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Citation: *Chaos: An Interdisciplinary Journal of Nonlinear Science* **16**, 043107 (2006); doi: 10.1063/1.2360503

View online: <http://dx.doi.org/10.1063/1.2360503>

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Frequency-selective response of FitzHugh-Nagumo neuron networks via changing random edges

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(Received 14 April 2006; accepted 12 September 2006; published online 12 October 2006)

We consider a network of FitzHugh-Nagumo neurons; each neuron is subjected to a subthreshold periodic signal and independent Gaussian white noise. The firing pattern of the mean field changes from an internal-scale dominant pattern to an external-scale dominant one when more and more edges are added into the network. We find numerically that (a) this transition is more sensitive to random edges than to regular edges, and (b) there is a saturation length for random edges beyond which the transition is no longer sharpened. The influence of network size is also investigated.

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Excitable neurons fire spikes spontaneously or when stimulated. The spontaneous firing is due to neural noise, such as noise caused by the stochastic opening and closing of ion channels on neuron membrane. The presence of neural noise could improve neurons' ability to detect subthreshold signals via stochastic resonance. Therefore, in the presence of neural noise and subthreshold stimulating signals, neurons can fire spikes either according to their spontaneous dynamics or to the period of the external stimulus. Because the mean firing rate of a spike sequence is one of the main manners for neural systems to encode information, it is important to understand the mechanism underlying the transition between the two time scales. In this paper, we investigate the influence of connections of neuron networks on the transition of its mean field's firing rate. We find the benefit of fast-switching due to random long-range edges. We also find that the random long-range edges need not be very long to bring about the fast-switching effect.

I. INTRODUCTION

The firing rate is the main manner for neurons to encode information in neuronal systems. Excitable neurons, if stimulated, can fire with a pattern either entrained by stimulus or according to their excitatory-refractory dynamics.¹ Therefore, the function of selective response between different temporal patterns is expected.^{2,3}

Noise, both internal, such as that resulting from random conformational changes of ion channels, and external, such as synaptic noise, has salient effects on neuron dynamics and its biological functions.⁴⁻⁷ Large enough noise would destroy the temporal structure of external stimulus or internal oscillations; therefore, the resulting firing pattern is meaningless.

However, an optimal level of noise could increase neurons' sensitivity to subthreshold stimulus, which is well known in the context of stochastic resonance (SR) and coherence resonance (CR).^{1,8,9} The mechanism of SR or CR requires an optimal noise intensity to maximize neurons' capacity to detect weak signals, but it is not as easy as in laboratory experiments to tune noise intensity *in vivo*. Thus, the prospective application of SR or CR in organisms seemed very difficult. However, many authors have discovered other mechanisms, such as summing network,¹⁰ system-size resonance (all-to-all coupled network),^{11,12} and feedback mechanism,¹³ to employ SR or CR with looser restriction of the requirement of an optimal level of noise.

In one of our previous papers,¹⁴ we studied how network size would influence the response of the globally (all-to-all) coupled networks of FitzHugh-Nagumo (FHN) neurons when both subthreshold periodic signals and noise are present. It is numerically proven that as the size of the coupled network is increased, the firing pattern of the mean field of the coupled network is first dominated by the internal time scale of the neurons [the internal-scale dominant (ID) case]. Then the external time scale manifests itself more and more frequently in the spike series, and with a certain network size, the spike series is most ordered and dominated by the external time scale [the external-scale dominant (ED) case], which means that the information transmitted by the mean field is mostly maximized. Further increasing network size would lead to disordered and meaningless spike series. If there are multiple external signals, some common multiples would be selected by certain network sizes. Thus, different firing rates are selected by the size of the globally coupled network.

