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Phil. Trans. R. Soc. B 2010 **365**, 1397-1403
doi: 10.1098/rstb.2009.0307

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2010) **365**, 1397–1403
doi:10.1098/rstb.2009.0307

Bacterial chemotaxis and entropy production

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Entropy production is calculated for bacterial chemotaxis in the case of a migrating band of bacteria in a capillary tube. It is found that the speed of the migrating band is a decreasing function of the starting concentration of the metabolizable attractant. The experimentally found dependence of speed on the starting concentration of galactose, glucose and oxygen is fitted with power-law functions. It is found that the corresponding exponents lie within the theoretically predicted interval. The effect of the reproduction of bacteria on band speed is considered, too. The acceleration of the band is predicted due to the reproduction rate of bacteria. The relationship between chemotaxis, the maximum entropy production principle and the formation of self-organizing structure is discussed.

Keywords: bacterial chemotaxis; reproduction rate; maximum entropy production principle

1. INTRODUCTION

Chemotaxis is the movement of microorganisms induced by some chemical attractant and is a basic and universal phenomenon among microorganisms (Eisenbach *et al.* 2004). The subject of this paper is chemotaxis of bacteria. Generally, in research of bacterial chemotaxis two lines of investigations have been taken. The first line is devoted to the collective behaviour of bacteria (see chapter IV in Eisenbach *et al.* 2004 and references therein) while the second one is devoted to the mechanisms of chemotactic response of the individual bacterium to the gradient of attracting or repelling chemicals (see chapter III in Eisenbach *et al.* 2004 and references therein).

Three types of collective effects in bacterial chemotaxis can be distinguished. The first type is associated with the introductory experiments performed by Adler (1966) and Nossal (1972) which have triggered an extremely high level of activity in research on chemotaxis. The second type makes complex patterns of spatial two-dimensional distribution of bacteria discovered by Budrene & Berg (1991, 1995). The third type is associated with different fractal patterns observed with bacteria colony spotted on medium containing relatively high agar concentrations (MacNeil *et al.* 1994; Ben-Jacob *et al.* 1995, 1998, 2000; Mendelson 1999; Matsyama & Matsushita 2001).

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One contribution of 17 to a Theme Issue 'Maximum entropy production in ecological and environmental systems: applications and implications'.

In theoretical approaches chemotaxis is usually described by kinetics equations. One writes the diffusion equations for concentrations of bacteria and attractants. Then the bacterial diffusion equations is extended with chemotactic and reproduction terms while the diffusion equation for attractant is extended by the reproduction term only. In these equations the chemotactic term plays the role of an additional thermodynamic force. From the mathematical point of view this is a system of two nonlinear diffusion equations. Using this approach the complex patterns, the aggregation, and the collapse of the swarm rings have been described (Budrene & Berg 1991, 1995).

Two objections can be raised against this approach. The first one relates to the chemotactic term. It is introduced *ad hoc* to explain chemotaxis. The second objection, connected with the first one, is the lack of a more basic principle underlying chemotaxis.

In order to avoid these objections we invoke maximum entropy production (MEP) principle as the key for understanding chemotaxis itself and the collective behaviour of bacteria in migrating bands.

The MEP principle states that the system with some degrees of freedom develops in such a way as to produce maximum possible entropy (Dewar 2003, 2005; Županović *et al.* 2005).

The basic features of *Escherichia coli* motion were discovered by Berg & Brown (1972). They found that it consists of an erratic turning stage (tumble) and a forward propulsion stage (run). A bacterium has sensors that detect the difference of concentration of the metabolizable chemicals (nutrients). In the tumble stage it explores the difference of the concentration of nutrient in, practically, all directions. It chooses the direction of

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the largest difference of nutrients for forward propulsion. A well-established feature of chemotaxis is the insensitivity of the tumbling frequency to the concentration of the metabolizable attractant (see Barkai & Liebler 1997 and references therein). It turns out that bacterium movement is not sensitive to the concentration of the chemoattractant but only to its gradient. Flux of nutrients is proportional to its gradient. In this way a bacterium moves through the region of the largest flux of chemoattractant.

