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Correlated input spike trains and their effects on the response of the leaky integrate-and-fire neuron

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Abstract

Correlation of neuronal activities is widely observed in the central nervous system and is likely to play a key role in its functioning. It is, thus, essential to understand the effects of correlated synaptic input on the response of neurons. Here, we model neuronal input as correlated Poisson processes, and assess their impact on the leaky integrate-and-fire neuron. We found that neuronal output firing rate typically is a non-monotonic function of the input correlation, and propose that the response of neurons is critically dependent on the input ensemble statistics. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Correlation; Integrate-and-fire; Input statistics; Neural coding

1. Introduction

Correlation of neuronal activities is ubiquitous in the central nervous system and is likely to play a central role in its functioning [4]. Also, it is known that correlated synaptic inputs can have a tremendous effect on the output firing rate and variability of model neurons [1,2,6,9,11]. Thus, an insight into the impact of input spike train statistics on the output firing rate is essential to understand potential neural codes. Here, we propose a simple model of correlated spike trains, and use it to assess the effect of correlation on the response rate of the leaky integrate-and-fire (I&F) neuron.

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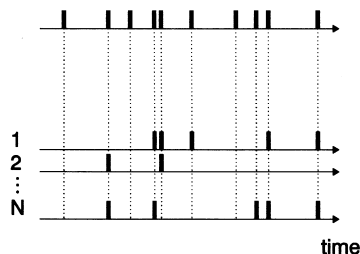


Fig. 1. A model of correlated spike trains: a realization of a Poisson point process (top) is thinned to give rise to N correlated processes (bottom).

2. A model of correlated spike trains

We modeled correlated spike trains as Poisson point processes, with homogeneous pairwise (zero-delay) correlations. A set of correlated spike trains was produced as follows: a realization of a Poisson process of rate α was used as “generating process” (Fig. 1, top). The correlated spike trains were obtained by thinning [3] the generating process, i.e. by deleting spikes with a fixed probability (Fig. 1, bottom). It can be shown that the diluted processes are again Poisson. If the probability of deletion is $1 - \beta$, each process generated in this manner has a rate $r = \alpha\beta$, and each pair of processes has a correlation coefficient β .

3. Neuron model and background activity

In this study, we used the leaky I&F model (see [11]) to assess the impact of correlated input on neuronal output. The neuronal parameter values were set to: $C = 500$ pF, $1/g_{\text{leak}} = 40$ M Ω , $U_{\text{rest}} = -70$ mV (see [8]). The time constant $\tau = RC$ of the membrane was thus 20 ms. The fast conductances responsible for the action potential generation were not modeled explicitly. Instead, when the membrane potential reached a threshold ($U_{\text{thresh}} = -50$ mV), it was temporarily clamped ($t_{\text{refr}} = 1.75$ ms) to a reset value ($U_{\text{reset}} = -60$ mV) to model the refractory period. Synaptic inputs were modeled as conductance changes [7,12]. For excitatory (resp. inhibitory) synapses, the reversal potential was set to 0 mV (resp. -70 mV). The synaptic conductances were parametrized by an alpha function [7,10] with a time constant of 1 ms for both excitatory and inhibitory synapses. The peak conductance for excitatory (inhibitory) synapses was set to 1 nS (3.4 nS). EPSPs and IPSPs had equal amplitude (0.30 mV) at a membrane potential of -54 mV.

Membrane potential fluctuations as observed in vivo [5] were reproduced by using a synaptic background of independent excitatory and inhibitory spike trains. It consisted of 9000 (5500) independent excitatory (inhibitory) neurons, both modeled as Poisson processes with a rate of 1 spike/s. This resulted in a mean membrane potential of -54.3 mV (standard deviation 1.4 mV) and a spontaneous firing rate of 1.2 spike/s. An average of 26 synchronous EPSPs was needed for the membrane potential to reach spike threshold.

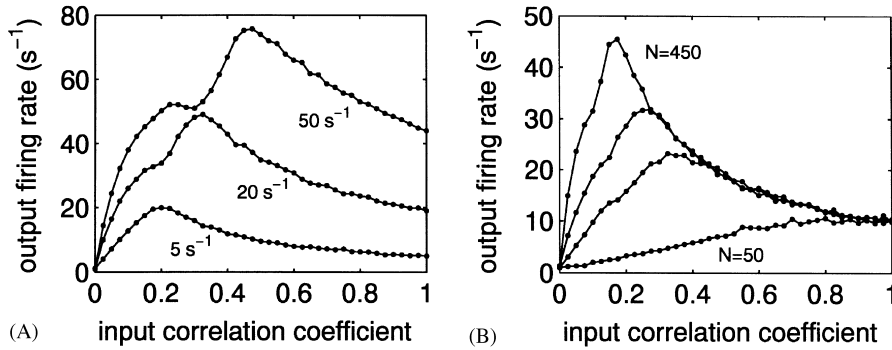


Fig. 2. Output firing rate is a non-monotonic function of input correlation. (A) Response rate of the model neuron as a function of the input correlation for different input rates ($r = 5, 20, 50$ spike/s). The size of the populations $N = 250$. (B) Same as in (A) but for different input sizes ($N = 50, 150, 250, 450$), with $r = 10$ spike/s.

In addition to this background activity, we stimulated the neuron with a pool of N excitatory and N inhibitory spike trains. Excitatory and inhibitory spike trains had identical firing rates r . We varied the correlation among the excitatory input population, while keeping the inhibitory inputs independent.

4. Output firing rate as a function of input correlation

A striking feature of the relation between input correlation and the neuron output rate is its non-monotonicity (Fig. 2). The initial increase in correlation leads to a rapid increase in output firing rate. However, beyond a critical correlation value (depending on the input rate and the input population size) additional input synchrony is detrimental to the output rate.

