Further Evidence That Rats Rely on Local Rather Than Global Spatial Information to Locate a Hidden Goal: Reply to Cheng and Gallistel (2005)

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Naive male Hooded Lister rats (Rattus norvegicus) were required to find a submerged platform in a right-angled corner between a long and a short wall of a pool in the shape of an irregular pentagon. Tests in a rectangular pool revealed a preference for the corners that corresponded with the correct corner in the pentagon. These findings indicate that rats identified the correct corner in the pentagon by local cues. They contradict the suggestion that rats navigate by moving in a particular direction relative to the principal axis of the shape of their environment.

Keywords: spatial learning, geometric module, navigation

Considerable theoretical significance has been attached to the discovery that animals can find a hidden goal by reference to the shape of their environment. The first experiment to demonstrate this ability was by Cheng (1986). Hungry rats were placed in a rectangular arena with food hidden in one corner and with a distinctive landmark in each corner. The rats soon learned to search in the correct corner of the arena, but initially they made rotational errors of searching in the corner that was diametrically opposite to this corner. Furthermore, when they were tested in the arena in the absence of the landmarks and food, rats showed a strong preference for the two corners that were geometrically equivalent to the corner that had previously contained food. Cheng (1986; see also Gallistel, 1990) proposed that these findings were a consequence of rats using the overall shape of the arena to identify where food was located. Learning about the shape of the environment was said to take place in a dedicated module, the exclusive purpose of which was to encode information about the geometric properties of the environment. Since the report by Cheng (1986), a number of similar experiments have been conducted and with a variety of species, including fish (Sovrano, Bisazza, & Volltigara, 2002), chicks (Volltignara, Zanforlin, & Pasti, 1990), rhesus monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001), and humans (Hermer & Spelke, 1994). The results from these experiments have been consistent with those reported by Cheng (1986), and they have been interpreted in much the same way (see Cheng & Newcombe, 2005, for a review). See also Cheng (2005a, 2005b) for accounts of navigation in a rectangular arena in which geometric and nongeometric information may interact.

There is, therefore, a widespread belief that many different species navigate with reference to the shape of the environment and that this ability reflects the existence of cognitive and neural mechanisms that are common to species as diverse as fish and humans. Set against this consensus are two reports of experiments that have been said to show that animals might not use the overall shape of the environment to find a hidden goal. If this is correct, then the justification for postulating the existence of a geometric module that processes global information based on the shape of the environment is seriously undermined.

Pearce, Good, Jones, and McGregor (2004) trained rats to find a submerged platform in one corner of a rectangular pool before the rats were tested in a pool in the shape of a kite. These shapes are shown in the top left and center panels of Figure 1, where the platform is located in a corner in the rectangle with a long wall to the left of a short wall. The kite-shaped pool was constructed from the same walls as the rectangular pool, and the corners between the short and long sides were both right angled. As a consequence, one of the right-angled corners (the correct corner) in the kite corresponded with the corner containing the platform in the rectangle, and the other right-angled corner in the kite (the incorrect corner) corresponded with the corners where the platform was never located. Pearce et al. (2004) argued that if rats found the platform in the rectangular pool by referring to its overall shape, then they should effectively be lost in the kite because of the lack of congruence between the shapes of the two environments. In contrast to this prediction, rats showed a clear preference for searching in the correct, rather than the incorrect, corner of the kite. Pearce et al. (2004) explained this outcome by proposing that during their training in the rectangular pool, rats identified the location of the platform by means of local information, rather than global information, such as the overall shape of the pool. For instance, the platform in the rectangle in Figure 1 could be found by swimming toward a corner with a long wall to the left of a short wall. Alternatively, it could be found by swimming to the right-hand end of a long wall. Either of these strategies would result in rats heading for the corner with the platform in the rectangle or to the
diagonally opposite corner from where they could then swim directly to the platform. Moreover, these strategies would lead rats to the correct, rather than the incorrect, corner in the kite.

