Nonequilibrium transition and pattern formation in a linear reaction-diffusion system with self-regulated kinetics

Shibashis Paul, Shyamolina Ghosh,* and Deb Shankar Ray†
Indian Association for the Cultivation of Science, Jadavpur, Kolkata-700032, India

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We consider a reaction-diffusion system with linear, stochastic activator-inhibitor kinetics where the time evolution of concentration of a species at any spatial location depends on the relative average concentration of its neighbors. This self-regulating nature of kinetics brings in spatial correlation between the activator and the inhibitor. An interplay of this correlation in kinetics and disparity of diffusivities of the two species leads to symmetry breaking non-equilibrium transition resulting in stationary pattern formation. The role of initial noise strength and the linear reaction terms has been analyzed for pattern selection.

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I. INTRODUCTION

Diffusion-induced instability of a homogeneous steady state under far from equilibrium condition forms the basis of the theory of morphogenesis proposed by Turing around the middle of the last century. This instability is caused by short-range activation and long range diffusion of the two chemically interacting species which are governed by reaction-diffusion equations [1–10]. Turing theory and its variants have been applied to several areas of physical, chemical, and biological sciences to understand a wide class of self-organized structures, e.g., waves, targets, spirals, stationary, and non-stationary patterns [1,2,11–15]. This has been the subject of a large body of literature over the last several decades. We refer to [1–15] for further details.

To put the present work in an appropriate perspective we begin with a note that the kinetics of two interacting species is an intrinsic characteristic of the reaction itself and the change in concentration of any one of them at a spatial location depends on their concentration at that site and hence the kinetics is local in nature. It is the diffusion that couples the concentration at the two different sites. In this paper we consider a class of kinetics, where the change in concentration of a species at a spatial location is guided by the average concentration of the two species around its immediate neighborhood. Thus the time evolution of concentration of the species is non-local and self-regulating in nature. This self-regulating kinetics has a close resemblance to self-propelled character of dynamical motion extensively studied in the context of collective behavior of a system of interacting particles resulting in an interesting class of phenomena of self-organization [16–19], e.g., bird flocks, fish schools, animal herds, movement of crowds, in general referred to as 'flocking'. These particles move at discrete time steps with constant speed and depending on the average alignment of their neighbors within an intermediate range of radius of interaction, align with them [16]. It is in this spirit that the kinetics of the reaction-diffusion system considered here is self-regulatory and points towards a close correspondence to the self-propelled dynamical motion of the particles undergoing flocking. We push this correspondence a little bit further to inquire whether symmetry-breaking of an homogeneous state can arise due to non-equilibrium transition in the reaction-diffusion system of two species following self-regulatory kinetics in the same way as symmetry-breaking gives rise to collective coherent behavior of a system of self-propelled particles, due to order-disorder non-equilibrium transition.

An important element in the study of the traditional reaction-diffusion systems is that they are, in general, non-linear in nature. The stability analysis of these systems is based on linearization of the equations around the steady state and depending on the nature of bifurcation one is led to varying spatio-temporal scenarios, like waves, stationary, and non-stationary pattern formation. In his original analysis of stationary patterns and wave instability, Turing [1] considered a simple linear system of two chemically interacting species with diffusion. However, such a system although predicts initiation of instability due to differential diffusivity under certain constraints, is characterized by exponential divergence, and neither saturation nor stationarity is ensured in the long time limit. It is the non-linearity which brings in saturation beyond the linear regime. Secondly, the nature of pattern itself (like spot or stripe, etc.) is determined by the detailed nature of non-linearity [13]. The first important point of the present analysis is that the reaction-diffusion system considered here is linear by construction but can lead to a stationary pattern. Another pertinent point needs to be emphasized here. Non-local interaction effects on pattern formation had been explored earlier in population dynamics where the origin of non-local aspects lies in the competitive interaction among individuals [20]. In a related issue [21] the interacting Brownian particle models with modification of birth and death rates have been introduced to understand clustering, advection and pattern formation. The non-local self-interaction arises in all these cases [20–22] via a non-linear integro-differential term. The non-local interaction in our proposed model of activator-

*Present address: University of Kansas, 1450 Jayhawk Blvd, Lawrence, KS 66045, USA.
†Corresponding author: pcdsr@iacs.res.in

inhibitor chemical dynamics, on the other hand is linear. Thus the present model is naturally distinct from the earlier non-local self-interaction models in terms of linearity and self-regulatory non-local kinetics of two interacting components. The physical origin of saturation in the long time limit here is thus not non-linearity but an interplay of non-local correlation and disparity of diffusion coefficients of these two species. Finally due to this non-locality it is possible to observe the existence of symmetry-breaking spatial structures beyond the limiting conditions for Turing pattern.

In what follows we consider a reaction-diffusion system governed by a linear, stochastic, self-regulatory kinetics of activator and inhibitor. Our numerical simulation shows that an interplay of spatial correlation of the reaction components via self-regulatory nature of kinetics and disparity of diffusion coefficients of the two species leads to symmetry-breaking of the homogeneous state resulting in pattern formation in a non-equilibrium steady state. This is independent of the relative rate of activation and inhibition of the two species. We examine the underlying instability in the light of Turing condition to show that spatial correlation of the activation and inhibition and diffusion play antagonistic role in the mechanism of pattern formation.

The outline of the paper is as follows. We introduce a model reaction-diffusion system with self-regulated activator-inhibitor kinetics in Sec. II. In Sec. III we carry out detailed numerical simulations to follow the spatio-temporal evolution of the dynamics and demonstrate how the system makes a non-equilibrium transition to reach a non-equilibrium steady state with pattern formation. The paper is concluded in Sec. IV.

II. A REACTION-DIFFUSION SYSTEM WITH SELF-REGULATED ACTIVATOR-INHIBITOR KINETICS

To begin with we consider a chemical reaction with two species U and V, where U is the activator and V is the inhibitor. In a generic activator-inhibitor model the kinetic part is defined by some explicit functional form of a reaction-diffusion equation as follows:

$$\frac{\partial U}{\partial t} = F(U,V) + D_U \nabla^2 U, \tag{2.1}$$

$$\frac{\partial V}{\partial t} = G(U,V) + D_V \nabla^2 V. \tag{2.2}$$

Here, $F(U,V)$ and $G(U,V)$ are the mathematical functions depending on U and V, which define the governing kinetics of the two species U and V and ∇^2 containing terms represent the diffusion of the respective components. For example, the functions F and G in the activator-inhibitor type model, first proposed by Gierer and Meinhardt [9,23] to describe morphogenesis in developmental biology have the form $F = \frac{U^2}{V} - U + \phi$ and $G = \mu(U^2 - V)$. Here, ϕ is the basic production term, μ is the relative removal rate. Activator and inhibitor are antagonistic in nature: with increase in the concentration of the activator U, the rate of formation of both the species increases and with increase in concentration of the inhibitor V, the rate of formation of both the species decreases. In our proposed model, We do not consider any explicit form of kinetics but assume that the reaction is non-local, i.e., the change in concentration of the activator or inhibitor at any given spatial location depends on the average local concentration of their neighbors.

