

Enhancement of Neural Synchrony by Time Delay

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In a network of neuronal oscillators with time-delayed coupling, we uncover a phenomenon of enhancement of neural synchrony by time delay: a stable synchronized state exists at low coupling strengths for significant time delays. By formulating a master stability equation for time-delayed networks of Hindmarsh-Rose neurons, we show that there is always an extended region of stable synchronous activity corresponding to low coupling strengths. Such synchrony could be achieved in the undelayed system only by much higher coupling strengths. This phenomenon of enhanced neural synchrony by delay has important implications, in particular, in understanding synchronization of distant neurons and information processing in the brain.

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Synchronization of coupled nonlinear oscillators is a widespread phenomenon occurring in physical and biological sciences [1–6]. The observations of synchronous neural activity in the central nervous system [5,7] have stimulated a great deal of theoretical work on synchronization in coupled neural networks. These observations suggest that neural activity is a cooperative process of neurons and synchronization plays a vital role in information processing in the brain, for example, in processing information from different sensory systems to form a coherent and unified perception of the external world. The information flow in coupled systems is not generally instantaneous. On the contrary, finite speed of signal transmission over a distance gives rise to a finite time delay. For example, the speed of signal conduction through unmyelinated axonal fibers is on the order of 1 m/s resulting in time delays up to 80 ms for propagation through the cortical network [8]. For experimental relevance, the questions of prime importance are then about the effects of time delays and the stability of synchronization. Some theoretical studies involving limit-cycle oscillators coupled via time delays have shown multistable behaviors and oscillator death as effects of time delays [9–11]. Recent experiments have confirmed several theoretical predictions of coupled time-delay oscillators [12,13]. In this study, we uncover a phenomenon of enhancement of synchrony by delay, that is, spike synchrony in Hindmarsh-Rose neurons [14,15] in a time-delay network at low coupling strengths. We provide stability equations to examine the stability of synchronized states for any linear coupling arrangement in time-delay networks.

The Hindmarsh-Rose model [15] of a neuron can exhibit fixed point, periodic, and chaotic (spiking and bursting) behaviors. To our knowledge, there have not been any general results for the synchronization behavior of complex neurons, such as Hindmarsh-Rose neurons in time-delay networks. Our focus is on (i) the synchronizing

behaviors of time-delayed neural networks as a function of time delays and coupling strengths and (ii) the stability of synchronized states. Although a time-delay system has an infinite number of Lyapunov exponents because of the infinite dimension of the phase space, we are interested in developing a general approach to examine the stability of the synchronized states by computing the maximum Lyapunov exponent following a similar scheme as proposed by Pecora and Carroll for nondelay coupled systems in Ref. [16].

In this Letter, we report a phenomenon of enhancement of spike synchrony as a result of time delays in a time-delay system of two chaotic Hindmarsh-Rose neurons. The computation of the maximum Lyapunov exponent for the transverse directions to the synchronization manifold shows an extended region of synchronized states at very low coupling strengths in $\epsilon - \tau$ parameter space (where ϵ is a coupling strength and τ is the time delay). We also formulate master stability functions for an arbitrary number of neurons in a time-delay network. The master stability equation allows us to calculate the maximum Lyapunov exponent and determine the stability of the system for any linear coupling scheme. The possible implications of these results are also discussed toward the end.

As an oscillator unit of our time-delay neural network, we choose the Hindmarsh-Rose (HR) neuron described by the following equations of motion [15]: $\dot{x} = y - ax^3 + bx^2 - z + I_{\text{ext}}$, $\dot{y} = c - dx^2 - y$, $\dot{z} = r[s(x - x_0) - z]$, where x is the membrane potential, y is associated with the fast current, Na^+ or K^+ , and z with the slow current, for example, Ca^{2+} . Here, $a = 1.0$, $b = 3.0$, $c = 1.0$, $d = 5.0$, $s = 4.0$, $r = 0.006$, $x_0 = -1.60$, and I_{ext} is the external current input. This system exhibits a multitime scaled burst-spike chaotic behavior for $2.92 < I_{\text{ext}} < 3.40$. We now consider two HR neurons coupled linearly via the x component as follows:

