

The Influence of Excitatory and Inhibitory Landmarks on Choice in Environments With a Distinctive Shape

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In two experiments rats were trained to find one of two submerged platforms that were located in diagonally opposite corners—the correct corners—of a rectangular pool. Additional training was given to endow two different landmarks with excitatory and inhibitory properties, by using them to indicate where a platform was or was not located in either a rectangular (Experiment 1) or a square pool (Experiment 2). Subsequent test trials, with the platforms removed from the pool, revealed that placing the excitatory landmark in each of the four corners of the rectangle resulted in more time being spent in the correct corners than when the four corners contained inhibitory landmarks. This result is contrary to predictions derived from a choice rule for spatial behavior proposed by Miller and Shettleworth (2007).

Keywords: spatial learning, choice, geometric cues

How one makes a choice between two alternatives is an important question in the area of decision making. The most widely-utilized model of how one weighs the pros and cons of each choice is based on a ratio of the magnitudes of each alternative. This ratio rule, sometimes referred to as the choice axiom (Luce, 1959, 1977), is shown in Equation 1, where P_A is the probability of choosing alternative A, and A and B are the strengths of each alternative.

$$P_A = \frac{A}{A + B} \quad (1)$$

Reminiscent of Thurstone's (1930) learning function, the ratio rule above, or derivations of this rule, have been used in a number of areas, ranging from statistics and economics (Halldin, 1974; McFadden, 1974) to animal behavior, including categorization in pigeons (Soto & Wasserman, 2010), and the matching law of operant conditioning (Herrnstein, 1970). The purpose of the present article is to explore the merits of an application of this ratio rule to spatial behavior that was proposed by Miller and Shettleworth (2007, 2008).

Figure 1 shows a rectangular arena where a goal may be hidden in a corner, say corner W. In order to ensure that only cues provided

by the shape of the arena are used to locate the goal, the orientation of the arena is normally varied randomly from trial to trial and it is surrounded by a curtain. When placed in this apparatus, a well-trained subject will head either to the corner containing the goal, corner W, or to the diagonally opposite corner, corner Y, which is geometrically equivalent to corner W. On failing to find the goal in corner Y, the subject will then head for corner W (e.g., Cheng, 1986; Pearce, Good, Jones, & McGregor, 2004). For the sake of discussion, corners W and Y will be referred to as the correct corners, and corners X and Z as the incorrect corners. Experiments have shown that species as diverse as ants (Wystrach, Cheng, Sosa, & Beugnon, 2011) and humans (Wang, Hermer, & Spelke, 1999) are able to locate successfully the goal in this kind of apparatus by reference to cues creating the rectangular shape of the arena.

To explain the preference shown by animals trained in this apparatus for searching in the correct rather than the incorrect corners, Miller and Shettleworth (2007) proposed that every visit to a corner provided the opportunity for the associative strength of the cues in that corner to be modified. If the visit resulted in reward then the associative strength of the cues would increase, but if there was no reward the associative strength of the cues would be reduced. The proposed rule governing these changes in associative strength is closely related to that proposed by Rescorla and Wagner (1972). Thus, after being trained in an arena similar to that depicted in Figure 1, the overall associative strengths of the cues relating to corners W and Y will be identical, as the two corners are equivalent. Moreover, given that visits to corner W will have been rewarded, the overall associative strengths of these two correct corners will be relatively high. In contrast, the associative strengths of the two identical incorrect corners, X and Z, will be low because all the visits to these corners will have been nonrewarded.

Performance on any trial was then said to be determined by a ratio rule based on Equation 1, where the probability of choosing

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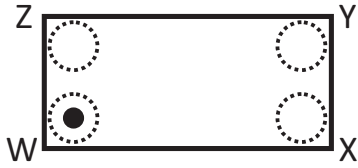


Figure 1. A schematic representation of the rectangular pool. W, X, Y, Z are the corners of the pool. The black filled circle is the submerged platform, and the dotted circles represent the area of the zones used for the analysis.

a correct location was determined by the overall associative strength of the corner in question, divided by the sum of the overall associative strengths of all the locations under consideration. In the case of choosing corner W in Figure 1, this relationship can be expressed as Equation 2, where P_W is the probability of choosing corner W, and V_W , V_X , V_Y , and V_Z , represent the overall associative strengths of corners W through Z, respectively.

$$P_W = \frac{V_W}{V_W + V_X + V_Y + V_Z} \quad (2)$$

Given the equivalence between the two correct corners W and Y, and the two incorrect corners, X and Z, the probability of choosing a correct corner, P_C , on any trial is then given by Equation 3, where V_C is the associative strength of the correct corners, and V_I the associative strength of the incorrect corners.

