MODELING REFRACTORINESS FOR STOCHASTICALLY DRIVEN SINGLE NEURONS

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Abstract. A description of the sequence of interspike intervals and of the subsequent firing times for single neurons is performed by means of an instantaneous return process in the presence of refractoriness. Every interspike interval consists of an absolute refractory period of fixed duration followed by a period of relative refractoriness whose duration is described by the first-passage time of the modeling diffusion process through a generally time-dependent threshold. In the cases of Wiener and Ornstein-Uhlenbeck processes, the interspike probability density functions and some of its statistical features are explicitly obtained for special monotonically non-increasing thresholds.

1 Introduction Stochastic models for neuronal firing in the presence of refractoriness have been the object of various investigations. The first attempt to study the effect of refractoriness in a point process is made in [22] and in [25] in which the authors consider the role played by the dead time in determining the distribution of the output when the input obeys a given distribution. Successively, an instantaneous return process, constructed on a diffusion, has been considered aiming to a quantitative description of neuron's membrane potential behavior. Within such a context, the presence of refractoriness has been included in two different ways. The first way assumes that the firing threshold acts as an elastic barrier that is partially transparent, i.e. such that its behavior is intermediate between total absorption and total reflection (cf. [3], [4], [5], [20]). Alternatively, the return process paradigm for the description of the time course of the membrane potential is analyzed by assuming that the neuronal refractoriness period is a random variable with a pre-assigned probability density (cf. [1], [10], [11], [15], [23]). Recently, in [2] and [16], the Wiener neuronal model in the presence of constant and of exponentially distributed refractoriness has been considered, and expressions for output distributions and for interspike interval densities have been obtained in closed form.

Customarily, the firing threshold has been viewed in the literature as a constant which may not be appropriate, especially for rapidly firing cells (cf. [7], [13], [14], [26]). Indeed, when a neuron releases an action potential, it becomes temporarily incapable of responding to further input signals. In fact, for a period of time, of the order of one or two milliseconds, the neuron is unable to respond to any stimuli (absolute refractory period). After that, for several successive milliseconds its sensitivity to the incoming stimuli is normally reduced, in some cases increasing successively. This type of after-firing behavior (after potentials) may last up to about 100 msec. In the present context we focus our attention on a constant absolute refractory period followed by a period of relative refractoriness that we model as a random variable. Hence, after a spike release, we assume that the neuron is unable to fire again during the absolute refractory period, while the firing threshold is assumed to decrease progressively as the inhibitory effect of the previous spike fades away.

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In Section 2 we provide a description of the sequence of interspike intervals $\{I_n, n = 0, 1, \dots\}$ by assuming that I_0 is described by the first-passage time of the modeling diffusion process through a monotonically non-increasing threshold $S(t)$, whereas the interspike interval I_n $(n = 1, 2, \dots)$ is characterized by the existence of two periods, R_n and F_n: the first represents the period of absolute refractoriness of fixed length; the second denotes the subsequent relative refractoriness whose duration is described by the first-passage time of the modeling diffusion process through the threshold $S(t)$ translated in the time. In Section 3 and 4 the interspike probability density functions are determined for the Wiener and Ornstein-Uhlenbeck processes and for particular thresholds.

2 Interspike distribution Let us denote by $\{X(t), t \geq 0\}$ a regular, time-homogeneous diffusion process defined over an interval $I = (r_1, r_2)$ and characterized by drift and infinitesimal variance $A_1(x)$ and $A_2(x)$, respectively, that we assume to satisfy Feller conditions [12].

As is well-known, the first passage time (FPT) of $X(t)$ to the continuous boundary $S(t)$ starting at $X(\tau) = \eta$ is defined as follows:

$$T = \inf_{t \geq \tau} \{t : X(t) \geq S(t)\}, \qquad X(\tau) = \eta < S(\tau). \tag{2.1}$$

Then,

$$g[S(t), t \mid \eta, \tau] = \frac{\partial}{\partial t} P(T < t), \qquad \eta < S(\tau) \tag{2.2}$$

is the FPT probability density function (pdf) of $X(t)$ through the boundary $S(t)$ conditional upon $X(\tau) = \eta$. In the neuronal modeling context the boundary $S(t)$ represents the neuron firing threshold, the FPT through $S(t)$ the firing time and $g[S(t), t \mid \eta, \tau]$ the firing time pdf. In the sequel we shall assume that $P(T < +\infty) = 1$ for all $\tau > 0$, so that the neuron's firing is a sure event.

Let $\{Z(t), t \geq 0\}$ be a return process in the presence of refractoriness. The process $Z(t)$ consists of recurrent cycles $\mathcal{F}_0, \mathcal{R}_1, \mathcal{F}_1, \mathcal{R}_2, \mathcal{F}_2, \dots$, where every period $\mathcal{R}_j$ $(j = 1, 2, \dots)$ of absolute refractoriness is characterized by fixed length ζ and where $\mathcal{F}_0, \mathcal{F}_1, \dots$ denote the periods of relative refractoriness. Starting at η at time zero, a firing takes place when $X(t)$ attains the threshold $S_0(t) = S(t)$ for the first time, with $\eta \in (r_1, S_0(0))$; then, an absolute refractory period occurs, after which $Z(t)$ is instantaneously reset to η. In general, the j-th subsequent evolution of the process goes on as described by $X(t)$, until the threshold $S_j(t)$, that coincides with the threshold $S(t)$ translated in the time, is again reached. A new firing then occurs, followed by the absolute refractory period, and so on.

We now provide a description of the sequence of interspike intervals $I_0, I_1, \dots$, where $I_0 = F_0$ and where $I_k = R_k + F_k$ $(k = 1, 2, \dots)$. Here $F_0, F_1, \dots$ denote the random variables describing the durations of the relative refractory periods $\mathcal{F}_0, \mathcal{F}_1, \dots$, whereas $R_1, R_2, \dots$ denote the durations of the absolute refractory periods $\mathcal{R}_1, \mathcal{R}_2, \dots$. To this purpose, let Θ_j $(j = 0, 1, \dots)$ be the random variable describing the $(j+1)$-th firing time of the neuron. The following relations hold:

$$\Theta_0 = I_0 = F_0, \qquad \Theta_j = F_0 + \sum_{k=1}^{j} (R_k + F_k) = \sum_{k=0}^{j} I_k \qquad (j = 1, 2, \dots). \tag{2.3}$$

In the sequel we shall assume that the firing thresholds are defined as follows:

$$S_0(t) = S(t), \qquad S_j(t) = \begin{cases} S\big(t - \theta_{j-1} - \zeta\big), & t > \theta_{j-1} + \zeta \\ +\infty, & \text{otherwise} \end{cases} \qquad (j = 1, 2, \dots), \tag{2.4}$$

where $\theta_0, \theta_1, \ldots,$ representing the successive firing times of the neuron, denote the values assumed by random variables $\Theta_0, \Theta_1, \ldots,$ respectively. Figure 1 shows the recurrent cycles of the process $Z(t)$.

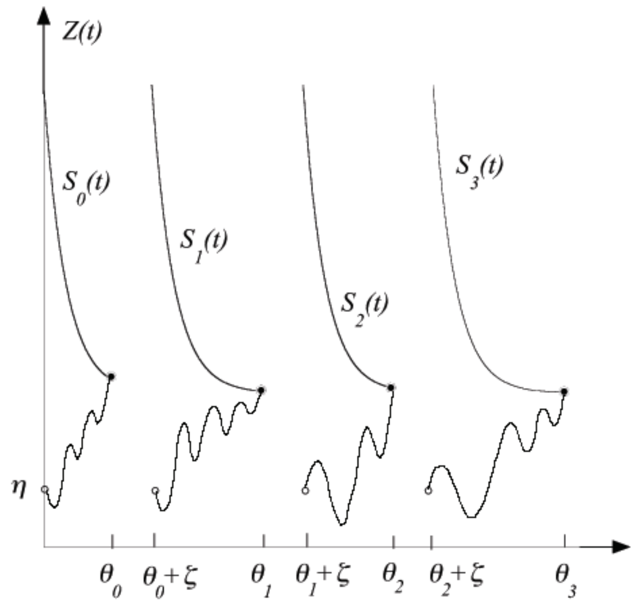


Figure 1: An hypothetical sample path of $Z(t)$. The instants $\theta_0, \theta_1, \ldots$ represent the firing times and ζ is the duration of the absolute refractory periods. The instantaneous reset value has been denoted by η.

