Pattern Cue and Visual Cue Competition in a Foraging Task by Rats

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Abstract In 4 experiments, rats searched for food located on top of 4 of 16 towers which were arranged in a 4×4 matrix. The location of the baited towers was cued by visual landmark cues (the baited towers were striped, the others white) and by pattern cues (the baited towers were located in a 2×2 pattern within the larger 4×4 matrix) or simply by pattern cues without visual landmark cues. In 3 of the experiments, visual cues, after being paired with pattern cues, were removed altogether (Experiment 1), put into competition with pattern cues (Experiment 2), or made noninformative (Experiment 3). In Experiment 4, it was the pattern cues that were made noninformative. Collectively, the data suggest strongly that whereas the pattern is learned, even when presumably more salient visual cues are present, the connection between pattern and food location is much weaker than that between visual cue and food location. These data are more easily explained by a model of learning that includes dedicated modules than by a single-system associative model.

Keywords Cue competition · Pattern recognition · Object recognition · Modularity · Rat

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Frequently, in both the laboratory and in nature, more than one type of information predicts some event, such as the location of food. Considerable interest has been attached to the question of how multiple and redundant cues come to control behavior. Rescorla and Wagner (1972) argued that in Pavlovian conditioning in which two conditioned stimuli (CSs) predicted an unconditioned stimulus (UCS), the more salient CS garnered most of the associative strength, leaving little for the less salient CS, and they supplied evidence that *overshadowing* of a less salient CS by a more salient CS was the typical outcome in Pavlovian studies involving compound CSs. But the opposite effect can also occur (Bouton, Dunlap, & Swartzentruber, 1987; Durlach & Rescorla, 1980).

These authors reported data in taste aversion conditioning studies in which the less salient CS conditioned more strongly than the more salient CS; that is, the more salient CS *potentiated*, rather than overshadowed, the less salient CS. This outcome was obtained in situations in which associations were formed between the two CSs before both were allowed to predict the UCS. All these approaches imply that there is a single associative processor that determines which redundant cues gain ascendancy (for reviews, see Escobar & Miller, 2004; R. A. Miller & Escobar, 2002).

The presence of redundant cues is not confined to Pavlovian conditioning, however. There has recently been considerable interest in how landmarks, which predict the location of food, and geometry of the surroundings, which are also cues to food location, interact. Early research (Cheng, 1986; Gallistel, 1990) provided evidence that suggested that geometry cues (i.e., the shape of the environment in which foraging occurs) were learned regardless of the presence of other potentially more salient cues. Cheng showed that when foraging in a rectangular box in which food was found in a corner that was both geometrically distinctive (e.g., long-wall-left-short-wall-right) and visually distinctive (i.e., a unique

landmark cue was located in that corner), rats tended to look in the geometrically correct corner rather than in the visually marked corner when the visual cues were rotated 90° clockwise or counterclockwise. Both Cheng (1986) and Gallistel (1990) went so far as to suggest that there was a *dedicated geometric module* in the brain that always processed geometric cues regardless of the presence of redundant and presumably more salient visual landmark cues. This approach, unlike single associative processor models, implies separate mechanisms for processing different kinds of cues. Although, no longer considered valid in its original form, the notion of separate but cooperating learning systems persists. A recent extension of the associative model originally proposed by Rescorla and Wagner (1972), and which resolves some if not all of the problems with the original model, has been advanced by N. Y. Miller and Shettleworth (2007, 2008; for reviews, see Cheng & Newcombe, 2005, and Cheng, Huttenlocher, & Newcombe, 2013).

Similar to environmental geometry, pattern of food location has also been used as a cue to the location of food. Brown and Terrinoni (1996) devised a foraging task in which rats searched for food located on top of four of 16 vertical poles all painted black and set out in a 4×4 matrix. This task is a variation on a task often referred to as a holeboard task. A comprehensive review of holeboard research tasks may be found in Van der Staay, Gierling, Pinzon, Nordquist, and Ohl (2012). The only cue as to the location of food in Brown and Terrinoni was the fact that the four baited poles were always in one of the nine 2×2 patterns possible within the larger 4×4 layout, although which one of the nine 2×2 sets of poles was baited varied randomly from trial to trial. Over 120 trials of training, the rats showed that they had learned the pattern. After finding the second baited pole, from among immediately adjacent and previously unvisited poles, the rats chose a previously unvisited pole that *could* have been baited more often than would have been expected by chance. Similarly, after finding the third baited pole, from among immediately adjacent and previously unvisited poles, the rats chose the only previously unvisited pole that was baited more often than would have been expected by chance.

Brown, Yang, and Digian (2002) used the same apparatus to look at cue competition. During the first phase, rats were randomly divided into groups. One group received the same treatment as the rats in the Brown and Terrinoni (1996) experiment; the only cue as to the location of the four baited poles was the fact that they were located in one of the 2×2 patterns that are possible within the larger 4×4 matrix of all-black poles. As in the Brown and Terrinoni experiment, the specific 2×2 pattern that was baited on any given trial changed randomly from trial to trial. Another group of rats also found the food atop poles arranged in a 2×2 pattern within the larger 4×4 matrix, but in addition, the baited poles were distinctively marked, having horizontal black and white stripes. After 45

trials, perhaps not surprisingly, the Visual + Pattern rats were performing better than the pattern-only rats, finding the fourth baited pole after significantly fewer looks. In the second phase, the visual cues were taken away from the Visual + Pattern rats so that the only cue available to them was the pattern cue, as had been the case, and continued to be the case, for the pattern-only rats. Not surprisingly, performance, in terms of looks to find the fourth baited pole, declined for the Visual + Pattern (now pattern-only) rats. Surprisingly, however, performance did not decline to a level lower than that seen in the pattern-only rats. Had the visual cues overshadowed the pattern cues during Phase 1, performance in the Visual + Pattern rats would have been lower than that continuing to be seen in the pattern-only rats. It might safely be assumed that visual cues are more salient than pattern cues, and to the extent that they were this outcome is not consistent with the predictions of the Rescorla–Wagner model. On the other hand, the data are consistent with the idea of separate learning modules (Cheng, 1986; Gallistel, 1990) for geometry and salient visual landmark cues.

