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Relation Between Firing Statistics of Spiking Neuron with Delayed Fast Inhibitory Feedback and Without Feedback

Alexander Vidybida* and Olha Shchur
*Bogolyubov Institute for Theoretical Physics
Metrologichna str. 14-B
Kyiv 03680, Ukraine
vidybida@bitp.kiev.ua

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We consider a class of spiking neuronal models, defined by a set of conditions typical for basic threshold-type models, such as the leaky integrate-and-fire or the binding neuron model and also for some artificial neurons. A neuron is fed with a Poisson process. Each output impulse is applied to the neuron itself after a finite delay Δ . This impulse acts as being delivered through a fast CI-type inhibitory synapse. We derive a general relation which allows calculating exactly the probability density function (pdf) $p(t)$ of output interspike intervals of a neuron with feedback based on known pdf $p^0(t)$ for the same neuron without feedback and on the properties of the feedback line (the Δ value). Similar relations between corresponding moments are derived.

Furthermore, we prove that the initial segment of pdf $p^0(t)$ for a neuron with a fixed threshold level is the same for any neuron satisfying the imposed conditions and is completely determined by the input stream. For the Poisson input stream, we calculate that initial segment exactly and, based on it, obtain exactly the initial segment of pdf $p(t)$ for a neuron with feedback. That is the initial segment of $p(t)$ is model-independent as well. The obtained expressions are checked by means of Monte Carlo simulation. The course of $p(t)$ has a pronounced peculiarity, which makes it impossible to approximate $p(t)$ by Poisson or another simple stochastic process.

Keywords: Spiking neuron; Poisson stochastic process; probability density function; delayed feedback; interspike interval statistics; variance.

1. Introduction

In the theory of neural coding, the rate coding paradigm dominated for a long time, [1–3]. In the framework of this paradigm, the essential neural signal is the mean number of impulses/spikes generated during some reference period, but not their

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exact position in time. If the temporal position of spikes does not matter, then it is natural to represent the seemingly random spike trains, produced by neurons, as Poisson processes, maybe with variable intensity, [4, 5]. In the course of gathering experimental data, it appeared that in some situations, the temporal structure of spike trains does have an essential role. For example, this is valid for echolocation, [6], early vision, [7], motor control, [8], late visual perception, [9]. A further, more rigorous examination of experimental data revealed that Poisson statistics, which does not have any temporal structure, is not suitable for modeling neuronal activity in some other brain areas, [10, 11], see also [12].

What might be the reason for appearing a temporal structure in neuronal spike trains? The two evident reasons are: (1) The threshold-type reaction to a stimulus; (2) A feedback presence, either direct or indirect, through intermediate neurons. Due to (1), more than a single input impulse is required for triggering. This makes it improbable to get a short output ISI, while for Poisson distribution, the shortest ISIs are the most probable. The second one may produce peculiarities in the pdf course for ISI length comparable with the feedback delay time. In this way, a fine temporal structure may appear in the spike trains even if primary stimulation is due to Poisson process. One more reason for a temporal structure in neuronal activity might be an adaptation of any kind, e.g., [13–15].

In this paper, we study the latter possibility. Namely, we consider a neuron with a fast inhibitory feedback and try to figure out what influence the feedback presence may have on statistical properties of its activity. Mathematically, we derive the ISI probability density function (pdf) for a neuron with feedback from its ISI pdf without feedback and the feedback line properties (see Fig. 1).

In the previous paper [16], the required relation has been obtained for the case when the feedback is excitatory and instantaneous, which allows calculating any one of the three pdfs, namely for stimulus, for output stream without feedback and for output stream with instantaneous feedback, provided the other two are given.

