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O.V. SHCHUR $^{1,\,2}$

- ¹ Bogolyubov Institute for Theoretical Physics, Nat. Acad. of Sci. of Ukraine (14b, Metrolohichna Str., Kyiv 03143, Ukraine; e-mail: olha.shchur@bitp.kiev.ua)
- ² Institute of Experimental Medicine (43, Szigony Str., 1083 Budapest, Hungary; e-mail: shchur.olha@koki.hu)

OUTPUT STREAM OF BINDING NEURON WITH THRESHOLD 2 STIMULATED WITH RENEWAL PROCESS

Information is transmitted between neurons in a brain via typical electrical impulses, which are called spikes. Since the activity of biological neurons is random, the statistics of neuronal activity, namely, the time intervals between neuron-generated consecutive spikes, is studied. A neuron transforms a random stream of input impulses into another stream, the output one. The input stream is described in this paper as a renewal point process. As a neuronal model, a binding neuron with threshold 2 is considered. A relationship between the Laplace transforms of the probability density functions of the interspike intervals in the input stream of impulses and the output stream generated as a response to this stimulus has been obtained. The derived relationship enables the determination of the probability density function and all of its moments. The resulting formulas are applied to the case where the input process is the Erlang one. In the considered case, the dependence of the regularity of the neuronal activity on the input stream parameters and the physical parameters of the neuron model is found.

Keywords: binding neuron, Poisson process, renewal process, interspike interval, probability density function, moments of a distribution.

1. Introduction

Most neurons transmit information by means of stereotypical short electrical impulses, which are called action potentials or spikes. Spikes can be generated when the voltage across the neuronal membrane reaches a certain threshold value. The generated action potential can be transmitted to other neurons along the neuron's dendrite, which is called axon.

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In this paper, we analyze how the neuron transforms the input sequence of impulses into the output one (see Fig. 1). As the neuronal model, we consider the binding neuron (BN) which was proposed in work [5]. In this model, every input pulse is stored unchanged in the neuron during a fixed time interval $\tau \in]0; \infty[$, which is called the internal memory storage time. After this interval, the input impulse disappears completely. The BN model is also characterized by the excitation threshold $N_0 \in \{2, 3, 4, ...\}$. The threshold value N_0 indicates how many input impulses must be stored in the neuron simultaneously in order to induce the generation of an output impulse. In this work, we consider only the case of threshold $N_0 = 2$.

The statistics of the activity of the BN with threshold 2 has already been studied earlier [6], however, only the stationary Poisson process, which is the simplest point process, was considered as an input stimulus. The intensity of a stationary Poisson process does not depend on the point process history (the arrival moments of previous impulses) and the time, being a constant. In this work, we extend the previously obtained result to the case where the input stimulus is a realization of a certain stationary renewal point process.

It is well known that, in any analytical problem concerning stochastic point processes, the substitution of the Poisson process by a more general one is a difficult task (see [4, p. 277] and [7, p. 5–6]). The intensity of a stationary renewal point process depends only on how much time has passed since the last event (the arrival of the last impulse). A stationary renewal process is completely described by the probability density function (PDF) of the intervals between the consecutive events. For a sequence of spikes, this time interval is called the interspike interval (ISI). Let us assume that we know the ISI PDF for the input renewal process and denote it as $p^{\rm in}(t)$, where t is the ISI duration.

The problem formulated in this work consists in finding a relationship between the PDF for the input sequence of impulses, $p^{\text{in}}(t)$, which is the realization of a certain renewal process, and the ISI PDF $p^{\text{out}}(t)$ for the output stream of spikes generated by the BN with threshold 2 in response to the stimulation with such a stream of impulses (see Fig. 1). The obtained results are applied to the case where the input ISIs are distributed according to the Erlang distribution. In

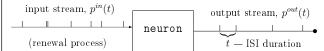


Fig. 1. Schematic diagram of a single spiking neuron that transforms the input stream of impulses with the ISI PDF $p^{\text{in}}(t)$, where t is the ISI duration, into an output stream with the ISI PDF $p^{\text{out}}(t)$

this case, besides the PDF of the output ISIs, all of its moments and the ISI coefficient of variation (CV) are determined.