These experiments were designed to provide further insight into the role that redundant cues, differing in salience, have in a laboratory-based foraging task. The purpose of Experiment 1 was to replicate the aforementioned experiment by Brown et al. (2002), but with a greater separation between adjacent food locations to see if the lack of overshadowing of pattern cues by visual cues that they reported could be demonstrated under these altered conditions. Experiment 2 was designed to put visual and pattern cues into conflict on nonreinforced probe trials in order to see which type of cue exerted stronger stimulus control over food location choices. Experiment 3 was designed to determine what effect rendering pattern cues noninformative would have on foraging choices. Finally, Experiment 4 was designed to find out what effect rendering visual cues noninformative, as opposed removing them entirely, as in Experiment 1, would have on foraging choices. The hope was that, collectively, these experiments might shed some additional light on the question of how redundant visual and pattern cues interact.

Experiment 1

Experiment 1 was designed to replicate the experiment by Brown et al. (2002), but with a greater separation between adjacent food sources. The separation between adjacent poles in the Brown et al. experiment was a mere 13.0 cm, and in their Discussion they suggested that the markings on the poles might have been primarily useful in bringing the rats into the vicinity of the 2×2 matrix. They went on to suggest, however, that once in the area of the baited poles, the visual markings might not have had any additional effect on the rats' behavior because they had only to rotate their bodies, remaining in an

erect position, to find an adjacent and baited pole. Except for a greater separation between adjacent food sites, and the fact that we used free-standing food towers located on the floor of a test room instead of the vertical poles set within a box, Experiment 1 was as much as possible an exact replication of the Brown et al. (2002) experiment. By separating the food towers so that the center-to-center distance between adjacent towers was 30 cm, we hypothesized that the visual markings on striped towers might be more salient, whereas the 2×2 pattern might become less salient. We thought it possible that the combined effect of increasing the salience of the visual cues and decreasing the salience of the pattern cues might produce overshadowing by the visual cues during the test.

Method

Subjects Eight male hooded rats of the Long-Evans strain, obtained from Charles River in Montreal, were used. The rats, which were all experimentally naïve, were reduced to 85 % of free-feeding body weight and were housed individually in two-rat shoe-box-style cages with ad lib water. The cage room was maintained at 23 °C with a 12-hour light-on-light-off cycle. The lights were red during the first and last hour of the lighted period. Testing was carried out during the light-off phase.

Apparatus As shown in Fig. 1, the apparatus consisted of 16 food towers with adjacent towers set 30 cm apart center to center and arranged in a 4×4 matrix. Each food tower

consisted of a block of cedar 10 cm $\times$ 10 cm $\times$ 20 cm high and coated with Varathane. Each tower was enclosed in a sleeve made of Bristol Board covered with clear packing tape.

These sleeves were either completely white or white with black stripes, each stripe being 3.0 cm wide and separated from the next stripe by 3.0 cm. A plastic food cup, 2.5 cm in diameter, 1.9-cm deep and created from a 35-mm film canister, was attached by means of a small screw to the center of the top of each tower. During this, and all subsequent experiments, four of the 16 towers were baited and 12 were sham baited. Cubes of Black Diamond Medium Cheddar cheese measuring 1 cm³ were used to bait or sham bait the towers. There were 12 disks, each 2.6 mm in diameter, and each containing 10, 3-mm-in-diameter holes, and were fashioned from the lids of 35 mm film canisters. These were used to cover a small piece of cheese placed in the food cups of the 12 sham-baited towers to control for odor cues. The disks were not used in the food cups of the four towers destined to be baited on a particular trial so that the cheese in those food cups was accessible. The matrix of towers was located in the center of a windowless room measuring 3.0 m $\times$ 3.0 m $\times$ 2.5 m high. The walls of the room were painted yellow, and there was a single gray painted door set into one wall that provided access to the test room. The two walls adjacent to the door wall were formed from cinder block, and an AC outlet covered with a stainless steel cover was located on one of these walls. The wall opposite to the door wall was faced with drywall.

The room was well illuminated by four light fixtures mounted on the ceiling, each of which contained four 120-cm long fluorescent tubes behind a translucent plastic lens.

Procedure

Preliminary training The rats were initially trained to eat from the food towers by placing three baited training towers that were 10-, 15-, and 20-cm high, respectively, in the test room. The rats were then placed one at a time into the arena and left there until they had visited all three towers. After five such trials, all rats went to all three towers, reared up, and removed and ate the cheese in the food cups.

Phase 1 training Following preliminary training, rats were randomly assigned to one of two groups ($N = 4$) and given four trials per day, two in the morning and two in the afternoon. Successive morning or afternoon trials were separated by at least 1 hour. For both groups four food towers were baited with cheese, and the four baited towers were always in one of the nine 2×2 patterns that are possible within a 4×4 matrix. We randomly determined which of the nine 2×2 patterns was baited on each trial but never baited the same two on two successive trials. The remaining 12 towers were sham baited. For rats in Group Visual + Pattern to Pattern

Fig. 1 Photograph of one of the nine possible 2×2 arrangements of the four baited and striped towers and the 12 plain towers for Group V + P $\rightarrow$ P in Phase 1 (bottom) and one of the nine possible 2×2 arrangements of the four plain baited towers and the 12 plain sham-baited towers that served for rats in Group P $\rightarrow$ P and for both groups (top) in Phase 2 of Experiment 1

Only ($V + P \rightarrow P$) the four baited towers were covered with striped sleeves. For rats in Group Pattern Only to Pattern Only ($P \rightarrow P$), the four baited towers were covered with the same white sleeves that covered the sham-baited towers. At the start of a trial, the rat was placed in the apparatus just inside the door and facing the rear wall. The door was then closed and the rat remained in the apparatus until it had visited the fourth baited tower or until it had made 48 choices. During the session, the experimenter observed the rat thorough the window in the door and recorded the order in which the rat visited towers. After being removed from the maze following the second afternoon session, the rats were weighed and given a ration of lab chow sufficient to maintain their body weights at 85 % of their original free-feeding weights. All rats were trained for 40 trials.

