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Interspike interval statistics of neurons driven by colored noise

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A perfect integrate-and-fire model driven by colored noise is studied by means of the interspike interval (ISI) density and the serial correlation coefficient. Exact and approximate expressions for these functions are derived for weak dichotomous or Gaussian noise, respectively. It is shown that correlations in the input result in positive correlations in the ISI sequence and in a reduction of ISI variability. The results also indicate that for weak noise, the noise distribution only shapes the ISI density but not the ISI correlations which are determined by the noise's correlation function.

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INTRODUCTION

One of the milestones in theoretical neurobiology was the introduction of the perfect integrate-and-fire (IF) neuron (or random walk) model by Gerstein and Mandelbrot [1]. In this model the voltage across the nerve membrane obeys a simple white-noise (WN) driven dynamics

$$\dot{v}=\mu+\eta(t) \qquad (1)$$

with $\mu>0$ being a constant input and $\eta(t)$ white Gaussian noise of intensity D, i.e., $\langle\eta(t)\eta(t')\rangle=2D\delta(t-t')$. The model is supplemented by the spike generator rule: whenever the voltage reaches a certain threshold v_T a δ spike is generated and the voltage is reset to zero.

In general, the output of a spike generator model like above is characterized by the statistics of the sequence of intervals between subsequent spikes, i.e., interspike intervals (ISIs), $\{\ldots,I_{j-1},I_j,I_{j+1},\ldots\}$ or, equivalently, by the statistics of the nth order intervals (sum of n subsequent intervals) $T_n=\Sigma_{j=1}^{n}I_j$. Furthermore, correlations among intervals can be quantified by the serial correlation coefficient (SCC)

$$\rho_k=\frac{\langle I_{j+k}I_j\rangle-\langle I_{j+k}\rangle\langle I_j\rangle}{\langle I_j^2\rangle-\langle I_j\rangle^2}. \qquad (2)$$

For Eq. (1) with WN driving, the probability density of the nth order interval can be exactly calculated [1,2]

$$g_n^{WN}(T_n)=\frac{nv_T}{\sqrt{4\pi DT_n^3}}\exp\left[-\frac{(T_n-nv_T/\mu)^2}{4(D/\mu^2)T_n}\right]. \qquad (3)$$

The variance and mean of this density are given by $\langle\Delta T_n^2\rangle_{WN}=2Dnv_T/\mu^3$ and $\langle T_n\rangle_{WN}=nv_T/\mu$, respectively. Furthermore, the SCC for the model with WN input is given by $\rho_k=\delta_{k,0}$. Since the driving process is uncorrelated and the reset erases any memory carried by the voltage variable, the model generates a renewal spike train [3] with statistically independent ISIs.

The perfect IF model is a good approximation for more complicated neuronal models if the mean input current μ is large. A severe limitation of Eq. (1), however, is the uncorrelated WN input. Massive spike train input received by cortical neurons, for instance, is filtered by a first-order synaptic dynamics, leading effectively to an Ornstein-Uhlenbeck process (OUP) [4,5], i.e., the input is an exponentially correlated (colored) Gaussian noise. Another example is a neuron receiving input from a randomly bursting neuron; in the simplest nontrivial case the input can be approximated by a dichotomous process (DP) with exponential correlations.

Recent work has shown that correlations in the input can affect spike count statistics [6,7] and signal transmission features [8] strongly and in unexpected ways, indicating the need for a deeper theoretical understanding of the effects of colored noise in neural systems (for classic results on colored noise in nonlinear dynamical systems, see Ref. [9]). So far, analytical results for (perfect or leaky) IF models have been reported for the ISI's mean and variance [4,10], for spike count and ISI statistics in case of a long-correlated (''static'') driving noise [6], and for the response to additional periodic stimuli [8]. A full characterization of the spontaneous (i.e., only noise driven) activity of a model neuron with colored noise of *arbitrary* correlation time by the ISI density and the SCC is still missing. In particular, it is not clear whether exponentially correlated noise processes like the OUP or DP increase or decrease the ISI variability compared to the WN case, whether they cause positive or negative ISI correlations, and how the noise distribution influences both ISI density and ISI correlations.