The other study was by Tommasi and Polli (2004), who trained chicks to search for food in one corner of an enclosure in the shape of a parallelogram (see the right-hand end of the top row of Figure 1). Test trials in a rectangular enclosure, with walls of the same length as the parallelogram, revealed a preference for searching in corners where the relationship between the short and long walls was the same as for the corner containing food in the original enclosure. Once again, if food was found in the parallelogram solely by reference to the shape of the environment, then the lack of congruence between a parallelogram and a rectangle would lead to subjects being unable to discriminate one pair of corners from the other on the test trial. The clear discrimination that was shown thus implies that subjects did not rely on the overall shape of the environment for finding food. Instead, they could have used either of the local strategies that were proposed for the study by Pearce et al. (2004). Tommasi and Polli also tested the chicks in a rhombus, with angles that were equivalent to those in the parallelogram. On this occasion, rats searched in the corners that were of the same angle as the corners where food had been hidden in the parallelogram, which suggests that they can use the local feature of the angle of a corner to find a goal.

In a comment on the findings by Pearce et al. (2004) and Tommasi and Polli (2004), Cheng and Gallistel (2005) agreed that the results from both studies rule out the possibility that generalization from one environment to another is mediated by the congruence between the global shapes of the two environments. They argued, however, that the transfer may have been based on a different global property of the environments, rather than on local features. One possibility is that during their training in an environment with a distinctive shape, rats identify its principal axis (Gallistel, 1990). The principal axis passes through the centroid of a shape and is also referred to as the long axis. The dashed lines superimposed on the shapes in the upper row of Figure 1 represent their principal axes, as identified by Cheng and Gallistel (2005). Once the principal axis of a shape has been identified, it is then assumed that the position of a hidden goal is defined relative to this axis. For instance, if the goal is located in the corner of a rectangular swimming pool where a long wall is to the left of a short wall, then rats might find this goal by looking for a corner at one end of the principal axis and as far as possible to the left. If the rat should then be placed in a kite, it should be evident from inspecting Figure 1 that the strategy just described will lead it to the correct corner or the apex. In keeping with this prediction, Pearce et al. (2004) observed that rats did indeed prefer these corners over the remaining two corners of the test arena. Of course, the outcome can also be explained if rats acquired the habit in the rectangular pool of swimming to a particular end of a long wall.

The results from Tommasi and Polli (2004) can also be explained by the proposals of Cheng and Gallistel (2005). For example, if chicks were trained to find food in a corner in the parallelogram where a long wall was to the left of a short wall, then they would learn to search away to the left at one end of the principal axis. The transfer of this strategy to the rectangular test environment would then encourage them to search in a corner where a long wall was again to the left of a short wall. The purpose of the following experiment was to test the proposal by Cheng and Gallistel (2005; Gallistel, 1990) that animals navigate with reference to the principal axis of the shape of their environment.

Rats were trained to find a submerged platform that was located in an irregular pentagon constructed inside a circular pool. The shape of the pentagon can be seen in the bottom left panel of Figure 1.
Figure 1, which shows the platform in one of the right-angled corners at the base of the pool. This corner will be referred to as the correct corner. The corner at the top of the pentagon will be referred to as the apex, the right-angled corner opposite the correct corner as the incorrect corner, the obtuse-angled corner near the correct corner as the obtuse-correct corner, and the remaining corner as the obtuse-incorrect corner. The dashed line shows the principal axis of the shape as computed by a Matlab function supplied by Gallistel (personal communication, October 2004). According to the proposals of Cheng and Gallistel (2005), rats will find the platform by swimming to one end of the principal axis and moving as far away as possible to the right.

The main purpose of the experiments was to examine how, once the subjects had been trained in the pentagon, they would behave when they were required to find the platform in one corner of the rectangular test pool shown in the remaining panel of Figure 1. The dimensions of the short and long walls of this pool were the same as for the short and long walls at the base of the pentagon. The corners in the rectangle have been labeled correct and incorrect because of their correspondence with these corners in the pentagon. If transfer of behavior between the pools is based on a response being made with reference to the principal axis, then subjects will swim to one end of the principal axis in the rectangle and turn to the corner on the right. Such a strategy will lead them to the incorrect rather than the correct corners. To test this prediction, we required half of the rats that had been trained in the pentagon—the consistent group—during three sessions of training to find the platform in a correct corner of the rectangle, and we required the remaining rats—the inconsistent group—to find the platform in an incorrect corner. If the proposals of Cheng and Gallistel (2005) are correct, then the inconsistent group should learn to head directly for the corner containing the platform, or the opposite corner, more rapidly than the consistent group. On the other hand, if the position of the platform is identified during the training stage by reference to local rather than global cues, then a different outcome to the experiment might be observed. The platform could be found in the pentagon, for example, by swimming toward the corner where the short wall is to the right of the long wall. Another possibility is that subjects would seek a wall of certain length—say, the one at the base of the pool—and then swim to the corner at its right-hand end. If either of these strategies should be adopted, then, at least initially, the consistent group will head directly for the corner containing the platform, or the opposite corner, more often than the inconsistent group. Prior to the final three sessions of training in the rectangular pool, individual test trials were conducted in which subjects were placed in an arena for 60 s in the absence of the platform. One purpose of these trials was to examine where rats would search for the platform in transformed versions of the pentagon, including a rectangle.

