Response of Spiking Neurons to Correlated Inputs

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The effect of a temporally correlated afferent current on the firing rate of a leaky integrate-and-fire (LIF) neuron is studied. This current is characterized in terms of rates, auto and cross-correlations, and correlation time scale \( \tau_c \) of excitatory and inhibitory inputs. The output rate \( \nu_{\text{out}} \) is calculated in the Fokker-Planck (FP) formalism in the limit of both small and large \( \tau_c \) compared to the membrane time constant \( \tau \) of the neuron. By simulations we check the analytical results, provide an interpolation valid for all \( \tau_c \) and study the neuron’s response to rapid changes in the correlation magnitude.

The neuron model and Input statistics. The depolarization membrane potential \( V(t) \) of a LIF neuron evolves from the reset voltage \( H \) according to

\[
\dot{V}(t) = -\frac{V(t)}{\tau} + I(t)
\]

where \( I(t) \) is the afferent and \( \tau \) is the membrane time constant \( \tau_c \). When the input drives the potential to a threshold value \( \Theta \), a spike is emitted and the neuron is reset to \( H \), from where it continues integrating the signal after a refractory time \( \tau_{\text{ref}} \). The afferent current \( I(t) \) is

\[
I(t) = \sum_{i=1}^{N_E} \sum_k \delta(t-t_i^k) - \sum_{j=1}^{N_I} \sum_l \delta(t-t_j^l)
\]

where \( t_i^{k(j)} \) represents the time of the \( k \)-th (l-th) spike from the \( i \)-th excitatory (j-th inhibitory) pre-synaptic neuron, and \( N_{E(I)} \) and \( J_{E(I)} \) respectively represent the number of inputs and size of the post-synaptic potentials from the excitatory (inhibitory) afferent populations. We work in the limit of infinitely fast post-synaptic currents, in which these are represented by delta functions. We consider stochastic spike trains with exponential auto-correlations with time constant \( \tau_c \)

\[
C_p(t, t') = \sum_{k, k'} \delta(t-t_i^k)\delta(t'-t_i^{k'}) - \nu_p^2 = \nu_p\delta(t-t') + \nu_p \left( \frac{F_p - 1}{2\tau_c} \right) e^{-\frac{|t-t'|}{\tau_c}}
\]

where \( \nu_p \) and \( F_p \) are the firing rate and Fano factors of the spike counts (for infinitely long time windows) of the individual trains from population \( p \). Notice that if \( F_p = 1 \) spikes are uncorrelated (Poisson process) and that for \( F_p > 1 \) spikes are positively correlated while for \( F_p < 1 \) they are negatively correlated. A similar expression for the autocorrelation of individual spike trains has been used in \( \tau_c \) in a study of the effect of synaptic filters. This problem is technically different from ours because those filters integrate out the Dirac delta in the correlation (see eq. (3) below). We also consider exponential cross-correlations

\[
C_{pq}(t, t') = \sum_{k, k'} \delta(t-t_i^{k_p})\delta(t'-t_i^{k_q}) - \nu_p\nu_q = \sqrt{\nu_p\nu_q} \left( \rho_{pq} \frac{F_p F_q}{2\tau_c} \right) e^{-\frac{|t-t'|}{\tau_c}}
\]

One of the most fundamental questions in neuroscience is to understand the way neurons communicate. There is growing evidence that temporal correlations in the spike emission times play a relevant role in the transmission of information (see, e.g. [1]). Although correlations are indeed present throughout cortex [2, 3], their functional role is controversial [4, 5, 6]. A relevant issue is how temporal correlations in a population affect the response of a postsynaptic neuron. Most of the work in this direction has been numerical, and little is known even for simple neuron models such as the LIF neuron [4, 5]. A better knowledge of how correlations affect the neuron’s input-output function would be useful, for instance, to study networks of these neurons, where correlations are unavoidable. A related issue is the speed with which changes in the correlations of inputs can be detected by a postsynaptic cell. In this letter we study both questions and interpret our results in the context of experiments on auditory processing [3]. The main conclusions are: 1) the neuron’s output rate is sensitive only to precisely synchronized inputs (\( \tau_c < \tau \)); 2) the response decreases (increases) with the timescale \( \tau_c \) for positive (negative) correlations, and increases (decreases) with their magnitude \( \alpha \); 3) this increase is larger for afferent currents in the fluctuation-dominated (balanced) state than for those in the drift-dominated (unbalanced) state; 4) the response increases until it reaches a saturation value if the magnitude and time scale of the correlations are increased simultaneously while keeping their ratio fixed; and 5) the neuron response to sudden changes in the size of the correlations is very fast, regardless of the magnitude of the change.

