

# Stochastic resonance in non-dynamical systems without response thresholds

Sergey M. Bezrukov\*† & Igor Vodyanoy\*‡§

\* Division of Computer Research and Technology, National Institutes of Health, Bethesda, Maryland 29892-0580, USA

† St Petersburg Nuclear Physics Institute, Gatchina, Russia 188530

‡ Office of Naval Research, Europe, 223 Old Marylebone Road, London NW1 5TH, UK

§ University College London, Gower Street, London, UK

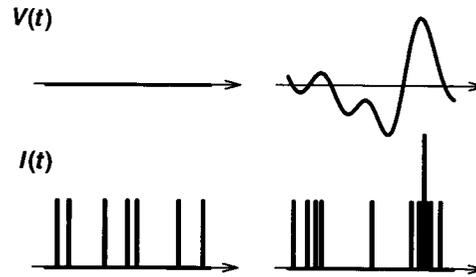
The addition of noise to a system can sometimes improve its ability to transfer information reliably. This phenomenon—known as stochastic resonance—was originally proposed to account for periodicity in the Earth's ice ages<sup>1</sup>, but has now been shown to occur in many systems in physics and biology<sup>2-4</sup>. Recent experimental and theoretical work has shown that the simplest system exhibiting 'stochastic resonance' consists of nothing more than signal and noise with a threshold-triggered device (when the signal plus noise exceeds the threshold, the system responds momentarily, then relaxes to equilibrium to await the next triggering event)<sup>4-6</sup>. Here we introduce a class of non-dynamical and threshold-free systems that also exhibit stochastic resonance. We present and analyse a general mathematical model for such systems, in which a sequence of pulses is generated randomly with a probability (per unit time) that depends exponentially on an input. When this input is a sine-wave masked by additive noise, we observe an increase in the output signal-to-noise ratio as the level of noise increases. This result shows that stochastic resonance can occur in a broad class of thermally driven physico-chemical systems, such as semiconductor p-n junctions, mesoscopic electronic devices and voltage-dependent ion channels<sup>7</sup>, in which reaction rates are controlled by activation barriers.

In contrast to threshold behaviour, where subthreshold forcing does not generate any output signal, threshold-free systems are able to respond to input signals of arbitrary small amplitude. We consider here threshold-free systems whose output can be described by a random train of identical pulses with the probability of pulse generation exponentially depending on the input signal. In particular, we assume that the pulse generation rate is given by:

$$r(V(t)) = r(0) \exp(V(t)) \quad (1)$$

where  $r(0)$  is the 'equilibrium rate' of the pulse generation and  $V(t)$  is dimensionless voltage or some other external parameter. This equation describes a broad variety of 'kT-driven' physico-chemical systems in which reaction rates are controlled by activation barriers whose heights are dependent on an external parameter. The classical examples include thermionic emission (the Richardson equation<sup>8</sup>), electron transfer across semiconductor p-n junctions<sup>9</sup>, and the generalized Eyring's rate theory<sup>10</sup>—a foundation for kinetic phenomena description in contemporary physical and biological chemistry. Among modern examples are ion channels<sup>7</sup> and mesoscopic electronic devices<sup>11</sup>.

Figure 1 illustrates the model with two examples of the output pulse train for  $V(t)$  equal to zero (on the left) and for  $V(t)$  randomly changing in time (on the right). It is seen that at zero input voltage the output current,  $I(t)$ , is represented by randomly arriving pulses. The input voltage encodes its properties into the pulse train, so that large positive deviations of the input voltage from zero substantially increase the probability of pulse generation. As a mathematical



**Figure 1** A time-dependent Poisson process is introduced via the voltage sensitivity of pulse generation rate. Randomly changing input voltage modulates the pulse arrival rate of an undisturbed stochastic process (tracks on the left) so that pulses start to group in time (tracks on the right). Large positive voltages increase the pulse rate to a degree where pulse overlapping is probable, and events with double (or multiple) amplitude appear in the output current.

object such a pulse train was introduced in 1955 by Cox who called it "doubly stochastic Poisson process"<sup>12</sup>. Following Cox, we do not discuss here the origin of initial stochasticity that leads to the pulse generation randomness—it may have different origins for different systems described by our approach, including some kind of internal fluctuation.

