Input-output Characteristics of LIF Neuron with Dynamic Threshold and Short Term Synaptic Depression

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Abstract. We consider a model of leaky integrate-and-fire neuron with dynamic threshold and a very simple realization of short term synaptic depression mechanism. Model simplicity makes possible creation of very large networks on its basis. Required general properties of these networks can be obtained due to the appropriate selection of neuron parameters. Knowledge of the dependence of neuron firing frequency on presynaptic activity for various neuron parameters is crucial for this selection. Since this dependence cannot be obtained in an exact analytical form we describe the process of building its empirical approximation using the multiple adaptive regression splines algorithm. This methodology can be used for other neuron models.

1 Introduction

Spiking neural networks (SNNs), the most biologically realistic class of neural network models, have one important distinctive feature. In contrast with more traditional neural networks like perceptron which can perform non-trivial tasks even if it consists of few dozen neurons only, practically applicable SNNs should include at least thousands or more likely millions of neurons. It is an inevitable consequence of information coding schemes used in SNNs and statistical nature of information processing, learning and self-organization mechanisms inherent in them. It is clear that detailed specification of all individual neuron properties, connections, synaptic weights is impossible in big neuronal ensembles. Usually, only their basic large scale properties like average number of excitatory and inhibitory connections, their mean strength, etc. are specified, while detailed network configuration is generated randomly inside the limits imposed by these large scale properties. Thus, as a rule, the simulated SNN is originally chaotic and should obtain structure necessary for performing some desired function due to self-organization process. One of the most important (and hardest) questions to be answered for achievement of necessary network behavior is how to select values of these basic network parameters. Naturally, it would be naïve to expect that setting them randomly we will get a network with acceptable properties which could demonstrate desired behavior after the respective evolution. Instead, it is most probable, that it will either stay silent because of insufficient excitatory synapses strength, or, on the contrary, show explosive total excitation growth to saturation level, or be involved in massive powerful oscillations suppressing any reaction to external signals. Many other negative scenarios are possible… To avoid them it is crucial to know relationship between properties of network as a whole and characteristics of

individual neurons and interneuron connections constituting it.

The most commonly used method for solution of this problem is based on the mean field equations. In this approach neurons are characterized by their input-output characteristics – the relationship between strength of stimulation of individual neuron and strength of its response. It is assumed that stimulation of different synapses is completely uncorrelated and corresponds to Poisson process so that it can be described by a single value - its total intensity (mean presynaptic spike frequency). More precisely, we need to find relationship between the steady state firing frequency of neuron, its parameters and the mean presynaptic spike frequency. This problem is not very difficult for simple leaky integrate-and-fire (LIF) neuron [1], but LIF neuron is too simple to create realistic or functionally rich SNNs. For this reason, several more realistic two-dimensional models have been proposed – like FitzHugh-Nagumo neuron [2] or Izhikevich neuron [3]. The model considered in this paper is also two-dimensional (it will be described formally in Section 2). It differs from LIF model by two features.

1. *Dynamic threshold.* Threshold value of membrane potential is incremented by a constant each time the neuron fires and decays exponentially to its baseline level. Models of this kind are described, for example, in [4]. It is an adaptive mechanism which allows controlling maximum firing frequency.
2. *Short Term Synaptic Depression (STD).* It was experimentally demonstrated that many types of synapses receiving high frequency spike train show different reaction to individual spikes in the train. While the first spike causes significant change of membrane conductance, effect of the subsequent spikes may be significantly weaker. This phenomenon is described in many works [5, 6]. In fact, it is characteristic for majority of synapses but in some kinds of synapses it is prevailed by the opposite effect, short term synaptic facilitation. Due to STD the impact of one synapse to neuron membrane potential value can be limited even in case when this synapse receives very intensive stimulation. It is a very important feature because neuron can perform non-trivial information processing only in case when it combines signals from different sources. Many formal models of STD have been proposed (see, for example [7]). As we will see in Section 2, the realization proposed in this paper is very simple and is based on requirement that the total contribution of one synapse to membrane potential is limited by a value proportional to the weight of this synapse (the similar approach was used by me in [8, 9]).

Having described the neuron model in Section 2 we consider procedure of finding its input-output characteristics in Section 3. In Section 4 we present and discuss the final result. At last, Section 5 contains conclusion and ideas how the obtained result could be utilized in further research.

