Within-compound associations explain potentiation and failure to overshadow learning based on geometry by discrete landmarks

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Abstract

In three experiments, rats were trained to locate a submerged platform in one of the base corners of a triangular arena above each of which was suspended one of two distinctive landmarks. In Experiment 1, it was established that these landmarks differed in their salience by the differential control they gained over behavior after being trained in compound with geometric cues. In Experiment 2, it was shown that locating the platform beneath the less salient landmark potentiated learning based on geometry compared with rats in a control group for which landmarks provided ambiguous information about the location of the platform. The presence of the more salient landmark above the platform for another group of animals appeared to have no effect on learning based on geometry. Experiment 3 established that these landmark and geometry cues entered into within-compound associations during compound training. We argue that these within-compound associations can account for the potentiation seen in Experiment 2, as well as previous failures to demonstrate overshadowing of geometric cues. We also suggest that these within-compound associations need not be of different magnitudes, despite the different effects of each of the landmarks on learning based on geometry seen in Experiment 2. Instead, within-compound associations appear to mitigate the overshadowing effects that traditional theories of associative learning would predict.

KEYWORDS: Cue competition, spatial learning, within-compound association, water maze, geometry

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Author note

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When two or more cues signal the same outcome, theories of associative learning most commonly predict that learning based on one of the cues will restrict learning based on the others (e.g., Pearce, 1994; Rescorla & Wagner, 1972). Although these theories of associative learning have been applied to conditions under which Pavlovian conditioning progresses, they do not specify the type of learning that the theory can explain, and are therefore considered to constitute general learning rules. Spatial learning might therefore be considered to follow the same general rules as Pavlovian conditioning. Examples of associative phenomena, such as pre-exposure effects, latent inhibition, and cue competition effects, such as overshadowing and blocking, have all been demonstrated in experiments in which an animal has navigate to the location of a hidden goal (e.g., Diez-Chamizo, Sterio, & Mackintosh, 1985; Prados, Redhead, & Pearce, 1999; Roberts & Pearce, 1999, review in Chamizo, 2003).

Although there are demonstrations of cue competition in spatial learning, there are circumstances under which failure to demonstrate cue competition is common. The best-documented example of such a case is when an animal has to learn the location of a hidden goal with reference to the shape of the environment. Many studies have demonstrated the ability of a variety of animals to use the geometric properties of the environment for navigation; examples include rats (e.g., Cheng, 1986), mice (e.g., Fellini, Schachner, & Morellini, 2006), birds (e.g., Vallortigara, Zanforlin, & Pasti, 1990), fish (e.g., Sovrano, Bisazza, & Vallortigara, 2002), monkeys (e.g., Gouteux, Thinus-Blanc, & Vauclair, 2001), and humans (e.g., Hermer & Spelke, 1996; Ratliff & Newcombe, 2005). When cues in addition to the geometry also indicate the goal’s location we might suppose, from the foregoing discussion about the associative nature of spatial learning, that these cues will restrict the amount learned about the geometry. However, a number of studies using a variety of species have failed to provide a consistent set of results when the cues trained in concert with geometric cues are of a non-geometric nature. Non-geometric cues have been previously defined as those cues that are not based on geometric relationships between the shape of the environment and the location of the goal, with examples including featural information from surfaces, such as wall color, and discrete objects within the environment. Often there was no evidence that additional non-geometric cues could restrict learning based on geometry (Hayward, McGregor, Good, & Pearce, 2003; Hayward, Good, & Pearce, 2004; McGregor, Horne, Esber, & Pearce, 2009; Pearce, Ward-Robinson, Good, Fussell, &Aydin, 2001; Wall, Botly, Black, & Shettleworth, 2004). Such evidence has been taken to support the notion that animals formed a representation of environmental geometry in a dedicated module that was impervious to the effects of learning based on non-geometric features (Cheng, 1986; Gallistel, 1990).

However, in some studies, when both the geometry of the arena and the color of its walls indicated the location of the goal, learning based on the geometry was disrupted by concurrent learning based on the wall color (Cole, Gibson, Pollack, & Yates, 2011; Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Pearce, Graham, Good, Jones, & McGregor, 2006). McGregor et al. (2009) suggested that non-geometric cues of this type might be integrated into a representation of geometry in a way not possible for discrete landmarks, although they argued such a proposal would lay open to question the validity of a purely geometric module for spatial learning. More recently, however, some studies have revealed evidence of the ability of discrete landmarks to compete for control over behavior with geometric cues (Horne & Pearce, 2009a; Kosaki, Austen, & McGregor, in press). Kosaki et al.’s results were particularly important because they identified the conditions under which overshadowing of geometry by landmarks should occur. In their Experiment 2 they trained rats to locate a platform in one of the two acute corners of a rhombus shaped pool. In addition to the geometric cues provided by the pool's shape, a landmark was always suspended over the platform, but not over the opposite acute corner. Thus, the landmark was a more valid predictor of the platform's location than the geometry. Another group was trained in a similar way but with the platform always located in one of the two obtuse corners. In a test trial the landmark and platform were removed from the pool and the time spent searching for the platform in the different corners of the pool was recorded. The performances of these overshadowing groups were compared with those of two control groups, one trained to locate the platform in one of the two acute corners and the other trained to one of the two obtuse corners. These control groups were trained in a similar way to their respective overshadowing groups but with a landmark suspended over each of the four corners of the pool. The control groups were expected to learn the significance of the geometric properties of the corner in which the platform was located to a greater extent than the overshadowing groups, for which the landmark was a more valid cue for locating the platform. The higher validity of the landmark resulted in overshadowing regardless of the angle of the corner. In a further experiment, Kosaki et al. controlled for differences in the relative validities of the landmarks and geometry between the overshadowing and control groups, and showed that the landmarks were only able to overshadow geometry for those animals trained to locate the platform in the obtuse corner, which they argued was of a lower salience than the acute corner. Therefore, the relative salience of the landmark cues in compound with the geometry is an important factor in determining the extent to which overshadowing of geometry can occur, in addition to differences in the relative validities of landmarks and geometry.

Although differences in relative validity and salience may offer an explanation for the frequent lack of overshadowing or blocking of geometry by landmarks, these difference are less able to explain the observation that learning based on non-geometric cues can enhance performance based on geometry (Cole et al., 2011; Graham, Good, McGregor, & Pearce, 2006, Horne & Pearce 2011; Pearce et al. 2006). This improvement in learning about one cue when trained in the presence of another cue is known as potentiation, and such an effect contradicts those theories of associative learning that utilize a global error term to predict that cues compete for control over behavior. As such, understanding the conditions under which potentiation occurs may allow us to determine the generality of associative learning principles with respect to spatial learning.

One theory put forward to explain these potentiation results is that of within-compound associations. Pearce et al. (2006) argued that during water maze training with a compound of geometric and non-geometric cues, the non-geometric cue entered not only into a direct association with the platform, but also into an association with the geometric cue with which it was paired. When animals were then tested in the absence of the platform and the non-geometric cue, the presence of the geometric cue associated with the platform should activate a memory of the non-geometric cue with which it was paired during training. This evokes a representation of the association between the non-geometric cue and the platform, which should enhance responding to the geometrically correct location. If the within-compound association is able to evoke a representation of the non-geometric cue, then any overshadowing of the geometry by this non-geometric cue may be counteracted by the boost in performance afforded through the within-compound association. Such an explanation can account for the lack of overshadowing of geometry by non-geometric cues in a variety of studies (e.g., Hayward et al., 2003; McGregor et al., 2009; Pearce et al., 2001). If the evoked representation of the non-geometric cue is particularly strong, then any overshadowing may be more than compensated for by this boost in performance, resulting in enhanced responding to the geometric cues (i.e., potentiation).

Direct evidence of the existence of these within-compound associations comes from an experiment by Horne and Pearce (2009b) in which rats were trained to locate a platform in a pool with reference to cues provided by its distinctive shape in addition to non-geometric cues provided by the colors of the arena's walls. Following training with reference only to the wall colors, during which the value of the wall colors was reversed, the rats lost their discrimination of the correct and incorrect geometric corners when tested with only the distinctive shape. Rats in a control group that received training with the wall colors that was consistent with their original training showed no such loss of discrimination. Rhodes, Creighton, Killcross, Good, and Honey (2009) extended the generality of this finding to an appetitive task. In their analysis of the circumstances under which potentiation and overshadowing of geometry learning occurred, Horne and Pearce (2011) proposed that the extent to which the non-geometric cue should overshadow the geometry is modulated by its salience. A salient non-geometric cue should overshadow geometry strongly, such that the within-compound association cannot compensate for this effect, which results in an overall overshadowing effect. Conversely, with a less salient non-geometric cue, the overshadowing effect should be weaker, such that it may be more than compensated for by the indirect association between the non-geometric cue and the platform, resulting in potentiation being observed. Although their results were consistent with an explanation based on within-compound associations, Horne and Pearce (2011) did not assess directly the extent to which within-compound associations were responsible for such an effect.

The purpose of the current article is to determine whether the frequently observed failure of discrete landmarks to overshadow learning based on geometry is the result of within-compound associations between the landmark and the geometry. We sought to test the generality of Horne and Pearce's (2011) analysis of the circumstances in which overshadowing and potentiation will occur to similar situations with discrete landmarks. Accordingly, in Experiment 1 we examined the relative saliences of two discrete landmarks. In Experiment 2 we predicted that overshadowing would be less apparent for the group trained with the landmark established in Experiment 1 as the less salient cue. The results of Experiment 2 confirmed that the less salient landmark potentiated geometry, but that, as McGregor et al. (2009) found after using a similar landmark, animals trained with the more salient landmark showed neither overshadowing nor potentiation. In Experiment 3 we tested if within-compound associations were able to form between the landmark and geometric cues used in Experiments 1 and 2.

