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Self-trapping of a single bacterium in its own chemoattractant

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Abstract. – Bacteria (*e.g.*, *E. coli*) are very sensitive to certain chemoattractants (*e.g.*, asparate) which they themselves produce. This leads to chemical instabilities in a uniform population. We discuss here the different case of a single bacterium, following the general scheme of Brenner, Levitov and Budrene. We show that in one and two dimensions (in a capillary or in a thin film) the bacterium can become self-trapped in its cloud of attractant. This should occur if a certain coupling constant g is larger than unity. We then estimate the reduced diffusion D_{eff} of the bacterium in the strong-coupling limit, and find $D_{\text{eff}} \sim g^{-1}$.

Introduction. – Budrene and Berg [1] studied an initially homogeneous population of *Escherichia coli* (*E. coli*) bacteria on an agar plate, in conditions where food (succinate) is available. Depending on the food content, they discovered various patterns such as moving rings or aggregates. These patterns were lucidly interpreted by Brenner, Levitov and Budrene [2]. They observed that in the (usual) conditions of rapid diffusion, the bacteria produce a concentration field of the chemoattractant, $c(r)$, which has the form of a gravitational field ($c(r) \sim 1/r$ in three dimensions). The bacteria attract each other and cluster by a "gravitational" instability. However, when a cluster ("star") is formed, food is depleted and the star then becomes dark in the center, a ring is created, etc.

Brenner *et al.* also discussed the spontaneous aggregation of a small group of bacteria, and found that they shall indeed aggregate if their number N is larger than a certain limit N^*. Because of the (rough) similarity with astrophysics, they called N^* the Chandrasekhar limit.

Our aim here is to discuss some properties of these small clusters and in particular the limit of a *single* bacterium. We point out that it may be trapped in its own cloud of asparate. This question has some weak similarity with a classical problem of solid-state physics and field theory, the *polaron* problem, defined first by Frolich [3] and analyzed by many theorists [4–6]. A polaron is an electron coupled to a phonon field in a solid. In the strong-coupling limit analyzed by Pekar [5], the electron builds up a distorted region, and is essentially occupying the lower bound state in the resulting (self-consistent) potential. However, the electron moves slowly: it has a large effective mass.

Our problem here is somewhat similar: if a certain coupling constant g is larger than unity, the bacterium sees a strong attractant cloud. We shall see that in three dimensions, it can always escape, but in one and two dimensions it cannot. The question of interest is then the *effective* diffusivity of the bacterium.

In the second section we start from the basic coupled equations for the bacteria and attractant [2, 7] (except for an alteration of the food kinetics). From this we investigate the possibility of a self-trapped state, define a coupling constant g and find that it can indeed be of order unity in some favorable cases. g is (except for coefficients) equal to $1/N^*$, where N^* is the Chandrasekhar limit of ref. [2]. We are interested in high g values ($N^* < 1$). If there are a number N of bacteria in one small droplet, g is multiplied by N and the large-g limit becomes easier to reach. In the third section we discuss this high-g limit and the renormalized diffusion constant.

Self-trapping. – *E. coli* colonies enjoying a large supply of food are governed by two coupled reaction-diffusion equations:

$$\frac{\partial \rho}{\partial t} = -\nabla \boldsymbol{J}, \quad \boldsymbol{J} = -D_b \nabla \rho + \kappa \rho \nabla c\,, \tag{1}$$

$$\frac{\partial c}{\partial t} = D_c \nabla^2 c + \beta \rho\,; \tag{2}$$

ρ and c are the number densities of the bacteria and chemoattractant fields, respectively, D_b and D_c are the diffusion constants of the bacteria and attractant, κ determines the strength of positive feedback and β is the production rate of the attractant by the bacteria.

Below we are interested in the case of fast attractant diffusion. In this limit, eq. (2) shows us that ρ and c relate to each other like charge density and potential in electrostatics. In this analogy ∇c is the force acting on a bacterium. For one bacterium at the origin and in two dimensions we find that

$$c = c_0 \ln\left(\frac{r_0}{r}\right) + \text{const}\,. \tag{3}$$

Here r_0 is the cutoff length. It is instructive to consider the steady state obtained when $\boldsymbol{J} = 0$. We find that ρ obeys the "Boltzmann distribution"

$$\rho = \tilde{\rho}_0 \exp\left[\frac{\kappa c}{D_b}\right] = \rho_0 \left(\frac{r_0}{r}\right)^g, \tag{4}$$

$$g = \frac{\kappa c_0}{D_b}\,. \tag{5}$$

Therefore, a self-trapped state exists if the coupling constant is $g \geq 2$. In order to know the value of g, we denote by e the thickness of the growth medium on the Petri dish, and equate the attractant flow out of a circular domain of radius r with the attractant production,

$$e D_c \cdot 2\pi r \nabla c \simeq 2\pi e D_c c_0 = \beta\,. \tag{6}$$

Thus, the coupling constant g can be written as

$$g = \frac{\kappa \beta}{2\pi e D_b D_c}\,. \tag{7}$$

Putting reasonable values for the parameters [2] $D_b \simeq 6.6 \cdot 10^{-6}\,\text{cm}^2/\text{s}$, $D_c = D_b$, $\beta = 10^3$ molecules/bacterium/s, $\kappa \simeq 10^{-14}\,\text{cm}^5/\text{s}$ and $e = 0.05\,\text{cm}$, we find that $g \approx 0.73$.

