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The synchronization of FitzHugh–Nagumo neuron network coupled by gap junction*

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It is well known that the strong coupling can synchronize a network of nonlinear oscillators. Synchronization provides the basis of the remarkable computational performance of the brain. In this paper the FitzHugh–Nagumo neuron network is constructed. The dependence of the synchronization on the coupling strength, the noise intensity and the size of the neuron network has been discussed. The results indicate that the coupling among neurons works to improve the synchronization, and noise increases the neuron random dynamics and the local fluctuations; the larger the size of network, the worse the synchronization. The dependence of the synchronization on the strength of the electric synapse coupling and chemical synapse coupling has also been discussed, which proves that electric synapse coupling can enhance the synchronization of the neuron network largely.

Keywords: synchronization, gap junction, FitzHugh–Nagumo model
PACC: 8730C, 8730E

1. Introduction

Synchronous activity among neurons is a very ubiquitous phenomenon and plays an important role in performing the remarkable computation of the brain. Many experiments suggest that it shapes the process of information in the brain, the sensory system and other neuronal networks.[1−5] For example, synchronization of γ oscillation (20–80 Hz) has been proved to relate to the object expression,[6] and simultaneous recordings in the primary motor cortex of monkeys during task performance demonstrate accurate spike synchronization.[7] As for its property, neuron can be described as a relaxation oscillator, which is essential for understanding some key issues in neuroscience. It is well known that the strong coupling can synchronize a population of nonlinear oscillators. In recent years, many theoretical studies have focused on the problem of to what extent the degree of synchronization can be controlled through the strength of the inter-oscillator coupling.[8] However, it has been argued that the transitions from the desynchronized state to the synchronized state are mediated not only by varying the coupling strength but also by changing the external stimulus applied to neurons.[9,10] The numerical simulations of coupled neurons indicated that synchronization can be achieved with optimally selecting noise intensity and coupling strength.[11−13] This idea implies that noise can play a significant role as a promoter of neuronal activity.

Diffusive interaction (electric synapse coupling) exists in neuron systems and is an important means of signal transmission between neurons. Many people have studied the effect of diffusive interaction on the neuronal and neuron network oscillation,[10−17] indicating that it can increase the synchronization from different aspects. In most studies, noise can be introduced by means of a fluctuating current. The phenomenological stochastic bifurcations have been investigated in noisy van der Pol–Bonhoeffer oscillators, and the results showed that external and/or synaptic noises can cause these systems to move along stochastic limit cycles determined by a set of parameters, where the deterministic equations do not show this behaviour at all. Thus, additive noise can indeed induce firing and drive the neurons to synchronize.[18]

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A small patch of cortex may contain thousands of similar neurons, each being connected with hundreds or thousands of other neurons. How to simulate so large a real system is a difficult problem. Computational neuroscientists have so far tried to understand the properties of neuron network by using two methods: (i) the direct numerical simulation; (ii) the analytical approaches such as mean-field (MF) theories and the Fokker–Planck equations (FPE). In the first method, it is difficult to simulate the real neuron network due to the limited computation ability; in the second method, the FPE are differential equations that are also difficult to solve. In 2003, Hasegawa[19] proposed a dynamical mean-field approximation (DMA) theory to simulate the activities of neuron network. The advantage of this method is that it can reduce the stochastic differential equations to the deterministic differential equations, cut down the number of differential equations largely and give a qualitative or semi-quantitative discussion about the properties of neuron network. And Hasegawa has proven that the larger the size of the network, the more accurate the computational results. Furthermore, the DMA theory based on the moments of local and global variables can be applied to more general stochastic systems besides neural networks.[20] However, the disadvantage is that it is hard to obtain explicit expressions for the spectrum of the population rate. To our knowledge, no explicit results have been derived like the power spectrum (or the autocorrelation function) of a single neuron, or the cross spectrum (or the cross correlation function) of two distinct neurons in the network.

Here we discuss the dependence of synchronization on the coupling strength, the noise intensity and the size of the network.