In any study of network dynamics, the issue of how the elements are connected is of crucial importance. The all-to-all coupling strategy (or summing strategy) that has been

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considered in the above-mentioned references is more an ideal model tractable for theoretical analysis than an approximate description of the real structure of neural systems. A network with local connections and some portion of long-range edges, i.e., a complex network, is a relatively more realistic model for neuronal systems.^{15–20} The study of complex networks has gained extensive attention in recent years. An intriguing type of complex networks is the small-world network (SWN).^{21,22} The main feature of a SWN is that it combines high clustering, which is usually found for regular lattices, and short characteristic path length, which is a typical property of random network. It has been shown that stochastic resonance²³ and synchronization²⁴ can be considerably improved on a small-world network, and a small-world network can greatly enhance the probability of spiral formation in excitable media,²⁵ order chaos,²⁶ and can eliminate oscillator death or introduce global oscillator death.²⁷ All these works show that the connectivity of the complex network plays a crucial role for the system's dynamics.

Neuron dynamics on complex networks have been studied by several authors. The small-world connectivity in the network of excitable integrate-and-fire neurons with unidirectional coupling is found to generate or inhibit, at low or high densities of random connections, persistent activity that is caused by a local stimulus.²⁸ In the numerical simulations of networks of Hodgkin-Huxley neurons, small-world connections that take advantage of regular and random networks are found to perform optimally, giving rise to fast response and coherent oscillations, while regular or random networks cannot do both.²⁹ SWN of FHN neurons also behaves optimally with respect to both stimulus response coherence and noise sensitivity,³⁰ and SWN of Hindmarsh-Rose neurons changes radically from local phase synchronization to global phase synchronization depending on the connections (rewiring probability) of the network.³¹

In the present study, we continue the research in Ref. 14 of frequency-selective response of neuronal networks by investigating the influence of connections of the network on the firing pattern of the mean field. The consideration of connections of a neuronal network as a control parameter has its theoretical and practical importance because plasticity in single neurons, synapses, and large circuits is common in the brain, over time scales ranging from milliseconds to years.^{32,33} Our numerical results suggest that frequency-selective response could be realized by changing the number or length of edges in the network. The transition of firing pattern from an internal-scale dominant (ID) to an external-scale dominant (ED) firing pattern could be realized by much fewer edges than that of an all-to-all coupled network, by much fewer random (long) edges than regular (short) edges, and more sensitively by random (long) edges than regular (short) edges. Moreover, there exists a saturation value, in the sense of the firing pattern transition, for the length of random edges that is much less than the diameter of the network.

The next part of the paper is devoted to a description of the model, in which we place some emphasis on the strategy of choosing dynamical parameters. Then we show illustratively the transition of firing patterns due to the variation of

the number of edges in a random network. Then we compare transitions on different network connections and come to the conjecture that random (long) edges in random, small-world, and scale-free networks are important for their superiority to regular networks. After that, we investigate two factors that have impact on the expense and functional capacities of the network: length limit of random edges and network size. The final section contains the conclusion of the paper.

II. MODEL DESCRIPTION

We choose the FHN model as an example because it provides a simple description of the dynamics of a large class of neurons. The equations are

$$\dot{x}_i = \frac{1}{\varepsilon} \left(x_i - \frac{1}{3}x_i^3 - y_i \right) + \frac{1}{\sum_j C_{ij}} \sum_j KC_{ij}(x_j - x_i) + D\xi_i(t), \quad (1)$$

$$\dot{y}_i = x_i + a + A \sin\left(\frac{2\pi}{T_e}t\right). \quad (2)$$

Here a and ε are parameters in the original FHN model, $\xi_i(t)$ is a Gaussian white noise with zero mean and unit variance, i.e., $\langle \xi_i(t) \rangle = 0$ and $\langle \xi_i(t)\xi_j(t') \rangle = \delta_{ij}\delta(t-t')$; D denotes the noise intensity, K is the coupling strength, and N is the number of elements in the network. T_e is the period of the input signal. The matrix $C = C_{ij}$ defines the connectivity of the network. If neuron i and neuron j are connected, we define $C_{ij} = C_{ji} = 1$; otherwise $C_{ij} = C_{ji} = 0$. C_{ii} is set to 1. For the collective behavior of the network, we investigate the mean field $X(t) = 1/N \sum_{i=1}^N x_i(t)$. The mean field of the coupled network is meaningful in the biological context because individual neurons receive convergent inputs from thousands of other neurons.

