Firing rate for a generic integrate-and-fire neuron with exponentially correlated input

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Abstract

The effect of time correlations in the afferent current on the firing rate of a generalized integrate-and-fire neuron model is studied. When the correlation time τ_c is small enough the firing rate can be calculated analytically for small values of the correlation amplitude α^2. It is shown that the rate decreases as $\sqrt{\tau_c}$ from its value at $\tau_c = 0$. This limit behavior is universal for integrate-and-fire neurons driven by exponential correlated Gaussian input. The details of the model only determine the pre-factor multiplying $\sqrt{\tau_c}$. Two model examples are discussed.

I. Introduction. Synchrony is a form of temporal correlation in the neuronal activity that occurs when a set of neurons tend to fire together within a time window of small size. It has been experimentally recorded throughout the cortex [1, 2]. Both the size of the population of neurons firing synchronously and the temporal precision of the synchronization may have important effects on the activity of the post-synaptic neurons. As a consequence of synchronization, the output rate of a post-synaptic neuron typically increases. This has been shown analitucally for example in [3, 4] and in simulations of leaky integrate-and-fire neurons in [5]. However, most of these studies obtain analytical results only for perfectly synchronized inputs where neurons tend to fire at the same time. The response of more complicated integrate-and-fire neuron models to a perfect synchronized input or to an input synchronized with finite temporal precision has, to our knowledge, only been treated in [4].

In this work we show that the rate of a generalized integrate-and-fire neuron (see eq. (1) below) increases with the precision of the synchronization in a universal way. Whithin this class of neuron models this increase in the response behaves as the squared root of the time window τ_c where the inputs are synchronized. The $\sqrt{\tau_c}$ behavior indicates that corrections to the perfectly synchronized case ($\tau_c = 0$) are important even for small τ_c. The universal $\sqrt{\tau_c}$ behavior of integrate-and-fire neurons in obtained using the diffusion approximation and the Fokker-Planck formalism. The constant pre-factor multiplying $\sqrt{\tau_c}$ depends on the details of the particular neuron model selected and can also be computed with our formalism. An example of this, corresponding to a leak proportional to the membrane potential, can be found in some previous work

[4]. Here we will also present a direct solution of another model corresponding to a simple non-leaky neuron which will be used to test the previous analytical results derived for small τ_c. We close this paper with a comparison between the two models.

II. The integrate-and-fire neuron and input statistics. Here we describe the generalized integrate-and-fire neuron model and present the statistic properties of the input current.

The integrate-and-fire neuron model. The depolarization membrane potential $V(t)$ evolves from the reset voltage H according to the stochastic equation [7, 8, 9]

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

where $f(V)$ is a voltage dependent term and $I(t)$ is the afferent current . When the potential reaches a threshold value Θ, a spike is emitted and the neuron is reset to H, from where it restarts to integrate the input signal after a refractory time τ_{ref}. Within the refractory time the voltage is fixed at H.

The input statistics. The neuron is driven by a stationary, correlated random current $I(t)$ coming from upstream neurons that can be written as a sum of spike events

$$I(t) = \sum_{i=1}^{N} J_i \sum_k \delta(t - t_i^k) \tag{2}$$

Here i denotes the i-th pre-synaptic neuron, the index k labels the arrival times of the individual pre-synaptic spikes, N is the number of connections, and J_i is the strength of the connection with neuron i. We assume that the cross-correlations between pairs of neurons have exponential decay with range τ_c, so that the two-point correlation of the current can be written as (for further details see [4])

$$C(t - t') \equiv\, < I^2(t) > - < I(t) >^2 = \sigma^2 \delta(t - t') + \sigma^2 \frac{\alpha^2}{2\tau_c}\, e^{-\frac{|t-t'|}{\tau_c}} \tag{3}$$

where σ^2 is a white noise variance and α^2 is the amplitude of the correlations (in the useful units of $\sigma^2/2\tau_c$) and measures the relative importance of the temporal correlations compared to white noise fluctuations. The exponential form in eq. (3) has been chosen first because it fully characterizes correlations by a timescale range τ_c (intuitively, it can be interpreted as the time window around which the synchronized spikes occur) and by the intensity factor α^2 and second because it makes the computations feasible. Note that the correlation function $C(t - t')$ describes a stationary property of the input statistics, a fact reflected in that it only depends on the difference between the two times.

