

# LABORPRAKTIKUM

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Some Active Motion and First-passage Time

August 2018 – version 1.0

Kevin Klein: *Laborpraktikum*, Some Active Motion and First-passage Time, © August 2018

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## LISTINGS

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## ACRONYMS

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SRW	Simple isotropic random walk
MSD	Mean square displacement
BRW	Biased random walk
PRW	Persistent random walk
CRW	Correlated random walk

## Part I

### PREPARATION

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## INTRODUCTION

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## ACTIVE MOTION

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*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.

### 2.1 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.

**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 America and the Neanderthal replacement in Europe has been studied [8].

**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.

More specific research concentrates on e.g. the movement of fish and crustaceans [23], the foraging behavior of squirrels [27], planktivorous fish [20], and foraging/moving animals in general [14, 24]. The search for prey has been studied for e.g. toads [16], different

*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.*

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

*TODO: "in great generality" that doesn't sound good*

*REZA: Articles on finding mates, shelter, habitats are missing. Do we need more examples here or is it too much already?*

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

ant-eating jumping spiders (*Salitricidae*) [13], buried bivalves [10], and predator search in general [1].

**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.

In the past 30 years there has been a focus on understanding migrational processes of cells and bacteria, the underlying mechanics and their properties [7, 9, 11, 12, 15, 17–19, 21, 22, 26, 28]. 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.

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.

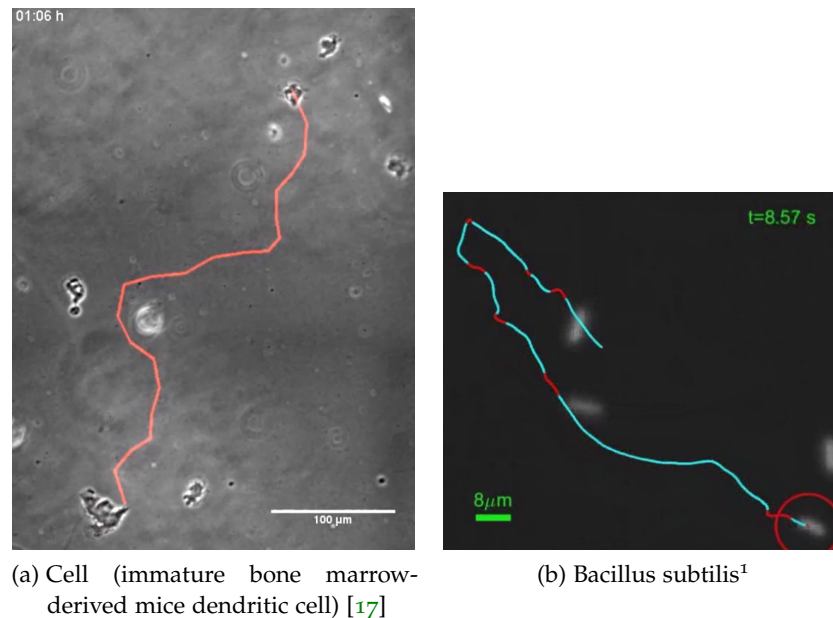


Figure 2.1: Directed migration paths.

**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.

## 2.2 MODELLING ACTIVE MOTION

The given examples above show the importance and relevance of understanding migration and motion in many different fields. 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.

### 2.2.1 The Simple Isotropic Random Walk

Consider a one-dimensional lattice which is split into discrete sites as it is shown in Figure 2.2. 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  $p = 1/2$ .

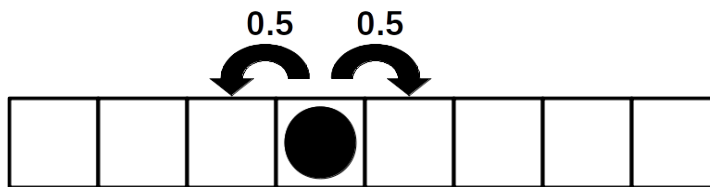


Figure 2.2: SRW on a one-dimensional lattice. Black arrows indicate the possible sites in the next step with according probabilities.

REZA: Should I define the random walk in a more mathematical approach?

<sup>1</sup> J. Najafi *et al.*, under review (2018)

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

$$\begin{aligned}\mathbb{E}[M_n] &= \sum_{m=-\infty}^{\infty} mp(m, n), \\ \mathbb{E}[M_n^2] &= \sum_{m=-\infty}^{\infty} m^2 p(m, n).\end{aligned}\tag{2.1}$$

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 [6] and therefore cannot be used for active, directed motion. However, it is still a good starting point for extended models.