2 Formal Neuron Model

Two main components of neuron state in our model are membrane potential u and dynamic part of membrane potential threshold h. Membrane potential is rescaled so that its rest value equals to 0 while firing threshold value after long period of inactivity is taken equal to 1. In general case the threshold value equals to $1 + h\ (h \geq 0)$. Thus, neuron fires when $u = 1 + h$. Just after firing, the membrane potential is reset to

0 and dynamic threshold is incremented:

$$u \leftarrow 0; h \leftarrow h+1 \,. \tag{1}$$

While neuron is silent its dynamic threshold decays exponentially with the time constant τ_h which determines (together with other parameters) relative refractoriness period of neuron.

The important feature of the considered model is dependence of synapse efficacy on the history of presynaptic spikes coming to it, more precisely, on the time passed since the most recent spike. To realize this dependence we introduce additional components of neuron state v_i $(0 \le v_i \le 1)$, one value per synapse; here i denotes synapse ordinal number. Just after reception of a new presynaptic spike by the synapse i its v_i is set to 1. In the absence of presynaptic spikes, v_i decay with the time constant τ_v (the membrane potential decay time constant). When the neuron fires, all v_i are reset to 0. Value of v_i determines contribution of the ith synapse to membrane potential:

$$u = \sum w_i v_i \,, \tag{2}$$

where w_i is weight of the ith synapse $(0 < w_i < 1)$. Thus, effect of presynaptic spike on membrane potential is less than w_i if the same synapse received a presynaptic spike some time t ago. In this case the membrane potential increment will be equal to $w_i\left(1 - \exp(-t/\tau_v)\right)$. Meaning of w_i here is ratio of the maximum contribution of one synapse to membrane potential to the baseline value of membrane potential threshold. Possibly, this realization of STD is a bit oversimplified but it reaches its main goal – to limit influence of a single synapse on neuron behavior even in case of its very strong stimulation. Besides, it has another valuable feature. Namely, the standard model of synaptic plasticity, STDP (spike timing dependent plasticity [1]), assumes that LTP (long term synapse potentiation) value is determined by the time interval between the most recent presynaptic spike obtained by the synapse and the postsynaptic spike emitted by the neuron. Therefore, synapses should store information about most recent presynaptic spike. It is clear that the values v_i in the discussed model represent the very convenient form of storing this information.

Thus, neuron state is characterized by values h and v_i whose dynamics obeys the following rules:

$$\frac{dh}{dt} = -\frac{h}{\tau_h}, \; \frac{dv_i}{dt} = -\frac{v_i}{\tau_v} \,;$$

$$v_i \leftarrow 1 \text{ when the } i\text{th synapse receives spike;}$$

$$\text{if } \sum_i w_i v_i = 1+h \text{ the neuron fires and } h \leftarrow h+1, \, v_i \leftarrow 0 \,. \tag{3}$$

Although this model is quite simple, the problem of finding its input-output characteristics is far from being trivial, as we will see in next section.

3 Finding Input-output Characteristics

Thus, we would like to find dependence of the steady state neuron firing frequency F on its properties and the frequency of presynaptic spikes f. In our model, neuron is characterized by its time constants τ_v and τ_h, the number of synapses n and the synaptic weights $w_i \, (1 \le i \le n)$. At first we consider case when the weights of all synapses are equal to the same value w.

Unfortunately, as we will see, the assumption of equal value of all weights does not help to formulate this dependence in a compact analytical form. It can be done only for certain particular cases, for example, if f is very great. To analyze this case it is convenient to imagine a very large ensemble of identical neurons stimulated by input signal with identical characteristics and to consider the steady state values of h and v_i averaged for the whole ensemble (v_i -also for all synapses). We denote them as $\bar{h}$ and $\bar{v}$, respectively. Since the stimulation is very strong, the neurons fire very frequently $1/F << \tau_h$ and $\bar{h}$ is also great. Then its steady state value can be determined from the equation

$$\bar{h}(1 - \exp(-\frac{1}{F\tau_h})) = 1 \,, \tag{4}$$

which for great $F\tau_h$ yields $\bar{h} = F\tau_h$. Dynamics of mean value of membrane potential includes 3 factors:

1. It grows due to incoming stimulation with the speed $fwn(1 - \bar{v})$ per neuron.

2. It decays with the speed $\frac{wn\bar{v}}{\tau_v}$ per neuron.

3. It is reset to 0 in the firing neurons that gives decrease speed $F(1 + \bar{h}) \approx F\bar{h} = F^2\tau_h$ per neuron.

