

Activity Driven Adaptive Stochastic Resonance

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(Received 13 February 2002; published 27 March 2003)

Cortical neurons *in vivo* show fluctuations in their membrane potential of the order of several millivolts. Using simple and biophysically realistic models of a single neuron we demonstrate that noise induced fluctuations can be used to adaptively optimize the sensitivity of the neuron's output to ensembles of subthreshold inputs of different average strengths. Optimal information transfer is achieved by changing the strength of the noise such that the neuron's average firing rate remains constant. Adaptation is fast, because only crude estimates of the output rate are required at any time.

DOI: 10.1103/PhysRevLett.90.120602

PACS numbers: 05.40.-a, 87.10.+e

Neurons often behave as threshold elements, which transmit information only when their membrane potential—driven by their inputs—crosses a certain threshold value. Input signals, which are too weak to sufficiently increase the membrane potential, are lost. One way to amplify weak inputs, however, is to add noise with a proper variance to the signal: Fluctuations of the membrane potential may lead to threshold crossings and to output spikes. Any modulation of the otherwise subthreshold input signals then leads to a modulation of the probability of generating these spikes and can be observed as a change in the neuron's output rate. If the fluctuations are too strong, signal transmission deteriorates. This phenomenon is called *stochastic resonance* (SR) (see [1] for a review). Stochastic resonance has been demonstrated in the context of neural systems [1–8], and there is a lively discussion in the current literature about its potential use (see, e.g., [5–7]). One basic cornerstone of an understanding of the role of SR in neural systems is the problem of adjusting the optimal level of noise. *Is there a simple way for a single neuron to calculate the proper noise level for a given ensemble of input signals, and would it be feasible for a neuron to adjust the noise level if the input is changing?* Using an abstract as well as a biophysically realistic neuron model we show that as long as the variance of the noise remains optimally adapted to the average strength of the inputs, the neuron's average output rate is approximately constant and independent of the ensemble of input signals. This suggests a simple adaptation principle for the neuron to properly adjust the variance of the noise: *The synaptic conductances of the noise inputs are strengthened if the neuron's average firing rate is below its target value and weakened otherwise.* Activity dependent weight regulation of this kind has been advanced in various theoretical and experimental studies [9–12].

Let us begin with the investigation of an abstract, but generic, model of a single neuron. We assume that all input spikes are generated by a Poisson process, and we describe the spike input by an instantaneous rate λ_s (for

the signal inputs) or λ_n (for the noise inputs). The rate λ_s is supposed to be low, so that the average membrane potential of the neuron remains subthreshold. The signal is “amplified” by the noise inputs which are assumed to be *balanced*; i.e., they consist of inhibitory and excitatory inputs with equal strength on average (for a more detailed discussion of balanced inputs to neurons see, e.g., [13]).

Signal and noise inputs are coupled to this model neuron via total synaptic weights w_s (signal) and w_n (noise). If the total rate of incoming spikes is large and the individual weights are small, the dynamics of the membrane potential is then given by an Ornstein-Uhlenbeck process with drift

$$\mu = w_s \lambda_s, \quad (1)$$

diffusion

$$\sigma^2 = w_n^2 \lambda_n \quad (\text{because } w_s^2 \lambda_s \ll w_n^2 \lambda_n) \quad (2)$$

(see [14]), and an upper absorbing boundary. Below the boundary, the evolution of the membrane potential V is governed by

$$dV(t) = \left(-\frac{V}{\tau} + \mu \right) dt + \sigma dW(t), \quad V(0) = 0, \quad (3)$$

where τ is the time constant and dW is the infinitesimal increment of the Wiener process. Once the membrane potential reaches a given value θ , the event is called a spike and the voltage is reset to $V_0 = 0$. A signal input μ is subthreshold if $\mu\tau < \theta$ and suprathreshold otherwise. The output rate, $f[\frac{\text{spikes}}{s}]$, of the Ornstein-Uhlenbeck neuron can be calculated using the expression

$$\frac{1}{f} = \tau \int_0^\infty du e^{-u^2} \frac{e^{(2y_\theta u)} - e^{(2y_r u)}}{u}, \quad (4)$$

where $y_\theta = (\theta - \mu\tau)/\sqrt{\sigma^2\tau}$, $y_r = (V_0 - \mu\tau)/\sqrt{\sigma^2\tau}$ (see [15]). Figure 1(a) shows the frequency-current (f - I) curve according to Eq. (4).

