

Delayed feedback causes non-Markovian behavior of neuronal firing statistics

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Abstract.

The instantaneous state of a neural network consists of both the degree of excitation of each neuron, the network is composed of, and positions of impulses in communication lines between neurons. In neurophysiological experiments, the neuronal firing moments are registered, but not the state of communication lines. But future spiking moments depend essentially on the past positions of impulses in the lines. This suggests, that the sequence of intervals between firing moments (interspike intervals, ISIs) in the network could be non-Markovian.

In this paper, we address this question for a simplest possible neural “net”, namely, a single neuron with delayed feedback. The neuron receives excitatory input both from the driving Poisson stream and from its own output through the feedback line. We obtain analytical expressions for conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, which gives the probability to get an output ISI of duration t_{n+1} provided the previous $(n + 1)$ output ISIs had durations t_n, \dots, t_1, t_0 . It is proven exactly, that $P(t_{n+1} | t_n, \dots, t_1, t_0)$ does not reduce to $P(t_{n+1} | t_n, \dots, t_1)$ for any $n \geq 0$. This means that the output ISIs stream cannot be represented as Markov chain of any finite order.

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1. Introduction

In a biological network, the main component parts are neurons and interneuronal communication lines – axons [1]. These same units are the main ones in most types of artificial neural networks [2]. If so, then the instantaneous dynamical state of a network must include dynamical states of all neurons and communication lines the network is composed of. The state of a 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. If it does conduct, then further information about how much time is required for the impulse to reach the end of the line (time to live) describes the line’s state.

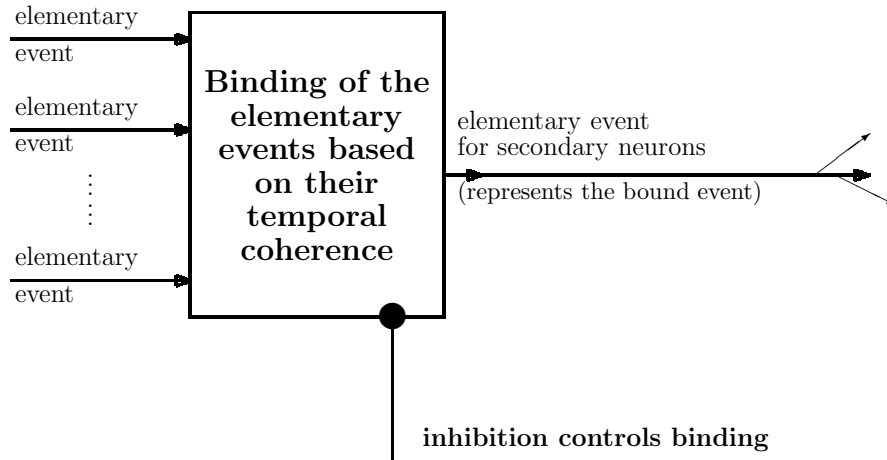


Figure 1. Signal processing in the binding neuron model [4].

In neurophysiological experiments, the triggering (spiking, firing) moments of individual neurons are registered. The sequence of intervals between the consecutive moments (interspike intervals, ISIs) is frequently considered as renewal stochastic process. Recently, based on experimental data it was offered that the ISIs sequence could be Markovian of order 4 or higher [3].

The presence of memory in the ISI sequence is not surprising, taking into account that information about triggering moments leaves unknown the states of communication lines at those moments. On the other hand, it is namely the impulses propagating in the communication lines that connect past firing moments with the future ones in a reverberating neural network. Without knowledge of communication line states, information about previous neuronal firing moments could improve our predicting ability of the next ones. The exact answer of what kind of memory could be expected in an ISI sequence of a neuron embedded in a reverberating neural network driven with some noisy stimulation requires rigorous mathematical treatment.

In this paper, we consider a simplest neural “net”, namely, a single neuron with delayed feedback, which is driven with Poisson process. As neuronal model we take binding neuron as it allows rigorous mathematical treatment. We study the ISI output stream of this system and prove that it cannot be presented as Markovian chain of any finite order. This suggests that activity of a more elaborate network, if presented in terms of neuronal firing moments, should be non-Markovian as well.

2. The object under consideration

2.1. Binding neuron model

The understanding of mechanisms of higher brain functions expects a continuous reduction from higher activities to lower ones, eventually, to activities in individual neurons, expressed in terms of membrane potentials and ionic currents. While this approach is correct scientifically and desirable for applications, the complete range of

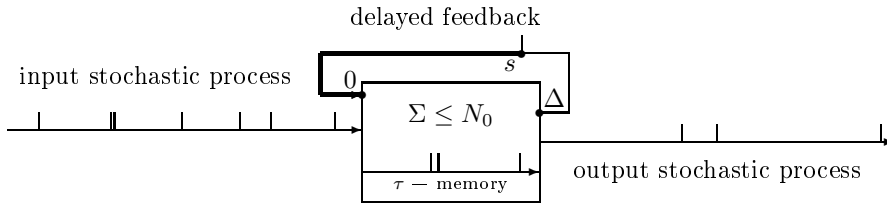


Figure 2. Binding neuron with feedback line under Poisson stimulation. Multiple input lines with Poisson streams are joined into a single one here. Δ is the delay duration in the feedback line.

the reduction is unavailable to a single researcher/engineer due to human brain limited capacity. In this connection, it would be helpful to abstract from the rules by which a neuron changes its membrane potentials to rules by which the input impulse signals are processed in the neuron. The coincidence detector, and temporal integrator are the examples of such an abstraction, see discussion in [5].

One more abstraction, the binding neuron (BN) model, is proposed as signal processing unit [6], which can operate either as coincidence detector, or temporal integrator, depending on quantitative characteristics of stimulation applied. This conforms with behavior of real neurons, see, e.g. [7]. 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 Figure 1. Mathematically, this 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 [8]. All input lines are excitatory. The neuron fires an output impulse if the number of stored impulses, Σ , is equal or higher than threshold value, N_0 . After that, BN clears its memory and is ready to receive fresh inputs. That is, every input impulse either disappears contributing to a triggering event, or is lost after spending τ units of time in the neuron's internal memory. It is clear, that BN fires when a bunch of input impulses is received in a narrow temporal interval. In this case the bunch could be considered as compound event, and the output impulse — as an abstract representation of this compound event. One could treat this mechanism as binding of individual input events into a single output event, provided the input events are coherent in time. Such interpretation is suggested by binding of features/events in largescale neuronal circuits [9, 10, 11].

Further, we expect that input stream in each input line is the 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 2.

For analytical derivation, we use BN with $N_0 = 2$. The case of higher threshold is considered numerically.

2.2. Feedback line action

In real neuronal systems, a neuron can have synaptic connection of its axonal branch at its own dendritic tree, see [12, 13] for experimental evidence. As a result, the neuron stimulates itself obtaining excitatory impulse after each firing with some propagation delay. We model this situation assuming that output impulses of BN are fed back into BN's input with delay Δ . This gives BN with delayed feedback, Figure 2. See also Supplementary Material for animation of BN with delayed feedback in action. Impulses from the feedback line have the same excitatory action on BN as those arrived from Poisson stream. Namely, each one of them is stored in BN's memory for time τ , after which it disappears completely, see section 2.1.

