Effects of reward amount and reward omission on short-term retention

WILLIAM S. TERRY and BRENT J. McSWAIN
University of North Carolina, Charlotte, North Carolina

A series of four experiments studied the retention of the response made on a just-preceding trial as a function of the presence, and amount, of food reward given on that trial. Rats were trained to alternate arm choices in a T-maze, and then were tested for alternation with 5- or 30-sec delays between runs. When the subjects had received prior experience with the reward amounts used in testing, larger rewards led to better retention than did small or no rewards. However, when reward omission first occurred during the test phase, it produced more alternation on the following trial than did reward presence. The results suggest that both reward amount and surprisingness determine short-term retention of responses paired with the rewards.

Much of the recent research on animal short-term memory (STM) has focused on variables presumed to affect retention of certain to-be-remembered stimuli. These target stimuli could be, for example, the color of a key light in a delayed matching-to-sample task (Roberts & Grant, 1976) or the arm of a maze recently entered in a spatial memory task (Olton, 1978; Terry & Anthony, 1980). Retention of the target stimulus has been found to be affected by the temporally proximal occurrence of other stimuli. Thus, stimuli that make the target especially "surprising" may increase its short-term retention (Terry & Wagner, 1975). The present experiments investigated the effects of one stimulus commonly presented along with the target—a food reinforcer.

A trial in a delayed-response task can be conceptually divided into three stages: a cuing phase, in which the subject is exposed to the target stimulus; a variable-length delay interval; and a test for the memory of the target. In the present experiments, the presence and amount of food given with the target stimulus during the cuing phase was varied, while the amount of reward given for correct responding on the retention test was held constant. Thus, one should be able to assess the effects of reward magnitude on processing of the target stimulus during the cuing phase, in the absence of differential reinforcement for retention of the target during the delay or added incentive for correct test trial responding.

Previous research with primates has shown reward magnitude to be an effective variable (see Fletcher,

1965, for a review). In these delayed-response experiments, the subject watched as food was concealed under the target stimulus. The use of larger rewards or more preferred foods during the cuing phase led to better test performance (e.g., Nissen & Elder, 1935). This effect was found even when the reward was changed during the delay interval, so that a constant reward was given on the test irrespective of the amount previously shown (Cowles & Nissen, 1937).

While these results may indicate better attention to or storage of the target stimulus during the cuing phase, it has been suggested that the subjects may have maintained anticipation better during the delay interval on large-reward trials (Spear, 1978, p. 126). It is possible that, having seen the target baited with a larger reward, there was more incentive to perform well on the subsequent memory test due to an expectancy for a larger reward (Tinklepaugh, 1928).

More recent studies suggest that reward occurrence may have little effect on short-term retention. Honig (1978), using an advance key procedure with pigeons, found only a small facilitating effect of reward presentation versus omission during the cuing phase. Walker and Olton (1979), using a radial maze to assess spatial working memory, found, on subsequent performance, no effect of reinforcing or not reinforcing the cuing arm exposures. While cuing phase rewards may be useful when initially training subjects to perform in the various STM tasks, there is a question as to whether reward plays a significant role in subsequent retention testing.

The present studies used a delayed-alternation procedure to assess the effects of reward amount on retention. In this task, rats are trained to alternate choices of goal arms in a T-maze. During the cuing run of each trial, the rat is forced to enter one goal, by blocking the alternate goal, and is there reinforced with food pellets. On the test run of the trial, the rat

This research was supported by a Faculty Grant from the foundation of the University of North Carolina at Charlotte. The authors wish to acknowledge the assistance of Shelley Droescher in running Experiment 3. Address reprint requests to: W. S. Terry, Department of Psychology, University of North Carolina at Charlotte, Charlotte, NC 28223.

must alternate to the arm not entered on the cuing run in order to be rewarded. In the present situation, the amount of food given on the cuing runs was varied and sometimes omitted. Since the delayed-alternation task typically produces higher error rates than does the radial-arm-maze task, it might prove more sensitive in detecting reward-magnitude effects.

