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Changes in attention to relevant and irrelevant stimuli during spatial learning

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Abstract

Rats were trained in two experiments to find a submerged platform that was situated in one of two of the four corners of a rectangular pool with a curved long wall. Different landmarks occupied two of the corners on every trial and the platform was always situated near a landmark. For the place group in each experiment, the location of the platform was indicated by the shape of the pool and stimuli outside the pool (place cues), but not the landmarks within the pool. For the landmark groups, the landmarks indicated where the platform could be found, but not the place cues. During Stage 2, two of the place cues were relevant, and two of the landmarks were irrelevant, for a new discrimination. The place cues gained better control over searching for the platform in the place than the landmark group when the place cues had initially been relevant by signalling the presence (Experiment 1) or the absence (Experiment 2) of the platform. The results are said to show that animals pay more attention to relevant than irrelevant cues.

Many of the discriminations made by animals involve some stimuli that are relevant to the solution, and some that are irrelevant. If the same stimuli are used for a new discrimination, then learning often progresses more readily with the previously relevant than irrelevant stimuli, (e.g. Lawrence, 1949; 1950). Furthermore, if relevant and irrelevant stimuli are from different dimensions, and the new discrimination involves novel stimuli from these dimensions, learning often progresses more readily with the novel stimuli that belong to the previously relevant rather than the previously irrelevant dimensions (e.g. Mackintosh & Little, 1969). These differences in conditionability, or associability, have been attributed to animals paying more attention to relevant than irrelevant stimuli during discrimination learning (e.g. Sutherland & Mackintosh, 1971; Mackintosh, 1975). The purpose of the present paper is to explore the generality of the circumstances that promote these changes in attention.

One source of support for the claim that animals pay more attention to relevant than to irrelevant stimuli is the intradimensional shift - extradimensional shift (IDS-EDS) effect. Typically, subjects receive a number of discriminations of the form AX+ BX−, AY+ BY−, where A and B represent values from one dimension, say colour, which is relevant to the solution of the discriminations and X and Y represent values from another, irrelevant dimension, say orientation. Once the initial discriminations have been mastered, subjects are transferred to a set of new discriminations involving novel values from the two dimensions.

It is generally found that animals receiving an IDS, where the significance of the two dimensions remains the same for both stages, acquire the second set of discriminations more readily than those receiving an EDS, where the significance of the dimensions is reversed for the second stage. Examples of this effect have been provided by Mackintosh and Little (1969) and George and Pearce (1999), using pigeons; Shepp and Eimas (1964) and Trobalon, Miguelez, McLaren, and Mackintosh (2003), using rats; and Roberts, Robbins, and Everitt (1988), using marmosets.

Demonstrations of an IDS-EDS effect normally take place in conditioning chambers, where visual stimuli presented on a display signal the presence or absence of reward. A series of experiments by Trobalon et al. (2003) has indicated, however, that this effect can be found in rather different circumstances. Rats were trained to find food at the end of one of two arms that were connected to a central platform. During the test phase the spatial position of the arms indicated where food could be found. For an IDS group, the position of the arms also indicated where food was situated during the previous training phase, but they occupied different locations to those used for testing. In addition, the texture of the floor of each arm was different and varied randomly with respect to food during the training stage. For an EDS group, the texture of the floor was relevant to the occurrence of food during the training stage, whereas the location of the arms was irrelevant. The former group, which received an IDS for the test phase, solved the test discrimination more rapidly than the latter group, which received an EDS.

The experiment by Trobalon et al. (2003) indicates that changes in attention to relevant and irrelevant cues are not confined to the conditioning chamber but, even in their study, the movement of the animals was constrained by the maze on which they were trained. It remains to be determined, therefore, whether similar changes can be seen when the animal must explore the entire environment in order to discover where reward is located. In order to address this issue, the experiments examined whether rats trained to escape from a pool of water, by swimming to a submerged platform, pay more attention to cues that are relevant rather than irrelevant for finding the platform.

Tests for an IDS-EDS effect are not always successful (see Hall & Channel, 1985; Couvillon, Tennant, & Bitterman, 1967; Sutherland & Andelman, 1969). Dopson, Esber, and Pearce (2010) have argued that this effect may be elusive because it depends upon a change in attention to one set of stimuli generalising to others from the same dimension. If the stimuli selected for the test phase differ too much from those used initially, then the difference in the degree of attention paid to the previously relevant and irrelevant stimuli might generalize only slightly to the new stimuli, and render the test for an IDS-EDS effect insensitive. To circumvent this obstacle, Pearce, Esber, George, and Haselgrove (2008; see also Dopson, Esber et al., 2010; Haselgrove, Esber, Pearce & Jones, 2010) devised an alternative method for revealing changes in attention to relevant and irrelevant stimuli. This method involved training pigeons on a number of discriminations, including: AW+ CW-, AX+ CX-, BW+ DW-. Following this training, subjects were given an AW+ AX- BW- test discrimination. All three test compounds were followed by food during the initial training, and it was therefore expected that responding during each of them would be similar at the outset of testing. Of interest was the rate at which the two sub-discriminations, AW+

AX– and AW+ BW–, were solved. It was expected that by the end of the initial training, A and B would be paid considerable attention, as these stimuli were relevant by virtue of consistently signalling food. W and X on the other hand should be paid little attention, as these stimuli were irrelevant to the delivery of food. Thus the AW+ BW– component of the test discrimination, which is based on cues A and B, should be acquired readily. In contrast, the AW+ AX– discrimination, which is based on cues W and X, should be acquired with difficulty. The results of Pearce et al. (2008) confirmed these predictions.

