Sex Differences in the Strategies Used by Rats to Solve a Navigation Task

Clara A. Rodríguez
Universitat de Barcelona

N. J. Mackintosh
University of Cambridge

Angélica Torres
University of Sevilla

V. D. Chamizo
Universitat de Barcelona

Rats were trained in a triangular-shaped pool to find a hidden platform, whose location was defined in terms of two sources of information, a landmark outside the pool and a particular corner of the pool. Subsequent test trials without the platform pitted these two sources of information against one another. This test revealed a clear sex difference. Females spent more time in an area of the pool that corresponded to the landmark, whereas males spent more time in the distinctive corner of the pool even though further tests revealed that both sexes had learned about the two sources of information by presenting cues individually. The results agree with the claim that males and females use different types of information in spatial navigation.

Keywords: sex differences, landmark learning, shape learning, Morris water-maze, rats

Both in the radial maze and in the Morris pool, there is evidence that male rats learn faster, and perform more accurately than females (in the Morris pool: Forcano, Santamaría, Mackintosh, & Chamizo, 2009; Saucier, Shultz, Keller, Cook, & Binsted, 2008; in the radial maze: Einon, 1980; Seymoure, Dou, & Juraska, 1996). This sex difference is usually small, and often depends on details of the way in which performance is measured. For example, Forcano et al. (2009), having trained rats to find the submerged platform in a Morris pool, a task which the males learned faster than the females, found no difference in the proportion of time during a 60-s test trial without the platform spent by males and females in the platform quadrant of the pool. However, males did spend more time in the platform quadrant than females over the first 30 s of the test trial. A number of other factors can also alter this pattern of male and female performance (i.e., an advantage for males), such as specific task parameters and rearing conditions (in the pool see Roof & Stein, 1999).

Perhaps even more interesting than any overall difference in speed of spatial learning in male and female rats is evidence that they may rely on different cues to solve spatial problems. For example, in a study by Williams, Barnett, and Meck (1990) with rats and a radial-maze, two manipulations were conducted after acquisition: alteration of the geometry of the testing room and rearrangement of the landmark cues. The results revealed that alteration of the geometry of the testing room affected the performance of normal males, but these changes did not affect normal females. Normal male rat performance was not impaired when landmark cues were rearranged, whereas normal female performance was impaired (for a similar result in the circular pool, see Roof & Stein, 1999). One reason why this finding is so interesting is that there are analogous data from human participants. It is, of course, well established that males and females differ in their performance on a variety of paper-and-pencil tests of spatial ability (Halpern, 1992). But such a difference has also been observed on a wide variety of other spatial tasks, including route and map learning (Dabbs, Chang, Strong, & Milun, 1998; Choi & Silverman, 2003; Galea & Kimura, 1993; Saucier, Green, Leason, MacFadden, Bell, & Elias, 2002), and computer based and/or virtual reality versions of the Morris pool (Astor, Ortiz, & Sutherland, 1998; Burkitt, Widman, & Saucier, 2007; Chai & Jacobs, 2009; Sandstrom, Kaufman, & Huettel, 1998; Wilson, Carter, Woulfe, & Southall, submitted). The important point is that here too, there is evidence not only of a difference in overall speed of learning and accuracy of performance, but also a difference in the cues used by males and females to solve these tasks. Galea and Kimura (1993); Sandstrom et al. (1998); Dabbs et al. (1998); Saucier et al. (2002); Jones and Healy (2006), and Wilson et al. (submitted), among others, all found that men were more likely to use geometrical information to solve a spatial task, and women were more likely to use visual features or landmarks.