Experiment 1

When two cues are trained in compound to signal an outcome, the strength of the association formed between each cue and the outcome after a given number of trials is assumed to be proportional to the salience of the cues (Rescorla & Wagner, 1972). To assess the relative saliences of the two different landmarks, we compared the control they acquired after being trained, in conjunction with geometric cues, to indicate the location of the hidden platform. Rats were trained to locate a submerged platform in one of the two base corners of an isosceles triangular-shaped arena, with the base wall created by the curved wall of the circular water maze. The rats were additionally presented with two different landmarks, one placed directly over each of the two base corners of the triangle. Following this compound training a single test trial was given in which the two landmarks were presented in the absence of the geometric cues provided by the arena. Animals should discriminate between the two landmarks more readily when the more salient landmark indicates the location of the hidden platform.

Method

Subjects

The subjects were ten male Lister Hooded rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, Oxfordshire, England). They were approximately nine weeks old at the start of testing, were tested for a total of six weeks, and were not used in any other study before the experiment began. The animals were housed in pairs in cages in which they had continuous access to food and water. These cages were in a light-tight holding room on a 12 h light:dark cycle, with lights coming on at 8:00 am. The animals were always tested when the lights were on in their holding room, and at a similar time each day.

Apparatus

A white fiberglass Morris water maze, with a diameter of 2 m and a depth of 60 cm, was mounted on a wooden platform 40 cm above the floor. Each day, the water maze was filled to a depth of 30 cm with water (25 ± 2 °C) to which was added 500 ml of white opacifier (OP 303B; Rohm & Haas, Dewsbury, England). After testing, the pool was drained and cleaned along with all other apparatus in contact with animals. The pool was fully surrounded by an opaque grey curtain which prevented the animals being able to utilize any visual extra-maze cues. This curtain fell 25 cm from the rim of the water maze and extended from the ceiling to 25 cm beneath the top of the water maze. Suspended directly above the pool, at a height of 1 m above the top of the walls, was a white circular polyurethane sheet, 2 m in diameter. This artificial ceiling contained eight 45 W spotlights (each 22.5 cm in diameter) arranged in a circular array with a diameter of 1 m, centered within the circular artificial ceiling. These spotlights illuminated the pool throughout the experiment. A 30 cm diameter circular hole in the center of this array allowed a wide-angled video camera, which was set 5 cm above the artificial ceiling, to relay an image of the water maze to a monitor, recording equipment, and a PC in the north-east corner of the room. Tracking software (EthoVision, Noldus, NL) was used to record the rats' swim paths during the experiment. The pool, curtains and artificial ceiling were situated in the approximate center of a room with dimensions 4.65 x 3.90 x 2.25 m high, with a door situated in the north 3.90 m wall. This room was illuminated by two strip lights (each 35 W), one attached to each of the long walls of the experimental room. These strip lights were 150 cm long and affixed 68 cm horizontally above, and parallel to, the floor.

To create a triangular-shaped arena within the circular water maze, two polyurethane boards, 180 cm in length, 59 cm high and 0.5 cm thick, were attached to square lengths of aluminium tubing (1.2 cm square cross-section), which extended 10 cm further than either end of the polyurethane boards in order to suspend the boards within the pool by resting the aluminium tubing on the top edge of the water maze. Two such boards were used to create a triangular arena, the third wall being formed from the curved wall of the circular water maze. In the landmark test at the end of training there were no polyurethane walls present and the entire circular water maze was used with the landmarks presented in diametrically opposite quadrants of the pool. The landmarks were suspended from thin white wires attached to the artificial ceiling such that the distance from the center of each landmark to the surface of the pool was 30 cm. These two landmarks were placed on an imaginary line that bisected the arena in a south-west to north-east direction. One landmark was suspended 63 cm from the south-west edge of the water maze and the other 63 cm from the north-east edge.

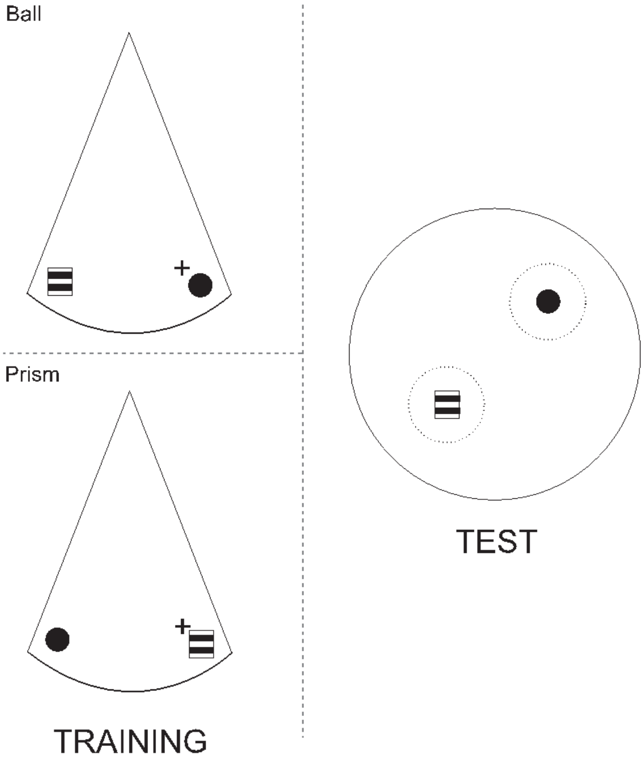

Figure 1: Procedure used in Experiment 1 to determine relative saliences of the ball and prism landmarks when trained in compound with geometry. Filled black circles represent the ball landmark, horizontally striped squares represent the prism landmark, ‘+’ signs denote the landmark under which the hidden escape platform is located, and the dotted areas denote the areas in which we query exploration times during the extinction phases.

During training, a circular Perspex platform, with diameter 10 cm, was submerged at a depth of 2 cm below the surface of the water. The surface of this platform consisted of concentric circular grooves to increase traction. Two landmarks were used in this study. One was a dense sponge ball, 9.5 cm in diameter, painted matte black. The other was a hollow octagonal prism, the inside and outside of which was painted white. The eight walls forming this prism were 9.5 cm tall, 4 cm wide, and 1 cm thick. A 5 mm-thick grey Perspex lid covered the top of the prism. The bottom of the prism remained open, with the exposed edges painted black. Two black stripes were painted horizontally around the center of the prism, each being

2.5 cm wide, with a 1 cm gap separating them. Both the ball and prism landmarks were suspended such that the center of each was 30 cm above the surface of the water. This was achieved by attaching each landmark to 8 mm diameter Perspex rods, which were attached horizontally to the aluminium tubing suspending the polyurethane walls. The landmarks were placed at a distance of 25 cm from the base corners of the triangular arena that were made up from one straight wall and the curved base, on a line bisecting each corner. Depending on the training condition, the platform was placed directly underneath one, or other, of the landmarks. A schematic of the arenas used for each phase of this experiment can be seen in Figure 1.

Procedure

At the beginning of the experiment the ten animals were split randomly into two equal groups based on the landmark beneath which the platform was located during compound training. Half of the animals always found the platform underneath the ball landmark (Group Ball), with the other half locating it underneath the prism landmark (Group Prism). It was not possible to fully counterbalance the corners in which the rats located the platform, so within each of the two groups, three animals were trained to find the hidden platform in one of the base corners of the triangle, with the straight wall to the left of the curved wall, with the other two animals in each group finding the hidden platform in the other base corner, which had the opposite arrangement of walls (see Figure 1). Across the two landmark groups, equal numbers of animals found the platform in each of the two base corners of the arena. The non-reinforced landmark was always present in the base corner that did not contain the platform during training. The platform could be located using the distinct shape of the arena, and also by discriminating between the landmarks.

At the beginning of a session, rats were transported in squads of five to the experimental room in separate compartments of a light-tight carrying box. This box was placed onto a table in the north-west corner of the room. During training a rat was removed from the carrying box and placed into the water maze at the center of one of the three walls, facing the wall. The rat swam until it located the platform, after which it was allowed to remain on the platform for 20 s until it was removed from the pool by the experimenter, dried, and returned to the carrying box for an inter-trial interval of approximately 5 minutes. If an animal failed to locate the platform within 60 s it was guided there by the experimenter. No training was required for the rat to follow the experimenter's hand. Animals received four trials per session, over the course of 18 sessions, with a single session per day. Throughout training, the curtains were drawn around the pool such that the animals were unable to use any cues beyond the curtain to locate the platform. Release points were counterbalanced such that for the four trials of a session, each release point (one from each wall, three in total) was used once, with the final release point being chosen randomly from the three options, with the stipulation that across three sessions each release point was used an equal number of times. The orientation of the arena was varied between trials, with each of the four possibilities (i.e., the apex of the arena pointing towards each cardinal compass point) used in each session, in a pseudorandom order. On session 19, the animals were given a single landmark extinction trial in the open circular pool, with both landmarks present, but with no platform present. For half of the animals, the prism landmark was in the north-east quadrant of the pool and the ball was in the south-west quadrant; this was reversed for the other half of the animals. Three of the five animals in each group experienced the correct landmark in the north-east quadrant of the pool, with the other two animals finding the correct landmark in the south-west. Animals were released from the center of the pool, equidistant from the two hanging landmarks, facing in a south-easterly direction. The time each animal spent searching for the platform underneath each landmark in circular zones, 50 cm in diameter and centered on each landmark, was recorded using EthoVision.

