Mosaic Pattern Formations in Multicellular Chemical Systems

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A 2-dimensional array of coupled Brusselators cells is studied numerically. A variety of stationary patterns are obtained depending on the coupling strength of an activator and an inhibitor. Mosaic patterns of different motifs, in a very complicated spatial arrangement, are discovered. The mechanism that leads to the formation of the mosaic patterns consists of the formation of rings by an oscillatory chemical medium, the breaking of rings, and the interaction with the cellular chemical medium.

Introduction

The experimental realization of Turing patterns,[1,2] which originate from the interaction between chemical kinetics and diffusion, has stimulated many important experimental and theoretical works. During just the past few years the dot pattern (with hexagonal or rhombic symmetry), stripes, the "black eye" pattern, and lamellar structures have been discovered.[3–7] Almost all previously discovered patterns consist of a single motif (dots, stripes) which are organized, more or less chaotically, on a 2-dimensional plane. The majority of theoretical works have been devoted to the simulation of experimental results computed from random initial conditions. Therefore, the problem of morphogenesis—the development of complex, nonchaotic structure from a simple perturbation—has not been properly addressed. In this paper we report the observation of complex patterns that are not the superpositions of the same motifs and that originate from a simple perturbation.

System of coupled oscillatory cells are interesting since they are related to biological systems. However, these discrete systems are less studied than continuous reaction diffusion systems where analytical methods[8–11] are applicable. Discrete systems probably require a more numerical approach, one similar to that used to study cellular automata.

Coupled oscillators form an important branch of nonlinear dynamics. Most experimental and numerical studies have been done for two coupled oscillators. This area is still a subject of interest.[12–14] Another area of intensive study is that of 1-dimensional arrays of oscillators.[15–20] Multiple coupled cells in a 2-dimensional arrangement are rarely studied due to experimental and theoretical difficulties. For such an array of coupled oscillators, many different behaviors may be observed depending on the coupling strength K. For large values of K the system will oscillate uniformly. If the coupling strength of the activator (U) is smaller than the coupling strength of the inhibitor (V), then the Turing pattern may develop in response to a proper perturbation. The K_i value may be consider as $D_i/(\mathrm{d}l)^2$, where D_i is the diffusion coefficient for a chemical species i and $\mathrm{d}l$ is a spatial increment corresponding to the size of a cell. A large K_i corresponds to a small $\mathrm{d}l$, and the system may be treated as uniform. This area is the subject of intensive studies. On the opposite end, when the K_i values are very small, the system may be treated as an n-dimensional torus where n is the number of coupled cells. When the K_i values are increased the torus is broken. The breaking of a torus has been studied in the 2-dimensional case, but in the multidimensional case the theory is not substantially developed.[21,22]

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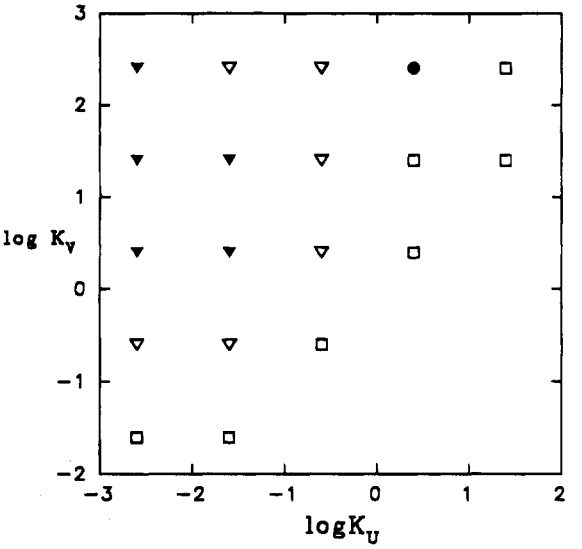

Figure 1. Phase diagram of the chemical multicellular system. K_U is the coupling constant for an activator species, and K_V is the coupling constant for a inhibitor species. Symbols: full circle, dot pattern (see Figure 2A); empty triangles, mosaic pattern (see Figure 2B–D); full triangles, stationary target pattern (see Figure 2E,F); empty squares, no stationary patterns.

