Information transfer with rate-modulated Poisson processes: A simple model for nonstationary stochastic resonance

Igor Goychuk*
Institute of Physics, University of Augsburg, Universitätsstrasse 1, D-86135 Augsburg, Germany
(Received 10 April 2001; published 24 July 2001)

Stochastic resonance in a simple model of information transfer is studied for sensory neurons and ensembles of ion channels. An exact expression for the information gain is obtained for the Poisson process with the signal-modulated spiking rate. This result allows one to generalize the conventional stochastic resonance (SR) problem (with periodic input signal) to the arbitrary signals of finite duration (nonstationary SR). Moreover, in the case of a periodic signal, the rate of information gain is compared with the conventional signal-to-noise ratio. The paper establishes the general nonequivalence between both measures notwithstanding their apparent similarity in the limit of weak signals.

DOI: 10.1103/PhysRevE.64.021909 PACS number(s): 87.10.+e, 87.16.−b, 05.40.−a, 02.50.Tt

I. INTRODUCTION

The problem of stochastic resonance (SR), i.e., a noise-improved signal transduction in nonlinear systems has produced a huge literature summarized by two recent reviews [1,2]. Especially, the search for similar effects in sensory biology became popular over the years [3–5]. Here, simple models are very useful, especially if they allow for an analytical treatment. The so-called nondynamical model of SR involving the Poisson process with the signal and noise dependent spiking rate [6–9] has been applied with various modifications to SR in sensory neurons [8] and ensembles of ion channels [9]. The attractive simplicity of this model still favors much interest in the SR community.

The problem of information transfer with the Poissonian spike train in sensory neurons has also been addressed [4,5,10]. In the related studies two different information measures have mainly been utilized: (i) the mutual information [4,5,10–12] and (ii) the so-called τ information [13,14] (see a clarifying note concerning the τ information in Ref. [15]). The latter one represents the difference of the τ entropies of the spike train in the absence and in the presence of a useful signal. τ information presents an unidirectional measure that describes the transfer of information from the input signal to the signal-modulated output Poissonian train. Since the τ entropy essentially depends on the time resolution of measurement $\Delta\tau$ and even diverges in the limit $\Delta\tau \to 0$ [16], the τ information suffers from this drawback as well. Thus, it cannot serve as an *objective* measure [15].

One of the possible solutions of this difficulty goes back to Shannon [17] and consists in the use of random input signals taken from a stationary distribution. Then, the mutual information (per unit of time) can be defined [10,17] (see also below) that represents a kind of *nonlinear cross-correlation* measure between the input and output stochastic signals. As such, this measure is bidirectional. It considers the input and output signals on the equal footing and thereby undermines the active role of input signal. Moreover, for the continuous-time information channels the mutual information is very difficult to find in an analytical form even for the simplest case of input signals with Gaussian statistics. Here practically no exact analytical results are available with the prominent exception provided by the Gaussian information channel with the Gaussian input signal [18,19]. For the Poissonian information channel considered in this work, an approximate analytical expression for the rate of mutual information has been obtained in the case of weak Gaussian signals only [10].

Is it possible to define a unidirectional measure of information transfer which, on the one hand, does not suffer from the above-mentioned drawback of the τ information and, on the other hand, can be used also for nonrandom, regular signals? An answer in the affirmative is represented by the so-called information gain, or relative (Kullback) entropy [15,20,21]. However, the exact analytical results here are very rare too. Recently, the information gain has been found in an exact analytical form for the two-state McNamara-Wiesenfeld model [22] of the stochastic resonance and applied to SR in single ion channels [15]. The use of this information measure allows one to characterize the *nonstationary* SR, i.e., SR with arbitrary signals of finite duration [15]. In the present work we show that the information gain can be found exactly also for another fundamental model of SR represented by rate-modulated Poisson process [8,9]. Moreover, we discuss the interrelation of this information measure with such popular measure of the conventional, periodic SR as signal-to-noise ratio (SNR) (cf. Refs. [1,2]).