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between the trains \((i,j)\) in populations \(p\) and \(q\) \((p,q = E,I)\). The magnitude of the cross-correlations is determined by the correlation coefficients \(\rho_{pq}\) of the spike counts. For simplicity, we consider all correlations in the problem to have the same time constant \(\tau_c\). The reason why the Fano factors appear in eq. (4) is that the time integral of the cross-correlation has to be zero if one of the trains does not have spike count fluctuations. The correlation of the total afferent current is:

\[
C(t,t') \equiv <I(t) - I(t')>(I(t') - I(t')>) = \sigma^2_w \delta(t - t') + \frac{\sigma^2_w}{2\tau_c} e^{-\frac{\mu(t')}{\tau_c}},
\]

where \(\sigma^2_w\) is a white noise variance and \(\Sigma_2\) is the contribution to the total variance, \(\sigma^2_{\alpha} = \sigma^2_w + \Sigma_2\), arising from correlations in the input spike trains:

\[
\begin{align*}
\sigma^2_w &= J_p^2 N_E \nu_E + J_I^2 N_I \nu_I \\
\Sigma_2 &= J_p^2 N_E \nu_E [ (F_E - 1) + f_{EE} (f_{EE} N_E - 1) F_E \rho_{EE}] \\
&+ J_I^2 N_I \nu_I [ (F_I - 1) + f_{II} (f_{II} N_I - 1) F_I \rho_{II}] \\
&- 2 J_E J_I f_{EI} f_{IE} N_E N_I \sqrt{\nu_{EE}} \sqrt{\nu_{II}} F_E F_I \rho_{EI}
\end{align*}
\] (6)

We suppose that only a fraction of presynaptic neurons can be correlated with each other. The four parameters \(f_{pq}\) denote the fraction of correlated neurons from populations \(p\) and \(q\). The input current \(I(t)\) is assumed to be Gaussian, condition which naturally holds when the neuron is receiving a large barrage of spikes per second \([3]\) each one inducing a membrane depolarization \(J\) very small compared to the distance between the threshold and reset potentials, i.e., qualitatively \(\frac{J E}{(E - H)}(1 + f N p) \ll 1\). Thus, the input can be described in terms of the mean \(\mu = J_E N_E \nu_E - J_I N_I \nu_I\), the variance \(\sigma^2_w\), the parameter \(k = \frac{\sqrt{\tau_c}}{\tau_c}\), and the correlation magnitude \(\alpha = \Sigma_2 / \sigma^2_w\) \([3]\).

### The analytical solution.

We express the input current \(I(t)\) as

\[
I(t) = \mu + \sigma_w \eta(t) + \sigma_w \frac{\beta}{\sqrt{2\tau_c}} \eta(t)
\]

\[
\dot{z}(t) = -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}} \eta(t)
\]

where \(\eta(t)\) is a white noise random process with unit variance, \(\beta = \sqrt{1 + \alpha - 1}\) and \(z(t)\) is an auxiliary colored random process which obeys eq. (1) with the same white input noise \(\eta(t)\). Using eqs. (1) \(\beta\) is easy to check that \(I(t)\) is exponentially correlated in the stationary regime, with correlations that read exactly as (1).

Associated to the stochastic diffusion process defined by eqs. (1) \(\beta\), \(\beta\), \(\beta\), we have the stationary FP equation \(\beta\)

\[
[L_x + \frac{L_z}{k^2} + \frac{2}{k} \frac{\partial}{\partial x} \frac{\partial}{\partial z} - \frac{\beta z}{2} ] f = -\tau (x - \sqrt{2H}) J(z)
\]

(9)

where \(L_x = \frac{\partial^2}{\partial x^2}\) and \(L_z = \frac{\partial^2}{\partial z^2}\). Besides, \(V = \mu \tau + \sigma_w \sqrt{2\tau}\), \(H = \frac{H - \nu}{\sigma_w \sqrt{\tau}}\) and \(\Theta = \frac{\Theta - \nu}{\sigma_w \sqrt{\tau}}\).