This rather striking parallel between rats and people deserves further exploration. The aim of the present experiments was to evaluate whether there are differences in the way that male and female rats solve a simple spatial task in the Morris pool. In both
studies, two white walls were inserted into the pool to create an area shaped like a right-angled triangle with a curved base. In Experiment 1, a submerged platform was located near the apex of this triangle, and a salient landmark was located above the pool at this position (see Figure 1A, left). Experiment 2 replicated the procedure of Experiment 1 but with a different landmark and with the platform located in a different corner of the pool (see Figure 2A top panel, left). Circular black curtains surrounded the pool, which was rotated from trial to trial, along with the landmark and the platform, so that the only indicators of the location of the platform were the landmark and the geometry of the triangle. Once the rats had learned to find the platform, they were given test trials without the platform, on which these two sources of information were put into opposition by presenting them 180° apart: the landmark was now positioned above the curved base of the triangle for Experiment 1 (see Figure 1A, right), and above the symmetrical corner of the pool for Experiment 2 (see Figure 2A top panel, right). The results of an opposition test, however, cannot tell us what the rats “know” (i.e., what they have learned), but rather about what they choose (i.e., how they perform). Therefore, a second purpose of Experiment 2 was to measure what males and females had learned about the two sources of information independently of their preferences. For this purpose, two additional test trials (Tests 2 and 3) were also conducted in Experiment 2. On one trial, the landmark was present in the circular pool

Figure 1.  Experiment 1: A schematic representation of the pool and the position of the landmark, X, as well as the hidden platform (P). A: Left panel, for acquisition; right panel, for test. B: Mean time spent in the two recording areas (shape and landmark) by the subjects during the test trial. C: Mean time spent in the two recording areas (shape and landmark) by the females (P, proestrus; M, metaestrus) during the test trial. Error bars denote standard error of means.
Figure 2. Experiment 2: A schematic representation of the pool and the position of the landmark, X, as well as the hidden platform (P). A (Top): Left panel, for acquisition; right panel, for Test 1. (Bottom): for Tests 2 and 3. B: Mean time spent in the two recording areas (shape and landmark) by the subjects during test Trial 1. C: Mean time spent in the two recording areas (shape or landmark and control) by the subjects during test Trials 2 and 3 (shape and landmark, respectively). Error bars denote standard error of means.
(i.e., in the absence of the triangular shape), and on the other trial, the triangular shape was present in the absence of the landmark (see Figure 2A bottom panel).

Method

Subjects

The subjects were naive Long Evans rats (*Rattus norvegicus*): 8 males and 8 females, approximately 7 months old at the beginning of Experiment 1; and 12 males and 12 females, approximately 5 months old at the beginning of Experiment 2. The animals were housed in standard cages, $25 \times 15 \times 50$ cm, in groups of two and were maintained on ad lib food and water, in a colony room with a 12:12-hr light–dark cycle. They were tested within the first 8 hrs of the light cycle.

Apparatus

The apparatus was a circular swimming pool made of plastic and fiberglass and modeled after that used by Morris (1981). It measured 1.58-m in diameter and 0.65-m deep, and it was filled to a depth of 0.49-m with water rendered opaque by the addition of 1 c/L of latex. The water temperature was maintained at 22 ± 1 °C. The pool was situated in the middle of a large room and mounted on a wooden platform 0.43-m above the floor. To create the triangular shape, two acrylic boards forming an angle of 90° were inserted in the pool resting on platforms at the base, which supported them vertically. The boards were 39.5 cm high, 0.5 cm thick and 112 cm long. The boards rose 9.5 cm above the water surface, so that their top coincided with the pool border. The pool was surrounded by black curtains reaching from the ceiling to the base of the pool and forming a circular enclosure 2.4-m in diameter. A single object was hung from a black false ceiling inside the black enclosure and around the curtains. It was suspended 35-cm above the surface of the water. For all rats in Experiment 1, the object, landmark X, was a plastic beach ball 35 cm in diameter with alternate blue, white, yellow, white, orange and white vertical segments. For all rats in Experiment 2 landmark X was a probably a less salient landmark, a ninepin, with blue and yellow segments. For all rats in Experiment 1, the two sources of information, the landmark and the triangular shape, were presented 180° apart, as shown in the left-hand panel of Figure 2A (Experiment 2). On the next, and the rat was placed in the pool in a different location on each trial, as far as possible equally often on the same or opposite side of the pool from the platform, and with the platform to the right or to the left of where the rat was placed. The rats were given five such pretraining trials over two days, with two trials on Day 1, and two on Day 2. Rats were run in squads of eight and spent the intertrial interval (ITI) in small individual compartments.

