Poison avoidance and patch (location) selection in rats

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Thirsty rats were tested on a four-armed radial maze with three water locations and one distinctive taste location (saccharin). Rats that were injected with lithium chloride after drinking a novel saccharin solution visited the saccharin location less than did unpoisoned animals, primarily during the later portions of the test sessions. When saccharin was moved to a different location, previously poisoned rats rapidly avoided the new saccharin location and increased visits to the original saccharin location, now rebaited with water. A similar pattern of learned avoidance and approach was obtained in Experiment 2 with three water locations and one vacant location (no water). These results indicate that: (1) sampling the contents of alternative patches mediates both learning to avoid the location of an aversive substance and returning to a newly viable patch, and (2) avoiding the location of a novel substance after a single poisoning occurs because the location does not contain an edible substance, not because of an aversion conditioned to environmental cues.

The study of foraging behavior has focused primarily on the determinants of choice of diet items or food patches in a stable environment (Krebs, Houston, & Charnov, 1981; Pyke, Pulliam, & Charnov, 1977). However, increasing attention has been directed to how animals allocate choices under changing food conditions (Krebs et al., 1981; Smith & Sweatman, 1974; Tinbergen, 1960). Several studies have documented a strategy of regular sampling of alternative food patches that presumably allows rapid tracking of changes in their profitability. This strategy has been observed in the field in bumblebees (Heinrich, 1979), howler monkeys (Glander, 1981), shorebirds (Goss-Custard, 1981), and hummingbirds (Gass & Montgomerie, 1981) and in the laboratory with great tits (Krebs et al., 1981), titmice (Smith & Sweatman, 1974), and rats (Barnett, Dickson, Marples, & Radha, 1978).

Although most research on the effects of changing patch quality has focused on variation in food density, another potentially important instance of changing food conditions is the ingestion of a novel substance followed by illness (Freeland & Janzen, 1974; Westoby, 1974, 1978). A vast body of research has shown that animals will avoid the taste and odor of a food item associated with illness (Domjan, 1980; Garcia & Koelling, 1966; Palmerino, Rusiniak, & Garcia, 1980; Rozin & Kalat, 1971). Although the evi-

dence is less extensive, a number of studies also have shown that animals learn about environmental cues associated with illness. For instance, Best, Best, and Mickley (1973) showed that illness associated with a distinctive chamber decreased rats' preference for that chamber. In a study showing the importance of environmental novelty, Rudy, Iwens, and Best (1977) found that exposure to novel exteroceptive stimuli prior to a taste-illness pairing decreased the magnitude of the subsequent illness-based taste aversion. However, these instances of illness-based aversions to environmental cues may have limited importance in natural foraging behavior, because the conditioning is based on repeated poisonings in the absence of ingestion.

Recently, though, several investigators, in testing the effects of devaluation of the reinforcer following illness, have found a taste-mediated decrease in the instrumental responses of barpressing and straight-alley running. Adams and his colleagues (Adams, 1982; Adams & Dickinson, 1981; Dickinson, Nicholas, & Adams, 1983) trained rats to barpress for sucrose reward and subsequently paired the sucrose with illness. Rats for which sucrose had been made aversive showed less barpressing than did control animals during a later extinction test. Chen and Amsel (1980) showed that speed of running a straight alley for a distinctive taste reward decreased on the first trial after that taste was paired with illness.

These studies suggest that the presence of a poisoned substance may be an important determinant of foraging behavior in rats. However, it is not clear whether such taste-mediated conditioning occurs in more complex choice situations, and whether the size of the effect is sufficient to modify overall choices of foraging locations. For instance, Slotnick, Brown, and Gelhard (1977) observed rats in a social living situation with three drinking loca-

tions. They found no apparent aversion to the drinking location previously associated with ingestion of saccharin solution paired with a single illness.

Furthermore, many questions concerning the role of environmental cues in poison avoidance remain unanswered in previous research. For instance, does the animal abandon the location of a novel substance the ingestion of which is followed by illness or does it continue to sample that location regularly? Does the animal respond rapidly to the appearance or disappearance of a known poisonous substance at a particular location? If avoidance of a patch containing a poisonous substance occurs, is it based on the aversion to the taste or odor of the substance transferred to the location or to the simple absence of an edible substance?

The intent of the present research was to examine how the introduction of a poisoned substance at different locations affected the choice behavior of rats in a laboratory analog of patch selection. Thirsty rats were tested while foraging for water in a four-armed radial maze. Experiment 1 attempted to determine the effects of introducing a novel conditioned aversive substance (saccharin) in one of the arms, and subsequently moving its location. Experiment 2 determined whether avoidance of the saccharin arm was significantly different from avoidance of an arm containing no water. Experiment 2 also carefully traced the time course of visits to each arm to determine to what extent avoidance could be attributed to initial daily sampling of the saccharin arm.

