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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 [11]. 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 [9]. Since this equation cannot in general be solved analytically, the authors resort to various plausible approximations to obtain analytical results in various extreme case [2, 5]. In this paper we outline a method that can produce the statistics of the inter-spikes time intervals for any input current and for a variety of synaptic noise types.

2 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.

2.1 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

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

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

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

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 [7]. 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 [3, 4] 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 next theorem.

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 $a(t)$ 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.

2.1.1 Constant intensity

In this case the membrane potential is the realization of an Ornstein-Uhlenbeck process. The function $a(r)$ is convex, hence the hypotheses of Durbin's theorem are satisfied. Moreover some analytical results have been obtained for the first moment of the law of the first passage time. In table 1, we show the successive approximations of the values of the integral of the law (which should be equal to 1); the mean value is found to be equal to 1.93 (which is the value found by the analytical formula found in, e.g., [8]). The values of the parameters are $\theta = \sigma = 2$, $\mu = \tau = 1$.

time-terms	3	5	7	9
10^3	0.86	0.86	0.86	0.86
10^5	0.98	0.95	0.95	0.95
10^7	1.12	0.97	0.98	0.98
10^9	1.44	1.01	0.99	0.99

Table 1: Values of the integral of the estimated pdf for $I_e = 0$. The left column indicates the range of the values of r, the first line the number of terms in the series approximation.

2.1.2 Periodic intensity

We choose $I_e(t) = \sin(2\pi f t)$. Table 2 is similar to 1. The parameters are the same as in the previous example, $f = 1$. It is seen that Durbin's series converges very quickly. Figure 1 shows the shape of the pdf of the first passage time and the first four terms in the series approximation. Tables 1 and 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.

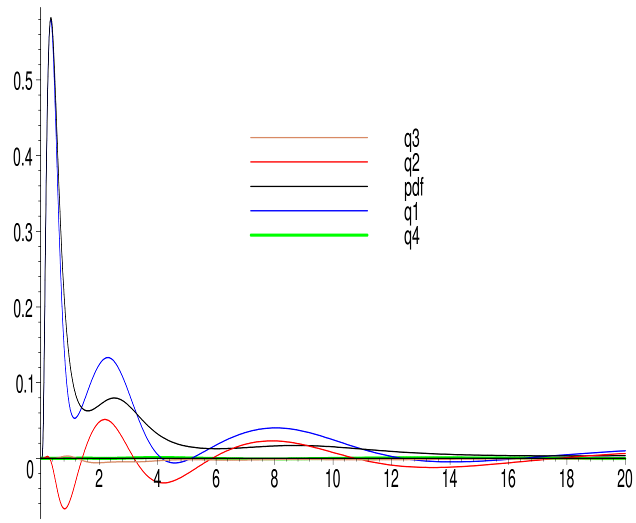

Figure 1: Four terms of the series approximation of the pdf when $I_e(t) = \sin(2\pi t)$ and the resulting pdf (the horizontal scale is in r units).

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 $I_e = \sin(2\pi t)$.

2.2 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.

We know that the process u_t is strongly Markovian (diffusion process with Lipschitz coefficients, see [7, 10]). Conditionally on the stopping time t_{n-1}, determining the interspike interval reduces to the problem of determining the first stopping time t_1. The only difference is that the random time shift t_{n-1} appears in the input I_e (but the conditioning allows us to apply the same method as before).

More precisely, we have for $r \geq 0$

$$u(t_{n-1}+r) = \mu(1-e^{-\frac{r}{\tau}}) + \tfrac{1}{\tau}\int_0^r e^{\frac{s-r}{\tau}} I_e(s+t_{n-1})\, ds + \tfrac{\sigma}{\tau}\int_0^r e^{\frac{s-t}{\tau}} dW(s). \tag{2}$$

Let r_n be the n$^{\text{th}}$ interspike interval. We have $t_n = t_{n-1} + r_n$. The same local martingale as in section 2.1 can be used. The Dubins-Schwarz' theorem yields the same change of variables and eventually the crossing condition reads :

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

where

$$\tilde{I}_e^{(n)}(s) = \frac{I_e\big(\frac{\tau}{2}\log\left(\frac{2}{\tau}s+1\right) + t_{n-1}\big)}{\sqrt{\frac{2}{\tau}s+1}}.$$

Finally, the problem of finding the sequence of stopping times $(t_n)_{n\geq 1}$ is equivalent to the problem of finding the first stopping time. Furthermore, we can see that the sequence (t_n) is a Markov chain, and that if the input is constant, the interspike intervals are independent and identically distributed.

