

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
FPT	First-passage time
MFPT	Mean first-passage time

Part I

PREPARATION

Not sure if an introduction is needed for the Laborpraktikum.

INTRODUCTION

Write some kind of intro here.

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.

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 purely random motion named after its famous discoverer Brown and his studies on the motion of pollen particles [6]. 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.

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.

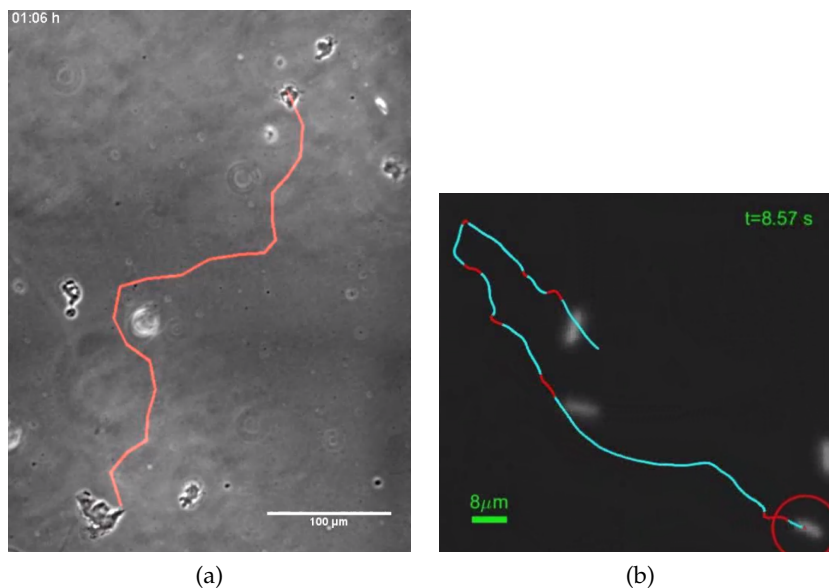


Figure 2.1: Directed and piecewise persistent migration paths for (a) an immature bone marrow-derived mice dendritic cell [24], and (b) a *Bacillus subtilis* bacterium [27].

In the following, reasons for active motion are given, a selection of research in different fields is presented and the search problem aspect is explained.

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. 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.

From this list one can extract that most of the time a specific *search problem* is the cause of active motion. 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 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 [11]. The total dispersal times as well as the effective velocity of dispersal, which have been derived within this study, are in good agreement with archaeological data and the given reference values.

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* [4] and the book *Animal Behavior* [5] which cover many interesting aspects such as *search, navigation, migration, dispersal, foraging, self-defense, mating*, and many more

in great generality. However, a wide variety of research also focuses on very specific topics with most of them being focused on foraging behaviour or other search problems requiring active motion or relocation.

In the early eighties animals were typically divided into the categories of *ambush* and *cruise* searchers depending on their foraging behaviour [12]. Animals that are constantly moving through the environment while searching for food or prey belong to the cruise search type (e. g. tuna, soaring hawks) whereas the ambush type remains stationary for long periods of time and waits for prey to get into strike range (e. g. herons, rattlesnakes).

Nonetheless, in a theoretical approach, Andersson (1981) [1] compared continuous travel to a search mode of alternating pause-travel in regard of energy consumption and prey detection efficiency. The results propose that, under given circumstances (prey density and detectability, energy expenditure during travel, etc.) a pause-travel tactic may become superior.

In studies of foraging behaviour in planktivorous fish such pause-travel or stop-and-go movement patterns, which cannot be associated with either the ambush nor the cruise search, have been observed [28]. This pattern is called *saltatory search* by Evans and O'Brien (1988) [10]. In fact many foraging species seem to perform some kind of saltatory motion during foraging. Even the movement of the human eye during the process of reading as the eye shifts focus along a line of type [17] or finding a specific letter sequence [7] can be described in such a saltatory manner. Analogously, it is even conceivable that e. g. soaring hawks, which are supposed to be cruise searcher, might be able to use saltatory eye movement to lock in on and scan an area for prey before they switch to a new area. Therefore, the saltatory search serves as an explanatory tool and supposedly all search behaviour can be placed on a saltatory continuum with the extremes being the cruise and the ambush search [28].

Indeed, the saltatory motion gives rise to a lot of research up to today. Observations of white crappie revealed alterations in speed, travel distance and pause times when feeding on prey of different sizes [19]. These adaptations were analyzed with regard to efficiency using a net energy gain simulation model and the results are believed to have considerable generality for other saltatory animals.

