

Asymmetry in the Discrimination of Length During Spatial Learning

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The ability of rats to solve a discrimination between two objects that differ in length was investigated in five experiments. Using a rectangular swimming pool, Experiment 1 revealed it is easier to locate a submerged platform when it is near the center of a long rather than a short wall. For Experiments 2–4, the objects were black or white panels pasted onto the gray walls of a square pool, with two long panels pasted to two opposing walls and two short panels pasted to the remaining walls. The platform was easier to locate when it was placed near the middle of a long rather than a short panel. This effect was found when the long panels were twice (Experiments 2–4) or four times the length of the short panels (Experiment 4). Experiment 5 demonstrated that rats can solve a discrimination between panels of length 15 and 45 cm more readily than when they are 70 and 100 cm. The results are consistent with the claim that generalization gradients based on stimulus magnitude are steeper for stimuli that are weaker rather than stronger than the stimulus used for the original training.

Keywords: spatial learning, cognitive map, magnitude discrimination, generalization of intensity

A prediction that is common to a variety of theories is that the acquisition of a discrimination between two stimuli from the same dimension will be unaffected by which of them is selected to signal the reinforcer (e.g., Blough, 1975; Pearce, 1994; Spence, 1936). There is, however, a small body of evidence that indicates this principle may not apply to discriminations involving stimuli differing in magnitude. Zielinski and Jakubowska (1977) trained rats using conditioned suppression and discovered that a discrimination between a loud noise that signaled shock and a weak noise followed by nothing was acquired more readily than when shock was signaled by the weak but not the loud white noise. The implication of this finding is that a discrimination between two stimuli that differ in magnitude is acquired more readily when the reinforcer is signaled by the stimulus of larger magnitude.

Support for this generalization can be found in a diverse range of tasks and species. Pelz, Gerber, and Menzel (1997) reported that a discrimination in honeybees with an odor of two different intensities was readily acquired when the reinforcer of sucrose was preceded by the intense odor, but when the weak odor indicated that sucrose would be delivered, there was no hint of the discrimination being solved. Turning to an experiment with birds, Watanabe (1998) trained four pigeons to discriminate between two and four red balls. The two birds who were trained with four balls

as the signal for food, and two balls as the signal for no food, acquired the discrimination more readily than the two birds who were trained with the opposite arrangement (for a related finding with bears as subjects, see Vonk & Beran, 2012). Finally, if a long duration stimulus is regarded as being of greater magnitude than one of shorter duration, then the asymmetry described above has also been reported with temporal discriminations. Kyd, Pearce, Haselgrove, Amin, and Aggleton (2007) and Todd, Winterbauer, and Bouton (2010) presented rats with an appetitive discrimination involving a short and a long auditory stimulus. The discrimination was acquired more readily when the occurrence of food was signaled by the long rather than short duration stimulus. For related findings, see Bouton and García-Gutiérrez (2006) and Bouton and Hendrix (2011).

This sparse, but diverse, collection of results points to the conclusion that discriminations based on differences in intensity, number, and duration do not follow the rules that are believed to apply to discriminations in general. We shall consider later why there may be an asymmetry in the ease with which discriminations based on stimulus magnitude are acquired, but first we want to determine whether this asymmetry can also be found in the spatial domain. In Experiment 1, rats were placed in a rectangular arena and required to solve a discrimination based on the short (S) and long (L) walls. One group received an L+ S− discrimination, where the goal was hidden beside the middle of a long, but not a short wall, whereas the other group was given the opposite training with an S+ L− discrimination. It seems natural to regard the long wall as being of larger magnitude than the short wall. On the basis of the foregoing findings, therefore, it would be expected that the L+ S− discrimination will be acquired more readily than the S+ L− discrimination. To our knowledge this prediction has never been tested in the proposed rectangular environment or, for that matter, any other environment where spatial learning has been investigated. The results from the experiment will thus be of interest because they might confirm the widespread generality of a

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phenomenon that poses a challenge to our understanding of how discriminations are solved.

A successful outcome to the experiment will also have important implications for theories concerned with spatial learning. A number of these theories assume that as they navigate through an environment animals construct a global representation, or map. Such a cognitive map might consist of all the salient landmarks that are encountered (e.g., Tolman, 1948; O'Keefe & Nadel, 1978) or be based principally on the boundaries surrounding the environment in question (Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990). In the case of Experiment 1, therefore, it would be assumed that animals will construct a representation of the overall shape of the rectangular arena, and identify on it where the goal is situated. As the theories stand, there is no reason to suppose that this task will be easier when the goal is near the middle of a long rather than a short wall, and thus it follows that the L+ S− discrimination will be acquired as readily as the S+ L− discrimination. A failure to confirm this prediction would suggest, at the very least, that this set of theories is in need of revision.

Experiment 1

Two groups of rats were trained to escape from a rectangular pool by swimming to one of two submerged platforms. For the L+ S− group the platforms were situated beside the centers of the two long walls, whereas for the S+ L− group, the platforms were placed beside the centers of the two short walls. If a discrimination based on stimulus magnitude is easier when the reinforcer is paired with the large rather than the small stimulus, then the L+ S− group will acquire a stronger preference for searching in the region where the platform is situated than the S+ L− group. This prediction was tested by placing the rats in the pool for a test trial in the absence of the platforms and recording how much time they spent near the center of each wall.

We were concerned that being required to find the centers of the walls without any additional cues might make the task too difficult for both groups. Accordingly, for all subjects an identical landmark was placed at the center of the top of each of the four walls of the arena. The landmarks would thus help rats to find the center of a wall, but they would not be of any assistance as far as identifying whether a platform was situated beside a short or a long wall.

Method

Subjects. The subjects were 24 male hooded Lister rats supplied by Harlan Olac (Bicester, Oxon, United Kingdom). They had previously been used for a conditioning experiment in operant chambers and were approximately 4 months old at the start of the experiment. All rats were housed in pairs in a temperature-controlled environment (approximately 20°C) that was continuously illuminated for 12 hr per day, with lights on at 07:00. Rats had free access to food and water throughout the experiment. They were randomly assigned in equal numbers to the two groups at the start of the experiment.

Apparatus. The experiment was conducted in a white circular pool that was 2 m in diameter and 60 cm deep. The pool was filled to a depth of 30 cm with a mixture of water and white opacifier (500 ml, OP303B, supplied by Rohm and Haas, United Kingdom).

This opaque mixture was maintained at a temperature of 25 °C (± 2 °C) and was changed daily. A white circular ceiling with a diameter of 2 m was suspended 1 m above the top edge of the pool, and was fitted with eight 45-W recessed spotlights. Each light was 22.5 cm in diameter. The lights were spaced evenly in a circle with diameter 1 m, concentric with the pool. In the center of the ceiling was a 30-cm hole into which a wide-angle video camera was fitted. Images from the camera were relayed to a monitor in an adjacent room, together with recording equipment, and a PC with tracking software (Watermaze Software, Edinburgh, United Kingdom). This software could be used to record each rat's swim path and to measure the amount of time spent in different areas of the pool. Four white polyurethane boards were inserted into the pool to create the rectangular arena. The longer walls were 1.8 m long, and the shorter walls were 90 cm; both had a height of 60 cm. The boards were suspended vertically into the pool by being attached to aluminum rods that rested on the upper edges of the pool. A gray curtain was drawn around the pool throughout the experiment to exclude any extramaze cues. It was hung at a distance of 25 cm beyond the edge of the pool and covered the entire height from the ceiling to below the pool's edge.

Two identical, circular, clear-Perspex platforms with a diameter of 10 cm were placed into the pool. Each platform was mounted on a column so that its upper surface was 2 cm below the surface of the water. Each platform was positioned with its center 15 cm from the midpoint of one of the four walls of the arena, on a notional line that was perpendicular to the wall.

Four identical balls, 10 cm in diameter and covered in colored cartoon characters, were used as landmarks. They were supported by Perspex horizontal rods attached to the middle of the top of each wall. The centers of the landmarks were positioned 15 cm away from wall to which they were attached. When a landmark was above a platform its center was directly above the center of the platform.

Procedure. The two platforms were situated beside the long walls for the L+ S− group and beside the short walls for the S+ L− group. Rats were trained for four trials per session, with an intertrial interval (ITI) of approximately 5 min. Each training trial started with a rat being released gently into the pool facing into a corner. Rats were released from each of the four corners once in a session, in a randomly selected sequence. Once the rat found the platform, it was allowed to remain on it for 20 s before being picked up, dried with a towel, and returned to a carrying cage for the duration of the ITI. If the rat failed to find the platform in 60 s, it was guided to the platform by the experimenter placing his finger just in front of the rat's snout. During the trials, the experimenter remained in a small room adjacent to the testing room, where the pool could be observed on a monitor. To ensure that subjects relied on the walls of the rectangular pool to find a platform, the arena was rotated between trials by 90, 180, or 270 degrees.

Training was conducted in the above manner for every trial of the first five sessions, and for the first three trials of Session 6. The final trial of Session 6 was a test in which the rat was released from the center of the pool in the presence of the landmarks, but not the platforms, and allowed to swim for 60 s.

