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Impact of synaptic properties, background activities and conductance effects on neural computation of correlated inputs

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Impact of Synaptic Properties, Background Activities and Conductance Effects on Neural Computation of Correlated Inputs

CHAN Ho Ka

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Philosophy

Principal Supervisor: Dr. ZHOU Changsong
Hong Kong Baptist University
May 2015
DECLARATION

I hereby declare that this thesis represents my own work which has been done after registration for the degree of MPhil at Hong Kong Baptist University, and has not been previously included in a thesis or dissertation submitted to this or any other institution for a degree, diploma or other qualifications.

Signature: ________________

Date: May 2015
Abstract

Neurons transmit information through spikes in neural networks through synaptic couplings. 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 in neuronal interaction is very little known. Through simulation of leaky integrate-and-fire (LIF) neurons, we have studied the effects of excitatory and inhibitory synaptic decay times, level of background activities and higher-order conductance effects on the output correlation of different time scales for neurons receiving correlated excitatory input. We also provided important understanding on the mechanism of how these factors influence neural computation of such correlated input.

We showed that when the conductance effects are totally ignored, increasing excitatory synaptic decay time jitters output spike time and shapes the output correlation of short to medium time scale, while the output correlation of very long time scale is determined by the membrane time constant. When conductance effects are considered, this is no longer the case as the effective membrane time constant becomes comparable to the excitatory decay time. We found that the ratio of long-term correlation to short-term correlation (synchrony) increases with excitatory synaptic decay time and decreases with the level of input activities due to the combined effects of jittered spike time. This observation can be associated with the time window and magnitude of the effects of a single input spike on membrane potential, and burst firing. In particular, it is possible for neurons with small excitatory synaptic decay time in high conductance state to respond to correlated input by solely giving extra precisely timed synchronous spikes without exhibiting correlation of longer time scale. In addition, we found that inhibitory synaptic decay time shapes correlation by controlling the relative contribution of excitatory and inhibitory input to output firing. As a result, both output correlation and synchrony increase with it. These results are qualitatively true for a wide range of input correlation and synaptic efficacies. Finally, we showed that fluctuations of conductance and membrane potential reduce output correlation, which can be explained by the reduced prevalence of burst firing.

These results suggest that spike initiation dynamics of neurons can be well characterized by their synaptic decay times and the level of input activities. These properties are therefore expected to influence neurons’ ability to code temporal information. These results also hint that correlation, in particular that of long time scale, would be lower if more realistic biophysical features like neural adaptations and network circuitry with feed-forward or recurrent inhibition are considered. It suggests that studies using single LIF neurons tend to overestimate output correlation and underestimate the ability of neurons in producing precisely timed output.
I would like to thank my supervisor Dr. Zhou Changsong for his efforts in helping with my study. I was inexperienced in research and unfamiliar with the field of computational neuroscience when I started the degree program. He patiently helped me get acquainted with the field and discussed important issues that can be researched on. He also helped me a lot in other aspects of my study and encouraged me to attend conferences and gives talks in meetings. He also devoted much time in reading the draft of manuscripts and thesis and gave valuable comments.

I would like to thank Dr. Yang Dong-ping for his guidance on my research work. We spent much time together discussing on interesting directions of research which ultimately helped me identify the direction of my work. He also shared with me recent literatures in the field and provided valuable suggestions about how I could improve my work. He also helped me learn some useful techniques which have been very useful to my study and research.

I would like to thank my other colleagues for discussing with me different issues in computational neuroscience, which helped me broaden my knowledge in other aspects in the field. They shared their experiences on their career and provided suggestions on my future career path.

Finally, I would like to thank my parents and friends for mentally supporting me during my study and helped me brace through hard time. I would also like to thank my parents for their support my finances and life so that I could concentrate on my study and research.
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<tr>
<td>ISI</td>
<td>interspike interval</td>
</tr>
<tr>
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<td>leak integrate-and-fire</td>
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Chapter 1 \hspace{1cm} Introduction

1.1 Ubiquity of correlated activities observed in our brain

Neurons transmit information among each other in the form of action potentials, also known as spikes. Interestingly, spike trains among neurons very often are not independent. Experimental work have reported that correlated activities are detected in different areas of our nervous systems, including visual cortex (Zohary et al, 1994; König and Engel, 1995; Bair et al, 2001; Kohn and Smith, 2005), motor cortex (König and Engel, 1995; Okun and Lampl, 2008), retina (Greschner et al, 2011) and olfactory bulb (Kazama and Wilson, 2009; Gerkin et al, 2013).

The origin of these correlated activities has been extensively studied. It has been shown that correlation observed in the visual cortex (Kohn and Smith, 2005; Smith and Kohn, 2008) and olfactory bulb (Kazama and Wilson, 2009; Gerkin et al, 2013) is stimulus-driven with additional contribution from recurrent connections and noise due to other common input. It is also reported that correlation and synchrony are strong for neurons having the same stimulus preferences (Kazama and Wilson, 2009; Denman and Contreras; 2014). Observed correlation is of many different time scales. The time scale of correlation is often associated with the origin of correlation and the neural network structures (Smith and Kohn, 2008; Giridar et al, 2011)

1.2 Possible functions and roles of correlated activities

The possible functions and roles of these observed correlated activities have been under much debate. One view is that correlation simply arises as a side product of an effective rate code, which is discussed in details by Shadlen and Newsome (1998). They proposed that the long membrane integration time of neurons
and noisy input render neural spike time too unreliable to transmit information about the temporal patterns of spike trains, including correlation. They argued that the statistics of input and output neurons should be indistinguishable so that quantities do not blow up or die out when being transmitted across the network. This is achieved through balanced excitation and inhibition with high input rate. The consequence is that it leads to irregular interspike interval (ISI), which means that neurons need to receive large populations of input, in which a substantial proportion are shared among each other, in order to accurately transfer rate code (See Fig.1.1). High input rate along with shared input create coincidental correlated spikes. It is proposed that such correlated spikes have modest effects on output firing statistics and instead introduce redundancy which reduces the information capacity of a group of neurons.

![Fig.1.1: The reason for the necessity of shared input: A, without shared input, an unrealistically high number of neurons are required to accurately carry out rate code. B, with shared input, the amount of input neurons and output neurons can be of the same order. Adopted from Fig. 7, Shadlen and Newsome, 1998](image)

However Salinas and Sejnowski (2000) showed that the result of the above-mentioned work can only be obtained when very specific parameters are chosen. In general, correlated activities modulate output firing rate in a feedforward network. It is supported by Reyes (2003) and Rossant et al. (2011) (See Fig.1.2). In a later work (Salinas and Sejnowski, 2001), they suggested that through modulating correlation by other mechanisms, the strength of signals and thus the flow of information can be regulated because correlation can modulate firing rate. Dipoppa and Gutkin (2013)
extended the idea and showed that changes in correlation enable selective information
gating by switching neural network activities between quiescent and persistent state, 
and hence enabling working memory operations.

![Graph](image)

Fig. 1.2: Output firing rate (left) and the standard deviation (right) of membrane potential substantially 
increases with input correlation. Adopted from Fig. 13c, Rossant et al, 2011.

On the other hand, Kuhn et al (2004) showed that neurons in high conductance state 
integrate input much more quickly than the measured membrane time constant often 
used in neuron models, as shown in Fig. 1.3, and therefore it is possible for such 
neurons to create precisely timed spikes in response to input, opening up the 
possibility for neural coding of temporal patterns of fine time scale. Similarly, Wolfe 
et al (2010) showed that neurons in cortical networks are extremely sensitive to 
correlated activities and are capable of producing precisely timed spikes in response.
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Panzeri et al (1999) and Averbeck et al (2006) demonstrated that correlation between neural spike trains may not necessarily introduce redundancy. Information capacity of a network of neurons can either be increased or reduced depending on the state of correlation between signals and noise. They developed analytical tools for calculating such changes in information capacity.

1.3 Previous work on computation and transmission of correlated input on single neuron level

Till now, how correlation is computed and transmitted among layers of neurons is not without controversy. This may be due to the fact that neurons are not biophysically identical and that they receive input of a wide variety of statistics. Through studying problems of correlation transfer using simplified neuron models like the leaky integrate-and-fire (LIF) model, we can gain better understanding of how neural computation and transfer of correlation depends on biophysical factors and input statistics. Very often, such studies involve investigation on single neuron level or simple feed-forward networks so as to make the problems analytically tractable and the results more transparent. In this section, I will summarize several works in this line of study. They provide the context for this work.
De la Rocha et al (2007) showed that the output correlation of cortical neurons in vitro and LIF neurons receiving excitatory correlated input increases with the baseline output firing rate. By considering input current consisting of a mean part and Gaussian white noise (diffusion approximation), found that the output correlation can be expressed as a function of output firing rate, which is independent of the mean and variance of input.

Ostojc et al (2009) studied how correlation transfer depends on the connectivity, synaptic properties and firing statistics of post-synaptic neurons. In doing so, they analytically expressed the cross-correlation function (CCF) (see Section 4.1) in terms of excitatory synaptic decay time and a constructed variable, which depends on both input statistics and neural properties and characterizes the time scale of the effects of input on membrane potential.

