

Overshadowing of geometric cues by a beacon in a spatial navigation task

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Abstract In three experiments, we examined whether overshadowing of geometric cues by a discrete landmark (beacon) is due to the relative saliences of the cues. Using a virtual water maze task, human participants were required to locate a platform marked by a beacon in a distinctively shaped pool. In Experiment 1, the beacon overshadowed geometric cues in a trapezium, but not in an isosceles triangle. The longer escape latencies during acquisition in the trapezium control group with no beacon suggest that the geometric cues in the trapezium were less salient than those in the triangle. In Experiment 2, we evaluated whether generalization decrement, caused by the removal of the beacon at test, could account for overshadowing. An additional beacon was placed in an alternative corner. For the control groups, the beacons were identical; for the overshadow groups, they were visually unique. Overshadowing was again found in the trapezium. In Experiment 3, we tested whether the absence of overshadowing in the triangle was due to the geometric cues being more salient than the beacon. Following training, the beacon was relocated to a different corner. Participants approached the beacon rather than the trained platform corner, suggesting that the beacon was more salient. These results suggest that associative processes do not fully explain cue competition in the spatial domain.

Keywords Spatial learning · Associative learning · Geometry · Landmarks · Overshadowing · Virtual watermaze

Overshadowing is an established phenomena within standard conditioning procedures (e.g., Kamin, 1969; Pavlov, 1927). For example, if a light–tone compound stimulus signals the delivery of food, both the tone and the light become associated with food. How strongly each cue is associated with the food is partly dependent on the relative saliences of the cues. If the tone is more salient than the light, the association between the light and food would be relatively weak. The standard associative account for this phenomenon is *cue competition* (see, e.g., Rescorla & Wagner, 1972): The two cues must compete for a finite amount of associative strength, and thus, the more associative strength that the salient tone acquires, the less the light can acquire.

Overshadowing has also been demonstrated in the spatial domain in both humans (e.g., Alexander, Wilson, & Wilson, 2009; Chamizo, Aznar-Casanova, & Artigas, 2003; Redhead & Hamilton, 2007, 2009) and nonhumans (e.g., Diez-Chamizo, Sterio, & Mackintosh, 1985; March, Chamizo, & Mackintosh, 1992; McGregor, Horne, Esber, & Pearce, 2009; Redhead, Roberts, Good, & Pearce, 1997; Roberts & Pearce, 1999). In a computer-generated version of the Morris water maze task, Redhead and Hamilton (2007) asked human participants to find the location of a platform that had a conspicuous visual cue (a beacon) placed directly above it. The location of the platform could also be defined in relation to other visual cues (referred to as *landmarks*) placed on the walls of the pool. During a test trial in which the beacon was removed, leaving only the landmarks to guide navigation, participants spent no more time in the platform area than would be expected by chance, suggesting that the beacon effectively overshadowed the, presumably less salient, landmark cues. Such competition between the cues involved in the control of navigation has led several authors (e.g., Chamizo,

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2003; Miller & Shettleworth, 2007; Pearce, 2009) to suggest that spatial learning follows the same rules as those described by associative-learning models.

Redhead and Hamilton (2007, 2009) went on to demonstrate a finding that has challenged this conclusion: The beacon did not overshadow the geometric cues provided by the walls of a triangular pool. The participants were required to locate a platform with a beacon placed in a corner of a pool shaped as an isosceles triangle. The platform's position could thus be determined either by the beacon or by the unique geometric cues formed by the walls of the pool. With the beacon removed, participants were still able to navigate to the platform, on the basis only of the geometric cues. Results showing a similar absence of overshadowing in triangular arenas (e.g., Hayward, McGregor, Good, & Pearce, 2003; McGregor et al., 2009; Pearce, Ward-Robinson, Aydin, Good, & Fussell, 2001) can be seen as being consistent with Cheng's (1986) and Gallistel's (1990) hypothesis concerning the notion of a *geometric module*. A key feature of this hypothesis is that geometric cues are processed separately from nongeometric cues. Such a proposal would mean that geometric cues are immune to competition from nongeometric cues such as beacons, and thus that a beacon would not overshadow geometric cues.

Several recent studies, however, have observed overshadowing of geometric cues when they are provided by more complex, four-sided shapes (Horne & Pearce, 2011; Pearce, Graham, Good, Jones, & McGregor, 2006; Wilson & Alexander, 2008, 2010). Increasing the number of sides of the arena may have reduced the salience of the geometric cues and diminished their resistance to cue competition. The notion of a separate geometric module does not readily encompass a role for relative salience effects, but the result would fit well with associative perspectives that have long recognized the contribution of relative stimulus salience to cue competition phenomena, in that weak cues are more easily overshadowed than comparatively strong cues (Mackintosh, 1976). It is possible that the geometric cues provided by a four-sided pool are less salient than those in the triangle, and thus are more easily overshadowed by the beacon (e.g., Wilson & Alexander, 2008). The absence of overshadowing in the triangle (e.g., Redhead & Hamilton, 2007) may result because the geometric cues formed by the triangular pool are more salient than the beacon. In the present series of experiments, we examined whether the occurrence of overshadowing in the spatial domain is determined by the relative saliences of the competing cues.

Experiment 1

In Experiment 1, we examined whether a beacon would overshadow geometric cues created by the walls of a pool,

both when the pool was a trapezium and when it was triangular. Experiment 1 was further designed to explore whether any difference in overshadowing can be explained by the saliences of the geometric cues in the two types of pool. The rate at which participants learned to locate the platform in the absence of the beacon was recorded in order to give an indication of the salience of the geometric cues within each pool type.

Participants navigated to a platform in a virtual water maze. For Groups Isosceles Overshadow and Isosceles Control, the walls of the virtual pool formed an isosceles triangle; for Groups Trapezium Overshadow and Trapezium Control, the walls formed a trapezium (see Fig. 1 for the pools and the platform layouts). For the two overshadow groups, a beacon marked the position of the platform, and participants could use both the beacon and the geometric cues of the pool shape to locate the platform. For the two control groups the beacon was not present, so participants could use only the geometric cues. If the geometric cues in the triangular pool were more salient than those in the trapezium, we would expect to see participants learn the position of the platform more rapidly in Group Isosceles Control than in Group Trapezium Control.

