Absence of overshadowing between a landmark and geometric cues in a distinctively shaped environment: A test of Miller and Shettleworth (2007)

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Abstract

Rats in the first two experiments, which were designed to test predictions from a model of spatial learning by Miller and Shettleworth (2007), had to escape from a triangular pool by swimming to a submerged platform in a geometrically unique corner. A spherical landmark was suspended above the platform for an overshadowing group. A control group was trained with the same arrangement and with a second, identical, landmark suspended in another corner. The platform could thus be found by reference to the landmark or the geometric cues in the overshadowing group, whereas the control group had to rely on geometric cues. There was no indication of overshadowing between the geometric cues and the landmark in the overshadowing group. The final two experiments revealed that the absence of overshadowing was not a consequence of the landmark being an ineffective cue for overshadowing. The results indicate either that the landmark and geometric cues were not in competition for the control they acquired over behaviour; or that an additional process compensated for any such competition that might have occurred in the overshadowing group. This additional process could involve between-cue associations, or the provision of a stable spatial framework.

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A wide range of experiments has shown that when two or more cues signal a particular outcome, then learning about at least one of them is restricted relative to a condition in which they individually signal the same outcome. Such overshadowing has been found with appetitive and aversive outcomes and with a variety of species. By far the most popular explanation for overshadowing is that stimuli must compete with each other for the control they acquire over behaviour, and the more control that is acquired by one stimulus, the less will be acquired by the other (e.g. Rescorla & Wagner, 1972).

Given the ubiquity of overshadowing, it is tempting to speculate that it is the result of an associative mechanism that operates in any context where learning takes place. There is, however, at least one set of findings that challenges this conclusion, by showing that overshadowing does not occur when a hidden goal must be found in an environment with a distinctive shape. Pearce, Ward-Robinson, Good, Fussell, and Aydin (2001) required rats to escape from a triangular pool of water by finding a submerged platform that was located in a geometrically unique corner. The task was performed with little difficulty, which indicates the rats were able to use cues provided by the shape of the pool – geometric cues – to find the hidden goal. Furthermore, this use of geometric cues was not at all affected by attaching a distinctive landmark to the platform. Even though the landmark could be used to find the platform with complete accuracy, its presence did not overshadow spatial learning based on the geometric cues.

Failures of a landmark to restrict learning based on the shape of the environment have been found with rats in a rectangular arena (Hayward, Good and Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003; Wall, Botly, Black & Shettleworth, 2004) and in a kite-shaped arena (Graham, Good, McGregor, & Pearce, 2006). This effect has also been revealed in a rectangular arena with pigeons (Kelly, Spetch, and Heth, 1998). Other studies have shown with rats (Cheng, 1986), goldfish (Sovrano, Bisazza, & Vallortigara, 2003), chicks (Tommasi & Vallortigara, 2003) and monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001) that the presence of a landmark does not prevent animals making use of geometric cues to find a hidden goal. The absence of an appropriate control condition, however, makes it impossible to determine whether the landmark had no effect at all on learning about the geometric cues.

These findings have led to the proposal that learning about the shape of the environment is governed by different rules to those that apply to learning in, say, conditioning chambers. Cheng (1986) and Gallistel (1990) have both proposed that information about the shape of the environment is encoded in a dedicated geometric module which is impervious to non-geometric information such as that provided by individual landmarks. Thus no matter how many landmarks surround a hidden goal, animals are assumed to learn about its location relative to the shape of the environment to the same degree as if no landmark is present (see also Wang and Spelke, 2002, 2003).

An alternative explanation for the failure to observe overshadowing when a landmark is situated near a goal in an environment with a distinctive shape has been proposed by Miller and Shettleworth (2007). This account is based on the supposition that learning about geometric cues adheres to the same principles that apply to all other cues. To justify this claim they demonstrated how a modified version of the Rescorla and Wagner (1972) theory can explain why a landmark should fail to overshadow geometric cues. Consider again, the experiment by Pearce et al. (2001). The experimental apparatus consisted of a circular pool containing two straight walls to create an isosceles triangle with a curved base. The three corners will be referred to as apex, correct and incorrect (see

Figure 1). The grey circle in the correct corner of Figure 1 represents the platform and the black circle represents a landmark above the platform. In Experiment 3 by Pearce et al. (2001), an experimental group was required to find the platform in this apparatus, whereas a control group received the same training in the absence of the landmark.

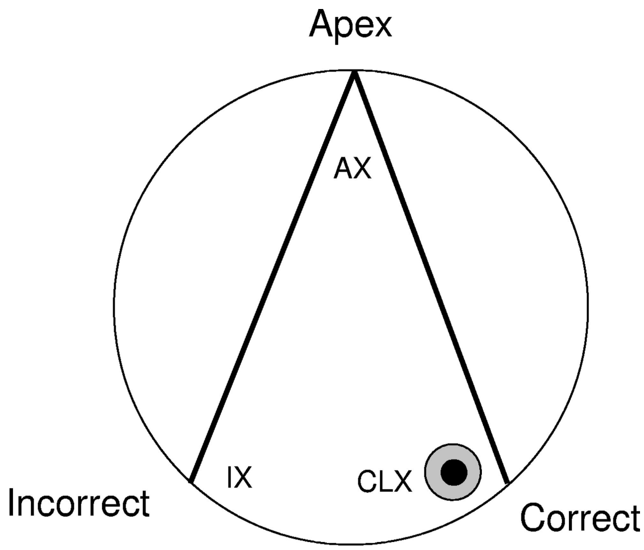

Figure 1. Plan of the apparatus used for the experiments. The grey circle depicts a submerged platform and the black circle depicts a landmark suspended above the platform. The letters refer to cues at the three corners: A = geometric cue at apex, C = geometric cue at correct corner, I = geometric cue at incorrect corner, L = landmark, X = cue that is common to all three corners.

According to Miller and Shettleworth (2007), the environment can be regarded as a set of cues. Each of the three corners was assumed to create its own, unique geometric cues, A, I, and C, and also a cue, X, that was common to each corner. In addition, the landmark provided a fifth cue, L, for the experimental group. Approaches to the apex were assumed to reduce the associative strength of A and X, approaches to the incorrect corner were assumed to reduce the associative strength of I and X, and approaches to the correct corner were assumed to increase the associative strength of C and X, and L if it was present. To predict behavior during a trial, Miller and Shettleworth (2007) suggested that the probability of a rat heading for a particular corner after being released into the pool is determined by the overall associative strength of the corner in question, divided by the sum of the associative strengths of all three corners. The probability of the experimental group heading for the correct corner is expressed in Equation 1, where each pair of brackets in the denominator expresses the overall associative strength for each of the three corners, and V represents the associative strength of the cue identified by the subscript. To determine the probability for the control group it would be necessary to remove V_L from the equation.[1]

$$P_{correct\ corner} = (V_C + V_L + V_X)/((V_A+V_X)+(V_I+V_X)+(V_C+ V_L +V_X)) \qquad 1$$

[1] In order to prevent the model from generating probabilities that lie outside the range from 0 to 1 (Dawson, Kelly, Spetch, & Dupuis, 2008), Miller and Shettleworth (2008) further suggested that when the combined associative strength of the cues in a corner is negative then they should be treated as having an overall associative strength of zero.