Rosenbaum and Josic (2011) considered simplified LIF neurons receiving pulse input and showed that the efficiency of correlation transfer is determined by the comparison of time scales between the firing rate of a neuron and the time it takes for the membrane potential distribution to relax to equilibrium after receiving an input spike. In other words, they relate the time scale and magnitude of output correlation with that of the effects of an input spike (on membrane potential).

Litwin-Kumar et al (2011) considered LIF neurons and cortical neurons in vitro with pulse input and showed that the conductance state of neurons receiving correlated input shapes both the magnitude and timescale of output correlation. In particular, they showed that the ratio of output correlation of long time scale to that of short time scale (synchrony) decreases with the total conductances that neurons receive.

Hong et al (2012) showed that neurons with different spike initiation dynamics respond to the mean and variance of input with different sensitivity, which they argued affect how the neurons compute correlations. They used high dimensional neuron models to study two neuron types, one being coincidence detectors and the other being integrators (See König et al, 1996 and also Section 6.1), and showed that
integrators exhibit output correlation of long time scale while coincidence detectors exhibit synchrony when they receive correlated input.

1.4 Objective of the thesis

How a neuron processes input depends primarily on two factors. First, it depends on how synaptic conductance changes when a presynaptic spike arrives (Moreno-Bote and Parga, 2004). 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 (Destexhe et al, 2003; Moreno-Bote and Parga, 2005), primarily affected by the level of synaptic bombardment by presynaptic input spikes (Paré et al, 1998; Destexhe and Paré, 1999). 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.

It is shown in the previous section that most of the previous work either focus on the effects of output firing activities (de la Racha, 2007; Rosenbaum and Josic, 2011) or level of input activities alone (Litwin-Kumar et al, 2011) on output correlation. They cannot account for the joint effects of synaptic filtering and level of conductance on output correlation.

An exception is Ostojic et al (2009), which attempted to study the above-mentioned effects analytically. In doing so, they made several assumptions. First, they assumed that synapses are fast compared to the membrane integration time, which is not generally true for biological neurons because of huge amount of synaptic input they receive (Destexhe et al, 2003). With such assumption, a large biologically plausible regime cannot be studied, since high order temporal correlation in the input is not negligible for slower synapses. Moreover, the higher order conductance effects arisen form conductance fluctuation on output correlation were unaccounted for because of
diffusion approximation of input current. Finally, the consideration of dominant
timescale only meant that the analytical approximation for output correlation may be
invalid for correlation of short time scale.

Therefore in this work, we directly tackle the problem through numerical simulation
of a pair of LIF neurons receiving partially common excitatory input. We intend to
explicitly study the effects of biophysical factors, namely the excitatory and
inhibitory synaptic decay times, level of input activities and higher order conductance
effects on neural computation of correlation, with emphasis on understanding the
mechanism of how these factors influence output correlation of different time scales.
Through numerical simulations, a large portion of biologically realistic regime can be
studied without constraints due to approximation as in analytical work.

In Chapter two, we will study a few variants of leaky integrate-and-fire (LIF) models
which will be used in this work to approximate neural dynamics. In particular, we
will look into what biophysical features have been taken into account by each of these
models. In Chapter three, we will examine the correlated excitatory input which we
give to the model neurons. We will first consider the statistics of a single spike train,
and then show how correlation between spike trains is generated, and finally discuss
how the balance between excitation and inhibition is achieved. In Chapter four, we
will show how the output correlation of different time scales can be characterized and
obtained from numerical results. We will also derive the relationship between
measures characterizing correlation used in this work and that in other works. In
Chapter five, we will study how the output correlation of different time scales
depends on the biophysical factors discussed in the last paragraph. We will show how
we can understand these results by considering the time window and magnitude of
the effects of a single input spike on membrane potential as well as the higher order
interactions between multiple spikes, in particular burst firing. In Chapter six, we will
discuss the implications of our results and suggest how the results of this work can be
extended to more realistic neurons and neural networks.
Chapter 2  Single neuron dynamics: The leaky integrate-and-fire model

Single neuron dynamics is by no means simple. It has been extensively studied in for example Izhikevich (2007). People have been building neuron models in order to quantitatively describe neuron dynamics and understand the mechanisms which drive neural activities.

Theoretically, it is possible to very accurately describe single neuron dynamics by building an extremely detailed model, using multiple differential equations to describe the dynamics of synaptic ion channels, spiking mechanisms, refractoriness and adaptations. However the model would be so complex that it becomes impossible to study the computational principles of neurons. Hodgkin and Huxley, in a Nobel Prize winning work (1952), studied spike initiation in squid giant axons and managed to very accurately describe single neuron dynamics using a 4-dimensional neuron model, which is simple enough to provide understanding on the important biophysical basis of how neurons integrate input.

However, inputs to biological neurons are highly variable. Instead of being constant or sine-wave currents, they are stochastic point processes. A neural network may exhibit structured activities, like synchronous burst firing and correlated oscillation. It is often hard to analyze how neurons compute such complex input. That is why simpler models which can capture the essential features of neural dynamics are required. The aim is to elucidate the computational principles of neurons receiving input with different statistics.

A popular choice for such simplified models is the leaky integrate-and-fire (LIF) model (see Burkitt (2006) for detailed discussions). In the model, neurons receive synaptic inputs. They modelled by input spikes which are stochastic point processes and can be excitatory, which tend to increase the membrane potential or inhibitory, which tend to do the opposite. The contribution of each input spike is summed up
linearly. The model neuron is leaky in the sense that, its membrane potential relaxes to a rest value at a rate proportional to the deviation of the membrane potential from the rest value when it receives no net input.

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 $t_{refra}$.

The leaky integrate-and-fire model has made several significant simplifications and as a result it fails to model several features observed in the dynamics of biological neurons. It does not take into account of neural adaptations. It ignores all the non-linear dynamics associated with spike initiation and refractoriness, and replaces them with an artificial spiking mechanism. It combines all the input from different ion channels into two types, excitatory and inhibitory, and thus misses many features of slower dynamics exhibited by biological neurons (Izhikevich, 2007). Nevertheless, its performance in modelling neurons is very often satisfactory and its simplicity makes problems easy to analyze, which explain its popularity and usefulness.

2.1 Conductance based model

The majority of the work in this thesis involves using the conductance based LIF model. The membrane potential of a model neuron is described by (Stein, 1967):

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

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.
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.

One of the objectives of this work is to study the effects of synaptic decay times, which are characterized by the synaptic time constants ($\tau_e$ for excitatory and $\tau_i$ for inhibitory). The contribution of each input to the conductance change is modelled by an alpha function and in most of the study, the integration (from $t = -\infty$ to $\infty$) of conductance change due to an input spike is kept constant, we have

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

where $A_s$ are synaptic efficacies, and the subscript $s$ can be chosen as e, referring to ‘excitatory’ or i, referring to ‘inhibitory’. $H(t)$ is the Heaviside step function. The expression in equation (2) ensures that the value of the integration of conductance change is $A_s \exp(1)$. Figure 2.1 shows the plot of $g_s(t)$ with different values of $\tau_s$.

In Section 4.5, we consider a different form of conductance change per synaptic input in relation to the synaptic time constants. More specifically, the peak of conductance change due to an input spike is kept constant, we then have

$$
g_s(t) = A_s \frac{t}{\tau_s} e^{1-\frac{t}{\tau_s}} H(t), \quad G_s(t) = \sum_j g_s(t - t_j) \quad \text{(3)}$$

Figure 2.1b shows the plot of $g_s(t)$ with different values of $\tau_s$. Note that $g_s(t)$ in equation (2) and (3), given a fixed $\tau_s$ differ by just a constant. Therefore switching from equation (2) and (3) can be considered equivalent to changing the synaptic efficacies of neurons. Unless otherwise specified, all the analysis in this work except Section 5.4 is based on conductance change in the form of equation (2).
Fig. 2.1: Left, the plot of $g_s(t)$ with different values of $\tau_s$. The area under the function is kept constant. Right, same as left but the peak under the function is kept constant. Note that for illustrative purposes $A_s$ take the value of 1 in both plots.

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

$$\tau_{eff}(t) \frac{d}{dt} V(t) = -V(t) + \frac{V_e G_e(t) + V_i G_i(t) + V_r G_l}{G_{total}(t)}$$  (4)

$\tau_{eff}(t)$ has the physical meaning of effective membrane time constant (Kuhn et al, 2004). It quantifies how fast the membrane of a model neuron responds to changes in synaptic conductance. Biologically, $\tau_{eff}(t)$ is much smaller than the membrane time constant $\tau_m = \frac{C}{G_l}$ owing to the high amount of synaptic input neurons typically receive (Destexhe et al, 2003).

2.2 Current based model

In Section 5.1, neurons whose dynamics are approximated by current based LIF model are considered. Their membrane potential is modelled by (Stein, 1967):
Chapter 2  Single neuron dynamics: The leaky integrate-and-fire model

\[ C \frac{d}{dt} V(t) - I(t) + [V(t) - V_r] G_l = 0 \]  \hspace{1cm} (5)

The current \( I(t) \) is modelled as:

\[ I(t) = \sum_j i_e(t - t_j) + \sum_k i_i(t - t_k), i_s(t) = B_s \frac{t}{\tau_s} e^{1 - \frac{t}{\tau_s}} H(t) \] \hspace{1cm} (6)

By inspecting equation (5) and (6), it is obvious that this model makes further simplification from the conductance based model. The most important feature of neural computation it does not take into account is the effects of the level of input activities on the effective membrane time constant, i.e. how fast a neuron integrates synaptic input. In this model, the rate which membrane integrate input is characterized by the membrane time constant \( \tau_m \), defined by \( \tau_m = \frac{C}{G_l} \), whose value is a constant. In Section 5.1, the results obtained by this model will be compared with that of the conductance based model, which would highlight the importance of the above-mentioned effects in shaping the output correlation of neurons receiving correlated input.