### 2.2.2 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 2.3.

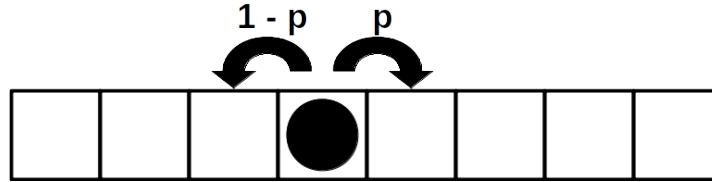


Figure 2.3: BRW on a one-dimensional lattice. Black arrows indicate the possible sites in the next step with according probabilities.

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

$$\sigma_n^2 = \sum_{m=-\infty}^{\infty} (m - \mathbb{E}[M_n])^2 p(m, n). \quad (2.2)$$

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 appropriate under certain circumstances and given certain requirements, which will be explained later on. For now, one more random walk model will be introduced.

### 2.2.3 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 *persistence* 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 2.4](#).

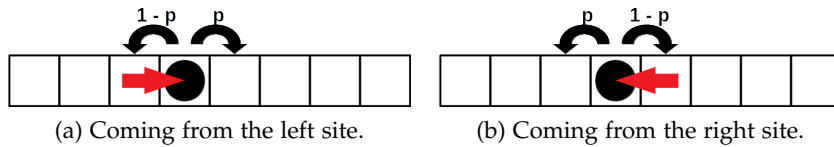


Figure 2.4: The two possible scenarios which can happen during the one-dimensional [PRW](#). Red arrows indicate the direction of movement in the previous step, black arrows indicate the possible sites in the next step with according probabilities.

Consequently, walks with  $p < 0.5$  tend to reverse the direction of movement leading to *anti-persistent motion*, while walks with  $p > 0.5$

*A [PRW](#) with persistence parameter  $p = 1/2$  is equivalent to the [SRW](#).*

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 [25]

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

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  $\alpha = 1 + \ln(1+p) / \ln 2$  [25]. 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, 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 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 2.5.

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.

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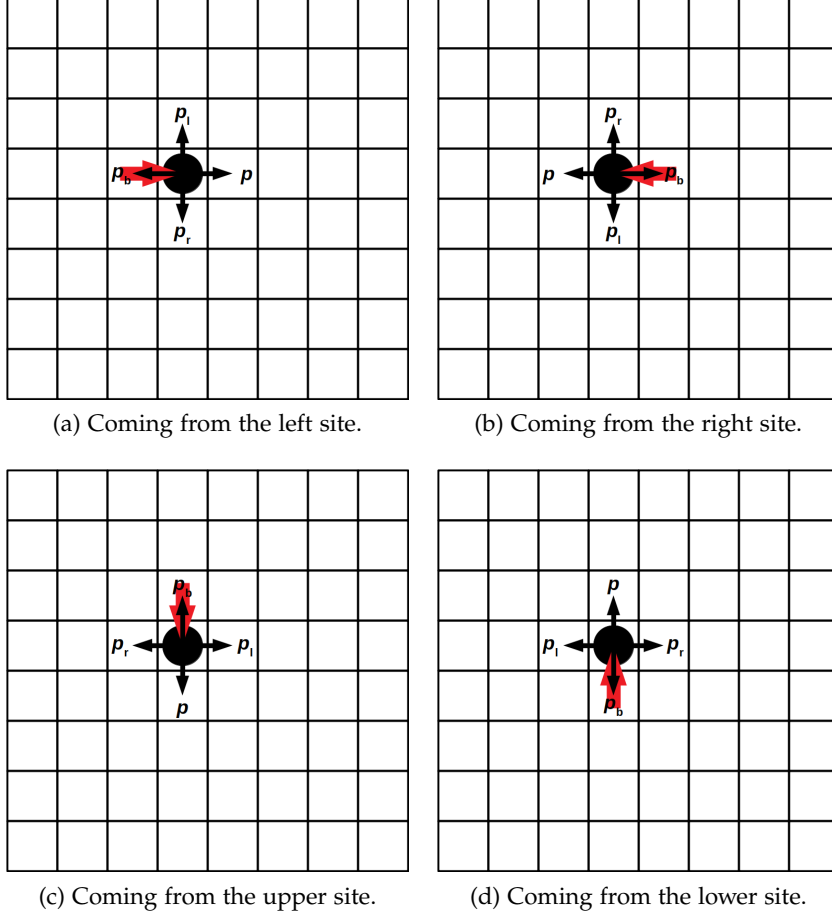


Figure 2.5: The four possible scenarios which can happen during the [PRW](#) on a two-dimensional lattice. Red arrows indicate the direction of movement in the previous step, black arrows indicate the possible sites in the next step with according probability.