Four experiments involving within-subject comparisons are reported, each including one or more test phases. During initial alternation training, when only a minimal delay intervened between the two runs of a trial, the amount of food on the cuing runs was varied across trials. This was done to give the subjects experience with certain amounts of reward prior to delay testing, or in some cases to minimize experience with those amounts. Subsequent test phases, on trials with 5- or 30-sec delays, compared larger rewards to either small rewards or reward omission.

EXPERIMENT 1

Method

Subjects. The subjects were 10 male Sprague-Dawley rats with preexperimental weights of 130-190 g. The animals were individually housed in standard laboratory cages, in a room kept on a 12-h light-dark cycle.

Apparatus. The subjects were trained in an E-shaped maze with interior dimensions of 14.1 cm wide $\times$ 12.5 cm high. The three legs of the maze (the horizontal bars of the E), each 31 cm long, were connected to the 103-cm-long stem. The maze was made of plywood painted flat black and had guillotine doors at the midpoint of each leg. The center leg was used as the startbox, and the outer legs served as the left and right goalboxes. Thus, reward was not visible from the choice point.

Procedure. The subjects were placed on a 23-h food-deprivation schedule beginning 2 days prior to training. Water was available ad lib except during the experimental sessions. The subjects received two 6-min periods of exploration in the maze, with food pellets available in the goal areas.

Subsequent sessions contained alternation training trials, with each trial having two runs in the maze. On the first run, the subject was forced to enter one of the goal arms, the opposite arm being blocked at the choice point, and there received an experimentally determined amount of food (described below). The subject was detained in the goalbox for 15 sec on all forced-choice runs to equate confinement time across trials. The subject was then replaced in the startbox, a 3-sec delay was timed, and the startbox door was opened to begin the second run. The subject was now allowed to enter either goal, with food being available only in the arm opposite that entered on the first run. In cases of errors, free choice runs were repeated until correct alternation occurred. The correct choice was varied over trials in a sequence that equated the number of left and right turns and balanced left-right transitions over 2-day blocks of trials.

During acquisition, the subjects received one, three, or five 45-mg Noyes food pellets on the forced-choice runs. Two trials with each amount occurred daily across eight sessions of training. The sequence of the three types of trials was balanced across subjects and days, and was orthogonal to the left-right sequence of correct turns. Three pellets were given as reinforcement on all free-choice runs.

Following this training, two delayed alternation test phases were given. The trial types in each phase were derived from 2×2 factorial combination of (1) length of the delay interval between free and forced choice runs, either 5 or 30 sec, and (2) the amount of food given on the forced choice runs, 5 pellets (in both phases)

versus 1 pellet (Phase 1) or no pellets (Phase 2). Each trial type occurred twice daily in a counterbalanced sequence. Three sessions of testing occurred in each phase. During the delay intervals, the rat was held in the startbox of the maze.

The subjects were run in squads of three or four animals, with an intertrial interval averaging 4 min. All sessions began 5 h into the light cycle.

Results

In this, and the subsequent experiments, the data are reported in terms of the mean percentages of correct choices (i.e., alternations) on free-choice trials. For statistical analyses, these percentages were square-root transformed. Statistical significance is defined as $p < .05$.

During acquisition, correct alternation increased from 71% across all trials of Days 1-2 to 87.5% on Days 6-8. The high initial rate was likely due to a spontaneous alternation tendency, and has been noted previously in alternation acquisition (Roberts, 1972). The amount of food on forced runs had little effect on free-choice performance at any point during training.

The results of the first test phase are shown in the left panel of Figure 1. Here, mean correct alternation on the 5- and 30-sec-delay trials is plotted as a function of the amount of food given on the run preceding the delay. As can be seen, 5-pellet rewards led to more correct choices than did 1-pellet rewards. This effect was relatively constant across the delay intervals tested. A delay $\times$ amount analysis of variance showed a significant difference between 1- and 5-pellet trials [$F(1,9) = 7.19$]. No other effects were reliable.

