7.1356167	40.0830298

Table 2: Values of the first 3 moments of the OU process and the empirical values, for the parameters: $\theta = \sigma = 2$, $V_{\text{rest}} = \tau_m = 1$, $I_e = 0$, see equation (2.2)

if sufficiently many terms are taken into account in Durbin's series expansion. We see that Volterra's method is the most accurate. It is also computationally the most efficient.

3.3.2 LIF neuron with instantaneous synaptic currents and periodic external input current

When $I_e(t) = \sin(2\pi ft)$ the hypotheses of theorem 3.3 are not satisfied. Table 3 shows the values of the integral of the estimated pdf for various times of integration and various orders of truncation of the series. The parameters are the same as in the previous example and $f = 1$. It seems to indicate that a very good approximation of the pdf can be obtained with only 5 terms in the series [22].

We have also noticed that Durbin's series converged very quickly, even if the associated boundary was neither convex nor concave. Figure 4 shows the shape of the pdf of the first passage time and the first four terms in the series approximation. The total computation time is 8 seconds on a 2GHz computer for 800 sample points.

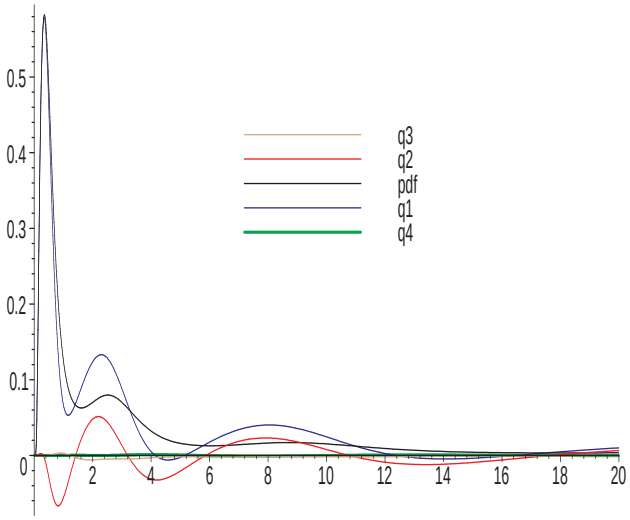


Figure 4: Four terms of the series approximation of the pdf when $I_e(t) = \sin(2\pi t)$ and the resulting pdf (the horizontal scale is in units of ρ, see text).

time-terms	3	5	7	9
10^3	0.86	0.88	0.88	0.88
10^5	0.86	0.97	0.96	0.96
10^7	0.82	1.00	0.98	0.98
10^9	0.88	0.97	1.00	0.99

Table 3: Values of the integral of the estimated pdf for $I_e = \sin(2\pi t)$.

Hence Durbin's method seems to converge even for non-convex boundaries. Nevertheless, to apply Durbin's expansion, one has to use the exponential time-change $\rho(t) = \frac{\tau_m}{2}\left(e^{2\frac{t}{\tau_m}} - 1\right)$. Hence evaluations are done on an exponential scale which is very inefficient.

In Figure 5 we compare three of the methods available for the LIF neuron: Durbin's method, Volterra's method and a Monte-Carlo simulation. We see that the simulation time is very high for both Monte-Carlo and Durbin's methods (around $10s$ for both, the Monte-Carlo simulation runs 10^6 sample paths and Durbin's method 800 sample points and 9 terms of the series). Volterra's method is very efficient and for 10^4 sample points, takes less than $0.02s$. We also see from the enlargement in the figure that the Monte-Carlo simulation does not have the expected regularity even at this level of precision.

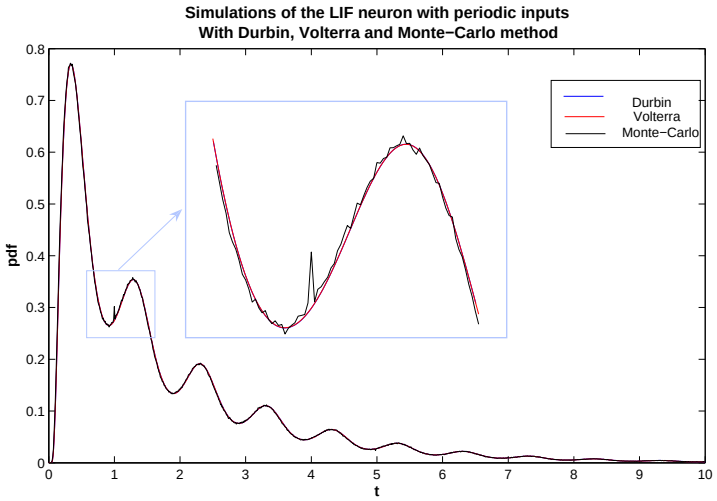


Figure 5: Graphical comparison with Monte-Carlo simulation and Durbin's simulations

3.4 Touboul-Faugeras Method

We present a new semi-analytical method for finding the probability density function of spikes of a LIF neuron with exponentially decaying synaptic conductances. This method is based on new results for the integrated Wiener process (IWP) introduced in section 2.2 and a new method of approximation of hitting times, inspired by very recent works on the Brownian motion hitting times. It has the following features:

(i). It generalizes the results obtained in the classical literature for the IWP to a large class of boundaries.

(ii). It builds a piecewise approximation of the general boundary which is in the class of (i) in each bin of the mesh.

(iii). It guarantees that the first hitting time of the process to the approximated boundary converges to the first hitting time of the process to the general boundary (and quantifies this convergence).

(iv). It extends these results to a general Double Integral Process (DIP).

For the Brownian motion, Wang and Potzelberger [67] build a piecewise affine approximation of the boundary and find an approximate expression for its first hitting time to a curved boundary. Later Novikov *et al* [48] found an expression for the convergence of this technique. These results have been generalized to a wider class of processes, with sharper error bounds but it is still a very active research subject [50, 6, 68]. Touboul and Faugeras [64] proposed a general approximation formula solving the problem of the statistics of spike trains for LIF neurons with exponentially decaying synaptic currents.

3.4.1 Approximating the first hitting time of the IWP to a general boundary

One of the main difficulties comes from the fact that the process is non-Markov, implying that we have to refer to the underlying Wiener process.

Lachal in [34] studies this problem in the case where the boundary is a constant. To make things more clear we define the process $U_t = (X_t + x + ty, W_t + y)$ where W_t a standard Brownian motion and X_t is the associated IWP. We denote by

$$\tau_a := \inf\left\{t > 0\ ;\ X_t + x + ty = a\right\}$$

the first passage time at a of the first component of the two-dimensional Markov process U_t. The work of Lachal [34] follows the work of McKean [43] who computed the joint law of the process (τ_a, W_{τ_a}) in the case $x = a$, and that of Goldman [28]. McKean's density can be written:

$$\begin{aligned}\mathbb{P}\Big[\tau_a \in dt\ ;\ |W_{\tau_a}| \in dz \Big| U_0 = (a,y)\Big] &\stackrel{\text{def}}{=} \mathbb{P}_{(a,\,y)}\left(\tau_a \in dt;\ |W_{\tau_a}| \in dz\right) \\ &= \frac{3z}{\pi\sqrt{2}t^2} e^{-(2/t)(y^2-|y|z+z^2)} \left(\int_0^{4|y|z/t} e^{-3\theta/2}\frac{d\theta}{\sqrt{\pi\theta}}\right) \mathbb{1}_{[0,+\infty)}(z)dzdt \quad (3.12)\end{aligned}$$

Lachal [34] extended this result and gave the joint distribution of the pair (τ_a, W_{τ_a}) in all cases. The quite complex formula reads:

$$\begin{aligned}\mathbb{P}_{(x,y)}\left[\tau_a \in dt\ ;\ W_{\tau_a} \in dz\right] = |z|\Big[&p_t(x,y;a,z) - \\ &\int_0^t \int_0^{+\infty} \mathbb{P}_{(0,-|z|)}\left(\tau_0 \in ds;\ W_{\tau_0} \in d\mu\right) p_{t-s}(x,y;a,-\varepsilon\mu)\Big]\mathbb{1}_A(z)dzdt \quad (3.13)\end{aligned}$$

where $A = [0, \infty)$ if $x < a$ and $A = (-\infty, 0]$ if $x > a$, $\varepsilon = \text{sign}(a - x)$, $\mathbb{P}_{(0,-|z|)}$ is given by McKean's formula (3.12), and p_t is defined by equation (2.13). We denote this density by $l^a_{x,y}(t, z)$.