Numerical Calculations

Calculations have been conducted for the Brusselator model of an oscillatory chemical system. The 2-dimensional model of Brusselators is given by the following set of differential equations:

$$\mathrm{d}U_L/\mathrm{d}t = A - (B+1)U_L + (U_L)^2V_L + K_U(\sum U_j - 4U_L)$$

$$\mathrm{d}V_L/\mathrm{d}t = BU_L - (U_L)^2V_L + K_V(\sum V_j - 4V_L)$$

We chose the parameters $B = 3.5$ and $A = 1.0$ and used the non-flux boundary conditions. The simple Euler method with four neighbors was applied . The Euler method, even with known insufficiencies, is a common tool for studying patterns formations in a chemical system due to computer time efficiency.[7,23] The time increment was chosen such that a decrease by a factor of 5 did not change the pattern. In most cases the time increment was equal to 0.001. Calculations were conducted until the stationary state had been obtained. Usually 60 000 steps were sufficient.

Results

The phase diagram for different values of K_U and K_V is presented in Figure 1. Before a perturbation has been applied,

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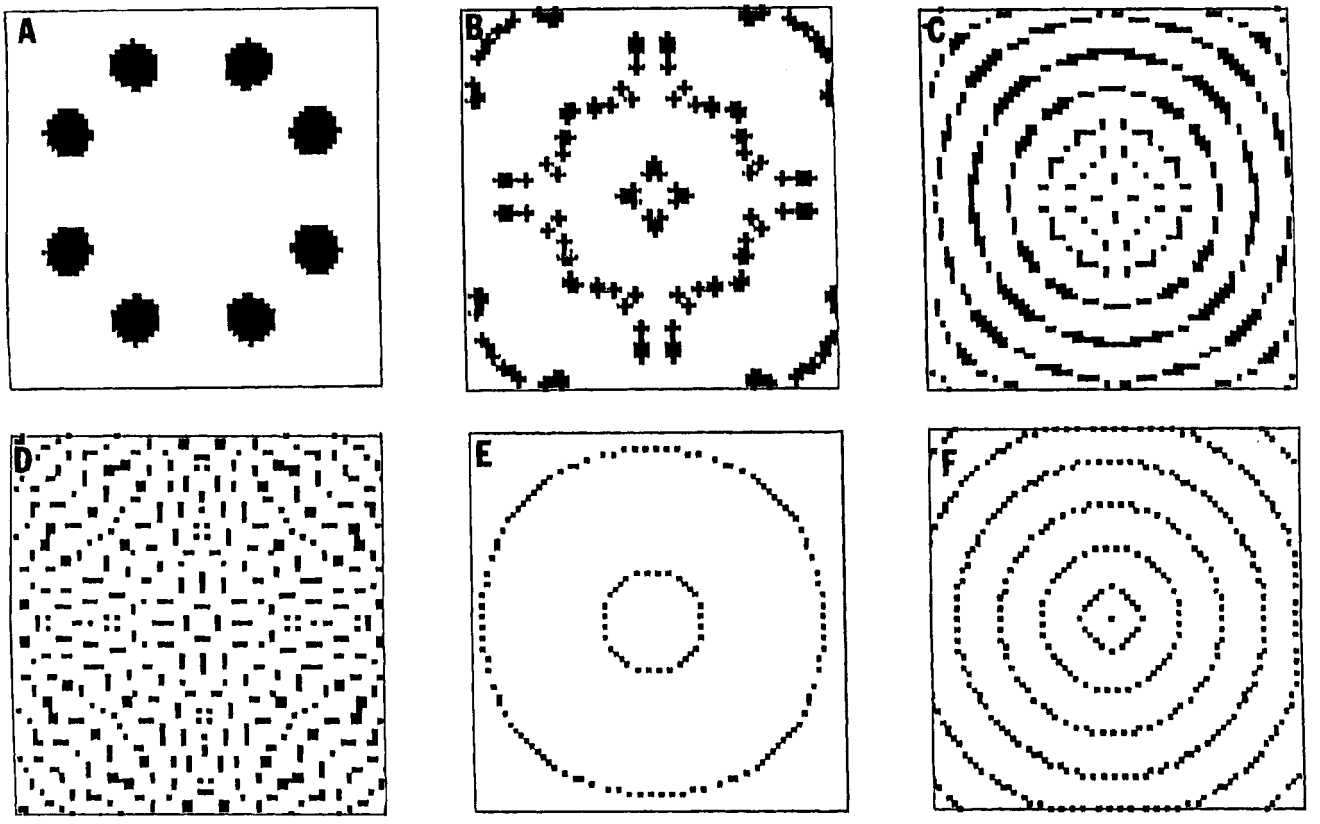