In keeping with our previous studies (e.g., Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001), training in the pentagon was initially conducted with curtains surrounding the arena in order to minimize the influence on behavior of cues outside the pool. One finding of the individual test trials was that proximity to the curtain was a salient cue that gained control over searching for the platform. Thus, subjects preferred to search in corners that were close to, rather than distant from, the curtain. In an attempt to encourage subjects to rely solely on the shape of the pool for finding the platform, we conducted further training with the curtains permanently open before the sessions of training in the rectangle. To prevent the cues beyond the arena from gaining control over searching for the platform, we changed the orientation of the arena randomly throughout the experiment. The results from the training sessions and test trials with the curtains closed are not reported.

Method

Subjects

The subjects were 20 experimentally naive male Hooded Lister rats (Rattus norvegicus) supplied by Harlan Olac (Bicester, United Kingdom). They were housed in pairs in a light-proof room in which the lights were on for 14.5 hr each day. Testing took place at the same time of day, 5 days a week, at a time when the lights were on in the holding room. Rats were allowed unrestricted access to food and water in their home cages throughout the experiment. One rat was excluded from the experiment because of illness.

Apparatus

The pool was 2 m in diameter and 60 cm deep. It was made of fiberglass, painted white, and mounted on a platform 60 cm above the floor in the center of a room that was 3 m × 4 m × 2.3 m high. The pool was filled to a depth of 30 cm with water to which was added 0.5 L of white food coloring E 308, supplied by Roehm and Haas Ltd (Dewsbury, United Kingdom). This mixture was changed daily and was maintained at a temperature of 25 °C (± 2 °C). A wide-angled video camera was fixed 1.75 m above the center of the pool, 5 cm above a 30-cm-diameter hole in a white circular ceiling with a diameter of 2 m. The image from the camera was relayed to recording equipment and a PC running tracking software (Watermaze Software; Morris & Spooner, 1990) in an anteroom. In the ceiling were eight 45-W, 22.5-cm diameter spotlights that were arranged at equal distances in a 1.6-m diameter circle with its center directly above the center of the pool. The spotlights were illuminated throughout the experiment. The pool was surrounded by a light blue curtain that hung from a rail around the circular ceiling at a distance of 25 cm beyond the edge of the pool. The lower edge of the curtain was 20 cm below the rim of the pool. When not in use, the curtain was pulled into the northeast corner of the room. The room was additionally lit by four 1.53-m strip lights, which were attached end to end in pairs on opposite walls of the room, parallel to the floor and 0.75 m above the floor. Posters of different shapes and patterns were attached to three walls of the room. A door was situated in the center of the fourth wall. Three of the walls and the ceiling were painted white. The fourth wall, and the door that was contained in it, was covered with a sheet of stainless steel. A portable screen that was 78 cm wide and that extended 52 cm above the top of the pool was placed in front of the door, 40 cm from the edge of the pool. The center of the screen was considered to be due north from the center of the pool. Throughout each trial, the experimenter sat behind the screen and observed the activity of the rat on a monitor in the corner of the room.

An irregular pentagon (see Figure 1) was created in the pool by inserting white polyurethane boards, 0.59 m high and 2 mm thick. The back of each board was attached along the top edge to a 2-cm square bar that extended 5 cm beyond each end of the board. The bar was used to suspend the board vertically in the pool. Two of the boards were 1.62 m long, two were 0.70 m long, and one was 1.40 m long. The 1.62-m boards were placed in the pool such that their ends made contact with the walls of the circular pool and met at one end, forming a corner with a 70° angle between the boards. The 1.40-m and 0.70-m boards were then placed in the pool in the manner shown in Figure 1. The corners where the 0.70-m boards met the 1.62-m boards were each 145°, and the distance between these corners and the apex of the pentagon was 1.22 m. An additional board of length 1.40 m
was used to create the rectangular test arena. A clear Perspex platform, 10 cm in diameter and mounted on a column, was submerged 2 cm below the water surface in one of the right-angled corners of the pentagon. The center of the platform was always 25 cm from the corner on a line that bisected the corner.