The feedback line either keeps one impulse, or keeps no impulses and cannot convey two or more impulses at the same time. 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 BN's input. If the line already keeps one impulse at the moment of firing, the just fired impulse ignores the line.

Any output impulse of BN with feedback line may be produced either with impulse from the line involved, or not. We assume that, just after firing and sending output impulse, the line is never empty. This assumption is selfevident for output impulses produced without impulse from the line, or if the impulse from the line was involved, but entered empty neuron. In the latter case, the second (triggering) impulse comes from the Poisson stream, neuron fires and output impulse goes out as well as enters the empty line. On the other hand, if impulse from the line triggers BN, which already keeps one impulse from the input stream, it may be questionable if the output impulse is able to enter the line, which was just filled with another impulse. We expect it does. This means that the refraction time of biological axon modelled as feedback line is equal Δ . Thus, at the beginning of any output ISI, the line keeps impulse with time to live s , where $s \in]0; \Delta]$. In this paper, we consider the case

$$\Delta < \tau \tag{1}$$

in order to keep expressions shorter.

3. Statement of the problem

The input stream of impulses, which drives neuronal activity is stochastic. Therefore, the output activity of our system requires probabilistic description in spite of the fact that both the BN and the feedback line action mechanisms are deterministic. We treat the output stream of BN with delayed feedback as the stationary process \ddagger . In order to describe its statistics, we introduce the following basic functions:

\ddagger The stationarity of the output stream results both from the stationarity of the input one and from the absence of adaptation in the BN 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.

- joint probability density $P(t_m, t_{m-1}, \dots, t_0)$ for $(m + 1)$ successive output ISI durations.
- 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 previous m ISIs had durations $t_{m-1}, t_{m-2}, \dots, t_0$, respectively.

Definition *The sequence of random variables $\{t_j\}$, taking values in Ω , is called the Markov chain of the order $n \geq 0$, 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 $n' < n$ (e.g. [14]). In the case of ISIs one reads $\Omega = \mathbb{R}^+$.

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

$$P(t_{n+1} | t_n, \dots, t_1, t_0) = P(t_{n+1} | t_n, \dots, t_1), \quad t_i \in \Omega, \quad i = 0, \dots, n + 1, \quad (2)$$

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

Theorem 1 *The output ISIs stream of BN with delayed feedback under Poisson stimulation cannot be represented as a Markov chain of any finite order.*

4. Proof outline

In order to prove the Theorem 1, we are going to show analytically, that the equality (2) does not hold for any finite value of n , namely, in the exact expression for conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, elimination of t_0 -dependence is impossible.

For this purpose we introduce the stream 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 ISI t_i starts. We consider the joint probability density $P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0)$ for realization 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.

Lemma 1 *Stream \mathbf{ts} is 1-st order markovian:*

$$\forall_{n \geq 0} \forall_{t_0 > 0} \forall_{s_0 \in [0; \Delta]} \dots \forall_{t_{n+1} > 0} \forall_{s_{n+1} \in [0; \Delta]} P(t_{n+1}, s_{n+1} | t_n, s_n; \dots; t_0, s_0) = P(t_{n+1}, s_{n+1} | t_n, s_n), \quad (3)$$

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

Proof Indeed, the value of s_{n+1} characterizes the state of the system at the moment of triggering, θ , and the value of t_{n+1} characterizes the system's behavior after that triggering, which means that, in physical time, s_{n+1} always gets its value before

than the t_{n+1} does. Once the value of s_{n+1} is known, the realization of t_{n+1} is completely determined by a unique realization of the input Poisson process after the θ .

At the same time, in $P(t_{n+1}, s_{n+1} | t_n, s_n, \dots, t_0, s_0)$ the value of s_{n+1} can be derived unambiguously from (t_n, s_n) (See Sections 2.2 and 5.2):

$$\begin{aligned} s_{n+1} &= s_n - t_n, & t_n < s_n, \\ &= \Delta, & t_n \geq s_n. \end{aligned} \quad (4)$$

Just after triggering, BN appears in the standard state (it is empty), the state of line is given by the value of s_{n+1} , and the state of input Poisson stream is always the same. Therefore, once the pair of values (t_n, s_n) is given, the state of the system at the moment of $(n+1)$ -th ISI beginning is determined completely, and knowledge of previous values of (t_i, s_i) , $i < n$ adds nothing to our predictive ability as regards the values of (t_{n+1}, s_{n+1}) , which proves (3).

In order to find the conditional probability density $P(t_{n+1} | t_n, \dots, t_1, t_0)$, the following steps should be performed:

- *Step 1.* Use property (3) for calculating joint probability of events (t, s) :

$$\begin{aligned} P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0) &= \\ &P(t_{n+1}, s_{n+1} | t_n, s_n) \dots P(t_1, s_1 | t_0, s_0) P(t_0, s_0), \end{aligned} \quad (5)$$

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 the joint probability density for successive output ISI durations as marginal probability by integration over variables s_i , $i = 0, 1, \dots, n+1$:

$$\begin{aligned} P(t_{n+1}, t_n, \dots, t_0) &= \\ &\int_0^\Delta ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_{n+1}, s_{n+1}; t_n, s_n; \dots; t_0, s_0). \end{aligned} \quad (6)$$

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

$$P(t_{n+1} | t_n, \dots, t_1, t_0) = \frac{P(t_{n+1}, t_n, \dots, t_0)}{P(t_n, \dots, t_0)}. \quad (7)$$

Taking into account Steps 1 and 2, for joint probability density $P(t_{n+1}, \dots, t_0)$ one derives

$$\begin{aligned} P(t_{n+1}, t_n, \dots, t_0) &= \\ &\int_0^\Delta ds_0 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k | t_{k-1}, s_{k-1}). \end{aligned} \quad (8)$$

In the next section, we are going to find the exact analytical expressions for probability densities $P(t, s)$ and $P(t_k, s_k | t_{k-1}, s_{k-1})$, and perform the integration in (8). Then we apply the Step 3, above, to find expressions for conditional probabilities $P(t_{n+1} | t_n, \dots, t_1, t_0)$. It appears, that the conditional probabilities have singular parts

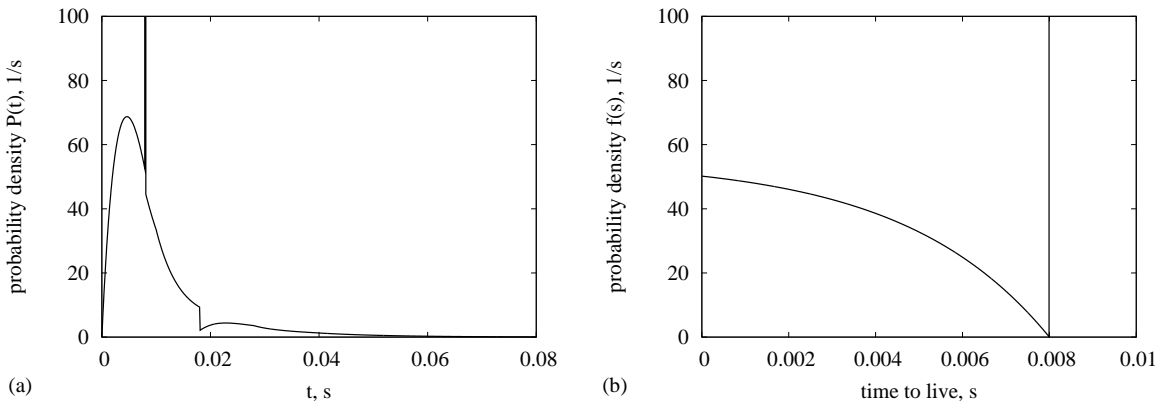


Figure 3. Output ISI probability density $P(t)$ (a) and probability density $f(s)$ for times to live of the impulse in the feedback line (b), found analytically in [15]. Here $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 150$ s $^{-1}$, $N_0=2$. The presence of δ -function in both densities is clearly visible.

of the Dirac's δ -function type. This is because the system's dynamics involves discrete events of obtaining impulse by neuron (see below). In order to prove that the equality (2) does not hold for any $n \geq 0$, we use the singular parts only.

