Turing instability in the reaction-diffusion network

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It is an established fact that a positive wave number plays an essential role in Turing instability. However, the impact of a negative wave number on Turing instability remains unclear. Here, we investigate the effect of the weights and nodes on Turing instability in the FitzHugh-Nagumo model, and theoretical results reveal genesis of Turing instability due to a negative wave number through the stability analysis and mean-field method. We obtain the Turing instability region in the continuous media system and provide the relationship between degree and eigenvalue of the network matrix by the Gershgorin circle theorem. Furthermore, the Turing instability condition about nodes and the weights is provided in the network-organized system. Additionally, we found chaotic behavior because of interactions between *I* Turing instability and *II* Turing instability. Besides, we apply this above analysis to explaining the mechanism of the signal conduction of the inhibitory neuron. We find a moderate coupling strength and corresponding number of links are necessary to the signal conduction.

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I. INTRODUCTION

In 1952, Turing tried to interpret the mechanism of animal skin pattern by analyzing the reaction-diffusion system [1]. And Othmer and Scriven found that the topology structure could induce Turing instability in the cellular network [2]. Isaac *et al.* investigated the role of the gene network in the evolution of pattern formation [3]. Then some general methods to analyze the Turing instability were obtained in the network-organized system [4,5]. Diego *et al.* proposed that the topology of the network determines the Turing system's properties [6]. Meanwhile, the eigenvalues and eigenvectors' distribution showed its role in the Turing instability [7–9], especially the maximal eigenvalue and the corresponding eigenvector [10–12]. Francesca *et al.* shown the increasing numbers of activated unstable modes leads to the Benjamin-Feir instability [13–15]. Fanelli *et al.* studied Turing instabilities from a limit cycle and the dynamics of a reaction-diffusion system on a multigraph [16,17]. Also, Turing instability conditions induced by a positive wave number were discussed in the different network [18–20]. Although propagation failure induced by anisotropy was investigated in discrete reaction-diffusion systems [21,22], the negative wave number's effect on pattern formation was seldom considered in the network-organized FitzHugh-Nagumo (FN) model.

The FN model is a reduced Hodgkin-Huxley system to explain the generation of action potential [23,24]. And some dynamical behavior induced by interior and external factors had been well studied, such as noise [25], delay [26], and synchronization [27]. Then, the FN model exhibited some rich dynamical behavior about pattern formation [28,29], and the shape and type of pattern formation were affected by dynamical parameters, external periodic forcing, and noise [30–34]. Also, Jing *et al.* exhibited the chaotic region and the complex bifurcation phenomena in discrete FitzHugh-Nagumo system [35]. Meanwhile, all the states of the coupled chaotic system were addressed in the synchronization of two FN systems coupled with gap junctions [36]. However, the chaotic dynamical behavior on the network was seldom considered in the FN model.

In general, Turing instability is that a steady state stable in the local system can become unstable in the presence of diffusion or network, and Turing instability is induced by the positive wave number in the reaction-diffusion system. But how the negative wave number shows its role in Turing stability (the firing of a neuron) remains to be solved. It is well known that neurons' interaction is like a vast network; there are two steady states for neurons: the resting state and the firing state. Also, neurons fire (namely, Turing instability) when some signals (including inhibitor and activator signals) are collected enough from others through the neural network. To further understand the mechanism of the firing of neurons and the Turing instability, we investigate the FN model's stability and show how the topology structure plays a vital role in the Turing instability. Then we take the weights and the number of links into account and obtain the firing region. The chaotic behavior induced by the interaction between *I* Turing instability (induced by the positive wave number) and *II* Turing instability (caused by the negative wave number) is studied. Finally, we try to explain the mechanism of the firing of neurons and Turing instability through the mean-field method.

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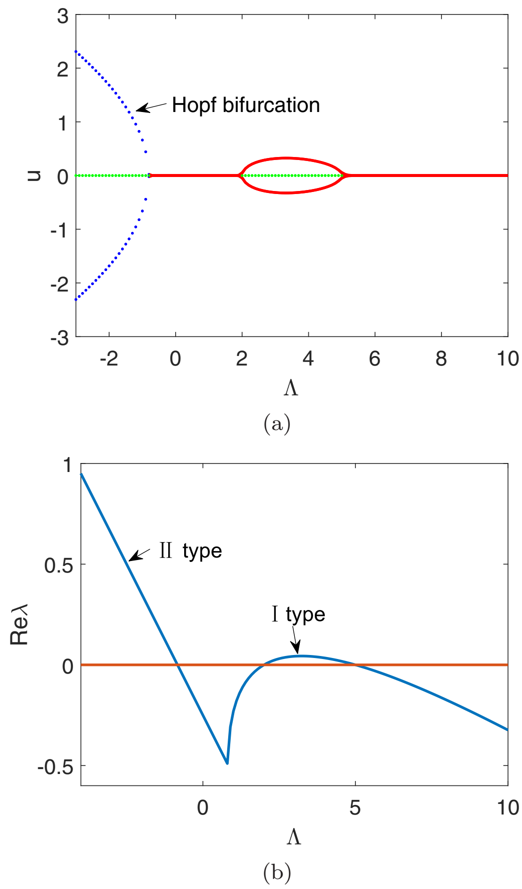


FIG. 1. The stability of system and Turing instability occurs when $\Lambda \in B = (-\infty, -0.8333) \cup (2, 5)$. (a) The bifurcation about eigenvalue Λ where the dotted line represents unstable equilibrium. (b) The stability region of system (2).

