Firing statistics of a neuron with delayed feedback inhibition stimulated with a renewal process

O. Shchur\textsuperscript{1} and A. Vidybida\textsuperscript{2}

\textsuperscript{1,2}Bogolyubov Institute for Theoretical Physics of the National Academy of Sciences of Ukraine, Kyiv, Ukraine
\textsuperscript{1}olha.shchur@bitp.kiev.ua
\textsuperscript{2}vidybida@bitp.kiev.ua, vidybida.kiev.ua

October 22, 2021

Abstract

In this paper, we study the impact of an inhibitory autapse on neuronal activity. In order to do this, we consider a class of spiking neuron models with delayed feedback inhibition stimulated with a series of excitatory impulses, representing a stochastic point renewal process. We calculate exactly the probability density function (PDF) \( p(t) \) for the distribution of output interspike intervals (ISIs). The calculation is based on the known PDF of ISIs \( p^0(t) \) for the same neuron without feedback and the PDF of ISIs for the input stream \( p^\text{in}(t) \). Obtained results are applied to the case of a neuron with threshold 2 when the time intervals between input impulses are distributed according to the Erlang-2 distribution. Further, for the binding neuron model with threshold 2 with delayed feedback inhibition stimulated with the Erlang-2 stream of excitatory impulses, the first two moments of the ISI PDF are computed. Our results indicate that depending on the time delay of the feedback inhibition, the spike regularity can lower or rise in comparison with the case of the neuron without delayed feedback inhibition.

Keywords: spiking neuron, delayed feedback inhibition, interspike interval, probability density function, coefficient of variation, spike regularity, renewal process, autapse.

1 Introduction

The brain consists of neurons that are wired together by axons with synapses and communicate with each other by electrical impulses, or spikes. There are two classes of neurons: excitatory and inhibitory. To execute cognitive tasks, in the cortex, the balance between excitation and inhibition must be maintained \cite{1,2}. Recently, the importance of cortical disinhibition, that is the temporary ceasing of inhibitory neurons activity, was recognized, for learning and memory \cite{3}, sensorimotor integration \cite{4}, locomotion \cite{5}, social behaviour \cite{6}, and attention \cite{7}.
Disinhibition can be achieved in different ways, for instance, by neuromodulation [5,6], long-range inhibitory input [8], and also at the level of local circuits. In the latter case, for some inhibitory neurons, their disinhibition is accomplished due to feedforward inhibition obtained from other neurons [9]. On the contrary, for parvalbumin-expressing (PV) inhibitory neurons, the main source of their inhibition is autaptic transmission [10]. The latter means that PV neurons send synaptic connections not only to other cells but also to themselves. Such inhibitory synapses are called autapses. They were also found in other parts of the brain [11–14]. However, the function of autapses outside the cortex are still to be discovered [15].

Most neurons in the brain are stimulated with sequences of spikes (spike trains) that appear random [16–22]. Mathematically such sequences are usually described as some stochastic point process [23]. Often the most simple case of a point process, a Poisson process, is used to describe a neuronal activity. For a Poisson process, its intensity, or infinitesimal rate at which events are expected to occur around a particular time is always the same. It does not depend on the prior history of the point process. In some cases, the description of neuronal activity with a Poisson process is experimentally approved [16–18] but in many others both experimental data [19–22] and theoretical considerations [24] exclude a possibility for a neuronal activity to have a Poisson statistics.

If a spike train is a realization of a Poisson process then the regularity of ISIs, or spike regularity, is low. However, there is an experimental evidence that some cortical neurons fire with a millisecond precision in response to sensory stimuli [25,26]. In [27] it was experimentally established that inhibitory autapses enhance spike timing precision on the millisecond scale. The latter is important in the situations where the precise spike timing carry information in the brain.

The effects of different types of autapses on the neuronal activity were studied extensively, see, for example, [28–37]. For instance, by computer modeling, it was discovered that excitatory autapse introduces a new firing pattern, namely, spike bursting, into the repertoire of behaviours of a lone Hodgkin–Huxley neuron [28]. It was proved rigorously that when a binding neuron with either an excitatory autapse [29] or inhibitory one [30] is stimulated with a Poissonian stream of excitatory impulses, the resulted output stream is non-Poissonian. For a Hodgkin–Huxley neuron with a slow excitatory autapse, it was discovered that the average firing rate can increase or decrease in comparison with the firing rate of the neuron without an autapse depending on the time delay of the feedback [31]. Also, when a Hodgkin–Huxley neuron with an autapse is stimulated with randomly distributed impulses, the neuron acts as a low-pass or band-pass filter [32]. Simulating an Izhikevich model neuron, it was observed that the spike regularity, measured by the coefficient of variation of ISIs, can increase or decrease for the neuron with inhibitory autapse depending on the time delay of the feedback [33]. Similarly, in [34] it was established that the value of the time delay of the feedback inhibition regulates firing patterns of the Wang-Buszaki neuron. For a Morris–Lecar neuron, the neuronal firing is intensified near the inverse Hopf bifurcation point when an inhibitory autapse is added to the neuron [35]. The autapses was observed to induce multiple coherence resonance in the scale-free neural network [36]. In a Hindmarsh–Rose neuron with time delay, changes in the time delay can lead to different types of bifurcations [37].

Although, theoretical studies of neurons with autapses are abundant, the
research was done by numerically or analytically investigating specified in a work particular neuronal model. In the current paper, we attempt to obtain analytical results for a wide range of neuronal models. We try to determine what kinds of statistics a neuron with delayed feedback inhibition might have if it is stimulated with input stream of excitatory impulses with non-Poisson, but renewal statistics. For the renewal point process, unlike Poisson process, the process intensity does depend on the prior history of the point process, namely, on the time at which the last event occurred. The consideration of a renewal point process instead of a Poissonian one presents analytic difficulties [23]. The emphasis of this work is made on the role of an inhibitory autapse, or delayed inhibitory feedback. That means that we take as given the probability density function (PDF) $p_0(t)$ of ISIs of that same neuron without feedback when it is stimulated with a stream of excitatory impulses distributed randomly according to its ISI PDF $p_{in}(t)$, see Fig. 1, upper panel. Here $p_{in}(t)dt$ and $p_0(t)dt$ give the probability to obtain the input and output ISI duration in the interval $[t; t+dt]$, respectively. Based on $p_{in}(t)$ and $p_0(t)$, we calculate the output ISI PDF $p(t)$ for the neuron with delayed inhibitory feedback, see Sec. 3.1. In this paper, we consider a $Cl$-type fast shunting inhibition, mediated via GABA_A receptors, see Sec. 2.2.

The answer is obtained for a class of spiking neuronal models, see Sec. 2.1, which includes a leaky integrate-and-fire model. The obtained general expression for $p(t)$ is checked analytically for already known case of a Poisson-type stimulation (see Sec. 3.2) as well as by numerical simulation of a stochastic process (see Fig. 3). Since the description of ISIs with the Gamma distribution is widely used in theoretical and experimental studies [39], obtained in this paper results are applied to the case of a neuron with threshold 2 when the time intervals between input impulses are distributed according to the Erlang-2 distribution, see Sect. 3.3. It is observed that spike regularity of a neuron with inhibitory autapse can decrease or increase in comparison with the case of the neuron without feedback, depending on the time delay of the feedback inhibition, see Fig. 4.