Phase 2 training During Phase 2, the rats in Group $P \rightarrow P$ continued as in Phase 1, having to rely only on pattern cues to find the food which remained in a 2×2 pattern. For rats in Group $V + P \rightarrow P$, however, the visual cues were removed. Thus, as for the rats in Group $P \rightarrow P$, all 16 towers were clad in white sleeves and the food continued to be located in a 2×2 pattern. Phase 2 was continued for 40 trials, again, at the rate of four trials per day.

Results

The mean choices to criterion (the number of choices, from the outset of the trial, required to find the fourth baited tower) for the first four blocks of 10 trials are shown in Fig. 2. In this, and in all subsequent experiments, immediate revisits were not counted as choices, but revisits that were not immediate were counted as choices. The data appear to show that whereas the $V + P \rightarrow P$ rats required fewer choices to find the fourth baited tower during Phase 1, there was no difference between

Fig. 2 Mean number of choices required to find the fourth baited tower as a function of blocks of trials for Group $V + P \rightarrow P$ and for Group $P \rightarrow P$ during Phases 1 and 2 in Experiment 1. Error bars represent standard errors of the mean

the groups in terms of choices to find the fourth baited tower in Phase 2 during which the rats in Group $V + P \rightarrow P$ no longer had the advantage of the visual cues.

The data from Phase 1 were subjected to a 2 (cue type) $\times$ 4 (blocks of 10 trials) split-plot ANOVA. This analysis revealed a significant main effect of cue type, $F(1, 6) = 217.0$, $p < .05$, $\eta^2_p = 0.97$, and a significant main effect of blocks of trials, $F(3, 18) = 13.2$, $p < .05$, $\eta^2_p = 0.69$, but no significant Cues $\times$ Blocks of Trials interaction, $F(3, 18) = 3.7$, $p > .05$, $\eta^2_p = 0.38$. This was interpreted to mean that during Phase 1, both groups showed improvement over trial blocks and that Group $V + P \rightarrow P$ outperformed Group $P \rightarrow P$.

The data from Phase 2 were also subjected to a 2 (cue type) $\times$ 4 (blocks of 10 trials) split-plot ANOVA. This analysis failed to reveal a main effect of blocks of trials, $F(3, 18) = 2.19$, $p > .05$, $\eta^2_p = 0.27$, or a Cues $\times$ Blocks of Trials interaction, $F(3, 18) = 0.70$, $p > .05$, $\eta^2_p = 0.11$, or a main effect of cue type, $F(1, 6) = 0.34$, $p > .05$, $\eta^2_p = 0.08$. These data were interpreted to mean that during Phase 2, there was no significant difference between the performance of $V + P \rightarrow P$ rats (now without their visual cues) and $P \rightarrow P$ rats.

Following Brown and Terrinoni (1996) an analysis of tower selection after discovery of the second tower was also undertaken for the Phase 1 data during Trials 21–40, during which choices to criterion data appeared to have stabilized. Two proportions were calculated for each rat over the last 20 trials of Phase 1. The first was the *expected probability* [$p(E)$] of finding a previously unvisited, possibly baited tower, after finding the second baited tower, based on chance. The numerator of this proportion was the number of (a) immediately adjacent towers that (b) had not previously been visited and that (c) could *possibly* have been baited. The denominator of this proportion was the number of (a) immediately adjacent towers that (b) had not been previously visited. The second proportion was the *obtained proportion* [$p(O)$] of discoveries of previously unvisited, possibly baited towers, after finding the second baited tower. The numerator of this proportion was the number of (a) immediately adjacent towers that (b) had not previously been visited and that (c) could *possibly* have been baited, and (d) which were chosen on the next visit. The denominator of this proportion was the number of (a) immediately adjacent towers that (b) had not been previously visited, and (c) which were chosen on the next visit. These two proportions were calculated for each rat during Trials 21–40, and the mean of each proportion calculated for Group $V + P \rightarrow P$ and Group $P \rightarrow P$. Mean $p(E)$ and mean $p(O)$ were also calculated for rats in each group for the choices immediately following discovery of the third tower. A more complete description of this statistic may be found in Brown and Terrinoni (1996).

The choice data following discovery of the second tower are shown in the left panel of Fig. 3. The data appear to show that after discovery of the second tower, the rats in both Group $V + P \rightarrow P$ and Group $P \rightarrow P$ chose the third baited tower

Fig. 3 Mean $p(\text{Expected})$ and $p(\text{Observed})$ values for $V + P \rightarrow P$ rats and $P \rightarrow P$ rats after finding the second baited tower (left panel) and after finding the third baited tower (right panel) during Trials 21–40 in Phase 1 of Experiment 1. Error bars represent standard errors of the mean

more often than would have been expected by chance. These data were subjected to a 2 (cue type) $\times$ 2 [$p(\text{E})$ vs. $p(\text{O})$] split-plot ANOVA. The main effect of $p(\text{E})$ versus $p(\text{O})$ was significant, $F(1, 6) = 39.68$, $p < .05$, $\eta^2_p = 0.87$. Neither the main effect of cue type, $F(1, 6) = 1.91$, $p > .05$, $\eta^2_p = 0.24$, nor the $p(\text{E})$ versus $p(\text{O}) \times$ Cue Type interaction, $F(1, 6) = 2.93$, $p > .05$, $\eta^2_p = 0.33$, was significant. These data were interpreted to mean that after the discovery of the second tower, rats in both cue groups chose the third baited tower more often than would be expected by chance.