In this paper, we consider the case of fast inhibitory feedback with a *non-zero* delay. Biological justification of this case is given in Sec. 2.3. For this case, we obtain general relation allowing to calculate the ISI pdf $p(t)$ of a neuron with feedback based on known pdf $p^0(t)$ for the same neuron without feedback stimulated with the same input Poisson stochastic process, see Eqs. (11) and (12). The general relation is

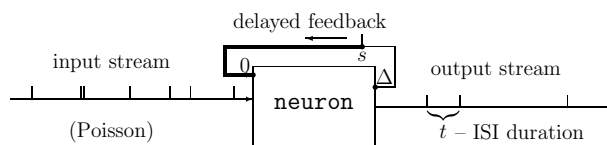


Fig. 1. Neuron with delayed feedback. As neuron in the figure, we consider any neuronal model, which satisfies the set of conditions Cond 0–Cond 4, above.

Firing Statistics of Spiking Neuron with Delayed Fast Inhibitory Feedback

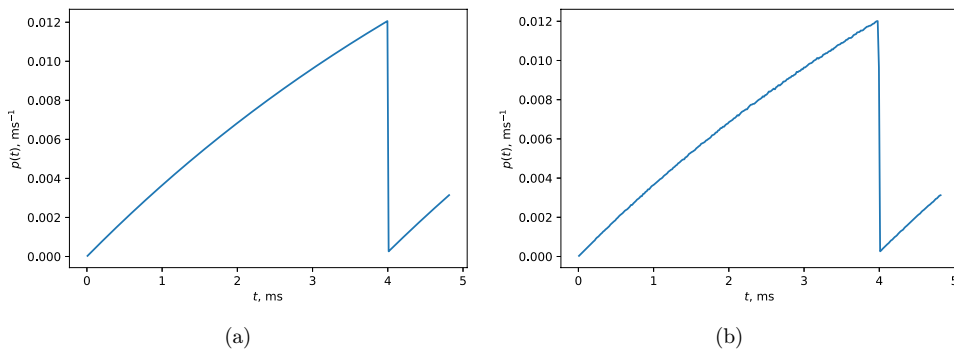


Fig. 2. Example of ISI PDF for the LIF neuron with threshold 2. (a) calculation in accordance with Eqs. (21) and (22). (b) Monte Carlo simulation (used 1000000000 output ISIs). For both panels: $\tau = 20$ ms, $V_0 = 20$ mV, $h = 11.2$ mV, (τ , V_0 and h are defined in Sec. 2.1) $\Delta = 4$ ms, $\lambda = 62.5$ s⁻¹.

obtained for a class of neuronal models, which includes the leaky integrate-and-fire and the binding neuron models,^a see Sec. 2.1, below.

Further, we analyze the pdf $p^0(t)$ of a neuron without feedback and discover that for any neuronal model, there exists initial interval $]0; T[$ of ISI values at which $p^0(t)$ does not depend on the neuronal model chosen, being completely defined by the input stream. Choosing Poisson stream as input, we calculate exactly that model-independent initial segment of $p^0(t)$, see Sec. 3.3. This allows us to calculate exactly the initial segment of $p(t)$, which is model-independent as well, see Sec. 3.5. A peculiarity in the $p(t)$ course for t close to the delay time is clearly seen in Fig. 2.

It appeared that the initial segment found for $p(t)$ is enough to express statistical moments of $p(t)$ through moments of $p^0(t)$, see Sec. 3.2, Eq. (14). In particular, we obtain in our approach the model-independent relation between the mean ISI of a neuron with and without feedback, which was known before for the binding neuron model only, see Eq. (23).

Finally, we check the exact expressions found for $p(t)$ by means of Monte Carlo simulation for the LIF neuron model, see Fig. 2.

2. Methods

2.1. Class of neuronal models

The neuronal state at the moment t is described by the depolarization voltage $V(t)$. If zero potential is chosen at the outer space of excitable membrane, then at the resting state $V \sim -70$ mV. In order to simplify expressions, we consider biased by 70 mV values of V . In this case, $V = 0$ at the resting state and depolarization is positive. This is similar (but not exactly the same) as in [18]. The input impulse

^aDefinition of the binding neuron model can be found in [17]. See also https://en.wikipedia.org/wiki/Binding_neuron.

