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MODELING OF BACTERIAL CHEMOTAXIS IN A MEDIUM WITH A REPELLENT

The bacterial chemotaxis in a one-dimensional system with a repellent has been considered. The process of bacterial redistribution in the system is analyzed, and a corresponding phenomenological model is proposed, which makes allowance for the diffusion of bacteria and their motion caused by the repellent gradient. The repellent injection into the system is governed by boundary conditions. In the framework of this model, the chemotaxis sensitivity function, a numerical characteristic, which describes the nonuniformity in the bacterial distribution, is calculated. A dependence of the chemotaxis sensitivity function on the repellent concentration at the system boundaries is obtained. A relation between the bacterial distribution and the parameters of repellent distribution is found.

K e y w o r d s: bacterium, chemotaxis, repellent, attractant, tumbling.

1. Introduction

Flagellate bacteria (e.g., *E. coli*) are known to be able to recognize certain chemicals. Such bacteria move in or opposite to the direction of the substance concentration gradient [1, 2]. If bacteria move in the direction of the substance concentration growth, such a substance is called an *attractant*. As an example, these are sugar, vitamins, and amino acids. If bacteria move in the direction of the substance concentration reduction, such a substance is called a *repellent*. Repellents include, e.g., alcohols, phenols, and some acids.

The chemotaxis problem has a long history. Among the first works in this area, there are works [3–5]. Nevertheless, the chemotaxis problem remains challenging till now [6–9]. For the decades of researches, a lot of interesting and promising results were obtained (see, e.g., works [10–13] and references therein). At the same time, there are important issues that have not been resolved yet. In particular, the mechanism governing the bacterial redistribution in accordance with the attractant or repellent gradient is quite complicated [2].

A bacterium has receptors that can sense an attractant or a repellent [14–17]. However, as a rule, the linear size of a bacterium is too small for the latter to "calculate" the gradient of the substance. This "rule" has exceptions (see, e.g., work [18]), but, in general, the reaction of bacteria to the repellent/attractant gradient has a multilevel character and is rather fine. It is based on the fact that, when a bacterium moves, its receptors register the attractant/repellent. As a result, the receptors transit into a certain active state. The active state of a receptor is a temporary phenomenon. In a certain time interval after its activation, the receptor returns into the inactive state. Therefore, when a bacterium moves, the number of its active receptors changes. This number is larger, if the concentration of an attractant/repellent registered by the bacterium during its motion is higher.

Concerning the laws of bacterium motion, bacteria move mainly uniformly and straightforwardly. However, the uniform motion is interrupted by the tumbling. At the tumbling, the bacterium stops and randomly changes the direction of its motion. The redistribution of bacteria according to the attractant/repellent gradient occurs by changing the tumbling frequency. The latter, in turn, depends on the number of active receptors and, thus, on the attractant/repellent concentration registered by the bacterium receptors during the motion of a bacterium in the medium. For example, if the bacterium receptors register a high attractant concentration, the tumbling frequency decreases [2]. As a result, a bacterium changes the direction of its motion more rarely in regions with a high attractant concentrations. For a repellent, the situation is inverse. Hence, bacteria obtain a "memory effect" [2, 19], when their behavior depends on the region where they were earlier.

There are two conceptual approaches to describe the motion of bacteria in a medium with an attractant/repellent. One of them is based on the software application [2]. Its advantage consists in that it is possible to set up an algorithm for the behavior of bacteria and, in such a way, maximally mimic the real system by an artificial one. The main disadvantage of this approach (apart from mere technical difficulties of its implementation) is associated with the impossibility to obtain analytical dependences. Therefore, the other approach that uses models based on nonlinear differential equations of the diffusion type [20, 21] is also popular and efficient. The corresponding equations contain a set of phenomenological parameters and involve the behavior of bacteria in a medium with an attractant/repellent by introducing specific terms into expressions for the bacterial flux.

In this work, a one-dimensional system containing bacteria and a repellent is considered. To elucidate the character and specific features of the bacterial distribution in the system (and their dependences on the repellent distribution), a mathematical model is proposed, which is based on a nonlinear differential equation. The models of this type were used earlier to study the bacterial behavior in a medium with an attractant [22–24]. A similar approach is used in this work, but now, when developing the model, we take into account that the repellent is dealt with.

