

Effect of spike-driven feedback on the firing statistics of noisy spike generators

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Abstract

We consider a general dynamical neuron model with noise and inhibitory feedback driven by its spikes (e.g. voltage-gated adaptation currents). Such feedback reduces the spike rate and can lead to negative ISI correlations. If certain characteristics of the neuron without feedback are known, the firing statistics in presence of a weak feedback can be inferred. For a white noise driven leaky integrate-and-fire model with current feedback, analytical results for mean, variance, ISI correlation coefficient, and spike train power spectrum display a good agreement with simulation results. This provides analytical insight into firing characteristics of stochastic neurons with adaptation or feedback.

General results

Given the ubiquity of feedback and noise in the nervous system, one of the most important but also challenging theoretical problems is the analysis of neuron models under the influence of both components. A study of a general deterministic spike generator with an additional adaptation (i.e. feedback) variable has recently been presented by Benda and Herz (2003). Other researchers have numerically explored specific models that include both noise and feedback (Liu and Wang, 2001; Chacron et al., 2001, 2003). Here we present a more general approach that permits conclusions from the properties of the neuron without feedback about the case with weak feedback.

We consider a stochastic neuron model governed by

$$\dot{v} = f(v, \vec{m}, a(t)) \quad (1)$$

where v is the membrane voltage and $\vec{m}(t)$ stands for additional variables, for instance, the gating variables in a Hodgkin-Huxley type model. The model generates a spike train $\sum_i \delta(t - t_i)$ (t_i denote the spike times) that is fed back through the feedback variable $a(t)$ obeying (Benda and Herz, 2003)

$$\tau \dot{a} = -a + A \sum_i \delta(t - t_i). \quad (2)$$

where A is a coupling strength, and τ is the feedback's time constant. The way in which $a(t)$ enters the dynamics depends on the model: it may stand, for instance, for a change in current, in conductance, or in the threshold value. We assume that there is noise in the function $f(\dots)$, e.g. white Gaussian noise or Poissonian spike trains. Furthermore, we take for granted that the neuron generates a renewal spike train (all ISIs of the spike train are mutually uncorrelated), if the feedback is switched off (i.e. $A = 0$) — this is a reasonable assumption for most neurons if the stimulus noise has a correlation time much shorter than the mean ISI.

Under these conditions the ISI's mean and variance, the spectrum of the spike train, and the serial correlation coefficient (SCC) can be found (Lindner et al., 2004)

$$\langle T \rangle = \langle T \rangle_0 - \frac{A/\tau}{1 - \rho_0(1/\tau)} \delta_1, \quad (3)$$

$$\langle \Delta T^2 \rangle = \langle \Delta T^2 \rangle_0 - \frac{A/\tau}{1 - \rho_0(1/\tau)} \delta_2 \quad (4)$$

$$S(\omega) = \frac{S_0(\omega)}{\left| 1 + A\chi(\omega) \left[1 - \frac{i\omega\tau}{1 + i\omega\tau} \right] \right|^2} \quad (5)$$

$$SCC_k = \frac{A\delta_1/\tau}{1 - \rho_0(1/\tau)} \left\{ \langle T \rangle_0 + \frac{d}{d\lambda} \ln(\rho_0(\lambda)) \Big|_{\lambda=1/\tau} \right\} \frac{\rho_0^k(1/\tau)}{\langle \Delta T^2 \rangle} \quad (6)$$

where $\langle T \rangle_0$, $\langle \Delta T^2 \rangle_0$, $S_0(\omega)$, $\rho_0(\lambda)$, and $\chi(\omega)$ are the ISI's mean and variance, the spike train's power spectrum, the Laplace transform of the ISI density, and the susceptibility, respectively, all taken for $A = 0$, i.e. for the system without feedback. The quantities δ_1 and δ_2 give the linear corrections to the ISI's mean and variance in the presence of a deterministic input $\exp[-(t - t_{last})/\tau]$ (t_{last} is the respective last firing time). The application of these formulas to an arbitrary neuron model eq. (1) requires the analytical or numerical determination of the quantities of the system without feedback. We note that for integrate-and-fire (IF) models, modified equations can be found that hold for a larger range of coupling strength; in this case numerically determined effective parameters of the unperturbed system take into account the static effect of the feedback. This is done in the next section, using a leaky IF model for which all of the functions of the system without feedback are analytically known (Lindner and Schimansky-Geier, 2001; Lindner et al., 2002; Lindner, 2003); details will be published elsewhere (Lindner et al., 2004).

