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Response of a LIF neuron to inputs filtered with arbitrary time scale

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Abstract

Neurons process their inputs with a variety of synaptic time scales. The presence of fast or slow filters provides the neuron with particular behaviors and changes quantitatively the output rate of the neuron. Here we study the effect of synapses with arbitrary time constant τ_s on the neuron response and give an analytical prediction of the firing rate for arbitrary values of τ_s.

Keywords: Integrate-and-fire neuron; Synaptic filtering; Neuron response; Fokker–Planck equation

1. Introduction

A neuron communicates with other neurons through synapses by generating synaptic currents. These currents manifest a wide variety of characteristic time scales. For example, AMPA-type receptors open during only 1–5 ms, while the activation of NMDA receptors lasts for $\sim$ 100 ms. Also, the effect of a spike on the post-synaptic neuron depends on the effective membrane time constant τ_m of this neuron [1]. We will show that the value of the ratio τ_m/τ_s sets the operating regime of a leaky integrate-and-fire (LIF) neuron model with added synaptic filters [4]. Besides, we prove that a perturbative expansion of its output firing rate in powers of $\varepsilon = \sqrt{\tau_m/\tau_s}$ does not exist.

2. Model and analytical solution

The membrane potential V of the model neuron obeys

$$\tau_m \dot{V} = -V + \tau_m I(t), \qquad (1)$$

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where $I(t)$ is the pre-synaptic current. When V reaches a threshold value Θ, the neuron produces a spike and V it is reset to a value H. If a large barrage of pre-synaptic spikes arrives at the neuron per unit time, the input can be approximated [5] by its mean μ and variance σ^2. Synapses filter this input through an exponential linear filter

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

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

$$\dot{x} = -\frac{x}{\tau_m} + \frac{z}{\sqrt{\tau_m\tau_s}}, \quad \dot{z} = -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}}\,\eta(t). \tag{3}$$

In these units, the threshold and reset potentials are: $\hat{\Theta} = \sqrt{2}(\Theta - \mu\tau_m)/\sigma\sqrt{\tau_m}$ and $\hat{H} = \sqrt{2}(H - \mu\tau_m)/\sigma\sqrt{\tau_m}$. The stationary Fokker–Planck equation (FPE) [6] associated to Eqs. (3) is

$$\left[\frac{\partial}{\partial x}(x - \varepsilon z) + \varepsilon^2 L_z\right] P(x,z) = -\tau_m J(z)\delta(x - \hat{H}), \tag{4}$$

where $\varepsilon = \sqrt{\tau_m/\tau_s}$ and $L_z = (\partial/\partial z)z + \partial^2/\partial^2 z$. $P(x,z)$ is the stationary probability density of having the neuron in the state (x,z). The probability current $J(z)$ is injected at the reset potential, and it equals the probability current escaping at the threshold. It is then calculated as

$$J(z) = \tau_m^{-1}(-\hat{\Theta} + \varepsilon z)P(\hat{\Theta}, z). \tag{5}$$

Because $J(z)$ cannot be negative, it has to be made zero by imposing that $P(\hat{\Theta}, z) = 0$ for $z < z_{\min} = \hat{\Theta}/\varepsilon$. The output firing rate is finally computed as

$$\nu_{out} = \int_{z_{\min}}^{\infty} dz J(z). \tag{6}$$

First we will see that an expansion of both $P(x,z)$ and $J(z)$ in powers of ε as

$$P = \tilde{P}_0 + \varepsilon\tilde{P}_1 + \cdots, \quad J = \tilde{J}_0 + \varepsilon\tilde{J}_1 + \cdots \tag{7}$$

does not exist for all input parameters. All coefficients of the expansion have to satisfy the following conditions:

$$\text{(i)}\ \tilde{P}_n(\hat{\Theta}, z) = 0 \quad \forall z < \hat{\Theta}/\varepsilon, \tag{8}$$

$$\text{(ii)}\ \tilde{J}_n(z) = \tau_m^{-1}(z\tilde{P}_{n-1}(\hat{\Theta}, z) - \hat{\Theta}\tilde{P}_n(\hat{\Theta}, z)), \tag{9}$$

$$\text{(iii)}\ \int_{-\infty}^{\hat{\Theta}} dx \int_{-\infty}^{\infty} dz \tilde{P}_n(x,z) = \delta_{n,0}, \tag{10}$$

$$\text{(iv)}\ \lim_{z\to\pm\infty} z\tilde{P}_n \to 0, \quad \lim_{x\to-\infty} x\tilde{P}_n \to 0. \tag{11}$$

