Firing Rate Adaptation without Losing Sensitivity to Input Fluctuations

Giancarlo La Camera, Alexander Rauch, Walter Senn, Hans-R Lüscher and
Stefano Fusi

Institute of Physiology, University of Bern, CH-3012 Bühlplatz 5, Switzerland
`{lacamera,rauch,senn,luescher,fusi}@pyl.unibe.ch`

Abstract. Spike frequency adaptation is an important cellular mechanism by which neocortical neurons accommodate their responses to transient, as well as sustained, stimulations. This can be quantified by the slope reduction in the *f-I* curves due to adaptation. When the neuron is driven by a noisy, *in vivo*-like current, adaptation might also affect the sensitivity to the fluctuations of the input. We investigate how adaptation, due to calcium-dependent potassium current, affects the dynamics of the depolarization, as well as the stationary *f-I* curves of a white noise driven, integrate-and-fire model neuron. In addition to decreasing the slope of the *f-I* curves, adaptation of this type preserves the sensitivity of the neuron to the fluctuations of the input.

1 Introduction

Many *in vivo* phenomena, like spontaneous activity, or the selective, delay activity observed in many cortical areas of behaving animals, are characterized by sustained spike activity throughout long intervals. During these intervals, the statistics of the input current is likely to be stationary or quasi-stationary, although originated by very irregular synaptic activity. When the activity of a neural network can be characterized in terms of mean output spike frequencies of subpopulations of neurons, the *f-I* response function (RF) has proved an invaluable tool to describe the network's stationary activity (see e.g. [1, 2]). At the same time, spike frequency adaptation (see e.g. [3, 6]) is an important cellular mechanism by which neocortical neurons accommodate their responses to transient, as well as sustained, stimulations. Adaptation should then be considered in the above framework, especially after that it proved to be essential for two models of integrate-and-fire (IF) neurons to fit the *in vitro* response of rat pyramidal neurons [5]. In addition to reducing the stationary spike frequency, adaptation could also affect the neuron's sensitivity to the fluctuations of the input. In this work we analyze this problem for the *linear* IF (LIF) model neuron with adaptation [5], driven by white noise, emulating the intense, irregular synaptic activity driving a cortical neuron *in vivo*.

2 The model

The sub-threshold behavior of the LIF neuron is fully described by the depolarization V, which obeys

$$CdV = -\lambda dt + I_\xi dt + I_\alpha dt \tag{1}$$

Here C is the capacitance of the membrane, λ a constant leak term, I_ξ the synaptic input and I_α a calcium dependent potassium current, responsible for spike frequency adaptation. I_α is proportional to intra-cellular calcium concentration $[Ca]$, $I_\alpha = \bar{g}[Ca]$. Upon emission of an action potential, an amount A_{Ca} of calcium immediately enters the cell and decays exponentially to zero with a slow time constant τ_{Ca} [5]:

$$\frac{d[Ca]}{dt} = -\frac{[Ca]}{\tau_{Ca}} + A_{Ca}\sum_k \delta(t - t_k) \tag{2}$$

where the sum goes over all spikes emitted by the neuron up to time t.

The synaptic current I_ξ is the result of the Poisson activation of (many) independent excitatory and inhibitory inputs, with average m, variance s^2 and time correlation length τ', corresponding to the decay time constant of a single post-synaptic potential. If τ' is very short, the correlation length of the current becomes negligible, and the current can be replaced by white noise [7, 5]:

$$I_\xi dt \to m dt + s\sqrt{2\tau'}\xi_t\sqrt{dt} \tag{3}$$

where ξ_t is a Gauss distributed variable with $E[\xi_t] = 0$ and $E[\xi_t \xi'_t] = \delta(t - t')$. Hereafter we set $\tau' = 1$ ms.

