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The Statistics Of Spikes Trains For Some Simple Types Of Neuron Models*†

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Abstract: This paper describes some preliminary results of a research program for characterizing the statistics of spikes trains for a variety of commonly used neuron models in the presence of stochastic noise and deterministic input. The main angle of attack of the problem is through the use of stochastic calculus and ways of representing (local) martingales as Brownian motions by changing the time scale.

Key-words: Integrate and fire neuron, Brownian motion, Integrate and fire with synaptic conductances, spikes statistics

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Statistiques de trains de spikes pour quelques types de modeles de neurones simples

Résumé : Ce rapport de recherche decrit les résultats preliminaires d'un travail visant a caracteriser les distributions statistiques des trains de spikes, pour certains modèles de neurones couramment utilisés, en présence de bruit stochastique et avec des entrées déterministes. Le principal angle d'attaque du problème est l'utilisation du calcul stochastique et la représentations des martingales (locales) comme un mouvement brownien via un changement de l'échelle de temps¶.

Mots-clés : Neurone integre et tire, integre et tire à conductances synaptiques, mouvement brownien, statistiques de spikes

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1 Introduction

The dynamics of the discharge of neurons in vivo is greatly influenced by noise. 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. The impact of noise on neuronal dynamics can be studied in detail in a simple spiking neuron model, the integrate-and-fire (IF) neuron [16]. For more complicated models the authors usually make use of the framework of the Fokker-Planck equation associated to a set of stochastic differential equations describing the dynamics of the neuron membrane potential in the presence of synaptic noise [14]. Since this equation cannot in general be solved analytically, the authors resort to some plausible approximations to obtain analytical results in various extreme case [3, 6]. In this paper we first give a general overview of methods arising from the stochastic calculus which we think can be very useful for studying this kind of problems. We then choose two of these methods and apply them to the description of the statistics of the inter-spikes time intervals for any input current and for a variety of synaptic noise types.

2 Stochastic calculus methods

2.1 Densities of hitting times

Stochastic diffusion models for neuron membrane potentials are widely admitted in the literature. For such a model the time of the first spike is the first time at which the diffusion process hits a determined threshold $\theta > 0$. Numerous authors consider that the probability density function (pdf) of this first hitting time conveys an important biological information.

In this section we briefly present a few mathematical tools which allow one, in some cases, to explicit this density function. As, in the sequel of the paper, we will deal with the Integrate and Fire model and variations thereof, we limit ourselves to consider diffusion processes of the type

$$X_t = X_0 + \int_0^t (\alpha(s) - X_s) ds + \sigma W_t,$$

where W is a a standard one dimensional Brownian motion W, σ is a positive real number, and $\alpha(s)$ is a real valued function of time. We search the pdf of the stopping time $T^{X,\theta} = \inf \{s \geq 0; X_s = \theta\}$. As shown in section 3 below, this question is equivalent to finding the pdf of the stopping time

$$T^{W,\phi} = \inf \{s \geq 0; W_s = \phi(s)\}$$

for some function ϕ which can easily be explicited in terms of $\alpha(s)$ and θ. Notice that Strassen [15] has actually shown that, when ϕ is of class C^1, then $T^{W,\phi}$ has a continuous pdf. Unfortunately there are only a few cases where one can explicit this pdf as we now explain.

We first consider the case where the function $\alpha(s)$ is such that ϕ is constant: $\phi(s) = a$ for all s. We write T^a for $T^{W,\phi}$. It is well known that the Laplace transform of a random variable fully characterizes its distribution. It is thus natural to search an explicit formula for the function $u(x) := \mathbb{E}_x \exp(-\lambda T^a)$ for all positive real number λ, where $\mathbb{E}_x$ is the expectation of the law of the

