Fluctuation and Noise Letters
Vol. 1, No. 1 (2001) L13–L19
© World Scientific Publishing Company

INFORMATION TRANSFER RATE OF NEURONS: STOCHASTIC RESONANCE OF SHANNON'S INFORMATION CHANNEL CAPACITY

LASZLO B. KISH
The Angstrom Laboratory, Uppsala University, POB 534, Uppsala, SE-75121, Sweden
Laszlo.Kish@angstrom.uu.se

GREGORY P. HARMER and DEREK ABBOTT
Centre for Biomedical Engineering (CBME) and EEE Department,
Adelaide University, Adelaide, SA 5005, Australia
{gpharmer,dabbott}@eleceng.adelaide.edu.au

Received 12 January 2001
Revised 14 March 2001
Accepted 14 March 2001

The information channel capacity of neurons is calculated in the stochastic resonance region using Shannon's formula. This quantity is an effective measure of the quality of signal transfer, unlike the information theoretic calculations previously used, which only characterize the entropy of the output and not the rate of information transfer. The Shannon channel capacity shows a well pronounced maximum versus input noise intensity. The location of the maximum is at a higher input noise level than has been observed for classical measures, such as signal-to-noise ratio.

Keywords: Information transfer; Stochastic resonance; Signal to noise ratio; Neural signals; Neurons; Nervous system.

1. Introduction

Stochastic resonance (SR) is a noise assisted signal propagation phenomenon which has recently attracted much attention due to its relevance in biology and sensing [1–19]. A stochastic resonator (STR) is a special nonlinear system (Fig. 1), which requires an optimal intensity of noise to be added to the input signal for the best signal transfer. Originally, the SR phenomenon was characterized by the signal-to-noise ratio (SNR) at the output of the STR by

$$SNR_{\text{out}}(f) \equiv \frac{P_{s,\text{out}}(f)}{S_{n,\text{out}}(f)}, \tag{1}$$

where $P_{s,\mathrm{out}}(f)$ is the mean-square (MS) signal amplitude of the periodic component of the output at the signal frequency f, and $S_{n,\mathrm{out}}(f)$ is the power spectral density (PSD) of the output noise at the same frequency. The noise power is described by its PSD because it is dependent on its bandwidth, whereas a sinusoidal signal (or component of) is not. The spectrum of the signal cannot be used since it is periodic and would result with a Dirac delta function, which means the height of the spike depends on the frequency resolution of the FFT during measurement. Conversely, we can not use the power measure for noise as this would include frequencies far from the signal frequency of interest. This mixed method is valuable because it gives information about the actual SNR at the signal frequency.

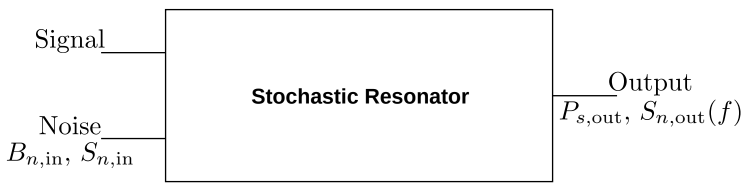

Fig 1. Stochastic resonator. The box represents a nonlinear system combining the signal and noise, usually involving a threshold. The notion is described in the text.

2. Comparison of metrics

It had been assumed that the SNR_{out} is a sufficiently good way of characterizing the quality of the output signal and that the best coherence between it and the input signal is achieved when the ratio of the SNR at the output versus the input is maximized. That is, the most information about the input signal is transferred though the system to the output, hence we have maximal information transfer. More recently, several new methods of characterization, which are similar in nature, have been proposed using entropy [16–19]. As an example, we discuss Stock's most recent method [16] that uses entropy difference,

$$I = H_{\mathrm{output}} - H_{\mathrm{lost}} \quad [\mathrm{bits}], \tag{2}$$

where H_{output} is the entropy of the noisy output signal and H_{lost} is the entropy lost during the transfer of the signal through the STR. This quantity has the same efficiency of output signal characterization as the SNR_{out} and I has a similar potential for characterization as the ratio of $SNR_{\mathrm{out}}/SNR_{\mathrm{in}}$ at the output versus the input.

