



Research report

Effects of rat sex differences and lighting on locomotor exploration of a circular open field with free-standing central corners and without peripheral walls

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ARTICLE INFO

Article history:

Received 11 August 2008

Accepted 1 September 2008

Available online 6 September 2008

Keywords:

Locomotor exploration

Sex differences

Behavior

Home base

Perimeter

Open field

Security

ABSTRACT

A typical open field consists of a square enclosure, bounded by four straight walls joined by identical corners. For decades behavioral researchers have used the open center and more sheltered perimeter of such fields to examine the effects of drugs, sex differences, and illumination on the behavioral expression of fear and anxiety. The present study “reversed” the relative security of the center and periphery of a circular field to re-examine the functional relation of open field behavior to experience, sex differences and lighting. Across six daily exposures, males in both the light and dark rapidly increased their preference for the center. Females in the light developed a similar pattern, though more slowly; females in the dark continued to spend the great majority of their time in the open periphery, including the edge of the field. The behavior of all groups, but especially the dark females, strongly supports the continued importance of environmental assessment in open field behavior.

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1. Introduction

Since 1920s locomotor behavior of domesticated Norway rats has been studied in standardized open fields [13]. These fields are typically a 1–2 m square enclosure with 40–60 cm high walls, located on the floor of a well-lit experimental room. Rats express the majority of their locomotion and rearing in close proximity to the walls, often taking up temporary residence in one or more corners. Disproportionate amounts of locomotion, rearing, and time spent near walls and corners, relative to in the center of the field, have been used to index fear and emotionality [1,13,20,30]. Such measures have found particular popularity in pharmacological studies examining the anxiety of drugged versus control groups of rodents [5–7,24]. The open field has also been used to identify differences in the behavior of individuals, strains, sexes, and species [17,18,29,30]. Manipulations of the standard open field environment, such as turning off the lights or placing objects in the field, have also been used to further investigate differences in behavior [9,10,30,32,33].

In the past few decades, published research using open fields has grown to include additional rodent species and functional analyses of structural elements of locomotion in the field. These elements

include looping patterns of locomotion, the tendency to organize movement around individually established home bases, and the role of movement in increasing security [2,8,11,12,26,27,31,34]. Recent research has used a variety of open field designs, including elevated tables without perimeter walls [11,23,31]. In empty elevated fields, rodents spend the majority of their time at the table’s exposed edge, where they establish home bases. Other research has placed free-standing corners in a standard open field and in a round field with curved walls. A free-standing corner, whatever its location in the field, is an attractive point for exploration; however, the home base is usually located at a perimeter corner, if available [31,32].

The present study merged recent lines of open field research to analyze further the role of security seeking, related to corners, and environmental assessment, related to free-standing corners and the perimeter, in determining locomotor behavior. The apparatus was an elevated circular field with free-standing corners arranged around the center of the field, but without a wall at the perimeter (see Fig. 1). This arrangement inverted the potential security functions of the center and periphery relative to other open fields. To further differentiate the functions of behavior at the center of the field, three of the six free-standing corners (every second one) faced the center while the other three faced the perimeter. These two kinds of corner were intended to differentiate the role of corners as a discontinuity in the environment to be explored from their role in increasing security. We hypothesized that the three corners opening to the center of the field were likely to be perceived as more secure (measured by time spent) than the corners opening toward

