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RETROACTIVE INTERFERENCE AND FACILITATION
IN PIGEON SHORT-TERM MEMORY

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of the requirements for

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RETROACTIVE INTERFERENCE AND FACILITATION IN PIGEON SHORT-TERM MEMORY

By

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ABSTRACT

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In three separate experiments, food-paired and non-paired conditional stimuli were interpolated during retention intervals while pigeons were performing in a successive delayed matching-to-sample task. It was expected that, dependent upon the sample stimulus and its relationship with the comparison stimulus, food-paired vs. non-paired stimuli would either retroactively facilitate or interfere with performance in the delayed matching task. Results showed that food-paired stimuli facilitated matching during trials when the sample stimulus predicted reinforcement but interfered with matching when the sample stimulus signalled extinction. A stimulus paired with the absence of food interfered with matching when the sample predicted reinforcement but did not interfere when the sample predicted extinction. With one exception, these results occurred whether a food sample signalled reinforcement and a house-light sample predicted extinction, or vice versa. These results were interpreted as supporting the notion that the interpolated conditional stimuli elicited expectancies that interacted with the sample-based expectancies. If the conditional stimulus and the sample elicited consistent expectancies, retroactive facilitation was the outcome. If the expectancies were inconsistent, retroactive interference with delayed matching occurred.

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INTRODUCTION

In recent years, the delayed matching-to-sample (DMTS) task has enjoyed increasing attention as a paradigm for assessing animal short-term memory (D'Amato, 1973; Grant & Roberts, 1976; Moe & Bierley, 1977; Roberts & Grant, 1976; Shimp, 1976a, b; Shimp & Moffitt, 1977). In two-choice DMTS, a delay intervenes between presentation of a sample stimulus and presentation of the comparison stimuli. A response to the comparison stimulus that matches the sample stimulus is required for reinforcement.

In order to perform well in this task, it is presumably necessary for an organism to actively remember the sample stimulus throughout the delay or retention interval. If this remembering process is in some way disrupted, matching accuracy typically suffers. For example, the most common way to disrupt DMTS has been to illuminate the retention interval by turning on the houselight in the operant chamber (D'Amato, 1973; D'Amato & O'Neil, 1971; Etkin, 1972; Grant & Roberts, 1976; Maki et al., 1977; Roberts & Grant, 1976, 1978). Although the amount of disruption is related to the total amount of interpolated illumination (Etkin, 1972; Maki et al., 1977), point of interpolation within the retention interval (Roberts & Grant, 1978), and to the intensity of the interpolated illumination (Grant & Roberts, 1976), the retention interval illumination effect is in general very powerful, often reducing matching accuracy to chance levels.

Retention interval illumination is generally interpreted as a source of retroactive interference. In some way, illumination during the retention interval retroactively interferes with an animal's memory for the sample stimulus. The conclusion that memory for the sample stimulus following a dark delay is superior to memory for the sample following an illuminated delay may not, however, be warranted. Baseline conditions in cited studies always included dark retention intervals and test conditions always included illuminated retention intervals. Consequently, sequence of exposure to delay-interval illumination conditions was not adequately controlled.

In some recent work conducted in the author's laboratory (Tranberg & Rilling, in press), it was shown that it is not the case that illumination per se, interpolated during the retention interval, interferes with matching performance. Rather, a change in retention interval illumination conditions during testing from those conditions that prevailed during the baseline appears to be the more important variable. In four different test conditions, either increasing or decreasing retention interval illumination from that which prevailed during the baseline equally disrupted delayed matching performance.

A reasonable conceptualization of animal short-term memory must, therefore, be able to explain why both increases and decreases in retention interval illumination effectively disrupt delayed matching performance. It would seem that an adequate theory that can encompass these data needs as a central concept the notion of expectancy. That is, when unexpected illumination, either an increase or a decrease, prevails during the retention interval, matching-to-sample is disrupted. When expected or familiar illumination conditions prevail during the retention interval then a retroactive interference effect is not obtained.

A recently developed information processing model of animal memory, which evolved out of the rabbit eyelid classical conditioning laboratory of Wagner and his colleagues (Terry & Wagner, 1975; Wagner, 1976; Wagner, Rudy, & Whitlow, 1973), does incorporate as central tenets the notions of "expectedness" vs. "surprisingness." Conceptually similar to familiar treatments of human memory (e.g., Atkinson & Shiffrin, 1968), Wagner's model distinguishes between a limited capacity short-term memory and a long term memory. Information is posited to be maintained in short-term memory via a process of rehearsal. A central concept of Wagner's model is the notion of "priming" short-term memory. According to Wagner, there are two ways that a stimulus will come to be rehearsed (i.e., primed in short-term memory): (a) as a result of recent presentation of that stimulus, self-generated priming, or (b) as a result of retrieval from long-term memory initiated by other cues with which the stimulus is associated, retrieval-generated priming.

The feature of Wagner's model that has particular importance to the retention interval illumination effect is his prediction that certain events will undergo differential rehearsal. According to Wagner (1976), unexpected events will be postperceptually processed more than will expected events. Thus, in a delayed matching task, when retention interval illumination is abruptly changed, the surprising aspect of this event engages the rehearsal process, takes up space in a limited capacity short-term memory, and prevents adequate rehearsal of the sample stimulus. Consequently, matching performance breaks down.

Most testing of Wagner's model has investigated the effects of introducing surprising vs. expected reinforcers into a learning situation (cf. Maki, 1979; Terry & Wagner, 1975; Wagner, Rudy & Whitlow, 1973). For example, in Maki's study, pigeons remembered food and no food sample stimuli better if their occurrence was incongruent rather than congruent with their past history.

Virtually no research has investigated retrieval-generated priming in the context of a short-term memory task such as DMTS. Animal research on retrieval processes has centered primarily on showing either interference or facilitation of memories stored in long-term memory (see Spear 1973, 1976 for reviews). The present set of experiments was motivated by an interest in studying retrieval-generated priming within a successive DMTS task. Food and no food (brief flash of houselight) served as the sample stimuli (see Maki et al., 1977 and Wilkie, 1978 for other delayed matching procedures with food as a sample stimulus). Off the DMTS baseline, stimuli paired with the presence and absence of food were established according to a standard classical conditioning discrimination procedure. It was hypothesized that a stimulus paired with food would become a retrieval cue for food whereas a stimulus paired with the absence of food would become a retrieval cue for no food. Testing consisted of interpolating the food paired and nonpaired stimuli during the retention intervals of the DMTS task. Dependent upon the sample stimulus, it was hypothesized that the interpolated stimuli would either retroactively interfere with delayed matching performance or retroactively facilitate performance. The food paired stimulus should facilitate performance on trials with food as the to-be-remembered event and interfere with performance on trials with no food as the sample stimulus. In a similar fashion, a stimulus paired with the absence of food should interfere with performance on food trials but facilitate performance on no food trials.

EXPERIMENT I

The purpose of Experiment I was to demonstrate retroactive interference and facilitation in pigeon short-term memory by interpolating stimuli paired with either the presence or absence of food during retention intervals of a successive DMTS task. Successive DMTS is different from two-choice DMTS in that only a single comparison stimulus is presented. Dependent upon the sample, responding is either reinforced or extinguished during the comparison stimulus. Rather than per cent correct, the dependent variable is rate of response during the comparison (see Nelson & Wasserman, 1978; Tranberg & Rilling, in press; and Wasserman, 1976 for examples of successive DMTS procedures). In the present experiment, food (S+) signalled reinforced responding during a white comparison stimulus and no food (houselight, S-) signalled extinction during white.

It was hypothesized that the mechanism responsible for short-term memory interference vs. facilitation may be, respectively, the retrieval of memories competitive with the to-be-remembered event vs. the retrieval of memories isomorphic with the to-be-remembered event. Pavlovian conditional stimuli (CS) served as potential retrieval cues. Adopting a theoretical stance developed by Konorski (1948, 1967) and elaborated by Rescorla (e.g., Holland & Rescorla, 1975; Rescorla, 1973, 1974; Rescorla & Heth, 1975) it was assumed that a CS elicits an internal representation of the event it is associated with, i.e., the unconditional stimulus (US). Therefore, a stimulus (CS+) that has been paired with food should elicit a representation of food; likewise, a stimulus (CS-) that has been paired with the absence of food should elicit a "no food" representation.

The question of interest is what happens to delayed matching performance when food paired and nonpaired stimuli are interpolated during the retention intervals of both matching-to-food and matching-to-no food trials. It was postulated that CS+ may elicit memories isomorphic with food but competitive with no food. Thus, it was predicted that CS+ interpolated during the delay interval of trials when food was the sample would result in retroactive facilitation and a high rate of response during the test stimulus; CS+ presented during retention intervals when no food was the sample should result in retroactive interference, a relatively high rate of response during the comparison stimulus.

A parallel set of predictions may be made for the conditions when CS- is interpolated during retention intervals. If food was the sample, CS- interpolated during the delay should retrieve competing memories and result in a reduced rate of response during the test stimulus. If no food was the sample, CS- should elicit isomorphic memories and an extremely low rate of response should occur to the test stimulus. In this case, since no food signalled extinction during the comparison, a low rate of response indicates retroactive facilitation.

Method

Subjects

The subjects were eight experimentally naive adult White Carneaux pigeons maintained at 80% of their free-feeding weights. Pigeons were individually housed in a temperature-controlled and constantly illuminated colony room with continuous access to grit and water.

Apparatus

The experimental space consisted of a standard three-key operant conditioning chamber for pigeons manufactured by Lehigh Valley Electronics with inside dimensions of 30 X 35 X 35 cm. The intelligence panel consisted of a 15 W houselight (GE 1820) that directed light towards the ceiling, circular speaker grill, and three circular, translucent response keys centered above and to the left and right of a 6 X 5 cm food magazine opening. During reinforcement, the magazine was illuminated with a Sylvania 48ESB lightbulb. Only the left, 2.5 cm response key, which required a minimum force of 15 g (.15 N) for activation, was used. The key could be transilluminated with white light. Access to the food hopper through the magazine opening was monitored by a photocell manufactured by Lehigh Valley Electronics. A piece of translucent acrylic was fastened over a 25 X 25 cm hole cut into the ceiling of the operant chamber. Lightbulbs (GE 40 W) colored red and green were mounted directly above the acrylic ceiling. Electromechanical equipment, located in an adjacent room, controlled experimental events. An exhaust fan provided ventilation and partially masked extraneous noises.