Equation (1) must be completed by boundary conditions: a spike is emitted when V is driven above a threshold θ, after which is reset to a value $0 < V_r < \theta$ and clamped there for a refractory time τ_r. V is confined in the range $[0, \theta]$ by a reflecting barrier at 0 (see [4]). Without adaptation ($I_\alpha \equiv 0$), the *f-I* curve of (1) is known and reads [4] (see also Fig. 1)

$$f = \Phi(m, s) = \left[\tau_r + \frac{\tau' s^2}{(m-\lambda)^2}\left(e^{-\frac{C\theta(m-\lambda)}{\tau' s^2}} - e^{-\frac{CV_r(m-\lambda)}{\tau' s^2}}\right) + \frac{C(\theta - V_r)}{m - \lambda}\right]^{-1} \tag{4}$$

The *f-I* curve gives the mean output spike frequency f as a function of m, s in stationary conditions. When adaptation is present, its effect can be taken into account in the RF using the fact that its dynamics is much slower compared to the other dynamic variables [3]. In particular, if $\tau_{Ca} \gg 1/f$, the fluctuations of $[Ca]$ can be neglected, $\bar{g}[Ca] \sim \bar{g}A_{Ca}\tau_{Ca} f \equiv \alpha f$. As a consequence, an additional negative current $\langle I_\alpha \rangle = -\alpha f$, proportional to the neuron's own frequency f, affects the mean current m which, in equation (4), has to be replaced by [3, 5]

$$m \to m - \alpha f \equiv m(f) \tag{5}$$

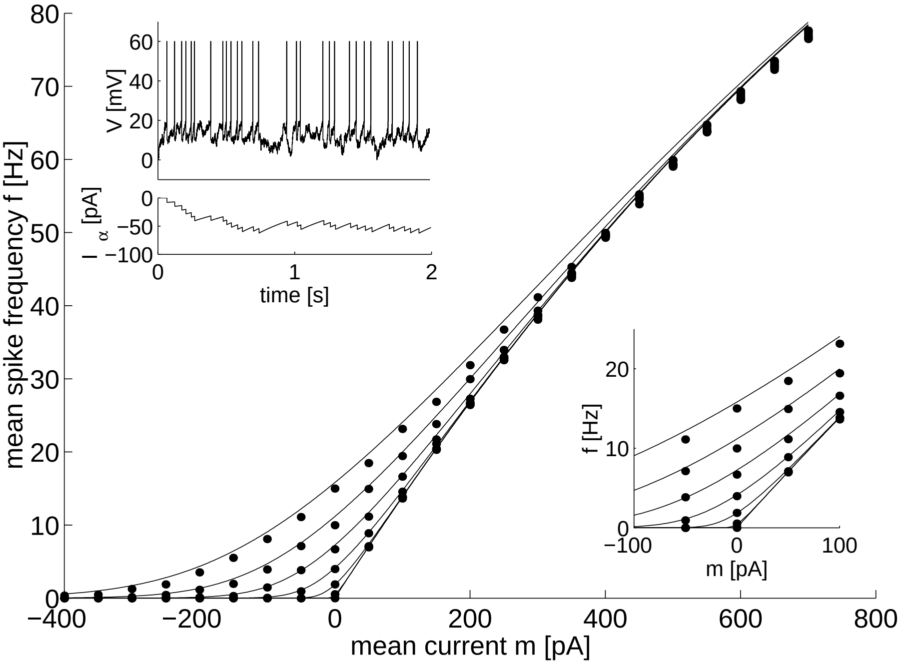

Fig. 1. *f-I* curves of the adapted LIF neuron, theory vs simulations. Mean output frequency plotted as a function of the mean current m at constant s (stepwise increasing from 0 to 600 pA). Lines: self-consistent solutions of equation (4-5) (f_{th}). Dots: simulations (f_{sim}). Adaptation parameters: $\tau_{ca} = 500$ ms, $\bar{g}A_{Ca} = 8$ pA (so that $\alpha = 4$ pA s). Neuron parameters: $\tau_r = 5$ ms, $C = 300$ pF, $\theta = 20$ mV, $V_r = 10$ mV, $\lambda = 0$. The right inset shows an enlargement around the rheobase $\tilde{m} = 0$. Left inset: sample of depolarization and I_α for the point $(m, s) = (100, 200)$ pA.

