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## Output stream of binding neuron with instantaneous feedback

A.K. Vidybida



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A.K. Vidybida<sup>a</sup>

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

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**Abstract.** The binding neuron model [A.K. Vidybida, *BioSystems* **48**, 263 (1998)] is inspired by numerical simulation of Hodgkin-Huxley-type point neuron [A.K. Vidybida, *Biol. Cybern.* **74**, 539 (1996)], as well as by the leaky integrate-and-fire (LIF) model [J.P. Segundo, D. Perkel, H. Wyman, H. Hegstad, G.P. Moore, *Kybernetik* **4**, 157 (1968)]. In the binding neuron, the trace of an input is remembered for a fixed period of time after which it disappears completely. This is in the contrast with the above two models, where the postsynaptic potentials decay exponentially and can be forgotten only after triggering. The finiteness of memory in the binding neuron allows one to construct fast recurrent networks for computer modeling [A.K. Vidybida, *BioSystems* **71**, 205 (2003)]. Recently, [A.K. Vidybida, *BioSystems* **89**, 160 (2007)], the finiteness is utilized for exact mathematical description of the output stochastic process if the binding neuron is driven with the Poisson input stream. In this paper, it is expected that every output spike of single neuron is immediately fed back into its input. For this construction, externally fed with Poisson stream, the output stream is characterized in terms of interspike interval (ISI) probability density distribution if the neuron has threshold 2. For higher thresholds, the distribution is calculated numerically. The distributions are compared with those found for binding neuron without feedback, and for leaky integrator. It is concluded that the feedback presence can radically alter spiking statistics.

**PACS.** 87.19.lj Models of single neurons and networks – 87.10.-e General theory and mathematical aspects – 87.10.Ca Analytical theories – 87.10.Mn Stochastic modeling

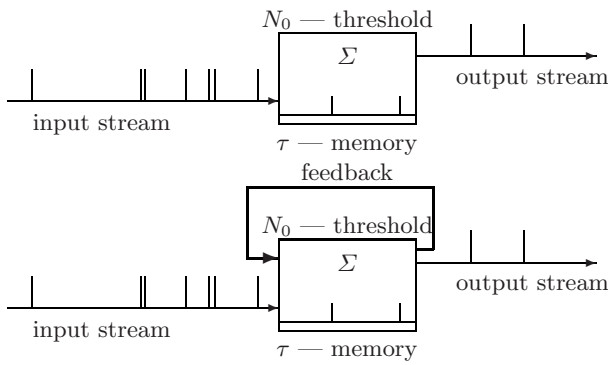
## 1 Introduction

The main function of a neuron is to receive signals and to send them out. In real neurons, this function is realized through concrete biophysical mechanism, the main parts of which are ion channels in excitable membrane and variations of ionic concentrations inside and outside of nerve cell and its processes, see [6] for details. The same function might be realized by means of any other mechanism able to support signals processing in the manner, which is characteristic of a real neuron. If so, then it would be interesting to develop a model, which realizes in an abstract form a concept of signal processing in real neurons, and is exempt from necessity to follow any biophysical mechanism supporting the processing. Such a model is necessary for quantitative mathematical formulation of what is going during signals/information processing in neural systems. Attempts to develop such a model are mainly concentrated around concepts of coincidence detector and temporal integrator, see discussion in [7]. One more model, the binding neuron (BN), is proposed as signal processing unit, 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. [8]. The BN model is inspired

by numerical simulation of Hodgkin-Huxley-type neuron stimulated from many synaptic inputs, as well as by the leaky integrate-and-fire model [3]. It describes functioning of a neuron in terms of events, which are input and output spikes, and degree of temporal coherence between the input events, see [1,2,5] for details. It is observed, that during processing of sensory signals, the spiking statistics of individual neurons changes substantially when the signal travels from periphery to more central areas (see, e.g. [9]). The changing of spiking statistics could underlie the information condensation, which happens during perception [10]. This transformation of statistics may happen due to feedforward and feedback connections between neurons involved in the processing. Having in mind such possibilities, it would be interesting to check what happens with spike train statistical properties when it passes neuronal structures with feedback connections.

Usually, feedback/recurrent connections are considered between several neurons. In this paper we consider the simplest possibility, namely, the single neuron with feedback. Such a configuration, can be found in real biological objects (see, e.g. [11,12]). As neuronal model we use binding neuron as it allows to obtain exact mathematical expressions, which may be suitable for further analysis. It is expected that input stream in any synapse of the neuron is Poisson one. In this case, from mathematical point of view, all input lines (input synaptic connections) can

