

## Optimal Spike Coherence and Synchronization on Complex Hodgkin–Huxley Neuron Networks

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In recent years, dynamic processes in complex networks have attracted growing attention.<sup>[1–3]</sup> Studies have focused on the small-world network (SWN)<sup>[4]</sup> and scale-free network (SFN)<sup>[5]</sup> due to their importance in explicitly mimicking highly complex structure of many realistic social,<sup>[6]</sup> biological,<sup>[7, 8]</sup> or electronic communication<sup>[9]</sup> networks. So far, studies on complex net-

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works can be divided into two main categories: In the dominant category, investigations are concerned with topological properties and the various mechanisms, which allow to determine the topology. Research in the other, more important category is engaged in understanding how the network topology influences the system's dynamic features.<sup>[2,10,11]</sup>

Any spreading rate can lead to the whole infection of disease on a "scale-free" network (SFN).<sup>[12]</sup> Stochastic resonance<sup>[13]</sup> and synchronization<sup>[14]</sup> can be considerably improved for SWN, and SWN can greatly enhance the probability of spiral wave formation in excitable media,<sup>[15]</sup> ordering chaos,<sup>[10]</sup> and oscillator death.<sup>[11]</sup> All these studies show that random shortcuts play a crucial role for the system's dynamics.

In biology, neural networks have always been an important subject of research. It is well-known that a single neuron in the vertebrate cortex connects to more than  $10^4$  postsynaptic neurons via synapses, forming complex networks.<sup>[16]</sup> Therefore, adding a number of long-range shortcuts among them is reasonable and feasible. Recently, the dynamics of coupled Hodgkin–Huxley (H–H) neurons on complex networks have gained much interest.<sup>[17,18]</sup> Two important dynamical phenomena, regarding the effects of random connectivity of networks, are the enhancement of temporal coherence and the spatial synchronization of action potentials (spikes). Coherence and synchronization of coupled excitable neurons may elucidate, how the coherent spontaneously synchronized oscillations, which have been observed in the brain cortex, are established in many neuronal systems.<sup>[19–21]</sup> Therefore, the study of coherence and synchronization of the H–H neurons on complex networks is of great significance for real neuronal systems.

Since Hodgkin's and Huxley's cornerstone paper<sup>[22]</sup> was published, numerous studies have been contributed to the dynamics of the H–H neurons. The dynamics of membrane potentials for a large and a small ion channel number can be described by the deterministic H–H equation<sup>[22]</sup> and the stochastic H–H model,<sup>[23,24]</sup> respectively. In the case of coupled neurons, fluctuations may be generated both from a small number of ion channels and from the synapses by stochastic effects in the transport of neurotransmitter through the synaptic cleft as well as by the relative small number of postsynaptic receptors. Since synaptic noise is extrinsic to the ion channel processes that generate the action potential, it appears as noise term in the equation for the membrane potential. Intrinsic channel noise appears in the equations for the gating variables.<sup>[23,24]</sup> A study of simple threshold-fire model neurons has shown that the maximal signal-to-noise ratio (SNR), found by varying the excitability at a given noise level, decreases monotonously with increasing noise.<sup>[25]</sup> Thus, adding noise externally is not the best strategy to optimize signal encoding. The dynamics of the stochastic H–H neuron model subjected to channel noise, arising from stochastic opening-closing of ion channel gates, has been extensively studied.<sup>[23–25]</sup> It is shown that the intrinsic channel noise can significantly alter the spiking activity of neurons. Interestingly and importantly, recent studies have demonstrated that optimal areas of ion channel clusters for subthreshold signal encoding exist.<sup>[31,32]</sup> Concerning the influence of intrinsic channel noise on the synchronization between the spik-

ing activity of the excitable membrane and an externally applied periodic signal, it is found that synchronization takes place only for sufficiently large ion channel assemblies.<sup>[33]</sup> A study of a system composed of two intrinsically noisy H–H neurons, which are coupled by a diffusive interaction, shows that the addition of sinusoidal forcing can change the system's statistical dynamics, giving rise to the statistical locking of random switching to the phase of the external signal.<sup>[34]</sup> It is also found that there exist both optimal clusters areas and an optimal number  $N$  of coupled neurons for the best coherence.<sup>[35]</sup> Note here that an optimal size of channel clusters corresponds to an optimal level of internal noise.