It was found by Forrest & Walker (1964) that the increase of the concentration of nutrients is associated with the increase of the entropy production of bacteria. Since entropy production is proportional to the flux of nutrients we can reinterpret the conclusion by Forrest & Walker by saying that entropy production of bacteria is proportional to the flux of nutrients. In the case of *E. coli* the direction of attractant concentration gradient is the direction of the largest flux of metabolizable chemoattractant and the direction associated with the largest possible entropy production. Since bacteria choose this direction, then, according to Forrest & Walker (1964), we can say that bacteria, considered as the system, develop in accordance with the MEP principle.

Bacteria live in colonies. Then, according to the MEP principle, one expects that a colony will consume nutrients in such a way as to ensure the maximum possible gradient of metabolizable chemicals. Indeed such behaviour was observed by Adler (1966).

The paper is divided into five sections, of which this is the first. Basic facts of the bacterial chemotaxis are briefly exposed in §2. Theoretical background and model assumptions are the subject of §3. Results are summarized in §4. The most relevant results are summarized in §5.

2. PHENOMENOLOGY OF BACTERIAL CHEMOTAXIS

In this paper, we consider only the first type of collective chemotactic effects, that is, the movement of bacteria along the capillary tube. Most of these experiments have been done by Adler (1966). They have been carried out using capillary tubes with a homogeneous solution of galactose (or glucose) and oxygen as metabolizable attractant. Tubes were inoculated at one end with *E. coli* bacteria. Soon afterwards, two clear bands of bacteria were observed moving from the point of origin. In these experiments the following quantities were measured: the speed of bands, and the concentration profiles of bacteria, galactose, glucose and oxygen along the capillary tube. Adler also performed chemotactic experiments with *E. coli* in the Petri plates. Spreading rings of *E. coli* were observed. However, the results of these experiments were reported only qualitatively. Speed of the swarm rings and concentration of the bacteria in the rings were measured by Nossal (1972).

3. THEORETICAL BACKGROUND AND MODEL ASSUMPTIONS

Standard descriptions of metabolic processes are based on the concept of free energy, but any other thermodynamic potential could also be used. Bacteria and the solution of nutrients, which serve as metabolizable attractants, with the surroundings can be considered as an isolated system. Entropy is the thermodynamic potential suitable for description of the processes in an isolated system. According to the second law of thermodynamics, entropy is an increasing function of time. The most important quantity for the description of non-equilibrium processes in isolated systems is the entropy production $\mathrm{d}_i S/\mathrm{d}t$, where $\mathrm{d}_i S$ is the change of the entropy due to irreversible processes in the system within the time interval $\mathrm{d}t$. The idea that entropy production, rather than energy, is important in biology has become attractive since the studies of Prigogine & Wiame (1946) and Prigogine (1967).

In the chemotaxis experiment, the speed of change in the spatial distribution of chemoattractants is much less than the speed of movement of an individual bacterium (Brenner *et al.* 1998). This fact enables quasistatic description of the chemotaxis phenomenon in contrast to the standard one, which includes time as an important parameter (Keller & Segel 1970; Nossal 1972; Brenner *et al.* 1998).

Here, we introduce two postulates:

— For a fixed time the concentration of bacteria is proportional to the flux of incoming nutrient molecules.
— An average rate of the entropy production of a bacterium is a decreasing function of the concentration of bacteria.

The first postulate is based on the well-known fact that the reproduction of bacteria is an increasing function of the rate of supplied food. The second one is based on the self-evident fact that the more bacteria are concentrated in the same volume, with a fixed concentration of nutrients, the lower is the rate of the incoming nutrients to an individual bacterium and that leads to its lower entropy production.

According to our first postulate, the concentration of bacteria is proportional to the flux of nutrients,

$$\rho(x,t) = d(t) j_{\mathrm{c}}(x,t). \tag{3.1}$$

Here $\rho(x, t)$ and $j_{\mathrm{c}}(x, t)$ are the concentrations of bacteria and the flux of nutrient at point x and moment t, respectively; $d(t)$ is the delay function. A bacterium needs time to respond to the change in the nutrient flow. For example, the abrupt change in the nutrient flow is followed by continuous change in the concentration of bacteria. The characteristic time for the change of function $d(t)$ is the inverse reproduction rate.

