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Temporal association in a network of neuronal oscillators

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Abstract

We investigate temporal association in a set of globally coupled neuronal oscillators, which retrieves time sequences of stored patterns. The asymmetry-to-symmetry ratio in the synaptic coupling as well as the total strength turns out to play a major role in these phenomena. By means of numerical simulations, we identify four different states: the memory-retrieval state, the temporal-association state, the mixed-memory state and the no-memory state, and obtain the corresponding phase boundaries on the plane of the asymmetry ratio and the coupling strength.

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1. Introduction

The oscillatory behaviours of neurons are believed to play important roles in information processing in biological systems [1, 2]. In general an assembly of oscillators with distributed natural frequencies can exhibit a coherent motion among the constituents, called collective synchronization [3, 4]; such synchronization observed in the cortex suggests that information processing is cooperative, involving many neurons. This has led to many attempts to explain such intriguing features of a brain as learning and memory in terms of collective properties of a network of neurons [5]. Among these, the associative memory, the function of which is to store and recall information in association with other information [6–8], and temporal association, which retrieves a sequence of embedded patterns successively [9, 10], have been much studied. Such recalling of temporal sequences can be endowed by introducing asymmetry in the synaptic coupling of the neural network, which may prevent the system from relaxing to the state of the minimum energy function. Most of these studies have been based on the Ising-type model of neural networks, where each neuron is considered to have two possible states [11]. In the phase model of neural networks, on the other hand, each neuron is regarded as a limit-cycle oscillator and its state described by the phase [12]. This is more convenient for addressing the oscillatory behaviour and naturally exhibits synchronization as a mechanism for memory storage.

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This paper presents an attempt to observe the temporal-association phenomena in the network of limit-cycle neuronal oscillators. We introduce asymmetry in the coupling and obtain the self-consistency equation for the order parameter, on the basis of which the collective synchronization behaviour is investigated. Particular attention is paid to the interplay of the symmetric coupling and the asymmetric one, and the schematic phase boundaries are obtained numerically on the plane of the asymmetry-to-symmetry ratio and the coupling strength. This reveals four different states in appropriate regions: the *memory-retrieval* state, where the state of the system has a nonzero correlation with only one specific pattern; the *temporal-association* state, where a temporal sequence of stored patterns is retrieved; the *mixed-memory* state, where the system has the same nonvanishing correlation with all the stored patterns, and the *no-memory* state, where the system has no appreciable correlation with any stored pattern.

There are four sections in this paper: section 2 introduces the network of coupled neuronal oscillators with asymmetric coupling and the order parameter, which measures collective synchronization in the system. The self-consistency equation for the order parameter is derived, and the corresponding behaviour of the order parameter is examined both analytically and numerically. Section 3, the main part of this paper, investigates the system with both symmetric and asymmetric couplings, revealing four different states including the temporal-association state. Typical behaviour of the order parameter in each state is shown, and the phase boundaries are obtained on the plane of the asymmetry-to-symmetry ratio and the coupling strength. Finally, a brief summary is given in section 4.

2. Asymmetric coupling

We consider a population of N neuronal oscillators, the ith of which is described by its phase ϕ_i $(i = 1, 2, \ldots, N)$:

$$\frac{\mathrm{d}\phi_i}{\mathrm{d}t} = \omega_i - \sum_{j=1}^{N} J_{ij} \sin(\phi_i - \phi_j) + \gamma_i(t). \tag{1}$$

The intrinsic frequency ω_i of the ith oscillator is randomly distributed over the whole system according to the distribution $g(\omega)$, which is assumed to be smooth and symmetric about $\omega = 0$. The second term on the right-hand side represents the coupling between the ith and the jth neurons. The third term represents the white noise with zero mean and correlation

$$\langle \gamma_i(t)\gamma_j(t') \rangle = 2T\delta_{ij}\delta(t-t')$$

where the noise strength T plays the role of the 'effective temperature' of the system.

In the case of the uniform coupling $J_{ij} = K/N$, equation (1) reduces to the simple oscillator system studied extensively [3,4]. The symmetric coupling in the form

$$J_{ij} = \frac{2J}{N} \sum_{\mu=1}^{p} \cos(\xi_i^\mu - \xi_j^\mu) \tag{2}$$

has been employed in the network of neuronal oscillators, storing p patterns [12]. The number ξ_i^μ $(\mu = 1, 2, \ldots, p)$ describes the state (phase) of the ith neuron in the μth pattern; they are random variables in the interval $[0, 2\pi)$, following the distribution $f_\mu(\xi^\mu)$. It has been shown that the system can indeed be in the memory-retrieval state characterized by a nonvanishing macroscopic correlation with only one specific pattern [12]. Here such a memory-retrieval state corresponds to the state in which collective synchronization sets in. Thus the transition between the memory-retrieval state and the no-memory state, where all components of the order parameter have vanishingly small values, is simply the synchronization–desynchronization transition prevalent in networks of oscillators.

