Cooperative Path Finding and
Time Delay Communication in Bacterial Chemotaxis

Cyrena Howland, Himanshu Sahni, Sheik Meeran Rasheed Abdul Rahuman, Róbert Fjölnir Birkisson, Vasiliki Kostara

Chalmers University of Technology, Complex Adaptive Systems, Simulation of Complex Systems \\

(Team Dolphins)

Abstract:

It remains poorly understood how the cooperative dynamics of bacteria populations help them navigate through an environment with obstacles to secure food. It has been shown that the time it takes a bacteria population to navigate towards a food source does not increase when obstacles are introduced and previous studies have come short of creating a suitable mathematical model that reproduces these experimental results in a biologically realistic way. Here we develop an agent-based model which introduces stochastic, yet directed behaviour of the bacteria towards an attractant (food source). This improves the relation between simulations and real-life behaviour of bacteria. We demonstrate that collaboration via time-delay communication reduces the amount of time it takes them to find a food source and, remarkably, also enables them to travel in an environment with obstacles in approximately the same amount of time as they would in an environment without obstacles. This has implications for distributed swarm-based computing and can motivate improved algorithms for self-autonomous robotic swarms.

I. INTRODUCTION

Agent-based modeling can be used as a base to describe various natural and artificial complex systems. Autonomous agents are brought to communicate and cooperate by perceiving signals from their environment as well as other agents [1]. Such systems can be bacterial colonies, delivery drones [2], or vehicles with cooperative cruise control [3].

Specifically, in bacterial ecosystems, chemotaxis plays a significant role in bacteria's adaptability in different environments. Bacterial chemotaxis is the biological mechanism, through which bacteria secrete different substances in order to indicate different signals. This ability plays a major role in their overall survival across different terrains[2].

To study this behavior, we developed an agent-based model with bacteria as our agents. In this manner, the bacteria are programmed to reach a certain goal in environments with different characteristics and we wanted to explore how communication between the agents would affect their ability to reach this goal.
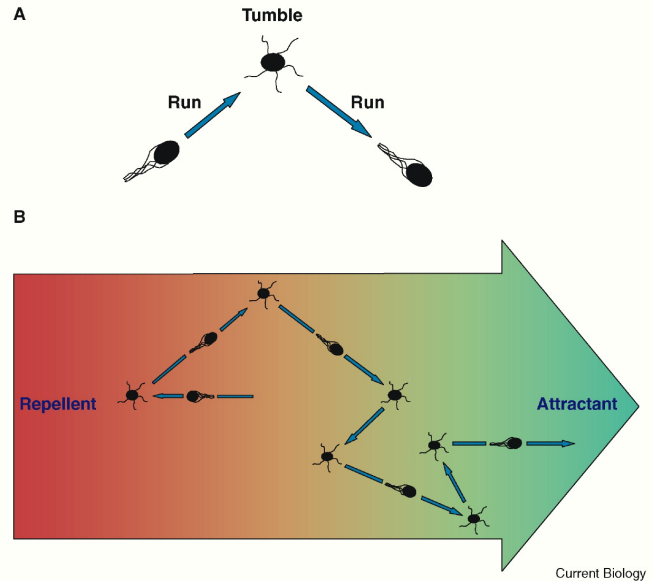

FIG. 1. *Chemotaxis —migration towards attractants and away from repellents. (A) Bacteria such as E. coli exhibit two modes of swimming: runs and tumbles. (B) Cells tend to continue on the course when running toward attractants; when swimming away from attractants they tend to tumble and change direction. –* [4]

II. BACKGROUND

A. Bacterial Chemotaxis

Chemotaxis is the directed movement of an organism either towards an environmental condition it finds attractive or away from one it finds repellent, using the detection of a chemical as its guide. Bacteria chemotaxis can be simplified into a sequence of longer "runs" punctuated by "tumbles" which last less than a second and randomize the direction of the next run [4]. As shown in figure 1, when the bacteria is moving away from an attractant, their tumble frequency increases, and the average angle of their random turn increases. When they move towards an attractant, such as a food source, they tumble less and have straighter trajectories.