Performance during the training trials was recorded in two ways: escape latency and correct choices. Escape latency was defined as the time taken by a rat to climb onto a platform after

being released into the pool, up to a maximum of 60 s. For the purposes of defining a correct choice, four circular search zones with a diameter of 30 cm were identified within the pool. The centers of the zones were directly beneath the centers of the four landmarks. If a zone normally contained a platform, it was regarded as a correct search zone; if a platform was never situated in a zone, it was regarded as an incorrect search zone. On every trial a record was taken of whether a rat entered a correct before an incorrect zone, which was regarded as a correct choice. During the test trial at the end of the experiment, the amount of time spent in each of the four search zones was recorded. Statistical analysis for every experiment was conducted with $p < .05$.

Results

The left-hand panel of Figure 1 shows the mean percentage of trials on which a correct choice was made by the two groups for the six sessions of the experiment. The performance of the L+ S- group was initially superior to that of the S+ L- group, but by the end of training both groups were heading directly toward a correct search zone on the majority of trials. A possible explanation for the relatively high percentage of correct choices on Session 1 by Group L+ S- is that this group for some reason had an unconditioned preference for the correct over the incorrect search zones. This possibility is made unlikely by the fact that on the first trial of Session 1, only 7 out of 12 rats headed directly for the correct search zones in the L+ S- group. To compare the performance of the two groups, the mean percentage of correct choices for the six sessions of the experiment combined was calculated for each rat. A comparison of these scores revealed a significant difference between the groups, $t(22) = 2.53$. Further analysis, using one-sample tests, revealed that each group headed directly toward a correct search zone on more than 50% of the trials, $ts(11) > 5.45$.

The center panel of Figure 1 shows the mean escape latencies for the two groups throughout the experiment. The latencies for both groups declined rapidly as training progressed. A two-way analysis of variance (ANOVA) found a significant effect of session, $F(5, 110) = 45.00$, but no difference between the two groups nor an interaction between these variables, $F_s < 1$.

The results of the single test trial at the end of the experiment are shown in the right-hand panel of Figure 1. The L+ S- group

displayed an overwhelming preference for the correct over the incorrect search zones, whereas S+ L- group spent roughly the same amount of time searching in both pairs of zones. This impression is supported by the results of a two-way ANOVA, which found a significant overall effect of group, $F(1, 22) = 25.05$, a significant overall difference between correct and incorrect zones, $F(1, 22) = 58.19$, and a significant Group \times Zone interaction, $F(1, 22) = 76.94$. Simple effects analysis revealed a difference between the correct and incorrect zones for the L+ S- group, $F(1, 22) = 134.47$; but not for the S+ L- group, $F < 1$.

Discussion

The results demonstrate for the first time that animals find it easier to approach a long than a short boundary wall of their environment, if a goal is situated near the former rather than the latter. This finding is consistent with the conclusion that discriminations based on stimulus magnitude progress more readily when the larger rather than the smaller stimulus is paired with reward. Moreover, they show for the first time that this conclusion applies to spatial learning.

Some comment is needed concerning the disparity between the results of the test trial, and the training trials for the S+ L- group. By the end of the training stage this group headed directly for a correct search zone on the majority of trials, which implies it was able to differentiate between the long and short walls. In contrast, when the test trial was conducted, the group failed to show any hint of a preference for the correct over the incorrect search zones, which implies a complete inability to tell the difference between the long and short walls. One possible explanation for this conflicting pattern of results is that on being released from a corner of the pool during the training stage, the S+ L- group acquired the habit of heading for the nearest landmark, which was always beside the short wall. The success of this strategy might then have overshadowed learning about the significance of the lengths of the walls for finding the platform. As subjects were released from the center of the pool for the test trial, adoption of this strategy by the S+ L- group would be unlikely to lead rats to the correct search zones and might even take them to the incorrect zones.

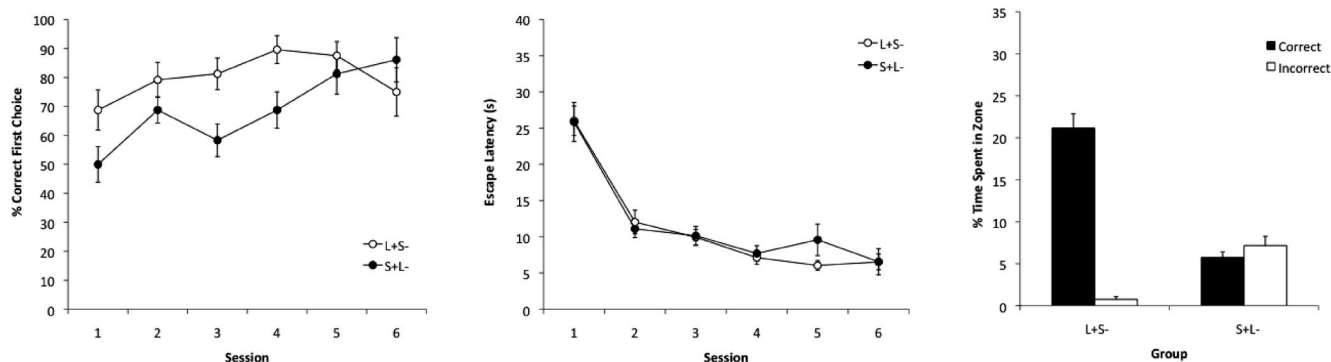


Figure 1. The mean percentages of correct choices (left-hand panel), and the mean escape latencies (center panel) for the 6 sessions of training for the two groups of Experiment 1, and the mean percentage of time spent by the two groups in the correct and incorrect search zones for the test trial of the experiment (right-hand panel). Error bars represent $\pm SEM$.

Experiment 2

Experiment 2 was conducted to overcome the foregoing shortcoming with the design of Experiment 1. The experiment was based on Experiment 1, except that rats were required to find a submerged platform in a square pool with four gray walls. Long white panels were attached to one pair of opposing walls and short white panels were pasted to the remaining two walls (Figure 2). A submerged platform was situated by the center of each of the long but not the short panels for the L+ S- group, whereas for the S+ L- group the platforms were situated by the centers of the short but not the long panels. After being trained to escape from the pool, rats received a test trial in the absence of the platforms. The use of a square pool ensured the distance from a corner to a platform beside a short panel was the same as for a platform beside a long panel. In contrast to the previous experiment, therefore, there is no good reason for believing that the layout of the pool will enable rats to solve the discrimination without making reference to the lengths of the panels. In keeping with Experiment 1, identical landmarks were attached to each of the four walls.

Method

Subjects. The subjects were 24 male rats from the same stock, housed in the same way, and of similar experience and age to those used for Experiment 1. They were allocated randomly to two groups of equal size at the start of the experiment.

Apparatus. The experiment was conducted in the pool that was used for Experiment 1. Four gray polyurethane boards were used to create the square-shaped arena. They were 141 cm in length, 60 cm high, and 4 mm thick. Each wall was partially covered by a panel of white plastic adhesive film (Deco d-c-fix)

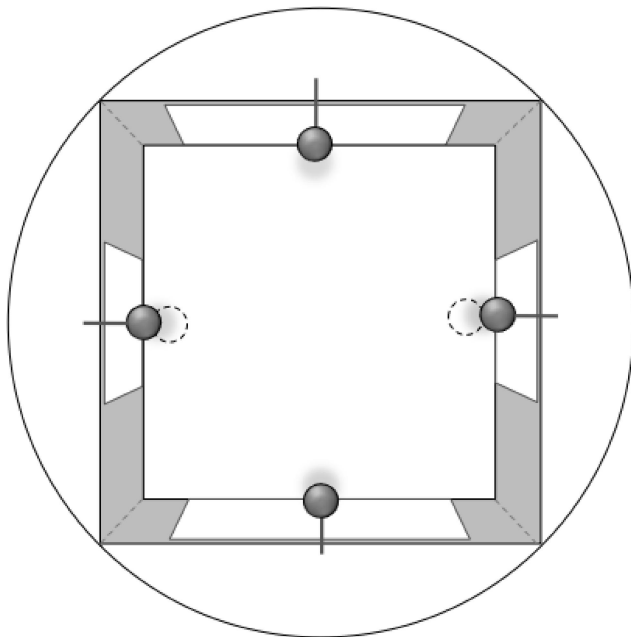


Figure 2. A plan showing the arrangement of landmarks (filled circles), platforms (dashed circles) and the short and long white panels in the square, gray pool for the S+ L- group of Experiment 2.

with a height of 45 cm and cut to lengths of either 50 cm or 100 cm. The center of each panel was superimposed on a notional vertical line passing through the center of the wall (Figure 2). The panels on each pair of opposing walls were of the same length. The bottom of the white panels extended below the water surface, and the top of the panel was 2 cm below the top edge of the wall. The remaining details concerning the apparatus, including the way in which the landmarks, the platforms and the search zones were positioned was the same as for Experiment 1.