Procedure

Rats were transported into the test room 5 at a time, in separate compartments of a light-tight carrying box that was placed on a table in the northwest corner of the room. The curtain was drawn around the pool throughout the first 35 sessions of the experiment, and it was pulled open for the remainder of the experiment. Each rat received 60 sessions of training in the pentagon, followed by 3 sessions in the rectangle. Each session consisted of four trials in which the rat had to escape from the water by climbing onto the platform. For the training in the pentagon, the platform was located in one of the right-angled corners for a randomly selected half of the rats, and in the opposite right-angled corner for the remaining rats. The animals were lowered gently into the pool from the midpoint of one of the walls, facing the wall. They were released from each of the five walls an equal number of times among sessions, in a pseudo-random order, and never from the same wall twice within a session. If a rat was unable to find the platform within 60 s, the experimenter placed a thumb about 5 cm in front of the animal and guided it to the platform. No training was required for this treatment to be effective. After finding the platform, each rat was allowed to remain there for 30 s before it was removed from the pool. It was then gently dried with a towel and returned to the light-tight carrying box where it waited until the remaining rats had received a single training trial. After the 5 rats had each received a trial, the arena was rotated. The extent of the rotation varied randomly from trial to trial and resulted in the apex pointing in the four principal points of the compass in a random sequence during the 35 sessions with the curtains drawn around the pool. During the subsequent 25 training sessions in the pentagon with the curtains open, the apex of the arena pointed once toward the eight principal points of the compass in every two sessions, again in a random sequence.

On Sessions 20, 21, and 25 of training with the curtains open, a single test trial followed the four training trials. The platform was removed from the pool, and the paths of the rats were tracked for 60 s. Subjects were released from the middle of the pool, and the principal axis of the test arena was always at right angles to the principal axis of the pentagon on the previous trial. Test 1 (Session 20 of training with the curtains open) was conducted in the rectangle that was located in the middle of the circular pool, with the principal axis aligned from north to south. Test 2 (Session 21) was conducted in the pentagon but with the 1.40-m wall at its base removed. Test 3 (Session 25) was conducted in the complete pentagon. For both of these tests, the apex of the arena pointed south.

The rats were assigned at random to two groups for the final three sessions of the experiment, which took place with the rectangle located in the middle of the circular pool and with the curtains open. There were four trials in each session. The orientation of the rectangle varied from trial to trial in the manner described for the pentagon in the previous stage. Rats were released from the middle of the four walls of the arena, with each release point being used once in a random sequence in each session. The platform was located in corners that were geometrically equivalent to the corner containing the platform in the pentagon for the consistent group (n = 9) and in the other corners for the inconsistent group (n = 10).

A record was taken on every training trial in the pentagon and in the rectangle, and on Test 1, of which corner a rat first swam to on release. To identify when a choice was made, we drew a notional circle in each corner with a radius of 15 cm and with its center 25 cm from the corner on a line bisecting the corner. A choice was deemed to have occurred whenever a rat’s snout entered this circle or crossed one of two tangents extending back to the walls from the circle that were parallel to the line bisecting the corner.

For the three test trials, circular search zones were created using the Watermaze Software, which measured the amount of time that was spent in a region with a diameter of 30 cm. The centers of these zones were located 25 cm from each corner on a line that bisected the corner. For Test 2, the search zones at the base of the arena were located at the corners where the straight walls met the curved wall of the pool.

Results

A Type I error of p < .05 was adopted for all statistical tests. In the final session of training with the curtains closed, the group mean percentages of trials on which each of the five corners were entered first were as follows: correct corner, 45%; incorrect corner, 8.75%; obtuse correct corner, 12.5%; obtuse incorrect corner, 25%; and apex, 13.75%. The group mean escape latency on this session was 10.8 s. The top left panel of Figure 2 shows, for each of the sessions of training in the pentagon with the curtains open, the mean percentages of trials on which all of the subjects headed for the five different corners. Throughout this stage of the experiment, subjects expressed a clear preference for swimming directly to the correct corner of the pentagon. There is also a suggestion that subjects entered first the obtuse-incorrect corner more often than the remaining corners. To examine this performance further, we calculated the mean percentage of trials on which each of the five corners was entered first for the 19 rats for the 25 sessions with the curtains open. Comparisons of these percentages revealed that subjects swam directly to the correct corner significantly more often than any other corner, Wilcoxon T(19) < 15. The obtuse-angled corners were each approached first significantly more often than either the apex or the incorrect corner, T(19) < 31, and the obtuse-incorrect corner was approached first more often than the obtuse-correct corner, T(19) = 14. The difference between the number of occasions on which the apex and the incorrect corner were visited first was not significant.