Results for an leaky integrate-and-fire neuron with current feedback

As specific example, we now consider an leaky IF model with inhibitory current feedback

$$\dot{v} = -v + \mu - a + \sqrt{2D}\xi(t), \quad (7)$$

where the time is measured in units of the membrane time constant, μ and D denote the constant base current and the intensity of the white Gaussian noise, respectively. Whenever the voltage crosses $v_T = 1$, a spike is fired and the voltage is reset to $v_R = 0$.

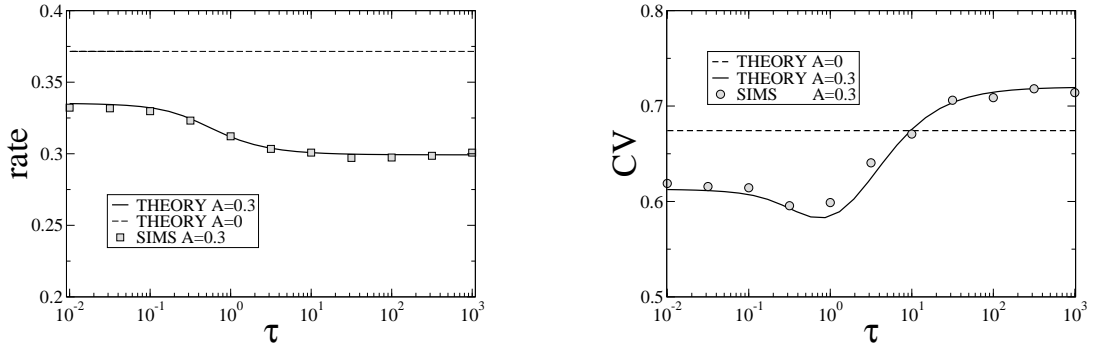


Figure 1: Spike rate (left) and CV (right) vs. time scale of the feedback variable. Analytical results (solid lines) compared to simulations (symbols, see legend); results for the unperturbed system (no dependence on τ) are shown by dashed lines. Parameters: $\mu = 0.8$, $D = 0.1$.

For this model, we can perform the refined approximation that involves the self consistent solution for the static parts of the feedback (Lindner et al., 2004). The system operates at an effective base current $\mu_{eff} < \mu$ that is determined by the feedback strength but also by the time scale τ . We choose a subthreshold $\mu = 0.8$, a moderate noise intensity $D = 0.1$, and a moderate coupling $A = 0.3$. In Fig. 1 we show the firing rate $r = 1/\langle T \rangle$ and the coefficient of variation $CV = \sqrt{\langle \Delta T^2 \rangle} / \langle T \rangle$ vs the feedback time constant. The rate drops with increasing τ ; a slow feedback is thus most efficient in reducing the firing. On the contrary, the CV can be smaller or larger than that in the absence of feedback (dashed line); moreover, it shows a minimum at $\tau \approx 1$ which corresponds in our nondimensional setup to the membrane time constant of the IF model. The theory shows a good agreement with numerical simulation results that were obtained from 10^5 ISIs, simulated using eq. (7), eq. (2), and the fire-and-reset rule explained above.

It can be shown, that in both limits of $\tau = 0$ and $\tau \rightarrow \infty$ correlations between ISIs vanish, i.e. in these limits the model generates a renewal spike train. For a finite value we observe negative correlations with an exponential decay towards zero (Fig. 2, left) in agreement with eq. (6). Such negative correlations reduce the spike count variability and can thus enhance the signal detection performance (Chacron et al., 2001).

