Auto- and Crosscorrelograms for the Spike Response of Leaky Integrate-and-Fire Neurons with Slow Synapses

Rubén Moreno-Bote[1] and Néstor Parga[2,3]

[1]Center for Neural Science, New York University, New York, New York 10003-6621, USA

[2]Departamento de Física Teórica, Universidad Autónoma de Madrid, Cantoblanco, 28049 Madrid, Spain

[3]Center for Theoretical Neuroscience, Center for Neurobiology and Behavior, Columbia University, New York 10032-2695, USA

(Received 1 August 2005; published 17 January 2006)

An analytical description of the response properties of simple but realistic neuron models in the presence of noise is still lacking. We determine completely up to the second order the firing statistics of a single and a pair of leaky integrate-and-fire neurons receiving some common slowly filtered white noise. In particular, the auto- and cross-correlation functions of the output spike trains of pairs of cells are obtained from an improvement of the adiabatic approximation introduced previously by Moreno-Bote and Parga [Phys. Rev. Lett. **92**, 028102 (2004)]. These two functions define the firing variability and firing synchronization between neurons, and are of much importance for understanding neuron communication.

DOI: 10.1103/PhysRevLett.96.028101 PACS numbers: 87.19.La, 05.40.−a, 84.35.+i

The variability of the spike trains of cortical neurons and their correlations might constrain the coding capabilities of the brain [1], but they can also reflect the strategies the brain uses to decipher the stimuli arriving from the world [2]. Neurons in cortex fire with high variability resembling Poisson spike trains [3] and nearby pairs of cortical neurons fire in a correlated fashion [1], reflecting the presence of some common source of noise. These variability and correlation of the spike trains affect the firing statistics of a neuron receiving those inputs [4,5]. It has been shown that the large variability observed *in vivo* can be accounted for by neuron models operating in a regime in which the membrane time constant, τ_m, becomes shorter or comparable to the synaptic decay constants, τ_s, due to spontaneous background activity ($\tau_s \geq \tau_m$) [6,7]. However, very little progress has been made in providing analytical tools to describe such variability and correlations found in cortex.

In this Letter we study analytically the variability and correlations in the firing responses of pairs of leaky integrate-and-fire (LIF) neurons receiving both common and independent sources of white noise input filtered by synapses in the regime $\tau_s \geq \tau_m$. For a single neuron we obtain the firing rate, the autocorrelation function of its output spike train (ACF), and the Fano factor of the spike count, F_N. For a pair of cells, we obtain the cross-correlation function of their output spike trains (CCF) and the correlation coefficient of their spike counts, ρ. These results characterize completely the firing response of these spiking neurons up to second order, and open the possibility for a principled way of including synchrony effects in the modeling of biologically plausible spiking neural networks.

The neuron and input models.—The membrane potential $V(t)$ of a single LIF neuron with membrane time constant τ_m and receiving an afferent current $I(t)$ obeys

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

A spike is generated when $V(t)$ reaches a threshold Θ, after which the neuron is reset to H, from where it continues integrating the current [8]. The external input is modeled by a white noise with mean μ and variance σ^2 [8], which is filtered by synapses with decay time constant τ_s, resulting in a current described by

$$\tau_s \dot{I}(t) = -I(t) + \mu + \sigma\eta(t), \tag{2}$$

where $\eta(t)$ is a Gaussian white noise with zero mean and unit variance. We simplify Eqs. (1) and (2) by performing the linear transformations $I = \mu + z\sigma/\sqrt{2\tau_s}$ and $V = \mu\tau_m + x\sigma\sqrt{\tau_m/2}$, obtaining

$$\dot{x} = \frac{1}{\tau_m}(-x + \gamma z), \tag{3}$$

$$\dot{z} = -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}}\eta(t), \tag{4}$$

with $\gamma = \sqrt{\tau_m/\tau_s}$. In the normalized potential, x, the threshold and reset read $\hat{\Theta} = \sqrt{2}(\Theta - \mu\tau_m)/\sigma\sqrt{\tau_m}$ and $\hat{H} = \sqrt{2}(H - \mu\tau_m)/\sigma\sqrt{\tau_m}$.

