ON THE FIRING ACTIVITY OF A STATE-DEPENDENT STOCHASTIC NEURONAL MODEL

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ABSTRACT. We address the problem of studying the number of excitatory stimuli producing a spike for a Stein-type stochastic model which includes a multiplicative state-dependent effect. Some results on the probability distribution of the number M of excitatory stimuli triggering a spike are obtained. We also evaluate the distribution of M conditional on the firing time, and disclose some properties of its mode. Finally, some results on the probability generating function of the conditional distribution are given.

1 Introduction A mathematical model based on Stein stochastic differential equation has been recently proposed in [5] to describe the firing activity of a neuronal unit. Similarly to Stein approach [15], such model includes the arrival of excitatory stimuli according to a Poisson process with an exponential decay in absence of stimuli. As an innovative feature, the model is characterized by a multiplicative state-dependent effect, since the depolarizations are random and depend on the voltage level at the stimulus time. This state-dependent effect is suitable to describe a behavior sometimes observed in neuronal dynamics (see, for instance, [14] where noisy stochastic conductance components are multiplicatively coupled to the membrane potential). Closed-form expressions for the distribution of the membrane potential level and for the firing density (in the case of homogeneous Poisson inputs) have been recently obtained in [5] for our model.

The state-dependent Stein-type model is considered here to study the distribution of the number of excitatory stimuli able to yield a neuronal firing. This provides a basic characterization of the relationship between environmental stimuli and neural response. For instance, it is well-known that spontaneous quantal transmitter release from the motor nerve endings follows the Poisson distribution and generates miniature potentials which contribute to the neuron postsynaptic potential [7]. The study performed in the present paper can be useful to face the question of what determines the post-synaptic response to the release of the quantal transmitter (see, for instance, [6] where an analysis of how retinal ganglion cells re-encode the received information is present). More generally, the obtained results are suitable to characterize the firing activity of a postsynaptic cell in networks of Stein-type neuronal units under ad hoc assumptions about the dynamics of presynaptic neurons (see [2], [3] and [4] where a simulation-based approach is used to investigate the synchronization between interacting neurons). The mathematical background of the present contribution is that of classical treatises on stochastic neuronal models, such as [12] and [13].

A brief review on the relevant results of [5] is presented in Section 2. In Section 3 we study the distribution of the number of stimuli producing the neuronal firing conditional on the firing time. We point out that the applicability of our results in the theory of neural

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dynamics depends on a reasonable choice of the parameters' values. In the treated cases, these are taken in agreement with the observed values of the firing time.

In Section 4 we obtain the probability distribution of the number of stimuli producing a spike, together with its mean value, and determine a condition ensuring the neuronal firing. Finally, some concluding remarks are given in Section 5.

2 The Stein-type model Let $\{V(t); t \ge 0\}$ be a stochastic process with state-space $(0, +\infty)$ describing the neuronal membrane potential, defined as

(1)
$$V(t) = v_0 \exp\left\{-\nu t + \sum_{k=1}^{N(t)} Z_k\right\}, \quad t > 0, \qquad V(0) = v_0$$

In this model excitatory stimuli, arriving according to a homogeneous Poisson process $\{N(t); t \ge 0\}$ with intensity λ , produce membrane potential jumps of positive amplitude. When the level of the membrane potential reaches the threshold value, an action potential is generated and a refractory period begins, after which the membrane potential is reset to the level $v_0 > 0$. In the absence of stimuli, the membrane potential exponentially decays to the resting level, assumed to be zero, with time constant $1/\nu$ ($\nu > 0$).

The random variables Z_k in the right-hand side of Eq. (1) are assumed to be independent and exponentially distributed with density $f_Z(x) = \alpha e^{-\alpha x}$, x > 0. The role of α is evident from Eq. (1): denoting by t_n the instant when the *n*-th stimulus occurs, it is $V(t_n) - V(t_n) = V(t_n) W_n$, where W_n is a Pareto-type random variable with shape parameter α . Hence, for a fixed membrane voltage $V(t_n)$, the mean value of the *n*-th depolarization is inversely proportional to α , so that large values of α reduce the effect of the excitatory activity (see Section 2 of [5] for some remarks on the role of α).

