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MOMENT-GENERATING FUNCTION OF OUTPUT STREAM OF LEAKY INTEGRATE-AND-FIRE NEURON

The statistics of the output activity of a neuron during its stimulation by the stream of input impulses that forms the stochastic Poisson process is studied. The leaky integrate-and-fire neuron is considered as a neuron model. A new representation of the probability distribution function of the output interspike interval durations is found. Based on it, the moment-generating function of the probability distribution is calculated explicitly. The latter, according to the Curtiss theorem, completely determines the distribution itself. In particular, explicit expressions are derived from the moment-generating function for the moments of all orders. The first moment coincides with the one found earlier. Formulas for the second and third moments have been checked numerically by direct modeling of the stochastic dynamics of a neuron with specific physical parameters.

Keywords: leaky integrate-and-fire neuron, stochastic Poisson process, interspike interval, moments of probability distribution, moment-generating function.

1. Introduction

Information in the brain is mainly represented in the form of neural impulses. All those impulses are roughly identical in their height and width and called spikes, see Fig. 1. The only thing which matters is the time when such an impulse has been generated or received. If neural impulses are recorded with proper biophysical instruments, one obtains a highly irregular sequence. It is called a spike train. It is difficult to find any rational meaning in these time moments of receiving spikes, or interspike intervals. The situation is even worse: In most cases, those sequences do not reproduce themselves, if the same stimulation is offered to an experimental animal several times. This might be the first reason why neuroscientists are mainly interested in the statistical properties of spike trains. Theoretical physicists as well try to predict which kind of statistics it could be and how it changes with changing stimuli or model parameters. In this direction, there is a long-standing discussion. What, indeed, represents the meaningful information in a spike train? Is it the mean number of spikes per time unit (rate coding), or are their exact temporal positions (time coding) essential? There is no clear answer to this question. Initially, we supposed that the rate coding operates at the periphery

of the nervous system. An example at the actuator periphery of the brain is the neuro-muscular junction in motoneurons [1, Sec. 5.01.12]. Namely, the only command passed to the muscle from the motoneuron is the contraction strength. But the contraction strength is determined by the neurotransmitter concentration, which is released from neural endings with each spike arrival. The more the spikes per time unit, the higher the neurotransmitter level, the higher the contraction strength. So, we have the rate coding here. An example at the sensory periphery of the brain is the olfactory receptor neuron [2], where the number of spikes per time unit depends on the odor concentration.

However, even at the sensory periphery, the time coding can be the coding paradigm. This is observed for the echolocation [3], where the temporal position of spikes from two ears should be kept with microsecond precision.

It is also clear that, in the time coding mechanism, a spike train can bear more information than in the rate coding one. This could be essential for more sophisticated intellectual tasks than muscle contraction or odor sniffing.

Unfortunately, most attempts to calculate the neuronal firing statistics exclude the possibility of the time coding due to utilizing the so-called diffusion approximation. In this approach, the neuronal stimulus

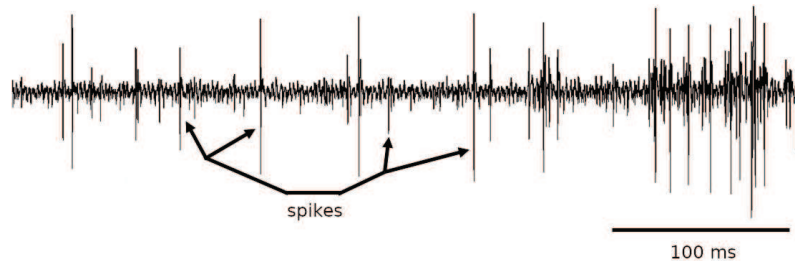


Fig. 1. Example of the electrical activity in the environment of neurons. The recording is made by an electrode, which is placed in the environment. Therefore, the activity of several neurons is registered simultaneously. In a case of a neuron generating an output impulse, its membrane potential changes drastically. At these time moments, the figure shows short-term jumps of voltage, or spikes. Different spikes have different heights because they belong to different neurons that are at different distances from the recording electrode. A single neuron generates spikes of the same height. Modified from: <https://backyardbrains.com/experiments/spikerbox>

