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Relation Between Firing Statistics of Spiking Neuron with Instantaneous Feedback and Without Feedback

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We consider a class of spiking neuron models, defined by a set of conditions which are typical for basic threshold-type models like leaky integrate-and-fire, or binding neuron model[a] and also for some artificial neurons. A neuron is fed with a point renewal process. A relation between the three probability density functions (PDF): (i) PDF of input interspike intervals ISIs, (ii) PDF of output interspike intervals of a neuron with a feedback and (iii) PDF for that same neuron without feedback is derived. This allows to calculate any one of the three PDFs provided the remaining two are given. Similar relation between corresponding means and variances is derived. The relations are checked exactly for the binding neuron model stimulated with Poisson stream.

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

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1. Introduction

Spiking statistics of various neuronal models under a random stimulation has been studied in the framework of two main approaches. The first one is named in [2, p. 38] as “Gaussian”, because it describes the random stimulation by means of Gaussian noise. This approach has developed into the well-known diffusion approximation methodology, see [3]. The second approach is named in [2, p. 38] as “quantal”, because it is based on the discrete nature of the influence any input impulse may have on its target neuron. For a recent review of the both approaches see [4]. As it may be concluded from [4], the quantal approach is not as rich with results as the Gaussian one. Recently, in the quantal approach for the binding neuron

[a] The binding neuron model is defined in the first paragraph of Sec. 4. Detailed description can be found in [1]. See also https://en.wikipedia.org/wiki/Binding_neuron.

model, the statistics of output stream is found if the stimulation is due to Poisson stream [5]. The stream of the output interspike intervals (ISIs) appears to be a renewal stochastic process for which an exact probability density function (PDF) is calculated. In the subsequent papers [6] and [7], the PDF is found for binding neuron model with instantaneous feedback. In both [6] and [7] distinct methods were used, not utilizing already available PDF for neuron without feedback.

In this paper, we offer a simple relation, which allows easy derivation of the output ISIs PDF for a model neuron with instantaneous feedback based on a known PDF for that same neuron without feedback. The relation connects three PDFs: for input ISIs, for output ISIs with and without feedback. The relation is valid for any renewal input stimulation and allows to calculate any of the three PDFs with the remaining two given. The relation becomes attractively simple for Poisson stimulation, see Eq. (4). Relations between mean and variance of the three PDFs are as well derived. Also, we do not specify a concrete neuronal model, only formulate a set of conditions the model must satisfy. Several basic threshold-type neuronal models do satisfy the formulated conditions.

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2. Assumptions and Definitions

The main function of a neuron is to transform its stream of input impulses (the stimulus) into its stream of output impulses. An output impulse is usually called "spike". When a neuron emits an output impulse, it is usually said that neuron is triggered and fires a spike. As regards to neuronal functioning, we assume that the following conditions are satisfied:

- COND1: Neuron is stimulated with excitatory input impulses which form a renewal point process. The process is described by means of a PDF of ISI, $p^{\mathrm{in}}(t)$, where t denotes an ISI duration.
- COND2: Neuron has a deterministic behavior: The same stimulus, which is a sequence of input impulses, gives the same result (the neuron either fires, or does not fire).
- COND3: After firing, neuron appears in its resting state, which does not evolve in time until next input impulse comes.
- COND4: Neuron may fire only at a moment when an input impulse comes.
- COND5: If neuron starts from its resting state, then more than one input impulse is required in order to trigger it.

The conditions COND1–COND5, above, are satisfied for basic neuronal models, such as perfect integrate-and-fire model, see [8], leaky integrate-and-fire model [2], and some of its modifications [9], and binding neuron model [5]. Condition COND5 means that the neuron makes some processing of sets of input impulses, instead of channelizing every input impulse into its output stream. It is clear from COND1–COND5 that we do not consider neuronal models able to produce an independent output activity due to oscillations on a periodic orbit.