The input current is completely described by its mean $\mu = < I(t) >$, its variance σ^2, and its second order correlations. This is justified because a typical neuron in the cortex receives a large barrage of spikes per second [6, 8]. Each spike induces a very small membrane depolarization J compared to the distance between the threshold and reset potentials. Moreover if the condition $\frac{J(1+\alpha^2)}{\Theta-H} < \frac{1}{10}$ holds, the correlations are weak enough for the diffusion approximation to be valid and thus the input current can be considered as Gaussian.

III. The analytical solution. A random Gaussian current $I(t)$ as described above, with correlations as in eq.(3), can be obtained as [10, 4]

$$I(t) = \mu + \sigma\eta(t) + \sigma\frac{\alpha^2}{\sqrt{2\tau_c}}z(t) \quad (4)$$

$$\dot{z}(t) = -\frac{z}{\tau_c} + \sqrt{\frac{2}{\tau_c}}\zeta(t) \quad (5)$$

where $\eta(t)$ and $\zeta(t)$ are two independent white noise random variables with unit variances $(< \eta(t) >=< \zeta(t) >= 0, < \eta(t)\eta(t') >=< \zeta(t)\zeta(t') >= \delta(t-t'),$ $< \eta(t)\zeta(t') >= 0)$ and $z(t)$ is an auxiliary random variable.

The diffusion process defined by eqs. (1, 4, 5) can be studied by means of the stationary Fokker-Planck equation [10, 4]

$$[\frac{\partial}{\partial V}(f(V)-\mu+\frac{\sigma^2}{2}\frac{\partial}{\partial V})+\frac{1}{\tau_c}\frac{\partial}{\partial z}(z+\frac{\partial}{\partial z})-\sqrt{\frac{2\sigma^2\alpha^2}{\tau_c}}\frac{\partial}{\partial V}]P = -\delta(V-H)J(z) \quad (6)$$

where $P(V,z)$ is the steady state probability density of having the neuron in the state (V,z) and $J(z)$ is the escape probability current, which integrated over z gives the firing rate of the neuron. It appears as a source term representing the reset effect: whenever the potential V reaches the threshold Θ, it is reset to the value H keeping the same distribution in the auxiliary variable z. If we suppose that the correlation time τ_c is very small compared to the refractory time τ_{ref} $(\tau_c << \tau_{ref})$ the escape current can be rewritten as $J(z) = \nu_{out}e^{-z^2/2}/\sqrt{2\pi}$ [11], where ν_{out} is the output firing rate of the neuron. This means that after one spike the variable z has enough time to relax to its stationary distribution (a normal distribution). The Fokker-Planck equation has to be solved with the normalization condition $\nu_{out}\tau_{ref} + \int_{-\infty}^{\Theta} dV \int_{-\infty}^{\infty} dz P(V,z) = 1$ (meaning that with probability $\nu_{out}\tau_{ref}$ the neuron is at the reset value, and with the complementary probability it is at some state (V,z)) and the condition that P vanishes at the threshold $P(\Theta, z) = 0$ [10, 4].