The function \(J(x,z)\) is the steady state probability density of having the neuron in the state \((x,z)\). The key quantity \(J(z)\) is the escape probability current. It appears in eq. (3) as a source term representing the reset effect: whenever the potential \(V\) reaches the threshold \(\Theta\), it is reset to the value \(H\) with a distribution in \(z\) that is unknown. The particular distribution of \(z\) will depend on the value of \(\tau_{\text{ref}}\). The escape current must be determined consistently using the normalization of the probability density, \(\tau_{\text{ref}} v_{\text{out}} + \int_{-\infty}^{\Theta} dx \int_{-\infty}^{\infty} dz f(x,z) = 1\), and the threshold vanishing condition, \(f(\sqrt{2\Theta},0) = 0\). The output firing rate is given by \(v_{\text{out}} = \int_{-\infty}^{\infty} dz J(z)\).

Small \(\tau_c\) expansion \((\tau_c \ll \tau)\). In this regime the quantities \(k\) and \(\alpha\) are treated as perturbative parameters. If we suppose that the correlation time \(\tau_c\) is very small compared to the refractory time \(\tau_{\text{ref}}\) \((\tau_{\text{ref}} \gg \tau_c)\), the escape current can be written as \(J(z) = v_{\text{out}} e^{-\frac{z^2}{2}} / \sqrt{2\pi}\). We find \(v_{\text{out}}\) analytically by expanding eq. (4) in powers of \(k = \sqrt{\tau_c / \tau}\), and calculating the terms exactly for all \(\alpha = \Sigma_2 / \sigma^2_w\) for the zero order, and perturbatively in \(\alpha \geq 0\) up to the first non trivial correction for the first order. The obtained firing rate can be written as

\[
\nu_{\text{out}} = \nu_{\text{eff}} - \alpha \sqrt{\tau_c \nu_{\text{ref}}^2} R(\Theta)
\]

(10)

Here \(R(t) = \sqrt{\frac{\tau}{\pi}} e^{t^2} (1 + \text{erf}(t))\), where \(\text{erf}(t)\) is the error function, and the rates \(\nu_{\text{eff}}\) and \(\nu_0\) are defined as

\[
\nu_{\text{eff}}^{-1} = \tau_{\text{ref}} + \frac{\sqrt{\pi} \tau}{\tau_{\text{eff}}} \int_{-\infty}^{\Theta_{\text{eff}}} dt e^{t^2} (1 + \text{erf}(t))
\]

\[
\nu_0^{-1} = \tau_{\text{ref}} + \frac{\sqrt{\pi} \tau}{\tau_{\text{eff}}} \int_{-\infty}^{\Theta} dt e^{t^2} (1 + \text{erf}(t))
\]

(11)

The effective reset and threshold are defined as \(\Theta_{\text{eff}} = \frac{\Theta - \nu}{\sigma_{\text{eff}} \sqrt{\tau}}\) and \(H_{\text{eff}} = \frac{H - \nu}{\sigma_{\text{eff}} \sqrt{\tau}}\). \(\nu_0\) is the mean firing rate of a LIF neuron driven by white noise \([8]\). Hence, eq. (10) implies that when \(\tau_c\) is 0 the problem is equivalent to considering an uncorrelated input with an effective signal variance \(\sigma^2_{\text{eff}} = \sigma^2_w + \Sigma_2\). In this case, our solution is exact for all \(\alpha\). When \(\tau_c \neq 0\), the expression is only correct for small values of both \(k\) and \(\alpha \geq 0\). Here the analytical result applies only when \(\alpha \geq 0\), but we checked by numerical simulations that the same formula for the output rate is also valid for \(\alpha < 0\).

Large \(\tau_c\) expansion \((\tau_c \gg \tau)\). In this limit the perturbative parameter is \(k^{-1}\). Now the escape probability current \(J(z)\) must be derived from the FP eq. (3). If we assume that \(\tau_{\text{ref}} \ll \tau_c\),

\[
J(z) = -\frac{1}{\tau} \frac{\partial}{\partial x} f(x,z) \big|_{x=\sqrt{2\Theta}}
\]

(12)
FIG. 1: Theoretical predictions and simulation results for \( \nu_{\text{out}} \) as a function of \( \tau_c \). **Left:** \( \alpha = 0.21 \) (upper curve) and \( \alpha = -0.19 \) (lower curve). **Top right:** same but for larger values of \( \tau_c \). **Bottom right:** the case \( \alpha = 0.21 \) for very small values of \( \tau_c \). Full lines: interpolations between the small and large \( \tau_c \) theoretical predictions performed at the interpolating time \( \tau_{\text{c,inter}} = 14 \text{ms} \). Dashed line: small \( \tau_c \) predictions from eq. (14). **Horizontal line:** response to white noise activation (\( \alpha = 0 \)). Other parameters are \( \tau = 10 \text{ms}, \tau_{\text{ref}} = 0 \text{ms}, \Theta = 1 \) (in arbitrary units), \( H = 0, \mu = 81.7 \text{s}^{-1}, \sigma_w^2 = 2.1 \text{s}^{-1} \).