In the final session of training in the pentagon, the mean percentages of trials in which the consistent and inconsistent groups, respectively, headed directly for the correct corner were 47.2% and 52.5%; for the incorrect corner, 11.1% and 5.0%; for the obtuse-correct corner, 16.7% and 25.0%; for the obtuse-correct corner, 16.7% and 5.0%; and for the apex, 8.3% and 12.5%. A comparison of the number of trials on which the two groups headed directly for each of these corners in the final session failed to reveal a difference between the groups, \( \chi^2(4, N = 19) = 4.39 \).

The bottom left panel of Figure 2 shows the mean escape latencies for all of the subjects for each session of training in the pentagon with the curtains open. The latencies were reasonably consistent throughout this stage of the experiment. In the final session of training in the pentagon, the mean escape latency for the consistent group was 10.3 s, and for the inconsistent group it was 9.5 s. This difference between the groups was not significant, \( \chi(17) = 0.61 \).

The results from the three test trials that took place in the pentagon with the curtains open can be seen in Figure 3. The left-hand column shows the mean percentages of time spent by all 19 subjects in the search zones of the different test arenas. For ease of presentation, the results have been normalized with reference to the shapes of the test arenas. Thus, the mean time spent by all subjects in the two correct corners of the rectangle during Test 1 is
shown in boldface in the corners where the long wall was to the left of the short wall, even though for some subjects the platform was located in a corner where the long wall was to the right of the short wall. The mean time spent in the incorrect corner is shown in roman font in the opposite corners.

The upper left-hand panel of Figure 3 indicates that subjects expressed a slight preference for searching in the correct rather than the incorrect corners during the test trial in the rectangle. Analysis of individual percentages of time spent in the two correct corners and the two incorrect corners revealed a significant preference for the former, \( t(18) = 2.10 \). Additional support for the claim that rats preferred the correct over the incorrect corners in the rectangle comes from the finding that after they were released, 15 rats headed directly for a correct corner and 4 headed directly for an incorrect corner. This preference was significant according to a binomial test.

The three remaining panels in the upper row of Figure 3 show the swim paths taken by 3 representative rats during the 60 s of Test 1. The highlighted circles show the location of the search zones in the two correct corners, and the remaining circles show the location of the search zones in the incorrect corners. The numbers beside the image indicate the time spent in each search zone. In every case, even though rats searched throughout the pool, they exhibited a preference for at least one of the correct corners.

The group mean results from Test 2, in which the wall at the base of the pentagon was removed, and Test 3, with the complete pentagon, are shown in the remaining two panels of the left-hand column of Figure 3. Subjects spent more time in the correct than
the incorrect corners at the base of the pentagon in Test 3, but this preference was eliminated when the wall at the bottom of the pentagon was removed in Test 2. A two-way analysis of variance was conducted using individual times spent in the five search zones during Tests 2 and 3. The effect of test trial was not significant, $F(1, 18) = 9.90$, and a significant Test Trial $\times$ Zone interaction, $F(4, 72) = 4.59$. Simple main effects analyses revealed that significantly less time was spent in the incorrect corner during Test 3 than during Test 2, $F(1, 18) = 8.08$. In addition, significantly more time was spent in the obtuse incorrect corner during Test 3 than during Test 2, $F(1, 18) = 13.1$. The amount of time spent in the remaining corners was not significantly affected by the nature of the test trial, $F(1, 90) < 2.38$. Tests of simple main effects also revealed that the amount of time spent in each of the five corners differed significantly for both test trials, $F(4, 144) > 6.44$. Subsequent comparisons between the results from pairs of corners revealed during Test 3 that significantly more time was spent in the correct than the incorrect corner, $t(18) = 3.06$. The equivalent comparison for Test 2 was not significant, $t(18) = 1.69$. Inspection of Figure 3 indicates that rats spent more time in the correct than the incorrect corner at the base of the pentagon than at the apex. In support of this observation, additional analyses revealed that significantly less time was spent in the search zone at the apex than in the corners at the base of the pentagon in Test 2, $t(18) < 2.95$, and in Test 3, $t(18) < 3.11$.