<sup>a</sup> e-mail: vidybida@bitp.kiev.ua



**Fig. 1.** Schematic representation of binding neuron (top) and BN with feedback (bottom).

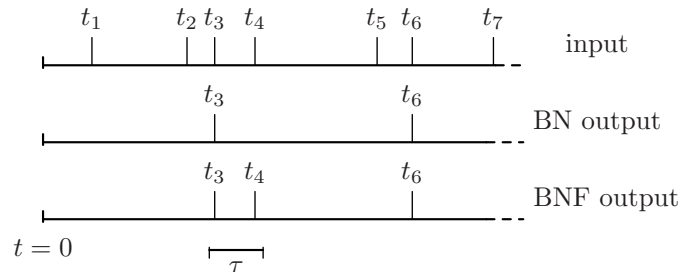
be replaced with a single one with Poisson stream in it, having its intensity equal to the sum of all intensities in the synapses (Fig. 1, top). The binding neuron works as follows. Any input impulse is stored in the neuron during time  $\tau$  and then it is forgotten. When the number of stored impulses,  $\Sigma$ , becomes equal to, or larger than the threshold one,  $N_0$ , the neuron sends out an output spike, clears its internal memory and is ready to receive impulses from the input stream. One obtains the binding neuron with feedback (BNF) by immediate feeding each output impulse to the neuron's input (Fig. 1, bottom). In this case, just after firing, the neuron has one impulse in its internal memory, and this impulse has time to live equal  $\tau$ .

The specifics of mathematical analysis of BN-type systems is due to presence in those systems both deterministic and stochastic dynamics. Namely, the neuron obtains its input from a random stream (stochastic component) and every impulse is stored for the same fixed period of time (deterministic component). This is in the contrast with the mass service theory [13], where the service time (counterpart of time to live,  $\tau$ ) is random, Poisson-distributed. The simultaneous presence of deterministic and random dynamics in real neurons is due to the fact that in real neurons the impulse existence in a neuron (exposed as the excitatory postsynaptic potential) is supported by electrochemical transient [14], which is deterministic, whereas the input impulses come from other neurons and external media in irregular (random) manner<sup>1</sup>.

## 2 Condensing of information with neurons

It is widely accepted that during flow of sensory signals in a hierarchical manner from sensory periphery to central brain areas, the information, which is present in the signals, becomes less analogue and more discrete, eventually resulting in representing discrete symbols or entities (see e.g. [10]). During this process, the amount of information within the flow must decrease in order to map various input spike trains from the sensory periphery into the same

<sup>1</sup> Compare with [15,16], where approach is adopted, which is consistent with mass service theory.



**Fig. 2.** Example of input spike train and corresponding output for binding neuron (BN), and binding neuron with feedback (BNF). In both cases  $N_0 = 2$ .

discrete entity. This process of consecutive reduction of information is known as condensation. Condensation of information represents a possible route to selforganization (compare with [17], No. 1.19). We now put a question: what could be the primary element in which the condensation takes place? It seems that single neuron is a suitable candidate for such an element. In the case of binding neuron this can be explained as follows.

Consider an input spike train like upper train in Figure 2. The train can be regarded as signal from a receptor neuron. After processing with the BN, the output spike train consists of two output impulses at moments  $t_3$  and  $t_6$ . The BNF gives three spikes at moments  $t_3, t_4$  and  $t_6$ . It is clear that the output trains contain less information than the input one. Nevertheless, having the output train for either BN, or BNF, one can make some condensed conclusions concerning the input train.

In the case of BN, the output spike at moment  $t_3$  tells us that there were input impulses at moments  $t_3$  and  $t^*$ , where  $t^* \in ]t_3 - \tau; t_3[$ , and the input impulse at moment  $t^*$  did not trigger an output one at the moment of its arrival. For realization shown in Figure 2,  $t^* = t_2$ . Information delivered in the output spike  $t_3$  is indeed condensed, because the presence and exact timing of this output spike does not change if position of  $t^*$  deviates remaining within interval  $]t_3 - \tau; t_3[$ . The same is about output spike at moment  $t_6$ .

In the case of BNF, the output spike at moment  $t_3$  tells us that there were input impulses at moments  $t_3$  and  $t^*$ , where  $t^* \in ]t_3 - \tau; t_3[$ , and the time interval  $]t^* - \tau; t^*[$  is free of input impulses. The same is about  $t_6$ . Two output spikes at moments  $t_3, t_4$ , where  $t_4 - t_3 < \tau$ , tell us additionally that in the input there were 3 successive impulses separated by intervals shorter than  $\tau$ . Similar conclusions can be made for binding neurons with  $N_0 > 2$ . Moreover, condensed conclusion about input, which is based on corresponding output spike train, can be formulated for other neuronal models, like Hodgkin and Huxley, or leaky integrator. The difference is that for binding neuron the conclusion admits formulation in precise and clear mathematical manner, whereas for other models it does not. A less precise, fuzzy formulation, which is suitable for any model is that the output spike signals about presence in the input train temporally coherent (distributed over short time interval) set of impulses (see [1,2] for discussion).

### 3 Output intensity of BNF with threshold 2

The intensity of output stochastic process can be defined by three different ways:

1. It is possible to define the instantaneous intensity (see [13]),  $\lambda_o(t)$ , as the probability to obtain an output impulse at moment  $t$  in infinitesimal interval  $s$  divided by  $s$ :

$$\lambda_o(t) = \lim_{s \rightarrow 0} \frac{w(s, t)}{s}, \quad (1)$$

where  $w(s, t)$  denotes the probability to obtain impulse in the interval  $[t; t + s[$ . We do not intend to analyze the  $\lambda_o(t)$  time dependence here.