Since the bacteria are too small to detect a chemical gradient in place, they use temporal sensing, keeping

track of the concentration through time and space. For example, a bacteria detects that it is moving towards an attractant by taking the difference between the concentration of the attractant chemical at its current position and its next position (after the run). If the concentration increases, it determines it's going in the correct direction and thus does not want to "tumble" away from its current path. If it decreases, it utilizes the tumble to try a new direction. This is essentially a biased random walk.

Bacteria are known to exhibit cooperative behavior by secreting molecules that benefit all individuals in their population. The chemical communication system the bacteria evolved is known as *quorum sensing* [5]. It has been shown that *Escherichia coli* (*E. coli*) cells, in the presence of a chemoattractant gradient, not only bias their random-walk swimming pattern as described above but when in a population of other *Escherichia coli* cells, actively secrete a potent chemoattractant of their own, which we will refer to as a *pheromone*, which increases the migration of nearby cells to the attractant of interest, such as the food source [2].

The bacteria's perception of the change in physical stimulus, be it a pheromone secreted by a neighboring cell, or chemicals produced by a food source, can be described by the Weber-Fechner Law [6]. The Weber-Fechner Law states, that the perceived changes in odor concentration are proportional to the log of stimulus increase. Therefore, a proxy for the signal the bacteria extracts from the environment is

$$P_C = \frac{1}{C} \cdot \frac{\Delta C}{t} \qquad (1)$$

where C is the concentration of the chemical of interest.

B. Models of Bacterial Chemotaxis

Previous work has been done in the development of mathematical models to explain collective bacterial chemotaxis [7] [8] [9] [10] [11], which simulations have shown do capture many important aspects of this behavior [12] [13]. These studies, however, neglect to account for how cooperation and communication among populations of cells contribute to their observed foraging behaviors. Not until recently have suitable models been developed that attempt to mathematically and computationally account for these dynamics [12] [13] [2]. These models utilize either an extended differential equations mode or model the process as a distributed gradient descent (DGD), and have been used to show that indeed communication among cells in a population can improve the average speed by which individual cells reach the attractant source.

While these studies have made considerable progress in understanding the phenomena, very few, namely

Rashid et. al [2], have focused on cells' ability to navigate in more complex environments such as those with obstacles. Previous models all predicted that the exit times of the bacteria would increase as more obstacles were introduced. Experiments done by Rashid et. al [2] found in fact this was not the case when studying real bacteria populations, and they were able to reproduce these results in simulations and mathematical models that modified the previously used DGD algorithm. Even though their model produced the desired results, it still fails to explain how bacteria utilize communication to navigate toward a food source in an obstacle-laden terrain. This is because their model of bacteria communication assumes they have knowledge that real bacteria couldn't possibly have. Specifically, their model assumes that each bacteria holds in its mind the exact coordinates of each of its fellow cells. In their model it is this information that each agent uses to sense the direction the secreted pheromone is coming from and what direction it should move.

With these building blocks in mind, an agent-based model was developed to be able to simulate the behavior of bacteria in a biologically realistic manner.

III. METHODS

For the simulation, a simple square environment is created to host the agents. In the central point of this environment, a source of a chemical with attracting properties is placed. The intensity of the source chemical forms a Gaussian distribution of the chemical concentration, C, at each step, i. By bearing a diffusion rate

$$C_i = 0.95C_{i-1} \qquad (2)$$

that spreads to its eight nearest neighbors and an evaporation rate

$$C_i = (1 - 0.001)C_{i-1} \qquad (3)$$

the source's concentration wanes as it's spreading. Thus, the central point of the environment becomes the primary focal point for the bacteria.