is modeled as a diffusion stochastic process such as the Wiener or Ornstein–Uhlenbeck one, see [4, 5]. In the diffusion process, any finite time interval contains infinitely many infinitesimal spikes obtained from the differentiation of the Wiener process. Therefore, there is no place for the time coding mechanism. At the same time, the output activity of a neuron stimulated with a diffusion process is represented by finite spikes emitted, when the neuronal membrane voltage crosses the firing threshold. The time intervals between those spikes are finite, see Fig. 2. Those spikes represent not a diffusion process, but the point one. Therefore, they cannot be fed into another neuron preserving the diffusion approximation approach. This means that the diffusion approximation approach is both incomplete and inconsistent. Therefore, an attempt was made to calculate firing statistics without diffusion approximation.

In the following sections, we will briefly formulate previously obtained results this work is based on. Preliminary results are related to the statistics of the activity of a leaky integrate-and-fire (LIF) neuron with a threshold of 2. In particular, earlier, [6, 7], the explicit expressions were obtained for the distribution function of the output interspike intervals (ISI) at the initial section of the values of the ISI duration. The distribution of input impulses is considered to be Poissonian. For larger values of ISI, the distribution function is represented as the sum of multiple integrals. This enabled us to calculate the first moment of the distribution function (mean ISI). In the current paper, we have found another representation of the distribution function, which provides the means to calculate the moment-generating function. Applying

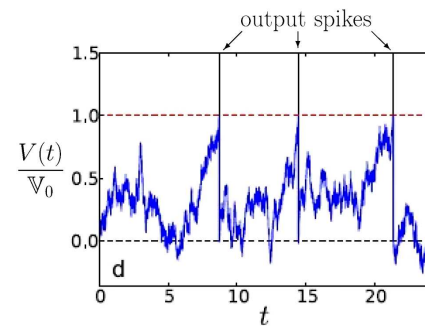


Fig. 2. Time course of the membrane potential simulated by the diffusion process. At the time moment when the membrane potential $V(t)$ reaches the firing threshold V_0 , the output impulse (spike) is generated. Modified from: A. Iolov, S. Ditlevsen & A. Longtin, DOI: 10.1186/2190-8567-4-4

the differentiation to it, a distribution moment of any order can be found. We note also that, according to the Curtiss theorem [8], the moment-generating function completely determines the distribution function itself.

2. Preliminary Results

2.1. Model description

The leaky integrate-and-fire neuron [9] is characterized by three positive constants: τ is the relaxation time; V_0 is the firing threshold; and h is the input impulse height.

At any given time t , the state of a LIF neuron is defined by the non-negative real number $V(t)$, which is a deviation of the transmembrane potential difference from the rest state toward the depolarization or, in other words, the magnitude of the excitation. Here, it

is assumed that $V = 0$ at rest, and the depolarization corresponds to a positive value of V . The presence of the leakage means that, in the absence of external stimuli, the value of $V(t)$ decreases exponentially:

$$V(t + s) = V(t)e^{-s/\tau}, \quad s > 0. \quad (1)$$

Input stimuli are input impulses. An input impulse obtained at the time t increases $V(t)$ by h :

$$V(t) \rightarrow V(t) + h. \quad (2)$$

The neuron is characterized by the firing threshold \mathbb{V}_0 . The latter means that, once the condition is met, i.e. $V(t) > \mathbb{V}_0$, the LIF neuron generates an output impulse and resets to the rest state, $V(t) = 0$. Regarding h and \mathbb{V}_0 , we make the following assumption:

$$0 < h < \mathbb{V}_0 < 2h. \quad (3)$$

From (1) and (2), it follows that the LIF neuron can generate an output impulse only at the time of receiving the input one. Condition (3) means that one input impulse, applied to the LIF neuron at rest, is not enough to generate the output impulse. However, even two input impulses obtained in a short time can excite the LIF neuron above the threshold and generate the output impulse. This means that the neuron has a threshold of 2^1 .

