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Modeling local interactions during the motion of cyanobacteria

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HIGHLIGHTS

- Phototactic cyanobacteria have quasi-random motion, not uniform motion toward light.
- Experimental data is analyzed to illustrate this unexplained motion.
- We propose two local interaction models accounting for quasi-random motion.
- Simulations suggest interaction distance between cells affects motion and patterns.

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ABSTRACT

Synechocystis sp., a common unicellular freshwater cyanobacterium, has been used as a model organism to study phototaxis, an ability to move in the direction of a light source. This microorganism displays a number of additional characteristics such as delayed motion, surface dependence, and a quasi-random motion, where cells move in a seemingly disordered fashion instead of in the direction of the light source, a global force on the system. These unexplained motions are thought to be modulated by local interactions between cells such as intercellular communication. In this paper, we consider only local interactions of these phototactic cells in order to mathematically model this quasi-random motion. We analyze an experimental data set to illustrate the presence of quasi-random motion and then derive a stochastic dynamic particle system modeling interacting phototactic cells. The simulations of our model are consistent with experimentally observed phototactic motion.

1. Introduction

Unicellular microorganisms have evolved to live in variable and extreme environments. Some are capable of intercellular signaling and appear to utilize group dynamics to achieve desired actions, such as moving toward a food source (Kaiser, 2008) or towards light (Bhaya, 2004). These group dynamics often result in emergent patterns which can be modeled and analyzed using mathematics. *Synechocystis* sp. Strain PCC6803 (hereafter *Synechocystis* sp.) is a well-studied unicellular freshwater cyanobacterium that displays the ability to move toward light, a phenomenon referred to as phototaxis, forming finger-like projections in the direction of a light source. *Synechocystis* sp. is a model organism for studying phototaxis in a laboratory setting and extensive genetic and microscopic analyses have been carried out to characterize the molecular bases for motility (Bhaya et al., 1999, 2000, 2001a). It has been demonstrated that this surface dependent motility requires Type IV pili, photoreceptors (Bhaya et al., 2001b; Ikeuchi and Ishizuka, 2008) and a number of other proteins necessary for phototaxis (Bhaya et al., 2001a). When wild type *Synechocystis* sp. is exposed to light, cells begin to move, although not necessarily in the direction of light. They instead form small aggregations of cells and eventually, with a time delay, cells may move toward light. At the front of a spot of plated cells, cells align along the boundary of the spot before forming the characteristic finger-like projections or swarms of cells (Burriesci and Bhaya, 2008). Yet the motion of individual cells is not as directed toward the light source as is the observed group behavior. Individual cells instead display a quasi-random motion, that is, they move in seemingly random directions. In this paper, we mathematically model the local interactions of *Synechocystis* sp. and observed quasi-random motion in order to address a series of questions:

1. If motile cells are not moving exclusively toward the light, are they moving in random directions or do they move following other non-random rules of motion?
2. Is there a characteristic distance, beyond which cells can no longer sense the presence and behavior of neighbors?
3. If such a distance exists, how do the patterns of motion vary with respect to this distance?

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An extensive amount of mathematical research has been conducted in related fields. Specifically, we would like to mention some works on animal flocking and on chemotaxis. The Couzin–Vicsek model of flocking (and its many extensions) allows animals or individual agents to be repelled by near neighbors, align with the average directional heading of not-so-near neighbors, and be attracted to far neighbors (Couzin et al., 2002; Vicsek et al., 1995). This model has lent itself to many applications as well as thorough mathematical analysis, for example, see Degond and Motsch (2008). Cucker and Smale offer a dynamical system which models the flocking of opinions in human networks (Cuker and Smale, 2007a,b); this model has also been subjected to significant analysis, for example, see Ha and Tadmor (2008) and Ha et al. (2009). Similar models of flocks and schools have been developed for a variety of self-propelling agents such as birds and fish, e.g. Aoki (1982), Huth and Wissel (1992), Li et al. (2008), Lukeman et al. (2010), and Parrish et al. (2002).

Chemotaxis, i.e., motion towards a chemical attractant, is also a field that has been extensively studied in recent decades, starting from the celebrated work of Patlak, Keller and Segel (Keller and Segel, 1971; Patlak, 1953). For completeness, we refer the interested reader to the following papers and to the references therein (Alber et al., 2002; Hillen and Painter, 2009; Horstmann, 2003; Othmer and Hillen, 2002; Tindall et al., 2008). Before migrating toward the light source, *Synechocystis* sp. form small aggregations whose location is unrelated to a spatial concentration of a chemoattractant as is the case with chemotactic motion. Consequently, most of the mathematical modeling and analysis on the topic is irrelevant in the present context.