To calculate the change in associative strength on any trial, Miller and Shettleworth (2007) advocated the modified version of the Rescorla-Wagner (1972) rule shown as Equation 2. The term ΔV_E represents the change in associative strength of an element at the corner that a subject has chosen, V_Σ is the sum of the associative strengths of all the elements at the chosen corner. In the experiments by Pearce et al. (2001), rats were allowed to search in the pool until they found the platform. Equation 2 must therefore take account of the fact that on any trial a rat might enter one or both corners without the platform before entering the corner with the platform. In view of this possibility, Miller and Shettleworth proposed that the change in associative strength of all the elements on any trial will be influenced by the probability of entering each corner throughout the entire trial, P_T. According to this multiple-choice model, the value of P_T for the elements at the correct corner is 1, because the trial terminates when the rat reaches the platform. The value of λ for the elements in the correct corner will be set at its maximum, because the correct corner contains the platform. For elements at the other two corners, the value of P_T will be less than one, and it will be determined by similar principles to those governing Equation 1, except the possibility rats that will enter two incorrect corners before heading for the correct corner must be considered (see Miller and Shettleworth, 2007, p. 199). The value of λ for the elements encountered on these incorrect choices will be zero. Finally, α in Equation 2 is a learning rate parameter with a value between 0 and 1.

$$\Delta V_E = \alpha\,(\lambda - V_\Sigma)P_T \qquad 2$$

Equation 2 predicts that when the experimental group approaches the correct corner, the presence of the landmark will restrict the gain in associative strength to C and result in the associative strength of C being less than in the control group. A test in the absence of the landmark might then be expected to reveal a rather weak preference for the correct over the incorrect corner by the experimental group, relative to the control group trained without any landmarks. However, the landmark in the experimental group will also restrict learning about the common cue, X. One effect of this disruptive influence on learning about X is that the probability of approaching the correct corner will be approximately the same for both groups, granted certain assumptions about the salience of X.

Miller and Shettleworth (2007) also show how Equations 1 and 2 can explain the reported failures of a landmark to overshadow and block geometric cues in a rectangular arena. The prediction concerning blocking depends upon the landmark gaining only a modest level of associative strength as a result of the initial training. The model has also been used with some success to explain why the control by geometric cue in a kite-shaped environment is potentiated by making the color of the walls of the correct corner different to the color of the other walls (Graham, et al., 2006), but see Horne and Pearce (in press) for an alternative explanation for this finding. The purpose of the present paper is to test further the model of Miller and Shettleworth (2007) by evaluating two specific predictions that it makes.

One prediction relates to an experimental design in which an overshadowing group receives the experimental treatment described above, and a two-landmark control group receives the same treatment but with a second, identical, landmark always located in the incorrect corner. The treatment for the control group will result in the landmark in the correct corner gaining associative strength whenever the platform is reached, and this strength can be expected to generalise fully to the opposite landmark. Subsequent failures to find the platform beneath the landmark in the incorrect corner will have two important consequences. First, they will reduce the associative strength of the landmark and thereby weaken its overshadowing influence on the geometric cue in the correct corner, C. Second, by virtue of the excitatory strength of the landmark, Equation 2 predicts that the geometric cue in the incorrect corner, I, will gain substantial negative associative strength. Should both groups then be given a test trial in the triangle without any landmarks or the platform, the model predicts for the control group that the relatively high associative strength of C, and the relatively low associative strength of I, will result in more time being spent in the vicinity of the correct corner than for the overshadowing group. In other words, using this control condition it should be possible to detect an overshadowing influence of the landmark in the experimental group.

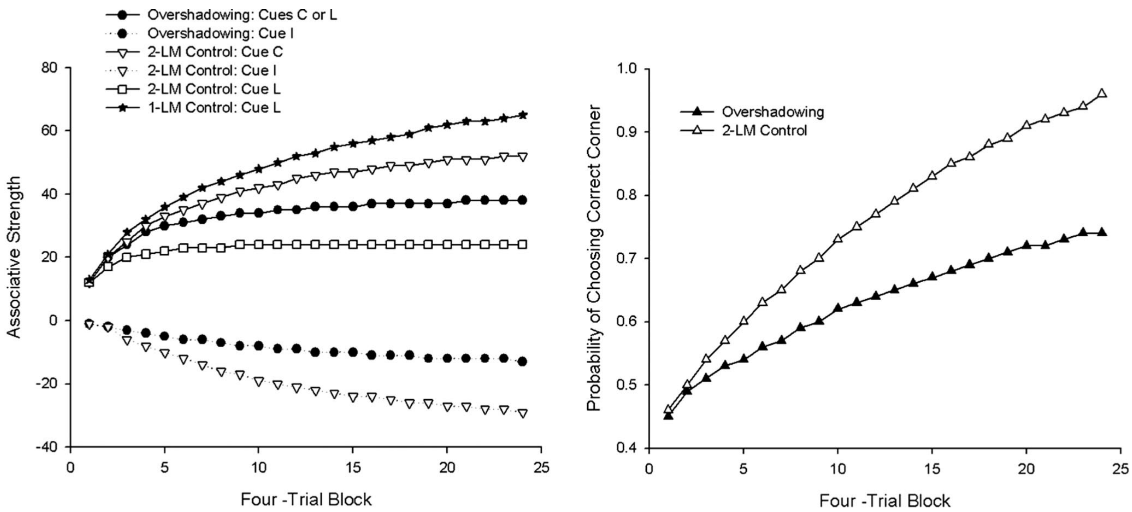

Figure 2. The results from computer simulations based on the associative model of geometry learning by Miller and Shettleworth (2007). Left-hand panel: The predicted acquisition of associative strength by some of the cues in the triangular arena for the overshadowing, and the one- and two-landmark control groups that were used in the experiments. Right-hand panel: The predicted probability of heading directly for the correct corner after being placed in the triangular arena in the absence of any landmarks, and after increasing amounts of training, for the overshadowing and two-landmark control groups of Experiment 1.

This prediction was verified with a computer simulation based on Equation 2, with λ set at 100 and with the remaining parameter values the same as those recommended by Miller and Shettleworth (2007). The left-hand panel of Figure 2 shows the predicted changes in associative strength as training progresses for the landmark and for the geometric cues at the correct and incorrect corners. These changes are shown for the overshadowing group, the two-landmark control group, and a one-landmark control group which will be considered shortly. In keeping with the predictions made in the previous paragraph, the positive associative strength of C is consistently greater in the control than the experimental group, and the same is also true for the negative associative strength of I. Note that the associative strength gained by the landmark and C in the overshadowing group is predicted to be the same because, following Miller and Shettleworth (2007), their saliencies were assigned the same value. The right-hand panel of Figure 2 shows the predicted effects of conducting test trials in the triangular arena without a landmark, after increasing amounts of training trials with the landmarks. With extended training the model predicts that the preference for the correct corner will become progressively stronger in the two-landmark than the overshadowing group. Of course, this difference will not be apparent during the training trials when the landmark is present.

An experiment by Pearce et al. (2001) included two groups that received the overshadowing and two-landmark control treatments just described, but its results are hard to interpret. During the first 15 s of a 60-s test trial that took place in an empty triangle, the overshadowing group exhibited a stronger preference for the correct over the incorrect corner than the control group, but for the remainder of the test trial this preference was reversed. Whether these differences reflect a stronger preference for the correct corner in one group than the other is hard to determine. Given the ambiguity of this finding, the purpose of Experiment 1 was to compare further the effects of the overshadowing and two-landmark control training treatments.

Thus far, experiments have focused on the question of whether a landmark will restrict learning about the geometric cues created by an environment with a distinctive shape. There has been little interest in the complementary question of whether geometric cues will overshadow learning about a landmark. To determine the prediction made by the model of Miller and Shettleworth (2007) concerning overshadowing of this sort, a computer simulation was conducted for a second control condition in which the platform, with a landmark always above it, moved randomly between the correct and incorrect corners throughout training in the triangle. This treatment ensures that the landmark is the only reliable cue for finding the platform and it should thus gain the maximum possible associative strength. The results from the simulation shown in the left-hand panel of Figure 2 include the predicted associative strength of the landmark in this one-landmark control condition. The magnitude of the associative strength of the landmark can be seen to be consistently greater for this group than for the overshadowing group. A further purpose of the reported experiments was to evaluate this prediction.

In fact the experiments failed to reveal any evidence of overshadowing between the geometric cues and the landmark. This finding raises the possibility that there was something unusual about the landmark that we used which makes it a poor cue for studying overshadowing. Two additional experiments are therefore reported which were designed to determine if the landmark is capable of overshadowing, and being overshadowed by, non-geometric cues.