Owing to the diffusion law, the flux is proportional to the gradient of the concentration of metabolizable attractants,

$$j_{\mathrm{c}}(x,t) = D|\nabla c(x,t)|, \tag{3.2}$$

where D is the diffusion constant of nutrients. Then we find that the concentration of bacteria is proportional to the gradient of the concentration of the nutrients,

$$\rho(x,t) = d(t) D|\nabla c(x,t)|. \tag{3.3}$$

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We note that the above relationship is different from the one derived by Nossal (1972). In the case of zero reproduction it follows from Nossal's (1972) equation that the concentration of bacteria is $\rho = a'(\nabla c/c)^2$. It is seen from this relationship that the concentration of bacteria is a function of the concentration of metabolizable attractant. This stands in contrast to the results of experiments done on individual bacteria (Barkai & Liebler 1997), and to the profile of bacteria concentration experimentally found in capillary tubes (Adler 1966).

Let us consider the experiments done by Adler (1966) with *E. coli* in capillary tubes. The capillary was inoculated at one end with bacteria. After a while, part of the bacteria separated into a migrating band. Bearing in mind the experimental fact that bacteria in a band leave a zero concentration of nutrient behind (Adler 1966), the above equation offers us the possibility to find the number of bacteria $N(t)$ in the band. Simple integration of equation (3.3) gives

$$N(t) = d(t)DAc_0, \tag{3.4}$$

where c_0 is the starting (or still non-consumed) concentration of nutrients and A is the capillary cross section. Thus $d(t)$ can be experimentally determined by measuring the number of bacteria in the band.

The density of entropy production is

$$\frac{\mathrm{d}_i s}{\mathrm{d}t} = \rho(x,t)\frac{\mathrm{d}_i s_\mathrm{b}}{\mathrm{d}t}. \tag{3.5}$$

Here $\rho(x, t)$ is the concentration of bacteria and $(\mathrm{d}_i s_\mathrm{b})/\mathrm{d}t$ is the mean entropy production per a bacterium owing to the dissipation of the chemical free energy of nutrients associated with bacterium metabolic activity, respectively. Entropy production due to the heat flux is not included.

In order to make the analysis as simple as possible, we assume the power-law dependence of mean entropy production per bacterium on the concentration of bacteria

$$\frac{\mathrm{d}_i s_\mathrm{b}}{\mathrm{d}t} = b\rho^{-n}, \tag{3.6}$$

where b is the characteristic constant for a given metabolizable attractant.

The non-physical divergence in the point with zero bacterium density has no significant effect at the final result since the relevant quantity is the density of entropy production. It is equal to

$$\frac{\mathrm{d}_i s}{\mathrm{d}t} = b\rho^{1-n}, \quad 0 < n < 1. \tag{3.7}$$

The requirement $1 > n > 0$ ensures that the entropy production is an increasing function of the concentration of bacteria. The total entropy production is

$$\frac{\mathrm{d}_i S}{\mathrm{d}t} = bA[d(t)D]^{1-n}\int |\nabla c|^{1-n}\,\mathrm{d}x. \tag{3.8}$$

The concentration of nutrients is given by

$$c(x,t) = c_0 f(x,t), \tag{3.9}$$

where $f(x, t)$ is a dimensionless function with asymptotes

$$\lim_{x\to-\infty} f(x,t) = 0 \quad \text{and} \quad \lim_{x\to+\infty} f(x,t) = 1. \tag{3.10}$$

Then we get

$$\frac{\mathrm{d}_i S}{\mathrm{d}t} = b[d(t)D]^{1-n}c_0^{1-n}IA, \tag{3.11}$$

where $I = \int_{-\infty}^{\infty}(\mathrm{d}f/\mathrm{d}x)^{1-n}\,\mathrm{d}x$.

