State differentiation by transient truncation in coupled threshold dynamics

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Dynamics with a threshold input-output relation commonly exist in gene, signal-transduction, and neural networks. Coupled dynamical systems of such threshold elements are investigated, in an effort to find differentiation of elements induced by the interaction. Through global diffusive coupling, novel states are found to be generated that are not the original attractor of single-element threshold dynamics, but are sustained through the interaction with the elements located at the original attractor. This stabilization of the novel state(s) is not related to symmetry breaking, but is explained as the truncation of transient trajectories to the original attractor due to the coupling. Single-element dynamics with winding transient trajectories located at a low-dimensional manifold and having turning points are shown to be essential to the generation of such novel state(s) in a coupled system. The universality of this mechanism for the novel state generation and its relevance to biological cell differentiation are briefly discussed.

I. INTRODUCTION

Differentiation of identical units through interaction is an important issue in both physics and biology. Through developmental processes, cells with identical genes start to take different chemical compositions; this process is known as cell differentiation [1,2]. Several distinct types of cells are generated that have different compositions of gene expressions. Theoretically, on the other hand, state differentiation of identical units has been studied in dynamical systems, by using a coupled dynamical system, such as coupled chaotic systems [3] or coupled oscillators [4].

In coupled dynamical systems with identical elements, there is a homogeneous state in which all elements take an identical value. If this homogeneous state is unstable, differentiation of elements follows. This has been studied extensively as symmetry breaking. For example, by losing the synchronization in oscillations, elements are differentiated into clusters with different phases of oscillation, in coupled chaotic or coupled oscillator systems [3,4]. Here the differentiation occurs with regard to the phase of oscillation.

In a biological cell, differentiation is more drastic. Different compositions of chemicals or, in other words, different types of gene expression appear, and the differentiation is not with regard to the phase of oscillation but in the fixed composition of chemicals (e.g., proteins). To describe cell differentiation as a coupled system of intracellular oscillatory dynamics, isologous diversification has been proposed [5,6], while its dynamical systems analysis is not as yet fully developed.

In the gene expression dynamics of a cell, the basic process is on-off output against input(s), with some threshold function, rather than oscillatory dynamics [7]. In the present paper, we present a mechanism for state differentiation by taking elements with such a threshold function [i.e., $y = \tanh(\beta x)$ with $\beta > 1$] and coupling them globally with each other through simple diffusion coupling. By varying several parameters, we find the generation of novel states in a coupled system that are not attractors of the original single-element dynamics. This differentiation of states is not explained as symmetry breaking and, indeed, the original attractor also remains stable. To explain such coupling-induced generation of novel stable states, we propose a transient truncation mechanism, which brings about stabilization of stagnation point(s) in transient trajectories, mediated by interaction with elements that have already fallen on the original attractor. We show how this mechanism works, and describe the condition for the generation and stabilization of novel states. The generality of this mechanism in a coupled threshold dynamics model is discussed, as well as its extension and relevance to cell differentiation.

II. MODEL

Gene expression [7] and signal transduction [8] as well as neural response [9] often follow threshold dynamics, where the output y can be represented by $y = \tanh(\beta x)$ where x is an input and $\beta \, (>1)$ is a parameter representing the sensitivity. The input to each variable (gene or neuron) comes from several genes (or neurons) that are connected through excitatory or inhibitory couplings. For such dynamics, the following threshold dynamics model is often adopted;

$$\dot{x}_i = \tanh\left(\beta \sum_{0 \leq j}^{M-1} J_{ij} x_j - \theta_i\right) - x_i, \qquad (1)$$

where x_i is the state of the ith variable (e.g., gene expression) with $i = 0, 1, \ldots, M-1$, while the component of the connection matrix J_{ij} goes from positive to negative values [10]. Here, we study the case in which J_{ij} is either -1 or 1, selected randomly, as is used in the spin-glass model [11], while the specific form of the distribution of J_{ij} is not important for discussion of the results. The threshold value θ_i is fixed, and is also distributed over $[-1, 1]$. The parameter β, representing the sensitivity, is fixed at 4 in the present paper, while the behavior to be discussed is unchanged as long as $\beta > 1$.