2.2. Distribution function of ISI durations²

We assume that the neuron described in Subsec. 2.1 is stimulated by a stream of input impulses, which forms a stochastic Poisson process of intensity λ . The latter means that the probability of obtaining the ISI of duration t with the precision dt at the input is given by the following expression:

$$e^{-\lambda t} \lambda dt,$$

and the input ISIs are statistically independent.

We introduce the following notations:

$$T_2 = \tau \ln \left(\frac{h}{\mathbb{V}_0 - h} \right), \quad T_3 = \tau \ln \left(\frac{\mathbb{V}_0}{\mathbb{V}_0 - h} \right),$$

$$\Theta_m = T_2 + (m - 3)T_3, \quad m = 3, \dots \quad (4)$$

¹ See [10], where the case of higher thresholds is considered.

² In the current section and below, t denotes the ISI duration.

In papers [6, 7], the following formula is obtained for the distribution function of output ISIs:

$$P(t)dt = \sum_{k=2}^{m-1} (P_k^0(t)\lambda dt - P_k^-(t)\lambda dt) + P_m^0(t)\lambda dt, \quad (5)$$

$$t \in]\Theta_m; \Theta_{m+1}], \quad m \geq 2,$$

where $P(t)dt$ is the probability to obtain an output ISI of duration t with the precision dt . Functions on the right-hand side of (5) are defined as follows:

$$P_{k+1}^0(t)\lambda dt = \int_{\Theta_{k+1}}^t P_k^-(s)\lambda ds e^{-\lambda(t-s)}\lambda dt, \quad (6)$$

$$t \geq \Theta_{k+1}, \quad k = 2, 3, \dots,$$

$$P_k^-(t)\lambda dt = e^{-\lambda t} \lambda^k dt \int_{\underline{t_1}}^{\overline{t_1}} dt_1 \int_{\underline{t_2}}^{\overline{t_2}} dt_2 \dots \int_{\underline{t_{k-1}}}^{\overline{t_{k-1}}} dt_{k-1}, \quad (7)$$

where the limits of integration are defined through the following inequalities:

$$\begin{cases} 0 \leq t_1 \leq t - \Theta_{k+1}, \\ T_2 + \tau \ln \left(\sum_{1 \leq j \leq i} e^{t_j/\tau} \right) \leq t_{i+1}, \\ t_{i+1} \leq \tau \ln \left(e^{(t - \Theta_{k+1} - i)/\tau} - \sum_{1 \leq j \leq i} e^{t_j/\tau} \right), \\ i = 1, \dots, k - 2. \end{cases} \quad (8)$$

Thus, the distribution function of the output ISI is completely determined by the function $P_k^-(t)$ for different $k = 2, 3, \dots$. Its physical meaning is as follows: if the neuron starts from the rest state, $V(0) = 0$, then the expression $P_k^-(t)\lambda dt$ gives the probability to obtain k consecutive input impulses from the Poisson input process in such a way that the last of them falls into the interval $[t; t + dt]$, and the neuron does not fire (the excitation threshold \mathbb{V}_0 has not been exceeded). In turn, $P_k^0(t)\lambda dt$ gives the probability to obtain k impulses, the last one within the interval $[t; t + dt]$ so that there is no firings up to and including the $(k - 1)$ -th impulse. Note that, in formula (7) for a fixed t , k cannot take values greater than k_{\max} , where

$$k_{\max} = \left[\frac{t - T_2}{T_3} \right] + 2,$$

and the square brackets denote the integer part of a number.