2. As limit, or mean output intensity one can choose the following

$$\lambda_o = \lim_{t \rightarrow \infty} \lambda_o(t). \quad (2)$$

3. In the definition of  $\lambda_o$  in (2), the role of time limit is to ensure that the initial state of the system is forgotten. In this case one can define/calculate  $\lambda_o$  as the factor in the expression  $\lambda_o dt$ , which gives the probability to obtain an output impulse in the infinitesimal interval  $dt$ , if nothing is known about previous states of the neuron.

It can be shown that both definitions 2 and 3 bring about the same value for  $\lambda_o$ . Therefore, we choose the third one here. Calculations based on the second definition can be fulfilled with the help of ([18], Part. XI, Sect. 8).

The probability to obtain an output impulse from the BNF with threshold 2 in the interval  $[t; t + dt[$ ,  $\lambda_o dt$ , can be calculated as product of probabilities of two independent events: (i) an input impulse,  $I_1$ , arrives in the interval  $[t - \tau; t[$ ; (ii) the next input impulse,  $I_2$ , arrives in the interval  $[t; t + dt[$ . Event (ii) has probability  $\lambda dt$ . Event (i) has the same probability as having in Poisson stream two successive events (here  $I_1, I_2$ ) separated by time interval, which is shorter than  $\tau$ . This probability is  $1 - e^{-\lambda\tau}$ . Thus,

$$\lambda_o = (1 - e^{-\lambda\tau})\lambda. \quad (3)$$

Interesting, that for high input rates ( $\lambda \rightarrow \infty$ ), the triggering rate becomes equal to the input one. This can be explained as follows. If input rate is very high, almost all input ISIs become shorter than  $\tau$ . In this case, any input, stored in the BNF will eventually give rise to output spike, which is immediately used as input for empty neuron due to feedback. This effectively doubles the input rate. Namely, any input impulse triggers the BNF, and then it is applied to empty BNF through feedback. As a result, the output stream for high  $\lambda$  literally reproduces the input one: any input spike becomes the output one without delay<sup>2</sup>. This same reasoning allows one to say that output rate of BNF with any threshold  $N_0$  approaches  $\lambda/(N_0 - 1)$  when  $\lambda \rightarrow \infty$ . Compare this with BN without feedback in [5], where corresponding limit output rate is  $\lambda/N_0$ .

<sup>2</sup> See also discussion section.

### 4 Distribution of output intervals for BNF with $N_0 = 2$

Let us consider a BNF with threshold  $N_0 = 2$  and internal memory  $\tau$ , which obtains its input from Poisson stream with intensity  $\lambda$ . Thus, the neuron fires every time when input impulse arrives  $\tau$ , or less units of time after its predecessor.

The output statistics can be described in terms of the probability density distribution to obtain an output interspike interval  $t$  with precision  $dt$ . For this purpose it is enough to calculate the probability,  $P_b(t, \tau)dt$ , of the following event: the next firing happens  $t$  units of time later than the previous one. Let the input impulses, which arrive after the previous firing, are numbered with numbers 1, 2, ... .

The above-mentioned event can be decomposed into several alternatives, which are numbered with the number  $k$  of input impulse, which triggers the next firing. Notice, that for  $t < \tau$  only one alternative is possible. It happens if the first input impulse arrives not later than  $\tau$  units of time after the previous firing. In this case, the neuron still keeps impulse from the previous firing, and the input secures the threshold to be achieved and BNF to fire. There is no other way to get output interval  $t$  shorter than  $\tau$ . Thus, for  $t \in [0; \tau[$ , the probability density distribution of ISI coincides with the distribution for the input Poisson stream:

$$P_b(t, \tau) dt = e^{-\lambda t} \lambda dt. \quad (4)$$

It is impossible to obtain output interval  $t > \tau$  with a single input impulse<sup>3</sup>. Thus, for  $t > \tau$ , possible alternatives are numbered with numbers 2, 3, ...,  $k_{max}$ , where  $k_{max} = [t/\tau] + 1$ , and  $[x]$  denotes the integral part of  $x$ .