The autocorrelation function.—To determine the ACF, first we describe the time evolution of the probability density of having the neuron in the state (x, z) at time t given that initially the neuron has just fired ($x = \hat{H}$) and $z = z_0$. The Fokker-Planck equation (FPE) for this density, $P(x, z, t|\hat{H}, z_0)$, is [9]

$$\tau_m \frac{\partial}{\partial t} P = \left[\frac{\partial}{\partial x}(x - \gamma z) + \epsilon^2 L_z\right] P + \tau_m J(z, t|z_0)\delta(x - \hat{H}), \tag{5}$$

where $\epsilon = \gamma = \sqrt{\tau_m/\tau_s}$ and $L_z = \frac{\partial}{\partial z} z + \frac{\partial^2}{\partial^2 z}$. $J(z, t|z_0)$ is the probability density of having a spike at time t along with a fluctuation z given that $z = z_0$ at time $t = 0$. This probability is expressed as a function of the density P as [9]

$$J(z, t|z_0) = \frac{1}{\tau_m}(-\hat{\Theta} + \gamma z)P(\hat{\Theta}, z, t|\hat{H}, z_0). \tag{6}$$

Solving the FPE (5) with $J(z, t|z_0)$ as a source term at $x = \hat{H}$ means that each time a spike is produced, the normalized potential x is reset to $\hat{H}$ while z keeps its same value.

The integral $\int dz J(z, t|z_0)$ expresses the probability of having a spike at time t conditioned to the fact that $z = z_0$ at time $t = 0$. We define the ACF, $C(t)$, as the probability density of firing a spike at time $t > 0$ conditioned to the fact that at time $t = 0$ there was a spike. Therefore, $C(t)$ is the average of $\int dz J(z, t|z_0)$ with the distribution of z_0 conditioned to the production of a spike at time $t = 0$, $B(z_0)$. Since $B(z)$ is the distribution of z at the *moment of a spike,* then $B(z) = J(z)/\nu$, where $J(z)$ is the limit $t \to \infty$ of $J(z, t|z_0)$, and ν is its normalizing factor $[\nu = \int dz J(z)]$ and also the firing rate of the LIF neuron defined by Eqs. (3) and (4). Therefore, the ACF is computed as

$$C(t) = \int dz_0 \frac{J(z_0)}{\nu} \int dz J(z, t|z_0). \tag{7}$$

The solution of the FPE (5) and Eq. (7) is simplified by noticing that z is a pure Ornstein-Uhlenbeck process, Eq. (4), and therefore its marginal distribution, $P(z, t|z_0)$, is (see, e.g., [8])

$$P(z, t|z_0) = \frac{1}{\sqrt{2\pi(1 - e^{-2t/\tau_s})}} e^{-[(z - z_0 e^{-t/\tau_s})^2/2(1 - e^{-2t/\tau_s})]}, \tag{8}$$

which broadens over time and for $t \gg \tau_s$ approaches a normal distribution, $p(z) = e^{-z^2/2}/\sqrt{2\pi}$.

The analytical solution.—We expand $P(x, z, t|\hat{H}, z_0)$ and $J(z, t|z_0)$ in powers of ϵ^2, as $P = P_0 + \epsilon^2 P_1 + 0(\epsilon^4)$ and $J = J_0 + \epsilon^2 J_1 + 0(\epsilon^4)$, following a technique introduced in [9] for the stationary FPE. In this expansion, the parameter γ in Eqs. (5) and (6) is assumed to be fixed. Only at the end, when the leading orders of the expansion have been found, γ is given its true value $\gamma = \sqrt{\tau_m/\tau_s}$.

The solution at zeroth order of the FPE (5) satisfying conditions (6) and (8) is

$$P_0(x, z, t|\hat{H}, z_0) = P(z, t|z_0)\delta(x - X(z, t)), \tag{9}$$

where $X(z, t)$ is the time evolution of the variable x obtained from Eq. (3) with *frozen* z and initial condition $\hat{H}$. Notice that $x = X(z, t)$ is a periodic function of t, because whenever $x = \hat{\Theta}$, x is reset to $\hat{H}$. Its period, $T(z) = \tau_m \ln(\hat{H} - \gamma z/\hat{\Theta} - \gamma z)$ $[T(z) = \infty$ for $z < \hat{\Theta}/\gamma]$, is the interspike interval (ISI) of a LIF neuron receiving a frozen z, and it is calculated from Eq. (3) as the first time T at which $X(z, T) = \hat{\Theta}$. After expressing the delta functions in terms of t, the probability density current, Eq. (6), at zeroth order becomes