2. System with Repellent

As was indicated above, a one-dimensional system with linear dimension L is considered. Accordingly, the coordinate along the system is varied within the interval $0 \le x \le L$. Let the function $b(x)$ describe the stationary distribution of bacteria, and the function $c(x)$ the stationary distribution of a repellent in the system. It is clear that there is a functional relation between the dependences $b(x)$ and $c(x)$, which is rather non-trivial. We proceed from the assumption that the flux of bacteria in the system, $\mathbf{j}_b$, is determined by both the distribution of bacteria $b(x)$ and by the distribution of a repellent $c(x)$. In particular, the following expression for the bacterial flux is used:

$$\mathbf{j}_b = -D\boldsymbol{\nabla} b(x) - k\frac{b(x)\boldsymbol{\nabla} c(x)}{(a+c(x))^2}, \tag{1}$$

where D is the diffusion coefficient, and k and a are phenomenological parameters of the model. The first term in the right-hand side of expression (1) corresponds to the bacterial diffusion, and the second term describes the flux component associated with the chemotaxis. We proceed from the assumption that the contribution of the chemotaxis to the bacterial flux is proportional to the repellent gradient $\boldsymbol{\nabla} c(x)$ and the bacterial concentration $b(x)$. The expression $(a+c(x))^2$ in the denominator of the second term is associated with the following fact. According to experimental data [2], if the concentration of an attractant or repellent is high, the "saturation effect" takes place: the bacteria cease to sense the gradient (in our case, of a repellent). It should also be noted that the type of functional dependence used by us for the chemotaxis term was well verified for models describing a system with an attractant [22–24]. In our case, we use an analogous expression, but it enters the general expression for the bacterial flux with the different sign.

If we are interested in the stationary distribution of bacteria in the system, the corresponding equation can be written as follows:

$$\mathrm{div}(\mathbf{j}_b) = 0. \tag{2}$$

In view of the one-dimensional geometry of the problem, it reads

$$D\boldsymbol{\nabla} b(x) + k\frac{b(x)\boldsymbol{\nabla} c(x)}{(a+c(x))^2} = \mathrm{const}. \tag{3}$$

In addition to this equation, we have to specify boundary conditions and to set the spatial distribu-

tion of a repellent. We proceed from the feasible conditions of physiological experiments [2]. In this case, let us consider a situation where the repellent is injected into the system at the left end $x = 0$, and bacteria at the right end $x = L$ (in the more general case, the parameters of the bacterial distribution are controllable). Suppose that the repellent concentration C_0 is given at the left boundary, and there is no bacterial flux through it. In addition, we assume that the total amount of a repellent, C, and the total number of bacteria, B, in the system are known.

Taking all that into account and making the substitutions $x = Lz$ $(0 \le z \le 1)$, $b(x) = Bm(z)/L$, and $c(x) = as(z)$, we can ultimately formulate the problem. It consists in finding the function $m(z)$ that satisfies the equation

$$\frac{dm}{dz} + \lambda \frac{m(z)\frac{ds}{dz}}{(1+s(z))^2} = 0, \tag{4}$$

where $\lambda = k/D/a$.

The repellent distribution in the system is described by the stationary diffusion equation. Therefore, the repellent concentration dependence on the coordinate is linear. In other words, the dependence $s(z)$ is given by the expression

$$s(z) = p(1-2z) + 2\alpha z, \tag{5}$$

where the parameter p determines the repellent concentration at the left end $(s(0) = p)$, and the dimensionless parameter $\alpha = C/L/a$ determines the total amount of a repellent in the system,

$$\int_0^1 s(z)dz = \alpha. \tag{6}$$

In addition, the function $m(z)$ is normalized,

$$\int_0^1 m(z)dz = 1. \tag{7}$$

From the formal viewpoint, this problem is not difficult. The solution $m(z)$ that satisfies all additional conditions looks like

$$m(z) = \frac{\exp\left(\frac{\lambda}{1+s(z)}\right)}{\int\limits_0^1 \exp\left(\frac{\lambda}{1+s(z)}\right)dz}, \tag{8}$$

where the function $s(z)$ is given by formula (5), and the parameters p and α are the known quantities.