The paper is organized as follows. In Section 2, an N-unit FitzHugh–Nagumo neuron network is developed, and the equations derived can be reduced to eight-dimensional deterministic differential equations by adopting DMA method. In Section 3, the synchronization of neuron network is analysed. The effects of the noise intensity, the coupling strength and the size of the network on the synchronization are studied in Section 4. In Section 5, the effects of the chemical synapse and the electric synapse on the synchronization are compared with each other. Section 6 presents the conclusion.

2. The FitzHugh–Nagumo neuron network

We assume a neuron network consisting of N-unit FitzHugh–Nagumo (FN) neurons. Dynamics of a single FN neuron i is described by the nonlinear differential equations

$$\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = F[x_i(t)] - cy_i(t) + \frac{w}{N}\sum_{j(\neq i)} G(x_j(t)) + I_i^{(e)}(t) + \xi_i(t), \tag{1}$$

$$\frac{\mathrm{d}y_i(t)}{\mathrm{d}t} = bx_i(t) - \mathrm{d}y_i(t) + e, \tag{2}$$

where $F[x(t)] = kx(t)[x(t)-a][1-x(t)]$, $k = 0.5$, $a = 0.1$, $b = 0.015$, $c = 1.0$, $d = 0.003$, and $e = 0$;[21,22] x_i is the fast (voltage) variable and y_i is the slow (recovery) variable. And the term for electric synapse coupling is $G(x_j(t)) = x_j(t) - x_i(t)$. The letter w denotes the coupling strength, and the self-coupling terms are excluded. N is the normalization factor and the size of network. The fourth term in Eq.(1) is the external current,

$$I_i^{(e)}(t) = A\Theta(t - t_{\mathrm{in}})\Theta(t_{\mathrm{in}} + T_{\mathrm{w}} - t), \tag{3}$$

where $\Theta(x) = \begin{cases} 1 & x > 0 \\ 0 & x \leq 0 \end{cases}$, A is the current, t_{in} is the input time and T_{w} is the spike width. The fifth term in Eq.(1) is the Gaussian white noise

$$\langle \xi_i(t) \rangle = 0, \langle \xi_i(t)\xi_j(t') \rangle = \beta^2 \delta_{ij}\delta(t - t'), \tag{4}$$

$\langle\ \rangle$indicates the average over stochastic random variables and β is the noise intensity.

The global variables for the network and their average can be defined as

$$X(t) = \frac{1}{N}\sum_i x_i(t), \tag{5}$$

$$Y(t) = \frac{1}{N}\sum_i y_i(t), \tag{6}$$

$$\mu_1(t) = \langle X(t) \rangle, \tag{7}$$

$$\mu_2(t) = \langle Y(t) \rangle. \tag{8}$$

Define the variances and covariances between local variables as

$$\gamma_{11} = \frac{1}{N}\sum_i \langle \delta x_i^2 \rangle,$$

$$\gamma_{22} = \frac{1}{N}\sum_i \langle \delta y_i^2 \rangle,$$

$$\gamma_{12} = \frac{1}{N}\sum_i \langle \delta x_i \delta y_i \rangle. \tag{9}$$

These variables express the spatial average of fluctuations in local variables of x_i and y_i.

We define the variances and covariances between global variables as

$$\rho_{11} = \langle \delta X^2 \rangle, \quad \rho_{22} = \langle \delta Y^2 \rangle, \quad \rho_{12} = \langle \delta X \delta Y \rangle. \quad (10)$$

They express the spatial average of fluctuations in global variables of X and Y. In Eqs.(9) and (10) we have

$$\delta x_i = x_i(t) - \mu_1(t), \quad \delta y_i = y_i(t) - \mu_2(t), \quad (11)$$
$$\delta X = X(t) - \mu_1(t), \quad \delta Y = Y(t) - \mu_2(t). \quad (12)$$

Numerical calculations demonstrate that the membrane voltage distribution of the single FN neuron obeys the Gaussian distribution for the weak noise intensity.[22,23] In this paper, adopting the DMA theory,[19] we reduce the $2N$-dimensional stochastic differential equations to eight-dimensional deterministic differential equations (the detailed calculation is given in the appendix).