On the other hand, the total entropy production of the band is proportional to the ratio of the consumed nutrient and the corresponding time interval. Since a barrier of nutrient moves with v_b, it follows that the entropy production is

$$\frac{\mathrm{d}_i S}{\mathrm{d}t} = v_\mathrm{b}c_0 A s_n, \tag{3.12}$$

where s_n is the entropy production associated with the dissipation of free chemical energy due to the consumption of one nutrient molecule. Then from equations (3.11) and (3.12) it follows that

$$v_\mathrm{b} = b\,[d(t)D]^{1-n}\,I\frac{1}{s_n c_0^n}. \tag{3.13}$$

It follows from equation (3.4) that the delay function $d(t)$ relates to the starting number of bacteria and the number of bacteria at the moment t, i.e.

$$N(t) = N(0)\frac{d(t)}{d(0)}. \tag{3.14}$$

Assuming that the elapsed time is much less than the reproduction time an exponential law of bacteria growth can be approximated with linear law. The same assumption regarding reproduction of bacteria during chemotaxis has been made by Burdene & Berg (1995). In terms of the reproduction factor r, we can write

$$N(t) = N(0)(1 + r\,t). \tag{3.15}$$

At the moment of the separation of the band from the colony its speed is $v_\mathrm{b}(0)$. Owing to reproduction, this value increases to v_b. In the case of the short time interval t, we can relate these two values with acceleration, $v_\mathrm{b}(t) = v_\mathrm{b}(0) + a_\mathrm{acc}t$. Here a_acc is band acceleration. It follows from equations (3.13)–(3.15) that acceleration of the band is

$$a_\mathrm{acc} = v_\mathrm{b}(0)(1 - n)r. \tag{3.16}$$

4. RESULTS

We focus on the experimental data from Adler's (1966) paper with oxygen considered as nutrient. These data suggest that concentrations of oxygen and *E. coli* are the unsymmetrical and symmetrical functions of coordinate x, respectively. The fact that these functions have different parities is in accordance with our equation (3.3). In order to check these results quantitatively, we have fitted experimental results with hyperbolic functions.

A concentration profile of oxygen taken from Adler's (1966) paper is fitted by the function $\tanh[(x - x_0)/\varepsilon]$ (see figure 1*a*). The corresponding

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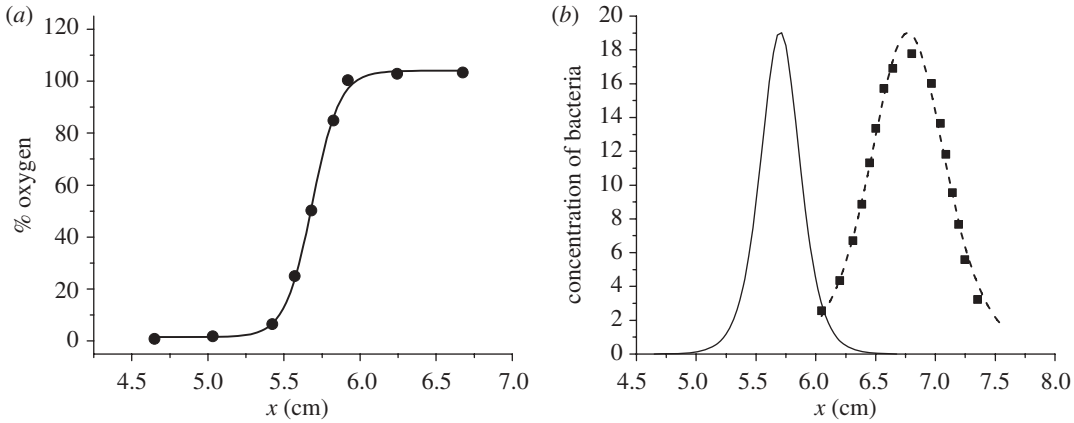

Figure 1. (*a*) The fit (solid line) of the experimentally determined data (dots) of the concentration of oxygen (Adler 1966) as the function of coordinate x with a hyperbolic function. Coordinate axis x is aligned along the capillary tube. (*b*) The concentration of *E. coli* as the derivation of the hyperbolic function from figure 1*a* (solid line) (see equation (3.3)) and the fit (dashed line) of the experimentally determined data (dots) of the concentration of *E. coli* (Adler 1966). The maximum of the function derived from equation (3.3) is equal to the maximum of the fitted curve. Note that peaks on this figure do not coincide. The shift is due to measurements of profiles of concentrations of oxygen and bacteria at different times. A difference in width of concentration of bacteria calculated from concentration profile of oxygen and measured concentration of bacteria is discussed in the text.