Results and Discussion

The time taken to locate the platform during training differed little between the two groups (Figure 2). A repeated measures Analysis of Variance (ANOVA) of Session x Landmark showed a significant main effect of session, $F(17, 136) = 50$, $p < .001$, with latencies to the hidden platform decreasing over the course of training. There was no main effect of landmark ($F < 1$). There was a significant interaction between session and landmark, $F(17, 136) = 2.0$, $p = .014$. Despite this interaction, on no sessions was there a significant difference in the time taken to find the hidden platform between animals trained with the ball correct and those trained with the prism correct, *F*s < 3.5, *p*s > .1.

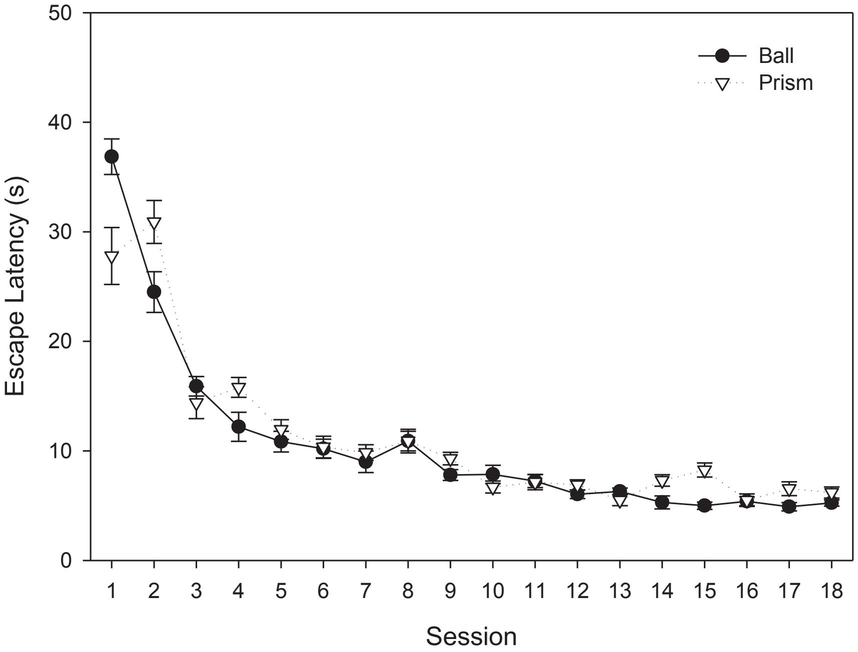

Figure 2: Escape latency data for the training stage, split by correct landmark. Error bars represent ± the Standard Error of the Mean.

Despite few differences between the two groups during training, Figure 3, which shows the results of the landmark test trial, reveals a greater preference for the landmark reinforced during training for Group Ball compared with Group Prism. A repeated measures ANOVA of Zone (landmark indicating the platform's presence during training, or the other landmark) x

Landmark (ball or prism indicating the presence of the platform during training) confirmed this observation by revealing an interaction between these main effects, $F(1, 8) = 5.6$, $p = .046$. Analysis of simple main effects showed that both groups discriminated between the correct and incorrect zones, $Fs(1, 8) > 9.4$, $ps < .02$. However, Group Ball spent significantly more time in the correct zone than Group Prism, $F(1, 8) = 6.8$, $p = .03$. Groups Ball and Prism spent an equal amount of time underneath the incorrect landmark, $F(1, 8) = 4.6$, $p = .07$. There were also main effects of zone, $F(1, 8) = 42$, $p < .001$, and landmark, $F(1, 8) = 7.2$, $p = .028$, with more time spent in the correct zone than the incorrect zone, and more time spent exploring landmarks by Group Ball than by Group Prism.

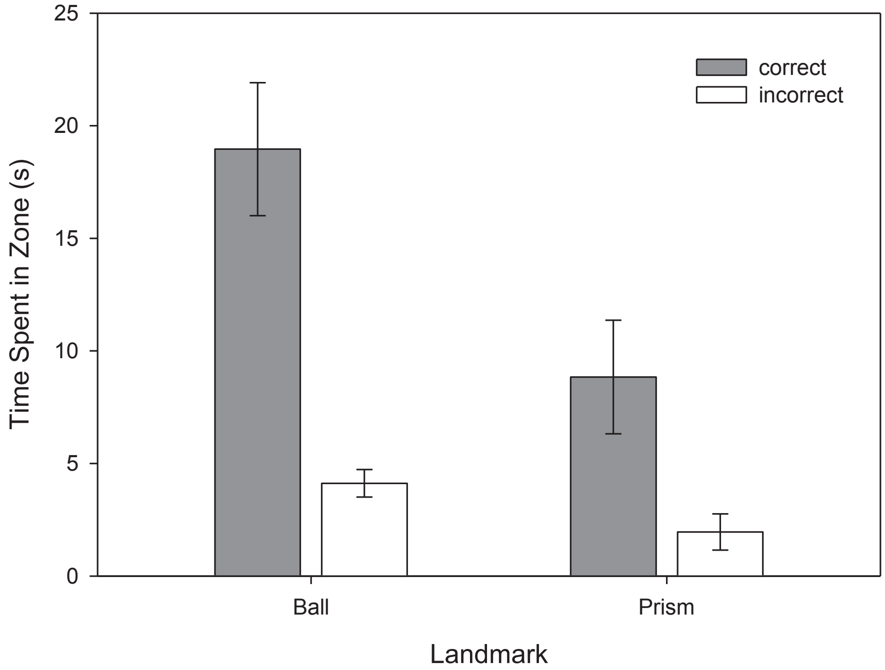

Figure 3: Time spent in the correct and incorrect zones in the landmark extinction trial, split by correct landmark during training. Error bars represent ± the Standard Error of the Mean.

The differences between the two groups in the landmark test suggest that those animals trained with the platform beneath the ball throughout training learned significantly more about the association between the ball and the platform than those trained with the prism learned about the association between the prism and the platform. This result reflects a difference in salience between the two cues, with more being learned about the more salient cue. We can infer from this that the ball landmark is relatively more salient than the prism landmark, when both are trained in compound with equivalent geometry cues. It is difficult to identify the reason for the difference in salience between the landmarks, although one possible reason is that the similarity between the features of the prism and those of the rest of the apparatus, such as the walls of the arena and the surrounding curtains, was greater than the similarity between the ball and the apparatus. As such, it is possible that the ball was a more intense stimulus than the prism.

Horne and Pearce (2011) found that a landmark of lower salience, when paired with geometry, should enhance geometry learning. If their findings also apply to a similar situation involving discrete landmarks, then we might predict that the prism used in Experiment 1 will be more likely to counteract overshadowing of geometry learning than the ball. Before considering the possible reasons for such an effect, we present Experiment 2, in which we tested the differential effect of the two discrete landmarks on geometry learning.

Experiment 2

Horne and Pearce (2011) attempted to examine the circumstances under which non-geometric panels attached to the walls of a rectangular arena potentiated or overshadowed geometry. They found that non-geometric cues of relatively low salience enhanced geometry learning, whereas those of high salience restricted the amount learned about geometry. Horne and Pearce (2011) appealed to their previous demonstration (Horne & Pearce, 2009b) of the presence of within-compound associations between the colors of the walls near the location of a submerged platform and the geometry of the arena to explain their potentiation results, although the nature of both the geometric and non-geometric cues differed between their studies.

In order to provide strong evidence for the role of within-compound associations in both failure to observe overshadowing, and potentiation, of geometry by non-geometric cues, it needs to be demonstrated that these cue competition effects and the presence of within-compound associations occur under the same circumstances. Therefore, in Experiment 2 we sought to examine how the differently salient landmarks from Experiment 1 would affect learning based on geometry. Given that a number of previous failures to demonstrate overshadowing of geometry have involved a triangular pool, these same geometric cues were used in Experiment 2. We trained rats to locate a platform hidden in one of the two base corners of the arena. In addition, for half of the animals in the experimental condition the ball landmark indicated the platform's position (with the prism over the other base corner) while the remainder received training with the prism indicating the platform's position, with the ball over the other base corner. Two further groups were trained to act as a control against which the experimental groups' performances could be compared. The platform was also hidden in one of the two base corners for these control groups, but the two landmarks over the base corners of the pool were identical. For half of the animals two balls were used, and for the remainder there were two prisms over the base corners (see Figure 4). During a test trial at the end of training, in which the landmarks and platform were removed for all of the animals, rats in these control groups were expected to have learned to rely on the geometry of the arena to locate the platform to a greater extent than those animals in the experimental groups, since the landmarks provided ambiguous information. The inclusion of these ambiguous landmark cues for the control groups allows us to control for generalisation decrement. In this regard, any differences between the control and experimental groups could not be explained by a greater difference between training and testing conditions for one group over the other, because landmarks were removed for all animals.

Standard models of associative learning would predict that the presence of the discriminable landmark cues for the experimental groups should restrict the amount learned about geometry. Therefore, the control groups, which can learn the position of the goal in reference only to the geometry, should demonstrate better geometry discrimination during the test trial, in which the non-geometric information is removed, than the experimental groups. However, given previous failures to observe overshadowing with similar geometric cues, and the demonstration by Horne and Pearce (2011) that the salience of the non-geometric cue alters the extent of overshadowing, it is difficult to make a prediction on the degree of cue competition we should observe here. One thing we can expect is that our lower salience landmark should overshadow geometry to a lesser extent than the higher salience landmark. In addition, the presence of within-compound associations may counteract any overshadowing effect observed.

