

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 neuron is studied. This current is characterized in terms of rates, autocorrelations, and cross correlations, and correlation time scale τ_c of excitatory and inhibitory inputs. The output rate ν_{out} is calculated in the Fokker-Planck formalism in the limit of both small and large τ_c compared to the membrane time constant τ of the neuron. By simulations we check the analytical results, provide an interpolation valid for all τ_c , and study the neuron's response to rapid changes in the correlation magnitude.

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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 [4–6]. 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 leaky integrate-and-fire (LIF) neuron [4,7]. 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 as follows: (1) the neuron's output rate is sensitive only to precisely synchronized inputs ($\tau_c < \tau$); (2) the response decreases (increases) with the time scale τ_c for positive (negative) correlations, and increases (decreases) with their magnitude α ; (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; (5) the neuron response to sudden changes in the size of the correlations is very fast, regardless of the magnitude of the change.

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

$$\dot{V}(t) = -\frac{V(t)}{\tau} + I(t), \quad (1)$$

where $I(t)$ is the afferent and τ is the membrane time constant [8]. When the input drives the potential to a

threshold value Θ , a spike is emitted and the neuron is reset to H , from where it continues integrating the signal after a refractory time τ_{ref} . The afferent current $I(t)$ is

$$I(t) = J_E \sum_{i=1}^{N_E} \sum_k \delta(t - t_i^k) - J_I \sum_{j=1}^{N_I} \sum_l \delta(t - t_j^l), \quad (2)$$

where $t_{i(j)}^{k(l)}$ represents the time of the k th (l th) spike from the i th excitatory (j th inhibitory) presynaptic neuron, and $N_{E(I)}$ and $J_{E(I)}$, respectively, represent the number of inputs and size of the postsynaptic potentials from the excitatory (inhibitory) afferent populations. We work in the limit of infinitely fast postsynaptic currents, in which these are represented by delta functions. We consider stochastic spike trains with exponential autocorrelations with time constant τ_c ,

$$\begin{aligned} C_p(t, t') &\equiv \left\langle \sum_{k, k'} \delta(t - t_i^k) \delta(t' - t_i^{k'}) \right\rangle - \nu_p^2 \\ &= \nu_p \delta(t - t') + \nu_p \left(\frac{F_p - 1}{2\tau_c} \right) e^{-(|t-t'|)/\tau_c}. \end{aligned} \quad (3)$$

Here $p = E, I$, and ν_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 [9] 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. (5) below]. We also consider exponential cross correlations

$$\begin{aligned} C_{pq}(t, t') &\equiv \left\langle \sum_{k_p, k_q} \delta(t - t_i^{k_p}) \delta(t' - t_j^{k_q}) \right\rangle - \nu_p \nu_q \\ &= \sqrt{\nu_p \nu_q} \left(\frac{\rho_{pq} \sqrt{F_p F_q}}{2\tau_c} \right) e^{-(|t-t'|)/\tau_c} \end{aligned} \quad (4)$$

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 ρ_{pq} of the spike counts. For simplicity, we consider all correlations in the problem to have the same time constant τ_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

$$\begin{aligned}\sigma_w^2 &= J_E^2 N_E \nu_E + J_I^2 N_I \nu_I, \\ \Sigma_2 &= J_E^2 N_E \nu_E [(F_E - 1) + f_{EE}(f_{EE} N_E - 1) F_E \rho_{EE}] + J_I^2 N_I \nu_I [(F_I - 1) + f_{II}(f_{II} N_I - 1) F_I \rho_{II}] \\ &\quad - 2 J_E J_I f_{EI} f_{IE} N_E N_I \sqrt{\nu_E \nu_I} \sqrt{F_E F_I} \rho_{EI}.\end{aligned}\quad (6)$$

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, a condition which naturally holds when the neuron is receiving a large barrage of spikes per second [8], each one inducing a membrane depolarization J very small compared to the distance between the threshold and reset potentials; i.e., qualitatively $\frac{JF}{(\Theta-H)}(1 + fN\rho) \ll 1$. 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 σ_w^2 , the parameter $k \equiv \sqrt{\tau_c}/\tau$, and the correlation magnitude $\alpha \equiv \Sigma_2/\sigma_w^2$ [10].

The analytical solution.—We express the input current $I(t)$ as

$$I(t) = \mu + \sigma_w \eta(t) + \sigma_w \frac{\beta}{\sqrt{2\tau_c}} z(t), \quad (7)$$

$$\dot{z}(t) = -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}} \eta(t), \quad (8)$$

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. (8) with the same white input noise $\eta(t)$. Using Eqs. (7) and (8), it is easy to check that $I(t)$ is exponentially correlated in the stationary regime, with correlations that read exactly as (5).

