Eur. Phys. J. B **69**, 29–35 (2009)
DOI: 10.1140/epjb/e2009-00049-y

**The European
Physical Journal B**

Regular Article

Nonstationary stochastic resonance viewed through the lens of information theory

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Received 9 December 2008

Abstract. In biological systems, information is frequently transferred with Poisson like spike processes (shot noise) modulated in time by information-carrying signals. How then to quantify information transfer by such processes for nonstationary input signals of finite duration? Is there some minimal length of the input signal duration versus its strength? Can such signals be better detected when immersed in noise stemming from the surroundings by increasing the stochastic intensity? These are some basic questions which we attempt to address within an analytical theory based on the Kullback-Leibler information concept applied to random processes.

PACS. 05.40.-a Fluctuation phenomena, random processes, noise, and Brownian motion – 87.10.Ca Analytical theories – 87.10.Vg Biological information

1 Introduction

Stochastic resonance (SR) [1] grew into extensive research domain on the border between many scientific disciplines, ranging from geophysics and climate dynamics, numerous physical, biophysical and engineering applications [2–4], including quantum SR in the deep quantum cold [5]. Nevertheless, more complex physical SR applications and timely SR applications to biological and climate complexity [6] as well as more insightful reasoning are still in the limelight. The original statement of the problem, i.e. a paradoxical amplification of the signal in a noisy background due to intrinsic [7], or added, external noise [2–4], has been contrasted with a synchronization framework [2–4,8]. *Postfactum* we can reformulate the original problem by asking the question of whether a stochastic bistable clock can resonate with an externally applied periodic driving via increasing the randomness of the underlying bistable clock dynamics.

The notion of a "Stochastic clock" [9] stems conceptually from the theory of continuous time random walk processes (see e.g. in Ref. [10], p. 245). It is characterized by a distribution of the sum of stochastic periods. The distribution of one period duration is a convolution of the residence times in the two clock states. Two subsequent transitions perform a cycle with a random duration. It is important to note that if the mean duration of a cycle $\langle \tau_{cycle} \rangle$ exists, the distribution of n cycles duration yields a sharp function, centered at $n\langle \tau_{cycle} \rangle$ in the limit $n \to \infty$. Intrinsic noise changes $\langle \tau_{cycle} \rangle$ and in some situations – e.g. for symmetric Markovian clock with an exponential distribution of the residence times and an exponential dependence of the mean cycle durations on the noise intensity – the stochastic clock can resonate with a weak periodic driving of period $\mathcal{T}_0$, when $\langle \tau_{cycle} \rangle = \mathcal{T}_0$. This is the benchmark of the stochastic resonance phenomenon. Then, the periodic signal is best detectable in the spectral power spectrum of the clock's bistable fluctuations and the stochastic transitions become more correlated with the periodic time course of the signal.

Whether the information transfer will be optimized at this resonance condition depends on how is information encoded. If a direct encoding is used, i.e. *locally* in the time domain, then the answer is "yes". However, if information is encoded in the frequency domain (like used in radio devices), then for the discussed bistable clock the answer is typically "no", at least for weak signals. The spectral signal-to-noise ratio (SNR) characterizes the Shannon information transfer for weak signals [11] (more precisely, the information capacity of an information channel which is the maximal rate of the Shannon's mutual information between the input and output signals for the fixed total power of the input signal). Stochastic resonance in the spectral SNR for the stochastic bistable system does not necessarily reflect a synchronization phenomenon [2–4,8]. More specifically, SNR does not directly reflect the matching between the stochastic time scale of the bistable clock dynamics and the time-scale of the deterministic, coherent signal dynamics. In contrast to SNR, the measure of spectral amplification [12,13], however, explicitly involves a dependence on the driving frequency. We also remark while within linear response (i.e. weak signals) the SR gain

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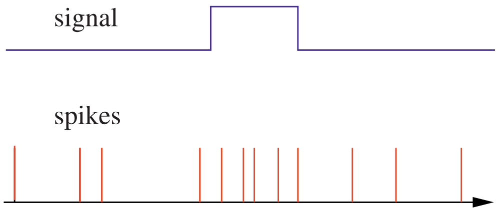

Fig. 1. (Color online) A step-like signal modulates an information-carrying spiking process, e.g. output of a sensory neuron [27].

determined by the "SNR output/ SNR input" cannot exceed unity [14] this is no longer the case for the nonlinear SR response [14,15].

Next we are dealing with SR in a wider sense, i.e. we shall study SR in a form which can broadly be characterized as a *relative* amplification of the information transfer through a noisy system. SNR for a weak sinusoidal signal predicts the information transfer for stationary, weak broadband stochastic signals [11,16,17]. As just noted, this remarkable analogy fails, however, for strong signals beyond the linear response approximation [14,15]. Nevertheless, it must be remarked that it is simply not feasible to extract more information (in the Shannon sense) from the output signal than was originally encoded in the input signal; this agrees with common sense and is corroborated with the information processing inequality [11].