The three remaining panels in the middle row of Figure 3 show the swim paths taken by the rats whose paths are shown in the top row of the panel during the test trial in the pentagon with its base removed. The panels in the bottom row show the paths taken by the same rats during the test trial in the complete pentagon. Subjects tended to search around the perimeter of the test arenas. More time was spent in the correct than the incorrect corner in the complete pentagon, but this was not the case for the incomplete pentagon.

The results from the three sessions of training in the rectangle are displayed in the top right panel of Figure 2, which shows that the consistent group swam directly to the corner containing the platform, or the diagonally opposite corner, more frequently than the inconsistent group. Analysis of individual mean percentages of trials on which rats swam directly to the corner with the platform, or the diagonally opposite corner, for the three sessions combined, revealed a significant difference between the groups, $U(9, 10) = 11$. In order to compare the two groups before they had a chance to learn about the position of the platform in the rectangle, we analyzed the results from the first test trial separately. All 9
subjects in the consistent group headed for the corner that contained the platform, or the opposite one, whereas only 3 out of 10 subjects in the inconsistent group swam directly to these corners. This difference between the groups was significant according to the Fisher exact probability test.

The bottom right panel of Figure 2 shows there was rather little difference between the mean escape latencies for the two groups during the three sessions of training in the rectangle. A two-way analysis of variance revealed that the effect of group ($F < 1$) and the Group $\times$ Session interaction, $F(2, 34) = 2.55$, were not significant, but the effect of trial was significant, $F(2, 34) = 4.75$.

**Discussion**

After being trained to find a submerged platform in a right-angled corner at the base of a pentagon, rats preferred to search for the platform in a rectangular arena in corners that were congruent, rather than incongruent, with the previously correct corner. This pattern of results is consistent with the claim that the correct corner was identified in the pentagon by its local properties, rather than by its position relative to the overall shape of the pool.

Further support for the foregoing conclusion can be found in the test trials that were conducted prior to the three sessions of training in the rectangle. For example, in Test 2, rats were placed in the pentagon with the wall at its base removed. Even though the principal axis of this new arena was aligned with the principal axis of the pentagon, there was no indication that subjects preferred to search in a region of the new arena that was equivalent to the correct corner of the pentagon. One interpretation of this finding is that subjects did not rely on the principal axis to find the platform in the pentagon, and thus there was no basis for transfer of searching preferentially in the relevant regions of the transformed arena. Instead, it is quite possible that, during the training trials, subjects identified the correct corner by certain local cues and that removing one of the walls creating this corner destroyed these cues and thus prevented transfer to the test arena.

As an alternative to the foregoing analysis, it might be argued that the transformation to the pentagon was so great that the control over behavior by the principal axis did not generalize to the new enclosure. An inspection of the results from the test in the transformed arena shows, however, that subjects spent more time in the two corners at the base of the test arena than in the apex. This aversion to the apex was presumably a result of subjects learning that the platform was never located in this corner, and they therefore avoided it. If the knowledge that a particular corner is to be avoided should generalize to the transformed pentagon, then it is hard to understand why learning about the significance of the principal axis should not also generalize to this test environment. Fortunately, the problem with interpreting the results from the test trial in the transformed pentagon does not apply to the results obtained in the rectangle. There was clear evidence that the effects of training in the pentagon transferred to the rectangle, but the nature of this transfer was opposite that predicted by Cheng and Gallistel (2005).

Previous studies of spatial learning based on the shape of the environment have, as a rule, taken steps to prevent subjects from being exposed to cues outside the environment. This was not the case for much of the present experiment, and we need to consider whether the presence of the cues provided by the room was responsible for the outcome of the experiment. During their training in the pentagon with the curtain open, subjects may have identified the eight locations of the platform relative to the room cues. Given the dimensions of the rectangle and the pentagon, it follows that the four corners of the rectangle were equidistant from these eight locations. The bias in the rectangle, of swimming toward the corners that were congruent with the correct corner in the pentagon, was therefore not a consequence of their being closer than the other corners to regions where the platform had previously been located. Instead, the only cues that could have been responsible for this bias must have been provided by the walls of the rectangle. Furthermore, in Tests 2 and 3, the pentagon was oriented in the same direction. Thus, if the preference shown in the pentagon for searching in the correct corner in Test 3 was a consequence of control by cues outside the arena, then a similar preference should have been seen in Test 2. In fact, during this test, rats showed a preference, at least numerically, for the incorrect rather than the correct corner.