Procedure

Pretraining. During magazine training, pigeons were trained to approach and eat mixed grain from the raised food tray. Birds were individually placed into the lighted test chamber with the food hopper elevated, lighted, and with mixed grain visible. The food tray lowered 2.5 sec after a pigeon broke a photocell beam by inserting its head into the magazine opening. Magazine training continued for 30, 2.5 sec food presentations with a mean duration of 45 sec separating each food delivery. Keypeck training, using the autoshaping method (Brown & Jenkins, 1968) began the day following magazine training. An autoshaping trial consisted of a 6-sec illumination of the left key with white light followed by the delivery of food. Trials were separated by a mean intertrial interval (ITI) of 60 sec. Keypecks during the ITI and during the white stimulus were recorded. Sixty light-food pairings constituted an autoshaping session. Autoshaping continued for 2-3 sessions. If during either the second or third auto-shaping session, 100 white keypecks occurred, the bird was placed into the next phase of training. If 100 keypecks did not occur by the third session, hand-shaping, by reinforcing successive approximations to a keypeck, was employed.

Operant discrimination: delayed matching-to-food. During this phase of training, a bird was required to learn to peck during the white keylight if food preceded its illumination but not to peck during white if a houselight flash had preceded its presentation. Food was the S+ sample and signalled the eventual availability of reinforcement whereas a brief houselight flash was the S- sample and signalled extinction during white. Figure 1 provides a diagram of the training and testing procedures. The sequence of events on an S+ trial was: fixed ITI of 50 sec followed by food; termination of food instituted the retention interval after which white illuminated the key for 20 sec; termination of white began another ITI. The temporal sequence of events during an S- trial was identical to S+ trials. Rather than food preceding the retention interval, during an S- trial, houselight flash occurred.

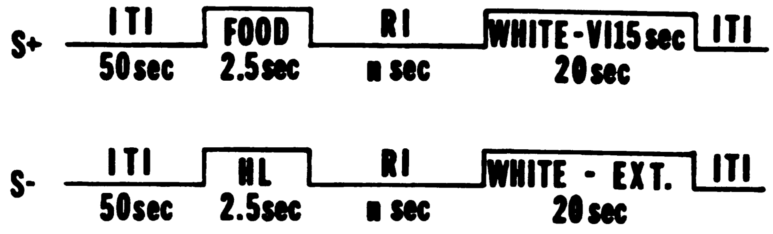
During S+ trials, a constant probability (Catania & Reynolds, 1968) variable interval (VI) 15 sec schedule of food reinforcement was in effect during the 20-sec white stimulus. It was possible for a bird to be rewarded from 0-2 times during white of an S+ trial. On S- trials, extinction was in effect during white of S- trials; no reinforcement was available to a bird during white of S- trials. The sample stimuli, access to food or houselight flash, were 2.5 sec in duration.

The dependent variable during delayed matching training was a discrimination ratio determined by the following formula:

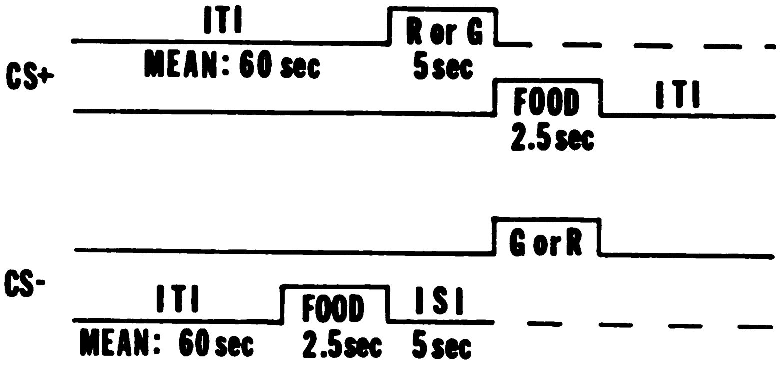
$$\frac{\text{Responses/minute during white (S+)}}{\text{Responses/minute during white (S+) plus white (S-)}} \times 100$$

Figure 1. Schematic of Experiment I's training and testing procedures (RI = Retention Interval; HL = Houselight; R = Red; G = Green; and C = Control).

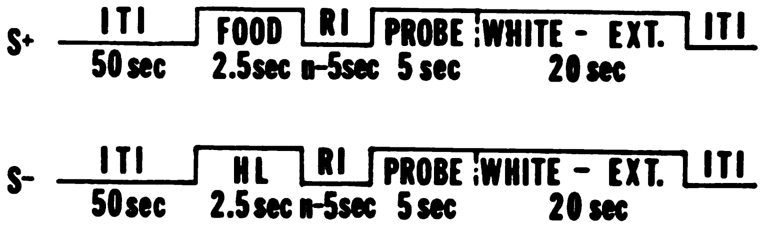
I. DELAYED MATCHING



II. PAVLOVIAN TRAINING



III. TESTING



A discrimination ratio of 100% implied a zero rate of response during S- trials whereas a ratio of 50% meant equal rates of response during S+ and S- trials. During the initial stages of training, the delay between termination of a sample and the white keylight was 2 sec. When a discrimination ratio for a bird reached 75%, the retention interval was increased by 1 sec. If possible, retention intervals were systematically increased in this fashion until a value of 15 sec was obtained. If at any time a bird's discrimination ratio fell below 75%, the retention interval was reduced by 1 sec.

The occurrence of S+ and S- trials was pseudo-randomly arranged such that S+ and S- occurred approximately the same number of times within a 50 trial session and S+ or S- never occurred in more than three consecutive trials.

Pavlovian training. During this phase of the experiment, sessions of Pavlovian discrimination training alternated with sessions of delayed matching. During Pavlovian sessions, birds were exposed to two CSs: CS+ signalled the occurrence of food and CS- signalled the absence of food. On CS+ trials, a 5-sec colored ceiling light was immediately followed by elevation of the food hopper whereas on CS- trials, termination of food instituted a 5-sec inter-stimulus interval (ISI) followed by a 5-sec colored ceiling light. Colored ceiling lights were red and green and their designation as either CS+ or CS- was counterbalanced between birds.

Trials were pseudo-randomly arranged such that CS+ and CS- occurred approximately the same number of times during a 60 trial session and neither stimulus occurred more than three times in succession. A mean ITI of 60 sec (range: 30-90 sec) separated trials.

The Pavlovian phase required a total of 20 sessions. Odd days were Pavlovian training and even days were delayed matching. The retention interval continued to increase in 1-sec increments during delayed matching sessions if 75% discrimination ratios were maintained.

Experimental phase. The general strategy during testing was to interpolate CS+ and CS- during the retention interval of matching-to-food vs. -houselight probe trials. A test session began on an even day and the first test trial occurred after 3-5 delayed matching warm up trials. Each pigeon was exposed to six types of probe trials: CS+, CS-, and control, interpolated equally often during S+ (food) and S- (houselight) delayed matching trials. For example, CS+ was interpolated during the retention interval of test trials when food was the sample and on test trials when the houselight was the sample. Probe stimuli occurred during the final 5 sec of the retention interval. During control probes, no probe stimulus was presented. Within a session, each probe was used four times for a total of 24 probe trials. Each bird was exposed to a different random order of probe trials and probe trials were separated from each other with 2-4 delayed matching trials. During all probe trials, extinction was in effect during the 20-sec white comparison stimulus. The dependent variable during test trials was responses/minute during white.

When food occurred during delayed matching or during Pavlovian training, access to the mixed grain was always 2.5 sec. The beginning and end of delayed matching and Pavlovian sessions was signalled by the offset and onset, respectively, of the standard houselight.

Results and Discussion

All the birds readily learned the delayed matching-to-food vs. houselight task with a 2-sec retention interval. The discrimination ratio criterion of at least 75% responding distributed to white when food was the sample stimulus was obtained after a mean of 4.75 sessions (range: 2-7 sessions). Performance remained relatively stable as retention intervals were satisfactorily increased to 15 sec for each bird prior to introduction of Pavlovian training. Final valued retention intervals after the 20 session Pavlovian phase ranged from 16 sec to 23 sec with a mean of 20.5 sec. The mean discrimination ratio on the last day of delayed matching training, prior to testing, was 78.8%. Thus, the delayed matching task proved not to be difficult, even at rather lengthy retention intervals.

Figure 2 shows the group data from the test session. Included in Figure 2 are mean rates of responding during the white stimulus during the four experimental and the two control probe trials. As is apparent from inspecting Figure 2, compared to respective

Figure 2. Group data from Experiment I's test session. The figure shows rate of response as a function of sample stimulus (food or houselight) and as a function of probe stimulus (control, CS+, or CS-).

control probes, interpolating CS+ vs. CS- during S+ (food) and S- (houselight) delayed matching retention intervals differentially affected rate of responding during the white test stimulus. For the moment, consider only the S+ (food) condition. When CS+ was presented during S+ (food) trials rate of response was similar to the rate obtained during control trials. When CS- was interpolated during S+ (food) trials, however, rate of white responding was considerably less than either the control probe or the CS+ probe.

A probe trial by subjects ANOVA on the S+ (food) data confirmed these conclusions, $\underline{F}$ (2,14) = 8.4, $\underline{p} < .005$. Subsequent analyses using the Neuman-Keuls procedure showed that the CS- rate of response was significantly lower than both the control and CS+ rates of responding ($\underline{p} < .01$ in both cases) but that the CS+ and control rates did not differ.