EXPERIMENT 1

The purpose of Experiment 1 was to determine whether a conditioned aversive substance affected rats' choices of drinking locations in a radial arm maze that had three water locations and one distinctive taste (saccharin) location. It seemed reasonable that poisoned rats should visit the location of the novel saccharin taste less often than unpoisoned animals, but the speed of development and completeness of this avoidance was an open question. One group of rats was tested after receiving a conditional pairing of saccharin and illness, and the other group was tested in the same way without taste aversion conditioning. Experiment 1 also examined the effect of a change in the location of saccharin following two initial test sessions. If rats sampled locations regularly, it was anticipated that they would return rapidly to the patch previously containing the poisoned substance. The development of avoidance of the new location containing saccharin should also reflect the regularity of sampling.

Method
Subjects. Sixteen male Long-Evans rats, 60 to 80 days old, were used as subjects. All rats were housed individually under a 12:12 light/dark cycle. Three days before the experiment, the subjects were maintained on a 23.25-h water-deprivation schedule, with free access to water for 45 min while in the home cage. Behavioral tests were conducted 3 h into the light cycle.

Apparatus. The apparatus was a plywood radial-arm maze with four arms radiating from alternate sides of a center octagonal plate. The octagonal center plate was 34 cm in diameter, and the individual arms were 52 cm long and 10 cm wide. The arms and parts of the octagonal center plate not connected to an arm had sides 10 cm in height. The entire maze was painted with unleaded glossy white paint. The floor of each arm was covered with plastic inserts to facilitate cleaning after each test session. The center floor was covered with .32-cm fiberboard.

The maze was situated inside a plywood box, 135 cm square and 40 cm high. A clear Plexiglas lid could be lowered onto the top of the maze to prevent rats from climbing out. The covering over the center plate was opaque.

Water feeders were centered 5 cm above the end of each arm. Each water feeder was a solenoid valve, which delivered approximately .1 ml to a brass nipple when operated. The water feeders were gravity fed in parallel via tubing from a common reservoir. The brass nipples protruded 3 cm into the maze from the end of each arm. Saccharin solution (1 g sodium saccharin per liter of water) was introduced to a particular feeder by replacing the water tube to the solenoid valve with a tube containing saccharin solution from a separate reservoir. Water feeders were operated individually by the experimenter from a four-button switchboard.

Procedure. Rats received one test session a day for 7 days. On Days 1 and 2, each rat was placed onto the center plate of the maze facing Arm 3 and the Plexiglas lid was lowered to cover the maze. The rat was then allowed to choose freely among the arms for 20 min, and .1 ml of water was delivered to the feeder following a response to any arm. A response was defined as all four paws onto the arm. Sequential visits to the same arm were counted only if the rat reentered the center plate before returning. The maze room was dimly illuminated during testing procedures. After 20 min, the rat was returned to its home cage, where it received free access to water for 45 min. Four rats that made fewer than 20 responses on Day 2 were not tested further. Half of the remaining 12 rats were assigned randomly to each of two drug treatment groups, a poisoned group and a saline group.

On Day 3, the most frequently visited arm during Day 2 (Test Day 0—T0) was baited with the saccharin solution and water was removed from the remaining arms. After 25 responses to the saccharin arm, each rat was taken from the maze and then allowed access to saccharin solution in the home cage for 45 min. Immediately after this drinking bout, rats in the poisoned group received an intraperitoneal (ip) injection of lithium chloride (LiCl .15M, 3% of body weight) and rats in the saline group received an ip injection of saline solution (NaCl .15M, 3% of body weight).

On Days 4 and 5 (Phase 1, maze testing—T1 and T2), each rat was placed into the maze and allowed to choose freely among the arms for 20 min. Saccharin was located in the same arm as on Day 3, and the other three arms now had water available. On Days 6 and 7 (Phase 2, maze testing—T3 and T4) the rats were again tested for 20 min in the maze. However, the most frequently chosen water arm during Phase 1 of maze testing was now baited with saccharin solution and the remaining arms contained water. Immediately after each day of maze testing, each rat was given simultaneous access to water and saccharin solution in the home cage for 45 min as a taste preference test. The position of each solution was always the same.