The difference at the shorter delay might be taken to indicate that nonmemory variables were affecting responding here. However, performance during the

Figure 1. Mean percentage correct alternation on free-choice runs during the first-test (left panel) and second-test (right panel) phases of Experiment 1 as a function of the number of food pellets given on the forced-choice runs.

immediately preceding training sessions was comparable on 1- and 5-pellet trials (85% and 83%, respectively, on Days 6-8), when an even shorter delay was used. Thus, differential forgetting may have occurred after 5 sec.

The above values suggest that performance on 5-pellet trials increased between training and the 5-sec test trials. This may be due to an unexplained drop in accuracy on Day 7 of training (which affected all trial types), and possibly to subsequent improvement in alternation with continued training over the test days.

The results of the second test phase are shown in the right panel of Figure 1. Here, at the 5-sec delay, 5 pellets produced more correct choices than did reward absence. However, after 30 sec, there was a substantial drop in performance following rewarded runs. No such decline occurred on the 0-pellet trials. Analysis showed a significant interaction of delay and amount of food [$F(1,9)=10.06$]. Planned post hoc tests, using the error term from the above analysis, showed that the 5- and 0-pellet trials were significantly different at the 30-sec delay ($t=2.29$) and marginally different at the 5-sec delay ($t=2.20$).

The results generally show that there is more accurate delayed responding following large rewards than following small rewards. However, this pattern was true only when the small reward was a lesser amount of food rather than absence of food.

EXPERIMENT 2

The purpose of the second experiment was again to assess delayed responding as a function of reward amount. Several changes in procedure were made: smaller animals necessitated using smaller rewards, 1 and 3 pellets; fewer training sessions were given, to reduce the possibility of a ceiling effect as was present for some subjects during Experiment 1; and the initial test sessions included reward-omission trials as well as the large- and small-reward trials. A second test phase compared reward omission and the larger reward.

Method

Apparatus and procedure remained unchanged unless noted below. The subjects were 10 male rats, weighing 75-90 g prior to the experiment. Three days of handling and maze-familiarization were given. Alternation training consisted of six trials daily, using large- and small-reward amounts on the forced runs and the larger reward on the free-choice runs. On Days 1-2, 1 and 5 pellets were used. However, since the rats sometimes failed to consume 5 pellets, or took an inordinate amount of time to consume this amount, 3-pellet rewards were substituted as the larger reward for the remainder of the experiment. Five total sessions of training were given.

The first test phase used a 2×2 design, with the variables being (1) 5- or 30-sec delays, and (2) 1- or 3-pellet rewards. Two of each trial type occurred daily across three test sessions. Two additional "probe" test trials were scheduled for each session, during which reward was omitted on the forced-choice run. One trial used a 5-sec delay, and the other, a 30-sec delay. The position of these trials

within sessions varied over days and subjects, so that the average position equaled that of the other trial types.

A second test phase compared 0- and 3-pellet forced runs, and was otherwise identical to the second phase of Experiment 1.

Results

During alternation training, there was again little effect of reward amount. Correct alternation increased from 68.8% on Days 1-2 to 80% on Day 5.

The results of the first test phase are shown in the left panel of Figure 2. In first considering the effects of discrete reward amounts, it can be seen that the 3-pellet rewards led to better performance after 30 sec than did 1 pellet. There was little difference between these amounts after 5 sec. The delay $\times$ amount interaction was significant [$F(1,9)=9.92$].

When reward omission trials were included, the interaction was again reliable [$F(2,18)=4.18$]. Reward omission led to slightly better performance than did reward presence after a 5-sec delay, and to much better accuracy than 1 pellet after the 30-sec delay. Tests of simple effects showed no significant difference on 5-sec trials ($F < 1$), but a reliable difference among reward amounts on 30-sec trials [$F(2,18)=6.35$]. Post hoc tests showed that the 3- and 0-pellet trials were superior to the 1-pellet trials after 30 sec ($t_s=3.24$ and 2.91 , respectively).