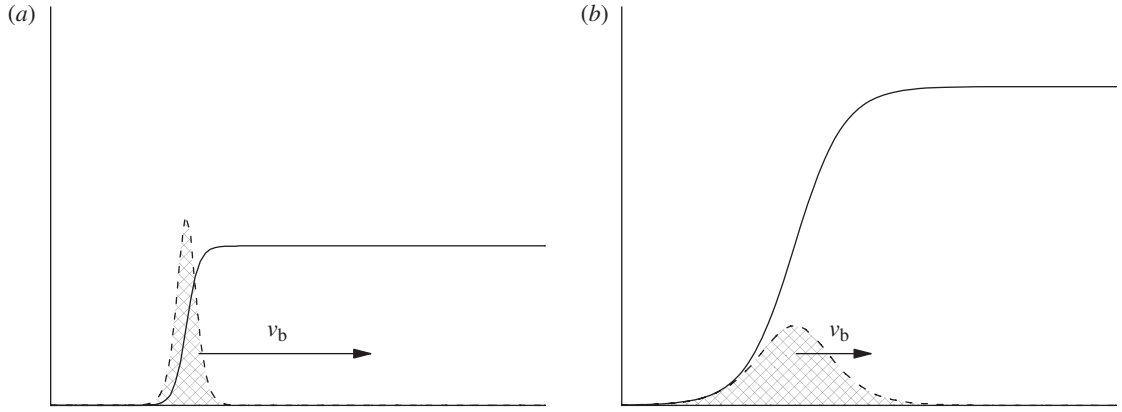

Figure 2. The decrease of band speed due to an increase in the concentration of nutrients (a → b).

concentration of the bacteria calculated as its derivation (equation (3.3)) is shown by the solid line in figure 1*b*.

The concentration profile of *E. coli* (fig. 2 in Adler's 1966 paper) is fitted with the derivation of the hyperbolic tangent function, $\cosh^{-2}[(x - x_0)/\varepsilon^*]$. Fit is shown by the dashed curve in figure 1*b*. The excellent fit proves that there is no significant asymmetry in the bell-shaped distribution of *E. coli* in the migrating band. If the concentration of bacteria were dependent on the concentration of nutrients, the bell-shaped function should be an asymmetrical one, owing to the large difference between the concentrations of oxygen at its edges. The discrepancy in widths between the experimentally determined profile of bacteria concentration and the one used to fit the experimentally determined concentration of oxygen (ε) can be attributed to the resolution of the measurement.

We note that, in contrast to the experiments with individual *E. coli* mentioned at the beginning of this section, the gradients of oxygen, galactose and glucose concentrations in Adler's experiments are not externally applied but are created by the metabolic activity of *E. coli* in an otherwise homogeneous solution of nutrients.

Table 1. The characteristic exponents n of the metabolizable attractants.

metabolizable attractant	n
oxygen	0.31
glucose	0.62
galactose	0.9

It follows from equation (3.13) that the speed of a band in a capillary is a decreasing function of the starting concentration of nutrients (see figure 2). We have used the power-law function to fit the experimentally determined dependence of the band speed on the starting concentration of the nutrient (see figs 9,10 and 12 in the reference Adler 1966). The exponent is the characteristic of the nutrient. The results are shown in table 1. We note that all values of exponent n fall into the interval (0,1), as predicted by our theory (compare equation (3.7) and table 1).

From this equation, it is clear that the higher exponent n means less acceleration. This result is in