Starting from there, the authors study in [64] the first hitting time problem of the IWP to a cubic boundary and find a closed form expression of its pdf using Girsanov's theorem A.7. We indicate in the sequel the main results without proofs, the mathematical aspects being very technical.

Theorem 3.4. *Let τ_C be the first hitting time of the standard IWP to the curve*

$$C(t) = a + b(t - s) + \frac{\alpha}{2}(t - s)^2 + \frac{\beta}{6}(t - s)^3, \quad t \geq s$$

Under the reference probability $\mathbb{P}$, the law of the random variable (τ_C, W_{τ_C}) satisfies the equation:

$$\mathbb{P}_{s,(x,y)}(\tau_C \in dt, W_{\tau_C} \in dz) = d^{\alpha,\beta}(s, x, y - b; t, C(t), z) \times \mathbb{P}_{s,(x,y-b)}(\tau_a \in dt, W_{\tau_a} - b + \alpha(\tau_a - s) + \frac{\beta}{2}(\tau_a - s)^2 \in dz) \quad (3.14)$$

where we noted:

$$d^{\alpha,\beta}(s, x, y; t, u, v) = \exp\Big(-\frac{1}{6}\beta^2(t^3 - s^3) - \frac{1}{2}\alpha\beta(t^2 - s^2) - \frac{1}{2}\alpha^2(t - s) - (\alpha + t\beta)v + (\alpha + s\beta)y + \beta(u - x)\Big) \quad (3.15)$$

and $\mathbb{P}(\tau_a \in dt, W_{\tau_a} \in dz)$ is given by Lachal's formula (3.13).

We remind the reader of the notation $\mathbb{P}_{s,(x,y)}$ used to indicate the probability law deduced from $\mathbb{P}$ by conditioning with respect to the event $\{(X_s, W_s) = (x, y)\}$ Hence we obtain a boundary with four free parameters. From this formula, we deduce an approximation formula for the first hitting time of the IWP to a general boundary.

3.4.2 Approximating the first hitting time of the DIP to a general boundary

Having solved the problem for the IWP lays the ground for its solution for a general Double Integral Process (DIP) to a general boundary f as follows.

The key observation, [64], is that the study of the first hitting times of a general DIP X_t is equivalent to the study of the simpler process:

$$Y_t = \int_0^t g(s) W_s \, ds, \quad (3.16)$$

where $g(\cdot)$ is a continuously differentiable function and W_t a standard Brownian motion. Let π be a partition of the interval $[0, T]$:

$$(\pi) := \quad \{0 = t_0 < t_1 < t_2 < \ldots < t_N = T\}$$

We denote by g^π the piecewise constant approximation of g:

$$g^\pi(t) = \sum_{i=0}^{N-1} g(t_i) \mathbb{1}_{[t_i, t_{i+1})}(t) \tag{3.17}$$

and by Y^π the associated process:

$$Y_t^\pi = \int_0^t g^\pi(s) W_s \, ds. \tag{3.18}$$

We also denote by f^π a cubic spline approximation of the boundary function f on the partition (π). The next proposition characterizes the convergence of the process Y_t^π

Proposition 3.5. The process Y_t^π converges almost surely to the process Y_t. Furthermore, there exists a real positive process Z_t such that:

$$\sup_{0 \le s \le t} |Y_s^\pi - Y_s| \le \delta(\pi) \; Z_t \tag{3.19}$$

With some technical calculations and the use of this proposition, we can prove the following approximation theorem:

Theorem 3.6. *The first crossing time τ^π of the process Y^π and the curve f^π tends in law to the first hitting time τ_f of the process Y to the curve f (see Fig.6).*

In the IWP case we can quantify the convergence as expressed in the

Theorem 3.7. *The first hitting time of the IWP to the curve $(f^\pi(t))$ before $T > 0$ converges in law to the first hitting time of the IWP to the curve f before T.*

Furthermore, if f is four times continuously differentiable, the convergence of this approximation is of order 4. More precisely, if $P(t, g)$ denotes the probability:

$$P(t, g) = \mathbb{P}\Big(X_t \ge g(t) \;\; \textit{for some } t \in [0, T]\Big),$$

for a real function g, there exists a constant $C(f)$ depending on the function f such that we have:

$$\boxed{|P(t, f^\pi) - P(t, f)| \le C(f) \; \delta(\pi)^4} \tag{3.20}$$

A closed-form expression for the law of τ^π is given in the following

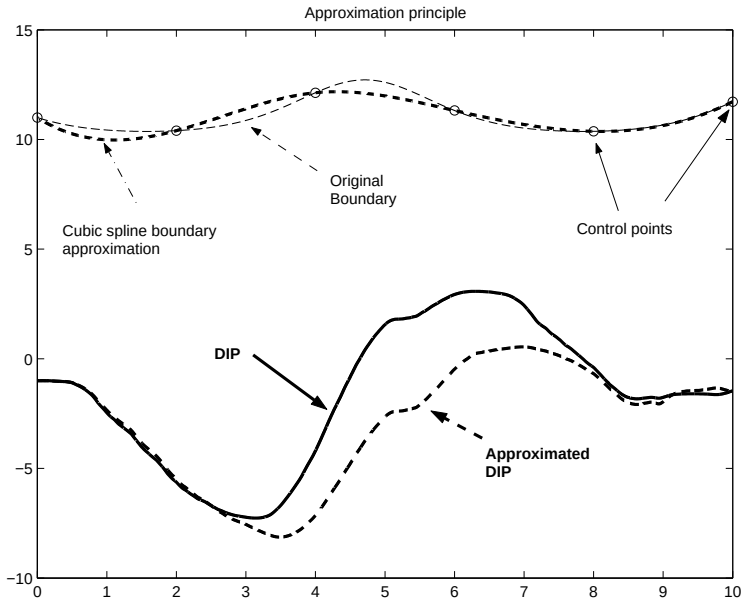


Figure 6: Approximation principle: the general DIP process is approximated and the boundary is approximated by its cubic spline interpolation

Theorem 3.8. *Let g be a Lipchitz continuous real function, $T > 0$ and π a partition of the interval $[0, T]$*

$$0 =: t_0 < t_1 < \ldots < t_p := T$$

Let f be a continuously differentiable function. The first hitting time τ^π of the approximated process Y^π defined by (3.18) to a cubic spline approximation f^π of f on the partition π satisfies the equation:

$$\mathbb{P}(\tau^\pi \geq T | U_0) = \int^{(2p)} \prod_{k=1}^{p} \left\{ p_{t_k - t_{k-1}}\Big(\frac{x_k - x_{k-1}}{g(t_{k-1})}, y_k - y_{k-1}; 0, 0\Big) - \int_{t_{k-1}}^{t_k} \int_{\mathbb{R}} p_{t_k - s}\Big(\frac{x_k - f^\pi(s)}{g(t_{k-1})}, y_k - y_s; 0, 0\Big) \mathbb{P}_{s,(0,y_s)}(\tau_{(f^\pi - x_{k-1})/g(t_{k-1})} \in ds,\ W_s \in dy_s) \right\} dx_k dy_k \tag{3.21}$$

where $\mathbb{P}(\tau_{f^\pi} \in ds,\ W_s \in dy_s)$ is given by equation (3.14).