We thoroughly assume that $\{N(t); t \ge 0\}$ and $\{Z_1, Z_2, \ldots\}$ are independent. Finally, for $n = 1, 2, \ldots$, we denote by T_n the *n*-th interarrival time of process $\{N(t); t \ge 0\}$ and by $f_{T_n}(t)$ its pdf.

The neuronal firing time is described as the first-passage time of V(t) through the constant firing threshold β :

(2)
$$T_V^{(\beta)} = \inf\{t \ge 0 : V(t) > \beta\}, \quad \beta > v_0.$$

This is the random time elapsing between the instant when the membrane potential resets to v_0 and the instant when an action potential is generated due to a crossing of the firing threshold β . As shown in [5], the firing density $g_V(\beta, t)$, that is the pdf of $T_V^{(\beta)}$, can be expressed as

$$g_V(\beta, t) = \sum_{n=1}^{+\infty} \gamma_n(t), \quad t > 0,$$

where

(3)
$$\gamma_n(t) := \frac{\partial^2}{\partial t_1 \partial t_2} \operatorname{P}\left\{T_V^{(\beta)} \le t_1, T_1 + \ldots + T_n \le t_2\right\} \Big|_{t_1 = t, t_2 = t}, \quad n = 1, 2, \ldots$$

is the sub-density of $T_V^{(\beta)}$ at the occurrence of the *n*-th stimulus. It has been proved that

(4)
$$\gamma_n(t) = \lambda^n \alpha^{n-1} e^{-(\lambda + \alpha\nu)t} \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{t^{n-1} \left(\nu t + n \log \frac{\beta}{v_0}\right)}{n! (n-1)!} \left(\log \frac{\beta}{v_0} + \nu t\right)^{n-2}, \quad t > 0,$$

and that, for t > 0 and $\beta > v_0$, the firing density is given by

(5)
$$g_{V}(\beta,t) = \frac{\lambda\nu t}{\log\frac{\beta}{v_{0}} + \nu t} e^{-(\lambda + \alpha\nu)t} \left(\frac{\beta}{v_{0}}\right)^{-\alpha} \times \left\{ \frac{I_{1}\left(2\sqrt{\lambda\alpha t}(\log\frac{\beta}{v_{0}} + \nu t)\right)}{\sqrt{\lambda\alpha t}(\log\frac{\beta}{v_{0}} + \nu t)} + \left(\log\frac{\beta}{v_{0}}\right) \frac{I_{0}\left(2\sqrt{\lambda\alpha t}(\log\frac{\beta}{v_{0}} + \nu t)\right)}{\nu t} \right\},$$

where $I_n(x)$, $n \ge 0$, denotes the modified Bessel function of the first kind.

The firing probability, i.e. the integral of the firing density over the positive half-line, equals 1 if and only if $\lambda \ge \alpha \nu$. In such a case, the mean firing-time is given by (see [5])

(6)
$$E\left[T_V^{(\beta)}\right] = \frac{1 + \alpha \log \frac{\beta}{v_0}}{\lambda - \alpha \nu}$$

3 The conditional firing activity In this section we investigate the number of stimuli producing a spike conditional on the firing time. Let M be the random variable that counts the number of excitatory stimuli producing the firing, and let

$$h_n(\beta, t) := P(M = n | T_V^{(\beta)} = t), \quad n \ge 1, \quad t > 0.$$

Recalling definition (3) and making use of Eqs. (4) and (5) it follows that, for t > 0, the conditional distribution of M is given by

(7)
$$h_n(\beta,t) \equiv \frac{\gamma_n(t)}{g_V(\beta,t)} = \frac{\left(\nu t + n\log\frac{\beta}{v_0}\right) \left[w(t)\right]^{2n-1}}{n!(n-1)! \left\{\nu t I_1(2w(t)) + \log\frac{\beta}{v_0} w(t) I_0(2w(t))\right\}},$$

where we have set

(8)
$$w(t) := \sqrt{\lambda \alpha t \Big(\log \frac{\beta}{v_0} + \nu t \Big)}.$$