Method

Subjects and Apparatus

Twenty experimentally naïve male Lister Hooded rats from the same stock as in Experiment 1 were used in this study. They were divided randomly in to four equal groups at the beginning of the experiment. Other details were the same as for Experiment 1. The apparatus was the same as in Experiment 1 with the exception that animals in the control groups received training with two identical landmarks over the base corners of the triangular pool. Duplicates of the ball and prism landmarks from Experiment 1 were created for these groups.

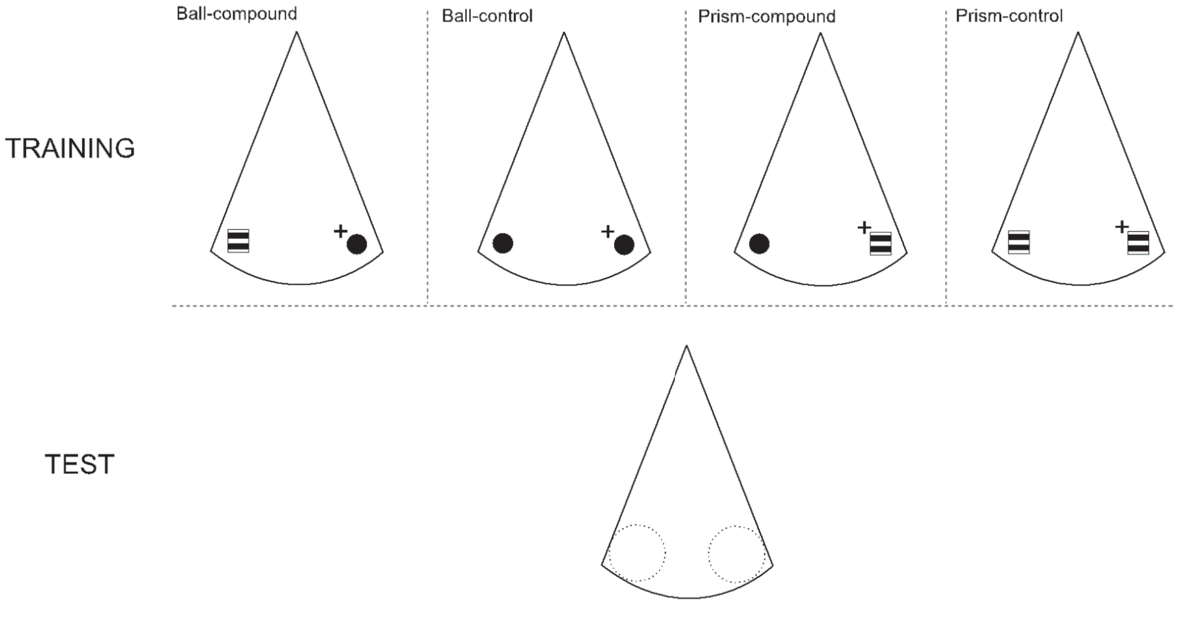

Figure 4: Standard overshadowing procedure used, in this case, to find potentiation of geometry learning by the presence of a distinct landmark cue, in Experiment 2. Filled black circles represent the ball landmark, horizontally striped rectangles represent the prism landmark, '+' signs denote the landmark under which the hidden escape platform is located, and the dotted areas denote the areas in which we query exploration times during the extinction phases.

Procedure

Animals were assigned randomly to one of four groups at the start of the experiment. Groups Ball-compound and Prism-compound received identical training to the Ball and Prism groups from Experiment 1. The other two groups of animals, Ball-control and Prism-control, were trained in a very similar manner, with the exception that instead of two discriminable landmarks they were presented with identical landmarks over each base corner, such that an accurate determination of the position of the hidden platform must be based on the shape of the arena alone. These control groups were not expected to differ in the extent to which they learned about the significance of the geometric cues for locating the platform, but their data are presented separately for clarity. Other details are as described for Experiment 1.

Following 18 sessions of training, all animals underwent a single geometry extinction trial. This took place in the same triangular arena as during training, with the apex facing south. There were no platforms or landmarks present during this extinction trial and, as during training, the curtains were drawn around the pool. Each animal was placed in the center of the water maze, facing south, and were allowed 60 s to search the arena. The animal was then removed from the north of the pool, dried, and returned to its carrying box. The time each animal spent searching for the platform in two 30 cm-diameter circular zones was recorded using EthoVision. These zones were located in the base corners of the triangle centered on the potential location of the platform during training.

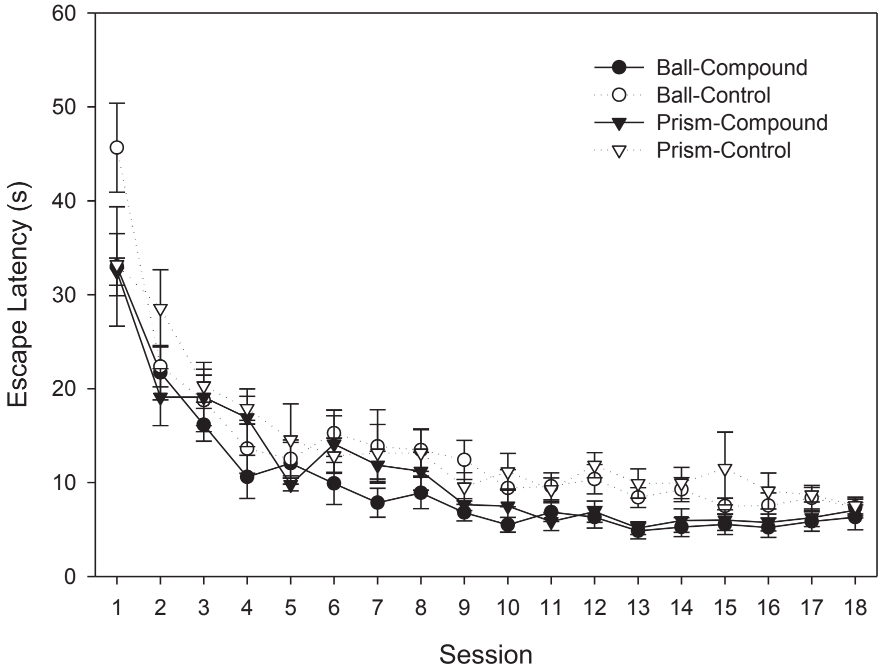

Figure 5: Escape latency data for the training stage, split by condition and landmark. Error bars represent ± the Standard Error of the Mean.

Results and Discussion

Latency to find the escape platform was recorded for each training trial. The mean escape latencies for each session, split by condition and landmark, can be seen in Figure 5. A repeated measures ANOVA of Session x Condition (compound or control) x Landmark (ball or prism) showed a significant main effect of session, $F(17, 272) = 68.70$, $p < .001$, with a decrease in latencies over sessions. There was also a significant main effect of condition, $F(1, 16) = 6.75$, $p = .019$, with compound-trained animals showing significantly lower latencies than control animals. There were no other main effects, and no interactions between any variables, *F*s < 1.7, *p*s > .05.

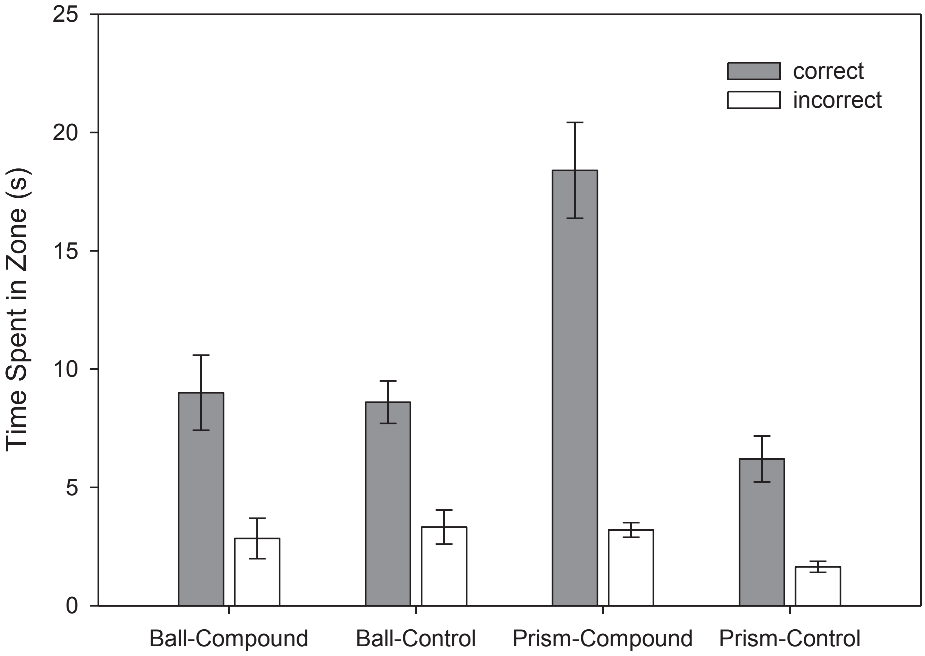

Figure 6: Time spent in the correct and incorrect corners in the geometry extinction trial, split by condition and correct landmark during training. Error bars represent ± the Standard Error of the Mean.