We note that F_0, correspondent to the first-passage time of the modeling diffusion process $X(t)$ through a monotonically non-increasing threshold $S(t) = S_0(t)$, is characterized by pdf

$$g[S_0(t), t \mid \eta, 0] \equiv g[S(t), t \mid \eta, 0], \qquad S_0(0) = S(0) > \eta, \tag{2.5}$$

whereas F_j, correspondent to the first-passage time of the modeling diffusion process $X(t)$ through a monotonically non-increasing threshold $S_j(t)$ given in (2.4), is characterized by pdf

$$g[S_j(t), t \mid \eta, \theta_{j-1} + \zeta] = \begin{cases} 0, & t < \theta_{j-1} + \zeta \\ g[S(t - \theta_{j-1} - \zeta), t \mid \eta, \theta_{j-1} + \zeta], & t > \theta_{j-1} + \zeta, \end{cases} \tag{2.6}$$

for $j = 1, 2, \ldots,$ where θ_{j-1} is the time in which the j-th spike has had place.

We denote by $\gamma_0(t \mid 0)$ the pdf of I_0, and by $\Gamma_j(t \mid \theta_{j-1})$ and $\gamma_j(t \mid \theta_{j-1})$ the conditional distribution function and the conditional pdf of I_j given $\Theta_{j-1} = \theta_{j-1}$ for $j = 1, 2, \ldots,$ respectively. From (2.3) and (2.5) it follows that I_0 is characterized by pdf:

$$\gamma_0(t \mid 0) := g[S(t), t \mid \eta, 0], \qquad S(0) > \eta. \tag{2.7}$$

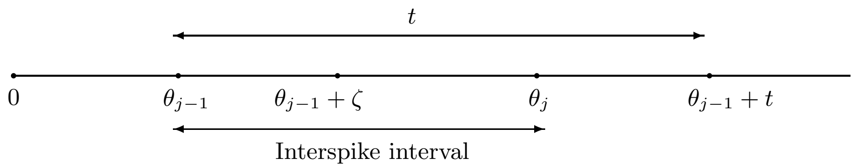


Figure 2: Starting at time θ_{j-1}, the duration of interspike interval is less than t.

Furthermore, recalling that $I_j = \zeta + F_j$, one has (cf. Figure 2):

$$\Gamma_j(t \mid \theta_{j-1}) := P(I_j < t \mid \Theta_{j-1} = \theta_{j-1}) = P(F_j < t - \zeta \mid \Theta_{j-1} = \theta_{j-1})$$

$$= \begin{cases} 0, & t < \zeta \\ \displaystyle\int_{\theta_{j-1}+\zeta}^{\theta_{j-1}+t} g[S_j(\tau), \tau \mid \eta, \theta_{j-1} + \zeta]\, d\tau, & t > \zeta \end{cases} \qquad (j = 1, 2 \ldots). \tag{2.8}$$

Hence, making use of (2.6), for $j = 1, 2, \ldots$ one obtains:

$$\gamma_j(t \mid \theta_{j-1}) := \frac{d\Gamma_j(t \mid \theta_{j-1})}{dt} = \begin{cases} 0, & t < \zeta \\ g[S(t-\zeta), t + \theta_{j-1} \mid \eta, \theta_{j-1} + \zeta], & t > \zeta. \end{cases} \tag{2.9}$$

The determination of the conditional pdf of interspike interval I_j $(j = 1, 2, \ldots)$ is in general unfeasible due to the memory effects present in the evolution of the process $Z(t)$. Hence, in the case of varying thresholds, analytical solutions are not available except in few cases. For this reason, in the sequel we shall consider special diffusion processes $X(t)$ and suitable varying thresholds, such that the FPT pdf (2.2) satisfies the following property:

$$g[S(t-\zeta), t + \theta \mid \eta, \theta + \zeta] = g[S(t-\zeta), t - \zeta \mid \eta, 0] \tag{2.10}$$

for all $t > \zeta$ and $\theta \geq 0$. Under assumption (2.10), from (2.9) one obtains:

$$\gamma_j(t \mid \theta_{j-1}) = \begin{cases} 0, & t < \zeta \\ g[S(t-\zeta), t - \zeta \mid \eta, 0], & t > \zeta \end{cases} \qquad (j = 1, 2, \ldots). \tag{2.11}$$

Eq. (2.11) shows that $\gamma_j(t \mid \theta_{j-1})$ is independent of the time θ_{j-1}, so that I_1 is independent of $\Theta_0 \equiv I_0$ and, in general, I_j is independent of $\Theta_{j-1} = I_0 + I_1 + \ldots + I_{j-1}$ $(j = 2, 3, \ldots)$. Hence, if (2.10) holds, the interspike intervals $I_0, I_1, \ldots$ are independently distributed random variables, with $I_1, I_2, \ldots$ also identically distributed.

Under assumption (2.10), we denote by I a random variable distributed as $I_1, I_2, \ldots$ and by $\gamma(t) \equiv \gamma_j(t \mid \theta_{j-1})$ its pdf. Hence, making use of (2.5) and (2.11), the first two moments of the interspike intervals $I_1, I_2, \dots$ follow:

$$
\begin{aligned}
E(I) &:= \int_0^{+\infty} t\,\gamma(t)\,dt = \int_\zeta^{+\infty} t\,g[S(t-\zeta), t-\zeta \mid \eta, 0]\,dt \\
&= \int_0^{+\infty} (u+\zeta)\,g[S(u), u \mid \eta, 0]\,dt = \zeta + E(\Theta_0), \\
E(I^2) &:= \int_0^{+\infty} t^2\,\gamma(t)\,dt = \int_\zeta^{+\infty} t^2\,g[S(t-\zeta), t-\zeta \mid \eta, 0]\,dt \\
&= \int_0^{+\infty} (u+\zeta)^2\,g[S(u), u \mid \eta, 0]\,dt = \zeta^2 + 2\,\zeta\,E(\Theta_0) + E(\Theta_0^2),
\end{aligned}
\tag{2.12}
$$

where Θ_0 is the FPT of $X(t)$ through the continuous boundary $S_0(t) = S(t)$ starting at $X(0) = \eta$. The variance of the interspike intervals $I_1, I_2, \dots$ is then $\mathrm{Var}(I) = \mathrm{Var}(\Theta_0)$.

If (2.10) holds, let $h_j(t)$ be the pdf of the random variable Θ_j describing the $(j+1)$-th firing time of the neuron, and let $H_j(\lambda)$ be its Laplace transform $(j = 0, 1, \dots)$. We note that $h_0(t) \equiv \gamma_0(t \mid 0)$. Furthermore, since $I_0, I_1, \dots$ are independently distributed random variables, recalling (2.3), (2.5) and (2.11), for $\lambda > 0$ one has:

$$
\begin{aligned}
H_j(\lambda) &:= \int_0^{+\infty} e^{-\lambda\,t}\,h_j(t)\,dt = \int_0^{+\infty} e^{-\lambda\,t}\,\gamma_0(t \mid 0)\,dt \cdot \left[\int_0^{+\infty} e^{-\lambda\,t}\,\gamma(t)\,dt\right]^j \\
&= \int_0^{+\infty} e^{-\lambda\,t}\,g[S(t), t \mid \eta, 0]\,dt \cdot \left[\int_\zeta^{+\infty} e^{-\lambda\,t}\,g[S(t-\zeta), t-\zeta \mid \eta, 0]\,dt\right]^j \\
&= e^{-j\lambda\,\zeta}\left[\int_0^{+\infty} e^{-\lambda\,t}\,g[S(t), t \mid \eta, 0]\,dt\right]^{j+1} = e^{-j\lambda\,\zeta}\left[\int_0^{+\infty} e^{-\lambda\,t}\,\gamma_0(t \mid 0)\,dt\right]^{j+1}
\end{aligned}
\tag{2.13}
$$

