Neural synaptic properties and conductance kinetics jointly influence how neurons process correlated input

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Abstract– Neurons transmit information through spikes. Given the prevalence of correlation among neural spike trains experimentally observed in different brain areas, it is of interest to study how neurons compute correlated input. Yet how it depends on the synaptic properties and conductance kinetics is very little known. Through simulation of leaky integrate-and-fire (LIF) neurons, we studied the effects of synaptic decay times, level of input activities and conductance fluctuation on the output correlation of different time scales for neurons receiving correlated excitatory input. We showed that the ratio of long-term correlation to short-term correlation (synchrony) increases with excitatory synaptic decay time due to the combined effects of jittered spike time and burst firing. In particular, it is possible for neurons with small excitatory synaptic decay time in high conductance state to give extra precisely timed synchronous spikes without exhibiting correlation of longer timescales in response to correlated input. In addition, we showed that burst firing greatly enhances output correlation but not synchrony, leading to an increase in correlation when conductance fluctuation is ignored.

1. Introduction

Many studies *in vivo* revealed that neurons in different brain areas often exhibit correlated activities [1-3]. However, the functions and consequences of correlation, and whether correlated input carries any information have long been debated. One of the key questions is how input correlation are computed and transmitted from a layer of neurons to another [4-7].

How a neuron processes input depends primarily on two factors. First, it depends on how synaptic conductance changes when a presynaptic spike arrives [8]. Second, it depends on how quickly the post-synaptic neuron integrates the synaptic conductance, culminating in changes in its membrane potential. This is widely known as synaptic filtering. It depends not only on the membrane capacitance, but also on the total conductance the neuron

receives, primarily affected by the level of synaptic bombardment by presynaptic input spikes [9]. Therefore, it can be expected that apart from input properties like input synchrony and correlation, neural synaptic properties and the level of input activities also play an important role in shaping the output of a neuron.

In this work, we studied the effects of several biophysical factors, namely the excitatory synaptic decay time, level of input activities and higher order conductance effects on neural computation of correlated input through numerical simulation of a pair of LIF neurons. In particular, we showed that when the synaptic time constant and effective membrane integration time constant are both small, neurons respond to correlated input solely by giving extra precisely timed synchronous spikes, suggesting the viability of synchrony coding by such neurons. Furthermore, we found that long-term correlation but not synchrony is greatly enhanced by burst firing. The effects of burst firing pose a challenge of studying the problem of correlation transfer analytically, and suggest that simplified model neurons, failing to take into account some observed biological features, like conductance fluctuation, may overestimate both the efficiency of correlation transfer and correlation-to-synchrony ratio of biological neurons.

2. Method

2.1. Neuron model

2.1.1. Conductance based LIF model

The membrane potential of a conductance based LIF model neuron [10] is given by:

$$C\frac{d}{dt}V(t) + [V(t) - V_e]G_e(t) + [V(t) - V_i]G_i(t) + [V(t) - V_r]G_l = 0, \qquad (1)$$

where C is the membrane capacitance, $V(t)$ is the membrane potential, V_r, V_e and V_i are the membrane rest

potential, excitatory synapse reverse potential and inhibitory synapse reverse potential respectively. G_l is the membrane leak conductance. To model the event of firing, a neuron is considered to have fired when its membrane potential reaches a hard threshold V_{th}. The membrane potential is then artificially brought to a reset potential V_{reset} and clamped to that value for a fixed refractory period t_{refra}.

In the model, inputs are modelled by conductances. The excitatory and inhibitory synaptic conductance, denoted by $G_e(t)$ and $G_i(t)$ respectively, are modelled by linear summation of conductance change due to each presynaptic input spike.

We can define a quantity $\tau_{eff}(t) = \frac{C}{G_{total}(t)}$, where $G_{total}(t) = G_l + G_e(t) + G_i(t)$. Expressing equation (1) in terms of $\tau_{eff}(t)$, we obtain

$$\tau_{eff}(t)\frac{d}{dt}V(t) = -V(t) + \frac{V_e G_e(t) + V_i G_i(t) + V_r G_l}{G_{total}(t)}. \quad (2)$$

$\tau_{eff}(t)$ has the physical meaning of effective membrane time constant [11]. It quantifies how fast the membrane responds to fluctuating conductance and is related to the total synaptic conductance which depends on the level of input activities.

2.1.2. Modified Current based LIF model

We may expand the membrane potential and synaptic conductance in equation (1) into tonic parts and fluctuation parts [12]. By assuming that the fluctuation parts are much smaller than the tonic parts, we obtain

$$<\tau_{eff}(t)>\frac{d}{dt}V(t) = -V(t) + \frac{V_e G_e(t) + V_i G_i(t) + V_r G_l}{<G_{total}(t)>}, \quad (3)$$

where $<>$ denotes the average over time. Equation (3) is to be called the 'modified current based model' in this work.