In the case of so-termed *aperiodic SR*, i.e. SR fed by stationary stochastic input signals (modeled, e.g., by Gaussian processes) the rate of mutual information can be used as a suitable quantifier [18]. How to proceed, however, if the signal is not stationary as it is intrinsically the case for fixed, deterministic or stochastic nonstationary inputs of finite duration? This latter situation is typical, e.g., for biological systems [2–4], cf. a typical situation depicted with Figure 1. Typical spectral measures as indicated above are then of limited use, or at best of approximate use only. The mutual information concept also cannot be applied whenever the input signal is strictly deterministic. In such a nonstationary situation one can characterize the information transfer by the change of the entropy between the process in absence of input and the output process when the input signal is applied. Then the difference of entropies can be regarded as the information gained from the input signal [11]. The Kullback-Leibler *relative* entropy [19–21], termed also the information gain is a suitable measure to characterize the corresponding entropy difference because it does not suffer from the subjective dependence on the discrete time-step $\Delta\tau$ used in approximating continuous time random processes [22,23]. This presents an advantageous fact when contrasted with using direct entropy differences [16]. The Kullback-Leibler entropy is just an analogue of the Boltzmann H-function for kinetic equations [24]. In the present context, it is applied not just to a single time probability density, but rather to the whole probability *functional* that determines the stochastic process under consideration. Like the H-function it characterizes the entropy difference from equilibrium in a well-defined manner, even if the equilibrium value of informational entropy itself is not precisely defined for continuous distributions. This is always the case if some fundamental "quantum-scale" (like the Planck constant for an elementary "area" in the phase space of a physical system, in the case of physical entropy) is absent. Moreover, the use of information gain if averaged over all possible realizations of a random input signal provides an upper bound for the mutual information transferred [22,23]. These facts predestine indeed the information gain as an adequate measure to characterize nonstationary SR.

With this present work, we investigate such nonstationary SR for an archetype setup of SR [2,23,25,26], by considering the renewal point processes for signal-modulated spike occurrences. This sort of modeling is relevant to signaling occurring in biological systems [16,27–29].

2 The model

We consider a renewal point process $\xi(t)$ defined by the spikes

$$\xi(t) = \sum_i \xi\delta(t - t_i) \tag{1}$$

occurring at random times t_i, see in Figure 2. One may safely assume that the spike width is negligible and its form is fixed by some total intensity (the time integral of the spike-form) ξ, i.e. the information is transferred with the spike occurrences. Put differently, rather than a specific shape of the spike it is the timing dynamics and not only the averaged number that is important in transferring information. The interspike intervals (ISI) $\tau_i = t_{i+1} - t_i$ are assumed to be uncorrelated (renewal assumption) and the whole process, generally a non-Markovian process, is completely characterized by the ISI distribution $\psi(t+\tau, t) := \psi(\tau|t)$, or equivalently by the corresponding survival probability $\Phi(t+\tau, t) := \Phi(\tau|t)$, $\psi(\tau|t) = -d\Phi(\tau|t)/d\tau$ [30,31]. The process is *non-homogeneous* in time what is reflected by its explicit dependence of the above quantities on the current time t via an input signal $V_s(t)$. For a time-homogeneous process we have in contrast $\psi(\tau|t) = \psi(\tau)$. The simplest example is given by the Poisson process with the time-dependent rate $r(t)$ [24,34], where

$$\Phi(\tau|t) = \exp\left(-\int_t^{t+\tau} r(t')dt'\right). \tag{2}$$

A popular SR model is [2,25,26]:

$$r(t) = r_0(U_0)\exp(qV_s(t)/D), \tag{3}$$

where

$$r_0(U_0) = k_0\exp(-U_0/D) \tag{4}$$

is the rate in the absence of signal. One further assumes that there is a threshold U_0 which upon crossing induces

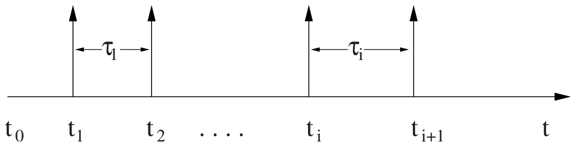

Fig. 2. Driven renewal process: spikes occur at random times t_i, the interspike time-intervals $\tau_i = t_{i+1} - t_i$ are assumed to be uncorrelated and described by a non-homogeneous ISI density $\psi(\tau|t)$.

a spike. Typical realizations are a conventional threshold detector [35], or the dynamics of the leaky integrate-and-fire model of neuron firing [27] driven, e.g., by synaptic noise. Some intrinsic noise of the intensity D produces spontaneous firing and the signal modulates the threshold height. A similar model applies also to the current spikes produced in a membrane by spontaneous electroporation facilitated by some ion channel forming peptides [26]. In the latter case the signal $V_s(t)$ is the voltage modulation, the quantity q is an effective gating charge, U_0 is the energy barrier to the channel formation, and $D = k_BT$. A similar model (modified for the refractory times) provides also a crude approximation to the activity of cortical and sensory neurons [27], spontaneous spiking of the ion channel clusters [36], and spontaneous calcium release spiking in living cells [29].