The results of the second test phase are shown in the right panel of Figure 2. Although there is little overall difference between 0- and 3-pellet trials, the rewarded trials did show more of a decrease in correct choices across delays. Analysis showed no significant differences among these conditions. However, it is of some interest that reward omission was again as effective as the larger reward, even though the first test phase found the larger reward to be better than a small reward.

Figure 2. Mean percentage correct alternation on free-choice runs during the first-test (left panel) and second-test (right panel) phases of Experiment 2, as a function of number of food pellets given on the forced-choice runs.

The present results differ somewhat from those of Experiment 1. A difference between small and large rewards appeared only at the longer delay, and reward omission was not superior to the larger reward tested. However, the general conclusions across experiments is similar: larger rewards led to better performance than small rewards, while no reward (at least sometimes) enhances performance above the level produced by rewarded cuing runs.

EXPERIMENT 3

In the first two experiments, reward-omission trials were introduced during the test phases, after the subjects had received prior experience with food always given on the forced-choice runs. The finding that reward omission could produce better alternation might in some manner be related to the novelty of these trials. In contrast, Finan (1942) found reward presentation to be better than reward omission, but with a procedure that had given extensive experience with omission on some trials.

In Experiment 3, the subjects were given explicit training with reward omission during acquisition, followed by delay testing with 0- and 5-pellet trials.

Method

The subjects were 11 male rats weighing 105-130 g. Three sessions of maze adaptation and five sessions of alternation training were given. The acquisition sessions had three trials each with nonrewarded or 5-pellet rewarded forced-choice runs. Three pellets were given on the free-choice runs.

The three test sessions included two of each trial type from the factorial combination of reward amount (0 vs. 5 pellets) and delay interval (5 vs. 30 sec). The trial sequences were counterbalanced with respect to the four types of trials, and with the left-right sequence of correct choices. Only a single test phase was given, since correct responding began to deteriorate during testing.

Results

During acquisition, correct choices increased from 67% on Days 1-2 to 79% on Days 4-5. Performance did not vary significantly between 0- and 5-pellet trials.

The delay-testing data are summarized in Figure 3. Both 0- and 5-pellet runs led to comparable performance after 5-sec delays. However, after 30 sec, there was superior performance following 5-pellet rewards as compared with no rewards. Analysis showed a significant delay $\times$ amount interaction [$F(1,10)=8.16$] and a significant difference at the 30-sec delay ($t=3.58$).

EXPERIMENT 4

The third experiment found that reward presence produced better delayed-alternation than did reward absence, using subjects with prior experience with cuing reward omission. In contrast, omitting food seemed to facilitate alternation in the first two experiments. One possible explanation for this pat-

Figure 3. Mean percentage correct alternation on free-choice runs as a function of number of food pellets on forced-choice runs, for subjects given 0- and 5-pellet acquisition trials.

tern of results is that reward omission was more "surprising" in Experiments 1 and 2, being encountered for the first time on the cuing runs of the test trials. The occurrence of omission may have been relatively more expected in Experiment 3. Previous research has suggested that surprising events are better retained in STM than are expected events (Maki, 1979; Terry & Wagner, 1975) and, of present relevance, that the surprising absence of a stimulus is better retained than an expected absence (Maki, 1979).

However, since the differing results across the present series of experiments could be due to other factors (e.g., variations in procedure, age of the animals, amount of pretraining), an explicit test of the surprise hypothesis seemed warranted. In Experiment 4, two groups of subjects were given different alternation training experiences and were subsequently tested with 0- and 5-pellet trials. One group received training with food present on all cuing runs, as was the case in Experiments 1 and 2. The second group received training with food omitted on some of the cuing runs, as was the case in Experiment 3. The delayed alternation phase would then test for differences attributable to the prior experience with reward omission.