However, according to Shannon, and Nyquist, [20,21] neither the $SNR_{\mathrm{out}}/SNR_{\mathrm{in}}$ nor I are sufficient measures of the effectiveness of channel capacity. They only provide information about the entropy of the signal versus the noise, and the degradation of this entropy during transfer. This is directly related to the potential information content of the output. However, it does not say anything about the channel capacity. Simply speaking, these quantities talk about the amount of information but they do not say anything about how frequently this information is refreshed. This fact is immediately obvious if we look at the dimension of I which is the bit. However, the proper dimension of the information transfer rate is bits/second. This is obvious from Shannon's formula (and the similar Nyquist formula), which was one of the most important milestones in information theory,

$$C = B_s \log_2(1 + \frac{P_s}{P_n}) \quad \text{[bits/second]}, \tag{3}$$

where C is the channel capacity, B_s is the maximal bandwidth of the signal, P_s is the maximal mean-square signal amplitude (called "signal power") and P_n is the mean-square noise amplitude (called "noise power"). According to Shannon, Eq. (3) can be interpreted as follows: half of the the logarithmic term is the information entropy and $2B_s$ is the frequency of refreshing this information. For the validity of Eq. (3) in practical cases, any noise outside the frequency bandwidth of the signal is removed by a linear filter. The bandwidth B_s in the Shannon formula is the key parameter which refers to the rate of refreshing the information and the logarithmic term refers to the potential amount of information available at each refreshment time. As a low value of the information can be compensated by a high refresh rate, that is by a large bandwidth, the amount of information alone is meaningless for the characterization of the quality of signal transfer. It is noted in [19], without using either the Shannon channel capacity or the signal-to-noise ratio, that the information refresh rate is important.

For example, the elements of Morse code can be described by two bits (short beep, long beep, short pause, long pause), so two bits are enough to communicate via this method. The two bits corresponds to the base of the logarithmic term in Shannon's formula. The information transfer rate will be determined by the mean frequency of beeps and pauses, which corresponds to the bandwidth B_s in the Shannon formula.

The aim of this Letter is to estimate the information transfer rate of neurons in the stochastic resonance region by using Shannon's formula. In this region, the input signal amplitude is less than the value of the threshold potential of the neuron. Moreover, the linear response approach will be used, which means that the input signal amplitude is less than the root-mean-square (RMS) noise amplitude. Thus, the signal response remains linear while that of the noise does not. A further assumption needed to ensure a linear response is that the firing rate of the neuron is much lower than the reciprocal of the refractory time.

For the calculations, Kiss' threshold crossing theory [5, 22] is used. This theory describes the SNR and bandwidth of the output voltage of a simple neuron model. The details of the calculations are presented in the Appendix. The main result of this Letter is the derivation of the channel capacity as follows,

$$C = \frac{B_{n,\text{in}}}{2\sqrt{3}} \exp\Big(\frac{-U_t^2}{2B_{n,\text{in}}S_{n,\text{in}}}\Big) \log_2\Big(1 + \frac{(2AU_t)^2}{(B_{n,\text{in}}S_{n,\text{in}})^2}\Big), \tag{4}$$

where $B_{n,\text{in}}$ is the bandwidth of input noise, U_t is the excitation threshold potential of the neuron, $S_{n,\text{in}}$ is the PSD of input noise and A is the RMS amplitude of the input signal. The main difference between our measure and others [16–19], is that they calculate an information content type of quantity, which is shown to have a maximum with noise intensity. What has been calculated is simply the signal-to-noise ratio expressed by other measures. When referring to optimized channel capacity, it is assumed that the signal bandwidth does not change. However, this is not the case, as shown by (A.5) the noise intensity indeed affects the signal bandwidth. Alternatively, according to theory [22] and analog simulations [5], the signal-to-noise ratio at the output is given as

$$SNR_{\rm out} = \frac{2}{\sqrt{3}} B_{n,\rm in} \frac{(AU_t)^2}{(B_{n,\rm in} S_{n,\rm in})^2} \exp\left(\frac{-U_t^2}{2B_{n,\rm in} S_{n,\rm in}}\right). \tag{5}$$