5. Main calculations

5.1. Probability density $P(t, s)$ for events (t, s)

The probability density $P(t, s)$ can be derived as the product

$$P(t, s) = F(t | s)f(s), \quad (9)$$

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 $F(t | s)$ are given in [15, Eqs.(5),(6) and (31)]. In this paper we need only singular parts of those expressions, which read:

$$F^{\text{sing}}(t | s) = \lambda s e^{-\lambda s} \delta(t - s), \quad (10)$$

$$f^{\text{sing}}(s) = a \cdot \delta(s - \Delta), \quad \text{where} \quad a = \frac{4e^{2\lambda\Delta}}{(3 + 2\lambda\Delta)e^{2\lambda\Delta} + 1}, \quad (11)$$

where a gives the probability to obtain the impulse in the feedback line with time to live equal Δ at the beginning of an arbitrary ISI, λ — is the input Poisson stream intensity.

The presence of δ -functions in $F(t | s)$ and $f(s)$ can be explained as follows. The probability to obtain an output ISI of duration t exactly equal s is not infinitesimally small. Due to (1), it equals to the probability to obtain exactly one impulse from the Poisson stream during time interval $]0; s[$, which is $\lambda s e^{-\lambda s}$. The second impulse comes from the line and triggers the neuron exactly after time interval s . So, we have the

non-zero probability to obtain an output ISI of duration exactly equal to s . This gives the δ -function at $t = s$ in the probability density $F(t | s)$.

The probability to have time to live, s , exactly equal Δ at the moment of an output ISI beginning is not infinitesimally small as well. 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 $t \geq s$ for the previous ISI. The set of realizations of the input Poisson process, each realization results in $t \geq s$, has non-zero probability a , see (11), and this gives the δ -function at $s = \Delta$ in the probability density $f(s)$.

The output ISI probability density $P(t)$ can be obtained as the result of integration of (9) (see [15] for details):

$$P(t) = \int_0^\Delta F(t|s)f(s)ds. \quad (12)$$

Examples of $P(t)$ and $f(s)$ graphs are given in Figure 3.

5.2. 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 (t_{k-1}, s_{k-1}) . By definition of conditional probabilities, the probability density wanted can be represented as the following product

$$P(t_k, s_k | t_{k-1}, s_{k-1}) = F(t_k | s_k, t_{k-1}, s_{k-1})f(s_k | t_{k-1}, s_{k-1}), \quad (13)$$

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 lifetime of impulse in the feedback line equal to s_k , and ii) previous (t, s) -event was (t_{k-1}, s_{k-1}) ; $f(s_k | t_{k-1}, s_{k-1})$ denotes conditional probability density for times to live of the impulse in the feedback line under condition ii). It is obvious, that

$$F(t_k | s_k, t_{k-1}, s_{k-1}) = F(t_k | s_k), \quad (14)$$

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 proof of Lemma 1).

In order to find the probability density $f(s_k | t_{k-1}, s_{k-1})$, let us consider different 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 ISI t_k , an output spike will enter the line and will have time to live equal $s_k = \Delta$ with probability 1. Therefore, the probability density contains the corresponding delta-function:

$$f(s_k | t_{k-1}, s_{k-1}) = \delta(s_k - \Delta), \quad t_{k-1} \geq s_{k-1}. \quad (15)$$

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 accurately equal to $s_k = s_{k-1} - t_{k-1}$, so

$$f(s_k | t_{k-1}, s_{k-1}) = \delta(s_k - s_{k-1} + t_{k-1}), \quad t_{k-1} < s_{k-1}. \quad (16)$$

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

$$\begin{aligned} P(t_k, s_k | t_{k-1}, s_{k-1}) &= F(t_k | s_k) \delta(s_k - \Delta), & t_{k-1} \geq s_{k-1}, \\ &= F(t_k | s_k) \delta(s_k - s_{k-1} + t_{k-1}), & t_{k-1} < s_{k-1}, \end{aligned} \quad (17)$$

where exact expression for $F(t | s)$ is given in [15, Eqs.(5),(6)].

5.3. Joint probability density $P(t_{n+1}, \dots, t_0)$

In this section, we are going to find the exact analytical expression for the joint probability density $P(t_{n+1}, \dots, t_0)$ at the domain

$$D_1 = \left\{ (t_0, \dots, t_n) \mid \sum_{i=0}^n t_i < \Delta \right\}. \quad (18)$$

It is worth to notice, that the set of $(n+1)$ successive ISI durations t_0, \dots, t_n has non-zero probability, $p_\Delta > 0$, to fall into the domain (18). Indeed, BN with threshold $N_0 = 2$ needs $2(n+1)$ input impulses within time window $]0; \Delta[$ to be triggered $(n+1)$ times within this window (condition (1) ensures that no input impulse is lost). BN receives impulses both from the Poisson stream and from the line. But no more than one impulse from the line may have time to reach BN's input during time interval less than Δ . Therefore, the other $(2n+1)$ impulses must be received from the Poisson stream. On the other hand, if $2(n+1)$ input impulses are received from the Poisson stream during time interval $]0; \Delta[$, the inequality (18) holds for sure, no matter is the impulse from the feedback line involved, or not. Therefore, $p_\Delta > p(2n+2, \Delta) > 0$, where $p(i, \Delta)$ gives the probability to obtain i impulses from the Poisson stream during time interval Δ [16]: $p(i, \Delta) = e^{-\lambda\Delta} (\lambda\Delta)^i / i!$.

Having in mind (18), let us split the integration domain for s_0 in (8) in the following way:

$$\int_0^\Delta ds_0 = \int_0^{t_0} ds_0 + \sum_{i=1}^n \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} ds_0 + \int_{\sum_{j=0}^n t_j}^\Delta ds_0,$$

and introduce the notations:

$$I_i = \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k | t_{k-1}, s_{k-1}), \quad i = 0, 1, 2, \dots, n, \quad (19)$$

$$I_{n+1} = \int_{\sum_{j=0}^n t_j}^\Delta ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} P(t_0, s_0) \prod_{k=1}^{n+1} P(t_k, s_k | t_{k-1}, s_{k-1}), \quad (20)$$

where we assume, that $\sum_{j=j_1}^{j_2} = 0$ for $j_1 > j_2$.