As a final note, equation (6) suggests that each input spike injects a constant amount of total charges to the membrane, resembling the form of conductance change as shown in equation (2).

2.3 Modified current based model

We may also approximate the conductance based model by a current based model using linear approximation. Neural dynamics obtained using this approximation, unlike that of the current based LIF model discussed in the last section, can capture the feature of reduction of effective membrane time constant due to the average level of synaptic bombardment. However, the higher order non-linear effects of fluctuation
of membrane potential and conductance on neural dynamics are still ignored (Richardson and Gerstner, 2005; Rossant et al, 2011).

First, we expand $V(t)$ and $G_s(t)$ in equation (1) into time-averaged parts $V_{\text{mean}}$ and $G_{0s}$ and fluctuation parts $V_{\text{fluc}}(t)$ and $G_{fs}(t)$. Equation (1) then becomes

$$ C \frac{d}{dt} V(t) + \left[ V_{\text{mean}} + V_{\text{fluc}}(t) - V_e \right] \left[ G_{0e} + G_{fe}(t) \right] + \left[ V_{\text{mean}} + V_{\text{fluc}}(t) - V_i \right] \left[ G_{0i} + G_{fi}(t) \right] + \left[ V(t) - V_l \right] G_l = 0 \quad (7) $$

Since biological neurons receive high level of synaptic bombardment (destexhe et al, 2003), we assume that fluctuation of $V(t)$ and $G_s(t)$ are small compared to their mean value. Hence higher order terms $V_{\text{fluc}}(t) \cdot G_{fs}(t)$ are negligible. Rearranging equation (7) gives

$$ \tau_{\text{eff}} \frac{d}{dt} V(t) + V(t) - V_e \frac{G_e(t) + V_i G_i(t) + V_r G_l}{G_{\text{total}}} + V_{\text{mean}} \frac{G_{fe}(t) + G_{fi}(t)}{G_{\text{total}}} = 0, \quad (8) $$

where $\tau_{\text{eff}} = \frac{c}{G_{\text{total}}}$ and $G_{\text{total}} = G_l + G_{0e} + G_{0i}$

The last term on the left hand side of equation (8), $\frac{V_{\text{mean}} \left[ G_{fe}(t) + G_{fi}(t) \right]}{G_{\text{total}}}$, is negligible once again because of our assumption $G_{fs}(t) \ll G_s(t)$. Hence we have

$$ \tau_{\text{eff}} \frac{d}{dt} V(t) = -V(t) + \frac{V_e G_e(t) + V_i G_i(t) + V_r G_l}{G_{\text{total}}}, \quad (9) $$

which will be called the ‘modified current model’ in this work. By comparing equation (9) with equation (4), it is clear that ignoring the higher order interactions between the membrane potential and conductance is effectively equivalent to ignoring conductance fluctuations and the resulting variations in the effective
membrane time constant. In Section 5.6, the results obtained by this model will be compared with that of the conductance based model and the ‘unmodified’ current-based model (equation (5)), allowing us to understand the effects of nonlinearity in membrane potential integration caused by fluctuating conductance and membrane potential on neural computation of correlated input.

Equation (9) is a current based model in a general sense, effectively replacing the membrane time constant $\tau_m = \frac{C}{g_l}$ in equation (5) by the usually much smaller $\tau_{eff}$ and scaling $B_s$ by a factor of $V_{mean}$.

Before ending this chapter, the numerical techniques in simulating the dynamics of LIF neurons will be briefly described. Finite difference method is used in integration. Heun’s method with time step $\Delta t$ is employed as the time-marching scheme (Shelley and Tao, 2001). It is a second-order method, so for consistency, spike time is linearly interpolated (Shelley and Tao, 2001). A transient period of $t_{tran}$ is added before results are taken to allow transient effects to sufficiently decay. See table 1 in the end of Chapter 4 for the values of the parameters used in this study.
Chapter 3 Generating correlated excitatory input

3.1 Statistics of the input spike trains

Spike time of neurons is highly variable. Experimental studies showed that the mean and variance of spike count in a specific time window are almost equivalent (Softky and Koch, 1993; Shadlen and Newsome, 1998) (see Fig. 3.1 (left)). Therefore the input spike trains can be well approximated by Poisson point processes. With such approximation, spikes are generated stochastically at a fixed rate $\lambda_s$, and the timing between successive spikes, the interspike interval (ISI), follows the exponential distribution (see Fig. 3.1 (right)).

Fig. 3.1: The mean and variance of spike count are almost equivalent (left) while the probability density of interspike intervals fits well to an exponential distribution (right). The data is obtained from 2-second recordings from a neuron in area MT of an alert monkey. Adopted from Fig. 3c and 3d, Shadlen and Newsome, 1998.

The value of $\lambda_s$ determines the level of synaptic bombardment on a neuron. By Campbell’s theorem (Papoulis, 1991), the time averaged total conductance $G_{total}$ can be expressed by

$$G_{total} = G_l + G_{oe} + G_{ol} = G_l + \lambda_e \int_0^\infty g_e(t) \, dt + \lambda_i \int_0^\infty g_i(t) \, dt$$

$$= G_l + \lambda_e A_e e + \lambda_i A_i e$$  \hspace{1cm} (10)
Since the total conductance is inversely proportional to the effective membrane time constant, it is hence confirmed that conductance based LIF neurons can capture the feature of neural computation being influenced by the level of input activities.

Biologically, neurons receive input from many synapses. Let’s say a neuron receives excitatory input from $N_e$ synapses, where the input rate for the $n^{th}$ synapse is $\lambda_{n,e}$, $n = 1, 2, 3, ..., N_e$ and inhibitory input from $N_i$ synapses, where the input rate for the $n^{th}$ synapse is $\lambda_{n,i}$, $n = 1, 2, 3, ..., N_i$. Then we will need to generate $N_e$ excitatory spike trains and $N_i$ inhibitory spike trains using the method described above. In this work, these spike trains are considered to be independent. Then, statistically it is equivalent to generate just one excitatory spike train and inhibitory spike train apiece, with input rate $\lambda_e = \sum_{n=0}^{N_e} \lambda_{n,e}$ and $\lambda_i = \sum_{n=0}^{N_i} \lambda_{n,i}$ respectively.

### 3.2 Generating correlated spike trains using SIP process

If we generate two spike trains using the method described in Section 3.1, they will be totally independent of each other. In this work, the output statistics of a pair of neurons receiving correlated excitatory input are studied. In order to add correlation to the spike trains which serve as input to the neurons, we adopt the Single Interaction Process (SIP) (Kuhn et al, 2003). 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 $c\lambda_e$. After summing the two spike trains, both neurons effectively receive an excitatory spike train with input rate $\lambda_e$, and the pairwise spike count correlation coefficient between the spike train is $\frac{c}{c+(1-c)} = c$.

Since inhibitory spike trains are not correlated in this work, the pair of neurons each only receives an independent inhibitory spike train with input rate $\lambda_i$ without additional common spike trains. See Figure 3.2 for an illustration for the structure of input to the neurons.
3.3 Balance between excitation and inhibition

Neural firing can be driven by two types of input, superthreshold and subthreshold input (Gerstner and Kistler, 2002). Superthreshold input can induce firing even in the absence of noise. Neural firing can be predominantly attributed to the mean of such input, which reliably drives the neurons above the firing threshold while noise only jitters the spike time by a little. Therefore neurons driven by superthreshold input fire very regularly (Gerstner and Kistler, 2002; Shadlen and Newsome, 1998) (see Fig. 3.3 (left)). It is often said that neurons receiving such input operate in the mean-driven regime.

Subthreshold input on the other hand cannot induce firing in the absence of noise. Neural firing is driven by the fluctuation of such input, whose mean is insufficient in depolarizing the membrane potential above the firing threshold. It is often said that neurons receiving such input operate in the fluctuation-driven regime.

There are evidences that biological neurons in our nervous systems mostly operate in the fluctuation-driven regime. First, the output spike trains of neurons receiving such input are shown to be highly variable (See Fig. 3.3 (right)) as observed in most biological neurons (Softky
and Koch, 1993; Shadlen and Newsome, 1998). Moreover, biological neurons show rich dynamics (Latham et al, 2000; Compte et al, 2003; Buzsáki and Draguhn; 2004). In fluctuation-driven regime, neural activities of a wide range of intensity (measured by firing rate) can be sustained in both single neurons (Kuhn et al, 2004; Shadlen and Newsome, 1998) and recurrent neural network (Amit and Brunel, 1997; Renart et al, 2007) set-ups, highly enriching neural dynamics.

![Graphs](image)

Fig. 3.3: The membrane potential (top) and the ISI distribution (bottom) for mean-driven (left) and fluctuation-driven (right) neurons. Adopted from Fig. 5.20, Gerstner and Kistler, 2002.

