

Security, Information, and Memory Determine  
Locomotor Exploration in *Rattus Norvegicus*

Jeff Alstott

4/10/2007

## **Abstract**

Since the 1930s, researchers have framed rat locomotion in a lit open field in terms of fear and anxiety. Modern studies have continued this interpretation, describing open field behavior in terms of security optimization. Since rats are a prey animal, such hypotheses certainly seem ecologically appropriate, and empirical research supports them. Rats placed in a new environment will spend most of their time next to walls or objects that provide some protection. However, the structure of rat movement in an open field cannot be predicted solely by fear reduction or "security optimization." The sex of the animal, the lighting conditions, and the temporal stability of the environment can all significantly affect the ambulation of rats in a novel or familiar environment devoid of food. Additionally, where the rats spend most of their time, their "home base," is a function not just of a location's relative security, but also of its familiarity. These results indicate that information gathering has a significant role in rodent exploration, which can supplement and potentially supersede evolutionary pressures to maximize security.

# Contents

<b>1</b>	<b>Behavior in the Open Field</b>	<b>2</b>
1.1	Components of Rats' Exploratory Behavior . . . . .	3
1.2	Components of Rats' Navigation System . . . . .	4
<b>2</b>	<b>Analyzed Factors</b>	<b>10</b>
2.1	Lighting . . . . .	10
2.2	Sex . . . . .	11
2.3	Familiarity . . . . .	11
<b>3</b>	<b>Materials and Methods</b>	<b>13</b>
3.1	Subjects . . . . .	13
3.2	Food Deprivation . . . . .	13
3.3	Apparatus . . . . .	14
3.4	Procedure . . . . .	18
3.5	Measures . . . . .	18
3.6	Statistics . . . . .	19
<b>4</b>	<b>Experiments</b>	<b>20</b>
4.1	Security: Sex and Sight . . . . .	20
4.2	Familiarity . . . . .	37
<b>5</b>	<b>Discussion</b>	<b>59</b>
5.1	Security . . . . .	59
5.2	Information . . . . .	60
5.3	Memory . . . . .	61
5.4	Conclusions . . . . .	61

# Chapter 1

## Behavior in the Open Field

The first researchers to study the behaviors of rats in an open field were primarily concerned with emotionality (Hall, 1934), and consequently framed them in terms of fear and anxiety (Archer, 1973; Crawley, 1985). Wall hugging behavior, in which the rats moved cautiously along the edges of the environment, and frequent defecation were the two main supports for this theory (Tobach, 1962). Open field research in the paradigm of fear reduction continues to the present day (Trullas and Skolnick, 1993), most notably in pharmacological studies testing the emotional effects of drugs (Prut and Belzung, 2003).

An alternative ecological approach to open field behavior has developed recently which seeks to understand rodent locomotion in an open field as a product of natural selection. As such, this approach treats the rodents' exploration as a complete behavioral and navigational system, built through evolution to maximize fitness. This approach has led to a host of discoveries related to the computational system of navigation in rodents, the neurological implementation of that system, and how rodents behave to maximize the system's effectiveness. What follows is a review of the key findings from that body of work. This background information is the starting point for the original research of this thesis, and provides context for the conclusions that it draws.

## 1.1 Components of Rats' Exploratory Behavior

### 1.1.1 The Home Base

When moving in a relatively open environment, rats tend to organize their locomotion around a "home base." The home base is a small area where the rat spends a disproportionate amount of its time, sitting, sleeping, grooming, defecating, and rearing (Eilam and Golani, 1989; Tchernichovski and Benjamini, 1998). In a generally featureless environment, such as an empty field in the dark, the location of the home base is idiosyncratic (Whishaw et al., 2006). In a lit environment with notable features, however, the location of the home base for all rats tends to converge to an area next to a salient landmark, such as a box, cone, or corner (Hines and Whishaw, 2005; Eilam and Golani, 1989). In the absence of proximal landmarks, rats will establish home bases in relationship to distant cues (Hines and Whishaw, 2005). With sufficient training, use of these home base locations will persist even if the cues are removed (Hines and Whishaw, 2005).

### 1.1.2 Trips

From the home base rats make frequent "trips" out into the environment and back (Eilam and Golani, 1989). The outward portion of a trip is slow, meandering, and contains frequent short stops, while the return segment is fast, without halts, and directly to the home base (Figure 1.1) (Tchernichovski and Benjamini, 1998). While the length of trips increases throughout a session, the number of stops in the outbound segment of the trip has a strong upper limit (8-10 in rats) (Tchernichovski et al., 1998; Golani et al., 1993). The home base/trip organization of locomotion is very robust, persisting throughout several environmental conditions, along with the number of stops per trip (Golani et al., 1993; Eilam, 2003). In addition to Norway rats, the general home base/trip system has been found in a variety of rodent species (Eilam, 2003; Zadicario, 2005; Avni et al., 2006). Differences in the implementation of the home base/trip behavior (stops per trip, trip frequency, etc.) have been used to ethologically distinguish species and genetic lines within a species (Kafkafi and Elmer, 2005).

### 1.1.3 Looping

In a small, lit open field, rodents typically establish home bases rapidly (Eilam and Golani, 1989), presumably because all relevant features of the environment are visible from the starting location. In a dark environment, however, rodents physically explore the environment in order to select a home base. The mechanism for this initial exploration is called "looping" (Figure 1.2), and consists of slowly meandering about the environment in roughly circular paths (loops), with occasional returns to previously visited locations (loop nodes) (Zadicario, 2005). These paths grow wider and wider, until they reach the boundaries of the environment. Loops and loop nodes can be thought of as trips centered around temporary home bases. As the rodent learns more about its environment, the home base moves around, until the rodent settles on a final location (Avni et al., 2006).

## 1.2 Components of Rats' Navigation System

Rats' physical behavior is not the only level on which we can account for their exploration. Looping, home base, and trip behaviors are all products of the cognitive mechanisms by which rats navigate. Below is a description of the aspects of the navigational system which most directly guide the behaviors discussed in this research.<sup>1</sup>

### 1.2.1 Local View

Local view is the animal's sensory experience when it is in a particular location in the environment. While the term used is local *view*, the sensory input does not need to be visual, but can include sounds, smells, etc<sup>2</sup> (Leonard, 1990; Goodale, 1990). In the laboratory, salient landmarks, such as bright posters, strong smells, and walls make up the bulk of local view information. For visual inputs, the distance to a landmark can be a particularly useful measure obtained from local view, as relatively accurate distances to three landmarks can pinpoint the animal's location (Redish, 1999). The rearing used by

---

<sup>1</sup>For a more complete review of the entire rat navigation system, including discussion of neurological implementation, see Redish's "Beyond the Cognitive Map" (Redish, 1999).

<sup>2</sup>In the majority of the experiments described in this paper, the rats are in complete darkness. This means the *only* possible inputs are nonvisual.

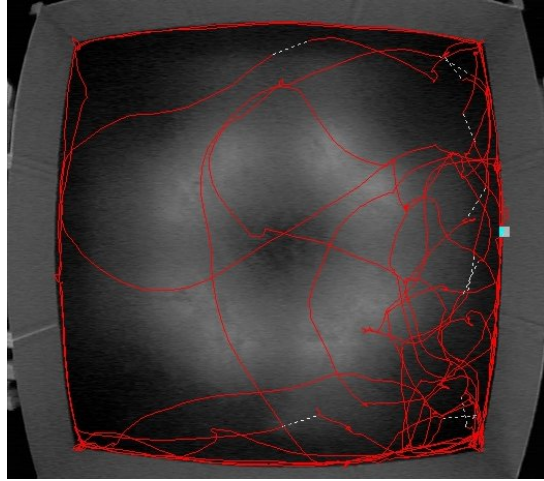
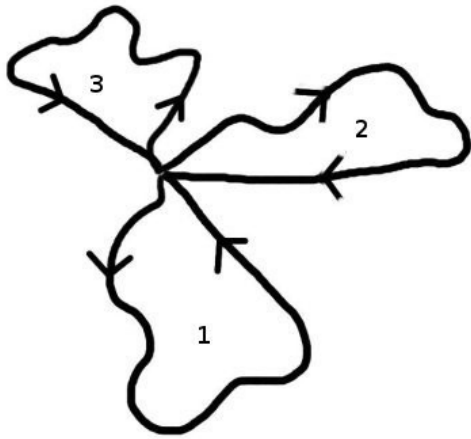


Figure 1.1: Idealized home base and trip behavior (left) and actual implementation (right) by a rat with a home base is in the lower right corner of an open field.

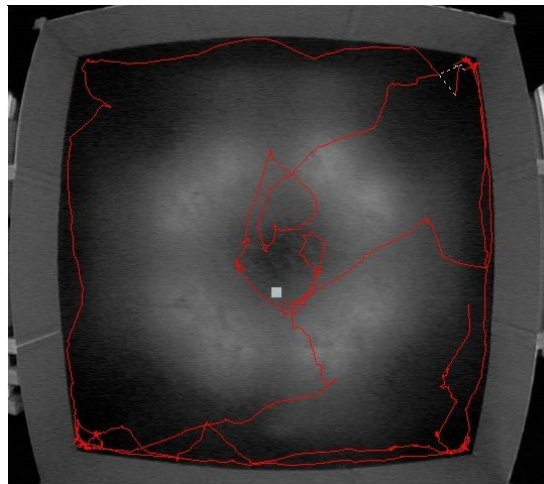
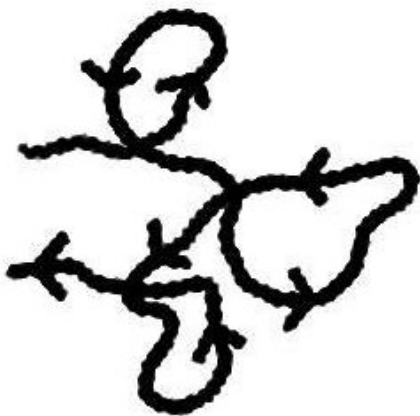


Figure 1.2: Idealized looping behavior (left) and actual implementation (right) by a rat released in the center of an open field.

the rat while in the home base may be used to accurately measure distances, as head movements while rearing could produce visual parallax, which can be used to determine distance (Goodale, 1990; Gallistel, 1990). For nonvisual inputs, information from landmarks distant from the rat is less accurate. As such, local view in a dark environment is largely limited to what is right under the rat's nose, including scents, sounds, vibrissae stimulus, etc.. The turning and rearing observed at home bases may be part of auditory and olfactory scanning, as well as increase vibrissae input from the immediate area, to produce a more complete nonvisual image.

### **1.2.2 Path Integration**

Path integration is the process of determining the present location relative to a starting point by summing the vectors traveled. Using accurate distance traveled measures for each leg of the journey, along with angles between each leg, it is possible to add each segment of the trip to compute a return segment directly to the starting location (Barlow, 1964; Etienne et al., 1998)(Figure 1.3). Path integration is not unique to rats; it has been documented in other mammals (including humans), birds, and insects (Jeffery, 2004; Loomis, 1993; Collett, 2000; Saint Paul, 1982). In all of these cases, however, path integration is not perfect. Because vector length and direction information can never be perfectly accurate, path integration will produce systematic errors (Figure 1.3). In rodents, path integration relates to the trip behavior. As the outward portion of the trip is marked by stops, this breaks the trip into a set of vectors. Summing these vectors allows for the quick, direct return portion of the trip. Additionally, increasing the number of vectors increases the calculation error, which is why there is an upper limit on the number of stops in a trip(Eilam et al., 2003). Too many stops, and the rat is increasingly inaccurate in returning to the home base.

### **1.2.3 Place Code and Self-Localization**

The place code is where local view and path integration meet, creating a coordinate system of an environment stored in memory (Redish, 1999). The cognitive representation



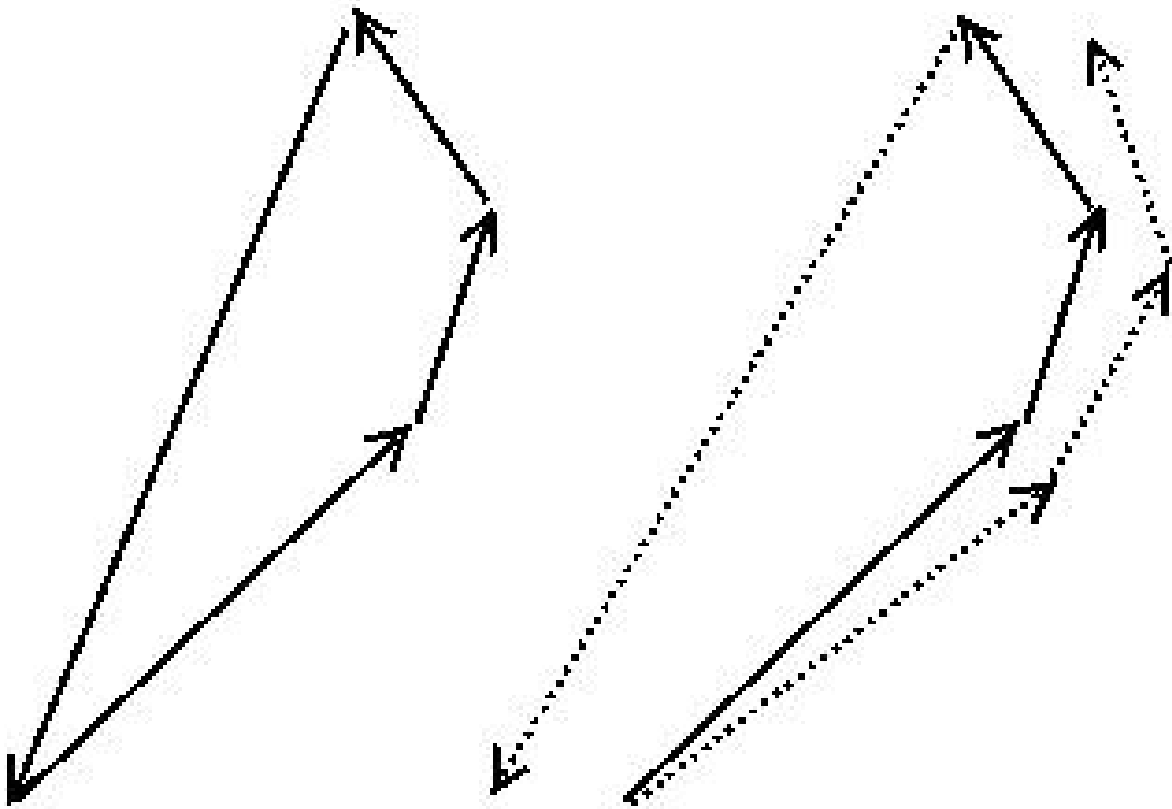


Figure 1.3: Path integration to return to a starting point. The three outward legs of the trip are summed and then reversed to obtain a return vector. In the right figure, inaccurate heading measures calculate an incorrect location, and thus a return vector that is too long and at too large of an angle.

of the rat's position, then, is a function of both the present local view and the position relative to a start location. Self-localization is the process of recalling the place code from memory using local view information. The path integration is then reset with the remembered location as the starting point, establishing the connection between the two subsystems (Touretzky, 1996).

Self-localization first occurs when entering into an environment (such as in the beginning of an open field experiment), in order to initially construct the place code. However, both local view and path integration are imperfect, and so the two systems can drift apart over time, destroying the coordinate system and disorienting the rat. In order to maintain an accurate place code, the local view and path integration connection must be periodically reset by self-localizing at a location where local view is well defined (Samsonovich, 1997). In rats, self-localization is achieved at the home base (Redish, 1999). As previously described, rats typically establish home bases next to a salient landmark, and maintain a very accurate local view while there, so there is minimal likelihood of misidentifying it by sensory inputs. The home/base trip behavior then, is a means of exploring new areas of environment, while frequently resetting the coordinate system, so as not to get lost.

#### **1.2.4 Thigmotaxis**

The previously described subsystems of rat navigation play a direct role in generating the home base/trip behavior. Thigmotaxis does not produce this behavior, but affects its implementation. Thigmotaxis has traditionally been thought of as an attraction to walls, producing "wall hugging" behavior. For example, in an enclosed open field rats spend most of their time next to the wall (Valle, 1970). Home bases are established in corners, and much of each trip is spent in contact with the wall. In a rectangular arena, a round trip from the home base may consist of sitting in a corner, moving in a straight line along all four walls, and returning to the starting corner (Eilam, 2003). Such wall hugging in rats has traditionally been attributed to fear, and more recently to the more general concept of security optimization, as walls and tall objects are presumed to provide

protection (Treit, 1998; Whishaw et al., 2006).

On the other hand, some ecologists have suggested that wall hugging can be thought of as a build up of activity at the boundaries of the environment (Calhoun, 1963). The rats have a characteristic natural range, the size of the area in which they naturally choose to live, and if a barrier prevents them from achieving this range, the unused locomotion will build up at the edges. Another explanation for wall hugging more narrowly defines thigmotaxis as an attraction to tactile stimuli, which for rats means objects that stimulate their vibrissae. The experiments described in this paper will show that in the dark rat behavior is not solely a function of security and wall hugging, but also familiarity, outer boundary buildup and simple contact-driven thigmotaxis. As described in experiment 4.1.1, female rats in the dark will readily leave a secure position in favor of exposed, precarious areas that have an edge, presumably because they stimulate the vibrissae. In experiment 4.2.4, rats will stay near more exposed, familiar over unfamiliar, protective walls.

# Chapter 2

## Analyzed Factors

In the past decade researchers have developed several computational models relating to rat exploration, including behavioral models of locomotion and neurological models of navigation (Tchernichovski and Benjamini, 1998; Tchernichovski et al., 1998; Redish, 1999; Touretzky, 1996). These models have done well in describing their particular domains, predicting the behaviors listed above and explaining their causes under limited conditions. However, there are still a considerable number of recognized factors which these models do not incorporate, yet do impact rat behavior. This paper focuses on three such factors - lighting, sex, and familiarity- in hopes of explaining their influence on how rats select and interact with their home bases. Several of the experiments in this paper are particularly aimed at the idea of security optimization, a recently developed mode of explaining the evolutionary causes for rat exploratory behavior(Whishaw et al., 2006). These experiments showed that while the need to not be eaten is a strong natural selector, it is not the complete explanation for rats' movements.

### 2.1 Lighting

Rats in the dark increase ambulation and rearing and decrease thigmotaxis and defecation compared to in the light (Valle, 1970). However, the great majority of rat open field studies have been done in light. The few rodent exploration studies done in darkness did not use rats, but gerbils and mice (Avni et al., 2006; Eilam, 2004). These studies

have shown that in the dark rodents significantly increase ambulation, spend less time by the walls, and are much slower to establish home bases. Experiments 4.1 will show how lighting can influence security seeking behavior in rats in several environments.

## **2.2 Sex**

Rats are sexually dimorphic in their behaviors, including behaviors relating to spatial task capabilities and open field locomotion (Stein, 1999; M., 1996; Slob AK, 1986; Valle, 1970; Calhoun, 1963). However, the bulk of research concerning home bases, trips, and looping in rodents has not discussed the possibility of sex differences in this set of behaviors, and most experiments have been run with males. In one case, females were run in addition to males, but the sexes were lumped into one group without analyzing their differences. Experiment 4.1.1 will directly compare males and females, and show that while females still use home bases, they spend much more of their time on trips. Possible reasons for this sex difference will be discussed, particularly as it relates to memory and familiarity.