II. MODEL

A rather simple and elegant model of SR based on the theory of random point processes has been introduced by Wiesenfeld, Pierson, Pantazelou, Dames, and Moss in Ref. [8] in an application to the stochastic resonance in sensory neurons. This model has been further generalized and applied to SR in ion channels by Bezrukov and Vodyanoy [9]. The approach consists in modeling some shot-noise-like events, for example, the neuron spike activity, or the ion current spikes across a membrane by a nonstationary Poisson

*Also at Bogolyubov Institute for Theoretical Physics, Kiev, Ukraine.

process. Let us consider such Poisson process of the current spikes $I(t)=I_0\Sigma_i\delta(t-t_i)$ [23] of strength I_0 occurring randomly within some time interval $[0,T]$. The spikes are assumed to occur at the time points t_i that are independently distributed with the exponential probability density function $f(t)=r(t)\exp[-\int_0^t r(\tau)d\tau]$. Here, the variable rate of spikes $r(t)$ has been introduced. This rate depends on the externally applied voltage signal $V_s(t)$ and the height U_0 of an activation barrier in the absence of signal; $r(t)=r(U_0)g[V_s(t)]$, where $r(U_0)>0$ is the rate in the absence of signal and $g(V)$ is some positive function, $g(V)>0, g(0)=1$.

One should note that the both functions, $r(U_0)$ and $g(V)$, depend also on the thermal noise intensity D [24]. The concrete form of $r(U_0)$ and $g(V)$ should be taken from experiments, or defined by an underlying microscopic model. For the purpose of illustration of our theory we will assume in this work the same model for the spiking rate as in Refs. [8,1], i.e.,

$$r(U_0)=r_0\exp\left(-\frac{U_0}{D}\right),$$

$$g(V_s)=\exp\left(\frac{qV_s}{D}\right). \tag{1}$$

In application to the ion channels [9], the noise intensity D corresponds to the temperature, $D=k_BT$ and q to the gating charge. If to apply an external Gaussian electric noise $V_n(t)$ with an extremely high corner frequency f_c and the noise intensity ζ, this will result in a renormalization of D, $D\rightarrow D+\delta D$, with $\delta D\propto\zeta$, i.e., in the local heating [25]. Although such a model assumption (local heating) is not quite realistic for the realm of ion channels, nevertheless it is useful to illustrate the main ideas [26]. Besides, the considered model is directly applicable (as it was originally proposed) to the information transfer in sensory neurons, cf. Ref. [8].

Furthermore, the probability density to have s spikes in the time interval $[0,T]$ is [27,28]

$$Q_s(T,t_s,t_{s-1},\ldots,t_1|V_s(t))=\frac{1}{s!}\exp\left[-\int_0^T r(t)dt\right]\times r(t_s)r(t_{s-1})\ldots r(t_1). \tag{2}$$

Since the spiking rate $r(t)$ depends on the input signal $V_s(t)$, the corresponding probability densities in Eq. (2) are in fact conditional. The corresponding probabilities $P_s(T)$ to have s spikes are given by the s-dimensional time integrals of $Q_s(T,t_s,t_{s-1},\ldots,t_1)$,

$$P_s(T|V_s(t))=\frac{1}{s!}\left[\int_0^T r(t)dt\right]^s\exp\left[-\int_0^T r(t)dt\right], \tag{3}$$

and are normalized to the unity. The hierarchy of distribution functions

$$\{Q_0(T|V_s(t)),Q_1(T,t_1|V_s(t)),\ldots,Q_s(T,t_s,t_{s-1},\ldots,t_1|V_s(t)),\ldots\}$$

defines the probability density functional (PDF) $P[I(t)|V_s(t)]$ of the current fluctuations.