The results from the test trial in the triangle can be seen in Figure 6. While all groups spent more time in the zone in the base corner that had contained the platform during training than that which did not, this discrimination was strongest in the Prism-compound group. It can be seen that the Prism-compound group discriminated between correct and incorrect corners more than the Prism-control group. Although there was no potentiation of geometry learning for the Ball-compound group, neither was there evidence that the ball had overshadowed learning about geometry for this group, when comparing its performance against that of the Ball-control group. These observations were confirmed by the results of a repeated measures Condition x Landmark x Zone ANOVA which revealed a three-way interaction between these main effects, $F(1, 16) = 10.92$, $p = .004$. Analysis of simple main effects showed that all four groups spent significantly more time in the correct zone than in the incorrect zone (*p*s< .01). They also showed that group Prism-compound spent significantly more time in the correct zone than group Ball-compound, *F*(1, 16) = 21.10, *p* < .001, or group Prism-control, *F*(1, 16) = 35.54, *p* < .001. There were no significant differences between the times any groups spent in the incorrect zone, *p*s> .05. The ANOVA also showed significant main effects of zone and condition, and significant interactions between zone and condition, zone and landmark, and condition and landmark, *F*s(1, 16) > 7.90, *p*s < .02. There was no main effect of landmark, *F*(1, 16) = 3.0, *p* = .10.

The results are the first to show potentiation of geometry by a discrete landmark. They also demonstrate that this potentiation is only evident when the landmark is of relatively low salience. The results are in line with those of Horne and Pearce (2011), who also showed potentiation of geometry learning by their least salient landmark. It may have been expected that training geometry in compound with the higher salience ball landmark would result in overshadowing of geometry learning, based on Horne and Pearce's (2011) similar design. However, their analysis of the causes of potentiation and overshadowing, as the result of within-compound associations counteracting different levels of overshadowing, provides a suitable explanation for such an apparent lack of overshadowing. Before accepting such an explanation, however, one other cause of the enhancement of geometry learning observed should be ruled out. Although our results are difficult to explain by appealing to traditional associative models, we may not have to accept that the superior performance of the Prism-compound animals was the result of potentiation as argued by Horne and Pearce (2011). From examination of the training results it is apparent that the compound-trained groups located the platform more rapidly than the control groups. If time taken to locate the platform is an indication of the extent to which learning has occurred then it may be argued that it is no surprise that compound-trained animals were superior in their discrimination of the correct and incorrect geometric corners of the pool in the geometry test. It should be noted, however, that although both Ball-compound and Prism-compound groups located the platform faster than the control groups, and as fast as each other, only the Prism-compound group showed any evidence that geometry learning was enhanced.

Therefore, the results of Experiment 2 are consistent with Horne and Pearce's (2011) demonstration of the circumstances in which potentiation of geometry occurs, and also provide the first clear demonstration of potentiation of geometry learning by discrete landmarks. We can apply this same analysis to explain how within-compound associations between the more salient ball landmark and geometry were able to counteract any overshadowing of geometry. Although Horne and Pearce's (2011) results are consistent with the within-compound association interpretation they provided, they did not measure the presence of the within-compound associations between their panel cues and the geometry of their arena. Accordingly, the purpose of Experiment 3 was to test for the presence of within-compound associations between our cues.

Experiment 3

In order to determine whether within-compound associations are a process by which potentiation and absence of overshadowing may occur in spatial learning, it is first necessary to demonstrate their presence using the same cues with which these effects are observed. Although within-compound associations have previously been shown in both an aversive water maze task (Horne & Pearce, 2009b) and an appetitive dry-maze task (Rhodes et al., 2009), their presence is unreported in a spatial task using the distinct compound of landmark and geometry cues that resulted in the potentiation observed in Experiment 2. It is important to note here that although within-compound associations have been implicated in the presence of potentiation, and absence of overshadowing, they have never been shown to exist between the cues most commonly used when observing these effects, that is spatially separate geometry and landmark cues.

Horne and Pearce (2009b) conducted an experiment that in part owed its design to a similar study by Durlach and Rescorla (1980), in which rats underwent flavor-odor aversion conditioning. Durlach and Rescorla observed that learning the relationship between the presentation of an odor and lithium chloride-induced illness was enhanced by the simultaneous presentation of a salient flavor, and supposed that this effect was the result of a within-compound association between the flavor and the odor. In the absence of the flavor rats learned little about the odor. To demonstrate the presence of the within-compound associations, following compound conditioning with the odor and flavor, they devalued one element of the compound, the flavor, by repeatedly presenting it in extinction. Subsequent testing with the odor alone demonstrated a reduced aversion to the odor than the same group of animals showed to a different odor that had previously been paired with a flavor, but for which the flavor had not undergone extinction. Similarly, Horne and Pearce (2009b) showed that, following training in a kite-shaped arena with both the geometry of the arena and the colors of the walls indicating the location of the platform, revaluation of the wall colors altered the rats' response to the presentation of the geometric cues in the absence of the wall colors. In the same geometry test, a similarly trained group of rats that had not undergone revaluation of the wall colors, continued to demonstrate a preference for the corner of the kite that had contained the platform during training. The explanation for both Durlach and Rescorla's and Horne and Pearce's results was that in the final test, experiencing the cue with which the revalued cue was paired during compound training activated the memory for the revalued cue via the within-compound association. This memory failed to evoke a conditioned response, however, because the revaluation resulted in the extinction of response to the revalued cue. Any remaining response was the result of a direct association between the odor and illness in Durlach and Rescorla's case, and between the geometry and the platform in Horne and Pearce's.

The purpose of Experiment 3 was to determine whether the same revaluation effect could be observed on the rats' response to geometric cues, having previously experienced geometric cues in compound with landmark cues. Should the observations made in Experiment 2 be the result of within-compound associations between the geometry and landmark, then reducing the value of the landmark cue should reduce the rats' response to the corner of the pool associated with the platform during training, shown by a reduced discrimination between geometric cues. We predicted that these within-compound associations would be shown to be present for all animals, regardless of the landmark beneath which the platform was located. Such a result would provide an explanation both for the potentiation of geometry by the prism seen in Experiment 2, and also for the lack of overshadowing of geometry by the ball in the same experiment. The role of such associations in failure to observe overshadowing, and observation of potentiation, has been a matter of conjecture previously (Horne & Pearce, 2011;

McGregor et al., 2009; Pearce et al., 2006) as the same cues have not been used to demonstrate both within-compound associations, and these cue competition effects.

The experiment followed a similar design to that of Horne and Pearce (2009b). Following compound training in the same environment as used in Experiment 2, the prism-trained and ball-trained animals were each split into two equal groups such that the performances of each group were matched (see Figure 7). One of each of these prism- and ball-trained groups then underwent further training with the landmark, but in the absence of the geometric cues that were present during compound training. These groups were trained consistently with their previous training from stage 1: on trials in which the landmark that previously indicated the location of the platform was present, the landmark continued to do so, while the previously unreinforced landmark was presented on other trials in the absence of the platform. The remaining animals were trained similarly, but with contingencies reversed: the previously reinforced landmark was presented on half the trials in extinction, while the previously unreinforced landmark was always presented with the platform beneath it, for the other half of the revaluation trials. For these inconsistently trained animals it was predicted that reversal training would result in a reduced discrimination between the base corners of the triangle when geometry alone was presented in a test trial at the end of the revaluation stage, compared with the consistently trained animals.

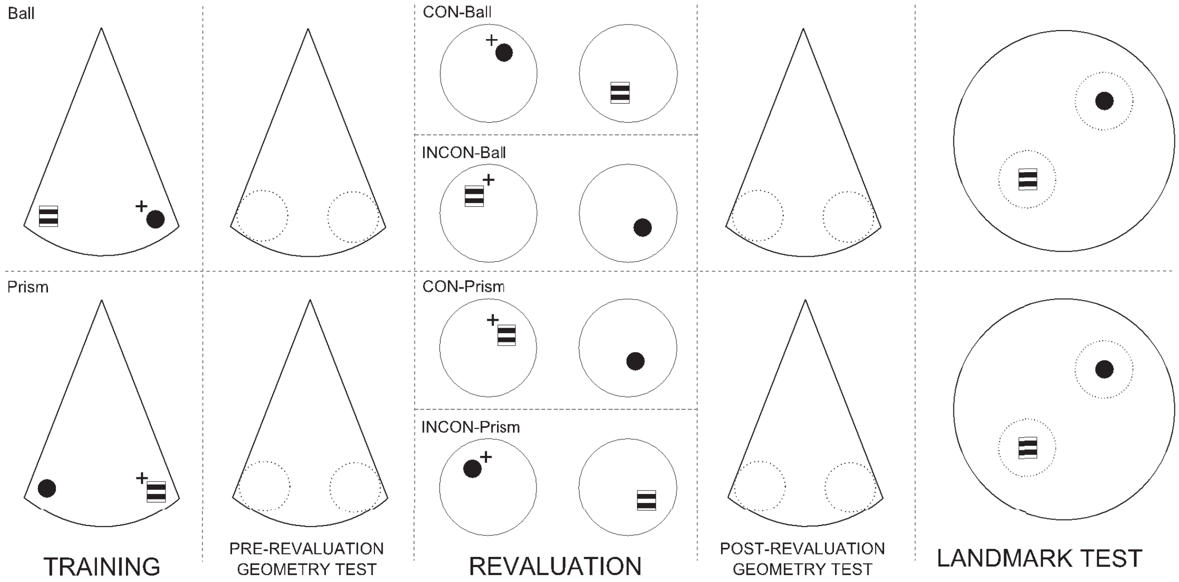

Figure 7: Procedure used for elucidating within-compound associations in Experiment 3. Filled black circles represent the ball landmark, horizontally striped squares represent the prism landmark, '+' signs denote the landmark under which the hidden escape platform is located, and the dotted areas denote the areas in which we query exploration times during the extinction phases.

In addition, Experiment 3 allowed us to examine the properties of any within-compound association formed between landmarks and geometry. Should a less salient landmark form a much stronger within-compound association with geometry than a more salient landmark, the results of Experiment 2 need not be explained by appealing to within-compound associations counteracting differential overshadowing effects, as suggested by Horne and Pearce (2011).