The power spectrum of the spike train (Fig. 2, right) shows a significant reduction of power at high frequencies and at low frequencies. Both are caused by the reduction of the spike rate; at low frequencies also the negative correlations in the ISI sequence contribute to the lowering of the power spectrum (Lindner and Longtin, 2003). Remarkably, the reduction of power is minimal for a frequency $\hat{\omega} \approx 2\pi/\tau$ close to the inverse time scale of the feedback variable.

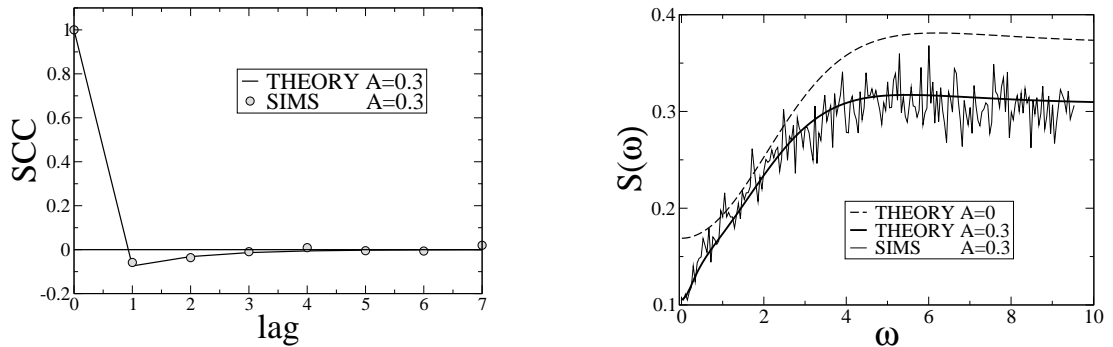


Figure 2: Serial correlation coefficient vs. lag (left) and power spectrum vs frequency (right) for $\mu = 0.8$, $D = 0.1$ and $\tau = 3.16$. Analytical results (thick lines) compared to simulations (symbols or thin line); results for the unperturbed system (no dependence on τ) are shown by dashed lines.

Our results show that already a weak feedback can have a significant effect on the spike train and ISI statistics of a stochastic neuron. Preliminary results on stochastic signal transmission indicate that feedback shapes the susceptibility of the neuron by a high-pass-like function, in agreement with previous results on deterministic models (Benda and Herz, 2003). The spectral signal-to-noise ratio, however, is robust against weak feedback; it is only slightly reduced. We will test these statements and apply the general results eq. (3)–eq. (6) to a multidimensional conductance-based model including an adaptation current.

References

- J. Benda and A. V. M. Herz. A universal model for spike-frequency adaptation. *Neural Comp.*, 15:2523, 2003.
- M. J. Chacron, A. Longtin, and L. Maler. Negative interspike interval correlations increase the neuronal capacity for encoding time-dependent stimuli. *J. Neurosci.*, 21:5328, 2001.
- M. J. Chacron, K. Pakdaman, and A. Longtin. Interspike interval correlations, memory, adaptation, and refractoriness in a leaky integrate-and-fire model with threshold fatigue. *Neural Comp.*, 15:253, 2003.
- B. Lindner. Moments of the first passage time under weak external driving. *arXiv:cond-mat/0312017, submitted to J. Stat. Phys.*, 2003.
- B. Lindner, J. Benda, and A. Longtin. *in prep.*, 2004.
- B. Lindner and A. Longtin. Nonrenewal spike trains generated by stochastic neuron models. In L. Schimansky-Geier, D. Abbott, A. Neiman, and C. V. den Broeck, editors, *Noise in Complex Systems and Stochastic Dynamics*, volume 5114, page 209, Bellingham, Washington, 2003. SPIE.

- B. Lindner and L. Schimansky-Geier. Transmission of noise coded versus additive signals through a neuronal ensemble. *Phys. Rev. Lett.*, 86:2934, 2001.
- B. Lindner, L. Schimansky-Geier, and A. Longtin. Maximizing spike train coherence or incoherence in the leaky integrate-and-fire model. *Phys. Rev. E*, 66:031916, 2002.
- Y.-H. Liu and X.-J. Wang. Spike-frequency adaptation of a generalized leaky integrate-and-fire model neuron. *J. Comp. Neurosci.*, 10:25, 2001.