The landmark for all of the experiments was a black sphere suspended above the platform. We opted for a landmark that rats could not reach because of the intention to test its associative strength. Pilot experiments revealed that rats will repeatedly make contact with a landmark on the surface of the water, even if it is novel. A sphere above the pool does not elicit this unconditioned activity. Thus the time spent in its vicinity should provide a more accurate indication of its conditioned properties than a landmark which the rat can touch.

Experiment 1

An overshadowing and a two-landmark control group were required to escape from a triangular pool by swimming to a submerged platform in one of the corners at the curved base (see Figure 1). A single landmark, which consisted of a black ball, was suspended directly above the platform for both groups. In addition, the two-landmark control group was trained with an identical ball to the one in the correct corner, but it was located in the incorrect corner. Upon the completion of 12 sessions of training a single test trial was conducted in which both groups were allowed to swim in the pool in the absence of the platform and the landmarks. During this trial a record was taken of the amount of time spent in two circular search zones that were located in the correct and incorrect corners. If the predictions from the theory of Miller and Shettleworth (2007) are correct, then during this trial the experimental group will spend less time in the search zone in the correct corner than the control group. The test failed to confirm this prediction. An inspection of the right-hand panel of Figure 2 indicates that the model of Miller and Shettleworth predicts that a difference between the test performance of the two groups is more likely to be evident after extended training. Accordingly, the two groups received a further 12 sessions of training before a second test trial was conducted.

Method

Subjects. The subjects were 20, experimentally naïve, male Hooded Lister rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, Oxfordshire, England). They were housed in pairs in a light-proof room in which the lights were on for 14.5 hours each day. They were tested for 5 days a week, at the same time each day, during the period when the lights were on in their holding room. The rats were randomly assigned to the two groups in equal numbers at the start of the experiment.

Apparatus The experiment was conducted in a white pool that was 2 m in diameter and 60 cm deep. It was made from fibreglass and mounted on a platform 60 cm above the floor in the center of a room that was 4 x 4 x 2.3 m high. The pool was filled to a depth of 27 cm with a mixture of water and 0.5 L of white coloring OP 308, supplied by Rohm and Haas Ltd (Dewsbury, UK). This opaque mixture was maintained at a temperature of 25 ^{o}C (± 2 C^{o}) and was changed daily. A white circular ceiling with a diameter of 2 m was suspended 1.5 m above the pool. Eight 45-W spotlights were recessed into the ceiling. They were each 22.5 cm in diameter and arranged symmetrically in a 1.6-m diameter circle with its center above the center of the pool. The room was additionally lit by four, horizontal, 1.53-m strip lights that were arranged end to end in pairs on opposite walls of the room. The lights were 75 cm above, the floor. In the center of the circular ceiling was a 30-cm diameter hole into which a wide-angled video camera was fixed. The image from the camera was relayed to a monitor, recording equipment, and a PC in an adjacent room. The PC could be used to record the rats' paths (Watermaze software; Morris & Spooner, 1990). A curtain that hung from a rail around the circular ceiling at a distance of 25 cm from the edge of the pool was drawn around the pool throughout the experiment. There was a sliding door in the center of one of the walls that did not support a strip light. The door provided access to an adjacent room where the experimenter would remain throughout each trial and where it was possible to observe the pool on a TV monitor. The center of the door was regarded as North for the purposes of the experiment.

Two white Perspex boards were used to create the straight walls of the triangular pool. They were 1.8 m in length, 59 cm high, and 2 mm thick. One of the long sides of each board was attached to a bar with a square cross section (2 x 2 cm) and which extended beyond the ends of the board by 5 cm. By resting the ends of a bar on the edge of the pool it was possible to suspend the boards within the pool. When they were placed in the pool the boards formed a triangular arena with two straight walls and a curved wall (see Figure 1). The distance between the corners created by the boards and the circular wall was 1.6 m. At the apex of the triangle one bar rested on the other, which resulted in the top edge of one board being 35 cm above the water at this point and the top edge of the other being 33 cm above the water. At their other end, the top of both boards was 33 cm above the surface of the pool.

A clear Perspex platform, 10 cm in diameter and mounted on a 3-cm diameter column, was submerged 2 cm below the surface of the water. The surface of the platform consisted of a series of concentric ridges. The center of the platform was located on an imaginary line that bisected a corner at the base of the pool, 25 cm from point where the two walls met. The landmarks were black foam-rubber balls, 8 cm in diameter, which were attached to horizontal clear Perspex rods with a diameter of 7 mm. The rods were clamped to the top of the Perspex panels so that the center of the ball was 25 cm from one of the corners at the base of the triangle, on a line that bisected the corner. The lowest point of the ball was 30 cm above the surface of the water.

Procedure. Rats were transported to the test room five at a time in separate light-tight compartments of a carrying box. The box was placed on a shelf in the room adjacent to the room with the pool. The rats were trained for 24 sessions. There were four trials in each session, with the exception of sessions 12 and 24 in which there were three training trials followed by one test trial. For each training trial, rats were required to escape from the pool by swimming to the submerged platform. The platform was always in the left-hand corner at the base of the triangle for half the rats in each group and in the opposite corner for the remaining rats. A single ball was situated above the platform for every training trial for both groups and, in addition, a second, identical, ball was located in the opposite corner at the base of the triangle for every trial for the two-landmark control group. On each training trial a rat was released from the mid-point of one of the three walls by being placed gently in the water facing the edge of the pool. The sequence in which the release points were used varied randomly from session to session, with the constraint that each release point was used at least once in every session and that across three successive sessions all release points were used four times. The order in which each start point was used was randomized within a session. The arena was always oriented along the North-South or East-West axis, and following each trial it was rotated clockwise through 90^o, 180^o, or 270^o. The orientation of the arena at the start of a session varied randomly, and within a session it was oriented only once in each of the four possible directions. If a rat failed to locate the platform within 60 s the experimenter placed a thumb approximately 5 cm in front of the rat's snout and guided it to the platform. No prior training was required for this treatment to be effective. Once it had reached the platform, the rat was allowed to remain on it for 20 s before it was removed from the pool, gently dried, and replaced into the carrying box. It remained there until all rats in the carrying box had completed a single trial. This cycle was repeated until all the rats had received four trials.

The first three trials of Sessions 12 and 24 were conducted as normal training trials. All rats then received a test trial in which the landmarks and platform were removed from the pool. The rats were released from the center of the pool and allowed to swim for 60 s.

Throughout the experiment, a record was taken of which corner a rat entered first after being released into the pool. A corner was deemed to have been entered if any part of the rat crossed a notional circular line with a radius of 40 cm and with its center at the point where the walls creating the corner met. For ease of exposition, the term correct choice will be used to refer to when a rat entered the correct corner before any other corner. The results from the test trial were analyzed by recording the time each rat spent in two circular search zones that were 30 cm in diameter. The centers of the zones were located 25 cm from the two corners at the base of the triangle, on lines that bisected the corners.

Results and Discussion

A Type 1 error rate of $p < .05$ was adopted for all statistical tests in this article.

The left-hand panel of Figure 3 shows the mean percentage of trials on which the two groups headed directly for the correct corner after being released into the pool. The overshadowing group was more likely than the two-landmark control group to head for the correct corner during the first half of the experiment, but this difference between the groups was negligible for the final sessions. In order to compare the performance of the two groups, the mean number of correct choices for the 24 sessions combined was calculated for each subject. A comparison of these individual means revealed they were significantly greater in the overshadowing than the two-landmark control group $U(10, 10) = 0$.