Associated with the stochastic diffusion process defined by Eqs. (1), (7), and (8), we have the stationary Fokker-Planck (FP) equation [11]

$$\left[L_x + \frac{L_z}{k^2} + \frac{2}{k} \frac{\partial}{\partial x} \left(\frac{\partial}{\partial z} - \frac{\beta z}{2} \right) \right] f = -\tau \delta(x - \sqrt{2}\hat{H}) J(z), \quad (9)$$

where $L_u = \frac{\partial}{\partial u} u + \frac{\partial^2}{\partial^2 u}$. Besides, $V = \mu\tau + \sigma_w \sqrt{x}$, $\hat{H} = \frac{H - \mu\tau}{\sigma_w \sqrt{\tau}}$, and $\hat{\Theta} = \frac{\Theta - \mu\tau}{\sigma_w \sqrt{\tau}}$.

The function $f(x, z)$ 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. (9) as a source term representing the reset effect: whenever the potential V reaches the threshold Θ , it is reset to the value H with a distribution in z that is unknown. The particular distribution of z will depend

$$\begin{aligned}C(t, t') &\equiv \langle (I(t) - \langle I(t) \rangle)(I(t') - \langle I(t') \rangle) \rangle \\ &= \sigma_w^2 \delta(t - t') + \frac{\Sigma_2}{2\tau_c} e^{-(t-t')/\tau_c},\end{aligned}\quad (5)$$

where σ_w^2 is a white noise variance and Σ_2 is the contribution to the total variance, $\sigma_{\text{eff}}^2 = \sigma_w^2 + \Sigma_2$, arising from correlations in the input spike trains:

on the value of τ_{ref} . The escape current must be determined consistently using the normalization of the probability density, $\tau_{\text{ref}} \nu_{\text{out}} + \int_{-\infty}^{\hat{\Theta}} dx \int_{-\infty}^{\infty} dz f(x, z) = 1$, and the threshold vanishing condition, $f(\sqrt{2}\hat{\Theta}, z) = 0$. The output firing rate is given by $\nu_{\text{out}} = \int_{-\infty}^{\infty} dz J(z)$.

Small τ_c expansion ($\tau_c \ll \tau$): In this regime the quantities k and α are treated as perturbative parameters. If we suppose that the correlation time τ_c is very small compared to the refractory time τ_{ref} ($\tau_{\text{ref}} \gg \tau_c$), the escape current can be written as $J(z) = \nu_{\text{out}} e^{-z^2/2} / \sqrt{2\pi}$ [9]. We find ν_{out} analytically by expanding Eq. (9) in powers of $k = \sqrt{\tau_c}/\tau$, and calculating the terms exactly for all $\alpha = \Sigma_2/\sigma_w^2$ for the zero order, and perturbatively in $\alpha \geq 0$ up to the first nontrivial correction for the first order. The obtained firing rate can be written as

$$\nu_{\text{out}} = \nu_{\text{eff}} - \alpha \sqrt{\tau_c} \tau \nu_0^2 R(\hat{\Theta}). \quad (10)$$

Here $R(t) = \sqrt{\frac{\pi}{2}} e^{t^2} [1 + \text{erf}(t)]$, where $\text{erf}(t)$ is the *error function*, and the rates ν_{eff} and ν_0 are defined as

$$\begin{aligned}\nu_{\text{eff}}^{-1} &= \tau_{\text{ref}} + \sqrt{\pi} \tau \int_{\hat{H}_{\text{eff}}}^{\hat{\Theta}_{\text{eff}}} dt e^{t^2} [1 + \text{erf}(t)], \\ \nu_0^{-1} &= \tau_{\text{ref}} + \sqrt{\pi} \tau \int_{\hat{H}}^{\hat{\Theta}} dt e^{t^2} [1 + \text{erf}(t)].\end{aligned}\quad (11)$$

The effective reset and threshold are defined as $\hat{\Theta}_{\text{eff}} = \frac{\Theta - \mu\tau}{\sigma_{\text{eff}} \sqrt{\tau}}$ and $\hat{H}_{\text{eff}} = \frac{H - \mu\tau}{\sigma_{\text{eff}} \sqrt{\tau}}$. ν_0 is the mean firing rate of a LIF neuron driven by white noise [8]. Hence, Eq. (10) implies that when $\tau_c = 0$ the problem is equivalent to considering an uncorrelated input with an effective signal variance $\sigma_{\text{eff}}^2 = \sigma_w^2 + \Sigma_2$. In this case, our solution is *exact* for all α . When $\tau_c \neq 0$, the expression is correct only 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 τ_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. (9). If we assume that $\tau_{\text{ref}} \ll \tau_c$,

$$J(z) = -\frac{1}{\tau} \frac{\partial}{\partial x} f(x, z) \Big|_{x=\sqrt{2}\hat{\Theta}}. \quad (12)$$