## **2.3 Familiarity**

The idea that the movements of rats could be a function of familiarity is not new (Tchernichovski et al., 1998; Tchernichovski and Benjamini, 1998). Tchernichovski et al.'s model describes the home base as an area with which the rat is highly familiar (has an accurate local view memory of) and makes explorations away from. As the rat makes successive trips, the surrounding environment becomes more familiar. To learn more about the environment, the rat must make progressively longer excursions into unfamiliar territory. Though these researchers argue that the rat's familiarity with its environment helps to generate the home base and trip behavior, they do not consider that familiarity is a factor in selecting the home base location. As many of the experiments this paper show, a region is not necessarily familiar because it is the home base; it can also become the home base because it is familiar.

Most research on rodent exploration has used single, long sessions to observe rodent locomotion, which does not work well for separating familiarity and habituation. In contrast, the experiments used to create the familiarity models used multiple, short, daily sessions, which are useful for measuring memory effects (Tchernichovski et al., 1998; Tchernichovski and Benjamini, 1998). However, these experiments did not use multiple sessions to its full advantage: the environment was never changed between sessions. In many of the experiments of this paper (4.2), rats are given multiple sessions to learn an environment, and then the environment is changed. In particular, several of these experiments alter the starting location of the rat within the same environment. Given the choice between an unfamiliar, nearby location and a familiar, distant location, rats will place their home bases in the familiar area. With repeated use of the new starting location, the area around it will become more familiar, and the home base will move from the old area to the new. The results and others indicate that familiarity plays a large factor in where rats will establish their home bases.

# Chapter 3

## Materials and Methods

### 3.1 Subjects

All subjects were male and female Norway rats between four and five months-old at the beginning of the study. All rats had previously participated in a behavioral study of spatial learning in the Morris Water maze. The rats received food and water libitum and housed individually in metal cages (9.5" deep, 8" wide, 7" high) in a colony room. The colony was lit from 7am-7pm and dark the remaining hours. The colony's temperature was maintained between 66-78°F.

### 3.2 Food Deprivation

Starting six days before the beginning of each experiment, rats were weighed daily in the mid afternoon, then fed an amount of food designed to reduce their body weight to 85 percent of their free feeding level. This typically occurred within four days (three days before the first day of the experiment), at which point the amount of food was slowly adjusted upward to maintain their target weight. For most rats this process involved lowering daily food intake to 5g in the first few days, then raising it to 10-12g for the rest of the experiment. The rats rapidly showed anticipation of this feeding time, with increasing alertness, locomotion, and grooming beginning in the afternoon hours. Throughout the experiments the rats were weighed before they were taken from the colony, and were fed

at least 15 minutes after their return.

## **3.3 Apparatus**

### **3.3.1 Room**

All experiments took place in the same laboratory room, which was 12' by 12' and 10' tall. The floor was tile painted black and sealed with a polyacrylic. All four walls were painted white, and were featureless except for a single door in the center of the east wall and a 3' by 4' whiteboard in the center of the west wall, 4' off the ground. The door's frame was constructed such that no outside light and minimum sound could enter the room when the door was shut. Experiments run in the light included a heavy, black, plastic curtain hung from the ceiling immediately in front of each wall. These curtains completely covered the walls, masking the door and whiteboard. Experiments run in darkness had these curtains pulled back to the corners of the room. Immediately in front of the curtains, in the center of the room, was a 10' by 10' enclosed arena, which was the open field used for most of the experiments (Figure 3.1). The walls of the arena were wooden, 2' tall, and painted gray.

The ceiling was white tile, and hosted eight fluorescent lights and four air vents. Only one of these vents was active, creating minimal air circulation. Hanging from the middle of the ceiling was a cylindrical cover made of wire mesh and duct tape (Figure 3.2). This cover, barely larger than a rat, was attached to a string which ran through a pulley system in the ceiling to outside the room. When introducing a rat into the environment, the experimenter would place the rat underneath the cover, then exit the room. From there, the experimenter would raise the cover by means of the string, releasing the rat to move about the exploration space.



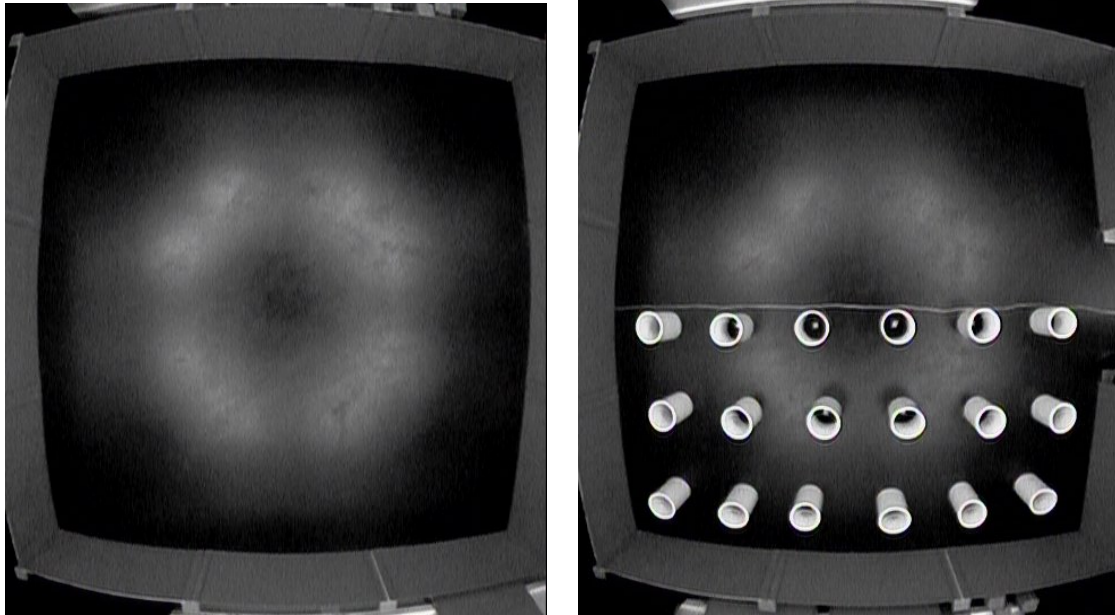


Figure 3.1: View from the tracking camera of the floor arena (left) and the floor arena with the forest on the south half (right). The picture of the forested arena shows a string marking the center of the arena, and a section of the wall pulled away at the location of the door. The string was removed and the wall section replaced during the running of the experiments.

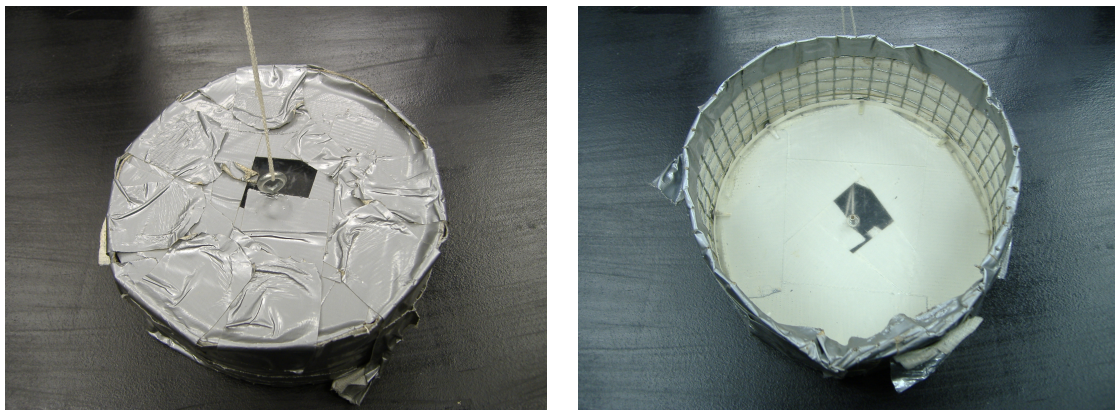


Figure 3.2: Top and bottom views of the cover used to release rats into the open fields.

### **3.3.2 Forest**

Some experiments in the floor arena used an artificial "forest", which was designed to mimic the difference between an area with trees and a more exposed region. In these experiments, half of the arena contained 18 PVC pipe segments, each 6.6" diameter and 12" long, standing on end. The pipes were sufficiently wide and bulky that a rat could not move them, and their top edge was higher than a rat could reach. The "trees" were arranged in an offset grid in the forested half, with roughly the same grid arrangement used across all experiments that used the forest (Figure 3.1).

### **3.3.3 Table**

Some experiments took place on a circular, wooden table, which was placed in the middle of the room. The table was 66" in diameter and raised 41" off the ground on sawhorses. Six 12" tall landmarks, consisting of two 4"x1" wooden segments nailed together at right angle, were mounted on end with pegs stuck into holes in the table equidistant from the edge and center of the table (Figure 3.3). The table and landmarks were also painted black and sealed with polyacrylic. The arrangement of the landmarks created a functional "inner circle" and "outer circle" whose border ran through the middle of the landmarks. These two regions were used in analysis of the rats' movements.

### **3.3.4 Tracking**

In the center of the ceiling hung an infrared LED bank, along with an IR sensitive Panasonic video camera. This camera was connected to a DVD recorder, monitor, and computer in an outside room. From this room the experimenter could observe the rats while the video feed was written onto DVD. The behavior of the rats was simultaneously digitally captured on the computer with Ethovision®, a tracking program which allowed for various analyzes of the rats movements. All experiments that were run in the light were illuminated by the eight fluorescent lights. All experiments run in the "dark" were illuminated by the infrared LED bank, which emits a wavelength of light that rats cannot

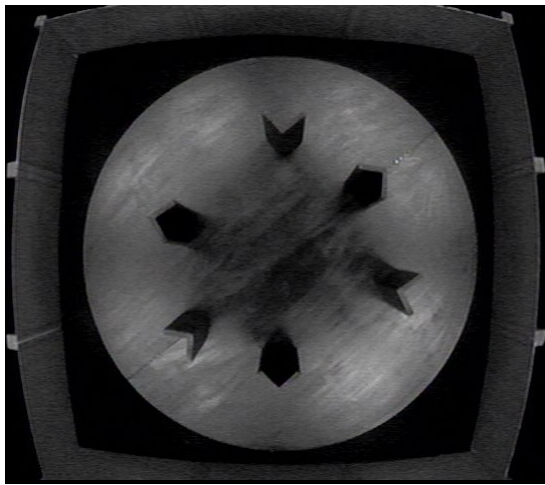
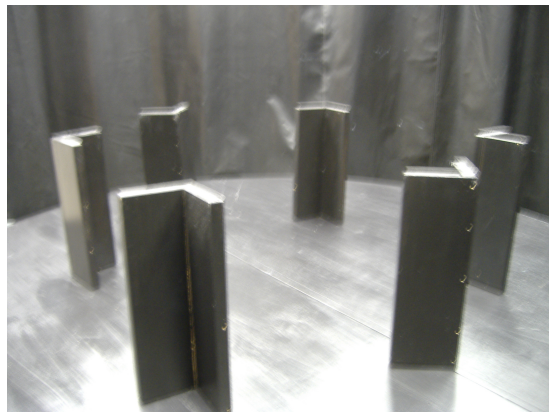
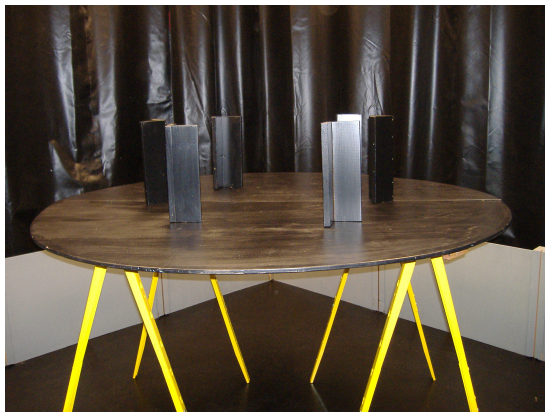


Figure 3.3: Side view of the table (top left), the six landmarks (top right), and a view from the tracking camera of the table (lower left).

see(Neitz, 1986).

### **3.4 Procedure**

All experiments took place in mid afternoon. All rats were removed from their cages and weighed, then carried to the lab in metal carriers, which featured individual compartments for each rat. The experimenter then took a single rat by hand from its carrier, carried it into the room used for the experiment, and placed it at its starting location on the table or floor, underneath the previously described metal covering. If the experiment was run in the dark, the room was dark while the experimenter brought in the rat. After placing the rat underneath the cover, the experimenter left the room, shut the door, and began recording on the DVD player. The experimenter then raised the cover, using the pulley-aided string, releasing the rat to move about the arena. Once the cover was pulled completely out of the camera's way (typically less than 2 seconds), the experimenter started Ethovision's tracking of the rat.

After Ethovision tracking started, the trial lasted 5 minutes before the experimenter entered the room (still in darkness, for those experiments run in the dark), picked up the rat, and put it back in the carrier. After each rat's trial, the experimenter cleaned away any feces and urine with paper towels and an organic acid cleaning solution, which was blotted dry. After all rats had been run, they were taken back in their carriers to the colony, where they were returned to their cages and later fed according to the food deprivation procedure described above. Because the rats traveled to and from the colony as a group, but had individual trials, there was some waiting time in the carriers. The rats waited 10 to 60 minutes before their trial, and 20 to 90 minutes before their return to the colony.

### **3.5 Measures**

For most of the following experiments, the primary measure analyzed was the percentage of time the rats spent in specific areas of the environment. Because a central characteristic

of the home base is that the rat spends the majority of its time there (Eilam and Golani, 1989), simply identifying what region the rat spends the most time in is sufficient to describe where home bases are located. The regions used in these measures are typically much larger than what a home base would be (ex. 50 square feet versus less than 1 square foot) for two reasons. First, the precise location of the home base can vary from rat to rat, making analysis of general home base locations complicated or impossible. Secondly, these experiments were designed such that finer distinctions between home base locations are unnecessary, namely because the environmental manipulations were so large.

### **3.6 Statistics**

All values and statistics reported are the least square means and p and F values calculated by a repeated measures ANOVA using Statistica<sup>tm</sup>. Effects with p values of less than .05 were considered significant.

# Chapter 4

## Experiments

Each of the factors detailed in Chapter 2 were addressed in this collection of experiments. The experiments in section 4.1 dissected how both lighting and the rat's sex can individually modify security related behaviors, eliciting highly adventurous or stimulus seeking behaviors. The experiments of section 4.2 analyzed how rats react to changes in the environment, giving them the option of a more secure location or one which they have more previous interaction with.

### 4.1 Security: Sex and Sight

#### 4.1.1 Table

This experiment, which took place in the table environment, analyzed how rats' security seeking behavior can be modified by both the sex of the animal and lighting conditions, and whether there is an interaction between the two factors. "Security seeking", in this case, was measured primarily by how much of their time rats spent in the more protected areas of the environment: by the landmarks and within the inner circle. In addition, this experiment shed some light on the wall following behavior of rats, particularly if the attraction is to walls or simply an edge.

## Procedure

Two groups of males (both  $n=9$ ) and two groups of female (both  $n=8$ ) were run on the table for 6 days. For each sex, one group was run in the dark, and the other in the light. For all trials the rats were released in the center.

## Results

*Inner Circle Percentage:* Males spent more time within the inner circle than females, and rats in the light spent more time within the inner circle than rats in the dark (Figure 4.1). For both conditions, the inner circle percentage was above chance (25%, as the inner circle had 1/4 the area of the outer circle). For light groups, the inner circle percentage was initially around that of the dark groups, but then grew over the 6 days (Figure 4.1). The dark groups maintained the same inner circle percentage throughout the experiment. There was a weak interaction of days and sex ( $F(5,150)=2.2437$ ,  $p=.05287$ ): males and females both started with a low inner circle percentage which increased over the experiment, but the males' increased faster. There was no significant interaction of days, sex, and lighting ( $F(5,150)=1.2951$ ,  $p>.2$ ). However, there was a significant effect of lighting in females ( $F(1,14)=6.7233$ ,  $p<.03$ ), as well as a days by lighting effect (Figure 4.2). In males, there was a significant effect of lighting ( $F(1,16)=14.722$ ,  $p<.002$ ), but only a weak interaction of days and lighting (Figure 4.3).

*Landmarks Percentage:* In the dark, the time spent by any landmark was roughly equal. For light groups, the protected corners on the inner circle were highly preferred (Figure 4.4). This preference for this kind of corner developed over the course of the experiment (Figure 4.5). There were no significant sex effects or other interactions.

*Edge Percentage:* Females in the dark spent much of their time within 4" of the table's edge, typically hanging their heads off the side. The other groups spent less than chance (22.7% by surface area) at the edge of the table (Figure 4.6). This produced significant main effects of lighting ( $F(1,30)=33.53$ ,  $p<.00000$ ) and sex ( $F(1,30)=31.570$ ,  $p<.00000$ ). Though the two male groups differed by less than 1% in this measure, there was still a significant difference between the light and dark groups ( $F(1,16)=15.726$ ,  $p=.00111$ ).