$$J_0(z, t|z_0) = P(z, t|z_0) \sum_{n=1}^{\infty} \delta(t - nT(z)). \tag{10}$$

This expression has a simple interpretation. The sum of delta functions in the index n represents a regular train of spikes with ISI $T(z)$, as if z were fixed. Therefore, the probability of having a spike along with a fluctuation z at time t, J_0, is given at a first approximation by the product of both the probability of finding at time t a spike of the train generated with frozen fluctuation z, and the probability of having such a fluctuation z at time t starting from the initial condition $z = z_0$, $P(z, t|z_0)$. Note that in Eq. (10) the noise is allowed to evolve in time following the distribution $P(z, t|z_0)$. It has been proved that the stationary (frozen) distribution of z can be employed to describe the firing rate of LIF neurons [9,6], and used the approximation that z is constant during the ISIs to describe the Fano factor of non-LIF neurons with weak noise [10]. However, freezing completely the noise z in Eq. (10) leads to very poor predictions in our problem (not shown).

To determine the ACF, Eq. (7), at zeroth order, $C_0(t)$, the zeroth order $J(z)$ is required, which is [9]

$$J_0(z) = \nu_0(z)p(z), \tag{11}$$

where $\nu_0(z) = 1/T(z)$ for $z \geq \hat{\Theta}/\gamma$ and $\nu_0(z) = 0$ otherwise. $C_0(t)$ is computed, after using Eqs. (7), (10), and (11), and evaluating the delta functions, as

$$C_0(t) = \sum_{n=1}^{\infty} \int \frac{dz_0 J_0(z_0)(\gamma z_n - \hat{H})(\gamma z_n - \hat{\Theta})}{\nu_0 \tau_m n\gamma(\hat{\Theta} - \hat{H})} P(z_n, t|z_0), \tag{12}$$

where $z_n \equiv z_n(t) \equiv \gamma^{-1}(\hat{\Theta} - \hat{H}e^{-t/n\tau_m})/(1 - e^{-t/n\tau_m})$. The z_ns are the roots of the equations $t = nT(z_n)$, the zeros of the delta functions in Eq. (10).

In Fig. 1 we plot the ACF for the output spike train of a LIF neuron computed using Eq. (12) and compare it with simulation results. The agreement is very good in both the subthreshold (left) and suprathreshold (right) regimes. In both regimes, the ACF shows a prominent peak after a relative refractory period of about 10 ms ($\sim\tau_m$). This means that the potential has to be integrated from reset to threshold to emit the first spike. The prominent peak indicates that the neuron is bursty, producing spikes that are grouped within short time intervals of 20 ms ($\sim\tau_s$) [9]. After the prominent peak, the ACF decays to a steady-state value either monotonically (left) or with a damped oscillation (right). Damped oscillations are a robust feature in the suprathreshold regime, as is their absence in the subthreshold regime. This reflects the fact that the neuron in the suprathreshold regime fires more regularly, and therefore the output spikes tend to occur at integer number of times the mean ISI (see the peaks of the oscillations in the ACF). For long times ($t \gg \tau_s$) the memory of the spike at time $t = 0$ has disappeared, and the ACF decays to the unconditioned probability of having a spike, that is, the firing rate of the LIF neuron.

The firing rate, Fano factor, and CV.—As it is clear, the firing rate can be obtained from the ACF, Eq. (12), in the