Initially, the bacteria spawn in random locations throughout the environment in search of the chemical food source. As stated before, this search can be described by a stochastic modification of distributed gradient descent (DGD) [13] [2] algorithm with "run" and "tumble" modes. However, this implementation relies only on the gradient of the different chemicals and not the position of the other agents. By each time step and, consequently location change ("run"), the bacteria evaluate their perception of the food source's chemical intensity and change their movement direction accordingly ("tumble"). In their new positions, if the perceived intensity is lower or equal to that of their previous positions,

their direction is changed randomly. However, if the perceived intensity is higher than that of their previous positions, their direction is restricted to change randomly in a smaller range of angles, indicating the desirable direction. Specifically, the direction of each bacteria, ϕ, in each step, i, is randomly picked from a Gaussian distribution of angles with a mean value

$$\mu_i = \phi_{i-1} \tag{4}$$

and standard deviation

$$\sigma_i = 2\pi e^{-S \cdot max\{0, \Delta P_C + \Delta P_c\}} \tag{5}$$

where S is a positive constant describing the chemical sensitivity of the bacteria, P_c is the perceived change in the concentration of the pheromones, discussed in the next paragraph and P_C is the perceived change in the concentration of the food source chemical. How the bacteria perceive the stimulus is described in Eq.1.

Introducing cooperation, the bacteria are able to secrete an attractant (pheromones). Specifically, a trail of pheromones can be deposited by each of the bacteria, when they detect an increase in chemical concentration is perceived. This pheromone concentration has a diffusion rate and an evaporation rate of its own. These rates are described by the exact same equation forms as those of the central food source, resulting in the disappearance of older parts of pheromone trails in the environment after a number of time steps. As a consequence of this behavior, other bacteria are able to perceive pheromone signals and adjust their movement to follow existing trails in addition to the search for the central source. Thus, bacteria without perception of the central source may perceive a transient pheromone, indicating the way to their primary goal, the food source, through a secondary chemical source.

To signify the importance of this kind of cooperation, a population of bacteria is set in the above simple environment with one central chemical source and is studied in two cases: first without pheromones and then with the ability to deposit pheromones. Moreover, the above cases are additionally studied within an environment that incorporates obstacles, which are static through the entirety of the simulation. Each obstacle occupies one random position throughout the environment as well as its four nearest neighbors, forming a cross. These obstacles prevent both the bacteria's movement and the propagation of chemicals (FIG 2).

The selected population ($n = 50$) is a small sample compared to experiments in vitro. However, it is a significant enough sample for the purposes of this simulation, enabling the deduction of clear results, aligned with existing literature. For the simulations, the program NetLogo [14] was used, as it specializes in agent-based simulations.
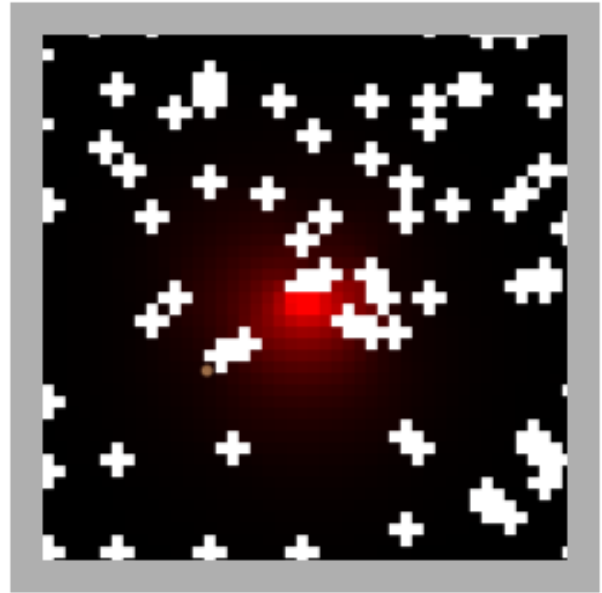

FIG. 2. *The propagation of the concentration signal (red) due to the central chemical source. White crosses represent obstacles (enlarged image).*

IV. OBSERVATIONS

During the trials, several phenomena are observed that can be pointed out. The small rainbow-colored dots represent the bacteria. The trajectories of each bacteria correspond to its color. The attractant chemical produced by the food source is indicated by the gradually fading red color (FIG 2). With communication active, the concentration of the pheromone is similarly indicated with green color, thus where the concentration of both is high, a yellow color will emerge. Lastly, white blocks represent the obstacles.

