

MODELING THE NAVIGATION OF A WEAVER ANT IN A SIMPLE,
UNFAMILIAR ENVIRONMENT



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วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต
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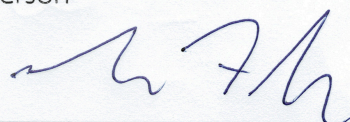
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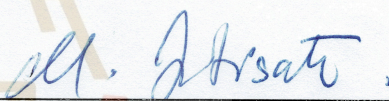
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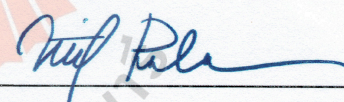
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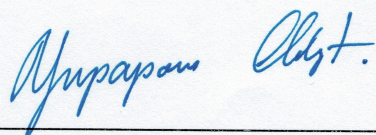
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มดสายพันธุ์ *Oecophylla smaragdina* หรือรู้จักกันโดยทั่วไปว่ามดแดง มดแดงเป็นมด
พื้นเมืองในแถบทวีปเอเชียและแอฟริกา มดเป็นที่รู้จักกันว่าเป็นสัตว์ที่มีความสามารถในการทำงาน
ร่วมกันสูง โดยเฉพาะมดแดงจะปรับตัวให้ทำงานร่วมกันเป็นจำนวนมากในการทำงานที่มีขนาดใหญ่
ให้สำเร็จ เมื่อมองในมุมมองของระบบที่มีจำนวนมากมดแดงได้ถูกนำมาศึกษาโดยนักวิจัยในหลายด้าน
เพื่อเป็นก้าวแรกในการทำความเข้าใจการเคลื่อนที่อย่างสอดคล้องกันของมดแดงงานวิจัยนี้จึงต้องการที่จะ
หารูปแบบการเคลื่อนที่ของมดแดงหนึ่งตัว จากการข้อมูลการติดตามตำแหน่งของมดหนึ่งตัวในพื้นที่
ปิดขนาดเล็กที่มีอยู่ นำไปสู่การเสนอแบบจำลองทางทฤษฎีอย่างง่ายที่ใช้ในการอธิบายการเคลื่อนที่
ของมดแดงหนึ่งตัว การสำรวจของมดแดงหนึ่งตัวสามารถอธิบายได้อย่างเหมาะสมด้วยจำลองแบบ
การเคลื่อนที่แบบบราวน์ หรือก็คือการเปลี่ยนแปลงความเร็วของมดเป็นผลมาจากแรงดลที่ได้รับการ
สุ่มอย่างอิสระจากฟังก์ชันการแจกแจงความน่าจะเป็นที่แน่นอน ด้วยการใช้จำลองการเคลื่อนที่แบบ
บราวน์ แนวโน้มของมดแดงที่จะอยู่บริเวณขอบสามารถอธิบายว่าเป็นผลมาจากการสุ่มเท่านั้น โดยที่
มดมีการหยุดที่ขอบของพื้นที่ซึ่งในการเคลื่อนไหวแบบสุ่มเป็นไปได้ยากที่จะนำมดกลับมายังบริเวณ
ภายในของพื้นที่ จากมุมมองในด้านคุณภาพการเคลื่อนที่ของมดแดงสามารถอธิบายด้วยแบบจำลอง
ดังกล่าว ด้วยจำนวนพารามิเตอร์ในแบบจำลองเพียงเล็กน้อยและปราศจากข้อสมมติฐานเรื่องจุดมุ่ง
หมายของมด

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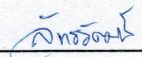
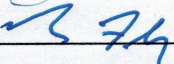
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The ant species *Oecophylla smaragdina*, commonly known as the weaver ant, is native to tropical Asia and Africa. All ants are known for highly-organized, co-operative behavior and weaver ants are particularly adept at working together, in numbers, to accomplish large-scale tasks. Considered an example of a many-body system, weaver ants have been studied by researchers in various fields. As a first step towards understanding weaver ant coordinated motion, this work want to find the algorithm that a single ant employs. Having previously tracked the motion of individual ants within a small, bounded arena, a simple theoretical model, which can describe this motion is presented. The navigation of a single ant can be adequately modeled as Brownian motion: the ant velocity changes by random impulses drawn independently from a robust probability distribution. Using established Brownian motion theory, the ant's tendency to remain near boundaries can be explained as a result of pure chance: having been stopped at the boundary, random motion is unlikely to bring the ant back to the arena interior. All qualitative aspects of ant motion are captured by a model with few parameters and without any assumptions about the ant's intent.

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Student's Signature

Advisor's Signature

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CHAPTER I

INTRODUCTION

The behavior of an ant colony has fascinated naturalists for hundreds of years and continues to motivate scientific research today. Even a casual observer recognizes that the colony is a highly organized society. Labor is divided effectively, with individuals performing specialized roles, so that projects requiring the effort of thousands can be accomplished. These endeavors require communication, and much ant research has focused on their methods of communication, which include using pheromones, and the responses of individuals to visual and tactile signals.

Experiments on ants are convenient (since ants are abundant and manageable) and, in addition to what they teach us about ants specifically, they can provide insight into more general many-body systems via analogy. The collective motion of ants may be compared to that of many other organisms that are more difficult to study, including birds and fish (Milinski and Heller, 1978) and microscopic examples like bacteria (Ryan et al., 2013; Sokolov and Aranson, 2012). Ant populations placed in danger manage to find effective strategies for evacuating enclosed areas, which may be emulated in methods of crowd-control among people (Parisi and Josens, 2015). More abstractly, a large group of ants is a system of correlated particles, representative of a class of natural systems of interest to chemistry, condensed matter physics and other fields (Czirók et al., 1999; Vicsek et al., 1999; Vicsek and Zafeiris, 2012; DeLellis et al., 2014). Some have even suggested that, since ant colonies appear to function effectively without hierarchical power structures, studies of ants may have applications in political science (Tokita and Tarnita, 2020).

When foraging ants successfully locate food and return to the nest, they direct others (in various ways) to follow the fruitful path. This means the algorithm that one ant uses to navigate is modified according to information received by others. The mechanism and efficiency of this communication has been a central point of interest for many studies.

Here we are interested in a much simpler, underlying, question: how

does an individual ant navigate within an unfamiliar environment? Originally, we viewed this as a first step in a systematic study of simple ant communication. The plan was first to analyze the navigation algorithm of a single ant, then to introduce a second ant and detect any changes in this algorithm that could be attributed to communication (Paisanapan et al., unpublished, 2022). We were surprised to discover that the motion of a single ant was, in itself, of considerable interest. This thesis will describe the motion of a single ant, and the quantitative model we developed to describe it.

Our group recently performed a set of experiments on weaver ants (Thiawatwanikul et al., 2020). The ant species *Oecophylla smaragdina*, commonly known as the weaver ant, is found in tropical Asia and Australia. Even when compared to those of other ants, their feats of cooperation are impressive. They build nests for the colony in trees by bending broad leaves and gluing them together into a spherical enclosure, which is where they get their name. To cross gaps or narrow streams, they can construct ‘living bridges’ using their own bodies: thousands of individuals form a single solid structure that spans the gap, and the entire colony manages to use it to cross. Their efforts have not gone unnoticed, they have been studied for decades (Cole and Jones, 1948; Holldobler, 1983; Kamhi et al., 2015). Weaver ants are a suitable subject for a study of communication and are conveniently found on the campus of our university.

Thiawatwanikul tracked the position of an individual weaver ant as it crawled in a small arena, which was a square floor tile bounded by a channel of water that the ant almost never tried to cross. Its position was measured as a function of time, over a period of $T = 5$ minutes, and its velocity and acceleration calculated. The experiment was repeated many times, using different ants on different tiles, and all data assembled in a statistical distribution. The time-averaged distribution over position and velocity did not depend significantly on T , and represents an equilibrium distribution that characterizes the dynamical system.

In this thesis, I present a theoretical and computational investigation of the navigation of individual weaver ants. With the data available, I developed a theoretical model of ant motion that aimed to explain the measured equilibrium distribution. Following the Langevin theory for Brownian particles, our model

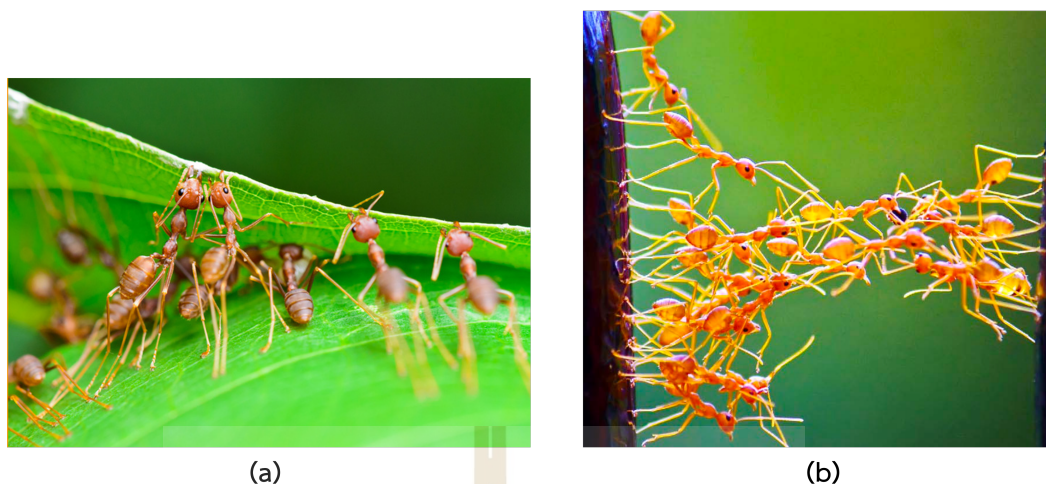


Figure 1.1 (a) *Oecophylla smaragdina*, ants aggregate to create their nest by gripping the leaf. The figure was retrieved from (Barker, 2014). (b) Asian weaver ants forming a living bridge. The figure was retrieved from (Peeters and Wiwatwitaya, 2012).

ants move according to Newton's law. They are subject to a trivial deterministic force, consisting of a linear drag term and a constant forward-driving force, and an uncorrelated random impulse drawn from a mathematically simple probability distribution. The key qualitative features of the experimental distribution were captured by the model.

In the experiment, ants had a high probability to be found near the edges of the arena. Our model distribution had the same position dependence. While one might be tempted to speculate about biological reasons for why an ant remains near the edge of the tile, our model ants had no preference whatsoever for one position over another. They remain near the edges because a Brownian particle, once forced to stop at a boundary, is statistically unlikely to move deep into the arena interior. That is, the dominant feature of the observed ant motion can be understood without making any assumption about the ant's intentions.

The measured velocity distribution of ants exhibited a sharp peak at zero velocity and broad, symmetric shoulders. This characteristic velocity dependence is reproduced by the model calculation and readily explained. The zero-velocity peak is the distribution of ants near the boundary while the

shoulder features result from members in the interior. The shoulder is located at the value of velocity where the drag and driving force are balanced.

In the next section I will review previous research on ants as a dynamical system give more details about Thiwatwanikul's experiment. After that I will present the theoretical model and describe the method I used to simulate it computationally.

1.1 Literature on ant navigation

The motion of ants has been studied extensively. While they move for many reasons, one aspect of their navigation that has received particular attention is their foraging behavior. Ant colonies typically disperse scouts that spread out over a large region surrounding the central colony in search of food. A successful scout returns to base and uses various means (the details of which vary from species to species) to recruit others to help collect the food. For example, the scout may lay down a pheromone trail during his return trip. Others pick up the trail, and whilst following it lay down their own pheromone stream to amplify the chemical signal.

There is a large literature on the subject but a good review of the strategies used by many species is provided by the textbook (and citing articles) of Hölldobler and Wilson, 1990 (Hölldobler and Wilson, 1990). Weaver ants, in particular, adjust their foraging motion in response to communication in several ingenious ways (Hölldobler and Wilson, ; Franks and Richardson, 2006; Gordon, 2010). While methods they use for foraging may or may not be employed when they wander about in an arena like our floor tile, it is at least clear that weaver ants can modify their navigational algorithms in response to communications they receive.

1.2 The Motivating Experiment

The thesis is a theoretical study, but it was strongly influenced by the work of (Thiwatwanikul et al., 2020). To understand the model presented below, it is necessary to know something about the setup and results of Thiwatwanikul's experiment.

Weaver ants, one-by-one, were selected from one of several nearby

colonies in the wild and safely transported into a laboratory. They were placed on a ceramic floor tile, square in shape with length $L = 30$ cm. The position $\mathbf{r} = x(t), y(t)$ at time t of the ant was recorded with a high-speed camera mounted above the center of the arena over a total duration $T = 300$ seconds with 15 frames per second—giving a time resolution of $\Delta t = 1/15$ s. The position origin will be defined as the center of the arena so $-L/2 < x(t), y(t) < L/2$ is the allowed range. These positional data were obtained via image-based tracking with detection of the center of an ant body in each image. Similar techniques are now commonly applied to investigate the motion of organisms (Dankert et al., 2009; Ballerini et al., 2008; Lukeman et al., 2010; Audira et al., 2018). After each 300 second trial, the ant was removed and another individual was placed (on a nearly-identical tile) and the process repeated. Dozens of individuals were studied in this way.

The trajectories of a single weaver ant were studied in two configurations: for the first configuration, a clean ceramic tile, the square arena is approximately homogeneous. For the second, the arena was partly coated with 1% w/w citronella oil. Citronella oil is detrimental but non-lethal for ants (Wang et al., 2015; Wang et al., 2016) and was used as a natural repellent. The repellent was coated evenly on a rectangular band at the center of arena that had a width along the x axis of $l = 10$ cm and a length along the y axis that spanned the arena (so positions with $|x| < l/2$ for all y were coated by the repellent). The band (in figure 1.2) is referred as zone R with $l = 10$ cm.

An individual ant continued moving throughout the experiment but tended to remain near the boundaries of the arena. It infrequently moved into the central region and rather appeared to patrol the perimeter. There was no evident change in its behavior over the trial duration T : it did not slow down or significantly alter its pattern of motion. Given this time-independence, every positional measurement (for any time t and any ant individual) can be included within a single large data set, to be studied statistically.