Eq.(6) is solved using an extension of the tecnique described in [4] for the leaky integrate-and-fire model. The probability density $P(V,z)$ is expressed in powers of $k = \sqrt{\tau_c}$ keeping the orders $O(k^0)$ and $O(k)$. At the end of a rather lengthy calculation one obtains that the output rate expands as $\nu_{out} = \nu_0 + \nu_1\sqrt{\tau_c}$ where

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$$\nu_0^{-1} = \tau_{ref} + \frac{2}{\sigma_{eff}^2} \int_H^\Theta du\, e^{\frac{2}{\sigma_{eff}^2}\int_\Theta^u dr(\mu - f(r))} \int_{-\infty}^u dv\, e^{-\frac{2}{\sigma_{eff}^2}\int_\Theta^v dr(\mu - f(r))}$$

$$\nu_1 = -\frac{\sqrt{2}\alpha^2\nu_0^2}{\sigma} \int_{-\infty}^\Theta dv\, e^{-\frac{2}{\sigma^2}\int_\Theta^v dr(\mu - f(r))} \tag{7}$$

Here appears the effective variance which is given by $\sigma_{eff}^2 = \sigma^2(1 + \alpha^2)$. Note that the analytical expression for the rate ν_0 is the same as in the white noise input case with mean input μ and variance σ_{eff}^2. At order $O(k)$, ν_1 has been calculated up to order $O(\alpha^2)$ in the amplitude of the correlations, so the expression is valid only for small values of α^2. However, the order $O(k^0)$ is exact for all α^2. The rate has been obtained in the Fokker-Planck formalism only for positive correlations ($\alpha^2 > 0$), which is the relevant case in this work. The mathematical tools for studying negative correlations are harder but with them it can be seen [4] that the expression for ν_0 is exact even for negative correlations.

The first term, ν_0, gives the response to a perfectly synchronized input. As was announced before, the correction to perfect synchronization behaves as $\sqrt{\tau_c}$ for any function $f(.)$, only the pre-factor ν_1 depends of the particular neuron model chosen. To exemplify this universal behavior we now discuss and compare two different models, the leaky and the non-leaky integrate-and-fire neurons.

The non-leaky neuron. In this model there is no voltage dependent decay, thus $f(V) = 0$, and we find

$$\nu_0^{-1} = \tau_{ref} + \frac{\Theta - H}{\mu}$$

$$\nu_1 = -\frac{\alpha^2\nu_0^2\sigma}{\sqrt{2}\mu} \tag{8}$$

The rate of the non-leaky neuron is known to be insensitive to input fluctuations [9], and here it is shown that the rate is also insensitive to perfectly synchronized inputs ($\tau_c = 0$), in fact ν_0 does not dependent on α. However, when synchronization is not perfect ($\tau_c \neq 0$), the first correction to the rate is negative. Since the rate at order $O(k^0)$ is the same as if the neuron received a white noise input, the effect of correlations is to decrease the rate as τ_c increases, what is a peculiarity of the non-leaky neuron with refractory time.

The interest in such a simple model comes from the fact that eq. (6) can be solved exactly for all τ_c in powers of α^2 when $J(z) = \nu_{out}e^{-z^2/2}/\sqrt{2\pi}$ (valid for $\tau_{ref} >> \tau_c$). This allows us to test the solution in eqs.(8) derived from the general expressions given in eqs. (7). The rate obtained in this way is

$$\nu_{out} = \nu_0 - \frac{\alpha^2\nu_0^2[1 - e^{(\gamma-\lambda)(\Theta-H)}]}{\mu(\gamma + \lambda)} + O(\alpha^4) \tag{9}$$
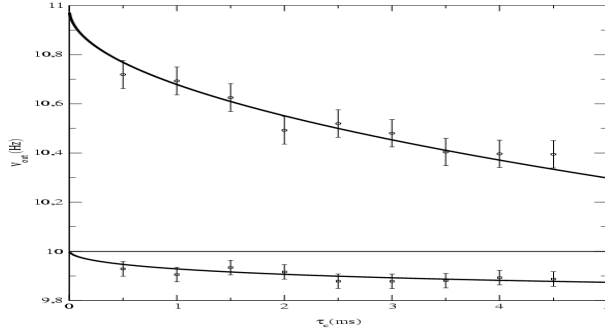
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Figure 1: Theoretical predictions and simulation results for ν_{out}/ν_0 as a function of α for the balanced and the unbalanced states. The neuron is much more sensitive to α in the balanced regime (full line, $\mu = 40s^{-1}$) than in the unbalanced regime (dashed line, $\mu = 110s^{-1}$). In both cases $\sigma_w^2 = 30s^{-1}$, $\tau_c = 1ms$ and the other parameters are as in Fig. **??**. With these parameters $\nu_0 = 16.9Hz$ in the balanced state and $\nu_0 = 69.5Hz$ in the unbalanced state.