III. INFORMATION GAIN AND MUTUAL INFORMATION

Let us assume first that the voltage signal $V_s(t)$ is not random and represents some arbitrary, but otherwise fixed function of time. Practically this means that the experiments are performed repeatedly applying one and the same time-dependent voltage form $V_s(t)$. PDF in the absence of signal can be denoted as $P_0[I(t)]$ with $\{Q_s^{(0)}(T,t_s,\ldots,t_1)\}$. Then, the information gain $K_T[V_s(t)]$ obtained from the observation of the current fluctuations in the absence and in the presence of voltage signal can be defined (in bits) by the functional integral

$$K_T[V_s(t)]=\int D[I(t)]P[I(t)|V_s(t)]\log_2\left(\frac{P[I(t)|V_s(t)]}{P_0[I(t)]}\right). \tag{4}$$

The information gain measures the deviation (lowering by $K[V_s(t)]$) of the entropy of current fluctuations from the equilibrium (defined by stationary current fluctuations in the absence of time-dependent voltage signal) due to the applied voltage. Since the entropy presents a measure of our uncertainty concerning the particular realization of $I(t)$ from the given ensemble, the lowering entropy (due to the signal) means getting information (about the signal).

To define the mutual information, one assumes that the input voltage signals are also random and can be characterized by the corresponding PDF $P_s[V_s(t)]$. The ensemble averaging over the voltage realizations is defined as $\langle\ldots\rangle_s := \int D[V_s(t)]\ldots P_s[V_s(t)]$. Then, the mutual information between $V_s(t)$ and $I(t)$ can be defined as the averaged information gain with respect to the statistical distribution of the current realizations *averaged* over $V_s(t)$, i.e., with respect to $P[I(t)]:=\langle P[I(t)|V_s(t)]\rangle_s$:

$$M_T[I(t):V_s(t)]=\left\langle\int D[I(t)]P[I(t)|V_s(t)]\times\log_2\left(\frac{P[I(t)|V_s(t)]}{P[I(t)]}\right)\right\rangle_s. \tag{5}$$

{Note the distinction between $P[I(t)]$ and $P_0[I(t)]$!} Moreover, noting that the joint PDF of $I(t)$ and $V_s(t)$ is obviously $P[I(t),V_s(t)]=P[I(t)|V_s(t)]P_s[V_s(t)]$, the latter definition can be recast in the form

$$M_T[I(t):V_s(t)]=\int\int D[I(t)]D[V_s(t)]P[I(t),V_s(t)] \times\log_2\left(\frac{P[I(t),V_s(t)]}{P[I(t)]P[V_s(t)]}\right). \tag{6}$$

This latter form makes transparent the fact that the mutual information is a symmetric measure with respect to its arguments and thus presents a nonlinear cross correlation between $I(t)$ and $V_s(t)$. This information measure is in fact bidirectional: ''What the output signal knows about input, the input signal knows about output.'

It is not difficult to prove that the averaged information gain gives an upper bound for the mutual information [15], i.e.,

$$M_T[I(t):V_s(t)]\leqslant\langle K_T[V_s(t)]\rangle_s . \tag{7}$$

This inequality is very important in the practice since not the mutual information in itself presents the main interest, but rather the information capacity. This latter quantity is defined as the maximum of mutual information over all possible input signals with the fixed root mean squared (rms) amplitude of signals (cf. [17,19]). The information capacity sets the *theoretical maximum* for information that can be transferred across the information channel within the given time interval $[0,T]$ [19]. In many cases it is simpler to find $\langle K[V_s(t)]\rangle_s$ and to establish in such a way the upper bound for the information capacity. Moreover, in some cases (e.g., for weak signals) this upper bound can coincide within the accuracy of the weak-signal approximation with the information capacity [15].

In the experimental realm, the finding of mutual information constitutes a rather formidable task because it assumes the two ensemble averaging, both over input (voltage) and output (current) signals. On the contrary, the practical feasibility of the information gain is beyond questions. This task can be accomplished, e.g., by building up the corresponding histograms of the current realizations with the given time resolution $\Delta\tau$, like in Ref. [14]. Then, there exist 2^N (where $N=T/\Delta\tau$) different realizations of ''all-or-nothing'' current records and in practice the respective functional integral is approximated by a multidimensional sum. The actual value of the information gain can be estimated from the calculation of the corresponding approximations at different $\Delta\tau$ by extrapolating those to the limit $\Delta\tau\to 0$. Unlike to the case of τ information in Refs. [13,14] (where such a limit does not exist in principle) the discussed limit should exist for the information gain. The information gain presents thus a reasonable alternative to the τ information that is *de facto* the most popular information measure at present [13,14].

