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MODEL OF CHEMOTAXIS IN A COMBINED ENVIRONMENT

We propose a model that describes the process of bacterial chemotaxis in a combined environment containing both an attractant and a repellent. The model is based on a system of differential equations that considers the effects of interaction of bacteria with both the attractant and the repellent. Within this approach framework, the chemotaxis effect turns out to be proportional to the concentration gradient of the corresponding substance (attractant or repellent). The model also revolves the saturation effect, when an increase in the concentration of the attractant or repellent reduces the bacterial response to the presence of a gradient in the concentration distribution of those substances. The chemotaxis sensitivity function has been used to analyze the heterogeneity of bacteria in the system. Its values are calculated at the system boundaries and, if there is an extremum in the bacterial distribution, at the extremum point. The dependence of the chemotaxis sensitivity function on the attractant and repellent concentrations has been analyzed. It is shown that this dependence is significantly nonlinear and differs qualitatively from similar dependences obtained earlier for systems containing only the attractant or the repellent.

K e y w o r d s: chemotaxis model, bacterium, attractant, repellent, concentration, distribution.

In theory, there is no difference between theory and practice. In practice, there is.
Yogi BERRA

1. Introduction

Recently, researchers have been interested in certain types of flagellated bacteria (such as *Escherichia coli* or *Salmonella enterica*), whose motility is provided by the rotational motions of their flagella [1–3]. Furthermore, the algorithm of bacterial motion depends on the parameters of the environment, where it occurs, and it is quite non-trivial. In particular, bacteria have receptors that can register certain substances to which the bacteria are sensitive. For example, such a substance is sugar for *Escherichia coli* bacteria, and the bacteria ultimately try to occupy an area, where the sugar concentration is maximum. Such a substance (which "attracts" bacteria) is called the *attractant*, and the corresponding phenomenon is called the *chemotaxis* [3–6]. There are also substances that bacteria try to avoid. A substance that "repels" bacteria is called the *repellent* [3, 4, 7].

As for the mechanisms of chemotaxis, the key fact is that bacteria, due to their relatively small size (of an order of a few micrometers), are not able to determine the presence of gradient in the attractant or repellent distribution and, hence, the direction in which they should move in order to enter

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the area with the highest attractant or the lowest repellent concentration. Therefore, bacteria use a certain algorithm, which allows them to move (on average) in the desired direction. Namely, a bacterium is not only able to register (using its receptors) the amount of attractant/repellent, but also to remember how much attractant/repellent it has registered during the motion. Technically, this mechanism is implemented through the number of receptors that enter the activated state as a result of the interaction with the attractant/repellent. The receptors remain in the activated state only temporarily. Therefore, actually, the bacterium "remembers" the amount of registered attractant/repellent for a certain time. Furthermore, since the total number of receptors is limited, there is a saturation phenomenon for bacteria, when all or almost all receptors enter the activated state, and the number of activated receptors does not increase further even in the presence of attractant/repellent [3, 6, 7].

The number of activated receptors (and, therefore, the amount of registered attractant/repellent) affects the character of the bacterial motion. In general, bacteria move evenly and rectilinearly. However, at some point, the bacterium stops and randomly changes the direction of its motion. This event is called *tumbling*. The tumbling frequency depends on the number of activated receptors: the more receptors are activated, the lower (for the attractant) or higher (for the repellent) the tumbling frequency. Since the number of activated receptors is determined by the amount of registered attractant/repellent, the tumbling frequency is lower/higher in those areas, where the attractant/repellent concentration is higher. More simply, the probability of changing the direction of bacterial motion decreases with the increase/decrease in the attractant/repellent amount [3].