The general behavior of the bacteria in each case can be observed in FIG 3. In the top left image, a simple environment with a central chemical source is created, where the bacteria have no means of communication. During their "run" and "tumble", the bacteria traverse paths equivalent to Brownian [1] motion in search of the source's signal. After they detect a change in chemical concentration, their path is visibly directed toward the source. In the top right image, the bacteria are placed in the same kind of environment, however, now they have the ability to deposit pheromones, as described in the methods section. Although a similar behavior as before can be observed close to their initial positions, their directed paths begin showing further away from the central source's signal. This behavior indicates the detection of the pheromones laid by other bacteria around the central chemical source.
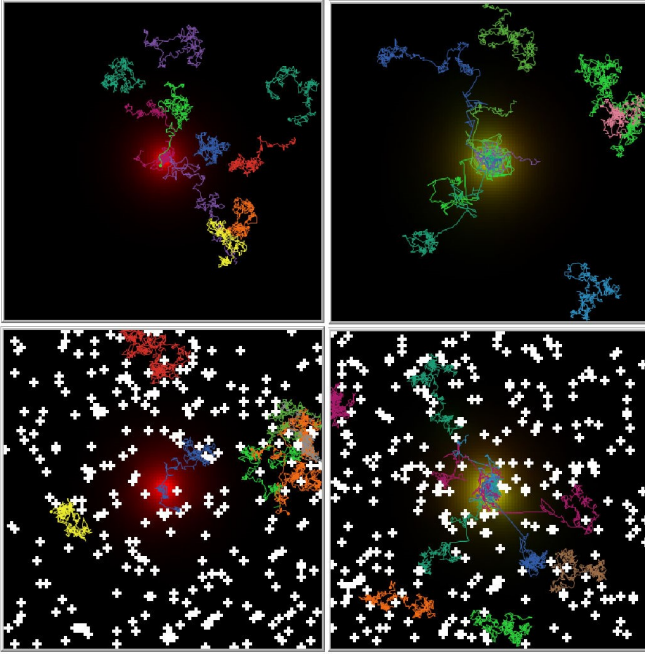
FIG. 3. *These images are all from different simulations, captured at the same time step.* **Top left:** *A simulation with no obstacles and no communication between agents.* **Top right:** *No obstacles but with communication.* **Bottom left:** *Obstacles with no communication.* **Bottom right:** *Obstacles with communication.*

FIG. 4. *The time-step evolution of a simulation where agents are able to secrete pheromones (green), starting from the top left image, followed by the right, then the bottom left, and, lastly, the bottom right image.*

Continuing to the bottom images of FIG 3, the environment is changed to include simple obstacles. Although the bacteria are barred from some paths through the environment, their behavior looks similar to the environment with no obstacles. Particularly, in the bottom left image, the trajectories of the bacteria are Brownian [1] as before and the obstacles seem to negligibly influence this behavior. Likewise, in the bottom right image, where now the agents can communicate with each other through pheromones, the obstacles seem to induce a minimal effect on their paths.