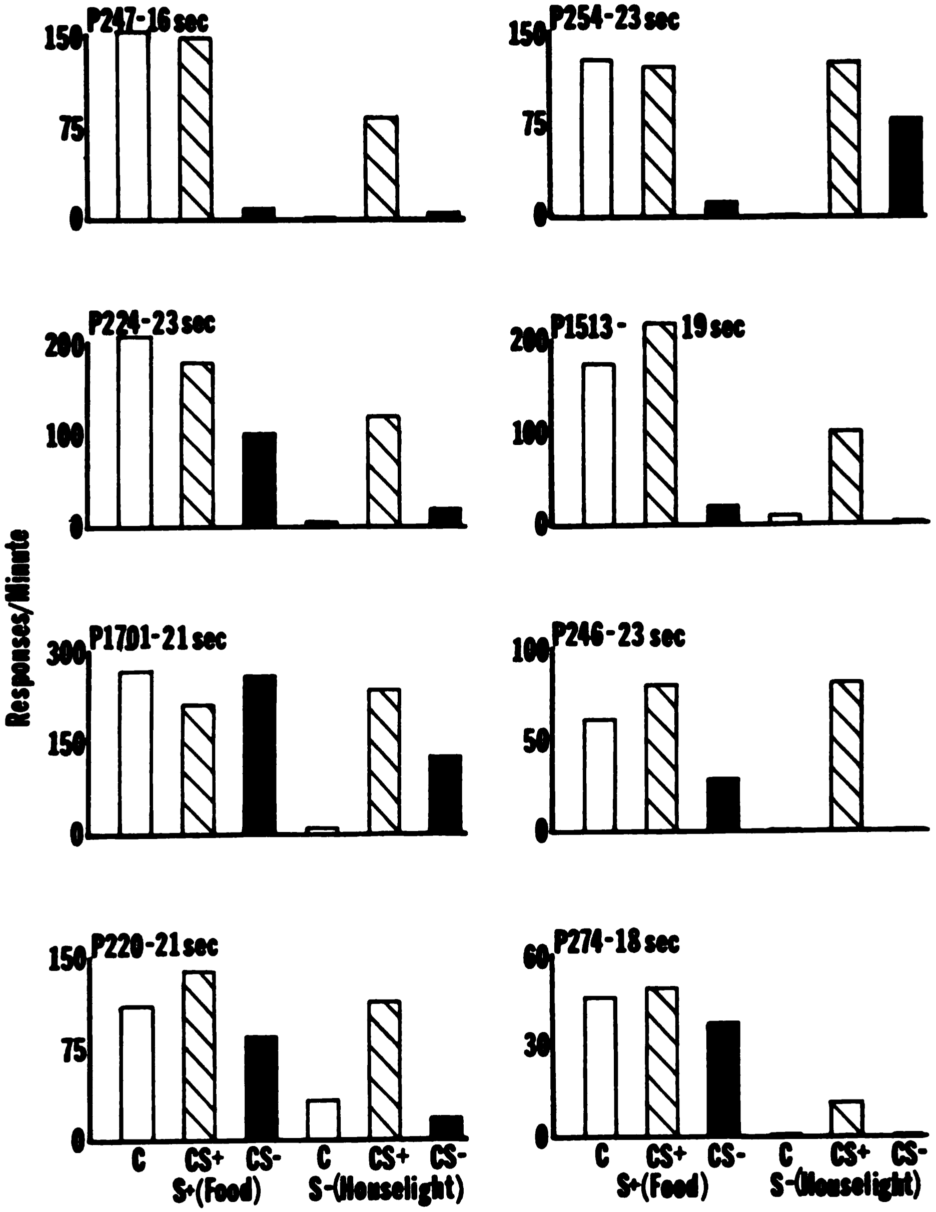
Next, consider the effects of probing the S- (houselight) condition. Relative to the control condition, interpolating CS+ during S- (houselight) trials greatly increased rate of responding during white whereas CS- increased rate of test stimulus responding only marginally. A treatment by subjects ANOVA on these data revealed that probe trial conditions significantly affected test stimulus response rate, $\underline{F}$ (2,14) = 20.2, $\underline{p} < .001$. A Neuman-Keuls analysis indicated that CS+ interpolated during S- (houselight) trials significantly increased rate of response relative to both the control condition and the CS- condition ($\underline{p} < .01$ in both cases) but that the CS- and control conditions did not differ.

Another question of interest is whether rates of responding induced by CS+ and CS- differed as a function of the sample stimulus. That is, did CS+ result in a higher rate of response on food trials than on houselight trials and did CS- result in a lower rate of response on houselight trials than during food trials? Figure 2 shows that CS+ presented during food trials resulted in a higher rate of response than CS+ interpolated during houselight trials. As is further indicated in Figure 2, CS- presented during houselight trials produced a lower rate of response than CS- presented during food trials.

These data were subjected to a 2 X 2 repeated measures ANOVA. Food vs. houselight was one factor and CS+ vs. CS- was the second factor. This analysis resulted in a significant food vs. houselight effect, $\underline{F}$ (1, 7) = 8.9, $\underline{p} < .05$, and a significant effect for CS+ vs. CS-, $\underline{F}$ (1, 7) = 25.1, $\underline{p} < .005$. Their interaction was not significant, $\underline{F} < 1$. Thus, CS+ resulted in a higher rate of response during S+ (food) trials than during S- (houselight) trials and CS- resulted in a lower rate of response during S- (houselight) trials than during S+ (food) trials.

Figure 3 provides individual subject data from the test session. Inspection of Figure 3 indicates that the group effects evident in Figure 2 are remarkably consistent within birds. The only exception to the general trends shown in the group data is pigeon 1701. This particular bird responded at a higher rate during the S+ (food) trial with a CS- probe stimulus than it did during either of the CS+ probe conditions.

Figure 3. Individual subject data from Experiment I. This figure shows each subject's rate of response in each of the six different probe conditions. The durations listed next to each bird's number are final valued retention intervals.


Responses/Minute
P247-16 sec
150
75
0
P254-23 sec
150
75
0
P224-23 sec
200
100
0
P1513-19 sec
200
100
0
P1701-21 sec
300
150
0
P246-23 sec
100
50
0
P220-21 sec
150
75
0
P274-18 sec
60
30
0
C
CS+
CS-
C
CS+
CS-
S+(Food)
S-(Houselight)
C
CS+
CS-
C
CS+
CS-
S+(Food)
S-(Houselight)

The results of Experiment I are in agreement with the predictions made. Interpolating a food-paired stimulus during food (S+) trials resulted in a high rate of response during the test stimulus whereas interpolating a stimulus paired with the absence of food during food trials resulted in a much lower rate of response. In a similar manner, a food-paired stimulus increased rate of responding on S- (houselight) trials but a stimulus paired with the absence of food resulted in a low rate of response during S- (houselight) trials.

One explanation of these data is the retrieval cue interpretation previously outlined. The retrieval cue interpretation rests on two basic assumptions. The first assumption is that memories play an important role in a delayed matching task. When faced with a test stimulus, a memory trace of the preceding sample persists and cues an animal how to respond (e.g., go or no-go in a successive task). The second assumption is that classically conditional stimuli elicit from long-term memory representations of the events they are associated with, namely the unconditional stimulus. A food-paired stimulus may elicit a representation of food and a stimulus paired with the absence of food (CS-) may elicit a representation of "no food." Accordingly, presenting a food-paired stimulus in the delay interval of a food trial may have retrieved a memory isomorphic with the food stimulus and, consequently, a high rate of response ensued during the test stimulus (i.e., retroactive facilitation). Presenting a stimulus paired with the absence of food during trials when food was the sample may have elicited competing memories that retroactively interfered with a food memory; hence, a somewhat lower rate of response resulted. A food-paired stimulus interpolated during no food trials may have elicited a representation of food that competed with a bird's memory for no food (i.e., houselight). Thus, retroactive interference occurred in the guise of an increase rate of response. Finally, presenting a stimulus paired with the absence of food on houselight trials may have resulted in a relatively low rate of response because a memory elicited by it was compatible with a memory for the no food houselight. In this case, retroactive facilitation is indicated by a very low rate or response.

It is also important to point out that CS+ and CS- did not simply elicit high vs. low rates of response during the test stimulus. The rate of response during CS+ trials was higher if food was the sample than if no food was the sample and, in a like manner, rate of response during CS- probes was lower during S- trials than during S+ trials. This finding is consistent with the notion that memories elicited by the probe stimuli interacted with sample memories. If the memories were isomorphic, facilitation occurred; if the memories were competitive, interference was the outcome.

Although the data collected in Experiment I are consistent with a retrieval cue interpretation, they do not necessarily rule out an alternative explanation. Probe stimuli, rather than eliciting memories isomorphic vs. competitive with sample stimuli memories, may have elicited isomorphic vs. competitive expectancies. An expectancy based interpretation is also able to explain the Experiment I data. This issue was directly addressed in Experiment II.

EXPERIMENT II

Although the results of Experiment I support a retrieval cue interpretation, the data do not necessarily rule out an alternative explanation offered by an extension of two-process learning theory (Trapold & Overmier, 1972). A prototypical experiment conducted by researchers in the two-process tradition was labelled by Trapold and Overmier (1972) a transfer of control experiment. In a transfer of control experiment there are three phases but the order of the first two phases is interchangeable: (a) an operant training phase in which an animal is rewarded for making a response in the presence of a specific stimulus; (b) a Pavlovian phase during which the operant discriminative stimulus is merely paired with the operant reinforcer; and (c) a transfer of control test phase in which the CS is tested for its tendency to evoke the operant response originally trained.

In terms of procedure, Experiment I was similar to a typical transfer of control experiment. During the first phase, birds learned a discrimination between an S+ (food) and an S- (houselight) stimulus; next, Pavlovian discrimination training was conducted; and finally, the Pavlovian CSs were superimposed on the operant baseline and their effects on operant responding were assessed. There were, however, several salient differences between Experiment I and a transfer of control experiment. First, Experiment I was a working memory experiment in which a delay intervened between the discriminative stimuli and the opportunity to engage in the operant response. Second, the Pavlovian CSs were not identical with the operant discriminative stimuli. Finally, the Pavlovian CSs were not superimposed during the test stimulus when the operant response was free to occur; rather, the CSs were superimposed during the retention interval.

These differences not withstanding, it remains reasonable to assume that the many similarities between the two types of experiments may warrant consideration of Trapold and Overmier's (1972) viewpoint. According to their theoretical framework, the Pavlovian stimuli conditioned in either the first or second phase of a transfer of control experiment become conditioned mediators with three primary characteristics: (a) they are specific to the properties of the reinforcer upon which they are based; (b) they possess distinctive stimulus properties specific to the signalled event, and (c) mediators control operant behavior via a cueing function based upon these distinctive stimulus properties. Another way of stating this last characteristic is that a CS elicits an expectancy for the reinforcer (US) upon which it is based. The expectancy then guides operant behavior in an appropriate direction. Several recent experiments provide strong support for the conditioned mediational role for CSs (Overmier, Bull, & Trapold, 1971; Peterson, Wheeler & Armstrong, 1978; Trapold, 1970).

In order for an elicitation of expectancies analysis to explain Experiment I's data, it must be assumed that: (a) during delayed matching training, S+ (food) and S- (houselight) samples established differential expectancies for reinforcement vs. nonreinforcement during the eventual test stimulus; (b) in the Pavlovian phase, CS+ established an expectancy for food and CS- established an expectancy for no food. According to this analysis, therefore, S+ and CS+ have a common mediational base as do S- and CS-. Thus, whenever probe stimuli elicited expectancies in accordance with sample produced expectancies, retroactive facilitation occurred. Likewise, whenever probe stimuli elicited expectancies that conflicted with sample engendered expectancies, retroactive interference was the outcome. In other words, CS+ and CS- may not have acted as retrieval cues for food vs. no food. CS+ and CS- may have elicited expectancies either consistent or inconsistent with S+ and S- produced expectancies.

A very simple change in Experiment I's design readily tests the retrieval cue vs. the expectancy interpretations. In Experiment II, the discriminative roles served by the food and houselight sample stimuli were reversed: Houselight (S+) signalled eventual reinforcement during the test stimulus whereas food (S-) signalled extinction. In all other respects, procedure for Experiment II was identical to Experiment I.