$$P_C = \frac{V_C}{V_C + V_I} \quad (3)$$

The purpose of the two reported experiments was to test whether the relationship expressed in Equation 3 provides an accurate account of how animals allocate their time between the correct and incorrect corners of a rectangular pool, after they have been trained to find reward in the correct corners. In two experiments, rats were trained to escape from a rectangular pool of water by swimming to one of two platforms that were submerged just below the water in two diagonally opposite corners, say corners W and Y in Figure 1. This training was expected to result in the associative strengths of the two correct corners being greater than of the two incorrect corners, with the consequence that on a test trial with the platforms removed from the pool, more time would be spent in the correct than the incorrect corners. At the same time, rats received training with landmarks which were intended to endow them with either positive or negative associative strength by serving, respectively, as signals for the presence or absence of the platform. Additional test trials were then conducted in which rats were placed in the pool, with the platforms removed, and with identical landmarks located in each of the four corners. The question of interest was how the amount of time spent in the correct corner was affected by whether the four landmarks were excitatory or inhibitory. If it is assumed that the associative strength of the landmark is V_K , then the preference for the correct corners on the test trial will be given by Equation 4

$$P_C = \frac{(V_C + V_K)}{(V_C + V_K) + (V_I + V_K)} \quad (4)$$

To appreciate the different predictions made by Equations 3 and 4 on the amount of time spent in the correct corner, P_C , during a test trial with or without the landmark present, a series of calculations were conducted in which the values of V_C , V_I and V_K were varied. The horizontal axis of Figure 2 depicts the value of P_C as given by Equation 3, for selected values of V_C and V_I that ensured P_C increased from 0 to 1 in steps of .05.¹ The vertical axis shows the values of P_C when the same values of V_C and V_I from each of the foregoing 20 calculations are transposed into Equation 4, with different values of V_K . The plot with black circles shows the outcome of these calculations when V_K was equal to zero, that is when the landmark was absent for the test trial. In this condition, Equations 3 and 4 make identical predictions concerning the value of P_C , and hence the plot is a straight line at 45 degrees to the abscissa and passes through the origin. The plot with open circles depicts the relationship between the two equations when V_K is positive (+20), and the filled triangles depict this relationship when V_K is negative (-20). When V_C is equal to V_I , then both equations predict that equal amounts of time will be spent in the correct and incorrect corners, no matter what the value of V_K . But when V_C is greater than V_I , which would be expected on the basis of the training that is given, then the probability of choosing a correct corner is predicted to be greater when V_K is negative than when it is positive. In other words, presenting an excitatory landmark in each corner of the pool is predicted to reduce the preference for the correct over the incorrect corners, and an inhibitory landmark is predicted to have the opposite effect.

Miller and Shettleworth (2007) equate the probability of choosing a corner with the amount of time that a subject will spend in that corner. It therefore follows from the above analysis that placing an excitatory landmark in each corner will result in less time being spent in the correct corner than when either no landmark or an inhibitory landmark is present. Conversely, placing an inhibitory landmark in each corner will result in more time being spent in the correct corner than when either no landmark or an excitatory landmark is present.

To our knowledge the foregoing predictions have not been tested. If the proposed experiments can confirm these predictions, then they will provide strong, novel support for the analysis of spatial learning in a rectangular environment proposed by Miller and Shettleworth (2007). Before describing the experiments, however, some additional comment is required concerning the relationships expressed in Figure 2. We have just seen the values of P_C , which are greater than .5 as predicted by Equation 3, indicate the probability of choosing the correct corner. It then follows that the value $1 - P_C$ will indicate the amount of time spent in the incorrect corners. Because this value will be less than .5 it follows that the left-hand side of Figure 1 can be used to determine the effect of adding an excitatory or an inhibitory landmark in all four corners of the rectangle on the time spent in the incorrect corners. The figure shows that when the added landmark is excitatory, its presence will increase the amount of time spent in the incorrect corners of the pool during the test trial, whereas an inhibitory

¹ For these calculations, we assumed the total amount of associative strength available was 100, thus the values of $(V_C + V_I)$ were held constant at 100. V_C ranged from 5 to 100 in increments of 5, and V_I ranged from 95 to 0 in decrements of 5.

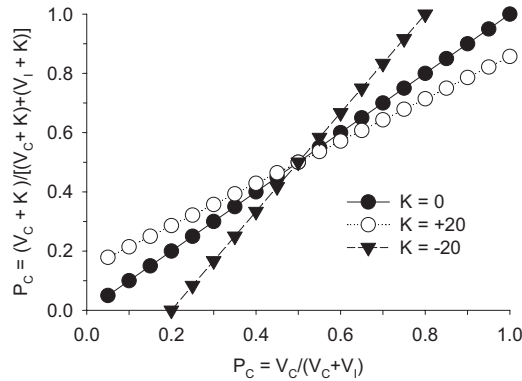


Figure 2. Predictions derived from the ratio rule for when a landmark (K) with a particular associative strength is added to each of the four corners of a rectangular environment. x -axis is the ratio prior to the addition of the landmarks, and the y -axis represents the ratio after the addition of the landmarks.

landmark will reduce the time spent in these regions. A further point to make is that different values of V_K do not affect qualitatively the predictions shown in Figure 1, but they do affect the slopes of the plots. The smaller the value of V_K , the closer the plot is to that shown for V_K equal to 0. The final point to make is that in keeping with the proposals of Miller and Shettleworth (2008), whenever the overall associative strength of a corner was negative then its value was set at zero.

Experiment 1

In the following experiment, rats were required to swim to one of two submerged platforms that were located in diagonally opposite corners of a rectangular swimming pool with gray walls. The platforms were situated in the same pair of corners, which are referred to as the correct corners, for all training trials. Pasted to the walls in each correct corner were two cards of a specific color, either black or white, and pasted to the walls in each of the remaining incorrect corners were two cards of the opposite color. The cards were intended to serve as landmarks which were expected to gain excitatory strength by virtue of being placed in the correct corners, or inhibitory strength by virtue of being placed in the incorrect corners. Following training, animals were given three test trials with the platform removed from the pool. The three tests included a trial without any landmarks, a trial with the excitatory landmarks located in each of the four corners, and a trial with the inhibitory landmarks located in each of the four corners. According to predictions derived from the proposals of Miller and Shettleworth (2007), rats will spend more time in the correct corners of the pool during the test with the inhibitory than the excitatory landmarks. Finally, tests were conducted by placing a single landmark in one of the correct corners of the pool in order to determine whether it had acquired excitatory or inhibitory properties during the initial training. An excitatory landmark was expected to result in rats spending more time in the correct corner containing the landmark than in the one without it. The opposite outcome was expected for the test with the inhibitory landmark.

