Low-Pass Filtering of Information in the Leaky Integrate-and-Fire Neuron Driven by White Noise

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Abstract The question of how noisy spiking neurons respond to external time-dependent stimuli is a central topic in computational neuroscience. An important aspect of the neural information transmission is, whether neurons encode preferentially information about slow or about fast components of the stimulus (signal). A convenient way to quantify this is the spectral coherence function, that in some experimental data shows a global maximum at low frequencies (low-pass information filter), in some other cases has a maximum at higher frequencies (band-pass or high-pass information filter); information-filtering defined in this way is related but not identical to the usual filtering of spectral power. Here I demonstrate numerically that the leaky integrate-and-fire neuron driven by white noise (a stimulus without temporal correlations) acts as a low-pass information filter irrespective of the dynamical regime (fluctuation-driven and irregular or mean-driven and regular firing).

1 Introduction

Nerve cells in our brain transduce information about time-dependent stimuli like visual or auditory signals into sequences of stereotype action potentials called spike trains. An important aspect of neural information transmission is what are the most important features that are encoded in the neural sequence of action potentials. One important feature is the preferred frequency band in which neurons transmit information or, put differently, whether neurons encode preferentially slow or fast components of a time-dependent stimulus (signal). Experimentally one has seen both

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kinds of low-pass and high-pass filtering of information (not to be confused with the common filtering of signal power). This raises the question about the properties of neural dynamics or network properties that may lead to specific forms of information filtering.

Simple neuron models like the stochastic integrate-and-fire model are able to reproduce spiking statistics of cells in response to noisy currents to an astonishing degree of accuracy [1, 2]. Upon changing the mean and variance of the current injection, IF models display transitions between distinct firing regimes: pacemaker-like regular firing, the near-Poisson irregular firing with low rate, and the burst-like firing with a coefficient of variation (Cv) beyond unity [3–5]. In the so-called nonlinear IF model different response behavior with respect to additional stimulation is possible: from non-resonant purely noise-controlled response function of the perfect IF model to the resonances of the leaky, quadratic or exponential IF models [6, 7].

Despite all these differences for different nonlinearities of the model and despite the existence of distinct firing regimes, a previous study [7] suggested that IF models seem to share one property: they transmit most information about slow signal components. This can be seen by looking at the coherence as a function of frequency: it attains its global maximum at zero frequency. For the leaky IF model with selected parameters, this has been found numerically already in the early 1970's [8].

Here in this chapter, I discuss the coherence for the leaky IF model as a function of mean and intensity of its input fluctuations. It is shown that this model is a low-pass filter of information in the sense that the maximum of the coherence is at zero frequency. I also discuss how the half-width of the coherence behaves and how it compares to other characteristic frequencies of the system, namely, the inverse membrane-time constant and the firing rate of the model neuron. These results establish that for a white-noise driven leaky IF model a high-pass filtering of information is not possible. If the latter is observed in a real neuron, this tells us that most likely a more complicated dynamics than a one-dimensional IF model is involved.

2 Model and Measures of Interest

I consider a leaky integrate-and-fire (LIF) model with a noisy current input

$$\dot{v} = -v + \mu + \sqrt{2D_{\text{bg}}}\xi_{\text{bg}}(t) + \sqrt{2D_{\text{st}}}\xi_{\text{st}}(t), \tag{1}$$

which is complemented by a fire-and-reset rule: whenever $v(t)$ crosses the threshold v_T, a spike is registered and the voltage is reset to v_R and, after an absolute refractory period τ_{abs} has passed, released to evolve again according to the above equation. To reduce the number of free parameters, voltage is here defined as the deviation from the reset (implying $v_R = 0$) and is measured in multiples of the reset-threshold distance (implying $v_T = 1$); time is measured in multiples of the membrane-time constant (see [5] for details of the transformation from the model with

physical dimensions to the non-dimensional model considered here). Input parameters are the constant base current μ, the intensity D_{bg} of the background noise $\xi_{bg}(t)$ (representing synaptic background fluctuations or channel noise), and the intensity D_{st} of the stimulus $\xi_{st}(t)$. Both background noise and stimulus signal are assumed as Gaussian white noise with $\langle \xi_i(t)\xi_j(t')\rangle = \delta_{i,j}\delta(t - t')$ (where $i, j \in \{bg, st\}$).

