A One-dimensional Discrete Model of Biased Random Walk Relating to Bacterial Chemo-taxis

Tomonobu Goto and Tonau Nakai

Tottori University, Japan

Abstract— A biased one-dimensional random walk model is proposed. This model adopts biased rules that include the features of bacterial chemo-taxis. In this model, a model cell moves along a discretized number line sensing whether it has approached or receded from the origin where a chemical attractant exists. A steady probability distribution function of the cell’s existence is analytically obtained and it is confirmed by numerical simulations. The biased rules introduce advection effect into random diffusive motion: the probability distribution indicates model cells’ accumulation around the origin, which corresponds to the spatial migration of bacterial cells around a chemical attractant.

Index Terms— Chemo-taxis, Bacterium, Random walk, Mathematical model

I. INTRODUCTION

Bacterial cells exhibit chemo-taxis in which they sense the density gradient of chemical molecules and swim to the higher concentration if the chemical is an attractant [1]. In an evenly dispersed concentration, bacterial cells swim in a random way, frequently changing directions. In the event that a chemical attractant diffuses from a source, the cells appear to be randomly swimming around that source. However, when a cell senses that it approaches a higher chemical concentration, the cell reduces the frequency in which it changes direction. Thus, each bacterial cell’s behavior results in a collective gathering around the source of the chemical.

In the present paper, a one dimensional model of the chemo-taxis by bacterial cells is proposed. This is a very simple mathematical model among many random walk models concerning biological behaviors [2]. The bacterial motion stochastically approaching the chemical attractant is modeled by simple rules. The probability distribution function around the chemical of a model cell that moves according to the rules is analytically obtained. The probability distribution function is numerically confirmed to be the distribution of a number of model cells that are governed by the rules. The model cells accumulate around the chemical. This distribution corresponds to the spatial migration of bacterial cells produced by the chemo-taxis.

II. BACTERIAL CHEMO-TAXIS

In this section, individual motion of bacterial cells and their chemo-taxis are briefly reviewed. Bacterial cells swim in aqueous media propelled by flagella. Each of bacterial cells, e.g. Escherichia coli or Salmonella typhimurium, possesses several flagella around its cell body. Each flagellum is driven by a rotary motor embedded on the surface of the cell body. The flagella which form a bundle with a helical shape rotate and propel the cell body much like the screw of a ship (e.g. [3], [4]). The flagellar bundle rotates counterclockwise when it is observed from the distal end. The bacterial cell swims almost straightly as shown in Figure 1(a). The swimming direction is parallel to the axis of the cell with a short cylindrical shape. When the rotary motors reversely rotate clockwise, the flagellar bundle comes apart as shown in Figure 1(b). During the process, the cell’s posture in the liquid medium randomly changes. Then, the cell

---

* Corresponding author: 4-101, Koyama-Minami, Tottori 680-8552, Japan, E-mail: goto@damp.tottori-u.ac.jp

---

Fig. 1. (a) A bacterial cell swims by using a bundle of flagella. This smooth motion is referred to as a ‘run’. (b) In a tumble, a bacterial cell changes its direction by loosening the flagellar bundle (e.g. [3], [4]). Thick open arrows in (b) indicate that time has elapsed.
swims to a different direction from the original track when the rotary motors return to rotate counterclockwise. Since the process is accomplished in a short time, it looks like that the cell suddenly changes its swimming direction. This process of sudden direction change is referred to as a ‘tumble’. Thus, a bacterial cell alternatively repeats ‘straight smooth swims (runs)’ and ‘random direction changes (tumbles)’.

Let us assume that a number of cells start from a point. The cells randomly swim and spread around. The distribution of the cells in a container will be uniform after a long time.

In contrast, if there is a source of a chemical attractant, the cells’ behavior changes. When a cell senses that it moves in a higher concentration of the chemical attractant, the cell reduces the tumble frequency and continues running [1]. Therefore, the random motion is biased to lead the cell to the source of the chemical as shown in Figure 2. Thus, cells accumulate around the source of the chemical. Their distribution concentrates at the source and the number density of the cells decreases as a function of the distance from the source.

