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Traveling Bands of Chemotactic Bacteria: A Theoretical Analysis

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Bands of motile *Escherichia coli* have been observed to travel at constant speed when the bacteria are placed in one end of a capillary tube containing oxygen and an energy source. Such bands are a consequence of a chemotatic mechanism which permits the bacteria to seek an optimal environment: the bacteria avoid low concentrations and move preferentially toward higher concentrations of some critical substrate. In this paper we develop a phenomenological theory of traveling bands starting with partial differential equations which describe the consumption of the critical substrate and the change in bacterial density due to random motion and to chemotaxis. The analysis shows that a band will form only if chemotaxis is sufficiently strong. The predicted band speed is shown to be in satisfactory agreement with observation. The analysis also predicts the shapes of the graphs of bacterial density and substrate concentration in the traveling band and shows how, from these shapes, one can determine a quantitative measure of the relative strength of chemotaxis.

1. Introduction

For almost a century, biologists have known that certain species of bacteria can move preferentially toward higher concentrations of oxygen, minerals and organic nutrients (see Weibull, 1960, for a review). A dramatic illustration of this phenomenon, generally referred to as chemotaxis, is the appearance of sharp migrating bands of motile bacteria, first observed by Beyerinck

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(1893) and more recently studied by J. Adler and his associates (Adler, 1966*a*,*b*, 1970; Adler & Dahl, 1967; Adler & Templeton, 1967).

In Adler's experiments, motile cells of *Escherichia coli* were placed at one end of a closed capillary tube filled with a medium capable of supporting motility (although not necessarily growth). The medium contained varying amounts of oxygen and an energy source, typically galactose, glucose or serine. Shortly after the introduction of the bacteria, a sharp band of cells, easily visible to the naked eye, was seen moving away from the end at constant speed. Under certain conditions, a second band was seen following the first. Some cells always remained at the end of the tube. If the amount of oxygen present was insufficient to oxidize all of the energy source, the first band totally (i.e. $> 99\%$) depleted the oxygen. Under those circumstances, a second band appeared only when the energy source was such that it could be used anerobically by the cells. This energy source was then exhausted by the second band. The bacteria in the first band create a steep gradient in the concentration of oxygen (and a lesser gradient in the concentration of energy source), and evidently move toward higher concentrations of one or both. The bacteria in the second band create a gradient in the concentration of the energy source alone, again moving preferentially in the direction of higher concentrations.

The purpose of this paper is to formulate a phenomenological model from which the existence and properties of migrating bands can be deduced. These properties can then be compared with the quantitative measurements of Adler and his associates. For simplicity we consider the motion of bacteria responding chemotactically to a single substrate, which we call the *critical substrate*. Since the same phenomena are observed in the absence of growth, we assume conditions in which no growth take place. The effects included in our description, then, are the chemotactic response of the bacteria, the non-chemotactic or "diffusive" motion of the bacteria, and the bacterial consumption of the substrate. Diffusion of the substrate is an effect which appears formally in our equations, but because it is a small effect compared to the "diffusive" random motion of the bacteria, it is ultimately ignored.

2. Formulation

We assume that the concentration $s(x, t)$ of the critical substrate is governed by the equation

$$\partial s/\partial t = -k(s)b + D[\partial^2 s/\partial x^2] \tag{1}$$

where $k(s)$ is the rate of consumption of the substrate per cell, $b(x, t)$ is the density of bacteria, D is the diffusion constant of the substrate, x is the distance along the tube, and t is the time. We assume that the concentration of substrate

is always sufficiently high so that its rate of depletion is limited by the ability of the bacteria to consume it, and not by the availability of substrate. This seems to be in accord with the kinetics of substrate consumption shown in Fig. 7 of Adler (1966*a*). The rate k will therefore be taken to be constant.