Various approaches are used to model and analyze the bacterial motion [8–14]. One of the fundamental approaches is based on the application of a system of nonlinear differential equations of the diffusion type, which describe the distributions of attractant/repellent and bacteria in the system [8, 9, 12, 15–21]. The advantage of this approach is that it makes it possible to obtain numerical solutions and study the influence of boundary and initial conditions on the system, as well as consider the effects of varying other model parameters. This possibility is important in the application aspect, since it allows the results of theoretical research to be connected with available experimental data. Furthermore, in the framework of this approach, an important methodological paradigm is implemented, which makes it possible to consider the chemotaxis phenomenon as isomorphic to diffusion phenomena in systems with a complicated structure (see, for example, works [22–24]) and some biophysical systems such as a chemical synapse [25–28]. Although this approach, like all others, has certain drawbacks (for example, it is most effective, if the attractant/repellent concentration gradients are small [3, 29, 30]), it seems promising in many cases.

In this article, a model is proposed in which a system with bacteria contains both an attractant and a repellent, and the bacteria can react with both of them. That is, such a combined environment contains components that have opposite effects on the behavior of bacteria. As will be shown below, this circumstance manifests itself through quite interesting, nonlinear effects that are not reduced to a simple "superposition" of the interactions of bacteria with the attractant and the repellent.

2. Initial Equations of the Model

Let us consider a one-dimensional spatially limited system of size L, with the spatial coordinate $0 \le x \le \le L$. The concentrations of bacteria, attractant, and repellent are denoted as $b(x)$, $a(x)$, and $r(x)$, respectively. Since the stationary case is considered, those quantities depend only on the spatial coordinate and do not depend on time.

In the general case, the distributions of the attractant, $a(x)$, and the repellent, $r(x)$, are determined from stationary diffusion equations. It is easy to show that; in the one-dimensional case where the attractant and repellent concentrations are fixed at the system boundaries, the corresponding dependences are linear in the coordinate x. As for the concentration of bacteria, a similar diffusion-type equation is used to determine their distribution, but this equation should invo the presence of the chemotaxis effect. In the framework of the applied model approach (see, for example, works [8–12, 15–21]), the chemotaxis effect is taken into account through the corresponding term in the expression for the bacterial flow. Since, in our case, a combined environment with both an attractant and a repellent is considered, there are two such

terms. Namely, we assume that the flow of bacteria is determined by the following relationship [3, 17]:

$$\mathbf{j}_b(x) = -D\nabla b(x) + \\ + k_a \frac{b(x)\nabla a(x)}{(a_0 + a(x))^2} - k_r \frac{b(x)\nabla r(x)}{(r_0 + r(x))^2}, \quad (1)$$

where D is the diffusion coefficient of bacteria, and k_a, a_0, k_r, and r_0 are model parameters. The first term in expression (1) describes the diffusion motion of bacteria, whereas the second and third terms describe the effect of chemotaxis due to the presence of attractant and repellent, respectively, in the system. We have considered that these contributions are proportional to the attractant/repellent concentration or the number of bacteria, and they decrease as the attractant/repellent concentration increase due to the saturation effect (a more detailed discussion of the specific form of the term describing the effect of chemotaxis can be found, for example, in work [3] and the references therein).

The basic equation for determining the distribution of bacteria taking axis into account can be obtained by setting the bacterial flux to zero (see, for example, works [8, 15–18]),

$$D\frac{db}{dx} = k_a \frac{b(x)\frac{da}{dx}}{(a_0 + a(x))^2} - k_r \frac{b(x)\frac{dr}{dx}}{(r_0 + r(x))^2}. \quad (2)$$

After simple transformations, we obtain the following relationship:

$$b(x) = C \exp\left(\frac{1}{D}\left(\frac{k_r}{r_0 + r(x)} - \frac{k_a}{a_0 + a(x)}\right)\right), \quad (3)$$

where C is an integration constant. Formula (3) describes the dependence of the bacterial concentration in the system on the attractant and repellent concentrations.

3. Dimensionless Dependences

To determine the features of the bacterial distribution in the system, it is necessary to specify the boundary conditions for the distributions of attractant, repellent, and bacteria themselves. Namely, we assume that the mode of attractant/repellent input into the system is regulated by fixing the attractant/repellent concentration at the system boundaries. From a practical point of view, such a mechanism is the most convenient and easiest to implement in an experiment [3].