We here examine how the asymmetric coupling affects the collective synchronization behaviour governed by equation (1) and probe the possibility of temporal association, which has not been observed in the system with symmetric coupling given by equation (2). For this purpose, we consider the asymmetric coupling of the form

$$J_{ij} = \frac{2J}{N} \sum_{\mu=1}^{p} \cos(\xi_i^{\mu} - \xi_j^{\mu-1}) \tag{3}$$

where the cyclic boundary condition $\xi_i^0 = \xi_i^p$ has been chosen for the random patterns $\{\xi_i^{\mu}\}$. (The system with both symmetric and asymmetric couplings will be considered in the next section.)

It is convenient to introduce the set of complex order parameters

$$\Psi^{\mu} \equiv \frac{1}{N} \sum_{j=1}^{N} \mathrm{e}^{\mathrm{i}(\phi_j \pm \xi_j^{\mu})} = m_{\pm}^{\mu} \mathrm{e}^{\mathrm{i}\theta_{\pm}^{\mu}} \tag{4}$$

which characterizes the collective behaviour of the N-oscillator network described by equation (1). Here m_-^{μ} measures the overlap between the state of the network and the pattern ξ^{μ} while m_+^{μ} are auxiliary order parameters. Thus a nonvanishing value of m_-^{μ} indicates the appearance of synchronization. Taking into account equations (3) and (4), we write equation (1) in the form

$$\frac{\mathrm{d}\phi_i}{\mathrm{d}t} = \omega_i - J \sum_{\mu=1}^{p} \left[m_-^{\mu-1} \sin(\phi_i - \theta_-^{\mu-1} - \xi_i^{\mu}) + m_+^{\mu-1} \sin(\phi_i - \theta_+^{\mu-1} + \xi_i^{\mu}) \right] + \gamma_i(t) \tag{5}$$

which, together with equation (4), constitutes the self-consistency equations for the order parameter.

To determine the stationary properties of equation (5), we consider the probability density $P(\phi, t; \omega, \xi^{\mu})$ for the distribution of oscillators with phase ϕ at time t, and instead of the Langevin equation (5), resort to the appropriate Fokker–Planck equation [13], which reads

$$\frac{\partial P}{\partial t} = \frac{\partial}{\partial \phi} \left(\frac{\partial V}{\partial \phi} + T \frac{\partial}{\partial \phi} \right) P \tag{6}$$

with the potential given by

$$V(\phi; \omega, \xi^{\mu}) \equiv -\omega\phi - J \sum_{\mu=1}^{p} \left[m_-^{\mu-1} \cos(\phi - \theta_-^{\mu-1} - \xi^{\mu}) + m_+^{\mu-1} \cos(\phi - \theta_+^{\mu-1} + \xi^{\mu}) \right]. \tag{7}$$

It is obvious that the stationary solution $P^{(0)}(\phi; \omega, \xi^{\mu})$ of the Fokker–Planck equation (6) satisfies

$$\left(\frac{\partial V}{\partial \phi} + T \frac{\partial}{\partial \phi} \right) P^{(0)} \equiv S \tag{8}$$

where S is determined by the normalization condition $\int_0^{2\pi} \mathrm{d}\phi\, P^{(0)} = 1$. We henceforth concentrate on the noiseless case ($T = 0$) and seek the solution for m_-^{μ} with $m_+^{\mu} = 0$ for all μ; this manifests the randomness of the distribution of ξ_i^{μ}. At $T = 0$ the stationary solution is given by

$$P^{(0)} = \begin{cases} \delta[\phi - \alpha - \sin^{-1}(\omega/JQ)] & \text{for} \quad |\omega| \leqslant JQ \\ \dfrac{\sqrt{\omega^2 - (JQ)^2}}{2\pi |\omega - JQ \sin(\phi - \alpha)|} & \text{for} \quad |\omega| > JQ \end{cases} \tag{9}$$

with Q and α defined according to

$$Qe^{i\alpha} \equiv \sum_{\mu=1}^{p} m_{-}^{\mu-1} e^{i(\xi^{\mu}+\theta_{-}^{\mu-1})}. \tag{10}$$

