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Stochastic resonance as an inherent property of rate-modulated random series of events

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Abstract

At the molecular level, processes in physics and biology are intrinsically random. Quite often they can be described as random series of elementary events, Poisson trains, whose event generation rate is a function of an input driving parameter. We analyze the transduction of weak signals by such trains in the presence of additive input noise in terms of transfer coefficient and output signal-to-noise ratio. We show that the noise-facilitated signal transduction, stochastic resonance (SR), is an inherent property of parameter-dependent Poisson trains with a nonlinear relationship between the event generation rate, $r(V(t))$, and the driving parameter, $V(t)$. We obtain a sufficient condition for the SR onset that shows that for the input noise with a sufficiently broad bandwidth, SR can be observed in a wide variety of such systems. If this relationship is represented by $r(V(t)) \propto 1+\sum_1^3 r_n V^n(t)$, then the system is capable of SR if $6r_3/r_1 - r_2 > 0$ Addition of small noise with a broad bandwidth to the system input increases the output signal quality. To highlight the mechanism of noise-facilitated signal transduction in such systems, we also analyze the "linearizing" effect of the additive noise on signal transduction in rate-modulated Poisson series. © 1998 Elsevier Science B.V.

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1. Introduction

Having been demonstrated in an increasing number of nonlinear systems in physics, chemistry, and biology, noise-facilitated signal transduction – stochastic resonance (SR) – has enjoyed renewed interest [1-3]. While altogether different in their nature, many of these systems share a common feature: from the excitation of electrons across a barrier in a back-biased solid-state diode, to ion channels of biological membranes, to neuronal spikes of nerve cells, their random activity can be described as a spontaneous succession of nearly uniform events whose generation rate is a function of some external variable – a driving parameter. Analysis of the temporal sequence of action potentials obtained from a nerve fibre in terms of a time-dependent or "inhomogeneous" Poisson process [4] has proved to be extremely fruitful [5].

If events are statistically independent and the event generation rate r is constant, the probability of observing exactly M events during time interval T is given by Poisson's law [6],

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$$p(M,t) = \frac{(rT)^M}{M!}\exp(-rT)\,,$$

Such time series are often referred to as stationary Poisson trains or stationary Poisson processes [7].

It was shown recently [8,9] that a Poisson train with an exponential dependence of event generation rate on input parameter shows all the basic features of stochastic resonance [1–3]. These include noise-facilitated signal transfer, noise-induced increase in the output signal quality, and the existence of a particular noise amplitude that optimizes signal transduction. Specifically, the Poisson train of identical events, e.g. current pulses, with the generation rate $r \equiv r(V(t))$ obeying

$$r(V(t)) = r(0)\exp(V(t)) \tag{1}$$

was considered. Such a process transduces a small signal in the driving parameter, e.g. input voltage $V(t)$, with a signal-to-noise ratio (SNR) that can be optimized by the addition of input noise. If the input voltage is a sum of a small slow sine-wave signal of amplitude V_S and zero-mean Gaussian noise $V_N(t)$ with a Lorentzian spectrum of bandwidth f_c,

$$V(t) = V_S\sin(2\pi f_S t) + V_N(t)\,, \tag{2}$$

then the output SNR at the signal frequency $f_S \ll f_c$ is [8,9]

$$\mathrm{SNR} = \frac{((V_S)^2 r(0)/2\Delta f_A)\,\exp(\sigma^2/2)}{2 + (2r(0)/\pi f_c)\exp(\sigma^2/2)\sum_1^\infty(\sigma^{2n}/n!n)}\,. \tag{3}$$

Here, σ is the r.m.s. noise amplitude and Δf_A is the measuring device spectral resolution. The SNR described by Eq. (3) shows noise-induced increase if the condition $f_c > 2r(0)/\pi$ holds (that is, the input noise has a sufficiently wide spectrum). The noise amplitude corresponding to an SNR maximum can be estimated by [9,10]

$$\sigma_{\mathrm{opt}} \simeq \sqrt{\ln\frac{\pi f_c}{2r(0)}}\,. \tag{4}$$

For input noise with a sharp spectral cutoff at frequency f_c, the factor $\pi/2$ must be omitted.

