Bacterial Motility via Diffusion Adaptation

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***Abstract*—Bacteria forage by moving towards nutrient sources in a process known as chemotaxis. The bacteria follow gradient variations by tumbling or moving in straight lines. Both modes of locomotion are affected by Brownian motion. Bacteria are also capable of interactions through chemical signaling. As the bacteria swim towards nutrients, they emit chemicals that can be sensed by their neighboring bacteria and used to adjust the direction of motion. In this paper, we propose schemes for cooperation and diffusion of information [1]–[7] and study their effect on bacteria motility. Because bacteria are limited in their abilities, we restrict the sharing of information to binary choices (such as whether to run or tumble). Simulation results suggest that cooperation among bacteria is critical for effective foraging to improve their decisions of movement.**

I. Introduction

Bacteria are single-cell microscopic organisms. They survive by foraging for nutrients in the environment in a manner that maximizes their energy intake per unit time [8]. In the process of foraging, motility plays a critical role. Bacterial movement is not purely random or arbitrary. Instead, bacterial cells exhibit directed movement in response to certain stimuli and away from others; a behavior known as "taxis" [9]. There are three types of taxes: chemotaxis, phototaxis, and magnetotaxis. Chemotaxis is the most common form of locomotion for bacteria [10]. It is the phenomenon by which bacteria move in response to certain chemicals in the environment.

Bacteria can move using a variety of mechanisms. Flagella are used for swimming through liquids; bacterial gliding and twitching motility move bacteria across surfaces; and changes of buoyancy allow vertical motion [11]. Because flagellum-dependent motility has been extensively studied, we will only focus on this kind of movement. Bacteria with flagella have two distinct modes of movement: forward movement if the flagella rotate clockwise and tumbling if the flagella rotate counter-clockwise. The two modes alternate and have different active durations. The mean run interval is about 1s, whereas the mean tumble interval is about 0.1s. Both times are exponentially distributed. The bacteria run and tumble, exhibiting a two-dimensional random walk. Although the change in angle generated by a tumble is approximately random, there is a slight forward bias. When, by chance, a bacterium moves up a spatial gradient of a chemical attractant, e.g., nutrients or other chemical signals, runs are extended. When, by chance, it moves the other way, running duration revert to the length observed in the absence of a gradient. Thus, the bias in the random walk enables bacteria to move up gradients. Finally, the behavioral response is temporal, not spatial. Bacteria do not determine whether there is more attractant, say, in front than in the back; rather, they determine whether the concentration increases when they move in a particular direction. Studies of impulsive stimuli indicate that a bacterium compares the concentration observed over the past 1s with the concentration observed over the previous 3s and responds to the difference [12].

Bacteria forage not only individually but also cooperatively to improve their sensing abilities. When a bacterium is far away from the nutrition, the density of nutrition will fall below a threshold that the bacteria can detect. Microbiologists have discovered that bacteria can communicate with each other by emitting and reacting to chemical signals in a process known as "quorum sensing" [13]–[18]. Bacteria use small molecules for extra- and intracellular signaling. They scan small molecule mixtures to access information about both their extracellular environment and their intracellular physiological status. Based on this information, they interpret the environment and react to the changes. This kind of interaction allows a group of bacteria to synchronize their behavior and act in coordination [13]–[18].

In summary, bacteria forage by moving towards the direction of increasing nutrients in response to chemical signaling. Their movement consists of two types of motion: run and tumble. In the long term, the motion can be viewed as a biased random walk. Besides, bacteria emit and react to chemical signals to communicate. And they cooperate and coordinate with others. They benefit from this inter-cell interaction to increase the chance of successful foraging.