Thus,

$$fwn(1 - \bar{v}) = \frac{wn\bar{v}}{\tau_v} + F^2\tau_h \approx F^2\tau_h \,. \tag{5}$$

The similar consideration of dynamics of $\bar{v}$ yields

$$f(1 - \bar{v}) = \frac{\bar{v}}{\tau_v} + F\bar{v} \approx F\bar{v} \,. \tag{6}$$

Combining (5) and (6), we obtain quadratic equation for F:

$$F\tau_h(F + f) = wnf \,. \tag{7}$$

Unfortunately, in general case we have to deal with complex transcendental equations (for example, because we cannot get rid of the exponent in (4)). Therefore, if we need analytical form of the input-output characteristics it can be only its approximation obtained by some method. I selected the most direct way - computer simulation of the neuron model described by (3) and measurement of its firing frequency during long time period. Since the model (3) is very simple it was easy to collect a large

dataset describing dependence of F on f for various values of τ_v, τ_h, n and w. After that, I applied to this table one of the most powerful modern methods for automated creation of non-linear regression models, multiple adaptive regression splines [10].

This procedure was carried out for the ranges of f, τ_v, τ_h, n and w, which can be potentially biologically realistic. They are summarized in Table 1.

Since the parameter boundaries differ by several orders of magnitude it was more convenient to work with their logarithms. It was also true for F because we needed to minimize its relative rather than its absolute error. Inside these limits the values of logarithm of parameters were chosen randomly and independently using uniform distribution. Simulation time step was chosen equal to 1 msec. Every simulation experiment corresponded to 1000 sec. The experiments where neuron did not fire at all or fired with the mean frequency greater than 300 Hz were not considered. Results of 5223 experiments satisfying these conditions were gathered in a single table which was loaded to the data mining system PolyAnalyst [11]. The empirical model obtained on these data by the multiple adaptive regression splines module of PolyAnalyst system is discussed in next section.

4 Empirical Approximation of Neuron Input-output Characteristics

Thus, as it was said, the method used to find dependence of F on f, τ_v, τ_h, n and w was multiple adaptive regression splines. In order to avoid danger of overfitting the complexity of the created model was limited by the following values. The maximum number of basis functions was set equal to 100, the maximum basis function order – to 3. The resulting formula itself cannot be inserted in the article (it would occupy about 1.5 pages) – it can be obtained from me by request (for example, in form of C code). While the model contains only few dozen degrees of freedom it appeared to be quite precise (standard deviation = 0.243, R^2 = 0.971). Values of measured and predicted firing frequency are depicted on Fig. 1. We see that quality of data fitting is very good everywhere except the region of very weak stimulation (< 1 Hz). However, good approximation is hardly possible there because of strong signal fluctuations.

Examples of the input-output characteristics calculated using the obtained model for different values of neuron parameters are shown on Fig. 2. We see that it is almost linear in some cases, while in other cases this curve may have plateau and even be non-monotonous. While negative val ue of derivative of this curve is a rare artefact,

Table 1. Ranges of Stimulation Intensity and Neuron Parameters for Which Neuron Firing Frequency Was Measured.

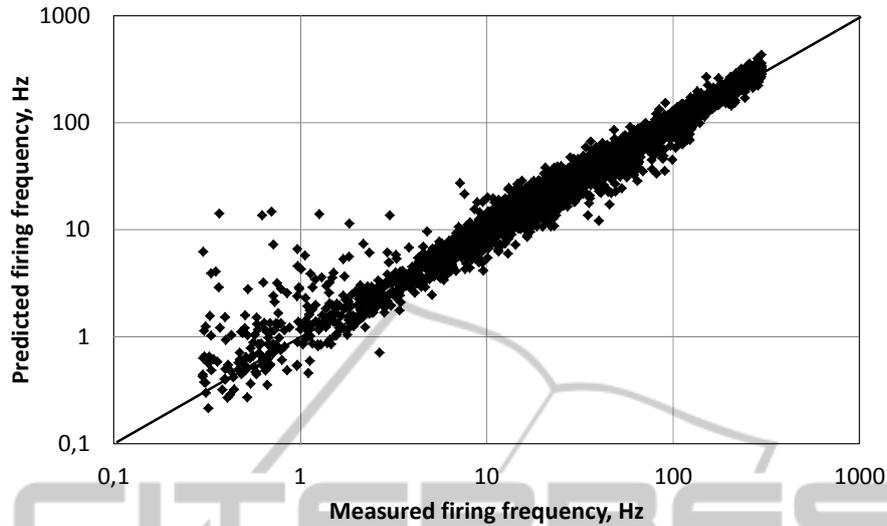| Parameter	Minimum value	Maximum value
F	1 Hz	300 Hz
N	10	3000
W	0.01	0.3
τ_v	3 msec	100 msec
τ_h	1 msec	100 msec