Results
Phase 1, maze testing. For each animal, the number of responses to the saccharin arm was divided by the total number of responses to all arms; the mean percentage scores for each condition are shown in Figure 1. The scores indicated on T0 are for the most preferred arm on the maze before the introduction of saccharin and drug
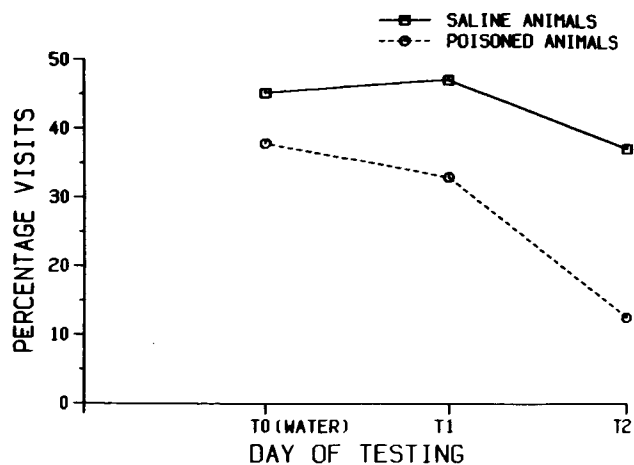
Figure 1. Mean percentage of visits to the preferred water arm before (T0) and after saccharin baiting and drug treatments (T1 and T2).

treatments. Scores on the following days (T1 and T2) show responding to the same arm now baited with saccharin and after drug treatments.

The percentage of visits to the most preferred water arm before saccharin baiting (T0) did not differ significantly between the poisoned and saline groups [t(10) = .84, p > .2]. However, after drug treatment (T1 and T2), the poisoned animals visited the saccharin arm less than did the saline animals [F(1,10) = 19.55, p < .001]. Also, both the poisoned and saline animals showed a decrease in the percentage of visits to the saccharin arm between T1 and T2 [F(1,10) = 18.16, p < .001], and there was no interaction between drug treatment and day of testing.

Phase 2 maze testing. The mean percentage of visits to the new saccharin arm are shown in Figure 2. As in Phase 1 of maze testing, the first day (T2) indicates responding to the most preferred water arm before saccharin baiting and the scores for T3 and T4 are for respond-
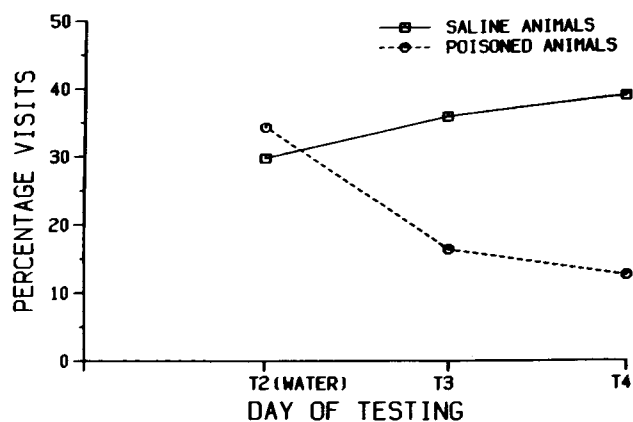

Figure 2. Mean percentage of visits to the new preferred water arm by poisoned and saline animals before (T2) and after saccharin baiting (T3 and T4).

ing to the same arm baited with saccharin. The percentage of visits to the most preferred water arm (T2) were slightly higher for poisoned animals, and this effect approached significance [t(10) = 1.89, p < .07]. As can be seen in Figure 2, the poisoned animals visited the saccharin arm less often than did the saline animals on T3 and T4 [F(1,10) = 34.34, p < .001]. Also, between T3 and T4, the poisoned animals showed a slight decrease in the percentage of visits to the saccharin arm, whereas the saline animals showed a slight increase, and this drug × days interaction approached significance [F(1,10) = 4.84, p < .06].

During Phase 2 of maze testing, we also measured the percentage of visits to the original saccharin location on the day before (T2) and the 2 days after (T3 and T4) this location had been rebaited with water. Figure 3 shows that the poisoned animals substantially increased the percentage of visits to the original saccharin location when it was rebaited with water between T2 and T3 [t(5) = 3.84, p < .01]. The poisoned animals also increased their percentage of visits to the rebaited water arm between T3 and T4 [t(5) = 5.32, p < .01]. The percentage of visits to the original saccharin arm by the saline animals did not differ significantly across T2, T3, and T4.

Taste preference tests. Each animal's saccharin intake score was computed by dividing the milliliters of saccharin consumed by total fluid intake (ml saccharin + ml water). The mean percentage of saccharin consumption for the two groups on T1 through T4 is shown in Table 1. As can be seen, the mean percentage of saccharin intake by poisoned animals was markedly depressed relative to the intake of the saline animals on each of the 4 days of taste preference testing [F(1,10) = 192.34, p < .001]. Also, there was a general increase in the percentage of saccharin intake across days of testing [F(3,30) = 7.99, p < .001].

Discussion

The results demonstrated that rats avoid the location of a conditioned aversive substance relative to the frequency with which they visit the location of a palatable substance. Poisoned animals entered the saccharin arm substantially less frequently than did the saline animals on all test days. This spatial avoidance of a poisoned substance had four characteristics. First, informal observation suggested that the avoidance was acquired *after* the rats had sampled the location of the poisoned substance, rather than as a direct result of illness. That is, a single poisoning did not retrospectively condition avoidance to the location previously associated with the novel substance. The failure to condition avoidance to environmental cues following a single poisoning is, of course, a fundamental finding in taste-aversion research (Domjan, 1980), but the present finding was particularly relevant to the role of this effect in a more realistic foraging situation (see, also, Slotnick et al., 1977).

