RAPID COMMUNICATIONS

PHYSICAL REVIEW E **76**, 055101(R) (2007)

Network structure formation in pulsating particle populations

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(Received 8 August 2007; published 30 November 2007)

Pattern formations in populations of "pulsating particles" which can autonomously vary their volumes were investigated. It was found that clusters of pulsating particles whose pulsation frequencies depend on the number of other particles in the vicinity form the following dynamical network structures: (i) void type networks exhibiting large voids, and (ii) branching type networks consisting of individual branches. Such global structures are formed through the annihilation and creation of local structures in the particle populations induced by tug-of-war-like interactions among them.

DOI: 10.1103/PhysRevE.76.055101 PACS number(s): 82.40.Ck, 05.45.Xt, 87.18.Hf, 82.40.Bj

Dynamical systems with many interacting nonlinear elements have been studied extensively. Such coupled dynamical systems often display a rich variety of spatial-temporal patterns by the interplay between the internal dynamics of the individual elements and their interactions. Several aspects of such pattern formation in systems where the elements are coupled spatially or construct several types of random networks have been uncovered recently [1–7].

In some complex systems, like biological systems, societies, etc., not only the internal state of each element but also the coupling properties among the elements vary temporally, in general. In several types of cell populations like bacteria populations, or brains or other internal organs in the multicellular organisms [8–11], each element (cell) has some internal degrees of freedom, such as chemical concentrations, shape, etc. In these systems, the couplings among the cells naturally vary temporally due to migration or deformation.

In order to consider such complex situations, a variety of coupled oscillator systems in which oscillator-oscillator connections vary temporally have been investigated [3,12–14]. One such system proposed populations of the oscillators which can move in space [3,14–18]. General aspects of such systems have been studied through abstract models in which the internal dynamics of each element are modeled by a chaotic or limit-cycle oscillator.

Such "mobile oscillator" models can be considered as metamodels of cell populations interacting through a chemical concentration field [8,9]. In recent models, however, the effects of the excluded volume, the shape, and their temporal variations in each cell have been mostly neglected. On the other hand, it is natural that these effects should play important roles in the pattern dynamics of cell aggregations, like the morphogenesis of multicellular systems.

In this paper, we study pattern formations in populations of mobile pulsating particles which have finite volumes and which can vary their volumes autonomously. Here, a "pulsation" is considered as one of the simplest descriptions of the effect of the autonomous shape variation as a result of the change in the internal states of cells, proteins, etc. [8–10]. In the following, we show that such simple systems can form various novel patterns, for instance, void type and branching type network patterns.

We introduce a model of pulsating particles in two-dimensional space. Of course, there exist many possible types of pulsating particle populations. In this paper, we consider an example dynamical system, defined by the following assumptions, with which we can obtain various interesting pattern formations.

First, we assume that each particle has a finite volume and that there is short-range attraction and hard core repulsion between two particles. Second, we assume that the frequency of the volume oscillation (pulsation) of a particle increases as the number of other particles in the vicinity of that particle increases. This dynamic rule is inspired by the observed effects of reaction-diffusion through the gap junction of living cells [8,10,11] and oscillations induced by the plasma streaming of Physarum plasmodium [19,20].

The time evolution of the center of mass of each particle is given by

$$\dot{\mathbf{x}}_{\mathbf{i}} = -\nabla_i\left(\sum_{i<j} V(r_i + r_j - |\mathbf{x}_{\mathbf{i}} - \mathbf{x}_{\mathbf{j}}|)\right), \tag{1}$$

where $\mathbf{x}_{\mathbf{i}}$ and r_i indicate the position and the radius of the ith particle, and V indicates the two-body interaction potential, given by

$$V(y) = \theta(y)(-cy^2 + dy^4). \tag{2}$$

Here, $\theta(y)$ is a step function. Figure 1(b) plots $V(r_i+r_j-|\mathbf{x}_{\mathbf{i}}-\mathbf{x}_{\mathbf{j}}|)$ as a function of $|\mathbf{x}_{\mathbf{i}}-\mathbf{x}_{\mathbf{j}}|$.

Now, we define the pulsation phase of the ith particle W_i as that which gives r_i:

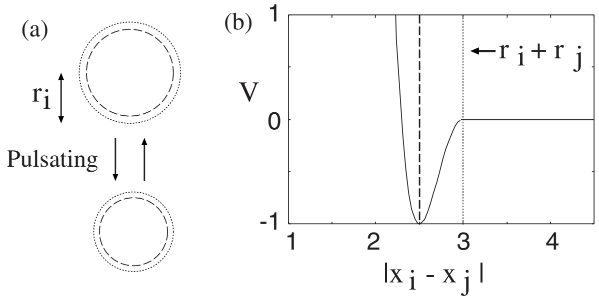

FIG. 1. (a) Illustration of pulsating particle, and (b) two-body interaction potential V as a function of $|\mathbf{x}_{\mathbf{i}}-\mathbf{x}_{\mathbf{j}}|$.