II. TURING INSTABILITY IN THE REACTION-DIFFUSION NETWORK

A general Turing system of the FN model in classical continuous media can be expressed as

$$\frac{\partial u}{\partial t} = f(u, v) + d_1 \nabla^2 u,$$
$$\frac{\partial v}{\partial t} = g(u, v) + d_2 \nabla^2 v, \quad (1)$$

where u, v could represent the local densities of activator and inhibitor species (population, chemical species, ion species, etc.), and the dynamics of them can be specified by $f(u, v)$ and $g(u, v)$, d_1, d_2 are the diffusion constants.

Based on the theory of stability, it is easy to know the dynamical behavior of the system (3) without diffusion is stable when $\mathrm{Re}\lambda < 0$. For reaction-diffusion system (2), we can obtain the Jacobian matrix [1,28],

$$B = \begin{pmatrix} a_{11} - d_1 k^2 & a_{12} \\ a_{21} & a_{22} - d_2 k^2 \end{pmatrix}.$$

where k^2 is a wave number (always positive), a_{11}, a_{12}, a_{21}, and a_{22} are the partial derivatives of $f(u, v)$ and $g(u, v)$.

In the present paper, a connected network is constructed to investigate Turing instability induced by the wave number.

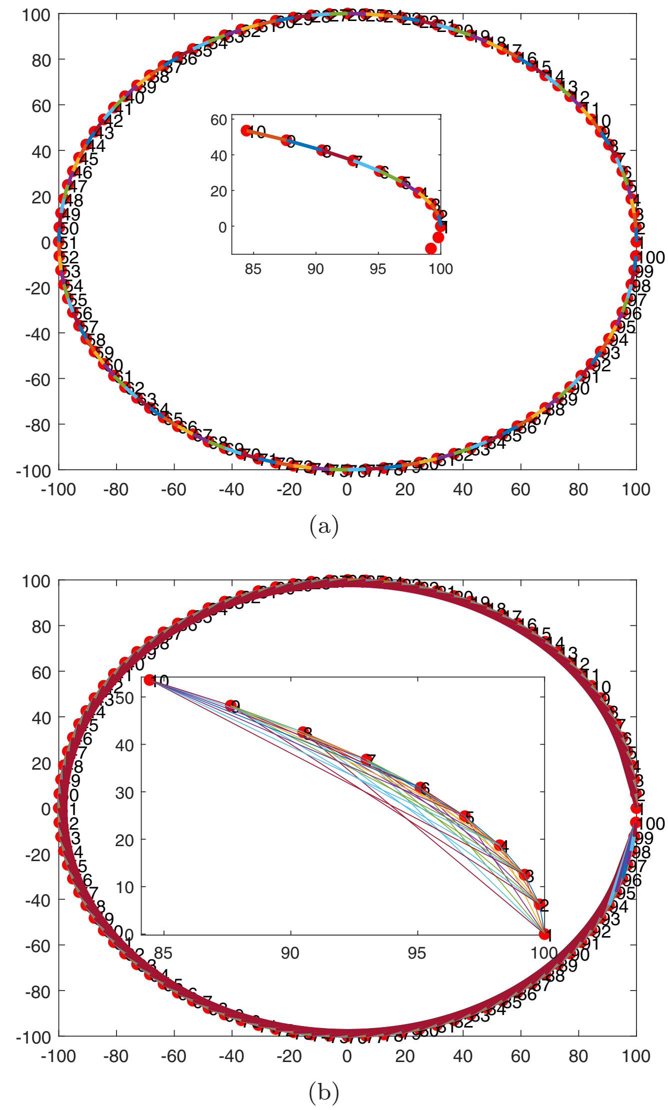


FIG. 2. The topology of the network. (a) The topology when $m = 1$. (b) The topology when $m = 7$.

One node connects the next m nodes with the weights p in the network. The network topology with N nodes can be defined by a symmetric matrix A, where $A_{ij} = p$ if $|i - j| \leqslant m$, otherwise $A_{ij} = 0$ and $A_{ii} = 0$, and the degree of node i is $k_i = \sum_{j=1}^{N} A_{ij}$. System (2) on the network can be rewritten as

$$\frac{du_i}{dt} = f(u_i, v_i) + d_1 \sum_j A_{ij} u_i,$$
$$\frac{dv_i}{dt} = g(u_i, v_i) + d_2 \sum_j A_{ij} v_i, \quad (2)$$

where A is the particular network's adjacency matrix, and the adjacency matrix's eigenvalues can be positive or negative, which is different from the positive wave number in the continuous media system. The positive and negative eigenvalues correspond to the positive (activator) and negative wave number (inhibitor), respectively.

Then a lemma and theorem are given in the following.

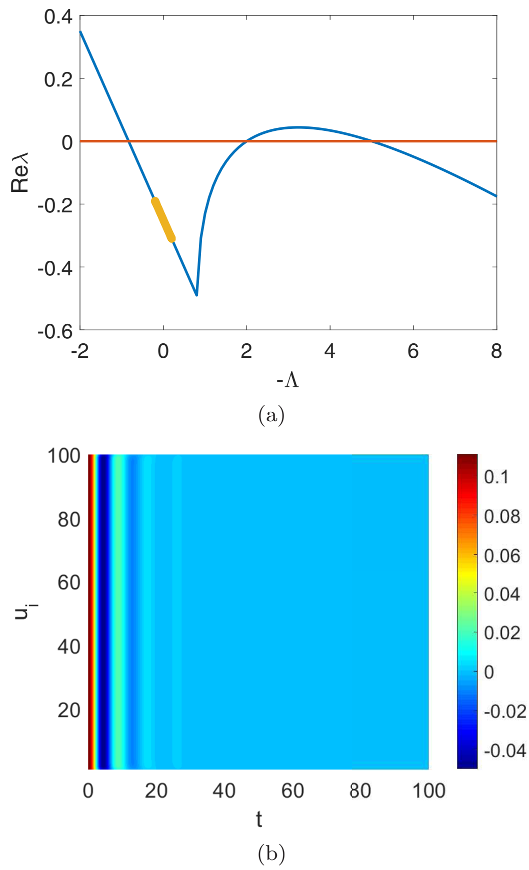


FIG. 3. The stability when the weights are $p = 0.1$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

