

NON-MARKOVIAN SPIKING STATISTICS OF A NEURON WITH DELAYED FEEDBACK IN PRESENCE OF REFRACTORINESS

KSENIIA KRAVCHUK AND ALEXANDER VIDYBIDA

Bogolyubov Institute for Theoretical Physics
Metrologichna str., 14-B, 03680 Kyiv, Ukraine

ABSTRACT. Spiking statistics of a self-inhibitory neuron is considered. The neuron receives excitatory input from a Poisson stream and inhibitory impulses through a feedback line with a delay. After triggering, the neuron is in the refractory state for a positive period of time.

Recently, [35, 16], it was proven for a neuron with delayed feedback and without the refractory state, that the output stream of interspike intervals (ISI) cannot be represented as a Markov process. The refractory state presence, in a sense limits the memory range in the spiking process, which might restore Markov property to the ISI stream.

Here we check such a possibility. For this purpose, we calculate the conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, and prove exactly that it does not reduce to $P(t_{n+1} | t_n, \dots, t_1)$ for any $n \geq 0$. That means, that activity of the system with refractory state as well cannot be represented as a Markov process of any order.

We conclude that it is namely the delayed feedback presence which results in non-Markovian statistics of neuronal firing. As delayed feedback lines are common for any realistic neural network, the non-Markovian statistics of the network activity should be taken into account in processing of experimental data.

1. Introduction. In a biological neural network, the component parts are neurons which communicate with each other through synapses. The main inter-neuronal communication unit — neuronal impulse — is initiated in the axonal hillock,[22] and then propagates to a synapse through an extended neuronal process, axon, with a finite speed. The finiteness of propagation speed results in a delay between starting of impulse in axonal hillock of presynaptic neuron and receiving final excitation/inhibition in the axonal hillock of corresponding postsynaptic neuron¹. This temporal interplay allows one to consider axon as communication line between somatic parts of two neurons. This point of view is utilized in most types of artificial neural networks [11]. In artificial neural networks, a model neuron corresponds to the soma/axonal hillock of biological neuron whereas communication line corresponds to axon. The axonal sprouting, which gives rise to multiple synapses is modeled as multiple communication lines starting at the same point and receiving identical inputs. If so, then the instantaneous dynamical state of a network must include dynamical states of somatic parts of all the neurons together with the states

2010 *Mathematics Subject Classification.* Primary: 60G55, 92C20; Secondary: 90C15.

Key words and phrases. Delayed feedback, non-Markovian statistics, reverberating neural networks, non-renewal statistics, ISI probability distribution, refractoriness.

¹To be precise, the total delay also includes a synaptic delay.

of communication lines the network is composed of. The state of a model neuron can be described as its degree of excitation. The state of a line consists of information of whether the line is empty or conducts an impulse [13], [24, I.1.2, II.7.2]. If it does conduct, then the state of the line can be described by the amount of time, which is required for the impulse to reach the end of the line and impinge on the target neuron.

In neurophysiological experiments, the triggering (spiking, firing) moments of individual neurons but not the states of communication lines are recorded. The sequence of intervals between the consecutive moments (inter-spike intervals, ISIs) is frequently considered as a renewal [14] or Markovian [7] stochastic process. For a renewal process, the consecutive ISIs are mutually statistically independent. On the other hand, the experimentally obtained spike trains in auditory [18] and visual [17] sensory systems do not support the ISIs' mutual independence. These observations can be associated with memory effects in the ISI sequence which arise from an underlying non-renewal process. Recently [27], such a possibility was analyzed for weakly electric fish electrosensory afferents using high-order interval analysis, count analysis, and Markov-order analysis. The authors conclude that the experimental evidence cannot reject the null hypothesis that the underlying Markov chain model is of order m or higher, or maybe non-Markovian. The limited data sets used in [27] allow to establish a lower bound for m as $m \geq 7$ for some fibers.

What could be possible sources of such non-renewal, or even non-Markovian, behavior in real neural network? First, this behavior could be inherited from non-renewal (non-Markovian) character of the input signal. Such a signal could be received through a sensory organ from external world. Second, intrinsic neuronal properties, such as adaptation, could be responsible. This is because due to adaptation neuron can memorize influence of previous inputs. One more reason for a network activity to be non-Markovian could be the presence of delayed recurrent interconnections. The simplest possible recurrent interconnection can be realized in a “network” composed of a single neuron sending its output impulses to its own input with a delay. Configurations of this type are ubiquitous in real biological neuronal networks, see [2, 26] and more references in Sec. 2.2. Here we prove that the presence of delayed feedback in an inhibitory neuron with refractoriness can be the possible source of the non-Markovian behavior. See also [16, 35], where this is proven for either inhibitory, or excitatory neuron, both without refractoriness.

The non-Markovian behavior of the ISI sequence from neuron in a network with delayed interconnections is not surprising. Indeed, the information about which neurons are spiking/silent at any given moment of time leaves unknown the position of impulses in the interconnection lines at that moment. And it is the previous firing moments which determine the states of interconnection lines, which in turn determine the next firing moments. Therefore, information about the previous neuronal firing moments could improve our predicting ability as regards the next firing moments.

We consider the simplest neural “net”, namely, a single inhibitory neuron with delayed feedback. The neuron receives excitatory impulses from a Poisson process² and sends its output inhibitory impulses to its own input through a feedback line with the fixed time delay Δ . As neuronal model we take binding neuron (see Sec.

²As Poisson process we mean the counting process with continuous time and independent and stationary increments, see [9, II.10].

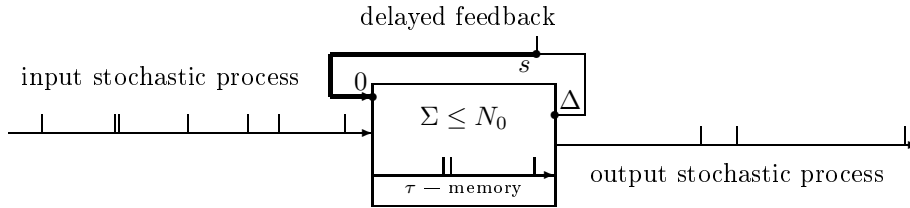


FIGURE 1. Binding neuron with feedback line under Poisson stimulation. Multiple input lines with Poisson streams are joined into a single one here. Δ is the delay duration in the feedback line, s is the time to live, see Definition 2.1.

2.1 for exact definition) as it allows rigorous mathematical treatment. We study the ISI output sequence of this system.

In our previous papers [35, 16], we considered the case when refractory period r of a neuron equals to zero, $r = 0$, which allows receiving and generating impulses immediately after the previous spike. We have proven in [35] that the sequence of output ISIs of excitatory binding neuron with delayed feedback cannot be represented as a Markov chain of any finite order. In [16], we prove the same issue for an inhibitory binding neuron with delayed feedback. In this work, we check if this result can be violated by presence of non-zero refractory period, $r > 0$. Let us first explain, why this violation could happen.

The feedback line acts as a kind of memory device. Namely, the impulse arrival from the line informs the neuron that there was an earlier spike Δ units of time before. In the case of no refractoriness, an ISI t may be arbitrarily short, $t > 0$, therefore, the earlier spike number, which the line is signaling about, can be arbitrarily distant from the current spike number.

In presence of refractory time $r > 0$, any ISI t is longer than r :

$$t > r,$$

therefore, the number of ISI, when the impulse entered the line, can differ from the number of ISI, when the line still contains the same impulse, by no more than n_{\max} ,

$$n_{\max} = [\Delta/r], \quad (1)$$

where $[x]$ gives an integer part of x . Thus, the ability of the impulse just arriving from the line to provide information about the earlier spikes is limited as compared with the case of no refractoriness. That is why, one could expect the finite Markov order to be found for the output ISI stream in the presence of refractoriness. The goal of this work is to check if this is the case.

The main result of this work is the proof that the sequence of output ISIs of inhibitory neuron with delayed feedback cannot be represented as a Markov chain of any finite order even in the presence of refractoriness. This suggests that activity of any network with delayed feedback interconnections, if represented in terms of ISIs, should be non-Markovian as well.

2. The object under consideration.

2.1. **Binding neuron model.** As a neuronal model we use here the binding neuron (BN). The BN model describes functioning of a neuron in terms of discrete events, which are input and output impulses, and degree of temporal coherence between the

input events, see [31] for detailed description. Mathematically, this model is realized as follows. We expect that all input impulses in all input lines are identical. Each input impulse is stored in the BN for a fixed time, τ . The τ is similar to the “tolerance interval” discussed in [20]. All input lines are excitatory. The neuron fires an output impulse if the number of stored excitatory impulses, Σ , is equal or higher than the threshold value, N_0 . After that, the BN clears its memory. That is, every input impulse either disappears contributing to a triggering event, or it is lost after spending τ units of time in the neuron’s internal memory. The latter case represents leakage. Here, the leakage is abrupt, while in more traditional models it is gradual.

Further, we expect that stream in each input line is a Poisson one with some intensity λ_i . In this case, all input lines can be collapsed into a single one delivering Poisson stream of intensity $\lambda = \sum_i \lambda_i$, see Figure 1.