The concentration of bacteria will be described by the equation

$$\frac{\partial b}{\partial t} = \frac{\partial}{\partial x}\left[\mu(s)\frac{\partial b}{\partial x}\right] - \frac{\partial}{\partial x}\left[b\chi(s)\frac{\partial s}{\partial x}\right]. \tag{2}$$

The first term on the right represents the motion of the bacteria in the absence of chemotaxis. The meaning of this term will perhaps be clearer if it is recognized that in the absence of a chemical gradient ($\partial s/\partial x = 0$), equation (2) becomes identical to the diffusion equation. Just as the seemingly random motion of molecules in a fluid results in a particle flux proportional to the density gradient, so too the seemingly random motion of bacteria unaffected by chemotaxis is hypothesized to result in a bacterial flux proportional to the gradient in bacterial density. The motility parameter, μ, takes the place of the diffusion coefficient as the proportionality factor. To allow for the possibility that μ varies with substrate concentration, we represent μ as a function of s. Although in principle μ could also vary with bacterial concentration, we expect that this will be a secondary effect that can safely be ignored.

Adler & Dahl (1967) have shown that under conditions in which the chemotactic response appears to be absent, the random motion of *E. coli* is similar to diffusion, and can roughly be characterized by a "motility" parameter such as that introduced in equation (2). The effect of substrate concentration on motility is not known at present. In the interests of simplicity, and in the absence of information to the contrary, we therefore take μ to be constant.† The values of μ obtained by Adler & Dahl are large compared to the diffusion constants of typical substrates. We therefore assume in looking for solutions to equations (1) and (2) that, to first approximation, D can be set equal to zero. (This approximation is discussed further in section 3.)

The second term on the right side of equation (2) describes the chemotactic response of the bacteria. Here it is assumed that that part of the bacterial flux which is a result of chemotaxis is proportional to the chemical gradient, by analogy with such physical laws as Fourier's law of cooling. Using the same reasoning as that which underlies the postulation of these physical laws, it can be shown that a gradient-proportional response is inevitable for sufficiently weak gradients (threshold effects aside). Since (neglecting

† As discussed elsewhere (Keller & Segel, 1971) the implications of this assumption may be of vital importance in the analysis of chemotactic effects. Measurement of the dependence of motility on substrate concentration would therefore be highly desirable for further theoretical considerations.

interference effects) the flux would necessarily be proportional to the density of bacteria, we write the flux due to chemotaxis as $b\chi(s)[\partial s/\partial x]$ where $\chi(s)$ is a measure of the strength of chemotaxis, and is hence termed the *chemotactic coefficient*.

For further discussion of equation (2) the reader is referred to Keller & Segel (1970) where this equation is used in a macroscopic analysis of the onset of aggregation in cellular slime mold. Another paper by Keller & Segel (1971) shows how various individual cell behaviors will result in a collective behavior which is described by equation (2).

The dependence of the chemotactic coefficient, χ, on substrate density, s, is of considerable importance in this analysis. It can be demonstrated (see Appendix) that under the assumptions made thus far, $\chi(s)$ must be sufficiently singular for equations (1) and (2) to yield traveling bands as a solution. In particular, if we denote the minimum value of s at which chemotaxis can take place by s_T, and if, for small values of $(s-s_T)$, we represent $\chi(s)$ by $\chi(s) \approx \delta(s-s_T)^a$, then traveling wave solutions exist only if $a \leq -1$. On the basis of this result we assume tentatively that the chemotactic coefficient is of the "least singular" form

$$\chi(s) = \delta(s-s_T)^{-1}, \tag{3}$$

where δ is a constant. Additional justification for this assumption comes from the pervasiveness of the Weber-Fechner law as an approximate description of biological response to stimulus. This law, whose formal expression is given by equation (3), states that the smallest change in an environmental factor or stimulus which is needed to cause a response is proportional to the intensity (in this case concentration) of the stimulus. Some confirmation that the Weber-Fechner law provides a valid description of bacterial chemotaxis already exists (see Weibull, 1960).

If the variable s is reinterpreted as the difference between the observed concentrations and the threshold value (presumably small), equation (3) becomes

$$\chi(s) = \delta s^{-1}. \tag{4}$$

The singularity is then at $s = 0$, and all other equations remain unchanged. Henceforth s will be so interpreted.