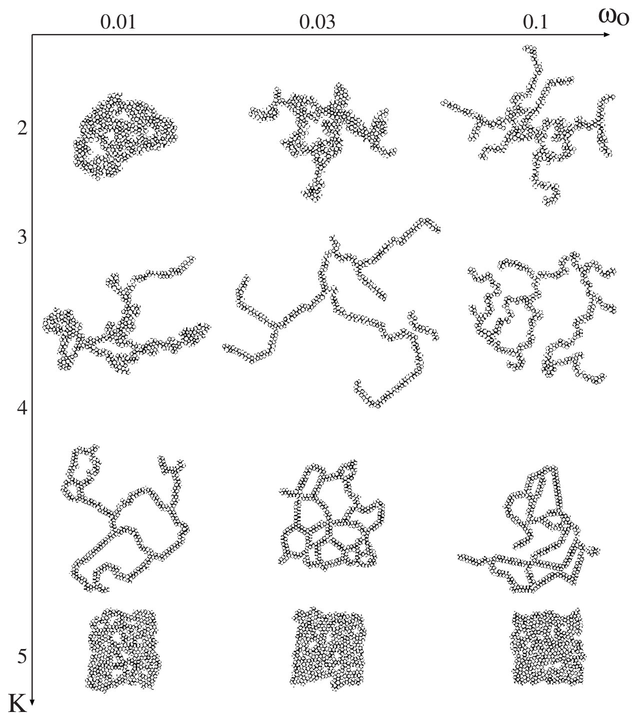

FIG. 2. Phase diagram with snapshots of the spatial structures of the system, for several values of ω_o and K.

$$r_i = r_o[1 - A\cos(2\pi W_i)]. \tag{3}$$

Here, r_o and Ar_o are the standard radius and the amplitude of the variation of the radius. We set A to be sufficiently smaller than 1. According to the second assumption, we assume the time evolution of W_i to be

$$\dot{W}_i = \omega_o\left(\sum_{i\neq j}\theta(\Delta)F(\Delta) - K\sin(2\pi W_i)\right). \tag{4}$$

Here, $\Delta = r_i + r_j - |\mathbf{x_i} - \mathbf{x_j}|$. In the following, we employ $F(\Delta)=1$ for simplicity. Qualitatively, the same results may appear if $F(\Delta)$ is an increasing function of Δ.

Now, we simulate the system using this model for several values of ω_o and K and fixed values $r_o=1.5$, $A=0.15$, $c=8$, and $d=16$. The characteristics of this model are qualitatively independent of these parameters. As the initial conditions, the centers of the particles are set to form a square and their radii are set to uniform random numbers between $r_o(1-A)$ and $r_o(1+A)$ (see Fig. 3).

Figure 2 shows a phase diagram of typical patterns as a function of ω_o and K (400 particles). The sample snapshots are shown for cases with $K=2$, 3.5, 4.5, and 5 and $\omega_o=0.01$, 0.03, and 0.1. Here, each circle represents one particle and the radius of each circle indicates that of each particle. This system exhibits the following four types of pattern formations: (i) When K is large, a small cluster of particles with some small voids appears. The shape of this cluster slightly varies from that at the initial condition (square). (ii) When K has an intermediate value, a large cluster of particles with voids larger than the particles appears. (iii) When K is small and ω_o is not so small, one or more large clusters of particles with some branches appears. (iv) When both K and ω_o are small, a small cluster exhibiting chaotic shape variation appears.