Method

Subjects. Thirty, experimentally naïve, male, hooded Lister Rats (*Rattus norvegicus*), obtained from Harlan Olac (Bicester, Oxon, United Kingdom), and weighing between 250 g - 300 g at the start of the experiment were used. Rats were housed in white plastic cages with secured metal grid lids and maintained on a 12-hr/12-hr light/dark cycle with lights on at 0700. Subjects were housed in pairs and had continuous access to food and water in their home cages.

Apparatus. A white, circular pool measuring 2 m in diameter and 0.6 m deep was used. The pool was mounted on a platform 0.6 m from the floor in the middle of the room (4 m × 4 m × 2.3 m). The pool was filled with water to a depth of 27 cm and was maintained at a temperature of 25 °C (± 2 °C). To make the water opaque, 0.5 L of white opacifer E308 (Roehm and Haas, Ltd., Dewsbury, United Kingdom) was used. The water was changed daily.

A white circular ceiling, measuring 2 m in diameter, was suspended 1.75 m above the floor of the pool. In the center of the ceiling was a hole measuring 30 cm in diameter in which a video camera with a wide-angled lens was situated. The lens of the camera was 25 cm above the hole and was connected to a video monitor and computer equipment in an adjacent room. During tests, the rats' movements were analyzed using Watermaze software (Morris & Spooner, 1990). The pool was illuminated by eight, 45-W lights that were located in the circular ceiling above the pool. The lights were 22.5 cm in diameter and were equidistant from each other in a 1.6 m diameter circle whose center was coincident with the center of the circular ceiling. Two platforms each measuring 10 cm in diameter and mounted on a column were used during all training trials. The surface of the platforms had a series of concentric ridges. For all trials, the base of the column rested on the bottom of the pool and the platform surface was 2 cm below the surface of the water. A white curtain was drawn around the pool during all training and test trials. The curtain, which was attached to the edge of the circular ceiling, was 1.5 m high and fell 25 cm below the edge of the pool. A number of black and white landmarks were used in this study. Each landmark consisted of two panels (21 cm × 29.7 cm) that could be attached (via surface tension) to the walls forming a corner in such a way that the longer edges of each panel made contact in the corner of the rectangle. The panels were composed of laminated A4 cards.

The training room was additionally lit by two 1.53-m strip lights connected end to end on each of the East and West walls. These lights ran parallel with the floor and were situated 75 cm above the floor. There was a door (1.75 m × 2 m) in the center of the South wall. Throughout the experiment rats were trained in a rectangular-shaped pool constructed from two gray, long Perspex boards (1.8 m long, 0.59 m high, and 2 mm thick) and two gray, short Perspex boards (0.9 m long, 0.59 m high, and 2 mm thick). Each board was placed vertically in the pool and suspended by bars that extended over the edge of the pool.

Procedure. Rats completed one session of four training trials each day. For each session they were carried into a room adjacent to the test room in groups of five in a light-tight box. They remained in this box between trials. Each rat was carried from the box to the pool and was released facing the center of a wall. The release point varied across trials with each wall being used once in a given

session. During a trial, the rat was required to swim to a submerged platform. Each trial lasted a maximum of 60 s. If the rat did not find the platform within 60 s, the experimenter guided it to the platform. After climbing on the platform the rat remained there for 20 s before being lifted from the pool, dried, and returned to its holding container. The intertrial interval for each rat was approximately 5 min. Between each trial, the experimenter rotated the arena 90°, 180°, or 270° clockwise. Four possible orientations were used (North, South, East or West). The orientation of the arena across trials varied randomly with the only stipulation being that each orientation was used once for any given session.

All rats received 26 sessions of training. The platforms were located 25 cm from two of the corners in the rectangle on an imaginary line that bisected the corner. For half of the rats, the platforms were located in the two corners where the short wall was to the left of the long wall. For the remaining rats, the platforms were located in the two corners where the short wall was to the right of the long wall. Situated in each corner was a landmark. Two of the diametrically opposite corners contained black landmarks while the other two corners contained white landmarks. For half of the rats, the black landmarks were in the corners where the platforms were located and the white landmarks in corners where there were no platforms. For the other half of the rats, the reverse arrangement was true. For ease of exposition, the landmarks located in the corners with the platforms will be referred to as excitatory landmarks, while the landmarks located in the two corners that did not contain the platforms will be referred to as inhibitory landmarks.

The first three trials of Session 17, 19, and 21 were conducted in the same manner as previous trials, but for the fourth trial a geometry test was conducted with the platforms removed from the pool. During each of the three test trials, 10 of the rats had an excitatory landmark (consisting of two adjacent cards) located in each of the four corners of the rectangle, 10 had an inhibitory landmark located in each of the four corners, and 10 had a test with no landmarks present in the pool. Over the course of the three tests each rat received all three testing conditions. For each test trial, rats were released from the center of the rectangular pool and allowed to swim for 60 s before being removed.