In the model, we construct an $N \times N$ grid and first locate (U_0, V_0) number of activator, inhibitor at all the spatial sites of the grid to start with. Time evolution of the system is started by applying a gaussian white noise (η) of strength σ at each site. In order to state mathematically the rules for successive updating of the concentration of activator and inhibitor at each time step, we first define a neighborhood $\mathbf{R}(r,t)$ of radius r centering around the grid point (i,j) at time t. Let $\langle U\rangle_{\mathbf{R},t}$ and $\langle V\rangle_{\mathbf{R},t}$ be the average concentrations of the activator (U) and the inhibitor (V), respectively, within the region $\mathbf{R}$ and at time t. The concentrations of the activator (U) and the inhibitor (V) at each site of the grid are updated in time by making use of the following rules:

for $\langle U\rangle_{\mathbf{R},t} \geqslant \langle V\rangle_{\mathbf{R},t}$,

$$U_{i,j}(t+\Delta t) = \{U_{i,j}(t) + \alpha\xi(t)\Delta t\} + D(\nabla^2 U)\Delta t, \tag{2.3}$$

$$V_{i,j}(t+\Delta t) = \{V_{i,j}(t) + \alpha\xi(t)\Delta t\} + (\nabla^2 V)\Delta t, \tag{2.4}$$

for $\langle U\rangle_{\mathbf{R},t} < \langle V\rangle_{\mathbf{R},t}$,

$$U_{i,j}(t+\Delta t) = \{U_{i,j}(t) - \beta\xi(t)\Delta t\} + D(\nabla^2 U)\Delta t, \tag{2.5}$$

$$V_{i,j}(t+\Delta t) = \{V_{i,j}(t) - \beta\xi(t)\Delta t\} + (\nabla^2 V)\Delta t. \tag{2.6}$$

Where $U, V \geqslant 0$.

According to Eqs. (2.1) and (2.2) it follows, when the average concentration of the activator within the finite region $\mathbf{R}(r,t)$ is greater than or equal to that of the inhibitor, there will be an increase in the concentration to both the activator and the inhibitor of amount $\alpha\xi(t)$ at the grid point (i,j). Here, $\xi(t)$ has a random real value ranging from 0 to 1 with uniform distribution and α is a constant defined as the rate of activation.

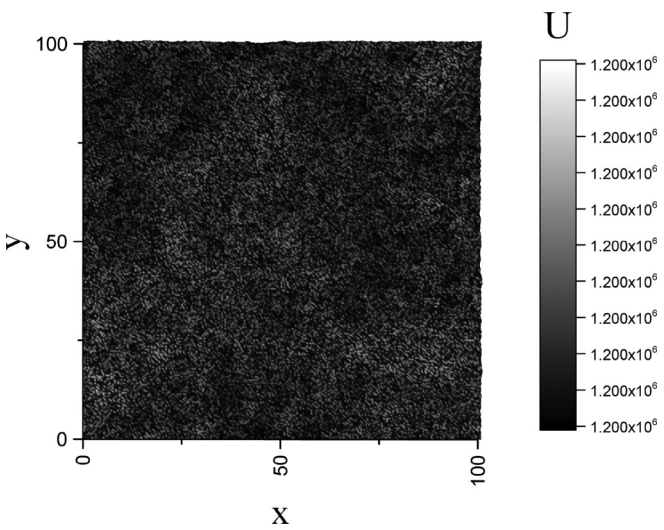

FIG. 1. Concentration profile of the activator U at 15000 time units for $D = 1.0$, $\alpha = 400.0$, $\beta = 400.0$, $r = 1.0$ (units arbitrary).

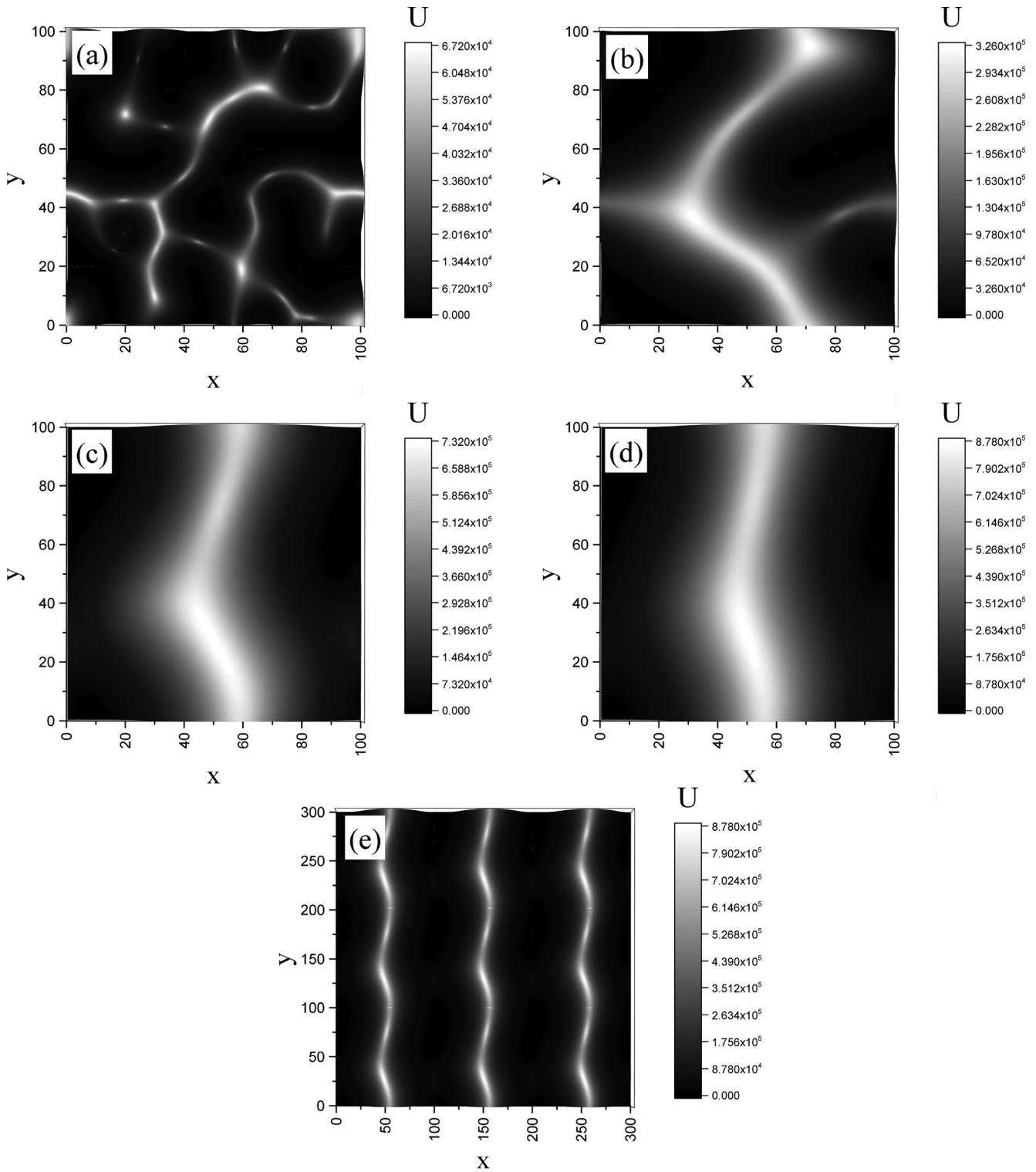

FIG. 2. Concentration profile of the activator U for $D = 0.05$, $\alpha = 400.0$, $\beta = 400.0$, $r = 1.0$ at the time units (a) $t = 1000$, (b) $t = 5000$, (c) $t = 12000$, (d) $t = 15000$, and (e) three repeating profiles of (d) in x and y directions (units arbitrary).