Since neurons mostly operate in high conductance state (Destexhe et al, 2003), the large amount of synaptic bombardment by excitatory input would be superthreshold and push the neurons into the mean-driven regime should there be no modulation from inhibitory input. For most of the biological neurons that operate in the fluctuation-driven regime, inhibition is required to counter the robust excitatory input so that the total input is subthreshold. In other words, excitatory and inhibitory input must be in some way balanced.

In this work, the balance between excitation and inhibition is achieved by adjusting the inhibitory input rate $\lambda_i$ such that the output firing rate $v_{out}$ 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 de la Rocha et al (2007). Keeping the firing rate constant allows us to focus entirely on the aim of studying the correlation of output spike trains due to synaptic decay time and conductance effects without worrying about the effects of extra factors which are irrelevant to the study, including $v_{out}$. A minor downside is that the total conductance would change slightly as $\lambda_i$ is varied, and as a result the effective membrane time constant is also changed. However, it turns out the required adjustment of $\lambda_i$ is small and the results are unaffected qualitatively.
Chapter 4  Characterizing output correlation

To quantify the correlation of output spike trains, we consider the cross-correlation function \( \text{CCF}(\delta t) \), defined by

\[
\text{CCF}(\delta t) = \langle n_1(t) n_2(t + \delta t) \rangle - \langle n_1(t) \rangle \langle n_2(t + \delta t) \rangle
\]

\[
= \langle n_1(t) n_2(t + \delta t) \rangle - \nu_{out}^2,
\]

where \( n_j(t) \) is the number of spikes per second in a spike train of the \( j^{th} \) neuron, and \( \langle \rangle \) denotes the average over time. In this work, the quantity \( \langle n_1(t) n_2(t + \delta t) \rangle \) is calculated from the numerically simulated output spike trains as follows:

\[
\langle n_1(t) n_2(t + \delta t) \rangle = \frac{1}{N_{\text{trial}}t_{\text{bin}}(t_{\text{total}} - |\delta t|)} \sum_{k=1}^{N_{\text{trial}}} \sum_{s=0}^{(t_{\text{total}} - \delta t)/t_{\text{bin}}} y_{1,k}(st_{\text{bin}}) y_{2,k}(st_{\text{bin}} + \delta t),
\]

where \( N_{\text{trial}} \) is the total number of simulated trials. \( t_{\text{total}} \) is the length of output spike trains per trial. \( t_{\text{bin}} \) is the size of time bin. \( y_{j,k}(t) = 1 \) if the spike time \( t_{\text{spike}} \) of any spike in the spike train of the \( j^{th} \) neuron lies within the corresponding time bin, i.e. \( t - \frac{t_{\text{bin}}}{2} \leq t_{\text{spike}} < t + \frac{t_{\text{bin}}}{2} \), and \( y_{j,k}(t) = 0 \) otherwise.

The value of the cross-correlation function has the physical meaning of ‘the number density of extra spike pairs per second’. In this work, if unspecified, ‘extra’ compares to the case where the input is totally uncorrelated, and ‘spike pairs’ here means the concurrence of two spikes, one from each neuron, fulfilling the condition that the spike from neuron 1 precedes that of the neuron 2 by \( \delta t \), where the choice of neuron 1 and neuron 2 is arbitrary but fixed once it is made. In some other work (de la Rocha et al, 2007; Tchumatchenko et al, 2010), the authors normalize the correlation function by the root of the product of the firing rate of each neuron. However it
is unnecessary here since \( v_{out} \) is always constant, adjusted by the inhibitory input rate \( \lambda_i \) as discussed above.

In order to separate the contribution of the partially common input to 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.

\[
corr = \int_{-T_{large}}^{T_{large}} n_1(t)n_2(t + \delta t) > -v_{out}^2 d(\delta t)
\]

\[
= \int_{-T_{large}}^{T_{large}} n_1(t)n_2(t + \delta t) > d(\delta t) - 2 T_{large} v_{out}^2
\]

\[
sync = \int_{-T_{small}}^{T_{small}} n_1(t)n_2(t + \delta t) > d(\delta t) - 2 T_{small} v_{out}^2
\]

They correspond to the number of extra spike pairs per second with the absolute spike time difference smaller than \( T \). When we integrate through a narrow time window where \( \delta t \) is small, only events in which two neurons almost simultaneously fire are counted. Hence \( sync \) detects extra synchronous spike pairs. Likewise \( corr \) detects extra correlated spike pairs. In this work, we choose \( T_{small} = 1.125ms \) for synchrony spiking detection and \( T_{large} = 10.125ms \) for correlated spiking detection. The extremely high precision of the time window chosen is merely a result of the binning system which keeps CCF(\( \delta t \)) strictly maximum at \( \delta t = 0 \). It has no biological significance, and would not qualitatively affect the results if other slightly different choices are made.

Some works use the Pearson pairwise correlation coefficients \( \rho_T \) (de la Rocha et al, 2007; Tchumatchenko et al, 2010) to describe output correlation of different time scales. Here we will show the relation between \( \rho_T \) and \( corr, sync \). By the definition of \( \rho_T \),
\[ \rho_T = \frac{\text{Cov}(N_1, N_2)}{\sqrt{\text{Var}(N_1)\text{Var}(N_2)}} = \frac{<N_1 N_2> - <N_1><N_2>}{\sqrt{\text{Var}(N_1)\text{Var}(N_2)}}, \]  

(15)

where \text{Cov} and \text{Var} denote covariance and variance respectively and \( N_j = \int_{-T}^{T} n_j(t) dt \). Since the input rate is constant, the average spike count within any time window is independent of the absolute time. Hence we have

\[ <N_j> = \int_{-T}^{T} n_j(t) dt = <n_j(t)> \int_{-T}^{T} dt = 2T v_{out} \text{ and} \]

\[ <N_1 N_2> = <\int_{-T}^{T} n_1(t) dt \int_{-T}^{T} n_2(t) dt> = \int_{-T}^{T} dt \int_{-T}^{T} d(\delta t) n_1(t)n_2(t + \delta t) >
\]

\[ = 2T \int_{-T}^{T} d(\delta t) <n_1(t)n_2(t + \delta t)> = 2T \int_{-T}^{T} d(\delta t) <n_1(t)n_2(t + \delta t)> \]

Neural spike counts are assumed to be Poisson distributed and the output firing rate for both neurons are \( v_{out} \), therefore \( \text{Var}(N_1) = \text{Var}(N_2) = 2v_{out}T \).

Finally, we obtain

\[ \rho_T = \frac{\int_{-T}^{T} d(\delta t) <n_1(t)n_2(t+\delta t)> - 2T v_{out}}{v_{out}}. \]  

(16)

Hence, by normalizing \text{corr} (sync) by the firing rate, \( \rho_{T_{\text{large}}} (\rho_{T_{\text{small}}}) \) can be obtained. Using \( \rho_T \) has the advantage of having taken into account the amount of coincidental correlation attributed to the level of firing activity, and also allowing direct comparison with the input correlation \( c \) since both are dimensionless. However, this does not apply to our work since \( v_{out} \) and \( c \) is kept constant in most parts of the work with the exception of Section 5.5 where \( c \) is varied. In that section, the quantities \( n_{corr} = \frac{\text{corr}}{v_{out}} \) and \( n_{sync} = \frac{\text{sync}}{v_{out}} \) are introduced to study the scaling of output correlation and synchrony with \( c \).
Table 4.1 lists the values of all the parameters used in this work.

<table>
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<tr>
<th>Parameters</th>
<th>Value</th>
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<tr>
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</tr>
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<td>$\frac{B_i}{G_l}$</td>
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</tr>
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<td>$\tau_i$</td>
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<td>ms</td>
</tr>
<tr>
<td><strong>Input statistics</strong></td>
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<td>$c$</td>
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</tr>
<tr>
<td>$T_{large}$</td>
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<td>ms</td>
</tr>
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</table>

Table 4.1: The values for all the parameters used in this work.
Chapter 5  Impact of conductance effects and synaptic decay time on output correlation

LIF neurons receiving completely identical input always fire together. If only a portion of excitatory input spikes are common, it is no longer the case because the neurons can be in different states when common input spikes arrive. However, they are still more likely to fire almost simultaneously (compared to the case where the inputs are totally independent). This is reflected by a bump centered at $\delta t = 0$ in the plots of CCFs. Figure 5.1 shows one such example.

![Figure 5.1: A plot of CCF. Conductance based LIF neurons with $\tau_e = 1.5 \text{ ms}, \tau_i = 5 \text{ ms}, \lambda_e = 12.5 kHz$ are considered.](image)

An intuitive explanation is that the arrival of a common excitatory input spike temporarily raises the firing probability of both neurons by skewing their steady state membrane potential distribution (i.e. the distribution without prior knowledge about the arrival of common input) towards the threshold. This idea was discussed and explored in details in Rosenbaum and Josic (2011). From this line of thought, the width of the bump in CCF, which characterizes the time
scale of output correlation, can therefore be related to the length of the time period during which a neuron experiences increased probability of firing as a result of an excitatory input spike. Similarly the size of the bump, which characterizes the magnitude of output correlation, is related to the total effects of an excitatory input spike on membrane potential, i.e. by how much the probability of firing is increased until the effects of the input spike fade. Furthermore, higher order interactions between multiple input and output spikes like burst firing also affect the time scale and magnitude of output correlation as we will show later. All the above factors, influenced by synaptic decay time and conductance effects, shape the output correlation of a neuron receiving correlated excitatory input.