The information transmission of this spiking model can be quantified by means of the spectral coherence function. To this end, one considers the Fourier transform in a time window $[0, T]$

$$\tilde{x}_T(\omega) = \int_0^T dt\, e^{i\omega t} x(t) \tag{2}$$

of the spike train

$$x(t) = \sum \delta(t - t_i) \tag{3}$$

where the t_i are the time instants of threshold crossings. The cross-spectrum of spike train and stimulus and the spike train power spectrum are defined as follows

$$S_{x,s}(\omega) = \lim_{T\to\infty} \frac{\langle \tilde{x}(\omega)\tilde{s}^*(\omega)\rangle}{T}, \quad S_{x,x}(\omega) = \lim_{T\to\infty} \frac{\langle \tilde{x}(\omega)\tilde{x}^*(\omega)\rangle}{T}. \tag{4}$$

The coherence function for the input signal and the output spike train is the squared correlation coefficient between input and output

$$C_{x,s} = \frac{|S_{x,s}(\omega)|^2}{S_{x,x}(\omega)S_{s,s}(\omega)} \tag{5}$$

and yields at each frequency a number between 0 and 1. Low or high information transmission in a certain frequency band is indicated by a coherence close to zero or one, respectively.

Generally, a system that shows under white-noise stimulation a coherence which decreases (increases) with frequency can be regarded as a low-pass (high-pass) filter of information. This kind of information filter is related but not identical with the commonly considered power filter. A linear bandpass-filter, for instance, driven by white background noise and a white noise stimulus would not act as an information filter—its coherence is simply flat. One formal reason for this is that the frequency dependences of cross-spectrum and power spectrum in Eq. (5) cancel out for a linear system. When both signal and noise pass through the same power filter, the filter cannot change the signal-to-noise ratio, which is what is essentially quantified by the coherence.

Despite the linearity of Eq. (1), the spiking LIF neuron model is *not* linear; it possesses the strong nonlinearity of the reset rule and thus we can expect that the LIF model performs one or the other kind of information filtering and that this information filter potentially depends on the firing regime that is set by the input parameters μ and

D. For the LIF driven by white Gaussian current noise, we fortunately know all the spectral functions of interest analytically. The cross-spectrum between input signal and output spike train is given by the product of input spectrum (just the constant $2D_{st}$) and the complex rate-modulation factor, the so-called susceptibility [9, 10]

$$S_{x,s}(\omega) = \frac{2D_{st}}{\sqrt{D}} \frac{r_0 i\omega}{i\omega - 1} \frac{\mathscr{D}_{i\omega-1}\left(\frac{\mu-v_T}{\sqrt{D}}\right) - e^{\Delta}\mathscr{D}_{i\omega-1}\left(\frac{\mu-v_R}{\sqrt{D}}\right)}{\mathscr{D}_{i\omega}\left(\frac{\mu-v_T}{\sqrt{D}}\right) - e^{\Delta}e^{i\omega\tau_{abs}}\mathscr{D}_{i\omega}\left(\frac{\mu-v_R}{\sqrt{D}}\right)} \tag{6}$$

where

$$\Delta = \frac{v_R^2 - v_T^2 + 2\mu(v_T - v_R)}{4D}$$

and $\mathscr{D}_a(x)$ is the parabolic cylinder function [11]. The firing rate r_0 is given by

$$r_0 = \left[\tau_{abs} + \sqrt{\pi} \int\limits_{(\mu-v_T)/\sqrt{2D}}^{(\mu-v_R)/\sqrt{2D}} dz\, e^{z^2}\, \mathrm{erfc}(z) \right]^{-1}. \tag{7}$$

Alternative expressions for the susceptibility with vanishing refractory period have been derived by Brunel et al. (see [12] and References there in).

The power spectrum of the spike train is given by [3]

$$S_{x,x}(\omega) = r_0 \frac{\left|\mathscr{D}_{i\omega}\left(\frac{\mu-v_T}{\sqrt{D}}\right)\right|^2 - e^{2\Delta}\left|\mathscr{D}_{i\omega}\left(\frac{\mu-v_R}{\sqrt{D}}\right)\right|^2}{\left|\mathscr{D}_{i\omega}\left(\frac{\mu-v_T}{\sqrt{D}}\right) - e^{\Delta}e^{i\omega\tau_{abs}}\mathscr{D}_{i\omega}\left(\frac{\mu-v_R}{\sqrt{D}}\right)\right|^2} \tag{8}$$

In both these expressions, $D = D_{bg} + D_{st}$ denotes the total noise intensity.