The fourth trial of Sessions 24 and 26 were landmark tests. These tests were conducted in the rectangle with a single landmark

present, but in the absence of the platforms. The landmark was located in one of the correct corners. For half the rats, the excitatory landmark was used for the first test, and the inhibitory landmark was used for the second test; the opposite sequence was used for the remaining rats.

Throughout the experiment, except for the test trials, a record was taken of whether after being released, a rat entered one of the correct corners of the pool first. A rat was deemed to have entered any of the four corners if its snout 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 those occasions when a rat entered one of the correct corners before any other corner. For the purpose of analyzing the results from the geometry tests in the rectangle, circular search zones were used. Each search zone had a diameter of 30 cm with its center positioned 25 cm from a corner on a line that bisected the corner. The percentage of time spent in the correct zones (the two where the platforms had been located during training trials) and incorrect zones (the remaining two corners) of the rectangular pool were analyzed. For the landmark tests, a very similar analysis was conducted. The percentage of time spent in the zone where the landmark was present (the landmark corner), and the time spent in the zone where the landmark was absent (the opposite corner) was recorded. A Type-I error rate of 0.05 was adopted for all reported statistical comparisons.

Results and Discussion

The left-hand panel of Figure 3 shows the average percentage of correct choices across the 26 sessions of training in the rectangle. Performance started off at chance and quickly improved. By the end of training, all rats were making correct choices on virtually every trial. A Wilcoxon matched pairs test revealed a significant increase in the mean percentage of correct choices from the first to the last session of the experiment, when the results from just these sessions were compared, $T(30) = 14.5$ ($z = 4.12$, $p < .001$).

The central panel of Figure 3 shows time spent in the correct and incorrect search zones during the three different test trials for the geometry test. More time was spent in the correct zones during the test with the excitatory landmarks than during either of the other

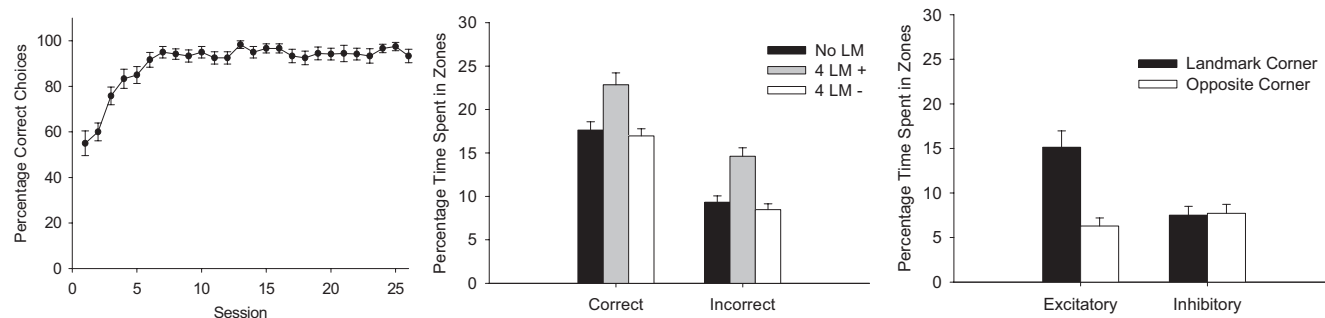


Figure 3. Left-hand panel: The mean (\pm SEM) percentage of correct choices upon being released into the pool across 26 sessions of training for Experiment 1. Center panel: The mean (\pm SEM) percentage of time spent in the correct and incorrect zones for the three test conditions in Experiment 1. Right-hand panel: The mean (\pm SEM) percentage of time spent in the zones during the landmark test of Experiment 1.

two test conditions. A one-way repeated measures ANOVA of the time spent in the correct zones revealed a significant difference among the test conditions, $F(2, 58) = 8.99$. A series of dependent t tests, with a Bonferroni alpha adjustment, revealed that during the test with the four excitatory landmarks more time was spent in the correct zones than during the other two test conditions, $t_s(29) > 3.10$, which did not differ, $t(29) = 0.51$. For the incorrect zones, an identical analysis was conducted and revealed a significant difference among the testing conditions, $F(2, 58) = 15.84$. Subsequent t tests revealed that the rats during the test with the excitatory landmarks spent significantly more time in the incorrect zone than during the other two test conditions, $t_s(29) > 4.32$, which did not differ, $t(29) = 0.90$.

The right-hand panel of Figure 3 shows the time spent in the landmark corner (corner with a landmark present), and in the opposite corner (the diagonally opposite corner with no landmark present) for the landmark tests. Considerably more time was spent in the corner containing the landmark than in the opposite corner for the test with the excitatory landmark. A paired t test based on individual times spent in each corner confirmed that this difference was statistically significant, $t(29) = 3.71$. During the tests with the inhibitory landmark there was very little difference between the time spent in the two corners, and this difference was not significant, $t(29) = 0.12$. During the landmark test the mean percentage of time spent in the two remaining zones was 3.37% for the test with the excitatory landmarks and 4.37% for the test with the inhibitory landmarks.