The expressions in theorem 3.8 involve integrals computed over $\mathbb{R}^{2p}$ if there are p points in the mesh. These have no closed-form expression. The numerical computation of these integrals can be quite intricate and inefficient, and this introduces another approximation besides that in theorem 3.6. The principle of the numerical approximation we use is to express these integrals as expectations with respect to some probability measure and to use a Monte-Carlo algorithm to compute this probability measure. The accuracy of this approximation can be assessed through standard procedures for Monte Carlo simulations [45, 53]. This idea leads to the following

Corollary 3.9 (of theorem 3.8)**.** Let g be a Lipchitz continuous real function, $T > 0$ and π a partition of the interval $[0, T]$

$$0 =: t_0 < t_1 < \ldots < t_p := T$$

Let f be a continuously differentiable function. The first hitting time τ^π of the approximated process Y^π defined by (3.18) to a cubic spline approximation f^π of f on the partition π can be computed as the expectation:

$$\mathbb{P}\Big(\tau^\pi \geq T \Big| U_0\Big) = \mathbb{E}\Big[h_p^{g,\pi}(X_{t_1}, W_{t_1}, \ldots, X_{t_p}, W_{t_p}) \Big| U_0\Big] \tag{3.22}$$

where the function $h_p^{g,\pi}$ is defined by:

$$h_p^{g,\pi}(x_1, \ldots, x_p) = \prod_{k=1}^{p} \left\{ \frac{p_{t_k - t_{k-1}}\Big(\frac{x_k - x_{k-1}}{g(t_{k-1})}, y_k - y_{k-1}; 0, 0\Big)}{p_{t_k - t_{k-1}}(x_k, y_k, x_{k-1}, y_{k-1})} - \int_{t_{k-1}}^{t_k} \int_{\mathbb{R}} \frac{p_{t_k - s}\Big(\frac{x_k - f^\pi(s)}{g(t_{k-1})}, y_k - y_s; 0, 0\Big)}{p_{t_k - t_{k-1}}(x_k, y_k, x_{k-1}, y_{k-1})} \mathbb{P}_{s,(0,y_s)}(\tau_{(f^\pi - x_{k-1})/g(t_{k-1})} \in ds,\ W_s \in dy_s) \right\} \tag{3.23}$$

where $\mathbb{P}(\tau_{f^\pi} \in ds,\ W_s \in dy_s)$ is given by equation (3.14).

The problem is now stated in terms of the expectation of a function of the Gaussian random vector $(X_0, W_0, X_{t_1}, W_{t_1}, \ldots, X_{t_p}, W_{t_p})$. This vector is Gaussian of mean 0 and covariance matrix defined by blocks by the expression:

$$K(t_1, \ldots, t_p) = \begin{pmatrix} \frac{1}{3}|t_j - t_i|^3 & \frac{1}{2}|t_j - t_i|^2 \\ \frac{1}{2}|t_j - t_i|^2 & |t_j - t_i| \end{pmatrix}_{(i,j)\in\{0\ldots p\}} \tag{3.24}$$

The Monte-Carlo algorithm we use to compute the expected probability is the following:

(i). Compute the square root $K(t_1, \ldots, t_p)^{1/2}$ of the covariance matrix (3.24) (using for instance a Cholesky decomposition)

(ii). Generate an i.i.d. sample $u = (u_1, u_2, \ldots, u_{2p})^T$ from the normal standard distribution $\mathcal{N}(0, 1)$.

(iii). Compute the transformation $x = K(t_1, \ldots, t_p)^{1/2} \cdot u$

(iv). Calculate $h_p^{g,\pi}(x)$

(v). Repeat steps (ii)-(iv) N times and calculate the frequency

$$P_N = \frac{1}{N} \sum_{\text{realizations}} h_p^{g,\pi}(x)$$

The probability $\mathbb{P}(\tau \geq T)$ is then estimated by P_N. The standard error of this estimator is given by :

$$\mathcal{E}(N) = \sqrt{\frac{\sum_{\text{realizations}} \left[h_p^{g,\pi}(x) - P_N\right]^2}{N(N-1)}} \tag{3.25}$$

Conclusion

In this paper we studied four different types of neuron models from the point of view of the stochastic calculus. We showed that characterizing the spikes times of a neuron was equivalent to solving a first hitting time problem for a stochastic process to a given continuous curve. We then presented four methods which can be applied to solve such problems. One of them, the Feynman-Kac method, is very restrictive, since it can only be applied to stationary boundaries (this is also the case of the Fokker-Planck equation formalism). The three other methods provide a unique solution and a way to compute this probability distribution. Durbin's method and Volterra's method are compared in the case of the LIF neuron with instantaneous synaptic currents. The last method presented is a new method wich enables

us to compute the distribution of the spikes times for the LIF neuron with exponentially decaying synaptic conductances. In this case, the only available and partial result is Brunel's who computed the stationary firing rate of this neuron model [12]. Nevertheless for the nonlinear models of types III and IV the stochastic calculus methods still fail to provide the complete statistical information about the spikes and one has to resort to the Fokker-Planck approximate formalism. We hope to be able to report new findings for these two cases in the near future and, despite these partially negative results, consider that the approach developed in this paper has enabled us to solve difficult open problems and has great potentials for applications to neuroscience.

A A crash course on Probabilities and Stochastic Calculus

We recall some of the basic definitions and results on stochastic processes. The aim of this section is not to be complete but to serve as a quick reference for readers with little background in stochastic calculus. Most of the proofs are omitted. The interested reader can find details in the extensive literature on the subject and follow the reading suggestions given within each section.

A.1 Probability Basics

This section heavily relies on Karatzas and Shreve's book [31] and on lecture notes by Jean-François Le Gall [38], where the interested reader can find all the theoretical material. We assume that the reader is familiar with elementary measure theory [55].

Probability theory is a branch of mathematics concerned with the analysis of random phenomena. The randomness is captured by the introduction of a measurable space $(\Omega, \mathcal{F})$, called the *sample space*, on which probability measures can be placed. Elements of Ω are denoted in general by ω. Subsets of Ω are called *events*. $\mathcal{F}$ is a σ-algebra of subsets of Ω.

Definition A.1. A probability measure $\mathbb{P}$ on $(\Omega, \mathcal{F})$ is a positive measure such that

$$\mathbb{P}(\Omega) = 1$$

. $(\Omega, \mathcal{F}, \mathbb{P})$ is called a probability space.

Definition A.2. A *random variable* is a measurable function from Ω to a measurable set $(X, \mathcal{X})$ called the state space.

Definition A.3. A *stochastic process* is a collection of random variables $X = \{X_t, t \in \mathbb{T}\}$ on $(\Omega, \mathcal{F})$ taking values in a state space $(X, \mathcal{X})$. The set $\mathbb{T}$ is called the *time set*. In the present paper, $\mathbb{T}$ is simply $\mathbb{R}^+$ and is referred to as the time of the process. The state space considered is the d-dimensional Euclidian space equiped with the σ-fields of Borel sets $(\mathbb{R}^d, \mathcal{B}(\mathbb{R}^d))$.

The temporal feature of a stochastic process suggests a flow of time, in which at every moment $t \geq 0$ we can talk about the past, present and future of the process. To quantify the *information flow* of the process, we can equip the sample space $(\Omega, \mathcal{F})$ with a *filtration*, i.e. a nondecreasing family $\{\mathcal{F}_t;\ t \geq 0\}$ of sub-σ-fields of $\mathcal{F}$:

$$\forall s \leq t;\ \ \mathcal{F}_s \subset \mathcal{F}_t \subset \mathcal{F}.$$

Given a stochastic process, the simplest choice of filtration is that generated by the process itself, i.e.,

$$\mathcal{F}_t^X := \sigma(X_s;\ 0 \leq s \leq t),$$

the smallest σ-field with respect to which X_s is measurable for every $s \in [0, t]$.