Procedure. There were 10 sessions of training with four trials per session. Each training trial started with a rat being released gently into the pool facing one corner, at a distance of 0, 25, or 50 cm from the corner. The distance of the release point from the corner was varied randomly, with the constraint that over three successive sessions each distance was selected on four occasions. The two platforms were situated beside the long panels for the L+ S- group and beside the short panels for the S+ L- groups. On the day after the completion of Session 10 of training, a single test trial was conducted with the platforms removed from the pool. Procedural details that have been omitted were the same as for Experiment 1.

Results

The left-hand panel of Figure 3 shows the mean percentage of correct choices for each group throughout the experiment. As might be expected, both groups headed directly for a correct search zone on approximately half the trials at the outset of the experiment. There was a slight improvement in this performance as training progressed for both groups. To compare the performance of the groups, the mean percentage of correct choices was calculated for each rat for the final five sessions of training. A comparison of these scores failed to reveal a statistically significant difference between the groups, $t(22) = 1.27$. Each group's performance during the final five sessions was further tested against chance performance of 50% using one-sample t tests. During the last five sessions, the first choice performance of S+ L- group was not different from chance, $t(11) = 1.69$, but L+ S- group did show a significant preference for the correct length above chance, $t(11) = 3.83$.

The mean escape latencies for the two groups are shown for the experiment in the center panel of Figure 3. The latencies were slightly shorter for the L+ S- than the S+ L- group, and this observation was supported by a two-way ANOVA with the factors of group and session. There was a significant effect of group, $F(1, 22) = 4.47$, and of session, $F(9, 198) = 41.42$, but the interaction was not significant, $F < 1$.

The right-hand panel of Figure 3 shows the mean percentages of time spent by the two groups in the correct and incorrect search zones during the test trial with the platforms removed from the pool. From the left-hand side of the figure it is evident that the L+ S- group spent considerably more time in the correct than the incorrect search zone, whereas the remaining results make clear that the S+ L- group spent a similar amount of time in the different zones. A two-way ANOVA supported this description, as it revealed a significant Group \times Zone interaction, $F(1, 22) = 7.51$, in addition to an overall effect of zone, $F(1, 22) = 9.57$, but not group, $F < 1$. Subsequent tests of simple main effects confirmed that the L+ S- group spent significantly more time in the

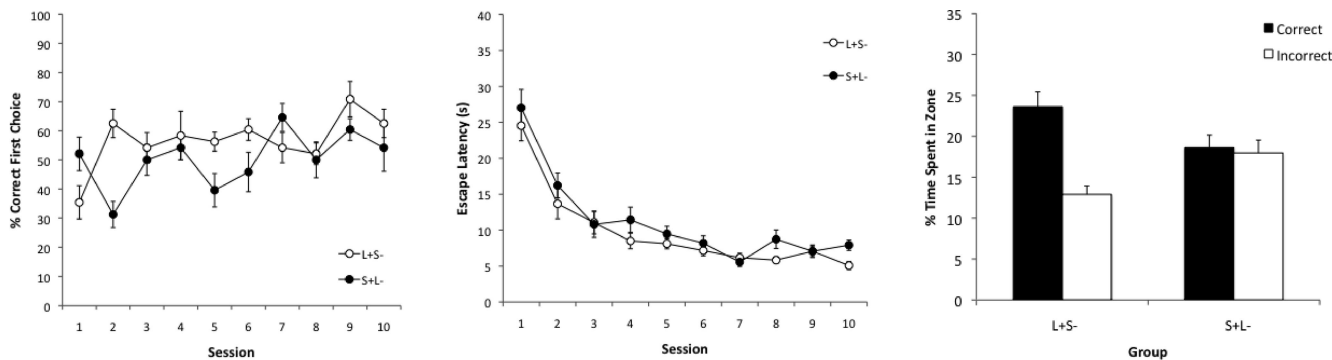


Figure 3. The mean percentages of correct choices (left-hand panel), and the mean escape latencies (center panel) for the 10 sessions of training for the two groups of Experiment 2, and the mean percentage of time spent by the two groups in the correct and incorrect search zones for the test trial of the experiment (right-hand panel). Error bars represent \pm SEM.

correct than the incorrect search zones, $F(1, 22) = 17.01$, but the S+ L- group did not, $F < 1$.

Discussion

Despite the use of a different arena, the results from the test trials of the present study revealed a similar outcome to that observed in Experiment 1. An L+ S- discrimination was again acquired more readily than the opposite S+ L- discrimination. It thus appears that the asymmetry in the acquisition of these discriminations is not a consequence of the manner in which the stimuli were arranged in Experiment 1. Instead, the results lend further support to the conclusion that discriminations based on the magnitude of a stimulus progress more readily when reward is signaled by the larger rather than the smaller member of the pair.

The results from the test trials of the first two experiments bear a striking similarity to each other, despite the differences in the apparatus that was used. Thus, in both cases, the L+ S- group exhibited a clear preference for the correct over the incorrect search zone, while the S+ L- group failed to show even a modest preference for one type of zone over the other. A comparison of the results from the training trials, however, reveals a different pattern of responding in the two experiments. The two groups in Experiment 1 displayed a substantially stronger tendency to head directly to a correct search zone after being released into the pool than their counterparts in Experiment 2. Presumably, this difference occurred because in Experiment 1 it was possible to find the platform by referring to the distance of the landmarks from the point of release, as noted in the discussion to Experiment 1. Such a strategy was not open to the rats in Experiment 2.

Experiment 3

One purpose of Experiment 3 was to replicate the findings from the previous study using black, rather than white panels. At first sight, this change might be thought to be unimportant and that it would have little effect on the outcome of the experiment. A study by Horne and Pearce (2011) implies, in contrast, that this manipulation might not be of trivial significance. Rats were trained to find a submerged platform in a gray, rectangular pool with A4 cards pasted to the walls beside the platform. If the cards were

white then they overshadowed learning about the significance of the shape of the pool for finding the platform, but if the cards were black then they enhanced such learning. Given this pattern of results it would be foolish to assume automatically that a replication of the previous experiment will be successful using black rather than white panels against the gray walls of the square.

A second purpose of the experiment was to assess the importance of the four identical landmarks that were situated at the midpoint of the four walls of the pools in Experiments 1 and 2. The landmarks were not expected to influence the discriminations in the two experiments because they were identical and thus gave no hint as to where the two platforms were located. On this basis, therefore, the results from both experiments would also be expected to occur if training took place in the absence of the landmarks. Four groups were used to test this prediction. A Landmark L+ S- and Landmark S+ L- group were trained and tested in the same way as their counterparts in Experiment 2, except that the panels attached to the walls of the square pool were black rather than white. The same training and testing was given to the remaining two groups, No Landmark L+ S- and No Landmark S+ L-, but with the landmarks absent throughout the experiment.

The results from the training stage of Experiment 2 provided rather little insight into how quickly the discrimination was acquired, because the increase in the percentage of correct choices as training progressed was slight. In the hope of improving performance during the training trials, the manner in which the rats were released into the pool was based on the procedure for Experiment 1, where a considerable improvement in performance during training was observed, rather than the different method used for Experiment 2. After five sessions of training it was evident that this manipulation was ineffective. Accordingly, in order to gain an indication of the effectiveness of the first five training sessions, a test trial was conducted after Session 5, as well as after Session 10.

Method

Subjects. The 36 rats were from the same stock, of approximately the same age and experience, and housed in the same way as for Experiment 1. The rats were assigned in equal numbers to the four groups at the start of the experiment.

Apparatus. The apparatus was the same as for Experiment 2, except that the white panels were replaced with black panels, which were of the same material and same dimensions as for Experiment 2.

Procedure. Apart from two differences, the training for the Landmark L+ S- and Landmark S+ L- groups was same as for the L+ S- and S+ L- groups, respectively, of Experiment 2. The first difference was the inclusion of a test trial between Sessions 5 and 6 of training, which took place on a separate day. The second difference was that for the training trials rats were always released from a corner of the pool. The No Landmark L+ S- and No Landmark S+ L- groups were trained and tested in the same way as first two groups, except that no landmarks were present in any session.

Results

Figure 4 shows the mean percentages of correct choices for the 10 sessions of training for the groups trained with the landmark

(upper left-hand panel), and without the landmark (lower left-hand panel). All four groups behaved as if the search zone they entered first was selected randomly. To compare the performance of the four groups, the mean percentage of correct choices made by each rat during the final five sessions of training was calculated. A two-way ANOVA with the factors of landmark (present or absent) and length (whether the short or long panel was correct) revealed no effect of landmark, length, or Landmark \times Length interaction, $F_s < 1$. Separate analyses were conducted to test each group's performance during the last five sessions against chance of 50% with one-sample t tests. The analyses revealed that none of the groups showed a preference that was significantly different from chance, $t_s(8) < 1.51$.