This estimate shows that the coupling between the bacterium and its own chemoattractant field can be rather strong in many experimental situations. Calculation along similar lines for the one-dimensional infinitely long "wire" with diameter d gives $c \sim |x|$ and confined bacterium, $\rho = \rho_0 \exp[-2\beta\kappa|x|/\pi d^2 D_b D_c]$. In three dimensions, however, $c \sim 1/r$ and a self-trapped state does not exist because $\rho \sim \exp[\kappa c/D_b]$ does not tend to zero at large distances. As we will see in the next section, the coupling of a moving bacterium with its chemoattractant leads to the appearance of a "drag force" acting on the bacterium, which is manifested by an effective, smaller, diffusion constant.

Effective mobility of a self-trapped bacterium in a film. – We have seen above that in favorable situations the coupling constant can be large, $g \gg 1$. This case occurs, for example, with a small drop (with diameter comparable to the thickness of the culture medium) containing a significant number of bacteria. In the following we consider the bacteria moving at a constant small velocity v, and look for the effective diffusion coefficient. The attractant profile is given by

$$\frac{\partial c}{\partial t} = D_c \nabla^2 c + \frac{\beta}{e}\delta(x - vt). \tag{8}$$

We write $c(r)$ as $c = \int c_{\boldsymbol{k}} \exp[i\boldsymbol{k}(\boldsymbol{r} - vt)]\mathrm{d}\boldsymbol{k}$ and obtain for the Fourier component $c_{\boldsymbol{k}}$

$$c_{\boldsymbol{k}} = \frac{\beta}{D_c k^2 - i\boldsymbol{k}\boldsymbol{v}} \simeq \frac{\beta}{eD_c k^2}\left(1 + \frac{i\boldsymbol{k}\boldsymbol{v}}{D_c k^2}\right). \tag{9}$$

The "force" f acting on the bacteria is

$$f = \nabla c = \int i\boldsymbol{k}c_{\boldsymbol{k}}\ \mathrm{d}\boldsymbol{k} = \frac{\beta}{eD_c^2}\int \frac{\boldsymbol{k}(\boldsymbol{k}\boldsymbol{v})}{k^4}\ \mathrm{d}\boldsymbol{k} = \frac{\pi\beta v}{2eD_c^2}\ln(k_{\max}/k_{\min}). \tag{10}$$

Approximating the logarithmic term by unity, we identify the effective mobility κ_{eff} as

$$\kappa_{\mathrm{eff}} = \frac{v}{f} = \frac{2eD_c^2}{\pi\beta}\,. \tag{11}$$

We may return for a moment to a problem of many bacteria with concentration $\rho(\boldsymbol{r})$ moving in an external concentration field $c_{\mathrm{ext}}(\boldsymbol{r})$. The bacteria density at steady state $\rho = \rho_0\exp[\kappa c_{\mathrm{ext}}/D_b]$ is the same if it is written in terms of the "effective" quantities κ_{eff} and D_{eff} instead of κ and D_b. This means that

$$\frac{\kappa_{\mathrm{eff}}}{D_{\mathrm{eff}}} = \frac{\kappa}{D_b}\,. \tag{12}$$

This relation tells us that the effective diffusion constant D_{eff} is given by

$$D_{\mathrm{eff}} = \frac{D_c}{\pi^2 g}\,. \tag{13}$$

Hence, bacterial diffusion is greatly diminished because of the chemoattractant cloud which is left behind.

Discussion. – Isolated bacteria moving in thin films (*e.g.* in the dental plaque) may be slowed down by their own chemoattractant at scales larger than the film thickness. This should be observable in experiments using fluorescent bacteria. In addition, clusters of a few bacteria are nearly stopped; this could be relevant for their ultimate fixation in the plaque.

We discussed some effects of the chemoattractant cloud. One may wonder whether there is an analogous effect related to the food problem: the bacterium eats some food, and this creates a depleted food region around it. If this "food hole" is lagging behind the bacterium, there will be more food available ahead, and the bacterium can go faster. (The corresponding transport is reminiscent of a hot wire anemometer.) However, the resulting food effect goes like v^2 (not v) and is thus irrelevant for our problem of mobility at low v.

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