The trapezium shape was chosen so as to match the triangle, in so far as possible, with respect to the geometric cues adjacent to the platform, such as the angles of the corners and the relative lengths of adjacent sides. Participants in the trapezium groups were divided into two further subgroups. For Subgroup 1, the platform was located at corner D in the trapezium (see Fig. 1). The platform corner was adjacent to the right of the shortest wall for this subgroup in both the trapezium and the triangular pool. For Subgroup 2, the

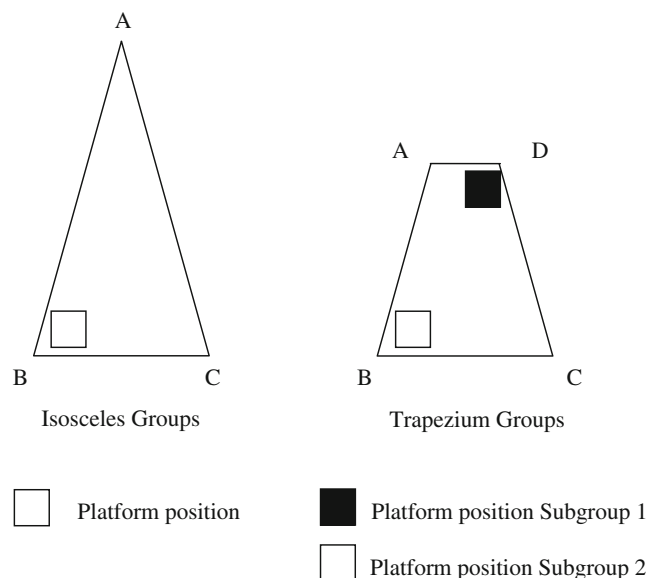


Fig. 1 Pool shapes and platform positions for the training trials in Experiment 1

platform was placed in corner B, and therefore the angle of the platform corner was the same for both this subgroup and the triangle groups.

Following training, all of the participants were given a test trial in which the platform and beacon were removed from the pool and the participants were required to go to the area of the pool where they thought the platform was located. The latency to first enter the platform area and the time spent in the area were taken as measures of how well participants had learned to use the geometric cues alone to locate the platform. If the beacon overshadowed the geometric cues, we would expect to observe shorter latencies and more time spent in the platform area for the control groups as compared to the overshadowing groups.

Some studies have demonstrated that sex is important in both animals and humans as to the type of cue predominantly used in navigation (e.g., Chai & Jacobs, 2009; Roof & Stein, 1999). Rodriguez, Chamizo, and Mackintosh (2011) illustrated that sex was important in determining whether a geometric or nongeometric cue would be the more salient in compound conditioning. Rodriguez et al. compared the behavior of male and female rats in a triangular pool. Overshadowing of the geometric cues by a single landmark was observed in female but not in male rats. These results suggest that males predominantly use geometric cues, while females predominantly use landmarks. The majority of the animal studies assessing overshadowing in a triangular pool have used male rats (e.g., Pearce et al., 2001). It may be that the absence of overshadowing in those studies might be due to this male bias for using geometric cues over landmarks. Human studies have shown a similar gender bias, with females predominantly using landmarks and males using both landmarks and geometric cues (e.g., Sandstrom, Kaufman, & Huettel, 1998). If the cue/gender bias were seen in the present study, we would expect to find a significant interaction between gender and the presence of the beacon. We might therefore expect to see overshadowing of geometric cues in females but not in males, irrespective of pool shape.

Method

Participants The participants were 82 undergraduate students, who received payment of £1.50 for participation and were divided into four main groups: Group Isosceles Control ($n = 18$; male = 7, female = 11); Group Isosceles Overshadow ($n = 15$; male = 6, female = 9); Group Trapezium Control, Subgroup 1 ($n = 18$; male = 8, female = 10) and Subgroup 2 ($n = 8$; males = 4, female = 4); and Group Trapezium Overshadow, Subgroup 1 ($n = 15$; male = 6, female = 9) and Subgroup 2 ($n = 8$; male = 4, female = 4). The mean age was 24.8 years (range 19–32 years).

Materials and apparatus The experiment was performed in a research cubicle (length 2.4 m, width 1.3 m, height 2 m) containing a chair in front of a 1.3-m-wide workbench attached to the wall opposite the entrance to the cubicle. A 15-in. color computer monitor and keyboard were placed on the workbench. The monitor was connected to an IBM-compatible PC placed beneath the bench. The virtual environment consisted of a pool in the shape of an isosceles triangle, for the isosceles groups, or a trapezium, for the trapezium groups. The layouts of the pools and the platform/beacon positions can be seen in Fig. 1. The isosceles triangle had long walls 140 units in length and a short wall of 60 units. The angles at which the walls intersected were 70° at corners B and C and 40° at corner A. For the trapezium groups, the pool was a trapezium with four beige walls. The wall between B and C was 60 units, the walls between B and A and between C and D were 90 units, and the wall between A and D was 25 units. Corners B and C were 70° angles, and corners A and D were 110° angles. For both pools, all of the walls were 15 units in height. The viewpoint of the participant was eight units above the surface of the water. The platform area was 10 units wide and 10 units long. For Subgroup 1 of the trapezium groups, the center of the platform was 17 units from corner D on a line at an angle of 43° from the wall between corners A and D. For the isosceles groups and for Subgroup 2 of the trapezium groups, the center of the platform was located 17 units from corner B on a line at an angle of 43° from the wall between corners B and C. For the overshadow groups, the beacon was a black cube, five units in height, width, and length, and was suspended three units above the center of the platform position. An opaque blue pattern was used to create the surface of the pool. Beyond the walls and above the pool the background was black, and no room contours were visible.

Navigation was controlled using the keyboard arrow keys. The UP arrow key was used to control forward motion, and the LEFT and RIGHT arrow keys controlled rotation. Backward navigation was not possible. One complete rotation took approximately 1.5 s to complete, and it took 3 s to cross 100 units of the pool.

Procedure Participants were led into the cubicle and asked to sit in front of the computer, after which the experimenter left the room. The following instructions were given to the participants in Group Isosceles Control via the computer screen:

In this experiment you will view a computer-generated environment on the monitor. You will be viewing the environment from a first-person perspective and you can move through the environment using the arrow keys on the keyboard (UP, LEFT, and RIGHT). You

will be placed in a triangular pool of water from which you must escape by climbing onto a submerged platform. When you cross the platform you will be stopped, raised out of the water, and you will see a message saying that you have found the platform. Your goal is to locate that platform and climb onto it as quickly as possible. You will be on the platform for a few moments during which time you can scan around the pool. The screen will then fade out and you will begin another trial. You will complete several trials. On each trial you will begin at the centre of the pool. Press the space bar when you are ready to start.

Participants in trapezium groups were given the same instructions, except they were told that the pool was a four-sided arena, and participants in the overshadow groups were also told that a beacon marked the position of the platform and that they would need to touch the beacon to end the trial.

Once participants had pressed the space bar, the computer screen displayed the water maze from the position of the center of the pool. Over the 16 acquisition trials, the participants initially were placed facing each of the corners within the pool at least four times. On reaching the platform, a bell sounded and the words “You have gained 10 points” appeared on the screen. The 10 points were added to a total displayed in the top right corner of the screen. Participants were then placed on top of the platform for 5 s before the screen went dark for 1 s, and the participants were again placed facing a corner for the start of the next acquisition trial. If the participants did not find the platform within 60 s, the platform became visible and the participants were instructed to swim toward it. The time to enter the platform area was recorded for each acquisition trial. At the end of training, a message appeared on the screen:

Please go to the area of the pool you think the platform should be. Please press the space bar to continue

Once the participants had pressed the space bar to begin the test trial, the screen displayed the pool from the center facing corner A. For the test trial, there was no platform or beacon in the pool, and the trial lasted for 45 s, after which the screen went blank except for a message requesting the participant to see the experimenter. The latency to cross into and the time spent in the platform area of the pool were recorded during the test trials.