The aim of this paper is to extend the above results for the WN case to a colored noise driven perfect IF neuron, assuming that the driving noise is weak. Exact or approximate expressions for the ISI density and the SCC are derived for the cases that $\eta(t)$ is not a WN but, (1), a DP, switching between two states $\pm\sigma$ with stationary density $p_0(\eta)=[\delta(\eta-\sigma)+\delta(\eta+\sigma)]/2$ or (2) an OUP with stationary density $p_0(\eta)=\exp[-\eta^2/(2\sigma^2)]/\sqrt{2\pi\sigma^2}$, respectively. Both processes are characterized by variance σ^2, correlation time τ, and an exponential correlation function $\langle\eta(t)\eta(t')\rangle=\sigma^2\exp[-(t-t')/\tau]$. On comparing with the WN case I shall use the *noise intensity* (i.e., the integral over the correlation function from 0 to infinity) given by $D=\sigma^2\tau$. The analytical approach is based on the assumption of a small noise variance, i.e., for $\varepsilon=\sigma^2/\mu^2$ one requires $\varepsilon\ll 1$ in case of an OUP and $\varepsilon\leqslant 1$ in case of a dichotomous driving.

THEORY

Since the dynamics, Eq. (1), does not explicitly depend on v, n subsequent passages from $v=0$ to $v=v_T$ (corresponding to the nth order interval T_n) are equivalent to *one* passage from $v=0$ to $v=nv_T$ *without* reset (see also Ref. [6]).

For a given initial value of the noise $\eta(0)=\eta_0$, the nth order interval density thus equals the first-passage-time density (FPTD) from $v=0$ to $v=nv_T$. For $n\rightarrow\infty$, the mean interval $\langle T_n\rangle$ approaches nv_T/μ [11] which can be regarded as a time average of lower order intervals; hence one can conclude that in general, $\langle T_n\rangle = nv_T/\mu$ as in the WN case and independent of the noise statistics.

For either driving processes the FPTD problem can be formulated in terms of a Fokker-Planck equation for the transition probability P_{tr} in the (v,η) plane with a reflecting boundary condition for $\eta<-\mu$ on the line $v=nv_T$ (this prevents multiple counting of realizations that have already reached nv_T and returned, see Ref. [4]). The FPTD is then given by the probability current in the v direction at $v=nv_T$ which is $(\eta_1+\mu)P_{tr}(nv_T,\eta_1,T_n|0,\eta_0,0)$ integrated over all possible final values η_1 of the noise. To obtain the true density of T_n, the FPTD has to be averaged with respect to the stationary density of noise values *upon firing* $P_F(\eta_0)$.

For small noise variance ($\varepsilon\ll 1$), values of η below $-\mu$ are highly unlikely; hence the reflecting boundary condition can be neglected and the transition probability of the *freely evolving process* $[v(t),\eta(t)]$ can be used. This is done throughout the remainder of the paper. Within the same approximation, the density $P_F(\eta_0)$ is proportional to the stationary probability current in the v direction; normalization yields

$$P_F(\eta_0)=\frac{\eta_0+\mu}{\mu}p_0(\eta_0), \tag{4}$$

where $p_0(\eta_0)$ is the stationary density of noise values. Putting all of these together, the nth order interval at small noise variance is given by

$$g_n(T_n)=\int\int d\eta_0 d\eta_1(\mu+\eta_1) \times P_{tr}(nv_T,\eta_1,T_n|0,\eta_0,0)P_F(\eta_0). \tag{5}$$

To keep the resulting expressions simple, these integrals are taken over the entire range of noise values. Note that this may lead to the occurrence of negative "probability" for two reasons: (1) our approximation of $P_F(\eta_0)$ is negative for $\eta_0<-\mu$; (2) the second integration (i.e., that with respect to η_1) includes the back flux of probability for $\eta_1<-\mu$ which is negative, too. These contributions, however, are negligible for $\varepsilon\ll 1$; they are completely absent for the dichotomous driving with $\varepsilon\leqslant 1$ in which case Eq. (5) is exact.

Knowledge of the nth order interval density also permits the calculation of the SCC ρ_k as follows: the variance of the nth order interval obeys [3] $\langle\Delta T_n^2\rangle/\langle\Delta T_1^2\rangle = n+2\Sigma_{k=1}^{n-1}(n-k)\rho_k$; from this relation, the SCC is found to be

$$\rho_k=\frac{\langle\Delta T_{k+1}^2\rangle+\langle\Delta T_{k-1}^2\rangle}{2\langle\Delta T_1^2\rangle}-\frac{\langle\Delta T_k^2\rangle}{\langle\Delta T_1^2\rangle}. \tag{6}$$