Method

The subjects were 14 male rats, weighing 240 to 260 g. Three sessions of maze adaptation were given as before, except that smaller quantities of food were available in the goalboxes. Thus, during these periods the rats consumed all the food in each goal. The subjects were then randomly assigned to two groups ($n=7$ each). Five sessions of alternation training were given, each containing three trials rewarded with 5 food pellets on the cuing runs. For subjects in Group 3-5, the other three trials daily had 3-pellet cuing rewards. For subjects in Group 0-5, these three trials had no food presented on the cuing run (i.e., 0-pellet condition). For the latter subjects, additional three-pellet rewards were given in the holding cages during the intertrial interval to equate total consumption during the training sessions. (This was not done on test days.) The

reward amount on free-choice runs was 5 pellets for all subjects on all trials of the experiment. The sequences of 0-5-pellet or 3-5-pellet trials and of left-right as correct turns were counterbalanced, as in the previous studies.

Following training, the subjects received four test sessions, using (as before) a factorial combination of 0- and 5-pellet cuing run rewards with a 5- or 30-sec delay interval. The test sequences were identical to those of Experiments 1 and 3.

The running order intermixed subjects from both groups during training and testing.

Results

The rate of alternation at the start of training averaged about 90% on Day 1, with little difference between the two groups. These high rates may have been due to the development of alternation during the maze-exploration sessions. On Days 4-5, correct alternation averaged 90% for Group 0-5 and 94% for Group 3-5, with no differences as a function of reward amount.

The delayed alternation test data are summarized in Figure 4, separately for each group. As can be seen in the left panel, the subjects given prior nonreward experience (Group 0-5) performed equivalently on 0- and 5-pellet trials after the shorter delay. However, after 30 sec, there was a substantial decrease in accuracy on the 0-pellet trials. These results are similar to those found in Experiment 3, which used comparable training and testing procedures.

The right panel of Figure 4 shows the performance of subjects not given prior training with reward absence on the cuing runs (Group 3-5). A very different pattern of results appears, with 0-pellet trials leading to more alternation than 5-pellet trials at both delay intervals, although the effect was somewhat greater at the 30-sec delay.

The statistical analysis of this data used the between-groups factor and the two within-subjects factors of

reward amount and delay. There was a significant effect of delay [$F(1,12) = 27.1$] and a groups $\times$ amount interaction [$F(1,12) = 7.68$]. No other effects in this analysis were significant. Post hoc tests of the interaction (collapsing across delays) showed, within each group, a marginally significant overall difference between 0- and 5-pellet trials ($t = 2.01$ for group 0-5 and $t = 2.08$ for Groups 3-5, $ps < .10$ two-tail). In a between groups comparison, there was significantly more alternation on 0-pellet trials by Group 3-5 subjects than by Group 0-5 subjects ($t = 2.36$).

Given that the previous experiments had suggested that larger effects would occur at the 30-sec delay, an additional planned analysis was done on the 30-sec data. Here there was a significant groups $\times$ amount interaction [$F(1,12) = 7.12$], with the 0- vs. 5-pellet difference being significant for Group 0-5 ($t = 2.73$) though not for Group 3-5 ($t = 1.56$).

Thus, performance on reward-omission trials, relative to that on rewarded trials, appears to be a function of prior experience with food absence in the experimental situation. The superiority of reward omission for Group 3-5 occurred at both delays. One possible reason could be that, given the higher rate of correct alternation throughout training and testing, relatively few nonrewarded free-choice runs occurred. Thus, reward absence may have been even more unexpected than in the other experiments.