Now, we consider an ensemble of elements, each of which follows the same equation (1) as single-element dynamics,

and introduce interaction among such elements. For example, consider N cells, each of which has identical gene expression dynamics. Then the global behavior of an ensemble of these cells is represented by the above intracellular dynamics and interaction among them. Instead of x_i, we need to study the dynamics of the variable $x_i(k)$, the state of the ith component (e.g., ith gene) of the kth element (cell). Here we take the simplest form of interaction, diffusive, global coupling, to all elements (cells). Now, the model we discuss is written as

$$\dot{x}_i(k) = \tanh\left(\beta \sum_{j=0}^{M-1} J_{ij}x_j(k) - \theta_i\right) - x_i(k) + D_i[\bar{x}_i - x_i(k)]$$

(2)

with $k = 1, 2, \ldots, N$, and $\bar{x}_i = (1/N)\Sigma_{\ell=1}^N x_i(\ell)$ is the average value of the ith component over all elements, while D_i is the strength of this diffusive coupling over elements. We use the present mean-field model (global coupling) as an idealized basic system.

Of course, another choice in the coupling form is spatially local interaction, such as the nearest-neighbor diffusion coupling among elements located on a lattice. Here, we use the above global interaction, because we are interested in the basic properties of coupled threshold dynamics and state differentiation. In general, with the choice of spatially local interaction, differentiation of state values by elements appears more easily, while the mechanism to be described for the global interaction works even for the local interaction case.

In a biological context, this type of model was discussed, for instance, by Mjolsness *et al.* [12] and Salazar-Ciudad *et al.* [13], in relationship with the problem of cell differentiation, where these authors chose the interaction J_{ij} and (local) cell-cell interaction to meet a specific biological situation. Here, we are interested in general features of this class of models, so that we have chosen the simplest situation, as described above. In a physics context, the above model (with local coupling) was studied analytically and numerically by Hansel and Sompolinsky [14], as a model for spatiotemporal chaos, where their interest is focused on the limit with $M \to \infty$, and fully chaotic behavior. Our interest in the present paper lies in the differentiation into distinct stable states (mostly fixed points) for a system with a relatively small M.

III. GENERATION OF NOVEL STATES BY TRANSIENT TRUNCATION MECHANISM

The single-element dynamics (1) [or the model (2) with $D_i = 0$ for all i] can have multiple attractors in general, which are either a fixed-point, a limit-cycle, or a strange attractor. To discuss the interaction-induced generation of novel states other than the attractor(s) of the single-element dynamics (1), however, it would be better to study the case with only one attractor at first.

In fact, the behavior of a coupled dynamical system has been studied extensively, when an element system has only one limit-cycle or chaotic attractor. If the attractor is a limit cycle, synchronization among elements often occurs through
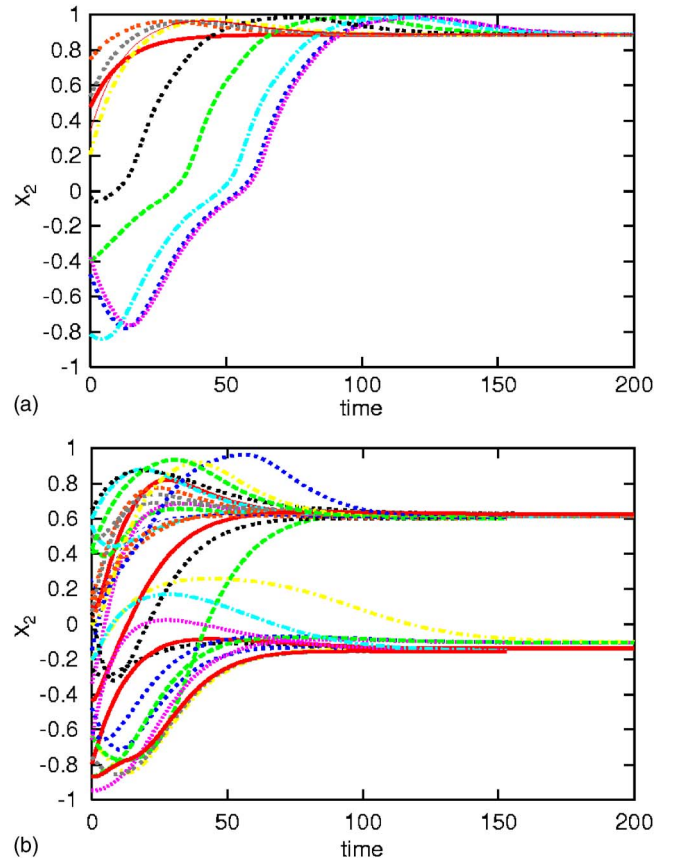

FIG. 1. (Color online) Time series of x_2 of the threshold dynamics model with $M = 5$. (a) Overlaid time series of single-element dynamics (1), from ten initial conditions chosen randomly. From all initial conditions, a single, fixed-point attractor is reached. (b) Time series of the coupled dynamics model (2) overlaid for 30 elements chosen from $N = 100$ elements, for a single initial condition. Other than the original fixed point of (a), another fixed-point state is reached, which is stabilized by the interaction. The matrix J and parameter values are chosen as shown in the text.

the coupling, while, if the attractor is chaotic, clustering of elements into several states can occur [3,4]. In the latter case, state values are differentiated by elements, as a result of the instability of the homogeneous (synchronized) state, while the differentiation is understood as symmetry breaking. Indeed, in our model (2), such clustering is generally observed when the single-element dynamics (1) shows chaotic or oscillatory dynamics.