We determined the instantaneous velocity components of an ant (in the x and y direction) using

$$v_x(t) = (x(t) - x(t - \Delta t)) / \Delta t \quad \text{and} \quad v_y(t) = (y(t) - y(t - \Delta t)) / \Delta t \quad (1.1)$$

. A detailed description of the overall dynamical system is provided by the

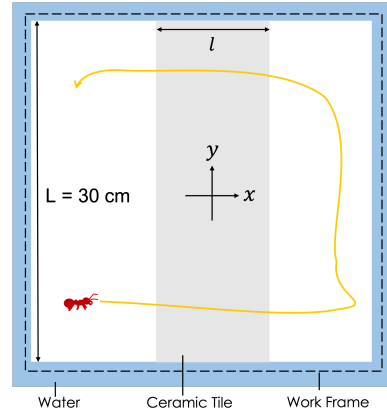


Figure 1.2 An illustration of an experimental setup for observing ant movement with a camera above the center of the arena, a square floor tile of length $L = 30$ cm. The position of an ant can be recorded marginally out the boundary of the tile, about 0.5 cm from the arena. The gray shaded band at centered along x is a repellent area with width $l = 10$ cm which be called R zone

equilibrium (i.e. time-averaged) distribution $\Pi(x, y, v_x, v_y)$, which gives the fraction of the data set found with a given value of position and velocity. This is a normalized probability distribution over four variables.

The full distribution $\Pi(x, y, v_x, v_y)$ can be integrated (i.e. summed over the large data set) over some of its variables to obtain more convenient measures. If we integrate over all possible velocity then we obtain a normalized density distribution $n(x, y)$, which gives the fraction of the data set found with a given position within the arena. A distribution over one position component $n(x)$ is obtained by integrating $n(x, y)$ over y . Similarly, if we integrate $\Pi(x, y, v_x, v_y)$ over all positions within the arena then we obtain a velocity distribution $P(v_x, v_y)$ that can be further reduced to $P(v_x)$ by integrating over v_y .

For an ant in the clean arena, the measured density is approximately square-symmetric: so $n(x, y) \approx n(-x, y) \approx n(x, -y) \approx n(y, x)$. Of course, this means $n(x) \approx n(y)$. The density $n(x)$ was sharply peaked near the arena boundary $x = \pm L/2$, and fell off rapidly with distance away from the boundary until it became approximately position-independent in the arena interior (seen in figure 1.3). That is, ants spent most of their time near the arena edges.

The approximate square symmetry of the distribution is important for data analysis and the development of a theoretical model. Many tiles were used, and a given tile was oriented arbitrarily within the laboratory. That is, the local x axis of a tile was aligned, at random, along the x , $-x$, y or $-y$ direction in the laboratory. So upon averaging over many tiles, square symmetry of the arena itself is understandable.

But the orientation of the Cartesian axes of the arena were fixed with respect to other objects in the room (such as the camera, window, air conditioner etc.). If the ants were using, to any significant extent, their long-range senses (like vision or the smell of the air) then the distribution should not have respected square symmetry. For example, if an ant was influenced by a light-intensity gradient, which would have a fixed direction in the laboratory (given that conditions in the room were maintained as constant as possible) then this should have been detected as a violation of square symmetry. The fact that the distribution was observed to obey square symmetry is evidence that the ants used only local sensory information to navigate.

In the case of coated arena, square symmetry was neither expected nor observed. The density $n(x)$, which reflects the effect of the repellent, was still peaked at the arena boundaries. It also exhibited an abrupt change at the border between the clean and coated regions.

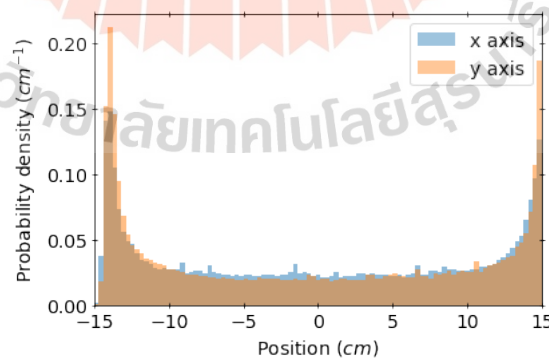


Figure 1.3 Normalized histograms of ant velocity derived from the position data with time resolution $\Delta t = 1/15$ s in x-axis (blue) of arena and y-axis (orange). The data are from (Thiwatwanikul et al., 2020).

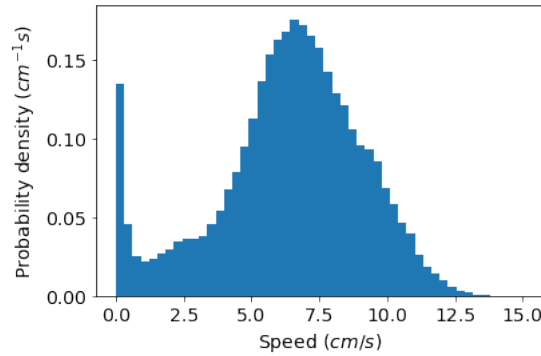


Figure 1.4 Normalized histograms of ant speed derived from the position data in the interior of arena with time resolution $\Delta t = 1/15s$. The data are from (Thiwatwanikul et al., 2020).

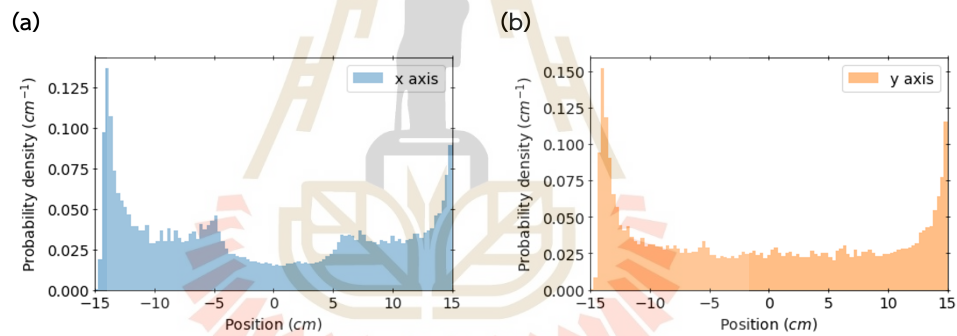


Figure 1.5 Normalized histograms of ant position for 68 ants in a coated arena with $l = 10$ cm. in x-axis (blue) of arena and y-axis (orange). The data are from (Thiwatwanikul et al., 2020).

The velocity histogram $P(v_x) \approx P(v_y)$ in the clean arena has a distinctive shape. It has a sharp, narrow central peak at $v_x = 0$. It decreased rapidly from this peak with increasing $|v_x|$ over a scale of 1 cm/s or so but then partly recovered to exhibit broad shoulder features centered at $v_x = 5 - 6$ cm/s (shown in figure 1.6). These shoulder features were notably missing from the $P(v_x)$ distribution for the coated arena. See figure 1.7

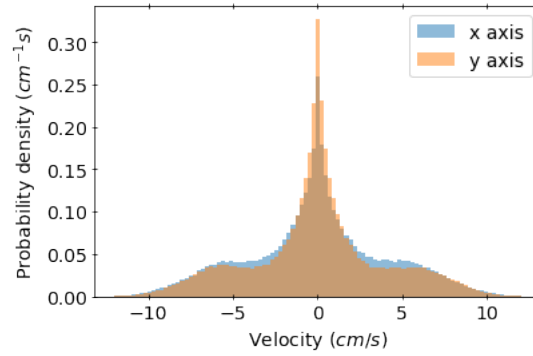


Figure 1.6 Normalized histograms of ants velocity derived from the position data with time resolution $\Delta t = 1/15s$ in x-axis (blue) of arena and y-axis (orange). The data are from (Thiawatwanikul et al., 2020).

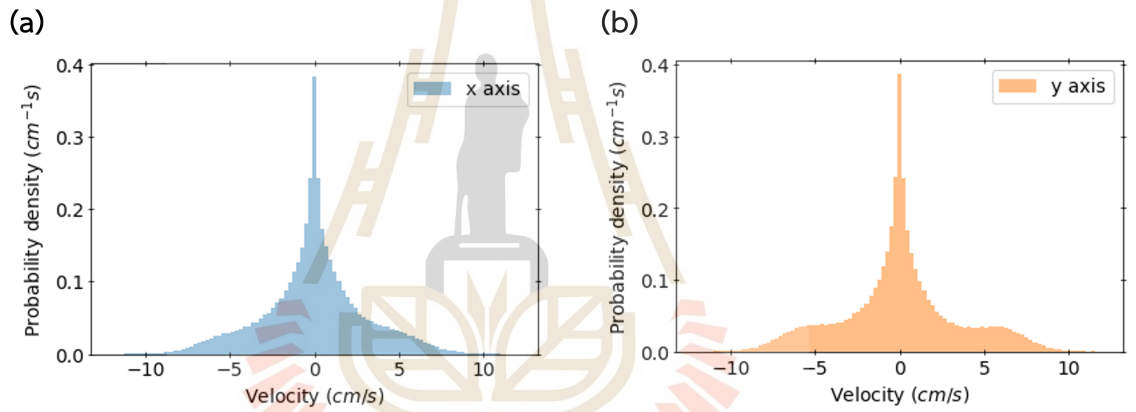


Figure 1.7 Normalized histograms of ants velocity derived from the position data of ants in arena with repellent ($l = 10$ cm) in x-axis (a) of arena and y-axis (b). The data are from (Thiawatwanikul et al., 2020).

We can go beyond the one-dimensional distributions discussed above using alternative plotting formats. A heat map is convenient for displaying a two-dimensional distribution, with color used to represent magnitude. The 2D heat map of the velocity distribution for all ants in the clean arena is shown in figure 1.8. The large values of velocity $P(v)$ mainly correspond to ants moving along the boundary, a heat map of velocity space has the shape of a ‘plus’ sign because members are usually moving along one of the square edges.

To better understand boundary effects, we divided data into two sets according to distance from the boundary. The interior data exhibit a zero

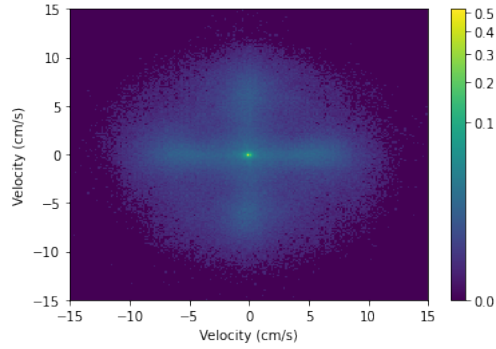


Figure 1.8 The heat maps of the distribution over velocity in x and y direction for 59 ants in clean arena. The data are from (Thiawatwanikul et al., 2020).

velocity peak surrounded by a valley. Beyond the valley there is a plateau and, outside the plateau the distribution rapidly decreases. The plateau corresponds to the shoulder features seen in 1D projections. The heat map for ants in the interior is isotropic. The boundary data is strongly anisotropic because ants tend to move along the boundaries.

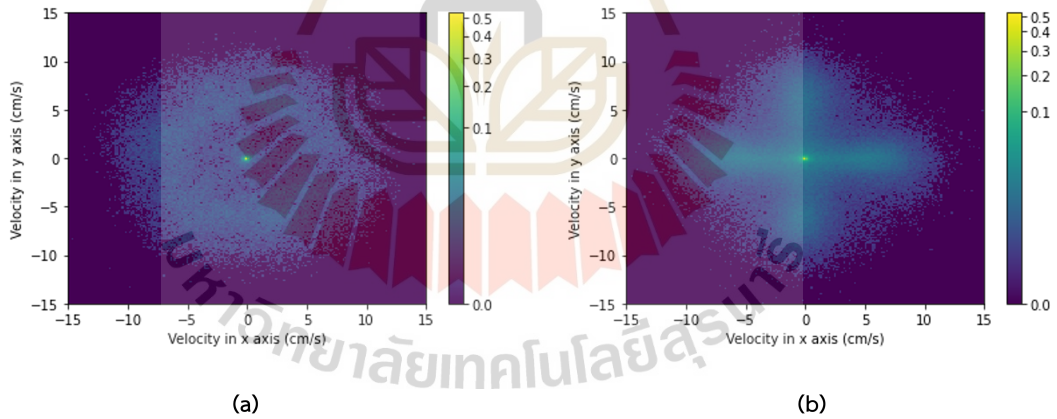


Figure 1.9 The heat maps of the distribution over velocity in x and y direction in (a) interior and (b) boundary of the ants in clean arena. The data are from (Thiawatwanikul et al., 2020).

Finally, Thiawatwanikul considered ant acceleration by defining velocity changes in Cartesian coordinate:

$$\Delta \mathbf{v}_{x,y}(t) = \mathbf{v}_{x,y}(t) - \mathbf{v}_{x,y}(t - \Delta t) = \Delta \mathbf{v}_x(t) + \Delta \mathbf{v}_y(t) \quad (1.2)$$

and finding the histogram $p(\Delta v_x)$ and $p(\Delta v_y)$ of this quantity (of course $\Delta v(t)$ is proportional to the acceleration). The result was a relatively simple mathematical shape: an even function $p(\Delta v) = p(-\Delta v)$ with a cusp-like peak at $\Delta v = 0$ that fell off smoothly with $|\Delta v|$ on the scale of 1 cm/s or so. Even more encouragingly, when the total data set was broken into subsets, we found that $p(\Delta v)$ was robust: no matter when or where ants were studied, their distribution of acceleration remained essentially the same. Also, it was seen that consecutive velocity changes, $\Delta v(t)$ and $\Delta v(t + \Delta t)$, were uncorrelated. They could be treated as independent events. Since $p(\Delta v)$ appeared qualitatively simple, and it was not dominated by boundary effects as the distributions $P(v_x)$ and $n(x)$ were, it became the starting point for our theoretical work.

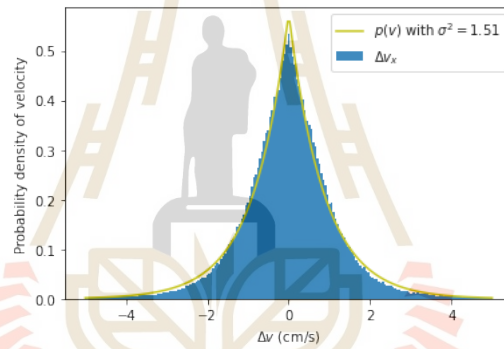


Figure 1.10 The blue is normalized histogram for velocity changes in x-direction with time step $\Delta t = 1/15$ s. The green line is the fit result for one-parameter in equation (2.10). The data are from (Thiwatwanikul et al., 2020).