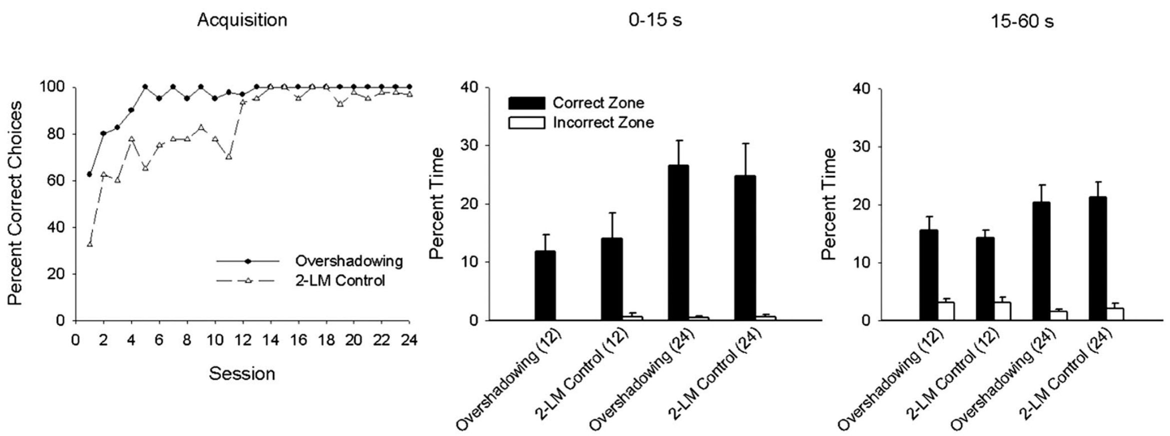

Figure 3. Left-hand panel: The mean percentage of trials on which the overshadowing and two-landmark (2-LM) control groups headed directly for the correct corner of the triangle during the 16 sessions of Experiment 1. Center panel: The mean percentage of time that the two groups of Experiment 1 spent the correct and incorrect search zones during the first 15 s of the test trials conducted after 12 sessions of training (overshadowing (12), 2-LM Control (12)) and after 24 sessions of training (overshadowing (24), 2-LM Control (24)). Right-hand panel: The equivalent results to those in the center panel, for the remaining 45 s of each test trial.

In keeping with the experiment of Pearce et al. (2001), the results from the first 15 s of the two test trials were examined separately from the results for the final 45 s. The center panel of Figure 3 shows the percentage of time spent by the two groups in the correct and incorrect search zones of the triangle during the first 15 s of both test trials. The right-hand panel shows the equivalent results for the remaining 45 s of the test trials. Substantially more time was spent in the correct than the incorrect search zone and there is no hint of a difference between the groups in the extent of this preference. A greater proportion of time was spent in the correct search zone during the second than the first test.

In support of these observations, a four-way ANOVA of individual percentages of time spent in the two search zones during the first 15 s and the last 45 s of each of the two tests revealed that the effect of group, and the seven interactions involving group were not significant, Fs < 1. There was a significant effect of search zone, $F(1, 18) = 104.59$, a significant effect of the number of training sessions, $F(1, 18) = 13.64$, and a significant interaction between these two effects, $F(1, 18) = 18.43$. Tests of simple main effects to examine the interaction revealed that significantly more time was spent in the correct search zone after 24 than 12 training sessions, $F(1, 36) = 31.79$, but this was not true for the incorrect search zone, $F < 1$. To return to the overall ANOVA, none of the remaining interactions, or the effect of interval within a trial, was significant, $Fs(1, 36) < 3.82$.

The results from the tests trials with the overshadowing group were identical to those from the two-landmark control group. Thus, being trained with a landmark directly above the goal, in the overshadowing group, did not at all disrupt learning based on geometric cues, relative to a group trained in the same way but with a second, identical landmark in the opposite corner at the base of the triangular pool. These findings contradict predictions that were derived from Miller and Shettleworth's (2007) associative model of geometry learning.

The results from the second test trial merit further consideration. Bearing in mind that if subjects searched for the platform at random they would be expected to spend 4.2% of their time in a search zone, it is evident from Figure 3 that both groups revealed a particularly strong preference for the correct search zone during the first 15 s of the test trial. This finding makes it unlikely that we failed to detect a difference between the groups because of inadequate training. In addition, during the final 45 s of this trial the preference for the correct over the incorrect zone was reduced relative to that during the first 15 s, yet there was still no hint of a difference between the results for the two groups. Such a finding makes it hard to argue that our failure to find a difference between the groups occurred because of a performance ceiling that masked a stronger preference for the correct zone in the control than the overshadowing group. The failure to confirm the predictions derived from Miller and Shettleworth (2007) is thus unlikely to be a consequence of an insensitive method of testing.

The experiment was based on a similar design to that by Pearce et al. (2001, Experiment 4) except that the landmark in the earlier study was a pole attached to the submerged platform. On that occasion, during the final 45 s of the trial the group trained with two landmarks in the pool showed a stronger preference for the correct corner of the pool than the overshadowing group. This effect, however, was obtained by examining the amount of time spent by the groups in quadrants occupying the lower half of the triangle, rather than circular search zones. A re-analysis of the present results using the results from the final 45 s of each test trial, and the time spent in quadrants of the pool revealed, contrary to the findings for Pearce et al. (2001), that the results for the two groups were remarkably similar. For the two test trials combined, the overshadowing group spent 63.7% of its time in the correct quadrant and the two-landmark control group spent 61.2% of its time in this quadrant. Likewise the two groups spent a similar amount of time in the incorrect quadrant during the final 45 s of the two test trials combined: 19.4% for the overshadowing group and 21.4% for the control group. Neither of these differences between the groups was significant, $ts(18) < .46$.

We are unable to offer an explanation for the poorer preference for the correct quadrant by the overshadowing than the control group during the final 45 s of the test trial conducted by Pearce et al. (2001), particularly as the opposite result was found during the first 15 s of the same trial. On the basis of the present results, however, the most reasonable conclusion to draw is that the training given to a two-landmark control group does not enhance spatial learning based on the geometric cues of a triangular arena to a greater extent than for an overshadowing group.

Experiment 2

The failure to observe a difference between the two groups of the previous experiment may have occurred because the salience of the ball was low relative to the salience of the geometric cues. Studies of Pavlovian conditioning with a compound composed of a strong and a weak stimulus generally reveal that the strong stimulus will overshadow the weak one, but the weak one will have little or no impact on conditioning with the strong one (e.g. Mackintosh, 1976). The model proposed by Miller and Shettleworth (2007) predicts a similar outcome. A computer simulation based on their equations revealed that the lower the salience of the landmark relative to the geometric cues, then the less effective will be the landmark as an agent for overshadowing geometric cues, and the more effective will be the geometric cues for overshadowing the landmark. If the failure of overshadowing in the previous experiment was a consequence of the relatively low salience of the landmark, then it should be possible to demonstrate that the overshadowing treatment results in the landmark being overshadowed by the geometric cues. One purpose of Experiment 2 was to test this prediction.

An overshadowing group of rats was trained in the same manner as its namesake for Experiment 1 before receiving a test trial of being placed into a circular pool with the landmark suspended above the pool some distance from the edge. The time that rats spent searching beneath the landmark was taken as the measure of its associative strength. A one-landmark control group was trained in the same way as the overshadowing group, except that the landmark and platform were moved, as one, randomly between the two corners at the base of the triangle. This treatment ensured that the geometric cues were irrelevant for finding the platform and should have prevented them from overshadowing learning about the position of the platform relative to the landmark. In keeping with this prediction, the left-hand panel of Figure 2 shows that the model of Miller and Shettleworth (2007) predicts that the associative strength of the landmark in the one-landmark group will be stronger than for the overshadowing group.

A third group was included in the experiment which was treated in the same way, and given the same name, as the two-landmark control group of Experiment 1. This group was included for two reasons. First, it provides an opportunity to test the reliability of the results from Experiment 1. Second, the simulation of the Miller and Shettleworth (2007) model described earlier revealed that the associative strength of the landmark in this group is predicted to be weaker than for the other two groups. If the test trial with the landmark should, for example, reveal a difference between the overshadowing and the two-landmark control group, then it will confirm that this novel test method is sufficiently sensitive to detect between-group differences in the associative strength of the landmark.

After being trained to find the platform in the triangle, therefore, the three groups received two test sessions. One test was conducted in order to examine the control acquired by the geometric cues in the triangle, and the other was conducted in a circular pool to assess the associative strength of the landmark. On the basis of the results from Experiment 1 we expected to find a similar, strong preference for the correct over the incorrect search zone in the triangular pool by the overshadowing and two-landmark control groups. Of course, the one-landmark control group would not be expected to exhibit a preference for either corner during this trial. If the failure to detect a difference between the results of the overshadowing and the two-landmark control group was a consequence of the salience of the landmark being less than of the geometric cues, then during the test in the circular pool the overshadowing group will spend less time searching beneath the landmark than the one-landmark group.