In this Letter we address different relationships between event generation rate and driving parameter. The main question we ask is: what are the other types of relationship that lead to SR. The answer we obtain is rather unexpected. The sharp exponential dependence is not necessary. A wide class of nonlinear relationships is sufficient for the SR onset if the input noise bandwidth is high enough. Given the universality of time-dependent random series of events in the description of various phenomena, this finding suggests that the noise-facilitated signal transduction is a general statistical phenomenon, rather than a specific property of particular systems.

First, we analyze small-signal transduction for a third-power polynomial at finite noise amplitudes. Then we use the obtained results to study the case of small noise intensities for an arbitrary dependence; we derive a condition for the onset of stochastic resonance. Second, to highlight the mechanisms of noise-facilitated signal transduction, we consider cases where the event generation rate is an even or an odd power of input voltage. We show that in the case of odd powers (greater than one) the system response can be "linearized" by the addition of input noise. In the appendix we present a simplified version of calculations based on an adiabatic approach with separate averaging over high and low frequencies.

Our approach is quite different from previous theories of stochastic resonance that deal with dynamical systems [11,12] or threshold devices [13,14]. We explore a nondynamical system (it could, for example, represent statistics of raindrops that are collected by a gadget with varying aperture). It also shows a threshold-free response [8,9]. The work that can be considered as a predecessor of our study is that by Weisenfeld et

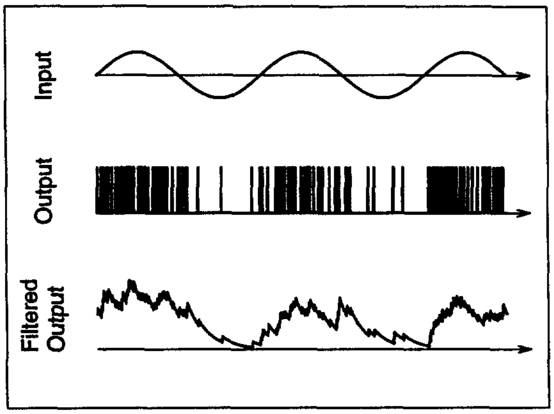

Fig. 1. Illustration of a time-dependent Poisson train (Output) with a linear rate dependence on a driving parameter (Input). The input signal (drawn here as a pure sine-wave) is transduced to the output and is contaminated by noise of random pulse generation (Filtered Output).

al. [15]. These authors examined "a modified version of the shot effect" where the event rate is modulated by a periodic signal. Noise strength defines the average rate by a Kramers-type formula for the threshold-crossings frequency [15] – the feature that makes their model to differ substantially from ours. For example, it cannot be used to account for the mixing between different spectral components of the input noise and to analyze several other effects described in the present Letter. Very recently, a new approach for the analysis of SR in intrinsically noisy systems was introduced [16]. It permits one to calculate signal-to-noise ratio for a variety of nondynamical systems; however, for an arbitrary dependence of output deterministic response and output noise on input voltage the approach is limited to small input signal and low input noise only [16].

2. Third-power polynomial dependence and a sufficient condition for stochastic resonance

Though the exponential relationship between the process rate and the driving parameter analyzed previously [8,9] seems to be the most important one for applications in physics and biology, other cases can also be of practical interest. Good examples are readily found in the field of auditory reception [17–19], where this relationship is often called "spike-generator function" [20]. The exponential spike-generation function is quite useful for modeling of auditory-nerve fiber activity [20], but it is long known that more accurate considerations must include saturation effects [21].