For numerical comparison, the units of s will be given in mmol/cm^3 and b in number/cm^3. The time t will be measured in hours. Hence k will have the units mmoles/hr/cell, and D, μ and δ will have the units cm^2/hr.

3. Solution

The non-linear parabolic system of differential equations (1) and (2) is a well defined mathematical problem only if appropriate initial and boundary

conditions are prescribed. It is convenient to choose co-ordinates so that the capillary tube lies along the x-axis from $x = 0$ to $x = L$. Then the initial conditions appropriate to this problem would be

$$s(x, 0) = s_0(x), \qquad b(x, 0) = b_0(x). \tag{5}$$

If the solution is initially well mixed, $s_0(x) =$ constant. The function b_0 describes the distribution of the initial inoculum of bacteria. The appropriate boundary conditions insure that neither bacteria nor critical substrate flow through the ends of the tube. They would be

$$\partial s/\partial x = 0, \qquad \partial b/\partial x = 0 \quad \text{at} \quad x = 0 \quad \text{and} \quad x = L. \tag{6}$$

We shall assume that D can be taken to be zero, keeping in mind the necessity of subsequent verification of the internal consistency of such an approximation. A consequence of this approximation is that the order of the differential equation (1) is reduced, and one of the boundary conditions must therefore be dropped.

The complete solution of the initial value problem described here, with or without the approximation $D = 0$, is a formidable task, and one not necessary for our present purposes. Instead we need only look for solutions in the form of a band moving without distortion in the direction of increasing x. (These are the "traveling waves" found in many physical contexts.) In doing so we make use of the fact that the capillary tube is long compared to the width of the band so that the tube may be assumed to be of infinite extent. We therefore let x vary from $x = -\infty$ to $x = +\infty$ and look for solutions of the form

$$b(x, t) = b(\xi), \qquad s(x, t) = s(\xi), \qquad \xi = x - ct, \tag{7}$$

where c is the constant band speed. With equation (7) the partial differential equations (1) and (2) are reduced to the non-linear† system

$$cs' = kb, \tag{8}$$

$$cb' = (\delta b s^{-1} s')' - \mu b'', \tag{9}$$

where the prime denotes differentiation with respect to ξ. Appropriate boundary conditions would now be

$$b \to 0, \qquad b' \to 0, \qquad s \to s_\infty \quad \text{as} \quad \xi \to \infty. \tag{10a, b, c}$$

That is, we assume that far in advance of the wave the concentration of bacteria is zero, the bacterial flux is zero, and the critical substrate concentration approaches the value s_∞, which is equal to its initial value s_0. Equations (8) to (10) can now be solved with relative ease.

† The non-linearity of equation (9) is crucial to the existence of traveling wave solutions. The importance of non-linearity for a variety of biological phenomena has often been stressed (see, e.g. Prigogine, 1969).

We first integrate equation (9) once, obtaining

$$cb = \delta b s^{-1} s' - \mu b' + \text{constant}.$$

According to equations (10) the constant of integration must be zero. We divide by b, integrate again, and find

$$b = Q s^{\bar{\delta}} e^{-\bar{\xi}} \quad \text{where} \quad \bar{\delta} = \delta/\mu, \qquad \bar{\xi} = c\xi/\mu, \tag{11}$$

and Q is a positive constant. Substituting into equation (8) and integrating a third time we obtain

$$s = [Qkc^{-2}(\delta - \mu)e^{-\bar{\xi}} + s_\infty^{1-\bar{\delta}}]^{-1/(\bar{\delta}-1)} \tag{12}$$

where equation (10c) has been used to determine a constant of integration.

Specification of Q is equivalent to specification of the origin of co-ordinates since the change to $\bar{\xi}^*$ co-ordinates via the axis translation

$$\bar{\xi} = \bar{\xi}^* + q$$

multiplies the first bracketed term in equation (12) by the factor $\exp(q)$. In equation (12), as well as in the corresponding expression for b, the effect of this translation is equivalent to redefining Q.