for $j = 0, 1, \dots$ Taking the inverse Laplace transform of (2.13) one is led to

$$
h_j(t) = \begin{cases} 0, & t < j\,\zeta \\ \left[\gamma_0(t - j\,\zeta)\right]^{(j+1)}, & t > j\,\zeta \end{cases} \qquad (j = 0, 1, \dots),
\tag{2.14}
$$

where exponent $(j+1)$ indicates $(j+1)$-fold convolution. In particular, if (2.10) holds, from (2.3) and (2.12), or equivalently from (2.13), one obtains the means and the variances of the subsequent firing times of the neuron in terms of the mean and of the variance of Θ_0:

$$
\begin{aligned}
E(\Theta_j) &= E(\Theta_0) + j\,E(I) = j\,\zeta + (j+1)\,E(\Theta_0) \\
\mathrm{Var}(\Theta_j) &= \mathrm{Var}(\Theta_0) + j\,\mathrm{Var}(I) = (j+1)\,\mathrm{Var}(\Theta_0)
\end{aligned}
\qquad (j = 1, 2, \dots).
\tag{2.15}
$$

In order to embody some physiological features of real neurons, several alternative models have been proposed in the literature (cf, for instance, [21], [24] and references therein). In the next two Sections we shall investigate the properties of the interspike intervals and of the subsequent firing times for the Wiener and Ornstein-Uhlenbeck neuronal models with refractoriness for particular choices of time-depending thresholds.

3 Wiener model In this Section we shall assume that the membrane potential of the neuron is modeled by a Wiener process $\{X(t), t \geq 0\}$, defined in $\mathbb{R}$, with drift and infinitesimal variance

$$
A_1 = \mu, \qquad A_2 = \sigma^2 \qquad (\mu \in \mathbb{R},\ \sigma > 0).
\tag{3.1}
$$

Preliminarily, we shall disclose some properties of the FPT of $X(t)$ through a linear boundary and subsequently consider a return process $Z(t)$ with refractoriness based on the Wiener process and linear firing thresholds.

3.1 FPT for the Wiener process through a linear boundary Let $\tilde{T}$ be the FPT of the Wiener process, defined in (3.1), through the threshold $\tilde{S}(t) = A\,t + B$ starting at $X(\tau) = \eta < \tilde{S}(\tau)$. The pdf of $\tilde{T}$ is given by (cf., for instance, [6] and [18]):

$$g[\tilde{S}(t), t \mid \eta, \tau] = g[A\,t + B, t \mid \eta, \tau] = \frac{A\,\tau + B - \eta}{\sigma\sqrt{2\,\pi\,(t-\tau)^3}}\,\exp\Big\{-\frac{[A\,t + B - \eta - \mu\,(t-\tau)]^2}{2\,\sigma^2\,(t-\tau)}\Big\}$$
$$[\tilde{S}(\tau) = A\,\tau + B > \eta]. \tag{3.2}$$

Remark 3.1 *For the Wiener process (3.1), for $A\,\tau + B > \eta$ and $\lambda > 0$ one has:*

$$\int_\tau^{+\infty} e^{-\lambda\,(t-\tau)}\, g[\tilde{S}(t), t \mid \eta, \tau]\, dt$$
$$= \exp\Big\{\frac{A\,\tau + B - \eta}{\sigma^2}\,(\mu - A) - \frac{A\,\tau + B - \eta}{\sigma^2}\,\sqrt{(\mu - A)^2 + 2\,\sigma^2\,\lambda}\Big\}. \tag{3.3}$$

Then,

$$P(\tilde{T} < +\infty) := \int_\tau^{+\infty} g[\tilde{S}(t), t \mid \eta, \tau]\, dt$$
$$= \begin{cases} 1, & A\,\tau + B > \eta,\ \mu \geq A \\[2ex] \exp\Big\{-\dfrac{2\,(A-\mu)\,(A\,\tau + B - \eta)}{\sigma^2}\Big\}, & \text{otherwise.} \end{cases} \tag{3.4}$$

Proof. From (3.2), for $\lambda > 0$ one has:

$$\int_\tau^{+\infty} e^{-\lambda\,(t-\tau)}\, g[\tilde{S}(t), t \mid \eta, \tau]\, dt = \frac{A\,\tau + B - \eta}{\sigma\sqrt{2\,\pi}}\,\exp\Big\{-\frac{(A-\mu)\,(A\,\tau + B - \eta)}{\sigma^2}\Big\}$$
$$\times \int_0^{+\infty} z^{-3/2}\,\exp\Big\{-\Big[\lambda + \frac{(A-\mu)^2}{2\,\sigma^2}\Big]\,z\Big\}\,\exp\Big\{-\frac{(A\,\tau + B - \eta)^2}{2\,\sigma^2\,z}\Big\}\,dz. \tag{3.5}$$

Since (cf. [9], page 146, no. 28)

$$\int_0^{+\infty} z^{-3/2}\, e^{-p\,z}\, e^{-\alpha/(4\,z)}\, dz = 2\sqrt{\frac{\pi}{\alpha}}\, e^{-\sqrt{\alpha\,p}} \qquad (\alpha > 0,\ p \geq 0), \tag{3.6}$$

choosing $p = \lambda + (A-\mu)^2/(2\,\sigma^2)$ and $\alpha = 2\,(A\,\tau + B - \eta)^2/\sigma^2$, (3.3) immediately follows from (3.5). Furthermore, by setting $\lambda = 0$ in (3.3), one obtains (3.4). □

Remark 3.2 *For the Wiener process (3.1), for $A\,\tau + B > \eta$ and $\mu > A$ one has:*

$$E(\tilde{T}^j) := \int_\tau^{+\infty} (t-\tau)^j\, g[\tilde{S}(t), t \mid \eta, \tau]\, dt = \frac{2\,(A\,\tau + B - \eta)^{j+1/2}}{\sigma\sqrt{2\,\pi}\,(\mu - A)^{j-1/2}}$$
$$\times \exp\Big\{-\frac{(A-\mu)\,(A\,\tau + B - \eta)}{\sigma^2}\Big\}\, K_{j-1/2}\Big(\frac{(A\,\tau + B - \eta)\,(\mu - A)}{\sigma^2}\Big) \qquad (j = 1, 2, \ldots), \tag{3.7}$$

where $K_\nu(z)$ denotes the modified Bessel function of the third kind. Then,

$$E(\tilde T)=\frac{A\,\tau+B-\eta}{\mu-A},\qquad E(\tilde T^2)=\Big(\frac{A\,\tau+B-\eta}{\mu-A}\Big)^2+\frac{(A\,\tau+B-\eta)\,\sigma^2}{(\mu-A)^3}\tag{3.8}$$

for $A\,\tau+B>\eta$ and $\mu>A$.

