Model and analysis of chemotactic bacterial patterns in a liquid medium

Rebecca Tyson¹, S. R. Lubkin², J. D. Murray³

¹Department of Applied Mathematics, Box 352420, University of Washington, Seattle, WA 98195-2420, USA (rebecca@amath.washington.edu)
²Biomathematics Program, Box 8203, North Carolina State University, Raleigh, NC 27695-8203, USA (lubkin@eos.ncsu.edu)
³Department of Applied Mathematics, Box 352420, University of Washington, Seattle, WA 98195-2420, USA (murrayjd@amath.washington.edu).

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Abstract. A variety of spatial patterns are formed chemotactically by the bacteria *Escherichia coli* and *Salmonella typhimurium*. We focus in this paper on patterns formed by *E. coli* and *S. typhimurium* in liquid medium experiments. The dynamics of the bacteria, nutrient and chemoattractant are modeled mathematically and give rise to a nonlinear partial differential equation system.

We present a simple and intuitively revealing analysis of the patterns generated by our model. Patterns arise from disturbances to a spatially uniform solution state. A linear analysis gives rise to a second order ordinary differential equation for the amplitude of each mode present in the initial disturbance. An exact solution to this equation can be obtained, but a more intuitive understanding of the solutions can be obtained by considering the rate of growth of individual modes over small time intervals.

Key words: Chemotaxis – Partial differential equations – Bacteria – Mathematical Modeling – Pattern formation

Introduction

In this paper we present a simple and intuitively revealing mathematical analysis of transient solutions to a chemotaxis model involving partial differential equations. Our model equations are motivated by experiments performed by Budrene and Berg [3], in which they
observed patterns formed by *Escherichia coli* and *Salmonella typhimurium*. When placed in a liquid medium and exposed to intermediates of the tricarboxylic acid (TCA) cycle, the bacteria arrange themselves into high density aggregates. The patterns appear, rearrange and eventually fade on a time scale which is short compared with the generation time of the bacteria.

The simplest patterns are produced when the liquid medium contains a uniform distribution of bacteria and TCA cycle intermediate. Of the latter, succinate and fumarate produced the strongest effect. Only a small amount is necessary, as the bacteria are merely exposed to the TCA cycle intermediate as a stimulant, and do not rely on it as a carbon source. The initially uniform distribution of bacteria begins to form a stranded pattern of higher-density regions. Subsequently, the pattern resolves into discrete clumps of roughly uniform size over the entire surface of the liquid, though the pattern often starts in one general area and spreads from there. Over time the aggregates coalesce, thus becoming larger and decreasing in number. Ultimately the pattern dissipates and cannot be induced to re-form.

Fluid dynamic convection cells are not believed to be responsible for these patterns (H. C. Berg, personal communication); we hypothesize instead a primarily chemotactic mechanism. It is known that the bacteria secrete aspartate, a potent chemoattractant, in response to the stimulant. A chemoattractant is a chemical which the cells seek, in the sense that they move up gradients of that chemical. This process tends to increase the local cell density, while diffusion tends to do the opposite. The competition between the two processes is the driving force behind the patterns observed. Thus the main players in the experiments are the cells, the stimulant (succinate or fumarate) and the chemoattractant (aspartate).

The disappearance of the pattern is thought to be due to saturation of the chemotactic response. Since cellular production of chemoattractant is not countered by any form of chemoattractant degradation (or inhibition), the amount of chemoattractant in the dish increases continuously. As a result, the chemotactic response eventually saturates, and diffusion dominates.

We represent the experiments mathematically as a reaction-diffusion chemotaxis model. The numerical and analytic solutions of the equations verify our interpretation of the experimental results.

### 1 The model: a perturbation approach

Careful study of these experiments [3] has revealed that the biological processes most crucial in the formation of these bacterial patterns are