Plots of the conditional distribution (7) for fixed values of parameters ν , v_0 , β and for different choices of (λ, t) and (α, t) are shown in Figures 1(a) and 1(b), respectively. We point out that the values of parameters in Eq. (7) should be fixed in agreement with the value of the firing time. For instance, by adopting a maximum likelihood approach, we consider the parameters' values in such a way that the mean firing time (6) is equal to the firing time t. Hence, for fixed ν , v_0 , β and t, the values of λ and α are chosen according to condition $1 + \alpha \log \frac{\beta}{v_0} = (\lambda - \alpha \nu)t$, with $\lambda > \alpha \nu$. From this assumption, when α is fixed and the firing time increases, the excitatory stimuli arrival rate λ decreases. Indeed, if the mean membrane depolarization is kept constant, a decreasing input arrival rate justifies an increasing firing time. On the contrary, if λ is fixed and the firing time increases, the value of α increases, this producing a reduction of the effects of the excitatory activity.

As shown in Figure 1, when the value of α (λ) is fixed, if the firing time t increases a large number of membrane potential jumps is expected. In particular, the mode of the conditional probability $h_n(\beta, t)$ increases very slowly in t for fixed α (see Figure 1(a)), whereas it exhibits a steep growth when λ is fixed (see Figure 1(b)).

A study on the mode of the conditional distribution $h_n(\beta, t)$ follows hereafter.

Theorem 3.1 The function $h_n(\beta, t)$ exhibits the following behavior:

• if $t \ge \tilde{t}$, then $\exists x \ge 1$ s.t. $h_n(\beta, t) \le h_{n+1}(\beta, t)$ for $1 \le n \le \lfloor x \rfloor$,



Figure 1: Conditional distribution $h_n(\beta, t)$ for $v_0 = 10 \ mV$, $\nu = 0.1 \ ms^{-1}$ and $\beta = 20 \ mV$. On the left-hand side (a) it is $\alpha = 2$ and (1) $(\lambda, t) = (2.5 \ ms^{-1}, 1 \ ms)$, (2) $(\lambda, t) = (1 \ ms^{-1}, 3 \ ms)$, (3) $(\lambda, t) = (0.7 \ ms^{-1}, 5 \ ms)$, (4) $(\lambda, t) = (0.5 \ ms^{-1}, 7 \ ms)$ (clockwise from top-left). On the right-hand side (b) it is $\lambda = 2 \ ms^{-1}$ and (1) $(\alpha, t) = (1.3, 1 \ ms)$, (2) $(\alpha, t) = (5, 3 \ ms)$, (3) $(\alpha, t) = (7.5, 5 \ ms)$, (4) $(\alpha, t) = (9.3, 7 \ ms)$ (clockwise from top-left).

• if
$$t < \tilde{t}$$
, then $h_n(\beta, t) \ge h_{n+1}(\beta, t)$ for $n \ge 1$,
where $\tilde{t} := \frac{\log \frac{\beta}{v_0}}{\nu} \left[-1 + \sqrt{1 + \frac{2\nu}{\lambda \alpha \log^2 \frac{\beta}{v_0}}} \right]$.

Proof. Let us set $\eta = (\log \frac{\beta}{v_0})/\nu$, $\theta = \eta \lambda \alpha \log \frac{\beta}{v_0}$ and $y = t/\eta$. For fixed t > 0 it is

9)
$$h_n(\beta, t) \le h_{n+1}(\beta, t) \text{ if } \varphi(n) \le 0$$

where

$$\varphi(x) = x^3 + a_2 x^2 + a_1 x + a_0,$$

and

$$a_{0} = -\lambda \alpha t \left(\log \frac{\beta}{v_{0}} + \nu t \right)^{2} / \log \frac{\beta}{v_{0}} = -\theta y (1+y)^{2},$$

$$a_{1} = \left[\nu t - \lambda \alpha t \log \frac{\beta}{v_{0}} \left(\log \frac{\beta}{v_{0}} + \nu t \right) \right] / \log \frac{\beta}{v_{0}} = y \left[1 - \theta (1+y) \right],$$

$$a_{2} = \frac{1}{\log \frac{\beta}{v_{0}}} \left(\log \frac{\beta}{v_{0}} + \nu t \right) = 1 + y.$$

