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HOW FAST CAN A NEURON TRANSFER INFORMATION: BANDWIDTH IS THE REAL ISSUE

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The information channel capacity of neurons is calculated in the stochastic resonance region by using the Shannon formula. This quantity is an effective measure of the quality of signal transfer, unlike signal-to-noise ratio or information entropy measures, which characterize only the resolution of the output and not the rate of information transfer. This fact has also been realized by some authors, however, until now, no published results exist for real stochastic resonators or neuron models. The most probable reason of missing results is the problem with defining the maximal bandwidth of the system. The trick we use is to applying Wiener's sampling theorem to define the maximal bandwidth. The channel capacity exhibits a well expressed maximum versus the input noise intensity, and the location of the maximum is at a higher input noise level than it was observed for classical measures, such as signal to noise ratio or entropy. In conclusion, more noise is needed for the optimal transfer than it has earlier been assumed.

1 Introduction

The present paper is an modified conference-version of a recently published paper [1]. 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

$$SNR_{out}(f) \equiv P_{s,out}(f) / S_{n,out}(f) \quad (1)$$

where $P_{s,out}(f)$ is the mean-square (MS) signal amplitude of the periodic component of the output at the signal frequency f , and $S_{n,out}(f)$ is the spectral density of the output noise background at the same frequency.

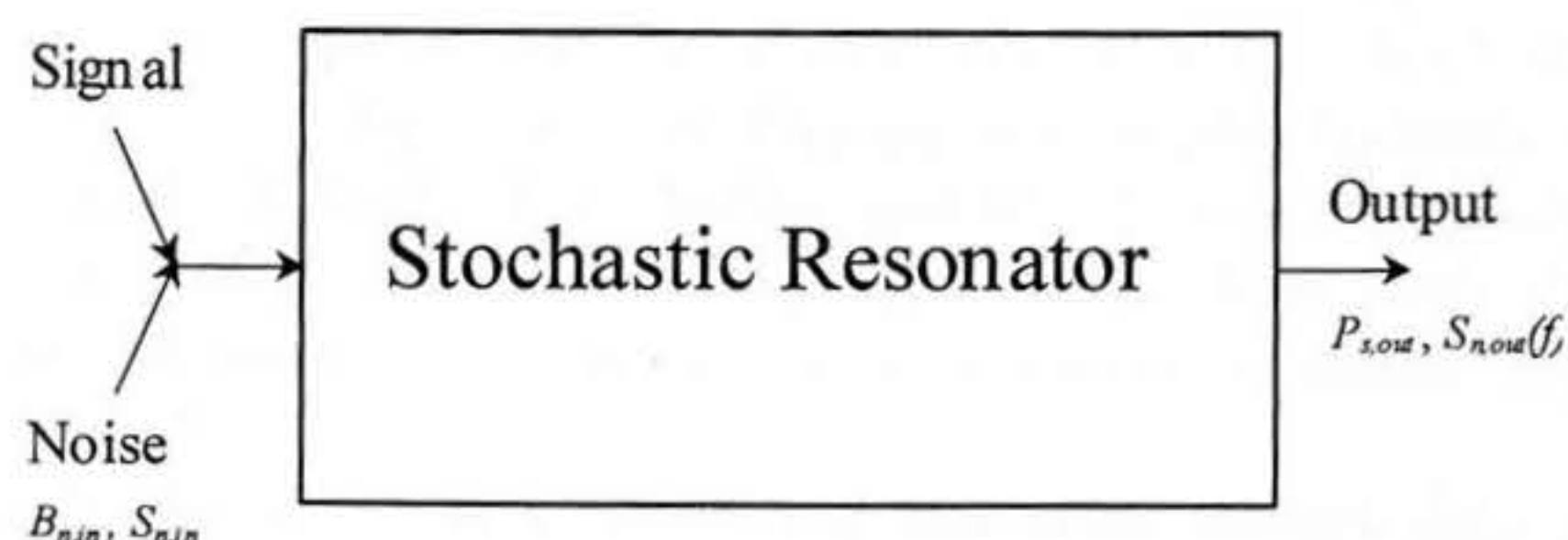


Figure 1. Stochastic resonator. The box represents a nonlinear system combining the signal and noise, usually involving a threshold. The notion is described in the text.