In particular, the study of dynamics of coupled H–H neurons on SWN has shown that random topologies give rise to fast response, if regular networks produce coherent oscillations on a slow time scale. Furthermore, random topology may speed the synchronization of neuron firings by taking advantage of a few long-range shortcuts.<sup>[17]</sup> Since the structural properties of complex networks, for example, the characteristic path length  $L(p)$  and clustering coefficient  $C(p)$  in SWN, vary together with  $p$ , the fraction of random shortcuts, it is important to study the effect of  $p$  on the dynamics of complex networks. An increase of  $p$  leads to an enhancement of coherence resonance and synchronization of neuron firings.<sup>[18]</sup> Thus, the intriguing question, if an optimal  $p$  for coherence and synchronization exists, raises. Herein, we really find such an optimal  $p$ , where neuron spikes achieve the best performance of coherence, by using the stochastic H–H neuron model subjected to channel noise. We demonstrate that appropriate random long-range shortcuts favor temporal coherence and hence subthreshold signal encoding.

The random neural network herein is constructed as follows. We start with a regular ring which comprises  $N=60$  identical H–H neurons. Each neuron has two nearest neighbors. Links are then randomly added between non-nearest vortices. In the limit case, when all neurons are coupled to each other, the network contains  $N(N-1)/2$  edges. Using  $M$  to denote the number of added random shortcuts, then the fraction of random shortcuts reads  $p=M/[N(N-1)/2]$ , which is chosen as the control parameter herein. One should note that for a given  $p$  a lot of network realizations exist.

It is known that in the presence of an external stimulus  $I(t)$ , the temporal evolution of the membrane potential  $V(t)$  for a single neuron is governed by the differential Equation (1):

$$C \frac{dV}{dt} = -g_{\text{Na}} m^3 h (V - V_{\text{Na}}) - g_{\text{K}} n^4 (V - V_{\text{K}}) - g_{\text{L}} (V - V_{\text{L}}) + I(t) \quad (1)$$

where the constants  $g_{\text{Na}}=120$ ,  $g_{\text{K}}=36$ , and  $g_{\text{L}}=0.3 \text{ mS cm}^{-2}$  are, respective, the maximal conductance of sodium, potassium, and leakage currents,  $C=1 \text{ } \mu\text{F cm}^{-2}$  is the membrane capacitance, and  $V_{\text{Na}}=50 \text{ mV}$ ,  $V_{\text{K}}=-77 \text{ mV}$ , and  $V_{\text{L}}=-54.4 \text{ mV}$  represent corresponding reversal potentials. We employ a periodic stimulus  $I=\sin(0.3t)$ , which is a subthreshold stimulus and does not trigger action potentials, if intrinsic channel noise is not taken into account. Note here that different subthreshold stimuli may cause a change in the spiking activity. However, it is shown that for a single neuron the interspike interval distri-

bution is not affected by the subthreshold stimulus for small patch sizes, and the influence of the stimulus is rather small even for larger patch sizes.<sup>[32]</sup> Accordingly, there may be small quantitative difference regarding the influence of different subthreshold stimuli on the coupled H–H neurons' spiking activity, but the qualitative result should remain the same.

According to Hodgkin and Huxley's work, the conductance of a potassium channel is gated by four independent and identical gates and, thus, if  $n$  is the probability of one gate to be open, the probability for a potassium channel to stay open is  $n^4$ . Similarly, sodium channels are assumed to be governed by three independent, identical gates with opening probability  $m$  and an additional different one, possessing the opening probability  $h$ . Accordingly, the opening probability of the sodium channel reads  $m^3h$ . To take into account the internal channel noise, the stochastic gating variables  $m$ ,  $h$ , and  $n$  obey the following Langevin equations [Eqs. (2a–2c)]:<sup>[22,23]</sup>

$$\dot{m} = \alpha_m(V)(1-m) - \beta_m(V)m + \xi_m(t) \quad (2a)$$

$$\dot{h} = \alpha_h(V)(1-h) - \beta_h(V)h + \xi_h(t) \quad (2b)$$

$$\dot{n} = \alpha_n(V)(1-n) - \beta_n(V)n + \xi_n(t) \quad (2c)$$

with the experimentally determined voltage-dependent transition rates, given in Equations (3a–3f):<sup>[22,27]</sup>