Let us assume that the zero attractant and repellent concentrations are maintained at the left boundary (at $x = 0$), i.e., $a(0) = 0$ and $r(0) = 0$. The constant concentration A of attractant and B of repellent are maintained at the right boundary (at $x = L$), i.e., $a(L) = A$ and $r(L) = R$. Then the spatial distributions of attractant and repellent concentrations are determined as follows:

$$a(x) = \frac{Ax}{L}, \quad (4)$$

$$r(x) = \frac{Rx}{L}. \quad (5)$$

The constant C in Eq. (3) is found from the condition that the concentration of bacteria in the system is constant and equal to B, i.e., $\int_0^L b(x)dx = B$:

$$C = \frac{B}{\int\limits_0^L \exp\left(\frac{1}{D}\left(\frac{k_r}{r_0 + \frac{Rx}{L}} - \frac{k_a}{a_0 + \frac{Ax}{L}}\right)\right)dx}. \quad (6)$$

For the further quantitative analysis, it is pertinent to make dimensionless all the above-mentioned relationships by putting $x = Lz$, $\alpha = \frac{k_a}{Da_0}$, $\beta = \frac{k_r}{Dr_0}$, and denoting $A_0 = \frac{A}{a_0}$ and $R_0 = \frac{R}{r_0}$. Also, instead of the dependence $b(x)$, we change to the dimensionless function $m(z) = \frac{Lb(x)}{B}$. Then, for the dependence $m(z)$, we obtain the following formula:

$$m(z) = \frac{\exp\left(\frac{\beta}{1+R_0 z} - \frac{\alpha}{1+A_0 z}\right)}{\int\limits_0^1 \exp\left(\frac{\beta}{1+R_0 z} - \frac{\alpha}{1+A_0 z}\right)dz}. \quad (7)$$

In fact, dependence (7) determines the spatial distribution of bacteria in the system. This distribution depends on the parameters A_0 and R_0, which are the values of the attractant and repellent concentration gradients, respectively.

4. Features of Bacterial Distribution

Even after the normalization, expression (7) contains some phenomenological parameters, so, its general analysis is of little interest. Let us consider a simplified, but at the same time important from a practical point of view, the case where the attractant and the repellent perform the actions of the same type, but differently directed. In particular, we will work in the

approximation $\alpha = \beta$ and $A_0 \approx R_0$. Then formula (7) can be written in the form

$$m(z) = \frac{\exp(f(z))}{\int\limits_0^1 \exp(f(z))dz}. \tag{8}$$

Here, we use the function

$$f(z) = \frac{\lambda z}{(1+kz)^2} \tag{9}$$

and denote $\lambda = \alpha(A_0 - R_0)$ and $k = A_0 \approx R_0$. Taking Eq. (8) into account, it is easy to understand that the extremum of the function $f(z)$, which is determined by Eq. (9, coincides with the extremum of the function $m(z)$ determined by Eq. (8). The function $f(z)$ has an extremum at the point $z = \frac{1}{k}$ (the maximum if $\lambda > 0$, and the minimum if $\lambda < 0$). However, for the argument z, there is the restriction $0 \le z \le 1$. Hence, the extremum of the bacterial distribution in the system occurs only if $k > 1$. Therefore, depending on the values of the parameters λ and k, the following types of bacterial distribution in the system are possible:

1) if $\lambda > 0$ and $k \le 1$, the bacterial concentration in the system monotonically increases as z increases from 0 to 1;

2) if $\lambda > 0$ and $k > 1$, the bacterial concentration in the system increases to a maximum located at $z = \frac{1}{k}$, and then it begins to decrease; in this case, the bacterial concentration at $z = 1$ is higher than that at $z = 0$;

3) if $\lambda < 0$ and $k \le 1$, the bacterial concentration in the system monotonically decreases as z increases from 0 to 1;

4) if $\lambda < 0$ and $k > 1$, the bacterial concentration in the system decreases to a minimum located at $z = \frac{1}{k}$, and then it begins to increase; in this case, the concentration of bacteria at $z = 1$ is lower than that at $z = 0$.