Here $P_n = 0$ for $n < 0$; besides, $\delta_{n,0} = 1$ for $n = 0$, and otherwise it is zero. Integrating Eq. (4) over x and imposing conditions (9) and (11) at all orders, one obtains an equation for $P(x,z)$ whose solution is

$$\int_{-\infty}^{\hat{\Theta}} \mathrm{d}x \tilde{P}_n(x,z) = \delta_{n,0} \frac{\mathrm{e}^{-z^2/2}}{\sqrt{2\pi}}. \tag{12}$$

This states that the marginal distribution of z is a normalized Gaussian. In what follows, we have to distinguish two different cases:

Suprathreshold regime: In this case, the mean depolarization, $\mu\tau_{\mathrm{m}}$, is above threshold ($\hat{\Theta} < 0$). Then, from Eq. (9) we obtain $\tilde{J}_0(z) = -\tau_{\mathrm{m}}^{-1}\hat{\Theta}\tilde{P}_0(\hat{\Theta},z)$, which is positive. Solving the FPE (4) at zeroth order leads to

$$\tilde{P}_0(x,z) = -\tau_{\mathrm{m}}\tilde{J}_0(z)\frac{H(x-\hat{H})}{x}. \tag{13}$$

Using conditions (6) and (12) for $n = 0$, we find $\tilde{J}_0(z) = \tilde{\nu}_0\mathrm{e}^{-z^2/2}/\sqrt{2\pi}$, from where we obtain that the zeroth-order firing rate is $\tilde{\nu}_0^{-1} = \tau_{\mathrm{m}}\log(\hat{H}/\hat{\Theta})$. Notice that $\tilde{\nu}_0$ is the rate of a LIF neuron driven by a noiseless current with mean μ. After solving the first and second orders, we obtain that the output firing rate up to second order is

$$\nu_{\mathrm{out}} \sim \tilde{\nu}_0 + \frac{\tau_{\mathrm{m}}^2\tilde{\nu}_0^2}{\tau_{\mathrm{s}}}\left[\tau_{\mathrm{m}}\tilde{\nu}_0(\hat{\Theta}^{-1}-\hat{H}^{-1})^2 - \frac{\hat{\Theta}^{-2}-\hat{H}^{-2}}{2}\right]. \tag{14}$$

This formula has also been obtained in [4] using a perturbative technique that is explained later.

Subthreshold regime: Now we prove that the perturbative expansion of the firing rate does not exist in this regime. Here, the mean depolarization is below threshold ($\hat{\Theta} > 0$). Because the probability current $J(z)$ cannot be negative, the zeroth-order probability current $\tilde{J}_0(z) = -\tau_{\mathrm{m}}^{-1}\hat{\Theta}\tilde{P}_0(\hat{\Theta},z)$ cannot be negative. Then, since $\hat{\Theta} > 0$, the density $\tilde{P}_0(\hat{\Theta},z)$ has to be zero, and also $\tilde{J}_0 = 0$. This implies that the zeroth-order rate is $\tilde{\nu}_0 = 0$ in the subthreshold regime. Assuming that $\tilde{P}_{\mathrm{m}}(\hat{\Theta},z) = 0$ for all $m < n$, it is easy to prove that $\tilde{P}_n(\hat{\Theta},z) = 0$: If $\tilde{P}_{\mathrm{m}}(\hat{\Theta},z) = 0$ for all $m < n$, then $\tilde{J}_n(z) = -\tau_{\mathrm{m}}^{-1}\hat{\Theta}\tilde{P}_n(\hat{\Theta},z)$ (see Eq. (9)). Since $J(z)$ cannot be negative and $\tilde{J}_m = 0$ for all $m < n$, the order $\tilde{J}_n$ cannot be negative. But since $\hat{\Theta} > 0$, $\tilde{P}_n(\hat{\Theta},z)$ has to be again zero, and in fact, all orders J_n are zero. This proves that the output firing rate in Eq. (6) does not admit an expansion in powers of ε in the subthreshold regime.

