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Learning in a navigation task: The role of salience of pairs of landmarks and sex differences*

Paola Crespo
Universitat Pompeu Fabra
Clara A. Rodríguez
V.D. Chamizo
Universitat de Barcelona

In two experiments rats were trained to find an invisible platform in the presence of four objects or landmarks which were centred at equal intervals around the edge of the pool. One pair of landmarks had more intrinsic salience than the other pair: The relative proximal from the platform landmarks were those with more intrinsic salience in Experiment 1 and those with less intrinsic salience in Experiment 2. In Experiment 1, the two proximal from the platform and with more intrinsic salience landmarks prevented learning about the two relatively distal from the platform and with less intrinsic salience landmarks. No sex differences were found. In Experiment 2, the two relatively distal and with more intrinsic salience landmarks did not prevent learning about the two proximal but with less intrinsic salience landmarks. No sex differences were found after extended training. These results have implications to understand spatial overshadowing among landmarks.
Keywords: *Spatial learning, overshadowing, landmark interference, sex differences, salience, relative distance, Morris pool, rats.*

Aprendizaje en una tarea de navegación: el papel de la saliencia de pares de puntos de referencia y diferencias de sexo

En dos experimentos se entrenó a unas ratas a encontrar una plataforma oculta en presencia de cuatro objetos o puntos de referencia, centrados a inter-

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Correspondence: Paola Crespo, Universitat Pompeu Fabra, DTIC, Roc Boronat 138, 08018, Barcelona (paola.crespo@upf.edu). V.D. Chamizo, Departament de Psicologia Bàsica, Universitat de Barcelona, IR3C, Passeig de la Vall d'Hebron, 171, 08035, Barcelona (victoria.diez.chamizo@ub.edu).

valos regulares alrededor del borde de la piscina. Una pareja de puntos de referencia tenía mayor saliencia intrínseca que el otro par: los objetos más próximos de la plataforma eran los que tenían más saliencia intrínseca en el Experimento 1 y los que tenían menos en el Experimento 2. En el Experimento 1, los dos objetos más próximos de la plataforma y con más saliencia intrínseca impidieron el aprendizaje de los dos objetos más alejados de la plataforma y con menos saliencia intrínseca. No se encontraron diferencias de sexo. En el Experimento 2 los dos objetos más alejados de la plataforma y con más saliencia intrínseca no impidieron el aprendizaje de los dos objetos más próximos de la plataforma aunque con menos saliencia intrínseca. No se encontraron diferencias de sexo con un entrenamiento prolongado. Estos resultados tienen implicaciones para entender el ensombrecimiento espacial entre puntos de referencia.

Palabras clave: *aprendizaje espacial, ensombrecimiento, interferencia entre puntos de referencia, diferencias de sexo, saliencia, distancia relativa, piscina de Morris, ratas.*

Introduction

A study by Chamizo, Rodrigo, Peris, and Grau (2006), with rats and a Morris pool, addressed the issue of how salience affects single landmark learning. Two aspects of the salience of a landmark were studied: Relative size and relative distance from a hidden platform, the goal. Experiment 1 tested whether the size of a landmark, a ball (small and big), and its relative distance from the platform (50 cm away and 110 cm away) are additive effects. On test, the rats' best performance was with a near and big ball; intermediate performance was with either a near and small ball or a far and big ball; and the worst performance was with a far and small ball. These results clearly showed that the effects of the two magnitudes studied (landmark size and relative distance from the hidden platform) were additive because it was found a better landmark control of the subjects' performance as the sum of the salience components of a landmark increased. Then, Experiment 2 eliminated an alternative explanation of Experiment 1 in terms of distance to the goal only (because the size of the two landmarks, the big ball and the small ball, was confounded with distance from the hidden platform). The authors concluded that salience seems to be equally important in the spatial domain as it is in the temporal domain.

In the learning and conditioning literature the term *salience* is not well defined, although normally refers to stimuli significance or noticeability. The salience of a stimulus is often increased by making it more intense or by increasing its capacity to attract the subjects' attention (Domjan, 2010 –but see Mackintosh, 1974, for additional complexities). One way to make a stimulus more salient is to make it more relevant to the biological needs of an organism. For example, animals become more attentive to the taste of salt if they suffer a nutritional salt deficiency (Kriekhaus & Wolf, 1968). A similar argument can apply to the Morris pool. Finding the platform not only allows an animal to escape from the water but also to rest on it (thus reducing its fatigue). Probably this is, at least partly, one reason why the spatial proximity of the landmarks to the platform seems to affect not only how well they can be used to locate the platform, but also its ability to prevent learning about other landmarks, a finding called overshadowing by relative spatial proximity (Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006; Leising, Garlick, & Blaisdell, 2011; Spetch, 1995).

