LABORPRAKTIKUM

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Some Active Motion and First-passage Time

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LISTINGS

ACRONYMS

SRW Simple isotropic random walk

MSD Mean square displacement

BRW Biased random walk

PRW Persistent random walk

CRW Correlated random walk

Part I

PREPARATION

Not sure if an introduction is needed for the Laborpraktikum.

1 INTRODUCTION

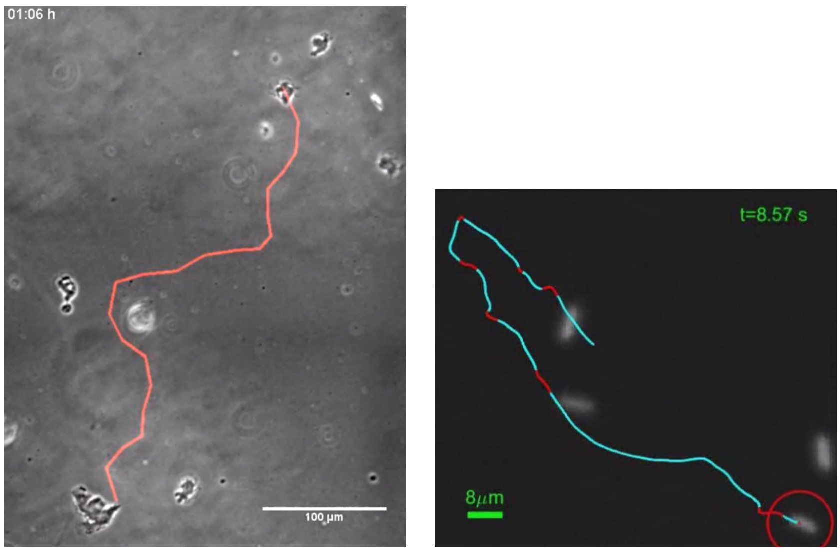
Write some kind of intro here.

2 ACTIVE MOTION

Active motion describes the process of converting energy resources into directed motion. Living beings using active motion are e. g. humans, animals and microorganisms such as cells or bacteria.

The motion of a human floating in a sea is only subject to the current, however, by using energy and muscle power the human can swim and therefore move directed.

While it is everyday experience that animals and humans are able to move directed, it is a non trivial fact for microorganisms. Especially considering cells and bacteria which are often surrounded by fluids and therefore experience thermal *diffusion*. The diffusion alone would lead to so called *Brownian motion*, a random motion named after its famous discoverer Brown and his studies on the motion of pollen particles [5]. However, in many experiments non-diffusive motion patterns have been observed for microorganisms. Figure 2.1 shows two examples of cells and bacteria for which directed and persistent motion has been recorded.



(a) Cell (immature bone marrow-derived mice dendritic cell) [18]

(b) Bacillus subtilis[1]

Figure 2.1: Directed and piecewise persistent migration paths for a cell and bacterium.

In the following, reasons for the necessity of active motion are given, a selection of research in different fields is presented and the efficiency of active motion is defined.

1 J. Najafi *et al.*, under review (2018)

2.1 MOTIVATION AND EXAMPLES

A mouse might need to hide or run from a fox while a human might be looking for lost keys.

The reasons for active motion are manifold and depend among others on the species and environmental conditions. Nevertheless, most of the time they are based on the task of searching something. Obviously the tasks which require active motion vary for humans, animals and microorganisms. They include:

- *Survival*: evading predators, escaping hazardous locations, finding shelter.
- *Foraging*: finding food or nutrients, hunting prey.
- *Reproduction*: finding mates.
- *Search*: searching for objects or locations of interest.
- *Migration*: finding and exploring new habitats and environments.
- *Biological tasks*: e. g. morphogenesis, wound healing, immune response, etc.

Furthermore, it is reasonable to assume that, depending on the motivation, also the movement patterns of active motion vary. To stick with the example of the mouse and the human: the movement pattern of a mouse running for its life will most certainly look different than that of a human looking for its lost keys. Therefore, there is a lot of research with the goal of quantifying and qualifying the many different kinds of active motion. Considering the tasks and functions of cells and bacteria, understanding their migrational properties is especially relevant in the fields of biology and medicine.

