Maze-solving by chemotaxis

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(Received 24 February 2010; revised manuscript received 9 April 2010; published 21 June 2010)

Here, we report on numerical simulations showing that chemotaxis will take a body through a maze via the shortest possible route to the source of a chemoattractant. This is a robust finding that does not depend on the geometrical makeup of the maze. The predictions are supported by recent experimental studies which have shown that by moving down gradients in *p*H, a droplet of organic solvent can find the shortest of multiple possible paths through a maze to an acid-soaked exit. They are also consistent with numerical and experimental evidence that plant-parasitic nematodes take the shortest route through the labyrinth of air-filled pores within soil to preferred host plants that produce volatile chemoattractants. The predictions support the view that maze-solving is a robust property of chemotaxis and is not specific to particular kinds of maze or to the fractal structure of air-filled channels within soils.

DOI: 10.1103/PhysRevE.81.062901 PACS number(s): 87.17.Jj

I. INTRODUCTION

Maze-solving is the act of finding a way through a maze from a starting location to a finishing location. Euler (1736) was the first to analyze mazes mathematically and in doing so made the first significant contributions to topology. There are now a number of different maze-solving algorithms, the best known of which are the "wall follower," the "pledge," and Tremaux's algorithm. Of these, only Tremaux's algorithm (a depth-first search) will find a solution for all mazes but not necessarily the shortest path when there are multiple paths. Shortest paths can be identified using a breadth-first search. A breadth-first search begins with an exploration of all locations in the neighborhood of an initial starting location. Then for each of these locations all unexplored neighboring locations are explored, and so on, until the goal is located. This algorithm may be implemented by the plasmodium of the slime mold *Physarum polycephalum*, a large amoebalike cell consisting of a dendritic network of tubelike structures (pseudopodia) [1]. More recently, it has been reported that positive chemotaxis will take a droplet of organic solvent or a biological organism to the source of chemoattractant via the shortest possible path through a maze [2,3]. Positive chemotaxis is a movement toward a higher concentration of attractant chemicals. The experimental study of Lagzi *et al.* [2] showed that a droplet of organic solvent can find its way through a complicated maze (approximately 2 cm^2 with channels that were 1.4 mm wide) to an acid source by moving down gradients in *p*H. The acid changes the surface tension of the oil droplet, but because of the *p*H gradient it affects opposite sides of the droplet unequally. This difference moves the droplet toward the acid source. It has long been recognized that chemotaxis is the primary means by which many biological organisms locate resources. Nematodes are, for example, attracted to plant roots via soluble and gaseous attractants produced by the root itself or by attendant rhizosphere microorganisms [4–8]. The numerical simulations of Reynolds *et al.* [3] suggest that chemotaxis will take nematodes and other soil-dwelling organisms to the source of a volatile chemoattractant via the shortest possible routes through the labyrinth of air-filled channels within a soil. These predictions are supported by experimental studies of the movement patterns of the root-knot nematodes *Meloidogyne incognita* and *M. graminicola* [3]. Nematodes were observed to take the shorter of possible two routes (one 2 cm long and one 4 cm long) to the roots of preferred host plants.

It is still unclear, however, whether the results from [2,3] depend on the particular maze constructed in [2] or on the fractal dimension of the air-filled pores in the soils modeled in [3]. Air-filled channels within soil are tortuous, having a fractal geometry and numerous dead ends, and so are quite different from the pathways through standard mazes [9]. Here, we report on numerical simulations showing that chemotaxis will take droplets of organic solvent and biological organisms via the shortest possible route through standard randomly generated mazes. Our findings support the view posited by Lagzi *et al.* [2] that chemotaxis is indeed the mechanism underlying maze navigation by droplets of solvent. We suggest that maze-solving is a robust property of chemotaxis and is not specific to particular kinds of mazes or to the particular geometry of air-filled channels found in soil.