How to find a formula valid for all regimes? Because the expansion is not defined in the subthreshold regime, we cannot replace $z_{\min}$ by infinity in Eq. (6) as τ_{s} increases. This suggests maintaining fixed the lower integration limit in Eq. (6) as τ_{s} increases. We implement this idea by rewriting the FPE (4) as

$$\left[\frac{\partial}{\partial x}(x-\gamma z) + \varepsilon^2 L_z\right]P(x,z) = -\tau_{\mathrm{m}}J(z)\delta(x-\hat{H}), \tag{15}$$

where we have introduced the new parameter γ in the drift term. At the same time, we express the escape probability current as in Eq. (5), but where ε is replaced by γ. Now the central idea becomes clear: We expand the density and the probability current in powers of ε^2 as

$$P = P_0 + \varepsilon^2 P_1 + \cdots, \quad J = J_0 + \varepsilon^2 J_1 + \cdots \tag{16}$$

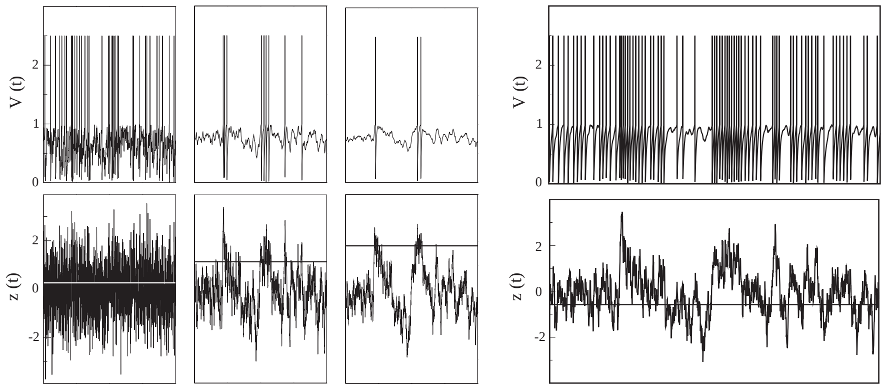

Fig. 1. Left: Membrane potential (top) and $z(t)$ (bottom) for a LIF neuron with a single synaptic type for $\tau_s = 1$, 20 and 50 ms from left to right. The horizontal lines in the bottom plots represent z_{min}. Parameters are $\tau_m = 10$ ms, $\Theta = 1$ and $H = 0$ (in arbitrary units), $\mu = 80$ s^{-1}, and $\sigma^2 = 12$ s^{-1}. The firing rates and coefficients of variation of the inter-spike-intervals are, from left to right: 20.5, 4.4 and 1.1 Hz, and 0.7, 1.1 and 1.2. Right: The same as before but for a suprathreshold LIF neuron for $\tau_s = 20$ ms and $\mu = 110$ s^{-1}. Notice that z_{min} is negative in this regime. The neuron fires at 38.5 Hz with $CV = 0.7$. In all cases the plotted time interval is 2 s.

maintaining fixed the auxiliary parameter γ. Only at the end, when the coefficients P_n and J_n have been determined, γ can be given its true value ε. We introduce this expansion into the FPE (15). Each order has to satisfy Eqs. (10) and (11), but conditions (8) and (9) have to be replaced by (i) $\tilde{P}_n(\hat{\Theta}, z) = 0 \ \forall z < \hat{\Theta}/\gamma$ and (ii) $J_n(z) = \tau_m^{-1}(\gamma z - \hat{\Theta}) P_n(\hat{\Theta}, z)$. After solving the leading order, one obtains (see [4] for further details) that the output firing rate at zeroth order is

$$\nu_{out,0} = \int_{\hat{\Theta}/\varepsilon}^{\infty} \frac{dz}{\sqrt{2\pi}} e^{-z^2/2} F_0(\hat{H} - \varepsilon z, \hat{\Theta} - \varepsilon z), \tag{17}$$

where $F_0^{-1}(a,b) = \tau_m \log(a/b)$. This is a remarkable result with a clear intuitive meaning that is discussed in [4]: Eq. (17) is an average over z—with a Gaussian distribution—of the firing rate, F_0, of a neuron receiving an effective noiseless current $I_{eff} = \mu + z\sigma/\sqrt{2\tau_s}$ [5]. As we have previously proved, it is possible to check that this formula does not admit an expansion in powers of τ_s^{-1} in the *subthreshold regime*, while in the *suprathreshold regime* the expansion does exist and is the same as in Eq. (14).