Results and discussion

All statistical tests were evaluated with respect to an alpha value of .05.

Figure 2 illustrates the group mean latencies to escape the pool by locating the platform across the training trials. The

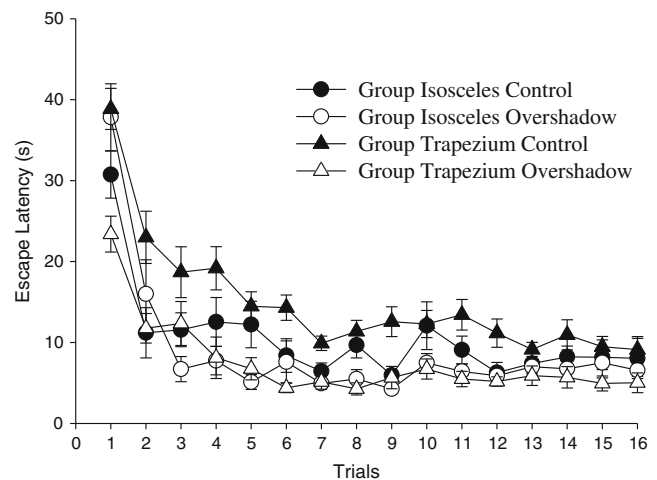


Fig. 2 Mean escape latencies during training in Experiment 1. The error bars show the standard errors of the means

subgroups in the trapezium pool are combined in Fig. 2 and in the subsequent training data analyses, as an initial 2 (presence of beacon) \times 2 (subgroup) \times 16 (trial) mixed-design analysis of variance (ANOVA) performed on the escape latencies of the trapezium groups revealed no main effect of subgroup, $F < 1$, nor any interaction with other factors [Beacon \times Subgroup, $F(1, 45) = 1.85$; Trial \times Subgroup, $F < 1$]. These results suggest that the difference in platform positions between the subgroups did not affect escape latencies. For all groups, the escape latencies decreased to an asymptote by the end of training. Group Trapezium Control appeared to have slightly longer escape latencies than did the other groups in the initial trials.

A 2 (gender) \times 2 (pool shape) \times 2 (presence of beacon) \times 16 (trial) mixed-design ANOVA was performed on the escape latency data. The effect of gender was found to be significant, $F(1, 74) = 6.19$: Males had shorter latencies ($M = 9.06$ s) than did females ($M = 11.5$ s). There was also a Gender \times Trial interaction, $F(15, 1110) = 3.56$, and simple main effects (Kepple, 1973) revealed that the gender difference was only significant on Trials 1 and 2, $F_s(1, 1184) > 11.88$. No other interaction involving gender was significant, indicating that gender had no significant impact on any other factor (all other interactions involving gender, $F_s < 1$, except Gender \times Shape \times Beacon, $F(1, 74) = 1.19$, and Gender \times Shape \times Beacon \times Trial, $F(15, 1110) = 1.13$).

A significant effect of trial, $F(15, 1110) = 48.48$, supported the observation that escape latencies decreased over trials, and an effect of beacon presence, $F(1, 74) = 20.46$, suggested that escape latencies were shorter when the beacon was present than when it was absent. The effect of pool shape was not significant, $F(1, 74) = 2.69$. There was, however, a significant Beacon \times Pool Shape interaction, $F(1, 74) = 8.14$. The Pool Shape \times Trial interaction was not significant, $F(15, 1110) = 1.58$, nor was the Beacon \times Trial

interaction, $F < 1$. The Pool Shape \times Beacon \times Trial interaction was significant, $F(15, 1110) = 2.31$. Simple main effects (Keppel, 1973) of the Pool Shape \times Beacon and Pool Shape \times Beacon \times Trial interactions revealed an effect of beacon in the trapezium groups, $F(1, 74) = 27.21$: Escape latencies were longer for Group Trapezium Control than for Group Trapezium Overshadow on Trials 1–6 and 8–12, $F_s(1, 1184) > 3.93$. The difference between the isosceles groups was not significant, $F(1, 74) = 1.39$. An effect of pool shape also emerged between the control groups, $F(1, 74) = 10.10$, with Group Trapezium Control having longer latencies than Group Isosceles Control on Trials 1–4, 6, and 9, $F_s(1, 1184) > 5.27$, suggesting that the geometric cues were less salient in the trapezium than in the triangular pool. The effect of shape was not significant in the overshadow groups, $F < 1$.

During the test trials, latencies to cross into the platform area (left-hand panel of Fig. 3) and percentages of time spent in the platform area (right-hand panel of Fig. 3) were recorded. The platform position subgroups in the trapezium pool are once again combined in both panels. A two 2 (subgroup) \times 2 (control vs. overshadow) between-group ANOVA on the latencies revealed no main effect of subgroup, $F < 1$, nor was the interaction between subgroup and condition significant, $F(1, 45) = 1.1$. A similar ANOVA on the percentages of time spent in the platform area revealed that the main effect of subgroup was not significant, $F(1, 45) = 3.21$, nor was the Subgroup \times Condition interaction, $F < 1$.

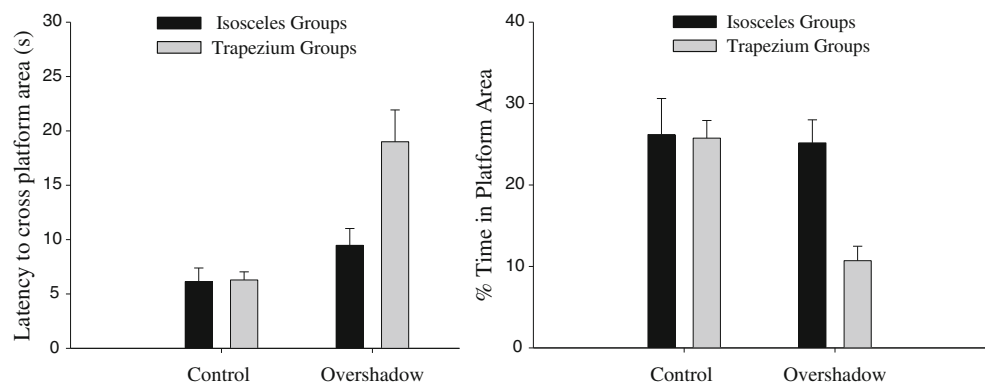
The left-hand panel of Fig. 3 suggests that the participants in Group Trapezium Overshadow took longer to locate the platform than did the participants from the other three groups. To confirm these observations, a 2 \times 2 \times 2 between-groups ANOVA was performed on the latencies to cross into the platform area, with gender, shape, and beacon presence the independent variables. The main effect of gender was not significant, $F(1, 74) = 1.49$, nor were the interactions between the other factors and gender, $F_s < 1$. We did find a significant effect of pool shape, $F(1, 74) = 6.00$, as well as an effect of beacon presence, $F(1, 74) = 15.57$, and an interaction between shape and beacon, $F(1, 74) = 5.56$. Further examination of the interaction via

simple main effects revealed that the participants in Group Isosceles Overshadow, $F(1, 74) = 11.56$, and Group Trapezium Control, $F(1, 74) = 19.87$, crossed the platform area before those in Group Trapezium Overshadow, suggesting that the beacon overshadowed the geometric cues in the trapezium.