The second terms of the equations incorporate diffusion into our model, where ∇^2 is the Laplacian, D is defined as the ratio of diffusion coefficients of the activator and the inhibitor and Δt represents the time step. On the other hand the scenario in which the inhibitor prevails within the region $\mathbf{R}(r,t)$, the rules given by Eqs. (2.5) and (2.6) are followed. According to these equations, both the activator and the inhibitor concentration at the grid point (i, j) decrease by an amount $\beta\xi(t)$. Here, β is defined as the rate of inhibition. Since the noise $\xi(t)$ is external the dynamical system is characteristically non-equilibrium in nature. Finally a clarification regarding the activator-inhibitor dynamics is pertinent. The dynamics governed by Eqs. (2.3) to

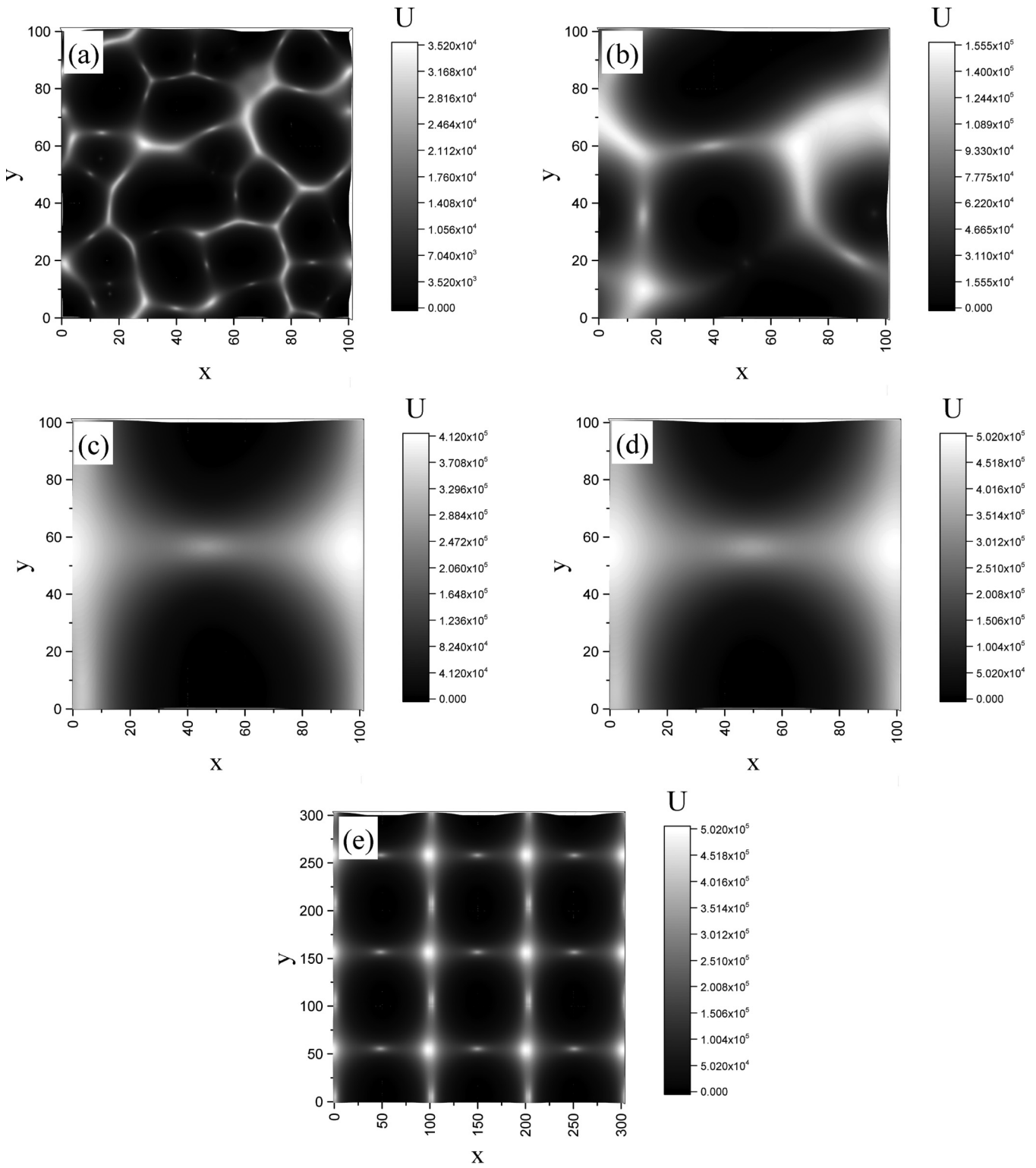

FIG. 3. Concentration profile of the activator U for $D = 0.05$, $\alpha = 200.0$, $\beta = 400.0$, $r = 1.0$ at the time units (a) $t = 1000$, (b) $t = 5000$, (c) $t = 12000$, (d) $t = 15000$, and (e) three repeating profiles of (d) in x and y directions (units arbitrary).

(2.6) is compatible with the linear reaction terms proportional to $(\alpha - \beta)$ at the deterministic level without any spatial resolution. This is in spirit with activator-inhibitor dynamics, in general. We now point out several conspicuous features of the present model.