A more formalized definition of the BN model can be given in the form of transfer function. A transfer function allows exact calculation of output in terms of input. In the case of neuron, input is a strictly increasing sequence of discrete arriving moments of standard impulses: $T_{in} = \{l_1, l_2, l_3, l_4, \dots\}$. The output is a sequence of discrete firing moments of BN: $T_{out} = \{f_1, f_2, \dots\}$. It is clear that $T_{out} \subset T_{in}$. The transfer function in our case could be the function $\sigma(l)$, $l \in T_{in}$, which equals 1 if l is the firing moment, $l \in T_{out}$, and 0 otherwise. For BN with threshold N_0 the required function can be defined as follows. It is clear that the first $N_0 - 1$ input impulses are unable to trigger neuron, therefore $\sigma(l_1) = 0, \dots, \sigma(l_{N_0-1}) = 0$. The next input impulse is able to trigger if and only if all first N_0 arriving moments are confined within a time interval, which is no longer than τ :

$$\sigma(l_{N_0}) = 1 \quad \text{if and only if} \quad l_{N_0} - l_1 \leq \tau.$$

In order to determine $\sigma(l_{N_0+k})$, $k \geq 1$, one must take into account previous input moments, therefore we use notation $\sigma_{T_{in}}$ instead of σ . The values of $\sigma_{T_{in}}(l_{N_0+k})$ can be determined recursively:

$$[\sigma_{T_{in}}(l_{N_0+k}) = 1] \quad \text{if and only if} \quad [l_{N_0+k} - l_{k+1} \leq \tau \quad \text{and} \\ \forall_{i \in \{k+1, \dots, N_0+k-1\}} [\sigma_{T_{in}}(l_i) = 0]].$$

For analytic derivation, we use BN with $N_0 = 2$ in order to keep mathematical expressions shorter. For this case, the above definition of transfer function looks as follows:

$$\sigma(l_2) = 1 \quad \text{if and only if} \quad l_2 - l_1 \leq \tau,$$

$$[\sigma_{T_{in}}(l_{k+2}) = 1] \quad \text{if and only if} \quad [l_{k+2} - l_{k+1} \leq \tau \quad \text{and} \quad \sigma_{T_{in}}(l_{k+1}) = 0], \quad k \geq 1.$$

It seems that cases with higher thresholds might be considered with the same approach, but even the case without feedback and with $N_0 = 3$ requires additional combinatorial efforts, see [32]. Therefore, cases of higher threshold are tested here only numerically.

As regards real biological neurons, the number of synaptic impulses able to trigger a neuron can be rather small. E.g., a single excitatory impulse may trigger a hippocampal inhibitory interneuron, [21].

2.1.1. *BN with refractoriness – BN(r)*. The neuron experiences refractoriness during r units of time after each firing. During the refractory time, the neuron is unable to both receive and send any impulses.

For short, we will use the notation $\text{BN}(r)$ for BN with refractoriness, $r > 0$. In the course of derivations, we will need to utilize some results, obtained before for BN without refractoriness, $r = 0$. We use the notation $\text{BN}(0)$ in this case.

2.2. Feedback line action. In real neuronal systems, a neuron can form synapses from its axonal branch to its own dendritic tree [2, 5, 8, 19, 25, 26, 29, 30]. Synapses of this type are called autapses. Some of the neurons forming autapses are known to be inhibitory, see [8, 26, 29] for experimental evidence. As a result, the neuron inhibits itself through an autapse after each firing with some propagation delay. We model this situation assuming that output impulses of $\text{BN}(r)$ are fed back into $\text{BN}(r)$'s input with delay Δ . This gives the inhibitory $\text{BN}(r)$ with delayed feedback model, Figure 1.

The action of an inhibitory feedback impulse is modeled in the following way. When the inhibitory impulse reaches $\text{BN}(r)$, it annihilates all excitatory impulses already present in the $\text{BN}(r)$'s memory and vanishes instantaneously, similarly as the Cl-type inhibition shunts depolarization of excitable membrane, see [28]. If at the moment of inhibitory impulse arrival, the neuron is empty, then the impulse disappears without any action, similarly as Cl-type inhibition does not affect membrane's voltage in its resting state. Such inhibition is "fast" in that sense, that the inhibitory impulses act instantaneously and are not remembered by neuron. Modeling the inhibition in this simple fashion is reasonable because of the relatively fast kinetics of the chlorine inhibitory postsynaptic currents [6].

The feedback line either keeps one impulse, or keeps no impulses and cannot convey two or more impulses at the same time. Biological correlates supporting to an extent this assumption could be a prolonged refractory period and/or short-term synaptic depression. The latter can have the recovery time up to 20 s [37].

Definition 2.1. The time to live of impulse in the feedback line, s , equals to the time necessary for the impulse to reach the end of the line and enter the neuron, see Fig. 1, where time to live is the temporal length of the thick part of the line.

This definition does not make sense if the line does not convey an impulse. On the other hand, if the feedback line is empty at the moment of firing, the output impulse enters the line, and after time interval equal Δ reaches the $\text{BN}(r)$'s input. If the line already keeps one impulse at the moment of firing, the just fired impulse ignores the line. This means, that *at the beginning* of an output ISI the feedback line is never empty, but keeps single impulse with time to live $s \in]0; \Delta]$.

We assume, that time delay Δ of impulse in the feedback line is smaller than the $\text{BN}(r)$'s memory duration, τ :

$$\Delta < \tau. \quad (2)$$

It allows to make analytic expressions shorter. Also, the assumption (2) is consistent with the case of direct feedback, not mediated by other neurons.

2.3. Relation between feedback and refractoriness parameters. In order to reveal the influence of refractoriness on the spiking statistics of a neuron with delayed feedback, we consider the following case

$$r < \Delta < 2r, \quad (3)$$

when no more than one output firing is possible while an impulse passes the feedback line, see (1). In this case, the refractoriness, taking more than half of the delay time within the feedback line, could reduce most correlations between the ISIs.

3. Statement of the problem. The input stream of impulses, which drives neuronal activity is a Poisson one. It is stochastic, therefore, the output activity of our system requires probabilistic description in spite of the fact that both the BN(r) and the feedback line action mechanisms are deterministic. We treat the output stream of inhibitory BN(r) with delayed feedback as a stationary process³. In order to describe its statistics, we introduce the following basic functions:

- the joint probability density $P(t_m, t_{m-1}, \dots, t_0)$ for $(m+1)$ successive output ISI durations, t_0 is the earliest one.
- the conditional probability density $P(t_m | t_{m-1}, \dots, t_0)$ for output ISI durations; $P(t_m | t_{m-1}, \dots, t_0)dt_m$ gives the probability to obtain an output ISI of duration between t_m and $t_m + dt_m$ provided the previous m ISIs had durations $t_{m-1}, t_{m-2}, \dots, t_0$, respectively.

Definition 3.1. The sequence of random variables $\{t_j\}$, taking values in Ω , is called a Markov chain of the order $n > 0$, if

$$\forall_{m>n} \forall_{t_0 \in \Omega} \dots \forall_{t_m \in \Omega} P(t_m | t_{m-1}, \dots, t_0) = P(t_m | t_{m-1}, \dots, t_{m-n}),$$

and this equation does not hold for any $n' < n$ (see e.g. [9]). In the case of output ISIs of the BN(r), one reads $\Omega =]r, \infty[$.

In particular, taking $m = n + 1$, we have the necessary condition,

$$P(t_{n+1} | t_n, \dots, t_1, t_0) = P(t_{n+1} | t_n, \dots, t_1), \quad t_i > r, \quad i = 0, \dots, n+1, \quad (4)$$

required for the stochastic process $\{t_j\}$ of ISIs to be the n -th order Markov chain.

Our purpose in this paper is to prove the following theorem.

Theorem 3.2. *The output ISIs stream of inhibitory BN(r) with delayed feedback under Poisson stimulation is not a Markov chain of any finite order.*

4. Main calculations. This section with Appendices contains the required proof of Theorem 3.2.

4.1. Proof outline. In order to prove the Theorem 3.2, we are going to show analytically that the equation (4) does not hold for any finite value of n . Namely, we will derive exact analytic expression for the conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$ and show that it depends on t_0 for any finite number n .

For this purpose we use the procedure, previously utilized in [35] and [16] for excitatory and inhibitory BN(0) with delayed feedback. We reproduce this section from [16], as it appears to be also suitable for the case with refractoriness.

So, let us introduce the stream \mathbf{ts} of events (t, s)

$$\mathbf{ts} = \{\dots, (t_i, s_i), \dots\},$$

where s_i is the time to live of the impulse in the feedback line at the moment, when the ISI t_i starts. At that moment, the feedback line always contains an impulse, see Definition 2.1 and paragraph next to it. Therefore, any ISI t_i can be attributed with time to live $s_i \in]0; \Delta]$, which is measured just at the beginning of that ISI. We consider the joint probability density $P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0)$ for realization

³ The stationarity of the output stream results both from the stationarity of the input one and from the absence of time-dependent parameters in the BN(r) model, see Section 2.1. In order to ensure stationarity, we also expect that system is considered after initial period sufficient to forget the initial conditions.

of $(n + 2)$ successive events (t, s) , and the corresponding conditional probability density $P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0)$ for these events.

Then, we prove the following lemma, which will be used in our calculations.

Lemma 4.1. *Stream \mathbf{ts} is the 1-st order Markovian:*

$$\forall_{n \geq 0} \forall_{t_0 > r} \forall_{s_0 \in]0; \Delta]} \dots \forall_{t_{n+1} > r} \forall_{s_{n+1} \in]0; \Delta]} P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0) = P(t_{n+1}, s_{n+1} | t_n, s_n), \quad (5)$$

where $\{t_0, \dots, t_{n+1}\}$ is the set of successive ISIs, and $\{s_0, \dots, s_{n+1}\}$ are the corresponding times to live.

See Appendix A for the proof.

Then, in order to find the conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, we perform the following steps:

- *Step 1.* Use the property (5) for calculating joint probability density of events (t, s) :

$$P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0) = P(t_{n+1}, s_{n+1} | t_n, s_n) \dots P(t_1, s_1 | t_0, s_0) P(t_0, s_0), \quad (6)$$

where $P(t, s)$ and $P(t_n, s_n | t_{n-1}, s_{n-1})$ denote the stationary probability density and conditional probability density (transition probability) for events (t, s) .

- *Step 2.* Represent $P(t_{n+1}, t_n, \dots, t_0)$ as marginal probability by integration over variables s_i , $i = 0, 1, \dots, n + 1$:

$$P(t_{n+1}, t_n, \dots, t_0) = \int_0^\Delta ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0). \quad (7)$$

- *Step 3.* Use the definition of conditional probability density:

$$P(t_{n+1} | t_n, \dots, t_1, t_0) = \frac{P(t_{n+1}, t_n, \dots, t_0)}{P(t_n, \dots, t_0)}. \quad (8)$$

Taking into account the Steps 1 and 2, one derives the following expression for the joint probability density:

$$P(t_{n+1}, t_n, \dots, t_0) = \int_0^\Delta ds_0 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k | t_{k-1}, s_{k-1}). \quad (9)$$

In the next sections, we are going to find the exact expressions for probability densities $P(t, s)$ and $P(t_k, s_k | t_{k-1}, s_{k-1})$. Then, we will consider separately cases, when $t_0 < \Delta$ and when $t_0 \geq \Delta$, and perform the integration in (9) for both of them. Then we will apply the Step 3, above, to find expressions for the conditional probability densities $P(t_{n+1} | t_n, \dots, t_0)$ in two domains characterized with $t_0 < \Delta$ and $t_0 \geq \Delta$. It will appear, that $P(t_{n+1} | t_n, \dots, t_1, t_0)$ does not depend on t_0 explicitly in any of the two domains. Nevertheless, the expression for $P(t_{n+1} | t_n, \dots, t_1, t_0)$ is different in each domain. The boundary between the two domains depends on t_0 , and this means that the whole function $P(t_{n+1} | t_n, \dots, t_1, t_0)$ considered in the union of the two domains, $D_l \cup D_m$, depends on t_0 .

