

A Simple Neuron Model with Memory of Firing

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Abstract—Cortical neurons in vivo generate highly irregular spike sequences. Recently, it was experimentally found that the local variation of interspike intervals, L_V , is nearly the same for every spike sequence for any given neuron [1]. To the contrary, the coefficient of variation, C_V , varies over different spike sequences. This suggests that short-term statistical characteristics of spike sequences are almost constant under rate modulation.

We show that the conventional leaky integrate-and-fire model does not fully account for the behaviors of C_V and L_V . Then, we introduce a new neuron model which generates the spike correlation by itself. The difference between the leaky integrate-and-fire model and the new model is whether a neuron resets the voltage after firing or not. As for the voltage resetting mechanism, a neuron loses the past firing memory, and it makes no significant difference between the behaviors of C_V and L_V . Since the new model possesses a memory of past firing and bursting property, its short-term statistical properties are invariant for rate modulation.

This model suggests that a biological neuron may possess such a memory, and the temporal correlation can be generated not only externally but also internally.

1. Introduction

Cortical neurons are driven by thousands of synaptic inputs. They generate highly irregular spike sequences.

Spike production can be considered as a two-step process. First, synaptic inputs are integrated by an extensive and complex dendric trees resulting in a total synaptic current. Second, the cell emits spikes in response to this synaptic current. A numerous number of single neuron models that can reproduce some aspects of spiking statistics of biological neurons have been produced, and most of them have largely focused on the latter.

The leaky integrate-and-fire model is one of the most well known models. It is shown that the leaky integrate-and-fire model with a balance of excitation and inhibition can reproduce spiking irregularity [2][3], and with temporally correlated inputs, it can reproduce the spiking statistics [4]. However, whether the leaky integrate-and-fire model is good enough is yet to be examined [5].

We attempted to determine whether the leaky integrate-and-fire model is satisfactory for reproducing the statistics of interspike interval (ISI). We focus on the spiking irregularity, C_V and L_V in this study.

We first introduce the spiking statistics, C_V and L_V in section 2.1. In section 2.2, we discuss the meaning of their behaviors. In section 3.1, we examine the leaky integrate-and-fire model and show that it does not fully account for the behaviors of C_V and L_V . In section 3.2, we introduce a new model and show that it explains their behaviors. This model can reproduce spike correlation by itself. In section 3.3, we consider the possibility of different intrinsic properties of neurons. In section 4, we discuss the differences between the leaky integrate-and-fire model and the new model, and conclude that the time correlation has much to do with neuron itself. This means that a neuron might have a memory of firing, and may be much cleverer than we have expected.

2. ISI Statistics

2.1. C_V and L_V

We first implement the measures of the spiking irregularity, C_V and L_V . Coefficient of variation C_V is a very common measure which has been employed by many researchers. Recently, a measure of local variation of ISIs, L_V , has been proposed and found to be experimentally useful [1]. C_V and L_V are defined as

$$C_V = \frac{\sqrt{\frac{1}{n-1} \sum_{i=1}^n (T_i - \bar{T})^2}}{\bar{T}} \quad (1)$$

$$L_V = \frac{1}{n-1} \sum_{i=1}^{n-1} \frac{3(T_i - T_{i+1})^2}{(T_i + T_{i+1})^2} \quad (2)$$

where T_i is the duration of the i th ISI, n is the total number of ISIs, and $\bar{T} = \frac{1}{n} \sum_{i=1}^n T_i$ is the mean ISI. C_V and L_V take 1 for purely Poisson process, and 0 for perfectly regular sequences. L_V indicates the local spiking irregularity, while C_V indicates the global spiking irregularity. For example, for a spike sequence which is locally quasi-regular but globally modulated, L_V takes a small value, while C_V

takes a large value. C_V of typical cortical neurons is close to 1. This means cortical neurons in vivo generates highly irregular spike sequences.