$\dot{x}_i = y_i - ax_i^3 + bx_i^2 - z_i + I_{\text{ext}} + \epsilon[x_j(t - \tau) - x_i]$, $\dot{y}_i = c - dx_i^2 - y_i$, and $\dot{z}_i = r[s(x_i - x_0) - z_i]$, where $\epsilon \geq 0$ is the coupling strength, $\tau \geq 0$ is a measure of the time delay, and the indices $i = 1, 2, j = 2, 1$. The first neuron receives the signal from the second neuron after a time delay τ and vice versa. The dynamics of the synchronized state, $(x_1, y_1, z_1) = (x_2, y_2, z_2)$, are then be represented by

$$\dot{x} = y - ax^3 + bx^2 - z + I_{\text{ext}} + \epsilon[x(t - \tau) - x], \quad (1)$$

$$\dot{y} = c - dx^2 - y, \quad (2)$$

$$\dot{z} = r[s(x - x_0) - z] \quad (3)$$

as the differences $|x_1 - x_2|, |y_1 - y_2|, |z_1 - z_2|$ vanish in the limit of $t \rightarrow \infty$. This occurs when the synchronization manifold becomes stable. If we now transform to $x_{\perp} = x_1 - x_2$, $y_{\perp} = y_1 - y_2$, and $z_{\perp} = z_1 - z_2$, in the limit when these variables are very small ($x_1^2 - x_2^2 \approx 2xx_{\perp}$ and $x_1^3 - x_2^3 \approx 3x^2x_{\perp}$), the motion transverse to the synchronization manifold can be described by the following equations:

$$\dot{x}_{\perp} = y_{\perp} - ax^2x_{\perp} + 2bxx_{\perp} - z_{\perp} + \epsilon[x_{\perp}(t - \tau) - x_{\perp}], \quad (4)$$

$$\dot{y}_{\perp} = -2dxx_{\perp} - y_{\perp}, \quad (5)$$

$$\dot{z}_{\perp} = r(sx_{\perp} - z_{\perp}). \quad (6)$$

The solutions of Eqs. (4)–(6) determine the stability whether the variations $(x_{\perp}, y_{\perp}, z_{\perp})$ will grow or shrink as $t \rightarrow \infty$. The minimal condition for stability of the synchronized state represented by Eqs. (1)–(3) is that the Lyapunov exponents associated with Eqs. (4)–(6) are negative for the transverse subsystem. Even though a delay system lives in an infinite dimensional space, we really need to calculate the largest transverse exponent, the sign of which will determine the stability of synchronized states. By solving Eqs. (4)–(6) in combination with Eqs. (1)–(3), we determine the maximum transverse Lyapunov exponent, shown in Fig. 1 for $\tau \geq 0$. In the numerical integration of these equations, we evolve a unit vector of $(x_{\perp}, y_{\perp}, z_{\perp})$ to 10^6 number of iterations or until the vector grows or shrinks to a size of $10^{\pm 8}$ in the finite dimensional phase space version of the infinite dimensional delay system. This procedure is repeated many times to collect the expansion or contraction rates of the vector, which approximately estimates the maximum Lyapunov exponent. Figure 1(a) shows that the synchronized state is stable at $\epsilon \geq 0.5$ for $\tau = 0$. Figure 1(b) is a plot of the maximum exponent in the $\tau - \epsilon$ parameter space: there are mainly two regions of negative exponents for small ϵ along the τ axis pointed out by an arrow and for small τ along the ϵ axis. Here, we see that even at very low coupling strengths, there is a region of stability (as