To facilitate subsequent treatment, we assume that  $V(t)$  is the sum of a slow zero-mean gaussian noise,  $V_N(t)$ , and a slow small-amplitude sine-wave signal, thus limiting ourselves to the adiabatic small-signal regime:

$$V(t) = V_N(t) + V_s \sin(2\pi f_s t) \quad (2)$$

where the signal amplitude  $V_s \ll 1$  and the signal frequency  $f_s$  is much smaller than all other characteristic frequencies in the model.

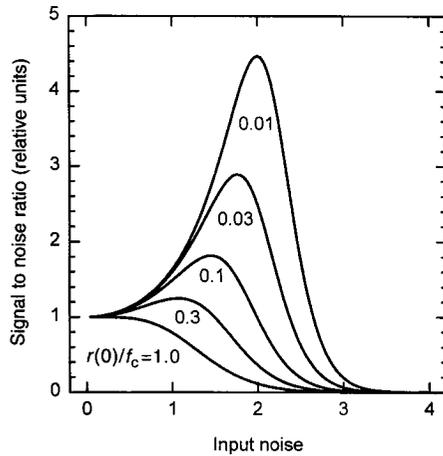
By analysing the statistical properties of such a pulse train we will describe the following features of signal transduction in these systems: (1) threshold-free response—the ability to transfer small signals with a transduction coefficient independent of signal amplitude; (2) noise-facilitated signal transduction—the property to increase the output signal amplitude by addition of noise to the system input; (3) noise-induced improvement in the output signal-to-noise ratio—the existence of particular input noise levels that optimize the output signal quality.

For a random train of identical pulses the statistical properties of the process are entirely defined by the moments of pulse arrival. The shape of the pulse gives only a multiplicative 'form-factor' important only at high frequencies that are comparable to inverse pulse time. To describe the signal transduction properties of our model we use the standard language of power spectral density<sup>2-7</sup>. At low frequencies around the signal frequency  $f_s$ , the power spectral density for this time-dependent Poisson process<sup>13</sup> can be written in the form:

$$S_i(f) = 2Q^2 \langle r(V(t)) \rangle + 4(Qr(0))^2 \times \int_0^\infty \langle \exp(V(t)) \exp(V(t + \tau)) \rangle \cos(2\pi f \tau) d\tau \quad (3)$$

where  $Q$  is single pulse area,  $\tau$  is the time delay and symbol  $\langle \rangle$  implies averaging over the ensemble representing the stochastic process. The first term here describes the frequency-independent component of noise expected from an uncorrelated time-independent train (Poisson wave) of pulses, the second one accounts for the pulse rate modulation induced by the input signal and noise (equations (1) and (2)).

For a small-amplitude signal and gaussian noise, the first term is easily expressed through the noise second moment or the root-



**Figure 2** Output signal-to-noise ratio (SNR) can be improved by addition of the input noise. Small-signal adiabatic theory predicts the existence of optimal noise intensity corresponding to a maximum in SNR. The magnitude of the optimal input noise is sensitive to the 'equilibrium pulse rate',  $r(0)$ , and the noise corner frequency,  $f_c$ .

mean-square fluctuation  $\sigma$ :

$$2Q^2\langle r(V(t)) \rangle = 2Q^2r(0) \exp(\sigma^2/2) \quad (4)$$

where  $\sigma$ , as all other voltages here, is dimensionless. To calculate the second term, we use relations for the probability density of two-dimensional normal distributions of  $X$  and  $Y$  (ref. 14) introducing the random vector  $(X, Y)$  as  $X \equiv V(t)$ ,  $Y \equiv V(t + \tau)$ . After some calculations, using the condition  $V_s \ll \sigma$ , we obtain:

$$\langle \exp(V(t)) \exp(V(t + \tau)) \rangle = \exp(\sigma^2(1 + \rho(\tau))) \quad (5)$$

For the band-limited 'white' noise with the corner frequency  $f_c = (2\pi\tau_F)^{-1}$ , the normalized autocorrelation can be written in the form:

$$\rho(\tau) = \exp(-\tau/\tau_F) + (V_s^2/2\sigma^2) \cos(2\pi f_s \tau) \quad (6)$$