2 Methods

2.1 Class of neuronal models

The neuron transforms the input stream of impulses into the output stream, see upper panel of Fig. 1. Instead of specifying a particular neuronal model, we consider a class of neuronal models, which satisfy the following conditions:

- **Cond0**: Neuron is deterministic: Identical stimuli elicit identical spike trains from the same neuron.
- **Cond1**: Neuron is stimulated with a renewal point stochastic process of excitatory impulses. The distribution of the intervals between those impulses is $p_{in}(t)$ where $t$ is a time between two consecutive impulses in the input stream.
- **Cond2**: Neuron can be triggered only at the moment of receiving an input impulse.
• Cond3: Just after triggering, neuron fires a spike and immediately appears in its resting state, and remains there until an input impulse is received.

• Cond4: Neuron’s output statistics is characterized by the output ISI PDF $p_0(t)$ where $t$ means an ISI duration.

Additionally, we assume here that, if starting from its resting state, a neuron requires more than one input impulse in order to be triggered and, consequently, emit an output spike.

The neuronal models that satisfy Cond0-Cond4 include a perfect integrator [40], a leaky integrate-and-fire neuron [40], and a binding neuron [41]. Notice that the considered class of neuronal models is a subset of renewal (non-adaptive) neurons as defined in [42].

2.2 Delayed feedback inhibition

In the current paper, we consider a neuron with delayed feedback. It means that every time the neuron generates a spike, it also enters the feedback line, if there is no impulse in the feedback line yet, see Fig. 1. The impulse in the feedback line needs $\Delta$ time units to enter the neuron.

The properties of the considered feedback inhibition line is inspired by autapses of PV neurons [43]. The transmission via them is mediated by GABA_A receptors permeable to $Cl^-$ ions. An impulse mediated through such receptors has shunting effect on the neuronal excitatory membrane. This means that excitation/depolarization, if any, decreases due to inhibitory input. Also, an inhibitory impulse has no effect on the neuronal state if it is the resting state. This is because the reversal potential for $Cl^-$ ions equals the resting potential. How much excitation is decreased due to the inhibitory impulse depends on the strength of the inhibitory synapse. In this paper, we assume that the inhibitory impulse is able to immediately diminish excitation entirely. After that, it does not have any influence on the neuronal state.

Therefore, inspired by GABA_A inhibition known in real neuronal systems, we assume that the feedback line has the following properties:

• Prop1: The time delay in the line $\Delta > 0$ is constant.
• Prop2: The line is able to convey no more than one impulse.
• Prop3: After receiving an impulse from the feedback line, the neuron appears in its resting state, and that impulse is immediately forgotten.

Note that because of Prop3 and Cond3 the case of instantaneous inhibitory feedback (i.e. $\Delta = 0$) corresponds to a neuron without any feedback.

3 Results

3.1 General expression for ISI PDF $p(t)$

We study a neuron with delayed feedback inhibition specified in Sec. 2.1, 2.2 in its stationary state. Also, it is worth to mention that when a neuron fires, an ISI starts anew.
Figure 1: Upper panel: Neuron without feedback. Lower panel: Neuron with delayed feedback. As neuron in the both panels of the figure, we consider any neuronal model, which satisfies the set of conditions Cond0 - Cond4, see Sec. 2.1. The neuron in both panels is stimulated with the same stream of excitatory impulses which is a realisation of some stochastic point renewal process. Thus time intervals between input impulses are indepent and randomly distributed according to the distribution $p^{\text{in}}(t)$, where $t$ denotes an ISI duration. As a result of the stimulation with the renewal input stream, the neuron without feedback (upper panel) produces the series of spikes which are distributed according to the distribution $p^0(t)$. Under the same stimulation, that same neuron but with delayed feedback inhibition with the time delay $\Delta$ of the feedback (lower panel) generates spikes with the ISI PDF $p(t)$. In case of the feedback line presence (lower panel), when the neuron generates spike, it also enters the feedback line if the line is empty.
To find the ISI PDF $p(t)$ for such a neuron, let us introduce a time-to-live $s$. It denotes the time the impulse in the feedback line needs to reach the neuronal input (see lower panel of Fig. 1). Note that at the beginning of an ISI, there is always an impulse in the feedback line with a time-to-live $s \in [0; \Delta]$. Then, in the stationary regime, $p(t)$ can be calculated as follows:

$$p(t) = \int_0^\Delta ds \ p(t|s)f(s).$$

Here $p(t|s)$ is the conditional probability density to get the output ISI of a duration $t$ if at the beginning of the ISI there was an impulse in the feedback line with a time-to-live $s$.

As regards $f(s)$, it is the PDF of times-to-live $s$ at the beginning of an ISI, i.e. just after spiking. We consider a stationary regime here. In the Appendix A, it is rigorously proven that if the condition (34) on the PDF for a neuron without feedback $p^0(t)$ and the time delay of the feedback $\Delta$ is met then in the course of neuronal activity $f(s)$ converges to a unique stationary distribution. When the stationary distribution is attained, $f(s)$ has the following form:

$$f(s) = g(s) + a \ \delta(\Delta - s).$$

Here $g(s) \in C([0; \Delta])$ is a solution of Eq. (35), which is given by the expression (36), see the Appendix A below. The coefficient $a \in [0; 1]$ can be found from the normalization condition on $f(s)$. Notice, that the expression (2) is in a sense universal. The same form of $f(s)$ has been used in [29, 38, 44, 45] for different neuronal models. But here we are able to prove that any initial distribution converges to a unique stationary distribution given by (2).

To find $p(t|s)$, let us consider three different cases, see Fig. 2. In Fig. 2, points 0 and $t$ on the time lines denote the start and the end of an ISI, respectively. Note that at the beginning of each ISI, i.e. at the moment 0, an input impulse has been received, and it triggers a neuron. Therefore at the moment 0, the input stochastic process starts anew, because it is renewal. Further, at that moment, the neuron is in its resting state, and there is an inhibitory impulse in the feedback line with a time-to-live $s \in [0; \Delta]$.

The first possible case is to get an output ISI $t < s$, see top panel of Fig. 2. The latter means that the impulse from the feedback line does not reach the neuron before the end of the ISI. Thus the probability $p(t)dt$ to obtain an ISI of duration within $[t; t + dt]$ for a neuron with feedback is the same as for the same neuron without feedback, i.e.

$$p(t|s) = p^0(t), \ \ t < s.$$

The second possible case is to obtain an output ISI $t > s$. Then two mutually exclusive scenarios should be considered. The first one is when there is no input impulses during the first $s$ time units after the start of the ISI, or, in other words, before the arrival of the impulse from the feedback line, see middle panel of Fig. 2. An event “to obtain the first output impulse at the moment $t > s$ if the first input impulse arrives after the one from the feedback line” consists of the continuum of the alternative events indexed with a parameter $s'' \in ]s; t[$, i.e. $s''$ denotes the arrival time of the first input impulse after the start of the ISI.
Figure 2: To calculate the conditional PDF $p(t|s)$ to get the output ISI of a duration $t$ if at the beginning of the ISI there was an impulse in the feedback line with a time-to-live $s$, one should consider three possible mutually exclusive events. Top panel: an event “to obtain the first from the beginning of an ISI output impulse at $t < s$”. Middle panel: an event “to obtain the first output impulse at $t > s$ if the first input impulse arrives after at $s'' > s$”. Bottom panel: an event “to obtain the first output impulse at the moment $t > s$ if the first input impulse arrives before $s$”. $s'$ and $s''$ are the arrival times of two consecutive input impulses, namely, the last one before and the first one after obtaining the impulse from the feedback line. Points 0 and $t$ on all three time lines denote the start and the end of an ISI, respectively. Points $s$ denote the arrival time of the impulse from the feedback line.
Each alternative event consists of the following two consecutive and statistically independent events:

1. The first input impulse is obtained at the time \( s'' \in ]s; t[ \). The event has the probability \( p^{in}(s'')ds'' \).