3. A New Representation of the Distribution Function

In this section, we will represent (7), (8) in a simpler form convenient for calculating the moment-generating function. For this reason, we introduce new integration variables:

$$z_i = e^{-\frac{t-\Theta_{k+2-i}}{\tau}} \sum_{1 \leq j \leq i} e^{\frac{t_j}{\tau}}, \quad i = 1, \dots, k-1.$$

The domain of integration (8) in terms of new variables takes the following form:

$$\begin{cases} e^{-\frac{t-\Theta_{k+1}}{\tau}} \leq z_1 \leq 1, \\ z_i \leq z_{i+1} \leq 1, \quad i = 1, \dots, k-2. \end{cases} \quad (9)$$

The Jacobian determinant of the transition to the new variables has the form

$$\left| \det \left\| \frac{\partial z_j}{\partial t_i} \right\| \right| = \frac{1}{\tau^{k-1}} z_1 \prod_{2 \leq i \leq k-1} (z_{i-1} - \beta z_i),$$

where $\beta = e^{-\frac{T_3}{\tau}}$. In view of this relation and (9), (7) can be expressed in the following form:

$$\begin{aligned} P_k^-(t) &= e^{-\lambda t} (\lambda \tau)^{k-1} \int_{B_k(t)} \frac{dz_1}{z_1} \int_{z_1}^1 \frac{dz_2}{z_2 - \beta z_1} \dots \\ &\dots \int_{z_{k-2}}^1 \frac{dz_{k-1}}{z_{k-1} - \beta z_{k-2}}, \end{aligned} \quad (10)$$

where

$$B_k(t) = e^{-\frac{t-\Theta_{k+1}}{\tau}}.$$

If the set of auxiliary functions $f_i(x)$ is introduced by the relations

$$f_0(x) \equiv 1, \quad f_{i+1}(x) = \int_x^1 \frac{dy}{y - \beta x} f_i(y), \quad i = 0, \dots, \quad (11)$$

then (10) can be written as

$$P_k^-(t) = e^{-\lambda t} (\lambda \tau)^{k-1} \int_{B_k(t)} \frac{dx}{x} f_{k-2}(x). \quad (12)$$

The latter with (5) and (6) are used below to calculate the moment-generating function.

4. Moment-Generating Function

The moments of the probability distribution $P(t)$ are the quantities μ_n given by the formula³

$$\mu_n = \int_{-\infty}^{\infty} t^n P(t) dt. \quad (13)$$

Here, the first moment is the mean of a random variable (in our case, of ISI). The calculation of moments can be difficult due to the complexity of the expression for $P(t)$. The moment-generating function simplifies the task.

According to the definition, the moment-generating function $M_t(z)$ is determined by the following formula:

$$M_t(z) = \mathbb{E}[e^{tz}] = \int_{-\infty}^{\infty} e^{tz} P(t) dt. \quad (14)$$

To find it, let us represent the distribution function $P(t)$ (5) in terms of the auxiliary functions $f_i(x)$ (11). To accomplish this, firstly, expression (6) for $P_k^0(t)$ should be rewritten through $f_i(x)$ (11), substituting (12):

$$\begin{aligned} P_{k+1}^0(t) &= \lambda(t - \Theta_{k+1}) P_k^-(t) + \\ &+ e^{-\lambda t} r^k \int_{B_{k+1}(t)} \frac{\ln(x)}{x} f_{k-2}(x) dx, \end{aligned} \quad (15)$$

where $r = \lambda \tau$.

By regrouping the terms in the sum on the right-hand side of (5) and substituting (12) and (15), the following expression for the distribution function $P(t)$ can be obtained in terms of the functions $f_i(x)$:

$$\begin{aligned} P(t) dt &= \lambda t e^{-\lambda t} dt + e^{-\lambda t} dt \times \\ &\times \sum_{k=3}^m r^{k-2} \int_{B_k(t)} \frac{dx}{x} f_{k-3}(x) (\lambda(t - \Theta_k) - 1 + r \ln(x)), \\ &t \in]\Theta_m; \Theta_{m+1}[, \quad m \geq 2. \end{aligned}$$

The latter is used in (14) to find the moment-generating function:

$$\begin{aligned} M_t(z) &= \frac{\lambda^2}{(\lambda - z)^2} + \\ &+ \frac{\lambda z}{(\lambda - z)^2} \sum_{m=3}^{\infty} r^{m-2} e^{-(\lambda-z)\Theta_m} I_m(z), \quad z < \lambda, \end{aligned} \quad (16)$$

³ In the considered case, $t \leq 0 \Rightarrow P(t) = 0$.