3. Qualitative Parameters of the System

Although we know a general solution for the bacterial distribution in the system, we are interested, first of all, in consequences following from this solution. From the practical viewpoint, we are interested in how the distribution of bacteria in the system is nonuniform and how the bacterial distribution nonuniformity depends on the repellent distribution. For this purpose, some numerical parameters should be used. In particular, the uniform character of the bacterial distribution in the system can be described by the chemotaxis sensitivity function [2, 22–24]. This function determines how much the average concentration of bacteria in a definite region deviates from the average concentration of bacteria over the whole system. If we are interested in the interval $x_1 \le x \le x_2$, the chemotaxis sensitivity function is defined as follows:

$$F(x_1, x_2) = \frac{\frac{1}{x_2 - x_1}\int\limits_{x1}^{x_2} b(x)dx}{\frac{1}{L}\int\limits_0^L b(x)dx} - 1. \tag{9}$$

The equality $F(x_1, x_2) = 0$ means that the average concentration of bacteria in the examined region is the same as in the whole system. The inequality $F(x_1, x_2) > 0$ demonstrates that the average bacterial concentration in this region is higher than the mean value over the system. Finally, the inequality $F(x_1, x_2) < 0$ indicates that the average concentration of bacteria in the region is lower than the average concentration over the system.

It is clear that the function defined by formula (9) depends on the size and location of the region, for which the function is calculated. But if the size $\Delta x = x_2 - x_1$ of the region tends to zero, we obtain the following formula for the chemotaxis sensitivity function:

$$F(x) = \frac{Lb(x)}{\int\limits_0^L b(x)dx} - 1. \tag{10}$$

In dimensionless variables,

$$F(z) = m(z) - 1 = \frac{\exp\left(\frac{\lambda}{1+s(z)}\right)}{\int\limits_0^1 \exp\left(\frac{\lambda}{1+s(z)}\right)dz} - 1. \tag{11}$$

Since the dependence $s(z)$ contains the parameters p and α (see formula (5)), the function $F(z)$ defined by Eq. (11) also depends on them. The corresponding solutions have a physical meaning at $p \leq 2\alpha$. At $p = \alpha$, we have $s(z) \equiv \alpha$, i.e. a uniform repellent distribution, so that $F(z) \equiv 0$.

From the technical viewpoint, it is the simplest way to carry out the measurements at the boundaries of the system. Therefore, let us consider the chemotaxis sensitivity function at the left boundary,

$$F_0(p,\alpha) \equiv F(z=0) = \frac{\exp\left(\frac{\lambda}{1+p}\right)}{\int\limits_0^1 \exp\left(\frac{\lambda}{1+s(z)}\right)dz} - 1, \qquad (12)$$

and, at the right boundary,

$$F_1(p,\alpha) \equiv \frac{\exp\left(\frac{\lambda}{1+2\alpha-p}\right)}{\int\limits_0^1 \exp\left(\frac{\lambda}{1+s(z)}\right)dz} - 1. \qquad (13)$$

It is easy to see that the equality $F_0(\alpha - q, \alpha) = F_1(\alpha + q, \alpha)$ holds true for any $0 \leq q \leq \alpha$, which means that the plots of the dependences $F_0(p, \alpha = \text{const})$ and $F_1(p, \alpha = \text{const})$ are specular reflections of each other with respect to the vertical line $p = \alpha$. This is an important fact, because it means that the functions $F_0(p,\alpha)$ and $F_1(p,\alpha)$ are not independent characteristics of the nonuniform character of the bacterial distribution in the system: from the known function $F_0(p,\alpha)$, we can obtain the function $F_1(p,\alpha)$ and vice versa.

4. Regime of Repellent Injection

Hence, the chemotaxis sensitivity function depends on the parameters p and α, which, in turn, are determined by the regime of repellent injection into the system. By changing one of them or the both, we can change the bacterial distribution in the system. Simultaneously, we can monitor those changes on the basis of the chemotaxis sensitivity function. Furthermore, the parameter λ also enters the corresponding formulas. However, unlike the parameters p and α, the parameter λ is not determined by the regime of repellent injection, but by the system properties of the system.