We interpret $A \in \mathcal{F}_t^X$ to mean that by time t, an observer of X knows wether or not A has occured. Hence $\mathcal{F}_t$ can be seen as the accumulated information up to time t.

A stochastic process X is said adapted to a filtration $(\mathcal{F}_t)_{t\geq 0}$ iff for all $t \geq 0$ the random variable X_t is $\mathcal{F}_t$-measurable.

A stochastic process X is said to be right-continuous (resp. left-continuous) iff almost every sample path is right- (resp. left-) continous.

Definition A.4 (Brownian Motion/Wiener process)**.** A standard one dimensional Brownian motion (also called a Wiener process) is a continuous adapted process $W = \{W_t,\ \mathcal{F}_t\, t \geq 0\}$ defined on some probability space $(\Omega, \mathcal{F}, \mathbb{P})$, with the properties that:

(i). $W_0 = 0$ a.s.

(ii). for all $0 \leq s \leq t$ the increment $W_t - W_s$ is independent of $\mathcal{F}_s$ and is normally distributed with mean 0 and variance $t - s$.

Let us now imagine that we are interested in the occurence of a certain phenomenon (e.g. a spike modeled as a threshold crossing of a given process in the present paper). We are thus forced to pay a particular attention to the random instant $\tau(\omega)$ at which the phenomenon manifests at the first time. Interesting models should be such that the event $\{\omega;\ \tau(\omega) \leq t\}$ is part of the information accumulated by that time. Random variables τ satifying this property are called *stopping times*:

$$\forall t \geq 0;\ \ \{\tau \leq t\} \in \mathcal{F}_t$$

Example. For instance, the first hitting time of a continuous stochastic process X to a given deterministic boundary g defined by:

$$\tau := \inf\{t \geq 0;\ \ X_t = g(t)\}$$

is is a stopping time with respect to the natural filtration of X. Indeed, the event $\{\tau \leq t\}$ is the same as $\{\exists s \in [0, t] X_s \geq f(s)\}$. From the continuity property, this last set is equal to $\{\exists s \in [0, t] \cap \mathbb{Q},\ X_s \geq f(s)\}$ which is a coutable union of sets of $\mathcal{F}_t^X$ and hence is contained in $\mathcal{F}_t^X$.

Definition A.5 (Conditional Expectation)**.** Let Y be a $\mathbb{L}^1$ random variable of $(\Omega, \mathcal{F}, \mathbb{P})$ and let $\mathcal{G}$ be a sub-σ-field of $\mathcal{F}$. There exists a unique element $\mathbb{E}(Y|\mathcal{G})$ of $\mathbb{L}^1(\Omega, \mathcal{G}, \mathbb{P})$ called conditionnal expectation of Y knowing $\mathcal{G}$, such that for all X bounded and $\mathcal{G}$-measurable:

$$\mathbb{E}(XY) = \mathbb{E}(\mathbb{E}(Y|\mathcal{G})X)$$

A process $\{X_t, \mathcal{F}_t,\ t \geq 0\}$ is called a *submartingale* (resp *supermartingale, martingale*) if for every $0 \leq s < t < \infty$ we have $\mathbb{P}$-almost surely $\mathbb{E}(X_t|\mathcal{F}_s) \geq X_s$ (resp $\mathbb{E}(X_t|\mathcal{F}_s) \leq X_s$, $\mathbb{E}(X_t|\mathcal{F}_s) = X_s$).

Theorem A.1 (Optional Sampling Theorem)**.** *Let $\{X_t,\ \mathcal{F}_t,\ t \geq 0\}$ be a right-continuous submartingale, S and T be two stopping times almost surely bounded (i.e. $\mathbb{P}(T < \infty) = 1$ and $\mathbb{P}(S < \infty) = 1$). Let X_T be the random variable defined by $X_T(\omega) = X_{T(\omega)}(\omega)$. Let $\mathcal{F}_S := \{A \in \mathcal{F}\ ;\ A \cap \{T \leq t\} \in \mathcal{F}_t\}$. Assume that $S \leq T$ amost surely. Then we have:*

$$\mathbb{E}(X_T|\mathcal{F}_S) \geq X_S \ \ a.s.\ \mathbb{P}.$$

Definition A.6. Let X be a stochastic process on a probability space $(\Omega, \mathcal{F}, \mathbb{P})$. Let $(\mathcal{F}_t)_{t\geq 0}$ be the natural filtration of the process X. The process X is a *Markov process* iff $\forall t \leq t_1 \leq \ldots \leq t_n < \infty$, for all $\Gamma_1, \ldots, \Gamma_n \in \mathcal{X}$,

$$\mathbb{P}\Big(X_{t_1} \in \Gamma_1, \ldots, X_{t_n} \in \Gamma_n \Big| \mathcal{F}_t\Big) = \mathbb{P}\Big(X_{t_1} \in \Gamma_1, \ldots, X_{t_n} \in \Gamma_n \Big| \sigma(X_t)\Big).$$

It is strongly Markovian if for all T stopping time for the $(\mathcal{F}_t)_t$, for all $\eta_1, \ldots \eta_n$ positive random variable $\mathcal{F}_\tau$-measurable, we have:

$$\mathbb{P}\Big(X_{\tau+\eta_1} \in \Gamma_1, \ldots, X_{\tau+\eta_n} \in \Gamma_n \Big| \mathcal{F}_\tau\Big) = \mathbb{P}\Big(X_{\tau+\eta_1} \in \Gamma_1, \ldots, X_{\tau+\eta_n} \in \Gamma_n \Big| \sigma(X_\tau)\Big).$$

Proposition A.2. The Brownian motion is strongly Markovian

Definition A.7. A process $(M_t, t \geq 0)$ is a continuous local martingale iff it is a continuous adapted process such that there exists an increasing sequence of stopping times $(T_n)_{n\in\mathbb{N}}$ such that $T_n \to_{n\to\infty} \infty$ and that for each $n \in \mathbb{N}$ $(M_{t\wedge T_n} - M_0)_t$ is a uniformly integrable martingale.

Theorem A.3. *Let M be a local martingale. There exists a unique non-decreasing process $\langle M\rangle_t$ such that $(M_t^2 - \langle M\rangle_t)_{t\geq 0}$ is a continuous local martingale. For M and N two continuous local martingales, there exists a unique finite variation process such that $(M_t\, N_t - \langle M, N\rangle_t)_t$ is a local martingale. Moreover, the application $(M, N) \mapsto \langle M, N\rangle$ is bilinear symetrical.*

Theorem A.4 (Stochastic Integral)**.** *Let M be a continuous local martingale and H a measurable process such that for all $t > 0$, $\int_0^t H_s^2 d\langle M\rangle_s < \infty$ (the set of such processes is denoted by $\mathbb{L}^2_{loc}(M)$).*

There exists a unique continuous local martingale $H \cdot M$ starting from 0 such that for all local martingale N we have:

$$\langle H \cdot M, N \rangle = H \cdot \langle M, N \rangle$$

This martingale is denoted $(H \cdot M)_t =: \int_0^t H_s dM_s$ and is called the stochastic integral of H with respect to the local martingale M.