Based on these facts, we now proceed to build a foraging model for bacteria. The model addresses four factors: motion, diffusion, observation, and decision. The motion model mimics the two-mode motility of bacteria. The diffusion model describes how bacteria diffuse information to each other over a network in an adaptive manner. The observation model characterizes how the bacteria receive information from others. And the decision model defines how bacteria make their decisions of movement in favor of foraging based on the information received from others. We propose diffusion and cooperation strategies to better understand the role of collaboration in bacteria foraging. We also present computer simulations to emulate the foraging behavior of bacteria and

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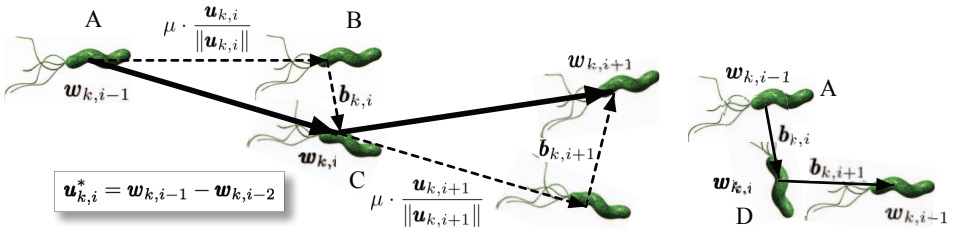


(a) Running mode (b) Tumbling mode

Fig. 1. Bacterial motion model with two modes of locomotion: running and tumbling.

compare cooperation strategies.

II. System Model

A. Motion model

During the running stage, the flagella rotate clockwise and the bacterium is pushed forward in its pointed direction. The moving direction is relatively fixed when the bacterium runs. During the tumbling stage, the flagella rotate counterclockwise and operate relatively independently of each other. As a result, the bacterium tumbles and has little displacement; its pointing direction would change randomly. A bacterium has limited control over its moving direction. The major aspect of its motion that it can control is whether to run in the current direction or to tumble around. Another prominent feature of bacteria motility is a Brownian motion effect, which is caused by the random hitting from the surrounding molecules in the medium. Even when the bacterium is in the running mode, its direction will still change in a random manner due to these collisions.

Based on these features, we model the motion of a bacterium k as follows:

$$\boldsymbol{w}_{k,i} = \boldsymbol{w}_{k,i-1} + \mu \frac{\boldsymbol{u}^*_{k,i}}{\|\boldsymbol{u}_{k,i}\|} e_k(i) + \boldsymbol{b}_{k,i}, \tag{1}$$

where $\boldsymbol{w}_{k,i} \in \mathbb{R}^2$ denotes the position in the plane of the kth bacterium at time i, $\boldsymbol{u}_{k,i}$ is a row vector that defines its pointing direction, μ is the size of the step it can move during one time interval, and $\boldsymbol{b}_{k,i} \in \mathbb{R}^2$ is an i.i.d Gaussian random vector modeling the Brownian motion and tumbling effect. The decision that the bacterium makes on whether to run or tumble is modeled by the variable $e_k(i)$, which takes the value of either 1 or 0 (depending on some assessment decision described in Sec III). For example, as shown on the left-side of Fig. 1, when $e_k(i) = 1$, the bacterium is running and aims to move from location A along the straight line determined by the direction $\boldsymbol{u}_{k,i}$ to location B. However, the Brownian motion effect adds a disturbance of $\boldsymbol{b}_{k,i}$, and the actual displacement ends up at C. On the other hand, when $e_k(i) = 0$, the bacterium is tumbling around and the displacement is $\boldsymbol{b}_{k,i}$; moving from A to D as shown on the right side of Fig. 1.

We assume the orientation of the bacterium is determined by the displacement vector during the last step, i.e.,

$$\boldsymbol{u}^*_{k,i} = \boldsymbol{w}_{k,i-1} - \boldsymbol{w}_{k,i-2}. \tag{2}$$

This means that, in the running mode, after moving from $\boldsymbol{w}_{k,i-1}$ to $\boldsymbol{w}_{k,i}$, the bacterium would continue to move in the direction of $\boldsymbol{w}_{k,i} - \boldsymbol{w}_{k,i-1}$ if there were no Brownian motion.