Figure 2. Different kinds of stationary patterns. Calculations have been conducted for an array of 71 × 71 chemical cells. (A) Dot pattern; K_U = 2.5. K_V = 25. (B) Mosaic pattern; K_U = 0.25, K_V = 25. (C) Mosaic pattern; K_U = 0.25, K_V = 2.5. (D) Mosaic pattern; K_U = 0.25, K_V = 1.5. (E) Stationary target pattern; K_U = 0.025, K_V = 25. (F) Stationary target pattern; K_U = 0.025, K_V = 2.5.

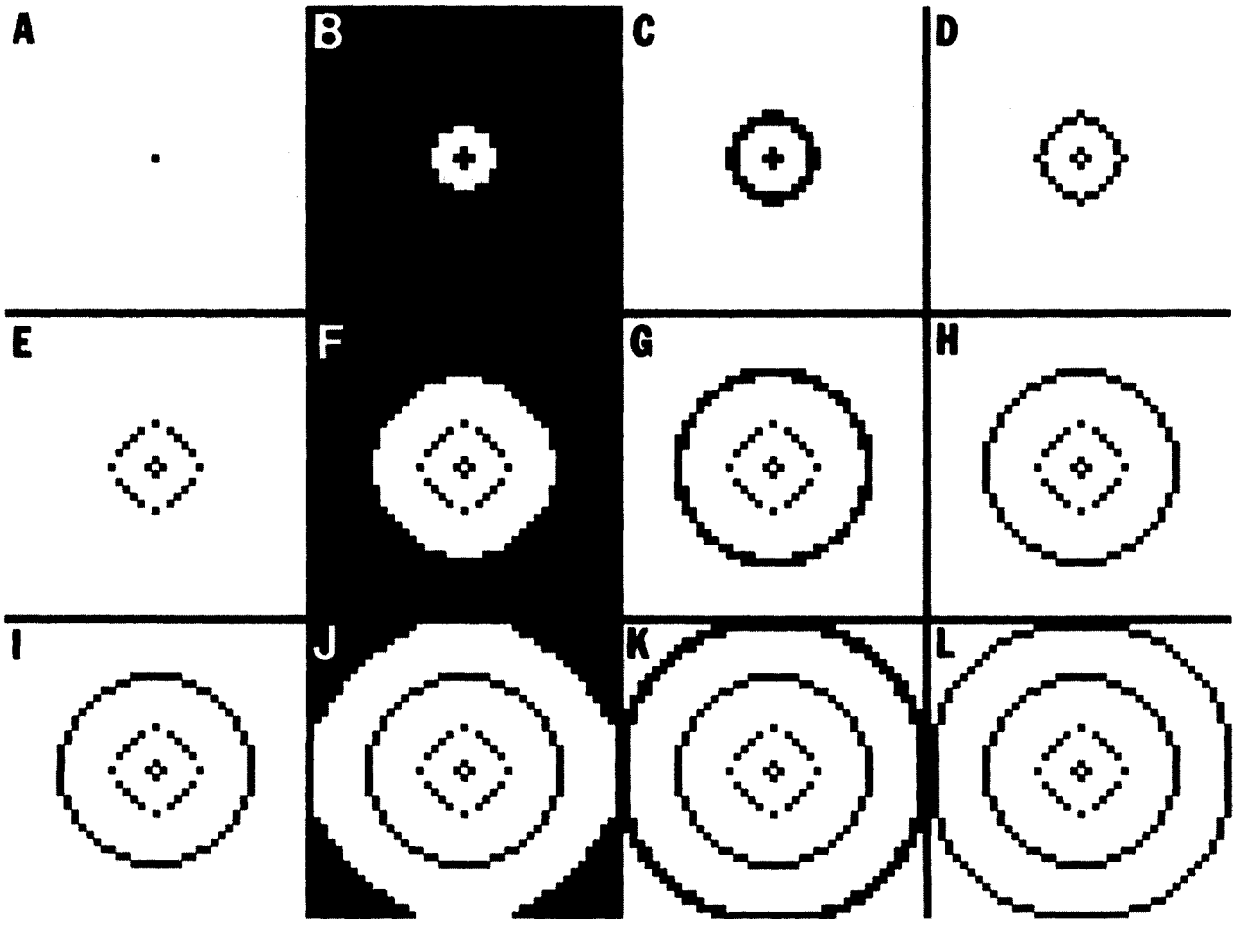

Figure 3. Origin of a stationary target pattern for an array of 41 × 41 chemical oscillators. (A) represents the initial perturbations. Pictures are separated by the 2 time units. K_U = 0.025, K_V = 2.5.