Instead, the stronger within-compound association could be assumed to allow a stronger representation of the non-geometric cue to be evoked from experience of the geometric cue. It is this stronger representation of the absent non-geometric cue that could result in potentiation of geometry learning. Should this be the case, then revaluation of the landmark following training to a compound of landmark and geometry cues should be more pronounced in the group trained with the landmark that produced greater potentiation. During the post-revaluation geometry test in the absence of the landmark cues, a stronger within-compound association should result in a more strongly evoked representation of the landmark cue. This representation should reduce the discrimination of geometry more than for the group that had formed a weaker within-compound association during compound training. As we have demonstrated that the less salient prism landmark potentiates geometry more strongly than the more salient ball landmark, we would expect a stronger revaluation effect for the prism, if within-compound association strength accounts for our previous results. Conversely, if the extent to which we observe potentiation is a result of differential overshadowing of geometry by landmark cues, then we would expect to see a similar revaluation effect, regardless of the identity of the correct landmark.

Method

Subjects and Apparatus

Twenty experimentally naïve male Lister Hooded rats (*Rattus norvegicus*) were the subjects in this study, from the same stock as those used in Experiments 1 and 2. They were divided randomly in to two equal groups at the beginning of the experiment, and were later sub-divided in to two further groups based on their performance at the end of stage 1 of training. Other details were the same as for Experiments 1 and 2. The apparatus was the same as in Experiment 1.

Procedure

Animals were split into two groups based on the identity of the landmark under which the platform was located, and were trained in an identical fashion to those in Experiment 1 for the first 18 sessions, with the landmarks and the geometry of the arena in compound predicting the location of the platform. All animals then underwent a single geometry extinction trial, as described in Experiment 2, on session 19 in order to determine a baseline performance for geometry learning prior to the effects of any revaluation. Using this pre-revaluation geometry test (which showed the animals' preference for a particular corner based on which corner was previously reinforced) combined with the data from the 18 training sessions, the animals from each landmark group were sub-divided equally into two very closely matched groups, creating four groups in total, split by landmark (Ball or Prism) and whether animals received revaluation that was consistent or inconsistent with their training contingency (CON or INCON): CON-Ball, CON-Prism, INCON-Ball, and INCON-Prism.

Immediately following the geometry extinction trial, rats in each group received revaluation training relevant to the condition into which they had been placed. For all animals the landmarks were presented in the circular water maze with the curtains drawn around it. The landmarks were suspended from wires, painted white, which were attached to hooks on the circular ceiling above the pool. Groups CON-Ball and CON-Prism received, per session, two trials in which the platform was placed under the landmark that was reinforced during stage 1 training. In the remaining two trials the landmark that did not signal the platform's location during stage 1 training was presented. In these trials, animals were required to swim in the pool for a duration of 60 s, in the presence of the landmark, but in the absence of the escape platform. Thus animals in the CON condition experienced direct reinforcement of the previously correct landmark, and direct extinction of the previously incorrect landmark. Groups INCON-Ball and INCON-Prism underwent similar revaluation treatment, but the reinforced landmark during stage 1 training was now presented in the absence of the platform, and the previously incorrect landmark was now presented with the platform beneath it. This treatment was intended to reverse stage 1 training regarding the location of the platform with respect to the identities of the landmarks. The revaluation stage lasted for five sessions, from session 20 to session 24. The rats were released from each of the four cardinal points of the pool once per session in a pre-determined random order. The landmarks could occupy any of twelve locations within the pool, chosen from 32 possible locations. The only stipulations on landmark position were that it should be no less than 28 cm from the center of the pool, no less than 40 cm from the edge of the pool, and not occupy the same quadrant of the pool for more than one trial per session.

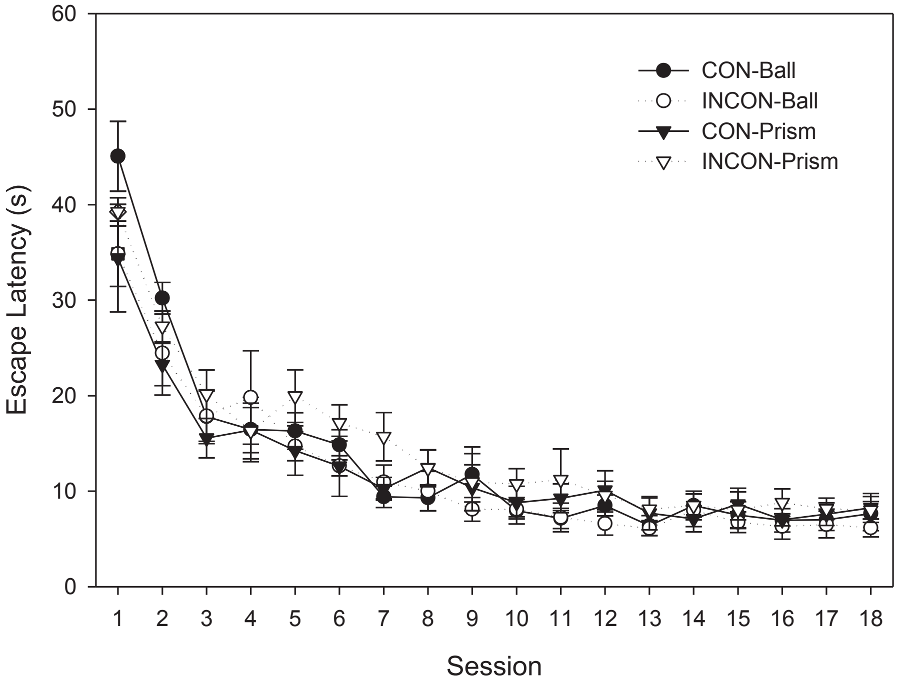

Figure 8: Escape latency data for the stage 1 training, split by revaluation and correct landmark. Error bars represent ± the Standard Error of the Mean.

Two extinction tests were presented following the conclusion of the revaluation stage, on sessions 25 and 26. The first was the critical post-revaluation geometry extinction test that was conducted in an identical fashion to the one conducted on session 19. Finally, a landmark extinction trial was presented, with both landmarks present but the platform absent. This test trial was conducted in an identical manner as the one described in Experiment 1 and was intended to provide a measure of the extent to which reversal learning had taken place during the revaluation stage for the INCON groups. A schematic diagram showing the order of the stages of the experiment is shown in Figure 7.

Results and Discussion

The time taken to find the hidden platform during stage 1 training was analysed using a repeated measures ANOVA of Session x Revaluation x Landmark. Animals were allocated to different conditions based on the results of the subsequent geometry extinction test, so it should be noted that to some extent the results are based on a post-hoc sub-division of animals, and as such, it was expected there would be no difference between conditions. The analysis showed a significant main effect of session, *F*(17, 272) = 91.18, *p* < .001, with latencies decreasing across sessions. There were no other significant main effects or interactions, *F*s ≤ 1.57, *p*s ≥ .178. These results are shown in Figure 8, and imply that all groups, regardless of condition or correct landmark, showed both the same level and rate of learning about the location of the hidden platform when trained with a compound of geometry and landmark cues.

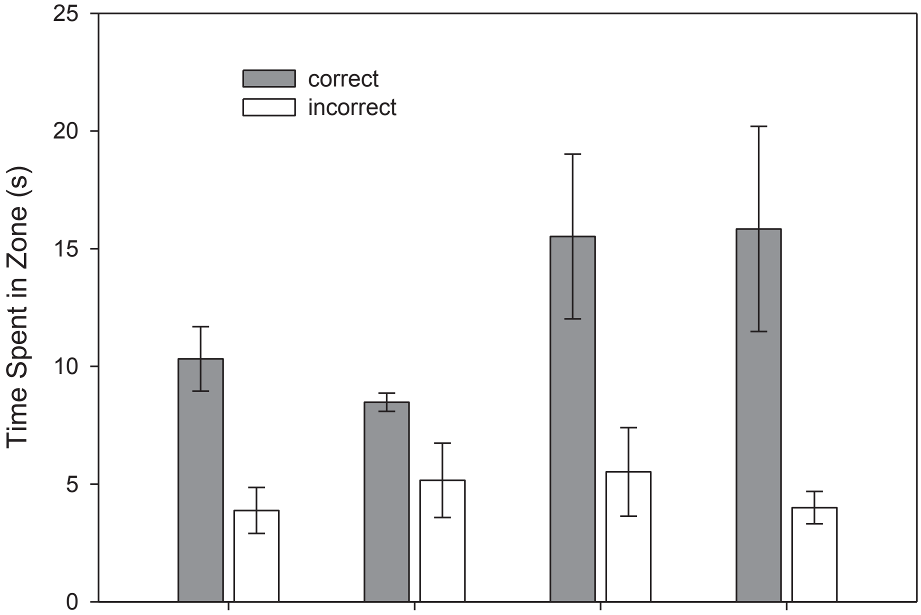

Figure 9: Time spent in the correct and incorrect corners in the pre-revaluation geometry test, split by revaluation and landmark. Error bars represent ± the Standard Error of the Mean.

Mean times spent in the correct and incorrect base corner zones during the first geometry extinction test are shown in Figure 9. A repeated measures ANOVA (Zone x Revaluation x Landmark) showed a significant main effect of zone, *F*(1, 16) = 18.17, *p* < .001, with more time spent in the correct zone than the incorrect zone. There was also a significant main effect of landmark, *F*(1, 16) = 6.43, *p* = .022, with more time being spent exploring the geometric cues by those animals trained with the prism landmark correct. This finding replicates Experiment 2, in which we observed potentiation of geometry learning by the presence of the prism landmark, but not when geometry was paired with the ball landmark. There were no other significant main effects, and no interactions between any other sets of variables, *F*s < 1.