2. The output impulse is produced at the time \( t > s'' \). At the moment \( s'' \), right after the receiving the input impulse, due to Cond3, the neuron is in the same state as at the beginning of an ISI in case of instantaneous excitatory feedback described in [46]. After the moment \( s \), the delayed feedback inhibition does not have any influence on the neuronal state. The input stochastic process also starts anew at \( s'' \). Thus the probability density to get the output ISI of duration \( t \) is \( p^{o-if}(t - s'') \), where \( p^{o-if}(t) \) is the PDF for the same neuron but with instantaneous excitatory feedback instead of inhibitory one. We use here notation from [46].

Therefore the probability of the considered alternative event indexed with the parameter \( s'' \) is \( p^{in}(s'')p^{o-if}(t - s'')ds''dt \). Its contribution to \( p(t|s) \) is as follows:

\[
p(t|s) = \int_s^t ds'' p^{in}(s'')p^{o-if}(t - s''), \quad t > s.
\]

The other scenario in case of \( t > s \) is an event “to obtain the first output impulse at the moment \( t > s \) if the first input impulse arrives before the one from the feedback line”. It consists of the continuum of the alternative events indexed with two parameters \( s' \in ]0; s[ \) and \( s'' \in ]s; t[ \), see bottom panel of Fig. 2. \( s' \) and \( s'' \) are the time moments of obtaining two consecutive impulses from the input line during one ISI, namely the last one before and the first one after obtaining the impulse from the feedback line, respectively. Each alternative event consists of three consecutive and statistically independent events:

1. The last impulse from the input line before the time moment \( s \) reaches the neuron at the moment \( s' < s \), and the neuron has not been triggered during the time interval \( ]0; s'[ \). Note that during the time interval \( ]0; s'[ \) the neuron is not influenced by the feedback and therefore can be considered as the one without feedback. We denote the probability density of such events (obtaining an input impulse at the moment \( s' \) before obtaining the impulse from the feedback line and the absence of firings during the time interval \( ]0; s'[ \)) as \( \tilde{F}^{0}(s') \).

2. The next impulse after the input impulse at \( s' \) is obtained from the input at the moment \( s'' > s \). The probability density of such events is \( p^{in}(s'' - s') \). It does not depend on the neuronal state or previous input impulses because the input stream is expected to be renewal.

3. The neuron is triggered at the time \( t > s'' \). At the moment \( s'' \), right after the receiving the impulse from the input, the neuron is in the same state as at the beginning of an ISI in case of instantaneous excitatory feedback. Therefore the probability density to get the output ISI of duration \( t \) is \( p^{o-if}(t - s'') \).
Thus the probability of the considered alternative event indexed with the
parameters \( s' \) and \( s'' \) is \( \tilde{P}(s')p^{in}(s'' - s')p^{o-2I}(t - s'')dx'ds'dt. \)

Finally, after examining three mutually exclusive events, the conditional
PDF \( p(t|s) \) can be written as follows:

\[
p(t|s) = \chi(s-t)p^0(t) + \int_s^t ds'' p^{o-2I}(t-s'') \left( p^{in}(s'') + \int_0^s ds' \tilde{P}(s')p^{in}(s'' - s') \right),
\]

where \( \chi(s-t) \) denotes a Heaviside step function.

In [46], the relation between the ISI PDF for a neuron without feedback \( p^0(t) \)
and the ISI PDF for the same neuron with instantaneous excitatory feedback
\( p^{o-2I}(t) \) was derived:

\[
p^0(t) = \int_0^t dt' p^{in}(t')p^{o-2I}(t - t').
\]

After applying the Laplace transform over the last expression, the Laplace
transform of the ISI PDF for the neuron with instantaneous excitatory feedback
\( p^{o-2I}(t) \) can be obtained:

\[
L\{p^{o-2I}\} = \frac{L\{p^0\}}{L\{p^{in}\}}.
\]

In order to calculate \( p(t) \), the exact expression for the distribution \( \tilde{P}(s') \) is
needed. It can be found as follows. The probability density of not trigerring a
neuron without feedback during the first \( t' \) time units of an ISI is a complemen-
tary cumulative distribution function (CCDF) of ISIs for the neuron without
feedback \( P^0(t') \):

\[
P^0(t') = 1 - \int_0^{t'} dt' p^0(t).
\]

The event of not trigerring the neuron during the first \( t' \) time units of an ISI
can be represented as a sum of two mutually exclusive events. The first one is
an event “to obtain no input impulses during the first \( t' \) time units of an ISI”. Its
probability density is the CCDF for the input stream:

\[
P^{in}(t') = 1 - \int_0^{t'} dt'' p^{in}(t'').
\]

The second event is an event “to not trigger a neuron during the first \( t' \)
time units of an ISI if at least one input impulse is fed into the neuron during
that time”. It can be represented as a set of alternative events indexed with a
parameter \( s' \in [0; t'] \). The alternative event consists of two consecutive inde-
pendent events. The first event is that at the moment \( s' \) the neuron obtains an
input impulse and has not been triggered during the time interval \([0; s'] \). The
probability of such an event is \( \tilde{P}^0(s')ds' \). The second event is the absence of input impulses during the time interval \([s';t']\). Note that at the moment \( s' \) the input stochastic process starts anew. Thus the probability of the second event is \( P_{in}(t' - s')dt' \).

Therefore \( \tilde{P}^0(s') \) can be derived by solving the following integral equation:

\[
P^0(t') = P_{in}(t') + \int_0^{t'} ds' \tilde{P}^0(s')P_{in}(t' - s').
\]  

(7)

Performing the Laplace transform over the last equation and using Eqs. (5) and (6), one can obtain the Laplace transform of \( \tilde{P}^0(s') \):

\[
L\{\tilde{P}^0\} = L\{p_{in}\} - L\{P^0\} \frac{1}{1 - L\{p_{in}\}}.
\]  

(8)

Substituting Eq. (3) for the conditional probability \( p(t|s) \) into Eq. (1) and taking into account that \( f(s) \) can be represented as in Eq. (2), the following expressions for the ISI PDF \( p(t) \) for the neuron with delayed feedback inhibition can be derived:

\[
p(t) = \int_0^t ds g(s) \int_s^t ds'' p^{Jf}(t - s') \left( p_{in}(s') + \int_0^{s'} ds' \tilde{P}^0(s')p_{in}(s'' - s') \right) + p^0(t) \left( \int_t^\Delta ds g(s) + a \right), \quad t < \Delta; \quad (9)
\]

\[
p(t) = \int_0^\Delta ds g(s) \int_s^t ds'' p^{Jf}(t - s') \left( p_{in}(s') + \int_0^{s'} ds' \tilde{P}^0(s')p_{in}(s'' - s') \right) + \int_t^\Delta ds'' p^{Jf}(t - s'') \left( p_{in}(s'') + \int_0^{s''} ds' \tilde{P}^0(s')p_{in}(s'' - s') \right), \quad t > \Delta.
\]  