The simplest expressions for $s(\bar{\xi})$ and $b(\bar{\xi})$ are obtained if we set

$$Qkc^{-2}(\delta - \mu) = s_\infty^{1-\bar{\delta}} \tag{13}$$

with which equation (12) becomes

$$\frac{s}{s_\infty} = (1 + e^{-\bar{\xi}})^{-1/(\bar{\delta}-1)}. \tag{14}$$

The corresponding expression for b is

$$\frac{b}{c^2 s_\infty (\mu k)^{-1}} = \frac{1}{\bar{\delta} - 1} e^{-\bar{\xi}} (1 + e^{-\bar{\xi}})^{-\bar{\delta}/(\bar{\delta}-1)}. \tag{15}$$

The maximum value of b, $b_{\max}$, is given by

$$b_{\max} = c^2 s_\infty / [\mu k \bar{\delta}^{\bar{\delta}/(\bar{\delta}-1)}]. \tag{16}$$

As $\bar{\xi} \to -\infty$ both s and b behave like constant multiples of $\exp[\bar{\xi}/(\bar{\delta}-1)]$. If solutions are to remain finite then we must have

$$\bar{\delta} > 1 \quad \text{or} \quad \delta > \mu. \tag{17}$$

If this requirement holds

$$\lim_{\bar{\xi} \to -\infty} s = 0, \qquad \lim_{\bar{\xi} \to -\infty} b = 0. \tag{18a, b}$$

By integrating equation (15) for b with respect to $\bar{\xi}$ from $-\infty$ to $+\infty$ or, much more easily, by performing this integration on differential equation (8)

and using equations (18a) and (10c), one obtains

$$c = Nk/(as_\infty) \tag{19}$$

where

$$N \equiv a \int_{-\infty}^{\infty} b(\xi)\mathrm{d}\xi \tag{20}$$

is the total number of bacteria found in the band and a is the cross-sectional area of the capillary tube. It is worth noting that equation (19) holds exactly even if substrate diffusion is considered, for retention of the diffusion term in equation (8) adds $Ds'(\infty) - Ds'(-\infty) = 0$ after integration.

We can see whether our neglect of substrate diffusion was consistent by using equations (14) and (15) to estimate $(D\mathrm{d}^2s/\mathrm{d}\xi^2)/kb$. This ratio varies from $(D/\mu)\bar{\delta}/(\bar{\delta}-1)$ to D/μ as ξ goes from $-\infty$ to ∞. Neglect of substrate diffusion is therefore a consistent approximation if D is small compared to μ. The fastest-diffusing critical substrate is oxygen. Its diffusion constant of about 5×10^{-2} cm^2/hr is just about small enough compared to a typical value of $\mu = 1/4$ cm^2/hr (see below) to allow us to assert that substrate diffusion does not play an important role except perhaps when chemotaxis is very weak.

Graphs of the right-hand-sides of equations (14) and (15) for s and b are given in Figs 1 and 2 for various values of $\bar{\delta}$. An interesting feature of these curves is that when $\bar{\delta} > 2$ the graph of b decreases from its maximum more rapidly toward the front of the band than the rear, while the opposite is the case when $\delta < 2$.