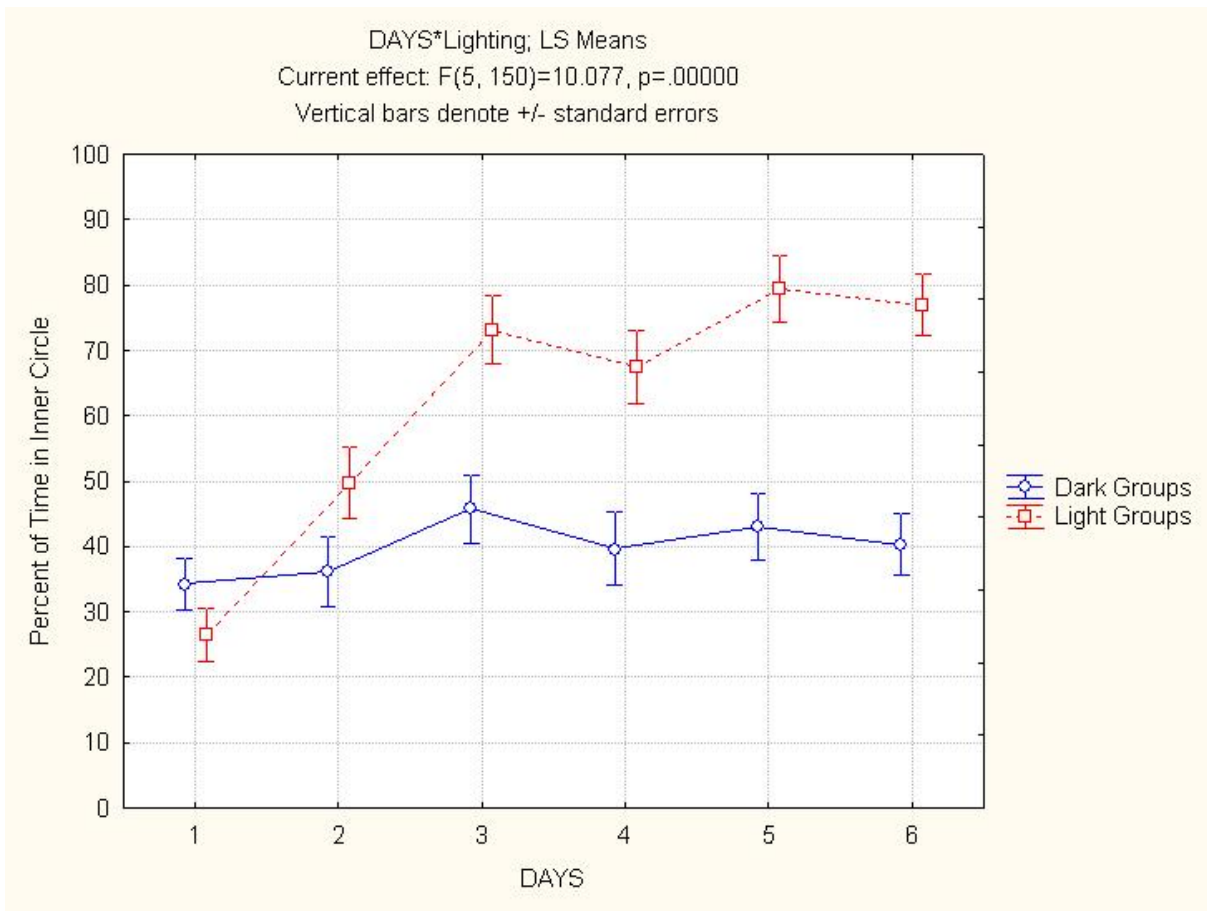


Figure 4.1: Light and Days interaction on Inner Circle Percentage for both sexes



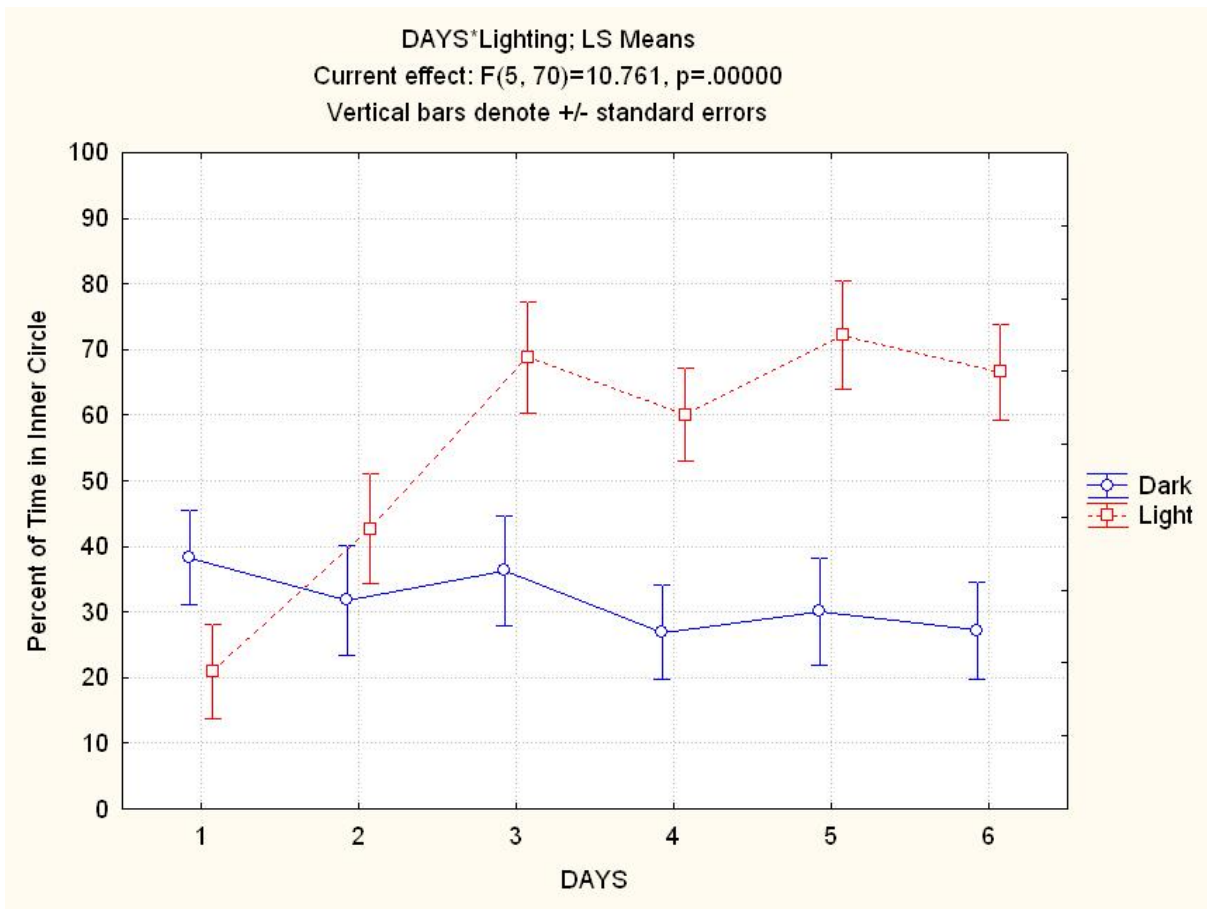


Figure 4.2: Light and Days interaction on Inner Circle Percentage in females

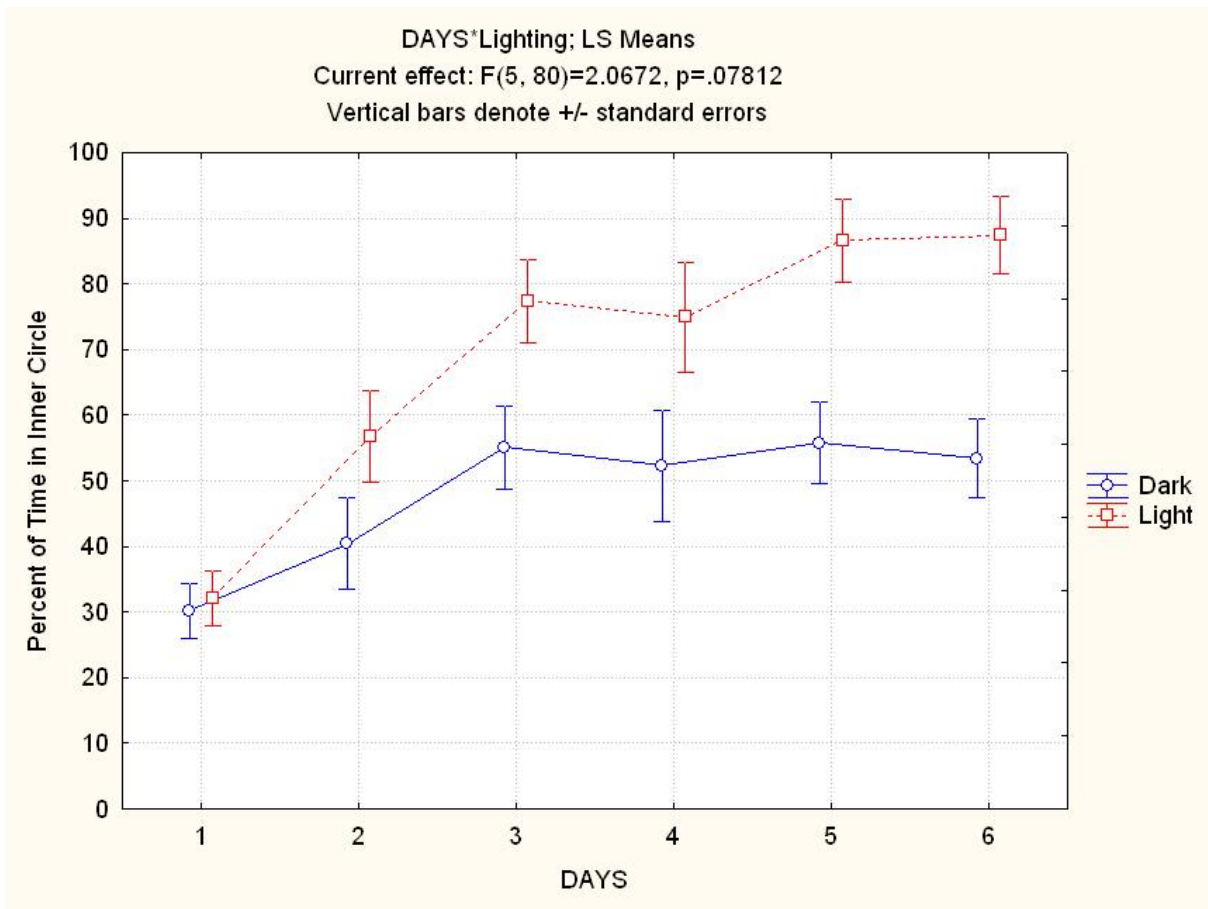


Figure 4.3: Light and Days interaction on Inner Circle Percentage in males

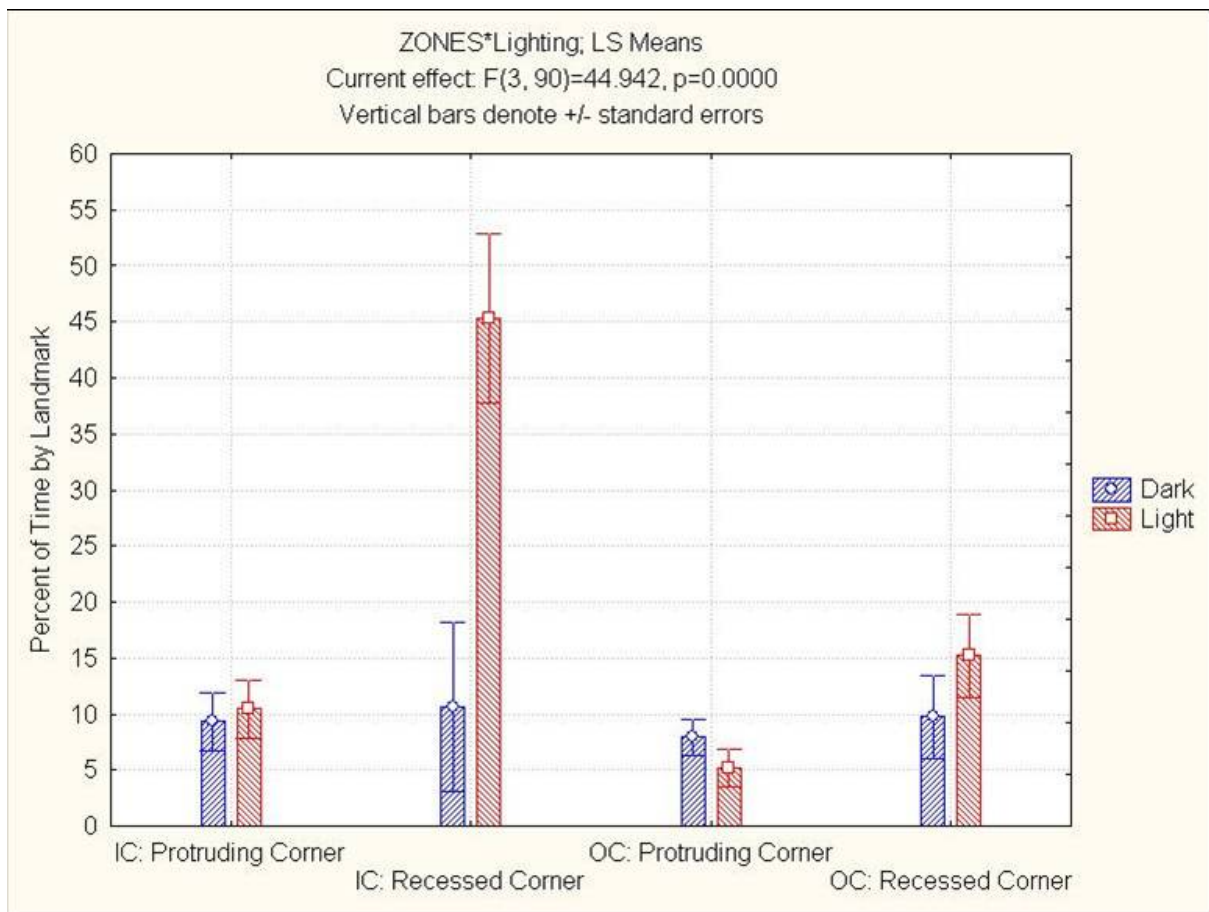


Figure 4.4: Light's effect on percent time by the four kinds of landmarks

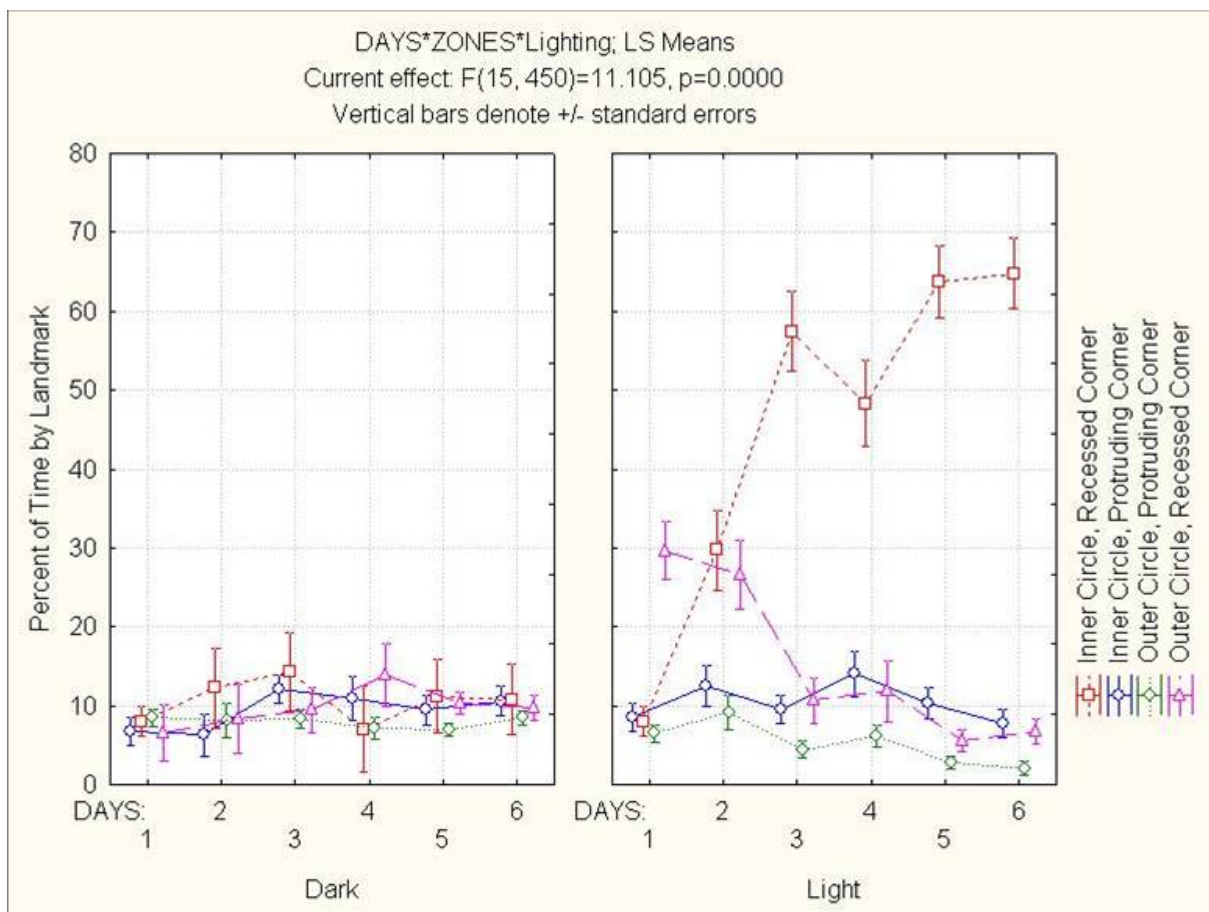


Figure 4.5: Light and Days interaction on percent time by the four kinds of landmarks

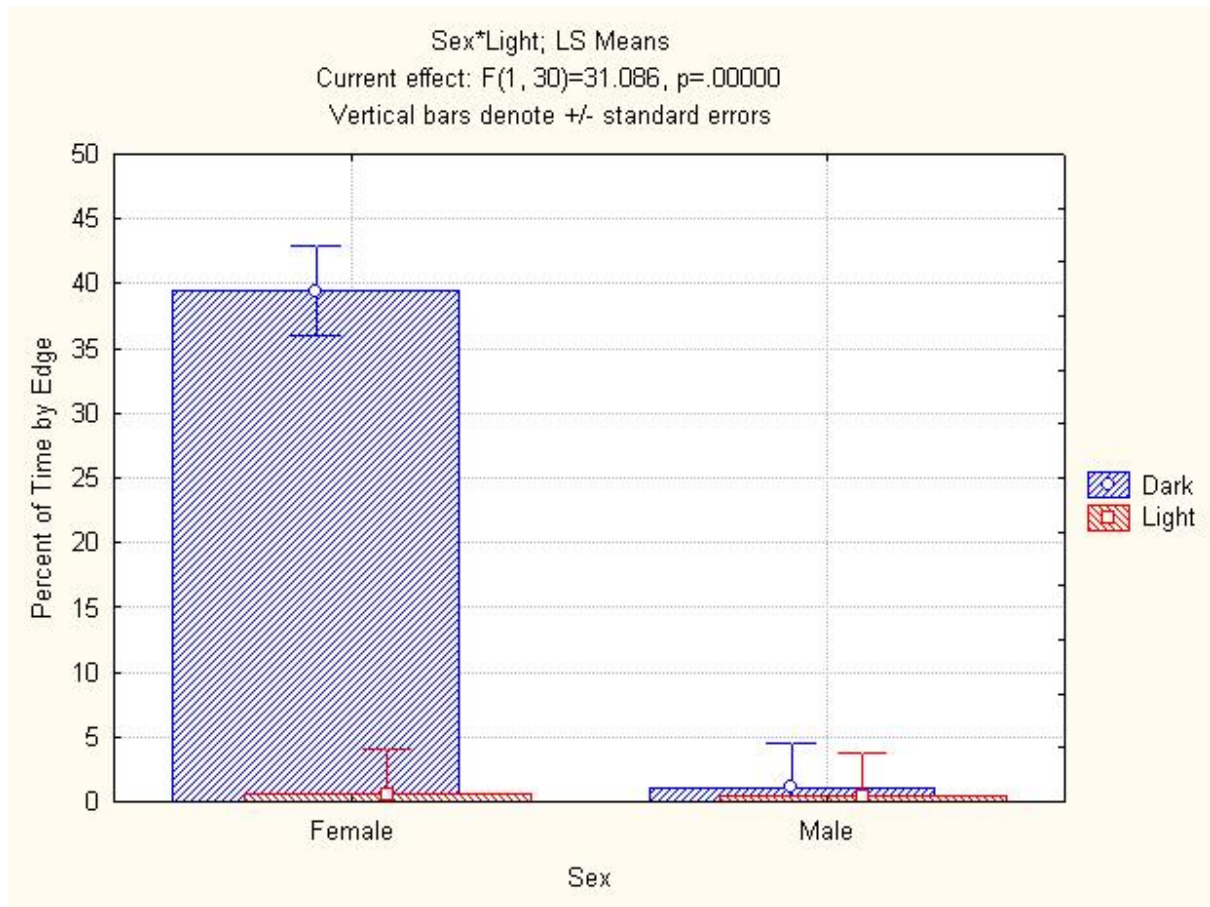


Figure 4.6: Light and Sex interaction on percent time with 4" of the table's edge. This region made up 22.7% of the table's surface area, making all groups except females in the dark below chance.