Combining Eqs. (6) and (8), the coherence of the LIF model reads:

$$C_{x,s} = \frac{2D_{st}}{D} \frac{r_0\omega^2}{1+\omega^2} \frac{\left|\mathscr{D}_{i\omega-1}\left(\frac{\mu-v_T}{\sqrt{D}}\right) - e^{\Delta}\mathscr{D}_{i\omega-1}\left(\frac{\mu-v_R}{\sqrt{D}}\right)\right|^2}{\left|\mathscr{D}_{i\omega}\left(\frac{\mu-v_T}{\sqrt{D}}\right)\right|^2 - e^{2\Delta}\left|\mathscr{D}_{i\omega}\left(\frac{\mu-v_R}{\sqrt{D}}\right)\right|^2} \tag{9}$$

It can be seen that the absolute refractory period does enter this expression only via the firing rate and, hence, has no effect on the frequency dependence of the coherence. Increasing τ_{abs} leads only to an overall reduction of the coherence. For this reason, we consider in the following the special case of a vanishing refractory period $\tau_{abs} = 0$.

If we want to graphically illustrate the above results, this requires the numerical evaluation of the parabolic cylinder function at complex-valued index, a nontrivial task that can be achieved using software like Maple^{TM} or Mathematica^{TM}. An alternative way to determine cross- and power spectra is the threshold-integration method

by Richardson [13], which can be easily implemented in common programming languages like C and can be readily extended to nonlinear IF models. In this work, I have mainly used the latter method but verified for selected parameter sets that this provides the same results as the explicit result evaluated in Maple16$^{\text{TM}}$.

Note that for fixed total noise intensity D the stimulus intensity D_{st} only scales the coherence function by a factor D_{st}/D . For this reason we set in the following $D = D_{\text{st}}$ implying $D_{\text{bg}} = 0$. With the same total noise intensity D, the coherence function with finite D_{bg} is obviously smaller than without intrinsic noise [8]. This is not in contradiction to the fact that the LIF displays stochastic resonance [9] because to see the latter phenomenon, we should keep the signal amplitude constant and vary the background noise intensity D_{bg}; in this case the total noise intensity is *not* fixed. Indeed, if $\mu < v_T$, the coherence at any frequency (proportional to the signal-to-noise ratio for periodic stimulation at this frequency) passes through a maximum as a function of D_{bg} [10].

3 Results

In Fig. 1 we show examples of power spectra, cross-spectra, and coherence functions for an LIF in the fluctuation-driven firing regime of high irregularity (a) and the mean-driven firing regime of rather regular firing pattern (b). For the setting in the fluctuation-driven regime, the steady state firing rate is $r_0 \approx 0.16$ and a coefficient of variation of the interspike interval is about $C_v \approx 0.835$ while for the parameters in Fig. 1b we have a higher firing rate $r_0 \approx 0.924$ and a considerably lower $C_v \approx 0.166$. Despite pronounced differences in the cross—and power spectra, that reflect differences in the spiking statistics and in the response to time-dependent signals, the
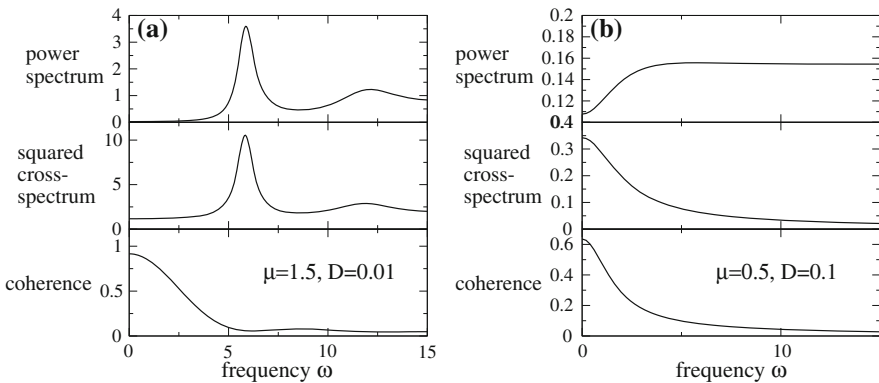

Fig. 1 Power spectrum (*top panel*), cross-spectrum (*mid panel*) and coherence as functions of frequency in the mean-driven regime (**a**) and the fluctuation driven regime (**b**) with mean input μ and total noise intensity as indicated in the figure.

coherence function in both cases attains its maximum at zero frequency and decays quite rapidly with increasing frequency.