The characteristic distributions of bacteria in the system are illustrated in Fig. 1.

It is important that the parameters λ and k are determined by the maximum attractant and repellent concentrations at the right boundary $z = 1$. The maximum attractant and repellent concentrations are relatively easy to be controlled in the experiment, so, we consider λ and k as the control parameters of the system. The values of these parameters qualitatively affect the bacterial distribution.

5. Chemotaxis Sensitivity Function

To analyze the character of the influence of boundary conditions on the features of the bacterial distribution in the system, it is convenient to use such a quantity as the *chemotaxis sensitivity function* [3,15–21]. In general, this function is defined for a certain spatial region S as the deviation of the average bacterial concentration over the region S from the average bacterial concentration over the system S_{tot}, normalized by the average bacterial concentration over the system:

$$F(S) = \frac{\frac{1}{S}\int_S b(\mathbf{r})d\sigma - \frac{1}{S_{\rm tot}}\int_{S_{\rm tot}} b(\mathbf{r})d\sigma}{\frac{1}{S_{\rm tot}}\int_{S_{\rm tot}} b(\mathbf{r})d\sigma} =$$

$$= \frac{S_{\rm tot}}{S}\,\frac{\int_S b(\mathbf{r})d\sigma}{\int_{S_{\rm tot}} b(\mathbf{r})d\sigma} - 1, \tag{10}$$

where $\int_S b(\mathbf{r})d\sigma$ is the integral of the bacterial concentration over the region S (for which the chemotaxis sensitivity function is defined), and $\int_{S_{\rm tot}} b(\mathbf{r})d\sigma$ is the integral over the entire system.

If the region for which the chemotaxis sensitivity function is defined is localized in a vicinity of the point $\mathbf{r}$, and the region measure $S \to 0$, then the expression for the chemotaxis sensitivity function transforms to the following form:

$$F(\mathbf{r}) = \frac{S_{\rm tot} b(\mathbf{r})}{\int_{S_{\rm tot}} b(\mathbf{r})d\sigma} - 1. \tag{11}$$

With regard for relationship (8) and the obvious fact that $\int_0^1 m(z)dz = 1$, we obtain the following formula

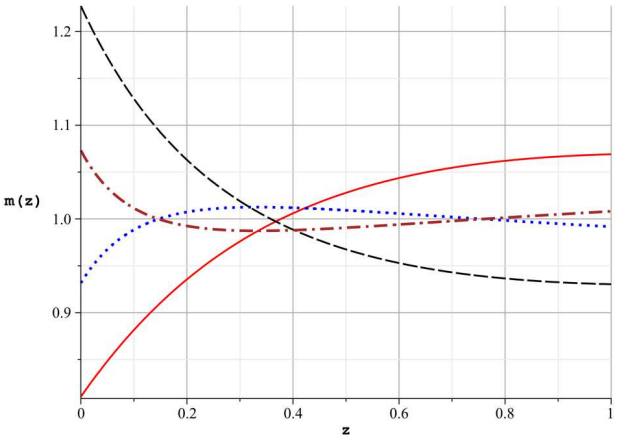

Fig. 1. Characteristic distributions of bacteria in the system with various parameters: $\lambda = 1$ and $k = 0.9$ (solid curve), $\lambda = 1$ and $k = 3$ (dotted curve), $\lambda = -1$ and $k = 0.9$ (dashed curve), $\lambda = -1$ and $k = 3$ (dash-dotted curve)