It is well known that if $a > 1$, the single FHN model stays at a stable fixed point that is excitable. For $a < 1$, a stable limit cycle, whose period is labeled by T_i , is created through a supercritical Hopf bifurcation, which changes from small amplitude quasiharmonic oscillation to spikes abruptly through canard explosion. We choose parameters to ensure the following. (a) Single FHN neurons stay at their excitable states and the quasiharmonic oscillation before canard explosion³⁴ occurs in a relatively wide range of a . Thus T_i increases slowly in a wide range of a . (b) The firing pattern of a single neuron (with the presence of the input signal and noise) is dominated by the internal time scale of FHN neurons T_i . (c) The firing pattern of the mean field of the all-to-all coupled network is dominated by T_e . In short, the mean field of the network can transmit external information while single neurons cannot. The key point to ensure this difference is to choose proper subthreshold signal (amplitudes and periods), noise intensities, and network size.¹⁴ Figure 1 shows our numerical result of thresholds to trigger spikes of single excitable FHN neurons as a function of signal periods. We are interested in how the firing pattern would change from the ID pattern to the ED pattern as the random edges are added into the network. Since the purpose is to investigate more details of the influence of the network connections on the mean field's firing pattern, we tend to choose a small

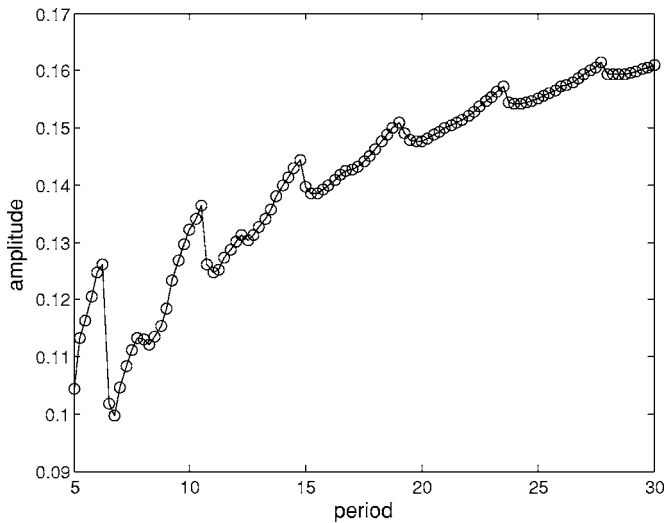


FIG. 1. Thresholds to trigger spikes of single excitable FHN neurons ($a=1.01, \epsilon=0.1$) as a function of signal periods.

network size to facilitate this study. Actually, the effect of a larger network size is similar to choosing smaller noise intensity [see Eqs. (4) and (5) in Ref. 12; the effective noise intensity on the mean field is D/\sqrt{N}].

In the following, we fix $a=1.01, \epsilon=0.1$. The elements in the network are excitable. The amplitude of the periodic signal is set to be subthreshold, namely, the signal alone, without noise, is not capable of triggering spikes. And to avoid being masked by the intrinsic period of the self-spiking behavior on the oscillatory side of the bifurcation point, which is $T_i=4$, the signal period is set to be larger than the former. So we set $T_e=9, A=0.112$ (the threshold is 0.1184), and $K=10$. The noise intensity D is fixed to 0.25; the network size is set to $N=41$ unless specified.

We numerically integrate the network by the explicit Euler-Murayama algorithm³⁵ with a time step 0.005, and then study the interspike intervals (ISI) or the Fourier coefficient Q . A spike is defined if a certain threshold (set to 0.1 in the following) of the mean-field voltage variable $X(t)$ is exceeded from below.