A variation of the method used by Pearce et al. (2008) was adopted for Experiment 1. The results were consistent with the claim that changes in attention to relevant and irrelevant stimuli can be found in a free exploration task. In order to extend further our understanding of the factors that promote changes in attention, Experiment 2 capitalised on the methodology of Experiment 1 to explore whether any enhancement of attention to cues that indicate the location of a goal, also occurs with cues that reliably indicate where the goal is not located. Thus far there is only a single report of such a change in attention, and this was obtained using autoshaping with pigeons (Dopson, Williams, Esber & Pearce, 2010).

Experiment 1

Two groups of rats were trained in the presence of cues provided by the experimental room to find a submerged platform in one corner of a swimming pool with a distinctive shape (see Figure 1). The orientation of the pool remained constant throughout the experiment. The shape was created by placing two short, grey walls and one long, grey wall in a circular pool to create an open rectangle, with the curved, white wall of the circular pool creating the fourth wall of the test enclosure (see Figure 1). The four corners where the platform could be situated are referred to as A, B, C and D. From here on, the term place cues will refer to the combination of stimuli at the four corners provided by the arena (e.g., geometric cues, colour of the walls) and by the room in which the arena was housed. In addition, pairs of laminated A4 cards could be attached to the walls of each corner to create four distinctive landmarks W, X, Y and Z. On any trial in Stage 1, there were two pairs of landmarks in the pool: either W and X (with one in Corner A and the other in Corner B) or Y and Z (with one in Corner C and the other in Corner D). The landmarks were presented equally often in each of the two permissible corners. The place group received place-relevant training in Stage 1, in which the platform could be found in Corner A when landmarks W and X were present, and Corner C when landmarks Y and Z were present (see Table 1). Thus to find the platform it was necessary to pay attention to the place cues and to ignore details of the landmarks. It is necessary to point out that the landmarks were not completely irrelevant for solving the task. When Landmark W was in Corner A, and Landmark X in Corner B, or *vice versa*, then the platform can be found in Corner A. If Landmark Y was in Corner C, and Landmark Z in Corner D, or *vice versa*, then the platform was in Corner C (see Table 1). Although place cues indicated where the platform was situated, the two landmarks that were present on any trial were not entirely irrelevant to the task because they narrowed down the search for the correct corner to a choice between two of the four corners. Even so, when selecting between these two corners it was necessary to focus on the place cues, rather than the landmarks. It would thus be a mistake to say that the landmarks were completely irrelevant, but they were of less relevance than the place cues for finding the platform. It is also a mistake to say that

the place cues were uniquely relevant, because in the absence of landmarks in Stage 1 it would be impossible to tell if the platform could be found in Corner A or C. The landmark group received landmark-relevant training in which the platform was always located beside landmark W (in Corner A or B), when W and X were present, and beside landmark Y (in Corner C or D), when Y and Z were present. For this training it was necessary to pay attention to the details of the landmarks in order to locate the platform, and to ignore information provided by the place cues.

In order to confirm that the rats had learned about the significance of the relevant stimuli for finding the platform in Stage 1 they received near the end of this stage a test trial in the absence of the platform. The test was conducted without the landmarks in the training arena for the place group, and with the landmarks in a square arena surrounded by a curtain for the landmark group.

In order to assess whether the foregoing treatments resulted in more attention being paid to relevant than irrelevant cues, a further stage of training was conducted, based on the method devised by Pearce et al. (2008). For this stage, a new place-relevant discrimination was introduced for which landmarks W and Y were located equally often in Corners A and C, and the platform was situated only in Corner A.

The place-relevant training in Stage 2 can thus be conceived as being composed of two simultaneous discriminations, AW+ CY– and AY+ CW–, where the task is to learn to approach A and avoid C. This is somewhat different to the test stage of training employed by Pearce et al. (2008). However, what is important and what is similar to Pearce et al. is that at the outset of the test phase for the two groups, each compound of the discrimination, AW, AY, CW, and CY was composed of one cue that, in Stage 1, signalled where the platform could be found and one cue that was irrelevant for finding the platform. Any differences that emerge during the test discrimination can not, therefore, be attributed to differences in the overall associative properties of the test compounds. If the place-relevant training in Stage 1 resulted in more attention being paid to the place cues than the landmarks, then the place group should solve the place-relevant discrimination in Stage 2 readily. In contrast, if the landmark-relevant treatment in Stage 1 resulted in animals paying more attention to the landmarks than the place cues, then the landmark group should find the place-relevant discrimination in Stage 2 difficult as it will start by paying more attention to the cues that are irrelevant, rather than relevant to its solution.