$$\frac{\mathrm{d}\mu_1}{\mathrm{d}t} = f_0 + f_2\gamma_{11} - c\mu_2 + I_i^{(e)}, \quad (13)$$
$$\frac{\mathrm{d}\mu_2}{\mathrm{d}t} = b\mu_1 - \mathrm{d}\mu_2 + e, \quad (14)$$
$$\frac{\mathrm{d}\gamma_{11}}{\mathrm{d}t} = 2f_1\gamma_{11} + 6f_3\gamma_{11}\gamma_{11} - 2c\gamma_{12} + \beta^2 + 2w(\rho_{11} - \gamma_{11}), \quad (15)$$
$$\frac{\mathrm{d}\gamma_{22}}{\mathrm{d}t} = 2b\gamma_{12} - 2\mathrm{d}\gamma_{22}, \quad (16)$$
$$\frac{\mathrm{d}\gamma_{12}}{\mathrm{d}t} = f_1\gamma_{12} + 3f_3\gamma_{11}\gamma_{12} - c\gamma_{22} + b\gamma_{11} - \mathrm{d}\gamma_{12} + w(\rho_{12} - \gamma_{12}), \quad (17)$$
$$\frac{\mathrm{d}\rho_{11}}{\mathrm{d}t} = 2f_1\rho_{11} + 6f_3\rho_{11}\gamma_{11} - 2c\rho_{12} + \frac{\beta^2}{N}, \quad (18)$$
$$\frac{\mathrm{d}\rho_{22}}{\mathrm{d}t} = 2b\rho_{12} - 2\mathrm{d}\rho_{22}, \quad (19)$$
$$\frac{\mathrm{d}\rho_{12}}{\mathrm{d}t} = f_1\rho_{12} + 3f_3\gamma_{11}\rho_{12} - c\rho_{22} + b\rho_{11} - \mathrm{d}\rho_{12}, \quad (20)$$

where $f_l = \left(\frac{1}{l!}\right) F^{(l)}(\mu_1)$.

These equations (13)–(20) can describe the properties of the neuron network. It is apparent that the dynamical properties are determined by the noise intensity β, the coupling strength w and the size of network N.

3. The synchronization

It is very easy to obtain from Eqs.(15) and (18) the following equation,

$$\rho_{k\lambda} = \begin{cases} \dfrac{\gamma_{k\lambda}}{N} \dfrac{w}{\beta^2} \to 0, \\ \gamma_{k\lambda} \dfrac{\beta^2}{w} \to 0. \end{cases} \quad (21)$$

Equation (21) is consistent with the central-limit theorem, and $\frac{\rho_{k\lambda}}{\gamma_{k\lambda}}$ will change as model parameters change. We will show that this change affects the degree of synchronous firing in neuron network.

Define the quantity $R(t)$ as

$$R(t) = \frac{1}{N^2} \sum_{ij} \langle [x_i(t) - x_j(t)]^2 \rangle = 2(\gamma_{11} - \rho_{11}). \quad (22)$$

When all neurons are in the completely synchronous state, we have $R(t) = 0$. In contrast, in the asynchronous (random) state, we have $R(t) = 2\left(1 - \frac{1}{N}\right)\gamma_{11} = R_0(t) > 0$. It can be seen that when $R(t) \to 0$, the response in the neuron network becomes synchronous.

Define the synchronization ratio as

$$S(t) = 1 - \frac{R(t)}{R_0(t)} = \frac{\left(\frac{\rho_{11}}{\gamma_{11}} - \frac{1}{N}\right)}{1 - \frac{1}{N}}. \quad (23)$$

When neurons are all in the synchronous state completely, we have $S(t) = 1$. In contrast, in the asynchronous (random) state, we have $S(t) = 0$. So the synchronization ratio is a parameter appropriate for describing the degree of synchronous firings in the neuron network.

4. Calculated results

From Eqs.(13)–(23), the synchronization ratio can be calculated. In this study, we pay our attention to the problem about the response of the FN neuron network to a single spike input. We see that there exists a critical magnitude of $A_c = 0.0442$ below which firings of neuron cannot take place without noise ($\beta = 0$).[19] Use the parameters of $A = 0.10$, $\theta = 0.5$, $t_{in} = 100$, $T_w = 10$. We adopt the 4th-order Runge–Kutta method to solve Eqs.(13)–(20), and all the calculated quantities are given dimensionless.

