



AQ: 1 Geometry Learning While Navigating: The Importance of Task Difficulty and Sex Differences

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Cheng (1986) trained male rats to search for food in a rectangular arena that also contained distinctive visual patterns. He found that the rats used mainly the geometric framework of the box itself to find the food and claimed that geometrical information is processed in a specialized module, which is independent of feature information. The aim of the present set of experiments was to check if the previous results with male rats and an appetitive task could be extended to an aversive task while using both male and female rats and three-dimensional landmarks. In Experiments 1 and 2, rats were trained in a rectangular-shaped pool to find a hidden platform that had a location defined in terms of two sources of information—landmarks of different salience (less salient in Experiment 1, more salient in Experiment 2) outside the pool and a particular corner of the pool. The results showed that both males and females used mainly the particular corner of the pool, supporting Cheng’s suggestion. In addition, in the two experiments, what the rats learned with respect to the landmarks was negligible. Experiment 3 used a more difficult triangular pool in addition to the rectangular pool, in the absence of landmarks. The results revealed sex differences in the triangular pool but not in the easier rectangular pool. These results suggest that task difficulty is a factor when it comes to finding sex differences in rats in spatial tasks.

Keywords: geometry learning, landmark learning, modified Morris pools, rats

Cheng (1986) was the first author to present evidence that rats can use geometrical information to locate a hidden goal. He trained male rats in a rectangular arena, where the two short walls of the arena and one of the long walls were black, while the other long wall was white. In addition, distinctive visual patterns, as well as other nongeometrical cues, were placed in each of the four corners of the arena. Food was buried in one corner, and the rats had to search for it. Although the rats rapidly learned to search in the

correct corner for the food, they also made frequent rotational errors searching in the corner diagonally across from the one where the food was hidden (i.e., the corner geometrically identical to the correct one). These results are surprising because the geometry of the arena gained control over the rats’ behavior even though there was a specific visual pattern, as well as other nongeometrical cues, in the correct corner, which were better predictors of the hidden food. Cheng (1986) concluded that the rats used the geometrical framework of the arena itself (see also Gallistel, 1990).

According to Cheng (1986) and Gallistel (1990; see also Cheng & Gallistel, 1984), learning about geometry (i.e., like the metric relations of distances and angles between a target place and the shape of an apparatus) occurs in a specialized module, which is impenetrable to nongeometrical information (although see Cheng, 2008; Cheng & Newcombe, 2005). Features such as landmarks are considered to be related to this featureless metric frame by means of address labels (see Cheng, 1986, p. 172). Subsequent work by Pearce et al. (for a review, see Pearce, 2009) has confirmed that male rats can use any pool geometry—like rectangular, triangular, and kite-shaped pools—to locate a hidden platform (i.e., aversive tasks). Most importantly, when cue competition effects (like

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McGregor, 2006), being the salience of both cues, geometrical and non-geometrical, critical variables (Horne & Pearce, 2009; Kosaki, Austen, & McGregor, 2013; Mesa, Osorio, Ballesta, Marimon, & Chamizo, 2017). In the study by Mesa et al. (2017), it was shown that changing the salience of a landmark could strongly affect the preference for a geometric cue over a landmark cue in male rats.

Importantly, neither Cheng (1986) nor any of the studies mentioned so far have examined sex differences when using rats trained to find a goal in the presence of geometrical and nongeometrical information simultaneously. What would have happened if the rats in Cheng's study—as well as those in the other studies reviewed—had been females? In a related study with female rats in a white rectangular arena, Golob and Taube (2002) trained the rats in a spatial delayed match-to-sample task, in a dry condition and also in a wet condition (in a modified Morris pool), where one short wall of the arena was black, a prominent visual cue. The results revealed that in the wet condition, female rats trained with the visual cue that provided information to differentiate the two geometrically identical corners of the arena learned about both the geometry and the visual cue. In other words, in the wet condition, Golob and Taube (2002) could not replicate Cheng's (1986) results: the rats did not make the frequent rotational errors searching in the corner geometrically identical to the correct one. The authors suggested that the confusion between geometrically equivalent corners may apply to appetitive tasks but may not be present in aversive tasks, such as a Morris pool. However, equally important could be to answer the following question: Was the previous result (Golob & Taube, 2002) obtained because the study was conducted only with female rats? Answering this question is important because it has been shown, in rodents and in humans, that when trained to find a hidden goal in the presence of geometrical and nongeometrical cues, in the two species mentioned, males seem more likely to rely on geometrical information to reach the goal, while females are more likely to use landmarks (in rats, see Rodríguez, Torres, Mackintosh, & Chamizo, 2010; Williams, Barnett, & Meck, 1990; in humans, Sandstrom, Kaufman, & Huettel, 1998; Ward, Newcombe, & Overton, 1986). Moreover, even when only landmark learning is addressed, males seem to learn different things than females about a single landmark that signals the location of a hidden platform (Chamizo, Rodríguez, Torres, Torres, & Mackintosh, 2014; Chamizo, Torres, Rodríguez, & Mackintosh, 2019).

In the study by Williams et al. (1990), rats were trained in a radial maze. After they had reached asymptotic performance, the rats were tested following various manipulations to the geometry of the room or to the landmarks. Provided the geometry of the room was unchanged, males' performance was unaffected by any change to the landmarks, but alteration of the geometry of the testing room disrupted their performance, even when the landmarks were still available for navigation. In contrast, females' performance was disrupted by rearrangement of the landmarks whether the geometry of the room was changed or not, although they were unaffected by the removal of the landmarks provided the geometry of the room was unchanged. The more recent study by Rodríguez et al. (2010) employed a different procedure to demonstrate rather similar effects.

Rodríguez et al. (2010) trained rats in a triangular-shaped pool to find a hidden platform, whose location was defined in terms of two sources of information: one landmark next to the platform, but

outside the pool, and one particular corner of the pool. Subsequent test trials without the platform pitted these two sources of information against one another. They revealed that females spent more time in an area of the pool next to the landmark, while males spent more time in the corner of the pool where the platform had originally been located. Two additional test trials with the two cues presented individually (i.e., learning tests) revealed that both sexes had learned about both cues: males performed significantly better on the shape than the landmark test, while females performed equally well on both. In addition, a clear male advantage was found on shape learning (i.e., the geometrical cue).

A subsequent study by Rodríguez, Chamizo, and Mackintosh (2011), where cue competition designs were used, confirmed the previous conclusion that shape is clearly more salient for males, and landmarks more salient for females. Employing the same apparatus and general procedure as Rodríguez et al. (2010), this new set of experiments showed an asymmetrical overshadowing effect in both sexes. In males, shape overshadowed landmark learning, but landmark learning did not overshadow learning about shape; while in females, landmark learning overshadowed learning about shape, but shape learning did not overshadow landmark learning. It was the more discriminable, salient, or preferred source of information (shape or pool-geometry for males and a landmark for females, as shown by Rodríguez et al. 2010) that overshadowed the less discriminable, salient, or preferred cue. Taken together, the clear implication is that the rules that govern learning about the shape of the environment (Cheng, 1986; Gallistel, 1990), or its boundaries (Doeller & Burgess, 2008), are not necessarily different to those that govern learning about landmarks. A question that deserves an answer is, can the previous sex differences be generalized to any pool shape, like a rectangular one?

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The aim of the present set of experiments was to replicate the study by Cheng (1986) but with both male and female rats and while employing a different apparatus, a modified Morris pool—as in the wet condition of Golob and Taube's (2002) work. The task was similar to that in Experiment 2 of Cheng's (1986) study—an appetitive reference memory task—although it was aversive instead of appetitive. The rats were trained in a rectangular-shaped pool to find a hidden platform that had a location defined in terms of two sources of information: one specific landmark next to the platform (a target landmark), but outside the pool, and one particular corner of the pool.

Importantly, we should mention that in previous studies (Rodríguez et al., 2010, Experiment 1; Rodríguez, Chamizo, et al. (2011), Experiments 1 and 2a), we examined the possibility that the estrus cycle of females could influence their performance. Before the experiments began, the rats were examined for 8 days to establish the estrus cycle by a daily collection of vaginal smears. During the experiments, they continued to be examined every day, and on test days, they were examined both before and after the experimental session to ensure that they did not change over to the next estrus cycle phase during testing. An ANOVA conducted on the female test data that included the variables of estrus cycle (i.e., high and low level of estradiol) and landmark versus shape revealed no significant effect of estrus cycle on preference for landmark or geometry in any of the experiments (for the same results with a similar or related task, see Keeley, Tyndall, Scott, & Saucier, 2013; Rodríguez, Aguilar, & Chamizo, 2011). Given these null

results, we did not measure the rats' estrus cycle in the present experiments in order to avoid unnecessarily stressing them.

Experiment 1

Experiment 1, a preliminary experiment, was conducted with male and female rats separately (Experiment 1a with males and Experiment 1b with females), using a rectangular-shaped pool and different landmarks placed in each of the four corners. The rats were trained to find a hidden platform that had a location defined by both a particular corner of the pool and a particular landmark. The aim of the experiment was to provide information about the basis of the rats' solution of this task.

Based on the results by Cheng (1986) and Rodríguez et al. (2010; see also Golob & Taube, 2002), we predicted that the searching behavior would be more strongly controlled by the shape of the pool than by the specific landmark only in male rats (i.e., in Experiment 1a), who would look for the platform both in the correct corner where the platform was hidden and in the corner diagonally across from it (i.e., the geometrical identical corner). However, such a differential control would not be found in females (i.e., in Experiment 1b), where less rotational errors were expected because the specific target landmark, the one placed very near the correct corner, would easily disambiguate the two geometrically identical corners. Would that be the case?