$$\alpha_m(V) = \frac{0.1(V + 40)}{1 - \exp[-(V + 40)/10]} \quad (3a)$$

$$\beta_m(V) = 4\exp[-(V + 65)/18] \quad (3b)$$

$$\alpha_h(V) = 0.07\exp[-(V + 65)/20] \quad (3c)$$

$$\beta_h(V) = \{1 + \exp[-(V + 35)/10]\}^{-1} \quad (3d)$$

$$\alpha_n(V) = \frac{0.01(V + 55)}{1 - \exp[-(V + 55)/10]} \quad (3e)$$

$$\beta_n(V) = 0.125\exp[-(V + 65)/80] \quad (3f)$$

where  $\xi_{i=m,n,h}(t)$  are Gaussian white noises with  $\langle \xi_i(t) \rangle = 0$ ,  $\langle \xi_i(t)\xi_j(t') \rangle_{i \neq j} = 0$ , and  $\langle \xi_i(t)\xi_i(t') \rangle = D_i\delta(t-t')$ .  $D_{i=m,n,h}$  represent the effective intensities of internal channel noises, which are inversely proportional to the total number of sodium or potassium channels in the membrane patch, shown in Equations (4a–4c):

$$D_m = \frac{2}{N_{Na}} \frac{\alpha_m\beta_m}{\alpha_m + \beta_m} \quad (4a)$$

$$D_h = \frac{2}{N_{Na}} \frac{\alpha_h\beta_h}{\alpha_h + \beta_h} \quad (4b)$$

$$D_n = \frac{2}{N_K} \frac{\alpha_n\beta_n}{\alpha_n + \beta_n} \quad (4c)$$

where  $N_{Na}$  and  $N_K$  are the total numbers of sodium and potassium channels present in a given patch of the membrane, respectively. With the assumption of homogeneous ion channels densities,  $\rho_{Na} = 60 \mu\text{m}^{-2}$  and  $\rho_K = 18 \mu\text{m}^{-2}$ ,  $N_{Na}$  and  $N_K$  are determined by using the membrane patch area  $S$  via  $N_{Na} = \rho_{Na}S$  and  $N_K = \rho_K S$ .

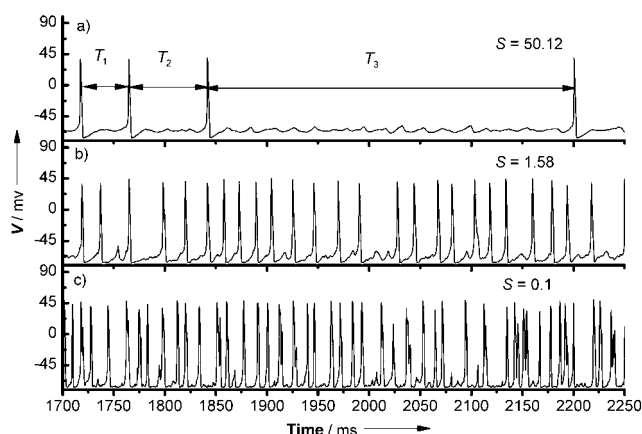
Now the membrane potential dynamics of coupled H–H neurons on the complex networks can be described by Equations (5a) and (5b):

$$C \frac{dV_i}{dt} = -g_{Na}m_i^3h_i(V_i - V_{Na}) - g_Kn_i^4(V_i - V_K) - g_L(V_i - V_L) + I + \sum_j \varepsilon_{ij}(V_j - V_i) \quad (5a)$$

$$\dot{x}_i = \alpha_{x_i}(V_i)(1-x_i) - \beta_{x_i}(V_i)x_i + \xi_{x_i}(t) \quad (5b)$$

