

Theory of input spike auto- and cross-correlations and their effect on the response of spiking neurons

RUBÉN MORENO-BOTE (1,2), ALFONSO RENART (2,3)
AND NÉSTOR PARGA (2)

- (1) Present Address: Center for Neural Science, New York University,
New York, NY 10003-6621, USA.
- (2) Dept. de Física Teórica. Universidad Autónoma de Madrid,
Cantoblanco 28049, Madrid, Spain
- (3) Present Address: Center for Molecular and Behavioral Neuroscience,
Rutgers, The State University of New Jersey, 197 University Avenue,
Newark, NJ 07102, USA

Abstract

Spike correlations between neurons are ubiquitous in the cortex, but their role is at present not understood. Here we describe the firing response of a leaky integrate-and-fire neuron (LIF) when it receives a temporarily correlated input generated by presynaptic correlated neuronal populations. Input correlations are characterized in terms of the firing rates, Fano factors, correlation coefficients and correlation timescale of the neurons driving the target neuron. We show that the sum of the presynaptic spike trains cannot be well described by a Poisson process. In fact, the total input current has a non trivial two-point correlation function described by two main parameters: the correlation timescale (how precise the input correlations are in time), and the correlation magnitude (how strong they are). Therefore, the total current generated by the input spike trains is not well described by a white noise Gaussian process. Instead, we model the total current as a colored Gaussian process with the same mean and two-point correlation function, leading to the formulation of the problem in terms of a Fokker-Planck equation. Solutions of the output firing rate are found in the limit of short and long correlation time scales. The solutions described here expand and improve our previous

results (Moreno et al., 2002) by presenting new analytical expressions for the output firing rate for general IF neurons, extending the validity of the results for arbitrarily large correlation magnitude, and by describing the differential effect of correlations on the mean driven or noise dominated firing regimes. Also the details of this novel formalism are given here for the first time. We employ numerical simulations to confirm the analytical solutions and to study the firing response to sudden changes in the input correlations. We expect this formalism to be useful for the study of correlations in neuronal networks and their role in neural processing and information transmission.

1 Introduction

A major problem in neuroscience is to understand the way neurons communicate with each other. Because neurons in the cortex are densely connected and share common inputs (White, 1989; Braitenberg and Schüz, 1991), some degree of correlation between their discharges is unavoidable. Indeed, correlations in the spiking activity of neurons are routinely observed throughout the cortex ((Zohary et al., 1994; deCharms and Merzenich, 1996; Lee et al., 1998; Usrey and Reid, 1999; Bair et al., 2001); for a review see Salinas and Sejnowski (2001); Averbek and Lee (2004)). Correlations could have an important functional role, as the temporal synchronization of neuronal activity has been shown to correlate with particular states of behaving animals (Vaadia et al., 1995; Riehle et al., 1997; Fries et al., 1997; Steinmetz et al., 2000; Fries et al., 2001). From a more traditional point of view, correlations have been considered as a coding dimension independent of the firing rate (deCharms and Merzenich, 1996; Wehr and Laurent, 1999; Laurent, 2001). However it remains still controversial whether correlated activity has a role in coding, or whether its main role is as a gating mechanism of the flow of information in cortical circuits (Salinas and Sejnowski, 2001; Averbek and Lee, 2004).

Before the functional role of correlations can be addressed, a prime question to solve is how correlations affect the firing properties of neurons. Previous work in this direction has revealed that neurons can be very sensitive even to weak correlations in their inputs (Burkitt and Clark, 1999; Feng and Brown, 2000; Salinas and Sejnowski, 2000). However, in most of these studies, only zero time lag correlated inputs (*perfect synchronization*) has been used. This means that when one spike arrives at one presynaptic terminal, another spike is more likely to be found *at the same time* in other

presynaptic terminal. This perfect synchrony is not expected to be exhibited by real neuronal systems, given their finite temporal precision. Instead, synchrony with a non zero time precision τ_c seems to be the realistic case, with $\tau_c \sim 15ms$ in monkey primary auditory cortex (deCharms and Merzenich, 1996), $\tau_c \sim 5ms$ in primary visual cortex of strabismic cats (Fries et al., 1997) (in this case the cross-correlogram is accompanied by an oscillatory pattern), τ_c with very broad values ranging from less than $15ms$ to more than $200ms$ mediating interactions between areas $V1$ and $V2$ in monkeys (Nowak et al., 1999), or $\tau_c \sim 10ms$ in the monkey visual area MT (Bair et al., 2001). In this case, if a spike arrives at time $t = 0$ at a presynaptic terminal, another spike is more, or less, likely than the chance level determined by the firing rate, to arrive within a time τ_c around $t = 0$ at other (or the same) terminal.

We have shown previously (Moreno et al., 2002) that the total current to a neuron generated by exponentially correlated afferent spike trains can be described (among other parameters) by the *correlation time*, τ_c , and the *correlation magnitude*, α (see definitions in Section (3)). Each parameter carries important information about the characteristics of the input correlations (either temporal or intensity information). Intuitively, a short correlation time τ_c means that afferent spikes synchronize within short time windows of size τ_c . Decreasing τ_c will enhance the temporal precision of correlations. The correlation magnitude, α , roughly represents how many spikes are expected above chance in a time window τ_c given that there was a spike centered in that time window. Therefore, it is a measure of the intensity of the correlations. For uncorrelated spike trains $\alpha = 0$, while for positively correlated spike trains $\alpha > 0$, and for negatively correlated $\alpha < 0$. As we will show, the correlation time and magnitude can also be related to the autocorrelograms (ACGs) and cross-correlograms (CCGs) of recorded spike trains. The correlation time measures the typical width of the CCG, while the correlation magnitude is proportional to the area under the CCG curve.

Both τ_c and α can affect the neuron's firing response in complicated ways. Separating their effects was crucial in our previous work (Moreno et al., 2002), where the effects of changing the timescale and the magnitude of the input correlations could be studied independently. In particular, one of the main qualitative results was that, if α is kept constant, neurons are sensitive to input correlations only when the correlation time is shorter than the membrane time constant. ¹.

¹ This mechanism is consistent with *coincidence detection* (Abeles, 1982;

The main problem studied in this paper is schematized in Fig.(1) and can be summarized as follows: What is the effect of the magnitude and the timescale of the input spike correlations on the neuron firing response? We answer this question by addressing consecutively several subproblems. First, after presenting the model (Sec 2), we describe the statistical properties of the afferent spike trains which drive a LIF neuron (Sec 3). The spike trains are characterized in terms of their firing rates, Fano factors, correlation coefficients and correlation timescale, and are assumed to have exponential auto- and cross-correlations. Correlated and uncorrelated Poisson spike trains are just special cases of these. The total current generated by the sum of the spike trains is described up to second order statistics (the two-point correlation function), and shows exponential correlations (Sec 3.2). Second, to solve the difficulties presented by the non-Markovian character of the input statistics, we seek to transform this input into a colored Gaussian input with the same mean and two-point correlation function as those generated by the original current. Two different Markovian stochastic processes that generate this colored Gaussian input are found (Sec 4). Then, we obtain the Fokker-Plank equations (FPEs) associated to each of these two processes and the voltage of the neuron (Secs 4.1 and 4.2). Third, the output firing rate is obtained by solving the FPEs in the limits of short and long values of the correlation timescale compared to the membrane time constant of the neuron (Sec 5). At this point we give a brief summary of the analytical expressions and their ranges of validity (Sec 6 and Table 1). An interpolation is then employed to join the two limits, and the analytical results are compared with numerical simulations (Sec 7.1). Finally, we also show that neurons can track fast changes in input correlations (Sec 7.2). In the discussion section (Sec 8) we summarize the main results and discuss possible applications. Several computational details are provided in a set of appendices.

Some of these results have been previously published in a brief format (Moreno et al., 2002). In the current work we extend the analytical techniques, obtain new results and present a more pedagogical version of our work to facilitate the use of the mathematical expressions as well as the understanding of their derivation. In particular, a more general expression for the output firing rate is found in the presence of exponentially correlated

Bernander et al., 1991; Softky and Koch, 1993; Softky, 1994). Note, however, that these authors consider input spike coincidence detection in the sub-millisecond range, while our results more generally concern the effect of correlation timescale of any size on a neuron with any membrane time constant

input spike trains that is valid for long τ_c and for all positive α (Sec 5.2). If the limit of small α is taken, this new expression becomes that found in (Moreno et al., 2002) in the case of long τ_c , and therefore generalizes and extends the latter for large correlation magnitudes. The effect of input correlations in the mean driven and noise dominated input regimes is found to be different, and those peculiarities are discussed here (Sec 7.1).

2 Model

We consider a LIF neuron with membrane potential $V(t)$ and membrane time constant τ_m . In the absence of input, the voltage decays exponentially toward the resting potential (here $V = 0$). In the presence of synaptic current, $I(t)$, the membrane potential evolves according to the equation

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

In the model, a spike is generated whenever the membrane potential $V(t)$ reaches a threshold value Θ . Following the spike, the potential is reset to a value H , from where, after an absolute refractory period τ_{ref} , the neuron can start integrating the synaptic current again.

We work in the limit of infinitely fast synaptic time constants, in which individual synaptic currents are represented by delta functions. Thus, 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 arrival time of the k -th (l -th) spike from the i -th excitatory (j -th inhibitory) presynaptic neuron, and $N_{E(I)}$ and $J_{E(I)}$ represent, respectively, the number of inputs and the size of the postsynaptic potentials from the excitatory (inhibitory) afferent populations.

We are interested in the case of stationary input statistics, so that the input firing rates do not depend on time (but see our simulation results for the case on non-stationary statistics in Sec. 7.2). Therefore, assuming that the excitatory and inhibitory presynaptic neurons fire at rates ν_E and ν_I respectively, the mean current $\langle I(t) \rangle$ is computed as

$$\mu = \langle I(t) \rangle = N_E J_E \nu_E - N_I J_I \nu_I . \quad (3)$$

This result is independent of the statistics of the afferent spike trains. For example, the mean current generated by correlated or independent Poisson spike trains is exactly the same, provided that the processes are stationary and described by the same firing rates. However, the second-order statistics of the current will be very sensitive to the second order statistical properties of the individual spike trains (e.g., their pair-wise correlations). In the next section we determine the two-point correlation function in terms of the statistical properties of the presynaptic spike trains.

3 Second-order statistical properties of the current

3.1 Auto-correlograms

This section is devoted to the description of the second order statistical properties of each individual spike train impinging on the LIF neuron. In the next section, we will consider the second order statistical properties of pairs of those spike trains. Here, we first define the Fano factor of the spike count of each input train. Then we introduce the auto-correlation function in the case of an exponentially correlated spike train. Finally, we show that the parameters defining the exponential auto-correlation function can be expressed in terms of the firing rate, Fano factor and correlation time of the spike train.

Most theoretical models have considered afferent spike trains (see eq. (2)) as stochastic Poisson processes (see e.g. (Ricciardi, 1977; Tuckwell, 1988; Brunel and Sergi, 1998; Feng and Brown, 2000; Nykamp and Tranchina, 2001; LaCamera et al., 2004; Richardson and Gerstner, 2005)). In this work, we relax this assumption. The Fano Factor is often used to quantify the reliability of neuronal discharge. The Fano factor of the spike count in a time window T is defined as the ratio between the variance of the spike count and the mean number of spikes in that time window, that is,

$$F_N(T) = \frac{\sigma_N^2(T)}{\langle N(T) \rangle} = \frac{\langle (N(T) - \langle N(T) \rangle)^2 \rangle}{\langle N(T) \rangle} , \quad (4)$$

where $N(T)$ is the number of spikes counted in the time window T in each

trial and brackets denote an average over trials. Note that, in practice, the mean and variance can also be computed using a single long spike train (with stationary firing rate) obtained in a single trial, where now the average is obtained using non-overlapping consecutive time windows instead of several trials. In either case, typically the time window T is taken to be large, so that at least tens of spikes are observed on average. A Poisson spike train has a Fano factor equal to one. However, Fano factors calculated from spike trains obtained from electrophysiological recordings *in vivo* usually exceed one, laying in the interval $F_N \sim 1 - 1.5$ throughout the cerebral cortex (Dean, 1981; Softky and Koch, 1993; Albright, 1993; Shadlen and Newsome, 1998; Compte et al., 2003), which is inconsistent with the Poisson hypothesis (see also (Amarasingham et al., 2006)).

Another important second-order statistical property of individual spike trains is the joint probability density of having spikes belonging to that same spike train at two times, t and t' , denoted $P(t, t')$. In fact, from it one can derive any other second-order statistical quantity, such as the Fano factor (see below). For a Poisson spike train with rate ν , $P(t, t')$ is a delta function at zero-time lag and flat otherwise, as

$$P_{Poisson}(t, t') = \nu\delta(t - t') + \nu^2. \quad (5)$$

The delta function at $t = t'$ serves to define $P(t, t')$ at all times; trivially, the probability density of having a spike at time t and a spike at time $t' = t$ is just the delta multiplied by the spike rate in that train, i.e., $\nu\delta(t - t')$; in other words, the presence of one spike is informative of the presence of a spike at that time (the same spike). For non-zero time lags ($t \neq t'$), this probability is just the product of the probability densities of having spikes at two different times, that is, ν^2 . For a general spike train we define the autocorrelation function as the quantity

$$C(t, t') = P(t, t') - \nu^2, \quad (6)$$

that is, the joint probability density of having spikes at times t and t' , from which the probability of finding them by chance (i.e., the rate to the square) is subtracted.

While Poisson trains have an autocorrelation with a single delta function at time lag zero and zero otherwise (i.e. $C_{Poisson}(t, t') = \nu\delta(t - t')$), auto-correlograms obtained from electrophysiological recordings show a decaying peak at non-zero time lags (disregarding refractory effects) sometimes

together with a damped oscillatory pattern. A centered decaying peak in an auto-correlogram means that spikes tend to occur close together in time, forming groups of several spikes. Experimental auto-correlograms with a single peak and without oscillations can be fitted to an exponential function (e.g. Bair et al. (2001)). We therefore consider stochastic spike trains with exponential autocorrelations with timescale τ_c

$$\begin{aligned}
C_p(t, t') &\equiv \left\langle \left(\sum_k \delta(t - t_i^k) - \nu_p \right) \left(\sum_{k'} \delta(t' - t_i^{k'}) - \nu_p \right) \right\rangle \\
&= \left\langle \sum_{k, k'} \delta(t - t_i^k) \delta(t' - t_i^{k'}) \right\rangle - \nu_p^2 \\
&= \nu_p \delta(t - t') + \nu_p \left(\frac{F_p - 1}{2\tau_c} \right) e^{-\frac{|t-t'|}{\tau_c}}, \tag{7}
\end{aligned}$$

as illustrated in Fig.(2 B). Since we assume that the input statistics is stationary, the input firing rates are time independent and the auto-correlation function only depends on time through the quantity $|t - t'|$, Here $p = E, I$; ν_p and F_p are the firing rate and the Fano factor of the spike count (for infinitely long time windows) of the individual trains coming from population p ². The connected two-point correlation function defined above is the joint probability density of finding one spike at time t and another at t' within the same spike train, from where the probability of observing them by chance, ν_p^2 , is subtracted. Note that this function has two contributions: a delta function at zero time lag, coming from the fact that spikes are point events, and an exponential dependence measuring the excess probability of finding a spike at t' when it is known that there is another spike at t . While normally spikes in the same train are positively correlated ($F_N > 1$), the auto-correlogram in eq. (7) also describes uncorrelated ($F_N = 1$, Poisson) and negatively correlated spikes ($F_N < 1$). With the parameterization we have chosen, fixing the Fano factor and changing the correlation time does not keep fixed the amplitude of the exponential term in eq. (7). However, this choice allows us to fix the variance of the spike count in a long time window for each individual spike train while varying the timescale of its correlations. To make this clearer,

²For renewal spike trains, the Fano factors in the above equations are related to the coefficients of variation of their inter-spike-intervals, CV_p , as $F_p = CV_p^2$. Note nevertheless that our formalism does not require that afferent spike trains are renewal.

consider the total number of presynaptic spikes arriving from the spike train i of the population p during a time window T , which is written as

$$N(T) = \int_0^T dt \sum_k \delta(t - t_i^k). \quad (8)$$

Notice that, since the arrival times t_i^k are random in such a way that the train has the autocorrelation of eq. (7), the number $N(T)$ is a random variable. Its mean value is

$$\langle N_p(T) \rangle = \left\langle \int_0^T dt \sum_k \delta(t - t_i^k) \right\rangle = \nu_p T, \quad (9)$$

and its variance can be calculated using the autocorrelation defined in eq. (7) as (Renart et al., 2007)

$$\begin{aligned} \sigma_{N,p}^2(T) &= \left\langle \int_0^T dt \int_0^T dt' \sum_{k,k'} \delta(t - t_i^k) \delta(t' - t_i^{k'}) \right\rangle - \langle N_p(T) \rangle^2 \\ &= \int_0^T dt \int_0^T dt' C_p(t, t') \\ &= \nu_p T + \nu_p (F_p - 1) (T - \tau_c (1 - e^{-T/\tau_c})). \end{aligned} \quad (10)$$

Therefore, the variance of the spike count grows linearly with T for long windows $T \gg \tau_c$, where it takes the value

$$\sigma_{N,p}^2(T) = F_p \nu_p T. \quad (11)$$

(see Fig.(2 C)). Thus, fixing only the Fano factor in the autocorrelation function keeps fixed the variance in the spike count for long T , as this variance is independent of τ_c . Changing τ_c does not alter the total spike count fluctuations, only the temporal precision in which they occur. Notice that the inclusion of the Fano factor in the autocorrelation function, eq. (7), is consistent with its definition for long T in eq. (4). Notice also from eq. (10), that the variance of the spike count is $\nu_p T$ for short $T \ll \tau_c$, and therefore the afferent spike train looks like a Poisson spike train when it is sampled during brief time windows. However, as soon as T is comparable with the correlation time, the variance of the spike count starts to take into account the temporal correlations in the spike train, and when T becomes very large, all effects are included and the variance is $F_p \nu_p T$, eq. (11) (see Fig.2). We

will show below that, for the LIF neuron we are considering, whether the input is seen as having significant temporal correlations or not depends on how the timescale of these correlations compares to the neuron’s membrane time constant.