In Experiment II, the expectancy hypothesis predicts results similar to Experiment I's data. S+ (houselight) should set up an expectancy for food, S- (food) should set up an expectancy for no food. Thus, CS+ should facilitate S+ performance and interfere with S- performance; similarly, CS- should facilitate S- performance and interfere with S+ performance. If however, CS+ and CS- retrieve memories of the sample stimuli, an opposite set of predictions result. When CS+ is presented during S- (food) trials, it should remind the bird that food was the sample stimulus. Since food in this situation predicts extinction, CS+ should facilitate performance by inhibiting pecking during the test stimulus. When CS+ is presented during S+ (houselight) trials, the conflicting memories should result in retroactive interference. A parallel set of predictions for the effects of interpolating CS- naturally follows. CS-, due to retrieving a representation of no food, should facilitate trials when food is not the sample stimulus and should interfere with trials when food is the sample stimulus.

The purpose of Experiment II was to pit the retrieval cue hypothesis against the expectancy hypothesis. The design was the same as Experiment I with one exception. In the delayed matching task, food signalled extinction and houselight signalled reinforced responding.

Method

Subjects

Eight experimentally naive adult White Carneaux pigeons, exposed to the same deprivation and living conditions as Experiment I birds, were used.

Apparatus

Same as Experiment I.

Procedure

Pretraining. Same as Experiment I.

Operant discrimination: delayed matching-to-food. The only change from Experiment I was reversed discriminative roles for the sample stimuli. In Experiment II, food (S-) signalled extinction during the white comparison stimulus and houselight (S+) predicted reinforced responding during white. All other procedural details were the same as Experiment I.

Pavlovian training. Same as Experiment I.

Experimental phase. Same as Experiment I.

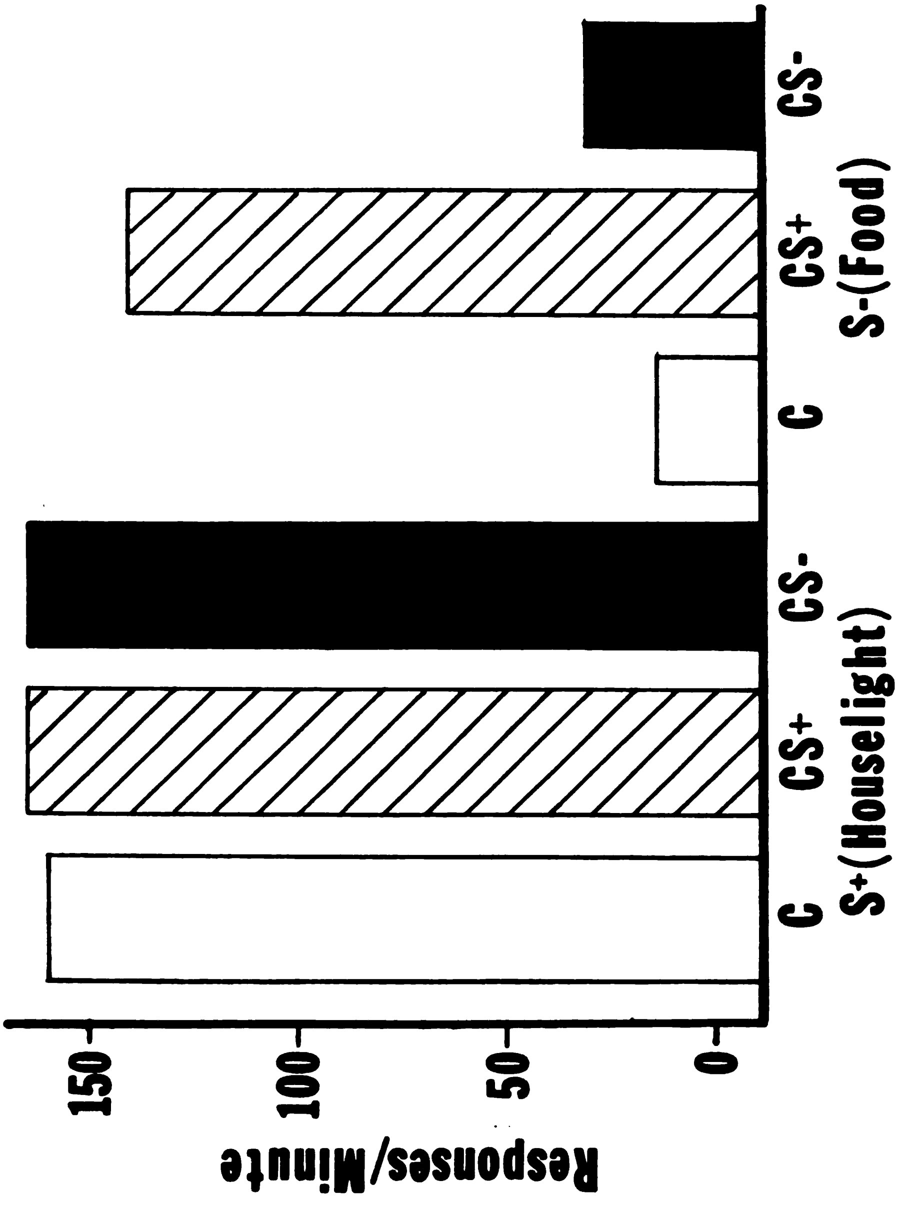
Results and Discussion

All eight birds learned the delayed matching task with a 2-sec retention interval. The discrimination ratio criterion of at least 75% responding distributed to white when the S+ (houselight) was the sample was obtained after a mean of 12.2 sessions (range: 8-20). Acquisition of the 75% criterion was slower for birds in Experiment II than it was for birds in Experiment I. In Experiment I, when food signalled reinforcement rather than extinction and houselight signalled extinction rather than reinforcement, birds acquired the criterion in 4.75 sessions (range: 2-7). The difference in days to criterion in the two experiments is significant, $t\ (14) = 4.8$, $p < .001$.

Matching performance of birds in Experiment II remained relatively stable as retention intervals were satisfactorily increased to 15 sec for all birds except one prior to introduction of Pavlovian training. Bird 413 only obtained a 6-sec retention interval before initiation of the Pavlovian phase. Final valued retention intervals following the 10 sessions of Pavlovian training alternated with 10 sessions of delayed matching ranged from 11 sec to 25 sec with a mean of 17.9 sec. Final valued retention intervals in Experiment II did not differ from those in Experiment I, $\underline{t}$ (14) = 1.5, $\underline{p} < .10$. The mean discrimination ratio on the last day of delayed matching training, immediately prior to the test session, was 83.8%. Thus, although the Experiment II delayed matching task was harder for birds to acquire than the Experiment I task, after the task was well learned, excellent matching performance at rather lengthy retention intervals was readily obtained.

Figure 4 shows the results from the test session. Included in Figure 4 are mean rates of responding during the white stimulus for each of the four experimental and for the two control probe trials. As this figure indicates, compared to respective control probes, interpolating CS+ vs. CS- during S+ (houselight) and S- (food) delayed matching trials differentially affected rate of responding only during test trials when food was the sample stimulus. Rates of responding during each of the three probes when the houselight was the sample were very similar; means of 159.8, 164.9, and 165.9 responses/minute were obtained, respectively, during control, CS+ and CS- probes. A probe trial by subjects ANOVA on the S+ (houselight) data shows no significant difference, $\underline{F} < 1$.

Figure 4. Group data from Experiment II's test session. The figure shows rate of response as a function of sample stimulus (houselight or food) and as a function of probe stimulus (control, CS+, or CS-).


Responses/Minute
150
100
50
0
C
CS+
CS-
S+(Houselight)
C
CS+
CS-
S-(Food)

Consider next the effects of probing the S- (food) condition. Relative to the control condition, interpolating CS+ during S- (food) trials greatly increased rate of responding during white whereas CS- increased rate of white responding only slightly. A treatment by subjects ANOVA on these data revealed that probe trial conditions significantly affected test stimulus response rate, $\underline{F}$ (2, 14) = 7.9, $\underline{p} < .025$. A Neuman-Keuls analysis indicates that CS+ interpolated during S- (food) trials significantly elevated rate of response relative both to the control condition and to the CS- condition ($\underline{p} < .01$ in both cases) but that CS- and the control conditions did not differ.

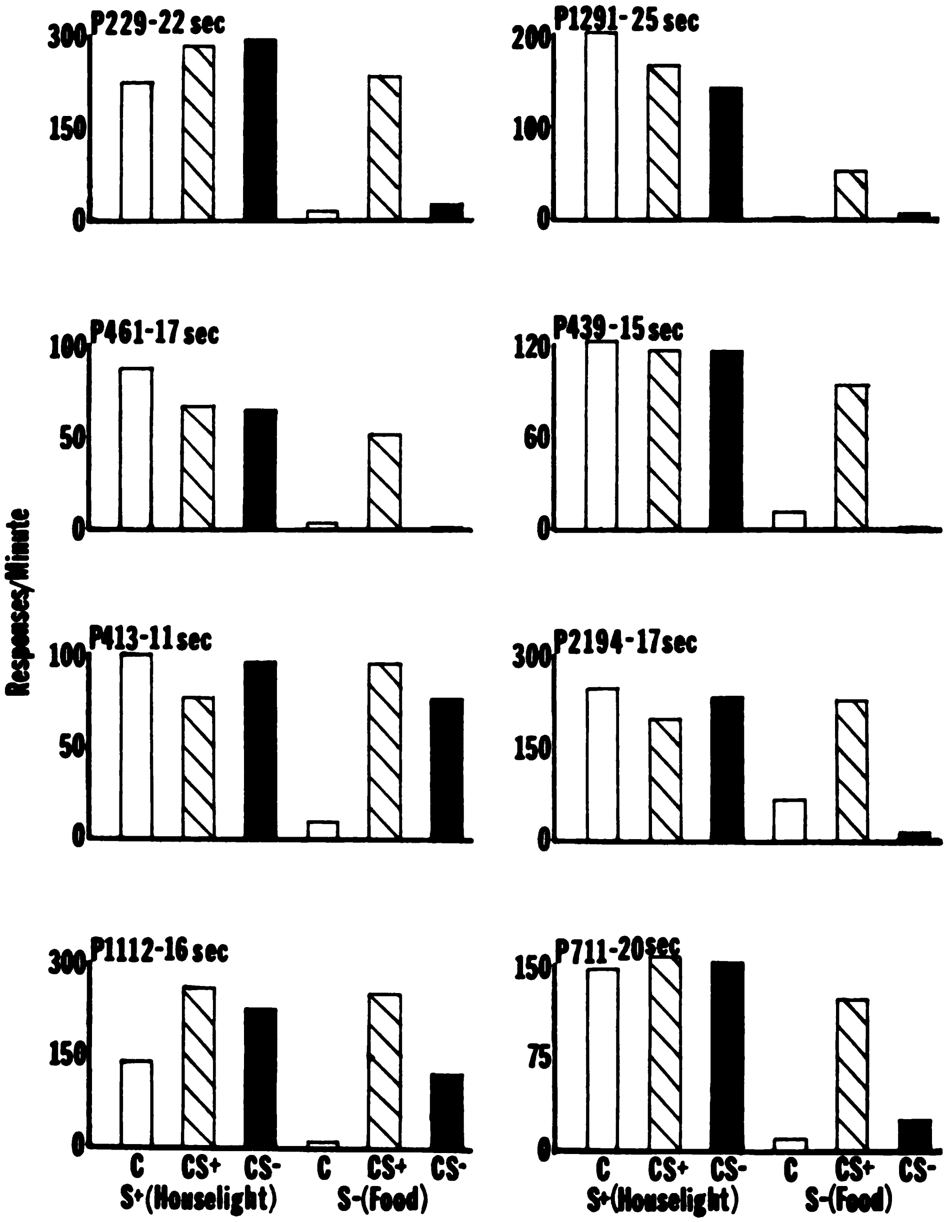
Whether CS+ vs. CS- induced different rates of responding dependent on sample stimulus condition was also analyzed. Figure 4 shows that CS+ resulted in a relatively high rate of response whether the sample was the houselight or was food. CS-, however, resulted in a high rate of response during S+ (houselight) trials but in a relatively low rate of response during S- (food) test trials. These data were subjected to a 2 X 2 repeated measures ANOVA. Food vs. houselight was one factor and CS+ vs. CS- was the second factor. This analysis resulted in a significant interaction, $\underline{F}$ (1, 7) = 13.0, $\underline{p} < .01$. Analysis of simple effects revealed that CS+ vs. CS- had a significant effect only during S- (food) trials, $\underline{F}$ (1, 7) = 40.1, $\underline{p} < .01$; furthermore, S+ (houselight) vs. S- (food) trial response rates differed only when CS- was the probe stimulus, $\underline{F}$ (1, 7) = 29.3, $\underline{p} < .01$ and not when CS+ was the probe stimulus, $\underline{F} < 1$.