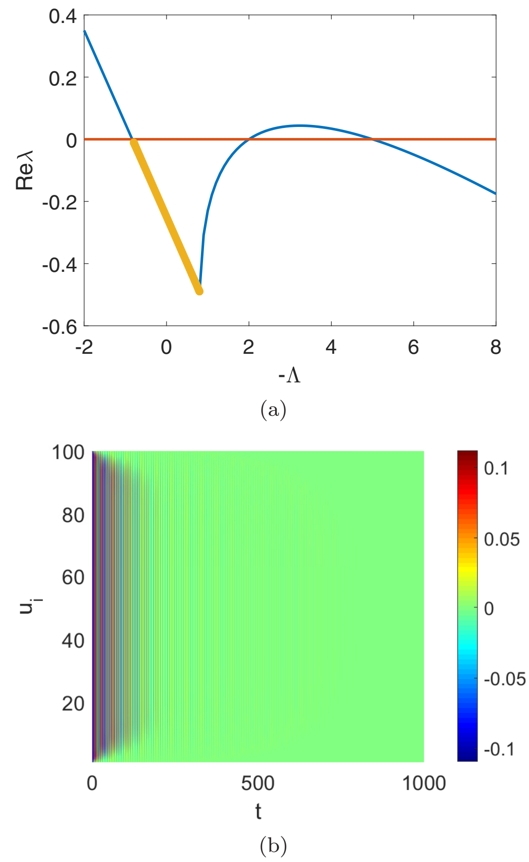


FIG. 4. The stability when the weights are $p = 0.4$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

Lemma 1. Gershgorin circle theorem [37]. Let A be a complex $N \times N$ matrix, let $R_i = \sum_{i \neq j} |a_{ij}|$ be the sum of the absolute values of the nondiagonal entries in the ith row, and let $D(a_{ii}, R_i)$ be a closed disk centered at a_{ii} with radius R_i. Therefore, every eigenvalue of A lies within, at least, one of the Gershgorin disks $D(a_{ii}, R_i)$. Namely, the eigenvalue Λ_i,

$$|\Lambda_i - a_{ii}| \leqslant R_i.$$

Theorem 1. For the above adjacency matrix A, $k = 2m$, and Λ is the eigenvalue of A. Therefore, $\Lambda \in C = \{\Lambda| -kp \leqslant \Lambda \leqslant kp\}$.

Proof. According to Lemma 1, we know $a_{ii} = 0$, $R_i = kp(i = 2, \dots, n-1)$, $R_1 = kp, R_n = kp$, and $|\Lambda| \leqslant R_i \leqslant kp$, namely, $-kp \leqslant \Lambda \leqslant kp$.

On the basis of Theorem 1, we obtain the region of the eigenvalues of the adjacency matrix, and then we consider the stability of system (3). We first consider the stability of a uniform stationary state (u_0, v_0) without a network, where $f(u_0, v_0) = g(u_0, v_0) = 0$. And the Jacobian matrix for every node at equilibrium (0,0) is

$$J = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

The characteristic function can be written as

$$\lambda_i^2 - B_i\lambda_i + C_i = 0, \tag{3}$$

where $B_i = a_{11} + a_{22},\ C_i = a_{11}a_{22} - a_{12}a_{21}$, and the eigenvalue is $\lambda_i = \frac{B_i \pm \sqrt{B_i^2 - 4C_i}}{2}$.

For the network-organized system, a general solution can be expressed as

$$u_i = \sum_{k=1}^{N} c_k \beta_k e^{\lambda_k t} \phi_i^k,$$

$$v_i = \sum_{k=1}^{N} c_k e^{\lambda_k t} \phi_i^k. \tag{4}$$

where $\sum_j A_{ij}\phi_j^k = \Lambda_k \phi_i^k$.

Substituting (5) into Eq. (3), the Jacobian matrix for every node can be written

$$B_i = \begin{pmatrix} a_{11} + d_1\Lambda_i & a_{12} \\ a_{21} & a_{22} + d_2\Lambda_i \end{pmatrix},$$

where Λ_i is the eigenvalue of matrix A, which corresponds to $-k^2$ in reaction diffusion, and $\Lambda_1 \leqslant \Lambda_2 \leqslant \cdots \leqslant \Lambda_N$.

Then the characteristic function of system (3) can be written as

$$\lambda^2 - B_i\lambda + C_i = 0, \tag{5}$$

where $B_i = a_{11} + a_{22} + d_1\Lambda_i + d_2\Lambda_i$, $C_i = d_1 d_2 \Lambda_i^2 + (a_{11}d_2 + a_{22}d_1)\Lambda_i + a_{11}a_{22} - a_{12}a_{21}$, and $\lambda(\Lambda_i) = \frac{B_i \pm \sqrt{B_i^2 - 4C_i}}{2}$.