IV. EXACT EXPRESSION FOR INFORMATION GAIN

The precise meaning of the functional integral in Eq. (4) for the studied model is as follows

$$K_T[V_s(t)]=Q_0(T|V_s(t))\log_2\frac{Q_0(T|V_s(t))}{Q_0^{(0)}(t)} +\sum_{s=1}^{\infty}\int_0^T d\tau_s\int_0^T d\tau_{s-1}\cdots \times\int_0^T d\tau_1 Q_s(t,\tau_s,\ldots,\tau_1|V_s(t)) \times\log_2\frac{Q_s(t,\tau_s,\ldots,\tau_1|V_s(t))}{Q_s^{(0)}(t,\tau_s,\ldots,\tau_1)}. \tag{8}$$

The calculation of integrals and series in Eq. (8) with the probability densities (2) is straightforward due to the factorization property in Eq. (2) and yields our main result

$$K_T[V_s(t)]=\frac{1}{\ln 2}\int_0^T\left[r(U_0)-r(t)+r(t)\ln\left(\frac{r(t)}{r(U_0)}\right)\right]dt. \tag{9}$$

Note that the result (9) is *exact* within the considered model. It can also be obtained from one found previously for the two-state Markov model in Ref. [15] in the limit where the two-state system is symmetric $[P_o(t)=P_c(t)=1/2]$ and the signal modulates the height of the activation barrier. Using this result we can address the general case of SR including nonstationary signals of finite duration, i.e., *nonstationary* SR. In particular, for weak signals we obtain approximately

$$K_T[V_s(t)]\approx R(U_0,D)\xi. \tag{10}$$

In Eq. (10),

$$R(U_0,D)=\frac{1}{2\ln 2}r(U_0)\left(\frac{\partial g(V_s)}{\partial V_s}\right)^2_{V_s=0} \tag{11}$$

is the form factor, which characterizes the system, and

$$\xi=\int_0^\infty V_s^2(t)dt \tag{12}$$

is the total intensity of input signal. For the model in Eq. (1) we obtain

$$R(U_0,D)=\frac{1}{2\ln 2}r_0\frac{q^2}{D^2}\exp\left(-\frac{U_0}{D}\right). \tag{13}$$

The form factor in Eq. (13) exhibits a typical stochastic resonance behavior versus the noise intensity D.

V. RATE OF INFORMATION GAIN AND THE SIGNAL-TO-NOISE RATIO

Let us consider now the case of a periodic input signal with the frequency Ω and the amplitude A,

$$V_s(t)=A\cos(\Omega t). \tag{14}$$

Then, one can define the rate of information gain

$$\mathcal{R}_I = \lim_{T\to\infty} \frac{K_T[V_s(t)]}{T}. \quad (15)$$

For the model in Eq. (1) an elementary calculation from Eq. (9) yields

$$\mathcal{R}_I = \frac{1}{\ln 2} r_0 \exp\left(-\frac{U_0}{D}\right)\left[1 - I_0\left(\frac{qA}{D}\right) + \frac{qA}{D} I_1\left(\frac{qA}{D}\right)\right], \quad (16)$$

where $I_{0,1}(z)$ are the modified Bessel functions. Note that the rate of information gain has the same dimensionality of frequency as SNR. Thus, it is interesting to compare the rate of information gain and SNR for the considered model. The corresponding expression for SNR has been obtained in Ref. [8] and in our notation (which follows the review [1]) reads

$$\mathcal{R}_{SN} = 4\pi r_0 \frac{I_1^2\left(\frac{qA}{D}\right)}{I_0\left(\frac{qA}{D}\right)} \exp\left(-\frac{U_0}{D}\right). \quad (17)$$

By comparison of Eq. (16) and Eq. (17) in the case of weak signals $qA \ll D$ one can establish the following important relation

$$\mathcal{R}_I \approx \frac{\mathcal{R}_{SN}}{4\pi \ln 2}, \quad (18)$$

where both the $\mathcal{R}_I$ and $\mathcal{R}_{SN}$ are proportional to $R(U_0, D)$ in Eq. (13) and both exhibit stochastic resonance.