Comparing Eqs. (4) and (5), it is obvious that both equations display a maximum versus the input noise intensity $S_{n,\rm in}$ given a fixed input noise bandwidth $B_{n,\rm in}$.

In Fig. 2, the C and the $SNR_{\rm out}$ functions are plotted versus $S_{n,\rm in}$. For high noise intensities, the value of C is zero when the MS amplitude of the output noise exceeds the MS amplitude of the output signal, i.e. when $P_s/P_n \ll 1$. The actual value and the shape of C can be modified by linear filtering the output to reduce the bandwidth when the signal is not fully utilizing all of the possible bandwidth. For all the channel capacity curves, the stochastic resonance peaks at higher input noise intensities than the $SNR_{\rm out}$ curve. Moreover, it is interesting to note that different shapes can be obtained at reduced bandwidths, where the difference in the behavior becomes pronounced at low noise levels and strong bandwidth reduction. In the large noise limit, the curves converge to the same level.

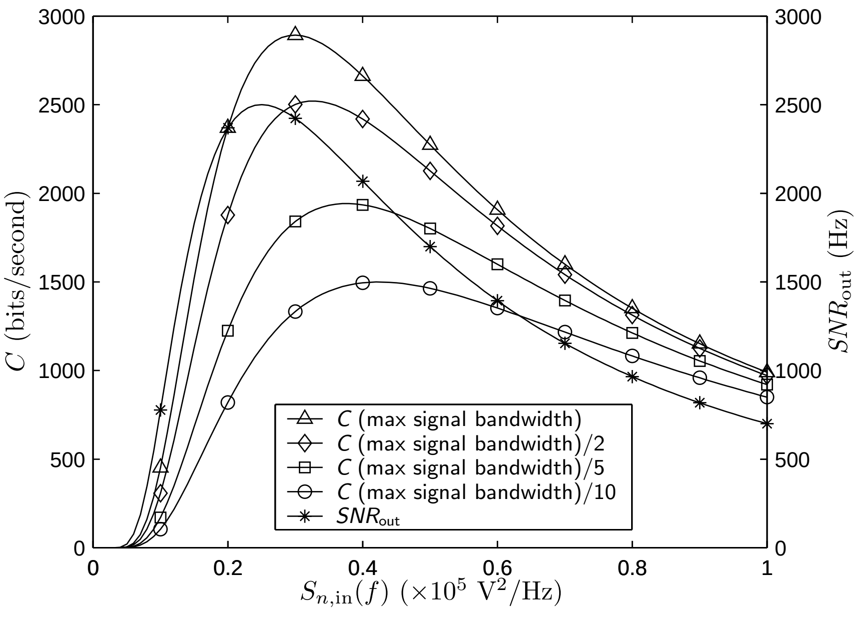

Fig 2. Channel capacity (maximal information rate) C and output signal to noise ratio ($SNR_{\rm out}$) of the neuron model (with signal amplitude 0.1 V, threshold 1.0 V, input noise bandwidth 100 kHz). The different C curves represent various fractions of the maximal signal bandwidth, where the unused band is removed by a linear low-pass filter.

3. Conclusion

We have highlighted that in order to correctly measure stochastic resonance using information theory metrics, one must consider the rate of information transfer. From first principles, the Shannon channel capacity can be expressed in terms of the output SNR and displays the characteristics of stochastic resonance. Unlike previous calculations that only consider the entropy, and hence only characterize the information content at the output, the channel capacity provides the rate of information transfer and thus is a more useful measure.