There was no significant difference between the sexes in the light ( $F(1,15)=.84277$ ,  $p=.37$ ).

*Other Measures:* Females and dark groups covered more ground, and males and dark groups spent more time moving (Table 4.1). The amount of time spent moving (velocity greater than 2cm/s) decreased over days (Figure 4.9). There was a weak interaction in movement between days and lighting ( $F(5,150)=2.0202$ ,  $p=.07894$ ), with light groups decreasing movement faster than dark groups. Males decreased their distance moved over the course of the experiment, while females did not (Figure 4.7) (Days effect for females:  $F(5,70)=1.3984$ ,  $p>.2$ ). This produced an overall significant effect of distance moved decreasing over days (Figure 4.8).

Table 4.1: Experiment 4.1.1 Parameters (Mean±Standard Error)

<b>Sex</b>	Male	Female	F(1,30)	p
I.C.P(%)	58.55±3.55	43.49±3.77	8.46	<b>.00678</b>
Distance Moved(cm)	1898.83±102.45	2243.88±108.66	5.34	<b>.02792</b>
% Time Moving	80.87±2.05	74.91±2.18	3.96	.05566
<b>Lighting</b>	Dark	Light	F(1,30)	p
I.C.P(%)	39.82±3.66	62.22±7.32	18.71	<b>.00016</b>
Distance Moved(cm)	2651.96±105.60	1490.75±105.60	60.46	<b>&lt;.00000</b>
% Time Moving	88.30±2.11	67.48±2.11	48.48	<b>&lt;.00000</b>

## Discussion

The inner circle percentages for all groups were above chance (25%), showing that across all the conditions rats have a preference for the more secure area. The strength of this preference, however, was strongly affected by lighting, the sex of the rat, and how familiar the rat was with the environment. Light groups started out as exploratory as dark groups, but developed more security-oriented behavior as they become more acquainted with the environment. This security seeking became rather extreme in later days, with rats spending 45% of their time by the recessed corners on the inner circle (the area with the most cover). Dark groups, on the other hand, showed a slight preference for secure locations over the entirety of the experiment, indicating that either the rats were not becoming as familiar with the environment as the light groups, or that familiarity had little influence on their movements.

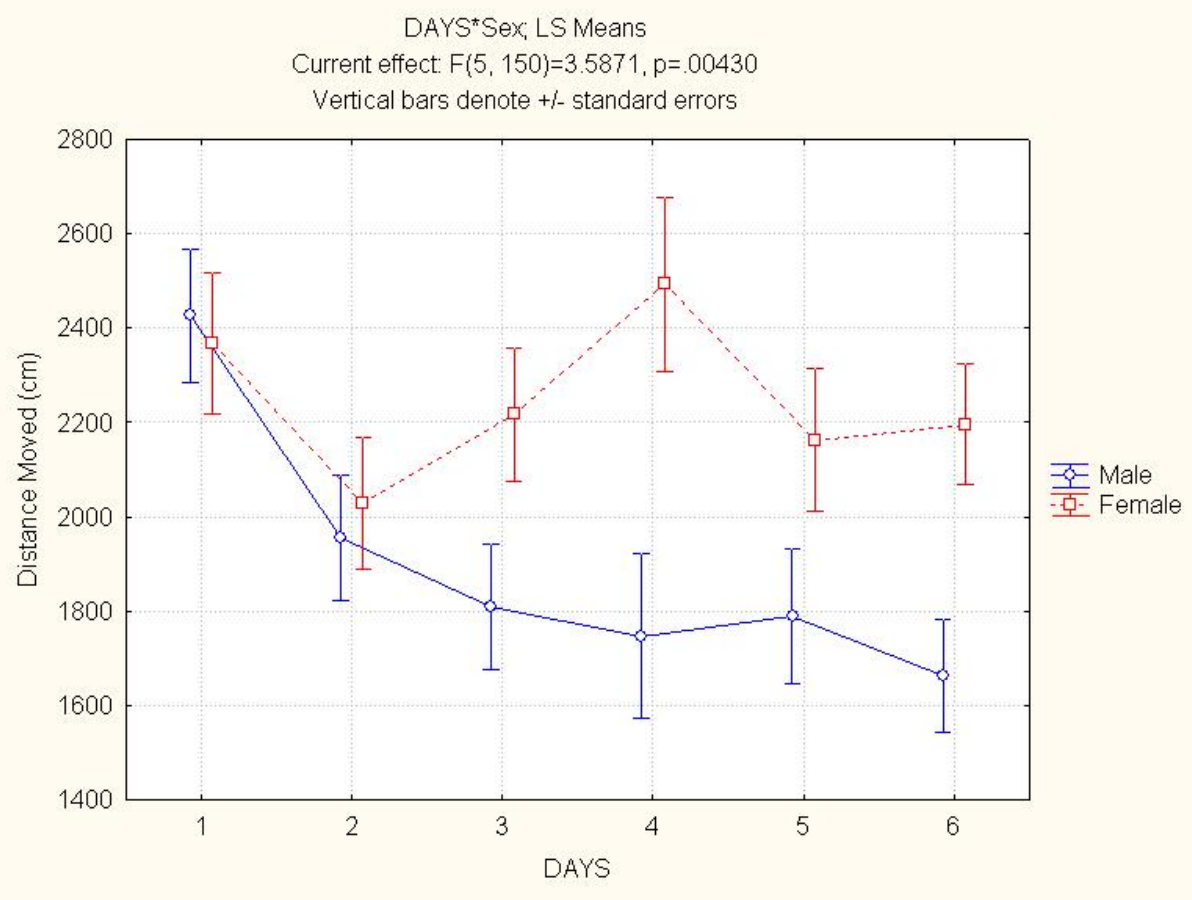


Figure 4.7: Sex and Days interaction in distance moved

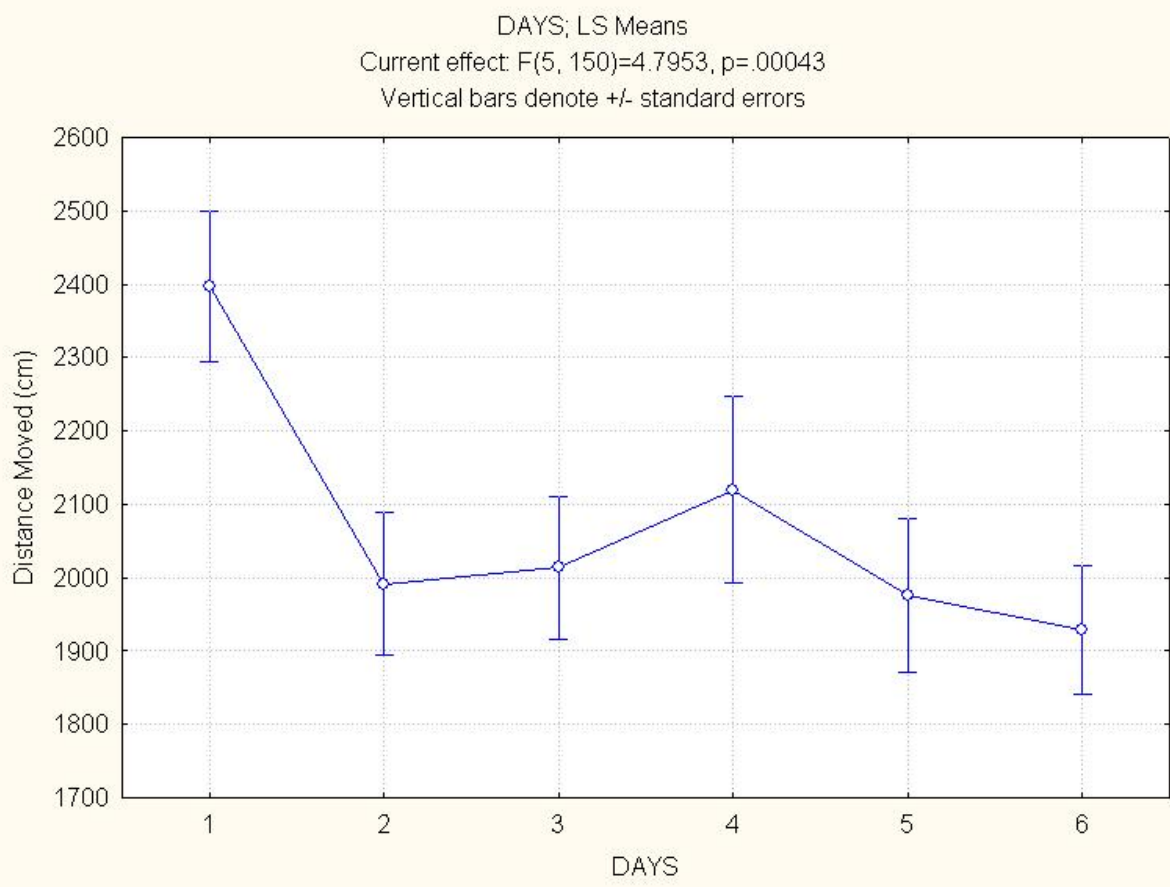


Figure 4.8: Days effect on distance moved



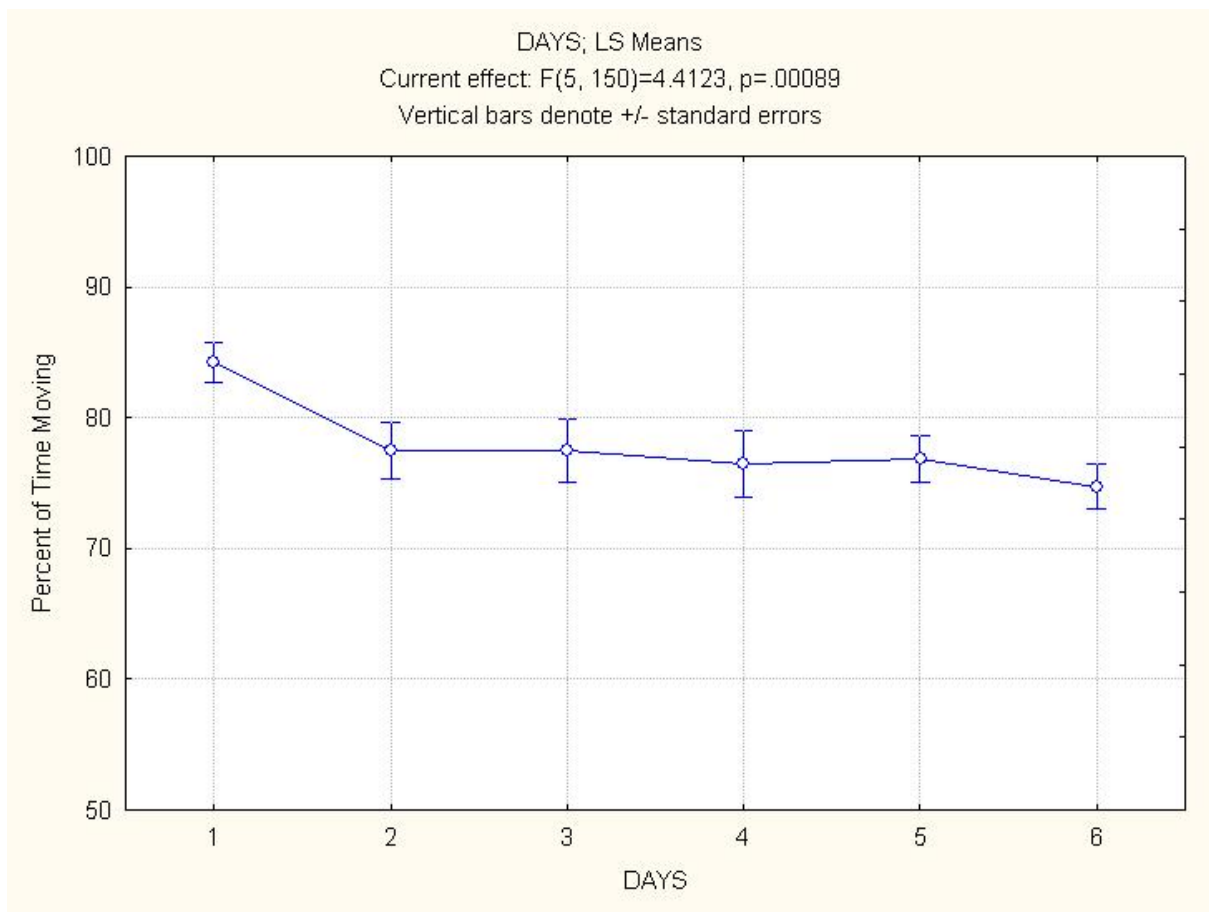


Figure 4.9: Days effect on percent of time moving (velocity greater than 2cm/s)

The fact that dark groups spent more time moving and covered more ground than light groups indicates that the dark groups' lower preference for the secure areas was due to increased exploration. Since the dark groups are unable learn about their environment without moving over it (they cannot see it from a distance, like the light groups), increased exploration would be necessary to have the same understanding of the area. This may also explain the interaction of inner circle percentage with both lighting and days: The light and dark groups are equally familiar with the environment, but the light groups (by virtue of their vision) can identify that the environment is the same as previous days without as much moving around. This leaves the light groups to move to the most secure area, while the dark groups are still confirming that nothing has changed from the previous day.

Males proved to be more security seeking than females in some respects. However, there could be alternative explanations for their behaviors. The males' higher inner circle percentage could be because they preferred the more protected area. But if this were the reason for the higher value, a sex difference in time spent by landmarks would seem appropriate, ideally with the males spending more time by the recessed corners on the inner circle. Given that males covered less ground in general and there were no sex differences by landmarks, it could be that the males stayed in the inner circle simply because it was the release area. The weak interaction of sex and days for the inner circle percentage might show that males became familiar with the release area faster than the females, accounting for their increased preference for the inner circle.<sup>1</sup> This explanation is supported by the males covering less ground over successive days, showing less exploration in general.

Females in the dark showed particularly security averse behavior, spending much of their time in a potentially dangerous area: At the very edge of the table, with their heading hanging off into the darkness. Males in the dark also exhibited this behavior, but not nearly to the same degree. This illustrates two points. First, security seeking is diminished in both sexes in the dark, but most significantly in females. Secondly,

---

<sup>1</sup>For more on how rats become familiar with an area solely by being released there, see Experiment 4.2.1.

the head behavior suggests that the rats were attracted to the table's outer rim perhaps because it provided a continuous edge to stimulate the rats' vibrissae. Such edge oriented behavior under certain conditions (females in the dark) may be evidence for touch driven thigmotaxis, as described in 1.2.4. This provides some background for Experiment 4.2.4, which more closely analyzes wall hugging behavior.

### **4.1.2 Forest**

This experiment continued the investigation of lighting's effect on security seeking behavior, this time in the floor arena. The PVC pipe forest was used to provide a relatively more protected area of the arena.

#### **Procedure**

Three groups of females (all  $n=8$ ) were run in the floor arena with a forest present. Two of the groups were run in the light for 3 days. The forest was in the south half of the arena for one group, and the north for the other (Light North and Light South). The remaining group was run in the dark for 6 days, with the forest in the south half of the arena throughout (Dark). For all trials the rats were released in the center.

#### **Results and Discussion**

*Forest Percentage:* Both Light groups quickly grew a preference for their respective forested halves (Figure 4.10). There was no difference between the two Light groups in the percentage of time spent in the forested half ( $F(1,16)=.9333$ ,  $p=.348374$ ). The Dark group, even when given twice as long to show a preference, spent equal time on both halves of the arena (Figure 4.11). As such, there was an interaction between the Light and Dark groups both when the Light groups were combined and left separated (Figure 4.12).

These results show that while the forest was an attractor to rats in the light, it had no attractive effect in the dark. This experiment, then, replicated the findings of Experiment 4.1.1, showing that rats pay more attention to security maximization when