III. RESULTS AND DISCUSSION

(a) *Selective response via changing the number of edges.* We show in Fig. 2 as an example of the trajectory and histogram of ISI distribution of the mean field of a random network, in which any edge is selected with equal probability $1/[N(N-1)/2]$. Denoting the number of edges by M , the ratio, $P=M/[N(N-1)/2]$, is a commonly used measure of connectedness of networks.^{36,37} All the results in this paper have been averaged over 50 different network realizations for each P . With the increased portion of random edges from $P=0.07$ (top) to 0.4 (bottom), the mean field first fires according to the internal spiking period $T_i=4$, then entrained to the external period $T_e=9$. With an intermediate portion of edges $P=0.1$, the firing pattern is a compound of two parts centered at T_i and T_e , respectively. Therefore, the frequency-selective response is realized by changing the number of random edges.

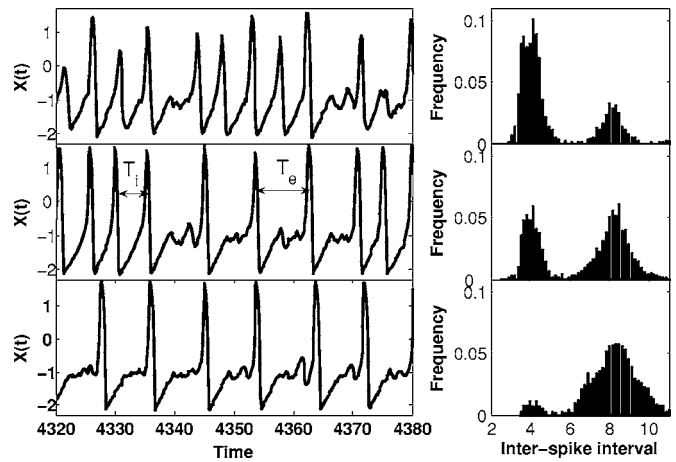


FIG. 2. (Left) time series of the mean field of the random network, $P=0.07$ (top), 0.1 (middle), 0.4 (bottom). (Right) corresponding histogram of ISI. Other parameters are $a=1.01, \epsilon=0.1, A=0.112, T_e=9, D=0.25, N=41, K=10$.

(b) *Compare regular edges with random edges.* To quantify how the pattern changes from autonomous firing to being locked to the signal period as connections change from non-couple to all-to-all couple, we calculate the Fourier coefficient Q ^{38,39} for the input signal, which quantifies how much external information is transmitted by the mean field. The definition of Q is

$$Q_{\sin} = \frac{1}{T} \int_0^T 2X(t) \sin\left(\frac{2\pi}{T_e} t\right) dt,$$

$$Q_{\cos} = \frac{1}{T} \int_0^T 2X(t) \cos\left(\frac{2\pi}{T_e} t\right) dt,$$

$$Q = \sqrt{Q_{\sin}^2 + Q_{\cos}^2}.$$

Here $X(t)$ is the mean field of the network, $[0, T]$ is the integral interval.

The $Q \sim P$ curves of different networks are present in Fig. 3(a) The regular network is constructed by adding edges from each neuron to its K nearest neighbors, where $K \in \{1, 2, \dots, N/2 \text{ or } (N-1)/2\}$. The small-world network is constructed by randomly adding edges on an underlying ring lattice (i.e., a regular network with $K=1$). The random network is the same as described in (a). The scale-free network is constructed following Goh⁴⁰ with $\gamma=2.3$. The curve of the random network shows nonmonotonic behavior when P approaches zero while other curves show monotone increasing behavior in that region. We can draw the following conclusions from Fig. 3(a). First, all the curves saturate before $P=0.6$ to the same value of Q (0.41), which indicates the capacity of the all-to-all coupled neuron network in responding to the external signal under the above conditions. Therefore, the all-to-all coupling strategy ($P=1$) is not a necessary condition for coupled networks to respond to an external signal. Secondly, small-world (square), random (circle), and scale-free (diamond) networks increase their Q values with faster speeds than regular networks as P is increased from 0.05 to 0.15. This is clearer in Fig. 3(b), which shows $\partial Q / \partial P$, the