Kramer and McLaughlin (2001) [21] use the term *intermittent locomotion* to describe the observed stop-and-go motion. They show that despite the fact that pausing adds acceleration and deceleration phases to locomotion, which are costly in terms of energy usage, it is still widespread among diverse species and can have benefits such as recovery from fatigue, improved detection of prey, predators and travel routes, and reduced detection by other organisms.

Juvenile plaice (*Pleuronectes platessa*) change their predatory behaviour

REZA: I might be too close to the original texts in some cases in the paragraph on cruise, ambush and stop-and-go search.

REZA: O'Brien, Browman, and Evans cited [17] and [7] in their work for the part with the reading and letter sequence, so do I need to cite them as well here or not since I already cited O'Brien, Browman, and Evans [28]?

The mentioned movement pattern has had many names throughout different works, namely saltatory search, intermittent locomotion, intermittent search, stop-go running, stop-and-go swimming, pause-travel locomotion, ...

and motion upon the discovery of a potential prey during search [14]. Several moves before an attack, the distance of moves is decreased, which gives rise to the assumption that plaice detect their prey more efficiently when stationary than while moving. Furthermore, the pauses between moves are shortened and the rate of turning per unit distance is increased.

Naturally, mathematical approaches and models describing saltatory or intermittent motion of animals have also emerged over the years, however, at this point they are not to be discussed (see e. g. [3, 32]).

Besides the saltatory search research, which is a topic to fill a whole book alone, there are further examples of research which include:

- A study on the depth vision and perception of the three dimensional environment of a toad revealed that in presence of a prey, the toad plans its route before starting to move and that the route is preprogrammed, meaning that once the toad has started moving, it does not correct its path even if the prey has relocated. [23]
- The movement of fish and crustaceans has been studied. [31]
- The control and function of *counterturning* (succession of alternating left and right turns), a feature in the flight of insects following a wind-borne odour, is discussed as there is unambiguous evidence only for the findings concerning a certain flying male moth. Furthermore, the main function of counterturning appears to be the redetection of an already perceived elusive odour. [20]
- Radiotagged red squirrels (*Sciurus vulgaris*) have been observed in coniferous and deciduous habitats in regard to activity pattern, activity budget and foraging behaviour. Food availability, food choice and feeding rate are then used to explain differences between habitats. [36]
- The prey-capture techniques and prey preferences of six different ant-eating jumping spiders (*Salitricidae*) have been studied in the laboratory. The results on the predatory behaviour as well as the preference for ants are discussed in consideration of the findings on other ant-eating spiders. [18]

TODO: Maybe find some finishing sentence here since it looks weird to stop with a list and continue with a new subsection?!

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

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REZA: [31] there is no abstract available online so maybe I should remove this resource because I don't know what their findings were!

REZA: Since source [20] is from 1983 I'm not sure if evidence has been found for other insects as well, this might be a problem?

not surprising as diffusive Brownian motion is highly inefficient in most (search) applications.

Understanding cell migration is of utmost importance as it has essential functions (not only) in the human body in regard to diverse health concerns. This importance is emphasized in many of the mentioned references below. Therefore, in the past 30 years there has been a focus on understanding migrational processes of cells and bacteria, the underlying mechanics and their properties, of which some excerpts are presented here.

- The migration of different *E. coli* strains on glass and solid surfaces differing in charge and hydrophobicity was studied in an *in vitro* system in order to gain insight on catheter-associated bacteriuria. The findings propose that prevention strategies should be based on inhibition of bacterial growth rather than on modifying the physicochemical properties of the catheter surface. [13]
- There are a few articles around which focus on explaining the mechanics, molecular processes and dynamics involved in cellular motion. Some topics covered include contractile forces and adhesion, the role of actin filaments and the cytoskeleton, polarization of the cell, molecular stimulation, membrane extension, and many others. [15, 16, 22, 26]
- In a study on the directional sensing of *Dictyostelium discoideum* amoebae it is concluded that the cell senses direction by spatial regulation of the activity of the signal transduction pathway. [29]
- The specific mechanisms and factors that promote directionally persistent as opposed to random cell migration are identified and examined. [30]
- In a study of cell motility a mathematical model is developed, which makes use of the analysis of live cell image sequences in order to gain information about collective biomechanical and molecular mechanisms of cell motion, such as e.g. molecular structures, dynamics, processes within the cell, and many more. Therefore, this model is supposed to allow drawing conclusions from the analysis of the cell motion alone. [9]
- In regard to the medical issue of removing infected prostheses from patients, bacterial cell migration has been observed and studied. For the migration from a colonized to a sterile plate, yeast and *Staphylococcus aureus*, which belongs to the bacteria that are responsible for most hospital infections, have been used. They suppose that infected prostheses in patients can be completely cleaned by this method in the near future. [34]