From (1) and (2), we obtain a recursion for $\boldsymbol{u}_{k,i}$:

$$\boldsymbol{u}^*_{k,i+1} = \mu \frac{\boldsymbol{u}^*_{k,i}}{\|\boldsymbol{u}_{k,i}\|} e_k(i) + \boldsymbol{b}_{k,i} \tag{3}$$

In the running mode, $e_k(i) = 1$. The self-propelled motion of the bacterium is generally much greater than the Brownian motion, i.e., $\mu \gg \|\boldsymbol{b}_{k,i}\|$. Therefore, the orientation of the bacterium will only change by a small amount, and the running directions in successive running steps are highly correlated. On the other hand, if the bacterium is tumbling around, then $\boldsymbol{u}^*_{k,i+1} = \boldsymbol{b}_{k,i}$, which is independent of $\boldsymbol{u}_{k,i}$, and the pointing of the bacterium will change randomly.

B. Problem formulation

From (1) and (3), we see that the main feature that the bacterium can control is the decision about whether to run or tumble around, namely, $e_k(i)$. This decision will generally be based on local stimuli (such as the nutritional gradient) and on information from the neighboring bacteria (through chemical signals). For the nutritional gradient, it is stated in [8] that the bacterium compares the nutritional density at location $\boldsymbol{w}_{k,i}$ say $J_n(\boldsymbol{w}_{k,i})$, with the previous density at location $\boldsymbol{w}_{k,i-1}$, and makes a decision based on the difference $J_n(\boldsymbol{w}_{k,i}) - J_n(\boldsymbol{w}_{k,i-1})$. The objective of the bacterium is therefore to design a sequence of decisions $e_k(i) \in \{0, 1\}$ $(i = 1, 2, \ldots)$ to adjust $\boldsymbol{w}_{k,i}$ so that the bacterium moves towards the maximum of the nutrition density, $J_n(\cdot)$.

III. Diffusion Adaptation

A. Measurement model

Bacteria communicate with each other through chemical signaling. If a bacterium wants to share information, it releases a chemical, which will remain in the environment until it decays. To characterize this effect, we assume the chemical field evolves in the following manner:

$$J_c(\boldsymbol{w}, i) = \lambda_c J_c(\boldsymbol{w}, i-1) + \sum_{\ell \in \mathcal{S}_D(i)} a(\boldsymbol{w}, \boldsymbol{w}_{\ell,i}) s_\ell(i) \tag{4}$$

where $J_c(\boldsymbol{w}; i)$ is the value of the chemical field at position $\boldsymbol{w}$ and time i, λ_c is the decay factor, $a(\boldsymbol{w}, \boldsymbol{w}_{m,i})$ is the chemical profile released by the mth bacterium, and $\mathcal{S}_D(i)$ is the set

of bacteria diffusing information at time i. Let $s_\ell(i) \in \{0,1\}$ indicate whether the ℓth bacterium diffuses information at time i. Then the chemical intensity measured by the kth bacterium at time i is

$$J_c(\boldsymbol{w}_{k,i}, i) = \lambda_c J_c(\boldsymbol{w}_{k,i}, i-1) + \sum_{\ell=1}^{N} a(\boldsymbol{w}_{k,i}, \boldsymbol{w}_{\ell,i}) s_\ell(i) \quad (5)$$

In (5), we assume that the bacteria only have the simple ability to decide whether to diffuse information or not by setting $s_\ell(i)$ to 1 or 0. They are not powerful enough to use "modulation" or "coding" schemes to broadcast messages with different contents. Still, we will see that such simple diffusion strategy works reasonably well.

It is shown in the literature that bacteria can sense different types of chemicals and are "multilingual" [15], [17]. For example, they can sense information from both the food source and the other bacteria independently by measuring nutrition and chemical densities, respectively. This mechanism is called "quorum sensing". Since we are denoting the density of nutrition at position $\boldsymbol{w}$ by $J_n(\boldsymbol{w})$, the observed nutrition density by the kth bacterium at time i will be

$$y_k^n(i) = J_n(\boldsymbol{w}_{k,i}) + v_k^n(i) \quad (6)$$

where $v_k^n(i)$ is the observation noise at the kth bacterium at time i when measuring the nutrition concentration. Likewise, the observed chemical intensity by bacterium k is

$$y_k^c(i) = J_c(\boldsymbol{w}_{k,i}, i) + v_k^c(i) \quad (7)$$

where $v_k^c(i)$ is observation noise for measuring the chemical signals. We assume that $\{v_k^n(i)\}$ and $\{v_k^c(i)\}$ are i.i.d Gaussian random variables with mean zero and variance σ^2 and σ_c^2, respectively, and that they are independent of each other.