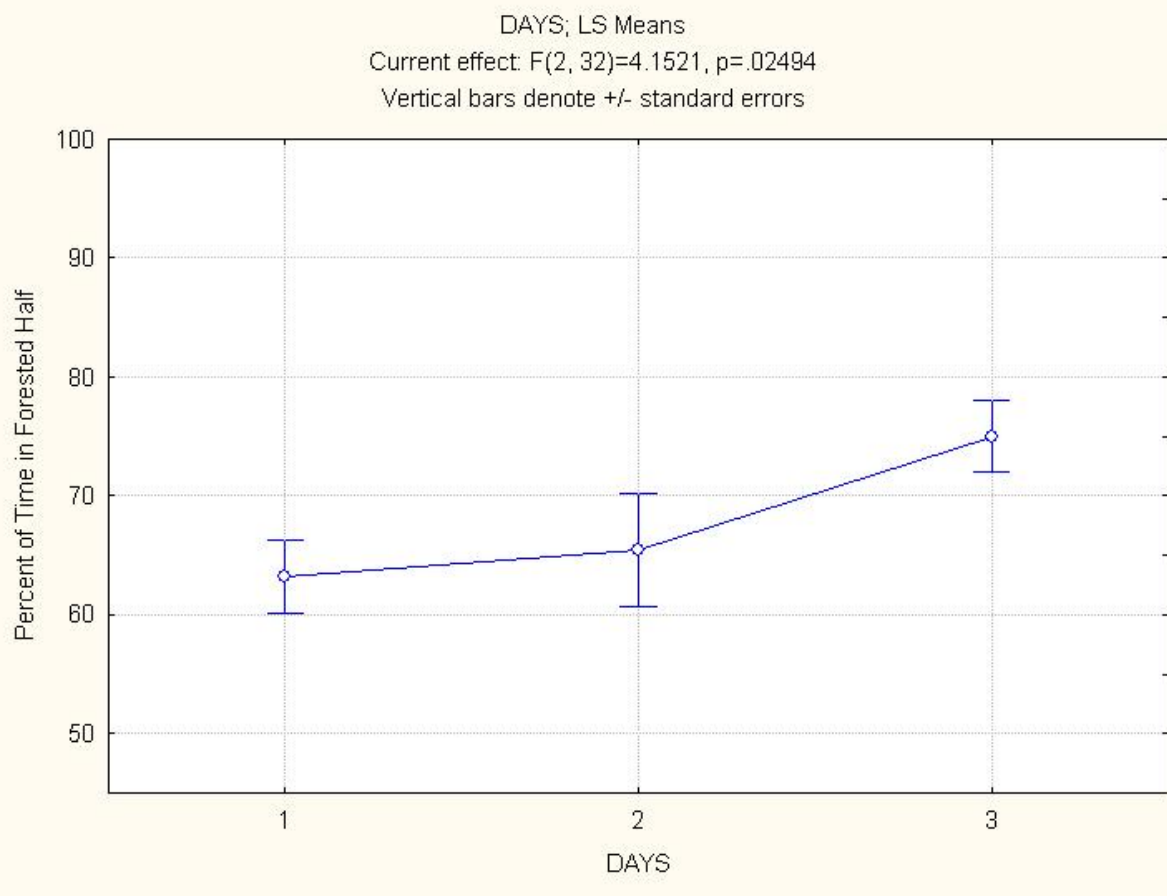


Figure 4.10: Days effect on Forest Half Percentage in the Light Groups

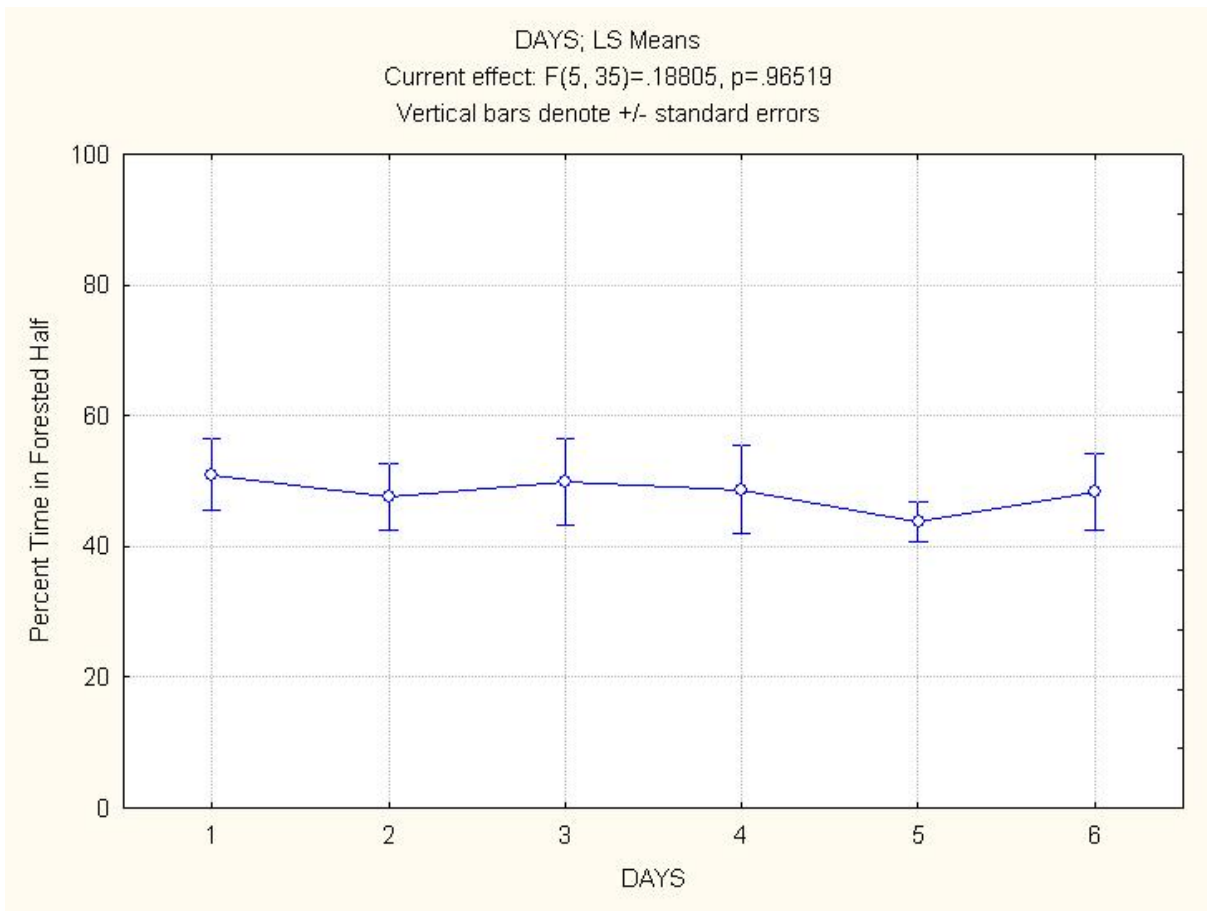


Figure 4.11: Days effect on Forest Half Percentage in the Dark Group

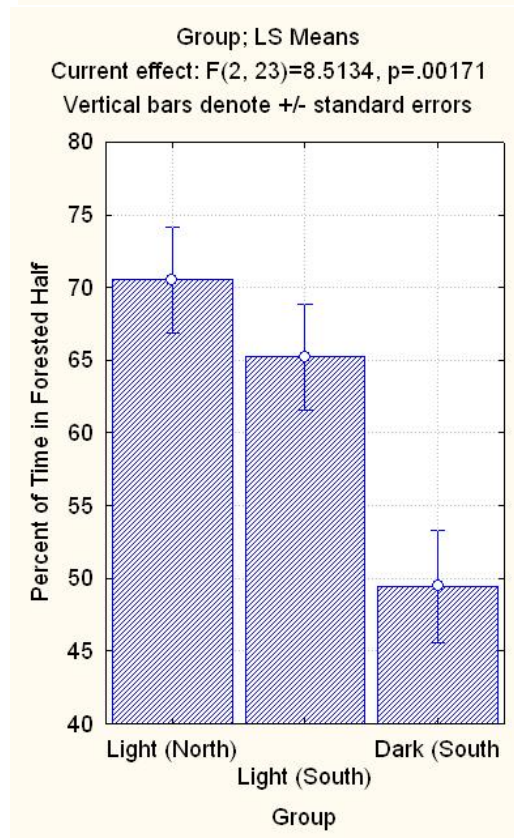
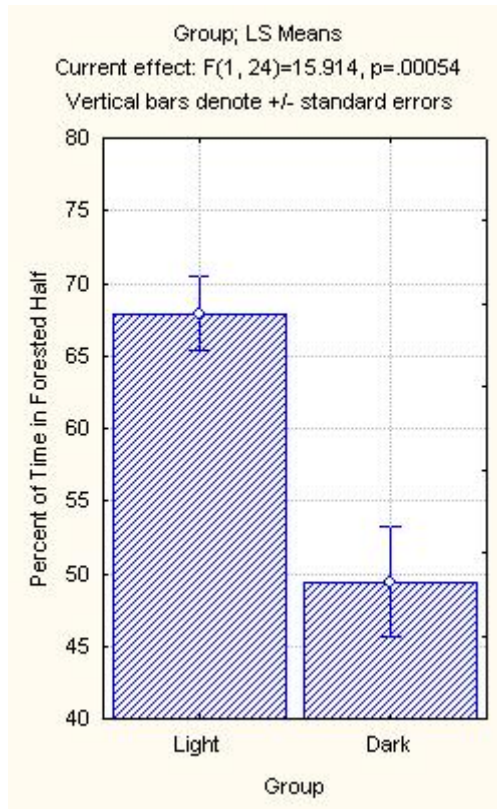


Figure 4.12: The amount of time spent in the forest by the Dark group was significantly different from the Light groups lumped together (top) and separately (bottom).

in the light than in the dark. An alternative explanation would be that rats pay just as much attention to their security in the dark, but they are less able to identify secure locations without the use of vision. While this is a possibility, there are a few facts that suggest otherwise.

First, all rats, regardless of lighting, interacted with the forest. In all 48 trials of the Dark group rats, there was only one in which a rat did not touch a PVC pipe. In the 47 trials where the rat did touch a PVC pipe, the rat frequently, though not always, stopped and examined the pipe. This indicates that the Dark group rats knew of the pipes, though they may have had a less precise understanding of their locations. Secondly, pipes were only 12" tall, just barely taller than the rats could reach while rearing. In the light, the rats could easily see the upper limits of the pipes, identifying just how tall and protective they were (not very). In the dark, however, the rats could not identify how tall the pipes were, making them any possible height, and so potentially good cover.

So, not only were the Dark group rats aware of the forest, but its perceived usefulness as cover could have been greater than that of the Light groups. These facts, along with the results from Experiment 4.1.1, show that decreasing lighting simultaneously decreases security seeking in rats.

## **4.2 Familiarity**

### **4.2.1 Halves**

In this experiment, the effect of the rats' familiarity with an area on its usability as a home base was tested. Rats were first made familiar with an area by repeatedly releasing them there, then were released at a distant location.

#### **Procedure**

Two groups of females (both  $n=8$ ) were run in the floor arena in the dark for 10 days. One group was released in the center of the south wall for 6 days, then in the center of the north wall for the remaining 4 days (South-North). The other group was the opposite,

with a release in the center of the north wall for 6 days, then in the center of south wall for the last 4 (North-South).

## Results and Discussion

*Starting Half Percentage:* Over the first 6 days both groups greatly increased the percentage of time spent in the release half (Figure 4.13). There was no group effect ( $F(1,14)=.3641$ ,  $p>.5$ ), but there was an indication of an interaction of days and group (Figure 4.14). On day 7, the release half preference disappeared, then started to grow again, more slowly than in first portion of the experiment (Figure 4.15). There were no group effects across all 10 days (Groups: $F(1,14)=.1270$ ,  $p>.7$ ), nor effects of group or days in the last four days (Groups:  $F(1,14)=.0030$ ,  $p>.9$  Days:  $F(3,42)=1.5743$ ,  $p>.2$ ).

At first, the rats were exploratory, spending roughly equal time in both halves of the arena. As a consequence of starting in one half of the environment, however, the rats became more familiar with that half than the other, which became apparent when the release point was changed. The evidence from this experiment indicates that this familiarity made the release half attractive for home bases, and thus the rats spent more time there later on. As the rats spent more time in the starting half, they became even more familiar with it over the other half, seemingly creating a snowball effect of preferring familiar regions, then becoming more familiar with those same regions, and so preferring them more. This effect had an asymptote at an almost 80/20 split between the release half and opposite half.

When the rats started on a new side, they "reset" to more exploratory locomotion, spending equal time in both halves. There are a few possible explanations for this. Changing the starting position could have caused the rats to not self-localize correctly when entering the environment, meaning they would not have recognized where they were. This could have affected their ability to recognize the arena at any point in the environment, meaning the rats had to relearn all the local views of the environment as though it were day one. However, this would not account for the difference between days 1-6 and 7-10 in how quickly the rats developed a preference for their release half.



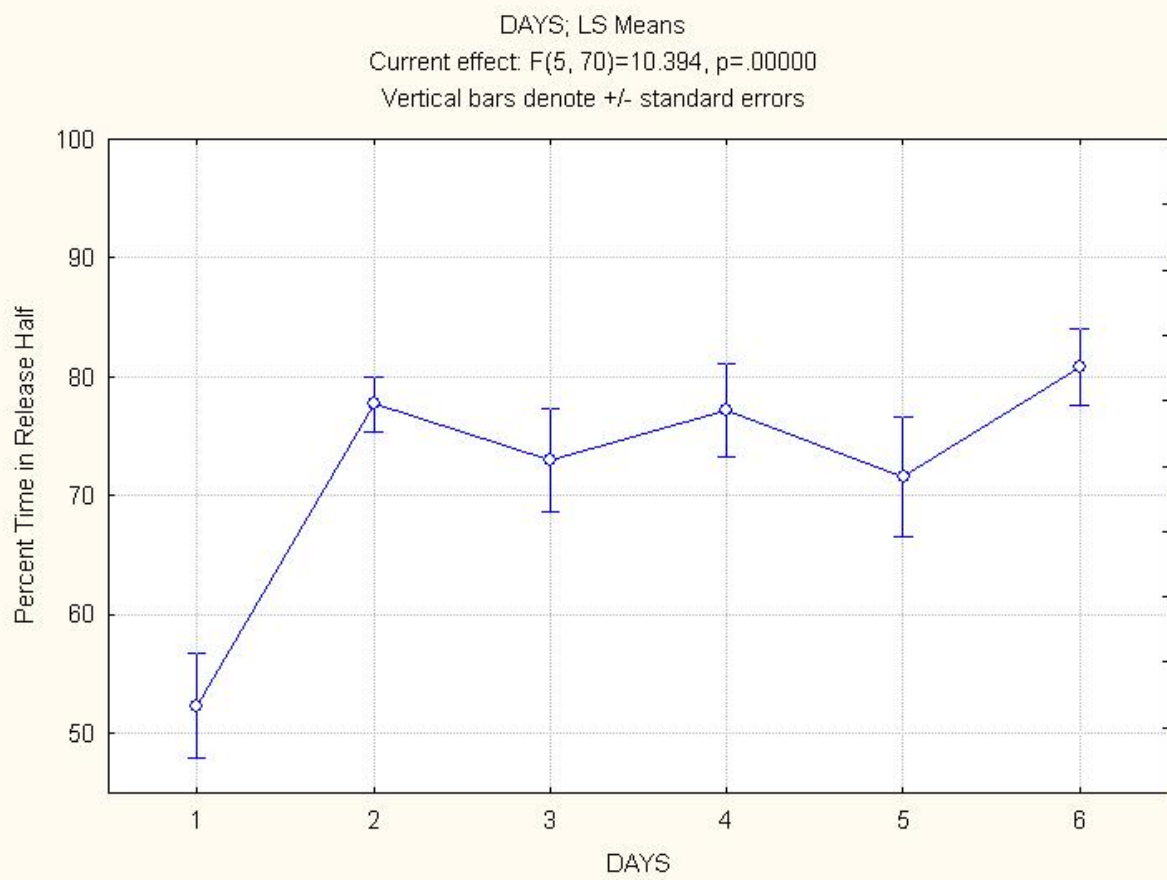


Figure 4.13: Days effect on percent time in release half for both groups

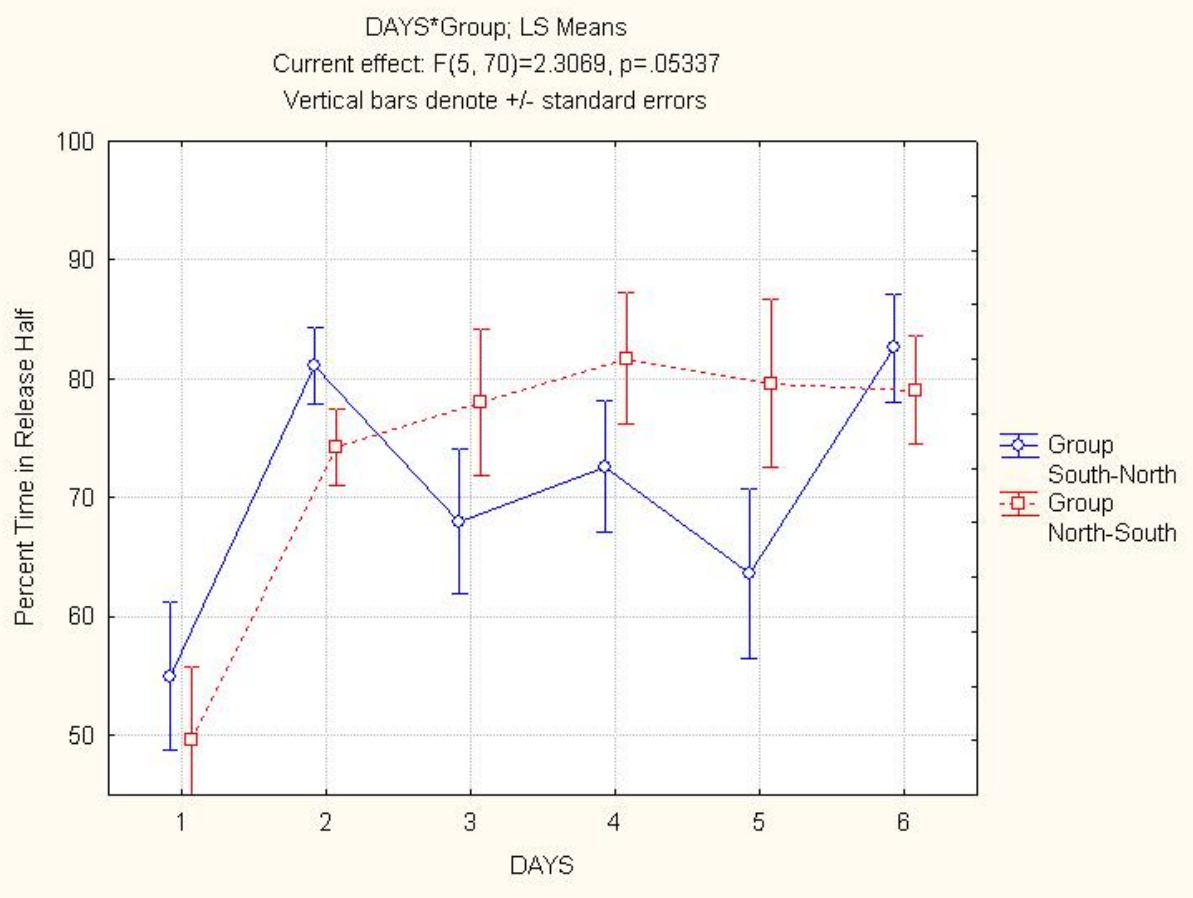


Figure 4.14: Days by Group effect on percent time in release half

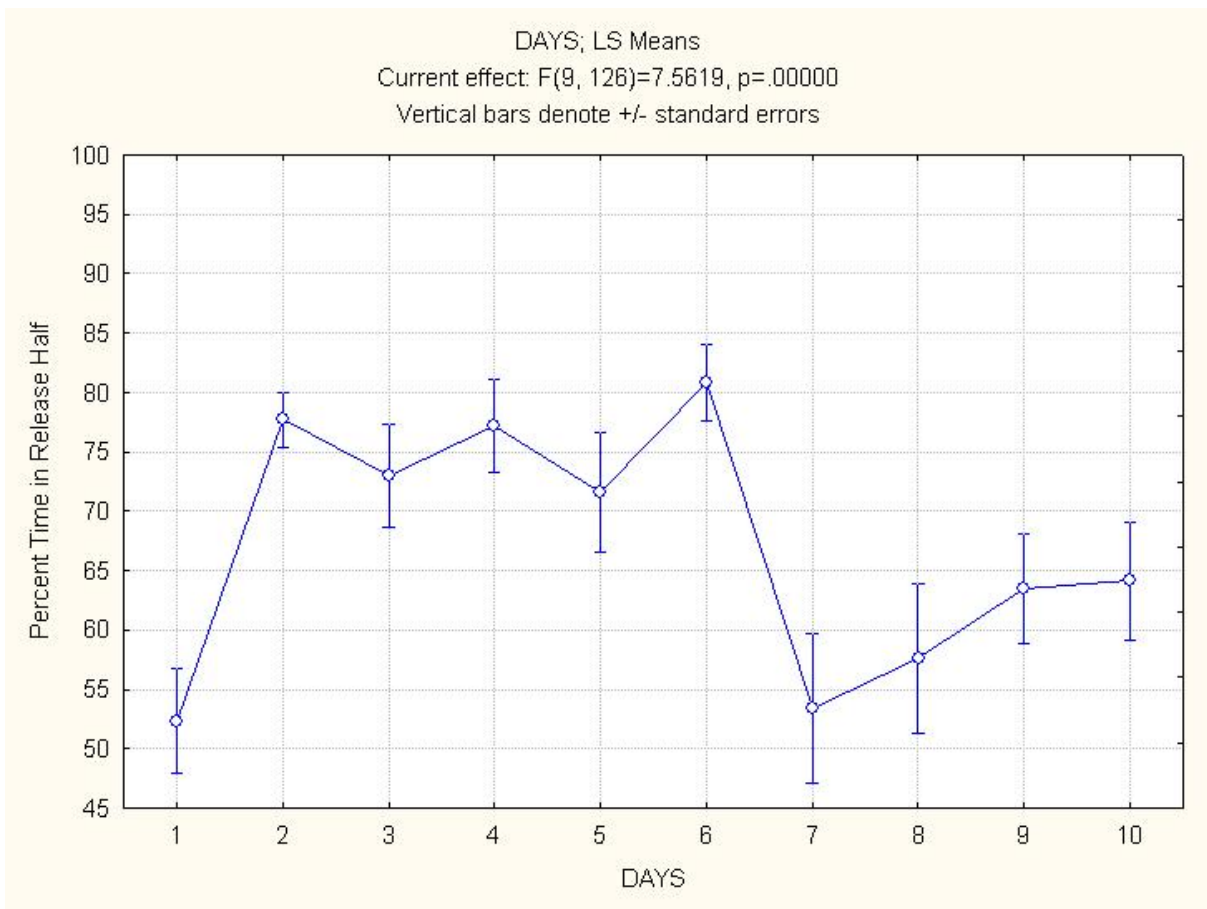


Figure 4.15: Days effect on percent time in release half for both groups. On day 7 both groups moved in starting position to the opposite half of the arena.