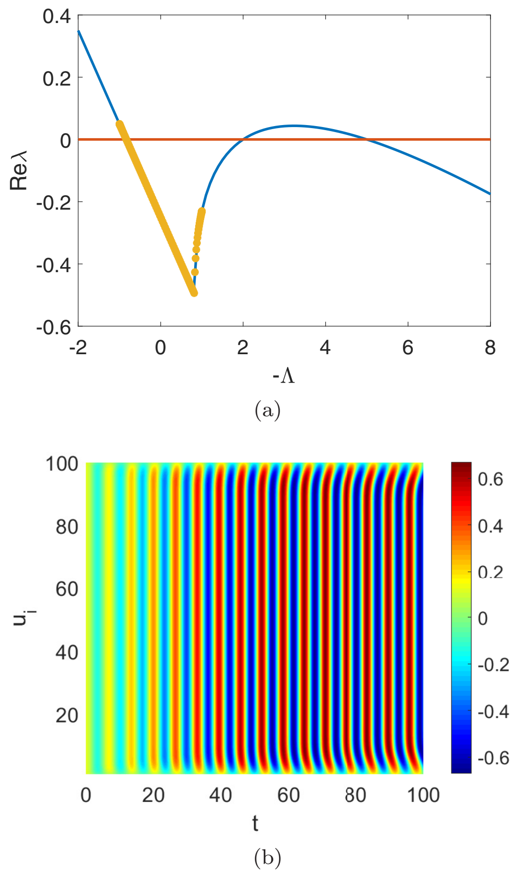


FIG. 5. The stability when the weights are $p = 0.5$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

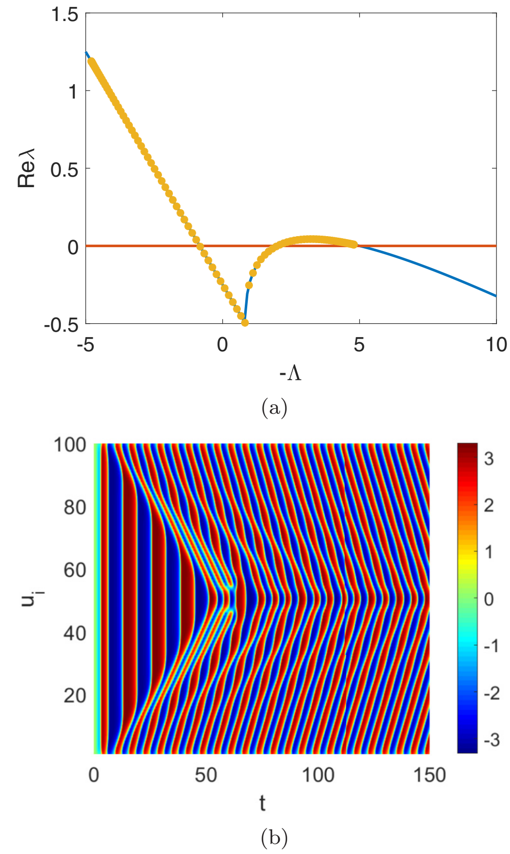


FIG. 6. The stability when the weights are $p = 2.4$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

It is well known that the Turing instability occurs if and only if there is, at least, a Λ_i to make the eigenvalue $\mathrm{Re}\lambda(\Lambda_i) > 0$ hold. In general, $-k^2 = \Lambda_k$ means the eigenvalues are always negative, namely, the wave number is positive. Also, we know there are three solutions λ_1, λ_2, λ_3 ($\lambda_1 \leqslant \lambda_2 \leqslant \lambda_3$) of $\mathrm{Re}\lambda(\Lambda_i) = 0$. $\mathrm{Re}\lambda(\Lambda_i) > 0$ holds if $\Lambda_i \in G = G_1 \cup G_2$, where $G_1 = \{\Lambda|\lambda_2 < \Lambda < \lambda_3$ and $G_2 = \Lambda < \lambda_1\}$. Namely, G is an instability region. For G_1, we know the following lemma.

Lemma 2 [20]. For a network system, the system is always stable when all the eigenvalues of the network matrix are not in the instability region $\Lambda \cap G_1 = \Phi$ (Φ represents the empty set), the instability occurs when $\Lambda \cap G_1 \neq \Phi$.

To find the origin of Turing instability (induced by the negative wave number) and the relationship between p and k, we rewrite system (3) by the mean-field approximation. Namely,

$$\frac{du_i}{dt} = f(u_i, v_i) + d_1\Lambda_i u_i,$$
$$\frac{dv_i}{dt} = g(u_i, v_i) + d_2\Lambda_i v_i. \qquad (6)$$

By linear stability analysis, we obtain the characteristic function,

$$\lambda^2 - b_i\lambda + c_i = 0, \qquad (7)$$

where $b_i = a_{11} + a_{22} + d_1\Lambda_i + d_2\Lambda_i$, $c_i = d_1d_2\Lambda_i^2 + (a_{11}d_2 + a_{22}d_1)\Lambda_i + a_{11}a_{22} - a_{12}a_{21}$, and $\lambda(\Lambda_i) = \frac{b_i \pm \sqrt{b_i^2 - 4c_i}}{2}$. Namely, the stability of system (7) depends on the sign of $\mathrm{Re}\lambda(\Lambda_i)$, which keeps consistent with system (5). If $\mathrm{Re}\lambda(\Lambda_i) > 0$, system (7) is unstable. However, system (7) is unstable when $\mathrm{Re}\lambda(\Lambda_i) < 0$, which means it does not work due to the interaction between the negative wave number and the positive wave number.