Method

Subjects. The subjects were naive Long Evans rats (*Rattus norvegicus*): eight males approximately 3 months old at the beginning of Experiment 1a and eight females approximately 3 months old at the beginning of Experiment 1b. Experiment 1a was conducted first, followed by Experiment 1b. The animals were housed in standard cages, 25 × 15 × 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 hr of the light cycle. In Experiment 1 (as well as in Experiments 2 and 3), all animal treatment and care abided by the ethical principles of the University of Barcelona regarding the care and use of animals for scientific purposes, as well as by the corresponding principles of the European Community (EEC Council Directive 86/609/EEC).

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 0.40 m deep, and it was filled to a depth of 0.30 m with water rendered opaque by the addition of 1 cL/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 rectangular shape, four acrylic boards forming a rectangle were inserted in the pool resting on platforms at the base, which supported them vertically. Two boards, the short ones, were 39.5 cm high, 0.5 cm thick, and 58 cm long. The resting two boards, the large ones, were 39.5 cm high, 0.5 cm thick, and 145 cm long. The top of the boards was 9.5 cm above the water surface—that is, at the same height as the outer wall of the pool. 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. In each of the four box's corners, a single object

was hung from a black false ceiling inside the black enclosure and around the curtains. They were suspended 35 cm above the surface of the water. Both in Experiment 1a and in Experiment 1b, four different objects or landmarks were used. They were located at positions A, B, C, and D as follows: at A, a 6.5-cm diameter white can, 12 cm high; at B, a white ninepin, 6 cm in diameter at the base and 16.5 cm in height, with the wider part measuring 26 cm in circumference; at C, a white funnel, 10 cm in diameter at the top and 14 cm in height, with the narrowest part at the base measuring 1 cm in diameter; and at D, an 8-cm diameter white cup, 9 cm high. Importantly, all four landmarks (as well as those used in Experiment 2) looked the same from all perspectives in order to avoid unwanted problems in the females (Chamizo et al., 2014; Torres, Rodríguez, Chamizo, & Mackintosh, 2014).

To ensure that the rats used the information provided by the two sources of information (the geometry of the pool and the landmarks) to locate the platform, rather than any inadvertently remaining static room cues (like noises from pipes and air conditioning), the landmarks, the four boards, and the platform were semirandomly rotated with respect to the room (90°, 180°, 270°, or 360°), with the restriction that all four positions of the room were used each day. A closed-circuit video camera with a wide-angle lens was mounted 1.75 m above the center of the pool inside the false ceiling, and its picture was relayed to recording equipment in an adjacent room. A circular platform 0.11 m in diameter and made of transparent Perspex was mounted on a base that was placed 0.38 m from the point formed by a corner of the pool, with a short wall to the left and a long wall to the right, on a line that bisected the center of the pool, with its top 1 cm below the surface of the water. The landmarks, the hidden platform (P), and the rectangular shape of the pool were situated as shown in Figure 1 (top).

Procedure. There were two types of trials: training and test trials. Training consisted of placing a rat into the rectangular pool with the landmarks present. The rat was given 120 s to find the platform, and once the rat had found it, it was allowed to stay on it for 30 s. If it had not found the platform within the 120 s, it was picked up, placed on it, and left there for 30 s. The platform, landmarks, and rectangular shape were rotated from one trial to the next, and the rat was placed in the pool in a different location on each trial (at I, II, III, and IV in Figure 1, top), as far as possible and equally often on the same or opposite side of the pool from the platform and with the platform to the right or left of where the rat was placed. Rats were given eight training trials over each of 3 days (a total of 24 trials). These trials had an intertrial interval (ITI) of 8–10 min. Rats were run in groups of eight and spent the ITI in small individual compartments.

Finally, there was a test day with eight training trials (identical to the training phase), followed by one test trial without the platform. The test trial was in the presence of the training configuration (i.e., geometry and landmarks) and was 60 s long. To measure the control gained by the geometry of the pool, the amount of time the rat spent in two different areas (i.e., correct and incorrect—C and I, respectively) was recorded, as shown in Figure 2 (top). The correct area was defined as having a short wall to the right and a long wall to the left. Two of the four corners correspond to this description (they are geometrically identical). These two corners were considered the "correct area" (C). The remaining two corners (also geometrically identical) were defined as having a

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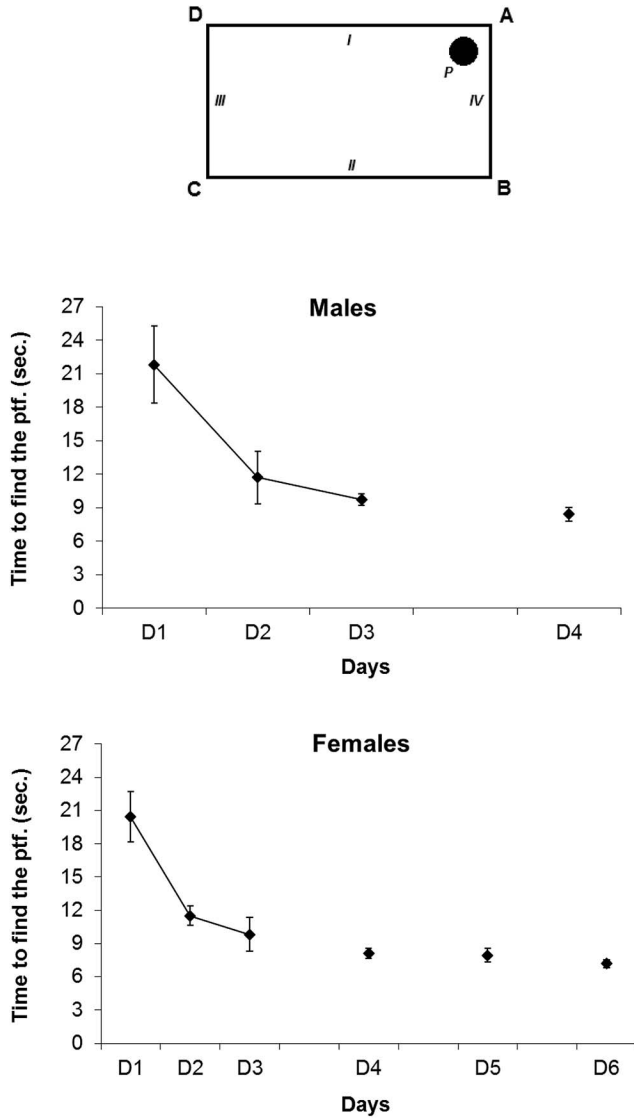


Figure 1. Experiment 1. Top: A schematic representation of the pool and the position of the four landmarks, A, B, C, and D, as well as the hidden platform, P (I, II, III and IV indicate the four starting positions) for acquisition. Middle: Mean escape latencies for the rats of Experiment 1a (males). Error bars denote standard errors of the means. Bottom: Mean escape latencies for the rats of Experiment 1b (females). Error bars denote standard errors of the means.

Statistical analysis. In Experiment 1 (as well as in Experiments 2 and 3), the data were analyzed using analysis of variance (ANOVA) and subsequent *t* tests and report partial eta squared (η_p^2) to estimate effect sizes. An alpha level of .05 was adopted for all the statistical analyses. The Bayes factor (BF) estimate has been included in statistical significance cases to complement significant ANOVA results. This value allows to show the likelihood of the model analyzed in relation, in this case, to the null model. It should be entered as a score that indicates the improvement implied by the proposed model in relation to the variance explained by each factor.

Results and Discussion

Unless otherwise stated, the results and statistics for Experiment 1a (i.e., males) are reported before those for Experiment 1b (i.e., females). **Figure 1** shows the mean escape latencies of the two sexes (1B males, 1C females—Experiments 1a and 1b, respectively)—in males, during both the training and the escape trials of the test day (day 4 in **Figure 1**, middle); in females, during the training, the escape trials of the first test day (day 4 in **Figure 1**, bottom), and the retraining day and the escape trials of the second test day (days 5 and 6 in **Figure 1**, bottom). Latencies (standard error of the

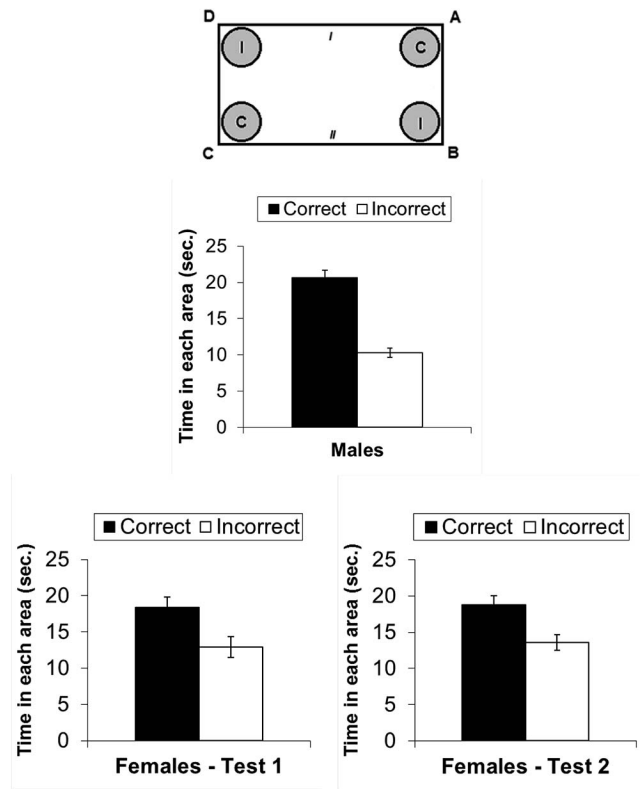


Figure 2. Experiment 1. Top: A schematic representation of the pool and the position of the four landmarks, A, B, C, and D (I, and II indicate the two starting positions) for testing the control gained by the geometry of the pool. Middle: Mean time spent in the two recording areas (Correct and Incorrect) by the male rats –Experiment 1a– during the test trial. Bottom: Mean time spent in the two recording areas (Correct and Incorrect) by the female rats –Experiment 1b– during the test trials.