In the sections below, how the time scale and magnitude of output correlation depends on synaptic decay time and conductance effects will be studied by bridging them using the mechanisms discussed in the previous paragraph.

### 5.1 Prelude: The effects of excitatory decay time ignoring conductance effects

To study the effects of excitatory decay time $\tau_e$ alone, current based LIF model, in which all conductance kinetics is ignored, is used to simulate the dynamics of neurons. As mentioned in Section 2.2, such neurons integrate input at fixed rate determined by $\tau_m$. Since $\tau_m$ is much larger than $\tau_e$, it can be expected that $\tau_e$ affects the profile of membrane potential shortly after the onset of a common input spike, and therefore affects output correlation of short time scale, while the output correlation of long time scale is dominantly dictated by $\tau_m$. Figure 5.2 shows the plot of CCF($\delta t$) for different $\tau_e$. We can observe that while $\tau_e$ has substantial effects on the CCFs at small $\delta t$, the tails of the CCFs are almost invariant with $\tau_e$, which is consistent with the above hypothesis.
To quantitatively study the output correlation of different time scales, we calculate the functions \textit{corr} and \textit{sync} as shown in Figure 5.3. It shows that output correlation is much larger than synchrony, which means that the timing of output spike pairs in response to the common input, which arrives synchronously at both neurons, is jittered. The jittering effect increases further with \( \tau_e \), as output synchrony decreases with \( \tau_e \) while correlation remains roughly constant. The results show that current based LIF neurons struggle to produce precisely timed spikes, consistent with some work using the same model (Shadlen and Newsome, 1998). Moreover, varying the excitatory input rate \( \lambda_e \) does not qualitatively change the above picture.

Nevertheless, Figure 5.3 shows some interesting features that cannot be explained by the above discussion. For instance, it shows that both correlation and synchrony increase with \( \tau_i \). The role of \( \tau_i \) will be studied in Section 5.3. Moreover, correlation is slightly stronger for high \( \lambda_e \). The mechanism which causes that will be investigated in Section 5.2.2.
Fig. 5.3: Output correlation and synchrony for current based LIF neurons with different $\tau_e$. Top, $\lambda_e = 3kHz$. Bottom, $\lambda_e = 60kHz$. 
5.2 The joint effects of excitatory decay time and conductance kinetics

The primary effect of conductance kinetics is that the time scale which neurons integrate input, $\tau_{\text{eff}}$, is no longer fixed. It becomes dependent on the level of input activity (Paré et al, 1998; Destexhe and Paré, 1999). This feature is well captured by conductance based LIF neurons (See Section 2.1 and also Kuhn, 2004) which will be used for the studies from Section 5.2 to 5.5.

The high level of synaptic bombardment on neurons means that $\tau_{\text{eff}}$ is often comparable or even smaller than $\tau_m$. The idea of differentiating the effects of $\tau_e$ and $\tau_{\text{eff}}$, or excitatory input rate $\lambda_e$ which primarily influences $\tau_{\text{eff}}$, into separate regimes of different time scales as we did in the last section thus would no longer work. $\tau_e$ and $\lambda_e$ jointly shape the output correlation of neurons.

Figure 5.4 shows the plot of CCFs for different $\tau_e$ and $\lambda_e$. When $\lambda_e$ is small, $\tau_{\text{eff}}$ is still larger than $\tau_e$, therefore the CCFs are qualitatively similar to that of current-based LIF neurons in Figure 5.2. However, when $\lambda_e$ is large, the picture becomes very different. First, the CCFs for neurons with small $\tau_e$ are significantly sharpened. Second, the tails of CCFs are no longer invariant with $\tau_e$ as opposed to the case of current-based LIF neurons. These significant differences confirm that conductance effects indeed cannot be ignored.
Fig. 5.4: CCFs for conductance-based LIF neurons with different $\tau_e$. $\tau_i = 5ms$. Top, $\lambda_e = 3kHz$. Bottom, $\lambda_e = 60kHz$.

We again consider the functions $corr$ and $sync$ as shown in Figure 5.5. As in the case of current-based LIF neurons, increasing $\tau_e$ has the effect of jittering the timing of output spike
pairs when $\lambda_e$ is small, illustrated by the decreasing synchrony and roughly unchanged correlation.

When $\lambda_e$ is large, the situation becomes complicated as several factors come into play. First, we note that at small $\tau_e$, the output correlation is much smaller compared to the case when $\lambda_e$ is 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. It means that correlation of long time scale is filtered out. In fact, Figure 5.5 (right) shows that $corr$ and $sync$ are almost equivalent for neurons with very small $\tau_e$, indicating that the such neurons indeed respond to the correlated input by creating extra precisely timed spikes without correlated spikes of longer time scale.

Next, it can be observed that correlation increases as $\tau_e$ increases. This can be understood by noting that synaptic filtering provides a lower bound for the time window of the effects of an input spike. No matter how quickly the membrane potential integrates input, it still needs to wait for the charges to slowly come through the synapses after an input spike arrives. In the next section, methods will be developed to support all the above arguments.

Finally, the behavior of output correlation becomes rather odd when $\tau_e$ is large, where it scales very strongly with both $\tau_e$ and $\tau_i$. It cannot be explained by synaptic filtering alone, since in extreme cases it increases beyond its counterpart observed in current based LIF neurons. These phenomena will be discussed in Section 5.2.2.
Fig. 5.5: Output correlation and synchrony for conductance based LIF neurons with different $\tau_e$. Top, $\lambda_e = 3kHz$. Bottom, $\lambda_e = 60kHz$. 
5.2.1 The ‘effect time window’ of excitatory input

In order to bridge the results in the previous section with the time window in which an excitatory input affects the membrane potential and hence post-synaptic firing, a new quantity describing the number of average effective excitatory input spikes bombarding a neuron before it fires, $s(t)$, is introduced. It is defined as an exponentially decaying function with time constant $\tau_e$ which jumps by the value of 1 whenever an excitatory input spike arrives. It contributes to the changes in excitatory conductance, constrained by our assumption of the form of conductance change due to an input spike in equation (2), by the following relation:

$$\tau_e \frac{d}{dt} g_e(t) = -g_e(t) + eA_e s(t)$$  \hspace{1cm} (17)

A neuron at any arbitrary moment is on average under the impact of $s_0 = \frac{g_{oe}}{eA_e}$ excitatory input spikes. According to equation (17), when $s(t) > s_0$, the excitatory conductance, and therefore the membrane potential, will tend to be driven above their mean value and vice versa. To allow easy comparison between the results, $s(t)$ is normalized such that $s(-20ms) = 0$ and $\max_{t \in [0,-20ms]} s(t) = 1$.

We can know the time window in which pre-synaptic input spikes can contribute to post-synaptic firing by finding the time $t_{eff}$ after which $s(t)$ starts to increase.

$$t_{eff} = \min T, \text{ where } T = \{t : s(t) \geq \epsilon\}, \epsilon = 0.1$$  \hspace{1cm} (18)

The exact value of $\epsilon$ is qualitatively unimportant as long as it is much smaller than 1.

We choose $t = 0$ to be the moment when the neuron fires so that $|t_{eff}|$ indicates how long before spiking does a neuron on average starts to integrate inputs which are capable of driving the membrane potential towards the threshold and eventually cause the neuron to fire.

Inputs arrived earlier than $|t_{eff}|$ before output spike time would have their effects almost completely decayed before the neuron fires and therefore unrelated to firing of the neuron. Such inputs serve only as maintaining the balance between excitation and inhibition. The power of this quantity is that it directly dictates the maximum spike time difference between any spike pairs to
which the very same common input spike can contribute, and hence predicts the time scale of output correlation (See discussion below and also Figure 5.7 for illustration).

The plots of $s(t)$ for conductance based LIF neurons with different $\tau_e$ and $\lambda_e$ are shown in Figure 5.6.
Fig. 5.6: The normalized number of effective excitatory input spikes a neuron receives before firing. Conductance based LIF neurons are considered. Top, $\tau_e = 4\text{ms}$. Bottom, $\tau_e = 0.5\text{ms}, \tau_i = 5\text{ms}$ for all cases.

It is shown that for cases of large $\tau_e$, $|t_{eff}|$ is larger than 15ms no matter what the input activity level $\lambda_e$ is, supporting the claim in the previous section that synaptic filtering provides a lower bound for the time window of the effects of an input spike. This also suggests that neurons with large $\tau_e$, while capable of responding to correlated input by exhibiting output correlation, cannot reliably give precisely timed spike as the spike time between spike pairs influenced by the same common input can be jittered within this (>15 ms) period. This gives rise to the low output synchrony to correlation ratio.

On the other hand, $\lambda_e$ plays a more important role when $\tau_e$ is small (Fig.5.6 (right)). When $\lambda_e$ is low, $|t_{eff}|$ is considerably less than the cases where $\tau_e$ is large, but it is still too large for reliable synchronous firing. However, when $\lambda_e$ is high, $|t_{eff}|$ can be as small as 2ms. Intuitively speaking, when such a neuron receives a presynaptic input spike, the change of conductance in the neuron is abrupt due to its small $\tau_e$, its membrane then integrates the (abrupt) conductance change rapidly due to its small $\tau_{eff}$. Therefore the effect of a presynaptic excitatory spike on the post-synaptic membrane potential is very short-lived. When a strong transient of common input acts on both neurons, they must fire within a short period of time, i.e. synchronously if the input is strong enough for both of them to fire. It is illustrated in Figure 5.7.
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Input arriving at time where the curve is flat does not contribute to spiking.