Assuming self-averaging, we now express the average in equation (4) in terms of the (stationary) probability distribution, which is expected to be valid in the zero-storage limit, i.e. for finite p in the thermodynamic limit ($p/N \to 0$), and write equation (4) in the form

$$m_{\pm}^{\mu} e^{i\theta_{\pm}^{\mu}} = \left\langle\!\!\left\langle \int_{0}^{2\pi} d\phi\, e^{i(\phi\pm\xi^{\mu})}\, P^{(0)}(\phi;\omega,\xi^{\mu}) \right\rangle\!\!\right\rangle_{\omega,\xi^{\mu}} \tag{11}$$

where $\langle\!\langle \cdots \rangle\!\rangle_{\omega,\xi^{\mu}}$ denotes the average over the distributions of ω and ξ^{μ}. It is then straightforward to compute the order parameter from equation (11) together with equation (9). Substitution of the latter into the former yields, to the lowest order,

$$m^{\mu} e^{i\theta^{\mu}} = \sqrt{\frac{\pi}{8}}\frac{J}{\sigma}\left\{1 - \frac{1}{8}\left(\frac{J}{\sigma}\right)^{2}\left[2\sum_{k=1}^{p}{}'(m^{k-1})^{2} + (m^{\mu-1})^{2}\right]\right\} m^{\mu-1} e^{i\theta^{\mu-1}} \tag{12}$$

where the frequency distribution and the pattern distribution have been chosen to be Gaussian with variance σ^2 and uniform, respectively: $g(\omega) = (\sqrt{2\pi}\sigma)^{-1}e^{-\omega^2/2\sigma^2}$ and $f_{\mu}(\xi^{\mu}) = 1/2\pi$ for $0 \leqslant \xi^{\mu} < 2\pi$. The prime in the summation represents the restriction $k \neq \mu$ whereas for simplicity the subscripts $(-)$ in m_{-}^{μ} and θ_{-}^{μ} have been dropped.

It is obvious that equation (12) does not bear the solution of the type $m^{\mu} \propto \delta_{\mu 1}$. Accordingly, unlike the symmetric coupling given by equation (2), the asymmetric coupling in equation (1) does not allow the memory-retrieval state. We instead search for the mixed-memory state, where all components of the order parameter tend to reach the same stationary value ($m^{\mu} = m$ for all μ). Equation (12) gives the solution for such a mixed-memory state:

$$m = \begin{cases} \sqrt{\dfrac{8}{2p-1}}\left(1 - \sqrt{\dfrac{8}{\pi}}\dfrac{\sigma}{J}\right)^{1/2}\dfrac{\sigma}{J} & \text{for } \frac{J}{\sigma} \geqslant \sqrt{\frac{8}{\pi}} \\ 0 & \text{for } \frac{J}{\sigma} < \sqrt{\frac{8}{\pi}}. \end{cases} \tag{13}$$

Thus the system with asymmetric coupling undergoes a transition from the no-memory state into the mixed-memory state as J/σ is increased beyond the critical value $\sqrt{8/\pi}$. For a given value of J/σ, the order parameter decreases with the number of stored patterns, proportional to $(2p-1)^{-1/2}$. Interestingly, in the system with symmetric coupling the critical value, separating the memory-retrieval state from the no-memory state, is also given by $(J/\sigma)_c \equiv \sqrt{8/\pi}$ [12], suggestive of the duality between the two cases.

To confirm the above analytical results, we have also performed numerical simulations, integrating directly the set of equations of motion (5) and computing the order parameter via equation (4). Equation (5) for a system of $N = 5000$ oscillators has been integrated with discrete time steps of $\Delta t = 0.01$. Various values of the coupling strength J as well as the number p of the stored patterns have been considered while the variance of the distribution of intrinsic frequencies have been set equal to unity ($\sigma = 1$).