The mean escape latencies for the two groups trained with the landmark are shown in the upper right-hand panel of Figure 4, while the results for the groups trained without the landmarks are displayed in the lower right-hand panel. There was a marked reduc-

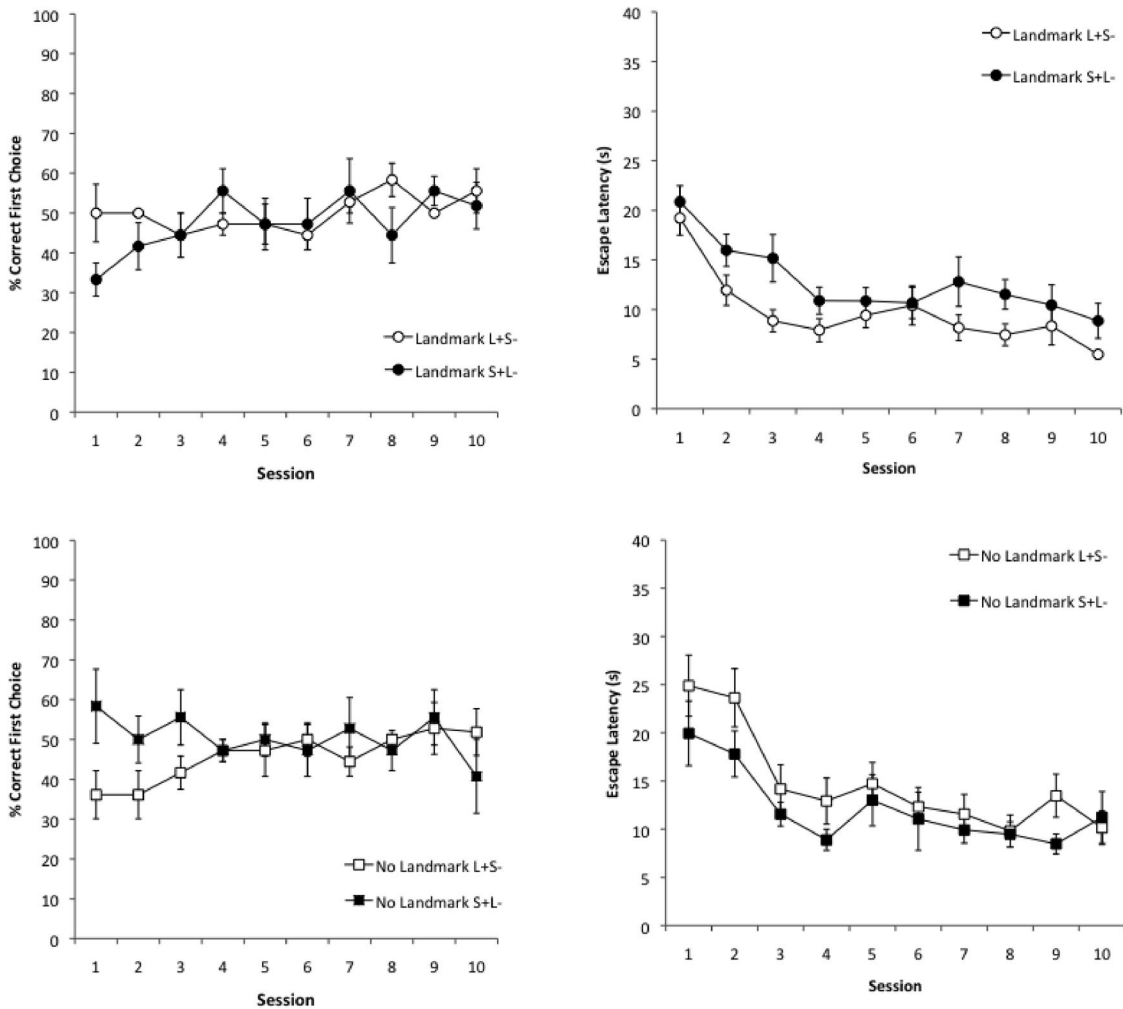


Figure 4. The mean percentages of correct choices (left-hand panels), and the mean escape latencies (right-hand panels) for the 10 sessions of training for the four groups of Experiment 3; the upper panels display the results for the groups trained with the landmarks in the arena, the results for the groups trained without the landmarks are displayed in the lower panels. Error bars represent \pm SEM.

tion in the latencies for each group as training progressed. A three-way ANOVA with the factors of landmark, length and session revealed a significant main effect of session, $F(9, 288) = 21.96$, as well as a Landmark \times Length interaction, $F(1, 32) = 5.91$. Analyses of simple main effects based on the significant interaction revealed that the escape latencies for the Landmark L+ S- group were significantly shorter than for the No Landmark L+ S- group $F(1, 32) = 9.20$. The remaining comparisons were not significant. $F_s(1,32) < 3.44$. Thus, the presence of the landmark reduced the time taken to find the platform in the groups received the L+ S-, but not the S+ L- discrimination. The ANOVA further revealed that the effect of landmark, $F(1, 32) = 3.46$, was not significant and nor were the interactions of Landmark \times Session, $F(9, 288) = 1.47$, Length \times Session, $F < 1$; and Landmark \times Length \times Session, $F < 1$.

The difference between the results from the two test sessions was slight, and they have therefore been combined for the sake of ease of presentation. The left-hand panel of Figure 5 shows the mean percentage of time spent in the correct and incorrect search zones for the two groups trained with the landmarks, while the equivalent results for the groups trained without the landmarks can be seen in the right-hand panel. From the figure it is evident that the only group to express a preference for the correct over the incorrect search zones was the Landmark L+ S- group. A three-way ANOVA with the factors of length, landmark and zone revealed a significant three-way interaction, $F(1, 32) = 5.41$. Analyses of simple main effects confirmed that Group Landmark L+ S- showed a significant discrimination of the different lengths, $F(1, 32) = 23.95$, but all other groups failed to do so, $F_s < 1$. The ANOVA also revealed significant effects of zone, $F(1, 32) = 15.36$, length, $F(1, 32) = 14.15$, and landmark, $F(1, 32) = 17.90$. The interactions of Zone \times Length, $F(1, 32) = 5.69$, Zone \times Landmark, $F(1, 32) = 4.67$, but not Length \times Landmark, $F(1, 32) = 1.09$, were also significant.

Discussion

The results from test trials for the two groups who were trained with the four landmarks attached to the walls of the square were

very similar to those from the previous experiment. The L+ S- discrimination was again acquired more successfully than the S+ L- discrimination. The fact that this outcome was found with black rather than white panels extends the generality of our findings. The asymmetry in the acquisition of the discrimination between the large and small panels was confined to the groups trained with landmarks. Neither of the groups trained without the landmarks showed any beneficial effect of the training they received. In view of the failure of the Landmark S+ L- group to make any progress with its discrimination, the poor performance in the No Landmark S+ L- is hardly surprising. The failure for the No Landmark L+ S- group to acquire the discrimination, however, is not so easy to understand, given the successful performance of the Landmark L+ S- group. The results from the two L+ S- groups thus suggest that the presence of landmarks is necessary if their discrimination is to be solved, even though the landmarks do not indicate which of the four search zones contain the platforms. The reason why the landmarks were so helpful for Group Landmark L+ S- is difficult to determine. Presumably, their absence in Group No Landmark L+ S- made it harder to find the center of the panels, but why this in turn should make it difficult to differentiate between the long and short panels is not clear.

The results from the two groups trained with the landmarks, together with the results from the previous experiments, make a strong case for believing that rats find it easier to solve an L+ S- than an S+ L- discrimination. The reasons for this asymmetry, however, remain to be determined. A mundane possibility is that the groups trained with the landmarks learned rather little about the significance of the length of the panels, and rather more about the significance of their color. For both groups, the platform was always situated by the black rather than gray segments of the walls of the pool. When the groups were placed in the pool for the test trial they might then have headed for any black panel, selected at random. Given that the long panels are, of necessity, larger than the short ones, rats would be more likely to look at and then head toward a long rather than a short panel. This tendency alone would

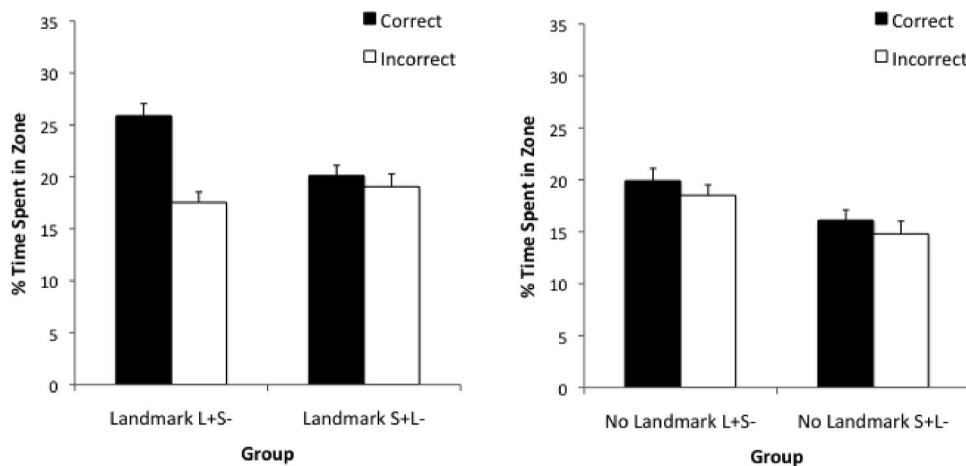


Figure 5. The mean percentage of time spent in the correct and incorrect search zones for the groups trained with (left-hand panel), and without the landmarks (right-hand panel) during the test trial of Experiment 3. Error bars represent SEM.

then result in superior performance in the L+ S− than the S+ L− condition.