In order to quantify information transmission in single neurons, Stemmler introduced a simple expression for a

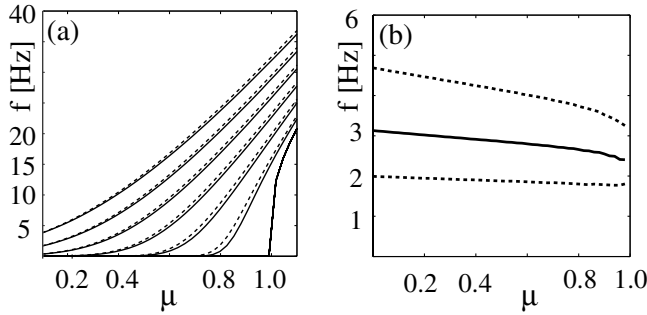


FIG. 1. (a) Output rate f [Hz] as a function of the input μ (f - I curve) for increasing values of $\sigma = 0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$. μ and σ are given in units of $\frac{\tau}{\theta}$ and $\sqrt{\tau}/\theta$, respectively. Solid lines: f - I curves according to Eq. (4). Dashed lines: f - I curves including signal dependent noise, $\sigma^2 = w_s^2 \lambda_s + w_n^2 \lambda_n = w_s \mu + w_n^2 \lambda_n$ with $w_s = 0.02$, as in [20]. $\mu = 1$ corresponds to the threshold, $\tau = 20$ ms, $\theta = 30$ mV. (b) Solid line: Optimal output rate f vs μ . For each μ , σ is adjusted such that J , Eq. (5), is maximal. Dashed line: f as a function of μ with σ adjusted such that J equals 95% of the maximum possible value for each μ . Parameters as in (a), $T = 200$ ms.

lower bound J on the Fisher information [16]. The Fisher information quantifies how well parameters of a data generating model can be inferred from the data (for an introduction, see, e.g., Ref. [17]). In spite of its being an approximation, it is shown numerically in [16] that the optimal noise level calculated from

$$J(\mu) = \frac{4T}{\sqrt{(\tau^3 \pi)}} \frac{(\theta - \mu\tau)^3}{\sigma^5} e^{(\theta - \mu\tau)^2 / \sigma^2 \tau} \quad (5)$$

deviates only negligibly from the one that would have resulted from the use of the mutual information [18,19] between the (Gaussian) spike count distribution and the distribution of small deviations from μ , for all sub-threshold μ . This property allows us to cover the whole parameter regime of interest, using only the simple expression Eq. (5), without the need to calculate the second moment of the first-passage-time density near the threshold for low noise, which is notoriously difficult (see, e.g., comments in [20]).

Figure 1(b), solid line, displays the output rate f vs μ using a noise level which maximizes J , Eq. (5), for every μ . The dashed lines correspond to output rates which belong to noise levels such that $J = 0.95J^{\max}$. Note that the output rate at the optimal noise level is almost a constant with respect to changing signal intensity. Because of the broad maximum of J , performance is only slightly degraded in case of a suboptimally chosen output rate.

It is far from trivial whether the above demonstrated property of the abstract single neuron model carries over to real neurons. In order to provide stronger evidence we employ an electric circuit model of a neuron, a so-called

Hodgkin-Huxley-type model, where we now use conductance rather than current noise, which is biologically more realistic. Models of this kind are highly successful in describing experimental data (for an introduction see [21]).