3 Integrate and fire with exponentially decaying synaptic conductances

We modify the model of section 2 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

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

3.1 The time of the first spike

We prove 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 a Brownian motion if we change the time scale: $X(t) = W\left((\tau - \tau_s)^2 e^{2\frac{t}{\tau}} - \tau_s(\tau + \tau_s) e^{2\frac{t}{\alpha}} + 4\tau\tau_s e^{\frac{t}{\alpha}} - \tau(\tau + \tau_s) \right)$.*

Proof This result is also a consequence of the Dubins-Schwarz' theorem. We provide a short elementary proof. By exchanging the order of integration in the definition of $X(t)$ (Fubini's theorem, which here is equivalent to an integration by parts) we obtain

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

and the result follows from the computation of $f(t) = \alpha^2 \int_0^t e^{2\frac{s'}{\tau_s}} (e^{\frac{t}{\alpha}} - e^{\frac{s'}{\alpha}})^2\, ds'$.
□

In the same line of idea as in section 2, we can express the problem of characterizing the time t_1 at which the membrane potential reaches the threshold θ as that at which

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

or equivalently at which

$$W(r) + \frac{\alpha\tau_s}{\sigma} I_s(0)(e^{\frac{f^{-1}(r)}{\alpha}} - 1) = \frac{\tau\tau_s}{\sigma} \left[(\theta - \mu)e^{\frac{f^{-1}(r)}{\tau}} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\, ds \right],$$

where f is the function defined in the proof of lemma 2 and

$$\tilde{I}_e(s) = e^{\frac{f^{-1}(s)}{\tau}} \frac{I_e(f^{-1}(s))}{f'(f^{-1}(s))}$$

It is easy to verify that if $\tau > \tau_s$, f is monotonously increasing. The time t_1 at which the membrane potential reaches the threshold θ for the first time is therefore obtained, conditionally on the random variable $I_s(0)$, from the time r_1 at which the Brownian motion reaches for the first time the curve $a(r)$ defined by the equation

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

by Durbin's theorem and the formula

$$t_1 = f^{-1}(r_1)$$

3.2 The times of the next spikes

As in the case of instantaneous synaptic conductances, we can extend our analysis and compute the conditional probabilities $p(t_n|t_{n-1})$, or rather $p(t_n|t_{n-1}, I_s(0))$, as follows. For $t > t_{n-1}$, let us denote $r = t - t_{n-1}$. We know that the process I_s is Markovian, hence conditionally on t_{n-1} and by the uniqueness of I_s we obtain:

$$I_s(t_{n-1}+r) = I_s(t_{n-1})e^{-\frac{r}{\tau_s}} + \frac{\sigma}{\tau_s}\int_0^r e^{\frac{s-r}{\tau_s}}\,dW(s).$$

Conditionally on t_{n-1} we can integrate the equation from this origin, and we obtain the following expression for the membrane potential:

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

Here again the problem is exactly the same as finding the first spike time. The only difference is that we condition on t_{n-1}, and this only amounts to change $I_s(0)$ to $I_s(t_{n-1})$ and $I_e(\cdot)$ by $I_e(\cdot + t_{n-1})$. The time t_n at which the membrane potential reaches the threshold θ for the first time after t_{n-1} is therefore obtained, conditionally on the random variables $I_s(0)$ and t_{n-1}, from the time r_n at which the Brownian motion reaches for the first time the curve $a(r)$ defined by the equation

$$y = a(r) = \frac{\tau\tau_s}{\sigma}\left[(\theta-\mu)e^{\frac{f^{-1}(r)}{\tau}} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e^{(n)}(s)\,ds\right] - \frac{\alpha\tau_s}{\sigma} I_s(t_{n-1})(e^{\frac{f^{-1}(r)}{\alpha}} - 1),$$

where $f(t) = \alpha^2\int_0^t e^{2\frac{s'}{\tau_s}}(e^{\frac{t}{\alpha}} - e^{\frac{s'}{\alpha}})^2\,ds'$ is the change of time scale used in the proof of lemma 2, and

$$\tilde{I}_e^{(n)}(s) = e^{\frac{f^{-1}(s)}{\tau}}\frac{I_e(f^{-1}(s)+t_{n-1})}{f'(f^{-1}(s))}.$$

Finally we obtain t_n by Durbin's theorem and the formula

$$t_n = t_{n-1} + f^{-1}(r_n)$$

Again, we can state that conditionally on the random variable $I_s(0)$ the sequence $(t_n)_{n\geq 0}$ is a Markov chain.

4 Conclusion

We have outlined a method for computing the pdf's of the spikes times of two variations of the integrate and fire neuron model with synaptic conductances. The method 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 [4] which provides a series approximation of the pdf. Numerical experiments show that the series converges rapidly. The method can be extended to more complex neuron models [1, 6].

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