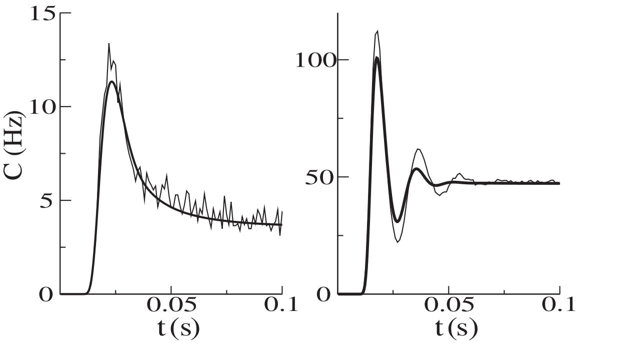

FIG. 1. ACF of a LIF neuron in the subthreshold (left) and suprathreshold regimes (right). The figures show the typical shape in both regimes: no oscillations and a large peak in the subthreshold regime ($\mu\tau_m < \Theta$) and damped oscillations in the suprathreshold regime ($\mu\tau_m > \Theta$). Thick lines are the analytical results obtained from Eq. (12) (the sum has been cut at $n = 200$ with $t = 200$ ms), and thin lines correspond to the numerical simulations of the same LIF neuron. Parameters for the subthreshold (suprathreshold) neuron are $\mu = 85$ Hz (115 Hz), $\sigma^2 = 6$ Hz (3 Hz). Other parameters are $H = 0$, $\Theta = 1$, $\tau_m = 10$ ms, and $\tau_s = 20$ ms.

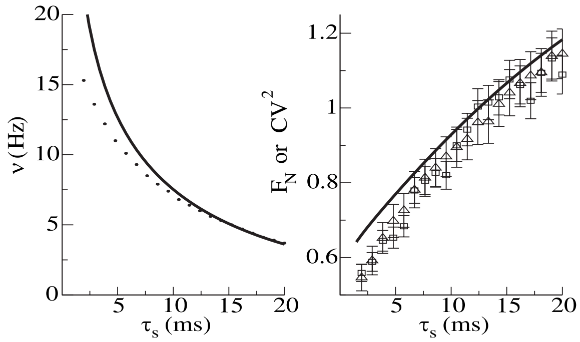

FIG. 2. The firing rate (left), the Fano factor (right), F_N, and the CV^2 (right) for the output spike train of a LIF neuron are plotted as a function of τ_s. The firing rate prediction (line) is calculated using both Eq. (13) and $\nu_0 = \int dz J_0(z)$, and it is compared with simulation results (points). The F_N predicted by Eqs. (14), (12), and (13) (line), is compared with the F_N (squares) and CV^2 (triangles) obtained from simulations. Parameters values are as in the subthreshold regime of Fig. 1.

limit of long times ($t \gg \tau_s$). This rate has the expression

$$\nu_0 = \lim_{t\to\infty} \sum_{n=1}^{\infty} \frac{[\gamma z_n(t) - \hat{H}][\gamma z_n(t) - \hat{\Theta}]}{\sqrt{2\pi}\,\tau_m n \gamma(\hat{\Theta} - \hat{H})} e^{-z_n(t)^2/2}. \quad (13)$$

A different expression for the firing rate can be computed using $\nu_0 = \int dz J_0(z)$ [9]. In fact, both expressions give identical results when they are plotted as a function of τ_s (continuous curve in Fig. 2, left). However, computationally, Eq. (13) is much faster because it involves only a sum that can be cut at $n \sim 200$ (using $t = 200$ ms). Naturally, the number of terms needed to approximate the ACF and the firing rate grows as t increases. Comparison of both expressions of ν_0 with simulation results shows that the prediction is very good even when $\tau_s \sim \tau_m$.

The Fano factor of the output spike train, F_N, defined as the ratio between the variance of the spike count and its mean evaluated for long time windows, is directly related to the time integral of ACF as ([11] and see, e.g., Eq. (3) of Ref. [5])

$$F_N = 1 + 2\int_0^{\infty} dt[C(t) - \nu]. \quad (14)$$

We have evaluated the zeroth order F_N in Eq. (14) using the zeroth order solutions of $C(t)$ and ν, Eqs. (12) and (13). The prediction fits very well the simulation results (right panel of Fig. 2). We have also computed the coefficient of variation of the ISIs, CV, of the neuron response using simulations (same panel). It is known that for renewal processes $F_N \equiv CV^2$ [e.g., for a Poisson process $F_N \equiv CV^2 = 1$, and $C(t) = \nu$]. Here we find that $F_N \sim CV^2$ even when the output response is not a renewal process. This is because, although the synaptic time scale introduces correlations in the successive ISIs, for low (but typical) rates $\tau_s < \nu^{-1}$ the correlation between successive ISIs is small. We also find that the firing variability is large when $\tau_s \geq \tau_m$ [6,7].