The only qualitative difference occurs around the frequency comparable to the firing rate: the LIF in the regular (mean-driven) firing regime possesses a local *minimum* at this frequency, whereas the coherence of the LIF in the irregular (noise-induced or fluctuation-dominated) firing regime decays monotonically with frequency. Given that coherence has a global maximum around zero in both cases and given that the main share of information is transmitted in this low-frequency range, these difference appear as rather unimportant.

How can we quantify whether this low-pass behavior of the coherence is present for all combinations of base currents and noise intensities? To this end, we can consider a number of characteristics of the coherence function that are illustrated in Fig. 2.

We can first of all find the global maximum of the coherence curve as a function of frequency for various combinations of base current μ and noise (signal) intensity D. In the broad range of values considered, this yields always $\omega = 0$ as the frequency
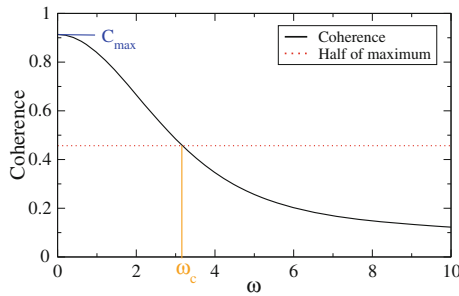

Fig. 2 Coherence function for $\mu = 1.2$ and $D = 0.1$. Indicated are the maximum, C_{max}, the half value of the maximum (*dotted line*), and the frequency ω_c at which this half value is attained (*vertical line*)
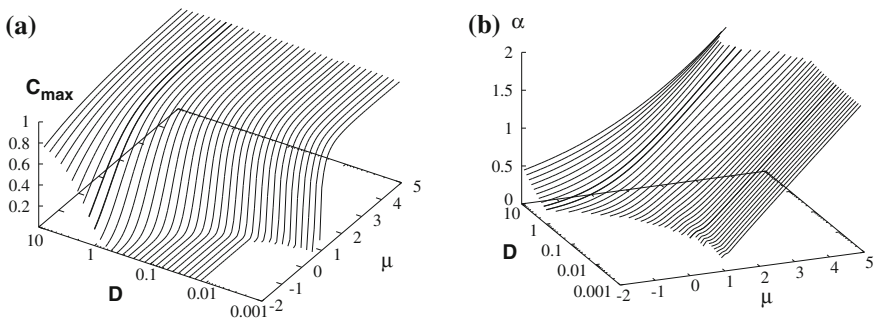

Fig. 3 The maximum (**a**) and the half-width (**b**) of the coherence between the driving noise and the output spike train as a function of the base current μ and the noise intensity D.

of this global maximum. In Fig. 3a, we show this maximum value of the coherence $C_{max} = C_{xs}(\omega = 0)$ as a function of the base current μ and the noise intensity D. This value increases both with the noise intensity (here also the signal amplitude) and the base current. In the limit of large base current, the coherence approaches one which agrees with the limit for a perfect IF model, in which a leak term is absent. The main reason for this increase in the maximum value of the coherence is the increase in firing rate with growing base current - with an increasing number of spikes per unit time it becomes possible to encode an arbitrary slow stimulus (corresponding to the coherence at $\omega = 0$, i.e. its maximum) arbitrarily reliable. In the opposite limit of negative base current, the firing rate becomes exponentially small and thus the coherence is essentially zero unless a large noise intensity compensates for the decrease in base current.