To give a few examples and an impression of the research that has been done, a small selection split into humans, animals and microorganisms is presented below.

HUMANS For humans almost any activity in everyday life is connected to active motion (e. g. doing groceries, sports, work, ...). However, on a macroscopic scale ancient migration and colonization can be analyzed as active motion. In this sense, the colonization of America and the Neanderthal replacement in Europe has been studied [8].

ANIMALS Here, the term animals includes all kinds of terrestrial animals, birds, fishes and insects.
There is quite a lot of literature on active motion of animals such as the *Encyclopedia of Animal Behavior* [3] and the book *Animal Behavior* [4] which cover many interesting aspects such as *search, navigation, migration, dispersal, foraging, self-defense, mating*, and many more in great generality.
More specific research concentrates on e. g. the movement of

fish and crustaceans [24], the 'zigzagging' and 'casting' in the flight of moths [14], the foraging behavior of squirrels [28], planktivorous fish [21], and foraging/moving animals in general [15, 25]. The search for prey has been studied for e. g. toads [17], different ant-eating jumping spiders (*Saliticidae*) [13], buried bivalves [10], and predator search in general [1].

MICROORGANISMS Directed and persistent motion has also been observed for microorganisms as it was stated before and shown in Figure 2.1. Considering the diverse tasks and functions of different microorganisms, this is not surprising as diffusive Brownian motion would be highly inefficient in most applications.
In the past 30 years there has been a focus on understanding migrational processes of cells and bacteria, the underlying mechanics and their properties. These include basic as well as specific studies of *in vitro* and *in vivo* experiments, the comparison of random and directed motion, migration in complex environments, theoretical and mathematical models, and many properties of microscopic migration in general [7, 9, 11, 12, 16, 18–20, 22, 23, 27, 29].

2.2 DEFINING EFFICIENCY

Most of the tasks requiring active motion can be described as search processes. The efficiency of a search can simply be measured by the time it takes to finish the search. Indeed, for many of the tasks listed in Section 2.1 it is crucial to to spend as little time as possible on the search, to be efficient. In the case of foraging, an inefficient search that takes too much time would lead to starvation. Cells that do not escape hazardous regions fast enough will die. Therefore, search strategies and active motion will be measured by the time needed, the best ones being those that need the lowest amount of time.

2.3 SOME EXAMPLES

The motivation for actively moving around the environment varies for different living beings and different environmental conditions. Also the types of motion are diverse. Accordingly, the variety of movement patterns and their purposes is immense. In this section, therefore, a small selection is presented.

REZA: Maybe one could highlight the paragraphs for animals humans etc more by indenting the text? See next section for alternative style.

HUMANS Nowadays there is an unlimited pool of trivial reasons for actively moving, whereby some are necessary, like e. g. getting food, and some are more or less by choice, like e. g. doing sports. Also (ancient) human migration and colonization is an example of macroscopic human active motion. In this sense the colonization of

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ANIMALS Animals is a very overall term for terrestrial animals, birds, fishes and here, is supposed to include insects as well. Some reasons for motion are:

- *Foraging / finding prey.*
- *Evading predators / hazards.*
- *Finding mates.*
- *Finding shelter / new habitats.*

Whereas the type of movement pattern not only depends on the motivation but also on the species. There is a lot of literature considering these topics such as the *Encyclopedia of Animal Behavior* [3] and the book *Animal Behavior* [4] which cover many interesting aspects such as *search, navigation, migration, dispersal, foraging, self-defense, mating*, and many more in great generality.

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Certain tasks within the human body require cells to move directed, like e. g. morphogenesis, wound healing, immune response, etc.

MICROORGANISMS The reasons for microorganisms to actively move are as diverse as their variety. For some bacteria it could be *finding food* in order to grow and multiply, whereas cells in the human body might be involved in *morphogenetic* processes.

Many microscopic organisms are surrounded by fluids and therefore experience thermal diffusion. This diffusion leads to so called *Brownian motion*, a random motion named after its famous discoverer Brown and his studies on the motion of pollen particles [5].

A random motion alone, though, would be highly inefficient considering the task of reaching to a certain location. Also some microorganisms do not experience diffusion in their environment and therefore they need to be able to move by themselves. Thus, it is not surprising that *directed, persistent migration* has been observed for many different microorganisms.