The percentages of time spent in the various search zones during the test trials in the absence of the platform were relatively small. One explanation for this finding is that the search zones were themselves small, relative to the area of the test arena. There is, in addition, a plausible explanation for the small amount of time that was spent in the correct corners that does not compromise the conclusions we wish to draw. As rats approached the correct corner during their training in the pentagon, if they failed to encounter the platform directly, they would rarely spend time in the corner searching for it. Rather, they would swim slowly through the corner and then continue in a loop, which could be quite large, until they returned to make another pass through the corner (see the swim paths in the bottom row of Figure 3). The transfer of this behavior to the rectangular test arena would make it difficult for subjects to spend substantially more time in the correct rather than the incorrect corners. Fortunately, results based on the amount of time spent in the correct and incorrect corners of the rectangle are bolstered by the finding that after being released into the rectangle, rats showed a robust tendency to head directly for a correct corner. This effect was evident in the final three sessions of the experiment and in the 60-s test trial in the rectangle. When these different measures of behavior in the rectangle are taken together, they point forcefully to the conclusion that training in the pentagon resulted in a preference for the correct over the incorrect corners of the rectangle.

It might be thought that because the two groups differed in the number of trials on which they headed directly for the corner in the rectangle containing the platform, or the diagonally opposite corner, their escape latencies should have differed during the final stage of the experiment. We generally find, however, that escape latency is not a particularly sensitive measure for discriminating between the performance of groups during test manipulations. For instance, many of the rats when released into the rectangle did not head directly for a corner, but instead they first swam in loops of varying length in the center of the pool. In addition, if subjects in the consistent group swam directly to a geometrically correct corner, then on approximately half of the trials, they would fail to find the platform. Even though this response would be regarded as a correct choice, recording of the escape latency would continue until the rat reached the platform—which might take some time if, as Figure 3 suggests, this journey involved swimming around the
perimeter of the pool. There was, therefore, considerable variability among individual escape latencies, and it is presumably for this reason that this measure failed to reveal a difference between the groups.

Once it is acknowledged that rats navigate with reference to local cues in an environment with a distinctive shape, then there is a need to specify the nature of these local cues. Suppose that the platform was in a corner where the short wall was to the right of the long wall. Possible local cues could be the corner itself, the long wall (which would require rats to swim to the corner at its right-hand end), or the short wall (which would require rats to swim to the corner at its left-hand end). In trying to choose between these alternatives, we are tempted to point to the finding during the training trials that, after the correct corner, the corner that was visited first most frequently was the obtuse-incorrect corner. If rats had learned to swim to a particular end of the short wall, then they should head frequently for this corner after being released into the pool. There was, however, no evidence from the test trial in the pentagon, or the transformed pentagon, of a preference for searching in one obtuse-angled corner rather than another. The tendency to swim directly to the obtuse-incorrect corner may thus have been a consequence of habits acquired during training. For instance, observation of the rats gave the impression that they were just passing through the obtuse-angled corners on their voyage around the pentagon to the correct corner. In support of this impression, note that during the later stages of training, both of the obtuse-angled corners were visited more frequently than the apex or the incorrect corner. On the basis of the available evidence, therefore, it is not possible to specify the local cue that enabled rats to identify the correct corner of the pentagon. The nature of this cue can, however, be identified as geometric because it involves information about the length of one or more sides of the pentagon and, perhaps, information about the relative position of these sides.

There can be no denying that the findings originally reported by Cheng (1986) have had a marked impact on the study of spatial behavior in animals. His results have prompted a number of related studies in distinctively shaped arenas that have investigated the spatial behavior of a variety of species. As noted in the introduction, the findings from these experiments have generally been regarded as evidence that animals navigate with reference to the overall shape of their environment, and the representation of this shape is constructed in a geometric module. The results from the present experiment contradict this explanation, even if it is assumed that the representation of the overall shape of the environment is not a direct copy of it but an abstraction, such as its principal axis. Until there is clear experimental evidence that animals use a global property of the shape of their environment for the purposes of navigation, the present results, together with those reported by Esber, McGregor, Good, Hayward, and Pearce (2005), Pearce et al. (2004), and Tommasi and Polli (2004), suggest it is sufficient to assume that animals rely solely on local cues.

References


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