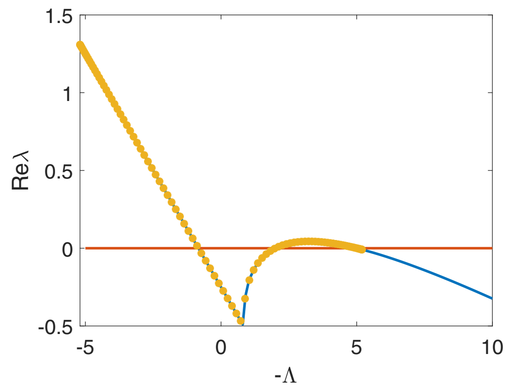
To further analyze the dynamic behavior of system (7), we treat the maximum (minimum) eigenvalue as the leading role to evaluate the Turing instability region. Because the range Λ depends on pk, the above system can be written as

$$\frac{du}{dt} = f(u, v) + d_1pku,$$
$$\frac{dv}{dt} = g(u, v) + d_2pkv. \qquad (8)$$

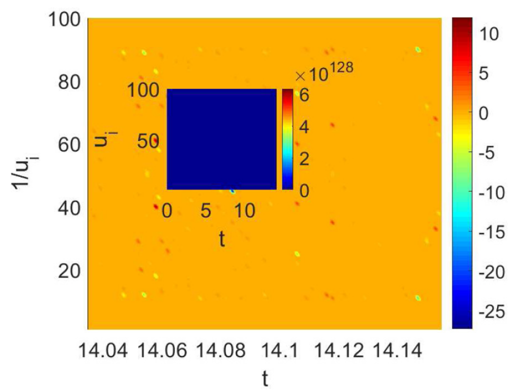
and

$$\frac{du}{dt} = f(u, v) - d_1pku,$$
$$\frac{dv}{dt} = g(u, v) - d_2pkv. \qquad (9)$$

In general, the stability of systems (9) and (10) determines the stability of system (3). We suppose $\Omega_1, \Omega_2, \Omega_3$ are sets, and system (3) is stable when $pk \in \Omega_1$ and $-pk \in$

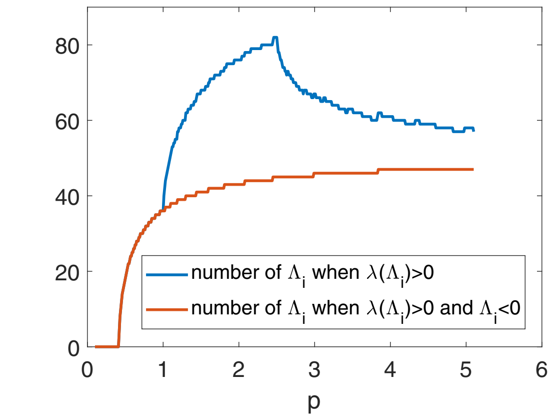


(a)

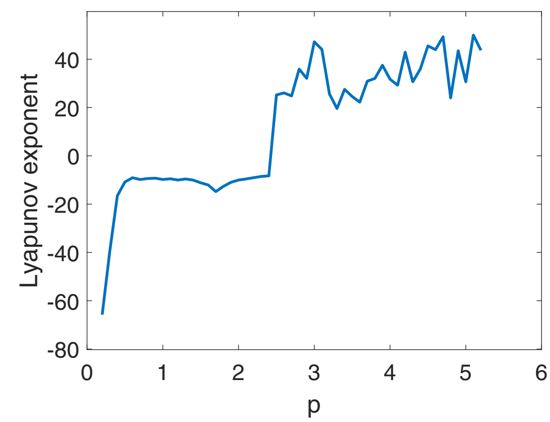


(b)

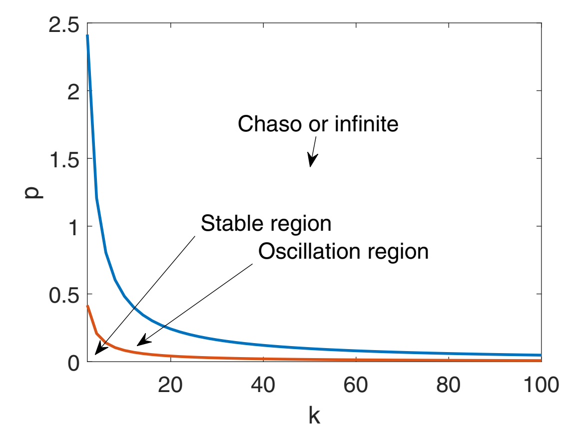
FIG. 7. The stability when the weights are $p = 2.6$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.



(a)



(b)



(c)

FIG. 8. (a) The number of eigenvalues Λ_i when $\mathrm{Re}\lambda_i > 0$. (b) The Lyapunov exponents about p when $dt = 0.01$. (c) The relationship between the p and the degree k.

Ω_1; system (3) is periodic oscillatory when $pk \in \Omega_2$ or $-pk \in \Omega_2$, and system (3) is chaotic or infinite when $pk \in \Omega_3$ or $pk \in \Omega_3$. Namely, system (3) is stable, periodic oscillatory, and chaotic or infinite, respectively, when $pk \in \Omega_1, \Omega_2, \Omega_3$. To a certain extent, the above results bring into correspondence with Benjamin-Feir instability [13–15]. We treat periodic oscillatory chaotic or infinite as Turing instability in this paper because the range of Ω_2, Ω_3 is challenging to determine. Moreover, the condition of Turing instability in a network-organized system can be described that Turing instability occurs in a continuous system, and one or more of the eigenvalues of the network lies in the Turing instability region in the network-organized system. Namely,

Theorem 2. (Sufficient condition of Turing instability). For a special network system, system (3) is always stable when $\pm pk \in \Omega_1$; Turing instability occurs when $pk \in \Omega_2 \cup \Omega_3$ or $-pk \in \Omega_2 \cup \Omega_3$. [System (3) is periodic oscillatory when $pk \in \Omega_2$; if $pk \in \Omega_3$, system (3) is chaotic or infinite.

