



Effects of correlated and synchronized stochastic inputs to leaky integrator neuronal model

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Abstract

We present an analysis of neuronal model behaviour with correlated synaptic inputs including the cases that correlated inputs are equivalent to exactly synchronized inputs and correlated inputs are *not* equivalent to exactly synchronized inputs.

For the former case,

- it is found that the fully (synaptically) correlated inputs assumption (see Section 1 for definition), which is used in most, if not all, theoretical and experimental work in the past few years, results in a waste of resources and might be an unrealistic assumption;
- with an exactly balanced excitatory and inhibitory, and synaptically correlated input, the integrate-and-fire model simply behaves as a synchrony detector in *certain* parameter regions;
- the well-known diffusion model, upon which most theoretical work is based, fails to approximate the model with synaptically correlated Poisson inputs. A novel way to approximate synaptically correlated Poisson inputs is then presented;
- an optimization principle on neuronal models with partially (synaptically) correlated inputs is proposed, which enables us to predict microscopic structures in neuronal systems.

For the latter case,

- with tightly synchronized inputs (see Section 1 for definition), the model behaviour depends on its integration time of input signals and could exhibit bursting discharge.
- for loosely synchronized inputs, we found that correlated inputs are equivalent to the post-spike voltage reset mechanism proposed in the literature.

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1. Introduction

In the past few years, we have seen a large body of literature devoted to studying single neuron models with stochastic inputs (see for example [Brown et al., 1999](#); [Destexhe and Pare, 1999](#); [Feng, 1997](#); [Feng and Brown, 1998a](#); [Harris and Wolpert, 1998](#); [Konig et al., 1996](#); [Mainen and Sejnowski, 1995](#); [Softky and Koch, 1993](#);

[Shadlen and Newsome, 1994, 1998](#); [Salinas and Sejnowski, 2000](#); [Stevens and Zador, 1998](#)), aiming to gain further insights into the coding problem. One popular assumption when studying neurons with stochastic inputs is that they receive synaptically correlated inputs, in contrast to conventional independent inputs ([Tuckwell, 1988](#)). Within the synaptically correlated input framework, many interesting results have been obtained: we ([Feng and Brown, 2000](#)), among others ([Destexhe and Pare, 1999](#); [Salinas and Sejnowski, 2000](#); [Stevens and Zador, 1998](#); [Shadlen and Newsome, 1998](#)), have shown that a small correlation between synaptical inputs could very efficiently drive a cell to fire irregularly. Despite the above-mentioned fact which

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indicates that it is clear now which cellular mechanism could result in an irregular firing, it is still intriguing to understand the functional role of exactly balanced inputs to a neuron.

The first question we wish to answer is what is the essential difference between neuronal responses with exactly balanced inputs compared with that of purely excitatory inputs. With a small correlation and in certain parameter regions, a neuron with integrate and fire mechanisms and with an exactly balanced input is simply a detector of input synchrony: it fires whenever a synchronous signal is presented and is completely silent otherwise. Shadlen and Movshon (1999) have recently argued that ‘Another flaw in the temporal binding hypothesis concerns the question of which neurons would read the binding signal, and how’. Our results indicate that by controlling its inhibitory input strength, a neuron could behave as a synchrony detector.

A second question is how to approximate a discrete process (a stochastic process with discontinuous trajectory), such as the integrate-and-fire model with a Poisson process input, with a continuous process. A discrete process is usually very difficult to deal with theoretically. Hence most, if not all, theoretical work is based upon using the Brownian motion (diffusion model) to approximate the Poisson process (random walk model). It is generally believed that this is a reasonable approximation, a basic assumption we employed before (Feng and Brown, 2000) as well. The advantage of the continuous process over the original, discrete one is obvious (Feng and Haderler, 1996): we could use the powerful theory of stochastic analysis to handle the model. Nevertheless, we find that with synaptically correlated inputs there are essential discrepancies between neuron models with discrete inputs and continuous inputs, which implies that conclusions developed in terms of continuous versions might be very misleading. A novel way to approximate synaptically correlated inputs is then proposed.

We then go a step further and analyse whether fully correlated inputs (Fig. 1) to a neuron is optimized or not. Here fully correlated inputs are in the sense that all active synapses are mutually correlated and optimization is maximizing efferent firing rates. We argue that fully correlated inputs (Fig. 1) to a neuron result in a waste of resources. An optimization principle—to maximize neuronal outputs with partially correlated inputs (see Fig. 1)—is then proposed. The principle enables us to investigate structures of neuronal systems: how many pre-synaptic neurons are synaptically correlated and projected to a post-synaptic neuron. We find that when every $V_{thre}/a + n$ neurons (see Section 3.2.1 for an exact definition of the number n) are fully correlated and send their outputs to a post-synaptic neuron, the post-synaptic neuron maximizes its firing rate, where V_{thre} is the threshold and a is the magnitude

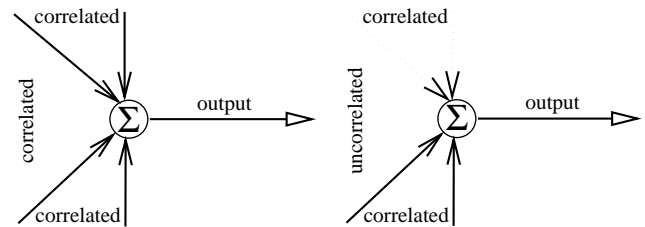


Fig. 1. Schematic representations of fully correlated inputs (left): all inputs are mutually correlated (indicated by the same line type); and partially correlated inputs (right): inputs are not all mutually correlated. Only inputs within the same group (indicated by the same line type) are mutually correlated. See also Fig. 2.

of EPSP (excitatory post-synaptic potential). Interestingly, under these circumstances, the coefficient of variation of efferent (CV) spike trains also attains a maximum. The conclusion is independent of input firing rates and correlation coefficients.

All results above are obtained under the assumption that correlation is equivalent to exact synchronization. Certainly correlation and synchronization are in general different, as pointed out in the literature (Brody, 1999). Loosely and tightly synchronized inputs are then taken into account (Fig. 2, also see Section 2.3 for exact definition). Basically, the neuronal integration time of input signals now plays an important role. With tightly synchronized inputs, the integrate-and-fire model exhibits bursting behaviour. With loosely synchronized inputs, the model behaviour is more or less similar to that with post-spike voltage reset mechanisms proposed in Troyer and Miller (1997). To drive a cell to fire irregularly, the post-spike voltage reset mechanism and synaptically correlated inputs are two predominant assumptions proposed in the literature. We demonstrate that the two assumptions are closely related.