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long wall to the right and a short wall to the left. These two corners were considered the “incorrect area” (I). To measure the control gained by the landmarks (especially by landmark A), the amount of time the rat spent in each of the four recording areas was also measured individually, as shown in **Figure 3** (top). Each of the four recording areas in **Figures 2** (top) and **3** (top) was 0.22 m in diameter, twice the hidden platform diameter. Rats were placed in the pool individually from one specific position (at I and II only, as shown in **Figures 2** and **3**, top). Following the test day, female rats received one further day of escape training (a total of eight trials), the procedure being the same as before, followed by a further test day, the same as before.

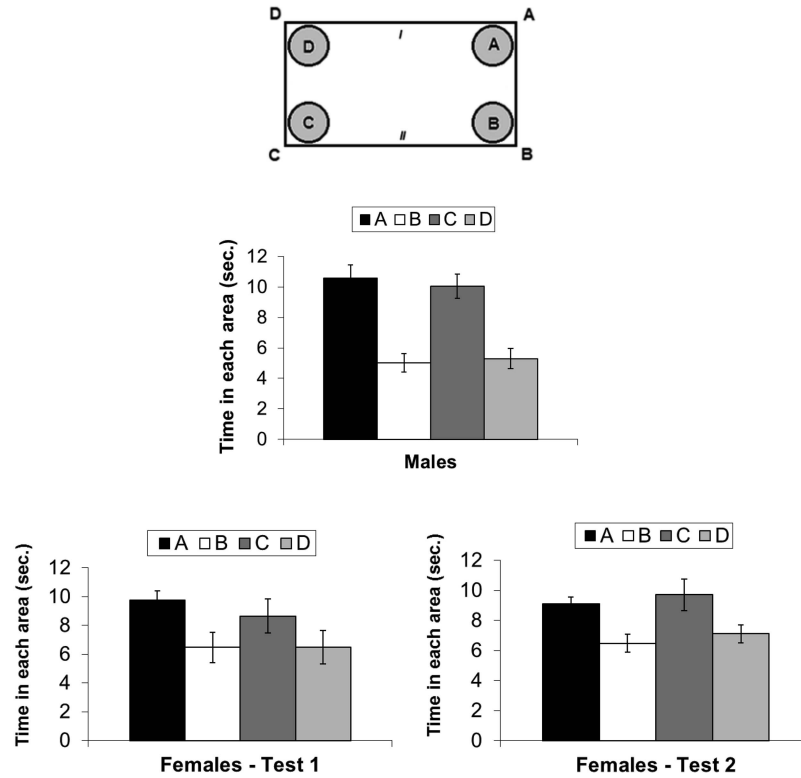


Figure 3. Experiment 1. Top: A schematic representation of the pool and the position of the four landmarks, A, B, C, and D (I, and II indicate the two starting positions) for testing the control gained by the landmarks. Middle: Mean time spent in the four recording areas (A, B, C, and D) by the male rats –Experiment 1a– during the test trial. Bottom: Mean time spent in the four recording areas (A, B, C, and D) by the female rats –Experiment 1b– during the test trials.

mean [sem]) to find the platform decreased over the course of the training days. Males decreased from a mean of 21.81 s on day 1 to a mean of 9.72 s on day 3, and females decreased from a mean of 20.44 s on day 1 to a mean of 9.83 s on day 3. These decreases in latencies were significant, $F(2, 14) = 11.20, p = .001, MSE = 30.01, \eta_p^2 = .62, BF_{10} = 60.28$; and $F(2, 14) = 19.07, p < .001, MSE = 13.65, \eta_p^2 = .73, BF_{10} = 774.27$. All rats improved their performance over the course of training (as shown in Figure 1, middle and bottom).

Figure 2 (middle: males; bottom: females) shows the time spent in the correct and incorrect areas (i.e., in C and I), while measuring the control gained by geometry, during the 60 s of the test trials. ANOVAS conducted on the data of the first test trial revealed that the two areas differed in males only, $F(1, 7) = 93.45, p < .001, MSE = 4.55, \eta_p^2 = .93, BF_{10} = 77,267.52$; in females, $F(1, 7) = 4.26, p = .078, MSE = 28.16, \eta_p^2 = .38, BF_{01} = 0.25$. Male rats spent more time looking for the platform in the correct area than in the incorrect area, as shown in Figure 2 (middle). The results of the second test trial by the females, given after an additional day of landmark training, are shown in Figure 2 (bottom right). An analysis on these data revealed that the correct and incorrect areas differed, $F(1, 7) = 5.66, p = .049, MSE = 19.29, \eta_p^2 = .45, BF_{10} = 8.00$. In the second test trial, female rats spent more time looking for the platform in the correct area than in the incorrect area.

Figure 3 (middle: males; bottom: females) shows the time spent in each of the four recording areas (i.e., A, B, C, and D), while measuring the control gained by the landmarks (specifically, by landmark A), during the 60 s of the test trials. ANOVAS conducted on the data of the first test trial revealed that the four recording areas differed in males only, $F(3, 21) = 15.35, p < .001, MSE = 4.65, \eta_p^2 = .69, BF_{10} = 14,604.24$; in females, $F(1, 7) = 2.04, p = .139, MSE = 10.60, \eta_p^2 = .23, BF_{01} = 0.77$. Additional comparisons in the males revealed that the rats spent the same time in A and C (in the correct area according to the geometry of the apparatus), $t(7) = 0.39, p = .709, d = 0.14, BF_{01} = 2.79$, but they spent more time in A than in B and D (in the wrong area according to the geometry of the apparatus), $t(7) = 4.77, p = .002, d = 1.69, BF_{10} = 23.14$, and $t(7) = 5.26, p = .001, d = 1.86, BF_{10} = 36.12$, respectively. The results of the second test trial by the females, given after an additional day of landmark training, are shown in Figure 3 (bottom right). An analysis on the data of the second test trial revealed that the four recording areas differed, $F(3, 21) = 3.79, p = .026, MSE = 5.06, \eta_p^2 = .35, BF_{10} = 7.53$. Additional comparisons revealed that the females spent the same time in A and C, $t(7) = -0.56, p = .593, d = -0.20, BF_{01} = 2.61$, but they spent more time in A than in B, $t(7) = 2.85, p = .025, d = 1.01, BF_{10} = 3.24$, and D (where a very clear tendency was found), $t(7) = 2.32, p = .053, d = 0.82, BF_{10} = 1.81$.

In conclusion, in Experiment 1a, male rats spent more time looking for the platform in the correct area (C) than in the incorrect one (I). This result reveals that geometry was very salient for the males. That was not the case with the landmarks because looking for the platform in front of A (a landmark that had always indicated the hidden platform during training) was the same as looking for the platform in front of landmark C (a landmark that had never indicated the hidden platform during training). Surprisingly, the same results were obtained in Experiment 1b, with female rats, after additional landmark training, in the second test trial. Therefore, we must conclude that the results of both males and females seem consistent with those obtained by Cheng (1986), working only with male rats and an appetitive task.

Experiment 2

In Experiment 1, we predicted that the searching behavior would be more strongly controlled by the shape of the pool than by the specific landmark only in male rats but that such a differential control would not be found in females, where less rotational errors (Cheng, 1986) were expected. Our predictions were confirmed in males but not in females. With enough training, all the rats spent more time looking for the platform in the correct area (C) than in the incorrect one (I), and landmark A, the target landmark, did not disambiguate the two corners neither for males nor for females.

However, admittedly, one problem in Experiment 1 could have been that the landmarks were not salient enough. In addition, they were not counterbalanced, and males and females were run separately. The aim of Experiment 2 was to address these problems, as well as to better clarify the results of the test trials by giving specific learning tests (i.e., by presenting the two cues, geometrical and nongeometrical, individually—the rectangular pool in the absence of the landmarks and the landmarks in a circular pool). The present experiment also incorporated three more procedural changes from Experiment 1. First, pretraining trials were introduced in order to reduce the possibility that on the landmark test, the use of a novel-shaped pool, a circular one, might disrupt the rats' performance. Moreover, these trials are a good control for thigmotaxis (i.e., wall hugging, rats' natural proclivity to stay near the perimeters of a novel environment; see Treit & Fundytus, 1988). Second, the experiment was run with only two bigger landmarks, counterbalanced (instead of four smaller ones as in Experiment 1), in the hope that this manipulation could facilitate landmark learning. Finally, the training phase lasted 4 days (instead of 3 as in Experiment 1), and it was followed by 3 test days. Following the training and test phase, the rats received 4 further days of escape training, followed by 3 further test days, all the same as before.