4.2. **Probability density $P(t, s)$ for events (t, s) .** The probability density $P(t, s)$ can be derived as the product

$$P(t, s) = F(t | s)f(s), \quad (10)$$

where $f(s)$ denotes the stationary probability density for time to live of the impulse in the feedback line at the moment of an output ISI beginning, $F(t | s)$ denotes conditional probability density for ISI duration provided the time to live of the impulse in the feedback line equals s at the moment of this ISI beginning. Exact expressions for both $f(s)$ and $F(t | s)$ for inhibitory BN(r) with delayed feedback are calculated in Appendices B and C. Particularly,

$$F(t | s) = \begin{cases} 0, & (t < r), \\ P^0(t - r), & (t > r \text{ and } s \leq r) \text{ or } (t \in]r; s[\text{ and } s > r), \\ (1 + \lambda(s - r)) e^{-\lambda(s-r)} P^0(t - s), & (t \geq s \text{ and } s > r), \end{cases} \quad (11)$$

where $P^0(t)$, $t > 0$, denotes an output ISI probability density for BN(0) without feedback, which was obtained in [32, Eq. (3)]. Explicit expressions for $P^0(t)$ are different for different domains of t . For example,

$$P^0(t) = \lambda^2 t e^{-\lambda t}, \quad t \in]0; \tau], \quad (12)$$

where λ is the input Poisson stream intensity. It is proven in [32], that $P^0(t)$ is a continuous function for whole range of ISI durations: $t \in]0; \infty[$.

It is essential for further study, that $F(t | s)$ considered as function of t has a jump discontinuity at $t = s$, when $s > r$. Indeed, using (11) and (12), one obtains

$$\begin{aligned} \lim_{t \rightarrow s-0} F(t | s) &= \lambda^2 (s - r) e^{-\lambda(s-r)} > 0, & 0 < r < s \leq \Delta, \\ \lim_{t \rightarrow s+0} F(t | s) &= 0. \end{aligned}$$

The presence of jump in $F(t | s)$ at $t = s$ can be explained as follows. According to the definition of $F(t | s)$, the inhibitory impulse from the feedback line arrives s units of time later than the corresponding ISI t starts. After the inhibitory impulse arrival, it is guaranteed, that the BN(r) is empty. To trigger the BN(r) just after that moment, it is necessary to get two impulses from the input stream within infinitesimally small time interval. This event has infinitesimally small probability for the Poisson process (as well as for any other point process). That is why, the value of probability density $F(t | s)$ drops to zero at $t = s+0$ and $F(t | s)$ experiences discontinuity at $t = s$.

It is important to emphasize, that $F(t | s)$ is a continuous function elsewhere except of the point $t = s$, where it has strictly negative jump. This follows from (11) and from the continuity of $P^0(t)$. The continuity of $F(t | s)$ at $t \in]0; s[$ and $t \in]s; \infty[$, and its jump at $t = s$ will be used later.

We also need an expression for $f(s)$, which is

$$f(s) = \begin{cases} g(s), & 0 < s < \Delta - r, \\ 0 & \Delta - r \leq s < \Delta, \\ a \cdot \delta(\Delta - s), & s \in]\Delta - \epsilon; \Delta], \end{cases} \quad (13)$$

where $\delta(\cdot)$ – is the Dirac delta-function, $g(s)$ – is a regular function, which vanishes out of interval $s \in]0; \Delta - r[$ (see Appendix C, eq. (37) for the exact expression), the a gives the probability to obtain the impulse in the feedback line with time to live

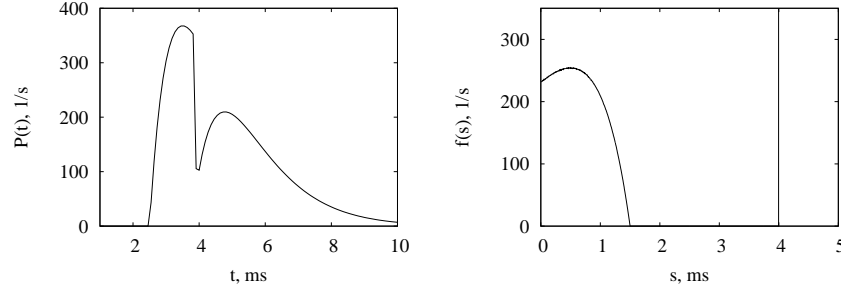


FIGURE 2. *Left:* output ISI probability density $P(t)$; *Right:* probability density $f(s)$ for times to live of the impulse in the feedback line. Here $\tau = 10$ ms, $\Delta = 4$ ms, $r=2.5$ ms, $\lambda = 1000$ s⁻¹, $N_0=2$.

equal Δ at the beginning of an arbitrary output ISI, $\frac{1}{2} < a < 1$. The expression for a is given in equation (39).

Let us explain the presence of Dirac δ -function type singularity in $f(s)$. The probability to have time to live, s , exactly equal Δ at the moment of an output ISI beginning is not infinitesimally small. Every time, when the line is free at the moment of an output ISI beginning, the impulse enters the line and has time to live equal Δ . For the line to be free from impulses at the moment of triggering, it is necessary that $t > s$ for the previous ISI. The set of realizations of the input Poisson process, each realization satisfying $t > s$, has non-zero probability a , see (13), and this gives the δ -function at $s = \Delta$ in the probability density $f(s)$.

It is worth to notice, that in the case (3) there are only two possible functional states, the feedback line can have at the beginning of an ISI. Namely, the line either keeps an impulse with time to live exactly equal Δ at the beginning of an ISI, or it does not affect the neuron within this ISI. Indeed, according to (13), the probability density for time to live s is positive only within the range $]0; \Delta - r[$ and at the point $s = \Delta$. But the condition (3) ensures, that

$$\Delta - r < r.$$

It means, that in the case $s \in]0; \Delta - r[$ the impulse from the feedback line will arrive during the refractory period and will not affect the neuron's state. This fact will be prominent in the final expression for $P(t_{n+1} | t_n, \dots, t_0)$, see discussion in Sec. 4.5.1.

The output ISI probability density $P(t)$ for inhibitory BN(r) with delayed feedback and with refractoriness can be obtained as the result of integration of (10):

$$P(t) = \int_0^{\Delta} F(t | s) f(s) ds. \quad (14)$$

Discontinuity of $F(t | s)$ at $t = s$ and δ -function type singularity at $s = \Delta$ in $f(s)$ result in discontinuity of $P(t)$ at $t = \Delta$.

Examples of $P(t)$ and $f(s)$ graphs can be found in Fig. 2.

4.3. Conditional probability density $P(t_k, s_k | t_{k-1}, s_{k-1})$. Here we find the conditional probability density $P(t_k, s_k | t_{k-1}, s_{k-1})$ for events (t_k, s_k) , which determines the probability to obtain the event (t_k, s_k) , with precision $dt_k ds_k$, provided

the previous event was exactly (t_{k-1}, s_{k-1}) . We reproduce this section from [36], where $P(t_k, s_k | t_{k-1}, s_{k-1})$ was obtained for the case $r = 0$. It appears, that the same considerations as those used in [36] are also valid for $r > 0$. Even the final expression (15) looks the same. But it is worth to notice, that explicit expressions for $F(t | s)$ in (15) will be different for $r > 0$ and $r = 0$.

By definition of conditional probabilities, the probability density wanted can be represented as the following product

$$P(t_k, s_k | t_{k-1}, s_{k-1}) = F(t_k | s_k, t_{k-1}, s_{k-1})f(s_k | t_{k-1}, s_{k-1}),$$

where $F(t_k | s_k, t_{k-1}, s_{k-1})$ denotes conditional probability density for ISI duration, t_k , provided i) this ISI started with time to leave of impulse in the feedback line equal to s_k , and ii) previous (t, s) -event was (t_{k-1}, s_{k-1}) ; the $f(s_k | t_{k-1}, s_{k-1})$ denotes conditional probability density for times to live of impulse in the feedback line under condition ii). It is obvious, that

$$F(t_k | s_k, t_{k-1}, s_{k-1}) = F(t_k | s_k),$$

because with s_k being known, the previous event (t_{k-1}, s_{k-1}) does not add any information, useful to predict t_k (compare with the proof of Lemma 4.1, Appendix A).

In order to find the probability density $f(s_k | t_{k-1}, s_{k-1})$, let us consider various possible relations between t_{k-1} and s_{k-1} . If $t_{k-1} \geq s_{k-1}$, the line will have time to get free from the impulse during the ISI t_{k-1} . That is why at the beginning of the ISI t_k , an output spike will enter the line and will have time to live $s_k = \Delta$ with probability 1. Therefore, the probability density contains the corresponding δ -function:

$$f(s_k | t_{k-1}, s_{k-1}) = \delta(s_k - \Delta), \quad t_{k-1} \geq s_{k-1}.$$

If $t_{k-1} < s_{k-1}$, than the ISI t_{k-1} ends before the impulse leaves the feedback line. Therefore, at the beginning of the t_k , the line still keeps the same impulse as at the beginning of t_{k-1} . This impulse has time to live being equal to $s_k = s_{k-1} - t_{k-1}$, so

$$f(s_k | t_{k-1}, s_{k-1}) = \delta(s_k - s_{k-1} + t_{k-1}), \quad t_{k-1} < s_{k-1}.$$

Taking all together, for the conditional probability density $P(t_k, s_k | t_{k-1}, s_{k-1})$ one obtains

$$\begin{aligned} P(t_k, s_k | t_{k-1}, s_{k-1}) &= F(t_k | s_k)\delta(s_k - \Delta), & t_{k-1} \geq s_{k-1}, \\ &= F(t_k | s_k)\delta(s_k - s_{k-1} + t_{k-1}), & t_{k-1} < s_{k-1}, \end{aligned} \quad (15)$$

where exact expression for $F(t | s)$ is given in (11).