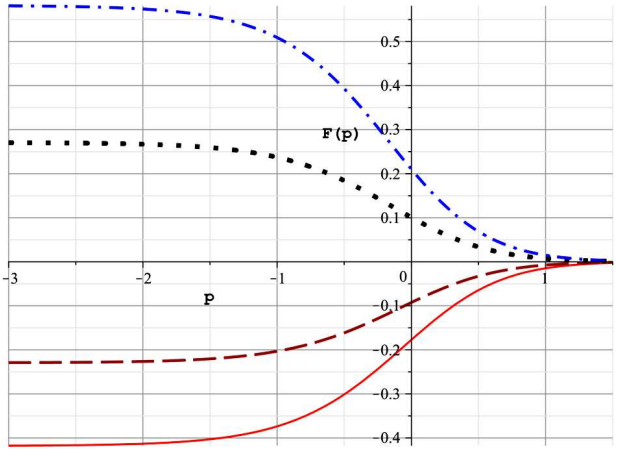

Fig. 2. Chemotaxis sensitivity function $F(p)$ at the left system boundary ($z = 0$) for various $\lambda = 1$ (solid curve), 0.5 (dashed curve), -0.5 (dotted curve), and -1 (dash-dotted curve)

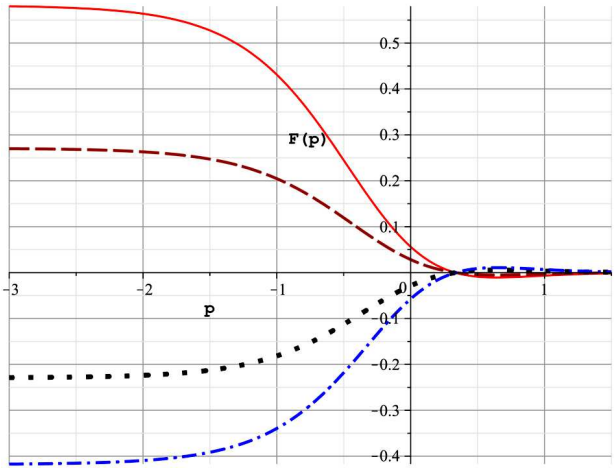

Fig. 3. Chemotaxis sensitivity function $F(p)$ at the right system boundary ($z = 1$) for various $\lambda = 1$ (solid curve), 0.5 (dashed curve), -0.5 (dotted curve), and -1 (dash-dotted curve)

for the chemotaxis sensitivity function at the point z in our specific case:

$$F(z) = m(z) - 1 = \frac{\exp(f(z))}{\int\limits_0^1 \exp(f(z)dz)} - 1. \tag{12}$$

On the one hand, this formula is trivial. However, it should be borne in mind that it is the dependence on the coordinate that is trivial. At the same time, the chemotaxis sensitivity function depends on the boundary conditions and, among other things, on the parameters λ and k. This dependence is not trivial in the general case [3, 15–21].

Let us consider the issue of the chemotaxis sensitivity function dependence on the parameters λ and k at the system boundaries and at those spatial points, where the bacterial concentration takes the highest and lowest values, if any. For convenience, let us put $k = 10^p$ and analyze the dependence of $F(z)$ on the parameter p. Figure 2 demonstrates the values that the chemotaxis sensitivity function takes on the left boundary of the system depending on the value of the parameter p for various values of the parameter λ. The dependences are monotonic: with the increase of the parameter p, the value of the chemotaxis sensitivity function $F(p)$ monotonically increases from negative values to zero if $\lambda > 0$, or monotonically decreases from positive values to zero if $\lambda < 0$. The value of the parameter λ affects the "amplitude" of the extreme value of the chemotaxis sensitivity function at $p \to -\infty$, which is equal, as can be easily shown, to

$$F(p = -\infty) = \frac{\lambda}{\exp(\lambda) - 1} - 1. \tag{13}$$

The chemotaxis sensitivity function behaves almost analogously at the right system boundary (with a change from the increase to the decrease, and vice versa when the sign of the parameter λ changes) when the parameter p grows. Namely, when p increases to zero, the chemotaxis sensitivity function monotonically decreases if $\lambda > 0$, and monotonically increases if $\lambda < 0$, as shown in Fig. 3.