The new spike frequency is found by iterating the equation $f = \Phi(m(f), s)$ until a fixed point is reached. [1] We have simulated the LIF neuron with calcium dynamics, equations (1-2-3), for different values of m, s and τ_{Ca}. Fig. 1 shows the agreement between theory (self-consistent solutions of equation (4-5)) and simulations. The good agreement for high s justifies the assumption that I_α affects only the mean current felt by the neuron or, equivalently, that fluctuations of I_α are negligible. In addition, calcium dynamics slower than ~ 100 ms leads to an error below 3% for four sample points of the (m, s)-plane (Fig. 2).

3 Effect of adaptation on the *f-I* curves

We next show that, contrary to the effect of the other parameters, adaptation allows the neuron to reduce its spike frequency, retaining most of its sensitivity

---

[1] The condition for any fixed point f^* to be stable is $\partial\Phi(m(f), s)/\partial f|_{f^*} = -\alpha\partial\Phi/\partial m|_{f^*} < 1$, which holds since Φ is an increasing function of m.

to fluctuations. Given a change in C, there is always a RF-equivalent change in the couple $\{\theta, V_r\}$, because the RF (4) is invariant under the scaling $C \to Ch$, $\{\theta, V_r\} \to \{\theta, V_r\}/h$, $h > 0$ constant. As a consequence, from now on we consider only changes in C, keeping θ and V_r fixed and such that their difference is finite.

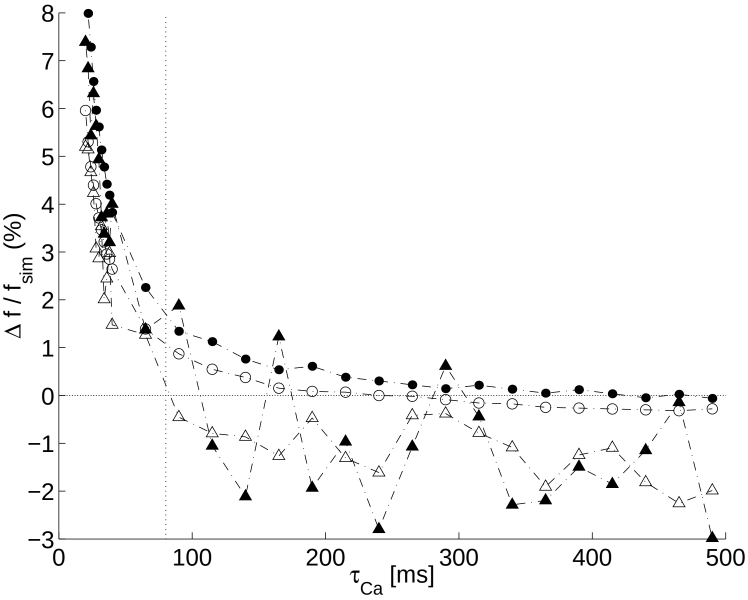

Fig. 2. Adapted LIF neuron, dependence of $(f_{sim} - f_{th})/f_{sim}$ (Fig. 1) on τ_{Ca}, theory vs simulations. As τ_{Ca} is varied, A_{Ca} is rescaled so that the total amount of adaptation ($\alpha = 4$ pA s) is kept constant. Parameters of the current: $m = 100$ pA (full symbols) and $m = 300$ pA (empty symbols); $s = 0$ (circles) and $s = 300$ pA (triangles). All other parameters as in Fig. 1. Mean spike frequencies assessed across 50 s, after discarding a transient of $10\tau_{ca}$. For $s > 0$ deviations from a monotonic behavior have to be expected, but the error is always below 3%. For $\tau_{Ca} < 80$ ms (vertical dotted line) the error is positive, meaning that $f_{sim} > f_{th}$: the neuron only slightly adapts because calcium decay is too fast.