The most important finding from the experiment is that during the geometry tests significantly more time was spent in the correct corners of the rectangle when all four corners contained an excitatory rather than an inhibitory landmark. This pattern of results is opposite to the prediction that was derived from the principles put forward by Miller and Shettleworth (2007). Two further predictions derived from these principles are that the amount of time spent in the correct corners during the test with no landmarks in the pool will be greater than during the test with the excitatory landmarks, and less than during the test with the inhibitory landmarks. The first of these predictions was contradicted by the present results, whereas for the second prediction, performance was unaffected by the presence of the inhibitory landmark.

A measure of support for the proposals of Miller and Shettleworth (2007) can be found in the amount of time spent in the incorrect corners during the geometry tests. It was predicted from these proposals more time would be spent in the incorrect corners during the test with the excitatory landmarks than the test with no landmarks. The results confirmed this prediction. It was also predicted that less time would be spent in these corners during the test with the inhibitory landmarks than with no landmarks. The results did not confirm this prediction, with the inhibitory landmarks appearing to have no effect on the amount of time spent in the incorrect corners.

The lack of influence on the outcome of the geometry tests by the inhibitory landmarks is consistent with the results of the landmark tests at the end of the experiment. When a single excitatory landmark was located in a correct corner, rats spent more time in this corner than the diagonally opposite corner, thus confirming that the treatment with this landmark successfully resulted in it acquiring excitatory properties. In contrast, when a similar test was conducted with an inhibitory landmark, rats spent an equal

amount of time in each of the correct corners. On the basis of this finding, it appears that the method of training did not endow the landmarks that were situated in the incorrect corners with any inhibitory properties, and they would not be expected to exert any influence when they were presented for the geometry tests. Support for this conclusion can be found in an experiment by Cheng (1986). In this experiment, a rat was required to search for a goal in a single corner of a rectangular arena. Each corner contained a distinct landmark in order to disambiguate the geometrically identical corners. Cheng found that the removal of landmarks situated in the geometrically correct corners resulted in equal preferences for both corners. However, the rats could have used the landmarks located in the two remaining, incorrect, corners to determine where to search for the goal. Thus it appears that animals attach little importance to cues that are situated in the incorrect corners of a rectangular arena. In view of this conclusion, Experiment 2 was based on the design of Experiment 1, but a different method for endowing landmarks with excitatory and inhibitory properties was employed.

Experiment 2

A group of rats was trained to find one of two submerged platforms that were situated in diagonally opposite corners of a rectangular pool with gray walls. At the same time, the rats received training in a square pool with a platform located in each of two diagonally opposite corners that was designed to endow different landmarks with either excitatory or inhibitory properties. For the excitatory training, which took place on half of the trials in the square pool, the landmarks were of one color and situated by the platforms. For the inhibitory training, which took place in the remaining trials in the square pool, the landmarks were of a different color and situated in the corners without the platforms. In order to confirm that both treatments had been successful, two test trials were conducted in the square pool with two identical landmarks in diagonally opposite corners, but with the platform removed from the pool. One test was with the landmarks that had been near the platforms and it was expected that rats would spend more time in the corners with the landmarks than in the corners without the landmarks. The other test was conducted with the landmarks that had been placed in corners without a platform—here rats were expected to prefer the corners without rather than with the landmarks.

The experiment then concluded with a series of test trials in the rectangular pool. The platforms were removed from the pool for these tests which involved no landmarks in the pool, excitatory landmarks in all four corners of the pool, and inhibitory landmarks in all four corners of the pool.

Method

Subjects and apparatus. Twenty-four experimentally naïve animals were maintained, housed, and from the same stock as in Experiment 1. The rectangular pool and landmarks that were used for Experiment 1 were used for the present experiment. We also used a square pool. The length of each wall of the square was 1.41 m and the height of the walls was the same as for the rectangle. The material and color of the walls for the square were the same as for the rectangle.

Procedure. Rats completed 27 sessions of training, the first six of which took place in the rectangular arena. For these sessions, each session consisted of four trials per day. For half of the rats, the platforms were located in the two corners where the long wall was to the right of the short wall and the remaining rats had the platforms in the other two corners. There were no landmarks in the rectangle for any training trial, but all other procedural details were the same as for Experiment 1. Training in the square pool commenced in Session 7. In keeping with the training in the rectangle, there were two platforms located in diagonally opposite corners for every training trial in the square. The centers of the platforms were above a point that was located 25 cm from the nearest corner on a line that bisected the corner. Half of the training trials in the square consisted of excitatory training, in which two identical landmarks were placed on the walls in the corners housing the platforms. The remaining trials consisted of inhibitory training in which the landmarks were attached to the walls of the two corners without the platforms. For half the rats, the excitatory landmarks were black and for the remaining rats, these landmarks were white. The opposite color was used for the inhibitory landmarks for each rat.

Sessions 7 to 27 contained six trials. Two trials were conducted in the rectangle, two in the square with the black landmarks, and two in the square with the white landmark. The order of the trials was selected randomly. On Sessions 18 and 20, each rat received two normal training trials in the square: one with the excitatory landmarks and one with the inhibitory landmarks. The third trial of these sessions was a landmark test. Testing took place in the square with the platform removed from the pool. For the test on Session 18, half of the rats were tested with the excitatory landmark half and with the inhibitory landmark. The test on Session 20 was conducted in the same manner except that the opposite landmark was used for each rat.

The first three trials of Session 23, 25, and 27 consisted of one of each of the different types of training trial. The fourth trial of these sessions was a test conducted in the rectangle in the same manner as in Experiment 1. Across the three tests, each rat received testing with no landmarks present in the arena, four excitatory landmarks present in each corner of the rectangle and four inhibitory landmarks in each corner. The sequence of the test trials was counterbalanced across the entire group of rats.