Method

Subjects. The subjects were 16 naive Long Evans rats (*Rattus norvegicus*): eight males and eight females approximately 3 months old at the beginning of the experiment. They were divided into two groups, Group Males and Group Females, matched for latency to find the platform on pretraining trials. The animals were housed in same-sex groups of two and kept and maintained as in

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Apparatus. The rectangular pool and the experimental room were the same as in Experiment 1. In two of the four box's corners

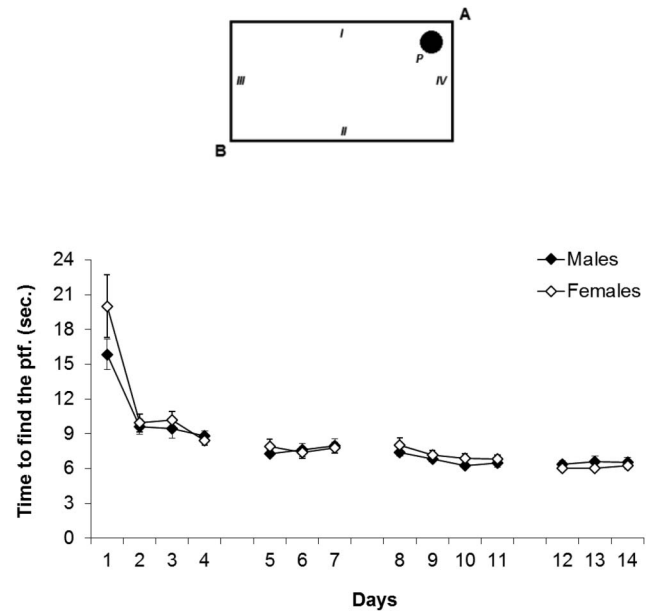


Figure 4. Experiment 2. Top: A schematic representation of the pool and the position of the two landmarks, A and B, as well as the hidden platform, P (I, II, III and IV indicate the four starting positions) for acquisition. Bottom: Mean escape latencies for the rats of Experiment 2. Error bars denote standard errors of the means.

(i.e., in the correct corner where the platform was hidden and in the corner diagonally across from it), a single object was hung from a black false ceiling inside the black enclosure and around the curtains. They were suspended 35 cm above the surface of the water. The two landmarks used were A: a white cylinder, 15.5 cm in diameter and 24.5 cm in height, and B: three yellow mopheads attached together, forming a cylindrical figure 12 cm in diameter and 22 cm high. The hidden platform (P), the landmarks, and the geometry of the pool were situated as shown in Figure 4 (top). F4

Procedure. There were three types of trials: pretraining, training (both escape trials), and test trials. Pretraining consisted of placing a rat into the circular pool without the landmarks or boards but with the hidden platform present. The rat was given 120 s to find the platform, and once the rat had found it, it was allowed to stay on it for 30 s. If it had not found the platform within the 120 s, it was picked up, placed on it, and left there for 30 s. The platform was moved from one trial to the next, and the rat was placed in the pool in a different location on each trial, as far as possible and equally often on the same or opposite side of the pool from the platform and with the platform to the right or left of where the rat was placed. Rats were given five such pretraining trials over 2 days, with two trials on day 1 and three on day 2.

The procedure for training was similar to that of pretraining, although with a few exceptions. The four boards forming the rectangular-shaped pool as well as the two landmarks were present, as shown in Figure 4 (top), and it lasted 4 days instead of 3 (as

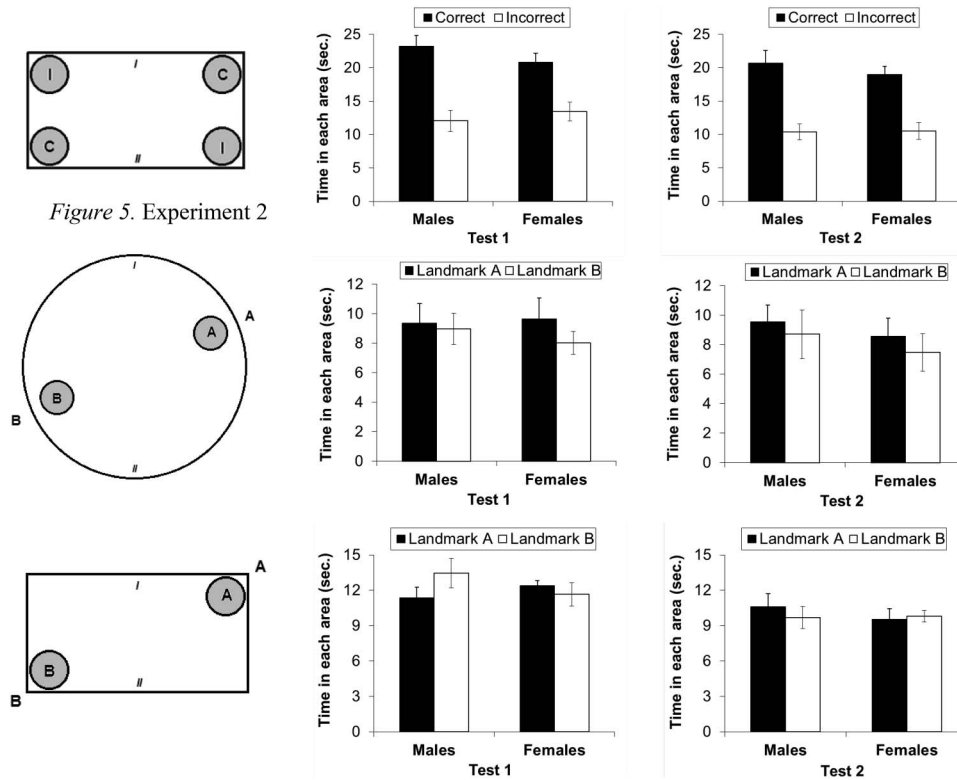


Figure 5. Experiment 2. Top: left, a schematic representation of the pool (I, and II indicate the two starting positions) for the geometry test; between, mean time spent in the two recording areas (Correct and Incorrect) by the rats during the first test trial; right, mean time spent in the two recording areas (Correct and Incorrect) by the rats during the second test trial. Middle: left, a schematic representation of the pool (I, and II indicate the two starting positions) for the landmark test; middle, mean time spent in the two recording areas (A and B) by the rats during the first test trial; right, mean time spent in the two recording areas (A and B) by the rats during the second test trial. Bottom: left, a schematic representation of the pool (I, and II indicate the two starting positions) for the training configuration test; middle, mean time spent in the two recording areas (A and B) by the rats during the first test trial; right, mean time spent in the two recording areas (A and B) by the rats during the second test trial. Error bars always denote standard errors of the means.

in Experiment 1). As in pretraining, the rat was placed in the pool in a different location on each trial, as far as possible and equally often with the platform to the right, to the left, where the rat was placed (at I, II, III, and IV of the previous figure). Rats were given eight trials per day over 4 days (a total of 32 trials). These trials had an ITI of 8–10 min, and the platform, landmarks, and rectangular shape were rotated between trials. Rats were run in groups of eight and spent the ITI in small individual compartments.

At the end of training, all the rats received 3 test days. Each day consisted of eight retraining trials (identical to the training trials), followed by a single test without the platform that was 60 s long. One day, the animals were tested in the rectangular pool, without the landmarks (i.e., a geometry learning test). Another day, the animals were tested in the circular pool, with landmarks A and B present (i.e., a landmark learning test). Finally, the animals were tested in the presence of the training configuration (i.e., in the rectangular pool and with A and B present), as shown in Figure 5 (left-hand panels of top, middle, and bottom, respectively). The three test trials were counterbalanced. When testing geometry learning, the amount of time the rat spent in two different areas

(i.e., correct and incorrect—C and I in the previous Figure 5, top left panel) was recorded. When testing landmark learning, the amount of time the rat spent in the recording areas in front of A and in front of B (A and B in the previous Figure 5, middle left panel) was recorded; this was also the case when testing the training configuration, the rectangular pool with the landmarks present (A and B in the previous Figure 5, bottom left panel). Each rat was placed in the pool from one specific position (at I and II only, as shown in the previous Figure 5, left-hand panels of top, middle, and bottom, respectively). Following the test days, all rats received 4 further days of escape training (a total of 32 trials), the procedure being the same as before, followed by 3 further test days, the same as before.

Results and Discussion

Latencies to find the platform decreased over the course of the five initial pretraining trials. Males decreased from a mean of 102.59 s on trial 1 to a mean of 46.51 s on trial 5, and females decreased from a mean of 104.41 s on trial 1 to a mean of 39.85

s on trial 5. A mixed ANOVA conducted on these data taking into account the variables trials (1–5) and sex showed that the only significant variable was trials, $F(4, 56) = 8.93, p < .001, MSE = 1134.56, \eta_p^2 = .39, BF_{10} = 6266.29$. No other main effect or interaction was significant ($F_s < 0.5$). All rats improved their performance as pretraining trials progressed. These results revealed that male rats achieved neither shorter latencies nor shorter path lengths in finding the platform, compared with female animals. Consequently, male and female rats did not differ in swim speed.