We focus on two observables, the slope ρ of the RF at the rheobase [2] ($\tilde{m} = m - \lambda = 0$) for $s = 0$ (which quantifies the amount of frequency reduction), and the *distance* d between two RFs at different s, or equivalently the dependence of the RF on s at $\tilde{m} = 0$, taken as a measure of the sensitivity to the fluctuations of the input current. [3] In the following it will be useful to use the notation

---

[2] The rheobase current I_{th} is the threshold current, i.e. $f = 0$ if $m < I_{th}$ when $s = 0$. For the LIF neuron $I_{th} = \lambda$.

[3] Since we are interested in the behavior at $\tilde{m} \approx 0$, the refractory period does not have an effect, and we set $\tau_r = 0$. The following formulae are also valid for $\tau_r > 0$ provided that the frequencies at the rheobase are not too large, say $f < 30$ Hz.

$\theta_n \equiv \theta^n - V_r^n$. For $s = 0$ the RF is linear in $\tilde{m}$, $f = \rho_\alpha \tilde{m}$ with

$$\rho_\alpha = \frac{1}{C\theta_1 + \alpha} = \frac{\rho_0}{(1 + \rho_0 \alpha)}$$

where $\rho_0 \equiv 1/C\theta_1$ is the slope with no adaptation ($\alpha = 0$). Whereas both C and α have a 'first order' effect on the slope, their effect on the distance d is very different. By expanding the *f-I* curve (4) around the rheobase, introducing adaptation and solving for f at $\tilde{m} = 0$, one gets the distance as a function of C and α:

$$d_\alpha = \frac{\sigma^2}{\theta_2} \frac{1}{1 + \rho_\infty \alpha} \equiv \frac{d_0}{1 + \rho_\infty \alpha}$$

where $\sigma^2 \equiv 2\tau' s^2/C^2$, $\rho_\infty \equiv 2\theta_3/3\theta_2^2 C$.