Assume, the  $k$ -th alternative is realized by input arrival times  $t_1, t_2, \dots, t_{k-1}, t_k \equiv t$ . Not all arrival times are admitted (see (5) and further, below). In accordance with the definition of Poisson process, the probability of such realization is given by the following expression:

$$e^{-\lambda t_1} \lambda dt_1 e^{-\lambda(t_2 - t_1)} \lambda dt_2 \dots e^{-\lambda(t - t_{k-1})} \lambda dt.$$

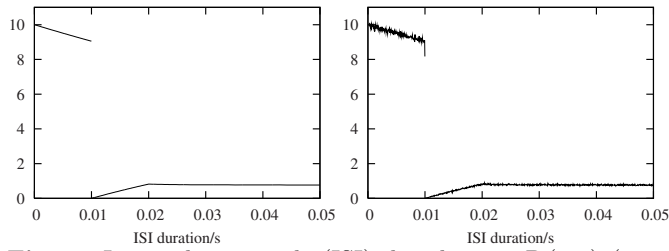
The probability  $P_{bk}(t, \tau)dt$  that the  $k$ -th alternative is realized with any admissible values of  $t_1, t_2, \dots, t_{k-1}$  can be calculated by integrating of the above expression over the region of  $(k - 1)$ -dimensional space with coordinates  $t_1, t_2, \dots, t_{k-1}$ , defined by the following conditions:

$$t_1 \geq \tau, \quad t_1 + \tau < t_2, \quad \dots, \quad t_{k-2} + \tau < t_{k-1} < t, \quad (5)$$

and  $t - t_{k-1} < \tau$ . The required integral over the region defined by (5) can be calculated exactly:

$$e^{-\lambda t} \lambda^{k-1} \int_{\tau}^{t-(k-2)\tau} dt_1 \int_{t_1+\tau}^{t-(k-3)\tau} dt_2 \dots \int_{t_{k-2}+\tau}^t dt_{k-1} \lambda dt = e^{-\lambda t} \lambda^{k-1} \frac{(t - (k-1)\tau)^{k-1}}{(k-1)!} \lambda dt. \quad (6)$$

<sup>3</sup> The value of  $P_b(\tau, \tau)$  can be chosen arbitrary.



**Fig. 3.** Interspike intervals (ISI) distribution  $P_b(t, \tau)$  (measured in  $\text{s}^{-1}$ ) for  $\tau = 10$  ms,  $\lambda = 10$   $\text{s}^{-1}$ ,  $N_0 = 2$ . Left – calculated in accordance with (4, 7), right – calculated numerically.

If  $k = k_{max}$ , then (5) ensures:  $(k - 1)$ -th impulse is in the interval  $]t - \tau; t[$ , and  $k$ -th impulse at moment  $t$  will cause firing. Thus, in this case

$$P_b k(t, \tau) dt = e^{-\lambda t} \lambda^{k-1} \frac{(t - (k-1)\tau)^{k-1}}{(k-1)!} \lambda dt, \quad k = k_{max}.$$

If  $k < k_{max}$ , then integral (6) includes also configurations for which  $t_{k-1} < t - \tau$ . For these configurations  $k$ -th input impulse at moment  $t$  will not cause firing. The contribution of these configurations into the integral (6) is given by the following expression

$$e^{-\lambda t} \lambda^{k-1} \int_{\tau}^{t-(k-1)\tau} dt_1 \int_{t_1+\tau}^{t-(k-2)\tau} dt_2 \cdots \int_{t_{k-2}+\tau}^{t-\tau} dt_{k-1} \lambda dt = e^{-\lambda t} \lambda^{k-1} \frac{(t - k\tau)^{k-1}}{(k-1)!} \lambda dt,$$

which should be subtracted from (6). Thus, for  $2 \leq k < k_{max}$ :

$$P_b k(t, \tau) dt = e^{-\lambda t} \frac{\lambda^{k-1}}{(k-1)!} ((t - (k-1)\tau)^{k-1} - (t - k\tau)^{k-1}) \lambda dt.$$

The total probability is calculated by summation over all alternatives. Notice, that  $k_{max}$  changes by 1 when  $t$  passes through integer multiple of  $\tau$ . Thus, for  $m = 1, 2, \dots$  the following statement is valid: if  $m\tau < t < (m+1)\tau$ , then

$$P_b(t, \tau) dt = e^{-\lambda t} \frac{\lambda^m}{m!} (t - m\tau)^m \lambda dt + \sum_{2 \leq k \leq m} e^{-\lambda t} \frac{\lambda^{k-1}}{(k-1)!} \times ((t - (k-1)\tau)^{k-1} - (t - k\tau)^{k-1}) \lambda dt. \quad (7)$$

For  $t \in [0; \tau[$  the function  $P_b(t, \tau) dt$  is given by (4). The distribution  $P_b(t, \tau) dt$ , which is given in equations (4, 7), is analogous to distribution  $P(t) dt = e^{-\lambda t} \lambda dt$  known for Poisson process. The graph of  $P_b(t, \tau)$  is shown in Figure 3.

## 5 Properties of the distribution

Notice that after firing, the neuron starts from standard state: it keeps a single impulse with time to live equal  $\tau$ .

Therefore, there is no correlation between successive interspike intervals. This fact depends crucially on the immediateness of feedback. For delayed feedback, as it could be suggested by [19], successive interspike intervals will be correlated.