The right panel in Fig. 3 appears to show that after discovery of the third tower, both $V + P \rightarrow P$ rats and $P \rightarrow P$ rats chose the fourth baited tower more often than would have been expected by chance during Trials 21–40 of Phase 1. These data were also subjected to a 2 (cue type) $\times$ 2 [$p(\text{E})$ vs. $p(\text{O})$] split-plot ANOVA. The main effect of $p(\text{E})$ versus $p(\text{O})$ was again significant, $F(1, 6) = 55.19$, $p < .05$, $\eta^2_p = 0.90$. In the absence of a significant main effect of cue type, $F(1, 6) = 0.01$, $p > .05$, $\eta^2_p = 0.002$, or a significant Cue Type $\times$ $p(\text{E})$ versus $p(\text{O})$ interaction, $F(1, 6) = 4.31$, $p > .05$, $\eta^2_p = 0.42$, this was interpreted to mean that the rats in both groups found the fourth tower after finding the third tower more often than would be expected by chance. Collectively, these data suggest that by the second half of Phase 1, the rats in both groups had learned the pattern, at least to some extent.

Discussion

The results of Experiment 1 replicated almost exactly the findings of Brown et al. (2002). They confirm the findings in that experiment that, whereas rats learned to find the fourth baited tower with fewer looks when they had visual cues to help them, the visual cues did not overshadow the pattern cues, because $V + P \rightarrow P$ rats performed no worse overall during Phase 2 after their visual cues had been removed than the $P \rightarrow$

P rats, that never had them in the first place. Moreover, the choice of third and fourth tower data confirms that rats were responding to the pattern. That our data so closely resemble the findings of Brown et al. (2002) is also interesting in view that the distance between adjacent towers was more than double the distance used by Brown et al. Brown et al. had suggested in their Discussion that the visual cues might have been less salient once the rat was among the visually marked towers. Our data suggest that the failure of the visual cues to overshadow the pattern cues was not likely due to food pole (tower) proximity.

These data thus extend and confirm the results of Brown et al. (2002) in demonstrating pattern learning by the presence of redundant and presumably more salient visual cues. Other research also using rats on a radial maze (Brown & Wintersteen, 2004) or in a pole task (Brown & Giumetti, 2006) and humans (Sturz, Brown, & Kelly, 2009; Sturz, Kelly, & Brown, 2010) using a variation of the pole task in both real and virtual environments has provided additional evidence that visual cues do not overshadow pattern cues. In fact, in the experiments that used humans, there was evidence that visual cues actually potentiated learning about pattern. Sturz et al. (2009) hypothesized that this potentiation might be due to the language abilities of humans, which may have facilitated the learning of the pattern.

In summary, Experiment 1 both replicated and extended the findings of Brown et al. (2002) and provide added support for a somewhat surprising failure to see overshadowing of what, on the face of it, would seem to be a less salient cue by a more salient cue. As such, these data are more consistent with modular learning than with single associative processing.

Experiment 2

The results of Experiment 1 almost exactly replicated the data reported by Brown et al. (2002) except that by making the adjacent food locations further apart, in all likelihood, the salience of the visual landmark cues was increased, whereas the salience of the pattern cues was potentially reduced. This suggests that the failure to document overshadowing of pattern cues by landmark cues by Brown et al. was not confined to the specific parameters of their experiment. The purpose of Experiment 2 was to provide evidence that the visual landmark cues were actually more salient than, and would exert stronger stimulus control than, the pattern cues in this situation. This was done by first training rats to find food locations in the 4×4 matrix of food towers in which both visual landmark cues (striped towers) and pattern (food was always in one of the 2×2 patterns within the larger 4×4 matrix). Following this, probe trials were inserted. On probe trials, one of the striped towers was moved outside of the 2×2 pattern, and a white tower put in its place. Following

discovery of the third striped tower, we were interested in observing the rats' next choice. Would it be the striped tower, now displaced from the 2×2 pattern, or the white tower that completed the pattern?

Method

Subjects Subjects were eight male hooded rats of the Long-Evans strain, obtained from Charles River in Montreal. The rats had all had prior experimental experience in an undergraduate laboratory course. First they learned to press a lever for food and then were exposed to a continuous reinforcement schedule for 40 minutes. Following that, the rats were placed on a multiple (variable interval 28 s—extinction) schedule for 10 sessions each, lasting 30 min, with the cue light on during the variable interval components and off during the extinction components. After that, the rats were exposed to a fixed-time 30-s schedule for 10 sessions each, lasting 30 min. Finally, the rats searched for cheese on an eight-arm radial maze for 20 trials. The rats were reduced to 85 % of free-feeding body weight and were housed as were the rats in Experiment 1 and were again tested during the light-off portion of the 12-hour light-on-light-off cycle.

Apparatus The 16 food towers were set out as in Experiment 1 in the same test room and in a 4×4 matrix, with adjacent towers again separated by 30 cm, center to center. Also, as in Experiment 1 for the $V + P \rightarrow P$ rats in Phase 1, four towers were clad with sleeves that had alternating black and white stripes, each 5 cm wide, whereas the other 12 towers were clad with plain white sleeves. Also, as in Experiment 1, perforated disks were inserted into the food cups located on top each of the 12 white towers and covered the 1 cm^3 cubes of Black Diamond Medium Cheddar Cheese used to sham bait these towers. The disks were not used in the food cups on top the four striped towers so that the 1 cm^3 cubes of cheese in those food cups were accessible to the rats.