Brownian motion W issued from x at time 0. To this end we consider the elliptic partial differential equation on $(-\infty, a)$:

$$\begin{cases} \frac{1}{2}\frac{d^2u}{dx^2}(x) - \lambda u(x) &= 0 \text{ for all } x < a, \\ u(a) &= 1, \end{cases} \tag{1}$$

with the limit condition:

$$\lim_{x \to -\infty} u(x) = 0.$$

The smooth solution to this PDE is $u(x) = \exp[\sqrt{2\lambda}(x-a)]$. Itô's formula applied to $\exp(-\lambda t)u(W_t)$ shows that this process is a martingale. Thus the Optional Stopping Theorem (see, e.g., [10]) implies

$$\mathbb{E}_x\left[\exp(-\lambda T^a)\right] = u(x) = \exp[\sqrt{2\lambda}(x-a)].$$

It now remains to invert the Laplace transform in order to get the density function of T^a:

$$\mathbb{P}_x\left(T^a \in dt\right) = \frac{a-x}{\sqrt{2\pi}t^{3/2}} \exp\left(-\frac{(a-x)^2}{2t}\right).$$

From this formula and Girsanov's theorem it is easy to deduce the pdf when ϕ is of the type $\mu t + c$. For more general functions ϕ we have to solve the two dimensional elliptic PDE

$$\begin{cases} \partial_t u(t,x) + \frac{1}{2}\frac{d^2u}{dx^2}u(t,x) - \lambda u(t,x) = 0 \\ \text{for all } x < \phi(t), \\ u(t, \phi(t)) = 1, \end{cases} \tag{2}$$

with the limit condition

$$\lim_{x \to -\infty} u(t,x) = 0.$$

If a smooth solution exists, we may apply Itô's formula to the process $\exp(-\lambda t)u(t, X_t)$ and prove that it is a martingale. We then get

$$\mathbb{E}_x\left[\exp(-\lambda T^{W,\phi})\right] = u(0,x).$$

The difficulty is to exhibit explicit solutions of (2) and to compute their inverse Laplace transform. However, Groeneboom [7] succeeded to treat the case $\phi(t) = -\frac{\gamma}{2}t^2$ and $x\gamma > 0$. Using Girsanov's Theorem, one easily sees that it is then enough to solve the one dimensional PDE

$$\begin{cases} \frac{1}{2}\frac{d^2u}{dx^2}(x) - (\gamma x + \lambda)u(x) &= 0 \text{ for all } x > 0, \\ u(0) &= 1, \end{cases} \tag{3}$$

with the limit condition: $\lim_{x\to\infty} u(x) = 0$. The solution can be explicited in terms of the decreasing sequence $(v_k)_{k\geq 0}$ of the negative zeros of the Airy function Ai (see, e.g., Borodin and Salminen for a definition). The Laplace transform inversion formula then leads to

$$\begin{aligned}\mathbb{P}_x\left(T^{W,\phi} \in dt\right) = & \left(2\gamma^2\right)^{1/3} \mathrm{e}^{-\frac{\gamma^2 t^3}{6}} \\ & \times \sum_{k=0}^{\infty} \frac{Ai\left(v_k + (2\gamma)^{1/3}x\right)}{Ai'(v_k)} \mathrm{e}^{2^{-1/3}\alpha^{2/3}v_k t} dt.\end{aligned}$$

A completely different methodoly is the Method of Images (see Lerche [11]). It consists in considering the function h defined by

$$h(t,x)dx = \mathbb{P}(T^{W,\phi} > t, W_t \in dx).$$

Notice that h solves the heat equation

$$\begin{cases} \frac{\partial}{\partial t} h(t,x) & = \frac{1}{2}\frac{\partial^2}{\partial x^2} h(t,x) \text{ for all } t > 0,\ x < \phi(t), \\ h(t,\phi(t)) & = 0, \\ h(0,x) & = \delta_0(x) \text{ for all } x < \phi(0). \end{cases} \tag{4}$$

Here we suppose that ϕ is concave and $\phi(0) > 0$.

