Signal Size Detection by Noisy Neurons

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Abstract

Signal transmission ability of stochastic model neurons is examined. Neurons with finite number of Markov ion channels are modeled and their input-output relationship are recorded. Based on the formulae obtained, reconstruction of unknown inputs from the output sequence of a neuronal population is carried out. The back-estimation shows a very good agreement with the actual input, and then it is concluded that a stochastic neuronal population can detect not only the signal timing but also the signal size.

Key words: Noise, Markov channel model, Temporal dynamics, Population coding, Stochastic resonance

1 Introduction

Noise is a sort of stochastic agitation which usually causes unwanted effects and is considered as a disturbance. However, recent studies have revealed that this villain can act as a supporter of dynamical systems by improving the signal detection ability. This phenomenon is called stochastic resonance (SR) and now observed in a broad range of areas including neuroscience [1][2].

There are three major sources of neuronal noise : thermal agitation, synaptic activity, and ion channel stochasticity [3]; the former two are external and the last one is internal. There have been quite a large number of studies corresponding noisy neurons [2][4][5][6][7]. Strassberg & DeFelice [4] compared the Markov channel model with the average conductance model and showed that the prediction of deterministic and continuous average models diverges from the prediction of the stochastic and discontinuous Markov channel models for small membrane patches.

Schneidman and colleagues [5] studied the effect of the channel stochasticity to the signal detection performance. They employed a model having an ensemble of fluctuating ion channels and showed that a stochastic neuron can respond, with high precision, to varying inputs. And then they concluded that stochastic neurons act as "smart" encoders using the inherent channel noise.

In this paper, we compare stochastic model neurons having finite number of ion channels with deterministic neurons and examine the signal detecting performance of a stochastic neuronal population. Our simulation consists of two parts. First we see the input-output relationship by changing the channel number (or the patch area) and the signal magnitude, and obtain two formulae relating (1) the input size and the output firing probability and (2) the input size and the average response time delay. Next, by employing the formulae gotten in the first step, we try to reconstruct the unknown input from the output sequence of a neuronal population and assess the signal transmission ability. The conclusion is that a population of stochastic neurons can transfer the information of not only the signal timing but also the signal size.

2 Simulation and Results I – Input-Output Relation of Neurons

First, we investigated the input-output relationship of model neurons. The neuronal membrane patch is assumed as isopotential and modeled as a capacitor, formulated by the well-known differential equation [3][8][9]:
$C_m \frac{dV}{dt} = I_{Na} + I_K + I_{leak} + I_{external}$, where C_m denotes the membrane capacitance, V the membrane potential, t time, and I_X specific currents. Each ionic current term is a product of three components: the single channel conductance, the potential term and the number of open channels (in the continuous model, this number is replaced by the fraction of the opening channels). The channels employed here are the fast sodium channels, whose behavior is depicted by the nine-state Markov model developed by Vandenberg & Bezanilla [10], and the delayed rectifier potassium channels described by the six-state Markov model by Perozo & Bezanilla [11]. Also the continuous version derived from these Markov dynamics are simulated for a comparative study (see, for example, [8] for detailed modeling procedures).

We change the patch area (or the number of channels in the patch) and the external input current size to obtain the responsivity and response delay statistics of the neuron (these values are defined in the next section). Patch area is chosen from 5 μm^2 to 160 μm^2. Input current shape is the so-called alpha-function $I(t) = At\exp(-\alpha t)$; the parameter α is fixed to 1/0.3 (msec^{-1}), and its maximum amplitude $H = A/e\alpha$ is changed from 0.00 pA/μm^2 to 0.25 pA/μm^2. The other parameters used in the simulation are listed in the appendix. The time length of each simulation is 200 seconds and the single time step is 1 microsecond. External currents are injected at every 200 milliseconds; namely, 1000 injections for one simulation. The initial channel states are all