The cross-correlation function and correlation coefficient.—A central issue to describe population dynamics is to understand the way neuron activity synchronizes. Here we study a *pair of identical LIF neurons* ($k = 1, 2$)

$$\tau_m \dot{V}_k = -V_k + \tau_m[I_k(t) + I_c(t)], \quad (15)$$

receiving both an independent source of current, $I_k(t)$, and a common source, $I_c(t)$. Each current is described by an equation identical to Eq. (2), with mean $\mu_{\rm ind}$ and variance $\sigma^2_{\rm ind}$ for the independent components, and mean μ_c and variance σ_c^2 for the common component. Each neuron receives a total mean current $\mu = \mu_{\rm ind} + \mu_c$ and total variance $\sigma^2 = \sigma^2_{\rm ind} + \sigma^2_c$.

The CCF of the output spike trains of the two neurons [denoted as $CC(\Delta)$] can be obtained by an analysis similar to that used for the ACF. The CCF is defined as the joint probability density of having a spike of neuron 1 at a given time and a spike from neuron 2 after a delay Δ. Here we summarize only the main results. First, we define the normalized fluctuations $u_k = (I_k + I_c - \mu)/\sigma$, having zero mean and unit variance. Notice that these are not independent because of the common input I_c. Second, if neuron 1 has a fluctuation u_1, the probability density that after a delay Δ neuron 2 has a fluctuation u_2, $P(u_2, \Delta | u_1)$, is a Gaussian distribution with mean $\langle u_2(\Delta, u_1)\rangle = u_1 e^{-\Delta/\tau_s}\sigma_c^2/\sigma^2$ and variance $\mathrm{Var}(u_2(\Delta)) = 1 - e^{-2\Delta/\tau_s}\sigma_c^2/\sigma^2$. Then, for long τ_s

$$CC_0(\Delta) = \lim_{t\to\infty} \int du_1 du_2 P(u_2, \Delta | u_1) p(u_1) \times \sum_{n,m=1}^{\infty} \delta(t - nT(u_1))\delta(t + \Delta - mT(u_2)), \quad (16)$$

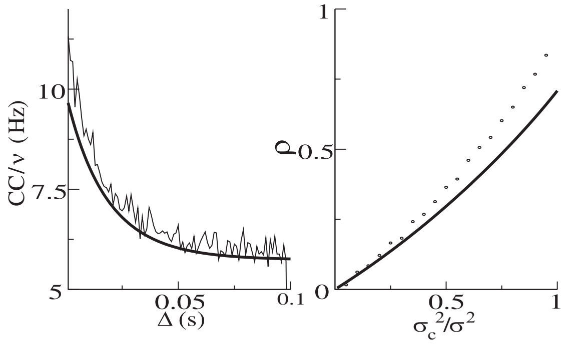

FIG. 3. Left: Theoretical [thick line, Eq. (17)] and simulated (thin line) CCFs normalized by the firing rate of one of the neurons as a function of time lag. Here $\sigma_c^2 = 2$ Hz. Right: Theoretical [line, Eq. (18)] and simulated (points) correlation coefficient, ρ, for the output spike trains of a pair of identical LIF neurons as a function of the fraction of common noise, σ_c^2/σ^2. The numerical ρ is calculated using Eq. (18) integrating the simulated CCF. Parameters for both figures are $\mu = 85$ Hz, $\sigma^2 = 9$ Hz, and the others as in Fig. 1.

where $T(u_k) = \tau_m \ln(\hat{H} - \gamma u_k/\hat{\Theta} - \gamma u_k)$ [$T(u_k) = \infty$ for $u_k < \hat{\Theta}/\gamma$] is the ISI of the neuron i receiving a *constant* fluctuation u_k, and $p(u_1)$ is a normal distribution describing the steady-state distribution of the fluctuations of neuron 1. The quantities γ, $\hat{H}$, and $\hat{\Theta}$ are defined as before. The two sums of delta functions in Eq. (16) can be interpreted as the product of two output spike trains with fixed ISI (determined by the input fluctuations), quantity which has to be averaged over all the possible fluctuations. The result of such an average is the CCF when the limit $t \to \infty$ is taken to allow randomization of the initial conditions, Eq. (16). This equation can be simplified by integration of the delta functions, obtaining