The CV enables the regularity of the renewal process to be determined quantitatively [4]. If the neuronal activity can be described as a Poisson process, then the ISI CV is equal to unity, and the neuronal activity is said to be irregular. The smaller the ISI CV is in comparison with unity, the more regular the neuronal activity is. Neurons located in different areas of the cerebral cortex are characterized by different ISI CV values [2, 3], which depend on the functional role played by the specific cerebral cortex region. Furthermore, the possibility to vary the neuronal activity is important for motor learning [8], as well as for the successful performance of delayed-response tasks, which require the information to be stored in the working memory [9].

In this work, it has been shown how the variability of the BN activity can be controlled. The relevant mechanism consists in the regulation of the slow somatic potassium inhibition level.

2. ISI PDF and Its Moments. General Relationships

In work [10], the Laplace transform of the output ISI PDF for a binding neuron with threshold 2 with instantaneous excitatory feedback was obtained in the case where the neuron is stimulated by a stochastic renewal point process,

$$\mathcal{L}\lbrace p^{o}_{-if}(t); s\rbrace = \frac{\mathcal{L}\lbrace \chi(\tau - t)p^{\mathrm{in}}(t); s\rbrace}{1 - \mathcal{L}\lbrace \chi(t - \tau)p^{\mathrm{in}}(t); s\rbrace},\tag{1}$$

where τ is the internal memory storage time in the BN model, $p^{\rm in}(t)$ is the ISI PDF for the input renewal process, and $\chi(t)$ denotes the Heaviside function. The presence of instantaneous feedback means that the BN already stores one impulse at the beginning of every ISI, and this impulse disappears after the time interval τ . In addition, in work [11], a relationship

was obtained for the Laplace transforms of the PDF of the output ISIs for the spiking neuron stimulated with a renewal process with instantaneous excitatory feedback, $p^{o}-^{if}(t)$, and the same neuron without feedback, $p^{o}(t)$, and the PDF of the input process, $p^{\text{in}}(t)$:

$$\mathcal{L}\lbrace p^o - if(t); s \rbrace = \frac{\mathcal{L}\lbrace p^o(t); s \rbrace}{\mathcal{L}\lbrace p^{\text{in}}(t); s \rbrace}.$$
 (2)

Note that $p^{o}(t)$ in formula (2) is identical to the sought distribution $p^{out}(t)$ defined above.

Hence, from Eqs. (1) and (2), the following expression can be obtained for the Laplace transform of the PDF for the output ISIs for a binding neuron with threshold 2 without feedback in the case where the neuron is stimulated with a stochastic renewal point process with the ISI PDF $p^{\text{in}}(t)$:

$$\mathcal{L}\{p^{\text{out}}(t);s\} = \frac{\mathcal{L}\{p^{\text{in}}(t);s\}\mathcal{L}\{\chi(\tau-t)p^{\text{in}}(t);s\}}{1 - \mathcal{L}\{\chi(t-\tau)p^{\text{in}}(t);s\}}.$$
 (3)

By inverting the Laplace transform in expression (3), it is possible to obtain the PDF $p^{\text{out}}(t)$ of the output ISIs for a BN with threshold 2 stimulated by a renewal stream. Furthermore, the Laplace transform of the PDF $p^{\text{out}}(t)$ makes it possible to calculate all of its moments,

$$\mu_m = \int_0^\infty t^m p^{\text{out}}(t) dt = (-1)^m \frac{d^m \mathcal{L}\{p^{\text{out}}(t); s\}}{ds^m} \bigg|_{s=0}.$$
(4)

Note that, in the infinite memory approximation, i.e., at $\tau \to \infty$, the Laplace transform of the PDF for the output stream, $\mathcal{L}\{p^{\text{out}}(t);s\}$, is the square of the Laplace transform of the PDF for the input stream, $\mathcal{L}\{p^{\text{in}}(t);s\}$. Therefore, the PDF of the output ISIs for a BN with threshold 2 is a PDF of the time up to the second renewal. Note that the case of infinite memory in the BN model is identical to the ideal integrator model described in work [12].

3. Poisson Input Stream

Let us consider a BN with threshold 2 stimulated with a stream of excitatory impulses, the latter being a realization of a Poisson point process with a constant intensity $\lambda>0$. Then the intervals between the input impulses are distributed exponentially according to the formula

$$p^{\rm in}(t) = \lambda e^{-\lambda t}. ag{5}$$

For this case, as it was already indicated above, explicit expressions for the PDF of the output ISIs, as well as for the mean ISI, were obtained in work [6]. Furthermore, in work [13], the corresponding ISI CV was also determined. Therefore, our task consists now in finding all other moments of the ISI PDF for a BN with threshold 2 stimulated with the Poisson process.