Here we only consider positively correlated inputs. For results on how a neuron might employ negative correlations between its input spike trains to exhibit the stochastic resonance phenomenon, we refer the reader to Feng and Tirozzi (2000). In Fig. 2 we summarize all cases of inputs considered in the present paper. A good review on correlated neuron activity is presented in Salinas and Sejnowski (2001).

2. Methods

2.1. Models

For two given quantities $V_{thre} > V_{rest}$ and when $v_t < V_{thre}$, the membrane potential v_t satisfies the following dynamics:

$$\begin{cases} dv_t = -\frac{v_t}{\gamma} dt + dI_{syn}(t), \\ v_0 = V_{rest}, \end{cases} \quad (2.1)$$

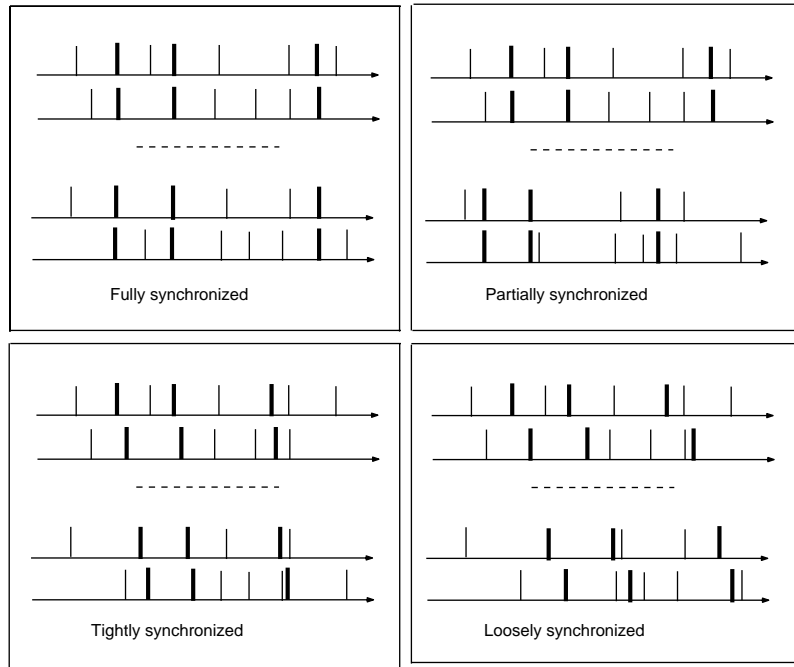


Fig. 2. Schematic representations of all cases of inputs considered in the present paper. Thick, vertical lines are correlated inputs. Thin, vertical lines are uncorrelated inputs. Upper panel: correlated input is equivalent to synchronized input, fully correlated input (left), partially correlated input (right); bottom panel: correlated input is not equivalent to synchronized input, tightly synchronized input (left) and loosely synchronized input (right).

where $\gamma > 0$, $I_{syn}(t)$ is the synaptic input given by

$$dI_{syn}(t) = a dE(t) - b dI(t) \quad (2.2)$$

with $a > 0$, $b > 0$ as the magnitude of single EPSP or IPSP, respectively, E, I are superposition of Poisson processes. A discussion on why we choose the Poisson process as an input to the model is outside the scope of the present paper and we simply refer the reader to theoretical papers, for example Abbott et al. (1997), and experimental data, for example Softky and Koch (1993), for more details. Basically an incoming EPSP will push the membrane potential to increase with an increment of a ; but an incoming IPSP at time t will reduce the membrane potential from v_t to $v_t - b$. The membrane potential decays with a time-scale of γ . For simplicity of notation we assume that $a = b$ from now on. Once v_t is greater than V_{thre} a spike is generated, and v_t is reset to V_{rest} . We also assume a lower bound V_{low} for v_t , i.e. $v_t = \max(v_t, V_{low})$.

2.2. Correlation = exact synchronization

Suppose a neuron receives excitatory inputs (Poisson processes) from p active dendrites with correlation coefficient c (Matthews, 1996; Zohary et al., 1994), i.e. all p active dendrites are mutually correlated (fully correlated, see Fig. 1 and Section 3.2), and $N_{E,i}$, a Poisson process, is the input EPSPs travelling along the i -th dendrite, $i = 1, \dots, p$. The total excitatory input

is then

$$E = \sum_{i=1}^p N_{E,i}. \quad (2.3)$$

According to results in Feng and Brown (1998b) Eq. (5.1) (see also Salinas and Sejnowski, 2000), we further have

$$E = \sum_{i=1}^p N_i^E + pN^E, \quad (2.4)$$

where N_i^E , $i = 1, \dots, p$ are identical and independent Poisson processes with a rate $(1 - c)\lambda_E$, and N^E is again an independent Poisson process with a rate $c\lambda_E$. The proof of Eq. (2.4) is quite straightforward. Denote $N_{E,i} = N_i^E + N^E$, we see that it is reasonable since the summation of two Poisson processes with a rate m_1 and m_2 , respectively, will be a Poisson process with a rate $m_1 + m_2$. Therefore, each $N_{E,i}$ is a Poisson process and the correlation coefficient between $N_{E,i}$ and $N_{E,j}$ is c provided that $i \neq j$. The total excitatory input is a composition of two point processes.

For p correlated inputs with a rate λ_E and correlation coefficient c , they are equivalent to a summation of

- p independent (asynchronous) inputs with a rate $(1 - c)\lambda_E$, reduced rate from λ_E to $(1 - c)\lambda_E$, and
- a common (synchronous) input with a rate $c\lambda_E$, enlarged amplitude from 1 to p .

Because of the factor p in front of the common input term N^E , it implies that the neuron sometimes receives pulsed inputs with a magnitude of ap , which is in general very large, compared to neuron's threshold. For example, suppose that around 40 EPSPs are needed for a neuron to cross the threshold (Shadlen and Newsome, 1994), starting from the resting potential, then the neuron will fire whenever it receives a common input, provided that $p > 40$.