A similar pattern of results can be seen in the right-hand panel of Fig. 3, depicting the percentages of time spent in the platform area; participants in Group Trapezium Overshadow spent less time in the platform area than did the participants in the other groups. A 2 \times 2 \times 2 between-groups ANOVA was performed on the percentages of time spent in the platform area, with gender, shape, and beacon presence the independent variables. The main effect of gender was not significant, $F(1, 74) = 3.71$, and no further significant interactions involved gender [Shape \times Gender, $F(1, 74) = 1.46$; all other interactions, $F_s < 1$]. We did find significant effects of pool shape, $F(1, 74) = 8.47$, and beacon presence, $F(1, 74) = 8.83$, as well as a significant interaction between shape and beacon, $F(1, 74) = 5.36$. Simple main effects performed to explore the interaction further showed that both Group Isosceles Overshadow, $F(1, 74) = 13.66$, and Group Trapezium Control, $F(1, 74) = 13.98$, spent more time in the platform area than did Group Trapezium Overshadow, suggesting once more that the beacon overshadowed the geometric cues only in the trapezium.

In Experiment 1, we examined whether a beacon could overshadow learning about geometric cues in two distinctively shaped pools. On the test trial, when the beacon was removed, Group Isosceles Overshadow spent the most time in the area of the pool indicated by the geometric cues. This group spent a similar amount of time in, and showed the same latency to cross into, the platform area as Group Isosceles Control, which had not received compound training with the beacon. All of these measures suggest no overshadowing by the beacon; Group Isosceles Overshadow had learned the position of the platform in reference to the geometric cues as well as the control group had. This was not the case for Group Trapezium Overshadow, which spent significantly less time in the platform area and crossed into

Fig. 3 Experiment 1: (Left) Mean latencies to cross into platform areas. (Right) Mean percentages of time spent in the platform areas. The error bars show the standard errors of the means



it significantly later than did Group Trapezium Control. Here the presence of the beacon had disrupted learning about geometric cues. This demonstration of disruption by a beacon is a novel finding in human navigation studies, and along with previous evidence of disruption to geometric cues by nongeometric cues (e.g., Horne & Pearce, 2011; Pearce et al., 2006; Wilson & Alexander, 2008, 2010), it challenges the claim that geometric cues are processed separately in a geometric module.

Although we found an effect of gender, with males generally outperforming females in the spatial tasks (shorter latencies in initial training), there was no Gender \times Beacon Presence interaction. The patterns of overshadowing were the same for both females and males. Therefore, we did not find the bias for females to use the beacon and males to use geometric cues that has been reported elsewhere (e.g., Sandstrom et al., 1998). If we had, we might have expected to see less overshadowing of geometric cues by the beacon in males. It is possible that our measure of such a bias was not sensitive enough; it remains the case, however, that the overall finding that a beacon overshadowed the geometric cues in a trapezium but not in a triangle was true across genders.

In an attempt to explain the absence of overshadowing seen in triangular pools (e.g., Hayward et al., 2003; McGregor et al., 2009; Pearce et al., 2001; Redhead & Hamilton, 2007), we suggested in the introduction that the geometric cues of a triangle maybe more salient than those created by a four-sided shape, where overshadowing has been demonstrated (e.g., Horne & Pearce, 2011). A comparison of the training trials in Experiment 1 supports this hypothesis. Group Trapezium Control had significantly longer escape latencies than did either Group Isosceles Control or Group Trapezium Overshadow, suggesting, first, that geometric cues were less salient in the trapezium than in the triangle, and second, that the geometric cues in the trapezium were less salient than was the beacon. However, while escape latencies differed between control groups over the first six trials, by the end of training, both groups had reached asymptote. This would explain why we found no difference between the control groups in the time spent in the platform area during the test trial. The excellent performance of Group Trapezium Control on the final training trial also suggests that the overshadowing effect observed in Group Trapezium Overshadow was not simply due to inadequate training. In Experiment 2, we explored an alternative explanation for the presence of overshadowing in the trapezium and its absence in the isosceles triangle.

Experiment 2

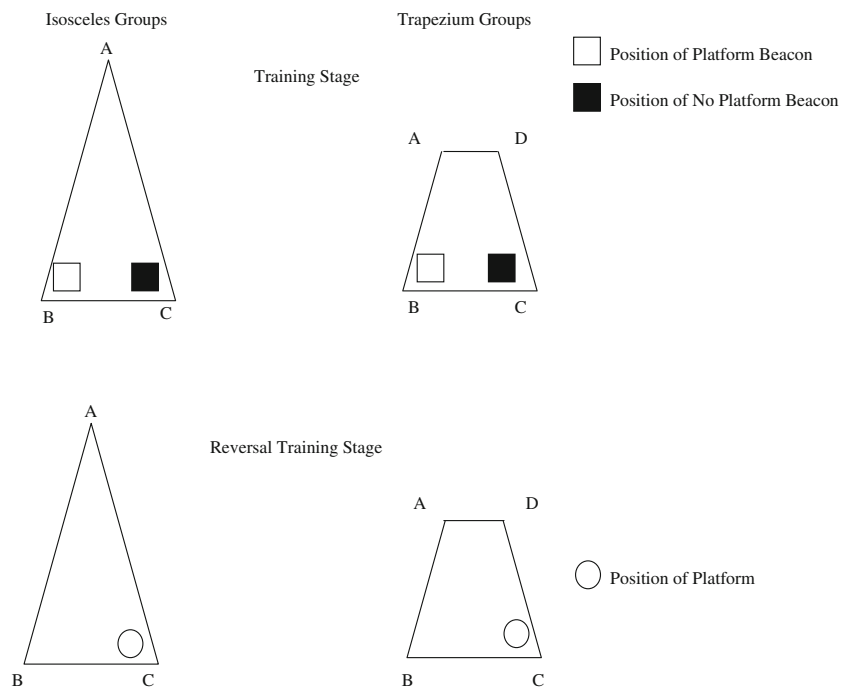
The results of Experiment 1 demonstrated that the beacon disrupted learning about the geometric cues in the trapezium.

An alternative explanation to the cue competition account for this effect could be offered in terms of a generalization decrement: Less associative strength will generalize to a stimulus in a test trial if the situation differs greatly from the training trial. For the overshadow groups in the test trial, associative strength might generalize poorly to an empty corner of the pool, given that training had required approaching a corner containing a beacon. This would not be the case for the control groups, for which training had required approaching an empty corner.

