



# Optimal network size for Hodgkin–Huxley neurons

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## Abstract

The collective behavior of an array of coupled Hodgkin–Huxley neurons, which are subject to subthreshold signal and external noise, is investigated by numerical methods. It is found that the network size, the number of Hodgkin–Huxley neurons in the network, has an optimal value, at which the collective behavior shows the best performance. The value of the optimal network size goes up when the coupling strength increases. Such a nontrivial dependence on the network size is not found if we only consider the response of an individual neuron in the network.

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## 1. Introduction

Hodgkin–Huxley model, a standard model of a neuron, is described by the Hodgkin–Huxley equations (HHE) [1], which are the standard mathematical tools in study dynamical behavior of biologically realistic neurons. In the last two decades, great attention has been paid to the constructive effects of noise (external or internal) on this nonlinear dynamic system, either isolated or coupled together [2–7]. A lot of interesting phenomena have been found, such as stochastic

resonance (SR) [2,3], which shows that the response of a stochastic generalization of the HHE to a periodic forcing can exhibit a resonance-like dependence on the noise intensity, coherence resonance (CR) or autonomous SR [4,5], where the system may have a maximal regularity in the present of noise even without external signal, and noise induced synchronization between an applied current stimulus and the spike dynamics of a cluster of ion channels [6], and noise induced synchronization between coupled Hodgkin–Huxley neurons [7], and so on. Some effects among those mentioned above have been observed in numerous experiments, and they may be very important for the signal processing in neuron system in vivo. The study of the Hodgkin–Huxley model is still

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going on, and new phenomenon is expected to be found.

Very recently, a new and quite interesting SR-like phenomenon, system size resonance, has gained much attention [2,8–16]. So far, mainly two types of ‘size resonance’ have been reported. On one hand, for chemical oscillating reactions taking place in small scale systems, stochastic oscillations can be observed and there is an optimal system size such that the stochastic oscillations show best performance [2,8–13]. For example, it was reported that ion-channel clusters of optimal sizes can enhance the encoding of a subthreshold stimulus [2,10], and optimal intracellular calcium signaling appears at a certain size or distribution of the ion-channel clusters [11,12]. On the other hand, Pikovsky et al. showed that in an array of coupled noise-driven bistable systems subjected to an external periodic forcing, an optimal response is obtained when the number of elements in the system had an optimal value [14]. Similar effects have also been reported in Refs. [15,16]. This effect was explained by reduction to the usual phenomena of stochastic and coherence resonances with an effective noise intensity depending on the number of coupled elements. The authors of Ref. [14] speculate that one possible field of application of this system size resonance is the neuronal dynamics, in which the neuronal connections or the coupling strengths between neurons can be tuned in order to achieve maximum sensitivity to external signals.

Motivated by the biological applications suggested in [14], we expect that this kind of system size resonance can also be observed in coupled Hodgkin–Huxley neurons. Thus in the present Letter, we consider the collective dynamic behavior of an array of linearly coupled Hodgkin–Huxley neurons, each subjected to uncorrelated external noise. We show that for an optimal network size, the number of neurons, the collective behavior of the system has a maximal order. The effect of coupling strength has also been investigated.

## 2. Model and results

In this Letter, we consider an ensemble of Hodgkin–Huxley neurons, which are coupled into a one-dimensional regular network. The dynamics of the

system can be described by,

$$\begin{aligned} C \frac{dV_i}{dt} &= -g_{\text{Na}} m_i^3 h_i (V_i - V_{\text{Na}}) - g_{\text{K}} n_i^4 (V_i - V_{\text{K}}) \\ &\quad - g_{\text{L}} (V_i - V_{\text{L}}) + I + D \xi_i(t) \\ &\quad + \varepsilon (V_{i-1} + V_{i+1} - 2V_i), \\ \dot{m}_i &= \alpha_{m_i}(V_i)(1 - m_i) - \beta_{m_i}(V_i)m_i, \\ \dot{h}_i &= \alpha_{h_i}(V_i)(1 - h_i) - \beta_{h_i}(V_i)h_i, \\ \dot{n}_i &= \alpha_{n_i}(V_i)(1 - n_i) - \beta_{n_i}(V_i)n_i, \quad 1 \leq i \leq N, \end{aligned} \quad (1)$$