The dashed spike does not contribute to the firing of neuron 2.

Neuron 1 and 2 almost fire simultaneously!  
Synchrony!
Fig 5.7: Pictorial descriptions of why neurons with long (short) integration time windows have high (low) output correlation to synchrony ratio. In the top panel, neurons having a large integration time window can be in different phases of their drifts towards the threshold when a common spike arrives. The common spike contributes to the firing of both neurons, but the output spikes greatly differ in time. The middle panel shows that this cannot be true for neurons with a small integration time window. Common spikes cannot contribute to the firing of both neurons if the timing of their output spikes does not align well. In other words, the spikes shown in the middle panel must be solely due to the fluctuation of the respective independent input of the neurons. The bottom panel reinforces the idea that the only condition which allows common spikes to contribute to the firing of both neurons requires them to fire synchronously. This explains why such neurons respond to common input solely by giving extra synchronous spikes without exhibiting correlation (of longer time scale).

To briefly sum up, this section provides understanding on the joint effects of \( \tau_e \) and \( \lambda_e \), except for the regime where both are very large, on the basis of the ‘effect time window’ of individual excitatory presynaptic input spike.

### 5.2.2 The effects of burst firing

To understand the strong scaling of output correlation with \( \tau_e \) and \( \tau_i \) when \( \lambda_e \) is large, we need to consider higher order interactions between multiple input and output spikes. One of such interactions is 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 section, how the prevalence of burst firing depends on the synaptic and membrane integration properties of neurons and more importantly, how the output correlation is affected will be studied.

To quantitatively describe the prevalence of burst firing in a spike train, we plot the probability distribution of ISI of an output spike train, and define the prevalence of burst firing (\( p_{\text{burst}} \)) as the probability of two randomly chosen consecutive spikes having an ISI of less than 16ms. It is illustrated in Figure 5.8. Since the output firing rate is kept constant at approximately 8Hz, the ISI of spikes defined as a part of burst firing are smaller than one eighth of their mean. Such spikes can be considered significantly clustered. Please note that the choice of 16ms is arbitrary. The concept of burst firing itself is biophysically ill defined and the point here is not to obtain
quantitatively accurate results but to understand qualitatively the relationship between burst firing and output correlation. Choosing other time windows would quantitatively affect the results but would not change the qualitative pictures.

Fig. 5.8: Illustration of the definition of $p_{\text{burst}}$. It is defined by the probability of two randomly chosen consecutive spikes with the interspike intervals between them smaller than 16ms.

Figure 5.9 shows how $p_{\text{burst}}$ depends on $\lambda_e$, $\tau_e$ and $\tau_i$. It is shown that $p_{\text{burst}}$ increases with all the three parameters. At the regime where $\lambda_e$, $\tau_e$ and $\tau_i$ are large, $p_{\text{burst}}$ can be almost 10 times as large as its counterpart in the regime where $\lambda_e$, $\tau_e$ and $\tau_i$ are small, indicating the strong scaling effects of $p_{\text{burst}}$ with these quantities. Another observation is that the scaling of $p_{\text{burst}}$ with $\tau_e$ and $\tau_i$ is much stronger when $\lambda_e$ is large. This is probably because neurons integrate input quickly when $\lambda_e$ is strong, allowing them to be very sensitive to input fluctuations. On the other hand, increasing $\tau_e$ and $\tau_i$ means that temporary imbalance of input tends to have prolonged effects on the membrane potential as a result of synaptic filtering. The longevity of input transients allows a neuron time to give multiple spikes (even after taking into account the refractive period) before the effect of inputs eventually fade.
Then how burst firing affects the output correlation and synchrony? We attempt to understand it qualitatively by reworking Section 5.2.1 using the same model except that the refractory period $\tau_{\text{refra}}$ is increased. The increase in refractory period provides a hard minimum for time between consecutive spikes, hence very much reduces the prevalence of burst firing, particularly in the regime where $\lambda_e$, $\tau_e$ and $\tau_i$ are large. We would like to again emphasize that though this is biologically unrealistic (See Section 6.2 for suggestions of biologically realistic mechanisms for neural adaption which may limit burst firing), the point here is to understand qualitatively the effects of burst firing instead of accurately modelling neural dynamics, and increasing $\tau_{\text{refra}}$ is the easiest way to modulate burst firing without resorting to higher dimensional neuron models which bring unnecessary complications.

Figure 5.10 shows how $\text{corr}$ and $\text{sync}$ change as $\tau_{\text{refra}}$ increases. All the neurons shown in the figure have large $p_{\text{burst}}$ ($p_{\text{burst}} > 0.12$) before $\tau_{\text{refra}}$ is increased. Upon reduction of $p_{\text{burst}}$, the change in output synchrony is very small. Only a slight decrease is observed when $\lambda_e$, $\tau_e$ and $\tau_i$ are very large. On the other hand, correlation substantially decreases. The reduction in correlation is notable for all neurons, but is particularly significant for those with large $\lambda_e$, $\tau_e$ and $\tau_i$, corresponding to the regime where $p_{\text{burst}}$ is the greatest before $\tau_{\text{refra}}$ is increased. Thus it can be concluded that burst firing greatly enhances output correlation but only have very modest effects on synchrony, and that a substantial portion of correlation observed at the regime of large $\lambda_e$, $\tau_e$ and $\tau_i$ in Figure 5.5 is due to strong burst firing (large $p_{\text{burst}}$).
Fig. 5.9: The prevalence of burst firing for conductance based LIF neurons with different $\lambda_e$, $\tau_e$ and $\tau_i$. 

![Diagram showing the prevalence of burst firing for conductance based LIF neurons with different $\lambda_e$, $\tau_e$ and $\tau_i$.](image-url)
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Fig. 5.10: The change of corr (top) and sync (bottom) when the refractory period increases for neurons with different \( \lambda_e, \tau_e \) and \( \tau_i \). In each of these cases, conductance based LIF neurons is considered and the inhibitory input rate \( \lambda_i \) is adjusted such that the output firing rate \( \nu_{out} \) remains constant (8 Hz).

Before ending this section, we will provide some intuitive understanding on why burst firing enhances correlation by considering equation (13). corr is defined in equation (13) as

\[
corr = \int_{-T_{large}}^{T_{large}} < n_1(t) n_2(t + \delta t) > d(\delta t) - 2 T_{large} \nu_{out}^2.
\]

The second term is a constant. For the first term, the non-linearity of \( < n_1(t) n_2(t + \delta t) > \) and large integration time window mean that if the burst clusters of the two neurons align well, a spike in a burst cluster can simultaneously be correlated to several other spikes in the same cluster. This has a multiplicative effect on corr. Common inputs to both neurons enhance the alignment of burst clusters, and hence output correlation. For sync, the time window is too small for that to happen. See Figure 5.11 for an illustration.
Fig. 5.1: Illustration of why burst firing enhances correlation. Top, Correlated pairs and synchronous pairs in a burst cluster. It is shown that correlation is much enhanced due to one spike being correlated with multiple other spikes in the same burst cluster if they align well due to common inputs. Bottom, Correlated pairs and synchronous pairs with larger ISIs, having the same total number of spikes as in the top panel. By comparing with the results in top panel, it can be seen that burst firing enhances correlation but not synchrony when neurons receive correlated input.
5.3 The effects of inhibitory synaptic decay time

The results in both sections 5.1 and 5.2 show that both correlation and synchrony increases with the inhibitory synaptic decay time constant $\tau_i$, suggesting that the effects of $\tau_i$ are independent of conductance kinetics. Figure 5.3 and 5.5 shows that the scaling of corr and sync with $\tau_i$ is almost invariant for different $\tau_e$ except for the regime where burst firing is prevalent. This suggests that the effects of $\tau_i$ are also independent of $\tau_e$, allowing it to be separately studied without the need of concerning about other parameters.

It may at first seem counter-intuitive that $\tau_i$ affects output correlation and synchrony, since in this study inhibitory inputs to the neurons are totally independent. In this section, it will be shown that the effects of $\tau_i$ exactly originate from the asymmetry between the statistics of excitatory and inhibitory inputs.

We consider the average inhibitory current acting on a neuron it fires, $I_i(t)$, defined by $I_i(t) = [V(t) - V_i]G_i(t)$, where $t = 0$ corresponds to be the moment when the neuron fires. As the name suggests, it indicates the amount of inhibition a neuron receives before firing. Increase in excitation and reduction in inhibition both contribute to neural firing to a different degree. Studying this quantity can allow us to know how much a neuron relies on reduction in inhibition on average when giving spikes. Since inhibitory inputs are uncorrelated in this study, output firing of the pair of neurons due to reduction in inhibition is also uncorrelated. Hence it is expected that neurons that rely less on reduction in inhibition to spike exhibit higher correlation and synchrony.