IF NEURON DRIVEN BY DICHOTOMOUS NOISE

For $\sigma\leqslant\mu$ (i.e., $\varepsilon\leqslant 1$), the transition probability can be derived from the solution $P_{\pm}(v,t)$ with $\mu=0$ and arbitrary initial conditions as, e.g., in Ref. [12]. In terms of $x_n(T)=nv_T-\mu T$, $\alpha_n(T)=\sqrt{\sigma^2T^2-x_n^2(T)}/(2\tau\sigma)$, and the Heaviside function [13] $\Theta=\Theta(\sigma T-|x_n(T)|)$ transitions from $v=0$ to $v=nv_T$ and various combinations of initial and final values of the noise (indicated by the first and last index, respectively) occur with probability

$$P_{\pm,\pm}=e^{-T/(2\tau)}\left[\delta(x_n(T)\mp\sigma T) + \Theta\frac{\sigma T\mp x_n(T)}{8\alpha_n(T)(\tau\sigma)^2}I_1(\alpha_n(T))\right], \tag{7}$$

$$P_{\pm,\mp}=e^{-T/(2\tau)}\Theta I_0(\alpha_n(T))/(4\tau\sigma), \tag{8}$$

where $I_0(z)$ and $I_1(z)$ are the modified Bessel functions [13]. Using the stationary distribution of noise values, one obtains from Eq. (5) (with the integrals reducing to sums because of the discrete nature of the DP) the following exact solution for the probability density of the nth order interspike interval for $\sigma\leqslant\mu$

$$g_n^{DP}(T_n)=\frac{e^{-T_n/(2\tau)}v_T}{4\sigma\tau^2\beta}\left[2\sigma\tau\left(\frac{\delta(T_n-T_n^+)}{\mu-\sigma}+\frac{\delta(T_n-T_n^-)}{\mu+\sigma}\right) + (n\beta-T_n/(2\tau))\frac{I_1(\alpha_n(T_n))}{\alpha_n(T_n)}+I_0(\alpha_n(T_n))\right]. \tag{9}$$

This holds for $T_n^+\leqslant T\leqslant T_n^-$ with $T_n^{\pm}=nv_T/(\mu\pm\sigma)$ while the density is zero outside this range. The parameter β is given by

$$\beta=\frac{v_T\mu/\tau}{\mu^2-\sigma^2}. \tag{10}$$

The δ spikes in the density correspond to realizations for which the noise value does not change during the passage from 0 to nv_T, while the continuous part in between those spikes results from at least one change of the noise value. The δ spikes will dominate at large correlation time (for $\tau\gg nv_T/\mu$ almost all probability is in the δ spikes). At small τ the continuous part of the density contains most probability and the δ spikes may be safely neglected.

In Fig. 1 (top) the ISI density [Eq. (9) with $n=1$] is shown for $\sigma^2=0.5$ and different values of correlation time by solid lines. This is compared to results of computer simulations (symbols) as well as to the density $g_1^{WN}(T)$ (dashed lines) of the WN driven IF neuron, Eq. (3), with noise intensity $D=\sigma^2\tau$. The simulation results confirm our analytical findings. Note that the noise intensity increases in proportion to the correlation time. It can therefore be expected that with growing correlation time the density becomes broader and ISIs become more variable. Indeed, starting at small correlation time $\tau=0.01$ I find a narrow density around the mean ISI ($\langle T\rangle=1$). Here the density coincides with $g_1^{WN}(T)$ within line thickness. Severe differences between $g_1^{DP}(T)$ and $g_1^{WN}(T)$ are already observed for $\tau=0.1$; due to the increase in noise intensity the finite support of noise values becomes apparent by a peak at $T=T_1^+$ beyond which no probability is present in marked contrast to the WN case. Also, the local

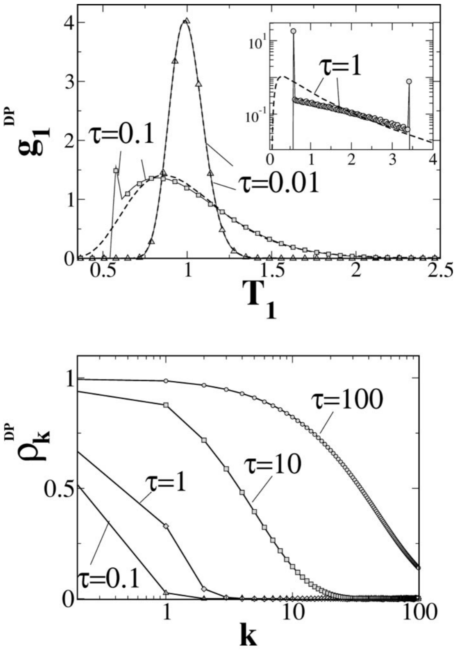

FIG. 1. ISI statistics for dichotomous noise and different values of the correlation time τ at $\mu = v_T = 1$. Top: ISI density (solid lines) for $\sigma^2 = 0.5$ compared to simulations (symbols) and the density of the WN case g_1^{WN} (dashed lines); for the latter, τ is not a correlation time but determines the noise intensity by $D = \sigma^2 \tau$. Inset: logarithm of density for τ=1. Bottom: SCC for $\sigma^2 = 0.5$, analytical result (solid lines) compared to simulation results (symbols).