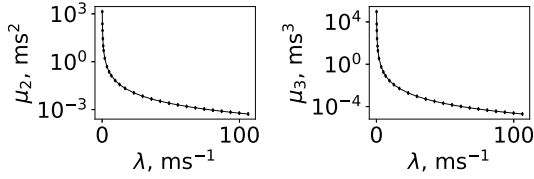


Fig. 3. Dependence of the second μ_2 and third μ_3 moments of the ISI duration distribution function on the intensity of the input stream λ . Diamonds denote the results of numerical simulation by the Monte Carlo method, solid line – calculations according to formulas (21) and (20) at $n = 3$. Here, $V_0 = 20$ mV, $h = 11.2$ mV, $\tau = 20$ ms

where the following auxiliary functions $I_m(z)$ are introduced:

$$I_m(z) = \int_0^1 dx f_m(x) x^{r-\tau z-1}, \quad m = 0, 1, \dots$$

To find a recurrent relation for $I_m(z)$, we substitute (11) into the last relation:

$$\begin{aligned} I_m(z) &= \Phi(\beta, 1, r - \tau z) I_{m-1}(z), \quad m = 1, 2, \dots; \\ I_0(z) &= \frac{1}{r - \tau z}. \end{aligned} \tag{17}$$

Here, $\Phi(\beta, 1, r - \tau z)$ denotes the Lerch transcendent:

$$\Phi(z, s, a) = \frac{1}{\Gamma(s)} \int_0^1 \frac{dx}{1 - zx} (-\ln(x))^{s-1} x^{a-1}.$$

It follows from the recurrent relation (17) that

$$I_m(z) = \frac{1}{r - \tau z} (\Phi(\beta, 1, r - \tau z))^m, \quad m = 0, 1, \dots$$

Let us substitute the last relation into (16) and use definition (4) of Θ_m :

$$\begin{aligned} M_t(z) &= \frac{\lambda^2}{(\lambda - z)^2} + \frac{\lambda z}{(\lambda - z)^2} \frac{r}{r - \tau z} e^{-(\lambda - z)T_2} \times \\ &\times \sum_{m=0}^{\infty} \left(r \beta^{r(1 - \frac{z}{\lambda})} \Phi(\beta, 1, r - \tau z) \right)^m. \end{aligned} \tag{18}$$

Here, the series $\sum_{m=0}^{\infty} \left(r \beta^{r(1 - \frac{z}{\lambda})} \Phi(\beta, 1, r - \tau z) \right)^m$ is convergent in some neighborhood of the point $z = 0$, since $r \beta^r \Phi(\beta, 1, r) < 1$. The latter is proved in Theorem 3 of [7].

Finally, after the summation on the right-hand side of (18), in some neighborhood of the point $z = 0$, the moment-generating function has the following form:

$$\begin{aligned} M_t(z) &= \frac{\lambda^2}{(\lambda - z)^2} + a^r \frac{\lambda z}{(\lambda - z)^2} \times \\ &\times \frac{r}{r - \tau z} \frac{e^{zT_2}}{1 - r \beta^r e^{zT_3} \Phi(\beta, 1, r - \tau z)}, \end{aligned} \tag{19}$$

where $a = e^{-\frac{T_2}{\tau}}$.

Since, in some neighborhood of zero, the moment-generating function is finite, then, according to the Curtiss theorem [8], the obtained moment-generating function (19) completely determines the distribution function $P(t)$.