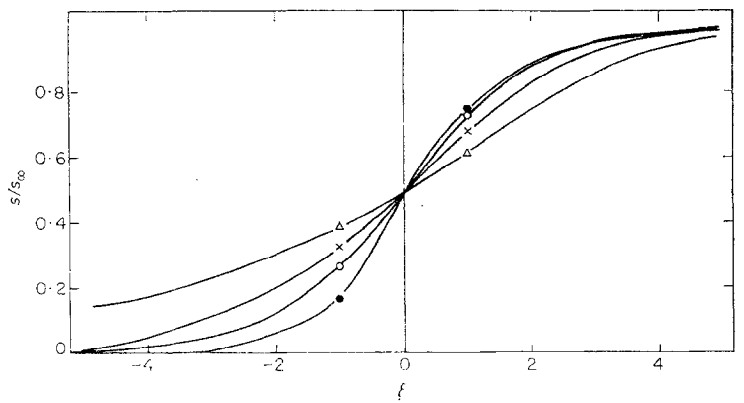

FIG. 1. Critical substrate concentration s divided by initial concentration s_∞ for $\delta/\mu = 4/3$ (●), 2 (○), 3 (×), 5 (△). Here δ is the proportionality factor relating the flux of the chemotactic cells to the relative concentration gradient and μ is a motility coefficient. Distance along the abscissa is marked in units of μc^{-1}, where c is the band speed. Typically, one unit is between 1/8 cm and 1/4 cm in length.

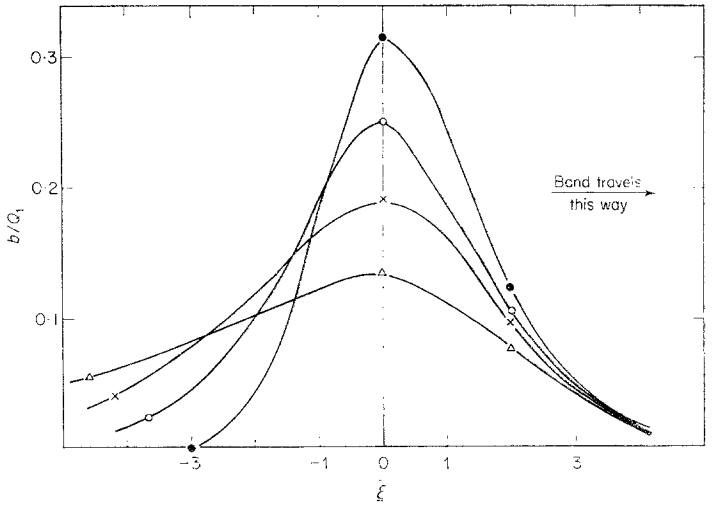

FIG. 2. Bacterial density b divided by the reference density $Q_1 \equiv c^2 s_\infty/\mu k$ for $\bar{\delta} \equiv \delta/\mu = 4/3$ (●), 2 (○), 3 (×), 5 (△). As in Fig. 1, the various curves have been translated to facilitate comparison between them. The bacterial density curve is symmetric when $\delta/\mu = 2$, and is steeper in the front (rear) if $\delta/\mu > 2(\delta/\mu < 2)$. The band is narrower when chemotaxis is relatively weaker.

4. Discussion

A number of specific predictions of our model can be compared with experimental results. Perhaps the simplest comparison is between calculated and observed band speeds, which can be made using equation (8) alone. We make this comparison using equation (19), remembering that this equation can be obtained simply by integrating equation (8). Calculation of the speed of the migrating bands from equation (19) requires specification of the values of s_∞, the initial concentration of critical substrate; k, the rate of substrate consumption; a, the cross-sectional area of the tube; and N, the total number of bacteria in the band. We have estimated these parameters from published data (Adler & Dahl, 1967; Adler, 1966*a*) and from data provided by Adler (private communication). These estimates being *ex post facto* are necessarily crude. In particular, the number of bacteria, N, is subject to a great deal of uncertainty, partly because of the intrinsic uncertainty in the assay procedure, and partly because of the fact that at least in some experiments, a certain amount of growth did take place, an effect not included in our model.

Nevertheless, the predicted band speed of our model is in rough agreement with the experimental findings. In one experiment described in Adler & Dahl (1967) a band is observed moving toward higher concentrations of oxygen at a speed of 0·9 cm/hr. Estimating k at 5×10^{-12} mmol/cell hr, a

at $2{\cdot}5\times10^{-3}$ cm^2 (Adler, private communication), N at $1{\cdot}5\times10^5$ (see Fig. 10, Adler & Dahl, 1967) and s_∞ at 2×10^{-4} mmol/cm^3 (using the saturation concentration of oxygen in water), we obtain from equation (19) a band speed of 1·5 cm/hr.