On the other hand, if the attractor of single-element dynamics (1) is a fixed point, a homogeneous state of the fixed point over all elements is always stable in the present diffusive coupling system. Then, the generation of novel states other than the fixed point is not possible by the symmetry-breaking mechanism. However, we have found several examples in which the coupled system (2) exhibits differentiation of state values, when started from initial conditions far from a homogeneous state. Inhomogeneous states with $x_i(k) \neq x_i(j)$ are observed, for some network J_{ij}, and for some values of $\{D_i\}$, and $\theta(i)$.

An example of such behavior is shown in Figs. 1 and 2, where $M = 5$. The corresponding single-element dynamics (1)
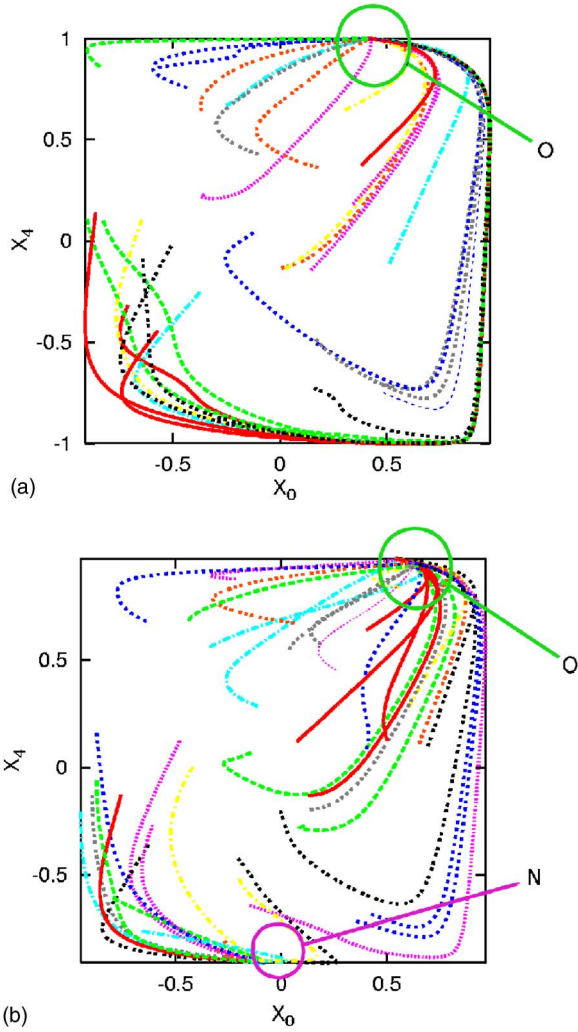
FIG. 2. (Color online) The trajectory of the model corresponding to Fig. 1. $(x_0(k), x_4(k))$ is plotted as a projection on a two-dimensional plane from the five-dimensional phase space. (a) Single-element dynamics corresponding to Fig. 1(a). Overlaid plot from 25 initial conditions. All the orbits are attracted to the fixed point denoted by O. (b) Coupled dynamics model corresponding to Fig. 1(b). Overlaid plot for 30 elements chosen from $N=100$. The orbits are either attracted to the original attractor shown as O (green circle), or to a novel fixed-point state denoted by N (represented by a violet circle). The latter is stabilized by the interaction. About one-third of the elements are attracted to N, while the others are attracted to the original attractor O. Note that the location of the state corresponding to the original attractor is slightly shifted by the coupling term with the elements at the novel state.

has only a fixed-point attractor. Here we choose

$$ J = \begin{pmatrix} + & - & - & + & + \\ - & - & - & + & + \\ + & - & - & - & + \\ + & + & - & + & + \\ - & + & - & + & + \end{pmatrix} \quad (3) $$

where $+$ denotes 1 and $-$ denotes -1, $\theta=(0.14, -0.75, 0.71, -0.78, 0.32)$, and $D=(0.95, 0.027, 0.30, 0.18, 0.95)$, while

several other choices of J, D_i, and $\theta(i)$ give rise to similar behavior. The time series of x_2 of a single-element dynamics (1) are plotted in Fig. 1(a) by taking a variety of initial conditions, which shows the relaxation to a single, fixed-point attractor. In Fig. 1(b), the time series of $x_2(k)$ over several elements are plotted. One can see differentiation of final state values into two fixed-point values, one of which corresponds to the original fixed-point value of the single-element dynamics (1), although the value of the fixed point is slightly shifted, due to the coupling term. The other fixed-point value, on the other hand, does not have a corresponding value in the single-element dynamics.