Acknowledgments

Comments of Peter Ruszczynski, Barbara Piechocinska and Bradley Ferguson are appreciated. LBK acknowledges the Swedish Natural Science Research Council (NFR). GPH and DA acknowledge funding by the Australian Research Council and the Sir Ross & Sir Keith Smith Fund.

Appendix A.

We start by giving the noise power as $P_n = S_n B_{n,\mathrm{eff}}$, where S_n is the power spectrum density of the noise (which is flat for white noise) and $B_{n,\mathrm{eff}}$ is the effective bandwidth of the noise. This means, that given the bandwidth of the signal we can simply limit the PSD of the noise by employing a simple linear filter with a cut-off frequency of the signal bandwidth. Thus, the noise bandwidth is equal to the signal bandwidth B_s, to give

$$P_n = S_n B_s. \tag{A.1}$$

Substituting (A.1) into the Shannon formula of (3) gives the information transfer rate as

$$C = B_s \log_2 \left(1 + \frac{P_s}{S_n B_s}\right). \tag{A.2}$$

Taking that at the output of the STR then P_s becomes $P_{s,\mathrm{out}}$ and S_n becomes $S_{n,\mathrm{out}}$ and using the signal-to-noise ratio given in (1) we have

$$C = B_s \log_2 \left(1 + \frac{SNR_{\mathrm{out}}}{B_s}\right), \tag{A.3}$$

which gives the channel capacity in terms of the output SNR and signal bandwidth.

To find the maximal bandwidth of the signal B_s, we need to consider Shannon's sampling theorem and the mean level crossing frequency $\nu(U_t)$, given in [22] as

$$\nu(U_t) = \frac{2}{\sigma} \exp\left(\frac{-U_t^2}{2\sigma^2}\right)\left(\int_0^\infty f^2 S(f)\,df\right)^{1/2}, \tag{A.4}$$

where the noise power $\sigma^2 = \int_0^\infty S(f)\,df = B_{n,\mathrm{in}} S_{n,\mathrm{in}}$. From the sampling theorem, B_s is approximately equal to half the mean spike frequency, which is half the mean level crossing frequency due to noise in any direction, thus $B_s = \nu(U_t)/4$. By direct integration we have

$$\frac{2}{\sigma}\left(\int_0^\infty f^2 S(f)\,df\right)^{1/2} = \frac{2}{\sqrt{3}} B_{n,\mathrm{in}},$$

then combining with (A.4) we find the signal bandwidth as

$$B_s = \frac{B_{n,\mathrm{in}}}{2\sqrt{3}} \exp\left(\frac{-U_t^2}{2B_{n,\mathrm{in}}S_{n,\mathrm{in}}}\right). \tag{A.5}$$

From Eq. (A.3.4) in [22], the output SNR is given as

$$\begin{aligned} SNR_{\mathrm{out}} &= \frac{\nu(0)(AU_t)^2}{\sigma^4} \exp\left(\frac{-U_t^2}{2\sigma^2}\right) \\ &= \frac{2}{\sqrt{3}} B_{n,\mathrm{in}} \frac{(AU_t)^2}{(B_{n,\mathrm{in}}S_{n,\mathrm{in}})^2} \exp\left(\frac{-U_t^2}{2B_{n,\mathrm{in}}S_{n,\mathrm{in}}}\right), \end{aligned} \tag{A.6}$$

where $\nu(0)$ can be found from (A.4). This can be given in terms of B_s by

$$SNR_{\mathrm{out}} = \frac{(2AU_t)^2}{(B_{n,\mathrm{in}}S_{n,\mathrm{in}})^2} B_s. \tag{A.7}$$

Substituting (A.7) and (A.5) back into (A.3) gives the desired channel capacity of Eq. (4).

References

[1] R. Benzi, A. Sutera and A. Vulpiani, *The mechanism of stochastic resonance*, *J. Phys. A* **14** (1981) 453–457.