maximum of the density is attained at slightly smaller ISI than for $g_1^{WN}(T)$. Going to an even larger correlation time of τ=1 (inset of Fig. 1, top) the density is dominated by the peaks (their height depends on the binning of ISIs) while in between the peaks there is a small continuous contribution that drops with increasing ISI. Obviously, this shape has nothing in common, anymore, with the ISI density of a WN driven IF neuron.

Further insights are provided by the interval variance which can be analytically calculated from Eq. (9)

$$\langle \Delta T_n^2 \rangle_{DP} = \langle \Delta T_n^2 \rangle_{WN} [1 - (1 - e^{-n\beta})/(n\beta)]. \qquad (11)$$

Note that the prefactor is exactly the variance of the WN driven IF neuron $\langle \Delta T_n^2 \rangle_{WN} = 2nDv_T/\mu^3$ (with $D = \sigma^2 \tau$). Since $\beta > 0$, the variance of the nth order interval is always smaller than for the WN case. Hence, compared to a WN driving, the IF neuron driven by dichotomous noise generates a less variable ISI.

From Eqs. (11) and (6) one can also obtain the following strikingly simple expression for the SCC ($k > 0$)

$$\rho_k^{DP} = 2e^{-k\beta} \sinh^2(\beta/2)/(\beta - 1 + e^{-\beta}). \qquad (12)$$

The correlations among intervals are evidently positive. The theoretical result is confirmed by simulations in Fig. 1 (bottom) for a fairly large noise variance corresponding to ε=0.5. Remarkably according to Eq. (12), the SCC *depends monotonously on all parameters only through* β given in Eq. (10), i.e., increasing β by increasing σ or decreasing τ weakens the positive correlations among the ISIs. This also implies that a decrease in correlation time can leave the correlations among ISIs unchanged if the noise variance is decreased at the same time such that β remains unchanged. This has been checked by simulating the system with $\sigma^2 = 0.25$, $v_T = \mu = 1$, and $\tilde{\tau} = 2\tau/3$ (τ stands for the values indicated in Fig. 1, bottom); indeed, the same data were obtained as shown in Fig. 1 (bottom).

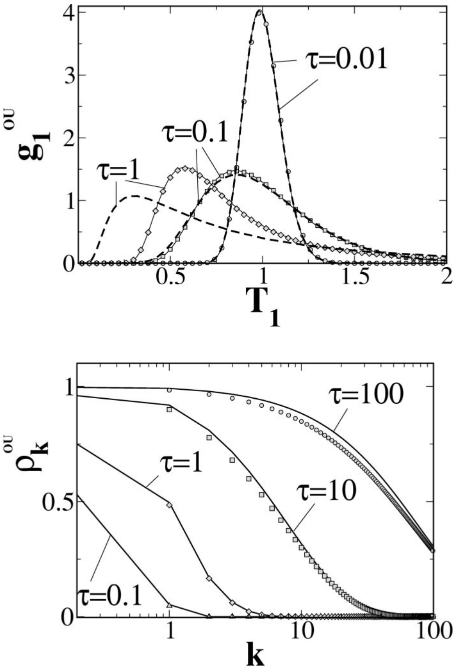

FIG. 2. ISI statistics for Ornstein-Uhlenbeck noise and different values of the correlation time τ at $\mu = v_T = 1$. Top: ISI density (solid lines) for $\sigma^2 = 0.5$ compared to simulations (symbols) and the density of the WN case g_1^{WN} (dashed); for the latter, τ is not a correlation time but determines the noise intensity by $D = \sigma^2 \tau$. Bottom: SCC for $\sigma^2 = 0.05$, analytical approximation (solid lines) compared to simulation results (symbols).