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increases the depolarization voltage by h :

$$V(t) \rightarrow V(t) + h, \quad (1)$$

where $h > 0$.

The input impulse decay is governed by a function $y(u)$, which is different for different neuronal models. It means that if the first (and single) impulse is received at the moment t , then for any $u > 0$

$$V(t + u) = V(t) + hy(u). \quad (2)$$

For instance, if we consider the LIF model, then

$$y(u) = e^{-\frac{u}{\tau}}, \quad (3)$$

where τ is the relaxation time.

The neuron is characterized by a firing threshold value V_0 : as soon as $V(t) > V_0$, the neuron generates a spike and $V(t)$ becomes zero.

Instead of specifying any concrete neuronal model (through specifying V_0 , h and $y(u)$), we consider a class of neuronal models, which (without feedback) satisfy the following conditions:

- Cond 0: Neuron is deterministic: Identical stimuli elicit identical spike trains from the same neuron.
- Cond 1: Neuron is stimulated with input Poisson stochastic process of excitatory impulses.
- Cond 2: Just after firing, neuron appears in its resting state.
- Cond 3: The function $y(u)$, which governs decay of excitation, see Eq. (2), is continuous and satisfies the following conditions:

$$\begin{aligned} y(0) &= 1, \\ 0 < u_1 < u_2 &\Rightarrow y(u_1) \geq y(u_2). \end{aligned} \quad (4)$$

The equality sign stays for the perfect integrator model.

- Cond 4: The pdf for output ISIs, $p^0(t)$, where t means an ISI duration, exists together with all its moments.

Note that we do not assume in Eq. (1) and Cond 1, above, that h is the same for all input impulses. Actually, h may depend on the number of input impulse, or on the corresponding input ISI either deterministically, or stochastically, as in renewal reward processes.

We keep this freedom as regards the input stimulation up to Sec. 3.2, below, where the general expressions are obtained. For concrete cases, used as examples, we assume that the height of input impulse h is the same for all input impulses. In this case, the whole set of neuronal models, satisfying the above conditions with different V_0 and h , can be decomposed into a set of disjoint subsets numbered by $n = 1, 2, \dots$ by means of the following relation:

$$(n - 1)h \leq V_0 < nh. \quad (5)$$

If a model satisfies (5) with some n , then that neuron is said to have threshold n . Indeed, in this case, n specifies the minimal number of input impulses necessary for triggering.^b

2.2. Type of feedback

The neuron is equipped with a delayed feedback line, see Fig. 1. We expect that the feedback line has the following properties:

- Prop1: The time delay in the line is $\Delta > 0$.
- Prop2: The line is able to convey no more than one impulse.
- Prop3: The impulse conveyed to the neuronal input is the fast Cl⁻-type inhibitory impulse. This means that after receiving such an impulse, the neuron appears in its resting state and the impulse is immediately forgotten.

2.3. Biological justification

It is known that neurons can form synaptic connections with their own body or dendrites. Synapses of this type are called “autapses”. For inhibitory neurons, see [19–22].

There are two types of inhibitory currents initiated by two types of synapses. Those currents are created by Cl⁻ and K⁺ ions. The K⁺ currents have rather slow kinetics, see [21, 23–25] with the rise time ranging from tens to hundreds of milliseconds and the decay constant between hundreds of milliseconds to minutes. On the other hand, the Cl⁻ current rise time is below 5 ms and the decay constant is up to 25 ms, [25]. Having this in mind, and taking into account that the Cl⁻ reversal potential is equal to the resting potential, we model the Cl⁻ action as immediately shunting any excitation present in the neuron and doing nothing if the neuron is in its resting state. This explains the Prop3, above. Hardware-based artificial neurons, like used in [26, 27], can be covered by our approach as well, provided that Cond 0–4 and Prop1–3, above, are satisfied.