For the purpose of analyzing the results from the landmark tests in the square, circular search zones (30 cm in diameter) were used. The zones were positioned in each of the four corners, where the center of the zone was 25 cm from the corner on a line that bisected that corner. The time spent in the two zones in corners with landmarks (landmark corners) was compared with the time spent in the two zones in corners without landmarks (remaining corners). The results from the tests in the rectangle were recorded and analyzed in the same way as for Experiment 1.

Results and Discussion

The left-hand panel of Figure 4 shows the group mean percentages of trials on which subjects headed directly for a corner containing a platform across the 27 sessions of training. Recall that during the first six sessions training took place in just the rectangle. By the end of training the group was heading for a correct corner on approximately 80% of the trials in the rectangle, in the square with the excitatory landmarks (Square - E), and in the square with the inhibitory landmarks (Square - I). A Friedman's Test, using the mean percentage of correct choices combined across the last three sessions of training, revealed no differences among the different types of trials, $\chi^2(2) = 3.96$.

The results of the landmark tests in the square pool are presented in the center panel of Figure 4. During the test with the excitatory landmarks considerably more time was spent in the corners that contained the landmarks than in the other two corners, but the opposite was found during the test with the inhibitory landmarks. A repeated measures ANOVA with the factors of test (excitatory or inhibitory landmark) and zone (landmark corners or remaining corners) revealed a significant effect of test, $F(1, 23) = 39.29$ and a significant Test X Zone interaction, $F(1, 23) = 55.15$. The zone effect was not significant, $F < 1$. Tests of simple effects revealed that during the test with the excitatory landmarks, significantly more time was spent in zones with rather than without a landmark, $F(1, 46) = 18.08$. In contrast, the test with the inhibitory landmarks resulted in significantly more time being spent in the corners without rather than with a landmark, $F(1, 46) = 23.24$. These results confirm that the training with both the excitatory and inhibitory landmarks in the square was effective.

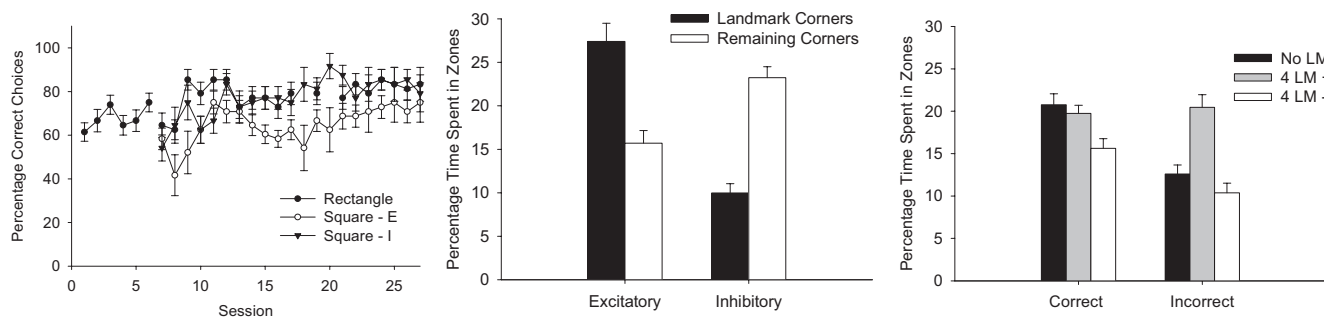


Figure 4. Left-hand panel: The mean (\pm SEM) percentage of correct choices upon being released into the pool for each trial type in the rectangle or square across training for Experiment 2. Center panel: The mean (\pm SEM) percentage of time spent in the zones during the landmark test of Experiment 2. Right-hand panel: The mean (\pm SEM) percentage of time spent in the correct and incorrect zones for the three test conditions in Experiment 2.

The right-hand panel of Figure 4 shows the group mean percentage of time spent in the correct and incorrect corners for the three test conditions in the rectangle. The amount of time spent in the correct corner was less for the test with the inhibitory landmark than for the tests with either no landmark or with the excitatory landmark, which did not differ noticeably. Turning now to the time spent in the incorrect corners, this was considerably greater for the test with the excitatory landmark than for the other two tests, the outcome of which was quite similar. A one-way ANOVA of individual percentages of time spent in the correct zones revealed a significant difference among the testing conditions, $F(2, 46) = 6.63$. Subsequent tests, using the Bonferroni correction, revealed that the time spent in the correct zone for the test with the four inhibitory landmarks was significantly less than for the other two tests, $t_s(23) > 3.01$, which did not differ, $t(23) = 0.68$. A similar analysis for the percentages of time spent in the incorrect corners revealed a significant difference among the test conditions, $F(2, 46) = 15.88$. The percentage of time spent in the incorrect zones for the test with the four excitatory landmarks was significantly greater than the other two tests, $t_s(23) > 3.66$, which did not differ, $t(23) = 1.55$.