Figure 1 presents the obtained behaviour of the order parameter with time for $J = 10$ and for (*a*) $p = 3$ and (*b*) $p = 10$. In both cases the system is in the mixed-memory state: each component of the order parameter, which measures the correlation of the state with each pattern, approaches the same value m after the initial transient time. For comparison, the behaviour of the order parameter in the system with the symmetric coupling given by equation (2) is shown in figure 2. Although the values of the parameters are the same ($J = 10$, $\sigma = 1$ and $p = 10$), one component reaches a value close to unity ($m^{\mu=1} \approx 1$) while the others remain

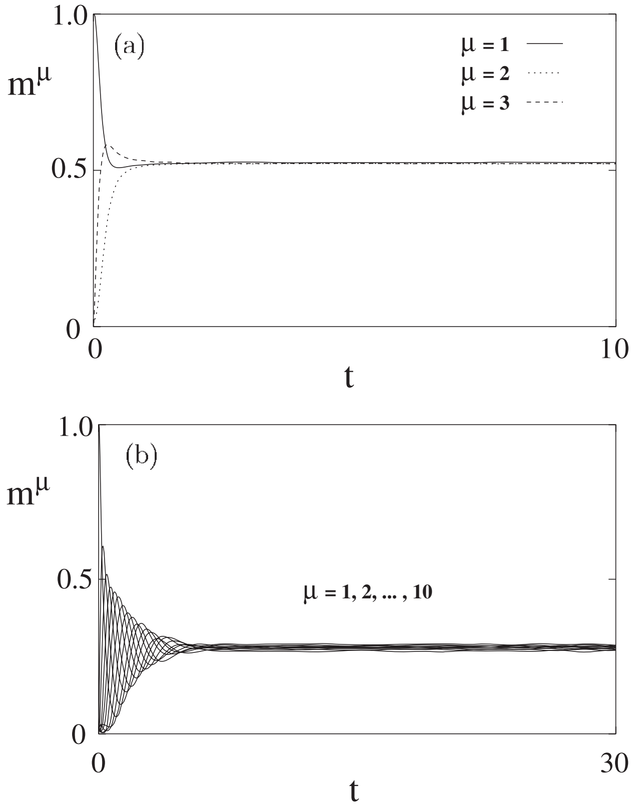

Figure 1. Behaviour of the order parameter with time in the mixed-memory state of the system with asymmetric coupling. The coupling strength is $J = 10$ whereas the number of stored patterns is (*a*) $p = 3$ and (*b*) $p = 10$. After the initial transient time all the components m^μ of the order parameter approach the same value.

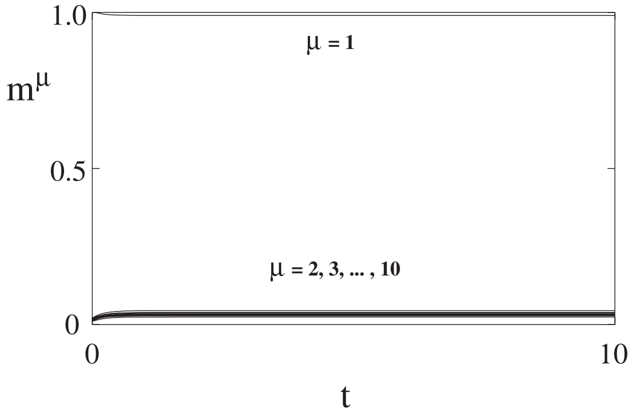

Figure 2. Behaviour of the order parameter in the memory-retrieval state of the system with symmetric coupling. The uppermost line near unity corresponds to $m^{\mu=1}$; other components ($\mu \neq 1$) are shown to be negligibly small. Parameter values are the same as those in figure 1(*b*).

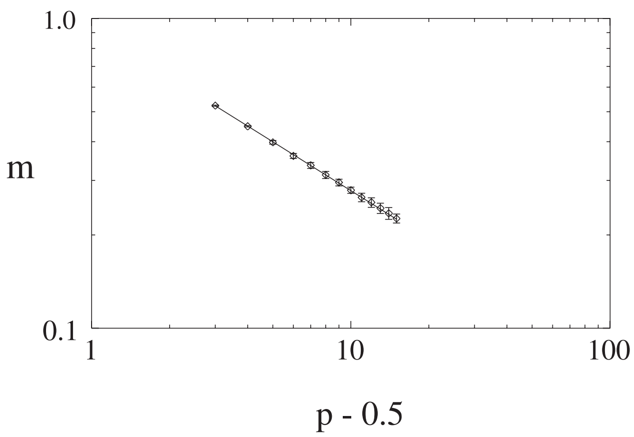

Figure 3. Dependence of the stationary value m of the order parameter upon the number p of stored patterns in the mixed-memory state. The data represented by diamonds, with the error bars estimated by the standard deviations, are shown to be well fitted to the line given by $m = 0.81 \times (p - 0.5)^{-0.47}$.

vanishingly small ($m^{\mu\neq 1} \approx 0$), thus indicating the memory retrieval state. Figure 3 shows the dependence of the stationary value of the order parameter upon the number of stored patterns in the mixed-memory state, which is consistent with the analytical result, $m \propto (2p-1)^{-1/2}$. We thus conclude that the system with only asymmetric coupling as well as that with symmetric coupling does not exhibit temporal association. To achieve temporal association, we need to consider the system with both symmetric and asymmetric couplings.