Method

Subjects—Twenty naïve, male, hooded Lister rats (*Rattus Norvegicus*), supplied by Harlan Olac (Bicester, UK) and weighing between 250 and 300 g at the outset of training were used. The rats were housed in pairs in white plastic cages with secured metal lids and maintained on a 12-hr light/dark cycle, with lights on at 07.00. Subjects had continuous access to food and water in their home cages

Apparatus—A white, circular pool 2 m in diameter and 0.6 m deep was used. The pool was mounted on a platform 0.6 m above the floor in the centre of the room (4 m × 4 m × 2.3 m). The pool was filled with water to 27 cm and maintained between 23 and 26°C. To make

the water opaque, 0.5 L of white opacifier E308 (Roehm and Haas, Ltd., Dewsbury, U.K.) was added. The water was changed daily.

A white circular ceiling, 2 m in diameter, was suspended 1.75 m above the pool floor. There was a hole in the center of the ceiling with a diameter of 30 cm. A wide-angled video-camera was secured 25 cm above the hole and connected to a video-monitor and computer in an anteroom. During testing, movements of the rats were analysed using Watermaze Software (Morris & Spooner, 1990). The pool was illuminated by eight 45-W lights located in the circular ceiling. The lights were 22.5 cm in diameter and equidistant from each other in a 1.6 m diameter circle whose centre was coincident with the centre of the circular ceiling. The arena was additionally illuminated by two 1.53-m strip lights connected end-to-end on both the east and west walls. These lights were positioned 75 cm above the floor and ran parallel to the floor. A sliding door (1.75 m $\times$ 2 m) leading to the anteroom was located in the centre of one of the walls.

A platform 10 cm in diameter and mounted on a column was used throughout training. The platform surface had a series of concentric ridges. The column base rested on the pool floor, maintaining the platform surface 2 cm below the water surface. To create the training arena three, grey, Perspex boards were suspended in the pool by bars extending over the pool edge (see Figure 1). There was one long board (1.8 m $\times$ 0.59 m $\times$ 2 mm), and two short boards (0.9 m $\times$ 0.59 m $\times$ 2 mm). The three boards always occupied the same position, relative to the room and, for all rats, the corners were labelled as shown in Figure 1. During Stage 1, four landmarks were used, each consisting of two sheets of laminated A4 (210 mm $\times$ 297 mm) paper which could be attached to the walls of the pool by surface tension after they had been made wet. The long side of one sheet made contact with the long side of the other in the appropriate corner of the pool, and the bottom edge of each sheet was 2 cm above the surface of the water. Landmark W was white, landmark X was black, landmark Y was horizontal black and white stripes of width 2 cm, and landmark Z was black spots arranged in columns and rows on a white background. The diameter of each spot was 1 cm and the distance between the centres of adjacent spots horizontally and vertically was 1.7 cm. Four additional boards (1.41 m $\times$ 0.59 m $\times$ 2 mm) of the same colour as those used to create the straight walls of the training arena were used to create a square pool for test trials with the landmarks. A curtain, attached to the edge of the circular ceiling, was drawn around the pool for the test trials in the square pool but was otherwise left open. The curtain was 1.5 m high and fell 25 cm below the top of the pool.

Procedure—Rats were transported to the test room in a light-tight carrying box with five compartments. The box remained on a shelf in the anteroom holding the rats between each trial. Training was conducted daily, for seven days a week, with four training trials in each daily session. For each trial, a rat was taken by hand from the carrying box to the pool and released facing the center of a wall. Release point varied across trials with the stipulation that each wall was used once in any given session. During a trial, the rat was required to swim to a submerged platform. The center of the platform was 25 cm from the corner of the rectangle on a notional line bisecting the corner. Each trial lasted a maximum of 60 s. If the platform was not located within 60 s, the experimenter placed a finger 2 cm from the rat's snout and guided it to the platform. After mounting the platform, the rat remained there for

20 s before being lifted, dried, and returned to its holding container. It remained there until all rats in the carrying box had completed a single trial. This cycle continued until four trials had been completed.