The results from the 60-s test trial in the previous experiment were analysed separately for the first 15 s and the final 45 s and revealed very similar findings. To simplify the presentation of the results for the remaining experiments, only the findings from the first 15 s will be considered.

Method

Subjects and apparatus. The subjects were 30 rats from the same stock and housed in the same manner as for Experiment 1. The rats had previously been used for an appetitive conditioning experiment in which their diet was restricted in order to maintain them at no less than 80% of their free-feeding weights. The rats were given unrestricted access to food for two weeks before training in the swimming pool began. At the start of the experiment the rats were assigned at random in equal numbers to the three groups. The apparatus was the same as for Experiment 1, except that the diameter of the black balls used as the landmarks was 11 cm rather than 8 cm. A circular test arena could be created by removing the two walls that formed the triangular pool. The curtains were drawn around the pool throughout the experiment.

Procedure. The method of training was the same as for the previous experiment for the overshadowing and the two-landmark control groups, except that there were 19 sessions and the fourth trial of Sessions 16 and 19 were test trials. The training for the one-landmark control group was based on that of the overshadowing group, except that for two trials in every training session the landmark and platform were located in one corner at the base of the triangle, and for the two remaining trials they were located in the opposite corner. The sequence with which the two corners were used varied randomly from session to session. Both groups received a test trial in the triangular pool in Session 16 in the manner described for Experiment 1. A second test was conducted in Session 19 which consisted of placing rats for 60 s in the circular pool without the platform but with the landmark. The landmark was suspended above the pool by being attached a horizontal, clear Perspex rod that was clamped to the edge of the circular pool. Its lowest point was 30 cm above the surface of the water and 50 cm from the edge of the pool. Procedural details of both the training and test trials that have been omitted were the same as for Experiment 1.

The method of recording behavior during the training and test trials in the triangle was the same as for the previous experiment. For the test trial in the circular pool, the amount of time that a subject spent in a circular search zone, with a diameter of 30 cm, was recorded. The center of the zone was directly below the center of the landmark.

Results and Discussion

The group mean percentages of trials on which a correct choice was made during the training stage are shown in the left-hand panel of Figure 4. The results are shown for every session of the experiment, apart from sessions 1 to 3 when the choices made by the rats were not recorded. Throughout the experiment, the performance of the overshadowing and one-landmark control group was similar, with both groups soon acquiring a strong tendency to head directly towards the correct corner. The results for the two-landmark control group were consistently inferior to those of the other two groups. Analysis of individual mean percentages of trials on which the corner containing the platform was approached first, for the final 16 sessions of the experiment revealed a significant difference among the groups, H(3) = 18.82. Subsequent comparisons revealed a significant difference between the results of the two-landmark control group and each of the other two groups, Us (10, 10) < 2, but no difference between the overshadowing and the one-landmark control group, U (10, 10) = 41 .

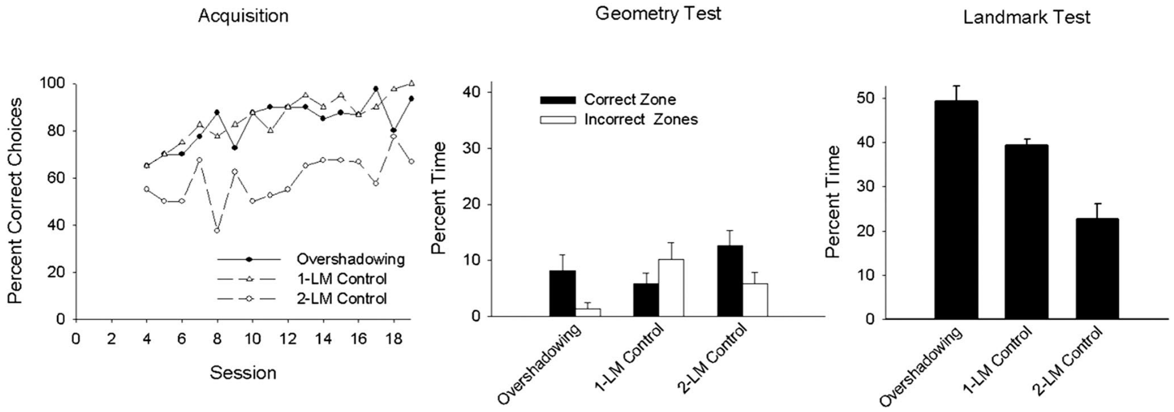

Figure 4. Left-hand panel: The mean percentage of trials on which the overshadowing, the one-landmark (1-LM) control and the two-landmark (1-LM) control groups headed directly for the correct corner of the triangle for Sessions 4 to 19 of Experiment 2. Center panel: The mean percentage time spent by the three groups of Experiment 2 in the correct and incorrect search zones during the test trial in the triangle. Right-hand panel: The mean percentage of time spent by the three groups of Experiment 2 in the search zone beneath the landmark during the test trial in the circular pool.

The mean percentage of time spent in the correct and incorrect search zones during the test trial in the triangle are presented in the center panel of Figure 4. The two groups that were trained with the platform always in the same corner – the overshadowing and the two-landmark control groups - showed a clear preference for this corner over the incorrect corner. There is an indication that the two-landmark group spent more time in each of the two search zones than the overshadowing group but, of particular importance, is the finding that the extent of the preference for the correct over the incorrect zone was similar in both groups. In support of these observations, a two-way ANOVA of individual percentages of time spent by the overshadowing and two-landmark control groups in the correct and incorrect search zones revealed a significant effect of zone, F(1, 18) = 7.84, but the effect of group, F(1, 18) = 4.19, and the interaction, F < 1, were not significant. In view of the treatment given to the one-landmark control group, there was no reason to expect it to show a marked preference for one corner at the base of the triangle over the other. The center panel of Figure 3 indicates a modest preference by this group for the incorrect corner, but this difference was not significant, t(9) = 1.21

The results depicted in the right-hand panel of Figure 4 are from the test trial in the circle. Bearing in mind that the search zone occupied 2.25% of the area of the entire pool, it is evident that all three groups spent substantially more time in the search zone than would be expected if they searched at random in the pool. In support of the additional observation that the groups spent different amounts of time in the search zone, a one-way ANOVA of individual times spent in the search zone revealed a significant difference among the groups, F(2, 27) = 21.79. Subsequent comparisons using the Newman-Keuls procedure revealed that the two-landmark control group spent significantly less time searching near the landmark than either the overshadowing or one-landmark control group. In addition, the overshadowing group spent more time near the landmark than the one-landmark control group.

The results from the first test with the overshadowing and two-landmark control groups replicate the findings from Experiment 1 and confirm that the different treatments given to the two groups do not result in the geometric cues gaining greater control over searching for the platform in one group than the other. The novel finding from the experiment concerns the test trial with the landmark in the circular pool. The overshadowing and one-landmark control groups spent a considerable amount of time searching in the vicinity of the ball, but there was no indication that this activity was stronger in the one-landmark control than the overshadowing group. To the contrary, the overshadowing group spent significantly more time than the one-landmark control group beneath the landmark during the second test. Possible reasons for this outcome will be considered in the General Discussion. For the present, it is evident that the presence of the geometric cues during the training with the overshadowing group did not restrict at all the associative strength of the landmark.

Experiment 3

The previous experiments have shown that when rats are required to find a submerged platform beneath a landmark in one corner of a triangular pool, then the presence of one of these cues does not restrict the control acquired by the other over searching for the platform. Before considering the implication of these findings, we must first examine the possibility that there is something unusual about the spherical landmark we used that makes it unsuitable for investigating overshadowing.