At the same time, at the right boundary,

$$F(p = -\infty) = \frac{\lambda \exp(\lambda)}{\exp(\lambda) - 1} - 1. \tag{14}$$

If $p > 0$, the corresponding dependences have an extremum. The situation is illustrated in Fig. 4.

As was also indicated, for the values $k > 1$ (and, hence, for $p > 0$), the distribution of bacteria has an extremum at the point $z = \frac{1}{k} = 10^{-p}$ (this is a maximum at $\lambda > 0$ and a minimum at $\lambda < 0$). In Fig. 5, the dependences $F(p)$ at the point $z = 10^{-p}$ are shown for positive p-values. One can see that these dependences are monotonic (decreasing at $\lambda > 0$ and increasing at $\lambda < 0$), with a characteristic plateau in the center, where the change of the parameter p value has little effect on the change of the chemotaxis sensitivity function value. These dependences are qual-

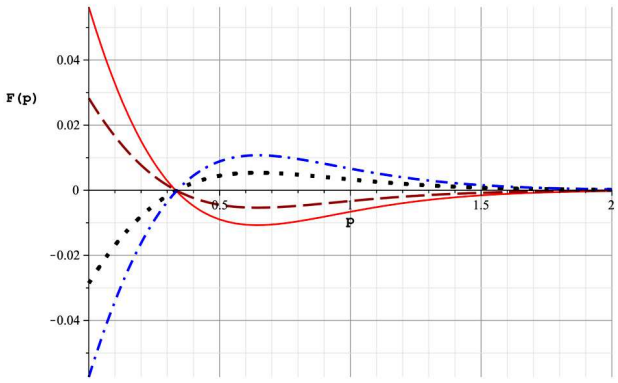

Fig. 4. Chemotaxis sensitivity function $F(p)$ at the right system boundary ($z = 1$) for $p \geq 0$ and various $\lambda = 1$ (solid curve), 0.5 (dashed curve), -0.5 (dotted curve), and -1 (dash-dotted curve)

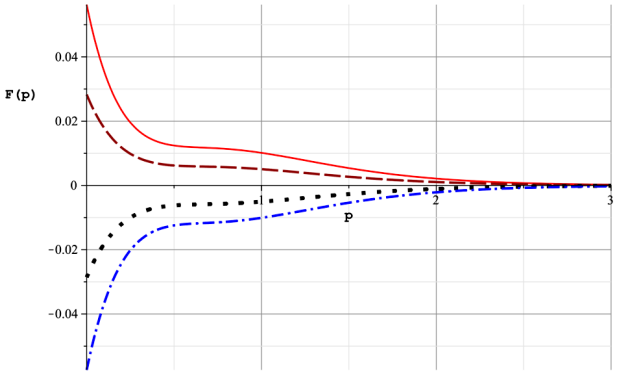

Fig. 5. Chemotaxis sensitivity function $F(p)$ at the internal extremum point ($z = 10^{-p}$) for $p \geq 0$ and various $\lambda = 1$ (solid curve), 0.5 (dashed curve), -0.5 (dotted curve), and -1 (dash-dotted curve)

itatively different from similar dome-shaped dependences obtained earlier for the chemotaxis sensitivity function of the systems containing only an attractant or a repellent [3, 15–21].

Figure 6 illustrates how the chemotaxis sensitivity function changes when the parameter p varies at the left boundary, at the point of maximum bacterial concentration, and at the right boundary, provided that $\lambda = 1$; only non-negative values of the parameter p are considered because the non-negativity of this parameter is a condition for the existence of an extremum in the bacterial distribution.

Similar dependences, but for $\lambda = -1$, are shown in Fig. 7. Of course, in this case, we deal with a minimum rather than a maximum in the distribution of bacteria.

In both cases, the behavior of the dependencies is quite predictable: as the parameter p increases, the inhomogeneity in the bacterial distribution decreases; as a result, the values of the chemotaxis sensitivity function at the system boundaries and at the extremum point tend to zero. This conclusion is also confirmed by the plots presented in Fig. 8 illustrating the chemotaxis sensitivity function values at the system boundaries in the absence of internal extremum at $\lambda = 1$ and negative p-values, and Fig. 9 illustrating the same dependences, but at $\lambda = -1$.