It is useful to mention that we follow here the quantal approach as it is defined in [2, p. 38]. Therefore, we expect that each input impulse abruptly increases the degree of excitation by some amount. In the case of current-type stimulation, this means that the current impulse has a Dirac's δ-function time course. In this context, as the perfect integrator model, we mean a model in which the degree of excitation (which in this case is a depolarization voltage) jumps upward after each input impulse, and remains constant between any two consecutive input impulses. The perfect integrator fires and resets its degree of excitation to zero when a threshold excitation is achieved. This is a little bit different of what is discussed in [8], where some degree of leakage is admitted.

From COND1–COND4, it follows that the output stream of ISIs will be as well a renewal stochastic process. Denote by $p^o(t)$ the PDF of ISIs in this stream.

The above construction can be extended by adding an instantaneous feedback line. The line sends any output impulse to the neuronal input without delay. This impulse is identical to any other input impulse.[b] In this case, we have a neuron with instantaneous feedback (IF), see e.g., [6]. Neurons, which send with a delay through autapses[c] their own output spikes to their own body or dendrites, are well known in physiology [10, 11]. If the input ISIs are much longer than the delay, then the instantaneous feedback could be a satisfactory approximation to what happens really. This substantiates the usefulness of relation we are looking for. Finally, it should be mentioned that any kind of afterspike "dead time", like refractoriness, nullifies the instantaneous feedback action. Therefore, we do not admit refractoriness here. On the other hand, our approach could be applied also to abstract neurons used in mathematical neural network studies, as well as to artificial neurons realized in electronic chips. In these two cases, the refractoriness is not a necessary

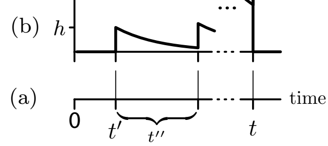

Fig. 1. Example for leaky integrate-and-fire neuron taken as a model. (a), the neuron without IF receives input impulses at the moments $t', t' + t'', \ldots, t$. (b), the depolarization voltage, V, time course. Between 0 and t' the neuron without IF is in its resting state. After receiving input spike at moment t', the neuron appears in the initial state of neuron with IF. This state evolves in time — excitation decays with time. At the moment t, neuron without IF fires its first output spike. h — is the input impulse magnitude; Th — is the firing threshold value.

[b] This means that we consider here excitatory neuron.
[c] Autapses — synapses which axon endings form at the cell the axon belongs to.

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feature. See e.g., [12, 13], where the binding neuron model without refractoriness is implemented in FPGA chip.

It is worth noticing that immediately after firing the neuron with IF as well appears in a standard initial state. This standard initial state is realized if a neuron without IF being in its resting state gets a single input impulse. See point t' at Fig. 1. This state can evolve in time.[d] Nevertheless, it is clear that the output stream of ISIs of a neuron with IF as well will be a renewal process. Denote by $p^{o\text{-if}}(t)$ the PDF of ISIs in this process, where “if” stands for the “instantaneous feedback”.

3. Relation Between PDFs

Our purpose is to establish a relation between $p^{\text{in}}(t)$, $p^{o}(t)$ and $p^{o\text{-if}}(t)$. Any of the three processes is a renewal one. If so, it is enough to analyze what happens between two consecutive firings of neuron without feedback.

Expect that neuron without feedback fires at moment 0. In order to fire next at moment in the time interval $[t; t+dt[$, the neuron must obtain an input impulse at this same moment (COND4), and this impulse is not the first one received after the moment 0 (COND5). The first one must be obtained earlier, at some moment $t' \in]0; t[$, see Fig. 1(a). The probability to receive this impulse in the interval $[t'; t'+dt'[$ is $p^{\text{in}}(t')dt'$. After receiving this impulse, the neuron appears in the standard initial state of neuron with instantaneous feedback. Now, firing next time at t means that a neuron with IF fires first time at t if starts at t'. This event does not depend on the event of receiving first input impulse and has probability $p^{o\text{-if}}(t-t')dt$. Therefore, for neuron without feedback, the compound event of receiving the first impulse at time $t' < t$ and firing first at time t has the following probability $p^{\text{in}}(t')dt' p^{o\text{-if}}(t-t')dt$. The latter allows to calculate $p^{o}(t)dt$ as convolution and to obtain the required relation:

$$p^{o}(t) = \int_0^t p^{\text{in}}(t')p^{o\text{-if}}(t-t')dt'. \tag{1}$$

3.1. *Inverting Eq.* (1)