The results of Thiwatranikul's experiment suggest that a reasonable theoretical model can be based on a Brownian motion picture. Particles undergoing Brownian motion move according to Newton's law, but experience random impulses because of collisions with molecules in the surrounding medium. This means their instantaneous acceleration is governed by the probability distribution of these random impulses.

1.3 Ant movement as Brownian motion

Brownian motion is a well-known physical phenomenon. It was first observed by Brown in 1827, who watched the motion of microscopic grains of pollen in water. Their motion appears random grains perform erratic three-dimensional walks within the fluid. In 1905, Einstein wrote a paper (Einstein, 1905) about the motion of microscopic bodies in water in which he attributed the random motion to the effects of collisions between the grain and water molecules. The quantitative agreement between the motion that Einstein predicted and the experimental trajectories had far-reaching implications. At the time, the existence of atoms was still in doubt, and the success of Einstein's picture (which included the thermal motion of molecules, described by statistical mechanics) went a long way towards proving that atoms were indeed real.

Within a few years, Langevin (Langevin, 1908) recast Einstein's theory in a modified form, which is more convenient for our purposes. Langevin wrote down a theory of motion, Newton's second law, for the grain. The grain is subject to random forces, due to the collisions with molecules, and to a deterministic drag force proportional to the speed of the grain (and directed opposite to its velocity). Langevin theory has since been applied to a huge range of natural phenomena, as well as to financial processes (prices can fluctuate randomly like a moving grain) and is in itself considered a branch of applied mathematics (Takahashi, 1996; Picozzi and West, 2002).

A quantum description of atoms and molecules suggests that randomness in nature is inescapable. But that is not necessary to understand why the grain motion is subject to random forces. Even in classical statistical physics, processes are considered random because we simply cannot acquire sufficient knowledge (about the microscopic state of a complex system) to predict them. Without this knowledge, one has no choice but to treat the effect of the collision with a water molecule as a random impulse. Of course, the fact that random variables enter a theory does not mean we cannot use the theory to understand experiments. If we have some knowledge of the *probability distribution* of the random variable then we can still make definitive predictions. Indeed, Einstein was able to predict the average diffusion of pollen grains and other statistical measures of motion.

In this thesis, we are studying the motion of ants. The ant may

well have good reasons to move as it does, perhaps each step it takes is done purposefully according to a precise plan. But we cannot read the ant's mind and we do not know the microscopic features to which the ant may be responding. This means that we do not have enough information to predict the precise trajectory of an ant. When we write down an equation of motion that determines this trajectory, we have no choice but to include random forces.

Since the distribution of velocity changes $p(\Delta v)$ occurring in a single time step Δt is robust and simple, we can interpret it as a distribution of random impulses (perfectly analogous to the results of collisions with molecules). So, we have some knowledge, from Thiawatwanikul's experiment, of the probability distribution of random impulses that steer the ant. The real physical origin for these impulses is likely some complex combination of the ant's personal decision-making and its response to the microscopic terrain of the arena.

But regardless of its origin, we can take the distribution of random forces as an experimental fact and use it to help predict average ant motion. We can develop a model based on Langevin theory to describe this motion. The parameters of the model can then be interpreted as properties of the ant's navigation algorithm. As parameters change in response to measurable factors (such as the arena boundaries, the mild chemical repellent that Thiawatwanikul introduced, the interactions with fellow ants, or other factors) we can begin to understand how the ant's navigational algorithm is designed to allow it to succeed in tasks like foraging.

CHAPTER II

THEORETICAL BACKGROUND

2.1 Overview of Langevin Theory

Langevin theory was originally devised to understand motion like that of a grain of pollen within water. The grain movement was observed by Robert Brown who saw the grains through a microscope - - their size was of order tens to hundreds of microns (which we now know to be much larger than a water molecule). This motion, so called Brownian motion, was characterized by erratic hops: the grain appears to undergo a random walk through the fluid. Like any classical particle, the grain obeys Newton's laws. So the original form of Langevin equation is just a model for the forces acting on a Brownian particle like this grain, and the appropriate statistical formulation of the effect of these forces. But a generalized form of Langevin's theory can be applied to many dynamic processes that undergo erratic change. It is used to model biomolecular systems, various types of diffusion, and even financial processes.

The dominant forces acting on the grain are imparted by the surrounding water. There is a net drag force (that is linear at small speeds) due to the water that is directed opposite to the grain velocity. Additionally, there are unpredictable forces acting for a very short time scale, which are treated as instantaneous impulses. These result from the collision between the grain and surrounding water molecules. The numerous, rapid collisions result in a distribution of random small impulses on the grain. They are random because it would be impossible (or at least incredibly difficult) to model the local molecular structure of the water environment and predict the effect of individual collisions. But the probability distribution of impulses is predictable because water molecules, in thermal equilibrium, have a well known distribution over velocity.

The ant moves under its own power when it crawls about and it also obeys Newton's laws. The most important forces acting on its body are the reaction forces of the ground on its feet (we treat the ant motion as

two-dimensional, so gravity and the normal force are assumed to always negate each other). These reaction forces are unpredictable because they depend on the precise manner in which the ant decides to move its legs. Since we are working with a coarse time resolution, these forces can be treated as instantaneous random impulses.

In two dimensions, we write

$$\frac{d}{dt}\mathbf{r} = \mathbf{v} \quad (2.1)$$

where $\mathbf{r}(t) = \mathbf{x}, \mathbf{y}$ is the ant position and $\mathbf{v}(t) = \mathbf{v}_x, \mathbf{v}_y$ its velocity at time t . When we relate differentials to experiment, we replace dt by $\Delta t = 1/15$ s, the experimental time step. A random impulse will be assumed to be delivered once each time step. We will also use a finite-resolution grid such that dx is replaced by $\Delta x \approx 0.1$ cm.

The Langevin equation for a body of unit mass is:

$$\frac{d}{dt}\mathbf{v} = \frac{\Delta \mathbf{v}}{\Delta t} = \mathbf{F}(t) = \frac{\eta(t)}{\Delta t} + \mathbf{F}_d(\mathbf{v}) - \nabla V(\mathbf{r}). \quad (2.2)$$

The first force term $\eta(t)/\Delta t$ is the random impulse (discussed in section 2.4). The second term and third terms add to give the deterministic force.

For the pollen grain, the deterministic force was a linear drag force $-\frac{\mathbf{v}}{\tau}$, where the constant τ , with the units of time, that indicates the strength of the drag force. We will also include such a force. It should not be literally interpreted as a physical drag acting on the ant—its purpose in our model is to ensure that the distribution of ant speed remains stable over long times. The deterministic force in Langevin theory could be modified to include the effects of gravity (or an electrical field acting on a charged grain). These are conveniently written in terms of a potential energy. We will also include a potential energy, $V(\mathbf{r})$ the last term above, in the deterministic force. Its main purpose will be to model the effect of the chemical repellent (see section 2.5). As long as the ant is moving in the clean arena, we can set $V(\mathbf{r}) = 0$.

A preliminary analysis of the experimental data indicated that a linear drag force was not sufficient to model the velocity dependence of the deterministic force for ants. (This is hardly surprising: the ant differs in many ways

from a passive pollen grain.) Ants in the interior of the arena were observed to tend towards a certain average terminal speed of approximately 7cm/s . A drag force alone would result in a terminal speed of zero—so a driving force was required in the model. Given that an ant's body has a defined orientation, and it always walks forwards, it seems reasonable to include a driving force in the forward direction. It is modeled in the simplest possible way: a constant force directed forward.

We model the velocity-dependent part of the deterministic force as:

$$\mathbf{F}_d(\mathbf{v}) = -\frac{v}{\tau}\hat{\mathbf{v}} + \frac{v_0}{\tau}\hat{\mathbf{v}} \quad (2.3)$$

Where in addition to the drag force v/τ we have the driving force with a strength controlled by the positive constant v_0 . The direction of the driving force is always the same as the ant velocity, i.e. it always points forward.

2.2 Orientation of velocity changes

The ant's body orientation introduces a preferred direction of motion. It tends to walk forward and rarely makes a sudden full turn. It is convenient to model its velocity change in a local orientation basis according to

$$\Delta\mathbf{v} = \Delta v_l\hat{\mathbf{v}} + \Delta v_n(\hat{\mathbf{z}} \times \hat{\mathbf{v}}) = \Delta v_l\hat{\mathbf{v}}_l + \Delta v_n\hat{\mathbf{v}}_n \quad (2.4)$$

The velocity change parallel to the velocity $\Delta\mathbf{v}_l = \Delta v_l\hat{\mathbf{v}}$ results in a change of speed. The velocity change perpendicular to velocity $\Delta\mathbf{v}_n = \Delta v_n(\hat{\mathbf{z}} \times \hat{\mathbf{v}})$ results in a change of direction. Since $\hat{\mathbf{z}}$ is a unit vector pointing up from the floor of the arena, we have defined a positive value of Δv_n to correspond to a leftward turn, see 1.2. When we want to work in terms of the global laboratory basis (i.e. standard Cartesian components) we use

$$\hat{\mathbf{v}}_l = \frac{v_x}{\sqrt{v_x^2 + v_y^2}}\hat{\mathbf{x}} + \frac{v_y}{\sqrt{v_x^2 + v_y^2}}\hat{\mathbf{y}} \quad (2.5)$$

and

$$\hat{\mathbf{v}}_n = -\frac{v_y}{\sqrt{v_x^2 + v_y^2}}\hat{\mathbf{x}} + \frac{v_x}{\sqrt{v_x^2 + v_y^2}}\hat{\mathbf{y}}. \quad (2.6)$$

We can obtain the magnitude (length) of the vector along each component by projection:

$$\Delta v_l = \Delta \mathbf{v}_{x,y} \cdot \hat{v}_l \quad \text{and} \quad \Delta v_n = \Delta \mathbf{v}_{x,y} \cdot \hat{v}_n \quad (2.7)$$

2.3 Modeling velocity changes in the local orientation basis

In an arena that is truly square-symmetric, the ant motion does not differentiate between the x and y directions. However, there is no symmetry requirement on velocity changes relative to the ant's body orientation. That is, the characteristic velocity change parallel and perpendicular to ant velocity need not be equal.

The 2D velocity change in our model is:

$$\begin{aligned} \Delta \mathbf{v}_n &= \eta_n(t)(\hat{z} \times \hat{v}) \\ \Delta \mathbf{v}_l &= \eta_l(t)\hat{v} + \Delta t(\mathbf{F}_d) \quad \text{where} \quad \mathbf{F}_d(v) = \left(-\frac{v}{\tau} + \frac{v_0}{\tau}\right)\hat{v} \end{aligned} \quad (2.8)$$

The random variables $\eta_n(t)$ and $\eta_l(t)$ will each be governed by a probability distribution that is described by equation (2.10). However, the root-mean-square (RMS) values of these variables will not be equal. We assign a value σ_l for the RMS of impulses parallel to velocity and σ_n for the RMS of impulses perpendicular to velocity.

The velocity-dependent deterministic force is always directed parallel to the velocity. As noted above, the value v_0 corresponds to a terminal speed because any ant moving with this speed feels zero deterministic force. In the presence of a repellent, an additional force will be included.

2.4 Random impulses for the ant

There are many ways one could model the random impulses seen in ant motion. In developing our model, we were guided by one basic principle: choose the simplest model that is plausibly consistent with qualitative experimental results. Particularly, we wanted to keep the number of model parameters to an minimum. (Models with many adjustable parameters can always be made to agree with data, but such agreement is meaningless.)

According to equation (2.2), a velocity change is

$$\Delta v(t) = \eta(t) - (\Delta t)\mathbf{F}_d - \Delta t \nabla v(\mathbf{r}). \quad (2.9)$$

For sufficiently small Δt , we see that Δv is dominated by the random impulse η . The other two forces, which are multiplied by Δt , are not important within a single time step. (They become important on longer time scales because their effects accumulate.) This greatly simplifies analysis, because it means that the normalized distribution of experimental velocity changes should be equal to the distribution of random impulses.

We described the experimental distribution of velocity changes $p(\Delta v_x) \approx p(\Delta v_y)$ above: it is sharply peaked at zero and appeared symmetric. Each component of this distribution can be well-described by Eq. (2.10).

$$p(\eta) = \frac{1}{\sqrt{2\sigma^2}} \exp\left(-\sqrt{\frac{2\eta^2}{\sigma^2}}\right), \quad (2.10)$$

which contains a single positive parameter, σ , and since

$$\int_{-\infty}^{\infty} d\eta \eta^2 p(\eta) = \sigma^2 \quad (2.11)$$

the value of σ is the RMS value. The distribution also satisfies

$$\int_{-\infty}^{\infty} d\eta p(\eta) = 1, \quad \int_{-\infty}^{\infty} d\eta \eta p(\eta) = 0. \quad (2.12)$$

That is, it is normalized and has a mean of zero

Given this experimental situation, we take each component of our model probability distribution for random impulses to be given exactly by Eq. (2.10). We use an RMS value of $\sigma = \sigma_l$ for velocity changes parallel to velocity and a value $\sigma = \sigma_n < \sigma_l$ for transverse velocity changes.

The equation (2.10) has a number of appealing properties. It is symmetric, with equal probability of an impulse in the positive or negative direction. This means that the time-averaged impulse is zero. It has a simple mathematical form that lends itself to analytic calculations and simple numerical computation. Most importantly, it is defined by a single parameter.

We should emphasize that our model would predict a distribution of velocity changes that is slightly different than the equation (2.10). This is because the model velocity change is determined by the deterministic force, in addition to the random impulse. However, we feel the overall experimental distribution of velocity changes gives an excellent indication for the distribution of random impulses that we should use in our model. Not only is it the case that the effect of the deterministic force within a single time step is small, one should also realize that the experimental distribution is effectively an average over all positions and velocities. In taking this average, the importance of the deterministic force (an odd function of velocity) would be further reduced.