Suppose now that the following representation holds true: for some $a > 0$,

$$h(t,x) = \frac{1}{\sqrt{t}}\eta\left(\frac{x}{\sqrt{t}}\right) - \frac{1}{\theta}\int_0^\infty \frac{1}{\sqrt{t}}\eta\left(\frac{x-s}{\sqrt{t}}\right) F(ds), \tag{5}$$

where $\eta(x) := \frac{1}{\sqrt{2\pi}}\exp(-x^2/2)$ and $F(ds)$ is a positive $\sigma-$finite measure such that $\int_0^\infty \eta(\sqrt{\epsilon s})F(ds) < \infty$ for all $\epsilon > 0$. In Lerche [11], it is shown that, if $z = \phi(t)$ is the unique solution of $h(t,z) = 0$ for all fixed t, then

$$\begin{aligned}\mathbb{P}_0\left(T^{W,\phi} \leq t\right) = & \ 1 - \eta\left(\frac{\phi(t)}{\sqrt{t}}\right) \\ & + \frac{1}{\theta}\int_0^\infty \eta\left(\frac{\phi(t)-s}{\sqrt{t}}\right) F(ds).\end{aligned} \tag{6}$$

The difficulty is to explicit the measure F which seems to have been possible for very particular functions ϕ only: see Patie [12] for a survey.

In conclusion, PDEs and Method of Images allow one to explicitly get the pdf of $T^{W,\phi}$ for restrcited families of functions ϕ. These families can be slightly enlarged by using the technical Doob's transform: see Alili and Patie [1].

An alternative approach consists in searching approximations of the pdf. This approach has been successfully developed by Durbin for concave or convex functions ϕ: see Theorem 1 below. An important challenge is to extend Durbin's results to general functions ϕ.

2.2 Monte Carlo simulations

As seen in section 2.1, explicit exact formulae or approximations of the pdf of $T^{W,\phi}$ are generally difficult to obtain. Monte Carlo simulations apply without restriction to the model and the function ϕ. Indeed, simulations of the stochastic model (or of accurate discretizations of the model) allow one to obtain empirical density functions of $T^{W,\phi}$.

For example, consider:

$$\begin{cases} dX_t &= (-X_t + 1 + \sin(2\pi t))dt + 2dB_t \\ X_0 &= 0. \end{cases}$$

And consider the stopping time $T = \inf\{t \geq 0; X_t \geq 2\}$ We obtain numerically an approximation of the pdf of T (see Fig. 1).

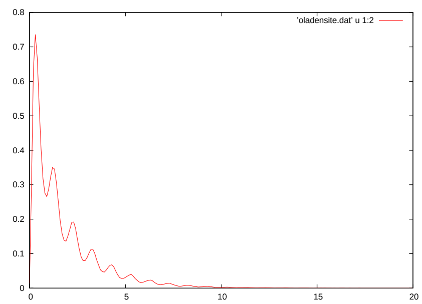

Figure 1: Approximation of the pdf of T with 10E6 Monte Carlo simulations

This method permits us to control the error (see Cramer bound). This method is robust, it does need no assumption of convexity.

3 Integrate and fire with instantaneous synaptic conductances

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

$$\tau du = (\mu - u(t))dt + I_e(t)dt + \sigma dW,$$

with initial condition $u(0) = 0$, where τ is the time constant of the membrane, μ a reversal potential, $I_e(t)$ the injected current and $W(t)$ a Brownian process representing synaptic input. The neuron emits a spike each time its membrane potential reaches a threshold θ. The membrane potential is then reinitialized to the initial value, i.e. 0. 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.

3.1 The time of the first spike

The problem of characterizing the first time t_1 when the membrane potential reaches the threshold θ is defined as

$$t_1 = inf\{t : t > 0, u(t) = \theta\},$$

where $u(t)$ is given by the following expression

$$u(t) = \mu(1 - e^{-\frac{t}{\tau}}) + \frac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_e(s)\, ds + \frac{\sigma}{\tau}\int_0^t e^{\frac{s-t}{\tau}} dW(s)$$

The condition $u(t) = \theta$ can be rewritten as

$$\int_0^t e^{\frac{s}{\tau}} dW = \frac{\tau}{\sigma}\left[(\theta - \mu)e^{\frac{t}{\tau}} + \mu - \frac{1}{\tau}\int_0^t e^{\frac{s}{\tau}} I_e(s)\, ds\right] \equiv b(t) \quad (7)$$

In order to characterize t_1 we need the following

Lemma 1 *Let* $X(t) = \int_0^t e^{\frac{s}{\tau}} dW(s)$ *The stochastic process* $X(t)$ *is a Brownian motion if we change the time scale:* $X(t) = W\left(\frac{\tau}{2}\left(e^{2\frac{t}{\tau}} - 1\right)\right)$.