Proof. If $P(\tilde T<+\infty)=1$, making use of (3.2) for $j=1,2.\dots$ one has:

$$\begin{aligned}E(\tilde T^j)&=\frac{A\,\tau+B-\eta}{\sigma\sqrt{2\,\pi}}\,\exp\Big\{-\frac{(A-\mu)\,(A\,\tau+B-\eta)}{\sigma^2}\Big\}\\&\times\int_0^{+\infty} z^{j-3/2}\,\exp\Big\{-\frac{(A-\mu)^2\,z}{2\,\sigma^2}\Big\}\,\exp\Big\{-\frac{(A\,\tau+B-\eta)^2}{2\,\sigma^2\,z}\Big\}\,dz.\end{aligned}\tag{3.9}$$

Recalling that (cf. [9], page 146, no. 29):

$$\int_0^{+\infty} z^{\nu-1}\,e^{-p\,z}\,e^{-\alpha/(4\,z)}\,dz=2\,\Big(\frac{\alpha}{4\,p}\Big)^{\nu/2}K_\nu(\sqrt{\alpha\,p})\qquad(\alpha>0,\ p>0)\tag{3.10}$$

after setting $p=(A-\mu)^2/(2\,\sigma^2)$, $\alpha=2\,(A\,\tau+B-\eta)^2/\sigma^2$ and $\nu=j-1/2$, from (3.9) one obtains (3.7). Furthermore, since (cf. [17], page 967 no. 8.468)

$$K_{n+1/2}(z)=\sqrt{\frac{\pi}{2\,z}}\,e^{-z}\sum_{r=0}^{n}\frac{(n+r)!}{r!\,(n-r)!\,(2\,z)^r}\qquad(n=0,1,\dots),$$

one has:

$$K_{1/2}(z)=\sqrt{\frac{\pi}{2\,z}}\,e^{-z},\qquad K_{3/2}(z)=\sqrt{\frac{\pi}{2\,z}}\,e^{-z}\,\Big(1+\frac{1}{z}\Big),$$

so that from (3.7) with $j=1,2$, relations (3.8) follow. □

3.2 Interspike intervals for the Wiener model For the Wiener model of single neuron activity, we consider a return process $Z(t)$ in the presence of refractoriness, with functions (2.4) chosen as follows:

$$\begin{aligned}&S_0(t)=S(t)=a\,t+b\\&S_j(t)=\begin{cases}a(t-\theta_{j-1}-\zeta)+b, & t>\theta_{j-1}+\zeta\\ +\infty, & \text{otherwise}\end{cases}\qquad(j=1,2,\dots),\end{aligned}\tag{3.11}$$

with $\theta_0,\theta_1,\dots$ representing the successive firing times. We assume $a\le 0$, so that the thresholds (3.11) are non-increasing functions (decreasing if $a<0$ and constant if $a=0$).

Recalling (2.7), by virtue of (3.2) with $A=a$, $B=b$ and $\tau=0$, we note that $I_0=\Theta_0$ is characterized by pdf:

$$\gamma_0(t\mid 0)=g[S(t),t\mid\eta,0]=\frac{b-\eta}{\sigma\sqrt{2\,\pi\,t^3}}\,\exp\Big\{-\frac{(a\,t+b-\eta-\mu\,t)^2}{2\,\sigma^2\,t}\Big\},\qquad b>\eta.\tag{3.12}$$

From (3.4) and (3.12) there follows that $P(\Theta_0<+\infty)=1$ if and only if $b>\eta$ and $\mu\ge a$.

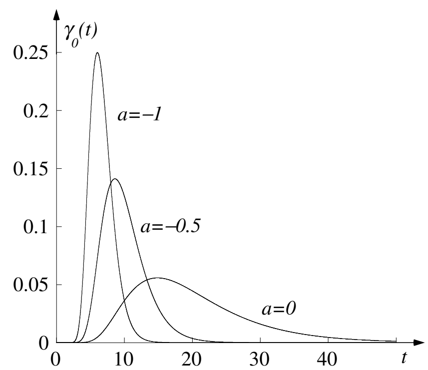


Figure 3: For the Wiener model with $\mu = 0.5\,\mathrm{mV/msec}$ and $\sigma^2 = 1\,\mathrm{mV^2/msec}$, $\gamma_0(t)$ is plotted for $\eta = -70\,\mathrm{mV}$, $b = -60\,\mathrm{mV}$, and $a = 0, -0.5, -1\,\mathrm{mV/msec}$.

Figure 3 shows the FPT pdf $\gamma_0(t) = g[S(t), t \mid \eta, 0]$ for the Wiener model (3.1) with $\mu = 0.5\,\mathrm{mV/msec}$ and $\sigma^2 = 1\,\mathrm{mV^2/msec}$ through the threshold $S(t) = (a\,t - 60)\,\mathrm{mV}$ starting from $\eta = -70\,\mathrm{mV}$ with $a = 0, -0.5, -1\,\mathrm{mV/msec}$.

Furthermore, if $b > \eta$ and $\mu > a$, the FPT moments are finite. Making use of (3.8) with $A = a$, $B = b$ and $\tau = 0$, there hold:

$$E(\Theta_0) = \frac{b-\eta}{\mu - a}, \qquad \mathrm{Var}(\Theta_0) = \frac{(b-\eta)\,\sigma^2}{(\mu - a)^3} \cdot \tag{3.13}$$

To analyze the interspike intervals $I_1, I_2, \dots$ and the firing times $\Theta_1, \Theta_2, \dots$ we first prove that the FPT pdf of the Wiener process (3.1) through the linear boundary $S(t) = a\,t + b$ satisfies relation (2.10). To this purpose we note that

$$\begin{aligned} g[S(t-\zeta), t+\theta \mid \eta, \theta+\zeta] &= g[a(t-\zeta) + b, t+\theta \mid \eta, \theta+\zeta] \\ &= g[a\,(t+\theta) - a(\theta+\zeta) + b, t+\theta \mid \eta, \theta+\zeta], \end{aligned}$$

from which, making use of (3.2) with $A = a$, $B = b - a\,(\theta+\zeta)$, $\tau = \theta + \zeta$ and final time chosen as $t + \theta$, we have:

$$\begin{aligned} g[S(t-\zeta), t+\theta \mid \eta, \theta+\zeta] &= \frac{b-\eta}{\sigma\sqrt{2\,\pi\,(t-\zeta)^3}} \exp\Big\{-\frac{[a\,(t-\zeta) + b - \eta - \mu\,(t-\zeta)]^2}{2\,\sigma^2\,(t-\zeta)}\Big\} \\ &\equiv g[S(t-\zeta), t-\zeta \mid \eta, 0] \qquad (b > \eta) \end{aligned}$$

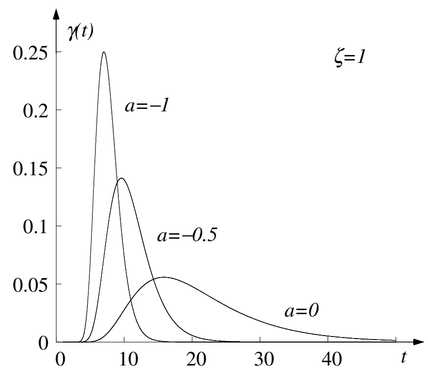
for all $t > \zeta$ and $\theta \geq 0$. Therefore, (2.10) holds.

By virtue of (2.11), for $b > \eta$ the pdf of interspike intervals I_j $(j = 1, 2, \dots)$ is:

$$\gamma(t) = \begin{cases} 0, & t < \zeta \\ \dfrac{b-\eta}{\sigma\sqrt{2\,\pi\,(t-\zeta)^3}} \exp\Big\{-\dfrac{[a\,(t-\zeta) + b - \eta - \mu\,(t-\zeta)]^2}{2\,\sigma^2\,(t-\zeta)}\Big\}, & t > \zeta. \end{cases} \tag{3.14}$$

From (3.4) and (3.14) there follows that $P(I_j < +\infty) = 1$ $(j = 1, 2, \dots)$ if and only if $b > \eta$ and $\mu \geq a$.

Figure 4 shows the interspike pdf $\gamma(t)$, given by (3.14), for the Wiener model (3.1) with $\mu = 0.5\,\mathrm{mV/msec}$ and $\sigma^2 = 1\,\mathrm{mV^2/msec}$ in the presence of the linear firing thresholds (3.11) in the case of $\eta = -70\,\mathrm{mV}$, $b = -60\,\mathrm{mV}$, $a = 0, -0.5, -1\,\mathrm{mV/msec}$ and $\zeta = 1\,\mathrm{msec}$ (on the left) and $\zeta = 10\,\mathrm{msec}$ (on the right). Figures 3 and 4 indicate that the difference between $\gamma_0(t \mid 0)$ and $\gamma(t)$ becomes more evident when the refractory period increases.