II. MAZE GENERATION, CHEMOTAXIS, AND MAZE-SOLVING

Perfect mazes containing no loops and so no inaccessible sections or open areas were generated in one of the two ways. The first approach is a randomized version of the depth-first search algorithm. In this approach the space for a maze is represented by a regular grid of square cells each with four walls. A random walker setting out from the central cell selects at random a neighboring cell that it has not visited previously, removes the adjoining wall, and moves to that cell. If the walker encounters a "dead end," i.e., a cell with no unvisited neighbors, then it backtracks until it reaches a cell with an unvisited neighbor before resuming its random walk. This backtracking creates a new junction. The progress ends and the maze is completed when the walker

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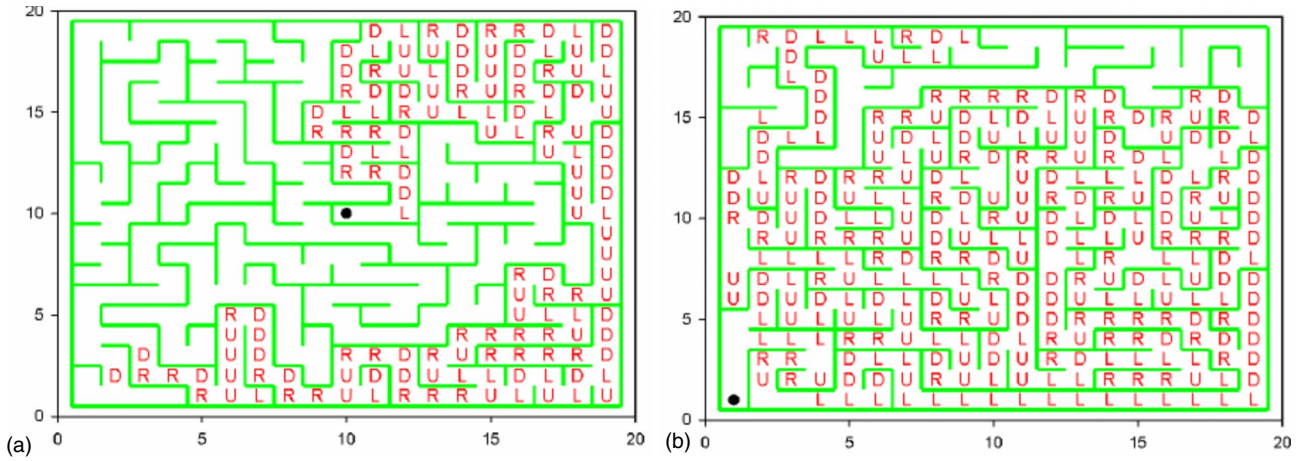

FIG. 1. (Color online) Examples of mazes produced by a randomized version of the depth-first search algorithm. The directions, up (U), down (D), right (R), and left (L), in which chemotaxis will take a droplet of organic solvent or a biological organism in response to a chemoattractant are indicated. Overall movement tracks from arbitrarily chosen starting locations can be seen by moving through the mazes in the directions indicated. Irrespective of their starting location, droplets and organisms always take the shortest most direct route to the source of the chemoattractant (●). In these simulations the chemoattractants have not yet diffused throughout the mazes entirely.

has visited every cell and is back at the origin of its walk. Although most paths lead to or from the center of these mazes, it can be difficult to find other locations. The second approach to maze generation is a recursive division method. In this approach the space for the maze is initially divided into two smaller spaces by the insertion of a randomly positioned wall that contains a randomly positioned opening. The process is then recursively repeated on the smaller spaces until all spaces are minimum sized. Mazes produced in this way have long straight walls. Examples of mazes produced by a randomized version of the depth-first search algorithm and by the recursive division method are shown in Figs. 1 and 2.

The diffusion of a chemoattractant from a source through the open channels in a maze was simulated using a discrete random-walk model. Random walks are equivalent to diffusion equations but are used here in preference to diffusion equations because they are easier to implement on complex geometries. In the random-walk model, discrete independent packets of chemoattractant move randomly to one of the adjacent available accessible spaces within a maze during each time step. Mean concentrations of chemoattractant at time $n=500$ due to the presence of a continuous source of chemoattractant which became active at time $n=0$ were calculated as follows. First, 10^4 packets of chemoattractant were tracked from the source over 1 time step and their final positions were recorded. This procedure was then repeated for $2,3,\ldots,500$ time steps. Finally, for each location (denoted by row i and column j) within the maze (e.g., see Fig. 1), the mean concentration of chemoattractant (i.e., the total number of packets present) was found by countering the number of packets having final position (i,j). For most locations within