It should be noted at once that the specific numerical value of the parameter λ does not affect the behavior of the obtained dependences at the qualitative level. At the same time, we can evaluate λ. For this purpose, let us consider the results of previous works for systems with an attractant [2, 22]. In particular, in work [2], the bacterial distribution in a system with a linearly distributed attractant was calculated. The cited work also contains data on the experimentally measured parameters of the bacterial distribution function. On the other hand, in work [22], an approach based on a phenomenological model was proposed, and a bacterial distribution function containing a phenomenological parameter, which corresponds to the parameter λ with an accuracy to its sign, was obtained. By comparing the bacterial distributions from works [2] and [22], the value of the indicated phenomenological parameter can be evaluated (the corresponding evaluation was made in works [22, 24]). Proceeding from the assumption that the reaction of bacteria to a repellent at the microscopic level is realized in a similar way as the reaction to an attractant, we may put $\lambda \approx 40$ by the order of magnitude.

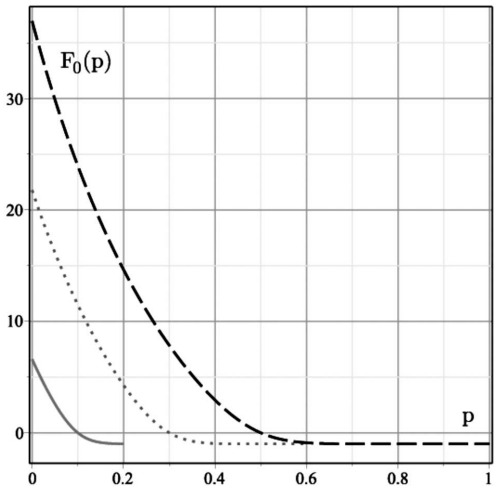

Fig. 1. Chemotaxis sensitivity function $F_0(p,\alpha)$ for various values of the parameter $\alpha = 0.1$ (solid curve), 0.3 (dotted curve), and 0.5 (dashed curve)

If the total amount of a repellent in the system is fixed ($\alpha = \text{const}$), the corresponding dependences $F_0(p)$ (for various α's) are shown in Fig. 1. Expectedly, the function $F_0(p, \alpha = \text{const})$ monotonically decreases with the growth of the parameter p. At $p < \alpha$, the repellent concentration profile $s(z)$ increases linearly with the coordinate z. Therefore, the bacteria

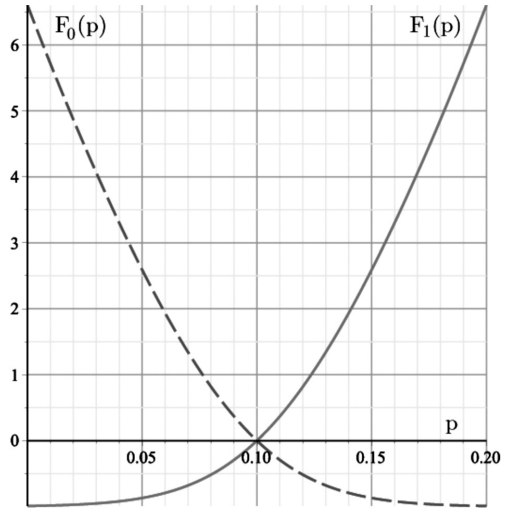

Fig. 2. Chemotaxis sensitivity function $F_1(p, \alpha)$ for the parameter $\alpha = 0.1$ (solid curve). For comparison, the function $F_0(p, \alpha = 0.1)$ is also plotted (dashed curve)