The results from the test trials in the rectangle replicate the most important finding from Experiment 1. More time was spent in the correct corners of the rectangle during the test in which an excitatory rather than inhibitory landmark was situated in each of the four corners. As stated earlier, this outcome is opposite to that expected on the basis of predictions derived from the analysis offered by Miller and Shettleworth (2007) for the way in which animals allocate their time to the corners of a rectangular arena when a goal is repeatedly hidden in one of its corners. There are, however, a number of differences between the current results and those from Experiment 1. On this occasion, the presence of an inhibitory landmark in each of the four corners of the rectangle resulted in less time being spent in the correct corners than during the test without any landmarks in the corners. The obvious explanation for the failure to find a similar effect in Experiment 1 is that the different method of training with the inhibitory landmarks in Experiment 2 was more effective than for Experiment 1. Certainly, the outcome of the landmark test in the present experiment indicates the success of the training with the inhibitory landmarks in the square. It is worth noting that the test with the inhibitory landmarks did not reduce the time spent in the incorrect zones, compared with that seen in the no landmark test. One explanation for this outcome is that rats spent such a small amount of time in the incorrect zones during the test without the landmarks that it was difficult for the inhibitory landmarks to suppress responding even further.

Another difference between the results of the two experiments is the failure in the present experiment of the test with the excitatory landmarks to enhance the time spent in the correct zones, relative to that seen in the no landmark test. The results of the test with the excitatory landmark in the square, and also the influence of this landmark on the time spent in the incorrect zones during the test in the rectangle, strongly suggest that the training with this landmark had been effective. Perhaps, on this occasion, the time spent in the correct zones during the no landmark test was so large that it was difficult for the excitatory landmark to augment it further. An alternative explanation for the failure of the excitatory landmarks to boost the time spent in the correct zones is that any beneficial

influence of its excitatory properties might have been counteracted by the fact that until the test trial, rats had never experienced a landmark in the correct corners of the pool. Any tendency to devote more time to searching in the correct corners may therefore have been countered by a generalization decrement brought about by the unusual presence of the landmarks. Whatever the reason for the failure to find a difference in the amount of time spent in the correct corners of the rectangle, with either excitatory or no landmarks, the comparison of the results from the tests with the excitatory and inhibitory landmarks remains of theoretical significance. The fact that more time was spent in the correct corners during the test with the excitatory than inhibitory landmarks stands in direct contrast to the predictions that were derived from the proposals of Miller and Shettleworth (2007).

General Discussion

In two experiments rats were trained to find a submerged platform in one of two diagonally opposite corners—the correct corners—of a rectangular pool. The experiments have shown that after this training the attraction of the correct corners is greater when an excitatory rather than an inhibitory landmark is situated in every corner. This result is novel, and it is of interest because it is the opposite outcome to that predicted by a currently influential formal model of how animals behave when they must find a goal in one corner of a rectangular arena (Miller & Shettleworth, 2007).

A possible shortcoming with the analysis offered by Miller and Shettleworth (2007) for spatial behavior in a rectangle is that the only locations that are assumed to influence performance on a test trial are the correct and incorrect corners. There are, however, many other locations in the pool that fill the space between these corners. It is not unreasonable to suppose that through stimulus generalization these locations acquire a measure of associative strength, and that this strength influences performance on the test trial. To capture this possibility, Equation 3 can be rewritten as Equation 5, which indicates the probability of heading toward a correct corner as determined by the associative strength of the correct and incorrect corners, V_C and V_I , and of all the other locations in the pool, V_O . Likewise, Equation 4 can be rewritten as Equation 6, which can be used to determine how the presence of the same landmark in each corner will affect the preference for the correct over the incorrect corners.

$$P_C = \frac{V_C}{V_C + V_I + V_O} \quad (5)$$

$$P_C = \frac{(V_C + V_K)}{(V_C + V_K) + (V_I + V_K) + V_O} \quad (6)$$

Replotting Figure 1 using the results from calculations based on Equation 6 does not alter qualitatively the predictions shown in that figure, and the point where all the plots cross is again when the values of both axes are .50. The difference now is that it is no longer safe to assume that animals will exhibit a preference for the correct over the incorrect zones only when the value of P_C in Equation 5 is greater than .50. Even if the value of P_C is less than .5, provided that it is greater than P_I , a preference for the correct over the incorrect corner will still be evident. Of course, this means there will be a probability of visiting a place other than a corner,

P_O , of value $1-(P_C + P_I)$, but this is not an unreasonable prediction. To return to the present experiments, if the value of P_C , as given by Equation 5, was less than .5 at the time of testing then it would follow from the relationships expressed in Figure 1 that the amount of time spent in the correct zones of the rectangle would be greater during the test with the excitatory rather than the inhibitory landmark. Such a prediction is entirely in keeping with the principal findings from both experiments. Thus, it appears that the model of Miller and Shettleworth (2007) is able to explain our results, once an account is taken of regions in the pool other than the four corners. The problem now is that it is not clear what value should be assigned to V_O in Equations 5 and 6. If this value is low, then it is likely that P_C will be greater than .5, and these equations will make the same predictions as Equations 3 and 4 concerning the present experiments. On the other hand, if the value of V_O should be relatively high then it may well result in P_C being less than .5 with the outcome of the present experiments now predicted to be opposite to that predicted when the value of V_O is low. Although the above modification to the proposals of Miller and Shettleworth (2007) might appear reasonable, until a method can be found for assessing the value of V_O , and V_I and V_C , it will be in the unfortunate position of being untestable as any experimental result can be explained by making appropriate assumptions about the values of these variables.