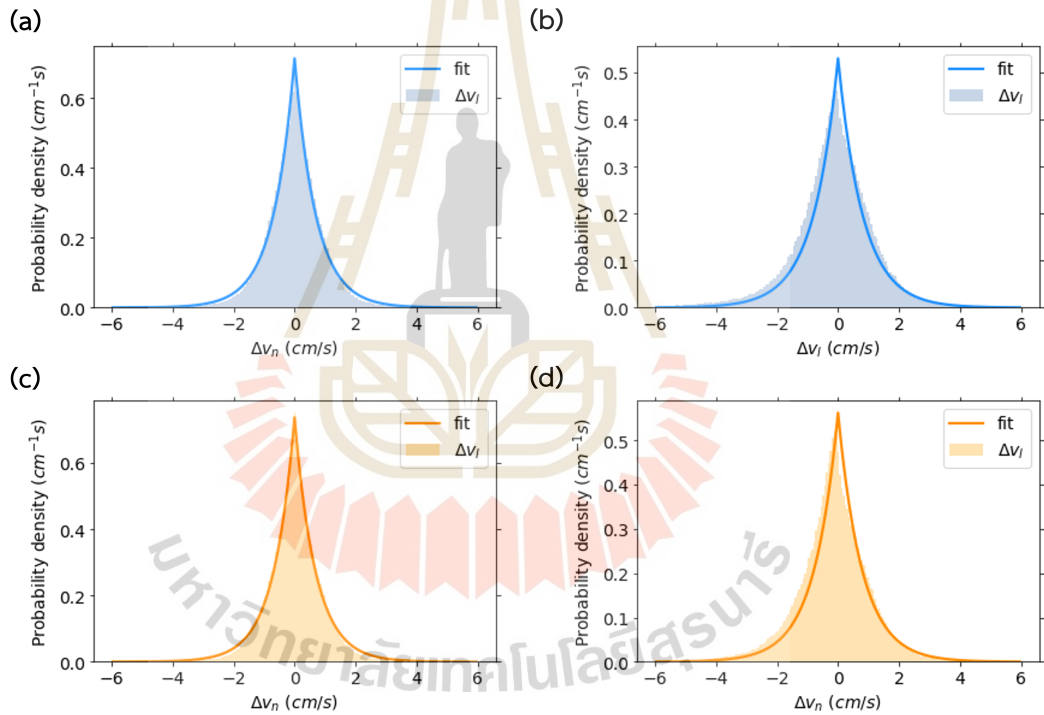


Figure 2.1 The histogram shows the probability density of changing in velocity over all times and all ants in clean arena (blue) and the coated arena with $l = 10$ cm (orange). The line curve is plotted by fitting probability density function in equation (2.10) for Δv_n (left) and Δv_l (right)

2.5 The effective potential

The potential $V(\mathbf{r})$ and associated force $\nabla V(\mathbf{r})$ in equation (2.2) is used to model an ant's interaction with the chemical repellent. The ant is averse to the citronella oil, and it is natural to associate this fact with a higher value for the potential energy. Given that the oil is coated evenly, the simplest model should assign two possible values for the potential energy: anywhere in the clean arena we will take $V(\mathbf{r}) = 0$ and anywhere within the repellent we will take $V(\mathbf{r}) = V_0 > 0$.

The band of repellent covered positions $|x| < l/2$ for all y . The potential then satisfies $V(\mathbf{r}) = V(x)$ with $V(x) = V_0$ for $|x| < l/2$ and $V(x) = 0$ for $|x| > l/2$. The repellent thus presents a square potential barrier that ants may overcome.

$$V(x) = \begin{cases} V_0, & \text{if in zone R.} \\ 0, & \text{otherwise.} \end{cases} \quad (2.13)$$

After encountering the step potential, an ant crosses into zone R, every member receives $\Delta v_x^2 = -2V_0$ opposite to the direction of its velocity. On the another hand, an ant that moves out off the R zone, will get a positive impulse with the same magnitude. The effect of potential is reducing probability of ants in zone R, since some are prevented from entering the zone: the ant with $v_x < \sqrt{2V_0}$ can't entry the R zone.

The force associated with the potential is equal to $-dV/dx$ and given by

$$-\frac{dV}{dx} = V_0 \left(-\delta(x + l/2) + \delta(x - l/2) \right). \quad (2.14)$$

So, only upon crossing in or out of zone R does the ant feel any effect of the repellent.

2.6 Consideration of the model

The model we have outlined above is conceptually and mathematically simplistic. We have defended this approach on the basis of minimizing the number of unknown parameters and avoiding speculative assumptions. But is

it possible that we are being unrealistic in applying this model to a complex living system? We have considered a number of factors that might be included in a more sophisticated theoretical description. We will briefly discuss some of them here.

First, we studied whether the erratic velocity changes exhibited by an ant are correlated in time. That is, if an ant makes an abrupt velocity change during the current time step, will it be more or less likely to do so during the next time step. Such time correlations would greatly increase the mathematical complexity of analysing motion. If they were large enough, they could undermine our entire approach.

As discussed in more detail in Thiawatwanikul's paper (Thiawatwanikul et al., 2020), we measured the statistical Gibbs' correlation between adjacent velocity changes (the correlation between $\Delta v_x(t)$ and $\Delta v_x(t + \Delta t)$ etc.) and found that these correlations were extremely weak. The distribution of a given velocity change was essentially independent of the corresponding values measured just before or after it. Thus, in our model calculation, we draw a given impulse $\eta(t)$ independently, using Eq. (2.10), at each time step.

Next, we considered whether the distribution of random velocity changes were dependent on time spent in the arena. By breaking the data into subsets according to time (ants that had been in the arena for less than 30 s, from 30 s to 60 s, etc.) we found that the shape of the distribution changed little with time.

For a clean arena, the standard deviation σ_l and σ_n trended weakly downward with time spent in the arena. In an arena with repellent, the descending trend of standard deviation is significantly stronger. The downward trends could be an indication that the ant gets tired or moves more circumspectly. But it is clear that σ does not change substantially over the duration of the experiment.

We were particularly interested in the possibility that ants change their dynamic parameters, such as σ , in the presence of the repellent. Certain bacteria, which move in the manner of a random walk, change their "run" and "tumble" frequencies depending on the local chemical environment. This behavior, an example of chemotaxis (Patteson et al., 2015), is an evolutionary strategy for avoiding harmful environments. However, we saw no strong evidence

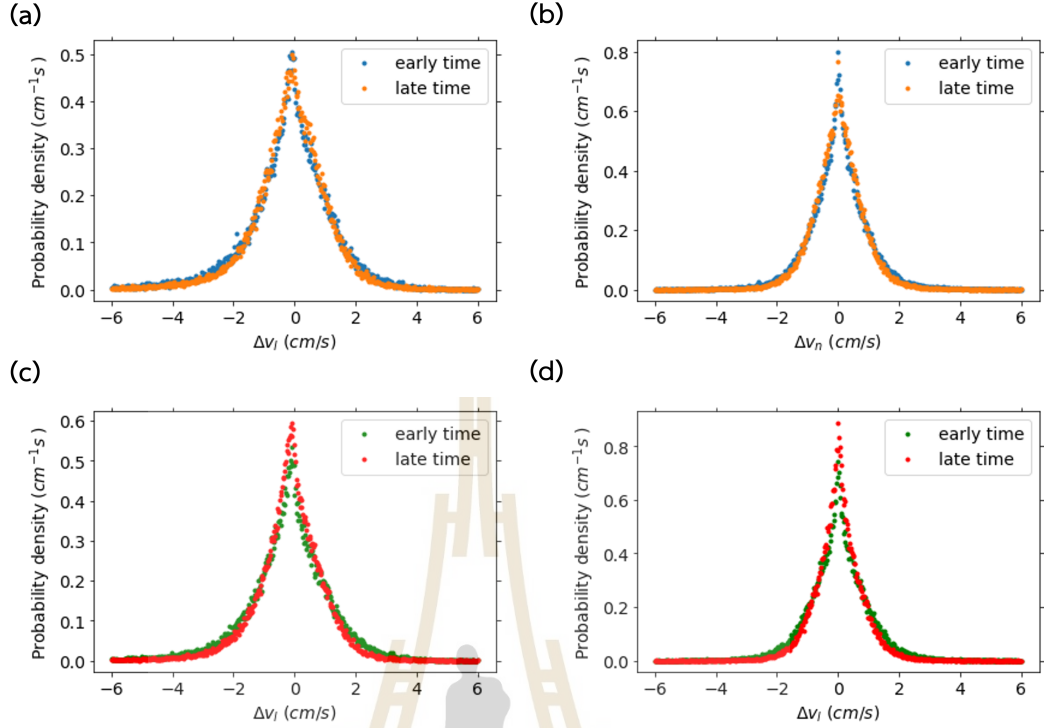


Figure 2.2 The probability distribution of changing in velocity in direction (a) parallel and (b) normal to velocity for early time (blue) and late time (orange) in clean arena. The probability distribution of changing in velocity in direction (c) parallel and (d) normal to velocity for early time (red) and late time (green) in coated arena. Δv_l

for this phenomenon. This is why our model only accounts for the repellent using the effective potential $V(x)$, discussed above.

When we looked for a change in the distribution of impulses depending on distance from the boundary we saw a similar, quantitative effect. A slight asymmetry was seen for members very near the boundary, owing to the limitation that large outward velocity changes were physically blocked by the boundary. But nothing we saw in the data lead us to conclude that qualitative behavior was dependent on position. In the model simulations, described below, the only effect of the boundary is to stop ants from proceeding further and force their normal velocity component to drop to zero.

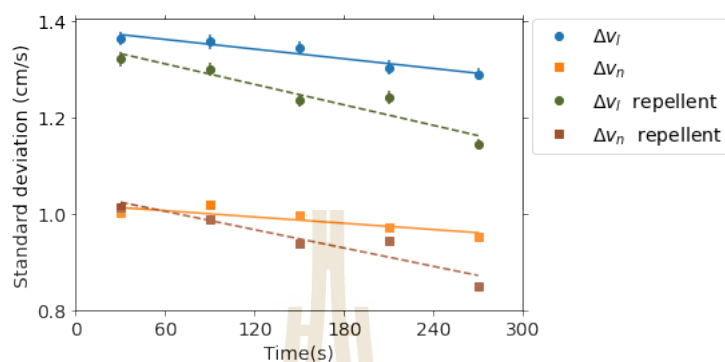


Figure 2.3 The standard deviation σ_l (circle) and σ_n (square) from fitting probability density function in equation (2.10) change over time for all ants in a clean arena (line) and coated arena (dash) for Δv_n (blue) and Δv_l (orange)

Table 2.1 A linear regression was done on σ values versus time t . The slope m and its uncertainty are indicated for σ obtained from Δv_n and Δv_l in the clean arena and the arena with repellent.

Linear curve fitting	$10^3 m_{\sigma_l} (\text{cm/s}^2)$	$10^3 m_{\sigma_n} (\text{cm/s}^2)$
Clean	-0.33 ± 0.05	-0.22 ± 0.07
$l = 10 \text{ cm}$	-0.7 ± 0.1	-0.6 ± 0.1

CHAPTER III

SIMULATION AND ANT-BOUNDARY PROTOCOL

We carried out numerical simulations of the model described in the previous chapter. The aim was to demonstrate that the model reproduces the qualitative behavior seen in the experiment. In this short chapter we provide the details about how the simulation was carried out.

Every simulated trajectory of the model ant used the same initial values: the ant was taken to be stationary at the middle of the arena: $\mathbf{r}(t = 0) = \mathbf{v}(t = 0) = (0, 0)$. The position and velocity were updated step wise in time intervals of Δt . That is, we found

$$\begin{aligned}\mathbf{r}(t + \Delta t) &= \mathbf{r}(t) + \mathbf{v}(t)\Delta t \\ \mathbf{v}(t + \Delta t) &= \mathbf{v}(t) + \Delta \mathbf{v}(t).\end{aligned}\tag{3.1}$$

The velocity change $\Delta \mathbf{v}(t)$, described in detail above, consists of a random impulse and the impulse due to the deterministic force

$$\Delta \mathbf{v}(t) = \eta(t) + \Delta t \mathbf{F}_d(t), \text{ with } \mathbf{F}_d(t) = \mathbf{F}_d(\mathbf{r}[t], \mathbf{v}[t]).\tag{3.2}$$

Where $\mathbf{F}_d(t)$ depends on velocity and, at the interface between clean and coated regions, on position.

A new random impulse is generated with each time step. The simulation continues until time T , where $T/\Delta t = 300$ is the experimental value but we often used much larger values in the simulation. After carrying out many such simulations we can build a distribution $\Pi(x, y, v_x, v_y, t)$ over a large ensemble by finding the fraction of members that have a given position and velocity at time t . At small times, this distribution is dependent on the initial state of the ant and it evolves with t . But after sufficiently long time, the distribution becomes independent of the initial conditions and of time, i.e. it approaches an equilibrium distribution. We calculate the time-average to find the equilibrium function $\Pi(x, y, v_x, v_y)$. Since T is large, the time averaged distribution is weakly dependent on T .

3.1 The generation of impulses

One minor technical challenge in carrying out the simulation was to generate two random numbers (one for the impulse parallel to velocity and one for the impulse normal to velocity) according to a particular probability distribution, equation (2.10). To do this, we first used a standard coin-flip random process to decide whether the impulse was positive or negative. Then we generated a random number q equally likely to have any value between 0 and 1. To connect this with a random number η that can have any positive value between 0 and $+\infty$ and has a governing probability distribution $p(\eta)$ we do the following.

We have the cumulative distribution

$$\tilde{p}(\eta) = \int_{-\eta}^{\eta} d\eta' p(\eta') \quad , \text{ with } \tilde{p}(0) = 0, \tilde{p}(\infty) = 1. \quad (3.3)$$

Now, suppose we divide the range of possible q values into 100 bins. There is a one percent chance that $0 < q < 0.01$ lies in the first bin, and a one percent chance that $0.99 < q < 1$ lies in the last bin. We can find a value η_1 by solving $\tilde{p}(\eta_1) - \tilde{p}(0) = 0.01$ and a value η_{99} by solving $\tilde{p}(\eta_{99}) - \tilde{p}(0) = 0.99$, which is equivalent to $\tilde{p}(\infty) - \tilde{p}(\eta_{99}) = 0.01$. There is a one percent chance that $0 < \eta < \eta_1$ lies in the first bin and a one percent chance that $\eta_{99} < \eta < \infty$ lies in the last bin. By making a one-to-one correspondence between the bins in this way, the random number q is transformed into a random number η with the correct probability distribution. The process is made particularly easy because i) equation (2.10) can be integrated analytically and ii) the distribution decays exponentially. So, too large η is rarely occur.

After following this procedure, we tested it by generating many η , plotting the resulting distribution and comparing it to equation (2.10). This is shown below.