To analyze the generality of SR in time-dependent Poisson trains, we consider a time-dependent series of identical pulses of area (charge per pulse, in the case of electric current) Q with the pulse generation rate depending arbitrarily on input voltage $V(t)$. A cartoon illustrating signal transfer in this model is shown in Fig. 1. We first analyze the following relationship between the rate and the voltage,

$$r(V(t)) = r(0)\left(1 + \sum_{1}^{3} r_n V^n(t)\right), \tag{5}$$

where $V(t)$ is given by Eq. (2). In the vicinity of the signal frequency, f_S, which is much smaller than all other characteristic frequencies or inverse times in this problem, the power spectral density of this doubly stochastic process [7,22] can be written in the form

$$S_I(f) = 2Q^2\langle r(V(t))\rangle + 4Q^2 \int_0^\infty \langle r(V(t))r(V(t+\tau))\rangle \cos(2\pi f\tau)\,\mathrm{d}\tau. \tag{6}$$

The first term is easily calculated because only even powers of $V(t)$ will contribute to the average generation rate, so that $\langle r(V(t))\rangle = 1 + r_2\sigma^2$. Using the Gaussian properties of the noise and keeping terms of Eq. (5) that are zero or first-order in V_S only, the correlator under the integral sign is

$$\langle r(V(t))r(V(t+\tau))\rangle = K^2\sigma^2\rho(\tau) + 2r_2^2\sigma^4\rho^2(\tau) + 6r_3^2\sigma^6\rho^3(\tau) + K^2(V_S^2/2)\cos(2\pi f_S\tau).$$

Here, constant (τ-independent) terms were omitted as not contributing to the spectral density around signal frequency; terms containing products of the type $V_S^2\rho^n(\tau)\cos(2\pi f_S\tau)$ were also neglected; they represent continuous spectra that are small compared to other continuous spectral components due to $V_S \ll \sigma$. For convenience we use two abbreviations,

$$K = r_1 + 3r_3\sigma^2, \tag{7}$$

and the normalized noise autocorrelation function,

$$\rho(\tau) = \exp(-\tau/\tau_c), \tag{8}$$

where τ_c is the noise correlation time.

For $Q = 1$, Eq. (6) can now be written

$$S_I(f) = 2r(0)(1 + r_2\sigma^2) + 4\tau_c(r(0))^2\sigma^2(K^2 + r_2^2\sigma^2 + 2r_3^2\sigma^4) + (r(0)K)^2(V_S^2/2)\delta(f - f_S). \tag{9}$$

Here, the first term represents the spectral density of a stationary (time-independent Poisson train) with the rate boosted to a higher (if r_2 is positive) value by the input noise. The second term accounts for the input noise transduced to the system output. The last term containing a δ-function shows signal transfer that depends on input noise intensity as $(r(0)K)^2$. This clarifies the meaning of K: it represents the system's small-signal (linear) transfer at $r(0) = 1$. It also makes clear that the second term describing noise transfer to the output, in addition to direct amplification of noise by $(r(0)K)^2$, also includes contributions from the mixing of noise components at different frequencies.

The output SNR is the ratio of the last term to the sum of the first two,

$$\mathrm{SNR}(\sigma) = \frac{r(0)K^2V_S^2/2\Delta f_A}{2(1 + r_2\sigma^2) + 2(r(0)/\pi f_c)\,\sigma^2(K^2 + r_2^2\sigma^2 + 2r_3^2\sigma^4)}, \tag{10}$$

where $f_c = 1/2\pi\tau_c$ and the "ideal" delta-function was substituted by the inverse frequency resolution of the analyzing device, that is, by $1/\Delta f_A$. At small noise intensities, $\sigma \to 0$, this expression gives a condition for stochastic resonance onset. If $\partial\mathrm{SNR}(\sigma)/\partial\sigma > 0$, small noise intensities improve the output signal quality. It is easy to show that this condition is equivalent to

$$\pi(6r_3/r_1 - r_2)f_c > r_1^2 r(0). \tag{11}$$

From here it follows that to obtain output signal improvement, input noise bandwidth must be sufficiently wide. Interestingly, at $r_1 = 0$, the input noise *always* increases the output signal SNR. This feature is easy to understand, because $r_1 = 0$ corresponds to zero small-signal transfer (see Eqs. (5) and (7)). In this case, without input noise there is no linear response. Addition of noise "linearizes" the system making the small-signal transfer coefficient finite thus increasing SNR from zero to the value given by Eq. (10).