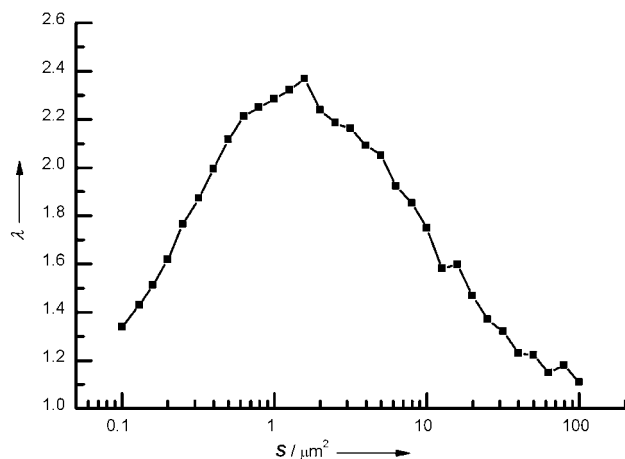
where  $x = m, n, h$  and  $1 \leq i \leq N$ . Here  $N$  is the number of neurons and  $\varepsilon_{ij}$  is the coupling strength between the two neurons  $i$  and  $j$ , which is determined by the coupling pattern of the system. If neuron  $i$  and  $j$  are connected, they have coupling strength  $\varepsilon_{ij} = 0.1$ ; otherwise the coupling strength is  $\varepsilon_{ij} = 0$ . Numerical integration of Equation (5) is carried out by using the explicit Euler method with time step 0.001 ms. Periodic boundary conditions are used and the parameter values for all the neurons are identical except for the noise terms  $\xi_{x_i}(t)$ .

Since action potentials can be generated by channel noise in the case of above subthreshold current input, we first briefly outline the effect of channel noise on the dynamics of a single H–H neuron. The patch area  $S$  is taken as a control variable and all other parameter values are as shown above. We have performed numerical integration of Equations (1)–(4), and obtained the spike oscillations of membrane potential and their regularity as a function of the patch area. Figure 1 plots the spike trains of the membrane potential  $V$  for three different patch areas. It is clearly shown that the spike firings appear relatively regular only at an intermediate patch area  $S = 1.58 \mu\text{m}^2$ . Usually, the regularity of a spike train is measured by the coef-



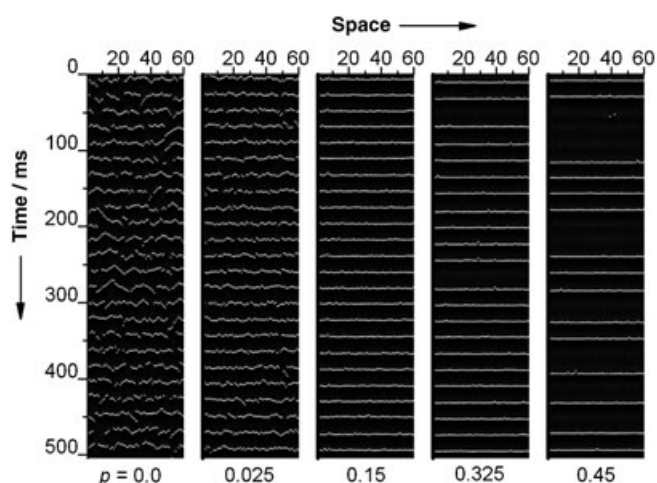
**Figure 1.** Membrane potential  $V$  for a single neuron with three different patch area  $S$ : a)  $S = 50.12 \mu\text{m}^2$ , b)  $S = 1.58 \mu\text{m}^2$ , and c)  $S = 0.1 \mu\text{m}^2$ . A regular spike train is observed for the intermediate patch areas.  $T_1$ ,  $T_2$ , and  $T_3$  in (a) are the examples of the interspike interval.

coefficient of variation defined as  $R = \sqrt{\langle T^2 \rangle - \langle T \rangle^2} / \langle T \rangle$ . Here we define  $\lambda = 1/R$  as our measure, simply to address the point that a larger  $\lambda$  corresponds to a better spiking regularity. The dependence of  $\lambda$  on the patch area  $S$  is displayed in Figure 2. It shows that  $\lambda$  goes through a maximum at around  $S \approx 1.58 \mu\text{m}^2$ , corresponding to the best regularity of the spike train. This phenomenon has been termed as "internal noise coherence resonance".<sup>[32]</sup>



**Figure 2.** Dependence of the variation coefficient  $\lambda$  on the patch area  $S$  in the presence of a subthreshold stimulus  $I = \sin(0.3t)$  for a single neuron. The maximal  $\lambda$  as a function of the patch area  $S$  is observed. This maximum shows the optimal  $S$  value for the encoding of small sinusoidal signals.