The study by Chamizo *et al*. (2006a) was conducted with single landmarks. Could the same results be obtained when dealing with multiple landmarks instead of single ones? For example, would the presence of a configuration formed by two salient landmarks during training decrease the amount the animals learned about a second configuration formed by two less salient landmarks? Would such an effect disappear when reducing the salience of the first configuration while augmenting that of the second? The aim of the present study was to answer these questions supposedly, early in training, when reaching asymptote, and after extended training. Moreover, because some studies (Blokland, Rutten, & Prickaerts, 2006; Roof & Stein, 1999; Williams, Barnett, & Meck, 1990) have shown that female rats are more likely than males to prefer proximal to distal landmarks, it was asked whether the results would differ in males and females.

In the two experiments presented here, all rats were trained in the presence of four landmarks (two of them with more intrinsic salience than the other pair of landmarks) and then tested with two landmarks only (and in a final test, with the four landmarks). A significance level of .05 was adopted for the statistical tests reported in both experiments.

Experiment 1

In Experiment 1 rats were trained to find a hidden platform in a Morris pool in the presence of four landmarks (three of them were used in Chamizo *et al*., 2006a) of different intrinsic salience (either because of their size or for their physical intensity), centred at equal intervals around the edge of the pool. The two landmarks with more intrinsic salience were those closer to the hidden platform (*A* and *D* in Figure 1[1], left panel), while the two landmarks with less intrinsic salience were those more distal from the platform (*b* and *c* in Figure 1, left panel). The rats received three training phases, each of them followed by two test trials with two landmarks only: With the landmarks with more intrinsic salience, which were proximal from the platform quadrant (*A* and *D*); and with the landmarks with less intrinsic salience, which were more distal from the platform quadrant (*b* and *c*). Finally, all rats received further training trials and a final test with the four

[1] The capital letters indicate the landmarks with more intrinsic salience (*A* and *D*) and the small letters the landmarks with less intrinsic salience (*b* and *c*).

landmarks. The prediction was that the two more salient landmarks (due both to their intrinsic salience and proximity from the platform), *A* and *D*, would prevent learning about the two less salient landmarks (due both to their smaller intrinsic salience and their distance from the platform), *b* and *c*. No prediction was made for the final test trial, with *AbcD*.

Method

Subjects

The subjects were 16 naive Long Evans rats: Eight males and eight females approximately 5 months old at the beginning of the experiment. Rats were maintained on *ad lib* food and water, in a colony room which had a 12:12-hr light-dark cycle, and were tested within the first 8 hrs of the light cycle.

Apparatus

The apparatus was a circular swimming pool, made of plastic and fibre glass, modelled after that used by Morris (1981). It measured 1.58 m in diameter and 0.65 m deep, and was filled to a depth of 0.49 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, mounted on a wooden platform 0.43 m above the floor, and it was surrounded by black curtains reaching from ceiling to the base of the pool and forming a circular enclosure 2.4 m in diameter. Inside the black enclosure, round the curtains, and hanging from a black false ceiling, either two or four objects were placed. These landmarks were suspended from the false ceiling, 23 cm above the surface of the water and had the mid-line directly above the wall of the pool. The four objects or landmarks used were: *A*: A 40 W light placed inside a white plastic inverted cone 11 cm in height and 13 cm in diameter at the base; *b*: A green plastic plant approximately 35 cm in diameter and 30 cm high; *c*: Three mop-heads attached together forming a cylindrical figure 12 cm in diameter and 22 cm height; and *D*: A 36 cm diameter plastic beach ball with alternate blue, white, yellow, white, orange, and white vertical segments. Landmarks *A* and *D* were more salient than landmarks *b* and *c* (landmarks *b* and *c* were directly compared by Chamizo, Rodríguez, Espinet, & Mackintosh, 2012).

For all rats, the four landmarks defined the location of the platform. In order to ensure that the animals used these landmarks, rather than any inadvertently remaining static room cues to locate the platform, the landmarks and platform were semi-randomly rotated with respect to the room (90°,180°, 270° or 360°), with the restriction that all four rotations were used equally each day. A closed-circuit video camera with a wide angle lens was mounted 1.75 m above the centre 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 rod and base, and could be placed in one quadrant of the pool, 0.38 m from the side, with its top 1 cm below the surface of the water. The platform was always situated as shown in Figure 1, left panel.