The procedure for training was similar to that of pretraining with two exceptions. The landmark, X, was always present, as well as the two boards forming the triangular shape, as shown in the left-hand panel of Figure 1A (Experiment 1), and the top panel of Figure 2A (Experiment 2). Finally, the rat was placed in the pool in a different location on each trial, as far as possible equally often with the platform to the right, to the left or in front of where the rat was placed (at I, II, and III of the previous figures). Rats were given eight trials per day over five days (a total of 40 trials). These trials had an ITI of 8–10 minutes, and the platform, landmark, and triangular shape were rotated between trials.

Test days consisted of eight training trials (which were identical to the training phase), followed by one test trial without the platform, which was 60 s long. On test trial one (the only test trial for Experiment 1), the two sources of information, the landmark and the triangular shape, were presented 180° apart, as shown in the right-hand panel of Figure 1A and the top panel of Figure 2A. The amount of time the rat spent in two different areas (each of them 0.22-m in diameter—twice the hidden platform diameter), one in front of the landmark and one in front of the shape, was recorded. Each rat was placed in the pool from one specific position (at I and II only, as shown in Figures 1A and 2A).

In Experiment 2 only, this test day was followed by a retraining day (which was identical to the training phase) and by two additional test days (Test Days 2 and 3). On both days, the rats were given eight training trials (which were identical to the training
phase), followed by a single 60-s test trial without the platform. On Test Day 2, 50% of the rats of each sex were tested in the circular pool with the landmark, while the remaining rats were tested in the triangular shaped pool with no landmark. On Test Day 3, all rats received the opposite test trial. The amount of time that the rats spent in the two different but identically sized areas (i.e., the target area close to either the landmark or the previously correct corner and a control area 180° apart, see Figure 2A bottom panel) was recorded in each test. The reason for measuring the time spent in the control area as well as the target area was to check that on the shape test rats could discriminate between these two corners of the triangle, and on the landmark test to check whether they were simply swimming in circles at a certain distance from the wall of the pool.

An alpha level of .05 was adopted for all statistical analyses. Unless otherwise stated, the results and statistics for Experiment 1 are reported before those for Experiment 2. Latencies (sem) to find the platform decreased over the course of the 5 initial pre-training trials. Males decreased from means of 111.0 (6.06) s and 81.4 (22.31) s on Trial 1 to means of 42.6 (14.25) s and 58.7 (27.20) s on Trial 5, and females decreased from means of 99.1 (14.68) s and 113.8 (6.22) s on Trial 1 to means of 20.8 (4.73) s and 69.5 (27.01) s on Trial 5. These decreases in latencies were significant, F(4, 56) = 11.12; F(4, 88) = 14.82. In Experiment 1 only, there was also an interaction between sex and trials, F(4, 56) = 3.04. Simple effects analysis showed that males and females differed on Trial 3 only, where males were faster to find the platform than females, F(1, 13) = 52.90.

Latencies (sem) to find the platform also decreased over the course of the training days. Males decreased from means of 17.7 (3.37) s and 23.7 (2.62) s on Day 1 to means of 8.0 (0.67) s and 7.7 (0.45) s on Day 5, and females decreased from means of 28.7 (3.81) s and 24.9 (4.82) s on Day 1 to means of 9.0 (0.98) s and 9.5 (0.43) s on Day 5. These decreases in latencies were significant, F(4, 56) = 11.12; F(4, 88) = 2.5. In Experiment 1 only, the variable sex (but not the interaction between sex and days) was close to significance (p = .07). Although all rats improved their performance over the course of training, males tended to reach the platform faster than females. In Experiment 2, no other main effect or interaction was significant (Fs < 1.0).

Figures 1B and 2B show the time spent in both the landmark area and the shape area by the two groups during the 60 s of the first test trial. ANOVAS with factors of landmark versus shape and male versus female conducted on these data revealed only a significant interaction between the two factors, F(1, 14) = 4.96; F(1, 22) = 18.68. Neither main effect was significant (Fs < 1.0; Fs < 1.5). Simple effects analysis of the interaction in Experiment 1 showed that female rats spent more time in the landmark area than in the shape area, F(1, 14) = 5.14, whereas males did not differ between the two (F < 1.0). In addition, males spent significantly more time searching for the platform in the shape area than females, F(1, 14) = 7.01. Simple effects analysis of the interaction in Experiment 2 showed that the effect of the two sources of information was significant in both males and in females (Fs(1, 22) = 14.24 and 5.47, respectively). While female rats spent more time in the landmark area than in the shape area, the reverse was true for males.