3.2 Cross-correlograms

We have also considered the possibility that spikes in different trains are correlated. When the activity of two neighbouring neurons is recorded, the cross-correlogram computed from their discharges can sometimes present a single peak with or without damped oscillations (e.g. (Perkel et al., 1967; Aersten et al., 1989; deCharms and Merzenich, 1996)). A prominent peak at zero time lag means that the two neurons tend to fire synchronously, while if a dip is observed, when one neuron fires the other is more likely to be silent. Very often, the cross-correlograms can be approximated by an exponential function (e.g. (deCharms and Merzenich, 1996; Bair et al., 2001)) The cross-correlogram is therefore modeled here as an exponential,

$$\begin{aligned}
C_{pq}(t, t') &\equiv \left\langle \left(\sum_{k_p} \delta(t - t_i^{k_p}) - \nu_p \right) \left(\sum_{k_q} \delta(t' - t_j^{k_q}) - \nu_q \right) \right\rangle \\
&= \left\langle \sum_{k_p, k_q} \delta(t - t_i^{k_p}) \delta(t' - t_j^{k_q}) \right\rangle - \nu_p \nu_q \\
&= \sqrt{\nu_p \nu_q} \left(\frac{\rho_{pq} \sqrt{F_p F_q}}{2\tau_c} \right) e^{-\frac{|t-t'|}{\tau_c}}, \tag{12}
\end{aligned}$$

where $C_{pq}(t, t')$ is the two-point correlation function between the trains (i, j) in populations p and q ($p, q = E, I$). This cross-correlation function is illustrated in Fig.(3 B). As in the case of the autocorrelation defined in eq. (7), the two-point correlation function expresses the probability density of finding a spike of a train in population p at time t along with a spike of a train in population q at time t' , from which the probability density of finding them by chance, $\nu_p \nu_q$, is subtracted. The magnitude of the cross-correlations is determined by the correlation coefficients ρ_{pq} of the spike counts (see its definition in eq. (14)). For the sake of simplicity, we take all the correlations in the problem to have the same time constant τ_c .

To better understand the effects of cross-correlations on the input statistics, we calculate the covariance between the count of spikes emitted by the neuron i from population p and the count of spikes emitted by the neuron j from population q as an integral of the cross-correlation function, eq. (12), as

$$\begin{aligned}
\langle (N_p(T) - \langle N_p(T) \rangle) (N_q(T) - \langle N_q(T) \rangle) \rangle &= \langle N_p(T) N_q(T) \rangle - \nu_p \nu_q T^2 \\
&= \left\langle \int_0^T dt \int_0^T dt' \sum_{k_p, k_q} \delta(t - t_i^{k_p}) \delta(t' - t_j^{k_q}) \right\rangle - \nu_p \nu_q T^2 \\
&= \int_0^T dt \int_0^T dt' C_{pq}(t - t') \\
&= \sqrt{\nu_p \nu_q} \left(\rho_{pq} \sqrt{F_p F_q} \right) \left(T - \tau_c (1 - e^{-T/\tau_c}) \right). \tag{13}
\end{aligned}$$

This covariance measures the correlation in the spike count fluctuations during a time T from two presynaptic spike trains. Notice that for T much shorter than the correlation time, this covariance is zero, that is, the spike counts of the two neurons become independent. This is true because for short T the spike trains look like uncorrelated Poisson trains. However, for time windows which are longer than the correlation time, the covariance is non-zero and approaches a linear behavior. This covariance as a function of the integration window is represented in Fig.(3 C).

The correlation coefficient is defined as the ratio of the covariance and the product of the deviations in the spike counts of both neurons, as

$$\rho_{pq} = \frac{\langle (N_p(T) - \langle N_p(T) \rangle) (N_q(T) - \langle N_q(T) \rangle) \rangle}{\sigma_{N_p}(T) \sigma_{N_q}(T)} \tag{14}$$

for long T . Notice from eq. (13) that the inclusion of the correlation coefficient in the cross-correlation, eq. (12), is consistent with the above definition. Changing the correlation time in the cross-correlation, eq. (12), changes its amplitude, but not the correlation coefficient between the two spike trains. The Fano factors appear in eq. (12) because the time integral of the cross-correlation has to be zero if one of the trains does not have spike count fluctuations ($F_N = 0$).

3.3 Writing the statistical properties of the total current

The two-point correlation function of the total afferent current, eq. (2), is defined as

$$C_{current}(t, t') \equiv \langle (I(t) - \langle I(t) \rangle)(I(t') - \langle I(t') \rangle) \rangle, \quad (15)$$

where the mean current $\langle I(t) \rangle$ is calculated as in eq.(3). The correlation function should take into account both the auto- and cross-correlations of the spike trains in the E and I populations given in eqs. (7, 12). In Fig. (4) we depict a diagram with the correlations present in the E and I neurons, whose spikes trains impinge on the same target neuron. There are N_E excitatory neurons firing at rate ν_E and N_I inhibitory neurons with rate ν_I . We assume that only a fraction f_{EE} (f_{II}) of the N_E (N_I) excitatory (inhibitory) neurons are correlated with other neurons within the same population, with a correlation coefficient ρ_{EE} (ρ_{II}). Also only a fraction f_{EI} of the excitatory neurons are correlated with a fraction f_{EI} of the inhibitory neurons, with a correlation coefficient $\rho_{EI} = \rho_{IE}$.

Then, the correlation function of the current, eq. (15), contains several contributions:

$$\begin{aligned} C_{current}(t, t') = & J_E^2 N_E C_E(t - t') + J_I^2 N_I C_I(t - t') \\ & + J_E^2 f_{EE} N_E (f_{EE} N_E - 1) C_{EE}(t - t') + J_I^2 f_{II} N_I (f_{II} N_I - 1) C_{II}(t - t') \\ & - 2 J_E J_I f_{EI} f_{IE} N_E N_I C_{EI}(t - t'). \end{aligned} \quad (16)$$

In this expression, the two first terms come from the auto-correlations of the spike trains in the E and I populations. The third and fourth terms take into account the cross-correlation between spike trains in the same E or I population. They are positive because both E and I inputs contribute positively to enhance fluctuations. The last term incorporates the cross-correlation between spike trains one from the E population and the other from the I neuronal population, and it is negative. Indeed, positive correlations between E and I neurons always reduce synaptic fluctuations because arrival of an excitatory spike can be cancelled out by arrival of another inhibitory spike, and this happens with higher than chance probability. Therefore, the effect of correlations within E or I neurons is always to increase $C_{current}(t, t')$ in the direction of their cross-correlation functions, $C_{EE}(t-t')$ and $C_{II}(t-t')$, whereas

the effect of correlations between E and I spike trains is always to lower the current correlation function in an amount proportional to $C_{EI}(t - t')$.

Using the choices given in eqs. (7, 12), the two-point correlation function of the total input current to the neuron can be written as

$$C_{current}(t, t') = \sigma_w^2 \left[\delta(t - t') + \frac{\alpha}{2\tau_c} e^{-\frac{|t-t'|}{\tau_c}} \right] , \quad (17)$$

where we call σ_w^2 the white noise variance, and α the *correlation magnitude*. They are expressed in terms of the model parameters as

$$\begin{aligned} \sigma_w^2 &= J_E^2 N_E \nu_E + J_I^2 N_I \nu_I \\ \alpha \sigma_w^2 &= J_E^2 \nu_E [(F_E - 1) + f_{EE} (f_{EE} N_E - 1) F_E \rho_{EE}] \\ &\quad + J_I^2 N_I \nu_I [(F_I - 1) + f_{II} (f_{II} N_I - 1) F_I \rho_{II}] \\ &\quad - 2 J_E J_I f_{EI} f_{IE} N_E N_I \sqrt{\nu_E \nu_I} \sqrt{F_E F_I \rho_{EI}} . \end{aligned} \quad (18)$$

We define the total variance of the current, σ_{eff}^2 , as the sum of the white noise variance and the variance generated by correlations, $\alpha \sigma_w^2$, that is,

$$\sigma_{eff}^2 = \sigma_w^2 (1 + \alpha) . \quad (19)$$

The sign of the correlation magnitude determines the sign of the correlations. If $\alpha > 0$, the current has *positive correlations*, while if $\alpha < 0$, the current has *negative correlations*. The minimum physically possible value for the correlation magnitude is $\alpha = -1$ ³. If $\alpha = 0$, the current is uncorrelated. Notice that σ_{eff}^2 is very sensitive to the fractions of correlated input trains, as these fractions are multiplied by the number of connections from each population to the square, which typically are of the order of $10^3 - 10^4$. Also, from eq. (18) it is possible to see that increasing the correlations between

³For large enough T ($T \gg \tau_c$), the variance of the integrated current, or accumulated charge $Q(t) = \int_0^T dt I(t)$, is calculated as

$$Var[Q(T)] = \int_0^T dt \int_0^T dt' C_{current}(t, t') = \sigma_{eff}^2 T . \quad (20)$$

Therefore, the variance of the current is just the proportionality factor σ_{eff}^2 . Notice that since the variance of the current is non-negative, the correlation magnitude has a lower bound at $\alpha = -1$. Lower values are not physically possible because the variance of a real-valued stochastic variable cannot be negative.

excitatory or inhibitory neurons (either increasing ρ_{EE} or ρ_{II}) enhances the total variance, whereas correlations between excitatory-inhibitory pairs (ρ_{EI}) always decrease it (Salinas and Sejnowski, 2000).

The parameters τ_c and α which appear in the definition of the correlation function of the current, eq. (17), fully characterize both the temporal range and the intensity of the correlations relative to the white noise variance σ_w^2 . Although it is important to understand the effect of these two parameters on the neuronal firing response separately, previous studies have not studied this problem. For instance, in Feng and Brown (2000) only the case $\tau_c = 0$ is considered, which precludes the characterization of the temporal scale of the correlations. On the other hand, Salinas and Sejnowski (2000) have changed simultaneously the values of τ_c and α in their simulations.

3.4 The sum of a large number of independent non-Poisson spike trains is not Poisson

One point deserves clarification at this moment. It refers to the way many simultaneous spike trains add up. The sum of many independent spike trains has been commonly approximated as a Poisson process (e.g. (Daley and Vere-Jones, 1988; Amit and Brunel, 1997a)). Although this is in some cases a good approximation, it is worth emphasizing that the sum of many independent point processes is not, in general, Poisson. Indeed, the conditions for the sum-process to be truly Poisson are rather restricted (see e.g., Daley and Vere-Jones (1988)). In particular, one of the conditions implies that, on any time interval, only one event can be observed from each individual point process. However, this is only expected to be a good approximation for time windows much shorter than the typical inter-spike-interval of each neuron. In general, a neuron will receive one, two or more spikes from the same presynaptic neuron before it fires, not just at most one spike, as the Poisson approximation strictly requires.

As expected from the rules of probability, adding up many independent spike trains results in a global spike train with an autocorrelation function which has exactly the same functional form as those of the individual trains (note, however, that higher order properties are not necessarily conserved, i.e., the sum of many renewal processes may not be renewal). In particular, when N independent spike trains with an autocorrelation $C(t, t')$ are added, the summed train has an autocorrelation $N \times C(t, t')$ ((Moreno et al., 2002),

see also eq. (16) with $C_{EE(II,EI)} = 0$ and $J_{E(I)} = 1$). We further noted that even in the diffusion limit (i.e. $N \rightarrow \infty$), when the individual firing rates ν are renormalized by ν/N to yield a finite two-point correlation function, the auto-correlation function of the total input has exactly the same shape as the auto-correlation function of the individual spike trains. Later works have also used this property (Renart et al., 2007; Lindner, 2006; Cateau and Reyes, 2006; Doiron et al., 2006), which is relevant to describe the temporal aspects of correlations in networks of spiking neurons.

Here we exemplify the above result using the expression for the correlation function of the current, eqs. (17-18). It is easy to see that the total current will show temporal correlations beyond the trivial delta function at zero time lag whenever α is different from zero and τ_c is not infinity. If the afferent spike trains are independent ($\rho = 0$) but they have exponential auto-correlations, as those in eq. (7), then α will be different from zero (see eq. (18)). This will happen for any choice of the number of connections and synaptic strengths (different from zero). Therefore, no matter which choices of the parameters are taken, the correlation-function of the total current can never correspond to a Poisson process with a larger rate, since an input Poisson process will produce a correlation function equal to $C_{current}(t, t') = \sigma_w^2 \delta(t - t')$. The above argument does not depend on the condition that the correlations are exponential, but rather the same conclusion can be achieved from eq. (16) using any plausible autocorrelation function $C_E(t, t')$ and $C_I(t, t')$ different from a delta function (i.e., different from the autocorrelation function of a Poisson process).

3.5 When the current can be approximated by a Gaussian current

We have described the statistical properties of the total current, $I(t)$, generated by correlated spike trains. However, the firing response of a neuron receiving that current is not yet completely determined by the mean and two-point correlation function of the current alone, eqs. (17-18). These quantities describe the statistical properties of a stationary current up to second order, but higher order statistics in the input could also play a role in shaping the firing response of the neuron. However, if the current $I(t)$ can be approximated by a Gaussian process, then, the current would be fully described by its mean and two-point correlation function. In fact, Gaussianity

naturally holds when the neuron is receiving a large barrage of uncorrelated spikes per second each one inducing a membrane depolarization J very small compared to the distance between the threshold and reset potentials, i.e., $J/(\Theta - H) \ll 1$ (Ricciardi, 1977). When inputs are correlated, the net effect of correlations is to increase effectively the size of the unitary depolarization (for positive correlations), since two or more spikes are more likely to occur together in time. We have estimated this renormalization in the size of J and determine that for the Gaussian approximation to be valid with correlated input spike trains the condition

$$\frac{JF}{(\Theta - H)}(1 + fN\rho) \ll 1 \quad (21)$$

should hold. This is a heuristic formula, and it is explained qualitatively as follows. The worst condition in the presence of correlations occurs when the correlation time τ_c is zero, that is, when there is some chance that two or more spikes arrive at the same time, increasing the effective size of each spike and worsening the Gaussian approximation. One can estimate the mean number of spikes arriving together to be $F(1 + fN\rho)$, which grows with the variability of the spike trains, the number of correlated pairs and their correlation coefficient. As long as this number multiplied by J is small compared to $\Theta - H$, i.e., eq.(21), the Gaussian approximation is expected to be appropriate. This indicates that if either F , fN or ρ increases too much, the Gaussian limit will be broken. When condition (21) is largely broken, as in (Kuhn et al., 2003), the Gaussian approximation is no longer valid. In particular in the limit of large N , it should hold that $\rho \sim 1/fN$, so the correlation coefficients cannot remain finite as the size of the population of neurons with significant cross-correlations increases. If condition (21) is satisfied, the input current in our problem can be described as a Gaussian stochastic current fully defined in terms of the mean $\mu = J_E N_E \nu_E - J_I N_I \nu_I$, the variance σ_w^2 , the correlation magnitude (α) and correlation time (τ_c), as expressed in eq. (17).