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Figure 2.1 shows two exemplary migration trajectories for a cell (immature bone marrow-derived mice dendritic cell) and *Bacillus subtilis*, which are directed and sectionally persistent.

ARTIFICIAL PARTICLES Nowadays researchers have even developed artificial active particles on the micro- and nanometer scale [2], which could turn out to be very useful in many different fields.

2.4 SOME EXAMPLES *alternative version*

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Figure 2.2 shows two exemplary migration trajectories for a cell (immature bone marrow-derived mice dendritic cell) and *Bacillus subtilis*, which are directed and sectionally straight.

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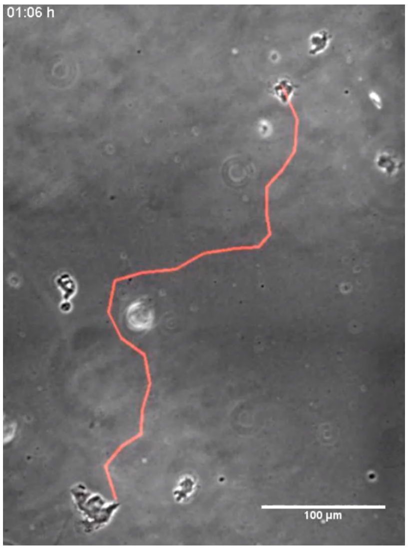
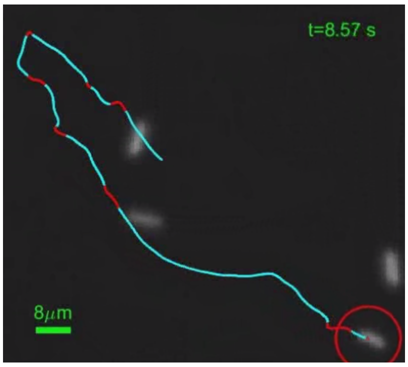


(a) Cell (immature bone marrow-derived mice dendritic cell) [18]



(b) Bacillus subtilis[1]

Figure 2.2: Directed migration paths.

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3

MODELING STOCHASTIC ACTIVE MOTION

In Chapter 2 the importance and relevance of understanding migration and motion in many different fields has been showed. In order to understand and analyze such processes mathematical modelling is a commonly used tool. A broad field of possible modelling approaches is based on the so called *Random Walk* and different extensions on it.

The random walk is a stochastic process that describes successive random steps on a mathematical space such as a hypothetical particle that walks on the integers $\mathbb{Z}$. The most basic version of the random walk is the *Simple isotropic random walk (SRW)*. It is unbiased (isotropic), meaning that the walker has no preference for one specific direction, and uncorrelated in direction, meaning that the history of previous steps' directions has no influence on the step direction at a given time.

More complex random walk versions build on the SRW and extend it.

3.1 THE SIMPLE ISOTROPIC RANDOM WALK

Consider a one-dimensional lattice which is split into discrete sites as it is shown in Figure 3.1. On this lattice, in each discrete timestep, a hypothetical particle (the *walker*) is able to jump from its current site to the neighbouring sites, each with equal probabilities $p = 1/2$. Therefore, the state of the walker can be described by the discrete time $n \in \mathbb{N}$ and position $m \in \mathbb{Z}$. Having the walker start at the origin ($m = 0$), after one time step, it will either be at site $m = -1$ or $m = 1$, each with probability $p = 1/2$. After another time step, accordingly, the walker can be at sites $m = -2$ or $m = 2$, each with probability $p = 1/4$, or at the origin $m = 0$ with probability $p = 1/2$.

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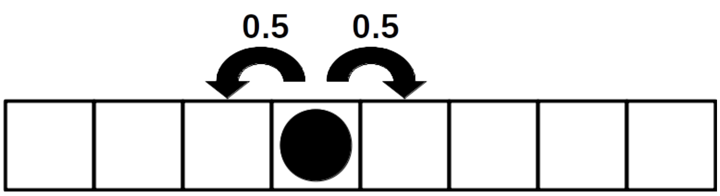


Figure 3.1: SRW on a one-dimensional lattice. Black arrows indicate the possible sites in the next step with according probabilities.