IF NEURON DRIVEN BY ORNSTEIN-UHLENBECK NOISE

The transition probability is given by the well-known transition probability of Brownian motion [14] with an additional bias, introduced by replacing the second spatial argument by $nv_T - \mu T$. Since this probability is Gaussian the integrals in Eq. (5) can be carried out yielding

$$g_n^{OU}(T_n) = \frac{1}{2\tau\sqrt{4\pi\varepsilon\gamma_1^3}} \exp\left[-\frac{(T_n - nv_T/\mu)^2}{4\varepsilon\tau^2\gamma_1} \right] \times \left[\frac{(\gamma_2(nv_T/\mu - T_n) + 2\gamma_1\tau)^2}{2\gamma_1\tau^2} - \varepsilon(\gamma_2^2 - 2\gamma_1 e^{-T_n/\tau}) \right], \qquad (13)$$

where $\gamma_1(T_n) = T_n/\tau + e^{-T_n/\tau} - 1$ and $\gamma_2(T_n) = 1 - e^{-T_n/\tau}$ are functions of the nth order interval. Equation (13) is strictly valid only for an asymptotically small noise variance (the second line becomes negative for a critical value of ε that depends on T_n and τ). Excluding the exponentially small tail of the density, we find, however, an excellent agreement to simulation results *even at a fairly large noise intensity* corresponding to $\varepsilon=0.5$ (Fig. 2, top). At small correlation time ($\tau=0.01$), the density, Eq. (13), coincides within line thickness with g_1^{WN} as it did for the DP driven neuron. Small differences show up for $\tau=0.1$, although not as pronounced as in the dichotomous case (cf. Fig. 1, top). For $\tau=1$, the OUP driven neuron does not display short ISIs as g_1^{WN} does. Since the variance of the noise is small, values of the ISI beyond $v_T/(\mu+\sigma)$ (corresponding to the noise staying below $-\sigma$ for an entire ISI) are unlikely irrespective of correlation time and hence also of noise intensity. Upon further increase of τ the shape of the density does not change much for the range of ISIs shown in Fig. 2 (top). Note that this large-τ density differs strongly from the WN *as well as* from the dichotomous case.

To second order in ε the variance is given by

$$\langle \Delta T_n^2\rangle_{OU}=\langle \Delta T_n^2\rangle_{WN}\left[1-\frac{1-e^{-n\delta}}{n\delta}+\varepsilon\left(e^{-n\delta}+\frac{(1-e^{-n\delta})(1-2e^{-n\delta})}{n\delta}\right)\right], \qquad (14)$$

where $\delta=v_T/(\tau\mu)$. Remarkably, for $\varepsilon\to 0$ this approaches the same function as the variance for dichotomous driving with $\varepsilon\to 0$ in β given in Eq. (10). Consequently, also the SCC approaches the *same functional form* for both driving processes in the weak noise limit. It can be furthermore shown, that at small but finite ε, the variance of the nth order interval of an OUP driven IF neuron is smaller than for an uncorrelated driving of the same noise intensity, i.e., the factor in brackets in Eq. (14) is generally smaller than unity.

Using Eqs. (14) and (6), the SCC reads ($k>0$)

$$\rho_k^{OU}=2\frac{\langle\Delta T_1^2\rangle_{WN}}{\langle\Delta T_1^2\rangle_{OU}}e^{-k\delta}\left[\sinh^2\left(\frac{\delta}{2}\right)+\varepsilon\left(2e^{-k\delta}\sinh^2(\delta)+(k\delta-3)\sinh^2\left(\frac{\delta}{2}\right)-\frac{\delta}{2}\sinh(\delta)\right)\right]. \qquad (15)$$

As in the dichotomous case, the correlations among ISIs are always positive, grow with increasing correlation time, and drop with increasing noise variance (note that also $\langle\Delta T_1^2\rangle_{OU}$ depends on ε). In Fig. 2 (bottom) Eq. (15) is compared to simulations at a small noise variance $\sigma^2=0.05$. While the theory and simulations agree well at small to moderate correlation time, discrepancies appear for large correlation time ($\tau=10$ or 100) and are expected to grow further with increasing τ. In general the theory overestimates the strength of correlations.

CONCLUSIONS

A perfect IF model driven by a weak exponentially correlated noise generates an ISI sequence with *exclusively positive* correlations implying a strictly positive SCC (this is somewhat surprising, since naively a correlation time of the order of the mean ISI could be expected to yield also negative correlations). The SCC is, furthermore, largely independent of the input's distribution (dichotomous or Gaussian), in marked contrast to the ISI and nth order interval densities that depend both on the input correlations *and* on the distribution of the input. In comparison to the simple WN case, the most important finding is the decreased ISI variability (ISI variance) for a colored noise input. It is known that ISI variability and ISI correlations of the spontaneous neuronal activity have a strong effect on signal transmission and detection through a neuron [7]. Hence, the analytical results achieved in this paper may help to understand the functional role of neural phenomena like synaptic filtering and presynaptic bursting that lead to input correlations and thus to a modification in the signal processing properties of a neuron.

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