### 5.1 Connection with BN distribution

It is interesting that function  $P(t, \tau)$ , which gives the probability density distribution for binding neuron without feedback (see [5], Eq. (6)) has simple interconnection with  $P_b(t, \tau)$ . In order to find this interconnection, denote restriction of  $P_b(t, \tau)$  onto interval  $[m\tau; (m+1)\tau[$  as  $P_{bm}(t, \tau)$ . (7) then means:

$$m\tau \leq t < (m+1)\tau \Rightarrow P_b(t, \tau) = P_{bm}(t, \tau), \quad m = 1, 2, \dots$$

Substitute here  $t + \tau$  instead of  $t$ :

$$m\tau \leq t + \tau < (m+1)\tau \Rightarrow P_b(t + \tau, \tau) = P_{bm}(t + \tau, \tau),$$

where  $m = 1, 2, \dots$ , or

$$(m-1)\tau \leq t < m\tau \Rightarrow P_b(t + \tau, \tau) = P_{bm}(t + \tau, \tau),$$

where  $m = 1, 2, \dots$ . Substitute here  $m$  instead of  $(m-1)$ :

$$m\tau \leq t < (m+1)\tau \Rightarrow P_b(t + \tau, \tau) = P_{b,m+1}(t + \tau, \tau), \quad m = 0, 1, 2, \dots$$

The explicit expression for  $P_{b,m+1}(t + \tau, \tau)$  can be obtained from (7):

$$P_{b,m+1}(t + \tau, \tau) = e^{-\lambda(t+\tau)} \frac{\lambda^{m+1}}{(m+1)!} (t - m\tau)^{m+1} \lambda + \sum_{2 \leq k \leq m+1} e^{-\lambda(t+\tau)} \frac{\lambda^{k-1}}{(k-1)!} \times ((t - (k-2)\tau)^{k-1} - (t - (k-1)\tau)^{k-1}) \lambda.$$

The last expression coincides with the corresponding term in the ([5], Eq. (6)) multiplied by  $e^{-\lambda\tau}$ . Thus, the following representation takes place:

$$\begin{cases} 0 \leq t < \tau \Rightarrow P_b(t, \tau) = e^{-\lambda t} \lambda, \\ \tau \leq t \Rightarrow P_b(t, \tau) = e^{-\lambda\tau} P(t - \tau, \tau). \end{cases} \quad (8)$$

The last expression together with the fact that  $P(t, \tau)$  from ([5], Eq. (6)) is normalized, allows one to check easily that  $P_b(t, \tau)$  is normalized as well:

$$\int_0^{\infty} P_b(t, \tau) dt = 1.$$

## 5.2 Mean interspike interval

Having for  $P_b(t, \tau)$  representation (8), one can easily calculate mean interspike interval,  $W$ , which is defined as

$$W = \int_0^{\infty} t P_b(t) dt.$$

Substitute here representation (8):

$$\begin{aligned} W &= \int_0^{\tau} t e^{-\lambda t} \lambda dt + \int_{\tau}^{\infty} t e^{-\lambda \tau} P(t - \tau, \tau) dt \\ &= \frac{1 - e^{-\lambda \tau}}{\lambda} - \tau e^{-\lambda \tau} + e^{-\lambda \tau} \int_0^{\infty} (t + \tau) P(t, \tau) dt \\ &= \frac{1 - e^{-\lambda \tau}}{\lambda} + e^{-\lambda \tau} \int_0^{\infty} t P(t, \tau) dt. \end{aligned}$$

The last integral is calculated in [5] Section 3.2. Use found there expression:

$$\begin{aligned} W &= \frac{1 - e^{-\lambda \tau}}{\lambda} + e^{-\lambda \tau} \frac{1}{\lambda} \left( 2 + \frac{1}{e^{\lambda \tau} - 1} \right) \\ &= \frac{1}{\lambda (1 - e^{-\lambda \tau})}. \end{aligned} \quad (9)$$

Compare this with (3).

## 5.3 Coefficient of variation

Coefficient of variation  $c_{fv}$  for obtained distribution (7) can be calculated as follows

$$c_{fv} = \sqrt{\frac{W_2}{W^2}} - 1, \quad (10)$$

where  $W$  is given in (9), and  $W_2$  is the second moment of distribution (7):

$$W_2 = \int_0^{\infty} t^2 P_b(t, \tau) dt.$$

Here use representation (8):

$$\begin{aligned} W_2 &= \lambda \int_0^{\tau} t^2 e^{-\lambda t} dt + e^{-\lambda \tau} \int_{\tau}^{\infty} t^2 P(t - \tau, \tau) dt \\ &= \frac{2 - ((\lambda \tau)^2 + 2\lambda \tau + 2)e^{-\lambda \tau}}{\lambda^2} \\ &\quad + e^{-\lambda \tau} \int_0^{\infty} (t + \tau)^2 P(t, \tau) dt. \end{aligned} \quad (11)$$

The second term here can be split into three:

$$\begin{aligned} e^{-\lambda \tau} \int_0^{\infty} \tau^2 P(t, \tau) dt &= e^{-\lambda \tau} \tau^2, \\ e^{-\lambda \tau} 2\tau \int_0^{\infty} t P(t, \tau) dt &= e^{-\lambda \tau} 2\tau \frac{1}{\lambda} \left( 2 + \frac{1}{e^{\lambda \tau} - 1} \right), \end{aligned}$$