Although the small \( \tau_c \) expansion requires \( \tau_{\text{ref}} \neq 0 \) the simulation shows that this prediction is good even for zero \( \tau_{\text{ref}} \).

This expression generates an additional constraint that should hold in addition to the conditions defined above.

Using standard perturbative techniques we find \( J(z) \) and the mean firing rate, up to \( O(k^{-2}) \):

\[
J(z) = \frac{e^{-z^2/2}}{\sqrt{2\pi}} [\nu_0 + \sqrt{\frac{\tau}{\tau_c}} \left( 2 + \beta \nu_0^2 (R(\hat{\Theta}) - R(\hat{H})) \right) - \nu_0 \tau_{\text{ref}}] z + \frac{C}{\tau_c} [\beta + \beta \tau_c (1 - \nu_0 \tau_{\text{ref}})] (z^2 - 1) \tag{13}
\]

\[
\nu_{\text{out}} = \nu_0 + \frac{C}{\tau_c} \tag{14}
\]

\[
C = \alpha^2 \nu_0^2 \left( \nu_0 (R(\hat{\Theta}) - R(\hat{H}))^2 - \frac{\hat{\Theta} R(\hat{\Theta}) - \hat{H} R(\hat{H})}{\sqrt{2}} \right) \tag{15}
\]

Note that \( \nu_{\text{out}} \) converges to \( \nu_0 \) when \( \tau_c \gg \tau \).

**Results and comparison with numerical simulations.** We have performed numerical simulations of a LIF neuron driven by Gaussian exponentially correlated input using eqs. (10,14) with a twofold motivation. First, they can be used to check the analytical results given in eqs. (10,14) and, second, they can be employed to determine higher order terms in the perturbative expansions by interpolating the output rate between the regimes of low and high \( \tau_c \). The interpolating curves have been determined by setting the firing rate in the small correlation time range \( (\tau_c < \tau) \) as \( \nu_{\text{out}} = \nu_{\text{eff}} + A_1 \sqrt{\tau_c} + A_2 \tau_c \) where \( A_1 \) and \( A_2 \) are unknown functions of \( \alpha \) and of the neuron and input parameters, while in the large correlation time limit \( (\tau_c > \tau) \) the expression given in eq. (14), \( \nu_{\text{out}} = \nu_0 + C/\tau_c \), was used. The functions \( A_1 \) and \( A_2 \) are determined by interpolating these two expressions with conditions of continuity and derivability at a convenient interpolation point \( \tau_{\text{c,inter}} \sim \tau \). Although we have calculated analytically the function \( A_1 \) (eq. (10)) for small \( \alpha \), this procedure takes into account higher order corrections which match more accurately the observed data for larger values of \( \alpha \). Fig. 1 shows an example the good agreement between theory and simulations. When positive correlations are considered \( (\alpha > 0) \), the interpolation procedure is robust to changes in \( \mu \) and \( \sigma_w^2 \). For negative correlations, changing these parameters sometimes results in lower quality fits. In these cases we have added to the expansion in eq. (14) an extra term, so that \( \nu_{\text{out}} = \nu_0 + C/\tau_c + B_1/\tau_c^2 \). This is used to match at \( \tau_{\text{c,inter}} \) the small \( \tau_c \) regime which is set as \( \nu_{\text{out}} = \nu_{\text{eff}} + B_2 \sqrt{\tau_c} \).

As it can be appreciated in Fig. 1, the response increases as \( \tau_c \) decreases (at fixed positive \( \alpha \)). This corresponds to the intuitive result that positive correlations between the pre-synaptic events produce a larger enhancement in the output firing rate as the temporal window over which they occur decreases. We have also considered a situation where the correlation magnitude increases with \( \tau_c \) as \( \alpha = \gamma \tau_c \), for a fixed \( \gamma > 0 \). Eqs. (14) and (15) suggest that the rate increases and saturates as a function of \( \tau_c \), because it depends only on the ratio \( \alpha/\tau_c \) in the long \( \tau_c \) limit. We checked this conclusion with simulations using the same parameters as in Fig. 1 (data not shown). Note, however, that this manipulation does not isolate the effect of changing the temporal range of the correlations, since now \( \alpha \), which depends on the pre-synaptic rates, Fano factors, etc., has to increase linearly with \( \tau_c \).

