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Pattern formation and Turing instability in an activator–inhibitor system with power-law coupling

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HIGHLIGHTS

- Activator–inhibitor systems with non-local coupling are studied in two dimensions.
- Linear stability analysis of spatial modes gives conditions for Turing instability.
- Numerical simulations are performed to study non-linear saturation of linearly growing modes.

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ABSTRACT

We investigate activator–inhibitor systems in two spatial dimensions with a non-local coupling, for which the interaction strength decreases with the lattice distance as a power-law. By varying a single parameter we can pass from a local (Laplacian) to a global (all-to-all) coupling type. We derived, from a linear stability analysis of the Fourier spatial modes, a set of conditions for the occurrence of a Turing instability, by which a spatially homogeneous pattern can become unstable. In nonlinear systems the growth of these modes is limited and pattern formation is possible. We have studied some qualitative features of the patterns formed in non-local coupled activator–inhibitor systems described by the Meinhardt–Gierer equations.

1. Introduction

One of the key questions in morphogenesis is how a single egg develops into a complex organism. Since all the cells belonging to the egg share an identical genetic code, some mechanism should account for the fact that the cells eventually become different from each other [1]. Translating this question into a mathematical language, this means how a spatially homogeneous pattern evolves into an inhomogeneous one [2]. Other biological examples of pattern formation are the skin pigmentation of animals, colony formation of small marine animals, and the regular spacing of leaves in a plant [3].

Minimal models aiming to mimic these and other related phenomena consist of two substances: one activator and one inhibitor. The pattern that is formed results from the interplay between the concentrations of these substances, whose spatio-temporal evolution is governed by coupled reaction–diffusion systems (activator–inhibitor models). In 1952 Alan Turing addressed this question from a linear stability analysis and found that a stable homogeneous pattern can become unstable (the so-called Turing instability) if the inhibitor diffuses more rapidly than the activator. In other words, if the diffusion coefficient of the inhibitor is greater than that of the activator by a given factor [4].

In activator–inhibitor models this factor can be as large as 10. Since the diffusion coefficient of most ions in water has nearly the same value ($circa 10^{-9}$ m^2/s), the production of Turing instability in the laboratory is a difficult task. A major

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progress was the observation that the introduction of a third substance fixed to a matrix in the solution can create a large difference between the diffusion coefficients of the activator and the inhibitor, since one of them binds reversibly to the immobile molecule and has an effectively smaller diffusion coefficient, in comparison with the substance which does not bind [5]. Indeed, the Turing instability has been observed in the Chlorine Dioxide–Iodine–Malonic Acid (CDIMA) reaction, for which the third substance was a starch indicator embedded in a gel matrix [6,7].

The simple existence of a Turing instability, however, is not sufficient *per si* to explain pattern formation. Since there is a strong positive feedback on the increase of the activator, there would be an unlimited increase of the latter. The presence of nonlinearities in the local dynamics, for example due to the inhibitor concentration, saturates the Turing instability into a stable and spatially inhomogeneous pattern. A model showing this kind of behavior was proposed by Meinhardt and Gierer and remains a paradigm for studies of activator–inhibitor systems [8–10].

Gierer and Meinhardt have shown that stable inhomogeneous patterns can be formed if the auto-catalytic production of the activator is short-ranged, while the formation of the inhibitor is long-ranged. In other words, the self-enhancing process involving the activator is chiefly local, whereas the inhibitor should have a long-range behavior characterized by rapid spreading, producing activator removal at long distances [11].

The role of the diffusion range is thus of central importance in the dynamics of activator–inhibitor systems. On the other hand, the mathematical modeling of reaction–diffusion equation involves Laplacian coupling, represented by second-order spatial derivatives. Such models are derived from a mass balance and Fick's law (the diffusion flux points from large to small concentration regions). However, in this class of models, the coupling is nevertheless of a local nature, characterized by interactions with the nearest-neighbor sites in a discrete lattice.

In this paper we present a more general formulation for the activator–inhibitor system, characterized by a non-local coupling: a lattice site can interact essentially with all its neighbors. The strength of this coupling is supposed to decrease with the lattice distance as a power-law, where a range parameter is introduced that can be varied so as to pass from a global (all-to-all) coupling to a local (nearest-neighbor) one [12–14].

We have previously described one-dimensional chains of nonlinear oscillators coupled according to this type nonlocal interaction [15]. In that work we found that global couplings spread information among oscillators more rapidly than local couplings, in such a way that globally coupled oscillators are less likely to present a Turing instability than locally coupled ones. Moreover, collective phenomena like frequency synchronization [16] are more likely to occur in the global case than in the local coupling [15].

However the one-dimensional case is rather idealized since spatio-temporal patterns of interest are typically two-dimensional, such as those observed in skin pigmentation, chemical cells, etc. In the present paper we investigate the occurrence of a Turing instability in a two-dimensional system of nonlocally coupled oscillators. We used a linear stability analysis to study the role of the effective range and the diffusion coefficients on the conditions for the occurrence of a Turing instability [17]. We also performed numerical simulations of the coupled system so as to investigate pattern formation and its dependence with range and diffusion.

This paper is organized as follows: in Section 2 we introduce the system of non-locally coupled activator–inhibitor oscillators and explore its limiting cases. Section 3 is devoted to the linear analysis of Fourier mode stability leading to conditions for the Turing instability involving both the range parameter and diffusion coefficients. In Section 4 we consider pattern formation for the Meinhardt–Gierer model of activator–inhibitor oscillators with power-law coupling. Our Conclusions are left to the final section.

2. Non-locally coupled oscillators

Activator–inhibitor systems with local coupling are usually described by coupled reaction–diffusion equations:

$$\frac{\partial u}{\partial t} = f(u, v) + D_u \nabla^2 u, \tag{1}$$

$$\frac{\partial v}{\partial t} = g(u, v) + D_v \nabla^2 v, \tag{2}$$

where $u(\mathbf{r}, t)$ and $v(\mathbf{r}, t)$ denote the local concentrations of the activator and inhibitor species, respectively. The functions $f(u, v)$ and $g(u, v)$ stand for the local dynamics of the system, in which the activator auto-catalytically enhances its own production and the inhibitor suppresses the activator growth [18]. The diffusion constants of the activator and inhibitor species are denoted, respectively, by D_u and D_v, and we assume them to be positive-defined.

A spatially homogeneous pattern becomes linearly unstable (Turing instability) if the ratio of the diffusion constants D_v/D_u exceeds a threshold value. The nonlinear terms in f and g, however, saturate the linear growth and produce a spatially inhomogeneous pattern, in which there are domains with high and low values of the activator concentration, with respect to a uniform background.

In the following, we will consider two-dimensional patterns in the x and y directions, along which we make a coarse-grained description of the spatial patterns. For a square lattice with local coupling, we link a given site to its nearest neighbors in both directions. There are N^2 cells of area Δ^2 and the variables are discretized as

$$u_{k,j}(t) = u(x = k\Delta, y = j\Delta; t), \qquad v_{k,j}(t) = v(x = k\Delta, y = j\Delta; t), \tag{3}$$