One way to equate the generalization decrement between the control and overshadow groups would be to require participants to locate a platform marked by a beacon during training in both groups. In Experiment 2, the control groups (Groups Trapezium Same and Isosceles Same) were presented with two identical beacons, only one of which marked the position of the platform (see Fig. 4 for the layouts of pools and the beacons). Participants had to use the geometric cues of the pool to identify which beacon marked the platform position. In the overshadowing groups (Groups Trapezium Different and Isosceles Different), the beacons were different colors, meaning that participants could learn either which geometric cues were associated with the platform position or which visually unique beacon was. Removing the beacons in the test trial would then result in similar levels of generalization decrement in both sets of groups. If overshadowing were still observed in the trapezium pool, it could not be attributed to unequal levels of generalization decrement between the control and overshadowing groups.

The absence of overshadowing in the isosceles triangle (in which generalization decrement might also be expected) requires consideration. One possibility is that, with this apparatus, generalization is countered by a potentiation effect. Several studies have demonstrated potentiation with cues from the spatial domain (Cole, Gibson, Pollack, & Yates, 2011; Graham, Good, McGregor, & Pearce, 2006; Pearce et al., 2006). For example, Horne and Pearce (2011) demonstrated potentiation of geometric cues by landmarks on the walls of a pool: Following training with the landmarks, rats spent more time searching near the geometric cues associated with the platform than if they had been trained only with the geometric cues. Pearce (2009) suggested that the cue associations formed between landmark and geometric cues during training meant that when rats viewed the geometric cues at test, this would evoke a memory for the landmarks that were strongly associated with the platform, and as a consequence the rats would approach the correct geometric cues. In Experiment 1, Group Isosceles Overshadow did not demonstrate potentiation by remaining in the geometric-cue corner longer than Group Isosceles Control. A possible reason might again be that the removal of the beacon resulted in a large generalization

Fig. 4 Pool shapes and positions of the platforms and beacons for the training trials in Experiment 2



decrement for Group Isosceles Overshadow, which counteracted any potentiation. Equalizing the generalization decrement across groups might allow potentiation to be observed in Group Isosceles Overshadow as compared to Group Isosceles Control.

Pearce et al. (2001) also demonstrated potentiation of geometric cues in a water maze, using a procedure in which, after an initial test trial, rats were given reversal-training trials in which they were trained to locate the platform in a new location. Pearce et al. (2001) found that the group that had received initial compound training, with beacon and geometric cues, took longer to locate the new position of the platform. The authors suggested that the original geometric cues had become more strongly associated with the platform position due to potentiation by the beacon. They also suggested that this procedure was likely to provide a sensitive test of potentiation, as there would be no performance ceiling (such as might occur in the no-platform test trials). Accordingly, our Experiment 2 included reversal training following initial compound training, in a further attempt to demonstrate potentiation.

Method

Participants The participants were 60 undergraduate students, who received payment of £1.50 for participation and were divided equally into four groups: Group Isosceles Same (male = 6, female = 9), Group Isosceles Different (male = 5, female = 10), Group Trapezium Same (male = 6, female = 9), and Group Trapezium Different (male = 6, female = 9). The

mean age was 22.8 years (range 19–32 years). Participants were not permitted to take part in the experiment if they had previously completed Experiment 1.

Materials and apparatus Details of the materials and apparatus were the same as in Experiment 1, except that all groups in Experiment 2 were presented with two beacons during training. For control groups, the two beacons were identical, and for the overshadow groups, the beacon above the platform was red, while the beacon in the other corner was green. Given the similarity in results between the trapezium subgroups in Experiment 1, for all participants the platform was placed in corner B during training and corner C during reversal training. For beacon positions and the pool layouts, see Fig. 4.

Procedure Participants received 21 training trials in which they were required to locate a platform marked by a beacon to end the trial. If participants touched the incorrect beacon, a message was displayed saying that they had lost 10 points. Training was followed by a test trial, in which the beacons and platform were removed from the pool and participants were asked to go to the area of the pool where they thought the platform should be. All participants then received three further training trials similar to the original training, to reduce any effect of the test trial on the associations formed between the platform and the geometric cues. Finally, they received nine training trials in which the platform was in the opposite corner than during initial training. In this training, the beacons were removed and participants had

to use geometric cues to identify the correct corner. All other details were the same as in Experiment 1.

Results and discussion

All statistical tests were evaluated with respect to an alpha value of .05.

Figure 5 (left-hand panel) illustrates the escape latencies across initial training. The escape latencies decreased over trials to the same point for all groups, suggesting that the groups learned the task at the same rate and to the same degree. A $2 \times 2 \times 21$ mixed-design ANOVA was performed on the escape latency data, with pool shape (isosceles or trapezium) and group (same vs. different) as between-subjects variables, and trial as a within-subjects variable. We found a significant effect of trial, $F(20, 1120) = 17.79$, supporting the observation that escape latencies decreased over trials. The effect of pool shape was not significant, $F(1, 56) = 2.38$, nor was the effect of group, $F(1, 56) = 1.10$. None of the interactions between the factors were significant [Group \times Pool Shape, $F < 1$; Group \times Trial, $F(20, 1120) = 1.09$; Pool Shape \times Trial, $F < 1$; Group \times Pool Shape \times Trial, $F < 1$]. These results support the observation that all four groups learned at the same rate and to the same level by the end of training.

The left-hand panel of Fig. 6 illustrates the latencies to cross into the platform area in the test trial. Participants in both control conditions, for whom the beacons had been identical during training, crossed to the platform area quite quickly, as did the participants in Group Isosceles Different. Participants in Group Trapezium Different, however, took longer to cross into the platform area than did the other groups. A 2×2 between-group design ANOVA was performed on the latencies to cross into the platform area, with pool shape and group

(same vs. different) as variables. An effect of pool shape emerged, $F(1, 56) = 7.24$, with the participants in the trapezium being slower overall to cross into the platform area. We found a significant effect of group, with the participants for whom the beacons were identical crossing into the platform area faster, $F(1, 56) = 8.29$, and the interaction between group and pool shape was also significant, $F(1, 56) = 4.48$. Further analysis of the interaction via simple mean effects revealed a significant effect of group only in the trapezium condition, $F(1, 56) = 12.48$, in that Group Trapezium Different crossed the platform later than did Group Trapezium Same. There was also a significant effect of pool shape only in the groups for which the beacons were different, $F(1, 56) = 11.58$; again, Group Trapezium Different had longer latencies to cross into the platform area.