First, we have not considered here any explicit form of kinetics which is an essential element of a traditional reaction-diffusion system. The growth and decay of concentration of any species at a given location is the characteristics of the reaction itself and is solely dependent, in general, on the

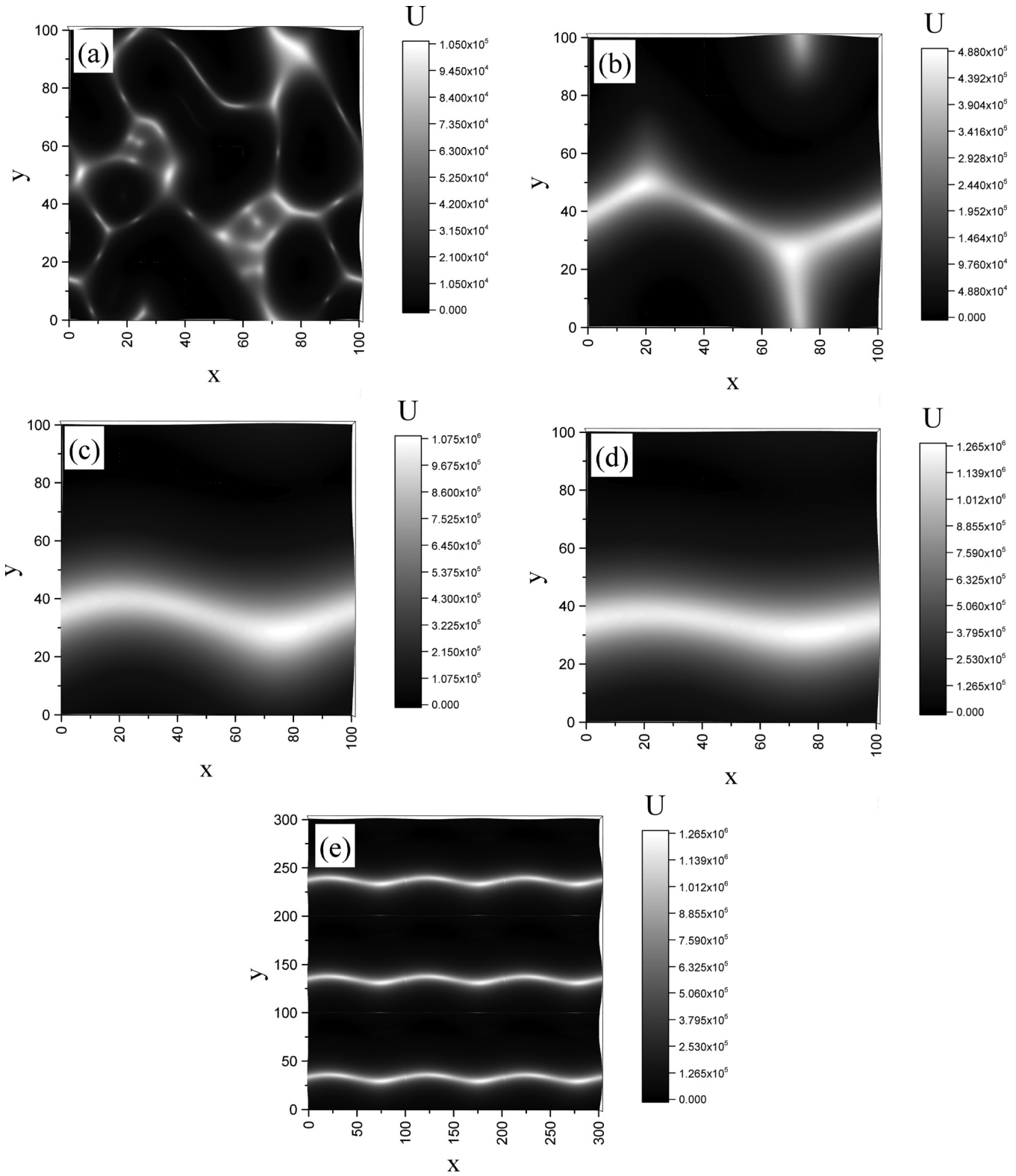

FIG. 4. Concentration profile of the activator U for $D = 0.05$, $\alpha = 600.0$, $\beta = 400.0$, $r = 1.0$ at the time units (a) $t = 1000$, (b) $t = 5000$, (c) $t = 12000$, (d) $t = 15000$, and (e) three repeating profiles of (d) in x and y directions (units arbitrary).

concentration of each species at that site. Since in the present model the growth and decay of a species at a spatial location is guided by the relative average concentration of the two species in its neighborhood, the kinetics is inherently non-local and self-regulating in character.

Second, the model is linear and the spatio-temporal evolution of the two species is governed by an interplay of spatial correlation in kinetics and diffusive transport.

Third, the kinetics considered here is stochastic rather than deterministic. The spatio-temporal evolution of the two species