Figure 1 shows that every neuron in the network is independent, and is stimulated by independent white noises. So in Fig.1(a), when $t < 100$, the average voltage of the neuron network is equal to zero. When a spike is input at $t = 100$, all the neurons will emit a spike immediately and the average voltage of the neuron network has a spike. After a refractory period, the global voltage returns to zero again. In Figs.1(b) and 1(c), the curves of γ_{11} and ρ_{11} have both double-peak. We may imagine that all the neurons are in the same state when there is no noise, and thus the average voltage will be equal to zero and does not show a peak. So the two peaks are caused by noise. The values of γ_{11} and ρ_{11} here satisfy Eq.(21).

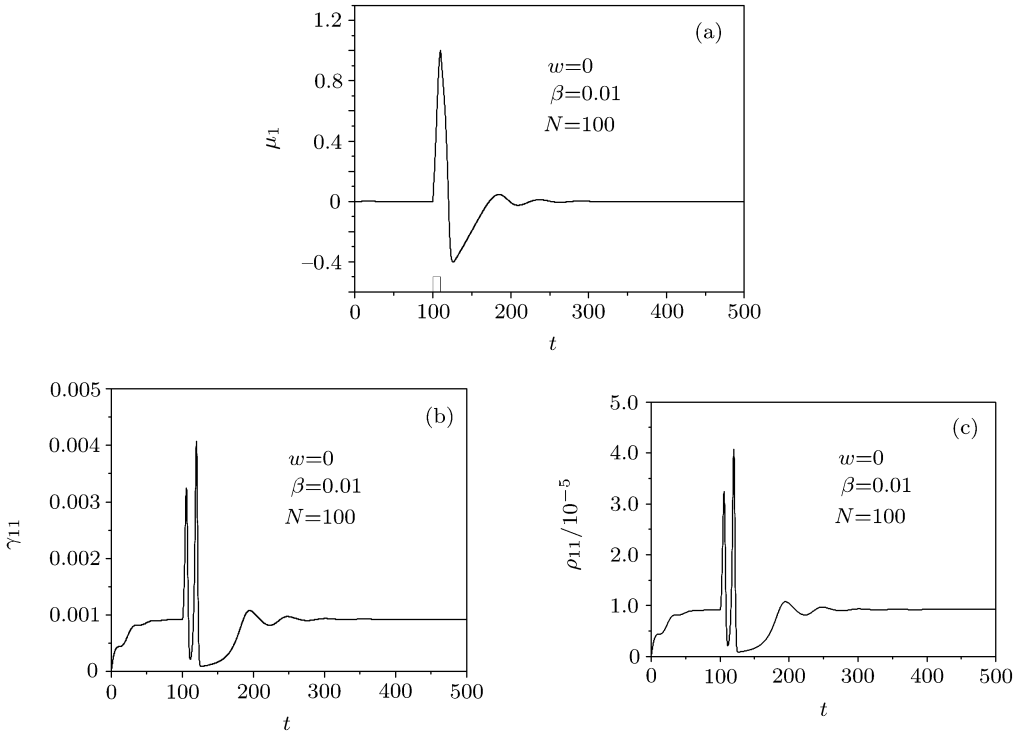


Fig.1. Variation of means, variance and covariance with time.

Figure 2 indicates that only when the noise acts on the neurons, are the responses of all neurons random, and their activities asynchronous , so $S(t) = 0$.

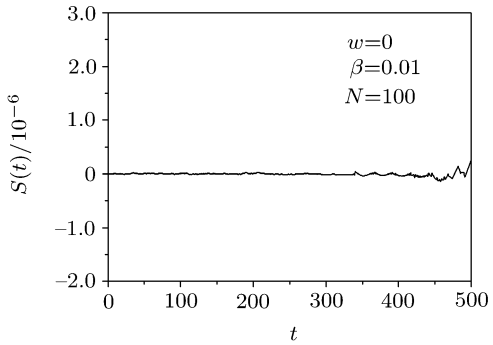


Fig.2. The synchronization ratio $S(t)$ as a function of time.