3.6 Choosing the connectivity and correlation parameters

Because we are dealing with a model with many free parameters (see eq. (18)), here we fix most of them or make choices within a range of real-

istic values. A single neuron receives typically $N_E \sim 5000 - 60000$ excitatory connections from other neurons (Cragg, 1967; DeFelipe and Fariñas, 1992). This accounts for 80 per cent of the total number of synapses; the remaining 20 per cent corresponds to inhibitory synapses (Abeles, 1991). The dynamical range of cortical neurons lies in the interval $\nu \sim 0 - 200Hz$ (Albright, 1993) although lower rates are much more probable than higher ones (Rolls and Treves, 1998). Synaptic strengths are between $J = 0.1 - 1mV$ ((Amit and Brunel, 1997a); see the references therein). Assuming a threshold of $20mV$ above the resting potential of the neuron, these unitary events represent a fraction in the range $J \sim 5 \cdot 10^{-3} - 10^{-2}$ of the total path to be travelled from rest to firing threshold.

Fano factors of the spike count lying in the interval $1 - 1.5$ reveal higher irregularity in the neuronal discharges than that expected from Poisson trains (Dean, 1981; Softky and Koch, 1993; Shadlen and Newsome, 1998; Albright, 1993; Stevens and Zador, 1998; Compte et al., 2003).

The timescale of correlations varies from a few to several hundred milliseconds, $\tau_c \sim 1 - 100ms$ (Ts'o et al., 1986; Gochin et al., 1991). For instance, in (deCharms and Merzenich, 1996) the correlated activity of pairs of neurons in primary auditory cortex in cats was recorded. The mean half-width at half-height of the cross-correlograms peaks computed from these pairs was $\sim 10ms$, which corresponds to a correlation time scale $\tau_c = 10ms/\ln 2 \sim 15ms$.

Zohary et al. (1994) have reported correlation coefficients of $\rho = 0.12$ between neighbouring cells in the middle temporal visual area (MT, or V5). If any pair of neurons in a group of thousand units were correlated with such a magnitude and projected to a same target neuron, the magnitude of the input fluctuations would be unrealistically large (see eq. (18)). In fact, the value $\rho = 0.12$ only holds for units within local circuits, because it is known that more distant neurons display much smaller correlation coefficients (Lee et al., 1998). Although a “mean” correlation coefficient could have been considered⁴, we have taken into account the heterogeneity of pairwise correlations observed in the cortex by assuming that only a fraction f_{pq} of neurons between populations p and q are indeed correlated with the same correlation coefficient ρ_{pq} . This fraction could represent the portion of presynaptic neurons located in the surroundings of the target neuron, and thus embedded in the

⁴A mean correlation coefficient can be obtained by averaging the ρ of each pair of neurons: $\langle \rho \rangle = \int f(\rho)d\rho$.

same local circuits as this neuron, or a far neuronal population displaying correlations between its units and projecting to the same target neuron. To bound the effects of input correlations, we assume that around one per cent of the presynaptic neurons can be correlated. Such a small value of f_{pq} still produces a large effect on the correlation magnitude (see eq. (18)), as will be also clear in section (7.2).

The values of μ , σ_w^2 and α therefore lie within rather broad intervals. As an example of the typical values they can take, if a neuron receives $N_E = 10^4$ excitatory connections, $N_I = 2 \cdot 10^3$ inhibitory connections, with synaptic strengths $J_E = 5 \cdot 10^{-3}$ and $J_I = 2 \cdot 10^{-2}$ (in units of the threshold), and they are firing at $\nu_E = \nu_I = 5Hz$, then $\mu = 50Hz$ and $\sigma_w^2 = 5.3Hz$. Assuming that there are only correlations between pairs of neurons in the E population ($\rho_{EI} = \rho_{II} = 0$), being $f_{EE} = 0.1$ the fraction of those which are correlated, then $\alpha = 0.85$ if $F_E = F_I = 1.5$ and the correlation coefficient is $\rho_{EE} = 0.01$, or $\alpha = 4$ if $\rho_{EE} = 0.1$. When we present results from numerical simulations, the parameter values considered will be of the order of the ones mentioned above.

4 Two ways of transforming the non-Markovian problem into a Markovian one

As we have explained in the introduction, we aim at calculating the output firing rate of a LIF neuron receiving a correlated input as described in the previous sections. The main technical problem to study the response properties of a neuron driven by correlated inputs analytically is that the stochastic process defined by eq. (1) with a current having correlations as in eq. (17) is non-Markovian, that is, the time derivative of the membrane potential at each time depends on the past history of the afferent current, not only on its present value. This fact complicates the solution of the problem. However, the process defined in eqs. (1, 17) can be expressed in a Markovian way by generating the current $I(t)$ with the help of an Ornstein-Uhlenbeck process (Moreno et al., 2002). The stochastic current $I(t)$ generated in this way displays exactly the same exponential correlations as eq. (17). This duplicates the number of variables, but puts the problem in a suitable form (see eqs. (22, 23) and (32, 33) below). We have found two different ways of representing the correlated Gaussian current $I(t)$ satisfying eq. (17). They

only differ in the values of α for which they hold. While one of them is more general because α can take any physical value (including both positive and negative correlations), the other is simpler, although it can be only used for $\alpha > 0$ (positive correlations).

4.1 The first Representation for the dynamics of $I(t)$

The first representation of the current $I(t)$ that we discuss here generates both positive ($\alpha > 0$) and negative ($\alpha < 0$) correlations. It has the form

$$I(t) = \mu + \sigma_w \eta(t) + \sigma_w \frac{\beta}{\sqrt{2\tau_c}} z(t) \quad (22)$$

$$\dot{z}(t) = -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}} \eta(t) , \quad (23)$$

where $\eta(t)$ is a white noise random process with mean zero and unit variance (i.e., $\langle \eta(t) \rangle = 0$ and $\langle \eta(t)\eta(t') \rangle = \delta(t - t')$), $\beta = \sqrt{1 + \alpha} - 1$ and $z(t)$ is an auxiliary colored random process which obeys the Ornstein-Uhlenbeck process (23) with the same white noise $\eta(t)$ (see, e.g., (Risken, 1989)).

It is easy to check that the current defined in eqs. (22, 23) generates a Gaussian waveform with mean $\langle I(t) \rangle = \mu$ and exponential correlations as in eq. (17). Defining $i(t) = (I(t) - \mu)/\sigma_w$ we have

$$\begin{aligned} \langle i(t) i(t') \rangle &= \left\langle \left[\eta(t) + \frac{\beta}{\sqrt{2\tau_c}} z(t) \right] \left[\eta(t') + \frac{\beta}{\sqrt{2\tau_c}} z(t') \right] \right\rangle = \delta(t - t') + \\ &\frac{\beta}{\sqrt{2\tau_c}} \langle \eta(t) z(t') \rangle + \frac{\beta}{\sqrt{2\tau_c}} \langle \eta(t') z(t) \rangle + \frac{\beta^2}{2\tau_c} \langle z(t) z(t') \rangle . \end{aligned} \quad (24)$$

Assuming that $t' > t$ without loss of generality (because $\langle i(t) i(t') \rangle$ is symmetric in the steady state), the third term on the right side of the eq. (24) vanishes. The second and fourth terms are calculated using the solution of the stochastic equation, eq. (23),

$$z(t) = \sqrt{\frac{2}{\tau_c}} e^{-t/\tau_c} \int_0^t ds e^{s/\tau_c} \eta(s) , \quad (25)$$

with the initial condition $z(0) = 0$. We find that in the stationary state ($t, t' \rightarrow \infty, t' - t = \text{constant} > 0$)

$$\begin{aligned}\langle \eta(t)z(t') \rangle &= \sqrt{\frac{2}{\tau_c}} e^{-(t'-t)/\tau_c} \\ \langle z(t)z(t') \rangle &= e^{-(t'-t)/\tau_c} .\end{aligned}$$

Using these identities, the correlation function of the current $I(t)$ defined in eqs.(22-23), denoted $C_{current}(t, t')$, can be written as

$$\begin{aligned}C_{current}(t, t') &\equiv \langle (I(t) - \mu)(I(t') - \mu) \rangle \\ &= \sigma_w^2 \left[\delta(t - t') + \frac{\beta(2 + \beta)}{2\tau_c} e^{-\frac{|t-t'|}{\tau_c}} \right] ,\end{aligned}\quad (26)$$

from where one sees that the correlation magnitude α is related to the new parameter β by $\alpha = \beta(2 + \beta)$, an equation which has two independent solutions, $\beta = \pm\sqrt{1 + \alpha} - 1$, both equally valid. We have chosen $\beta = \sqrt{1 + \alpha} - 1$. Remember that α has a lower bound in -1 , which is obtained with $\beta = -1$. For each solution there is a one-to-one mapping from $\alpha \in [-1, +\infty)$ to β , and thus, all physically realizable positive and negative correlations are included in this formalism.

The joint process defined by eqs. (1, 22, 23) is Markovian and driven by white noise. Thus, the problem of finding the output firing rate can be formulated according to its associated stationary Fokker-Planck equation (FPE) (Risken, 1989). The system of eqs. (1, 22, 23) can be simplified by the linear transformation

$$V = \mu\tau_m + \sigma_w \sqrt{\frac{\tau_m}{2}} x \quad (27)$$

to obtain the set of stochastic equations

$$\begin{aligned}\dot{x}(t) &= -\frac{x(t)}{\tau_m} + \sqrt{\frac{2}{\tau_m}} \eta(t) + \frac{\beta}{\sqrt{\tau_m \tau_c}} z(t) \\ \dot{z}(t) &= -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}} \eta(t) .\end{aligned}$$

The FPE associated to these two equations is derived in detail in Appendix B, and is given by

$$[L_x + \frac{L_z}{k^2} + \frac{2}{k} \frac{\partial}{\partial x} (\frac{\partial}{\partial z} - \frac{\beta z}{2})] P_\beta(x, z) = -\tau_m \delta(x - \sqrt{2}\hat{H}) J_\beta(z) , \quad (28)$$

where the differential operator L_u is defined as $L_u = \frac{\partial}{\partial u} u + \frac{\partial^2}{\partial^2 u}$, and $k \equiv \sqrt{\tau_c/\tau_m}$. Besides, $\hat{H} = \frac{H - \mu\tau_m}{\sigma_w \sqrt{\tau_m}}$ and $\hat{\Theta} = \frac{\Theta - \mu\tau_m}{\sigma_w \sqrt{\tau_m}}$. The true reset and threshold values in the new variable x are $\sqrt{2}\hat{H}$ and $\sqrt{2}\hat{\Theta}$, respectively. The function $P_\beta(x, z)$ is the steady state probability density of having the neuron in the state (x, z) . Since the problem cannot be solved exactly as in the one-dimensional diffusion case (see e.g. (Ricciardi, 1977; Risken, 1989)), we have used a perturbative expansion of the FPE in powers of $k^{-1} = \sqrt{\tau_m/\tau_c}$.

A key quantity is the escape probability density flux at fixed z , $J_\beta(z)$. Associated to the FPE (28) there is a probability density vector flux $\vec{J}_\beta(x, z)$ defined at each point on the plane (x, z) (Risken (1989), Chapter 6, pag. 133). It measures the direction and the intensity of the probability density flux at each point (x, z) . For our FPE it has the expression

$$\vec{J}_\beta(x, z) = \frac{1}{\tau_m} \left[-\frac{\partial}{\partial x} - x - \frac{1}{k} \left(\frac{\partial}{\partial z} - \beta z \right) , \quad -\frac{1}{k^2} \left(\frac{\partial}{\partial z} + z \right) - \frac{1}{k} \frac{\partial}{\partial x} \right] P_\beta(x, z) . \quad (29)$$

The probability density flux satisfies the so-called continuity equation

$$\vec{\nabla} \cdot \vec{J}_\beta(x, z) + \tau_m \delta(x - \sqrt{2}\hat{H}) J_\beta(z) = 0 , \quad (30)$$

where $\vec{\nabla} = [\frac{\partial}{\partial x}, \frac{\partial}{\partial z}]$ is the divergence operator. Eq. (30) is equivalent to the FPE (28), and expresses the conservation of the total probability over time. The escape probability density flux $J_\beta(z)$ is just the x -component of the probability density flux (29) evaluated at threshold:

$$J_\beta(z) = \frac{1}{\tau_m} \left(-\frac{\partial}{\partial x} - x - \frac{1}{k} \left(\frac{\partial}{\partial z} - \beta z \right) \right) P_\beta(x, z) |_{x=\sqrt{2}\hat{\Theta}} . \quad (31)$$

The escape probability density flux appears in eq. (28) as a source term representing the reset effect: whenever the potential V reaches the threshold Θ , it is reset to the value H with the same z distribution that it had when it escaped. This holds because the particular value of z at the moment of the generation of each spike has to be conserved for the next inter-spike interval since, as opposed to V , z is not reset after an action potential.

Crucially, this self-consistency condition complicates the solution of the FPE (28). The escape probability density flux in eq. (31) is exact if $\tau_{ref} = 0$ (or approximately if $\tau_c \gg \tau_{ref}$, because in this case the variable z has slow dynamics and therefore its probability distribution at a time τ_{ref} after the emission of an output spike is very similar to its distribution at the moment of the spike).

Let us notice that this first representation of $I(t)$ can be used not only for analytical calculations but also for the numerical generation of exponentially correlated currents, as it is shown in Fig. (5), where we show the exponential two-point correlation function of a current $I(t)$ generated numerically by eqs. (22, 23) and that predicted by eq. (26). Additionally, in a later section this representation will be employed in the numerical analysis of the response of LIF neuron to negative and positive correlations (Sec 7).

4.2 The second Representation for the dynamics of $I(t)$

An afferent current $I(t)$ with non-negative exponential correlations obeying eq. (17) can also be generated by the set of equations

$$I(t) = \mu + \sigma_w \eta(t) + \sigma_w \sqrt{\frac{\alpha}{2\tau_c}} y(t) \quad (32)$$

$$\dot{y}(t) = -\frac{y}{\tau_c} + \sqrt{\frac{2}{\tau_c}} \zeta(t). \quad (33)$$

Here $\eta(t)$ and $\zeta(t)$ are two independent white noise processes with mean zero and unit variance. The two-point correlation of $I(t)$ can be calculated as in eq. (24), with the exceptions that β in eq. (24) is replaced by $\sqrt{\alpha}$ and the two white noises are not correlated. Then, only the terms analogous to the first and fourth terms in eq. (24) are nonzero. Because $\sqrt{\alpha}$ is a real number, the correlation magnitude α has to be positive in this representation.

From the set of eqs. (1, 32, 33) and making the linear transformation defined in eq. (27) we obtain the FPE (the derivation is similar to the one presented in Appendix B)

$$\left[L_x + \frac{L_y}{k^2} - \frac{\sqrt{\alpha} y}{k} \frac{\partial}{\partial x} \right] P_\alpha(x, y) = -\tau_m \delta(x - \sqrt{2} \hat{H}) J_\alpha(y). \quad (34)$$

The linear differential operator L_u has been defined as in Sec. 4.1, and again $k \equiv \sqrt{\tau_c/\tau_m}$. As in the previous representation, the escape probability

density flux $J_\alpha(y)$ acts as a source term injecting current at the reset potential at the same rate and with the same distribution in y as when it escaped (here we have to assume that $\tau_{ref} = 0$, or $\tau_c \gg \tau_{ref} = 0$). It represents the probability current in the direction of x evaluated at threshold. The probability density vector flux for this FPE is

$$\vec{J}_\alpha(x, y) = \frac{1}{\tau_m} \left[-\frac{\partial}{\partial x} - x - \frac{\sqrt{\alpha}y}{k} , -\frac{1}{k^2} \left(\frac{\partial}{\partial y} + y \right) \right] P_\alpha(x, y) . \quad (35)$$

Its continuity equation is

$$\vec{\nabla} \cdot \vec{J}_\alpha(x, y) + \tau_m \delta(x - \sqrt{2}\hat{H}) J_\alpha(y) = 0 , \quad (36)$$

equivalent to the FPE (34), and the escape probability density flux is defined as

$$J_\alpha(y) = \frac{1}{\tau_m} \left(-\frac{\partial}{\partial x} - x - \frac{\sqrt{\alpha}y}{k} \right) P_\alpha(x, y) |_{x=\sqrt{2}\hat{\Theta}} , \quad (37)$$

The FPE (34) will be useful for finding a perturbative solution to the first passage time problem in powers of $k = \sqrt{\tau_c/\tau_m}$, that is, for short τ_c . We have found this representation especially useful for this purpose, since this limit is harder to obtain from the first representation.