3 Theory

We start out from the trajectory description of $\xi(t)$ considering a finite time interval $[t_0, t)$. The elements of the probability space are the trajectories with spikes occurring at some random times $t_1, t_2, ..., t_n$. The probability to have spike occurring during the prescribed interval (starting out from a no spike event at time t_0) is $P_0(t, t_0) = \Phi(t, t_0)$. The probability density of trajectories with one spike occurring at t_1, $t_0 < t_1 < t$ is

$$Q_1(t, t_1, t_0) = \Phi(t, t_1)\psi(t_1, t_0),$$

yielding for the corresponding probability

$$P_1(t, t_0) = \int_{t_0}^{t} Q_1(t, t_1, t_0)dt_1.$$

Furthermore, the probability density of trajectories with two events at t_1 and t_2, $t_0 < t_1 < t_2 < t$, reads

$$Q_2(t, t_2, t_1, t_0) = \Phi(t, t_2)\psi(t_2, t_1)\psi(t_1, t_0),$$

and the probability to have two events within $[t_0, t)$ becomes

$$P_2(t, t_0) = \int_{t_0}^{t} dt_2 \int_{t_0}^{t_2} dt_1 Q_2(t, t_2, t_1, t_0).$$

Other probability densities and probabilities are constructed akin, using the semi-Markov, renewal character of the underlying process. The normalization condition $\sum_{n=0}^{\infty} P_n(t, t_0) = 1$ can be readily verified; it is done by showing that the derivative of the l.h.s. with respect to t is zero upon using $P_0(t_0, t_0) = 1$, $P_{n\neq 0}(t_0, t_0) = 0$. We thus obtain a complete description of the considered time-inhomogeneous, nonstationary process with the probability density functional

$$P[\xi(t)] = [P_0(t, t_0), Q_1(t, t_1, t_0), ..., Q_n(t, t_n, ..., t_1, t_0), ...].$$

For this rate-modulated Poisson process the densities read

$$Q_n(t, t_n, ..., t_1, t_0) = \exp\left(-\int_{t_0}^{t} r(t')dt'\right) \prod_{i=1}^{n} r(t_i), \quad (5)$$

and the number of spikes exhibits a Poisson distribution

$$P_n(t, t_0) = \frac{\langle n(t, t_0)\rangle^n}{n!} \exp\left[-\langle n(t, t_0)\rangle\right] \quad (6)$$

with mean $\langle n(t, t_0)\rangle = \int_{t_0}^{t} r(t')dt'$.

3.1 τ-entropy

The definition of the entropy of any continuous variable which has a physical dimension requires to introduce some arbitrary bin $\Delta\tau$ (a measurement unit). The entropy of $\xi(t)$ can be defined (in natural units, nats) as a functional integral [37]

$$\begin{aligned} S_{\Delta\tau}(t, t_0) = &-P_0(t, t_0) \ln P_0(t, t_0) \\ &- \sum_{n=1}^{\infty} \int_{t_0}^{t} dt_n \int_{t_0}^{t_n} dt_{n-1} ... \int_{t_0}^{t_2} dt_1 \quad (7) \\ &\times Q_n(t, t_n, ..., t_0) \ln[Q_n(t, t_n, ..., t_0)(\Delta\tau)^n]. \end{aligned}$$

Upon differentiating equation (7) with respect to time t we arrive after some algebra at the following expression for the rate of entropy production

$$\begin{aligned} \frac{d}{dt} S_{\Delta\tau}(t, t_0) &= F(t, t_0) + \int_{t_0}^{t} F(t, t_1)\Psi(t_1, t_0)dt_1 \\ &= F(t, t_0) + \sum_{n=1}^{\infty} \int_{t_0}^{t} dt_n \int_{t_0}^{t_n} dt_{n-1} ... \int_{t_0}^{t_2} dt_1 \frac{F(t, t_n)}{\Phi(t, t_n)} \\ &\quad \times Q_n(t, t_n, ..., t_0). \quad (8) \end{aligned}$$

In equation (8),

$$F(t, t_1) := \dot{\Phi}(t, t_1) \ln\left(\frac{-\Delta\tau\dot{\Phi}(t, t_1)}{e\Phi(t, t_1)}\right) \quad (9)$$

where $\dot{\Phi}(t, t_1) \equiv d\Phi(t, t_1)/dt < 0$ and

$$\begin{aligned} \Psi(t, t_0) = \sum_{n=1}^{\infty} \int_{t_0}^{t} dt_n \int_{t_0}^{t_n} dt_{n-1} ... \int_{t_0}^{t_2} dt_1 \\ \times \prod_{i=1}^{n} \psi(t_i, t_{i-1}). \quad (10) \end{aligned}$$

Using that

$$\Phi(0|t)=1,\quad \lim_{\tau\to\infty}\Phi(\tau|t)=0,$$

one can show that $S_{\Delta\tau}(\psi|t)=\int_0^\infty F(t+\tau,t)d\tau$ has the meaning of the entropy of the time-inhomogeneous ISI, i.e.

$$S_{\Delta\tau}(\psi|t)=-\int_0^\infty \psi(\tau|t)\ln[\psi(\tau|t)\Delta\tau]d\tau. \quad (11)$$