Rats were randomly assigned to the place group ($n=10$), and the landmark group ($n=10$). For the first four sessions of the 17 sessions of Stage 1 every rat was exposed to four different trials. For one trial, landmark W was in Corner A and landmark X was in Corner B (AW and BX), and for another trial this combination was reversed (AX and BW). For a third trial, landmark Y was in Corner C and landmark Z was in Corner D (CY and DZ), and this relationship was reversed for the final trial (CZ and DY). The sequence in which the trials were presented varied randomly from session to session. For the place group the platform was located in Corner A when the landmarks occupied Corners A and B, and in Corner C when the landmarks occupied Corners C and D. For the rats receiving landmark-relevant trials, the platform was located beside landmark W when the landmarks W and X were present and beside landmark Y when landmarks Y and Z were present. As Stage 1 progressed, unusually long latencies to reach the platform were recorded. To amend this, from Session 5 onwards rats were trained with only one pair of landmarks, W and X or Y and Z, for the four trials of any session. Although this change was accompanied by a reduction in escape latencies, it did not lead, as had been anticipated, to rats heading directly for the corner with the platform once they were released into the pool. Instead, they tended to swim around the boundary of the pool to the goal, often passing on the way through corners without the platform. In contrast to our previous studies (e.g. Horne & Pearce, 2010), the corner approached first after being released was thus of little interest and an account of this behaviour has been omitted from the present report.

Until Session 14, the four trials in each session for all groups involved landmarks W and X on odd numbered sessions and landmarks Y and Z on even numbered sessions. A summary of the place-relevant training is shown in the upper panel of the left-hand column of Table 1, while the lower panel summarizes the landmark-relevant training.

Session 15 of Stage 1 contained two normal training trials with landmarks W and X followed by a test trial. The place group was released into the training pool with the landmarks and the platform removed, and the landmark group was released into a square pool, surrounded by curtains, and with two landmarks in diagonally opposite corners but no platform. For half of the rats tested in the square pool the landmarks were W and X, and for the other half they were Y and Z. All rats were released into the centre of the pool for the test trial, and were allowed to swim for 60 s. The remaining two sessions of Stage 1 consisted of four trials of normal training with landmarks W and X in Session 16 and with landmark Y and Z in Session 17.

The final three sessions of the experiment, which commenced on the day following Session 17 of Stage 1, were conducted in the pool that was used for Stage 1, but with landmarks W and Y, in Corners A and C. For two randomly selected trials of each session landmark W was in Corner A and landmark Y was in Corner C (AW and CY), and for the remaining two trials this relationship was reversed (AY and CW). The platform was always situated in Corner A for both groups. The Stage-2 treatment for the two groups is shown in the middle

column of Table 1. A fifth trial, which served as a test, was presented immediately after the completion of Session 3. For both groups, the test trial was conducted in the same manner as the test trial for the place group in the training pool in Session 15.

The time taken to reach the platform after being released into the pool was recorded on every training trial throughout the experiment. If a rat failed to reach the platform within 60 s, then a time of 60 s was recorded. During each of the test trials in Stage 1 and Stage 2, the time spent in circular zones, 30 cm in diameter, that were located in selected corners of the test arena was recorded. The centre of the zone was situated 25 cm from the nearest corner of the pool, on a line that bisected the corner. The results from test trials in Stages 1 and 2 were analysed with individual discrimination ratios, which were computed by dividing the amount of time spent in what is referred to as the correct zone by the sum of the time spent in the correct and incorrect zones. For the test trial in the square in Stage 1, the correct zone was situated by the landmark which had previously been paired with the platform; the incorrect zone was in the diagonally opposite corner, beside the landmark that had not been paired with the platform during the immediately preceding training. For the test in the training arena in Stage 1, the two zones where the platform had previously been located were regarded as the correct zones, and the remaining two zones were regarded as the incorrect zones. For the Stage-2 test trial in the training arena, the correct zone was in the corner where the platform had been located for this stage, and the incorrect zone was in the diagonally opposite corner.

A Type-I error rate of 0.05 was adopted for all reported statistical analyses.

Results and Discussion

Mean escape latencies for the two groups for each of the 17 sessions of Stage 1 are shown in the left-hand panel of Figure 2. Both groups reached the platform more rapidly as training progressed and it is evident that the change in the method of training between Sessions 4 and 5 was accompanied by an improvement in performance. A two-way ANOVA using individual mean escape latencies for the 13 sessions of training from Session 5 onwards with the factors of session and group revealed a significant effect of session, $F(12, 216) = 7.44$ and a significant Session X Group interaction, $F(12, 216) = 3.49$. The effect of group was not significant, $F(12, 216) = 1.85$. Subsequent tests of simple main effects revealed that on Sessions 10, 12, 14, and 17, the mean escape latencies for the landmark group were significantly longer than for the place group. Landmarks W and X were employed for all the sessions on which a significant effect was recorded.

During the first test trial in the square pool, the landmark group spent more time in the search zone beside the landmark that had previously been paired with the platform – the correct zone, than in the zone beside the landmark that had never been paired with the platform – the incorrect zone. The mean time spent in the correct and incorrect zones during the test trial is shown by the left-hand pair of bars in the left-hand panel of Figure 3. The mean discrimination ratio based on the times spent in the two zones was .67. Single-sample *t*-tests based upon individual discrimination ratios indicated that the ratios were significantly greater than .5 (which is the value expected when there is no preference for one corner over the other), $t(9) = 5.67$.