Using the data from a different experiment pertaining to a second band moving toward higher concentrations of serine (Adler, 1966*a*), comparison can again be made between observed and calculated band speeds. In this experiment k is estimated from a plot of the anerobic consumption of serine (see Fig. 7, Adler, 1966*a*) at $k=2\times10^{-11}$ mmol/cell hr, s_∞ is given as 2×10^{-3} mmol/cm^3, and N is estimated from Fig. 3 of Adler (1966*a*) at 3×10^5, half the total viable count after two hours. The observed speed at that time is approximately 2 cm/hr, and the speed calculated on the basis of these estimates is 1·2 cm/hr. In this case and that of the previous paragraph, agreement seems to be as close as could reasonably be expected. However, it is obvious that the parameter estimates made here are too crude to provide a definitive confirmation of equation (19). What is required is a repeat of these experiments, under conditions which do not permit growth, in which N is measured as accurately as possible.

In the context of the present analysis, measurement of the width of the migrating bands provides a means for estimating $\bar{\delta}=\delta/\mu$, the ratio of the chemotactic strength to motility. Again, given the measurements which exist, only an order of magnitude estimate can be made. Using the data in Figs 5 and 6 of Adler (1966*a*), the width of the oxygen band, W, is approximately 0·5 cm and its speed is 2 cm/hr. (The band width is here defined as the distance between the points at which s is one-tenth and nine-tenths of s_∞.) Using the average value of the motility quoted by Adler & Dahl (1967), $\mu=0{\cdot}25$ cm^2/hr, and noting that $\bar{\xi}=c\mu^{-1}(x-ct)$, equation (14) enables us to find $\bar{\delta}$. Comparison with Table 1 shows that these estimates yield a value of $\bar{\delta}$ between 1 and 2. Similarly, the data from the same experiment on the

TABLE 1

The width of the band as measured from the substrate curve (W_s) *and the bacterial density curve* (W_b) *for various ratios of strength of chemotactic response* (δ) *to motility coefficient* (μ).

$\bar{\delta}\equiv\delta/\mu$	W_b	W_s
1·33	5·5	3·5
2	7·5	4
3	9·5	6
5	12	9

The widths are in units of μc^{-1}, where c is the band speed.

second band, in which the critical substrate is serine, shows a band width for serine of approximately 1·2 cm. The band speed is roughly 2 cm/hr as in the previous case. Using the same value for the motility as before, comparison with the Table 1 yields a value of $\bar{\delta}$ in the neighborhood of 3.†

That different values of $\bar{\delta}$ are associated with the two bands is particularly interesting because, as is evident from Table 1 and Figs 1 and 2, when c and μ are constant the bacterial band width is expected to increase with increasing $\bar{\delta}$, and furthermore, when $\bar{\delta} > 2$, the leading edge of the band is predicted to be steeper than the lagging edge, the relative steepness increasing with $\bar{\delta}$. (When $1 < \bar{\delta} < 2$, the back of the band is expected to be steeper.) It is clear from inspection of the densitometer tracings (Fig. 4, Adler, 1966*a*) that both of these predictions are borne out. The second band is clearly wider than the first, and in that band the front edge is considerably steeper than the rear. In contrast, the first band seems relatively symmetric, perhaps even somewhat steeper in back. Although the exact values of $\bar{\delta}$ calculated cannot be taken too seriously, the success of such qualitative predictions as these is encouraging.

A possibly significant source of error in the computation of $\bar{\delta}$ arises from ambiguities in the measurement of μ. In the observations of Adler & Dahl (1967) the bacterial motion deviates somewhat from ordinary diffusion. The estimate they quote is of the "fastest motility", and may well be an overestimate. (If so, our theoretical values of $\bar{\delta}$ are underestimates.) In particular, it is assumed that chemotactic motion is absent in these experiments since no bands are formed. According to our analysis, however, chemotaxis could be present, even though bands do not form, if $0 < \delta < \mu$. The presence of some degree of chemotaxis could perhaps explain the difference Adler & Dahl found between their measurements of μ and measurements to be expected from diffusion theory.