(10)

Notice that, according to Eqs. (9) and (10), the obtained ISI PDF \( p(t) \) has a jump type discontinuity at a point corresponding to the output ISI that is equal to the delay in the feedback line \( \Delta \):

\[
\lim_{t \to \Delta^-} p(t) - \lim_{t \to \Delta^+} p(t) = a p^0(\Delta).
\]

To summarize, if the output ISI PDF for the same neuron without feedback \( p^0(t) \) and the input ISI PDF \( p_{in}(t) \) are known then the output ISI PDF \( p(t) \) for the neuron with delayed feedback inhibition can be calculated as follows:

1. to find the stationary PDF of times-to-live \( f(s) = g(s) + a \delta(\Delta - s) \), first, calculate \( g(s) \) using Eq. (36), then find \( a \) from the normalization condition on \( f(s) \);
2. reverse the Laplace transform of \( p^{\omega\mathcal{F}}_{\text{oi}}(t) \) in Eq. (4);

3. reverse the Laplace transform of \( \tilde{P}_0(t) \) in Eq. (8);

4. substitute all mentioned above into Eqs. (9) and (10) to calculate \( p(t) \).

### 3.2 Case of Poissonian input

To verify the results obtained in Sec. 3.1 above, consider a neuron stimulated with a stream of excitatory impulses which is a realization of a Poisson point process with a constant rate \( \lambda > 0 \). Then intervals between the input impulses are exponentially distributed:

\[
p^{\text{in}}(t) = \lambda e^{-\lambda t}.
\]

(11)

According to [46], the relation between the ISI PDF \( p^0(t) \) for a neuron without feedback stimulated with a Poisson stream and the ISI PDF \( p^{\omega\mathcal{F}}_{\text{oi}}(t) \) for the neuron with instantaneous feedback looks as follows:

\[
p^{\omega\mathcal{F}}_{\text{oi}}(t) = p^0(t) + \frac{1}{\lambda} \frac{d}{dt} p^0(t).
\]

(12)

Substituting Eqs. (11) and (12) into Eq. (3), and taking into account Eq. (7), the conditional probability density \( p(t|s) \) can be obtained:

\[
p(t|s) = \chi(s-t)p^0(t) + p^0(t-s)P_0(s),
\]

which is the same expression for \( p(t|s) \) as it was obtained before in [45] for the case of the Poisson input. Notice that in the considered case the expression for the conditional probability density \( p(t|s) \) is simplified compared to the more general case of the renewal input, see Eq. (3). As regards \( f(s) \), the starting point (Eq. 30) of the proof, given in the Appendix A, is valid in the case of the Poisson input. Thus the considered here general case of the renewal input includes the case of a Poisson one studied previously in [45].

### 3.3 Case of a neuron with threshold 2 stimulated with Erlang-2 stream

To illustrate the case when the input stream is renewal but non-Poissonian, firstly, consider a neuronal model without feedback that satisfies Cond0-4, see Sec. 2.1 above. Input ISIs are assumed to be distributed according to the Erlang-2 distribution:

\[
p^{\text{in}}(t) = \lambda^2 t e^{-\lambda t}, \quad \lambda > 0.
\]

(13)

Hereinafter it is assumed that the neuron has threshold 2. It means that 2 input impulses may trigger the neuron. This can be realized, for instance, for the standard leaky integrate-and-fire model satisfying the condition \( h < V_0 < 2h \), where \( V_0 \) is the firing threshold, and \( h \) is the height of stimulating impulses.

In the considered case of the neuron with threshold 2, there is a domain of ISIs \( t \in [0; T_2] \) such that the second after the beginning of an ISI input impulse received at the moment \( t \) will definitely trigger an output spike. For instance, for
the binding neuron model $T_2 = \tau$ [47], where $\tau$ is the storage time of the internal memory. For the mentioned above leaky integrate-and-fire neuron model [48],

$$T_2 = \tau \ln \frac{h}{V_0 - h},$$

where $\tau$ is the membrane relaxation time.

From the definition of $T_2$, it follows that for the ISIs of a duration less than $T_2$ time units, the event of the neuron trigerring consists of two consecutive independent events of obtaining an input impulse. Therefore, in such a case, for the neuron without feedback the ISI PDF $p_0(t)$ is as follows:

$$p_0(t) = \lambda e^{-\lambda t} \left(\frac{\lambda t}{3!}\right)^3, \quad t < T_2.$$  \hspace{1cm} (14)

The latter together with Eq. (13) allows a calculation of the PDF $\tilde{P}_0(s')$ for $s'<T_2$. Since Eq. (8) is valid, the distribution $\tilde{P}_0(s')$ is given by

$$\tilde{P}_0(s') = p_{in}(s'), \quad s'<T_2.$$  \hspace{1cm} (15)

Further, for the ISIs shorter than $T_2$, the event of triggering the neuron with instantaneous excitatory feedback is the event of obtaining an input impulse (one impulse is already fed into the neuron at the beginning of an ISI due to the instantaneous feedback). Thus the output ISI PDF for the neuron with instantaneous excitatory feedback $p_{o_{if}}(t)$ is the same as the input ISI PDF $p_{in}(t)$ (13):

$$p_{o_{if}}(t) = p_{in}(t), \quad t < T_2.$$  \hspace{1cm} (16)

Secondly, consider the case when the delayed inhibitory feedback line is added to the neuron discussed right above. Assume that the delay in the feedback line $\Delta$ fulfills the following condition:

$$\Delta < T_2.$$  \hspace{1cm} (17)

Note that, to find the PDF of times-to-live $f(s)$, the explicit expression for $p_0(t)$ is needed only for the arguments within the interval $[0; \Delta]$. Thus, if the condition (17) holds, the PDF of times-to-live $f(s) = g(s) + a \delta(\Delta - s)$ can be found in the considered case of the neuron with threshold 2 stimulated with the Erlang-2 stream. After the substitution of the expression (14) for $p_0(t)$ into Eqs. (36), (37) of the Appendix A, where the expression for $g(s)$ is given, one can obtain the following:

$$g(s) = \frac{a\lambda e^{-\lambda(\Delta-s)}}{2} (\sinh(\lambda(\Delta-s)) - \sin(\lambda(\Delta-s))), \quad s \in [0; \Delta],$$  \hspace{1cm} (18)

where

$$a = \frac{8}{2e^{-\lambda\Delta} (\cos(\lambda\Delta) + \sin(\lambda\Delta)) + 2\lambda \Delta + e^{-2\lambda\Delta} + 5}.$$  \hspace{1cm} (19)

Finally, the expressions for $p_{in}(t)$ (13), $p_0(t)$ (14), $\tilde{P}_0(t)$ (15), $p_{o_{if}}(t)$ (16), and $g(s)$ (18) can be substituted into Eq. (9) to find the PDF for the neuron.
with delayed inhibitory feedback $p(t)$ for the ISIs $t < \Delta$:

$$p(t) = \frac{a e^{-\lambda(2\Delta + t)}}{2880} \left( -45(2 + \lambda t) + 45e^{2\lambda t} \left( 2 + \lambda t\left( -3 + \lambda t(1 + \lambda t) \right) \right) + \lambda^2 t^2 \left( 45 + \lambda t\left( 75 + 2e^{2\lambda \Delta}(150 - 30\lambda t + 60\lambda \Delta + \lambda^3 t^3) \right) \right) + 60e^{\lambda \Delta} e^{\lambda t^3} \cos(\lambda(t - \Delta)) + 3\lambda t(-4 + \lambda^2 t^2) \cos(\lambda \Delta) - 3e^{\lambda t}\left( -4 + \lambda t(-2 + \lambda t) \right) \sin(\lambda(t - \Delta)) + \left( 12 + \lambda^2 t^2(-6 + \lambda t) \right) \sin(\lambda \Delta) \right),$$  