The results from Stage-1 test trial in the training pool for the place group are shown by the right-hand pair of bars in the left-hand panel of Figure 3. The group spent more time in the correct than the incorrect zones during the test trial. Discrimination ratios, derived from the time spent in Corners A and C divided by the time spent in all four corners had a mean value of .77, which was significantly different from chance, $t(9) = 5.98$. The results summarised in the left-hand panel of Figure 3 thus demonstrate that the Stage-1 discrimination training based on either the landmarks or the place cues was successful.

The group mean escape latencies for the two groups during the three sessions of Stage 2 can be seen in the right-hand panel of Figure 2. Both groups performed similarly and showed a marginal reduction in escape latencies across the three sessions. A two-way ANOVA similar to the one conducted for Stage 1 revealed a significant session effect, $F(2, 36) = 12.37$. The effect of Type of training in Stage 1 and the interaction was not significant, $F(2, 36) < 1$.

The most important results from the experiment concern the outcome of the test trial at the end of Stage 2. The right-hand panel of Figure 3 shows the mean amount of time spent by the two groups in the correct zone, A, where the platform and a landmark had been located throughout Stage 2, and in the incorrect zone, C, where a landmark but not the platform was located in Stage 2. Both groups spent more time in the correct than the incorrect zone, but the extent of this preference was greater for the place group. Discrimination ratios were derived from the time spent in Zone A, divided by the sum of the time spent in Zones A and C. The mean ratio for the place group was .87 and for the landmark group it was .70, which indicates that by the end of Stage 2 training, the discrimination between the cues distinguishing Corner A from C had been acquired to a greater extent when the place cues had been previously relevant, rather than previously irrelevant. In support of this conclusion, analysis of individual discrimination ratios for the test trial revealed a significant difference between the groups, $t(18) = 2.86$. In addition, single-sample t-tests indicated that the discrimination ratios for each of the two groups were significantly greater than .5, $t_s(9) > 3.90$, thus confirming that both groups solved the discrimination.

The results from the place and the landmark group are in keeping with the claim that Stage-1 training resulted in more attention being paid to the place cues than the landmarks by the former group, and more attention to the landmarks than the place cues by the latter group. These differences in attention would then make it easier to discriminate between the correct place, A, and the incorrect place, C, for the place than the landmark group in Stage 2. The experiment thus provides, for the first time, an indication that changes in attention to relevant and irrelevant stimuli, which hitherto have been detected only in a confined environment, can also be found in a free exploration task.

Experiment 2

The possible changes in attention that were recorded during Experiment 1 concerned cues that had previously signalled where the platform was situated, and cues that had previously been irrelevant. Experiment 2 was conducted in order to explore the generality of this finding by determining how attention to place cues is affected when they reliably signal the absence, rather than the presence, of the platform. It is possible that the initial training will

result in these cues receiving little attention. Experiments have revealed that animals will withdraw from a stimulus that signals the absence of food (e.g. Hearst and Franklin, 1977), and it is likely they will do the same for cues that signal the absence of an escape platform. By actively avoiding such cues, animals may pay them little attention. The results of an experiment by Dopson, Williams, et al. (2010) suggest that an alternative outcome might be observed. These authors gave pigeons similar training to that in the experiment by Pearce et al. (2008) described earlier, that is, AW+ CW−, AX+ CX−, BW+ DW− discriminations. This training was followed by the test discrimination CW+ CX− DW−, which involved three trial types that had previously been nonreinforced. Of the stimuli used at test, C and D had been relevant during the initial training, by virtue of consistently signalling the absence of food, and W and X had been irrelevant. Dopson, Williams et al. found that the CW+ DW− component of the test discrimination, which was based on stimuli C and D, was acquired more readily than the CW+ CX− component, which was based on stimuli W and X. Thus the results were in keeping with the expectation that animals pay more attention to relevant stimuli – even those that signal the absence of food – than irrelevant stimuli.

To our knowledge, the experiment by Dopson, Williams, et al. (2010) is unique in investigating the changes in attention that take place to stimuli that are of relevance by reliably signalling the absence of an outcome. Experiment 2 thus provides an opportunity to establish the reliability and generality of this finding, and also a further opportunity to examine if the principles of learning and attention established in the conditioning chamber extend to spatial learning during free exploration in a swimming pool.

The experiment again included a place group and a landmark group which received the same discriminations in Stage 1 as their namesakes in Experiment 1. For Stage 2, the landmarks, X and Z, which in Stage 1 had either been irrelevant (place group), or signalled the absence of the platform (landmark group), occupied Corners B and D, which had either been irrelevant (landmark group) or signalled the absence of the platform (place group). The platform was located in Corner B. A summary of the treatment for both stages is presented in the right-hand column of Table 1. On the basis of the findings reported by Dopson, Williams et al. (2010), it was anticipated that the discrimination in the test phase would be acquired more readily by the place than the landmark group.

Method

Subjects and apparatus—Thirty-two experimentally naïve rats of the same stock and approximate weight as those in Experiment 1, housed in the same manner, were used. The apparatus was identical to Experiment 1, but without the boards for forming the square arena.