A measure of support for this possibility can be found in an experiment by Timberlake , Sinning, and Leffel (2007). They demonstrated that a wedge-shaped landmark suspended over the platform in a swimming pool was an ineffectual cue for blocking, when the additional cues were objects such as posters suspended in front of a curtain enclosing the pool. They further demonstrated that this shortcoming could be overcome by attaching the wedge to the platform with a rod. Timberlake et al. (2007) suggested that attaching the wedge to the platform made it more salient, and thus increased its effectiveness for blocking (see Hall, Mackintosh, Goodall, & Martello, 1977). Applying this reasoning to the present studies makes it possible to explain why the sphere failed to overshadow the geometric cues, but if the sphere was of low salience then it should have been overshadowed by the geometric cues. The previous experiment failed to reveal any support for this prediction which makes it unlikely that appealing to the salience of the landmark will account for the results thus far. Of course, there may be some other property of the landmark that prevents it from overshadowing, and being overshadowed, by other cues. Experiments 3 and 4 were conducted in order to test this possibility.

In Experiment 3 an overshadowing group of rats was trained to find a submerged platform beneath the spherical landmark in one corner of a square pool with two black walls, which were adjacent, and two white walls. The platform and landmark were always located in the corner created by the two white walls – the white corner. The purpose of this experiment was to assess whether the landmark would overshadow, or be overshadowed by, the color of the walls of the arena. The color of the walls was selected as the cue for investigating overshadowing because Pearce, Graham, Good, Jones, and McGregor (2006) have already shown that this cue is capable of overshadowing geometric cues provided by a rectangular pool. On the basis of this finding it is likely that the color of the walls will overshadow the landmark.

In order to test this outcome a one-landmark control group received similar treatment to the overshadowing group, but the landmark was suspended above the platform in different corners of the square from one trial to the next. Hence, the landmark in the one-landmark control group was expected to gain considerable associative strength because it uniquely signalled where the platform could be found. Both groups received a test trial in the circular pool with the landmark suspended over the surface of the water some distance from the edge. If the one-landmark group should spend more time than the overshadowing group searching beneath the ball, then the conclusion could be drawn that the color of the walls overshadowed learning about the landmark.

A third group was included in the experiment in order to determine if the landmark was capable of overshadowing the color of the walls. For this no-landmark control group, the platform was always in the white corner, and the landmark was located at random in each of the four corners. Towards the end of training, a test trial was conducted in the black and white square with the landmark and platform removed. If the no-landmark control group should spend more time searching in the correct corner than the overshadowing group, then it would demonstrate that the color cues were indeed overshadowed by the landmark during the training trials.

Method

Subjects. The 30 animals in this experiment were from the same stock and were housed in the same way as for the previous experiments. They were experimentally naïve at the beginning of the experiment.

Apparatus. The experiment was conducted in the same swimming pool and with the same landmark as Experiment 1. A square was created within the wall of the swimming pool by suspending four acrylic boards vertically into the pool from bars that extended over the pool's edge. The boards were built of the same material and constructed in the same manner as the straight walls of the triangle in Experiment 1, except that the length of each wall was 1.41 m. Two of the boards were black, the remaining two were white. To create the square pool, the two black boards were adjacent to each other, and so were the two white boards. The square thus contained a black corner, a white corner, and two black and white corners.

Throughout training the center of the platform was 25 cm from the appropriate corner on a line that bisected the corner. The landmark was always suspended above the pool with its lowest point 30 cm above the surface of the water. During training the center of the landmark was 25 cm from the appropriate corner, on a line that bisected the corner; for the test in the circular pool the center of the landmark was 50 cm from the edge of the pool, suspended by a thread attached to the ceiling.

Procedure. The three groups received 24 sessions of training in the square pool. The platform was always located in the white corner for the overshadowing group, directly beneath the landmark which was present for every training trial. The platform was also located in the white corner for the no-landmark control group, but the position of the landmark varied randomly among the four corners with the constraint that it was located once in every corner in every session. The position of the landmark varied in a similar fashion for the one-landmark control group, but the platform was always directly beneath it. Rats were released once from the center of each of the four walls of the arena in each session. The curtains were drawn around the pool throughout the experiment and the orientation of the arena was changed between trials in the same manner as for the previous experiments. Other details of the training procedure were the same as for the previous experiments.

The first three trials of session 18 were conducted in the way just described. The fourth trial was a test trial with the platform removed from the pool. For half of the animals in each group the test took place in the square in the absence of the landmark. For the remaining animals the square arena was removed from the pool and the test was conducted in the circular pool in the presence of the landmark. On session 24, three standard training trials were again followed by a test trial. Those animals that received the test trial in the square were now tested in the circular pool. The remaining animals were tested in the square. Other details of the test trial were the same as previously described. The manner of recording behavior during the training and test trials was the same as for the previous experiments.

Results and Discussion

The left-hand panel of Figure 5 shows the mean percentage of trials on which the three groups headed directly for the corner containing the platform, for each session of the experiment. The performance of the overshadowing group was superior to that of the one-landmark control group, which was superior to that of the no-landmark control group. A Kruskal-Wallis test of individual mean correct choices for the 24 sessions combined revealed a significant difference among the groups, $H(3) = 25.55$. Subsequent tests revealed the no-landmark control group made significantly fewer correct choices than either of the other two groups, $Us\ (10, 10) = 0$. In addition, the one-landmark control group made fewer correct choices than the overshadowing group, $U\ (10, 10) = 1.0$.

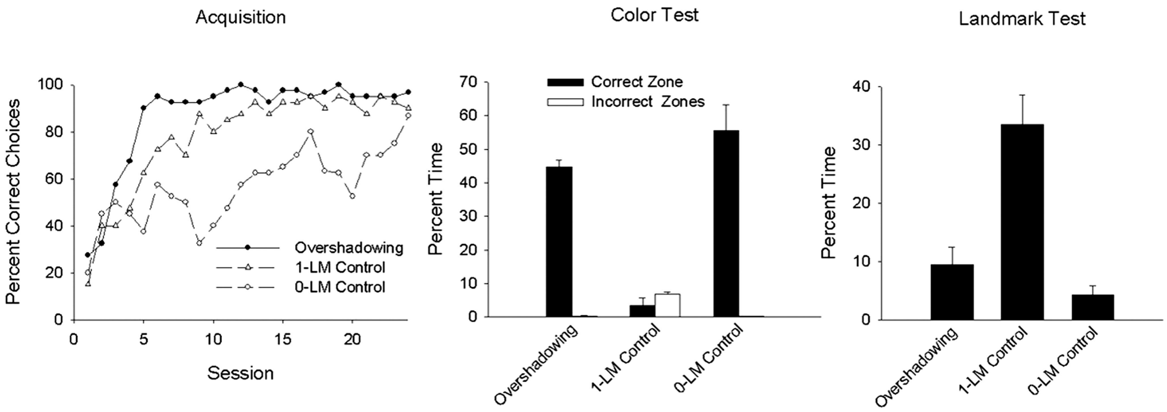

Figure 5. Left-hand panel: The mean percentage of trials on which the overshadowing, the one-landmark (1-LM) control and the no-landmark (0-LM) control groups headed directly for the correct corner of the black and white square for the 24 sessions of Experiment 3. Center panel: The mean percentage time spent by the three groups of Experiment 3 in the correct and incorrect search zones during the test trial in the black and white square. Right-hand panel: The mean percentage of time spent by the three groups of Experiment 3 in the search zone beneath the landmark during the test trial in the circular pool.

For the test in the square, the percentage of time spent by each rat in each of the four corners was recorded. The middle panel of Figure 5 shows the mean percentage of time spent by the three groups in the correct corner (the white corner), and the average of the mean percentages of time spent in the three remaining corners. The overshadowing and the no-landmark control groups showed a substantial preference for the correct corner over the other corners. There is a suggestion that the extent of this preference was greater in the no-landmark group than the overshadowing group, but this difference was not significant. A two-way ANOVA for the two groups based on individual mean percentages of time spent in the correct corner, and the other three corners combined, revealed a significant effect of corner, $F(1, 18) = 163.42$, but the effect of group, $F(1, 18) = 1.95$, and the interaction, $F(1, 18) = 1.94$, were not significant. In view of the treatment it received, there was no reason to expect the one-landmark control group to acquire a preference for the white corner of the square. Indeed, from the center panel of Figure 5 it appears that this group spent less time in this corner than the other corners, but this difference was not significant, $t(9) = 1.42$.