Corresponding to these time series, we have plotted a two-dimensional projection of orbits from the five-dimensional phase space. Figure 2(a) again shows the single-element dynamics (1) without interaction. Each line represents the time evolution of (x_0, x_4) starting from different initial conditions, while Fig. 2(b) shows the evolution of the coupled system (2), where an orbit from a single initial condition is plotted, with each line as an orbit of each element. One can again see clearly that a novel attracting state (N) other than the original fixed-point attractor $x_i(k)=x_i^*$ (O) is created through the interaction.

Recall that the homogeneous state with $x_i(k)=x_i^*$ for all elements k is always stable. Indeed, when the initial condition is set so that the states of all elements are located near this fixed point, the attractor $x_i(k)=x_i^*$ is always reached. In this sense, the present mechanism differs distinctly from the clustering or other mechanisms based on spontaneous symmetry breaking. In addition to the stable homogeneous state, there appears a macroscopic state consisting of both the elements at the original fixed point and a novel fixed point, when the initial condition of elements is set far from homogeneity. (In most examples, we choose a random initial condition where $x_i(k)$ is taken randomly from $[-1,1]$.) Here the novel fixed point N is stabilized by the coupling with other elements located at O.

Indeed, by taking a variety of networks J_{ij}, we have observed several examples of formation of such novel state(s), and found a common mechanism. The mechanism of the generation of novel state(s) other than the original fixed-point attractor is explained as follows.

Consider the case in which a single unit dynamics has long-winding transient trajectories before they reach the original unique fixed point (O), as shown in Fig. 2(a). During the transient process, the orbit has (a few) turning points at which the motion of $x_i(t)$ is slowed. While some elements have reached the original fixed point fast, others are still on the route to it. At some turning points, the relaxation of an element take a course once going farther away from the original fixed point O. On the other hand, diffusive coupling with elements that have already reached the original final fixed point drives the transient element toward it (see Fig. 3 for a schematic representation). This coupling suppresses the relaxation of single-element dynamics toward the original fixed point. When the directions of the original relaxation and the attraction to the original fixed point are opposite, the two driving forces may balance each other around a turning point where the motion is stagnated (see stagnation point S in
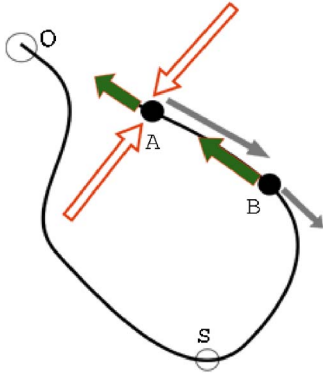
FIG. 3. (Color online) Schematic representation of transient truncation mechanism. Original relaxation of single-element dynamics takes a course $A \rightarrow B \rightarrow S \rightarrow O$, while the interaction with elements near O hinders the relaxation from A to S.
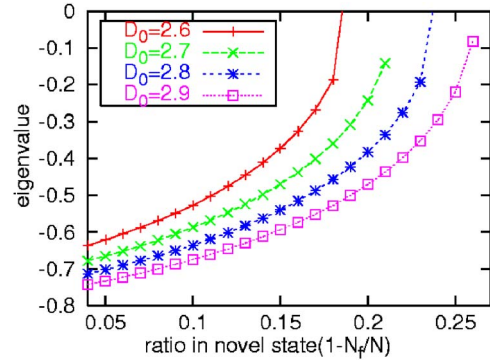

FIG. 4. (Color online) Dependence of the stability of the novel state upon N_f, the number of elements located at the original fixed-point attractor. By using the same model for Figs. 1 and 2, we have computed the largest eigenvalue of the Jacobi matrix of the novel fixed-point state, by fixing the number of elements at the original attractor at N_f. Here the eigenvalue is plotted as a function of $(N - N_f)/N$, i.e., the fraction of the number of elements at the novel state. When the eigenvalue exceeds zero, the state is no longer stabilized, and the exponent is not computed. Different symbols correspond to different sets of diffusion coupling D_i, which is changed by fixing $D_1/D_0 = 0.448$, $D_2/D_0 = 0.19$, $D_3/D_0 = 0.078$, $D_4/D_0 = 0.052$, and changing only D_0, as shown in the figure.