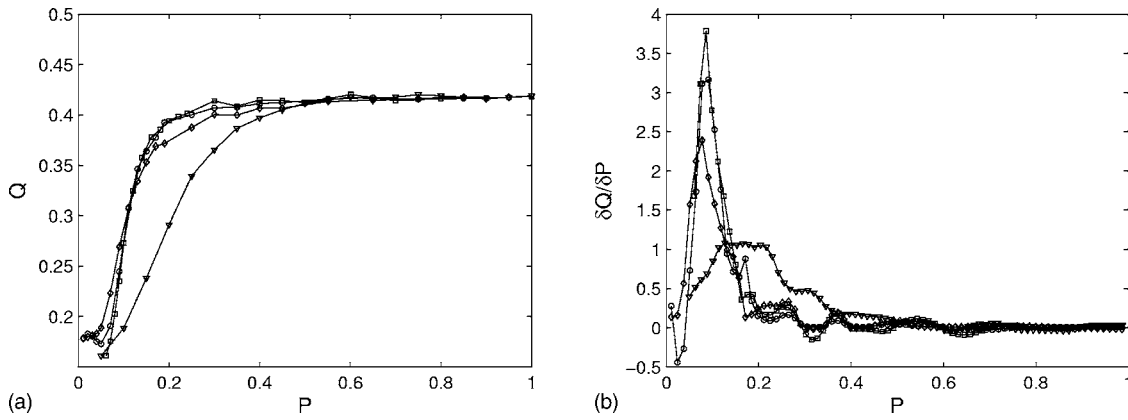


FIG. 3. (a) Q of random (circle), small-world (square), scale-free (diamond), and regular (triangle) network as a function of P . (b) $\delta Q / \delta P$ for these networks. These curves are plotted after interpolation. Markers are the same as in (a). Parameters are the same as in Fig. 2.

rate of Q versus P , for these networks. The curve of regular networks has a low and broad plateau while other curves share the feature of a high and narrow peak. We could contribute the fast increase of Q in small-world (square), random (circle), and scale-free (diamond) networks to random (long) edges in these networks other than their network structures since their behavior shows little difference here.

We have also done simulations for different external signal periods to investigate the robustness of the above phenomena. As long as signal amplitudes and periods (see Fig. 1) are properly chosen, the results are approximately the same as those in Figs. 2 and 3.

(c) *Length limit for random edges.* We have shown that changing the number of edges switches the firing pattern and random edges can increase the capacity of responding to external signals more efficiently to reach the full capacity than regular edges. To get more details on the influence of random edges, we set an upper limit for the length of the random edges. Here we define the length of a random edge in such a way: We index neurons by $1, 2, \dots, N$; the length of an edge that connects neurons i and j ($j > i$) is $d = \min[j - i, N - (j - i)]$. We term the longest length $[N/2$ or $(N - 1)/2]$ as the diameter of the network. With an upper limit, the random edges could not reach beyond the limit. The consideration of confining the edges in a certain area in the network here makes sense when the random edges are physical and energy-consuming. The results obtained from a random network ($N = 41$) are shown in Fig. 4.

As the length limit is increased from 7 to 11, the Q value increases. The Q curve, whose length limit is 11, is almost the same as the fully random network (i.e., the network without length limit for random edges). Decreasing noise intensity from 0.25 (solid lines) to 0.15 (dashed lines) raises the curves and brings little variation to their relative position. Therefore, we could define an effective diameter of the random network, in terms of the dynamical measurement Q , beyond which the $Q(P)$ curves saturate to that of the fully random network. We calculate

$$R = \{ \langle [Q^{lim}(p) - Q^{full}(p)] / Q^{full}(p) \rangle \},$$

where curly brackets means an average over 50 different network realizations, and angular brackets means average

over different values of P , which includes 9 points linearly spaced between 0.01 and 0.09 plus 15 points linearly spaced between 0.1 and 0.8. The superscript *full* means the value of the fully random network, the superscript *lim* means the value of the network with a length limit for random edges. If $R > -1\%$ for the first time, we then define the corresponding length limit as the effective diameter of the random network. Figure 5 shows the effective diameter as a function of network size.

