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Dynamics of Neural Systems with Discrete and Distributed Time Delays*

B. Rahman[†], K. B. Blyuss[†], and Y. N. Kyrychko[†]

Abstract. In real-world systems, interactions between elements do not happen instantaneously, due to the time required for a signal to propagate, reaction times of individual elements, and so forth. Moreover, time delays are normally nonconstant and may vary with time. This means that it is vital to introduce time delays in any realistic model of neural networks. In order to analyze the fundamental properties of neural networks with time-delayed connections, we consider a system of two coupled two-dimensional nonlinear delay differential equations. This model represents a neural network, where one subsystem receives a delayed input from another subsystem. An exciting feature of the model under consideration is the combination of both discrete and distributed delays, where distributed time delays represent the neural feedback between the two subsystems, and the discrete delays describe the neural interaction within each of the two subsystems. Stability properties are investigated for different commonly used distribution kernels, and the results are compared to the corresponding results on stability for networks with no distributed delays. It is shown how approximations of the boundary of the stability region of a trivial equilibrium can be obtained analytically for the cases of delta, uniform, and weak gamma delay distributions. Numerical techniques are used to investigate stability properties of the fully nonlinear system, and they fully confirm all analytical findings.

Key words. neural network, stability, discrete and distributed time delays, uniform and weak gamma distributions

AMS subject classifications. 92B20, 34K99, 37N25

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1. Introduction. The emergence of self-organized behavior in networks of coupled systems is a very current and fascinating topic stemming from direct applications in various scientific disciplines [1]. The fascination comes from the fact that, by themselves, uncoupled elements may exhibit very simple and well-understood behavior, and yet, when coupled together, they produce a wealth of new dynamical regimes, such as full and/or partial synchronization, clustering, localized pattern formation, and chimera states. Collective emergence of self-organized behavior is of fundamental importance, and it appears in a wide range of systems, including circadian pacemaker cells within the brain, Josephson junction arrays, and metabolic yeast cells [2, 3].

A neural network can be described as an information processing structure, which consists of processing elements connected together through a particular network topology. Each processing element has an input, which supplies the information required to produce a desired output through the network via connections depending on the configuration. Applications of

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neural networks range from classification, associative memory, image processing, and pattern recognition to parallel computation and optimization problems [4, 5]. Mathematically, neural networks can be represented by systems of coupled neurons, and such modelling approaches help reveal the networks' stability and synchronization properties [6, 7, 8].

In recent years, a number of researchers have studied neural network models with time delays to represent the time required for communication between neurons [9, 10, 11, 12, 13, 14]. Time delays are used to account for the fact that in the majority of real-world networks, some processes do not happen instantaneously due to a finite speed of signal propagation, times required for information processing, etc., and their inclusion leads to significant changes in the dynamics of the system [15, 16, 17, 18, 19, 20].

It has long been established that introduction of time delays often leads to additional instabilities in the system when compared with its nondelayed analogue, and there are numerous studies devoted to the analysis of coupled systems with discrete or constant time delays [18, 21, 22]. However, in many real situations the time delays are not constant; they may change over time and/or depend on system parameters [23, 24]. In the context of neural networks, the presence of many parallel pathways with different axon sizes and lengths results in different distributions of transmission velocities, which can be studied using models with distributed time delays [25, 26, 27].

Using the average time delay as a bifurcation parameter, Liao, Wong, and Wu [28] have shown that a Hopf bifurcation occurs when this parameter passes through a critical value. Furthermore, they have investigated the direction of Hopf bifurcation and the stability of the bifurcating periodic orbits by applying the normal form approach and the center manifold reduction theory. Ruan and Filfil [29] have studied the stability of steady-state solutions in a two-neuron system with discrete and distributed delays. They have shown the existence of periodic oscillations that arise through a Hopf bifurcation of the steady state. Kyrychko, Blyuss, and Schöll [30, 31, 32] have analyzed a generic system of coupled oscillators with distributed-delay coupling represented by identical and nonidentical Stuart-Landau oscillators and have shown how different distribution kernels affect the shape of the amplitude death islands, where periodic oscillations are quenched and the previously unstable trivial steady state is stabilized. Li and Hu [33] have investigated the stability of the trivial equilibrium and Hopf bifurcations in a neural network by using the time delay as the bifurcation parameter.

An often quoted general rule is that a system with distributed delays is inherently more stable than the same system with a discrete delay. Despite the developments in the field of differential equations with either discrete or distributed delays, there are just a few results with regards to coupled networks which include both discrete and distributed time delays. Cooke and Grossman [12] have compared the behavior of a scalar equation with one discrete delay to that of the corresponding equation with a gamma distributed delay. They have shown that increasing the discrete delay in the model destabilizes the trivial solution, and it can never be restabilized. For the distributed delay, increasing the mean time delay can also destabilize the trivial solution; however, it will always be restabilized for a large enough mean time delay. Bernard, Bélair, and Mackey [10] analyzed the linear stability of a scalar system with one and two delays characterized by the distribution kernel properties, such as mean, variance, and skewness. For uniform and continuous distributions, they have shown that stability regions are larger than those in the case of a discrete delay. Jirsa and Ding [13] have analyzed an

 $n \times n$ linear system with linear decay and arbitrary connections with a common delay. They have shown that, under some mild assumptions, the stability region of the trivial solution for any distribution of time delays is larger and contains the stability region for a discrete delay.

Atay [34] has studied a system consisting of two simple oscillators with gap junctional coupling. He has shown that it is easier to quench oscillations in a system with distributed delays than in a system with a discrete time delay, in the sense that there is a larger region of coupling strengths for which the steady state can be stabilized. In particular, it was deduced that as the variance of the distribution increases, the size of the stability region increases. Meyer et al. [14] have found that distributed delays enhance the stability of the system, so that with the increased width of distribution of delays, the system converges faster to a fixed point and converges slower toward a limit cycle. Moreover, the introduction of distributed delays leads to an increased range of the average values of time delays for which the equilibrium point is stable. The dynamics of the system is then determined almost exclusively by the mean and the variance of the delay distribution and shows very little dependence on the particular type of the distribution.

The simplest time-delayed model which describes neural interaction can be written in the form

$$\dot{u}_1(t) = -u_1(t) + a_{12}f(u_2(t-\tau)),$$

$$\dot{u}_2(t) = -u_2(t) + a_{21}f(u_1(t-\tau)),$$

where u_i , i = 1, 2, describe the voltage input of the neuron i, a_{12} and a_{21} are synaptic weights or connection strengths, τ is the synaptic time delay, and $f : \mathbb{R} \to \mathbb{R}$ is a nonlinear activation/transfer function. This model can be used to describe a Hopfield network, where individual neurons are connected to each other through an activation (or transfer) function with certain weights [35]. The time delay τ is assumed to be positive, and the connection strengths a_{12} and a_{21} can be positive or negative, describing excitatory or inhibitory connections, respectively. The dynamical properties of the system (1.1), such as stability of the steady states and existence of the Hopf bifurcation, have been extensively studied by several authors (for example, [36, 37, 38] and references therein).

Despite a large number of results related to neural network models of the type shown in (1.1), systems of coupled subnetworks have received less attention. In particular, in the majority of models considered in the literature, the connection time delay is assumed to be constant; see, for example, Song, Tade, and Zhang [5]. In this paper, we focus on the role of the distribution of delay times between the two subnetworks, rather than the influence of discrete time delays inside a single subnetwork. Furthermore, we analyze the dynamics of a system where both discrete and distributed time delays are simultaneously present.

We expand the Hopfield-type model (1.1) and its modification considered in [5] by introducing a distribution of time delays in the feedback connection *between* the two subnetworks, and within each subnetwork the neurons are coupled with a constant time delay. Explicitly

incorporating the above assumptions leads to the following model:

$$\dot{u}_{1}(t) = -u_{1}(t) + a_{12}f(u_{2}(t-\tau)) + \alpha \int_{0}^{\infty} g(s)f(u_{4}(t-s))ds,$$

$$\dot{u}_{2}(t) = -u_{2}(t) + a_{21}f(u_{1}(t-\tau)),$$

$$\dot{u}_{3}(t) = -u_{3}(t) + a_{12}f(u_{4}(t-\tau)) + \alpha \int_{0}^{\infty} g(s)f(u_{2}(t-\tau))ds,$$

$$\dot{u}_{4}(t) = -u_{4}(t) + a_{21}f(u_{3}(t-\tau)),$$

where u_i are voltages of neurons $i, i = 1, \ldots, 4$; a_{12} and a_{21} denote the strength of connections between neurons within each subnetwork, where they can be positive or negative; and α measures the strength of the long-range coupling between the two subnetworks. We assume that locally a time delay τ arising due to a finite speed of signal propagation between individual neurons inside each subnetwork is a nonnegative constant, while the long-range transmission delays between the subnetworks are characterized by a distribution with the kernel $g(\cdot)$. In the most general formulation, all neural interactions (both within and between the subnetworks) could be represented by distributed time delays. However, due to the close proximity of neurons inside each subnetwork, it is reasonable to assume that the variation of the time delays in the connection between them is negligibly small compared to the variation of the time delays in the long-range connections between subnetworks [39]. This justifies the choice of a discrete time delay within the subnetworks and distributed time delays in the interactions between them, and makes analytical investigations more tractable.

The synaptic transfer function $f: \mathbb{R} \to \mathbb{R}$ is assumed to be \mathcal{C}^1 and sigmoidal with a maximum slope at zero [36, 40]. For the linear stability analysis, we require only f(0) = 0, $f'(0) \neq 0$ and use a particular choice of $f(\cdot) = \tanh(\cdot)$ in the numerical simulations.

Without loss of generality, the distribution kernel $g(\cdot)$ is assumed to be positive-definite and normalized to unity; i.e.,

$$g(s) \ge 0,$$

$$\int_0^\infty g(s)ds = 1.$$

A schematic sketch of system (1.2) is shown in Figure 1. If the distribution kernel is taken in the form of the Dirac delta function, that is $g(s) = \delta(s)$, one recovers the instantaneous coupling between the two subnetworks, where the two subnetworks interact without time delays. If $g(s) = \delta(s - \tau)$, the coupling takes the form of a discrete time delay $\alpha f(u_i(t - \tau))$, i = 2, 4. Song, Tade, and Zhang [5] have considered the case of discrete time delays in system (1.2) and derived conditions for stability, Hopf bifurcation, and emergence of spatio-temporal patterns from bifurcating periodic solutions.

The outline of the paper is as follows. In section 2 we derive general conditions for stability of the trivial steady state of system (1.2) for any distribution kernel. Section 3 is devoted to the analysis of model (1.2) with Dirac delta distributed kernel, and we show how one can obtain explicit conditions on the system parameters that ensure the stability of the trivial steady state. In sections 4 and 5 we consider the cases of uniform and weak gamma

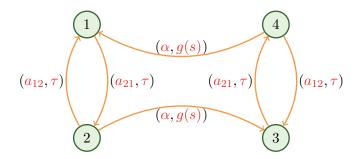


Figure 1. Diagrammatic sketch of the Hopfield-type neural network described by system (1.2). The delays τ inside each of the subnetworks are assumed to be constant and discrete, and long-range interactions between the two subnetworks are represented by the distributed delay kernel q(s).

distribution kernels, find conditions on stability of the trivial steady state, and numerically identify stability regions in the parameter space. Numerical simulations of the full nonlinear system (1.2) are presented in section 6, and the paper concludes with the summary and discussion of results in section 7.