Figure 4 (bottom) shows the mean escape latencies of the two sexes during the two training phases (days 1–4 and days 8–11 in Figure 4, bottom) as well as the escape trials of all the test days (days 5–7 and days 12–14 in Figure 4, bottom). Latencies (sem) to find the platform decreased over the course of the training days. A mixed ANOVA conducted on these data taking into account the variables days (1–4) and sex revealed that the only significant variable was days, $F(3, 42) = 24.75, p < .001, MSE = 11.95, \eta_p^2 = .64, BF_{10} = 3.034e + 8$. All rats improved their performance over the course of training (days 1–4). No other main effect or interaction was significant ($F_s < 2.5$). A second mixed ANOVA conducted on these data taking into account the variables days (8–11) and sex again showed that the only significant variable was days, $F(3, 42) = 6.67, p < .001, MSE = .64, \eta_p^2 = .32, BF_{10} = 61.35$. All rats improved their performance over the course of this second training phase (days 8–11). No other main effect or interaction was significant ($F_s < 1.5$). Figure 4 (bottom) also shows a stable performance by all rats during the escape trials of the test days (days 5–7 and days 12–14, respectively; $F_s < 1.0$).

Figure 5 (top) shows the correct and incorrect areas, C and I (left panel), and the time spent in these areas (i.e., in C and I) during the 60 s of the geometry test trials (middle panel, first geometry test trial; right panel, second geometry test trial). A mixed ANOVA ($2 \times 2 \times 2$) was carried out on the geometry test trials to analyze the effect of the two tests, the effect of the variable area (C and I), and the between-factor sex. The results revealed that the variable tests was significant, $F(1, 14) = 6.72, p = .021, MSE = 11.97, \eta_p^2 = .32, BF_{10} = 1.31$, as well as the variable area, $F(1, 14) = 43.43, p = .001, MSE = 32.01, \eta_p^2 = .76, BF_{10} = 2.015e + 10$. No other main effect or interaction was significant ($F_s < .99$). In the two geometry test trials, all the rats spent more time in the correct area (C) than in the incorrect one (I), thus revealing good geometry learning. Moreover, for all rats, the performance on the first test phase was better than the performance on the second test phase.

Figure 5 (middle) shows the A and B areas in the circular pool (left panel) and the time spent in front of landmark A and in front of landmark B (i.e., in the recording areas A and B) during the 60 s of the landmarks test trials (middle panel, first landmarks test trial; right panel, second landmarks test trial). A second mixed ANOVA ($2 \times 2 \times 2$) was carried out on the landmark test trials to analyze the effect of the two tests, the effect of the variable area (A and B), and the between-factor sex. The results revealed that no main effect or interaction was significant ($F_s < 1.30$). In the landmark test trials, all the rats spent the same time in front of landmark A as in front of landmark B, thus revealing deficient landmark learning.

Figure 5 (bottom) shows the A and B areas in the rectangular pool (left panel) and the time spent in front of landmark A and in front of landmark B (i.e., in the recording areas A and B) during

the 60 s of the training configuration test trials (middle panel, first training configuration test trial; right panel, second training configuration test trial). A final mixed ANOVA ($2 \times 2 \times 2$) was carried out on the training configuration test trials to analyze the effect of the two tests, the effect of the variable area (A and B), and the between-factor sex. The results revealed that the variable tests was significant, $F(1, 14) = 23.56, p = .001, MSE = 3.60, \eta_p^2 = .63, BF_{10} = 44.65$. No other main effect or interaction was significant ($F_s < 2.39$). In the training configuration test trials, all the rats spent the same time in the A and B recording areas, thus revealing that the animals could not discriminate between the two landmarks, A and B. Moreover, for all rats, the performance on the first test phase was better than the performance on the second test phase.

In conclusion, in Experiment 2, both males and females replicated the main results already obtained in Experiments 1a and 1b, but in a single experiment. In the geometry test trials, all rats spent more time in the correct corners of the pool (in C) than in the incorrect ones (in I). This result shows geometry learning. In addition, the landmarks test trials as well as the training configuration test trials revealed that landmarks did not seem to control such behavior. Geometry learning seems to have clearly interfered with learning about the target landmark (i.e., the landmark that was in front of the hidden platform during the escape trials). It is worth noting that the lack of an effect of sex (or interactions with sex) in the different ANOVAs was surprising. As in Experiment 1, these results were expected in male rats, but they were totally unexpected in females.

Experiment 3

One possible explanation of the results of the previous experiments, where no sex differences were found, is to appeal to the concept of task difficulty. If we assume that learning in the present rectangular pool is easier than learning in the unusual triangular pool employed by Rodríguez et al. (2010)—because the swimming surfaces are very different—the results of Experiments 1 and 2 could be consistent with Coluccia and Louse's (2004) suggestion that sex differences tend to appear only when the task is difficult (for a demonstration in a Morris pool, see Forcano, Santamaría, Mackintosh, & Chamizo, 2009). Therefore, navigation tasks that have a high cognitive demand are expected to show sex differences, while navigation tasks with lower cognitive demand are not. We conducted two separate pilot experiments with 32 rats (one experiment with 16 males and another experiment with 16 females) to show that they were slower to find the platform in the more difficult triangular pool (the one used by Rodríguez et al., 2010)—the swimming surface was half the size in the rectangular pool than in the triangular pool. If this factor could determine the level of difficulty of the two tasks, we expected a difference in the speed with which males and females would learn to locate the platform during training: faster in the rectangular pool than in the triangular pool, as was the case. The aim of Experiment 3 was to replicate the major results of the pilot experiments in a single experiment. We predicted a difference in the speed with which males and females would learn to locate the platform during training: faster in the rectangular pool than in the triangular pool. Most importantly, we also predicted a difference in the speed with which male and female rats learned in the triangular pool (i.e., the

more difficult task) but not in the rectangular pool (i.e., the easier task).

Previous research in our laboratory in the triangular pool in the absence of landmarks had shown ambiguous results in the speed with which males and females learned to locate the platform during training. While Rodríguez, Chamizo, et al. (2011) found a significant difference favoring males, Rodríguez and Chamizo (2013) did not find sex differences—in spite of a clear sex difference favoring males on a subsequent test trial. In the only experiment carried out in the rectangular pool (Rodríguez & Chamizo, 2013), no sex differences were found during training. Employing the same triangular-shaped pool as in Rodríguez et al. (2010) and Keeley et al. (2013) found significant differences favoring males, both in the latency to reach the hidden platform and in the length of the trajectories.

Method

Subjects. The subjects were naive Long Evans rats (*Rattus norvegicus*): 16 males and 16 females approximately 5 months old at the beginning of the experiment. They were divided into four groups, Group Triangle males, Group Triangle females, Group Rectangle males, and Group Rectangle females, matched for latency to find the platform on pretraining trials. The animals were housed in same-sex groups of two and kept and maintained as in Experiments 1 and 2.

Apparatus. The rectangular pool and the experimental room were the same as in Experiments 1 and 2. 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. A circular platform 0.11 m in diameter and made of transparent Perspex was mounted on a base that was placed in the triangular shape 0.38 m from the point formed by the corner of the pool, with a straight wall to the left and the circular base of the pool, on a line that bisected the center of the pool, with its top 1 cm below the surface of the water. The hidden platform (P) and the two shapes of the pool were situated as shown in Figure 6 (top; i.e., as in Rodríguez et al., 2010, although without any landmark present).

Procedure. There were two types of trials: pretraining and training (both escape trials). Pretraining consisted of placing a rat into the circular pool without boards but with the hidden platform present. The rat was given 120 s to find the platform, and once the rat had found it, it was allowed to stay on it for 30 s. If it had not found the platform within the 120 s, it was picked up, placed on it, and left there for 30 s. The platform was moved from one trial to the next, and the rat was placed in the pool in a different location on each trial, as far as possible and equally often on the same or opposite side of the pool from the platform and with the platform to the right or left of where the rat was placed. Rats were given five such pretraining trials over 2 days, with two trials on day 1 and three on day 2.

The procedure for training was similar to that of pretraining, although with a few exceptions. The two boards forming the triangular-shaped pool or the four boards forming the rectangular-shaped pool were present, as shown in Figure 6 (top), and it lasted 4 days. As in pretraining, the rat was placed in the pool in a different location on each trial, as far as possible and equally often

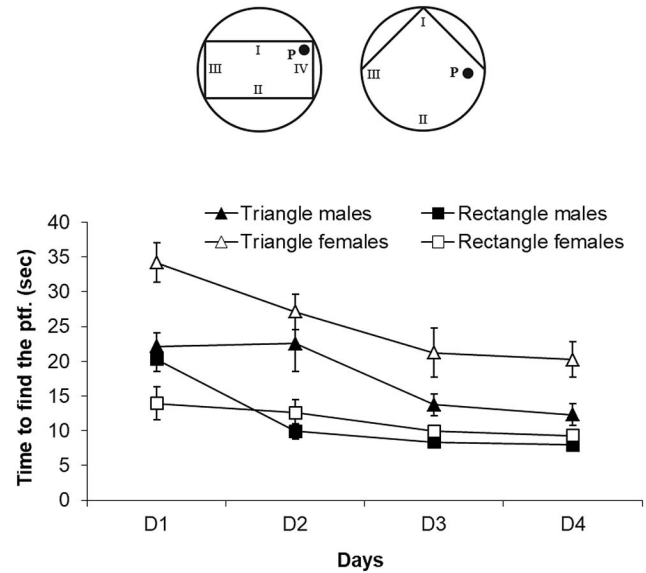


Figure 6. Experiment 3. Top: left, A schematic representation of the rectangular pool, as well as the hidden platform, P (I, II, III and IV indicate the four starting positions); right: A schematic representation of the triangular pool (as in Rodríguez et al., 2010), as well as the hidden platform, P (I, II, and III indicate the three starting positions). Bottom: Mean escape latencies for the rats of Experiment 3. Error bars denote standard errors of the means.

with the platform to the right, to the left, or in front of where the rat was placed (at I, II, III, and IV in the rectangular pool and at I, II, and III in the triangular pool—as shown in Figure 6, top). Rats were given eight trials per day over 4 days (a total of 32 trials). These trials had an ITI of 8–10 min, and the platform and the shapes of the pool were rotated between trials. Rats were run in groups of eight and spent the ITI in small individual compartments.