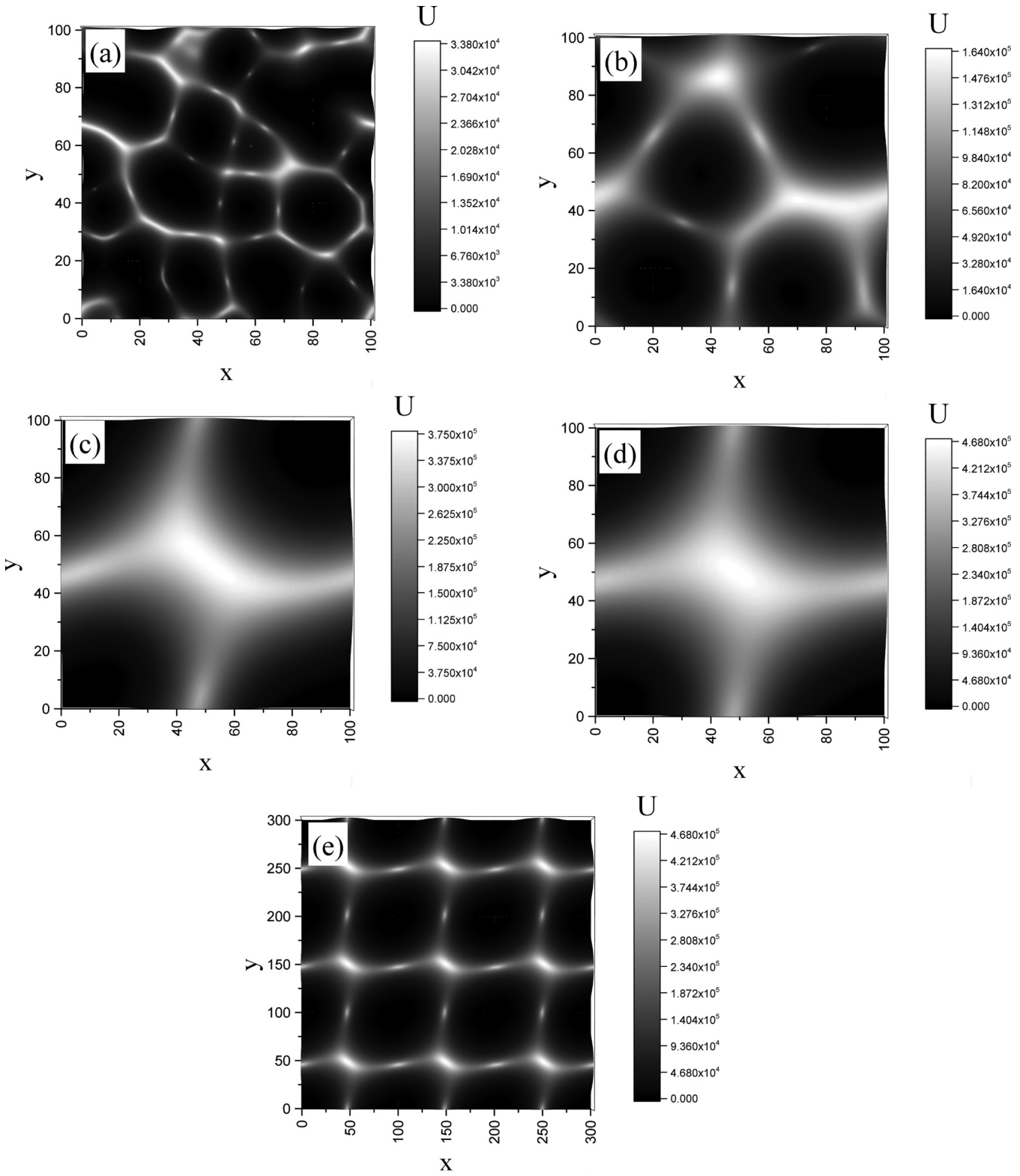

FIG. 5. Concentration profile of the activator U for $D = 0.05$, $\alpha = 200.0$, $\beta = 400.0$, $r = 0.5$ at the time units (a) $t = 1000$, (b) $t = 5000$, (c) $t = 12000$, (d) $t = 15000$, and (**e**) three repeating profiles of (d) in x and y directions (units arbitrary).

is probabilistic in nature. The scheme does not make any special reference to any homogeneous steady state which needs to be specified for a typical reaction-diffusion system with non-linear kinetics.

III. NUMERICAL SIMULATIONS: SPATIO-TEMPORAL INSTABILITY AND STATIONARY PATTERN FORMATION

In order to explore the symmetry breaking non-equilibrium transition leading to stationary pattern formation we have

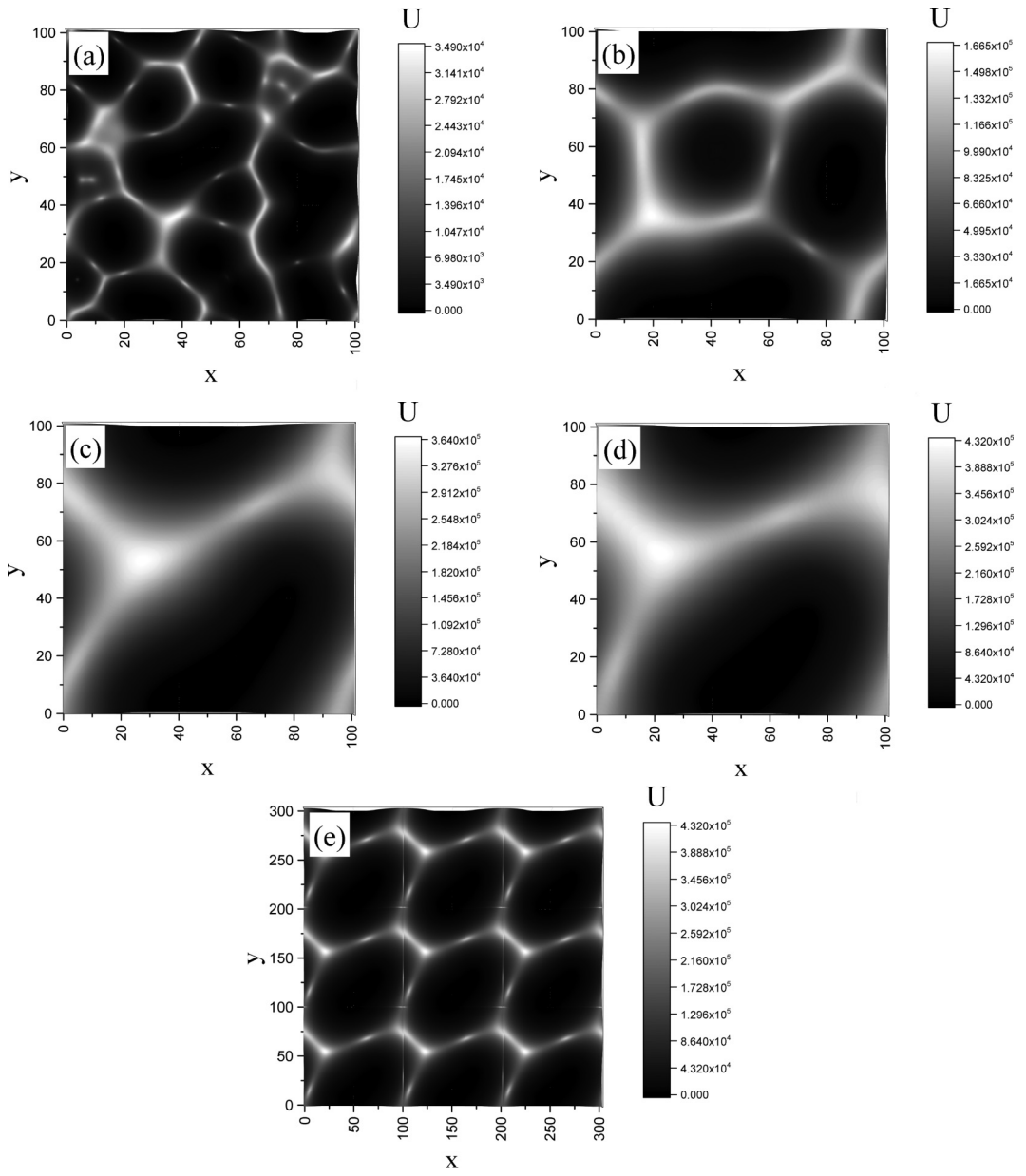

FIG. 6. Concentration profile of the activator U for $D = 0.05$, $\alpha = 200.0$, $\beta = 400.0$, $r = 1.5$ at the time units (a) $t = 1000$, (b) $t = 5000$, (c) $t = 12000$, (d) $t = 15000$, and (e) three repeating profiles of (d) in x and y directions (units arbitrary).

performed numerical simulations of this linear, stochastic, self-regulating kinetic model with diffusion for different parameter values. Throughout the simulations periodic boundary condition has been maintained and the standard central difference formulas are used to evaluate the Laplacians $(\nabla^2 U)$ and $(\nabla^2 V)$. For the present purpose a 250×250 array with grid size $\Delta X = 0.4$ and $\Delta Y = 0.4$ has been chosen. To begin with a homogeneous state the concentration of the activator $U_0 = 5.0$ and that of the inhibitor $V_0 = 5.0$ are set at all sites. This state is perturbed by a Gaussian white noise, $\eta(t)$ with zero mean, $\langle \eta \rangle = 0$ and noise correlation as $\langle \eta(t)\eta(0) \rangle = 2\sigma\delta(t)$, σ being the strength of noise which is set as $\sigma = 0.01$. The inhibition rate β and the time step for numerical simulation Δt are fixed at 400.0 and 0.0025, respectively, all throughout our calculations.