3. Interplay of symmetric and asymmetric couplings

In this section we consider a network of neuronal oscillators with the synaptic coupling given by the (weighted) sum of equations (2) and (3), and examine the interplay of the symmetric coupling and the antisymmetric one. When both couplings are present, the set of equations of motion (1) in the absence of noise assumes the form

$$\begin{aligned}\frac{\mathrm{d}\phi_i}{\mathrm{d}t} &= \omega_i - J\sum_{\mu=1}^{p}\left[m_-^{\mu}\sin(\phi_i - \theta_-^{\mu} - \xi_i^{\mu}) + m_+^{\mu}\sin(\phi_i - \theta_+^{\mu} + \xi_i^{\mu})\right] \\ &\quad - \lambda J\sum_{\mu=1}^{p}\left[m_-^{\mu-1}\sin(\phi_i - \theta_-^{\mu-1} - \xi_i^{\mu}) + m_+^{\mu-1}\sin(\phi_i - \theta_+^{\mu-1} + \xi_i^{\mu})\right] \qquad (14)\end{aligned}$$

where λ measures the asymmetric coupling strength relative to the symmetric one. The limit $\lambda \to 0$ corresponds to the case of symmetric coupling [12]; in the opposite limit $\lambda \to \infty$ with λJ finite, equation (14) reduces to equation (5) describing the system with asymmetric coupling. When both couplings are present, equation (14) resists simple analytical treatment, making it inevitable to obtain numerically the behaviour of the order parameter. We have thus integrated directly equation (14) with discrete time steps of $\Delta t = 0.01$ and compute the components of the order parameter m_-^{μ}, varying the asymmetry-to-symmetry ratio λ and the coupling strength J.

Figure 4 presents the obtained behaviours of the order parameter in the system of $N = 5000$ oscillators, with $p = 10$ stored patterns. Again the Gaussian distribution with unit variance and the uniform distribution have been taken for the distributions of intrinsic frequencies and of