The same formulation holds true for inhibitory inputs with a ratio $r, 0 \leq r \leq 1$, i.e. IPSPs travel with a rate $r\lambda_E$. In particular, when $r = 0$ the neuron receives exclusively excitatory inputs; when $r = 1$ the inhibitory and excitatory input is exactly balanced.

The input is decomposed into two parts: asynchronous input $\sum_{i=1}^p N_i^E$ and synchronous input N^E . Denote t_i^s as the time (inter EPSP intervals) of synchronous input, i.e.

$$N^E(t) = \sum_k I_{\{\sum_{j=1}^k t_j^s < t\}}, \quad (2.5)$$

where I_A is the indicator function of a set A . Let

$$\mathcal{T} = \{t_i, i = 1, \dots\} \quad (2.6)$$

be the set of efferent interspike intervals

$$\begin{cases} \mathcal{T}^s = \{t_i^s, i = 1, \dots, & \text{if } \sum_{k=1}^i t_k^s \in \{\sum_{k=1}^j t_k\} \\ t_k, j = 1, \dots\}, \\ \mathcal{T}^a = \{t_i, i = 1, \dots, & \text{if } \sum_{k=1}^i t_k \notin \{\sum_{k=1}^j t_k\} \\ t_k^s, j = 1, \dots\} = \mathcal{T} - \mathcal{T}^s. \end{cases} \quad (2.7)$$

Roughly speaking \mathcal{T}^s is the set of spike intervals resulting from synchronous inputs and \mathcal{T}^a is due to asynchronous inputs. An explanation of Eq. (2.7) is presented in Fig. 3.

Finally we emphasize that Eq. (2.4) is obtained under the assumption that correlation is equivalent to exact synchronization.

2.3. Correlation \neq exact synchronization

Essentially Eq. (2.4) relies on the assumption that correlations are equivalent to synchronization, a prevailing assumption used in neuroscience. Certainly correlation and synchronization are in general different, as it has been pointed out in the literature (Brody, 1999) (see below). As a generalization of results in the previous subsection, we also consider the following form of correlated inputs:

$$E = \sum_{i=1}^p N_i^E + \sum_{i=1}^p N_{i,\varepsilon}^E, \quad (2.8)$$

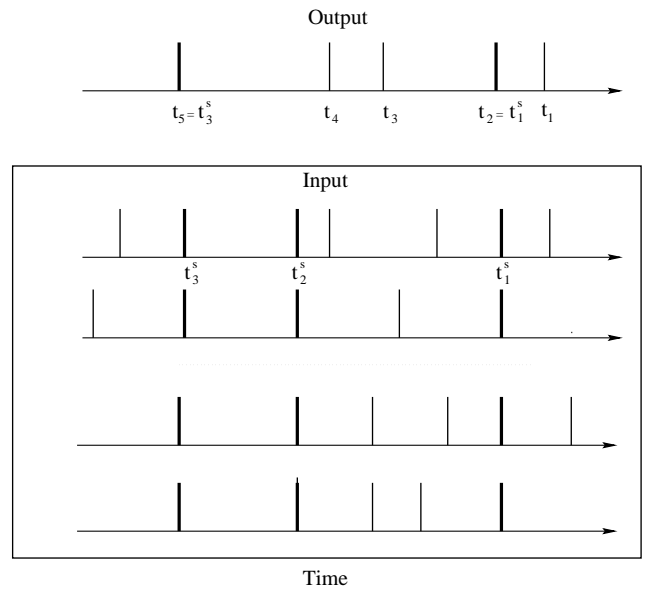


Fig. 3. Schematic representations of \mathcal{T} , \mathcal{T}^s and \mathcal{T}^a . $\mathcal{T} = \{t_1, t_2, t_3, t_4, t_5\}$, $\mathcal{T}^s = \{t_1^s = t_2, t_3^s = t_5\}$, we then have $\mathcal{T}^a = \{t_1, t_3, t_4\}$.

where

$$\begin{aligned} N_{1,\varepsilon}^E &= \sum_{j=1}^{\infty} I_{\{t > \sum_{k=1}^j t_k^s\}} \\ N_{i,\varepsilon}^E &= \sum_{j=1}^{\infty} I_{\{t > \sum_{k=1}^j t_k^s + (i-1)\varepsilon\}}. \end{aligned} \quad (2.9)$$

It is easily seen that $N_{i,\varepsilon}^E$ and $N_{j,\varepsilon}^E$, $i \neq j$, $\varepsilon > 0$ are correlated but not synchronized. The meaning of Eq. (2.9) is clear. If the neuron receives a pulse input from the first synapse, say at time $\sum_{k=1}^j t_k^s$, then at time

$$\sum_{k=1}^j t_k^s + \varepsilon, \dots, \sum_{k=1}^j t_k^s + (p-1)\varepsilon,$$

there is an EPSP arrives along a synapse. When $\varepsilon = 0$, Eq. (2.8) is exactly Eq. (2.4). Essentially, we consider two cases of ε : ε is small enough, corresponding to the exact synchronization case discussed in the previous subsection (see Fig. 2, bottom panel, left); otherwise the neuron receives pulsed inputs with time difference ε (see Fig. 2 bottom panel, right). Assume that the bottom spike trains (thick vertical lines) in Fig. 2 bottom panel (right) are $t_k^s, k = 1, 2, 3$. We then see that there is a delay in time for the second spike trains (thick vertical lines in the second spike trains, from bottom to up), namely the input spikes are $t_k^s + \varepsilon, k = 1, 2, 3$.

2.4. Summary of notation

For clarity, we provide a list of notation and explanations used in the current paper (see Table 1).