Moreover, we have for all $t > 0$ and $0 =: t_0^n < t_1^n < \ldots < t_{p_n}^n := t$ sequence of nested mesh whose step tends to 0, we have in the sense of probability:

$$\int_0^t H_s dM_s = \lim_{n \to \infty} \sum_{i=1}^{p_n} H_{t_{i-1}^n} (X_{t_i^n} - X_{t_{i-1}^n})$$

Theorem A.5 (Itô formula)**.** *Let $X = (X^1, \ldots, X^n)$ be n continuous semi-martingales and $F : \mathbb{R}^n \mapsto \mathbb{R}$ a C^2 map. Then we have:*

$$F(X_t) = F(X_0) + \sum_{j=1}^n \int_0^t \frac{\partial F}{\partial x^j}(X_s) dX_s^j + \frac{1}{2} \sum_{j=1}^n \sum_{k=1}^n \int_0^t \frac{\partial^2 F}{\partial x^j \partial x^k}(X_s) d\langle X^j, X^k \rangle_s$$

Theorem A.6 (Dubins-Schwarz)**.** *Let M be a continuous local martingale such that $\langle M \rangle_\infty = \infty$ a.s. Then there exists a Brownian motion B such that*

$$M_t = B_{\langle M \rangle_t}$$

Theorem A.7 (Girsanov)**.** *Assume that $\mathbb{Q} \sim \mathbb{P}$ on $\mathcal{F}$. Let $D_t = \frac{d\mathbb{Q}}{d\mathbb{P}}\Big|_t$ and L be the unique local martingale such that $D = exp(L - \frac{1}{2}\langle L \rangle)$. Then for all M $\mathbb{P}$-local martingale continuous, the process $M - \langle M, L \rangle$ is a $\mathbb{Q}$-local martingale continuous.*

In particular if M is a $\mathbb{P}$-Brownian motion, then $M - \langle M, L \rangle$ is a $\mathbb{Q}$-Brownian motion.

Definition A.8 (Stochastic Differential Equation)**.** Let B be a d-dimensional Brownian motion, $\sigma : \mathbb{R}_+ \times \mathbb{R}^d \mapsto \mathbb{R}^{d \times m}$ and $b : \mathbb{R}_+ \times \mathbb{R}^d \mapsto \mathbb{R}^d$ two measurable locally bounded functions. The Stochastic Differential Equation (SDE) associated to σ and b is defined by:

$$dX_t = \sigma(t, X_t)\, dB_t + b(t, X_t)\, dt$$

This expression is a notation and means:

$$X_t = X_0 + \int_0^t \sigma(s, X_s)\, dB_s + \int_0^t b(s, X_s)\, ds$$

Under suitable conditions on the coefficients σ and b (for instance if both are continuous and (locally) Lipschitz), we have existence and (pathwise) uniqueness of a solution. In the Lipschitz case, then the solution is strongly Markovian.

A.2 Stochastic processes and Partial Differential Equations

The aim of this section is to show the link between some functionals of a diffusion process X and PDEs. For more details on diffusion processes we refer to the excellent book of Bass [4]. Interested readers are also refered to [29, 62]. The diffusion process studied here satisfies the equation:

$$dX_t = b(X_t)dt + \sigma(X_t)dB_t \tag{A.1}$$

where $B := ((B_t^{(i)})_{t\geq 0})_{i=1,\dots,d}$ is a d-dimensionnal Brownian motion. This process (X) is called a multi-dimensional *diffusion process*.

We assume that b and σ are bounded and at least $\mathcal{C}^1$. We define $\mathcal{L}$ to be the diffusion operator associated to the diffusion process (A.1)

$$\mathcal{L}f(x) := \frac{1}{2}\sum_{i,j=1}^{d} a_{ij}(x)\frac{\partial^2}{\partial x_i \partial x_j}f(x) + (b(x)\cdot\nabla)f(x) \tag{A.2}$$

where $a(x) = (a_{ij}(x))_{i,j} \in \mathcal{M}_d$ is the symmetrical matrix defined by $a(x) = \sigma(x)\sigma^T(x)$.

Let us now define a real function q, called potential, in reference with Schrödinger's theory.

We consider the operator, called *Schrödinger's operator*, defined by:

$$\mathcal{G}u(x) := \mathcal{L}u(x) + q(x)u(x) \tag{A.3}$$

We have the

Theorem A.8. *Let D be a smooth bounded domain, q a $\mathcal{C}^2$ function on $\bar{D}$, f a continuous function on ∂D. Let τ_D be the first hitting time of the border ∂D of D by the process X :*

$$\tau_D := \inf\{t > 0; X_t \in \partial D\} = \inf\{t > 0; X_t \in \partial D\}$$

Let u be the solution of the PDE equation with Dirichlet condition :

$$\begin{cases} \mathcal{L}u(x) + q(x)u(x) = 0 & \forall x \in D \\ u(x) = f(x) & \forall x \in \partial D \end{cases} \tag{A.4}$$

If q is such that :

$$\mathbb{E}_x\left[e^{\int_0^{\tau_D} q^+(X_s)ds}\right] < \infty \tag{A.5}$$

where $q^+(x) := max(q(x), 0)$, then u, solution of (A.4), can be written:

$$u(x) = \mathbb{E}_x\left[f(X_{\tau_D})e^{\int_0^{\tau_D} q(X_s)ds}\right] \tag{A.6}$$

We provide the proof of this theorem because it is simple and because it is a good example of the use of the notions we introduced in section A.1.

Proof. Let $Y_t := \int_0^t q(X_s)ds$ and consider the stochastic process $e^{Y_t}u(X_t)$. Itô's formula gives the following expression for this process:

$$\begin{aligned} e^{Y_t}u(X_t) &= u(X_0) + \int_0^t e^{Y_s}u(X_s)dY_s + M_t + \int_0^t e^{Y_s}\mathcal{L}u(X_s)ds \\ &= u(X_0) + M_t + \int_0^t e^{Y_s}(\mathcal{L}u(X_s) + q(X_s)u(X_s))ds \\ &= u(X_0) + M_t + \int_0^t e^{Y_s}\mathcal{G}u(X_s)ds \qquad \text{(A.7)} \\ & \qquad \text{(A.8)} \end{aligned}$$

where M_t denotes an associated local martingale:

$$M_t = \sum_{i=1}^{d} \int_0^t e^{Y_s} b_i(X_s) \frac{\partial u}{\partial x_i}(X_s)ds$$

Let us stop the process under consideration at the stopping time τ_D. Let $S_n := \inf\{t; \text{dist}(X_t, \partial D) < 1/n\}$. We clearly have $S_n \underset{n\to\infty}{\nearrow} \tau_D$. Then since $u \in \mathcal{C}^2(\bar{D})$ we have the property that $M_{t\wedge S_n}$ is a martingale for all $n \in \mathbb{N}$. Let us take the expectation and apply the optimal stopping theorem to (A.7). Stopping the process at time S_n ensures us that $\mathcal{G}u(X_s)$ is 0 because X_s is always inside the domain D. We then have

$$\begin{aligned} e^{Y_{t\wedge S_n}}u(X_{t\wedge S_n}) &= u(X_0) + M_{t\wedge S_n} \quad \text{, and taking the expectation} \\ \mathbb{E}_x\left[e^{Y_{t\wedge S_n}}u(X_{t\wedge S_n})\right] &= u(x) \end{aligned}$$

Finally, letting $n \to \infty$ and using Lebesgue's theorem (the function u is bounded inside the domain D and the hypothesis (A.5) ensures us to have a $\mathbb{L}^1$ bound) we get :

$$\mathbb{E}_x\left[e^{Y_{t\wedge\tau_D}}u(X_{t\wedge\tau_D})\right] = u(x) \quad \forall t > 0$$

We can conclude letting $t \to \infty$, since the expectation converges by Lebesgue's theorem. □

There is also an interesting connection between the Laplace transform and the diffusion operator associated to a one-dimensional diffusion process. Let $X = (X_t;\ t > 0)$ be a one-dimensional diffusion process given by the equation :

$$dX_t = b(X_t)dt + \sigma(X_t)dB_t \qquad \text{(A.9)}$$

where $B = (B_t)_{t\geq 0}$ is a standard one-dimensional Brownian motion.