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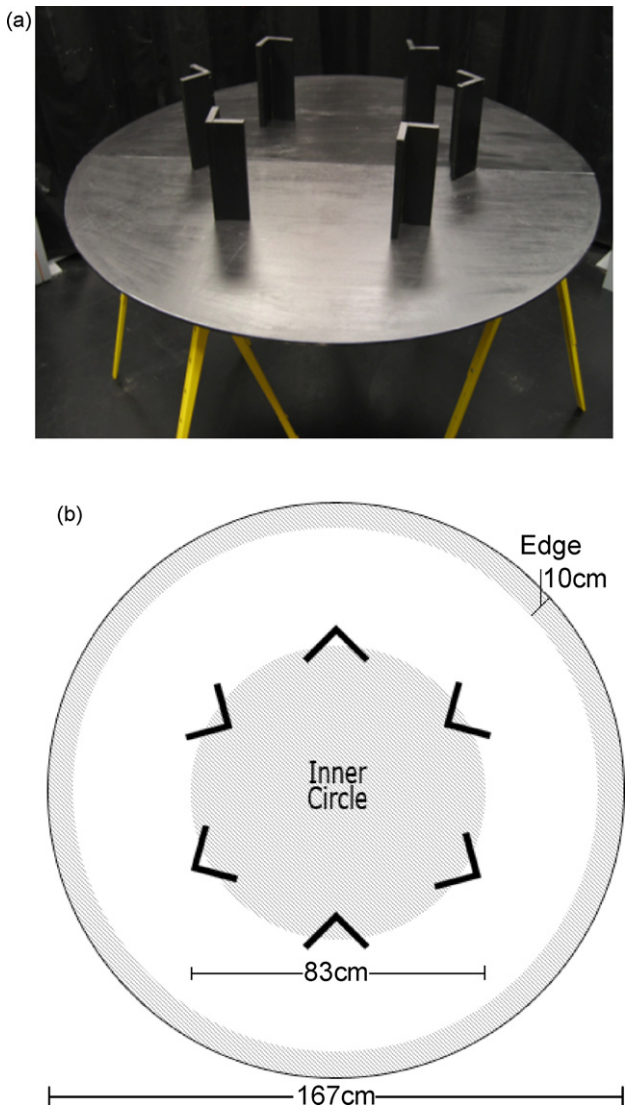


Fig. 1. Side view of the table (left) and a diagram of the table as viewed from the ceiling (right).

the edge of the field (measured by time spent). Further, because the perimeter of the field lacked both walls and corners, we were able to examine the extent to which repeated locomotion and time spent approaching and exploring the open perimeter of the field reflects assessment of the field's limits. Finally, because open field research has often related sex differences and lighting effects to fear and emotionality, we tested the same variables by running male and female groups in light or darkness for six daily 5 min exposures.

To the extent that the primary goal of rat behavior in an open field is safety and security seeking, rats should spend proportionally more time in the center of our "reversed" open field, with greater time spent inside the free-standing corners facing the center than inside those facing the periphery. Similarly, rats should avoid differentially the periphery of the field beyond the area, particularly the edge of the perimeter. On the other hand, to the extent that assessing the limits of the space in which an animal finds itself on a daily basis is an important determinant of its behavior, we expect to see persistent time spent in the outer circle of the field, including sniffing and whisker contact at the edge of the field. Finally, based on past results, we expect males to show more "security seeking" than females, spending more time in the center and the center-facing

corners, and groups run in the dark to spend less time in the center of the field than comparable groups run in the light [4,9,15,21,30].

2. Materials and methods

2.1. Subjects

The subjects were 18 male and 16 female lab rats (*Rattus norvegicus*) between 4 and 5 months old at the beginning of the study. All rats had previously participated in a behavioral study of spatial learning in a Morris water maze. Rats were housed individually in metal cages (24 cm deep, 20 cm wide, 18 cm high) in a colony room, where they received food and water ad libitum. The colony was lit from 7 a.m. to 7 p.m. and dark the remaining hours. Colony temperature was maintained between 66 and 78 F.

2.2. Food deprivation

Starting 6 days before the beginning of the experiment, food was no longer available ad libitum. The rats were weighed daily 10 to 20 minutes before their regular afternoon feeding, then given a daily amount of food designed to reduce and maintain their body weight at 85% of their free feeding level. The rats rapidly showed anticipation of this feeding time, with increasing alertness, locomotion, and grooming beginning in the afternoon hours. Throughout the experiment the rats were weighed before they were taken from the colony, and were fed at least 15 min after their return.