The right-hand panel of Fig. 6 illustrates a similar pattern of results for the percentages of time spent in the platform area: Participants in Group Trapezium Different spent less time in the platform area than did those in any of the other groups, suggesting that they had learned the position of the platform in relation to the geometric cues more poorly than the other groups. These observations were confirmed by a 2×2 between-group design ANOVA performed on the time spent in the platform area, with group and pool shape as independent variables. We found an effect of pool shape, in which participants in the isosceles triangle spent more time overall in the platform area than did those in the trapezium, $F(1, 56) = 14.26$. The effect of group was not significant, $F(1, 56) = 2.80$, but the interaction between pool shape and group was, $F(1, 56) = 4.06$. Further analysis of the interaction via simple main effects revealed a significant effect of group only for the participants in the trapezium pool, with Group Trapezium Same spending longer in the platform area than did Group Trapezium Different, $F(1, 56) = 6.81$. We also found a significant effect of pool shape only for the

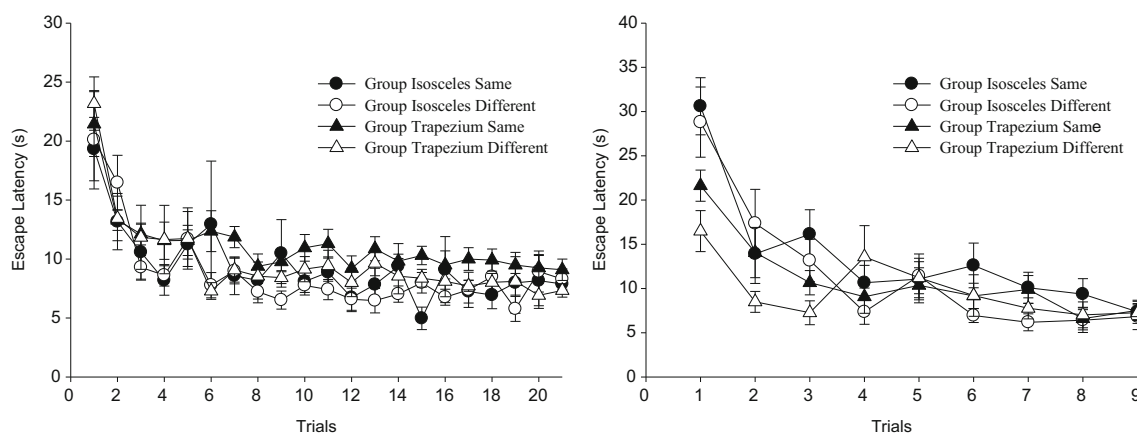
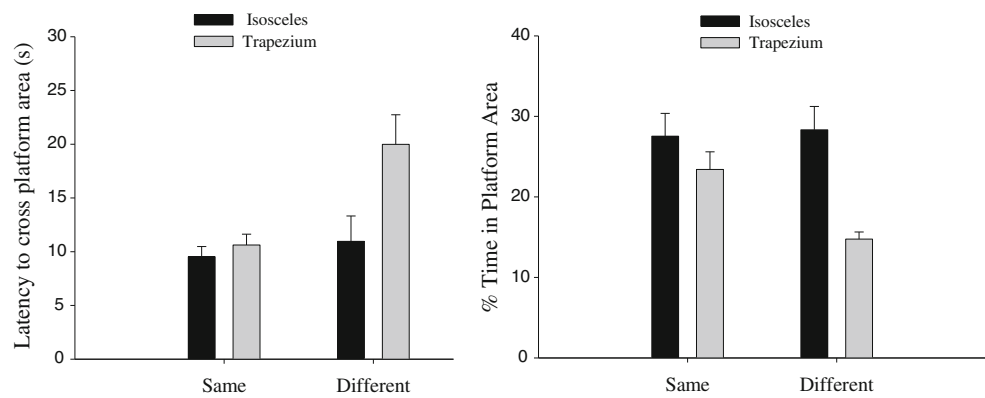


Fig. 5 Mean escape latencies during training (*left-hand panel*) and reversal training (*right-hand panel*) in Experiment 2. The error bars show the standard errors of the means

Fig. 6 Experiment 2: (Left) Mean latencies to cross into platform areas. (Right) Mean percentages of time spent in the platform areas. The error bars show the standard errors of the means



participants with differently colored beacons; Group Isosceles Different spent longer in the platform area than did Group Trapezium Different, $F(1, 56) = 16.77$.

The right-hand panel of Fig. 5 illustrates the escape latencies during the reversal-learning stage. Generally, there appears to be little difference among the groups, although on the initial trials, the isosceles groups' mean escape latencies are numerically longer than those of the trapezium groups, suggesting that the isosceles groups had possibly associated the original position of the platform with the geometric cues more strongly than had the trapezium groups. These observations were confirmed by a 2 (group) \times 2 (pool shape) \times 9 (trial) mixed-design ANOVA performed on the escape latencies. A significant effect of trial emerged, $F(8, 448) = 29.78$, supporting the observation that participants learned the new position of the platform over trials. The effect of pool shape was not significant, $F(1, 56) = 3.67$, nor was the effect of group, $F < 1$, nor the interaction between group and pool shape, $F(1, 56) = 1.88$. The interaction between pool shape and trial was significant, $F(8, 448) = 4.39$, but the interactions between group and trial, $F(8, 448) = 1.66$, and between pool shape, group, and trial, $F < 1$, were not significant. Further analysis of the Pool Shape \times Trial interaction via simple main effects revealed an effect of pool shape on Trials 1, 2, and 3, with the isosceles groups having significantly longer latencies than did the trapezium groups, $F_s(1, 504) > 4.15$.

It was suggested that the poor performance observed in Group Trapezium Overshadow in Experiment 1 might have been due to a generalization decrement caused by the removal of the beacon during the test trial. Despite training both trapezium groups to approach a beacon marking a platform position, poorer performance was still found only in Group Different Trapezium, suggesting that generalization decrement was not responsible for the poor performance in Group Trapezium Overshadow in Experiment 1. Overall, the results suggest that the poor performance here was due to the unique beacon overshadowing the geometric cues of the trapezium.

As in Experiment 1, no evidence emerged that the beacon had overshadowed the geometric cues in the triangle. We

suggested that this might be due to potentiation of the shape cues by the beacon. No evidence of potentiation was observed in Experiment 1, but this, again, might have been due to a disparity in generalization decrements between the two groups. Despite making the generalization decrement in the test trials similar for the isosceles groups in Experiment 2 and using a second, and possibly more sensitive, measure of potentiation, we still found little evidence of potentiation of the shape cues by the beacon. Although Group Isosceles Different spent somewhat more time in the platform corner during the test trial than did Group Isosceles Same, this difference was not significant. The latency to cross into the platform area was numerically shorter in Group Isosceles Same, but again this difference between the two groups was not significant. In the reacquisition trials, we found little evidence that the two groups learned the new position of the platform at different rates.

Experiments 1 and 2 suggest that the less salient geometric cues created by the walls of the trapezium could have been overshadowed by the beacon, a result that is inconsistent with the suggestion that a geometric module processes geometric cues separately, but that is consistent with a simple cue competition account. That the beacon did not overshadow the geometric cues created by the walls of the isosceles triangle would be expected if these cues were more salient than those of the trapezium. It might also be expected that the geometric cues within the triangle should be more salient than the beacon. Experiment 1 suggested, however, that the geometric cues in a triangular pool are approximately equal in salience to a beacon, since escape latencies during training were the same whether or not the beacon was present. Experiment 3 directly tested the saliences of a beacon and geometric cues by comparing the control that each has over navigation.

Experiment 3

Hamilton, Akers, Weisend, and Sutherland (2007) demonstrated that the position of a platform in relation to the walls of a circular water maze and to distal directional cues

controlled search behavior much more than did a beacon attached to the platform. They trained rats to locate a platform with an attached beacon placed a set distance from the west side of a circular water maze. In a test trial, the beacon was moved to the east side of the pool. The rats' initial trajectories were uniformly directed toward the location where the platform had been during training (west) rather than toward the beacon (east).