Second, the conditioned avoidance of the location of a poisoned substance developed rapidly, since poisoned
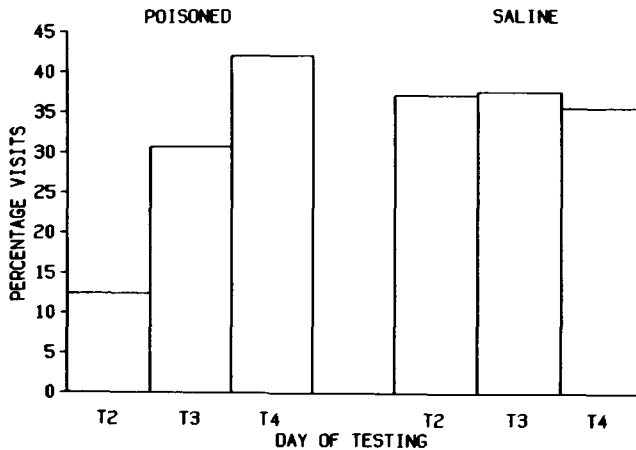
Figure 3. Mean percentage of visits to the original saccharin arm by poisoned and saline animals before (T2) and after water rebaiting (T3 and T4).

rats made fewer visits to the saccharin location than saline animals on the first day after poisoning. Third, control of this location avoidance appeared to depend on the continued presence of saccharin; the conditioned avoidance did not show any permanent transfer to environmental cues. For instance, when the location of saccharin was moved and the original saccharin location was rebaited with water, rats rapidly avoided the new saccharin arm and substantially increased the number of visits to the original saccharin arm within a single test session. Similarly, Slotnick et al. (1977) found that rats readily resumed drinking a palatable substance at a location that had previously contained a poisoned substance.

Finally, avoidance of the saccharin location was never complete. This finding suggests a critical role of sampling alternative foraging locations in allowing rats to adjust readily to changes in the spatial distribution of palatable and unpalatable substances, at least among familiar locations. It also should be noted that avoidance of saccharin intake was not complete. Poisoned rats consumed between 15% and 30% saccharin during the taste-preference tests. In short, the conditioning of avoidance of the location of a poisoned substance did not appear to be based directly on the poisoning experience, but proceeded rapidly with subsequent sampling of the location. However, the conditioning of location avoidance was also incomplete in that

Table 1
Mean Percentage of Saccharin Intake as a Function of
Drug Treatment and Day of Testing

Day	Drug Treatment	
	Poisoned	Saline
T1	15	67
T2	17	77
T3	23	80
T4	31	83

animals continued to visit the location of poison, and the avoidance reversed readily with changes in the spatial distribution of palatable and unpalatable substances in the environment.

Some of these results appear to contrast with studies in which barpressing or alley running was decreased by the pairing of a distinctive reward with illness (Adams, 1982; Adams & Dickinson, 1981; Chen & Amsel, 1980; Dickinson et al., 1983). It should be noted that those studies used repeated or relatively high dosages of poison, a single practiced appetitive behavior, and that the effect was not robust with respect to type of schedule or training (Adams, 1980, 1982; Chen & Amsel, 1980; Garcia, Kovner, & Green, 1970; Holman, 1975). Perhaps most importantly, the poisoning manipulation only decreased the rate of pressing or running rather than altering the choice of location.

EXPERIMENT 2

Experiment 2 defined further the cues controlling rats' spatial avoidance of a poisoned substance, and examined the time course of visits to the saccharin location within each test session to clarify the nature of this sampling. One obvious strategy by which animals could monitor the spatial distribution of palatable and unpalatable resources is to visit all locations early in each test session and then exploit the profitable (water) locations (Barnett et al., 1978). If this is the case, poisoned animals should visit the saccharin location less often than saline animals, primarily during the latter intervals of each test session.

Second, informal observations from Experiment 1 showed that poisoned rats rarely drank the saccharin solution on the maze after initial visits to that location. This observation raised the question of whether rats avoided the saccharin location because the environmental cues or odors associated with the saccharin became aversive (Garcia & Rusiniak, 1980; Palmerino et al., 1980) or simply because the saccharin location no longer contained an edible substance. Accordingly, to determine whether avoidance of the saccharin arm was significantly different from avoidance of an arm containing no water, Experiment 2 tested rats under a condition in which three locations contained water and one location was vacant (no fluid).