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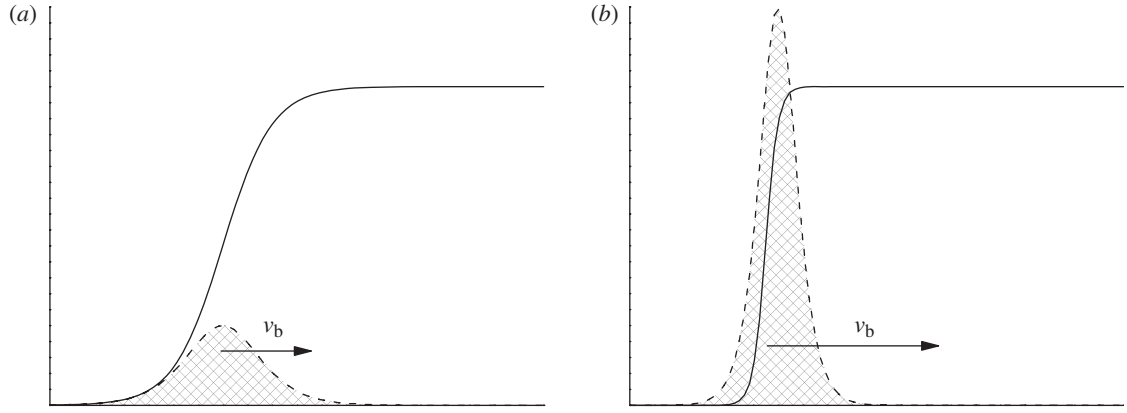

Figure 3. The increase of the slope of the barrier of nutrient (a → b) and the acceleration of the migrating band due to the reproduction of bacteria at a fixed concentration of the nutrient.

accordance with the experimental fact that the band consuming oxygen ($n = 0.31$) is faster than the one consuming galactose ($n = 0.9$) (see fig. 2 from Adler 1966).

The acceleration of the migrating band can easily be interpreted in terms of the entropy production of the whole band. Owing to reproduction of the bacteria, the total entropy production of the band increases. In the case of a fixed concentration of the non-consumed nutrient c_0, the band needs to accelerate in order to meet the increased need in entropy production (see equation (3.12)). The acceleration of the band, or barrier of nutrient, is accompanied by an increase in the diffusion flux. Using the law of diffusion (equation (3.2)), we find that the acceleration of the band is accompanied by an increase in the nutrient barrier slope (see figure 3). We note, in addition, that the acceleration of the bands was experimentally detected by Nossal (1972) and Budrene & Berg (1995) in the case of metabolizable and non-metabolizable attractants, respectively. Furthermore, qualitative analysis based on figure 3 suggests that acceleration of the band is accompanied by a narrowing of the barrier of the metabolizable attractant. The width of the barrier defines the width of the band. This means that acceleration is accompanied by an increase in the total number of bacteria and by the shrinkage of the band. Indeed, in the case of spreading swarm rings, this effect was observed (Nossal 1972).

In order to be more specific, we use equation (3.16) to find that the ratio between speeds of bands consuming different nutrients is

$$\frac{v_1}{v_2} = \frac{a_{\mathrm{acc1}}}{a_{\mathrm{acc2}}} = \frac{v_{\mathrm{b1}}(0)(1-n_1)r_1}{v_{\mathrm{b2}}(0)(1-n_2)r_2}. \tag{4.1}$$

Assuming that starting speed is not a function of chemoattractant and the same reproduction factors $r_1 = r_2$, we can roughly estimate the ratio between speeds of bands

$$\frac{v_1}{v_2} = \frac{(1-n_1)}{(1-n_2)}. \tag{4.2}$$

By means of table 1 our rough estimation is that speed of the first band in Adler's experiment should be 7 times greater than the speed of the second band. This result is in accordance with the measured values which show that the ratio of speeds is approximately 5.

5. CONCLUSIONS

Biochemical processes in living species occur far from the thermodynamic equilibrium. In order to describe them, one must resort to non-equilibrium thermodynamics. In this paper, thermodynamic analysis of the motion of the migrating bands is done in terms of entropy production only. There are two important results of this paper.

The first one considers the speed of the band as the function of the starting concentration of nutrients. The power-law dependence is used. From the thermodynamic consideration, it follows that the exponent should be within the interval $0 < n < 1$. The exponents of the power-law functions are obtained by fitting experimental results obtained by Adler (1966). It was found that they were indeed within the predicted interval.

The second result is the prediction of band acceleration caused by the reproduction of bacteria. In the case of constant rate reproduction, a simple relationship between acceleration, initial speed and rate of reproduction is predicted. We note that acceleration of the ring in the Petri plate with metabolizable attractant, accompanied by the reproduction of bacteria, has been observed (Nossal 1972).