Consider the fixed sequence of ISIs, (t_0, \dots, t_n) , which belongs to D_1 . Domain of s_0 values covered by I_i , $i = 0, \dots, n$, corresponds to the scenario, when impulse, which was in the feedback line at the beginning of interval t_0 (with time to live s_0), will reach BN during interval t_i . In this process, after each firing, which starts ISI t_k , $k \leq i$, the time to live of the impulse in the feedback line is decreased exactly by t_{k-1} . This means, that variables of integration $\{s_0, \dots, s_{n+1}\}$, above, are not actually independent, but must satisfy the following relations:

$$s_k = s_0 - \sum_{j=0}^{k-1} t_j, \quad k = 1, \dots, i, \quad (21)$$

which are ensured by δ -function in the bottom line of (17). Next to s_i time to live must be equal Δ :

$$s_{i+1} = \Delta, \quad (22)$$

and this is ensured by δ -function in the top line of (17). The next to s_{i+1} times to live again are decreased by corresponding ISI with each triggering. Due to (18), this brings about another set of relations:

$$s_k = \Delta - \sum_{j=i+1}^{k-1} t_j, \quad k = i+2, \dots, n+1, \quad (23)$$

which are again ensured by δ -function in the bottom line of (17). Relations (21), (22) and (23) together with limits of integration over s_0 in (19) ensure that at D_1 the following inequalities hold:

$$\begin{aligned} s_k &> t_k, & k = 0, \dots, i-1, \\ s_i &\leq t_i, \\ s_k &> t_k, & k = i+1, \dots, n. \end{aligned} \quad (24)$$

Inequalities (24) allow one to decide correctly which part of rhs of (17) should replace each transition probability $P(t_k, s_k \mid t_{k-1}, s_{k-1})$ in (19), and perform all but one integration. This gives:

$$\begin{aligned} I_i &= \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} ds_0 \int_0^\Delta ds_1 \dots \int_0^\Delta ds_{n+1} F(t_0 \mid s_0) f(s_0) \prod_{k=1}^i F(t_k \mid s_k) \delta(s_k - s_0 + \sum_{j=0}^{k-1} t_j) \\ &\times F(t_{i+1} \mid s_{i+1}) \delta(s_{i+1} - \Delta) \prod_{k=i+2}^{n+1} F(t_k \mid s_k) \delta(s_k - \Delta + \sum_{j=i+1}^{k-1} t_j) \\ &= F(t_{n+1} \mid \Delta - \sum_{j=i+1}^n t_j) F(t_n \mid \Delta - \sum_{j=i+1}^{n-1} t_j) \dots F(t_{i+2} \mid \Delta - t_{i+1}) F(t_{i+1} \mid \Delta) \end{aligned}$$

$$\times \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} F(t_i | s_0 - \sum_{j=0}^{i-1} t_j) F(t_{i-1} | s_0 - \sum_{j=0}^{i-2} t_j) \cdots F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0,$$

$$i = 0, 1, 2, \dots, n. \quad (25)$$

The last expression might be obtained as well by means of consecutive substitution of either top, or bottom line of (17) into (19), without previously discovering (21) – (24).

Finally, integral I_{n+1} corresponds to the case, when at the beginning of interval t_{n+1} , the line still keeps the same impulse as at the beginning of t_0 . Therefore, I_{n+1} comprises the rest of scenarios contributing to the value of $P(t_{n+1}, \dots, t_0)$ in (6). Here, the bottom line of (17) ensures that values of variables of integration $\{s_0, \dots, s_{n+1}\}$, which contribute to the I_{n+1} , should satisfy the following relations:

$$s_k = s_0 - \sum_{j=0}^{k-1} t_j, \quad k = 1, \dots, n+1, \quad (26)$$

which taken at the domain D_1 , defined in (18), results in inequalities

$$s_k > t_k, \quad k = 0, \dots, n. \quad (27)$$

Equations (17) and (27) allow one to perform integration in (20) and to obtain:

$$\begin{aligned} I_{n+1} &= \int_{\sum_{j=0}^n t_j}^{\Delta} ds_0 \int_0^{\Delta} ds_1 \cdots \int_0^{\Delta} ds_{n+1} F(t_0 | s_0) f(s_0) \prod_{k=1}^{n+1} F(t_k | s_k) \delta(s_k - s_0 + \sum_{j=0}^{k-1} t_j) \\ &= \int_{\sum_{j=0}^n t_j}^{\Delta} F(t_{n+1} | s_0 - \sum_{j=0}^n t_j) F(t_n | s_0 - \sum_{j=0}^{n-1} t_j) \cdots F(t_1 | s_0 - t_0) \\ &\quad \times F(t_0 | s_0) f(s_0) ds_0. \end{aligned} \quad (28)$$

Taking into account (25) and (28), one obtains the following expression for joint probability density $P(t_{n+1}, \dots, t_0)$:

$$\begin{aligned} P(t_{n+1}, \dots, t_0) &= \sum_{i=0}^{n+1} I_i \\ &= \sum_{i=0}^n F(t_{i+1} | \Delta) \prod_{k=i+2}^{n+1} F(t_k | \Delta - \sum_{j=i+1}^{k-1} t_j) \\ &\quad \times \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} F(t_0 | s_0) f(s_0) \prod_{k=1}^i F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) ds_0 \\ &\quad + \int_{\sum_{j=0}^n t_j}^{\Delta} F(t_0 | s_0) f(s_0) \prod_{k=1}^{n+1} F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) ds_0, \quad \sum_{i=0}^n t_i < \Delta, \end{aligned} \quad (29)$$

where we assume, that $\sum_{j=j_1}^{j_2} = 0$ and $\prod_{j=j_1}^{j_2} = 1$ for $j_1 > j_2$.

Using (7), for conditional probability density $P(t_{n+1} | t_n, \dots, t_0)$ one derives:

$$\begin{aligned}
P(t_{n+1} | t_n, \dots, t_0) &= \frac{1}{P(t_n, \dots, t_0)} \cdot \left(\sum_{i=0}^n F(t_{i+1} | \Delta) \prod_{k=i+2}^{n+1} F(t_k | \Delta - \sum_{j=i+1}^{k-1} t_j) \times \right. \\
&\times \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} F(t_0 | s_0) f(s_0) \prod_{k=1}^i F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) ds_0 \\
&+ \left. \int_{\sum_{j=0}^n t_j}^{\Delta} F(t_0 | s_0) f(s_0) \prod_{k=1}^{n+1} F(t_k | s_0 - \sum_{j=0}^{k-1} t_j) ds_0 \right), \\
&\sum_{i=0}^n t_i < \Delta, \quad (30)
\end{aligned}$$

where expression for $P(t_n, \dots, t_0)$ can be obtained from (29) with $(n-1)$ substituted instead of n .