A third, potentially important, issue was whether the location avoidance actually depended on the prior association of a particular location with the poisoned substance or whether the odor of saccharin at the center platform determined maze choices. In Experiment 2, a strong saccharin solution was placed behind each of the water feeders so that rats could smell, but not contact, the saccharin in all locations. If the results of Experiment 1 were due to differential olfactory cues among the arms, both poisoned and saline animals should visit the saccharin location equally often because no differential olfactory cues existed among the arms in Experiment 2.

Method

Subjects. Twenty male Sprague-Dawley rats served as subjects in Experiment 2. The ages of these rats, the housing conditions, and the water-deprivation procedures were the same as in Experiment 1.

Apparatus. A different testing room and apparatus were used for Experiment 2. The apparatus was a larger four-armed radial maze constructed of plywood and painted gray. A center platform, 86 cm in diameter, was elevated 63 cm above the floor. Four individual arms extended from the center platform, as described in Experiment 1. The arms were 10 cm wide and 68 cm long and had siding 3 cm in height.

The design and control of the watering system were similar to those of Experiment 1, but a different type of water receptacle—a .5-cm-deep brass well centered 2.5 cm from the end of each arm—was used. Water (.1 ml) or .15% sodium saccharin solution was delivered to the well through plastic tubing. To provide similar olfactory cues for each arm in the saccharin conditions, a paper towel, dressed with about 5 ml of .5% sodium saccharin solution, was placed 10 cm below the end of each arm. The maze room was well illuminated during all testing procedures.

Procedure. All animals were subjects in the vacant-arm condition and in either the poisoned or saline conditions. Ten animals were tested in the vacant-arm condition before they were placed in one of the saccharin conditions. The remaining 10 animals were tested in the reverse order.

The procedures in Experiment 2 were the same as in Experiment 1, with the exceptions noted below. On Day 1, the animals were allowed to explore the maze in groups of two or three for 10 min without water or saccharin in the arms. On Day 2, the animals were tested individually on the maze, and responses to the arms (defined as in Experiment 1) produced .1 ml of water. Each animal was tested daily until it showed 40 responses within a test session. The arm that was the most frequently visited by each animal on 3 consecutive days of testing was designated as its "preferred" arm. There were not large differences in preferences among the arms. The mean percentage of visits to the least preferred arm during these 3 days for poisoned animals was 19.4.

Phases 1 and 2 of maze testing were performed as in Experiment 1, with the exceptions noted below. For the vacant-arm condition, the supply of water to the preferred arm was terminated and the remaining arms contained .1 ml of water per visit. In Phase 1, the animals were tested for 20 min for 2 days, with one vacant location and three water locations. On the first day of Phase 2, the location of the vacant arm was changed according to the procedure used in Experiment 1 and the supply of water to the previously vacant arm was replaced. In Phase 2, the animals were tested for 20 min daily on 4 consecutive days. The animals received free access to water for 45 min in the home cage after all days of maze testing.

In the saccharin conditions, each animal's preferred arm was baited with saccharin and the remaining arms contained water. Also, the animals were tested for 20 min on the first day of saccharin baiting. Immediately after maze testing, the animals were given free access to saccharin solution in their home cages for 45 min. The 10 animals in the poisoned group received ip injections of .15M LiCl at 2% of body weight, and the 10 animals in the saline group received ip injections of .15M saline solution at 2% of body weight. The animals received their exposures to saccharin and drug treatments on the day after the preferred arm was determined. There was a slight decrease in responding to the novel saccharin arm on the day of drug treatments (about 4% from T0), and Phase 1 began the following day. It should be noted that Phase 1 testing began on the first day after the preferred water arm was determined in the vacant-arm condition. The remaining procedures for Phases 1 and 2 of maze testing in the saccharin conditions were the same as for Experiment 1, except that there were 6 days of Phase 2 maze testing.

Results

The scores for responding to the saccharin or vacant arm were calculated as in Experiment 1. The scores for responding to the preferred water arm represent the mean of the 3 days before saccharin baiting or the vacant arm manipulation (i.e., the scores shown for T0). A within-groups analysis compared the performance of the rats in the poisoned group with their performance in the vacant condition. A between-groups analysis compared the performance of the rats in the poisoned group with the performance of the saline animals in the vacant condition. There were generally no differences in the statistical conclusions yielded by the repeated and independent measures analysis.

Phase 1 maze testing. Figure 4 shows the mean percentage of visits to the preferred arm before (T0) and after (T1 and T2) the saccharin manipulation or the vacant-arm manipulation. Responding to the saccharin arm is shown for the days after drug treatment.

As indicated in Figure 4, there were no significant differences among the three conditions in the percentage of visits to the preferred water arm (T0). However, poisoned animals visited the saccharin location less often than the saline animals after drug treatments (T1 and T2) [$F(1,18) = 32.67$, $p < .001$].