We claim in this paper that bacterial chemotaxis is rooted in the MEP principle. To be more specific let us reconsider the experiments done by Adler (1966). The migrating band comes from the colony of *E. coli* that is placed at one end of a capillary tube. For pedagogical reasons, we call it the left end. Initially, a small number of *E. coli* bacteria at the free border of the colony create a small gradient in nutrient concentration. Owing to the chemotaxis effect, this small gradient attracts other *E. coli* bacteria from the colony, which reinforces this gradient. In this way positive feedback is established in the system. Owing to the positive feedback the gradient becomes as high as possible. This means that the flux of nutrients is the maximum possible. The speed of the barrier of

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nutrients is the maximum possible, too. Then, according to equation (3.12), entropy produced by bacteria is the maximum possible. In other words, the stationary state is established when entropy production reaches its maximum possible value. We have considered briefly accelerated bands. Accelerating bands are tightly connected with the reproduction of bacteria. At a certain concentration of bacteria reproduction diminishes to zero and a band finds itself in a stationary state. Acceleration of a band is just its transient state to the stationary state. We point out that analysis of experimental results obtained on both individual *E. coli* and on colonies of *E. coli* in capillary tubes show that the chemotaxis induced by a metabolizable attractant is in agreement with the MEP principle. We note that the conclusion drawn by Forrest & Walker (1964) is in accordance with the MEP principle, too.

This principle has been successfully applied in climatology (Paltridge 1981; Kleidon *et al.* 2003). Paltridge found excellent fit of measured values for annual average distribution of temperatures at the Earth surface with predictions from the MEP principle.

Shimokawa & Ozawa (2001) have applied this principle to the problem of oceanic circulation.

Linear non-equilibrium thermodynamics covers processes close to equilibrium in physics and chemistry. In this case, established distribution of the fluxes is associated with the maximum possible entropy production (Županović *et al.* 2004, 2005; Botrić *et al.* 2005).

The MEP principle and principles similar to the MEP principle are associated with several different theories of development of biological systems (see reference Martyushev & Seleznev 2006 and references cited therein).

Among these theories, we single out Swenson's theory. This theory is based on two principles (Swenson 1997):

— The universe develops in such a way as to achieve the final state as soon as possible.
— The appearance of ordered subsystems leads to more efficient realization of the former principle.

These statements are nothing but qualitative interpretation of the MEP principle. As an example, Swenson describes a tornado as an illustration of his principles. A tornado, in contrast to ordinary wind, is higher in the hierarchy of organized atmospheric structures. It is not just movement of air mass from the place of high pressure to the place of low pressure, but includes many finer details in its clearly visible structure. However, this organized structure produces entropy much more efficiently than less organized structures such as ordinary wind. A similar example is the formation of Bénard convection cells that appear as spontaneously arising structures in a liquid layer when heat is applied from below. At the critical temperature gradient the heat conduction is replaced with the convection that produces entropy much more efficiently than heat conduction. A migrating band in bacterial chemotaxis is also a spontaneously formed structure. As we have explained above this structure produces entropy most efficiently. In other words bacterial chemotaxis is another example of the Swenson (1997) theory.

The principle of maximum information entropy formulated by Jaynes (1957*a*,*b*) has proved itself a useful predictive method in ecology (Shipley *et al.* 2006) and theory of information (Ishwar & Moulin 2005). The application of this principle to non-equilibrium thermodynamics led to the derivation of the maximum entropy production principle (Jones 1983; Dewar 2003, 2005; Županović *et al.* 2006). According to the MEP principle, a system develops in such a way as to produce the maximum possible entropy. This principle has been so far successfully applied in physics (Županović *et al.* 2004, 2005; Botrić *et al.* 2005), chemistry (Županović & Juretić 2004), biology (Juretić & Županović 2003; Županović & Juretić 2004; Dewar *et al.* 2006), climatology (Paltridge 1981; Kleidon *et al.* 2003) and oceanography (Shimokawa & Ozawa 2001). A very nice review on the MEP principle and its applications in physics, chemistry and biology has been written by Martyushev & Seleznev (2006).

The present work was supported by the bilateral research project of Slovenia-Croatia Cooperation in Science and Technology, 2007–2008 and Croatian Ministry of Science grant no. 177-1770495-0476 to DJ.

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