The distribution of C_V from the same area exhibits strong similarities. But the C_V from a single neuron were observed to vary significantly with time. Therefore, C_V is not useful for classification of individual neurons. However, L_V is nearly the same for every spike sequence for any given neuron [1]. We examine whether the neuron models express the behaviors of C_V and L_V in section 3.

2.2. What Makes L_V Constant?

What makes L_V almost constant compared with C_V ? The difference of C_V and L_V behaviors indicates that there exist the correlations which are valid only locally.

One possibility that makes L_V almost constant is, strong correlation of neighboring spikes. For example, bursting neurons exhibit strong correlation between spikes. For the bursting neuron, when input increases, the period of bursting become longer and C_V fluctuates rapidly since it measures global irregularity and reflects every bursting sequences. To the Contrary, L_V is a measure of local variation, and mainly reflects the boundaries of bursting and non-bursting. When the input increases, although the period of bursting becomes longer, the boundaries of bursting and non-bursting do not change greatly. Therefore, L_V is much more constant than C_V with respect to neurons that have strong correlations such as a bursting neuron. In this case, it is important not to burst too long. When the period of bursting becomes too much longer, C_V increases when the input increases. However, experimental facts that C_V changes rapidly and L_V is constant are feasible when there is a moderate correlation.

In order to make correlation between spikes, there are two methods.

The first method is to give temporally correlated inputs to neurons. If the input is correlated, the output would be naturally correlated. The leaky integrate-and-fire model with temporally correlated inputs uses this method. However, in this method, the output variability is fully dependent on input, and it seems changeable for the rate modulation.

The other method is to make the correlation by the neuron itself. For this way, output variability is not fully dependent on input variability, and it seems much more robust under the rate modulation. The leaky integrate-and-fire model with a stochastic noise produces a renewal process, therefore it is impossible to apply this method.

3. The Model and its Numerical Analysis

3.1. Leaky Integrate-and-Fire Model

We first examine whether the conventional leaky integrate-and-fire model expresses the behaviors of C_V and L_V .

The mechanism of the leaky integrate-and-fire model is as follows: incoming spiking signals to a neuron raise its membrane potential, and when the membrane potential exceeds a certain threshold(= θ), the neuron fires and emits a spike. The potential is then resets to a resting potential(= V_0).

$$\tau \frac{dV(t)}{dt} = -V(t) + \eta(t) \quad (3)$$

$$V(t) = \theta \rightarrow \text{firing} \rightarrow V(t + \Delta t) = V_0 \quad (4)$$

For the input $\eta(t)$, we use the Ornstein-Uhlenbeck process(OUP), so the input is an exponentially correlated (colored) Gaussian noise. $\eta(t)$ is written as $\langle \eta(t) \cdot \eta(t') \rangle > \alpha e^{-\frac{|t-t'|}{s}}$ and $\langle \eta(t) \rangle = \mu$. It is shown that leaky integrate-and-fire model given correlated inputs of order 100msec can reproduce spiking statistics [4]. Therefore, we adopted 100msec as the time correlation parameter s .

Now, we change the average ISI by modulating the average input μ . The result is given in figure 1.

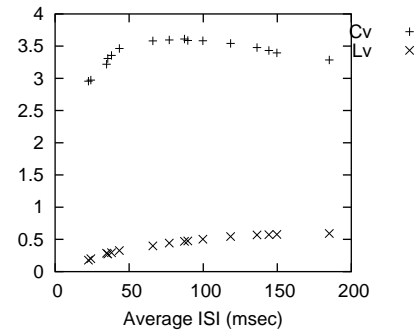


Figure 1: C_V and L_V obtained from LIF+OUP

Figure 1 shows the C_V and L_V obtained from the leaky integrate-and-fire model with the OUP input. If the average ISI is short, C_V increases rapidly compared with L_V as the ISI becoming longer. This accounts for their experimental behaviors. On the other hand, if the average ISI is long, C_V decreases as the ISI becoming longer. This is because it has too strong correlation, and it doesn't fire except in the period of bursting. If the input increases, the period of bursting becomes longer, and C_V increases since the global irregularity increases. When the input increases to some rate, C_V turns to decrease since the period of each bursting gets close to the average ISI, so that global irregularity decreases. This fact in the high ISI contradicts with the experimental fact that L_V is constant compared with C_V [1]. This means that the leaky integrate-and-fire model with correlated inputs does not explain behaviors of C_V and L_V .