Table 1
A summary of main notation, definition, first appearance and relationships between notation

Notation	Definition	First appearance	Relationship with other notation
E	Total excitatory inputs	Eq. (2.2)	Eq. (2.3)
$N_{E,i}$	EPSPs along the i -th synapse	Eq. (2.3)	Eq. (2.3)
N_i^E	Independent EPSPs along the i -th synapse	Eq. (2.4)	Eq. (2.4)
N^E	Common EPSP input for all synapses	Eq. (2.4)	Eq. (2.4)
t_i^s	i -th synchronous input	Eq. (2.5)	Eqs. (2.5) and (2.7)
\mathcal{T}^s	Efferent spike trains generated by synchronous inputs	Eq. (2.7)	Eq. (2.7)
\mathcal{T}^a	Efferent spike trains generated by asynchronous inputs	Eq. (2.7)	Eq. (2.7)
\mathcal{T}	Efferent spike trains	Eq. (2.7)	Eq. (2.7)
t_k	k -th efferent spike	Eq. (2.6)	Eqs. (2.6) and (2.7)
$N_{i\epsilon}^E$	i -th afferent spike trains with a delay ϵ	Eq. (2.9)	Eq. (2.9)
$N_{i\epsilon}^E$	Synchronous afferent spike trains in a block	Eq. (3.6)	Eq. (3.6)

3. Results

3.1. Fully correlated inputs: correlation = exact synchronization

3.1.1. Synchrony detector

We first fix a few parameters of the model $\gamma = 20$ ms, $V_{thre} = 20$ mV, $V_{rest} = 0$ mV, $V_{low} = -10$ mV, $\lambda_E = 100$ Hz, $c \in [0, 1]$, $r \in [0, 1]$. See for example Brown et al. (1999) and references therein for the choice of these parameters. The model is solved using an Euler scheme (Albeverio et al., 1995) of step size (integration time of input signals) $h = 0.001$ and 20 000 interspike intervals are generated for calculating mean interspike intervals (ISIs) and CV.

When a neuron receives an exactly balanced, independent ($c = 0$, $r = 1$) input, from Fig. 4 we see that it fires extremely slowly. From the results of the previous subsection, we know that when a neuron receives fully correlated inputs, it will fire with a rate greater than $c\lambda_E$ provided that

$$ap > (V_{thre} - V_{low}). \tag{3.1}$$

Eq. (3.1) is true in our set-up of the model if $a > 0.3$. In other words when $a > 0.3$ we have

$$\mathcal{T}^s = \{t_i^s, i = 1, \dots, \} \tag{3.2}$$

(compare with Eq. (2.7)). Because the firing resulting from independent inputs is so slow, we could expect that the neuron with synaptically correlated inputs fires if and only if it receives synchronous inputs. In other words, it acts as a synchrony detector: firing if and only if a synchronous input is present. Fig. 4 with $a = 0.5$ confirms the claim. When $c = 0.1$, the synchronous input is 10 Hz, the model fires with a mean interspike interval of 96 ms; when $c = 0.5$, the synchronous input is 50 Hz, the cell fires with a rate of 50 Hz.

In terms of the notation of the previous subsection we see that when $r = 1$ and $a = 0.5$ we have

$$\mathcal{T} \sim \mathcal{T}^s = \{t_i^s, i = 1, \dots, \}.$$

We go a step further to consider the extreme case of $a = 2.0$ mV (Fig. 5). Now the situation is different. Without synchronous inputs, the cell fires relatively fast. For example, when $r = 1$, and $c = 0$, the cell fires with a mean INIs between 10 and 15 ms. Adding a synchronous signal with small rate, $c\lambda_E$ (c is usually small), only slightly modifies the firing property, i.e. mean and CV.

Hence for exactly balanced synaptic inputs, when the magnitude of EPSPs is in certain regions ($0.3 \text{ mV} \leq a \leq 0.5 \text{ mV}$), the cell acts as a synchrony detector (see Section 3.2.1 for more results with different p -values).

3.1.2. Break down of the usual approximation

The diffusion approximation to synaptically correlated inputs can be written as (Feng and Brown, 2000; Salinas and Sejnowski, 2000)

$$du_t = -\frac{1}{\gamma} u_t dt + (ap\lambda_E - bpr\lambda_E) dt + \sqrt{a^2 p\lambda_E(1 + (p-1)c) + b^2 pr\lambda_E(1 + (p-1)c)} dB(t), \tag{3.3}$$

where $B(t)$ is the standard Brownian motion. When $c = 0$ Eq. (3.3) gives rise to the exact result as in the literature (Tuckwell, 1988) for independent inputs.

Fig. 6 shows that when there is no correlation in inputs, diffusion inputs and Poisson inputs agree well with each other (Musila and Lánský, 1994; Ricciardi and Sato, 1990; Tuckwell, 1988). But with synaptically correlated inputs, the situations are totally changed. Even when $c = 0.1$, a small correlation, we see that the discrepancy between Poisson and diffusion inputs is obvious: a much higher CV and output firing frequency are obtained from the model with diffusion inputs.

In theory we know that the diffusion approximation is true only when the rate of the Poisson process is high and its magnitude is small. Nevertheless, a limit theory does not tell you that exactly when it holds true and when it fails. The input has two parts: asynchronous input with a small magnitude and a fast rate (when c is

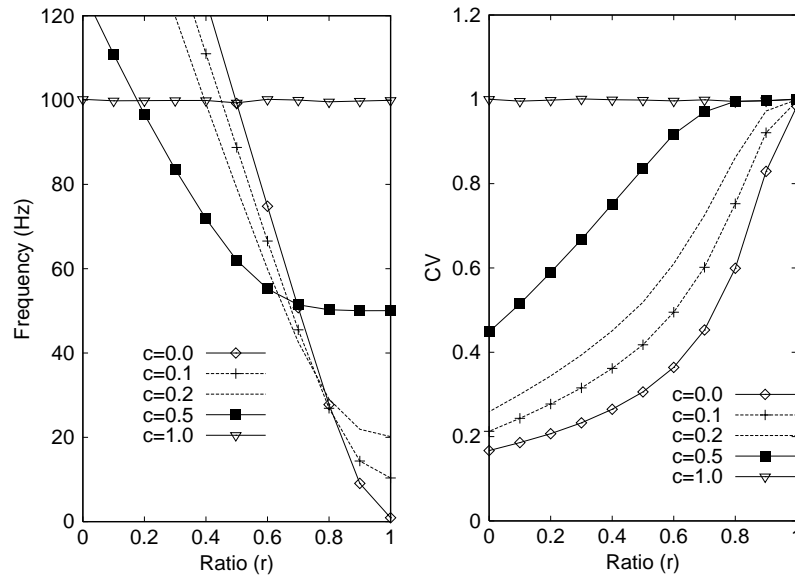


Fig. 4. Mean ISIs and CV of the integrate-and-fire model with $a = 0.5$ mV, $p = 100$ and $c = 0.0, 0.1, 0.2, 0.5, 1$. Note that when $r = 1$, the neuron fires if and only if there is a synchronous input.