Eq. (11) provides a sufficient condition for stochastic resonance in systems with various relations between event generation rate and driving parameter. For example, by substituting coefficients for the exponential relationship, that is, $r_n = 1/n!$, we have

$$f_c > 2r(0)/\pi ,$$

reported earlier [8,9].

Most importantly, Eq. (11) implies that noise-facilitated signal transduction, SR, is an inherent property of of a wide class of nonlinear time-dependent random trains of events.

3. Linearizing odd power-law dependence by input noise

To understand better the noise facilitated signal transduction in time-dependent Poisson trains, consider the following, simplified relation between event generation rate and the driving parameter,

$$r(V(t)) = r(0)(1+\alpha V^n(t)) , \qquad (12)$$

where n is an integer. Again, we calculate signal transduction and the output SNR using Eq. (6). Assuming weak signals we keep only terms from Eq. (12) that are zero and first power in V_S, .

$$r(V(t)) \simeq r(0)(1+\alpha(V_N^n(t) + nV_N^{n-1}V_S\sin(2\pi f_S t))) .$$

For even n, the correlator is now

$$\langle r(V(t))r(V(t+\tau))\rangle = (r(0))^2 + (r(0))^2\alpha^2\sigma^{2n}\left(\frac{n!}{2^{n/2}(n/2)!}\right)^2(1+((n/2)!)^2)\sum_{k=1}^{n/2}\frac{2^{2k}}{2k!}\frac{1}{((n/2-1)!)^2}\rho^{2k}(\tau) + (r(0))^2n^2\alpha^2\sigma^{2n-2}\frac{V_S^2}{2}\left(\frac{(n-1)!}{2^{(n-1)/2}}\right)^2\sum_{k=1}^{n/2}\frac{2^{2k-1}}{(2k-1)!}\frac{1}{((n/2-k)!)^2}\rho^{2k-1}(\tau)\cos(2\pi f_S\tau) .$$

The only term of this expression that contains V_S is the last one. It gives the following output spectral components,

$$(r(0))^2\alpha^2\sigma^{2n-2}\frac{V_S^2}{2}\sum_{k=1}^{n/2}A_k\left(1+\frac{(f^2+f_S^2)}{(2k-1)^2f_c^2}\right)\left[\left(1+\frac{(f-f_S)^2}{(2k-1)^2f_c^2}\right)\left(1+\frac{(f+f_S)^2}{(2k-1)^2f_c^2}\right)\right]^{-1} ,$$

where A_k are numerical coefficients. Analysis of this expression shows that for n even the input signal contributes only to a broad-band output noise that is small in comparison with other components because of the condition $V_S \ll \sigma$.

For odd n, the situation is qualitatively different. The correlator can be calculated as described above to give the following expression for the power spectral density ($Q = 1$),

$$S_I(f) = 2r(0) + 4(r(0))^2\alpha^2\sigma^{2n}\frac{(n!)^2}{2^n}\sum_{k=1}^{(n+1)/2}\frac{2^{2k-1}}{(2k-1)!}\frac{1}{(((n+1)/2-k)!)^2}\frac{1}{2\pi f_c(2k-1)} \times\frac{1}{1+(f/f_c(2k-1))^2} + \frac{V_S^2}{2}(r(0))^2\alpha^2n^2\sigma^{2n-2}\left(\frac{(n-1)!}{2^{(n-1)/2}((n-1)/2)!}\right)^2\delta(f-f_S) .$$