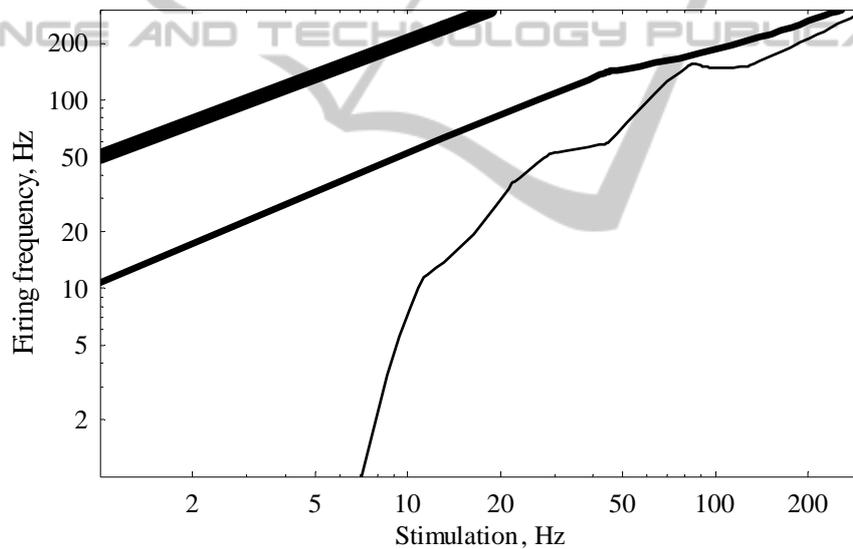**Fig. 1.** Predicted vs. real values of neuron firing frequency.

Fig. 2. Empirical approximation of neuron input-output characteristics for different values of neuron parameters. The thin line corresponds to $\tau_v = 24.5$ msec, $\tau_h = 10$ msec, $n = 2032$, $w = 0.0348$; the thick line – to $\tau_v = 71$ msec, $\tau_h = 69$ msec, $n = 348$, $w = 0.0893$; the very thick line – to $\tau_v = 36$ msec, $\tau_h = 8$ msec, $n = 68$, $w = 0.0467$.

presence of plateau is explainable. In some circumstances increased stimulation may have very weak impact on firing frequency because, at the same time, it leads to growth of dynamic threshold. This situation is observed for thin line on Fig. 2 in case of stimulation intensity close to 100 Hz. It illustrates why dynamic threshold may be a useful stabilizing factor preventing uncontrolled excitation growth.

At last we should discuss how the obtained result could be extended to case of non-uniform synaptic weight values. Since all input signals have identical properties and are not correlated, the most important value determining the firing frequency is the sum of all synaptic weights. Number of synapses plays its role only because it determines fluctuation magnitude in input stream, the fewer synapses, the stronger fluctuations. But the process of transformation of presynaptic spikes to postsynaptic spikes can be treated as information flow. Postsynaptic spikes contain information about presynaptic spikes in form of conditional probabilities $P_i = P$(postsynaptic spike | presynaptic spike on the synapse i). But, $P_i \sim y_i = \dfrac{w_i}{\sum w_i}$. Hence, the volume of this information flow and, therefore, the magnitude of its fluctuations is determined by a value proportional to $-\sum y_i \log y_i$. It follows from this discussion that for our purpose neuron with n synapses having different weights w_i can be approximated by neuron with n^* identical synapses with weight w^*, where

$$\log n^* = -\sum y_i \log y_i , \tag{8}$$

$$w^* = \frac{1}{n^*} \sum w_i . \tag{9}$$

5 Conclusion

In this paper, we considered a very simple model of spiking neuron which, despite its simplicity, has a number of valuable properties. It can perform non-trivial information processing in wide range of presynaptic signal intensity due to limitation of single synapse contribution to membrane potential; it can help preventing uncontrolled excitation growth due to dynamic threshold, and it is convenient for implementation of STDP rule. Thanks to its simplicity, simulation experiments with large ensembles of such neurons can be carried out. To predict general properties of these ensembles it is crucial to know input-output characteristics of a single neuron. Since this characteristics cannot be formulated in analytical form, we obtained its empirical approximation collecting experimentally measured values of neuron firing frequency under various conditions and processing these data using multiple adaptive regression splines algorithm. The resulting empirical dependence can be included in the mean field equations describing large neuronal ensembles for analysis of basic properties of their dynamics (using respective numeric methods). It can also be utilized to evaluate acceptable stimulation intensity range in simulation experiments and for other purposes. This empirical law is an important component of numeric models of SNN dynamics used in our ongoing research projects.

The described methodology for determination of neuron input-output characteristics can be applied to other neuron models, as well, – in cases when it cannot be obtained in exact analytical form.

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