For the revaluation stage, sessions consisted of both reinforced and non-reinforced trials. For the reinforced trials, learning about the landmark was measured using latency to find the platform (Figure 10). A repeated measures ANOVA (Session x Revaluation x Landmark) showed a significant main effect of session, *F*(4, 64) = 20.48, *p* < .001, with latencies to find the hidden platform showing a general decrease over sessions. There was also a significant main effect of revaluation, *F*(1, 16) = 7.27, *p* = .016, with those animals in group CON taking less time to find the hidden platform than those in group INCON. The interaction between session and revaluation variables approached significance, *F*(4, 46) = 2.33, *p* = .065, the simple main effects of which showed that animals in group CON found the platform significantly more quickly than those in INCON on session 1, *F*(1, 16) = 4.94, *p* = .041, session 4, *F*(1, 16) = 546, *p* = .033, and almost session 2, *F*(1, 16) = 4.34, *p* = .054. There was no difference between conditions on either session 3 or 5, *F*s(1, 16) < 2.7, *p*s > .12. There were no other significant main effects or interactions, *F*s < 1.1, *p*s > .33.

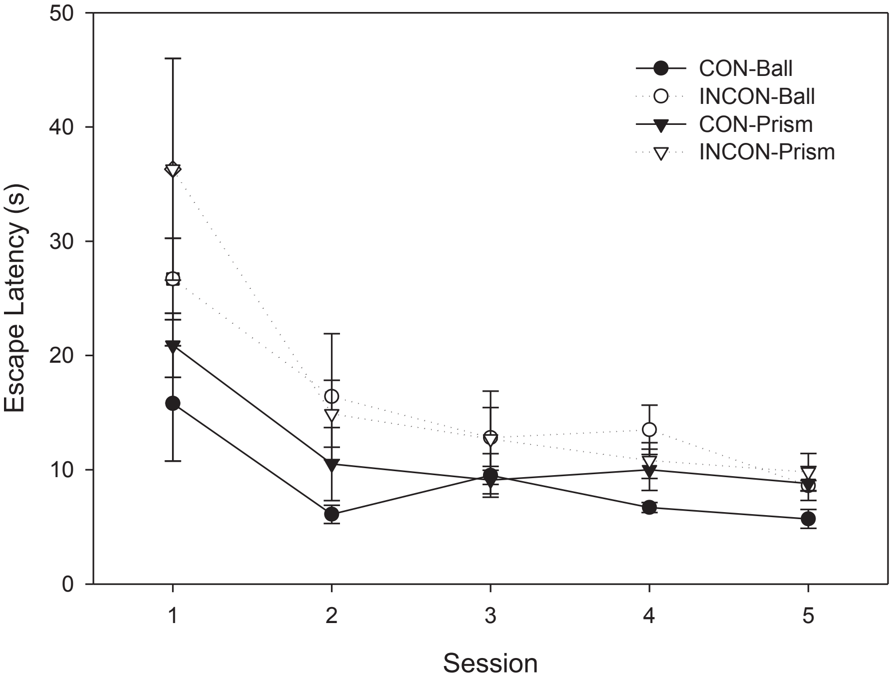

Figure 10: Escape latency data for the reinforced trials of the revaluation phase, split by revaluation and landmark. Error bars represent ± the Standard Error of the Mean.

In the crucial post-revaluation geometry test, the assignment of the correct and incorrect zones conformed to that of stage 1 of training (Figure 11). Importantly for our prediction of within-compound associations having formed between landmark and geometry cues during compound training, a repeated measures ANOVA of Zone x Revaluation x Landmark showed that there was a significant interaction between zone and revaluation, *F*(1, 16) = 6.51, *p* = .021. Analysis of the simple main effects of this interaction showed that group CON was able to discriminate between the correct and incorrect corners, *F*(1, 16) = 10.20, *p* = .006, whereas INCON lost their ability to perform this discrimination, *F* < 1, despite being equally as competent as group CON at this discrimination in the pre-revaluation geometry test. Although there was no difference in the amount of time CON and INCON spent exploring in the correct zone, *F* < 1, INCON spent significantly more time in the incorrect zone than did CON, *F*(1, 16) = 13.30, *p* = .002. There were no other significant main effects or interactions from this analysis, *F*s(1, 16) < 3.86, including no three-way interaction involving the reinforced landmark during stage 1 training. This implies the effect of revaluation was equal between Ball- and Prism-trained groups.

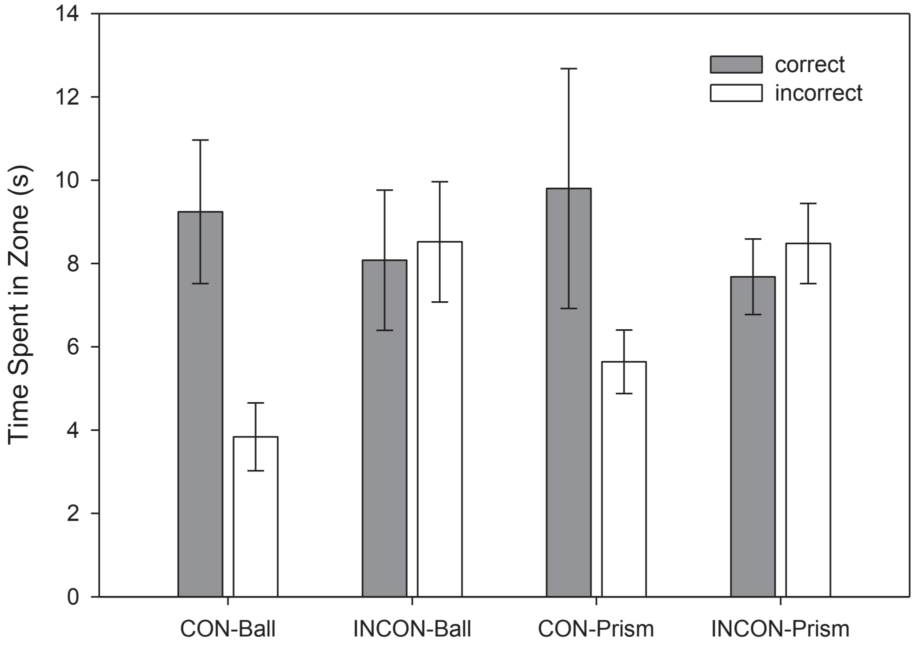

Figure 11: Time spent in the correct and incorrect corners in the post-revaluation geometry test, split by revaluation and landmark. Error bars represent ± the Standard Error of the Mean.

In order to ensure that the landmark revaluation procedure had produced the required reversal of landmark preference for group INCON, and the effect was equal between groups INCON-Ball and INCON-Prism, the final landmark test trial recorded time spent searching for the platform underneath each of the two landmarks (see Figure 12). In addition, the test was intended to indicate that CON-trained animals retained the landmark discrimination they had learned during stage 1 training and had reinforced during the revaluation stage. A repeated measures ANOVA (Zone x Revaluation x Landmark) showed a significant Zone x Revaluation interaction, *F*(1, 16) = 169, *p* < .001. Analysis of simple main effects showed that whilst CON groups spent significantly more time searching for the hidden platform underneath the landmark that was correct during stage 1 training, *F*(1, 16) = 127, *p* < .001, INCON groups spent significantly more time searching underneath the landmark that was incorrect during stage 1 training, *F*(1, 16) = 50.8, *p* < .001. Additionally, CON groups spent significantly more time searching underneath the correct landmark than INCON groups, *F*(1, 16) = 65.0, *p* < .001, whereas INCON groups spent significantly more time in the proximity of the incorrect landmark than CON groups, *F*(1, 16) = 93.7, *p* < .001. The interpretation of this interaction is that the revaluation stage successfully reversed the landmark preference that INCON groups should have developed during initial training, with the preference now in favor of the landmark that was correct during the revaluation stage. Conversely, CON groups retained their preference for the landmark that was correct during initial training, as it remained correct during the revaluation sessions.

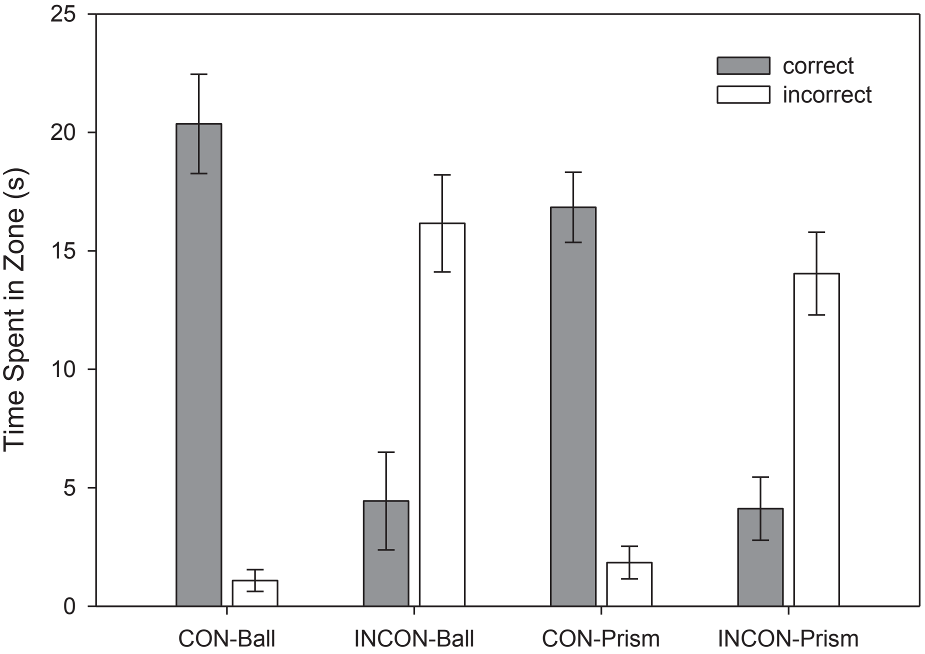

Figure 12: Time spent in the correct and incorrect zones during the landmark test, split by revaluation and landmark. Error bars represent ± the Standard Error of the Mean.