Procedure

Preliminary training As in Experiment 1, the rats were initially trained to eat from the food towers by placing three baited towers that were 10-, 15-, and 20-cm high, respectively, haphazardly within the room. The rats were then placed one at a time into the room and left there until they had visited all three towers. After five such trials, all rats reared up, removed, and ate the cheese contained on all three towers.

Phase 1 training Following preliminary training, all rats were given a total of 100 trials of training, at the rate of four trials per day. Successive trials were separated by at least 1 hour. Of these, 84 trials were regular training trials, with one of the nine possible 2×2 baiting patterns randomly selected for each trial,

with the four baited towers clad in striped sleeves as the $V + P \rightarrow P$ group during Phase 1 in Experiment 1. Also, as in Experiment 1, on each such training trial, rats were allowed to search for food until they had discovered the fourth baited tower. The other 16 trials were nonrewarded probe trials. Beginning with Trial Blocks 21–25, each block of five trials contained one probe trial, the remaining four trials being regular trials. Of the five trials within a block, a probe trial was randomly determined. On probe trials, one of the striped towers located in one of the randomly selected 2×2 patterns was moved from its position to an adjacent position outside of the pattern, and in its place was set the white tower. Both the white tower that completed the pattern and the displaced striped tower were sham baited with inaccessible bait to control for odor cues. There were eight such probe arrangements, and the pattern used was randomly determined for each probe trial with the caveat that each was used only twice. These eight arrangements are shown in Fig. 4. On probe trials, rats were allowed to search until they had found the three striped and baited towers and beyond that until they had gone to either the white tower that completed the 2×2 pattern or the striped tower that was located outside the pattern.

Phase 2 training Following Trial 100, the striped sleeves were removed from the baited towers for all rats, and an additional 20 trials of training, at the rate of four trials per day with a minimum of 1 hour between trials, were given during which only the 2×2 pattern served as a cue as to the location of the food. This phase was not integral to the question being addressed in this experiment but rather was done to enable a comparison between the performance of these rats with that of the $V + P \rightarrow P$ rats in Experiment 1.

Results

Figure 5 shows the number of choices required to find the fourth baited tower during the first 40 regular trials of Phase 1 and all 20 trials of Phase 2 in blocks of 10 trials. Only the first 40 trials of Phase 1 are shown to facilitate a comparison with Phase 1 for the $P + V \rightarrow P$ rats in Experiment 1. The figure shows that over the first four blocks of 10 trials of Phase 1, performance appeared to improve, and the overall curve is similar to that seen for the $V + P \rightarrow P$ rats in Experiment 1 despite that there were four probe trials during Blocks 3 and 4.

These data were subjected to a one-way ANOVA, with blocks of trials as the predictor variable. This resulted in a significant effect of blocks of trials, $F(3, 21) = 22.6$, $p < .05$, $\eta_p^2 = 0.76$. Of all the pairwise comparisons among trial blocks, using t tests for correlated means, only the one between Block 3 and Block 4 was not significant at the 0.05 level.

Figure 5 also shows that during Trial Blocks 1 and 2 of Phase 2, after the striped sleeves had been removed, there was

Fig. 4 The eight tower arrangements during probe trials in Experiment 2

a decline in performance again comparable to that seen in Group V + P → P during the first two blocks of 10 trials in Phase 2 of Experiment 1 after the visual cues had been removed.

An analysis of the choice data during the 16 probe trials in Phase 1 was also undertaken. The data depicted in Fig. 6 show the number of trials for all eight rats combined on which, following the discovery of the third baited and striped tower in the 2×2 pattern, the displaced visually marked tower or the unmarked tower that completed the 2×2 pattern was selected on the next choice. These data are further broken down into four groups: (1) those on which neither target tower had previously been visited; (2) those on which the visual but not the pattern tower had previously been visited; (3) those on which the pattern but not the visual tower had previously been visited; and (4) those on which both of the target towers had previously been visited. The most important of these four statistics is the first one, which shows which of the two target towers was selected on the very next choice after finding the

third baited tower when neither target tower had previously been visited.

It is clear from Fig. 6 that there was a preference for selecting the visual as opposed to the pattern tower on the next choice when neither had been visited previously ($\sim P \sim V$). These data were subjected to a goodness-of-fit test, which revealed that the preference for the visual tower was statistically significant, $\chi^2(1) = 12.3, p < .05$. It is also apparent in Fig. 6 that even during trials in which the striped tower, but not the white tower that completed the pattern, had previously been visited ($\sim PV$), the rats still showed a preference for the displaced striped tower over the white tower that completed the pattern on their very next choice. Again, this difference was also statistically significant, $\chi^2(1) = 15.7, p < .05$.

Discussion

The results of Experiment 2 suggest that the visual cues were more salient than the pattern cues. Even when the striped tower that had been displaced out of the 2×2 pattern had

Fig. 5 Mean number of choices to find the fourth baited tower in blocks of 10 trials during the first 40 training trials in Phase 1 and in blocks of 10 trials during all 20 trials of Phase 2 of Experiment 2. Error bars represent standard errors of the mean

Fig. 6 Number of choices of the displaced visually marked tower and the unmarked tower that completed the 2×2 pattern immediately after finding the third baited tower. Data are shown for trials on which neither of these towers ($\sim P \sim V$), only the pattern-completing tower ($P \sim V$), only the visually marked tower ($\sim PV$), and both of these towers (PV) had been visited previously

already been visited and found empty of accessible bait, and the white tower that completed the 2×2 pattern had not previously been visited, the rats still showed an overwhelming preference for the striped tower. Thus, in view of these data, the hypothesis that in Experiment 1, and in the experiment by Brown et al. (2002), overshadowing did not occur because the visual cues were not as salient as the pattern cues does not seem viable. It does appear, however, that the pattern was learned in Experiment 1 and in the Brown et al. (2002) experiment even in the face of salient visual cues, which is not consistent with Rescorla–Wagner theory, nor with other similar cue-competition theories (e.g., Mackintosh, 1975; Pearce & Hall, 1980).