In general case, the Eq. (1) can be inverted by means of Laplace transform:

$$\mathcal{L}(p^{o})(s) = \mathcal{L}(p^{\text{in}})(s)\mathcal{L}(p^{o\text{-if}})(s),$$
$$\mathcal{L}(p^{o\text{-if}})(s) = \mathcal{L}(p^{o})(s)/\mathcal{L}(p^{\text{in}})(s). \tag{2}$$

In order to find exact expression for $p^{o\text{-if}}(t)$, it is necessary to apply the inverse Laplace transform to the right-hand side of Eq. (2). This operation can be accomplished depending on the explicit expressions for the $p^{\text{in}}(t)$, $p^{o}(t)$.

[d]This state does evolve with time for any neuronal model (received with impulse excitation decays in time), except of the perfect integrator.

3.2. *Poissonian input case*

In this case $p^{\text{in}}(t) = \lambda e^{-\lambda t}$, where λ is the intensity of the input Poisson stream — the mean number of input spikes per unit time interval. The Laplace transform of $p^{\text{in}}(t)$ is as follows: $\mathcal{L}(p^{\text{in}})(s) = \frac{\lambda}{s+\lambda}$, which gives after using in Eq. (2)

$$\mathcal{L}(p^{o\_\text{if}})(s) = \mathcal{L}(p^o)(s) + s\mathcal{L}(p^o)(s)/\lambda. \tag{3}$$

Notice that from COND1, COND5 it follows that $p^o(0) = 0$. If so, then Eq. (3) gives

$$p^{o\_\text{if}}(t) = p^o(t) + \frac{1}{\lambda}\frac{d}{dt}p^o(t). \tag{4}$$

4. Example: Binding Neuron with Threshold 2

The binding neuron (BN) model is characterized with a time interval $\tau > 0$ during which an input impulse is stored in the neuron without decay. After that time, it is removed. The BN with threshold 2 fires a spike at the moment of receiving an input impulse, provided at that moment the previous input impulse is still stored in the neuron. Just after firing, BN is free of stored impulses. If BN is stimulated with a Poisson stream, then the COND1–COND5 are satisfied.

Exact expression for the $p^o(t)$ can be found in [5, Eq. (3)]. It is different for different intervals of t value. Namely, if $m\tau < t \le (m+1)\tau$, where $m = 0, 1, 2, \ldots,$ then

$$\begin{aligned} p^o(t) &= e^{-\lambda t}\frac{\lambda^{m+2}}{(m+1)!}(t - m\tau)^{m+1} \\ &\quad + e^{-\lambda t}\sum_{2\le k\le m+1}\frac{\lambda^k}{(k-1)!}\left((t-(k-2)\tau)^{k-1} - (t-(k-1)\tau)^{k-1}\right). \end{aligned} \tag{5}$$

Exact expression for the $p^{o\_\text{if}}(t)$ can be found in [6, Eqs. (4) and (7)], or in [7, Eq. (10)]: for $m = 0, 1, 2, \ldots$, if $m\tau < t \le (m+1)\tau$ then

$$\begin{aligned} p^{o\_\text{if}}(t) &= e^{-\lambda t}\frac{\lambda^{m+1}}{m!}(t - m\tau)^m \\ &\quad + e^{-\lambda t}\sum_{2\le k\le m}\frac{\lambda^k}{(k-1)!}((t-(k-1)\tau)^{k-1} - (t-k\,\tau)^{k-1}). \end{aligned} \tag{6}$$

Now, the validity of Eq. (4) for BN model can be directly checked by substituting (5) and (6) into it.