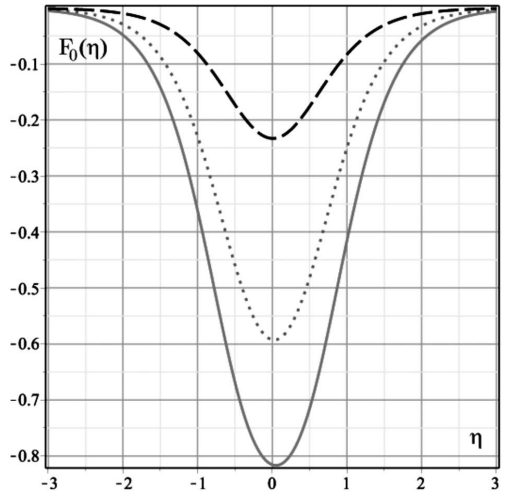

Fig. 3. Chemotaxis sensitivity function $F_0(\eta)$ for various values of the parameter $\xi = 0.75$ (solid curve), 0.85 (dotted curve), and 0.95 (dashed curve)

are located closer to the coordinate origin. At $p = \alpha$, the repellent distribution is uniform, so that the bacteria are also uniformly distributed over the system, and the chemotaxis sensitivity function equals zero. Finally, at $\alpha < p \leq 2\alpha$, the repellent concentration linearly decreases with the distance, so that the bacteria move to the end of the system. Accordingly, the bacterial concentration at the left boundary becomes lower than the average one, and the chemotaxis sensitivity function becomes negative.

The situation at the right boundary of the system is inverse. Figure 2 demonstrates plots for the dependences $F_0(p)$ and $F_1(p)$ with the same value of the parameter $\alpha = 0.1$. As was marked above, the plot of the function $F_1(p)$ is a specular reflection of the plot of the function $F_0(p)$ with respect to the vertical line $p = \alpha$. At $p < \alpha$, the repellent concentration increases, as the coordinate grows. Therefore, the bacteria move to the left boundary of the system. Accordingly, the chemotaxis sensitivity function $F_1(p)$ acquires negative values. At $\alpha < p \leq 2\alpha$, the repellent concentration in the system decreases, as the coordinate grows. Therefore, the bacteria move to the right boundary of the system in this case, and the chemotaxis sensitivity function $F_1(p)$ increases.

It is evident that if the total amount of a repellent in the system is fixed, the variation of its concentration at the boundary can result in the redistribution of bacteria only within certain limits. More interesting is a situation where the variation of the repellent concentration at the left boundary of the system is synchronously accompanied by the variation of the repellent amount in the whole system. In particular, let us consider a situation where a variation of the repellent concentration at the left boundary gives rise to a proportional variation of the repellent concentration at the right boundary,

$$s(0) = p, \tag{14}$$

$$s(1) = \xi p, \tag{15}$$

where the parameter ξ is fixed. In this case, the total amount of a repellent in the system is determined by the formula

$$\alpha = \frac{(1+\xi)p}{2}. \tag{16}$$

For the sake of convenience, we put $p = 10^{\eta}$ and introduce the notation

$$F_i(\eta) = F_i\Big(10^{\eta}, \frac{(1+\xi)10^{\eta}}{2}\Big), \tag{17}$$

where $i = 0$ and 1.

The dependences $F_0(\eta)$ for various values of the parameter ξ are plotted in Fig. 3. The function $F_0(\eta)$ has only negative values. It has a well-shaped profile with a minimum. The negativity of the function $F_0(\eta)$ follows from the fact that, under the given boundary conditions, the repellent concentration decreases

along the system. As a result, the bacterial concentration at the left boundary of the system is lower than the average concentration over the whole system. The well-shaped profile of the curve has the following explanation. With an increase of the repellent concentration at the left boundary of the system, the repellent concentration gradient also increases. Therefore, the nonuniformity in the bacterial distribution grows, and the chemotaxis sensitivity function decreases (increases by the absolute value). However, an increase of the repellent concentration at the left boundary also results in an increase of the total repellent amount in the whole system. Hence, the bacteria begin to demonstrate the saturation effect, when the repellent gradient is not sensed enough against a significant repellent concentration background. As a result, the bacterial distribution becomes more uniform, and the chemotaxis sensitivity function returns back to zero. As to the influence of the parameter ξ, it is evident that its smaller values correspond to larger values of the repellent concentration gradient, so that the extremum of the chemotaxis sensitivity function becomes more pronounced.

A similar situation takes place for the function $F_1(\eta)$. The only correction consists in that the function $F_1(\eta)$ accepts positive values. The plots of the function $F_1(\eta)$ for various ξ are shown in Fig. 4.