5.4. Singular part of $P(t_{n+1}, \dots, t_0)$

In order to obtain the singular part of expression, defined in (29), let us first derive singular parts for all I_i , $i = 0, \dots, n$ and I_{n+1} separately. In order to keep the expressions shorter, we represent I_i as follows

$$I_i(t_0, \dots, t_{n+1}) = X_i(t_0, \dots, t_i) \cdot Y_i(t_{i+1}, \dots, t_{n+1}), \quad i = 0, 1, \dots, n, \quad (31)$$

where

$$X_i \equiv \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} F(t_i | s_0 - \sum_{j=0}^{i-1} t_j) F(t_{i-1} | s_0 - \sum_{j=0}^{i-2} t_j) \dots F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0, \quad (32)$$

$$Y_i \equiv F(t_{n+1} | \Delta - \sum_{j=i+1}^n t_j) F(t_n | \Delta - \sum_{j=i+1}^{n-1} t_j) \dots F(t_{i+2} | \Delta - t_{i+1}) F(t_{i+1} | \Delta). \quad (33)$$

It is clear, that at D_1 , X_i is the part of the probability density for $(i+1)$ successive ISI durations, which corresponds to the case when the impulse, which was in the line at the beginning of the first ISI, reaches the neuron's input within the last one. And the Y_i gives the probability density for $(n+1-i)$ successive ISI durations provided the impulse enters the line just at the beginning of the first one of these ISIs.

At the domain considered, namely, for $\sum_{i=0}^n t_i < \Delta$, the expressions for $F(t_n | \Delta - \sum_{j=i+1}^{n-1} t_j)$, \dots , $F(t_{i+2} | \Delta - t_{i+1})$ and $F(t_{i+1} | \Delta)$ have no singularities, see (10). Therefore

$$Y_i^{\text{sing}} = F^{\text{sing}}(t_{n+1} | \Delta - \sum_{j=i+1}^n t_j) F^{\text{sing}}(t_n | \Delta - \sum_{j=i+1}^{n-1} t_j) \dots F^{\text{sing}}(t_{i+2} | \Delta - t_{i+1}) F^{\text{sing}}(t_{i+1} | \Delta). \quad (34)$$

At the same time, intergration limits in (32) ensure that $X_i^{\text{sing}} = 0$. Indeed, each integral X_i (and, originally, I_i), $i = 0, 1, \dots, n$, covers the half-open interval $s_0 \in$

$]\sum_{j=0}^{i-1} t_j; \sum_{j=0}^i t_j]$. The only singularity of integrand in (32) at this domain is $\delta(\sum_{j=0}^i t_j - s_0)$ provided by $F(t_i | s_0 - \sum_{j=0}^{i-1} t_j)$, see (10), and it disappears after intergration. Therefore

$$\begin{aligned} I_i^{\text{sing}} &= F^{\text{sing}}(t_{n+1} | \Delta - \sum_{j=i+1}^n t_j) F(t_n | \Delta - \sum_{j=i+1}^{n-1} t_j) \dots F(t_{i+2} | \Delta - t_{i+1}) F(t_{i+1} | \Delta) \\ &\times \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} F(t_i | s_0 - \sum_{j=0}^{i-1} t_j) F(t_{i-1} | s_0 - \sum_{j=0}^{i-2} t_j) \dots F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0, \\ & \quad i = 0, 1, \dots, n. \end{aligned} \quad (35)$$

In the same way, for the singular part of integral I_{n+1} one obtains

$$I_{n+1}^{\text{sing}} = a \cdot F^{\text{sing}}(t_{n+1} | \Delta - \sum_{j=0}^n t_j) F(t_n | \Delta - \sum_{j=0}^{n-1} t_j) \dots F(t_1 | \Delta - t_0) F(t_0 | \Delta), \quad (36)$$

where a is the δ -function's mass in $f(s)$, see (11).

Taking into account (10), (35) and (36), for the singular part of the probability density $P(t_{n+1}, \dots, t_0)$ one obtains

$$\begin{aligned} P^{\text{sing}}(t_{n+1}, t_n, \dots, t_0) &= \sum_{i=0}^{n+1} I_i^{\text{sing}} \\ &= \sum_{i=0}^n A_i \cdot \delta\left(\sum_{j=i+1}^{n+1} t_j - \Delta\right) + A_{n+1} \cdot \delta(t_{n+1} + \dots + t_0 - \Delta), \\ & \quad \sum_{i=0}^n t_i < \Delta, \end{aligned} \quad (37)$$

where A_i and A_{n+1} denote regular factors, defined by the following expressions:

$$\begin{aligned} A_i &= \lambda t_{n+1} e^{-\lambda t_{n+1}} \cdot F(t_n | \Delta - \sum_{j=i+1}^{n-1} t_j) \dots F(t_{i+2} | \Delta - t_{i+1}) F(t_{i+1} | \Delta) \\ &\times \int_{\sum_{j=0}^{i-1} t_j}^{\sum_{j=0}^i t_j} F(t_i | s_0 - \sum_{j=0}^{i-1} t_j) F(t_{i-1} | s_0 - \sum_{j=0}^{i-2} t_j) \dots F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0, \\ & \quad i = 0, 1, \dots, n, \end{aligned} \quad (38)$$

$$A_{n+1} = a \cdot \lambda t_{n+1} e^{-\lambda t_{n+1}} \cdot F(t_n | \Delta - \sum_{j=0}^{n-1} t_j) \dots F(t_1 | \Delta - t_0) F(t_0 | \Delta). \quad (39)$$

Obviously, each factor A_i , $i = 0, \dots, n$, gives the probability to obtain $(n + 1 - i)$ successive output ISIs of overall duration exactly equal Δ . And A_{n+1} gives the probability to obtain $(n + 2)$ successive output ISIs of overall duration exactly equal Δ .

The presence of δ -functions in joint probability density $P(t_{n+1}, \dots, t_0)$ can be additionally explained as follows. If at the beginning of $(i + 1)$ -th ISI, the impulse enters the line, then output interval t_{n+1} will start with that same impulse in the feedback line with time to live equal $s_{n+1} = \Delta - \sum_{j=i+1}^n t_j$. To trigger BN after time exactly equal

s_{n+1} after that, it is necessary to obtain one impulse from the Poisson stream during time interval s_{n+1} . This event has non-zero probability, therefore we have the non-zero probability of an output ISI exactly equal to s_{n+1} : $t_{n+1} = \Delta - \sum_{j=i+1}^n t_j$. This gives the corresponding δ -functions in ISI probability density. The term with $\delta(t_{n+1} + \dots + t_0 - \Delta)$ corresponds to the case, when the impulse enters the line at the beginning of t_0 .

From (7) and (37) one can easily derive the following expression for the conditional probability density:

$$\begin{aligned}
 P^{\text{sing}}(t_{n+1} | t_n, \dots, t_0) &= \frac{1}{P(t_n, \dots, t_0)} \sum_{i=0}^n A_i \cdot \delta\left(\sum_{j=i+1}^{n+1} t_j - \Delta\right) \\
 &+ \frac{A_{n+1}}{P(t_n, \dots, t_0)} \cdot \delta(t_{n+1} + \dots + t_0 - \Delta), \quad \sum_{i=0}^n t_i < \Delta, \quad (40)
 \end{aligned}$$

where A_i and A_{n+1} are defined in (38) and (39). It should be outlined, that joint probability density $P(t_n, \dots, t_0)$ has no singularities at the domain $t_n < \Delta - \sum_{i=0}^{n-1} t_i$, see (37) with $(n-1)$ substituted instead of n .