- The coherence of cell migration speed and cell persistence is shown based on experimental data *in vitro* and *in vivo*. Additionally, using a theoretical model a generic phase diagram of cell trajectories is obtained which represents the whole range of observed migration patterns. [24]
- In a preview the distinct motility modes exhibited by migrating cells and their ability to switch between modes according to physical or chemical cues is discussed. [37]
- It is physiologically reasonable that cells move through crowded and complex environments, typically in three-dimensional fibrillar networks. A review on the progress of understanding single-cell migration through such environments is given. [25]

TODO: Maybe find some finishing sentence here since it looks weird to stop with a list and continue with a new subsection?!

Artificial particles

Inspired by microorganisms researchers have developed artificial self-propelled active particles with similar properties and behaviour in regard to motility. These could turn out to be very useful in many different fields such as e. g. health care, sustainability, and security. In a review, the development of artificial self-propelled micro- and nanoparticles, their application to the study of nonequilibrium phenomena, and open challenges are discussed. While doing so the focus lies on the basic physical features of the interactions with crowded and complex environments. [2]

At this point it is worth emphasizing again that many of the given examples for active motion are dealing with search problems and in the course of evolution, as an answer, the creativeness of Mother Nature has yielded many different search types and strategies which will be partly addressed later on. Hence, understanding their main qualitative and quantitative properties is beneficial to many fields of research and will be a main focus of this work.

MODELING STOCHASTIC DYNAMICS OF ACTIVE MATTER

In [Chapter 2](#) the importance and relevance of understanding migration, motion and search strategies in many different fields has been outlined. 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 $p = 1/2$. In this manner one can continue in order to find the probabilities for being at each site at a given time.

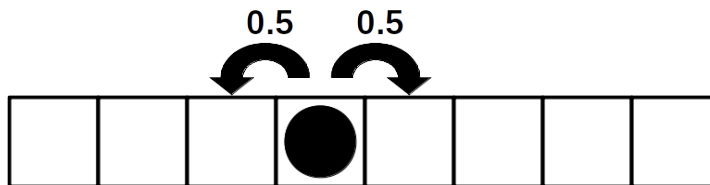


Figure 3.1: [SRW](#) on a one-dimensional lattice. Black arrows indicate the possible sites in the next step with according probabilities.

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

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

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

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

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

which illustrates the isotropy or absence of a bias, and

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

the typical property of *diffusion* (MSD linear in time). Indeed, the SRW is used to model diffusive motion [8] 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.

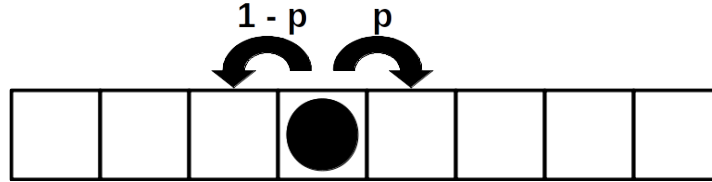


Figure 3.2: BRW on a one-dimensional lattice. Black arrows indicate the possible sites in the next step with according probabilities.

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

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

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

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

and thus $\mathbb{E}[M_n^2] \propto n^2$, 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

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

This quantity is easily obtainable as well and one derives

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

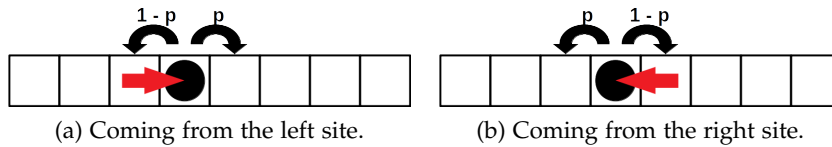
This shows that the dispersal about the mean position is only linear in time and therefore the walker diffuses about its mean position. In other words: in its own rest frame the walker performs diffusive motion.

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 site, 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](#).

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 [33]

$$\begin{aligned}\mathbb{E}[M_n] &= 0, \\ \mathbb{E}[M_n^2] &= \frac{1+p}{1-p}n + \frac{2p}{(1-p)^2}(p^n - 1).\end{aligned}$$

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

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

where $\alpha = 1 + \ln(1+p) / \ln 2$ [33]. 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 ($n \rightarrow \infty$) 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, the model is extended to two dimensions and a model in continuous space is introduced.