The dynamics of the membrane potential V is given by

$$C_m \frac{dV}{dt} = -I_{\text{leak}} - I_{\text{Na}} - I_{\text{Kd}} - I_M - I_{\text{syn}} + I_{\text{app}}. \quad (6)$$

The left-hand side of the equation describes the influence of the membrane's capacitance, while all ionic currents through the cell's membrane are summed on the right-hand side. I_{Na} and I_{Kd} are the sodium and potassium currents through the membrane, which are responsible for the neuron's ability to produce a spike. I_M is a potassium current typical for cortical pyramidal cells and I_{leak} summarizes all other (unspecific) currents through the membrane. Any incoming spike also causes a change in the conductance of the neuron's membrane. This causes currents flowing through the membrane, which are summarized in the total synaptic current I_{syn} . I_{app} , finally is the applied signal current.

I_{syn} is responsible for the noise input,

$$I_{\text{syn}} = g_e(t)(V - E_e) + g_i(t)(V - E_i). \quad (7)$$

It is mediated by time dependent excitatory [$g_e(t)$] and inhibitory [$g_i(t)$] conductances which change as a result of the incoming spikes. E_e and E_i are the reversal potentials of the excitatory and inhibitory synapses. The effect of the incoming spikes of the noise inputs is not modeled in detail, but effectively described by an Ornstein-Uhlenbeck process, as in [22],

$$dg_{e,i}(t) = -\frac{1}{\tau_{e,i}} [g_{e,i}(t) - \bar{g}_{e,i}(t)] dt + \sigma_{e,i} dW, \quad (8)$$

where $\bar{g}_{e,i}$ are average conductances, $\tau_{e,i}$ are time constants, and dW is the infinitesimal increment of the Wiener process. Parameters are given in the Appendix. They were chosen to match basic properties of cortical pyramidal cells; see [22].

In this more realistic model the notion of balanced input is not as straightforward as in the abstract model. Balance requires excitation and inhibition to be the same on average. According to Eq. (7), this is possible only for a fixed voltage V . For any other average membrane potential the input is not totally, but partly balanced. For the given neuron model balance would be achieved at the voltage threshold at $\bar{g}_i/\bar{g}_e = 2.4$. In the following, however, we choose a ratio of $\bar{g}_i/\bar{g}_e = 3.1$, which corresponds to balanced conditions for 3.5 mV below threshold and is a realistic value in the sense that the membrane potential of cortical pyramidal cells is often seen close below the threshold; see [23]. Figure 2(a) displays the frequency-current curve for the above choice of parameters for different noise conditions.

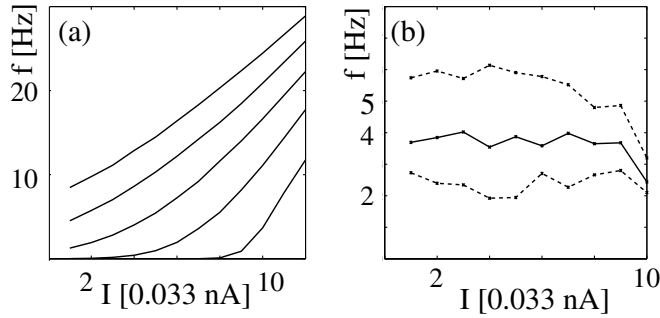


FIG. 2. (a) Output rate as a function of the “signal” input current for five different levels of noise. Different noise conditions due to a change of the conductances by a (gain) factor α , $\alpha \times (\bar{g}_e, \bar{g}_i)$, are modeled by a corresponding change in the standard deviations $\alpha \times (\sigma_e, \sigma_i)$; here $\bar{g}_e = \alpha \times 0.01 \mu\text{S}$, $\bar{g}_i = \alpha \times 0.032 \mu\text{S}$, $\sigma_e = \alpha \times 0.003 \mu\text{S}/\sqrt{\text{ms}}$, $\sigma_i = \alpha \times 0.0085 \mu\text{S}/\sqrt{\text{ms}}$, with $\alpha = 0.35, 0.75, 1.15, 1.55, 1.95$. The current threshold is at 0.33 nA. (b) Solid line: *Optimal* output rate as a function of the “signal” input current. The level of noise was always chosen such that information transmission was optimal. Dashed lines: output rate at noise levels that give 95% of the performance, in terms of d , compared to the optimal case.