An ANOVA conducted on the female test data in Experiment 1 (see Figure 1C) that included the variables of estrous cycle (i.e., proestrus and metaestrus phases) and landmark versus shape revealed no significant effect (Fs < 5.5).

Figure 2C shows the time spent in the two recording areas (i.e., the target area and the control area) on each test (i.e., landmark and shape) by the two groups of Experiment 2 during the 60 s of test Trials 2 and 3. Males’ performance is shown in the left-hand panel of Figure 2C, whereas females’ performance is shown in the right-hand panel. T tests were used to compare rats’ performance in each target area with its control area. The time in the target areas differed significantly from that in the control areas on all test trials [t(11) = 8.50, 9.26, 10.92, and 12.33; males target shape vs. control, males target landmark vs. control, females target shape vs. control, and females target landmark vs. control, respectively]. The implication is that both males and females had learned about both the landmark and the correct corner. But Figure 2C also suggests that males’ performance on the shape test was better than their performance on the landmark test, and better than females’ performance on either test. An ANOVA on the time spent in the target area on landmark and shape tests showed that performance on the shape test was better than on the landmark test, F(1, 22) = 5.10, males performed better than females, F(1, 22) = 9.23, and that there was a significant interaction between these two factors, F(1, 22) = 7.57. Simple effects analyses showed that males performed better on the shape test than the landmark test, F(1, 22) = 12.55, but that females did not differ on the two tests (p = .73). In addition, males spent more time searching for the platform in the target area on the shape test than females, F(1, 22) = 11.22, whereas males and females did not differ on the landmark test (F < 1).

Although the results of Figure 2B might be taken to show that males had learned the spatial task by geometry only, and females had learned by landmark only, the results of Figure 2C provide a quite different picture. In spite of the different preferences shown in Figure 2B, it is clear from Figure 2C that both males and females had learned to find the platform using both sources of information (i.e., the landmark and the shape of the pool). When the two sources of information were tested one by one, the searching behavior was more strongly controlled by the shape of the pool than by the landmark in male rats, while such a differential control was not found in females. In addition, a clear male advantage was found on shape learning.

**Discussion**

In both experiments reported here, there was little or no difference between males and females in their initial speed of learning to find the submerged platform in the Morris pool—either during pretraining in the circular pool with no landmarks present, or during subsequent training when the platform was located in one particular corner of the triangular-shaped pool, next to a landmark situated outside the pool. This suggests that females are no more likely than males to spend time exploring the pool rather than swimming directly to the platform (for the same result, see Forcano et al., 2009).

The more important result, obtained in both experiments, was that when rats were tested without the platform in the presence of the landmark and the shape, put into conflict by presenting them 180° apart, a clear sex difference appeared. Males tended to use the geometric information given by the shape of the pool, whereas
female rats relied more on the landmark. Thus, Experiments 1 and 2 showed that males and females differ in their preference for using a landmark or geometry when solving a simple spatial task. These results are in agreement with previous findings showing that male and female rats do not use the same cues when solving spatial tasks (Williams et al., 1990; Roof & Stein, 1999).

The further tests given in Experiment 2 revealed that both males and females had learned to find the platform using both sources of information. When the landmark and the shape were tested alone, the results showed that both males and females had learned something about their less preferred source of information. This finding seems to contradict the claim of Williams et al. (1990), who suggested that whereas male rats are predisposed to attend to a single aspect of the environment (global shape), female rats use multiple environmental cues (global shape and landmarks). According to these authors, when multiple sources of information are presented together, male rats learn the geometric relations between food and the overall shape of the environment, and that these sources of information overshadow all other cues. In contrast, they suggested, female rats process and use both geometric and nongeometric sources of information when they are presented together. The results of Tests 2 and 3 of Experiment 2 showed that both males and females process and use both geometric and nongeometric sources of information when they are presented together. It is true that the different measures of the three test trials gave quite different results, showing a clear distinction between learning and performance. On test Trial 1, female rats showed no evidence of having learned much about shape, whereas males did not seem to know much about the landmark. Test Trials 2 and 3, however, clearly revealed that such was not the case. Using a variety of tests was crucial to know what the rats had learned. Experiment 2 did, however, confirm a clear male advantage on shape learning. On the test trial with the triangular pool and no landmark, males were significantly more accurate than females.