A solution to the foregoing problem would be to divide the entire arena into four quadrants of equal area—two correct and two incorrect—and to record the amount of time spent by animals in each of them during the test trials. Once this change has been made it would be quite reasonable to use Equation 3 to derive predictions concerning the effects of our experimental manipulations, as the only regions that could be visited by the animals would be correct or incorrect. With this solution in mind, we reexamined the results from both experiments on the basis of the time spent in quadrants of the pool. During the test with the excitatory landmark in Experiment 1 rats spent 35.5 sec of the 60 sec test trial in the correct quadrants (and of course 24.5 sec in the incorrect quadrants), whereas this value was 36.2 for the test with the inhibitory landmarks. The difference between the amounts of time spent in the correct quadrants during the two tests was not significant. Likewise for Experiment 2, 30.2 sec of the test trial with the excitatory landmark was spent in the correct quadrants, although for the test with the inhibitory landmarks this value was 33.2 sec. This difference, too, was not significant. It thus appears that dividing the pool into such large regions renders insensitive our behavioral test of the predictions that were derived from Equation 3 at the beginning of this article.

Experiment 1 revealed that the presence of an excitatory landmark in each corner of the pool enhanced the time spent in both the correct and incorrect corners, relative to when there was no landmark in the corners. In Experiment 2, the presence of the inhibitory landmark in each corner had the opposite effect of reducing the time spent in the correct and incorrect corners. According to the ratio rule adopted by Miller and Shettleworth (2007), the landmarks should have one effect in the correct corner and the opposite effect in the incorrect corner. An increase in the time spent in the correct corners, say, on a test trial should have been matched by a corresponding reduction in the time spent in the incorrect corners. The failure to confirm this prediction can, however, be remedied by appeal to Equation 6. If it is assumed that the value of V_O is

greater than the sum of V_C and V_I then the equation predicts the presence of an excitatory landmark will augment the time spent in every corner, whereas an inhibitory landmark will have the opposite effect.

To demonstrate how their model works, Miller and Shettleworth (2007) applied it to experiments in which the test arena contained regions other than the correct and incorrect corners (e.g., Graham, Good, McGregor, & Pearce, 2006; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001). When calculating the predicted preference for the correct over the incorrect corners for these experiments, Miller and Shettleworth took no account of the opportunity to visit these additional regions of the pool. It would thus appear that the predictions we initially derived from the model were in keeping with the manner in which the authors intended it to be used, and it would be unreasonable to argue that we have used their model inappropriately. Furthermore, the findings from the present experiments imply that by ignoring the associative properties of the regions outside the correct and incorrect corners of a distinctively shaped arena, Miller and Shettleworth (2007) may have overlooked an important influence on how choices between these corners are made.

Horne and Pearce (2010) describe an experiment in which rats were trained to swim to the correct corners of a rectangular pool, with inhibitory landmarks situated in those corners. A subsequent test revealed a stronger preference for the correct corners than when the treatment with the inhibitory landmarks was omitted. Although this demonstration of superconditioning can be understood in terms of the Rescorla and Wagner (1972) theory, Horne and Pearce demonstrated that the opposite outcome to the experiment is predicted by the proposals of Miller and Shettleworth (2007, 2008). The reasons behind this incorrect prediction are complex and need not concern us here, but it is worthy to note that a different outcome to the experiment is predicted if it is assumed that Equation 5 determines choice behavior in a rectangular pool, and that V_O is of some positive value.

Horne and Pearce (2010) did not consider the foregoing possible explanation for their results. Instead they suggested that choice behavior was determined by the overall associative strength of the correct corners minus the overall associative strength of the incorrect corners, $V_C - V_I$. Although this rule was able to account successfully for the results described by Horne and Pearce, it does not fare well with the current experiments. Adding the same landmark to each of the four corners of a rectangular pool will alter the magnitudes of the overall associative strengths of the correct and incorrect corners, but will not alter the magnitude of the difference between their overall associative strengths. Accordingly, adding either an excitatory or an inhibitory landmark to the four corners of the arena should not have altered the time spent in the correct corners. In both experiments, however, the time spent in these corners was greater when there was an excitatory than an inhibitory landmark in every corner.

Another possibility is that the time spent in a corner of a rectangular pool is determined solely by the overall associative strength of that corner. The results from both experiments can be explained in this way, and so too can the results described by Horne and Pearce (2010). An implication of this proposal is that once a rat has selected a corner, the time it spends there will be not be affected at all by the associative properties of the other corners. In the case of both experiments, for example, the amount of time

spent in a correct corner will be the same when there is an excitatory landmark in each of the four corners, as when there is an excitatory landmark in the two correct corners and an inhibitory landmark in the two incorrect corners. Unfortunately, we do not know of any evidence that bears on this prediction which, at face value, appears implausible.

When an animal is permitted a limited amount of time to search in a rectangular arena for a hidden goal then inevitably the amount of time spent in the incorrect regions of the arena will detract from the time available for searching in the correct regions. Equation 3 captures this relationship succinctly but, as we have seen, it leads to incorrect predictions when the effects of adding landmarks of identical associative strength to the four corners are considered. It is possible to modify Equation 3 to explain the results we have described by acknowledging that, in addition to the correct and incorrect corners, there are other regions in the pool where an animal may choose to spend its time. Unfortunately, the success of this modification for predicting our results depends upon untestable assumptions being made about the associative strength of these additional regions. Therefore, until a method can be found for assessing the associative properties of these regions, the modification we have suggested to the proposals of Miller and Shettleworth (2007) should be regarded as speculative. Moreover, if this modification is accepted, then it will be difficult to derive unambiguous predictions from it.

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