For the Poisson model, $\Psi(t,t_0)=r(t)$ and equation (8) simplifies to

$$\frac{d}{dt}S_{\Delta\tau}(t,t_0)=r(t)\ln\left(\frac{e}{r(t)\Delta\tau}\right)=r(t)\overline{S}_{\Delta\tau}(\psi|t), \quad (12)$$

where $\overline{S}_{\Delta\tau}(\psi|t)$ is the entropy of the ISI distribution which is calculated with the *frozen* rate $r(t)$, i.e. with $\psi(\tau)=r(t)\exp(-r(t)\tau)$ instead of $\psi(\tau|t)$ in equation (11). This result has a simple interpretation: namely that the *rate of entropy production = spiking rate × entropy of ISI distribution for instant rate* $r(t)$. For the "background" process, i.e. the resulting process with no signal applied, the rate is r_0 and the entropy of the spike train of duration $\mathcal{T}$ is given by the well-known MacKay and McCulloch result [16,38]

$$S_0=N(\mathcal{T})\ln\left(\frac{e}{r_0\Delta\tau}\right), \quad (13)$$

where $N(\mathcal{T})=r_0\mathcal{T}$ is the averaged number of spikes. A popular definition of the information $I_{\Delta\tau}(\mathcal{T})$ transferred with spikes [16,17] amounts to take the difference

$$\begin{aligned}I_{\Delta\tau}(\mathcal{T})&=S_0-S_{\Delta\tau}(t_0+\mathcal{T},t_0)\\&=\int_{t_0}^{t_0+\mathcal{T}}\left[r_0\ln\left(\frac{e}{r_0\Delta\tau}\right)-r(t)\ln\left(\frac{e}{r(t)\Delta\tau}\right)\right]dt. \quad (14)\end{aligned}$$

One can see that the dependence on the finite time bin $\Delta\tau$ does generally not cancel [23,30], unlike in the case of an n-dimensional probability distribution. The reason is that the probability P_n to have n spikes is changed, i.e. probability is redistributed between different n-dimensional "slices" of the hyper-dimensional probability space. Troublesome is further the finding that the above difference can readily become negative (i.e. for $r(t)>r_0$ and for a sufficiently small $\Delta\tau$). This should then be interpreted as a loss of information. Of course, a proper definition should always yield a positive information, because the spikes become more ordered due to the application of the input signal. The interpretation problem is an artefact of this $\Delta\tau$ dependence. This is precisely why we prefer to define the entropy difference for stochastic processes via the Kullback-Leibler relative entropy, see below. Before we proceed with a suitable definition along our posed objective we derive next a generalization of the MacKay and McCulloch result for different, nondriven (i.e. $V_s(t)=0$) point processes.

3.2 Rate of entropy production for stationary renewal point processes

Using the exact result (8) one can find also the asymptotic rate of entropy production for time-homogeneous processes in the limit $t\to\infty$ for any $\psi(\tau)$ with a *finite* mean ISI $\langle\tau\rangle=\int_0^\infty\tau\psi(\tau)d\tau$. In this case $F(t+\tau,t)=F(\tau)$, $\Psi(t+\tau,t)=\Psi(\tau)$, and for the Laplace-transformed rate of the entropy production $\dot{S}_{\Delta\tau}(t,0)$ we obtain

$$\tilde{R}(s)=\frac{\tilde{F}(s)}{1-\tilde{\psi}(s)}. \quad (15)$$

The asymptotic rate of entropy production follows as

$$\lim_{t\to\infty}\frac{d}{dt}S_{\Delta\tau}(t,0)=\lim_{s\to 0}[s\tilde{R}(s)]=\frac{1}{\langle\tau\rangle}S_{\Delta\tau}(\psi), \quad (16)$$

which is a natural generalization of the relation (12). The role of the mean spiking rate is taken on by $1/\langle\tau\rangle$. The result in (13) is thus generalized to read

$$S_0=N(\mathcal{T})S_{\Delta\tau}(\psi), \quad (17)$$

where $N(\mathcal{T})=\mathcal{T}/\langle\tau\rangle$. This latter result is applicable also in the case of fractal-rate renewal processes [39], where the mean rate does not exist, i.e. where $\tilde{\psi}(s)\approx 1-(s\tau^*)^\alpha$, for $s\to 0$; $0<\alpha<1$ and τ^* is some scaling time parameter [10]. The only difference is that the number of spikes within a long time interval $\mathcal{T}$ scales sub-linearly with its length, i.e. $N(\mathcal{T})\propto(\mathcal{T}/\tau^*)^\alpha$. Generally, for the considered renewal processes we find that *entropy of spike train = number of spikes × entropy of ISI*. One can also infer that the Poisson process is the maximum entropy point process, for fixed $\langle\tau\rangle$ and $\Delta\tau$. This is so, because the exponential ISI distribution displays the maximum entropy distribution from all one-sided distributions under such constraints.