The results of the present experiments are consistent with the human literature, which shows that men outperform women in a number of spatial tasks (for reviews see Kimura, 1999; Mackintosh, 1998). In the spatial domain, a crucial question to answer is how an environment is represented by males and by females. Dabb et al. (1998) suggested that women focus on factors related to personal, concrete representations of the environment (e.g., left-right and landmarks), whereas men focus on abstract factors related to a Euclidean representation of the environment (e.g., distance and cardinal directions). Furthermore, they found that when people give navigational instructions to others, men use more cardinal directions, such as north or south, and women use more topological/landmark descriptions, such as buildings and other visual objects along a route (i.e., list learning). Men and women seem to differ in their use of topographic or Euclidian navigation strategies. The sexes also differ in geographical knowledge, even when education, region of residence and travel experience has been controlled (Beatty & Troster, 1987). Moreover, when self-report questionnaires have been used, males show greater confidence than females in their own spatial ability, whereas females show higher levels of spatial anxiety, more fear of getting lost (Lawton, 1994; Schmitz, 1997).

We have noted in the introduction that the human sexual dimorphism has been observed on a wide variety of spatial tasks, including route and map learning, computer based or virtual reality versions of the Morris pool, and other virtual tasks. Moreover, a similar difference has also been obtained in experiments conducted in real environments: buildings, big mazes and university campuses (e.g., Lawton, Charleston, & Zieles, 1996; Saucier et al., 2002; Schmitz, 1997). Saucier et al. (2002) asked whether the observed differences in navigational skill between males and females were caused by differences in preferred strategy or by differences in spatial abilities. Their participants were required to follow either landmark- or Euclidean-based instructions during a navigation task (either in the real-world, Experiment 1, or on paper, Experiment 2). The results showed that men performed best when using Euclidean information (distances and directions), whereas women performed best when using landmark information. The authors suggested that there is a systematic difference in the ability to use these two types of spatial information. Subsequent research (Saucier, Bowman, & Elias, 2003) has found that women rely on linguistic information more than men when navigating, regardless of the type of instruction. Dabb et al. (1998) suggested that the different strategies result from dimorphic exploration and encoding of spatial information by men and women. Such hypothesis was seriously questioned after one experiment by MacFadden, Elias, and Saucier (2003) in which eye movements were recorded as people studied routes on a map, and then the participants were asked to provide directions along those routes. The map contained intersections, traffic lights, landmarks and a legend with a distance scale and compass. The results showed that although male and female participants later described routes with different terms and strategies, their eye movements did not reveal systematic differences in how the map was explored. Thus, no evidence was found that sex-related navigation strategies are related to selective exploration of the map.

An important claim (Coluccia & Louse, 2004) is that sex differences tend to appear only when the task is difficult. In other words, that orientation tasks high in cognitive demands are accompanied by sex difference while orientation tasks low in cognitive demands are not. The present results provide little support for this suggestion. Whereas it is not obvious what would count as an easy or a difficult task, in both the present experiments, rats swam rapidly to the platform within 40 training trials, and performed accurately on subsequent test trials. Finding this difference in rats perhaps suggests that the difference in people has nothing to do with language. Both the human and the rat data are consistent with the hypothesis that a sex difference in spatial cognition arises only when there is a difference between the sexes in range size: in people that difference arises largely because men hunted and women gathered; in other animals it could arise from the fact of a polygynous mating system requiring males that mate with more than one female in a single breeding season to have larger ranges. But both have the same consequence—a difference in range size, which is the more proximal cause of the difference in spatial cognition.

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