Alternatively, the rats recognized the arena as the same from previous days, and as such tried to move to the preferred half (the old release half). However, without being released in that half, the rats lacked path integration data to get back there, and so spent longer than normal in the new release half, initially using the new release half as a path integration reference, then switching to the old. As the rats continued to be released in the new half, the same phenomenon of becoming more familiar with the release point occurred, and so the rats developed a preference for the new release half. This preference grew more slowly than in days 1-6 because the old release half was still a draw for the rats, as it was also familiar. It would take more than just two days for the rats to become much more familiar with the new release half than the old. This explanation accounts for the different half preference acquisition rates between days 1-6 and 7-10.

The weak days by group interaction in the first 6 days, showing a slightly stronger release half preference in Group North-South, may indicate that the north half of the room was slightly preferable to the south half. The slightly higher forest half percentages from the Light North group in Experiment 4.1.2 also point towards a slight inequality between the halves of the room. This small skew towards the north half of the room does not question any of the results. Rather, this is an indication of the slight variation across the room (Due to such factors as air flow, etc.) which possibly aides the rats in differentiating the areas of the environment.

## **4.2.2 Forest**

While previous experiments show a main effect of dark vs. light in time by a secure location, there is still the possibility that security, lighting, and familiarity could interact. In this experiment, the same rats from experiment 4.1.2 were run for several more days, this time with a slightly different environment from before.

### **Procedure**

The same rats from experiment 4.1.2 were run for several additional days under slightly altered conditions. Recall that there were two light groups (Light North and South),

that were run for 3 days in the floor arena with the forest. These groups were run for an additional 3 days, with the forest moving to the opposite half. The result was two light groups run for 6 days with the forest on one side of the arena for 3 days, then on the other side for the remaining three. In one of these groups, the forest moved from north to south, and the other from south to north (North-South and South-North).

The dark group rats from experiment 4.1.2 were also run for an additional 4 days, with the forest now on the north half of the arena. This created a dark group run for 10 days, with the forest in the south for the first 6 days, and in the north for the remaining 4.

## Results and Discussion

*Forest Percentage:* Across all 6 days, the Light groups showed behavior similar to the rats of Experiment 4.2.1, quickly showing a preference for one side, then "resetting" this preference when the position of the forest changed (Figure 4.16). Within the Light groups there were no group effects across all 6 days ( $F(1,16)=.100$ ,  $p>.75$ ) or the last 3 days ( $F(1,16)=.1601$ ,  $p>.6$ ). Looking at the last 3 days alone, the increase in forest half percentage across days was significant ( $F(2,32)=3.4037$ ,  $p=.045685$ ).

Again, the first three days of the Light groups showed a preference for the forested halves. The increase in this preference over the first three days, and a resetting on day 4 similar to the rats of Experiment 4.2.1, indicates that they had grown a familiarity with the old forested half. On day 4, the attraction of the security of the forest and the familiarity of the old forested half balanced out, resulting in a 50/50 split between the halves. As the rats spent more time in the new forested half (which they were attracted to for its security), they became familiar with it, eventually negating the familiarity effect of the old forested half.

The fact that the forest percentage hung at 50% on both day 4 and 5 (as opposed to just the first day after the manipulation, as seen in Experiment 4.2.1) before increasing may be because both halves were significantly altered by the change of the forest's position. As such, the rats' remembered local views of both halves became partially in-

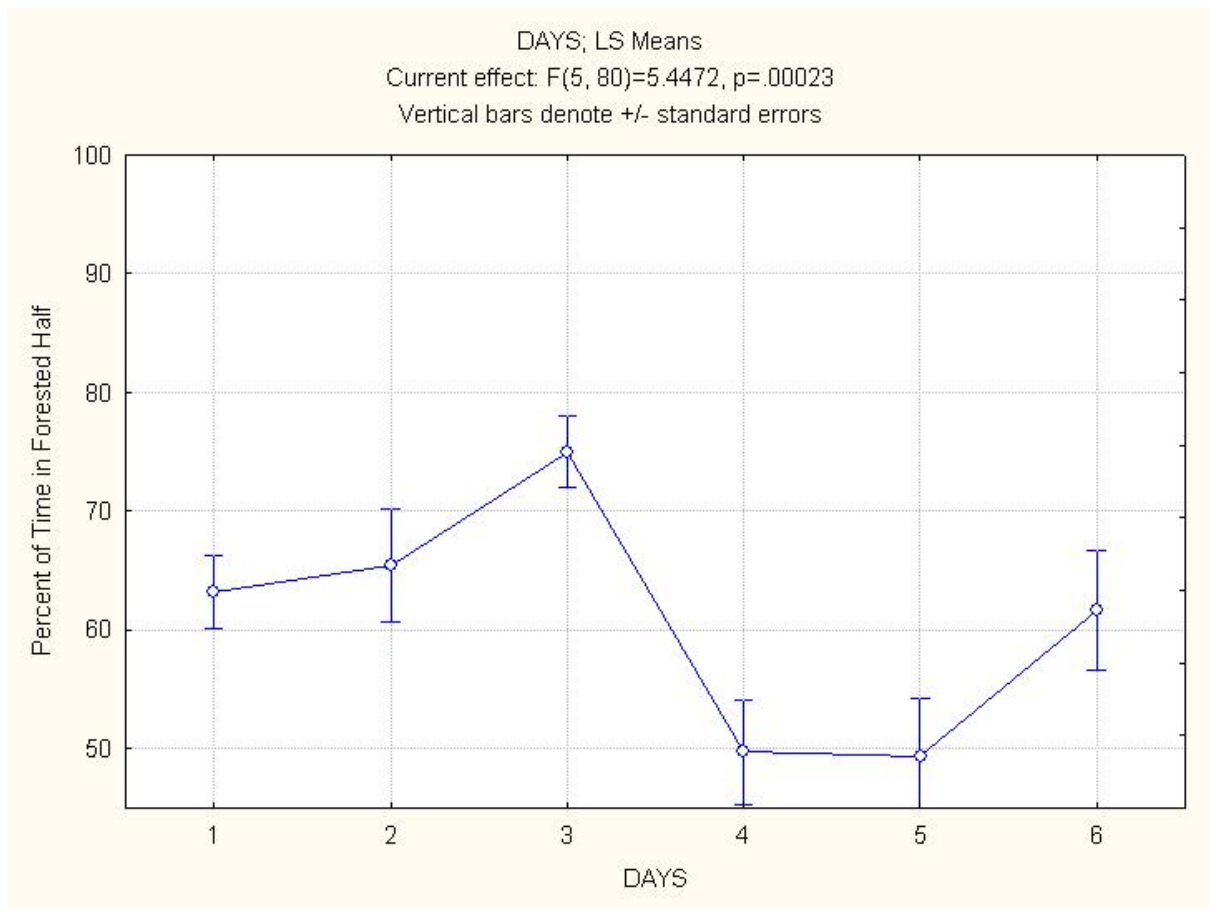


Figure 4.16: Days effect on Forest Half Percentage in both Light groups. On day 4 the forest moved to the opposite half of the arena.

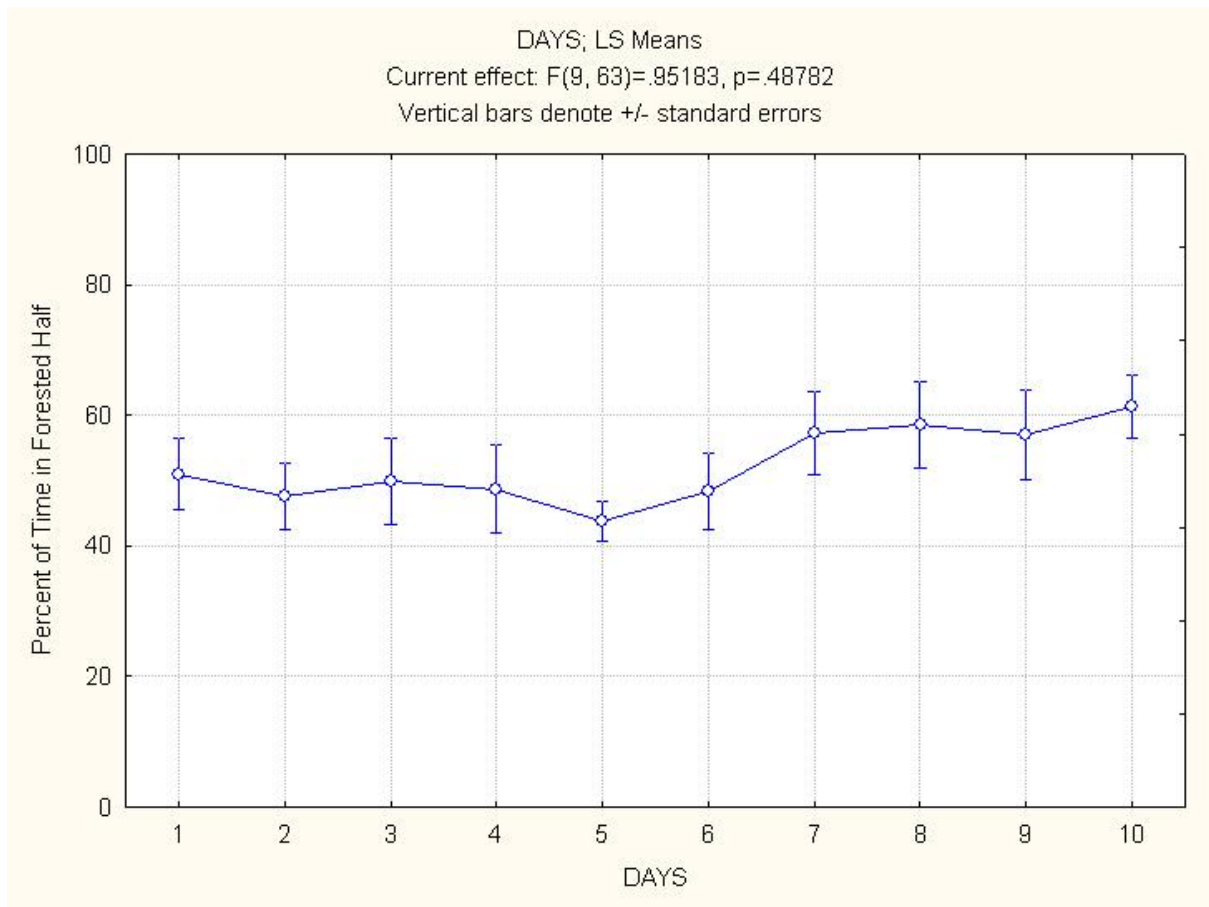


Figure 4.17: Days effect on Forest Half Percentage in the Dark group. On day 7 the forest moved to the opposite half of the arena.

accurate. For the old forested half, these local views were well-remembered, and so even after a significant change in the environment were still useful for recognizing the area. For the new forested half (previously the unforested half), less time had been spent there, so the local views were not well-remembered. As such, when the environment changed significantly by gaining the forest, the weakly remembered local views of the area were useless for navigating. As such, the rats had to learn the new forested half from scratch, taking longer to gain time from the familiar old forest half. Why the more familiar half would have equal draw to the "novel" forested half for multiple days is unclear.

In the Dark group, there was still no preference for either the forested or unforested half of the arena (Figure 4.17), nor showed any reaction to the forest moving. In the last 4 days, while the forest was in the north half of the arena, the average forest percentage went up sharply, but was too variable between individuals to be significant. This is another bit of evidence, just outside of significance, that the north half of the arena may have been slightly preferable.

### **4.2.3 Halves and Forest**

While experiment 4.2.1 showed rats have a preference for their starting half, and experiment 4.2.2 indicated that rats ignore the forest in the dark, they did not test for a possible interaction of starting location and security in the dark. This experiment tested if a moving forest, while not significantly attractive to rats in the dark, could cause some perturbation in starting half preference.

#### **Procedure**

Two groups of females (both  $n=8$ ) were run in the floor arena in the dark with a forest for 10 days. One group was released in the center of the south wall for all 10 days (South), and the other was released in the center of the north wall for all 10 days (North). For both groups the forest was in the south half of the arena for the first 6 days, then in the north half for the remaining 4 days.



## Results and Discussion

*Starting Half Percentage:* There was no significant difference between the groups ( $F(1,14)=.6600$ ,  $p>.4$ ), with both groups showing a preference for their respective release halves in a few days, ignoring the forest (Figure 4.18). Day 8 may seem out of place, but there was no effect of days in the last 4 days, after the forest moved ( $F(3, 42)=.7644$ ,  $p>.5$ ).

As further evidence that the forest was ignored by both groups in selecting home bases, the first 6 days of this experiment show no difference from the first 6 days of Experiment 4.2.1 in this measure, which had no forest at all. <sup>2</sup> Between all four groups, there was no group effect ( $F(3,28)=.287$ ,  $p>.8$ ), nor interaction between days and groups ( $F(15,140)=1.619$ ,  $p>.075$ ).

These results reiterate the findings of Experiments 4.2.1 and 4.2.2: Rats will choose a more familiar location over a less familiar one, and they will not pay attention to the forest (and potentially other cover) in the dark.

### 4.2.4 Two Walls

Rats' different familiarity with various areas in the environment has proven to be a key component in establishing a home base (Experiments 4.2.1 and 4.2.2). Additionally, rats will spend much of their time by the walls in an enclosed arena, as well as the edges of a table. This experiment attempted to identify if rats are attracted to walls because they are an edge, because they are the boundary of the environment, because they are protective, or for some other reason. This was done by providing two disconnected, continuous walls, both of which were an edge, one of which was potentially more protective and the outer boundary of the environment. Additionally, this experiment tested if rats would differentially familiarize with walls like they do halves of the environment.

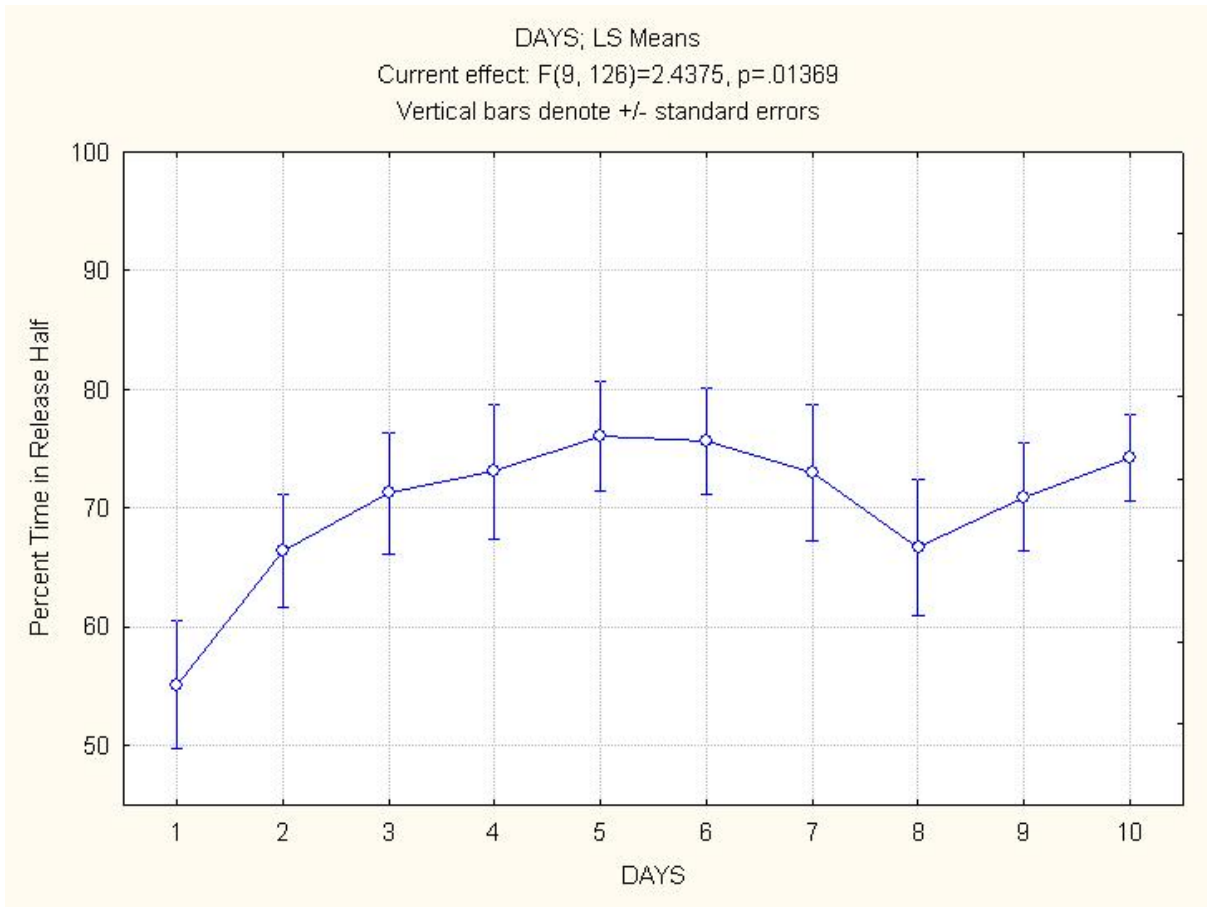


Figure 4.18: Days effect on percent time in release half for both groups. On day 7 the forest moved to the opposite half.