2.3. Experimental room

The experiment took place in a 3.65 m × 3.65 m sound insulated room with a black floor, designed to minimize uncontrolled sensory cues. All four walls were covered by heavy, black, vinyl curtains hung from a track in the ceiling immediately in front of each wall. In trials run in darkness, three of the curtains were pulled back to the corners of the room to increase the illumination provided by the infrared LED light bank for the infrared-sensitive video camera. The remaining curtain covered the insulated door on all trials to further deaden sound and prevent light leaks. The 3-m high ceiling was white tile and hosted four air vents and eight fluorescent light fixtures with four 17 W bulbs each. Lights and vents were symmetrically arranged, though only one vent was active. Suspended from the middle of the ceiling was a circular start cage, 10 cm tall and 26 cm in diameter, made of wire mesh covered in duct tape. This cage, with a diameter slightly larger than the length of a rat, was attached to a string which ran through a pulley system in the ceiling to outside the room. To introduce a rat into the environment, the experimenter would place the rat underneath the start cover at the center of the field, exit the room, and raise the cover to the ceiling from outside using the string.

2.4. Table

The experiment proper took place on a circular, wooden table, placed in the middle of the room. The table was 1.67 m in diameter and raised 1 m off the ground on two metal sawhorses. Six free-standing corners were arranged around a virtual circle on the table with a diameter half the diameter of the table (see Fig. 1). The corners were 30.5 cm tall, consisted of two 10 cm × 2.5 cm wooden segments nailed together at right angle, and were mounted on end with pegs stuck into holes in the table equidistant from the edge and center of the table. The corners were sufficiently tall that rats did not climb on top of them. The table and corners were painted black and sealed with polyacrylic. The arrangement of the corners created a center area half the diameter of the apparatus, the "inner circle," and a peripheral area, the "outer circle". The corners alternated directions, with three corners opening in to the center and three opening out to the periphery.

2.5. Tracking

As noted, an infrared-sensitive Panasonic video camera was placed at the center of the ceiling with an infrared LED bank hung near it. The camera was connected to a DVD recorder, monitor, and computer outside the room. The experimenter observed the rat on the screen while the video feed was written onto a DVD. The behavior of the rats was simultaneously digitally captured on the computer with a tracking program (Ethovision, by Noldus Information Technologies, NL) which provided the ability to analyze the rat's movements in the field. Trials run in the light were illuminated by the fluorescent lights. All trials run in the dark were illuminated by the infrared LED bank, which emitted a wavelength of light longer than rats can see [22]. The only entry door to the room was designed with gaskets to block sound and light and was covered by a black vinyl curtain, as previously described. The camera had no visible indicator lights which might have provided a beacon to the rats.

2.6. Procedure

All rats were individually released on the table environment for one 5 min trial on each of six successive days. The trials were run in mid-afternoon, within the 2 h

before the rats' feeding time. On each day each rat was removed from its home cage and carried to the lab in metal carrying cages with four individual compartments. For each trial, the experimenter removed a single rat from its compartment, carried it into the experimental room, and placed it on the center of the table, beneath the start cover. For animals to be run in the dark, the room was dark when the experimenter entered with the rat. After placing the rat underneath the cover, the experimenter left the room, covered and shut the door, and began recording on the DVD player. The experimenter then raised the cover, using the pulley-aided string, to release the rat to move about the arena. Once the cover was pulled completely out of the camera's way (approximately 2 s), the experimenter started Ethovision's tracking of the rat. After Ethovision tracking started, the trial lasted 5 min before the experimenter entered the room (still in darkness, for rats run in the dark), picked up the rat using light from the open doorway, and returned it to the carrier. The experimenter then cleaned away any feces and urine with paper towels and an organic acid cleaning solution. This solution removed odors and was blotted dry before the next trial. After all rats had been run they were returned in their carriers to the colony and placed in their cages to be fed later 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 10–60 min before their trial, and 20–90 min before their return to the colony. The order in which the rats were run varied, meaning the exact time waited by any individual rat was unpredictable within this range from day to day.

2.7. Measures

The primary measure was the amount of time the rats spent in central and peripheral areas of the field, presented as a percentage of the 5 min in each trial. These areas included the "inner circle" and "outer circle," as previously described in Section 2.4. The inner circle had a radius of 83 cm (half the table's width) and covered 25% of the table's surface area. The outer circle covered the remaining 75% of the table. The inner circle was identified as more secure because the surrounding six free-standing corners provided cover, while the outer circle was exposed and included the "cliff" at the perimeter. The outer 10 cm of the outer circle, which covered 22.7% of the total table surface area, was designated as the "edge" and also recorded.