Now we turn to the present coupled H–H neurons on the complex networks. To mainly investigate the effect of the network topology, we fixed the patch area at  $S = 6 \mu\text{m}^2$ , and we let  $p$  variable. All other parameters are the same as given above. The spatiotemporal evolution of the membrane potentials of all the 60 coupled H–H neurons on the networks is presented in Figure 3. The left panel in Figure 3 corresponds to



**Figure 3.** Spatiotemporal evolution of membrane potentials of 60 coupled H–H neurons on the network. The spatial synchronization is enhanced with increasing  $p$ , and temporal coherence becomes most pronounced for an intermediate  $p$  value.

the regular lattice case ( $p = 0$ ). It shows rather irregular and nonsynchronous spikes. However, if certain random shortcuts are added (e.g.,  $p = 0.025$ , i.e., number of shortcuts  $M = 45$ ), the system shows a more regular spatiotemporal pattern, which is nearly synchronized in space and almost periodic in time. When the number of random shortcuts increases to  $M = 270$  (see the panel for  $p = 0.15$ ), the synchronization is more enhanced and the performance of temporal regularity becomes the best. However, if the number of random shortcuts is further increased, the spikes are irregular in time although the neurons are still spatially synchronized (see the panels for  $p = 0.325$  and  $0.45$ ). The temporal regularity is apparently lost.

To quantitatively characterize these two behaviors, we introduce the standard deviation  $\sigma$  and the coefficient of variation  $\lambda_c$  to measure the spatial synchronization and the regularity of collective spike firings, respectively. Here  $\sigma$  is defined as Equation (6):

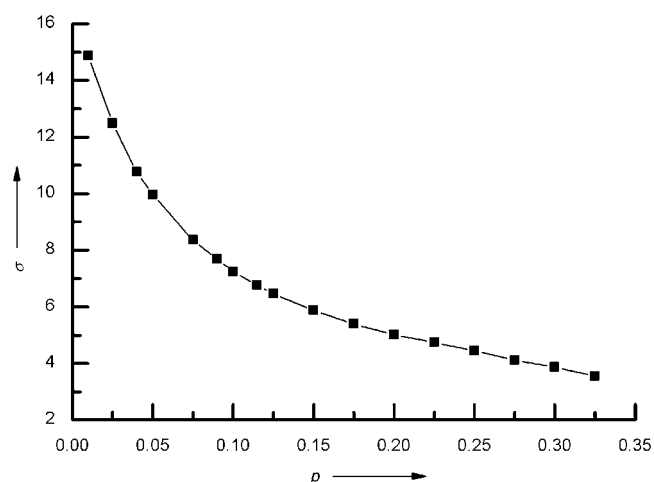
$$\sigma = [\langle \sigma(t) \rangle] \quad \text{with} \quad \sigma(t) = \sqrt{\frac{\frac{1}{N} \sum_{i=1}^N V_i(t)^2 - \left( \frac{1}{N} \sum_{i=1}^N V_i(t) \right)^2}{N-1}} \quad (6)$$

where  $\langle \cdot \rangle$  denotes the average over time and  $[\cdot]$  the average over 50 different network realizations for each  $p$ . The value of  $\sigma(t)$  measures the spatial synchronization of neurons' spikes at a fixed time  $t$ . Large values of  $\sigma(t)$  represents large deviation between the neurons, and small values of  $\sigma(t)$  shows good synchronization.  $R$  is used to measure the regularity of the collective spikes in time, which herein is defined as Equation (7):

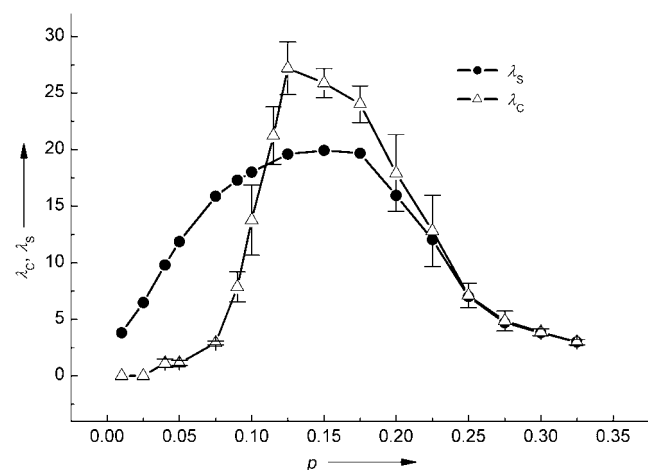
$$\lambda_c = [\lambda'] \quad \text{with} \quad \lambda' = \frac{\langle T \rangle}{\sqrt{\langle T^2 \rangle - \langle T \rangle^2}} \quad (7)$$

here  $T$  is the interspike interval,  $\langle T \rangle$  and  $\langle T^2 \rangle$  are its mean and mean-squared values, respectively. A spike occurs per definition, when the average membrane potential  $V_{\text{ave}}$  crosses 0 mV from below, where  $V_{\text{ave}}(t) = \frac{1}{N} \sum_{i=1}^N V_i(t)$  is the average action potential. Note that  $\lambda_c$  measures the regularity of the spike train of  $V_{\text{ave}}$  spikes and thus represents the collective temporal coherence of the system, which is of much biological significance since it is related to the spike timing precision of the information processing in the H–H neuron system.