2 On Different Metrics of Information Transfer

It has recently been realized by Goychuk and Hanggi [18] that Shannon's information channel capacity is the proper measure to be applied for stochastic resonators. However, until now, no published results exist for real stochastic resonators or neuron models. The most probable reason of missing results is the problem with defining the maximal bandwidth of the system. Very recently, this problem has successfully been solved in [1]. Here we present the detailed argumentation without mathematical details.

Originally, 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. Several new methods of characterization, which are similar in nature, have been proposed using, in various ways, the entropy [16-19]

$$H = \frac{1}{2} \log_2 \left(1 + \frac{P_s}{P_n} \right) \quad [\text{bits}], \quad (2)$$

where H is the entropy of the noisy signal at the input (H_{in}) or at the output (H_{out}), P_s is the maximal mean-square signal amplitude (called "signal power") and P_n is the mean-square noise amplitude (called "noise power"). This quantity has the same efficiency of signal quality characterization as the SNR given on a deciBell scale, which is called resolution in technical fields. However, according to Shannon, and Nyquist, [20,21] neither the comparison of SNR_{out} with SNR_{in} nor the comparison of H_{out} with H_{in} are sufficient measures of the effectiveness of channel capacity. They only provide information about the degradation of the signal resolution during the transfer. However, it does not say anything about the information 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 H 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,

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

where C is the channel capacity and B_s is the maximal bandwidth of the signal. 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, because the equation is for continuous signals where Wiener's sampling theorem holds. 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 (resolution) 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 paper 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.