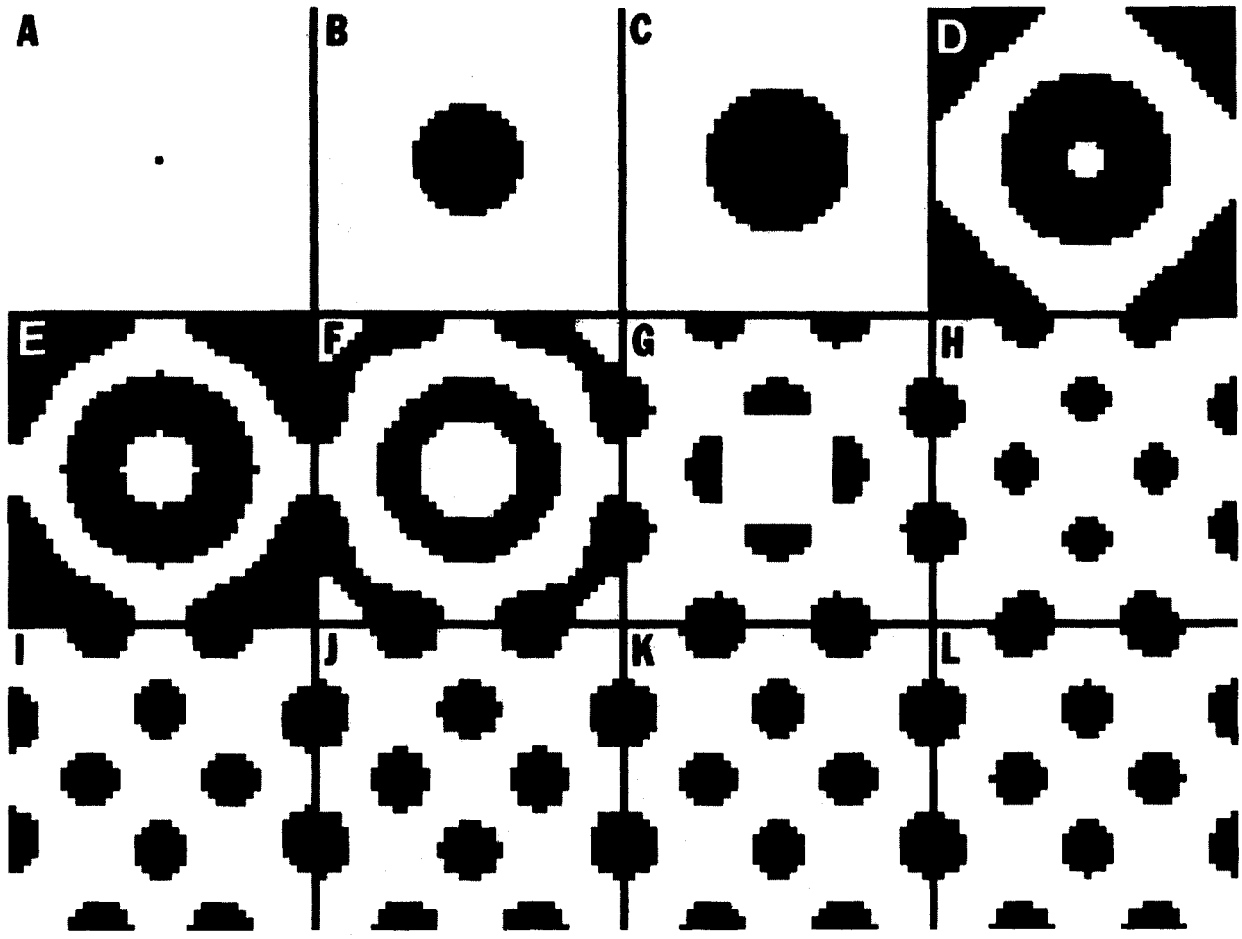

Figure 4. Development of a dot pattern for an array of 41 × 41 chemical cells. Pictures are separated by 1 time unit. $K_U = 2.5$, $K_V = 25$.

the system oscillated uniformly. The central cell was perturbed with U value equal to 10. Developed patterns, which are stable only when K_U is smaller then K_V , are presented in Figure 2. Figure 2A represents a dot pattern with circular symmetry. This pattern exists for higher values of K_U . Figure 2B−D represents the complex mosaic pattern, whereas Figure 2E,F represents stationary target patterns with different wavelengths.

The origin of stationary target patterns has been studied in more detail and is presented in Figure 3. In the top row the origin of a first ring is demonstrated. From the initial perturbation, the pattern grows slowly, changing the concentrations of chemicals in the surrounding area. When the medium oscillates uniformly (see Figure 3B), then the ring is formed around the affected area. This process is repeated for the next oscillations with the formation of more rings. Depending on the value of K_V, the affected area grows slower or faster, forming rings with different spacing. This is illustrated in Figure 2E,F.

The origin of a dot pattern is presented in Figure 4. The first interior ring originates from the initial perturbation (Figure 4A−F). The second ring is formed by the oscillation of the chemical medium (Figure 4D,E). Next both rings are broken into dots (Figure 4F,G). A similar structure may be observed for the stationary target patterns as can be seen in Figure 2E,F. Dots are always separated by one cell or are connected by corners. In this case the pattern is characterized by two wavelengths: one wavelength is equal to the separation of the rings, and the other wavelength is equal to the one that separates dots on a ring.

The important factor is the relation between a size of dot and a size of a cell. If the dot is big compared to the size of a cell, dl, then the dot pattern similar to homogeneous system can be observed. However, if a dot is of the size of a cell, then the broken stationary target pattern may develop. The intermediate situation, when a dot is of the size of several cells, is the most interesting. In this case the more complex mosaic patterns will develop.

The origin of the mosaic pattern is presented in Figure 5. We may also observe the two mechanisms discussed above: the origin of rings and the breaking of rings. However, because of the interactions with the nonhomogeneous media, the developed pattern does not exhibit dots, but a more complex structure develops. After some transient period, this structure becomes stationary starting from the center of the pattern. Figure 2C exhibits a pattern where a mosaic develops in the area around the initial perturbation. Farther from the perturbation point, the pattern preserves circular symmetry. This suggests that the process of the breaking of a ring depends on the curvature of the ring.