3. Results

3.1. Pdf: General relation

If the feedback line conveys an impulse, let s denote the time necessary for that impulse to reach the end of the line and act upon the neuron. Below, we call s “time to live”. Note that at the beginning of any ISI, the line is never empty. Let $f(s)$ denote the distribution of s at the beginning of ISI in the stationary regime. For calculating the pdf, we introduce the conditional probability density $p(t|s)$, which gives the probability to get the ISI t units of time long provided that at its beginning, the line bears an impulse with the time to live s . In the stationary regime, the

^bActually, the threshold expressed in terms of membrane voltage is always the same, but it is the height of input impulse h which varies for the different subsets.

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required ISI pdf $p(t)$ can be calculated as follows:

$$p(t) = \int_0^\Delta ds p(t|s)f(s). \quad (6)$$

The function $p(t|s)$ for the fast CI-type inhibitory feedback has been found previously in [28]. It looks as follows:

$$p(t|s) = \chi(s-t)p^0(t) + P^0(s)p^0(t-s), \quad (7)$$

where

$$P^0(s) = 1 - \int_0^s dt p^0(t), \quad (8)$$

$p^0(t)$ is the pdf without feedback and $\chi(t)$ is the Heaviside step function.

The pdf $f(s)$ satisfies the following equation, see [29]:

$$f(s) = \int_s^\Delta ds' p^0(s'-s)f(s') + \delta(s-\Delta) \int_0^\Delta ds' P^0(s')f(s'). \quad (9)$$

It appears from (6), (7) and (9) that it is only the exact expression for pdf without feedback $p^0(t)$ which is needed for finding the pdf with fast CI-type inhibitory feedback.

It follows from (9) that the $f(s)$ should have the following form:

$$f(s) = g(s) + a\delta(s-\Delta), \quad (10)$$

where $a > 0$ and $g(s)$ is bounded and vanishes out of interval $]0; \Delta]$. After substituting Eq. (10) into (9) and separating terms with and without δ -function, we obtain the following system of integral equations for unknown a and $g(s)$:

$$\begin{cases} a = \int_0^\Delta ds' P^0(s')g(s') + aP^0(\Delta); \\ g(s) = \int_s^\Delta ds' p^0(s'-s)g(s') + ap^0(\Delta-s). \end{cases} \quad (11)$$

After substituting (7) and (10) into (6) and taking into account that $p^0(t)$ equals to zero for negative argument, one can obtain the following:

$$p(t) = \begin{cases} \int_0^t ds P^0(s)p^0(t-s)g(s) + p^0(t) \left(\int_t^\Delta ds g(s) + a \right), & t < \Delta \\ aP^0(\Delta)p^0(t-\Delta) + \int_0^\Delta ds P^0(s)p^0(t-s)g(s), & t > \Delta. \end{cases} \quad (12)$$

This gives the straightforward algorithm for finding $p(t)$ from known $p^0(t)$:

- a: Calculate $P^0(t)$ according to Eq. (8).
- b: Substitute $P^0(t)$ and $p^0(t)$ into Eq. (11) and find a and $g(s)$.
- c: Substitute all into Eq. (12) and take the integrals.

In Secs. 3.3–3.5, we illustrate this in a situation when $p^0(t)$ is known exactly.