The roots of the polynomial equation $\varphi(x) = 0$ are real or complex according to the sign of $q^3 + r^2$, with

$$q := a_1/3 - a_2^2/9, \qquad r := (a_1a_2 - 3a_0)/6 - a_2^2/27.$$

Since

$$q^{3} + r^{2} = -y \left\{ 4\theta + (1 - 8\theta^{2})y + (-2 - 8\theta - 44\theta^{2} + 4\theta^{3})y^{2} + (1 - 8\theta - 72\theta^{2} + 12\theta^{3})y^{3} + (12\theta^{3} - 44\theta^{2})y^{4} + (4\theta^{3} - 8\theta^{2} + 4\theta)y^{5} \right\} / 108,$$

the condition $y \ge \left(-1 + \sqrt{\frac{2+\theta}{\theta}}\right)$ ensures the existence of a real root of $\varphi(x)$ greater than or equal to 1. Recalling the expressions of y, η and θ , the proof immediately follows. \Box

Remark 3.1 By assuming the firing time equals to the mean firing time (6), and setting

- $\bar{t} := \left[-\left(3\alpha \log \frac{\beta}{v_0} + 1\right) + \sqrt{8 + \left(\alpha \log \frac{\beta}{v_0} 1\right)^2} \right] / (2\alpha\nu), \text{ due to Theorem 3.1 we have}$
 - if $\alpha \log \frac{\beta}{v_0} \ge (-1 + \sqrt{5})/2$ and t > 0, then $\exists x \ge 1$ s.t. $h_n(\beta, t) \le h_{n+1}(\beta, t)$ for $1 \le n \le \lfloor x \rfloor$,
 - if $0 < \alpha \log \frac{\beta}{v_0} < (-1 + \sqrt{5})/2$ and $t \ge \overline{t}$, then $\exists x \ge 1$ s.t. $h_n(\beta, t) \le h_{n+1}(\beta, t)$ for $1 \le n \le \lfloor x \rfloor$,
 - if $0 < \alpha \log \frac{\beta}{v_0} < (-1 + \sqrt{5})/2$ and $t < \overline{t}$, then $h_n(\beta, t) \ge h_{n+1}(\beta, t)$ for $n \ge 1$.

As suggested by Remark 3.1, when the mean membrane depolarization is large, this yielding a large value of \bar{t} , a single excitatory stimulus is likely to trigger the spike.

Hereafter we discuss the limit behavior of $h_n(\beta, t), n \ge 1$.

Remark 3.2 (i) As $t \to +\infty$ there holds:

$$h_n(\beta, t) \sim \frac{2\nu\sqrt{\pi}}{(\nu + \sqrt{\lambda\alpha\nu}\log\frac{\beta}{v_0})} \frac{e^{-2t\sqrt{\lambda\alpha\nu}}(\sqrt{\lambda\alpha\nu}t)^{2n-1/2}}{n!(n-1)!},$$

whereas, for $t \to 0^+$, one has:

$$h_n(\beta, t) \sim \frac{\left(\lambda \alpha t \log \frac{\beta}{v_0}\right)^{n-1}}{(n-1)!(n-1)!}.$$

(ii) As $\alpha \to +\infty$, it is

$$h_n(\beta, t) \sim \frac{2\sqrt{\pi} \left(\nu t + n\log\frac{\beta}{\nu_0}\right)}{\log\frac{\beta}{\nu_0}} \frac{\mathrm{e}^{-2w(t)} \left[w(t)\right]^{2n-3/2}}{n!(n-1)!},$$

where w(t) is defined in (8), and for $\alpha \to 0^+$

$$h_n(\beta, t) \sim \left(\nu t + n \log \frac{\beta}{v_0}\right) \left(\log \frac{\beta}{v_0} + vt\right)^{n-2} \frac{(\lambda \alpha t)^{n-1}}{n!(n-1)!}$$

Let us now obtain the probability-generating function of M given that a spike has occurred at time t. Making use of Eq. (7), and recalling definition (8), it is not hard to see that for $|s| \leq 1$ there holds