3.2 The arena boundary protocol

The last aspect of the model that must be specified is the interaction between the ant and the boundary. Following our guiding principle of choosing

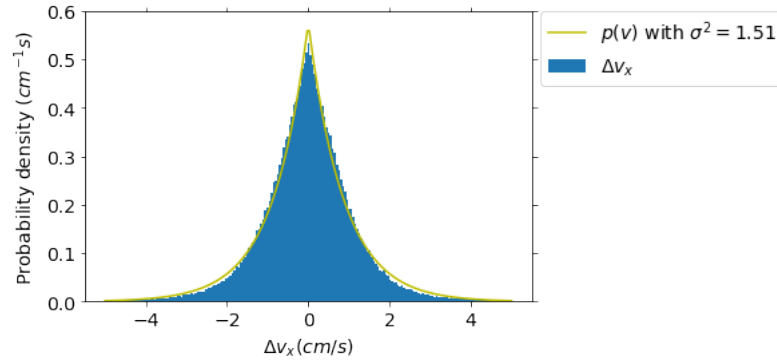


Figure 3.1 The histogram shows the probability density of random impulse was created via Numpy random library which number of sample is 10000. The green curve is plotted with probability density function in equation (2.10) with $\sigma = 1.41\text{cm/s}$

the simplest plausible description, we do the following. If a model ant moves across a boundary then it is returned to the boundary and its velocity component normal to the boundary is set equal to zero. No other parameters are modified. For example, suppose after updating position and velocity to $\mathbf{r}(t)$, $\mathbf{v}(t)$ we find that $x(t) > L/2$. We respond by setting $x(t) = L/2$ and $v_x(t) = 0$ while leaving $y(t)$ and $v_y(t)$ as they were. We then apply equation (3.1) as usual to determine $\mathbf{r}(t + \Delta t)$, $\mathbf{v}(t + \Delta t)$. The corresponding transformation is carried out at any of the four sides of the square arena. It is exceedingly rare that a model ant leaves via the corner, i.e. crosses two boundaries simultaneously. If it does then we apply the above protocol to both violated boundaries.

This description of the ant-boundary interaction is equivalent to a totally-inelastic collision between a particle and a wall. Because of translational symmetry, the particle momentum parallel to the wall is conserved. But the momentum of the particle perpendicular to the wall drops to zero. A quick observation of the behavior of an actual ant near our arena boundary appears roughly consistent with this interaction. (Certainly, it is a much closer description of the observed interaction than would be an elastic collision, which would have ants reflecting from boundaries without a change of speed.)

It is important to notice that this ant-boundary interaction is modeled to be as simplistic and unobtrusive as possible. A model ant does not see the

boundary until it runs into it. Upon colliding with the wall it is forced to stop. But it immediately resumes its motion without being any wiser. The model ants have no tendency whatsoever to be drawn towards boundaries. (Such a tendency could easily be introduced via the effective potential, but we found that it was not needed to explain the data.) The boundary stops the ant but does not affect its motion in any other way.

From a observation of Thiwiratnakul's experiment, one immediately sees that the ants tend to remain near the water channel that defines the arena boundaries. There are numerous "explanations" for this behavior that might come to mind. Perhaps ants keep a boundary to one side of them as a partial shield against predators, or they stay near a source of water in case they should need it. It could be that they follow the 1D feature to avoid getting lost in an unfamiliar 2D environment, or that they are using their eyes to see beyond the arena and are trying to escape the confining tile and return to their nest. We emphasize that none of these factors has to be considered to explain the observed behavior. Because a model that contains none of them can account for the experimental distribution. This finding is somewhat counter intuitive, and we like it for this reason. Also, perhaps it serves as a warning against speculative biological (and likely anthropomorphic) reasoning in some cases.

3.3 Velocity evolution in laboratory coordinates

While, the velocity in the next time step of our model is updated using local coordinates: components normal and parallel to the ant velocity axis, the ant-boundary protocol in the square arena must be done in global coordinates. We have to transform the velocity change in the model to be operable in global (laboratory) coordinates.

Recall that the ant only moves forward, so its body orientation is parallel to its velocity. If the ant has zero speed, we can still define the direction of its body orientation. In the simulation, the ant begins with zero speed and its body orientation is selected randomly, i.e. a random angle from 0 to 2π is the angle θ between its initial velocity $\mathbf{v}$ and the x axis of the laboratory. We consider the simulated ant at time t with velocity $\mathbf{v}(t)$ and direction θ (illustration in figure 3.2). For the next time step, the speed of ant

$v(t + \Delta t)$ is equal to

$$v(t + \Delta t) = \sqrt{(v(t) + \Delta v_l(t))^2 + v_n^2(t)} \quad (3.4)$$

with angular $\theta + \phi$ where ϕ can evaluated by:

$$\phi = \arctan\left(\frac{\Delta v_n(t)}{v(t) + \Delta v_l(t)}\right) \quad (3.5)$$

The arctangent function is undefined where the denominator is zero, but we can practically set the angle ϕ is $\pi/2$ or $-\pi/2$ if the normal of velocity changing is positive or negative respectively. Therefore, the velocity in x and y components at time $t + \Delta t$ can be simply written as:

$$\begin{aligned} v_x(t + \Delta t) &= v(t + \Delta t) \cos(\theta + \phi) \\ v_y(t + \Delta t) &= v(t + \Delta t) \sin(\theta + \phi) \end{aligned} \quad (3.6)$$

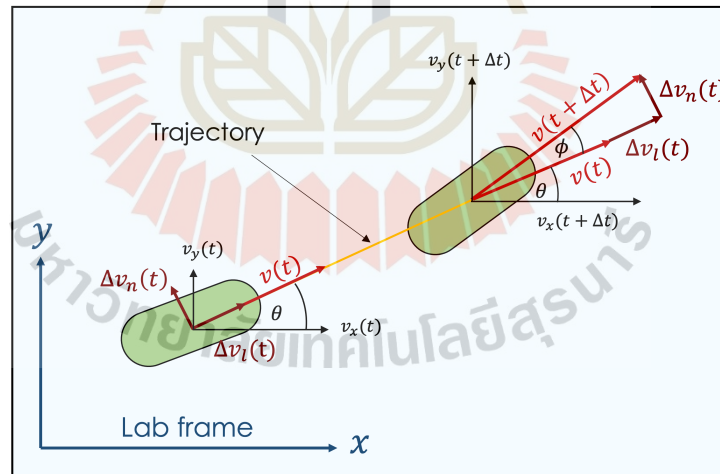


Figure 3.2 An illustration of updating velocity and angular between velocity and x axis of lap frame in a small time step Δt .

CHAPTER IV

RESULTS AND DISCUSSION

In this chapter, we report the results of our simulations and give a more detailed comparison between these results and the data. The simulations, repeated many times, were used to calculate the equilibrium distribution $\Pi(x, v_x, y, v_y)$ and its projections.

4.1 Unbounded arena

We start by studying a simpler system: a clean *unbounded* arena that is completely homogeneous: each position is symmetry-equivalent to every other position. For a real arena with boundaries, ants deep in the interior should have a distribution that is similar to that of the unbounded arena. So the unbounded arena helps us understand the ideal distribution to which ants should be approaching as they move further from the boundaries.

We show results for both a 1D and 2D unbounded arena. The 1D arena is a circle of circumference L . So an ant that moves a distance L gets back to where it started. For the one dimensional case, the distribution $\Pi(x, v)$ is calculated using $x(t + \Delta t) = x(t) + v(t)\Delta t$, and $v(t + \Delta t) = v(t) + \Delta v(t)$ where

$$\Delta v(t) = \eta(t) + \Delta F_d(t), \text{ with } F_d(t) = \eta(t) - v/\tau + (v_0/\tau)\text{sign}(v[t]) \quad (4.1)$$

and the random impulse $\eta(t)$ is governed by the probability distribution in equation (2.10).

The 2D unbounded arena can be viewed as the square arena bent into the surface of an ideal torus with a circumference (in both directions) equal to L . An ant that moves a distance L in either the x or y direction returns to the position from which it started. The distribution $\Pi(x, y, v_x, v_y)$ is simulated exactly as described in the previous chapter.

The equilibrium distribution of the unbounded arena must be inde-

pendent of position. In the absence of a driving force, i.e. with $v_0 = 0$, the equilibrium distribution can be calculated analytically and found to be equal to the Gaussian $\exp(-v^2/2v_\infty^2)$ where

$$v_\infty = \sqrt{\frac{\sigma^2 \tau}{2\Delta t}}. \quad (4.2)$$

In the presence of a driving force, the 1D equilibrium distribution is split into two Gaussians: it is proportional to $\exp(-v^2/2v_\infty^2 + |v|v_0/v_\infty^2)$, so the distribution has peaks at $v = \pm v_0$. These analytic results (not derived here because they are beyond the scope of this thesis) can be used to check the reliability of our simulations.

Our simulation results for the unbounded arena are shown in figure 4.1. There is no position dependence to the distribution, so we show only the distribution over velocity $P(v)$ in 1D and $P(v_x, v_y)$ in 2D. We started every simulation with the ant having zero velocity. We carried out many simulations and averaged them to obtain the distribution. Here we show how the distribution evolves with time in figure 4.2 and approaches its equilibrium form, which is exactly the split Gaussian described above. The parameters are indicated in the figure captions.

4.2 Clean bounded arena

Now we add boundaries to the arena, again showing the result for both 1D and 2D arenas. The 1D arena is just a line of length L while the 2D arena is the square of length L described above. The boundary protocol, discussed in section 3.4, is applied. (The 1D version of this procedure is obvious: if $x(t) > L/2$ then $x(t) = L/2$ and $v(t) = 0$.)

The simulations all started with an ant at the center of arena with zero velocity. That is, the initial distribution in 1D was $\Pi(x, v, t = 0) = \delta(x)\delta(v)$ and in 2D was $\Pi(x, v_x, y, v_y, t = 0) = \delta(\mathbf{r})\delta(\mathbf{v})$. With time, this distribution rapidly spreads. After long times, it approaches its equilibrium state.

For the 1D arena, the time-averaged position distribution $n(x)$ shows a high probability to find ants near the boundary. This density $n(x)$ decreases with distance from boundaries, becoming position independent within the arena

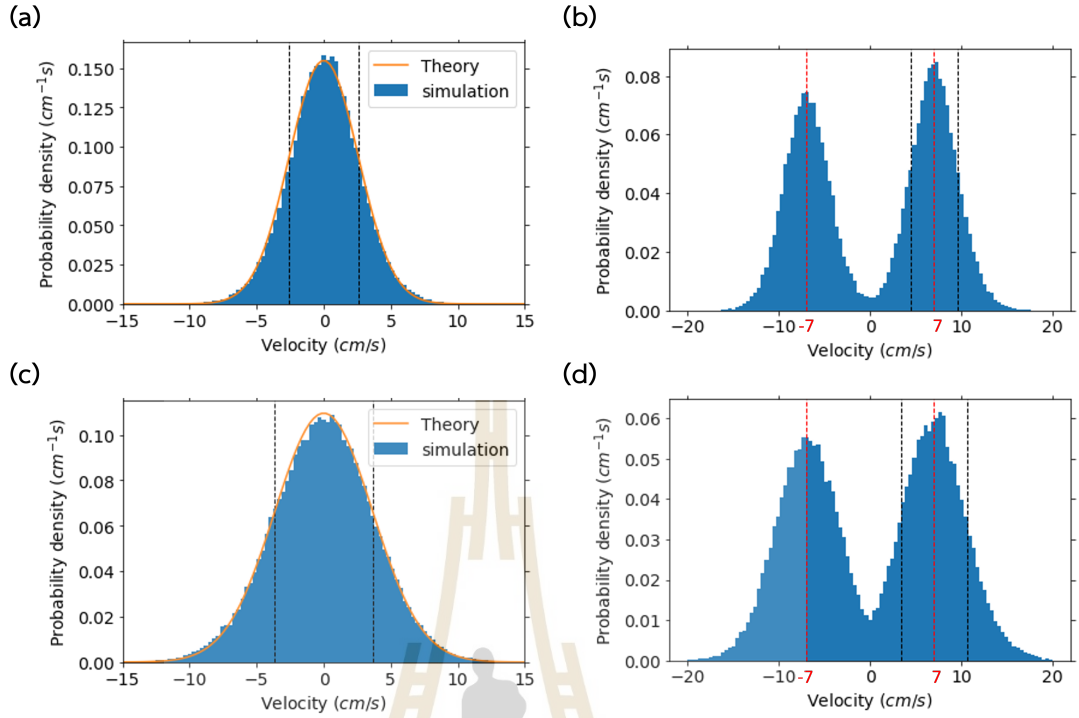


Figure 4.1 (Top) The probability distribution of velocity with parameters $\Delta t = 1/15$ s, $\sigma = 1.33$ cm/s, $\tau = 0.5$ s, (a) $v_0 = 0$ cm/s and (b) $v_0 = 7$ cm/s. (Bottom) The probability distribution of velocity by changing $\tau = 1$ s. Those show that the root mean square is proportional to $\sqrt{\tau}$. The orange curve is result of fitting with the normal distribution: (a) standard deviation is 2.58 cm/s (b) standard deviation is 3.64 cm/s that are correspond to the equation 4.2. (The length between black dash lines is the standard deviation v_∞ in case of $v_0 = 0$ cm.)

interior. The 2D density has exactly the same behavior. (We do not show a heat map of the 2D distribution $n(x, y)$ because you cannot see much: the peaks at the boundary dominate the color mapping.) Once again, this striking behavior results from the statistics of Brownian motion in our model. The model ants do not prefer to be near boundaries, but they end up near them because of their aimless movement.