2. Stability analysis. Equilibria of system (1.2) satisfy $\dot{u}_i = 0$, i = 1, 2, 3, 4. Under the assumption f(0) = 0, system (1.2) always has a trivial or rest steady state $(u_1, u_2, u_3, u_4) = (0, 0, 0, 0)$. The importance of this trivial steady state lies in the fact that it represents a state of background activity, which is fundamental for many neural processes [41, 42]. Depending on the signs of the coupling weights/strengths a_{ij} , i, j = 1, 2, and the specific form of the transfer function f, there may exist a number of other nontrivial steady states, but their existence is not guaranteed in general [39, 40]. Therefore, we concentrate our analysis on the stability of the trivial steady state, and similar considerations can be made for all other steady states when they are permitted by the model. The linearization of system (1.2) near the trivial steady state has the form

(2.1)
$$\dot{\mathbf{u}}(t) = L_0 \mathbf{u}(t) + L_1 \mathbf{u}(t-\tau) + M \int_0^\infty g(s) \mathbf{u}(t-s) ds,$$

with $\mathbf{u} = (u_1, u_2, u_3, u_4)$, $L_0 = -I$, where I is the 4×4 identity matrix and L_1 and M are given by

$$L_1 = \begin{pmatrix} 0 & a_{12}\beta & 0 & 0 \\ a_{21}\beta & 0 & 0 & 0 \\ 0 & 0 & 0 & a_{12}\beta \\ 0 & 0 & a_{21}\beta & 0 \end{pmatrix}, \quad M = \begin{pmatrix} 0 & 0 & 0 & \alpha\beta \\ 0 & 0 & 0 & 0 \\ 0 & \alpha\beta & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

where $\beta = f'(0) \neq 0$. The characteristic matrix can now be calculated as

$$\Delta(\tau,\lambda) = (\lambda+1)I - L_1 e^{-\lambda\tau} - M\widehat{G}(\lambda),$$

where

$$\widehat{G}(\lambda) = \int_0^\infty e^{-\lambda s} g(s) ds$$

is the Laplace transform of the function $g(\cdot)$. The corresponding characteristic equation factorizes as follows:

(2.2)
$$\det[\Delta(\tau,\lambda)] = \Delta_{-}(\tau,\lambda) \cdot \Delta_{+}(\tau,\lambda) = 0,$$

where $\Delta_{-}(\tau,\lambda)$ and $\Delta_{+}(\tau,\lambda)$ are given by

(2.3)
$$\Delta_{-}(\tau,\lambda) = (\lambda+1)^{2} - a_{12}a_{21}\beta^{2}e^{-2\lambda\tau} - \widehat{G}(\lambda)a_{21}\alpha\beta^{2}e^{-\lambda\tau}.$$

(2.4)
$$\Delta_{+}(\tau,\lambda) = (\lambda+1)^{2} - a_{12}a_{21}\beta^{2}e^{-2\lambda\tau} + \widehat{G}(\lambda)a_{21}\alpha\beta^{2}e^{-\lambda\tau}.$$

It it easy to see that λ is a root of the characteristic equation (2.2) if and only if it is a root of either Δ_+ or Δ_- .

Lemma 2.1. $\lambda = 0$ is a solution of (2.2) if and only if $|a_{21}\alpha\beta^2| = |1 - a_{12}a_{21}\beta^2|$.

Proof. From the factorization of the characteristic equation $\det[\Delta(\tau,\lambda)] = \Delta_+(\tau,\lambda) \cdot \Delta_-(\tau,\lambda) = 0$ it follows that either $\Delta_+(\tau,\lambda) = 0$ or $\Delta_-(\tau,\lambda) = 0$. Computing $\widehat{G}(\lambda)$ at $\lambda = 0$ yields

$$\widehat{G}(0) = \int_0^\infty g(s)ds = 1.$$

Substituting this into $\Delta_{+}(\tau,0) = 0$ and $\Delta_{-}(\tau,0) = 0$ given in (2.3) and (2.4), one finds that either

$$\Delta_{+}(\tau,0) = 1 - a_{12}a_{21}\beta^{2} + a_{21}\alpha\beta^{2} = 0$$

or

$$\Delta_{-}(\tau,0) = 1 - a_{12}a_{21}\beta^2 - a_{21}\alpha\beta^2 = 0.$$

The last two expressions imply

$$|a_{21}\alpha\beta^2| = |1 - a_{12}a_{21}\beta^2|,$$

which completes the proof.

Theorem 2.2. If either $|a_{21}\alpha\beta^2| > |1 - a_{12}a_{21}\beta^2|$ or $|a_{21}\alpha\beta^2| < a_{12}a_{21}\beta^2 - 1$, then the characteristic equation (2.2) has a root with positive real part for any $\tau \geq 0$.

Proof. Substituting $\lambda = 0$ into (2.3) and (2.4) gives

$$\det[\Delta(\tau,0)] = \Delta_{+}(\tau,0) \cdot \Delta_{-}(\tau,0) = (1 - a_{12}a_{21}\beta^{2} + a_{21}\alpha\beta^{2}) \cdot (1 - a_{12}a_{21}\beta^{2} - a_{21}\alpha\beta^{2}).$$

Under the assumption $|a_{21}\alpha\beta^2| > |1 - a_{12}a_{21}\beta^2|$, we have either

$$\Delta_{+}(\tau,0) > 0$$
 and $\Delta_{-}(\tau,0) < 0$

or

$$\Delta_{+}(\tau,0) < 0$$
 and $\Delta_{-}(\tau,0) > 0$,

which both imply that $det[\Delta(\tau,0)] < 0$. On the other hand,

$$\lim_{\lambda \to \infty} \det[\Delta(\tau, \lambda) = \lim_{\lambda \to \infty} \left[\Delta_+(\tau, \lambda) \cdot \Delta_-(\tau, \lambda) \right] = \infty.$$

Since $\det[\Delta(\tau,\lambda)]$ is a continuous function of λ , there exists $\lambda^* > 0$ such that $\det[\Delta(\tau,\lambda^*)] = 0$ for any $\tau \geq 0$ and $|a_{21}\alpha\beta^2| > |1 - a_{12}a_{21}\beta^2|$. Thus, the characteristic equation (2.2) has a real positive root.

In the case when $|a_{21}\alpha\beta^2| < a_{12}a_{21}\beta^2 - 1$, we have

$$\Delta_{+}(\tau,0) < 0 \text{ and } \Delta_{-}(\tau,0) < 0$$

Since

$$\lim_{\lambda \to \infty} \Delta_+(\tau, \lambda) = \lim_{\lambda \to \infty} \Delta_-(\tau, \lambda) = \infty,$$

this implies that both $\Delta_{+}(\tau, \lambda)$ and $\Delta_{-}(\tau, \lambda)$ will cross zero at some positive λ^* , which completes the proof.

In order to make further analytical progress, we need to specify the kernel of the delay distribution. There are three main distribution kernels used in the literature, namely, delta function, uniform distribution, and gamma distribution [10, 11, 12, 34, 43]. We shall start our analysis by considering the distribution kernel in system (1.2) in the form of the delta function.

3. Delta function distribution. In the case of the delay distribution being given by the Dirac delta function, we have to consider two different cases. In the case $g(s) = \delta(s - \tau)$, system (1.2) reduces to the case of a system with discrete time delay. Song, Tade, and Zhang [5] have shown that if $|a_{21}\alpha\beta^2| > 1 - a_{12}a_{21}\beta^2$, the trivial steady state of system (1.2) with $g(s) = \delta(s - \tau)$ is unstable for all $\tau \geq 0$; if $a_{12}a_{21}\beta^2 - 1 < |a_{21}\alpha\beta^2| \leq a_{12}a_{21}\beta^2 + 1$, the trivial steady state is asymptotically stable for all $\tau \geq 0$; and if $1 + a_{12}a_{21}\beta^2 < |a_{21}\alpha\beta^2| < 1 - a_{12}a_{21}\beta^2$, there exists $\tau_0 > 0$ such that the trivial steady state is asymptotically stable for all $\tau \in [0, \tau_0)$ and unstable for $\tau > \tau_0$.

Considering the distribution kernel of the form $g(s) = \delta(s)$, i.e.,

(3.1)
$$\int_{0}^{\infty} \delta(s) f(\mathbf{u}(t-s)) ds = f(\mathbf{u}(t)),$$

system (2.1) reduces to a system with discrete time delay of the form

$$\dot{\mathbf{u}}(t) = L_0 \mathbf{u}(t) + L_1 \mathbf{u}(t - \tau),$$

where $\mathbf{u} = (u_1, u_2, u_3, u_4)$ and L_0 and L_1 are given by

$$L_0 = \begin{pmatrix} -1 & 0 & 0 & \alpha\beta \\ 0 & -1 & 0 & 0 \\ 0 & \alpha\beta & -1 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix}, \quad L_1 = \begin{pmatrix} 0 & a_{12}\beta & 0 & 0 \\ a_{21}\beta & 0 & 0 & 0 \\ 0 & 0 & 0 & a_{12}\beta \\ 0 & 0 & a_{21}\beta & 0 \end{pmatrix}.$$

The characteristic equation of system (3.2) can be factorized in a manner similar to (2.2):

(3.3)
$$\det[\Delta(\tau,\lambda)] = \Delta_{-}(\tau,\lambda) \cdot \Delta_{+}(\tau,\lambda) = 0,$$

where

(3.4)
$$\Delta_{-}(\tau,\lambda) = (\lambda+1)^2 - a_{12}a_{21}\beta^2 e^{-2\lambda\tau} - a_{21}\alpha\beta^2 e^{-\lambda\tau}$$

and

(3.5)
$$\Delta_{+}(\tau,\lambda) = (\lambda+1)^{2} - a_{12}a_{21}\beta^{2}e^{-2\lambda\tau} + a_{21}\alpha\beta^{2}e^{-\lambda\tau}.$$

Lemma 3.1. Let $|1 - a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$. If

$$(3.6) 1 + a_{12}a_{21}\beta^2 > 0 and a_{12}a_{21}\beta^2 \neq 1$$

or

(3.7)
$$1 + a_{12}a_{21}\beta^2 < 0 \quad and \quad \tau \neq \tau_d = -\frac{2}{1 + a_{12}a_{21}\beta^2},$$

then $\lambda = 0$ is a simple root of the characteristic equation (3.3). If

$$(3.8) a_{12}a_{21}\beta^2 = 1$$

or

$$(3.9) 1 + a_{12}a_{21}\beta^2 < 0 and \tau = \tau_d,$$

then $\lambda = 0$ is a double root of the characteristic equation (3.3).

Proof. It follows from Lemma 2.1 that whenever the condition $|1 - a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$ holds, $\lambda = 0$ is a root of the characteristic equation (3.3). In order to determine the multiplicity of this root, we compute

(3.10)
$$\frac{d\Delta}{d\lambda}\Big|_{\lambda=0} = 2(1 - a_{12}a_{21}\beta^2)[2 + \tau(1 + a_{12}a_{21}\beta^2)].$$

If the condition (3.6) holds, then $d\Delta(\tau,0)/d\lambda \neq 0$ for any τ , implying that $\lambda = 0$ is a simple root of the characteristic equation (3.3). Likewise, if the condition (3.7) holds, it follows from (3.10) that

$$\frac{d\Delta}{d\lambda}\Big|_{\lambda=0} > 0 \quad \text{for } \tau < \tau_d,$$

$$\frac{d\Delta}{d\lambda}\Big|_{\lambda=0} < 0 \quad \text{for } \tau > \tau_d.$$

Hence, $\lambda = 0$ is a simple root. When the condition (3.8) is satisfied, we have

$$\frac{d\Delta}{d\lambda}\Big|_{\lambda=0} = 0, \qquad \frac{d^2\Delta}{d\lambda^2}\Big|_{\lambda=0} = 8(\tau+1)^2 > 0,$$

and, therefore, $\lambda = 0$ is a double root. Finally, if the condition (3.9) holds, one has

$$\left. \frac{d\Delta}{d\lambda} \right|_{\lambda=0,\tau=\tau_d} = 0, \qquad \frac{d^2\Delta}{d\lambda^2} \right|_{\lambda=0,\tau=\tau_d} = \frac{4(1-a_{12}a_{21})(a_{12}^2a_{21}^2-4a_{12}a_{21}-1)}{(1+a_{12}a_{21})^2} > 0,$$

which means that $\lambda = 0$ is a double root of (3.3). This completes the proof.