$$CC_0(\Delta) = \lim_{t\to\infty} \sum_{n,m=1}^{\infty} \frac{(\gamma a_n - \hat{H})(\gamma b_n - \hat{H})}{nm\tau_m^2 \gamma^2 (\hat{\Theta} - \hat{H})^2} \times (\gamma a_m - \hat{\Theta})(\gamma b_m - \hat{\Theta}) P(b_m, \Delta | a_n) p(a_n), \quad (17)$$

where $a_n \equiv z_n(t)$ and $b_m \equiv z_m(t + \Delta)$, with $z_n(t)$ as in Eq. (12). The theoretical CCF matches very well the simulated one (Fig. 3, left). Typically, the prediction underestimates the central peak at time lag zero (notice that the CCF is symmetric around $\Delta = 0$). The peak decays within a time of the order of τ_s. This is because the synaptic input, being slower than the neuron dynamics, sets its own time scale in the dynamics of interactions of the two neurons. The existence of a single peak is robust for low values of σ_c^2 in both the subthreshold and suprathreshold regimes, but other side secondary peaks arise when all the noise is essentially common. For long Δ, the CCF converges to the product of the firing rates at zeroth order, ν_0^2 [see Eq. (13)], because the neurons fire independently.

The correlation coefficient, ρ, of the spike counts for long time windows of the output spike trains of two identical neurons can be computed from their CCF ([11] and see, e.g., Eq. (4) of Ref. [5])

$$\rho = \frac{2}{F_N \nu} \int_0^\infty ds[CC(s) - \nu^2]. \quad (18)$$

For the two neurons in Eq. (15) it can be computed at zeroth order using the zeroth orders of $CC(\Delta)$, Eq. (17), F_N, and ν. We have compared the theoretical and simulated ρ as the fraction of common noise increases (Fig. 3, right). The prediction is good for low values of common noise and departs from the simulations for larger values. As the common noise increases, ρ increases monotonically and reaches $\rho = 1$ when the common noise equals the total input noise. Correlation coefficients of ~ 0.1 as those found in cortex [1] are predicted accurately, and they are obtained when the common noise represents $\sim 20\%$ of the total synaptic noise entering into the neuron, which can be a realistic value [1]. Therefore, the right plot at Fig. 3 provides a valuable tool to estimate the fraction of common noise from the correlations of the spike trains of pairs of neurons, a quantity that otherwise is not available experimentally.

R. M. thanks N. Rubin and J. Rinzel for their hospitality at the CNS. We thank A. Renart for his comments. R. M. and N. P. are supported by the Swartz Foundation and N. P. also by the Spanish Grant No. BMF 2003-06242.

[1] M. N. Shadlen and W. T. Newsome, J. Neurosci. **18**, 3870 (1998); E. Zohary and M. N. Shadlen, Nature (London) **370**, 140 (1994).
[2] W. Singer, Neuron **24**, 49 (1999); E. Salinas and T. J. Sejnowski, Nat. Rev. Neurosci. **2**, 539 (2001).R. C. deCharms and M. M. Merzenich, Nature (London) **381**, 610 (1996).
[3] W. Softky and C. Koch, J. Neurosci. **13**, 334 (1993).
[4] E. Salinas and T. J. Sejnowski, J. Neurosci. **20**, 6193 (2000).
[5] R. Moreno, J. de la Rocha, A. Renart, and N. Parga, Phys. Rev. Lett. **89**, 288101 (2002).
[6] R. Moreno-Bote and N. Parga, Phys. Rev. Lett. **94**, 088103 (2005).
[7] G. Svirskis and J. Rinzel, Biophys. J. **79**, 629 (2000); A. Destexhe, M. Rudolph, and D. Paré, Nat. Rev. Neurosci. **4**, 739 (2003).
[8] L. M. Ricciardi, *Diffusion Processes and Related Topics in Biology* (Springer-Verlag, Berlin, 1977).
[9] R. Moreno-Bote and N. Parga, Phys. Rev. Lett. **92**, 028102 (2004).
[10] J. W. Middleton, M. J. Chacron, B. Lindner, and A. Longtin, Phys. Rev. E **68**, 021920 (2003).
[11] D. R. Cox, *Renewal Theory* (John Wiley, New York, 1962).