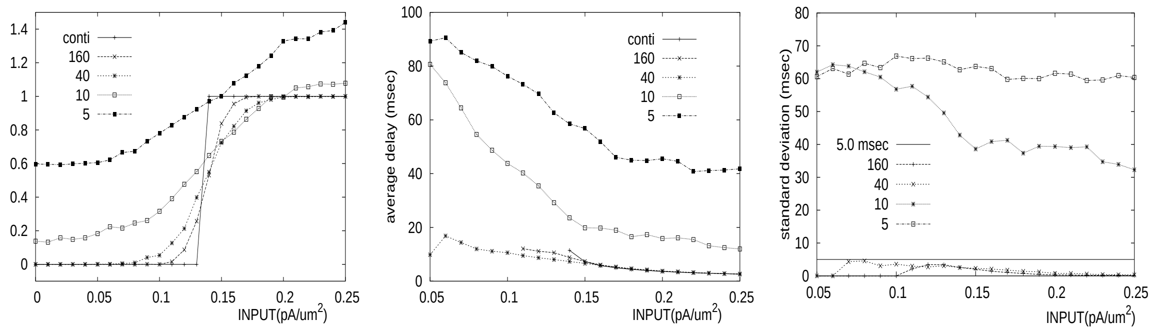

Fig. 1. **(Left)** Firing responsivity, defined as: (Total number of spikes)/(Total number of current injection times = 1000). **(Center)** Average response time delay to current injection. Response delay is defined as: (Spike generation time)-(Last current injection time). **(Right)** Standard deviation (SD) of response delay. This SD is exactly zero for the continuous model. The line numbers of each panel indicate the isopotential membrane patch area (μm^2).

closed for both sodium and potassium channels (indicated as C_1 in [10] and C_0 in [11]). The initial membrane potential is fixed at -70 mV. It should be noted that our result does not depend on these initial conditions.

The left panel of Figure 1 shows the firing responsivity of the neuron, which is defined as the fraction of total number of spikes to the total number of current injections (fixed to 1000 here). This value is a measure for '*how sensitive the neuron is*'. There are three important findings. (1) The responsivity of a stochastic neuron is positive even for subthreshold inputs which cannot cause spikes in the continuous model (as reported by [5]). (2) Smaller membrane patch generates more number of APs than input times because the potential fluctuation is large enough to make spontaneous firings. (3) The responsivity increases monotonously as the input size increases.

The average response delay, defined as the average time lag of the spike timing from the last stimuli timing, is shown in the center panel of Figure 1. We should note its monotonous decrease to the input size. The right panel of Figure 1 shows the standard deviation (SD) of the response delay. The value is below 5.0 (msec) for the membrane with 40 (μm^2) or larger patch. This means that a neuron with smaller fluctuation responds quite precisely to stimuli. On the other hand, due to the spontaneous firing, average and SD of the response delay is very large for smaller membrane patch.

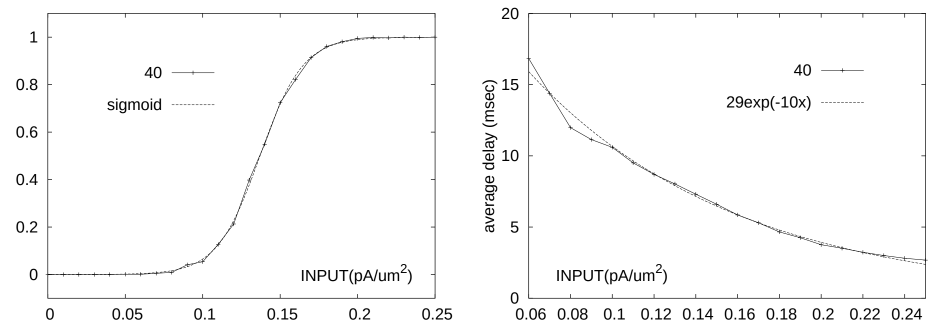

Fig. 2. **(Left)** Firing responsivity of 40(μm^2) membrane patch and approximating sigmoid function $y = 1/(1 + \exp(-72(x - 0.137)))$. **(Right)** Average response delay of 40(μm^2) membrane patch and approximating exponential function $y = 29\exp(-10x)$.