(20)

and into Eq. (10) to find $p(t)$ for the ISIs $t \in \Delta; T_2$:

$$p(t) = \frac{a e^{-2\lambda(t+\Delta)}}{2880} \left( 15e^{\lambda t}\left( -6 + \lambda t\left( -3 + \lambda t(3 + 5\lambda t) \right) \right) + e^{\lambda t+2\Delta}\left( 90 + 5\lambda^3 t^3(45 + 2\lambda \Delta(3 + \lambda \Delta))(9 + 2\lambda \Delta) \right) + 60\lambda \Delta\left( -15 + \lambda \Delta(15 + \lambda \Delta(10 + \lambda \Delta)) \right) - 15\lambda^2 t^2\left( 3 + 2\lambda \Delta\left( -15 + \lambda \Delta(\lambda \Delta(10 + \lambda \Delta) + 15) \right) \right) + 3\lambda t\left( 255 + 2\lambda \Delta(\lambda \Delta(5 + \lambda \Delta)(-45 + \lambda \Delta(15 + 2\lambda \Delta)) - 135) \right) + 60e^{\lambda t+\Delta}\left( 3\lambda t(-4 + \lambda^2 t^2) \cos(\lambda \Delta) + (12 + \lambda^2 t^2(-6 + \lambda t) \right) \sin(\lambda \Delta) \right),$$  

(21)

where the coefficient $a$ is given by Eq. (19).

Notice that expressions for the ISI PDF $p(t)$ (20) and (21) have been obtained without specifying the exact neuronal model. For example, instead of the leaky integrate-and-fire model, we might consider the perfect integrator or the binding neuron model. It means that at some initial interval of ISI durations, the PDF $p(t)$ is the same for the whole considered in this section class of neuronal models with delayed inhibitory feedback. The further course of $p(t)$ will depend on the ISI PDF for the neuron without feedback $p^0(t)$, which is different for different models.

The expressions (20) and (21) for $p(t)$ have been checked numerically by means of the Monte Carlo simulation for the binding neuron model with threshold 2 stimulated with the Erlang-2 stream (13), and with delayed inhibitory feedback specified in Sec. 2.2. The model parameters have been set to fulfill the conditions (17) and (34). The results of the simulation are displayed in Fig. 3.

### 3.3.1 The mean and the coefficient of variation

Additionally, in the considered case of the neuron with threshold 2 with delayed feedback inhibition stimulated with the Erlang-2 stream, one can calculate the
Figure 3: Example of the ISI PDF for the input Erlang-2 stream (a), Eq. (13) is used, and for the output stream of the binding neuron with threshold 2 with delayed inhibitory feedback, stimulated with the Erlang-2 stream (b), Eqs. (20) and (21) are used. For both panels: \( \tau = 8 \text{ ms} \), \( \lambda = 1 \text{ ms}^{-1} \). \( \Delta = 2.5 \text{ ms} \) in (b). (c): results of the Monte Carlo simulation for the same neuron as in (b) (1 000 000 output ISIs were obtained). The total probability under the curves is 0.996981 (a) and 0.905041 (b), (c). As it can be seen from the plot (b), the delayed feedback inhibition causes a jump type discontinuity of the ISI PDF at a point corresponding to the output ISI that is equal to the delay in the feedback line \( \Delta \). The analytical results for the neuron with feedback inhibition (b) are in concordance with the results of the numerical simulation (c).

moments of the output ISI PDF \( p(t) \):

\[
\mu_n = \int_0^{\infty} \text{d}t \, t^n p(t), \quad (22)
\]

where \( \mu_n \) denotes the \( n \)-th moment of the ISI PDF for the neuron with delayed inhibitory feedback. The first moment \( \mu_1 \) is the mean ISI. It can be used together with the second moment \( \mu_2 \) to calculate the coefficient of variation (CV) of ISIs:

\[
CV = \frac{\sqrt{\mu_2 - \mu_1^2}}{\mu_1}. \quad (23)
\]

Actually, after substituting Eqs. (9) and (10) for the ISI PDF \( p(t) \) into Eq. (22), one obtains the relation between the moments for the neuron with delayed inhibitory feedback and that same neuron with instantaneous excitatory feedback. Then, from Eq. (4), the moments for the neuron with instantaneous excitatory feedback can be derived:

\[
\mu_n^{\text{o,\text{f}}} = (-1)^n \left. \frac{d^n \mathcal{L}\{\mu_n^{\text{o,\text{f}}}(z)\}}{dz^n} \right|_{z=0} = (-1)^n \left. \frac{d^n \mathcal{L}\{\mu^0(z)\}}{dz^n} \right|_{z=0},
\]

Here \( \mu_n^{\text{o,\text{f}}} \) denotes the \( n \)-th moment of the ISI PDF for the neuron with instantaneous excitatory feedback. It follows from the equation right above that, for the considered input stream, namely, specified by Eq. (13), the following relation between the moments of the output ISI PDF for the neuron with instantaneous feedback \( \mu_n^{\text{o,\text{f}}} \) and without feedback is valid:

\[
\mu_n^{\text{o,\text{f}}} = \mu_n^0 - \frac{2n}{\lambda} \mu_{n-1}^0 + \frac{n(n-1)}{\lambda^2} \mu_{n-2}^0, \quad n \geq 2, \quad (24)
\]
where $\mu_0^n$ is the $n$-th moment of the ISI PDF for the neuron without feedback.

The latter together with Eqs. (9), (10), (13), (14), (15), (16), and (18) can be substituted into Eq. (22) to calculate moments $\mu_n$ of the output ISI PDF for the neuron with threshold 2 with delayed inhibitory feedback stimulated with the Erlang-2 stream, assuming that the condition (17) on $\Delta$ is met. For example, the mean ISI $\mu_1$ is given by

$$\mu_1 = \frac{a}{2\lambda} (-1 + 2\lambda(\mu_1^0 + \Delta) + e^{-2\lambda\Delta}), \quad (25)$$

and the second moment $\mu_2$ is as follows:

$$\mu_2 = \frac{ae^{-2\lambda\Delta}}{2\lambda^2} (-7 + 4\lambda\mu_1^0 + e^{2\lambda\Delta}(-17 + 2\lambda(4\mu_1^0 + 5\Delta + \lambda\mu_2^0)) + 4e^{\lambda\Delta}(8 - 4\lambda\mu_1^0 + (-1 + \lambda\mu_1^0)\cos(\lambda\Delta) + (1 - \lambda\mu_1^0)\sin(\lambda\Delta))). \quad (26)$$

The coefficient $a$ in Eqs. (25) and (26) is given by Eq. (19).