where  $V_i(t)$  is the transmembrane potential of  $i$ th neuron, of which the temporal evolution is governed by the first differential equation of (1).  $m_i$ ,  $h_i$ , and  $n_i$  are corresponding gating variables (probabilities) governed by two-state, ‘‘opening–closing’’ dynamics, as shown in the last three equations of (1). The experimentally determined voltage transition rates are given explicitly by the expressions

$$\begin{aligned} \alpha_{m_i}(V_i) &= \frac{0.1(V_i + 40)}{1 - \exp[-(V_i + 40)/10]}, \\ \beta_{m_i}(V_i) &= 4 \exp[-(V_i + 65)/18], \\ \alpha_{h_i}(V_i) &= 0.07 \exp[-(V_i + 65)/20], \\ \beta_{h_i}(V_i) &= \{1 + \exp[-(V_i + 35)/10]\}^{-1}, \\ \alpha_{n_i}(V_i) &= \frac{0.01(V_i + 55)}{1 - \exp[-(V_i + 55)/10]}, \\ \beta_{n_i}(V_i) &= 0.125 \exp[-(V_i + 65)/80]. \end{aligned} \quad (2)$$

$C = 1 \mu\text{F}/\text{cm}^2$  denotes the membrane capacitance per unit area;  $g_{\text{Na}} = 120 \text{ mS}/\text{cm}^2$  and  $g_{\text{K}} = 36 \text{ mS}/\text{cm}^2$  are maximum conductance of the sodium and potassium channel per unit area, respectively; and the constant  $g_{\text{L}} = 0.3 \text{ mS}/\text{cm}^2$  stands for the maximum leakage conductance per unit area which is associated with the remaining ion channels. Moreover,  $V_{\text{Na}} = 50 \text{ mV}$ ,  $V_{\text{K}} = -77 \text{ mV}$  and  $V_{\text{L}} = -54.4 \text{ mV}$  are the reversal potentials associated with sodium, potassium, and leakage conductance, respectively.  $I$  represents a periodic stimulus current delivered externally to the neuron, which reads  $I = 6.0 + \sin(0.3t)$  in the present Letter.  $N$  is the number of the system’s elements,  $\varepsilon$  is the coupling strength,  $D$  is the noise strength of the external Gaussian white noise  $\xi_i(t)$  with zero mean value and unit variance. Periodic boundary conditions are adopted in our numerical simulations. To study the collective response of the coupled system, we introduce the average transmembrane potential  $V_{\text{out}}(t) =$

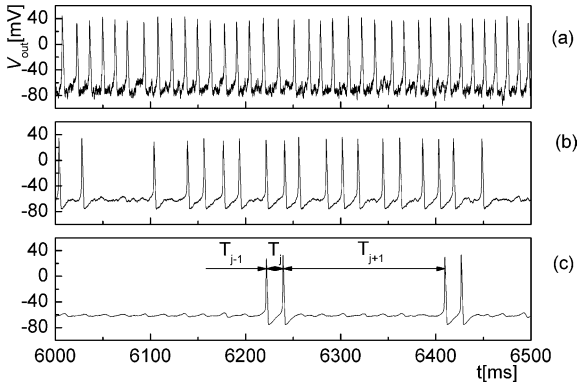


Fig. 1. The spike trains of the output  $V_{out}$  of a single Hodgkin–Huxley neuron for different noise strengths: (a)  $\log(D) = 1.0$ , (b)  $\log(D) = 0.2$ , (c)  $\log(D) = -0.5$ . With the noise strength  $D$  increasing, the number of the spikes increases.