This behavior could be a result of the specific input statistics, or of particular features of the neuron model (e.g. the membrane potential threshold and reset mechanism), or both. In order to disambiguate these different possibilities, we suppressed the spiking and reset of the neuron model, and considered the process formed by the “free” membrane potential (i.e. without spiking).

5. Amplitude distribution of the membrane potential

We simulated the membrane potential U of a leaky integrator, i.e. a leaky I&F model without thresholding the membrane potential. Fig. 3 shows membrane potential traces and the corresponding amplitude distributions for independent input (Fig. 3A) and two levels of correlated inputs ($\beta = 0.3$, Fig. 3B, and $\beta = 0.8$, Fig. 3C). For increasing correlation, the membrane potential showed larger fluctuations, due to the

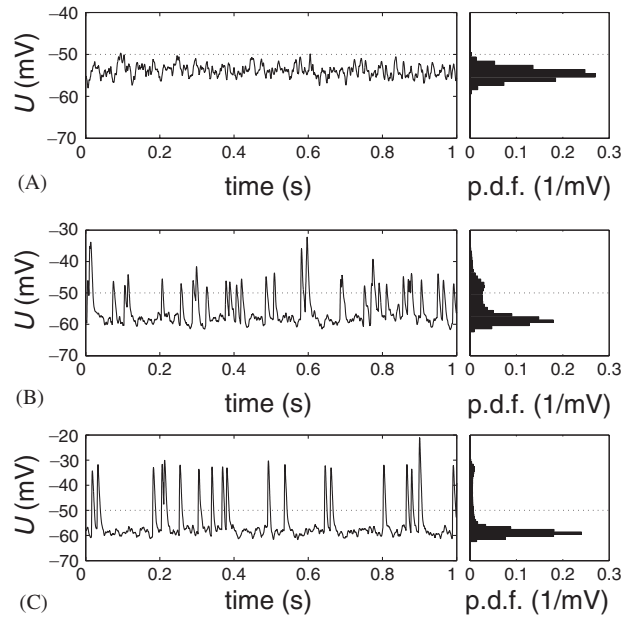


Fig. 3. The distribution of the free membrane potential with correlated synaptic input is asymmetric. (A) 1 s run of the membrane potential (left). The input consists of 300 independent excitatory and 300 independent inhibitory spike trains at 15 spike/s, in addition to the background input. The probability density function of the amplitude distribution is plotted on the right. (B) same as in (A) with an input correlation coefficient of 0.3. (C) same as in (A) with an input correlation coefficient of 0.8. In all panels, the dotted lines indicate the threshold level of the I&F neuron.

simultaneous occurrence of presynaptic spikes. Correspondingly, the variance of the amplitude distribution increased and the distribution became asymmetric.

Obviously, the cumulative probability P_U of the membrane potential being above threshold is related to the firing rate of the neuron model. Thus, we investigated the dependence of P_U on the input correlation. The input parameters were kept as in the simulations of the spiking neuron. We found that, similar to the output firing rate, P_U is a non-monotonic function of the input correlation (Fig. 4). Note the (qualitative) similarity of the firing rate response (Fig. 2) and the P_U response (Fig. 4).

Thus, the non-monotonicity observed in the spiking response is primarily due to the input statistics. The average number of simultaneous presynaptic spikes (given by βN) increases with correlation. Concurrently, the rate of occurrence of these clusters (given by $\alpha = r/\beta$) decreases, resulting in a decreasing output rate. For an input correlation of 1, the neuron model responds with a spike to almost every input cluster and, thus, has an output rate approximately equal to the individual input rate r (cf. Fig. 2). Observe that, for large input rates, the output firing rate can have more than one maximum, again reflecting the statistical properties of the input (Kuhn et al., in preparation).

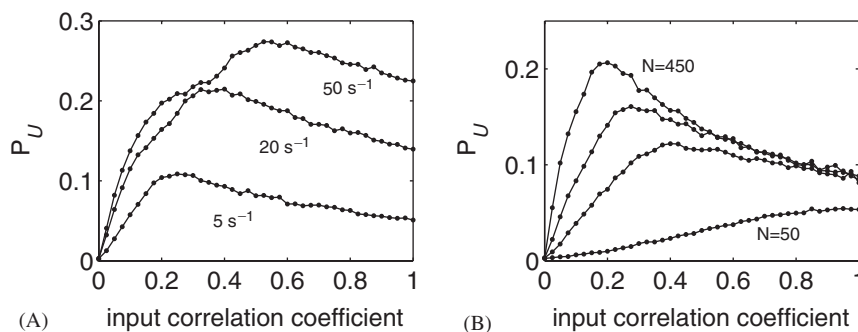


Fig. 4. The cumulative probability of the membrane potential above threshold decreases for larger input correlation. (A) Impact of input correlation on P_U for different input rates and (B) different sizes of the input ensemble. The parameters are the same as in Fig. 2.

6. Discussion

We have shown that for our model of correlated excitatory inputs:

- (1) the output firing rate of the leaky I&F neuron increases for low input spike train correlation, and decreases for larger input correlation, and
- (2) this non-monotonic dependence on the correlation is predominantly governed by the input statistics, and not by the threshold and reset mechanism of the leaky I&F.

A detrimental effect of synchrony, though under somewhat different input conditions, had already been demonstrated by Murthy and Fetz [9]. Note that we modeled zero-delay correlation only. A jitter in synchronization could modulate the effects of input correlation [1].

In conclusion, we propose that the response of the leaky I&F critically depends on the input firing statistics. As a corollary, drawing conclusions about the potential effect of input correlation in the working brain necessitates a better knowledge of the statistical structure of spiking activity in large neuronal ensembles.

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