In Experiment 3, we utilized a method similar to that used by Hamilton et al. (2007) to assess whether the geometric cues in the triangular pool were more salient than the beacon used in Experiment 1. Participants in Group Isosceles were trained to locate a platform, with a beacon marking the platform position, in an isosceles-shaped pool. The platform was placed in corner B of the isosceles triangle (see Fig. 7). In the test trial, the beacon was moved to corner C and the platform was removed. If the geometric cues were more salient than the beacon, it might be expected that they would have more control over search behavior, and thus that participants would search more in corner B than C. Such a result would lend further support for the hypothesis that the lack of overshadowing in the triangular pool in Experiments 1 and 2 was a result of the geometric cues being more salient than the beacon.

A further group, Group Trapezium, received similar training, but in the trapezium pool. As with Group Isosceles, the platform and beacon were placed in corner B for training, and then in the test trial, the platform was removed and the beacon was moved to corner C (see Fig. 7). As the beacon has

previously overshadowed the geometric cues in the trapezium pool, it might be expected that here the beacon would control search behavior and that participants would spend more time searching corner C.

Method

Participants The participants were 24 undergraduate students, who received payment of £1.50 for participation and were divided equally into two groups: Group Isosceles (male = 5, female = 7) and Group Trapezium (male = 3, female = 9). The mean age was 24.7 years (range 20–32 years). Participants were not permitted to take part in the experiment if they had previously completed either Experiment 1 or 2.

Materials and apparatus Details of the materials and apparatus were the same as in Experiment 1, except that for all participants the position of the platform in training was marked by a beacon, and during test trials, the beacon remained in the pool but was moved to a different corner.

Procedure The participants received nine training trials. This was fewer than in previous experiments, as it had been found in Experiment 1 that escape latencies for participants trained with a beacon were at asymptote by Trial 9. During training, the participants were required to locate a platform marked by a beacon to end the trial. Training was followed by a test trial in which the platforms were removed from the pool and the

Fig. 7 Pool shapes and positions of the platforms and beacons in the training and test trials of Experiment 3

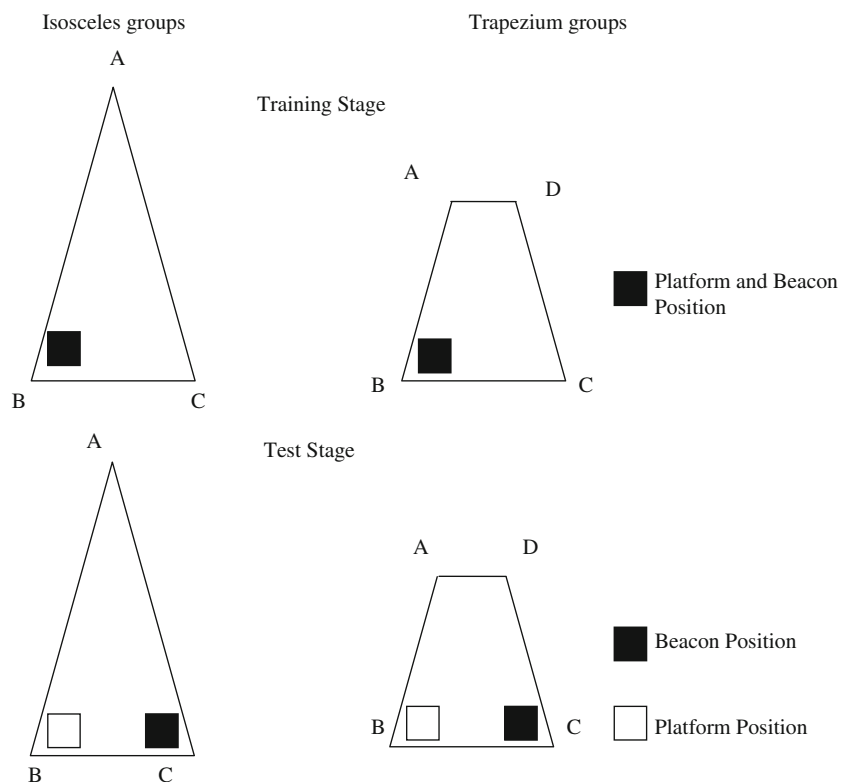
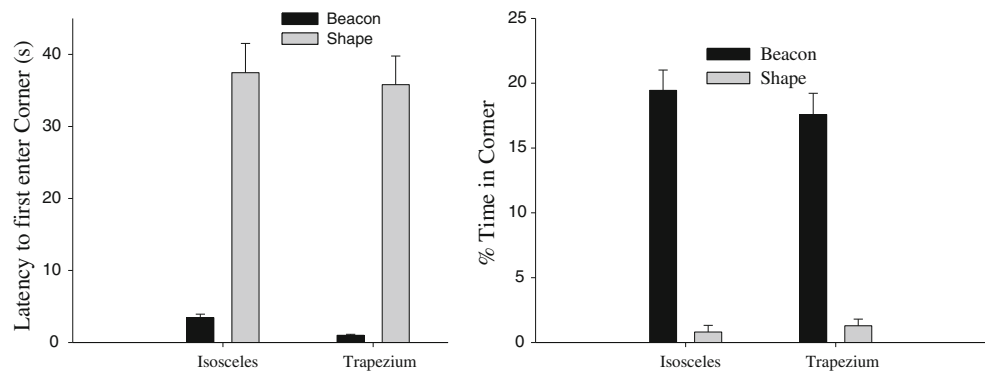


Fig. 8 Experiment 3: (Left) Mean latencies to cross into the beacon corner (black bars) and the shape corner (gray bars) for Groups Isosceles and Trapezium. (Right) Mean percentages of time spent in the beacon corner (black bars) and the shape corner (gray bars) for Groups Isosceles and Trapezium. The error bars show the standard errors of the means



black beacon marking the position of the platform in corner B was moved to corner C. Participants were asked to go to the area of the pool where they thought the platform should be. All other details were the same as in Experiment 1.

Results and discussion

All statistical tests were evaluated with respect to an alpha value of .05.

In Fig. 8, the left panel illustrates the latencies to cross into the platform areas indicated by the geometric cues (corner B) and by the black beacon (corner C) during the test trial. The right panel illustrates the time spent in these areas. It is apparent that for both Groups Isosceles and Trapezium, the latency was shorter to cross into the beacon corner than the geometric-cue corner, and again for both groups, more time was spent in the beacon corner. This suggests that the beacon was more salient than the geometric cues in both shapes of pool. To test this interpretation of the results, two 2×2 mixed-design ANOVAs were performed, with the latencies to cross into and the times spent in the respective corners as the two dependent variables. For both analyses, the independent variables were shape of pool (between subjects) and beacon or geometric-cue corner (B or C; within subjects).