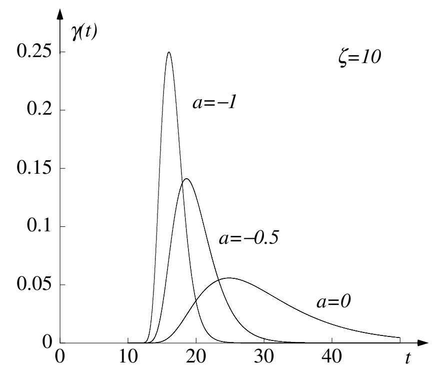


Figure 4: For the Wiener model with $\mu = 0.5\,\mathrm{mV/msec}$ and $\sigma^2 = 1\,\mathrm{mV^2/msec}$, $\gamma(t)$ is plotted for $\eta = -70\,\mathrm{mV}$, $b = -60\,\mathrm{mV}$, $a = 0, -0.5, -1\,\mathrm{mV/msec}$ and $\zeta = 1\,\mathrm{msec}$ (on the left) and $\zeta = 10\,\mathrm{msec}$ (on the right).

Furthermore, if $b > \eta$ and $\mu > a$, making use of (3.13) in (2.12), one obtains the mean and the variance of the interspike intervals:

$$E(I) \equiv E(\Theta_0) + \zeta = \frac{b-\eta}{\mu - a} + \zeta, \qquad \mathrm{Var}(I) \equiv \mathrm{Var}(\Theta_0) = \frac{(b-\eta)\,\sigma^2}{(\mu-a)^3}\,\cdot \tag{3.15}$$

In order to obtain the pdf of $\Theta_1, \Theta_2, \ldots$, we first determine the Laplace transform of $\gamma_0(t \mid 0)$. From (3.12), recalling (3.3) with $A = a$, $B = b$ and $\tau = 0$, one obtains:

$$\begin{aligned}\int_0^{+\infty} e^{-\lambda\, t}\, \gamma_0(t \mid 0)\, dt &= \int_0^{+\infty} e^{-\lambda\, t}\, \frac{b-\eta}{\sigma\sqrt{2\,\pi\, t^3}}\, \exp\Big\{-\frac{(a\,t + b - \eta - \mu\, t)^2}{2\,\sigma^2\, t}\Big\}\, dt \\ &= \exp\Big\{\frac{(\mu-a)\,(b-\eta)}{\sigma^2} - \frac{b-\eta}{\sigma^2}\sqrt{(\mu-a)^2 + 2\,\sigma^2\,\lambda}\Big\} \qquad (b > \eta).\end{aligned} \tag{3.16}$$

Hence, from (2.13) for $\lambda > 0$ there follows:

$$H_j(\lambda) = e^{-\lambda\, j\, \zeta}\, \exp\Big\{\frac{(\mu-a)\,(b-\eta)\,(j+1)}{\sigma^2} - \frac{(b-\eta)\,(j+1)}{\sigma^2}\sqrt{(\mu-a)^2 + 2\,\sigma^2\,\lambda}\Big\} \tag{3.17}$$

for $b > \eta$. Then, taking the inverse Laplace transform of (3.17), for $b > \eta$ the pdf of the random variable Θ_j is obtained:

$$\begin{aligned} h_j(t) &= \int_0^t \delta(\tau - j\zeta)\, g\big[a(t-\tau) + b(j+1), t - \tau \mid \eta(j+1), 0\big]\, d\tau \\ &= \begin{cases} 0, & t < j\,\zeta \\[2ex] g\big[a(t - j\,\zeta) + b(j+1), t - j\,\zeta \mid \eta(j+1), 0\big], & t > j\,\zeta, \end{cases}\end{aligned}$$

or equivalently:

$$h_j(t) = \begin{cases} 0, & t < j\,\zeta \\ \dfrac{(b-\eta)\,(j+1)}{\sigma\sqrt{2\,\pi\,(t-j\,\zeta)^3}}\,\exp\Big\{-\dfrac{[a\,(t-j\,\zeta)+(b-\eta)\,(j+1)-\mu\,(t-j\,\zeta)]^2}{2\,\sigma^2\,(t-j\,\zeta)}\Big\}, & t > j\,\zeta \end{cases}$$

$$(j=0,1,\dots;b>\eta). \tag{3.18}$$

We note that $h_0(t)$ coincides with $\gamma_0(t \mid 0)$, previous obtained in (3.12). Furthermore, (3.17) yields $P(\Theta_j < +\infty) = 1$ $(j = 0, 1, \dots)$ if and only if $b > \eta$ and $\mu \geq a$.

Figure 5 shows the pdf $h_j(t)$ $(j = 0, 1, \dots, 5)$ for the Wiener model (3.1) with $\mu = 0.5\,\mathrm{mV/msec}$ and $\sigma^2 = 1\,\mathrm{mV^2/msec}$ in the presence of the linear firing thresholds (3.11) in the case of $a = -0.5\,\mathrm{mV/msec}$, $b = -60\,\mathrm{mV}$, $\eta = -70\,\mathrm{mV}$ and $\zeta = 1\,\mathrm{msec}$ (on the left) and $\zeta = 10\,\mathrm{msec}$ (on the right).

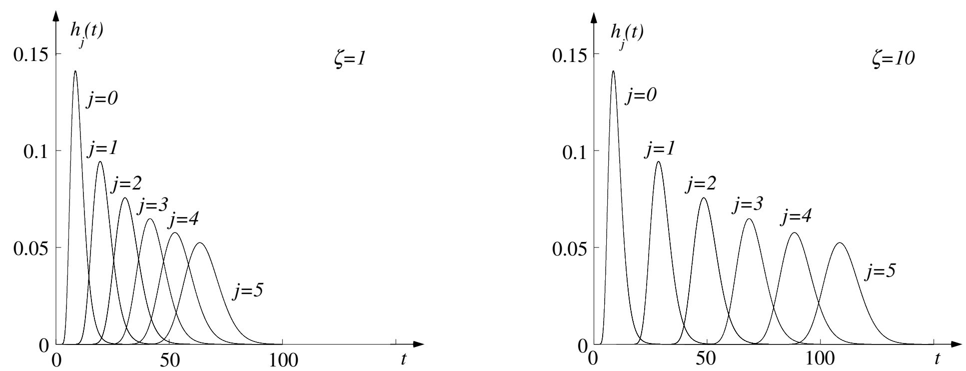


Figure 5: For the Wiener model with $\mu = 0.5\,\mathrm{mV/msec}$ and $\sigma^2 = 1\,\mathrm{mV^2/msec}$, $h_j(t)$ $(j = 0, 1, \dots, 5)$ is plotted for $\eta = -70\,\mathrm{mV}$, $b = -60\,\mathrm{mV}$, $a = -0.5\,\mathrm{mV/msec}$ and $\zeta = 1\,\mathrm{msec}$ (on the left) and $\zeta = 10\,\mathrm{msec}$ (on the right).

Finally, if $b > \eta$ and $\mu > a$ the mean and the variance of the random variable Θ_j, describing the $(j+1)$-th firing time of the neuron, follow from (2.15) and (3.13):

$$E(\Theta_j) = j\,\zeta + (j+1)\,\frac{b-\eta}{\mu-a}, \qquad \mathrm{Var}(\Theta_j) = (j+1)\,\frac{(b-\eta)\,\sigma^2}{(\mu-a)^3} \qquad (j=0,1,\dots). \tag{3.19}$$

4 Ornstein-Uhlenbeck model A more refined model that includes the spontaneous exponential decay of the neuron's membrane potential is the Ornstein-Uhlenbeck (OU) neuronal model, namely the diffusion process $\{X(t), t \geq 0\}$, defined in $\mathbb{R}$, characterized by drift and infinitesimal variance

$$A_1(x) = -\frac{x-\varrho}{\beta}, \qquad A_2 = \sigma^2 \qquad (\varrho \in \mathbb{R},\ \beta > 0,\ \sigma > 0). \tag{4.1}$$

Differently from the Wiener model, in the absence of inputs the membrane potential exponentially decays to the resting potential ϱ with a time constant β. We shall preliminarily obtain some properties of the FPT of $X(t)$ through an hyperbolic boundary and subsequently we shall consider a return process $Z(t)$ with refractoriness based on the OU process and hyperbolic firing thresholds.