The time spent within 10 cm of the six free-standing corners was the final location measure. The corners each had two sides: a "recessed" side (presumed more secure) and a "protruding" side (presumed less secure). These two sides were further differentiated by whether the side was in the inner or outer circle (see Fig. 1). This created four corner-related positions for the rat, ranging from the least secure "outer circle, protruding corner" to the most secure "inner circle, recessed corner." In addition to corner-related measures, we recorded two locomotion measures: total distance covered and percent of time spent moving. "Moving" was defined as occurring when the rat's sampled velocity was greater than 2 cm/s. The results for all measures failed Mauchly's test of sphericity ($p \leq 0.05$). Therefore, all measure values and statistics reported are the estimated marginal means and p - and F -values calculated by a multivariate analysis of variance.

3. Results

3.1. Inner circle

On the first day all four groups spent roughly equal time in the inner circle (Fig. 2), all near the 25% level expected by chance, based on the area of the inner circle relative to the whole table. Over subsequent days, males and females in the light quickly increased time spent in the inner circle to nearly 90% for the males and 70% for the females. Males in the dark also increased their inner circle time over trials, but more slowly and to a notably lower asymptote of 55%. Surprisingly, females in the dark actually decreased time spent in the inner circle over the next 5 days ($F(5, 27) = 2.88$, $p = 0.033$), eventually spending only around 15% of the trial there. Disregarding lighting differences, there was a weak interaction of days and sex ($F(5, 27) = 2.278$, $p = 0.075$): males and females both started with a low inner circle time that increased over daily trials, but the males increased their time more rapidly. There was no interaction of sex and lighting independent of days ($F(1, 30) = 2.128$, $p = 0.155$).

3.2. Free-standing corners

While initially rats showed little preference for any corner, by the fifth day both sexes in the light came to spend over 60% of their time at the recessed (safest) free-standing corners in the inner cir-

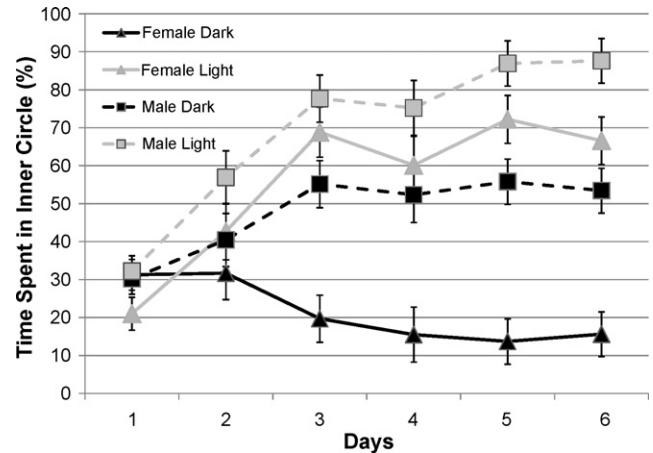


Fig. 2. Inner circle time for both sexes and lighting conditions by days. Vertical bars denote standard errors.

cle (Fig. 3). Over the course of the experiment, males and females in the light spent, respectively 50 and 40% of their total time, at the recessed corners in the center ($F(1, 31) = 16.65$, $p < 0.001$). These three corners were the areas of the field with the most cover. In contrast, neither males nor females in the dark showed any preference for a corner type throughout the experiment; females spent no more than 5% of trial time by any given corner type, and males spent no more than 11% ($F(5, 27) = 10.88$, $p < 0.001$).