The right-hand panel of Figure 5 shows the mean percentage of time the three groups spent searching beneath the landmark during the test trial in the circular pool. The one-landmark control group spent more time in the search zone than either of the other two groups. A one-way ANOVA of individual times spent in the search zones revealed a significant difference among the groups, $F(2, 27) = 20.38$. Newman-Keuls comparisons then revealed a significant difference between the one-landmark control group and each of the two other groups.

The difference between the results from the overshadowing and the one-landmark control group, during the test in the circular pool, demonstrates that the presence of the color cues during the training stage overshadowed learning about the position of the platform with reference to the landmark in the overshadowing group. To our knowledge this is the first occasion that spatial learning based on a discrete landmark has been overshadowed by the presence of other cues. Such a demonstration thus confirms that there is nothing unique about the landmark that prevented it from being overshadowed by the geometric cues in Experiment 2. Some other explanation must therefore be sought for the failure of the geometric cues to overshadow the landmark in that experiment.

Inspection of the center panel of Figure 5 indicates that the overshadowing group spent less time searching in the correct corner during the test in the black and white square than the no-landmark control group. This difference, however, was not significant, and we must conclude that the landmark did not overshadow learning about the position of the platform with respect to the color cues. Before reaching the additional conclusion that a ball suspended over a platform is not an effective cue for overshadowing in any circumstances, it must be acknowledged that color may be a particularly difficult cue for a landmark to overshadow. The fact that color overshadowed the landmark in the present experiment implies that the former was more salient than the latter (Mackintosh, 1976), in which case one might not expect to find overshadowing in the opposite direction. Accordingly, for the final experiment, we assessed whether the ball landmark could overshadow cues which have already been shown to be capable of being overshadowed by a different landmark.

Experiment 4

Redhead, Roberts, Good and Pearce (1997) trained an overshadowing group of rats to find a submerged platform with a rod attached to it as a landmark in a circular pool that was surrounded by cues provided by the experimental room. A two-landmark control was treated in a similar fashion, except that a second landmark, identical to the first was situated in a fixed location some distance from the platform. A subsequent test without a landmark or the platform in the pool revealed that the overshadowing group spent less time searching in the quadrant of the pool where the platform had previously been located than the control group. The present experiment was conducted in order to determine if a similar overshadowing effect can be found when the landmark is the sphere used for the previous experiments.

Method

Subjects and apparatus. The subjects were 20 rats from the same stock, with similar experience, and housed in the same manner as for Experiment 1. The experiment took place in a different room to the one used for the previous experiments. The circular pool, and the suspended circular ceiling above it, were of the same design and dimensions as for Experiment 1. The room in which the pool was housed was 4 x 3 x 2.3 m high. Three of the walls of the room were painted white and hung with posters of different shapes and patterns. The fourth wall, with a door in its center, was covered with a sheet of aluminium. The center of the door defined north for the purposes of the experiment. A curtain, which could enclose the pool, was tied back in the north-east corner of the room. Illumination of the room was provided, in part, by eight 45-W spotlights, arranged in the circular ceiling in the same manner as for Experiment 1. Additional illumination was provided by four, horizontal, 1.53-m strip lights that were arranged end to end in pairs on opposite 4-m walls of the room. They were 75 cm above the floor. A video camera was located above the pool in the same manner as for Experiment 1. The image from the camera was relayed to a monitor in the north-east corner of the room. A 2-m high, 1.5-m wide screen was situated 30 cm from the pool in the north-east corner. Video recording equipment and a computer were located outside the room. The computer could be used to record the rats' paths using the same software as for Experiment 1.

Procedure. Rats were transported to the room five at a time in separate compartments of a light-tight carrying box which was placed on a trolley in the north-west corner of the room. The rats were trained for 15 sessions. For half of the subjects in each group the platform was located in the south-east quadrant of the circular pool, and for the remainder it was located in the north-west quadrant. The platform was located 50 cm from the edge of the pool on a radius that bisected the relevant quadrant. For both groups, a black ball was suspended directly above the platform by a thread from the ceiling, with its lowest point 30 cm above the surface of the water. In addition, for the two-landmark control group, a second ball was suspended in a similar manner to the first ball, but in the diametrically opposite location. Rats were released into the pool from start points that were located on the edge of the pool that corresponded to the four main compass points. The order in which each start point was used was randomized within each session. Throughout each trial the experimenter observed the rat on the monitor from behind the screen.

The first three trials of Session 16 were conducted in the same manner as for the preceding sessions. All rats then received a test trial in the absence of any landmark and the platform. Each rat was released from the center of the pool, and allowed to swim for 60 s. In the previous experiments the performance of the rats was monitored during the training trials by noting whether they entered first the correct or incorrect corner after being released into the pool. The use of a circular pool for training prevented this method from being used in the present experiment. Instead, the time taken for a rat to climb onto the escape platform after being released into the pool was recorded on every training trial.

Results and Discussion

The mean escape latencies for the two groups for the sixteen sessions of the experiment are shown in the left-hand panel of Figure 6, where it is evident that there was rather little difference between the groups. A two-way ANOVA revealed a significant effect of session, F (15, 270) = 164.36, but no difference between the groups, F (1, 18) = 2.13, and no interaction, $F < 1$.

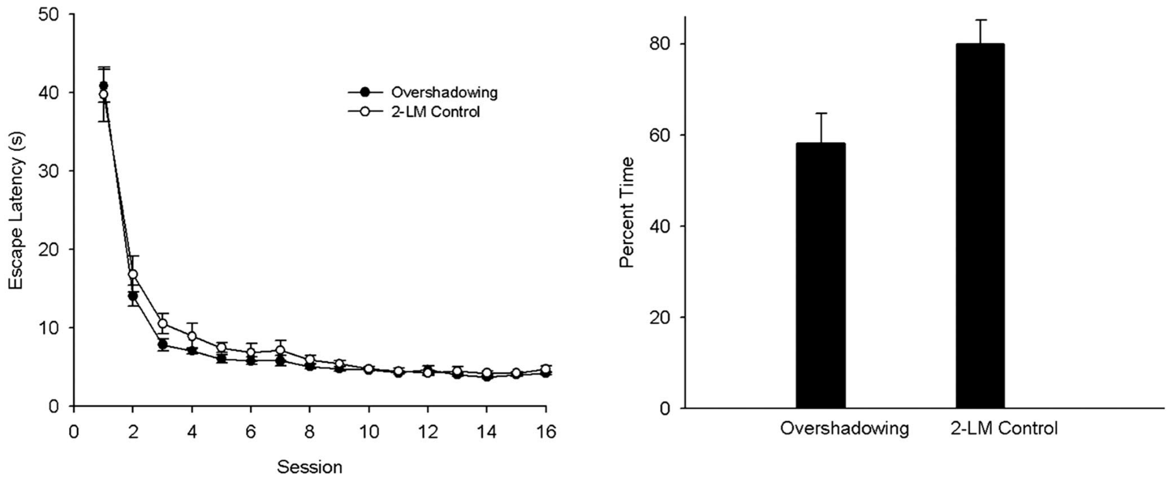

Figure 6. Left-hand panel: The mean escape latencies for the overshadowing and the two-landmark (2-LM) control groups of Experiment 4 during the 16 sessions of training in the circular pool. Right-hand panel: the mean percentage of time searching in the quadrant where the platform had previously been located during the test trial for the two groups of Experiment 4, according to whether the platform had been located in the south-east or north-west quadrant.

The results from the first 15 s of the test trial are presented in the right-hand panel of Figure 6 which shows that the overshadowing group spent less time in the correct quadrant than the two-landmark control group. This difference was statistically significant, $t(18)= 2.46$.

In keeping with the findings of Redhead et al. (1997), the results show that the presence of a black sphere suspended above a hidden platform can overshadow learning about the position of the platform with reference to distal cues provided by the room in which the pool is housed. This finding thus implies that the failure of the same landmark to overshadow geometric cues in Experiments 1 and 2 was not due to some inherent property that prevents it from acting as an agent for overshadowing.