Another interesting phenomenon arises due to the secretion of pheromones (FIG 4). As expected, bacteria close enough to the central source, start depositing pheromones along their paths and continue this behavior, even after they have reached their goal. Thus, as more bacteria gradually gather there, the pheromones close to the central source get summed up. Early on, the central source of the attracting chemical gets overpowered by the intensity of the summed pheromone secretions. The effect of this behavior is the continuous expansion of the total pheromone concentration radius along with the progress of time. Consequently, bacteria still located far away from the center are more likely to detect pheromone concentrations as time goes on and thus can make their way towards the food source.
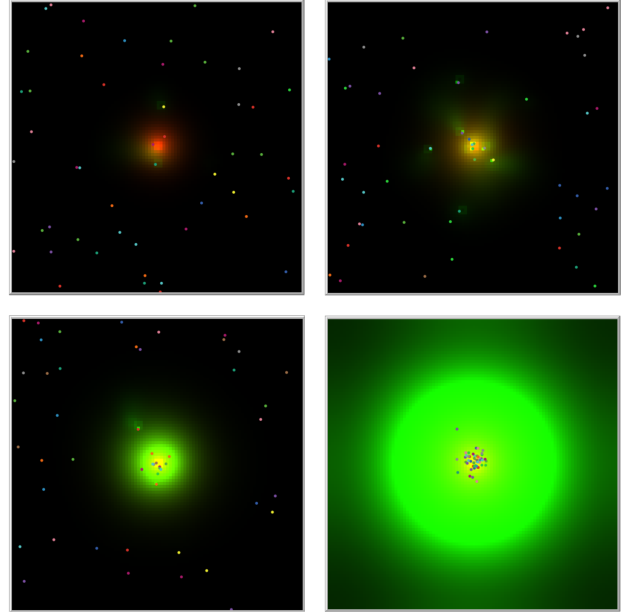
V. RESULTS

In order to quantify the visual outputs of the simulations, the average positions of the bacteria were recorded over a certain amount of time steps. The reference point of the system is the central chemical source. For each case, a population of $n = 50$ bacteria was initialized. Then, the average position of all the bacteria was recorded for 10^4 time steps. Each of the four cases (with or without bacteria or pheromones) was run ten times. Finally, the ten sets of positions were averaged again for each time step, to form the graph below (FIG 5). Environments without obstacles are indicated with orange color, and environments with obstacles are indicated with blue color. The dotted lines correspond to bacteria without cooperation, while the continuous lines correspond to bacteria with cooperation.

As is observed, there is quite a notable difference between bacteria that do secrete pheromones and those that do not. Specifically, when bacteria employ their attracting chemicals, their majority reaches their destination rapidly. On the other hand, without any form of cooperation, the majority of the bacteria mostly remain away from the source, reaching it at a dramatically slower pace.

Concerning the implementation of obstacles, the bacteria's average position is not affected significantly. Especially in the case of a lack of cooperation, the
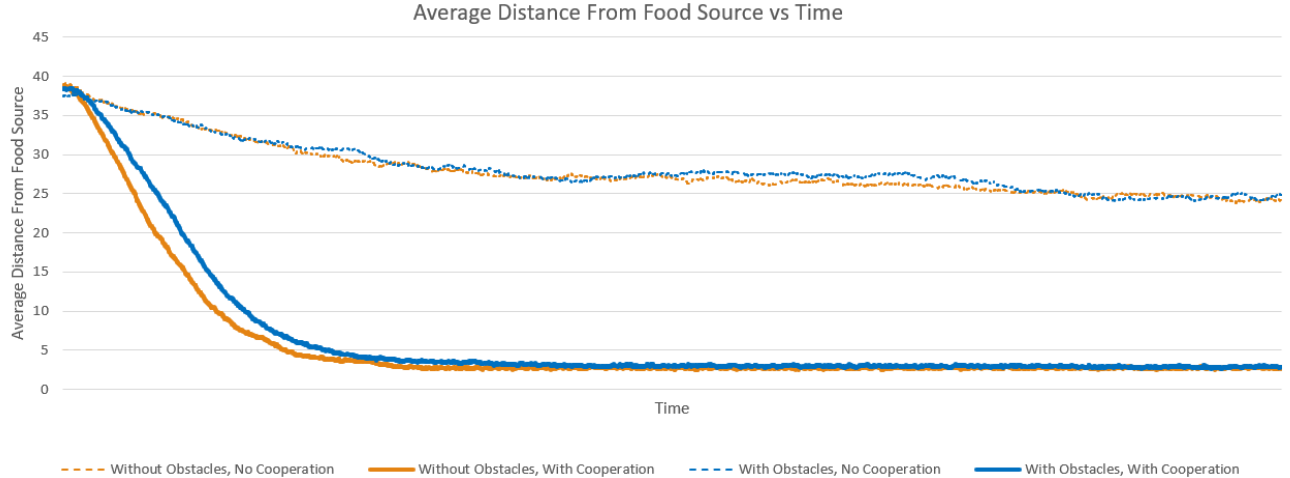
FIG. 5. *This figure presents the average distance from the central (food) source of the bacteria over a total time of 10^4 time steps. Environments without obstacles are indicated with orange color and environments with obstacles are indicated with blue color. The dotted lines correspond to bacteria without cooperation, while the continuous lines correspond to bacteria with cooperation.*