The velocity distribution $P(v)$ in 1D and $P(v_x, v_y)$ in 2D is also plotted. The peak at zero velocity is seen along with the shoulder features. To better understand the origin of these respective features, we have broken the model data into two subsets: one for ants in arena interior and one for ants near

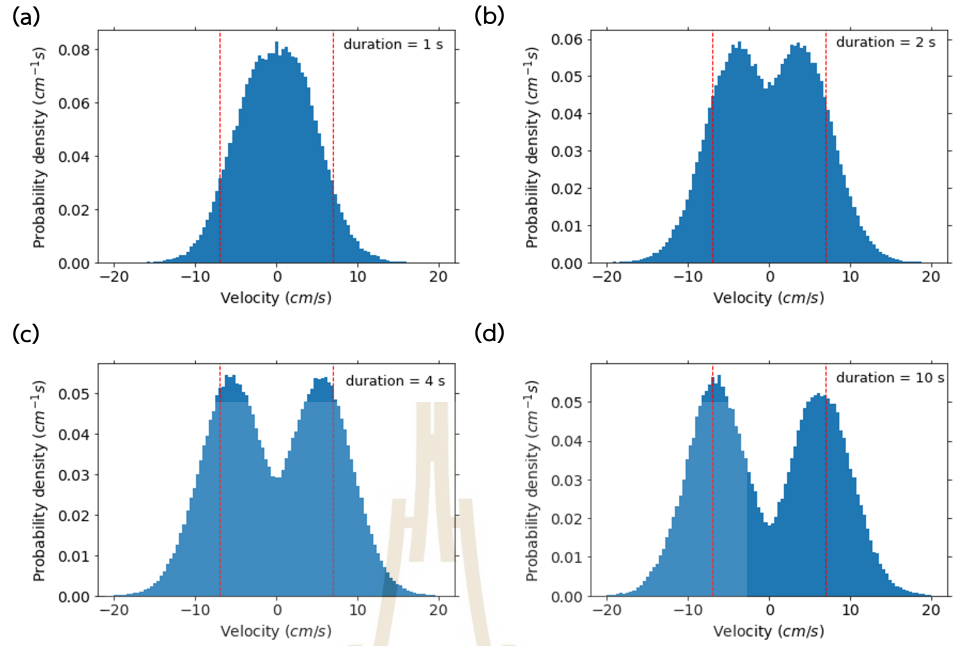


Figure 4.2 The evolution of velocity probability distribution in the unbounded arena is shown with parameters $\Delta t = 1/15$ s, $\sigma = 1.33$ cm/s, $\tau = 1$ s and $v_0 = 7$ cm/s. The peak of velocity distributions are separated and move to $\pm v_0$ over times. (The red dash line represents the terminal speed on average $\pm v_0$)

the boundaries.

The model result $P(v_x, v_y)$ for the distribution of ants in the arena interior is qualitatively similar to the corresponding experimental data. The distribution is isotropic and exhibits the shoulder features discussed above. Ants deep in the interior have a characteristic terminal velocity, at which the drag and driving forces balance. It does not matter which direction the ant is moving: for any direction it has the same preferred speed of v_0 .

When we plot the distribution for ants near the boundary, we see the general features anticipated above. The sharp peak at $v = 0$ (for the 1D simulation) and $v_x, v_y = 0$ (for 2D) is simply explained: near a given boundary we find a dominate fraction of ants that have recently come in contact with this boundary. After they contact it and are forced to stop, it is unlikely that they will receive a long sequence of impulses in the same direction to push them deep into the interior. Rather, they will receive just as many impulses

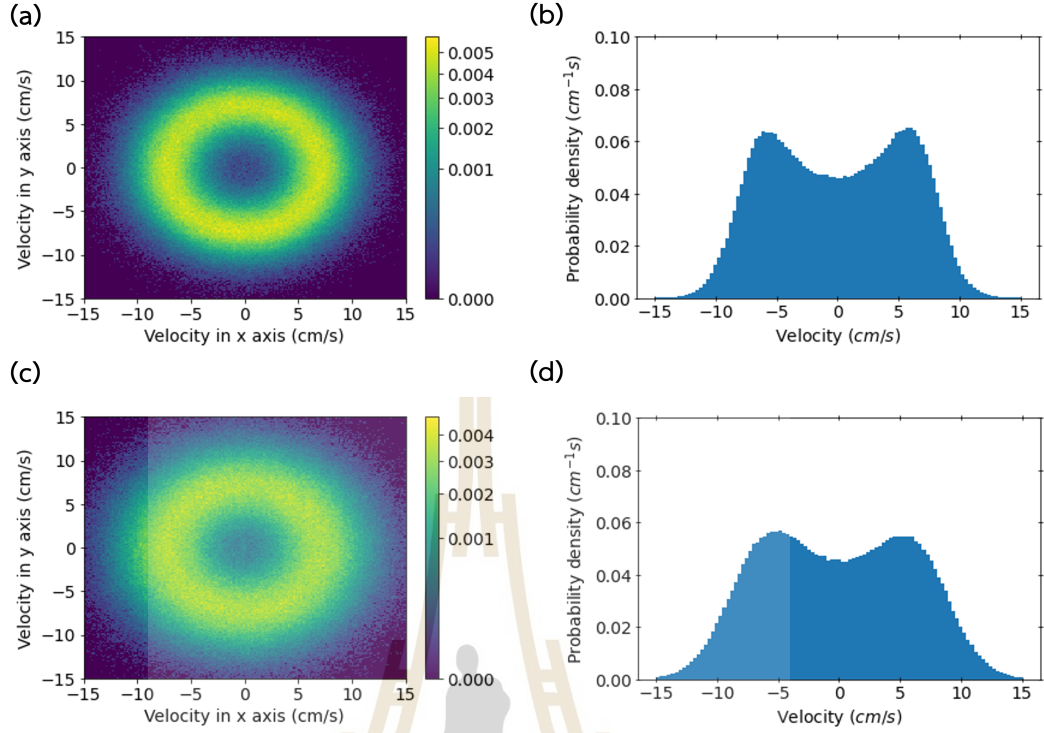


Figure 4.3 The 2D map of velocity distribution (left) and velocity distribution in x axis (right) in the unbounded arena with parameters $\Delta t = 1/15$ s, $\sigma = 1$ cm/s, $v_0 = 7$ cm/s, $\mathcal{T} = 0.5$ s (top) and $\mathcal{T} = 1$ s (bottom)

pushing them outwards. Their typical motion is to repeatedly move away from, then back into, the same boundary. As a result, the component of their velocity normal to the boundary always remains small. The 2D heat map for the boundary population exhibits the characteristic “plus sign” seen in the experiment. In this idealized model description, the sharpness of this feature is exaggerated.

We also present the distribution in a slightly different way, by plotting the ensemble averages of v_x^2 , v_y^2 and $v^2 = v_x^2 + v_y^2$ as functions of position. That is, we broke the model data into subsets according to position, then found the statistical average of velocity squared within each subset. (The average of velocity would be very nearly equal to zero because of rotational symmetry, so the squared velocity is more illuminating.) The results indicate that the average $\{v_x^2\}$ is very nearly zero at $x = \pm L/2$. All ants at the boundary have zero velocity normal to it. With distance from the boundary, $\{v_x^2\}$ increases and approaches its plateau value associated with equilibrium distribution of the

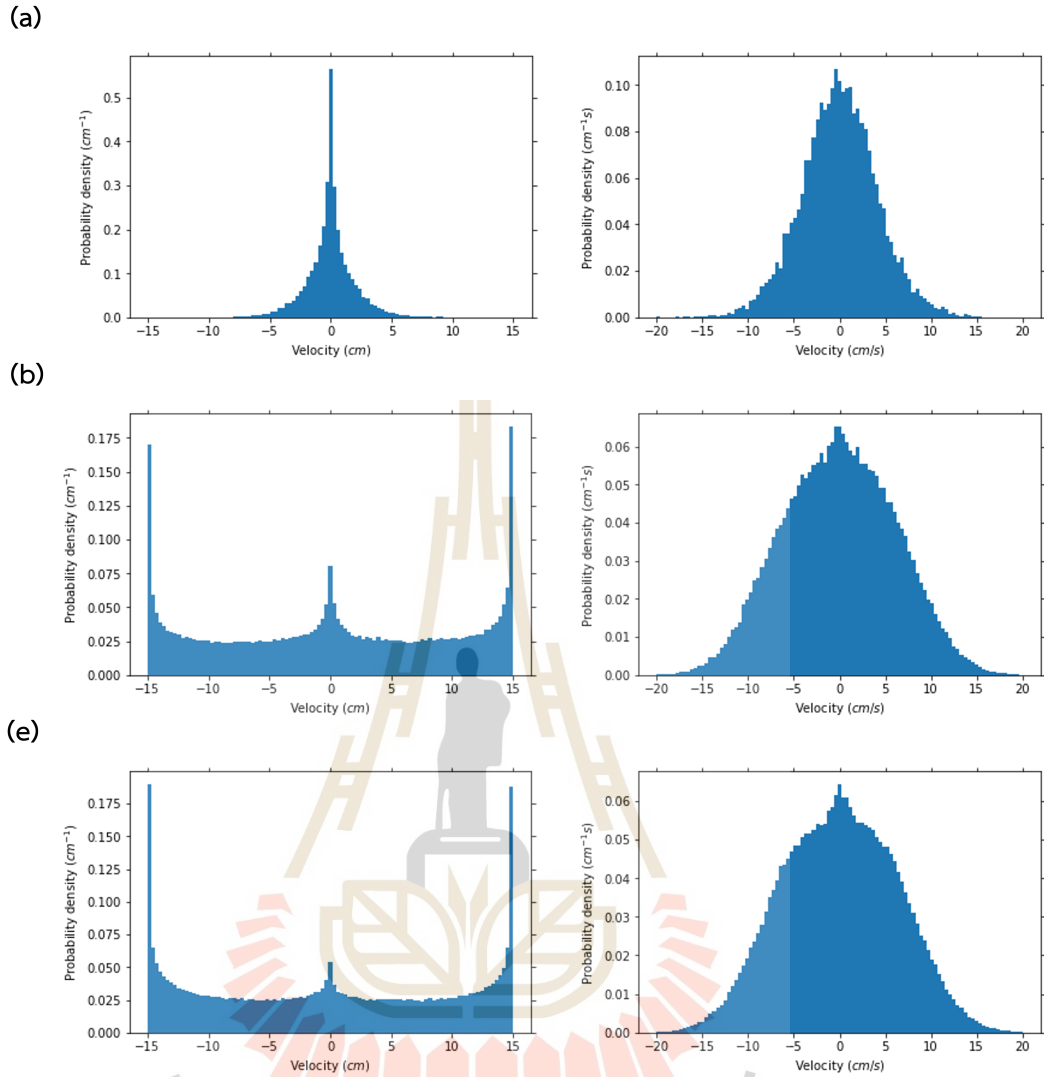


Figure 4.4 The evolution of probability distribution in finite arena length $L = 30$ cm with parameters $\Delta t = 1/15$ s, $\sigma = 1.33$ cm/s, $\tau = 2$ s and $v_0 = 7$ cm/s for (a) 1 s, (b) 10 s and (c) 100 s

unbounded arena. Because of the square symmetry of the overall distribution $\{v_y^2\}$ is weakly dependent on x and vice versa (figure 4.9).

4.3 Coated bounded arena

The effect of the chemical repellent in the R zone is modeled by adding a potential barrier in equation (2.13). The height of the barrier must increase according to how “unpleasant” the ants find the citronella oil. Obviously,

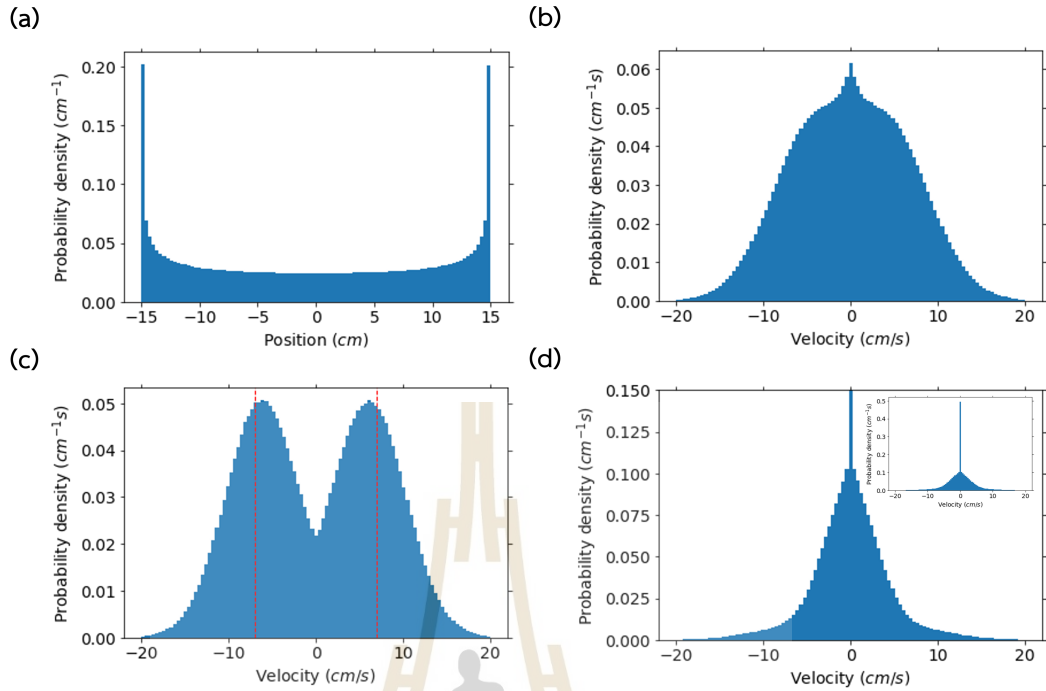


Figure 4.5 The simulation results in finite arena length $L = 30$ cm with parameters $\Delta t = 1/15$ s, $\sigma = 1.33$ cm/s, $\tau = 2$ s and $v_0 = 7$ cm/s. **(a)** The probability distribution of position was sharply peaked near the arena boundary and decay over distant far from the boundary. The probability distribution of velocity for **(b)** all arena **(c)** interior of arena ($|x| < 7$) (this result is similar to the unbounded arena) **(d)** near the boundary (2 cm from the boundary) for probability distribution from 0.00 to $0.14 \text{ cm}^{-1}\text{s}$ (inserted figure for over all).

we have not way of knowing this parameter. But at a qualitative level, we can check whether a significant potential barrier could produce the behavior seen in the experimental distribution.