(d) *Influence of number of neurons.* As for the expense of the network, not only the length of edges, but also the number of neurons may be crucial in some cases. We plot Q as a function of P for random networks with various network sizes in Fig. 6.

With the increasing of N , the saturation value of Q is increased, indicating that the network's full capacity of responding to the external signal is increased. At the same time, the value of P where the saturation of Q is first reached is decreased. That is to say, a larger network could respond

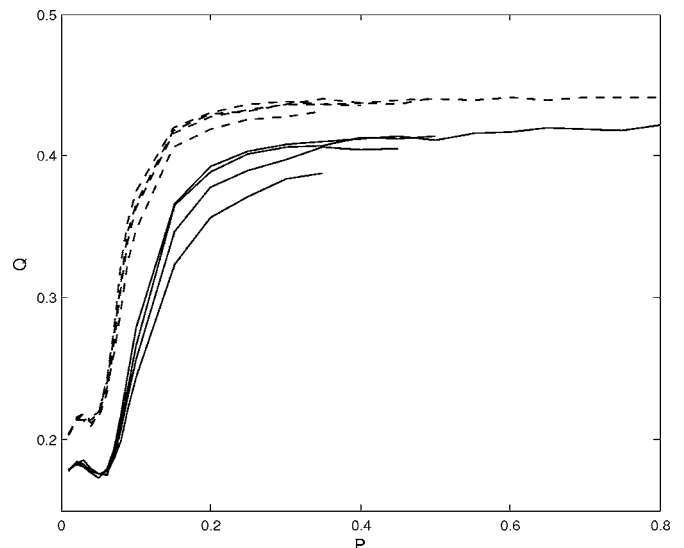


FIG. 4. Q as a function of P for networks with different length limit. Solid lines are $D = 0.25$, dashed lines are $D = 0.15$. From bottom to top, the length limits are 7, 9, 11, and 20, respectively. Other parameters are the same as in Fig. 2.

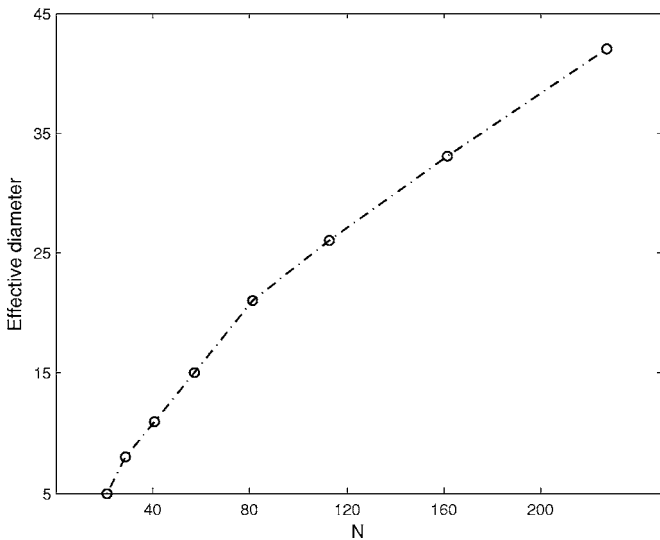


FIG. 5. Effective diameter of random networks as a function of network size. Other parameters are the same as in Fig. 2.

fully to an external signal with fewer portions of random edges. Also the sensitivity of the switch, in view of P , is enhanced as the size is increased. Considering the results in Ref. 14, Fig. 1(a), further increasing the network size would lead to a low Q value when P is close to 1. Therefore, a peaking behavior would appear in the $Q(P)$ curve when the network size is increased to such a degree that the external signal plus the effective noise is too small to trigger the spiking response. Figure 7 shows alternative curves of this situation, in which we choose smaller noise intensities to avoid excessively long CPU time caused by very large network sizes. So, from the point of view of functional gain (sensitive switch), there exists an optimal network size, as noise intensity cannot be tuned easily in many cases. Considering the balance between the cost of the network, including the number of neurons, the number of edges, and the