GENERAL DISCUSSION

The major findings of these experiments can be summarized briefly. With respect to delayed responding, when subjects have had prior experience with the to-be-tested reward amounts, larger rewards lead to more correct alternation than do small or no rewards. This was shown in all four experiments, in comparisons variously involving 5 or 3 pellets versus 1 or no pellet. The present results complement previous reports of primate delayed responding (Cowles & Nissen, 1937; Finan, 1942). Since reward amount varied only on the cuing runs and not on the free-choice runs, one could argue that the larger rewards influenced memory processes at the time of cuing or during the retention interval, and were not differentially affecting incentive to perform accurately at the time of the test run.

A second major finding was that when reward omission on the cuing runs was first introduced during the test sequences, it led to better performance than did a 5-pellet (Experiments 1 and 4) or 1-pellet (Experiment 2) reward, particularly after a 30-sec delay. Only when subjects had had prior experience with reward omission on the cuing runs did reward occurrence prove superior. Although all subjects had had some experience with nonreward on the free-choice runs, these nonrewards were shortly followed by a correction run during which food was available. With a 15-sec detention in the goalbox on the cuing

Figure 4. Mean percentage correct alternation on free-choice runs for subjects that had had prior training with no-food cuing runs (Group 0-5, left panel), and for subjects without prior training with nonrewarded cuing runs (Group 3-5, right panel).

runs, a longer interval typically intervened before reward was obtained.

As noted earlier, some studies have shown little effect of reward variation on short-term retention (e.g., Honig, 1978; Walker & Olton, 1979). The present results could be due to any of several differences. Using the same two maze choices repetitively may have induced more between-trials interference (Terry & Anthony, 1980), thus increasing error rates. Also, comparisons of reward and reward omission in any given situation could show equal levels of correct performance, but in each case due to different sources. For example, large rewards might produce stronger memory traces, while reward absence could lead to sudden changes in attention or arousal (i.e., frustration) and thereby enhance retention.

Reward amount had little discernible effect during the acquisition phases of these studies. This suggests that, at very short delays, there were no differences attributable to attention or motivation on small-versus large-reward occasions which could complicate interpretation of the retention test data. The acquisition procedure also ensured that poor test performance with small, familiar rewards was not due to the novelty of a particular reward amount (i.e., generalization decrement).

In an attempt to provide a more sensitive test of reward-magnitude effects during training, data were combined across several experiments. Within-subjects comparisons were made between the smallest and largest reward used within a given study. On Day 1, a superiority of small rewards versus large rewards was found for subjects in Experiments 1, 2, and 4 (80.4% vs. 67.9%), and similarly for no food versus the large rewards in Experiments 3 and 4 (84.3% vs. 75%). However, across Days 2-5, no differences were found between the small and large rewards (80% and 80.6%) or between no food and large rewards (76.5% and 78.8%).

There are two current forms of memory theory that would seem to be especially applicable to the present results: variable rehearsal theory and temporal discrimination theory. Wagner (e.g., Wagner, 1978; Wagner, Rudy, & Whitlow, 1973) has suggested that there may be rehearsal of stimulus representations in STM. Variations in the degree or duration of rehearsal can occur, and one could reasonably assume that stimulus intensity should be a determining variable. Thus, larger rewards may provoke more rehearsal than smaller (or no) rewards. The novel theoretical statement needed to incorporate the present results would be that larger rewards also enhance rehearsal of other stimuli occurring contemporaneously with the rewards. That is, larger rewards would lead to more rehearsal of the location of the food, and not just of the food itself.

One reason for the development of variable rehearsal theory is to describe the acquisition of long-term memories. Thus, longer periods of rehearsal

would allow more opportunity for stronger long-term associations to be formed (Wagner & Terry, 1975). With respect to the present findings, one would be led to conclude that just as larger rewards seemingly enhance short-term retention, they should also enhance long-term conditioning. Indeed, many studies have demonstrated the effects of reward magnitude on the acquisition of instrumental conditioning (e.g., see Mackintosh, 1974).

