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

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An analytical description of the response properties of simple but realistic neuron models in the presence of noise is still lacking. We determine completely the firing response of pairs of leaky integrate-and-fire neurons receiving some common slowly filtered white noise. These results characterize completely the firing response through the linear transformations $I = \mu + z\sigma/\sqrt{2}\tau$, where $\mu$ and variance $\sigma^2$ are the filtered by synapses with decay time constant $\tau_s$, resulting in a current described by

$$\tau_s i(t) = -I(t) + \mu + \sigma \eta(t),$$

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 $I = \mu + z\sigma/\sqrt{2}\tau$, and $V = \mu\tau_m + x\sigma\sqrt{\tau_m}/2$, obtaining

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

$$\dot{z} = -\frac{z}{\tau_s} + \frac{\gamma}{\tau_s} \eta(t),$$

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

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 $(x = \tilde{H})$ and $z = z_0$. The Fokker-Planck equation (FPE) for this density, $P(x, z, t|\tilde{H}, z_0)$, is [9]

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

where $\epsilon = \sqrt{\tau_m/\tau_s}$ and $L_z = \frac{\partial^2}{\partial z^2} + \frac{\gamma^2}{\tau_s^2}$. $J(z, t|z_0)$ 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]
\[ J(z, t|z_0) = \frac{1}{\tau_m} (-\hat{\Theta} + \gamma z)J(\hat{\Theta}, z, t|\hat{H}, z_0). \]  
(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 \( \int dzJ(z, t|z_0) \) 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 \( \int dzJ(z, t|z_0) \) 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 \( \nu \) is its normalizing factor \( \{\nu = \int dzJ(z)\} \) and also the firing rate of the LIF neuron defined by Eqs. (3) and (4). Therefore, the ACF is computed as

\[ C(t) = \int dz_0 \frac{J(z_0)}{\nu} \int dzJ(z, t|z_0). \]  
(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])

\[ P(z, t|z_0) = \frac{1}{\sqrt{2\pi(1 - e^{-2\tau/s})}} e^{-[(z - z_0 - e^{-\tau/s})^2/2(1 - e^{-2\tau/s})]}, \]  
(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 \( \epsilon^2 \), 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 \( \gamma \) in Eqs. (5) and (6) is assumed to be fixed. Only at the end, when the leading orders of the expansion have been found, \( \gamma \) 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

\[ P_0(x, z, t|\hat{H}, z_0) = P(z, t|z_0) \delta(x - X(z, t)), \]  
(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, \( T(z) = \tau_m \ln(\hat{H} - \gamma z/\hat{\Theta} - \gamma z) \), 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

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

\[ J_0(z) = \nu_0(z)p(z). \]  
(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

\[ C_0(t) = \frac{\sum_{n=1}^{\infty} \int dz_0 J_0(z_0)(z_{n}-\hat{H})(z_n-\hat{\Theta})}{\nu_0^2 \tau \sum_{n=1}^{\infty} p(z_n, t|z_0)}, \]  
(12)

which \( z_n \equiv z_n(t) \equiv y^{-1}(\hat{\Theta} - \hat{H} e^{-t/\tau_m})/(1 - e^{-t/\tau_m}) \). The \( z_n \)'s 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 (\( \approx \tau_m \)). 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 (\( \approx \tau_m \)) [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 (\( t \gg \tau_m \)) 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
threshold (suprathreshold) neuron are 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 $\tau_c = 20$ ms.

The prediction fits very well the simulation results (right panel of Fig. 2). The Fano factor of the output spike train, $\text{FN}$, 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 (111) and see, e.g., Eq. (3) of Ref. [5])

$$F_N = 1 + 2 \int_0^\infty dt \langle C(t) - \nu \rangle.$$ (14)

We have evaluated the zeroth order $F_N$ in Eq. (14) using the zeroth order solutions of $C(t)$ and $\nu$ 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 $\tau_e < \nu^{-1}$ the correlation between successive ISIs is small. We also find that the firing vairability is large when $\tau_s \gtrsim \tau_m$ [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 $k = 1, 2$

$$\tau_m V_k = -V_k + \tau_m [I_k(t) + I_c(t)].$$ (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 $\mu_{\text{ind}}$ and variance $\sigma^2_{\text{ind}}$ for the independent components, and mean $\mu_c$ and variance $\sigma^2_c$ for the common component. Each neuron receives a total mean current $\mu = \mu_{\text{ind}} + \mu_c$ and total variance $\sigma^2 = \sigma^2_{\text{ind}} + \sigma^2_c$.

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 $\Delta$. 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 $\Delta$ neuron 2 has a fluctuation $u_2$, $P(u_2, \Delta | u_1)$, is a Gaussian distribution with mean $(u_2(\Delta, u_1)) = u_1 e^{-\Delta/\tau_c \sigma^2_c/\sigma^2}$ and variance $\text{Var}(u_2(\Delta, u_1)) = 1 - e^{-2\Delta/\tau_c \sigma^2_c/\sigma^2}$. Then, for long $\tau_s$

$$CC(\Delta) = \lim_{\nu \to 0} \int udud\nu P(u_2, \Delta | u_1) p(u_1) \times \sum_{n,m=1}^{\infty} \delta(t - nT(u_1)) \delta(t + \Delta - mT(u_2)).$$ (16)
The quantities $T(u_k) = \tau_m \ln(\hat{H} - \gamma u_k/\hat{\Theta} - \gamma u_k)$ for $u_k < \hat{\Theta}/\gamma$ is the ISI of the neuron $i$ to receive 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 $\gamma$, $\hat{H}$, 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

$$CC_0(\Delta) = \lim_{t \to \infty} \sum_{n,m=1}^{\infty} \frac{(ya_n - \hat{H})(yb_n - \hat{H})}{nm\sigma^2_{a_n}\gamma'(\hat{\Theta} - \hat{H})^2} \times (ya_n - \hat{\Theta})/(yb_n - \hat{\Theta})P(b_m, \Delta \lvert a_n)p(a_n),$$  

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 $\tau_s$. 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 $\sigma_\Delta^2$ in both the subthreshold and supra-threshold regimes, but other side secondary peaks arise when all the noise is essentially common. For long $\Delta$, the CCF converges to the product of the firing rates at zeroth order, $\rho^2$ [see Eq. (13)], because the neurons fire independently.

The correlation coefficient, $\rho$, 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])

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

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 $\nu$. We have compared the theoretical and simulated $\rho$ 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, $\rho$ 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.

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