As one can see, function $P(t_{n+1} | t_n, \dots, t_0)$ contains singularity at $t_{n+1} = \Delta - t_n - t_{n-1} - \dots - t_0$. The dependence of the singular part of function $P(t_{n+1} | t_n, \dots, t_0)$ on t_0 cannot be compensated by any regular summands, therefore, the whole conditional probability density $P(t_{n+1} | t_n, \dots, t_0)$ depends on t_0 . It means, that the condition (2) does not hold for any n for the output stream of BN with delayed feedback. The Theorem 1 is proven.

6. Particular cases

In previous section, we have proven the impossibility to represent the stream of output ISI durations for BN with delayed feedback as a Markov chain of any finite order. In particular, output ISI stream is neither a sequence of independent random variables, and therefore is non-renewal, nor it is the first-order Markovian process.

In the course of proving Theorem 1 (see Sections 4 and 5), we have obtained the expression for $P(t_{n+1} | t_n, \dots, t_0)$ at the domain $\sum_{i=0}^n t_i < \Delta$ in general case of an arbitrary n , see (30).

In this section, we consider the two particular cases of $P(t_{n+1} | t_n, \dots, t_0)$ when $n=0$ and $n=1$, namely, the single-moment conditional probability density $P(t_1 | t_0)$ and the double-moment conditional probability density $P(t_2 | t_1, t_0)$ and obtain the expressions for $P(t_1 | t_0)$ and $P(t_2 | t_1, t_0)$ for domain (18), as well as for all other possible domains, which were omitted in general consideration.

6.1. Conditional probability density $P(t_1 | t_0)$

In order to derive the exact expression for conditional probability density $P(t_1 | t_0)$ for neighbouring ISI durations, we take Steps 1–3, outlined in Section 4, for $n=0$. In the case of $P(t_1 | t_0)$, there are only three domains, on which the expressions should be

obtained separately, namely cases $t_0 < \Delta$, $t_0 > \Delta$ and $t_0 = \Delta$. Performing intergration in (8), one obtains the following expressions for $P(t_1, t_0)$ at these domains:

$$P(t_1, t_0) = F(t_1 | \Delta)P(t_0), \quad t_0 \geq \Delta, \quad (41)$$

$$\begin{aligned} &= F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0)f(s_0)ds_0 \\ &+ \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0)F(t_0 | s_0)f(s_0)ds_0, \quad t_0 < \Delta. \end{aligned} \quad (42)$$

Then, by definition of conditional probability densities, one obtains:

$$P(t_1 | t_0) = F(t_1 | \Delta), \quad t_0 > \Delta, \quad (43)$$

$$\begin{aligned} &= \frac{1}{P(t_0)} \left(F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0)f(s_0)ds_0 \right. \\ &\left. + \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0)F(t_0 | s_0)f(s_0)ds_0 \right), \quad t_0 < \Delta. \end{aligned} \quad (44)$$

It should be outlined, that the output ISI probability density $P(t_0)$ has no singularities at the domain $t_0 < \Delta$. Indeed, due to (10)–(12), the only δ -function contained in $P(t_0)$ is placed at $t_0 = \Delta$, see Figure 3 (a).

In vicinity of the point $t_0 = \Delta$, the single-moment conditional probability density can be derived as

$$P(t_1 | t_0 = \Delta) = \lim_{\epsilon \rightarrow 0} \frac{\int_{\Delta-\epsilon}^{\Delta+\epsilon} dt_0 P(t_1, t_0)}{\int_{\Delta-\epsilon}^{\Delta+\epsilon} dt_0 P(t_0)}, \quad (45)$$

which just gives δ -functions' masses both in numerator and denominator, and delivers

$$P(t_1 | t_0) = F(t_1 | \Delta), \quad t_0 = \Delta. \quad (46)$$

Expressions (43), (44) and (46) can be understood as follows. Since $t_0 \geq \Delta$, one can be sure that the line has time to get free from impulse during t_0 , therefore at the moment of next firing (at the beginning of t_1) the impulse enters the line and has time to live equal Δ . In the case of $t_0 < \Delta$, see (44), two possibilities arise. The first term corresponds to the scenario, when the feedback line discharges conveyed impulse within time interval t_0 , and the second one represents the case when at the beginning of t_1 the line still keeps the same impulse as at the beginning of t_0 .

It can be shown, that the following normalization conditions take place:

$$\int_0^{\infty} dt_1 P(t_1 | t_0) = 1, \text{ and } \int_0^{\infty} dt_0 P(t_1, t_0) = P(t_1).$$

The singular part of $P(t_1 | t_0)$ can be easily extracted:

$$P^{\text{sing}}(t_1 | t_0) = e^{-\lambda \Delta} \lambda \Delta \cdot \delta(t_1 - \Delta), \quad t_0 \geq \Delta, \quad (47)$$

$$\begin{aligned} &= \frac{\lambda t_1 e^{-\lambda t_1}}{P(t_0)} \left(\int_0^{t_0} F(t_0 | s_0)f(s_0)ds_0 \cdot \delta(t_1 - \Delta) + \right. \\ &\left. + a F(t_0 | \Delta) \cdot \delta(t_0 + t_1 - \Delta) \right), \quad t_0 < \Delta. \end{aligned} \quad (48)$$

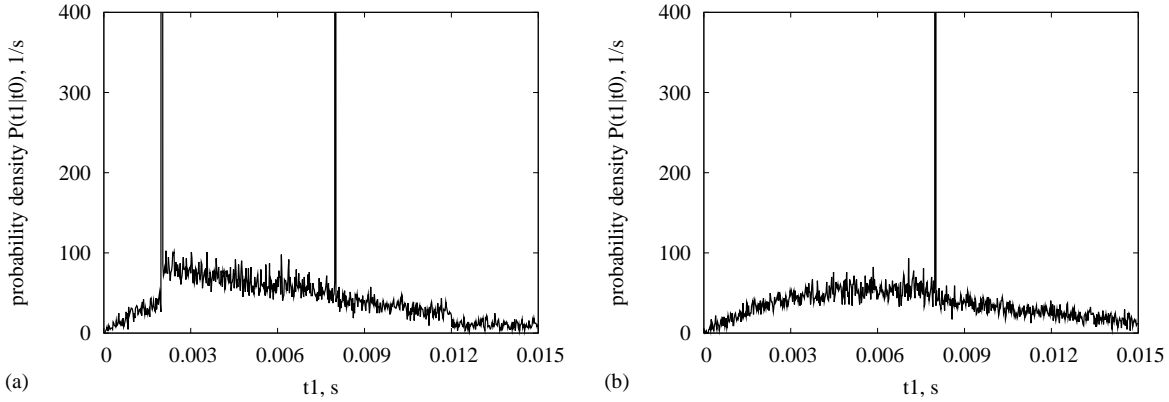


Figure 4. Conditional probability density $P(t_1 | t_0)$ for $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 150$ s $^{-1}$, $N_0 = 2$, $t_0 = 6$ ms (a) and $t_0 = 11$ ms (b), found numerically by means of Monte-Carlo method (the number of firings accounted $N = 30\,000$).