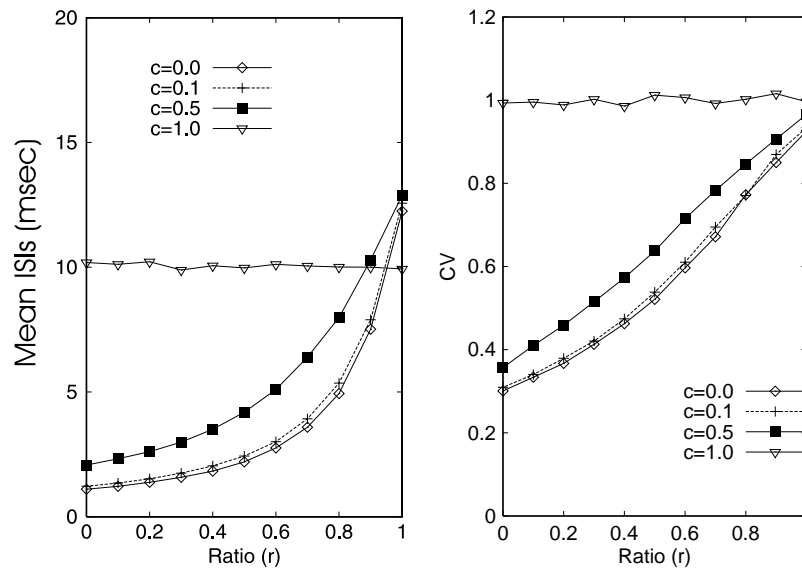


Fig. 5. Mean ISIs and CV of the integrate-and-fire model with $a = 2$ mV, $p = 100$.

small); synchronous input with a (relative) large magnitude and slow rate (see the previous subsection). It is the synchronous input term which violates the condition of the validity of the diffusion approximation.

Many, if not all, theoretical developments are confined to the case of the model with diffusion inputs. It is thus of vital importance to develop a theoretically tractable way to approximate the model with Poisson inputs. We introduce the following approximation:

$$\sum_{j=1}^p dN_j^E - \sum_{j=1}^p dN_j^I = \mu dt + \sigma dB_t, \quad (3.4)$$

where $\mu = a(1 - c)p\lambda_E(1 - r)$, $\sigma^2 = a^2(1 - c)p\lambda_E(1 + r)$.

$$dV_t = -\frac{V_t}{\gamma} dt + \mu dt + \sigma dB_t + ap dN^E - ap dN^I. \quad (3.5)$$

Eq. (3.5) is a Markov process with diffusion and jump components (see for example, Eq. (9.124) in Tuckwell, 1988). In Fig. 7, we see that the approximation defined by Eq. (3.5) is excellent. Surely the idea behind Eq. (3.5) is simple. The synchronous inputs part breaks down the diffusion approximation and we have to retain its original form of jump processes, but for the asynchronous inputs part, we could safely approximate it by a diffusion process.

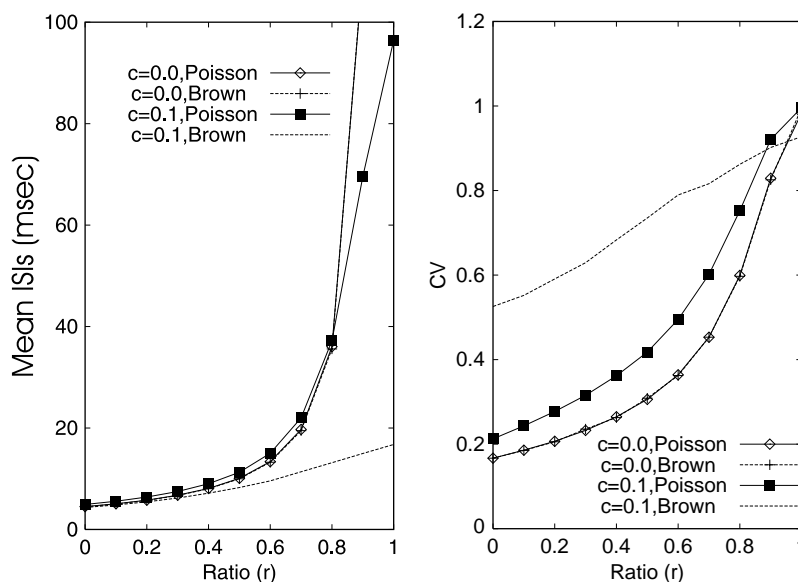


Fig. 6. Mean ISIs and CV of the integrate-and-fire model with $a = 0.5$ mV, $p = 100$. Breaking down of the diffusion model even when $c = 0.1$. When $c = 0$ a quite good approximation is obtained between diffusion inputs (Brown) and Poisson inputs.

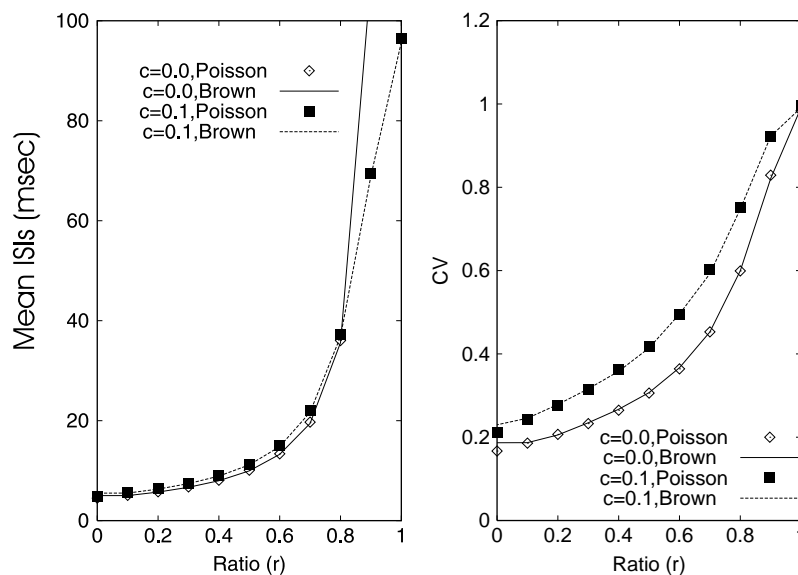


Fig. 7. Mean ISIs and CV of the integrate-and-fire model with $a = 0.5$ mV, $p = 100$. A comparison between the model with Poisson inputs and with inputs as defined in Eq. (3.5).