We also applied those statistical measures to a leaky integrate-and-fire model with uncorrelated inputs. In this case, behaviors of those two measures didn't have significant difference. This is because integrate-and-fire with

stochastic noise produce a renewal process so that there has no correlation between spikes. Therefore, there is no difference between local and global irregularity.

These facts indicates that leaky integrate-and-fire model does not explain behaviors of C_V and L_V .

3.2. New Model

For the leaky integrate-and-fire model with uncorrelated inputs, the correlation coefficient, which is a measure of mutual dependence of consecutive ISIs, is 0. The correlation coefficient is expected to vanish in the renewal process, in which individual ISIs are generated independently from each other. However, many biological data exhibit an anomalously large value of positive correlation coefficient. In order to solve this problem, correlated inputs are used.

Now we introduce the new model which exhibit positive correlation coefficient even with uncorrelated inputs. This means that the new model is able to generate the spike correlation by itself.

New model is defined as

$$\tau \frac{dV(t)}{dt} = -V(t) + \eta(t) + \xi(t) \quad (5)$$

$$\frac{d\eta(t)}{dt} = -a \quad (6)$$

$$V(t) = \theta \rightarrow \text{firing} \rightarrow V(t + \Delta t) = V_0 \quad (7)$$

$$\rightarrow \text{if } \eta(t) = 0, \eta(t + \Delta t) = \eta_0 \quad (8)$$

The mechanism of this model is very simple(cf.figure 2).

The leaky integrate-and-fire model can be interpreted as a motion of a particle in a potential. If it reaches the threshold(=fire), it resets to a resting potential. For the new model, $\eta(t)$ becomes a positive rate η_0 after spiking, so that a particle gets easily to climb the potential for a while. This non-resetting mechanism causes spike correlation. $\eta(t)$ decays with a constant rate a , so that it prevents from too strong correlation.

The new model has a tendency to fire easily after firing, compared with leaky integrate-and-fire model. We can interpret $\eta(t)$ as internal dynamics, not external input since it depends on the spike generation, which is not natural for the external phenomenon.

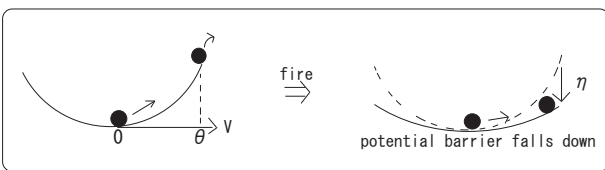


Figure 2: new model

We examine the C_V and L_V behaviors for the new model. White Gaussian noise $\xi(t)$ is used for the uncorrelated input.

We modulate the average input μ , and change average ISI. The result is given in figure 3.

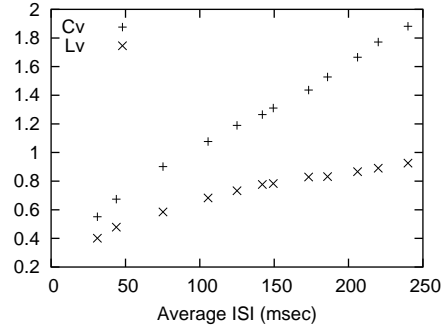


Figure 3: C_V and L_V obtained from new model

Figure 3 shows the C_V and L_V obtained from the new model. The L_V value is constant compared with C_V value. This fact indicates that the new model can explain the behaviors of C_V and L_V to some extent.

3.3. Intrinsic Properties of Neurons

It is shown that L_V is one of the measure of the neuron's intrinsic properties [1]. There are two kinds of neurons, high L_V values, and low L_V values. What causes this difference?