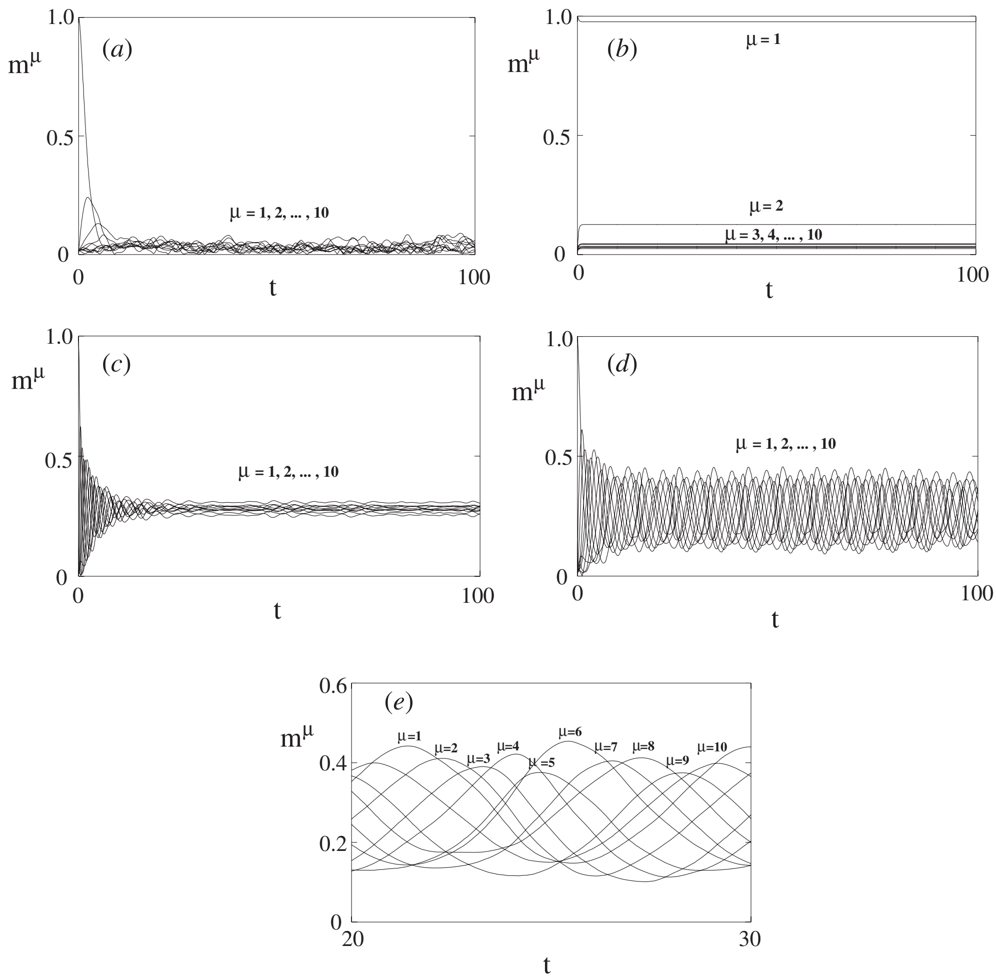

Figure 4. Behaviour of the order parameter in the system with both symmetric and asymmetric couplings. Simulations have been performed on the system of $N = 5000$ oscillators with $p = 10$ stored patterns, while the coupling strength J and the asymmetry-to-symmetry ratio λ are set equal to (*a*) $J = 1$ and $\lambda = 0.4$; (*b*) $J = 10$ and $\lambda = 0.1$; (*c*) $J = 10$ and $\lambda = 0.7$ and (*d*) $J = 10$ and $\lambda = 0.4$. All components of the order parameter assume negligibly small values in (*a*), describing the no-memory state. (*b*) and (*c*) correspond to the memory-retrieval state and the mixed-memory state, respectively. In (*d*), the details of which are shown in (*e*), each component m^μ of the order parameter reaches its maximum in succession, displaying temporal association.

stored patterns, respectively. In the plot the subscript $(-)$ in the notation m_-^μ has been dropped for convenience. Depending upon the values of λ and J, a variety of behaviours are displayed: for weak coupling, each oscillator tends to oscillate according to its natural frequency rather than displaying synchronization. The order parameter thus remains vanishingly small in the resulting no-memory state, shown in figure 4(*a*). On the other hand, strong coupling gives rise to collective synchronization characterized by nonvanishing values of the order parameter, leading to the memory-retrieval state, the mixed-memory state or the temporal-association state. When λ is small, the system is in the memory-retrieval state, which has a nonzero overlap with only one specific pattern. Figure 4(*b*) shows that only one component ($\mu = 1$) of the order

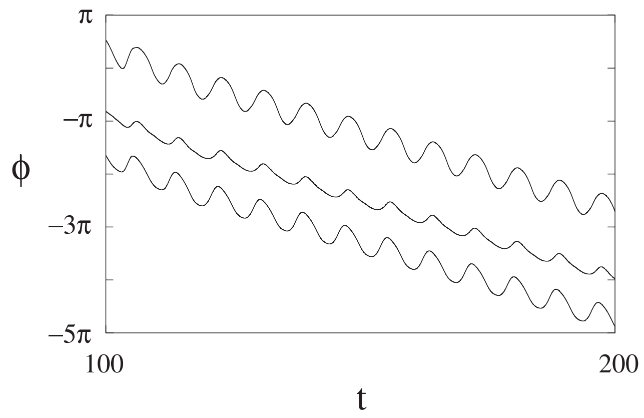

Figure 5. Time evolution of three arbitrarily chosen oscillators in the temporal-association state shown in figure 4(*d*).

parameter takes the stationary value near unity, while the others ($\mu \neq 1$) remain substantially small. Comparison of figures 2 and 4(*a*) shows that the presence of weak asymmetric coupling does not alter the overall features of the memory-retrieval state, although it tends to raise the stationary value of other components ($\mu \neq 1$). For large values of λ, the asymmetry can be strong enough to make all components reach more or less the same stationary value. The resulting mixed-memory state is presented in figure 4(*c*), the comparison of which with figure 1(*b*) again indicates that the presence of weak symmetric coupling does not alter the overall features of the mixed-memory state.