Although it is hard to refute the foregoing explanation for the two groups trained with a landmark, if it is correct then a similar pattern of results should have been seen with the two groups trained without a landmark. Indeed, according to this account, it is particularly hard to understand why the No Landmark L+ S− group failed to exhibit a preference for the long over the short panels during the test trial. It is not the case that the group trained without the landmarks failed to appreciate the significance of the centers of the panels. Each search zone occupied 3.55% of the area of the pool. Hence, if subjects searched at random during the test trials they would spend 7.1% of their time in the correct search zones, as well as in the incorrect search zones. Inspection of Figure 5 indicates that this figure is substantially lower than the actual time spent in both pairs of zones, which confirms that the two groups trained without landmarks appreciated the importance of searching near the centers of the panels. Thus, if the asymmetry in the acquisition of the discrimination observed with the groups trained with landmarks was attributable to nothing more than the long black panels being easier to detect than the short ones, then a similar effect should have been seen in the groups trained without landmarks.

Experiment 4

A surprising aspect of the results from all of the above experiments is the failure of the groups trained with the S+ L− discrimination to show any preference at all for the search zones by the short rather than the long panels, or walls. Conceivably, whatever was responsible for this failure, was also responsible for the asymmetry in the ease of acquisition of the L+ S− and S+ L− discriminations. If this were the case, then finding a way of helping rats to solve the S+ L− discrimination might result in it being acquired as readily as the converse L+ S− discrimination. With this rationale in mind, the next experiment included four groups, all of which were trained with the landmarks used for the above experiments, and with black panels. Groups 100+ 50− and 50+ 100− were trained in the square pool with two 100-cm panels on opposite walls, and two 50-cm panels on the remaining walls. A platform was placed beside each of the long panels for the 100+ 50− group, and beside each short panel for the 50+ 100− group. This treatment is the same as for the two groups trained with the landmarks in Experiment 3, and we anticipated that the 100+ 50− group would acquire a preference for the correct search zones, while the 50+ 100− group would not.

The remaining two groups received the same training, but with panels that were either 100 cm or 25 cm in length. For the 100+ 25− group the platforms were located beside the long panels, and it was expected this group would acquire a strong preference for the long over the short panel. The use of panels of such different lengths was expected to facilitate the solution of the S+ L− discrimination, and thus enable the 25+ 100− group to exhibit a preference for the short over the long panels during the test trials. If the asymmetry observed in the previous experiments depends solely on the failure to master the S+ L− discrimination, because the difference between the lengths of the panels was too small, then there may now be no difference between the performance of the 100+ 25− and 25+ 100− groups. On the other hand, if the

asymmetry observed in the previous experiments is a manifestation of a general characteristic of discriminations based on stimulus magnitude then, once again, the L+ S− discrimination will be acquired more readily than S+ L−.

The two previous experiments that took place in the square pool involved 10 sessions of training. In the present study this number was increased to 15 to determine whether extended training might result in a difference between the L+ S− and S+ L− conditions being evident during the training trials.

Method

Subjects. The subjects were 24 rats from the same stock, of approximately the same age, and of the same experience as those for Experiment 1. They were housed in the same manner as for the previous experiments. At the start of the experiment rats were randomly assigned in equal numbers to the four groups.

Apparatus. The apparatus, including the landmarks, was the same as for Experiment 3, except that panels with a width of 25 cm were included in the experiment. In keeping with the other panels, they were attached to the middle of the gray walls and extended from below the surface of the water to 2 cm from the top edge of the wall. All the panels were black.

Procedure. The procedure was the same as for the two groups trained with the landmarks in Experiment 3, with the exception that there were 15 sessions of training, rather than 10. A test trial was conducted on the day following Sessions 5, 10, and 15. For the 100+ 50− and the 50+ 100− groups, one pair of opposing walls of the pool displayed panels that were 100 cm wide and the other pair displayed panels that were 50 cm wide. For the 100+ 25− and the 25+ 100− groups the opposite walls of the square displayed panels that were 100 cm and 25 cm wide. The platform was situated beside the short panels for the 25+ 100− and 50+ 100− groups, and beside the long walls for the 100+ 50− and the 100+ 25− groups.

Results

The mean percentage of correct choices for the 15 sessions of training can be seen in the upper left-hand panel of Figure 6 for the 100+ 50− and 50+ 100− group, and in the lower left-hand panel for the 100+ 25− and the 25+ 100− groups. Despite the extended training, neither of the groups trained with short panels of 50 cm acquired a preference for heading toward a correct than incorrect search zone. There was, however, an indication of such a preference developing in the groups trained with short panels of 25 cm. In order to compare the performance of the four groups individual mean percentages of correct choices were calculated for the final five training sessions. A two-way ANOVA of these data with the factors of arena (whether the short panel was 25 or 50 cm) and length (whether the platform was beside a short or long panel) revealed a significant effect of arena, $F(1, 20) = 22.25$, reflecting that the choice accuracies were overall higher in 100+ 25− and 25+ 100− groups. There was also a significant effect of length, $F(1, 20) = 5.95$, reflecting the better choice performance from the two L+ S− groups compared with the S+ L− groups. Analyses with one-sample *t* tests (two-tailed) against chance of 50% revealed that choice accuracies were higher than the chance level in all groups, $t(5) > 2.71$, except Group 50+ 100−, $t(5) = -1.00$.

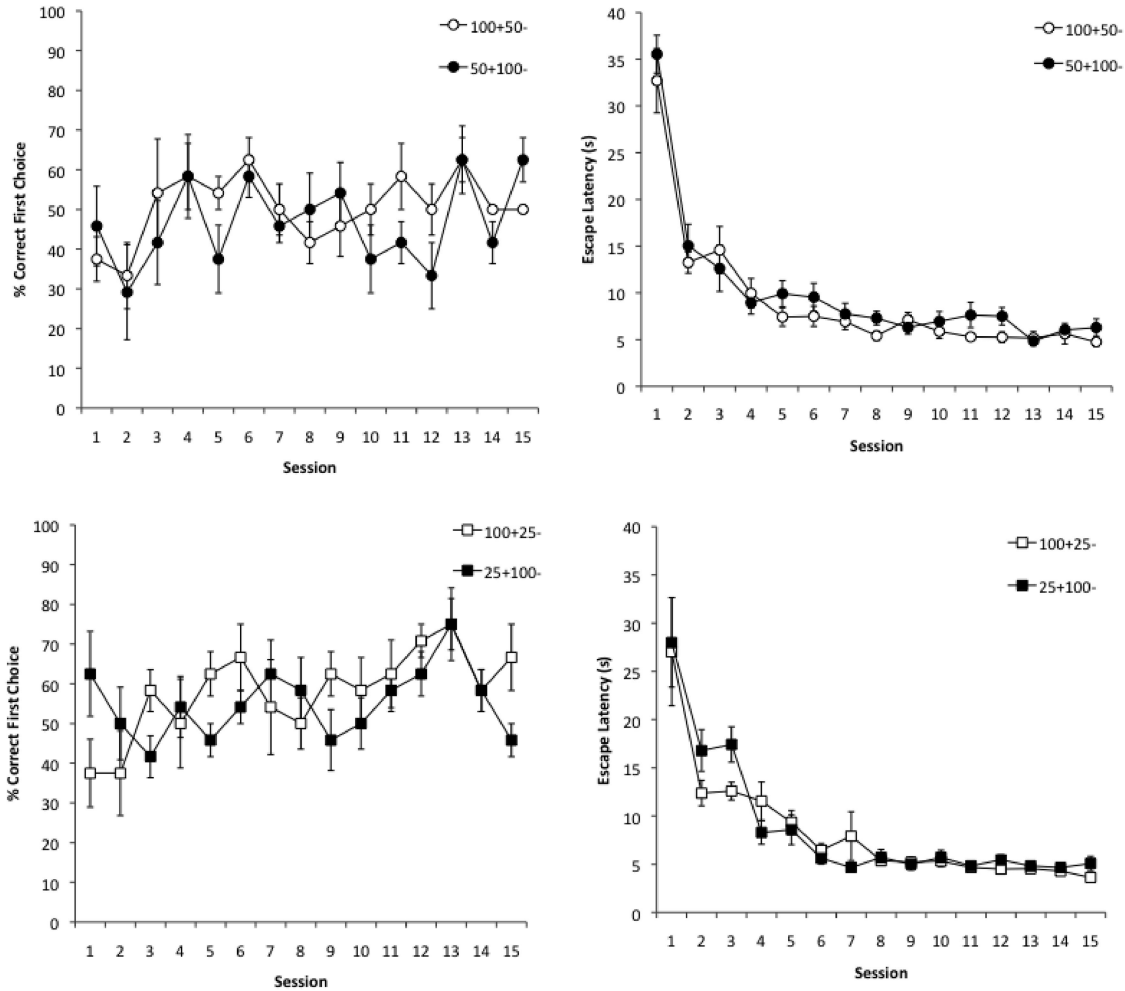


Figure 6. The mean percentages of correct choices (left-hand panels), and the mean escape latencies (right-hand panels) for the 15 sessions of training for the four groups of Experiment 4; the upper panels display the results for the groups trained with the 50-cm short panels, the results for the groups trained with the 25-cm short panels are displayed in the lower panels. Error bars represent \pm SEM.