To understand the role of diffusion coefficients which couple the concentration at different spatial sites, the simulation is first carried out for activation rate $\alpha = 400.0$ and $r = 1.0$ for equal diffusivities, i.e., $D = 1.0$ for a long time. The results are presented in Fig. 1 depicting the snapshot of the concentration profile of u at $t = 15000$ time units. We observe that the system remains homogeneous. The simulations have been repeated for several other values of α to check that for equal diffusivities of the activator and the inhibitor, homogeneity is not disturbed in any such case. This observation is in agreement with the basic condition for Turing instability of a homogeneous steady state.

We now introduce disparity in the values of diffusivities of the activator and inhibitor by setting the ratio $D = 0.05$. The simulations are carried out keeping all other parameters same and the results are shown in Figs. 2(a)–2(d). The concentration

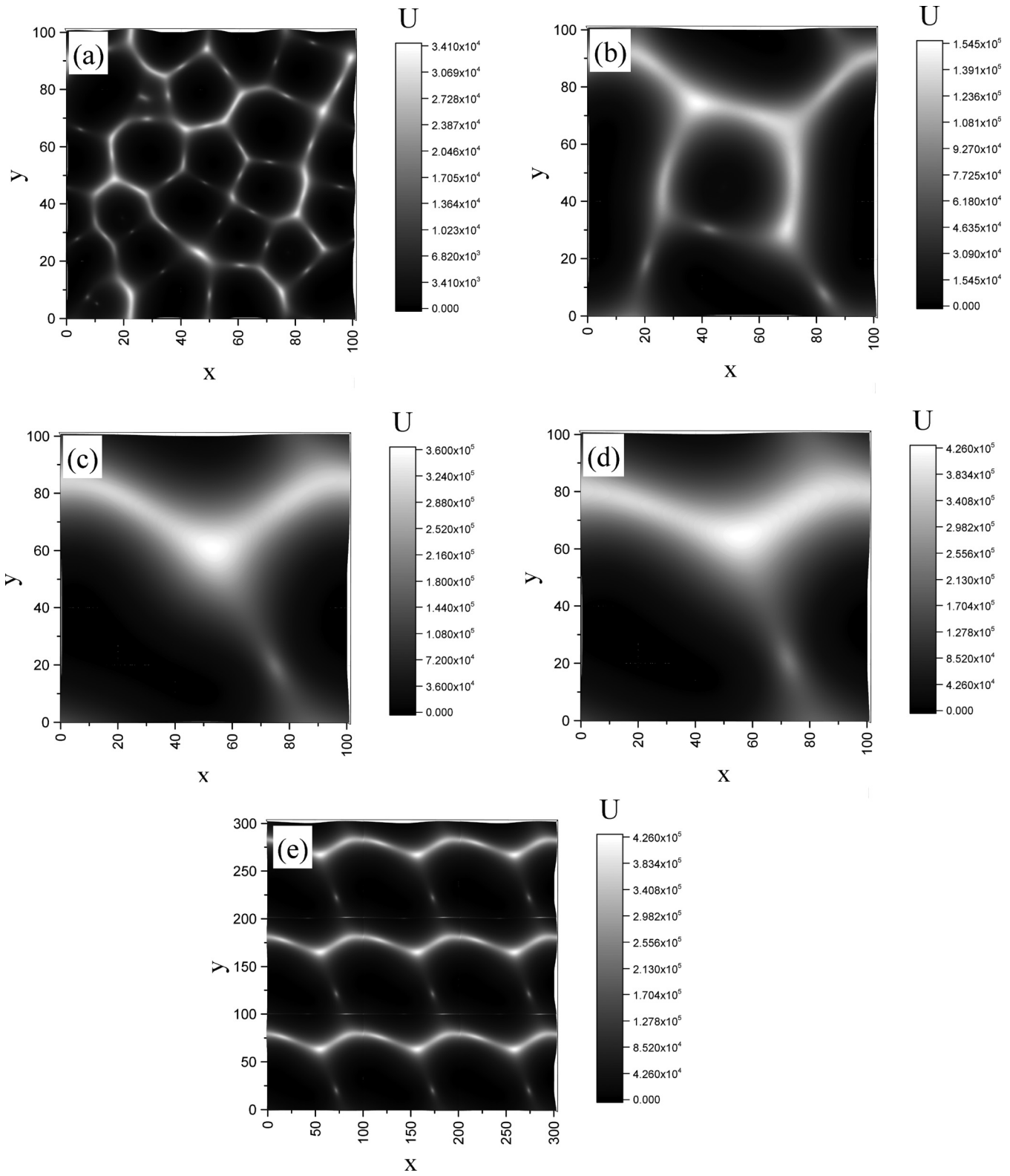

FIG. 7. Concentration profile of the activator U for $D = 0.05$, $\alpha = 200.0$, $\beta = 400.0$, $r = 2.0$ at the time units (a) $t = 1000$, (b) $t = 5000$, (c) $t = 12000$, (d) $t = 15000$, and (e) three repeating profiles of (d) in x and y directions (units arbitrary).

profiles of activator U at $t = 1000$, 5000, 12000, and 15000 time units clearly reveal the emergence of inhomogeneity resulting in stripe patterns which finally settle down to a stationary or non-equilibrium steady state. We emphasize an important point at this stage. Although disparity of diffusivities has been maintained ($D = \frac{D_U}{D_V} < 1$), the rate of activation and rate of inhibition are set equal ($\alpha = 400.0, \beta = 400.0$). The realization of stationary patterns in Fig. 2 points out a