$I_i(t)$ for neurons with different $\tau_i$, whose $\tau_e = 4$ ms and $\lambda_e = 3$ kHz is shown in Figure 5.12. These neurons are particularly good for illustrating the effects of $\tau_i$ since their curves of $I_i(t)$ are very different as $\tau_i$ varies. For the neurons with small $\tau_i$, the inhibitory current on average substantially decreases before they fire, suggesting that they on average can solely rely on reduction of inhibition to spike. For the neurons with large $\tau_i$, $I_i(t)$ increases for a long period instead, suggesting that for such neurons, extra excitation is necessary on average to push the membrane potential towards threshold and facilitate firing. The relative reliance on inhibition and excitation to spike explains the higher correlation and synchrony observed when $\tau_i$ is larger.
Intuitively thinking, neurons with small $\tau_i$ integrate inhibitory input quickly. In such neurons, changes in inhibitory conductance tend to be abrupt. These events of abrupt and significant reduction of inhibition cause temporary large imbalance towards excitation, allowing the neuron to quickly fire. On the other hand, the pre-synaptic current for neurons with large $\tau_i$ tends to fluctuate less abruptly with smaller peaks. While initially this may still allow the neuron to slowly edge towards the threshold, it is more likely that the inhibitory current would cease to decrease at some point even as the inhibitory conductance decreases, thanks to the voltage dependent term $[V(t) - V_i]$. Combining with the membrane leakage term $[V(t) - V_i]G_i$, the drift of membrane potential towards threshold would be stopped more easily if without extra contribution from a surge of excitatory spikes. Therefore fluctuation in inhibitory input tends to contribute less to spiking for neurons with large $\tau_i$.

Finally, please note that the form of $I_i(t)$ shown in Figure 5.12, where the slope changes sign as $\tau_i$ increases, is not general. Our argument on the relative contribution of inhibition and excitation to spiking is nevertheless general. For instance, at higher $\lambda_e$, $I_i(t)$ is increasing for all $\tau_i$ as
shown in Figure 5.13. Nevertheless, it always increases more for neurons with larger $\tau_i$, indicating that such neurons rely more on excitation than their counterparts with smaller $\tau_i$ when they spike.

![Graph showing $I_i(t)$ for neurons with different $\tau_i$.](image)

Fig. 5.13: $I_i(t)$ for neurons with different $\tau_i$. Conductance based LIF neurons with $\tau_e = 0.5\ ms, \lambda_e = 60kHz$ are considered.
5.4 Synaptic input with constant peak of conductance change

In the above sections, the integration of total conductance change due to a synaptic input spike is kept constant (See equation (2)). One of the reasons for making this choice is that it allows $G_{\text{total}}$ and hence $\tau_{\text{eff}}$ to be a function of $\lambda_e$ but independent of $\tau_e$ as shown in equation (10), so that varying $\tau_e$ will only change the time scale of synaptic filtering but not $\tau_{\text{eff}}$, allowing us to independently modulate the time scale of synaptic filtering and membrane integration.

However, the integration of conductance change may not necessarily be invariant for biological neurons. The synaptic efficacies of neurons can take a large range of values as a result of plasticity and homeostasis. Thus, it will be of interest to study the case where the peak of the conductance change due to an input spike is kept constant instead, described by equation (3).

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

The output correlation for neurons having other values of synaptic efficacies can then be approximated by interpolating the results of this section and Section 5.2.

Figure 5.1 shows the CCFs for neurons with different $\tau_e$ and $\lambda_e$. They are qualitatively similar to Figure 5.4 (the case of constant integration of conductance change) in many ways, like the sharpening of CCFs at high $\lambda_e$ and the different dependence of the tails of CCFs on $\tau_e$ as $\lambda_e$ varies. The key difference is that the CCFs grow in size as $\tau_e$ increases. This is well illustrated by considering the functions $corr$ and $sync$ as shown in Figure 5.15.
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Fig. 5.14: CCFs for conductance based LIF neurons with different $\tau_e$. Conductance change is defined by equation (3). $\tau_i = 5\, ms$. Top, $\lambda_e = 3\, kHz$. Bottom, $\lambda_e = 60\, kHz$. 

$\tau_i (ms)$
- $0.5$
- $1.5$
- $4$

CCF (1/s²)

$\delta t$ (ms)

CCF (1/s²)

$\delta t$ (ms)
Fig. 5.15: Output correlation and synchrony for conductance based LIF neurons with different $\tau_e$. Conductance change is defined by equation (3). Top, $\lambda_e = 3kHz$. Bottom, $\lambda_e = 60kHz$.

For both small and large $\lambda_e$, $sync$ almost remains unchanged while $corr$ substantially increases as $\tau_e$ increases. This is clearly different from the case where the integration of conductance
change is constant (Figure 5.5). Now increasing $\tau_e$ has the effect of inducing extra correlation instead of simply jittering the timing of spikes. This can intuitively be understood by examining the plot of the excitatory conductance change $g_e(t)$ in the right panel of Fig. 2.1. $g_e(t)$ is similar for all $\tau_e$ at small $t$, which means that the effects of excitatory input on membrane potential are almost invariant with $\tau_e$ for a short period after the arrival of an input spike. The differences in $g_e(t)$ for different $\tau_e$ become apparent as $t$ increases, where the effects of input spikes fade for neurons with small $\tau_e$ but prolonged for their counterparts with large $\tau_e$. The prolonged effects of input, absent for neurons with small $\tau_e$, induce the extra correlation for neurons with larger $\tau_e$.

This can also explain the other notable difference of Figure 5.15 from Figure 5.5, the absence of scaling of output correlation and synchrony with $\tau_i$. As $\tau_i$ increases, the effect of an inhibitory input spike is not spread thin across time but rather is prolonged, maintaining the drive required for the membrane potential to reach threshold. The plot of $I_i(t)$ in Figure 5.16 shows that neurons with both large and small $\tau_i$ rely on reduced inhibition to spike to a similar degree, characterized by the similar average level of inhibition right before a neuron fires.

![Fig.5.16: $I_i(t)$ for neurons with different $\tau_i$. Conductance based LIF neurons with $\tau_e = 0.5$ ms, $\lambda_e = 3$ kHz are considered. Conductance change is defined by equation (3).](image-url)
Finally, we note that as the synaptic efficacies increase (by switching the form of conductance change from equation (2) to equation (3)), it is the magnitude of effects of input that is altered given a fixed $\tau_e$, and the primary outcome is that magnitude of CCF but not its time scale is changed given fixed $\lambda_e$ and $\tau_e$. That said, the qualitative pictures of integration time window and burst firing in Section 5.2 are unchanged as they are ‘time scale dependent’ only, and the discussions in Section 5.2, while technically may not be totally accurate, can be applied to this section with suitable modifications on the magnitude of correlation and synchrony.

5.5 The effects of input correlation

So far the input correlation, characterized by the input correlation coefficient $c$, has been kept constant. It would be of interest to know whether the above results still hold if $c$ is altered. The quantities $n_{corr} = \frac{corr}{c_{out}}$ and $n_{sync} = \frac{sync}{c_{out}}$ are introduced to study the scaling of output correlation and synchrony with $c$.

Figure 5.17 shows how $n_{corr}$ and $n_{sync}$ depend on $c$ for neurons with different $\lambda_e$, $\tau_e$ and $\tau_i$. It is shown that all the plots have small positive slopes, indicating that output correlation and synchrony scale with $c$ slightly superlinearly. The slopes of the plots considering neurons with different parameters are mostly similar except for a few outliers, suggesting that in most cases $\lambda_e$, $\tau_e$ and $\tau_i$ only weakly affect the scaling of output correlation and synchrony with $c$. Considering that the outliers indicate an increased sharpening effect on CCFs for neurons with small $\tau_e$ as $c$ increases, which does not alter our qualitative pictures in Section 5.2, we hence conclude that the discussions and results in previous sections hold over a wide range of input correlation.

The reasons for the superlinear scaling of output correlation on input correlation are not rigorously studied in this work. A possible explanation is that the reliance of neurons on reduction of inhibitory input to spike does not scale with $c$. Moreover, higher order interactions between multiple spikes like burst firing may also have complicated scaling with input correlation.
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Fig. 5.17: The scaling of $n_{corr}$ (top) and $n_{sync}$ (bottom) with $c$ for different $\lambda_e$, $\tau_e$ and $\tau_i$. Conductance based LIF neurons are considered.
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5.6   Higher order conductance effects

The primary effect of conductance kinetics is the reduction of the average effective membrane time constant $\tau_{eff}$. This effect can still be observed after linear approximation of the conductance based LIF model which yields the ‘modified current based LIF model’ described by equation (9) (See also Chapter 2).

The modified current based LIF model reads: $\tau_{eff} \frac{d}{dt} V(t) = -V(t) + \frac{V_{e}G_{e}(t)+V_{i}G_{i}(t)+V_{r}G_{l}}{G_{total}}$

If higher order conductance effects on neural computation of correlated input are negligible, it would be highly beneficial in using the modified current based LIF model in analyzing such problems since it is more analytically tractable than conductance based LIF model. In this section, it will be shown that the effects of high order conductance kinetics are in fact not negligible.

Figure 5.18 shows the plot of the functions $corr$ and $sync$ for different $\tau_{e}$ and $\lambda_{e}$ for modified current based LIF neurons. By comparing Figure 5.18 with Figure 5.5, it can be shown that while the results are qualitatively similar, $corr$ is much higher for modified current based LIF neurons. This is well illustrated in Figure 5.19.
Fig.5.18: Output correlation and synchrony for modified current based LIF neurons with different $\tau_e$. Top, $\lambda_e = 3kHz$. Bottom, $\lambda_e = 60kHz$. 
Fig. 5.19: Difference in output correlation between conductance based LIF and modified current based LIF neurons. Positive values indicate that modified current based LIF neurons exhibit higher output correlation than their conductance based counterpart, particularly in the regime where burst firing is prevalent.