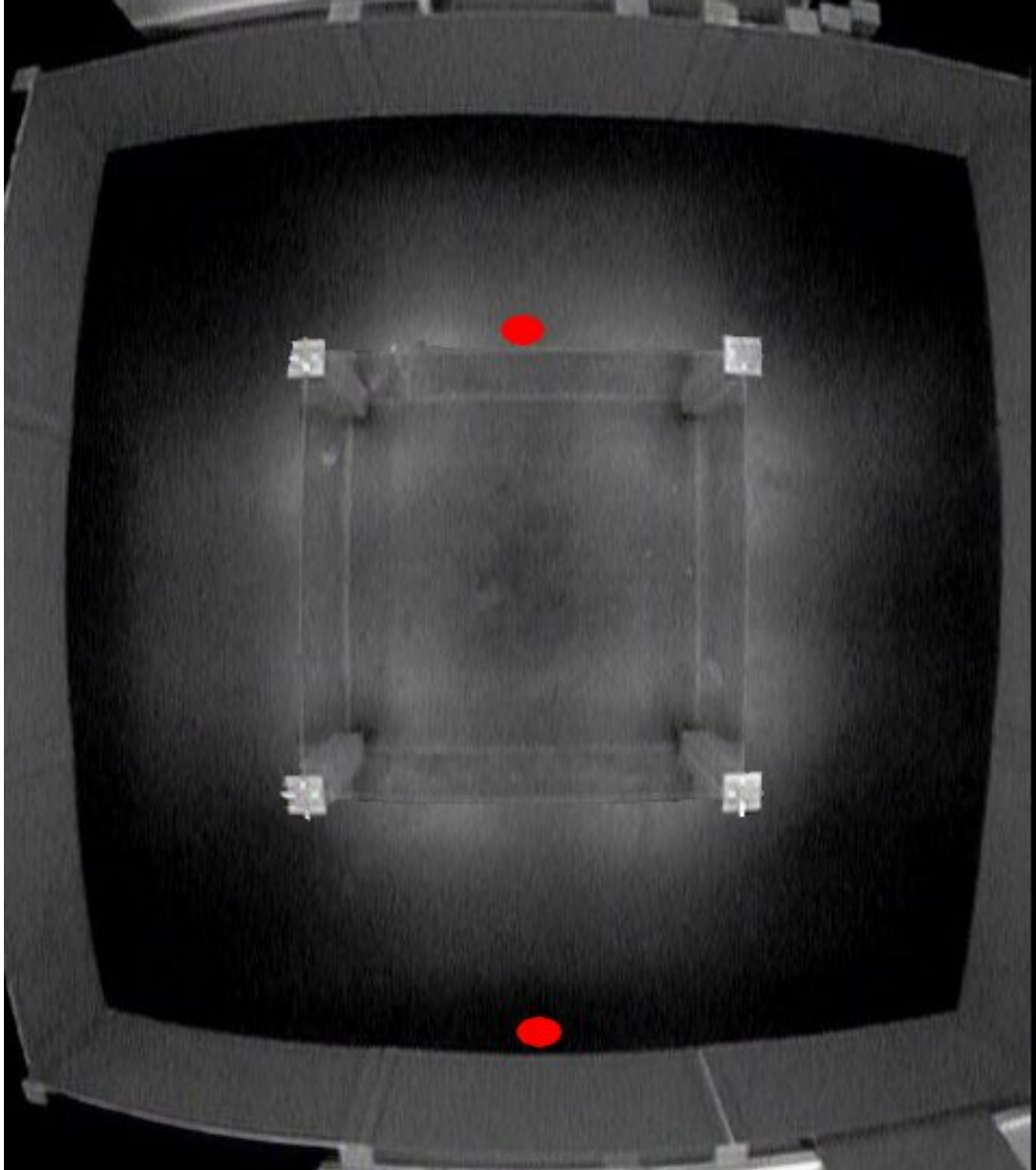


Figure 4.19: The floor arena with an inner plexiglass wall. The release points by the inner and outer walls are marked as red circles.

## Procedure

Two groups of females (both  $n=8$ ) were run in a modified version of the floor arena in the dark for 10 days. This arena featured an additional set of walls in its center (Figure 4.19), one third the perimeter of the outer wall. This inner wall was made of plexiglass, so that the camera could see the rat even if it was up against the wall. This additional wall created a ring arena with two separate, continuous walls. One group of rats was released by the outer wall for 6 days, then by the inner wall for 4 days (Outer-Inner). The other group was reversed, with a release by the inner wall for 6 days, and the outer wall for 4 (Inner-Outer). The central measure examined in this experiment was the percentage of the rats' time spent by each wall (within 8").

## Results and Discussion

*Wall Percentage:* In the first 6 days, the Outer-Inner group showed a strong preference for its starting wall, while the Inner-Outer group was more ambivalent (Figure 4.20). In the last 4 days both groups altered their behavior slightly, spending more time on their new starting wall, but the same overall group differences remained (Figure 4.22). There was a days by group effect in this first portion of the experiment, which shows the Inner-Outer group starting to spend more time by its starting wall (Figure 4.21). Days had only a weak interaction with wall percentages in the last 4 days ( $F(3,42)=2.571, p>.066$ ). Over all 10 days, both groups remained distinct in their time spent by both walls (Figure 4.23).

Unlike the halves of the floor arena or the circles of the table, the two walls of this open field created two discontinuous regions separated by an open area just over 3' across. Had each wall been attractive solely by virtue of being the rats' release point, both groups should have shown equal preference for their respective starting wall. However, the difference in starting wall preference between the groups shows that the outer wall was attractive to all of the rats, regardless of whether it was the starting wall or not.

Why was the outer wall attractive? The outer wall could have been preferred simply

---

<sup>2</sup>Only the first 6 days of each experiment were used because on day 7 the rats of Experiment 4.2.1 changed starting location, which had a significant effect on behavior.

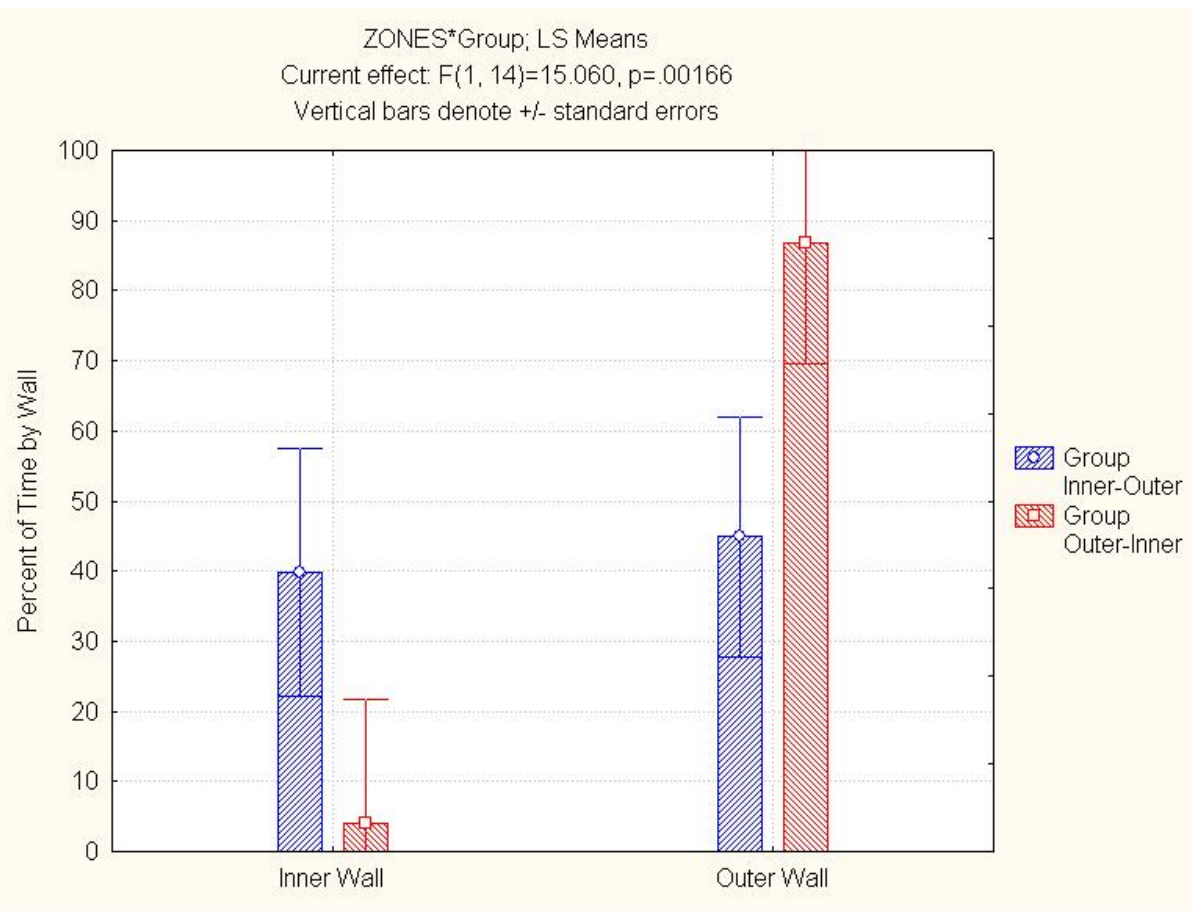


Figure 4.20: Wall preference in the first 6 days

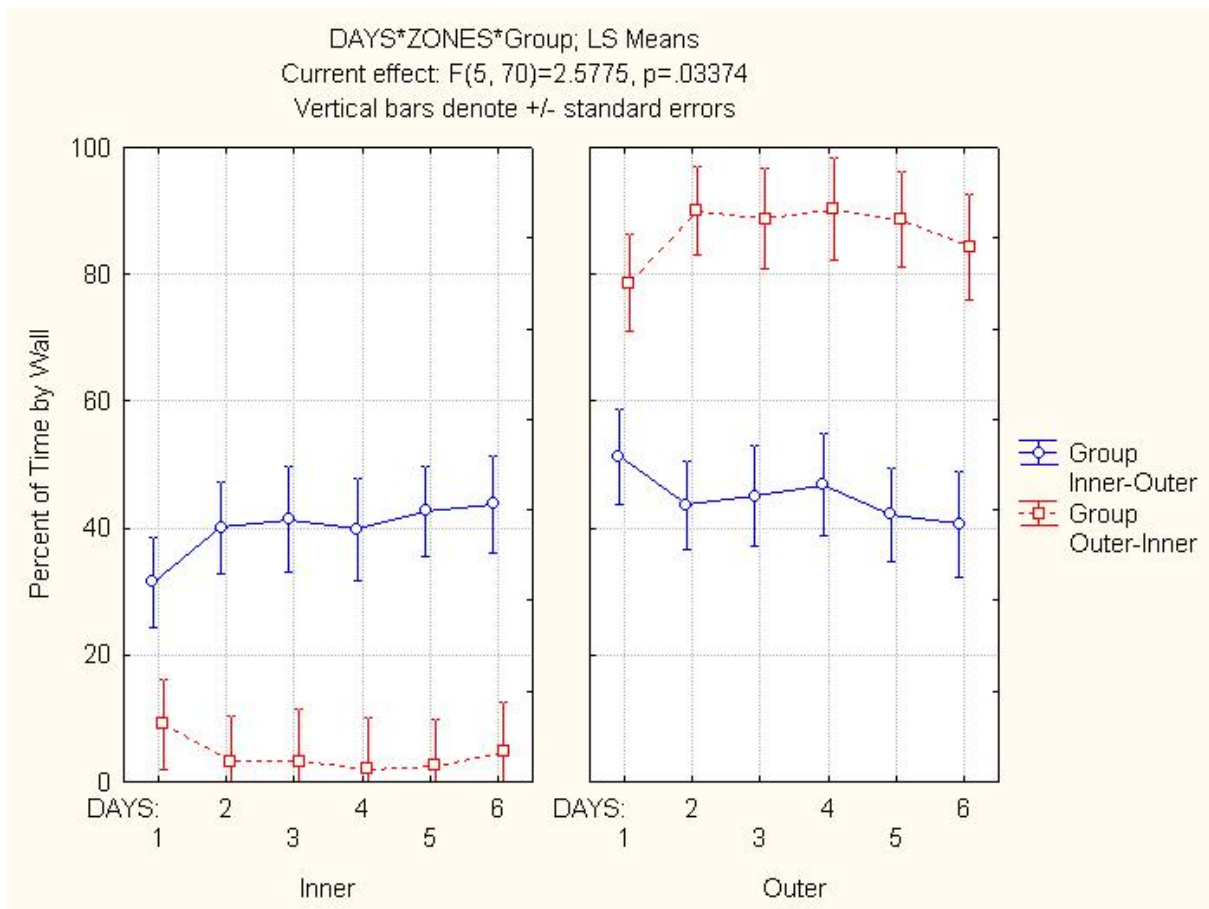


Figure 4.21: Wall preference across the first 6 days

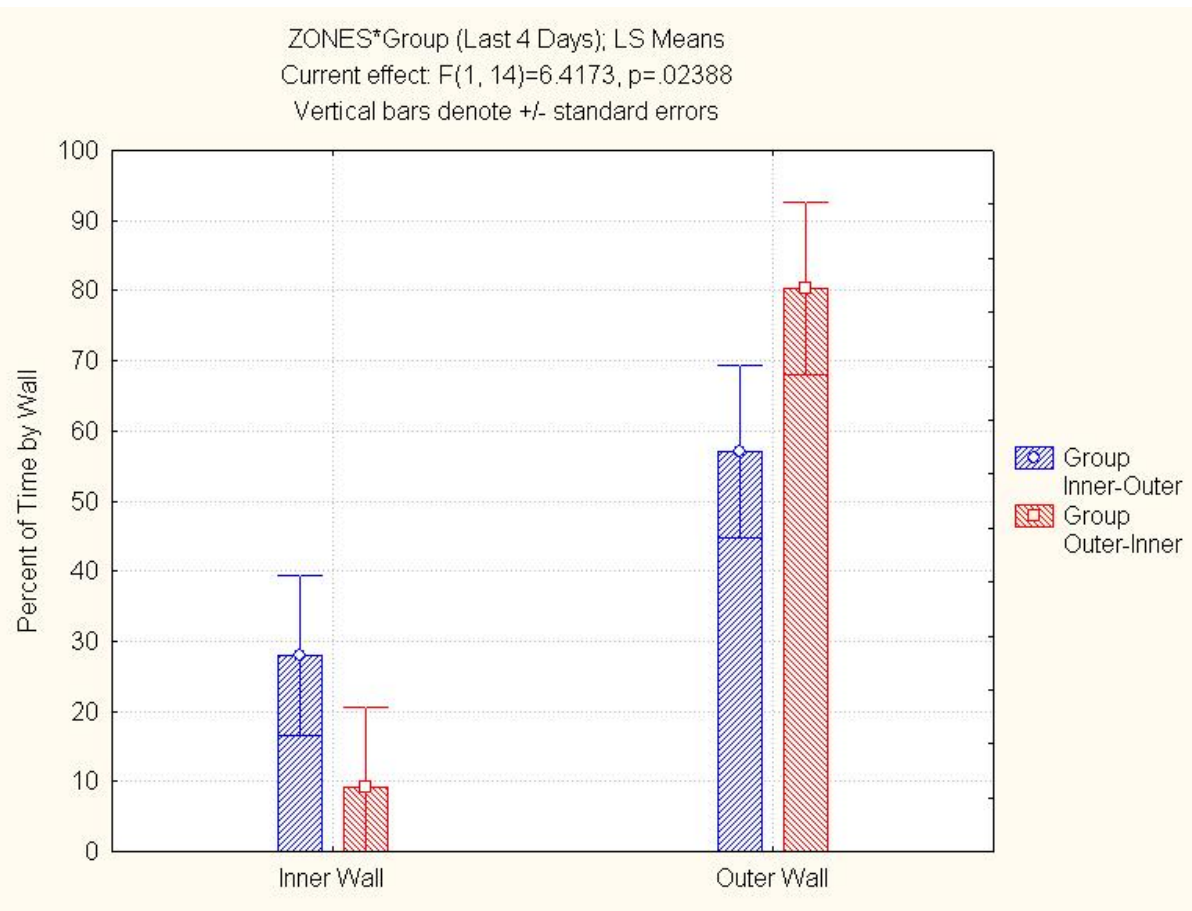


Figure 4.22: Wall preference in the last 4 days

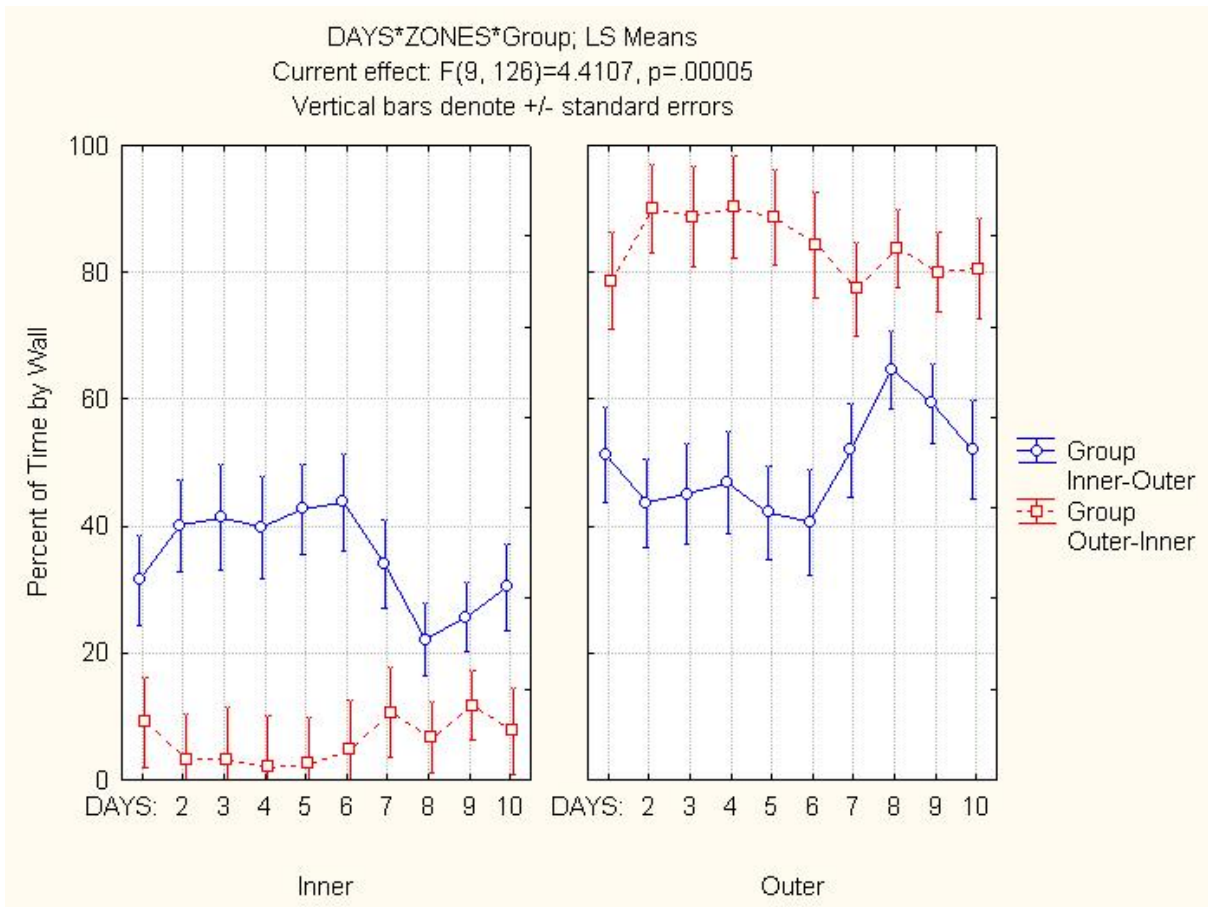


Figure 4.23: Wall preference across all 10 days



because there was more of it. However, even if the outer wall percentage is weighted downward, to account for its higher area, the Outer-Inner group still has a significantly higher outer wall percentages in the first 6 days ( $F(1,14)=17.8908$ ,  $p<.001$ ), the last 4 days ( $F(1,14)=7.2577$ ,  $p<.02$ ), and across all 10 days ( $F(1,14)=14.892$ ,  $p<.002$ ). It could be more secure, as it contained four recessed corners, as opposed to the four protruding corners of the inner wall. However, a corner preference was not significantly shown by the female dark group in Experiment 4.1.1 ( $F(1,7)=3.43081$ ,  $p>.1$ ). If the outer wall were protective simply by being a tall object to press against, not only would the inner and outer walls both be attractive (with the inner wall having a proportionately lower percentage only because of its smaller perimeter), but the Dark group in Experiment 4.1.2 would have been attracted to the forest, which had similar properties. If the wall was attractive only because it was an edge to follow along, then the inner wall should have shown a higher percentage in the Outer-Inner group. As it was, the Outer-Inner group's mean inner wall percentage never went above chance (11.25%). One remaining explanation for both groups' attraction to the outer wall is that it was the outer boundary of the environment, and the rats were building up their excess range beside it, as described in section 1.2.4.

