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Basis of self-organized proportion regulation resulting from local contacts

Mayuko Iwamoto[a,c,*], Daishin Ueyama[b,c]

[a] Department of Mathematics and Computer Science, Interdisciplinary Graduate School of Science and Engineering, Shimane University, 1060 Nishikawatsu Matsue-city, Shimane 690–8504, Japan
[b] Department of Mathematical Engineering, Faculty of Engineering, Musashino University, 3-3-3 Ariake Kohtoh-ku, Tokyo 135–8181, Japan
[c] Meiji Institute for Advanced Study of Mathematical Sciences (MIMS), 4-21-1 Nakano, Nakano-ku, Tokyo 164–8525, Japan

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ABSTRACT

One of the fundamental problems in biology concerns the method by which a cluster of organisms can regulate the proportion of individuals that perform various roles or modes as if each individual is aware of the overall situation without a leader. In various species, a specific ratio exists at multiple levels, from the process of cell differentiation in multicellular organisms to the situation of social dilemma in a group of human beings. This study determines a common basis for regulating collective behavior that is realized by a series of local contacts between individuals. In this theory, the most essential behavior of individuals is to change their internal mode by sharing information when in contact with others. Our numerical simulations regulate the proportion of population in two kinds of modes. Furthermore, using theoretical analysis and numerical calculations, we show that asymmetric properties in local contacts are essential for adaptive regulation in response to global information such as group size and overall density. Particle systems are crucial in allowing flexible regulation in no-leader groups, and the critical condition that eliminates overlap with other individuals (the excluded volume effect) also affects the resulting proportion at high densities. The foremost advantage of this strategy is that no global information is required for each individual, and minimal mode switching can regulate the overall proportion. This simple mechanism indicates that proportion regulation in well-organized groups in nature can be realized through and limited to local contacts, and has the potential to explain various phenomena in which microscopic individual behavior results in orderly macroscopic behavior.

1. Introduction

An old Roman proverb exhorts us to “Learn wisdom by the follies of others.” The same may be equally true of other social animals. One of the fundamental problems in nature is the regulation of the proportion of individuals who perform multiple roles or modes within a cluster of organisms. In general, social organizations contain hierarchies that are generally managed through a direct chain of command with a clearly identified superior. Collective organisms found in nature, however, can self-regulate their proportions for multiple roles without the need for a central control. Examples include the proportion of prestalk and prespore cells in the slug of the cellular slime mold (Bonner, 1957; Bonner and Slifkin, 1949; Nanjundiah and Bhogle, 1995; Oohata, 1995; Ráfols et al., 2000; Raper, 1940; Stenhouse and Williams, 1977), “active” and “inactive” workers (Hayashi et al., 2015; Ishii and Hasgawa, 2013; Prigogine, 1984) and task allocation (Gordon, 1987; Gordon, 1989; Gordon, 1996; Wilson, 1971) in ant colonies, “aggressive” and “docile” female spiders (Pruitt and Goodnight, 2014), and the producer–scrounger foraging strategy found in bird crowds (Giraldeau et al., 1994).

As reported in experimental research on the proportion of certain species (Bonner and Slifkin, 1949; Gordon, 1987; Gordon, 1989; Gordon, 1996; Nanjundiah and Bhogle, 1995; Oohata, 1995; Pruitt and Goodnight, 2014; Ráfols et al., 2000; Stenhouse and Williams, 1977), these regulating systems may act as a response to global and temporal properties, e.g., group size and density, which can be changed by external disturbances. This is sometimes referred to as “collective intelligence,” as the proportion can adapt as if the total number of individuals were known. Self-organizing proportion regulation in collective behavior can be universal at multiple levels, such as cellular and individual levels. This would indi-

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[*] Corresponding author at: Shimane University, Department of Mathematics and Computer Science, Interdisciplinary Graduate School of Science and Engineering, 1060 Nishikawatsu Matsue-city, Shimane 6908504 Japan.
E-mail address: miwamoto@riko.shimane-u.ac.jp (M. Iwamoto).

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cate that the coexistence of multiple modes in suitable proportions is deeply involved in evolution and natural selection.

In addition, the temporal dynamics of internal modes appear in diverse species (Nakamura et al., 2007; Shimada et al., 1995; Sims et al., 2008; Viswanathan et al., 1996), and it has been reported that each cell or individual in some species can change its mode after physically close contact with others through specific substances (Gordon, 2011; Hayashi et al., 2015; Hojo et al., 2015; Inoue, 1989; Kay and Jermyn, 1989). From observations of the transdifferentiation between two cell types of cellular slime molds (Brown and Firtel, 1999) and the suggestion that contact between two ants changes their tasks (Gordon, 2011), proportion regulation models have been developed that maintain the idea of local interaction between individuals (Gordon et al., 1992; Goto and Kaneko, 2013; Nanjundiah and Bhogle, 1995). However, as these models implicitly include a global property, it remains a mystery how each individual can know the overall status.