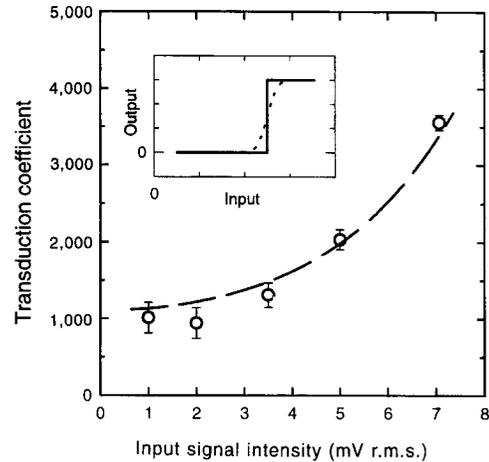
At  $f \ll f_c$ , equation (3) becomes:

$$S_i(f) = 2Q^2r(0) \exp\left(\frac{\sigma^2}{2}\right) + \frac{(Qr(0)\sigma)^2}{f_c} \exp(\sigma^2) \times \sum_1^\infty \frac{\sigma^{2n-2}}{n!n} + \frac{(Qr(0)V_s)^2}{2} \exp(\sigma^2) \delta(f - f_s) \quad (7)$$

Here, the first term on the right-hand side accounts for the noise expected from the time-independent train of pulses with the rate of  $r(0)\exp(\sigma^2/2)$ . The second term represents the external input voltage noise,  $V_N(t)$ , transduced to the output. It includes not only a small-signal part of the noise transduction but also contributions from the crosstalk between different spectral noise components. Signal transduction at  $f = f_s$  is described by the term containing a delta-function. It shows that the power of the output signal grows exponentially with  $\sigma^2$  and is finite at zero input noise. A d.c. component of the output is ignored.

The last two terms of equation (7) reflect the coding of the input stimulus (signal plus noise) in the pulse train. If the 'equilibrium rate'  $r(0)$  were not disturbed at all, that is, if  $\sigma$  and  $V_s$  were zeros, these terms would vanish and would not contribute to the system output. The second term goes away also for the input noise with negligible correlations—in this case  $\sigma$  is held constant, but the noise corner frequency is increased to an extent where  $f_c \gg r(0)\sigma^2$ .

Output signal-to-noise ratio, SNR, is now easily obtained from the left part of equation (7) as the ratio of its last term to the



**Figure 3** Signal transduction predicted by the model at zero input noise as a function of input signal intensity (dashed line) compared to those for threshold systems from electronics<sup>18</sup> (solid line) and biology<sup>17</sup> (dotted line) shown in the inset. The threshold-free character of the model is clearly seen. The points show the gain ratio measured as described in ref. 7 with the parallel array of alamethicin ion channels reconstituted in a planar lipid bilayer at 110 mV. The interrupted line is calculated for  $kT/ne = 3.3$  mV.

first two:

$$\text{SNR} = \frac{\frac{V_s^2 r(0)}{2\Delta f_A} \exp\left(\frac{\sigma^2}{2}\right)}{2 + \frac{r(0)}{f_c} \sigma^2 \exp\left(\frac{\sigma^2}{2}\right) \sum_1^\infty \frac{\sigma^{2n-2}}{n!n}} \quad (8)$$

where  $\Delta f_A$  stands for the unit-frequency window width of the spectrum analyser that is to be used in measurements. It is seen that, except for the trivial dependence on the input signal amplitude ( $V_s$ ) and the details of measurement technique ( $\Delta f_A$ ), the SNR can be controlled by the noise intensity ( $\sigma$ ), its frequency width ( $f_c$ ), and 'equilibrium pulse rate' ( $r(0)$ ).

Figure 2 shows the signal-to-noise ratio at different values of  $r(0)/f_c$  as a function of input noise intensity. In the figure, the SNR is normalized to its magnitude at  $\sigma = 0$ . It can be seen that external input noise can improve the output signal quality. Noise intensity corresponding to a maximum in the output SNR increases with  $f_c$  but decreases with  $r(0)$ . Interestingly, however good the initial statistics (large  $r(0)$ ), the output signal quality can be further improved if (and only if) the bandwidth of input noise is high enough for the condition  $f_c > r(0)$  to hold.