(10)
$$G(s) := E\left(s^{M} \mid T_{V}^{(\beta)} = t\right) = \frac{\sqrt{s} \,\nu \,t \,I_{1}\left(2\,w(t)\sqrt{s}\right) + s \,\log\frac{\beta}{v_{0}}\,w(t)\,I_{0}\left(2\,w(t)\sqrt{s}\right)}{\nu \,t \,I_{1}\left(2w(t)\right) + \log\frac{\beta}{v_{0}}\,w(t)\,I_{0}\left(2\,w(t)\right)}$$

From Eq. (10), the conditional mean value immediately follows:

(11)
$$E(M \mid T_V^{(\beta)} = t) = \frac{w(t) \left\{ \log \frac{\beta}{v_0} w(t) I_1(2w(t)) + \left(vt + \log \frac{\beta}{v_0}\right) I_0(2w(t)) \right\}}{\nu t I_1(2w(t)) + \log \frac{\beta}{v_0} w(t) I_0(2w(t))}.$$

It is not hard to see that the mean value (11) is increasing in α , with

$$\lim_{\alpha \to 0^+} E(M \mid T_V^{(\beta)} = t) = 1 \quad \text{and} \quad \lim_{\alpha \to +\infty} E(M \mid T_V^{(\beta)} = t) = +\infty.$$

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Similarly,

$$\lim_{t \to 0^+} E(M \mid T_V^{(\beta)} = t) = 1 \text{ and } \lim_{t \to +\infty} E(M \mid T_V^{(\beta)} = t) = +\infty.$$

We shall now discuss the behavior of the conditional mean by assigning specific values to the parameters in agreement with some experimental results. In [6], Freed describes how a retinal mammalian ganglion cell receives information about a white-noise stimulus as a flickering pattern of glutamate quanta and performs a study about how such information is re-encoded. For a brisk cell (capacitance $C_m \sim 38 \, pF$, resistance $R_m \sim 25 \, M\Omega$) an average quantal rate of about $112 \pm 19 \, s^{-1}$ is recorded. Since the observed spike rate is 13 ± 7 spikes s^{-1} [9], Freed concludes that about 10 glutamate quanta are sufficient to trigger a spike. Making use of these experimental data, and recalling the expression of the mean firing time (6), we have the following estimates: $\hat{\nu} = 1.05 \, ms^{-1}$, $\hat{\lambda} = 0.1 \, ms^{-1}$, $\hat{t} = 100 \, ms$ and $\hat{\alpha} = 0.09$. The level attained by the membrane potential after a refractory period is set to $\hat{v}_0 = 20 \, mV$, whereas the firing threshold is $\hat{\beta} = 30 \, mV$. Hence, the difference between the threshold and the initial value is $10 \, mV$, in agreement with several previous studies (see [10], [11] and references therein). From Eq. (11) it follows that $E(M \mid T_V^{(\beta)} = \hat{t}) = 10.2$, which is in a good agreement with the value obtained in [6].

4 Number of stimuli producing a spike Let us now study the probability distribution of the number of excitatory stimuli which produces a neuronal firing.

Theorem 4.1 For $n \ge 1$ one has:

(12)
$$p(n) := P(M = n) = \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda^n \alpha^{n-1} \left(\log \frac{\beta}{v_0}\right)^{2n-1}}{\nu^n (n-1)!} \\ \times \left\{\Psi\left(n+1; 2n; \log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right) + \Psi\left(n; 2n-1; \log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right)\right\}$$

where $\Psi(\cdot;\cdot;\cdot)$ denotes the confluent hypergeometric function of the second kind.