Figure 2 focuses on the response of the 40 (μm^2) membrane patch. Its responsivity shows a remarkable agreement with a sigmoidal function $y = 1/(1 + \exp(-72(x - 0.137)))$, and the average response delay is also approximated very well by an exponential function $y = 29\exp(-10x)$.

3 Simulation and Results II – Backward Estimation of Input Size and Timing

Based on the findings in the last section, we next examine the signal transmission performance of a population of noisy neurons. 100 independent neurons

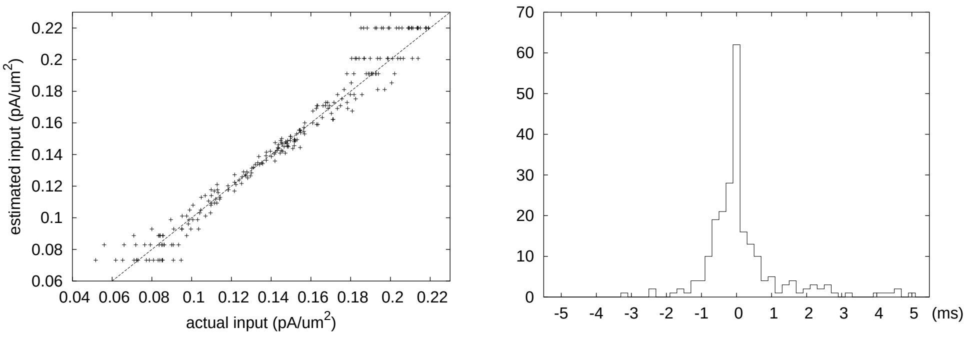

Fig. 3. **(Left)** Relationship between actual input size and estimated input size. The dashed line is $y = x$. The correlation coefficient is 0.978. **(Right)** Histogram of the difference between estimated input timing and actual input timing. Average : 0.237 (msec), SD : 1.791 (msec). The sample number is 237 for both panels. 63 inputs (out of 300) are too small to cause any spikes.

receiving the same input are simulated. Each neuron has the area of 40 μm^2, and the input current with random magnitude (0.04 to 0.22 pA/μm^2) is injected 300 times at random timing. From the output spike sequence of the population, we reconstruct the input by using the estimation procedure below. (1) Slide a time window of 20 msec and count $N(t)$, the number of spikes occurred in the window (This length of the window is set as over four times as large as the SD of the timing delay). (2) Take each local maximum of $N(t)$ as the response of the neuronal population to a input signal and estimate the signal size by the function $\tilde{I}(r)$, where $r = N(t)/100$, the fraction of firing neurons, and $\tilde{I}(r)$ is the inverse function of the responsivity, defined as 0.0 (if $r = 0.00$), $0.137 - \log(1/r - 1)/72$ (if $0.1 \leq r \leq 0.99$), 0.22 (if $r = 1.00$). (3) Calculate the average timing of the spikes in the time window and then estimate the input timing by using approximating function of the average response delay $\tilde{d} = 29\exp(-10\tilde{I})$.

The results of this simulation are shown in Figure 3. The left panel is the correlation diagram of the actual input and the estimated input calculated by the rule explained above. The correlation coefficient between actual and estimated input is 0.978. The estimation rule works very well, especially for intermediate inputs (0.12 to 0.16(pA/μm^2)). The right panel of Figure 3 is the histogram of the lag between actual and estimated input timing. This estimation error is less than 1 msec for about 80% of the cases.