TABLE I. *This table shows the time steps needed for the first bacteria to reach the central chemical source averaged, as well as the average initial and the average final position of the bacteria in reference to the central chemical source in the absence or existence of obstacles or pheromones.*

Obstacles	Pheromones	Avg Time Steps (AU)	Avg Initial Position (AU)	Avg Final Position (AU)
no	no	3488	38.95	24.28
no	yes	762	38.54	2.69
yes	no	3935	37.39	24.88
yes	yes	990	38.40	2.86

lines are almost indistinguishable. Then, in the case of cooperation, although obstacles impede the bacteria's search only slightly, their average position follows the same trend as without obstacles and they reach the source almost as rapidly.

In the table (TABLE I), three particular variables are presented. *Average Time Steps* is the time needed for the first bacteria to reach the central chemical source which is averaged over all the runs. *Average Initial Position* and *Avg Final Position* of all the bacteria are in reference to the central chemical source for each of the four cases. It is noted that in the cases of no cooperation, some bacteria actually reach the central food source within the total time steps of the simulation and, due to the trend of the upper parts of the graph (FIG. 5), it can be safely concluded that the majority of the population is due to finally reach the central source, though after a larger amount of time steps.

For bacteria that leave trails of pheromones, the first bacteria appears to reach the central source approximately four times faster than the first bacteria that does not leave pheromones. In addition, even though populations in all cases appear in similar average initial positions after the simulations have ended it is visible that

general populations of bacteria that secrete pheromones have reached positions very close to the source.

VI.   DISCUSSION

Although the data from the simulations show clear results, there are shortcomings that must be addressed. We were able to reproduce the results found in previous experiments, where cooperative bacteria were able to navigate in an environment with obstacles in the same time as without. However, they attributed this to the introduction of cooperative dynamics, whereas we see the trend regardless of them. This could be the result of the stochastic navigation algorithm paired with the stochastically placed obstacles. In real-world experiments [15], obstacles are often predefined structures with walls and paths instead of randomly placed small blocks but this algorithm was chosen to model micro-environments, in which real bacteria might find themselves in. What is clear is that cooperation decreases the amount of time taken to navigate to the food source.

In order to resolve the question as to whether the way the obstacles were placed are responsible for the lack

of difference between the time taken with and without obstacles, other types of obstacles should be tried. For example, mazes and fractal structures [15] could be tested.

In addition, bacteria that utilize chemotaxis often have different types of pheromones to communicate the presence of obstacles and food, namely avoidant pheromones and attractant pheromones. However, the simulation only makes use of attractant pheromones as avoidant pheromones were out-of-scope for this project but they could be added in future projects and could give a better understanding of how real bacteria move.

All in all, our results closely match the results of studies in vitro and provide a satisfactory framework with which to study bacteria in environments, that would be hard to observe and control in real-world scenarios.

VII. CONCLUSION

In conclusion, chemical communication helps bacteria in reaching a food source quickly and we see a significant drop in the time taken when compared to path-finding without cooperation. Another important observation is the presence of randomly generated obstacles with predefined shapes did not have a notable impact on the time taken to get to the source.

In the future, this algorithm can be used in a base model to deploy in real-world scenarios which involve path-finding with communication. For example, chemotaxis is currently being used by drones to help search-and-rescue operations, where they have to locate trapped victims in emergency situations. [16] [17]

VIII. ACKNOWLEDGEMENTS

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IX.   SUPPLEMENTARY MATERIAL

We included the code used in our simulation in a separate file *code.pdf* which can be run through the open-source platform *Netlogo* [14].