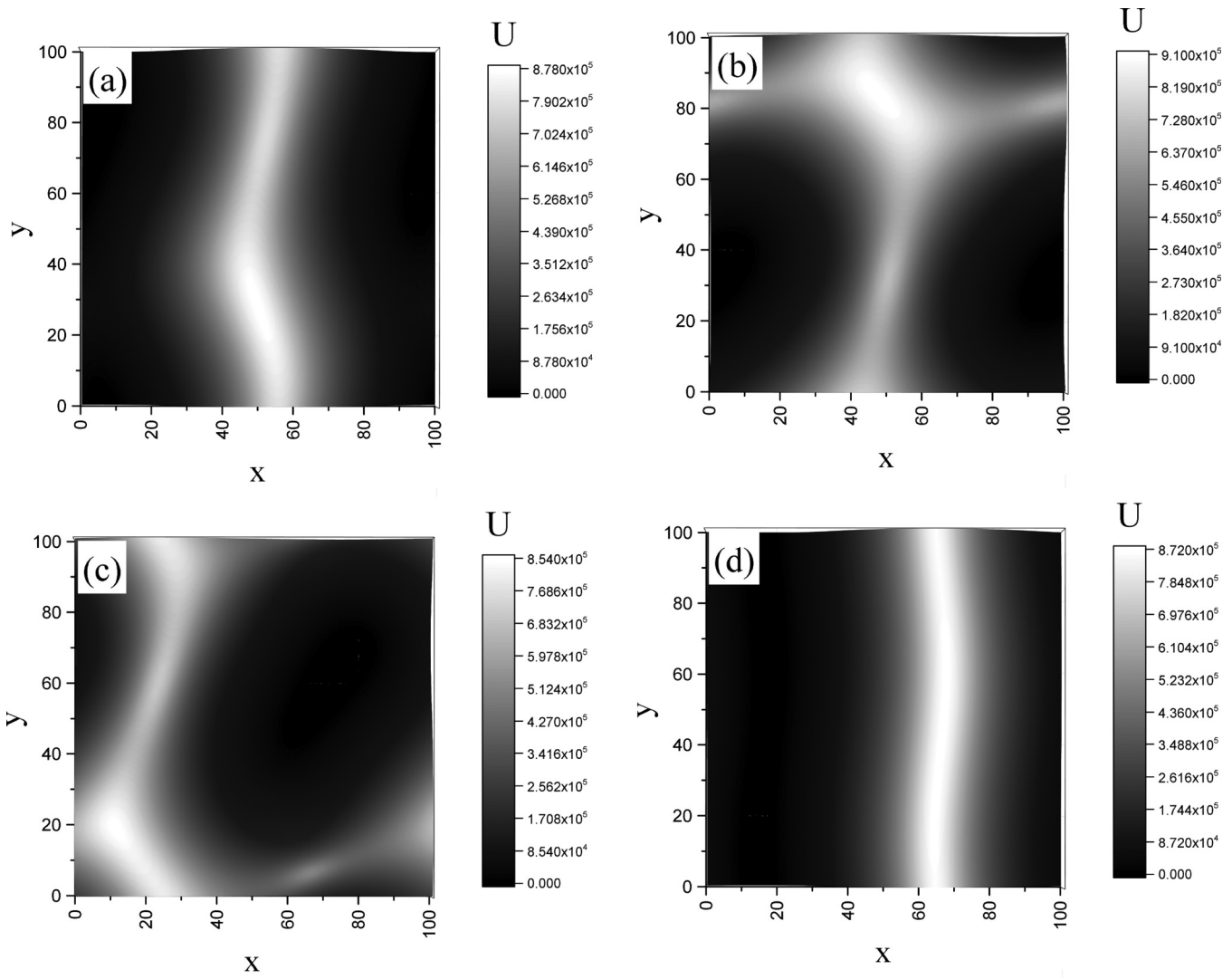

FIG. 8. Stationary ($t = 15000$ t.u.) concentration profile of the activator U for $D = 0.05$, $\alpha = 400$, $\beta = 400$, $r = 1.0$ for initial Gaussian noise strength σ (a) 0.01, (b) 0.05, (c) 0.10, and (d) 0.20 (units arbitrary).

significant departure from the Turing condition that $\frac{D_U}{D_V} < \frac{|F_U|}{|G_V|} < 1$, where F_U and G_V are the partial first derivatives of F and G of Eqs. (2.1)–(2.2) with respect to U and V, respectively. The ratio $\frac{|F_U|}{|G_V|}$ in the present case is $\frac{\alpha}{\beta} = 1$. In order to get a clear view of the stationary pattern as shown in Fig. 2(d) we arrange the profile in a sequence of three repeating units in both x and y directions in Fig. 2(e). The pattern appears as wavy stripes.

Keeping in view of the above observations we now consider further two cases by putting the ratio of the rate of activation to the rate of inhibition (α/β) less than and greater than unity. To this end we first set $\alpha = 200.0$ keeping all other parameters as in Fig. 2. The simulation results are shown in Figs. 2(a)–2(d) for $\frac{\alpha}{\beta} < 1$. The concentration profiles of U at time $t =$ 1000, 5000, 12000, and 15000 time units clearly reveal how the short-time honey-comb structure of the patterns change over to a stationary profile. We extend our simulations for $\alpha =$ 600.0, i.e., for $\frac{\alpha}{\beta} > 1$, while the other parameters remain same. From Figs. 4(a)–4(d) it is apparent that the homogeneous state goes over to the stationary patterned state as in the above two cases. Figures 3(e) and 4(e) where the stationary profiles of Figs. 3(d) and 4(d) have been shown as three repeating units in longitudinal and transverse directions, clearly reveal that the stationary patterns in Figs. 3(d) and 4(d) are spots and wavy stripes, respectively. The initial parameter ratio, $\frac{\alpha}{\beta}$, therefore plays a determining role in pattern selection.

An important element of the present scheme is that the concentration of a species at a space point is guided by that of its neighbors. It would therefore seem that the radius of the length of interaction would play an important role in the spatio-temporal evolution due to non-local kinetics. To explore this aspect we have varied the radius of interaction over $r = 0.5$, 1.5 and 2.0 for numerical simulations. In Figs. 5, 6, and 7 we present the snapshots of concentration profiles of activator U for $\alpha = 200.0$ and $\beta = 400.0$, respectively, at time $t = 1000$, 5000, 12000, and 15000 time units. The results remain qualitatively same in all cases. The patterns as shown in Figs. 5(e), 6(e), and 7(e) as in the earlier cases, appear to be stationary honeycomb structures.

Another aspect of the present study is the role of the noise in the simulation. The noise at the initial condition has a particular