4.3 Conditions over the probability density distribution and probability density flux

For both representations of exponential correlations, the probability density and the escape probability density flux must be determined such that they obey the set of conditions:

1. Normalization of the probability density,

$$\tau_{ref} \nu_{out} + \int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx \int_{-\infty}^{\infty} dw P_r(x, w) = 1 \quad (38)$$

2. Threshold vanishing condition,

$$P_r(\sqrt{2}\hat{\Theta}, w) = 0 \quad (39)$$

3. The output firing rate is given by

$$\nu_{out} = \int_{-\infty}^{\infty} dw J_r(w). \quad (40)$$

4. The escape probability density flux has the form

$$J_r(w) = -\frac{1}{\tau_m} \frac{\partial}{\partial x} P_r(x, w)|_{x=\sqrt{2}\hat{\Theta}} \quad (41)$$

where $r = \alpha, \beta$ is the representation label, and w stands for both z and y . Condition (38) is a normalization condition stating that with probability $\tau_{ref}\nu_{out}$ the neuron is in the refractory period. Condition (39) states that at the firing threshold, the probability density has to be zero (notice that the density can be defined to be zero above threshold, so this condition is a continuity condition at the threshold boundary). This is so because otherwise the flux in eq. (41), which includes a derivative evaluated at threshold, would be infinity. The output firing rate of the neuron, ν_{out} , is obtained by integrating the escape probability density flux over w , condition (40). To write down $J_r(w)$ in condition (41) we have used the condition (39) applied to eqs. (31) and (37). Notice that precisely because of condition (39), the escape probability density flux, eq. (41), has exactly the same expression in both representations.

While solving the FPEs in both representations, it is usually easier to employ the exact condition

$$\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx P_r(x, w) = (1 - \nu_{out}\tau_{ref}) \frac{e^{-w^2/2}}{\sqrt{2\pi}}, \quad (42)$$

which is directly obtained from the equations for z or y (eqs. (23) and (33) respectively) and the condition that there is a fraction $\nu_{out}\tau_{ref}$ of neurons in the refractory state. Eq. (42) states that the marginal distribution of w is a normal distribution, as it corresponds to the stationary distribution of an Ornstein-Uhlenbeck process (eqs. (23,33)). Notice that it is consistent with eq. (38).

5 Output firing rate for long and short τ_c

The next step is to compute the output firing rate using the FPEs. We found feasible to evaluate it from the first representation, eq. (28), for long

correlation times ($\tau_c \gg \tau_m$), and from the second representation, eq. (34), for both short and long correlation times. In the two cases we propose a perturbative expansion of the solution $P_r(x, w)$ in powers of a representative temporal scale parameter (a convenient power of $k \equiv \sqrt{\tau_c/\tau_m}$).

5.1 Long τ_c limit using the first representation

In this limit we expand both the probability density and the escape probability density flux as a series in powers of $k^{-1} = \sqrt{\tau_m/\tau_c}$,

$$P_\beta(x, z) = h_0(x, z) + k^{-1}h_1(x, z) + k^{-2}h_2(x, z) + O(k^{-3}) \quad (43)$$

$$J_\beta(z) = J_{0,\beta}(z) + k^{-1}J_{1,\beta}(z) + k^{-2}J_{2,\beta}(z) + O(k^{-3}) . \quad (44)$$

Each term $J_{i,\beta}$ in this expansion must satisfy the condition (41),

$$J_{i,\beta}(z) = -\frac{1}{\tau_m} \frac{\partial}{\partial x} h_i(x, z)|_{x=\sqrt{2}\hat{\Theta}} . \quad (45)$$

Let us proceed to the calculation by replacing the expansions (43, 44) into the FPE (28). This substitution generates a set of equations for $P_{i,\beta}$ that can be solved consistently with conditions (38 - 40). The main steps of the procedure are given in Appendix C.

The resulting escape probability density flux $J_\beta(z)$ is found to be, up to $O(k^{-2})$

$$J_\beta(z) = \frac{e^{-z^2/2}}{\sqrt{2\pi}} \left[\nu_0 + \sqrt{\frac{\tau_m^3}{\tau_c}} \frac{(2 + \beta)\nu_0^2(R(\hat{\Theta}) - R(\hat{H}))}{1 - \nu_0\tau_{ref}} z \right. \\ \left. + \frac{\alpha}{\tau_c} C + \frac{\alpha C}{\beta^2\tau_c(1 - \nu_0\tau_{ref})} (z^2 - 1) \right] , \\ C \equiv \tau_m^2\nu_0^2 \left[\frac{\tau_m\nu_0(R(\hat{\Theta}) - R(\hat{H}))^2}{1 - \nu_0\tau_{ref}} - \frac{\hat{\Theta}R(\hat{\Theta}) - \hat{H}R(\hat{H})}{\sqrt{2}} \right] .$$

Here $R(t) = \sqrt{\frac{\pi}{2}} e^{t^2}(1 + \text{erf}(t))$, where $\text{erf}(t) = \frac{2}{\sqrt{\pi}} \int_0^t du e^{-u^2}$ is the error function. The rate ν_0 is just the firing rate of a LIF neuron driven by a white noise input with variance σ_w^2 (Ricciardi, 1977)

$$\nu_0^{-1} = \tau_{ref} + \sqrt{\pi}\tau_m \int_{\hat{H}}^{\hat{\Theta}} dt e^{t^2}(1 + \text{erf}(t)) . \quad (46)$$

Notice that C is independent of τ_c .

We then use condition (40) to find the output firing rate valid for long τ_c and fixed α

$$\nu_{out} = \nu_0 + \frac{\alpha}{\tau_c} C . \quad (47)$$

Several important conclusions can be extracted from this simple expression. First, the effect of correlations is linear on α for long τ_c . That is, doubling α doubles the firing rate above the rate without correlations, ν_0 . Notice also that α can be positive or negative, so for negative correlations the effect on the rate is the opposite than for positive correlations. Second, the firing rate of a LIF neuron with exponentially correlated input approaches the firing rate in the absence of input correlations as the correlation time increases. This happens because, as the correlation time becomes longer than the membrane time constant ($\tau_c \gg \tau_m$), the neuron filters out the fluctuations provoked by input correlations. As a consequence, in the long τ_c limit and for finite correlation magnitude, the correlated input to the neuron can be approximated by a white noise process. Therefore, in this limit, the observation of only the output firing rate of the neuron does not allow to distinguish a correlated input from other generated by the sum of many Poisson point processes in the diffusion limit. This result is important, as it determines when inputs with complex correlation structure (i.e., with several correlation timescales) can be approximated by white noise.

5.2 Long τ_c limit using the second representation

In this section we calculate the firing rate in the long τ_c limit using the FPE (34). Although the FPE (34) is more restrictive than the FPE (28) (it only describes positive correlations, $\alpha > 0$), it is analyzed here because it is much simpler and can also be solved in the limit in which α/τ_c is constant, i.e., for arbitrarily large α . In fact, the FPE (28) has been studied in the limit in which α/τ_c approaches to zero as τ_c rises, because the correlation magnitude was constant in that case. The real advantage of using the second representation is that the predicted firing rate is valid for larger values of α , compared to the formula (47).

We start from the FPE (34) and assume that the factor $\sqrt{\alpha}/k$ is constant ($k \equiv \sqrt{\tau_c/\tau_m}$). We thus define

$$\gamma = \frac{\sqrt{\alpha}}{k}. \quad (48)$$

Inserting this parameter in the FPE (34) we obtain

$$\left[L_x - \gamma y \frac{\partial}{\partial x} + \frac{L_y}{k^2} \right] P_\alpha(x, y) = -\tau_m \delta(x - \sqrt{2}\hat{H}) J_\alpha(y), \quad (49)$$

where $J_\alpha(y)$ reads as in eq. (41). The solution of the FPE (49) along with the conditions (38-42) in the long τ_c limit is found by expanding $P_\alpha(x, y)$ and the escape probability density flux $J_\alpha(y)$ in powers of k^{-2} while keeping γ fixed as

$$\begin{aligned} P_\alpha(x, y) &= r_0(x, y) + k^{-2} r_1(x, y) + O(k^{-4}) \\ J_\alpha(y) &= J_{\alpha,0}(y) + k^{-2} J_{\alpha,1}(y) + O(k^{-4}). \end{aligned} \quad (50)$$

To obtain the coefficients $r_i(x, y)$ and $J_{\alpha,i}(y)$ we proceed as in section (5.1). In particular, conditions (38 - 41) are imposed order by order. The main steps of the calculation are given in Appendix D. The results are here summarized up to order k^0 . The density $P_\alpha(x, y)$ up to $O(k^0)$ is

$$P_\alpha(x, y) = \tau_m J_\alpha(y) e^{-\frac{(x-\gamma y)^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} du e^{\frac{(u-\gamma y)^2}{2}} \mathcal{H}(u - \sqrt{2}\hat{H}), \quad (51)$$

($\mathcal{H}(t) = 1$ if $t > 0$ and it is zero otherwise) where the escape probability density flux $J_\alpha(y)$ up to the same order is

$$J_\alpha(y) = \frac{1}{\sqrt{2\pi}\tau_m} e^{-\frac{y^2}{2}} \left[\int_{\sqrt{2}\hat{H}-\gamma y}^{\sqrt{2}\hat{\Theta}-\gamma y} du e^{\frac{u^2}{2}} \int_{-\infty}^u dve^{-\frac{v^2}{2}} \right]^{-1}. \quad (52)$$

The output firing rate at leading order is obtained by integrating $J_\alpha(y)$ over y as

$$\nu_{out} = \frac{1}{\sqrt{2\pi}\tau_m} \int_{-\infty}^{\infty} dy e^{-\frac{y^2}{2}} \left[\int_{\sqrt{2}\hat{H}-\gamma y}^{\sqrt{2}\hat{\Theta}-\gamma y} du e^{\frac{u^2}{2}} \int_{-\infty}^u dve^{-\frac{v^2}{2}} \right]^{-1}. \quad (53)$$

Notice that this formula has been derived for $\tau_{ref} = 0$. Notice also that only the leading order k^0 has been calculated. This order, however, gives a firing

rate which is much more accurate than the firing rate obtained using the first representation in the same limit, eq. (47). This is true because the firing rate in eq. (53) depends on γ , which is a function of the parameters α and k ($\gamma \equiv \sqrt{\alpha}/k$). If the zero-th order firing rate in eq. (53) is expanded in powers of k^{-1} for fixed α , the same firing rate in eq. (47) is found when correlations are positive (In particular, if $\alpha = 0$, then $\gamma = 0$ and ν_{out} equals ν_0 , i.e., the well-known expression for the firing rate of a LIF neuron driven by white noise (Ricciardi, 1977)). This means that eq. (53) is exact up to $O(k^{-2})$, and therefore the corrections to the firing rate arising from the terms $O(k^{-2})$ in the expansion (50) should vanish. This is indeed the case, as shown in Appendix D. In addition, the higher order corrections found in the expansion of eq. (53) improve the prediction provided by eq. (47), especially when α is very large, or when α/τ_c is kept constant (i.e. γ constant) in the long τ_c limit.

The firing rate in eq. (53) has a very simple interpretation. Since y is slow compared to the voltage dynamics ($\tau_c > \tau_m$), the firing rate of a LIF neuron receiving correlated noise can be calculated by multiplying the firing rate of the LIF neuron receiving a frozen current proportional to y (plus mean μ and white noise with amplitude σ_w ; this corresponds to the function in the square brackets, divided by τ_m (Ricciardi, 1977)⁵) and the probability density of having the value y , which in this case is a normal distribution because y obeys an Ornstein-Uhlenbeck process, eq (33). This expression, obtained here to describe the effect of exponentially correlated inputs, has also been used to describe the effects of synaptic filtering with both fast and slow linear synapses on the output firing rate of a LIF neuron (Moreno-Bote and Parga, 2004).

One important feature of the firing rate in the long τ_c limit, eq. (53), is that it does not change as γ is kept fixed, that is, as the ratio α/τ_c is kept constant. This means that to obtain the same output firing rate for a longer correlation time, one has to increase proportionally the correlation magnitude so that the loss of temporal precision is counterbalanced by an increase in the excess of synchronous afferent spikes. This suggests a proportionality law that could be tested experimentally using *in vitro* current injections in which both the magnitude and the temporal precision can be controlled independently (using e.g. eqs. (23)). Furthermore, for non-exponential cor-

⁵Note that the function within the brackets can be expressed in terms of the error function, similarly to eq. (46)

relation functions (e.g. oscillatory), it might be possible to define an effective correlation magnitude and an effective correlation time so that the output firing rate of the neuron will not depend on them individually, but on their ratio.

5.3 Short τ_c limit using the second representation

In the regime of short τ_c the FPE (34) is employed to find the output firing rate. Although the set of eqs. (1, 32, 33) only generates positive exponential correlations, we use them because its associated FPE can be solved perturbatively in powers of $k = \sqrt{\tau_c/\tau_m}$ and $\sqrt{\alpha}$. We have found the FPE (28) including both positive and negative correlations too involved to be studied in the small k limit. Although the firing rate computed in this limit from the FPE (34) is derived only for positive correlations, when the same formula is employed for negative correlations, one finds an excellent agreement with the numerical results. This fact suggests that the analytical continuation of our formula to negative correlations ($\alpha < 0$) could match the true expression for that case.

Even when using the FPE (34), valid for positive correlations, the short τ_c expansion is not easy to obtain. This is because of the self-consistency condition (41), which is hard to deal with. However, if the correlation time τ_c is short compared to the refractory time τ_{ref} ($\tau_{ref} \gg \tau_c$), the escape probability density flux can be written as (Doering et al., 1987)

$$J_\alpha(y) = \nu_{out} \frac{e^{-y^2/2}}{\sqrt{2\pi}}, \quad (54)$$

which solves automatically the conditions (40 - 41). This approximation is good because after a spike the variable y approaches its Gaussian stationary distribution in a time τ_c , which we are taking shorter than τ_{ref} .

We now look for a solution of the FPE (34) of the form

$$P_\alpha(x, y) = f_0(x, y) + k f_1(x, y) + O(k^2), \quad (55)$$

and at the same time we expand the escape probability density flux J_α in powers of k or, equivalently, the unknown output firing rate as

$$\nu_{out} = \nu_{eff} + k \nu_1 + O(k^2). \quad (56)$$

It can be shown that the solution $f_1(x, y)$ obtained from the perturbative expansion does not satisfy the vanishing boundary condition (39) (see Appendix E). To address this problem, we extend the formalism described in (Doering et al., 1987) to solve the short τ_c limit. As in (Doering et al., 1987), our problem does not have a perturbative solution for short τ_c , and it is necessary to solve a boundary layer problem. Details of these calculations are given in Appendix E. Briefly, the solution $P_\alpha^{total}(x, y)$ is obtained as the sum of the perturbative and an additional solution, valid close to the threshold, that we call *boundary solution* $f_1^b(x, y)$:

$$P_\alpha^{total}(x, y) = f_0(x, y) + k[f_1(x, y) + f_1^b(x, y)] + O(k^2). \quad (57)$$

It is now possible to satisfy the condition (39) up to order k . Finally, the firing rate up to order k can be calculated using the condition (38), resulting

$$\nu_{out} = \nu_{eff}(\alpha) - \alpha\sqrt{\tau_c\tau_m}\nu_0^2R(\hat{\Theta}), \quad (58)$$

where ν_0 is defined as in eq. (46) and

$$\nu_{eff}^{-1}(\alpha) = \tau_{ref} + \sqrt{\pi}\tau_m \int_{\hat{H}_{eff}}^{\hat{\Theta}_{eff}} dt e^{t^2} (1 + \text{erf}(t)). \quad (59)$$

The effective reset and threshold potentials are defined as $\hat{\Theta}_{eff} = \frac{\Theta - \mu\tau_m}{\sigma_{eff}\sqrt{\tau_m}}$ and $\hat{H}_{eff} = \frac{H - \mu\tau_m}{\sigma_{eff}\sqrt{\tau_m}}$. An important implication of eq. (58) is that when $\tau_c = 0$ the output rate is $\nu_{eff}(\alpha)$, equivalent to that of a LIF neuron receiving an *uncorrelated* input (white noise) with an effective signal variance

$$\sigma_{eff}^2 = \sigma_w^2(1 + \alpha). \quad (60)$$

In this case, the solution is *exact* for all α . When $\tau_c \neq 0$, it is correct only for small values of both k and $\alpha > 0$. This expression indicates that when the correlation time is zero, the effect of the input correlations is to increase the white noise variance by a factor equal to $1 + \alpha$.

A general expression for the firing rate of any IF neuron is presented in Appendix F. Again, for $\tau_c = 0$, the firing rate is that of the IF neuron with input white noise but with a renormalized variance as in eq. (60). From this maximum firing rate at optimal synchronization, the firing rate decreases as $-\sqrt{\tau_c}$ for fixed α (eq. (99), analogous to eq. (58) for a LIF neuron), showing that this large sensitivity to variations in the correlation time of the inputs is a general property of IF neurons.