3.2. Moments of pdf: General relations

Denote W_n and W_n^0 the n th moment of $p(t)$ and $p^0(t)$, respectively. Using (12) within different time domains $[0; \Delta[$ and $[\Delta; \infty[$, the moments of $p(t)$ can be found as follows:

$$\begin{aligned} W_n &= \int_0^\infty dt t^n p(t) \\ &= \int_0^\Delta dt t^n \int_0^t ds P^0(s) p^0(t-s) g(s) + \int_0^\Delta dt t^n p^0(t) \left(\int_t^\Delta ds g(s) + a \right) \\ &\quad + a P^0(\Delta) \int_\Delta^\infty dt t^n p^0(t-\Delta) + \int_\Delta^\infty dt t^n \int_0^\Delta ds P^0(s) p^0(t-s) g(s) \\ &= A_1 + A_2 + A_3 + A_4. \end{aligned}$$

Consider first A_3 . After replacing the integration variable t by $(t - \Delta)$, one can obtain the following:

$$A_3 = a P^0(\Delta) \int_0^\infty dt (t + \Delta)^n p^0(t).$$

Using the moments' definition for pdf without feedback, W_n^0 , and taking into account that W_0^0 is a normalization coefficient and equals 1, one has

$$A_3 = a P^0(\Delta) \sum_{k=0}^n \binom{n}{k} W_k^0 \Delta^{n-k}.$$

In A_4 , we change the integration order:

$$A_4 = \int_0^\Delta ds P^0(s) g(s) \int_\Delta^\infty dt t^n p^0(t-s),$$

and then we replace the integration variable t by $(t - s)$:

$$A_4 = \int_0^\Delta ds P^0(s) g(s) \int_{\Delta-s}^\infty dt (t+s)^n p^0(t).$$

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Note that $\int_{\Delta-s}^{\infty} dt = \int_0^{\infty} dt - \int_0^{\Delta-s} dt$. Using this, normalization of $p^0(t)$ and definitions for W_n^0 , one gets:

$$A_4 = \int_0^{\Delta} ds P^0(s)g(s) \sum_{k=0}^n \binom{n}{k} W_k^0 s^{n-k} - \int_0^{\Delta} ds P^0(s)g(s) \times \int_0^{\Delta-s} dt (t+s)^n p^0(t). \quad (13)$$

Now, change the integration order in A_1 . This gives the same expression as the second term in (13). Finally, after cancellation, we have

$$W_n = \int_0^{\Delta} dt t^n p^0(t) \left(\int_t^{\Delta} ds g(s) + a \right) + \sum_{k=0}^n \binom{n}{k} W_k^0 \left(a P^0(\Delta) \Delta^{n-k} + \int_0^{\Delta} ds g(s) P^0(s) s^{n-k} \right). \quad (14)$$

3.3. Initial segment of $p^0(t)$ for Poisson input

Here, we consider a situation with the feedback line removed. Obviously, according to (2) and (4), the neuronal firing may happen only at the moment of receiving an input impulse. Assume that Eq. (5) is valid with some fixed $n > 1$ for our neuronal model. Let the last firing happen at the moment 0. After the last firing, the neuron requires at least n impulses in order to be triggered again. Denote as t the interval between the last and the next firing. The probability density function of this t is just^c $p^0(t)$. The first firing at the moment t may be triggered by the input impulse $\#n$, or greater. But for any neuron satisfying Conds 0–4, there exists an initial interval of t values, $[0; T_n]$. Those values can be achieved by triggering *only* due to the input impulse $\#n$. The latter is clear for very small values of t . For infinitesimally small t , the input impulse $\#n$ ensures excitation since $nh > V_0$, leaving no chances for the impulse $\#(n+1)$ to trigger the first firing. T_n is the maximum of such t (ISI, which is achievable by the n th input impulse only). The situation here is similar to discussed earlier for the LIF neuron in [30, Theorem 2].

To figure out the exact length of that initial interval, consider the situation when the first $(n-1)$ input impulses are obtained immediately after the last firing. Now, T_n is the maximum value of t , such that impulse $\#n$ delivered at t still triggers.

At the moment T_n , the first $(n-1)$ impulses ensure excitation $(n-1)hy(T_n)$. Now, T_n can be found from the following equation:

$$(n-1)hy(T_n) = V_0 - h,$$

^cNote that neuron without feedback has a renewal stochastic process as its output.

or

$$T_n = y^{-1}\left(\frac{V_0 - h}{(n-1)h}\right),$$

where the function y^{-1} is the inverse of y . For the perfect integrator, $T_n = \infty$.