2.2. Synaptic input

The contribution of each input to the conductance change is modelled by an alpha function and the integration (from $t = -\infty$ to ∞) of conductance change due to an input spike is kept constant. The total conductance change is modelled by linear summation of conductance change due to each presynaptic input spike.

$$g_s(t) = A_s \frac{t}{\tau_s^2} e^{1-\frac{t}{\tau_s}} H(t), \quad G_s(t) = \sum_j g_s(t - t_j), \quad (4)$$

where A_s are synaptic efficacies, τ_s are synaptic time constant and the subscript s can be chosen as e, referring to 'excitatory' or i, referring to 'inhibitory'. $H(t)$ is the Heaviside step function. t_j, referring to the timing of input spikes, is assumed to have Poisson statistics.

2.3. Input correlation

In order to add correlation to the input spike trains, we adopt the Single Interaction Process [13]. Each neuron receives an independent excitatory spike train with input rate $(1 - c)\lambda_e$. In addition, they receive a common excitatory spike train with input rate $c\lambda_e$. The pairwise spike count correlation coefficient between the spike train is then c. Inhibitory spike trains are not correlated in this work.

2.4. Balance between excitation and inhibition

Most biological neurons operate in the fluctuation driven regime [4]. It means that excitation and inhibition must be balanced. In this work, this is achieved by adjusting the inhibitory input rate λ_i such that the output firing rate ν_{out} remains constant for different parameters. The reason of doing so is that output correlation is sensitive to the base-line firing rate of the post-synaptic neurons as shown by [5].

2.5. Characterizing output correlation

To quantify the correlation of output spike trains, we consider the cross-correlation function CCF(δt), given by

$$CCF(\delta t) = <n_1(t)n_2(t + \delta t)> - <n_1(t)><n_2(t + \delta t)> = <n_1(t)n_2(t + \delta t)> - \nu_{out}^2, \quad (5)$$

where $n_j(t)$ is the number of spikes per second in a spike train of the jth neuron. In order to further separate output synchrony from correlation of longer time scale (please note that 'correlation of longer time scale' will be simply referred to as 'correlation' in the following sections unless otherwise specified) quantitatively, we introduce two quantities, $corr$ and $sync$, by integrating the area below the graph of CCF from time $\delta t = -T_{large}$ to T_{large} and from $\delta t = -T_{small}$ to T_{small} respectively, where T_{large} (T_{small}) is chosen to have a large (small) value. These quantities correspond to the strength of output correlation and synchrony respectively.

Parameters chosen are listed below: $V_r = -70mV, V_e = 0, V_i = -75mV, V_{th} = -50mV, V_{reset} = -60mV$, $t_{refra} = 2ms$ (unless otherwise specified), $\frac{C}{G_l} = 20ms$, $\frac{A_e}{G_l} = 0.1, \frac{A_i}{G_l} = 0.3, c = 0.2$.

3 Results

3.1. Spike timing is jittered as τ_e increases

The ratio of correlation to synchrony, describing the time scale of correlation, increases as τ_e increases, as shown in Figure 1.

When τ_e increases, charge flow through the synapses due to presynaptic excitatory spikes takes place for a longer period, which causes a prolonged change in the membrane potential. The timing of extra spikes attributed to common input is then getting more easily jittered by 'noises' from other independent input, resulting in an increase of the time scale of correlation.

3.2. Synchronous output firing when τ_e is small and λ_e is large

Figure 1 shows that the ratio of correlation to synchrony approaches 1, corresponding to synchrony firing, at small τ_e only when given the condition that λ_e is large. Since λ_e is approximately inversely proportional to the effective membrane time constant, it means that the correlated input leads to extra synchronous output firing when the time scale of synaptic filtering and membrane integration is both small. This is because such neurons integrate (and forget) input quickly such that the effects of an excitatory input spike on the membrane potential are short-lived. As a result correlation of long time scale is filtered out as seen in Figure 2, where output correlation decreases with λ_e when τ_e is small.

3.3 Burst firing enhances correlation but not synchrony

Figure 2 shows that correlation is very large when both τ_e and λ_e are large. It turns out this can partly be attributed to burst firing, which refers to the phenomenon where more than one spikes are given in quick succession when a neuron experiences a temporary strong imbalance in excitation. In this work, it is defined by the probability of two randomly chosen consecutive spikes with interspike interval of less than 16ms. Burst firing is the most prevalent when the time scale of synaptic filtering is comparable or larger than that of the membrane integration, that is when both τ_e and λ_e are large (results not shown).

To illustrate that burst firing enhances correlation, we repeat the simulation with increased t_{refra}. This creates a hard minimum for the interspike interval and suppresses burst firing. Figure 3 shows that correlation indeed decreases while synchrony remains almost unaffected as t_{refra} increases.