Consider what happens when an ant tries to enter the R zone at $x = -l/2$. It feels a change in its velocity of $dv_x = -F_d dt$ so after writing $dt = dx/v_x$ we integrate from just before to just after the ant passes $x = -l/2$ and find

$$\frac{1}{2} \int_{v_{x1}^2}^{v_{x2}^2} dv_x^2 = \frac{1}{2} (v_{x2}^2 - v_{x1}^2) = v_0 = \int_{x1}^{x2} dx \delta(x + l/2) \quad (4.3)$$

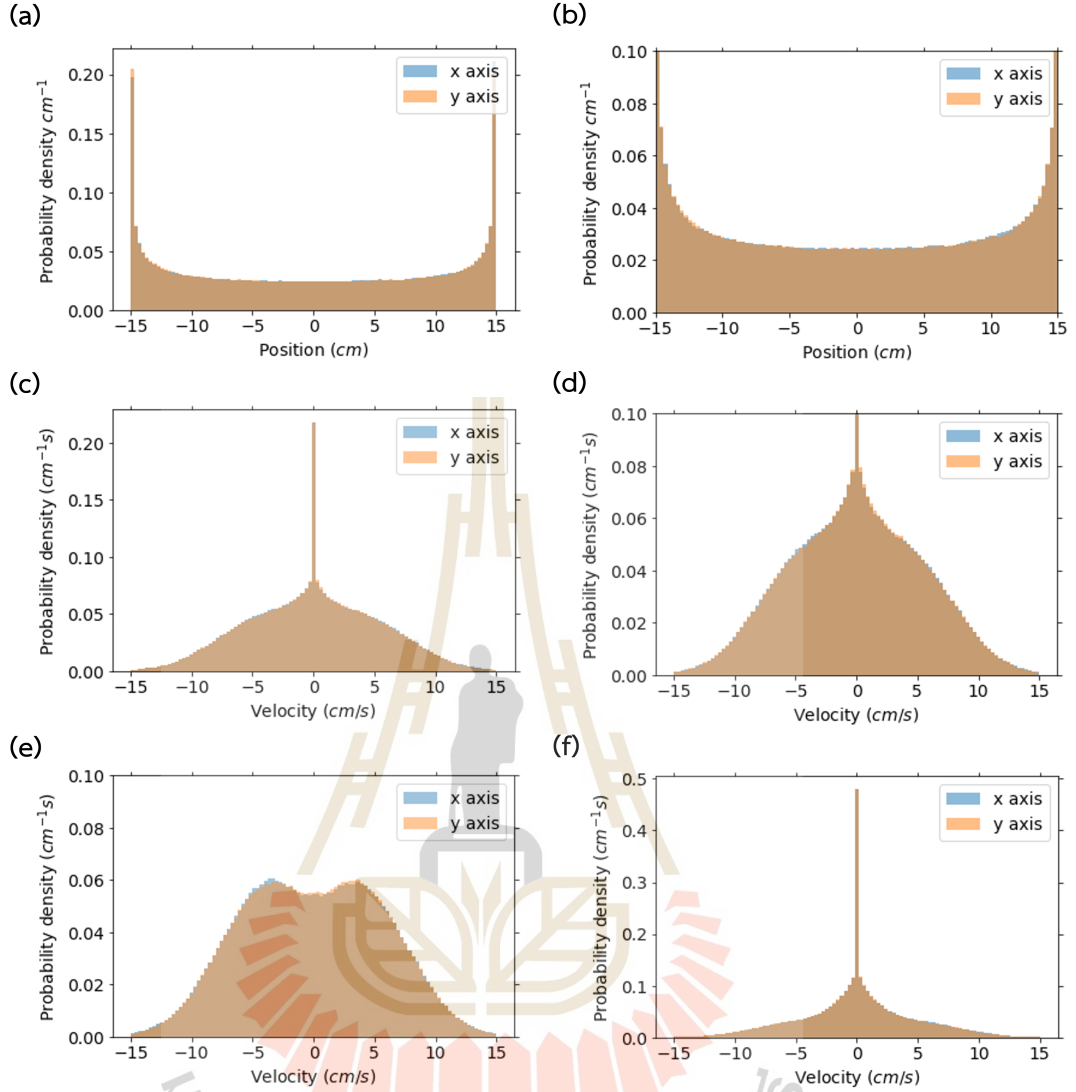


Figure 4.6 The simulation results in 2D finite arena length $L = 30$ cm with parameters $\Delta t = 1/15$ s, $\sigma_r = 1.33$, $\sigma_n = 0.99$ cm/s, $\tau = 1$ s and $v_0 = 7$ cm/s. **(a)** The probability distribution of position **(b)** for the density from 0.00 to 0.10 cm^{-1} for ant in all area of arena. **(c)** The probability distribution of velocity for all arena **(d)** for the density from 0.00 to 0.10 cm^{-1} s, **(e)** interior of arena and **(f)** near the boundary cm^{-1} s. The peak in **(c)** is over estimated, compared to the result in 1D arena. The shoulder feature in **(d)** is formed by the contributions from **(e)** and **(f)**

where v_{x1} and v_{x2} is its x velocity component before and after passing into the R zone. If the ant approached the square barrier with a velocity $v_{x1} < \sqrt{2v_0}$

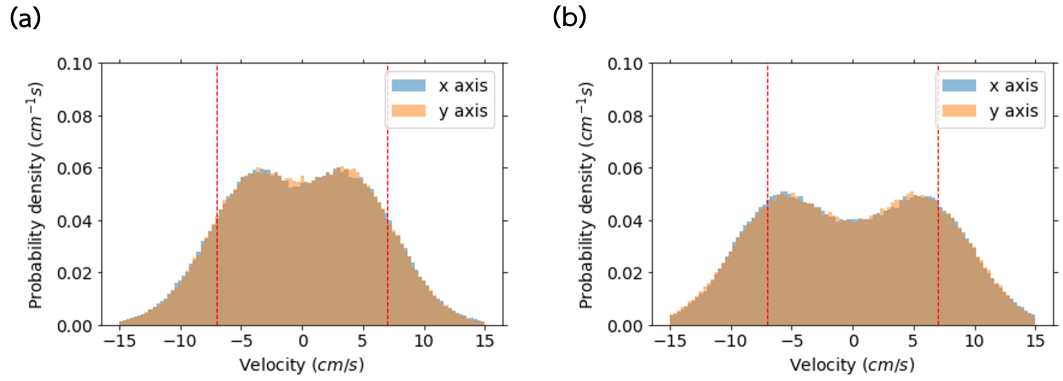


Figure 4.7 From simulation with $\Delta t = 1/15$ s, $\tau = 0.5$ s, $v_0 = 7$ cm/s, $\sigma_l = 1.33$ cm/s, $\sigma_n = 1.00$ cm/s (a) and $\sigma_n = 2.00$ cm/s (b), the velocity in central arena distributions (bottom) are slightly changed the peak position by the σ_n . (the red dash line is vertical line at v_0 .)

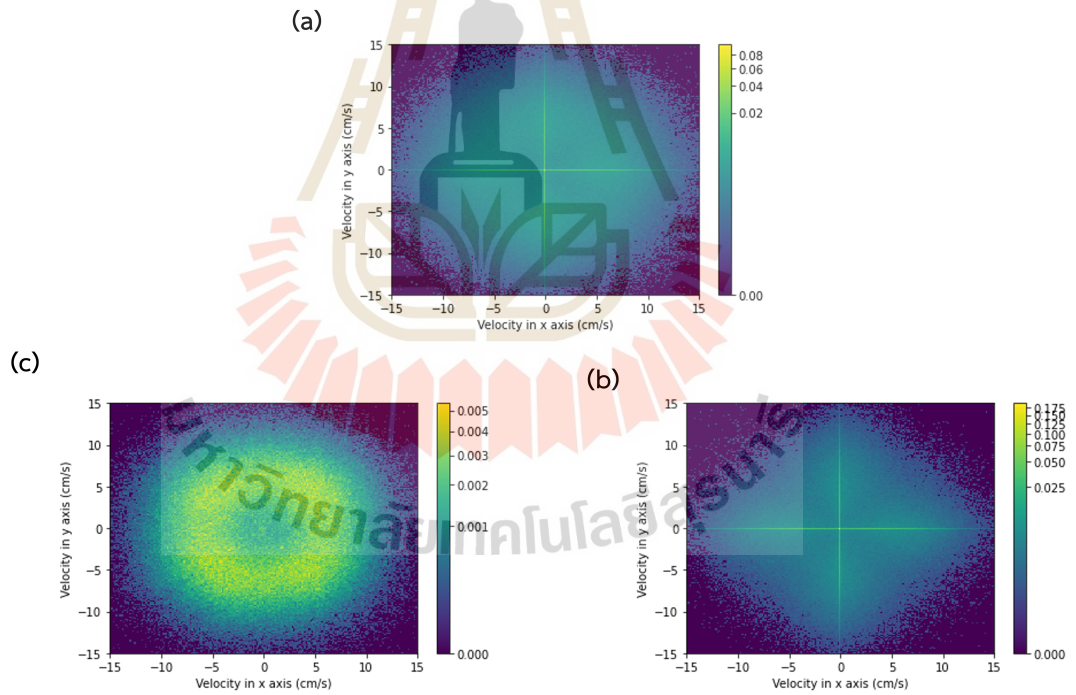


Figure 4.8 The 2D heat map of the velocity distribution from simulation results in finite arena length $L = 30$ cm with parameters $\Delta t = 1/15$ s, $\sigma_l = 1.33$ cm/s, $\sigma_n = 0.99$ cm/s, $\tau = 0.5$ s and $v_0 = 7$ cm/s for (a) all area (b) interior of arena (c) near the boundary.

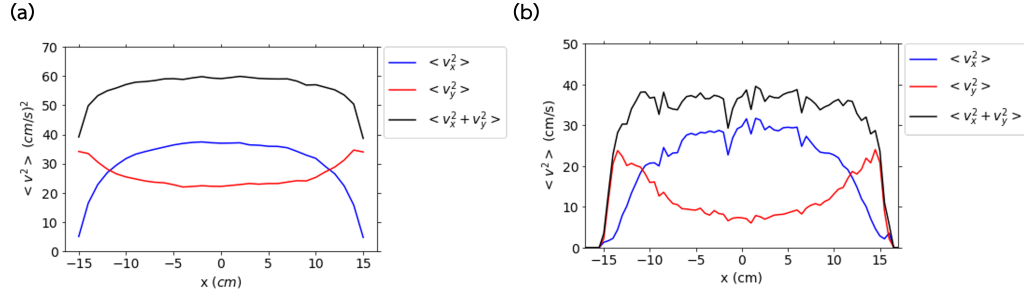


Figure 4.9 The mean of velocity square in x (red) and y (blue). **(a)** simulation results in 2D length $L = 15$ cm with parameters $\Delta t = 1/15$ s, $\sigma_l = 1.33$ cm/s, $\sigma_n = 0.99$ cm/s, $\tau = 1$ s and $v_0 = 7$ cm/s. **(b)** the data are from (Thiawatwanikul et al., 2020).

then this equation suggests that its velocity v_{x2} will be complex. This means that the ant cannot overcome the square barrier unless it has a sufficient velocity towards it.

Those ants with $v_x < \sqrt{2V_0}$ fail to clear the boundary, and a significant number of members accumulate at the foot of the barrier. Ants with $v_x > \sqrt{2V_0}$ are able to overcome the barrier, but their velocity is reduced. As ants move deeper into zone R, they once again approach the velocity distribution of the unbounded arena. Those ants moving out of the R zone enjoy a boost in their outward velocity component by the same amount (use Eq. (4.3) but switch the meanings of v_{x1} and v_{x2} for this case).

The interface between the clean and coated regions acts like a gentler version of the boundary. There is a local peak of density $n(x)$ that is due to many slow ants at the feet of the square potential barrier. The presence of the repellent band leaves ants with less space in which to achieve the distribution of the unbounded arena. As a result, the features associated with the interior are suppressed relative to those features resulting from boundaries. This provides an explanation for why the shoulder features in $P(v_x)$ were less prominent in experiments done in the coated arena.

The simulation results for the density $n(x, y)$ and velocity distribution $P(v_x, v_y)$ are shown in figure 4.10. The features described above are all seen. In particular, consider the heat map of $P(v_x, v_y)$. The obvious vertical features in this plot result from the abrupt change in the velocity distribution resulting

from the square barrier—the feature is located at $v_x = \pm\sqrt{2V_0}$.

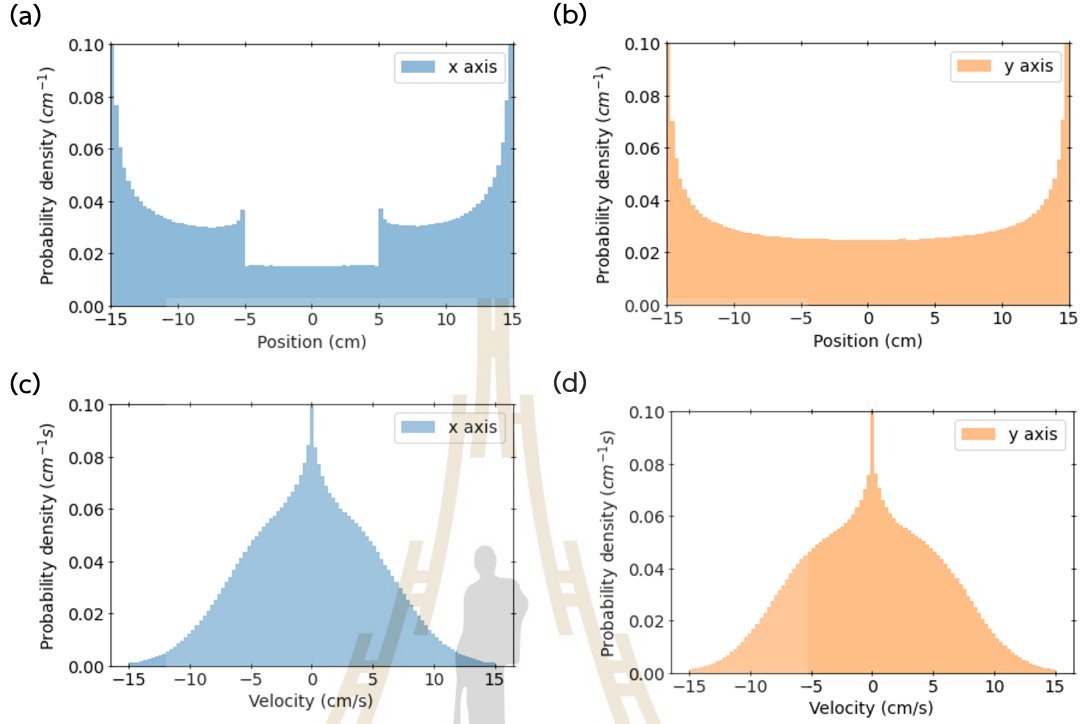


Figure 4.10 The simulation results in repellent arena length $L = 15$ cm and $l = 10$ cm parameters $\Delta t = 1/15$ s, $\sigma_n = 1.25$ cm/s, $\sigma_l = 0.96$ cm/s, $\tau = 0.5$ s, $v_0 = 7$ cm/s and $V_0 = 8$ (cm/s)². The position distribution (top) in x axis (left) is dropped in coated area while the position distribution in y axis (right) is the same as clean arena. The velocity distribution (bottom) in x axis has a smaller “shoulder” then the y-distribution.