While there may be differences in the detailed contact and mode switching mechanisms, we consider there to be a common mechanism throughout the regulation systems of various living creatures. On this basis, we recognize that it is important to determine whether the system must know the global properties of the proportion in response to the overall situation. Even today, however, the mechanism underlying proportion regulation from purely local contacts has not been fully elucidated.

Our view of this regulating mechanism in nature is the creature-like behavior whereby the mode of operation can be changed to produce other behavior that expanded the kinetic theory of molecules in chemical reactions. This study investigates a simple but plausible mechanism for the self-organized proportion regulation between two modes. In this mechanism, the overall result comes from a series of local contacts between individuals exhibiting distinct behavior. The most important question is whether global information is required for a global response.

We have found that a discrete system is necessary to understand the proportion regulation mechanisms, although a part of the issue can be explained by a continuous model. Using observation data from cellular slime mold as an example, simulation results with our cellular automata model show that the system can exhibit global responses without any global information. Finally, we discuss an idea for the regulation mechanism across multiple tasks, which could be applied to the control of a swarm of self-driven robots and autonomous cars.

2. Methods

To investigate the mechanism of self-organizing proportion regulation, we use the following three assumptions: 1) there is no leader in a group; 2) the total number of individuals is conserved; and 3) each individual has its own mode (e.g., prestalk or prespore cells in cellular slime mold), and can freely switch to another mode. In addition, based on previous research (Brown and Firtel, 1999; Gordon, 2011; Hayashi et al., 2015; Hojo et al., 2015; Inoue, 1989; Kay and Jermyn, 1989), we consider that each individual is able to elicit mode information about other individuals through contact, and that individuals cannot acquire global information, such as the group size or density.

2.1. Concept for regulation mechanism

Under the above assumptions, we consider a bounded swarm of individuals whose total number is constant, as shown in Fig. 1a, where each individual is denoted by a circle. Each individual can assume either of two internal modes, mode A or mode B. We assume that individuals can switch modes based on their contact with others in the neighborhood. In any contact between two individuals, there are three possible combinations of modes, i.e., A-A, A-B (or B-A), and B-B. After gaining mode information through contact with others, an individual changes its mode based on some probability or threshold. This study uses probability-based investigations, but threshold-based mode switching works on a similar principle.

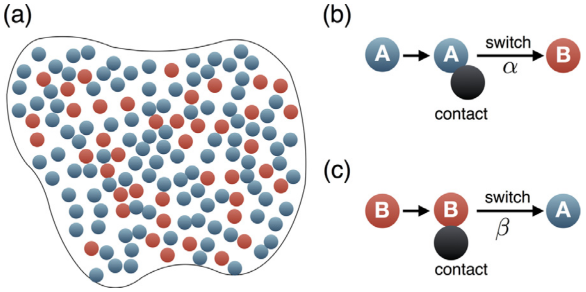

Fig. 1. Conceptual schemes of model. (a) A swarm of individuals within a boundary. Mode switching from (b) mode A to mode B and (c) mode B to mode A occurs stochastically after appropriate contact with other individuals. Variables α and β are the mode switching probabilities.

Whether mode switching occurs is dependent on the modes of the other individuals who are physically contacted. As an example, we consider the following four conditions for physical contact and the acquisition of information about other individuals' modes, as shown in Fig. 1b and c.

1. If an individual in mode A contacts another individual in mode A, no mode switching will occur.
2. If an individual in mode A contacts an individual in mode B, the first individual will switch to mode B with probability α (Fig. 1b).
3. If an individual in mode B contacts another individual in mode B, the first individual will switch to mode A with probability β (Fig. 1c).
4. If an individual in mode B contacts an individual in mode A, no mode switching will occur.

The mode switching probabilities α and β remain constant, and would be determined at the gene level in actual phenomena. The important concept is the creature-likeness of individual behavior. For instance, the above rules seem to describe "synchrony," "imitation," "repulsion," and "insensitivity," respectively. These actions are widely observed in living creatures such as human beings. Therefore, this study shows that these traits are essential for order formation through communication in social animals. Note that this study does not discuss the detailed method of contact that would lead to mode switching.

2.2. Monte Carlo algorithm for cellular automata model simulations

The concept of the mechanism for proportion regulation, which was suggested in this paper, is an expansion of chemical reaction systems into a biological sense. Namely, although the concept cannot be achieved by any chemical reactions, it would be not difficult for animals. We believe that such a little bit difference makes creatures creature-likeness. Particle systems, e.g., probabilistic lattice gas cellular automata (LGCA) is one of the most useful method for realizing and understanding chemical reaction systems from a microscopic perspective (Deutsch and Dormann, 2005; Kier et al., 2005; Lawniczak et al., 1991). LGCA simulations indicate a constant value as an equilibrium constant of reversible reaction (Lawniczak et al., 1991) and pattern formations that can be generated by autocatalytic reaction (Deutsch and Dormann, 2005).