Couplings among neurons can improve the synchronous dynamics and suppress local fluctuations, as shown Fig.3. When the noise intensity is fixed, the synchronization ratio $S(t)$ increases with the increase of coupling strength and the synchronous activities. When $t = 100$, all neurons are injected into the same current at the same time and response at the same time, thus the curve of $S(t)$ has a spike. From this figure, we also find that the maximal value of $S(t)$ increases with increasing coupling strength, thus it can be used to express the network synchronization, as denoted by $S_{\max}$.

It can be seen from Fig.4 that when the size of network is fixed, the value of $S_{\max}$ increases with increasing coupling strength, which is consistent with the results in Fig.3. It is also very clear that when the coupling strength is fixed, the synchronization improves with the decrease of network size. This is very easy to understand.

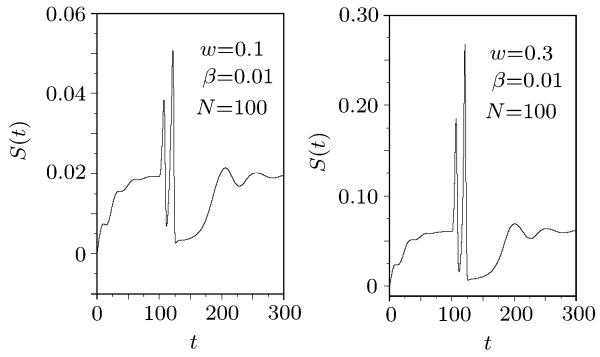


Fig.3. The variation of synchronization ratio with time for different coupling strengths.

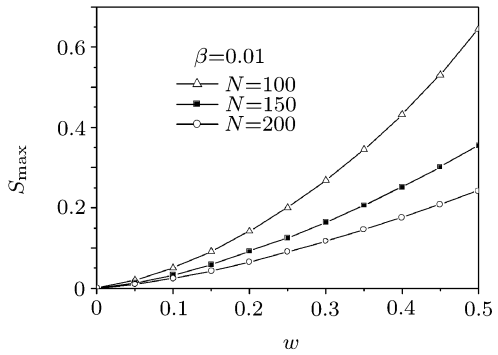


Fig.4. The dependence of $S_{\max}$ on w.

The network synchronization is determined by the coupling strength and the noise intensity jointly. When the coupling strength is fixed, the larger the noise intensity, the more random the response of neuron. And the correlation of the neuron activity becomes smaller and smaller with decreasing $S_{\max}$. The correlation and the $S_{\max}$ increase with increasing coupling strength, from the analysis above, we know that the synchronization increases with increasing coupling strength and decreases with increasing noise intensity and the network size.

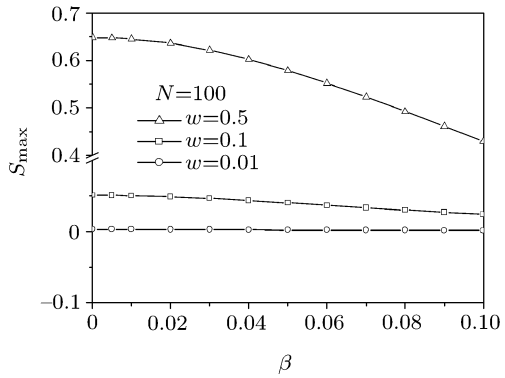


Fig.5. The dependence of $S_{\max}$ on β.

5. The different effects of electric and chemical synapse couplings on the synchronization

Synapse propagates information among the neurons and can be divided into two types: chemical synapse and electric synapse.

Chemical synapse coupling is nonlinear. The mechanism is that only when the membrane voltage of the presynaptic neuron reaches the threshold value, can it emit a spike, stimulate the release of neuron transmitter and have an effect on postsynaptic neuron. This coupling is always denoted by the S function, adopted in Ref.[19] and expressed as

$$G(x) = \frac{1}{1+\exp(-(x-\theta)/\alpha)}, \tag{24}$$

where θ is the threshold value and α is the function width.

Comparing the effects of electric synapse and chemical synapse couplings on the synchronization, we have the result as follows: when the coupling strength is the same for the two types of synapse, $S_{\max}$ of the electric synapse coupling is larger than that of the chemical synapse coupling, indicating that the electric synapse coupling has a larger effect on the synchronization. And this effect will increase with increasing coupling strength.