It should be noted here that for small and slow signals the results of our calculations are exact. The presented model is applicable to a wide variety of systems with exponential statistics. In the case of biological ion channels the exponential statistics are due to an interaction between the part of channel molecule containing so called 'gating charges'<sup>15</sup> and the electric field applied across the membrane in which this molecule is embedded. For such voltage-dependent ion channels  $Q$  becomes the total charge transported through a single channel during its conductive state, and all voltages in the problem are now expressed in units of  $kT/ne$ , where  $ne$  is an effective gating charge of the channel<sup>7</sup>.

Figure 3 shows signal transduction predicted by our model (dashed line) with experimental data obtained for voltage-dependent ion channels (data points) and demonstrates its threshold-free character. To highlight the qualitative difference, the solid and dashed lines in Fig. 3 inset describe examples of two threshold devices taken from electronics and biology; they demonstrate

the output signal of a level-crossing detector (adapted from ref. 16 for the case of zero external noise) and a nerve cell as a function of the input signal amplitude. The nerve cell is represented by the 'Hodgkin-Huxley axon' in the presence of electrical noise<sup>17</sup> whose magnitude determines the width of the threshold transition. It is seen that at zero external noise, the threshold devices are silent at small signals, whereas voltage-dependent ion channels transduce them with a finite coefficient. □

Received 15 July; accepted 22 November 1996.

1. Benzi, R., Sutera, S. & Vulpiani, A. *J. Phys. A* **14**, L453–457 (1981).
2. Bulsara, A. R. & Gammaitoni, L. *Phys. Today* **49**, 39–45 (1996).
3. Wiesenfeld, K. & Moss, F. *Nature* **373**, 33–36 (1995).
4. Moss, F., Pierson, D. & O'Gorman, D. *Int. J. Bifurc. Chaos* **4**, 1383–1397 (1994).
5. Wiesenfeld, K., Pierson, D., Pantazelou, E., Dames, C. & Moss, F. *Phys. Rev. Lett.* **72**, 2125–2128 (1994).
6. Gíngl, Z., Kiss, L. B. & Moss, F. *Europhys. Lett.* **29**, 191–196 (1995).
7. Bezikov, S. M. & Vodyanoy, I. *Nature* **378**, 362–364 (1995).
8. Nye, J. F. *Physical Properties of Crystals* 236–240 (Clarendon, Oxford, 1976).
9. Benedict, R. R. *Electronics for Scientists and Engineers* 80–85 (Prentice-Hall, Englewood Cliffs, 1976).
10. Glasstone, S., Laidler, K. J. & Eyring, H. *The Theory of Rate Processes* 1–27 (McGraw-Hill, London, 1941).
11. Reznikov, M., Heiblum, M., Shtrikman, H. & Mahalu, D. *Phys. Rev. Lett.* **75**, 3340–3343 (1995).
12. Cox, D. R. *J. R. Statist. Soc. B* **17**, 129–164 (1955).
13. Cox, D. R. & Lewis, P. A. W. *The Statistical Analysis of Series of Events* 28–29, 102–112 (Methuen, London, 1996).
14. Rice, S. O. in *Selected Papers on Noise and Stochastic Processes* (ed. Wax, N.) 133–294 (Dover, New York, 1954).
15. Hille, B. *Ionic Channels of Excitable Membranes* 54–47, 372–503 (Sinauer Assoc., Sunderland, 1992).
16. Jung, P. *Phys. Lett. A* **207**, 93–104 (1995).
17. Lecar, H. & Nossal, R. *Biophys. J.* **11**, 1048–1067 (1971).

**Acknowledgements:** We thank V. A. Parsegian for discussions and encouragement at all stages of this work; G. Weiss and M. Taqqu for consultations; V. Aguilera, B. Altshuler, C. Houdre, S. Leikin, R. Nossal, R. Podgornik and H. Strey for their suggestions and comments on the manuscripts. This work was supported by the US Office of Naval Research.

Correspondence should be addressed to S.M.B. (e-mail: bezrukov@helix.nih.gov).