According to the definition of T_n , any n input impulses received within $]0; T_n]$ evoke firing at the moment of receiving the last one. Therefore, the pdf $p^0(t) dt$ for $t \in [0; T_n]$ is the probability to receive $(n-1)$ input impulses within $]0; t[$ and the impulse $\#n$ within $[t; t + dt[$, whatever the $y(u)$ might be. In particular, for Poisson input with intensity λ , we have on the initial segment, a γ -distribution:

$$p^0(t) dt = e^{-\lambda t} \frac{(\lambda t)^{n-1}}{(n-1)!} \lambda dt, \quad t \leq T_n. \quad (15)$$

This is in concordance with [30, Eq. (21)], [31, Eq. (3)], where $p^0(t)$ within $]0; T_2]$ is found for the LIF and the binding neuron, respectively.

It is worth noticing that features of a concrete neuronal model are present in Eq. (15) only through the value of T_n . The time course of $p^0(t)$ within $]0; T_n]$ does not depend on neuron's physical properties (the manner of decaying of input stimuli governed by function $y(u)$ in (2)), but is completely determined by the input stochastic process.

As regards to the T_n value, for the LIF neuron model, $y(u)$ is defined by Eq. (3), from which we have

$$T_n = \tau \log\left(\frac{(n-1)h}{V_0 - h}\right).$$

3.4. Distribution of times to live

Here and further, we expect that

$$\Delta < T_n. \quad (16)$$

This allows us to obtain exact expressions in the case of Poisson stimulation without specifying an exact neuronal model.

In order to find the distribution $f(s)$ for time to live, one has to solve the system (11). It is clear from (11) that it determines the pair $(a, g(s))$ only up to arbitrary coefficient. In order to fix that uncertainty, we use the normalization condition:

$$1 = \int_0^\Delta ds g(s) + a. \quad (17)$$

Let us rewrite the second equation in (11) by replacing the unknown function with $\tilde{g}(s) = g(s)/a$:

$$\tilde{g}(s) = \int_s^\Delta ds' p^0(s' - s) \tilde{g}(s') + p^0(\Delta - s). \quad (18)$$

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Due to (16), we may use Eq. (15) with certain n in Eq. (18) in order to find the bounded part of the distribution of times to live $f(s)$. For a neuron with threshold $n = 2$, we have

$$\tilde{g}(s) = \lambda^2 e^{\lambda s} \int_s^\Delta ds' e^{-\lambda s'} s' \tilde{g}(s') - \lambda^2 e^{\lambda s} s \int_s^\Delta ds' e^{-\lambda s'} \tilde{g}(s') + \lambda^2 e^{-\lambda(\Delta-s)} (\Delta - s).$$

The solution is

$$\tilde{g}(s) = \frac{\lambda}{2} (1 - e^{-2\lambda(\Delta-s)}). \quad (19)$$

From Eq. (17)

$$a = \frac{4e^{2\lambda\Delta}}{1 + e^{2\lambda\Delta}(2\lambda\Delta + 3)}. \quad (20)$$

It is interesting to see that the last two equations are the same as in [32, Eqs. (15) and (16)], where those are obtained by another method for the binding neuron model with threshold 2.

3.5. Initial segment of $p(t)$ for threshold 2

We can find the pdf $p(t)$ for threshold 2 within $]0; \Delta]$ after substituting (15) with $n = 2$, (19) and (20) into the first equation in (12):

$$p(t) = \frac{2\lambda e^{-\lambda t}}{3 + 2\Delta\lambda + e^{-2\lambda\Delta}} \left(\frac{1}{6} \lambda^3 t^3 - \frac{1}{2} \lambda^2 t^2 + \lambda^2 t \Delta + \lambda t \right. \\ \left. \times \left(\frac{3}{2} + \frac{1}{4} e^{-2\lambda\Delta} + \frac{1}{4} e^{-2\lambda(\Delta-t)} \right) \right), \quad t < \Delta. \quad (21)$$

This is in concordance with what was obtained in [33, Eq. (21)] for the binding neuron. Here we have proven that this same distribution of ISIs is valid for all neuronal models satisfying the conditions of Sec. 2.1, above.