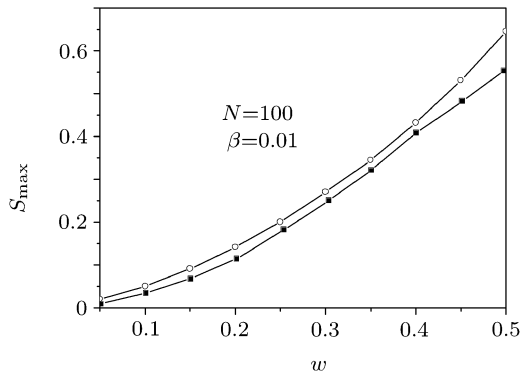


Fig.6. $S_{\max}$ versus w for the electric synapse and the chemical synapse couplings (black squares: the chemical synapses (data from Ref.[19]); open circles: electric synapse).

In order to analyse this effect clearly, we make the following approximation. For the chemical synapse coupling, the coupling term for the ith neuron in the network is given by

$$G(x_j) = \frac{1}{1+\exp(-(x_j-\theta)/\alpha)}. \tag{25}$$

We can expand Eq.(25) around the value x_i until the first-order term in case that all neuron activities are synchronous and $x_j \approx x_i$. Then Eq.(25) can be rewritten as

$$G(x_j) = \frac{1}{\alpha}\frac{\exp(-(x_i-\theta)/\alpha)}{[1+\exp(-(x_i-\theta)/\alpha)]^2}(x_j - x_i) + \frac{1}{1+\exp(-(x_i-\theta)/\alpha)}. \tag{26}$$

Comparing only the first term in Eq.(26) with the electric synapse coupling $G(x_j(t)) = x_j(t) - x_i(t)$, we can find that it is α and θ that make the differences between the chemical synapse and the electric synapse. In Eqs.(25) and (26) θ is determined by the chemical synapse mechanism and the value of α reflects the delay time. They cannot be neglected in chemical synapse. Considering the higher order term, we obtain the same results. Due to the different mechanisms, the chemical synapse and the electric synapse can induce different dynamics in network, such as stochastic coherence, etc.[24]

For the network of neurons coupled by the chemical synapse, there is a characteristic delay time in the propagation of spikes. For this delay, all the neurons in the network are difficult to synchronize. For the electric synapse, the spikes also show slight propagation delay, but much smaller than that in the chemical synapse case. If we increase the value of the coupling strength, the system would remain synchronous for a larger system size. This would not happen in the chemical synapse case, because the delay is intrinsic for the synapses and does not depend on the coupling strength. This is a fundamental qualitative difference between chemical coupling and electrical coupling, which is worth being highlighted.

6. Conclusion

Synchronization is a very ubiquitous phenomenon in the fields of physics and biology. Adopting the DMA theory, we have studied the dependence of the synchronization on the coupling strength, the network size and the noise intensity. The simulation suggests that with the increase of coupling strength and the decrease of size and noise intensity, the synchronization of neurons in the network is improved greatly. The different effects of the electric synapse and the chemical synapse couplings on the synchronization have been discussed, which proves that the electric synapse coupling can increase the synchronization of the neurons in the network greatly.

Appendix

We may expand Eqs.(1) and (2) around the average value to the third-order terms

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = F(\mu_1) + F'(\mu_1)\delta x_i + \frac{1}{2}F^{(2)}(\mu_1)\delta x_i^2 + \frac{1}{6}F^{(3)}(\mu_1)\delta x_i^3 - c\mu_2 - c\delta y_i + I_i^{(c)} + I_i^{(e)} + \xi_i, \tag{A1}$$

$$\frac{\mathrm{d}y_i}{\mathrm{d}t} = b\mu_1 - \mathrm{d}\mu_2 + b\delta x_i - \mathrm{d}\delta y_i + e, \tag{A2}$$

where

$$I_i^{(c)} = \frac{w}{N}\sum_{j(\neq i)}\delta x_j(t) - w\left(1-\frac{1}{N}\right)\delta x_i(t). \tag{A3}$$

With the formulae (5) and (6), we can have

$$\frac{\mathrm{d}\mu_1}{\mathrm{d}t} = \left\langle \frac{1}{N}\sum_i \frac{\mathrm{d}x_i}{\mathrm{d}t}\right\rangle, \tag{A4}$$

$$\frac{\mathrm{d}\mu_2}{\mathrm{d}t} = \left\langle \frac{1}{N}\sum_i \frac{\mathrm{d}y_i}{\mathrm{d}t}\right\rangle. \tag{A5}$$

Using Eqs.(A1) and (A4), we can obtain Eq.(13). From Eqs.(A2) and (A5), we can obtain Eq.(14).