The inability of the INCON-trained groups to discriminate between the corners of the arena during the post-revaluation geometry test implies that their previous geometry preference had been abolished as a result of the landmark revaluation training, despite no difference between INCON- and CON-trained groups in their experience of which geometric cues were associated with the presence of the platform throughout training. The marked difference in the behaviors of the INCON and CON groups is consistent with an account based on the formation of within-compound associations between the geometry and landmark cues during initial compound training. According to this account, in the post-revaluation geometry test the presentation of the corner that had contained the platform during training evoked a representation of the landmark with which it was paired in stage 1 training. For INCON-trained animals this evoked representation was not consistent with a representation for the presence of the platform, and thus the discrimination of geometric cues was poorer than that of the CON-trained animals, for which the evoked representation of the landmark was consistent with the platform's presence. The magnitude of the landmark revaluation appeared to be the same regardless of the identity of the landmark that had indicated the location of the platform during stage 1 training. This pattern of results is discussed further in the General Discussion.

General Discussion

In each experiment rats were trained to locate a submerged platform in one of the base corners of a triangular arena above each of which was suspended one of two distinctive landmarks. In Experiment 1 a landmark test in the absence of geometric cues established that the discrimination of the landmarks was more pronounced for those animals for which the platform was associated with the ball than with the prism. This finding led to the conclusion that the ball was a more salient landmark than the prism. In Experiment 2 rats trained to locate the platform beneath the prism in the same triangular pool subsequently showed superior geometry discrimination compared with rats in a control group for which landmarks provided ambiguous information about the location of the platform, and were therefore expected to learn the platform's location with reference only to the geometry of the arena. The presence of the ball above the platform for another group of animals appeared to have no effect on learning based on geometry. Experiment 3 tested the presence of within-compound associations under the same training conditions as Experiments 1 and 2 and suggested they had formed between both the ball and geometry and the prism and geometry. The results provide the first evidence, as far as we are aware, that the apparent immunity to cue competition between landmarks and geometry demonstrated elsewhere may in fact be the result of within-compound associations abrogating the overshadowing effect that is predicted by theories of associative learning. These results fail to support those theories that suppose learning based on discrete landmarks to progress independently of learning based on geometry (Cheng, 1986; Doeller & Burgess, 2008; Wang & Spelke, 2002, 2003).

Our series of experiments is especially pertinent to the current spatial learning literature, as in the majority of studies that have failed to demonstrate an effect of non-geometric cues on learning based on geometry, the non-geometric cue was a discrete landmark, physically and visually separate from the walls that formed the arena's shape (Hayward et al., 2003, 2004; McGregor et al. 2009; Pearce et al., 2001). Cheng (1986) and Gallistel (1990) proposed that learning based on geometry was impervious to learning based on any other non-geometric feature. However, some theories of spatial learning are more specific, postulating that it is only learning based on individual landmarks that fails to enter the same representation as geometric cues, and thus learning based on geometry progresses independently of these landmarks. For example, Wang and Spelke (2002, 2003) proposed that learning locations based on individual landmarks takes place egocentrically, while an allocentric representation of geometry is necessary only for reorientation. Similarly, Doeller and Burgess (2008) claim that a representation of location based on vectors derived from a uniform boundary is not influenced by a representation of location based on landmark position. Doeller, King, and Burgess (2008) further suggested that boundary-learning and landmark-learning processes were independent of one another because the neural substrates for landmark- and boundary-learning are independent. In each of these cases, then, it is to be assumed that learning based on discrete landmarks will have no influence on learning based on geometry. Clearly, these theories have difficulty in explaining the recent work by Kosaki et al. (in press) that demonstrated overshadowing of geometry by discrete landmarks, and the work presented in the current study, in which the landmark and geometry cues must interact to form within-compound associations.

Although the results are not consistent with those theories that suppose spatial learning to hold a special status in learning and memory, other accounts assume no special role for learning based on geometry. For example, Miller and Shettleworth (2007) proposed a theory that was based on the Rescorla and Wagner (1972) error-correction theory with the addition of a probability rule to determine the likelihood of experiencing particular cue contingencies. Although their theory is able to explain the presence of potentiation between geometric and non-geometric cues within arenas with ambiguous geometric information, such as a rectangle, simulations of their model using our non-ambiguous geometric cues produces only overshadowing. McGregor et al. (2009) presented simulations of Miller and Shettleworth’s model that also apply to our Experiment 2, with an overshadowing group compared against a control group with two identical landmark cues paired with the geometry. These simulations showed that the associative strength of the correct geometry for the control group is always higher than that of the overshadowing group, thus the model predicts overshadowing of the geometric cue by the concurrently trained landmark cue. In addition, the account of cue competition put forward by Miller and Shettleworth cannot explicate the results of our Experiment 3.

It has also been argued that template-matching can explain various aspects of spatial behavior within arenas of a distinctive shape (Cheung, Stürzl, Zeil, & Cheng, 2008; Stürzl, Cheung, Cheng, & Zeil, 2008). Template-matching theory would propose that an animal takes a snapshot of its surroundings while at the goal location. On future trials, the animal then moves around the arena in an attempt to match their current view with the stored view at the goal location. Minimizing the discrepancy between the current- and goal-views should lead the animal back to the goal location. However, all animals in Experiment 2 experienced a similar change in their environment between training and test conditions: all landmark cues were removed. It is unclear how this would cause poorer discrimination of geometry cues by the control group than by the compound group, and especially why this would depend upon the salience of the landmark above the platform in the manner observed. Additionally, there is no process within the template-matching account that could explain the change in discrimination between the base corners of the arena in Experiment 3 following revaluation of the landmarks. It is therefore unlikely that template-matching is able to explain any of our results.

One objection to the interpretation of Experiment 1 regarding the salience of landmarks is that the within-compound associations formed between geometry and landmarks during compound training affected their discrimination during the test trial. Such an interpretation is perfectly valid, since we would not expect within-compound associations to affect the discrimination of geometry and not the discrimination of landmarks. However, the results of Experiment 3 show that the strength of the within-compound associations does not differ depending on the identity of the landmark. As such, while the presence of within-compound associations might have boosted discrimination for both Group Ball and Group Prism, the size of this effect should be equal for both groups. Any differences between the groups, therefore, can be ascribed only to differences in landmark salience.

The finding that reduction of the value of the landmarks in Experiment 3 affected geometry discrimination to the same extent regardless of the identity of the landmark suggests that the within-compound associations that formed between the ball and geometry, and the prism and geometry, were of an equal strength. We can infer from this that the mechanism by which within-compound associations affect cue competition is not based on differing strengths of the within-compound associations formed. Therefore, we argue that the reason our less salient landmark potentiates learning about geometry, whereas our more salient landmark merely counteracts overshadowing, is due to differing degrees of overshadowing caused by these differently salient landmarks. Together with the results of Kosaki et al. (in press) and Horne and Pearce (2011), our results provide an explanation for cue interaction effects observed between geometry and any non-geometric cue. The relative saliences of the cues determine both the degree of overshadowing, and the extent to which within-compound associations counteract overshadowing.

An explanation for the results of Experiment 3 in terms of within-compound associations having to overcome different degrees of overshadowing is consistent with accounts of within-compound associations in flavor-odor aversion conditioning, such as that offered by Durlach and Rescorla (1980). However, there is some discrepancy between our potentiation results and those of Durlach and Rescorla in terms of the relative saliences of the potentiating and potentiated cues. Whilst we observe potentiation of geometry cues by the least, but not the most, salient landmark, in flavor-odor aversion conditioning the opposite appears to be true. Durlach and Rescorla show potentiation of aversion learning of a low salience odor cue via compound conditioning with a relatively higher salience flavor cue. Despite this discrepancy, the observed potentiation is accounted for in a similar manner to ours, and that of Horne and Pearce. These accounts suggest that testing in the presence of the non-revalued cues evokes representations of the revalued, but absent, cues, and it is these representations that affect discrimination of the non-revalued cues. This associative chain account supposes that when rats experience the correct geometric corner a memory for the absent landmark cue is evoked, and it is this landmark’s negative association with the escape platform that prevents animals from exploring this corner in preference to the incorrect corner. This account may be contrasted with one in which a configural representation of the landmark and geometry cues forms as a result of those cues being trained in compound. The revaluation of the landmark cue alone activates this configural representation, and the configuration of geometry and landmark cues is revalued. Experience of the geometry cues alone, during test, activates this configural representation, which has been revalued, resulting in animals failing to discriminate between correct and incorrect geometric cues (for a detailed discussion, see Dwyer, Burgess, & Honey, 2012). Currently our data are unable to differentiate between these two mechanisms by which within-compound associations may have altered behavior towards geometric cues. It is possible that the apparent differences between conditions under which within-compound associations form in spatial and in non-spatial learning reflect the differences in these mechanisms. Understanding the mechanisms by which within-compound associations affect behavior is therefore an important step in determining whether the rules that govern spatial learning are unique.

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