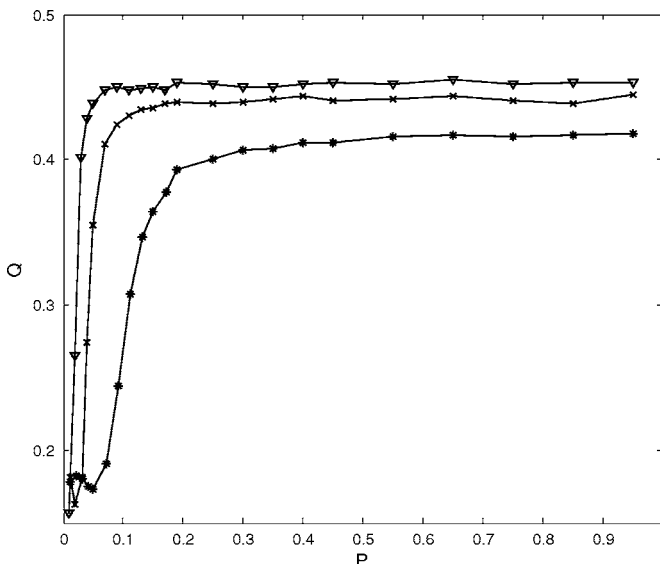


FIG. 6. Q as a function of P for different network sizes of random networks. From top to bottom, $N=201$, 101, and 41. Other parameters are the same as in Fig. 2.

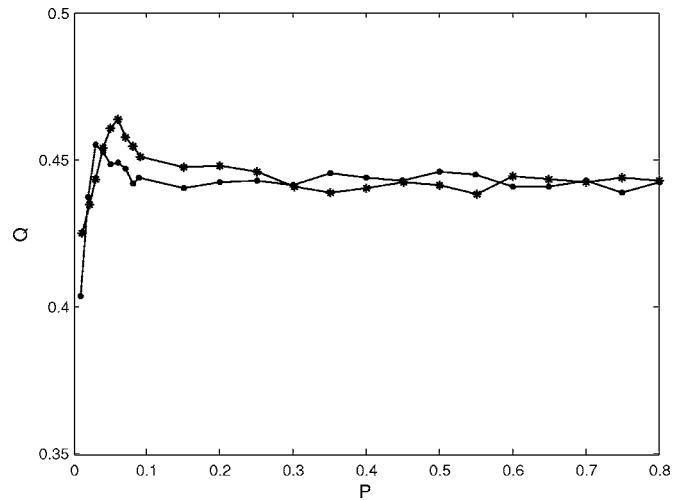


FIG. 7. $Q \sim P$ curves of random networks to illustrate the effect of very large network size in the alternative way of choosing a smaller noise intensity, because the effect of large network size is similar to that of a smaller noise intensity. $N=221$, $D=0.05$ (dot); $N=41$, $D=0.01$ (star). Other parameters are the same as in Fig. 2.

length of edges, and the functional gain of the system, one may propose a certain strategy to design an “optimal” working network.

IV. CONCLUSION

In conclusion, we have studied numerically the influence of network connections on the function of frequency-selective response. The pattern of the mean field depends on the number or length of the edges in the network. We have shown that the capacity of responding to external signals of an all-to-all coupled network could be reached by many fewer random (long) edges than regular (short) edges. And the switch in the regular network is slow while the switches in random, small-world, and scale-free networks are much steeper. Those fast switches between two firing patterns demonstrate some type of ultrasensitivity of the networks’ dynamics to their connections.³¹ Moreover, we find that the length of random edges could be bounded for the purpose of cost-saving, while the network’s capacity of information transmission and sensitive switch is not reduced. Network size, which could adapt to the changes of noise intensity, has an optimal value with regard to the cost of the network and its functional capacities. The tradeoff between cost of the network and its full capacity may set up a building strategy for an “optimal” network.

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