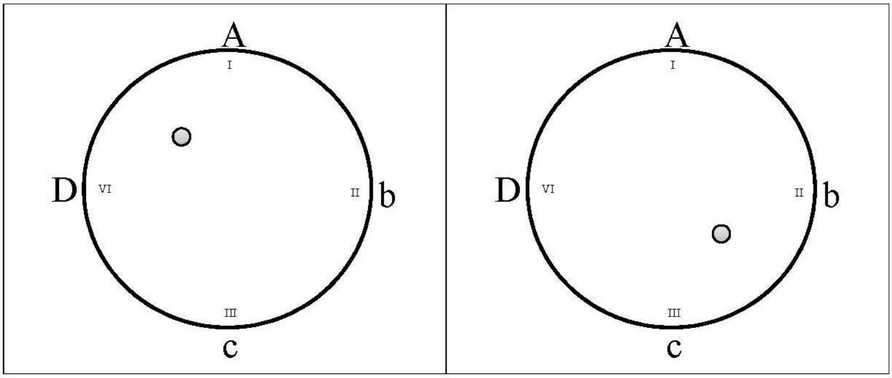


Figure 1. A schematic representation of the pool and the position of the four landmarks in Experiment 1 (A, b, c, and D), as well as the hidden platform and the starting positions (I, II, III, IV) for Experiment 1 (Left) and for Experiment 2 (Right).

Procedure

We examined the possibility that the estrus cycle of females could influence their performance. For this reason, we divided the eight females into two groups: Proestrus females (*n*=4) and estrus females (*n*=4). Following the procedure of Sava and Markus (2005), verification of the phase of the estrus cycle began approximately 8 days before pretraining in the pool. A vaginal lavage was used in females while males received similar handling; they were turned upside down to expose the perineal region, and then the scrotum was wiped with a cotton swab (during the experiment these manipulations were carried out prior to any daily session).

There were three types of trial: Pretraining, training, and test trials.

Pretraining consisted of placing a rat into the pool, without landmarks but with the hidden platform present. The rat was given 120 s to find the platform, and once it had found 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 (at I, II, III, and IV in Figure 1, left panel), 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. Rats were given five such pretraining trials over two days, with two trials on Day 1, and three on Day 2.

The procedure for training trials was similar to that of pretraining with the exception that the four landmarks, *AbcD*, were always present, as shown in Figure 1, left panel. There were three training phases in which the rats received eight trials per day over four days (a total of 32 trials each phase). These trials had an inter-trial-interval (ITI) of 8-10 minutes, and the platform and the landmarks were rotated between trials. After each of the training phases, rats received a test phase with two test days each phase. A test day consisted of eight training trials (which were identical to those of the training phases), followed by one test trial without the platform, which lasted 60 seconds. On the first test day of each phase, 50% of males and 50% of females were tested in the presence of *A* and *D*, whereas the remaining animals were tested with *b* and *c*. On the second test day of each test phase, the animals that the day before had been tested with *A* and *D* were tested with *b* and *c*, and vice versa. After test phase-3, one day of retraining with eight training trials identical to those of the three training phases was conducted, and then a final test day, which consisted of eight training trials followed by a test trial, without the platform, and with the four training landmarks simultaneously presented. In this final test trial the variable estrus cycle was controlled.

Results and Discussion

Figure 2A shows the latencies for finding the platform by males and females during all the escape trials of the experiment. Initially, three ANOVAs were made, one for each training phase, taking into account the variables Sex and Days (1-4). Only in training-1, the variable Days was significant, $F(3,42)=3.62$. No other main effect or interaction was significant ($F < 1.5$). *T* tests were used to analyze the rats' performance during training-1, reflecting that the latency to reach the platform on days 1 and 2 differed from that on day 4. Additional ANOVAs of the escape latencies of the two days of each test phase taking into account the variables Sex and Days, showed that no variable or interaction was significant, max $F(1,14)=3.85$. Further ANOVAs of the escape latencies of the last retraining day and of the final test day showed that males and females did not differ, Fs(1,14)=3.57 and 3.83, respectively.