3.3 Kullback-Leibler relative entropy

As discussed above, τ-entropy of the spike train is not exactly defined, being dependent on $\Delta\tau$. However, its deviation from equilibrium can be defined unambiguously via the relative entropy, given by the functional integral:

$$\begin{aligned}&K_{[t_0,t]}[\xi(t)|\xi_0(t)]=\\&\int D[\xi(t)]P[\xi(t)|V_s(t)]\ln\left(\frac{P[\xi(t)|V_s(t)]}{P[\xi_0(t)]}\right)\\&=P_0(t,t_0|V_s)\ln\left(\frac{P_0(t,t_0|V_s)}{P_0^{(0)}(t,t_0)}\right)\\&\quad+\sum_{n=1}^{\infty}\int_{t_0}^{t}dt_n\int_{t_0}^{t_n}dt_{n-1}...\int_{t_0}^{t_2}dt_1Q_n(t,t_n,...,t_0|V_s)\\&\quad\times\ln\left(\frac{Q_n(t,t_n,...,t_0|V_s)}{Q_n^{(0)}(t,t_n,...,t_0)}\right)\geq 0. \quad (18)\end{aligned}$$

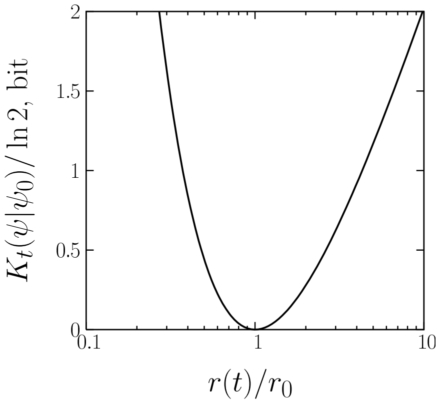

Fig. 3. Kullback-Leibler entropy per one spike as a function of the frozen rate $r(t)$.

Here, the super-index (0) refers to the background process $\xi_0(t)$ in the absence of signal $V_s(t)$. Relative entropy is always non-negative. It is zero iff the both distribution functionals $P[\xi_0(t)]$ and $P[\xi(t)|V_s(t)]$ coincide [19], i.e. in the absence of signal. The rate of the relative entropy production for the rate-modulated Poisson process can be easily calculated with equation (5) in (18) [23]. It reads,

$$\frac{d}{dt}K_{[t_0,t]}[\xi(t)|\xi_0(t)] = r(t)K_t(\psi|\psi_0) \geq 0, \tag{19}$$

where

$$\begin{aligned} K_t(\psi|\psi_0) &= \int_0^\infty d\tau\psi(\tau)\ln\left(\frac{\psi(\tau)}{\psi^{(0)}(\tau)}\right) \\ &= \frac{r_0}{r(t)} - 1 + \ln\left(\frac{r(t)}{r_0}\right) \end{aligned} \tag{20}$$

is the Kullback-Leibler entropy of the ISI distribution with the *frozen* rate $r(t)$ with respect to the unperturbed ISI distribution with the rate r_0. The meaning of the result in equation (19) is as follows: the *rate of information transduction = spiking rate × relative change of the ISI entropy.* Notably it does not depend of the time bin $\varDelta\tau$. The total information about signal is the time-integral of equation (19). Figure 3 depicts the relative entropy for the exponential distribution as a function of $r(t)/r_0$. Notice that the information transferred per one spike can in principle exceed one bit for a strong rate-modulation, in accordance with [16]. This is because the information is transferred not only via the spike occurrence, but also with its *timing* (and time is a continuous variable). For the weak signals ($qV_s < D$), the information transfer per one spike, however, does not exceed one bit, independently of the time resolution $\varDelta\tau$.

3.4 Rate of information gain for a two-state process

A generalization of the above result for the two-state Markovian rate-modulated process $x(t)$ can also be obtained [22]. The Markovian two state dynamics is governed by the master equation

$$\dot{p}_1(t) = r_2(t)p_2(t) - r_1(t)p_1(t), \;\; p_2(t) = 1 - p_1(t), \tag{21}$$

with the time-dependent transition rates $r_{1,2}(t)$ detailed e.g. for SR gating in ion channels in reference [22]. Using the present notation the rate of information gain then emerges as

$$\frac{d}{dt}K_{[t_0,t]}[x(t)|x_0(t)] = \sum_{i=1,2} r_i(t)K_t(\psi_i|\psi_i^{(0)})p_i(t), \tag{22}$$

where the relative entropy is given again by equation (20) for the residence time distributions in the two states, reading $\psi_{1,2}(\tau) = r_{1,2}(t)\exp[-r_{1,2}(t)\tau]$ with the frozen rates $r_{1,2}(t)$, and $\psi_{1,2}^{(0)}(\tau) = r_{1,2}^{(0)}\exp(-r_{1,2}^{(0)}\tau)$ are the rates in the absence of the signal. In [22] this result has been applied to investigate the problem of stochastic resonance in biological ion channels [26] from an information theory perspective.