In the latency analysis, we found no significant effect of pool shape, $F < 1$, but there was a significant effect of corner, $F(1, 22) = 141.84$, indicating that the participants in both groups entered the beacon corner (C) earlier than the geometric-cue corner (B). The interaction between the factors was not significant, $F < 1$. For time spent in the corners, no effect of pool shape emerged, $F < 1$, but there was an effect of corner, $F(1, 22) = 200.50$, indicating that the participants in both groups spent more time in the beacon corner. The interaction was not significant, $F < 1$. These results suggest that the beacon was more salient than the geometric cues in both pools.

The main finding from Experiment 3 was that in both the isosceles triangle and the trapezium, participants approached the beacon first, rather than the geometric cues associated with the platform, and both groups spent more time in the beacon corner during the test trial. This suggests that the beacon

controls spatial navigation and is more salient than the geometric cues. The absence of overshadowing seen in the isosceles triangle in Experiments 1 and 2 cannot be explained by the geometric cues being more salient than the beacon.

General discussion

The results of Experiment 1 demonstrated that the geometric cues associated with a trapezoidal arena could be overshadowed by a beacon marking the position of the platform. Though overshadowing and blocking in four-sided enclosures have been demonstrated before (e.g., Home & Pearce, 2011; Pearce et al., 2006; Wilson & Alexander, 2008, 2010), Experiment 1 in the present study has been the first to show overshadowing of geometric cues via a beacon in a human spatial-navigation study. The findings add to the evidence suggesting that geometric cues are not processed separately from other spatial cues in a geometric module.

In Experiment 2, we tested an alternative explanation for the poor performance of Group Trapezium Overshadow in Experiment 1: The generalization decrement may have been greater for groups trained to approach the beacon, due to the disruption caused by its removal in the test trial. In Experiment 2, both the control and overshadow groups were required to approach a beacon during training, and we still found a disruption of performance in the overshadow group trained in the trapezium, as compared to the equivalent control group.

Experiment 1 also demonstrated the absence of overshadowing within an isosceles triangle. The suggestion that the pattern of overshadowing was due to the relative saliences of the two sets of geometric cues was supported by the escape latencies in the training stages of both control groups. In the absence of the beacon, participants learned the position of the platform more slowly in the trapezium than in the isosceles pool, suggesting that the geometric cues in the isosceles pool were more salient, and thus less prone to overshadowing by the beacon.

In Experiment 2 we examined whether the lack of overshadowing in the isosceles triangle could be explained by potentiation of the geometric cues by the beacon. In Experiment 1, no evidence emerged that the overshadowing group

performed better than the control group in the test stage, as would be predicted if potentiation had occurred. However, an increased generalization decrement in the overshadow group, due to the absence of the beacon in the test trial, might have countered any potentiation. In Experiment 2, generalization decrements were equated by marking the position of the platform with a beacon in both groups during training. We still found, however, no evidence that the overshadow group (Group Isosceles Different) performed significantly better than the control group (Group Isosceles Same) in the test stage. Pearce et al. (2001) had demonstrated potentiation with rats in a triangular pool in a different manner; they found that reversal learning was slower following compound training with the beacon, suggesting that the animals had formed a stronger association between the platform and its original position than had those in the control group. In Experiment 2 of the present study, no difference was found in the rates at which reversal learning progressed, suggesting that the lack of overshadowing in the pool was not due to potentiation.

The discrepancy between nonhuman studies, such as that of Horne and Pearce (2011), in which potentiation has been demonstrated, and the present study with human participants, in which there was no evidence of potentiation, may be due to differences in motivation to complete the task. The water maze is a mildly aversive procedure for the animals, possibly leading them to be more motivated to learn the relationships between all cues and the platform position, and thus leading to stronger within-cue associations. Motivation might also have been high in the study by Rhodes, Creighton, Killcross, Good, and Honey (2009), which produced evidence of potentiation of geometric cues in a maze in which hungry rats were trained to locate sucrose pellets from locations within the maze. The reward for locating the platform in the virtual water maze task of the present study was merely to receive points. It might be that such a low-motivation task could lead to a lack of attention to peripheral cues and to increased overshadowing. Chamizo et al. (2003), in their virtual water maze task, used an unpleasant auditory stimulus to better simulate the aversive nature of an escape trial in a real water maze. Using such a procedure might produce potentiation if motivation is a factor.

Miller and Shettleworth (2007) suggested that potentiation happens early within training, due to feature enhancement. For example, in Experiment 1, participants in Group Isosceles Overshadow might have chosen to enter the correct corner first on a trial more often than the control group did due to the presence of the salient beacon. According to Miller and Shettleworth (2007, p. 194), this would lead “the associative strength of the geometry to increase faster than it would have if the subject had relied only on geometry.” They suggested that this potentiation is transient and is apparent only when the associative strengths are relatively small. It may be argued that in the present experiments we were testing too late to detect potentiation. If we were to give several test trials throughout training, we might be more

successful in detecting potentiation. Miller and Shettleworth went on to suggest that normal associative processes take over later in training, so that overshadowing is likely to be observed. It again may be suggested that if we were to provide extended training, we might be more likely to observe overshadowing in the isosceles pool. There was some variation in the length of training in these experiments: In Experiment 1 testing occurred after 16 trials, and in Experiment 2, after 21. We found no difference in the results, but maybe we would need a wider variation in the number of training trials.

The fact that no evidence of overshadowing of geometric cues by the beacon was found in the triangular pool leads to the suggestion that the geometric cues of the triangle were more salient than those in the trapezium, and also more salient than the beacon. This suggestion was not supported by the results of Experiment 3. Following training with the beacon in the pool, the beacon was placed in another area of the pool, so as to test which cue the participants would use to locate the platform, the beacon or the geometric cues. The participants showed a strong preference for the beacon over the geometric cues in both pools, suggesting that the beacon was more salient than the geometric cues. This was true for both the trapezium and the triangle.

Although overshadowing of geometric cues in the trapezium by a nongeometric cue is not consistent with the notion of a geometric module (Cheng, 1986), the absence of overshadowing in the triangle by the more salient beacon suggests that associative-learning models (e.g., Pearce, 1994; Rescorla & Wagner, 1972) might not fully explain cue competition within the spatial domain. Hamilton, Rosenfelt, and Whishaw (2004) demonstrated that rats would use cues sequentially in navigating to a platform in a water maze: First they would use distal landmarks to calculate the initial heading directions, and later in the swim path would use a beacon to modify their final approach to the platform. Hamilton, Johnson, Redhead, and Verney (2009) reported eyetracking data suggesting that human participants use a similar two-stage process to locate a platform in a virtual water maze. If participants do use cues sequentially, it might be predicted that there would be little cue competition; they could learn about the geometric cues to provide the initial trajectory, and about the beacon to provide information on approach.

Such a navigational strategy might explain why overshadowing was obtained in the trapezium but not in the triangle, since the geometric cues of the trapezium were shown to be less salient than those in the triangle in the training trials of Experiment 1. Even though the geometric cues around the platform might be similar in the trapezium and the triangle, the apex of the triangle might have provided a particularly discriminable initial orienting cue. In the absence of such an orienting cue in the trapezium, participants might simply scan the pool until they see the beacon. Such a strategy would not require participants to discriminate between corners in the trapezium, and thus, when tested without the beacon, they would be unable to identify the platform corner.

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