4.4. Joint probability density $P(t_{n+1}, \dots, t_0)$. In this section, we are going to find the exact analytic expressions for the joint probability density $P(t_{n+1}, \dots, t_0)$ at two following domains:

$$D_1 = \left\{ (t_0, \dots, t_n, t_{n+1}) \mid t_1 < \Delta, \dots, t_n < \Delta, t_0 < \Delta, \right\}, \quad (16)$$

$$D_m = \left\{ (t_0, \dots, t_n, t_{n+1}) \mid t_1 < \Delta, \dots, t_n < \Delta, t_0 \geq \Delta, \right\}. \quad (17)$$

Notice, that coordinate t_{n+1} is not included to the condition here. The notations D_1 and D_m are introduced in correspondance to the sign between t_0 and Δ , – “1” for $t_0 < \Delta$, and “m” for $t_0 \geq \Delta$. It is also worth to notice, that within the introduced model, it is impossible to obtain any ISI of duration $t < r$, which follows directly from the meaning of refractoriness, sec. 2.1.1 and can be derived from (11).

Therefore, the conditions $t_i < \Delta$ in (16) and (17) actually mean $r < t_i < \Delta$, $i = 0, 1, \dots, n$ and $i = 1, \dots, n$, respectively. Hereinafter we will keep this in mind, considering domains D_l and D_m .

It is worth to notice the following:

Lemma 4.2. *The set of $(n+2)$ successive ISI durations t_0, \dots, t_n, t_{n+1} has non-zero probability to fall into the domain D_* , where $*$ means either l , or m .*

See Appendix D for the proof.

4.4.1. $P(t_{n+1}, \dots, t_0)$ at D_l . Before we start derivation of $P(t_{n+1}, \dots, t_0)$, it is worth to notice, that in the case (3) considered here, the following inequalities hold:

$$\Delta - t_i < r, \quad i \in \mathbb{Z}^+, \quad (18)$$

$$t_i + t_j > \Delta, \quad i, j \in \mathbb{Z}^+. \quad (19)$$

Indeed, $t_j > r$, $j = 0, 1, \dots$, and due to relation (3), $r \leq \Delta < 2r$. Combining these inequalities, one obtains (18), (19). We will keep in mind relations (18), (19), while performing integration in (9).

So, consider a fixed $(n+2)$ -tuple $(t_0, \dots, t_n, t_{n+1}) \in D_l$. Substituting $P(t_0, s_0)$ and $P(t_k, s_k | t_{k-1}, s_{k-1})$ from expressions (10) and (15) to (9) and performing integration over variables s_1, \dots, s_{n+1} using (19), one obtains

$$\begin{aligned} P(t_{2k}, \dots, t_0) &= \prod_{i=1}^k F(t_{2i} | \Delta - t_{2i-1}) F(t_{2i-1} | \Delta) \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 \\ &+ F(t_{2k} | \Delta) \prod_{i=1}^{k-1} F(t_{2i+1} | \Delta - t_{2i}) F(t_{2i} | \Delta) \times \\ &\times \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0, \quad k = 0, 1, \dots, \end{aligned} \quad (20)$$

$$\begin{aligned} P(t_{2k+1}, \dots, t_0) &= F(t_{2k+1} | \Delta) \prod_{i=1}^k F(t_{2i} | \Delta - t_{2i-1}) F(t_{2i-1} | \Delta) \times \\ &\times \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 \\ &+ \prod_{i=1}^k F(t_{2i+1} | \Delta - t_{2i}) F(t_{2i} | \Delta) \times \\ &\times \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0, \quad k = 0, 1, \dots, \end{aligned} \quad (21)$$

where $F(t | s)$ and $f(s)$ were defined in (11) and (13). We assume here, that $\prod_i^j = 1$, when $j < i$. Note, that formula (20) with $k = 0$ gives an expression (14) for $P(t_0)$.

At the domain D_l , all the differences $(\Delta - t_i)$, $i = 0, \dots, n$, take values within interval $]0; r[$, see (18). Therefore, according to (11), all $F(t_{2i} | \Delta - t_{2i-1})$ and

$F(t_{2i+1} | \Delta - t_{2i})$ in (20) and (21) should be substituted with $P^0(t_{2i} - r)$ and $P^0(t_{2i+1} - r)$, respectively.

Similarly, at the domain D_1 , all $t_i < \Delta$, $i = 0, \dots, n$, see (16). Therefore, according to (11), all $F(t_j | \Delta)$, $j = 2k, 2k+1$, in (20) and (21) should be substituted with $P^0(t_j - r)$.

Now, consider integral in the first term of (20) and (21). Probability density $f(s)$ is zero within interval $[\Delta - r; \Delta[$, see (13). So, the integration domain in the first term should be narrowed to $s_0 \in]0; \Delta - r[$. At this domain, $s_0 < r$, as it follows from relation (3). Therefore, $F(t_0 | s_0)$ should be substituted with $P^0(t_0 - r)$ and carried out from the integral. Finally, we use, that $f(s)$ is normed:

$$\int_0^{\Delta-r} ds_0 f(s_0) = 1 - a,$$

where a was defined in (13) and (39).

Taking into account all the considerations above, and using (13) for integration in the second term, one obtains:

$$\begin{aligned} P(t_{n+1}, \dots, t_0) &= P^0(t_{n+1} - r) \prod_{i=0}^n P^0(t_i - r) \cdot (1 - a) \\ &\quad + F(t_{n+1} | \Delta) \prod_{i=0}^n P^0(t_i - r) \cdot a, \quad n = 2k + 1, \\ P(t_{n+1}, \dots, t_0) &= F(t_{n+1} | \Delta) \prod_{i=0}^n P^0(t_i - r) \cdot (1 - a) \\ &\quad + P^0(t_{n+1} - r) \prod_{i=0}^n P^0(t_i - r) \cdot a, \quad n = 2k, \quad k = 0, 1, \dots \end{aligned} \quad (22)$$

4.4.2. $P(t_{n+1}, \dots, t_0)$ at D_m . Consider a fixed $(n+2)$ -tuple $(t_0, \dots, t_n, t_{n+1}) \in D_m$. Applying the similar considerations as in Sec. 4.4.1 to perform the intergration in (9), one obtains

$$P(t_{n+1}, \dots, t_0) = \begin{cases} \prod_{i=1}^{n+1} P^0(t_i - r) \cdot P(t_0), & n = 2k + 1, \\ F(t_{n+1} | \Delta) \prod_{i=1}^n P^0(t_i - r) \cdot P(t_0), & n = 2k, \end{cases} \quad (23)$$

where $P(t_0) = a \cdot F(t_0 | \Delta) + (1 - a) \cdot P^0(t_0 - r)$, compare with the top line of (22)

4.5. $P(t_{n+1} | t_n, \dots, t_0)$ at domains D_1 and D_m . The expressions (22) and (23) give the joint probability density $P(t_{n+1}, \dots, t_0)$ for consecutive ISI durations for an arbitrary n at the domains D_1 and D_m , respectively. Therefore, the conditional probability density $P(t_{n+1} | t_n, \dots, t_0)$ at D_1 and D_m can be obtained readily, see equation (8). One just needs to take (22) and (23) with $(n-1)$ substituted instead of n to find $P(t_n, \dots, t_0)$, and use, that $F(t_n | \Delta) = P^0(t_n)$ at both D_1 and D_m . Substituting obtained expressions for $P(t_{n+1}, \dots, t_0)$ and $P(t_n, \dots, t_0)$ to (8), one

	$(t_0, \dots, t_n) \in D_1$	$(t_0, \dots, t_n) \in D_m$
$n = 2k,$ $k = 0, 1, \dots$	$P^0(t_{n+1} - r) \cdot a + F(t_{n+1} \Delta) \cdot (1 - a)$	$F(t_{n+1} \Delta)$
$n = 2k + 1,$ $k = 0, 1, \dots$	$F(t_{n+1} \Delta) \cdot a + P^0(t_{n+1} - r) \cdot (1 - a)$	$P^0(t_{n+1} - r)$

 TABLE 1. Expressions for $P(t_{n+1} | t_n, \dots, t_0)$ at domains D_1 and D_m .

obtains

$$P(t_{n+1} | t_n, \dots, t_0) \Big|_{D_1} = \begin{cases} P^0(t_{n+1} - r) \cdot a + F(t_{n+1} | \Delta) \cdot (1 - a), & n = 2k, \\ F(t_{n+1} | \Delta) \cdot a + P^0(t_{n+1} - r) \cdot (1 - a), & n = 2k + 1, \end{cases} \quad (24)$$

$$P(t_{n+1} | t_n, \dots, t_0) \Big|_{D_m} = \begin{cases} F(t_{n+1} | \Delta), & n = 2k, \\ P^0(t_{n+1} - r), & n = 2k + 1, \end{cases} \quad (25)$$

where $k = 0, 1, \dots$, and a ranges within 0.5 and 1, see Appendix C. Expressions for $P(t_{n+1} | t_n, \dots, t_0)$, given in (24) and (25), are arranged in the Table 1.

We can see, that for $t_1 < \Delta, \dots, t_n < \Delta$ the conditional p.d.f. $P(t_{n+1} | t_n, \dots, t_0)$ can be represented as a linear combination of functions $P^0(t_{n+1} - r)$ and $F(t_{n+1} | \Delta)$, with coefficients, which depend on whether $t_0 < \Delta$ or $t_0 \geq \Delta$ and on the parity of n . Functions $P^0(t_{n+1} - r)$ and $F(t_{n+1} | \Delta)$ are different and they have different properties. Namely, $P^0(t_{n+1} - r)$ is a continuous function at all its domain, and $F(t_{n+1} | \Delta)$ contains a jump at the point $t_{n+1} = \Delta$, see an example of $P^0(t_{n+1} - r)$ at Fig. 6, right, and an example of $F(t_{n+1} | \Delta)$ at Fig. 3, right⁴. This means, that $P(t_{n+1} | t_n, \dots, t_1, t_0)$ changes its value when t_0 changes its value from $t_0 < \Delta$ to $t_0 \geq \Delta$. Therefore conditional p.d.f. $P(t_{n+1} | t_n, \dots, t_1, t_0)$ does depend on the condition t_0 . This means, that the condition (4) does not hold for any n for the output stream of BN(r) with delayed feedback. The Theorem 3.2 is proven. \square

4.5.1. *Discussion of result for $P(t_{n+1} | t_n, \dots, t_0)$.* In this section, we are going to explain additionally, how the results (24) and (25) for the conditional p.d.f. $P(t_{n+1} | t_n, \dots, t_0)$ should be understood.