Proof. Based on the above assumption and Lemma 2, the maximum eigenvalue $\Lambda_{\max} = pk$ and the minimum eigenvalue $\Lambda_{\min} = -pk$ lie in Ω_1. Namely, all the eigenvalues stay at Ω_1, and the system is stable. Otherwise, Turing stability occurs.

III. SIMULATION

In this section, we consider the above system in the Fizhugh-Nagumo model,

$$f(u, v) = c\left(u - \frac{u^3}{3} - v\right),$$
$$g(u, v) = c(au - bv),$$

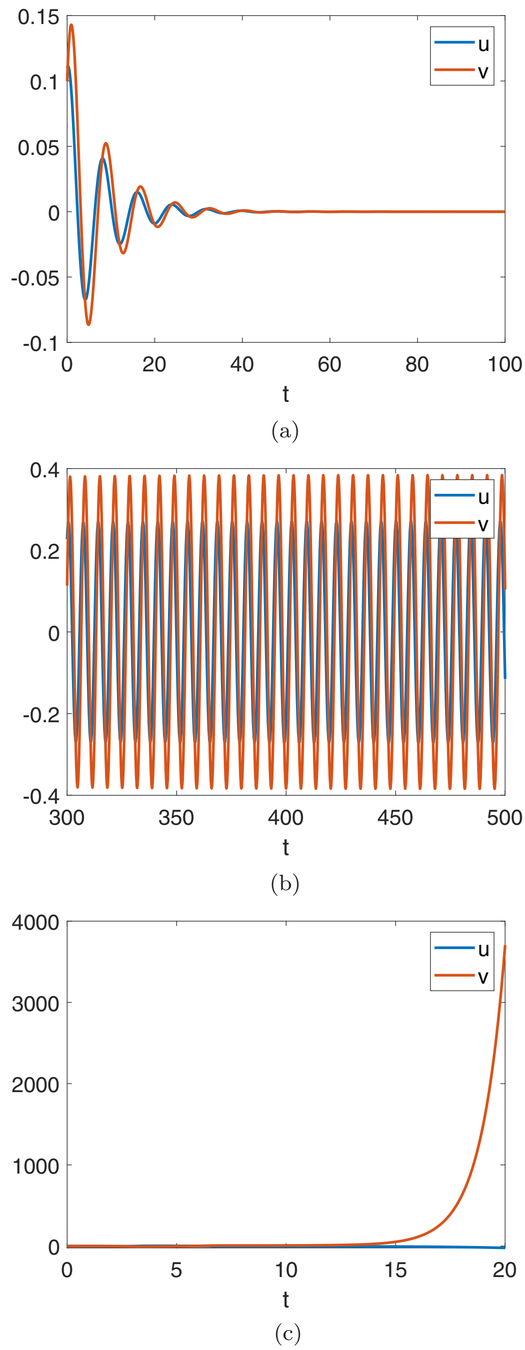


FIG. 9. The stability about pk. (a) System (9) is stable when $pk = 0.4$. (b) System (9) is a periodic oscillation when $pk = 0.85$. (c) System (9) is unstable when $pk = 4.85$.

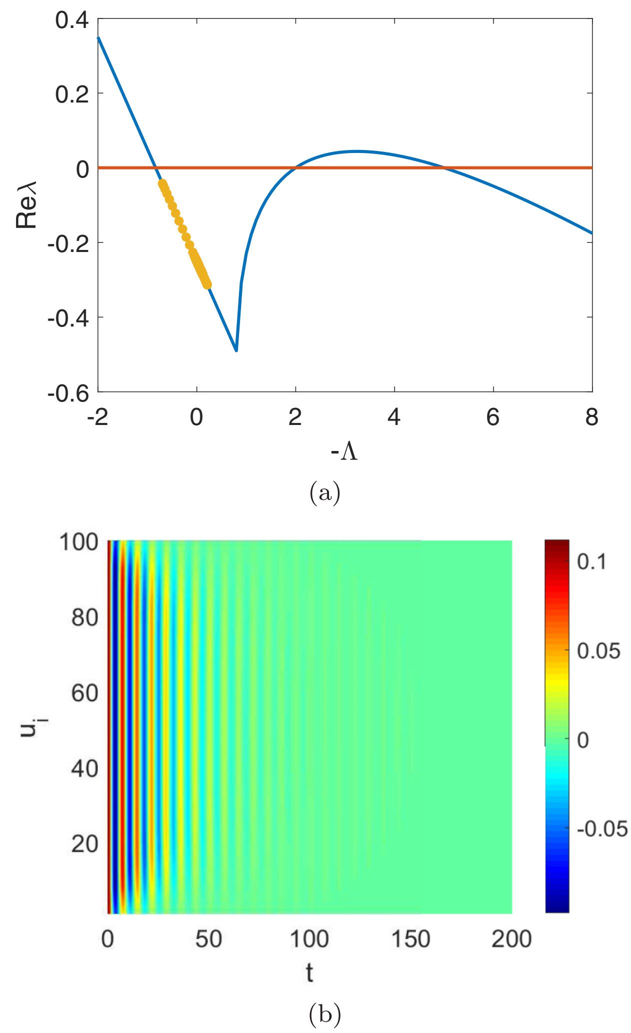


FIG. 10. The stability when the weights are $p = 0.05$, $m = 7$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

where variables u and v are the voltage (activator) and recovery voltage (inhibitor).