Proof. Recalling Eq. (4) we have

$$p(n) = \int_0^{+\infty} \gamma_n(t) dt = \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda^n \alpha^{n-1}}{(n-1)!(n-1)!} \left\{\frac{\nu}{n} \int_0^{+\infty} t^n \mathrm{e}^{-(\lambda+\alpha\nu)t} \left(\log\frac{\beta}{v_0} + \nu t\right)^{n-2} dt \right\}$$

$$(13) \qquad \qquad +\log\frac{\beta}{v_0} \int_0^{+\infty} t^{n-1} \mathrm{e}^{-(\lambda+\alpha\nu)t} \left(\log\frac{\beta}{v_0} + \nu t\right)^{n-2} dt \left\}.$$

From Eq. (13), by setting $z = \nu t / \log \frac{\beta}{v_0}$, it results

$$p(n) = \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda^n \alpha^{n-1} \left(\log \frac{\beta}{v_0}\right)^{2n-1}}{\nu^n (n-1)! (n-1)!} \left\{ \int_0^{+\infty} \frac{z^n}{n} (1+z)^{n-2} \left(\frac{\beta}{v_0}\right)^{-\frac{(\lambda+\alpha\nu)z}{\nu}} \mathrm{d}z + \int_0^{+\infty} z^{n-1} (1+z)^{n-2} \left(\frac{\beta}{v_0}\right)^{-\frac{(\lambda+\alpha\nu)z}{\nu}} \mathrm{d}z \right\}.$$

Since (see, for instance, Eq. 13.2.5 of [1])

$$\Psi(a;\gamma;x) = \frac{1}{\Gamma(a)} \int_0^{+\infty} e^{-xw} w^{a-1} (1+w)^{\gamma-a-1} dw, \quad a > 0,$$

Eq. (12) thus follows after some calculations.



Figure 2: Probability distribution p(n) with $v_0 = 10 \, mV$, $\nu = 0.1 \, ms^{-1}$, $\beta = 20 \, mV$, $\lambda = 1 \, ms^{-1}$ and $\alpha = 0.5, 1, 2, 3$ (clockwise from top-left).

Figure 2 shows plots of p(n) for various choices of α . Note that when α is small, there is a high probability that a single excitatory stimulus produces the neuronal firing. On the contrary, when α increases, the probability mass spreads over the *n* axis. In this case, due to a reduction of excitatory stimuli effects, it is likely that a spike is triggered for a wide range of large values of *n*.

The limit behavior of p(n) when α varies is studied in the following remark.

Remark 4.1 Let us assume that parameters λ , β , ν and v_0 are fixed. (i) If $\alpha \to +\infty$, and $n \ll \alpha$, it is (see Eq. (1"), p. 105, of [16])

$$p(n) \sim \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha \nu} \frac{\left(\lambda \log \frac{\beta}{v_0}\right)^{n-1}}{(n-1)!},$$

(which is a somewhat remainder of a Poisson distribution). (ii) If $\alpha \to +\infty$ and $n \to +\infty$, with $\alpha/n \to 1$, we have (see Eq. (23), p. 128, of [16])

$$p(n) \sim \frac{\lambda}{\nu} \frac{(\log \frac{\beta}{v_0})^{3/2}}{(4 + \log^2 \frac{\beta}{v_0})^{1/4}} \frac{w}{\sqrt{2w+1}} \left(\frac{\beta}{v_0}\right)^{-[w(1+\lambda/\nu)+1]} \\ \times \frac{\mathrm{e}^n}{\sqrt{n(n-1)!}} \left[\frac{\lambda}{\nu} \log \frac{\beta}{v_0} \left(\frac{\beta}{v_0}\right)^{-(w+1)} (2w+1)\right]^{n-1}$$

where

$$w = \left(2 - \log\frac{\beta}{v_0} + \sqrt{4 + \log^2\frac{\beta}{v_0}}\right) / \left(2\log\frac{\beta}{v_0}\right).$$

For the probability distribution obtained in Theorem 4.1, we now study the probability that the spike is due to a finite number of stimuli.