Figure 4 depicts the dependence of the standard deviation  $\sigma$  on  $p$  of the network topology. One can see that  $\sigma$  decreases monotonously when  $p$  is increased, approaching zero as  $p \rightarrow 1$ , that is, the synchronization of coupled H–H neurons is enhanced more and more as  $p$  increases. This is in qualitative agreement with the result in ref. [18]. Figure 5 displays the evolution of  $\lambda_c$  as a function of  $p$  within the range  $p = 0 - 0.325$ . Interestingly, it is shown that  $\lambda_c$  in this case undergoes a maximum, which demonstrates the existence of a narrow range of optimal fraction around  $p \approx 0.125$ , where the H–H neurons behave most periodically in time. This implies that for an optimal  $p$  the H–H neurons on the complex networks would exhibit the best performance in subthreshold signal encoding and collective information processing.



**Figure 4.** Dependence of the standard deviation  $\sigma$  on the fraction  $p$ .  $\sigma$  decreases with increasing  $p$ . This behavior indicates that the spatial synchronization is more and more enhanced.



**Figure 5.** Dependence of  $\lambda_c$  and  $\lambda_s$  on  $p$ . Both variables undergo a maximum as  $p$  is increased. For large  $p$  values they tend to be completely the same.

We have also calculated the averaged spike coherence  $\lambda_s = \left[ \frac{1}{N} \sum_{i=1}^N \lambda_i \right]$ , where  $\lambda_i$  is the spike coherence of the interspike intervals for the  $i$ th individual neuron's potential  $V_i(t)$ , and  $[\cdot]$  has the same interpretation as above. The result obtained is also plotted in Figure 5. One sees that an optimal fraction is present around  $p \approx 0.15$  where  $\lambda_s$  reaches its maximum, which indicates the occurrence of the best performance of spike coherence. One should note that in the range of small  $p$  the values of  $\lambda_c$  and  $\lambda_s$  are not the same, however, they tend to be completely the same for large  $p$  values. The reason for this observation is that for large  $p$  values the spikes become completely spatially synchronized, consequently, the response of the system's collective behavior will certainly become the same as that of an individual neuron.

The results obtained sufficiently demonstrate that increasing  $p$  would enhance the spatial synchronization of spiking activity of the coupled H–H neurons on the complex networks. On the other hand, optimal  $p$  would mostly enhance the temporal co-

herence of the system. Note that when the temporal coherence reaches the best level,  $\sigma$  already decreases to a relatively low value, that is, the spatial synchronization is already good. Therefore, the spatiotemporal order of the system's collective behavior reaches its best performance at an optimal value of  $p$ , as already shown in Figure 3.

In conclusion, we have studied the temporal coherence and the spatial synchronization of the stochastic Hodgkin–Huxley model subjected to channel noise on complex networks. We find that coherence and synchronization, which are absent in the regular network, can be enhanced by random shortcuts. More interestingly, a novel phenomenon has been found. With increasing  $p$  the temporal coherence displays the best performance for an optimal  $p$ . We have defined here  $\lambda$ , the inverse value of the “coefficient of variation”, and calculated  $\lambda_c$  for the collective spike coherence of the array and  $\lambda_s$  for individual neuron's spike coherence as well. Apparently, they all undergo a maximum as  $p$  is increased, which demonstrates that there are optimal random shortcuts where the collective spike coherence and individual one conduct the best temporal coherence. This phenomenon is somewhat similar to that of the channel noise stochastic resonance in a single H–H neuron.<sup>[31,32]</sup> The existence of optimal random shortcuts for the spike coherence of the H–H neurons reveals that the neurons may exhibit a rhythmic spiking activity and thus conduct best subthreshold signal encoding under optimal random shortcuts.

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