3.2. Partially correlated inputs: correlation = exact synchronization

As we have pointed out before, fully correlated input assumption is not realistic in the sense that a neuron sometimes receives a huge EPSP which results in a big jump in its membrane potential (see the previous subsection). We therefore consider the following partially correlated input model (see Fig. 1 for more explanations).

$$E = \sum_{i=1}^p N_i^E + k \sum_{i=1}^{p/k} N_{,i}^E. \quad (3.6)$$

For $i = 1, \dots, p/k, ik + 1, \dots, (i + 1)k$ neurons are in the i -th block (see Fig. 1). The meaning of Eq. (3.6) is clear: within each block, all synaptic inputs are correlated and are independent in different blocks. The first term in Eq. (3.6), $\sum_{i=1}^p N_i^E$, gives rise to a Poisson process with rate $(1 - c)p\lambda_E$ and magnitude a , the second term with a rate $c\lambda_{EP}/k$ and magnitude ak .

It is interesting to have a comparison between Eqs. (2.4) and (3.6). The first term, asynchronous term, is identical for two equation. The difference is in the second term. For Eq. (2.4) there is only single Poisson process N^E in the second term, but in Eq. (3.6) there are p/k Poisson processes.

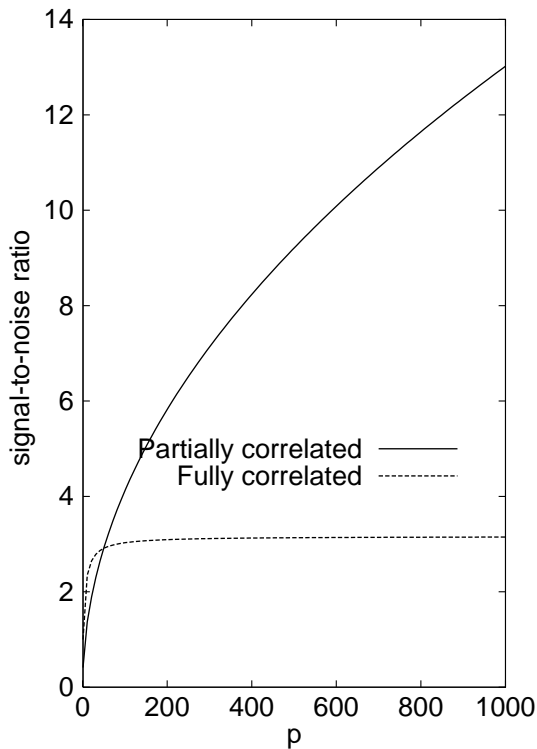


Fig. 8. Signal-to-noise ratio vs. p for partially correlated input = $p/\sqrt{p(1+(k-1)c)}$ with $k=50$ and fully correlated input = $p/\sqrt{p(1+(p-1)c)}$ where $c=0.1$.

In Zohary et al. (1994) the authors have argued that when $c=0.1$, the signal-to-noise ratio of efferent spike trains is saturated when a neuron receives 100 synaptic inputs (see Fig. 8). Here the signal-to-noise ratio is defined by

$$SNR = \frac{\text{mean of input}}{\text{standard deviation of input.}}$$

Hence for fully correlated input we have $SNR = p/\sqrt{p(1+(p-1)c)}$ and for partially correlated input $SNR = p/\sqrt{p(1+(k-1)c)}$. Nevertheless, as we have pointed out, the fully correlated input is an unrealistic assumption provided that correlated inputs are equivalent to synchronized inputs. Even the fully correlated assumption is true for pre-synaptic neurons, we articulate that only a proportion of neurons which are correlated with each other send their outputs to a post-synaptic neuron. In the next subsection we are going to discuss how to optimize the number of neurons inside a block. Fig. 8 depicts the case of $k=50$. Totally different from the conclusions in Zohary et al. (1994) where the authors claimed that, for example, when $c=0.1$, the noise-to-signal ratio is stabilized when $p \geq 100$. We find that the larger the p is, the better the signal-to-noise ratio, provided that neurons are partially correlated.

Finally, we point out that results in the previous subsection can be applied here, provided that $ak > V_{thre}$ (see next subsection). All the results are valid in the circumstances that correlation is equivalent to synchronization.

3.2.1. An optimization principle

Despite the fact that synaptically correlated model has been extensively considered in the literature, dated back to the publications of Barlow (1986), it is usually investigated under the assumption of fully correlated inputs. Under the assumption of partially correlated inputs, a natural question to ask is then how many neurons should be in each block. Here we propose a simple optimization principle: *the number of neurons in each block, which send their outputs to a post-synaptic neuron, ensures the optimization of the output of the post-synaptic neuron activity.* By neuron activity, we mean its output firing rate or output variability of interspike intervals, or other functions of \mathcal{T} . For simplicity of notation we only consider mean firing rates. Note that the number of neurons in each correlated block is irrelevant, instead the number of neurons they actually sent their outputs *together* to a post-synaptic neuron is the quantity we take into account.

We first consider the case of $k=10, 20, \dots, p$. For $a=0.5$ mV, we have the following cases.

- When $k > 50$, we see that $ak > V_{thre}$. The model fires slowly since these EPSPs with $k=51, 52, \dots$ have no impact on the model behaviour and are wasted.
- When $k < 40$, i.e. $ak < V_{thre}$, we see that a synchronous input is not large enough to push the neuron to cross the threshold.

Therefore the optimal number k which ensures the neuron to fire with its largest firing rate should satisfy $ak > V_{thre}$ and $ak \sim V_{thre}$. In other words, the optimal number of neurons in each block should be $k=50$, provided that $a=0.5$ mV, $V_{thre}=20$ mV. Numerical simulations (Fig. 9) confirm our conclusions. When $k=50$, the model emits spike trains with its largest firing rates, averaging over $r \in [0, 1]$.

It is very interesting to note that optimizing firing rates also maximizes the irregularity of efferent spike trains (Fig. 9). It should point out that from the conclusions above, we know that $k=50$ optimizes neuronal output activity is independent of c , p and λ_E .