The mean escape latencies for the four groups during the 15 sessions of training are shown in the right-hand panels of Figure 6. An Arena \times Length \times Session ANOVA revealed a significant effect of arena, $F(1, 20) = 4.73$, reflecting that the groups trained with 100- and 25-cm panels found the platform more swiftly than the other two groups trained with 100- and 50-cm panels. There was also a significant effect of session, $F(14, 280) = 81.55$. There was no other significant main effect or interaction, $F_s(1,20) < 1.89$, and $F_s(14,280) < 1.49$.

The results of the three test trials were similar and they have therefore been combined for ease of presentation. The left half of Figure 7 displays a now familiar pattern of results for the groups for whom the length of the short panel was 50 cm. The 100+ 50- group exhibited a strong preference for the correct over the incorrect search zones during the test trials, whereas the 50+ 100- group spent approximately equal amounts of time in each of the zones. A similar asymmetry in the acquisition of the discrimination was also seen with the 100+ 25- and 25+ 100- groups but, on

this occasion, both groups expressed a preference for the correct over the incorrect search zones.

An ANOVA with the factors of arena, length and zone revealed a significant effect of zone, $F(1, 20) = 59.74$, but the effects of length and arena were not significant, $F_s(1,20) < 3.99$. The Arena \times Zone, $F(1, 20) = 10.07$, and the Length \times Zone, $F(1, 20) = 12.77$, interactions were significant, but the Length \times Arena and the three-way interaction were not significant, $F_s < 1$. The significant Length \times Zone interaction shows that for both groups combined training with the L+ S- discrimination was more successful than with the S+ L- discrimination. The significant Arena \times Zone interaction indicates that the discrimination by the two groups trained with a 25-cm short panel was more pronounced than for the groups trained with the 50-cm short panel. Finally, comparisons for individual groups of the time spent in the two search zones showed that all groups spent significantly more time in the correct than the incorrect search zones, $t_s(5) > 4.04$, apart from Group 50+ 100-, $t(5) = 0.72$.

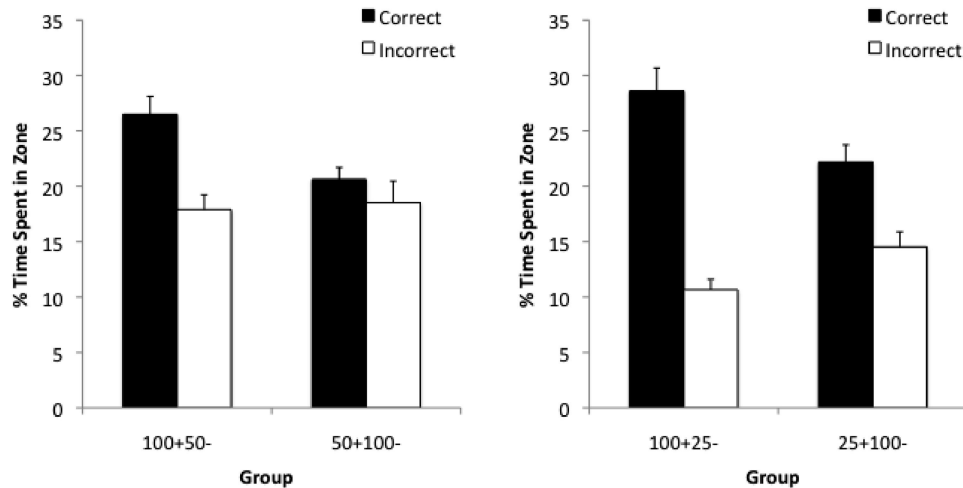


Figure 7. The mean percentage of time spent in the correct and incorrect search zones for the groups trained with the 50-cm short panels (left-hand panel), and with the 25-cm short panels (right-hand panel) during the test trial of Experiment 4. Error bars represent *SEM*.

Discussion

The results from the 100+ 50– and 50+ 100– groups merit little comment, as they replicate findings from Experiments 2 and 3 using very similar methods of training. The results from the remaining two groups are of more interest because they demonstrate the asymmetry in performance recorded in the previous experiments can be found when the small stimulus is only one quarter of the length of the long stimulus, rather than half the length. This larger difference between the short and long stimuli enabled the S+ L– discrimination to be mastered in the 25+ 100– group. Even so, the discrimination was not acquired as effectively as for the 100+ 25– group. The present experiment thus confirms that the asymmetry in the acquisition of discriminations based on short and long stimuli does not depend upon the S+ L– task being impossible to solve. The asymmetry can also be seen when subjects are capable of acquiring a preference for the short over the long stimulus.

The results from the 50+ 100– and the 25+ 100– groups are also relevant to an issue raised in the discussion to Experiment 3. It was suggested that rats trained in the S+ L– condition find it difficult to express a preference for the short over the long panel because on being released into the pool they merely search for a black panel. Since the long panels occupy a greater area of the walls than the short panels, it is likely that by chance they will select a long panel in preference to a short panel, which will disrupt the acquisition of the S+ L– discrimination. It follows from this account, however, that the greater the disparity between the lengths of the long and short walls, the more likely will be the rat to head toward a black panel on being released into the pool. On this basis, therefore, it would be expected that the 25+ 100– group would not perform as well as the 50+ 100– groups during the test trials, whereas the opposite was found.

Experiment 5

We have argued that the discrimination of length in spatial learning is equivalent to any discrimination in which one magni-

tude is contrasted with another. If this is correct, then the ease with which a discrimination based on length is mastered will be governed by Weber's Law. That is, for a given difference between a pair of lengths, the discrimination will be easier to solve when the two lengths are of small rather than large magnitude. Experiment 5 tested this prediction with two groups, which both received an S+ L– discrimination in the same manner as for the previous experiment. For Group 15+ 45– the short walls were 15 cm wide, and the long walls were 45 cm wide; whereas for Group 70+ 100– the widths of the short and long walls, respectively, were 70 and 100 cm. According to Weber's Law, even though the difference between the two pairs of stimuli is the same value of 30 cm, the 15+ 45– discrimination will be acquired more readily than 70+ 100–. While such a result might not be surprising, it will lend force to our proposal that the discrimination of length during spatial learning can be regarded essentially as a magnitude discrimination. Furthermore, we argue shortly that the anticipated result may pose a problem for at least one account of how discriminations are solved.

Method

Subjects. The subjects were 32 male rats from the same stock, of the same age and experience, and housed in the same way as for Experiment 1. They were randomly assigned in equal numbers to the four groups at the start of the experiment.

Apparatus. The apparatus, including the landmarks, was the same as for the previous experiments, except that pairs of black panels with lengths of 15, 45, 70, and 100 cm were used. All the panels were 45 cm high, and panels of the same length were attached to opposite walls of the pool. In keeping with the previous experiments, the sides of each panel were equidistant from the corners created by the walls to which they were attached.

Procedure. There were 10 sessions of training, which were conducted in the same manner as for the previous experiment. The two test sessions, each of which contained a single test trial, took place on the day following the completion of Sessions 5 and 10 of training. The panels were 15 cm and 45 cm wide for the 15+ 45–

group, and 70 cm and 100 cm wide for the 70+ 100- group. A platform was situated beside the midpoint of each of the walls displaying a short panel for both groups.

Results

The mean percentages of correct choices and the mean escape latencies for the two groups during the training sessions can be seen in the left-hand and center panels, respectively, of Figure 8. There was an indication of a modest improvement in the number of correct choices, as training progressed, for the 15+ 45- group but not the 70+ 100- group. The mean escape latencies throughout the training stage were similar for the two groups.

A comparison of individual mean percentages of correct choices for the final five sessions of the experiment revealed a significant difference between the groups, $t(30) = 3.39$. Comparisons using one-sample tests revealed that the percentage of correct choices was no greater than that expected on the basis of chance for the final five sessions for Group 15+ 45-, $t(15) = 1.89$, but the choice accuracy of Group 70+ 100- was significantly below chance, $t(15) = -3.06$. A two-way ANOVA of individual mean escape latencies for each of the 10 sessions revealed a significant effect of session, $F(9, 270) = 60.66$. The effect of group, $F < 1$, and the Group \times Session interaction, $F(9, 270) = 1.73$, were not significant.