It is obvious that the mixed-memory state is stable in the asymmetric limit ($\lambda \to \infty$ with λJ finite), whereas the memory-retrieval state is stable in the symmetric limit ($\lambda \to 0$). In between the two limits, i.e., for intermediate values of λ, each component m^μ of the order parameter oscillates with the same frequency, reaching its maximum in succession. Such temporal association is manifested in figure 4(*d*), the details of which are shown in figure 4(*e*). It should be pointed out that the temporal association cannot be achieved by either symmetric or asymmetric coupling alone. The symmetric coupling tends to lead the system to the memory-retrieval state by assigning different stationary values for the order parameter components (see figure 2), while the asymmetric coupling encourages all the components to take the same value (see figure 1). These two different tendencies are necessary for obtaining temporal association. To characterize the temporal-association state, we have examined how the phase of each oscillator evolves with time. In the memory-retrieval state, it evolves monotonically, decreasing linearly with time. In contrast, figure 5, which displays the time evolution of three arbitrarily chosen oscillators in the temporal-association state, reveals that each phase exhibits an oscillation, with the same frequency as the order parameter, superposed with linear behaviour. We have also probed the robustness of temporal association against noise. The noise effects on temporal association are shown in figure 6, displaying the temporal behaviour of the order parameter for the noise strength $T = 1.2$. It is observed that, although noise induces fluctuations in the behaviour of the order parameter, the temporal-association state persists for moderate noise. Obviously, noise of sufficiently large strength destroys such a state, resulting in the no-memory state.

We have performed extensive simulations for various values of the coupling strength J and the ratio λ, with the number of stored patterns set equal to $p = 10$. The obtained phase

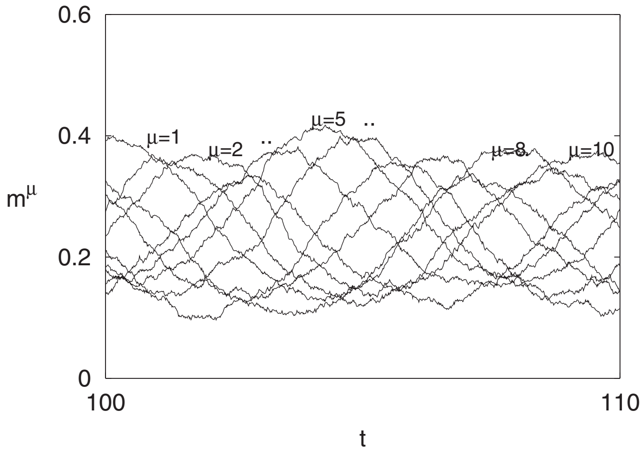

Figure 6. Behaviour of the order parameter in the presence of noise, displaying temporal association. Simulations have been performed on the system of $N = 5000$ oscillators with $p = 8$ stored patterns and the noise strength $T = 1.2$, while the coupling strength J and the asymmetry-to-symmetry ratio λ are set equal to $J = 10$ and $\lambda = 0.4$, respectively.

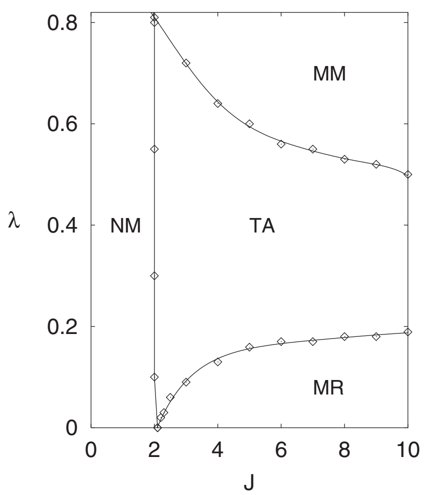

Figure 7. Schematic phase diagram on the plane of the coupling strength J and the asymmetry ratio λ, exhibiting boundaries between the four states: the memory-retrieval state (MR), the temporal-association state (TA), the mixed-memory state (MM) and the no-memory state (NM). Solid curves are merely guides to the eye. Simulations have been performed on the system of $N = 5000$ oscillators with $p = 10$ stored patterns.