Figure 5.19 indicates that the overestimation of correlation is the most significant in the regime of large $\lambda_e$, $\tau_e$ and $\tau_i$, which is exactly where burst firing is the most prevalent. It is shown in Figure 5.20 that $p_{\text{burst}}$ is higher in modified current based LIF neurons than its conductance based counterpart with the same parameters. The increased prevalence of burst firing hence explains the higher correlation observed in modified current based LIF neurons.
The above analysis suggests that higher order conductance kinetics, namely the nonlinearity in membrane potential integration caused by fluctuating conductance and membrane potential reduces the prevalence of burst firing. An intuitive way to understand this result is that the voltage dependence terms in the conductance based model $[V(t) - V_s]$ tend to reduce excitation and enhance inhibition when the membrane is depolarized, and thus reduce the probability of firing. When adding such effects to neural dynamics, average inhibition needs to be weakened to account for the reduced probability of firing so that the output firing rate can remain constant. At the same time, however, such weakening of inhibition is not enough to overcome the reduction of burst firing which has becomes much rarer, since input now needs to be large enough to overcome the non-linear effects more than once in quick succession. Note that this description fits well with the work of Richardson and Gerstner (2005), which showed that conductance fluctuation skews the distribution of the free membrane potential such that it has a shorter tail, corresponding to lower prevalence of burst firing.

To sum up this section, higher order conductance kinetics reduces the prevalence of burst firing of neurons and hence reduces output correlation. Modified current based LIF neurons, having
ignored this effect, therefore tend to exhibit higher correlation than their conductance based counterparts.

As a final note, we transformed the conductance based model into the modified current based model by assuming the mean potential $V_{\text{mean}}$ to be $-52.5 \text{mV}$. The average membrane potential for conductance based LIF neurons with different parameters ranged from $-51 \text{mV}$ to $-55 \text{mV}$. This approximation would lead to underestimation of correlation and synchrony for neurons with very small $\tau_e$ and $\tau_i$, and overestimation in the other extreme. Simulation where $V_{\text{mean}}$ is taken to be $-54 \text{mV}$ instead is also performed and it is found that the discrepancy of results is small (around 5% for most cases and never exceeds 10%), and more importantly, it would not dispute the observed differences between the results of conductance based and modified current based model. We did not adopt more accurate approximation of the mean potential during model transformation (Richardson and Gerstner, 2005) because we need to adjust the inhibitory input rate such that the output firing rate between the two models is equivalent (See Section 3.3), rendering the parameters of the two models slightly different anyway.
Chapter 6 Discussion

In this work, we focus on studying the joint effects of synaptic properties and conductance kinetics on neural computation of correlated excitatory input. To this end, we employed different LIF models and showed how the output correlation and synchrony depend on biologically meaningful parameters, namely the excitatory and inhibitory synaptic decay time constants ($\tau_e$ and $\tau_i$) and excitatory input rate ($\lambda_e$). We provided crucial understanding on the mechanisms of how they influence neural computation of correlated inputs, namely the modulation of the time window and the magnitude of the effects of a single input spike on membrane potential as well as higher order interactions between multiple spikes, in particular burst firing, which can explain the above dependence.

We found that at low $\lambda_e$, increasing $\tau_e$ has the effect of jittering the output spike time. While at high $\lambda_e$, in addition to the above effect, increasing $\tau_e$ greatly enhances output correlation which can be largely attributed to burst firing. In particular, it is shown that neurons can respond to correlated input solely by giving extra synchronous spikes without exhibiting output correlation of longer time scale given that $\tau_e$ and $\lambda_e$ are both sufficiently small. On the other hand, we have shown that $\tau_i$ affects output correlation by changing how much do neurons rely on the uncorrelated inhibitory input to spike, originated from the asymmetry between the statistics of excitatory and inhibitory input. Next we show that the qualitative picture of the effects of $\lambda_e$, $\tau_e$ and $\tau_i$ on neural computation of correlated input is not affected by the size of input correlation and synaptic efficacies. Finally, we have shown that higher order conductance kinetics reduce output correlation by subduing burst firing.

6.1 Implication on spike initiation dynamics and coding

Neurons can be classified according to their spike initiation dynamics (König et al, 1996; Hong et al, 2012; Ratté et al, 2013). On one extreme lies the coincidence detecting neurons whose firing must be caused by synchronous presynaptic input. On the other extreme are the integrators
who integrate input for tens of milliseconds before firing. This work suggests that the spike initiation dynamics of a neuron can be satisfactorily characterized in a one-dimensional conductance based model by its excitatory decay time and the level of input activities: Neurons with small $\tau_e$ and high $\lambda_e$ are effective coincidence detectors, and both increasing $\tau_e$ and decreasing $\lambda_e$ would make them more integrator-like (See Figure 5.4 and 5.5).

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. Some earlier work (Shadlen and Newsome, 1998) argued that temporal features of spike trains cannot be coded since neurons are incapable of producing precisely timed spikes. Neurons used in such work often have large synaptic time constant and the results in this work are consistent with them in the sense that in such a regime, the correlation of output spike trains of neurons who receive partially common input is mostly of long time scale. If we consider the common input as signal, it means that the timing of the responses, the correlated output spikes, is imprecise. However, we have shown that it is possible, at high conductance state and when $\tau_e$ is sufficiently small, that the output spike trains exhibit synchronous spiking without any extra correlation of longer time scale. This suggests that information that may be contained in correlation in neural spike trains can be reliably transmitted to the next layer of neurons with suitable properties in the form of synchronous spikes. With a suitable network structure, these synchronous spikes may act as common input for a third layer of neurons. Synchrony coding is thus viable should this process be able to iterate.
6.2 Possible effects of other biophysical features on neural computation of correlated input

A major advantage of neuron modeling is that we can study biological features that are most relevant to experimental observations through means of analytical calculations and numerical simulation. As a trade-off, discrepancy in neural computation inevitably arises.

The current based LIF model is a popular choice for neuron modeling since it can both reasonably mimic the experimental results and is analytically tractable. However this work shows that it is unsatisfactory in modeling neural computation of correlation. By totally ignoring conductance effects, model neurons can no longer act as coincidence detectors and reliably produce synchronous output without extra correlation of longer time scales. The performance of the modified current based LIF model (equation (9)) somewhat improves. However, by neglecting higher-order conductance effects, correlation is still substantially overestimated, and the regime for neurons being effective coincidence detectors shrinks. This work has illustrated two important effects of the non-linearity of conductance integration which can be captured by the more realistic conductance based model: reducing burst firing and enhancing neurons’ ability in coincidence detecting.

In this work, it is shown that burst firing enhances correlation. Biologically, there are several mechanisms for neural adaptation which reduces the prevalence of burst firing. For example, slow potassium hyperpolarizing currents which activate when the membrane potential is depolarized may regulate repetitive firing (Storm, 1990; Goldberg et al, 2008). Increase of membrane threshold due to preceding spiking activities (Henze and Buzsáki, 2001; Badel et al, 2008) and short-term depression due to depletion of neurotransmitters (Rosenbaum et al, 2013) have similar effects. If these biological features are taken into account by models of higher dimensions like the Morris-Lecar model (Prescott et al, 2008) or models with variable spiking threshold (Platkiewicz and Brette, 2010), it can be expected that output correlation would be smaller than the results obtained in this work.
6.3 Correlation between inhibitory input and between excitatory and inhibitory input

In this work, only correlation between excitatory inputs is considered. From the symmetry of the model, it can be expected that correlation between inhibitory inputs would have similar effects. Increasing $\tau_i$ would lead to increased output correlation of longer time scale but decreased synchrony, while increasing $\tau_e$ would increase both output correlation and synchrony if partially common inhibitory input is used instead.

Another interesting case is to consider correlation between excitatory and inhibitory inputs. Biologically, it can be implemented by network circuitries with feed-forward or recurrent inhibition. Take feed-forward inhibition (Okun and Lampl, 2008) as an example. In such networks, input from a layer of neurons simultaneously excites the neurons in the next layer as well as inhibitory interneurons which are also connected to the neurons in the next layer. When an output neuron receives an excitatory spike from an input neuron, the probability that it would receive an inhibitory input a few milliseconds later increases since the interneurons are also excited by the very same input spike. In the context of this work, this can be mimicked by letting the two post-synaptic neurons each receive a common excitatory spike train and an inhibitory one, in which the spikes are partially copied from its excitatory counterpart with a time delay. From the results of several studies (Pouille and Scanziani, 2001; Kremkow et al, 2010; Middleton et al, 2012), we predict that correlation of long time scale would be much reduced compared to the case where only excitatory input is correlated, as output spikes induced by the common input might be ‘silenced’ by the oncoming inhibition unless they occur within a small time window right after the onset of the above-mentioned input (Pouille and Scanziani, 2001). Decorrelation may also result from recurrent inhibition. Studies showed that network circuitries with inhibitory feedback exhibit reduced correlation (Tezlaff et al, 2012) and favor correlated activities of short time scale (Giridhar et al, 2011). Because of these previous works, we believe that more realistic neuron network set-up with feed-forward or recurrent inhibition would soften the constraints of neural properties that allow precisely timed spikes to be given.
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