	<i>First Representation</i>	<i>Second Representation</i>
Short τ_c	Not found	$\nu_{out} = \nu_{eff}(\alpha) - \alpha\sqrt{\tau_c\tau_m}\nu_0^2R(\hat{\Theta})$, eq. (58). Valid for small and positive α , and <i>exact</i> for all positive α when $\tau_c = 0$.
Long τ_c	$\nu_{out} = \nu_0 + \frac{\alpha}{\tau_c}C$, eq. (47). Valid for small α , positive and negative.	$\nu_{out} = \frac{1}{\sqrt{2\pi\tau_m}} \int_{-\infty}^{\infty} dy e^{-\frac{y^2}{2}}$ $\left[\int_{\sqrt{2}\hat{H}-\gamma y}^{\sqrt{2}\hat{\Theta}-\gamma y} du e^{\frac{u^2}{2}} \int_{-\infty}^u dv e^{-\frac{v^2}{2}} \right]^{-1}$, with $\gamma = \sqrt{\alpha\tau_m/\tau_c}$, eq. (53). Valid for all (even large) positive α .

Table 1: Analytical expressions for the output firing rate of a LIF neuron receiving exponentially correlated inputs with magnitude α and correlation timescale τ_c for the two representations of the current in both the short and long τ_c limits.

6 Summary of the analytical results

The analytical results, obtained in the first and second representations of the current, and in the short and long τ_c limits, along with the conditions upon which they are valid, are summarized in Table (1).

The second representation allows one to calculate the firing rate for both short and long τ_c , while the first representation only allows the calculation of the firing rate for long τ_c . In (Moreno et al., 2002) we used the second representation to obtain the firing rate for short τ_c , and therefore the expression shown here is the same at that found there. On the other hand, using the second representation for long τ_c , here we have been able to find a new expression for the firing rate, eq. (53), which can be applied for arbitrarily large α , while that found in (Moreno et al., 2002) using the first representation, eq. (47), could only be applied for small α . The expressions valid for

long τ_c , eq. (47) and eq. (53), are in fact equivalent when the limit $\alpha \rightarrow 0$ is taken (Appendix D). Note, however, that eq. (47) can be employed for negative α , while eq. (53) can only be used for positive α .

7 The effect of correlations on the firing response of spiking neurons

In this section we take advantage of the machinery developed in the previous sections. First, the prediction of the firing rate as a function of the timescale and magnitude of input correlations is used to study the role of synchrony on the stationary firing response of a LIF neuron. Second, we study the firing response to modifications of the correlation magnitude. Numerical solutions of the voltage and noise equations to generate exponentially correlated noise are employed in this case.

7.1 Stationary firing response

Although we have calculated the output firing rate both in the limit $\tau_c \ll \tau_m$ and in the limit $\tau_c \gg \tau_m$, before the effect of τ_c and α on the firing rate is described, we develop an interpolation procedure that allows us to use a single expression for all values of τ_c . The interpolating curves have been determined by setting the firing rate in the short correlation time range ($\tau_c < \tau_m$) as

$$\nu_{out} = \nu_{eff} + A_1 \sqrt{\tau_c} + A_2 \tau_c, \quad (61)$$

where A_1 and A_2 are unknown functions of α and of the neuron and input parameters, while in the long correlation time limit ($\tau_c > \tau_m$) the expression given in eq. (47),

$$\nu_{out} = \nu_0 + \alpha C / \tau_c, \quad (62)$$

was used. The functions A_1 and A_2 are determined by interpolating these two expressions with conditions of continuity and differentiability at a convenient interpolation point $\tau_{c,inter} \sim \tau_m$. Although we have calculated analytically the function A_1 (eq. (58)) for small α , this procedure takes into account higher order corrections which match more accurately the observed data for larger values of α , as those used in some of our simulations (see below). Therefore, eqs. (61-62) provide an analytical formula for the output firing

rate of a LIF neuron receiving exponentially correlated input which is valid for all τ_c .

We have performed numerical simulations of a LIF neuron driven by Gaussian exponentially correlated input using eqs. (1, 22, 23). We use them to check the analytical results given in eqs. (47, 53, 58) and validate the interpolation made between the regimes of short and long τ_c , provided by eqs. (61-62). When positive correlations are considered ($\alpha > 0$), the interpolation procedure is robust against changes in μ and σ_w^2 . Crucially, the interpolating point $\tau_{c,inter} \sim \tau_m$ does not vary too much, so that it can be maintained approximately fixed for all input parameters. For negative correlations we have found more convenient to add to the expansion in eq. (62) an extra term: $\nu_{out} = \nu_0 + \alpha C/\tau_c + B_1/\tau_c^2$. Then, this expression is made to match at $\tau_{c,inter} \sim \tau_m$ the short τ_c regime given by the equation $\nu_{out} = \nu_{eff} + B_2\sqrt{\tau_c}$.

This interpolation is compared with simulation results in Fig. (6), providing good fits. The firing rate 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. On the other hand, when negative correlations are present in the input, the effect of τ_c is reversed: the firing rate increases as τ_c increases. Negative correlations produce a deficit in current fluctuations that decreases the firing rate. This deficit is not noticeable if τ_c is very long compared with τ_m . These results show that correlations with *fixed* magnitude α have different effects on a target neuron depending on the value of their correlation timescale. Correlations are not perceived by neurons if the temporal precision they occur is larger than the membrane time constant of those neurons. As it can be appreciated in Fig. (6), when τ_c is of the order of $40ms$ (twice longer than τ_m) the output firing rate of the neuron approaches the firing rate obtained by an input without correlations ($\alpha = 0$, dashed-dotted line). Only if $\tau_c < \tau_m = 20ms$, the presence of correlations is noticeable. As noted above, this implies that, from the point of view of the output firing rate, correlations in the input can be neglected, i.e., a white-noise input description is appropriate, when τ_c is significantly longer than τ_m (note, however, that there is not an absolute value of τ_c for which correlations can be neglected, rather, this value will increase with α).

In Fig. (7) we use the predictions of eqs. (47,53) valid for long τ_c . Here, large values of correlation magnitude, α , are used. The predictions

are compared with simulations of neurons in the subthreshold (left) and the suprathreshold (right) regimes. The subthreshold and suprathreshold regimes are defined by $\mu\tau_m < \Theta$ and $\mu\tau_m > \Theta$ respectively, and they correspond to the fluctuation and drift dominated regimes. The prediction by eq. (53) is very good even for intermediate $\tau_c \sim \tau_m$ in both regimes. In contrast, the firing rate for long τ_c given in eq. (47), provides poorer fits (dotted line in the left panel) in the subthreshold regime, and even poorer in the suprathreshold regime when very large values of α are used (not shown). This is because the second prediction of the firing rate was obtained for fixed α .

The figure also shows that the effect of correlations is quite different for a neuron receiving subthreshold or suprathreshold inputs. For subthreshold inputs, positive correlations always increase the firing rate relative to the case without correlations, and the firing rate decreases as the timescale of correlations becomes broader. However, for suprathreshold inputs a different qualitative behavior is observed, at least for small white noise variances. Positive correlations with long enough τ_c give an output firing rate smaller than the basal rate without correlations, although this effect is very small (notice the large values of α that have been used). A minimum firing rate is attained when the correlation timescale is longer than the membrane time constant of the neuron, and the exact value of τ_c at which the minimum occurs is roughly predicted by the analytical formula (53). When the white noise variances become larger, this counterintuitive effect of correlations disappears, and the profile is much more similar to the subthreshold case, but with much smaller correlation-induced changes.

Overall, this analysis shows that neurons are more sensitive to correlations in the subthreshold than in the suprathreshold regime, what is not surprising, since in the first regime spiking is driven by input fluctuations and correlations enhance them (Moreno et al., 2002; Salinas and Sejnowski, 2001).

7.2 Transient firing response

Another important question is how fast a neuron can respond to *pure* changes in the correlation magnitude α , that is, when both the afferent mean current and white noise variance σ_w^2 are fixed. In our work (Moreno et al., 2002) we have shown that changes in correlation magnitude can be transmitted very fast by the firing rate of spiking neurons even when the timescale of those

correlations is quite large. Those firing responses are also compared here with the response to sudden jumps in mean input current.

Let us write the instantaneous firing rate for the time dependent FPE, either in the first or in the second representation, as (see eq. (41))

$$\nu_{out}(t) = -\frac{\sigma_w^2(t)}{2} \frac{\partial}{\partial V} \int_{-\infty}^{\infty} dw P(V, w, t)|_{V=\Theta} . \quad (63)$$

For the sake of clarity, we have come back to the physical quantity V and used its distribution $P(V, w, t)$ ($w = z, y$). A similar equation for the instantaneous firing rate of a one-dimensional FPE has been used by Silberberg et al. (2004) to predict that any instantaneous modification in the white noise variance, $\sigma_w^2(t)$, produces an immediate change in the output firing rate of the neuron. Besides, as we have shown before, the exact form of eq. (63) for $\tau_c = 0$ corresponds to a neuron receiving (uncorrelated) input white noise with effective variance $\sigma_{eff}^2 = \sigma_w^2(1 + \alpha)$, eq. (19). This gives (Moreno et al., 2002)

$$\nu_{out}(t) = -\frac{\sigma_{eff}^2(t)}{2} \frac{\partial}{\partial V} \int dw P(V, w, t)|_{V=\Theta} . \quad (64)$$

Now it is clear that any change in α will produce an immediate change in $\nu_{out}(t)$, because the distribution $P(V, t) = \int dw P(V, w, t)$ can only experience a smooth change (notice that the trajectories generated by the equations for V (e.g, see eqs. (1, 22, 23)) are continuous under changes in α). This means that when $\tau_c = 0$, changes in the correlation magnitude (α) will be felt immediately by the firing response of the neuron. By analyticity arguments, the response under changes in α will be also fast for non-zero τ_c .

These predictions have been tested with numerical simulations, whose results are shown in Fig. (8). Initially the input statistics is white noise, and some time later either the mean current μ (bottom curve), or the white noise variance σ_w (upper curve), or the correlation amplitude α (two intermediate curves) are changed independently. Changing abruptly the mean current only produces a slow response with a timescale of the order of the membrane time constant. However, in the absence of correlations, the firing rate changes instantaneously under a sudden modification in the variance of the injected current (σ_w^2). In agreement with our prediction, for short τ_c the response is also very quick when the correlation changes from $\alpha = 0$ to a positive value. To quantify how fast the response is, we computed the time t_{cross} at which the instantaneous rate reaches for the first time the value of the final

stationary firing rate. The inset in Fig. (8) shows that, as a function of τ_c , t_{cross} initially grows but it soon saturates at about $3ms$, even when τ_c is several hundred milliseconds long. Thus, the correlation time is not a limiting factor for fast transmission of information contained in correlation changes. This result shows that information carried by correlated input patterns can be transmitted with a timescale that is not limited by the membrane time constant, what is not the case for signals embedded in the mean input current (Moreno et al., 2002). In (Rudolph and Destexhe, 2001) the authors show that correlation changes can be followed very rapidly by a spiking neuron. Because they consider the case of perfect synchrony, $\tau_c = 0$, their conclusions are similar to those by (Silberberg et al., 2004), because the case $\tau_c = 0$ corresponds to a simple renormalization of the current variance (σ_w^2), as we have explained before (see eq. (19)).

These results show that fast information transmission in cortex using spike correlations is theoretically possible. As we have shown, changing the mean afferent current produces slow responses if the neuron is in the subthreshold regime, because the mean current has to be integrated in a timescale τ_m . However, because of their fast transmission rate, correlation modulations can be an ideal candidate for transmitting information rapidly. The fact that changes in μ do not evoke rapid responses does not mean that rate codes are inefficient for transmitting information rapidly. Rather, changes in the firing rate of "noisy" input spike trains (e.g., as in a Poisson train) involve both changes in μ and in fluctuations σ_w (Ricciardi, 1977) and indeed also in α (see their definitions in eqs. (18)). Such white noise variance and correlation magnitude modulations can be transmitted very fast, while the mean current modulations produce a slower response. Therefore, an increase in the firing rate of an irregularly spiking presynaptic population will produce an output rate change which contains information in at least two different timescales (one short and another slow).

8 Discussion

In this paper we have provided and thoroughly analyzed a theoretical framework to understand how temporal correlations affect the output firing response of neurons. The main qualitative results we found are

- The neuron's output rate is very sensitive to precisely synchronized inputs with $\tau_c < \tau_m$.

- The response decreases (increases) with the timescale τ_c for positive (negative) correlations, and increases (decreases) with their magnitude α .
- The neuron response to sudden changes in the size of the correlations is very fast, regardless of the magnitude of the change and on the correlation time.

An important question is how our results can be incorporated into the modeling of neural networks. Temporal and spatial correlations are presumably relevant to correctly describe the dynamics of realistic recurrent neuronal networks. Recently in (Renart et al., 2007) we have proposed an extended mean-field approach to determine the firing rate and spiking variability of a large network of LIF neurons. In the classical mean-field theory, the neurons in the network are assumed to fire in a Poisson and independent manner (Amit and Brunel, 1997b; Renart et al., 2003), so that the only free dynamical parameter in the dynamics of an homogeneous population of neurons is its population firing rate. Our extension goes beyond the classical mean field theory by adding as a free parameter the spiking variability of the network, that is, the coefficient of variation of the inter-spike-intervals, CV . Then, the firing rate as well as the variability of the network can be studied without the assumption that the spike trains are Poisson, corresponding to the particular case $CV = 1$. In particular, stationary states with $CV > 1$ would correspond to states of high spiking variability, while stationary states of the network with $CV < 1$, would correspond to more regular spiking regimes of the neuronal dynamics. The formalism presented in (Renart et al., 2007) is based on the result that when the correlation time of the spike trains is short enough ($\tau_c \ll \tau_m$), then the input variability can be expressed as (see eqs. (60,18); (Moreno et al., 2002))

$$\sigma_{eff}^2 = J_E^2 N_E CV_E^2 \nu_E + J_I^2 N_I CV_I^2 \nu_I, \quad (65)$$

assuming that there is no cross-correlations ($\rho = 0$). Since the output firing rate and the output CV of an integrate-and-fire neuron can be calculated exactly when the input is white noise (Ricciardi, 1977), then a mapping between the input rates and CV , and the output rates and CV can be constructed as

$$\nu_{out} = f_\nu(\nu_{in}, CV_{in})$$

$$CV_{out} = f_{CV}(\nu_{in}, CV_{in}), \quad (66)$$

where the functions f_ν and f_{CV} are the expressions for the output firing rate and CV of the IF neuron receiving white noise input. These equations define an input-output mapping of the neuronal dynamics with independent variables ν and CV . Therefore, under the conditions described above, a mean-field theory for the dynamics of the mean and variability of the spiking response can be formulated. Doiron et al. (2006) have also recently used our renormalization technique of the input variance, as defined in eqs. (65,66), to describe the transmission of the activity of non-leaky IF neuron in feed-forward networks. As we have said above, (Renart et al., 2007) have addressed the problem of self-consistency in firing rate and CV in recurrent networks of LIF neurons. Other works have also studied this problem using different approaches to find self-consistent equations for the spiking variability of the network (Lerchner et al., 2006).

However, further extensions of our mean-field theory (Renart et al., 2001; Moreno et al., 2002; Renart et al., 2007) are required to consider in a self-consistent way the second order statistics of the neuronal activity in spiking recurrent networks. A first step has been made in (Moreno-Bote and Parga, 2006), where the auto- and cross-correlation functions of the output response of a pair of spiking neurons receiving independent as well as common sources of noise have been analytically determined⁶. The self-consistent treatment of spike cross-correlation functions (i.e., the input and output cross-correlation functions should also match each other) to describe more realistic recurrent neuronal networks seems to be an unavoidable step to understand how neurons' interactions give rise to network behaviors. The problem can be formally stated as follows: find the set of mean-field equations mapping the input values of the relevant dynamical variables of the network (firing rate, F_N and ρ) to their output values

$$\begin{aligned} \nu_{out} &= f_\nu(\nu_{in}, F_{N,in}, \rho_{in}) \\ F_{N,out} &= f_{F_N}(\nu_{in}, F_{N,in}, \rho_{in}) \\ \rho_{out} &= f_\rho(\nu_{in}, F_{N,in}, \rho_{in}). \end{aligned}$$

This set of equations are now available at least for a LIF neuron receiving colored noise (Moreno-Bote and Parga, 2006).

⁶For different approximations of this computation see (Lindner et al., 2005; Masuda, 2006)

In this work we have considered decaying (exponential) correlations, while in cortex, damped oscillatory cross-correlograms are also observed (see e.g. (Vaadia et al., 1995; Riehle et al., 1997; Fries et al., 1997)). This problem could be addressed by introducing a stochastic current which obeys a second-order equation driven by white noise: the well-known damped oscillator. A current generated in this way can have a cross-correlogram with exponentially decaying oscillations, with frequency and damping value controlled by the parameters of the equation. Although relevant, we do not study this problem here, since the new system would involve solving a more complicated FPE having now three independent variables.

Here we have not studied neuron models with conductance-based synapses either. However, an analogous expression for the firing rate at long τ_c can be obtained if the noise enters multiplicatively, instead of additively (although we do not present the derivation here, the FPE for neuron models with conductance-based synapses can be solved using the techniques in Appendix D). Qualitatively, the effect of the correlation magnitude and correlation timescale in conductance-based models is not different from their effects in current-based models. Note, however, that in the first case correlations are strongly effective only when τ_c is shorter than the effective membrane time constant of the neuron, which now depends on the total conductance (see e.g. (Moreno-Bote and Parga, 2005)).