The substitution of the input ISI PDF (5) into expression (3) for the Laplace transform of the output ISI PDF makes it possible to determine all moments of this distribution with the help of relationship (4). Namely,

$$\mu_{m} = \frac{m!}{\lambda^{m}} \sum_{k=0}^{m} \frac{1}{k!} \left(\sum_{j=0}^{k} \frac{(-1)^{j} j!}{(e^{\lambda \tau} - 1)^{j+1}} \times B_{k,j}(g_{1}, g_{2}, ..., g_{k-j+1}) \right) \times \left((-1)^{k} (e^{\lambda \tau} - 1)(m - k + 1) + \sum_{l=1}^{m-k} \frac{(-1)^{k+l} (m - k - l + 1)}{l!} e^{\lambda \tau} (\lambda \tau)^{l} \right),$$
 (6)

where

$$g_l = (\lambda \tau)^l e^{\lambda \tau} + (-1)^{l+1} l!,$$

and $B_{k,j}(g_1, g_2, ..., g_{k-j+1})$ denote the incomplete exponential Bell polynomials. Here, $B_{0,0}=1$ and $B_{k,0}=0$ for $k\geq 1$. Putting m=1 in expression (6), we get a formula for the average ISI, which coincides with the previously obtained result [6, p. 1823]. According to Eq. (6), the second moment (m=2) in the case of stimulation with a Poisson process looks like

$$\mu_2 = \frac{6e^{2\lambda\tau} + e^{\lambda\tau}(2\lambda\tau - 6) + 2}{\lambda^2(1 - e^{\lambda\tau})^2},\tag{7}$$

and the third moment (m = 3) reads

$$\mu_3 = \frac{3}{\lambda^3 (e^{\lambda \tau} - 1)^3} \left(-2 + 8e^{3\lambda \tau} + e^{\lambda \tau} (8 - 2\lambda \tau + \lambda^2 \tau^2) + e^{2\lambda \tau} (-12 + 6\lambda \tau + \lambda^2 \tau^2) \right). \tag{8}$$

Figure 2 illustrates (solid curves) the dependences of the second, μ_2 (panel a), and third, μ_3 (panel b), moments on the intensity of the input Poisson process, λ , calculated according to formulas (7) and (8),

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respectively. Those formulas were verified by numerically simulating the stochastic dynamics of a BN with threshold 2 and the internal memory storage time $\tau=20$ ms for various λ -values. The results of numerical simulation are depicted using diamonds. Figure 2 demonstrates a good coincidence of the analytical formulas obtained in this work with the results of numerical simulation.

4. Erlang Input Stream

Since the description of ISI PDF with the help of the gamma distribution is widely applied in theoretical [14] and experimental [2] studies, let us also consider the case where the input ISIs are distributed according to the Erlang distribution of the n-th order (Erlang-n),

$$p^{\text{in}}(t) = \lambda e^{-\lambda t} \frac{(\lambda t)^{n-1}}{(n-1)!}, \ \lambda > 0, \ n = 1, 2, \dots$$
 (9)

which is a partial case of the gamma distribution. The Erlang distribution of order 1 (Erlang-1) corresponds to the case of Poisson process considered above.

By substituting expression (9) as the PDF of input ISIs into formula (3), we obtain the following expression for the Laplace transform of the PDF for the output ISIs:

$$\mathcal{L}\lbrace p^{\text{out}}(t); s \rbrace = \frac{\lambda^n}{(s+\lambda)^n} \times \frac{\lambda^n}{(s+\lambda)^n} - e^{-\tau(\lambda+s)} \lambda^n \sum_{k=0}^{n-1} \frac{\tau^k}{k!(s+\lambda)^{n-k}} \times \frac{1 - e^{-\tau(\lambda+s)} \lambda^n \sum_{k=0}^{n-1} \frac{\tau^k}{k!(s+\lambda)^{n-k}}}{1 - e^{-\tau(\lambda+s)} \lambda^n \sum_{k=0}^{n-1} \frac{\tau^k}{k!(s+\lambda)^{n-k}}}.$$
(10)