Results and Discussion

Latencies (sem) to find the platform decreased over the course of the five initial pretraining trials. Males that will train with the rectangular-shaped pool decreased from a mean of 69.75 s on trial 1 to a mean of 44.06 s on trial 5, and males that will train with the triangular-shaped pool decreased from a mean of 95.04 s on trial 1 to a mean of 41.56 s on trial 5. Females that will train with the rectangular-shaped pool decreased from a mean of 100.42 s on trial 1 to a mean of 56.47 s on trial 5, and females that will train with the triangular-shaped pool decreased from a mean of 91.44 s on trial 1 to a mean of 57.47 s on trial 5. An ANOVA conducted on these data, taking into account the variables trials (1–5), group (rectangle, triangle), and sex, showed that only the variable trials was significant, $F(4, 112) = 6.43, p < .001, MSE = 1459.94, \eta_p^2 = .19, BF_{10} = 873.47$. The variable sex was close to significance, $F(1, 28) = 3.13, p = .088, MSE = 4781.77, \eta_p^2 = .10, BF_{10} = 0.54$. No other main effect or interaction was significant ($F_s < 3.0$). All rats improved their performance over the course of pretraining trials.

Figure 6 shows the mean escape latencies of the rats during training. An ANOVA conducted on these data taking into account

the variables days (1–4), group (triangle, rectangle), and sex revealed that the variables days, $F(3, 84) = 19.92, p < .001, MSE = 35.58, \eta_p^2 = .42, BF_{10} = 7.125e + 7$; group, $F(1, 28) = 83.85, p < .001, MSE = 39.24, \eta_p^2 = .75, BF_{10} = 599259.71$; and sex, $F(1, 28) = 12.43, p = .001, MSE = 38.24, \eta_p^2 = .31, BF_{10} = 17.04$, were significant, as well as the triple interaction, $F(3, 84) = 2.86, p = .042, MSE = 35.58, \eta_p^2 = .09, BF_{10} = 1.62$. No other main effect or interaction was significant ($F_s < 2.0$). The analysis of the triple interaction showed that the interaction Group \times Sex was significant on days 1 and 4, $F(1, 28) = 16.67, p < .001, MSE = 40.73, \eta_p^2 = .37, BF_{10} = 78.98$, and $F(1, 28) = 4.37, p = .046, MSE = 21.01, \eta_p^2 = .14, BF_{10} = 5.71$, respectively (see

T1, AQ: Table 1 for the analysis of these interactions), on which the males reached the platform faster than the females only in the triangular pool. A final analysis from the very first trial (i.e., day 1, trial 1) revealed that males and females in the triangular-shaped groups did not differ, $t(14) = -1.35, p = .197, BF_{01} = 1.29$. This result suggests that males learned faster than females throughout the following trials.

An additional ANOVA was conducted in order to clarify these results. In this analysis, all the trials corresponding to starting position IV of the rectangular pool (the one being very close to the hidden platform in Figure 6) have been eliminated, both in males and in females, in order that the two pool shapes can be more safely compared. The results of this new analysis are similar to the previous one: days, $F(3, 84) = 20.05, p < 0.001, MSE = 39.43, \eta_p^2 = .42, BF_{10} = 1.509e + 8$; group, $F(1, 28) = 75.39, p < .001, MSE = 41.13, \eta_p^2 = .73, BF_{10} = 229275.77$; and sex, $F(1, 28) = 9.35, p = .005, MSE = 41.13, \eta_p^2 = .25, BF_{10} = 12.63$, were significant, as well as the interaction Group \times Sex, $F(1, 28) = 16.05, p < .001, MSE = 41.13, \eta_p^2 = .36, BF_{10} = 22.96$. No other main effect or interaction was significant ($F_s < 2.0$). Additional comparisons revealed that the males differed in the two pools, $t(14) = 4.95, p < .001, d = 2.46, BF_{10} = 101.21$, as well as the females, $t(14) = 7.20, p < .001, d = 3.60, BF_{10} = 2639.78$. Most importantly, males performed better than females only in the triangular pool, $t(14) = -4.21, p < .001, d = -2.11, BF_{10} = 32.765$.

All rats improved their performance over the course of training, with rectangle groups reaching the platform faster than triangle groups. These results replicate those of the pilot experiments and clearly indicate a distinct level of difficulty in the two shaped pools. Most importantly, Experiment 3 explicitly shows that males performed better than females only in the triangular pool (i.e., in the more difficult task); males and females did not differ in the

rectangular pool (i.e., in the easier task). In conclusion, males and females learned equally rapidly when they were trained in the rectangular pool, but geometry learning took place more readily in males than in females in the triangular pool. This experiment agrees with the claim that sex differences tend to appear only when the task is difficult, therefore offering an explanation to the results of Experiments 1 and 2.

General Discussion

In Experiment 1 reported here we predicted that the searching behavior would be more strongly controlled by the rectangular shape of the pool than by a specific landmark (i.e., landmark A, the one placed very near the correct corner), only in male rats (Cheng, 1986) but that such a differential control would not be found in females (Golob & Taube, 2002; Rodríguez et al., 2010), where less rotational errors were expected due to landmark A, that would be easily disambiguating the two geometrically identical corners. However, our predictions were not fulfilled. With sufficient training, on the test trials both males (Experiment 1a) and females (Experiment 1b) spent more time looking for the platform in the correct area (C) than in the incorrect one (I), which indicates that geometry was very salient for all the rats. That was not the case with the landmarks, neither for males nor for females, because on test trials looking for the platform in front of landmark A was the same as looking for the platform in front of landmark C (a landmark that had never indicated the hidden platform during training). These results were expected in male rats but totally unexpected in female rats.

Several major changes of procedure were introduced in Experiment 2, which consisted of two groups, one of male rats and another of female rats. There was 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 rectangular-shaped pool, next to a target landmark situated outside the pool. This suggests that females are no more likely than males to spend time exploring the pool rather than swimming to the platform (for the same result, see Forcano et al., 2009). The more important findings obtained in Experiment 2 were that when rats were tested without the platform in the presence of the rectangular shaped-pool alone, the results showed that both males and females had learned equally well about the shape of the pool: all rats spent more time in the correct corners of the pool (in C) than

Table 1
Results of the Triple Interaction (Days \times Group \times Sex) on Days 1 and 4 of Experiment 3

Training	Pool shape/sex	Results	$F(1, 14)$	p	η_p^2	MSE	BF_{10}
Day 1	Triangle:	Males > Females	12.62	0.003	.47	581.53	12.04
	Rectangle:	Males \leq Females	4.58	0.050	.25	162.12	1.74
	Males:	Rectan. = Trian.	0.50	0.493	.03	13.27	0.51
	Females:	Rectan. > Trian.	29.94	<.001	.68	1,639.44	222.67
Day 4	Triangle:	Males > Females	7.18	0.018	.34	251.46	3.46
	Rectangle:	Males = Females	1.32	0.270	.09	6.79	0.66
	Males:	Rectan. > Trian.	6.40	0.024	.31	75.52	2.84
	Females:	Rectan. > Trian.	16.96	0.001	.55	481.47	28.31

Note. BF = Bayes factor; MSE = mean square error. Bolded values represent $p \leq 0.05$.

in the incorrect ones (in I). In addition, when rats were tested without the platform in the circular pool in the presence of the landmarks A and B, the results revealed that both males and females did not differ: for all rats, the landmarks did not seem to control the searching behavior. The same result was found when the learning configuration was tested: for all rats, the landmarks did not seem to control such behavior. In conclusion, Experiment 2 replicated twice and with a better procedure, the main results already obtained in Experiment 1. Geometry learning was superior to landmark learning in Experiments 1 and 2. These results do not replicate the main findings obtained by Golob and Taube (2002) in the wet condition. In this condition, female rats trained with a prominent visual cue that provided information to differentiate the two geometrically identical corners of the rectangular pool learned about both geometry and the visual cue. It is important to note that there are many differences between the present experiments and those of Golob and Taube's work (in the task, in the procedures, in the measures carried out, in the nature of the so-called "nongeometric cue," etc.) that could be responsible for the different results. The present results support Cheng's (1986) suggestion (see also Cheng & Gallistel, 1984; Gallistel, 1990) that rats mainly use geometrical information to locate a hidden goal. We wondered why this is the case in a rectangular pool, but the results are far from clear (Rodríguez et al., 2010; see also Chamizo, Rodríguez, Sánchez, & Mármol, 2016; Keeley et al., 2013; Rodríguez, Chamizo, et al., 2011; Rodríguez, Chamizo, & Mackintosh, 2013; Torres et al., 2014) in a specific triangular pool.