3.3. Edge and outer circle

All groups spent much less time than chance within 10 cm of the table's edge, with an average of 1.02% time spent at the edge versus the 22.7% of the table's surface area the region occupied (Fig. 4, white bars). Further, during the 6 days of exposure the average portion of time spent at the edge (combining sexes and lighting conditions) was nearly halved, 1.68% on day 1 and 0.82% on day 6 ($F(1, 27) = 3.36$, $p = 0.017$). In the dark, though, both sexes spent more time by the edge, with females almost doubling the time spent by males ($F(1, 30) = 6.62$, $p = 0.015$). Additionally, for both sexes the most frequently observed behavior at the edge of the table in the dark was hanging the head over the edge, turning the neck until their vibrissae contacted the side and underside of the table. There were no significant interactions involving days, sex, and/or light-

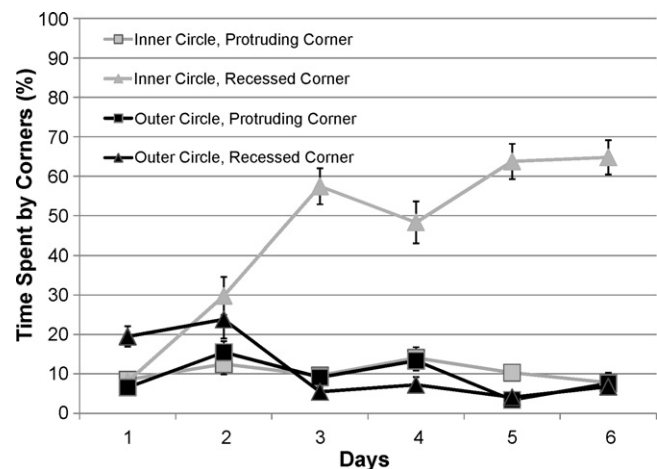


Fig. 3. Time spent by the four kinds of corners in a lit environment by days, combining both sexes.

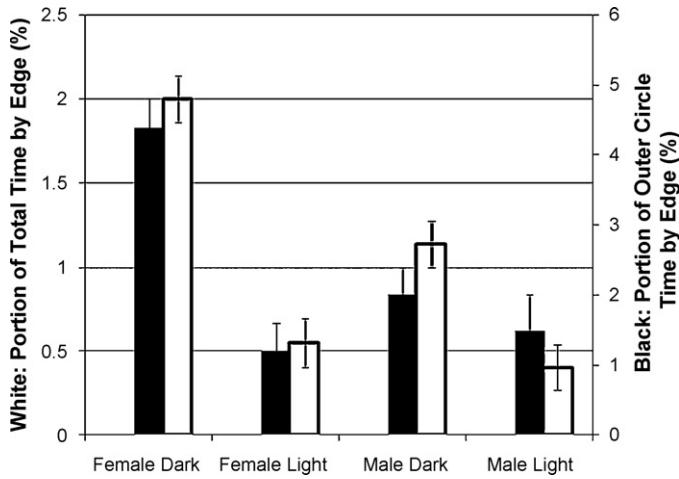


Fig. 4. Time spent within 10cm of the table's edge, both as percent of total time (white) and relative to time in the outer circle (black). This region made up 22.7% of the table's surface area, making time spent in all groups far below chance.

ing. Finally, because the edge region is contained within the outer circle, we evaluated whether differences in time spent at the edge of the field by different groups simply reflected time spent in the outer circle. To examine this, we tested the ratio of the time spent at the edge to the time spent in the outer circle (see Fig. 4, black bars). All reported effects were still significant, indicating that the behavior at the edge did not simply reflect the behavior of the rat in the outside circle.

3.4. Locomotion measures

Fig. 5 shows that for all groups distance moved decreased slightly over the six daily trials, though significantly more for males than for females ($F(5, 27) = 2.92, p = 0.031$). Although both sexes covered roughly equal ground in the light, in the dark females moved a significantly greater distance than males (Fig. 5) ($F(1, 30) = 5.35, p = 0.028$). Additionally, as shown in Fig. 6, all groups slightly decreased time spent moving (velocity greater than 2 cm/s) during the 6 days, from an average of 86% on day 1–74% on day 6 ($F(5, 27) = 6.92, p < 0.001$). There was no significant effect of the sexes on time spent moving, nor an interaction of days with sex or lighting. However, combining sexes, rats in the dark spent 90% of their time moving, while those in the light moved only 67% of the time ($F(1, 30) = 62.39, p < 0.001$) (Fig. 6).