5. Summary and Conclusions

Precise characterizations of motility and chemotaxis are used in our mathematical analysis of traveling bands. Motility and chemotactic coefficients are defined in terms of the *flux* of cells, i.e. the rate of passage of cells across a unit area. The motility coefficient μ is the flux of cells per unit gradient in bacterial density, in the absence of chemotaxis. In a uniform distribution of bacteria, the chemotactic coefficient χ is the flux of cells per unit gradient of the concentration of the critical substrate, divided by the local cell density.

† Strictly, one should here use a value for the motility obtained for anerobic consumption of serine. Unfortunately such a measurement is unavailable. Since it is known that motility is somewhat less under such circumstances, the true value of μ is somewhat lower than that used. The "true" value of $\bar{\delta}$ would hence be somewhat greater than 3.

The virtue of these definitions is that, once defined, μ and χ are subject to experimental measurement. Such measurements are essential for a more accurate theoretical analysis. In general, both μ and χ depend on the critical substrate concentration. Lacking experimental evidence, we have assumed that μ is constant, and $\chi(s) = \delta(s-s_T)^{-1}$ where δ is a constant and s_T is the threshold for chemotaxis. The latter assumption says, in accordance with the Weber-Fechner law, that the chemotactic flux is proportional to the relative concentration gradient. Our analysis shows that, *given these assumptions*, steadily traveling bands cannot appear unless δ exceeds μ. In retrospect, a condition of this type might appear to be necessary. The ordering of motion caused by chemical gradients must be sufficient to outweigh the disordering diffusive consequences of random motion. The more vigorously an individual cell moves at random, the greater is the tendency of a collection of these cells to distribute themselves uniformly over the space available to them, and the more powerful must be any organizing tendency.

In the present analysis we have taken as (experimentally) given that steadily traveling bands exist and have determined the consequences. It should be possible to predict the appearance of such bands from a study of the initial value problem given by equations (1), (2), (4), (5) and (6) (with $L = \infty$). The initial values would be those corresponding to the situation in which the substrate is at first evenly distributed throughout the tube and the bacteria are concentrated at one end. Study of the initial value problem has more than mathematical interest, for it should reveal the way in which it happens that some bacteria remain at the origin while others join the band. Such a study is in progress.

We have shown how measurements of the widths of either the bacterial or substrate bands can be used to determine the ratio $\bar{\delta} = \delta/\mu$, thus giving a numerical measure of the relative strength of chemotaxis. The value of $\bar{\delta}$ also determines the shape of the bacterial bands, providing another means of comparison between theory and experiment. If $\bar{\delta} > 2$ the band is steeper in front and if $1 < \bar{\delta} < 2$ the band is steeper behind. The predicted changes in shape with increasing $\bar{\delta}$ are found to be consistent with observation.

The primary purpose of this paper is to present a theoretical framework for the description of chemotactic bands. The authors have previously shown that the same framework, in a different context, is capable of providing a description of the onset of aggregation in cellular slime mold (Keller & Segel, 1970).† In both cases, in order to obtain an explicit solution, certain simplify-

† The simplified equations used in Keller & Segel (1970) are almost identical to those used here [i.e. equations (1) and (2)]. The only difference is between equation (1) and the analogous equation in the slime mold analysis. There, $k(s)$ is negative, corresponding to the production of acrasin, and an extra term is included which represents the degradation of acrasin. Equation (2) is unchanged.

ing assumptions were made. In neither case do these assumptions critically bear on the ability of the theory to describe the phenomena in question. In the present analysis, we have made explicit assumptions concerning the functions $k(s)$, $\mu(s)$ and $\chi(s)$. Although the qualitative agreement between our results and existing experimental data is encouraging, these assumptions cannot be considered to be justified by such agreement, but must await further experimental work for independent verification.

