How much power does neural signal propagation need?*

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Abstract
Two well known, biologically inspired non-dynamical models of stochastic
resonance, the threshold-crossing model and the fluctuating rate model, are
analyzed in terms of channel information capacity and dissipation of energy
necessary for small-signal transduction. Using analogies to spike
propagation in neurons we postulate the average output pulse rate as a
measure of dissipation. The dissipation increases monotonically with the
input noise. We find that for small dissipation both models give a close to
linear dependence of the channel information capacity on dissipation. In
both models the channel information capacity, as a function of dissipation,
has a maximum at input noise amplitude that is different from that in the
standard signal-to-noise ratio versus input noise plot. Though a direct
comparison is not straightforward, for small signals the threshold model
gives appreciably higher density of information per dissipation than the
exponential fluctuating rate model. We show that a formal introduction of
cooperativity in the rate fluctuating model permits us to imitate the response
function of the threshold model and to enhance performance. This finding
may have direct relevance to real neural spike generation where, due to a
strong positive feedback, the ion channel currents add up in a synchronized
way.

1. Introduction

Noise-facilitated signal transduction, or stochastic resonance
(SR) [1], is attracting significant attention (for reviews
see [6, 18, 19]). Here we consider two well known non-
dynamical models of noise-facilitated signal transduction from
the point of view of energy dissipation. The first model,
introduced six years ago [7, 10], is a threshold model where a
pulse (or a spike) is generated every time the input parameter
comprised of signal and noise reaches the threshold voltage
value [12]. The second model, described four years ago [2–4],
is a threshold-free model of signal transduction. It is based on
the so-called inhomogeneous Poisson process. In this process
the rate of pulse generation is modulated by the input parameter
in a continuous manner. By bypassing a discussion of the

mechanistic origins of such processes, this model shows that a
number of non-linear dependences between the input stimulus
and the process rate lead to SR demonstrating its universal
character [2]; see also in another article [5].

Pulse generation in both electronics and biology is a
non-equilibrium process that dissipates energy. For example,
a rough estimate that uses typical times ($\sim$1 ms), current
densities ($\sim$1 mA cm^{-2}) and voltages ($\sim$0.1 V) for a squid
giant axon [9] shows that, to produce a spike, the axon
dissipates about 10^{-7} J cm^{-2}. The free energy of adenosine
triphosphate (ATP) hydrolysis is close to 3×10^4 J mol^{-1} [17],
therefore propagation of an action potential over a square
centimeter of axon surface requires hydrolysis of about $2 \times
10^{12}$ ATP molecules. This is the cost of an elementary
step in biological information processing. Guided by this
consideration, we will compare the two SR models taking the
rate of output pulse generation as a measure of dissipation.

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2. Comparison of the models

In the present paper, we restrict our considerations to the case of small and adiabatically slow signals. We start with Shannon's formula for the channel information capacity I to show that, for small signals, this measure coincides with the signal-to-noise ratio (SNR). The channel information capacity characterizes the rate of information transmission (dimensions: bits/second) and, for a white spectral distribution of the output noise, can be written in the form[13]

$$I = B_{out} \log_a\left(1 + \frac{P_s}{S_{n\,out}B_{out}}\right), \qquad (1)$$

where B_{out} is the output frequency bandwidth, P_s is the output signal power and $S_{n\,out}$ is the spectral density of the output noise. It is clear that for small harmonic signals with $S_s(f) = (A^2/2)\delta(f - f_s)$, where A is signal amplitude and f_s is signal frequency, the integration of equation (1) gives

$$I \cong \frac{1}{\ln a}\frac{A^2/2}{S_{n\,out}}. \qquad (2)$$

It is interesting that due to the low signal limit, which has a key importance in practical biological applications, this expression differs from the standard definition of the SNR frequently used in noise-facilitated signal transduction studies only by a factor $1/\ln a$ which accounts for the choice of the base of the information measure.

In the small-signal adiabatic approximation the analytical expression describing channel information capacity in the threshold-crossing model is obtained from its output SNR as [11]

$$I_{th} = \frac{\text{SNR}_{th}}{\ln 2} = \frac{2}{\sqrt{3}\ln 2}B_n\frac{(AU_t)^2}{(B_nS_n)^2}\exp\left(\frac{-U_t^2}{2B_nS_n}\right), \qquad (3)$$

where the corresponding mean firing rate characterizing the dissipation is as follows:

$$D_{th} = \langle r_{th}(t)\rangle = \frac{B_n}{\sqrt{3}}\exp\left(\frac{-U_t^2}{2B_nS_n}\right). \qquad (4)$$

Here B_n and S_n are frequency bandwidth and spectral density of the input noise and U_t is the threshold height. A rectangular spectral shape of the input noise is assumed here. For the input noise represented by an Ornstein–Uhlenbeck process the numerical multiplicative factor is different [10].