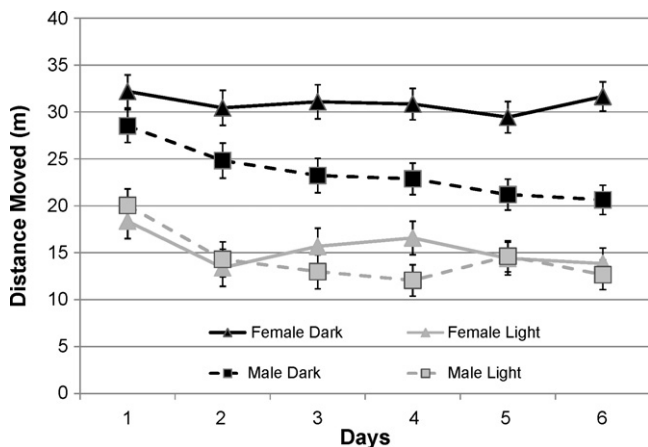


Fig. 5. Distance moved for both sexes and lighting conditions by days.

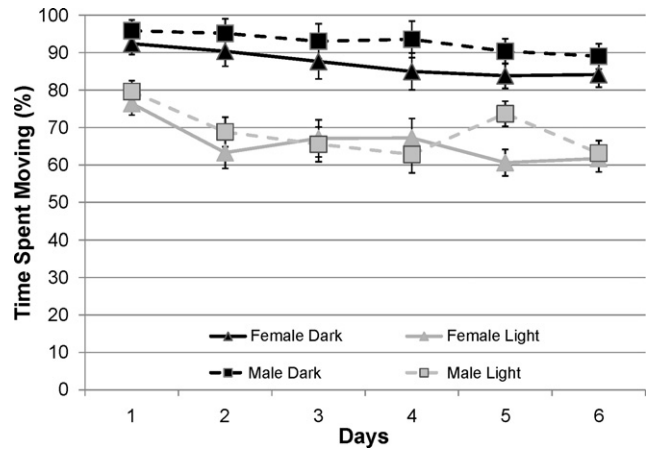


Fig. 6. Time spent moving for both sexes and lighting conditions by days.

4. Discussion

In an open field, rats typically spend the largest portion of their time by cover. However, when cover is completely unavailable, in the form of an empty field with no walls, rats instead spend the largest portion of their time at the edge, a cliff [23,31]. Just as enclosed open fields place the protective wall at the perimeter, previous research placing cover in an open field without walls has positioned the cover at the edge, overlapping the draw of cover with the possible attraction of assessing the perimeter [23,31]. This study sought to differentiate and compare cover and the perimeter as determinants of exploration in rats by physically separating these two features. A circular, elevated open field without walls was used, in the middle of which stood a circle of six free-standing corners. To test an array of preferences for security and exploration, both female and male groups of rats were exposed to the field in the light or in the dark for 6 days.

On the first experimental day, regardless of sex or illumination, all groups spent a proportion of time in the inner and outer circles roughly equal to chance (25 and 75%), showing extensive movement throughout the entire field. After the first day, though, both sexes in the light and males in the dark spent increasingly more time in the protective inner circle, with males in the light spending almost 90% of each trial in the most secure area (Fig. 2). Additionally, rats in the light spent approximately 60% of each trial at the recessed corners of the inner circle, the area with the most cover (Fig. 4). In contrast to their security seeking behavior in the light, females in the dark spent slightly less time than chance in the inner circle, overall spending more time in the exposed outer circle. Furthermore, both females and males in the dark had no preference for the more secure free-standing corners. Increased activity in exposed areas by females in the dark has been observed previously in standard, enclosed open fields, but not in such a marked fashion [30].

4.1. Lighting Effects

The observed effects of light in depressing locomotion conform well to reports from previous research [4,9,21,30]. These differences in behavior between the light and dark groups are likely due in part to a balance between immediate access to information provided by light and the rat's evolutionary history of avoidance of brightly illuminated areas. Darkness is an excellent cover against visual predators, so remaining near or in protective locations likely has a smaller impact on fitness in the dark than in the light. As a result, we might expect rats in the dark to be less security seeking and/or "fearful" than in the light.