3.3.1 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 probabilities 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 then computed by $p_b = 1 - p - p_l - p_r$. 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.

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.

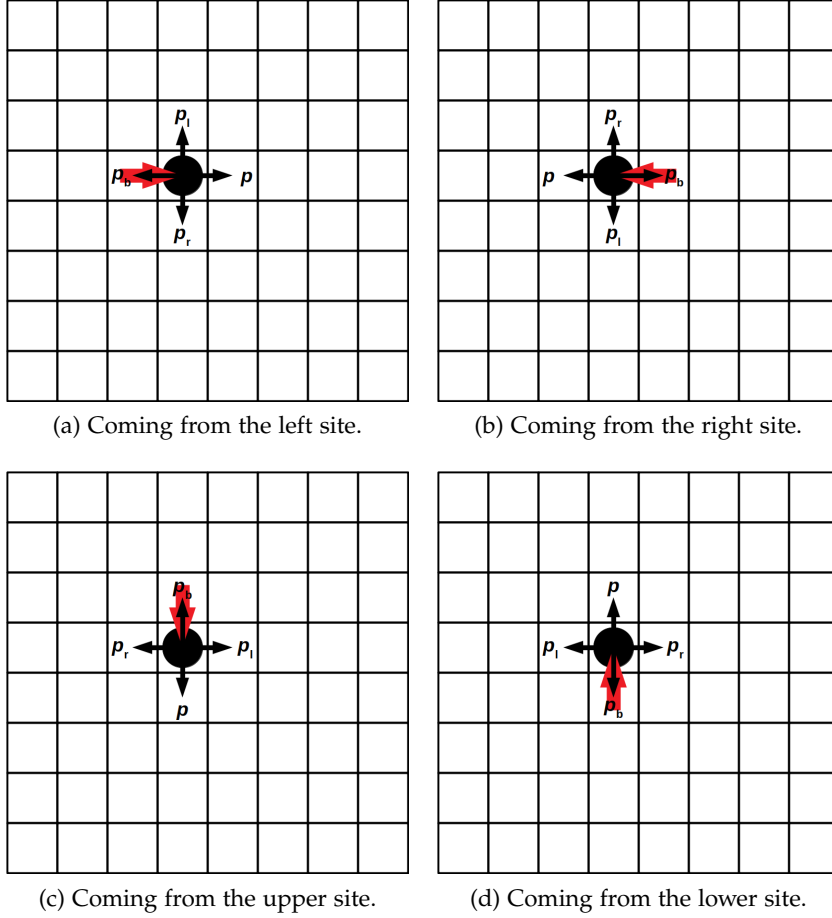


Figure 3.4: The four possible scenarios which can happen during the PRW on a two-dimensional lattice. Red arrows indicate the direction of movement in the previous step, black arrows indicate the possible sites in the next step with according probability.

3.3.2 Two-dimensional continuous space

For the two-dimensional continuous PRW, instead of hopping probabilities, 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

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

From these quantities one can extract information about the PRW. The mean sine measures the relative probability of clockwise and anti-clockwise 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 quantity 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.

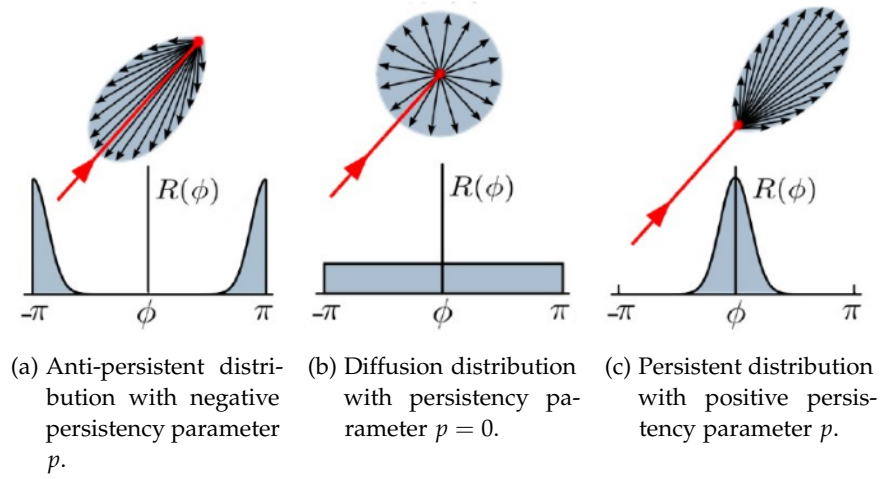


Figure 3.5: Exemplary turning angle distributions and directions of movement in the context of the two-dimensional continuous PRW. Red arrows indicate the direction of movement in the previous step, black arrows indicate possible directions of movement in the next step, with length being proportional to the probability. [33]