Let us first consider $P(t_{n+1} | t_n, \dots, t_0)$ at D_m , expression (25). The condition $t_0 \geq \Delta$ in (17) ensures, that the impulse will leave the feedback line during ISI t_0 , no matter what its time to live was at the beginning of t_0 (compare with considerations in the proof of Lemma 4.2, Appendix D). So, at the next firing, the line will start to conduct a new impulse with time to live equal $s_1 = \Delta$. As $t_1 < \Delta$ at D_m , then at the beginning of the next ISI, the line will still conduct the same impulse with time to live $s_2 = \Delta - t_1 < \Delta - r < r$, where we use (3) and $t_1 > r$. At the next firing, the line will start to conduct a new impulse with time to live equal $s_3 = \Delta$, and due to the condition $t_3 < \Delta$ will contain the same impulse at the beginning of ISI t_4 with time to live $s_4 = \Delta - t_3 < r$, see Fig. 9 in Appendix D.

⁴ We use here, that $P(t_{n+1} | t_n, \dots, t_0) = P^0(t_{n+1} - r)$ for $n = 2k + 1$ and $P(t_{n+1} | t_n, \dots, t_0) = F(t_{n+1} | \Delta)$ for $n = 2k$ at D_m , expression (25).

Proceeding with such considerations, one concludes, that the states of the feedback line at the beginning of ISIs t_1, \dots, t_n alternate; namely, $s_i = \Delta$ for an odd and $s_i < r$ for an even number i . So, if we take $n = 2k$, $k = 0, 1, \dots$, in (25), an ISI t_{n+1} will start with time to live $s_{n+1} = \Delta$. Ones s_{n+1} is known, the conditions t_1, \dots, t_n do not add any information, useful to predict t_{n+1} , compare with the proof of Lemma 4.1. Formally, it means, that all the conditions t_n, \dots, t_0 in $P(t_{n+1} | t_n, \dots, t_0)$ should be substituted with the condition $s_{n+1} = \Delta$, which gives the top line of (25).

Now, if we take $n = 2k + 1$, $k = 0, 1, \dots$, in (25), an ISI t_{n+1} will start with time to live $s_{n+1} < r$. Inequality $s_{n+1} < r$ ensures, that the feedbacked impulse will enter the neuron during refractory period and therefore will disappear without any action. Therefore, the probability to obtain an output ISI of definite duration for $\text{BN}(r)$ with delayed feedback is the same as for $\text{BN}(0)$ without feedback, which started to receive impulses at the moment r (after the end of refractoriness). This explains the bottom line of (25).

Now, let us consider $P(t_{n+1} | t_n, \dots, t_0)$ at D_1 , expression (24). Using the same considerations as for D_m , one can conclude, that the states of the feedback line at the beginning of ISIs t_0, t_1, \dots, t_n also alternate. But in the case of D_1 , the condition $t_0 < \Delta$ leaves unknown the state of the feedback line at the beginning of t_1 , and eventually at the beginning of any later ISI, as the conditions $t_1 < \Delta, \dots, t_n < \Delta$ hold. So, at the beginning of t_0 the line either has an impulse with time to live $s_0 = \Delta$, with probability a , or it contains an impulse with time to live $s_0 < r$, with probability $(1 - a)$. Here we use (13) and normalization condition (38). If $s_0 = \Delta$, then $s_{n+1} = \Delta$ for $n = 2k + 1$ and $s_{n+1} < r$ for $n = 2k$, $k = 0, 1, \dots$, which explains the first term in top and bottom lines of (24). Otherwise, if $s_0 < r$, then $s_{n+1} < r$ for $n = 2k + 1$ and $s_{n+1} = \Delta$ for $n = 2k$, which corresponds to the second term in top and bottom line of (24).

5. Numerical simulation. In order to check the correctness of obtained analytic expressions, and also to investigate whether the output ISIs stream is non-Markovian for inhibitory $\text{BN}(r)$ with higher thresholds as well, numerical simulations were performed. A C++ program, containing class, which models the operation manner of inhibitory $\text{BN}(r)$ with delayed feedback, was developed. Object of this class receives the sequence of pseudorandom numbers with Poisson probability density to its input. The required sequences were generated by means of utilities from the GNU Scientific Library⁵ with the Mersenne Twister generator as source of pseudorandom numbers.

Program contains function, the time engine, which brings system to the moment just before the next input signal, bypassing moments, when neither external Poisson impulse, nor impulse from the feedback line comes. So, only the essential events are accounted. It allows one to make exact calculations faster as compared to the algorithm where time advances gradually by adding small time-steps.

The conditional probability densities, $P(t_1 | t_0)$ and $P(t_2 | t_1, t_0)$, are found by counting the number of output ISI of different durations and normalization (see Figures 3 – 7). Obviously, for calculation of conditional distributions only those ISIs are selected, which follow one or two ISIs of fixed duration, t_0 for $P(t_1 | t_0)$ and $\{t_1, t_0\}$ for $P(t_2 | t_1, t_0)$. The single- and double-ISI conditional probability densities, found numerically for inhibitory $\text{BN}(r)$ with threshold 2, coincide with

⁵<http://www.gnu.org/software/gsl/>

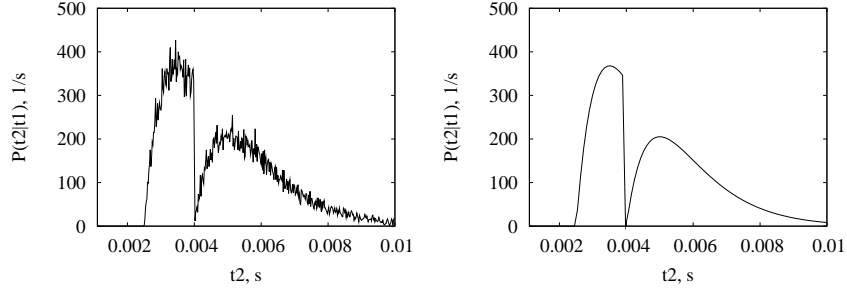


FIGURE 3. Conditional probability density $P(t_2 | t_1)$ for $\tau = 10$ ms, $\Delta = 4$ ms, $\lambda = 1000 \text{ s}^{-1}$, $N_0 = 2$, $r=2.5$ ms, $t_1=5$ ms, $t_1 \in D_m$, found numerically by means of Monte-Carlo method (left) and derived analytically using (25) (right). The number of firings accounted in numerical simulation $N = 30\,000$.

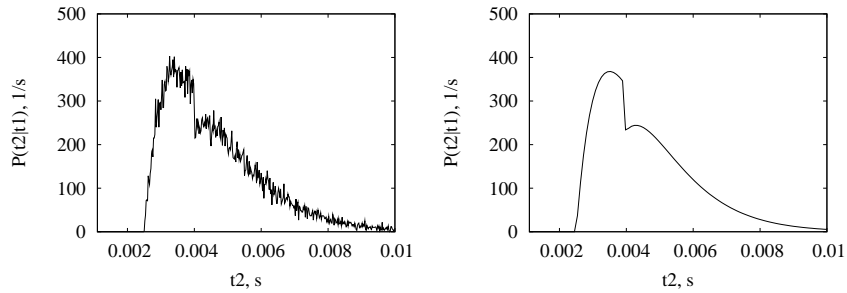


FIGURE 4. Conditional probability density $P(t_2 | t_1)$ for $\tau = 10$ ms, $\Delta = 4$ ms, $\lambda = 1000 \text{ s}^{-1}$, $N_0 = 2$, $r=2.5$ ms, $t_1=3.5$ ms, $t_1 \in D_1$, found numerically by means of Monte-Carlo method (left) and derived analytically using (24) (right). The number of firings accounted in numerical simulation $N = 30\,000$.

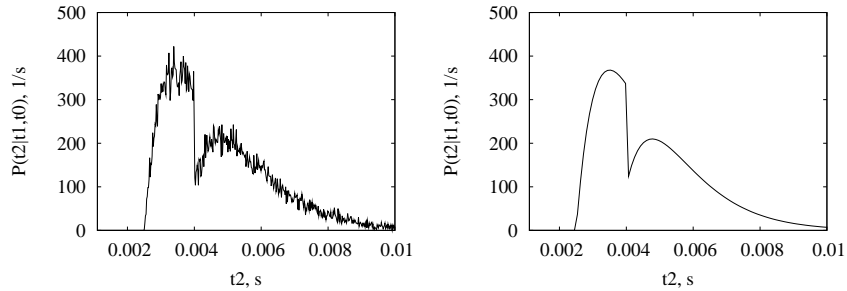


FIGURE 5. Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 4$ ms, $\lambda = 1000 \text{ s}^{-1}$, $N_0 = 2$, $r=2.5$ ms, $t_1=3.5$ ms, $t_0=3$ ms, $(t_0, t_1) \in D_1$, found numerically by means of Monte-Carlo method (left) and derived analytically using (24) (right). The number of firings accounted in numerical simulation $N = 30\,000$.

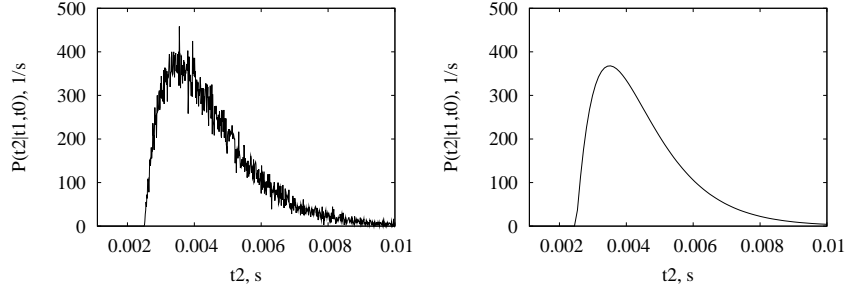


FIGURE 6. Conditional p.d.f. $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 4$ ms, $\lambda = 1000$ s $^{-1}$, $N_0 = 2$, $r = 2.5$ ms, $t_1 = 3.5$ ms, $t_0 = 5$ ms, $(t_0, t_1) \in D_m$, found numerically by means of Monte-Carlo method (left) and derived analytically using (25) (right). The number of firings accounted in numerical simulation $N = 30\,000$.