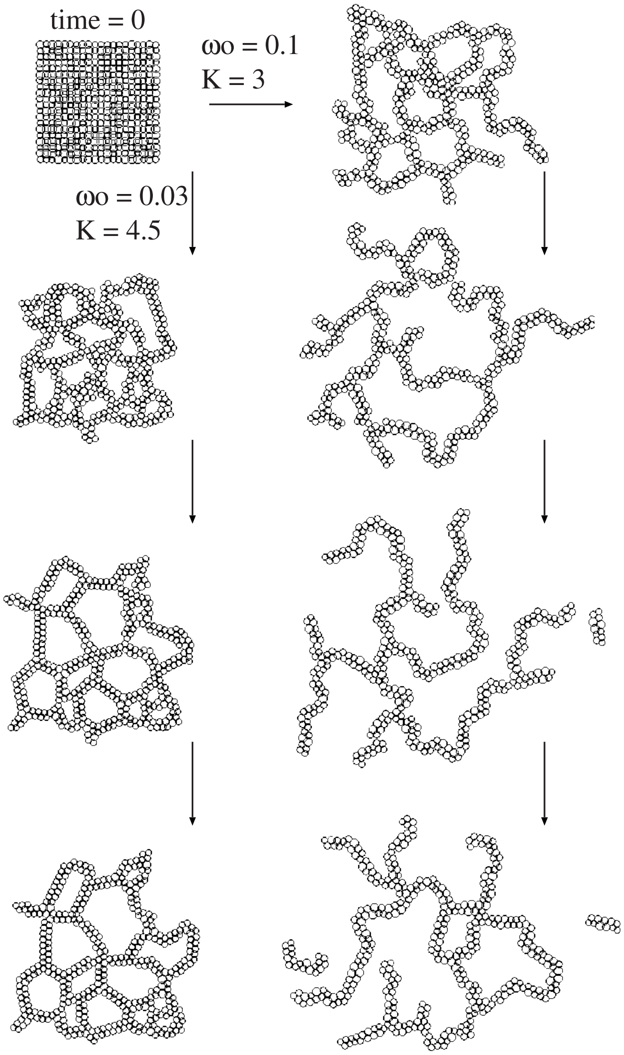

FIG. 3. Typical temporal evolutions of the void type network and the branching type network.

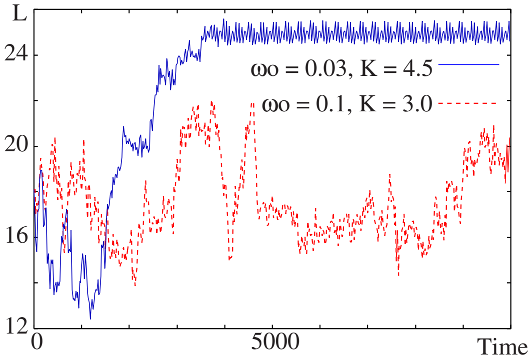

FIG. 4. (Color online) Typical temporal evolutions of L for the void type network (blue solid curve) and the branching type network (red dashed curve).

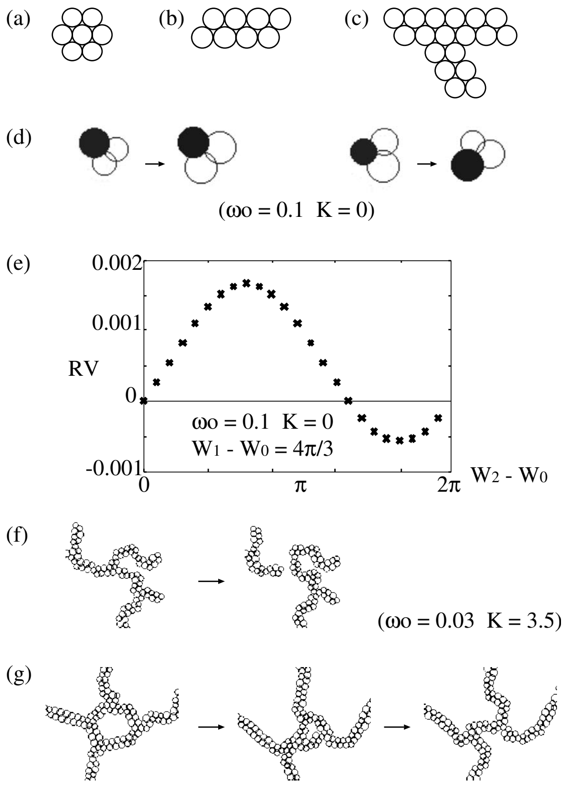

FIG. 5. (a)–(c) Illustration of typical local structures. (d) The rotational motions of a three-particle system (one of the particles is filled to show it clearly) in cases where the pulsation phases of two (white) particles are the same (left) and where those of all particles are different (right). (e) Rotational velocity (RV) as a function of the pulsation phase difference between two of the particles (positive RV indicates the clockwise rotation). (f), (g) Examples of the destruction of local structures (junctions) and void shrinking.

Thus the various types of patterns are formed by the interplay between migration and pulsation of the particles. In particular, the networklike patterns in (ii) and (iii) are often observed in many biological systems [8,9,19,20]. We name the pattern shown in (ii) a void type network and that in (iii) a branching type network, after their shapes.

Now, the dynamical aspects of the void type networks and the branching type networks are considered. Figure 3 shows typical temporal evolutions of the system for large K (ω_o=0.03 and K=4.5) and those for small K (ω_o=0.1 and K=3.0), and Fig. 4 shows typical temporal evolutions of the distance between two sample particles L for these cases. As shown in Fig. 3, the void type networks are formed at an early stage in both cases. If K is large, such void type networks are sustained, as seen in Fig. 3 (left). In such cases, the temporal evolution of L (blue solid curve in Fig. 4) eventually becomes periodic. This means that the structures are stable.