Discussion

The origin of dots in a chemical system has lately been the subject of intensive theoretical and experimental studies. A dot grows from the perturbation point and later divide into two dots. This mechanism attracted a lot of attention because of its similarity with biological cell division.[23−25] Furthermore, the generation and annihilation of dots are an important feature of spatiotemporal chaos. In this paper we report a new "route" to a dot pattern that consists of the successive formation and breaking of rings. However, the most important result of our studies is the discovery of mosaic patterns that originate from single perturbations. These mosaic patterns are built from many

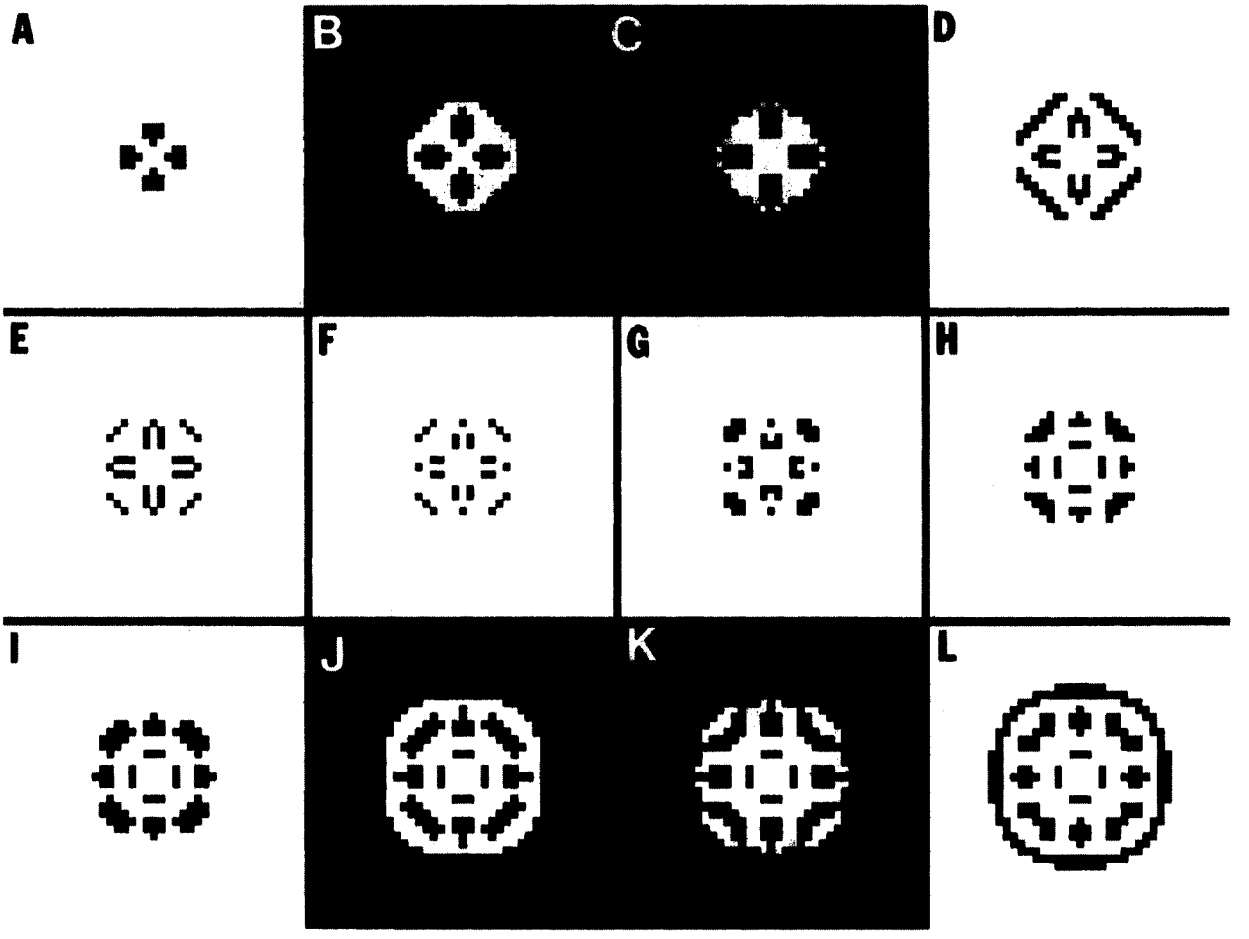

Figure 5. Development of a mosaic pattern for an array of 41 × 41 cells. Pictures are separated by 1 time units. $K_U = 0.25$, $K_V = 1.5$.

different motifs. Arrangement of these elements looks chaotic, nevertheless, it must be considered to be a very high order spatial organization.

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