Figure 5 provides individual subject data from the test session. In general, each subject's data are consistent with the general trends apparent in the group data. Particularly worthy of note is the finding that CS- interpolated during S+ (houselight) trials resulted in a relatively high rate of response for all birds. Thus, the lack of statistical differences attributable to CS+ vs. CS- interpolated during S+ (houselight) trials is not due to wide individual variability. Rather, the finding that CS+ vs. CS- do not differentially affect S+ (houselight) rate of responding is consistent within birds.

The results of Experiment II are not entirely clear. Data obtained during three of the four experimental probes clearly support the expectancy interpretation whereas the other experimental probe data appear to support the retrieval cue explanation. The findings that CS+ interpolated during either S+ (houselight) or S- (food) trials resulted in a high rate of response (i.e., retroactive facilitation and interference, respectively) is in agreement with the expectancy explanation. Furthermore, low rates of responding during S- (food) trials with CS- probes also confirms the expectancy prediction. The somewhat anamalous outcome was the finding that CS- interpolated during S+ (houselight) trials resulted in a high rate of response. According to the expectancy interpretation, the expectancies elicited by an S+ sample vs. a CS- should be competitive and their interaction should have produced a low rate of responding.

The retrieval cue explanation does make the prediction that CS- interpolated during S+ (houselight) probe trials should result in a

Figure 5. Individual subject data from Experiment II. This figure shows each pigeon's rate of response in each of the six different probe conditions. The durations listed next to each bird's number are final valued retention intervals.


Responses/Minute
P229-22 sec
300
150
0
P1291-25 sec
200
100
0
P461-17 sec
100
50
0
P439-15 sec
120
60
0
P413-11 sec
100
50
0
P2194-17 sec
300
150
0
P1112-16 sec
300
150
0
P711-20 sec
150
75
0
C
CS+
CS-
C
CS+
CS-
S+(Houselight)
S-(Food)
C
CS+
CS-
C
CS+
CS-
S+(Houselight)
S-(Food)

high rate of response. Such is the case because a stimulus paired with the absence of food should not interfere with matching performance on trials when food is not the sample stimulus. That is, the retrieval cue hypothesis assumes that the representation of no food elicited by CS- and the memory for an S+ which is not food are not inconsistent; hence, they should not be competitive.

It seems somewhat hard to understand, however, why the expectancy hypothesis was confirmed in three of the conditions whereas the retireval cue explanation was confirmed in the other condition. The nature of the two hypotheses seems to preclude mutual confirmation. The consistency of the effects in Experiment II does indicate, however, a systematic relationship. For every bird in Experiment II, CS- interpolated during S+ (houselight) trials resulted in a high rate of response. Thus, alternative explanations of the present data need to be entertained.

It might be argued that CS- in the present experiments did not become an active inhibitor of food related activities and did not retrieve a "no food" representation. That is, perhaps CS- did not become a conditioned inhibitor and predict a period of time when food would necessarily be absent. Regarding CS-, Pavlovian training may have been functionally equivalent to a latent inhibition treatment (Lubow, 1973; Lubow & Moore, 1959; Tranberg & Rilling, 1978) and birds may simply have learned that CS- was irrelevant (Mackintosh, 1973). If CS- was ignored in the present experiments one would expect matching performance to be unaffected by its interpolation within the retention interval. One can in fact draw the conclusion from Experiment II's data that CS- did not have any effect. In neither the S+ (houselight) condition nor the S- (food) condition did CS- reliably change rate of responding relative to the respective control conditions. In Experiment I, however, rate of response during S+ (food) trials when CS- was interpolated was reliably lower than its control condition. It does not appear reasonable to conclude, therefore, that birds learned to ignore CS- in the present procedures. In addition, recent research has shown that backwards pairing of a US and CS effectively produces a conditioned inhibitory stimulus (Maier, Rapaport, & Wheatley, 1976; Plotkin & Oakley, 1975; Siegel & Domjan, 1971, 1975).

Observational data collected during Pavlovian training in both Experiments I and II are also consistent with the notion that CS- actively predicted the absence of food. If pigeons are presented with localized visual signals that predict either food or the absence of food approach to the positive stimulus and withdrawal from the negative stimulus is typically observed (Wasserman, Franklin, & Hearst, 1974). Although localized stimuli that could be either approached or withdrawn from were not used in the present experiments, differential behaviors during CS+ and CS- were observed. Typical behaviors during CS+ included orienting along the magazine wall, "nibbling" the extended houselight fixture, and pecking in the magazine. In contrast, typical CS- behaviors included moving away from the magazine wall, circle turning, facing the back wall or the window wall, and pecking the floor. It would appear, therefore, that birds readily discriminated CS+ and CS- and engaged in behaviors appropriate to each signal's predictive value.

It might also be argued that the ceiling light Pavlovian stimuli had so many elements in common with the houselight sample stimulus that during testing, generalization occurred. For example, the Pavlovian stimuli shared onset and offset characteristics with the houselight and both the Pavlovian stimuli as well as the houselight provided general, ambient illumination. The generalization hypothesis predicts, therefore, that during testing, response rates following CS+ and CS- probes should be in accord with response rates typically produced by the houselight sample. This notion is able to account for the anomalous data in Experiment II. In Experiment II, the houselight predicted reinforced responding; hence, a high rate of response usually occurred during white when preceded by the houselight sample. Consistent with the generalization hypothesis, both CS+ and CS- probes in Experiment II resulted in a high rate of response during S+ (houselight) trials. That is, birds may have responded on these trials at a high rate due to stimulus generalization between the houselight sample and the Pavlovian probe stimuli.

The generalization hypothesis is unable to explain, though, why CS- resulted in a low rate of response during S- (food) trials in Experiment II and why, in Experiment I, CS+ resulted in relatively high rates of response during S+ (food) trials and S- (houselight) trials. The generalization hypothesis predicts the opposite in each of these examples. It appears, therefore, that the generalization explanation for the anomalous data is untenable.

At the present time, I do not have a satisfactory explanation for the high rate of response obtained when CS- was interpolated during S+ (houselight) trials in Experiment II. The preponderance of the evidence collected in Experiment II supports, however, the Expectancy hypothesis. For the most part, if sample stimuli and probe stimuli yielded similar expectancies, no disruption in matching performance was obtained; if sample stimuli and probe stimuli elicited competitive expectancies, retroactive interference was obtained. Since the results of Experiment II primarily support the expectancy interpretation it must furthermore be concluded that Experiment I's results are better explained via the expectancy interpretation rather than the retrieval cue hypothesis.

Experiments I and II may have been designed such that support for the expectancy rather than the retrieval cue hypothesis was the more likely result. In Experiments I and II, pigeons did not necessarily have to remember the sample stimuli. Following termination of the food or houselight sample stimuli, birds only had to remember whether responding would be reinforced or would not be reinforced during the white comparison. In other words, birds simply had to remember the instruction to peck or not to peck as designated by the sample (cf. Honig, 1978). This problem was avoided in Experiment III through employment of a conditional successive DMTS procedure.

EXPERIMENT III

Ultimately, experimental support for either an expectancy based hypothesis or a retireval cue hypothesis is equally important. A fair test of the relative merits of these two hypotheses may not, however, have been provided in the first two experiments. The first test of the retireval cue hypothesis would be a situation wherein an animal is forced to actively remember the sample stimulus throughout the retention interval. When Pavlovian probe stimuli are subsequently presented during test retention intervals, representation of the samples would be maintained in memory. It would thus be possible for the representations elicited by probe stimuli to interact with the sample-produced memories.

In Experiments I and II, it was not necessary for birds to actively remember the sample stimuli throughout the retention interval. Since the delayed matching tasks essentially consisted of a go/no go discrimination, those tasks may be classified as working memory paradigms wherein animals needed only to remember the instruction of "what to do" when the test stimulus was presented (Honig, 1978).

Since pigeons were able to base their decision to respond or not respond during the test stimulus independent of differential memories for the sample stimuli in Experiments I and II it seems entirely likely that CS+ and CS- interpolated during the delay intervals may not have retrieved memories for food and no food. Rather, CS+ and CS- may simply have elicited additional expectancies for food or no food. These expectancies may have simply interacted with the sample-produced expectancies and resulted, respectively, in either retroactive facilitation or retroactive interference.

In order to preclude the formation of simple, sample-produced expectancies or instructions and to ensure that birds actively remembered the sample stimuli throughout the retention interval, in Experiment III a conditional delayed matching task was employed. By using this task, birds were forced to wait until the test stimulus and then respond or not respond based on the conditional relationship between the sample and test stimulus. For example, if a vertical line comparison stimulus followed a food sample, responding was reinforced; if a horizontal line test stimulus followed the no food (houselight) sample, responding was also reinforced. Extinction was in effect both when the horizontal line followed food and when the vertical line followed the houselight.

The purpose of Experiment III, therefore, was to assess the role played by CS+ and CS- probe stimuli when pigeons had differential memories for the sample stimuli uncontaminated by simple differential expectancies produced by these same stimuli.