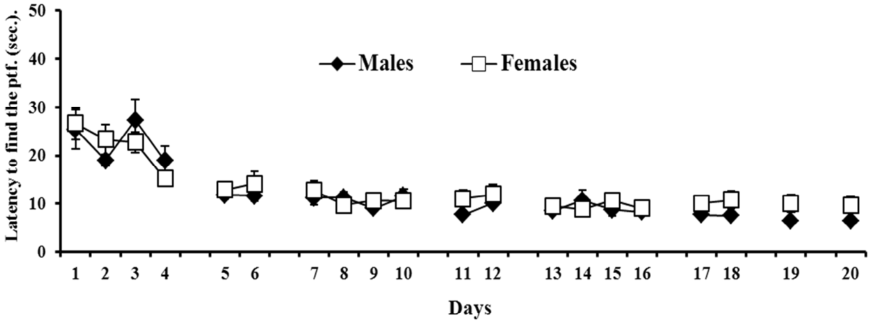
Figure 2B shows the time spent in the platform quadrant by males and females during the 60 s test trials of each of the three tests phases. Student *t* tests were used to compare rats' performance with chance (i.e., 15 s searching in the platform quadrant) in order to evaluate whether the test results reflected significant spatial learning. Rats differed from chance in the presence of landmarks *A* and *D* only[2]: In test phase-1, $t(7)=4.38$ and 5.89; in test phase-2, $t(7)=13.91$ and 5.89; and in

[2] The capital letters P- and D- in the graph indicate relative distance of the landmarks from the platform (proximal and distal).

test phase-3, $t(7)=8.63$ and 8.38, males and females respectively. Three different ANOVAs were conducted, one for each test phase, taking into account the variables Sex and Platform position with respect to the landmarks (proximal, distal). The ANOVA for test phase-1 showed that the only significant variable was Platform position, $F(1,14)=60.67$, reflecting that both males and females learned more about landmarks *A* and *D* than about landmarks *b* and *c*. The ANOVA for test phase-2 revealed that the variable Platform position was significant, $F(1,14)=158.75$; as well as the interaction Platform position x Sex, $F(1,14)=5.21$. The analysis of this interaction showed that the variable Platform position was significant in both males and females, $Fs(1,7)=242.27$, and 34.49, respectively, reflecting that all rats spent more time in the platform quadrant in the presence of *A* and *D* than in the presence of *b* and *c*. With landmarks *A* and *D* males and females were close to differ ($p=.07$). Finally, the ANOVA for test phase-3 showed that the variable Platform position was significant, $F(1,14)=203.18$, as well as the interaction Platform position x Sex, $F(1,14)=5.03$. The analysis of this interaction showed that the variable Platform position was significant in both males and females, $Fs(1,7)=157.81$, and 63.40, respectively, reflecting that all rats spent more time in the platform quadrant in the presence of *A* and *D*, than in the presence of *b* and *c*. With landmarks *A* and *D* males and females were close to differ ($p=.10$).

Figure 2C shows the time spent in the platform quadrant by the two subgroups of females (proestrus, estrus) during the 60 s of the final test trial with the training configuration of landmarks, *AbcD*. Student *t* tests were used to compare females' performance with chance (i.e., 15 s searching in the platform quadrant). Both subgroups showed significant spatial learning, $t(3)=7.61$ and 5.56, proestrus and estrus rats, respectively. An ANOVA conducted on these data showed that these two subgroups did not differ ($F < 0.5$). An additional ANOVA taking into account the data of the two subgroups of females combined and those of males revealed that the two sexes did not differ when tested with landmarks *AbcD* ($F < 1.5$).

A



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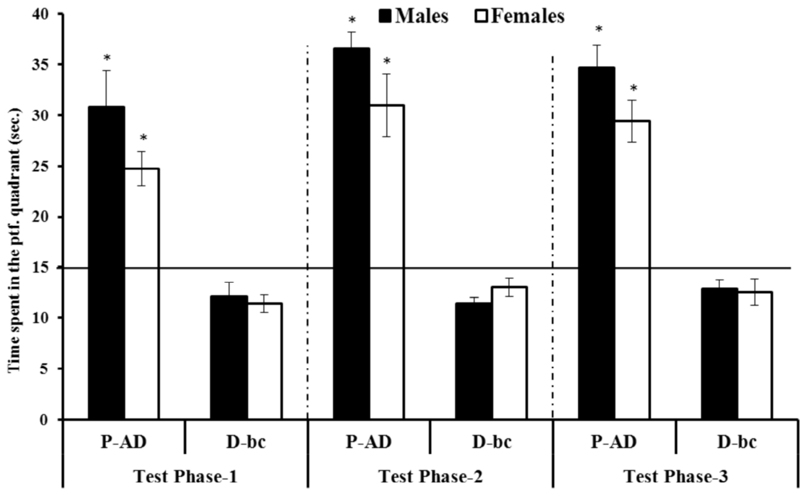