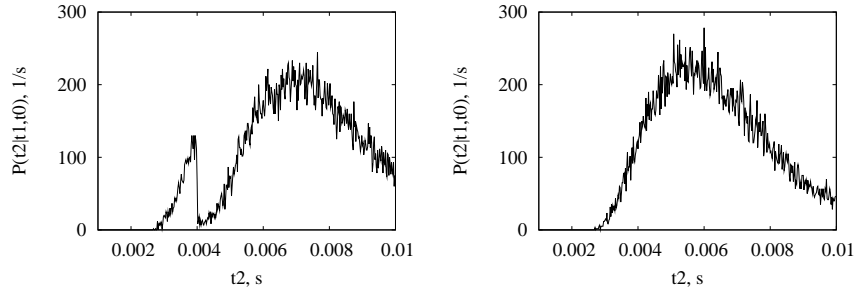


FIGURE 7. Conditional p.d.f. $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 4$ ms, $\lambda = 1000$ s $^{-1}$, $N_0 = 4$, $r = 2.5$ ms, $t_1 = 3.5$ ms, $t_0 = 3$ ms, $(t_0, t_1) \in D_1$ (a) and $t_1 = 3.5$ ms, $t_0 = 5$ ms, $(t_0, t_1) \in D_m$ (b), found numerically by means of Monte-Carlo method ($N = 30\,000$).

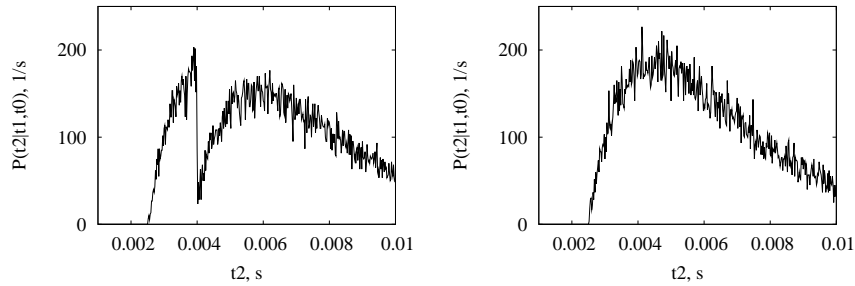


FIGURE 8. Conditional p.d.f. $P(t_2 | t_1, t_0)$ for the LIF model found numerically by means of Monte-Carlo method ($N = 30\,000$). Here $\lambda = 500$ s $^{-1}$, $r = 2.5$ ms, $\tau_M = 10$ ms, $y_0 = 4$ mV, $V_0 = 5$ mV; (a) $t_0 = 3$ ms, $t_1 = 3.5$ ms, $(t_0, t_1) \in D_1$, (b) $t_0 = 5$ ms, $t_1 = 3.5$ ms, $(t_0, t_1) \in D_m$.

those obtained analytically in (25) and (24), compare left and right panels in Figs. 3–6.

For $N_0 > 2$, conditional probability densities $P(t_1 | t_0)$ and $P(t_2 | t_1, t_0)$ are similar to those, found for $N_0=2$. In particular, both the availability and position of discontinuity coincide with those obtained for inhibitory BN(r) with threshold 2, as expected, compare Figure 7, left with Figure 5 and Figure 7, right with Figure 6.

In order to compare results for the BN neuron with the leaky integrate-and-fire (LIF) model, numerical simulation was performed for the LIF model as well. The LIF neuron was simulated in its simplest version. Namely, the neuron's state at any moment of time ϑ is completely characterized by its membrane voltage at that moment, $V(\vartheta)$. Without stimulation, the $V(\vartheta)$ decays exponentially to the resting state with $V = 0$:

$$V(\vartheta + t) = e^{-t/\tau_M} V(\vartheta),$$

where τ_M – is the membrane relaxation time. An input impulse advances V by a fixed value, y_0 , instantaneously:

$$V \rightarrow V + y_0,$$

where y_0 mimics the EPSP peak value. If the resulting voltage satisfies the inequality

$$V + y_0 > V_0,$$

where V_0 – is the firing threshold, then the LIF neuron fires an output spike and appears in the resting state.

For numerical simulations we choose $\tau_M = 10$ ms, $y_0 = 4$ mV, $V_0 = 5$ mV. These values are comparable with those found in the inhibitory interneurons of CA3 hippocampal region, [21]. The relation between V_0 and y_0 ensures that two input impulses are able to trigger the LIF provided they are close in time (which corresponds to $N_0 = 2$ in BN model). For the inhibitory interneurons, this is because of their depolarized resting state, [15]. It is reported, [12], that even single impulse from a pyramidal cell may trigger interneuron of this type. Interesting, that selfinhibition is found in the inhibitory interneurons also, but in the neocortex, [3].

The result, obtained for the LIF model, Fig. 8, conforms with non-Markov behavior, obtained for the BN model.

6. Conclusions. Our results reveal the influence of delayed feedback presence on the neuronal firing statistics. In the contrast to the cases of BN(0) without feedback [33] and BN(0) with instantaneous feedback [34], the neighbouring output ISIs of inhibitory BN(r) with delayed feedback are mutually correlated, compare with [4]. This means that even in the simplest possible reverberatory network with random stimulation the output ISI stream is not as a renewal one.

The non-renewalness of experimentally registered spike trains was observed for neuronal activity in various CNS areas in mammals [18, 10, 23] and fish [17, 27]. The simplest stochastic processes which are not renewal are the Markov processes of various order. The order of underlying Markov process was estimated in [27] for activity in the weakly electric fish electrosensory system. It was found in [27] that for some neural fibers the Markov order should be at list seven, which does not exclude that the genuine order is higher, or that the activity is non-Markovian.

Actually, for proving based on experimental data that a stochastic activity has Markov order m , one needs increasing amount of data with increasing m . If

so, it seems impossible to prove experimentally that a stochastic activity is non-Markovian. Similarly as it is impossible to prove experimentally that a number is irrational. We prove here that the output ISI stream of inhibitory BN(r) with delayed feedback is non-Markovian based on complete knowledge of the mechanism which generates the output stream. In a sense, to have this knowledge is equivalent as to have an unlimited amount of experimental data.

It is worth to notice, that the activity of excitatory BN(r) with delayed feedback would be non-Markovian as well. We conclude, that it is namely the delayed feedback presence, which results in non-Markovian statistics of neuronal firing. One should take this facts into account during analysis of neuronal spike trains obtained from any reverberatory network.

7. Discussion. The relative simplicity of expressions for $P(t_{n+1} | t_n, \dots, t_0)$, see (24), (25) and Table 1, are due to the relationship (3) between the temporal length of the feedback line, Δ , and the refractory period, r . Due to this relationship, the feedback line can act in a binary mode only. Namely, the only state of the line at the beginning of any ISI, which can influence the subsequent firing activity, is the state with $s = \Delta$. All other values of s , $0 < s < \Delta$, (actually, $0 < s < \Delta - r < r$), are equally unable to influence the firing process, and therefore, can be qualified as belonging to the same unique state. In the opposite to (3) situation, when $\Delta > 2r$, among the states with $s < \Delta$, there appears a continuum of states with $r < s < \Delta - r$, which are able to influence the firing process in distinguishable manner. In that case, the feedbacked impulse can provide more detailed information about the previous events and the correlations and memory effects in the ISI sequence would be stronger. Therefore, as the non-Markovian behavior was found for the case (3), one would expect the same in the case $\Delta > 2r$.

In this paper, we have proven that the memory time scale of the output ISIs stream is infinite, provided a delayed feedback is involved. It is possible to try to approximate a non-Markov process with a Markov process. An interesting question would be to estimate how good such an approximation could be. The answer depends on what is expected to calculate with the initial non-Markov process and its Markov approximation. E.g., a so called Markovian projection [1] offers a good approximation if a stochastic volatility of prices is calculated, but it is not clear what could it mean for a neuronal system. A simpler task would be to estimate correlations between different ISIs, and how fast do the correlations decay with order/temporal distance between the ISIs. This is expected to try in another work.

Appendix A. Proof of Lemma 4.1. We reproduce this proof literally from [36], as all the considerations from [36] for the case $r = 0$ are also valid for $r > 0$.

In the compound event (t_{n+1}, s_{n+1}) , the time to live s_{n+1} always gets its value before than the t_{n+1} does. The value of s_{n+1} can be determined unambiguously from the (t_n, s_n) value (See Sections 2.2 and 4.3):

$$s_{n+1} = \begin{cases} s_n - t_n, & t_n < s_n, \\ \Delta, & t_n \geq s_n. \end{cases} \quad (26)$$

The only two factors, which determine the next ISI duration, t_{n+1} , are (i) the value of s_{n+1} , and (ii) the behavior of the input Poisson stream under the condition $(t_n, s_n; \dots; t_0, s_0)$ after the moment θ , when the t_{n+1} starts. The s_{n+1} value does not depend on $(t_{n-1}, s_{n-1}; \dots; t_0, s_0)$, see above. As regards the input Poisson stream,

condition $(t_n, s_n; \dots; t_0, s_0)$ imposes certain constraints on its behavior before the θ . But what do we need in the definition of the $P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0)$, it is the conditional probability to obtain input impulses at definite moments after the θ . For a Poisson stream this conditional probability does not depend on conditions before the θ . For example, conditional probability to obtain the first after θ impulse at $\theta + t$ equals $e^{-\lambda t} \lambda dt$, whatever conditions are imposed on the stream before the θ . This proves (5). \square

Appendix B. Derivation of $F(t | s)$. In order to derive conditional p.d.f. $F(t | s)$, we are going to consider separately cases $s \leq r$ and $s > r$.