In case of the binding neuron model, the moments of the output ISI PDF for the neuron with inhibitory feedback $\mu_n$ can be calculated explicitly by substituting the corresponding moments. Indeed, it has been shown in [49] that the Laplace transform of the output ISI PDF $p_{\text{o}^{\text{if}}}(t)$ for the binding neuron with threshold 2 with instantaneous excitatory feedback stimulated with a renewal stream is given by

$$\mathcal{L}\{p_{\text{o}^{\text{if}}}(t)\} = \frac{\mathcal{L}\{\chi(\tau - t)p_{\text{in}}(t)\}}{1 - \mathcal{L}\{\chi(t - \tau)p_{\text{in}}(t)\}}, \quad (27)$$

where $\tau$ is the storage time of the internal memory in the binding neuron model. Eq. (27) allows calculation of $p_{\text{o}^{\text{if}}}(t)$ and, consequently, utilizing Eq. (4), $p_0(t)$ as well as their moments, $\mu_{\text{o}^{\text{if}}}^n$ and $\mu_0^n$, respectively. For instance, if the input ISI PDF is the Erlang-2 distribution (13), then Eq. (27) together with the relation (24) gives the following first two moments $\mu_1^0$ and $\mu_2^0$ for the binding neuron with threshold 2 without feedback:

$$\mu_1^0 = \frac{4e^{\lambda\tau} - 2 - 2\lambda\tau}{\lambda(e^{\lambda\tau} - 1 - \lambda\tau)}, \quad (28)$$

and

$$\mu_2^0 = \frac{20e^{2\lambda\tau} + 6(1 + \lambda\tau)^2 + 2e^{\lambda\tau}(-9 - 9\lambda\tau + 2\lambda^2\tau^2)}{\lambda^2(1 - e^{\lambda\tau} + \lambda\tau)^2}. \quad (29)$$

Eqs. (28) and (29) have been used to check numerically the relations (25) and (26) by running the Monte Carlo simulations for the binding neuron model with threshold 2 with delayed inhibitory feedback. The simulations were performed for different values of the feedback line delay $\Delta$. The values were chosen to meet the condition (34), in order for obtained in the current section results to be valid (for more details on the condition (34), see the Appendix A). In Fig. 4, the results for the mean $\mu_1$, the second moment $\mu_2$, and the CV are displayed.

4 Discussion

In the present paper, the obtained analytical results are valid if the condition (34) is fulfilled, which ensures the existence of the unique stationary distribution
of times-to-live \( f(s) \). Actually, the condition (34) is equivalent to the requirement that the input ISIs smaller than \( \Delta \) have low probability. This condition is in line with biological details of the synaptic transmission. Indeed, when a synapse mediates impulses at high frequency, i.e. short input ISIs are highly probable, the time of the synaptic transmission can be prolonged up to the hundreds of ms due to the asynchronous synaptic release. It was shown that the latter may happen to autapses of PV neurons [50]. However, in the current paper, we assume that the impact of an inhibitory impulse from the feedback line on a neuron is momentary (see property Prop3 of the feedback line, Sec. 2.2 above).

As it can be seen in Fig. (4), panel (c), in the presence of the delayed inhibitory feedback, the CV and, consequently, spike regularity can decrease or increase in comparison with the case of the same neuron without feedback (the point \( \Delta = 0 \) on the Fig. 4) depending on the time delay of the feedback inhibition. Additionally, there is an optimal value of the time delay \( \Delta \) for enhancing the spike regularity. The increase of spike regularity is consistent with experimental observation that inhibitory autapses enhance spike timing precision on the millisecond scale [27]. Analogous dependence of the spike regularity on the feedback time delay was observed previously, for example, in the computer simulation of an Izhikevich model neuron [33]. Similarly, for the Wang-Buszaki neuron, the existence of optimal strength of autaptic inhibition for spiking regularity was revealed [34]. Also, increased spike regularity was observed for other neuronal systems. For example, in the network of excitatory neurons the time delays of the neuronal connections determine whether or not neurons will fire regularly and fast [51].

Acknowledgments. This work was supported by the Programs of Basic Research of the Department of Physics and Astronomy of the National Academy of Sciences of Ukraine “Mathematical models of nonequilibrium processes in open systems”, № 0120U100857, and “Noise-induced dynamics and correlations in nonequilibrium sys-
A The convergence of $f(s)$ to a stationary distribution

Suppose that there is an ensemble of identical neurons. Each of them has an impulse in the feedback line with some value of time-to-live $s$. Also, suppose that, at the beginning, these times-to-live $s$ have a distribution $f_0(s)$. It is clear that the distribution of $s$ can be changed only after triggering. Denote the distribution obtained after the $n$-th triggering of every neuron in the ensemble as $f_n(s)$. Here we prove that $f_n(s)$ converges$^1$ to a distribution $f(s)$ which remains the same after further triggerings (is stationary).

In the work [44], to find the distribution of times-to-live $f(s)$, the transition function $P(s|s')$ was introduced. It gives the probability density to find an impulse in the feedback line at the beginning of an ISI with a time-to-live $s$ provided that, at the beginning of the previous ISI, there was an impulse with a time-to-live $s'$. Thus, if the distribution of times-to-live at the beginning of an ISI was $f_n(s)$, then at the beginning of the next ISI it is given by

$$f_{n+1}(s) = \int_0^\Delta ds' P(s|s')f_n(s') =$$

$$= \int_s^\Delta ds' P^0(s'-s)f_n(s') + \delta(s - \Delta) \int_0^\Delta ds' P^0(s')f_n(s'),$$

(30)

where the explicit form of $P(s|s')$ was taken into account.

Since $f_n(s)$ is a PDF, it is normalized:

$$\int_0^\Delta ds f_n(s) = 1.$$

With the help of Eq. (30), it can be checked that a norm of the distribution of times-to-live at the beginning of each ISI does not change:

$$\int_0^\Delta ds f_{n+1}(s) = \int_0^\Delta ds f_n(s).$$

(31)

According to Eq. (30), $f_n(s)$ can be represented as follows:

$$f_n(s) = g_n(s) + a_n\delta(s - \Delta),$$

where $g_n(s) \in C([0; \Delta])$, and $a_n \in [0; 1]$. Then Eq. (30) can be rewritten as the following system of equations on $g_n(s)$ and $a_n$:

$$\begin{cases}
  a_{n+1} = \int_0^\Delta ds' P^0(s')g_n(s') + a_nP^0(\Delta); \\
  g_{n+1}(s) = \int_s^\Delta ds' P^0(s'-s)g_n(s') + a_nP^0(\Delta - s).
\end{cases}$$

(32)

$^1$The regular part of $f_n(s)$ converges in $C([0; \Delta])$ and the singular part (the $\delta$-function mass) converges in $R^1$.\[17]
However, since (31) is valid, $a_n$ can be determined through $g_n(s)$:

$$a_n = 1 - \int_0^\Delta ds \, g_n(s),$$

which, after substitution into the second equation of the system (32), gives the self-contained expression for the sequence $\{g_n(s)\}$:

$$g_{n+1}(s) = \int_s^\Delta ds' \, p^0(s' - s)g_n(s') + p^0(\Delta - s)(1 - \int_0^\Delta ds' \, g_n(s')).$$  \hspace{1cm} (33)

Let us assume that $p^0(s) \in F = C([0; \Delta]), \ s \in [0; \Delta]$. Then Eq. (33) can be rewritten in terms of an operator $M : \mathcal{F} \to \mathcal{F}$:

$$(Mg)(s) = \int_s^\Delta ds' \, p^0(s' - s)g(s') + p^0(\Delta - s)(1 - \int_0^\Delta ds' \, g(s')).$$