Below we concentrate on analysis of the equation

(3.11)
$$\Delta_{-}(\tau,\lambda) = (\lambda+1)^2 - a_{12}a_{21}\beta^2 e^{-2\lambda\tau} - a_{21}\alpha\beta^2 e^{-\lambda\tau} = 0,$$

and the same analysis applies to the case of $\Delta_{+}(\tau,\lambda)=0$. In order to identify further stability changes, we look for solutions in the form $\lambda=i\omega,\ \omega\neq0$. When $\tau=0,\ \Delta_{-}(\tau,\lambda)=0$ turns into

(3.12)
$$\Delta_{-}(0,\lambda) = (\lambda+1)^2 - a_{21}\alpha\beta^2 - a_{12}a_{21}\beta^2 = 0.$$

The following lemma can be easily obtained using the Routh-Hurwitz criterion.

Lemma 3.2. Assume $a_{21}\alpha\beta^2 < 1 - a_{12}a_{21}\beta^2$. Then all roots of (3.12) with $\tau = 0$ always have negative real parts.

When $\tau \neq 0$, an iterative procedure can be employed to find a new function $F(\omega)$, whose roots ω give the Hopf frequency associated with purely imaginary roots of the characteristic equation (3.11). The procedure for finding the function $F(\omega)$ works as follows. Consider a general transcendental characteristic equation [21, 44, 45],

(3.13)
$$\Delta(\tau, \lambda) = \sum_{k=0}^{n} p_k(\lambda) e^{-k\lambda\tau},$$

where $\tau \geq 0$; $p_k(\lambda)$, $k = 0, 1, 2, \ldots$, are polynomials in λ ; and $|p_k(\lambda)/p_0(\lambda)| < 1$, $k = 1, 2, \ldots, n$, for $|\lambda| \to \infty$ and $Re(\lambda) \geq 0$. Substituting $\lambda = i\omega$ into (3.13) and conjugating $\Delta(\tau, i\omega)$ gives

$$\Delta(\tau, i\omega) = \sum_{k=0}^{n} p_k(i\omega) e^{-ki\omega\tau}, \qquad \overline{\Delta(\tau, i\omega)} = \sum_{k=0}^{n} \overline{p_k(i\omega)} e^{ki\omega\tau}.$$

Clearly, $\Delta(\tau, i\omega) = 0$ if and only if $\overline{\Delta(\tau, i\omega)} = 0$. Define $\Delta^{(j)}(\tau, i\omega)$ recursively as

$$\Delta^{(1)}(\tau, i\omega) = \overline{p_0(i\omega)}\Delta(\tau, i\omega) - p_n(i\omega)e^{-ni\omega\tau}\overline{\Delta(\tau, i\omega)} = \sum_{k=0}^{n-1} p_k^{(1)}(i\omega)e^{-ki\omega\tau},$$

$$\vdots$$

$$\Delta^{(j)}(\tau, i\omega) = \overline{p_0^{(j-1)}(i\omega)}\Delta^{(j-1)}(\tau, i\omega) - p_{n-j+1}^{(j-1)}(i\omega)e^{-(n-j+1)i\omega\tau}\overline{\Delta^{(j-1)}(\tau, i\omega)}$$

$$= \sum_{k=0}^{n-j} p_k^{(j)}(i\omega)e^{-ki\omega\tau},$$

$$\vdots$$

$$\Delta^{(n-1)}(\tau, i\omega) = p_0^{(n-1)}(i\omega) + p_1^{(n-1)}(i\omega)e^{-i\omega\tau}.$$

From $p_0^{(j+1)}(i\omega)$ we obtain

$$p_0^{(j+1)}(i\omega) = |p_0^{(j)}(i\omega)|^2 - |p_{n-j}^{(j)}(i\omega)|^2, \quad j = 0, 1, 2, \dots, n-2.$$

Moreover, from $\Delta^{n-1}(\tau, i\omega)$, let

$$F(\omega) = |p_0^{(n-1)}(i\omega)|^2 - |p_1^{(n-1)}(i\omega)|^2.$$

If $\Delta(\tau, i\omega) = 0$, then ω is a root of $F(\omega) = 0$.

Returning to (3.11), we can use the same argument as above with n=2 to find the function $F(\omega)$:

(3.14)
$$F(\omega) = |p_0^1(i\omega)|^2 - |p_1^1(i\omega)|^2,$$

where

$$p_0^1(i\omega) = (\omega^2 + 1)^2 - a_{12}^2 a_{21}^2 \beta^4,$$

$$(3.15)$$

$$p_1^1(i\omega) = a_{21}\alpha\beta^2 [(\omega^2 - 1) - a_{12}a_{21}\beta^2 + 2i\omega].$$

The function $F(\omega)$ is explicitly given by

(3.16)
$$F(\omega) = \omega^8 + 4\omega^6 + a_1\omega^4 + a_2\omega^2 + a_3,$$

where the coefficients a_i , i = 1, 2, 3, are expressed through the parameters of system (1.2) in the following way:

$$a_1 = 6 - 2a_{12}^2 a_{21}^2 \beta^4 - a_{21}^2 \alpha^2 \beta^4, \qquad a_2 = 2(2 - 2a_{12}^2 a_{21}^2 \beta^4 - a_{21}^2 \alpha^2 \beta^4 + a_{21}^3 \alpha^2 a_{12} \beta^6),$$

$$a_3 = 1 - 2a_{12}^2 a_{21}^2 \beta^4 + a_{12}^4 a_{21}^4 \beta^8 - a_{21}^2 \alpha^2 \beta^4 - 2a_{21}^3 \alpha^2 a_{12} \beta^6 - a_{21}^4 \alpha^2 a_{12}^2 \beta^8.$$

Lemma 3.3. If $a_3 < 0$ in (3.16), then the function $F(\omega)$ given by (3.16) has at least one positive root ω ; i.e., $F(\omega) = 0$.

Proof. Assumption $a_3 < 0$ implies that $F(0) = a_3 < 0$. Since $F(\omega)$ as defined by (3.16) is a continuous function of ω , and also $\lim_{\omega \to \infty} F(\omega) = \infty$, this means that there exists a positive root $\omega > 0$ of the equation $F(\omega) = 0$.

Let us now consider the case when the assumption $a_3 < 0$ does not hold. Introducing the notation $s = \omega^2$, the equation $F(\omega) = 0$ can be rewritten as

(3.17)
$$h(s) = s^4 + 4s^3 + a_1s^2 + a_2s + a_3 = 0.$$

From (3.17), we have

$$(3.18) h'(s) = 4s^3 + 12s^2 + 2a_1s + a_2s^2$$

Existence and the number of positive roots of (3.17) depend on the coefficients a_1 , a_2 , a_3 , which themselves depend on system parameters.

Without loss of generality, suppose that (3.17) has four positive roots denoted by s_1, s_2, s_3, s_4 . Then the equation $F(\omega) = 0$ will have four positive real roots,

$$\omega_1 = \sqrt{s_1}, \quad \omega_2 = \sqrt{s_2}, \quad \omega_3 = \sqrt{s_3}, \quad \omega_4 = \sqrt{s_4}.$$

On the other hand, substituting $\lambda = i\omega$ into (3.11) gives

$$(3.19) (i\omega + 1)^2 - a_{21}\alpha\beta^2 e^{-i\omega\tau} - a_{12}a_{21}\beta^2 e^{-2i\omega\tau} = 0.$$

Separating this equation into real and imaginary parts yields

$$-\omega_k^2 + 1 = a_{21}\alpha\beta^2 \cos(\omega_k \tau_k) + a_{12}a_{21}\beta^2 \cos(2\omega_k \tau_k),$$

$$(3.20)$$

$$-2\omega_k = a_{21}\alpha\beta^2 \sin(\omega_k \tau_k) + a_{12}a_{21}\beta^2 \sin(2\omega_k \tau_k),$$

where k = 1, 2, 3, 4. Using trigonometric formulas, the system (3.20) can be rewritten in the form

$$\cos(\omega_k \tau_k) = \frac{-a_{21} \alpha \beta^2 \pm \sqrt{a_{21}^2 \alpha^2 \beta^4 + 8a_{12}^2 a_{21}^2 \beta^4 + 8a_{12} a_{21} - 8a_{12} a_{21} \omega_k^2}}{a_{12} a_{21} \beta},
(3.21)$$

$$\sin(\omega_k \tau_k) = \frac{4\omega_k}{\beta \left(-a_{21} \alpha \beta^2 \pm \sqrt{a_{21}^2 \alpha^2 \beta^4 + 8a_{12}^2 a_{21}^2 \beta^4 + 8a_{12} a_{21} - 8a_{12} a_{21} \omega_k^2}\right)}.$$

Dividing the second equation in (3.21) by the first equation there, we obtain

(3.22)
$$\tau_k^j = \frac{1}{\omega_k} \left[\arctan\left(\frac{-2\omega_k}{1 - \omega_k^2 + a_{12}a_{21}\beta^2}\right) + j\pi \right],$$

where $k = 1, 2, 3, 4, j = 0, 1, 2, \ldots$. Therefore, the solutions of (3.19) are pairs (τ_k^j, ω_k) , where $\lambda = \pm i\omega_k$ are pairs of purely imaginary roots of (3.11) with $\tau = \tau_k^j$. Define

$$\tau_0 = \tau_{k_0}^0 = \min_{1 \le k \le 4} \{ \tau_k^0 \}, \quad \omega_0 = \omega_{k_0}, \qquad k_0 \in \{1, 2, 3, 4\}.$$

Then τ_0 is the first value of the time delay τ for which the roots of the characteristic equation (3.11) cross the imaginary axis. Let $\lambda(\tau) = \alpha(\tau) \pm i\omega(\tau)$ be the root of (3.4) near $\tau = \tau_k^0$ satisfying $\alpha(\tau_k^0) = 0$, $\omega(\tau_k^0) = \omega_0$. It can be easily shown that the following transversality condition holds.

