Adaptive Regulation for Noise-Aided Weak Signal Detection in Spiking Neurons *

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Spiking neurons usually change their membrane properties, especially ion channel activity, during adaptation or synaptic modification to improve information processing and transmission. Using simple and biophysically realistic models, our analyses reveal that activity-dependent regulation of membrane properties contributes to sensitivity adaptation that improves the neuron ability of detecting sub-threshold signals in the presence of background noises. The improvement is achieved by regulating the conductance of ion channels on the membrane, dependent on the neuron firing activity.

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Noise-aided signal detection has been well documented in the past two decades since it was first proposed in meteorological research and termed as "stochastic resonance" (SR).[1] Apart from numerous theoretical analyses, there are also many reports for SR phenomena observed in biological systems, from single neurons to cerebral neural networks, for a review see Ref. [2]. Among the literature dealing with SR in biological systems, the neurons or neural networks were treated as passive nonlinear systems in most cases, i.e., the intrinsic properties of the system were invariant. However, it has been revealed that most biological systems are highly adaptive and flexible, with modifiability being one of the fundamental characteristics.[3,4]

In the present study, we demonstrate that the regulation of ion-channel activity could contribute to the modification of the sensitivity of a spiking neuron and probably improve its ability for signal detection.

In the classic Hodgkin–Huxley (H-H) equations,[5]

$$\begin{aligned} C_i dv/dt &= -g_{\rm Na}(v-v_{\rm Na}) - g_{\rm K}(v-v_{\rm K}) \\ &\quad - g_L(v-v_L) + I(t) + \xi(t), \\ g_{\rm Na} &= \bar{g}_{\rm Na} m^3 h, \\ g_{\rm K} &= \bar{g}_{\rm K} n^4, \\ dx/dt &= \alpha_x(v)(1-x) - \beta_x(v)x, \quad x = m, h, n, \end{aligned} \tag{1}$$

where C_i is the membrane capacitance, v represents the membrane potential; $I(t)$ is the input signal; $\xi(t)$ is a noise term; $v_{\rm Na}$, $v_{\rm K}$, and v_L are respectively the equilibrium potentials for sodium, potassium and leakage currents, which are constant; m, h, and n are the variables representing processes such as sodium channel activation, sodium channel inactivation, and potassium channel activation, respectively; g and $\overline{g}$ denote the channel conductance and maximal conductance respectively; α and β are the rate variables describing each dynamic process, which are voltage dependent and take the following forms:

$$\begin{aligned} \alpha_m &= \frac{0.1(v+40)}{1-\exp[-(v+40)/10]}, \\ \beta_m &= 4\exp[-(v+65)/18], \\ \alpha_h &= 0.07\exp[-(v+65)/20], \\ \beta_h &= \frac{1}{1+\exp[-(v+35)/10]}, \\ \alpha_n &= \frac{0.01(v+55)}{1-\exp[-(v+55)/10]}, \\ \beta_n &= 0.125[-(v+65)/80]. \end{aligned}$$

Here the membrane potential and rate constants are in units of mV and $\rm ms^{-1}$, respectively.

Following these equations, the neuron output can be calculated and the power spectral density (PSD) of the output spike train is computed. In the present study, the signal-to-noise ratio (SNR) of the system output was measured to be $10\log_{10}(S/B)$, where S is the PSD value at the input signal frequency f_i and B is the level of background noise at that frequency.[6–8]

We first used Eq. (1) for calculation, with all model parameters following the ones introduced in the classic Hodgkin–Huxley equation: $C_i = 1.0\,\mu\rm F/cm^2$, $\overline{g}_{\rm Na} = 120\,\rm mS/cm^2$, $v_{\rm Na} = 50\,\rm mV$, $\overline{g}_{\rm K} = 36\,\rm mS/cm^2$, $v_{\rm K} = -77\,\rm mV$, $g_L = 0.3\,\rm mS/cm^2$, $v_L = -54.4\,\rm mV$. Since the nervous system is full of noises caused by transmitter release, ion channel activity changes, etc., which can be equivalently modelled as a Gaussian white noise with zero mean:

$$\begin{aligned} &\langle \xi_i(t) \rangle = 0, \\ &\langle \xi_i(t_1)\xi_j(t_2) \rangle = \sigma^2 \delta_{ij}\delta(t_1 - t_2), \end{aligned}$$

where $\langle \cdots \rangle$ represents the ensemble average over the noise distributions and σ^2 indicates the noise intensity as deviation. The stimulus current applied in this study therefore included two components: a periodic input signal $I(t) = A_i \sin(2\pi f_i t)$ with A_i and f_i being its amplitude and frequency respectively, together