boundaries for the system of size $N = 5000$ are shown in figure 7, where the memory-retrieval state (MR), the temporal-association state (TA), the mixed-memory state (MM) and the no-memory state (NM) are identified on the (J, λ) plane. In determining the phase boundary between the temporal-association state and the mixed-memory state, we have used the following criterion: the system is considered to exhibit temporal association if the maximum value of each order parameter component is larger than the minimum value of any component during the time evolution. To check the size effects, we have also considered systems of various sizes, from $N = 625$ to 20 000, via extensive simulations, which shows that the overall phase boundaries do not change qualitatively. Quantitatively, it is revealed that the critical coupling strength $(J/\sigma)_c$, beyond which the symmetric system ($\lambda = 0$) is in the memory-retrieval state, in general decreases with the system size N. Figure 8 manifests that the critical coupling strength approaches the value $(J/\sigma)_c = 1.617$ as the size N grows; this agrees well with

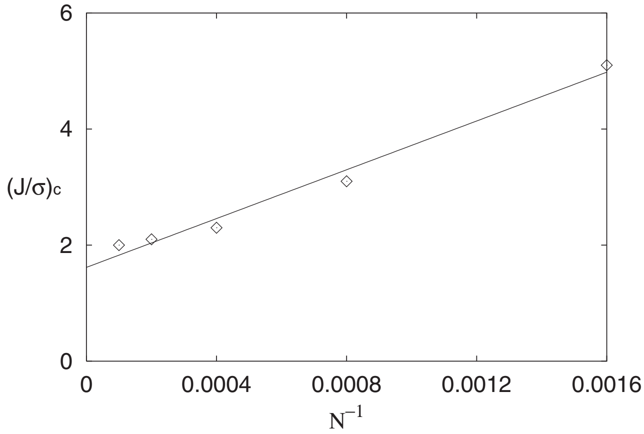

Figure 8. Dependence of the critical coupling strength $(J/\sigma)_c$ upon the inverse system size N^{-1}. The least-squares fit, represented by the solid curve, demonstrates that $(J/\sigma)_c$ approaches 1.617 as N is increased.

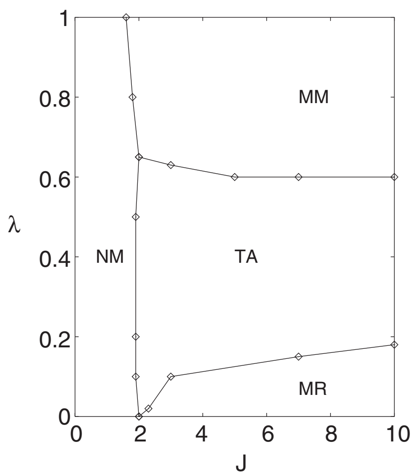

Figure 9. Schematic phase diagram for the system of $N = 5000$ oscillators with $p = 8$ stored patterns.

the analytical result $(J/\sigma)_c = (8/\pi)^{1/2}$, valid in the thermodynamic limit ($N \to \infty$). In addition, the location of the boundary between the temporal-association state and the mixed-memory state tends to shift toward smaller values of λ, as the size is increased from $N = 625$ to $N \simeq 2500$. For $N \gtrsim 5000$, on the other hand, the phase boundaries appear to saturate, indicating that finite-size effects are not substantial for $N \gtrsim 5000$.

We have further investigated the dependence of the phase boundaries on the number of stored patterns. Displayed in figure 9 is the schematic phase diagram, obtained from numerical simulations on the system of $N = 5000$ oscillators with $p = 8$ stored patterns. Comparison with figure 7, corresponding to the case of $p = 10$, shows that the region of temporal association shrinks near $J \simeq 2$ and $\lambda \gtrsim 0.6$. However, the overall boundaries still remain the same qualitatively.

4. Summary

We have studied the memory retrieval behaviour of a network of limit-cycle neuronal oscillators with symmetric and asymmetric coupling. In the absence of the latter, the system exhibits a transition from the no-memory state to the memory-retrieval state as the coupling strength is increased. In the absence of the symmetric coupling, on the other hand, the self-consistency equation for the order parameter can still be solved analytically, yielding the mixed-memory state at strong (asymmetric) coupling strengths. In the presence of both, their interplay gives rise to the additional temporal-association state, where the phase of each oscillator evolves non-monotonically with time. The temporal-association state has been shown to be robust against noise, persisting in the presence of even moderate noise. By means of extensive simulations, we have obtained schematic phase boundaries between these four different states on the plane of the asymmetry-to-symmetry ratio and the coupling strength. Here the size effects as well as the dependence on the number of stored patterns have been examined. Also pointed out is the apparent correspondence between the asymmetric limit and the symmetric one, with the mixed-memory state as the counterpart of the memory-retrieval state; this raises the interesting possibility of the duality present in the system, the investigation of which is left for further study.

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