Now, inverting the Laplace transform (10), we can obtain an expression for the PDF $p^{\text{out}}(t)$. The analytical form of this expression depends on the output ISI duration t. In particular, for m=0,1,2,..., if $m\tau \leq t < (m+1)\tau$, we obtain

$$\begin{split} p^{\text{out}}(t) &= \lambda^{n(m+2)} e^{-\lambda t} \times \\ &\times \sum_{m_0 + m_1 + \dots + m_{n-1} = m} \binom{m}{m_0, m_1, \dots, m_{n-1}} \times \\ &\times \frac{\sum\limits_{k=0}^{n-1} k m_k}{\prod\limits_{k=0}^{n-1} (k!)^{m_k}} \frac{(t - m\tau)^{n(m+2) - \sum\limits_{k=0}^{n-1} k m_k - 1}}{\left(n(m+2) - \sum\limits_{k=0}^{n-1} k m_k - 1\right)!} + \end{split}$$

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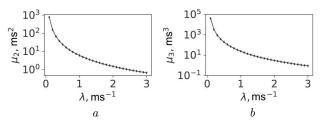


Fig. 2. Examples of the dependences of the second, μ_2 (a), and the third, $\mu_3(b)$, moment of the ISI PDF for a BN with threshold 2 stimulated with a Poisson process on the intensity λ of this process. Diamonds correspond to the results of a numerical simulation using the Monte Carlo method, and solid curves to the results of calculations according to formulas (7) and (8). $\tau = 20$ ms

$$+e^{-\lambda t} \sum_{l=2}^{m+1} \lambda^{nl} \times \left(\sum_{m_0+m_1+\ldots+m_{n-1}=l-2} \binom{l-2}{m_0, m_1, \ldots, m_{n-1}} \right) \times \left(\frac{\sum_{m_0+m_1+\ldots+m_{n-1}=l-2}^{n-1} km_k}{\sum_{k=0}^{n-1} km_k} \binom{\left(t-(l-2)\tau\right)^{nl-\sum_{k=0}^{n-1} km_k-1}}{\left(nl-\sum_{k=0}^{n-1} km_k-1\right)!} - \sum_{p=0}^{n-1} \frac{\tau^p}{p!} \frac{\left(t-(l-1)\tau\right)^{nl-p-\sum_{k=0}^{n-1} km_k-1}}{\left(nl-p-\sum_{k=0}^{n-1} km_k-1\right)!} \right).$$

$$(11)$$

By putting n=1 in this formula, we obtain an expression for the PDF for a BN with threshold 2 stimulated with a Poisson stream of spikes, which completely coincides with the expression previously obtained in work [6, eq. (3)].

In Fig. 3, a, one can see the distribution of input ISIs Erlang-2 with a given intensity. Figure 3, b demonstrates the PDF of the output ISIs for a BN with specific values of physical parameters under stimulation with the Erlang-2 process, which was calculated according to the obtained analytical formula (11) where n=2. The plot in Fig. 3, c shows the same distribution obtained as a result of the numerical simulation, using the Monte Carlo method, of the stochastic dynamics of a BN with the same physical parameters. Here, one can see again a complete agreement between the analytical and numerical results.

Again, using relation (4) between the moments and the Laplace transform of the PDF – in this case, the Laplace transform is given by expression (10) – we

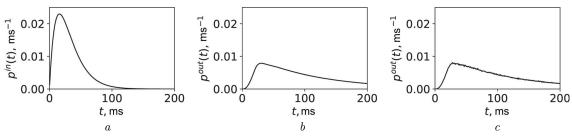


Fig. 3. Examples of the ISI PDFs for the Erlang-2 input stream using Eq. (9) with n=2 (a) and the output stream of a BN with threshold 2 stimulated with the Erlang-2 input stream (b) [Eq. (11) with n=2]. $\lambda=62.5~{\rm s}^{-1}$ for both panels, and $\tau=20$ ms for panel b. (c) Results of a Monte Carlo simulation of the stochastic behavior of a BN with the same physical parameters as in panel b

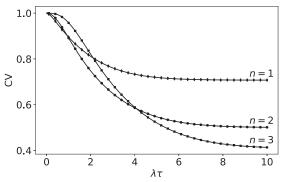


Fig. 4. Examples of the dependence of the CV for a BN with threshold 2 stimulated with the Erlang process on the quantity $\lambda \tau$ for various orders n of the input process. Solid curves are the results of analytical calculations according to formula (16) with the corresponding n-value. Symbols are the results of a numerical simulation of the stochastic dynamics of a BN with threshold 2 stimulated by the Poisson process (diamonds), the Erlang-2 process (circles), and the Erlang process of order 3 (squares). $\tau = 20$ ms and $\lambda \in \in [0.005; 0.5]$ ms⁻¹