Experiment 3

Although the results of Experiment 2 confirmed that the visual cues were likely more salient than the pattern cues, they do not address the question of whether the pattern learning or the visual cue learning in Experiments 1 and 2 was the more robust. Experiments 3 and 4 were designed to answer this question. The general approach in Experiment 3 was to make both the visual landmark cues and the pattern cues redundant and equally reliable guides to the location of the baited towers during Phase 1. Then, in Phase 2, because it would not be possible to remove the pattern cues altogether in a 4×4 matrix, to make them unreliable so that the visual cues provided the only reliable information as to the location of the food. To the extent that the association between the visual cues and food location is strong, and that between pattern cues and food location is weak, this should lead to little decline in performance.

Method

Subjects Eight male hooded rats of the Long-Evans strain were used, obtained from Charles River in Montreal, and although different rats, they had had the same prior experiences as the rats in Experiment 2 in both operant chambers and on a small eight-arm radial maze. The rats were reduced to 85 % of free-feeding body weight and were housed as the rats in Experiments 1 and 2, and were tested during the light-off portion of the 12-hour light-on-light-off cycle.

Apparatus The apparatus, baits, and the test room were exactly the same as the previous experiments.

Procedure

Preliminary training Preliminary training was the same as in previous experiments.

Phase 1 training Four rats were randomly assigned to either the Visual + Pattern $\rightarrow$ Visual + Pattern Unreliable ($V + P \rightarrow V + PU$) or the Visual + Pattern Unreliable $\rightarrow$ Visual + Pattern Unreliable ($V + PU \rightarrow V + PU$) group, and each was given 40 training trials at the rate of four trials per day. For Group $V + P \rightarrow V + PU$, training during Phase 1 was exactly the same as it had been for Group $V + P \rightarrow P$ during Phase 1 in Experiment 1, with the four baited towers being striped and set out in one of the nine 2×2 patterns. For Group $V + PU \rightarrow V + PU$, during Phase 1, the four baited towers were striped but not arranged in a 2×2 pattern. There were nine arrangements of the striped towers, and the one that was used on a given trial varied randomly. In both groups, rats remained in the apparatus on each trial until finding the fourth baited tower.

Phase 2 training For Group $V + P \rightarrow V + PU$, the striped towers remained present, and were baited, but they were no longer arranged in a 2×2 pattern but rather in one randomly chosen of the nine patterns used for Group $V + PU \rightarrow V + PU$. Rats in Group $V + PU \rightarrow V + PU$ continued to be exposed to a randomly chosen one of these nine random arrangements of striped towers during Phase 2. Phase 2 consisted of 40 trials at the rate of four per day. Figure 7 shows examples of the arrangements for both groups of rats during Phases 1 and 2.

Results

As Fig. 8 shows, during Phase 1, there appears to have been little difference between the performance of Group $V + P \rightarrow V + PU$ and Group $V + PU \rightarrow V + PU$ during any of the four blocks of trials. On the other hand, performance in both

Fig. 7 Examples of the baiting and tower location arrangements in Phase 1 and Phase 2 of Experiment 3 for rats in the $V+P \rightarrow V+PU$ and $V+PU \rightarrow V+PU$ groups

Fig. 8 Mean number of choices required to find the fourth baited tower as a function of blocks of trials for Group $V+P \rightarrow V+PU$ and for Group $V+PU \rightarrow V+PU$ during Phases 1 and 2 in Experiment 3. Error bars represent standard errors of the mean

groups appears to have improved over trial blocks. The Phase 1 data were subjected to a 2 (group) $\times$ 4 (blocks of 10 trials) split-plot ANOVA. The analysis revealed a significant effect of trial blocks, $F(3, 18) = 34.22$, $p < .05$, $\eta^2_p = 0.85$, but neither the main effect of group, $F(1, 6) = 0.23$, $p > .05$, $\eta^2_p = 0.04$, nor the Group $\times$ Trial Blocks interaction, $F(3, 18) = 1.89$, $p > .05$, $\eta^2_p = 0.25$, was significant. These results were interpreted to mean that, whereas both groups showed improvement over trial blocks, the addition of the pattern cues to the visual cues during Phase 1 did not appear to have profited Group $V+P \rightarrow V+PU$. Moreover, Fig. 8 also suggests that when the pattern cues were taken away from Group $V+P \rightarrow V+PU$, during Phase 2, their performance appeared to be little affected. The Phase 2 data were also subjected to a 2 (group) $\times$ 4 (blocks of 10 trials) split-plot ANOVA. This analysis also revealed a significant effect of trial blocks, $F(3, 18) = 5.2$, $p < .05$, $\eta^2_p = 0.47$, but neither the main effect of group, $F(1, 6) = 0.04$, $p > .05$, $\eta^2_p = 0.01$, nor the Group $\times$ Trial Blocks interaction, $F(3, 18) = 1.86$, $p < .05$, $\eta^2_p = 0.24$, was significant. These data were interpreted to mean that, whereas both groups showed additional improvement over trial blocks in Phase 2, the groups did not differ in performance.