(used same expression as for calculating (9)), and

$$e^{-\lambda \tau} \int_0^{\infty} t^2 P(t, \tau) dt.$$

The ISI distribution's second moment for BN without feedback can be calculated similarly as it is done for its first moment. This gives

$$\int_0^{\infty} t^2 P(t, \tau) dt = \frac{2}{\lambda^2} \frac{3e^{2\lambda \tau} + (\lambda \tau - 3)e^{\lambda \tau} + 1}{(e^{\lambda \tau} - 1)^2}. \quad (12)$$

Substitute this into (11). This gives

$$W_2 = \frac{2e^{\lambda \tau}}{\lambda^2} \frac{e^{\lambda \tau} + \lambda \tau}{(e^{\lambda \tau} - 1)^2}. \quad (13)$$

Substitute this and (9) into (10), this gives

$$c_{fv} = \sqrt{2\lambda \tau e^{-\lambda \tau} + 1}.$$

Coefficient of variation gets its maximum value,  $c_{fv m}$ ,

$$c_{fv m} = \sqrt{2e^{-1} + 1} \approx 1.32$$

at  $\lambda \tau = 1$  (Fig. 5, left).

It is also possible, by using equation (12), to calculate coefficient of variation,  $c_v$ , for BN without feedback:

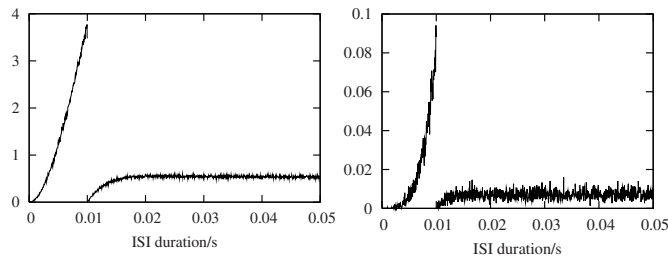
$$c_v = \sqrt{\frac{2\lambda \tau e^{\lambda \tau} + 0.5}{4e^{2\lambda \tau} - 4e^{\lambda \tau} + 1} + \frac{1}{2}}.$$

The  $c_v$  gets its maximum value equal to 1 at  $\lambda \tau = 0$ , and decreases monotonically when  $\lambda \tau$  increases (Fig. 5, left).

## 6 Numerical simulations

Numerical simulations were carried out here for several purposes. The first purpose was to check numerically correctness of the expressions found analytically in previous sections. A C++ program was developed, which allows to calculate the  $P_b(t, \tau)$ . The Poisson streams were generated by transformation of uniformly distributed sequences of random numbers (see, e.g. Eqs. (12.14) in [20]). Those sequences were produced with the system pseudo-random number generator from `libc` library in the Linux operating system, as well as with the Mersenne Twister,





**Fig. 4.** ISI distribution  $P_b(t, \tau)$  (measured in  $s^{-1}$ ) found numerically for  $\tau = 10$  ms,  $\lambda = 50$   $s^{-1}$ . Left –  $N_0 = 4$ , right –  $N_0 = 6$ . Notice the discontinuity at  $t = \tau$ . 30 000 000 triggerings were taken in both cases.

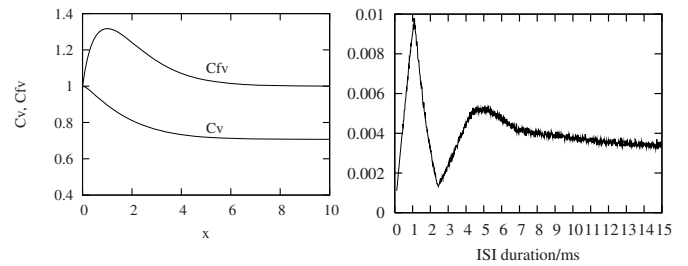
mt19937 [21]. The two methods give indistinguishable results. The program includes the BNF class, which analyzes the input stream and fires in accordance with the rules, described above. With the help of that class, output stream samples were produced by calculating  $N = 30\,000\,000$  output spikes. The samples are scanned for interspike intervals of various duration, and the probability density distribution is then calculated by normalization. The numerically obtained ISI distributions are in good agreement with analytical expression, as it can be seen in Figure 3. Also, the second moment of  $P_b(t, \tau)$  was calculated numerically for several values of  $\lambda$ ,  $\tau$ . Deviation of numerically found values from analytical expression (13) is within  $0.01\% \div 0.1\%$  range.