For the evaluation of signal transmission in the Hodgkin-Huxley–type model we choose the discriminability d ,

$$d = 2 \frac{\mu_N(\mu + \Delta\mu) - \mu_N(\mu)}{\sigma_N(\mu + \Delta\mu) + \sigma_N(\mu)}. \quad (9)$$

The discriminability is calculated from the average (output) spike count (μ_N) and the spike count variability (σ_N^2) for mean inputs μ and $\mu + \Delta\mu$, and relates to J , as $d = \Delta\mu\sqrt{J}$ for small $\Delta\mu$; see [16].

In Fig. 2(b) the output rate at the noise level which maximizes the discriminability d is plotted versus the injected current (solid line). Like in the abstract model, the “optimal” output rate is constant over a wide range of average signal inputs. The dashed lines indicate the output firing rates in the case of suboptimally adjusted noise; here the noise is adjusted to yield 95% performance in terms of the optimal value of d . Thus the width of the maximum in d is fairly broad. The resulting *optimal* frequency is ≈ 4 Hz, which is close to the spontaneous activity of cortical neurons.

If the noise level is optimized for a certain signal strength, it is guaranteed that the discriminability for small deviations from this input intensity is maximal. Input statistics may change with time, thus the optimal noise level may have to change as well. Here we consider a scenario in which the mean input intensity may change with time. Signals are then considered to be small deviations from this mean; time scale and statistics (of the changing mean) are assumed to be such that one noise level may be optimal for many signals. Adaptation to the

mean of a signal distribution is common in nature; see, e.g., contrast adaptation [24].

The low optimal output rate immediately leads to two questions: (i) Can a neuron use such a low output rate to adapt to new stimulus distributions without averaging for unrealistically long time intervals? (ii) Would a readout mechanism be able to infer the existence of a signal within a reasonable time?

The latter depends on the number of neurons receiving correlated (signal) input. The performance for single neurons would be poor. In populations (sizes go up to some hundred neurons per population [25]) the performance can be arbitrarily good.

Figures 3(a)–3(e) demonstrate that adaptation to some mean input intensity is possible well within biologically realistic time scales. The figure shows the dynamics of adaptation of the noise level for a single model neuron to three different mean input intensities. Adaptation is based on an estimate f_{est} of the average output activity