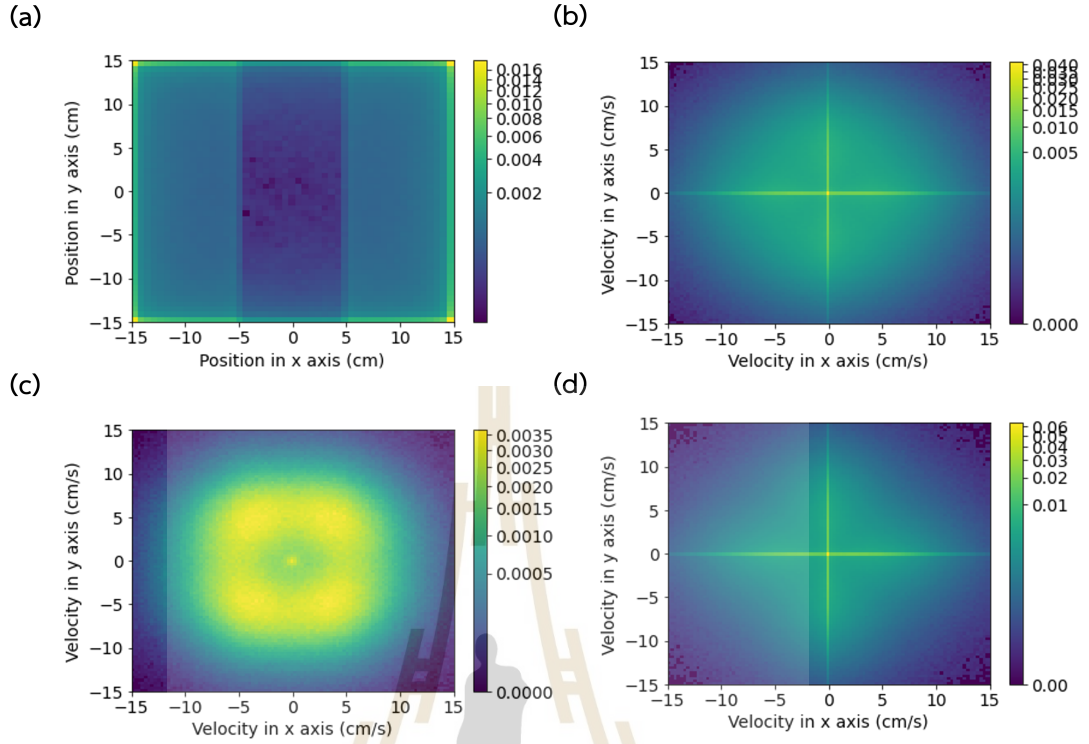


Figure 4.11 The 2D heat map of the position distribution (a) and the 2D heat map of the velocity distribution from simulation results in arena length $L = 30$ cm, the coated length $l = 10$ cm, with parameters $\Delta t = 1/15$ s, $\sigma_n = 1.25$ cm/s, $\sigma_l = 0.96$ cm/s, $\tau = 0.5$ s, $v_0 = 7$ cm/s and $V_0 = 24.5$ (cm/s)² for (b) all area (c) interior of arena (d) near the boundary.

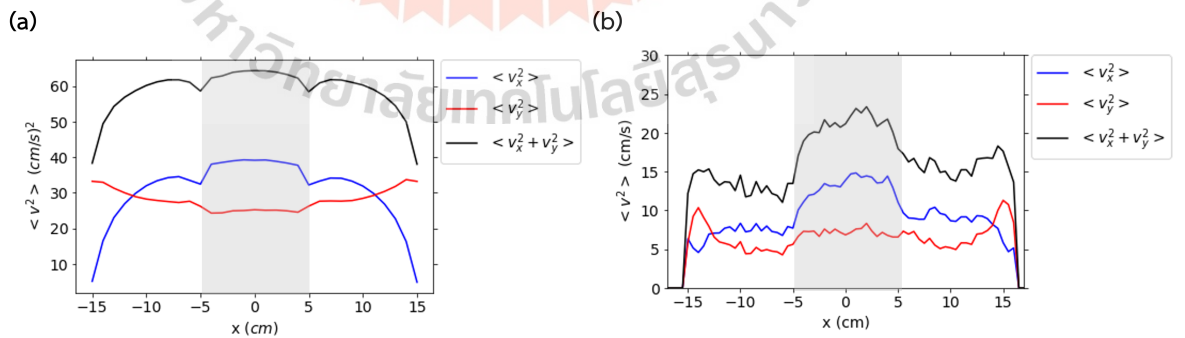


Figure 4.12 The mean of velocity square in x (red) and y (blue) and the mean square of $v_x + v_y$ (black) (a) simulation results in 2D length $L = 15$ cm with parameters $\Delta t = 1/15$ s, $\sigma_n = 1.25$ cm/s, $\sigma_l = 0.96$ cm/s, $\tau = 1$ s and $v_0 = 5$ cm/s $V_0 = 8$ (cm/s)² and (b) the data from (Thiawatwanikul et al., 2020). The green dash line is v_0 cm/s and light blue line is average speed.

CHAPTER V

CONCLUSION

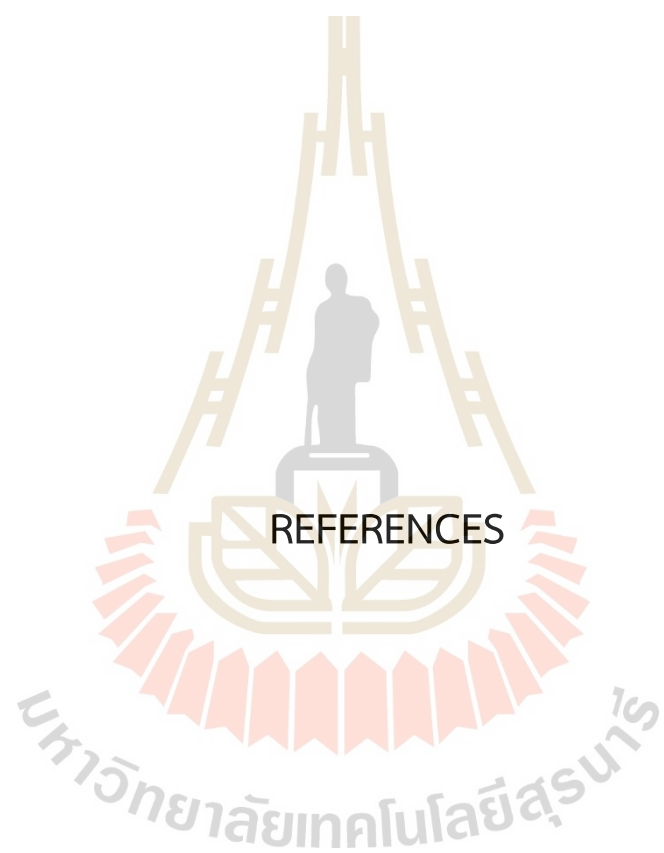
The motion of an individual weaver ant, of the species *Oecophylla smaragdina*, was previously tracked experimentally. In this thesis, we developed a model of its motion—essentially a model of the algorithm it uses to navigate within a simple, unfamiliar environment. Our model was based on the theory of Brownian motion. Accordingly, the total force on the ant was written as a sum of a random component and a deterministic component. We obtained, from experiment, a probability distribution for the impulses caused by the random component—they have zero time average and a mathematically simple distribution. In the deterministic force we included a linear drag term and a constant, forward-directed driving force. To model the effect of a mild chemical repellent we introduced an effective potential energy—the potential is higher when citronella oil, a repellent, is present. We carried out numerical simulations of the motion of our model ants and compared them to the experimental distribution of ants over position and velocity.

Our remarkably simple model accounted for all qualitative properties of the measured distribution. In the experiment, ants tended to remain near the boundaries of the square arena. The model explains this behavior as a basic property of bounded Brownian motion: when an ant is stopped at the boundary, the random impulses tend to make it remain there. The experimental distribution over velocity had a sharp zero-velocity peak and broad shoulder features. The former are explained by the model as a contribution from ants near boundaries, moving slowly because they were recently forced to stop. The latter are characteristic of ants near the arena interior: the shoulders mark the terminal velocity at which the drag and driving forces add to zero. The features of the distribution associated with a band of chemical repellent painted across the arena were similarly explained. The simple effective potential, a square barrier, produced similar features in the model distribution.

Throughout this project, we were guided by the principle of simplicity. We tried to develop a minimal quantitative model. Our model included very

few free parameters: we had two parameters corresponding to the RMS impulse parallel and perpendicular to ant velocity, two corresponding to the strength of drag and driving force, and one to the height of the effective barrier (i.e. the degree to which the citronella oil was unpleasant to ants). We avoided the temptation to classify the ant motion into qualitative phases (searching, resting, etc.) as is often done in analyses of animal behavior. We feel that to do so is to introduce subjective judgement into observation. Also, we refrained from making assumptions about the intentions of the ant, and based our model only on observed quantitative tendencies. The fact that we were able to account for the complex characteristics of experiment, despite being constrained by these guiding principles, is the main positive result of this thesis.

The work was intended as a first step in a study of one aspect of a ant's communication project: a study of how communication of ants affects their navigation. We hope to continue this effort. But the thesis might also have value, in itself, towards understanding the motion of individual ants. It provides a basis for understanding how ants move in unfamiliar territory and might be useful for predicting how they disperse and how their motion may be directed by physical barriers and chemical repellents. Also, we might be bold enough to claim that our approach, which emphasized objective quantitative analysis and simple theoretical modeling, should be followed by other biophysical researchers.



REFERENCES

REFERENCES

- Audira, G., Sampurna, B. P., Juniardi, S., Liang, S.-T., Lai, Y.-H., and Hsiao, C.-D. (2018). A simple setup to perform 3d locomotion tracking in zebrafish by using a single camera. *Inventions*, 3(1), 11.
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M., et al. (2008). Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Animal behaviour*, 76(1), 201–215.
- Cole, A. and Jones, J. (1948). A study of the weaver ant, *Oecophylla smaragdina* (fab.) 1. *American Midland Naturalist*, pages 641–651.
- Czirók, A., Vicsek, M., and Vicsek, T. (1999). Collective motion of organisms in three dimensions. *Physica A: Statistical Mechanics and its Applications*, 264(1-2), 299–304.
- Dankert, H., Wang, L., Hoopfer, E. D., Anderson, D. J., and Perona, P. (2009). Automated monitoring and analysis of social behavior in *Drosophila*. *Nature methods*, 6(4), 297–303.
- DeLellis, P., Polverino, G., Ustuner, G., Abaid, N., Macri, S., Boltt, E. M., and Porfiri, M. (2014). Collective behaviour across animal species. *Scientific reports*, 4(1), 1–6.
- Einstein, A. (1905). Über die von der molekularkinetischen theorie der wärme geforderte bewegung von in ruhenden flüssigkeiten suspendierten teilchen. *Annalen der Physik*, 322(8), 549–560.
- Franks, N. R. and Richardson, T. (2006). Teaching in tandem-running ants. *Nature*, 439(7073), 153–153.
- Gordon, D. M. (2010). *Ant encounters: interaction networks and colony behavior*, volume 1. Princeton University Press.

- Hölldobler, B. (1983). Territorial behavior in the green tree ant (*Oecophylla smaragdina*). *Biotropica*, pages 241–250.
- Hölldobler, B. and Wilson, E. O. The multiple recruitment systems of the african weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 3(1), 19–60.
- Hölldobler, B. and Wilson, E. O. (1990). *The ants*. Harvard University Press.
- Kamhi, J. F., Nunn, K., Robson, S. K., and Traniello, J. F. (2015). Polymorphism and division of labour in a socially complex ant: neuromodulation of aggression in the Australian weaver ant, *Oecophylla smaragdina*. *Proceedings of the Royal Society B: Biological Sciences*, 282(1811), 20150704.
- Langevin, P. (1908). Sur la théorie du mouvement brownien. *Compt. Rendus*, 146, 530–533.
- Lukeman, R., Li, Y.-X., and Edelstein-Keshet, L. (2010). Inferring individual rules from collective behavior. *Proceedings of the National Academy of Sciences*, 107(28), 12576–12580.
- Milinski, M. and Heller, R. (1978). Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature*, 275(5681), 642–644.
- Parisi, D. R. and Josens, R. (2015). Human-ant behavior in evacuation dynamics. In *Traffic and Granular Flow '13*, pages 203–211. Springer.
- Patteson, A., Gopinath, A., Goulian, M., and Arratia, P. (2015). Running and tumbling with *E. coli* in polymeric solutions. *Scientific reports*, 5(1), 1–11.
- Picozzi, S. and West, B. J. (2002). Fractional Langevin model of memory in financial markets. *Physical Review E*, 66(4).
- Ryan, S. D., Sokolov, A., Berlyand, L., and Aranson, I. S. (2013). Correlation properties of collective motion in bacterial suspensions. *New Journal of Physics*, 15(10), 105021.

- Sokolov, A. and Aranson, I. S. (2012). Physical properties of collective motion in suspensions of bacteria. *Physical review letters*, 109(24), 248109.
- Takahashi, M. (1996). Non-ideal brownian motion, generalized langevin equation and its application to the security market. *Financial Engineering and the Japanese Markets*, 3(2), 87–119.
- Thiwatwanikul, T., Paisanpan, P., Suksombat, S., and Smith, M. (2020). Modeling navigation by weaver ants in an unfamiliar, featureless environment. *Physical Review E*, 101(5), 052404.
- Tokita, C. K. and Tarnita, C. E. (2020). Social influence and interaction bias can drive emergent behavioural specialization and modular social networks across systems. *Journal of The Royal Society Interface*, 17(162), 20190564.
- Vicsek, T., Czirók, A., Farkas, I. J., and Helbing, D. (1999). Application of statistical mechanics to collective motion in biology. *Physica A: Statistical Mechanics and its Applications*, 274(1), 182–189.
- Vicsek, T. and Zafeiris, A. (2012). Collective motion. *Physics reports*, 517(3-4), 71–140.
- Wang, S., Cao, S., Wang, Q., Lian, L., and Song, W. (2016). Effect of exit locations on ants escaping a two-exit room stressed with repellent. *Physica A: Statistical Mechanics and its Applications*, 457, 239–254.
- Wang, S., Lv, W., and Song, W. (2015). Behavior of ants escaping from a single-exit room. *PloS one*, 10(6), e0131784.

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