Proof This lemma is in fact a direct consequence of the Dubins-Schwarz theorem [9]. We provide an elementary proof for completeness. Let $r = \frac{\tau}{2}\left(e^{2\frac{t}{\tau}} - 1\right)$, it is a monotonously increasing function of t equal to 0 for $t = 0$. For all times $0 < r_1 < r_2 < \cdots < r_n$, the random variables $X(r_1)$, $X(r_2) - X(r_1)$, $\ldots X(r_n) - X(r_{n-1})$ are independent because W is a Brownian motion. Finally, it is easy to see that $X(t_2) - X(t_1)$ is distributed as $N(0, \int_{t_1}^{t_2} e^{2\frac{s}{\tau}}\, ds)$ which implies that $X(r_2) - X(r_1)$ is distributed as $N(0, r_2 - r_1)$.
□

We can now rewrite the threshold crossing condition above as

$$W(r) = \frac{\tau}{\sigma}\left[(\theta - \mu)\sqrt{\frac{2}{\tau}r + 1} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\, ds\right],$$

where

$$\tilde{I}_e(s) = \frac{I_e(\frac{\tau}{2}\log\left(\frac{2}{\tau}s + 1\right))}{\sqrt{\frac{2}{\tau}s + 1}}$$

The time t_1 at which the membrane potential reaches the threshold θ is obtained from the time r_1 at which the Brownian motion W reaches for the first time the curve $a(r)$ defined by the equation

$$y = a(r) = \frac{\tau}{\sigma}\left[(\theta - \mu)\sqrt{\frac{2}{\tau}r + 1} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\, ds\right],$$

by the formula

$$t_1 := \frac{\tau}{2}\log(\frac{2}{\tau}r_1 + 1)$$

The corresponding problem has been studied in particular by Durbin [4, 5] who provides an integral equation for the probability density function (pdf) of r_1. From this integral equation he deduces a series approximation of the pdf and proves convergence when the curve is concave or convex.

This result is summarized in the

Theorem 1 (Durbin) *Let $W(\tau)$ be a standard Brownian motion for $\tau \geq 0$ and $y = a(\tau)$ be a boundary such that $a(0) > 0$ and $a(\tau)$ is continuously differentiable for $\tau \geq 0$. The first-passage density $p(t)$ of $W(\tau)$ to $a(t)$ is solution of the following integral equation*

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

which can be written as

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

where

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

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

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

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

$$f_0(t) = (2\pi t)^{-1/2}\exp(-a(t)^2/2t),$$

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

$$f(t|s) = f_0(s)(2\pi(t - s))^{-1/2}\exp(-(a(t) - a(s))^2/(2(t - s))).$$

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

As an application of the above, we consider two examples.

3.1.1 Constant intensity

In this case the membrane potential is the realization of an Ornstein-Uhlenbeck (OU) process. The function $a(r)$ is convex, hence the hypotheses of Durbin's theorem are satisfied. The moments of the pdf of the hitting time can be computed analytically [13], see the next theorem.

Theorem 2 *Let us define $\alpha := \frac{\mu}{\sigma}$ and $\beta := \frac{\sigma}{\theta\sqrt{\tau}}$ and the three following functions:*

$$
\begin{aligned}
\Phi_1(z) &:= \frac{1}{2}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})(z-\alpha)^n \\
\Phi_2(z) &:= \frac{1}{2}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})\left(\Psi(\frac{n}{2})-\Psi(1)\right)(z-\alpha)^n \\
\Phi_1(z) &:= \frac{3}{8}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})(z-\alpha)^n \rho_n^{(3)}
\end{aligned}
$$

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

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

A comparison of the values of the first three moments computed from the pdf of the hitting time obtained from Durbin's theorem or by simulation with the analytical values (obtained by truncating the series Φ_i) is shown in table 1. This table shows that the theoretical values can be closely

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 realisations, step = 10^{-4}	1.932180	7.139402	40.079556

Table 1: Values of the first 3 moments of the OU process and the empirical values, for the parameters: $\theta = \sigma = 2$, $\mu = \tau = 1$

approximated if sufficiently many terms are taken into account in Durbin's series expansion.