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with a zero-mean Gaussian white noise $\xi(t)$. The parameters for the sub-threshold periodic stimulus $I(t)$ were chosen arbitrarily such that $A_i = 1.1\,\mu\mathrm{A/cm^2}$ and $f_i = 40\,\mathrm{Hz}$. The standard deviation (STD) σ of the applied noise sequence was chosen at reasonable levels (ranging from a minimum value of 1.8 to a maximum of 17.6).

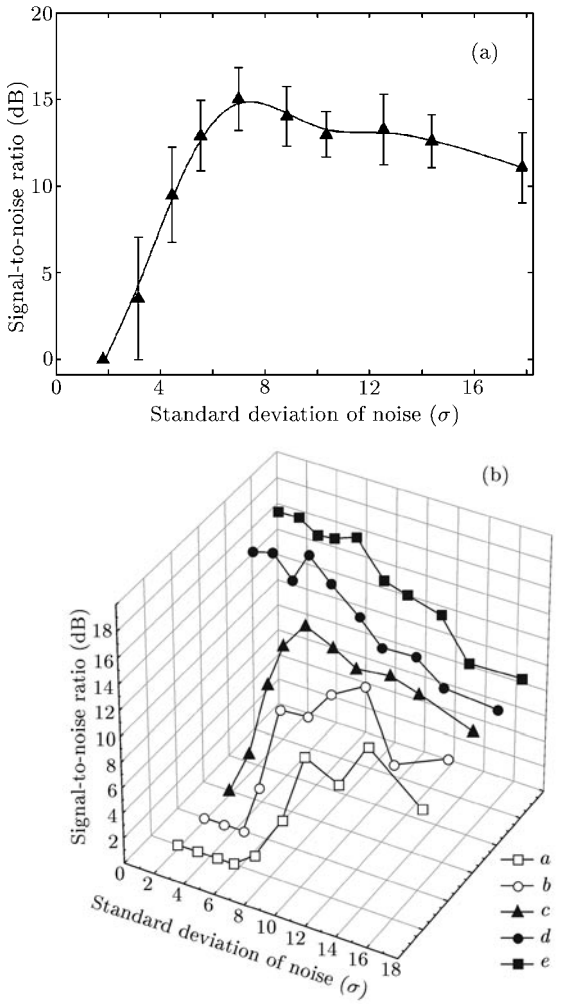

Fig. 1. (a) The relationship between the noise intensity and the model neuron SNR. (b) The relationship between the neuron SNR and the noise intensities with various regulations of g_{Na} and g_{K}, where curve c is the same as the one in (a).

Figure 1(a) illustrates the relationship between the output SNR and the intensity σ of noise added (ten different levels of noise intensity were applied, and twenty noise sequences were applied for each intensity level to provide averaged SNR values (mean $\pm$ STD)). Obviously, there is an optimal noise level ($\sigma \approx 7.0$) for aiding weak signal detection which is consistent with the previously reported stochastic resonance phenomena in classic H–H model[8] and also other neuronal model systems.[6,7]

Biological systems are highly adjustable, and neuronal responses to stimulation generally show significant adaptation, being characterized by membrane activity changes.[3] A key issue in this study is that conductances of the ion channels are not constant, but rather changeably depending on both the membrane potential and neuron's firing behaviour:[3]

$$g'_{\mathrm{Na}} = p(r) \cdot \overline{g}_{\mathrm{Na}}, \quad g'_{\mathrm{K}} = q(r) \cdot \overline{g}_{\mathrm{K}}, \tag{2}$$

where $p(r)$ and $q(r)$ both are the functions of firing frequency, indicating that the conductances of the ion channels are dependent on activity, and can be defined as 100% in general conditions and have variation within a certain range when relevant regulatory processes occur.[4] In order to investigate the effect of membrane conductance changes on neuron's sensitivity in signal detection, we chose to modify the conductance of sodium and potassium channels within the physiological range.[9] Because increasing sodium conductance generally lowers the neuron threshold for discharge and increasing potassium conductance should have exactly the opposite effect, we chose to modify these channel conductances in opposite directions for simplicity. The maximum changes of conductance regulation is defined as $p(r) = 120\%$ and $q(r) = 80\%$ and vice versa, considering the experimental results of Desai *et al.*[9] The corresponding neuron performance for signal detection is clearly shown in Fig. 1(b), in which the maximal value of SNR decreases with its peak shifting towards higher noise level when sodium