Discussion

The fact that during Phase 1 the presence of the pattern cues did not improve performance by Group $V+P \rightarrow V+PU$ over that seen in Group $V+PU \rightarrow V+PU$ suggests that the presence of the pattern cues exerted little stimulus control over searches. Moreover, the fact that when their removal during Phase 2 was accompanied by no decline in performance by Group $V+P \rightarrow V+PU$, as evidenced by the lack of a Group $\times$ Blocks of Trials interaction adds further weight to the argument that the visual cues exerted more stimulus control over behavior than did the pattern cues.

Experiment 4

Experiment 4 was designed to complement Experiment 3. In Experiment 3, redundant pattern cues were made unreliable for Group $V+P \rightarrow V+PU$. This resulted in little change in performance by the rats in Group $V+P \rightarrow V+PU$. In Experiment 4, it was the visual cues that were made unreliable in Phase 2. This experiment was necessary because in Experiment 1, visual cues had been removed entirely, in Group $V+P \rightarrow P$. Because in Experiment 3, pattern cues had not been removed, but rather just made unreliable, it was necessary to see what would happen when visual cues were made unreliable, rather than being removed entirely. If the visual cues are more important than the pattern cues, as was suggested by the results of Experiment 3, then making them unreliable ought to lead to a considerable decrement in performance relative to rats that were not able to use visual cues from the outset.

Method

Subjects Eight male hooded rats of the Long-Evans strain were used, obtained from Charles River in Montreal, and with the same prior experiences as the rats in Experiments 2 and 3 in both operant chambers and on a small eight-arm radial maze. The rats, which were not the same rats used in Experiments 1, 2, and 3, were reduced to 85 % of free-feeding body weight and were housed as were the rats in all the previous experiments and, as in the previous experiments, were tested during the light-off portion of the 12-hour light-on-light-off cycle.

Apparatus The apparatus, baits, and the test room were exactly the same as in Experiment 1.

Procedure

Preliminary training Preliminary training was the same as in previous experiments.

Phase 1 training Four rats were randomly assigned to each of the Visual + Pattern $\rightarrow$ Visual Unreliable + Pattern ($V+P \rightarrow VU+P$) and Visual Unreliable + Pattern $\rightarrow$ Visual Unreliable + Pattern ($VU+P \rightarrow VU+P$) groups, and each was given 40 training trials at the rate of four trials per day. For Group $V+P \rightarrow VU+P$ during Phase 1, training was exactly the same as it had been for Group $V+P \rightarrow P$ in Experiment 1, with the four baited towers being striped and set out in one of the nine 2×2 patterns. For Group $VU+P \rightarrow VU+P$ during Phase 1, four towers were visually striped but unbaited and not arranged in a 2×2 pattern. The baited towers were white and arranged in a randomly selected, one of nine possible 2×2 patterns. In both

groups, rats remained in the apparatus on each trial until finding the fourth baited tower.

Phase 2 training For Group $V + P \rightarrow VU + P$ during Phase 2, the striped towers remained present and also remained baited but were no longer arranged in a 2×2 pattern, the same condition that had been in place for the rats in Group $VU + P \rightarrow VU + P$ during Phase 1 of this experiment. Rats in Group $VU + P \rightarrow VU + P$ continued to be exposed to this arrangement during Phase 2. Phase 2 consisted of 40 trials at the rate of four trials per day. Figure 9 shows examples of these arrangements during Phases 1 and 2.

Results

Figure 10 shows that during Phase 1, there appears to be a large difference between the performance of Group $V + P \rightarrow VU + P$ and Group $VU + P \rightarrow VU + P$ during all four blocks of trials.

Also, performance of both groups appeared to have improved over trial blocks. These data were subjected to a 2 (group) $\times$ 4 (blocks of 10 trials) split-plot ANOVA. This analysis revealed a significant effect of group, $F(1, 6) = 48.42, p < .05, \eta^2_p = 0.89$. In addition, the analysis revealed a significant effect of trial blocks, $F(3, 18) = 18.34, p < .05, \eta^2_p = 0.75$, but the Group $\times$ Trial Blocks interaction, $F(3, 18) = 2.99, p > .05, \eta^2_p = 0.33$, was not significant. These data were interpreted to mean that both groups showed improvement over trial blocks, but that Group $V + P \rightarrow VU + P$ performed better throughout Phase 1 than did Group $VU + P \rightarrow VU + P$. More significantly, Fig. 10 also suggests that when the visual cues were made

unreliable in Group $V + P \rightarrow VU + P$, their performance was greatly negatively affected during at least the first two blocks of Phase 2. These data were also subjected to a 2 (group) $\times$ 4 (blocks of 10 trials) split-plot ANOVA. This analysis revealed a significant main effect of group, $F(1, 6) = 16.91, p < .05, \eta^2_p = 0.74$. The analysis also revealed a significant effect of trial blocks, $F(3, 18) = 7.68, p < .05, \eta^2_p = 0.56$, and Group $\times$ Trial Blocks interaction, $F(3, 18) = 5.42, p < .05, \eta^2_p = 0.48$. Subsequent *t* tests revealed that the difference between the means of Groups $V + P \rightarrow VU + P$ and $VU + P \rightarrow VU + P$ was significant during Block 1, $t(6) = 4.57, p < .05$, and Block 2, $t(6) = 4.15, p < .05$, but not during Block 3, $t(6) = 1.68, p > .05$, and Block 4, $t(6) = 0.84, p > .05$.

Discussion

The superior performance by the rats in Group $V + P \rightarrow VU + P$ over those in Group $VU + P \rightarrow VU + P$ in Phase 1 suggests that the presence of the visual cues played a major role in learning where the food was. The added fact that performance in this group dropped to a level well below that of Group $VU + P \rightarrow VU + P$ when the visual cues were rendered noninformative, but were still present, adds weight to this argument. It took until the third block of 10 trials before the performance by Group $V + P \rightarrow VU + P$ was no longer significantly worse than that of Group $VU + P \rightarrow VU + P$. Unlike in Experiment 1, when the visual cues were removed entirely in Phase 2, they remained present in Phase 2 of this experiment, albeit uninformative. In short, the rats had to learn to ignore these formerly informative but now noninformative cues.