It is worth noting that for weak Gaussian signals with the rms amplitude $A_{rms}=A$, the information gain in Eq. (18) defines, after averaging over the signal realizations, also the information capacity (with the factor of 2 [29]). This fact can be proven making use of the Shannon's formula for the mutual information rate [19]. The Shannon's formula has been originally derived, strictly speaking, for Gaussian information channels only (cf. Ref. [30]). However, it has been shown in Ref. [10] that the Shannon's formula applies also for the considered Poissonian information channel if the input Gaussian signals are weak.

To sum up, in the limit of weak signals the knowledge of SNR for a harmonic signal completely determines both the rate of information gain for the periodic signal and the information capacity for the Gaussian aperiodic signals. Besides, SNR characterizes also the information gain for small signals with finite duration. This remarkable result is illustrated in Fig. 1.

Nevertheless, for strong signals the analogy between SNR and information gain breaks down. To demonstrate this fact we used the following parameters that resemble (although are *not* directly related to) that used for the Schmitt trigger in Ref. [21]. We set the barrier height to $U_0=150$ meV, the gating charge to the elementary charge, $q=e$, and the signal amplitude to $A=100$ mV. The numerical comparison between the rate of information gain and SNR is depicted in Fig. 2. It explains in principle the *nonequivalence* between

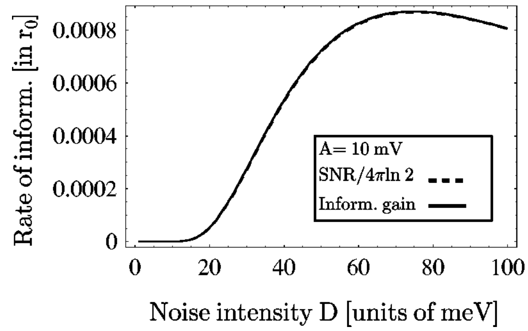

FIG. 1. Dependence of the rate of information gain and the scaled signal-to-noise ratio on the background noise intensity D in the case of a weak periodic signal. The barrier height is set to $U_0=150$ meV.

the SNR and the information gain (Kullback entropy) for *strong* signals, beyond the linear response regime, which has been observed in the numerical experiments [21]. It is interesting to note that both in this work and in Ref. [21] the maximum of the information gain is attained at $D \approx 45$ meV (cf. Fig. 4 in [21]), while the maxima of SNR are somewhat different. One has to stress that it is not possible to compare the both situations directly, because in the case of Schmitt trigger the input signal modulates the energy difference between two states, rather than the energy barrier between two states with equal energy. Nevertheless, the general tendency becomes rather obvious.

The *nonequivalence* between the information gain and SNR is especially clearly demonstrated in Fig. 3 for the signal amplitude $A=150$ mV. In this case, the maximum in the information gain disappears, whereas the $\mathcal{R}_{SN}$ still exhibits a maximum. For the suprathreshold amplitude $A>158$ mV the stochastic resonance in the signal-to-noise ratio disappears as well (not shown).

VI. CONCLUSIONS

In this work we have addressed a simple model of stochastic resonance in sensory neurons [8] or ion channels [9] from the point of view of the information transfer. The model considers some shot-noise-like events as nonstationary Poisson process with the signal-dependent spiking rate. This rate depends on the background noise intensity as a parameter, i.e., it is assumed that neither background noise, nor signal

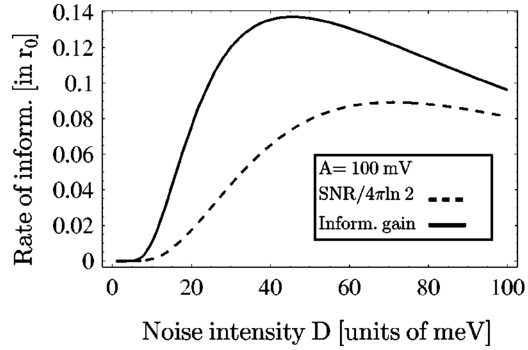

FIG. 2. Same as Fig. 1, in the case of a strong signal.