While part of the higher activity of the dark groups was likely due to a release of the inhibitory effects of light on movement it is worth considering that dark groups cannot use vision to initially acquire and daily reacquire information about the nature of their environment. In contrast, light groups can relatively quickly determine they are in a familiar environment without moving around extensively [4]. This may account for the rapid movement of the light animals over days to a secure area. In contrast, the dark groups must patrol the environment daily to establish that little has changed. By this argument, the impact of prior exposure to the environment on total locomotion should be less for rats in darkness, which it was.

4.2. Sex differences

As expected from previous data, males showed more security seeking behavior than females, as evidenced by more time spent in the inner circle and in the recessed corners. Interestingly, although in the light males spent slightly more time in the inner circle than females (see Fig. 2), males spent relatively even more time in the inner circle than females in the dark. Thus, although the light data showed trends conforming to previous literature reporting that males are more cautious and fearful than females [15,19,30], it seemed odd that males should be relatively even more fearful in the dark than females. This suggests there may be another contributor to differences in male and female open field behavior.

The weak interaction of sex and days with regard to time in the inner circle (males increasing inner circle times faster than females), may indicate that males adapted to the environment more quickly than females. Given that all groups behaved similarly on the first day, the subsequent difference between the sexes may not originate from different overall preferences or levels of emotionality, but from disparities in certainty of knowledge of the environment. Previous research has shown a male advantage in spatial memory, due in part to several differences in neural structures, as well as the memory disrupting effects of estrous cycles [3,14,16,25,28]. Finally, in the present experiment, comparison of time spent moving relative to distance covered shows that males move more slowly, possibly exploring more thoroughly. For these reasons, males may better retain information about the spatial environment than females, and so spend relatively less time renewing it in the dark.

4.3. Females in the dark

It seems possible that the remarkable behavior of females in the dark reflects an interaction of lighting with sex differences. At the end of the experiment males in the light spent around 30% more time in the inner circle relative to males in the dark, while females in the light spent greater than 50% more time in the inner circle than in the dark. At the same time, females in the dark spent more time than any other group at the edge of the outer circle. The traditional explanation for such differences in activity would be that rats are more cautious in the light than in the dark, and that males appear more cautious than females [9,15,19,21,30]. However, as noted above, these hypotheses do not precisely fit the results we obtained.

In the present study, female rats in the dark spent an unexpectedly large amount of time in the outer circle of the field and at the edge, despite the absence of safety or cover in these areas. While research in traditional open fields has shown that females in the dark spend more time in the open than male rats, they do not show as large a preference for exposed areas as found in the present experiment. A possible contributor to the present effect is that females simply seek more information about the surrounding

environment than males. However, as mentioned above, females are not as adept at remembering the spatial aspects of the open field as males, perhaps especially without visual cues present. As a result, females in the dark may spend more time and movement to assess salient features of the environment, such as objects, cover and the periphery.

5. Conclusion

Our data provide additional evidence that cover and security are important determinants of both male and female rat locomotor exploration under conditions of both light and dark. In the traditional open field, four walls and corners make up the perimeter of the environment, simultaneously providing cover and an opportunity to assess the limits of the field. In the present study, we reversed the location of cover by placing free-standing corners in the center and removing walls and corners from the periphery. This change reversed the dominant location of time spent in an open field from the periphery to the center. In the light, both males and females spent by far the most time in the “secure” inward facing corners relative to all other corners. However, both sexes continued to check the periphery of the field, including the edge, daily, assessing the limits of the environment.

In contrast, in the dark both sexes showed less security seeking behavior, spending more time outside the inner circle and at the edge, even though the field had no attractive perimeter wall. These females spent by far more time in the outer circle and at the edge than any other group. The size of the difference suggests that female rats in the dark are not simply less fearful than females in the light or male rats in the light or dark (although that could be so), but differentially motivated to persist in exploring the peripheral areas of a dark environment. Thus, while female rats may be uniquely less cautious than males in the dark, they may also acquire environmental information in more depth, more slowly, and/or with poorer retention in the absence of visual data.

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