The chemo-taxis by bacteria possesses some distinct properties. First, a bacterial cell needs to move a certain distance to sense chemical concentration distribution. The size of a cell is too small to sense the spatial distribution of the chemical at a time using two or more sensors. The cell senses the concentration at two different times and compares the concentration values. It needs to swim for a certain time period to determine whether it does tumble or does not. Second, a bacterial cell changes its direction randomly during a tumble. The cell’s posture after the tumble is determined by the fluid force exerted on the deforming flagella, and the cell body’s new posture will be random. The cell is not able to choose a proper direction to approach the chemical source. Whether to approach or to leave the chemical source is a stochastic process. Third, a cell does not stop even if the cell reaches the highest concentration of the chemical. The size of a cell may be smaller than the size of a local unevenness in chemical distribution. Not stopping at one position seems to be a suitable behavior to prevent it from being trapped at one point where the chemical concentration is at a local maximum value.

III. MATHEMATICAL MODEL: ONE-DIMENSIONAL DISCRETE MODEL

In our one-dimensional model, the motion of a bacterial cell is modeled as the discrete motion along a number line sectioned at equal intervals as shown in Figure 3. The distance between two adjacent intervals is $a$. The model cell moves one interval during one time step period $\Delta t$.

This setting appears in the classical mathematical model to deal with random walk (e.g. [5]). A model cell moves one interval during one time step period along a number line. The direction of its forward motion is randomly chosen, i.e. whether to move to the right-hand side or to move to the left-hand side is determined with the same probability of 1/2. The model produces diffusion process. When a number of model cells start from a position, the distribution of the cells becomes the normal distribution (Gaussian distribution) and its standard deviation is proportional to the square root of the time.

![Chemical attractant](image1)

![Chemical attractant](image2)

![Chemical attractant](image3)

**Fig. 2.** Bacterial chemo-taxis. (a) Two-dimensional schematic of the behavior of a bacterial cell. The dashed lines are iso-concentration lines of a chemical attractant that diffuses from a point. The red circles indicate tumbles. When the cell senses that the concentration of the chemical attractant increases as the cell moves, the cell reduces the frequency of tumbles. (b) Three-dimensional schematic on the bacterial cells’ accumulation. Left: without any stimulus, the bacterial cells are evenly distributed. Right: the cells gather around the source of a chemical attractant.

![Bias random walk](image4)

**Fig. 3.** The rules for the biased random walk in the present study. When a cell approaches the origin in a time step, it continues to move in the same direction in the next time step (purple). When a cell goes away from the origin, it changes its direction with probability of 1/2 (green).
In the present study, a chemical attractant is introduced into the setting. The source of the chemical is assumed to be at the origin of the number line; the concentration of chemical attractant is highest at the origin, and it gradually decreases as the distance from the origin increases.

Two biased rules shown in Figure 3 are applied: if the model cell approaches the origin in one time step, the cell will move in the same direction in the next time step (purple); if the cell recedes from the origin in one time step, the cell will randomly move to the right or to the left with the same 1/2 probability (green). The latter rule stands for a ‘tumble’ in which the direction is randomly changed. The former rule stands for smooth swimming without tumbles. This is an extreme case in which the tumble frequency is reduced to zero when a cell approaches the origin.

Three properties of bacterial motion (see Section III.) are included in the model. The cell moves to sense whether it approaches the origin or recedes from the origin. When the cell senses that it recedes from the origin, it randomly changes direction. The cell does not stop even it reaches the origin.

IV. ANALYTICAL RESULTS

A. Probability

Figure 4 indicates the time-position diagram of a model cell. In this diagram, the position is indicated by use of non-dimensional position number $i$ ($x = i\Delta$), and the time is expressed as non-dimensional time step number $n$ ($t = n\Delta$).

Let us assume that a model cell moving from the left-hand side has just arrived at the origin. Since the cell has approached the origin on the previous leg, it continues to move to the right-hand side and moves to position $i = 1$.