One possibility derived from our model is the difference of inputs. We change the ratio of correlated inputs and uncorrelated inputs. Figure 4 shows the result. When the ratio of incoming correlated and uncorrelated inputs changes, L_V changes significantly. The difference of L_V may be caused from these inputs. Temporally correlated inputs can be interpreted as a transiently synchronous inputs. Therefore, neurons may be classified into two groups: those that mainly receive synchronous inputs and those that mainly receive asynchronous inputs. We can interpret the former for the group using temporal coding, and the latter for that of using rate coding. Therefore, the difference of L_V may be caused from their coding manners.

Another possibility that our model suggest is, the potential shapes. We modulate the shape of potential U by modulating asymmetric parameter A .

$$U = \frac{1}{2}V^2 + A \sin(\pi V) \quad (9)$$

The potential shape that we used in section 3.2 is $A=0$, therefore symmetric.

Figure 5 shows L_V for potentials that changing the asymmetric parameter. If the asymmetry of the potential increases, the L_V decreases. This is because if we increase the asymmetric parameter, a particle tends to move forward [6], and fires regularly. High and low L_V may be

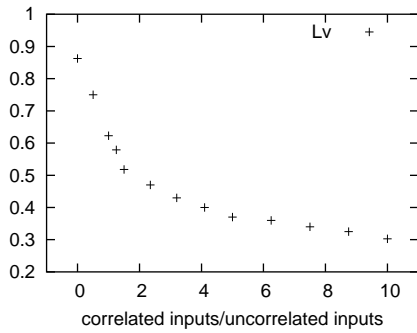


Figure 4: L_V and correlated/uncorrelated inputs

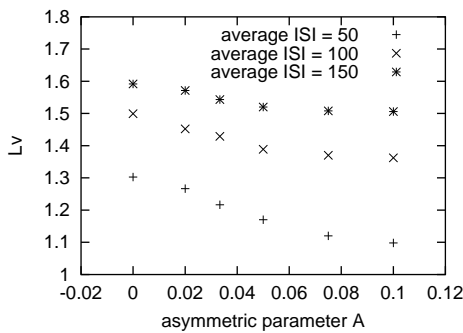


Figure 5: L_V and potential asymmetry

caused from the difference of the potential shapes, asymmetry for example.

4. Discussion

In Section 3, we have shown that the leaky integrate-and-fire model can not explain behaviors of C_V and L_V , and have introduced the new model to explain their behaviors.

The leaky integrate-and-fire model with a stochastic noise produces a renewal process. It has no spike correlation if the input is uncorrelated. This fact shows that there is no difference between local and global spiking irregularity.

On the other hand, the new model has a tendency to fire easily after firing. Therefore, it is likely to burst even in low input. As mentioned in section 2.2, bursting neurons exhibit constant L_V compared with C_V .

The behaviors of C_V and L_V indicates that a neuron may have a memory of its firing. This fact is not unreasonable. Slow synaptic processes which are related with metabolic changes in ion channels have been reported, and it seems possible to generate slow fluctuations inside the neuron, for example, the Ca^{2+} ion concentration and the dynamics of ion permeation membrane which depends on it. Ca^{2+} ion concentration varies slowly compared with the voltage inside the cell. Its variation is not fully dependent on the volt-

age. Therefore, though influenced by a spike generation, they vary almost independently. This may be the memory of a neuron. To understand cortical ISI variability, we must focus on not only the inputs, but also the spike generation mechanism, therefore, neuron itself.

Although it is not yet known what properties of neurons L_V measures, it is important to know what causes the different L_V values in models. We mentioned two possibility in section 3.3. Both different potential shapes and different inputs can be interpreted as different functional roles of neurons.

We have introduced a new model instead of the leaky integrate-and-fire model to explain behaviors of C_V and L_V . This model can reproduce spike correlation by itself.

The advantage of using this model is not just explaining behaviors of C_V and L_V . As mentioned earlier, it is easy to generate bursting. It would be a future problem to examine plausibility of this model by experimental spiking data.

Acknowledgments

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