Procedure—Rats were assigned at random to the place group (n=16) and the landmark group (n=16). Experiment 2 was based on Experiment 1, but with a number of changes. First, the method of training in which only Corners A and B were used on odd-numbered sessions, and C and D on even-numbered sessions, was adopted from the outset of Stage 1. Second no test trials were administered towards the end of the Stage 1, as the previous experiment had already confirmed the effectiveness of Stage-1 training. Third, a total of 14,

rather than 17 sessions of training were given in Stage 1. Fourth, both groups received place-relevant training in Stage 2, with landmarks X and Z, being located in Corners B and D. Landmark X was placed in Corner B, and landmark Z in Corner D, for two trials in each Stage-2 session, while these relationships were reversed for the remaining trials. Finally, apart from the test trial at the end of Stage 2, which was conducted in the same manner as for the equivalent groups of Experiment 1, the platform was placed in Corner B throughout Stage 2.

Results and Discussion

The mean escape latencies for the two groups throughout the 14 sessions of Stage 1 can be seen in the left-hand panel of Figure 4. At the outset of the experiment the time taken to reach the platform was marginally faster in the place than the landmark group, but as the performance of both groups improved with continued training this difference diminished. A two-way ANOVA revealed a significant effect of session, $F(13, 390) = 72.93$, a significant effect of group, $F(1, 30) = 4.65$, and a significant Group $\times$ Session interaction, $F(13, 390) = 2.48$. Subsequent tests of simple main effects revealed a significant difference between the groups on Sessions 1, 2, 3 and 6, $F_s(1, 420) > 4.37$.

The mean escape latencies for the three sessions of Stage 2 are presented in the right-hand panel of Figure 4 for the two groups. From the outset of this stage, both groups found the platform relatively quickly but the latencies for the place group were marginally shorter than for the landmark group. The performance of both groups improved with continued training. A two-way ANOVA revealed a significant effect of group, $F(1, 30) = 7.27$, and of session, $F(2, 60) = 26.94$, but the interaction was not significant, $F < 1$.

The outcome of the test trial can be seen in Figure 5. The figure shows that both groups spent considerably more time in the correct corner, B, of the apparatus, where the landmark and the platform had been situated in Stage 2, than in the incorrect corner, D, where only a landmark had been situated for this stage. Of more importance is the observation that the extent of this difference was greater for the place than the landmark group. In support of this observation the discrimination ratio for the place group, which was calculated in the same manner as for the place group of Experiment 1, had a value of .96, while for the landmark group the value of the ratio was somewhat lower at .87. Analysis of individual discrimination ratios revealed a significant difference between the groups, $t(30) = 2.98$. In addition, the ratio for each group was significantly greater than .5, $t_s(15) > 13.6$. Thus both groups solved the discrimination, but to a greater extent in the place than the landmark group.

The results are consistent with those from Experiment 1, by showing that rats can acquire a discrimination between two places more readily if those places had been relevant, rather than irrelevant during a previous spatial discrimination. In the first experiment, the place cues were initially made relevant by signalling where a hidden goal could be found, whereas for the present experiment they were made relevant by consistently signalling the absence of the platform.

General Discussion

The experiments have shown that rats can find a platform in a corner of a distinctively shaped arena by referring either to landmarks situated in the corners, or to place cues provided by the walls of the arena and the room in which it was housed. The ease with which learning took place with these cues in a new discrimination was influenced by their significance in a previous discrimination. If the place cues had been relevant to the solution of the original discrimination, and the landmarks irrelevant, then both experiments revealed that a new discrimination, for which some of the place cues were again relevant, was acquired more readily than if the place cues originally had been irrelevant, and the landmarks relevant.

Given the nature of the experimental design, it is not possible to tell whether the results were due to the enhanced conditionability of cues that were relevant in Stage 1, or to the reduced conditionability of those that were irrelevant during this stage. A third possibility is that both of these processes contributed to the outcome of the experiments. Despite this uncertainty, the results are nonetheless consistent with the claim that animals pay more attention to relevant than irrelevant cues, and that the more attention is paid to a stimulus the higher will be its conditionability. Support for these conclusions has already been found in experiments where the movement of an animal has been constrained by the walls of a conditioning chamber, or by a maze. The above results, in contrast, provide the first indication that the conclusions may also be true for free exploration tasks. If changes in attention were indeed responsible for the present results, then these changes appear to take place in a wide range of circumstances.

Experiment 2 revealed that the conditionability of the place cues in two corners of the arena that had previously signalled the absence of the platform was greater than when the same cues had previously been irrelevant for finding the platform. It thus appears that animals will pay considerable attention to cues that are relevant, even if they are relevant by signalling the absence of an important event. To our knowledge, the findings from only one other study, which used autoshaping with pigeons, have pointed to a similar conclusion (see Dopson, Williams et al., 2010).