5. Moments of Distribution

Denote $W_n^{\{\text{in},o,o\_\text{if}\}}$ the nth moment of the corresponding distribution. Using Eq. (1) one obtains

$$W_n^o = \int_0^\infty dt t^n p^o(t) = \int_0^\infty dt t^n \int_0^t dt' p^{\text{in}}(t')p^{o\_\text{if}}(t-t')$$

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$$= \int_0^\infty dt' p^{\text{in}}(t') \int_{t'}^\infty dt t^n p^{o\_\text{if}}(t-t')$$
$$= \int_0^\infty dt' p^{\text{in}}(t') \int_0^\infty dt (t+t')^n p^{o\_\text{if}}(t) = \sum_{k=0}^{n} \binom{n}{k} W_k^{\text{in}} W_{n-k}^{o\_\text{if}}.$$

In particular, for $n = 1, 2$ one has

$$W_1^o = W_1^{o\_\text{if}} + W_1^{\text{in}}, \tag{7}$$
$$W_2^o = W_2^{o\_\text{if}} + W_2^{\text{in}} + 2W_1^{\text{in}} W_1^{o\_\text{if}}. \tag{8}$$

For binding neuron with threshold 2 fed with Poisson stream, (7) can be checked explicitly. It is clear that here $W_1^{\text{in}} = \frac{1}{\lambda}$. The W_1^o is found in [5, Sec. 2]:

$$W_1^o = \frac{1}{\lambda}\left(2 + \frac{1}{e^{\lambda\tau} - 1}\right).$$

The $W_1^{o\_\text{if}}$ is found in [6, Eq. (9)] or [7, Eq. (11)]:

$$W_1^{o\_\text{if}} = \frac{1}{\lambda(1 - e^{-\lambda\tau})}.$$

The validity of Eq. (7) can now be checked by substituting these expressions into it. Similarly, [6, Eqs. (12) and (13)] give:

$$W_2^o = \frac{2}{\lambda^2} \frac{3\,e^{2\lambda\tau} + (\lambda\tau - 3)e^{\lambda\tau} + 1}{(e^{\lambda\tau} - 1)^2}, \quad W_2^{o\_\text{if}} = \frac{2e^{\lambda\tau}}{\lambda^2} \frac{e^{\lambda\tau} + \lambda\tau}{(e^{\lambda\tau} - 1)^2}.$$

Also, $W_2^{\text{in}} = \frac{2}{\lambda^2}$. The validity of Eq. (8) for binding neuron with threshold 2 fed with Poisson stream can now be checked by substituting these expressions into it.

Finally, denote $\sigma^2_{\{\text{in},o,o\_\text{if}\}}$ the variance of corresponding distribution. Then from (7), (8) the following relation can be derived:

$$\sigma^2_{o\_\text{if}} = \sigma^2_o - \sigma^2_{\text{in}}. \tag{9}$$

6. Conclusions

In this paper, a relation is offered, which connects firing statistics of an excitatory neuron with instantaneous feedback and that same neuron without feedback, provided both are driven with the same renewal stream of input impulses, see Eq. (1). The relation can be used for some basic models of biological neurons, like leaky integrate-and-fire model. The set of possible models is restricted by conditions COND1–COND5, above. Yet, the relation is rather universal. This is because conditions COND1–COND5 do not specify any concrete firing mechanism, which makes the relation applicable to some abstract mathematical neuronal models, as well as to neurons implemented with electronic chips. Also, any renewal process can be used for stimulation. For the case of Poisson stimulation, Eq. (1) turns into even a simpler form of Eq. (4). The latter is checked for the binding neuron model, for which both the statistics are already known.

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The relation found is mathematically exact and can be safely used in a relevant situation. As an immediate application, it could be used for calculating $p^{o\text{-if}}(t)$ for the leaky integrate-and-fire neuron stimulated with Poisson stream of strong impulses, when already two input impulses may trigger the neuron ($r = 2$ in notations of paper [2]). The corresponding $p^o(t)$ is calculated in [14, Eqs. (14), (19)–(23)].

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