B. Decision model

The decision model characterizes how a bacterium processes the received information and how it responds to the information. The information available to a bacterium is $y_k^n(i)$ and $y_k^c(i)$. The objective is to use the data to estimate the location of the maximum of $J_n(\boldsymbol{w})$ and to move in that direction. First, we need to recover J_n and J_c from the noisy measurements $\{y_k^n(i), y_k^c(i)\}$.

Since the densities $J_n(\boldsymbol{w}_{k,i})$ and $J_c(\boldsymbol{w}_{k,i}, i)$ are nonnegative, we can use this information to improve the estimation quality. If we assume the probability density functions of $J_n(\boldsymbol{w}_{k,i})$ and $J_c(\boldsymbol{w}_{k,i}, i)$ are flat over the positive axis and zero over the negative axis, i.e., we have no other information besides them being nonnegative, then the maximum a posterori estimates for these two variables are:

$$\hat{J}_{n,MAP}(\boldsymbol{w}_{k,i}) = \max\{y_k^n(i), 0\} \quad (8)$$

$$\hat{J}_{c,MAP}(\boldsymbol{w}_{k,i}, i) = \max\{y_k^c(i), 0\} \quad (9)$$

This step is equivalent to performing a *detection* on the observation, and then truncating it to zero if it is negative. Otherwise, we use the observation as the estimate.

For simplicity, we shall write $\hat{J}_n$ and $\hat{J}_c$ to represent the estimated values in the sequel. Based on the estimates $\hat{J}_n$ and $\hat{J}_c$, the bacterium then makes a decision on two aspects: whether to diffuse information, and whether to run.

For the diffusion decision, we assume the bacterium sets $s_\ell(i)$ in (5) as follows:

$$s_k(i) = I[e_k^n(i-1)] = \begin{cases} 1, & e_k^n(i-1) > 0 \\ 0, & e_k^n(i-1) \le 0 \end{cases}$$

where

$$e_k^n(i-1) = \hat{J}_n(\boldsymbol{w}_{k,i-1}) - \hat{J}_n(\boldsymbol{w}_{k,i-2}) \quad (10)$$

This means that, if the bacterium senses that the estimated nutrition density has increased during the last step of movement, then the bacterium diffuses the information out. In this way, the bacteria moving in the right direction towards the food will diffuse information to announce their likely discovery of the path. Since the chemical will remain in the environment for a while, the diffusion adds information about the nutrition source to the chemical field, which serves as a "food map" for the "unlucky" bacteria to find the food.

Another decision making for the bacterium is to determine which motility mode to use in the next step: running or tumbling. We assume the bacterium sets $e_k(i)$ by examining the nutritional gradient $e_k^n(i-1)$ in (10) and the chemical gradient defined by

$$e_k^c(i-1) = \hat{J}_c(\boldsymbol{w}_{k,i-1}, i-1) - \hat{J}_c(\boldsymbol{w}_{k,i-2}, i-2) \quad (11)$$

Based on the two increments $\{e_k^n(i-1), e_k^c(i-1)\}$, we consider several strategies to select $e_k(i)$ for this decision step:

- *Emphasis on nutrition and signaling*:

$$e_k(i) = \lambda_L \cdot I[e_k^n(i-1)] + (1-\lambda_L) \cdot I[e_k^c(i-1)] \quad (12)$$

  where $0 < \lambda_L < 1$. In this case, $e_k(i)$ is a convex combination of the indicator functions of the two increments.

- *Emphasis more on nutrition*:

$$e_k(i) = I[e_k^n(i-1)] + \delta[e_k^n(i-1)] \cdot I[e_k^c(i-1)] \quad (13)$$

  where $\delta(\cdot)$ is the Kronecker delta function. In this case, if the bacteria is certain about the change of nutrition density in the last step (either increase or decrease), it will ignore all chemical signals. In the next section, this strategy is combined with maximum a posterori estimation for decision making.

