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## Evaluation of bacterial run and tumble motility parameters through trajectory analysis

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## ABSTRACT

In this paper, a method for extraction of the behavior parameters of bacterial migration based on the run and tumble conceptual model is described. The methodology is applied to the microscopic images representing the motile movement of flagellated *Azotobacter vinelandii*. The bacterial cells are considered to change direction during both runs and tumbles as is evident from the movement trajectories. An unsupervised cluster analysis was performed to fractionate each bacterial trajectory into run and tumble segments, and then the distribution of parameters for each mode were extracted by fitting mathematical distributions best representing the data. A Gaussian copula was used to model the autocorrelation in swimming velocity. For both run and tumble modes, Gamma distribution was found to fit the marginal velocity best, and Logistic distribution was found to represent better the deviation angle than other distributions considered. For the transition rate distribution, log-logistic distribution and log-normal distribution, respectively, was found to do a better job than the traditionally agreed exponential distribution. A model was then developed to mimic the motility behavior of bacteria at the presence of flow. The model was applied to evaluate its ability to describe observed patterns of bacterial deposition on surfaces in a micro-model experiment with an approach velocity of 200  $\mu\text{m/s}$ . It was found that the model can qualitatively reproduce the attachment results of the micro-model setting.

### 1. Introduction

Understanding the motile behavior of bacteria has implications in several areas of science including but not limited to pathogenic risk assessment, water treatment, biopesticides, and soil and groundwater bio-remediation (Andersen et al., 2003; Ashrafuzzaman et al., 2009; Au, 2004; Josenhans and Suerbaum, 2002; Oyanedel-Craver and Smith, 2007; Singh and Olson, 2008; Singh et al., 2006; Witt et al., 1999). Bacterial motility behavior via flagella movement in aqueous systems have been traditionally conceptualized based on the “run and tumble” model (Lovely and Dahlquist, 1975; Turner et al., 2000). This model assumes that the movement of bacteria is composed of two modes: runs consisting of near straight movement followed by tumbles consisting of random changes in direction. Modeling studies proposed for simulating bacterial motility can be mainly classified into two groups. Some researchers have focused on the detailed hydrodynamics of individual swimming cells (Dillon et al., 1995; Lauga et al., 2006; Lauga and Powers, 2009). Others have looked at the problem on bacterial motility in aqueous phase under chemotaxis effects at continuum scale by

constructing models representing the spatial evolution of concentrations of bacterial population (Chen et al., 1998; Ford and Harvey, 2007). Based on the later approach, in macro-scale, motility can be represented by modifying the effective diffusion coefficient (Arabagi et al., 2011; Kim and Breuer, 2004; Strobel et al., 2011; Valdés-Parada et al., 2009) and adding an extra advection (drift) term to the advection-dispersion equation when chemotaxis is present (Berg and Turner, 1990; Cates, 2012; Chen et al., 1998; Ford and Harvey, 2007; Keller and Segel, 1971).

Quantifying the run and tumble model parameters is a necessary step in up-scaling the transport from micro-scale to macro-scale. Several attempts have been made to characterize the parameters of the run and tumble model using experimental data. Lovely and Dahlquist (1975) provided a detailed conceptual model of run and tumble to be used for estimation of its parameters. They assumed perfectly straight runs with a constant travel speed and an exponential probability distribution for the run-time, and instantaneous tumbles. In the early 1980s, Alt's (1980) model assumed bacterial tumbling frequency (number of tumbles in a given time) to follow a Poisson distribution with a constant

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swimming speed which results in an exponentially distributed run-time. Block et al. (1983) also found out that the distributions of run and tumble intervals were exponential. Zonia and Bray (2009) modeled the deviation angle in tumbling events according to a random number generated by a Gaussian distribution based on the experimental values described by Turner et al. (2000). Other models (e.g. Martens et al., 2012) drawn the new direction of the bacteria from a uniform distribution independently from the previous direction. Wilson et al. (2011) used Schulz distribution for velocity of motile bacteria to parameterize a normalized intermediate scattering function used to extract bacterial motility parameters from imaging data. However, few parameters of physical models were derived from the real data.

In this paper, an attempt to extract the run and tumble motility parameters of flagellated *Azotobacter vinelandii* based on microscopic images of a large number of cells is presented. The frequency distributions of the following quantities have been extracted from images representing bacterial movement trajectories: transition time (the time spent in each state of run and tumble), deviation angle distribution during run and tumble states, the velocity distribution as well as the temporal velocity correlation which is captured using a copula approach. It is assumed that the bacterial cells can deviate (change direction) during both runs and tumbles based on the observation from the movement paths in the images. However, it is expected that the variance of deviation angles to be larger during the tumble state compared to the run state. For the purpose of estimating motility behavioral distributions, an unsupervised cluster analysis has been applied to fractionate each bacterial trajectory into run and tumble states. After that, the distributions for each mode can be extracted by fitting mathematical distributions which best representing the data. A model was then developed to mimic the motility behavior of bacteria at the presence of flow. The proposed model was applied to a micro-model collector experiment to determine its ability to explain the observed spatial distribution of bacterial deposition on the collector surfaces (Lu et al., 2015a).