The fact that with the growth of the parameter p, the non-uniformity in the bacterial distribution decreases (with a possibility to have an extremum at positive p-values) has a non-trivial explanation. This occurs, because larger p-values mean an increase in

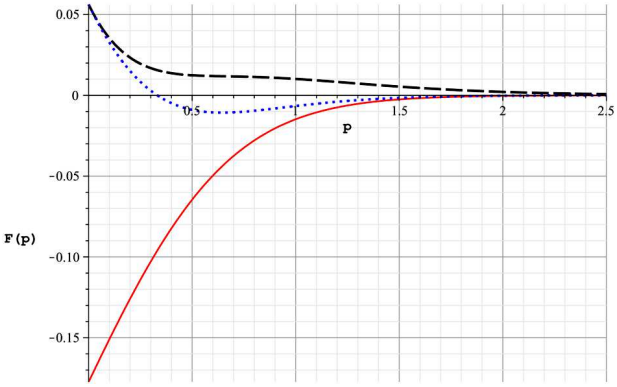

Fig. 6. Chemotaxis sensitivity function $F(p)$ at the left boundary (solid curve), the right boundary (dotted curve), and the point of maximum bacterial concentration (dashed curve). $\lambda = 1$ and $p \geq 0$

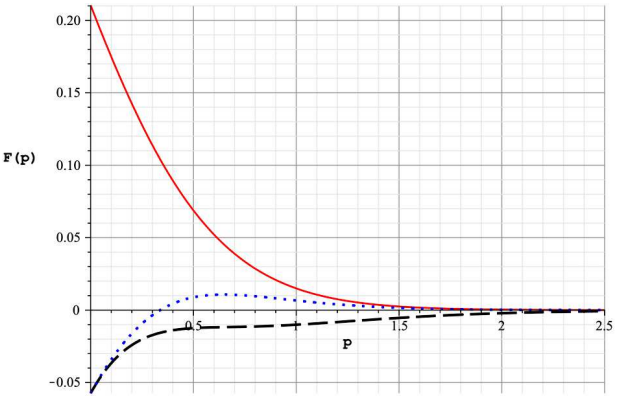

Fig. 7. Chemotaxis sensitivity function $F(p)$ at the left boundary (solid curve), the right boundary (dotted curve), and the point of minimum bacterial concentration (dashed curve). $\lambda = -1$ and $p \geq 0$

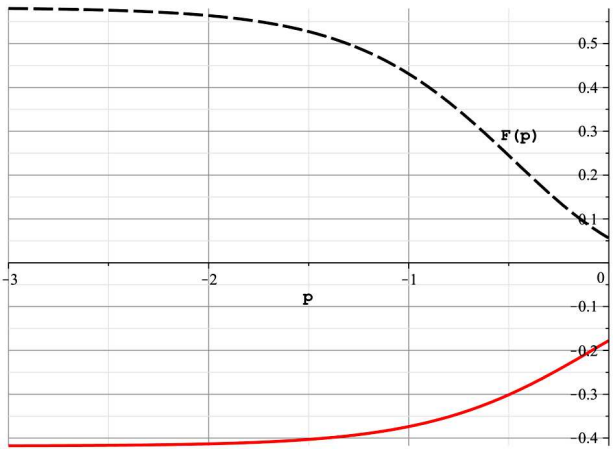

Fig. 8. Chemotaxis sensitivity function $F(p)$ at the left boundary (solid curve) and the right boundary (dashed curve). $\lambda = 1$ and $p \leq 0$