The second purpose of numerical calculations is to obtain ISI distributions for higher thresholds. The above mathematical reasoning for BNF with threshold  $N_0 = 2$  becomes extremely cumbersome for thresholds  $N_0 = 3$ , or higher. It seems that there should be a more efficient mathematical approach for higher thresholds. Meanwhile, it is possible to calculate numerically the probability density distribution for any threshold value. Examples of calculated densities are shown in Figure 4. These densities are in qualitative agreement with what is found analytically for  $N_0 = 2$ , except of the fact that the initial part of ISI distribution is increasing for  $N_0 > 2$ , whereas for  $N_0 = 2$  it is decreasing. The initial (for  $t < \tau$ ) part of the probability density distribution  $P_b(t, \tau)dt$  can be easily found analytically for any threshold  $N_0$ . Indeed, denote the moment of the previous firing as 0. At this moment BNF stores one impulse with time to live  $\tau$ . The next firing happens at moment  $t < \tau$  iff  $N_0 - 2$  input impulses arrive within the interval  $]0; t[$ , and one more impulse within  $]t; t + dt[$ . The probability of such event for Poisson process is known, which gives for any  $N_0 \geq 2$

$$P_b(t, \tau) dt = e^{-\lambda t} \frac{(\lambda t)^{N_0-2}}{(N_0-2)!} \lambda dt, \quad t < \tau.$$

This function is decreasing for  $N_0 = 2$  and increasing for higher  $N_0$ , which explains seeming qualitative disagreement between  $N_0 = 2$  and  $N_0 > 2$  cases.

The third purpose was to compare the ISI distributions found here for the binding neuron model with those for leaky integrate and fire (LIF) model. In the program developed, the BNF class was replaced with LIF class,



**Fig. 5.** Left: coefficient of variation as function of  $x = \lambda\tau$  for BN ( $C_v$ ) and BNF ( $C_{fv}$ ). Right: ISI distribution  $P_b(t)$  (measured in  $s^{-1}$ ) found numerically for leaky integrate and fire model with feedback. Used 30 000 000 output spikes. Firing threshold,  $C = 20$  mV, input intensity,  $\lambda = 0.1$   $s^{-1}$ , membrane time constant,  $\tau_M = 6$  ms, input impulse amplitude,  $y_0 = 7.5$  mV.

which reproduces the simplest version of the LIF model. Namely, the LIF neuron is characterized by a threshold,  $C$ , and every input impulse advances by  $y_0$  the LIF membrane voltage,  $V$ . Between input impulses,  $V$  decays exponentially with time constant  $\tau_M$ . The LIF neuron fires when  $V$  becomes greater or equal  $C$ , and  $V = 0$  just after firing. Examples of the ISI distribution obtained for various parameter values are shown in Figures 5 (right) and 6 (left).

## 7 Conclusions

We calculated here intensity and output interspike intervals distribution for binding neuron with instantaneous feedback, which is stimulated with Poisson stream. For BNF with threshold  $N_0 = 2$  this is done analytically, for higher thresholds – numerically. It is interesting to compare the obtained distributions with those known for a single neuron without feedback. Such distributions are obtained numerically for LIF model in [3], and analytically for binding neuron in [5]. In both cases distributions are continuous and uni-modal. By comparing these distributions with those found here for BNF (see also comparison of coefficients of variation in Sect. 5.3), one could conclude that even the simplest possible feedback excitation is able to change radically statistical properties of spiking process. This gives a hint about what could take place with spiking statistics of individual neurons in networks, where feedback due to recurrent excitation (mediated by neighbor neurons) is typical feature. Numerical calculations made for the LIF model with feedback (Fig. 5, right, and Fig. 6, left) suggest, that introducing feedback might result in qualitative changing of spiking statistics for other neuronal models as well.

## 8 Discussion

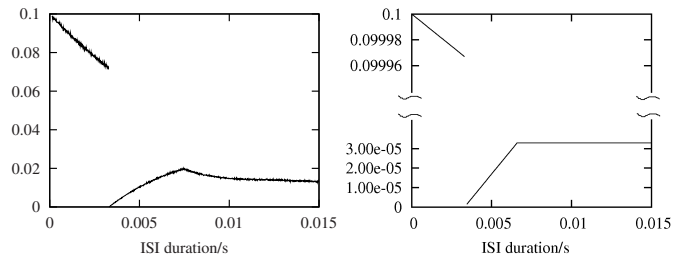
The problem of mathematically rigorous description of firing statistics of a model neuron seems to be interesting for several reasons. Firstly, it is because that statistics can be estimated experimentally. Statistical characteristics, such

as mean, dispersion, coefficient of variation in the ISIs distribution, and ISIs distribution itself are of interest. Unfortunately, obtaining exact mathematical expressions for those quantities is difficult task, mainly due to threshold-type behavior of real neurons, which must be present in any neuronal model. A substantial progress in obtaining analytical expressions for those quantities is made for diffusion models only, see [22–26]. If input to a model neuron (usually, leaky integrate and fire one) is chosen as diffusion stochastic process, then contribution of individual input impulses is infinitesimally small, which is compensated by a possibility to have infinite number of input impulses during finite time interval, see [27]. The validity of such a situation could be approved if in reality a neuron obtains large number of inputs during short time intervals, or at least the number of inputs, which is necessary for triggering is large. This is tightly connected with the well-known spike code – rate code paradigms. In the case of rate coding, the diffusion approximation is suitable, and in the case of spike coding it does not. Available data suggest that in nervous system both paradigms coexist, see discussion in [7]. This is also supported by experimental findings of how many synaptic impulses is necessary to trigger a neuron. The number varies from one [28], through fifty [29], to 60–180 [30], and 100–300 [31].