Variations in rehearsal have most often been attributed to the "surprisingness" of the stimulus events: a surprising occurrence of a reinforcer has been found to be better retained than an expected occurrence (Maki, 1979; Terry & Wagner, 1975). Less research has been done on the complementary possibility that surprising omissions of reward may be better retained than expected omissions (but see Maki, 1979), although an extensive literature attests to the persisting aftereffects of frustrative nonreward (e.g., Amsel, 1972). The enhanced retention following reward omission in Experiments 1, 2, and 4 (Group 3-5) could be due to the expectancy established during training for food presentation on the cuing runs. However, in Experiments 3 and 4 (Group 0-5), food omission was made relatively more expected by the explicit training with nonreward, and thus would not be especially rehearsed during testing. Conversely, the occurrence of reward was made less predictable in Experiments 3 and 4, so that food presentations might have been better rehearsed than in the other conditions.

The temporal discrimination hypothesis (D'Amato, 1973; Worsham, 1975) could also provide an account of the present findings. This theory does not require a short-term/long-term memory dichotomy. Rather, correct performance on delayed response tasks depends on a discrimination in memory of the most recent cuing stimulus from traces of other stimuli that have previously occurred. Across longer delay intervals, delayed retention accuracy drops because of the difficulty in discriminating among several recent prior traces. As applied to the present case, one might argue that large-reward cued trials might leave more discriminable traces, thus allowing for better performance. Similarly, the uniqueness of reward omission might allow these trials to be more easily differentiated from traces of reward trials. However, this novelty might not work as a memory aid if nonrewarded trials were fairly common, as they were for groups receiving training experience with reward omission.

The present studies of the effects of reward amount on STM have parallels in several other literatures on performance after longer delays. For example, Gleitman (1971) has noted apparent retention of different reward magnitudes across 1-day delays, but forgetting across 68-day delays. Presumably also in the delayed-alternation task, equivalent forgetting among the several reward amounts could be obtained with longer delays. The present results are also con-

ceptually related to reward contrast effects (see Flaherty, 1982, for a comprehensive review). On the face of it, the use of within-subject designs and relatively brief intervals between trials could lead to depressed performance on small-reward trials, analogous to negative contrast, or to enhanced performance on large-reward trials, analogous to positive contrast. Alternatively, the levels of performance observed when food absence is suddenly introduced might better predict when contrast would appear in other tasks (such as the runway) in which a smaller reinforcer is substituted. Thus, while the present procedures contain the elements of contrast, the relationship of the present results to contrast is still unclear.

Finally, it must be acknowledged that delayed spatial alternation may reflect memory processes and also be affected by certain biological or species-typical predispositions of the subjects used. For example, untrained spontaneous alternation has been found to occur more often following small rewards (Richter & Kay, 1980) or reward absence (Gaffan & Davies, 1981). Olton, Handelman, and Walker (1981) have noted that rats' food-searching patterns seem to be more affected by food absence at a given location than by food presence. The present results in groups without prior reward-omission training are consistent with the above findings, and suggest further that the surprisingness of reward absence may be a determining factor. This interpretation is congruent with that of Gaffan and Davies (1981), who have implicated frustration or contrast effects in the production of such reward-magnitude effects on alternation behavior. However, it is also possible that the extensive training received in the present studies degraded the contribution of spontaneous response tendencies on test performance. As noted earlier, on Day 1 of training, small rewards led to more alternation than did large rewards, at a time when spontaneous alternation effects should be maximal. This difference disappeared over subsequent days of training. In any event, the present results suggest that studies of animal spatial behavior may have to consider not only reward presence or absence (Gaffan & Davies, 1981; Walker & Olton, 1979), but also the previous experience with these reward amounts in the test situation.