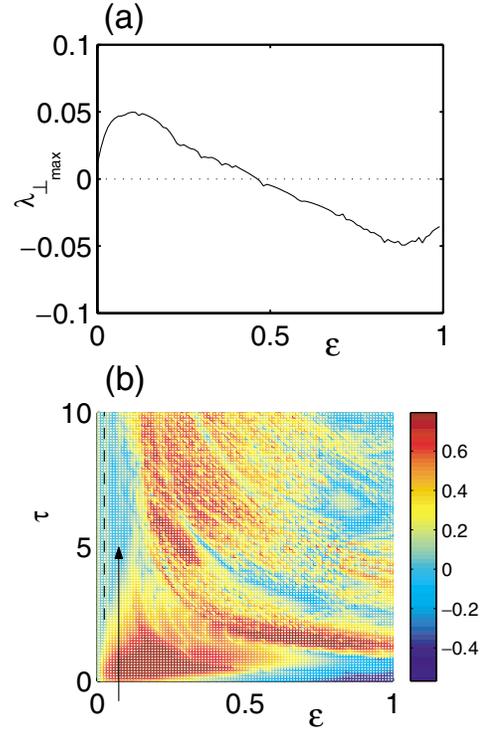


FIG. 1 (color online). The maximum transverse Lyapunov exponent $\lambda_{\perp, \text{max}}$. (a) $\lambda_{\perp, \text{max}}$ versus ϵ for $\tau = 0$ and (b) intensity represents the values of $\lambda_{\perp, \text{max}}$ in $(\tau - \epsilon)$ parameter space. The arrow points to the region of synchrony at very low coupling strengths, revealing the phenomenon of enhancement of synchrony via time delay. The dashed line drawn at $\epsilon \approx 0.036$ to the left of this region is the zero-exponent contour line that separates this stable region with the unstable one, where $\lambda_{\perp, \text{max}}$ at $\epsilon = 0.0$ is ≈ 0.17 .

shown by the arrow) for synchronized states. Figures 2(a)–2(d) show the time series and their correlations at $\tau = 0$ and $\tau = 8.0$ for the same low coupling strength, $\epsilon = 0.1$. As an example, Figs. 2(b) and 2(d) show that the HR neurons synchronize completely via time delay even at $\epsilon = 0.1$. On the other hand, there is no synchrony when $\tau = 0$ at the same ϵ , shown in Figs. 2(a) and 2(c). This underscores the point that time delay can also enhance synchrony in multitime scale oscillations such as coupled HR neurons. The bifurcation analysis of the synchronized state [Eqs. (1)–(3)] as a function of ϵ at different time delays reveals that much of the parameter space prevails with periodic oscillations and time delays stabilize the dynamics in one of the least unstable periodic orbits.

Following a similar scheme used by Pecora and Carroll in Ref. [16], we now turn to formulate general master stability functions for a time-delay network that has a self-time-delay term. The equation is as follows:

$$\dot{\mathbf{x}}_i = \mathbf{F}(\mathbf{x}_i) + \epsilon \sum_j G_{ij} \mathbf{H}(\mathbf{x}_j(t - \tau)), \quad (7)$$

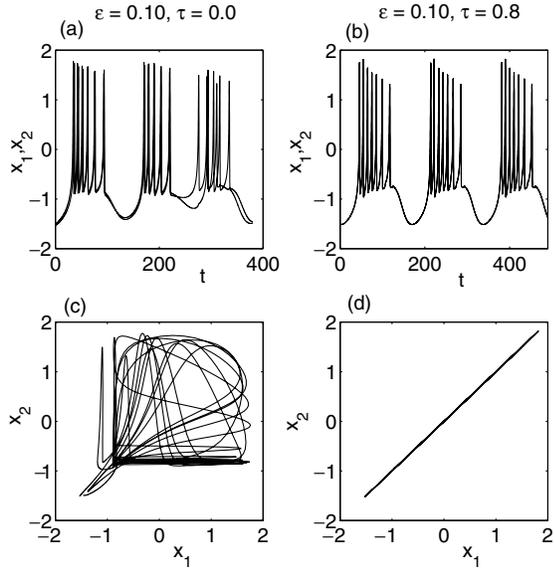


FIG. 2. Time series and membrane potential correlation between neurons: a complete synchrony at very low coupling strengths for $\tau \neq 0$. (a) x_1 and x_2 versus t at $\tau = 0$, $\epsilon = 0.1$, (b) x_1 and x_2 versus t at $\tau = 8.0$, $\epsilon = 0.1$, (c) x_2 versus x_1 at $\tau = 0$, $\epsilon = 0.1$, and (d) x_2 versus x_1 at $\tau = 8.0$, $\epsilon = 0.1$.

where \mathbf{x}_i is the dynamical variable vector of m dimensions for site i in an N oscillator array. The isolated dynamics for each node is $\dot{\mathbf{x}}_i = \mathbf{F}(\mathbf{x}_i)$. ϵ is the coupling strength, $H: R^m \rightarrow R^m$ is the coupling function, and \mathbf{G} is an $N \times N$ matrix which determines node-to-node coupling. The $N - 1$ constraints $\mathbf{x}_1 = \mathbf{x}_2 = \dots = \mathbf{x}_N$ define the synchronization manifold of the state \mathbf{x}_1 . For the invariance of the synchronization manifold, the rows of G_{ij} all sum to zero: $\sum_{j=1}^N G_{ij} = 0$, which also guarantees the diagonalizability of \mathbf{G} . Considering variations in all possible directions to the synchronized state \mathbf{x} and diagonalizing \mathbf{G} block by block, we arrive at the generic block-diagonalized variational equation for transverse modes as follows:

$$\dot{\xi}(t) = D\mathbf{F}(\mathbf{x})\xi(t) + (\alpha + \sqrt{-1}\beta)D\mathbf{H}(\mathbf{x}_\tau)\xi_\tau, \quad (8)$$

where $\mathbf{x}_\tau = \mathbf{x}(t - \tau)$, ξ is the multidimensional perturbations, $\xi_\tau = \xi(t - \tau)$, and $(\alpha + \sqrt{-1}\beta)$ is the eigenvalue of $\epsilon\mathbf{G}$. Imaginary eigenvalues arise from asymmetric couplings. $D\mathbf{F}(\mathbf{x})$ is the Jacobian matrix evaluated on the synchronization manifold and $D\mathbf{H}(\mathbf{x}(t - \tau))$ is an $m \times m$ matrix \mathbf{E} that determines which of the oscillator components are coupled. For example, for x -component coupling in a network of HR neurons, only the first element is unity and all the rest are zero. Separating ξ into real part ξ_r and imaginary part ξ_i , we get

$$\dot{\xi}_r = D\mathbf{F}(\mathbf{x})\xi_r + \alpha D\mathbf{H}(\mathbf{x}_\tau)\xi_{r\tau} - \beta D\mathbf{H}(\mathbf{x}_\tau)\xi_{i\tau}, \quad (9)$$

$$\dot{\xi}_i = D\mathbf{F}(\mathbf{x})\xi_i + \alpha D\mathbf{H}(\mathbf{x}_\tau)\xi_{i\tau} + \beta D\mathbf{H}(\mathbf{x}_\tau)\xi_{r\tau}, \quad (10)$$

where $\xi_{r\tau} = \xi_r(t - \tau)$ and $\xi_{i\tau} = \xi_i(t - \tau)$. The maxi-

imum transverse Lyapunov exponent ($\lambda_{\perp\max}$) can be estimated from Eqs. (9) and (10), which are the master stability equations. $\lambda_{\perp\max}$ is a function of α , β , and τ . For given coupling strength and delay times, one can locate a point in (α, β) space and identify the sign of $\lambda_{\perp\max}$ at that point. The negative value of $\lambda_{\perp\max}$ confirms that all the transverse eigenmodes are stable and the synchronous state is stable at this point.

Figure 3(a) shows a master stability function in (α, β) -parameter space at $\tau = 0$ for x -coupled HR neurons. The zero-stability curve represents the boundary between the stable region on the left and the unstable region on the right. The negative equistability curves are roughly symmetrical in the β directions about the α axis. $(\alpha, \beta) = (0, 0)$ corresponds to a completely uncoupled state and $\lambda_{\perp\max}$ is greater than zero at this point. Figure 3(b) shows a master stability function for $\tau = 8.0$. The equistability curves are all positive and symmetrical in the β directions about the α axis. It appears from these symmetrical curves that there would be a tiny stable region close to the α axis on the negative side near the origin. However, our numerics with a grid of 500×500 in (α, β) -parameter space could not establish that for this network with the self-time-delay coupling term.

On the other hand, the master stability equations for an array of N neurons without the overall self-delayed interaction coupled in a similar way as the two-neuron system described by Eqs. (1)–(3) can be written as follows:

$$\dot{\mathbf{x}}_i = \mathbf{F}_1(\mathbf{x}_i, \epsilon) + \mathbf{F}_2(\mathbf{x}_{i\tau}, \epsilon) + \epsilon \sum_j G_{ij} \mathbf{H}(\mathbf{x}_{j\tau}), \quad (11)$$