For the fluctuating rate model [3, 4], where the pulse generation rate $r(t)$ is the function

$$r_{fr}(t) = r(0)\exp(\beta V(t)), \qquad (5)$$

of the input parameter $V(t)$, the dissipation is

$$D_{fr} = \langle r_{fr}(t)\rangle = r(0)\exp\left(\frac{\beta^2 B_nS_n}{2}\right). \qquad (6)$$

In the same approximation as above the channel information capacity is given by

$$I_{fr} = \frac{\text{SNR}_{fr}}{\ln 2} = \frac{(\beta A)^2}{2\ln 2}\frac{r(0)\exp\left(\frac{\beta^2 B_nS_n}{2}\right)}{2 + \frac{r(0)}{B_n}\exp\left(\frac{\beta^2 B_nS_n}{2}\right)\sum_1^\infty \frac{(\beta^2 B_nS_n)^m}{m!m}}. \qquad (7)$$
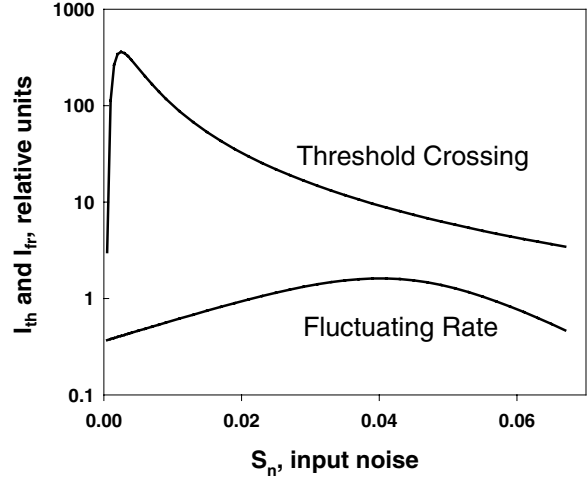

Figure 1. Maxima in the information capacity in the two models differ by two orders of magnitude with about tenfold different optimal spectral densities of the input noise.

We can compare two models using the following parameters: $U_t = 1$, $\beta = 1$, $r(0) = 1$, $B_n = 100$. Figure 1 shows the channel information capacity as a function of the input noise spectral density demonstrating two features. The information capacity is given in relative units representing $(A/\mu_t)^2 bit/sec$ and $(\beta A)^2$ bit/sec, for the threshold-crossing and fluctuating rate models, correspondingly. First, the threshold-crossing model gives an information capacity maximum at about ten times smaller input noise intensity than the fluctuating rate model. Second, the information capacity at the threshold-crossing model maximum is significantly higher. This qualitative behaviour is observed at every combination of $r(0)$ and B_n, as long as the condition $r(0) < B_n$, necessary for the SR onset in the fluctuating-rate model, is fulfilled [2, 4].

The dissipation, as a function of the input noise spectral density, is presented in figure 2. It is obvious that the qualitative behaviour in the two models is quite different. The threshold-crossing model demonstrates saturation to a level, which is expected in the case of strong input noise, where the number of crossings is defined by the noise spectral composition [12]. The fluctuating-rate model shows exponential growth of dissipation.

Figure 3 displays the information capacity as a function of dissipation. It can be seen that, in the two models, the maxima in information capacity occur at close values of dissipation. However, the ratio of information capacity to dissipation is about two orders of magnitude higher in the threshold-crossing model.

Figure 4 illustrates the information capacity versus dissipation at small dissipations. It is seen that in the fluctuating rate model the relationship is linear and in the threshold-crossing model it is close to linear. Using equations (3)–(7), it is easy to show that at small dissipations and for $B_n \gg r(0)$

$$I_{th} \cong \frac{8}{\ln 2}\left(\frac{A}{U_t}\right)^2(\ln D_{th})^2 D_{th} \qquad (8)$$