If we introduce an operator $\tilde{M} : \mathcal{F} \to \mathcal{F}$ such as $M = Inv \tilde{M} Inv$, where $(Inv g)(s) = g(\Delta - s)$, then the previous equation can be rewritten as follows:

$$(\tilde{M}g)(s) = \int_0^s ds' \, p^0(s - s')g(s') + p^0(s)(1 - \int_0^\Delta ds' \, g(s')).$$

If the condition

$$\int_0^\Delta p^0(s)ds + \Delta \sup_{s \in [0; \Delta]} p^0(s) < 1 \hspace{1cm} (34)$$

is fulfilled, then the operator $\tilde{M} : \mathcal{F} \to \mathcal{F}$ is a contraction in $C([0; \Delta])$. Consequently, the sequence $\{g_n(s)\}$ defined by $g_{n+1}(s) = (Mg)(s)$ converges to a fixed point of the operator $\tilde{M}$. This proves the existence and uniqueness of the PDF $f(s)$ in the stationary regime. The stationary $g(s)$ is a solution of the following equation:

$$g(s) = \int_0^s ds' \, p^0(s - s')g(s') + p^0(s)(1 - \int_0^\Delta ds' \, g(s')).$$  \hspace{1cm} (35)

The solution of Eq. (35) is given by [52, p. 631]:

$$g(s) = \frac{g^0(s)}{1 + \int_0^\Delta g^0(s')ds'},$$  \hspace{1cm} (36)

where

$$g^0(s) = \sum_{k=0}^{\infty} (V^k p^0)(s),$$  \hspace{1cm} (37)

and an operator $V$ is defined as follows:

$$(V\phi)(s) = \int_0^s ds' \, p^0(s - s')\phi(s'), \ \ \phi \in \mathcal{F}.$$  

It can be easily shown that $||V|| < 1$ in $C([0; \Delta])$, which ensures convergence in (37).
References

[1] Isaacson, J.S., Scanziani, M.: How Inhibition Shapes Cortical Activity. Neuron 72(2), 231–243 (2011). https://doi.org/10.1016/j.neuron.2011.09.027

[2] Atallah, B.V., Scanziani, M.: Instantaneous Modulation of Gamma Oscillation Frequency by Balancing Excitation with Inhibition. Neuron 62(4), 566–577 (2009). https://doi.org/10.1016/j.neuron.2009.04.027

[3] Lützkus, J.J., Wolff, S.B.E., Lüthi, A.: Disinhibition, a Circuit Mechanism for Associative Learning and Memory. Neuron 88(2), 264–276 (2015). https://doi.org/10.1016/j.neuron.2015.09.024

[4] Lee, S., Kruglikov, I., Huang, Z.J., Fishell, G., Rudy, B.: A disinhibitory circuit mediates motor integration in the somatosensory cortex. Nat. Neurosci. 16(11), 1662–1670 (2013). https://doi.org/10.1038/nn.3544

[5] Fu, Y., et al.: A Cortical Circuit for Gain Control by Behavioral State. Cell 156(6), 1139–1152 (2014). https://doi.org/10.1016/j.cell.2014.01.050

[6] Marlin, B.J., Mitre, M., D’Amour, J.A., Chao, M.V., Froemke, R.C.: Oxytocin enables maternal behaviour by balancing cortical inhibition. Nature 520(7548), 499–504 (2015). https://doi.org/10.1038/nature14402

[7] Sridharan, D., Knudsen, E.I.: Selective disinhibition: A unified neural mechanism for predictive and post hoc attentional selection. Vision Res. 116, 194–209 (2015). https://doi.org/10.1016/j.visres.2014.12.010

[8] Zhang, S., et al.: Long-range and local circuits for top-down modulation of visual cortex processing. Science 345(6197), 660–665 (2014). https://doi.org/10.1126/science.1254126

[9] Pfeffer, C.K., Xue, M., He, M., Huang, Z.J., Scanziani, M.: Inhibition of inhibition in visual cortex: The logic of connections between molecularly distinct interneurons. Nat. Neurosci. 16(8), 1068–1076 (2013). https://doi.org/10.1038/nn.3446

[10] Deleuze, C., et al.: Strong preference for autaptic self-connectivity of neocortical PV interneurons facilitates their tuning to γ-oscillations. PLOS Biol. 17(9), e3000419 (2019). https://doi.org/10.1371/journal.pbio.3000419

[11] Pouzat, C., Marty, A.: Autaptic inhibitory currents recorded from interneurones in rat cerebellar slices. J. Physiol. 509(3), 777–783 (1998). https://doi.org/10.1111/j.1469-7793.1998.777bm.x

[12] Cobb, S.R., et al.: Synaptic effects of identified interneurons innervating both interneurons and pyramidal cells in the rat hippocampus. Neuroscience 79(3), 629–648 (1997). https://doi.org/10.1016/S0306-4522(97)00055-9

[13] Park, M.R., Lighthall, J.W., Kitai, S.T.: Recurrent inhibition in the rat neostriatum. Brain Res. 194(2), 359–369 (1980). https://doi.org/10.1016/0006-8993(80)91217-2

[14] Karabelas, A.B., Purura, D.P.: Evidence for autapses in the substantia nigra. Brain Res. 200(2), 467–473 (1980). https://doi.org/10.1016/0006-8993(80)90935-X

[15] Bekkers, J.M.: Synaptic Transmission: Functional Autapses in the Cortex. Curr. Biol. 13(11), R433–R435 (2003). https://doi.org/10.1016/S0960-9822(03)00363-4

[16] Liley, A.W.: An investigation of spontaneous activity at the neuromuscular junction of the rat. J. Physiol. 132(3), 650–666 (1956). https://doi.org/10.1113/jphysiol.1956.sp005555
[17] Drongelen, W.: Unitary recordings of near threshold responses of receptor cells in the olfactory mucosa of the frog. J. Physiol. 277(1), 423–435 (1978). https://doi.org/10.1113/jphysiol.1978.sp012282

[18] Shadlen, M.N., Newsome, W.T.: The Variable Discharge of Cortical Neurons: Implications for Connectivity, Computation, and Information Coding. J. Neurosci. 18(10), 3870–3896 (1998). https://doi.org/10.1523/JNEUROSCI.18-10-03870.1998

[19] Baddeley, R., et al.: Responses of neurons in primary and inferior temporal visual cortices to natural scenes. Proc. R. Soc. B Biol. Sci. 264, 1775–1783 (1997). https://doi.org/10.1098/rspb.1997.0246

[20] Maimon, G., Assad, J.A.: Beyond Poisson: Increased Spike-Time Regularity across Primate Parietal Cortex. Neuron 62(3), 426–440 (2009). https://doi.org/10.1016/j.neuron.2009.03.021

[21] Shinomoto, S., et al.: Relating Neuronal Firing Patterns to Functional Differentiation of Cerebral Cortex. PLoS Comput. Biol. 5(7), e1000433 (2009). https://doi.org/10.1371/journal.pcbi.1000433

[22] Mochizuki, Y., et al.: Similarity in Neuronal Firing Regimes across Mammalian Species. J. Neurosci. 36(21), 5736–5747 (2016). https://doi.org/10.1523/JNEUROSCI.0230-16.2016

[23] Johnson, D.H.: Point process models of single-neuron discharges. J. Comput. Neurosci. 3(4), 275–299 (1996). https://doi.org/10.1007/BF00161089