Within $]\Delta; T_2[$, $p(t)$ is obtained by integrating the second equation from (12):

$$p(t) = \frac{2\lambda e^{-\lambda t}}{3 + 2\Delta\lambda + e^{-2\lambda\Delta}} \left(\lambda t \left(\frac{1}{2} \lambda^2 \Delta^2 + \frac{5}{2} \lambda \Delta + \frac{7}{4} + \frac{1}{4} e^{-2\lambda\Delta} \right) \right. \\ \left. - \frac{1}{3} \lambda^3 \Delta^3 - 2\lambda^2 \Delta^2 - 2\lambda \Delta \right), \quad \Delta < t < T_2. \quad (22)$$

Since $T_2 = \infty$ for the perfect integrator, in that case, we have obtained the desired pdf within entire positive time semi-axis.

3.6. The first and the second moments for threshold 2

To find the moments of pdf $p(t)$, one should substitute (15) with $n = 2$, (19) and (20) into (14). Note that in (14), one needs to know $p^0(t)$ only for $t \leq \Delta$, which for Poisson input and restriction (16) is given in (15).

Thus, after taking all the integrals, we obtain the following expression for mean W_1 of $p(t)$:

$$W_1 = a(W_1^0 + \Delta) = \frac{4e^{2\lambda\Delta}}{1 + e^{2\lambda\Delta}(2\lambda\Delta + 3)}(W_1^0 + \Delta). \quad (23)$$

This is in concordance with [33, Eq. (23)] obtained for the binding neuron with threshold 2. The output intensity can be now found as

$$\lambda^{\text{out}} = \frac{1}{W_1}.$$

Similarly, one can obtain the following for the second moment W_2 :

$$W_2 = \frac{2(-1 + 2W_1^0\lambda + 8e^{\Delta\lambda}(1 - W_1^0\lambda) + e^{2\Delta\lambda}(-7 + 6\lambda(W_1^0 + \Delta) + 2W_2^0\lambda^2))}{\lambda^2(1 + e^{2\lambda\Delta}(2\lambda\Delta + 3))}. \quad (24)$$

Thus to find the moments of pdf for the neuron with feedback, it is enough to know the corresponding moments for the neuron without feedback. For example, one can find the output intensity for the LIF neuron with inhibitory feedback by means of substituting the expression for mean without feedback, [30, Eq. (46)], into (23).

4. Conclusions and Discussion

In this paper, we have derived general mathematical expressions, see Eq. (12), for calculating pdf $p(t)$ of output ISI distribution for a neuron with delayed fast inhibitory feedback stimulated with a Poisson stream of input impulses based on the pdf for that same neuron without feedback. The expression found is valid for a class of neuronal models defined by a set of natural conditions, see Conds 0–4 in Sec. 2.1. Standard threshold-type models, like the leaky integrate-and-fire model or the binding neuron model, satisfy the conditions mentioned above. Similar general expressions are derived for moments of the pdf found, Sec. 3.2. In the case of Poisson input stimulus, we obtain a model-independent exact expression for the initial segment of $p(t)$ and its moments, provided that a model is characterized by threshold 2, Eqs. (21)–(24).

The course of the pdf found, see Fig. 2, has clearly seen peculiarity — a jump for ISI $t = \Delta$, which excludes a possibility to describe the output ISI stream by a Poisson-like, or other simple distribution. Our findings add to the discussion about such a possibility, see [10, 11].

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