As a measure of the bandwidth over which the LIF transmits the stimulus, I consider the (minimal) frequency ω_c at which the coherence attains half of its maximal value (cf. Fig. 2); ω_c is in the following referred to as the *half-width*. Also of interest is the ratio of this (cyclic) frequency to the frequency associated with the inverse membrane time constant (which we set to one):

$$\alpha = \frac{\omega_c}{2\pi}. \tag{10}$$

The parameter α will tell us whether the half-width is constrained by the inverse membrane time constant or not. In Fig. 3b α is plotted as a function of μ and D illustrating that for low firing rate (for $\mu < 1$ and small noise intensity D), the coherence halfwidth is smaller than the inverse membrane time constant, while at higher firing rate (in the mean-driven firing regime with $\mu > 1$) the information bandwidth is not limited by the membrane-time constant. In particular in this latter regime it is also instructive to compare ω_c to another typical frequency in the system, namely the firing rate:

$$\beta = \frac{\omega_c}{2\pi r_0}. \tag{11}$$

Because r_0 is also measured in multiples of the membrane time constant, the latter drops out of the ratio β.

Fig. 4 Halfwidth normalized by the firing rate as a function of base current μ and noise intensity D
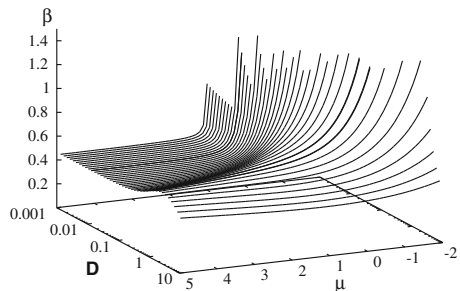
In Fig. 4 it becomes apparent that at high firing rate (large μ, small D), the halfwidth is determined mainly by the firing rate - the inverse membrane time constant does not play a role in this limit. There seems to be a saturation at about half of the width of the firing rate, i.e. frequencies sufficiently below the firing rate (smaller by a factor of two or three) are transmitted reliably ($C(\omega) > 0.5$). Expressed in multiples of the firing rate, the information bandwidth diverges in the opposite limit of vanishing firing rate. Here, however, one should keep in mind that in terms of the inverse membrane-time constant the halfwidth is still very small in this limit (cf. Fig. 3b).

4 Summary and Conclusions

In this chapter I have inspected the coherence function of a leaky integrate-and-fire neuron driven by white Gaussian noise. In accordance with previous findings at selected parameter sets [7] I have found that the LIF neuron acts as a low-pass filter on information about a time-dependent uncorrelated Gaussian stimulus for a broad range of input parameters. I have studied the magnitude and halfwidth of the coherence function. At low firing rate (subthreshold μ and small noise intensity D) the coherence is generally low and its half-width is constrained by the inverse membrane time constant (which was one in our units). At high firing rate (for suprathreshold $\mu > 1$), information transmission is high up to frequencies that are well below the firing rate; for large μ, the halfwidth seems to be given by $\omega_c \approx \pi r_0$.

Results from Ref. [7] indicate that low-pass information filtering is also prevailing in other integrate-and-fire models, as for instance, the perfect and the quadratic IF neurons. The bandwidth inspected here, however, may certainly differ. It is, for instance, known that the coherence of the perfect IF model at zero frequency is always one irrespective of the parameter values (similar to what seems to be the limit of the LIF model for $\mu \to \infty$). Furthermore, the halfwidth is solely controlled by the noise intensity [7]. The numerical methods by Richardson [13], which were applied here to the LIF can be also applied to the perfect and quadratic IF models as well as to the so-called exponential IF model [2, 6].

Desirable would be also to analytically study the coherence of a general nonlinear IF model at low frequencies: the conjecture of low-pass information filtering entails a negative curvature of the coherence at low frequencies that may be provable by perturbation methods. Unfortunately, this is already highly nontrivial for the LIF model for which we know the exact result for the coherence, namely, Eq. (9) but lack a simple small-frequency expansion that would permit to determine the sign of the curvature at $\omega = 0$.

The results achieved in this paper indicate that the LIF model is unable to reproduce cases of information highpass-filtering that have been observed in experiments. At the population level the coding by synchronous spikes provides a coherence function that is suppressed at low frequencies [14], an experimental observation that has been modeled and theoretically analyzed with populations of LIF neurons [15]. At the single-cell level possible candidates for information filtering are short-term synaptic

plasticity (however, see [16] but also [17]), spike-frequency adaptation [18], or sub-threshold oscillations [19, 20]. Also the effect of temporally correlated background spiking [21] or synaptic filtering of uncorrelated input [22] will result in colored instead of white background noise and may thus lead to a decrease or increase of the coherence at low frequencies compared to the case of white noise. Filtering of information, regarded as a simple form of information processing, could thus assign (an additional) functional role to certain biophysical features of the neural dynamics.