Let us start with $s \leq r$. In this case, inhibitory impulse from the feedback line does not affect the neuron, as it arrives during refractory period. According to our model (Sec. 2.1.1), BN(r) is unable to receive and send any impulses during refractory period, so $F(t | s) = 0$ if $t < r$. As the line is free of impulse at the moment when neuron recovers from its refractory period, the probability to obtain ISI of definite duration $t > r$ is the same as for BN(0) without feedback, which started to receive excitatory impulses at the moment r . So, the expression for $F(t | s)$ can be readily obtained:

$$F(t | s) = \begin{cases} 0, & t \leq r \text{ and } s \leq r, \\ P^0(t - r), & t > r \text{ and } s \leq r, \end{cases} \quad (27)$$

where $P^0(t)$ is the probability density for output ISI durations for BN(0) without feedback, which was derived in [32].

Now consider the case, when $s > r$. Again, it is impossible to obtain any ISI of duration less than r , so $F(t | s) = 0$ if $t < r$. Until the feedbacked impulse arrives, the neuron is unaffected by the feedback line, therefore $F(t | s) = P^0(t - r)$ if $t \in]r; s[$. Finally, in order to obtain an ISI of duration $t > s$, the following conditions must be satisfied: i) BN(0) without feedback, which started to receive impulses at the moment r , should not fire until moment s , ii) BN(0) without feedback, which started to receive impulses at the moment s fires for the first time at the moment t . The probability of event i) is $\Pi^0(s - r)$, where $\Pi^0(t)$ gives the probability to obtain an ISI longer than t at the output of BN(0) without feedback:

$$\Pi^0(t) \equiv \int_t^\infty P^0(t') dt'.$$

The expression for $\Pi^0(t)$ is different for different domains of t . In this work, we need only the expression for the domain $t < \tau$. This can be calculated with the usage of (12) and the fact that $P^0(t)$ is normalized to 1:

$$\Pi^0(t) = 1 - \int_0^t P^0(t') dt' = (1 + \lambda t) e^{-\lambda t}, \quad t < \tau.$$

The probability of event ii) is simply $P^0(t - s) dt$.

Taking all together, one obtains for $s > r$:

$$F(t | s) = \begin{cases} 0, & t \leq r, \\ P^0(t - r), & t \in]r; s[, \\ \Pi^0(s - r) P^0(t - s), & t \geq s. \end{cases} \quad (28)$$

Note, that p.d.f. $F(t | s)$, given in (27) and (28), is normalized: $\int_0^{\infty} F(t | s) dt = 1$.

Appendix C. Stationary probability density $f(s)$. In order to derive $f(s)$, let us define transition probability densities $P(s' | s)$. Namely, $P(s' | s) ds'$ gives the probability to find the impulse in the feedback line with time to live within interval $[s'; s' + ds']$ at the beginning of some ISI, provided that at the beginning of the previous ISI, time to live of the impulse in the feedback line was s .

Ones $P(s' | s)$ is known, stationary probability density $f(s)$ can be found as a normalized to 1 solution of the following equation:

$$\int_0^{\Delta} P(s' | s) f(s) ds = f(s'). \quad (29)$$

C.1. Derivation of the transition probability densities $P(s' | s)$. In order to derive $P(s' | s)$, let us again consider different domains of s and s' values separately.

Consider $s < \Delta$ at the beginning of some ISI. Depending on the duration t of this ISI, time to live s' at the beginning of the next ISI can take different values (See Sections 2.2 and 4.3):

$$s' = \begin{cases} s - t, & t < s, \\ \Delta, & t \geq s, \end{cases} \quad (30)$$

compare with (26).

Namely, if $t < s$, then $s' = s - t$ and ISI t is generated without the feedback line involved. As the probability to obtain an ISI of duration $t \leq r$ is zero, then

$$P(s' | s) = 0 \quad \text{for} \quad 0 < s - s' \leq r.$$

To obtain an ISI of duration $t = s - s' > r$, it is necessary, that the BN(0) without feedback, which started to receive impulses at the moment r , fires for the first time at the moment t . The probability of this event is $P^0(t - r) dt$, therefore

$$P(s' | s) = P^0(s - s' - r), \quad \text{when} \quad 0 < s' < s - r.$$

On the other hand, if $t \geq s$, then the feedback line will get free from its impulse during ISI t . So, at the beginning of the next ISI, new impulse will enter the line and will have time to live exactly equal $s' = \Delta$. This results in δ -function in the conditional p.d.f. $P(s' | s)$ at the point $s' = \Delta$. The mass of this δ -function is the overall probability to obtain any ISI of duration $t \geq s$, given that at the beginning of this ISI time to live of the impulse in the feedback line was s . This probability can be calculated as follows:

$$\int_s^{\infty} F(t | s) dt = \begin{cases} 1, & s \leq r, \\ \Pi^0(s - r), & s > r, \end{cases}$$

were we substituted $F(t | s)$ from (28) and (27) and used the normalization condition $\int_0^{\infty} P^0(t) dt = 1$.

Finally, as it follows from Section 2.2 and can be seen in (30), it is impossible to obtain $s \leq s' < \Delta$.

Taking all together, one obtains:

$$P(s' | s) = \begin{cases} 0, & s \leq s' < \Delta, \\ 0, & 0 < s - s' \leq r, \\ P^0(s - s' - r), & 0 < s' < s - r, \\ A(s, r)\delta(s' - \Delta), & s' \in]\Delta - \epsilon; \Delta], \end{cases} \quad (31)$$

where

$$A(s, r) = \begin{cases} 1, & s \leq r, \\ \Pi^0(s - r), & s > r. \end{cases}$$

Note, that p.d.f. $P(s' | s)$, given in (31), is also normalized: $\int_0^\Delta P(s' | s) ds' = 1$.

C.2. Derivation of the $f(s)$. In order to solve equation (29), we present $f(s)$ in the following form:

$$f(s) = g(s) + a \cdot \delta(\Delta - s), \quad (32)$$

where $\delta(\cdot)$ – is the Dirac delta-function, $g(s)$ – is a regular function, which vanishes out of interval $s \in]0; \Delta]$, a – some constant, which will be defined from normalization condition.

Substituting (32) to (29) and separating terms without δ -function, one obtains equation for the regular part $g(s)$ of probability density $f(s)$:

$$g(s') = a \cdot F(s' | \Delta) + \int_r^\Delta P^{\text{reg}}(s' | s) g(s) ds,$$

where $P(s' | s)$ is defined by (31), and superscript “reg” denotes its regular part (without δ -function).

One should consider cases $0 < s' < \Delta - r$ and $\Delta - r \leq s' \leq \Delta$ separately, as the expressions for $P(s' | s)$ are different for different domains. Let us start with $s' \in [\Delta - r; \Delta]$. Substituting $P(s' | s)$ from (31), one obtains the trivial result:

$$g(s') = 0, \quad s \in [\Delta - r; \Delta], \quad (33)$$

which simply reflects the impossibility to obtain an ISI of duration less than r .

Now consider the case $0 < s' < \Delta - r$. Substituting corresponding expressions for $P(s' | s)$ from (31), one obtains

$$g(s') = a \cdot \lambda^2(\Delta - s' - r)e^{-\lambda(\Delta - s' - r)} + \lambda^2 \int_r^\Delta (s - s' - r)e^{-\lambda(s - s' - r)} g(s) ds, \quad (34)$$

where we used (12). In order to solve this equation, let us represent $g(s)$ as

$$g(s') = e^{\lambda s'} \phi(s'), \quad 0 < s' < \Delta. \quad (35)$$

Substituting (35) to (34), one obtains

$$\phi(s') = a \cdot \lambda^2(\Delta - s' - r)e^{-\lambda(\Delta - r)} + \lambda^2 e^{\lambda r} \int_r^\Delta (s - s' - r)\phi(s) ds, \quad 0 < s' < \Delta - r, \quad (36)$$

or after double differentiation

$$\frac{d^2}{ds'^2} \phi(s') = \phi(s' + r), \quad 0 < s' < \Delta - r.$$

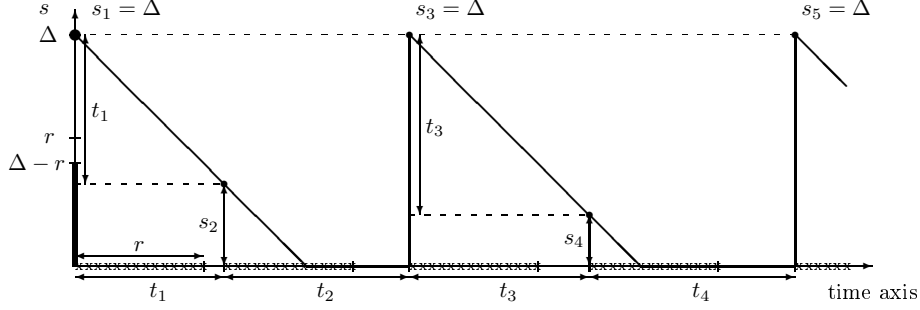


FIGURE 9. Relation between s_1, s_2, \dots and t_1, t_2, \dots at the domain D_m , (17). Each ISI starts with refractory time r , indicated by “xxxxxx” at the time axis. The values the s can take at the beginning of any ISI are indicated by solid line and dot at s -axis. The states of the feedback line at the beginning of t_1, t_2, \dots alternate: the line keeps an impulse with time to live either equal Δ , or less than r . In the latter case the feedbacked impulse arrives during refractory period and does not affect neuron.

But $\phi(s' + r) \equiv 0$, see (33). Therefore, for $g(s)$ one obtains:

$$g(s') = a \cdot \lambda^2 (\Delta - s' - r) e^{-\lambda(\Delta - s' - r)}, \quad 0 < s' < \Delta - r, \quad (37)$$

where we used (36). Taking together (32), (33) and (37), one obtains (13).

