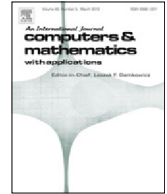




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Linear stability of delayed reaction–diffusion systems

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ABSTRACT

A common feature of pattern formation in both space and time is the destabilization of a stable equilibrium solution of an ordinary differential equation by adding diffusion or delay, or both. Here we study linear stability of general reaction–diffusion systems with off-diagonal time delays. We show that a delay-stable system cannot be destabilized by diffusion, and that a diffusion stable system is also stable with respect to delay, if the diffusion is sufficiently fast. A system with direct negative feedback which is strongly stable with respect to diffusion can be destabilized by off-diagonal delay.

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1. Introduction

Since the seminal work of Turing in 1952 [1] it has been known that stable equilibrium solutions of ordinary differential equations can be destabilized in a spatial setting by the introduction of diffusion with different diffusion constants for different species. Later works have proposed specific reaction mechanisms exhibiting Turing instability, for instance the well-known activator–inhibitor model introduced originally by Gierer and Meinhardt [2]. The mechanism for Turing instability in general systems for n interacting species has been studied in [3–6]. The typical results are necessary or sufficient conditions for a change in the spectrum of a matrix with respect to the imaginary axis. For more examples of possible reaction kinetics and sample applications, see the book by Murray [7].

Instability caused by time delays has also been studied in some recent works such as [8] for neural networks, [9] for general chemical networks and [10] for a model of human respiration. Commonly, instabilities caused by delays are associated with oscillations of the solutions of a system of delay differential equations. The linear stability of general delay systems has been studied in [11], where the authors give necessary and sufficient conditions for the null solution of a linear delay system to be asymptotically stable for any choice of off-diagonal delays. The interaction of delay and diffusion effects often occurs simultaneously, in particular in models inspired by biological problems. For some recent works that investigate both diffusion and delay together we refer to [12–18]. These works exhibit many different techniques to derive results, such as the use of Lyapunov functions, and a large number of applications, such as modeling of infectious diseases.

In this paper, we investigate the relationship between different kinds of linear stability of reaction–diffusion systems with delays. Haderl and Ruan in [13] showed that for 2-dimensional systems, stability with respect to off-diagonal delay implies stability with respect to diffusion. We extend this result from two dimensional reaction–diffusion systems with off-diagonal delays to general n -dimensional systems. Our results apply to systems with non-negative diffusion coefficients and non-negative off-diagonal delays. The theory on linear stability for delay systems developed in [11] is instrumental in many of the proofs.

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In Section 2, we review some definitions of matrix stability. In Sections 3 and 4, we discuss stability and instability results for general reaction–diffusion systems and delay systems, respectively. Section 5 is devoted to the study of reaction–diffusion systems with delays. There we prove the main results of this paper about the relationships between the different stability concepts. Finally, in Section 6, we present an example illustrating the main results.

2. Matrix definitions and stability

The stability of equilibrium solutions of differential equations can often be described in terms of matrix stability. In this section we give the relevant definitions and review some results on matrix stability. Let $D = \text{diag}(d_1, \dots, d_n)$ be a diagonal matrix with entries d_i , $i = 1, 2, \dots, n$. We will write $D \geq 0$ if all $d_i \geq 0$ and $D > 0$ if all $d_i > 0$. We use the common notations like $x > 0$ to indicate inequalities for all components of a vector or a matrix.

Definition 1. A matrix $A \in \mathbb{R}^{n \times n}$ is called

- (a) *stable* if all eigenvalues of A have negative real part,
- (b) *strongly stable with respect to diffusion* if $A - D$ is stable for every non-negative diagonal matrix D ,
- (c) *excitable with respect to diffusion* if it is stable, but not strongly stable with respect to diffusion.

Matrices that are strongly stable with respect to diffusion have been characterized up to order $n = 3$ in [19].

Recall that a submatrix of a matrix is called a *principal submatrix* if rows and columns with the same indices are deleted. The determinant of a submatrix is called a *minor*, thus the determinant of a principal submatrix is a *principal minor*. If $I \subset \{1, \dots, n\}$ is a subset of indices, then $\det A[I]$ denotes the corresponding principal minor, which is formed by the rows and columns with indices in I . Let the complementary set to I be $I^c = \{1, \dots, n\} \setminus I$. Then $\det A[I^c]$ denotes the corresponding *complementary principal minor*, where the rows and columns with indices in I have been removed. The empty matrix is defined to have determinant 1. The quantity $(-1)^{|I|} \det A[I]$ where $|I|$ is the number of indices in I is called the *signed principal minor*.

The *companion matrix* of a matrix A is defined as in [20],

$$\mathcal{M}(A) = \begin{cases} -|a_{ij}| & \text{if } i \neq j \\ |a_{ii}| & \text{otherwise.} \end{cases}$$

We will need the following definitions throughout the paper. The second set of definitions is taken from [20].

- Definition 2.** (a) A $n \times n$ -matrix is called *irreducible*, if the directed graph of the corresponding adjacency matrix is strongly connected, that is, every vertex can be reached from every other vertex along a directed path.
- (b) A matrix A is called a *Z-matrix* if $a_{ij} \leq 0$ for $i \neq j$.
 - (c) A matrix A is called a *M-matrix* if it is of the form $A = sI - B$ where $s \geq \varrho(B)$ and $B \geq 0$, [21]. Here ϱ denotes the spectral radius.
 - (d) A matrix A is called an *H-matrix* if the companion matrix $\mathcal{M}(A)$ is an *M-matrix*.
 - (e) A matrix A is called a *P-matrix* if all principal minors are positive. A matrix A is of class P_0 if all its principal minors are non-negative.

We note that the labeling of the matrix classes is not uniform across the literature. A *Z-matrix* for which all eigenvalues have positive real part is indeed a nonsingular *M-matrix*. We refer to the book by Fiedler [22] for many equivalent conditions for a matrix with non-positive off-diagonal entries to have only positive, respectively only non-negative principal minors, where these classes are denoted by K , respectively K_0 . The K -matrices are also known as nonsingular *M-matrices* (see Definition 2(c)).

3. Reaction–diffusion systems and Turing instability

Let $u = (u_1, \dots, u_n)$ denote, for example, the vector of non-negative species concentrations or populations. If variations in the concentration in space are neglected, the species interactions are given by the ordinary differential equation

$$\frac{du}{dt} = f(u), \quad (1)$$

where $f(u)$ is a smooth function. Let $A = \frac{\partial f_i}{\partial u_j}(u^*)$ be the Jacobi matrix of f , evaluated at the equilibrium point u^* . We assume that u^* is a hyperbolic equilibrium of (1), that is, A has only eigenvalues with nonzero real part. By linearizing (1) at u^* we obtain

$$\frac{du}{dt} = Au.$$

Now we assume that species concentrations $u_i(x, t)$, $i = 1, \dots, n$ vary within a bounded domain $\Omega \subset \mathbb{R}^k$ with smooth boundary, and that species i diffuses with rate constant $\tilde{d}_i \geq 0$. The reaction–diffusion system with the same dynamics as

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