We have modelled input spike trains as delta functions (point-processes) without any further temporal synaptic filtering. This means that the cross-correlation function of the total input current displays a delta function at zero time lag, as shown in eq. (17). When the input spike trains are filtered by synapses with a finite synaptic time constant τ_s , they generate a train of exponential-like current waveforms into the neuron. The delta function in the correlation function, eq. (17), becomes then an exponential with the same time constant as that of the synaptic filter, τ_s (see e.g. (Brunel and Sergi, 1998; Moreno-Bote and Parga, 2004)). At the same time, the exponential term in the correlation function results after filtering in two additional exponentials, with time constants τ_c and τ_s , respectively. Then, the result of (linearly) filtering correlated input spike trains is an input current whose correlation function has two kind of exponentials, each with a different time constant (τ_c and τ_s). Particular cases of this interesting problem (e.g. when the two timescales are disparate) could be addressed analytically by using the techniques developed to study simultaneous fast and slow synaptic filtering (Moreno-Bote and Parga, 2004).

Two differences are expected when synaptic filters are present in the model. First, synapses filter out fluctuations in the input whose timescale is shorter than τ_s and convert them into fluctuations with timescale τ_s . Fluctuations that are slower than τ_s will pass the synapses. Therefore, fast fluctuations produced by precise input synchronization (i.e., short $\tau_c \leq \tau_m$) will not be seen by the neuron: effectively the sharp synchronization of timescale τ_c is converted into a coarser synchronization with timescale τ_s . Then, we expect that for $\tau_c < \tau_s$ the firing rate will depend very little on τ_c in that range. However, when $\tau_c > \tau_s$ the rate vs. τ_c curve will decay fast until τ_c crosses τ_m , after which the effect of input correlation on the rate will be small, similarly to Fig. (6). Second, filters introduce a delay in the transient firing response to sudden increases of input synchrony. We have run simulations with fast filters ($\tau_s \leq 5ms$) and found that the response was still fast and was delayed by the time constant of the synapses.

In future work it would be desirable to develop a complete theory that describes the firing statistics of integrate-and-fire neurons with conductance-based synapses and finite synaptic timescales driven by correlated spike trains. The effect of input correlations in this more complex system could be evaluated by extending and combining the techniques developed in this and the above quoted works.

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Appendices

A Numerical procedures

The equations for the voltage of the integrate-and-fire neuron and the correlated Gaussian noise are numerical solved using a simple Euler integration procedure, along with a Monte-Carlo method. This procedure gives an excellent estimate of the the output firing rate (time dependent or independent), which can be compared to the theoretical predictions. As an example, the dy-

namics of the voltage of a LIF neuron in eq. (1) with the current $I(t)$ defined in eqs. (22,23) is integrated using a small time step ($\delta t = 5 \cdot 10^{-4} \text{ms} \ll \tau_m$) as

$$V(t + \delta t) = V(t) - \frac{V(t)}{\tau_m} \delta t + I(t) \delta t, \quad (67)$$

$$I(t) = \mu + \sigma_w \frac{\omega(t)}{\sqrt{\delta t}} + \sigma_w \frac{\beta}{\sqrt{2\tau_c}} z(t), \quad (68)$$

$$z(t + \delta t) = z(t) - \frac{z}{\tau_c} \delta t + \sqrt{\frac{2}{\tau_c}} \omega(t) \sqrt{\delta t}, \quad (69)$$

with the reset condition $V = H$ after a spike is generated (when $V \geq \Theta$). The initial value of the noise variable z is that at the time of the previous spike, i.e, z is not reset after each spike. The variable $\omega(t)$ is a random variable taken values $+1$ and -1 with equal probability $1/2$ at each time step δt , and being drawn independently from time step to time step. Therefore $\langle \omega(t) \rangle = 0$, $\langle \omega^2(t) \rangle = 1$ and $\langle \omega(t)\omega(t') \rangle = 0$, where $t \neq t'$. This means that the quantity $\omega(t)/\sqrt{\delta t}$, which appears in the expression for the current $I(t)$ above, is an approximation to the delta function, since $\langle \omega(t)/\sqrt{\delta t} \rangle = 0$, $\langle \omega^2(t)/\delta t \rangle = 1/\delta t$, and $\langle \omega(t)\omega(t')/\delta t \rangle = 0$. The procedure described above is robust and converges to the true stationary process as δt decreases. The Monte-Carlo simulations were run using Fortran90 custom code. Special care has to be taken in choosing an appropriate random generator for $\omega(t)$.

B Derivation of the FPEs

The FPE (28) is here derived for the set of equations

$$\begin{aligned} \dot{x}(t) &= -\frac{x(t)}{\tau_m} + \sqrt{\frac{2}{\tau_m}} \eta(t) + \frac{\beta}{\sqrt{\tau_m \tau_c}} z(t) \\ \dot{z}(t) &= -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}} \eta(t), \end{aligned} \quad (70)$$

corresponding to the first representation of the current. The FPE (34) associated to the second representation of the current can be obtained using

the same rules described in this section. More formal derivations of similar FPEs can be found in (Ricciardi, 1977; Risken, 1989).

The system defined by eqs. (70) is fully described by the probability density function $P_\beta(x, z, t)$. This function expresses the probability density of having the neuron in the state (x, z) at time t . The FPE is an equation which precisely describes the dynamics (i.e., time evolution) of such a density. A first step toward the derivation of the FPE consists in discretizing the time in the dynamics, similarly as it has been done in Appendix A. This leads to

$$\begin{aligned} x(t + \delta t) &= x(t) - \frac{x(t)}{\tau_m} \delta t + \sqrt{\frac{2}{\tau_m}} \omega(t) \sqrt{\delta t} + \frac{\beta}{\sqrt{\tau_m \tau_c}} z(t) \delta t \\ z(t + \delta t) &= z(t) - \frac{z}{\tau_c} \delta t + \sqrt{\frac{2}{\tau_c}} \omega(t) \sqrt{\delta t}, \end{aligned} \quad (71)$$

where δt represents an infinitesimal time increment, and $\omega(t)$ is a random variable taken values $+1$ and -1 with probability $p(w = \pm 1) = 1/2$ and drawn independently at every infinitesimal time step. The terms in eqs. (71) proportional to $\sqrt{\delta t}$ are approximations to the delta functions in eqs. (70) integrated during the infinitesimal time increment.

To determine the FPE associated to eqs. (70), one has to relate the density at time $t + \delta t$, $P_\beta(x, z, t + \delta t)$, with the density at a previous time t , $P_\beta(x', z', t)$. First, we realize that the probability that we find a neuron in an infinitesimal square $\delta x' \delta z'$ around state (x', z') at time t has probability $P_\beta(x', z', t) \delta x' \delta z'$. Second, the state square centered at (x', z') with surface $\delta x' \delta z'$ will be projected at the successive time $t + \delta t$ into another square centered at (x, z) with surface $\delta x \delta z$ close to the previous one, obeying the rules defined in eqs. (71). Therefore, by conservation of the probability, we have that

$$P_\beta(x, z, t + \delta t) \delta x \delta z = \sum_{w=\pm 1} p(w) P_\beta(x'(w), z'(w), t) \delta x' \delta z', \quad (72)$$

where

$$\begin{aligned} x'(w) &= x + \frac{x}{\tau_m} \delta t - \sqrt{\frac{2}{\tau_m}} \omega \sqrt{\delta t} - \frac{\beta}{\sqrt{\tau_m \tau_c}} z \delta t \\ z'(w) &= z + \frac{z}{\tau_c} \delta t - \sqrt{\frac{2}{\tau_c}} \omega \sqrt{\delta t}. \end{aligned}$$

Notice that the states $(x'(w), z'(w))$ ($w = \pm 1$) defined above are the only ones from where one can arrive to the state (x, z) after an infinitesimal amount of time δt . In addition, the box around state (x', z') is compressed to the box around the final state (x, z) by a factor $\delta x \delta y = (1 - \delta t / \tau_m)(1 - \delta t / \tau_c) \delta x' \delta y'$, given by the decaying term in eqs. (70).

After expanding the densities in eq. (72) in powers of $\sqrt{\delta t}$, we find that all terms which are order $\sqrt{\delta t}$ are equal to zero (since $\langle \omega \rangle = 0$), while the terms order δt do not vanish (either they do not depend on ω , or they are proportional to ω^2 , and therefore $\langle \omega^2 \rangle = 1$). After equating the terms at $O(\delta t)$, one obtains the FPE

$$\tau_m \frac{\partial}{\partial t} P_\beta(x, z, t) = [L_x + \frac{L_z}{k^2} + \frac{2}{k} \frac{\partial}{\partial x} (\frac{\partial}{\partial z} - \frac{\beta z}{2})] P_\beta(x, z, t). \quad (73)$$

In the time-independent case, $\frac{\partial}{\partial t} P_\beta(x, z, t) = 0$. However, to establish a stationary probability density function which does not depend on time, the probability density flux escaping at threshold (probability density flux in the direction of the variable x calculated at threshold) should be reinjected into the reset voltage. This enforces conservation of the total probability, that is, $\int \int dx dz \rho(x, z, t) = 1$ at all times, and leads to the self-consistent stationary FPE (28).

C Long τ_c expansion using the first representation

Here we detail the main steps for calculating the firing rate in eq. (47). Introducing the expansions (43, 44) in eq. (28) we obtain

$$L_x h_n + L_z h_{n-2} + 2 \frac{\partial}{\partial x} (\frac{\partial}{\partial z} - \frac{\beta z}{2}) h_{n-1} + \tau_m \delta(x - \sqrt{2} \hat{H}) J_{\beta, n-1}(z) = 0 \quad (74)$$

($h_n \equiv 0$ for $n < 0$). The solution to these equations is obtained order by order in such a manner that the conditions (38 - 41) are satisfied. After solving them up to order k^2 using the conditions (39, 41) and the fact that the h_n 's have to be normalizable, we obtain that

$$h_0(x, z) = k_0(x) J_{\beta, 0}(z),$$

$$\begin{aligned}
h_1(x, z) &= k_0(x)J_{\beta,1}(z) + k_1(x)\left(2\frac{\partial}{\partial z} - \beta z\right)J_{\beta,0}(z) , \\
h_2(x, z) &= k_0(x)J_{\beta,2}(z) + k_1(x)\left(2\frac{\partial}{\partial z} - \beta z\right)J_{\beta,1}(z) \\
&\quad + k_2(x)\left(2\frac{\partial}{\partial z} - \beta z\right)^2 J_{\beta,0}(z) , \tag{75}
\end{aligned}$$

where the functions k_i are

$$\begin{aligned}
k_0(x) &= \tau_m e^{-\frac{x^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2}} H(y - \sqrt{2}\hat{H}) , \\
k_1(x) &= e^{-\frac{x^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2}} k_0(y) , \\
k_2(x) &= e^{-\frac{x^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2}} k_1(y) .
\end{aligned}$$

The coefficients $J_{i,\beta}(z)$ in eq. (75) have still to be calculated. This is done by integrating first the h_n 's over x from $-\infty$ to $\sqrt{2}\hat{\Theta}$ and using the condition (42). After using the condition (40), we find

$$\begin{aligned}
J_0(z) &= \nu_0 Z_0(z) , \\
J_1(z) &= \frac{(2 + \beta)\nu_0 \int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_1(x)}{\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_0(x)} z Z_0(z) , \\
J_2(z) &= \left[\frac{\alpha}{\tau_m} C + \frac{\alpha C}{\beta^2 \tau_m (1 - \nu_0 \tau_{ref})} (z^2 - 1) \right] Z_0(z) , \\
C &= \tau_m \nu_0^2 \left[\frac{(\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_1(x))^2}{\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_0(x)} - \int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_2(x) \right] , \tag{76}
\end{aligned}$$

where $Z_0(z) = e^{-z^2/2}/\sqrt{2\pi}$. Finally, integrating again $J_{i,\beta}(z)$ over z gives the contributions to the output firing rate in eq. (47). In the next section we calculate the integrals appearing in the parameter C in eq. (76).

C.1 Integrals

Here we only present some intermediate steps and the final results for the integrals appearing in C , eq. (76). The last two integrals can be expressed in terms of the function $R(t) = \sqrt{\frac{\pi}{2}} e^{t^2} (1 + \text{erf}(t)) = e^{t^2} \int_{-\infty}^{\sqrt{2}t} ds e^{-s^2/2}$ as

1.
$$\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_0(x) = \tau_m \int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx e^{-\frac{x^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2}} H(y - \sqrt{2}\hat{H}) = \frac{1 - \nu_0 \tau_m}{\nu_0} .$$
2.
$$\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_1(x) = \int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx e^{-\frac{x^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2}} k_0(x) = \tau_m \int_{\sqrt{2}\hat{H}}^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2}} \int_{-\infty}^y dx e^{-\frac{x^2}{2}} (y - x) = \tau_m (R(\hat{\Theta}) - R(\hat{H})) .$$
3.
$$\int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx k_2(x) = \int_{\sqrt{2}\hat{H}}^{\sqrt{2}\hat{\Theta}} \frac{\tau_m}{2} dy e^{\frac{y^2}{2}} \int_{-\infty}^y dx e^{-\frac{x^2}{2}} (y - x)^2 = \tau_m \left(\frac{\hat{\Theta}}{\sqrt{2}} R(\hat{\Theta}) - \frac{\hat{H}}{\sqrt{2}} R(\hat{H}) \right) .$$

D Long τ_c expansion using the second representation

In this section we derive the output firing rate formula (53) using the FPE (34). Here, we take the ratio $\gamma \equiv \sqrt{\alpha}/k$ to be a parameter independent of k , that is, it is fixed. This will allow us to study the case of large α in the long τ_c limit. From the FPE (34,49) we develop a systematic expansion of the probability distribution $P_\alpha(x, y)$ and the escape probability density flux $J_\alpha(y)$ in powers of k^{-2} (see the expansion in (50)), in which γ is considered a fixed parameter independent of k . Inserting the expansion in eq. (50) into the FPE (49) produces

$$[L_x - \gamma y \frac{\partial}{\partial x}] r_n + L_y r_{n-1} + \tau_m \delta(x - \sqrt{2}\hat{H}) J_{\alpha,n}(y) = 0 \quad , \quad (77)$$

where $r_n \equiv 0$ if $n < 0$. For simplicity, the set of conditions (38 - 42) is used here when $\tau_{ref} = 0$. Solving the zero-th order in eq. (77) with conditions (39, 41) gives

$$r_{\alpha,0}(x, y) = \tau_m J_{\alpha,0}(y) e^{-\frac{(x-\gamma y)^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} du e^{\frac{(u-\gamma y)^2}{2}} H(u - \sqrt{2}\hat{H}) \quad , \quad (78)$$

where the escape probability density flux $J_{\alpha,0}(y)$ has yet to be determined. This is done by using the condition (42) with $\tau_{ref} = 0$ at zero-th order, to obtain

$$J_{\alpha,0}(y) = \frac{1}{\sqrt{2\pi\tau_m}} e^{-\frac{y^2}{2}} \left[\int_{\sqrt{2}\hat{H}-\gamma y}^{\sqrt{2}\hat{\Theta}-\gamma y} du e^{\frac{u^2}{2}} \int_{-\infty}^u dv e^{-\frac{v^2}{2}} \right]^{-1}. \quad (79)$$

Repeating the same steps as above, the n -th ($n > 0$) order escape probability density flux is found to be

$$J_{\alpha,n+1}(y) = \left[\int_{\sqrt{2}\hat{H}-\gamma y}^{\sqrt{2}\hat{\Theta}-\gamma y} du e^{\frac{u^2}{2}} \int_{-\infty}^u dv e^{-\frac{v^2}{2}} \right]^{-1} \int_{-\infty}^{\sqrt{2}\hat{\Theta}} dx e^{-\frac{(x-\gamma y)^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dv e^{-\frac{(v-\gamma y)^2}{2}} L_y \int_{-\infty}^u dv r_n(v, y). \quad (80)$$

and the density r_n is computed as

$$r_n(x, z) = e^{-\frac{(x-\gamma y)^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} dv e^{-\frac{(v-\gamma y)^2}{2}} L_y \int_{-\infty}^u dv r_{n-1}(v, y) + \tau_m J_{\alpha,n}(y) e^{-\frac{(x-\gamma y)^2}{2}} \int_x^{\sqrt{2}\hat{\Theta}} du e^{-\frac{(u-\gamma y)^2}{2}} H(u - \sqrt{2}\hat{H}).$$

The zero-th order rate is obtained by integrating over y the zero-th order escape probability density flux in eq. (79). This gives the firing rate in eq. (53). For fixed α , the parameter γ decreases as τ_c grows. In this limit, we could expand the zero-th order firing rate in powers of γ . The firing rate obtained from this expansion has a dominant order k^{-2} ($O(\gamma^2)$). However, other contributions to the total firing rate at order k^{-2} could also come from the non zero-th order firing rate from the expansion (50). In particular, the first order ($n = 1$) rate in the expansion (50) is order k^{-2} . However, it is possible to see that an expansion in powers of γ in the term with $n = 1$ in eq. (80) also leads to an extra dominant order k^{-2} , that multiplied by k^{-2} yields finally a correction to the firing rate bigger than $O(k^{-2})$. This finally proves that the leading correction to the firing rate for fixed α when τ_c approaches infinity is order k^{-2} and it is given by the expansion of the zero-th order rate (53). Naturally, this expansion matches the output firing rate formula (47) for positive correlation magnitudes.