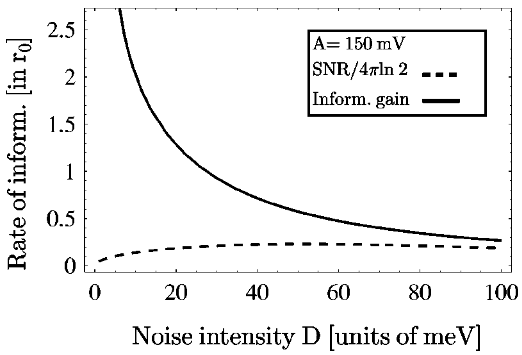

FIG. 3. Same as Fig. 1, in the case of signal with the threshold amplitude.

can introduce the correlations among spikes. Of course, this is an idealization. Nevertheless, such a simple model is very useful as one of the basic models for the stochastic resonance, cf. [1]. The meaning of the noise is context dependent. In application to the ion channels, it is the thermal noise. If the external noise is added [9], one assumes that the corner frequency of this added noise is so high that it results in the renormalization of the thermal noise intensity only.

The main result of this work is the expression (9) for the information gain that measures the lowering of the entropy of the Poissonian spike train due to the applied signal. Since the signal can be of arbitrary form and duration, our result allows to quantify the *nonstationary* SR. Here, in the case of weak signals, an approximate result in Eqs. (10)–(12) readily follows. This latter result has a remarkable feature. The occurrence of stochastic resonance depends merely on the form factor (11). In the case of an Arrhenius rate in Eq. (1) this form factor has the same functional form as $\mathcal{R}_{SN}$ in Ref. [8] and displays a typical SR behavior, like in Fig. 1. Another interesting point is that the information gain depends in the discussed case only on the total intensity of the signal given by Eq. (12). This means that the signals of equal intensity produce equal information gains, no matter how different the form of signals is.

Furthermore, the consideration of the rate of information gain in the case of a periodic signal allows one to find the similarity and the distinction between the rate of information gain and the signal-to-noise ratio. Namely, we have shown that in the case of a weak signal both measures behave identically in their dependences on the noise intensity, cf. Fig. 1. This similarity is remarkable indeed, because the meaning of both measures is quite different. In fact, the discussed similarity is virtually known in the literature (although for a different information measure—information capacity, cf. [19,4,10,30]). However, in this work we have explicitly shown that this similarity holds in the case of weak signals only. For strong signals it is not valid anymore, cf. Fig. 2, Fig. 3, and Eq. (16) vs Eq. (17). This fact becomes especially clear for the signal with the threshold amplitude (Fig. 3), where SNR still displays the stochastic resonance behavior, whereas the information gain does not.

ACKNOWLEDGMENTS

This work has been supported by Deutsche Forschungsgemeinschaft, SFB 486, project A10. It is my pleasure to acknowledge the hospitality of Dr. Sergey Bezrukov and the National Institutes of Health (Bethesda, U.S.A.), where this work has been written, as well as the fruitful discussions with Professor Peter Hänggi and Professor Sergey Bezrukov.