The right-hand panel of Figure 8 shows the mean percentage of time spent by the two groups in the correct and incorrect search zones for the two test trials combined. More time was spent in the correct than incorrect search zones by the 15+ 45- group, but not the 70+ 100- group. A two-way ANOVA revealed a significant Group \times Zone interaction, $F(1, 30) = 8.95$. Subsequent analyses showed that the 15+ 45- group spent significantly more time in the correct zone than in the incorrect zone, $F(1, 30) = 10.60$, but Group 70+ 100- did not, $F < 1$. In addition, the 15+ 45- group spent significantly more time in the correct zone than did Group 70+ 100-, $F(1, 30) = 4.69$, and less time in the incorrect zone, $F(1, 30) = 5.90$.

Discussion

Rats were able to solve an S+ L- discrimination when the stimuli were relatively short, 15 and 45 cm, but not when they were long, 70 and 100 cm, even though the difference between the stimuli was the same across each pair. Such a result is consistent with Weber's law, which stipulates that the size of the difference between two stimuli required for one to be regarded as larger than the other is proportional to the magnitude of the stimuli.

Although the results from the present experiment are hardly surprising, they pose a problem for certain theories of learning, including the influential Rescorla-Wagner theory (Rescorla & Wagner, 1972). A longstanding theoretical assumption is that when animals are presented with a discrimination between two stimuli, they will each excite a set of elements that can enter into associations with the trial outcome (e.g., Estes, 1950). To keep matters simple, the 15+ 45- discrimination might be regarded as a feature-negative, A+ AC-, discrimination in which A represents the set of elements created by the 15-cm wide panels, and C represents the additional elements that extend A by 30 cm to create a panel that is 45-cm wide. Likewise, the 70+ 100- discrimination can be regarded as B+ BC-, where B represents the elements created by the 70-cm wide panel and C represents the same elements as its namesake from the A+ AC- discrimination, which will again be necessary in order to extend the short panel by 30 cm to create the long panel. The salience of B might also be regarded as being greater than of A, because it represents a larger area. Given these assumptions, the Rescorla-Wagner (1972) theory then predicts that the B+ BC- discrimination will be acquired more readily than the A+ AC- discrimination. This prediction follows because, on each reinforced trial, B will gain more excitatory strength than A, which will then result in C gaining inhibitory strength more rapidly during B+ BC- than A+ AC- training. Because the difference in the predicted strength of responding on reinforced and nonreinforced trials is determined by the magnitude of the inhibition associated with C, it then follows that the B+ BC- (70+ 100-) discrimination will develop more rapidly than A+ AC- (15+ 45-). That is, the wrong outcome of the exper-

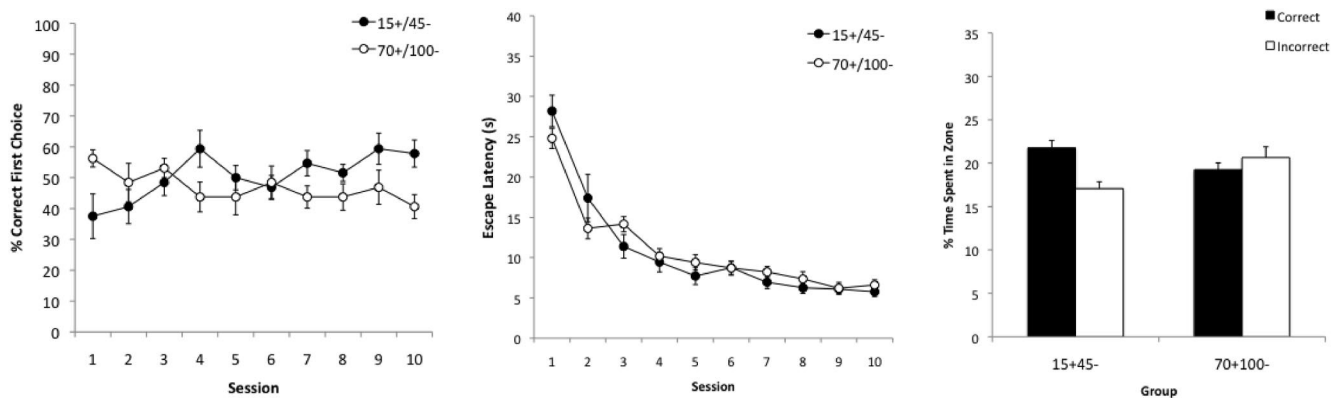


Figure 8. The mean percentages of correct choices (left-hand panel), and the mean escape latencies (center panel) for the 10 sessions of training for the two groups of Experiment 5, and the mean percentage of time spent by the two groups in the correct and incorrect search zones for the test trial of the experiment (right-hand panel). Error bars represent \pm SEM.

iment is predicted. An obvious response to this conclusion is to argue that the above characterization of the two discriminations is unsatisfactory in some way. It must be said, however, that we have adopted what may be regarded as the simplest, most straightforward method for decomposing the stimuli into elements, and it is not immediately clear how the Rescorla-Wagner (1972) theory might explain the results from Experiment 5.

Furthermore, treating the 15+ 45− and the 70+ 100− discriminations as A+ AC− and B+ BC−, respectively, does not pose a problem for all theories of conditioning. According to Pearce (1994), a discrimination between two patterns of stimulation involves each pattern entering into an association with the trial outcome. The ease with which the discrimination is solved is then related to the similarity between the two patterns. In the case of the foregoing feature-negative discriminations, the similarity between the reinforced and nonreinforced patterns will be determined by the relative salience of the common and the unique cue. When the common cue is weak relative to the unique cue, which will be the case for the 15+ 45− discrimination, then the similarity between the reinforced and nonreinforced patterns will be slight and the discrimination will be easy to solve. In the case of the 70+ 100− discrimination, the salience of the common cue will be high relative to the unique cue, the similarity between the reinforced and nonreinforced patterns will be strong, and the discrimination will be difficult to solve. Although the theory of Pearce (1994) can thus explain the results from the present experiment, it is unable to explain our remaining findings. A cardinal feature of the theory is the assumption that a discrimination between any two patterns of stimulation will be unaffected by which of them is paired with reward. It then follows that a S+ L− discrimination will be no more difficult than L+ S−.

An unexpected finding from the experiment is that toward the end of the training stage, the percentage of trials on which the 70+ 100− group headed directly toward a correct search zone was significantly less than expected on the basis of chance. In contrast, the same group did not show a preference for one search zone over the other during the test trial. In view of this conflicting pattern of results, little can be gained by discussing further the unexpected, and intriguing, significant effect.

General Discussion

In each of five experiments, rats were required to find a goal beside one of a pair of objects that differed in length. This discrimination was remarkably successful when the goal was beside the long object, but when the goal was beside the short object, it proved more difficult to solve. This asymmetry in the ease of solving the discriminations was demonstrated when the objects were the walls of a rectangular pool, and when they were panels attached to the walls of a square pool. Moreover, the asymmetry was found when the objects were black, and when they were white. The experiments provide the first demonstration of an asymmetry in the ease of acquisition of a spatial, long-short discrimination, but they are similar to findings from other discriminations involving stimulus magnitude. A small number of experiments were reviewed in the Introduction which involved discriminations based on intensity, number, and time. In each of these studies a discrimination was acquired more successfully when the reinforced stimulus was of larger magnitude than the nonreinforced stimulus. In

the first part of this discussion we shall consider explanations for this asymmetry; in the second part, we shall consider the implications of our findings for the proposals that animals navigate by means of either cognitive maps (e.g., Tolman, 1948) or mental snapshots (e.g., Collett & Collett, 2002).

According to a variety of authors, the solution to a discrimination based on a single dimension depends either upon individual stimulus elements (e.g., Blough, 1975; Hall, 1991; McLaren & Mackintosh, 2002; Rescorla, 1976) or configurations of elements (e.g., Pearce, 1994) entering into associations with an outcome. An important corollary of these proposals is that a discrimination between two stimuli, A and B, from the same dimension will be acquired just as readily when reward is signaled by A or B. To extend this analysis to the present experiments requires the elements that represent length to be specified. In the absence of any previous attempts to meet this challenge, it might be suggested that specific lengths are represented by different elements in the same way that different frequencies of light, say, are assumed to excite different elements. On this basis, then, the solution of a discrimination based on length should progress in the same way as one based on color, and a S+ L− discrimination will be acquired as readily as the opposite L+ S−. The failure to confirm this prediction suggests the need for an alternative way of understanding how discriminations based on lengths of objects are solved.

To explain why a discrimination between stimuli of different durations is easier when food is signaled by the longer rather than the shorter of the two (e.g., Bouton & García-Gutiérrez, 2006; Kyd et al., 2007), Bouton and Hendrix (2011) appealed to the feature-positive effect; their explanation can also be applied to the present results. They suggested that when a discrimination involves two stimuli of different durations then the short one can be construed as being composed of element A, and the long one as element A plus an element representing the difference between the long and short stimulus, B. A temporal L+ S− discrimination then becomes a feature positive, AB+ A−, discrimination and a S+ L− discrimination becomes a feature negative, A+ AB− discrimination. Because it is well established that a feature-positive discrimination is acquired more readily than a feature-negative discrimination (e.g., Hearst, 1978; Jenkins & Sainsbury, 1970)—the feature positive effect—it then follows that an L+ S− discrimination will be easier to acquire than S+ L−.