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 $O(k^{-2})$,

$$J(z) = \frac{e^{-z^2/2}}{\sqrt{2\pi}} \left[\nu_0 + \sqrt{\frac{\tau^3}{\tau_c}} \frac{(2 + \beta)\nu_0^2(R(\hat{\Theta}) - R(\hat{H}))}{1 - \nu_0\tau_{\text{ref}}} z + \frac{C}{\tau_c} + \frac{(2 + \beta)C}{\beta\tau_c(1 - \nu_0\tau_{\text{ref}})} (z^2 - 1) \right], \quad (13)$$

$$\nu_{\text{out}} = \nu_0 + \frac{C}{\tau_c}, \quad (14)$$

$$C \equiv \alpha\tau^2\nu_0^2 \left[\frac{\tau\nu_0(R(\hat{\Theta}) - R(\hat{H}))^2}{1 - \nu_0\tau_{\text{ref}}} - \frac{\hat{\Theta}R(\hat{\Theta}) - \hat{H}R(\hat{H})}{\sqrt{2}} \right].$$

Note that ν_{out} converges to ν_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. (1), (7), and (8) with a twofold motivation. First, they can be used to check the analytical results given in Eqs. (10) and (13) 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 τ_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 α 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 $\tau_{c,\text{inter}} \sim \tau$. Although we have calculated analytically the function A_1 [Eq. (10)] for small α , this procedure takes into account higher order corrections which match more accurately the observed data for larger values of α . Figure 1 shows an example of the good agreement between theory and simulations. When positive correlations are considered ($\alpha > 0$), the interpolation procedure is robust to changes in μ and σ_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 $\tau_{c,\text{inter}}$ the small τ_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 τ_c decreases (at fixed positive α). This corresponds to the intuitive result that positive correlations between the presynaptic 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 τ_c as $\alpha = \gamma\tau_c$, for a fixed $\gamma > 0$. Equations (10) and (14) suggest that the rate increases and saturates as a function

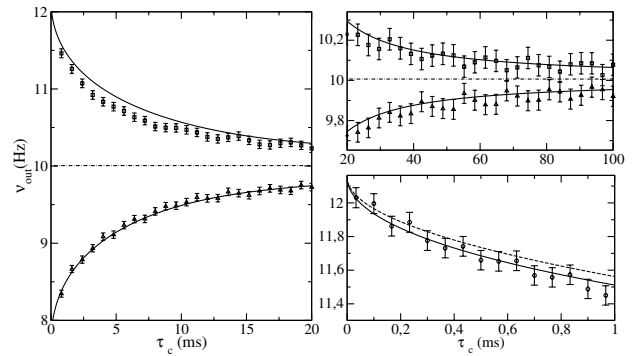


FIG. 1. Theoretical predictions and simulation results for ν_{out} as a function of τ_c . Left: $\alpha = 0.21$ (upper curve) and $\alpha = -0.19$ (lower curve). Top right: same but for larger values of τ_c . Bottom right: the case $\alpha = 0.21$ for very small values of τ_c . Full lines: interpolations between the small and large τ_c theoretical predictions performed at the interpolating time $\tau_{c,\text{inter}} = 14$ ms. Dashed line: small τ_c predictions from Eq. (10). Horizontal line: response to white noise activation ($\alpha = 0$). Other parameters are $\tau = 10$ ms, $\tau_{\text{ref}} = 0$ ms, $\Theta = 1$ (in arbitrary units), $H = 0$, $\mu = 81.7$ s $^{-1}$, $\sigma_w^2 = 2.1$ s $^{-1}$. Although the small τ_c expansion requires $\tau_{\text{ref}} \neq 0$, the simulation shows that this prediction is good even for zero τ_{ref} .

of τ_c , because it depends only on the ratio α/τ_c in the long τ_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 α , which depends on the presynaptic rates, Fano factors, etc., has to increase linearly with τ_c .

At fixed τ_c , the rate increases with α , as shown in Fig. 2. The mean current, μ , and the white noise variance, σ_w^2 , have been chosen so that the afferent current puts the neuron either in the fluctuation-dominated or in the drift-dominated regime [4]. Notice that the response is more sensitive to changes in the correlation magnitude (α) in the balanced than in the unbalanced state, in agreement with the findings in [7] for similar neuron models.