Lemma 3.4. Suppose $h'(s_0) \neq 0$ and $p_0^1(\omega_0) \neq 0$, where h(s) and $p_0^1(\omega_0)$ are defined in (3.15) and (3.17), respectively, and $s_0 = \omega_0^2$. Then the following transversality condition holds:

$$\operatorname{sgn}\left\{\frac{dRe[\lambda(\tau)]}{d\tau}\bigg|_{\tau=\tau_h^0}\right\} = \operatorname{sgn}\left[p_0^1(\omega_0)h'(s_0)\right].$$

Proof. Substituting $\lambda(\tau)$ into the characteristic equation (3.11) and taking the derivative with respect to τ gives

$$\left\{\frac{d\lambda(\tau)}{d\tau}\right\}^{-1} = -\frac{2\lambda + 2}{2a_{12}a_{21}\beta^2\lambda e^{-2\lambda\tau} + a_{21}\alpha\beta^2\lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda}.$$

From this equation, one can find

$$\left\{ \frac{dRe\{\lambda(\tau)\}}{d\tau} \right\}_{\tau=\tau_{k}^{0}}^{-1} = Re\left\{ -\frac{2\lambda + 2}{2a_{12}a_{21}\beta^{2}\lambda e^{-2\lambda\tau} + a_{21}\alpha\beta^{2}\lambda e^{-\lambda\tau}} \right\}_{\tau=\tau_{k}^{0}} - Re\left\{ \frac{\tau}{\lambda} \right\}_{\tau=\tau_{k}^{0}}$$

$$=\frac{2\omega_{0}\left[2\omega_{0}a_{12}a_{21}\beta^{2}\cos(2\omega_{0}\tau_{k}^{0})+2a_{12}a_{21}\beta^{2}\sin(2\omega_{0}\tau_{k}^{0})+\omega_{0}a_{21}\alpha\beta^{2}\cos(\omega_{0}\tau_{k}^{0})+a_{21}\alpha\beta^{2}\sin(\omega_{0}\tau_{k}^{0})\right]}{\left[2\omega_{0}a_{12}a_{21}\beta^{2}\sin(2\omega_{0}\tau_{k}^{0})+\omega_{0}a_{21}\alpha\beta^{2}\sin(\omega_{0}\tau_{k}^{0})\right]^{2}+\left[2\omega_{0}a_{12}a_{21}\beta^{2}\cos(2\omega_{0}\tau_{k}^{0})+\omega_{0}a_{21}\alpha\beta^{2}\cos(\omega_{0}\tau_{k}^{0})\right]^{2}}.$$

Using (3.20) and (3.21), this expression can simplified into

$$\left\{ \frac{dRe\{\lambda(\tau)\}}{d\tau} \right\}_{\tau=\tau_k^0}^{-1} = \frac{\omega_0^2 \left[4\omega_0^6 + 12\omega_0^4 + 2(6 - 2a_{12}^2 a_{21}^2 \beta^4 - a_{21}^2 \alpha^2 \beta^4) \omega_0^2 \right]}{\Lambda(\omega_0^4 + 2\omega_0^2 + 1 - a_{12}^2 a_{21}^2 \beta^4)}$$

$$+\frac{\omega_0^2\left[2(2-2a_{12}^2a_{21}^2\beta^4-a_{21}^2\alpha^2\beta^4-a_{21}^3\alpha^2a_{12}\beta^6)\right]}{\Lambda(\omega_0^4+2\omega_0^2+1-a_{12}^2a_{21}^2\beta^4)}=\frac{s_0\left[4s_0^3+12s_0^2+2a_1s_0+a_2\right]}{\Lambda p_0^1(\omega_0)},$$

where

$$\Lambda = \left[2\omega_0 a_{12} a_{21} \beta^2 \sin(2\omega_0 \tau_k^0) + \omega_0 a_{21} \alpha \beta^2 \sin(\omega_0 \tau_k^0) \right]^2 + \left[2\omega_0 a_{12} a_{21} \beta^2 \cos(2\omega_0 \tau_k^0) + \omega_0 a_{21} \alpha \beta^2 \cos(\omega_0 \tau_k^0) \right]^2$$

and $p_0^1(\omega_0) = (\omega_0^2 + 1)^2 - a_{12}^2 a_{21}^2 \beta^4$. Since $s_0 = \omega_0^2 > 0$ and $\Lambda > 0$, this implies

$$\operatorname{sgn}\left\{\frac{dRe[\lambda(\tau)]}{d\tau}\bigg|_{\tau=\tau_b^0}\right\} = \operatorname{sgn}\left\{\frac{dRe[\lambda(\tau)]}{d\tau}\bigg|_{\tau=\tau_b^0}\right\}^{-1} = \operatorname{sgn}\left\{\frac{1}{\Lambda p_0^1(\omega_0)}h'(s_0)\right\} = \operatorname{sgn}[p_0^1(\omega_0)h'(s_0)],$$

which completes the proof.

By Lemmas 3.2 and 3.4, we have the following result regarding the stability of the trivial steady state of the system (1.2) and the existence of the Hopf bifurcation.

Theorem 3.5. Suppose $|a_{21}\alpha\beta^2| < |1 - a_{12}a_{21}\beta^2|$. If (3.17) has at least one positive root, $p_0^1(\omega_0) \neq 0$, and $h'(s_0) \neq 0$, then the trivial steady state of system (1.2) is stable for $0 \leq \tau < \tau_0$ and undergoes a Hopf bifurcation at a critical value of the time delay $\tau = \tau_0$.

In order to illustrate the effects of varying the coupling strength α and the time delay τ on the stability of the trivial steady state, we numerically compute stability boundaries of this steady state in the $\alpha - \tau$ plane using a pseudospectral algorithm developed by Breda, Maset, and Vermiglio in [46].

Figure 2(a) shows a closed stability region in the α - τ plane for the case when $a_{12}=2$, $a_{21}=-0.55$, and $\beta=1$. We can observe that the steady state is stable inside the colored region, where color corresponds to $[-\max\{Re(\lambda)\}]$. For small values of the time delay τ , there is a large interval of the coupling strength values where the steady state is stable. As τ gets larger, the stability region become narrower, and eventually, for large enough values of the time delay τ , the trivial steady state becomes unstable independently of the value of the coupling strength α . The situation for any values of the parameters a_{12} , a_{21} , and β satisfying $a_{12}a_{21}\beta^2 < -1$ is qualitatively the same as that shown in Figure 2(a).

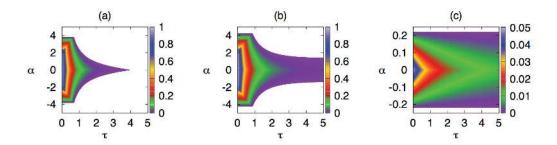


Figure 2. Stability regions of the trivial steady state of system (1.2) with delta distribution $g(s) = \delta(s)$ and $a_{12} = 2$, $\beta = 1$. (a) $a_{21} = -0.55$. (b) $a_{21} = -0.45$. (c) $a_{21} = 0.45$. Color code denotes $[-\max\{Re(\lambda)\}]$.

In the case when the parameters of system (1.2) satisfy the condition $-1 \le a_{12}a_{21}\beta^2 < 0$, the stability region is as illustrated in Figure 2(b). One can see that compared to the case $a_{12}a_{21}\beta^2 < -1$, the stability region is larger, and for all values of the time delay τ there is always a range of values of the coupling strength α for which the trivial steady state of system (1.2) is stable. It is noteworthy that whenever a_{12} and a_{21} have opposite signs, the boundary of the stability region consists of two parts. The trivial steady state can lose its stability via a Hopf bifurcation, in accordance with Theorem 3.5, or undergo a steady-state bifurcation, as described in Lemma 3.1. In Figures 2(a) and (b), the horizontal part of the stability boundary corresponds to $|1 - a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$.

If $0 \le a_{12}a_{21}\beta^2 \le 1$, the trivial steady state can lose its stability only via a steady-state bifurcation, as shown in Figure 2 (c). Once again, the horizontal boundaries are defined by $|1-a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$. Finally, for $a_{12}a_{21}\beta^2 > 1$, the trivial steady state is always unstable independently of the time delay τ , following the results of Theorem 2.2.

4. Uniformly distributed delay. In this section we consider system (1.2) in the case of the uniformly distributed kernel of the form

$$g(s) = \begin{cases} \frac{1}{2\rho} & \text{for } \tau - \rho \le s \le \tau + \rho, \\ 0 & \text{elsewhere.} \end{cases}$$

Taking the Laplace transform of the uniform distribution g(u) given in (4.1), we obtain

(4.2)
$$\widehat{G}(\lambda) = \frac{1}{2\rho\lambda} e^{-\lambda\tau} (e^{\lambda\rho} - e^{-\lambda\rho}) = e^{-\lambda\tau} \frac{\sinh(\lambda\rho)}{\lambda\rho}.$$

Lemma 4.1. Let $|1 - a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$. If $a_{12}a_{21}\beta^2 \neq 1$, then $\lambda = 0$ is a simple root of the characteristic equation (2.2) with the delay kernel (4.1); otherwise, it is a double root.

The proof of Lemma 4.1 is analogous to the proof of Lemma 3.1.

Substituting the Laplace transform (4.2) into the characteristic equation (2.3) and looking for solutions in the form $\lambda = i\omega$ yields

$$(4.3) (i\omega + 1)^2 - [a_{12}a_{21}\beta^2 + a_{21}\alpha\beta^2\gamma(\omega, \rho)]e^{-2i\omega\tau} = 0,$$

where

$$\gamma(\omega, \rho) = \frac{\sin(\omega \rho)}{\omega \rho}.$$

Separating (4.3) into real and imaginary parts gives

$$-\omega^{2} + 1 = [a_{12}a_{21}\beta^{2} + a_{21}\alpha\beta^{2}\gamma(\omega, \rho)]\cos(2\omega\tau),$$

$$(4.4)$$

$$-2\omega = [a_{12}a_{21}\beta^{2} + a_{21}\alpha\beta^{2}\gamma(\omega, \rho)]\sin(2\omega\tau).$$

Squaring and adding the last two equations gives a transcendental equation for the Hopf frequency ω :

(4.5)
$$\omega^2 + 1 = \pm [a_{12}a_{21}\beta^2 + a_{21}\alpha\beta^2\gamma(\omega, \rho)].$$

In a similar way, dividing the second equation in (4.4) by the first equation, we obtain

(4.6)
$$\tan(2\omega\tau) = \frac{2\omega}{\omega^2 - 1}.$$

To illustrate the effects of changing the coupling between the two subnetworks α and the time delay τ on stability of the trivial steady state, we numerically find the stability boundary in the α - τ plane parameterized by the Hopf frequency ω . We rewrite the linearized system with the uniformly distributed kernel as follows:

(4.7)
$$\dot{\mathbf{u}}(t) = L_0 \mathbf{u}(t) + L_1 \mathbf{u}(t-\tau) + \frac{\alpha}{2\rho} \int_{-(\tau+\rho)}^{-(\tau-\rho)} M \mathbf{u}(t+s) ds,$$

where $\mathbf{u} = (u_1, u_2, u_3, u_4)$, $L_0 = -I$, I is the 4×4 identity matrix, and L_1 and M are given by

$$L_1 = \begin{pmatrix} 0 & a_{12}\beta & 0 & 0 \\ a_{21}\beta & 0 & 0 & 0 \\ 0 & 0 & 0 & a_{12}\beta \\ 0 & 0 & a_{21}\beta & 0 \end{pmatrix}, \qquad M = \begin{pmatrix} 0 & 0 & 0 & \beta \\ 0 & 0 & 0 & 0 \\ 0 & \beta & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

The system (4.7) is now in the form suitable for computing the maximum real part of the characteristic eigenvalues using the algorithm described in [46] and implemented in the traceDDE suite in MATLAB.

