

**On the Propagation Theory for Bands of Chemotactic Bacteria\***

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ABSTRACT

By exhibiting exact analytical expressions for the planar wave solutions to the governing equations, it is shown that the theory for the propagation of bands of chemotactic bacteria requires an effective  $m$ th order process for the degradation of the critical substrate chemotactic agent, with  $m$  less than unity but greater than a certain function of the diffusional transport coefficients.

1. INTRODUCTION

The propagation of bands of chemotactic bacteria [1,2] has been associated with the diffusional transport and rate equations [3]

$$\frac{\partial b}{\partial t} = \mu \nabla^2 b - \delta \nabla \cdot (b \nabla \ln S), \tag{1}$$

$$\frac{\partial S}{\partial t} = -kb, \tag{2}$$

where  $b$  denotes the density of bacteria cells,  $S$  denotes the concentration of the critical substrate chemotactic agent, and  $\mu$ ,  $\delta$ , and  $k$  are positive constant parameters. For  $\delta > \mu$  Eqs. (1) and (2) yield the solitary wave solution<sup>1</sup> that

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<sup>1</sup>The existence of solitary wave solutions to nonlinear partial differential equations was first studied systematically in [5].

describes the propagation of a planar band of bacteria [3],

$$b = [c^2 S_\infty / k(\delta - \mu)] e^{-\xi} (1 + e^{-\xi})^{-\delta/(\delta - \mu)}, \quad (3a)$$

$$S = S_\infty (1 + e^{-\xi})^{-\mu/(\delta - \mu)}, \quad (3b)$$

in which the independent variable is the dimensionless quantity

$$\xi \equiv c\mu^{-1}(x - ct) + (\text{a disposable constant}),$$

the positive constant parameter  $S_\infty$  in (3a) and (3b) is the prescribed critical substrate concentration at  $x = +\infty$ , and the constant velocity of the band propagation is given by

$$c = kS_\infty^{-1} \int_{-\infty}^{\infty} b dx.$$

An alternative to the rate equation (2),

$$\frac{\partial S}{\partial t} = -kbS, \quad (2')$$

has been proposed more recently [4], and indeed it is logical that a positive power of  $S$  should appear in the equation for  $\partial S/\partial t$ ; the rate equation (2) has the obvious shortcoming of admitting a finite negative value for  $\partial S/\partial t$  in the limit  $S \rightarrow 0$  if  $b$  remains finite, and hence (2) may be inapplicable in the region of the band where  $S \ll S_\infty$ . However, this theoretical shortcoming is not rectified by the rate equation (2'), because the latter equation does not engender a solitary wave solution for the propagation of a planar band of bacteria, as shown below. On the other hand, if (2) is replaced by the rate equation for an effective  $m^{\text{th}}$ -order process,

$$\frac{\partial S}{\partial t} = -kbS^m \quad [m \geq 0], \quad (2'')$$

then solitary wave solutions homologous to the solution (3) follow for  $[1 - (\delta/\mu)] < m < 1$ , as shown in Section 3 below. Hence, a rate equation of the form (2'') with  $[1 - (\delta/\mu)] < m < 1$  is admissible theoretically for the propagation of bands of chemotactic bacteria.

## 2. SOLUTION FOR PLANAR BACTERIAL PROPAGATION WITH A FIRST-ORDER RATE EQUATION

Supplemented with (2'), eq. (1) yields the planar wave solution

$$b = b_{-\infty}(1 + e^{\xi})^{-1}, \quad (4a)$$

$$S = S_{\infty}(1 + e^{-\xi})^{-\mu/\delta}, \quad (4b)$$

where the positive constant parameter  $b_{-\infty}$  denotes the density of bacteria cells at  $x = -\infty$ , and the constant velocity of the wave front propagation is given by

$$c = (k\delta b_{-\infty})^{1/2}.$$

Similar in form to the distribution function for the temperature in a one-dimensional laminar flame [6], or for the density of a biological species in a one-dimensional population growth process [7], the solution (4) does not depict the propagation of a finite band of bacteria. Chemotactic bacteria propagation of a type described by (4) has not been observed and reported to date, and thus the first-order rate equation (2') is precluded in a theory for the recent experimental findings [1,2].

## 3. SOLUTIONS FOR PLANAR BACTERIAL PROPAGATION WITH AN $m$ th-ORDER RATE EQUATION

Supplemented with (2''), eq. (1) yields the solitary wave solutions

$$b = (c^2 S_{\infty}^{1-m} / k\gamma) e^{-\xi} (1 + e^{-\xi})^{-\delta/\gamma}, \quad (5a)$$

$$S = S_{\infty} (1 + e^{-\xi})^{-\mu/\gamma}, \quad (5b)$$

provided that the quantity  $\gamma \equiv \delta - (1-m)\mu$  is in the range  $0 < \gamma < \delta$ , or equivalently, if

$$[1 - (\delta/\mu)] < m < 1. \quad (6)$$

The constant velocity of the band propagation is obtained by integrating (5a)<sup>2</sup>,

$$c = (1 - m)k S_{\infty}^{m-1} \int_{-\infty}^{\infty} b dx.$$

That the solutions (5) are homologous to the solution (3) for  $m$  in the range prescribed by (6) is a consequence of the fact that Eqs. (1), (2) are mapped into Eqs. (1), (2'') by letting  $S \rightarrow (1 - m)^{-1} S^{1-m}$  and  $\delta \rightarrow (1 - m)^{-1} \delta$ . If  $\delta > \mu$ , then (6) admits the  $m = 0$  solution (3) as a special case in (5).

#### 4. BIOLOGICAL IMPLICATION

The mathematical analysis presented above shows that a rate equation of the form (2'') with  $[1 - (\delta/\mu)] < m < 1$  is required for the propagation of bands of chemotactic bacteria. An effective  $m^{\text{th}}$ -order process with  $m < 1$  for the degradation of the critical substrate chemotactic agent may be associated with many physio-chemical and biological mechanisms, for example, an adsorption coefficient (for molecules of the chemotactic agent at the surface of a bacterium cell membrane [8,9]) which depends inversely on a fractional power of  $S$ . It is clear that a suitable new experiment is needed to reveal the physio-chemical or biological mechanism that makes  $m < 1$  and thus engenders the propagation of bands of bacteria for certain chemotactic agents.

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<sup>2</sup>Using the estimated experimental values for *E. coli* attracted by oxygen [Ref. 3, pp. 242-243]  $c = 0.9$  cm/hr,  $kS_{\infty}^m = 5 \times 10^{-12}$  mmol/cell-hr,  $S_{\infty} = 2 \times 10^{-4}$  mmol/cm<sup>3</sup>,  $\int_{-\infty}^{\infty} b dx = 1.5 \times 10^5$  cells/ $2.5 \times 10^{-3}$  cm<sup>2</sup> =  $6 \times 10^7$  cells/cm<sup>2</sup>, this formula yields  $m = 0.4$ , a value for the exponent in the rate equation (2'') consistent with (6) for  $\delta > (0.6)\mu$ . On the other hand, the estimated experimental values of the quantities in the formula for *E. coli* attracted by serine [Ref. 3, p. 243] appear to require an inadmissible negative value for  $m$ , a discrepancy that may stem from a low estimate for the value of  $\int_{-\infty}^{\infty} b dx$ . More accurate experimental measurements are required to check the validity of this formula.

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