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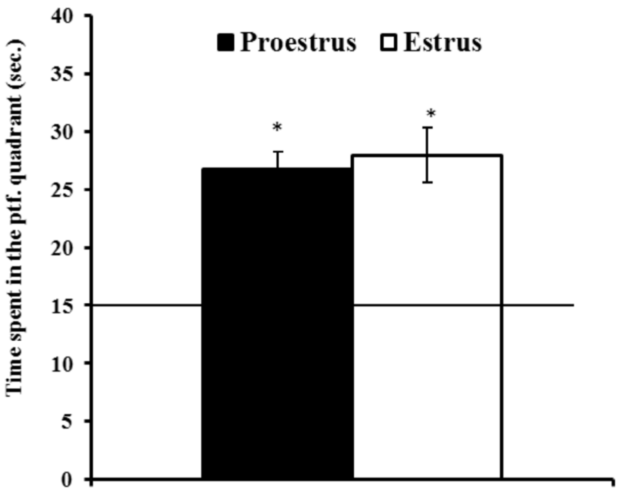


Figure 2. A: Mean escape latencies made by the subjects in Experiment 1 during both the three training and the test phases. Error bars denote standard error of means. B: Mean time spent in the platform quadrant by the subjects in Experiment 1 during the three test phases. Error bars denote standard error of means. C: Mean time spent in the platform quadrant by two subgroups of female rats in the last test trial of Experiment 1. Error bars denote standard error of means. (A small asterisk above each bar indicates whether the rats' performance differed significantly from chance).

Experiment 2

In Experiment 1 the landmarks with more intrinsic salience, *A* and *D*, were those closer to the hidden platform and the two with less intrinsic salience, *b* and *c*, those more distal from the platform (as shown in Figure 1, left panel). In the three test phases, those landmarks with more total salience, *A* and *D*, prevented learning about those landmarks with less total salience, *b* and *c*. No significant sex differences were found and extended training did not affect the results. In Experiment 2 the relationship between the landmarks and the hidden platform was swapped (as shown in Figure 1, right panel). Landmarks *A* and *D* are now those more distal from the platform, while landmarks *b* and *c*, those closer to the platform. Thus, the total sa-lience of both configurations of landmarks was altered: The salience of landmarks *A* and *D* was reduced (because their relative distance from the platform had been increased), while the salience of landmarks *b* and *c* was augmented (because their relative distance from the platform had been reduced). Assuming that the effects of differential salience affects equally to individual landmarks (Chamizo *et al*., 2006a) than to configurations of landmarks, the prediction was that landmarks *A* and *D* should now fail to prevent learning about landmarks *b* and *c*. Would that be the case? As in Experiment 1, no prediction was made for the last test trial, with *AbcD*.

Method

Subjects and apparatus

The subjects were 24 Long Evans rats: 12 males and 12 females approximately 7 months old at the beginning of the experiment. Four male rats had previously participated in a taste aversion experiment, the rest were naive. The apparatus and the four landmarks were the same as in Experiment 1.

Procedure

In this experiment we also examined the possibility that the estrus cycle of females could influence their performance. For this reason, we divided the 12 females into two groups: Proestrus females (*n*=6) and estrus females (*n*=6). The procedure for the determination of the estrus cycle was the same as used in Experiment 1.