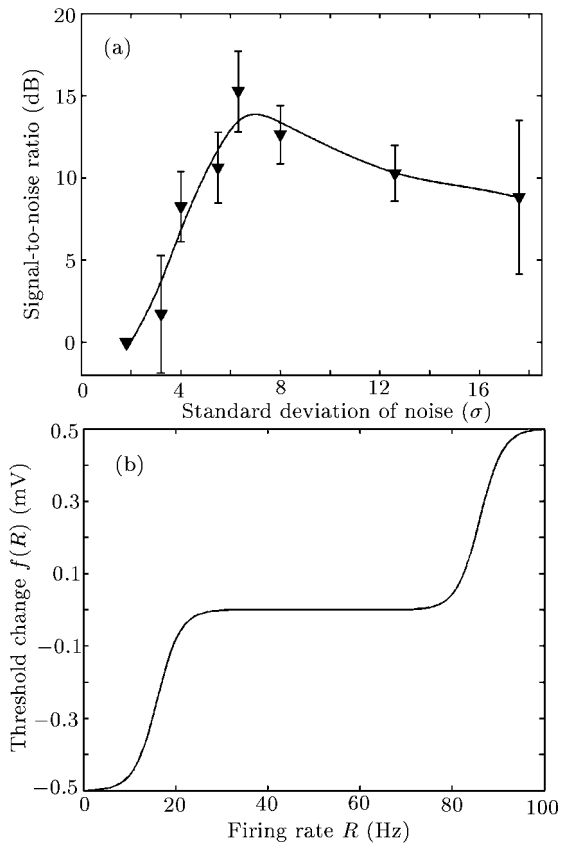

Fig. 2. (a) The relationship between noise level and SNR in an I-F neuron response. (b) The double-sigmoid function (Eq. (5)) describing the relationship between the threshold modification $\Delta\theta$ and the system firing rate R.

channel activity is suppressed and potassium channel activity is enhanced ($p(r) = 80\%$ and $q(r) = 120\%$ curve a, $p(r) = 90\%$ and $q(r) = 110\%$ curve b, compared to $p(r) = q(r) = 100\%$ of curve c in Fig. 1(b)), where curve c is the same as the one shown in Fig. 1(a). On the other hand, SNR increases and shifts towards lower noise level side when sodium channel activity is up-regulated with potassium channel activity being down-regulated ($p(r) = 110\%$ and $q(r) = 90\%$ curve d, $p(r) = 120\%$ and $q(r) = 80\%$ curve e, in Fig. 1(b)). This result indicates that the modification of neuron's membrane properties can potentially regulate the neuron ability for weak signal detection, which supports that the neuronal system can be adjusted to an optimal sensitive state for signal processing through the property modulations.[8]

In order to further illustrate the effect of activity-dependent regulation processes on neuron's signal detection performance, we construct a simple model which employs a classic integrate-and-fire (I-F) model with an additional firing-activity-dependent feedback component for the threshold regulation. In the traditional leaky integrate-and-fire model, the neuron behaviour can be described by[10]

$$C_s \frac{dv}{dt} = -g \cdot v + S(t) + \xi(t), \tag{3}$$

where C_s is the cell membrane capacitance, v is the membrane potential, $g \cdot v$ is the leakage term (g is the conductance), $S(t)$ is the input signal, and $\xi(t)$ again is a zero-mean Gaussian white noise with a standard deviation of σ. Once the membrane potential reaches its threshold θ, an action potential is fired and the membrane potential will then quickly return to its resting value V_e, which is set to be zero in this study, for simplicity. We add an activity-dependent feedback system for threshold regulation, which can be described by

$$\Delta\theta = f(R), \quad \theta_{n+1} = \theta_n + \Delta\theta, \tag{4}$$

where R is the neuron firing rate, and $\Delta\theta$ is the magnitude of the threshold change.