4 Nonstationary SR

Now we are sufficiently equipped in order to address the questions posed in the abstract. We adhere here to the Poisson model and apply a transient step-like signal of the amplitude A and the duration τ_0 depicted with Figure 1, i.e. $V_s(t) = A$ for $t_0 < t_{in} < t < t_{in} + \tau_0$, $V_s(t) = 0$ otherwise, and where t_{in} is the time instant when the signal is applied. The signal can be either positive, $A > 0$ (activating signal), or negative, $A < 0$ (inhibiting signal). In terms of the averaged number of background spikes, $N_0 = r_0\tau_0$, occurring within a typical time interval of the duration τ_0 in the absence of signal, the total information gain is evaluated to read

$$K = K_{[t_0,\infty]}[\xi(t)|\xi_0(t)] = N_0[r(A)/r_0]K(\psi|\psi_0), \tag{23}$$

where $r(A) = r(t) = const$ for $t_{in} < t < t_{in} + \tau_0$ and $K(\psi|\psi_0)$ is given by equation (20) with $r(t) = r(A)$. This is result after integrating equation (19). Its structure is illuminating; in terms of N_0 the signaling information transfer involves both the change of the spiking rate with applied signal $r(A)$ and the relative change of the ISI-entropy. Interestingly, for $r(A)/r_0 < 1$ (inhibiting signal) the information transferred per one background spike cannot exceed one nat, cf. Figure 4. Put differently, then each disappeared background spike bears no more than one nat of information, in accord with intuition.

Furthermore, for the popular model in equations (3), (4), we obtain a practical result, reading

$$K = k_0\tau_0\exp\left(-\frac{U_0}{D}\right)\left[1 - \exp\left(\frac{qA}{D}\right)\left(1 - \frac{qA}{D}\right)\right]. \tag{24}$$

For very weak signals, $q|A| \ll D$, it displays the well-known, bell-shaped SR dependence on the noise intensity D [2]

$$K \approx k_0\tau_0\frac{(qA)^2}{D^2}\exp\left(-\frac{U_0}{D}\right), \tag{25}$$

being proportional to the SNR in the case of sinusoidal signal with the same amplitude [2,23,25]. The latter result

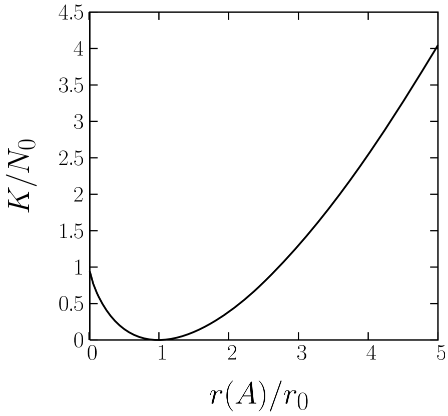

Fig. 4. Information gain K per one spike of the undriven Poisson process (in nats) as function of the relative change of the spiking rate $r(A)/r_0$.

confirms the fact that the use of SNR indeed describes information transfer for weak signals. In order to detect a signal, the total information gain should intuitively be no less than one bit. This clearly poses a bound on the signal duration τ_0 depending on its amplitude strength A. This bound can be found from equation (24): weak signals should last for a sufficiently long time τ_0 (many affected spikes accumulate the corresponding information), otherwise such signals cannot be detected within environmental noise. In Figure 5, we depict the information gain K versus the noise strength D for several values of the signal strength A. The threshold barrier U_0 is set to $U_0 = 75$ meV. Assuming that q is equal to the elementary charge, the signal strength is measured in mV.

The presence of wide sense SR is clearly detectable in Figures 5a–5c, for both activating and inhibiting signals. For an activating signal of the threshold strength, $qA = U_0$, in Figure 5d, nonstationary SR disappears. The increase of the information transfer by increasing the randomness of the background process has an instructive explanation. Namely, the increase of the spontaneous spiking rate leads to more spikes occurring within the signal duration τ_0. They altogether transfer more information about the signal. From the value of K in Figure 5a one can realize that many spikes are required in order to transfer information of $K = 1$ nat (approximately 0.7 bit) about the corresponding weak signal. Namely, one needs $k_0\tau_0 > 2 \times 10^4$. This clearly poses a bound $\tau_0 > 2\times10^4/k_0$ on its duration. Assuming that $k_0 = 20\ \mathrm{m\,s^{-1}}$ (such that $r_0 \approx 1\ \mathrm{m\,s^{-1}}$ at $D = 25$ meV), this yields the bound $\tau_0 > 1$ s, i.e. such a faint signal should last at least for about 1000 spikes to become detectable. However, if to increase the strength of the signal to 10 mV, the corresponding bound for τ_0 drops by two orders of magnitude, as it can be deduced from Figure 5b. In other words, such a stronger input signal (being, however, still much below the threshold) can be detected already with a few spikes, in principle. Moreover, nonstationary SR can help to detect such signals which would otherwise far too short lived at a non-optimal noise intensity D.