- *Emphasis only on nutrition (nocooperation)*:

$$e_k(i) = I[e_k^n(i-1)] \quad (14)$$

  In this case, the bacterium only relies on its measurement of the increment of nutrition. All chemical signals released by the other bacteria are ignored. This can be

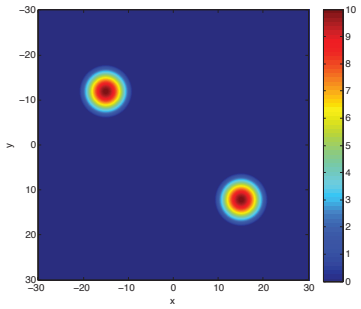
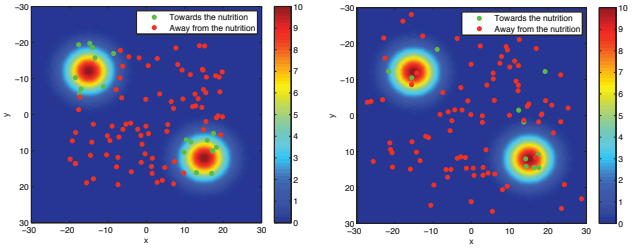
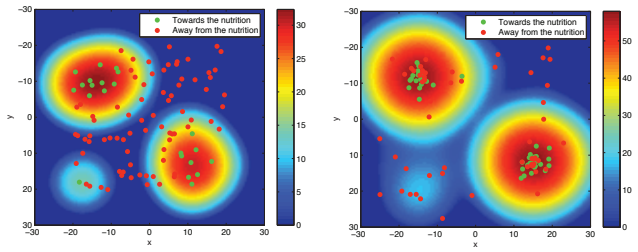


Fig. 2. The distribution of nutrition density.



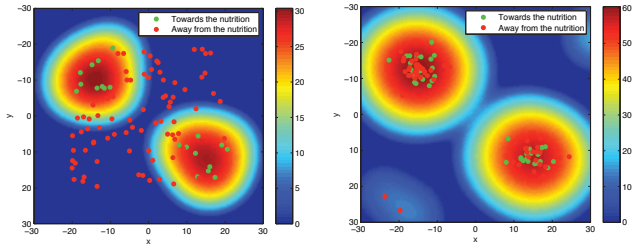
(a) Initial stage($T = 1$) (b) Final stage ($T = 1000$)

Fig. 3. Dynamic behavior based on model (14); emphasis is on nutrition only.



(a) Initial stage ($T = 1$) (b) Final stage ($T = 1000$)

Fig. 4. Dynamic behavior based on (12); emphasis is on both nutrition and chemical signaling.



(a) Initial stage ($T = 1$) (b) Final stage ($T = 1000$)

Fig. 5. Dynamic behavior based on (13); more emphasis is given to nutrition.

considered as a special case of linear cooperation with $\lambda_L = 1$.

In summary, $e_k(i)$, as a function of $e_k^n(i)$ and $e_k^c(i)$, aims to appropriately combine these two sources of information so that the decision strategy can result in a biased random walk towards the food.

IV. Simulation Results

In this section, we simulate the bacterial foraging behavior for the different cooperation strategies.

A. Simulation profile

Two identical nutrition sources are placed at locations $(-15, -12)$ and $(15, 12)$, respectively. Each source generates a nutrition field in the shape of a two-dimensional Gaussian distribution. Accordingly, the density of nutrition at location $w = (x, y)$ is given by

$$J_n(x,y) = b_{\max} \exp\left(-\frac{(x-x_1)^2 + (y-y_1)^2}{2\sigma_b^2}\right) + b_{\max} \exp\left(-\frac{(x-x_2)^2 + (y-y_2)^2}{2\sigma_b^2}\right),$$

where $(x_1, y_1) = (-15, -12)$, $(x_2, y_2) = (15, 12)$, $b_{\max} = 10$, and $\sigma_b = 4$. The nutrition field is shown in Fig. 2. Although the bacteria consume food during the foraging process, we assume that the density of nutrition is not affected appreciably. This can be achieved by, for example, continually replenishing the nutrition level.