Two different shaped-pools were used in Experiment 3, which consisted of four groups, two of male rats and two of female rats. This experiment addressed only geometry learning (in the absence of the landmarks) and suggested a possible explanation to the previous results: If rats, both males and females, were trained to locate the platform in a rectangular pool, learning was faster than in a triangular pool. The implication is that for all rats geometry learning in the two shaped-pools had a different level of difficulty: reaching the hidden platform in the rectangular pool was easier (i.e., and therefore the rats were faster) than in the triangular pool. Most importantly, a clear male advantage on shape learning was confirmed only when the task was relatively difficult. When learning in the triangular pool (with no landmark present), males showed significant shorter latencies to find the platform than females. This result was not obtained in the rectangular pool, where males and females did not differ. These findings are consistent with Coluccia & Louse's (2004) suggestion that sex differences in the spatial domain tend to appear only when the task is difficult. A study by Forcano et al. (2009) conducted in a Morris pool supports the previous suggestion. Forcano et al. (2009) have shown that when rats were trained to find a hidden platform located some distance away from a single landmark, males learned to swim to the platform faster than females. However, when the problem was made easier by locating the platform closer to the solitary landmark, then males and females learned to swim to the platform equally rapidly. The results of the present Experiments 1 and 2 showed that both males and females had learned only about geometry. This finding seems to contradict a claim of Williams et al. (1990) while working in a radial maze.

Williams et al. (1990) were pioneers in suggesting that whereas male rats are predisposed to attend to a single aspect of the environment (global shape), female rats use multiple environmen-

tal cues (global shape and landmarks). According to Williams et al. (1990), when multiple sources of information are presented together, male rats learn the geometric relations between food and the overall shape of the environment (as claimed by Cheng, 1986), and 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. Partly contradicting these results, in a related set of highly controlled experiments conducted in an unusual triangular pool (i.e., the one used here in Experiment 3), Rodríguez et al. (2010) have shown that both males and females process and use a geometrical and a nongeometrical cue (i.e., the pool shape and one landmark): on test trials without the platform, with the two cues presented individually (i.e., learning tests), performance was always well above chance. In addition, males performed significantly better on the shape than the landmark test, while females performed equally well on both. They also found a clear male advantage on shape learning (i.e., the geometrical cue). However, following training in the rectangular pool in the presence of several landmarks, the results of the test trials of the present Experiments 1 and 2 show that both males and females have processed and used only the geometric source of information, the shape of the pool. The landmarks seem to have been "ignored" by all rats. We are inclined to conclude that the reason is because learning in the rectangular pool is an easy task (see Experiment 3), as first claimed as an interpretative hypothesis by Coluccia and Louse (2004; see also Forcano et al., 2009). This hypothesis can explain the phenomenon of the presence/absence of sex differences in spatial learning depending on the level of difficulty of a task. The swimming surface was half the size in the rectangular pool than in the triangular pool. Moreover, there is also the question of having to discriminate one corner from another—two geometrically different corners in the rectangular pool but three in the triangular pool.

To explain what controls spatial search behavior, an approach emphasizing local features has been proposed (for a review, see Pearce, 2009) instead of an approach emphasizing a global geometrical representation, as claimed by Cheng (1986). According to Pearce, when multiple sources of information are presented together, rats navigate with reference to local rather than global cues provided by their environment. Experiments conducted in areas of distinctive shapes support this claim (Pearce, Good, Jones, & McGregor, 2004), and similar results have been obtained with shapes created by individual landmarks (Esber, McGregor, Good, Hayward, & Pearce, 2005). A clear implication of the previous findings is that rats do not seem to rely on a global representation of their environment. On the contrary, they appear to search for a hidden goal on the basis of its spatial relationship with local cues (for a different claim in humans, see Buckley, Holden, Spicer, Smith, & Haselgrove, 2019). It is therefore possible that in the present experiments, the target landmark and the correct corner of the pool could be regarded simply as beacons of different salience that the rats learned to approach (i.e., beacons are "objects" situated so near the goal that the animal simply has to perceive them in order to locate the goal). Therefore, the rats could learn an instrumental stimulus-response association. The instrumental response would be elicited by the most salient beacon (any geometrically correct corner of the pool for all rats in Experiments 1 and 2, with the rectangular pool). A similar argument could also apply

to Experiment 3, without landmarks, although this experiment deserves further consideration.

Research in both humans and nonhuman animals suggests that the hippocampus is involved in geometry learning. For example, the study by Keeley et al. (2013), with male and female rats, has shown a significant correlation between all measures taken in the triangular-shaped pool and the entorhinal cortex (i.e., EC, the main input region to the hippocampus) volume, but only in males (for a similar result, see Lugo, Torres, & Chamizo, 2018). Because both sexes preferentially used the geometry strategy in this study (Keeley et al., 2013), according to the authors, this suggests a sexual divergence of the reliance on EC for geometric cue-biased spatial navigation. We agree with this suggestion. If males have more sensitivity than females to Euclidean geometry-like distance, sense, and angles (in humans, see Saucier et al., 2002), it could be argued that the use of the hippocampus in the triangular pool probably favors the speed at which male rats localize the hidden platform. Therefore, the previous divergence found in males and females (Keeley et al., 2013) could help to explain the sex differences obtained in the present Experiment 3. All the previous results are consistent with the claim that males and females often rely on and use different neural structures for spatial navigation. Female rats tend to be more caudate-dependent animals than male rats, who are more hippocampal-dependent animals (for a pioneering study, see Roof, Zhang, Glasier, & Stein, 1993). The present experiments imply that the caudate nucleus could be compensating a decreased hippocampal function in the females in the easy task (i.e., in the rectangular-shaped pool) but not in the more difficult one (i.e., in the triangular-shaped pool). Research in male rodents has suggested that the caudate nucleus and the hippocampus can function independently (Packard & McGaugh, 1996; White & McDonald, 2002; in human navigation, see Bohbot, Del Balso, Conrad, Konishi, & Leyton, 2013; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003).

There is abundant research (both in rodents and in humans) showing that males and females often use different types of information in spatial navigation. Males prefer geometry as a source of information, whereas females tend to focus on landmarks (which are often near to a goal objects). However, the present research goes beyond the work in this literature by showing that when the spatial task is relatively easy, the use of geometry as a source of information can be equally preferred by both males and females. Rephrasing Wall et al. (2004), we wondered if the “geometric module” (Cheng, 1986) could have a special status, but only when easy spatial tasks are concerned. This is an open question that deserves more research. For example, a natural progression of the present study would be to dissociate geometry and landmark use in the easy versus difficult task and investigate the sex differences in this setting.

There is enough agreement that the work with rodents helps to understand human sexual dimorphism in the spatial domain. In both cases, rodents and humans, although for different reasons, one biological hypothesis is gaining prominence (for reviews, see Chamizo & Rodrigo, 2019; Halpern, 2012; Jones, Braithwaite, & Healy, 2003; Kimura, 1999; Mackintosh, 2011). As Kimura (1999) has claimed, let us always keep in mind that our brains are essentially the same as those of our ancestors 50,000 years ago and more and that men and women probably had different selection pressures:

Men and women have a very long evolutionary history of division of labor, with men more actively involved in hunting or scavenging, which could take them further from their home base. They also appear to have been better at throwing projectiles of various kinds. Early women, in contrast, stayed nearer the settlement and contributed to the food supply primarily by gathering. Their most crucial contribution would have been the care of infants and small children. It is likely that the average difference between the sexes in cognitive pattern and in motor skills arose chiefly out of such complementary evolutionary histories. (p. 16) **AQ: 17**

However, men should not be regarded as more highly spatially specialized than women but differently specialized, as claimed by Silverman and Eals (1992). In other animals, like rodents, the most frequent explanation to understand sexual dimorphism refers to a polygynous mating system requiring promiscuous males to have larger ranges. Yet in both cases, humans and rodents, a difference in range expansion between males and females is associated with a difference in spatial cognition.

Fortunately, our wonderful technology allows us to look to the future with hope. It has been shown (West et al., 2018) that 90 hr of action video games can shrink the hippocampus. What could be expected from an appropriate 90-hr video games intervention in the hippocampus of women and girls? Future research will have to answer this question.

References

- Bohbot, V. D., Del Balso, D., Conrad, K., Konishi, K., & Leyton, M. (2013). Caudate nucleus-dependent navigational strategies are associated with increased use of addictive drugs. *Hippocampus*, *23*, 973–984. <http://dx.doi.org/10.1002/hipo.22187>
- Buckley, M. G., Holden, L. J., Spicer, S. G., Smith, A. D., & Haselgrove, M. (2019). Crossing boundaries: Global reorientation following transfer from the inside to the outside of an arena. *Journal of Experimental Psychology: Animal Learning and Cognition*, *45*, 322–337. <http://dx.doi.org/10.1037/xan0000206>
- Chamizo, V. D., & Rodrigo, T. (2019). Spatial orientation. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1–11). New York, NY: Springer. http://dx.doi.org/10.1007/978-3-319-47829-6_1416-1 **AQ: 18**
- Chamizo, V. D., Rodríguez, C. A., Sánchez, J., & Mármol, F. (2016). Sex differences after environmental enrichment and physical exercise in rats when solving a navigation task. *Learning & Behavior*, *44*, 227–238. <http://dx.doi.org/10.3758/s13420-015-0200-3>
- Chamizo, V. D., Rodríguez, C. A., Torres, I., Torres, M. N., & Mackintosh, N. J. (2014). What makes a landmark effective? Sex differences in a navigation task. *Learning & Behavior*, *42*, 348–356. <http://dx.doi.org/10.3758/s13420-014-0152-z>
- Chamizo, V. D., Torres, M. N., Rodríguez, C. A., & Mackintosh, N. J. (2019). What makes a landmark effective in adolescent and adult rats? Sex and age differences in a navigation task. *Learning & Behavior*, *47*, 156–165. <http://dx.doi.org/10.3758/s13420-018-0364-8>
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, *23*, 149–178. [http://dx.doi.org/10.1016/0010-0277\(86\)90041-7](http://dx.doi.org/10.1016/0010-0277(86)90041-7)
- Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences*, *12*, 355–361. <http://dx.doi.org/10.1016/j.tics.2008.06.004>
- Cheng, K., & Gallistel, C. R. (1984). Testing the geometric power of an animal's spatial representation. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 409–423). Hillsdale, NJ: Erlbaum.
- Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1–23. <http://dx.doi.org/10.3758/BF03196346>