where $\gamma = \frac{\mu}{\sigma^2}$, $\lambda = \sqrt{\gamma^2 + \frac{2}{\sigma^2 \tau_c}}$ and ν_0 is the same as in eq. (8). Expanding eq. (9) for small τ_c one obtains the same universal $\sqrt{\tau_c}$ behavior as predicted, and the same prefactor as in eq. (8).

The leaky neuron. This neuron is characterized by a voltage dependent decay $f(V) = V/\tau$, where τ is the membrane time constant ($\tau \sim 10ms$). From eq.(8) we obtain

$$
\begin{aligned}
\nu_0^{-1} &= \tau_{ref} + \sqrt{\pi}\tau \int_{\hat{H}_{eff}}^{\hat{\Theta}_{eff}} du\, e^{u^2}(1 + erf(u)) \\
\nu_1 &= -\alpha^2 \nu_0^2 \sqrt{\frac{\pi\tau}{2}} e^{\hat{\Theta}^2}(1 + erf(\hat{\Theta}))
\end{aligned}
\tag{10}
$$

Here $erf(t)$ is the error function. Besides, $\hat{\Theta}_{eff} = \frac{\Theta - \mu\tau}{\sqrt{\sigma_{eff}^2 \tau}}$, $\hat{H}_{eff} = \frac{H - \mu\tau}{\sqrt{\sigma_{eff}^2 \tau}}$ and $\hat{\Theta} = \frac{\Theta - \mu\tau}{\sqrt{\sigma^2 \tau}}$. This result agrees with what was found in [4]. For positive correlations the firing rate grows, meaning that correlated spikes are more effective in driving the leaky neuron than uncorrelated ones. Some numerical results and comparison between leaky and non-leaky rates are shown in Fig. 1.

IV. Discussion. This work points to a better understanding of the role of correlations in driving neurons. The main result is that the firing rate of an integrate-and-fire neuron decreases as $\sqrt{\tau_c}$ from the rate obtained at $\tau_c = 0$. This behavior is universal and it indicates that even small departures from the perfect synchronized input case are important and need to be considered.

References

[1] A. Aertsen and M. Arndt. Curr. Opin. Neurobiol. **3**, 586-594 (1993).

[2] E. Salinas and T. J. Sejnowski. Nature Reviews Neuroscience **2**: 539-550 (2001).

[3] J. Feng and D. Brown, Neural Computation **12**, 671-692 (2000).

[4] R. Moreno, A. Renart, J. de la Rocha and N. Parga, submitted, 2002.

[5] E. Salinas and T. J. Sejnowski, The Journal of Neuroscience **20**, 6193-6209 (2000).

[6] M.N. Shadlen and W.T. Newsome, J. Neurosci. **18**, 3870-3896 (1998).

[7] B. W. Knight, The Journal of General Physiology **59**, 734-778 (1972)

[8] L. M. Ricciardi, *Diffusion processes and related topics in biology* (Springer-Verlag, Berlin, 1977).

[9] H. C. Tuckwell, *Introduction to Theoretical Neurobiology II* Cambridge University Press, Cambridge, UK, 1988

[10] H. Risken, *The Fokker-Planck equation* (Springer-Verlag, Berlin. Second ed., 1989)

[11] N. Brunel and S. Sergi, J. Theor. Biol. **195**, 87-95 (1998).