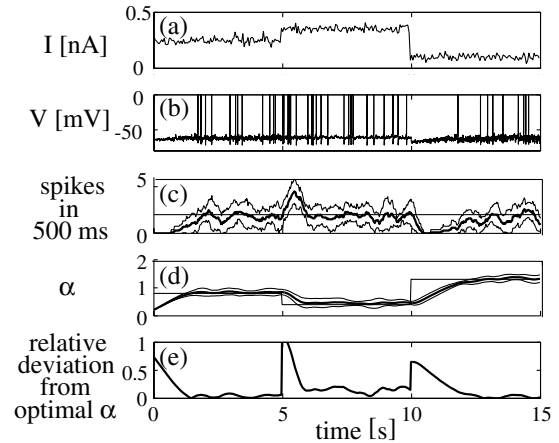


FIG. 3. Demonstration of adapting the noise level. There are three distinct time scales: Fast membrane potential fluctuations according to Eq. (8), “signal” inputs changing every 50 ms, such that many “signals” correspond to deviations from the same mean, and adaptation of the noise level on the slowest time scale. (a) Brief “signal” current injections, I_{app} , of duration 50 ms, randomly drawn from normal distributions with mean 0.25, 0.35, 0.1 nA (left to right) and variance 0.0005 nA^2 , one every 50 ms. (b) Example of a voltage trace of the Hodgkin-Huxley model, Eq. (6), as a consequence of current injections and adaptation. (c) Estimated output rate f_{est} , based on a 500 ms average of the recent past; f_{est} is evaluated every 25 ms. Thick line: mean over 10 independent runs; thin lines: corresponding standard deviations; straight lines: $f_{\text{opt}} = 4$ Hz. (d) Noise amplification α (see caption of Fig. 2), according to Eq. (10), with $\epsilon = 0.007$. The update occurs in the same time step as f_{est} is evaluated, every 25 ms. Thick line: mean over 10 independent runs. Thin lines: corresponding standard deviation. Straight line: optimal noise amplification (with respect to mean of stimulus distribution) $\alpha_{\text{opt}} = 0.8, 0.4, 1.3$ (left to right), changing every 5 s according to stimulation. (e) Relative deviation from optimal noise level: $\frac{|\alpha_{\text{opt}} - \alpha|}{\alpha_{\text{opt}}}$.

calculated from the number of output spikes in the preceding 500 ms. The synaptic conductances of the noise inputs are strengthened if the neurons average firing rate is below the optimal output activity f_{opt} and weakened otherwise. The simplest possible (formal) update rule for the noise amplification parameter α is given by

$$\delta\alpha(t_n) = \epsilon[f_{\text{opt}} - f_{\text{est}}(t_n)]; \quad n \text{ is integer}, \quad (10)$$

where ϵ determines the time scale for adaptation and α determines the variance of the membrane potential (see caption of Fig. 2). At times t_n , f_{est} is evaluated and the update applies. As can be seen in Fig. 3(d), the neuron succeeds in adapting the noise level to different signal distributions well within approximately 2 s, despite a low output rate. An adaptation time of 2–3 s is well within realistic time scales [24].

Until now we have focused on the subthreshold regime, but would an adaptation rule similar to Eq. (10) make sense in case of suprathreshold stimuli? Suprathreshold stimuli result in output rates that are higher than the optimal rate in the stochastic resonance regime. As a consequence, the noise level would be reduced as much as possible such that suprathreshold inputs are not disturbed by (unnecessary) additional noise.

In summary, we have demonstrated that the optimal noise level, in terms of information maximization, is a function of the average output rate of a neuron, a measure that is readily available everywhere within each single neuron. We showed, using an abstract but generic model, that the spike rate at the optimal noise level depends only weakly upon the average strength of the signal distribution, and we demonstrate that these results carry over to a biophysically more plausible framework. Hence simple mechanisms which stabilize a neuron's output rate may be sufficient to adjust the noise level in order to optimally exploit the phenomenon of stochastic resonance in the nervous system.

The authors thank T. Hoch, L. Schwabe, and O. Shriki for fruitful discussions. This work was supported by Wellcome Trust (061113/Z/00) and DFG (SFB 618). Part of the work was done while G.W. was a participant of the *EC Advanced Course in Computational Neuroscience*.

Appendix.—Electric circuit models, model details, and parameters:

$$\begin{aligned} I_{\text{leak}} &= g_{\text{leak}}(V - E_{\text{leak}}), & I_{\text{Na}} &= \bar{g}_{\text{Na}} m^3 h(V - E_{\text{Na}}), \\ I_{\text{Kd}} &= \bar{g}_{\text{Kd}} n^4 (V - E_{\text{K}}), & I_{\text{M}} &= \bar{g}_{\text{M}} p(V - E_{\text{K}}), \\ C_m &= 1 \mu\text{F}/\text{cm}^2, & g_{\text{leak}} &= 0.045 \text{ mS}/\text{cm}^2, \\ E_{\text{leak}} &= -80 \text{ mV}, & E_e &= 0 \text{ mV}, & E_i &= -75 \text{ mV}, \\ \tau_e &= 2.7 \text{ ms}, & \tau_i &= 10.5 \text{ ms}. \end{aligned}$$

All simulations were performed in the NEURON simulation environment [26]. The model neuron's code is available from <http://senselab.med.yale.edu/senselab/>.

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