[2] B. McNamara and K. Wiesenfeld, *Theory of stochastic resonance*, *Phys. Rev. A* **39** (1989) 4854–4869.

[3] P. Hänggi, P. Jung, C. Zerbe and F. Moss, *Can colored noise improve stochastic resonance?*, *J. Stat. Phys.* **70** (1993) 25–51.

[4] M. I. Dykman, R. Mannella, P. V. E. McClintock, N. D. Stein and N. G. Stocks, *Probability distributions and escape rates for systems driven by quasimonochromatic noise*, *Phys. Rev. E* **47** (1993) 3996–4009.

[5] Z. Gingl, L. B. Kiss and F. Moss, *Non-dynamical stochastic resonance: Theory and experiments with white and arbitrarily coloured noise*, *Europhys. Lett.* **29** (1995) 191–196.

[6] S. M. Bezrukov and I. Vodyanoy, *Noise-induced enhancement of signal-transduction across voltage-dependent ion channels*, *Nature* **378** (1995) 362–364.

[7] J. J. Collins, C. C. Chow and T. T. Imhoff, *Aperiodic stochastic resonance in excitable systems*, *Phys. Rev. E* **52** (1995) 3321–3324.

[8] A. R. Bulsara and L. Gammaitoni, *Tuning into noise*, *Physics Today* **49** (1996) 39–45.

[9] K. Loerincz, Z. Gingl and L. B. Kiss, *A stochastic resonator is able to greatly improve signal-to-noise ratio*, *Phys. Lett. A* **224** (1996) 63–67.

[10] F. Chapeau-Blondeau and X. Godivier, *Theory of stochastic resonance in signal transmission by static nonlinear systems*, *Phys. Rev. E* **55** (1997) 1478–1495.

[11] S. M. Bezrukov, *Stochastic resonance as an inherent property of rate-modulated random series of events*, *Phys. Lett. A* **248** (1998) 29–36.

[12] L. Gammaitoni, P. Hänggi, P. Jung and F. Marchesoni, *Stochastic resonance*, *Revs. of Modern Physics* **70** (1998) 223–287.

[13] P. Jung, A. Cornall-Bell, F. Moss, S. Kadar, J. Wang and K. Showalter, *Noise sustained waves in subexcitable media: From chemical waves to brain waves*, *Chaos* **8** (1998) 567–575.

[14] G. P. Harmer and D. Abbott, *Simulation of circuits demonstrating stochastic resonance*, *Microelectronics J.* **31** (2000) 553–559.

[15] L. B. Kish and S. M. Bezrukov, *Flows of cars and neural spikes enhanced by colored noise*, *Phys. Lett. A* **266** (2000) 271–275.

[16] N. G. Stocks, *Suprathreshold stochastic resonance in multilevel threshold systems*, *Phys. Rev. Lett.* **84** (2000) 2310–2313.

[17] M. DeWeese and W. Bialek, *Information flow in sensory neurons*, *Il Nuovo Cimento D* **17D** (1995) 733–741.

[18] I. Goychuk and P. Hänggi, *Stochastic resonance in ion channels characterized by information theory*, *Phys. Rev. E* **61** (2000) 4272–4280.

[19] S. P. Strong, R. Koberle, R. R. de Ruyter van Steveninck and W. Bialek, *Entropy and information in neural spike trains*, *Phys. Rev. Lett.* **80** (1998) 197–200.

[20] C. E. Shannon and W. Weaver, *The mathematical theory of communication*, The University of Illinois Press, 1949.

[21] C. E. Shannon, *Communication in the presence of noise*, *Proc. IRE* **37** (1949) 10–21.

[22] L. B. Kiss, *Possible breakthrough: significant improvement of signal to noise ratio by stochastic resonance*, in Chaotic, Fractal, and Nonlinear Signal Processing, Proc. Am. Institute Phys., ed. R. Katz, Mystic, Connecticut, USA, **375** (1996) 382–396.