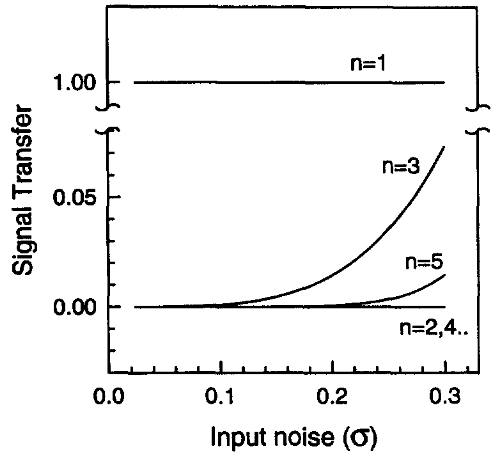

Fig. 2. Signal transfer in Poisson trains with power-law relationships between input voltage and pulse generation rate. Zero-mean Gaussian noise input noise has a "linearizing effect" on signal transfer in the case of odd powers higher than one (n = 3, 5, 7,...) but does not induce small-signal transfer in the case of even n.

The last term of this expression represents noise-facilitated small-signal transduction. This "linearizing effect" is demonstrated in Fig. 2 that shows the ratio of output spectral density at signal frequency to the signal's input spectral density at $r(0)\alpha = 1$. The corresponding SNR is the ratio of the last term to the first two in the limit of low frequencies,

$$\mathrm{SNR}(\sigma) = \left[\frac{V_S^2}{2\Delta f_A} r(0)\alpha^2 n^2 \sigma^{2n-2}\left(\frac{(n-1)!}{2^{(n-1)/2}((n-1)/2)!}\right)^2\right] \times \left(2 + 2\frac{r(0)}{\pi f_c}\alpha^2\sigma^{2n}\frac{(n!)^2}{2^n}\sum_{k=1}^{(n+1)/2}\frac{2^{2k-1}}{(2k-1)!}\frac{1}{(((n+1)/2-k)!)^2}\frac{1}{(2k-1)}\right)^{-1}. \tag{13}$$

Analysis of this equation shows that at finite α and odd $n > 1$, $\partial\mathrm{SNR}(\sigma)/\partial\sigma$ is positive at $\sigma = 0$. It means that addition of small-intensity input noise always increases the output signal quality. But for $n = 1$, that is, for a linear system, $\mathrm{SNR}(\sigma) \propto 1/(1+\sigma^2\alpha^2 r(0)/\pi f_c)$ is a monotonically decreasing function of noise intensity. As expected, introduction of noise to the input of a linear system deteriorates output signal. Only for higher odd n does input noise improve signal transduction. Comparison of output SNR for a linear system and nonlinear systems corresponding to n = 3, 5, and 7 is shown in Fig. 3 for $\tau_c = 1$, $\alpha = 1$, and $r(0) = 10$ [8]. It is seen that the output SNR of nonlinear systems showing stochastic resonance is always smaller than the corresponding value for the linear system. The noise value optimizing signal transduction depends on both the initial process rate $r(0)$ and the noise bandwidth f_c, similarly to that in the case of the exponential dependence (Eq. (4)) studied earlier [9,10]. For example, for $n = 3$,

$$\sigma_{\mathrm{opt}} = \sqrt[6]{\frac{2\pi f_c}{11\alpha^2 r(0)}}.$$

To conclude, our analysis gives a sufficient condition (Eq. (11)) for noise-induced improvement of output signal SNR in systems that can be represented by Poisson trains of events with arbitrary dependence of event generation rate on a driving parameter. It shows that stochastic resonance is an inherent property of time-dependent Poisson trains with a nonlinear relationship between the pulse generation rate and the driving parameter.