Figure 4 also shows that responding to the vacant arm was similar to that of the poisoned animals to the saccharin arm. The percentage of visits to the vacant arm was slightly higher than that of the poisoned animals to the saccharin arm on T1 (ps $<$ .05) but not on T2.

Phase 2 maze testing. Figure 5 shows the mean percentage of visits to the new saccharin and vacant arms. Animals in the poison and vacant-arm conditions showed slightly more responding than did saline animals to this location on the day before saccharin baiting and the vacant-arm manipulation (T2). Poisoned animals visited the new saccharin location less than did saline animals
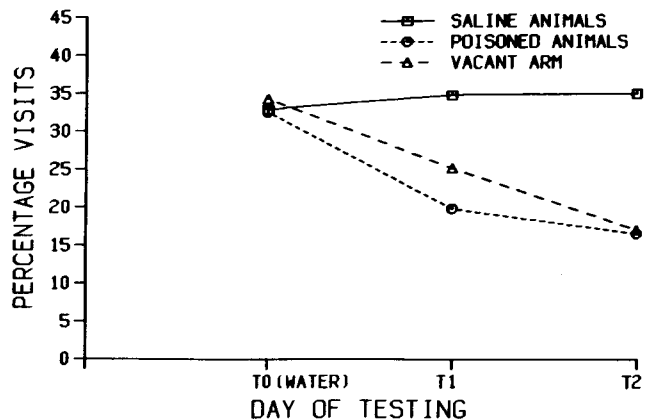

Figure 4. Mean percentage of visits to the preferred water arm before (T0) and after saccharin baiting and drug treatment or removal of water (T1 and T2). Scores shown for the vacant-arm condition represent the mean of the 20 animals tested.
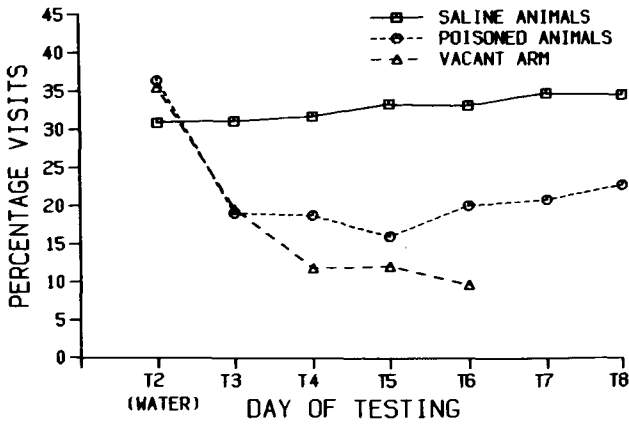
Figure 5. Mean percentage of visits to the new preferred arm by saline and poisoned animals before (T2) and after saccharin baiting or removal of water (T3 through T8).

on all days of Phase 2 [F(1,18) = 35.18, p < .001]. Also, both poisoned and saline animals showed a significant increase in responding to the saccharin arm between T3 and T8 [F(5,90) = 3.61 , p < .01]. Figure 5 also shows the pattern of responding to the vacant arm. As can be seen, responding to the vacant arm was equivalent to the responding of poisoned animals to the saccharin arm on T3, but was actually less than the responding of the poisoned animals to the saccharin arm in the later days of Phase 2 [F(3,54) = 4.78, p < .01].

The percentage visits to the original saccharin or vacant arm on the day before (T2) and the 2 days after (T3 and T4) the water rebaiting procedures are shown in Figure 6. As can be seen, the poisoned animals showed a significant increase in responding between Days T2 and T3, when the original saccharin arm was rebaited with water [t(9) = 5.00, p < .01]. There was no significant difference in responding between Days T3 and T4 for poisoned animals.
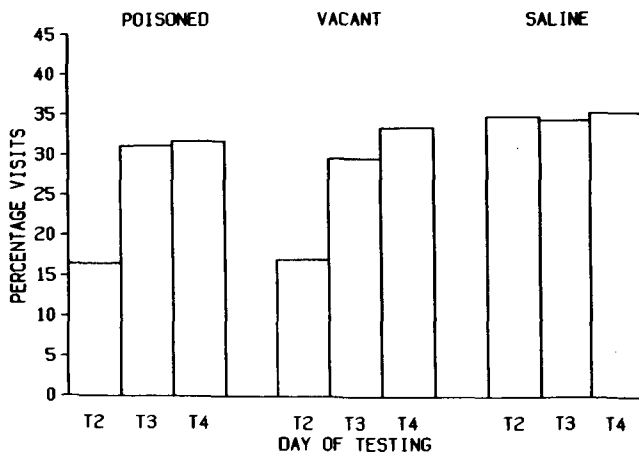

Figure 6. Mean percentage of visits to the original saccharin/vacant arm by poisoned and saline animals before (T2) and after water rebaiting (T3 and T4).