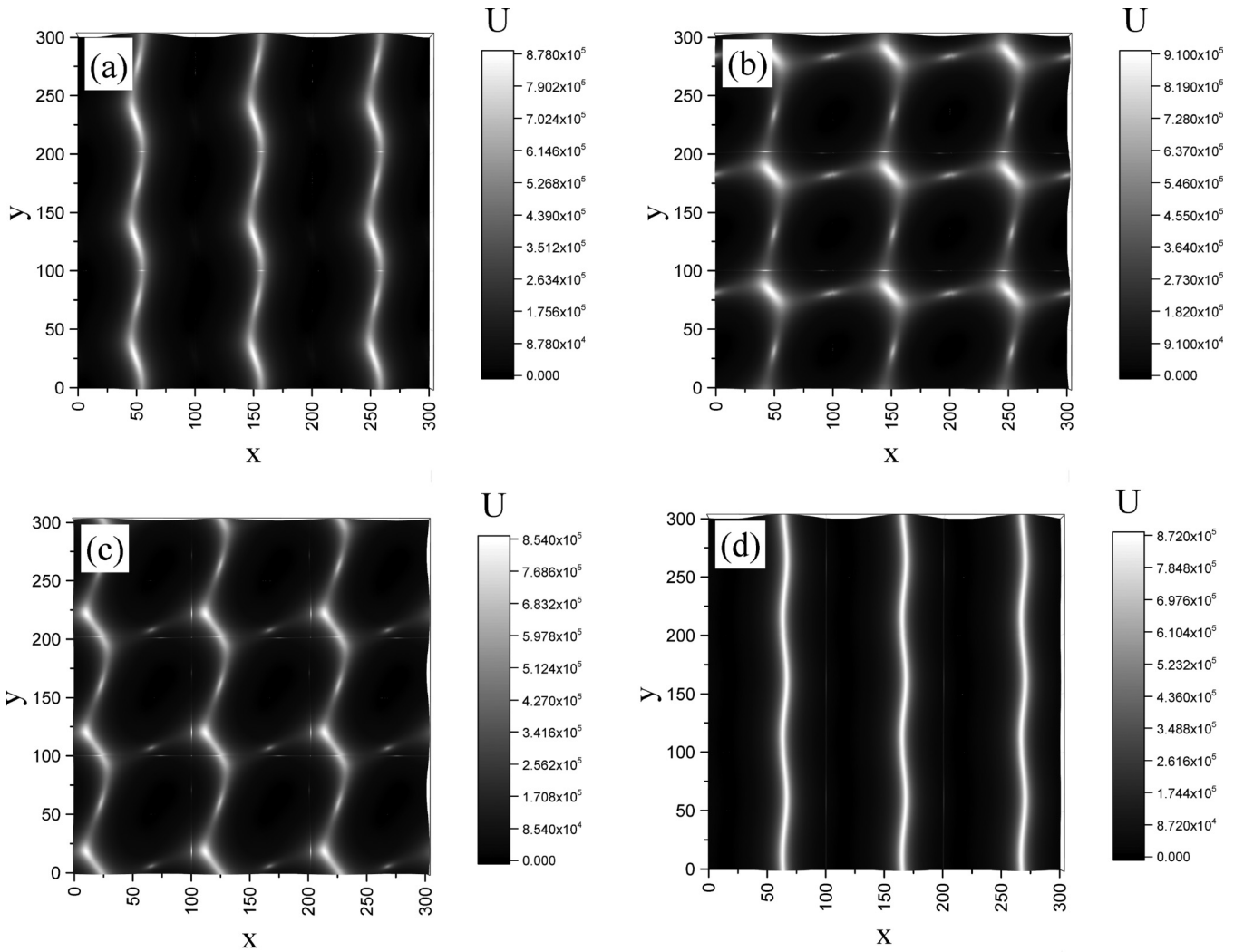

FIG. 9. (a) Three repeating profiles of Fig. 8(a) in x and y directions showing wavy stripe pattern for $\sigma = 0.01$, (b) same as in (a) but for Fig. 8(b), ($\sigma = 0.05$) showing honey-comb-like spots, (c) same as in (a) but for Fig. 8(c), ($\sigma = 0.10$) showing honey-comb-like spots, and (d) same as in (a) but for Fig. 8(d), ($\sigma = 0.20$) showing wavy stripes (units arbitrary).

influence on the nature of the spatio-temporal evolution leading to stationary pattern, particularly pattern selection. To this end we vary the strength (σ) of the initial Gaussian noise over $\sigma = 0.01$, 0.05, 0.10, 0.20 for $\alpha = 400.0$, $\beta = 400.0$, $D = 0.05$, and $r = 1.0$. The results for the stationary patterns at $t = 15000$ t.u. shown in Figs. 8(a)–8(d) reveal that the nature of the patterns changes from stripes for low and high intensity of noise to honeycomb spots for intermediate range of noise strength as apparent from Figs. 9(a)–9(d) where each of the profiles of Figs. 8(a)–8(d) have been arranged as three repeating units over x and y directions. This observation is indicative of the fact that the pattern forming instability is due to the noise-induced transition in the system and honeycomb-like structure is formed for optimal strength of noise.

Summarizing the above observations, it is apparent that non-locality of chemical reaction and diffusive transport of the species with unequal diffusivities lead to a symmetry-broken state, i.e., a stationary patterned state. The stationarity is ensured by the fact that the nature of spatio-temporal profiles at $t = 12000$ and $t = 15000$, i.e., in the long time limit remains almost the same. The reason for attainment of stationarity is not apparently obvious since model is linear and there is no scope of nonlinear saturation which prevails in the long time limit and normally overwhelms the linear divergence at short time that initiates the instability in a non-linear model. The primary condition for instability leading to the formation of stationary pattern is the disparity of diffusivities of the two species. This is irrespective of the ratio of the rate of activation and the rate of inhibition. Another point regarding non-locality of the kinetics is pertinent. The spatio-temporal evolution of the activator and inhibitor appears to be independent according to Eqs. (2.3)–(2.6) since there is no explicit kinetic or diffusive coupling between them. However, a closer look at the scheme makes it clear that non-locality of the reaction term gives rise to spatial correlation between the species at different sites and couples the concentration as the updating of concentration of one species at a spatial location is guided by that of its neighbors which include both the activator and the inhibitor. In the spirit of self-propelled motion the symmetry-breaking may be viewed as non-equilibrium transition between disordered homogeneous state to ordered pattern state.

IV. CONCLUSION

Non-linear reaction-diffusion systems with two reacting components serve as prototypical models for study of self-organization phenomena under far from equilibrium condition. In this paper we have considered a linear reaction-diffusion system with self-regulatory kinetics of activator and inhibitor whose growth and decay of concentration depends on the relative average concentration of their neighbors. The model does not make use of any explicit form of deterministic kinetics but relies on stochastic variations of concentration at each time step. In presence of external noise the system undergoes a non-equilibrium transition between the homogeneous and the patterned state due to the symmetry-breaking, a scenario which captures partly the features of Turing bifurcation and partly the features of order-disorder transition in non-equilibrium system of self propelled particles. To highlight this aspect we may term the phenomena as non-equilibrium Turing transition. We now summarize the main conclusions of this study.

First, linear, non-local and self-regulatory nature of the kinetics brings in spatial correlation of concentration of activator and inhibitor in the dynamics. This is a significant point of departure from traditional kinetics in a reaction-diffusion system, where diffusive transport is only responsible for spatial correlation of concentration.

Second, the spatio-temporal instability of the homogeneous state arises due to the spatial correlation of concentration and disparity of diffusivities of the activator and inhibitor, rather than local activation and long-range diffusion.

Third, the nature of stationary pattern is determined by the linear reaction terms of the activator-inhibitor dynamics as well as the strength of noise as initial condition. While low and high noise intensity gives rise to wavy stripes, honeycomb-like structure is favored for an intermediate range of noise strength.

Fourth, the non-equilibrium symmetry-breaking transition gives rise to self-organized structures in the form of stationary patterns irrespective of the rate of activation or inhibition. The attainment of stationarity here cannot be due to non-linear saturation in the long time limit in this linear model. This is quite distinct from the stationarity in the usual reaction-diffusion systems with non-linear kinetics.

Finally, we note that the present theoretical scheme also serves as a bridge between the two classes of self-organization phenomena, one, in the non-linear dynamics of reaction-diffusion systems and other in the non-equilibrium statistical mechanics of self-propelled particles where the common link lies in the symmetry-breaking transition and formation of non-equilibrium ordered structure. Since the reaction-diffusion systems encompass a variety of problems in chemical, biological and ecological sciences, this simple model can be generalized appropriately by suitable modification of the time-updating rules and stochasticity of the governing kinetics.

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