We must return briefly to discuss the place-relevant training in Stage 1. For this stage, rats were placed in a four-cornered pool with different landmarks in two of the corners, and required to find the platform in one of the corners with a landmark. We noted in the Introduction that this training ensured the place cues were not solely relevant and the landmarks were not entirely irrelevant for finding the platform. However, we argued that the place cues would be of greater relevance than the landmarks. The results from both experiments support this conclusion by showing that the place-relevant training in Stage 1 was sufficient to encourage more rapid learning about the place cues in the subsequent test by the place than the landmark group.

We have assumed thus far that the superior performance of the place than the landmark groups at the end of the test stage in both experiments was a consequence of the initial training resulting in more attention being paid to relevant than irrelevant stimuli. In fact, as

the foregoing discussion makes clear, the design of the experiments is more complicated than for other studies which have been said to show that more attention is paid to relevant than irrelevant stimuli. Given the unusual design of our task, we should consider whether our results can be explained without appealing to changes in attention to relevant and irrelevant stimuli. One possibility, at least for Experiment 1, is that the results from the final test were a consequence of nothing more than stimuli competing for a limited pool of associative strength, as envisaged, for example, by the Rescorla-Wagner (1972) theory. In order to explore the implications of this theory for our results, computer simulations were conducted based on the associative model for spatial learning put forward by Miller and Shettleworth (2007). This model is based on the Rescorla-Wagner (1972) theory, but it incorporates a modification to take account of the fact that animals choose which corners to enter during every training trial. Miller and Shettleworth suggested, therefore, that Equation 1 determines the changes in associative strength of both the landmarks and the place cues in a task such as the one we employed

$$\Delta V = \alpha \beta (\lambda - V_{\Sigma}) \cdot P_L \quad 1$$

In this equation, ΔV is the change in associative strength of a particular stimulus, α and β are learning rate parameters with values varying between 0 and 1, λ is the asymptote of conditioning, and V_{Σ} is the sum of the associative strengths of all the cues in the corner containing the stimulus under consideration. The term, P_L , represents the probability of entering a given corner. The value of P_L is given by Equation 2, where V_L is the overall associative strength of all the cues in a corner, and $\Sigma V_{L'}$ is the sum of the overall associative strengths of all four corners.

$$P_L = \frac{V_L}{\Sigma V_{L'}} \quad 2$$

Computer simulations, based on Equations 1 and 2, were conducted to determine the predicted changes in associative strength for the place-relevant and landmark-relevant training in Stage 1 of both experiments. The multiple-choice model of Miller and Shettleworth (2007) was used, which allows an animal to enter more than one place on each trial. Each corner and each landmark was represented by a unique cue, making eight cues, and a final cue was used to represent the common features of the four places (see Miller and Shettleworth, 2007). For all the simulations that follow, the value of α was .2, the value of β and λ was 1, and the associative strength of the common cue was .1 at the start of training for Stage 1 (with the exception of α , these values were taken from Miller & Shettleworth, 2007, who proposed that α is .15). We followed Miller and Shettleworth in assigning the same value of α to the landmarks and place cues. The final associative strengths for each cue were then carried over to the start of the simulations for Stage 2.

Figure 6 shows the simulations for the training of both the landmark (left-hand panel) and place (right-hand panel) groups of Stage 1. These simulations involved the four sequences of trials in the upper panel of the left-hand column of Table 1 for the place group, and the four sequences in the lower panel for the landmark group. Equation 1 can result in the overall

associative strength of all the cues at a corner having negative associative strength, which will adversely affect the calculation of probabilities in Equation 2. When making calculations based on Equation 2, therefore, the minimum value of the overall associative strength of a corner was set at zero (see Dawson, Kelly, Spetch, & Dupuis, 2008; Miller and Shettleworth, 2008).

The important point to note from Figure 6 is that Stage-1 training for the place group is predicted to endow the place cues associated with the platform with positive associative strength, and the place cues associated with the absence of the platform with negative associative strength. The training for the landmark group, on the other hand, is predicted to leave all four place cues with virtually no associative strength. These differences are important because they determine the predicted outcome of Stage 2 of the experiments. The top two panels in Figure 7 depict the predicted changes in associative strength during Stage 2 of Experiment 1 for the landmark group (left-hand panel) and the place group (right-hand panel). It is evident that the initial difference for the two groups between the associative strengths of place cue, A, which signalled where the platform could be found in Stage 2, is also predicted to be evident at the end of training. In contrast, for Experiment 2, because the associative strength of the correct place cue, B, in Stage 2 for the place group starts off with a negative value, it is predicted to be of a lower value throughout Stage 2 than for the landmark group (see the two bottom panels of Figure 7). The simulations thus predict that the place group should exhibit a stronger tendency to approach the correct corner during the final test trial than the landmark group in Experiment 1, but the opposite outcome should be observed in Experiment 2. The first of these predictions, but not the second, was confirmed by the results of the final test trials.