It is interesting to note that the conditions experienced by Group $VU + P \rightarrow VU + P$ were similar to those that human participants were exposed to by Katz, Brown, and Sturz (2014). In their experiment, people searched for four “baited” bins set out in a 5×5 array. The “baited” bins were always in a

Fig. 9 Examples of the baiting and tower location arrangements in Phase 1 and Phase 2 of Experiment 4 for rats in the $V + P \rightarrow VU + P$ and $VU + P \rightarrow VU + P$ groups

Fig. 10 Mean number of choices required to find the fourth baited tower as a function of blocks of trials for Group $V + P \rightarrow VU + P$ and for Group $VU + P \rightarrow VU + P$ during Phases 1 and 2 in Experiment 4. Error bars represent standard errors of the mean. Asterisks represent significant differences between cell means

2×2 diamond pattern within larger array of locations. Among the 25 bins, there were four red bins, the rest being white. The four red bins were never baited. In the experimental group, the red bins were also in a diamond pattern, whereas in the control group they were in no particular pattern. The experimental group outperformed the control group in terms of choices to find the fourth “baited” bin, choices to find the second “baited” bin, and choices to find the third baited bin. The conditions experienced by the control group in the Katz et al. experiment were similar to those offered to our control rats in Experiment 4. Like their control humans, our control rats did not perform well.

General discussion

Overall, the results of these experiments have accomplished several goals. First, they verify and extend the results of previous research and provide some new insight into the role of visual landmark cues and pattern of food location cues in a foraging situation for rats.

Experiment 1 confirmed and extended the results of an experiment by Brown, et al. (2002). To begin with, our data confirmed the findings in that research that pattern cues are learned in a situation in which there are supposedly more salient visual landmark cues, a somewhat surprising finding in that such data are not consistent with the predictions of Rescorla–Wagner theory, nor with the predictions of other similar cue-competition theories (e.g., Mackintosh, 1975; Pearce & Hall, 1980); rather, the data are more consistent with the idea of a dedicated geometric module (Cheng, 1986; Gallistel, 1990). Second, the results of Experiment 1 extended these findings by showing that they were obtained even when the separation between adjacent food sites was more than doubled. The effect of this separation should have been to increase the salience of the visual landmark cues, because with the towers further apart, rats had to actually do more than just rotate in a reared position to find adjacent towers. At the same time, the increased separation might have made the 2×2 patterns more difficult to discern, hence decreasing their salience. Yet, in spite of all that, the pattern was still learned, as evidenced by the data, which showed that the probability of selecting a possibly baited tower after finding the second tower and the probability of selecting the fourth baited tower after finding the third one, for both groups, was greater than would be expected by chance.

Experiment 2 was designed to answer the following question: Do the visual cues or the pattern cues exert more stimulus control in this situation? The data clearly showed that, given a choice between the fourth position in the pattern containing an unmarked tower and a marked, but out-of-position tower, after finding the third baited tower, the rats overwhelmingly chose the visually marked tower over the tower occupying the fourth

position that completed the pattern. Although this does not make it certain that the visual cues were more salient than the pattern cues, any argument that they were less salient, simply to make the results of Experiment 1 consistent with Rescorla–Wagner theory, would be a weak one.

Experiments 3 and 4 addressed a question that was not answered in Experiments 1 and 2: Specifically, during the learning of food locations, are visual landmarks or are patterns of food location more useful to the animal? In Experiment 1, the visual cues clearly helped the rats find the food, but when they were removed altogether, performance declined, but not below the level of performance seen in rats that had been exposed only to pattern cues from the outset. What was needed was a complementary experiment in which the pattern cues were removed altogether; but that presents a problem because there are always patterns in any array of elements, and these patterns cannot be removed in the same way that visual cues can be eliminated. Experiment 4 was designed to not remove but to make pattern cues unreliable as guides to the location of food. Experiment 1 would not provide a suitable comparison for this manipulation because the visual cues in Experiment 1 were completely removed, not merely made unreliable. So, Experiment 3 was designed to make visual cues unreliable instead of being removed altogether. The data from these two experiments spoke clearly to the question. Making pattern cues unreliable in Experiment 3 led to little change in performance, whereas making visual landmark cues unreliable in Experiment 4 led to an immediate albeit temporary decline in performance. The conclusion was that the connection between visual landmark cues and the location of food is more substantial than that between pattern cues and food location.

It is interesting to note here that the findings in Experiments 3 and 4 are not consistent with the results of a series of experiments by Hurley and Healy (2002), who found evidence that hummingbirds (*Selasphorus rufus*) were guided more by the location of an artificial flower baited with sucrose, relative to the locations of other flowers not baited with sucrose, than by the visual distinctiveness of the artificial flowers in the array of locations. Whether the flowers were visually distinctive or all the same had little effect on performance, but changing the location of the baited flowers within the array caused a deficit in performance. Of course, the species used and the details of the foraging situations were different, and further research will be required to tease out the reasons for this discrepancy. One factor that might be relevant had to do with the separation between adjacent food sites. In our research, that separation was 30 cm, whereas Hurley and Healy found that patterns exerted more stimulus control than visual cues only when the flowers were less than 30 cm apart.

The conclusion that derives from our research is that although pattern cues do not seem to be overshadowed by visual landmark cues, the latter appear to exert stronger stimulus control in foraging by rats in the Brown and Terrinoni

(1996) paradigm. Such a finding is clearly more easily explained by a model of learning that includes dedicated modules than by a single-system associative model.

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