E Short τ_c expansion using the second representation

E.1 The Free Solution

We introduce an expansion of the form (55, 56) into the FPE (34) and find the set of equations:

$$L_y f_0 = 0 , \quad (81)$$

$$L_y f_1 = \sqrt{\alpha} y f_0 , \quad (82)$$

$$L_y f_2 = -L_x f_0 + \sqrt{\alpha} y f_1 - \tau_m \delta(x - \sqrt{2}\hat{H}) \nu_{eff} Z_0(y) , \quad (83)$$

$$L_y f_3 = -L_x f_1 + \sqrt{\alpha} y f_2 - \tau_m \delta(x - \sqrt{2}\hat{H}) \nu_1 Z_0(y) , \quad (84)$$

where $Z_0(y) = e^{-y^2/2}/\sqrt{2\pi}$. After solving eq. (81) we find that the only normalizable solution is

$$f_0(x, y) = g_0(x) Z_0(y) , \quad (85)$$

where g_0 has yet to be determined. The equation at order k gives the expression for f_1

$$f_1(x, y) = [g_1(x) - \sqrt{\alpha} y \frac{\partial}{\partial x} g_0(x)] Z_0(y) . \quad (86)$$

Again, g_1 is unknown. The equation at second order satisfies

$$\begin{aligned} L_y f_2(x, y) &= -\alpha y g_1(x) Z_0(y) \\ &- [L_x g_0(x) + \alpha \frac{\partial^2}{\partial x^2} g_0(x) - \tau_m \delta(x - \sqrt{2}\hat{H}) \nu_{eff}] Z_0(y) . \end{aligned} \quad (87)$$

Using that the integral $\int dy L_y f_2(x, y)$ has to equal zero in order for f_2 to be integrable, we can integrate eq. (87) over y and obtain the condition

$$\left[\frac{\partial}{\partial x} x + (1 + \alpha) \frac{\partial^2}{\partial x^2} \right] g_0(x) + \tau_m \nu_{eff} \delta(x - \sqrt{2}\hat{H}) = 0 . \quad (88)$$

This equation is the same as that obtained when solving the FPE for a LIF neuron driven by white noise input (Ricciardi, 1977), but where the variance

of the noise has been renormalized by a factor $1 + \alpha$. This equation is solved exactly for all α using the condition (39):

$$g_0(x) = \frac{\tau_m \nu_{eff}}{1 + \alpha} e^{-\frac{x^2}{2(1+\alpha)}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2(1+\alpha)}} H(y - \sqrt{2}\hat{H}) . \quad (89)$$

The firing rate ν_{eff} (the zero-th order in the expansion in powers of k) is obtained by applying the condition (38) to f_0 in eq. (85).

Similarly, while solving eq. (84) a condition over g_1 is obtained, from where g_1 is determined, except for an unknown constant D :

$$g_1(x) = D e^{-\frac{x^2}{2(1+\alpha)}} + \frac{\tau_m \nu_1}{1 + \alpha} e^{-\frac{x^2}{2(1+\alpha)}} \int_x^{\sqrt{2}\hat{\Theta}} dy e^{\frac{y^2}{2(1+\alpha)}} H(y - \sqrt{2}\hat{H}) . \quad (90)$$

The constant D is needed to match the boundary condition at threshold (39).

Now it is crucial to realize that the first order solution f_1 does not satisfy the boundary condition at threshold (39) for any value of D . Thus, we have to add a *boundary solution* f_1^b so that the total solution (57) satisfies it up to order k . This boundary solution, found in the next section, serves to fix the value for D as

$$D = \alpha \nu_{eff} \tau_m e^{\frac{\hat{\Theta}^2}{(1+\alpha)}} . \quad (91)$$

Using the normalization condition (38) on the term order k in the expansion of $P_\alpha(x, y)$, eq. (57) leads to the firing rate at order k in eq. (58)⁷. In that equation we have approximated ν_{eff} by ν_0 and also all α appearing in eq. (90) have been made equal to zero. These two approximations are justified because expanding ν_{eff} and eq. (90) in powers of α gives corrections to the firing rate at order k that are higher than $O(\alpha)$.

E.2 The Boundary Solution

Here we find the boundary solution, f_1^b , for the FPE (34) valid close to threshold and for small k . The FPE in this limit takes the form

$$\left[\frac{\partial^2}{\partial r^2} - \sqrt{\alpha} y \frac{\partial}{\partial r} + \frac{\partial^2}{\partial y^2} - y \frac{\partial}{\partial y} + O(k, k^2) \right] u(r, y) = 0 . \quad (92)$$

⁷Notice below that $\int \int u(r, z) = O(k)$, and for this reason we can neglect its contribution to the rate at order k .

We have replaced $f_1^b(x, y) = u(r, y)Z_0(y)$ and we have made the linear transformation $r = (x - \sqrt{2}\hat{\Theta})/k$. A complete basis for this linear differential operator is not known, but if $\sqrt{\alpha} = 0$ a complete basis for an integrable function of $r \in [-\infty, 0], y \in [-\infty, \infty]$ is given by the set of functions $e^{\sqrt{nr}} H_n(y/\sqrt{2})$ for all $n > 0$, where H_n are the Hermite polynomials⁸. We insert into eq. (92) a solution u of the form $u = u_0 + \sqrt{\alpha}u_1 + \alpha u_2 + O(\alpha^{3/2})$ to obtain

$$\left[\frac{\partial^2}{\partial r^2} + \frac{\partial^2}{\partial y^2} - y \frac{\partial}{\partial y} \right] u_{i+1}(r, y) = y \frac{\partial}{\partial r} u_i(r, y). \quad (94)$$

The solution f_1^b has to be added to the perturbative solution f_1 , eq (86), to match the boundary condition (39), that is

$$D e^{-\frac{\hat{\Theta}^2}{1+\alpha}} - \sqrt{\alpha} y \frac{\partial}{\partial x} g_0|_{x=\sqrt{2}\hat{\Theta}} + u(0, y) = 0. \quad (95)$$

Defining $d = D e^{-\frac{\hat{\Theta}^2}{1+\alpha}}$ and expanding it in powers of $\sqrt{\alpha}$ as $d = d_0 + \sqrt{\alpha}d_1 + \alpha d_2 + O(\alpha^{3/2})$, as well as the others terms in eq. (95), we obtain the set of conditions

$$\begin{aligned} d_0 + u_0(0, y) &= 0, \\ d_1 + \nu_{eff} \tau_m y + u_1(0, y) &= 0, \\ d_2 + u_2(0, y) &= 0. \end{aligned}$$

Now we express each order u_i as a linear combination of the functions $e^{\sqrt{nr}} H_n(y/\sqrt{2})$ plus a particular solution as $u_i(r, y) = \sum_1^\infty A_{n,i} e^{\sqrt{nr}} H_n(y/\sqrt{2}) + u_{i,part}(r, y)$.

We find

$$\begin{aligned} u_0 &= 0, \quad d_0 = 0 \\ u_1 &= -\nu_{eff} \tau_m y e^r, \quad d_1 = 0 \\ u_2 &= -\nu_{eff} \tau_m [y^2 - 1] e^{\sqrt{2}r} + \nu_{eff} \tau_m [y^2 - 2] e^r, \quad d_2 = \nu_{eff} \tau_m. \end{aligned}$$

⁸The Hermite polynomials satisfy the equation

$$\left(\frac{\partial^2}{\partial y^2} - y \frac{\partial}{\partial y} \right) H_n \left(\frac{y}{\sqrt{2}} \right) = -n H_n \left(\frac{y}{\sqrt{2}} \right). \quad (93)$$

The first three polynomials $H_0(y) = 1$, $H_1(y) = 2y$ and $H_2(y) = 4y^2 - 2$ are used in our calculations.

With these solutions, we finally found the value of D up to order α , eq. (91).

F Short τ_c limit for a generic IF neuron.

In this section we extend the formalism described in Appendix E to calculate the firing rate of a generic IF neuron receiving a Gaussian exponentially correlated input in the short τ_c limit (Moreno and Parga, 2002). A generic IF neuron can be defined by the leak function, $f(V)$, that determines how the voltage behaves in absence of any input. In this model, the depolarization membrane potential $V(t)$ evolves from the reset voltage H according to the stochastic equation

$$\dot{V}(t) = -f(V) + I(t) , \quad (96)$$

where $I(t)$ is the synaptic current with exponentially temporal correlations as in eq. (17). When the Gaussian current is expressed using the second representation, as it is defined in Section (4.2), the FPE associated to this model neuron is

$$\left[\frac{\partial}{\partial V} (f(V) - \mu + \frac{\sigma_w^2}{2} \frac{\partial}{\partial V}) + \frac{1}{\tau_c} \frac{\partial}{\partial y} (y + \frac{\partial}{\partial y}) - \sqrt{\frac{2\sigma_w^2 \alpha}{\tau_c}} \frac{\partial}{\partial V} \right] P = -\delta(V-H) J(y) . \quad (97)$$

Using the same procedure as in Appendix E, we find that the output firing rate of such a generic neuron is

$$\nu_{out} = \nu_{eff} + \nu_1 \sqrt{\tau_c} \quad (98)$$

where

$$\begin{aligned} \nu_{eff}^{-1} &= \tau_{ref} + \frac{2}{\sigma_{eff}^2} \int_H^\Theta du e^{-\frac{2}{\sigma_{eff}^2} \int_\Theta^u dr (f(r) - \mu)} \int_{-\infty}^u dv e^{-\frac{2}{\sigma_{eff}^2} \int_\Theta^v dr (f(r) - \mu)} \\ \nu_1 &= -\frac{\sqrt{2\alpha} \nu_0^2}{\sigma_w} \int_{-\infty}^\Theta dv e^{-\frac{2}{\sigma_w^2} \int_\Theta^v dr (f(r) - \mu)} , \end{aligned} \quad (99)$$

which is valid whenever the above integrals are defined. This general formula, that has been previously found in our work (Moreno and Parga, 2002), shows that the $\sqrt{\tau_c}$ decay of the firing rate is *universal* for IF models with hard

threshold. Using this general formula it is possible to obtain the firing rate in the short τ_c limit given by eq. (58) for a LIF neuron.

Using a different procedure we have been able to calculate exactly the firing rate of a non-leaky IF neuron ($f(V) = 0$) with exponential correlations without the need of the boundary solution to fit the boundary condition at threshold. This formula is valid for *all* τ_c and for small α . We still require the condition $\tau_c \ll \tau_{ref}$. This exact formula, however, allows us to check the technical procedure described above, and it naturally gives the same result. This firing rate is expressed as

$$\nu_{out} = \nu_{eff} - \frac{\alpha \nu_0^2 [1 - e^{(\gamma-\lambda)(\Theta-H)}]}{\mu(\gamma + \lambda)} + O(\alpha^2) \quad (100)$$

where $\gamma = \frac{\mu}{\sigma_w^2}$, $\lambda = \sqrt{\gamma^2 + \frac{2}{\sigma_w^2 \tau_c}}$ and ν_{eff} is defined below, eq.(101). An expansion of eq. (100) for small τ_c leads to the same universal $\sqrt{\tau_c}$ decay law, and the coefficients are identical to those produced by eqs. (99):

$$\begin{aligned} \nu_{eff}^{-1} &= \tau_{ref} + \frac{\Theta - H}{\mu} \\ \nu_1 &= -\frac{\alpha \nu_0^2 \sigma_w}{\sqrt{2}\mu}. \end{aligned} \quad (101)$$

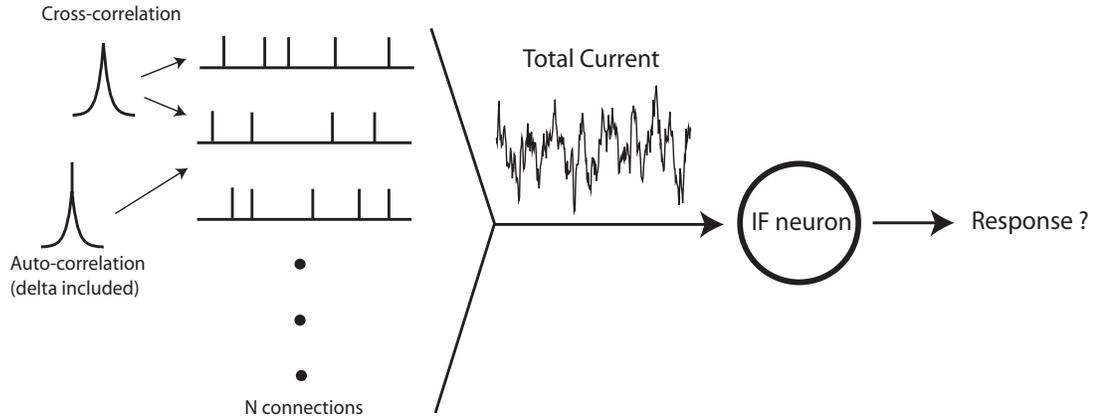


Figure 1:

Caption 1: Illustration of the problem studied in this paper (a fully detailed description is given in the text). A set of afferent presynaptic spike trains impinges on a LIF neuron. Each individual spike train has exponentially-shaped auto-correlations, describing the joint probability density of having two spikes separated by a particular time lag (a delta function should be included at zero time lag because the train is made of point events; see text). A fraction of the trains also have exponential cross-correlations, describing non-independent firing of some of the presynaptic neurons. The total current generated by the presynaptic bombardment is replaced by a Gaussian process with the same mean and two-point correlation function than that generated by the superposition of all presynaptic spike trains. The goal is to characterize the spiking response properties of the LIF neuron as a function of the global magnitude and timescale of the input correlations.