If $\rho = 0$, the last term in (4.7) becomes $\alpha M \mathbf{u}(t - \tau)$, and system (1.2) reduces to the system with a single discrete time delay τ , which was analyzed in [5]. When $\rho \neq 0$, we have to consider separately different values of $a_{12}a_{21}\beta^2$ and compute the stability of the trivial steady state of the system (1.2) as the distribution width ρ is varied. Figure 3 shows the stability boundary when the condition $a_{12}a_{21}\beta^2 < -1$ is satisfied. In this case, when $\rho = 0$, the stability region is the same as in the case of a single discrete time delay and coincides with Figure 2(a), where for $\tau = 0$ there is an interval of α values for which the trivial steady state of system (1.2) is stable. As ρ is increased, the stability region detaches from the α -axis, and for $\tau = 0$ it is not possible to stabilize the trivial steady state, as shown in Figure 3(b). In Figures 3(c) and (d), increasing ρ further still leads to shrinking of the stability region in

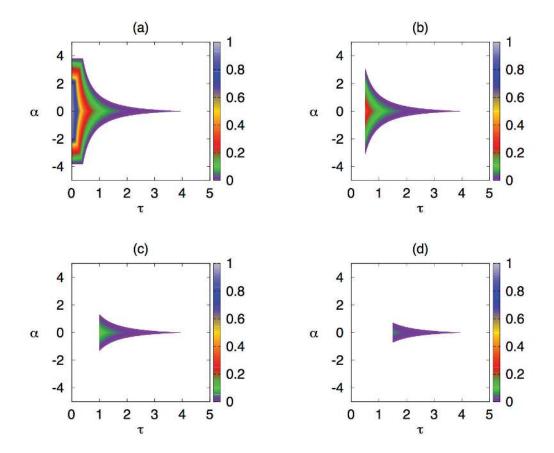


Figure 3. Stability region of the trivial steady state of system (1.2) with the uniform distribution (4.1) for $a_{12}=2,\ a_{21}=-0.55,\ and\ \beta=1$. Color code denotes $[-\max\{Re(\lambda)\}]$. (a) $\rho=0$, (b) $\rho=0.5$, (c) $\rho=1$, and (d) $\rho=1.5$.

the α - τ plane, thus reducing the range of α values for which the trivial steady state of system (1.2) is stable.

In the case when parameter values of system (1.2) satisfy the condition $-1 \le a_{12}a_{21}\beta^2 < 0$ with $\rho = 0$, we again recover the case of a single discrete time delay, and the stability region shown in Figure 4(a) is the same as that in Figure 2(b). As the distribution width is increased, as shown in Figures 4(b)–(d), it is no longer possible to stabilize the trivial steady state with $\tau = 0$ for any values of the coupling strength α . Moreover, the larger the distribution width, the smaller is the interval of α values where the stability is observed. However, unlike the situation when $a_{12}a_{21}\beta^2 < -1$, in this case, the stability region does not become an isolated island but rather becomes a narrow stretch in the α - τ plane. For $0 \le a_{12}a_{21}\beta^2 \le 1$ the stability region does not depend on the time delay τ and is identical to the one shown in Figure 2(c), and for $a_{12}a_{21}\beta^2 > 1$ the trivial steady state is unstable for any $\tau \ge 0$ and any ρ .

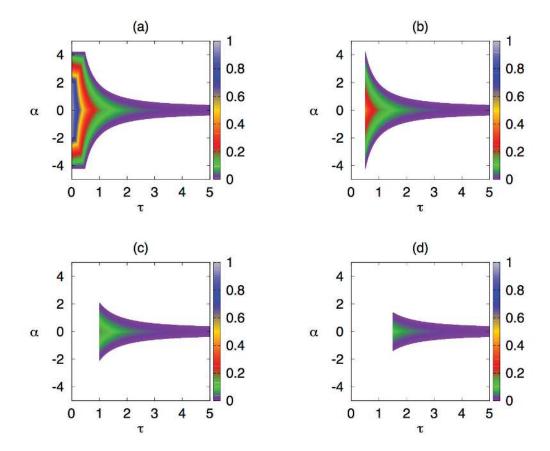


Figure 4. Stability region of the trivial steady state of system (1.2) with the uniform distribution (4.1) for $a_{12}=2,\ a_{21}=-0.45,\ and\ \beta=1$. Color code denotes $[-\max\{Re(\lambda)\}]$. (a) $\rho=0$, (b) $\rho=0.5$, (c) $\rho=1$, and (d) $\rho=1.5$.

5. Weak gamma distributed delay. The gamma distribution kernel, as commonly used in the literature [10, 11, 12, 43], can be written as follows:

(5.1)
$$g(s) = \frac{s^{p-1}\gamma^p e^{-\gamma s}}{(p-1)!},$$

where $\gamma, p \geq 0$ and p is integer. For p = 1, this is an exponential distribution, also called a weak delay kernel. The delay distribution (5.1) has the mean delay

(5.2)
$$\tau_m = \int_0^\infty sg(s)ds = \frac{p}{\gamma}$$

and the variance

(5.3)
$$\sigma^2 = \int_0^\infty (s - \tau_m)^2 g(s) ds = \frac{p}{\gamma^2}.$$

The stability analysis of the trivial steady state of system (1.2) with the gamma distributed delay kernel (5.1) can be performed either by taking the Laplace transform of the distribution kernel, which gives

(5.4)
$$\widehat{G}(\lambda) = \left(\frac{\gamma}{\lambda + \gamma}\right)^p,$$

or by using the *linear chain trick* described in [47]. The linear chain trick allows one to replace the original system with discrete and distributed delays by the system of delay differential equations with discrete time delay only. In this section we will concentrate on the case of the weak gamma distributed kernel. Introducing the new variables

$$u_5(t) = \int_0^\infty \gamma e^{-\gamma s} u_2(t-s) ds,$$

$$u_6(t) = \int_0^\infty \gamma e^{-\gamma s} u_4(t-s) ds$$

allows one to rewrite the system (1.2) as follows:

$$\begin{cases}
\dot{u}_1(t) = -u_1(t) + a_{12}\beta u_2(t-\tau) + \alpha\beta u_6(t), \\
\dot{u}_2(t) = -u_2(t) + a_{21}\beta u_1(t-\tau), \\
\dot{u}_3(t) = -u_3(t) + a_{12}\beta u_4(t-\tau) + \alpha\beta u_5(t), \\
\dot{u}_4(t) = -u_4(t) + a_{21}\beta u_3(t-\tau), \\
\dot{u}_5(t) = \gamma u_2(t) - \gamma u_5(t), \\
\dot{u}_6(t) = \gamma u_4(t) - \gamma u_6(t).
\end{cases}$$

The characteristic equation (2.2) for the system (5.5) with weak distribution kernel has the form

(5.6)
$$\det[\Delta(\tau,\lambda)] = \Delta_{-}(\tau,\lambda) \cdot \Delta_{+}(\tau,\lambda) = 0,$$

where

(5.7)
$$\Delta_{-}(\tau,\lambda) = (\lambda + \gamma)(\lambda + 1)^{2} - (\lambda + \gamma)a_{12}a_{21}\beta^{2}e^{-2\lambda\tau} - \gamma a_{21}\alpha\beta^{2}e^{-\lambda\tau}$$

and

(5.8)
$$\Delta_{+}(\tau,\lambda) = (\lambda + \gamma)(\lambda + 1)^{2} - (\lambda + \gamma)a_{12}a_{21}\beta^{2}e^{-2\lambda\tau} + \gamma a_{21}\alpha\beta^{2}e^{-\lambda\tau}.$$

Lemma 5.1. Let
$$|1 - a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$$
. If
$$-1 \le a_{12}a_{21}\beta^2 \le 1 + 2\gamma \quad and \quad a_{12}a_{21}\beta^2 \ne 1,$$

or

$$a_{12}a_{21}\beta^2 > 1 + 2\gamma$$
 or $a_{12}a_{21}\beta^2 < -1$ and $\tau \neq \tau_{\gamma} = \frac{a_{12}a_{21}\beta^2 - 2\gamma - 1}{\gamma(1 + a_{12}a_{21}\beta^2)}$,

then $\lambda = 0$ is a simple root of the characteristic equation (5.6). If

$$a_{12}a_{21}\beta^2 = 1$$

or

$$a_{12}a_{21}\beta^2 > 1 + 2\gamma$$
 or $a_{12}a_{21}\beta^2 < -1$ and $\tau = \tau_{\gamma}$,

then $\lambda = 0$ is a double root of the characteristic equation (5.6).

The proof of Lemma 5.1 is similar to the proof of Lemma 3.1.

We will analyze the case of $\Delta_{-}(\tau, \lambda)$ given by (5.7), and the analysis is the same for $\Delta_{+}(\tau, \lambda)$ in (5.8). The transcendental equation for eigenvalues λ for $\Delta_{-}(\tau, \lambda)$ has the form

$$(5.9) \qquad \Delta_{-}(\tau,\lambda) = (\lambda + \gamma)(\lambda + 1)^{2} - (\lambda + \gamma)a_{12}a_{21}\beta^{2}e^{-2\lambda\tau} - \gamma a_{21}\alpha\beta^{2}e^{-\lambda\tau} = 0.$$

Note that when $\tau = 0$, this equation reduces to

$$(5.10) \lambda^3 + (\gamma + 2)\lambda^2 + (2\gamma + 1 - a_{12}a_{21}\beta^2)\lambda + \gamma(1 - a_{12}a_{21}\beta^2 - a_{21}\alpha\beta^2) = 0.$$

In view of the Routh-Hurwitz criterion, we have the following result.

Lemma 5.2. Assume that condition

$$(5.11) a_{21}a_{12}\beta^2 < \min\{2\gamma + 1, 1 - a_{21}\alpha\beta^2\}$$

holds. Then all roots of (5.10) have negative real part.

When $\tau > 0$, we can use the same technique as in the case of the delta distributed kernel in order to calculate $F(\omega)$ as follows:

$$p_0^1(i\omega) \, = \left[\gamma - (\gamma + 2)\,\omega^2\right]^2 + \left[\omega^3 - (2\,\gamma + 1)\,\omega\right]^2 - \left(\gamma^2 + \omega^2\right)a_{21}{}^2\beta^4a_{12}{}^2,$$

$$(5.12) p_1^1(i\omega) = -a_{21}\alpha \, \beta^2 \gamma^2 + a_{21}\alpha \, \beta^2 \gamma^2 \omega^2 + 2 \, a_{21}\alpha \, \beta^2 \gamma \, \omega^2 - a_{21}^2\alpha \, \beta^4 a_{12} \gamma^2$$

$$+ \left(-a_{21}\alpha \beta^2 \gamma \omega^3 + 2 a_{21}\alpha \beta^2 \gamma^2 \omega + a_{21}\alpha \beta^2 \gamma \omega - a_{21}^2 \alpha \beta^4 a_{12} \gamma \omega \right) i,$$

and hence

(5.13)
$$F(\omega) = \omega^{12} + b_1 \omega^{10} + b_2 \omega^8 + b_3 \omega^6 + b_4 \omega^4 + b_5 \omega^2 + b_6,$$

where

$$b_1 = 2\gamma^2 + 4$$
, $b_2 = -2a_{12}^2a_{21}^2\beta^4 + 8\gamma^2 + \gamma^4 + 6$,

$$b_3 = -4\,a_{12}{}^2a_{21}{}^2\beta^4 + 4 + 12\,\gamma^2 + 4\,\gamma^4 - a_{21}{}^2\alpha^2\beta^4\gamma^2 - 4\,a_{12}{}^2a_{21}{}^2\beta^4\gamma^2,$$

$$b_4 = 1 + 6\,\gamma^4 - 8\,a_{12}{}^2a_{21}{}^2\beta^4\gamma^2 - 2\,\gamma^4a_{12}{}^2a_{21}{}^2\beta^4 - 2\,a_{12}{}^2a_{21}{}^2\beta^4 + a_{12}{}^4a_{21}{}^4\beta^8 - 2\,a_{21}{}^2\alpha^2\beta^4\gamma^2 + 8\,\gamma^2 - a_{21}{}^2\alpha^2\beta^4\gamma^4 - 2\,a_{21}{}^3\alpha^2\beta^6\gamma^2a_{12},$$

$$b_5 = 4\gamma^4 + 2\gamma^2 - 4\gamma^4 a_{12}^2 a_{21}^2 \beta^4 + 8a_{21}^3 \alpha^2 \beta^6 \gamma^3 a_{12} + 2a_{12}^4 a_{21}^4 \beta^8 \gamma^2 - a_{21}^2 \alpha^2 \beta^4 \gamma^2 + 2a_{21}^3 \alpha^2 \beta^6 \gamma^4 a_{12} - a_{21}^4 \alpha^2 \beta^8 a_{12}^2 \gamma^2 2a_{21}^2 \alpha^2 \beta^4 \gamma^4 - 4a_{12}^2 a_{21}^2 \beta^4 \gamma^2 + 2a_{21}^3 \alpha^2 \beta^6 \gamma^2 a_{12},$$

$$b_6 = -a_{21}^2 \alpha^2 \beta^4 \gamma^4 - 2a_{21}^3 \alpha^2 \beta^6 \gamma^4 a_{12} - 2\gamma^4 a_{12}^2 a_{21}^2 \beta^4 - a_{21}^4 \alpha^2 \beta^8 a_{12}^2 \gamma^4 + a_{12}^4 a_{21}^4 \beta^8 \gamma^4 + \gamma^4.$$

Lemma 5.3. Assume that $b_6 < 0$. Then the equation $F(\omega) = 0$ has at least one positive root.