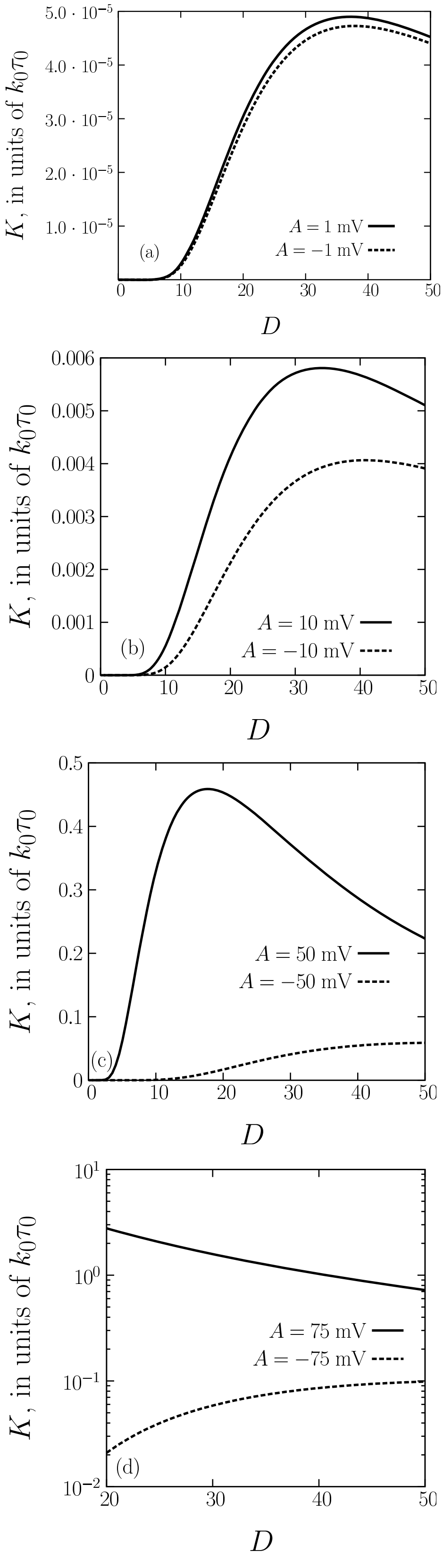

Fig. 5. Information gain K (in nats) versus the noise strength D (in meV) in one of the basic SR models [2,25], cf. equations (3), (4), for different values of the signal strength A. Information gain is scaled in the units of $k_0\tau_0$.

5 Conclusion

In this work, we considered a basic model for nonstationary SR, i.e. for the case of deterministic but aperiodic signals of finite duration. Information theory helped us to shed light on the very possibility and the origin of such nonstationary SR, as well as other critical issues such as the existence of a bound on the signal duration τ_0 versus its strength A. The obtained results may be of a broad importance in the context of information transduction in biological systems on the cellular level and in sensory systems.

This work has been supported by the Deutsche Forschungsgemeinschaft through the SFB 486, and by the German Excellence Initiative via the Nanosystems Initiative Munich (NIM).