Method

Subjects

Eight experimentally naive adult White Carneaux pigeons, reduced to 80% of their free-feedings weights, were used. The birds were exposed to the same living conditions as birds in the previous two experiments.

Apparatus

The only apparatus change from Experiments I and II was the comparison stimuli in the successive DMTS task. Rather than a white light, arrangements of three white dots on a black surround were presented on the left key. The three dots were arranged either horizontally or vertically and were projected by a Lehigh Valley Electronics (Model #: 10-OW78-1820-L) miniprojector.

Procedure

Pretraining. The only change was in autoshaping. Birds were equally autoshaped to the vertical and horizontal arrays of dots.

Delayed-matching. The most important procedural change from the first two experiments was the inclusion of a conditional successive DMTS task. Four types of trials were possible: (a) Food as the sample and vertical dots as the comparison (Food-Vertical); (b) Food as the sample and horizontal dots as the comparison (Food-Horizontal); (c) Houselight as the sample followed by the horizontal comparison stimulus (Houselight-Horizontal); and (d) Houselight sample with vertical comparison (Houselight-Vertical). Responding was reinforced according to the VI 15 sec schedule during the 2-sec comparison stimulus in Food-Vertical and Houselight-Horizontal trials. Extinction was in effect during Food-Horizontal and Houselight-Vertical trials.

Several parameters were changed in order to allow a reasonable number of each trial type per session while maintaining weights at 80%. Access to mixed grain was always for 2 sec rather than 2.5 sec. Thus, duration of the houselight flash as a sample stimulus was also for 2 sec. Each session consisted of 64 trials with a 32-sec ITI. Within a session, each trial type occurred 16 times pseudo-randomly arranged such that no more than three reinforced or extinction trials occurred consecutively and no more than two identical trials occurred in succession.

The initial value of the retention interval was set at 2 sec for all birds. If a discrimination ratio was 75% or better, the value of the retention interval was increased in 0.5-sec increments with the restriction that each retention interval was used for a minimum of two sessions. The value of the retention interval was reduced by 0.5 sec if birds failed to maintain 75% discrimination ratios. Eight seconds was the maximum retention interval that was potentially obtained for each bird prior to introduction of Pavlovian training.

Pavlovian training. In order to maintain satisfactory discrimination ratios, Pavlovian discrimination training alternated with training on delayed matching within sessions rather than between sessions. Thirty trials of Pavlovian training immediately followed 32 delayed matching trials. The duration of the ceiling light conditional stimuli was reduced to 3 sec and the ISI between food and CS- was set at 3.5 sec. The mean ITI remained at 60 sec but the range was changed to a minimum of 40 and a maximum of 80 sec. As in the previous experiments, this phase required 20 sessions. All other procedural details were the same as Experiment I.

Experimental phase. The same general strategy employed in the previous experiments was used. The first probe trial occurred after 4-7 delayed matching warm up trials. Each pigeon was exposed to three types of probe trials, CS+, CS- and control, interpolated equally often during Food-Vertical and Food-Horizontal delayed matching trials. No probes were conducted when the houselight was the sample stimulus. Probe stimuli were inserted during the final 3 sec of the retention interval. All other aspects of the procedure were the same as Experiment I.

Results and Discussion

All eight birds readily learned the conditional successive delayed matching-to-sample task at the 2-sec retention interval. Table 1 contains data from three different stages in the acquisition of the matching task. Stage I refers to data collected on the first day that birds obtained the discrimination ratio criterion of at least 75% total responses distributed to the comparison stimulus on S+ trials. A mean of 12.2 sessions (Range: 8-20) was required for birds to initially obtain this criterion. As Table 1 shows,

Table 1

Group Means and Standard Errors in Responses and Reinforcements/Minute and Discrimination Ratios at Three Different Stages of Training

	S+ Trials		S- Trials		
Training Stage	HL[a] - Hor Resp - Rft	Food-Vert Resp - Rft	HL-Vert Resp	Food-Vert Resp	Ratio %
I[b]					
Means	195.7 - 3.1	184.6 - 3.5	21.2	73.7	79.6
Error	23.2 - 0.2	23.4 - 0.1	5.3	12.7	1.6
II[c]					
Means	211.2 - 3.0	211.7 - 3.2	31.2	57.3	81.0
Error	32.7 - 0.1	28.0 - 0.2	7.4	19.8	2.2
III[d]					
Means	223.9 - 3.4	227.3 - 3.1	33.3	61.6	81.8
Error	35.0 - 0.1	32.9 - 0.1	2.8	14.6	3.0

[a] HL = Houselight sample stimulus.

[b] Stage I includes data from first session birds obtained 75% discrimination ratios at 2-sec retention intervals.

[c] Stage II are data from final session of training at 2-sec retention interval.

[d] Stage III are data from last five sessions of training at final valued retention intervals.

after these 12.2 sessions, the group mean discrimination ratio was 79.6%. It was decided not to automatically increase retention intervals to 2.5 sec, however, because response rates during S- trials were unequal. On Food-Horizontal trials vs. Houselight-Vertical trials, response rates were 73.7 vs. 21.2 responses/minute, respectively. This difference is significant, $\underline{t}$ (7) = 3.3, $\underline{p}$ < .02.

Birds were exposed to a mean of 10.5 (Range: 8.21) additional sessions prior to increasing retention intervals to 2.5 sec. Stage II in Table I shows data collected on the final day of exposure to the 2-sec retention interval. As Table 1 indicates, even after additional training, response rates during Food-Horizontal vs. Houselight-Vertical trials were still quite different, 37.5 vs. 31.2 responses/minute, respectively. This difference remains significant, $\underline{t}$ (7) = 2.4, $\underline{p}$ < .05.

Performance in delayed matching remained relatively stable for six of the eight birds as retention intervals were increased to their final values and the Pavlovian Phase was carried out. Two birds were eventually dropped from the experiment because they failed to maintain satisfactory discrimination ratios at retention intervals greater than 2.5 sec. Final retention intervals for the remaining six birds ranged from 5-8 sec with a mean of 6.2 sec. Stage III in Table 1 contains mean data from the last 5 sessions of training prior to the test session. As Table 1 shows, responding during reinforced trials, dependent on whether the houselight sample preceded horizontal or the food sample preceded vertical, was very similar, 223.9 compared to 227.3 responses/minute, respectively.

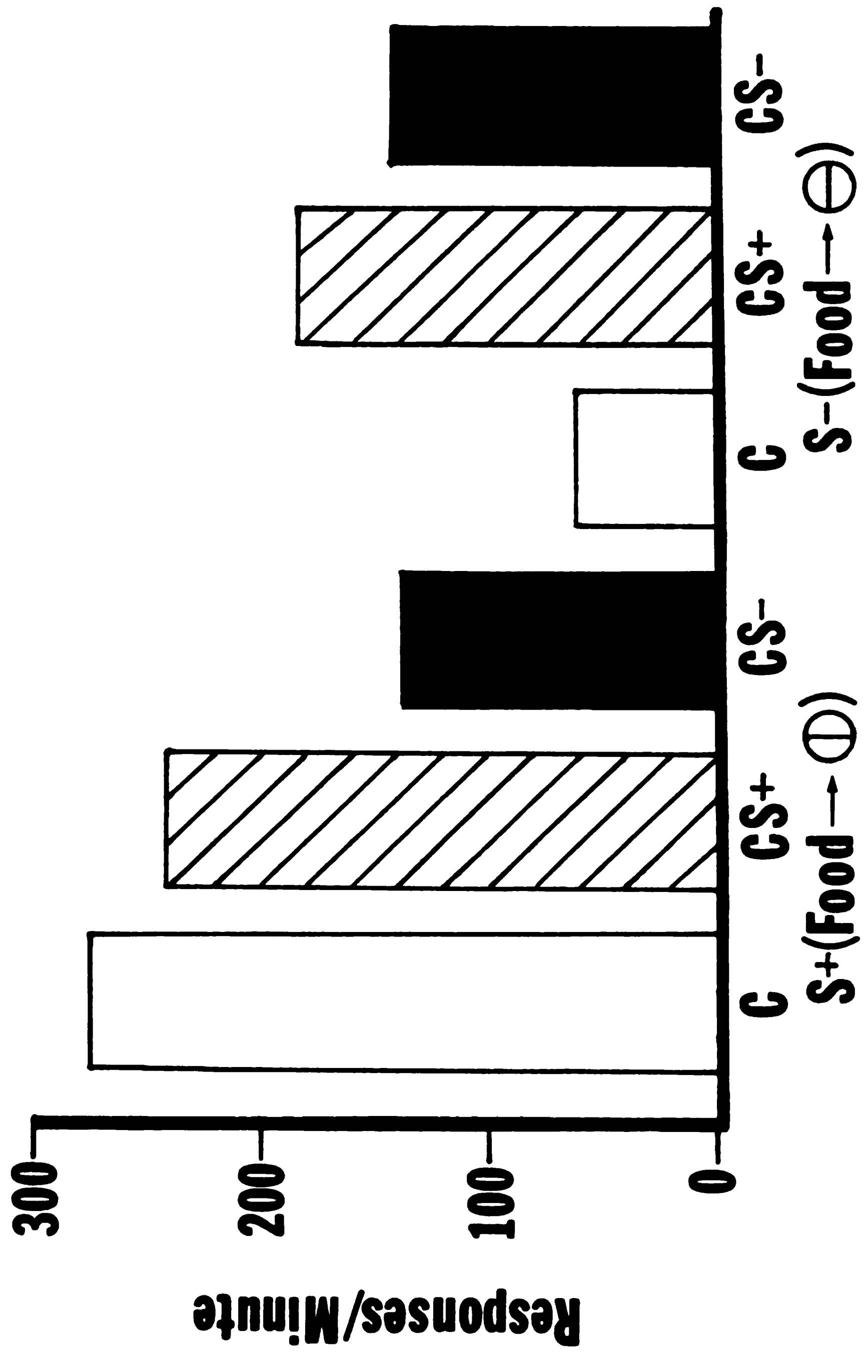
As Table 1 further indicates, responding during S- trials continued to differ, 33.3 vs. 61.6 responses/minute during, respectively, Houselight-Vertical vs. Food-Horizontal trials. This difference, however, is not significant, $\underline{t}$ (5) = 2.1, $\underline{p} > .05$.

The finding in Experiment III that more training is required for birds to learn not to peck during an S- comparison stimulus when food was the sample than when houselight was the sample is a within subject confirmation of the acquisition data collected between groups in Experiments I and II. Birds in Experiment II, wherein food signalled extinction, required significantly more sessions to learn the delayed matching task than did birds in Experiment I, wherein houselight signalled extinction.