As a final note, we stress that neurons with long hard refractory period are biologically unrealistic. We intend to show the effects of burst firing without resorting to higher dimensional and more complicated models. Moreover, the

inhibitory input rate is slightly adjusted so that the output firing rate remains a constant, thereby preventing changes in correlation as a result of reduced output firing rate [19].
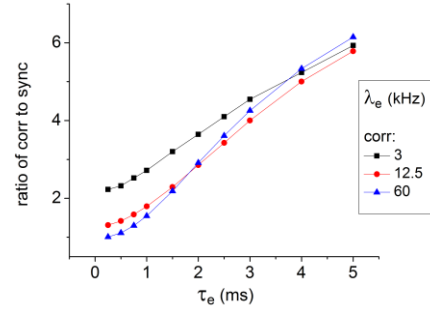

Fig.1: Ratio of correlation to synchrony increases with τ_e, and approaches unity when τ_e is small while λ_e is large. $\tau_i = 10ms$.
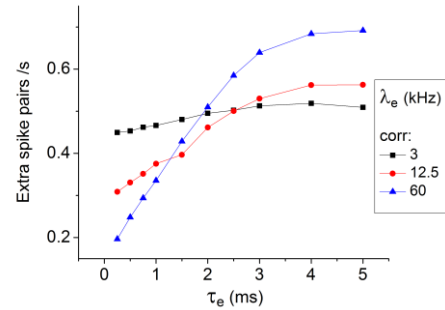

Fig.2: Output correlation greatly increases with both τ_e and λ_e. $\tau_i = 10ms$.
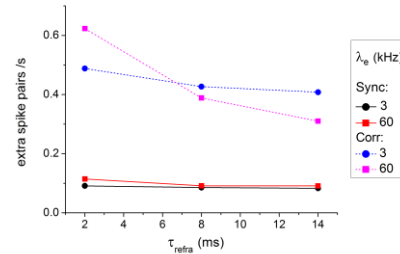

Fig.3: Changes in output correlation and synchrony when burst firing is suppressed. It is shown that correlation is reduced while synchrony is almost unaffected. $\tau_i = 8ms$.
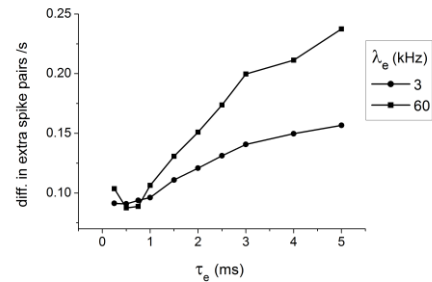

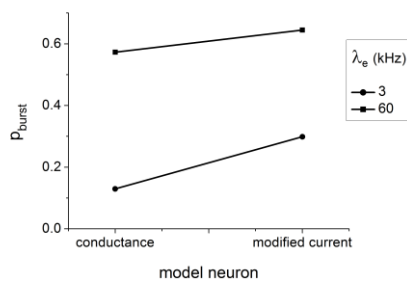Fig.4: Increase in output correlation when conductance fluctuation is ignored. $\tau_i = 8ms$.

Fig.5: Conductance fluctuation suppressed burst firing. $\tau_i = 8ms$.

3.4. Conductance fluctuation leads to reduced correlation

To study the effects of conductance fluctuation arisen from the multiplicative interaction between time-dependent terms $V(t)$ and $G_s(t)$ in equation (1), we repeat the simulation with modified current based model as shown in equation (3). Figure 4 shows that correlation is enhanced in general compared to the results using conductance based model. The enhancement is the most significant when τ_e is small and λ_e is large, which coincides with the regime where burst firing is the most prevalent. Figure 5 shows that burst firing increases when conductance fluctuation is ignored, suggesting that conductance fluctuation reduces correlation by suppressing burst firing.

4. Discussion

4.1. Implication on neural coding

An important question often discussed is neural coding. We would like to know what information in the spike trains can be reliably computed by neurons and transmitted from one layer of neurons to another.

We have shown that neurons at high conductance state with small synaptic decay time can exhibit extra synchronous spiking without correlation of longer time scale when they receive correlated input. This suggests that information that may be contained in correlation in neural spike trains can be reliably transmitted to the next layer of neurons in the form of synchronous spikes, which can easily and quickly transmit through neuron layers since they can induce postsynaptic firing easily. On the other hand, when the time scale of synaptic filtering is comparable or larger than that of membrane integration, output correlation is strong. Output spikes are more likely to cluster and their statistics become less Poissonian as a result of burst firing. Its implication on coding can be a subject of study.

4.2. Analytical study of correlation transfer

It is often challenging to study the output statistics of LIF neurons analytically without making further approximations. One common strategy is to approximate the neural dynamics as diffusion processes [5-6, 14]. In doing so, the temporal correlation in the input due to synaptic filtering is ignored. Another strategy is to use linear perturbation to study the influence of a single input spike on the membrane potential distribution, and hence the probability of output firing and correlation [6-7]. Such approach assumes that an input spike can contribute to at most one output spike. However, biological neurons may have slow synapses, rendering the above assumptions invalid. This work further shows that burst firing resulting from slow synaptic filtering has profound effects on output correlation. How to incorporate the effects of burst firing and conductance fluctuation into analytical studies of correlation transfer is therefore very important for our understanding on the subject.

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