Proof. Assumption $b_6 < 0$ implies that $F(0) = b_6 < 0$. Since $F(\omega)$ as defined by (5.13) is a continuous function of ω , and also $\lim_{\omega \to \infty} F(\omega) = \infty$, this means that there exists a positive root $\omega > 0$ of the equation $F(\omega) = 0$.

Let $s = \omega^2$; then the equation $F(\omega) = 0$ becomes

(5.14)
$$h(s) = s^6 + b_1 s^5 + b_2 s^4 + b_3 s^3 + b_4 s^2 + b_5 s + b_6 = 0.$$

Without loss of generality, suppose that (5.14) has six positive roots, denoted by s_1 , s_2 , s_3 , s_4 , s_5 , s_6 . This implies that $F(\omega) = 0$ also has six positive real roots given by

$$\omega_1 = \sqrt{s_1}, \quad \omega_2 = \sqrt{s_2}, \quad \omega_3 = \sqrt{s_3}, \quad \omega_4 = \sqrt{s_4}, \quad \omega_5 = \sqrt{s_5}, \quad \omega_6 = \sqrt{s_6}.$$

At the same time, substituting $\lambda = i\omega$, $\omega > 0$ into (5.9), we obtain

$$(5.15) (i\omega + \gamma)(i\omega + 1)^2 e^{i\omega\tau} - \gamma a_{21}\alpha\beta^2 - (i\omega + \gamma)a_{12}a_{21}\beta^2 e^{-i\omega\tau} = 0.$$

Separating this equation into the real and imaginary parts gives

$$\gamma(-\omega^{2}+1) - 2\omega^{2} - \gamma a_{21}\alpha\beta^{2}\cos(\omega\tau) = \gamma a_{12}a_{21}\beta^{2}\cos(2\omega\tau) + \omega a_{12}a_{21}\beta^{2}\sin(2\omega\tau),$$
(5.16)
$$\omega(-\omega^{2}+1) + 2\gamma\omega + \gamma a_{21}\alpha\beta^{2}\sin(\omega\tau) = \omega a_{12}a_{21}\beta^{2}\cos(2\omega\tau) - \gamma a_{12}a_{21}\beta^{2}\sin(2\omega\tau).$$

Using trigonometric formulas, system (5.16) can be simplified as follows:

$$(1 - \omega^2 + a_{12}a_{21}\beta^2)\gamma - 2\omega^2$$

= $\left[\gamma a_{21}\alpha\beta^2 + 2\gamma a_{12}a_{21}\beta^2\cos(\omega\tau) + 2\omega a_{12}a_{21}\beta^2\sin(\omega\tau)\right]\cos(\omega\tau),$

$$\omega(1 - \omega^2 + 2\gamma - a_{12}a_{21}\beta^2) = -\left[\gamma a_{21}\alpha\beta^2 + 2\gamma a_{12}a_{21}\beta^2\cos(\omega\tau) + 2\omega a_{12}a_{21}\beta^2\sin(\omega\tau)\right]\sin(\omega\tau).$$

Dividing the second of these equations by the first gives

(5.17)
$$\tan(\omega\tau) = -\frac{\omega(1-\omega^2+2\gamma-a_{12}a_{21}\beta^2)}{(1-\omega^2+a_{12}a_{21}\beta^2)\gamma-2\omega^2}$$

We can now define

(5.18)
$$\tau_k^j = \frac{1}{\omega_k} \left[\arctan\left(-\frac{\omega_k (1 - \omega_k^2 - a_{12} a_{21} \beta^2 + 2\gamma)}{(1 - \omega_k^2 + a_{12} a_{21} \beta^2) \gamma - 2\omega_k^2} \right) + j\pi \right],$$

where k = 1, ..., 6, j = 0, 1, 2, ... The pairs (τ_k^j, ω_k) are the solutions of the characteristic equation (5.15), and $\lambda = \pm i\omega_k$ are pairs of purely imaginary roots of the characteristic equation (5.9) for $\tau = \tau_k^j$. Let

(5.19)
$$\tau_0 = \tau_{k_0}^0 = \min_{1 \le k \le 6} \{ \tau_k^0 \}, \qquad \omega_0 = \omega_{k_0},$$

where $k_0 \in \{1, ..., 6\}$. Then $\tau = \tau_0$ is the first value of the time delay such that (5.9) has purely imaginary roots. Using the time delay τ as the bifurcation parameter, let $\lambda(\tau) = \alpha(\tau) \pm i\omega(\tau)$ be the root of (5.9) near $\tau = \tau_0$ such that $\alpha(\tau_0) = 0$, $\omega(\tau_0) = \omega_0$. In order to show that we have a Hopf bifurcation at $\tau = \tau_0$, we have to show that $dRe[\lambda(\tau_0)]/d\tau > 0$.

Theorem 5.4. Suppose that the conditions of Lemma 5.2 hold, and $h'(s_0)p_0^1(i\omega_0) > 0$, where h(s) and $p_0^1(i\omega)$ are defined in (5.12) and (5.14), respectively, and $s_0 = \omega_0^2$. Then the trivial steady state of system (5.5) is linearly asymptotically stable for $\tau \in [0, \tau_0)$ and undergoes a Hopf bifurcation at $\tau = \tau_0$.

Proof. Lemma 5.2 ensures that at $\tau=0$ all eigenvalues of the characteristic equation have negative real part. From the definition of τ_0 in (5.19) it follows that τ_0 is the first positive value of τ for which the characteristic equation (5.9) has a pair of complex conjugate eigenvalues $\lambda=\pm i\omega_0$. In this case, however, it does not prove possible to use the direct computation as in the proof of Lemma 3.4 to show that $\lambda=i\omega_0$ is a simple root of the characteristic equation (5.9). Following the methodology of Li, Zhang, and Wang [44] instead, we introduce a function

$$S_1(\omega) = \operatorname{sgn}[\omega F'(\omega) p_0^1(i\omega)],$$

which determines possible changes in the number of roots with positive real part of (5.9). From the definition of the function h(s), we have

$$F(\omega) = h(\omega^2) \implies F'(\omega) = 2\omega h'(\omega^2) = 2\omega h'(s),$$

which under the assumptions of the theorem implies

$$S_1(\omega_0) = \operatorname{sgn}[\omega_0 F'(\omega_0) p_0^1(i\omega_0)] = \operatorname{sgn}[2\omega_0^2 h'(s_0) p_0^1(\omega_0)] = \operatorname{sgn}[h'(s_0) p_0^1(i\omega_0)] > 0.$$

From Theorem 2 in [44] it then follows that

$$\operatorname{sgn}\left\{\frac{dRe[\lambda(\tau)]}{d\tau}\bigg|_{\tau=\tau_0}\right\} > 0,$$

which suggests that the trivial steady state of system (5.5) undergoes a Hopf bifurcation at $\tau = \tau_0$.

In order to illustrate how the stability of the trivial steady state of system (5.5) changes in the case of the weak gamma distribution kernel, we illustrate in Figure 5 the stability boundary for different values of $a_{12}a_{21}\beta^2$. In the case when $a_{12}a_{21}\beta^2 < -1$, the trivial steady state is stable inside the region bounded by the surface shown in Figure 5(a) and unstable outside this region. For $-1 \le a_{12}a_{21}\beta^2 \le 1$, there are two nonoverlapping surfaces, and the trivial steady state is stable for any parameter values lying inside the region bounded by these surfaces, as shown in Figures 5(b) and (c). For $a_{12}a_{21}\beta^2 > 1$, the trivial steady state is unstable for any $\tau \ge 0$, γ , and α .

To get a better understanding of how eigenvalues are changing inside the stability region, we show in Figure 6 numerically computed eigenvalues of the characteristic equation for the cases shown in Figure 5 and one particular value of $\gamma = 1$. Figure 6(a) shows that in the case when $a_{12}a_{21}\beta^2 < -1$, as the value of the discrete time delay increases, the stability region

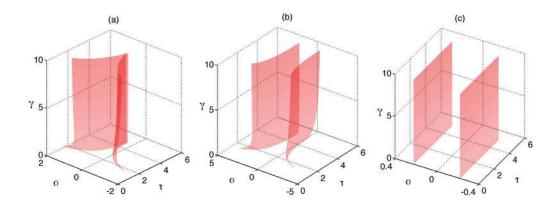


Figure 5. Stability boundary of the trivial steady state of system (1.2) with weak delay distribution kernel (5.1) (p = 1) and $a_{12} = 2$, $\beta = 1$. (a) $a_{12}a_{21}\beta^2 < -1$ with $a_{21} = -0.55$. (b) $-1 \le a_{12}a_{21}\beta^2 < 0$ with $a_{21} = -0.45$. (c) $0 \le a_{12}a_{21}\beta^2 \le 1$ with $a_{21} = 0.45$. The trivial steady state is stable inside the region restricted by the boundaries and unstable outside this region.

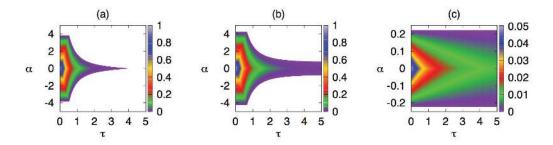


Figure 6. Stability region of the trivial steady state of system (1.2) with weak delay distribution kernel (5.1) (p = 1) with $\gamma = 1$, $a_{12} = 2$, $\beta = 1$. (a) $a_{12}a_{21}\beta^2 < -1$ with $a_{21} = -0.55$. (b) $-1 \le a_{12}a_{21}\beta^2 < 0$ with $a_{21} = -0.45$. (c) $0 \le a_{12}a_{21}\beta^2 \le 1$ with $a_{21} = 0.45$. Color code denotes $[-\max\{Re(\lambda)\}]$.

shrinks, and for sufficiently large values of the discrete time delay τ , the trivial steady state of system (5.5) is unstable for any value of the coupling strength α . In the parameter region where $-1 \le a_{12}a_{21}\beta^2 < 0$, as the discrete time delay increases, the region of stability of the trivial steady state of system (5.5) becomes smaller, but there is always a range of coupling strength values α at which the steady state is stable, as shown in Figure 6(b). In the case $0 \le a_{12}a_{21}\beta^2 \le 1$, the region of stability is bounded by $|1 - a_{12}a_{21}\beta^2| = |a_{21}\alpha\beta^2|$ and is independent of τ and γ .