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Proposition 4.1 There holds:

(14)
$$P_M(\beta) := \sum_{n=1}^{+\infty} p(n) = \frac{2\lambda}{\lambda + \alpha\nu + |\lambda - \alpha\nu|} \left(\frac{\beta}{v_0}\right) \frac{\lambda - \alpha\nu - |\lambda - \alpha\nu|}{2\nu}$$

Proof. As (see Eq. (2'), p. 87, of [16])

(15)
$$\Psi(m; n+1; z) = (-1)^{n-m} (n-m)! z^{-n} \mathcal{L}_{n-m}^{-n}(z), \quad m \le n,$$

where $\mathcal{L}_n^a(z)$ is the generalized Laguerre polynomial, we obtain

$$P_{M}(\beta) = \left(\frac{\beta}{v_{0}}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha\nu} + \left(\frac{\beta}{v_{0}}\right)^{-\alpha} \frac{\lambda^{2} \alpha \log \frac{\beta}{v_{0}}}{(\lambda + \alpha\nu)^{2}} \sum_{m=0}^{+\infty} \frac{(-\nu)^{m}}{m+1} \left[\frac{\lambda\alpha}{(\lambda + \alpha\nu)^{2}}\right]^{m}$$

$$(16) \qquad \times \left\{\frac{\nu}{\log \frac{\beta}{v_{0}}(\lambda + \alpha\nu)} \mathcal{L}_{m}^{-2m-3}\left(\log \frac{\beta}{v_{0}} \frac{(\lambda + \alpha\nu)}{\nu}\right) + \mathcal{L}_{m}^{-2m-2}\left(\log \frac{\beta}{v_{0}} \frac{(\lambda + \alpha\nu)}{\nu}\right)\right\}.$$

Recalling that (see Eq. 22.7.31 of [1], for instance)

(17)
$$\mathcal{L}_{n}^{a}(z) = \frac{1}{z} \{ (n+a)\mathcal{L}_{n}^{a-1}(z) - (n+1)\mathcal{L}_{n+1}^{a-1}(z) \}$$

from Eq. (16) we have

$$P_{M}(\beta) = \left(\frac{\beta}{v_{0}}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha\nu} + \left(\frac{\beta}{v_{0}}\right)^{-\alpha} \frac{\lambda^{2}\alpha\nu}{(\lambda + \alpha\nu)^{3}} \sum_{m=0}^{+\infty} (-1)^{m+1} \left[\frac{\lambda\alpha\nu}{(\lambda + \alpha\nu)^{2}}\right]^{m} \\ \times \left\{ \mathcal{L}_{m}^{-2m-3} \left(\log\frac{\beta}{v_{0}} \frac{(\lambda + \alpha\nu)}{\nu}\right) + \mathcal{L}_{m+1}^{-2m-3} \left(\log\frac{\beta}{v_{0}} \frac{(\lambda + \alpha\nu)}{\nu}\right) \right\} \\ = \left(\frac{\beta}{v_{0}}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha\nu} \sum_{m=0}^{+\infty} \left[-\frac{\lambda\alpha\nu}{(\lambda + \alpha\nu)^{2}}\right]^{m} \\ (18) \qquad \times \left\{ \mathcal{L}_{m}^{-2m-1} \left(\log\frac{\beta}{v_{0}} \frac{(\lambda + \alpha\nu)}{\nu}\right) - \frac{\lambda\alpha\nu}{(\lambda + \alpha\nu)^{2}} \mathcal{L}_{m}^{-2m-3} \left(\log\frac{\beta}{v_{0}} \frac{(\lambda + \alpha\nu)}{\nu}\right) \right\}.$$

Since (see Eq. 48.17.4 of [8])

(19)
$$\sum_{k=0}^{+\infty} \xi^k \mathcal{L}_k^{c-2k}(x) = \frac{1}{u} 2^{-c-1} (1+u)^{c+1} \mathrm{e}^{(1-u)x/2}, \qquad u = (1+4\xi)^{1/2},$$

after some calculations Eq. (14) follows from Eq. (18).

Note that Eq. (14) is identical to the firing probability obtained in [5]. Indeed, we find again that condition $\lambda \ge \alpha \nu$ ensures that the firing occurs with probability 1.

By calculations similar to those in the proof of Proposition 4.1, it is not hard to evaluate the mean number of excitatory stimuli producing a spike.