Let $\tau_a(X)$ be the first passage-time of X to the fixed barrier a and let $u_\lambda(x)$ be the Laplace transform of $\tau_a(X)$ conditionally on the fact that $X_0 = x$.

$$\tau_a(X) := \inf\{t > 0; X_t = a\}$$

$$u_\lambda(x) := \mathbb{E}_x\left[e^{-\lambda\tau_a(X)}\right] \quad , \ \lambda \geq 0 \tag{A.10}$$

Theorem A.9. *Assume that $x < a$. The Laplace transform $u_\lambda(x)$ is solution of the following PDE together with limit conditions :*

$$\begin{cases} \mathcal{L}u_\lambda(x) - \lambda u_\lambda(x) = 0 \\ u_\lambda(a) = 1 \\ \lim\limits_{x\to-\infty} u_\lambda(x) = 0 \end{cases} \tag{A.11}$$

Remark 1. The case $x > a$ can be treated in the same way with only a few changes as stated in the beginning of the section.

Theorem A.10. *The Laplace transform of the hitting time of a diffusion with generator $\mathcal{L}$ can be written:*

$$\mathbb{E}_x\left[e^{-\lambda\tau_a(X)}\right] = \frac{\Psi_\lambda(x)}{\Psi_\lambda(a)} \tag{A.12}$$

where $\Psi_\lambda(\cdot)$ is proportional to the unique increasing positive solution of

$$\mathcal{L}\Psi_\lambda = \lambda\Psi_\lambda$$

(i.e. the eigenfunction of the diffusion operator $\mathcal{L}$ associated to the eigenvalue λ).

Let us now consider section a one-dimensional diffusion process $X = (X_t;\ t > 0)$ given by the equation :

$$X_t = b(X_t)dt + \sigma(X_t)dB_t \tag{A.13}$$

where $B = (B_t)_{t\geq 0}$ is a standard one-dimensional Brownian motion.

Let $a(t)$ be the boundary, and $\tau_a(X)$ the first passage time of X to the boundary.

We denote $u_\lambda(x)$ be the Laplace transform of $\tau_a(X)$ conditionally on the fact that $X_0 = x$.

$$\tau_a(X) := \inf\{t > 0; X_t = a(t)\}$$

$$u_\lambda(x) := \mathbb{E}_x\left[e^{-\lambda\tau_a(X)}\right] \quad , \ \lambda \geq 0 \tag{A.14}$$

Theorem A.11. *Assume that $x < a(0)$. Then the Laplace transform $u_\lambda(x) = v_\lambda(0,x)$ where $v_\lambda(t,x)$ is solution of the following PDE together with limit conditions :*

$$\begin{cases} \partial_t v_\lambda(t,x) + \mathcal{L} v_\lambda(t,x) - \lambda v_\lambda(t,x) = 0 \\ v_\lambda(t,a(t)) = 1 \\ \lim\limits_{x\to-\infty} v_\lambda(t,x) = 0 \end{cases} \tag{A.15}$$

Proof. The proof of the necessary condition, i.e. assuming that a regular solution ($C^{1,2}$), the proof is very similar to the one of theorem A.9.

To prove this theorem we only have to use Itô's formula to the (assumed) $C^{1,2}$ function $e^{-\lambda t} v(t, X_t)$. The local martingale will be a real martingale (it is necessary to bound the process X also to get a martingale, as we did in the last proof), and the optimal stopping theorem will apply and we will eventually get:

$$\mathbb{E}_x\left[e^{-\lambda \tau_a(X)}\right] = v_\lambda(0,x)$$

□

In the present paper we also use several times the Fokker-Planck partial differential equation. This equation which governs the transition probability density of a given process can be deduced straightforwardly form the previous theory.

Theorem A.12 (Fokker-Planck equation)**.** *Let X be a diffusion process solution of the stochastic differential equation:*

$$dX_t = b(X_t)\,dt + \sigma(X_t)\,dW_t. \tag{A.16}$$

Under suitable conditions on b and σ, the process X is uniquely defined by (A.16)*, strongly Markovian with stationnaty increments. Its transition function is:*

$$P(t,x,\Gamma) := \mathbb{P}\Big(X_{t+s} \in \Gamma \Big| X_s = x\Big)$$

We assume that this probability has a density with respect to Lebesgue's measure $P(t,x,\Gamma) = \int_\Gamma p(t,x,y)\,dy$ and that this density satisfies regularity conditions on $\frac{\partial p}{\partial t}$, $\frac{\partial p}{\partial x^i}$ and $\frac{\partial^2 p}{\partial x^i \partial x^j}$. In this case, the transition density probability is the fundamental solution (Green's function) of the equation:

$$\frac{\partial p(t,x,y)}{\partial t} = \frac{1}{2}\sum_{i,j} a^d_{i,j=1}(x)\frac{\partial^2 p(t,x,y)}{\partial x^i \partial x^j} + \sum_{j=1}^{d} b_j(x)\frac{\partial p(t,x,y)}{\partial x^j}. \tag{A.17}$$

i.e. $\frac{\partial p(t,x,y)}{\partial t} = \mathcal{L}_x p(t,x,y)$. This equation is called forward Kolmogorov equation.

Under regularity conditions on $\frac{\partial p}{\partial t}$, $\frac{\partial p}{\partial y^i}$ *and* $\frac{\partial^2 p}{\partial y^i \partial y^j}$, *the transition probability density is the fundamental solution (Green's function) of the backward Kolmogorov equation, or* Fokker-Planck equation*:*

$$\frac{\partial p}{\partial t} = \frac{1}{2}\sum_{i,j=1}^{d} \frac{\partial^2 a_i, j(y) p(t,x,y)}{\partial y^i \partial y^j} - \sum_{j=1}^{d} \frac{\partial b^i(y) p(t,x,y)}{\partial y^i} \tag{A.18}$$

or:

$$\frac{\partial p(t,x,y)}{\partial t} = \mathcal{L}_y^* p(t,x,y)$$

.

B Hermite's function

The special functions used in previous sections are recalled below and we refer to [39] for most of the results and proofs.

Definition B.1. The Hermite function $\mathcal{H}_\nu$ is defined by :

$$\mathcal{H}_\nu(z) \stackrel{\text{def}}{=} \frac{2^\nu \Gamma(\frac{1}{2})}{\Gamma(\frac{1-\nu}{2})} \phi\left(-\frac{\nu}{2}, \frac{1}{2}; z^2\right) + \frac{2^{\nu+\frac{1}{2}} \Gamma(-\frac{1}{2})}{\Gamma(\frac{-\nu}{2})} z\phi\left(\frac{1-\nu}{2}, \frac{3}{2}; z^2\right) \tag{B.1}$$

where ϕ denotes the confluent hypergeometric function (or Kummer's function of the first kind) and Γ the gamma function.

$$\begin{aligned}\phi(a,b;z) &\stackrel{\text{def}}{=} 1 + \frac{a}{b}z + \frac{a(a+1)}{b(b+1)}\frac{z^2}{2!} + \frac{a(a+1)(a+2)}{b(b+1)(b+2)}\frac{z^3}{3!} + \dots \\ &\stackrel{\text{def}}{=} \sum_{k=0}^{\infty} \frac{(a)_k}{(b)_k}\frac{z^k}{k!}\end{aligned}$$

Proposition B.1. Hermite function satisfies the following relations :

i. The Hermite function has the following series representation :

$$\mathcal{H}_\nu(z) = \frac{1}{2\Gamma(-\nu)} \sum_{m=0}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m-\nu}{2}\right) (2z)^m, \quad |z| < \infty \tag{B.2}$$

ii. The following recurrence relations hold :

$$\frac{\partial \mathcal{H}_\nu(z)}{\partial z} = 2\nu \mathcal{H}_{\nu-1}(z) \tag{B.3}$$

$$\mathcal{H}_{\nu+1}(z) = 2z\mathcal{H}_\nu(z) - 2\nu\mathcal{H}_{\nu-1}(z) \tag{B.4}$$

iii. $\mathcal{H}_\nu(z)$ and $\mathcal{H}_\nu(-z)$ are fundamental solutions of the ordinary so called Hermite equation :

$$f''(z) - 2zf'(x) + 2\nu f = 0 \tag{B.5}$$

Proof. The series expansion of i. comes from the definition of the ϕ function.