At time $n = 0$, the model cell which has come from the origin is at position $i = 1$. Since the cell has receded from the origin, the cell will tumble. The cell will move to the right-hand side (to $i = 2$) with 1/2 probability, or the cell will move to the left-hand side (to $i = 0$) with 1/2 probability at time $n = 1$. Thus, the probability of the model cell is at position $i = 2$ at time $n = 1$ is $p_{i=2}^{n=1} = 1/2$. Similarly, $p_{i=0}^{n=1} = 1/2$.

The cell at position 0 at time $n = 1$ came from the position $i = 1$. Since the cell has approached the origin, the cell will move to the left-hand side and will be at position $i = -1$ at time $n = 2$. Thus, $p_{i=-1}^{n=2} = 1/2$.

The probability of being at a given position at each time step is sequentially obtained in the analysis.

B. Expectation (average position)

The expectation is defined as

$$E(n) = \sum_{i=0}^{\infty} i p_i^n.$$  \hfill (1)

When many model cells start at time $n = 0$ at position $i = 0$, this value $E(n)$ means the average position of the cells. Because the probability $p_i^n$ is sequentially obtained as demonstrated in the previous IV. A, we get $E(n)$ as

$$E(n) = \sum_{i=0}^{\infty} i p_i^n = \frac{1}{2n+1} (n \geq 1).$$  \hfill (2)

After many time steps ($n \rightarrow \infty$), the average position $E(n)$ tends to 0 as it is intuitively expected.

C. Variance

The variance $\sigma^2(n)$ is defined by

$$\sigma^2(n) = \sum_{i=0}^{\infty} (i - E(n))^2 p_i^n \geq \sum_{i=0}^{\infty} i^2 p_i^n = \sum_{i=0}^{\infty} \left( p_i^n + p_i^0 \right).$$  \hfill (3)

Here, $E(n) \rightarrow 0$ is considered in the approximation. The analytical solution of the variance depends on whether $n$ is even or odd:

If $n$ is even, $n = 2m$,

$$\sigma^2(n) = \frac{1}{2^n} (n+1)^2 + \sum_{j=1}^{m} 3 \cdot 2^{3j-2} n^{2j-1} \cdot (n - (2j - 1))^2$$

$$= \frac{1}{2^n} (n+1)^2,$$  \hfill (4)

and, as $n \rightarrow \infty$,

$$\lim_{n \rightarrow \infty} \sigma^2(n) = 0 + 12 \cdot \frac{20}{27} - 12 \cdot \frac{4}{9} + 3 \cdot \frac{1}{3} = \frac{41}{9} \approx 4.55\ldots.$$  \hfill (5)

If $n$ is odd, $n = 2m+1$,


\[ \sigma^2(n) = \frac{1}{2^n} (n+1)^2 + \sum_{j=1}^{m} \frac{3 \cdot 2^{j-2}}{2^n} |n - (2j - 1)|^2 \]

\[ = \frac{1}{2^n} (n+1)^2 + 6 \sum_{k=1}^{m} \frac{k^2}{2^k} \quad . \quad (6) \]

\[ \lim_{n \to \infty} \sigma^2(n) = 0 + 6 \cdot \frac{20}{27} = \frac{40}{9} \approx 4.44\ldots \]

Depending on whether \( n \) is even or odd, two close but different variance values are obtained. When \( n \) is even, the probability that the cells exist at the positions of even \( i \) (i.e. \( i = -2, 0, 2, 4, \ldots \)) is zero as it appears in Figure 4. In contrast, when \( n \) is odd, the probability that the cells exist at the positions of odd \( i \) (i.e. \( i = -3, -1, 1, 3, \ldots \)) is zero. As a result, the probability distributions at even \( n \) and odd \( n \) are different.

The standard deviation \( \sigma(n) \) approximately converges to the following as the time step \( n \) tends to infinity:

\[ \lim_{n \to \infty} \sigma(n) \approx 2.1 . \quad (7) \]

This means that if a number of cells independently move in the stochastic manner according to the two biased rules defined in Section III. (see Figure 3), some amount of the cells will gather around the origin even after a long elapsed time. This accumulation corresponds to the spatial distribution of bacterial cells produced by the chemo-taxis.