Some important and useful quantities are the mean position $\mathbb{E}\left[M_n\right]$ and the *Mean square displacement (MSD)* $\mathbb{E}\left[M_n^2\right]$, which are defined as

$$\begin{aligned}\mathbb{E}\left[M_n\right] &= \sum_{m=-\infty}^{\infty} mp\left(m,n\right), \\ \mathbb{E}\left[M_n^2\right] &= \sum_{m=-\infty}^{\infty} m^2 p\left(m,n\right).\end{aligned} \tag{3.1}$$

Here, $p\left(m,n\right)$ denotes the *probability mass function*.

As the single steps of the walk are independent from each other, these quantities are easily derived. One obtains

$$\mathbb{E}\left[M_n\right] = 0,$$

which illustrates the isotropy or absence of a bias, and

$$\mathbb{E}\left[M_n^2\right] = n,$$

the typical property of *diffusion* (MSD linear in time). Indeed, the SRW is used to model diffusive motion [6] and therefore cannot be used for active, directed motion. However, it is still a good starting point for extended models.

3.2 THE BIASED RANDOM WALK

The SRW is a special case of the BRW for $p = 1/2$.

By introducing a hopping probability $p \neq 1/2$ in the SRW one obtains the *Biased random walk (BRW)*. The situation for the one-dimensional case is depicted in Figure 3.2.

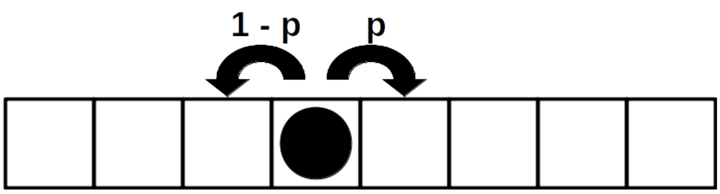


Figure 3.2: BRW on a one-dimensional lattice. Black arrows indicate the possible sites in the next step with according probabilities.

Again one can easily derive the mean position and the MSD. One obtains

$$\mathbb{E}\left[M_n\right] = n\left(2p-1\right),$$

which is nonzero (except for $p = 1/2$) as a result of the introduced asymmetrical hopping rates. This drift to one side illustrates the walker's preference for one direction. For the MSD one gets

$$\mathbb{E}\left[M_n^2\right] = 4np\left(1-p\right) + n^2\left(4p^2-4p+1\right),$$

and thus $\mathbb{E}\left[M_n^2\right] \propto n^2$, which is typical for *ballistic* motion. However, since the mean position drifts, in this case it is more meaningful to take a look at the dispersal about the mean position, which is defined as

$$\sigma_n^2 = \sum_{m=-\infty}^{\infty} \left(m - \mathbb{E}\left[M_n\right]\right)^2 p\left(m, n\right). \tag{3.2}$$

This quantity is easily obtainable as well and one derives

$$\sigma_n^2 = 4np\left(1-p\right).$$

This shows that the dispersal about the mean position is only linear in time and therefore the walker diffuses about its mean position. In other words: in its own rest frame the walker performs diffusive motion.

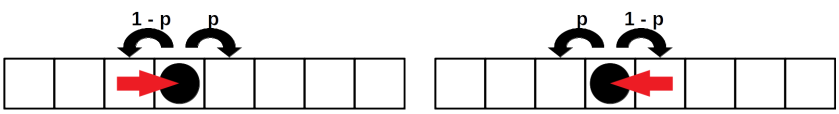
Because of its drift component the BRW is a possible model to describe directed motion, however, it is only applicable under certain circumstances and given certain requirements, which will be explained later on. For now, one more random walk model will be introduced.

3.3 THE PERSISTENT RANDOM WALK

So far the introduced random walk models have been uncorrelated and steps were independent from each other. In the Persistent random walk (PRW) (or also Correlated random walk (CRW)) this is not the case. Instead, at a given time the probabilities for the different directions of the next step are dependent on the direction of the very previous step. In other words: it matters from which direction the walker came from in the previous step, the walker has some kind of short memory.

The PRW model defines a *persistency* parameter $p \in [0, 1]$ which gives the probability to keep going in the same direction. Therefore, in the one-dimensional case there are two possible ways of how a walker has reached its current side, leading to two possible scenarios of how it will continue its walk which are shown in Figure 3.3.