- Coluccia, E., & Louse, G. (2004). Gender differences in spatial orientation: A review. *Journal of Environmental Psychology, 24*, 329–340. <http://dx.doi.org/10.1016/j.jenvp.2004.08.006>
- Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 5909–5914. <http://dx.doi.org/10.1073/pnas.0711433105>
- Esber, G. R., McGregor, A., Good, M. A., Hayward, A., & Pearce, J. M. (2005). Transfer of spatial behaviour controlled by a landmark array with a distinctive shape. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology, 58*, 69–91. <http://dx.doi.org/10.1080/02724990444000069>
- Forcano, L., Santamaría, J. J., Mackintosh, N. J., & Chamizo, V. D. (2009). Single landmark learning in rats: Sex differences in a navigation task. *Learning and Motivation, 40*, 46–61. <http://dx.doi.org/10.1016/j.lmot.2008.05.003>
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Golob, E. J., & Taube, J. S. (2002). Differences between appetitive and aversive reinforcement on reorientation in a spatial working memory task. *Behavioural Brain Research, 136*, 309–316. [http://dx.doi.org/10.1016/S0166-4328\(02\)00184-5](http://dx.doi.org/10.1016/S0166-4328(02)00184-5)
- Halpern, D. F. (2012). *Sex differences in cognitive abilities* (4th ed.). New York, NY: Psychology Press.
- Hayward, A., McGregor, A., Good, M. A., & Pearce, J. M. (2003). Absence of overshadowing and blocking between landmarks and the geometric cues provided by the shape of a test arena. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology, 56*, 114–126. <http://dx.doi.org/10.1080/02724990244000214>
- Horne, M. R., & Pearce, J. M. (2009). A landmark blocks searching for a hidden platform in an environment with a distinctive shape after extended pretraining. *Learning & Behavior, 37*, 167–178. <http://dx.doi.org/10.3758/LB.37.2.167>
- Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience, 23*, 5945–5952. <http://dx.doi.org/10.1523/JNEUROSCI.13-13-05945.2003>
- Jones, C. M., Braithwaite, V. A., & Healy, S. D. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience, 117*, 403–411. <http://dx.doi.org/10.1037/0735-7044.117.3.403>
- Keeley, R. J., Tyndall, A. V., Scott, G. A., & Saucier, D. M. (2013). Sex difference in cue strategy in a modified version of the Morris water task: Correlations between brain and behaviour. *PLoS ONE, 8*(7), e69727. <http://dx.doi.org/10.1371/journal.pone.0069727>
- Kimura, D. (1999). *Sex and cognition*. Cambridge, MA: The MIT Press. <http://dx.doi.org/10.7551/mitpress/6194.001.0001>
- Kosaki, Y., Austen, J. M., & McGregor, A. (2013). Overshadowing of geometry learning by discrete landmarks in the water maze: Effects of relative salience and relative validity of competing cues. *Journal of Experimental Psychology: Animal Behavior Processes, 39*, 126–139. <http://dx.doi.org/10.1037/a0031199>
- Lugo, F., Torres, M. N., & Chamizo, V. D. (2018). Two strategies used to solve a navigation task: A different use of the hippocampus by males and females? A preliminary study in rats. *Psicológica, 39*, 319–339. <http://dx.doi.org/10.2478/psicolj-2018-0014>
- Mackintosh, N. J. (2011). *IQ and human intelligence* (2nd ed.). New York, NY: Oxford University Press.
- Mesa, V., Osorio, A., Ballesta, S., Marimon, J. M., & Chamizo, V. D. (2017). Geometric vs. non-geometric information: Explaining male rats' selective preferences in a navigation task. *Learning and Motivation, 60*, 23–33. <http://dx.doi.org/10.1016/j.lmot.2017.09.001>
- Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation, 12*, 239–260. [http://dx.doi.org/10.1016/0023-9690\(81\)90020-5](http://dx.doi.org/10.1016/0023-9690(81)90020-5)
- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory, 65*, 65–72. <http://dx.doi.org/10.1006/nlme.1996.0007>
- Pearce, J. M. (2009). The 36th Sir Frederick Bartlett lecture: An associative analysis of spatial learning. *The Quarterly Journal of Experimental Psychology, 62*, 1665–1684. <http://dx.doi.org/10.1080/17470210902805589>
- Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: Implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30*, 135–147. <http://dx.doi.org/10.1037/0097-7403.30.2.135>
- Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 201–214. <http://dx.doi.org/10.1037/0097-7403.32.3.201>
- Pearce, J. M., Ward-Robinson, J., Good, M., Fussell, C., & Aydin, A. (2001). Influence of a beacon on spatial learning based on the shape of the test environment. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 329–344. <http://dx.doi.org/10.1037/0097-7403.27.4.329>
- Rodríguez, C. A., Aguilar, R., & Chamizo, V. D. (2011). Landmark learning in a navigation task is not affected by the female rats' estrus cycle. *Psicológica, 32*, 279–299. Retrieved from <http://www.uv.es/psicologica/paraARCHIVES/2011.html>
- Rodríguez, C. A., & Chamizo, V. D. (2013). Male advantage in geometry learning? A preliminary study in rats. *Revista Argentina de Ciencias del Comportamiento, 5*, 30–39. <http://dx.doi.org/10.32348/1852.4206.v5.n2>
- Rodríguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2011). Overshadowing and blocking between landmark learning and shape learning: The importance of sex differences. *Learning & Behavior, 39*, 324–335. <http://dx.doi.org/10.3758/s13420-011-0027-5>
- Rodríguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2013). Do hormonal changes that appear at the onset of puberty determine the strategies used by female rats when solving a navigation task? *Hormones and Behavior, 64*, 122–135. <http://dx.doi.org/10.1016/j.yhbeh.2013.05.007>
- Rodríguez, C. A., Torres, A., Mackintosh, N. J., & Chamizo, V. D. (2010). Sex differences in the strategies used by rats to solve a navigation task. *Journal of Experimental Psychology: Animal Behavior Processes, 36*, 395–401. <http://dx.doi.org/10.1037/a0017297>
- Roof, R. L., Zhang, Q., Glasier, M. M., & Stein, D. G. (1993). Gender-specific impairment on Morris water maze task after entorhinal cortex lesion. *Behavioural Brain Research, 57*, 47–51. [http://dx.doi.org/10.1016/0166-4328\(93\)90060-4](http://dx.doi.org/10.1016/0166-4328(93)90060-4)
- Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research, 6*, 351–360. [http://dx.doi.org/10.1016/S0926-6410\(98\)00002-0](http://dx.doi.org/10.1016/S0926-6410(98)00002-0)
- Saucier, D. M., Green, S. M., Leason, J., MacFadden, A., Bell, S., & Elias, L. J. (2002). Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behavioral Neuroscience, 116*, 403–410. <http://dx.doi.org/10.1037/0735-7044.116.3.403>
- Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 531–549). New York, NY: Oxford Press.

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- Torres, M. N., Rodríguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2014). Landmark vs. geometry learning: Explaining female rats' selective preference for a landmark. *Psicológica*, *35*, 81–100. Retrieved from <http://hdl.handle.net/2445/53867>
- Treit, D., & Fundytus, M. (1988). Thigmotaxis as a test for anxiolytic activity in rats. *Pharmacology, Biochemistry and Behavior*, *31*, 959–962. [http://dx.doi.org/10.1016/0091-3057\(88\)90413-3](http://dx.doi.org/10.1016/0091-3057(88)90413-3)
- Wall, P. L., Botly, L. C., Black, C. K., & Shettleworth, S. J. (2004). The geometric module in the rat: Independence of shape and feature learning in a food finding task. *Learning & Behavior*, *32*, 289–298. <http://dx.doi.org/10.3758/BF03196028>
- Ward, S. L., Newcombe, N., & Overton, W. F. (1986). Turn Left at the Church, Or Three Miles North: A Study of Direction Giving and Sex Differences. *Environment and Behavior*, *18*, 192–213. <http://dx.doi.org/10.1177/0013916586182003>
- West, G. L., Konishi, K., Diarra, M., Benady-Chorney, J., Drisdelle, B. L., Dahmani, L., . . . Bohbot, V. D. (2018). Impact of video games on plasticity of the hippocampus. *Molecular Psychiatry*, *23*, 1566–1574. <http://dx.doi.org/10.1038/mp.2017.155>
- White, N. M., & McDonald, R. J. (2002). Multiple parallel memory systems in the brain of the rat. *Neurobiology of Learning and Memory*, *77*, 125–184. <http://dx.doi.org/10.1006/nlme.2001.4008>
- Williams, C. L., Barnett, A. M., & Meck, W. H. (1990). Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience*, *104*, 84–97. <http://dx.doi.org/10.1037/0735-7044.104.1.84>

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