**TWO-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

$$\begin{aligned}
 c &= \mathbb{E}[\cos(\phi)] = \int_{-\pi}^{\pi} \cos(\phi) R(\phi) d\phi, \\
 s &= \mathbb{E}[\sin(\phi)] = \int_{-\pi}^{\pi} \sin(\phi) R(\phi) d\phi.
 \end{aligned} \tag{2.3}$$

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  $\phi_{\text{mean}}$  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 2.3 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 2.6.

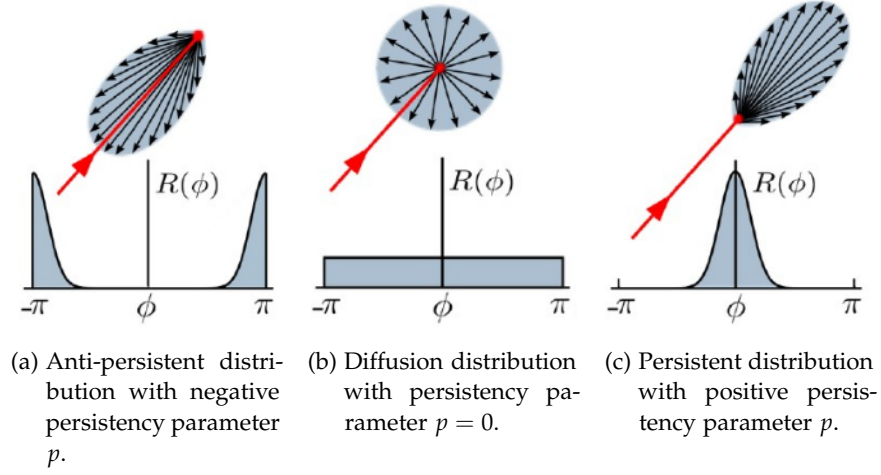


Figure 2.6: Exemplary turning angle distributions and directions of movement in the context of the two-dimensional continuous PRW. Red arrows indicate the direction of movement in the previous step, black arrows indicate possible directions of movement in the next step, with length being proportional to the probability. [25]

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

### 2.3 A TWO-DIMENSIONAL LATTICE MODEL



2.4 SOME EXAMPLES *alternative version*

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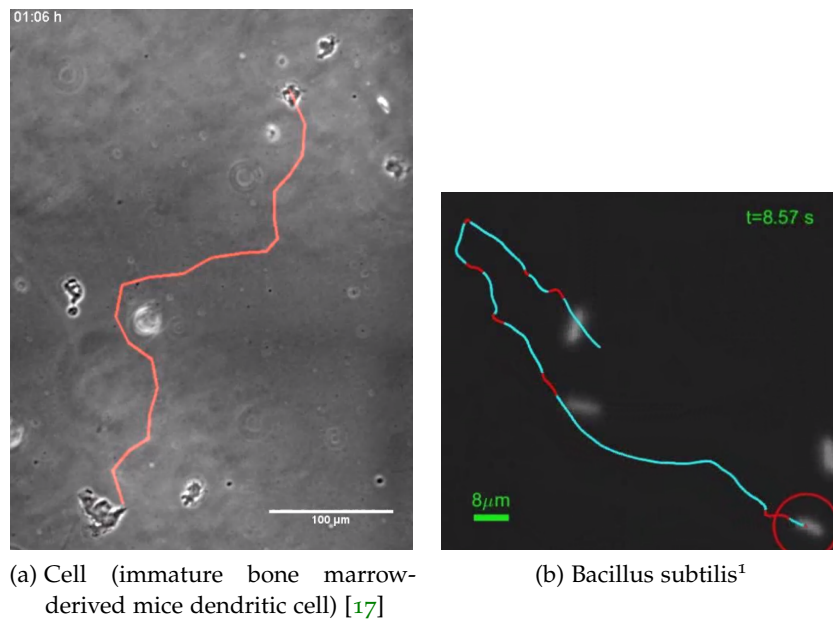


Figure 2.7: Directed migration paths.

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<sup>1</sup> J. Najafi *et al.*, under review (2018)

## Part II

### PART<sub>2</sub>



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