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

3.1.2 Periodic intensity

We choose $I_e(t) = \sin(2\pi f t)$. Table 2 shows the values of the integral of the estimated pdf. The parameters are the same as in the previous example, $f = 1$. It is seen that Durbin's series converges very quickly. Figure 2 shows the shape of the pdf of the first passage time and the first four terms in the series approximation. Table 2 indicate that a very good approximation of the pdf can be obtained with only 5 terms in the series. The total computation time is 8 seconds on a 2GHz computer for 800 sample points.

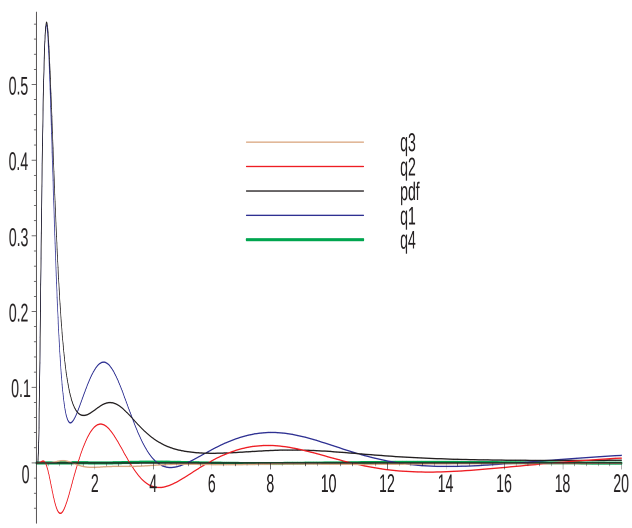

Figure 2: Four terms of the series approximation of the pdf when $I_e(t) = \sin(2\pi t)$ and the resulting pdf (the horizontal scale is in r units).

3.2 The times of the next spikes

The previous analysis and results can be extended to the times $t_2, \ldots t_n$ of the next spikes. We discuss how to determine t_n given t_{n-1}, i.e. how to compute $p(t_n|t_{n-1})$. The scenario is similar to the one used to compute t_1. For $t > t_{n-1}$, $u(t)$ is given by the following expression

$$u(t) = \mu(1 - e^{-\frac{t-t_{n-1}}{\tau}}) + \tfrac{1}{\tau}\int_{t_{n-1}}^{t} e^{\frac{s-t}{\tau}} I_e(s)\,ds + \frac{\sigma}{\tau}\int_{t_{n-1}}^{t} e^{\frac{s-t}{\tau}} dW(s)$$

After some algebra, the condition for crossing the threshold can be written

$$X(t) = \int_{t_{n-1}}^{t} e^{\frac{s}{\tau}}\,dW(s) = b(t) + h(t_{n-1}),$$

where

$$h(t_{n-1}) = \frac{\tau}{\sigma}\left(\frac{1}{\tau}\int_0^{t_{n-1}} e^{\frac{s}{\tau}} I_e(s)\,ds + \mu(e^{\frac{t_{n-1}}{\tau}} - 1)\right),$$

and $b(t)$ is defined in (refeq:bt). Consider the stochastic process $Y(t') = X(t' + t_{n-1})$, using once again the Dubins-Schwarz theorem, $Y(t') = W(r')$ where $r' = \int_0^{t'} e^{2\frac{s'+t_{n-1}}{\tau}}\,ds' = e^{\frac{2t_{n-1}}{\tau}}\frac{\tau}{2}(e^{\frac{2t'}{\tau}} - 1)$. The next threshold crossing time t_n is the first crossing time of $W(r')$ with the boundary $b(t' + t_{n-1}) + f(t_{n-1}) = b(\frac{\tau}{2}\log(\frac{2}{\tau}e^{-\frac{2t_{n-1}}{\tau}}r' + 1) + t_{n-1}) + h(t_{n-1})$.