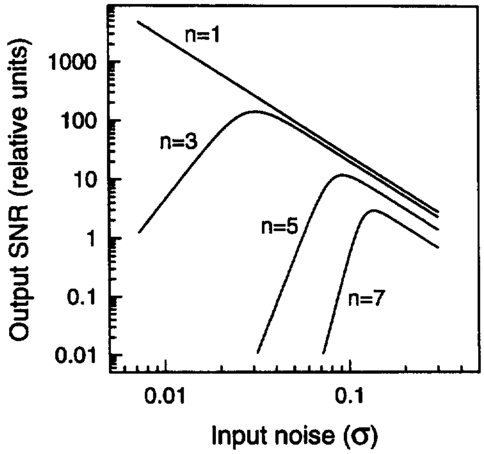

Fig. 3. Output signal-to noise ratio (SNR) for Poisson trains with power-law relationships between input voltage and pulse generation rate. In the case of a linear relationship, input noise only deteriorates output signal. For odd powers higher than one, input noise increases output SNR. The optimal noise value depends on the ratio between noise bandwidth and initial pulse generation rate (see text).

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Appendix A. Simplified adiabatic approach with separate averaging over fast and slow processes

Consider the case of small noise amplitudes only, $\sigma \ll 1$. We are interested in the value of $r(V(t))$ averaged over all processes that are faster than the input signal $f > f_S$. It is intuitively clear that in the limit of very slow signals, $f_S/f_c \to 0$, and in case of input noise with a "white" low-frequency spectrum, this averaging is exact. For the second and the third momentum of input voltage, we have

$$\langle V^2(t)\rangle_{\text{fast}} = \sigma^2 + V_S^2 \sin^2(2\pi f_S t) \tag{A.1}$$

and

$$\langle V^3(t)\rangle_{\text{fast}} = 3\sigma^2 V_S \sin(2\pi f_S t) + V_S^3 \sin^3(2\pi f_S t) \tag{A.2}$$

as the averages of all odd powers of noise signal are zeros. The condition $V_S \ll 1$ allows us to ignore all powers of the signal except for the first one, so that we have

$$\langle r(t)\rangle_{\text{fast}} = r(0)\,[\,1 + r_2\sigma^2 + (r_1 + 3r_3\sigma^2)V_S \sin(2\pi f_S t)\,]\,. \tag{A.3}$$

This expression shows that the small input sine-wave signal is transduced to the system output with a noise-dependent coefficient $r(0)(r_1 + 3r_3\sigma^2)$ in accordance with Eq. (7) above.

We find the output SNR as a ratio of input signal spectral density, $V_S^2/2\Delta f_A$, multiplied by the square of transduction coefficient, to the output noise spectral density. The latter is represented by the sum of two terms. The first one is a "shot-noise" expected from a Poisson pulse train with the initial rate $r(0)$ boosted by the factor $1 + r_2\sigma^2$ by the input noise (Eq. (A.3), first two terms in brackets) to give $2r(0)(1 + r_2\sigma^2)$. The second one is the low-frequency spectral density of input noise, $S_{\text{NI}}(0) = 2\sigma^2/\pi f_c$, multiplied by the square of transduction coefficient. This procedure gives

$$\mathrm{SNR}(\sigma) = \frac{(r(0)K)^2 V_S^2/2\Delta f_A}{2r(0)(1+r_2\sigma^2) + (2\sigma^2/\pi f_c)\,(r(0)K)^2}, \tag{A.4}$$

where $r(0)K$ is a small-signal transduction coefficient with K defined by Eq. (7). This expression differs from Eq. (10) because, considering small noise amplitudes only, we neglected contributions from mixing of different noise spectral components. Neglecting terms containing σ^4 and σ^6 and solving $\partial\mathrm{SNR}(\sigma)/\partial\sigma > 0$, we obtain Eq. (11). For the case of noise with a sharp frequency offset $S_{\mathrm{NI}}(0) = \sigma^2/f_c$. The corresponding condition for SR onset is now derived from Eq. (11) where f_c has to be replaced by $2f_c/\pi$ and is $f_c > r(0)$ [8,9].

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