Fig. 3). Then, the relaxation to the original fixed point is truncated, and some elements remain around this stagnation point, to create an interaction-induced novel state, as shown in Figs. 2 and 3.

This transient truncation mechanism works under the following conditions.

The loci of transient orbits are restricted within a low-dimensional manifold: If the transient trajectories cover a high-dimensional region in the phase space, orbits from different elements approach the original attractor from a variety of directions, and the transient truncation by diffusion coupling does not work effectively. When the transient truncation mechanism works, many points reach the original attractor, taking a specific course restricted within a low-dimensional region in the phase space, as displayed in Fig. 2. Contraction to the low-dimensional manifold is so strong that each element is located within a low-dimensional manifold, as shown schematically in Fig. 3 (as thick red arrows toward A).

The transient orbit has one or several turning points. At some turning point, the single-element motion stagnates where the orbit stays for a long time, so that the driving force by the single-element dynamics is weak there. Hence, the diffusive coupling to the original fixed point is sufficient to stop the original relaxation course. See Fig. 2 for example.

The direction of transient orbit around this stagnation point is roughly opposite to the direction to the original fixed point, attracted by the diffusive coupling. Then, the orbit is trapped around this stagnation point, as shown in Fig. 2.

Since the interruption of transient dynamics is caused by the diffusive coupling to the elements already fallen on the original fixed point, the degree of interruption depends on the number of such elements, which is denoted by N_f.

To study how the stability of the novel state changes with N_f, we have computed the largest eigenvalue of the Jacobi matrix of the evolution equation at this novel fixed point (N) induced by coupling. If the eigenvalue is negative, this novel fixed-point state is stable. This eigenvalue depends on the number N_f (or more generally, on the ratio N_f/N). We have plotted this eigenvalue against the ratio $1 - N_f/N$, i.e., the fraction of the elements at the novel state. As shown in Fig.

4, the eigenvalue is negative only if N_f is larger than some threshold, while it decreases with increase of N_f. In other words, the novel state is sustained only under the existence of a moderate number of the elements at the original fixed point. Existence of the threshold number for N_f is natural, since the new state is sustained by an "attractive force" to the original fixed point.

According to the above mechanism, the appropriate strength of diffusion coupling is necessary to stabilize the novel state. Indeed, the present transient truncation mechanism works only for a given range of diffusion constants. If it is too small, the attraction to the original fixed point is too weak to interrupt the relaxation course of the single-element dynamics, so that all the elements fall on the original fixed point. On the other hand, when the diffusion coupling is too large, the diffusion coupling dominates so that all the elements take the same value. Then, the dynamics follow the single-element dynamics (1), so that all elements fall on the original fixed point. [See Fig. 5 for the diffusion constant dependence of the existence of the novel state, where D_i is changed by keeping the proportion among the D_i's (i.e., fixing D_i/D_j)].

IV. GENERALIZATION

We have studied the behavior of the model (2) by taking a variety of networks and by changing N and M, to find that the generation of novel states by the mechanism of the last section is general. We have computed the fraction of the networks that show the generation of novel state(s) from fixed-point attractor(s), by the above mechanism. The fraction of the network (and θ_j) for such behavior remains at 1–5 %, when M is changed from 8 to 64. Here, we have computed 100 networks for each M, and the transient truncation
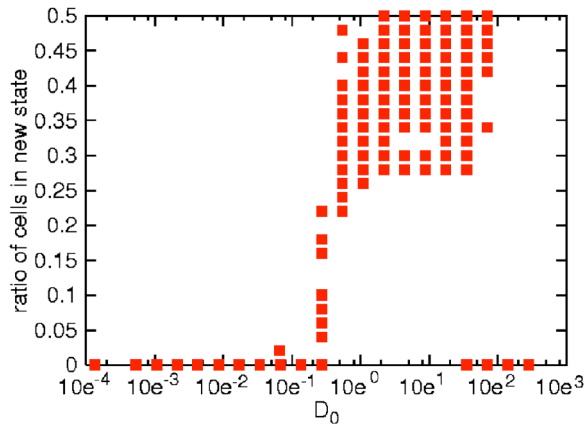
FIG. 5. (Color online) Fraction of elements falling on the novel state is plotted against the strength of diffusion coupling. The fraction is measured over 50 randomly chosen initial conditions. Diffusion strength D_i is changed by fixing D_i/D_0 and varying D_0, in the same way as in Fig. 4, and changing only D_0 as shown. The fraction is plotted against D_0. For $D_0 < 0.1$ and $D_0 > 100$, the novel fixed-point state does not exist, and all the elements fall on the original fixed point.

mechanism from fixed point attractor(s) is observed for 1–5 networks among them. We also note that the present mechanism also works, even if the coupling J_{ij} is sparse, in the sense that many J_{ij}'s are set at 0. For example, we have observed the novel state generation by transient truncation, with a similar fraction, for a system with $J_{ij} = 0$ for 70% of the matrix.