Figure 6 shows a similar pattern of responding to the vacant arm. There was a significant increase in responding between Days T2 and T3, when the original vacant arm was rebaited with water [t(19) = 4.88, p < .01] and no change in responding between days T3 and T4. Finally, it can be seen that saline animals showed no significant change in responding to the original saccharin arm after it was rebaited with water.

Within-session responding. Figure 7 shows the mean percentage of visits to the preferred arm during each 5-min interval within Sessions T0 (water in all arms) and T1 through T5 (one arm vacant or baited with saccharin). As can be seen, there were no differences among the conditions within Session T0 when the preferred arm contained water.

Poisoned animals visited the saccharin arm less than did saline animals primarily during the later intervals of testing on T1 and T2 [group × interval interactions, F(3,54) = 3.30, F(3,54) = 3.78, ps < .02]. Figure 7 indicates that poisoned animals visited the saccharin arm less than saline animals during the first 5 min of T1, but this effect was not significant. There were no significant differences between the vacant and poisoned conditions within Session T1 or Session T2.

Within-session responding after the location of the saccharin or vacant arm was changed is shown under T3 through T5. As can be seen, the poisoned animals visited the new saccharin arm less often than did the saline animals, but this was primarily during the later intervals on T3 and T4 [group × internal interactions, F(3,54) = 6.24, F(3,54) = 6.28, ps < .001]. On T5, the poisoned animals visited the saccharin location less often than the saline animals throughout the session [F(1,18) = 22.39, p < .001]. There were no significant overall differences between responding in the vacant and poisoned conditions on T3. However, it can be seen that there was less responding in the vacant than in the poisoned condition during the first half but not during the second half of T4 [F(3,54) = 4.44, p < .01]. Finally, it can be seen that there were fewer visits in the vacant condition than in the poisoned condition throughout T5, but this trend was not significant.

Taste-preference tests. Table 2 shows the mean percentage of saccharin intake by poisoned and saline animals. Poisoned animals drank less saccharin than saline animals on all test days [F(1,18) = 139.64, p < .001]. Both groups showed an increase in saccharin intake across test days [F(7,126) = 6.87, p < .001].

Discussion

The results replicated the findings of Experiment 1 and permitted several further conclusions about rats' reactions to changing foraging conditions in a radial arm maze. First, the olfactory cues available at the center platform were not a critical determinant of poisoned animals' avoidance of the saccharin location, because they learned to avoid the saccharin location even with a common saccharin odor in each arm.
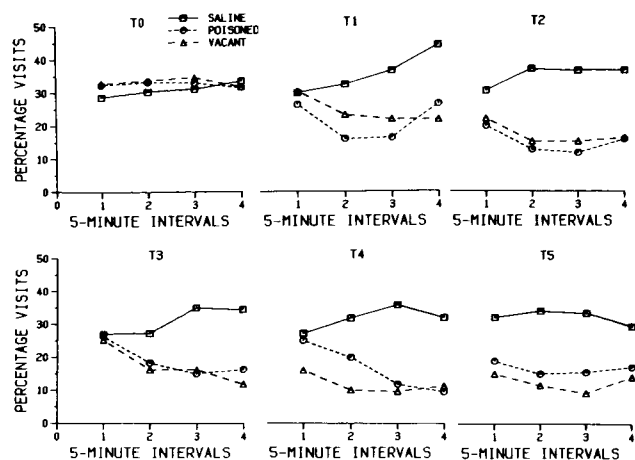
Figure 7. Time course of visits to the preferred arm within Sessions T0 through T5 for the poisoned, saline, and vacant-arm conditions. The mean percentage of visits to the preferred arm is shown for the first, second, third, and fourth 5-min interval of each test session. T0 shows responding to the preferred water arm, T1 and T2 represent Phase 1, and T3 through T5 represent Phase 2 maze testing.

Second, the time course of visits to the saccharin arm strongly suggested the importance of daily sampling in determining foraging patterns in rats. The within-session data showed that there were no differences between poisoned and saline animals early in the initial test sessions. However, poisoned animals showed progressively less responding to the saccharin location relative to saline animals toward the end of initial test sessions (T1, T3, and T4). The poisoned animals did show an increase in the percentage of visits to the saccharin arm at the end of T1, but their responding remained substantially less than that of the saline animals. The poisoned animals also showed fewer visits to the saccharin arm than did the saline animals during the first 5 min, but only on later test days (T2 and T5). Thus, avoidance of the saccharin location required substantial sampling both within and between test sessions.