Here the Lyapunov exponent in network-organized system can be defined as

$$L = \ln\left\{\frac{\sqrt{\sum_{i=1}^{n}\left[\left(\frac{df_i(u,v)}{dt}\right)^2 + \left(\frac{dg_i(u,v)}{dt}\right)^2\right]}}{2n}\right\}, \tag{10}$$

where the system is stable or periodic oscillation when $L < 0$, chaos or infinity appear when $L > 0$, and dt is the initial perturbation.

According to the above theoretical analysis, the equilibrium point $(u_0, v_0) = (0, 0)$ of system (2) without diffusion is stable when $1 < b < a$, then the parameters can be set as $a = 2$, $b = 1.5$, $c = 1$, $m = 1$. And Turing instability occurs $(\Lambda > 0)$ in the continuous reaction-diffusion system when $d_1 = 0.1$, $d_2 = 0.5$. Meanwhile the wave number could induce the Hopf bifurcation and pitchfork bifurcation [Fig. 1(a)]. Also, the positive eigenvalue (the negative wave number) could induce Turing instability (Turing instability occurs when $\Lambda < 0$) (Fig. 1). Finally, we call I type Turing instability induced by the positive wave number, and II type Turing instability induced by the negative wave number [Fig. 1(b)].

First, we construct a special network with $n = 100$ although one node just connects its next node with the weights p in the present paper [Fig. 2(a)], and one node just connects its next seven nodes [Fig. 2(b)]. The same is true in other cases. Here we mainly consider the case $m = 1$, and system (3) can

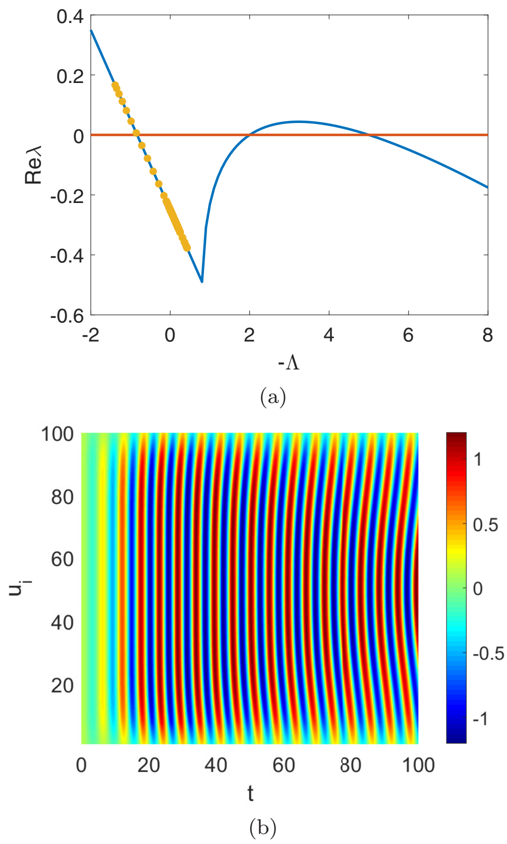


FIG. 11. The stability when the weights are $p = 0.1$, $m = 7$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

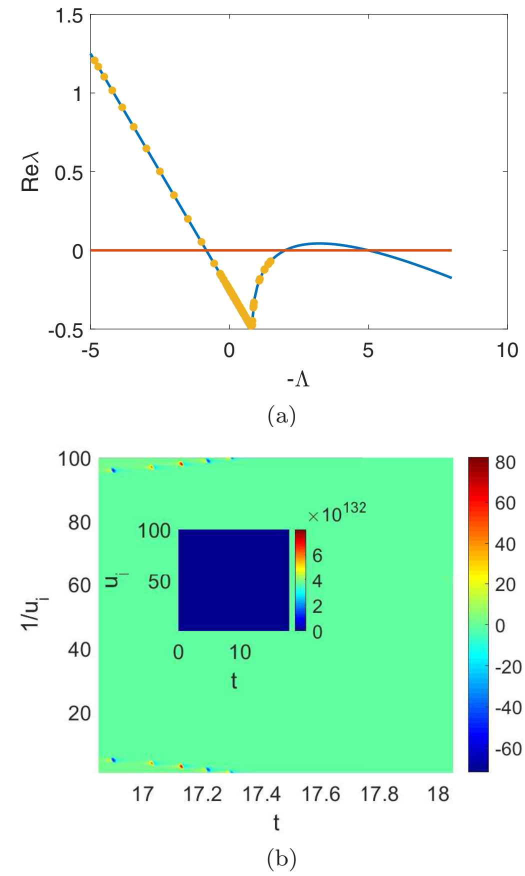


FIG. 12. The stability when the weights are $p = 0.35$, $m = 7$. (a) The intersection region with the eigenvalues of the network matrix. (b) The corresponding pattern formation.

be written as

$$\frac{du_i}{\partial t} = f(u_i, v_i) + d_1 \sum_j A_{ij} u_i,$$

$$\frac{dv_i}{\partial t} = g(u_i, v_i) + d_2 \sum_j A_{ij} v_i, \tag{11}$$

where $A_{ij} = p$ when $|i - j| \leqslant 1$ and $i \neq j$, $p > 0$ are weights, otherwise $A_{ij} = 0$.