and

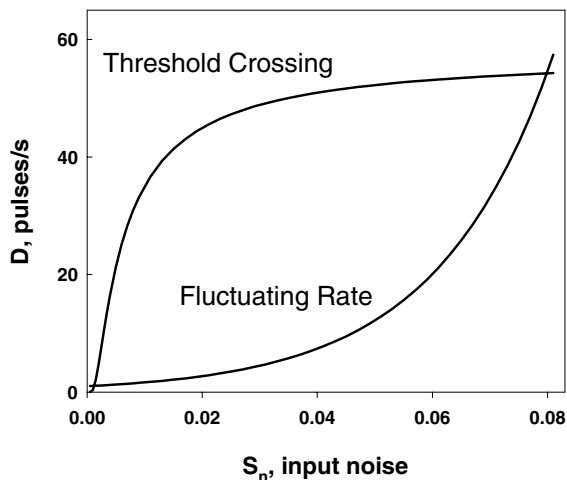$$\Delta I_{fr} \cong \frac{(\beta A)^2}{4\ln 2}\Delta D_{fr} \qquad (9)$$

Figure 2. Dissipation as a function of the input noise spectral density shows quite different qualitative behaviour.
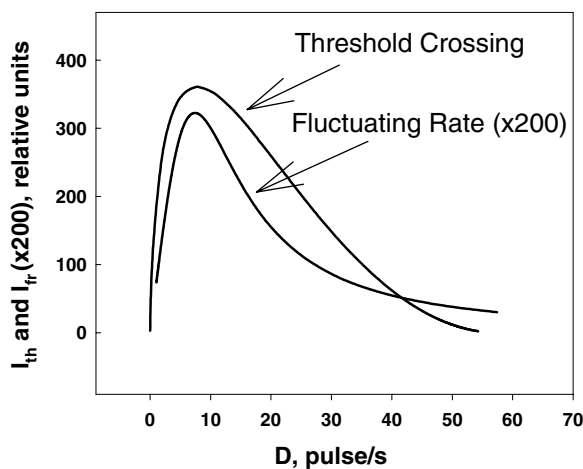

Figure 3. Information capacity as a function of dissipation is qualitatively similar.

where ΔI_{fr} and ΔD_{fr} are the noise-induced increments in information capacity and dissipation (in the case of the threshold-crossing model $\Delta I_{th} = I_{th}$ and $\Delta D_{th} = D_{th}$). The comparison of figures 1–3 and equations (8) and (9) shows that the threshold-crossing model serves as a much more efficient signal transducer in terms of information-to-dissipation ratio. Indeed, the threshold characteristic can be seen as a limiting case of exponential dependence where parameter β is large. For the rest of the parameters as specified above and at dissipations close to optimal (figure 3), the fluctuating rate model gives information-to-dissipation ratios similar to those in the threshold-crossing model at $\beta \approx 7$.

The encoding of information into nerve pulse trains is a vividly discussed unsolved problem [15, 16]. The results discussed above relate to the pulse rate modulation mechanism, believed to be dominating in many studied examples [14]. By comparing the information content of the transduced signals with the corresponding dissipation we show that the two models, both using basically the same pulse rate modulation mode of signal encoding, are significantly different in their efficiency.
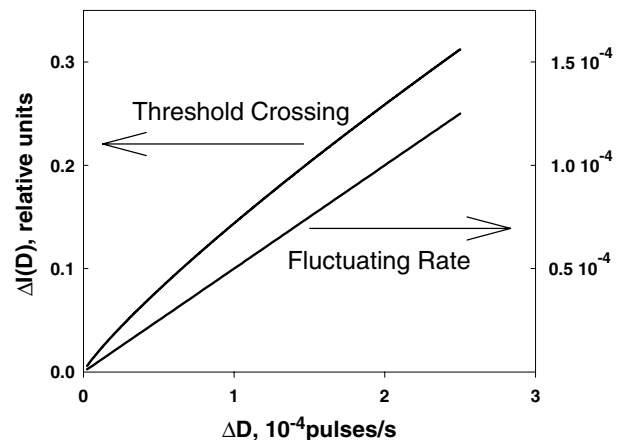
Figure 4. In both models gain in the information capacity in the limit of low dissipation is approximately proportional to dissipation.

As an immediate biological application—nerve pulse generation—is concerned, the following paradox is now apparent. Ion channel dynamics can be approached by the fluctuating rate model ([4], see [8] for a more elaborate treatment) and neuron firing dynamic by the threshold model [12]. On the other hand, neuron firing events, which are dissipation optimized, are collective phenomena of ion channel opening events, which have poor dissipation performance. It is clear that the dissipation, produced by ion channel transient opening/closing events, adds up to give the overall dissipation during neuron firing. Therefore, the nontrivial question is how a system can be optimized for dissipation while its elements seem to be not. The possible solution of this paradox is that during pulse generation ion channels act cooperatively because of a strong positive feedback via the membrane potential of the excitable nerve cell.

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