Explanations of the dome-shaped profile of the function $F_1(\eta)$ remain the same as for the function $F_0(\eta)$. It should also be noted that the effect obtained in our case is similar to that obtained for systems with an attractant [22–24].

5. Discussion of the Results Obtained

The model proposed in this work allows the bacterial distribution in the system to be calculated provided that the system contains a repellent. Despite the phenomenological character of the basic model, we have good grounds to hope for that the results obtained can be useful, while processing experimental data and predicting the behavior of bacteria in a repellent environment. Such hopes are based on the qualitative agreement between the simulation results and modern ideas concerning the behavior of bacteria in an active medium, as well as on the results of computer simulations for a system with an attractant [2]. Notwithstanding that, as for a repellent, the model used by us is similar to that proposed for a system with

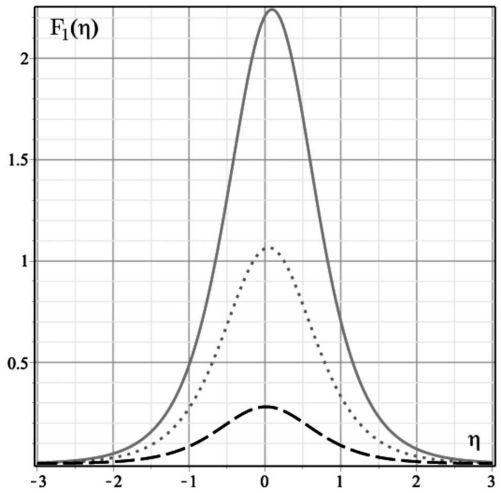

Fig. 4. Chemotaxis sensitivity function $F_1(\eta)$ for various values of the parameter $\xi = 0.75$ (solid curve), 0.85 (dotted curve), and 0.95 (dashed curve)

an attractant and had shown a good agreement of its predictions with the available results of numerical and real experiments [22–24].

The approach used in this work to calculate the chemotaxis sensitivity function also has a specific application value, because, in practice, it is much easier to measure the concentration of bacteria at a certain point than over the whole system. Concerning a possible experiment, its technique should be associated with the counting of the number of bacteria in a region, where an attractant or a repellent is injected [2] (in our case, this is one of system's ends). Therefore, the estimates obtained for the chemotaxis sensitivity function and their dependences on the repellent concentration at system's boundaries can be used directly for the processing of experimental data.

6. Conclusions

The results of calculations presented above testify that, by controlling the repellent distribution, it is possible to affect the bacterial redistribution. The regime of repellent injection is important in this case. If a variation of the repellent concentration does not change the ratio of concentrations on system's boundaries, then the dependence of the nonuniformity of the bacterial distribution, which is determined by the chemotaxis sensitivity function, on the repellent concentration is substantially nonlinear. At low repellent concentrations, an important factor is the

repellent concentration gradient. Due to the growth of the repellent concentration gradient, the bacterial distribution becomes more nonuniform. The increase in the total amount of a repellent leads to a lower sensitivity of bacteria to the repellent concentration gradient because of the saturation mechanism, so that the bacterial distribution becomes uniform again. It should also be emphasized that the described results were obtained provided that the total number of bacteria and the total amount of a repellent in the system are constant. If at least one of those conditions is violated in a real experiment, the corresponding changes have to be introduced into the model.

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МОДЕЛЮВАННЯ БАКТЕРІАЛЬНОГО ХЕМОТАКСИСУ В СЕРЕДОВИЩІ З РЕПЕЛЕНТОМ

Р е з ю м е

Розглядається хемотаксис бактерій в одновимірній системі за умови наявності там репеленту. Досліджується процес просторового перерозподілу бактерій в системі. Для цього пропонується феноменологічна математична модель. В моделі враховується дифузія бактерій та їх рух, пов'язаний із наявністю градієнту репеленту. Режим підведення репеленту в систему реалізується за рахунок граничних умов. Для такої системи розраховано функцію чутливості хемотаксису – числову характеристику, яка описує неоднорідність розподілу бактерій. Отримано залежність функції чутливості хемотаксису від концентрації репеленту на границях системи. Знайдено зв'язок між характеристиками розподілу репеленту та розподілом бактерій.