The recurrence relations of ii. come from the fundamental relation on Γ : $\Gamma(1+z) = z\Gamma(z)$ and the series expansion (B.2) : on one hand we have

$$\begin{aligned}\frac{\partial \mathcal{H}_\nu(z)}{\partial z} &= \frac{1}{2\Gamma(-\nu)} \sum_{m=1}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m-\nu}{2}\right) 2m(2z)^{m-1} \\ &= \frac{-2}{2\Gamma(-\nu)} \sum_{m=0}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m+1-\nu}{2}\right) (2z)^m \text{ changing } m \text{ to } m+1\end{aligned}$$

On the other hand,

$$2\nu\mathcal{H}_{\nu-1}(z) = \frac{2\nu}{2\Gamma(1-\nu)} \sum_{m=0}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m-\nu+1}{2}\right) (2z)^m$$

And conclude with the relation $\Gamma(1-\nu) = -\nu\Gamma(-\nu)$.

The second recurrence relation comes also from those two relations. To check this relation we compare the coefficient of the power of $2z$ of the series expansion of the two sides of (B.4) and play with the fundamental relation of Γ.

Finally, the ordinary differential equation (B.5) is no more than (B.4), writing $\mathcal{H}_{\nu-1}$ and $\mathcal{H}_{\nu-2}$ in terms of derivatives of $\mathcal{H}_\nu$ using (B.3). □

C Some calculations

Proposition C.1. The two-dimensionnal process (X_t, M_t) is a Gaussian Markov process.

Proof. First of all, note that if $\mathcal{F}_t^X$ (resp. $\mathcal{F}_t^M$) defines the canonical filtration associated to the process X (resp. M) then it is clear that $\forall t \geq 0$, $\mathcal{F}_t^X \subset \mathcal{F}_t^M$.

It is also clear that M is a martingale, and satisfies the Markov property. Let $s \leq t$. We have:

$$\begin{aligned}X_t &= \int_0^t g(u)M_u du \\ &= \int_0^s g(u)M_u du + \int_s^t g(u)M_u du\end{aligned}$$

$$\boxed{X_t = X_s + \int_s^t g(u)(M_u - M_s)du + M_s \int_s^t g(u)du} \tag{C.1}$$

Conditionnaly to M_s, the process $\int_s^t g(u)(M_u - M_s)du$ is independant of $\mathcal{F}_s^M$ so the law of X_t knowing (X_s, M_s) is independant of the filtration $\mathcal{F}_t^{(X,M)}$ and so does M, so eventually the couple (X, M) is Markov.

The pair is clearly a Gaussian process since its two components are. Indeed, M is Gaussian as the limit of the Riemann sums of Brownian increments, which are Gaussian, and X is also the limit of Riemann sums of a Gaussian process, namely M, with the weights given by g.

□

Remark 2. In the proof of proposition C.1, we also proved that conditionally to M_s, the increment $(X_t - X_s, M_t - M_s)$ are independent of the σ-field $\mathcal{F}_s$. The proof also shows that X_t is non-Markov since its law depends on M_t.

References

[1] L. F. Abbott and C. van Vreeswijk. Asynchronous states in a network of pulse-coupled oscillators. *Phys. Rev. E*, 48:1483–1490., 1993.

[2] L. Alili, P. Patie, and J. L. Pedersen. Representations of the first hitting time density of an ornstein-uhlenbeck process. *Stochastic Models*, 21:967–980, 2005.

[3] R. S. Anderssen, F. R. De Hood, and R. Weiss. On the numerical solution of brownian motion processes. *Journal of Applied Probability*, 10:409–418, 1973.

[4] Richard F. Bass. *Diffusions and Elliptic Operators*. Springer, 1998.

[5] Patrick Billingsley. *Convergence of Probability Measures*. Wiley series in probability and statistics, 1999.

[6] K. Borovkov and Alexander Novikov. Explicit bounds for approximation rates for boundary crossing probabilities for the wiener process. *Journal of Applied Probability*, 42:82–92, 2005.

[7] L. Breiman. First exit times from a square root boundary. *Fifth Berkeley Symposium*, 2:9–16, 1967.

[8] R. Brette and W. Gerstner. Adaptive exponential integrate-and-fire model as an effective description of neuronal activity. *J Neurophysiol*, 94:3637–3642, 2005.

[9] N Brunel. Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons. *J. Comp. Neurosci.*, 8:183–208, 2000.

[10] N Brunel and V Hakim. Fast global oscillations in networks of integrate-and-fire neurons with low firing rates. *Neural Comp.*, 11:1621–1671, 1999.

[11] N Brunel and P Latham. Firing rate of noisy quadratic integrate-and-fire neurons. *Neural Computation*, 15:2281–2306, 2003.

[12] N. Brunel and S. Sergi. Firing frequency of leaky integrate-and-fire neurons with synaptic currents dynamics. *J. Theor. Biol.*, 195:87–95, 1998.

[13] Guido Bugmann, Chris Christodoulou, and John G. Taylor. Role of temporal integration and fluctuation detection in the highly irregular firing of a leaky integrator neuron model with partial reset. *Neural Computation*, 9(5):985–1000, 1997.

[14] A. Buonocore, A. G. Nobile, and L. M. Ricciardi. A new integral equation for the evaluation of first-passage-time probability densities. *Advances in Applied Probability*, 19(4):784–800, December 1987.

[15] B. Delisle Burns and A. C. Webb. The spontaneous activity of neurones in the cat's cerebral cortex. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 194:211–223, 1976.

[16] C.C. Chow and J.A. White. Spontaneous action potentials due to channel fluctuations. *Biophysical Journal*, 71:3013–3021, 1996.

[17] Alain Destexhe, Zachary F. Mainen, and Terrence J. Sejnowski. *Methods in Neuronal Modeling*, chapter Kinetic models of synaptic transmission, pages 1–25. MIT Press, Cambridge, 1998.

[18] Alain Destexhe and Denis Paré. Impact of network activity on the integrative properties of neocortical pyramidal neurons in vivo. *Journal of Neurophysiology*, 81:1531–1547, 1999.

[19] J.L. Doob. Heuristic approach to the kolmogorov-smirnov theorems. *Ann. Math. Statist.*, 20:393–403, 1949.

[20] J. Durbin. The first-passage-density of a continuous Gaussian process to a general boundary. *J. Appl. Prob.*, 22:99–122, 1985. Correction in volume 25 (1988), 840.

[21] J. Durbin. The first-passage density of the brownian motion process to a curved boundary. *J. Appl. Prob.*, 29:291–304, 1992.

[22] Olivier Faugeras, Theodore Papadopoulo, Jonathan Touboul, Mireille Bossy, Etienne Tanre, and Denis Talay. The statistics of spikes trains for some simple types of neuron models. In *NeuroComp 2006*, 2006.

[23] L. Favella, M.T. Reineri, L.M. Ricciardi, and L. Sacerdote. First passage time problems and related computational methods. *Cybernetics and Systems*, 13:95–128, 1982.

[24] Nicolas Fourcaud and Nicolas Brunel. Dynamics of the firing probability of noisy integrate-and-fire neurons. *Neural Computation*, 14:2057–2110, 2002.

[25] G.L. Gerstein and B. Mandelbrot. Random walk models for the spike activity of a single cell. *Biophys. J.*, 4:41–68, 1964.