There was also a familiarity effect. While both groups were attracted to the outer wall, the Inner-Outer group was also attracted to the inner wall, even after moving to the outer wall in days 7-10. This behavior shows that rats will regulate much of their locomotion near the starting location, which they are the most familiar with. In addition, it shows that rats will follow along a wall if started next to it, even if that wall is not the outermost boundary. The edge following behavior of females in the dark in Experiment 4.1.1 may be the cause for the Inner-Outer group's attraction to the inner wall. Because they started next to the inner wall, they followed along the edge, which made them familiar with the area. Upon leaving the inner wall, the rats found the outer wall attractive both for its edge and because it was the boundary of the environment. The inner wall, however, was still familiar, and so was used as a home base. When the rats switched starting locations, this familiarity effect drew them to their previous starting walls. Because the distance

between the walls was so small (just over 3'), it was easy for the rats to return to their old starting wall to organize their movements around.

## 4.2.5 Table

This experiment tested the limits of familiarity effects, using a procedure very similar to experiment 4.2.1, but in a much smaller area with the two starting locations closer together. This experiment also tested if the results from experiment 4.1.1 were biased toward high inner circle percentages, as all the rats in that experiment started in the middle.

### Procedure

One group of females (n=8) was run on the table for 10 days in the dark. The rats started by the edge of the table for the first 6 days, and in the center the remaining four. The Female Dark group from experiment 4.1.1 was run for an additional 4 days, this time starting from the edge. This created two groups, both running for 6 days in one starting location and 4 in another (Side-Center and Center-Side). For both groups, the switch in starting location involved moving just 33".

### Results and Discussion

*Inner Circle Percentage:* In the first 6 days there was no main effect of group ( $F(1,14)=.84384$ ,  $p>.37$ ), but there was an interaction between group and days (Figure 4.24). While the two groups initially started out apart, tending more towards their starting areas, they moved together over the 6 days. Over the course of the entire 10 days, which includes both groups switching starting locations, there continued to be no main effect of groups ( $F(1,14)=.33032$ ,  $p>.5$ ), and the interaction of days and group became insignificant ( $F(9,126)=1.59459$ ,  $p>.1$ ).

These behaviors provide a contrast to those seen in Experiment 4.2.1, showing that release points' effect on familiarity differences across the environment disappear when the release points are relatively close together. In this case, the release points were not much

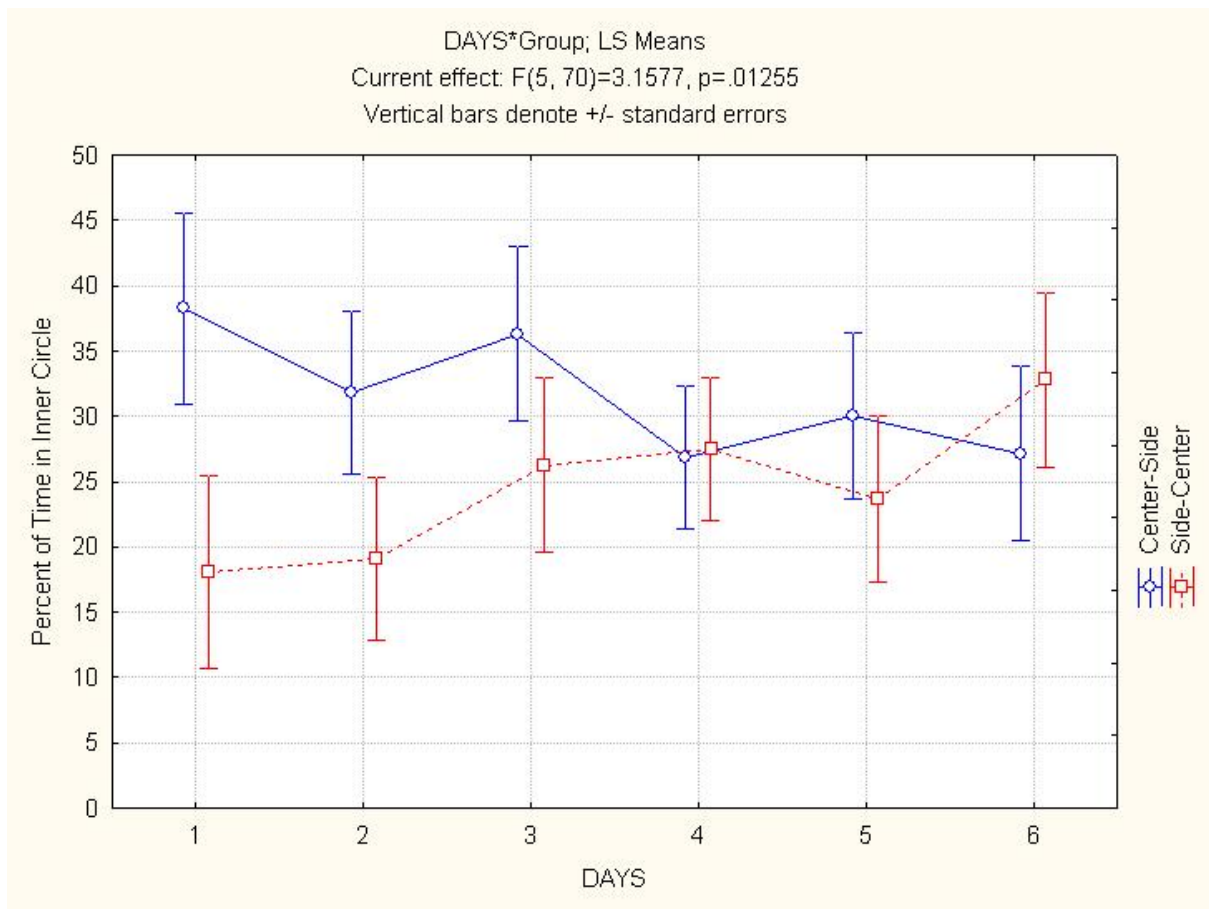


Figure 4.24: The two groups initially preferred their respective starting areas, then grew together over

more than three rat lengths apart, and changing release point had no effect on where the rats went. While the two starting points differentiated the behaviors of rats on the first few days, once the rats learned the environment, such distinctions became insignificant.

# Chapter 5

## Discussion

The experiments presented here have shown that while Norway rats do have a general preference for more protective areas over less secure ones, this preference can be greatly modified by a number of factors. The results of Experiments 4.1.1 and 4.1.2 show that in the dark rats are significantly less security seeking than in the light. Additionally, Experiment 4.1.1 illustrated how there is a difference in security seeking between the sexes, with males spending significantly more time in a generally more secure region of the table. Experiment 4.2.1 showed that a rat's familiarity with an area will also modify how much time it spends there. Experiments 4.2.2 and 4.1.1 indicated that this familiarity effect can interact with a rat's attraction to a secure area, conflicting with the attraction to a moving protective area and increasing the draw of a stationary location. Lastly, Experiments 4.2.4 and 4.1.1 together showed that rats' interactions with the walls of an enclosed area is not simply because they are protective, but due to a complex interaction of several forces, one of which can be familiarity. These results paint an overall picture of rat exploratory behavior that is not driven just by security, but also information and memory (of which lighting, sex, and familiarity play a part).

### 5.1 Security

Maintaining access to a protected location is one aspect of rat exploration, as shown by the above chance time spent in the inner circle by all groups in Experiment 4.1.1.

However, the lack of security seeking behavior in some situations reveals that rats most likely do not have an "understanding" of security, but only respond to stimuli in a way that typically increases safety in their natural ecology. The edge following behavior of both sexes, but most notably the females, in Experiment 4.1.1 is one example. Nowhere in rats' natural history was the ability to survive on a 66" diameter table a selecting force. However, possessing effective tunneling and trail following behavior was. These behaviors in the rats natural environment produce security maximization(Calhoun, 1963), but on the table such edge following is hazardous.

In addition, experiments in the light and dark (4.1.1 and 4.1.2) show that security seeking is significantly diminished or disappears in the dark. This could be partially attributed to the fact that rats are largely nocturnal, using the darkness itself as protection from predators. While this would explain lower selective pressure for safety oriented behaviors in the dark, this selection would not be zero, as there are still numerous predators that hunt at night. As such, there must have been some other selector creating lower security seeking in the dark. This was information and memory.

## 5.2 Information

In addition the need to be safe, the need to know about the environment also drives rat exploration. Both Experiments 4.1.1 and 4.1.2 found rats in the dark to be more exploratory than those in the light, not only in time spent in a secure area, but also in distance moved and ambulation<sup>1</sup>. As previously discussed, this difference could be caused not just by the fact that rats are nocturnal, but also by the difference in information acquisition in the light and the dark. In the light, the rat can view much or all of the environment without changing its position, but in the dark, the rat must physically move about in order to learn about its surroundings. These findings suggest that information is a key factor in rat locomotive exploration. If this were not the case, the dark groups should not have shown increased exploration over the light groups, instead using only the

---

<sup>1</sup>As measured by time spent in both halves of the arena. Equal time in both halves is highly ambulatory, while a bias shows lower overall exploration

limited information they could attain without vision.

## 5.3 Memory

Information, however, is only useful if it is remembered. Throughout all of these experiments, the rats' behaviors changed over days, indicating that they remembered the environment from previous trials. Experiment 4.2.1 showed this most simply, with rats preferring some areas simply because they were more familiar than other areas. Other experiments showed that the rat's memory of an environment will affect behavior in a variety of situations, including a varying environment (Days 4-6 in Experiment 4.2.2), a stable environment (Time by landmarks in Experiment 4.1.1), and in differentiating gross environmental features (The two walls in Experiment 4.2.4). However, if the environment is sufficiently small, initially significant familiarity effects will disappear as the rat learns the entirety of the environment equally well (Experiment 4.2.5)

Additionally, males, which have been shown to have better spatial memory, altered their behavior more over days than females, decreasing their activity. This is probably because the males remembered the environment better than the females, and so had less need to explore it. The same explanation can be used for the change of behavior over days seen in the light groups of Experiment 4.1.1. Since the light groups had a more complete understanding of the environment (they could see it, in addition to feel/smell/hear it), their remembered local views were more comprehensive, and more easily compared to the local views perceived each day.

## 5.4 Conclusions

From these experiments it is apparent that rat exploration is heavily influenced by the rat's processing of environmental information and recalling that information later. In interacting with an environment over several days, especially one that is prone to change, these aspects of the rat's navigational system can result in behavior that is not security maximizing. While safety seeking behavior is part of the rat's exploratory repertoire,

they can be overshadowed by the more basic factors of information gathering and memory. Given that these two elements can temporarily supersede security oriented behavior (such as in Experiment 4.2.2) and security optimization has not been shown to trump information gathering, it follows that the navigational aspects of rat exploration are the product of stronger selective pressures than safety. While security remains a viable way of interpreting some elements of rat exploration, information and memory is often a more effective paradigm for analyzing rats' movements in an open field.



## Acknowledgements

This research was funded by the Howard Hughes Medical Institute, the Indiana University Hutton Honors College, and the Indiana University Cognitive Science Department. Many of these experiments were run by Indiana University students Tammy Marnell, Lisa Huang, and Rachael Keith. Thanks to Bill Timberlake for guiding me through this research process, and Joe Leffel for invaluable help with Ethovision and Statistica.

# Bibliography

- J. Archer. Tests for emotionality in rats and mice - review. *Animal Behaviour*, 21(May): 205–235, 1973. ISSN 0003-3472.
- Reut Avni, Pazit Zadicario, and David Eilam. Exploration in a dark open field: a shift from directional to positional progression and a proposed model of acquiring spatial information. *Behavioural brain research*, 171(2):313–23, August 2006. ISSN 01664328.
- J.S. Barlow. Inertial navigation as a basis for animal navigation. *Journal of Theoretical Biology*, 6:76–117, 1964.
- J Calhoun. *The Ecology and Sociology of the Norway Rat*. Public Health Service, Bethesda, MD, 1963.
- M. Collett, T.S.; Collet. Path integration in insects. *Current Opinion in Neurobiology*, 10:757–762, 2000.
- J Crawley. Exploratory behavior models of anxiety in mice. *Neuroscience & Biobehavioral Reviews*, 9:37–44, 1985.
- D. Eilam and I. Golani. Home base behavior of rats (*rattus norvegicus*) exploring a novel environment. *Behavioural Brain Research*, 34(3):199–211, September 1989.
- David Eilam. Open-field behavior withstands drastic changes in arena size. *Behavioural brain research*, 142(1-2):53–62, June 2003. ISSN 01664328.
- David Eilam. Locomotor activity in common spiny mice (*acomys cahirinuse*): the effect of light and environmental complexity. *BMC ecology*, 4(1):16, November 2004. ISSN 14726785.

David Eilam, Maya Dank, and Roland Maurer. Voles scale locomotion to the size of the open-field by adjusting the distance between stops: a possible link to path integration. *Behavioural brain research*, 141(1):73–81, April 2003. ISSN 01664328.

A. S. Etienne, R. Maurer, J. Berlie, B. Reverdin, T. Rowe, J. Georgakopoulos, and V. Seguinot. Navigation through vector addition. *Nature*, 396(6707):161–164, November 1998. ISSN 0028-0836.

C.R. Gallistel. *The Organization of Learning*. MIT Press, 1990.

Ilan Golani, Yoav Benjamini, and David Eilam. Stopping behavior: constraints on exploration in rats (*rattus norvegicus*). *Behavioural Brain Research*, 53(1-2):21–33, February 1993.

D.P. Goodale, M. A.; Carey. *The Cerebral Cortex of the Rat*, pages 309–340. MIT Press, 1990.

C Hall. Emotional behavior in the rat I Defecation and urination as measures of individual differences in emotionality. *Journal of Comparative Psychology*, 18:385–403, 1934.

Dustin J. Hines and Ian Q. Whishaw. Home bases formed to visual cues but not to self-movement (dead reckoning) cues in exploring hippocampectomized rats. *European Journal of Neuroscience*, 22(9):2363–2375, 2005.

Ariane S. Etienne; Kathryn J. Jeffery. Path integration in mammals. *Hippocampus*, 14: 180–192, 2004.

N. Kafkafi and G. I. Elmer. Texture of locomotor path: a replicable characterization of a complex behavioral phenotype. *Genes, Brain & Behavior*, 4(7):431–443, October 2005. ISSN 16011848. URL <http://bert.lib.indiana.edu:2048/login?url=http://search.ebscohost.com/login.aspx?d>

B.L. Leonard, B; McNaughton. *Neurobiology of Comparative Cognition*, chapter Spatial representation in the rat: Conceptual, behavioral, and neurophysiological perspectives, pages 363–422. Erlbaum, 1990.

- M.J Loomis. Nonvisual navigation by blind and sighted: assessment of path integration ability. *Journal of Experimental Psychology: General*, 122:73–91, 1993.
- Perrot-Sinal TS; Kostenuik MA; Ossenkopp KP; Kavaliers M. Sex differences in performance in the morris water maze and the effects of initial nonstationary hidden platform training. *Behavioral Neuroscience*, 110:1309–1320, 1996.
- G.H. Neitz, J.; Jacobs. Reexamination of spectral mechanisms in the rat (*Rattus norvegicus*). *Journal of Comparative Psychology*, 100:21–29, 1986.
- Laetitia Prut and Catherine Belzung. The open field as a paradigm to measure the effects of drugs on anxiety-like behaviors: a review. *European journal of pharmacology*, 463 (1-3):3–33, February 2003. ISSN 00142999.
- A. David Redish. *Beyond the Cognitive Map*. MIT Press, 1999.
- U.V. Saint Paul. *Avian Navigation*, chapter Do geese use path integration for walking home?, pages 298–307. Springer, 1982.
- A.V. Samsonovich. *Attractor map theory of the hippocampal representation of space*. PhD thesis, University of Arizona, 1997.
- Van der Werff ten Bosch JJ. Slob AK, Huizer T. Ontogeny of sex differences in open-field ambulation in the rat. *Physiology and Behavior*, 37:313–315, 1986.
- Robin L. Roof; Donald G. Stein. Gender differences in morris water maze performance depend on task parameters. *Physiology & Behavior*, 68:81–86, 1999.
- O Tchernichovski, Y Benjamini, and I Golani. The dynamics of long-term exploration in the rat. part I. a phase-plane analysis of the relationship between location and velocity. *Biological cybernetics*, 78(6):423–32, June 1998. ISSN 03401200.
- Ofer Tchernichovski and Yoav Benjamini. The dynamics of long term exploration in the rat: part II. an analytical model of the kinematic structure of rat exploratory behavior. *Biological Cybernetics*, 78(6):433–440, 1998. ISSN 03401200.

T.C. Tobach, Ethel; Schneirla. *Roots of Behavior*, chapter Eliminative Responses in Mice and Rats and the Problem of "Emotionality", pages 211–231. Harper and Brothers, 1962.

D Touretzky, D; Redish. Theory of Rodent Navigation Based on Interacting Representations of Space. *Hippocampus*, 6:247–271, 1996.

M Treit, D; Fundytus. Thigmotaxis as a test for anxiolytic activity in rats. *Pharmacology, Biochemistry, and Behavior*, 31:959–962, 1998.

Ramon Trullas and Phil Skolnick. Differences in fear motivated behaviors among inbred mouse strains. *Psychopharmacology*, 111(3):323–331, June 1993.

Fred Valle. Effects of Strain, Sex, and Illumination on Open-Field Behavior of Rats. *American Journal of Psychology*, 83(1):103–111, March 1970.

Ian Q Whishaw, Omar A Gharbawie, Benjamin J Clark, and Hugo Lehmann. The exploratory behavior of rats in an open environment optimizes security. *Behavioural brain research*, 171(2):230–9, August 2006. ISSN 01664328.

R; Zadicario Zadicario, P; Avni. 'Looping' - an exploration mechanism in a dark open field. *Behavioral Brain Research*, 159:27–36, 2005.