To understand why the feature-positive effect occurs, Bouton and Hendrix (2011) turned to the Rescorla-Wagner (1972) theory. It follows from this theory that the difference between the strength of responding to A and to AB, and hence the magnitude of the discrimination between them, will be determined by the absolute magnitude of the associative strength of B. It further follows from the theory that B in an AB+ A− discrimination will acquire excitatory strength more rapidly than it will acquire inhibitory strength in an A+ AB− discrimination. Combining these principles then leads the theory to predict that an A+ AB− discrimination will be acquired more slowly than an AB+ A− discrimination. If a short panel is regarded as element A, and a long panel as compound AB, then this analysis leads to the prediction it will be easier to solve a L+ S− than a S+ L− discrimination.

The results from Experiment 5 pose a problem for this account. If the Rescorla-Wagner (1972) is to be used to explain the asymmetry between the ease of acquisition of a S+ L− and a L+ S− discrimination, then it should also be able to explain why the 15+

45– discrimination was easier to solve than the 70+ 100– discrimination. The discussion to Experiment 5, however, indicated that at least one way of applying the theory to the results of that experiment led to it predicting the wrong outcome. Until it can be shown that this theory is able to explain the findings of Experiment 5, the explanation we have derived from the proposals of Bouton and Hendrix (2011) for our remaining results should be viewed with a degree of caution.

A relatively straightforward way to explain the results from the five experiments can be developed from findings described by Grice and Saltz (1950). Different groups of rats were trained to pass through a door displaying a white circle with an area of either 20 cm² or 79 cm². When later tested with circles whose areas ranged between these values, the rats trained with the larger circle showed monotonically decreasing level of responding as the test stimulus was made progressively smaller. By contrast, the rats trained with the smaller stimulus initially showed an increase in responding as the stimulus became larger which then reduced with the more extreme values of the test stimuli. The implication of this finding is that generalization gradients based on stimulus magnitude are asymmetrical. Excitation falls off rapidly when generalization tests are conducted with stimuli less intense than the one used for training, but when the test stimuli are more intense, excitation will fall off more slowly (and may even increase for a while) as their similarity to the test stimulus is reduced. Turning now to the present experiments, it follows from the foregoing analysis that there will be rather little generalization of excitation from the long to the short stimulus for the L+ S– discrimination, whereas generalization from the short to the long stimulus for the S+ L– discrimination will be considerable. Given this asymmetry in generalization, it then follows that the L+ S– discrimination will be acquired more readily than S+ L–.

The foregoing account begs the question of why should generalization gradients based on stimulus intensity be asymmetrical. One possible answer to this question is provided by Mackintosh (1974) and based on proposals put forward by Perkins (1953) and Logan (1954). If conditioning is conducted with a single stimulus of given intensity, S+, then this training can be regarded as an S+ S_x– discrimination, where the stimulation provided by the absence of the stimulus, S_x–, is of lower intensity than S+. If a test trial is then conducted with a novel stimulus, it will receive more inhibition through generalization from S_x– if it is weaker, rather than stronger, than S+, and thus the generalization gradient will be sharper for stimuli that are weaker than S+ than for those that are stronger. Mackintosh (1974) goes on to show that this type of account even predicts that stimuli which are stronger than S+ might also elicit a stronger response than S+ through peak shift (Hanson, 1959). Such an effect has been recorded on more than one occasion (e.g., Grice & Salz, 1950).

We turn now to discuss the implication of our results for theories of spatial learning. It may seem surprising but, to our knowledge, the present results provide a rare confirmation that animals are indeed sensitive to the lengths of objects. There is abundant evidence that animals can use the shape of a rectangular arena to find a goal hidden in one of the corners (e.g., Cheng, 1986; Pearce, Good, Jones, & McGregor, 2004), and Experiment 1 has shown that they can also find a goal when it is hidden beside the middle of the long, but not the short walls of a rectangle. These results make it clear that animals can differentiate between long

and short walls, but they do not confirm that this differentiation is based on an appreciation of the lengths of the walls. Lee, Sovrano, and Spelke (2012) make the point that such a discrimination might be controlled by the distance of the target wall from the one opposite it—long walls are necessarily nearer each other than short walls in a rectangle; or it might be based on the proximity of the wall in question to the middle of the arena—long walls are necessarily nearer the center than short walls. The results from Experiment 2 to 5 are not open to this ambiguity of interpretation because the distance between the long panels was the same as between the short panels. In addition, all four panels were the same distance from the center of the pool. By default, therefore, the successful discrimination between the long and short panels that was seen in each of the final four experiments must have been based on the ability to judge the lengths of the panels directly.

The question now arises as to how the length of an object is represented. One suggestion is that the length of an object is encoded as a component of a cognitive map which, according to Gallistel (1990, p. 171–172), is a record of the “geometric relations among the points, lines, and surfaces that define the macroscopic shape of the animal’s behavior space.” An animal in possession of such a record would be well equipped for identifying the location of a goal anywhere in a familiar environment, including beside the middle of a wall of certain length. Thus, a cognitive map would allow the animal to solve the discriminations employed above, but unless additional properties are assigned to the map, it is not clear why its use would result in a L+ S– discrimination being solved more readily than S+ L–. The results from an additional test trial from Experiment 3 pose a further problem for the suggestion that animals found the goal in the present experiments by means of a cognitive map. Upon the completion of Experiment 3, the Landmark L+ S– group was trained for two further sessions in the same manner as for the immediately preceding sessions, with two long panels on one pair of opposite walls, and two short panels on the remaining pair. The group then received a test trial in the square pool with a short panel on one wall, a long panel on the opposite wall, and no panels on the remaining walls. If rats found the platforms by reference to a cognitive map, then the considerable rearrangement of cues would be expected to reduce substantially the correspondence between the original map and the new test environment, and thus make it difficult for rats to identify where the correct search zone was located. In fact, on this trial rats spent 21.4 (± 3.3 SEM) s in the single correct search zone, and 9.5 (± 1.6) s in the single incorrect zone. This difference, which was statistically significant, $t(8) = 2.67$, strongly suggests that rats were able to identify the correct zone without reference to a map of their environment.

Collett and Collett (2002; see also Stürzl, Cheung, Cheng, & Zeil, 2008) suggested that when an animal is at a goal it takes a snapshot of its surroundings. On being returned to the environment, it is then assumed to find the goal by moving in a direction that enhances the match between its current view and the snapshot. The present results provide mixed support for this account. It is possible to explain the poor performance of the S+ L– group in Experiment 2, say, with this type of account, if it is assumed that rats take a snapshot of the nearest panel when they reach the platform. When the S+ L– group was released into the center of the pool, for a test trial, the visual angle subtended by the edges of 100-cm long panels would be 70°, while for the 50-cm short panel

it would be 40°. The comparable angle when the short panel is viewed from the platform is just under 120°. Thus, when placed in the center, the view that most closely corresponds to the snapshot taken of the goal is provided by a long panel, and subjects might therefore head directly for it. If they were to put their heads down and make no further comparisons they would end up in the wrong search zone. The problem with this account is that it makes a similar prediction for the 25+ 100– group of Experiment 4. Indeed, it might even be expected from this account that the 25+ 100– group will perform particularly poorly because, when viewed from the platform, the short panel will subtend a visual angle of approximately 80° which is close to the visual angle subtended by the long panel when viewed from the center of the pool, 70°. In contrast to this prediction, the experiment revealed that the 25+ 100– group was able to solve its discrimination and perform significantly better than the 50+ 100– group. Rather than restrict their snapshots to a local view, such as that provided by a single panel, Stürzl et al. (2008) argued that animals will take a panoramic snapshot of the entire arena when they are at the goal. At first sight, it is hard to see how this proposal can accommodate the findings from the above experiments, but it must be acknowledged that it is not easy to draw precise predictions from the proposals of Stürzl et al. and there may be a way in which they can explain why a L+ S– discrimination is easier than S+ L–. Having said that, the results from the test trial just mentioned in the discussion of cognitive maps might pose a particular problem to this account. By changing the arena substantially for the test trial, it would seem likely that the snapshots taken during the test trial would provide a poor match with the remembered snapshot and thus result in a weak discrimination between the correct and incorrect search zones. In fact, performance on this test was remarkably good. In summary, then, it appears that none of the accounts of animal navigation that we have considered is able to explain our findings.

The results from the experiments demonstrate for the first time that a discrimination between two objects that differ in length progresses more readily when reward is signaled by the longer rather than the shorter of the two. This finding poses a problem for current theories of discrimination learning, and for current theories of spatial learning. The results can, however, be explained if it is assumed that the long object provides a greater magnitude of stimulation than the short one, and that the generalization gradients based on these magnitudes are asymmetrical.

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