References

1. L. Badel, S. Lefort, R. Brette, C.C.H. Petersen, W. Gerstner, M.J.E. Richardson, Generalized integrate-and-fire models of neuronal activity approximate spike trains of a detailed model to a high degree of accuracy. J. Neurophysiol. **92**, 959 (2004)
2. L. Badel, S. Lefort, R. Brette, C.C.H. Petersen, W. Gerstner, M.J.E. Richardson, Dynamic I-V curves are reliable predictors of naturalistic pyramidal-neuron voltage traces. J. Neurophysiol. **99**, 656 (2008)
3. B. Lindner, L. Schimansky-Geier, A. Longtin, Maximizing spike train coherence or incoherence in the leaky integrate-and-fire model. Phys. Rev. E **66**, 031916 (2002)
4. A. N. Burkitt, A review of the integrate-and-fire neuron model: I. homogeneous synaptic input. Biol. Cyber. **95**(1) (2006)
5. R.D. Vilela, B. Lindner, Are the input parameters of white-noise-driven integrate & fire neurons uniquely determined by rate and CV? J. Theor. Biol. **257**, 90 (2009)
6. N. Fourcaud-Trocmé, D. Hansel, C. van Vreeswijk, N. Brunel, How spike generation mechanisms determine the neuronal response to fluctuating inputs. J. Neurosci. **23**, 11628 (2003)
7. R.D. Vilela, B. Lindner, A comparative study of three different integrate-and-fire neurons: spontaneous activity, dynamical response, and stimulus-induced correlation. Phys. Rev. E **80**, 031909 (2009)
8. R.B. Stein, A.S. French, A.V. Holden, The frequency response, coherence, and information capacity of two neuronal models. Biophys. J. **12**, 295 (1972)
9. B. Lindner, L. Schimansky-Geier, Transmission of noise coded versus additive signals through a neuronal ensemble. Phys. Rev. Lett. **86**, 2934 (2001)
10. B. Lindner, J. García-Ojalvo, A. Neiman, L. Schimansky-Geier, Effects of noise in excitable systems. Phys. Rep. **392**, 321 (2004)
11. M. Abramowitz, I.A. Stegun, *Handbook of Mathematical Functions* (Dover, New York, 1970)
12. N. Fourcaud, N. Brunel, Dynamics of the firing probability of noisy integrate-and-fire neurons. Neural Comp. **14**, 2057 (2002)
13. M. J. E. Richardson, Spike-train spectra and network response functions for non-linear integrate-and-fire neurons. Biol. Cybern. (to appear) **99**, 381–392 (2008)
14. J.W. Middleton, A. Longtin, J. Benda, L. Maler, Postsynaptic receptive field size and spike threshold determine encoding of high-frequency information via sensitivity to synchronous presynaptic activity. J. Neurophysiol. **101**, 1160 (2009)
15. N. Sharafi, J. Benda, B. Lindner, Information filtering by synchronous spikes in a neural population. J. Comp. Neurosci. **34**, 285 (2013)
16. B. Lindner, D. Gangloff, A. Longtin, J.E. Lewis, Broadband coding with dynamic synapses. J. Neurosci. **29**, 2076 (2009)
17. R. Rosenbaum, J. Rubin, B. Doiron, Short term synaptic depression imposes a frequency dependent filter on synaptic information transfer. PLoS Comput. Biol. **8**, e1002557 (2012)

18. J. Benda, A.V.M. Herz, A universal model for spike-frequency adaptation. Neural Comp. **15**, 2523 (2003)
19. M.J.E. Richardson, N. Brunel, V. Hakim, From subthreshold to firing-rate resonance. J. Neurophysiol. **89**, 2538 (2003)
20. T.A. Engel, L. Schimansky-Geier, A.V.M. Herz, S. Schreiber, I. Erchova, Subthreshold membrane-potential resonances shape spike-train patterns in the entorhinal cortex. J. Neurophysiol. **100**(3), 1576 (2008)
21. B. Lindner, Superposition of many independent spike trains is generally not a poisson process. Phys. Rev. E **73**, 022901 (2006)
22. N. Brunel, S. Sergi, Firing frequency of leaky integrate-and-fire neurons with synaptic current dynamics. J. Theor. Biol. **195**, 87 (1998)