Another type of nontrivial behavior of the coupled system (2) is clustering of elements into different phases of oscilla-
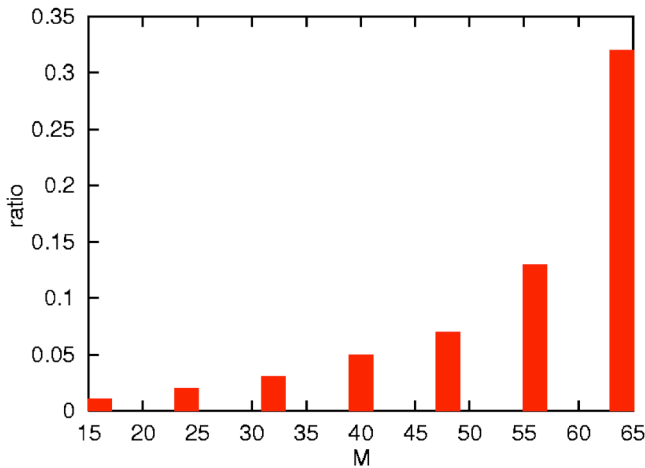

FIG. 6. (Color online) Fraction of networks that exhibit oscillatory dynamics for single-element dynamics. For each value of M, we have chosen 100 networks with randomly chosen J_{ij}, and carried out the simulation without coupling, to check if there is a limit cycle or a chaotic attractor. For the corresponding coupled system, clustering of elements into a few groups is observed with the increase of the coupling strength, and then a synchronized state over elements appears for the further increase of coupling, as is studied in globally coupled maps [3]. N is fixed at 128.
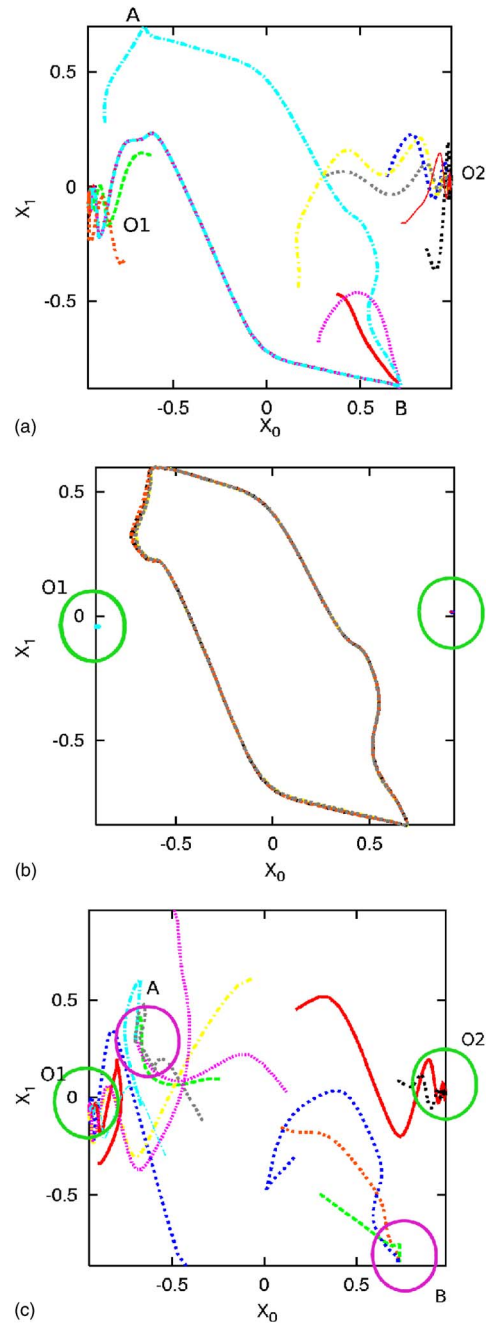

FIG. 7. (Color online) The trajectories $(x_0(k)(t), x_4(k)(t))$ are plotted, as a projection on a two-dimensional plane from the M-dimensional phase space ($M = 10$). (a) Single-element dynamics (1), overlaid plot over 20 initial conditions. (b) Coupled dynamics model (2) corresponding to (a), with the coupling values $D = (0.20, 0.27, 0.66, 0.41, 0.26, 0.15, 0.32, 0.29, 0.096, 0.33)$. Final states are plotted for all 100 elements. The original fixed-point attractors are shown as $O1$ and $O2$. In (a), there are winding transient orbits that fall on the attractor $O1$ or $O2$. In (b), a novel limit cycle is generated. (c) The trajectories of a coupled dynamical system with the same set of J_{ij} and $\theta(i)$, but a different set of D_i, i.e., $D = (0, 0.30, 0.0037, 0, 0.79, 0, 0, 0.0070, 0.80, 0.0028)$. With the coupling, novel fixed-point states A and B are generated, besides the original fixed points, instead of the limit cycle in (b). Trajectories of 12 elements among 100 are plotted. The matrix J and parameter values are chosen as shown in the text.