To measure the chemotactic coefficient one could perhaps impose a known or calculable gradient of substrate on a uniform mixture of bacteria and measure the bacterial flux. To establish a constant gradient one might layer samples with the same bacterial density but differing substrate concentrations (the highest on top because of gravity) and assay the bacterial concentration on the top layer periodically. One could do this at different average concentrations and thus get the dependence of the flux on s. Since the sedimentation constant of bacteria is known, the effect of gravity could be computed and eliminated.

The fact that our theoretical framework is capable of describing both chemotactic bands of motile bacteria and the onset of aggregation in slime mold gives reason to believe that the same framework can be used to describe other collective chemotactic phenomena. Two examples of such phenomena are the following: (1) Adler (1970) reports a new assay for chemotaxis in which a capillary tube containing attractant is pushed into a suspension of bacteria on a slide. The bacteria in the tube are counted after a fixed period. Adler's measurements can be related to χ and μ by solving equations (1) and (2) subject to appropriate initial and boundary conditions; (2) a rate test for assaying the effect of the attractant acrasin on cellular slime molds (Bonner, Kelso & Gillmor, 1966) begins by placing a Cellophane square uniformly covered with motile test cells at the bottom of a Petri dish. The dish contains an acrasin solution of known concentration. The leading cells leaving the square form a rather sharp edge and appear to move at constant speed. This speed is measured and correlated with acrasin concentration. It appears likely that this test can be analyzed as a traveling band phenomenon governed by equation (2) plus equations (Keller & Segel, 1970) which describe the production, reaction and diffusion of acrasin and the relatively heavy enzyme which deactivates it.

Our theoretical framework thus seems to have the capability of relating various assays of chemotaxis to each other and to a precisely defined measure of the strength of chemotaxis.

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Appendix

Under the assumptions $\mu(s)$, $k(s) = \text{constant}$, and $D = 0$, the existence of traveling waves which have the property $s \to 0$ at $-\infty$ implies that the chemotactic function $\chi(s)$ must have a singularity of order one or greater at $s = 0$. To show this we assume the existence of a traveling wave solution to equations (1) and (2) as before, but we now leave $\chi(s)$ arbitrary. We obtain

$$b = Qe^{g(s)/\mu}e^{-\bar{\xi}}, \qquad g' \equiv \chi, \tag{A1}$$

instead of equation (11). From equation (8)

$$ds/d\xi = Qkc^{-1}e^{g(s)/\mu}e^{-\bar{\xi}}. \tag{A2}$$

Thus s is monotonic increasing, so we can regard $\bar{\xi}$ as a function of s. We find

$$\bar{\xi} = \ln \{Qk\mu c^{-2} / \int_s^{s_\infty} \exp [-g(p)/\mu] dp\}. \tag{A3}$$

If s is to approach zero as $\bar{\xi} \to -\infty$, the integral in (A3) must diverge as $s \downarrow 0$. Suppose

$$\chi(s) \approx \delta s_1^q \quad \text{when } s \text{ is small}, \tag{A4}$$

for some constants δ and a. Then the integral in (A3) becomes

$$\int_s^{s_\infty} \exp\left[-\frac{\delta}{\mu}\frac{p^{a+1}}{a+1}\right] dp, \qquad a \neq -1,$$

which diverges as $s \downarrow 0$ if and only if $a+1 < 0$. When $a = -1$, as was assumed in the text, the integral (A3) also has the appropriate behavior. Thus, if a traveling band is to exist for motile organisms which are characterized by a chemotactic function satisfying equation (8) then $a \leq -1$.

By examining the asymptotic behavior of the integral in (A3) for small values of s, and substituting the result into (A1), we can show that b behaves like a constant multiple of s^{-a} as $x \to -\infty$. By measuring the decay of bacterial count and substrate density behind the advancing band, then, one can in principle determine whether the Weber-Fechner law holds approximately ($a = -1$) or whether there is a significant deviation from this law. Such measurements could in principle give information about the behavior of χ at all values of substrate density but, in accord with intuition, the material of this Appendix shows that only behavior at relatively low values of s has a significant influence on the phenomenon.