A PRW with persistency parameter $p = 1/2$ is equivalent to the SRW.



(a) Coming from the left site. (b) Coming from the right site.

Figure 3.3: The two possible scenarios which can happen during the one-dimensional PRW. Red arrows indicate the direction of movement in the previous step, black arrows indicate the possible sites in the next step with according probabilities.

Consequently, walks with $p < 0.5$ tend to reverse the direction of movement leading to *anti-persistent motion*, while walks with $p > 0.5$ reinforce the direction of movement leading to *persistent motion*. For the trivial cases of $p = 0$ the walker only jumps back and forth and for $p = 1$ it keeps going in one direction without ever reversing, which is a ballistic flight.

For the mean position and the MSD one obtains [26]

$$\mathbb{E}\left[M_n\right] = 0,$$
$$\mathbb{E}\left[M_n^2\right] = \frac{1+p}{1-p}n + \frac{2p}{(1-p)^2}\left(p^n - 1\right).$$

The result for the mean position is not surprising as there is no bias or preferred direction in the PRW. However, the result for the MSD is more interesting. Here one needs to differentiate between short and long term behavior.

For short times one derives

$$\mathbb{E}\left[M_n^2\right] \propto n^\alpha,$$

where $\alpha = 1 + \ln(1+p) / \ln 2$ [26]. Considering only the non-trivial case of $p \in (0,1)$ gives $\alpha \in (1,2)$ and therefore the short term behavior is *superdiffusive*.

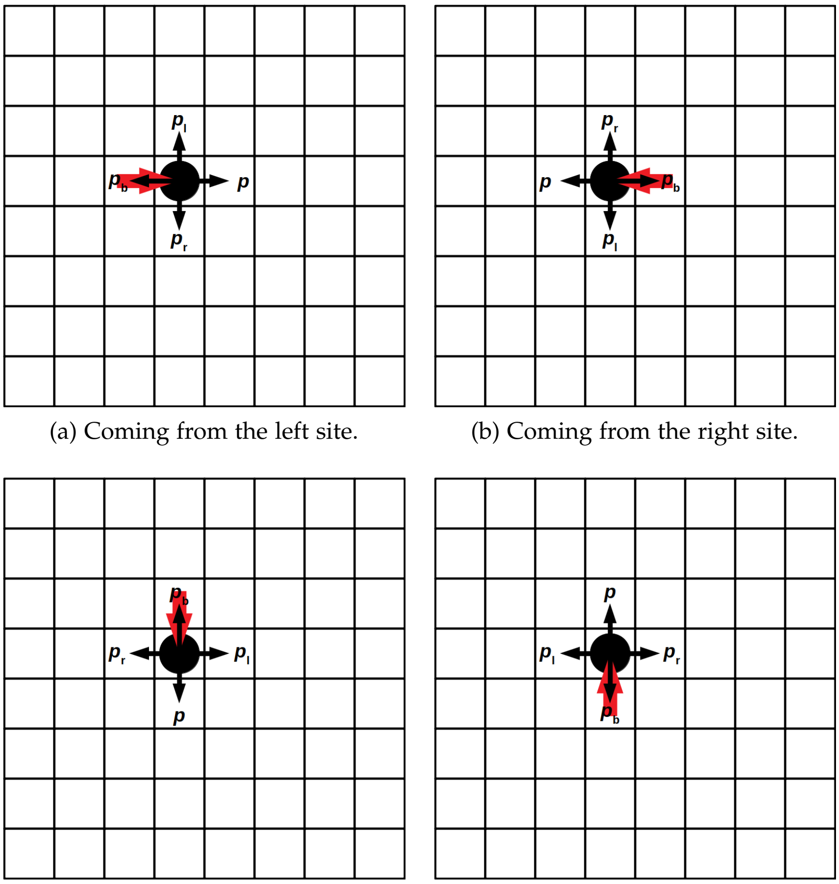
For long times ($n \to \infty$) the second part of the right-hand side becomes a constant and the first part defines the behavior. This means that the MSD is linear in time and the motion becomes diffusive.

Therefore, the PRW shows a transition from superdiffusive to diffusive motion, which makes it a possible model to describe active, persistent motion. And indeed, later on, it will be the model of choice in order to study different aspects of motion. For this purpose, one needs to extend the model to two dimensions and consider not only discrete but also continuous space.