The general strategy exhibited by the poisoned animals was *initial sampling* of *all* locations before avoidance of the poison location. As a more direct measure of initial sampling, we calculated the number of different arms

Table 2
Mean Percentage of Saccharin Intake as a Function of
Drug Treatment and Day of Testing

	Drug Treatment	
Day	Poisoned	Saline
T1	21	72
T2	22	81
T3	16	81
T4	31	81
T5	30	76
T6	41	81
T7	47	85
T8	47	85

visited during the first four choices on the first day after poisoning (T1). Poisoned animals visited a mean of 3.9 different arms during their first four maze choices on T1. This finding provides further evidence that an aversive taste does not affect initial choice of location in the present foraging situation. The rats' general foraging strategy also involved continued sampling of the saccharin location. Indeed, poisoned animals maintained a relatively high percentage of visits to the saccharin arm (about 15%) even during the latter portions of test session.

Finally, the within-session time course of avoidance and the rapid elimination of spatial avoidance to the previously poisoned location suggested that the animals treated the saccharin location as containing no edible substance rather than as a dangerous or aversive stimulus. This view is strongly supported by the similarity of visits to vacant and poisoned patches. Responding to a vacant arm was similar to the responding of poisoned animals to the saccharin arm within and between sessions. There were fewer visits to the vacant arm than to the poisoned saccharin arm on T4, T5, and T6, but this may have been due to some extinction of the conditioned taste aversion, a possibility supported by the increased saccharin consumption of the poisoned animals.

The most convincing evidence of the similarity between the vacant-arm and poison conditions came from an analysis of responding within test sessions. Responding in the vacant-arm and poison conditions was about the same as it was in the saline condition early in the test session. However, in both the vacant-arm and poison conditions, responding decreased progressively across the session relative to the responding of the saline animals. This similarity between the time course of responding in the poison and vacant-arm conditions was particularly striking on the first day after a change in the location of saccharin or the vacant arm (T3).

There was also a similar pattern of responding in the vacant and poison conditions on the first day after the water rebaiting procedures. Animals in both these conditions showed a substantial increase in responding to the original vacant/saccharin arm on the first day after water was returned to that location.

GENERAL DISCUSSION

Taken together, these results clearly show that rats learned to decrease the frequency of their visits to the location of a conditioned aversive substance. The rats also rapidly learned to avoid a new location of this substance, even after 2 days of exposure to the substance in its original location which were not followed by illness. This learned avoidance of the location of a poisoned substance has several interesting characteristics. First, unlike the case for taste and odor of a novel substance, the conditioned avoidance of a poisoned location is not due simply to illness following ingestion (e.g., Best et al., 1973). Rather, rats continued to sample the location and the substance before decreasing their visits to the location over

time within the test sessions. A similar pattern of avoidance occurred when the location of the poisoned substance was changed.

A related, and important, characteristic was that the spatial avoidance of the poisoned substance was incomplete. Poisoned animals continued to sample all arms each day. The tendency to sample was especially high early in the initial test sessions, but continued intermittently even during the later days of testing. As mentioned previously, it appeared that continued visits to the saccharin location allowed poisoned rats to detect changes in the quality of substance in that location. Thus, in addition to rapidly learning to avoid the location of a "poisonous" substance, rats also learned rapidly to return to the same location when the poison was replaced by water (see, also, Smith & Sweatman, 1974).

The third interesting characteristic was that the spatial avoidance did not appear to be due to a typical secondary conditioned aversion based on the taste or odor of saccharin but rather to a simple avoidance of the location because it did not contain an edible substance. Experiment 2 showed that animals avoided an arm that contained no substance at least as much as they did an arm that contained a poisoned substance. Moreover, avoidance of the vacant arm also appeared to be based on the same daily sampling of alternative locations exhibited by the poisoned animals.

The rapid increase in visits to the initially poisoned location after rebaiting with a palatable substance (water) also supports the interpretation that avoidance of the location of a poisonous substance was not based on a conditioned aversion related to illness. As mentioned previously, other studies have reported that an aversive substance can decrease the instrumental responses of straight alley running and barpressing (Adams, 1982; Adams & Dickinson, 1981; Chen & Amsel, 1980; Dickinson et al., 1983). However, the present results indicate that any such effects of an aversive taste on appetitive behavior either do not extend to the rat's choice of location in a foraging situation or were too small to be measured in the present paradigm.

In short, rats did not learn to avoid the location of a novel substance based on a single illness. Rather, the animals decreased their visits to the poisoned location only after continued sampling of that location. The relative avoidance of the location of a poisoned substance first appeared during the latter intervals of the initial test sessions, and then increasingly across the entire session on later days of testing. It is important to emphasize that this avoidance was relative to choices of alternative arms rather than absolute, and that the avoidance appeared to be based on the absence of an edible substance and not a typical conditioned aversion related to a negative outcome such as shock. Thus, the present results can be attributed to a strategy of regular sampling of alternative feeding locations and, secondarily, to a transient learned avoidance of a location containing a poisoned substance.

Such a foraging strategy would allow rats to adjust rapidly to changes in the spatial distribution of palatable and unpalatable substances.

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