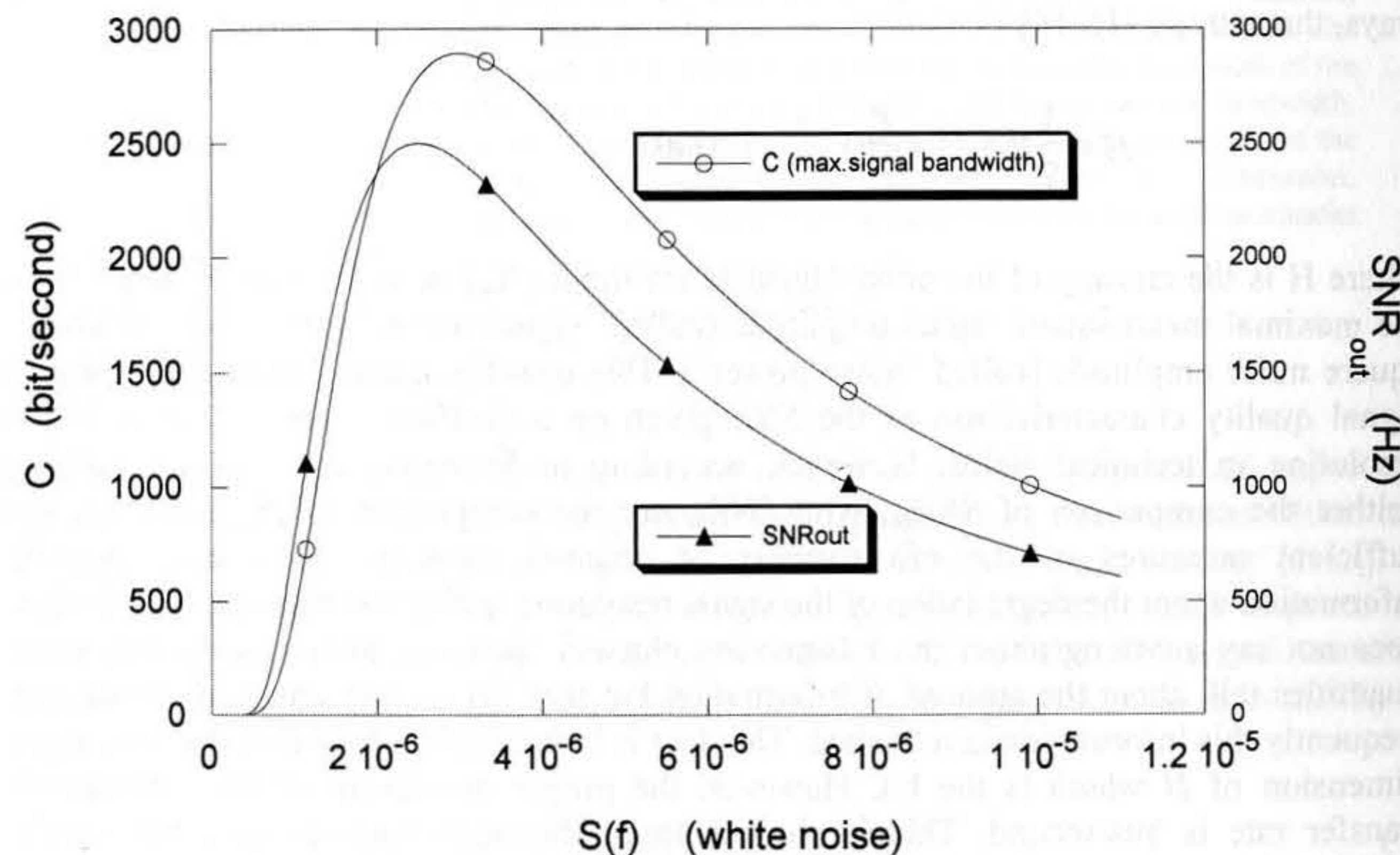


Figure 2. Channel capacity (maximal information rate) C and output signal to noise ratio (SNR_{out}) of the neuron model (with signal amplitude 0.1 V, threshold 1.0 V, input noise bandwidth 100kHz). C has its maximum at a higher input noise intensity, because the larger the input noise the greater the bandwidth of signal transfer through the neuron. Note, at these systems, it is the standard way that the input noise intensity is characterized by its spectrum, because it is a bandlimited white noise with fixed cut-off frequency.

For the calculations [1], Kiss' threshold crossing theory [5,22] was used. This theory describes the SNR and bandwidth of the output voltage of a simple neuron model. The applied trick to get the bandwidth is applying Wiener's sampling theory, that is, the bandwidth is half of the repetition frequency of generated spikes at the output. The main result of this paper is the channel capacity:

$$C = \frac{B_{n,in}}{4\sqrt{3}} \exp\left(\frac{-U_t^2}{2B_{n,in}S_{n,in}}\right) \log_2 \left[1 + 4 \frac{(AU_t)^2}{(B_{n,in}S_{n,in})^2} \right], \quad (4)$$

where $B_{n,in}$ is the bandwidth of input noise, U_t is the excitation threshold potential of the neuron, $S_{n,in}$ is the PSD of input noise and A is the RMS amplitude of the input signal. The main difference between our measure and the results of others [16-19] on various systems, is that the Shannon channel capacity, which is our measure, takes into the account the variation of the bandwidth versus the input noise intensity and cut-off frequency. As the output spike frequency is a monotonically increasing function of the input noise intensity, a higher input noise means a higher bandwidth. This effect yields a higher intensity of the optimal input noise for maximal information transfer capacity, as it can be seen in Fig. 2.

3 Conclusion

It has been shown that the additive noise is better for stochastic resonator systems and biological information transfer than it was earlier assumed. The reason for the increased benefit is the increasing effective bandwidth with increasing input noise.

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