Then we consider the stability of the network-organized system (12) in the following. Based on Theorem 1, the range of an eigenvalue Λ_i of the adjacency matrix in system (12) is in $[-2p, 2p]$. And due to Theorem 2, the system is always stable when all the eigenvalues of the network matrix are not in the instability region $\Lambda \cap B = \Phi$ [Fig. 3(a)], the pattern formation is uniformly distributed [Fig. 3(b)]. Meanwhile, all the neurons remain in the resting state, and no action potential occurs when the coupling strength $p = 0.1$ is weak. But the damped oscillations occur and become stable [Fig. 4(b)] when $[-2p, 2p]$ approaches the instability region [Fig. 4(a)]. Namely, some neurons' spiking occurs, but it was not enough to conduct completely (conduction failure). It is easy to know $(-\infty, -0.8333) \cap \Lambda \neq \Phi$ and $(2, 5) \cap \Lambda \neq \Phi$ [Fig. 5(a)] when $p = 0.5$, *II* type Turing instability occurs, and the system rapidly reaches a stable periodic oscillation [Fig. 5(b)]. Namely, the signal conduction is expected when the coupling strength of the neuron is moderate. Then *I* type Turing instability and *II* type Turing instability occur at the same time when $p = 2.4$ [Fig. 6(a)], the corresponding pattern formation and dynamical evolution are different [Fig. 6(b)]. Although the spiking of neurons occurs, it is not synchronous. Also, the number of intersections $B \cap \Lambda$ becomes large. And the number of the intersections $B \cap \Lambda$ becomes larger when $p = 2.6$ [Fig. 7(a)], and the chaos or infinity phenomenon occurs [Fig. 7(b)], which can be verified by the Lyapunov exponents [Fig. 8(a)]. That means the larger coupling strength of neurons could induce the chaotic system or nerve disease. The inhibitory neurons comprise 20%–30% of the neurons, and they are believed to be important in regulating the action potential [38,39]. The negative wave number corresponds to inhibitory neurons, and the positive wave number corresponds to excitatory neurons. And we may safely conclude that the number of negative wave numbers (the inhibitory neurons) should stay within a certain range. From [Fig. 8(a)], only the number of the negative wave numbers is few at the beginning when $\text{Re}\lambda(\Lambda_i) > 0$, and the inhibitory neurons could effectively regulate the conduction of signal transmission [Fig. 5]. Otherwise, conduction failure may occur [Figs. 4 and 8]. Meanwhile, the above findings illustrate the importance of the inhibitory neurons in regulating the action potential [38,39]. Also, the Lyapunov exponent is given, which means the neural system may become a chaotic state when the inhibitory neurons are larger [Figs. 8(a) and 8(b)]. Finally, the numerical ranges are obtained through $pk = 0.8333$ and $pk = 4.838$. Namely, the system is stable when $0 < pk < 0.8333$, and the system is periodic oscillation (chaotic or infinite) when $0.8333 < pk < 4.838$ ($pk > 4.838$). Above all, Theorem 2 is a novel approach to Turing instability in a network-organized system.

To investigate the Turing instability mechanism in the network-organized system, the region of stability about p and k is obtained, divided into three parts: stable region, periodic oscillation region, and chaos or infinity region. So what determines the stability of the network-organized system? Then we will consider the bifurcation point in the mean-field system. It is easy to know that the stability of system (3) is determined by the stability of systems (9) and (10). And the theoretical results indicate that system (3) is stable when $0 < pk < 0.8333$ [Fig. 9(a)]. Although the mean-field system's bifurcation point determines the network-organized system's critical values, we only find the critical value (bifurcation point) between the stable and the unstable regions. For the critical value between periodic oscillation [Fig. 9(b)] and infinity phenomenon (or chaos) [Fig. 9(c)] in the mean-field system, it is different from system (3). Maybe the chaos phenomenon (or infinity phenomenon) of the network-organized system is induced by the interaction of network nodes or the interaction between I Turing instability and II Turing instability. The term pk can be treated as an external stimulus of the FN model, and the conduction failure occurs when the stimulus strength is stronger or weaker. Namely, the moderate coupling strength is necessary for the signal conduction. Finally, we consider the network-organized system with $m = 7$, which is more complicated. But the dynamical behavior and conditions of the Turing instability are the same as $m = 1$, system (3) is stable [Fig. 10] when $pk < 0.8333$, periodic oscillation [Fig. 11], and the chaos or infinity [Fig. 12] occur when $pk > 0.8333$.

IV. CONCLUSION

We know that the neural network plays an essential role in the neural system. However, the role of the coupling weights in Turing instability and the importance of inhibitory neurons in conduction failure remain mysteries. To understand the mechanism of the Turing instability and the origin of the conduction failure, the theoretical analysis of Turing instability and a detail has been investigated in a network-organized Turing system. This numerical analysis reveals the effects of the weights on pattern formation and explained conduction failure mechanism in the inhibitory neurons for the FN model. Initially, we found the range of network wave number (the adjacency matrix) using Theorem 1. The stability analysis of the Turing system in a network-organized system was given by Theorem 2, and these analytical results are numerically validated. Additionally, the stability of the organized-network system is determined by the stability of the mean-field systems (9) and (10) and this dynamical behavior is determined by the range pk. We found Turing instability appears with increasing the negative wave number. The inhibitory neurons could effectively regulate the conduction of signal transmission, and the moderate coupling strength is necessary to the signal conduction. We also reveal the presence of chaotic phenomenon due to the interaction of network nodes or the interaction between I Turing instability and II Turing instability. Meanwhile, the above methods can be used for other models and networks.

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