TWO-DIMENSIONAL LATTICE On a two-dimensional lattice the persistency parameter p gives the probability to keep going in the same direction. However, instead of only one probability for the reversal of movement, there are two additional probabilites for turning to the right or left in respect to the direction of movement. To distinct between them, they will be denoted by p_l and p_r, respectively. The probability of reversing the direction of motion is than computed by $p_\mathrm{b} = 1 - p - p_\mathrm{l} - p_\mathrm{r}$. This means that for a walker at any given time there are four possible ways of how it has reached its current site and therefore there are four possible scenarios of how it will continue its walk which are shown in Figure 3.4.

REZA: I might want to use a smaller grid in Figure 3.4 to save some space

Here, the analytical derivation of the mean position and the MSD is much more complex than in the one-dimensional case and, since those quantities are not of much importance now, will be skipped. However, there are different other meaningful quantities that can be derived under certain simplifications, which will be explained below.



(a) Coming from the left site. (b) Coming from the right site.

(c) Coming from the upper site. (d) Coming from the lower site.

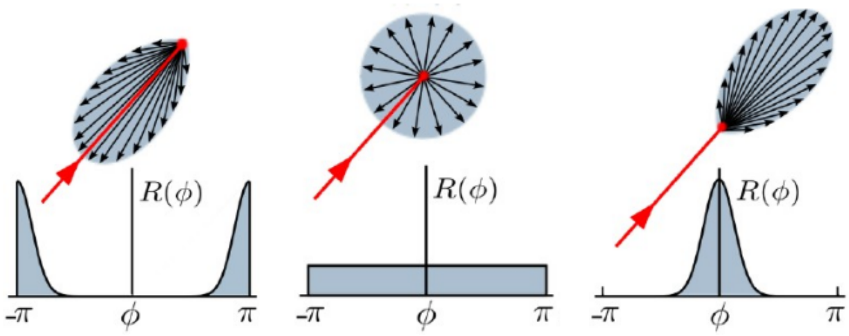
Figure 3.4: The four possible scenarios which can happen during the PRW on a two-dimensional lattice. Red arrows indicate the direction of movement in the previous step, black arrows indicate the possible sites in the next step with according probability.

TWO-DIMENIONAL CONTINUOUS SPACE For the two-dimensional continuous PRW, instead of hopping probailities, one needs a continuous turning angle distribution in order to determine the direction of movement. Additionally, the step-length can be chosen from a step-length distribution. Nevertheless, one can still define a persistency parameter.

Considering the turning angle distribution $R(\phi)$, one can define the mean cosine c and mean sine s of the turning angle as

$$\begin{aligned} c &= \mathbb{E}\left[\cos(\phi)\right] = \int_{-\pi}^{\pi} \cos(\phi)\, R(\phi)\, \mathrm{d}\phi, \\ s &= \mathbb{E}\left[\sin(\phi)\right] = \int_{-\pi}^{\pi} \sin(\phi)\, R(\phi)\, \mathrm{d}\phi. \end{aligned} \tag{3.3}$$

From these quantities one can extract information about the PRW. The mean sine measures the relative probability of clockwise and anticlockwise turns. For most applications, however, the turning angle distributions are symmetric and, hence, the mean turning angle ϕ_{mean} as well as the mean sine s are zero. In this case, the quantitiy c is a measure of the correlation or persistency and therefore, the mean cosine c as defined in Equation 3.3 will be called persistency parameter p hereinafter. Note that $p \in [-1, 1]$ can be negative and depending on its value the motion is either anti-persistent, diffusive or persistent. An example distribution for each regime is shown in Figure 3.5.



(a) Anti-persistent distribution with negative persistency parameter p.

(b) Diffusion distribution with persistency parameter $p = 0$.

(c) Persistent distribution with positive persistency parameter p.

Figure 3.5: Exemplary turning angle distributions and directions of movement in the context of the two-dimensional continuous PRW. Red arrows indicate the direction of movement in the previous step, black arrows indicate possible directions of movement in the next step, with length being proportional to the probability. [26]

Now that these models and methods have been briefly introduced, the two-dimensional lattice model will be slightly modified and discussed in more detail.

Part II

PART 2

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