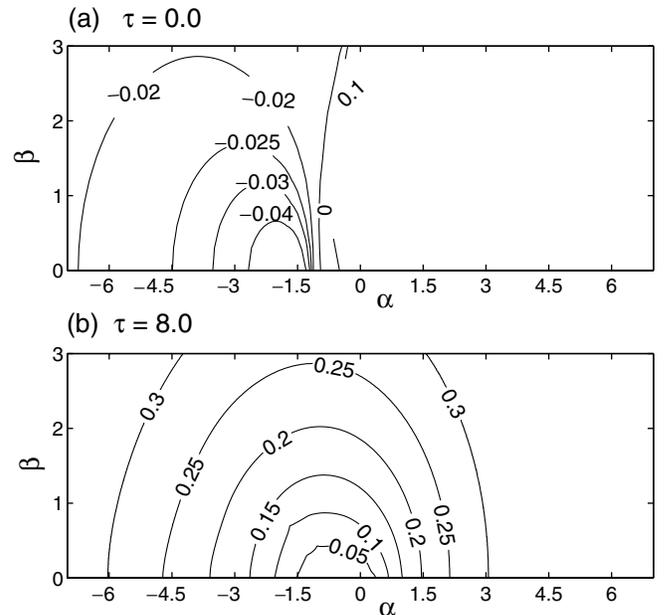


FIG. 3. Master stability functions at (a) $\tau = 0.0$ and (b) $\tau = 8.0$ for x -coupled Hindmarsh-Rose neurons. The lines are isoclines for the constant maximum Lyapunov exponent.

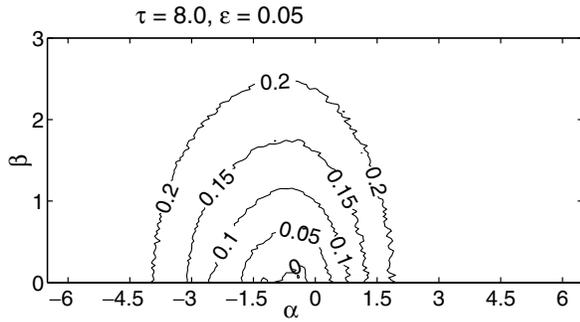


FIG. 4. Master stability functions at $\tau = 8.0$ and $\epsilon = 0.05$ for x -coupled Hindmarsh-Rose neurons. Notice the stable region close to the α axis near the origin in the negative side.

where, for an x -component coupling, for instance, $\mathbf{F}_1(\mathbf{x}_i, \epsilon) = \mathbf{F}(\mathbf{x}_i) + \epsilon G_{ii}[1 \ 0 \ \cdots \ 0]\mathbf{x}_i$, and $\mathbf{F}_2(\mathbf{x}_i, \epsilon) = -\epsilon G_{ii}[1 \ 0 \ \cdots \ 0]\mathbf{x}_{i\tau}$. Here, the synchronized state is $\dot{\mathbf{x}} = \mathbf{F}_1(\mathbf{x}, \epsilon) + \mathbf{F}_2(\mathbf{x}_\tau, \epsilon)$. This results in the following master stability equations:

$$\dot{\xi}_r = D\mathbf{F}_1(\mathbf{x}, \epsilon)\xi_r + [D\mathbf{F}_2(\mathbf{x}_\tau, \epsilon) + \alpha D\mathbf{H}(\mathbf{x}_\tau)]\xi_{r\tau} - \beta D\mathbf{H}(\mathbf{x}_\tau)\xi_{i\tau}, \quad (12)$$

$$\dot{\xi}_i = D\mathbf{F}_1(\mathbf{x}, \epsilon)\xi_i + [D\mathbf{F}_2(\mathbf{x}_\tau, \epsilon) + \alpha D\mathbf{H}(\mathbf{x}_\tau)]\xi_{i\tau} + \beta D\mathbf{H}(\mathbf{x}_\tau)\xi_{r\tau}. \quad (13)$$

The maximum transverse Lyapunov exponent ($\lambda_{\perp, \max}$) can be estimated from these equations. The synchronized state also depends on the ϵ value. Figure 4 shows the master stability curves for such a system at $\tau = 8.0$, $\epsilon = 0.05$. There is a stable region close to the α axis near the origin in the negative side. This is evidence that time delay does not always destabilize synchronized states, but also it stabilizes the synchronized states for the right choice of parameters. Thus, the phenomenon of enhancement of synchrony by delay can be observed in a coupled system of N HR neurons.

In any physical or biological systems, time delays are unavoidable in signal transmission. Neural synchronization was reported to occur between the brain areas separated by distances up to several centimeters [17–19]. Visuomotor integration was found to be associated with zero time-lag synchronization of signals recorded from the visual and parietal areas, and motor and parietal areas of the awake cat [20]. Time delay seems to facilitate synchronization between the distant cortical areas. Our results suggest that this long-range neuronal synchronization is possible between those areas which are coupled with predominantly low connectivity strengths.

In conclusion, we have uncovered a phenomenon of enhancement of spike synchrony by time delay in a coupled system of neurons. Even for significant time delays, a stable synchronized state exists at a very low coupling strength, which may account for long-range neural synchrony observed in experiments. We formulate

master stability functions for an arbitrary linear coupling arrangement in time-delay networks of a large number of bursting neurons.

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