Proposition 4.2 If $\lambda > \alpha \nu$, it is

(20)
$$E[M] = \frac{\lambda(1 + \alpha \log \frac{\beta}{v_0})}{\lambda - \alpha \nu}.$$

Proof. From Eqs. (12) and (15) we obtain

$$E[M] = 2 - \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha\nu} + \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda^2 \alpha\nu}{(\lambda + \alpha\nu)^3} \sum_{m=1}^{+\infty} m(-1)^{m+1} \left[\frac{\lambda \alpha \nu}{(\lambda + \alpha\nu)^2}\right]^m \times \left\{ \mathcal{L}_m^{-2m-3} \left(\log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right) + \mathcal{L}_{m+1}^{-2m-3} \left(\log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right) \right\}.$$

Hence, due to Eq. (17), we have

$$E[M] = 2 - \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha\nu} + \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda^2 \alpha \log \frac{\beta}{v_0}}{(\lambda + \alpha\nu)^2} \sum_{m=1}^{+\infty} \left[-\frac{\lambda \alpha \nu}{(\lambda + \alpha\nu)^2}\right]^m \mathcal{L}_m^{-2m-2} \left(\log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right) + 2\left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda^2 \alpha\nu}{(\lambda + \alpha\nu)^3} \sum_{m=1}^{+\infty} \left[-\frac{\lambda \alpha \nu}{(\lambda + \alpha\nu)^2}\right]^m \mathcal{L}_m^{-2m-3} \left(\log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right) - \left(\frac{\beta}{v_0}\right)^{-\alpha} \frac{\lambda}{\lambda + \alpha\nu} \sum_{m=1}^{+\infty} \left[-\frac{\lambda \alpha \nu}{(\lambda + \alpha\nu)^2}\right]^{m+1} \mathcal{L}_{m+1}^{-2m-3} \left(\log \frac{\beta}{v_0} \frac{(\lambda + \alpha\nu)}{\nu}\right).$$

Finally, making use of (19), we obtain Eq. (20).

As we expect, from (6) and (20), it is
$$E[M] = \lambda \cdot E[T_V^{(\beta)}]$$
, i.e. the mean number of stimuli
triggering a spike is equal to the arrival rate of excitatory stimuli times the mean firing time.
The mean value (20) is increasing for $\alpha \in (0, \lambda/\nu)$, whereas it decreases as function of λ .
In particular it goes to 1 as $\alpha \downarrow 0$ and diverges as $\alpha \uparrow \lambda/\nu$. Hence, if the effect of excitatory
inputs is a large mean membrane depolarization, a single excitatory stimulus is expected
to trigger the neuronal firing. For fixed α , it results $\lim_{\lambda \to +\infty} E[M] = 1 + \alpha \log \frac{\beta}{v_0}$, so, even
if the arrival rate of excitatory stimuli is large, the mean number of membrane potential
jumps required to reach the firing threshold is linearly increasing with α . Finally, we note
that $E(M)$ diverges as $\lambda \downarrow \alpha \nu$.

5 Concluding remarks In the present paper the relevant question on the relationship between stimuli and neural response is faced by studying the number of excitatory stimuli producing a spike. The model proposed is based on Stein equation and includes a state-dependent synaptic transmission. The membrane potential is described as a stochastic process which exponentially decays in absence of stimuli and performs jumps of random positive amplitude at the occurrence of excitatory stimuli.

Our main results are the probability distribution of the number M of excitatory stimuli triggering a spike and the distribution of M conditional on the firing time. The values of the involved parameters have been considered as fixed in agreement with the value of the firing time t. In particular, they have been chosen so that the mean firing time is equal to t. The given results are in agreement with an a priori expected fact: namely, when excitatory stimuli produce a large mean membrane depolarization, a single excitatory stimulus triggers the spike. On the contrary, if the excitatory activity effect is a small mean membrane depolarization, a large number of stimuli is required to trigger the spike.

Through the calculation of the probability generating function, we have obtained the conditional mean value of M and performed a discussion on its behavior by assigning to the parameters specific values suggested by experimental studies. In this case, the value of

the conditional mean turned out to be in a good agreement with the available experimental results.

Finally, for the mean number of stimuli producing the spike, we have obtained some results on its limit behavior as α and λ vary. In particular, if the arrival rate of excitatory stimuli goes to infinity, the mean value E(M) is shown to increase linearly with α .

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