Here is a summary of our observations. Suppose that a group of neurons are divided into a number of blocks (columns, see Albright et al., 2000; Feng et al., 1996; Sheth et al., 1996) and inside each block all neuronal activities are mutually correlated. From each block, k

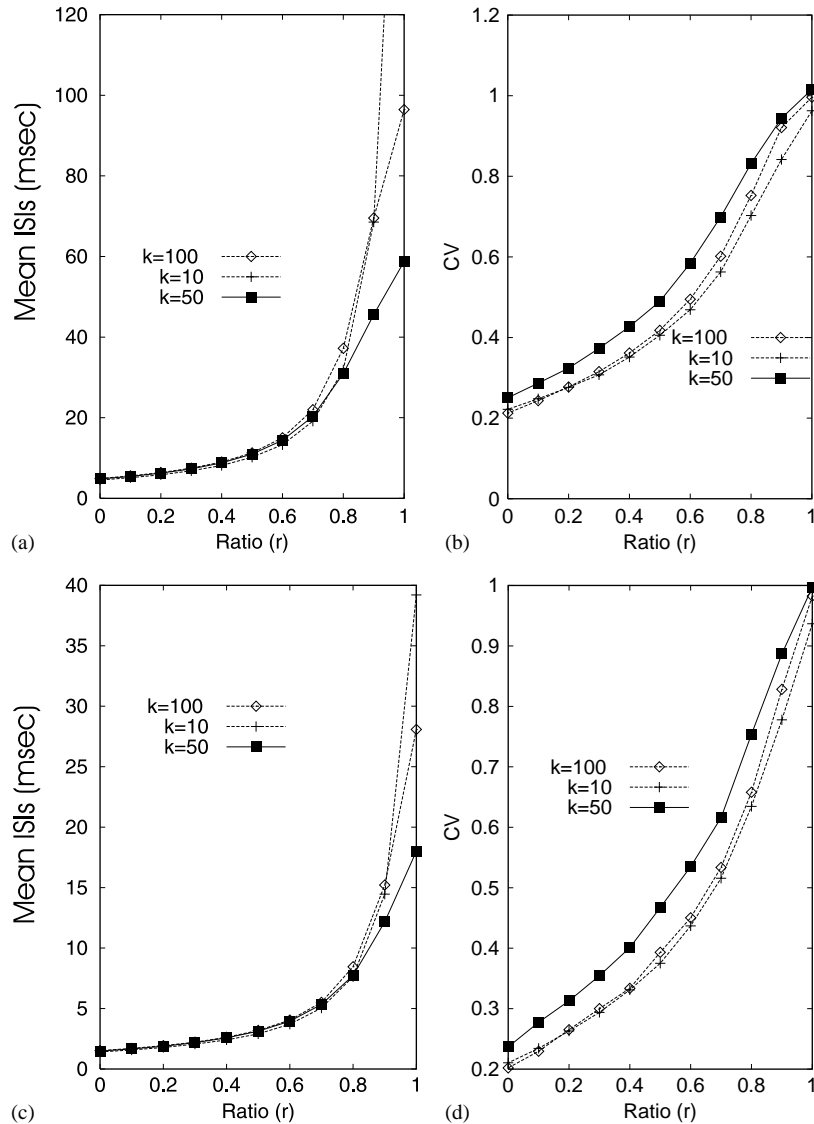


Fig. 9. Mean ISIs and CV of the integrate-and-fire model with partially correlated inputs ($k = 10, 50, 100$), $c = 0.1$ and $a = 0.5$ mV, $p = 100$ (a, b), $a = 0.5$ mV, $p = 300$ (c, d). It is easily seen that both the efferent frequency and CV are maximized (optimized) when $k = 50$.

neurons send out their outputs to a post-synaptic neuron, where k satisfies $ak > V_{thre}$, $ak \sim V_{thre}$. As such, the post-synaptic neuron activities are optimized.

The next question is for a given total number of synapses p , what is the optimal value of synapses k in each block? A complete and rigorous answer is outside the scope of the current paper and k depends on the ratio r as well. However, in one specific case $r = 1$, the exactly balanced case, and $0.3 \text{ mV} < a \leq 0.5 \text{ mV}$, we can have an exact answer here. From results in the previous section we know that the neuron fires if and only if a synchronous input arrives. Hence to drive the neuron to fire as fast as possible, it is required that $ka > V_{thre}$, but $ka - a < V_{thre}$, i.e. k is uniquely determined by

$$k = [V_{thre}/a] + 1,$$

where $[\cdot]$ is the integer part of a number. For example, when $V_{thre} = 20$ and $a = 0.5$, the optimal value of k is 41.

3.3. Correlation \neq exact synchronization

According to Section 2.3, the integrate-and-fire model behaviour now depends on the *asynchronization parameter* ε and its integration time h of input signals. In the sequel we consider two cases: $h \sim \varepsilon$ (loosely synchronized) and $h \sim p\varepsilon$ (tightly synchronized).

- Loosely synchronized (with a large asynchronization parameter) inputs.

If ε is too large, inputs are correlated, but are remotely separated in time, we could expect that the model behaviour is now similar to that of independent inputs. When $h \sim \varepsilon$, this case could be related to the post-spike voltage resetting mechanism proposed, i.e. after the membrane reaches the threshold it is reset to a value which is higher than the resting potential, see for example [Troyer and Miller \(1997\)](#). Suppose that $h = \varepsilon$ and at time t , the neuron fires a spike due to the arrival of an EPSP, say $t = t_1^s + \dots + t_k^s$. Then in the time interval $[t, t + (p - 1)\varepsilon]$ there is a positive current present. This effectively reduces the threshold from V_{thre} to $V_{thre} - a$. Therefore our results here provide a natural explanation of the post-spike voltage resetting mechanism proposed in [Troyer and Miller \(1997\)](#), without involving any biophysical mechanisms of a cell (see [Fig. 10](#)).