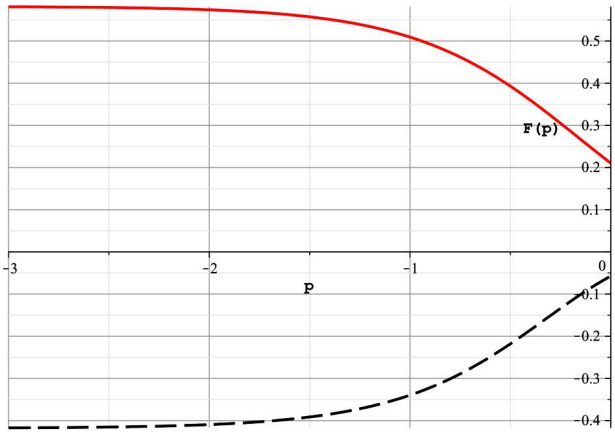

Fig. 9. Chemotaxis sensitivity function $F(p)$ at the left boundary (solid curve) and the right boundary (dashed curve). $\lambda = -1$ and $p \leq 0$

the attractant and repellent concentrations at the right system boundary (due to the relationship $k = 10^p$). According to Eqs. (4) and (5), this means that the gradients of the attractant and repellent distribution also increase. By formula (1), the terms describing the chemotaxis effect are proportional to the concentration gradient of the attractant or the repellent. However, since those terms contain the attractant/repellent concentration in the denominator, the growth in the total concentration of those substances reduces the chemotaxis effect. Therefore, actually, we have two oppositely directed effects. Furthermore, the presence of both the attractant and the repellent in the system also neutralizes their cummulative effect and does it in a nonlinear manner.

6. Conclusions

The model proposed in this paper can explain the peculiarities of the bacterial distribution in a system with a combined environment (in the presence of both the attractant and the repellent). The model involves the chemotaxis effects made by the attractant and the repellent, which have opposite directions, but their cummulative effect is not reduced to a simple superposition. To characterize the nonhomogeneity of the bacterial distribution in the system, the chemotaxis sensitivity function is applied, which is calculated at the system boundaries and, if there is an extremum point in the bacterial distribution, at this point. The change in the attractant and repellent concentrations at the right system boundary, where the attractant and repellent are introduced into the system, nonlinearly affects the chemotaxis sensitivity function. In this case, several competing effects take place. First, an increase in the gradient of the attractant or repellent concentration enhances the chemotaxis effect, but also causes an increase in the total amount of the attractant or repellent in the system, which brings the bacterial receptors into a saturation state and weakens the effect obtained from the larger concentration gradient of the corresponding substance. Second, the simultaneous presence of both the attractant and the repellent in the system partially compensates the combined effect of those substances. As a result, the behavior of the chemotaxis sensitivity function for a system with a combined environment (with the attractant and the repellent) differs substantially from that in the case of a system with only the attractant or the repellent.

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МОДЕЛЬ ХЕМОТАКСИСУ
В КОМБІНОВАНОМУ СЕРЕДОВИЩІ

У статті пропонується модель, яка описує процес хемотаксису бактерій у комбінованому середовищі, яке містить одночасно як атрактант, так і репелент. Модель ґрунтується на системі диференційних рівнянь, які враховують ефекти від взаємодії бактерій як з атрактантом, так і репелентом. У рамках цього підходу ефект від хемотаксису пропорційний до градієнта концентрації відповідної речовини (атрактанту чи репеленту). Також модель враховує наявність ефекту насичення, коли збільшення концентрації атрактанту чи репеленту зменшує відгук бактерій на наявність градієнта в розподілі концентрації цих речовин. Для аналізу неоднорідності розподілу бактерій в системі використовується функція чутливості хемотаксису. Її значення обчислюється на межах системи та, за наявності екстремуму у розподілі бактерій, в точці такого екстремуму. Аналізується залежність значення функції чутливості хемотаксису від концентрації атрактанту та репеленту. Показано, що така залежність є ступінчасто нелінійною і якісно відрізняється від аналогічних залежностей, отриманих раніше для систем, що містять лише атрактант чи репелент.

Ключові слова: модель, хемотаксис, бактерія, атрактант, репелент, концентрація, розподіл.