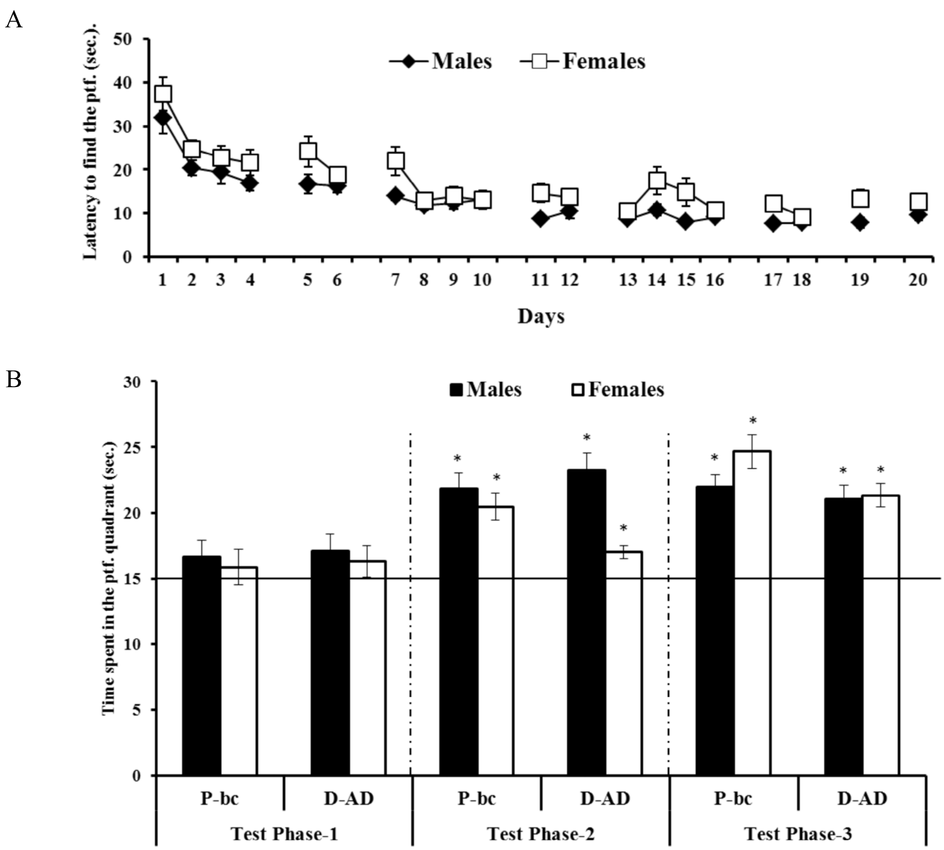
The general procedure was the same as that in Experiment 1, with the main exception that the arrangement of the landmarks with respect to the platform was modified. Unlike in the previous experiment (where the landmarks with more intrinsic salience, *A* and *D*, were located relatively proximal from the platform, while the landmarks with less intrinsic salience, *b* and *c*, relatively distal from the platform), in the present experiment the landmarks with less intrinsic salience (*b* and *c*) are those located relatively proximal from the platform, while the landmarks with more intrinsic salience (*A* and *D*) are those relatively distal from the platform (as shown in Figure 1, right panel).

Results and Discussion

Figure 3A shows the latencies for finding the platform by males and females during all the escape trials of the experiment.

Initially, three ANOVAs were made, one for each training phase, taking into account the variables Sex and Days (1-4). In training-1, the variable Days was significant, $F(3,66)=13.36$; as well as the variable Sex, $F(1,22)=5.13$, reflecting that males reached the platform faster than females. In training-2, the variable Days was significant, $F(3,66)=5.95$; as well as the interaction Sex x Days, $Fs(3,66)=3.02$, reflecting that males reached the platform faster than females on the first day of this phase, $F(1,22)=5.84$. In training-3, the variable Days was significant, $F(3,66)=6.19$; as well as the interaction Sex x Days, $F(3.66)=3.11$, reflecting that males reached the platform faster than females only on the third day of this phase, $F(1,22)=4.59$. Additional ANOVAs of the escape latencies of the 2 days of each test phase, taking into account the variables Sex and Days, showed that the variable Sex was significant only in test phase-2, $F(1,22)=6.32$, reflecting that males reached the platform faster than females. No other main effect or interaction was significant (Fs < 0.5). Further ANOVAs of the escape latencies of the last retraining day and of the final test day showed that the groups did not differ neither in the escape trials of the last retraining day ($F < 0.5$) nor in the escape trials of the final test day ($F < 1.5$).

Figure 3B shows the time spent in the platform quadrant by males and females during the 60 s test trials of each of the three tests phases. Student t tests were used to compare rats' performance with chance (i.e., 15 s searching in the platform qua-drant) in order to evaluate whether the results reflected significant spatial learning. Rats differed from chance in both test trials of test phase-2 and test phase-3 only. (Test phase-1 reveals that the present task is more difficult for all rats in comparison to Experiment 1.) In test phase-2, in the presence of *b* and *c*: $t(11)=5.54$ and 5.28; and with *A* and *D*: $t(11)=6.37$ and 3.95, males and females respectively. In test pha-se-3, in the presence of *b* and *c*: $t(11)=8.20$ and 8.56; and with *A* and *D*: $t(11)=6.4$ and 8.72, males and females respectively. Three different ANOVAs were conducted, one for each test phase, taking into account the variables Sex and Platform position with respect to the landmarks (proximal, distal). The ANOVA for test phase-1 sho-wed that no variable or interaction was significant ($Fs < 0.5$). The ANOVA for test phase-2 revealed that the variable Sex was significant, $F(1,22)=8.43$; as well as the interaction Platform position x Sex, $F(1,22)=10.91$. The analysis of this interaction revealed that males had a better performance than females in the test with *A* and *D*, $F(1,22)=20.09$ (for a similar result, with humans and virtual navigation, see Chamizo, Artigas, Sansa, & Banterla, 2011). Moreover, females showed a better performance in the test with the proximal from the platform landmarks (*b* and *c*) than with the distal ones (*D* and *A*), $F(1,11)=16.66$, reflecting that the proximal landmarks, those with less intrinsic salience, are learned first and then, those more distal from the platform (as shown in test phase-3). This result supports previous findings (Blokland *et al*., 2006; Roof & Stein, 1999; Williams *et al*., 1990) showing that female rats often prefer proximal to distal landmarks. Males had a similar performance in both tests. Finally, the ANOVA of test phase-3 showed that the variable Platform position was significant $F(1,22)=6.70$, reflecting that all rats spent more time in the platform quadrant in the presence of *b* and *c* than in the presence of *A* and *D*, which shows that after extended training the sex difference disappeared and proximity to the goal was the main determinant of landmark control.