Figure 6 shows the group data from the test session. Included in Figure 6 are mean rates of responding during the comparison stimuli when food was the sample stimulus during the four experimental and two control probe trials. Figure 6 shows that, compared to respective control probes, interpolating CS+ vs. CS- during S+ (Food-Vertical) and S- (Food-Horizontal) retention intervals differentially affected rates of responding during the comparison stimuli.

When CS+ was presented during S+ (Food-Vertical) trials, rate of response was similar to the rate obtained during control trials. When CS- was interpolated during S+ (Food-Vertical) trials, however, rate of responding during vertical was considerably less than either the control probe or the CS+ probe. A probe trial by subjects ANOVA on the S+ (Food-Vertical) data confirmed that type of probe trial

Figure 6. Group data from Experiment III's test session. The figure shows rate of response as a function of delayed matching trial (Food-Vertical or Food-Horizontal) and as a function of probe stimulus (Control, CS+, or CS-).


Responses/Minute
300
200
100
0
C
CS+
CS−
S+(Food→⊕)
C
CS+
CS−
S−(Food→⊖)

affected rate of responding *F* (2, 10) = 6.7, *p* < .025. Subsequent analyses using the Neuman-Keuls procedure showed that the CS- probe trial rate of response was significantly less than both the control and CS+ rates of responding (*p* < .05 in both cases) but that CS+ and control rates did not differ.

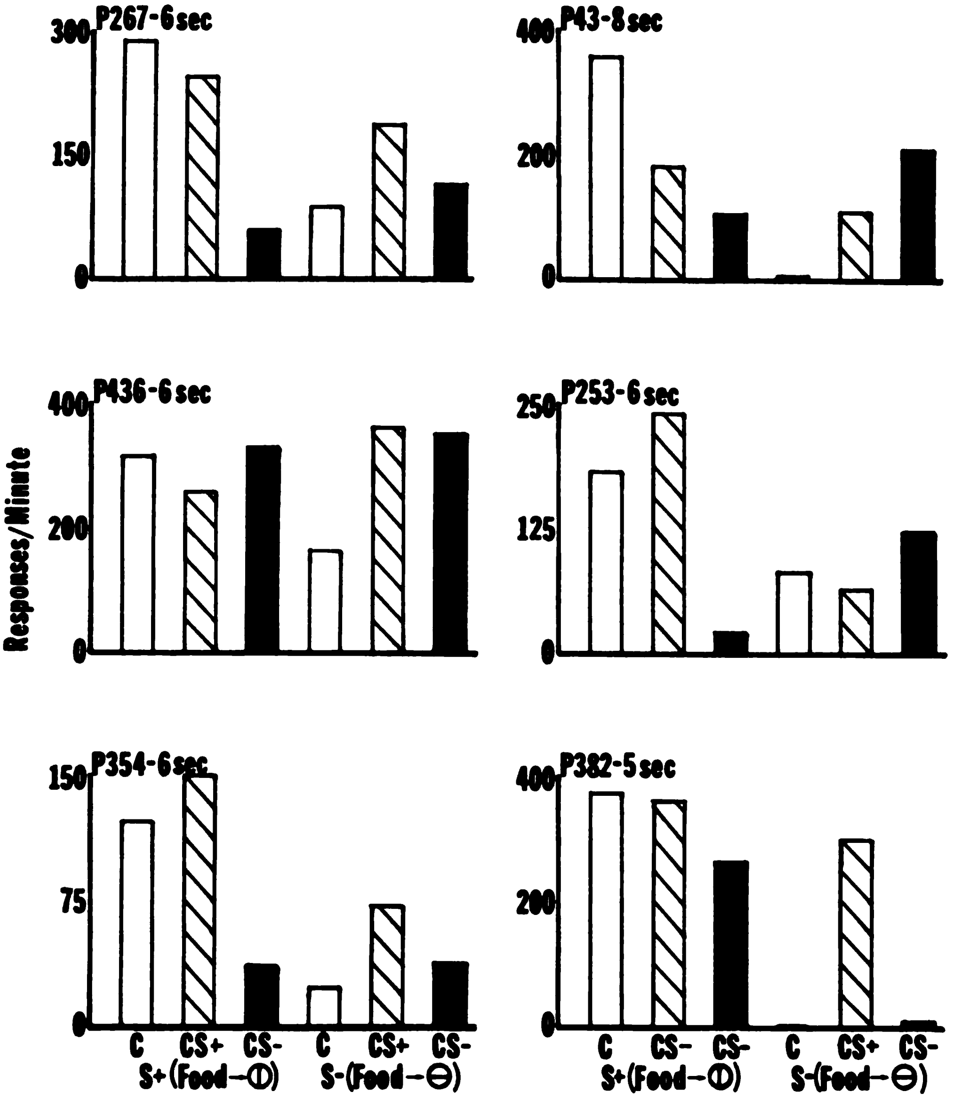
Consider next the effects of probing the S- (Food-Horizontal) condition. Relative to the control condition, interpolating either CS+ or CS- during the retention interval resulted during the horizontal comparison stimulus in a higher rate of response. A treatment by subjects ANOVA on these data did not show, however, that probe trial conditions significantly affected test stimulus response rate, *F* (2, 10) = 3.4, *p* > .05 < .10. Dunnet's *t* tests were used to compare the two experimental treatments to the control in the S- (Food-Horizontal) condition. This analysis did reveal that CS+ resulted in a higher rate of response than the control probe, *t* (10) = 2.6, *p* = .05, but that CS- and control probes did not differ, *t* (10) = 1.7, *p* > .05.

A further question of interest is whether rates of responding induced by CS+ vs. CS- differed as a function of whether the food sample meant responding was reinforced during vertical or extinguished during horizontal. Figure 6 shows that CS+ presented during S+ (Food-Vertical) trials resulted in a somewhat higher response rate than CS+ interpolated during S- (Food-Horizontal) trials. Furthermore, Figure 6 indicates that CS- interpolated during either S+ (Food-Vertical) trials or S- (Food-Horizontal) trials resulted in similar rates of response. These data were subjected to a

2 X 2 repeated measures ANOVA. S+ vs. S- was one factor and CS+ vs. CS- was the second. This analysis did not result in a significant S+ vs. S- effect, $\underline{F} < 1$. There was a trend in the direction of CS+ resulting in a higher rate of response than CS-, $\underline{F}(1, 5) = 4.4$, $\underline{p} < .10$, but the interaction was not significant, $\underline{F} < 1$.

Figure 7 provides individual subject data from the test session. The duration listed next to each bird is that bird's final valued retention interval. Inspection of Figure 7 reveals that the group effects elaborated in Figure 6 are not altogether consistent within birds. The data of Birds 267 and 354 show patterns that closely resemble the group data. Pigeons 43 and 253 show patterns consistent with the group data with the exception that, for both birds, CS- resulted in a higher rate of response than CS+ during S- (Food-Horizontal) trials. The within S+ (Food-Vertical) probe trial comparisons and the within S- (Food-Horizontal) probe trial comparisons for pigeon 382 are consistent with the group data except, perhaps, for the extremely large quantitative difference engendered by CS+ vs. CS- during S- (Food-Horizontal) trials. Between S+ (Food-Vertical) and S- (Food-Horizontal) trials, however, pigeon 382 shows an inconsistency with the group data: CS- during S+ trials resulted in a much higher rate of response than CS- during S- trials. Bird 436's data are, in general, quite aberrant. All probe trials for this bird resulted in a high rate of response. Remarkably, the lowest probe trial rate of response for Bird 436 was when CS+ was interpolated during S+ (Food-Vertical) trials.

Figure 7. Individual subject data from Experiment III. This figure shows each pigeon's rate of response in each of the six different probe conditions. The durations listed next to each bird's number are final valued retention intervals.


P267-6sec
300
150
0
P43-8sec
400
200
0
Responses/Minute
P436-6sec
400
200
0
P253-6sec
250
125
0
P354-6sec
150
75
0
C CS+ CS- C CS+ CS-
S+(Food—⊕) S-(Food—⊖)
P382-5sec
400
200
0
C CS- CS- C CS+ CS-
S+(Food—⊕) S-(Food—⊖)

One other aspect of the data presented in Figure 7 warrants consideration. Although neither S+ vs. S- nor CS+ vs. CS- main effects reached conventional levels of statistical significance in the 2 X 2 repeated measures ANOVA, Figure 7 does show that five out of six birds obtained a higher rate of response when CS+ was interpolated during S+ (Food-Vertical) trials than when CS+ was presented during S- (Food-Horizontal) trials. The only exception to this trend was Bird 436, whose data altogether were quite anomalous. Thus, a qualified conclusion may be drawn that CS+ interpolated during delayed matching retention intervals did not simply elicit a high rate of response during the comparison stimulus. Rather, five of six birds showed a higher rate of response following a CS+ probe if responding had normally been reinforced rather than extinguished during the comparison stimulus.

The results of Experiment III are in close agreement with predictions made by the expectancy hypothesis as opposed to the retrieval cue explanation. CS+ vs. CS-, interpolated during S+ (Food-Vertical) delayed matching retention intervals resulted, respectively, in high vs. low rates of response during the vertical comparison stimulus. According to the expectancy interpretation, these outcomes may have occurred because CS+ elicited an expectancy consistent with the mediated expectancy elicited by the vertical comparison when food was the sample stimulus (i.e., both CS+ and the vertical comparison may have elicited expectancies for food). Similarly, CS- may have elicited an expectancy inconsistent with the mediated expectancy elicited by the vertical comparison when food was the sample stimulus (e.g., "no food" vs. food, respectively).

CS+ vs. CS-, presented during S- (Food-Horizontal) trials resulted, respectively, in medium high vs. medium low rates of responding during the horizontal comparison stimulus. According to the expectancy interpretation, these outcomes may have occurred because CS+ vs. CS- elicited expectancies either competitive or isomorphic with the mediated expectancy elicited by the horizontal comparison stimulus when food was the sample. The horizontal comparison stimulus, preceded by a food sample, should have elicited a "no food" expectancy. The expectancy for food that CS+ may have elicited may have competed with this "no food" expectancy; hence, retroactive interference occurred in the guise of an increased rate of response. The expectancies for the absence of food that both CS- and the horizontal stimulus may have elicited are consistent with each other; therefore, no interference and a low rate of response occurred.

The evidence most damaging to the retrieval cue interpretation is provided in the data collected when CS+ was presented during S- (Food-Horizontal) trials. If CS+ elicited a representation of food that simply served to remind the birds that food was the sample stimulus, then a very low rate of response should have occurred. The finding that CS+ increased the rate of response above the control in the S- (Food-Horizontal) condition strictly contradicts the retrieval cue hypothesis.

GENERAL DISCUSSION

In three separate experiments the effects of interpolating food paired and nonpaired stimuli during retention intervals of successive delayed matching-to-food vs. -a houselight was investigated. It was expected that, dependent upon the sample stimulus, food-paired vs. non-paired stimuli would either retroactively facilitate or interfere with performance in the delayed matching task.