AUTO-CORRELATION FUNCTION

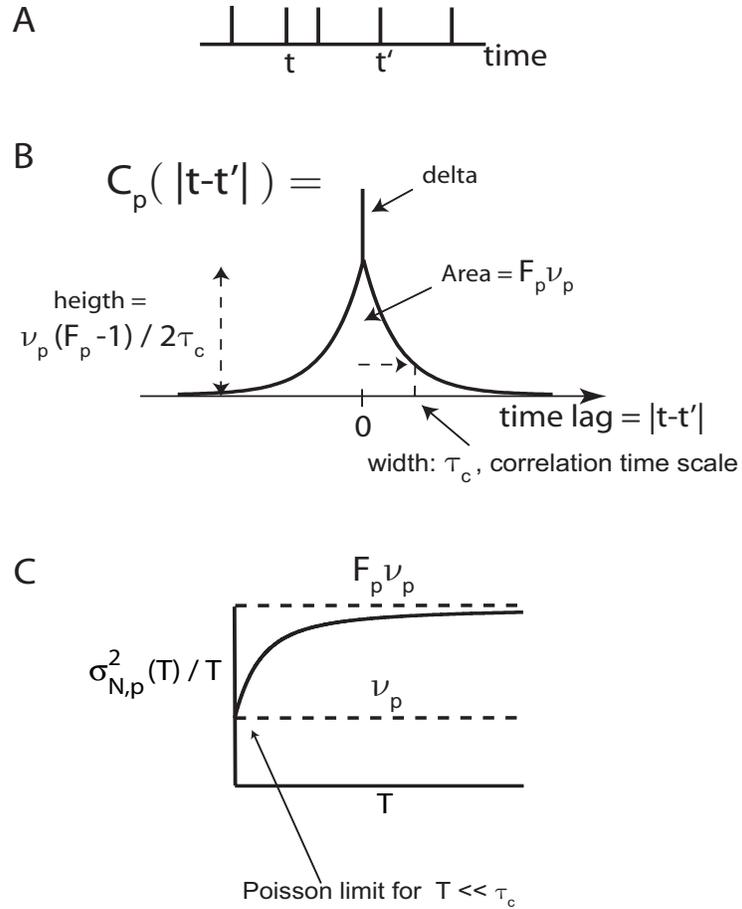


Figure 2:

CROSS-CORRELATION FUNCTION

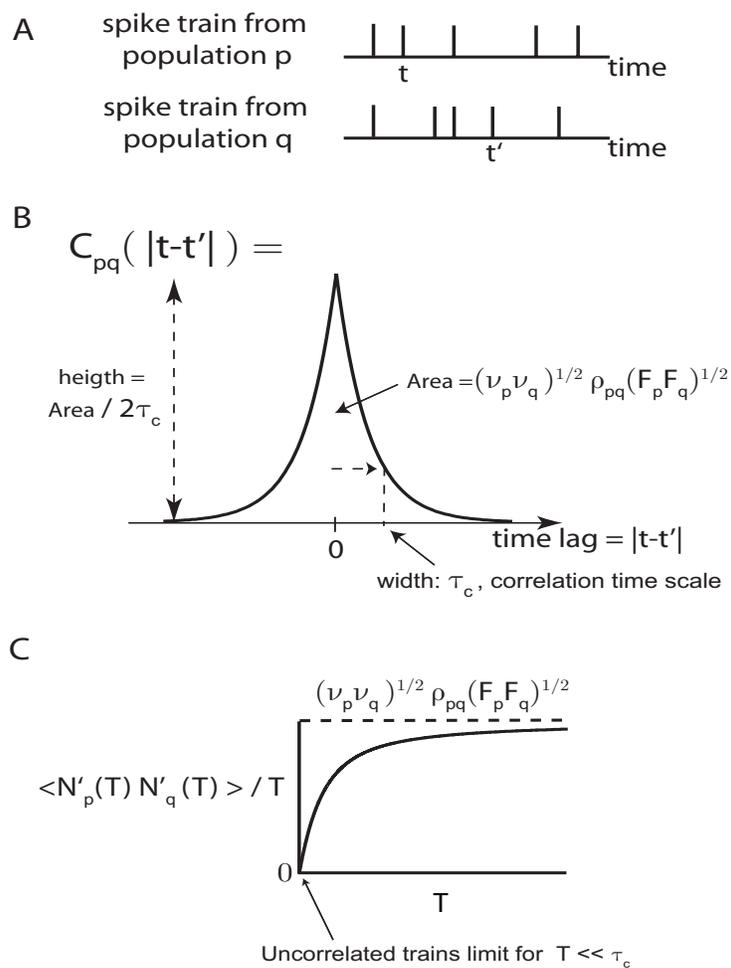


Figure 3:

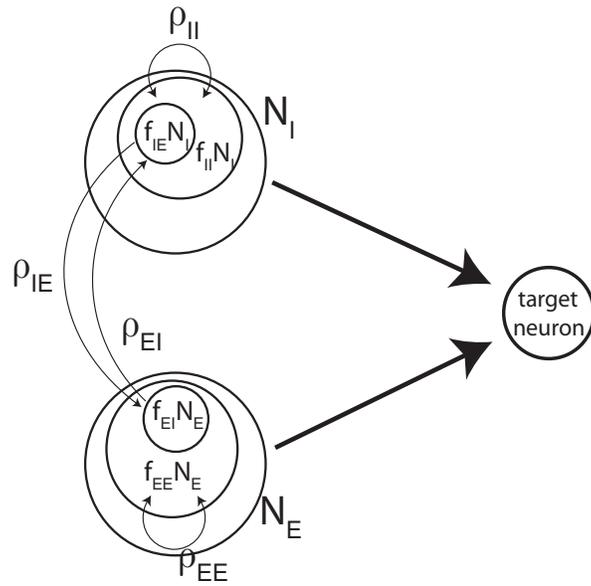


Figure 4:

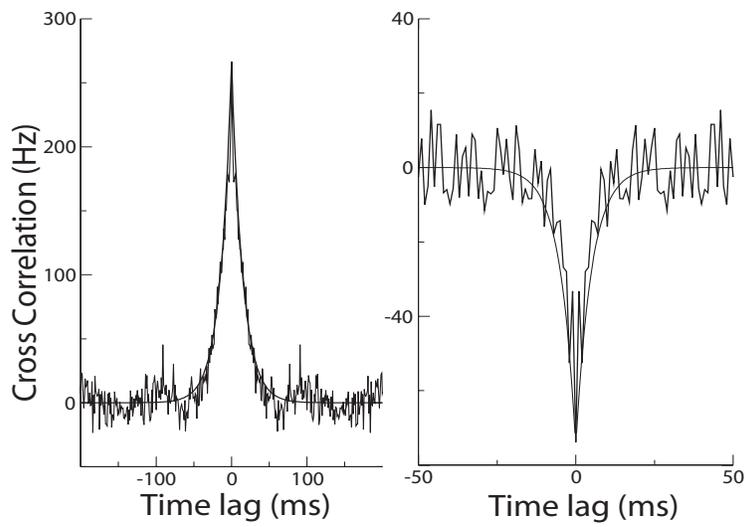


Figure 5:

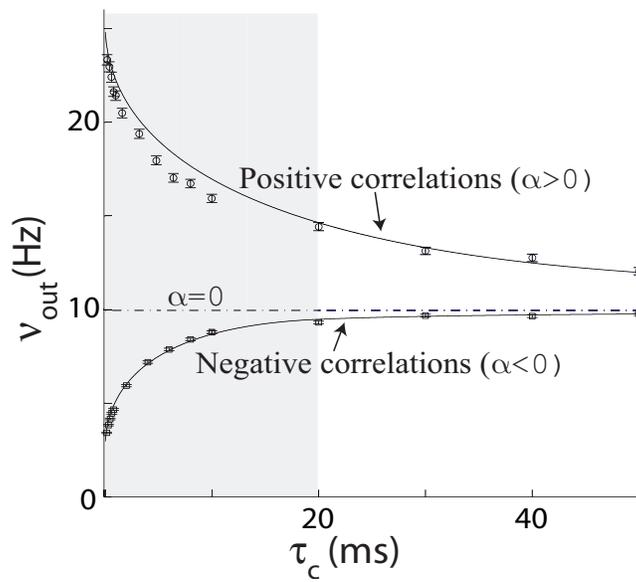


Figure 6:

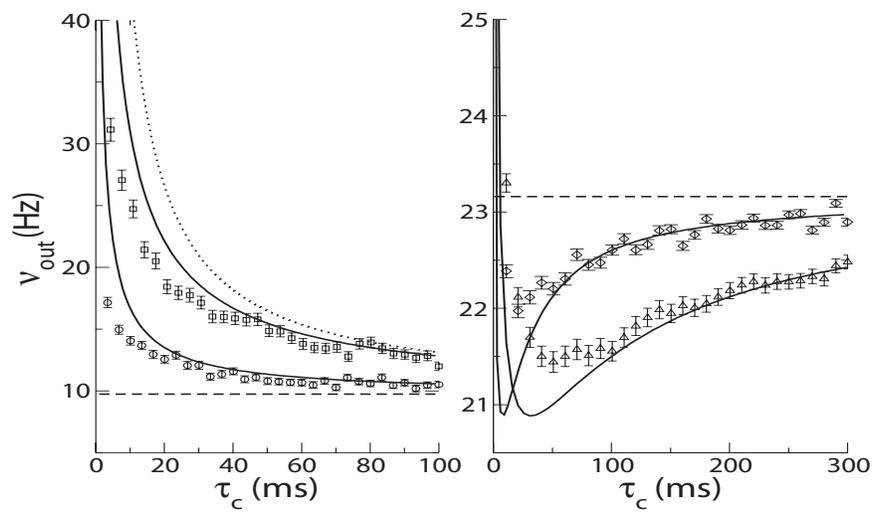


Figure 7:

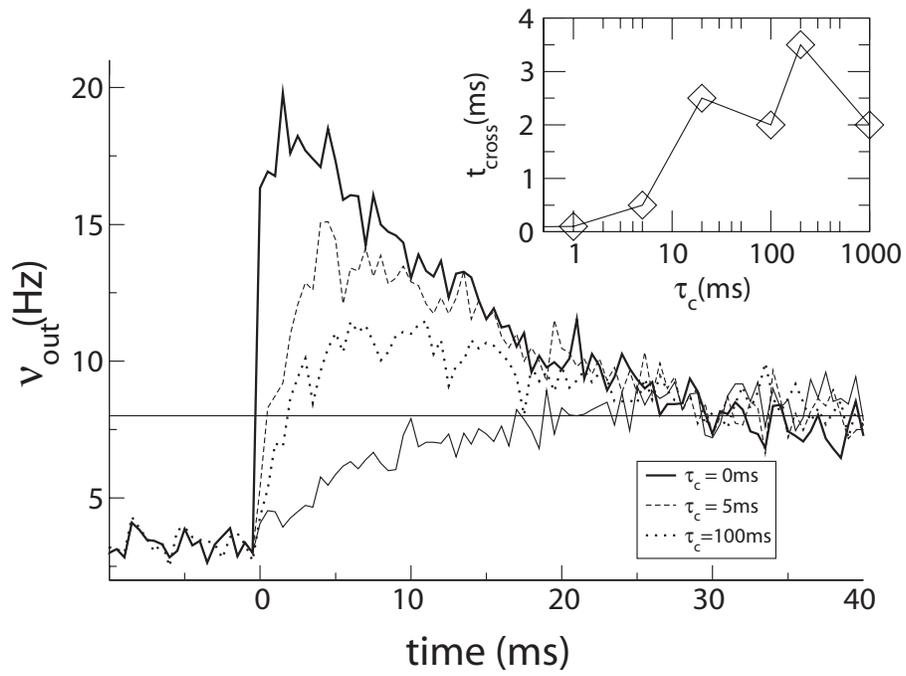


Figure 8:

Caption 2: (A): An individual afferent spike train from population p could show correlations between two times, t and t' : the probability of finding a spike at one of those times depends on the existence of a spike at the other time. (B): This temporal correlation is described by the auto-correlation function, $C_p(t - t')$, assumed to have an exponential shape. The firing rate, ν_p , Fano factor, F_p , and correlation time, τ_c , enters in the definition of the shape and size of the exponential as described in the plot. The delta function present at zero time is proportional to ν_p , and participates in the total area of the autocorrelogram. (C): When the spike count of the spike train is integrated over a time window T , the variance of the count divided by T goes exponentially from ν_p to $F_{N,p}\nu_p$. For small time windows, the count variance converges to that of a Poisson spike train, which is equal to $\nu_p T$. However, for longer time windows than the correlation time τ_c , the count variance scales as $F_{N,p}\nu_p$, indicating that then the effect of temporal correlations is fully visible.

Caption 3: (A): The probability of having a spike at time t in an afferent spike train belonging to population p could depend on the existence of having a spike at time t' on other spike train from population q . (B). This correlation is described by the cross-correlation function, $C_{pq}(t - t')$, assumed to have exponential shape. The firing rates, Fano factors, correlation coefficient of the spike counts, ρ_{pq} , and correlation time, τ_c , determine the shape of the exponential, as illustrated in the figure. (C): When the spike counts of the spike trains in the top panel are integrated over a time window T , their covariance divided by T increases exponentially from zero to a finite value proportional to the correlation coefficient (here we define $N'(T) = N(T) - \langle N(T) \rangle$). For short time windows, the covariance is zero and therefore it resembles that of two independent spike trains. However, for time windows longer than τ_c , correlations are fully visible and the covariance is non-zero.

Caption 4: Diagram of correlations in excitatory (E) and inhibitory (I) neuronal populations presynaptic to the same target neuron. The presynaptic E and I populations make N_E and N_I contacts respectively with the target neuron. A fraction $f_{EE(II)}$ of these $N_{E(I)}$ excitatory (inhibitory) neurons are correlated with each other with a correlation coefficient $\rho_{EE(II)}$. Also there are $E-I$ correlations, with a fraction f_{EI} participating from the E population and a fraction f_{IE} from the I population, for which the correlation coefficient is ρ_{EI} ($= \rho_{IE}$). Since all E neurons in the fraction f_{EI} are correlated with any given I neuron in the fraction f_{IE} , these E neurons necessarily have $E-E$ correlations. Therefore, they are considered here to be a group within the fraction f_{EE} , as shown in the figure. The same applies for the I neurons.

Caption 5: Normalized correlation functions of the current $I(t)$ numerically generated by simulating the process defined in eqs. (22 - 23). The normalized correlation function of the current is defined as $\hat{C}_{current}(s) = C_{current}(s)/\sigma_w^2 - \delta(s)$, where $C_{current}(s)$ is defined in eq. (26). The variable s is the time lag $s = t - t'$. With this normalization, the correlation function has units of Hz . For positive correlations (left) we took $\beta = 2$, which yields a correlation magnitude $\alpha = 8$; $\tau_c = 15ms$. For negative correlations (right) we took $\beta = -0.5$, which corresponds to $\alpha = -0.75$; here $\tau_c = 5ms$. In both cases, numerical results are compared with the exponential functions predicted by eq. (26) (non-fluctuating curves).

Caption 6: Theoretical predictions (lines) and simulation results (points) for the output firing rate of a LIF neuron driven by exponentially correlated inputs as a function of the correlation timescale. Here we use eq. (61) for short τ_c and eq. (62) for long τ_c , along with a continuous and smooth interpolation between the two limits (the interpolation is made at an intermediate $\tau_{c,inter} \sim \tau_m$). The rate decreases when the input correlations are positive ($\alpha > 0$, upper curve) and increases when correlations are negative ($\alpha < 0$, lower curve). When there are no correlations ($\alpha = 0$), the neuron fires at a rate of $10Hz$ (dashed-dotted line). Maximum rate differences relative to the rate with no input correlations are attained when $\tau_c = 0$, that is, when the input correlation is exquisitely precise. Differences are substantial whenever the correlation time is shorter than the membrane time constant of the neuron ($\tau_m = 20ms$ for this case; shaded region). When the correlation time becomes longer than τ_m , relative changes are much smaller, and the neuron becomes less sensitive to the input correlations. Correlation magnitudes are $\alpha = 8$ (upper curve) and $\alpha = -0.75$ (lower curve), and interpolations between the short and long τ_c theoretical predictions were performed at the interpolating time $\tau_{c,inter} = 40ms$ and $20ms$ respectively. Other parameters are $\tau_{ref} = 0ms$, $\Theta = 1$ (in arbitrary units), $H = 0$, $\mu = 42s^{-1}$, $\sigma_w^2 = 2s^{-1}$. Although the short τ_c expansion requires $\tau_{ref} \neq 0$ the simulation shows that this prediction is good even for zero τ_{ref} .

Caption 7: Theoretical predictions and simulation results for the firing rate of a LIF neuron as function of the correlation timescale for the sub- (left) and the suprathreshold regimes (right). Here we use eqs. (47,53), valid for long τ_c . For the subthreshold regime, the effect of increasing the correlation time is always to decrease the rate. However, for the suprathreshold regime and when the input noise is small, the effect is the opposite for long τ_c . As the input noise increases, this effect disappears and the curve becomes as in the subthreshold regime (data not shown). The theoretical predictions (full lines) are obtained using the firing rate given in eq. (53) without any interpolation, and the discrete points are the simulation results with the same parameters as in the theoretical curves. Parameters for the subthreshold regime are: $\mu = 0Hz$, $\sigma_w^2 = 50.5Hz$, and $\alpha = 4$ (top full line and squares), $\alpha = 1$ (bottom full line and circles) and $\alpha = 0$ (straight line). The dotted line has the same parameters as the top full line, but it has been obtained from the expression of the rate in eq. (47). Notice that the prediction from eq. (53), strictly only valid for long τ_c , is also good even when $\tau_c \sim \tau_m$, and it is better than that provided by eq. (47) for all τ_c . Parameters for the suprathreshold regime are: $\mu = 100.7Hz$, $\sigma_w^2 = 0.05Hz$, and a very large correlation strength $\alpha = 36$ (bottom line and triangles), a moderate correlation strength $\alpha = 9$ (intermediate line and diamonds) and $\alpha = 0$ (straight line). The other parameters are as in Fig. (6), except for $\tau_m = 10ms$.

Caption 8: Averaged transient firing responses of a LIF neuron to changes in the input statistics. Below $t = 0$ the input is white noise ($\alpha = 0$) with $\mu = 16s^{-1}$ and $\sigma_w^2 = 0.81s^{-1}$. Upper curve: instantaneous response when σ_w^2 is increased up to $\sigma_w^2 = 3.8s^{-1}$. Second (third) curve: quick response to correlation changes, with $\tau_c = 5ms$ ($100ms$) and $\alpha = 6.8$ (52.3). Bottom curve: slow response when μ is changed from $\mu = 16s^{-1}$ to $\mu = 19.9s^{-1}$ and σ_w^2 is kept constant. These values were chosen so that the evoked firing rates in the final steady state are roughly the same ($\sim 8Hz$, straight line). Inset: time when the firing rate response reaches for the first time the value of the final stationary rate as a function of τ_c . When the correlation timescale is very short, t_{cross} is very small, and it saturates for long τ_c . Neuron parameters are $\tau_m = 50ms$, $\tau_{ref} = 0$, $\Theta = 1$ and $H = 0$ (dimensionless).

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