We can also infer how fast a LIF neuron responds to changes in the correlation magnitude α at fixed afferent mean current and white noise variance σ_w^2 . It is easy to verify that the instantaneous rate for the time dependent FP equation can be expressed as [for the sake of clarity we have come back to the physical quantity V and used its distribution $P(V, z, t)$]

$$\nu_{\text{out}}(t) = -\frac{\sigma_w^2(t)}{2} \frac{\partial}{\partial V} \int_{-\infty}^{\infty} dz P(V, z, t) |_{V=\Theta}. \quad (15)$$

As we have seen, the exact solution for $\tau_c = 0$ corresponds to a renormalization of σ_w^2 to σ_{eff}^2 . This gives $\nu_{\text{out}}(t) = -\frac{\sigma_{\text{eff}}^2(t)}{2} \frac{\partial}{\partial V} \int dz P(V, z, t) |_{V=\Theta}$. Now it is clear that any change in σ_{eff}^2 will produce an immediate change in ν_{out} [12]. This means that when $\tau_c = 0$ changes in both correlation magnitude (α) and white noise

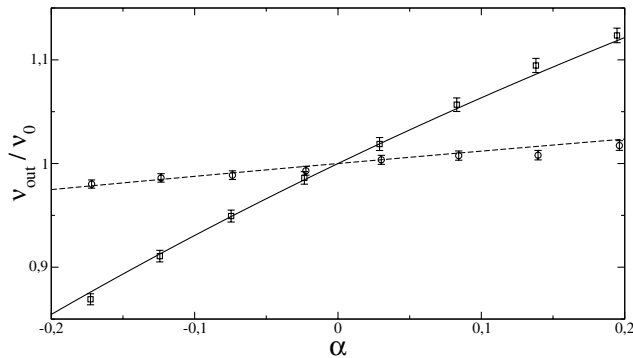


FIG. 2. Theoretical predictions and simulation results for v_{out}/v_0 as a function of α for the balanced and the unbalanced states. The neuron is much more sensitive to α in the balanced regime (full line, $\mu = 40 \text{ s}^{-1}$) than in the unbalanced regime (dashed line, $\mu = 110 \text{ s}^{-1}$). In both cases $\sigma_w^2 = 30 \text{ s}^{-1}$, $\tau_c = 1 \text{ ms}$ and the other parameters are as in Fig. 1. With these parameters $\nu_0 = 16.9 \text{ Hz}$ in the balanced state and $\nu_0 = 69.5 \text{ Hz}$ in the unbalanced state.

variance (σ_w^2) will be felt immediately by the firing response of the neuron. By analyticity arguments, the response under changes in α will also be fast for nonzero, small τ_c .

These predictions have been tested with numerical simulations in the context of the experimental results found in [3]. 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 α (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. 2, this final rate increases with α , but the velocity of the response is independent of it (see inset of 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 [13] 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 τ_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, nonzero τ_s (e.g., 2 ms) are considered.

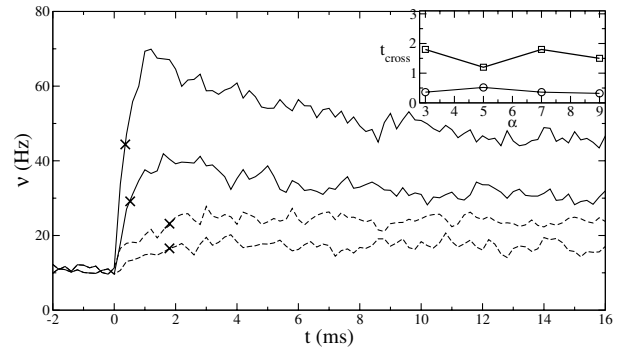


FIG. 3. Trial averages of the transient responses of a LIF neuron to changes in the input correlations. Below $t = 0$ the input has only autocorrelations, described by $\mu = 40 \text{ s}^{-1}$, $\sigma_w^2 = 19.3 \text{ s}^{-1}$, $\alpha = 0.56$, and $\tau_c = 15 \text{ ms}$ (representing independent bursty input spike trains with, e.g., $\nu_E = \nu_I = 10 \text{ Hz}$, $N_E = 10^4$, $N_I = 2 \times 10^3$, $F_E = 4$, $F_I = 1$, $J_E = 6 \times 10^{-3}$, $J_I = 2.8 \times 10^{-2}$). Full lines: quick responses when α 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 α 's (corresponding to different tone frequencies) can be obtained with $\rho_{EE} = 0.34$ and $\rho_{EE} = 0.13$, respectively, and in both cases $f_{EE} = 5 \times 10^{-2}$, $f_{II} = f_{EI} = f_{IE} = 0$. Dashed lines: the same as above but $\tau_c = 15 \text{ ms}$ after $t = 0$, in agreement with [3]. The responses are slower, but still fast in comparison with τ . Other parameters are as in Fig. 1. Inset: t_{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 α . Upper curve: $\tau_c = 15 \text{ ms}$; bottom curve: $\tau_c = 1 \text{ ms}$.

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