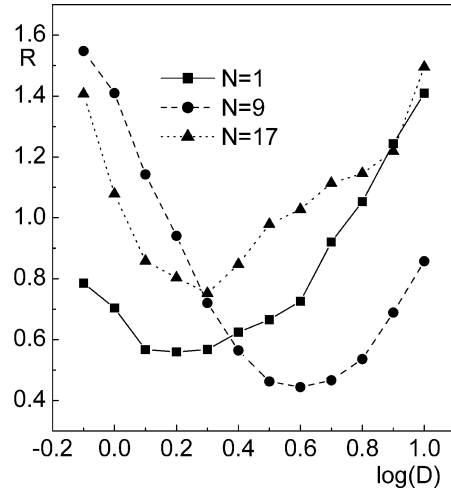
$\frac{1}{N} \sum_{i=1}^N V_i(t)$  as the signal output. Numerical integration of Eq. (1) is carried out by explicit Euler method with a time step 0.001 s.

For a single Hodgkin–Huxley neuron ( $N = 1$ ), Ref. [17] already discussed the bifurcation in the Hodgkin–Huxley neuron to a constant  $I$  in the absence of noise ( $D = 0$ ), from which we know that there is only a globally stable fixed point for  $I < I_c = 6.2$ . For  $I$  larger than  $I_c$ , one observes potential spikes. Therefore the periodic stimulus  $I = 6.0 + \sin(0.3t)$  is a subthreshold signal for the Hodgkin–Huxley neuron to trigger a large-amplitude spike in the absence of noise. However, in the presence of external noise, noise-induced spikes can be observed as shown in Fig. 1, and the number of the spikes increases with the increment of  $D$ . To characterize the regularity of the spike train, we have calculated the coefficient of variance  $R$ , which is defined as follow,

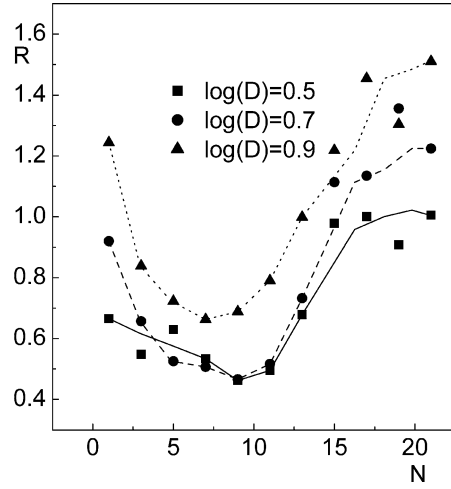
$$R = \frac{\sqrt{\langle T^2 \rangle - \langle T \rangle^2}}{\langle T \rangle} \quad (3)$$

here  $\langle T \rangle$  and  $\langle T^2 \rangle$  are the mean and mean-squared interspike intervals, respectively, and a spike occurs each time  $V_{out}$  crosses 0 mV from below. Note that  $R$  represents a measure of the spike coherence. The more ordered is the spike train, the smaller  $R$  is obtained. For a purely periodic signal,  $R$  equals zero.

Let us now study the effects of  $N$  and  $D$  on the array of coupled Hodgkin–Huxley neurons by calculating the spike coherence  $R$  of the spike train of  $V_{out}$ . The results for  $\varepsilon = 2.0$  are depicted in Fig. 2. In



(a)



(b)

Fig. 2. (a) The spike coherence  $R$  versus  $D$  for given  $N$ . (b) The spike coherence  $R$  versus  $N$  for given  $D$ . (a) and (b) display the stochastic resonance and system size resonance, respectively. In this picture, the coupling strength is  $\varepsilon = 2.0$ .

Fig. 2(a), we show how the spike coherence  $R$  depends on the noise intensity for fixed network size  $N = 1, 9$ , and  $17$ . All the curves show that spike coherence  $R$  has a minimum for a certain noise strength  $D$ , namely, there is an optimal external noise level at which the collective behavior is the most ordered. On the other hand, we have also investigated how the spike coherence changes with the network size when the noise intensity is fixed. For instance, the results for  $\log(D) = 0.5$ ,  $\log(D) = 0.7$  and  $\log(D) = 0.9$ , are displayed in