Using formulae (11), (A1), (A2), (A3) and (A4), we have

$$\frac{\mathrm{d}\delta x_i}{\mathrm{d}t} = f_1\delta x_i + f_2(\delta x_i^2 - \gamma_{11}) + f_3\delta x_i^3 - c\delta y_i + \delta I_i^{(c)} + \xi_i, \tag{A6}$$

$$\frac{\mathrm{d}\delta y_i}{\mathrm{d}t} = b\delta x_i - \mathrm{d}\delta y_i, \tag{A7}$$

where

$$\delta I_i^{(c)} = \frac{w}{N}\sum_{j(\neq i)}\delta x_j(t) - w\left(1-\frac{1}{N}\right)\delta x_i(t). \tag{A8}$$

From Eqs.(A6)–(A8), we can derive

$$\frac{\mathrm{d}\gamma_{11}}{\mathrm{d}t} = \frac{1}{N}\sum_i\left\langle 2\delta x_i\frac{\mathrm{d}\delta x_i}{\mathrm{d}t}\right\rangle, \tag{A9}$$

$$\frac{\mathrm{d}\gamma_{22}}{\mathrm{d}t} = \frac{1}{N}\sum_i\left\langle 2\delta y_i\frac{\mathrm{d}\delta y_i}{\mathrm{d}t}\right\rangle, \tag{A10}$$

$$\frac{\mathrm{d}\gamma_{12}}{\mathrm{d}t} = \frac{1}{N}\sum_i\left\langle \delta y_i\frac{\mathrm{d}\delta x_i}{\mathrm{d}t} + \delta x_i\frac{\mathrm{d}\delta y_i}{\mathrm{d}t}\right\rangle, \tag{A11}$$

$$\frac{\mathrm{d}\rho_{11}}{\mathrm{d}t} = \frac{1}{N^2}\sum_j\sum_i\left\langle 2\delta x_i\frac{\mathrm{d}\delta x_j}{\mathrm{d}t}\right\rangle, \tag{A12}$$

$$\frac{\mathrm{d}\rho_{22}}{\mathrm{d}t} = \frac{1}{N^2}\sum_j\sum_i\left\langle 2\delta y_i\frac{\mathrm{d}\delta y_j}{\mathrm{d}t}\right\rangle, \tag{A13}$$

$$\frac{\mathrm{d}\rho_{12}}{\mathrm{d}t} = \frac{1}{N^2}\sum_j\sum_i\left\langle \delta y_j\frac{\mathrm{d}\delta x_i}{\mathrm{d}t} + \delta x_i\frac{\mathrm{d}\delta y_j}{\mathrm{d}t}\right\rangle. \tag{A14}$$

We have adopted the following Gaussian decoupling and mean-field approximation.[19]

The fourth-order variances are assumed to be

$$\frac{1}{N}\sum_i \langle \delta x_i^4 \rangle \cong 3\gamma_{11}\gamma_{11}, \tag{A15}$$

$$\frac{1}{N}\sum_i \langle \delta x_i^3 \delta y_i \rangle \cong 3\gamma_{11}\gamma_{12}, \tag{A16}$$

$$\frac{1}{N^2}\sum_j \sum_i \langle \delta x_i \delta x_j^3 \rangle \cong 3\gamma_{11}\rho_{11}, \tag{A17}$$

$$\frac{1}{N^2}\sum_j \sum_i \langle \delta y_i \delta x_j^3 \rangle \cong 3\gamma_{11}\rho_{12}. \tag{A18}$$

other fourth-order terms being set to zero.

The third-order variances and terms higher than fourth order are neglected.

Using Eqs.(A6–A8) and (A9–A17), we can obtain Eqs.(15–20).

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