References

1. R. Benzi, A. Sutera, A. Vulpiani, J. Phys. A **14**, L453 (1981); C. Nicolis, G. Nicolis, Tellus **33**, 225 (1981)
2. L. Gammaitoni, P. Hänggi, P. Jung, F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998)
3. V.S. Anishchenko, A.B. Neiman, F. Moss, L. Schimansky-Geier, Sov. Phys. Usp. **42**, 7 (1999)
4. P. Hänggi, Chem. Phys. Chem. **3**, 285 (2002)
5. R. Löfstedt, S.N. Coppersmith, Phys. Rev. E **49**, 4821 (1994); M. Grifoni, M. Sassetti, P. Hänggi, U. Weiss, Phys. Rev. E **52**, 3596 (1995); M. Grifoni, P. Hänggi, Phys. Rev. Lett. **76**, 1611 (1996); M. Grifoni, P. Hänggi, Phys. Rev. E **54**, 1390 (1996); M. Grifoni, L. Hartmann, S. Berchtold, P. Hänggi, Phys. Rev. E **53**, 5890 (1996); M. Grifoni, L. Hartmann, S. Berchtold, P. Hänggi, Phys. Rev. E **56**, 6213 (1997); I. Goychuk, P. Hänggi, Phys. Rev. E **59**, 5137 (1999)
6. R.B. Alley, S. Anadakrishnan, P. Jung, Paleoceanography **16**, 190 (2001); A. Ganopolski, S. Rahmstorf, Phys. Rev. Lett. **88**, 038501 (2002)
7. G. Schmid, I. Goychuk, P. Hänggi, Europhys. Lett. **56**, 22 (2001)
8. J.A. Freund, L. Schimansky Geier, P. Hänggi, Chaos **13**, 225 (2003)
9. L.B. Kiss, A. Ambrózy, in *Noise in Physical Systems and 1/f Noise – 1985*, edited by A. D'Amico, P. Mazzetti (North-Holland, Amsterdam, 1986), pp. 501–504
10. B.D. Hughes, *Random Walks and Random Environments* (Clarendon Press, Oxford, 1995), Vol. 1
11. C. Shannon, Bell System Technical J. **27**, 379 (1948); C. Shannon, Bell System Technical J. **27**, 623 (1948); C. Shannon, Proc. IRE **37**, 10 (1949)
12. P. Jung, P. Hänggi, Europhys. Lett. **8**, 505 (1989)
13. P. Jung, P. Hänggi, Phys. Rev. A **44**, 8032 (1991); P. Jung, P. Hänggi, Phys. Rev. A **41**, 2977 (1990)
14. J. Casado-Pascual, C. Denk, J. Gomez-Ordonez, M. Morillo, P. Hänggi, Phys. Rev. E **67**, 036109 (2003)
15. K. Loerincz, Z. Gingl, L.B. Kiss, Phys. Lett. A **224**, 63 (1996); P. Hänggi, M. Inchiosa, D. Fogliatti, A. Bulsara, Phys. Rev. E **62**, 6155 (2000); J. Casado-Pascual, J. Gomez-Ordonez, M. Morillo, P. Hänggi, Phys. Rev. Lett. **91**, 210601 (2003); J. Casado-Pascual, J. Gomez-Ordonez, M. Morillo, P. Hänggi, Phys. Rev. E **68**, 061104 (2003)
16. F. Rieke, D. Warland, R. de Ruyter van Steveninck, W. Bialek, *Spikes: Exploring the Neural Code* (MIT Press, Cambridge, MA, 1997)
17. W. Bialek, A. Zee, J. Stat. Phys. **59**, 103 (1990); W. Bialek, M. DeWeese, F. Rieke, D. Warland, Physica **200**, 581 (1993); M. DeWeese, W. Bialek, Nuovo Cimento D **17**, 733 (1995)
18. J.J. Collins, C.C. Chow, T.T. Imhoff, Nature (London) **376**, 236 (1995); A.R. Bulsara, A. Zador, Phys. Rev. E **54**, R2185 (1996); J.E. Levin, J.P. Miller, Nature (London) **380**, 165 (1996); I. Goychuk, P. Hänggi, New J. Phys. **1**, 14 (1999); L.B. Kish, G.P. Harmer, D. Abbott, Fluct. Noise Lett. **1**, L13 (2001)
19. S. Kullback, R.A. Leibler, Ann. Math. Stat. **22**, 79 (1951); S. Kullback, *Information Theory and Statistics* (Wiley, New York, 1959)
20. D.J.C. MacKay, *Information theory, Inference, and Learning Algorithms* (Cambridge University Press, New York, 2003)
21. A. Neiman, B. Shulgin, V. Anishchenko, W. Ebeling, L. Schimansky-Geier, J. Freund, Phys. Rev. Lett. **76**, 4299 (1996)
22. I. Goychuk, P. Hänggi, Phys. Rev. E **61**, 4272 (2000)
23. I. Goychuk, Phys. Rev. E **64**, 021909 (2001)
24. N.G. Van Kampen, *Stochastic Processes in Physics and Chemistry* (North-Holland, Amsterdam, 1992)
25. K. Wiesenfeld, D. Pierson, E. Pantazelou, Ch. Dames, F. Moss, Phys. Rev. Lett. **72**, 2125 (1994)
26. S.M. Bezrukov, I. Vodyanoy, Nature (London) **378**, 362 (1995); S.M. Bezrukov, I. Vodyanoy, Nature (London) **385**, 319 (1997); S.M. Bezrukov, I. Vodyanoy, Chaos **8**, 557 (1998)
27. C. Koch, *Biophysics of Computation. Information Processing in Single Neurons* (Oxford University Press, New York, 1999)
28. M. Gopalakrishnan, P. Borowski, F. Juelicher, M. Zapotocky, Phys. Rev. E **76**, 021904 (2007)
29. A. Skupin, M. Falcke, Genome Informatics **18**, 44 (2007)
30. I. Goychuk, P. Hänggi, Phys. Rev. E **69**, 021104 (2004)
31. Notice that the process $\langle \xi(t) \rangle_{V_s}$ *averaged* over the stationary fluctuations of some signal $V_s(t)$ is *not* a renewal process, i.e. the signal induces correlations among the interspike intervals in the corresponding *averaged* process. This is the reason why it was not possible thus far to find an *exact* expression for the rate of mutual information for this model. For weak Gaussian signals the Shannon-Pinsker formula for the transinformation rate [11,16,18,32] provides but a valid approximation [17] which serves as a lower bound [33] for the mutual information
32. M.S. Pinsker, Dokl. Akad. Nauk SSSR **99**, 213 (1954) (in Russian); M.S. Pinsker, *Information and Information Stability of Random Variables and Processes* (Holden-Day, San Francisco, 1964)
33. P.P. Mitra, J.B. Stark, Nature (London) **411**, 1027 (2001)
34. A. Papoulis, *Probability, Random Variables, and Stochastic Processes*, 2nd edn. (McGraw-Hill Book Company, New York, 1984)
35. Z. Gingl, L.B. Kiss, F. Moss, Europhys. Lett. **29**, 191 (1995)
36. C.C. Chow, J.A. White, Biophys. J. **71**, 3013 (1996)
37. P. Gaspard, X.-J. Wang, Phys. Rep. **235**, 292 (1993)
38. D.M. MacKay, W.S. McCulloch, Bull. Math. Biophys. **14**, 127 (1952)
39. S.B. Lowen, M.C. Teich, Phys. Rev. Lett. **63**, 1755 (1989)