The diffusion approximation has an advantage, that it allows to obtain conclusions for a range of threshold values in a uniform manner. Considering individual input spikes as significant, requires to develop separate mathematical approach for each individual value of threshold, see [32], where output intensity is calculated for BN with  $N_0 = 3$ . In principle, diffusion approximation could be applied for binding neuron as well. Numerical simulations made for BN with thresholds up to 20 (unpublished data) suggest that ISIs distribution for BN stimulated with diffusion process will be qualitatively similar to what was obtained in [3,5]. But it will be difficult to preserve diffusion process paradigm while feeding back individual output spikes in BNF. At the same time, consideration of individual spikes as significant, allows new behavior to appear in leaky integrate and fire neuron as well (Fig. 5, right, and Fig. 6, left).

The exact discontinuities in the output ISI distributions, which can be seen in Figures 3, 4, are due to abrupt loss of feedback input influence  $\tau$  units of time after triggering. Output ISI, which is shorter than  $\tau$ , is created with the feedback spike involved. The longer ISIs are created without feedback spikes. Therefore, the jump is in the direction of smaller probabilities. In the models, in which the influence of input spike diminishes gradually, one could expect the decreasing region of probability density function course in the range, where role of feedback inputs becomes small. This could cause a bimodal distribution of output ISIs, like shown in Figure 5, right. Nevertheless, for special parameter values, the genuine discontinuity can be as well observed for the LIF model, like in Figure 6, left<sup>4</sup>.

<sup>4</sup> For the LIF model, the presence of discontinuity in ISI distribution in Figure 6, left, can be proved mathematically rigorously.



**Fig. 6.** Left: ISI distribution  $P_b(t)$  found numerically for leaky integrate and fire model with feedback. Used 30 000 000 output spikes. Firing threshold,  $C = 20$  mV, input intensity,  $\lambda = 0.1$  s<sup>-1</sup>, membrane time constant,  $\tau_M = 3$  ms, input impulse amplitude,  $y_0 = 15$  mV. Right: BNF ISI distribution in accordance with equations (4) and (7) displayed for comparison. Here  $\lambda = 0.1$  s<sup>-1</sup>,  $\tau = 3.3$  ms. Both densities are measured in s<sup>-1</sup>. Compare also with Figure 3.

It is worth noticing the high variability of the BNF ISIs distribution, which can be seen in Figure 5, left, which is similar to experimentally observed for real neurons, [33]. The coefficients of variation dependence on  $x = \lambda\tau$ , which is found for BN and BNF, can be explained as follows. For  $x \rightarrow 0$  both BN, and BNF output streams become Poisson. Indeed, consider the BN case. The BN will generate an output spike in interval  $[t; t + dt[$  if three conditions are satisfied: (i) there is input spike in  $[t; t + dt[$ , (ii) the previous input was received at  $t - \tau$ , or later, (iii) the previous input did not trigger BN. Violation of cond. (iii) with (i), (ii) satisfied is improbable when  $\lambda\tau \rightarrow 0$ , because this means appearance of two successive input ISIs, both shorter than  $\tau$ , which is small compared to  $1/\lambda$ . For Poisson input this may happen with probability  $(1 - e^{-\lambda\tau})^2$ , and for small  $x$  may be neglected. In this case the desired probability of output is  $(1 - e^{-\lambda\tau}) \lambda dt$ , which describes Poisson stream with intensity  $\lambda' = (1 - e^{-\lambda\tau}) \lambda$ . For this stream, coefficient of variation is 1. Similar reasoning is valid for BNF. In the opposite case, when  $\lambda\tau \rightarrow \infty$ , violation of condition (iii) for BN cannot be ignored. Actually, for high stimulation rates, the BN will act as perfect integrator. The output stream of perfect integrator is  $\gamma$ -distributed, with  $c_v < 1$ . For BNF at high stimulation rates, every feedbacked spike will combine with next input one, and trigger next output spike<sup>5</sup>. This possibility was mentioned as “dancing in step” in [34] page 43. In such a regime, output stream exactly reproduces the input one, hence, is Poisson stream with  $c_{fv} = 1$ . For intermediate values of  $\lambda\tau$  the “dancing in step” will be interrupted from time to time by waiting longer than  $\tau$  for the next input spike. The triggering, which is next to this event, must happen without feedback involved. Combination of this two possibilities gives maximum variability of output stream at  $\lambda\tau = 1$ .

Finally, it would be interesting to compare ISI distributions found here with those observed experimentally. The

<sup>5</sup>  $N_0 = 2$  is expected. See also reasoning at the end of Section 3.



configurations with feedback are known for real biological objects, [11,12]. The self-excitatory neurons described in the cited papers are incorporated in a complicated network. Thus, their spiking statistics is influenced by other neurons. Therefore, a more developed network model is needed in order to compare with experimental data.

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