Figure 7 shows that as the coupling strength α between the two subnetworks is increased, in the case of the weak distribution kernel, the stability region of the trivial steady state becomes smaller in the γ - τ plane.

6. Numerical simulations. In order to illustrate and confirm the results of our analytical findings, we perform direct numerical simulations of system (1.2) for different cases of delay distribution. Let $f(\cdot) = \tanh(\cdot)$, which implies that $\beta = f'(0) = 1$ and $g(s) = \delta(s)$. Then

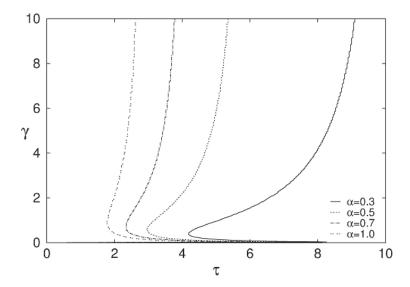


Figure 7. Boundary of stability in the τ - γ plane for the weak delay distribution kernel (5.1) (p = 1), for different values of α , $a_{12} = 2$, $a_{21} = -0.5$. The trivial steady state is stable to the left of the boundary and unstable to the right of it.

system (1.2) takes the form

(6.1)
$$\dot{u}_{1}(t) = -u_{1}(t) + a_{12} \tanh(u_{2}(t-\tau)) + \alpha \tanh(u_{4}(t)),
\dot{u}_{2}(t) = -u_{2}(t) + a_{21} \tanh(u_{1}(t-\tau)),
\dot{u}_{3}(t) = -u_{3}(t) + a_{12} \tanh(u_{4}(t-\tau)) + \alpha \tanh(u_{2}(t)),
\dot{u}_{4}(t) = -u_{4}(t) + a_{21} \tanh(u_{3}(t-\tau)).$$

First, we consider the case when $a_{12}a_{21}\beta^2 < -1$ holds, for example, $a_{12} = 2$, $a_{21} = -0.55$, and $\alpha = \pm 2$; then the expression (3.17) has the form

$$h(s) = s^4 + 4s^3 + 2.3700s^2 - 5.922s + 0.032.$$

In this case, h(s) = 0 has only one positive real root $s_0 = 0.882$, and $\omega_0 = 0.939$, $\tau_0 = 1.159$, $h'(s_0) = 10.331 > 0$, $p_0^1(i\omega_0) = 2.331 > 0$. Therefore, from Theorem 3.5 it follows that the trivial solution of system (6.1) is stable when $0 \le \tau < \tau_0$, and undergoes a Hopf bifurcation when τ crosses through the critical value of the time delay $\tau_0 = 1.159$, giving rise to a stable periodic solution, as illustrated in Figures 8(a)–(b). In a similar manner, when the parameter values of system (1.2) satisfy $-1 \le a_{12}a_{21}\beta^2 < 0$, e.g., $a_{12} = 2$, $a_{21} = -0.45$, and $\alpha = \pm 2$, the expression (3.17) becomes

$$h(s) = s^4 + 4s^3 + 3.57s^2 - 2.318s + 0.028.$$

Hence, h(s) = 0 has one positive real root $s_0 = 0.416$, and $\omega_0 = 0.645$, $\tau_0 = 2.062$, $h'(s_0) = 3.02 > 0$, $p_0^1(i\omega_0) = 1.196 > 0$. Theorem 3.5 implies that the trivial solution of system (6.1) is stable when $0 < \tau < \tau_0$ and undergoes a Hopf bifurcation at $\tau_0 = 2.062$, once again resulting in a stable periodic solution, as shown in Figures 8(c)–(d).

In the case $0 \le a_{12}a_{21}\beta^2 \le 1$, system (6.1) approaches the stable trivial steady state provided that $|a_{21}\alpha\beta^2| < |1 - a_{12}a_{21}\beta^2|$, as illustrated in Figure 8(e). If $|\alpha| > |\alpha_{\rm c}|$, where

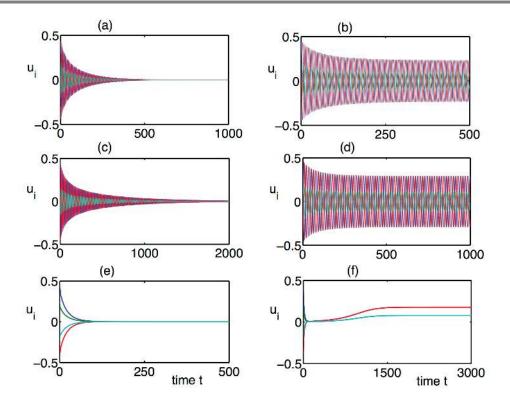


Figure 8. (a)–(b) Solution of system (6.1) in the case when $a_{12}a_{21}\beta^2 < -1$. Parameter values are $a_{12} = 2$, $a_{21} = -0.55$, $\alpha = \pm 2$, and $\tau_0 = 1.159$. (a) $0 < \tau = 1.1 < \tau_0$. (b) $\tau = 1.2 > \tau_0$. (c)–(d) Solution of system (6.1) in the case when $-1 \le a_{12}a_{21}\beta^2 < 0$. Parameter values are $a_{12} = 2$, $a_{21} = -0.45$, $\alpha = \pm 2$, and $\tau_0 = 2.062$. (c) $0 < \tau = 2 < \tau_0$. (d) $\tau = 2.3 > \tau_0$. (e)–(f) Solution of system (6.1) in the case when $0 \le a_{12}a_{21}\beta^2 \le 1$. Parameter values are $a_{12} = 2$, $a_{21} = 0.45$, and $\tau = 1$. (e) $\alpha = 0.15$. (f) $\alpha = 0.25$.

 $\alpha_{\rm c}$ satisfies $|a_{21}\alpha_{\rm c}\beta^2|=|1-a_{12}a_{21}\beta^2|$, the trivial steady state is unstable via a steady-state bifurcation, and system (6.1) tends to one of its stable nontrivial steady states, as shown in Figure 8(f). One should note that it is possible for this system to simultaneously have multiple stable steady states for the same parameter values, and the solutions will approach one of them depending on the initial conditions. For $a_{12}a_{21}\beta^2 > 1$, the behavior of system (6.1) is similar to the case shown in Figure 8(f).

In order to illustrate the dynamics in the case of the weak gamma distribution kernel, we again take $f(\cdot) = \tanh(\cdot)$, $\beta = f'(0) = 1$ and rewrite the system (1.2) as

(6.2)
$$\begin{cases} \dot{u}_{1}(t) = -u_{1}(t) + a_{12} \tanh(u_{2}(t-\tau)) + \alpha \tanh(u_{6}(t)), \\ \dot{u}_{2}(t) = -u_{2}(t) + a_{21} \tanh(u_{1}(t-\tau)), \\ \dot{u}_{3}(t) = -u_{3}(t) + a_{12} \tanh(u_{4}(t-\tau)) + \alpha \tanh(u_{5}(t)), \\ \dot{u}_{4}(t) = -u_{4}(t) + a_{21} \tanh(u_{3}(t-\tau)), \\ \dot{u}_{5}(t) = \gamma u_{2}(t) - \gamma u_{5}(t), \\ \dot{u}_{6}(t) = \gamma u_{4}(t) - \gamma u_{6}(t). \end{cases}$$

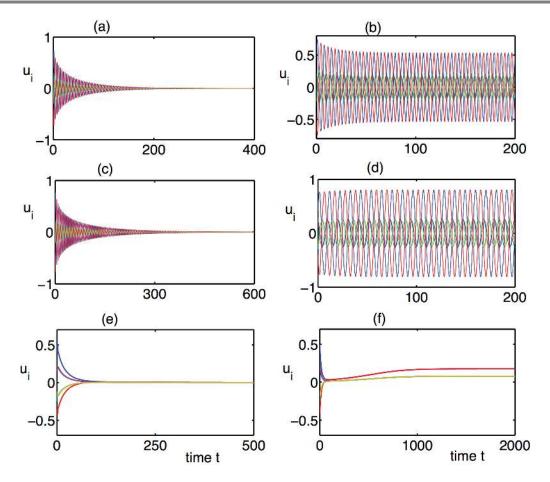


Figure 9. (a)–(b) Solution of system (6.2) in the case when $a_{12}a_{21}\beta^2 < -1$. Parameter values are $a_{12} = 2$, $a_{21} = -0.55$, $\alpha = \pm 2$, and $\tau_0 = 0.873$. (a) $0 < \tau = 0.8 < \tau_0$. (b) $\tau = 1 > \tau_0$. (c)–(d) Solution of system (6.2) in the case when $-1 \le a_{12}a_{21}\beta^2 < 0$. Parameter values are $a_{12} = 2$, $a_{21} = -0.45$, $\alpha = \pm 2$, and $\tau_0 = 1.286$. (c) $0 < \tau = 1.2 < \tau_0$. (d) $\tau = 2 > \tau_0$. (e)–(f) Solution of system (6.2) in the case when $0 \le a_{12}a_{21}\beta^2 \le 1$. Parameter values are $a_{12} = 2$, $a_{21} = 0.45$, and $\tau = 1$. (e) $\alpha = 0.15$. (f) $\alpha = 0.25$.

In the case when $a_{12}a_{21}\beta^2 < -1$ (for example, $a_{12} = 2$, $a_{21} = -0.55$, and $\alpha = \pm 2$) we find $\omega_0 = 0.947$, $\tau_0 = 0.873$, $h'(s_0)p_0^1(i\omega_0) = 277.94 > 0$. Using Theorem 5.4, one can conclude that the trivial steady state is stable when $0 < \tau < \tau_0$ (see Figure 9(a)), and at $\tau = \tau_0$ it loses stability via a Hopf bifurcation, which results in a stable periodic solution (Figure 9(b)). In the same way, when parameters of the system (6.2) satisfy $-1 \le a_{12}a_{21}\beta^2 < 0$ —for example, $a_{12} = 2$, $a_{21} = -0.45$, and $\alpha = \pm 2$ —we have $\omega_0 = 0.769$, $\tau_0 = 1.286$, $h'(s_0)p_0^1(i\omega_0) = 9.337 > 0$. It is possible to use Theorem 5.4 to conclude a Hopf bifurcation of the trivial steady state and a transition to a stable periodic solution at $\tau = \tau_0$, as illustrated in Figures 9(c)–(d). Figures 9(e) and (f) depict the case when $0 \le a_{12}a_{21}\beta^2 \le 1$, and we observe the loss of stability of the trivial steady state through a steady-state bifurcation, which results in a stable nontrivial equilibrium.

7. Discussion. In this paper we have analyzed a generalized model of coupled neural networks with discrete and distributed time delays for a general distribution kernel. We have analytically obtained a characteristic equation determining the stability of the trivial steady state for any general distribution kernel. In order to further understand the dynamics of the system, we have studied in detail the cases of the three commonly used distribution kernels, i.e., delta, uniform, and weak gamma distributions. For each of these distributions, we have obtained analytical conditions for stability of the null solution in terms of system parameters and the time delays. The results suggest that stability of the zero steady state depends on the synaptic weights, strength of the connection between the two subnetworks, and time delays in the connection. In the case of the Dirac delta distribution kernel, the stability region of the trivial steady state becomes larger with increasing product of the synaptic weights.