D. Probability distribution function

The probability distribution function after a long elapsed time will be described as a function of the non-dimensional distance from the origin.

Figure 5(a) is the probability distribution of cells existence at position \( i (i \geq 0) \), where

\[ p(n,i) = \frac{p^n_0 + p^{2n}_i}{2} \quad (i \geq 1) \].

\[ p(n,0) = p^n_{i=0} \quad (i = 0) \]

Since the distribution should be symmetric about the origin, the probabilities at positive and negative position numbers with the same distance from the origin are averaged. As mentioned in the previous Section IV. C, there are two probability distributions depending on whether the time step number \( n \) is even or odd. Figure 5(a) shows that each of the distributions quickly converges as the time step proceeds. Within seven time steps, each of the probability distributions seems to converge to two different distributions in the region around the origin. (The probability distributions interminably spread in the outlying region where \( i \) is of great value. However, the probability significantly decreases at such a point.)

We seek a probability distribution function of a cell model that is equivalent to the distribution of many model cells. If a number of cells start at different time steps, i.e. \( n \) is odd or even, the probability distribution should be the mean of the two distributions. This is shown in Figure 5(b).

The probability distribution function \( p(i) \) after many time steps is defined as

\[ p(i) = \lim_{n \to \infty} p(n,i) . \quad (9) \]

This \( p(i) \) should have a property

\[ p(0) + 2 \sum_{i=1}^{\infty} p(i) = 1 . \quad (10) \]

Figure 5(c) shows the probability distribution function. This graph corresponds to the number density distribution of the cells if an infinite number of cells are in the region. The explicit formula of \( p(i) \) is

---

Fig. 5. The probability distribution function after a long elapsed time. (a) The distributions alternate depending on the time step \( n \). They converge to two distributions indicated by blue and green. (b) The mean probability of the two consecutive distributions in (a). (c) Probability distribution function \( p(i) \) after infinite elapsed time.
This is a geometric progression with the common ratio 1/2. Moreover, it satisfies Equation (10).

The variance \( \sigma^2 \) and the standard deviation \( \sigma \) are calculated by using the values in Equation (11):

\[
\sigma^2 = 2 \sum_{i=1}^{\infty} i^2 p(i) = \frac{9}{2} = 4.5, \quad \sigma \approx 2.1.
\]

This value is the average of the two values in Equations (5) and (6).

V. SIMULATION RESULTS

The biased rules defined in Section III. (see Figure 3) was implemented as a program. \( 10^6 \) model cells were produced in the program at \( n = 0 \). The number of the model cells, \( 10^6 \), was sufficient to capture the cells’ distribution. The model cells did not interact with one another. Two initial distributions were applied: (i) The cells started from the origin. This corresponds to the condition imposed in Section IV. (ii) The cells were initially distributed within the range \( |i| \leq 30 \). The distributions of the cells at each time step were calculated for the two initial distributions.

Figure 6(a) is the simulation result for the case in which the cells start from the origin. The vertical axis indicates the number of the cells at position \( i (i \geq 0) \). Since two positions of the same distance from the origin, i.e. positive \( i \) and negative \(-i\), exist on a number line, the two numbers of the cells at the two positions are averaged like being done in Equation (8). The numbers of the cells at even \( n \) time step at even \( i \) positions are zeros. Alternatively, the numbers of the cells at odd \( n \) time step at odd \( i \) positions are zeros. The two distributions that appear every other time step are both steady. The average of the two distributions amount to a steady distribution that is expressed by a geometric sequence with the common ratio 1/2. The result agrees with the analytical formula provided in
Equation (11) and Figure 5(c). Figure 6(b) is the result of a random walk (not biased) to be compared with the result of the present biased random walk. The distribution spreads as the time step proceeds. This is a commonly recognized diffusion process.