## 2. Materials and methods

The research was conducted in two stages: Firstly, data acquisition and processing. Image processing and trajectory analysis was used to 1) discriminate the mode of motion (i.e run/tumble) and 2) extract the statistical distribution of factors controlling the motility behavior in each mode. Secondly, simulation model development. A discrete particle tracking model was developed based on the results of the analysis in the first stage and applied to the hydrodynamic field surrounding a single cylindrical collector. The spatial distribution of cells on the collectors were qualitatively compared with the results of a micro-model experiment (Lu et al., 2015a).

### 2.1. Data collection

A soil bacterial strain, *Azotobacter vinelandii*, was used as our model bacterium. The transport and fate of this bacterium has been our continuous research quest in understanding the interplay of bacterial motility, transport, and horizontal gene transfer (Massoudieh et al., 2013; Lu et al., 2015a,b; Liang et al., 2015).

*A. vinelandii* cells were grown on modified (no molybdenum) Burks medium Strandberg and Wilson (1968) plates with addition of 0.013 M ammonium acetate at 30 °C for 2 days and then in liquid media of modified (no molybdenum, no iron) Burks medium (Strandberg and Wilson, 1968) with addition of 0.013 M ammonium acetate shaking at 170 rpm for 18 to 20 h (Lu et al., 2013). The cell suspension (2.7 10<sup>7</sup> to 4.2 10<sup>7</sup> cells/mL) in 3-mor-pholinopropane-1-sulfonic acid (MOPS) buffer solution with 100 mM KCl at pH 7.2 was continuously pumped into the micromodel at a Darcy's velocity of 200 μm/s. The experimental conditions used in previous studies (Massoudieh et al., 2013; Lu et al., 2015a,b; Liang et al., 2015) were followed to facilitate comparability across studies to investigate the effects of motility. The micromodel consists of a regular array of 1440 cylindrical collectors to mimic the porous structures in the subsurface soil and the bacterial movement around one of the collectors was continuously recorded using an inverted Axio Observer microscope (Carl Zeiss, Oberkochen, Germany) and a camera (Andor Technology iXon 897, Belfast, UK) controlled by Solis software (Andor Technology). Each image stack of 1000 pictures were taken per 31-second duration, and the stack was obtained with a 0.4 μm per pixel size resolution.

#### 2.1.1. Image analysis

Cell locations in each frame were extracted using a particle tracker plugin, initially developed by MOSAIC group, Sep, 2014 release (Sbalzarini and Koumoutsakos, 2005) for ImageJ (Abràmoff et al., 2004; Rasband, 1997; Sbalzarini and Koumoutsakos, 2005; Schneider et al., 2012). The bacteria profile in this study are similar to colloidal spheres. The estimation of the bacteria location is done by finding the local intensity maxima in the analyzed image. For example, the location is estimated as the brightest pixel within a distance and if its intensity is in the upper user defined percentile of intensity values of the current frame. To refine the location, an approximation of offset is given by the distance to the centroid of the noise-reduced image. Brownian motion was treated as a Gaussian Noise and reduced with filter during image processing. Visual inspection indicated that the particles were well detected from the background and shadows. Fig. 1 shows an example of original image taken by the inverted Axio Observer microscope and the detected cells by the particle tracker's particle detection function.

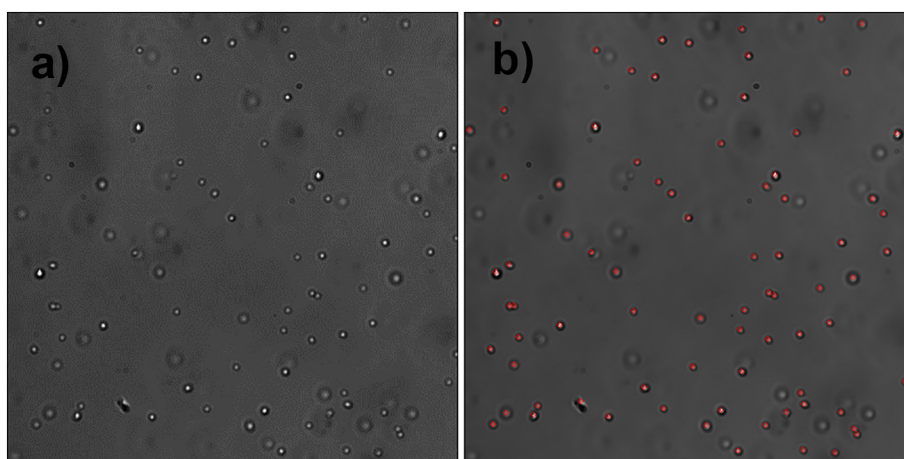


Fig. 1. (a) Sample original image of bacteria and (b) segmentation result by ImageJ.

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