Furthermore, phototaxis has not been extensively subjected to mathematical modeling. Only a few models of phototaxis have been developed, for example, see Burkhart and Hader (1980) and Maree et al. (1999); however, these models do not consider the intercellular group dynamics. A recent agent-based model of phototaxis considers cell interactions by transmission of light by individual cells (Fatehi et al., 2010). In a series of papers we have developed several families of mathematical models for describing phototaxis (Bhaya et al., 2008; Burriesci and Bhaya, 2008; Levy and Requeijo, 2008a,b; Levy and Ha, 2009). In all these models, the primary focus was on the phase of the initiation of the motion towards a light source (including the associated time delay) and the resulting overall migration of the colony of cells towards the light source (including the modeling of the finger formation). The emphasis of these analyses was on the role of the group dynamics, as opposed to what can be associated with the behavior of the individual cell. Missing from these analyses was the description of what happens in regions of low to medium cell density. The purpose of this paper is to develop, present, and study mathematical models for such regions.

Our mathematical models follow the time-discrete dynamics of a finite set of particles that are interacting in a two-dimensional domain according to rules that involve certain random terms. The rules for the local interactions between particles are based on our experimental observations given by the analysis of time-lapse movies of the bacteria under a plethora of controlled conditions.

The structure of the paper is as follows. In Section 2 we present the biological background, describe the experimental setup, demonstrate some of the experimental results, and formulate a

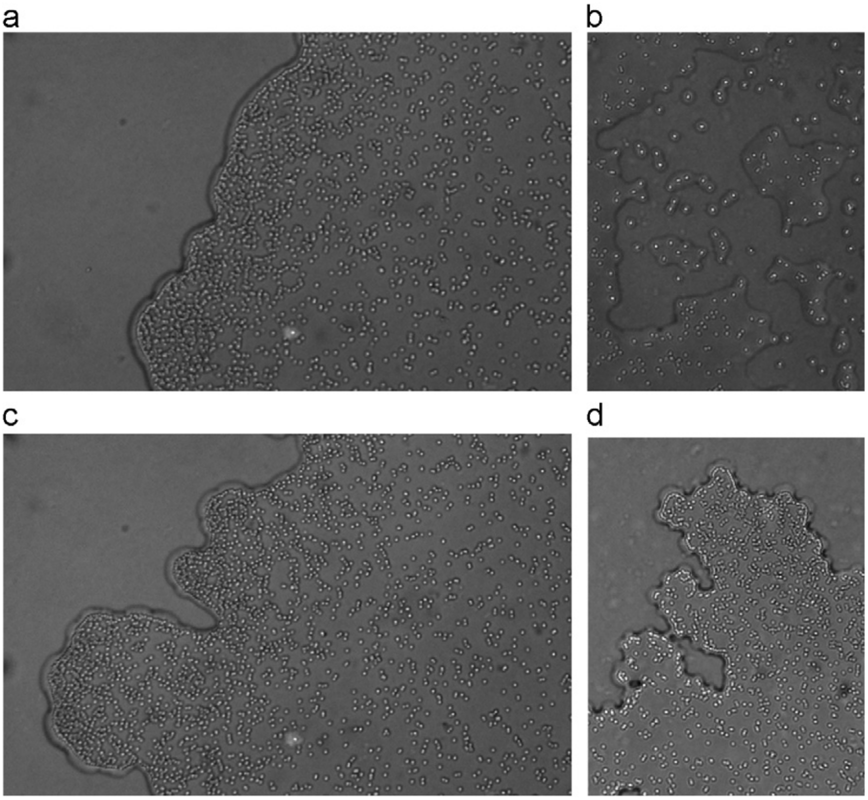

Fig. 1. Experimental results illustrating (a) beginnings of finger-like projection formation, (b) surface dependence, and (c/d) aggregation and finger formation. The bacteria within a matrix of extracellular polysaccharides appear as white dots or circles. The bacteria are approximately 1 μm in diameter. Each image contains wild type cells exposed to a light source radiating from the upper left corner of each image. (a) Shows the front of a spot of cells 48 h after plating. (c) Shows the exact same spot frame as (a), 24 h later. (b) and (d) Depict different sections of the same spot at different times. In (b), the density of cells is very low and surface dependence is observable—the cells are surrounded by polysaccharides formed by the cells in the liquid cultures, a process that continues after the cells are placed on the agarose plate. The formation of this “slime” facilitates motility and is necessary for the cells to move onto the non-pre-wetted surface. In (c) (as well as in (a) and (d)), the cells are observed to form small aggregations as a precursor to the finger of cells pushing the boundaries of wetted surface toward the direction of light.