[1] L. Gammaitoni, P. Hänggi, P. Jung, and F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998).
[2] V.S. Anishchenko, A.B. Neiman, F. Moss, and L. Schimansky-Geier, Sov. Phys. Usp. **42**, 7 (1999) [Usp. Fiz. Nauk. **169**, 7 (1999)].
[3] J.L. Douglass, L. Wilkens, E. Pantazelou, and F. Moss, Nature (London) **365**, 337 (1993).
[4] J.E. Levin and J.P. Miller, Nature (London) **380**, 165 (1996).
[5] J.J. Collins, C.C. Chow, and T.T. Imhoff, Nature (London) **376**, 236 (1995); Phys. Rev. E **52**, R3321 (1996).
[6] Z. Gingl, L.B. Kiss, and F. Moss, Europhys. Lett. **29**, 191 (1995).
[7] P. Jung, Phys. Lett. A **207**, 93 (1995).
[8] K. Wiesenfeld, D. Pierson, E. Pantazelou, Ch. Dames, and F. Moss, Phys. Rev. Lett. **72**, 2125 (1994).
[9] S.M. Bezrukov and I. Vodyanoy, Nature (London) **378**, 362 (1995); **385**, 319 (1997); Chaos **8**, 557 (1998).
[10] W. Bialek and A. Zee, J. Stat. Phys. **59**, 103 (1990); W. Bialek, M. DeWeese, F. Rieke, and D. Warland, Physica A **200**, 581 (1993); M. DeWeese and W. Bialek, Nuovo Cimento D **17**, 733 (1995).
[11] A.R. Bulsara and A. Zador, Phys. Rev. E **54**, R2185 (1996).
[12] L.B. Kish, G.P. Harmer, and D. Abbott, Fluct. Noise Lett. **1**, L13 (2001).
[13] F. Rieke, D. Warland, R. de Ruyter van Steveninck, and W. Bialek, *Spikes: Exploring the Neural Code* (MIT Press, Cambridge, MA, 1997).
[14] S.P. Strong, R. Koberle, R.R. de Ruyter van Steveninck, and W. Bialek, Phys. Rev. Lett. **80**, 197 (1998).
[15] I. Goychuk and P. Hänggi, Phys. Rev. E **61**, 4272 (2000).
[16] P. Gaspard and X.-J. Wang, Phys. Rep. **235**, 292 (1993).
[17] C. Shannon, Bell Syst. Tech. J. **27**, 379 (1948); **27**, 623 (1948).
[18] M.S. Pinsker, Dokl. Akad. Nauk SSSR **99**, 213 (1954); *Information and Information Stability of Random Variables and Processes* (Holden-Day, San Francisco, 1964).
[19] C. Shannon, Proc. IRE **37**, 10 (1949).
[20] S. Kullback and R.A. Leibler, Ann. Math. Stat. **22**, 79 (1951); S. Kullback, *Information Theory and Statistics* (Wiley, New York, 1959).
[21] A. Neiman, B. Shulgin, V. Anishchenko, W. Ebeling, L. Schimansky-Geier, and J. Freund, Phys. Rev. Lett. **76**, 4299 (1996).
[22] B. McNamara and K. Wiesenfeld, Phys. Rev. A **39**, 4854 (1989).

[23] We assume here the spikes be modeled by the Dirac's δ function. This particular choice is not principal for the information theory. The spikes of finite width could be considered without further complications. This would not affect the calculation of the information gain. However, the finite width of spikes would, strictly speaking, modify the calculation of the spectral measures such as signal-to-noise ratio in Eq. (17).
[24] Poisson-like process results from the activated barrier crossings due to some background thermal noise. It is assumed that the time scales of the thermal noise, barrier crossing, and interspike intervals are well separated.
[25] P. Reimann and P. Hänggi, in *Surmounting Fluctuating Barriers: Basic Concepts and Results*, edited by L. Schimansky-Geier and T. Pöschel, Lecture Notes in Physics (Springer, Berlin, 1997), Vol. 484, pp. 127–139.
[26] The main distinction between the two models in Ref. [8] and in Ref. [9] is that in Ref. [9] the time scale of the *added* noise can interfere with the time scale of spikes. This introduces the mutual correlation among the interspike intervals. Such a complication is beyond the scope of present work. For simplicity we assume that the discussed time scales are well separated (added noise is much faster than the spiking rate) and thus neglect such induced correlations.
[27] R.L. Stratonovich, *Topics in the Theory of Random Noise* (Gordon and Breach, New York, 1963), Vol. 1.
[28] N.G. Van Kampen, *Stochastic Processes in Physics and Chemistry*, 2nd, ed. (North-Holland, Amsterdam, 1992).
[29] The factor of 2 appears because the mutual information and the information capacity are defined with the rms amplitude A_{rms} of random signals whereas the SNR is defined with the corresponding *amplitude* of periodic signal $A = A_{rms}$, cf. Ref. [30].
[30] I. Goychuk and P. Hänggi, New J. Phys. **1**, 14 (1999).