[26] Wulfram Gerstner and Werner M. Kistler. *Spiking Neuron Models*. Cambridge University Press, 2002.

[27] M.T. Giraudo, L. Sacerdote, and C. Zucca. A monte-carlo method for the simulation of first passage time diffusion processes. *Methodology and computing in applied probability*, 3:215–231, 2001.

[28] Malcolm Goldman. On the first passage of the integrated Wiener process. *Ann. Mat. Statist.*, 42:2150–2155, 1971.

[29] Kiyosi Itô and Henry P. MacKean. *Diffusion processes and their sample paths*. 1996.

[30] Eugene M. Izhikevich. *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting*. The MIT Press, 2006. To appear.

[31] I. Karatzas and S. Shreve. *Brownian motion and stochatic calculus*. Springer, 1987.

[32] Peter Kloeden and Eckhard Platen. *Numerical solution of stochastic differential equations*. Springer-Verlag, Berlin, 1992.

[33] B. W. Knight. Dynamics of encoding in a population of neurons. *J. Gen. Physiol.*, 59:734–766, 1972.

[34] Aimé Lachal. Sur le premier instant de passage de l'intégrale du mouvement brownien. *Annales de l'IHP, section B*, 27:385–405, 1991.

[35] Aimé Lachal. Quelques martingales associÃ©es Ã l'intÃ©grale du processus d'ornstein-uhlenbeck. application Ã l'Ã©tude des premiers instants d'atteinte. *Stoch. Stoch. Rep.*, 58:285–302, 1996.

[36] Aimé Lachal. Les temps de passages successifs de l'intÃ©grale du mouvement brownien. *Ann. I. H. P. Sect. B*, 33:1–36, 1997.

[37] L Lapicque. Recherches quantitatifs sur l'excitation des nerfs traitee comme une polarisation. *J. Physiol. Paris*, 9:620–635, 1907.

[38] Jean-François Le Gall. Mouvement Brownien et Calcul Stochastique. Lecture notes, January 1997.

[39] N.N. Lebedev. *Special functions and their applications.* Dover publications, 1972.

[40] Mario Lefebvre. First-passage densities of a two-dimensional process. *SIAM Journal on Applied Mathematics*, 49:1514–1523, 1989.

[41] Peter Linz. *Analytical and Numerical Methods for Volterra Equations.* SIAM studies in applied mathematics, 1985.

[42] P. Marsalek, C. Koch, and J. Maunsell. On the relationship between synaptic input and spike output jitter in individual neurons. *PNAS*, 94:735–740, 1997.

[43] H. P. McKean. A winding problem for a resonator driven by a white noise. *J. Math. Kyoto Univ.*, 2:227–235, 1963.

[44] E. Di Nardo, A. G. Nobile, E. Pirozzi, and L. M. Ricciardi. A computational approach to first passage time problems for Gauss-Markov processes. *Advances in Applied Probability*, 33:453–482, 2001.

[45] Harald Niederreiter. *Random number generation and quasi-Monte Carlo methods.* Society for Industrial and Applied Mathematics, Philadelphia, PA, USA, 1992.

[46] A. G. Nobile, L. M. Ricciardi, and L. Sacerdote. Exponential trends of first-passage-time densities for a class of diffusion processes with steady-state distribution. *Journal of Applied Probability*, 22:611–618, 1985.

[47] A. G. Nobile, L. M. Ricciardi, and L. Sacerdote. Exponential trends of ornstein-uhlenbeck first-passage-time densities. *Journal of Applied Probability*, 22:360–369, 1985.

[48] A. Novikov, V. Frishling, and N. Kordzakhia. Approximations of boundary crossing probabilities for a brownian motion. *Journal of Applied Probability*, 36:1019–1030, 1999.

[49] H. E. Plesser. *Aspects of signal processing in noisy neurons.* PhD thesis, Georg-August-Universität, 1999.

[50] Klaus Pötzelberger and Liqun Wang. Boundary crossing probability for brownian motion. *Journal of Applied Probability*, 38:152–164, 2001.

[51] L.M. Ricciardi, L. Sacerdote, and S. Sato. On an integral equation for first passage time probability density function. *Journal of Applied Probability*, 21:302–314, 1984.

[52] Luigi M. Ricciardi and Shunsuke Sato. First-passage time density and moments of the ornstein-uhlenbeck process. *Journal of Applied Probability*, 25(1):43–57, March 1988.

[53] Brian D. Ripley. *Stochastic simulation.* John Wiley & Sons, Inc., New York, NY, USA, 1987.

[54] A. Ronveaux, editor. *Heun's Differential Equations.* Oxford University Press, 1995.

[55] Walter Rudin. *Principles of Mathematical Analysis.* McGraw-Hill, 1976.

[56] M. Samuelides and B. Cessac. Random recurrent neural networks. *European Physical Journal - Special Topics*, 142:7–88, 2007.

[57] M. Shadlen and W. Newsome. The variable discharge of cortical neurons: Implications for connectivity. *J. Neurosci*, 18:3870–3896, 1998.

[58] M. N. Shadlen and W. T. Newsome. Noise, neural codes and cortical organization. *Curr Opin Neurobiol*, 4(4):569–579, August 1994.

[59] A.J.F. Siegert. On the first passage time probability problem. *Physical Review*, 81:617–623, 1951.

[60] William R. Softky and Christof Koch. The highly irregular firing of cortical cells is inconsistent with temporal integration of random epsps. *Journal of Neuroscience*, 13:334–350, 1993.

[61] R. B. Stein. A theoretical analysis of neuronal variability. *Biophysics Journal*, 5:173–194, 1965.

[62] Daniel W. Stroock and S.R.S. Varadhan. *Multidimensional diffusion processes*. Springer, 1979.

[63] Jonathan Touboul. Bifurcations analysis of a general class of nonlinear integrate-and-fire neurons. *Siam Appl. Math. (submitted)*, 2007.

[64] Jonathan Touboul and Olivier Faugeras. First hitting time of the integrated wiener process to curved boundaries. *(in preparation)*, 2007.

[65] Todd Troyer and Kenneth D. Miller. Physiological gain leads to high ISI variability in a simple model of a cortical regular spiking cell. *Neural Computation*, 9(5):971–983, 1997.

[66] H. C. Tuckwell. *Introduction to theoretical neurobiology*. Cambridge University Press, 1988.

[67] Liqun Wang and Klaus Pötzelberger. Boundary crossing probability for brownian motion and general boundaries. *Journal of Applied Probability*, 34:54–65, 1997.

[68] Liqun Wang and Klaus Potzelberger. Crossing probabilities for diffusion processes with piecewise continuous boundaries. 2006.

Unité de recherche INRIA Sophia Antipolis
2004, route des Lucioles - BP 93 - 06902 Sophia Antipolis Cedex (France)

Unité de recherche INRIA Futurs : Parc Club Orsay Université - ZAC des Vignes
4, rue Jacques Monod - 91893 ORSAY Cedex (France)
Unité de recherche INRIA Lorraine : LORIA, Technopôle de Nancy-Brabois - Campus scientifique
615, rue du Jardin Botanique - BP 101 - 54602 Villers-lès-Nancy Cedex (France)
Unité de recherche INRIA Rennes : IRISA, Campus universitaire de Beaulieu - 35042 Rennes Cedex (France)
Unité de recherche INRIA Rhône-Alpes : 655, avenue de l'Europe - 38334 Montbonnot Saint-Ismier (France)
Unité de recherche INRIA Rocquencourt : Domaine de Voluceau - Rocquencourt - BP 105 - 78153 Le Chesnay Cedex (France)

Éditeur
INRIA - Domaine de Voluceau - Rocquencourt, BP 105 - 78153 Le Chesnay Cedex (France)
http://www.inria.fr
ISSN 0249-6399