At fixed \( \tau_c \), the rate increases with \( \alpha \), as shown in Fig. 2. The mean current, \( \mu \), and the white noise variance, \( \sigma_w^2 \), have been chosen so that the afferent current puts the neuron either in the fluctuation-dominated or in the drift-dominated regime. Notice that the response is more sensitive to changes in the correlation magnitude (\( \alpha \)) in
We can also infer how fast a LIF neuron responds to the input has only autocorrelations, described by \( \mu = 40 \text{s}^{-1} \), \( \alpha = 19.3 \text{s}^{-1} \), \( \alpha = 0.56 \), and \( \tau_c = 15 \text{ms} \) (representing independent bursting input spike trains with, e.g., \( \nu_E = \nu_l = 10 \text{Hz} \), \( N_E = 10^4 \), \( N_l = 2.1 \times 10^3 \), \( F_E = 4 \), \( F_l = 1 \), \( J_E = 6.10^{-3} \), \( J_l = 2.8.10^{-2} \)). **Full lines:** quick responses when \( \alpha \) is suddenly changed at \( t = 0 \) to \( \alpha = 7 \) (upper curve) and to \( \alpha = 3 \) (bottom curve) and synchronization occurs in a precise way \( (\tau_c = 1 \text{ms}) \). These two \( \alpha \)’s (corresponding to different tone frequencies) can be obtained with \( \rho_{EE} = 0.34 \) and \( \rho_{EE} = 0.13 \) respectively, and in both cases \( f_{EE} = 5.10^{-2} \), \( f_{I} = f_{EI} = f_{IE} = 0 \). **Dashed lines:** the same as above but \( \tau_c = 15 \text{ms} \) after \( t = 0 \), in agreement with \( \tau_c \). The responses are slower, but still fast in comparison with \( \tau \). Other parameters are as in Fig. 1. Inset: \( t_{\text{cross}} \), time when the response hits for the first time the value of the stationary rate (crosses in the main graph), as a function of \( \alpha \). Upper curve: \( \tau_c = 15 \text{ms} \), bottom curve: \( \tau_c = 1 \text{ms} \).

As we have seen, the exact solution for \( \tau_c = 0 \) corresponds to a renormalization of \( \sigma_w^2 \) to \( \sigma_{\text{eff}}^2 \). This gives \( v_{\text{out}}(t) = -\frac{\sigma_w^2(t)}{2} \frac{\partial}{\partial V} \int_{-\infty}^{\infty} dz P(V, z, t)|_{V = \Theta} \). Now it is clear that any change in \( \sigma_{\text{eff}}^2 \) will produce an immediate change in \( v_{\text{out}} \). This means that when \( \tau_c = 0 \), changes in both correlation magnitude \( (\alpha) \) and white noise variance \( (\sigma_w^2) \) will be felt immediately by the firing response of the neuron. By analyticity arguments, the response under changes in \( \alpha \) will be also fast for non-zero, small \( \tau_c \).

These predictions have been tested with numerical simulations in the context of the experimental results found in [9]. In this experiment, neurons in primary auditory cortex (AI) are recorded under stimulation by a pure tone. After the stimulus onset, a change in the cross-correlogram is observed while the rate changes very little. The results shown in Fig. 3 correspond to the response of a LIF neuron integrating a current which emulates the activity in AI. The input initially contains autocorrelations but not cross-correlations and the output rate is low. When at \( t = 0 \) a tone is presented, there is a sudden increase in \( \alpha \) (due to a synchronization of a subpopulation in AI, which depends on the tone frequency). The neuron responds by firing at a higher output rate. As expected from Fig. 3 this final rate increases with \( \alpha \), but the velocity of the response is independent of it (see inset Fig. 3). This means that the reaction is equally fast for any stimulation tone. As a consequence of this dynamics, the correlation coding present in AI is transformed into a rate coding by the postsynaptic neuron.

In [12] the same *synchrony reading* problem was discussed with AI cells making depressing synapses with the reading neuron. The authors show an example where a neuron with static synapses fails to respond to the tone. We have checked that the results in Fig. 3 (dashed lines) hold for parameter values that can represent the experimental results.

Our results could be extended by including the effect of finite synaptic time constants \( \tau_s \); our work takes \( \tau_s = 0 \) and thus it is the zeroth order in an expansion in this parameter. Indeed, we have numerically checked that our conclusions hold qualitatively if small, non-zero \( \tau_s \) (e.g. 2 ms) are considered.

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