In Fig. 1 (left) we plot $V(t)$ and $z(t)$ and show the dependence of the neuron response on τ_s in the *subthreshold regime*. For long τ_s, the neuron fires whenever $z(t) > z_{min} \sim 1$ and, then, it acts as a *detector* of particular rare events. If z is high enough, the neuron emits a burst of spikes. In this mode, the neuron fires with high output variability. However, for short τ_s the neuron does not always detect $z(t) > z_{min}$, and the output variability is lower. In the *suprathreshold regime* the neuron behaves as an *integrator*, because its firing is driven by the mean input current, and it is not very sensitive to the value of $z(t)$, as it can be seen in Fig. 1 (right).

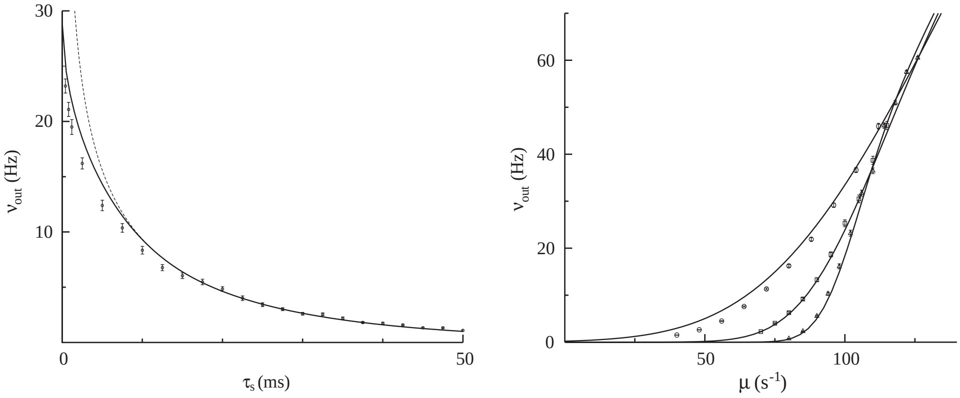

Fig. 2. Left: Output firing rate as a function of τ_s for a neuron in the subthreshold regime with $\mu = 80$ s^{-1} and $\sigma^{-1} = 12$ s^{-1}. Full line is the interpolation prediction with $\tau_{inter} = 15$ ms and dash line is the long τ_s prediction given by Eq. (17). Besides, $\tau_m = 10$ ms, $\Theta = 1$ and $H = 0$. Right: Output firing rate as a function of μ. The synaptic time constant is $\tau_s = 10$, 40 and 150 ms for the upper, intermediate and bottom curves. In the three cases the input variance $\sigma^2 = 30$ s^{-1} and the other parameters are as above.

3. Short τ_s, interpolation procedure and results

Using a technique introduced by [2], the output firing rate of a LIF has been calculated in the short τ_s limit [3], and it is

$$\nu_{out} = \tilde{\nu}_0 - 1.46\sqrt{\tau_s \tau_m}\,\tilde{\nu}_0^2 \left[R\left(\frac{\hat{\Theta}}{\sqrt{2}}\right) - R\left(\frac{\hat{H}}{\sqrt{2}}\right) \right], \quad (18)$$

where $R(t) = \sqrt{\pi/2}\,e^{t^2}(1 + \mathrm{erf}(t))$, and $\mathrm{erf}(t)$ is the error function. An interpolation between the long and short limits, Eqs. (17) and (18), has been performed in [4], and here we summarize the procedure. First, we set the firing rate for short τ_s as $\nu_{out} = \tilde{\nu}_0 + A\sqrt{\tau_s} + B\tau_s + C\tau_s^{3/2}$, where the constant A is the same as in formula (18), and then B, C are chosen to obtain a continuous and derivable function at an intermediate $\tau_s = \tau_{inter}$. In Fig. 2 (left) we compare the result of this interpolation procedure with the simulation data obtained using Eqs. (1) and (2). In Fig. 2 (right) the output firing rate is shown as a function of μ for three different τ_s. In this last case, the prediction is just the long τ_s firing rate, Eq. (17). In both graphs the prediction is good even for intermediate values of the synaptic time constant, $\tau_s \sim \tau_m$.

4. Conclusions

We have showed that a neuron with slow filters acts as a detector of rare events in the subthreshold regime, since it responds only when large fluctuations in the synaptic drive are present. This response could be particularly useful when the system is engaged in coding rare but meaningful events in the external world. Also, the neuron is particularly designed to detect large afferent fluctuations in a time scale τ_s. This makes reasonable that long synaptic time constants in the nervous system are present to read information and selects it in the behavioral relevant time scale of hundreds of milliseconds.

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