Obviously, expression (48) could be obtained directly from (38)–(40) by substituting $n = 0$.

As it can be seen from (47) and (48), the number of δ -functions in $P(t_1 | t_0)$ and their positions depend on t_0 , therefore the conditional probability density $P(t_1 | t_0)$ cannot be reduced to output ISI probability density $P(t_1)$. Therefore, the neighbouring output ISIs of BN with delayed feedback are correlated, as expected.

Examples of $P(t_1 | t_0)$, found for two domains numerically, by means of Monte-Carlo method (see Section 7 for details), are placed at Figure 4.

6.2. Conditional probability density $P(t_2 | t_1, t_0)$

In order to derive the exact expression for conditional probability density $P(t_2 | t_1, t_0)$ for the successive ISI durations, we take Steps 1–3, outlined in Section 4, for $n = 1$. In the case of $P(t_2, t_1, t_0)$, there are six domains, on which the expressions should be obtained separately, namely, the domain

$$D_1 = \{t_1, t_0 \mid t_1 + t_0 < \Delta\},$$

which was already utilized in Section 5, and five remaining:

$$D_2 = \{t_1, t_0 \mid t_0 \geq \Delta \quad \text{and} \quad t_1 \geq \Delta\},$$

$$D_3 = \{t_1, t_0 \mid t_0 < \Delta \quad \text{and} \quad t_1 \geq \Delta\},$$

$$D_4 = \{t_1, t_0 \mid t_0 \geq \Delta \quad \text{and} \quad t_1 < \Delta\},$$

$$D_5 = \{t_1, t_0 \mid t_0 < \Delta \quad \text{and} \quad \Delta - t_0 < t_1 < \Delta\},$$

$$d = \{t_1, t_0 \mid t_0 + t_1 = \Delta\}.$$

In the case, when the exact equality $t_0 + t_1 = \Delta$ holds, namely, if $(t_1, t_0) \in d$, the product $P(t_2 | t_1, t_0)dt_2$ gives the probability to obtain an output ISI of duration within interval $[t_2; t_2 + dt_2[$, provided the overall duration of two previous ISIs accurately equals Δ .

Expressions for $P(t_2 | t_1, t_0)$ can be found exactly on each domain:

$$P(t_2 | t_1, t_0) = F(t_2 | \Delta), \quad (t_0, t_1) \in D_2, \quad (49)$$

$$= F(t_2 | \Delta), \quad (t_0, t_1) \in D_3, \quad (50)$$

$$= F(t_2 | \Delta), \quad (t_0, t_1) \in d, \quad (51)$$

$$= F(t_2 | \Delta - t_1), \quad (t_0, t_1) \in D_4, \quad (52)$$

$$\begin{aligned} &= \frac{1}{P(t_1, t_0)} \left(F(t_2 | \Delta - t_1) F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 \right. \\ &\quad \left. + F(t_2 | \Delta) \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0 \right), \quad (t_0, t_1) \in D_5, \quad (53) \end{aligned}$$

$$\begin{aligned} &= \frac{1}{P(t_1, t_0)} \left(F(t_2 | \Delta - t_1) F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 \right. \\ &\quad \left. + F(t_2 | \Delta) \int_{t_0}^{t_0+t_1} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0 \right. \\ &\quad \left. + \int_{t_0+t_1}^{\Delta} F(t_2 | s_0 - t_0 - t_1) F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0 \right), \\ &\quad (t_0, t_1) \in D_1. \quad (54) \end{aligned}$$

where $P(t_1, t_0) = F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 + \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0$, according to (44).

The probability density $P(t_1, t_0)$ contains δ -function at the domain d , see (48). In (51), the two-time conditional probability density was derived as

$$P(t_2 | t_1, t_0) = \lim_{\epsilon \rightarrow 0} \frac{\int_{\Delta-t_0-\epsilon}^{\Delta-t_0+\epsilon} dt_1 P(t_2, t_1, t_0)}{\int_{\Delta-t_0-\epsilon}^{\Delta-t_0+\epsilon} dt_1 P(t_1, t_0)}, \quad (t_0, t_1) \in d,$$

compare with (45).

It is worth to notice, that $P(t_1, t_0)$ is regular function on both D_1 and D_5 , see (53) and (54). Indeed, from (47) and (48) one can see, that $P(t_1, t_0)$ may include singularities only at the points $t_1 = \Delta$ and $t_1 = \Delta - t_0$. None of these points belongs to D_1 , or D_5 .

It can be shown, that the following normalization conditions take place:

$$\int_0^{\infty} dt_2 P(t_2 | t_1, t_0) = 1, \quad \text{and} \quad \int_0^{\infty} dt_0 P(t_2, t_1, t_0) = P(t_2, t_1).$$

The singular part of the conditional probability density $P(t_2 | t_1, t_0)$ can be derived as follows:

$$P^{\text{sing}}(t_2 | t_1, t_0) = e^{-\lambda t_2} \lambda t_2 \cdot \delta(t_2 - \Delta), \quad (t_0, t_1) \in D_2 \cup D_3 \cup d, \quad (55)$$

$$= e^{-\lambda t_2} \lambda t_2 \cdot \delta(t_1 + t_2 - \Delta), \quad (t_0, t_1) \in D_4. \quad (56)$$

$$\begin{aligned} &= \frac{e^{-\lambda t_2} \lambda t_2}{P(t_1, t_0)} \cdot \left(F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 \cdot \delta(t_1 + t_2 - \Delta) \right. \\ &\quad \left. + \int_{t_0}^{\Delta} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0 \cdot \delta(t_2 - \Delta) \right) \end{aligned}$$

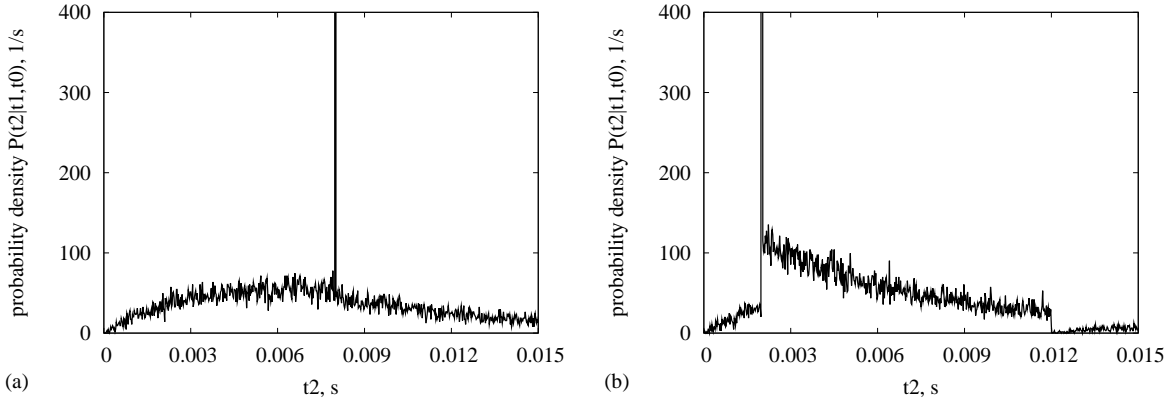


Figure 5. Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 150$ s $^{-1}$, $N_0 = 2$, $t_1 = 13$ ms, $t_0 = 13$ ms (a) and $t_1 = 6$ ms, $t_0 = 13$ ms (b), found numerically by means of Monte-Carlo method ($N = 30\,000$).