At the beginning, bacteria are randomly and uniformly distributed over a 40×40 rectangular region centered at $(0, 0)$. Their Brownian motion is modeled as i.i.d. two-dimensional Guassian random variable with zero mean and 0.1 standard deviation. The step size is $\mu = 0.8$. Moreover, $v_k^n(i)$ in (6) is modeled as i.i.d. Guassian random variable with zero mean and unit variance.

The density of the chemical signals emitted by the bacteria is also modeled as a two-dimensional Guassian distribution. The chemical signal generated by the k-th bacterium is modeled as

$$a(\boldsymbol{w}, \boldsymbol{w}_k) = a_{\max} \exp\left(-\frac{(x-x_k)^2 + (y-y_k)^2}{2\sigma_a^2}\right), \quad (15)$$

where $\boldsymbol{w} = (x, y)$, $\boldsymbol{w}_k = (x_k, y_k)$ is the position of the kth bacterium, $a_{\max} = 5$, and $\sigma_a = 5$. The chemical signals generated by all bacteria are accumulated and decay exponentially according to (5), with $\lambda_c = 0.9$. Similar to $v_k^n(i)$, the noise $v_k^c(i)$ in (7) is also modeled as i.i.d. Guassian random variable with zero mean and unit variance. Finally, λ_L in (12) is set to 0.8.

B. Dynamic behavior of bacterial foraging

We simulate 200 bacteria and record the initial and final stage of the bacterial colony, as shown in Fig. 3–5.

Fig. 3 shows the case of no cooperation. Obviously, this mechanism does not work well–only a small fraction of the bacteria can successfully forage while the others fail to locate the nutrition source after 1000 iterations.

Figs. 4–5 correspond to the cases when the bacteria cooperate; we also plot the distribution of the chemical field. Fig. 4 is for the case that emphasizes both nutrition and chemicals. The figure shows that cooperation improves the precision of

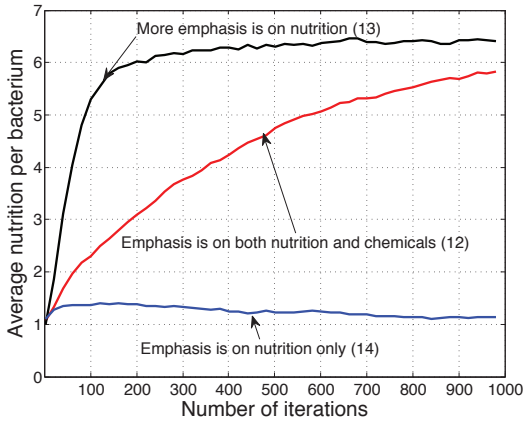


Fig. 6. Convergence speed of different diffusion and decision strategies.

foraging, but the bacteria that are far away from the nutrition sources still cannot find the target. Fig. 5 shows the case that emphasizes more on nutrition. It has the best performance and most bacteria converge to the nutrition sources.

C. Convergence speed of different strategies

We compare the convergence speed of different cooperation strategies by plotting $\frac{1}{N}\sum_{k=1}^{N} J(\boldsymbol{w}_{k,i})$ against i in Fig. 6. Obviously, the best strategy is (13). After 200 iterations, this strategy achieves a steady state where on average every bacterium enjoys a rather high (> 6) nutrition density. The strategy in (12) is inferior to the best case. It can achieve an average nutrition density value between 5 and 6 after 1000 iterations. The scheme without communication does not work well.

According to these results, we observe that communication between bacteria plays a critical role in their foraging behavior. By emitting and reacting to chemical signals, bacteria can efficiently share information and enhance the sensing and foraging ability of the group.

With inter-cell communication, it is important to choose the right combination strategy for local stimuli and neighborhood information. Our simulation shows that the one that emphasizes more on nutrition is effective, which can extract useful information from the noisy communication environment more efficiently.

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