4 Integrate and fire with exponentially decaying synaptic conductances

We modify the model of section 3 to include exponentially decaying synaptic conductances.

$$\begin{cases} \tau du &= (\mu - u(t))dt + I_e(t)dt + I_s(t)dt \\ \tau_s dI_s &= -I_s(t)dt + \sigma dW \end{cases}$$

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

$$u(t) = \mu(1 - e^{-\frac{t}{\tau}}) + \tfrac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_e(s)\,ds + \tfrac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_s(s)\,ds,$$

the second equation can be integrated as

$$I_s(t) = I_s(0)e^{-\frac{t}{\tau_s}} + \frac{\sigma}{\tau_s}\int_0^t e^{\frac{s-t}{\tau_s}} dW(s),$$

where $I_s(0)$ is a given random variable. We define $\frac{1}{\alpha} = \frac{1}{\tau} - \frac{1}{\tau_s}$. Replacing in the first equation $I_s(t)$ by its value in the second equation we obtain

$$u(t) = \mu(1 - e^{-\frac{t}{\tau}}) + \tfrac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_e(s)\,ds + \frac{I_s(0)}{1 - \frac{\tau}{\tau_s}}(e^{-\frac{t}{\tau_s}} - e^{-\frac{t}{\tau}}) + \frac{\sigma}{\tau\tau_s}e^{-\frac{t}{\tau}}\int_0^t e^{\frac{s}{\alpha}}\left(\int_0^s e^{\frac{s'}{\tau_s}} dW(s')\right) ds$$

4.1 The time of the first spike

The previous method must be slightly modified because of the following

Lemma 2 *Let $X(t) = \int_0^t e^{\frac{s}{\alpha}} \left(\int_0^s e^{\frac{s'}{\tau_s}} dW(s') \right) ds$, the stochastic process $X(t)$ is not a martingale. It is a continuous Gaussian process with covariance function $\rho(r,t)$ for $0 \leq r \leq t$ given by*

$$\frac{1}{\alpha^2}\rho(r,t) = \frac{\tau_s}{2} e^{\frac{r+t}{2}} (e^{\frac{2r}{\tau_s}} - 1) + \frac{\alpha\tau_s}{2(\alpha+\tau_s)} e^{\frac{2r(\alpha+\tau_s)}{\alpha\tau_s}} - 1) - \\ (e^{\frac{r}{\alpha}} + e^{\frac{t}{\alpha}})(e^{\frac{r(2\alpha+\tau_s)}{\alpha\tau_s}} - 1)$$

Proof By exchanging the order of integration in the definition of $X(t)$ (Fubini's theorem) we obtain

$$X(t) = \int_0^t e^{\frac{s'}{\tau_s}} \left(\int_{s'}^t e^{\frac{s}{\alpha}} ds \right) dW(s') = \\ \alpha \int_0^t e^{\frac{s'}{\tau_s}} (e^{\frac{t}{\alpha}} - e^{\frac{s'}{\alpha}}) \, dW(s'),$$

This expression is of the form $X(t) = \int_0^t f(t,s)\, dW(s)$ and therefore $X(t_1) - X(t_2)$ is not independent of $X(t_2)$ for $0 \leq t_2 < t_1$. Because of the properties of the Brownian motion it is a continuous zero-mean Gaussian process whose covariance function $\rho(r,t)$ for $0 \leq r \leq t$ is

$$\mathbb{E}[X(r)X(t)] = \mathbb{E}\left[\int_0^r f(r,s)\, dW(s) \int_0^t f(t,s)\, dW(s) \right] = \\ \mathbb{E}\left[\int_0^r f(r,s) f(t,s)\, d < W, W >_s \right] = \int_0^r f(r,s) f(t,s)\, ds$$

and the result follows from the computation of the last integral.
□

In the same line of idea as in section 3, we can express the problem of characterizing the time t_1 at which the membrane potential reaches the threshold θ as that at which the Gaussian process X reaches for the first time the curve $a(\tau)$ defined by the equation

$$y = a(\tau) = -\frac{\alpha\tau_s}{\sigma} I_s(0)(e^{\frac{t}{\alpha}} - 1) + \\ \frac{\tau\tau_s}{\sigma}\left[(\theta - \mu) e^{\frac{t}{\tau}} + \mu - \frac{1}{\tau}\int_0^t e^{\frac{s}{\tau}} I_e(s)\, ds \right],$$