In this study, parameters for the original I-F model described by Eq. (3) are such that $C_s = 1.0\,\mu\mathrm{F/cm^2}$, $g = 1.0\,\mathrm{mS/cm^2}$. $A_s = 0.5\,\mu\mathrm{A/cm^2}$, $f_s = 40\,\mathrm{Hz}$ are chosen for the sub-threshold input $S(t) = A_s \sin(2\pi f_s t)$. Initial threshold potential was set to be a fixed value $\theta_0 = 3.0\,\mathrm{mV}$. Figure 2(a) illustrates the system ability to detect a sub-threshold periodic signal $S(t)$ in the presence of noise (eight different levels, twenty repeats for each), when the neuron spiking threshold is fixed.

Equation (4) is then introduced in to describe this regulation via a firing-rate-dependent mechanism. The relationship between the threshold modification $\Delta\theta$ and the system firing rate R is defined using a sigmoid function (Eq. (5)) as shown in Fig. 2(b). We propose that the system threshold will be elevated when the neuron firing rate exceeds 70 Hz, and it is lowered in the case that the firing rate is less than 30 Hz. For simplicity, this threshold level was renewed every 500 ms in our calculation.

$$f(R) = \begin{cases} 0.5/(\exp((-R+15)/2.5+1) - 0.5, & R \le 30, \\ 0, & 30 < R < 70, \\ 0.5/(\exp((-R+85)/2.5)+1), & R \ge 70. \end{cases} \tag{5}$$

Figure 3(a)–3(h) demonstrate this adaptive regulatory process in the system signal detection behaviour when $S(t)$ is given in the presence of noises with $\sigma_1 = 3$ and $\sigma_2 = 8$ respectively. Comparison is made between the original and modified I-F models, for the detection of signal $S(t)$, in exposure to various noise levels. As illustrated in Fig. 4(a), the activity-dependent modification of threshold significantly improves the model detection behaviour when the additive noise is with very low intensities.

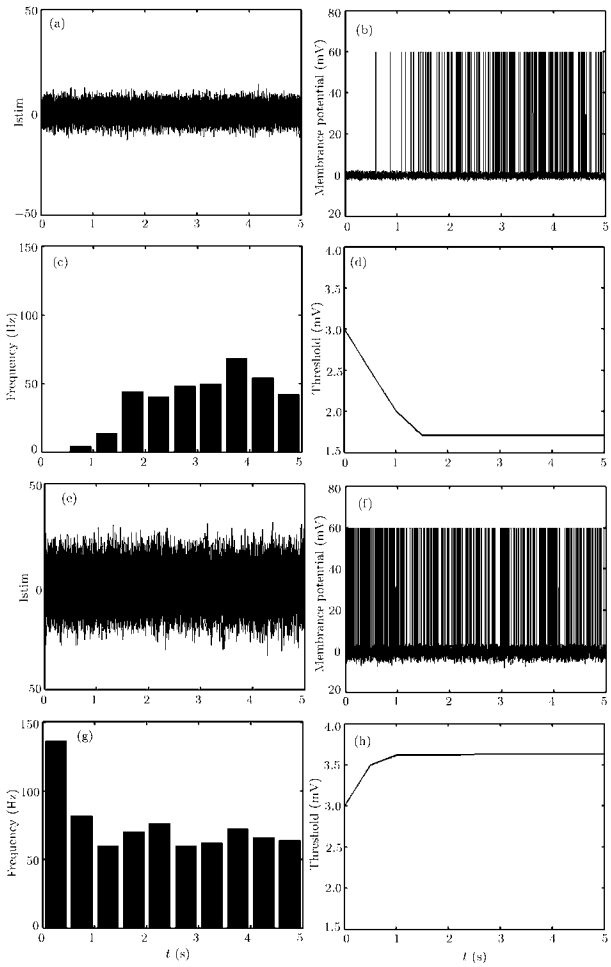

Fig. 3. The adaptive regulation process in the system detection of signal $S(t)$ in the presence of noises. (a) The stimulus signal $S(t)$ in the presence of noise with $\sigma_1 = 3$; (b) 5-s data of the cell spiking response to the signal presented in (a); (c) the spiking histogram with time bin being 500 ms; (d) the neuron discharge threshold change in the investigated time interval, which is adjusted based on the firing rate for every 500 ms; (e)–(h) the corresponding aspects for neuron response to stimulus signal $S(t)$ in the presence of noise with $\sigma_2 = 8$.