In the case of the uniformly distributed kernel, the stability properties of the trivial steady state strongly depend on the width of the distribution. In particular, as the width of the distribution becomes larger, the stability region shrinks and becomes an isolated bubble in the τ - α plane. As one of the synaptic weights is increased, enlarging the distribution width leads to a smaller region of stability, but it never becomes an isolated island.

In the case of the weak gamma distribution kernel, we have obtained analytical and numerical results on the stability properties of the system and have shown that the strength of the connection between the two subnetworks plays an important role. Increasing the coupling reduces the size of the stability region, in which the trivial steady state is stable and no oscillations are possible. We have also performed direct numerical simulations that confirm our analytical findings and illustrate the dynamics of the system inside and outside the stability regions for all distribution kernels presented in the paper. Notably, for some parameter values, when the trivial steady state becomes unstable, the system can support stable nontrivial steady states.

It is worth noting that while the cases of delta and weak gamma distribution exhibit similar types of stability, in the case of the uniform distribution it is not sufficient to consider only the mean time delay, as the width of the distribution also plays a profound role in defining the region of stability. The combination of discrete and distributed time delays considered in this paper shows that stability regions for wider uniform distributions are characterized by smaller ranges of coupling strengths, which is in contrast to the results obtained in [30, 31, 34], where the authors observed an increase in the stability region for wider uniform distributions.

Neural networks are often used to model associative memories or pattern recognition, where information is represented by stable equilibria of the system. In order to retrieve a memory, the system should start with an initial condition lying within a basin of attraction of a stable steady state. If the steady state is unstable, this renders the retrieval of the memory impossible [35]. In light of this observation, the results obtained in this paper provide important insights into the circumstances where neural networks with discrete and distributed time delays can support successful memory retrieval.

There are several directions in which current work can be extended to yield a better understanding of neural systems. One possibility would be to consider a large system of coupled neurons consisting of several subgroups with different types of delayed connections within and between subgroups. Such systems are known to be able to support rich dynamics including chimera states, where some nodes of the network have coherent dynamics while others remain chaotic. The question of how such dynamics can be affected by the combination

of discrete and distributed delays remains an open problem. Another practically important issue is that of dynamic synchronization in systems with time-delayed connections. We have recently developed a formalism for analysis of synchronization in systems with distributed delay coupling [32], and it would be insightful to generalize this approach to systems that include both discrete and distributed time delays between nodes.

Efficient pattern recognition relies on the presence of multistability in the system [48] and, hence, requires a careful analysis of the basins of attraction of different steady states. Understanding the structure of these coexisting attractors in systems with discrete and distributed delays would explain how such neural networks perform the complex task of pattern recognition.

REFERENCES

- [1] S.H. Strogatz, Exploring complex networks, Nature, 410 (2001), pp. 268–276.
- [2] C. Hermann, R. Saccon, P.R. Senthilan, L. Domnik, H. Dircksen, T. Yoshii, and C. Helfrich-Foerster, *The circadian clock network in the brain of different Drosophila species*, J. Comp. Neurol., 521 (2013), pp. 367–388.
- [3] S.H. Strogatz, Sync: The Emerging Science of Spontaneous Order, Hyperion, New York, 2003.
- [4] P.K. SIMPSON, Artificial Neural System: Foundation, Paradigms, Applications and Implementations, Pergamon Press, New York, 1990.
- [5] Y. Song, M.O. Tade, and T. Zhang, Bifurcation analysis and spatio-temporal patterns of nonlinear oscillations in a delayed neural network with unidirectional coupling, Nonlinearity, 22 (2009), pp. 975– 1001.
- [6] S. BOCCALETTI, The Synchronized Dynamics of Complex Systems, Elsevier, Amsterdam, 2008.
- [7] E.A. Martens, S. Thutupalli, A. Fourrière, and O. Hallatschek, *Chimera states in mechanical oscillator networks*, Proc. Natl. Acad. Sci. USA, 110 (2013), pp. 10563–10567.
- [8] O.V. Popovych, S. Yanchuk, and P.A. Tass, Delay- and coupling-induced firing patterns in oscillatory neural loops, Phys. Rev. Lett., 107 (2011), 228102.
- [9] I. OMELCHENKO, Y.L. MAISTRENKO, P. HÖVEL, AND E. SCHÖLL, Loss of coherence in dynamical networks: Spatial chaos and chimera states, Phys. Rev. Lett., 106 (2011), 234102.
- [10] S. BERNARD, J. BÉLAIR, AND M.C. MACKEY, Sufficient conditions for stability of linear differential equations with distributed delay, Discrete Contin. Dyn. Syst. Ser. B, 1 (2001), pp. 233–256.
- [11] S.A. Campbell and R. Jessop, Approximating the stability region for a differential equation with a distributed delay, Math. Model. Nat. Phenom., 4 (2009), pp. 1–27.
- [12] K.L. Cooke and Z. Grossman, Discrete delay, distributed delay and stability switches, J. Math. Anal. Appl., 86 (1982), pp. 592–627.
- [13] V.K. JIRSA AND M. DING, Will a large complex system with delays be stable?, Phys. Rev. Lett., 94 (2004), 070602.
- [14] U. MEYER, J. SHAO, S. CHAKRABARTY, S.F. BRANDT, H. LUKSCH, AND R. WESSEL, Distributed delays stabilize neural feedback systems, Biol. Cybern., 99 (2008), pp. 79–87.
- [15] F.M. Atay, ed., Complex Time-Delay Systems, Springer, Berlin, 2010.
- [16] M. SORIANO, J. GARCIA-OJALVO, C. MIRASSO, AND I. FISCHER, Complex photonics: Dynamics and applications of delay-coupled semiconductor lasers, Rev. Modern Phys., 85 (2013), pp. 421–470.
- [17] A. ZAKHAROVA, I. SCHNEIDER, Y.N. KYRYCHKO, K.B. BLYUSS, A. KOSESKA, B. FIEDLER, AND E. SCHÖLL, Time delay control of symmetry-breaking primary and secondary oscillation death, Europhys. Lett., 104 (2013), 50004.
- [18] T. Erneux, Applied Delay Differential Equations, Springer, New York, 2009.
- [19] Y.N. KYRYCHKO AND S.J. HOGAN, On the use of delay equations in engineering applications, J. Vibr. Control, 16 (2010), pp. 943–960.
- [20] V. Flunkert, S. Yanchuk, T. Dahms, and E. Schöll, Synchronizing distant nodes: A universal classification of networks, Phys. Rev. Lett., 105 (2010), 254101.
- [21] K. Gu, L. Kharitonov, and L. Chen, Stability of Time-Delay System, Birkhäuser, Boston, 2003.

- [22] G. Stépán, Retarded Dynamical Systems: Stability and Characteristic Functions, Longman Press, London, 1989.
- [23] A. GJURCHINOVSKI AND V. URUMOV, Variable-delay feedback control of unstable steady states in retarded time-delayed systems, Phys. Rev. E, 81 (2010), 016209.
- [24] S.A. GOURLEY AND J.W.-H. So, Extinction and wavefront propagation in a reaction-diffusion model of a structured population with distributed maturation delay, Proc. R. Soc. Edinburgh, 133 (2003), pp. 527–548.
- [25] H. Zhao, Global asymptotic stability of Hopfield neural network involving distributed delays, Neural Netw., 17 (2004), pp. 47–53.
- [26] F.M. Atay and A. Hutt, Neural fields with distributed transmission speeds and long-range feedback delays, SIAM J. Appl. Dyn. Syst., 5 (2006), pp. 670-698.
- [27] A. Hutt and L. Zhang, Distributed nonlocal feedback delays may destabilize fronts in neural fields, distributed transmission delays do not, J. Math. Neurosci., 3 (2013), 9.
- [28] X. Liao, K. Wong, and Z. Wu, Bifurcation analysis on a two-neuron system with distributed delays, Phys. D, 49 (2001), pp. 123–141.
- [29] S. Ruan and R.S. Filfil, Dynamics of a two-neuron system with discrete and distributed delays, Phys. D, 191 (2004), pp. 323–342.
- [30] Y.N. KYRYCHKO, K.B. BLYUSS, AND E. SCHÖLL, Amplitude death in systems of coupled oscillators with distributed-delay coupling, Eur. Phys. J. B Condens. Matter Phys., 84 (2011), pp. 307–315.
- [31] Y.N. KYRYCHKO, K.B. BLYUSS, AND E. SCHÖLL, Amplitude and phase dynamics in oscillators with distributed-delay coupling, Phil. Trans. R. Soc. A, 371 (2013), 20120466.
- [32] Y.N. KYRYCHKO, K.B. BLYUSS, AND E. SCHÖLL, Synchronization of networks of oscillators with distributed delay coupling, Chaos, 24 (2014), 043117.
- [33] X. LI AND G. Hu, Stability and Hopf bifurcation on a neuron network with discrete and distributed delays, Appl. Math. Sci., 5 (2011), pp. 2077–2084.
- [34] F.M. Atay, Distributed delays facilitate amplitude death of coupled oscillators, Phys. Rev. Lett., 91 (2003), 094101.
- [35] J.J. Hopfield, Neurons with graded response have collective computational properties like those of twostate neurons, Proc. Natl. Acad. Sci. USA, 81 (1984), pp. 3088–3092.
- [36] C.M. Marcus and R.M. Westervelt, Stability of analog neural networks with delay, Phys. Rev. A, 39 (1989), pp. 347–359.
- [37] T. Faria, On a planar system modelling a neuron network with memory, J. Differential Equations, 168 (2000), pp. 129–149.
- [38] J. WEI AND S. RUAN, Stability and bifurcation in a neural network model with two delays, Phys. D, 130 (1999), pp. 255–272.
- [39] Y. Song, V.A. Makarov, and M.G. Velarde, Stability switches, oscillatory multistability, and spatiotemporal patterns of nonlinear oscillations in recurrently delay-coupled neural networks, Biol. Cybern., 101 (2009), pp. 147–167.
- [40] J. BÉLAIR, S.A. CAMPBELL, AND P. VAN DEN DRIESSCHE, Frustration, stability and delay-induced oscillations in a neural network model, SIAM J. Appl. Math., 56 (1996), pp. 245–255.
- [41] H.R. Wilson and J.D. Cowan, Excitatory and inhibitory interactions in localized populations of model neurons, Biophys. J., 12 (1972), pp. 1–24.
- [42] F. Zenke, G. Hennequin, and W. Gerstner, Synaptic plasticity in neural networks needs homeostasis with a fast rate detector, PLoS Comput. Biol., 9 (2013), e1003330.
- [43] K.B. Blyuss and Y.N. Kyrychko, Stability and bifurcations in an epidemic model with varying immunity period, Bull. Math. Biol., 72 (2010), pp. 490–505.
- [44] J. Li, L. Zhang, and Z. Wang, Two effective stability criteria for linear time-delay systems with complex coefficients, J. Syst. Sci. Complex., 24 (2011), pp. 835–849.
- [45] Y. KUANG, Delay Differential Equations with Applications in Population Dynamics, Academic Press, New York, 1993.
- [46] D. Breda, S. Maset, and R. Vermiglio, Pseudospectral approximation of eigenvalues of derivative operators with non-local boundary conditions, Appl. Numer. Math., 56 (2006), pp. 318–331.
- [47] N. MACDONALD, Time Lags in Biological Systems, Springer, New York, 1978.
- [48] C.-Y. Cheng, K.-H. Lin, and C.-W. Shih, Multistability in recurrent neural networks, SIAM J. Appl. Math., 66 (2006), pp. 1301–1320.