4 Concluding Discussion

"When the stimulus is large enough, a neuron generates a full spike, and when the stimulus is not large enough, a neuron generates nothing" – this "all-or-none law" is true for ideal deterministic/continuous model neurons, but not true for stochastic/discontinuous model neurons and real neurons [3][9]. Our simulation showed that instead of having a clear threshold, a stochastic neuron has a response probability which monotonously depends on the stimulus size. Using this input size-output probability relationship (Fig.1 left, Fig.2 left) and input size-output delay relationship (Fig.1 center, Fig.2 right), one can estimate the input size and timing very precisely from the output spike sequence of neuronal population.

It should be noted that this back-calculation can be achieved only when we use stochastic neurons because the responsivity function of a continuous neuron is not an injective mapping and therefore it does not have a inverse function necessary for estimation rule. (A continuous neuron also has the input-delay relationship, so the input-responsivity relationship is crucial.) We do not know whether we can say this result as stochastic resonance. However, it is also a noise enhancement of signal detection performance.

A real neuron is very noisy due to both internal and external causes. Our finding implies that instead of being irritated by unavoidable noise, a neuronal population can positively employ the stochastic nature to transmit not only the signal timing but also the signal size.

A Simulation parameters

The fixed parameters used in the simulations are: membrane capacitance per area $C_m = 1\ \mu\mathrm{F/cm}^2$, Na channel density $\sigma_{Na} = 60$ channels/$\mu\mathrm{m}^2$, K channel density $\sigma_K = 18$ channels/$\mu\mathrm{m}^2$, single Na channel conductance $\gamma_{Na} = 6$ pS/channel, single K channel conductance $\gamma_K = 20$ pS/channel, maximum Na conductance per area $\bar{g}_{Na} = 36\ \mathrm{mS/cm}^2$, maximum K conductance per area $\bar{g}_K = 36\ \mathrm{mS/cm}^2$, leakage conductance per area $\bar{g}_{leak} = 0.3\ \mathrm{mS/cm}^2$, Na reversal potential $E_{Na} = +50.0$ mV, K reversal potential $E_K =$ -90.0 mV, leakage current reversal potential $E_{leak} =$ -70.0 mV.

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References

[1] K. Wiesenfeld & F. Moss, Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDs., Nature, **373**, 33-36, 1995.

[2] M. Rudolph & A. Destexhe, Do neocortical pyramidal neurons display stochastic resonance?, J. Comput. Neurosci., **11**, 19-42, 2001.

[3] W. Gerstner & W. Kistler, Spiking Neuron Models., Cambridge, 2002.

[4] A.F. Strassberg and L.J. DeFelice, Limitations of the Hogkin-Huxley formalism: Effects of single channel kinetics on transmembrane voltage dynamics., Neural Comput., **5**, 843-855, 1993.

[5] E. Schneidman, B. Freedman, & I. Segev, Ion channel stochasticity may be critical in determining the reliability and precision of spike timing., Neural Comput., **10**, 1679-1703, 1998.

[6] P.N. Steinmetz, A. Manwani, C. Koch, M. London & I. Segev, Subthreshold voltage noise due to channel fluctuations in active neuronal membranes. J. Comput. Neurosci., **9**, 133-148, 2000.

[7] G. Ashida & M. Kubo, Neuronal dynamics based on individual stochastic ion channels, in Proceedings of 9th International Conference on Neural information Processing (ICONIP'02), #1387, 2002.

[8] B. Hille, Ion channels of excitable membranes (3rd. ed.), Sinauer, 2001.

[9] C. Koch, Biophysics of computation, Oxford, 1999.

[10] C.A. Vandenberg & F. Bezanilla, A model of sodium channel gating based on single channel, macroscopic ionic, and gating currents in the squid giant axon., Biophys. J., **60**, 1511-1533, 1991.

[11] E. Perozo & F. Bezanilla, Phosphorylation affects voltage gating of the delayed rectifier K^+ channel by electrostatic interaction., Neuron, **5**, 685-690, 1990.