This problem has been studied by Durbin [4] and is summarized in the following theorem

Theorem 3 (Durbin) *Let $X(\tau)$ be a continuous zero-mean Gaussian process with covariance function $\rho(r,t)$ for $0 \leq r \leq t$ and $y = a(\tau)$ be a boundary such that $a(\tau)$ is continuous in $0 \leq \tau < t$*

and left differentiable at t. Under some mild assumptions on ρ the first-passage density $p(t)$ of $X(\tau)$ to $a(t)$ is solution of the following Volterra integral equation of the second kind

$$p(t) = p_1(t) + \int_0^t [a'(t) - \beta_1(s,t)a(s) - \beta_2(s,t)a(t)] f(t|s) p(s)\, ds,$$

where β_1 and β_2 are given by

$$\begin{bmatrix} \beta_1(s,t) \\ \beta_2(s,t) \end{bmatrix} = \begin{bmatrix} \rho(s,s) & \rho(s,t) \\ \rho(s,t) & \rho(s,s) \end{bmatrix}^{-1} \begin{bmatrix} \rho_2(s,t) \\ \rho_1(s,t) \end{bmatrix},$$

ρ_1 and ρ_2 are the first order partial derivatives of ρ with respect to the first and second variables, and

$$p_1(t) = f_0(t) b_1(t),$$

where

$$b_1(t) = \frac{a(t)}{\rho(t,t)} \frac{\partial \rho(s,t)}{\partial s}|_{s=t} - a'(t)$$

$f_0(t)$ is the density of $X(t)$ on the boundary and $f(t|s)$ is the conditional density of $X(t)$ at $a(t)$ given that $X(s) = a(s)$.

4.2 The times of the next spikes

As in the case of instantaneous synaptic conductances, we can extend our analysis and compute the conditional probabilities $p(t_n|t_{n-1})$, in effect $p(t_n|t_{n-1}, I_s(0))$, as follows. For $t > t_{n-1}$. The expression for the membrane potential is

$$u(t) = \mu(1 - e^{-\frac{t-t_{n-1}}{\tau}}) + \frac{1}{\tau}\int_{t_{n-1}}^t e^{\frac{s-t}{\tau}} I_e(s)\, ds + \frac{I_s(0)}{1-\frac{\tau}{\tau_s}}(e^{-\frac{t-t_{n-1}}{\tau_s}} - e^{-\frac{t-t_{n-1}}{\tau}}) + \frac{\sigma}{\tau\tau_s} e^{-\frac{t}{\tau}} \int_{t_{n-1}}^t e^{\frac{s}{\alpha}} \left(\int_0^s e^{\frac{s'}{\tau_s}} dW(s') \right) ds$$

The analysis proceeds as follows using theorem 3 instead of 1.

5 Conclusion

We have sketched out a number of techniques borrowed from the field of stochastic calculus that we believe to be useful in the analysis of spikes trains generated by neural models. We have applied two variations of one of these methods to the computation of the pdfs of the spikes times of two instances of the integrate and fire neuron model with synaptic conductances. The first variation is based upon representing the membrane potential as the sum of a deterministic function and a local martingale. Due to a theorem by Dubins and Schwarz, by changing the time scale we can turn the local martingale into a Brownian motion and the problem of computing the pdfs of the spikes times into that of computing the first-passage density of the Brownian motion to a curved boundary. This particular problem can be solved through a method due to Durbin [5] which provides a series approximation of the pdf. Numerical experiments show that the series converges rapidly. A comparison with the results obtained by Monte-Carlo simulation is provided. The second variation is based upon representing the membrane potential as the sum of a deterministic function and a zero-mean continuous Gaussian process. Due to another theorem by Durbin the problem is shown to be equivalent to solving a Volterra integral equation of the second kind. These ideas can probably be extended to more complex neuron models [2, 8].

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