It is previously proposed that voltage-dependent

conductances might have adaptive changes to maximize the information encoded by neuronal activities.[11] Wenning and Obermayer[12] have proposed one kind of adaptive stochastic resonance in which they construct a firing-rate-dependent feedback mechanism to regulate the input synaptic noise. Optimal information transfer is achieved by changing the strength of noise such that the neuron average firing rate is kept to be constant.[12] In this study, by introducing in adaptive changes of channel conductance and the consequent spiking threshold, we demonstrate that neurons tend to improve its responsibility to weak signals in changing environment.

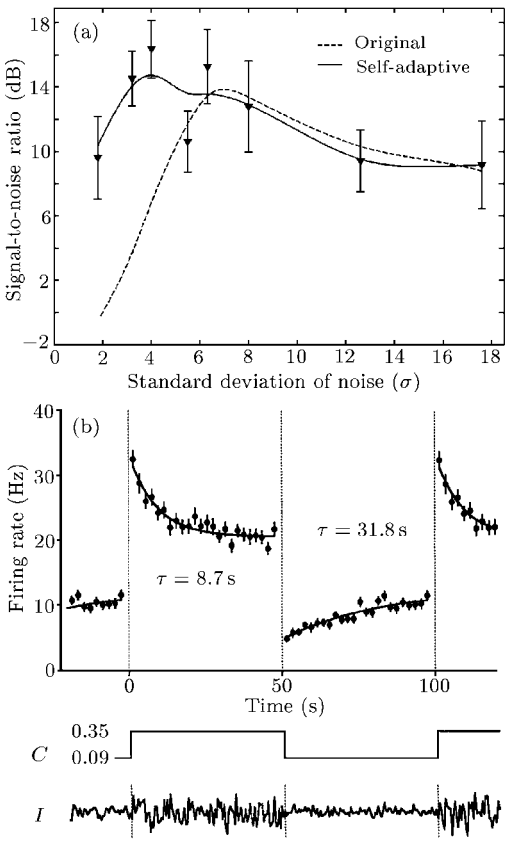

Fig. 4. (a) Comparison between the original (dashed line) and modified (solid line) I-F models, for the detection effects of signal $S(t)$ in the presence of various noise levels. (b) Firing rate of a retinal ganglion cell under flicker stimulation (taken from Ref. [13]), alternating every 50 s between contrast values of 0.09 and 0.35, here τ is the decay time constant of firing rate. The curve in the middle of (b) shows the time course of contrast C, and the bottom curve demonstrates the time course of flickering intensity I. This sensitivity regulation in the retinal ganglion cell has been suggested to be dependent on the ion channel activity change.

Adaptation is one of the general properties of sensory system, from single neuron to neural network, even to higher perception level. The bidirectional regulation mechanism proposed here has been observed in retina[13−15] and other preparations.[4,9] One possible underlying mechanism may involve Ca^{2+}-dependent dynamical modification exerted on relevant channels properties.[4] In the present study, firstly we show that the modulation of ion channel conductance can regulate the neuron ability for weak signal detection and we further illustrate that this kind of modification could be achieved by neuronal firing-activity-dependent feedback, in a self-adaptive manner. Physiological observations show that, given a stimulus of high noise level, the retinal neuron will decrease its firing activity and sensitivity during adaptation process (see Fig. 4(b), taken from Ref. [13]), which is similar to the activity-dependent modification proposed in our adapted I-F model (Figs. 3(e)–3(h)). When the retina is stimulated with a lower noise level, the retinal neuron will gradually increase its firing activity by increase its sensitivity, which is consistent with the process plotted in Figs. 3(a)–3(d) of our model. Our present results suggest that this process may greatly improve the system ability for weak signal detection (see Fig. 4(a)). These results were consistent with the theory of the functional role that visual adaptation optimizes the information transmission.[16]

Taking together, the results of this study suggest that the sensory system may employ the internal and external noises to help to detect the weak periodic stimulation, in a self-adaptive manner. Furthermore, this study could help to extend our understanding for some stochastic resonance phenomena observed in the sensory system, and the biologically inspired detection mechanism presented may also give some new insights in the development of intelligent signal detection instruments.

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