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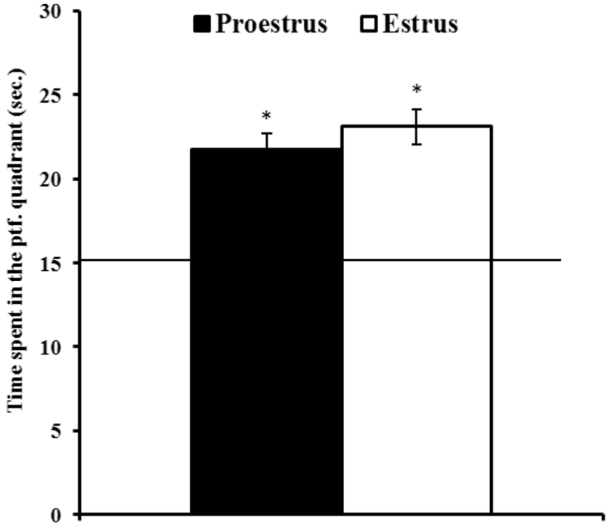

Figure 3. A: Mean escape latencies made by the subjects in Experiment 2 during both the three training and the test phases. Error bars denote standard error of means. B: Mean time spent in the platform quadrant by the subjects in Experiment 2 during the three test phases. Error bars denote standard error of means. C: Mean time spent in the platform quadrant by two subgroups of female rats in the last test trial of Experiment 2. Error bars denote standard error of means. (A small asterisk above each bar indicates whether the rats' performance differed significantly from chance).

Figure 3C shows the time spent in the platform quadrant by the two subgroups of females (proestrus, estrus) during the 60 s of the final test trial with the training configuration of landmarks, *AbcD*. Student *t* tests were used to compare females' performance with chance (i.e., 15 s searching in the platform quadrant). Both subgroups showed significant spatial learning, $t(5)=7.34$ and 7.75, proestrus and estrus rats, respectively. An ANOVA conducted on these data showed that these two subgroups did not differ ($F < 1.0$). An additional ANOVA taking into account the data of the two subgroups of females combined and those of males revealed that the two sexes did not differ with landmarks *AbcD* ($F < 3.0$).

General Discussion

As expected, the results of the present experiments show that by increasing the distance of those landmarks with more intrinsic salience, *A* and *D* (Experiment 2), the clear interference effect found in Experiment 1, disappeared. These results are in agreement with those studies, classical conditioning studies, where more standard stimuli are used (Mackintosh, 1976). In standard Pavlovian experiments the degree of associative overshadowing depends on the relative salience of both the overshadowing and the overshadowed stimuli (Mackintosh, 1976). Mackintosh found that the presence of an intense noise during training decreased the amount the animal learned about a light-shock association by comparison with a control group which received training with just the light. And only when the noise was intense did its presence detract from the amount the rats learned about the light-shock association. In a similar way, the present results show that a more valid configuration of landmarks (i.e., the one formed by the two proximal landmarks which, in addition, had high intrinsic salience –A and D in Experiment 1), one configuration which better predicts finding the hidden platform, interferes with a less valid configuration (i.e., the one formed by the two more distal landmarks which, in addition, had less intrinsic salience than the previous pair of landmarks –b and c in Experiment 1). The degree of interference (or overshadowing) seems to depend on the relative salience of the two configurations of landmarks: The more salient configuration prevents or overshadows learning about the other, less salient configuration of landmarks.