Figure 7 displays the simulation result for the case in which the cells start from the region within $|i| \leq 30$. Two converged distributions alternatively appear at every time step; i.e. odd $n$ (open marks) and even $n$ (solid marks). At a given time step, the probabilities at even $i$ positions and odd $i$ positions are independent of each other (see Figure 4). Therefore, each of the two distributions is decomposed into two sets of probability. Consequently, four steady probability distributions at every two spatial intervals are obtained. They are all expressed by geometric progression with the common ratio $1/2^2$; the square corresponds to two spatial intervals. The result is also in accord with the distribution provided in Equation (11). Moreover, this result suggests the existence of a steady distribution which is common for both even and odd $n$.

VI. CONCLUSIONS

A discrete one-dimensional model of biased random walk was proposed. In this model, a model cell moves one interval along a number line during one time step period like the classical one-dimensional random walk model. The present model employs two biased rules which are determined according to the properties of chemo-taxis by bacterial cells. Assuming that a chemical attractant exists at the origin of the number line, we analytically obtained the probability that a cell is at a given position after a long elapsed time. Three features were revealed:

(a) The probability distribution as a function of the distance from the origin converges after several time steps.

(b) The probability of model cell’s existence at a position closer to the origin is higher. This corresponds to the bacterial cells’ migration around the source of a chemical attractant.

(c) This probability is halved as the distance increases one interval length. Therefore, the probability is expressed as a geometric progression with the common ratio $1/2$.

The features (a)-(c) were confirmed in the distribution of the number of cells calculated by simulations in which $10^6$ model cells moved according to the biased rules.

The aim of this paper is to propose a mathematical model of the biased random walk motion in one-dimension, and present some results about the cells’ distribution around a chemical attractant. The present model adopts the two rules determined after bacterial chemo-taxis. However, in order to apply the present mathematical model to measure the bacterial chemo-taxis, we need to expand and modify the present model in three directions at least.

First, the intensity of the biased motion will be defined. The probability distribution according to the present biased rules is produced by the balance between the diffusion and the advection (or drift) towards the origin. In the model shown in Figure 3, the model cell was ruled to continue to move when it approached the origin without tumbling. This is equivalent to the most intense advection. However, bacterial cells in nature do not quit tumbling when they approach the chemical attractant; they only reduce the frequency of tumbling. The probability of motion towards the origin after approaching motion is a candidate as a parameter adjusting the intensities of the diffusion and the advection. The probability was set to be one in this study. Varying the probability in the range from one to zero, one could change the distribution from the most concentrated distribution affected by the advection to the distribution dominated by the diffusion.

Second, in the present mathematical model, the motion of a model cell is limited in one-dimension. When bacterial cells are contained in a capillary tube and its diameter is small enough, the bacterial cells’ distribution would be one dimensional because the radial motion is restricted. The suitable diameter of the capillary is not yet known. The bacterial cells’ distribution obtained in conventional capillary assay is two/three dimensional. Developing multi-dimensional mathematical model and accumulating the observed data will be complementary to measure the bacterial chemo-taxis. Further investigation will be necessary to obtain the observed bacterial distribution which is adequate to be compared with the model cells’ distribution according to the present model.

Third, although the time period and the swimming speed during one ‘run’ is assumed to be constant and be same between cells in the present model, they may vary and be different. We need to collect these values for individual bacterial cells. These data would help us modify the present model to include the fluctuations in $a$ and $\Delta t$.

Moreover, the interference between bacterial cells is not taken into account in the present model. The number density of the bacterial cells near the chemical attractant will be high and the interference between the bacterial cells would not be negligible. Moreover, considering bacterial size of order of micrometers, it seems difficult to provide a chemical attractant at a spot in an experiment. Such a region near the chemical attractant may be inadequate to measure the cells’ distributions.

Resolving these problems in future, we will determine bacterial chemo-taxis quantitatively by comparing the observed cells’ distribution to the probability distribution revealed by the present model.
Acknowledgement
This work was partly supported by JSPS KAKENHI
Grant Number 15K05796, 15K17975.

References