tions, when the single element shows (chaotic) oscillation, as was discussed in globally coupled maps [3]. The fraction of networks showing the clustering also increases with M, as shown in Fig. 6. This is natural, since chaotic behavior is more frequently observed in a single-element dynamics [14]. In other words, the network only with fixed-point attractors for single-element dynamics decreases with M. Hence, among the networks having only fixed-point attractors, the fraction showing the transient truncation mechanism slightly increases with M [15].

Although the generation of coupling-induced novel state(s) is common to the networks above, it is often more complicated than the simple example in the last section where the original single-element dynamical system has only a single, fixed-point attractor.

Even if the single-element dynamics has multiple attractors, the transient truncation mechanism still works. Indeed, when M is large, we observed the case in which novel states are generated by coupling in addition to the original multiple attractors. For example, when there are two fixed-point attractors in the original dynamics, other fixed-point or limit-cycle states are stabilized due to the coupling, as a result of transient truncation. An example is shown in Fig. 7, where we choose

$$J = \begin{pmatrix}
- & - & + & + & + & + & - & - & - & + \\
+ & - & + & - & + & + & + & + & - & + \\
+ & + & - & + & + & + & - & + & - & + \\
+ & + & + & + & + & - & - & - & - & - \\
- & - & - & + & - & + & - & + & + & + \\
- & + & - & + & - & - & + & + & + & - \\
- & - & - & + & + & + & - & + & - & - \\
+ & - & - & - & + & - & - & - & - & + \\
+ & + & - & - & + & + & - & + & - & + \\
- & + & + & - & - & + & - & + & - & -
\end{pmatrix} \tag{4}$$

with $\theta = (-0.27, 0.98, 0.22, -0.25, -0.92, 0.63, 0.44, 0.64, 0.74, -0.73)$.

In this example, there are two fixed points, denoted by $O1$ and $O2$, in the original single-element dynamics (1). There are transient trajectories that have a few turning points, and that are attracted to $O2$, as shown in Fig. 7(a). With the coupling to elements located at $O1$ and $O2$, the transient trajectory is truncated, and a limit cycle is generated for the remaining elements, as shown in Fig. 7(b). This truncation is possible only if the numbers of elements at $O1$ and $O2$ are within some range, but the range is rather broad, so that the coupling-induced limit-cycle state is observed just by starting from random initial conditions. Furthermore, we have observed this type of novel limit-cycle state in a variety of networks.

Formation of multiple novel states is also possible in some networks (and with suitable choice of diffusion). In Fig. 7(c), we show an example of formation of two fixed-point states, by using the same network as in Figs. 7(a) and 7(b), but by taking a different set of diffusion couplings $(D_0, D_1, \ldots, D_{M-1})$ given in the figure caption. Here, two fixed-point states A and B are generated around two stagnation points. By starting from some initial conditions, both of these two stagnation points become stable due to the interaction with other elements.

Here, the novel fixed-point state A exists under the presence of B; otherwise the elements located around A cannot stay there, but move toward B. Hence there is ordering between A and B. The latter states are necessary for the former, but not vice versa. Generally, when there are several stagnation points $S1, S2, \ldots$, along a low-dimensional transient orbit, and coupling-induced novel states are formed accordingly as $N1, N2, \ldots$, there is ordering with regards to their existence, as $N1$ exists under the presence of $N2, N3, \ldots$, and $N2$ exists under $N3, N4, \ldots$, and so forth.

In some other networks, novel states A and B mutually stabilize each other; the state A exists under the presence of elements at B, and vice versa. By removing all elements taking the state A, elements taking the state B become unstable and are absorbed into the original fixed point, and removing the elements taking B also results in the destabilization of the state A.

Finally, the original attractor of the single-element dynamics need not necessarily be a fixed point. The mechanism of the transient truncation can work even if the original attractor is not a fixed point, but a limit cycle, as long as there are stagnation points along the transient orbits satisfying conditions (1)–(3) in the last section.