The foregoing predictions are based solely on the predicted associative strength of the correct corner, but there were four corners in the arena. It is thus possible that the associative properties of the remaining three corners might influence the preference that is predicted to be shown for the correct corner. To explore this possibility, the predicted probability of approaching the correct corner under the conditions of a test trial, was calculated for every trial of Stage 2. The calculations were based on Equation 2 and the predicted associative strengths of the various cues as depicted in the top and bottom rows of Figure 7. The outcome of these calculations can be seen in Figure 8, which shows that for Experiment 1 the place group is predicted to show a marginally stronger preference for the correct corner than the landmark group after a few training trials, but this difference soon disappears with both groups showing a complete preference for the correct corner. Of more importance are the predictions concerning Experiment 2. Here, the landmark group is predicted to show a sustained and considerably stronger preference for the correct corner than the place group. Such an outcome is opposite to the results from the test trial that was conducted at the end of Experiment 2. Furthermore, this outcome was predicted by additional simulations where α for the landmarks (.1) was half that of the place cues (.2), and where this relationship was reversed.

The results from Experiment 2, therefore, can not be explained by a theory of learning which assumes that the conditionability of stimuli remains constant throughout training. One ready explanation for the results from this study is that during Stage 1 the place group paid

considerable attention to the place cues B and D as they reliably, and uniquely, signalled that the platform could not be found in their vicinity (e.g. Mackintosh, 1975). The same cues would not be expected to receive a similar level of attention in the landmark group as they were intermittently paired with the platform in the presence of landmarks that reliably signalled where the platform was located. If more attention was paid to B and D in the place than the landmark group, then it would follow that the former group would acquire the discrimination in the test phase more rapidly than the latter.

The main purpose of the present experiments has been to explore the generality of the finding that discriminations are acquired more readily with stimuli that are similar, or the same, as those that have been relevant rather than irrelevant to the solution of a previous discrimination. The experiments have confirmed for the first time that this effect can be found when the discriminations take place in a task where subjects must freely explore the entire environment in order to find the goal. They have also confirmed the findings of Dopson, Williams et al. (2010) that the animals will solve a new discrimination readily if it is based on stimuli that were previously relevant by signalling the absence of reward. When the results of both experiments are taken together, they reveal that a full understanding of how animals learn to locate a goal in an open environment must take account not just of the associations that are formed, but also of the changes in the associability of the stimuli that enter into those associations.

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Figure 1.

Scale diagram of the arena and experimental room. The large circle represents the pool and smaller open circles represent the zones used for the analysis of the results from test trials. The solid black circle represents the platform. A, B, C, D refer to the four corners. The wavy lines represent a curtain that was open for training. Distal landmarks located at the corners of the room and in the centre of the East and West walls were all different black and white abstract posters. The door on the South wall led to the anteroom.

Figure 2. Mean escape latencies for the two groups of Experiment 1 during Stage 1 (left-hand panel) and Stage 2 (right-hand panel).

Figure 3. Mean time spent in the correct and incorrect search zones during the test at the end of Stage 1 (left-hand panel) and the end of Stage 2 (right-hand panel) for Experiment 1.

Figure 4. Mean escape latencies for the two groups of Experiment 2 during Stage 1 (left-hand panel) and Stage 2 (right-hand panel).

Figure 5.
Mean time spent in the correct and incorrect search zones during the test at the end of Stage 2 for the two groups of Experiment 2.

Figure 6.

Computer simulations based on Equations 1 and 2 for Stage 1 training for the landmark group (left-hand panel) and the place group (right-hand panel). The values of the parameters were $\lambda = 1$, $\alpha = 0.2$, $\beta = 1$. The initial associative strength of all cues was zero, except for the common cue which was .1.

Figure 7.

Computer simulations based on Equations 1 and 2 for Stage 2 for the place and landmark groups Experiment 1 (top row) and Experiment 2 (bottom row). The values of the parameters were $\lambda = 1$, $\alpha = 0.2$, $\beta = 1$. The initial associative strength of all cues was carried over from the end of the simulation of Stage 1.

Figure 8.
The predicted probabilities for approaching the correct corner during the test trial of Stage 2 derived from simulations based on Equations 1 and 2.

Table 1

Summary of the training given to the two groups for the two stages of Experiments 1 and 2. Each row depicts the configurations of stimuli that were used for one of the four training trials used in Stage 1, or the two training trials in Stage 2 (A, B, C and D = corners of the training arena; W, X, Y and Z = landmarks that could be attached to the corners; + and – = corners where the platform was located, or not located, respectively, on a given trial).

Group	Stage 1 (Experiments 1 & 2)	Stage 2 (Experiment 1)	Stage 2 (Experiment 2)
Place	AW+ BX– C– D–	AW+ B– CY– D–	A– BX+ C– DZ–
	AX+ BW– C– D–	AY+ B– CW– D–	A– BZ+ C– DX–
	A– B– CY+ DZ–		
	A– B– CZ+ DY–		
Landmark	AW+ BX– C– D–	AW+ B– CY– D–	A– BX+ C– DZ–
	AX– BW+ C– D–	AY+ B– CW– D–	A– BZ+ C– DX–
	A– B– CY+ DZ–		
	A– B– CZ– DY+		