4.1 FPT for the OU process through a hyperbolic boundary Let $\tilde{T}$ be the FPT of the OU process, defined in (4.1), through the threshold $\tilde{S}(t) = \varrho + A\,e^{-t/\beta} + B\,e^{t/\beta}$ starting from $X(\tau) = \eta < \tilde{S}(\tau)$. The pdf of $\tilde{T}$ is given by (cf., for instance, [6], [8]):

$$g[\tilde{S}(t), t \mid \eta, \tau] = g\big[\varrho + A\,e^{-t/\beta} + B\,e^{t/\beta}, t \mid \eta, \tau\big] = \frac{2\left[\varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} - \eta\right] e^{-(t-\tau)/\beta}}{\beta\sqrt{\pi\,\sigma^2\,\beta\left(1 - e^{-2\,(t-\tau)/\beta}\right)^3}}$$

$$\times \exp\left\{-\frac{\left[A\,e^{-t/\beta} + B\,e^{t/\beta} - (\eta - \varrho)\,e^{-(t-\tau)/\beta}\right]^2}{\sigma^2\,\beta\left(1 - e^{-2\,(t-\tau)/\beta}\right)}\right\} \tag{4.2}$$

with $\tilde{S}(\tau) = \varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} > \eta$.

Remark 4.1 *For the OU process (4.1) one has:*

$$P(\tilde{T} < +\infty) = \begin{cases} 1, & \varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} > \eta,\ B \le 0 \\ \exp\left\{-\dfrac{4\,B\,e^{\tau/\beta}\,(\varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} - \eta)}{\sigma^2\,\beta}\right\}, & \text{otherwise.} \end{cases} \tag{4.3}$$

Proof. From (4.2) one obtains:

$$\begin{aligned} P(\tilde{T} < +\infty) &= \int_\tau^{+\infty} g[\tilde{S}(t), t \mid \eta, \tau]\,dt \\ &= \frac{\varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} - \eta}{\sqrt{\pi\,\sigma^2\,\beta}}\,\exp\left\{-\frac{2\,B\,e^{\tau/\beta}\,(A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} + \varrho - \eta)}{\sigma^2\,\beta}\right\} \\ &\quad \times \int_0^{+\infty} y^{-3/2}\exp\left\{-\frac{B^2\,e^{2\,\tau/\beta}\,y}{\sigma^2\,\beta}\right\}\exp\left\{-\frac{\left[\varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} - \eta\right]^2}{\sigma^2\,\beta\,y}\right\}dy, \end{aligned} \tag{4.4}$$

where the last equality follows after the change of variable $y = e^{2\,(t-\tau)/\beta} - 1$. Recalling (3.6) with $p = B^2\,e^{2\,\tau/\beta}/(\sigma^2\,\beta)$ and $\alpha = 4\left(\varrho + A\,e^{-\tau/\beta} + B\,e^{\tau/\beta} - \eta\right)^2/(\sigma^2\,\beta)$, (4.3) immediately follows from (4.4). ◻

Remark 4.2 *For the OU process (4.1), if* $\tilde{S}(t) = \varrho + A\,e^{-t/\beta}$ *with* $\varrho + A\,e^{-\tau/\beta} > \eta$, *one has:*

$$\begin{aligned} \int_\tau^{+\infty} e^{-\lambda\,(t-\tau)}\,g[\tilde{S}(t), t \mid \eta, \tau]\,dt &= \frac{2^{\lambda\,\beta/2}}{\sqrt{\pi}}\,\Gamma\Big(\frac{1}{2} + \frac{\lambda\,\beta}{2}\Big)\,\exp\left\{\frac{(\varrho + A\,e^{-\tau/\beta} - \eta)^2}{2\,\sigma^2\,\beta}\right\} \\ &\quad \times D_{-\lambda\beta}\Big(\frac{\varrho + A\,e^{-\tau/\beta} - \eta}{\sigma}\,\sqrt{\frac{2}{\beta}}\Big), \end{aligned} \tag{4.5}$$

where $D_\nu(z)$ *denotes the parabolic cylinder function, and*

$$\begin{aligned} E(\tilde{T}) &= \beta\left[\sqrt{\pi}\,\varphi_1\Big(\frac{\varrho + A\,e^{-\tau/\beta} - \eta}{\sigma\sqrt{\beta}}\Big) - \psi_1\Big(\frac{\varrho + A\,e^{-\tau/\beta} - \eta}{\sigma\sqrt{\beta}}\Big)\right], \\ E(\tilde{T}^2) &= 2\,\beta^2\left[\sqrt{\pi}\,\ln 2\,\varphi_1\Big(\frac{\varrho + A\,e^{-\tau/\beta} - \eta}{\sigma\sqrt{\beta}}\Big) - \sqrt{\pi}\,\varphi_2\Big(\frac{\varrho + A\,e^{-\tau/\beta} - \eta}{\sigma\sqrt{\beta}}\Big)\right. \\ &\qquad \left. + \psi_2\Big(\frac{\varrho + A\,e^{-\tau/\beta} - \eta}{\sigma\sqrt{\beta}}\Big)\right], \end{aligned} \tag{4.6}$$

where we have set:

$$\varphi_1(z)=\sum_{k=0}^{\infty}\frac{z^{2\,k+1}}{(2\,k+1)\,k!},\qquad \varphi_2(z)=\sum_{n=0}^{\infty}\frac{z^{2n+3}}{(n+1)!\;(2n+3)}\;\sum_{k=0}^{n}\frac{1}{2k+1},$$
$$\psi_1(z)=\sum_{n=0}^{\infty}\frac{2^n\,z^{2n+2}}{(n+1)\;(2n+1)!!},\qquad \psi_2(z)=\sum_{n=0}^{\infty}\frac{2^n\,z^{2n+4}}{(2n+3)!!\;(n+2)}\;\sum_{k=0}^{n}\frac{1}{k+1}. \tag{4.7}$$

Proof. If $B=0$ and $\varrho+A\,e^{-\tau/\beta}>\eta$, from Remark 4.1 it follows $P(\tilde{T}<+\infty)=1$. Furthermore, the FPT pdf for the OU process (4.1) through the threshold $\tilde{S}(t)=\varrho+A\,e^{-t/\beta}$ starting from $X(\tau)=\eta<\tilde{S}(\tau)$ immediately follows from (4.2):

$$\begin{aligned} g\big[\varrho+A\,e^{-t/\beta},t\mid\eta,\tau\big]&=\frac{2\,\big[\varrho+A\,e^{-\tau/\beta}-\eta\big]e^{-(t-\tau)/\beta}}{\beta\sqrt{\pi\,\sigma^2\beta\,\big(1-e^{-2\,(t-\tau)/\beta}\big)^3}}\exp\Big\{-\frac{\big[A\,e^{-t/\beta}-(\eta-\varrho)e^{-(t-\tau)/\beta}\big]^2}{\sigma^2\,\beta\,\big(1-e^{-2\,(t-\tau)/\beta}\big)}\Big\}\\ &\equiv\widehat{g}\big(0,t-\tau\mid\varrho+A\,e^{-\tau/\beta}-\eta\big), \end{aligned}\tag{4.8}$$

where $\widehat{g}(0,t\mid x_0)$ denotes the FPT pdf through 0 at time t starting from x_0 at the initial time zero for the OU process $\widehat{X}(t)$ characterized by drift $\widehat{A}_1(x)=-x/\beta$ and infinitesimal variance $\widehat{A}_2=\sigma^2$ $(\beta>0,\ \sigma>0)$. Hence, from (4.8) one has:

$$\int_\tau^{+\infty}e^{-\lambda\,(t-\tau)}\,g[\tilde{S}(t),t\mid\eta,\tau]\,dt=\int_0^{+\infty}e^{-\lambda\,u}\,\widehat{g}(0\mid\varrho+A\,e^{-\tau/\beta}-\varrho)\,du, \tag{4.9}$$

with $\varrho+A\,e^{-\tau/\beta}-\eta>0$. Since (cf., for instance, [19]):

$$\int_0^{+\infty}e^{-\lambda\,t}\,\widehat{g}(0,t\mid x_0)\,dt=\frac{2^{\lambda\,\beta/2}}{\sqrt{\pi}}\,\Gamma\Big(\frac{1}{2}+\frac{\lambda\,\beta}{2}\Big)\,\exp\Big\{\frac{x_0^2}{2\,\sigma^2\,\beta}\Big\}\,D_{-\lambda\beta}\Big(\frac{x_0}{\sigma}\sqrt{\frac{2}{\beta}}\Big)\qquad(x_0>0),$$