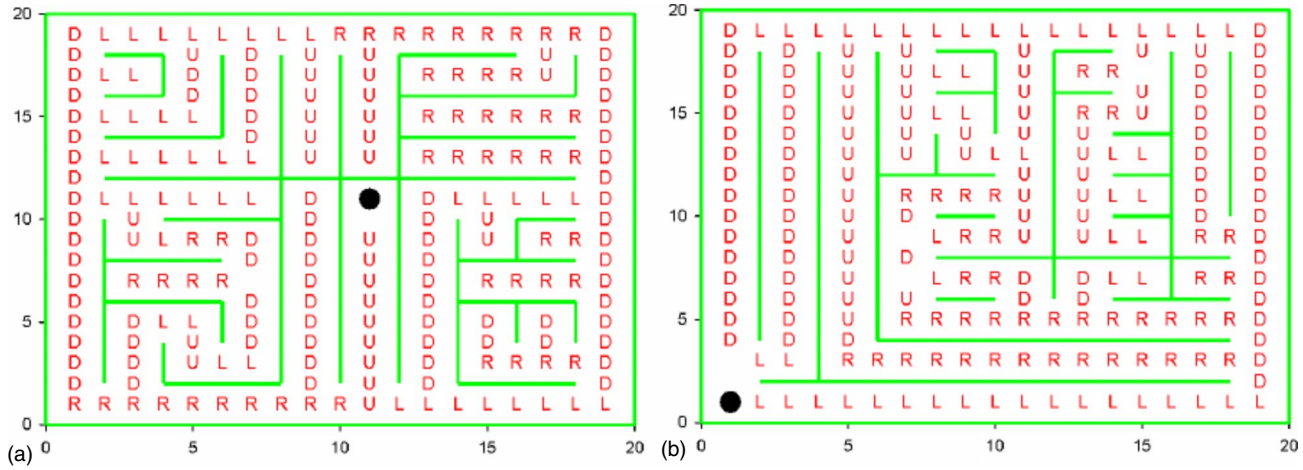

FIG. 2. (Color online) Examples of mazes produced by a recursive division method. The directions, up (U), down (D), right (R), and left (L), in which chemotaxis will take a droplet of organic solvent or a biological organism in response to a chemoattractant are indicated. Overall movement tracks from arbitrarily chosen starting locations can be seen by moving through the mazes in the directions indicated. Irrespective of their starting location, droplets and organisms always take the shortest most direct route to the source of the chemoattractant (●).

the 20×20 mazes considered here, the signs of the concentration gradients did not change at later times. When far fewer packets were tracked and for much earlier times, gradients in chemoattractant at some locations were found to be affected by stochastic fluctuations in concentration. These fluctuations led to chemotactic followers occasionally becoming trapped.

Some examples of simulated movement patterns within mazes due to chemotaxis are shown in Figs. 1 and 2. The overall movement tracks from arbitrarily chosen starting locations can be seen by moving through the mazes in the directions indicated. Examination of these tracks reveals that irrespective of starting location, chemotaxis takes a body through a maze to the source of a chemoattractant via the shortest possible route. This suggests that the maze-solving capacity of chemotaxis does not depend sensitively on maze geometry.

III. SUMMARY

Many organisms use chemotaxis to locate resources. When movements are unhindered by obstructions, chemotaxis will take an organism along a straight-line path (the shortest possible path) to the source of a chemoattractant. Here, in support of the recent experimental studies of Lagzi *et al.* [2] and the experimental and theoretical work of Reynolds *et al.* [3], it was found that chemotaxis can take a droplet of organic solvent or a biological organism along the shortest possible path through a maze to the source of a chemoattractant. This is a robust finding and does not depend on the geometrical makeup of the maze. This finding helps to elucidate how soil-dwelling organisms can move effectively through air-filled pores within soil to locate resources and how some ground-dwelling invertebrates can navigate effectively through leaf litter to locate prey and potential mates. Sophisticated navigational skills are not required. All that is required is the establishment of statistical stationary gradients in concentration, the ability to resolve all gradients in chemoattractant, at all concentration levels (i.e., no minimum detection threshold and no saturating maximum threshold), and to be able to move through all of the passages through which the chemoattractant diffuses.

ACKNOWLEDGMENT

Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council.

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