$$\begin{aligned}
 & (t_0, t_1) \in D_5, \tag{57} \\
 & = \frac{e^{-\lambda t_2} \lambda t_2}{P(t_1, t_0)} \left(\int_{t_0}^{t_0+t_1} F(t_1 | s_0 - t_0) F(t_0 | s_0) f(s_0) ds_0 \cdot \delta(t_2 - \Delta) \right. \\
 & + F(t_1 | \Delta) \int_0^{t_0} F(t_0 | s_0) f(s_0) ds_0 \cdot \delta(t_1 + t_2 - \Delta) \\
 & \left. + a \cdot F(t_1 | \Delta - t_0) F(t_0 | \Delta) \cdot \delta(t_0 + t_1 + t_2 - \Delta) \right), \\
 & (t_0, t_1) \in D_1. \tag{58}
 \end{aligned}$$

Obviously, expression (58) could be obtained directly from (38)–(40) by substituting $n = 1$.

As one can see, the singular part of $P(t_2 | t_1, t_0)$ depends on t_0 , therefore $P(t_2 | t_1, t_0)$ cannot be reduced to $P(t_2 | t_1)$, which means that the output stream is not first-order Markovian.

Examples of $P(t_2 | t_1, t_0)$, found numerically for different domains, are placed at Figures 5 and 6.

7. Numerical simulation

In order to check the correctness of obtained analytical expressions, and also to investigate whether the output ISIs stream is non-Markovian for BN with higher thresholds as well as for $N_0 = 2$, numerical simulations were performed. A C++ program, containing class, which models the operation manner of BN 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 Library§ with the Mersenne Twister generator as source of pseudorandom numbers.

§ <http://www.gnu.org/software/gsl/>

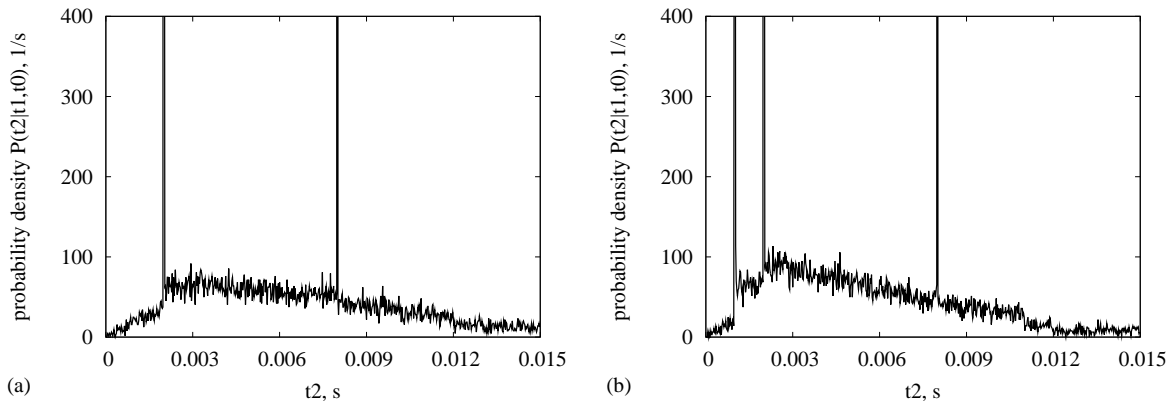


Figure 6. Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 150$ s $^{-1}$, $N_0 = 2$, $t_1=6$ ms, $t_0=3$ ms (a) and $t_1 = 6$ ms, $t_0 = 1$ ms (b), found numerically by means of Monte-Carlo method ($N = 30\,000$).

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 discrete events are accounted. It allows one to make exact calculations faster as compared to the algorithm where time advances gradually by adding small timesteps.

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 4 – 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 quantity, the position and the mass of delta-functions, obtained in numerical experiments for BN with threshold 2, coincide with those predicted analytically in (47), (48) and (55) – (58).

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 quantity and position of delta-functions coincide with those obtained for BN with threshold 2, as expected, compare Figures 7 and 6.

8. Conclusions and discussion

Our results reveal the influence of the delayed feedback presence on the neuronal firing statistics. In contrast to the cases of BN without feedback [17] and BN with instantaneous feedback [18], the neighbouring output ISIs of BN with delayed feedback are mutually correlated. It means that even in the simplest possible recurrent network the ISI stream cannot be treated as the renewal one. The presence of nearest ISIs correlation was reported for spike trains of a neurons in different CNS and peripheral NS structures [19, 20].

Moreover, we prove, that the output ISI stream of BN with delayed feedback cannot

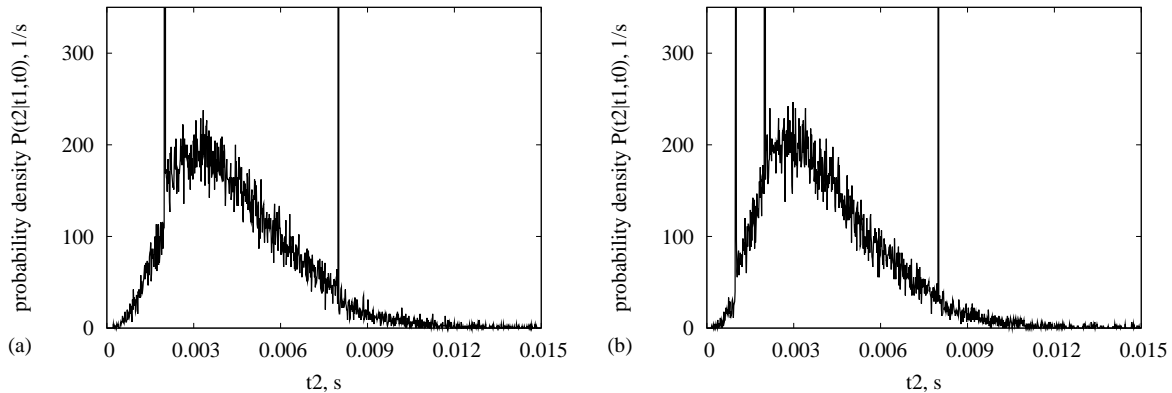


Figure 7. Conditional probability density $P(t_2 | t_1, t_0)$ for $\tau = 10$ ms, $\Delta = 8$ ms, $\lambda = 800$ s $^{-1}$, $N_0 = 4$, $t_1 = 6$ ms, $t_0 = 3$ ms (a) and $t_1 = 6$ ms, $t_0 = 1$ ms (b), found numerically by means of Monte-Carlo method ($N = 30\,000$).

be represented as the Markov chain of any finite order. This is in accordance with rare attempts of experimental estimation of the Markov order of neuronal spike trains (see, e.g. [3], where it is established that the order, if any, must be greater than 3).

We expect the same non-markovian property for firing statistics of any single neuron with delayed feedback, whatever neuronal model is used, and conclude that it is namely the delayed feedback presence results in non-markovian statistics found. One should take this fact into account during analysis of neuronal spike trains obtained from any recurrent network.

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