General Discussion

Experiments 1 and 2 failed to find any evidence of overshadowing between a discrete landmark and the geometric cues provided by the shape of a triangular arena. The failure of a landmark to overshadow geometric cues has been reported on a number of occasions (e.g. Pearce et al., 2001), but this is the first time that a failure of geometric cues to overshadow a landmark has been described. The principal purpose for conducting the experiments was to test the associative model of geometry learning proposed by Miller and Shettleworth (2007). According to this model, overshadowing between a discrete landmark and geometric cues should have been observed in each of the first two experiments. As they stand, therefore, the results imply that, at best, the model proposed by Miller and Shettleworth (2007) provides an incomplete account of the factors that govern the acquisition of associative strength by cues during spatial learning.

The foregoing conclusion, as far as overshadowing of geometric cues by the landmark is concerned, must be tempered by the fact that it is based on a set of null results. This shortcoming of our findings was considered in the discussion to Experiment 1 and there is little to add here, except to repeat that the failure of the landmark to overshadow the geometric cues was unlikely to be a consequence of the use of an insensitive test. The possibility remains, however, that a subtle change to the design of the experiments would reveal overshadowing, but it is hard to know what this change should be.

One way of reconciling the present results with Miller and Shettleworth's (2007) model is to appeal to the influence of within-compound associations. It is conceivable, for example, that the landmark overshadowed the geometric cues in the overshadowing groups of Experiments 1 and 2 but at the same time associations developed between the geometric cues and the landmark. Even though the sight of the correct corner, during a test trial in the triangle, might then elicit a relatively weak tendency to approach it, the sight of this corner might also activate a representation of the landmark and the attractiveness of this cue would compensate for the effects of overshadowing. In other words, the presence of one cue might potentiate learning based on the other (e.g. Rescorla and Durlach, 1981).

There are several strands of evidence in support of this explanation for the present results. First, the test trial in the circular pool of Experiment 2 revealed that potentiation can result from our method of training. It was found that the landmark exerted significantly more control over searching for the platform in the overshadowing than the one-landmark control group (see Figure 4, right-hand panel). Second, potentiation has been found in other spatial learning studies. Thus Graham, Good, McGregor and Pearce (2006) report that the control acquired by the geometric cues of a kite-shaped pool over searching for a platform was enhanced if the color of the walls could also be used to identify the location of the platform. The final strand of evidence comes from studies showing that between-cue associations develop during spatial learning. Horne and Pearce (in press), for example, found that performance in the presence of geometric cues is influenced by the associative properties of non-geometric cues, when the latter are present during training but not testing (see also Rhodes, Creighton, Killcross, Good, & Honey, in press).

A rather different explanation for potentiation in spatial learning has been put forward by Timberlake et al. (2007), who proposed that satisfactory spatial learning depends upon the development of a stable framework of background cues. If subjects are first trained to locate a goal with reference to a set of relatively weak cues then they may learn rapidly about the significance of cues that are subsequently introduced because they will be introduced against a stable spatial framework. Timberlake et al. (2007) further acknowledge that this process can operate in opposition to associative learning about the cues that would be governed by, say, the Rescorla-Wagner (1972) equation. In the case of the landmark in the present studies, therefore, the geometric cues may have disrupted its influence through overshadowing, but compensated for this effect by providing a stable framework against which learning about the position of the platform relative to the landmark could take place.

Thus far we have considered the possibility that learning about geometric cues and landmarks is governed by the same competitive rule that has been shown to govern other types of learning (e.g., Rescorla & Wagner, 1972). Given the pattern of results that we found, it might be more reasonable to conclude that learning about these cues is not governed by a competitive rule. Animals make use of a variety of sources of information in order to navigate towards a goal and, as Shettleworth (1998) points out, information that is relevant to different strategies might be processed in different cognitive modules. If these modules were to operate independently of each other, then learning about the significance of a cue that is important for one strategy should not influence the control acquired by a cue that is important for a different strategy (Shettleworth & Sutton, 2005). Perhaps the simplest interpretation of the present results is to assume, as mentioned in the Introduction, that learning about the shape of the environment takes place in a dedicated module that is unaffected by the presence of non-geometric stimuli (e.g. Cheng, 1986; Gallistel, 1990). An obvious implication of this proposal is that learning about geometric cues will progress independently of learning about discrete landmarks and that the presence of one would not be expected to overshadow the other.

Although appeal to a geometric module can explain the failure of a landmark to overshadow geometric cues, it is worth noting that the existence of such a module has by no means gained universal acceptance. For instance, the claim that learning about the shape of the environment takes place in a module dedicated to geometric information is clearly at odds with the discovery by Graham et al. (2006), mentioned above, that the color of the walls creating a kite-shaped environment influences learning based on geometric cues (see also Cheung, Stürzl, Zeil, and Cheng, 2008; Pearce, Graham, Good, Jones, & McGregor, 2006). To explain this outcome it must then be assumed that some non-geometric cues, such as the color of walls, are allowed to enter the module, but others are not, such as discrete landmarks. Once this assumption is made, however, it becomes questionable whether the term geometric module can be used meaningfully. Indeed, Gallistel (1990, p. 208) has specifically argued against this assumption, by asserting that information about the properties of the objects creating a shape will be denied access to the geometric module. A rather different challenge to the existence of a geometric module was raised by Pearce, Good, Jones and McGregor (2004, see also McGregor, Jones, Good & Pearce, 2006) who argued that animals may not navigate by means of a global representation of their environment and would thus have no need for the module.

Another possibility is to acknowledge that as an animal moves towards its goal it relies on a sequence of different cues that are used in a hierarchical fashion (Shettleworth, 1998). For example, rats in the overshadowing groups of the present experiments may have learned to use the shape of the pool to guide them to the correct corner, and then as they reached the corner they may have switched their attention to the landmark for the purpose of fine tuning their search for the platform. Given such a possibility, it would not seem unreasonable to conclude that learning about the geometric cues will fail to interfere with the landmark, and *vice versa*. Moreover, by appealing to such mechanisms as higher-order conditioning, serial learning, and conditioned reinforcement, it would be possible to understand this hierarchical use of cues from the perspective of associative learning theory.

The present results may be of relevance to template matching accounts of navigation (e.g. Cartwright and Collett, 1983). When an animal is at a goal it is assumed to take a snapshot of its surroundings. To find the goal again the animal must then move in a direction that transforms its current view into one that matches the snapshot. See Stürzl, Cheung, Cheng, & Zeil (2008) and Cheung et al. (2008) for an application of these ideas to environments with a distinctive shape. Turning to Experiment 2, the test trial in the circular pool revealed considerable control by the landmark in both the overshadowing and one-landmark control groups. Since this test took place in an environment with very different geometric properties to the training environment, it would be hard to find a horizontal view on the test trial that matched the snapshot taken of the goal during the training trials. This failure to match the snapshot might then be expected to weaken searching beneath the landmark through generalization decrement. To explain the strong response on this test trial, one might argue that the snapshot involved the view from platform looking upwards at the landmark, in which case the geometric cues would form a relative minor component of the snapshot. The natural implication of this analysis is that the removal of the landmark from the triangle will produce a large generalization decrement and result in overshadowing, yet this effect was not observed.

There are a number of explanations for the failure to observe overshadowing between a landmark and geometric cues. Some are based on the assumption that cues compete for the control they acquire over searching for a hidden goal (Miller and Shettleworth, 2007). To explain the present results it is necessary for these explanations to appeal to an additional mechanism, such as between-cue associations, that will compensate for the effects of cue competition. Other explanations assume that landmarks and geometric cues govern different strategies which are not in competition with each other, and which may be processed by different modules. A problem that confronts all of these explanations is that, as Experiments 3 and 4 have demonstrated, cue competition effects can be found with the spherical landmark when the other spatial cue is not provided by the shape of the test arena. Any satisfactory account of spatial learning will need to make clear why overshadowing is seen in some spatial tasks, but not others.

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