According to (32) and (37), the normalization condition can be written as

$$\int_0^{\Delta - r} g(s) ds + a = 1, \quad (38)$$

which results in

$$a = \frac{e^{\lambda(\Delta - r)}}{2 e^{\lambda(\Delta - r)} - 1 - \lambda(\Delta - r)}. \quad (39)$$

Analyzing expression (39) and using $\lambda(\Delta - r) > 0$, one can find, that constant a takes values within interval

$$\frac{1}{2} < a < 1.$$

Appendix D. Proof of Lemma 4.2. Let us first consider D_m . The condition $t_0 \geq \Delta$ in (17) ensures, that the feedback line will discharge its impulse during ISI t_0 . So, at the next firing, new impulse will enter the line, and will have time to live equal $s_1 = \Delta$. But at the domain D_m , $t_1 < \Delta$, which means, that ISI t_1 was generated without the feedbacked impulse involved. At the beginning of the next ISI, the line still conducts the same impulse with time to live $s_2 = \Delta - t_1 < \Delta - r < r$, where the conditions (3) and $t_1 > r$ are used, see Fig. 9. Inequality $s_2 < r$ means, that the feedback line will not affect BN during ISI t_2 (compare with the end of Section 4.2). Proceeding with such considerations, one concludes, that ISIs t_1, t_2, \dots, t_n are generated without feedback line involved (with Poissonian impulses only).

BN(0) with threshold $N_0 = 2$ requires 2 input impulses from the Poisson stream within time window $]r; \Delta[$ to be triggered within this window (condition (2) ensures that no one input impulse will be lost). This event has the probability $\lambda^2(\Delta - r)^2$.

$e^{-\lambda(\Delta-r)}/2$. Therefore, the probability to have n ISIs each within interval $]r; \Delta[$, is given by $\lambda^{2n}(\Delta-r)^{2n} \cdot e^{-n\lambda(\Delta-r)}/2^n$.

The state of the feedback line at the beginning of t_0 is unknown. But no matter the state was, it is guaranteed, that after Δ units of time after the ISI beginning, the inhibitory impulse is already utilized and BN proceeds driven by the Poisson process only, until the next spike will be generated. The lower bound for the probability to obtain $t_0 \geq \Delta$ can be estimated as $\Pi^0(\Delta-r) \int_{\Delta}^{\infty} P^0(t-\Delta) = \Pi^0(\Delta-r) = (1 + \lambda(\Delta-r))e^{-\lambda(\Delta-r)}$.

Therefore, the set of $(n+2)$ successive ISI durations t_0, \dots, t_n, t_{n+1} has non-zero probability,

$$\text{Prob}[(t_0, \dots, t_{n+1}) \in D_m] > \frac{\lambda^{2n}(\Delta-r)^{2n}}{2^n} \cdot e^{-(n+1)\lambda(\Delta-r)} > 0$$

to fall into the domain D_m .

Now, consider the domain D_1 . Applying the similar considerations as in the case of D_m , one can conclude, that at D_1 all the ISIs t_0, t_1, \dots, t_n are generated without feedback line involved. Therefore the lower bound for the probability to fall into this domain can be estimated as

$$\text{Prob}[(t_0, \dots, t_{n+1}) \in D_1] > \frac{\lambda^{2(n+1)} \cdot (\Delta-r)^{2(n+1)}}{2^{n+1}} \cdot e^{-(n+1)\lambda(\Delta-r)} > 0$$

This proves Lemma 4.2. □

REFERENCES

- [1] A. Antonov and T. Misirpashaev, *Markovian projection onto a displaced diffusion: Generic formulas with applications*, working paper series, (2006).
- [2] V. Aroniadou-Anderjaska, M. Ennis and M. T. Shipley, *Dendrodendritic recurrent excitation in mitral cells of the rat olfactory bulb*, J. Neurophysiol. **82** (1999), 489–494.
- [3] A. Bacci, J. R. Huguenard and D. A. Prince, *Functional autaptic neurotransmission in fast-spiking interneurons: A novel form of feedback inhibition in the neocortex*, J. Neurosci., **23** (2003), 859–866.
- [4] E. Benedetto and L. Sacerdote, *On dependency properties of the ISIs generated by a two-compartmental neuronal model*, Biological Cybernetics, **107** (2013), 95–106.
- [5] J. M. Bekkers and C. F. Stevens, *Excitatory and inhibitory autaptic currents in isolated hippocampal neurons maintained in cell culture*, PNAS, **88** (1991), 7834–7838.
- [6] G. G. Borst, J. C. Lodder and K. S. Kits, *Large amplitude variability of GABAergic IPSC in melanotrophs from Xenopus laevis: Evidence that quantal size differs between synapses*, J. Neurophysiol., **71** (1994), 639–655.
- [7] T. Britvina and J. J. Eggermont, *A Markov model for interspike interval distributions of auditory cortical neurons that do not show periodic firings*, Formal Aspects of Computing, **96** (2007), 245–264.
- [8] V. Chan-Palay, *The recurrent collaterals of Purkinje cell axons: A correlated study of rat's cerebellar cortex with electron microscopy and the Golgi-method*, Z. Anat. Entwicklungsgesch., **134** (1971), 210–234.
- [9] J. L. Doob, “Stochastic Processes,” John Wiley & Sons, Inc., New York; Chapman & Hall, Limited, London, 1953.
- [10] F. Farkhooi, M. F. Strube-Bloss and M. P. Nawrot, *Serial correlation in neural spike trains: Experimental evidence, stochastic modelling, and single neuron variability*, Phys. Rev. E, **79** (2009), 021905.
- [11] S. Ghosh-Dastidar and H. Adeli, *Spiking neural networks*, International Journal of Neural Systems, **19** (2009), 295–308.
- [12] A. I. Gulyas, R. Miles, A. Sik, K. Tóth, N. Tamamaki and T. F. Freund, *Hippocampal pyramidal cells excite inhibitory neurons through a single release site*, Nature, **366** (1993), 683–687.

- [13] A. L. Hodgkin, “The Conduction of the Nervous Impulse,” Liverpool University Press, Liverpool, 1971.
- [14] A. V. Holden, “Models of the Stochastic Activity of Neurones,” Lecture Notes in Biomathematics, Vol. 12, Springer-Verlag, Berlin-New York, 1976.
- [15] P. Jonas, J. Bischofberger, D. Fricker and R. Miles, *Fast in, fast out temporal and spatial signal processing in hippocampal interneurons*, Trends in Neurosciences, **27** (2004), 30–40.
- [16] K. G. Kravchuk and A. K. Vidybida, *Firing statistics of inhibitory neuron with delayed feedback. II: Non-Markovian behavior*, BioSystems, **112**, 3 (2013), 233248.
- [17] M. W. Levine, *Firing rates of a retinal neuron are not predictable from interspike interval statistics*, Biophys. J., **30** (1980), 9–26.
- [18] S. B. Lowen and M. C. Teich, *Auditory-nerve action potentials form a nonrenewal point process over short as well as long time scales*, J. Acoust. Am., **92** (1992), 803–806.
- [19] J. Lübke, H. Markram, M. Frotscher and B. Sakmann, *Frequency and dendritic distribution of autapses established by layer 5 pyramidal neurons in the developing rat neocortex: Comparison with synaptic innervation of adjacent neurons of the same class*, J. Neurosci., **16** (1996), 3209–3218.
- [20] D. M. MacKay, *Self-organization in the time domain*, in “Self-Organizing Systems” (eds. M. C. Yovitts and G. T. Jacobi, et al.), Spartan Books, Washington, (1962), 37–48.
- [21] R. Miles, *Synaptic excitation of inhibitory cells by single CA3 hippocampal pyramidal cells of the guinea-pig in vitro*, J. Physiol., **428** (1990), 61–77.
- [22] J. W. Moore, N. Stockbridge and M. Westerfield, *On the site of impulse initiation in a neurone*, J. Physiol., **336** (1983), 301–311.
- [23] M. P. Nawrot, C. Boucsein, V. Rodriguez-Molina, A. Aertsen, S. Grün and S. Rotter, *Serial interval statistics of spontaneous activity in cortical neurons in vivo and in vitro*, Neurocomputing, **70** (2007), 1717–1722.
- [24] J. G. Nicholls, A. R. Martin, B. G. Wallace and P. A. Fuchs, “From Neuron to Brain,” Sinauer Associates, Sunderland, 2001.
- [25] R. A. Nicoll and C. E. Jahr, *Self-excitation of olfactory bulb neurones*, Nature, **296** (1982), 441–444.
- [26] M. R. Park, J. W. Lighthall and S. T. Kitai, *Recurrent inhibition in the rat neostriatum*, Brain Res., **194** (1980), 359–369.
- [27] R. Ratnam and M. E. Nelson, *Nonrenewal statistics of electrosensory afferent spike trains: Implications for the detection of weak sensory signals*, J. Neurosci., **20** (2000), 6672–6683.
- [28] R. F. Schmidt, “Fundamentals of Neurophysiology,” Springer Study Edition, Springer, 1981.
- [29] G. Tamás, E. H. Buhl and P. Somogyi, *Massive autaptic self-innervation of GABAergic neurons in cat visual cortex*, J. Neurosci., **17** (1997), 6352–6364.
- [30] H. Van der Loos and E. M. Glaser, *Autapses in neocortex cerebri: Synapses between a pyramidal cell’s axon and its own dendrites*, Brain Res., **48** (1972), 355–360.
- [31] A. K. Vidybida, *Inhibition as binding controller at the single neuron level*, BioSystems, **48** (1998), 263–267.
- [32] A. K. Vidybida, *Output stream of a binding neuron*, Ukrainian Mathematical Journal, **59** (2007), 1819–1839.
- [33] A. K. Vidybida, *Input-output relations in binding neuron*, BioSystems, **89** (2007), 160–165.
- [34] A. K. Vidybida, *Output stream of binding neuron with instantaneous feedback*, Eur. Phys. J. B, **65** (2008), 577–584; Erratum: Eur. Phys. J. B, **69** (2009), 313.
- [35] A. K. Vidybida and K. G. Kravchuk, *Delayed feedback causes non-Markovian behavior of neuronal firing statistics*, Ukrainian Mathematical Journal, **64** (2012), 1587–1609.
- [36] A. K. Vidybida and K. G. Kravchuk, *Firing statistics of inhibitory neuron with delayed feedback. I. Output ISI probability density*, BioSystems, **112**, 3 (2013), 224–232.
- [37] Y. Wu, F. Kawasaki and R. W. Ordway, *Properties of short-term synaptic depression at larval neuromuscular synapses in wild-type and temperature-sensitive paralytic mutants of drosophila*, J. Neurophysiol., **93** (2005), 2396–2405.

Received December 14, 2012; Accepted June 24, 2013.

E-mail address: vidybida@bitp.kiev.ua

E-mail address: kgkravchuk@bitp.kiev.ua