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Characterization of spatial patterns produced by a Turing instability in coupled dynamical systems

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ABSTRACT

We quantify the degree of spatial order of patterns at fixed time generated by lattices of coupled dynamical systems, using correlation-based and recurrence-based numerical diagnostics. These patterns are obtained through numerical integration of differential equations describing the interplay between activator and inhibitor species generating Turing patterns. We consider different types of coupling: linear (diffusive) interaction with nearest-neighbors, global (all-to-all) coupling and intermediate (nonlocal) coupling. Numerical simulations are performed in one and two spatial dimensions. The effects of noise are briefly discussed. We introduce a recurrence-based quantity (recurrence-rate matrix) to characterize two-dimensional spatial patterns.

1. Introduction

The time evolution of spatial patterns is a problem of major importance in many scientific areas. In morphogenesis, for example, an initially homogeneous pattern common to a single cell evolves with time in a distinct way for different groups of cells, yielding the diversity of forms and functions that characterize our organs and bodily systems [1]. There are many examples of systems, from flame fronts to roughening surfaces, which evolve from a homogeneous state toward an inhomogeneous and often disordered pattern [2].

The fact that most spatial patterns occurring in experimental or natural circumstances are neither totally ordered nor completely disordered demands the use of diagnostics for characterization of the order or disorder of some spatial pattern. There are techniques to analyze profile roughness, like the interface width, which is the rms fluctuation in the surface height [3]. The interface width quantifies the profile smoothness degree, but it smears out the pattern irregularities. Hence such quantities often cannot properly describe spatially complex patterns, since they focus on gross features of the pattern.

We have used, to quantify spatial patterns generated by coupled dynamical systems (like coupled map lattices), quantities based on adaptations of diagnostics developed originally for time series analysis, like the spatial correlation function [4]. Moreover, we have introduced recurrence-based diagnostics for spatial patterns, which are extensions of the idea of dynamical recurrences (for time series) to the realm of spatial profiles [5].

In this work we apply the analysis of correlation-based and recurrence-based diagnostics of spatial patterns to quantify the degree of disorder present in arrays of coupled cells for different kinds of coupling prescriptions. Each cell undergoes a dynamical process involving two substances: an activator and an inhibitor, whose interplay generates a given output (e.g., the color of an animal skin) [6]. An array of these cells can evolve from a spatially homogeneous to an inhomogeneous pattern through a Turing instability [7]. The latter causes the exponential growth of a number of unstable modes, but this growth saturates due to the nonlinear terms in the dynamics and eventually produces a stationary pattern.

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Usually the study of the spatial patterns generated by Turing instability is made in systems with local interactions, where the spatial units, or cells, are coupled locally by diffusive forces described by Fick's law [8]. However, there are more complex situations for which the coupling cannot be limited to the nearest neighbors only. This is the case, for example, in which an assembly of cells interact through a chemical substance which is both produced and absorbed by the cells, and which diffuses in the intercellular medium [9].

The abovementioned kind of situation requires the use of nonlocal couplings, in which a given cell interacts with other cells, the interaction depending on the spatial distance between two sites [10]. We use in this work a kind of nonlocal coupling where the interaction decays with the spatial distance as a power-law, whose exponent can be varied from a global (all-to-all) coupling to a local (diffusive) coupling [11]. We have analyzed the conditions for the occurrence of a Turing instability in arrays of coupled dynamical systems by this nonlocal scheme [12].

In this work we investigate the formation of spatial patterns in such systems due to a Turing instability and characterize the spatial order/disorder using both correlation-based and recurrence-based diagnostics. We identify, for both local and nonlocal couplings, a transition between partially disordered and partially ordered patterns as the diffusion coefficient is varied.

This paper is organized as follows: in Section 2 we introduce the dynamical model we use for describing the spatio-temporal evolution of cells with nonlocal coupling in one spatial dimension. Section 3 presents ordered and disordered spatial patterns obtained by numerical integration and analyzing how a linear Fourier analysis can give some information about the modes which become unstable due to a Turing instability. Section 4 deals with correlation-based diagnostics of the spatial patterns obtained, with a discussion of the effects of noise. In Section 5 we show the recurrence-based diagnostics for the same situations, identifying a transition from disordered to ordered patterns as the diffusion coefficient of an activator is increased. Section 6 deals with two-dimensional patterns and their characterization using spatial recurrences. Our Conclusions are left to the final Section.

2. A dynamical model for evolving spatial patterns

In this work we study a nonlinear activator-inhibitor dynamical system proposed by Meinhardt and Gierer [6] as a model for pattern formation related to skin pigmentation:

$$\frac{dx}{dt} = f(x,y) = \rho_x \frac{x^2}{y} - \mu_x x, \tag{1}$$

$$\frac{dy}{dt} = g(x,y) = \rho_y x^2 - \mu_y y, \tag{2}$$

where $x = [X]$ and $y = [Y]$ are the concentrations of the activator and inhibitor substances, respectively, and $\rho_{x,y}, \mu_{x,y}$ are positive constants.

The activator undergoes an auto-catalytic reaction, its time rate being thus proportional to the square of the concentration at a given time. The inhibition caused by the substance Y is represented by the y^{-1} dependence on the reaction rate of the substance X. Moreover, the inhibitor reaction rate also increases with the activator concentration, i.e. it is also influenced by the auto-catalytic process of X. The parameters $\rho_{x,y}$ quantify those influences. Since $\mu_{x,y}$ are both positive, it is assumed that the concentrations of both X and Y decay spontaneously with time.

There are two equilibrium points for the coupled Eqs. (1) and (2): one is the origin and another is

$$x^* = \frac{\rho_x \mu_y}{\rho_y \mu_x}, \quad y^* = \frac{\rho_x^2 \mu_y}{\rho_y \mu_x^2}, \tag{3}$$

the latter representing a dynamical tradeoff between activation and inhibition which yields a time-independent behavior. In the following we shall fix the values as $\rho_x = 0.01$, $\rho_y = 0.02$, $\mu_x = 0.01$, and $\mu_y = 0.02$. For these values the equilibrium at the origin is unstable, whereas the second equilibrium point $(x^*, y^*) = (1,1)$ is asymptotically stable.

The spatio-temporal evolution of this activator-inhibitor dynamical system can be described by introducing spatial diffusion through Laplacian terms, yielding two coupled partial differential equations of the reaction–diffusion type

$$\frac{\partial x}{\partial t} = f(x,y) + \tilde{D}_x \nabla^2 x, \tag{4}$$

$$\frac{\partial y}{\partial t} = g(x,y) + \tilde{D}_y \nabla^2 y, \tag{5}$$

where $\tilde{D}_{x,y}$ are diffusion coefficients for the activator and the inhibitor, respectively.

In the one-dimensional case, and representing by z the spatial direction, we can divide the interval of interest into N cells of length Δ and discretize the variables for each cell:

$$x_j(t) = x(z = j\Delta, t), \quad y_j(t) = y(z = j\Delta, t), \tag{6}$$

where $j = 0, 1, 2, \ldots (N-1)$ and we adopt periodic boundary conditions, such that $x_N = x_0$. On redefining the diffusion constants