V. SUMMARY AND DISCUSSION

In the present paper we have studied a coupled threshold dynamics model, to find emergence of novel states stabilized by the coupling. Although we have adopted just a simple

global diffusive coupling which tends to homogenize all the element values, there appears differentiation of the state values, induced by the coupling. The mechanism of the generation of novel states is explained as the truncation of transient orbits that are located on a low-dimensional manifold in the phase space. The interaction with the elements that have fallen on the original attractor suppresses the relaxation process of the remaining elements at some stagnation point, to make it a novel fixed point (or a limit cycle).

The transient truncation mechanism is based just on the existence of winding transient orbits on a low-dimensional manifold, with several turning points. Hence, the coupling-induced formation of novel stable states by this mechanism is not restricted to the present model. It should be generally possible in coupled dynamical systems, with the above class of transient orbits at a single-element level.

Still, we have not found such differentiation in the previous studies on coupled dynamical systems in which a much simpler element is adopted (such as the logistic map [3]). At least, one can conclude that the present transient truncation appears more frequently in the coupled threshold dynamics model given by Eq. (2). We expect that this is because of the typical nature of transient orbits in (1). Indeed, in threshold dynamics, each variable tends to approach either 1 or −1. At some points with $x_i \simeq 1$ or −1 for some i's, the change in the variable values is slowed, and then the trajectory departs from them. The transient dynamics of a single element often involve such switchings between +1 and −1 with stagnation of motion. Thus the requirement on transients discussed in Sec. III is more easily satisfied in the present model than in coupled oscillators or coupled chaos.

Another clear example of such stagnation is a heteroclinic cycle [17–19]. Although the heteroclinic cycle itself is not a transient orbit to a fixed point required here, slight structural perturbation on the heteroclinic cycle can lead to transient orbits on low-dimensional manifold with some stagnation points. At this point, it is interesting to recall that a class of threshold-network dynamics can generally produce heteroclinic cycles [20].

Of course, generation of novel states is important in the study of biological cell differentiation. As the number of cells increases through the developmental process, they interact with each other, and some cells start to exhibit different gene-expression patterns. Indeed, the spontaneous cell differentiation process has been discussed theoretically as isologous diversification [5,6].

Considering that Eq. (1) is a simplified form of gene-expression dynamics, the present mechanism of state differentiation may be relevant to cell differentiation, since novel states stabilized by the (cell-cell) interaction have gene-
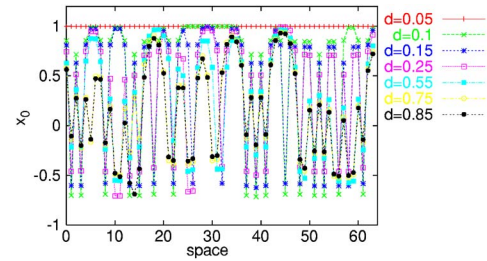

FIG. 8. (Color online) Snapshot pattern of x_0 for the model (3), with one-dimensional nearest-neighbor interaction. $M = 10$ and $N = 64$ with a periodic boundary condition. When d_i is less than some value (~ 0.07), there exists only a single attractor with a spatially homogeneous state with $x_0 \approx 1$. On the other hand, for larger d_i, spatially inhomogeneous patterns are reached as attractors for most initial conditions.

expression patterns distinct from those of the original attractor. Indeed, mutual stabilization and hierarchical ordering of cell types, observed in the present model, may be important to the discussion of robustness and irreversibility in the cell differentiation process [16]. Here, it is interesting to note that long transient dynamics on a low-dimensional manifold has recently been observed in a gene network model constructed from biological data [21].

To close the paper, we again note that inclusion of spatially local interaction in the present study is quite straightforward. In a one-dimensional lattice, one can adopt a nearest-neighbor diffusive interaction model as given by

$$\dot{x}_i(k) = \tanh\left(\beta \sum_{j=0}^{M-1} J_{ij} x_j(k) - \theta_i \right) - x_i(k)$$

$$+ d_i \left(\frac{x_i(k+1) + x_i(k-1)}{2} - x_i(k) \right). \quad (5)$$

In this case, generation of novel states by the present mechanism works. Without coupling (i.e., by taking $d_i = 0$), only a homogeneous state with a stable fixed point exists, while with coupling spatially inhomogeneous pattern appears, depending on the initial condition. "Spots" of novel states are distributed with some distance, leading to spatial configuration of differentiated elements (see Fig. 8 as an example). Note again that this pattern formation is not a result of symmetry breaking as in the Turing pattern [22].

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[15] Generation of novel states by the transient truncation mechanism can also occur even if the attractor of single-element dynamics is a limit cycle. However, we have not systematically counted the fraction of such cases, since automatic detection for such a case is not so easy.

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