REFERENCES

- AMSEL, A. (1972). Behavioral habituation, counterconditioning, and a general theory of persistence. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II*. New York: Appleton-Century-Crofts.
- COWLES, A. T., & NISSEN, H. W. (1937). Reward expectancy and delayed responses of chimpanzees. *Journal of Comparative Psychology*, **24**, 345-347.
- D'AMATO, M. R. (1973). Delayed matching and short-term memory in monkeys. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 7). New York: Academic Press.
- FINAN, J. L. (1942). Delayed response with pre-delay re-enforcement in monkeys after the removal of the frontal lobes. *American Journal of Psychology*, **55**, 202-214.
- FLAHERTY, C. F. (1982). Incentive contrast: A review of behavioral changes following shifts in reward. *Animal Learning & Behavior*, **10**, 409-440.
- FLETCHER, H. J. (1965). The delayed-response problem. In A. M. Schrier, H. F. Harlow, & F. Stollnitz (Eds.), *Behavior of non-human primates* (Vol. 1). New York: Academic Press.
- GAFFAN, E. A., & DAVIES, J. (1981). The role of exploration in win-shift and win-stay performance on a radial maze. *Learning and Motivation*, **12**, 282-299.
- GLEITMAN, H. (1971). Forgetting of long-term memories in animals. In W. K. Honig & P. H. R. James (Eds.), *Animal memory*. New York: Academic Press.
- HONIG, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, NJ: Erlbaum.
- MACKINTOSH, N. J. (1974). *The psychology of animal learning*. New York: Academic Press.
- MAKI, W. S. (1979). Pigeons' short-term memories for surprising vs. expected reinforcement and nonreinforcement. *Animal Learning & Behavior*, **7**, 31-37.
- NISSEN, H. W., & ELDER, J. H. (1935). The influence of amount of incentive on delayed response performance of chimpanzees. *Journal of Genetic Psychology*, **47**, 49-72.
- OLTON, D. S. (1978). Characteristics of spatial memory. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, NJ: Erlbaum.
- OLTON, D. S., HANDELMANN, G. E., & WALKER, J. A. (1981). Spatial memory and food searching strategies. In A. C. Kamil & T. D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches*. New York: Garland.
- RICHTER, M. L., & KAY, E. J. (1980). The roles of expectancy and aftereffects in alternation. *Learning and Motivation*, **11**, 503-521.
- ROBERTS, W. A. (1972). Spatial separation and visual differentiation of cues as factors influencing short-term memory in the rat. *Journal of Comparative and Physiological Psychology*, **78**, 284-291.
- ROBERTS, W. A., & GRANT, D. S. (1976). Studies of short-term memory in the pigeon using the delayed matching-to-sample procedure. In D. L. Medin, W. A. Roberts, & R. T. Davis (Eds.), *Processes of animal memory*. Hillsdale, NJ: Erlbaum.
- SPEAR, N. E. (1978). *The processing of memories: Forgetting and retention*. Hillsdale, NJ: Erlbaum.
- TERRY, W. S., & ANTHONY, S. G. (1980). Arousal and short-term memory: Effects of caffeine and trial spacing on delayed-alternation performance. *Animal Learning & Behavior*, **8**, 368-374.
- TERRY, W. S., & WAGNER, A. R. (1975). Short-term memory for "surprising" versus "expected" unconditioned stimuli in Pavlovian conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, **1**, 122-133.
- TINKLEPAUGH, O. L. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology*, **8**, 197-202.
- WAGNER, A. R. (1978). Expectancies and the priming of STM. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, NJ: Erlbaum.
- WAGNER, A. R., RUDY, J. W., & WHITLOW, J. W. (1973). Rehearsal in animal conditioning. *Journal of Experimental Psychology*, **97**, 407-426.
- WAGNER, A. R., & TERRY, W. S. (1975). Backward conditioning to a CS following an expected vs. a surprising UCS. *Animal Learning & Behavior*, **3**, 370-374.
- WALKER, J. A., & OLTON, D. S. (1979). The role of response and reward in spatial memory. *Learning and Motivation*, **10**, 73-84.
- WORSHAM, R. W. (1975). Temporal discrimination factors in the delayed-matching-to-sample task in monkeys. *Animal Learning & Behavior*, **3**, 93-97.