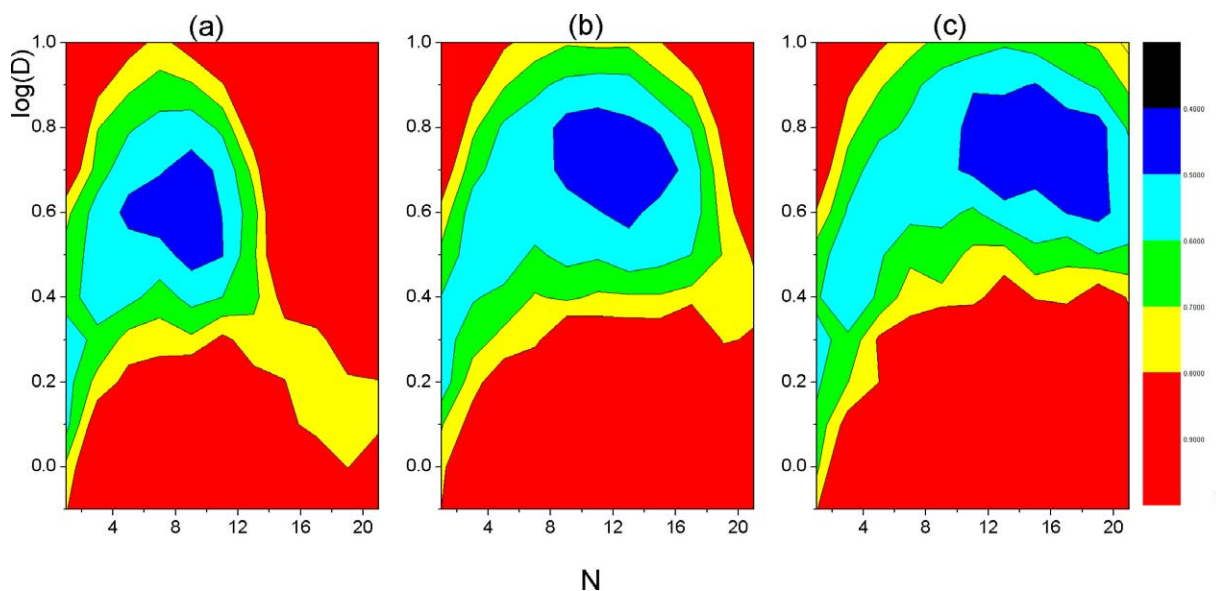


Fig. 3. The spike coherence as a function of  $N$  and  $D$  for different coupling strength: (a)  $\varepsilon = 2.0$ , (b)  $\varepsilon = 4.0$ , and (c)  $\varepsilon = 6.0$ .

Fig. 2(b). Clearly, the spike train is the most regular when the network size  $N$  has an optimal value, demonstrating the existence of system size resonance. To get a global view, we have scan the network size  $N$  and noise strength  $D$  simultaneously over a relatively wide parameter range, keeping other parameters unchanged. The results are shown in Fig. 3(a) for  $\varepsilon = 2.0$ . We see a clear ‘optimal island’ in the  $N$ – $D$  parameter plane where the value of  $R$  reaches the bottom of a valley, indicating that the collective behavior become even better ordered when both the network size and the external noise have optimal values, i.e., *optimal number of neurons subjected to optimal external noise works the best for their collective information processing*.

To further demonstrate this behavior, we have also investigated the effect of the coupling strength, and the results are also shown in Fig. 3. For Fig. 3(b) and (c), the coupling strength read  $\varepsilon = 4.0$  and  $\varepsilon = 6.0$ , respectively. For different coupling strength we obtained similar results, except that the island’s position shifts along the direction of the increasing network size  $N$  and the coupling strength.

In addition, we find that the existence of an optimal network size, i.e., the system size resonance, depends on the choice of dynamical behavior under investigation. In the present Letter, we have focused on

the collective dynamics defined by the average transmembrane potential, as those done in the study of system size resonance of coupled bistable or excitable elements. However, such a nontrivial dependence on the network size does not occur if we only consider the dynamics of an individual neuron in the network. We have also calculated the averaged spike coherence  $\langle R \rangle = \frac{1}{N} \sum_{i=1}^N R_i$ , here  $R_i$  is the coefficient of variance of the  $i$ th individual neuron. The results are displayed in Fig. 4, where the parameters are same as those in Fig. 2. As shown in Fig. 4(a), an optimal noise strength still exists for a given network size. But in Fig. 4(b), one does not see minima in the  $R$ – $N$  curves, indicating that there is no optimal network size at which the individual neuron’s behavior has maximal order. Fig. 4(c) depicts the spike coherence as a function of network size and external noise. No optimal island exists in this case. Therefore, only when we consider the network as a whole, can one find the resonance with the network size. The main reason for this difference between a single neuron in the network and the network as a whole is that the neurons do not spike synchronously. Of course, when the coupling strength is very strong, the network will reach a complete synchronized state, such that the response of an individual neuron and the whole network may behave the same with the change of the network size [18].