can find all moments μ_m of the PDF of output ISIs, $p^{\text{out}}(t)$, under stimulation with an Erlang-n stream:

$$\mu_{m} = \frac{m!}{\lambda^{m}} \sum_{n_{1}=0}^{m} \frac{1}{n_{1}!} \sum_{j=0}^{n_{1}} \frac{(-1)^{j} j!}{\left(e^{\lambda \tau} - \sum_{k=0}^{n-1} \frac{(\lambda \tau)^{k}}{k!}\right)^{j+1}} \times \\ \times B_{n_{1},j}(f_{1}, f_{2}, ..., f_{n_{1}-j+1}) \left(\sum_{n_{2}=0}^{m-n_{1}} (-1)^{n_{1}+n_{2}} e^{\lambda \tau} \times \right) \\ \times (\lambda \tau)^{n_{2}} \frac{(2n+m-n_{1}-n_{2}-1)!}{n_{2}!(m-n_{1}-n_{2})!(2n-1)!} - \\ - \sum_{n_{2}=0}^{\min(n-1,m-n_{1})} \frac{(-1)^{n_{1}+n_{2}}(2n+m-n_{1}-n_{2}-1)!}{n_{2}!(m-n_{1}-n_{2})!(2n-1)!} \times \\ \times \sum_{k=0}^{n-1-n_{2}} \frac{(\lambda \tau)^{k+n_{2}}}{k!}, \qquad (12)$$

where

$$f_l = (\lambda \tau)^l e^{\lambda \tau} (-1)^l \sum_{k=0}^{n-1} (\lambda \tau)^k \frac{(n-k+l-1)!}{k!(n-k-1)!}.$$

If the input ISIs are distributed according to the Erlang-2 distribution [Eq. (9) with n=2], Eq. (12) yields the following first two moments of the PDF:

$$\mu_1 = \frac{4e^{\lambda\tau} - 2 - 2\lambda\tau}{\lambda \left(e^{\lambda\tau} - 1 - \lambda\tau\right)} \tag{13}$$

and

$$\mu_2 = \frac{20e^{2\lambda\tau} + 6(1+\lambda\tau)^2 + 2e^{\lambda\tau}(-9 - 9\lambda\tau + 2\lambda^2\tau^2)}{\lambda^2(1 - e^{\lambda\tau} + \lambda\tau)^2}$$
(14)

5. ISI Coefficient of Variation

The mean ISI μ_1 together with the second moment μ_2 of the ISI PDF can be used to calculate the ISI coefficient of variation

$$CV = \frac{\sqrt{\mu_2 - (\mu_1)^2}}{\mu_1}.$$
 (15)

For a BN with threshold 2 stimulated with an Erlang process of order n, the CV reads

$$CV = \frac{1}{\sqrt{n} \left(2 - e^{-\lambda \tau} \sum_{k=0}^{n-1} \frac{(\lambda \tau)^k}{k!} \right)} \times \left(2 + (n-3)e^{-\lambda \tau} \sum_{k=0}^{n-1} \frac{(\lambda \tau)^k}{k!} + \frac{2(\lambda \tau)^n e^{-\lambda \tau}}{(n-1)!} + \left(e^{-\lambda \tau} \sum_{k=0}^{n-1} \frac{(\lambda \tau)^k}{k!} \right)^2 \right)^{\frac{1}{2}}.$$
 (16)

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If the input process is Poisson (n = 1), this expression yields a formula for the CV, which is completely consistent with the formula obtained earlier in work [13], where two cases of the statistics of the activity of a BN with threshold 2 stimulated with a Poisson process were compared: in the presence and in the absence of instantaneous excitatory feedback.

Examples of the dependence of the CV on the quantity $\lambda \tau$ for various orders n of the Erlang input process are shown in Fig. 4. The solid curves exhibit analytical results [formula (16) with n=1,2,3], and the diamonds, circles, and squares are used to present the corresponding results of a numerical simulation of the dynamics of BNs with specific physical parameters using the Monte Carlo method. The results of numerical simulation testify to the reliability of formula (16) obtained in this work.

6. Conclusions and Discussion

In this work, a relationship between the Laplace transforms of the ISI PDFs for an input impulse stream, which is a realization of a certain renewal process, and for the output stream of a BN with threshold 2 stimulated with the former stream is obtained [see Eq. (3)]. This relationship makes it possible to find not only the PDF of the output ISIs, but also all of its moments. The resulting formulas are applied to the case where the input ISIs are distributed according to the Erlang distribution. In particular, the corresponding dependence of the ISI CV on the input stream parameters and the physical parameters of the neuron model is found. The analytical results obtained in this work are verified by numerically simulating the stochastic dynamics of the neuron.