Eq. (4.5) immediately follows from (4.9). Furthermore, making use of (4.8) , for $j=1,2,\dots$ one has:

$$\begin{aligned} E(\tilde{T}^j)&=\int_\tau^{+\infty}(t-\tau)^j\,g\big[\varrho+A\,e^{-t/\beta},t\mid\eta,\tau\big]\,dt\\ &=\int_0^{+\infty}z^j\,\widehat{g}\big(0,z\mid\varrho+A\,e^{-\tau/\beta}-\eta\big)\,dz=\tilde{t}_j\big(0\mid\varrho+A\,e^{-\tau/\beta}-\eta\big), \end{aligned}\tag{4.10}$$

where $\tilde{t}_j(0\mid x_0)$ denotes the j-th moment of FPT for the OU process $\widehat{X}(t)$ from x_0 to the state 0. Finally, recalling the expressions of $\tilde{t}_j(0\mid x_0)$ for $j=1,2$ (cf., for instance, [19]), from (4.10) one immediately obtains (4.6). ◻

4.2 Interspike intervals for the OU model For the OU model of single neuron activity, a return process $Z(t)$ in the presence of refractoriness is considered, where the functions (2.4) are chosen as:

$$\begin{aligned} S_0(t)&=S(t)=\varrho+a\,e^{-t/\beta}+b\,e^{t/\beta}\\ S_j(t)&=\begin{cases}\varrho+a\,\exp\Big\{-\dfrac{t-\theta_{j-1}-\zeta}{\beta}\Big\}+b\,\exp\Big\{\dfrac{t-\theta_{j-1}-\zeta}{\beta}\Big\}, & t>\theta_{j-1}+\zeta\\ +\infty, & \text{otherwise,}\end{cases} \end{aligned}\tag{4.11}$$

for $j = 1, 2, \dots$, where $\theta_0, \theta_1, \dots$ represent the successive firing times. We assume that $b \le 0$ and $a \ge b$, so that the thresholds (4.11) are non-increasing functions.

Recalling (2.7), by virtue of (4.2) with $A = a$ and $B = b$ and $\tau = 0$, we note that $I_0 \equiv \Theta_0$ is characterized by pdf:

$$\gamma_0(t \mid 0) = \frac{2\,(\varrho + a + b - \eta)\, e^{-t/\beta}}{\beta\sqrt{\pi\,\sigma^2\,\beta\,(1 - e^{-2\,t/\beta})^3}} \exp\left\{-\frac{\left[a\, e^{-t/\beta} + b\, e^{t/\beta} - (\eta - \varrho)\, e^{-t/\beta}\right]^2}{\sigma^2\,\beta\,(1 - e^{-2\,t/\beta})}\right\} \tag{4.12}$$

with $\varrho + a + b > \eta$. Due to (4.3) and (4.12), $P(\Theta_0 < +\infty) = 1$ if and only if $\varrho + a + b > \eta$ and $b \le 0$.

Figure 6 shows the FPT pdf $\gamma_0(t \mid 0) = g[S(t), t \mid \eta, 0]$ for the OU model (4.1) with $\beta = 5\,\text{msec}$, $\varrho = -60\,\text{mV}$ and $\sigma^2 = 1\,\text{mV}^2/\text{msec}$ through the firing threshold $S(t) = (-60 + a\, e^{-t/5})\,\text{mV}$ starting from $\eta = -70\,\text{mV}$ with $a = 0, 50, 100\,\text{mV}$.

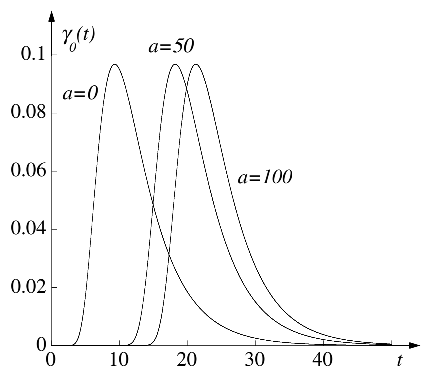


Figure 6: For the OU model with $\beta = 5\,\text{msec}$, $\varrho = -60\,\text{mV}$ and $\sigma^2 = 1\,\text{mV}^2/\text{msec}$, $\gamma_0(t \mid 0)$ is plotted for $b = 0\,\text{mV}$, $\eta = -70\,\text{mV}$ and $a = 0, 50, 100\,\text{mV}$.

In order to analyze the interspike intervals $I_1, I_2, \dots$ and the firing times $\Theta_1, \Theta_2, \dots$ we first prove that the FPT pdf of the OU process (4.1) through the hyperbolic boundary $S(t) = \varrho + a\, e^{-t/\beta} + b\, e^{t/\beta}$ satisfies relation (2.10). To this purpose, we note that

$$\begin{aligned} g[S(t-\zeta), t+\theta \mid \eta, \theta+\zeta] &= g\left[\varrho + a\, e^{-(t-\zeta)/\beta} + b\, e^{(t+\zeta)/\beta}, t+\theta \mid \eta, \theta+\zeta\right] \\ &= g\left[\varrho + a\, e^{(\theta+\zeta)/\beta}\, e^{-(t+\theta)/\beta} + b\, e^{-(\theta+\zeta)/\beta}\, e^{(t+\theta)/\beta}, t+\theta \mid \eta, \theta+\zeta\right], \end{aligned}$$

from which, making use of (4.2) with $A = a\, e^{(\theta+\zeta)/\beta}$, $B = b\, e^{-(\theta+\zeta)/\beta}$, $\tau = \theta + \zeta$ and final time chosen as $t + \theta$, we obtain:

$$\begin{aligned} g[S(t-\zeta), t+\theta \mid \eta, \theta+\zeta] &= \frac{2\,(\varrho + a + b - \eta)\, e^{-(t-\zeta)/\beta}}{\beta\sqrt{\pi\,\sigma^2\,\beta\,(1 - e^{-2\,(t-\zeta)/\beta})^3}} \\ &\quad\times \exp\left\{-\frac{\left[a\, e^{-(t-\zeta)/\beta} + b\, e^{(t-\zeta)/\beta} - (\eta - \varrho)\, e^{-(t-\zeta)/\beta}\right]^2}{\sigma^2\,\beta\,(1 - e^{-2\,(t-\zeta)/\beta})}\right\} \\ &\equiv g[S(t-\zeta), t-\zeta \mid \eta, 0], \qquad \varrho + a + b > \eta. \end{aligned}$$

for all $t > \zeta$ and $\theta \ge 0$. Therefore, (2.10) holds.

Making use of (2.11), for $\varrho + a + b > \eta$ the pdf of interspike interval I_j $(j = 1, 2, \dots)$ is zero for $t < \zeta$, whereas for $t > \zeta$ one has:

$$\gamma(t) = \frac{2\left(\varrho + a + b - \eta\right) e^{-(t-\zeta)/\beta}}{\beta\sqrt{\pi\,\sigma^2\,\beta\left(1 - e^{-2\,(t-\zeta)/\beta}\right)^3}}\exp\left\{-\frac{\left[a\,e^{-(t-\zeta)/\beta} + b\,e^{(t-\zeta)/\beta} - (\eta-\varrho)\,e^{-(t-\zeta)/\beta}\right]^2}{\sigma^2\,\beta\left(1 - e^{-2\,(t-\zeta)/\beta}\right)}\right\} \tag{4.13}$$

From (4.3) and (4.13) it follows that $P(I_j < +\infty) = 1$ if and only if $\varrho + a + b > \eta$ and $b \le 0$.