The term overshadowing refers to a phenomenon in which one stimulus interferes with the conditioning of another with which it is presented in compound (Pavlov, 1927; Kamin, 1969). The main explanation for this phenomenon refers to associative competition. But overshadowing can also be explained in terms of generalization decrement: Animals trained with an AB compound and tested with B alone, experience a greater change from training to test than those trained and tested with B alone (Pearce, 1987, 1994). In the spatial domain, a number of studies have shown overshadowing. Some of them (Chamizo *et al*., 2012; Sánchez-Moreno, Rodrigo, Chamizo, & Mackintosh, 1999; Leising *et al*., 2011) have conducted specific controls to test for generalization decrement. Associative overshadowing supports the view that the spatial landmarks seem to interact competitively, according to an error-correcting rule (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). The study by Sánchez-Moreno *et al*. (1999), with rats and a Morris pool, clearly suggests that when two landmarks occupy the same spatial position reciprocal overshadowing by associative competition is possible.

In the study by Leising *et al*. (2011), pigeons were trained to find a target when its location was indicated either by X + A (where A was positioned between X and the target) or by Y alone (where Y was the same distance from the target as X). Performance was significantly worse on test trials to X than to Y. These results indicate that the control over the response acquired by a landmark a given distance from the target was reduced by the presence of another landmark closer to the target. In this study, poor spatial control by X at test was not found to be attributable to generalization decrement from training on the AX compound to testing on element X. Test trials of a novel compound BY in which Y, but not B, had been trained as a landmark revealed equally strong control by the BY compound as by Y itself. These last results support associative overshadowing.

In the Chamizo *et al*. (2012) study, with four landmarks centred at equal intervals around the edge of the pool (as in the present experiments), a preliminary experiment was conducted to ensure that the four landmarks used (i.e., a cube, an artificial plant, a ball, and three mop-heads attached together) were of similar salience. Rats were trained with one of the four objects, which was always placed in the same location (approximately 50 cm away from the hidden platform). Following acquisition, a test trial without the platform revealed that the four landmarks acquired the same control of the rats' performance, both in males and in females. In spite of this null result, to the human eye, two of the landmarks, the cube and the mop-heads looked more salient as they contrasted more sharply with the black curtains. Therefore in all the subsequent experiments, these two were always the distal from the platform landmarks, while the plant and the ball were always the proximal to the platform landmarks (perhaps this manipulation could explain the absence of overshadowing by relative spatial proximity observed in Experiments 1-3). In Experiment 1, one pair of groups was trained with the four landmarks while a second pair was trained with two landmarks only, either relatively close to or distal from the hidden platform. After extensive training, both male and female rats showed a reciprocal overshadowing effect: On a test with two landmarks only (either proximal or distal from the platform), rats trained with four landmarks spent less time in the platform quadrant than those trained with only two. Then, Experiment 2 showed that animals trained with two landmarks and then tested with four also performed worse on test than those trained and tested with two landmarks only. This result clearly suggests that generalization decrement, rather than associative competition, provides a sufficient explanation for the overshadowing observed in Experiment 1 (due to the amount of change between training and testing). Experiment 3 provided a within-experiment replication of the results of Experiments 1 and 2. Finally, Experiment 4 showed that rats trained with a configuration of two landmarks learn their identity. Thus, with landmarks of similar intrinsic salience occupying different spatial positions overshadowing by generalization decrement is possible.

Importantly, on Experiment 2, test phase-2, female rats had a significantly worse performance when tested in the distal condition than male animals. Then, on test phase-3, the performance by male and female rats did not differ. Extended training eliminated the previous sex difference (for a related finding where sex differences disappear after extended training, see Chamizo *et al.*, 2012, Experiment 1). How can this be? A recent study (Andersen, Dahmani, Konishi, & Bohbot, 2012) on human virtual navigation, using an eye tracking procedure, has shown that women rely more on landmarks to navigate than men; and that they spend more time looking at landmarks than men. The same could be true in rats, thus explaining, at least partly, our results.

As in previous studies conducted in the Morris pool in our laboratory (Rodríguez, Aguilar, & Chamizo, 2011; Rodríguez, Chamizo, & Mackintosh, 2011), the present experiments show that the estrus cycle does not influence the female rats' performance in a highly controlled navigation task based on four landmarks. The final test trial of both Experiment 1 and Experiment 2 revealed that there was no difference between females with high hormonal levels and females with low hormonal levels.

The results of the present experiments favour an explanation in terms of associative competition by the different total salience of the two configurations of landmarks: An appeal to generalization decrement seems insufficient because the amount of change between training and testing (i.e., from four to two landmarks) was the same in all test trials. Although this study constitutes inconclusive work (control groups were not included in the experiments), it certainly reveals that further research is needed to fully understand overshadowing among spatial landmarks.

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