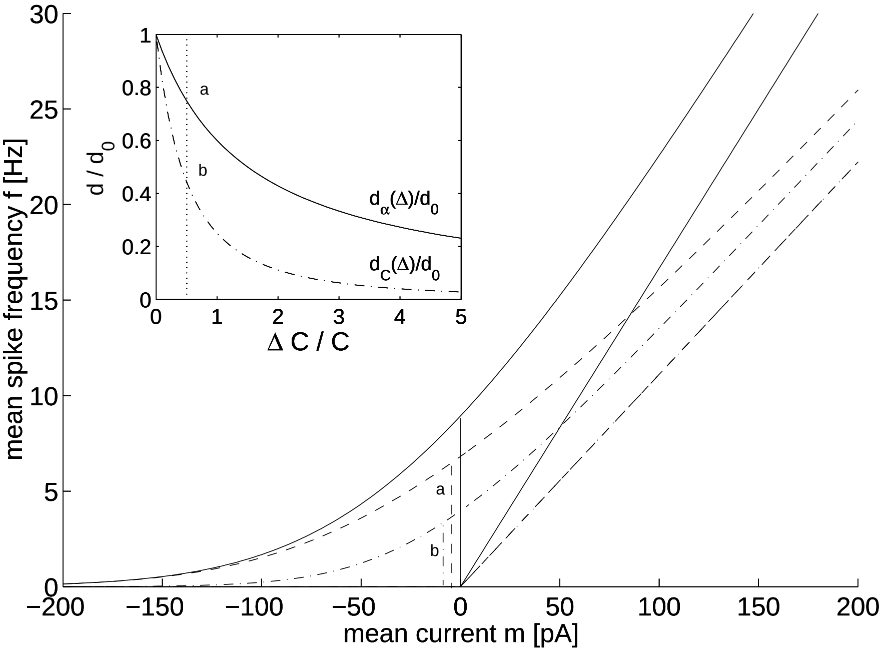

Fig. 3. Adaptation only slightly affects the sensitivity to fluctuations. Full lines: RFs without adaptation, $C = 300$ pF, $\theta_1 = \theta = 20$ mV, $\tau_r = 0$, $s = 0$ and 400 pA. Vertical line: distance at the rheobase d_0. Dashed lines: same as full lines but with adaptation $\alpha = 3$ pA s. The distance is reduced to only 80% of d_0 (see inset, a). Dot-dashed lines: $C = 450$ pF, no adaptation, a slope-equivalent change to the previous case (a). The distance is approximately halved (inset, b). The inset shows $d_\alpha(\Delta)/d_0$ (full line) and $d_C(\Delta)/d_0$ (dot-dashed line) as a function of slope-equivalent changes expressed in $\Delta C/C$ for the parameters of the main figure. Inset's vertical line: $\Delta C/C = 0.5$. Note that $d_C(\Delta) \leq d_\alpha(\Delta)$ approximately by a factor $(1 + \rho_0 \alpha \eta)^{-1} = (1 + \Delta C/C)^{-1}$ (see text)

This exposes the difference between the 'quadratic' ($1/C^2$) behavior in C (or θ because of the scaling properties of the RF), and the 'first order' behavior in α: the price to be payed, to reduce the slope without adaptation, is a decreased sensitivity to fluctuations, as implied by a reduced distance between the curves. This is apparent by comparing the change in d caused by slope equivalent changes in α ($\alpha \to \alpha(1+\eta)$) and C ($\Delta C/C = \rho_0 \alpha \eta$) respectively (see inset of Fig. 3):

$$d_\alpha(\Delta) = \frac{d_0}{1+\rho_\infty \alpha + \rho_\infty \alpha \eta} \quad , \quad d_C(\Delta) = \frac{d_0}{(1+\rho_0 \alpha \eta)(1+\rho_\infty \alpha + \rho_0 \alpha \eta)}$$

4 Conclusions

We have analyzed a simple model of spike frequency adaptation, due to a *slow* calcium dependent potassium current I_α, for the IF neuron with a linear decay. I_α enters the RF only as a negative, feedback current which depends on the neuron's own spike frequency. We showed that there is an excellent agreement between the theoretical frequencies, as predicted through the RF, and the ones obtained by simulations of the neuron dynamics, up to large values of the amplitude of the input fluctuations, and for slow enough calcium dynamics. In addition, we have shown that adaptation reduces the slope of the RF retaining most of neuron's sensitivity to the fluctuations of the input current. We have also found that the same results hold for the classical IF neuron with leakage proportional to V (not shown here). These two model neurons with adaptation have been recently proved able to fit the spike frequencies of rat neocortical pyramidal neurons *in vitro* injected with Gauss distributed current resembling the white noise (3) [5].

References

1. Amit D.J. and Tsodyks M.V., Quantitative study of attractor neural network retrieving at low rates I: Substrate - spikes, rates and neuronal gain, *NETWORK* **2**: 259 (1991)
2. Brunel, N., Persistent activity and the single-cell frequency-current curve in a cortical network model, *NETWORK* **11**: 261-280 (2000)
3. Ermentrout, B., Linearization of *f-I* curves by adaptation, *Neural Comp.* **10**: 1721-1729 (1998)
4. Fusi S. and Mattia M., Collective behavior of networks with linear (VLSI) Integrate and Fire Neurons, *Neural Comp.* **11**: 643-662 (1999)
5. Rauch A., La Camera G., Lüscher, H-R., Senn W. and Fusi S., Neocortical pyramidal cells respond as integrate-and-fire neurons to *in vivo*-like input current, *submitted* (2002)
6. Wang, X.J., Calcium coding and adaptive temporal computation in cortical pyramidal neurons, *J. Neurophysiol.* **79**: 1549-1566 (1998)
7. Tuckwell, H.C., Introduction to theoretical neurobiology, vol II, *Cambridge: Cambridge University Press* (1988)

This article was processed using the LaTeX macro package with LLNCS style