Regarding the regular character of the activity of a BN with threshold 2 stimulated with an Erlang process, it follows from expression (16) that the ISI CV depends only on the product $\lambda \tau$. It can be shown that the CV monotonically decreases from 1 to $\frac{1}{\sqrt{2n}}$, where n is the order of the input Erlang process, when $\lambda \tau$ increases. The same behavior also takes place for the separate dependences of the CV on only λ or τ . Note that if $\tau \to \infty$ (i.e., if the memory is infinite) or $\lambda \to \infty$, we obtain the same CV as in the case of the Erlang process of order 2n; namely, $\text{CV} = \frac{1}{\sqrt{2n}}$. This behavior is in total agreement with the fact that the output stream for a BN with threshold 2 and infinite memory stimulated with the Erlang process of order

n is an Erlang process of order 2n with the same intensity as the input process has 1.

From expression (16) for the CV, one can see that if the input stream is Poisson, the output stream is always more regular owing to the processing of the former by the binding neuron. In addition, since the CV equals $\frac{1}{\sqrt{n}}$ for the Erlang process of order n and the CV for the output stream of a BN with threshold 2 stimulated with this process varies from $\frac{1}{\sqrt{2n}}$ to 1, the regularity of the neuronal activity can be both higher and lower than the regularity of the input Erlang process (9), which depends on its intensity λ and the BN internal memory storage time τ . In turn, the internal memory storage time τ in the BN model is governed by the level of slow somatic potassium inhibition [5]. Therefore, by varying the level of the BN inhibition, it is possible to control the regularity of the BN activity.

In the recent paper [15], a relationship between the ISI PDFs for a neuron with delayed inhibitory feedback stimulated by a renewal process, for an identical neuron but without feedback, and for an input renewal process, was found. The problem was solved for a whole class of non-adaptive spiking neurons, which includes the BN model and the leaky integrate-and-fire neuron [12]. The solution of this problem makes it possible to calculate the ISI PDF for a neuron with feedback, if the PDF for a neuron without feedback is known. However, no PDFs of output ISIs have been found yet for a lone neuron belonging to the class considered in work [15] and stimulated with a renewal process. In particular, an ISI PDF was determined for the leaky integrate-and-fire neuron only provided its stimulation with a Poisson process [16–18]. An analogous situation occurs for the BN model [6].

The results obtained in this work allow the study of the activity statistics of a neuron with delayed inhibitory feedback stimulated with a renewal process, which was started in work [15], to be continued.

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As was already indicated in Section 2, the PDF of the output ISIs for BNs with threshold 2 and infinite memory is equivalent to the PDF of the times up to the second spike for the input renewal process.

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О.В. Щур

ВИХІДНИЙ ПОТІК ЗВ'ЯЗУЮЧОГО НЕЙРОНА З ПОРОГОМ 2, СТИМУЛЬОВАНОГО ПРОЦЕСОМ ВІДНОВЛЕННЯ

Інформація в мозку передається між нейронами за допомогою стереотипних електричних імпульсів, які називаються спайками. Оскільки активність біологічних нейронів є випадковою, ми вивчаємо статистику нейронної активності, а саме часових інтервалів між послідовно згенерованими нейроном спайками. Нейрон перетворює випадковий потік вхідних імпульсів в інший, вихідний потік. Вхідний потік у цій роботі описується як точковий процес відновлення. У якості нейронної моделі розглядається модель зв'язуючого нейрона з порогом 2. Отримано зв'язок між перетвореннями Лапласа функцій розподілу міжспайкових інтервалів для вхідного потоку імпульсів та для вихідного потоку, згенерованого у відповідь на цей стимул. Отримане співвідношення дозволяє знайти саму функцію розподілу та всі її моменти. Отримані формули були застосовані до випадку, коли вхідний процес є процесом Ерланга. Зокрема, для розглянутого випадку було знайдено залежність регулярності нейронної активності від параметрів вхідного потоку та фізичних параметрів нейронної моделі.

Kлючові слова: зв'язуючий нейрон, процес Пуассона, процес відновлення, міжспайковий інтервал, функція розподілу ймовірностей, моменти функції розподілу.