In Experiment I, a food-paired stimulus facilitated matching when a food sample signalled reinforced responding during the test stimulus but interferred with matching when a houselight sample signalled extinction. Also in Experiment I, a stimulus paired with the absence of food interferred with matching during trials when food predicted reinforced responding but did not interfere during trials when a houselight predicted extinction. The results of Experiment II were generally consistent with Experiment I. A food-paired stimulus facilitated matching during trials when a houselight sample predicted extinction. The stimulus paired with the absence of food, interpolated during delayed matching trials of Experiment II, did not interfere with matching when food predicted extinction nor did it interfere with matching when the houselight predicted food reinforcement. This latter result was not anticipated.

In Experiment III, a conditional successive delayed matching task was employed. In this experiment, the food-paired and non-paired stimuli were interpolated during retention intervals of trials with food as either an S+ or an S- sample. Whether responding was normally reinforced or extinguished during the comparison stimulus depended on the conditional relationship between food and the comparison stimulus. Although the task demands were more difficult, the results of Experiment III confirmed the data collected in Experiment I. The food-paired stimulus facilitated matching on trials when the relationship between the food sample and the comparison mediated reinforced responding but interfered with matching when the relationship between the food sample and the comparison mediated extinguished responding. The stimulus paired with the absence of food interfered with matching on trials when the sample-comparison relationship predicted reinforcement but did not interfere during trials when the sample-comparison relationship predicted extinction.

The theoretical principle tested in the present set of experiments was whether classically conditional stimuli, either paired with food or with the absence of food, retrieved representations of or elicited expectancies for the events upon which they were based. The two viewpoints were named, respectively, the retrieval cue hypothesis and the expectancy hypothesis. The retrieval cue hypothesis predicted that interpolated conditional stimuli would facilitate or interfere with delayed matching dependent upon whether the representation retrieved by the cue was either isomorphic or competitive with the sample stimulus memory. For example, a food-paired cue may elicit a representation isomorphic with a memory for a food sample. The expectancy hypothesis predicted that interpolated conditional stimuli would facilitate or interfere with delayed matching dependent upon whether the expectancy elicited by the probe stimulus was either isomorphic or competitive with the expectancy elicited by the sample stimulus (or the mediated expectancy in Experiment III). For example, an S+ sample, whether food or houselight, would elicit an expectancy isomorphic with the expectancy for food elicited by a food-paired conditional stimulus.

The preponderance of the evidence collected in the present set of experiments clearly supported the expectancy hypothesis and disconfirmed the retrieval cue explanation. Food-paired and non-paired stimuli resulted in retroactive facilitation or retroactive interference if the expectancies elicited by the interpolated stimuli were either consistent or inconsistent with the sample-based expectancies. Two theoretical viewpoints are consistent with these data: Denny's (1967) Elicitation Theory and Trapold and Overmier's (1972) extension of Two-Process Learning Theory.

According to Elicitation Theory, approach vs. withdrawl responses, acquired through a backchaining process, may have mediated the retention interval of the delayed matching tasks. If the sample was an S+, then appetitive chains of food-related approach responses may have mediated during the delay. If the sample stimulus predicted extinction, then a chain of nonfood-related withdrawal responses probably occurred throughout the retention interval. When classically conditional stimuli, paired either with food or the absence of food, were subsequently presented during delayed matching trials, Elicitation Theory makes predictions consistent with the results obtained. It must merely be assumed that the approach vs. withdrawal responses elicited by CS+ vs. CS- were either consistent or inconsistent with the chain of responses that mediated the retention interval. For example, Elicitation Theory must assume that the responses elicited by CS+ were compatible with the mediated chain of approach responses on S+ trials but incompatible with the mediated chain on S- trials. Likewise, Elicitation Theory must assume that the withdrawal responses elicited by CS- were incompatible with an S+ based chain of responses but compatible with an S- based chain.

Trapold and Overmier (1972) posit that discrimination learning is mediated by reward expectancies elicited by discriminative stimuli and based on the eventually obtained reinforcer. A series of experiments has shown that a consistent stimulus-reinforcer relationship is crucial for the rapid acquisition of a discrimination (Overmier, Bull, & Trapold, 1971; Peterson et al., 1978; Trapold, 1970). For example, in the Peterson et al. study, pigeons readily learned a two-choice conditional delayed matching-to-sample task when one reinforcer was consistently associated with one of the correct choices and a different reinforcer was consistently associated with the other correct choice. Large within subject decrements in performance were shown when reinforcers were subsequently inconsistently associated with the correct choices.

According to Trapold and Overmier, consistent reward training allows differential reward expectancies to develop to each cue whereas inconsistent reward training prevents the formation of differential reward expectancies. Differential reward expectancies, therefore, are presumably important in the acquisition of a discrimination.

A straightforward application of Trapold and Overmier's (1972) theory may be used to explain the present set of results. In Experiments I and II, it need only be assumed that the S+ and S- samples elicited expectancies for food and no food during the eventual test stimulus; in Experiment III, reward expectancies may have been formed based on the conditional relationship between the sample stimuli and the comparison stimuli. Furthermore, it naturally follows from Trapold and Overmier's perspective that CS+ and CS- elicited expectancies for food and the absence of food, respectively. When the Pavlovian stimuli were subsequently interpolated on the delayed matching baseline, Trapold and Overmier make the appropriate facilitation and interference predictions based on whether the sample and Pavlovian probe stimulus expectancies were, respectively, consistent or inconsistent. Therefore, the present results extend Trapold and Overmier's data base to include retroactive interference and facilitation in pigeon short-term memory.

Although the theoretical positions espoused by Denny (1967) and Trapold and Overmier (1972) both predict the results obtained in the present experiments, conceptually, the two theories differ at the most basic level. According to Elicitation Theory, stimulus-response associations were responsible for the facilitation and interference effects obtained whereas Trapold and Overmier posit that stimulus-reinforcer associations were responsible for those same effects. Unfortunately, the present data do not allow one to choose between these two disparate positions.

If future research is to decide whether stimulus-response or stimulus-reinforcer associations were responsible for the interference and facilitation effects obtained, it may be necessary to adopt a theoretical position concerning the nature of stimulus-reinforcer expectancies other than Trapold and Overmier's. According to Trapold and Overmier, a conditioned mediator is _specific_ to the reinforcer upon which it is based, it possesses distinctive stimulus properties _specific_ to the signalled event, and it controls operant behavior via a cueing function based on these distinctive stimulus properties. This notion of stimulus-reinforcer specificity seems to necessarily bind Trapold and Overmier into making the same predictions as Denny's Elicitation Theory, at least within the context of procedures similar to those employed in the present research. A somewhat liberalized viewpoint of stimulus-reinforcer expectancy learning, recently developed by Fowler (1978) may, based on future research, allow a decision to be made concerning the merits of stimulus-response vs. stimulus-reinforcer interpretations of the present results.

Fowler (1978) suggests that animals process appetitive and aversive conditional stimuli through a central expectancy state that characterizes the incentive features of associated unconditional stimuli. For example, an appetitive CS+ and an aversive CS- both elicit expectancies for "good" outcomes (e.g., the occurrence of food and the omission of shock, respectively); an appetitive CS- and an aversive CS+, according to Fowler, both elicit expectancies for "bad" outcomes (e.g., no food and shock, respectively).

A typical experiment in Fowler's lab consists of presenting either a previously trained aversive CS+ or CS- contingent on correct or incorrect responses in a T-maze. No shock occurs during T-maze training. Food is the reinforcer for a correct turn in the T-maze and extinction occurs for wrong responses. The general findings are that an aversive CS+ presented for a wrong response and an aversive CS- presented for a correct response both block conditioning to the discriminative stimuli associated with incorrect or correct responses whereas an aversive CS- presented contingent on an incorrect response and an aversive CS+ presented for a correct response both produce superconditioning to the appropriate discriminative stimuli.

Fowler interprets these data in accordance with Wagner's (1978) "surprise" model of animal conditioning. For example, consider the situation when an animal makes an incorrect response in Fowler's T-maze and does not get fed. An aversive CS- presented following an incorrect response elicits an expectancy for a "good" outcome (i.e., no shock) but a "bad" outcome, no food, occurs. This expectancy-outcome discrepancy of "good"-"bad" is surprising to an animal; hence, the rehearsal mechanism is instigated and conditioning readily accrues to the T-maze discriminative stimuli. A similar analysis may be applied to the other three conditions listed above. Blocking (Kamin, 1968) occurs whenever the expectancies elicited by the aversive conditional stimuli are affectively consistent with the outcomes incurred in the instrumental task while superconditioning occurs whenever the expectancies elicited by the aversive conditional stimuli are affectively inconsistent with the instrumental outcomes.

It should be relatively clear how Fowler's position generates interesting predictions concerning facilitation and interference in short-term memory. Whenever a sample-based expectancy and an expectancy elicited by a probe stimulus are affectively consistent, retroactive facilitation in delayed matching should occur; if a sample produced expectancy and a probe stimulus expectancy are affectively inconsistent, retroactive interference in a short-term memory task would be predicted. As an example, an aversive CS+, which should elicit an expectancy for shock--a "bad" event--should interfere with matching when food reinforcement is expected but facilitate performance when extinction is the expected outcome of the matching trial. An entire set of predictions of this nature may be generated based on the nature of the instrumental reinforcer and based on whether the Pavlovian stimuli are aversive or appetitive.

Fowler's (1978) stimulus-reinforcer position on the nature of expectancies makes, therefore, predictions at odds with Denny's (1967) stimulus-response Elicitation Theory. Since the responses elicited by an aversive CS+ or an aversive CS- would never be (necessarily) consistent with chains of approach responses that mediate a delayed matching for food vs. extinction retention interval, Elicitation Theory would not in this case, predict specific interference and facilitation effects. Rather, since the aversive conditional stimuli would elicit responding (more than likely) inconsistent with the chains of retention interval behaviors, it seems as if Elicitation Theory would simply predict a general interference effect in all conditions.

In summary, data collected in the present set of experiments supported the notion that appetitive conditional stimuli elicit responses consistent vs. inconsistent with delay-interval chains of responses ala Elicitation Theory (Denny, 1967) and also support the notion that appetitive conditional stimuli elicit expectancies either isomorphic or competitive with expectancies elicited by S+ and S- sample stimuli (Trapold and Overmier, 1972). In order for future research to determine whether the retroactive facilitation and interference effects obtained in the present experiments were due to stimulus-response (Denny, 1967) vs. stimulus-reinforcer variables, Trapold and Overmier's stimulus-reinforcer position was discarded in favor of Fowler's (1978) affective theory of stimulus-reinforcer expectancy learning.

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