[24] Softky, W.R., Koch, C.: Cortical Cells Should Fire Regularly, But Do Not. Neural Comput. 4(5), 643–646 (1992). https://doi.org/10.1162/neco.1992.4.5.643

[25] Petersen, R.S., Panzeri, S., Diamond, M.E.: Population coding in somatosensory cortex. Curr. Opin. Neurobiol. 12(4), 441–447 (2002). https://doi.org/10.1016/S0959-4388(02)00338-0

[26] Arabzadeh, E., Zorzin, E., Diamond, M.E.: Neuronal Encoding of Texture in the Whisker Sensory Pathway. PLoS Biol. 3(1), e17 (2005). https://doi.org/10.1371/journal.pbio.0030017

[27] Bacci, A., Huguenard, J.R.: Enhancement of Spike-Timing Precision by Autaptic Transmission in Neocortical Inhibitory Interneurons. Neuron 49(1), 119–130 (2006). https://doi.org/10.1016/j.neuron.2005.12.014

[28] Herrmann, C.S., Klaus, A.: Autapse turns neuron into oscillator. Int. J. Bifurcat. Chaos 14(2), 623–633 (2004). https://doi.org/10.1142/S0218127404009338

[29] Vidybida, A.K., Kravchuk, K.G.: Output stream of binding neuron with delayed feedback. Eur. Phys. J. B 72(2), 279–287 (2009). https://doi.org/10.1007/s10059-009-0309-8

[30] Vidybida, A.K., Kravchuk, K.G.: Firing statistics of inhibitory neuron with delayed feedback. I. Output ISI probability density. BioSystems 112(3), 224–232 (2013). https://doi.org/10.1016/j.biosystems.2012.12.006

[31] Hashemi, M., Valizadeh, A., Azizi, Y.: Effect of duration of synaptic activity on spike rate of a Hodgkin-Huxley neuron with delayed feedback. Phys. Rev. E. 85(2), 021917 (2012). https://doi.org/10.1103/PhysRevE.85.021917

[32] Wang, H., Wang, L., Chen, Y., Chen, Y.: Effect of autaptic activity on the response of a Hodgkin-Huxley neuron. Chaos 24(3), 033122 (2014). https://doi.org/10.1063/1.4892769

[33] Guo, D., et al.: Regulation of Irregular Neuronal Firing by Autaptic Transmission. Sci. Rep. 6(1), 26096 (2016). https://doi.org/10.1038/srep26096

20
[34] Guo, D., Chen, M., Perc, M., Wu, S., Xia, C., Zhang, Y., Xu, P., Xia, Y., Yao, D.: Firing regulation of fast-spiking interneurons by autaptic inhibition. EPL (Europhysics Lett.) 114(3), 30001 (2016). https://doi.org/10.1209/0295-5075/114/30001

[35] Zhao, Z., Jia, B., Gu, H.: Bifurcations and enhancement of neuronal firing induced by negative feedback. Nonlinear Dyn. 86(3), 1549–1560 (2016). https://doi.org/10.1007/s11071-016-2976-x

[36] Yilmaz, E., Ozer, M., Baysal, V., Perc, M.: Autapse-induced multiple coherence resonance in single neurons and neuronal networks. Sci. Rep. 6(1), 30914 (2016). https://doi.org/10.1038/srep30914

[37] Li, Y., Wei, Z., Zhang, W., Perc, M., Repnik, R.: Bogdanov–Takens singularity in the Hindmarsh–Rose neuron with time delay. Appl. Math. Comput. 354, 180–188 (2019). https://doi.org/10.1016/j.amc.2019.02.046

[38] Schchur, O., Vidybida, A.: First Passage Time Distribution for Spiking Neuron with Delayed Excitatory Feedback. Fluct. Noise Lett. 19(1), 2050005 (2020). https://doi.org/10.1142/S0219477520500054

[39] Lansky, P., Sacerdote, L., Zucca, C.: The Gamma renewal process as an output of the diffusion leaky integrate-and-fire neuronal model. Biol. Cybern. 110(2), 193–200 (2016). https://doi.org/10.1007/s00422-016-0690-x

[40] Burkitt, A.N.: A Review of the Integrate-and-Fire Neuron Model: I. Homogeneous Synaptic Input. Biol. Cybern. 95(1), 1–19 (2006). https://doi.org/10.1007/s00422-006-0068-6

[41] Vidybida, A.: Binding Neuron. In: Khosrow-Pour, M. (ed.) Encyclopedia of Information Science and Technology, Third Edition. pp. 1123–1134. IGI Global (2015). http://doi:10.4018/978-1-4666-5888-2.ch107

[42] Gerstner, W., Kistler, W.M., Naud, R., Paninski, L.: Neuronal Dynamics. Cambridge University Press, Cambridge (2014). https://doi.org/10.1017/CBO9781107447615

[43] Bacci, A., Huguenard, J.R., Prince, D.A.: Functional Autaptic Neurotransmission in Fast-Spiking Interneurons: A Novel Form of Feedback Inhibition in the Neocortex. J. Neurosci. 23(3), 859–866 (2003). https://doi.org/10.1523/JNEUROSCI.23-03-00859.2003

[44] Vidybida, A.K.: Activity of Excitatory Neuron with Delayed Feedback Stimulated with Poisson Stream is Non-Markov. J. Stat. Phys. 160(6), 1507–1518 (2015). https://doi.org/10.1007/s10955-015-1301-2

[45] Vidybida, A., Schchur, O.: Relation Between Firing Statistics of Spiking Neuron with Delayed Fast Inhibitory Feedback and Without Feedback. Fluct. Noise Lett. 17(1), 1850005 (2018). https://doi.org/10.1142/S0219477518500050

[46] Vidybida, A.: Relation Between Firing Statistics of Spiking Neuron with Instantaneous Feedback and Without Feedback. Fluct. Noise Lett. 14(4), 1550034 (2015). https://doi.org/10.1142/S0219477515500340

[47] Vidybida, O.K.: Output stream of a binding neuron. Ukr. Math. J. 59(12), 1819–1839 (2007). https://doi.org/10.1007/s11253-008-0028-5

[48] Vidybida, A.K.: Output Stream of Leaky Integrate-and-Fire Neuron Without Diffusion Approximation. J. Stat. Phys. 166(2), 267–281 (2017). https://doi.org/10.1007/s10955-016-1698-2

[49] Arunachalam, V., Akhavan-Tabatabaei, R., Lopez, C.: Results on a Binding Neuron Model and Their Implications for Modified Hourglass Model for Neuronal Network. Comput. Math. Methods Med. 2013, 374878 (2013). https://doi.org/10.1155/2013/374878
[50] Manseau, F., et al.: Desynchronization of Neocortical Networks by Asynchronous Release of GABA at Autaptic and Synaptic Contacts from Fast-Spiking Interneurons. PLoS Biol. 8(9), e1000492 (2010). https://doi.org/10.1371/journal.pbio.1000492

[51] Sun, X., Perc, M., Kurths, J., Lu, Q.: Fast regular firings induced by intra- and inter-time delays in two clustered neuronal networks. Chaos An Interdiscip. J. Nonlinear Sci. 28(10), 106310 (2018). https://doi.org/10.1063/1.5037142

[52] Polyanin, A.D., Manzhirov, A.V.: Handbook of Integral Equations, Second Edition. CRC Press, Boca Raton (2008). https://doi.org/10.1201/9781420010558