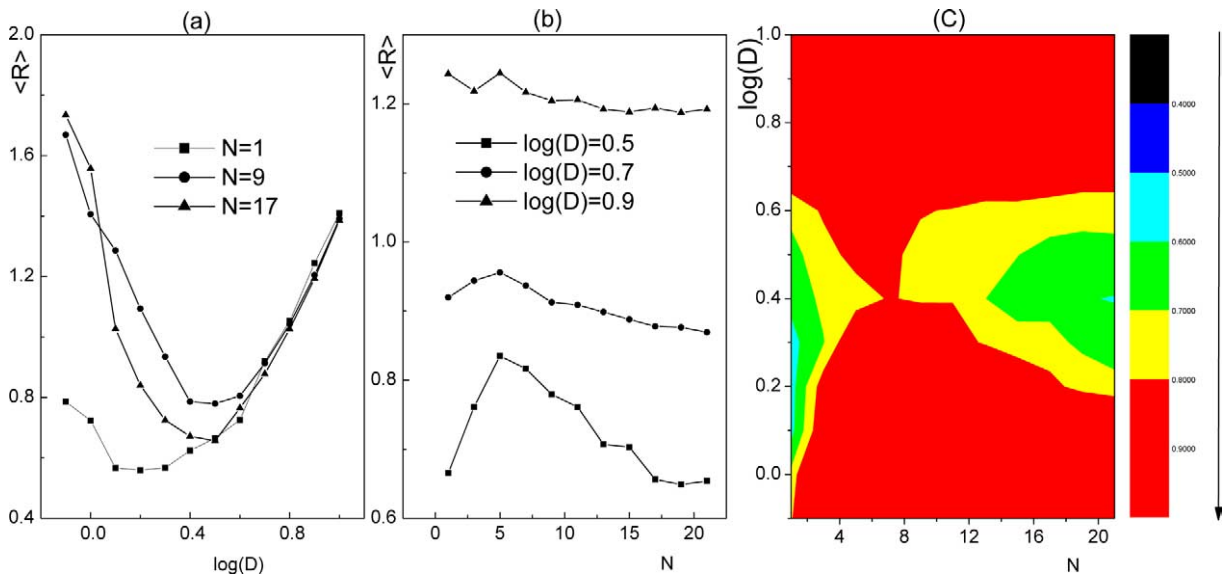


Fig. 4. The averaged spike coherence  $\langle R \rangle$ , which is defined as  $\langle R \rangle = \frac{1}{N} \sum_{i=1}^N R_i$ . (a)  $\langle R \rangle$  versus  $D$  for different given network size:  $N = 1, 9$ , and  $17$ . (b)  $\langle R \rangle$  versus  $N$  for different given external noise strength:  $\log(D) = 0.5, 0.7$ , and  $0.9$ . (c)  $\langle R \rangle$  as a function of  $N$  and  $D$ .

### 3. Conclusion

In conclusion, we have studied the collective dynamics of Hodgkin–Huxley neurons on regular one-dimensional network by numerical simulation methods. We find that the collective behavior of the system is the most regular when the network size, here is the number of the neurons in the network, has an optimal value. The effect of the coupling strength has also been investigated, and the existence of an optimal network size is robust. The value of the optimal network size becomes larger when the coupling strength increases. In addition, we find that such an optimal network size does not exist if we investigate the response of an individual neuron in the network rather than the collective dynamics. Hence, optimal number of neurons works the best for their collective information processing. Since many real neuronal systems may be coupled into network and response to the external single as a whole, our study may be useful to understand how the neuronal network works in praxis.

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