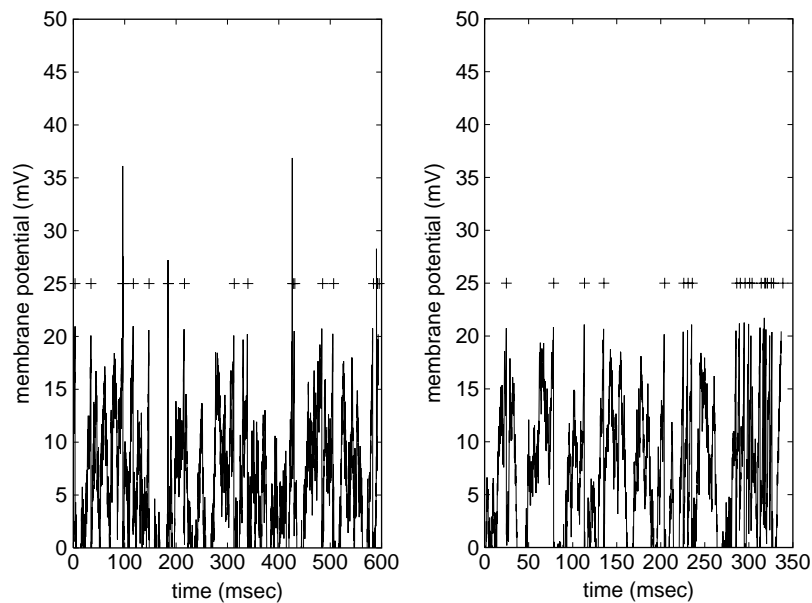
- In the literature, two mechanisms are proposed to explain the observed experimental results of irregular firing of a neuron in the cortex. One is the post-spike voltage resetting; the other is correlated inputs. Our analysis here unifies these two mechanisms and indicates that the correlated input is the key.
- Tightly synchronized inputs (with a small asynchronization parameter).
 1. When $p\varepsilon \leq h$, we have the exactly synchronized case, which we have fully discussed in the previous subsection.
 2. When $p\varepsilon \sim h$, now the inputs could be highly clustered and, as a result, the output is also very irregular. In fact, we could easily see that the model exhibits bursting behaviour. In [Fig. 10](#) we

see that two spikes are close to each other, with a time lag of ε . Note that we could choose different asynchronization parameter ε for different synaptic inputs and so bursting could be more widely separated in time (with refractory periods).

[Fig. 11](#) shows numerical results of tightly ($\varepsilon = 0.0024$) and loosely ($\varepsilon = 0.1$) synchronized inputs. It is interesting to note that the accuracy of the diffusion approximations presented in [Section 3.1.2](#) is significantly improved, comparing with exactly synchronized inputs (see [Fig. 6](#)).

4. Discussion

We have studied neuronal models with partially and fully correlated inputs. With an exactly balanced excitatory and inhibitory, and synaptically correlated input, we have found that the integrate-and-fire model simply behaves as a synchrony detector in certain parameter regions. A novel way to approximate synaptically correlated Poisson inputs has been proposed. The most interesting result discussed here is probably the optimization principle, which enables us to find out the optimal number in each fully correlated blocks and gives us a clue on how the nerve system might be organized ([Albright et al., 2000](#); [Feng et al., 1996](#); [Sheth et al., 1996](#)). We have also presented results on the model with tightly and loosely synchronized inputs.



[Fig. 10](#). Membrane potential of the model with tightly synchronized inputs $\varepsilon = 0.0024$ (upper panel), $h = 0.1$, $c = 0.1$ and $a = 0.5$ mV, $p = 100$, $r = 0.8$ and loosely synchronized inputs $\varepsilon = 0.1 = h$ (bottom panel). Bursting, two spikes occur with a time lag of ε , is indicated by vertical lines higher than 25 mV when $\varepsilon = 0.0024$. Note that when $\varepsilon = 0.1$ and t around 300 ms, the membrane potential seems not be set back to the resting potential.

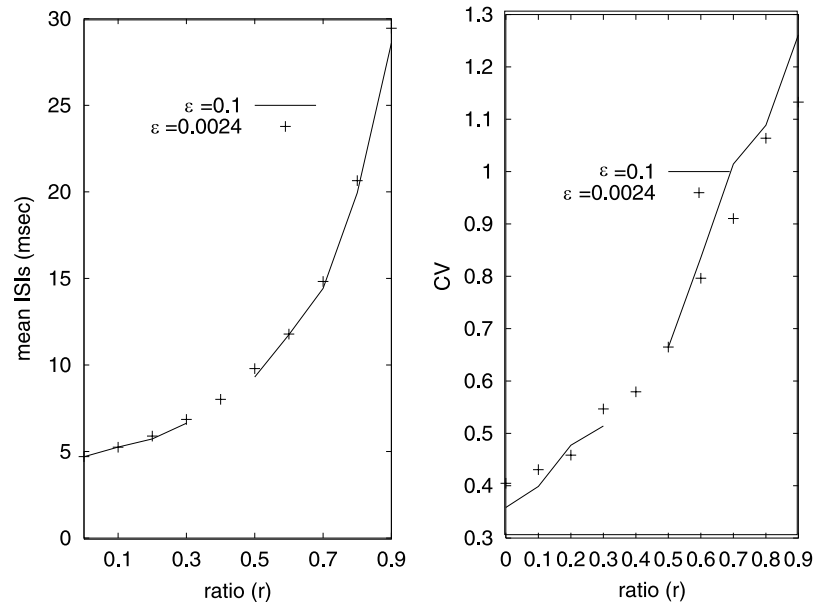


Fig. 11. Mean ISIs and CV of the integrate-and-fire model with tightly $\epsilon = 0.0024$ and loosely $\epsilon = 0.1$ synchronized inputs; $h = 0.1$, $c = 0.1$ and $a = 0.5$ mV, $p = 100$.

Although neuronal models with stochastic inputs have been extensively studied in the literature, it seems the issues discussed here have not been addressed before. With the availability of multi-unit recording data, we start to understand how neurons interact with each other. Synchronization or correlation, the second or higher order statistics, is bound to play a more important role in neuron modelling. Our results presented here could serve as a milestone for further rigorous study.

We emphasize here that the integrate-and-fire model is a Type I model, i.e. the output firing rate is a continuous function of input current, and it is generally believed that most neurons in the cortex are of the same type. Much as it is not saying that all results found here for the integrate-and-fire model can be generalized to more complex, biophysical models, we have learnt a lot from studying simple models, as demonstrated here and, for example, in Abbott et al. (1997).

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