On the other hand, if K is small, the void type networks are broken and the branching type networks appear. In such cases, the temporal evolution of L is nonstationary, as shown in Fig. 4 (red dashed curve). This indicates that the shape of each branching type network is not stable but varies gradually, as shown in Fig. 3 (right).

Next, we focus on the formation processes of the void type networks and the branching type networks in order to consider the mechanisms of these pattern formations. In this model, each particle starts to pulsate when the number of other particles in its vicinity becomes larger than K, as given in Eq. (4). In the following, we mainly focus on the K dependency of the pattern dynamics.

If $K>6$, no particles can pulsate because the number of other particles in the vicinity of each particle cannot be greater than 6 in two dimensional space. On the other hand, when $4<K<6$, hexagonal structures [Fig. 5(a)] are not stationary because the particles at the interior pulsate. However, rodlike structures [Fig. 5(b)] remain stable because the number of other particles in the vicinity of each particle is 4. Then, some voids can emerge.

In such situations, some junctions of the rods [Fig. 5(c)] appear. Here, the particle at the interior of each junction pulsates. Then, these junctions pulsate and interact with each other, that is, pushing or pulling, through the rods. By such a tug-of-war-like interaction among the junctions, some of them often move along the rods or disappear, causing growth of the voids. When the pulsation phases of the surviving junctions are balanced, the structures formed, namely, the void type networks, becomes stable and sustain their periodic oscillation.

Next, we consider cases with $K<4$, where the system shows more complex motions than the cases above. In this case, not only the particles at the interior of the junctions but also the other particles constructing the junctions or the rods can pulsate. Here, it is notable that the pulsation frequencies of the particles at the interior and those at the surface of these structures are different because the number of other particles in the vicinity of each particle is different. Thus these local structures show multiple time-scale shape variations in general.

Moreover, it should also be noted that the pulsation of particles induces rotation of the local structures. This is one example of the rotation with zero angular momentum induced by the deformation of an object, which has been studied mathematically [21]. Here, the rotational velocities and the directions depend on the differences among the pulsation phases of the particles, as shown in the following simple example.

Figure 5(d) shows the rotational motions of a cluster consisting of three particles (i=0, 1, and 2) with K=0 and ω_o=0.1. Here, the pulsation frequencies are always the same because the numbers of other particles in the vicinity are the same. When the pulsation phases of these particles, W_0, W_1, and W_2, are not the same, as seen at the right in Fig. 5(d), the cluster may rotate. Figure 5(e) shows the rotational velocity of the cluster as a function of W_2-W_0 for $W_1-W_0=4\pi/3$. (Note that W_i-W_j is temporally constant because the pulsation frequencies of these particles are always the same now.) As shown in this figure, this rotation tends to be faster when the pulsation phases of the particles disperse [22].

From these facts, the local structures exhibit several time-scale shape variations and rotations when $K<4$. Such motions induce the complex tug-of-war among the local structures. Then, destruction of the rods or the junctions [Fig. 5(f)] and shrinking of the voids [Fig. 5(g)] often occurs, which causes the emergence and growth of the branches in the particle cluster. Thus for such small K, the branching type networks appear due to the destruction of transient void-type networks. Moreover, such a tug-of-war among local structures also induces collisions between them, which create new junctions. Then, the shapes of the branching-type networks vary in a nonstationary manner.

In this paper, the network structure formations of populations of mobile pulsating particles were studied. It was found that a system consisting of particles whose pulsation frequency depends on the number of other particles in the vicinity shows some different network structure formations.

The presented model can also be considered as a model of temporally evolving networks [3,12,13,15] if we regard the junctions and the rods as the nodes and the links, respectively. Unlike recent temporally evolving network models, however, this model does not assume the existence of the nodes and links explicitly. This model is a metadynamical system that can realize the creation, annihilation, and variation of mesoscale structures like nodes and links by the microscale (particles) dynamics. The mathematical analysis of such systems is an important issue for future study.

The creation and annihilation of nodes and links by the interactions among them should play an important role in networklike structure formation of cytoskeletons, tube morphogenesis in Physarum plasmodium, etc. The presented model should also provide some hints for the mechanical aspects of the morphogenesis [8,9,19,20] of multicellular systems. Of course, this model is too simple for the detailed study of such real systems. More complex models in which the states of the mobile elements are regulated by complex inner chemical reactions and complex interactions like chemotaxis, Notch-Delta-like interactions, etc. should be investigated in the future.

The author thanks D. Tanaka and T. Shibata for useful discussions. This research was supported in part by a Grant-in-Aid for Young Scientists (B) (Grant No. 19740260).

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