Using the moment-generating function (19), the moments of the distribution function can be found as

$$\begin{aligned} \mu_n &= \left. \frac{d^n M_t(z)}{dz^n} \right|_{z=0} = \frac{(n+1)!}{\lambda^n} + \\ &+ \frac{n! a^r}{2\lambda^n} \frac{1}{1 - r \beta^r \Phi(\beta, 1, r)} \sum_{m=0}^{n-1} \frac{(\lambda(T_2 - T_3))^m}{m!} \times \\ &\times \sum_{k=0}^{n-1-m} (n-m-k)(n-m-k+1) \left(\delta_{k,0} + \right. \\ &+ \left. \frac{1}{k!} \sum_{l=1}^k \frac{(-1)^l l!}{(1 - r \beta^r \Phi(\beta, 1, r))^l} B_{k,l}(g_1, g_2, \dots, g_{k-l+1}) \right), \\ g_m &= (-\lambda T_3)^m - m! r^{m+1} \beta^r \Phi(\beta, m+1, r), \end{aligned} \tag{20}$$

where μ_n denotes the n -th moment, and $B_{k,l}(g_1, g_2, \dots, g_{k-l+1})$ are incomplete exponential Bell polynomials.

Setting $n = 1$ in the last expression, for the first moment, we have

$$\mu_1 = \frac{2}{\lambda} + \frac{1}{\lambda} \frac{a^r}{1 - r \beta^r \Phi(\beta, 1, r)},$$

which coincides with the obtained previously one in [7, Eq. (46)]. Notice that, in the notations used in [7], $I(a, r) = \beta^r \Phi(\beta, 1, r)$.

According to (20) for $n = 2$, the second moment takes the form

$$\begin{aligned} \mu_2 &= \frac{6}{\lambda^2} + \frac{2}{\lambda^2} \frac{a^r}{1 - r \beta^r \Phi(\beta, 1, r)} \left(3 + \lambda T_2 + \right. \\ &+ \left. \frac{r \beta^r \Phi(\beta, 1, r)}{1 - r \beta^r \Phi(\beta, 1, r)} \left(\lambda T_3 + r \frac{\Phi(\beta, 2, r)}{\Phi(\beta, 1, r)} \right) \right). \end{aligned} \tag{21}$$

5. Numerical Verification

To numerically verify the obtained formulas, a program was written that simulated the dynamics of the membrane potential of a neuron stimulated by a stream of input impulses that form the stochastic Poisson process. The behavior of the neuron was simulated for such a time that, as a result, 1000 000 output impulses were obtained, which allowed the calculation of the probability density $P(t)$ and its moments, as shown in (13). The simulation was repeated for different values of the input stream intensities λ . The results of calculating the 2nd and 3rd moments and their comparison with formulas (21) and (20) for $n = 3$ are shown in Fig. 3.

6. Conclusions

In the current paper, the statistics of the activity of a leaky integrate-and-fire neuron during its stimulation by input impulses, which form the stochastic Poisson process, is considered. For the model of a neuron with a threshold of two, a comprehensive description of the statistics of the durations of interspike intervals in terms of the moment-generating function is obtained. The latter is found explicitly, Eq. (19). The obtained formulas have been verified by the numerical modeling of the neuron dynamics with specific physical parameters.

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ТВІРНА ФУНКЦІЯ МОМЕНТІВ ДЛЯ СТАТИСТИКИ ВИХІДНОЇ АКТИВНОСТІ ІНТЕГРУЮЧОГО НЕЙРОНА З ВТРАТАМИ

Досліджується статистика вихідної активності нейрона при його стимуляції потоком вхідних імпульсів, що утворюють стохастичний процес Пуассона. В ролі моделі нейрона взято інтегруючий нейрон з втратами. Знайдено нове представлення функції розподілу ймовірностей довжин вихідних між-імпульсних інтервалів. На його основі обчислено в явному вигляді твірну функцію моментів ймовірнісного розподілу. Остання, за теоремою Куртіса, повністю визначає сам розподіл. Зокрема, на основі твірної функції знайдено явні вирази для моментів всіх порядків. Момент першого порядку збігається із знайденим раніше. Формули для моментів другого і третього порядків перевірено чисельно шляхом прямого моделювання стохастичної динаміки нейрона з конкретними фізичними параметрами.

Ключові слова: інтегруючий нейрон з втратами, стохастичний процес Пуассона, міжспайковий інтервал, моменти функції розподілу, твірна функція моментів.