3.4 A TWO DIMENSIONAL LATTICE MODEL

At this point, all the requirements are given to introduce a minimal model, which has been used by Tejedor, Voituriez, and Bénichou (2012) [35] in their work on “Optimizing Persistent Random Searches.” It is based on the persistent random walk on a two dimensional lattice and will serve as an example of how to use modeling in order to acquire information about the motion and search problem.

As introduced in Section 3.3.1, the model includes a persistent random walker in discrete time and space, moving on a two dimensional lattice of volume $V = X^2$, where $X \gg 1$ (see Figure 3.6). Periodic boundary conditions are used and there is a fixed single target site within the system. However, we will consider the search problem later on. Here, we want to look at the persistent random walk only.

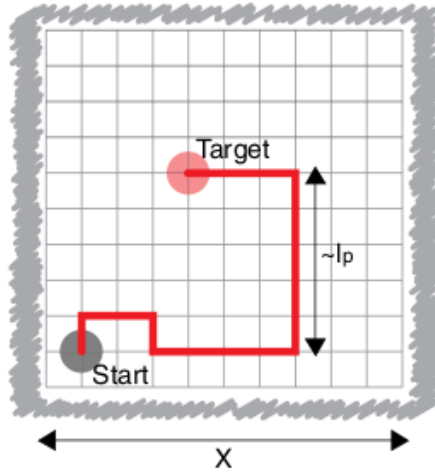


Figure 3.6: Example trajectory for a persistent random walker walking on a two dimensional discrete lattice.

The persistent random walker is described by its persistency parameter $p \in [0, 1]$, which gives the probability for taking a step in the persistent direction. For the other three directions the probabilities are assumed to be equal and therefore it is $p_b = p_l = p_r = \frac{1-p}{3}$. In this case one can derive the probability of having l consecutive steps in the same direction as

$$P(l) = (1 - p) p^{l-1}.$$

Using this probability, one can then define the *persistence length* as

$$l_p = \sum_{l=1}^{\infty} l P(l) = \frac{1}{1 - p}, \quad (3.4)$$

which is the mean length of ballistic excursions and is a descriptive quantity of persistent random walks.

As the walker will necessarily (TODO: Do I need to prove this necessity?) encounter the target site during its walk, this model can serve as a simple search problem model. In ?? the search time was declared to be one of the interesting quantities of search problems. Therefore, using this model, an adequate method of calculating the search time is needed. This will be covered in [Chapter 4](#).

In [Chapter 2](#) *search problems* and the term *search time* have been mentioned as important concerns of this work. In order to model a search problem, in the first place we needed a method of modeling motion as motion is a prerequisite for exploring space. This has been done in [??](#). Now the last component of a simple complete search problem is the search time.

In random walk models like the two dimensional lattice one introduced in [Section 3.4](#), the time it takes to find the target is often referred to as *First-passage time (FPT)* (the time it takes to first visit and pass the target site). However, in most cases it is more meaningful to consider the average search time, which is accordingly called *Mean first-passage time (MFPT)*. Depending on the complexity of the search problem, the *MFPT* can be derived analitically or numerical methods are needed.

Consider, for example, a *SRW* on a constrained one dimensional lattice of length $L = 4$. For the four sites $i \in [0, 3]$ one can easily write down the transition probabilities $P_l(i)$ and $P_r(i)$ to the neighbouring sites (see [TODO: create figure and refer here](#)). The boundaries shall be reflective, which means that for the outer sites the probabilities are $P_l(0) = 0$ and $P_r(0) = 1$ (analogously for site $i = 3$). For the two inner sites it is $P_l(1) = 1/2$ and $P_r(1) = 1/2$ (analogously for site $i = 2$). Now the question could be, *What is the average time it takes to move from site $i = 0$ to site $i = 3$?*, which could be compared to a very simple random search problem in which the target is located at the right side of the confinement while the searcher starts its search on the left side. In this simple case, using backward equations, one can quickly derive the average number of steps it takes the walker to reach site $i = 4$, here namely nine steps.

The problem of determining the search time in the scope of a model in which the searcher performs a random walk to find the target is often called a random search problem.

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