Figure 7 shows the interspike pdf $\gamma(t)$, given in (4.13), for the OU model (4.1) with $\beta = 5\,\text{msec}$, $\varrho = -60\,\text{mV}$ and $\sigma^2 = 1\,\text{mV}^2/\text{msec}$ in the presence of the hyperbolic firing thresholds (4.11) in the case of $\eta = -70\,\text{mV}$, $b = 0\,\text{mV}$, $a = 0, 50, 100\,\text{mV}$ and $\zeta = 1\,\text{msec}$ (on the left) and $\zeta = 10\,\text{msec}$ (on the right). Figures 6 and 7 show that the difference between $\gamma_0(t \mid 0)$ and $\gamma(t)$ becomes more evident as the refractory period increases.

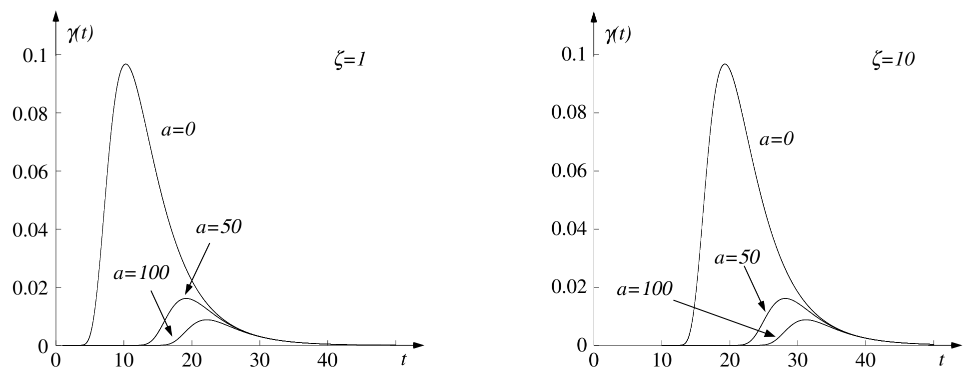


Figure 7: For the OU model with $\beta = 5\,\text{msec}$, $\varrho = -60\,\text{mV}$ and $\sigma^2 = 1\,\text{mV}^2/\text{msec}$, $\gamma(t)$ is plotted for $\eta = -70\,\text{mV}$, $b = 0\,\text{mV}$, $a = 0, 50, 100\,\text{mV}$ and $\zeta = 1\,\text{msec}$ (on the left) and $\zeta = 10\,\text{msec}$ (on the right).

If $b = 0$ and $\varrho + a > \eta$, the FPT moments are finite and, making use of (4.6) with $A = a$ and $\tau = 0$, one has:

$$E(\Theta_0) = \beta\left[\sqrt{\pi}\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \psi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\right]$$

$$E(\Theta_0^2) = 2\,\beta^2\left[\sqrt{\pi}\,\ln 2\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \sqrt{\pi}\,\varphi_2\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) + \psi_2\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\right].$$

where φ_1, φ_2 and ψ_1, ψ_2 are given in (4.7). Furthermore, if $b = 0$ and $\varrho + a > \eta$, making use of (4.14) in (2.12) one obtains the mean and the variance of the interspike intervals:

$$\begin{aligned} E(I) &= \zeta + E(\Theta_0) = \zeta + \beta\left[\sqrt{\pi}\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \psi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\right], \\ \mathrm{Var}(I) &= \mathrm{Var}(\Theta_0) = 2\,\beta^2\left[\sqrt{\pi}\,\ln 2\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \sqrt{\pi}\,\varphi_2\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) + \psi_2\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\right] \\ &\quad - \beta^2\left[\sqrt{\pi}\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \psi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\right]^2. \end{aligned} \tag{4.14}$$

In order to obtain the pdf of $\Theta_0, \Theta_1, \dots$ for $\beta = 0$, we first evaluate the Laplace transform of $\gamma_0(t \mid 0)$. Recalling (4.5) with $A = a$ and $\tau = 0$, from (4.12) for $\beta = 0$ one obtains:

$$\begin{aligned}\int_0^{+\infty} e^{-\lambda t}\gamma_0(t \mid 0)\, dt &= \int_0^{+\infty} \frac{2\, e^{-\lambda t}\, \big(\varrho + a - \eta\big)\, e^{-t/\beta}}{\beta\sqrt{\pi\,\sigma^2\,\beta\,\big(1 - e^{-2\,t/\beta}\big)^3}} \exp\Big\{-\frac{\big[a\, e^{-t/\beta} - (\eta - \varrho)\, e^{-t/\beta}\big]^2}{\sigma^2\,\beta\,\big(1 - e^{-2\,t/\beta}\big)}\Big\}\, dt \\ &= \frac{2^{\lambda\beta/2}}{\sqrt{\pi}}\,\Gamma\Big(\frac{1}{2} + \frac{\lambda\beta}{2}\Big)\,\exp\Big\{\frac{(\varrho + a - \eta)^2}{2\,\sigma^2\,\beta}\Big\}\, D_{-\lambda\beta}\Big(\frac{\varrho + a - \eta}{\sigma}\sqrt{\frac{2}{\beta}}\Big).\end{aligned} \tag{4.15}$$

Hence, from (2.13) for $\lambda > 0$ one has:

$$H_j(\lambda) = e^{-j\lambda\zeta}\,\Big[\frac{2^{\lambda\beta/2}}{\sqrt{\pi}}\,\Gamma\Big(\frac{1}{2} + \frac{\lambda\beta}{2}\Big)\, D_{-\lambda\beta}\Big(\frac{\varrho + a - \eta}{\sigma}\sqrt{\frac{2}{\beta}}\Big)\Big]^{j+1}\exp\Big\{\frac{(\varrho + a - \eta)^2 (j+1)}{2\,\sigma^2\,\beta}\Big\},$$

so that taking the inverse Laplace transform, for $j = 0, 1, \dots$ one is led to

$$h_j(t) = \begin{cases} 0, & t < j\,\zeta \\ \Big[\dfrac{2\,\big(\varrho + a - \eta\big)\, e^{-(t - j\,\zeta)/\beta}}{\beta\sqrt{\pi\,\sigma^2\,\beta\,\big(1 - e^{-2\,(t - j\,\zeta)/\beta}\big)^3}}\exp\Big\{-\dfrac{\big[a\, e^{-(t - j\,\zeta)/\beta} - (\eta - \varrho)\, e^{-(t - j\,\zeta)/\beta}\big]^2}{\sigma^2\,\beta\,\big(1 - e^{-2\,(t - j\,\zeta)/\beta}\big)}\Big\}\Big]^{(j+1)} & \\ & t > j\,\zeta. \end{cases} \tag{4.16}$$

Finally, if $b = 0$ and $\varrho + a > \eta$ the mean and the variance of the random variable Θ_j, describing the $(j+1)$-th firing time of the neuron $(j = 0, 1, \dots)$ follow from (2.15) and (4.14):

$$\begin{aligned} E(\Theta_j) &= j\,\zeta + (j+1)\,\beta\,\Big[\sqrt{\pi}\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \psi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\Big], \\ \mathrm{Var}(\Theta_j) &= 2\,\beta^2\,(j+1)\,\Big[\sqrt{\pi}\,\ln 2\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \sqrt{\pi}\,\varphi_2\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) + \psi_2\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\Big] \\ &\quad - \beta^2\,(j+1)\,\Big[\sqrt{\pi}\,\varphi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big) - \psi_1\Big(\frac{\varrho + a - \eta}{\sigma\sqrt{\beta}}\Big)\Big]^2. \end{aligned} \tag{4.17}$$

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